Levels of interaction between episodic and semantic memory:
an electrophysiological and computational investigation.

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University of Edinburgh
2007
Abstract

There is compelling evidence that memory is supported by multiple, functionally independent subsystems that distinguish declarative from non-declarative memories (Tulving, 1972). The declarative subsystems, episodic and semantic memory, have been studied intensively, largely in isolation from each other. Relatively little attention has been paid to the interplay between episodic and semantic memory.

This thesis constitutes a series of behavioural, neuroimaging, and computational investigations aimed at elucidating the factors and mechanisms that mediate interactions between episodic and semantic memory. Event-Related Potentials (ERPs) are used to isolate processes implicated in episodic and semantic memory interactions on the basis of known ERP effects. Experimental investigations vary factors that target semantic memory either directly or indirectly. Direct manipulations alter the semantic content of word pairs by modulating their lexicality (words vs. non-words) or coherence (categorical vs. non-categorical). Indirect manipulations focus episodic encoding towards semantic or non-semantic aspects of the to-be-encoded word pairs. This thesis investigates whether such manipulations influence episodic memory and if so, in what form.

The behavioural and ERP data provide clear evidence for distinct episodic and semantic interactions at the level of semantic organisation and lexical representation. Episodic retrieval, which is supported by recollection and familiarity according to dual process theories (Yonelinas, 2002), reveals enhanced familiarity for semantically organised stimuli. This effect is dependent on semantically deep encoding strategies. By contrast differences in the lexicality of stimuli modulated both familiarity and recollection.

To provide an account for why different types of interactions are obtained a computational memory model is proposed. This model uses a single network to simulate a dual process model of episodic retrieval and gives insight into processes that may support interactions between episodic and semantic memory. Thus, this thesis provides novel evidence for different types of episodic and semantic memory interactions dependent on the kind of semantic manipulation and specifies the mediating mechanisms leading to such interactions.
Acknowledgements

First of all I would like to thank the Doctoral Training Centre (DTC, financially supported by EPSRC and MRC) for providing such a unique and supportive scientific environment, which enabled me to define and pursue my personal research interests. It has been a privilege to be a part of the DTC from its very beginning and see it grow throughout the years to such an active and vibrant research community. Special thanks go to Mark van Rossum whose ambition and dedication allowed the DTC to become what it is today and whose supervision of my PhD project was invaluable in helping me to create this thesis.

My sincere gratitude goes to the Psychological Imaging Lab at Stirling University, especially to David I. Donaldson for supervising my research. I would like to thank David for his encouragement, support and advice he gave me throughout my PhD. The countless discussions about memory and cognitive neuroscience have greatly shaped the research I conducted during my PhD and have certainly influenced my view of the field. I also benefited from his practical support that taught me how to conduct ERP research and how to communicate and present this research in a clear and effective manner. Furthermore, I would like to thank him for all the given opportunities to be introduced and meet other people in the field.

My work has also benefited from the interaction with many different individuals. I would like to thank Paulo Aguiar, Kit Longden and Matthijs van der Meer for some very enlightening ‘Hippocampus lunches’; Cindy Gray, Graham Mackenzie, Sinead Rhodes, Richard Sharp, Lucy McGregor and all the other members of the PIL lab for their discussion, help and company; Ruth Durie and Martin Guthrie for all the time we spent together in the office working on our PhDs and finally Catriona Bruce and Pat Ferguson for their technical, administrative and moral support.

I am very grateful to people outside the academic field whose friendship and encouragement have given me an invaluable source of energy and motivation. A very special thanks goes to Fiona Blair, who was never tired to listen or ask about the progress in my PhD and who taught me ‘how to step’ outside it. Equally, I would
like to thank Sarah Maisey, Mareile H. Knees, Sadaf Baybori and Tanja Lazarevic for their patience and long-term friendship even in times when my PhD seemed to take over my life. Most importantly, I would like to sincerely thank my family for their unconditional help, support and encouragement, which allowed me to pursue my own goals.

My deepest gratitude, however, goes to Tim Smith who provided me with priceless emotional and practical support in writing this PhD. I would like to thank him for the numerous times of reading, correcting and commenting on several drafts of this thesis. I am immensely grateful for him being there for me.
Declaration

I declare that this thesis was composed by myself, that the work contained herein is my own except where explicitly stated otherwise in the text, and that this work has not been submitted for any other degree or professional qualification except as specified.

(Andrea Greve)
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1 Introduction

Human declarative memory supports the conscious retrieval of information from the past and is widely believed to consist of two distinct systems: Episodic and Semantic memory (Roediger & Bergman, 1998; Gobet, 1998; Vargha-Khadem et al., 1997; but see Squire & Knowlton, 1995). Episodic memory refers to retrieval of personally experienced events embedded in the context of their acquisition, e.g. remembering a specific party, whereas semantic memory is based on retrieval of knowledge about the world without reference to any specific event, e.g. information about what generally happens at parties.

Episodic and semantic memory are well characterised functionally, with behavioural and neuropsychological evidence strongly suggesting that they are dissociable. Evidence that distinct systems support declarative memory comes from patient data (Mayes & Montaldi, 2001). Intact semantic but impaired episodic memory occurs in children with early-onset amnesia (Vargha-Khadem et al., 1997), whereas the opposite pattern of impairment occurs in semantic dementia or cases suffering from developmental amnesia (Temple & Richardson, 2004). Furthermore, amnesic patients with impaired episodic memory are associated with bilateral hippocampal damage (Vargha-Khadem et al., 1997), whereas semantic dementia patients with impaired semantic memory have temporal lobe atrophy (Simons, Graham, Galton, Patterson, & Hodges, 2001; Graham, Simons, Pratt, Patterson, & Hodges, 2000). This neuropsychological evidence suggests that episodic and semantic memory are supported by functionally and anatomically distinct brain systems. The proposal for anatomically distinct systems underlying episodic and semantic memory remains contentious, however the data clearly demonstrate a functional dissociation between episodic and semantic memory in patient populations. This dissociation does not, of course, exclude the possibility that episodic and semantic memory interact in healthy participants.

Interactions between episodic and semantic memory may take many forms. For instance events might be encoded by the episodic memory system in
coordination with information provided by the semantic memory system. An interaction between episodic and semantic memory might occur when such complementary semantic information alters episodic memory. The nature of semantic and episodic memory interactions can be studied by investigating the effects of episodic manipulations on semantic memory or by examining the influence of semantic manipulations on episodic memory. Expertise effects (for review see Gobet, 1998) have provided some evidence that semantic memory has an impact on episodic performance. Similarly, several well established neuropsychological tests (e.g. the California Verbal Learning Test, Delis, Kramer, Kaplan, & Ober, 1987) assess the tendency to utilize semantic information inherent in the material that is studied and tested within an episodic memory paradigm. Nevertheless, it remains unclear which parameters evoke, and what processes facilitate such interactions between episodic and semantic memory. These questions will be investigated during this thesis by examining the influence of semantic manipulations on episodic memory.

The underlying processes that mediate the influence of semantic manipulations on episodic retrieval are assessed in the light of dual process models, which describe episodic retrieval as being contingent upon familiarity and recollection (Yonelinas, 2002). Familiarity refers to a fast acting process that reflects a quantitative assessment of memory strength, whilst recollection is the retrieval of qualitative contextual information about a previous event. Thus, the question at stake is whether familiarity or recollection support the interaction between episodic and semantic memory. It is of course possible that both processes exhibit a differential or combined influence dependent on the type of semantic manipulations employed.

Current behavioural findings, most notably from Levels of Processing (LOP) studies (Craik & Lockhart, 1972), suggest that manipulations of semantic memory influence episodic retrieval largely by modulating recollection. The LOP theory states that episodic memory retrieval is influenced by semantic memory processing at encoding, with enhanced recognition for deep, semantically meaningful encoding (e.g. semantic categorization) compared to shallow non-semantic encoding (e.g. letter discrimination). Evidence suggests that deep encoding evokes recognition
based on familiarity and recollection, whilst shallow encoding leads to recognition based primarily on familiarity (Toth, 1996; Mulligan & Hirshman, 1995; for review see Yonelinas, 2002). Thus, LOP strongly suggests an interaction between episodic and semantic memory which influences recollection to a greater extent than familiarity.

In contrast to the LOP account, other data provide evidence that familiarity may also play a role. The Speed-Accuracy Trade-off (SAT) method has been used to test recognition for semantically related and unrelated word pairs, revealing a maximum false-alarm rate to semantically related lures at short retrieval deadlines (Dosher, 1984). Retrieval based on recollection is relatively slow, whereas familiarity is regarded as a fast acting process. This suggests that the false alarms to semantically related pairs are due to familiarity and, therefore, that it is familiarity, not recollection that might be more affected by manipulations of semantic memory. In general, previous studies do not provide a conclusive account as to which episodic retrieval process (familiarity or recollection) mediates the interaction between semantic and episodic memory. In fact, very few attempts have been made to systematically investigate the variables that elicit and modulate episodic and semantic memory interactions.

Event-Related Potentials (ERPs) provide an ideal method to investigate the engagement of distinct processes associated with episodic and semantic memory. The most prominent ERP effect indexing specific semantic processes is the N400 (Kutas & Hillyard, 1980). This N400 elicits a negative deflection at about 400ms over central scalp locations, which is inversely related to the level of semantic expectancy. A second more parietally located effect is often reported at about 600ms, typically in response to language processes in sentences. Although the functional significance of this effect is still debated, it is interpreted to index either language specific effects of syntactic integration (Osterhout, McLaughlin, & Bersick, 1997) or language unspecific effects linked to attention (Coulson, King, & Kutas, 1998b). In addition to semantic processes, ERP effects indexing efficient episodic encoding are reported by ‘Differences in memory’ (Dm) effects. Although the precise timing and scalp distribution seems to depend on individual experimental manipulations, classic
Dm effects occur from about 300ms onwards over frontal scalp locations (Paller, 1990; Friedman, 1990).

In relation to episodic retrieval, distinct ERP old/new effects (contrasting hits and correct rejections) have been identified as indexes of familiarity and recollection (see Donaldson, Allan, & Wilding, 2002; Rugg, 1995; Johnson, 1995 for reviews). Familiarity is reflected by an early frontal ERP old/new effect, elicited around 300-500ms post stimulus onset, with maximum amplitude over frontal scalp sites (Nessler, Mecklinger, & Penney, 2001; Curran, 2000, although see Tsivilis, Otten, & Rugg, 2001). Whilst debate continues as to whether the early frontal ERP old/new effect reflects familiarity when non-verbal stimuli are employed (e.g., faces, see Yovel & Paller, 2004), the effect has been widely used as a reliable index of familiarity in experiments using verbal stimuli (e.g. in studies of the revelation effect, see Azimian-Faridani & Wilding, 2004). ERPs can also be used to identify recollection. The left parietal old/new effect, elicited around 500-800ms post stimulus onset, with maximum amplitude over the left tempo-parietal region is believed to index recollection (Rugg et al., 1998; Wilding, Doyle, & Rugg, 1995; Paller & Kutas, 1992; for a review see: Curran, 1999; Allan, Wilding, & Rugg, 1998).

This thesis investigates the influence of semantic memory on episodic memory by systematically varying semantic factors that target semantic memory either directly or indirectly. Behavioural and electrophysiological data provide compelling evidence for the existence of interactions between semantic and episodic memory. By identifying known ERP effects, insight into the processes involved in these interactions can be gained but an understanding of why they are involved and how they operate remains elusive. Computational modelling can be used to provide such an understanding by explicitly representing the processes of episodic retrieval. In this thesis, a computational model will be developed that suggests how recollection and familiarity may be affected by semantic manipulations.

The thesis opens with a review of important concepts, methods and findings in memory research with regards to the current investigation (Chapter 2). Furthermore, ERP methods (Chapter 3) and relevant results obtained in memory
research using ERPs (Chapter 4) are introduced. The main body of the thesis reports empirical investigations testing the effects of direct or indirect semantic manipulations on episodic encoding and retrieval mechanisms.

The first experiment employs a direct manipulation of semantic memory, varying the semantic coherence of the stimuli by presenting pairs of words that described exemplars of either the same or different categories (Chapters 5 and 6). This manipulation is associated with memory representations that are either congruent or incongruent with the category specific organisation of the semantic memory system. Modulations in semantic processing indexed by the N400 and P600 effects occur during encoding. Furthermore, differences in efficient encoding were obtained with Dm effects that predicted superior familiarity based recognition for congruent stimuli (Chapter 5). These data were in line with the behavioural and ERP findings at retrieval, indicating enhanced recognition primarily due to increased familiarity processes for congruent stimuli (Chapter 6).

The second experiment examined the question of whether the familiarity driven effect obtained in the first investigation is contingent upon episodic encoding strategies that gate the availability of semantic information by focussing encoding processes towards a lexical/semantic or non-lexical/perceptual level. Thus an indirect semantic memory manipulation was employed by amending the type of semantic encoding strategies (an LOP manipulation) in addition to the manipulation of semantic coherence. The encoding data revealed a dependency between the semantic processes and the encoding strategy employed. Deep encoding conditions revealed differences in semantic processing for congruent vs. incongruent stimuli indexed by the N400 and P600, similar to the first experiment. Shallow encoding conditions, by contrast, failed to elicit any modulations in semantic processing. Encoding efficiency, examined by Dm effects, also differed between encoding strategies. Dm effects associated with elaborative processing occurred for deep conditions, while Dm effects linked to familiarity based retrieval were obtained under shallow conditions (Chapter 7). The retrieval data confirmed that the stimulus driven influence of semantic coherent material is conditional on the level of semantic processing employed. In line with the first experiment, deep encoding evoked
increased recognition performance of coherent stimuli primarily based on familiarity. However, no selective engagement of familiarity or recollection based processes were obtained under shallow encoding conditions (Chapter 8). This suggests that the lexicality or non-lexicality of the encoding process has a significant impact on the interaction between episodic and semantic memory.

A third experiment employed a direct semantic manipulation of lexicality by testing categorically unrelated pairs of words (that contain lexical/semantic representations) and non-words (that do not contain lexical/semantic representations). By comparison, the first two experiments investigated stimuli that were associated with lexical/semantic representations but varied in their coherence and consequently in their degree of semantic feature overlap (i.e. categorical representations). Differences in stimulus lexicality influenced encoding processes, which exhibited modulations in the N400 and P600. Equally, a modulation in subsequent memory effects was obtained, which indicate efficient encoding processes related to familiarity based retrieval of non-lexical, visual/orthographic features (Chapter 9). Furthermore, retrieval processes revealed better recognition for words compared to non-words. This advantage was supported by familiarity and recollection based retrieval, which was, however, conditional on the temporal lag separating study and test conditions (Chapter 10).

In addition to the empirical investigation of episodic and semantic memory interactions, a computational model will be presented, which simulates retrieval processes inherent to episodic memory (Chapter 11). Although the behavioural and ERP data provide compelling evidence for multiple episodic and semantic memory interactions, they fail to explain how and why such interactions occur. By providing an explicit account of the mechanisms that support episodic retrieval the proposed model aims to contribute to the understanding of the mechanisms underlying the interactions between episodic and semantic memory. The model demonstrates that it is possible to simulate familiarity and recollection as two distinct retrieval processes that operate upon a single memory representation. Furthermore, the familiarity process demonstrates a higher susceptibility to feature overlaps and the
recombination of information, which provides a window into understanding the mechanisms by which semantic memory may influence episodic retrieval.

In general, this thesis provides evidence that episodic and semantic memory interact in multiple ways, dependent on the level of semantic information in the to-be-encoded stimuli, or the level to which this information is processed during episodic encoding. The data presented here reveal that interactions occur at the level of semantic organisation as well as lexical/semantic representation. These interactions are contingent upon indirect semantic manipulations such as episodic encoding operations that do or do not facilitate processing of semantic information. In the attempt to provide an account for why different types of interactions are obtained a computational memory model is proposed. An underlying assumption of the model is that the level of semantic manipulation during encoding has a differential influence on the representation of semantic information. Manipulations targeting the organisation of lexical representations are likely to vary the feature overlap between semantic representations, while modulations in lexicality may change the amount of information associated with that representation. Thus, the different levels of interaction between episodic and semantic memory potentially reflect the sensitivity of a particular retrieval process to characteristics inherent in the underlying semantic representations upon which memory is based.
1 Introduction
2 Introduction to Memory

The process of learning, storing and retrieving information from memory has captured the interest of writers, philosophers and scientists for hundreds of years. This is not surprising considering the important role memory plays in our life. Memory is both essential to our survival, by indicating and circumventing dangerous situations, and is an integral part of our being as it holds personal information of past experiences and provides general knowledge about the world. Over the last few decades scientific research has significantly advanced our understanding of memory. Recently, this has been primarily driven by increasingly sophisticated methods used in the field of neuroscience, neurophysiology and neuroimaging. By taking into account the underlying brain processes, these methods allowed insights into the nature and organization of memory. One such insight is that memory is not unitary but can be fractioned into multiple dissociable systems. Also particular brain areas have been associated with specific memory performance. Thus, recent findings seem to suggest that memories are manifested in multiple ways, in multiple functionally and anatomically distinct brain systems.

This chapter is devoted to the empirical evidence that has led to the notion of multiple memory systems by reviewing psychological findings which have reported memory tasks and tests that supported the division of memory into several subsystems. A main focus of this thesis and this chapter is the declarative memory system. The episodic and semantic subsystems comprising declarative memory are reviewed and discussed individually, before the functional relation and dependency between those two subsystems are discussed. First, however, this chapter will introduce the line of research that has led to the currently held view of multiple memory systems.
2.1 Psychological dissociations of memory

One of the earliest theories that advocated different forms of memory was proposed by the French philosopher Maine de Biran (1804/1929, for discussion see Schacter and Tulving, 1994). He argued that instead of a single function or structure, memory is divided into three different but independent entities: representative memory (conscious recollection of facts or events), sensitive memory (emotional reactions) and mechanical memories (habitual behaviours). Although this theory remained largely unknown and had therefore very little influence on the current view of multiple forms of memory, there are striking parallels between them. To date numerous forms of memory or memory systems have been postulated including episodic and semantic memory (Tulving, 1983; Tulving, 1972), taxon and locale memory (O'Keefe & Nadel, 1978) working memory and long-term memory (Baddeley, 1986) implicit and explicit memory (Graf & Schacter, 1985), declarative and non-declarative (Squire, 1992) or procedural memory (Eichenbaum, Cohen, Otto, & Wible, 1992a) fast and slow memory systems (McClelland, McNaughton, & O’Reilly, 1995). However, this wealth of proposals raises the questions of: how many memory systems are there, and how are they organised? The following sections will address these two questions, by first outlining criteria which are necessary and sufficient for proposing memory systems, and secondly, by introducing a taxonomy which classifies and organises distinct forms of memory into a general framework.

In the past the multiple memory system approach has been contrasted with the ‘processing approach’ which focuses on particular operation demands evoked by a specific task rather than general memory systems (Roediger, Rajaram, & Srinivas, 1990). However, the systems and processing approach are now seen as complementary rather than incompatible (Roediger, Buckner, & McDermott, 1999; Schacter, 1992; Schacter, 1990). While the systems approach describes processes that operate across broad domains, the processing approach focuses on specific operations that may function in one or more systems.
2 Introduction to Memory

2.2 Criteria for Memory Systems

The proposal that memory is not unitary but supported by multiple systems has to be grounded in a precise conceptual definition of what a ‘memory system’ refers to. Schacter and Tulving (1994) addressed this question and argued that memory systems should be distinguished primarily on their psychological characteristics under consideration of the following three criteria: ‘class inclusion operations’, ‘properties and relations’, and ‘convergent dissociations’.

The first criterion, ‘class inclusion operations’, states that a memory system should be able to perform tasks or functions within a particular class or domain. The second criterion of ‘properties and relations’ requires that each memory system should exhibit unique functional properties including the rules by which a system operates, the type of information that falls into a domain, the neuronal substrate and the function of the system. Finally, the criterion of ‘convergent dissociations’ constitutes the necessity to demonstrate dissociations between classes of tasks that distinguish memory systems from one another. These three criteria make it possible to discriminate the restricted concept of a ‘memory system’ from the more open notion of a ‘form of memory’ which is used on a more heuristic basis as for example the form of spatial memory.

2.3 Framework of Memory Systems

Under consideration of the defining criteria for memory systems, two memory taxonomies have been proposed by Schacter and Tulving (1994) and Squire and Zola-Morgan (1991), which have been proven to be useful classification to guide memory research (see Table 2-1 and Figure 2-1).
## 2 Introduction to Memory

<table>
<thead>
<tr>
<th>System</th>
<th>Other terms</th>
<th>Subsystems</th>
<th>Retrieval</th>
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<td>simple associative learning</td>
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<td>nondeclarative</td>
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<td>episodic</td>
<td>personal, event</td>
<td>autobiographic</td>
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</tbody>
</table>

| **Table 2-1:** The memory taxonomy proposed by Schacter and Tulving (adapted from Schacter and Tulving, 1994). |

Although these two taxonomies are partially overlapping, they also include classifications which are unique to their particular framework. However, there are experimental findings which support both taxonomies and disclose characteristic features of the proposed memory systems.

![Memory Taxonomy](image)

**Figure 2-1:** The memory taxonomy introduced by Squire and Zola-Morgan (adapted from Squire and Zola-Morgan, 1991)
2.4 Declarative and Procedural memory

The taxonomy of Squire and Zola-Morgan (1991) explicitly defines the counterpart of declarative memory as procedural memory. According to this taxonomy, procedural memory is further divided into skills, priming, classical conditioning and others. However, it is worth noting that Schacter and Tulving (1994) propose that procedural memory in combination with perceptual representations form the non-declarative counterpart to declarative memories. This results in an incoherent employment of the term procedural memory across the two taxonomies. In the remainder of this chapter the term procedural memory will be used to describe the counterpart of declarative memory, consistent with the classification of Squire and Zola-Morgan (1991). Besides defining a precise terminology, it is essential to understand the concepts described by this terminology. Declarative and procedural memory are broad categories which refer to memories of prior events or episodes that can either be explicitly accessed (declarative memory) or become implicitly manifested in altered preferences or performances (procedural memory). Some of the most convincing evidence supporting this distinction has been reported in studies with amnesic patients (Corkin, 1984; Milner, Corkin, & Teuber, 1968; Scoville & Milner, 1957). Corkin (1968), for example, reported amnesic patients that have an impaired capacity for declarative memory, which includes facts and events that can be brought to conscious recollection and explicitly articulated. In contrast, procedural memory, involving the acquisition of skills and preferences that can only be expressed unconsciously, remained spared in amnesia.

Notably, the distinction between declarative and procedural memory is characterised by the difference in memory access or expression. A further fundamental distinction is given by the nature of the memory representation. Cohen (1984) argued that declarative representations permit comparisons among learned events which are encoded in relations to other items and events. Thus declarative representations are relational in nature and entail an interconnected network with links to associated items (Cohen & Eichenbaum, 1993; Eichenbaum, Cohen, Otto, & Wible, 1992b; Eichenbaum et al., 1992a).
However, declarative representations can be expressed independent of the circumstances in which they were initially acquired (Cohen, 1984). Therefore, regardless of the current context, an external sensory cue or even purely internal cue is able to activate declarative memories. This relates to a further defining property of declarative memory: representational flexibility, which describes the ability of flexible usage and manipulation of memories. After outlining the general differences between declarative and procedural memory, the next section will focus on the subtypes defining the procedural memory system.

2.5 Procedural memory

A unique case study which has guided memory research since the late 1950s is the report of the amnesic patient H.M. (Milner et al., 1968; Scoville & Milner, 1957). After a bilateral medial temporal lobe removal H.M. exhibited selective memory impairments characterised by intact perceptual, motor, and cognitive functions; intact immediate memory but severe and global anterograde amnesia¹; temporally graded retrograde amnesia¹; and spared remote memory. The case study of H.M. was groundbreaking because it demonstrated that specific memory functions are dissociable from one another. In addition, the ability of H.M. to perform successful sensorimotor and perceptual learning even in the presence of severe global amnesia suggests that certain learning abilities are spared in amnesia. This has lead to

¹Amnesia is traditionally classified in two major categories: retrograde and anterograde. Retrograde amnesia refers to the case in which a person is unable to remember details that were learned prior to the event that caused the amnesia. Anterograde amnesia describes the condition in which a person seems unable to learn new information after a brain trauma. It is common for both kinds of amnesia to be present simultaneously to different degrees.
dissociations between declarative memory and several subtypes of procedural memory such as skill learning, conditioning and repetition priming.

Procedural memory is generally supported by various types of learning and different kinds of memories. The acquisition of procedural memories is not limited to general skill learning, such as motor or perceptual skills, but also includes learning of habits, conditioning and priming. Besides slow incremental improvements, procedural memories can also be gained by one trial learning, as demonstrated by repetition priming studies.

Furthermore, procedural memories are not limited to a particular category of material but include a broad range of stimuli including words, non-words, objects, patterns or pictures. The domain of procedural memory, which is preserved in amnesic patients compared to declarative memory, is global and not specific to the modality of information, speed of acquisition or specificity of memory. Instead complex and higher order properties such as form of memory expression, extent of conscious access to memories or structure of memory representation define procedural memories. Procedural memories are distinct from declarative memories, which will be reviewed in the following section.

2.6 Declarative memory

Declarative memory resembles closely the meaning of the word ‘memory’ as used in everyday language because it refers to the conscious recollection of facts and events. Declarative memories are characterised as explicit and accessible to conscious awareness so that facts or episodes can be brought to mind verbally as propositions or nonverbally as images. Procedural memory, in contrast, is implicit and only accessible through performance which engages knowledge embedded in skills or operations. Furthermore, declarative memory orchestrates rapid formations of relational representations and enables the flexible use of information whereas procedural memories are neither flexible nor relational in nature. Declarative and procedural memory are also distinct in terms of the different kinds of information they process and the principle by which they operate. While the underlying principle
for declarative memory is the ability to detect and encode aspects which are unique to a single event, procedural memory is dedicated to the gradual extraction of the common elements from a series of separate events.

Declarative memories are divided further into two distinct subsystems constituting episodic memory for personally experienced events and semantic memory for general facts and knowledge. These two subsystems have many features in common, for example, both represent complex system that have a large capacity to stored information, in contrast to the limited storage capacity of working memory. Furthermore, both the episodic and semantic memory systems enable the acquisition of information through different sensory modalities.

Due to the fact that episodic and semantic memory are regarded as two distinct systems, experimental investigations have primarily concentrated on researching either the episodic or the semantic memory system. Therefore, theories of episodic memory have predominantly evolved in isolation and independent from theories of semantic memory. It is known, however, that people have access to their personal past not only in terms of episodic remembering but also in terms of semantic knowledge. An overlap between semantic and episodic memory seems to occur with the semantic content of episodes. When new information is encountered during specific events, such as watching the news or reading a paper, retrieval can occur from one of the memory systems or from both. Consequently, it is likely that the episodic memory system interacts with semantic representations and an investigation of such possible interaction is the endeavour of the present thesis.

Although some theories describe episodic and semantic memory as two parallel subsystems of declarative memory (Squire, 1987), others view episodic memory as a unique extension of semantic memory (Tulving, 1984). However, before the relations between episodic and semantic memory can be discussed further, the subsequent sections first review the concepts and models proposed for episodic and semantic memory systems, which might serve as basis for possible interactions between them.
2.6.1 Episodic memory

The episodic memory system enables the acquisition and retrieval of information about personally experienced events which are embedded in a particular spatial and temporal context (Tulving, 1983; Tulving, 1972). Thus, episodic memory entails information about what, when and where an event took place, and is also accompanied by autonoetic consciousness, the ability to undergo a self-aware mental journey through time. Such autonoetic consciousness is regarded as one defining feature of episodic memory as it gives rise to mental re-enactment of experienced events, which is distinguished from noetic consciousness, the awareness of specific knowledge per se (Tulving & Markowitsch, 1998; Wheeler, Stuss, & Tulving, 1997; Tulving, 1983). This suggests that a conscious, voluntary re-experience of prior events, which are embedded in a particular context, is central to the concept of episodic memory. A second defining feature of episodic memory (and one which will be particularly important for the computational modelling presented in this thesis) is the nature of stored information, which contain unique past events that have been acquired in a single learning incident. Besides defining the content of episodic memory, memory theories also have to characterize the encoding, storage and retrieval processes mediated by episodic memory.

Episodic encoding associates very different kinds of experienced information, including perceptual, semantic, temporal and spatial information, into a coherent episode. The formation of episodic memories, which is evoked by a single experience of an event, can occur without a deliberate intent. After encoding, storage processes are engaged to maintain or consolidate this information into memory traces, which persist over time and can be retrieved subsequently. While the term retrieval refers to the access of stored information, retrieval processes describe the means of using stored information. For a long time memory research was guided by the assumption that the result of a memory test indicates the content of stored information. These theories, which ascribe failures to remember information to problems in encoding and storage but not to retrieval, are referred to as ‘trace-dependent’ theories (Tulving, 1974). An alternative ‘cue-dependent forgetting’ theory embodies the assumption that memory relies upon two sources: the memory
trace and the retrieval cue (Tulving, 1974). The basic idea behind this theory is that both the stored memory traces and information presented by the cue are critical for successful remembering. Subsequent memory research focused on investigating different types of retrieval processes by employing distinct methods such as repeated testing of studied material, the presentation of different retrieval cues, comparison of different instructions at retrieval and the analysis of judgements made during retrieval.

2.6.1.1 Retrieval tests

One of the first systematic investigations of repeated memory testing was conducted by Brown (1923), who presented subjects with a recall test immediately after learning, which was followed 30 minutes later by a second test. This free recall test simply instructed subjects to remember as many previously studied items as possible. Surprisingly, the results showed that more items were recalled in the second test compared to the first test. This result, which has been replicated many times, indicated that a single memory test is not a perfect indicator of stored information per se. Attempts to explain this effect came from Roediger and Thorpe (1978) who proposed that people employ subjective and internally generated cues to guide their retrieval process. However, it is difficult to evaluate this proposal using tests of free recall, since it is impossible to control the nature of the retrieval cues. This has encouraged studies to investigate retrieval processes through manipulating overt retrieval cues, known as cued recall studies.

Experiments of cued recall typically present identical sets of study material and study instructions, while systematically manipulating the retrieval condition, e.g. by providing different retrieval cues. Studies have shown that the number of retrieved items doubles when the same stimulus material is tested with cued recall compared to free recall (Tulving & Pearlstone, 1966). This difference in performance indicates that information is available (i.e. stored) but not always accessible (i.e. retrieved) during free recall. Presenting not only parts but the entire stimulus itself in the test conditions, might occur as an extreme form of cued recall, but is regarded as a different type of test called recognition test.
This distinction between cued recall and recognition test is grounded in the different nature of the responses. Since generating or completing stimuli is no longer required, recognition tests typically assess memory performance using judgements about whether or not a test stimulus has been previously studied. A recognition test can take the form of an Alternative Forced Choice (AFC) or a yes-no recognition test. While the AFC test presents a studied item together with one or multiple alternative distractors, the yes-no recognition test displays only a single item which either was or was not presented in the study list and subjects are required to indicate whether an item is old (previously studied) or new (not studied). Consequently, the yes-no recognition test contains two classes of correct responses and two classes of incorrect responses (see Table 2-2).

<table>
<thead>
<tr>
<th>Test Item</th>
<th>old</th>
<th>new</th>
</tr>
</thead>
<tbody>
<tr>
<td>old</td>
<td>hit</td>
<td>miss</td>
</tr>
<tr>
<td>new</td>
<td>false alarm</td>
<td>correct rejection</td>
</tr>
</tbody>
</table>

Table 2-2: Possible outcome of a yes-no recognition test. Hits refer to old responses for truly old items, false alarms are old responses to truly new items, misses describe new responses for truly old items and correct rejections indicate new responses to truly new items. The probability of a hit equals the probability of (1-miss). Similarly, the probability of a false alarm equals the probability of (1-correct rejection).

However, the particular task of a yes-no recognition test can influence or bias performance. For instance, if the experiment associates false alarms with high costs or losses, subjects are more likely to adopt a conservative response bias, which leads to increased ‘new’ responses. This has to be taken into account when analysing experimental data and ideas from ‘Signal detection theory’ (Green & Swets, 1966) have been proven particularly useful in dealing with these issues. The following section will outline the basic principles of the signal detection theory and its application to recognition memory tests.
2.6.1.2 Signal detection Theory

The signal detection theory (SDT) (Abdi, 2007; McMillan & Creelman, 2005; Green & Swets, 1966) can be used to analyse data from recognition tests, which require categorisation of ambiguous stimuli. Such categorisation might either be performed on the basis of successful retrieval (called signal) or by chance (called noise in the SDT framework). For example, the signal can correspond to the feeling of familiarity for previously studied stimuli, whereas the noise relates to the feeling of familiarity evoked by new stimuli. The SDT assumes that the old and new signal form two distinct normal distributions (see Figure 2-2). The objective of this detection theory is to estimate two parameters: d’ and C, which will be discussed in the following. These parameters not only provide a description of the experimental data but also enable quantitative comparisons across different studies.

The mean difference of the old and new distribution divided by their standard deviation provides d’ (“dee prime”), a measure of bias-free discrimination. A d’ equal to 0 describes completely overlapping old and new distributions, suggesting that subjects can not discriminate between them. A greater difference between the two distributions leads to a larger d’ and a better discrimination between old and new items. Consequently, the report of correctly recognised old items (hits) itself is not sufficient to assess memory performance, and the proportion of correct rejections or false alarms has to be taken into account. Dependent on the false alarm rate, smaller hit rates could indicate a better discrimination than larger hit rates. For example, a hit rate of 50% with 2% false alarms reflects better discrimination performance than a hit rate of 90% with 90% false alarms.
Figure 2-2: Signal detection theory applied to yes-no recognition memory tests. Old items are assumed to appear on average more familiar than new items, although there is some overlap. The distance between the means of the two distributions is $d'$; a measure of discriminability. Participants adopt a criterion and items falling above it will be judged as familiar (yes response) and items below it are classified as novel (new response).

As mentioned previously, not only the discrimination ability $d'$ but also the response bias $C$ determines the proportion of hit and false alarm rates. $C$ reflects the average between the mean of the old distribution and the mean of the new distribution. A value of $C$ greater than 0 indicates a conservative response bias, the tendency to respond ‘new’ more often than ‘old’, whereas a value of $C$ smaller than 0 reflects a liberal response bias, the tendency to respond ‘old’ more often than ‘new’.

Despite its power and simplicity, the signal detection theory is not the only way of analysing yes-no recognition responses particularly in circumstances where the underlying assumptions, that the old and new distributions are normally distributed and have the same variance, might not always be given.

An alternative approach is the two-high-threshold model (Green & Swets, 1966; Egan, 1958) which assumes that the decision space is characterised by a few discrete states, rather than the continuous dimension underlying the detection theory. This approach proposes two thresholds, one for new items and one for old items and only items that exceed both thresholds will be recognised. The discrimination measure or corrected recognition score in the two-high-threshold model is called ‘Pr’, which reflects the difference between the hit and false alarm rate. The bias
measure in this model is named ‘Br’, and is calculated by the false alarm rate divided by 1-Pr. Values of Br greater than 0.5 indicate a liberal response bias, while Br values less than 0.5 signify a conservative response bias.

2.6.1.3 Models of retrieval

The question of whether the signal detection model or the two-high-threshold model is better suited for calculating discrimination ability and response bias clearly depends on which model more appropriately reflects the underlying characteristics of the data. Theoretical models which try to incorporate and explain a wide variety of experimental findings largely attempt to characterise recognition data, and thereby outline retrieval processes that can account for empirical results. The following, therefore, will summarise some of the most influential models, outlining the current view of episodic retrieval and the different processes that contribute to it.

2.6.1.3.1 Single Process Models

Early theories of recognition memory can be summarised as single process models which describe recognition memory as contingent upon a single search process. For example, the tagging model of recall and recognition (Yntema & Trask, 1963) assumes that every encoded item is associated with a tag which contains not only the information that an item was studied, but also the time of its occurrence. This model can account for accurate judgements of presentation order (Yntema & Trask, 1963). It further explains the incorrect classification (false alarms) to words which are similar to the target word, by proposing that a tag is not only attached to a studied word but also to all related words that comes to mind during study. A second type of single process models, called strength theory models, characterise more recently experienced items as stronger or more familiar (Wickelgren & Norman, 1966). At test each memory item is retrieved and compared with the test item and judged as ‘old’ or ‘new’. Strength in this model provides a memory signal which is evaluated in a signal detection type analysis.
Although single process models have the advantage of parsimony, their key limitation is that only one process must account for all memory findings. Thus, single process models predict that the same manipulation should cause the same effect regardless of the task, a prediction that is inconsistent with experimental findings. One study, for example, demonstrates that recall is higher for intentional compared to incidental learning, whereas the opposite is true for recognition (Eagle & Leiter, 1964). Equally, high-frequency words are recalled better than low-frequency words, while low-frequency words are recognised more accurately than high-frequency words (Gregg, 1976; Deese, 1961). Single process models can not account for these results, as they predict that learning task or word frequency have to effect recall and recognition in a similar way. In order to overcome this limitation a class of two-stage models know as generate-recognize models has been proposed that have largely replaced single process models.

2.6.1.3.2 Generate-Recognize Models

The generate-recognize models (Anderson & Bower, 1972; Kintsch, 1970) assume that recall involves two processes while recognition entails only one process. The two processes supporting recall involve first a generation of a set of plausible candidates, and second, a confirmation or selection of which candidate word is finally recalled. Recognition, in contrast, involves only candidate confirmation but not candidate generation, because a plausible candidate has already been provided in the test. Such models can explain why recall and recognition are differentially influenced by altered learning tasks or changes in word frequency.

Despite their obvious plausibility, a major limitation of these models is their prediction that a recalled item must also be recognised. Because both recall and recognition have the second stage in common, it has to follow that once a word can be recalled it must also be recognised. However, studies have demonstrated a phenomenon known as recognition failure of recalled words, which shows that even though subjects fail to recognize a studied word previously, they may nonetheless be able to recall it in a cued recall test (Watkins & Tulving, 1975). This suggests that both recognition and recall depend on the cues available at test. One possible
extension of the generate-recognize model could entail a search process for the recognition phase, so that both recall and recognition rely on a search and a confirmation process (Jacoby & Hollingshead, 1990). Nevertheless, it seems unlikely that items are always retrieved via an extensive memory search because subjects are able to identify very quickly and with great confidence items that were not studied (Atkinson & Juola, 1974). Therefore, several researchers have proposed that recognition can be based on a search process but can also rely on a simple familiarity process (Mandler, 1980; Atkinson & Juola, 1973). The models that support this proposal are known as dual-process models (Yonelinas, 2002).

2.6.1.3.3 Dual process models

Dual process models are based on the idea that recognition performance is supported by two different types of retrieval processes: familiarity and recollection. Familiarity is widely believed to be a fast acting process, which produces memory judgements based on the quantitative assessment of strength or confidence that a memory has been encountered previously. Recollection, in contrast, entails retrieval of qualitative contextual information about a previous event. A variety of dual process models have been proposed, for example the Atkinson model (Atkinson & Juola, 1974; Atkinson & Juola, 1973), the Mandler model (1980), the Jacoby model (Jacoby & Kelley, 1992; Jacoby & Witherspoon, 1982; Jacoby & Dallas, 1981) or the Yonelinas model (Yonelinas, 1994).

Probably the most prominent dual process theory to date is the Yonelinas model (Yonelinas, 2002; Yonelinas, 1999; Yonelinas, 1997), which suggests that familiarity and recollection provide different types of information and engage two qualitatively distinct processes. Familiarity is thought to operate on quantitative information, i.e. memory strength, and is proposed to be well described by a signal detection process. Recollection, in contrast, is assumed to recover qualitative information about a previously studied episode and is characterised as a threshold-like retrieval process. In addition to the type of information, familiarity and recollection are associated with different levels of recognition confidence. While recollection is coupled with high confidence ratings of a recognition decision,
familiarity covers a wide range of confidence responses. Furthermore, the Yonelinas model assumes that familiarity and recollection become initiated in parallel but function independently from each other, with familiarity being faster than recollection.

In general, all the aforementioned dual-process models are in good agreement with respect to a number of key issues and are often treated as slight variations of the same basic theory. For example, they all agree that familiarity is faster than recollection, and even though the Atkinson model proposes that familiarity is completed before recollection, all the remaining models assume that familiarity and recollection are initiated in parallel and act independently from each other. Furthermore, familiarity is mostly described to reflect a continuous index of memory strength, while recollection is associated with retrieval of specific information about a study event. Also, some models, like the Atkinson and Mandler model, assume that familiarity and recollection reflect perceptual and conceptual processes respectively, whereas the view of the Jacoby suggests that familiarity includes both perceptual and conceptual processes. There are of course also considerable points of disagreement, for example concerning the extent to which a process can support novel learning, and how familiarity is related to implicit memory (for a more extensive review see Yonelinas, 2002).

**2.6.1.3.4 Global Matching Model**

In opposition to dual-process models Gillund and Shiffrin (1984) argued that recognition performance could be solely explained by a ‘search of associative memory’ (SAM) model (Gillund & Shiffrin, 1984; Raajmakers & Shiffrin, 1981). This model is part of the so-called global matching models, which describe the attempt to model human memory in a formal and quantitative fashion in a variety of different task, including both recall and recognition. Common to all these models is the basic principle of recognition memory, which is based on two claims. The first claim, called the interactive-cue assumption, concerns the way multiple cues are combined to probe memory. The second claim concerns the way information is accessed, which is referred to as global matching assumption.
More traditional matching models usually assume that a test probe undergoes a serial or parallel matching process with every single item stored in memory (Flexser & Tulving, 1978). The obtained strength of every individual match is compared to a threshold. Recognition failure occurs when no match exceeds the threshold. In general, global matching models can be divided into two types based on whether items are stored individually followed by a multiple-match process (separate storage models), or whether all information is stored in a distributed fashion and the matching process is based on a composite (distributed memory models) (see Figure 2-3).

SAM (Raajmakers & Shiffrin, 1981) and MINERVA2 (Hintzman, 1984) are examples of separate-storage models, while TODAM (Murdock, 1983; Murdock, 1982), CHARM (Eich, 1982) or the Matrix model (Pike, 1984) describe distributed memory models. Although all these models differ in their specific assumptions and the way the global matching process is implemented (for more detailed description or
comparison of theses models see Humphreys et al., 1989; or Clark et al., 1996), they all predict, in agreement with other single process models, that recognition memory relies on only one single retrieval process.

However, this view is in conflict with the previously discussed dual process models. Empirical evidence is required to answer the question of whether recognition memory is contingent upon a single process or on dual processes. Therefore, the subsequent section will review empirical findings that have lead to the view that recognition memory depends on two distinct retrieval processes.

2.6.1.4 Retrieval processes: familiarity and recollection

Recent work seems to provide empirical evidence that two distinct retrieval components support recognition memory. Such evidence comes from so called remember/know procedure, which requires participants to judge the source that a recognition response is based on. A further line of research that is difficult to account for with single process models are ‘Receiver Operating Characteristics’ (ROCs). The remainder of this section will concentrate on the underlying logic of the remember/know procedure and ROC curves and discuss the findings gained from these methods. Finally, the Process Dissociation Procedure (PDP) will be introduced as a behavioural technique to separate the contribution of familiarity and recollection to recognition memory performance.

2.6.1.4.1 Remember/Know procedure

The two retrieval processes, familiarity and recollection have been found to differ in their phenomenological experience. While recollection is accompanied by the awareness of qualitative information about a study event, familiarity is lacking this type of awareness and is only associated with a sense of oldness. This difference in awareness is captured by the remember/know procedure, which asks participants to introspect about their recognition response (Gardiner, 1988; Tulving, 1985). This procedure requires ‘remember’ response whenever qualitative information of a previously studied item is recollected, and a ‘know’ response when items seem
familiar even though no further details can be retrieved about them (Yonelinas, 2002). Interestingly, Tulving’s (1985) original account of the remember/know procedure related remember responses to the conscious state of awareness associated with the output from the episodic memory system, while know responses reflect a state of awareness associated with the output from the semantic memory system. However, nowadays the remember/know procedure is typically employed in the context of dual-process theories and is regarded as an index of different episodic retrieval processes.

Participants seem to be able to consistently employ remember and known responses. Source memory studies, for instance, report that participants can correctly identify presentation details such as relative position or spatial location for items that are claimed to be remembered, while this is not the case for items that are claimed to be known (Mather, Henkel, & Johnson, 1997; Perfect, Mayes, Downes, & Eijk, 1996).

Many studies have reported dissociations for remember and know responses across different variables and have tried to reveal the relation between these two types of responses with confidence or trace strength. For example, level of processing manipulations have a large effect on remember but no effect on know judgements (Rajaram, 1993; Gardiner, 1988), whereas the same versus different study/test modality evoked a large difference in knowing but no difference in remembering (Gregg & Gardiner, 1994). A further experiment testing lists of words and pronounceable non-words demonstrated no considerable overall difference in recognition performance, but revealed a strong differential effect on the two types of responses. While words evoked more remember than know responses, non-words gave rise to more know than remember responses (Gardiner & Java, 1990). Finally, an investigation testing the effect of an increased number of study trials reported enhanced overall recognition performance due to an elevation in both remember and know responses (Gardiner & Radomske, 1999).

The empirical data suggest that the two distinct states of awareness might relate to different types of retrieval. Given that remember responses require retrieval of specific details, it is reasonable to assume that it provides a measure of
recollection. In contrast, know responses do not reflect a direct index of familiarity because subjects are not instructed to use this response whenever an item is familiar but whenever an item is familiar without being recollected. Consequently, the proportion of known responses will underestimate the probability that an item is familiar. To compensate for this underestimation, the proportion of ‘know’ responses should be divided by the total number of responses that were given in the absence of recollection² (Yonelinas & Jacoby, 1995).

Overall, the remember/know procedure is employed in many studies as a method of estimating the contribution of familiarity and recollection during a memory test. However, this procedure is not the only line of empirical evidence that advocates the view that recognition memory is supported by familiarity and recollection. Further evidence is provided by Receiver Operating Characteristics.

2.6.1.4.2 Receiver Operating Characteristics (ROCs)

ROC curves plot, across different levels of decision confidence, the probability of a correct recognition response to a target (i.e. hit rate) against the probability of an incorrect response to a non-target (i.e. false alarm). A point on a ROC curve describes effectively the ability to discriminate between hits and false alarms, which is also known as the sensitivity measure d’ (see Section 2.6.1.2). In other words, a ROC curve plots d’ as a function of decision confidence as it is systematically shifted along the old and novel distribution, starting at very conservative or confident responses and moving towards more and more liberal or

---

² As subjects are instructed to make a ‘remember’ response whenever an item is recollected (R), the proportion of a remember response is indexing the probability of recollection: R = ‘remember’. However, as subjects are instructed to make a ‘know’ response when an item is familiar (F) in the absence of recollection (1-R), the proportion of know responses divided by the number of possible known responses indexes the probability of familiarity: F = ‘know’/ (1-R).
less confident responses. Thus, the leftmost point of a ROC curve reflects the most confident discrimination performance and the further right a point is positioned on the curve the less confidence is associated with the discrimination (see Figure 2-4).

![Figure 2-4: Receiver Operating Characteristics curves (ROC) derived from the Signal detection model (SDM). ROC curves (right panel) are generated by plotting the probability of hits against the probability of false alarms systematically across different point of the decision space in the SDM (left panel). The leftmost point on a ROC curve reflects the most confident decision (compare the red point on the ROC curve with the red decision criterion of the SDM) and the further right a point is positioned on the curve the less confident the response (compare the green point on the ROC curve with the green decision criterion of the SDM). The right panel shows multiple ROC curves for different levels of discrimination ability of the SDM indicated by $d'$.

Furthermore, the shape of ROC curves is informative about the type and level of discrimination. When performance is at chance ($d'=0$), the ROC curve is identical to the major diagonal where hit and false alarm rates are equal. With increasing performance the ROC curve shifts towards the upper left corner, where discrimination becomes perfect (hit rate = 1 and false alarm rate =0). ROC curves are often expressed in the representation of z-transformed curves named z-ROC curves, which are sensitive to changes in hits relative to changes in false alarms. Such z-ROCs, which are generated on the basis of z-transformed hit and false alarm scores, take the shape of a straight line (if the underlying distributions are Gaussian). The
Intercept of z-ROCs provide a measure of discriminability, and the slope reflects the symmetry of ROC curves which indicate how false alarm rates will change in relation to hits.

Z-ROC curves with unit slope are symmetrical around the negative diagonal, which means that if they are folded along the negative diagonal, they will produce a reflection onto themselves. ROC curves with unit slope are generated for instance by gaussian old and new distributions of equal variances. If the slope of the ROC curves is different from 1, the sensitivity changes along the decision axis and the curve is no longer symmetrical around the negative diagonal. Such asymmetric ROC curves can occur for different reasons. For example, the signal detection theory predicts asymmetric ROC curves if the underlying distributions contain unequal variances. An alternative explanation is given by threshold theories, which assume that the decision space is characterised by discrete states. While some states reflect decisions purely based on hits, others reflect a proportional contribution of hits and false alarms. This also predicts asymmetric ROC curves.

Recently, ROC curves have found an increased application in recognition memory research. Some early studies have reported curvilinear and approximately symmetrical ROCs for recognition memory (Murdock & Duffy, 1972), which can be described by solely one signal detection parameter d’ (according to the equal variance signal detection model). Further studies, however, revealed overall curvilinear but asymmetric ROC curves that appear to be pushed up the y-axis. Importantly, the degree of asymmetry varies across different experimental manipulations. In some cases, ROC curves become more asymmetric as performance increases, for example, due to changes in study-test lag (Donaldson & Murdock, 1968), word frequency (Ratcliff, McKoon, & Tindall, 1994; Glanzer & Adams, 1990) or concreteness (Glanzer & Adams, 1990). However, other manipulations evoked an increase in performance without changing the symmetry of ROC curves, for example, study duration (Yonelinas & Jacoby, 1994; Ratcliff et al., 1994; Ratcliff, Sheu, & Gronlund, 1992) or item repetition (Egan, 1958).

As these studies demonstrate that the symmetry of ROC curves changes across some manipulations but remains constant across others, they are difficult to
account for with just a single recognition parameter. Asymmetrical ROC curves are not necessarily inconsistent with a single process model when they appear in the context of an unequal-variance signal detection model. If, for example, the variance of the old-item distribution is always greater than the variance of the new-item distribution, asymmetric ROC curves will be observed even though the recognition accuracy is still appropriately reflected in $d^\prime$. Similarly, if the asymmetry is a function of accuracy (e.g. increased accuracy leads to increased asymmetry), recognition performance could still be measured with a single parameter $d^\prime$. Nevertheless, the studies mentioned above demonstrate a functional independence between the asymmetry of ROC curves and the level of recognition accuracy, which can not be accounted for by a single memory parameter. More importantly, curvilinear and symmetrical ROC curves have been reported for amnesic patients who have deficits in recollection and rely predominantly on familiarity (Yonelinas, Kroll, Dobbins, Lazzara, & Knight, 1998; but see Wais, Wixted, Hopkins, & Squire, 2006). This provides empirical evidence that familiarity likely reflects an equal-variance signal detection process.

However, the reported asymmetric ROC data are in agreement with the proposal of a second retrieval process. Such a proposal implies that recognition memory is not solely based on assessments of familiarity but is also supported by a separate recollection process (Yonelinas, 1997; Yonelinas, 1994). Retrieval based on recollection is assumed to reflect an all-or-none process, so that retrieval of a studied event either succeeds or fails. In the case of successful retrieval, recognition is associated with highly confident responses. Consequently, recollection would tend to increase the number of those old items eliciting high-confidence responses without influencing false-alarm rates. This would move the ROC curves further up on the y-axis and produce an asymmetry like the one that has been reported in empirical findings. Familiarity, on the other hand is assumed to be well described by the equal-variance signal detection model. Recollection and familiarity are further regarded to contribute independently to recognition judgements (for a discussion of this assumption see Cowan and Stadler, 1996; Jacoby et al., 1993; Jacoby et al., 1994; Jacoby 1997).
In general, ROC curves are thought to reflect components of two independent processes: a symmetric, curvilinear component associated with familiarity and an asymmetrical, linear component reflecting recollection. Increasing recollection will force the ROC curve to become more asymmetrical, whereas increasing familiarity will influence the shape of the ROC curve to be more symmetrical. This can therefore account for the findings that an increase in recognition performance can be accompanied either by a change in symmetry or no change in symmetry, depending on whether performance is primarily based on familiarity or recollection.

Further support for this account comes from studies that demonstrate a direct relationship between familiarity and recollection and the shape of the ROC curves. Estimates of familiarity and recollection gained with the remember/know procedure revealed that changing the size of geometric shapes between study and test leads to a decrease in both familiarity and recollection (Yonelinas & Jacoby, 1995). The ROC analysis of these data showed no change in slope or symmetry, as performance decreased. A related experiment, which presented study lists of different lengths, reported estimates of familiarity and recollection which revealed enhanced recollection but no change in familiarity (Yonelinas & Jacoby, 1994). This increase in recollection was accompanied with better overall recognition performance and more asymmetric ROC curve.

In summary, these studies demonstrate that the dual process model proposed by Yonelinas (1994), in contrast to single process models, is able to account for the pattern of the observed ROC curves. The studies furthermore illustrate that the proposed link between the shape of ROC curves relative to familiarity and recollection is consistent with empirical estimates of familiarity and recollection, even when different estimation methods are used. This is the case, as estimates of familiarity and recollection of the earlier mentioned study of list length (Yonelinas & Jacoby, 1995), were generated with a so-called Process Dissociation Procedure (PDP), which shall be explained in the following section.
2.6.1.4.3 Process Dissociation Procedure (PDP)

Jacoby (1991) developed a technique for separating two different processes that contribute to a specific task. This technique, called the Process Dissociation Procedure (PDP), contrasts the performance of two different types of tests. The logic behind this procedure is that an inclusion test permits the contribution of two processes (e.g. familiarity (F) and recollection (R)), whereas a second exclusion test is designed to involve only one of the two processes (e.g. familiarity). By comparing performance on these two tests, it becomes possible to separate the contribution of the individual processes with the following equations:

\[
P(\text{hit} \mid \text{inclusion}) = R + (1-R)F \\
P(\text{false alarm} \mid \text{exclusion}) = (1-R)F
\]

The probability of correctly accepting an item in the inclusion task is equal to the probability that an item is recollected plus the probability that an item is familiar in the absence of recollection. In contrast, the probability that an item is incorrectly identified as old in the exclusion task is given by the probability that an item is not recollected but accepted on the basis of familiarity. Estimates of familiarity and recollection can be gained by contrasting the inclusion and exclusion performance as follows:

\[
R = P(\text{hit} \mid \text{inclusion}) - P(\text{false alarm} \mid \text{exclusion}) \\
F = P(\text{false alarm} \mid \text{exclusion}) / (1 - R)
\]

These equations are based on the assumption that familiarity and recollection are independent, so that there should be variables that produce dissociations on the estimates of familiarity versus recollection. This has indeed been observed and factors that evoke changes in recollection but do not alter familiarity have been identified such as for example aging (Jacoby, 1999; Jennings & Jacoby, 1997), response time (Yonelinas & Jacoby, 1994), divided attention (Jacoby & Kelley,
1992) or study duration (Jacoby, 1998). In comparison solving an anagram rather than simply reading a word increases both familiarity and recollection estimates (Jacoby, 1991).

Similarly, an elevation of both familiarity and recollection occurs for semantic compared to shallow processing (Toth, 1996), as well as for the picture-superiority effect, which reflects better word recognition if the object the word refers to was previously studied as a picture compared to a word (Wagner, Gabrieli, & Verfaellie, 1997). Finally, differences in familiarity without changes in recollection have been observed for the revelation effect, which describes better recognition of previously studied items if they are presented disguised at test and become only gradually revealed (Lecompte, 1995).

However, the assumption underlying the process-dissociation procedure, that familiarity and recollection independently contribute to performance, has been controversial (Jacoby, Begg, & Toth, 1997; Jacoby & Shrout, 1997). Curran and Hintzman (1995), for example, found a correlation between familiarity and recollection which was interpreted as a violation of the independence assumption, which evoked an artifactual dissociation. However, a subsequent debate established that although the independence assumption of the process dissociation procedure could be violated in some circumstance, correlations between familiarity and recollection are not able to detect such violations (Jacoby et al., 1997; Jacoby & Shrout, 1997). However, it is not entirely clear what impact violations of the independence assumption have on the outcome of the process dissociation procedure (McBride, Dosher, & Gage, 2001).

Generally, in most experimental conditions familiarity and recollections are found to operate independently (Jacoby, 1998). The validity of the process dissociation procedure is supported by experiments in which the estimates obtained by the process dissociation procedure agree with the estimates obtained with other methods (Yonelinas, 2001).
2.6.1.5 Conclusion

In summary, this section described the episodic memory system which defines one of the two subsystems constituting declarative memory. A main emphasis was placed on episodic retrieval. Studies demonstrate that memory performance is dependent on the type of memory test employed. The amount of retrieved information is smaller when participants perform free recall, compared to cued recall and is highest for recognition. Such performance differences indicate that information might be stored but can not be accessed unless the right type of retrieval cue is used at test. These findings have motivated an increased use of recognition memory paradigms. Data acquired by recognition memory tests and their interpretation or analysis are discussed in reference to signal detection theory.

Nevertheless, over the past decades different models of retrieval have been proposed to account for empirical data. Single process or global matching models, for example, propose that data from a recognition memory test can be accounted for by a single parameter provided by the signal detection theory. Dual process models, in contrast, assume that recognition performance relies on two different types of retrieval processes: familiarity and recollection. Recent empirical evidence seems to support the proposal of two distinct retrieval processes. Such findings have been reported using the remember/know procedure, ROC curves and PDP estimates. In conclusion, although there is no definite consensus about which is the best model to describe episodic memory retrieval, there is increasing evidence that at least two processes are engaged during episodic retrieval.
2.6.2 Semantic memory

According to Tulving’s proposal (1972), episodic memory defines only one half of the declarative system; the second half is defined by semantic memory. The term semantic memory is used to denote comprehension of language including memory for words and concepts. In contrast to episodic memories, semantic memories are not associated with autobiographical references or the context of acquisition, instead it encompasses information about facts, objects, concepts or general knowledge about the world. Thus, semantic memory is detached from the learning context and can be flexibly retrieved in a variety of contexts.

2.6.2.1 Organisation of semantic memory

Early research into semantic memory focused on finding distinctions between semantic memory and other memory systems without addressing the content or organization of semantic memory per se. Recently, however, large efforts have been made to characterise the underlying structure of the semantic memory system. The influential neuropsychological studies from Warrington and colleagues (1975), who reported patients with impaired comprehension of nonliving things but relatively spared comprehension of living things, provided the foundation for this research.

More contemporary debates on semantic memory concern the format of semantic representations, their association with underlying sensory-motor processes, as well as their categorical organization in semantic memory. Besides semantic storage, a further topic of ongoing research is the mechanism that guides semantic retrieval; automatic vs. controlled processes. However, before describing the principles of semantic retrieval in more detail, this section will start with a brief review of empirical findings supporting the currently held view that semantic memories are organised in a distributed, associative network that links conceptual representation of semantic knowledge.
2 Introduction to Memory

2.6.2.1.1 Sensor-motor processes and semantic representations

Conceptual semantic representations are clearly distinct from the sensory-motor processes that are involved in the acquisition of these representations. However, there is no clear consensus about the format semantic representations take, or how semantic representations relate to their preliminary sensor-motor processes. Research in this area is guided by two different stances.

One stance is based on the assumption that perceptual and conceptual processes result from two interrelated but completely independent systems (Humphreys & Riddoch, 1988; Snodgrass, 1984; Pylyshyn, 1973; Anderson & Bower, 1973). According to this view, a first process of perceptual analysis is performed in different hierarchical stages. This analysis can reach the level of a three-dimensional structural description before a second process performs recognition of that item. This recognition process is performed on semantic representations which are regarded as abstract, amodal and propositional and therefore completely distinct from the sensor-motor representations the first process is acting upon.

In contrast, the second stance rejects the idea of abstract, amodal semantic representations and assumes that semantic information is associated with a similar format to that which it was first perceived in. Some more radical interpretation of this stance suggest that semantic memory contains multiple modality-specific systems, which represent objects in exactly the same format they were perceived in (Shallice, 1988; Warrington, 1975). However, this view implies that information will be duplicated within separate modality-specific systems. In contrast to this modality specific model, a second more moderate interpretation proposes that semantic memory is based on activity patterns which are distributed across the perceptual and motor domain (Allport, 1985; Kolers & Brison, 1984). This so called multimodal model does not assume that the semantic system contains modality specific representations, rather it describes a multimodal network, in which different areas are accessed by each modality and store modality specific information.

Whether the amodal model, the modality-specific model, or the multimodal model describes the semantic memory system more appropriately can be determined
by their compatibility with empirical findings. Data that conflict with the amodal model have been reported in clinical studies of optic aphasia (Beauvois, 1982). In this condition patients fail to name visually presented objects, although they are able to identify them when presented non-visually (e.g. mime). Warrington and Shallice (1979), suggest that this dissociation reflects the contribution of two different semantic subsystems: the visual semantic and the verbal semantic system.

Caramazza (1990), by contrast, explains these data with a unified, amodal model named: the Organised Unitary Conceptual Hypothesis (OUCH). This model assumes that a particular modality of input (e.g. visual input) has privileged access to a subset of information (e.g. perceptual or functional information), which does not necessitate modality-specific storage of the information (Caramazza, Hillis, Rapp, & Romani, 1990). Nevertheless, this OUCH model cannot fully account for why the ability to name objects presented in non-visual modalities is selectively spared in optical aphasia.

Semantic dementia, which is a selective disorder of semantic memory manifested in focal degeneration of the frontal lobes (Snowden, Goulding, & Neary, 1989) offers further important data to this debate (Hodges, Patterson, Oxbury, & Funnell, 1992). Patients suffering from semantic dementia demonstrate difficulties understanding the name of an object, yet they are able to recognize pictures of those same objects (Lauro-Grotto, Piccini, & Shallice, 1997; McCarthy & Warrington, 1988). However, the opposite pattern of results has been reported in other groups of patients, which exhibit greater difficulties in identifying pictures compared to understanding words (Warrington & McCarthy, 1994; McCarthy & Warrington, 1986). This double dissociation has been interpreted as evidence for models of modality-specific semantic systems.

However, such dissociations are rarely observed in absolute terms. Often, semantic dementia affects both words and pictorial stimuli, albeit to different degrees. In addition, some studies report high correlations between knowledge elicited from pictures and words (Lambon, Graham, Patterson, & Hodges, 1999), which goes against the proposal that knowledge is stored in separate verbal and visual semantic systems as assumed by modality-specific models. Therefore, these
data might be open to alternative explanations consistent with unitary, amodal models. Indeed, such models predict superior performance for pictures, because pictures afford certain properties of objects, whereas words do not. On the other hand, this implies that the reversed effect of superior performance for words compared to pictures can not be explained by amodal models. Consequently, neither the modality-specific nor the amodal models can fully account for this double dissociation.

A study by Snowden and colleagues (1994) attempted to clarify this conflict and demonstrated a clear relationship between the level of performance for different classes of stimuli and lesions in particular brain areas. Patients with predominant left temporal lobe atrophy performed better with faces, whereas patients with larger right temporal lobe atrophy performed better for words. Such stimulus specific deficits caused by distinct brain lesions are inconsistent with a unitary, amodal model. The data are also not completely compatible with a strict modality specific model, since memory performance was only reduced but not completely abolished. However, these data support a multimodal model comprising a single interconnected network with dedicated brain regions representing modality specific information.

In summary, recent clinical and experimental data regarding the relationship between semantic representations and their underlying sensory-motor processes cast serious doubt on models that propose a unitary, amodal and abstract format for semantic representations. These models fail to explain, for example, the spared abilities observed in patients with optic aphasia, and cannot account for the fact that some patients show superior performance for words compared to pictures. Therefore, these findings do not support the hypothesis of complete independence between modality specific processes of sensory-motor information and amodal, abstract and propositional representations of conceptual knowledge. An increasing number of studies report findings consistent with models that suggests conceptual knowledge is stored in a similar format to that in which it was perceived, or is, at least still associated with the perceptual representations through which it was acquired. Although there is no clear consensus as to whether the format of semantic memory is better described by a modality-specific model or a multimodal model, recent findings
seem to advocate the latter model. Beside the debate of how semantic representations relate to the sensory-motor processes through which they were acquired, a second central discussion focuses on the question how semantic representations are organised in semantic memory.

### 2.6.2.1.2 Categorical organisation of semantic representation

A significant body of research regarding the structure and organisation of semantic memory has been reported by Warrington (1975), who proposed that semantic memory is categorically organised in the brain. This proposal was motivated by the fact that different brain lesions provoke distinct category-specific deficits, which selectively impaired performance for abstract words (Warrington, 1981; Warrington, 1975), action names or verbs (McCarthy & Warrington, 1985; Baxter & Warrington, 1985), living things (Warrington & Shallice, 1984), (McCarthy & Warrington, 1991) and man-made things (Warrington & McCarthy, 1987; Warrington & McCarthy, 1983).

This work has lead to the ‘differential weighting hypothesis’, which accounts for the mechanisms causing semantic disorders. This hypothesis assumes that concepts are linked to the perceptual systems though which they are acquired, but emphasizes that sensory modalities are differently weighted or involved when distinct semantic categories are acquired. This view, for example, explains the dissociation between living and non-living categories as a consequence of the distinct weighting of visual-perceptual and functional properties for living and non-living things.

The severe inability to recognize a living being and the preserved capacity to identify man-made objects, is the most frequently reported dissociation (Kolinsky et al., 2002; Forde, Francis, Riddoch, Rumiati, & Humphreys, 1997; Gainotti & Silveri, 1996; Warrington & Shallice, 1984). The reverse dissociation of impaired recognition of non-living things but intact identification of living things has been reported much less frequently (Sacchett & Humphreys, 1992; Hillis & Caramazza, 1991; Warrington & McCarthy, 1983). It has been suggested that these category specific impairments may simply represent an artefact of the stimulus material,
because living things tend to be of lower frequency, lower familiarity and greater visual complexity (Stewart, Parkin, & Hunkin, 1992; Funnell & Sheridan, 1992). However, the fact that some patients do show deficits for the supposedly easier category of non-living things argues against a simple stimulus artefact account. Even when frequency, familiarity and visual complexity are carefully matched for living and non-living things, many patients continue to show difficulties in naming or recognising living things (Gainotti & Silveri, 1996; Laiacona, Barbarotto, & Capitani, 1993; Warrington & Shallice, 1984). Equally, some studies demonstrate double dissociations in category deficits when testing groups of patients with the same stimuli (Gainotti & Silveri, 1996; Hillis & Caramazza, 1991). Therefore, the category specific deficits appear to reflect specific disruptions of knowledge following specific kinds of brain lesions.

Nevertheless, the interpretation or explanation of such categorical impairments remains controversial. The previously introduced ‘different weighting hypothesis’, has been challenged by two other accounts. One is the hypothesis of ‘domain specific knowledge system’ proposed by Caramazza and Shelton (1998), who rejected the ‘different weighting hypothesis’ on the basis that patients who fail to recognize living things do not necessarily show greater impairments of visual-perceptual properties. This ‘domain specific knowledge system’ assumes different evolutionary-adapted neuronal mechanisms for the domains of animals (possible predators), plant life (potential food and medicine) and non-living things. Category-specific defects, according to this view, reflect a disruption of these different evolutionary-adapted neuronal mechanisms.

The second account that challenged the ‘different weighting hypothesis’ is the hypothesis of ‘inter-correlations among semantic features’ (Gonnerman, Anderson, Devlin, Kempler, & Seidenberg, 1997). This hypothesis proposes that semantic representations contain features (i.e. perceptual and functional features), which have different levels of interconnectivity for living and non-living categories. For example, in living things eyes and ears might be correlated with the function of seeing and hearing, whereas this interconnection is less important for non-living things that have eyes and ears. According to Gonnerman and colleagues (1997) these
different interconnections between living and non-living categories might be more important for explaining category-specific disorders than the differential weighting of perceptual and functional attributes.

In summary, there is a general consensus that semantic knowledge is organised into specific clusters or categories. Category specific impairments have been reported for patients with damages to circumscribed brain areas. The nature of the resulting deficits describes the inability to recognize a semantic category. However, the dissociated categories also differ along other possible dimensions such as their defining features (visual features for living things and functional features for non-living things) according to the ‘different weighting hypothesis’, their evolutionary-adapted neuronal mechanisms according to the ‘domain specific knowledge system’ hypothesis, or their correlation or interconnectivity between specific perceptual and functional feature according to the ‘inter-correlations among semantic features’ hypothesis. Whether one of these hypotheses can describe the organisational principle or structure of semantic knowledge remains to be shown. Nevertheless, identifying the structure and organisation of semantic knowledge is of wider importance, as they are likely to influence the way those representations are accessed by semantic retrieval processes.

2.6.2.2 Controlled and automatic retrieval processes

The previous section (see 2.6.2.1) outlined key features of how semantic memories are represented and organised. Yet, it remains unclear how relevant information is accessed or retrieved from semantic memory. The ability to comprehend stimuli requires a system that can guide access to relevant knowledge. Dependent on the task demand and context, retrieval of relevant semantic knowledge is thought to be dependent on two basic processes: automatic semantic retrieval and controlled semantic retrieval. The following will examine the cognitive and behavioural findings which provide evidence that semantic meaning can be recovered by these two processes.
2.6.2.2.1 Automatic semantic retrieval

Automatic semantic retrieval occurs when a cue is strongly associated with a stored representation, either due to the strength of prior pairing or because of feature overlaps. This association between the cue and representation initiates bottom up activation which results in the recovery of the related knowledge. However, it is possible that a cue is associated with several stored representations which become active by a process of relatively automatic and involuntary spreading activation. Thus, automatic retrieval is characterised by rapid occurrence, it is oblivious to conscious control and occurs independent of the task context (Carr, 1992; Neely, 1991).

Empirical evidence for automatic cue-driven activation of semantic memories have been reported in a number of different paradigms, for example, lexical decision tasks (Neely, 1991; Meyer & Schvaneveldt, 1971). Such lexical decision tasks (LDT) present an initial prime word followed by a target word which participants have to identify as either being a word or nonword. The measure of interest in this task is the reaction time for the target identification, which is typically faster when the target word is semantically related to the prime word (Neely, 1991). This semantic priming effect is thought to emerge if a prime word is strongly associated to the target, thereby facilitating the retrieval of the target. The strength of an association between two concepts can be determined by free association norms, which indicate the likelihood that one words leads to the free recall of the other word. The association strength between two representations is positively correlated with the degree of automatic semantic retrieval, so that stronger associations between prime and target lead to greater magnitudes of semantic priming (Moss, Ostrin, Tyler, & Marslen-Wilson, 1995; McNamara, 1992).

However, automatic retrieval does not engage conscious control and is therefore unaffected by manipulations of the task context or expectancy. This has been demonstrated in a lexical decision experiment where subjects were presented with two different classes of primes naming two different categories. A ‘match’ prime displays a word which describes the category of the subsequent target word, whereas a ‘shift’ prime shows the word of the opposite category which does not
describe the subsequent target (Favreau & Segalowitz, 1983; Neely, 1977). Participants were aware of whether a prime was a ‘match’ or a ‘shift’ prime. The logic of this experiment is that shift primes should create the expectancy that the subsequent word belongs to the opposite category. Nevertheless, the results revealed priming effects only for targets that were preceded by a prime of the same category. Although the target was predictable in the shift conditions, no priming effect was observed, as the actual presented prime described a different category than the target. These results suggest that expectancy has no influence on automatic semantic retrieval processes, which yields priming for related targets regardless of the expectancy. However, if the same experiment is conducted with a long intervals between prime and target, facilitated responses to targets also occurred in the shift conditions (Favreau & Segalowitz, 1983; Neely, 1977). This suggests that the time between prime and target (the Stimulus Onset Asynchrony - SOA) determines the degree of controlled and automatic semantic processing in semantic tasks. While only automatic retrieval is evident at shorter SOAs, controlled semantic retrieval becomes engaged if more time is available between prime and target.

2.6.2.2.2 Controlled semantic retrieval

In contrast to automatic retrieval, controlled semantic retrieval is sensitive to expectancy effects, as demonstrated in the above mentioned experiment. Generally, controlled semantic retrieval is assumed to occur when a retrieval task (or a retrieval cue) requires the activation of a certain conceptual representation (and automatic processes are insufficient to meet the task demands). Therefore, controlled semantic retrieval depends on a top-down mechanism that represents the task expectations or goal, which facilitates the controlled processing of task-relevant information (Neely, 1991). Hence, controlled semantic retrieval is characterised, in contrast to automatic semantic retrieval, as a slow and more effortful process, which is able to direct retrieval towards task relevant information and can inhibit retrieval of task irrelevant information.

The different temporal dynamic between automatic and controlled semantic retrieval has not only been reported in the previously described expectancy
experiment, but also occurs in studies investigating the relatedness proportion effect, which predicts increased semantic priming when the proportion of related compared to unrelated targets increases (den Heyer, 1985; Neely, 1977). However, this relatedness proportion effect, which is thought to foster a greater expectancy that a prime is followed by a target, is only evident for long SOA intervals.

Finally, the contribution of controlled and automatic retrieval processes to semantic memory have been investigated with dual-task experiments, which require participants to accomplish two tasks simultaneously and therefore divide their attention between them. These experiments are based on the assumption that participants have only a limited capacity for processing information and the simultaneous execution of two tasks should compromise controlled retrieval processes, as they are resource demanding. Empirical data confirm this prediction and show in lexical decision tasks that controlled retrieval is reduced under divided attention (Herdman, 1992; Becker & Killion, 1977), whereas automatic retrieval processes remain unaffected (McCann, Remington, & Van Selst, 2000). In addition to that, long-term conceptual repetition priming effects are also compromised during divided attention (Mulligan, 1997), which supports the interpretation that control processes might contribute to the priming effect.

In summary, this section discussed evidence that semantic knowledge is accessed by both automatic and controlled retrieval processes. Automatic processes are thought to reflect cue-driven, bottom-up activation, which is dependent on the associative strength between the cue and the representation. Furthermore, automatic processes occur rapidly and are not influenced by conscious control or the task context. By contrast, controlled retrieval processes are sensitive to the task context or expectancy and are thought to depend on top-down mechanisms that represent task goals. In comparison to automatic retrieval, controlled retrieval describes a slow and more effortful process which can extract task relevant information and exclude irrelevant associations. Thus, access of semantic knowledge is guided by two processes that differ in their processing demands, temporal dynamic and control over the retrieval output.
2.6.2.3 Conclusion

This section discussed the semantic memory system which stores concepts and general knowledge about the world. In contrast to episodic memories, semantic memories do not contain specific contextual information. Recent debates about semantic memory have focused on two main topics: the format of semantic representations and the mechanisms that guide semantic retrieval.

Investigations concerning the format of semantic representation tried to reveal how semantic representations relate to their preceding sensory-motor processes. Although there is as yet no clear consensus, recent findings cast serious doubt on models that propose a unitary, amodal and abstract format for semantic representations. An increasing number of studies report findings consistent with models suggesting that conceptual knowledge is stored in a similar format as the perceptual representations through which they were acquired. Furthermore, patients exhibiting deficits for constrained categories suggest that semantic knowledge is organised in a category specific manner. However, some studies suggest that category specific deficits are not driven by impaired semantic categories per se but reflect impairments in the underlying defining features or correlations between features which are more prominent in some categories. Nevertheless there is a general agreement that semantic knowledge is structured according to some principles that lead to category specific deficits.

Semantic memory access is believed to be guided by either controlled or automatic semantic retrieval. Automatic retrieval processes reflect cue-driven, bottom-up activation that is dependent on the strength of association between the cue and a particular representation. By comparison, controlled retrieval processes are task dependent and reflect top-down mechanisms directed towards a specific task goal. In general these two retrieval mechanisms are characterised to differ in their processing demands, temporal dynamic and the ability to control the retrieval output.
2.7 General Discussion and Conclusion

In general, this chapter reviewed empirical findings which have led to the proposal of multiple memory systems, and discussed models that have tried to account for these empirical data. After defining the term ‘memory system’, this chapter highlighted two memory taxonomies proposed by Schacter and Tulving (1994) and Squire and Zola-Morgan (1991). Although these taxonomies differ in their specifics, they both agree on a general dichotomy between a declarative and procedural memory system. This chapter focussed on the declarative memory system, which is defined by two distinct subsystems called episodic and semantic memory that differ in the type of information that they store.

The majority of previous research has investigated episodic and semantic memory in isolation. Yet, in real life knowledge about objects or facts are often encoded and retrieved in the context of particular episodes or events. However, it remains unclear how differences in semantic memory may influence the experience of, and therefore the encoding of, episodic memories. Furthermore, not just encoding but also the retrieval of episodic events might be susceptible to processes and properties inherent to semantic memories. Seeing that the access of semantic representations is influenced by their organisation in semantic memory, it is conceivable that this also affects the access of semantic representations during episodic retrieval. In other words, the content of semantic information may influence or interact with processes supporting episodic retrieval. However, theories and models of episodic memory have evolved in isolation from semantic memory, which raises questions about latent functional relationships between the episodic and semantic memory system.

A relationship between episodic and semantic memory has been proposed in the context of memory acquisition. For example, new facts about the world might be learned though repeated episodic experience, which predicts that semantic learning depends on episodic encoding. Findings and theories that support the dependence between semantic and episodic memory acquisition are outlined in the first part of this general discussion section. However, even if episodic and semantic memories are assumed to be functionally independent, this does not rule out the possibility that
potential relationships and interactions may exist among those systems. This possibility will be discussed in the second section.

### 2.7.1 Functional dependency of episodic and semantic memory

The distinction between episodic and semantic memory constitutes the standard model of declarative memory organization. Nevertheless, some problems arise from this classification. It is not clear, for example, whether episodic and semantic information are acquired through distinct systems or whether both types of memories are obtained through a common process.

Initially, episodic and semantic memories were assumed to rely on common encoding processes that differed only in their rate of learning (Tulving, 1972). According to this view, episodic memories result from a single exposure, while semantic memories are the product of repeated exposure to stimuli indexing the same knowledge. However, a revised version of this proposal defined episodic and semantic memory as two functionally distinct systems, which enable the acquisition and storage of different kinds of information and is supported by separate neuronal mechanisms (Tulving, 1984).

Data from single-case studies have shown that patients with severely impaired episodic memory caused by anterograde amnesia can acquire new semantic information, which advocates the complete independence of semantic knowledge from episodic memory (Haslam, Coltheart, & Cook, 1997; Verfallie, Croce, & Milber, 1995; Knowlton & Squire, 1994). This view is supported by findings in developmental amnesia, which demonstrate that children with severe loss of episodic memory are able to attend mainstream schools and obtain factual knowledge and literacy skills (Vargha-Khadem et al., 1997).

Some data, however, seem to contradict the proposal of independent episodic and semantic memory acquisition. Cases of semantic dementia show that episodic memory is able to preserve or restore meaning. For example, if semantic dementia patients repeatedly experience autobiographical events that contain certain semantic information, they exhibit partial knowledge of this information, which becomes retained in semantic memory (Snowden, Griffiths, & Neary, 1994). Similarly,
another study demonstrated that semantic dementia patients were significantly better at retrieving information that was acquired in recent time periods compared to that from distant time periods (Hodges & Graham, 1998; Graham & Hodges, 1997). This finding questions the independent nature of semantic memory as autobiographic experience seems to update semantic knowledge in cases of semantic dementia. This raises the question of whether semantic memory is a static store of abstract information or whether it is a dynamical system that constantly integrates episodic experiences, which would imply that the mechanisms of semantic and episodic memory acquisitions are partially overlapping.

In accordance with that, some views come to the conclusion that episodic and semantic memory are two end points of a continuum, which expand from completely context dependent episodes to truly general knowledge (Funnell, 2001; Kintsch, 1980). In general, although a large number of studies support the dichotomy between the episodic and semantic memory system, some authors (Graham & Hodges, 1997; Snowden et al., 1994) question this distinction and acknowledge that there might be an overlap between the acquisition of episodic and more general semantic memories.

### 2.7.2 Relations between Episodic and Semantic memory

Tulving (1983) rejected the view that episodic and semantic memories form the end points of a continuum reaching from completely context-dependent episodes to general knowledge and instead claimed that the underlying memory systems are functionally distinct. Nevertheless, this view does not deny possible relationships between episodic and semantic memory. In fact, Tulving proposed a model which formalizes process specific relations among the episodic and semantic memory system (Tulving & Markowitsch, 1998; Tulving, 1995). The central idea of this model is that episodic and semantic memory perform ‘Serial encoding’ (S), ‘Parallel storage’ (P) and ‘Independent retrieval’ (I); thus the model is referred to as the SPI model. In addition to episodic and semantic memory, this model also includes perceptual memories and proposes a hierarchical arrangement with the perceptual system at the lowest level and the episodic system at the highest level.
Information is encoded serially into these three systems, which implies that the products of encoding can either be stored at the encoded level, be transmitted to the next higher level, or both. Hence, not all perceptually processed information need necessarily reach the semantic system and similarly not all semantic information will reach the episodic system in this model. The transmission of information is thought to be influenced by factors of encoding like ‘bottom-up’ processes, initiated for example by the novelty of incoming information (Tulving, Markowitsch, Kapur, Habib, & Houle, 1994) and ‘top-down’ factors, such as ‘Levels Of Processing’ (Craik & Lockhart, 1972), which will be discussed in a more detail shortly.

The storage process in the SPI model assumes that different aspects of information become consolidated separately in different systems. Hence information about conceptual and semantic features are stored in the semantic system, whereas experiences of events are stored in the episodic system. Consequently, a single event is not represented in a ‘single’ memory trace but is stored as a number of hierarchically organised features. Finally, the retrieval process in the SPI model is proposed to be independent, which is in line with the assumption of parallel storage. Therefore, information retrieved from the semantic systems has no influence on retrieval of information from the episodic system. Although information from different systems might equally contribute to memory for a specific situation, their contribution is regarded as additive and independent.

However, although the SPI model outlines a framework of possible relations among episodic and semantic memory it fails to specify the particular process by which semantic information influences episodic memories (given that episodic memory is thought to require multiple dissociable retrieval processes). It further predicts that any possible interaction is directional, in that only semantic information can contribute to episodic memories but not vice versa.

A second line of evidence that episodic memories might be influenced by semantic memory comes from the previously mentioned ‘Levels Of Processing’ (LOP) theory. This LOP theory predicts an interaction between episodic and semantic memory which is determined by the nature of processing applied to incoming information. This theory proposes that ‘deeper’ or more semantically based
processing leads to better episodic retrieval than ‘shallow’ or more perceptually based processing. Thus the degree of semantically meaningful encoding influences the process of episodic retrieval. Furthermore, empirical studies have investigated the underlying retrieval process that supports this LOP effect and report that deep encoding leads to recognition based on familiarity and recollection, whilst shallow encoding leads to recognition based primarily on familiarity (Yonelinas, 2001; Toth, 1996). Thus, LOP predicts an interaction between episodic and semantic memory which influences recollection to a greater extent than familiarity. Nevertheless, the LOP theory describes such interactions only in terms of semantic top-down mechanisms causing encoding processes to engage strategic semantic processes to a different degree. By contrast, it is unknown whether episodic and semantic memories might also interact via bottom-up processes, driven by the semantic properties of the stimuli, and if so whether such interactions are qualitatively different from those described for modulations in semantic top-down processes.

These questions will be addressed in the present thesis, which investigates potential interactions between episodic and semantic memory processes with a series of experiments. The experiments test whether and how the semantic content of information embedded within an episodic event influences the processes guiding retrieval from episodic memory. Since we rely on our memory capabilities as a source to guide ongoing behaviour and future actions, it is important to study and understand the specific functions and interaction between different memory systems like episodic and semantic memory.
3 Event-Related Potentials (ERPs)

The first attempt to measure electrical activity of the human brain was undertaken in 1929 by Hans Berger (Berger, 1929). Berger placed electrodes on the scalp, amplified the recorded signal and plotted the changes in voltage over time. This electrical activity is generally referred to as an Electroencephalogram (EEG).

Over the past decades, EEG recordings have proven to be a very useful tool for clinical and scientific investigations. However, EEG data cannot be used to identify the neuronal processes related to specific sensory, cognitive or motor events as EEG data represent an accumulation of activation across various different neural sources, which decreases the strength of the signal of interest. To extract such specific neuronal processes from EEG, data averaging techniques can be employed. The resulting Event-Related Potentials (ERPs) are averaged electrical potentials associated with particular events. A great amount of research has been devoted to developing not only appropriate methods for recording and analysing ERP data, but also to identify various cognitive ERP components and refine our knowledge and understanding of these components.

Like other neuroimaging techniques, ERPs are not suitable for answering all cognitive neuroscience questions. ERP recordings have a high temporal resolution which makes them optimal for investigating dynamical differences between cognitive processes. However, questions regarding the neuronal source of a cognitive process are very difficult to address with ERPs due to their poor spatial resolution. In order to appreciate the potential and limitations of interpreting ERP data it is important to understand the neuronal origin of the signal reflected in ERP recordings.

This chapter provides a general introduction to ERP data and methods. The goal of this chapter is to present a broad overview of the source of the ERP signal, the recording and processing procedures which enable the extraction of clean ERP data, and the analysis techniques that permit inferences regarding the cognitive process of interest. The intention of this chapter is to highlight the scope and limitation of ERP data and methods with respect to their ability to answer questions of interest to cognitive neuroscience.
3.1 Origin of ERP data

Over the past centuries, biological research has revealed a large amount of detailed knowledge about the central nervous system. Cajal’s influential proposal of the ‘Neuron doctrine’ (Cajal, 1909) identified the neuron as a basic structural and functional unit of the central nervous system. Neurons are described as discrete cells consisting of a soma, axon and dendrites (see Figure 3-1). The excitable cell membrane enables neurons to generate and propagate electrical signals from dendrites to axons. The extensive branching of the dendritic tree allows the neuron to receive thousands of inputs from many other neurons.

![Figure 3-1: The structure of a typical neuron, which contains a dendrite, cell body (soma) and axon. Incoming activation is passed on to the cell body via the extensively branched dendrites. In some circumstances, the cell body generates an action potential which becomes propagated along the axon as illustrated by the arrows (adapted from Lodish et al., 2000).](image)

An electrical potential is present across the cell membrane as the ion composition of the intracellular and extracellular fluid differs and the cell membrane has only a selective permeability to the cellular ions. The resting membrane potential is typically about -60mV on the inside, which is mainly due to the large number of
open $K^+$ channels in the membrane. Current flowing into the cell changes the membrane potential towards more positive values which depolarise the cell. If the depolarization raises the membrane potential above a certain threshold, a positive feedback process is initiated and the neuron generates an action potential. An action potential, also known as a spike, is a rapid fluctuation of about 100mV in electrical potential across the cell membrane lasting for about 1ms. Such action potentials result from the sequential opening and closing of voltage-gated channels. This depolarisation phase is followed by a short period of hyperpolarisation which changes the cell membrane towards more negative values below the resting potential. Action potentials which propagate along the axon are passed on to different neurons via synapses. A synapse is the junction connecting two neurons and permits information from a sending neuron (presynaptic cell) to be passed on to a receiving neuron (postsynaptic cell). When an action potential arrives at a synapse, the opening of ion channels produces an influx of Calcium Ions ($Ca^{2+}$) leading to the release of neurotransmitters. The neurotransmitters bind to receptors at the postsynaptic side where the opening of ion-channels initialise postsynaptic potentials. Depending on the type of ion flow, synapses can either be excitatory or inhibitory.

**Figure 3-2:** An action potential as shown in (a) is a sudden, transient depolarization of the membrane followed by a short period of hyperpolarization before the membrane potential is returning to the resting potential of about $-60 \text{ mV}$. (b) Action potentials move down the axon at speeds up to 100 meters per second. Their arrival at a synapse causes release of neurotransmitters that bind to receptors in the postsynaptic cell, generally depolarizing the membrane (making the potential less negative) and tending to induce an action potential in it (adapted from Lodish et al., 2000).
The neuronal activity of individual cells can be recorded (‘single-unit’ recordings) intracellularly or extracellularly. Such recordings extract action potentials arising from a single neuron but do not measure their postsynaptic potentials. If recordings are taken from a close proximity of many neurons simultaneously it is possible to measure either their summed postsynaptic potential (‘local field potential’ recordings) or their action potential (‘multi-unit’ recordings). Activity recorded at the surface of the scalp will not reflect action potentials due to the timing of spikes and the spatial arrangements of axons. This is based on the fact that if two action potentials are propagated along two axons at precisely the same time, their voltage summates and the surface electrode records activity twice as large as for a single action potential. If, however, the two action potentials occur with a slight time delay, which is virtually always the case, the depolarization of one action potential will coincide with a hyperpolarization of the other action potential. Thus, the activation of the two action potentials will partially cancel out and produce a much smaller signal at the recording electrode.

In contrast to action potentials, postsynaptic potentials occur instantaneously and last anywhere between tens to hundreds of milliseconds. A specific spatial alignment of the neurons enables summation of postsynaptic potentials which can be recorded by scalp electrodes. The actual signal picked up by the scalp electrodes is generated by dipoles (a pair of positive and negative charges separated by a small distance) which evolve from postsynaptic potentials as follows: when an action potential is transmitted to the postsynaptic cell, positive current flows into the dendrites, which generates negativity in the extra-cellular fluid. This, in turn, causes current to flow out of the cell body, which creates positivity in that area. Together, the negativity at the dendrites and the positivity at the cell body form a small dipole. Nevertheless, activity at the scalp is only recordable if thousands or millions of neurons are active at approximately the same time and, most importantly, have the same spatial alignment. If neurons have a similar orientation, known as an ‘open field’, their dipoles will sum and produce activation that is recordable at the scalp (see Figure 3-3). However, if neurons are randomly orientated, known as ‘closed
field’, positivity of one neuron is likely to be aligned with negativity of another neuron, leading to cancellation. Some brain structures, such as the cerebral cortex or cerebellum, contain neurons in an arrangement that support the summation and propagation of their electrical activity because the neurons share the same orientation and are aligned perpendicular to the cortical surface. Other structures, for instance the thalamus and midbrain nuclei, contain an arrangement of neurons that most certainly prevent detection of activity at distant recording electrodes.

In general, scalp recorded activation reflects postsynaptic potentials produced by a large population of synchronously firing neurons of identical orientation. It is important to note that as the relative difference in orientation between diploes increases, the cancellation effect might result in complete cancellation at 180 degrees, under the assumption that the two dipoles are located in virtually the same place.

Figure 3-3 This figure shows the predicted current flow and potential field produced by synchronous depolarisation of the cell bodies of a row of neurons with parallel orientation (open field), a group of cell bodies clustered in the centre and dendrites spreading radially (close field), and a group of cell bodies of mixed orientation (open-closed field), adapted from (Allison, Wood, & McCarthy, 1986).

3.2 Recording ERP data

Voltage describes the difference in electrical potential between two points in an electric field. Therefore, at least two electrodes are required to measure the voltage at one scalp location. However, the voltage recorded at the scalp will not only reflect brain activity but will also include background “noise”. To extract this “noise” a
third ground electrode is used. One electrode ($E_L$) is placed in the desired location on the scalp, a second reference electrode ($E_R$) is positioned in a different site on the scalp while a third ground electrode ($E_G$) is attached anywhere on the subject’s head or body. Differential amplifiers are then used to record the activity from the three electrodes and amplify the difference in activation measured at the pair of electrodes ($E_L, E_G$) minus ($E_R, E_G$). Any fluctuation in activity originating from the ground electrode will be eliminated by the subtraction, leaving only the voltage between a chosen location and reference site. When recordings are taken from multiple electrode locations they are referenced to the same electrode. However, before discussing the characteristics of a suitable reference electrode a brief description of recording electrodes in general and their placement on the scalp is provided. The third and final part in this section discusses the process of amplifying, filtering and digitizing electrical activity once it is recorded.

### 3.2.1 Recording electrodes

Scalp electrodes are small metal disks, usually made out of silver with a thin silver-chloride coating (Ag/AgCl electrodes), attached to a wire. The recording electrodes are attached to the surface of the scalp where voltages are picked up via a conductive gel. As electrical activity follows the path of least resistance, it is important to have small impedances (impediment to current flow) between scalp and electrodes, ideally below $5 \text{k}\Omega$. Increased skin impedance is primarily caused by the outer layer of dead skin cell and their removal by gentle abrasion usually reduces the impedance below $5 \text{k}\Omega$.

In order to capture electrical activity occurring at different locations on the scalp it is necessary to simultaneously record activity from multiple electrodes positioned at different areas on the scalp. The most common system for placing and naming electrode sites is the 10/20 system (Jasper, 1958). 21 electrodes are located at the 10% and 20% points of the latitudinal and longitudinal contours of the scalp (see Figure 3-4).
The development of multi-channel EEG hardware systems and the advancement of topographical methods has necessitated a system that could accommodate a larger number of channels. An extension of the 10/20 system was proposed which included up to 74 electrodes (Chatrian, Lettich, & Nelson, 1985). This so called ‘extended 10/20 system’ introduces additional contours and positions electrodes at every 10% along the contours. This system is currently regarded as the standard by the American Electroencephalographic Society (American Electrophysiology Society, 1994) and the International Federation of Societies for Electroencephalography and Clinical Neurophysiology (Nuwer et al., 1998) (see Figure 3-5). All ERP data reported in this thesis is recorded using the extended 10/20 system.
3 Event-Related Potentials (ERPs)

Figure 3-5: Location and nomenclature of the intermediate 10% electrodes of the extended 10/20 system, as standardized by the American Electroencephalographic Society. In this standardization, four electrodes have different names compared to the 10-20 system; these are T7, T8, P7, and P8. These electrodes are drawn black with white text in the figure (adapted from Sharbrough, 1991).

3.2.2 Reference Electrodes

All recording electrodes are linked with a reference electrode which, ideally, should pick up as little activity as possible, so as not to bias the recordings. However, there is no truly neutral reference site in the human body. Therefore it is important to choose a reference site that is not biased by one hemisphere and that is convenient and consistent across several experiments or experimenters. This makes the subsequent comparison of recorded data easier.

A commonly used reference site is the mastoid (the bony protrusion behind each ear). To avoid a bias in the recording electrodes over the left and right hemisphere, reference electrodes are placed at both the left mastoid (ML) and right mastoid (MR), which is called the ‘linked mastoids’. The data are often recorded in reference to the left mastoid but become re-referenced offline with an average of ML and MR.

Beside the linked mastoids there are alternative methods for referencing recording sites. For instance, the average voltage across all recording electrodes can
be used as a reference. If this type of reference is applied, the average voltage of the recording electrodes has to be zero at any given point in time. Consequently, when using average referencing an increase in voltage at one site is coupled with a decrease in voltage at other sites and thus requires caution when interpreting the data. In addition, the average voltage approach leads to serious distortions of the referenced recordings if data are sampled only from a subset of the head. Nevertheless, such distortions can be avoided by sampling with a dense array of electrodes which obtain good estimate of average voltage of the entire head (Dien, 1998).

The data reported in this thesis are recorded with linked mastoid reference which facilitates the interpretation and comparison of the data with published ERP studies investigating memory.

### 3.2.3 Amplifying, Filtering and Digitizing the Signal

Once electrical activity is picked up by scalp electrodes, the recorded microvolt signals need amplification so that the continuous analog voltage can be converted into a discrete digital signal allowing further processing. For this conversion, each electrode is amplified by a separate EEG channel and the amplifier gain is adjusted to the input range of the analog-to-digital (A/D) converter. An A/D converter translates voltages into numerical representations and is mostly based on 12 bits (4096 values), which specifies the number of discrete values that can be produced over a range of voltages. Thus the gain of the amplifiers should be chosen so that the range of the A/D converter (e.g. ± 5 V) is not exceeded, but is high enough to prevent significant noise. The applied high-pass filter also contributes to whether the recorded signal will exceed the A/D range. High-pass filters attenuate low frequencies while passing high frequencies. This type of filter decreases gradual shifts in voltage (drift) caused by changes in skin potentials. Besides using analog high-pass filters, it is possible to apply a digital high-pass filter after the data are digitised.

The EEG data are digitised at a sequence of discrete time points (samples). The time between consecutive samples is referred to as sampling period (e.g., 5ms) and
the number of samples taken per second is the sampling rate (e.g., 200 Hz). According to the Nyquist theorem, all information in an analog signal can be captured digitally if the sampling rate is at least twice as great as the highest frequency in the signal. Lower sampling rates, however, will induce artificially low frequencies. Thus the sampling rate is dependent on the highest frequency in the signal. To avoid sampling artefacts due to noisy and arbitrarily high frequencies, most EEG amplifiers contain low-pass filters which attenuate high frequencies and filter out low frequencies.

3.3 Processing ERP data

The recorded EEG data itself discloses very little information about ERP waveforms without further processing, because ERP signals are very small and easily overshadowed by noise or other activity. Therefore, further processing such as averaging is needed to increase the signal of interest and obtain clear ERP waveforms. Beside random noise, systematic noise or artefacts such as ocular artefacts, voltage drift, amplifier saturation or muscle activity also have to be minimised to enable the identification of ERP components. This section will discuss the methods and assumptions underlying the averaging and artefact reduction process.

3.3.1 Averaging

Event-Related Potentials are small components embedded within a larger EEG signal. It is possible to isolate these ERP components with specific processing procedures, for example signal averaging. EEG epochs for a given type of event (presented stimulus) are extracted from ongoing EEG recordings. These epochs are then aligned with similar epochs with respect to a time-lock of the events and a point by point average of the waveforms is produced. As EEG data are assumed to reflect the ERP activity in addition to random noise, averaging over many trials should reduce the noise and provide a clearer signal of the ERP component.
However, this procedure relies on the assumption that the ERP signals have stable characteristics, such as identical waveform morphology, amplitude and latency across single trials so that only the noise varies from trial to trial. In practice this is very rarely the case as single trials show a great variability in their characteristics. Nevertheless, changes in morphology and amplitude across individual trials are not problematic as the averaged ERP waveform can be interpreted to reflect the mean amplitude and mean morphology of all trials.

Figure 3-6: Simulation of latency variation. Panel A and B show 4 single trial waveforms (t1 - t4) together with the average waveform. The single trial waveforms in panel A and B are identical but there is greater latency variability for A compared to B. Panel C illustrates that greater latency variability (Average A) causes a smaller peak amplitude and broader temporal distribution in the average waveform compared to smaller latency variations (Average B) (inspired by Luck et al., 2005)

More problematic, however, is trial-to-trial variability in latency across experimental conditions, which causes the peak amplitude of the average component to be reduced and leads to distortions in shape (see Figure 3-6). Thus, differences in average ERP amplitudes between experimental conditions may reflect a difference in latency instead of a real difference in component amplitude. In contrast to peak amplitude measures, area amplitude measures are not susceptible to latency variability. Area amplitude measures benefit from the fact that the area under an averaged ERP component is equivalent to the average area of ERP components from individual trials. The caveat, however, is that the latency range used to measure the area has to span the entire range of the component, which is difficult when multiple overlapping ERP components are present. Also, multiphasic components (e.g. with
positive and negative portions) are misrepresented by those measures. Beside the area measures, response-locked averages, Woody filter techniques (Woody, 1967)\(^3\) and time-locked spectral averaging are further alternatives to avoid effects of latency variability.

An important issue related to signal-averaging is the question of how many trials should be included in an average. To answer this question it is important to consider changes in signal and noise when several trials are averaged together. As the signal is unaffected by the averaging process and the noise decreases as a function of the square root of the number of trials, the signal-to-noise ration (SNR) increases as a function of the square root of the number of trials. Thus a two-fold increase in the SNR is reached by an average of four trials, a four-fold increase of the SNR by an average of sixteen trials and a five-fold increase by an average of twenty five trials. This demonstrates the dependency of the SNR on the number of trials, which suggests that there is a trade-off between the increase in the number of trials and the improvement of the SNR. The ERP data presented in this thesis contain at least a four-fold increase in the SNR by defining the minimum number of trials as sixteen.

3.3.2 Artefacts

Electrical activity recorded at the scalp is not only generated by brain activity but also by blinks, eye movements, muscle activity and skin potentials, all of which are regarded as artefacts. It is essential to minimize these artefacts as their large activity decreases the SNR and they may occur systematically rather than at random.

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\(^3\) A Woody filter is based on an iterative procedure that locates the signal on each single trial by moving a template (initially the signal average) along the time points of a trial to find the latency of maximum correlation. A new average is then formed by aligning trials on the identified signal latencies, and the new average is used as a new template.
(so that averaging would not eliminate them). To minimize artefacts, contaminated trials can either be excluded from the ERP averaging process (artefact rejection) or the influence of the artefacts can be estimated and subtracted from the averaged ERP waveform (artefact correction).

### 3.3.2.1 Ocular Artefacts

Ocular artefacts such as eye blinks and eye movements result from the electrical gradient of the eye, which is positive at the front and negative at the back of the eye. The movement of the eyes or eyelid causes changes in the voltage gradient across the scalp which can be monitored by obtaining recordings from electrodes below and above the eye as well as electrodes lateral to both eyes. Electrical activity caused by eye blinks are characterised as a deflection of 50-100 μV lasting for 200-400ms. Eye movements show voltage deflections at the eye channels of approximately 16 μV for each degree of eye movement and the voltage decreases linearly with increasing distance between the electrode site and the eyes (Lins, Picton, Berg, & Scherg, 1993). Most eye movements are evoked by saccades in one direction followed by a return of the eyes to the fixation point, which results in a rectangular shaped deflection in the recorded activation. There are several methods to minimize ocular artefacts.

First, their occurrence can be reduced by asking subjects to actively suppress blinks given an appropriate experimental design that provides frequent rest breaks for blinks. This approach is problematic, however, for groups of subjects (e.g. children, psychiatric patients) who are not able to easily control their blinking. Also the active process of monitoring and suppressing eye blinks might engage cognitive activity which could affect, or be falsely attributed to, the experimental manipulation.

Second, trials which are contaminated with eye blinks and eye movements can be discarded. This, nevertheless, could lead to unrepresentative samples of the dataset, could result in insufficient number of artefact free trials and would exclude experimental designs where blinks and eye movements are integral to the task.

Third, instead of rejecting ocular artefacts they can be corrected. Voltage caused by eye blinks and movements are propagated to the scalp electrodes so that
the voltage at a given electrode site is equal to the voltage at the eye electrodes multiplied by a propagation factor, plus EEG activity recorded at that electrode. Ocular artefacts can be corrected by calculating the propagation factor between eyes and scalp electrodes and subtracting the corresponding proportion of ocular activity from each scalp electrode. This method is used to correct the data presented in this thesis for ocular artefacts. A limitation of this correction method is that the eye electrodes also record brain activity in addition to true ocular activity, thus the subtraction includes brain responses as well as ocular artefacts. There are more sophisticated methods of ocular artefact corrections which avoid these problems, for example the dipole modelling procedures (Berg & Scherg, 1991) or independent component analysis (ICA) (Joyce, Gorodnitsky, & Kutas, 2004; Jung et al., 2000).

3.3.2.2 Voltage Drift

A slow drift in voltage can be caused by changes in the impedance of the skin or electrodes. Decreased skin impedance occurs when subjects start sweating and the resulting slow voltage drift is called a skin potential. Skin potentials can be avoided by reducing the skin impedance before applying the electrodes (Picton & Hillyard, 1972). It is also important to adjust the room temperature to avoid unnecessary sweating.

A second factor which causes voltage drift is any change in electrode position, e.g. due to movements by subjects. The repositioning of an electrode results in a voltage shift if the impedance of the two electrode positions is different. Minimizing the movements of subjects is the obvious solution for this problem, but also high-pass filtering during data acquisition should avoid saturation due to voltage drift. Nevertheless, trials with a sudden shift in voltage should be rejected.

3.3.2.3 Amplifier Saturation and Muscle Activity

Voltage drift can cause saturation of the amplifiers which prohibits the recording of EEG activity. Such saturated trials should be rejected by selecting all trials with a voltage that exceeds a value set just below the amplifiers saturation
point. This was applied to the data presented in this thesis, as including trials with amplifier saturation in the ERP average would cause serious distortions of the true signal.

A further source causing distortion of the signal is voltage created by muscle activity, called electromyogram or EMG. Fortunately, this voltage is very high in frequency and can be eliminated by the amplifier’s low-pass filter. Also providing a comfortable seat and asking the subject to relax as much as possible can help to reduce muscle activity. If it is necessary to actively reject trials with EMG, it is possible to perform a Fourier transform on each trial and reject the amount of high frequency power.

### 3.4 Interpreting ERP data

Once ERP data are collected and artefacts are minimised the challenge to successfully interpret these data arises. The interpretation is dependent on the experimental design and the hypothesis tested by the design. Average ERP data are waveforms that consist of a series of peaks and troughs, which reflect the sum of several underlying, so-called latent, components. Even though there is no commonly accepted definition of what constitutes an ERP component, it mostly describes a part of an ERP waveform that has a confined scalp distribution and co-occurs with specific experimental variables. Some ERP components are associated with a specific cognitive process. However, it is also possible to gain meaningful interpretations of ERP data without knowing the functional significance of a waveform. For example, two experimental conditions can be dissociated on the basis of distinct ERP signatures, even if the meaning of those signatures is not fully understood. Successful interpretations of ERP experiments have to consider the strengths and limitations of inferences that can be made from ERP data. These will be discussed in the next section.
3.4.1 Possible Inferences from ERP data

ERP components do generally permit three kinds of inferences about underlying cognitive processes: their timing, their functional equivalence, and their degree of engagement. These inferences are based on ERP differences between conditions in time course, distribution across the scalp, and amplitude, respectively. This inference is based on the fundamental assumption that an invariant pattern of neuronal activity is associated with a specific cognitive process. Thus ERP differences between conditions indicate differences in the cognitive processes that are engaged.

Inferences regarding the timing of cognitive processes take advantage of the high temporal resolution of ERP waveforms. Latency differences in the ERP waveforms between two conditions indicate changes in the temporal engagement of the underlying cognitive process. Inferences based on scalp distributions determine whether processes engaged across conditions are functionally dissociable. Differences in scalp distributions imply that distinct patterns of neuronal activity are associated with the two conditions. Beside changes in scalp distributions across conditions, differences can also arise across time points within conditions, indicating that multiple, qualitative different functional processes are engaged at different points in time.

The final type of inference entails the amplitude. ERP components with identical scalp distributions but dissimilar amplitudes reflect quantitative but not qualitative differences in cognitive processes. Differences in amplitude suggest that the experimental conditions engaged the same cognitive process but to a different degree.

3.4.2 Limitation of Inferences from ERP data

Inferences from ERP data are constrained by their underlying assumptions and the scope of the data itself. As always, null results have to be interpreted with caution. The absence of an effect could be attributed to a lack of experimental power, could result from an insufficient quantification or analysis of the effect, or might
occur because the ERP data cover only a subset of the total brain activity. More specifically, the latter point demonstrates that neurally distinct generators can be inferred from different scalp distributions, whilst the opposite conclusion is not warranted because different neuronal generator do not necessarily evoke distinct scalp distributions. Thus, identical scalp distributions do not necessarily imply the same underlying generator and such data have to be interpreted with caution.

Reliable differences in scalp distributions are open to alternative interpretations as they could either signify anatomically distinct generators or reflect differences in the relative contributions of components from a common set of generators.

When interpreting the polarity of an ERP component, it is important to keep in mind that the location of the reference electrode, the baseline and the orientation of the intracerebral source, all contribute to the observed polarity. Also, the intracerebral source is not straightforwardly related to the electrical activity observed at the scalp. ERP activity that is maximal over frontal scalp sites is not necessarily evoked by a source in the frontal cortex.

Inferences based on amplitude have to be treated with caution because amplitude changes can occur even when the strength of the underlying neuronal activity is identical. As discussed previously, averaging trials with varied latencies leads to changes in amplitude. Furthermore, it is possible that amplitude differences could reflect different proportions of trials that do or do not carry an effect of constant amplitude. This suggests that the amplitude does not reflect the degree to which a process is engaged but the probability of its engagement in a single trial.

A further important notion is that ERP data are inherently correlational: a certain neural activity is correlated with a cognitive process but is not regarded as its direct manifestation. This is important because the obtained neuronal activity could reflect a cognitive process which arises downstream from the process of interest. To be able to use brain activity to investigate a cognitive process it is necessary to make assumptions about their mapping between neuronal activity and cognitive process. The assumption that different patterns of neuronal activity indicate qualitatively different cognitive processes implies a one-to-one mapping. The alternative
assumption that the same cognitive processes can be evoked by different neuronal activity makes inferences of cognitive process more difficult. Some studies have isolated distinct patterns of neuronal activity that were associated with the same cognitive process (Mangun & Hillyard, 1995). This demonstrates that distinct scalp distributions are a necessary but not sufficient requirement for inferring distinct cognitive processes across conditions.

3.5 Statistical analysis of ERP data

Once ERP differences are identified between conditions their reliability has to be assessed with statistical analyses. Although the optimal statistical test is dependent on the specific experimental design, the most commonly applied test is the repeated measure analysis of variance (ANOVA) which is described in the following section.

3.5.1 Repeated measure analysis of variance (ANOVA)

The repeated measure analysis of variance (ANOVA) partitions the variance of the data into components related to the effect of interest and noise, and tests whether the effect of interest can explain a significant amount of the variance. The ANOVA is based on the assumption that the sample data are normally distributed with equal variance. However, a repeated measure ANOVA necessitates the additional assumption of sphericity, which requires the variance of difference scores between all possible pairs of variables to be equal. In other words, all possible pairs of variables should be correlated to the same degree. This assumption is clearly violated in ERP data because data from adjacent electrodes are likely to be more correlated than data from distant electrodes. Such differences in correlation arise because activity at one electrode site will spread to neighbouring electrodes more than to distant electrodes. However, the violation of the sphericity assumption can be addressed with a Greenhouse-Geisser correction (Jennings & Wood, 1976) which adjusts increased false positives (the error of accepting something that should have
been rejected) by decreasing the degree of freedoms and hence increasing the p-value.

The ANOVA calculates individual p-values for all factors and the likelihood that one reaches significance by chance increases with the number of factors. Thus, it is sensible to collapse data across irrelevant factors. Individual electrodes can be grouped together in a single factor, but it is more informative to divide electrodes into separate factors that correspond to different spatial location: left and right hemisphere, frontal and parietal location, inferior and superior sites. When an ANOVA reveals significant effects subsequent analyses, e.g. additional ANOVAs on a subset of the data, allow further characterisation of these effects. Effects involving electrode by condition interactions are ambiguous as the difference in mean amplitude could be caused by an additive or multiplicative effect. An additive effect reflects the contribution of a different generator, which for example increases the voltage evoked by the first generator on two electrode sites by 1μV from \( E_1=1\mu V \), \( E_2=3\mu V \) to \( E_1=2\mu V \), \( E_2=4\mu V \). However, a multiplicative change in amplitude occurs when the activation of one generator changes in magnitude. For example, a twofold increase in activity of the same generator could enhance the voltage on two electrode sites twofold from \( E_1=1\mu V \), \( E_2=3\mu V \) to \( E_1=2\mu V \), \( E_2=6\mu V \). Thus, whether differences in electrode sites really reflect differences in generator source or topography has to be tested by normalizing the data, removing the overall amplitude difference (McCarthy & Wood, 1985).

### 3.5.2 Topographical analysis

McCarthy and Wood (1985) show that amplitude differences between conditions might result from differences in generator strength but not differences in the spatial distribution of generators. In order to assess real differences in scalp distribution, McCarthy and Wood (1985) suggested rescaling ERP data. An appropriate rescaling procedure should eliminate absolute voltage differences across conditions but preserve the pattern of relative voltage difference within conditions. The Max-Min method provides such normalisation by finding the maximum and
minimum value in each condition, subtracting the minimum from every data point, and dividing it by the difference between maximum and minimum.

A further normalisation method is the Vector scaling approach which represents ERP data as points on a multidimensional scale (Glaser et al., 1976). Recordings from N electrodes are represented by an N-dimensional vector. The amplitude of a distribution is given by the length (norm) of a vector, while the shape of a distribution is reflected in the orientation of a vector. The vector length (norm) method computes the square root of the sum of squared voltages over each electrode. Absolute voltage differences between conditions can be eliminated by scaling the voltages in each distribution by its vector length. This scaling by vector length will preserve the relative voltage differences between electrodes in each condition and should produce equivalent results to the Max-Min normalisation.

However, Urbach and Kutas (2002) expressed serious concerns whether different scalp topographies, even after amplitude normalization, would allow the reliable inference of different source configurations. During EEG recordings, the signal might exhibit slow shifts over time, causing the zero level to differ considerably across channels and time. Baseline correction procedures adjust such fluctuations by defining a baseline interval (e.g. preceding an event) and subtract the mean activity of that baseline interval from the signal at all time points of the subsequent event epoch. Urbach and Kutas (2002) argue that differences in baseline introduce serious confounds, as subtracting a baseline that is different from zero will cause a change in vector orientation. Thus differences in vector orientation do not necessarily reflect differences in generators. Increased levels of noise are also problematic. As the vector length is a function of the squared amplitude, positive and negative noise components will not cancel out and will bias the normalised data. Urbach and Kutas (2002) demonstrate that amplitude normalisation permit inferences of different scalp distributions only under the assumption that the generators in two conditions have the same location, the same polarity and differ in strength by the same multiplicative factor. Urbach and Kutas (2002) advocate the discontinuation of data rescaling as differences in scalp topographies (even after amplitude
normalization) do not allow a reliable inference of differences in the spatial configuration of neuronal generators.

However, this view has been challenged by Wilding (2006) and Dien and Santuzzi (2005) who offer alternative recommendations. Dien and Santuzzi (2005) argue that baseline potentials are an inherent and unavoidable problem for all ERP analysis. In contrast, Wilding (2006) proposes that the baseline problem can be circumvented with experimental designs that test between-condition differences. Under the assumption that the two experimental conditions are associated with the same baseline distribution, creating between-condition differences will effectively cause the baselines to cancel out. Nevertheless, Urbach and Kutas (2006) point out that the assumption of identical baseline distributions is not only sufficient but also necessary for a valid rescaling of between-condition differences. Urbach and Kutas (2006) reemphasise their call for discontinuation of data rescaling on the basis that inferences regarding the questions of interest are not warranted. Thus, whether rescaling can address questions regarding the engagement of different neuronal generators remains an issue of ongoing debate and research.

3.6 Localizing ERP data

Understanding how and which specific neuronal population supports a cognitive process is a major objective in cognitive neuroscience. Thus, besides employing topographical analysis to test whether distinct neuronal generators are engaged in different conditions, it seems desirable to specify the locus of neuronal activity. Even though ERP data lack a high spatial resolution they do provide some information which can be used by source localisation techniques to identify the voltage source in the cortex. However, the task of source localisation is not trivial. While a specific source evokes a unique distribution of voltage at the scalp (knowing the forward problem), a single scalp distribution can be produced by an infinite number of different cortical sources (knowing the inverse problem). If the number of sources is not known the inverse problem can not be solved as there is no unique solution to this problem. For a known number of sources the inverse problem can be
approximated by solving the forward problem. In doing so the forward solution for intentionally placed sources is compared with the observed scalp distribution and the placement of the sources becomes iteratively adjusted to reduce the discrepancy between the predicted and observed scalp distributions. The forward solution relies on a model of the head, mostly approximated by a sphere, which has to account for variations in its conductive properties (e.g. the brain, dura, skull).

Besides using a detailed model of the head, accuracy of source localisation can be improved by increasing the number of recording electrodes or by introducing constraints to the solution. Simulations have shown that an increased number of recording electrodes is beneficial for source localisation because more information about the underlying source is available (Laarne, Tenhunen-Eskelinen, Hyttinen, & Eskola, 2000). About a hundred electrodes are required to effectively sample the voltage topography across the scalp (Gevins, 1990). Enhancing source localisation by constraining the solution can be as trivial as rejecting dipole solutions that are located outside the head, as advanced as constraining the number of dipoles by using principle component analysis (PCA)\(^4\), or using findings from elsewhere in the literature (e.g. neuroimaging data).

In general, source localisation is very complex and difficult. It entails generating models of the internal configuration of electrical activity, and these models have to be evaluated with respect to how well they satisfy certain constraints. Unfortunately, the number of generators is mostly unknown so that infinitely many internal configurations could often explain an observed scalp distribution. Nevertheless, in some cases source localisation can be very helpful to provide converging evidence for a well specified hypothesis.

\(^4\) The principal component analysis (PCA) describes a method for simplifying datasets by reducing the dimensionality of the dataset. This reduction is based on a linear transformation which projects the data to a new coordinate system such that the greatest variance of the data lies on the first coordinate (called the first principle component).
3.7 Summary

The current chapter about Event-Related Potentials started by identifying the neuronal origin of ERP data as a large group of spatially aligned neurons that fire synchronously at approximately the same time. The resultant electrical activity, which propagates to the surface of the skull, reflects postsynaptic potentials. This activity can be simultaneously recorded from multiple electrode sites which are linked to a suitable reference site. Once the signal is recorded, amplified, filtered and digitised the data require further processing to isolate the small ERP components which are embedded in random and systematic noise. While the processing step of signal averaging reduces the influence of random noise, systematic noise components have to be eliminated with artefact reduction or rejection methods. Interpretations and inferences from the resulting ERP components are constrained by the scope of the data and the assumption of how different patterns of neural activity indicate qualitatively or quantitatively different cognitive processes. The reliability of differences in ERP components has to be confirmed with statistical analysis.

Finally, questions regarding the engagement of different neural generators or even the precise location of neural generators can be addressed with topographical analysis and source localisation techniques. Even though these latter methods do not remain unchallenged, they refer back to where we started: the neural origin of ERP data, with the general goal of identifying how a specific cognitive process is supported by particular neural populations.
3 Event-Related Potentials (ERPs)
4 ERP findings in memory research

The preceding chapter introduced concepts and methods underlying the acquisition and analysis of ERP data. It discussed the measurable aspects of ERP components: amplitude, latency and scalp distribution. Whilst amplitude provides an index of the extent to which a neuronal process is engaged, component latency reveals the timing of this activation and scalp distribution provides an overall pattern of brain activation. Different ERP components with distinct amplitude, latency and scalp distributions in response to certain experimental manipulations have been linked to various sensory, cognitive and motor processes.

Over the past decades many researchers have attempted to gain further knowledge of cognitive and neuronal process supporting human memory by using ERP recordings. ERP data can supplement behavioural findings by revealing differences between conditions even in the absence of behavioural differences. For example, this measure of covert information processing has been used to examine the episodic encoding processes and their impact on episodic retrieval. ERP components associated with semantic memory have been similarly explored. Together these components have advanced our understanding of memory.

This chapter summarises the key findings of ERP studies investigating episodic and semantic memory. The goal is to review the central ERP components regarding memory and to discuss the evidence for their associated functional interpretation. The first part of this chapter is concerned with episodic memory studies. These studies are subdivided into those studies that identified ERP components evoked by encoding processes and those evoked by retrieval processes. The second part of this chapter focuses on ERP components which have been reported in studies of semantic memory.
4.1 Episodic Memory

4.1.1 ERP findings and episodic encoding

Encoding describes the process by which incoming information is transformed into a permanent memory representation. Interestingly, this process does not seem to be perfect and certain factors seem to limit or enhance the likelihood that we will remember an event subsequently. Although multiple factors could influence the ability to retrieve information, one essential question is whether a memory trace was successfully formed in the first place. Insights into successful memory formation can be gained by monitoring brain activity during encoding and relating this activity to subsequent behavioural evidence of effective retrieval. Studies which have analysed encoding trials depending on subsequent memory performance have identified differential neuronal responses during encoding for events that were subsequently remembered compared to those that were subsequently forgotten (for review see Friedman and Johnson, 2000; Wagner et al., 1999).

One of the first studies investigating neural differences during encoding as a function of subsequent retrieval was reported by Sanquist and colleagues (1980). They obtained, with an incidental encoding task, larger positive amplitudes over midline electrodes (Fz, Cz, Pz) during encoding for subsequently remembered items compared to subsequently forgotten items. This effect was replicated in many further studies, such as Paller et al. (1987), who labelled this effect “Difference in subsequent memory” or the “Dm” effect. These results suggest that ERPs recorded at study can discriminate items as early as 250-300ms after stimulus onset on the basis of their probability of subsequent retrieval. However, different scalp distributions have been reported for the Dm effect. In some studies the Dm effect takes the form of a sustained frontal positivity whilst in others the effect has been evenly distributed over the midline or exhibited a posterior maximum. Consecutive studies have also demonstrated that the relationship between encoding and retrieval is not only complex but also moderated by many factors, e.g. stimulus material, encoding task or type of memory test. These factors will now be discussed in turn. The question of interest concerns the degree to which subsequent memory effects differ according to
these factors, which indicate whether episodic encoding relies on a single neuronal system or whether it is supported by multiple, task specific systems.

4.1.1.1 Stimulus material

Different stimulus materials have been shown to display different Dm effects. Studies testing verbal material report Dm effects predominantly at midline parietal electrodes (Fabiani & Donchin, 1995; Friedman, 1990; Johnson, Pfefferbaum, & Kopell, 1985). This effect reflects a greater positivity for subsequently remember compared to forgotten items and co-occurs with, but extends beyond a P300\(^5\) component. Some studies, however, suggest that the Dm effect for verbal material is more left-lateralised, especially over temporal-parietal regions (Paller, Kutas, & Mayes, 1987; Neville, Kutas, Chesney, & Schmidt, 1986). An additional later positive going component has been observed over frontal areas when subjects are explicitly instructed to attempt to remember items (Friedman, 1990; Münte, Heinze, Scholz, & Kunkel, 1988).

Compared to verbal material, pictorial stimuli of objects elicit a Dm effect with a 200ms post stimulus onset. This effect modulates the parietal P300 component and a later negativity (Friedman & Sutton, 1987). Recordings from intracranial electrodes, placed in the lateral and anterior medial temporal lobe (MTL)\(^6\), revealed more positive going amplitudes of an N400-like component for subsequently remembered items. However, this amplitude modulation was lateralised by the type

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\(^5\) The P300 is related to unexpected events and is elicited by rare targets in a series of common ‘standard’ stimuli (for review see Donchin and Coles, 1988; Kok, 2001). The P300 for targets shows a positivity peaking at around 400ms after stimulus onset and is largest over centro-parietal sites.

\(^6\) The medial temporal lobe includes a system of anatomically related structures that are essential for declarative memory retrieval (conscious memory for facts and events). The system consists of the hippocampal region (CA fields, dentate gyrus, and subicular complex) and the adjacent perirhinal, entorhinal, and parahippocampal cortices.
of stimulus material: the left anterior MTL was correlated with later recognition of words, whereas the right anterior MTL was correlated with later recognition of pictures (Elger et al., 1997). This suggests that different stimulus material elicit Dm effects which are supported by different neuronal structures, but more importantly it implies that the Dm effect originates in brain areas which also contribute to declarative memory retrieval. Interestingly, studies testing abstract or symbol like visual stimuli have failed to observe Dm effects (Van Petten & Senkfor, 1996; Fox, Michi, & Coltheart, 1990). Contrasting these results with the presence of Dm effects for pictures with known conceptual or semantic content may suggest that Dm effects require, at least to some extent, access to conceptual and semantic knowledge. This hypothesis is consistent with observations, reported in the following section, that the magnitude of Dm effects is enhanced for encoding tasks which promote elaborative semantic processing (Weyerts, Tendolkar, Smid, & Heinze, 1997; Paller et al., 1987).

4.1.1.2 Encoding task

The extent to which a stimulus is processed depends on the encoding task. For example, the encoding task can enhance or limit the processing of semantic meaning of a presented stimulus (‘depth’ of processing manipulations, Craik & Lockhart, 1972). Studies using incidental encoding tasks that manipulate depth of processing, by encouraging processing in terms of meaning (deep processing) rather than surface features (shallow processing), report clear Dm effects from 400-800ms after stimulus onset which are significantly greater for semantic compared to non-semantic encoding tasks (Paller & Kutas, 1992; Paller et al., 1987). However, even though extensive semantic processing enhances Dm effects it is not essential for the effect to occur as Dm effects have also been reported for shallow encoding tasks (Friedman, Ritter, & Snodgrass, 1996).

In addition to single item encoding, semantically related word pairs which are encoded under associative and non-associative conditions only revealed Dm effects for associatively encoded pairs (Weyerts et al., 1997). The Dm effect occurred at 200-1600ms post stimulus onset and was apparent over central parietal areas but most pronounced at frontal electrode sites. Such frontally distributed Dm effects
have been mostly reported for intentional encoding tasks (Friedman & Trott, 2000; Fernandez et al., 1998; Van Petten & Senkfor, 1996).

Studies contrasting Dm effects of incidental and intentional encoding tasks reveal Dm effects for both types of encoding. Surprisingly, the effect is significantly stronger for incidental compared to intentional encoding and had different topographic and temporal characteristics (Paller, 1990; Friedman, 1990; Münte et al., 1988). Incidental encoding conditions produced Dm effects which started at about 200ms post stimulus and peaked at about 1000ms with a maximum at midline Cz and Pz electrodes. Intentional encoding conditions, by contrast, produced Dm effects with a later peak and a maximum at frontal locations (Fz). This difference in Dm strength might emerge because of increased between- and within-subject variability in how items are attended, evaluated or processed in intentional compared to incidental encoding conditions. A further contributing factor might be the processing time, which is likely to be limited to the stimulus presentation in the incidental encoding task, whereas intentional effort to memorise an item can extend beyond the stimulus presentation. Thus, it is hypothesised that the frontally distributed Dm effect in intentional encoding tasks might reflect subsequent elaborative processing, which is in line with findings that elaborative rehearsal evokes frontally distributed components (Fabiani, Karis, & Donchin, 1990).

4.1.1.3 Type of memory test

Considering that neuronal responses during encoding can predict subsequent memory performance, it is conceivable that this prediction is dependent on the type of memory test. Several studies have investigated different types of explicit memory test such as free recall and recognition (Fabiani & Donchin, 1995; Münte et al., 1988; Paller et al., 1987) or free and cued recall (Paller, 1990). These studies report larger amplitudes of the Dm effect for free recalled items compared to recognised items with low confidence ratings. A possible explanation for this difference in Dm effect is that some recognised items are based on guesses instead of actual item memory, which diminishes their Dm effect compared to recalled items. Alternatively, it has been hypothesised that the Dm effect is modulated by ‘encoding strength’, which
would explain the larger Dm effects for recalled items (Paller, McCarthy, & Wood, 1988).

In contrast to explicit tests, there is very little agreement on whether Dm effects occur for implicit tests such as stem completion tasks, which present a stem of a word (such as ST__) and requires a completion of that stem with the first word that comes to mind. While some studies do observe Dm effects for implicit tasks (Friedman et al., 1996; Paller et al., 1987) others fail to report such effects (Paller & Kutas, 1992; Paller, 1990). Therefore, further examinations of the Dm effect are needed to shed light on whether explicit and implicit memory tests modulate subsequent memory effects.

### 4.1.1.4 Conclusion

In general, a number of studies clearly demonstrate that electrophysiological correlates, referred to as Dm effects, reflect differences in neuronal activity at the time of learning and that this predicts subsequent memory performance. Such Dm effects take the form of a more positive going deflection for remembered compared to forgotten items. The precise timing and scalp distribution of this effect varies across studies and experimental manipulations. It seems likely, therefore, that multiple neuronal generators and thus multiple cognitive processes contribute to subsequent memory effects. The degree to which Dm effects vary across different experimental manipulations gives insight into factors that modulate encoding processes. The preceding section reviewed findings of temporal and topographical differences in Dm effects elicited by different stimulus material, encoding task or type of memory tests.

Different classes of stimuli, for example, evoke a Dm effect as early as 200ms over parietal locations but with a left lateralised distribution for words and a right lateralised distribution for non-words. However, no Dm effects have been reported for symbols or abstract stimuli, suggesting a potential link between Dm effects and semantic processing. Furthermore, incidental encoding evokes Dm effects from 200ms onwards with a maximum at midline Cz, Pz electrodes, while intentional encoding elicits Dm effects from about 400ms onwards with a maximum over frontal
locations. Also, the magnitude of Dm effects differs with the type of employed memory test. Stronger Dm effects have been reported for free recall relative to recognition test. Although the precise variation and functional significance of the Dm effect is not fully understood, the current data demonstrate that Dm effects are able to forecast which items will or will not be retrieved in a subsequent memory test. The following section discusses electrophysiological correlates in relation to retrieval processes.

4.1.2 ERP findings and episodic retrieval

Effective encoding of events into memory is only one of many influential factors which determine retrieval success. The retrieval cue and the processes engaged during a retrieval attempt, such as retrieval mode and retrieval orientation, are equally important for retrieval success. The neuronal activity associated with these aspects of retrieval processing is discussed in the following section of ‘Processes leading to retrieval’. In the context of dual process models (see Chapter 2), successful retrieval itself is contingent upon different processes: familiarity and recollection. The section ‘Processes engaged during retrieval’ reviews and discusses ERP evidence that suggests distinct neuronal correlates for familiarity and recollection, which supports the notion of two separate retrieval processes. Finally, the section ‘Processes evaluating retrieval results’ concerns ERP correlates which are assumed to reflect processes that act upon the retrieval outcome. The objective of the present section is by no means to present an exhaustive summary of the existing ERP literature, (for example it does not discuss ERP findings from implicit memory studies). Nevertheless, this section offers an overview of the main ERP components related to explicit episodic memory retrieval and discusses their associated functional interpretation.

4.1.2.1 Processes leading to retrieval

In general it is believed that episodic retrieval is the outcome of an interaction between retrieval cues and stored memory representations. This interaction is more
likely to result in successful retrieval of information if, first, a specific cognitive state called ‘retrieval mode’ is adopted and, second, the retrieval cue is effective in accessing a memory representation which can be accomplished with a specific ‘retrieval orientation’. Retrieval orientation aligns cue processing with the demands of a particular retrieval goal by specifying the way a retrieval cue is processed. The process reflecting retrieval success itself can be informative as it denotes how effective a retrieval cue is in accessing a specific memory representation. The following section discusses the neuronal activity associated with these processes, which together lead to retrieval of information from episodic memory.

**4.1.2.1 Retrieval mode**

Retrieval mode refers to a tonically maintained state which ensures that the processing of a retrieval cue is directed toward retrieving information from a specific class of memories, e.g. episodic or semantic memories (Tulving, 1972). The question of whether different retrieval modes are associated with different neuronal activity has been investigated by studies contrasting blocks of items engaging episodic retrieval with blocks of items requiring semantic retrieval (Duezel et al., 2001; Duezel et al., 1999). These studies report that neuronal activity for retrieval cues differed with respect to the engaged retrieval conditions. This difference was focused over the right frontal scalp with a more positive going deflection at about 300-500ms post stimulus onset for episodic compared to semantic retrieval cues. As this positive deflection was maintained during the entire retrieval episode but did not vary with a specific type of retrieval task or retrieval cue, it has been interpreted as an electrophysiological correlate of retrieval mode.

Studies testing changes in retrieval mode on a trial-by-trial basis report similar findings (Morcom & Rugg, 2002), but only for the second successive trial on which subjects were performing the recognition task. This finding encouraged the proposal that a retrieval task has to be completed on at least one preceding trial before a retrieval mode can be successfully adopted. Subsequent investigations have supported this proposal and excluded the possibility that time limits in the preparatory period might have prevented the observation of retrieval mode effects.
4 ERP findings in memory research

(Herron & Wilding, 2006). In general, these studies have demonstrated that electrophysiological correlates over the right frontal scalp correlate with a tonically maintained state of retrieval.

4.1.2.1.2 Retrieval orientation

The ability to change the way a retrieval cue is processed requires the adoption of different retrieval orientations, which describe a mental operation that biases the processing of a retrieval cue towards a specific retrieval goal (Rugg & Wilding, 2000). This process can be investigated when the same retrieval cue is used to probe memory retrieval for different kinds of information. Rugg and Wilding (2000) argued that this investigation should be performed on new but not previously studied items in order to avoid confounds with retrieval success. Several studies have reported ERP effects in response to differential processing of a retrieval cue when source memory was tested for different encoding manipulation (Johnson, Kounios, & Nolde, 1997), contrasts of specific vs. general information (Ranganath & Paller, 1999) or for different types of encoding judgement (Wilding, 1999). All these studies revealed task related ERP differences over the frontal scalp region, mostly left lateralised, with an onset of about 400ms.

Similarly, a study investigating different encoding manipulation using a yes/no recognition test without employing source memory judgements reports comparable task related ERP differences (Rugg, Allan, & Birch, 2000) even when a possible confound of test difficulty is removed (Robb & Rugg, 2002). This effect has also been observed for new items when a specific retrieval task was performed on a test lists that contained different retrieval cues (Herron & Rugg, 2003). There is evidence, though, that different retrieval orientations can not be switched on a trial-by-trial basis but only over multiple successive trials (Wilding & Nobre, 2001).

Together, these findings demonstrate that neuronal activity, prominent over left frontal electrodes, is modulated when processing of the same retrieval cue is directed towards different aspects of the information that could be retrieved. This neuronal activity, which onsets about 400ms post stimulus, is thought to index retrieval orientation.
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4.1.2.1.3 Retrieval success

Appropriate retrieval cue processing facilitates the successful recovery of an event from episodic memory, which is coupled with the subjective experience of remembering. The majority of ERP studies investigating episodic memory measure successful episodic retrieval by contrasting neuronal activity elicited for correctly classified old items with activity from correctly rejected new items. In order to link specific ERP modulations to processes of familiarity and recollection, which are thought to support recognition memory according to dual-process models (Yonelinas, 2002), experimental designs and manipulations need to be employed which are known to separate familiarity driven from recollection based recognition.

The subsequent section, ‘processes engaged during retrieval’, will give a more elaborate review of their results. Overall, these studies reveal two distinct ERP components associated with retrieval success: a left parietal component indexing successful recollection and an early frontal component reflecting familiarity-based retrieval success, which will be discussed now in more detail.

4.1.2.2 Processes engaged during retrieval

Most studies investigating the neuronal basis of retrieval processes report a modulation of ERP responses if an item is recognised. More precisely, correctly detected old items demonstrate more positive going ERP deflections compared to correctly rejected new items (for review see Rugg, 1995; Johnson, 1995; Friedman and Johnson, 2000; Rugg and Allan, 2000; Donaldson et al., 2003; Friedman, 2004; Curran, 2006). This group of ERP components is called old/new effects, and have been further divided into several subcomponents on the basis of their distinct time course, scalp distribution and sensitivity to experimental variables.

The functional significance of these old/new subcomponents has been framed mainly in the context of dual process models which describe retrieval as contingent upon two distinct processes: familiarity and recollection (reviewed by Yonelinas, 2002). As described in Chapter 2, while familiarity is thought to be a relatively fast-acting process, reflecting retrieval of items without contextual details, recollection is
regarded as an effortful and slower-acting process, indicating retrieval of items accompanied by contextual information in which the episode was initially experienced. The following section reviews experimental findings which suggest that familiarity and recollection are associated with distinct ERP old/new effects.

**4.1.2.2.1 Left parietal old/new effects and recollection**

An ERP old/new effect, which occurs in the time window of 500-800ms post stimulus onset with the largest amplitude over left parietal electrodes (see Figure 4-1), has been consistently reported to be modulated by experimental manipulations thought to alter recollection. Early findings which supported this idea were observed by Smith (1993). He demonstrated that the left parietal old/new effect is greater for ERPs elicited for recognised items associated with ‘remember’ compared to ‘know’ responses and inferred therefore that this effect is closely tied to recollection. A similar conclusion was reached by Paller and Kutas (1992), who reported that the left parietal old/new effect is sensitive to a ‘depth of processing’ manipulation which is assumed to selectively alter recollection. However, it should be noted that in addition to modulations in recollection a large number of studies indicate also a small but consistent change in familiarity in response to LOP manipulations (Yonelinas, 2001; Yonelinas et al., 1998; Toth, 1996).

![Figure 4-1: ERP waveforms for the left parietal old/new ERP effect, the putative correlate of recollection. The graph on the left side illustrated the scalp topography of the left parietal old/new effect, reflecting differences in voltage for correctly recognised old items studied under deep conditions (deep hit) and correctly recognised old items studied under shallow conditions (shallow hit). The graph on the right side demonstrated that the latency of this left parietal difference in voltage is in the range of 500-800ms post stimulus onset (adapted from Rugg et al., 2003).](image-url)
Additional support for these early findings is given by source memory studies which entail retrieval of contextual information, such as the format or modality of the original study event. Items which are recognised with the correct source are assumed to engage recollection, whereas correctly recognised items which are attributed with a wrong source are believed to be based on familiarity. The results of ERP studies testing source memory demonstrate larger left parietal old/new effects associated with recollection compared to familiarity, irrespective of whether the source was temporal (Trott, Friedman, Ritter, Fabiani, & Snodgrass, 1999), comprised gender of voices (Wilding & Rugg, 1996), or spatial locations (Van Petten, Senkfor, & Newberg, 2000).

Further evidence consistent with the view that the left parietal old/new effect is closely linked to recollection comes from ERP studies of associative memory which tests subject’s memory for pairs that were presented in the same arrangement as studied compared to pairs that have been rearranged, i.e. recombined into pairs that were not presented at study (Rugg et al., 1998; Rugg, Schroerscheidt, Doyle, Cox, & Patching, 1996). The logic underlying these experiments is that correctly identified words that maintained their pairing between study and test (same pairing) are more likely to elicit recollection compared to rearranged pairs. The ERP findings revealed larger left parietal old/new effects for the same compared to rearranged pairs.

In summary, all these findings provide supporting evidence that the left parietal old/new effect, which is a positivity evoked by hits compared to correct rejections at about 500-800ms after stimulus onset over parietal scalp locations, is closely linked to recollection. Interestingly, this effect has never been reported for ERPs elicited by old items incorrectly identified as new (misses) or by new items incorrectly judged old (false alarms). It therefore does not reflect stimulus repetition as such but seems to be related to retrieval of information which permits accurate recognition judgements.
4.1.2.2 Early frontal old/new effects and familiarity

An increasing number of recent ERP investigations have reported ERP old/new effects of distinct time course and topography which are thought to separate the two processes involved in recognition memory: recollection and familiarity. The previous section summarised experimental evidence that a so called left parietal old/new effect, indexes recollection. A second so called early frontal old/new effect has been dissociated from the left parietal old/new effect and is considered to reflect familiarity. This early frontal old/new effect typically arises at about 300-500ms post stimulus onset and is bilaterally distributed over the frontal region of the scalp (see Figure 4-2).

![Figure 4-2](image)

**Figure 4-2** ERP waveforms for the early frontal old/new ERP effect which is thought to index familiarity. The graph on the left side illustrated the scalp topography of the early frontal old/new effect, reflecting differences in voltage for correctly recognised items studied under shallow encoding conditions (shallow hit) and items that were misclassified as new (new). The graph on the right side demonstrates that the latency of this effect is in the range of 300-500ms post stimulus onset (adapted from Rugg et al., 2003).

One of the first findings providing evidence that this ERP effect is associated with familiarity has been reported in a ‘depth of processing’ study (Rugg et al., 1998). An early frontal effect between 300-500ms post stimulus was found to be more positive going for recognised old items compared to correctly rejected new items or misses. However, in contrast to the left parietal old/new effect, this early frontal old/new effect was insensitive to the depth of processing manipulations,
which were thought to selectively influence recollection. It therefore provided the basis for the proposal of a functional relationship between the early frontal old/new effect and familiarity. However, this proposal was called into question by accumulating evidence that depth of processing manipulations do not only modulate recollection but also familiarity (Yonelinas et al., 1998; Toth, 1996).

Nevertheless, further evidence supporting the view that the early frontal old/new effect is linked to familiarity was provided by studies using lure items that were similar but not identical to previously studied items. Under the assumption that familiarity reflects a global assessment of the similarity between study and test items, lures are expected to elicit familiarity. Several studies have observed an early frontal old/new effect for studied items and similar lures, for example, studies presenting lures with plurality changes (Curran, 2000), semantically related lures (Nessler et al., 2001) and lures in the form of pictures presented in reversed orientation (Curran & Cleary, 2003). These findings strengthen the proposal that the early frontal old/new effect is related to familiarity.

Additional evidence came from ERP studies employing behavioural measures capable of dissociating familiarity and recollection based retrieval, such as the remember/know paradigm (Trott et al., 1999). While remember responses reflect recollection that may be accompanied by familiarity, known responses are based only on familiarity. Trott et al. (1999) reported similar early frontal old/new effects for remember and known responses while robust left parietal effect were present only for remember but absent for known responses. This demonstrates that the early frontal old/new effect is unlikely to index recollection but is consistent with the functional interpretation of familiarity.

Recently, however, some ERP studies have challenged the hypothesis that the early frontal old/new effect reflects familiarity. Behavioural experiments have shown that divided attention during study adversely affects familiarity and recollection, but has a stronger effect on recollection (Yonelinas, 2001). An ERP study testing this effect with visually presented words, reported differences in the left parietal old/new effect but failed to demonstrate changes in the early frontal old/new effect, even though behavioural estimates of familiarity, tested with the remember/know
procedure, were reduced for divided compared to full attention (Curran, 2004). Although it is very difficult to interpret null results, this study highlights an inconsistency between behavioural estimates of familiarity and the early frontal old/new effect.

Serious questions regarding the proposal that the early frontal old/new effect reflects familiarity have also been raised by Yovel and Paller (2004). In their ERP study, which paired faces with verbally presented occupations, recollection was inferred from correctly recognised faces when accompanied by correct recall of the associated occupation or other specific details. In contrast, familiarity was assessed by correctly recognised face that failed to evoke recall of specific information. The results from this study by Yovel and Paller (2004) failed to reveal any sign of an early frontal old/new effect which was interpreted as strong evidence against the link between familiarity and the early frontal old/new effect. However, as mentioned previously null results have to be interpreted with caution as they could be attributed to several experimental details. A more compelling proof that the early frontal old/new effect does not reflect familiarity could be provided by demonstrations that the early frontal old/new effect is present but not in concurrence with behavioural modulations of familiarity. It has been suggested that rather than indicating familiarity this early frontal old/new effect might reflect conceptual priming (Olichney et al., 2000). This proposal is challenged, however, by experiments reporting significant early frontal old/new effects for faces and non-semantic ‘blobs’ (Johansson, Mecklinger, & Treese, 2004; Curran, Tanaka, & Weiskopf, 2002). This suggests that a solely conceptual or linguistic origin of the early frontal old/new effect seems unlikely.

A further set of recent studies have also raised doubts on the association of the early frontal old/new effect with familiarity. These studies report an old/new effect that appears to be related to familiarity based processes but occurs earlier than the early frontal old/new effect (Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Curran & Dien, 2003; Tsivilis et al., 2001). Tsivilis et al. (2001) tested pictures of common objects that were presented on top of a background scene. The recognition of rearranged pairings of old objects and old background as well as
systematic variation of the old/new status of objects and background, elicited an early frontal old/new effect only for the rearranged but not old/new pairs. However, an even earlier old/new effect, occurring between 100-300ms post stimulus onset, was reported with a distinct scalp distribution over fronto-polar scalp regions (see Figure 4-3). This effect was argued to be more consistent with familiarity than the early frontal old/new effects, as it was modulated by pairs that contained at least one previously studied object or background.

Figure 4-3 ERP waveforms for the fronto-polar old/new ERP effect, which has been reported to be associated with familiarity. The graph on the left side illustrated the scalp topography of the fronto-polar old/new effect, reflecting differences in voltage between new items (New/New) and the mean of all other conditions which contained at least one old item. The graph on the right side demonstrated that the latency of this fronto-polar difference in voltage is in the range of 100-300ms post stimulus onset (adapted from Tsivilis et al., 2001).

Also Duarte et al. (2004) report an early fronto-polar old/new effect between 150-300ms when pictures of common objects were recognised. The magnitude of this fronto-polar effect did not vary across recognised items that were associated with either remember or known judgements, suggesting a link to familiarity processes. The early frontal old/new effect was equally associated with familiarity based responses and no significant topographic differences were found between the fronto-polar and the early frontal old/new effect.

However, Curran et al. (2003) examined auditorally and visually studied words, using a visual word recognition test, under the premise that familiarity is an amodal process and therefore should reveal neuronal correlates of similar magnitude regardless of the study modality. The early frontal old/new effect confirmed this
prediction, whilst the modulation of a fronto-polar old/new effect, present between 170-260ms post stimulus onset, was modality specific it was only observed for visually studied words. Thus, unlike the early frontal old/new effect, the fronto-polar old/new effect demonstrates response patterns which are more consistent with repetition priming than familiarity. Taken together, there is some evidence suggesting that the fronto-polar old/new effect might reflect familiarity. However, some studies report conflicting findings and further studies are required to elaborate on the functional significance of this effect.

In general, an increasing body of evidence has proposed that the early frontal old/new effect may be associated with familiarity-driven processes. However, this familiarity hypothesis is not unchallenged. Some studies have concluded that the early frontal old/new effect is connected to conceptual priming whilst others have argued that an even earlier component, the fronto-polar old/new effect, occurring between 100-300ms post stimulus onset, is primarily associated with familiarity processing. Undoubtedly, further investigations are needed to elucidate the significance of the early frontal old/new effect with regards to familiarity driven retrieval. The present thesis aims to advance our understanding in that respect.

4.1.2.3 Processes evaluating retrieval results

Despite the ERP old/new effects discussed so far, investigations of episodic memory retrieval have repeatedly reported the occurrence of a further, so called ‘right frontal old/new effect’, with a late onset (e.g. 900ms post stimulus), sustained amplitude largest over the right frontal scalp. This effect has been reported for tests including source memory (Senkfor & Van Petten, 1998; Wilding & Rugg, 1997; Wilding & Rugg, 1996), associative recognition (Donaldson & Rugg, 1998), simple old/new decisions (Allan & Rugg, 1997) as well as across different study material (Schloerscheidt & Rugg, 2004; Mecklinger & Meinshausen, 1998; Schloerscheidt & Rugg, 1997). In a source memory experiment, Wilding and Rugg (1996) reported larger right frontal old/new effects for correctly judged sources compared to incorrectly judged sources. The presence of the frontal old/new effect was attributed to the explicit task requirement of retrieving information about the
study context. Hence, the right frontal old/new effect was functionally interpreted to reflect processes that operate on the product of retrieved information, and was regarded to be essential for the successful recovery of contextual information of a studied item. This interpretation is supported by findings from exclusion tasks which demonstrate that the right frontal old/new effect is only present for targets (Wilding & Rugg, 1997), which implies that this effect is not elicited by episodic retrieval per se, but is selective to retrieval success.

However, this interpretation conflicts with studies reporting greater right frontal old/new effects for unsuccessful source retrieval compared to successful source retrieval (Trott et al., 1999) and it also fails to account for right frontal old/new effects which were elicited in recognition test that did not require retrieval of specific information (Ranganath & Paller, 1999). Similarly, a number of studies have reported that new items can evoke late sustained positivities of the same magnitude as old items (Tendolkar, Doyle, & Rugg, 1997; Allan & Rugg, 1997; Wilding & Rugg, 1996). Although these studies report that both old and new items do exhibit a clear late positive shift, their findings are difficult to reconcile with the claim that the later right frontal modulation is exclusively associated with old items. Consequently, some researchers have concluded that this late frontal old/new effect is not essential for episodic memory retrieval per se (Johnson, Kreiter, Russo, & Zhu, 1998; Tendolkar et al., 1997).

However, these results are in line with the interpretation that the late right frontal old/new effect might reflect post-retrieval monitoring operations (Wilding, 1999). This interpretation was suggested by a study that presented different types of source information. Although, this study revealed that different types of source retrieval modulate the right frontal effect, this modulation was equally present for hits and correctly rejected new items. As it is impossible to retrieve contextual information for correctly rejected new items, this study demonstrates that the modulation of the right frontal old/new effect is not directly related to successful retrieval of information but indicates monitoring processes for certain kinds of retrieval information (Wilding, 1999).
False memory studies, which report greater right frontal activity for false rather than true recognition (Goldmann et al., 2003; Fabiani, Stadler, & Wessels, 2000) do support this post-retrieval operation hypothesis, as monitoring processes are likely to be increased during false recognition. Additional evidence comes from reports of larger right frontal old/new effects for high performers, who discriminate well between studied and unstudied items, compared to low performers (Mecklinger & Meinshausen, 1998). Finally, the time course of the right frontal old/new effect, which is typically later onsetting and extends beyond the left parietal old/new effect is consistent with the proposal that the right frontal old/new effect reflects a post-retrieval process.

Overall, several studies have reported a right frontal old/new effect, such as studies of simple old/new decisions (Allan & Rugg, 1997), source memory (Wilding & Rugg, 1996), associative memory (Donaldson & Rugg, 1998) and false memory (Fabiani et al., 2000). These studies engaged different types of experimental manipulations and report that the right frontal old/new effect is not task specific. Even though the original interpretation, that linked this effect with the recovery of contextual information for successfully retrieved items, became revised towards the post-retrieval monitoring hypothesis, the exact meaning and potential dissociations of this right frontal old/new effect is still a subject of ongoing research.

**4.1.3 Conclusion**

In summary, this section reviewed studies which have identified ERP components that index ‘processes that lead to retrieval’ such as retrieval mode and retrieval orientation. The adoption of a retrieval mode, which is a tonically maintained state that directs the processing of a retrieval cue towards a specific class of memories, is correlated with right frontal scalp activity at about 300-500ms. In contrast, neuronal activity associated with retrieval orientation, which directs the processing of a retrieval cue towards specific aspects of information, is prominent over the left frontal brain regions at about 400ms after stimulus onset.

Besides the ‘processes leading to retrieval’, retrieval success or ‘processes engaged during retrieval’ have been discussed in the light of spatially and temporally
distinct old/new effects. Several studies have provided supporting evidence that a left parietal old/new effect, which occurs at about 500-800ms post stimulus over left parietal scalp locations, indexes recollection. In addition, an early frontal old/new effect has been associated with familiarity driven processing, though these findings have not remained unchallenged. Some studies argue that the early frontal old/new effect is more related to conceptual priming. Other studies have proposed an even earlier component to index familiarity processes: a fronto-polar old/new effect which occurs at 100-300ms post stimulus.

The final part in this section focused on ‘processes evaluating retrieval results’ and discussed evidence that a right frontal old/new effect might reflect processes which act upon the retrieval outcome. Although, the right frontal old/new effect, like most ERP components and their associated functional interpretations are still subject to ongoing research, they still provide a useful and promising path for investigating processes supporting recognition memory. Nevertheless, not only processes engaged in episodic memory but also processes supporting semantic memory might be linked to electrophysiological correlates. The second part of this chapter is devoted to ERP findings that reflect neuronal activation engaged in semantic memory processes.
4.2 Semantic Memory

Memory is fundamental to our life not only because it enables us to remember every day events in form of episodic memories, but also because it gives us the ability to accumulate general facts and knowledge about the world in our semantic memory. A critical difference between these two memory systems is that episodic recall is generally accompanied by contextual information such as time or place an event was experienced whereas such information does not accompany semantic memories.

Behavioural and neuropsychological evidence suggest that episodic and semantic memory describe two distinct memory systems (see Chapter 2) which implies that they are mediated by distinct neural activity. This section describes findings from electrophysiological studies of semantic memory. Specific consideration is given to ERP components and their functional interpretation with respect to the nature, organisation and timing of semantic memory. Investigations of semantic memory do not typically distinguish between processes that lead to retrieval, processes engaged during retrieval and processes following retrieval, like episodic memory research does. In fact, most of the semantic memory investigations are tightly linked to linguistic studies. ERP correlates of semantic memory are foremost reported in the context of linguistic manipulations. Thus, before discussing ERP correlates and their functional significance for semantic memory processes, ERP modulations in response to linguistic manipulations will be reviewed.

4.2.1 The N400 and contextual information

Semantic processing is linked to a broadly distributed ERP effect that is maximal at about 400ms over centro-parietal locations. Kutas and Hillyard (1980), who were the first to describe this so-called N400 effect, reported larger negative
deflections for words that were incongruent compared to those that were congruent within the semantic context of a sentence. Thus, the N400 amplitude is negatively correlated with the cloze probability\(^7\) of a sentence (Kutas & Hillyard, 1984). Several studies have replicated and extended this finding by demonstrating that the N400 effect occurs not only at the sentence but also the lexical level (Kutas and Hillyard, 1980, 1983, 1984; for review see Kutas and Federmeier, 2000).

In particular, studies focussing on the lexical level have reported larger N400 modulations for pronounceable non-words relative to unexpected or unprimed words, while N400 effects were the smallest or nearly absent for expected or primed words (Rugg, 1990; Bentin, 1987). The N400 is also a reliable index of semantic relatedness between word pairs, as several studies reported reduced N400 amplitudes for semantically related compared to unrelated words (Bentin, Kutas, & Hillyard, 1995; Brown & Hagoort, 1993). It should be noted though, that these findings are based on investigations that principally confound semantic and associative relations. A study that carefully separated semantic from associative relations demonstrated that the N400 is sensitive to associative relations (irrespective of additional semantic relations), while no N400 modulations were obtained for purely semantic relations after confounding associative relations were removed (Rhodes & Donaldson, submitted).

The functional significance of the N400 effect is still the subject of ongoing debate, which favours different interpretations dependent on the lexical or sentence level of occurrence. At the lexical level, some studies suggest that the N400 component reflects automatic processing of semantic spreading activation; others argue that the N400 reflects post-lexical processes of semantic matching and integration. The automatic spreading activation account is founded on the

\(^7\) The cloze probability of a word in a sentence refers to the probability that a participant, given the linguistic context of the sentence up to that word, would complete the sentence with that word (Taylor, 1953).
observation that associative primes modulate the N400 effects even when the experiment does not necessitate access to the meaning of words. Bentin and colleagues (1995), by contrast, argue for a post-lexical semantic integration account based on their observation that N400 modulations are dependent on attentional processes. Further support for the semantic integration account comes from masked priming (Brown & Hagoort, 1993), level of processing (Chwilla, Brown, & Hagoort, 1995) and backward priming effects (Chwilla, Hagoort, & Brown, 1998).

Studies examining N400 modulations at the sentence level broaden the functional perspective of this component. Studies show that N400 effects are not only elicited by semantically unexpected sentence-final words (Kutas & Hillyard, 1980) but also by words in other sentence positions (Kutas & Hillyard, 1983). This has lead to the interpretation that the N400 reflects the accumulation of semantic context of sentences with the N400 amplitude indexing the effort required to integrate every successive word into the general meaning of the sentence. Words at the end of the sentence benefit from previous semantic context, and therefore elicit a larger N400 effect compared to words occurring earlier in the sentence (Van Petten & Kutas, 1991). This interpretation is in good agreement with findings from the discourse level which report larger N400 effect for words that fit the context of a sentence but are unexpected in the wider context of the discourse (van Berkum, Zwitserlood, Hagoort, & Brown, 2003; Federmeier & Kutas, 1999). Thus, findings at the sentence and discourse level support the functional interpretation that the N400 reflects contextual integration processes.

In general, the processing of almost any type of meaningful, or potentially meaningful stimuli is associated with an N400, including visual and auditory words, line drawings, photographs, faces, environmental sounds and odours (for review see Kutas and Federmeier, 2000). The amplitude of the N400 for these stimuli is reduced as a function of associative, semantic and repetition priming as well as the amount of congruous information provided by the preceding context. Thus, the N400 seems to be related to cognitive processes that incorporate information of a stimulus into a preceding semantic context.
4.2.2 The N400 and memory

Besides indexing linguistic processing, there are several lines of evidence that the N400 effect is also informative for semantic memory processes. The first line of evidence comes from studies using sentence verification paradigms which require accuracy judgements of category membership statements such as ‘a rose is a flower’ (Kounios, 1996; Kounios & Holcomb, 1992; Fischler, Bloom, Childers, Roucos, & Perry, 1983). These studies revealed that the N400 amplitude is reduced when the exemplar is a member of the category irrespective of whether or not the statement is true. In other words, the statement ‘a rose is a flower’ evokes the same N400 amplitude reduction as the statement ‘a rose is not a flower’. Thus, the N400 did not vary with semantic correspondence between item and context, but was sensitive to associations between item and context.

Second, stronger N400 modulations have been reported for between category violations (e.g. unexpected words that came from a different, but related semantic category as the expected word) compared to within category violations (e.g. unexpected words that came from the same semantic category as the expected word) (Federmeier & Kutas, 1999). Since the functional and physical similarity between two members of a category seems to alter the N400 amplitude, this effect is sensitive to the organisation of semantic memory.

Finally, the topography of the N400 effect varies across sensory modalities of stimulus presentations. Auditory stimuli elicit a more evenly distributed N400 compared to visual stimuli, which have a clear centro-parietal maximum (Domalski, Smith, & Halgren, 1991). Similarly, pictures and faces evoke a more frontal N400 than words (Ganis, Kutas, & Sereno, 1996) whilst unexpected concrete words elicit a more frontal N400 compared to unexpected abstract words (Holcomb, Kounios, Anderson, & West, 1999). These findings are in line with semantic memory models that assume modality specific storage of information (see Chapter 2).

In summary, the N400 is sensitive to the ease of accessing information from semantic memory, since the N400 amplitude is modulated by the frequency of word usage and number of stimulus repetition (Van Petten & et al., 1991). Although linguistic studies propose that the N400 indexes processes that incorporate stimulus
information into a preceding semantic context, the N400 is modulated by the association between an item and context but not the semantic correspondence per se (e.g. the truth value of a statement). Furthermore, the N400 seems to be sensitive to the way items are organised in semantic memory and supports a modality specific account of information storage.

4.2.3 Additional semantic memory effects

Besides the N400 effect other ERP components have been reported to index linguistic processes, notably the P600 or Syntactic Positive Shift (SPS), which in the following will be referred to as P600. A number of studies report this ERP effect in relation to syntactic violations, which evoke a positive going deflection at around 500ms following the onset of an anomalous word and persisting for several hundred milliseconds over centro-parietal scalp regions (for review, see Osterhout et al., 1997). The amplitude of the P600 is inversely related to the syntactic congruency between a target word and the preceding sentence and is elicited by anomalies involving number and gender agreements, phrase structure, verb subcategorisation, verb tense and case.

While some researchers believe that the P600 reflects a language specific brain response (Osterhout et al., 1997; Osterhout, McKinnon, Bersick, & Corey, 1996), others support the proposal that the P600 is in fact a member of the P300 family (Coulson et al., 1998b). The P300 is not a unitary component, but is divided into multiple subcomponents generated by different neuronal sources (Johnson, 1993; Johnson, 1989; Sutton & Ruchkin, 1984). One subcomponent, the P3b reflects a striking similarity with the P600, as both components are broadly distributed over centro-parietal areas and occur at around 500ms after stimulus onset. The functional significance of the P300, and the P3b in particular, is thought to reflect brain activity indexing the update of a context maintained in working memory (Donchin, Karis, Bshore, Coles, & Gratton, 1986). Although there is little consensus in the debate as to whether the P600 is a manifestation of the P3b, it is possible that the P600 reported in numerous linguistic studies is closely linked to memory processes which constantly update contextual information.
4.2.4 Summary

The N400 is an electrophysiological correlate of semantic meaning which is processed at various contextual levels such as lists of words, sentences or in discourse. This component describes a negative deflection between 250 and 500ms post stimulus which has been mostly reported to occur over central areas of the scalp, although the precise topographical distribution is dependent on stimulus modality. The N400 is thought to constrain and pre-activate semantic information or meaning that is congruent with a preceding context and the ease of processing expected information leads to a reduction in the amplitude. The N400 has also been linked to the ease of accessing information from semantic memory and is reported to be sensitive to associative and semantic relationships between items. Thus, there is general agreement that the N400 is related to the retrieval of semantic information and indexes processes that integrate meaning into a preceding semantic context.

Besides the N400, a second ERP component, the P600, may also be linked to semantic memory processes. Although P600 effects are predominantly reported in linguistic studies examining syntactic violations in sentences, some support the view that the P600 is not a language specific component but belongs to the family of the P300. This line of research interprets the P600 to index memory processes which constantly update contextual information.

4.3 Conclusion

This chapter reviewed prominent ERP components which are associated with episodic and semantic memory. The first part of this chapter focussed on ERP components, referred to as difference in memory ‘Dm’ effects, which are evoked by episodic encoding processes. Such effects exhibit more positive going deflections for remembered compared to forgotten items. Dm effects are able to indicate at the time of encoding whether an item will be subsequently remembered but the precise timing and scalp distribution is influenced by different variables.

Following encoding, this chapter reviewed different ERP components associated with episodic retrieval. These included processes that lead to retrieval,
processes engaged during retrieval and processes evaluating retrieval results. Most importantly, this section reported ERP findings indexing putative ERP correlates for familiarity and recollection (the early frontal and left parietal old/new effect, respectively). Such correlates suggest that ERP methods are a vital tool for investigating episodic retrieval in the light of dual-process theories, by providing independent measures of familiarity and recollection.

The second part discussed ERP findings in relation to semantic memory. The N400, which is a negative deflection between 250-500ms post stimulus onset, has been shown to index semantic meaning and contextual integration processes at various different levels: word, sentence or discourse. The N400 is linked to the ease of accessing information from semantic memory and appears to be sensitive to semantic relations between items.

In general, most of the reviewed ERP effects which relate to episodic and semantic memory processes are not entirely understood in terms of their functional meaning and significance. Nevertheless, the current chapter has revealed some consistent interpretations of ERP modulations across multiple studies and experimental manipulations. Therefore, the outlined ERP effects might play an important role in elucidating potential interactions between the episodic and semantic memory system, which is the main intent of this thesis. For instance, N400 effects should indicate whether semantic memory processes were successfully modulated by an experimental paradigm. The question of how such modulations affect episodic retrieval can be addressed at the stage of encoding by investigating modulations in Dm effect, or at the stage of retrieval by examining changes in the ERP correlates for recollection and familiarity. If specific semantic memory processes alter episodic retrieval, such influence should elicit modulations in the ERP correlates for encoding and retrieval. The predicted direction of change for individual encoding and retrieval correlates is dependent on the experimental manipulations employed and will be discussed independently for the individual studies. Overall, this chapter provides evidence that ERP methods offer insightful information, capable of overtly or covertly examining whether and how semantic and episodic memory processes interact with each other.
4 ERP findings in memory research
5 Encoding of semantic relations

5.1 Introduction

Some events we experience in the course of our lives will enter and persist in our memory, while others go unnoticed and evoke hardly any memories at all. Efforts have been made to identify mechanisms that relate enduring memories to operations of encoding, storage and retrieval (Squire, 1987; Tulving, 1983). Encoding refers to processes that initiate the formation of memory traces and is thought to involve distinct sub-processes. First, multi-sensory inputs from different brain areas have to be transformed into a cohesive internal representation, possibly by mechanisms of temporal synchronization (Engel & Singer, 2001; Tallon-Baudry & Bertrand, 1999). Second, the resulting perceptual representations need to be related to stored representations or knowledge. Hence, perceptual and conceptual features as well as contextual information related to the episode are activated during encoding. Processes of encoding are therefore likely to be sensitive to the encoding strategy employed and the properties of the to-be-encoded material, including their match to previously stored knowledge. The current study concentrates on the latter factor and investigates whether semantic knowledge of the to-be-encoded material alters the actual process by which information is encoded into memory.

Neuronal mechanisms supporting encoding of different semantic material can be assessed with ERPs. The ability to successfully remember a specific stimulus class better than others are sometimes associated with modulations in neuronal activity during encoding. Thus, differences in neuronal activity elicited by different semantic material at study may reflect changes in encoding processes. For example, previous studies have repeatedly shown that the contrast of semantically congruent and incongruent material reveals a modulation of the N400 component (Kutas & Hillyard, 1980). The N400 effect is a negative deflection peaking approximately 400ms after stimulus onset for semantically unrelated or unexpected material. It is possible that this change in neuronal activity in response to different semantic material influences encoding, potentially affecting later storage and retrieval of such information.
A more direct approach to investigate how encoding processes may influence successful retrieval is the subsequent memory paradigm. This approach separates neuronal correlates elicited at encoding for items that were subsequently remembered from those that were subsequently forgotten. ERP studies employing subsequent memory paradigms have reported more positive going deflections for items subsequently remembered than subsequently forgotten (Paller et al., 1987; Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980). More precisely, two distinct classes of “differences in memory” (Dm) effects have been identified: one occurring at about 300-800ms post stimulus distributed over centro-parietal areas of the scalp, and a second occurring at a similar latency range but distributed over frontal areas (for reviews see Friedman, 1990; Paller and Wagner, 2002).

These frontal and centro-parietal Dm effects are associated with neuronal generators in different brain regions, presumably serving distinct cognitive functions. The frontal subsequent memory effect, for example, is more pronounced when participants are explicitly instructed to remember items (Friedman & Johnson, 2000), under elaborative encoding compared to rote rehearsal (Fabiani, Karis, & Dochin, 1990), for deep compared to shallow encoding (Sanquist et al., 1980), and for associative compared to non-associative encoding tasks (Kounios, Smith, Yang, Bachman, & D'Esposito, 2001). Parietal Dm effects have been observed in incidental encoding but not in intentional encoding tasks which only show a frontal Dm effect (Münte et al., 1988). Similarly, semantic encoding tasks have been reported to evoke frontal subsequent memory effects whereas perceptual encoding tasks are associated with small and often unreliable parietal subsequent memory effect (Paller et al., 1987; Sanquist et al., 1980). The parietal subsequent memory effect, furthermore, has been dissociated from implicit memory, semantic processing and distinctiveness. Furthermore, the size of the parietal Dm effect appears to be positively related to the demand of declarative memory (Fernandez et al., 1998; Paller, 1990; Neville et al., 1986).

Although frontal and parietal subsequent memory effects are likely to subserve different functions in memory encoding, the precise underlying cognitive processes are not well understood. Nevertheless, the parietal Dm effect, which seems to be
linked to MTL activity (Fernandez & Tendolkar, 2001; Tendolkar et al., 2000; Fernandez et al., 1999), appears to be specifically related to declarative memory formation, as the size of the effect correlates positively with the demand on declarative memory (Paller, 1990). Conversely, the frontal Dm effect, presumably reflecting PFC activity (Kounios et al., 2001; Duezel et al., 1999; Knight, 1984), is modulated by elaborative compared to rote encoding (Fabiani et al., 1990) and deep compared to shallow encoding (Sanquist et al., 1980). Therefore, frontal Dm effects seem to relate to operations supporting effortful encoding.

Following this line of argument the current study investigates whether pre-existing semantic knowledge alters the process of encoding, as indexed by changes in Dm effects. During the encoding phase subjects were instructed to perform a semantic classification task on visually displayed word pairs that contained different degrees of semantic relation to a previously presented category name. Changes in encoding activity were assessed via multiple sets of ERP analyses.

First, this chapter contrasts the electrical activity elicited during encoding of the three stimulus conditions. The defining difference between these stimuli is their semantic coherence and therefore their congruence with stored semantic knowledge. Modulations in ERP activity across stimulus conditions would indicate differences in encoding processing, suggesting that the semantic coherence of stimuli potentially influences memory performance.

Since the current data demonstrate difference in encoding activity the question arises as to whether such differences are contingent upon conscious processing of the semantic relations. Alternatively, such differences might relate to more automatic processing and thus emerge independent from correct or incorrect classifications of semantic relations. This was tested in a second set of analyses contrasting correct vs. incorrect classification of the word type during encoding. The results highlight two ERP modulations, one that was and another that was not susceptible to the accuracy of classification performance.

A final set of analyses investigated subsequent memory effects giving more direct indication of whether encoding activity is predictive for subsequent memory performance. The results demonstrate that stimuli that are congruent with pre-
existing semantic knowledge elicit effects that are different from those seen for incongruent stimuli.

5.2 Materials and Methods

5.2.1 Participants

All participants were right-handed native English speakers, ranging from 18 to 35 years in age, with normal or corrected-to-normal vision and no known neurological problems. Informed consent was required, and payment provided at a rate of £5 per hour. Twenty two participants performed the ERP study; three were excluded due to technical failure, and the remaining 19 (6 female) subjects had an average age of 24 years.

5.2.2 Materials

Stimuli consisted of the presentation of a category name followed by a word pair. Each word pair was classed as being either semantic-two (both words related to the category), semantic-one (one word related to the category) or non-semantic (both words unrelated to the category) as shown in Figure 5-1. Word pairs were constructed from 864 nouns, 4-6 letters in length, with a frequency between 10 and 30 occurrences per million (Kucera and Francis, 1967). A third (288) of the nouns were category exemplars (12 nouns for each of 24 categories), the remainder (576) were unrelated to the categories.

Stimuli were created for 6 blocks, each containing a single study list of 16 semantic-two, 16 semantic-one and 32 non-semantic word pairs (randomly intermixed), matched with a corresponding test list of 12 semantic-two, 12 semantic-one and 24 non-semantic word pairs. Test lists were created for each condition (semantic-two, semantic-one and non-semantic) in the following way: 8 pairs were re-presented at test in the same pairings as at study, providing 8 intact word pairs. 16 pairs shown at study were recombined to create 8 rearranged word pairs by taking one word from each of two study pairs (maintaining word position in each case) and
discarding the other member of each study pair. To be clear, rearranged study word pairs A-B and C-D would be recombined to form A-D, discarding B and C. The first and second word of a study pair were discarded equally often. The remaining 8 pairs were used to create 8 new word pairs, by combing the first member of each pair (always discarding the second member of the pair) with a previously unstudied word. The resulting semantic-two, semantic-one and non-semantic word pairs for each of the intact, rearranged and new conditions were randomly intermixed within each test list.

![Experimental design and materials](image)

**Figure 5-1** Experimental design and materials. During the study phase each trial involved the presentation of a category name followed by a word pair. Either both of the words were semantically related to the category (semantic-two), one of the words was semantically related to the category (semantic-one), or neither of the words contained a semantic relation to the category (non-semantic). During the test phase the same trial procedure was employed and three types of word pairs were presented: intact pairs, which were previously presented at study, rearranged pairs, which were constructed by recombining words from two study pairs and new pairs, which were constructed by combining a member of a studied pair with an unstudied word. Intact, rearranged and new word pairs were constructed separately for the semantic-two, semantic-one and non-semantic conditions (Figure adapted from Greve et al., 2007).

### 5.2.3 Procedures

The experiment was implemented using E-Prime and a PST Serial Response Box. All stimuli were displayed in white, using upper case Courier New 18 point font, against a black background. Category names were displayed in central vision,
and word pairs were displayed one above the other, slightly above and below central vision. The category name associated with an individual word was held constant between study and test (pairs were rearranged within each category). At the viewing distance of approximately 1 metre, the stimuli subtended a maximum visual angle of $3.7^\circ$ horizontally and $1.4^\circ$ vertically. The 6 study-test blocks were presented in a random order for each participant. An additional practice list was always shown first to familiarize participants with the procedure. Figure 5-1 illustrates the design. The factors of relationship (semantic-two, semantic-one, non-semantic) and pairing (intact, impaired, new) were fully crossed within participants.

Each study trial started with a fixation cross (+) displayed for 750ms in the centre of the screen, followed by a blank screen for 250ms. The category name was then presented for 1500ms before being replaced by a word pair for 2000ms. Participants were instructed to indicate by button press (within 5750ms of word pair onset) whether none, one or two of the words were related to the category name. The study task was intended to ensure that the semantic meaning of the word pairs was encoded. Once a response was made the screen went blank for 250ms, and the next trial began. Participants were informed that their memory would be tested.

Each test trial started with an initial 750ms fixation cross, followed by a 250ms blank screen, a 1500ms category name, and then a word pair for 2000ms. Category names were re-presented at test. Participants were instructed to indicate by button press (within 7750ms of word pair onset) whether each word pair was a target (respond: old) or a non-target (respond: new). Targets were defined as intact word pairs; non-target as rearranged and new word pairs. The mapping of buttons to old and new responses was counterbalanced across participants. Once a response was made a short (250ms) delay occurred, and participants were then prompted to rate their response confidence by button press on a five point scale (1 = guess, 2 = unsure, 3 = think so, 4 = pretty sure, 5 = certain). Once a confidence response was made the screen went blank for 250ms, and the next trial began. Participants were asked to respond as quickly and accurately as possible, and the mapping of buttons to old and new responses was counterbalanced across participants.
5.2.4 ERP recording and analysis

Scalp EEG was recorded from 61 Silver/Silver-Chloride electrodes embedded in a cap based on the extended international 10-20 system (Jasper, 1958): Fz, FCz, Cz, CPz, Pz, POz, Oz, FP1, FP2, AF7, AF8, AF3, AF4, F7, F8, F5, F6, F3, F4, F1, F2, FT7, FT8, FC5, FC6, FC3, FC4, FC1, FC2, T7, T8, C5, C6, C3, C4, C1, C2, TP7, TP8, CP5, CP6, CP3, CP4, CP1, CP2, P7, P8, P5, P6, P3, P4, P1, P2, PO7, PO8, PO5, PO6, PO3, PO4, O1, O2. Data were recorded and processed using Neuroscan 4.2 software. EEG was recorded using a left mastoid reference, but EEG was also recorded from the right mastoid, allowing re-referencing off-line to recreate linked mastoid recording. Electrooculogram (EOG) electrodes were located above and below the left eye for monitoring eye blinks and on the outer canthi of both eyes to monitor lateral eye movements. Electrode impedances were adjusted below 5kΩ, and all data were recorded with a bandpass filter of 0.1-40 Hz and digitised (16 bit) at a rate of 8ms per point. Eye-blinks artefacts were removed using a regression procedure (Neuroscan Ocular Artifact Reduction), calculating an average blink from a minimum of 32 blinks for each participant, and removing the contribution of the blink from all other channels on a point-by-point basis.

Continuous EEG data was separated into 2000ms epochs, beginning 200ms before the onset of each word pair. Individual epochs were baseline corrected and smoothed over 5 points. Epochs were excluded (average 9%, ranging from 4% to 19%) when eye movements were present (horizontal EOG effects greater than 100 μV), when any channel became saturated (exceeding ±495 μV), or when baseline drift (absolute difference in amplitude between the first and last data point of each individual epoch) was greater than 75 μV on any EEG channel. A minimum of 16 artefact-free trials were required from each participant in each condition to ensure an acceptable signal-to-noise ratio. To minimize EEG artefacts participants were asked to relax, minimise body, head and eye movements, and to fixate on the centre of the screen.

As noted above, the experiment was designed to examine differences in ERP components associated with the encoding of semantic-two, semantic-one and non-semantic word pairs, thus ERPs were formed for these three stimulus conditions.
Further ERP analyses were designed to investigate the patterns of subsequent memory effects elicited at study. On the basis of visual inspection of the waveforms, data at study were analysed over 3 consecutive time windows (300-600ms, 600-1000ms, 1000-1800ms).

All statistical tests were conducted with a significance level of 0.05. Analysis of ERP data employed the Greenhouse-Geisser correction for non-sphericity, and corrected df and p values are reported as appropriate. Topographical analyses were performed on difference scores (subtracting the ERPs for subsequent incorrectly identified word pairs from subsequent correctly identified word pairs) and these effects were normalised prior to analysis using the Max-Min method (McCarthy and Wood, 1985).

5.3 Results at study

5.3.1 Comparison of the three stimulus conditions

This first set of analysis contrasted the three stimulus conditions with respect to differences in behavioural performance as well as changes in electrical activity recorded during the study phase. Modulations in behavioural performance or ERP activity during study would advocate the view that altered encoding processes are engaged for the three stimulus conditions.

5.3.1.1 Behavioural data

Figure 5-2 shows the likelihood for correctly classifying the word pairs during study. The results of an ANOVA testing the factor of stimulus (non-semantic, semantic-one, semantic-two) reveal no significant difference in classification accuracy. The three types of word pairs revealed an average of 83 per cent correct responses.
Figure 5-2 Behavioural data showing the mean probability (and standard error) of correct responses in the semantic classification task at study. Participants were required to classify the semantic relation between a presented word pair and a preceding category name. For the non-semantic, semantic-one and semantic-two relations no significant difference in task performance was found.

However, the three stimulus conditions demonstrated differences in reaction times (RT), as illustrated in Figure 5-3. An ANOVA testing the factor of stimulus (non-semantic, semantic-one, semantic-two) verified the statistical significance of this difference \(F(2,38)=5.143, p<0.05\). Follow-up contrasts revealed no RT differences between correctly identified semantic-one and semantic-two pairs, which both evoked significantly faster classifications than non-semantic pairs \(t(19)=2.2, p<0.05; t(19)=2.8, p<0.01\) respectively). Furthermore, RTs were significantly faster across all three stimulus conditions for correctly compared to incorrectly classified pairs (non-semantic pairs: \(t(19)=2.2, p<0.05\); semantic-one pairs: \(t(19)=3.1, p<0.01\); semantic-two pairs: \(t(19)=2.6, p<0.05\), see Figure 5-3.
In sum, the behavioural data demonstrated that participants can discriminate between the different types of word pairs as semantic relations were classified correctly with a high degree of accuracy. Significantly faster RTs for semantic-two and semantic-one pairs compared to non-semantic pairs suggest that the processing of semantic-two and semantic-one pairs may have been easier than non-semantic pairs.

5.3.1.2 ERP data

Grand average ERPs elicited for the three stimulus conditions are shown in Figure 5-4. The mean numbers of trials contributing to the average waveforms are 115 for the non-semantic, 58 for the semantic-one and 57 for the semantic-two condition.

Figure 5-4 Grand average ERPs elicited for non-semantic (black), semantic-one (blue) and semantic-two (red) word pairs during study. ERP waveforms presented here and in subsequent graphs of this kind are shown for 61 electrodes, displayed as if looking down onto the top of the head. Differences between the waveforms are present over frontal and parietal locations, indicating changes in neuronal activity when different semantic word pairs become encoded.
ERP activity elicited for semantic-two and semantic-one conditions departed from non-semantic conditions between 300 to 600ms post stimulus onset over frontal electrodes (see Figure 5-5 for enlarged illustration of select electrodes). All three stimulus conditions diverge between 600 and 1000ms, eliciting waveforms with graded levels of activity across parietal sites. The semantic-two condition elicits more positive going ERPs compared to the semantic-one condition, which in turn reveals more positive going ERP waveforms compared to the non-semantic condition. Finally, from around 1000ms onwards differences between the three stimulus conditions become apparent over right lateralised frontal sites. Subsequent statistical analyses investigate those ERP differences by contrasting average voltages calculated over three consecutive epochs (300-600ms, 600-1000ms, 1000-1800ms) for each stimulus condition.

**Figure 5-5** Grand average ERPs elicited for non-semantic (black), semantic-one (blue) and semantic-two (red) word pairs during study. Unless stated otherwise, ERP waveforms are presented here and in the following graphs of this kind over 3 frontal (F1, Fz, F2) and 3 parietal (CP1, CPz, CP2) electrodes, whose locations are highlighted in green on the schematic top down view of the head. Frontal electrodes show a negative deflection for non-semantic compared to semantic-one and semantic-two pairs. Parietal electrodes, in contrast, reveal a graded positive deflection, which is largest for semantic-two condition, followed by the semantic-one condition and smallest for the non-semantic condition.
### 5.3.1.2.1 Analysis over frontal locations

Analyses over frontal electrodes were performed individually across all three time windows by employing an ANOVA with the factors of condition (non-semantic, semantic-one, semantic-two), hemisphere (left, right) and site (inferior, mid, superior). Significant effects and interactions with the factor of condition were obtained across the first and third epoch but not the second epoch (see Table 5-18). When contrasting the activity for stimulus conditions (collapsed over frontal electrodes9) in the first time window (300-600ms), the non-semantic condition evoked significantly more negative activity compared to the semantic-one and semantic-two condition (t(18)=−2.8, p<0.05, t(18)=−2.2, p<0.05 respectively), but no significant difference was present between the semantic-one and semantic-two condition. Figure 5-5 indicates that this early effect is symmetrically distributed over frontal electrodes, which is confirmed by the absence of significant condition by hemisphere or condition by hemisphere by site interactions (see Table 5-1).

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Table 5-1 This table shows significant interactions with the factor of condition separated for the three epochs at frontal electrodes, resulting from an ANOVA with the factor of condition, hemisphere and site.

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8 For reasons of transparency only ‘p-values’ are reported for this analysis. More detailed information regarding the ‘F-values’ and ‘df-values’ of this analysis can be found in Appendix A (Section 15.1.1)

9 This analysis was performed on a virtual electrode reflecting the average activity of the following six frontal electrodes: F1, F2, F3, F4, F5, F6.
While the second epoch fails to reveal any significant effect or interaction with condition, differences over frontal locations reappear in the third epoch (see Table 5-1). Figure 5-5, and more clearly Figure 5-6, indicate that the semantic-one condition shows a stronger later positivity compared to the semantic-two or non-semantic conditions. Auxiliary analyses contrasting the level of activity (collapsed over frontal electrodes\(^9\)) revealed no significant differences between conditions. However, more focused right frontal comparisons (collapsed over right frontal electrodes: F2, F4, F6) demonstrated significantly more positive activity for semantic-one than semantic-two conditions (\(t(18)=-2.2, p<0.05\)), while all other contrasts were not significant.

![Figure 5-6](image)

**Figure 5-6** Grand average ERPs elicited for non-semantic (black), semantic-one (blue) and semantic-two (red) word pairs during study. ERP waveforms are displayed over 6 frontal (FP2, AF4, AF8, F2, F4, F6) locations, marked in green on the schematic top down view of the head. The waveforms reveal a late positivity for semantic-one compared to semantic-two and non-semantic conditions.

### 5.3.1.2.2 Analysis over parietal locations

Modulations at parietal electrodes were analysed individually across all three time windows using an ANOVA with the factor of condition (non-semantic,
5 Encoding of semantic relations

semantic-one, semantic-two), hemisphere (left, right) and site (inferior, mid, superior). Significant effects and interactions with the factor of condition were present across the first and second, but not the third epoch (see Table 5-2\textsuperscript{10}). Figure 5-5 shows that the three stimulus conditions exhibit graded modulations in activity within the second epoch. The semantic-two condition elicits more positive going activity compared to the semantic-one condition, which in turn reveals more positive ERPs relative to the non-semantic condition. Subsequent analysis verified the significance of this graded modulation by contrasting the activity (collapsed over parietal electrodes\textsuperscript{11}) elicited for semantic-two and semantic-one conditions ($t$(18)=4.6, $p<0.001$) as well as semantic-one and non-semantic conditions ($t$(18)=2.3, $p<0.05$). This difference is symmetrically distributed over the parietal scalp (see Figure 5-4 and Figure 5-5) as the lack of significant condition by hemisphere or condition by hemisphere by site interactions suggest (see Table 5-2).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>parietal location</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>300-600ms</td>
</tr>
<tr>
<td>cond.</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>cond. by hem.</td>
<td>-</td>
</tr>
<tr>
<td>cond. by site</td>
<td>p&lt;0.05</td>
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<tr>
<td>cond. by hem. by site</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

Table 5-2 This table shows significant interactions with the factor of condition separated for the three epochs at parietal electrodes, resulting from an ANOVA with the factors of condition, hemisphere and site.

\textsuperscript{10} For reasons of transparency only ‘p-values’ are reported for this analysis. More detailed information regarding the ‘F-values’ and ‘df-values’ can be found in Appendix A (Section 15.1.2).

\textsuperscript{11} This analysis was performed on a virtual electrode reflecting the average activity of the following six parietal electrodes: CP1, CP2, CP3, CP4, CP5, CP6.
However, analyses over parietal electrodes not only reveal condition effects in the second but also the first epoch. Follow-up analyses (collapsed over parietal electrodes\textsuperscript{11}) demonstrate that the non-semantic condition elicits more negative activity compared to the semantic-one and semantic-two conditions ($t(18)=-4.9$, $p<0.001$; $t(18)=-5.3$, $p<0.001$ respectively), while no significant difference was present between the semantic-one and semantic-two condition.

This pattern of results suggests that the early difference between non-semantic vs. semantic-one and semantic-two conditions reported over the frontal electrodes appears to be broadly distributed and extends to more central and parietal electrodes. This ERP effect is consistent with a modulation of an N400 component, a negative going deflection which is maximal over central-parietal electrodes between 300-500ms post stimulus (for review see Kutas and Van Petten, 1994).

### 5.3.1.2.3 Analysis of the N400

In order to establish that the modulations obtained in the first time window resembles the distribution of an N400 component, additional analysis was performed across two rings of central electrodes (see Figure 5-7). An ANOVA with the factors of condition (non-semantic, semantic-one, semantic-two), ring (inner, outer) and site (FCZ, FC2, C2, CP2, CPZ, CP1, C1, FC1 and FZ, F4, C4, P4, PZ, P3,C3, F3) was employed. Beside a main effect of condition [$F(1.7,31.3)=12.1$, $p<0.001$], a significant condition by epoch by ring interaction [$F(1.9,33.8)=4.2$, $p<0.05$] was obtained. This indicates that the N400 component is maximal over the superior ring of electrodes and is modulated by the stimulus conditions within the first epoch. More importantly, subsequent analysis within the first epoch (separated across ring) revealed significant main effects of condition for the inner and outer ring [$F(1.8,33.1)=11.3$, $p<0.001$; $F(1.8,33.9)=10.0$, $p<0.001$, respectively] but no condition by site interactions. This confirms a broad and symmetric distributed of the effect around the centre of the scalp, a pattern that strongly resembles the N400 effect.
Figure 5-7 A schematic outline of the recording montage and analysis strategy for the N400 effect. This figure displays all 61 electrodes, displayed as if looked down onto the top of the head. ERP analysis investigating N400 effects included electrodes located in two rings, each containing 8 electrodes (Inner Ring highlighted in light green: FCZ, FC2, C2, CP2, CPZ, CP1, C1, FC1; Outer Ring highlighted in dark green: FZ, F4, C4, P4, PZ, P3, C3, F3), allowing the central maximum of the effect to be identified.

5.3.1.2.4 Topographical analysis

The pattern of results described above suggests that the different stimulus conditions show changes in activity over time, starting with an early centrally distributed N400 effect, followed by a later parietal and an even later frontal component. Topographic analyses were performed to confirm that these findings reflect a qualitative difference in the pattern of neural generators engaged over time (see Figure 5-8 for topographic maps). Analyses were performed on three difference waveforms contrasting non-semantics vs. semantic-one, non-semantic vs. semantic-two, and semantic-one vs. semantic two conditions, using rescaled data to avoid confounding effects of size. The profile of spatio-temporal differences between stimulus conditions was tested with ANOVAs comparing the first and second epoch, including the factors of epoch (1st epoch vs. 2nd epoch), location (front, central, parietal), hemisphere (left, right) and site (inferior, mid, superior). The analyses, which were performed separately across all three difference waveforms, revealed significant interaction between epoch, location and hemisphere for the non-semantic vs. semantic-one contrast \( [F(1.5,26.4)=5.2, p<0.01] \), epoch, location, hemisphere and site for non-semantic vs. semantic-two contrast \( [F(1.5,26.4)=5.2, p<0.01] \) and epoch by hemisphere \( [F(1.5,26.4)=5.2, p<0.01] \) and epoch by location \( [F(1.5,26.4)=5.2, p<0.01] \).
p<0.01] interactions for semantic-one vs. semantic-two contrasts. Since all three stimulus conditions revealed interactions between the factors of epoch, location and hemisphere, this analysis suggests that the neuronal generators giving rise to the early N400 effect is spatially and temporally distinct from the neuronal generators evoking the later emerging parietal modulation.

The corresponding ANOVAs contrasting the second and third epoch also revealed significant interactions between epoch, location, and site for both non-semantic vs. semantic-one [F(1.5,26.4)=5.2, p<0.01] and non-semantic vs. semantic-two [F(1.5,26.4)=5.2, p<0.01] conditions, whereas the semantic-one vs. semantic-two condition showed significant interactions between epoch and site [F(1.3,22.9)=9.9, p<0.001] as well as location and hemisphere [F(1.6,28.7)=12.8, p<0.001]. These results suggest that the parietal and late frontal modulations are also generated by spatially and temporally dissociable neural sources.

Finally, a third set of ANOVAs analogous to the previous ones was performed over the first and third epoch, testing whether or not the same neuronal generator underlying the early frontal effects is engaged in the late time window. The results revealed significant interactions between epoch, location and hemisphere [F(1.6,28.0)=11.3, p<0.01] for the non-semantic vs. semantic-one condition and significant epoch by hemisphere by site interaction for both the non-semantic vs. semantic-two [F(1.4,24.5)=6.9, p<0.01] and semantic-one vs. semantic-two [F(1.3,23.7)=5.0, p<0.05] condition, whereby the latter condition also revealed a location by hemisphere interaction [F(1.6,29.0)=11.8, p<0.01]. This pattern of results confirms that the early N400 effect originates from a neuronal source that is spatially and temporally dissociable from the neuronal generators eliciting the late frontal differences between the stimulus conditions. Overall, the topographical analysis confirms that the early N400 effect and the successive parietal and late frontal differences are associated with qualitatively distinct neuronal generators.
5.3.2 Contrasting correct and incorrect classifications

The previous analysis demonstrated that the level of semantic coherence modulates encoding activity, potentially causing changes in memory performance. However, it remains unclear whether such differences in encoding activity relate to conscious or automatic processes. Contrasting encoding activity for correctly and incorrectly identified pairs may give more insight into that question as automatic processes would predict no change in activity.

Thus, the following analysis compared ERP activity elicited by correctly and incorrectly classified conditions. However, only a very low proportion of stimuli were incorrectly classified (see Section 5.3.1.1). In order to enable statistical analysis of ERP data with sufficient trial numbers (averaging over at least 16 trials), the data
for semantic-one and semantic-two conditions were collapsed, to form a general semantic condition. Overall, a subgroup of 10 (3 female) participants with an average age of 24 qualified for this contrast by showing at least 16 artefact free trials in every condition. This subgroup of participants revealed no significant difference in behavioural performance compared to the complete group of participants.

5.3.2.1 ERP data

Grand average ERPs elicited for correctly and incorrectly classified semantic and non-semantic conditions are shown in Figure 5-9 and Figure 5-10. The mean numbers of trials contributing to the average waveforms are 106 for correct semantic, 112 for correct non-semantic, 28 for incorrect semantic and 27 for incorrect non-semantic classifications.

![ERP data](image)

**Figure 5-9** Grand average ERPs showing electrical activity elicited for correctly classified semantic word pairs (red) and incorrectly classified semantic word pairs (black). Differences between the waveforms emerge over parietal electrodes, indicating changes in encoding activity when semantic relations are correctly identified.
Figure 5-10 Grand average ERPs showing electrical activity elicited for correctly classified non-semantic word pairs (blue) and incorrectly classified non-semantic word pairs (black). Although, differences emerge over anterior frontal electrodes between waveforms for correctly and incorrectly identified non-semantic words, previously reported effects that reveal changes in activity for the encoding of semantic or non-semantic word pairs are not modulated by correct or incorrect non-word classification.

As Figure 5-9 and Figure 5-10 show, in the early epoch (300-600ms) no clear differences exist in ERP activity between correctly and incorrectly classified items for both semantic and non-semantic conditions. Correct and incorrect responses to semantic conditions, however, diverge over parietal electrodes in the second epoch (600-1000ms), with the correct responses eliciting more positive going ERPs. Non-semantic conditions, in contrast, reveal no modulation in activity between correct and incorrect responses (see also Figure 5-11 and Figure 5-12 for more detailed illustration).
Figure 5-11 Grand average ERPs elicited for correctly classified semantic word pairs (red) and incorrectly classified semantic word pairs (back). Parietal electrodes reveal a strong positive deflection peaking at about 800ms post stimulus onset, for correctly compared to incorrectly classified semantic word pairs.

Figure 5-12 Grand average ERPs elicited for correctly classified non-semantic word pairs (blue) and incorrectly classified non-semantic word pairs (black). Neither frontal nor parietal electrodes show differences between correctly and incorrectly classified non-words at the location and time of interest.
Finally, from around 1000ms onwards variations in ERP activity are evident over left lateralisated frontal sites. More positive going ERP activity was evident for correctly than incorrectly identified semantic condition. The reverse pattern of activity emerges for non-semantic conditions, revealing more positive going ERP deflections for incorrectly compared to correctly classified stimuli (see Figure 5-13).

![Figure 5-13](Grand average ERPs elicited for correctly classified semantic (red) and non-semantic (blue) word pairs as well as incorrectly classified semantic (black) and non-semantic (black) word pairs. Semantic word pairs demonstrate more positive going ERP activity for correctly compared to incorrectly classified pairs, while the opposite pattern of activity is present for non-semantic word pairs.)

To establish the statistical significance of these apparent differences in ERP activity, voltages were averaged over three consecutive epochs (300-600ms, 600-1000ms, 1000-1800ms) for semantic and non-semantic stimulus conditions.
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5.3.2.1.1 ERP analyses

The aim of this set of ERP analysis was to test whether the early central N400, the subsequent parietal and late frontal ERP components, reported in the previous set of analysis (see Section 5.3.1.2), are sensitive to correct and incorrect classification of the stimuli, which may be informative for what type of processes these components may reflect. To test this, subsequent analyses were performed over frontal locations (collapsed across 6 frontal electrodes)\(^{12}\) and parietal locations (collapsed across 6 parietal electrodes)\(^{12}\) examining whether the individual stimulus conditions showed differences in ERP activity for correct and incorrect responses.

No significant difference in ERP activity was observed in the early time window of 300-600ms for correct vs. incorrect responses for either the semantic or non-semantic conditions, at frontal or parietal locations. The second time window of 600-1000ms also failed to reveal significant differences for correct vs. incorrect responses at frontal locations, but parietal electrodes showed significantly more positive activity for correctly vs. incorrectly identified semantic word pairs (t(9)=3.7, p<0.01), whereas no such difference was present in non-semantic conditions. Finally, similar to the early time window, the 1000-1800ms epoch demonstrated that semantic and non-semantic conditions elicited no significant differences in ERP activity when correct responses are contrasted with incorrect responses over frontal and parietal locations.

Overall, modulations in ERP activity between correct and incorrect semantic classifications were obtained at parietal electrodes at 600-1000ms, but not frontal electrodes. Neither the N400 (300-600ms) nor late frontal effect (1000-1800ms) revealed modulation in activity.

\(^{12}\) The analysis was performed by collapsing over 6 frontal electrodes (F6, F5, F4, F3, F2, F1) and 6 parietal electrodes (CP6, CP5, CP4, CP3, CP2, CP1).
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Figure 5-14: Topographic distributions of differences in encoding between correctly and incorrectly classified word pairs. The maps illustrate distributional difference in activity between correct and incorrect non-semantic word pairs as well as correct and incorrect semantic word pairs in separate columns. The rows represent averages over different time windows (300-600ms, 600-1000ms and 1000-1800ms). Maps are shown as if looking down onto the top of the head, with individual electrode locations indicated by black dots, and a scale bar shows amplitude range. Topographic differences occur in the early 300-600ms time window over anterior frontal electrodes, while from 600-1000ms differences exist over parietal electrodes only for semantic word pairs. The late 1000-1800ms time window reveals differences at right frontal electrodes, particularly in the non-semantic condition.

5.3.3 Summary

This analysis assessed changes in encoding activity evoked by stimulus material containing different degrees of semantic relatedness. The question addressed here was whether stimulus material congruent with our semantic knowledge evokes encoding processes that are different to those observed for stimulus material that does not map onto the structure of our semantic knowledge (i.e., organised coherently or not). If this is the case, stimulus material with different semantic characteristics may indeed be encoded differently, potentially affecting the subsequent storage and retrieval of information.
The results revealed three different ERP effects that were modulated by the semantic content of the stimulus material. First, an early centrally distributed effect (300-600ms), revealing a stronger negative deflection for non-semantic pairs compared to semantic-one and semantic-two pairs. Second, a later difference emerged over parietal areas (600-1000ms), which showed graded levels of activity. Specifically, the semantic-two condition elicited a more positive going deflection compared to the semantic one condition, which in turn was associated with more positive activity than the non-semantic condition. Third, a late right lateralised frontal activity was obtained (1000-1800ms), revealing a stronger positive deflection for semantic-one conditions compared to semantic-two or non-semantic conditions.

These three effects differ in time course, topography and sensitivity to changes in semantic stimulus coherence a property of the to-be-encoded information. This suggests that these effects index processes of distinct functionality during encoding. As mentioned previously the first effect likely reflects modulations of the N400 component associated with the ease of integrating semantic information into a general context. Less obvious, however, is what functional interpretation can be assigned to the second and third component.

To gain further insight into this question a second set of analysis investigated whether any of the ERP effects were sensitive to correct and incorrect classification of the semantic relations. In other words, the second analysis tested whether the presence of a semantic relationship in the stimulus material was sufficient to evoke the observed modulations, or whether it was essential that subjects explicitly identified the semantic relationship correctly. The results of this analysis demonstrated no clear differences in the early central component. This is consistent with an N400 interpretation of this effect, which differed between semantic and non-semantic conditions, appeared centrally distributed over the scalp and occurred regardless of the accuracy of the semantic classification task. The later parietal component, in contrast, revealed a more positive going deflection for correctly compared to incorrectly identified semantic relations in semantic pairs. This difference only occurred for semantic but not non-semantic pairs. In contrast to the early N400 effect, the positive deflection over the parietal location appears to be

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related to the conscious detection and processing of semantic relations, as this effect was modulated by the accuracy of the semantic classification task. Finally, the late right lateralised frontal difference was not susceptible to correct or incorrect classification performance for either the semantic or non-semantic stimuli. Hence, similar to the initial N400 effect, the late frontal difference may reflect more automatic processes triggered by the semantic characteristics inherent to the stimulus material per se. Nevertheless, the distinct pattern of activity obtained for semantic and non-semantic pairs in the early and late time window suggests that the N400 and later frontal component index distinct (i.e. two distinct aspects of) automatic processes at encoding.

In general, the present results support the view that the pattern of processes engaged at encoding is susceptible to the semantic content of the to-be-encoded stimulus material. However, changes in activity at encoding need not necessarily reflect changes in encoding efficiency per se. An important question concerns whether such differences in activity recording during encoding will actually lead to changes in memory performance. To be clear, although the ERP effects are seen at the time of encoding they need not necessarily play any causal role in encoding into memory, but may reflect incidental or epiphenomenomal processing. The subsequent memory paradigm allows this issue to be addressed and this question is investigated in the following section.

5.4 Subsequent memory effects

Although the previous analyses have demonstrated that semantic coherence modulates encoding activity it is not given that this will alter later memory. The subsequent memory paradigm is able to establish a more direct link between encoding activity and subsequent retrieval success. This subsequent memory paradigm is effectively a reanalysis of the study data; however by using information from the test phase, it is possible to contrast study activity for subsequently remembered versus subsequently forgotten stimuli. Since this type of comparison is determined by the number of correctly and incorrectly remembered items at test, a
subgroup of 12 subjects (4 female, overall average age of 24) qualified for the subsequent memory analysis (i.e. containing at least 16 artefact free trials in every condition).

### 5.4.1 Behavioural Results

The next chapter (Chapter 6) of this thesis reports the behavioural and electrophysiological findings obtained at the test phase. As the behavioural recognition performance is included in that chapter, these data will not be presented at this stage. Nevertheless, recognition performance at test reveals whether an item is successfully remembered or not, and this information is utilised here to classify the study material into groups of subsequently remembered or forgotten items. The following section investigates differences in neural encoding activity between those remembered and forgotten items, which is predictive for accurate memory performance at test.

### 5.4.2 ERP data contrasting semantic and non-semantic stimuli

Grand average ERPs recorded at study for subsequent correctly and incorrectly recognised items are contrasted across semantic and non-semantic stimuli (see Figure 5-15 for semantic pairs and Figure 5-17 for non-semantic pairs). In the following, study activity leading to correct and incorrect recognition performance will be simply referred to as correct and incorrect conditions. However, it is important to note that the labels correct and incorrect relate to test performance which is used to separate the ERP activity at study.

The mean number of trials for correct and incorrect waveforms was 53 and 54 for semantic, and 59 and 47 for non-semantic word pairs respectively. Figure 5-15 shows that ERP activity for semantic test conditions is more positive going for incorrectly compared to correctly identified pairs, from around 300ms onwards, over parietal locations (see Figure 5-16 for enlarged illustration of selective electrodes). At a first glance these results seem surprising given that subsequent memory effects typically reveal more positive activity for correct compared to incorrectly recognised
stimuli. Nevertheless, the current analysis was collapsed across intact and rearranged test conditions, which are likely to have engaged different processes leading to correct and incorrect responses.

Whilst intact conditions require ‘old’ responses, rearranged conditions demand ‘new’ responses, since two previously studied words are portrayed in a new configuration. Consequently, incorrect responses to rearranged pairs may in fact reflect some item memory for individual words, leading to the incorrect classification of the entire word pairs as ‘old’. As behavioural data (see behavioural results in Chapter 7) show increased false alarm rates for rearranged relative to intact conditions, it is likely that the more positive activity for incorrect responses may predominantly reflect partial recognition for words presented in rearranged pairs.

Figure 5-15 Grand average ERPs showing subsequent memory effects for subsequent correctly (red) and incorrectly (black) identified semantic word pairs. Stimuli that are subsequently incorrectly remembered are associated with more positive going ERP waveforms at encoding over parietal electrodes compared to correctly identified semantic word pairs.
5 Encoding of semantic relations

![Graph showing ERP activity over time and parietal electrodes for correctly (red) and incorrectly (black) identified semantic word pairs.](image)

**Figure 5-16** Grand average ERPs illustrating subsequent memory effects for correctly (red) and incorrectly (black) identified semantic word pairs. Subsequently incorrectly compared to correctly identified stimuli reveal more positive going deflections over parietal electrodes. This deflection is a long lasting positivity which onsets at about 300ms post stimulus.

In contrast to semantic pairs, non-semantic pairs (see Figure 5-17) reveal no difference in ERP activity for correctly compared to incorrectly identified pairs over frontal or parietal locations (see Figure 5-22 for an enlarged illustration of selective electrodes). This failure to detect subsequent memory effects for non-semantic pairs might be a consequence of collapsing across intact and rearranged test conditions. Therefore, a second set of analysis tested for subsequent memory effects individually in the intact and rearranged test conditions. It is worth noting, however, that the current analysis does indeed reveal a modulation in subsequent memory effects for semantic compared to non-semantic conditions. A parietal subsequent memory effect is present for semantic pairs, but absent for non-semantic word pairs. To characterise this difference in subsequent memory using statistical methods, average voltages were calculated for each condition over two consecutive epochs (300-600ms, 600-1000ms).
5 Encoding of semantic relations

**Figure 5-17** Grand average ERPs showing subsequent memory effects for subsequently correctly (blue) and incorrectly (black) identified non-semantic word pairs. During study, the ERP waveforms show no clear modulation in electrical activity for subsequently correctly and incorrectly identified word pairs.

**Figure 5-18** Grand average ERPs illustrating subsequent memory effect for correctly (blue) and incorrectly (black) identified semantic word pairs. Subsequently correctly compared to correctly identified stimuli reveal no difference in electrical activity over either frontal or parietal locations.
5.4.2.1 ERP analysis separated by stimulus condition and location

Differences in subsequent memory effects across semantic and non-semantic stimuli were assessed at frontal and parietal locations by using an ANOVA with the factors of response (correct, incorrect), epoch (300-600ms, 600-1000ms), hemisphere (left, right) and site (inferior, mid, superior). The results show a response by epoch by site interaction [F(1.2,13.9)=3.9, p<0.05] for non-semantic conditions, reflecting late frontal changes in activity between correct and incorrect responses over inferior electrode sites. This pattern of activity does not relate to the previously reported subsequent memory effects. In contrast the semantic condition reveals a subsequent memory effect which shows a similar temporal and spatial distribution, but not polarity, to the previously reported subsequent memory effect. The ANOVA for the semantic conditions reveals a main effect of response over parietal locations [F(1,11)=4.2, p=0.06]. Thus, this analysis suggests that semantic but not non-semantic pairs reveal subsequent memory effects over parietal scalp locations, which contrary to what might have been predicted, demonstrate more positive going activity for incorrectly compared to correctly recognised items. This subsequent memory effect persists over a long period of time; no response by epoch interaction was observed. In general, the modulation of subsequent memory effects between semantic and no-semantic stimulus conditions suggests that pre-existing semantic knowledge may indeed alter the process by which information is encoded into memory. Interestingly, semantic pairs reveals more positive activity for incorrect than correct responses. As mentioned previously, this modulation may predominantly reflect incorrect ‘old’ responses to rearranged pairs, which is tested in the following set of analyses.
5 Encoding of semantic relations

5.4.3 ERP data contrasting intact and rearranged test conditions

Grand average ERPs for correctly vs. incorrectly identified intact and new conditions are shown in Figure 5-19 and Figure 5-21 respectively. The mean number of trials contributing to the waveform for subsequent correct and incorrectly identified trials was 49 and 23 for intact, and 63 and 78 for rearranged test conditions respectively. Figure 5-19 demonstrates that ERP activity for intact test conditions is more positive going for correctly compared to incorrectly identified pairs from around 300ms onwards over frontal locations (see Figure 5-20 for enlarged illustration of selective electrodes).

Figure 5-19 Grand average ERPs showing subsequent memory effects for correctly (green) and incorrectly (black) identified stimuli under intact test conditions. Stimuli that are subsequently correctly remembered are associated with more positive going ERP waveforms over frontal location during encoding.
Figure 5-20 Grand average ERPs illustrating subsequent memory effect for correctly (green) and incorrectly (black) identified test stimuli with intact test conditions. Subsequent correctly compared to incorrectly identified stimuli reveal more positive going activity over frontal electrodes. This effect demonstrates a long lasting positivity which onsets at about 300ms post stimulus.

However, recombined test conditions (see Figure 5-21) reveal more positive going ERP activity for incorrectly compared to correctly identified pairs over parietal locations, with an onset of about 300ms (see Figure 5-22 for an enlarged illustration of selective electrodes). For subsequent statistical analyses, average voltages were calculated for each condition over three consecutive epochs (300-600ms, 600-1000ms, 1000-1800ms).
5 Encoding of semantic relations

Figure 5-21 Grand average ERPs showing subsequent memory effects for correctly (purple) and incorrectly (black) identified stimuli tested under rearranged conditions. Subsequent incorrectly compared to correctly identified stimuli are associated with more positive going ERP activity over parietal locations.

Figure 5-22 Grand average ERPs illustrating subsequent memory effect for correctly (purple) and incorrectly (black) identified stimuli assessed under rearranged test conditions. Subsequent incorrectly compared to correctly identified stimuli reveal more positive going activity over parietal electrodes. This positive deflects onsets at about 300ms post stimulus and is sustained over a long period of time.
5.4.3.1 ERP analysis separated by test condition and location

The pattern of subsequent memory effects across individual test conditions and locations was assessed with ANOVAs including the factors of response (correct, incorrect), epoch (300-600ms, 600-1000ms, 1000-1800ms), hemisphere (left, right) and site (inferior, mid, superior). Intact test conditions revealed a significant response by site interaction \[F(1.7,18.2)=8.3, p<0.01\] over the frontal location, while no significant effect of response was observed over parietal locations. In contrast, recombined test conditions, revealed no significant response effects over frontal locations, but a significant main effect of response at parietal locations \[F(1,11)=8.2, p<0.05\].

Consequently, this pattern of results indicates that the subsequent memory effect for the intact test condition occurs over frontal scalp locations, with more positive going activity for correctly compared to incorrectly recognised items. In contrast, subsequent memory effects for the rearranged test condition occurs over parietal locations, revealing more positive going activity for incorrectly compared to correctly recognised items. Notably, these consecutive analyses failed to reveal any response by epoch interactions, suggesting a long-lasting modulation between correct and incorrect conditions.

5.4.3.2 Topographical analyses

The analyses in the previous section revealed spatially distinct subsequent memory effects for intact and recombined test conditions: a frontal effect for intact pairs showing a more positive going deflection for correctly recognised items and a parietal effect for recombined pairs revealing a more negative going deflection for correctly recognised items. Topographic analyses were performed to test whether these effects engaged qualitatively different neural generators. Analyses were performed on difference waveforms contrasting correct vs. incorrect conditions, using rescaled data to avoid confounding effects of size.

The ANOVA including the factors of test condition (intact, rearranged), epoch (300-600ms, 600-1000ms, 1000-1800ms), location (frontal, parietal),
hemisphere (left, right) and site (inferior, mid, superior), revealed a significant main effect of location \([F(1,11)=7.9, \ p<0.05]\) and a test by site interaction \([F(1.3,14.9)=5.3, \ p<0.05]\). The main effect of location is in agreement with two spatially distinct subsequent memory effects. Nonetheless, the absence of any significant location by test interactions suggests that intact and rearranged test conditions show no qualitatively distinct engagement of these generators for the subsequent memory effects. In other words, the topographic analysis failed to provide evidence that qualitatively distinct sets of generators support the subsequent memory effects observed for intact and rearranged test conditions. Thus, there is no evidence permitting the conclusion that the subsequent memory effects obtained under intact and rearranged test conditions, engage qualitatively distinct neuronal generators.

**Figure 5-23** Topographic distribution of the subsequent memory effects. The maps illustrate the difference in topographical distribution of encoding activity to stimuli that were either subsequently correctly or incorrectly recognised when tested either under intact or rearranged test conditions. The topographical maps are displayed over a time window of 300-1000ms. Maps are shown as if looking down onto the top of the head, with individual electrode locations indicated by black dots, and the scale bar shows amplitude range. Topographical differences occur over frontal locations for intact test conditions and parietal locations for rearranged test conditions.

**5.4.4 Summary**

The subsequent memory analysis tested whether encoding activity differs for subsequent correctly and incorrectly remembered stimuli. In particular, this investigation was concerned with the question of whether the presence of to-be-encoded stimuli which relates to pre-existing semantic knowledge alters the process of encoding, as measured by differences in subsequent memory effects. The first
analysis contrasted subsequent memory effects for semantic and non-semantic stimuli, and revealed a Dm effect over parietal locations for semantic stimuli only. Interestingly, this effect had a reversed polarity to previously reported Dm effects, with incorrectly identified items eliciting a more positive going deflection compared to correctly identified items. Nevertheless, under consideration that the subsequent memory contrast included correct and incorrect responses performed under intact and rearranged test conditions, it is possible that incorrect responses to rearranged pairs may have engaged memory processes. This possibility arises from the different task demands placed on intact and rearranged test conditions. While intact test conditions necessitate ‘old’ responses to previously studied pairs, rearranged conditions require ‘new’ responses, since rearranged word pairs are not displayed in their originally studied configuration. Nevertheless, individual words within a rearranged pair have been encountered previously. Thus, if rearranged pairs are incorrectly classified as old, it is possible that memory retrieval for individual words may have governed this decision and this could explain the more positive deflection to incorrectly identified pairs.

To explicitly test this hypothesis, a second set of analysis was performed contrasting subsequent memory performance for intact and rearranged test conditions. As predicted, rearranged test conditions elicited a subsequent memory effect over parietal locations, displaying a more positive going deflection for incorrectly compared to correctly recognised items. Intact test conditions, however, did not reveal such differences. In contrast, intact test conditions evoked a frontally located subsequent memory effect, characterised by more positive going ERP activity to subsequently correctly relative to incorrectly identified items. This effect was not present under rearranged test conditions.

In general, the subsequent memory analysis demonstrates that stimuli that relate to pre-existing semantic knowledge elicit different patterns of Dm effects than stimuli that do not directly map onto the structure of our semantic knowledge. This suggests that to-be-encoded material may alter the process of encoding, depending on the extent to which the to-be-encoded stimuli relate to pre-existing semantic knowledge.
5.5 Discussion

This study investigated whether the mapping between pre-existing semantic knowledge and the content of to-be-encoded stimulus material alters the actual process of encoding. This question was investigated in two stages. First, general changes in electrical activity during encoding were examined in stimulus conditions containing different semantic relations. The second stage employed the subsequent memory paradigm to assess whether changes in encoding activity between semantic stimulus conditions can predict subsequent memory performance.

The first stage of analysis identified three different ERP effects which revealed modulations in encoding activity across semantic and non-semantic stimuli. These three effects comprised an early centrally distributed component occurring between 300-600ms post stimulus onset, characterised by a strong negative deflection for non-semantic compared to semantic-one and semantic-two word pairs. This effect is likely to reflect an N400 based on the temporal, spatial and functional characteristics of the effect. Secondly, a parietal component occurred at about 600-1000ms post stimulus onset, showing graded levels of activity, with the strongest positive deflection for semantic-two, followed by semantic-one and non-semantic pairs. Finally a late, right lateralised frontal component was observed at about 1000ms post stimulus onset, revealing a stronger positive deflection for semantic-one conditions compared to semantic-two or non-semantic conditions.

These three effects emerged at the encoding phase, during which subjects performed a semantic classification task designed to ensure that the different semantic relations in the stimulus material were attended to. Thus, in an attempt to functionally interpret the observed ERP differences it seems to be a good starting point to consider linguistic ERP components indexing semantic processing of word pairs.
5.5.1 The early central effect and the N400

Previous research has proposed distinct ERP components in relation to specific linguistic processes, for example, semantic and syntactic analysis during sentence processing (for reviews see Hagoort and Brown, 1994; Osterhout, 1994). Manipulations of semantic variables, thereby, have consistently evoked a modulation of the so-called N400 component (Kutas & Hillyard, 1980), a negative deflection peaking approximately 400ms after stimulus onset. Although, the N400 component was originally observed in response to semantic anomalies (Kutas & Hillyard, 1980), subsequent studies have reported N400 modulations in response to semantic priming and found that the amplitude of the N400 was inversely related to the cloze probability\textsuperscript{13} of a word in a sentence (Kutas & Hillyard, 1984). Furthermore, the N400 component is sensitive to category membership and is elicited whenever a presented word does not fit into the context of a particular category, established either by lists of words (Polich, 1985) or by sentences (Kounios & Holcomb, 1992; Fischler et al., 1983). Interestingly, the N400 is not modulated by the truth value of a sentence itself but is predominantly sensitive to the relatedness between subjects and predicates within the sentence. In addition to category membership, the N400 is also modulated by the associative strength between a category and exemplars, as stronger N400 deflections have been observed for atypical exemplars compared to typical exemplars (Fujihara, Nageishi, Koyama, & Nakajima, 1998; Heinze, Muente, & Kutas, 1998). Taken together, these results suggest that the N400 amplitude is modulated by the degree of semantic relatedness and has been repeatedly reported in experiments studying semantic categorisation effects.

The early central effect reported in this study appears to be an N400 effect as the temporal and spatial distribution of this effect is in agreement with the

\textsuperscript{13} The cloze probability of a word refers to the frequency with which a word is chosen to complete a particular sentence.
characteristics of the N400 effect. In addition, the pattern of activity (revealing more negative going deflections for non-semantic compared to semantic word pairs) is in consonance with the eliciting conditions of the N400 effect, which is reported to be sensitive to category membership, revealing a negative deflection to words that do not fit into the context of a particular category. Hence, the difference in the early central effect reported in this experiment most likely reflects the modulation of the N400 component, highlighting a difference in semantic processing between the non-semantic and semantic word pairs. Interestingly, this N400 component in the present study was not modulated by response accuracy within the semantic classification task, suggesting that irrespective of correctly or incorrectly identified semantic relations the N400 component exhibited a more negative going deflection for non-semantic compared to semantic word pairs. This supports the view that the N400 component indexes an automatic process of semantic analysis which does not directly reflect the explicit classification decision performed by the subjects.

In contrast to the early central effect it is more challenging to relate the later parietal effect to an existing ERP component. The main difficulty lies in matching the pattern of activity associated with the parietal effect to the multitude of proposed components revealing comparable spatial and temporal distributions but distinct functional interpretations. The following section briefly summarises ERP components containing spatial and temporal distributions overlapping with the parietal component identified here.

5.5.2 The later parietal effect and the P600/P300

Consistent with the linguistic view that semantic processing is distinct from syntactic processing, researchers have reported ERP components related to syntactic manipulations, labelled as either P600 or Syntactic Positive Shift (SPS), which in the following will be referred to as the P600. A multitude of syntactic anomalies have been identified to elicit a positive going deflection at around 500ms following the onset of an anomalous word and persisting for several hundred milliseconds over centro-parietal scalp regions (for review, see Osterhout et al., 1997). The amplitude of the P600 is inversely related to the syntactic congruency between a target word
and the preceding sentence and is elicited, for example, by anomalies involving number and gender agreements, phrase structure, verb subcategorisation, verb tense and case.

This P600 is clearly distinct from the N400 as the two components are temporally and spatially dissociable. Less clear, however, is the relationship between the P600 compared to the family of P300 components. The P300 is elicited by a variety of attended, task-relevant stimuli (for review, see Dochin, 1981) and its amplitude is modulated for items whose properties deviate from the preceding stimuli (Johnson, 1993). A variety of studies have associated the P300 with a range of cognitive processes such as decision making, target selection, sensory discrimination and match-mismatch processing (for review, see Picton, 1992). Careful comparisons across different experiments, however, revealed that the P300 is not a unitary component, but is divided into at least three subcomponents each generated by different neuronal sources (Johnson, 1993; Johnson, 1989; Sutton & Ruchkin, 1984).

These three subcomponents are characterised by a fronto-centrally distributed P3a (Squires, Squires, & Hillyard, 1975), a centro-parietally distributed P3b, and a later and long lasting positive slow wave (Squires et al., 1975). The P3b component, in particular, has attracted a lot of attention and is predominantly reported to reflect a broadly distributed positive going component that onsets at about 500ms post stimulus with a centro-parietal maximum. The P3b amplitude is sensitive to stimulus properties such as task relevance/difficulty, salience and probability (Donchin & Coles, 1988), favouring the functional interpretation of uncertainty resolution or task-relevant surprise effects evoked by novel stimuli. In more general terms, the P300, and the P3b in particular, are thought to reflect brain activity indexing the update of a context maintained in working memory (Donchin et al., 1986). The basic idea underlying this context updating hypothesis is that if attributes of presented stimuli do not change compared to their preceding stimuli, a general neuronal code representing the stimuli is maintained. If, however, a change in attributes occurs, attentional mechanisms are engaged to update the neuronal stimulus representation, which elicits a P3b.
The topographical and functional characteristics of the P3b reflect striking similarities with the previously introduced P600, as both components are broadly distributed over centro-parietal areas and occur at around 500ms after stimulus onset. Moreover, a commonality in eliciting conditions can be described as the perception of unexpected but task relevant events, insofar as the word that makes a sentence ungrammatical is relatively rare and unexpected. Thus, while some researchers consider the P600 to reflect a language specific brain response (Osterhout et al., 1997; Osterhout et al., 1996), others support the proposal that the P600 is in fact a member of the P300 family. The latter proposal is also known as the identity thesis (Coulson et al., 1998b). Although there are several ways to examine the distinctiveness of two brain responses (for example by comparing their scalp distributions, assessing the influence of a particular task manipulation, or testing for additive effects between components) to date there is little consensus in the debate as to whether the P600 is a manifestation of the P3b, or whether the P600 reflects an independent but language specific component (Osterhout, 1999; Coulson et al., 1998b; Coulson, King, & Kutas, 1998a; Osterhout et al., 1997).

Irrespective of this debate, the P600 and P3b component are both associated with a temporal and spatial distribution similar to the later parietal component observed in the present study. The experimental paradigm in the current study does not involve sentences or encourage the encoding of word pairs in the context of sentences. Thus, it is unlikely that the experimental stimulus material would engage syntactic processing which therefore prohibits a functional interpretation in terms of syntactic violations as suggested by the linguistic P600 component. In contrast, the functional significance of the P3b is thought to reflect brain activity indexing the updating of context information maintained in working memory (Donchin et al., 1986).

It seems reasonable therefore to interpret the parietal component reported in the present experiment as a modulation of the P3b. As summarised previously, a number of different eliciting conditions have been reported in relation to the P3b component that indicate differences in presentation probability. In the present experiment non-semantic word pairs were twice as likely to occur as semantic-two or
semantic-one word pairs, which occurred with equal probability. Nevertheless, the obtained parietal effect can not be explained by the differences in presentation probability between stimulus conditions precisely because the semantic-one and semantic-two conditions occur with an equal probability but demonstrate significant modulation of this effect.

More likely, however, is the prospect that the semantic classification task performed across the three stimulus conditions places different processing demands on working memory and attentional mechanisms. For instance, all three stimulus conditions necessitate an active maintenance of the category word in working memory to enable the semantic classification of the subsequent word pair. The actual evaluation process of semantic relatedness, however, may engage different working memory and attentional mechanisms. For example, variations could arise because semantically related pairs can be successfully integrated into the categorical context, while this is not the case for non-semantic pairs. Such integration may place higher demands on working memory, indexed by more positive going deflections over parietal electrode sites. This interpretation is supported by the finding that only correctly identified semantic pairs elicit a more positive going ERP deflection over parietal locations. Thus, when the semantic pairs are identified as such, additional integration processes are recruited to relate the individual words into a coherent context. By this view, since the semantic-one condition contains only one semantically related word, the contextual integration process is reduced and evokes a diminished positive deflection over the parietal area compared to semantic-two conditions.

Although, an interpretation in terms of contextual integration is able to account for the reported pattern of parietal activity, this interpretation has to be treated with caution as it reflects a post-hoc explanation of the data. It is important, for example, to note that the reaction time data in the semantic classification task are significantly longer for non-semantic compared to semantic word pairs, possibly indicating higher processing demands for non-semantic pairs. Nevertheless, such increased processing demand could reflect the unsuccessful attempt of performing contextual integration, evoking prolonged reaction times in the semantic
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classification task. Consequently, this interpretation implies that the parietal positivity is only elicited for successful integrations, which is in line with the absence of the effect for incorrectly identified semantic pairs.

5.5.3 The late frontal effect

Finally, the third effect that was modulated by the different semantic stimulus conditions occurred at about 1000ms post stimulus onset and revealed a stronger positive deflection for semantic-one compared to semantic-two or non-semantic conditions. Previous studies have repeatedly reported a late frontal ERP effect of similar latency and topography in studies investigating memory processes including source memory (Senkfor & Van Petten, 1998; Wilding & Rugg, 1997; Wilding & Rugg, 1996), associative recognition (Donaldson & Rugg, 1998), simple old/new decisions (Allan & Rugg, 1997) as well as across different study material (Schloerscheidt & Rugg, 2004; Mecklinger & Meinshausen, 1998; Schloerscheidt & Rugg, 1997). This late frontal effect is often observed over the right hemisphere, eliciting more positive going deflections to old compared to new items during episodic memory tests. Although the exact meaning and potential dissociations of this right frontal old/new effect is still a subject of ongoing research it is thought to reflect post-retrieval monitoring operations and strategic evaluation processes for certain kinds of retrieved information (Wilding, 1999).

In the same spirit, it is possible to hypothesise that the late frontal ERP effect in the present study may reflect strategic evaluation processes. Although, the semantic classification task employed here did not engage episodic retrieval per se, information had to be accessed from semantic memory and a semantic judgement had to be performed upon the retrieved information. When adopting this functional interpretation of the late frontal effect, the data suggest that operations of strategic evaluation were less involved for non-semantic and semantic-two word pairs compared to semantic-one pairs. This could reflect the fact that the classification of semantic-one pairs was more difficult because category congruent as well as incongruent information are presented within those pairs.

In sum, the first stage of analysis provides supporting evidence that pre-existing semantic knowledge of to-be-encoded material does indeed alter the pattern
of encoding process engaged. A modulation in the N400 component occurred between non-semantic and semantic word pairs suggesting that non-semantic pairs violate semantic expectations generated by the preceding category word. Subsequent to the N400, neuronal activity appeared over parietal areas, which was interpreted to reflect contextual integration processes based upon attentional and working memory operations. Contextual integration was more successful for semantic-two compared to semantic-one word pairs, but least successful for non-semantic pairs, as reflected by the graded positivity over the parietal location. Finally, a late frontal component, thought to index strategic evaluation processes, revealed a more positive going ERP waveform for semantic-one compared to semantic-two or non-semantic word pairs. This modulation might be elicited because semantic-one word pairs are difficult to classify, since they contain category congruent as well as incongruent information. In general, although these findings suggest that the encoding process is sensitive to the type of semantic material, the critical question of whether subsequent storage and retrieval processes might be affected by such differences in encoding activity remains unanswered. Therefore a second stage of analysis was performed to investigate whether differences in encoding activity impact upon successful memory performance.

5.5.4 Subsequent memory effects across semantic stimuli

As outlined in the introduction, previous studies have identified two distinct classes of subsequent memory effects. One is elicited at about 300-800ms after stimulus onset with a centro-parietal distribution, while the second one occurs at a similar latency over frontal scalp regions (for reviews see Friedman, 1990; Paller and Wagner, 2000). Although, it is likely that these two subsequent memory effects are associated with distinct functional aspects of memory encoding, the precise cognitive process supporting these Dm effects are currently not well understood. Nevertheless, complementary neuropsychological and neuroimaging studies support the view that the parietal Dm effect may reflect modulations in neuronal activity generated by the medial temporal lobe (MTL) (Fernandez & Tendolkar, 2001), while the frontal Dm effect appears to be linked to activity in the prefrontal cortex (PFC) (Kounios et al.,
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2001; Duezel et al., 1999; Knight, 1984). Taking into account the functional role these neuroanatomical areas play in memory processing, the parietal Dm effect is inferred to reflect operations related to the formation of declarative memories and appears to be positively related to episodic encoding demands (Paller, 1990). The frontal Dm effect, however, is thought to index operations that support effortful encoding, as larger frontal effects occur for elaborative compared to rote encoding (Fabiani et al., 1990) as well as for deep compared to shallow encoding (Sanquist et al., 1980).

The subsequent memory paradigm employed for semantic and non-semantic stimulus conditions in the present study revealed only a parietal subsequent memory effect for semantic stimuli. Surprisingly, this effect was of reversed polarity compared to previously reported subsequent memory effects. However, potential differences in task demand between intact and rearranged test conditions may account for this reversal, which raises questions about the nature of the information that was retrieved, and which lead to incorrect classifications more prominently for semantic relative to non-semantic word pairs.

Dual process theories attribute the failure of correctly rejecting rearranged word pairs to the process of familiarity (Yonelinas, 2002). Consequently, incorrectly identified semantic and non-semantic pairs tested under rearranged conditions are supported by familiarity-based retrieval. Nevertheless, solely semantic pairs show significant signs of differences in encoding, indexed by a positive deflection over parietal areas, which predicts and possibly even facilitates subsequent retrieval based on familiarity. The hypothesis that differences in encoding activity may facilitate subsequent familiarity processing of semantic pairs is supported by the finding that significantly more false alarms were observed for semantic compared to non-semantic pairs. Hence, semantic pairs are associated with different encoding activity compared to non-semantic pairs, which results in subsequent superior familiarity processing for semantic pairs. As rearranged pairs elicit significantly higher proportions of false alarms compared to intact pairs, the parietal positivity of the subsequent memory effects is assumed to primarily reflect activation evoked by rearranged test conditions.
5.5.5 Subsequent memory effects across test conditions

A second set of subsequent memory analysis tested this assumption by separating intact and rearranged test conditions. While rearranged test conditions revealed a subsequent memory effect over parietal locations, no such differences were obtained for intact pairs. This confirms that the parietal positivity reported in the previous analysis is primarily driven by the rearranged test conditions. If encoding of semantic pairs enhances subsequent familiarity processing, as hypothesised here, it may be expected that parietal differences should also occur for intact pairs. However, correctly identified semantic and non-semantic word pairs revealed no significant parietal modulations under intact conditions. This could be explained by the fact that recognition responses to intact pairs engage retrieval based on familiarity and recollection. Hence, the relative contribution of familiarity in the intact test condition may not have been sufficient to detect subsequent memory differences between semantic and non-semantic pairs.

Intact pairs did however reveal subsequent memory effects over frontal locations. This effect was absent in the subsequent memory analysis contrasting stimulus conditions, suggesting that those items that engage increased frontal activity during encoding, whether semantic or non-semantic, are likely to be better recognised in a subsequent memory test. Such enhanced frontal activity is likely to reflect more elaborative encoding of individual stimuli.

In sum, the subsequent memory analysis contrasting semantic test conditions demonstrated differences in the parietal Dm effect. Analyses across different test conditions, however, showed that this parietal effect is predominantly elicited by rearranged but not intact test conditions. Thus, the parietal Dm effect for incorrectly identified rearranged word pairs is interpreted as indexing the likelihood that familiarity based retrieval processes are subsequently engaged. This likelihood differs between semantic and non-semantic pairs, predicting more familiarity based processing for semantic compared to non-semantic pairs. Additionally, a frontal subsequent memory effect was elicited in intact test conditions over frontal scalp locations, which is likely to reflect more elaborative encoding for subsequently correctly remembered items.
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5.6 Summary and Conclusion

In general, the present study provides evidence that the presence vs. absence of pre-existing semantic knowledge within to-be-encoded information alters the pattern of process engaged at encoding. During encoding an early automatic process indexed by the N400 component dissociates semantically congruent from incongruent information. Subsequent contextual integration operations, reflected by parietal activity, relate semantically congruent material, which has been consciously identified as such, into a coherent episode. In contrast, contextual integration processes are less effective in combining incongruent information, and these stimuli are therefore associated with less parietal activity. Since the encoding procedure employed in the present experiment required a semantic judgement, differences in electrical activity reflecting operations of strategic evaluation were observed over late frontal scalp regions. Word pairs containing one semantically related and one semantically unrelated word showed the highest demand for strategic evaluation operations.

Subsequent memory analyses demonstrated differences in Dm effects between semantic and non-semantic word pairs over parietal scalp locations. Incorrectly identified rearranged test conditions, which are supported by familiarity-based retrieval processes, revealed more positive going Dm effects for semantic compared to non-semantic pairs. This subsequent memory effect reveals a striking similarity to the parietal component indicating contextual integration during encoding. It may well be that this parietal activity during semantic encoding facilitates the positive deflection obtained in the Dm effect. Speculatively, it may be suggested that because the parietal Dm effect relates to familiarity based retrieval, the parietal encoding activity may equally relate to encoding mechanisms specifically supporting familiarity. Even for topographically identical components, however, ERP data per se do not permit the inference that two components are generated by the same neuronal source. Therefore, complementary neuroimaging and neuropsychological investigations are required to substantiate this proposal.
6 Retrieval of semantic relations

6.1 Introduction

A considerable controversy over the cognitive and neuronal organisation of declarative memory has emerged from research into the processes underlying encoding, storage and retrieval of information. As reviewed earlier (Chapter 2), the majority of neuropsychological and neuroimaging work to date supports the multiple memory systems account (Tulving, 1983; Tulving, 1972). Tulving proposed the fractioning of declarative memories into two distinct types of memory: episodic and semantic. Episodic memories, thereby, contain personally experienced events, which are accessed either on the basis of familiarity (feeling of previous encounter) or recollection (retrieval of detailed information), according to dual-process theories (Yonelinas, 2002).

Semantic memories, by contrast, hold general, culturally shared knowledge about the world such as the meaning of symbols, objects, concepts or facts. Semantic memory loss has been observed in many distinct neurological patient groups with very different lesion profiles. Depending on the precise locus of the damage it has been shown that some types of information are impaired to a greater extent than others. Selective deficits regarding knowledge of people, names, faces, building, living or non-living things are reported in the literature (Thompson-Schill, 2003; Warrington & McCarthy, 1987; Warrington & McCarthy, 1983). Those findings give insight into how semantic knowledge is represented and stored in the brain and has furthered our understanding by suggesting that the semantic system is organised in a category specific manner.

The relationship between episodic and semantic memory is highly controversial and the question of whether these two memory systems are cognitively and neurally dissociable has received a lot of attention (Graham et al., 2000; Squire & Zola, 1998; Tulving, 1995; Tulving, 1983). Recent evidence favours the view that semantic and episodic memories are supported by two functionally independent systems (Temple & Richardson, 2004; Graham et al., 2000; Vargha-Khadem et al., 1997). Although this evidence suggests that episodic and semantic memories are in
principle dissociable, it is possible that both types of memory function in concert or even interact with each other in normal cognition. Surprisingly few studies have addressed such potential interactions directly. It remains unclear, for instance, whether the category specific organisation of the semantic memory system has any consequence for the interaction between episodic and semantic memory. Furthermore, it is not known whether primarily familiarity or recollection based retrieval would mediate a potential influence of semantic memories on episodic retrieval.

Thus, to investigate these issues the following study sets out to examine the interaction between episodic and semantic memory by manipulating the semantic coherence of to-be-remembered information. The experimental design requires the retrieval of categorically related vs. unrelated word pairs during an associative recognition test. Neuroimaging (event-related potentials) and behavioural (process dissociation procedure) measures are used to provide convergent evidence that semantic memory does in fact influence episodic retrieval.

6.2 Material and Methods

6.2.1 Participants

The same group of participants as described in the previous chapter (Chapter 5) performed the recognition memory task presented in this study. Seven out of the twenty two participants who performed the ERP study had to be excluded due to either technical failure or EEG artefacts. The remaining 15 (6 female) participants had an average age of 24 years. An additional 12 participants (8 females, mean age 21) performed a follow up behavioural study using the Process Dissociation Procedure.

6.2.2 Material

Exactly the same material as described in the previous chapter was employed in the current recognition memory task (see Section 5.2.2).
6.2.3 Procedure

The experimental procedure is already described in the methods section of the previous chapter (Section 5.2.3). This procedure was followed by a behavioural study based on the Process Dissociation Procedure, PDP (Jacoby, 1991), allowing estimates of the contribution of familiarity and recollection to be calculated based on differences in performance in ‘exclusion’ and ‘inclusion’ tests. The ERP paradigm was an exclusion test, in which rearranged pairs had to be excluded as non-targets. The inclusion test is identical to this exclusion test with exception of the task instructions given to participants. In the inclusion version an ‘old’ response is required for intact and rearranged word pairs (target trials), while a ‘new’ response is required only for new word pairs (non-target trials).

By comparing performance on exclusion and inclusion tasks PDP provides estimates of the contribution of recollection and familiarity. PDP estimates are based on the assumption that an ‘old’ response to recombined pairs is given in the inclusion task when either the pair was recollected (R) or when the pair was familiar (F) in the absence of recollection (1-R), i.e.: prob. (old | inclusion)=R + (1-R)F. In contrast, an ‘old’ response to recombined pairs in the exclusion task should only be evoked by familiarity (F) in the absence of recollection (1-R), i.e.: P (old | exclusion)=(1-R)F. Recollection of the precise pairing in the exclusion task would lead to a correct rejection of the recombined pair. These processing differences for inclusion and exclusion responses allow the derivation of the following estimates for familiarity and recollection:

\[
\text{Recollection} = P(\text{old} | \text{inclusion}) - P(\text{old} | \text{exclusion}).
\]

\[
\text{Familiarity} = \frac{P(\text{old} | \text{exclusion})}{(1-R)}.
\]

Inclusion and exclusion experiments are typically performed within participants, to avoid differences in response bias across tasks and to allow statistical analysis of the resulting estimates. An additional behavioural experiment was therefore carried out to obtain PDP estimate of familiarity and recollection using the
same stimuli as in the ERP study. Only two changes were made from the original paradigm. First, subjects performed both inclusion and exclusion versions of the experiment, as outlined above; task order was counterbalanced across participants. Second, because two tasks were being performed by each participant rather than one, the number of inclusion and exclusion trials was reduced by half (leaving the total number of trials the same).

6.2.4 ERP recording and analysis

The recording technique used to collect the ERP data was outlined in chapter 5. In contrast to chapter 5 the current study focussed on the examination of ERP old/new effect associated with the retrieval of semantic and non-semantic word pairs. This difference in focus necessitated a different analysis strategy.

ERPs were formed for correct responses to intact and new word pairs. ERP analyses were designed to investigate the pattern of old/new effects in the semantic and non-semantic conditions, revealing any differences in the engagement of the generators of the left parietal and early frontal ERP old/new effects. ERPs to rearranged pairs were not examined because there were insufficient artefact free trials in this condition. Based on previous findings and visual inspection of the waveforms, data were analysed over 4 consecutive time windows (300-600ms, 600-900ms, 900-1200ms and 1200-2000ms). The first two time windows capture the ERP correlates of familiarity and recollection; the early frontal and left parietal old/new effects. As other late-onsetting old/new effects have been reported, the later time windows were also included in the analysis. All statistical tests were based on the criteria described in section 5.2.4.
6.3 Results at retrieval

6.3.1 Behavioural data

Figure 6-1 shows the probability of a correct response (bars) for intact, rearranged and new word pairs, along with associated reaction times (lines). The data are shown separately for semantic and non-semantic word pairs, demonstrating a clear improvement in recognition performance for semantically related compared to unrelated pairs. Importantly, analysis revealed that participants were able to discriminate between the different types of word pair in both conditions (paired t-tests comparing hits (intact) vs. false alarms (rearranged), and hits (intact) vs. false alarms (new) were significant (p<0.001) in all comparisons).

Old/new discrimination accuracy \[\text{Pr} = \text{Hit} – \text{FA}\] and response biases \[\text{Br} = \frac{\text{FA}}{1 - \text{Pr}}\] were computed for semantic and non-semantic conditions, whereby Hit is the probability of ‘old’ response to an intact pair, and FA is the probability of an ‘old’ response to a new pair. Discrimination accuracy was significantly better for the semantic (0.48) than non-semantic (0.29) conditions (t(14)=4.68, p<0.001). Similarly, response bias was significantly higher for the semantic (0.56) than non-semantic (0.41) conditions (t(14)=3.77, p<0.05). The two high threshold model might not provide a suitable fit for the target/new discrimination, as it assumes discrete ‘states’ of remembering. Participants are thought to either remember that word pairs were studied in the combination presented at test, or they remember that pairs were studied in a different combination or they fail to remember and guess. The signal detection theory offers an alternative approach that does not assume the adoption of discrete ‘states’ of knowledge. Thus, a measure of response bias based on detection theory was also calculated. The pattern of results remained the same, however with a more liberal response bias for the semantic condition. Whether this difference in performance for semantic and non-semantic pairs is reflected in the ERP data will be discussed later.
Figure 6-1 Mean (and standard error) probability of a correct response (bars) and mean (and standard error) reaction times (lines) during the test phase, shown for intact, rearranged, and new word pairs. Participants were required to only respond old to intact pairs. Responses are shown separately for the semantic (red) and non-semantic (blue) conditions, indicating a clear enhancement in recognition of intact pairs for the semantic compared to non-semantic condition.

The statistical analysis of the behavioural data was performed with an ANOVA including the factors of relationship (semantic, non-semantic) and pairing (intact, impaired, new). Results revealed a significant main effect of pairing \( [F(2,28)=21.31, p<0.001] \), no main effect of relationship \( [p>0.05] \), but a significant interaction between relationship and pairing \( [F(2,28)=33.82, p<0.001] \). As Figure 2 shows, intact pairs were better remembered when semantically related \( (t(14)=7.56, p<0.001) \). By contrast, rearranged pairs were more difficult to reject when semantically related \( (t(14)=4.38, p=0.001) \), and new pairs were equally well rejected in the semantic and non-semantic conditions \( (p>0.05) \).

Reaction time data is shown in Figure 6-1 (lines), revealing no clear influence of the manipulation of semantic relatedness. An ANOVA testing the factors of relatedness (semantic, non-semantic) and pairing (intact, impaired, new) revealed no significant main effects or interactions \( [p>0.05 \text{ in all cases}] \). Nonetheless, the behavioural results clearly demonstrate that semantically related word pairs were better remembered than unrelated pairs.
Confidence ratings for the semantic and non-semantic pairs were also compared. The analysis tested whether the memory advantage for semantic vs. non-semantic intact pairs is carried solely by the ‘high confidence old’ ratings, which are expected to reflect recollection in addition to familiarity, or by ‘middle range confidence old’ (i.e., 2 to 4) ratings, which just indicate the contribution of familiarity. The probability of confidence ratings for all semantic hits was contrasted with the probability of confidence ratings for all non-semantic hits. An ANOVA with the factors of condition (semantic, non-semantic) and confidence rating (ratings 1-5) for correctly identified intact pairs revealed a main effect of condition \([F(1,14)=36.76; p<0.001]\), a main effect of confidence \([F(4,56)=11.23; p<0.001]\), and an interaction between confidence and condition \([F(4,56)=16.60; p<0.001]\), suggesting that the pattern of confidence ratings did vary across conditions. Importantly, a t-test confirmed that there was indeed an increase in confidence for the semantic compared to non-semantic condition at the middle range confidence category 4 \((t(14)=2.43, p=0.029)\). This difference did not reach significance for confidence category 2 and 3, but given the increase in category 4 ratings, it is likely that there was less opportunity for ratings at category 2 and 3. Nonetheless, this suggests that semantic pairs did attract more ratings in the middle range, particularly at higher confidence levels, reflecting stronger familiarity for semantic pairs. Finally, a t-test contrasting the ‘high confidence ratings’ also reveals increased confidence ratings for semantic pairs \((t(14)=6.32, p<0.001)\). Since familiarity as well as recollection is likely to contribute to ‘high confidence ratings’ it is difficult to determine which process is accountable for this difference. Nevertheless, semantic pairs were associated with a shift in confidence ratings towards medium and higher values consistent with an increase in either familiarity alone, or familiarity and recollection.
6.3.2 ERP data

Grand average ERPs for correct responses to intact and new word pairs are shown for the semantic condition in Figure 6-2 (for a detailed illustration of particular electrodes see Figure 6-3), and for the non-semantic condition in Figure 6-4 (for enlarged illustration of specific electrodes see Figure 6-5). The mean number of trials contributing to the intact and new waveforms were 32 and 29 for semantic, and 24 and 31 for non-semantic.

![Figure 6-2](image-url) Grand average ERPs for semantic word pairs. ERPs are shown for correct responses to intact (red) and new (black) word pairs, differences between the waveforms revealing a characteristic pattern of ERP old/new effects, with a early frontal ERP effect followed by a strong left parietal effect.
Figure 6-3 Grand average ERPs elicited for correctly recognised intact (red) and correctly rejected new (black) semantic stimuli. The frontal electrodes show more positive going deflections for intact compared to new stimuli, onsetting at about 300ms post stimulus. Parietal electrodes also reveal more positive going activity for intact compared to new stimuli, showing considerable modulations between 600 and 900ms.

Figure 6-2 and Figure 6-4 show that the ERPs evoked in both semantic and non-semantic conditions are more positive going for intact compared to new word pairs from around 300ms. The old/new effects are initially bilaterally distributed and largest over frontal electrodes for the semantic condition, with a more central focus for the non-semantic condition. From around 600ms however, the positive shift for intact pairs exhibits a clear left parietal maximum in both conditions. The intact and new waveforms converge around 900ms, but differences appear to remerge from around 1200ms onwards. To characterise the pattern of old/new effects for each condition average voltages were calculated over four consecutive epochs (300-600ms, 600-900ms, 900-1200ms, 1200-2000ms), at 4 separate locations, representing average activity over 3 electrodes: left-frontal (LF: F1, F3, F5), right-frontal (RF: F2, F4, F6), left-parietal (LP: CP1, CP3, CP5), and right-parietal (RP: CP2, CP4, CP6), as illustrated in Figure 6-6A.
Figure 6-4 Grand average ERPs for non-semantic word pairs. ERPs are shown for correct responses to intact (blue) and new (black) word pairs, exhibiting a different pattern of ERP old/new effects compared to those seen for semantic word pairs. Whilst a clear left parietal effect is present, there is little evidence of an early frontal ERP effect.

Figure 6-5: Grand average ERPs elicited for correctly recognised intact (blue) and correctly rejected new (black) non-semantic stimuli. Parietal electrodes demonstrate more positive going activity for intact compared to new stimuli predominantly between 600 and 900ms.
6.3.3 ERP analyses

An initial high-level analysis was designed to identify whether old/new effects varied across conditions and epochs, using ANOVA with the factors of condition (semantic, non-semantic), epoch (300-600ms, 600-900ms, 900-1200ms, 1200-2000ms), old/new (intact, new), location (frontal, parietal) and hemisphere (left, right). Results revealed significant ERP old/new effects; a main effect of old/new \[ F(1,14)=8.41, p=0.012 \], a 2-way interaction between old/new and location \[ F(2.67,37.35)=7.5, p=0.001 \], and three 3-way interactions between condition, epoch and old/new \[ F(2.18,30.5)=5.01, p=0.011 \], epoch, old/new and location \[ F(2.50,34.93)=4.3, p=0.016 \], and old/new, location and hemisphere \[ F(1,14)=4.75, p=0.047 \]. The presence of significant interactions involving factors of both old/new and epoch strongly suggests that a changing pattern of old/new effects exists over the four epochs, varying across the semantic and non-semantic conditions, and varying across frontal and parietal locations.

![Figure 6-6](image-url) Schematic of the recording montage and analysis strategy. Filled electrodes are used in specific analyses. A: ERP analyses investigating the early frontal ERP old/new effect and left parietal old/new effects were performed over four regions, each representing average activity over 3 electrodes: left-frontal (LF: F1, F3, F5), right-frontal (RF: F2, F4, F6), left-parietal (LP: CP1, CP3, CP5), and right-parietal (RP: CP2, CP4, CP6). B: ERP analysis investigating N400 effects included electrodes located in two rings, each containing 8 electrodes (Inner Ring: FCZ, FC2, C2, CP2, CPZ, CP1, C1, FC1; Outer Ring: FZ, F4, C4, P4, PZ, P3, C3, F3), allowing the central maximum of the effect to be identified.

To further investigate the pattern of old/new effects, a second level of analysis was performed on the data from each epoch, using ANOVA with the factors of old/new (intact, new), location (frontal, parietal) and hemisphere (left, right). This
analysis aimed to demonstrate whether old/new effects were present within each epoch. The results presented in Table 6-1 show in both of the early epochs the factor of old/new interacts with location (albeit marginally significant for the first epoch), suggesting that the pattern of old/new effects varies at frontal and parietal electrodes. This pattern of results is consistent with the presence of an early effect over frontal scalp, and a later effect (which varies by hemisphere) over parietal scalp. To demonstrate that this is indeed the case, and to investigate whether these old/new effects differ across semantic and non-semantic conditions, a final set of analysis was performed separately at frontal and parietal locations during the 300-600ms and 600-900ms epochs. These data are highlighted in Figure 6-7.

<table>
<thead>
<tr>
<th>Old/New effects</th>
<th>300-600</th>
<th>600-900</th>
<th>900-1200</th>
<th>1200-2000</th>
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<tr>
<td>Old/New</td>
<td>&lt;0.05</td>
<td>&lt;0.05</td>
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<td>Old/New by Loc</td>
<td>0.071</td>
<td>&lt;0.05</td>
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<tr>
<td>Old/New by Loc by Hem</td>
<td>-</td>
<td>&lt;0.05</td>
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Table 6-1 Statistical analyses of the old/new effects. Results of ANOVA with the factors of old/new (intact, new), location (frontal, parietal) and hemisphere (left, right) over four successive time windows. The data reveal significant old/new effects during the 300-600ms and 600-900ms epochs, but not for the later two time windows. In both of the early epochs the old/new effects interact with location, suggesting that the pattern of old/new effects varies at frontal and parietal electrodes.

Analysis of the data from 300-600ms employed ANOVA with the factors of condition (semantic, non-semantic), old/new (intact, new) and hemisphere (left, right). Analysis at frontal electrodes revealed a significant main effect of old/new [$F(1,14)=20.32$, $p<0.001$], and an interaction between old/new and condition [$F(1,14)=6.30$, $p=0.025$]. As Figure 6-7 shows, old/new effects are present over frontal scalp sites from 300-600ms, and these effects are significantly larger for the semantic condition. This result was confirmed with an additional focused analysis (collapsed across frontal electrodes) that directly compared the magnitude of the old/new difference across conditions ($t(14)=2.45$, $p=0.028$). By contrast, analysis at
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parietal electrodes revealed a significant effect of old/new [F(1,14)=33.57, p<0.001] but no interactions. This pattern of results is important; it reveals differences in the old/new effects exhibited by semantic and non-semantic conditions only at frontal electrodes. The topographic distribution of the old/new effects are illustrated in Figure 6-8, highlighting a bilaterally distributed old/new effect over frontal locations for the semantic condition only, and a more posterior effect that is present for both the semantic and non-semantic conditions.

**Figure 6-7** Early frontal ERP old/new effect and left parietal old/new effects. A: Average ERP waveforms from left-frontal (LF: F1, F3, F5), right-frontal (RF: F2, F4, F6), left-parietal (LP: CP1, CP3, CP5), and right-parietal (RP: CP2, CP4, CP6) locations. The early frontal ERP old/new effect (300-600ms) is more pronounced for semantic compared to non-semantic conditions, while the left parietal old/new effect (600-900ms) is similar in both cases. B: Bar charts display the magnitude of the old/new effects (error bars show S.E.), averaged from the data shown in panel A. The early frontal ERP old/new effect (i) is significantly larger for the semantic compared to non-semantic conditions in the 300-600ms epoch. The parietal old/new effect (ii) found from 600-900ms reveals no reliable differences between the semantic and non-semantic conditions.
Analysis of the data from 300-600ms revealed significant old/new differences at centro-parietal locations, though these effects did not differ in the semantic and non-semantic conditions. This old/new difference is particularly visible in Figure 6-8 for the non-semantic condition, where there is little sign of additional overlapping frontally distributed effects. Examination of the waveforms (see Figure 6-4) suggests that, in this case, the difference appears to be restricted to a time window from 300-500ms and is largest over central electrodes. This pattern of old/new differences is consistent with a modulation of the N400 component, a negative going peak (maximal over central-parietal electrodes between 300 and 500ms post stimulus) which is known to vary with the ease with which the meaning of words can be integrated into a given context (for review see Kutas and Van Petten, 1994). To be clear, the N400 component (the negative going peak) is distinct from the N400 old/new effect (a modulation of the N400 component). Given the pattern of data shown in Figure 6-7 and Figure 6-8, it seems likely that the small frontally distributed old/new differences seen for the non-semantic condition most likely reflects residual spread of activity from the N400 old/new effects seen for intact pairs (where the words have already been integrated) compared to new pairs (where integration is required).

Based on the pattern of effects seen at central and frontal electrodes, two possible interpretations of the data exist. First, both the semantic and non-semantic conditions are associated with activity over frontal electrodes that reflect spread of activity from the N400 old/new effects, but that for the semantic condition this is overlaid with additional early frontal activation from a second more frontally distributed generator. Second, both the semantic and non-semantic conditions are associated with activity over frontal electrodes that reflect spread of activity from the N400 old/new effects, and the increased old/new effect at frontal electrodes in the semantic condition simply results from a spread of a stronger N400 old/new component, without the presence of any additional early frontal activation.

To discriminate between the two possibilities outlined above, additional analyses were performed on data from 300-500ms, over two rings of electrodes that capture the distribution of the N400 component (see Figure 6-6B). ANOVA were
performed with the factors of condition (semantic, non-semantic), old/new (intact, new), ring (inner, outer) and site (FCZ, FC2, C2, CP2, CPZ, CP1, C1, FC1 and FZ, F4, C4, P4, PZ, P3, C3, F3). Analyses revealed a significant effect of old/new \[F(1,14)=28.95, p<0.001\], a two way interaction between old/new and ring \[F(1,14)=27.51, p<0.001\] and a three way interaction between old/new, ring and site \[F(4.1,58.3)=3.35, p=0.014\]. These analyses a) confirm the characteristic distribution of the N400 component, maximal over a superior central ring of electrodes, b) demonstrate that the N400 component is modulated by the old/new status of the test items, and c) reveal that this modulation of the N400 component does not differ between semantic and non-semantic conditions. Thus, as can be seen in Figure 6-8, non-semantic word pairs reflect only a centrally distributed N400 old/new effect in the early time-window, whereas the semantic pairs reflect a comparable centrally distributed N400 old/new effect combined with an additional early frontal ERP old/new effect.

![Figure 6-8](image)

**Figure 6-8** Topographic distribution of the old/new effects. Each map represents the difference in activity between intact and new waveforms, averaged over time (300-600ms and 600-900ms). The topographical distribution in the early 300-600ms time window shows symmetric frontal activity in the semantic compared condition, compared to a more central parietal effect in the non-semantic condition. By contrast, in the 600-900ms time window the ERP old/new effects show a left parietal distribution, with no significant differences between the semantic and non-semantic conditions.
Data from 600-900ms were analysed using equivalent ANOVAs with the factors of condition (semantic, non-semantic), old/new (intact, new) and hemisphere (left, right). These analyses revealed no significant old/new effects over frontal electrodes, but a significant main effect of old/new \([F(1,14)=25.25, p<0.001]\) and a significant interaction between old/new and hemisphere \([F(1,14)=4.67, p=0.049]\) at parietal sites. As can be seen in Figure 6-7, these findings reveal that old/new effects are present from 600-900ms, exhibiting a left greater than right asymmetry characteristic of the left parietal old/new effect. Importantly, no old/new effects were present at frontal sites, and no differences were found between the old/new effects exhibited in the semantic and non-semantic conditions during the 600-900ms epoch. The topographic distribution of the left parietal old/new effects is shown in Figure 6-8 for both semantic and non-semantic conditions.

6.3.4 Topographic analyses

The pattern of results described above strongly suggests differences in the ERP old/new effects found for semantic and non-semantic conditions during the 300-600ms epoch. As Figure 6-7 and Figure 6-8 illustrate, an early frontal ERP old/new effect is present for the semantic condition, and this is not apparent for the non-semantic condition. Further, the results suggest a change in activity over time for the semantic condition, from an early frontal effect to a later left parietal effect. Additional topographic analyses were performed to confirm that this finding reflects a genuine qualitative difference in the pattern of neural generators engaged over time. Analyses were performed for the semantic condition on difference waveforms (intact minus new) from the 300-600 and 600-900ms epochs, using rescaled data (removing confounding effects of size). ANOVA with the factors of epoch, location and hemisphere revealed a significant 3-way interaction \([F(1,14)=10.08, p<0.01]\). This analysis confirms that the early frontal ERP old/new effect is statistically distinct from the later parietal effect, demonstrating the presence of two spatio-temporally dissociable memory processes.
6.3.5 Additional behavioural experiment

The additional within-subjects PDP experiment was designed to provide estimates of recollection and familiarity, and the behavioural data are therefore reported in brief (see Figure 6-9). Statistical analysis of the exclusion data revealed the same pattern of results as observed in the ERP experiment. ANOVA including the factors of relationship (semantic, non-semantic) and pairing (intact, impaired, new) revealed a significant main effect of pairing \([F(2,22)=18.87, p<0.001]\), no main effect of relationship \([p>0.05]\), but a significant interaction between relationship and pairing \([F(2,22)=14.22, p<0.001]\). As was the case for the ERP experiment, intact pairs were better remembered when semantically related \((t(11)=2.79, p=0.018)\) while rearranged pairs were more difficult to reject when semantically related \((t(11)=3.97, p=0.002)\).

The inclusion task also revealed differences in recognition performance for semantic and non-semantic word pairs. ANOVA with the factors of relationship (semantic, non-semantic) and pairing (intact, impaired, new) revealed a significant main effect of relationship \([F(1,11)=5.32, p=0.041]\) and a significant interaction between relationship and pairing \([F(2,22)=4.41, p=0.025]\). Intact pairs were better remembered when semantically related \((t(11)=2.11, p=0.059)\). In contrast to the exclusion task, rearranged pairs were associated with better performance for semantically related compared to unrelated pairs \((t(11)=3.91, p=0.002)\), as would be expected given the changes in task instruction.
Figure 6-9 Mean (and standard error) probability of a correct response (bars) and mean (and standard error) reaction times (lines) during the test phase, shown for intact, rearranged, and new word pairs. Participants were required to respond old to intact and rearranged pairs. Responses are shown separately for the semantic (red) and non-semantic (blue) conditions, indicating a clear enhancement in recognition of intact and rearranged pairs for the semantic compared to non-semantic condition.

6.3.5.1 PDP estimates

Based on the combined performance from the exclusion and inclusion studies, the process dissociation procedure (PDP) can be used to provide an estimate of the contribution of familiarity and recollection to performance. These data are illustrated in Figure 6-10, showing that familiarity estimates increased from 0.53 to 0.72 for non-semantic compared to semantic pairs, while estimates for recollection remained stable at 0.26 and 0.24 for non-semantic and semantic pairs. Clearly, the PDP data exhibit a considerable increase in familiarity from non-semantic to semantic conditions (0.19) but only a small difference in recollection (0.02). The PDP estimates were subjected to statistical analysis using an ANOVA with the factors of condition (semantic vs. non-semantic) and estimate (familiarity vs. recollection), revealing a main effect of condition [F(1,11)=7.35, p=0.02], a main effect of estimate [F(1,11)=11.62, p<0.01] and a significant interaction between condition and estimate [F(1,11)=14.23, p<0.01]. Subsidiary analysis confirmed a statistically significant increase in familiarity from non-semantic to semantic conditions (t(11)=6.13, p<0.001) and no significant difference in recollection (t(11)=0.48, p>0.05). Thus, consistent with the pattern of ERP effects, behavioural
estimates suggest that episodic retrieval is modulated by the manipulation of semantic versus non-semantic word pairs, and that this is driven primarily by changes in familiarity rather than recollection.

![Figure 6-10](image)

**Figure 6-10:** PDP estimates of familiarity and recollection. PDP estimates (mean and standard error) of familiarity and recollection are shown for the semantic (red) and non-semantic (blue) condition. The estimates, which are derived from the behavioural inclusion and exclusion experiments, demonstrate a significant difference between semantic and non-semantic conditions in familiarity but not recollection.

### 6.4 Summary

In sum, semantic and non-semantic stimuli exhibit significant differences in ERP activity for correctly identified intact and new test conditions in the first two time windows (300-600ms, 600-900ms). While both components reveal centrally distributed N400 components of equivalent magnitude, only the semantic condition exhibits an additional early frontal old/new effect. Topographical analysis confirmed that this early frontal old/new effect is based on a neuronal generator which is statistically distinct from a generator giving rise to a subsequent left parietal old/new effects emerging in the second time window (600-900ms). Both semantic and non-semantic conditions exhibit a significant left parietal old/new effect with no difference in magnitude across conditions. The remaining two time windows (900-1200ms, 1200-2000ms) failed to elicit further differences in ERP activity between intact and new test conditions for both semantic and non-semantic stimulus conditions.
6.5 Discussion

The present study investigated the functional and neural interaction between episodic and semantic memory in normal cognition. By manipulating whether word pairs were categorically related, the results demonstrated that associative recognition memory is enhanced for semantically coherent information. A second aim of this study was to establish whether this interaction produced changes in recollection or familiarity. The data revealed that the influence of semantic memory was to modulate the extent of familiarity based retrieval, leaving recollection relatively unaffected. In short, the findings presented here provide novel evidence for an interaction between semantic and episodic memory, demonstrating that the semantic organisation of information influences the engagement of episodic memory by modulating familiarity based retrieval.
6.5.1 Convergent evidence that manipulating semantic memory modulates familiarity

The results are particularly compelling because they reflect convergent behavioural and electrophysiological evidence. Estimates derived from the Process Dissociation Procedure (Jacoby, 1991) revealed a considerable increase in familiarity, alongside a negligible change in recollection. Whilst the behavioural findings are indirect, the neuroimaging data provide a direct record of the underlying neural activity associated with performance. As would be expected on the basis of previous findings (Donaldson & Rugg, 1999), the data provide clear evidence of significant left parietal old/new effects during associative recognition memory (see Figures 6 and 7). Importantly, however, there was no evidence for a significant difference in the left parietal old/new effect elicited by semantic and non-semantic word pairs; consistent with the behavioural data, ERPs revealed comparable levels of recollection. By contrast, the semantic and non-semantic conditions were dissociable on the basis of the early frontal ERP old/new effect, which was only present for the semantic condition. The ERP findings are particularly clear; the semantic and non-semantic conditions exhibited a selective modulation of the early frontal ERP old/new effect, suggesting that recognition of the semantic word pairs was enhanced due to an increase in familiarity.

Although the PDP and ERP findings both point towards the conclusion that semantic coherence influences familiarity rather than recollection, it is important to recognise that the reasons for reaching this conclusion are quite different in each case. Whilst the ERP findings are restricted to analysis of the intact pairs, the PDP estimates stem primarily from performance on the rearranged pairs (the likelihood of hits and false alarms to this class of stimuli during the inclusion and exclusion tasks respectively). In some respects the difference between these two measures is a strength: the two findings provide genuinely independent (yet convergent) evidence using methods that rely on very different assumptions. Nonetheless, drawing any direct correspondence between the ERP and PDP data relies on a strong assumption, namely that the selective familiarity advantage for rearranged pairs from the
6 Retrieval of semantic relations

semantic versus non-semantic condition seen in the PDP data also holds for the intact pairs in the ERP data.

To address this issue, and provide a more direct link between the behavioural and electrophysiological evidence, an additional examination of the confidence judgements made during the ERP task was carried out. Recollection is associated mostly with high confidence judgements, whereas familiarity typically covers a range of confidence judgements (Yonelinas, 2002; Yonelinas, 1997). If, as is assumed in this case, familiarity shows an increased contribution to intact semantic pairs compared to non-semantic pairs, this should be reflected in the pattern of confidence judgements. Consistent with this view, analysis of the confidence ratings revealed differences between semantic and non-semantic pairs for confidence ratings which are typically assumed to reflect responses based on familiarity. This finding adds weight to this conclusion, providing added behavioural evidence that the putative change in familiarity based responding is evident for both the rearranged and intact pairs. Given this confidence analysis, the ERP findings alone provide strong evidence for an increase in familiarity for the semantic, compared to non-semantic, condition.

6.5.2 Unitisation, bias and task difficulty

One potential objection to the current findings is that, traditionally, associative recognition tests are thought to require recollection (Mandler, 1991; Mandler, 1980; Atkinson & Juola, 1974), with familiarity playing little or no role in performance. Recent evidence suggests however that this is not always the case; familiarity can sometimes contribute to associative recognition. Yonelinas et al. (1999) demonstrated that familiarity can play a significant role in associative recognition if the separate elements of a stimulus are unitized into a single larger representation (e.g. complex stimuli such as faces can be familiar when processed as a whole, but not when processed in parts). The results present here are consistent with this view; enhanced performance and increased familiarity for the semantically coherent stimuli may reflect the benefits of unitisation. Caution is necessary in interpreting the findings in this way however, because the extent and limits of
unitisation are not well understood to date. For example, it is unclear what kinds of stimulus relationships support unitised representations, or whether a brief learning phase (as employed in the present experiment) would allow unitization of item-item associations to occur (see Mayes et al., 2004, for an argument that unitization is sufficient but not essential for an engagement of familiarity in associative recognition). Regardless, a unitisation account need not sit in opposition to the present interpretation of the data; rather, the unitisation hypothesis may offer an explanation of the way in which semantic memory influences episodic retrieval.

The findings are, of course, open to alternative interpretations. It could be argued that the current findings reflect little more than changes in either task difficulty or response bias. Were the lower levels of performance in the non-semantic condition, and thus the lower estimates of familiarity, simply due to increased task difficulty? Task difficulty is notoriously hard to define a priori, and is typically introduced as an a posteriori explanation of changes in performance. In the present case, although performance is poorer in the non-semantic condition overall (consistent with a change in difficulty), reaction times are not significantly different in the semantic and non-semantic conditions (suggesting no overall change in difficulty). More importantly, both the behavioural and ERP findings suggest that the manipulation of semantic coherence had a selective effect; unlike familiarity, recollection did not vary across condition. By contrast, a task difficulty account would predict changes in both familiarity and recollection, and not a selective change in familiarity.

An alternative interpretation of the obtained data is that the ERP findings reflect little more than the influence of response bias. As reported above, the behavioural data reveal a high response bias for semantic pairs and a low response bias for non-semantic pairs. How might bias influence the ERPs measured at retrieval? Perhaps the most straightforward view would be that changes in bias should directly influence the probability of responding old on the basis of familiarity (a more liberal bias leading to an increased likelihood of items being accepted as old on the basis of a lower level of familiarity). The data do, superficially, fit such a simple bias account; the more liberal bias found for the semantic condition was
associated with better performance and an increase in familiarity. Thus, assuming that changes in response bias exhibit more influence on familiarity than recollection, encountering a semantic relationship between the category name and word pair may have resulted in a relaxed criterion for responding ‘old’ overall, producing a change in the size of the early frontal old/new effect. From this perspective, the semantic condition is seen as being associated with increased familiarity based responding (as indexed by the early frontal old/new effect), but this is simply a consequence of changes in response bias.

Whilst a response bias account is plausible, it seems to be difficult to sustain. The presented data do not reveal a change in bias alone; the behavioural results show both a change in bias and a change in discriminability, with significantly higher discrimination in the semantic compared to non-semantic condition. Moreover, the behavioural results for the semantic and non-semantic conditions show no significant differences in false alarm rate. A full account of the data would therefore require an explanation that goes beyond response bias. Moreover, it is clear from previous findings that ERPs are sensitive to changes in response bias at frontal recording sites, but that the neural correlates of response bias may be distinct from those of familiarity, with the former seen only in responses to new items (cf. Johansson et al., 2004), or occurring in opposite directions for old and new items (cf. Windmann, Urbach, & Kutas, 2002). In the present case, careful examination of the data reveals that the change in the pattern of early frontal old/new effects across semantic and non-semantic conditions is driven by the old conditions (see Figure 6). Additional analysis comparing the magnitude of activity across the two correct rejection waveforms from 300-600ms at frontal electrodes revealed no significant difference between the semantic and non-semantic conditions (means of -2.1μV and -1.9μV respectively; F(1,14)=0.13, p>0.05). If the early frontal old/new effect was modulated by bias, this would be expected to be evident in the ERPs to correct rejections. Thus, although differences in bias are present across conditions, and this could theoretically underlie the change in familiarity that is seen, the obtained data can not be fully accounted for by a bias account. Finally, it should be noted that it does not matter a great deal for the central conclusion, which is that the change from
semantic to non-semantic conditions is associated with an increase in familiarity, rather than recollection. Whether this turns out to be associated with changes in unitisation, bias, task difficulty, or other factors, remains an interesting question to be investigated.

6.5.3 Dissociating the early frontal ERP old/new effect and N400 old/new effects

One important aspect of the presented data is the clear dissociation between the early frontal ERP old/new effect and the N400 old/new effect. The N400 component is typically seen in studies of language comprehension, and reflects the difficulty with which the meaning of words can be integrated with the current context (for review see Kutas & Van Petten, 1994). Given the manipulation, overall differences in the N400 component are to be expected in the semantic and non-semantic conditions (with a larger N400 for non-semantic compared to semantic pairs). Of more concern was the possibility that differences in the old/new effects across condition might simply have reflected a change in the pattern of N400 old/new effects. Modulation of the N400 component elicited by intact and new pairs (i.e., N400 old/new effects) are reasonable, as semantic integration for intact pairs (where words have already been integrated during study) is easier compared to new pairs (where additional integration is required). It was, therefore, critical that the observed N400 old/new effect did not vary across the semantic and non-semantic conditions. Any such difference would have suggested that the stimulus manipulation merely influenced the ease of semantic integration and not episodic retrieval itself.

The present findings are, consequently, significant in ruling out interpretations of the early frontal ERP old/new effect as nothing more than a reduction of the N400 component (e.g., as suggested by Yovel & Paller, 2004). In the present data changes in the N400 component (i.e., N400 old/new effects) occurred in both semantic and non-semantic conditions, exhibiting a temporal overlap with the early frontal ERP old/new effect. The early frontal ERP old/new effect was, however, only present in the semantic condition, and thus cannot reflect a
modulation of the N400 component per se. By contrast, the ERP data are, in principle, consistent with the possibility that the early frontal ERP old/new effect reflects summation of the N400 old/new effect with anterior fronto-polar effect (cf. Curran & Dien, 2003). This anterior fronto-polar effect is, however, associated with visual (perceptual) priming, and there seems little reason to expect differences in visual priming across our semantic and non-semantic conditions. Regardless, the present data clearly suggest that the early frontal ERP old/new effect is driven by a different neural source than that which underlies the N400 component.

Whilst the early frontal ERP old/new effect is interpreted here as reflecting familiarity, other studies have suggested that it reflects conceptual priming. One source of support for this view is the idea discussed above, that the early frontal ERP old/new effect is actually produced by an N400 reduction (Yovel & Paller, 2004), which the obtained data clearly militate against. In addition, in the current context a conceptual priming account would predict differences in the magnitude of the early frontal old/new effect between the semantic and non-semantic new pairs – the former are preceded by a semantically related category cue, but the later are not. Examination of the ERPs for correctly rejected new pairs revealed no differences over mid-frontal electrodes however, suggesting that the early frontal old/new effect is not elicited by conceptual priming. Moreover, evidence from normal (Wolk et al., 2004) and amnesic (Olichney et al., 2000) participants suggests that conceptual priming modulates the N400 component, separate from the early frontal ERP old/new effect. There are also clear examples of dissociations between conceptual priming and episodic memory retrieval using other neuroimaging methods (Donaldson, Petersen, & Buckner, 2001) and neuropsychological data (Levy, Stark, & Squire, 2004). Therefore, this interpretation of the data favours the view that, at least for verbal material, the conscious experience of familiarity and the unconscious activation associated with conceptual priming are both functionally and neurally distinct.
6.5.4 Multiple interactions between semantic and episodic memory

The findings presented in the current chapter stand in striking contrast to results from Levels Of Processing studies, which typically reveal an interaction between episodic and semantic memory that is driven largely by a modulation of recollection. For example, Rugg et al., (Rugg et al., 1998); see also (Rugg et al., 2000) measured ERP old/new effects during an LOP study (sentence generation vs. alphabetic judgement), and revealed a modulation of the left parietal effect but no change in the early frontal ERP old/new effect. In LOP studies the way in which information is processed is manipulated during learning. By contrast, the present study manipulated the type of information that had to be remembered, whilst holding processing demands constant. Thus, whilst changes in semantic processing during learning lead to a modulation of recollection, it appears that changes in the semantic coherence of material results in a modulation of familiarity. Of considerable interest is whether this result extends to other manipulations of semantic memory. Regardless, it is clear that the way in which semantic memory is manipulated has a critical impact on the interaction between episodic and semantic memory.

Neuropsychological and neuroimaging studies suggest that semantic knowledge is organised as categorical representations (Okada et al., 2000; for a review see Capitani, Laiacona, Mahon, & Caramazza, 2003). This type of organisation is observable neuroanatomically (Laiacona, Barbarotto, & Capitani, 1998; Warrington & McCarthy, 1983) and effects psychological processing, as demonstrated in semantic priming experiments (Collins & Loftus, 1975). The current findings suggest that this organisation of semantic knowledge has a significant impact on the normal functioning of episodic memory retrieval. The data go further, however, to suggest a mechanism that underlies this interaction in healthy subjects, namely familiarity. In general, familiarity can be interpreted as a consequence of the functional overlap amongst representations. Familiarity may arise when subjects become exposed to an item that matches (or largely overlaps with) previously stored representations. As mentioned above, semantic memory is categorically organised and items belonging to the same category are thought to share overlapping
representations. By this view it is plausible that the process of familiarity is particularly sensitive to the presence or absence of semantic relations between stimuli per se.

Finally, it is of interest to examine the consequences that different types of manipulation of semantic memory have on behaviour. The present study distinguished between manipulations of semantic content, which are inherent to the stimulus material and their representations, and manipulation of semantic context, which are dependent on the way stimuli are processed. In general, this difference might explain why processing manipulations in LOP studies (semantic deep vs. shallow encoding process) lead to recollection based interactions, while changes in material as applied in the current study (categorically related vs. unrelated word pairs) facilitate familiarity based interactions. These findings have potentially important practical implications, for example, in relation to alleviating the memory impairments associated with aging. Processing manipulations require the active and intentional use of internal mental strategies, whereas material manipulations are external and independent from the engagement of strategies. As old people exhibit particular difficulty in strategic processing, manipulating the semantic organisation of to-be-remembered material might prove a more effective way to enhance their episodic remembering.
6.6 Conclusion

In real life, when required to remember an important piece of information, one may strategically engage in elaborate thought to increase the likelihood of recollecting the information later. More often, however, memory operates without such intent. In this case, one of the important factors in determining whether information is remembered or forgotten is the characteristics of the information itself. Some of the information that we are required to remember maps onto our semantic knowledge about the world; it is coherently organised around a semantic theme or category. Alternatively, information can be relatively incoherent, without obvious relationship to existing knowledge, or any clear theme or category structure. The present study has shown that the nature of to-be-remembered information is important for how we remember; when information contains a coherent semantic structure we are better able to remember it. Unlike changing the way in which information is processed, however, making information more semantically coherent simply causes it to become more familiar.
6 Retrieval of semantic relations
7 Deep and shallow encoding of different classes of semantic stimuli

7.1 Introduction

Human memory comprises a set of complex cognitive functions that are inherently inter-twined with other mental processes guiding our thoughts and interactions within the world. It is often even difficult to define where information processing such as language and attentional operations ends and memory encoding begins. Memory, in general, refers to a function that unfolds over time, whereupon information processing at one point in time (encoding) influences processing at a later stage (retrieval). While encoding refers to the initial processing of information that instantiates a memory trace, retrieval denotes later processes accessing (or resulting from) prior encoded information. Within the context of human memory research, several studies have tried to elucidate how information processing at encoding influences subsequent retrieval processes. This research embraces different levels of description ranging from neuronal brain functions to cognitive approaches.

The ‘Levels Of Processing’ (LOP) theory (for more detailed review see Section 2.7.2), is one of the most influential cognitive accounts linking encoding and retrieval. LOP proposes that ‘deeper’ or more semantically-based processing at encoding leads to better episodic retrieval than ‘shallow’ or more perceptually-based processing (Craik & Lockhart, 1972). The theory predicts a relationship between encoding and retrieval operations, mediated by the type of processing applied to incoming information. Nevertheless, the LOP theory focuses on the type of processing applied to the encoding material, but does not predict how differences in encoding material may alter memory performance. The study reported in the previous chapter of this thesis (Chapter 6) demonstrated very clearly that the mapping between pre-existing semantic knowledge and the content of to-be-encoded stimuli influences the way information is processed and encoded into memory. It remains unknown whether such stimulus driven effects are also modulated by the
type of encoding task that is performed, as might be predicted on the basis of the LOP theory.

This question is addressed in the following study, which investigates whether encoding strategies alter the encoding processes and assesses their sensitivity to the type of material encoded. Thus, the current study investigates how encoding activity and subsequent memory effects differ when semantic vs. non-semantic stimuli are studied using either a semantic or non-semantic encoding strategy. The hypotheses tested with this experiment predicts that both the encoding strategy itself and the interaction between encoding strategy and the precise nature of the to-be-encoded stimuli will govern encoding related differences in memory.

7.2 Material and Methods

7.2.1 Participants

All participants were right-handed native English speakers, ranging from 18 to 35 years in age, with normal or corrected-to-normal vision and no known neurological problems. Informed consent was required, and payment provided at a rate of £5 per hour. Twenty one participants performed the ERP study. Five participants were excluded due to technical failure or excessive noise in the acquired data. The remaining 16 (5 female) subjects had an average age of 24 years.

7.2.2 Materials

The stimulus material and resulting study and test lists were created similar to those presented in the previous study (Section 6.2.2). Nevertheless, an increased number of word pairs were presented. In this experiment word pairs were constructed from 1044 nouns, 4-8 letters in length, with a frequency between 10 and 35 occurrences per million (Kucera & Francis, 1967). About a third (324) of the nouns were category exemplars, the remainder (720) were unrelated to the categories.

Stimuli were created for 16 blocks, each comprising a single study and test list. Individual study lists contained 6 semantic-two, 6 semantic-one and 12 non-
semantic word pairs (randomly intermixed), matched with a corresponding test list of 6 semantic-two, 6 semantic-one and 12 non-semantic word pairs. The 12 non-semantic pairs presented at test were constructed in the following way: 6 pairs were re-presented at test in the same pairings as at study, 2 pairs shown at study were altered to create 2 rearranged word pairs by recombining the first word from a studied pair (maintaining word position in each case) with a second word from the second studied pair and vice versa\textsuperscript{14}. The remaining 4 pairs of the non-semantic condition were used to create 4 new word pairs, by combing the first member of each pair (always discarding the second member of the pair) with a previously unstudied word.

Non-semantic conditions were presented in the test list intermixed with semantic-one and semantic-two conditions. Each of the 6 semantic-one and 6 semantic-two conditions were constructed in the following manner: 3 pairs were represented in the test list in exactly the same pairing as at study. One pair was altered to create a rearranged word pair by recombining the first word from a studied pair (maintaining word position in each case) with a second word from a different studied pair. Finally, the remaining 2 pairs were used to create 2 new word pairs, by combing the first member of each pair (always discarding the second member of the pair) with a previously unstudied word.

### 7.2.3 Procedures

The experiment was implemented similar to the previous experiment (Section 6.2.3). The trial structure, however, was slight changed to accommodate the different

\textsuperscript{14} In general, the rearranged condition was included in the experimental paradigm to prevent strategic old/new responses. The rearranged condition was not intended to be subject of subsequent analysis, however. Without the rearranged condition, participants could have performed the task correctly by simply classifying the second word of the pair as old or new (ignoring the precise pairing).
encoding instructions so that: each study trial started with a fixation cross (+) displayed for 750ms in the centre of the screen, followed by a blank screen for 250ms. The category name was then presented for 1500ms, before being replaced by a word pair for 2000ms. For deep encoding conditions participants were instructed to indicate by button press (within 4000ms of word pair onset) whether none, one or two of the words were related to the category name. Shallow encoding conditions, however, required a judgement as to whether the second word of the pair was the same length, longer or shorter than the first word presented in the pair. The two encoding conditions were employed to focus encoding process either towards the semantic meaning or perceptual characteristics of the word pairs. Once a response was made the screen went blank for 250ms, and the next trial began. Participants were informed that their memory would be tested afterwards. The presentation of the test trials was identical to the previous study (Section 6.2.3) with the exception that no confidence responses were required.

7.2.4 ERP recording and analysis

Scalp EEG was recorded in precisely the same form as described in the previous Chapter (Section 6.2.4). ERP waveforms were formed separately for shallow and deeply encoded semantic-two, semantic-one and non-semantic word pairs. Furthermore, encoding activity was separated by subsequent memory performance across different encoding conditions and stimulus types. On the basis of visual inspection of the waveforms, data at study were analysed over 3 consecutive time windows (300-500ms, 500-800ms, 800-1800ms). These time windows capture the effects of interest in the current data most appropriately, although they diverge slightly from the time windows (300-500ms, 500-1000ms, 1000-1800ms) specified in the previous experiment (Section 6.2.4).
7.3 Results at study

7.3.1 Comparison of the stimulus conditions

Potential differences in encoding activity between non-semantic, semantic-one and semantic-two stimulus conditions were examined across shallow and deep encoding strategies. Behavioural and electrophysiological measures were used to establish whether encoding processes engaged for the three conditions differ when deep vs. shallow encoding strategies were employed.

7.3.1.1 Behavioural data

Figure 7-1 shows the likelihood of correct task performance for non-semantic, semantic-one and semantic-two pairs studied under deep and shallow encoding conditions. An ANOVA testing the factors of encoding (deep, shallow) and stimulus (non-semantic, semantic-one, semantic-two), revealed a significant encoding by stimulus interaction [F(2,30)=4, p<0.05].

Follow up analysis contrasting individual stimulus conditions showed, under shallow encoding, significantly more correct responses for semantic-one compared to semantic-two and non-semantic pairs (t(15)=-3.2, p<0.01; t(15)=6.1, p<0.001 respectively). Deep encoding, by contrast, elicited significantly more correct responses for non-semantic compared to semantic-one as well as semantic-two conditions (t(15)=2.1, p<0.05; t(15)=2.3, p<0.05 respectively). Overall, the level of performance demonstrated a high likelihood of accurate classification, ranging from 79 to 93 percent correct responses.
Figure 7-1 Behavioural data showing the mean of correct responses for shallow and deep encoding of non-semantic, semantic-one and semantic-two pairs. The shallow encoding task required a judgement of word length, while the deep encoding task involved decisions concerning the semantic relation of words presented in a pair. Mean probability (and standard error) of correct task performance reveal significantly more correct responses for shallowly encoded semantic-one conditions and deeply encoded non-semantic conditions.

RT differences (see Figure 7-2) were assessed with an ANOVA employing the factors of encoding (shallow, deep), stimulus (non-semantic, semantic-one, semantic-two) and accuracy (correct, incorrect), which resulted in a significant 3-way interaction \[ F(2,30)=8.1, \ p<0.01 \]. Subsidiary analyses performed on shallow encoding conditions revealed significantly faster RTs for semantic-two relative to non-semantic \((t(15)=-3.2, \ p<0.01)\) or semantic-one conditions \((t(15)=3.1, \ p<0.01)\). Significantly longer RTs occurred further for incorrectly compared to correctly identified non-semantic \((t(15)=3.9, \ p<0.01)\) and semantic-one pairs \((t(15)=3.6, \ p<0.01)\). Although deep encoding conditions failed to show any differences in RTs between the three stimulus conditions, correct relative to incorrect responses revealed significantly longer RTs for semantic-one \((t(15)=3.5, \ p<0.01)\) and semantic-two pairs \((t(15)=6.5, \ p<0.001)\).
In general, the behavioural data suggest that participants were able to complete the shallow and deep encoding task with a high degree of accuracy. Shallow encoding revealed significantly faster classification performance for the semantic-two condition. Common to deep and shallow encoding conditions were overall faster RTs for correct compared to incorrect responses, with the exception of shallowly encoded semantic-two and deeply encoded non-semantic conditions.

![Figure 7-2](image-url)  
**Figure 7-2** Behavioural data showing reaction times (RT) for correctly (c) and incorrectly (i) performed shallow and deep encoding tasks. Mean (and standard error) reaction times are displayed for non-semantic, semantic-one and semantic-two stimulus conditions. In general, correct responses are significantly faster than incorrect responses, but shallow encoding conditions produced overall faster RTs compared to deep encoding conditions. Shallow encoding condition produced faster RTs for semantic-two than semantic-one or non-semantic pairs, whereas no such difference was found under deep encoding conditions.
7 Deep and shallow encoding of different classes of semantic stimuli

7.3.1.2 ERP data

Grand average ERPs elicited for deep encoded non-semantic, semantic-one and semantic-two word pairs are shown in Figure 7-3. The mean numbers of trials contributing to the average waveforms are 54 for non-semantic, 30 for semantic-one and 26 for semantic-two pairs.

![Figure 7-3](image.png)

Figure 7-3 Grand average ERPs for deeply encoded non-semantic (black), semantic-one (blue) and semantic-two (red) pairs. Here, and in all subsequent graphs of this kind, ERP waveforms are shown for 61 electrodes, displayed as if looking down onto the top of the head. Differences between the waveforms emerge over frontal, central and parietal locations, signifying changes in neuronal activity when different semantic word pairs become deeply encoded.

ERP activity for the three stimulus conditions depart over frontal electrodes between 300 and 500ms (see Figure 7-4 for enlarged illustration). Semantic-two pairs seem to reveal slightly more negative going deflections for non-semantic relative to semantic-one pairs, which in turn exhibit more positive going ERP waveforms compared to semantic-two pairs. The subsequent time-window between 500-800ms indicates some differences between all three stimulus conditions (non-semantic, semantic-one and semantic-two pairs). The semantic-two condition elicits more positive going ERP activity compared to the semantic-one condition, which in
Deep and shallow encoding of different classes of semantic stimuli

turn elicit more positive going deflections compared to non-semantic conditions. Finally, while differences over parietal locations decrease from 800ms onwards, right frontal locations exhibit differences in encoding activity until the end of the recording epoch. Significant differences in ERP activity were assessed statistically by using average voltages calculated over three consecutive epochs (300-500ms, 600-900ms, 900-1800ms). These epochs are similar to those employed in the previous experiment (Section 6.2.4) and capture the present changes in activity.

Grand average ERPs obtained for shallow encoded non-semantic, semantic-one and semantic-two word pairs are displayed in Figure 7-5. The mean numbers of trials contributing to the average waveforms are 61 for non-semantic, 34 for semantic-one and 33 for semantic-two pairs.
No clear differences in encoding activity were evident between the three stimulus conditions (see Figure 7-6 for enlarged illustration). Nevertheless, to allow statistical comparisons between deep and shallow encoding conditions, average voltages were calculated over three consecutive epochs (300-500ms, 500-800ms, 800-1800ms), analogous to the deep encoding conditions.
7 Deep and shallow encoding of different classes of semantic stimuli

7.3.1.2.1 Analysis of shallow encoding conditions

Shallow encoding conditions failed to elicit any significant main effect or interactions with the factor of stimulus in an ANOVA testing the factors of stimulus (non-semantic, semantic-one, semantic-two), epoch (300-500ms, 500-800ms, 800-1800ms), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior). This result suggests that under shallow encoding ERP waveforms elicited by the three stimulus conditions do not differ in their electrical activity.

7.3.1.2.2 Analyses of deep encoding conditions

Analogous analyses of deep encoding conditions revealed multiple 2-way and 3-way interactions involving the factors of stimulus (see Table 7-1), along with a 5-way interaction between stimulus, epoch, location, hemisphere and site \([F(2.4,36.2)=3.0, p=0.05]\). These results advocate that under deep encoding ERP waveforms differ across the three stimulus conditions as a function of time, location, hemisphere and sites. A subsidiary set of analysis was performed separately across frontal and parietal locations.
7 Deep and shallow encoding of different classes of semantic stimuli

Table 7-1 This table shows significant effects and interactions with the factor of stimulus for deeply encoded word pairs, resulting from an ANOVA with the factors of stimulus, epoch, location, hemisphere and site.

<table>
<thead>
<tr>
<th>Effect</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>stim.</td>
<td>12.5</td>
<td>1.6</td>
<td>23.4</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>stim. by epoch</td>
<td>3.2</td>
<td>2.5</td>
<td>37.4</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>stim. by hem.</td>
<td>5.1</td>
<td>1.8</td>
<td>26.6</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>stim. by site</td>
<td>5.3</td>
<td>2.2</td>
<td>33.2</td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td>stim. by loc. by hem.</td>
<td>3.8</td>
<td>1.4</td>
<td>21.2</td>
<td>p=0.05</td>
</tr>
<tr>
<td>stim. by hem. by site</td>
<td>5.5</td>
<td>2.4</td>
<td>36.6</td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td>stim. by epoch by loc. by hem. by site</td>
<td>3.0</td>
<td>2.4</td>
<td>36.2</td>
<td>p=0.05</td>
</tr>
</tbody>
</table>

7.3.1.2.3 Analysis over frontal locations

Frontal electrodes were tested across individual time widows with an ANOVA employing the factor of stimulus (non-semantic, semantic-one, semantic-two), hemisphere (left, right) and site (inferior, mid, superior). The first epoch showed a main effect of stimulus and a stimulus by hemisphere interaction (see Table 7-2\(^ {15} \)). Subsequent analyses (collapsed across frontal electrodes\(^ {16} \)) failed to reveal any significant difference between the non-semantic and semantic-one word pairs, but both the non-semantic and semantic-one pairs evoked significantly more negative activity compared to semantic-two word pairs (t(15)=−4.3, p<0.05, t(15)=−2.9, p<0.05 respectively).

\(^ {15} \) In order to enable a straightforward comparison between the different time windows, this table only reports the ‘p-values’ of the statistical analysis. For a more comprehensive report, which also includes the corresponding ‘F-values’ and ‘df-values’ see Appendix A (Section 15.3.1).

\(^ {16} \) This analysis was performed on a virtual electrode reflecting the average activity of the following six frontal electrodes: F1, F2, F3, F4, F5, F6.
7 Deep and shallow encoding of different classes of semantic stimuli

Table 7-2 This table shows significant effects and interactions with the factor of stimulus separated for the three epochs across frontal locations, resulting from an ANOVA with the factors of stimulus, hemisphere and site.

<table>
<thead>
<tr>
<th>Effect</th>
<th>300-500ms</th>
<th>500-800ms</th>
<th>800-1800ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>stim.</td>
<td>p=0.001</td>
<td>p&lt;0.001</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>stim. by hem.</td>
<td>p&lt;0.05</td>
<td>p&lt;0.01</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>stim. by site</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>stim. by hem. by site</td>
<td>-</td>
<td>p&lt;0.05</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

Furthermore, the stimulus by hemisphere interaction (see Table 7-2) suggests an asymmetric distribution of the frontal effect. A pair wise comparison of the left and right hemisphere was performed over two virtual electrodes, one averaging activity over left frontal (F1,F3,F6) and the other over right frontal electrodes (F2,F4,F6). This comparisons revealed, across all three stimulus conditions and time windows, no significant difference between non-semantic and semantic-one conditions over the left hemisphere, while differences emerged (although only marginally significant) over the right hemisphere for non-semantic vs. semantic-one (t(15)=3.1, p<0.01) and non-semantic vs. semantic-two contrasts (t(15)=3.3, p<0.01).

The results of the ANOVA in the second and third epoch were similar to the outcome reported for the first epoch. A main effect of stimulus, a stimulus by hemisphere interaction and a stimulus by hemisphere by site interaction reached statistical significance (see Table 7-2). Thus, the pattern of activity described for the first epoch appears to be long lasting as it spreads over the second and third epoch.
7.3.1.2.4 Analysis over parietal locations

Activity at parietal electrodes were tested separately across the three time windows by employing an ANOVA with the factors of stimulus (non-semantic, semantic-one, semantic-two), hemisphere (left, right) and site (inferior, mid, superior). The results demonstrated significant stimulus effects and interactions including the factors of stimulus, hemisphere and site in the second and third but not first epoch (see Table 7-3\textsuperscript{17}).

<table>
<thead>
<tr>
<th>Effect</th>
<th>parietal location</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1.epoch</td>
</tr>
<tr>
<td>stim.</td>
<td>-</td>
</tr>
<tr>
<td>stim. by hem.</td>
<td>-</td>
</tr>
<tr>
<td>stim. by site</td>
<td>-</td>
</tr>
<tr>
<td>stim. by hem. by site</td>
<td>-</td>
</tr>
</tbody>
</table>

\textbf{Table 7-3} This table shows significant main effects and interactions including the factor of stimulus, separated for the three epochs over parietal locations, resulting from an ANOVA with the factors of stimulus, hemisphere and site.

Follow up comparisons (collapsed across parietal electrodes\textsuperscript{18}) revealed significantly more positive activity for the semantic-two compared to the semantic-one condition ($t(15)=3.2$, p<0.001) and for the semantic-one compared to the non-semantic condition ($t(15)=2.4$, p<0.05). This difference is more left lateralised over

\textsuperscript{17} This table only reports the ‘p-values’ of the statistical analysis for reasons of better comparisons across epochs. A comprehensive report of the statistical data, including ‘F-values’ and ‘df-values’, is listed in Appendix A (Section 15.3.2).

\textsuperscript{18} This analysis was performed on a virtual electrode reflecting the average activity of the following six frontal electrodes: CP1, CP2, CP3, CP4, CP5, CP6.
7 Deep and shallow encoding of different classes of semantic stimuli

parietal electrodes (see Figure 7-3 and Figure 7-4) and is stronger at superior electrodes as the significant stimuli by hemisphere by site interaction indicates (see Table 7-3).

Analyses over parietal electrodes revealed significant effects involving the factor of stimulus beyond the second time window. It is evident in Figure 7-3 and Figure 7-4 that the prolonged positivity of the semantic-two condition gives rise to this stimulus effect. Pair wise contrasts were performed over two virtual electrodes, one averaging activity over left parietal (CP1,CP3,CP6) and the other over right parietal electrodes (CP2,CP4,CP6). Significant differences between non-semantic and semantic-two conditions occurred in the third epoch over the left \( t(15)=2.1, p<0.05 \) and right hemisphere \( p(15)=4.2, p<0.001 \). Also the contrast between semantic-one and semantic-two conditions remains significant in the third epoch but only over the right hemisphere \( t(15)=2.2, p<0.05 \) but not the left hemisphere. This reflects a more pronounced positivity of the semantic-two condition over the right compared to the left hemisphere.

Taking together, the pattern of activity over frontal and parietal locations indicates the presence of two spatially distinct ERP effects. Further inferences as to whether qualitative distinct neural generators gave rise to these effects require further analyses using rescaled data.

7.3.1.2.5 Topographical analysis

Topographical analyses were performed on difference waveforms contrasting non-semantics vs. semantic-one, non-semantic vs. semantic-two, and semantic-one vs. semantic two conditions using normalised data. A set of ANOVAs tested these contrasts by employing the factor of epoch (1st epoch, 2nd epoch), location (front, parietal), hemisphere (left, right) and site (inferior, mid, superior). All three difference waveforms exhibited significant interactions with epoch. The non-semantic vs. semantic-one condition revealed an epoch by hemisphere \( F(1,15)=6.3, p<0.05 \) and a location by hemisphere interaction \( F(1,15)=12.7, p<0.01 \). This indicates that electrical activity differs qualitatively with time and across hemisphere. Furthermore, frontal differences between the non-semantic and semantic-one
condition is spatially distinct from the parietal difference. As no epoch by location interaction was observed, frontal and parietal locations can not be inferred to be generated by temporally dissociable sources.

Nevertheless, the non-semantic vs. semantic-two contrasts exhibited a 4-way interaction between the factors of epoch, location, hemisphere and site [F(1.5,23)=4.6, p<0.05], and the semantic-one vs. semantic-two conditions showed an epoch by location interaction [F(1,15)=6.3, p<0.05]. Thus, the neuronal generators underlying the frontal activity for the semantic-two condition in contrast to the semantic-one and non-semantic conditions seems to be spatially and temporally dissociable from the neuronal generators evoking the later emerging parietal modulation for the semantic two condition.

The ANOVA comparing the second and third epoch included the factors of epoch (2nd epoch, 3rd epoch), location (front, parietal), hemisphere (left, right) and site (inferior, mid, superior), and demonstrated for the non-semantic vs. semantic-one contrast a location by hemisphere interaction [F(1.5,22.3)=18.1, p<0.001] without any significant epoch effects. Thus, although spatially distinct generators were engaged those did not change over time. The non-semantic vs. semantic-two conditions revealed in the second vs. third epoch a 4-way interaction between the factors of epoch, location, hemisphere and site [F(1.9,27.9)=10.7, p<0.001], while the semantic-one vs. semantic-two contrast revealed a location by hemisphere by site interaction [F(1.6,24.2)=6.4, p<0.01]. Taken together, these results indicate that the difference across the second and third epoch between the non-semantic and semantic-two condition are generated by spatially and temporally distinct sources. Such evidence is not present for the non-semantic vs. semantic-one contrast or the semantic-one vs. semantic-two contrast, which both reveal spatially but not temporally distinct generator.

In general, the topographical analysis confirmed that the early frontal and later parietal effects are associated with qualitatively distinct generators (i.e. with different spatial distributions). In addition, the semantic-two condition reveals not only spatially but also temporally distinct generators for the frontal and parietal component when contrasted with semantic-one or non-semantic conditions.
7.3.2 Comparison of the two encoding conditions

The ERP modulations described so far for the encoding of different stimulus conditions do not permit inferences as to whether distinct encoding processes were engaged in the present experiment. Therefore, specific difference in electrical activity between shallow and deep encoding conditions are examined and characterised more closely in the following set of analyses.

7.3.2.1 Behavioural data

The likelihood of performing the encoding task correctly has been already analysed in the former section (Behavioural data 7.3.1.1), which revealed significant encoding by stimulus interactions (compare Figure 7-1). An ANOVA employing the factors of encoding (deep, shallow) and stimulus (non-semantic, semantic-one, semantic-two) disclosed significant effects of encoding for semantic-one \( [F(1,15)=79.3, \ p<0.001] \) and semantic-two conditions \( [F(1,15)=16.3, \ p<0.01] \), indicating more accurate responses for shallow compared to deep encoding tasks. Non-semantic conditions, however, revealed no significant differences in encoding.

Furthermore, RT data revealed a significant interaction between encoding, stimulus and accuracy \( [F(2,30)=8.1, \ p<0.01] \) (see Section 7.3.1.1). Pair wise contrasts of individual stimulus conditions indicated significantly faster RTs to shallow compared to deep encoding tasks for non-semantic \( (t(15)=-11.5, \ p<0.001) \), semantic-one \( (t(15)=-6.3, \ p<0.001) \) as well as semantic two conditions \( (t(15)=-10.8, \ p<0.001) \). Moreover, when encoding was contrasted across correctly and incorrectly classified stimulus conditions, every single comparison (over correct as well as incorrect responses) showed significantly faster RTs for shallow compared to deep encoding \( [p<0.05, \ in \ all \ cases] \) (see Figure 7-2).

In general, the statistical analysis of the behavioural data indicates that task performance differs between shallow and deep encoding conditions. The shallow encoding task was largely performed with a higher degree of accuracy (with exception of the non-semantic stimulus condition) and evoked shorter RTs relative to the deep encoding condition. This may reflect the fact that shallow encoding
conditions are associated with less processing demands than deep encoding conditions. Overall, the behavioural data reveal very clearly that the way stimulus material is processed is modulated by shallow and deep encoding conditions. This confirms that participants have successfully processed the stimuli with different strategies across the two encoding conditions.

7.3.2.2 ERP data

Grand average ERPs contrasting deep and shallow encoding activity for non-semantic stimuli are presented in Figure 7-7. The mean numbers of trials contributing to the average waveforms are 54 for deep and 61 for shallow encoded non-semantic pairs.

![Grand average ERPs](image)

**Figure 7-7** Grand average ERPs elicited for deeply encoded (black) and shallowly encoded (grey) non-semantic pairs. Long lasting differences between the waveforms emerge over frontal, central and parietal locations, signifying changes in neuronal activity when non-semantic stimuli are studied under different encoding conditions.
Deep and shallow encoded non-semantic stimuli show clear differences in encoding activity starting at around 300ms (see Figure 7-8 for enlarged illustration). Compared to shallow encoding conditions, deeply encoded non-semantic stimuli reveal a large negative deflection most prominent over frontal locations maximal at around 400ms. At the same time, shallow relative to deep encoding conditions exhibited substantial positive ERP deflection. Although the effect size decreases noticeably at about 800ms over frontal and parietal locations, encoding related ERP differences do display small sustained differences particularly over centrally located electrode sites until the end of the recording epoch.

Figure 7-8 Grand average ERPs elicited for deeply encoded (black) and shallowly encoded (grey) non-semantic word pairs. The frontal electrodes show a more negative deflection for deep compared to shallow encoding conditions (max. at 400ms). Parietal electrodes reveal (from 400ms onwards) beside the negative deflection for deep encoding conditions, a positive deflection for the shallow encoding condition, which amplifies the difference in electrical activity between encoding conditions.

Grand average ERP waveforms displaying encoding differences for semantic-one pairs are shown in Figure 7-9. The mean numbers of trials contributing to the average waveforms are 30 for deep and 34 for shallow encoded pairs.
Figure 7-9 Grand average ERPs are displayed for deeply encoded (blue) and shallowly encoded (black) semantic-one pairs. Similar to non-semantic pairs, differences in ERP activity for semantic-one pairs emerge over frontal, central and parietal locations, suggesting that the neuronal activity elicited for semantic-one pairs is dependent on the encoding condition.

Similar to non-semantic pairs, semantic pairs revealed from about 300ms onwards divergences in frontal activity with a stronger negative deflection for deep compared to shallow encoded pairs (see Figure 7-10 for enlarged illustration). Shallow encoding conditions, on the other hand, elicited an increased positivity over parietal locations evoking large differences between shallow and deep conditions. However, in contrast to non-semantic stimuli differences in encoding activity disappears for semantic-one stimuli at about 800ms over frontal and 1000ms over parietal locations.
Figure 7-10 Grand average ERPs elicited for deeply encoded (blue) and shallowly encoded (black) semantic-one pairs. Frontal electrodes show a more negative deflection for deep compared to shallow encoding conditions (max. at 400ms). This is followed by a positive deflection for shallow encoding conditions over parietal electrodes suggesting difference in electrical activity between encoding conditions.

Finally, differences in encoding activity between deep and shallow conditions were also examined for semantic-two conditions. The corresponding grand average ERP waveforms are displayed in Figure 7-11. The mean number of trials contributing to the average waveforms was 26 for deep and 33 for shallow encoded pairs.
Surprisingly, deep and shallow encoding conditions seem to reveal the smallest difference in encoding activity for semantic-two compared to semantic-one or non-semantic stimuli. Although a small difference between encoding conditions seems to occur at about 300ms over parietal locations, the largest divergence in ERP activity occurs over mid-frontal locations between 400 and 1000ms (see Figure 7-12 for enlarged illustration). The frontal modulation for semantic-two pairs is elicited by a larger positivity for deep compared to shallow encoding conditions. No further differences seem to be present between encoding conditions beyond 1000ms post stimulus onset.

Figure 7-11 Grand average ERPs elicited for deeply encoded (red) and shallowly encoded (black) semantic-two pairs. Differences in activity appear over frontal locations between 500 and 800ms. Deep encoding conditions reveal a more positive going deflection relative to shallow encoding conditions, which indicates a difference in encoding activity dependent on the encoding condition.
Figure 7-12 Grand average ERPs elicited for deeply encoded (red) and shallowly encoded (black) semantic-two pairs. Frontal electrodes elicit a more positive going deflection for deep compared to shallow encoding conditions between 500 and 800ms, suggesting a difference in encoding activity between conditions.

The different word pairs studied under shallow encoding conditions were contrasted by their average voltages calculated over three consecutive epochs (300-500ms, 500-800ms, 800-1800ms).

7.3.2.2.1 Analysis over frontal locations

The analysis over frontal locations, based on an ANOVA including the factors of encoding (shallow, deep), hemisphere (left, right) and site (inferior, mid, superior) was performed across individual time windows. Significant effects of encoding are summarised in Table 7-4\textsuperscript{19}. The non-semantic and semantic-one

\textsuperscript{19}To allow a straightforward comparison between the different time windows, this table only reports the ‘p-values’ of the statistical analysis. For a more comprehensive report, which also includes the corresponding ‘F-values’ and ‘df-values’, see Appendix A (Section 15.4.1).
condition revealed significant effects of encoding in the first epoch, which progressed to significant encoding by hemisphere by site interactions in the second epoch, which was present for semantic-one pairs even in the third epoch. These encoding effects reflect a more negative going deflection for deep compared to shallow encoding conditions (see Figure 7-7 and Figure 7-9).

<table>
<thead>
<tr>
<th>Effect</th>
<th>frontal location</th>
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<tbody>
<tr>
<td></td>
<td>Non-semantic</td>
</tr>
<tr>
<td>epoch</td>
<td>1. 2. 3</td>
</tr>
<tr>
<td>enc.</td>
<td>&lt;0.01 =0.001</td>
</tr>
<tr>
<td>enc. by hem.</td>
<td>- - -</td>
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<tr>
<td>enc. by site</td>
<td>- - =0.01</td>
</tr>
<tr>
<td>enc. by hem. by site</td>
<td>- &lt;0.05 -</td>
</tr>
</tbody>
</table>

**Table 7-4** Significant effects and interactions with the factor of encoding are shown separately across the three time epochs (1. = 300-500ms, 2. = 500-800ms, 3. = 800-1800ms) and stimulus conditions (non-semantic, semantic-one, semantic-two) over frontal locations. These effects result from an ANOVA with the factors of encoding, hemisphere and site.

Changes in the distribution of encoding effects in the second time window were assessed across all six frontal electrodes (F1, F2, F3, F4, F5, F6). For non-semantic pairs encoding effects were present at all electrodes, this was also the case for semantic-one pairs, with the exception of electrodes F1 and F6. As Figure 7-13 illustrates, larger modulations in electrical activity were present over the right hemisphere for non-semantic pairs, whereas semantic-one pairs reveal stronger encoding differences over the left hemisphere.
Figure 7-13 The magnitude of encoding effects (difference in electrical activity between shallow vs. deep encoding) are shown for the second epoch over six frontal electrodes. Three electrodes were located over the left (F5, F3, F1) and further three over the right (F2, F4, F6) hemisphere. The displayed mean (and standard error) of the encoding effects illustrates increased effect sizes over the right hemisphere for non-semantic pairs, while semantic-one pairs show a slightly stronger differences in encoding related activity over the left hemisphere.

Rather surprisingly, semantic-two pairs failed to elicit any significant effect of encoding, although the grand average waveforms seem to suggest a divergence in activity (see Figure 7-13). It is possible that the specified time windows may not fully capture the frontal modulations and re-analyses were based on the following three time windows: 300-600ms, 600-1300ms, 1300-1800ms. The second time window (600-1300ms) fully captures the frontal effect. Yet again, statistical tests failed to reveal any significant effect of encoding even when activity was compared at individual electrode sites, suggesting that the observed frontal modulation is statistically unreliable.

In sum, frontal electrodes reveal in the first epoch stronger negative deflections for deep compared to shallow encoding conditions for non-semantic and semantic-one pairs. This difference continued to exist in the second time window but was focused over the right hemisphere for non-semantic pairs and the left hemisphere for semantic-one pairs.
7 Deep and shallow encoding of different classes of semantic stimuli

7.3.2.2 Analysis over parietal locations

Analogous to the analysis performed over frontal locations, data from parietal locations were subjected to an ANOVA including the factors of encoding (shallow, deep), hemisphere (left, right) and site (inferior, mid, superior), which was performed across individual time windows. Significant encoding effects (summarised in Table 7-5\textsuperscript{20}) were present for all three stimulus conditions across all three time windows with the exception of the semantic-two condition, which disappeared in the third time window. These encoding differences reflect more positive going ERP activity for shallow compared to deep encoding conditions (see Figure 7-8 and Figure 7-10).

<table>
<thead>
<tr>
<th>Effect</th>
<th>parietal location</th>
<th>epoch</th>
<th>Non-semantic</th>
<th>Semantic-one</th>
<th>Semantic-two</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1.</td>
<td>2.</td>
<td>3.</td>
<td>1.</td>
</tr>
<tr>
<td>statistic</td>
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<td>p</td>
<td>p</td>
<td>p</td>
<td>p</td>
</tr>
<tr>
<td>enc.</td>
<td></td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.05</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>enc. by hem.</td>
<td></td>
<td>-</td>
<td>-</td>
<td>=0.01</td>
<td>=0.05</td>
</tr>
<tr>
<td>enc. by site</td>
<td></td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>=0.01</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>enc. by hem. by site</td>
<td></td>
<td>-</td>
<td>&lt;0.05</td>
<td>&lt;0.05</td>
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</tr>
</tbody>
</table>

Table 7-5 Significant effects and interactions with the factor of encoding are shown split across the three time epochs and stimulus conditions over parietal locations. These effects result from an ANOVA with the factors of encoding, hemisphere and site.

The encoding by hemisphere by site interaction suggests hemispheric differences. In the first epoch, contrasts for semantic-two conditions across all six

\textsuperscript{20} To allow a straightforward comparison between the different time windows, this table only reports the ‘p-values’ of the statistical analysis. For a more comprehensive report, which also includes the corresponding ‘F-values’ and ‘df-values’ see Appendix A (Section 15.4.2).
parietal electrodes (CP1, CP2, CP3, CP4, CP5, CP6) revealed significant differences at all electrodes, with the exception of CP4 and CP6, suggesting a left lateralised distribution. The second epoch shows for non-semantic and semantic-one stimuli significant encoding effects that are larger over the right compared to the left hemisphere (see Figure 7-14). This trend continues to exist for non-semantic stimuli in the third epoch, where all parietal electrodes showed significant differences in encoding activity, with the exception of electrode CP5 and CP3.

![Figure 7-14](image)

**Figure 7-14** The magnitude of encoding effects (difference in electrical activity between shallow vs. deep encoding) are shown for the second epoch over six parietal electrodes. Three electrodes were located over the left (CP5, CP3, CP1) and right (CP2, CP4, CP6) hemisphere. The displayed mean (and standard error) of the encoding effects illustrates increased effect sizes over the right compared to the left hemisphere for non-semantic and semantic-one pairs.

Overall, parietal locations demonstrated larger positive deflections for shallow compared to deep encoding conditions in the first time window for all three stimulus conditions. This activity persists in the second time window, and for non-semantic pairs even in the third time window. While these encoding effects are bilaterally distributed for semantic-one pairs, the semantic-two condition reveals a left lateralised distribution, while the non-semantic condition elicits stronger right lateralised effects.

In conclusion, the pattern of electrical activity over frontal and parietal locations designates the presence of two distinct encoding effects. Rescaled data
were used to investigate whether qualitatively distinct neural generators may have elicited these distinct encoding components.

### 7.3.2.2.3 Topographical analyses

Topographical analyses were performed on difference waveforms contrasting shallow and deep encoding conditions. An ANOVA including the factors of stimulus (non-semantic, semantic-one, semantic-two), location (front, parietal), hemisphere (left, right) and site (inferior, mid, superior) was performed across all individual time windows.

The first epoch revealed significant location by site interactions \([F(1.3,18.8)=4.1, p=0.05]\), while the second and third epoch demonstrated significant location by hemisphere by site interactions \([F(1.9,28.1)=6.7, p<0.01]\), \([F(1.9,28)=7.1, p<0.01]\) respectively. These results suggest that distinct neuronal sources gave rise to frontal and parietal modulations in all time windows.

Subsidiary analysis investigated whether encoding effects change with time over frontal and parietal locations by employing an ANOVA with the factors of stimulus (non-semantic, semantic-one, semantic-two), epoch (300-500ms, 500-800ms, 800-1800ms), hemisphere (left, right) and site (inferior, mid, superior). Frontal locations revealed a significant interaction between epoch and hemisphere \([F(1.7,26.8)=5, p<0.05]\), as well as between stimulus, epoch and site \([F(2.8,42.1)=3.2, p<0.05]\). Parietal locations also demonstrated a significant epoch by hemisphere interaction \([F(1.4,22.4)=6.7, p<0.01]\), in combination with an epoch by hemisphere by site interaction \([F(2.1,30.8)=7.7, p<0.01]\), but failed to elicit significant stimulus effects. This pattern of results indicates that qualitative different sources contribute to the encoding effects over time.

In general, topographic analysis confirms that frontal and parietal encoding effects are generated by spatially distinct neuronal sources which differ qualitatively across time. The temporal modulation in neuronal activity differs across stimulus conditions over frontal locations, while the same neuronal source seems to contribute to all stimulus conditions over parietal locations.
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7.3.3 Summary

The first part of this chapter examined behavioural and electrophysiological differences elicited by deep and shallow encoding of word pairs comprising three different types of semantic relations (non-semantic, semantic-one, semantic-two). Analyses focussed on two different contrasts: one comparing the three stimulus conditions and the other assessing differences between the two encoding tasks.

The first contrast failed to reveal any differences in electrical activity between non-semantic, semantic-one and semantic-two conditions for shallow encoding. Nevertheless, deep encoding conditions demonstrated two distinct modulations in electrical activity, one over frontal and one over parietal locations. Frontal locations exhibited early onsetting (about 300ms post stimulus) and long lasting differences in electrical activity, reflecting stronger negative deflections for non-semantic and semantic-one relative to semantic-two pairs. No significant differences, however, were obtained between non-semantic and semantic-one pairs.

Parietal locations demonstrated later onsetting modulations in ERP activity (about 500ms post stimulus) characterised by a graded deflection, comprising more positive activity for semantic-two, followed by semantic-one and finally non-semantic conditions. This parietal difference was more temporally confined as differences between non-semantic and semantic-one conditions disappeared after 800ms (although positive deflection of the semantic-two compared to semantic-one and non-semantic conditions continued to exist until the end of the recording epoch).

In sum, the first contrast showed that deeply encoded semantic stimuli elicit two qualitatively distinct components over frontal and parietal locations. These two components are generated by two spatially dissociable neuronal generators as topographical analysis confirmed. Furthermore, in the semantic-two condition spatially and temporally distinct generators were obtained.

The second contrast focussed on ERP differences elicited by deep and shallow encoding conditions. Frontal locations revealed early onsetting differences (at about 300ms) evoked by stronger negative deflections for deep compared to shallow encoding conditions. This difference was present for non-semantic and semantic-one conditions, but it did not occur for semantic-two conditions. These frontal differences
continued to exist in later time windows but with a more lateralis
distribution. Parietal locations also demonstrated early onset
ting modulations (at about 300ms) across all three stimulus
conditions. These differences were based on larger positive
deflections for shallow compared to deep encoding conditions, which
were long lasting and remained present across the second and even the third time
window for non-semantic pairs. In summary, the second contrast revealed
differences over frontal and parietal locations. Topographical analyses confirmed
that these two modulations are supported by qualitatively different neuronal
generators which are spatially and temporally distinct.

The contrasts comparing electrical activity across different stimulus and
encoding conditions at study revealed qualitatively distinct frontal and parietal
modulations in encoding activity. These results demonstrate that processes engaged
at encoding are sensitive to both encoding strategy and stimulus type. The observed
pattern of ERP activity for encoding and stimulus conditions resembled a striking
similarity. It should be noted here though that not all electrical activity obtained
during study necessarily reflects activity related to memory encoding. It is
conceivable that other cognitive functions like linguistic or attentional processes may
become engaged and modulated when participants study different classes of stimuli
under distinct encoding conditions. These processes might be peripheral to the actual
process of successful encoding per se and therefore irrelevant to subsequent memory
performance.

The following part of this chapter uses the subsequent memory paradigm to
examine whether successfully encoded items elicit different brain activity when
those items were of a semantic or non-semantic nature. If that was the case for deep
encoding conditions, the current experiment would replicate the finding of the study
reported in the previous chapter. Importantly, it is of interest whether the precise
encoding task modulates activity for successful and unsuccessful encoding, and if so,
whether this activity interacts with stimulus driven encoding differences.
7.4 Subsequent memory effects

Similar to the analysis reported in the earlier chapter (Chapter 5), the subsequent memory analysis undertaken here investigated whether electrical activity elicited during study predicts successful retrieval. The following analysis investigates differences in subsequent memory effects between shallow and deep encoding conditions across non-semantic, semantic-one and semantic-two conditions.

7.4.1 Comparison of the stimulus and encoding conditions

The subsequent memory paradigm takes into account information from the test phase in order to contrast the study activity for subsequently remembered and forgotten items. Since this type of analysis relies on the number of correctly and incorrectly remembered items at test, a subgroup of 11 (4 female) subjects with an average age of 24 qualified for the subsequent memory analysis by exhibiting at least 16 artefact free trials in every condition.

7.4.1.1 Behavioural data

Two distinct sets of behavioural performances are of potential significance for subsequent memory analysis. One set describes the recognition performance in the subsequent memory test, whereas the other set focuses on performance of the study task. The behavioural memory performance at test is described in the next chapter of this thesis (Chapter 8) and will therefore not be discussed at this point. With regards to study performance, the subgroup of participants revealed no significant differences in performance compared to the complete group of participants reported earlier (see Section 7.3.1.1).
7.4.1.2 ERP data

Grand average ERPs examining subsequent memory effects for deeply encoded non-semantic word pairs are shown in Figure 7-15. The mean number of trials contributing to the average waveforms were 43 for subsequent correctly and 25 for subsequent incorrectly recognised word pairs.

![Figure 7-15](image)

**Figure 7-15** Grand average ERPs for subsequent incorrectly (black) and correctly (green) remembered non-semantic pairs, studied under deep encoding. No difference in electrical activity was observed for correctly and incorrectly recognised non-semantic pairs, suggesting that subsequent memory effects are absent.

ERP waveforms at study reveal no difference in electrical activity for subsequently remembered and forgotten pairs at frontal or parietal locations (see Figure 7-16 for enlarged illustration). Whether this absence of subsequent memory effects is due to the nature of the presented stimuli or the type of encoding task remains unclear at this point, but will be investigated subsequently.
Figure 7-16 Grand average ERPs for subsequent incorrectly (black) and correctly (green) remembered non-semantic pairs, studied under deep encoding. This closer view of the ERP waveforms illustrates that correctly and incorrectly recognised non-semantic pairs show no difference in electrical activity over frontal or parietal locations.

Subsequent memory effects were also investigated for deeply encoded semantic word pairs. The corresponding grand average ERP waveforms are displayed in Figure 7-17, which contained an average of 54 trials for subsequent correctly and 25 trials for subsequently incorrectly recognised word pairs.
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**Figure 7-17** Grand average ERPs elicited for subsequent incorrectly (black) and correctly (purple) remembered semantic pairs, studied under deep encoding. More positive going ERP waveforms occur for correctly compared to incorrectly recognise semantic pairs over frontal and parietal locations, suggesting the presence of subsequent memory effects.

At about 400ms, frontal and parietal locations exhibit differences in ERP activity (see Figure 7-4 for enlarged illustration). Correctly recognised pairs elicited a stronger positive deflection compared to incorrectly recognised pairs. At frontal locations this difference is long lasting and present until the end of the recording epoch. Parietal electrodes, however, demonstrate a more circumscribed effect occurring between 500 and 800ms. This pattern of activity suggests that semantic word pairs do elicit differences in encoding activity, which is predictive for subsequent memory performance. Nevertheless, the lack of subsequent memory effects for deep encoded non-semantic pairs suggests that subsequent memory effects are highly dependent on the nature of the encoding task the stimulus material is studied with.
Grand average ERP waveforms for subsequent memory effects for shallow encoded non-semantic pairs are displayed in Figure 7-19, which include an average of 53 trials for subsequent correctly and 25 trials for subsequently incorrectly recognised non-semantic pairs.

ERP activity seems to differ to some extent over frontal locations between 800 and 1200 ms (see Figure 7-20 for enlarged illustration). Correctly recognised non-semantic pairs appear to elicit a stronger positive deflection over frontal electrodes compared to incorrectly recognised pairs. Parietal electrodes, however, demonstrated no clear differences in encoding activity.
Figure 7-19 Grand average ERPs elicited for subsequent incorrectly (black) and correctly (green) remembered non-semantic pairs, studied under shallow encoding. ERP waveforms display a small divergence over frontal electrode sites with more positive going ERP deflections for correctly compared to incorrectly recognise semantic pairs.

Figure 7-20 Grand average ERPs elicited for subsequent incorrectly (black) and correctly (green) remembered non-semantic pairs, studied under shallow encoding. Frontal electrodes show small differences in electrical activity between correctly and incorrectly recognised semantic stimuli. No modulation in activity was present over parietal electrode sites.
Finally, grand average ERPs for shallow encoded semantic stimuli, displayed in Figure 7-21, were examined for potential differences in electrical activity predicting subsequent memory performance. The mean number of trials contributing to the average waveforms were 49 for subsequent correctly and 23 for subsequently incorrectly recognised word pairs.

Figure 7-21 Grand average ERPs elicited for subsequent incorrectly (black) and correctly (light purple) remembered semantic pairs, studied under shallow encoding. Difference in electrical activity emerge very late (about 1200ms post stimulus onset) over parietal electrode sites revealing more positive going ERP waveforms for correctly compared to incorrectly recognised non-semantic pairs.

As can be seen in Figure 7-21, ERP waveforms reveal no clear difference in electrical activity over frontal locations (see Figure 7-22 for enlarged illustration). Parietal electrodes, however, seems to exhibit differences in activity with a very late onset at about 1200ms post stimulus interval, reflecting more positive going ERP activity for correctly compared to incorrectly recognised items.
Figure 7-22 Grand average ERPs elicited for subsequent incorrectly (black) and correctly (light purple) remembered semantic pairs, studied under shallow encoding. Differences in electrical activity between correctly and incorrectly recognised non-semantic stimuli appear with a very late onset over parietal but not frontal locations.

The electrical activity elicited by the different word pairs studied under shallow encoding conditions was compared by contrasting average voltages calculated over three consecutive epochs (300-600ms, 600-1000ms, 1000-1800ms).

7.4.1.2.1 Analysis over separate stimuli and locations

In order to test for subsequent memory effects at frontal and parietal locations individually across semantic and non-semantic conditions, an ANOVA was designed with the factors of encoding (shallow, deep), response (correct, incorrect), epoch (300-600ms, 600-1000ms, 1000-1800ms), hemisphere (left, right) and site (inferior, mid, superior).
Non-semantic stimuli

For non-semantic stimuli, the results of this ANOVA revealed no significant interactions with the factor of response over frontal locations, and only a response by epoch interaction over parietal locations \( [F(1,10)=5.7, p<0.05] \), suggesting that changes in the subsequent memory effects occur over time at parietal locations but not across encoding conditions.

Subsidiary analysis over parietal locations using an ANOVA with the factors of response (correct, incorrect), hemisphere (left, right) and site (inferior, mid, superior) was performed individually for deep and shallow encoding conditions over all three time windows. The results revealed no significant effect of response in the first or third time window. The second epoch of 600-1000ms, however, did reveal a significant response by site interaction \( [F(1.2,18.9)=6, p=0.05] \) but only for the shallow encoding conditions. This suggests that the electrical activity for correctly and incorrectly recognised non-semantic pairs differ over inferior, mid and superior sites when studied under shallow encoding conditions. Nevertheless, focused analysis on shallow encoded pairs directly compared the level of activity between correctly and incorrectly recognised stimuli by using a t-test over left and right parietal locations\(^\text{21}\). The results failed to demonstrate significant differences in electrical activity. Consequently, there is no statistical evidence that subsequent memory effects occurred when non-semantic stimuli were studied with shallow versus deep encoding tasks.

\(^\text{21}\) This analysis was performed on a virtual electrode by collapsing over three left parietal (CP1, CP3, CP5) and right frontal (CP2, CP4, CP6) electrodes.
Semantic stimuli

Over frontal locations semantic stimuli demonstrated a significant 4-way interaction between the factors of encoding, response, epoch and hemisphere [F(1,10)=6, p=0.05], while parietal locations revealed a 4-way interaction between encoding, response, epoch and site [F(1.3,13.4)=4, p=0.05]. Hence, subsequent memory effects do significantly differ between shallow and deep encoding conditions but only when semantic word pairs are studied.

Follow-up analysis based on an ANOVA including the factors of response (correct, incorrect), epoch (300-600ms, 600-1000ms, 1000-1800ms), hemisphere (left, right) and site (inferior, mid, superior) revealed, for shallow encoding, no significant effects or interactions with the factor of response over frontal locations. Parietal locations, however, demonstrated a significant response by site [F(1.7,17.2)=5, p<0.05] and response by epoch by site interaction [F(2.2,22.6)=3.3, p<0.05]. Subsidiary analysis performed individually over all three time windows (employing an ANOVA with the factors of response (correct, incorrect), hemisphere (left, right) and site (inferior, mid, superior)) revealed a marginally significant main effect of response [F(1,10)=4.4, p=0.06] and a response by hemisphere interaction [F(2,20)=9, p<0.01] in the third epoch. Overall, the findings indicate more positive going activity for subsequent correctly vs. incorrectly remembered items over parietal locations, which are more pronounced over the right than the left hemisphere. Individual t-tests comparing electrical activity at all six parietal electrodes [CP6 CP5 CP4 CP3 CP2 CP1] showed significant differences between subsequent correctly and incorrectly recognised pairs at superior electrodes sites CP1 (t(10)=2.67, p<0.05) and CP2 (t(10)=2.64, p<0.05) (see Figure 7-23).
Figure 7-23 The differences in shallow encoding activity for subsequent correctly and incorrectly recognised semantic pairs are shown across the third epoch (1000-1800ms) over six parietal electrodes. Three electrodes were located over the left (CP5, CP3, CP1) and right (CP2, CP4, CP6) hemispheres. The displayed mean (and standard error) of the encoding activity illustrates significant differences in encoding activity at superior electrode sites.

Deeply encoded semantic pairs, by contrast, revealed a significant response by hemisphere interaction over frontal locations $[F(1,10)=7.2, p<0.05]$, indicating larger positive deflections for correctly compared to incorrectly recognised items, which was more pronounced over the left than right hemisphere (see Figure 7-17). This subsequent memory effect seems to endure over a long period of time as no significant response by epoch interactions emerged. Subsidiary analyses employing an ANOVA with the factor of response (correct, incorrect), hemisphere (left, right) and site (inferior, mid, superior) showed, only for the second epoch, a significant response by hemisphere interaction $[F(1,10)=10.6, p<0.01]$. 

In sum, non-semantic stimuli failed to reveal any subsequent memory effects as no significant effects or interactions with response were obtained. Semantic stimuli, however, exhibited differences in encoding activity predictive for subsequent memory performance over frontal and parietal locations. Additional topographical analyses are required to allow inferences regarding the nature of neuronal sources giving rise to these effects.
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7.4.1.2.2 Topographical analysis

Topographic analyses tested whether the frontal and parietal effect obtained under deep and shallow encoding respectively were generated by two qualitatively distinct neural generators. Analyses were performed on difference waveforms contrasting study activity for subsequent correctly vs. incorrectly recognised items (using rescaled data to eliminate effects of size). An ANOVA was performed with the factors of encoding (shallow, deep), epoch (300-600ms, 600-1000ms, 1000-1800ms), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior).

The results demonstrated marginally significant interactions between the factors of encoding, epoch, location and site [F(1.8,18.5)=3.2, p=0.066], which was followed up with focused contrasts directly comparing frontal and parietal differences across deep and shallow encoded semantic stimuli. These tests exhibited no significant location effects across all three time epochs [p>0.05, in all cases]. Therefore, the topographical analyses failed to provide statistical evidence that spatially distinct neuronal generators contribute to the frontal and parietal subsequent memory effect.

7.4.2 Summary

The purpose of the subsequent memory analyses reported here was twofold. First, it was of importance to establish whether ERP activity under deep encoding conditions elicits subsequent memory effects similar to those reported in Chapter 5. Since the encoding task of the present study was comparable to the one employed in the previous experiment, it was predicted that an analogous pattern of ERP activity should be obtained. The results revealed early onsetting subsequent memory effects over frontal locations for deeply encoded semantic but not non-semantic conditions. This finding is indeed compatible with the results reported in the previous study. It should be noted here that the current comparison was limited to intact test conditions. No rearranged pairs were examined. In the previous experiment, rearranged pairs exhibited subsequent memory effects over parietal locations. Nevertheless, parietal
subsequent memory effects were also found in the current experiment for shallowly studied semantic pairs. The possible interpretation of this finding will be discussed shortly.

Secondly, this study aimed to extend previous findings by investigating how encoding strategies might amend stimulus induced subsequent memory. Thus it was of interest whether stimulus conditions modulate subsequent memory effects regardless of the type of encoding task employed. The results demonstrate very clearly that this was not the case, as different subsequent memory effects were obtained under deep and shallow encoding conditions. In fact, non-semantic stimuli failed to elicit subsequent memory effects altogether, whereas semantic stimuli revealed modulations in subsequent memory dependent on the type of encoding task. While deeply encoded semantic stimuli elicited subsequent memory effects over frontal locations, such differences were absent under shallow encoding. Parietal subsequent memory effects, however, were observed for shallowly encoded semantic stimuli but remained absent for deep encoding conditions.

Taken together, the results revealed a dependency of the subsequent memory effect on the nature of the encoding task as well as the nature of the stimuli. This suggests that if the content of the to-be-remembered material matches the structure of pre-existing semantic knowledge, information processing is modulated with respect to subsequent memory performance. However, this modulation is sensitive to, and conditional on, the encoding task employed.
7.5 Discussion

The study presented in this chapter aims to clarify how pre-existing semantic knowledge of to-be-encoded stimuli influences successful memory encoding. The previous study revealed modulations in ERP activity during encoding of word pairs comprising different semantic relations. Furthermore, distinct subsequent memory effects were obtained when semantic pairs were contrasted across different test conditions. The present study was designed to validate these results, but also intended to extend those findings by testing how different encoding strategies alter stimulus induced modulations in encoding activity.

This chapter reports two sets of analyses, one investigating ERP modulations generally elicited during encoding and the other focussing on changes in encoding activity that predicts subsequent memory performance. The discussion will start with the first set of analysis, which included two separate contrasts examining either the three stimulus conditions or the two encoding tasks.

7.5.1 Comparing stimulus conditions

The contrast of all three stimulus conditions failed to reveal any differences in encoding activity under shallow encoding. Deep encoding, however, elicited two distinct modulations, comprising a long lasting frontal component onsetting at about 300ms post stimulus which was characterised by a stronger negative deflection for non-semantic and semantic-one pairs compared to semantic-two pairs (see Figure 7-24).
7.5.1.1 The early frontal effect

The early frontal effect elicited under deep encoding of different semantic stimulus conditions exhibited temporal and spatial distributions typical for an N400 component. As reported previously (see Sections 4.2 and 5.5.1) the N400 component describes a negative deflection at about 400ms after stimulus onset, indexing violations in expectancy or category membership (Polich, 1985; Kutas & Hillyard, 1984; Kutas & Hillyard, 1980). The results obtained here are consistent with the
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functional interpretation of the N400 component, as a stronger negative deflection was elicited for non-semantic pairs which did not fit into the context of a particular category. Semantic-two pairs, in contrast, elicited less negative going deflections while comprising words that are congruent with a particular category. Thus, similar to the frontal differences reported in the previous experiment, the present frontal effects are interpreted to reflect an N400 modulation.

Hence, the present study replicates findings of the first study, although subtle differences regarding the distribution and deflection of the N400 component emerged. While the previous experiment reported centrally distributed N400 components, the results of the current experiment revealed a more frontally distributed N400 component since no differences between stimulus conditions were obtained over parietal locations in the first time window (300-500ms). Furthermore, the non-semantic condition elicited a more negative going ERP deflection compared to semantic-one and semantic-two conditions in the previous study, whereas the present experiment demonstrated more negative going deflections for non-semantic and semantic-one conditions relative to the semantic-two condition. Both these disparities are attributed to minor changes in the experimental design between the first and second experiment. Such changes included a reduced number of trials in individual experimental blocks which was offset by an increased number of blocks in the second experiment. The desired effect of this alteration was a diminished degree of difficulty which enabled satisfactory levels of performance under shallow encoding conditions, but consequently also heightened the level of performance under deep encoding conditions. This alteration in task difficulty might be responsible for the discussed differences in the N400 component across the two experiments.

Furthermore, the total number of trials was slightly reduced to keep the overall length of the experiment within reasonable bounds (below 90 minutes) but allowed testing of both deep and shallow encoding conditions within subjects. The decreased number of incorrectly classified items did not permit ERP contrasts of correctly and incorrectly performed encoding tasks. Although the previous study suggests that the
N400 component is not modulated by response accuracy, the present study cannot speak to this finding.

Nevertheless, the present experiment was able to compare the frontal N400 activity under deep and shallow encoding conditions. While deep encoding reveal modulations in N400 components between stimulus conditions, shallow encoding failed to elicit such frontal differences. This suggests that the N400 component is task specific and emerges only when the semantic content of the word pairs is intentionally processed. It also implies that no processing differences appeared between the different classes of stimuli under shallow encoding as they showed no difference in the cognitive processes indexed by the N400.

### 7.5.1.2 The later parietal effect

In concert with the previous experiment, deep encoding conditions revealed not only frontal but also parietal differences. These parietal modulations (starting at about 500ms) were characterised by a graded deflection with more positive going activity for semantic-two, followed by semantic-one and non-semantic conditions. This pattern of results replicates the parietal modulation reported in the first experiment. As discussed in the previous chapter (Chapter 5) the functional interpretation of this parietal component is more challenging. As far as semantic classification tasks performed across the three stimulus conditions place different processing demands on working memory and attentional mechanisms, parietal ERP effects may index a modulation of the P3b component. As discussed in the previous study (Section 5.5.2) working memory and attentional mechanisms might be engaged to a different degree between the three stimulus conditions, depending on how successfully the pair can be integrated into a given semantic context. As semantic-two pairs can become integrated completely into the categorical context, they are associated with more positive going P3b deflections than semantic-one pairs which in turn lead to more positive parietal activity compared to non-semantic pairs.

Additional insight into the functional interpretation of this parietal modulation may be gained by comparing different encoding conditions. Under the premise that parietal modulations index successful contextual integration, this component should
be more likely to occur for encoding tasks that demand such integration, e.g. semantic categorisation tasks. The shallow encoding condition in the present experiment demonstrates that parietal differences are indeed absent when different semantic stimuli are encoded with a task requiring word length judgements instead of semantic categorisation. This finding is in accordance with the contextual integration hypothesis, although it does not necessarily prove that this is the only possible interpretation.

The current findings indicate that encoding activity is sensitive to the type of semantic material but only when encoded under specific encoding tasks. In addition to that it is possible that encoding activity is modulated when different encoding tasks are contrasted. It is conceivable that deep and shallow encoding conditions cause global modulations that occur across all stimulus conditions to the same degree. Such differences would not have been detected by the analyses contrasting individual stimulus conditions performed so far. If encoding tasks elicit modulations in electrical activity distinct from modulations between different classes of stimuli, it would suggest that encoding tasks and stimulus condition exhibit an independent influence on encoding processes. Alternatively, an interaction between encoding task and stimulus condition would reflect a functional dependence of the two manipulations.

### 7.5.2 Comparing encoding conditions

The second contrast, examining differences in ERP activity between deep and shallow encoding conditions, revealed modulations over frontal and parietal locations, which were surprisingly similar to the modulations reported in the first contrast. Frontal locations elicited stronger negative deflections for deep compared to shallow encoding conditions for non-semantic and semantic-one pairs, but failed to elicit such differences for semantic-two word pairs. These frontal modulations emerged at about 300ms and remained present in later time windows but with a more lateralised distribution. In addition to frontal effects, parietal locations revealed early onsetting differences (at about 300ms) reflecting more positive going waveforms for shallow compared to deep encoding conditions across all three stimulus conditions.
Topographical analyses confirmed that the frontal and parietal modulations were supported by qualitatively distinct neuronal generators that differed not only in spatial but also temporal distribution (see Figure 7-25).

![Figure 7-25](image)

**Figure 7-25** Significant differences in ERP activity between shallow and deep encoding conditions are shown across different classes of stimuli (non-semantic, semantic-one, semantic-two). Modulations in study activity are present for all three stimulus classes which, however, reveal differences in the temporal and spatial distribution of the effect.

### 7.5.2.1 The frontal effect

The early frontal effect elicited during deep compared to shallow encoding conditions revealed an interaction with stimulus conditions. Encoding differences were only present for non-semantic and semantic-one but not semantic-two pairs, suggesting that alterations in encoding activity do not reflect global changes in activity but emerge as a result of altered stimulus related activity. To be precise, the frontal difference between deep and shallow encoding conditions reflects the presence or absence of N400 deflections. Deeply encoded non-semantic and semantic-one conditions are associated with a stronger N400 component compared to
7 Deep and shallow encoding of different classes of semantic stimuli

semantic-two pairs. Shallow encoding conditions, however, failed to elicit N400 deflections all together. Consequently, frontal differences in activity between deep and shallow encoding conditions result from a stronger N400 deflection for deeply encoded non-semantic and semantic-one pairs. As this frontal N400 effect is functionally interpreted as a violation of categorical expectancy, the lack of encoding differences in semantic-two conditions reflects the absence of categorical violations for deeply encoded semantic-two pairs in combination with an absence of categorical expectancy for shallow encoded semantic-two pairs.

7.5.2.2 The parietal effect

Parietal differences between encoding conditions occurred for all three classes of stimuli revealing more positive going waveforms for shallow compared to deep encoding conditions. The size of the parietal effect varied in concert with parietal modulations obtained for the three deep encoded stimulus conditions. As semantic-two conditions elicited more positive going parietal deflections compared to semantic-one or non-semantic pairs, the overall size of the encoding effect was decreased for semantic-two compared to semantic-one or non-semantic conditions. Hence, parietal encoding effects are inter-twined with parietal stimulus effects. But what is the functional interpretation of this parietal encoding component?

A first starting point to answering this question might be the functional interpretation of the parietal modulation between classes of stimuli. This effect has been hypothesised here to reflect a P3b component indexing working memory and attentional processes engaged for successful integration of items into a given semantic context. Although shallow encoding conditions require no semantic integration, working memory processes might still be engaged when comparing the word length of the two words presented in the pair. It is unclear, however, why in general more positive activity is elicited for shallow compared to deep encoding conditions. Larger positive deflections for deeply encoded semantic word pairs were interpreted as reflecting a higher level of working memory load and attentional resources compared to deeply encoded non-semantic pairs. Keeping to this line of argument, even stronger positive deflections for shallow encoded word pairs would
consequently imply that shallow encoding conditions engaged more working memory loads and attentional resources than deep encoding conditions. This seems in conflict with the behavioural data, which reveal higher levels of accuracy and more importantly significantly faster reaction times for shallow compared to deep encoding conditions. This indicates that smaller working memory loads and attentional resources were recruited for shallow compared to deep encoding conditions. This is inconsistent with the interpretation of the more positive going parietal deflections for shallow compared to deep encoding conditions. A possible explanation for this inconsistency might be that different mechanisms contribute to verbal and visual working memory processes (Baddeley, 1986; Baddeley & Hitch, 1974) which reveal changed levels in parietal activity.

In general, the findings discussed so far indicate that encoding activity is sensitive to the type of semantic material and the type of encoding task the material is studied with. Thus it is not possible to infer how to-be-remembered material with semantic characteristics that map onto pre-existing semantic knowledge influences encoding processes without taking into account the precise encoding task under which the material was studied. The question how subsequent storage and retrieval processes may be affected by distinct encoding tasks and classes of stimuli has not been addressed so far. Therefore, a second stage of analysis was performed to investigate whether differences in subsequent memory activity were present when semantic or non-semantic word pairs were studied under deep and shallow encoding conditions.

7.5.3 Subsequent memory: encoding and stimulus conditions

The second part of this chapter investigated differences in subsequent memory effects. Although it was important to verify that subsequent memory effects obtained in the previous study are also present in the current study, the analyses aimed to elucidate how certain types of encoding conditions may contribute or alter subsequent memory effects. Similar to the previous study, the current results show that deep encoding conditions elicited early onsetting subsequent memory effects over frontal locations for semantic but not non-semantic word pairs tested under
intact conditions (see Figure 7-26). Other than a more left lateralised distribution this frontal effect showed similar characteristics to the subsequent memory effect observed in the previous experiment. It was hypothesised in the former experiment that frontal effects indicate elaborate encoding that leads to subsequent retrieval processes primarily driven by recollection, while additional parietal subsequent memory effects, which appeared for rearranged conditions, index subsequent recognition driven by familiarity.

The evaluation of subsequent memory effects for rearranged test conditions could not be performed with the present data, as the experimental design deliberately excluded rearranged test pairs from statistical analysis in order to limit the length of the experiment. Nevertheless, it was essential to include rearranged test pairs in the experimental paradigm per se to prevent strategic memory performance based on only the first word of the pair. The present study confirms that frontal subsequent memory effects occur for intact test pairs when studied under deep encoding conditions.

When comparing deep with shallow encoding conditions, it becomes apparent that the type of encoding task does indeed affect subsequent memory effects. In contrast to deep encoding, shallow encoding conditions failed to elicit frontally distributed subsequent memory effects. However, shallow conditions did elicit parietal subsequent memory effects for semantic compared to non-semantic pairs which were not present under deep encoding conditions (see Figure 7-26). This confirms that the specific type of encoding employed at study modulates subsequent memory effects.

Interestingly, the parietal difference obtained under shallow encoding resembles activity reported across parietal locations for rearranged pairs in the previous study. This effect was interpreted as indexing an increased likelihood of familiarity based recognition in the subsequent memory test. When adopting the same functional interpretation, the present results would suggest that shallowly encoded semantic pairs are more likely to engage familiarity driven retrieval relative to non-semantic pairs. Although this interpretation is not in conflict with the present data, there is little evidence directly supporting this conclusion. For instance, if more
familiarity-based recognition occurred for semantic compared to non-semantic pairs, it might be expected that semantic pairs should show superior behavioural performance compared to non-semantic pairs. However, no significant difference in behavioural performance (neither mean percent correct nor RT) was obtained between shallow encoded semantic and non-semantic word pairs. Whilst, such null effects have to be treated with caution (as the behavioural data may have had insufficient power to reveal existing behavioural differences), it is possible that ERP waveforms are sensitive to modulations in brain activity that do not necessarily lead to changes in behavioural performance. Thus, the absence of behavioural difference between shallowly encoded semantic and non-semantic pairs does not prohibit the association of parietal subsequent memory effects to familiarity related processing.

Subsequent memory effect

comparison of the stimulus and encoding condition

Deep encoding

non-sem

Shallow encoding

non-sem

300-600 600-1000 1000-1800

correct

incorrect
In general, the subsequent memory analysis demonstrates that encoding strategies do influence the pattern of subsequent memory effects. While deep encoding evokes frontal modulations in subsequent memory components for semantic but not non-semantic pairs, shallow encoding conditions demonstrated parietal subsequent memory effect for semantic compared to non-semantic pairs. Hence, changes in subsequent memory effects that emerge between classes of stimuli also depend on the precise encoding task used to study the stimuli. This confirms the claim that encoding processes which predict subsequent retrieval are sensitive to stimulus conditions as well as the encoding tasks employed.

7.6 Summary and Conclusion

The goal of the current study was to investigate whether the successful encoding of semantic and non-semantic word pairs is modulated by depth of processing. The data show that information processing during encoding is dependent on the semantic nature of the stimuli as well as the semantic processing demands of the encoding task, which both seem to elicit modulations in common ERP components. Further analyses employed the subsequent memory paradigm to examine how the different encoding tasks and stimulus conditions influenced effective encoding processes. The results revealed two distinct patterns of subsequent memory effects which were dependent on the nature of the encoding task. Deep and shallow encoding conditions reveal more positive going activity for subsequently remembered compared to forgotten items, but only for semantically related stimuli. This finding strongly suggests that the set of cognitive processes used to facilitate subsequent memory for semantic stimuli are not engaged for non-semantic stimuli. The dependence of the subsequent memory effect on the type of encoding condition supports the conclusion that pre-existing semantic knowledge does alter the process of successful encoding. These results are in line with the findings reported in the
foregoing study. Nevertheless, the current data extend previous findings by demonstrating that stimulus driven modulations evoke different subsequent memory effects under deep and shallow encoding conditions. While deep encoding elicited frontal subsequent memory effects, shallow encoding resulted in parietal subsequent memory effects. Thus, whether semantic stimuli alter encoding processes is ultimately dependent on the particular encoding strategy.
7 Deep and shallow encoding of different classes of semantic stimuli
8 Retrieval of shallow and deep encoded classes of stimuli

8.1 Introduction

Episodic memory contains rich representations of previously encountered events. The results of the former chapter showed that semantic coherence or interrelatedness of elements within events significantly influences the formation and retrieval of episodic memories. The proposal of this thesis is that semantic coherence influences episodic retrieval through cognitive and neuronal operations typically associated with familiarity processing. This relationship will be further explored in the rest of this chapter.

Under consideration that specific knowledge or facts embedded in an episodic memory are likely to be represented and activated in our semantic memory system, it seems possible that the episodic and semantic memory systems interact with one another. The precise cognitive and neuronal operations supporting such interactions, however, remain unclear. Previous proposals about a potential interplay between episodic and semantic memory have focused mainly on interactions evoked by semantic and non-semantic levels of processing (LOP) (Craik & Lockhart, 1972). According to such proposals, an event is better recognised, by means of increased recollection, when studied under semantically deep encoding conditions. Thus, recollection is more strongly modulated by semantic compared to non-semantic encoding processes. Craik and Lockhart (1972) concluded that the efficacy of episodic memory formation depends on the depth of processing engaged during encoding, with semantic processing forming the deepest level. Evidence supporting such proposals has been provided by behavioural and neuroimaging experiments (Kirchhoff, Schapiro, & Buckner, 2005; Craik, 2002; Schott, Richardson-Klavehn, Heinze, & Duzel, 2002; Rugg et al., 2000).

Whilst the importance of semantic encoding strategies is not in doubt, the means by which they interact with semantically organised or semantically coherent stimuli remains unclear. Recent evidence, presented in this thesis, suggests that
interactions between semantic and episodic memories are not only driven by internal mental processes such as encoding strategies, but also by external factors like the semantic nature of the stimuli. Semantically coherent stimuli facilitate recognition performance primarily on the bases of enhanced familiarity processes (Greve, van Rossum, & Donaldson, 2007)\textsuperscript{22}. This highlights an important distinction between the types of semantic manipulations that might be employed when investigating episodic and semantic memory interactions. Manipulations of semantic content inherent to the stimuli and their representations appear to modulate familiarity driven interactions between episodic and semantic memory. Manipulations of semantic context or strategy, which is dependent on the way stimuli are processed, seem to engage more recollection driven interactions according to LOP studies (Yonelinas, 2002).

It may well be that the semantic organisation of stimuli influences episodic retrieval only when a particular encoding context or strategy is adopted. This would imply that modulations in episodic retrieval evoked by semantic stimuli are dependent on the level of processing applied to them. Consequently, an interaction between semantic stimuli and semantic encoding strategy should be obtained. Alternatively, stimulus driven differences in episodic retrieval may emerge independent from a particular encoding strategy. Under this premise semantic stimuli and semantic encoding strategies constitute two independent sources of episodic and semantic memory interactions.

The present study attempts to differentiate between these two potential scenarios. To test the influence of semantic stimuli in the context of different semantic encoding strategies, the current study contrasts retrieval related activity elicited for semantic vs. non-semantic stimuli when studied either under deep or shallow encoding conditions. ERP measures are employed, similar to previous experiments reported in this thesis. It was predicted that semantic compared to non-

\textsuperscript{22} See Appendix B for a reprint of the paper.
Semantic stimuli should be better recognised under deep encoding due to an increased level of familiarity. Furthermore, deep compared to shallow encoded stimuli are expected to reveal overall enhanced levels of recognition performance, primarily on the basis of increased recollection, according to the LOP theory. It is unclear, however, whether changes in recognition performance will occur between semantic and non-semantic stimuli under shallow encoding conditions, establishing either an encoding dependent or independent influence of semantic stimuli on episodic and semantic memory interactions.

In the present study, participants encoded word pairs at two different levels of processing: one requiring judgement of the word length (shallow encoding condition) and the other involving judgement of semantic relatedness (deep encoding condition). As mentioned above, memory retrieval is expected to be less likely following shallow compared to deep encoding tasks. The LOP theory holds that perceptual and lexical levels of processing precede the conceptual level typically engaged for deep encoding conditions. LOP effects should therefore reflect differential activity in neuronal structures responsible for conceptual processing. The present experiment addresses the question of whether the influence of semantically coherent stimuli is limited to conceptual levels of processing. The current study is expected to yield new information about the relationship between internal and external semantic manipulations and their influence on episodic and semantic memory interactions.

### 8.2 Material and Methods

#### 8.2.1 Participants

The same group of participants as reported in the previous chapter performed the recognition memory task described in the current chapter. Thus, the following results describe the performance of 16 (5 female) subjects, who had an average age of 24 years.
8.2.2 Material and Procedures

This study was based on an experimental procedure and stimuli that were identical to the one reported in the previous chapter (Chapter 7).

8.2.3 ERP recording and analysis

Scalp EEG was recorded in exactly the same manner as described in the previous Chapters (Sections 5.2.4 and 7.2.4). The ERP analyses were designed to investigate possible differences in retrieval activity evoked by correctly identified intact (previously studied) and new (previously not studied) semantic and non-semantic pairs of words that were either studied under shallow or deep encoding conditions. The data at test were analysed over 4 consecutive time windows (300-600ms, 600-900ms, 900-1200ms, 1200-2000ms) chosen based on previously reported effects and because they are expected to capture differences in activity in the present data based on visual inspection.

8.3 Results at retrieval

8.3.1 Behavioural data

The likelihood of correct task performance for previously studied (intact) and non-studied (new) pairs of semantic and non-semantic word pairs encoded either under deep or shallow conditions are displayed in Figure 8-1. An ANOVA including the factors of encoding (shallow, deep), stimulus (non-semantic, semantic) and test (intact, new) showed a significant interaction between the factors of encoding and stimulus [F(1,15)=10.2, p<0.01], encoding and test [F(1,15)=42.7, p<0.001], as well as test and stimulus [F(1,15)=23.5, p<0.001], in addition to main effects of stimulus [F(1,15)=8.9, p<0.01] and test [F(1,15)=4.9, p<0.05].

Subsidiary analyses focused on differences in recognition performance across stimulus conditions by performing a pair-wise semantic vs. non-semantic contrast for individual encoding and test conditions. While shallow encoding failed to show any significant stimulus effects for intact or new test condition, deep encoding evoked a
highly significant stimulus effect ($t(15)=5.9$, $p<0.001$) solely for intact pairs. This difference in performance across stimuli reflects significantly higher levels of correct recognition for deeply encoded semantic compared to deeply encoded non-semantic pairs. Furthermore, analysing differences in task performance between encoding conditions revealed significant encoding effects for semantic ($t(15)=6.4$, $p<0.001$) as well as non-semantic stimuli ($t(15)=2.1$, $p<0.05$) under intact test conditions. These effects are driven by a significantly higher proportion of hits for deep compared to shallow encoding conditions. New test conditions also exhibited significant encoding effects for semantic ($t(15)=6.4$, $p<0.001$) as well as non-semantic conditions ($t(15)=6.4$, $p<0.001$).

These behavioural results suggest that recognition performance is enhanced when stimuli were semantically coherent, but only when such stimuli were studied under deep encoding conditions. Furthermore, deep encoding conditions reveal an overall increase in hits and a decrease in correct rejections across semantic and non-semantic stimuli.

![Figure 8-1](image)

Figure 8-1 Behavioural data showing mean correct responses for previously studied (intact) and new (new) words encoded under shallow and deep conditions. Mean probability (and standard error) of correct task performance reveal significantly more correct responses for deeply encoded semantic than non-semantic intact conditions. Overall performance shows significant differences across shallow and deep encoding conditions for intact as well as new test conditions.
8.3.2 ERP data

Grand average ERPs elicited for correctly recognised intact and correctly rejected new non-semantic stimuli studied under shallow encoding conditions are shown in Figure 8-2. The mean number of trials contributing to the average waveforms is 28 for intact, and 29 for new pairs.

![Grand average ERPs](image)

**Figure 8-2** Grand average ERPs elicited for correctly recognised intact (blue) and correctly rejected new (black) non-semantic stimuli that were studied under shallow encoding conditions. Differences between the waveforms emerge over frontal and parietal locations, highlighting modulations in neuronal activity for successfully recognised stimuli.

ERP activity for shallowly encoded non-semantic stimuli demonstrates more positive going activity for correctly identified intact compared to new conditions. This difference emerges over frontal locations and onsets at about 300ms post stimulus (see Figure 8-3 for enlarged illustration of selected electrode sites). Parietal locations also show more positive going ERP activity for correctly identified intact compared to new conditions as early as 300ms, but this difference is maximal.
between 600 and 900ms post stimulus. While parietal modulations in activity start to decrease at about 900ms, right frontal electrodes still exhibit small differences in retrieval activity until the end of the recording epoch.

Figure 8-3 Grand average ERPs elicited for correctly recognised intact (blue) and correctly rejected new (black) non-semantic stimuli studied under shallow encoding conditions. ERP waveforms are displayed at 3 frontal (F1, Fz, F2) and 3 parietal (CP1, CPz, CP2) electrodes, whose locations are highlighted in green on the schematic top down view of the head. The frontal electrodes show more positive going deflections for intact compared to new stimuli, onsetting at about 300ms post stimulus. Parietal electrodes also reveal more positive going activity for intact compared to new stimuli, which seems to diverge at about the same time as frontal differences, but shows considerable modulations between 600 and 900ms.

Grand average ERPs elicited for correctly recognised intact and correctly rejected new semantic stimuli studied under shallow encoding conditions are shown in Figure 8-4. The mean number of trials contributing to the average waveforms is 29 for intact, and 28 for new pairs.
Figure 8-4 Grand average ERPs elicited for correctly recognised intact (red) and correctly rejected new (black) semantic stimuli that were studied under shallow encoding conditions. Modulations in ERP activity emerge over frontal and parietal locations, which indicates changes in neuronal activity for successfully recognised stimuli.

Figure 8-5 Grand average ERPs elicited for correctly recognised intact (red) and correctly rejected new (black) semantic stimuli that were studied under shallow encoding conditions. The frontal electrodes show more positive going deflections for intact compared to new stimuli, onsetting at about 300ms post stimulus. Parietal electrodes also reveal more positive going activity for intact compared to new stimuli, which shows a considerable divergence between 600 and 900ms.
Semantic stimuli studied under shallow encoding conditions show more positive going activity for correctly identified intact compared to new word pairs, bilaterally distributed over frontal electrodes (see Figure 8-5 for a more detailed illustration of selected electrode sites). This difference onsets at about 300ms post stimulus and is sustained over a long period of time. In addition to persisting frontal differences, more positive going waveforms emerge for correctly identified intact vs. new word pairs across parietal locations at about 600ms post stimulus. While these parietal differences disappear at about 1200ms, frontal modulations, particularly at right frontal electrodes, are sustained until the end of the recording epoch.

Grand average ERPs for correctly recognised intact and correctly rejected new non-semantic stimuli which were studied in the context of a deep encoding task are displayed in Figure 8-6. The mean number of trials contributing to the average waveforms is 32 for intact, and 25 for new pairs.

**Figure 8-6** Grand average ERPs elicited for correctly recognised intact (blue) and correctly rejected new (black) non-semantic stimuli that were studied under deep encoding conditions. Differences in ERP activity emerge primarily over parietal electrodes, showing changes in neuronal activity for successfully recognised stimuli.
Correctly identified intact compared to new non-semantic word pairs, which were studied under deep encoding conditions, demonstrate more positive going ERP activity at parietal locations between 600ms and 900ms post stimulus. No divergence in frontal activity is apparent prior to this parietal modulation (see Figure 8-7 for a more detailed illustration of selected electrode sites). Nevertheless, frontal activity seems to fluctuate between intact and new conditions from about 1200ms onwards.

![Figure 8-7](image)

Figure 8-7 Grand average ERPs elicited for correctly recognised intact (blue) and correctly rejected new (black) non-semantic stimuli that were studied under deep encoding conditions. The frontal electrodes show no obvious difference in ERP activity between intact and new test conditions. Parietal electrodes, however, reveal more positive going activity for intact compared to new stimuli between 600 and 900ms.

Finally, grand average ERPs for correctly recognised intact and correctly rejected new semantic stimuli studied under deep encoding conditions are shown in Figure 8-8. The mean number of trials contributing to the average waveforms is 39 for intact, and 25 for new pairs.
Figure 8-8 Grand average ERPs elicited for correctly recognised intact (red) and correctly rejected new (black) semantic stimuli that were studied under deep encoding conditions. Modulations in ERP activity appear over frontal and parietal a location, suggesting differences in neuronal activity for successfully recognised stimuli.

Under deep encoding conditions, a more positive modulation in activity is present for correctly identified intact compared to new semantic word pairs over frontal locations from about 300ms onwards (see Figure 8-9 for enlarged presentation of specific electrode sites). Subsequent to this frontal divergence, parietal locations also reveal more positive going ERP activity for correctly identified intact compared to new word pairs from about 600ms onwards. While parietal differences disappear at about 1200ms, left frontal electrodes exhibit small differences in encoding activity towards the end of the recording interval.
Following the visual inspection, changes in electrical activity were characterised by means of statistical analyses. For this purpose, average voltages were calculated over four consecutive epochs (300-600ms, 600-900ms, 900-1200ms, 1200-2000ms), which were in line with previously reported studies (Sections 5.2.4 and 7.2.4) and are furthermore expected to capture the obtained changes in electrical activity.
8.3.3 ERP analyses

8.3.3.1 Shallow encoding conditions

Statistical analyses were performed to examine differences in ERP activity evoked by individual stimulus conditions studied under shallow encoding by employing an ANOVA with the factors of test (old = hit, new = correct rejection), epoch (300-600ms, 600-900ms, 900-1200ms, 1200-2000ms), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior). Non-semantic stimuli revealed a range of significant interactions with the factor of test, of which the most noteworthy was a test by epoch by location by hemisphere interaction \[F(2.2, 32.6)=4.2; \ p<0.05\]. Similarly the semantic conditions exhibited a variety of significant interaction with the factor of test, including a test by epoch by location by hemisphere by site interaction \[F(3.0, 44.9)=4.1; \ p<0.05\]. These results indicate changes in the pattern of the old/new effects across time and locations for both stimulus conditions.

Subsequent analyses specifically explored the pattern of temporal and spatial modulation of ERP old/new effects by employing ANOVA with the factors of test (old, new), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior) across the four consecutive time windows. The resulting effects obtained for non-semantic and semantic stimulus conditions are presented below.

8.3.3.1.1 Non-semantic stimuli

Recognition performance for non-semantic stimuli previously studied under shallow encoding conditions revealed significant interactions involving the factor of test across all four time windows (see Table 8-1). The pattern of interactions suggests that modulations in ERP activity for intact and new test conditions differ depending on specific locations, hemispheres and sites. A subsidiary set of analysis separated the data over frontal and parietal locations and employed an ANOVA with the factors of test (old, new), hemisphere (left, right) and site (inferior, mid, superior).
Table 8-1 This table shows significant effects and interactions with the factor of test for non-semantic stimuli, which were previously studied under shallow encoding conditions. The significant effects resulted from an ANOVA with the factors of test, location, hemisphere and site, which are displayed separately for all four epochs.

Analyses conducted across frontal locations elicited significant effects and interactions with the factor of test within all four time windows (see Table 8-2). These effects and interactions demonstrate more positive going deflections for intact compared to new non-word pairs throughout the entire recording epoch. Nevertheless, pair-wise comparisons of ERP activity between intact and new conditions indicate a shift in the distribution from more central towards right frontal locations as recording time progresses. More precisely, the first time window reveals significant differences in ERP activity for intact and new conditions across all six frontal electrode sites (p<0.05, in all cases). The second time window shows a similar profile of significant differences (p<0.05, in all cases except F5). The last two time windows, however, demonstrated significant differences in the pair-wise comparisons only at right frontal electrode site F6 (t(15)=3.0, p<0.01), F4 (t(15)=3.2, p<0.01), F2 (t(15)=2.5, p<0.05) within the third time window as well as F6 (t(15)=2.3, p<0.05) and F4 (t(15)=2.8, p<0.05) in the fourth time window.
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Table 8-2 This table shows significant effects and interactions with the factor of test for non-semantic stimuli, which were previously studied under shallow encoding conditions. The significant effects resulted from an ANOVA with the factors of test, hemisphere and site, which are shown separately for all four epochs.

<table>
<thead>
<tr>
<th>Effects for non-semantic stim.</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>at frontal locations</td>
<td>300-600</td>
</tr>
<tr>
<td>test</td>
<td>p=0.001</td>
</tr>
<tr>
<td>test by hem</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>test by site</td>
<td>p&lt;0.001</td>
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</tbody>
</table>

Parietal electrodes also elicited significant effects and interactions with the factor of test across all four time windows (see Table 8-3). The first three time windows demonstrated a significant effect of test, in combination with a test by site interaction. The last time window showed a slight variation in the pattern of activity; a significant effect of test and a test by hemisphere by site interaction was obtained. Follow up comparisons, including pair-wise contrasts of electrical activity for intact vs. new stimuli, revealed significant differences at all individual electrode sites across the first three time windows (p<0.05, in all cases). Differences in the fourth time window, however, were limited to right parietal electrodes: CP6 (t(15)=3.3, p<0.01), CP4 (t(15)=2.7, p<0.05), CP2 (t(15)=2.2, p<0.05).

Table 8-3 This table shows significant effects and interactions with the factor of test over parietal locations for non-semantic stimuli, which were previously studied under shallow encoding conditions. The significant effects resulted from an ANOVA with the factors of test, hemisphere and site, which are shown separately for all four epochs.

<table>
<thead>
<tr>
<th>Effects for non-semantic stim.</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>at parietal locations</td>
<td>300-600</td>
</tr>
<tr>
<td>test</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>test by site</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>test by hem. by site</td>
<td>-</td>
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</tbody>
</table>
Overall, recognition performance for non-semantic stimuli, studied under shallow encoding conditions, revealed a significant bilateral frontal difference in concert with a bilateral parietal difference between intact and new conditions from about 300ms onwards. These differences were long lasting and remained present in the subsequent second and third time window. With progression in time, the distribution of these effects gradually shifted from a bilateral towards more right hemispheric activity in the fourth time window.

### 8.3.3.1.2 Semantic stimuli

Semantic stimuli studied under shallow encoding conditions demonstrated significant effects and interactions involving the factor of test across all four time windows (see Table 8-4). The results indicate modulations in intact vs. new effects across time, hemisphere, location and electrodes. Subsidiary analyses separated the data over frontal and parietal locations and employed an ANOVA with the factors of test (old, new), hemisphere (left, right) and site (inferior, mid, superior).

<table>
<thead>
<tr>
<th>Effects for non-semantic stim.</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shallow encoding</td>
<td>300-600</td>
</tr>
<tr>
<td>test</td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td>test by hem</td>
<td>-</td>
</tr>
<tr>
<td>test by site</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>test by loc. by hem. by site</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 8-4 This table shows significant effects and interactions with the factor of test for semantic stimuli, which were previously studied under shallow encoding conditions. The significant effects resulted from an ANOVA with the factors of test, location, hemisphere and site are displayed separately for all four epochs.

The statistical results at frontal electrodes revealed significant effects and interactions with the factor of test in all four time windows (see Table 8-5). These effects and interactions reflect more positive going activity for intact compared to
new word pairs. Follow-up analyses focussing on individual electrodes revealed significant differences between intact vs. new conditions only within the first two time windows. For the first time window, significant differences were found at nearly all electrodes (p<0.05, in all cases except F5), while the second time window demonstrated significant differences across frontal locations primarily at right-central electrodes: F1 (t(15)=2.3, p<0.05), F2 (t(15)=2.9, p<0.05), F4 (t(15)=2.7, p<0.05). Differences in the third and fourth time window, however, failed to elicit significant differences in activity at single electrodes. Thus frontal activity seems to reveal robust differences in the beginning of the recording epoch with a slight bias towards the right hemisphere. This difference undergoes changes in the second half of the recording epoch and is only obtained in the form of a test by hemisphere by site interaction and is not significant at any individual electrode (see Table 8-5).

<table>
<thead>
<tr>
<th>Effects for semantic stim.</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>at frontal locations</td>
<td>300-600</td>
</tr>
<tr>
<td>test</td>
<td>p=0.01</td>
</tr>
<tr>
<td>test by hem</td>
<td>-</td>
</tr>
<tr>
<td>test by site</td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td>test by hem. by site</td>
<td>-</td>
</tr>
</tbody>
</table>

*Table 8-5* This table shows significant effects and interactions with the factor of test over frontal locations for semantic stimuli, which were previously studied under shallow encoding conditions. The significant effects resulted from an ANOVA with the factors of test, hemisphere and site, which are displayed separately for all four epochs.

Similar to frontal locations parietal locations indicate significant effects and interactions with the factor of test, within the first three time windows (see Table 8-6). While the first two time windows exhibit a significant effect of test and a test by site interaction, the third time window reveals a main effect of test. Comparisons performed at individual electrodes revealed significant differences between intact vs. new activity at all individual electrodes within the first three time windows (p<0.05,
in all cases). ERP activity for intact conditions is more positive going compared to new conditions. As all electrodes revealed significant differences, the test by site interaction obtained with the ANOVA in the first two time windows does not reflect the presence or absence of the effect across electrodes, but it rather indicates a larger difference in activity between intact and new stimuli towards central electrode sites.

Table 8-6 This table shows significant effects and interactions with the factor of test over parietal locations for semantic stimuli, which were previously studied under shallow encoding conditions. The significant effects resulted from an ANOVA with the factors of test, hemisphere and site, which are displayed separately for all four epochs.

<table>
<thead>
<tr>
<th>Effects for semantic stim.</th>
<th>time window in ms</th>
<th>300-600</th>
<th>600-900</th>
<th>900-1200</th>
<th>1200-2000</th>
</tr>
</thead>
<tbody>
<tr>
<td>at parietal locations</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>test</td>
<td>p&lt;0.001</td>
<td>p&lt;0.001</td>
<td>p&lt;0.01</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>test by site</td>
<td>p&lt;0.05</td>
<td>p&lt;0.05</td>
<td>-</td>
<td>-</td>
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</tr>
</tbody>
</table>

In general, semantic stimuli studied under shallow encoding conditions exhibit significant modulations in activity for intact vs. new conditions across frontal electrodes, especially within the first two time windows. The topography of the frontal modulations shows a slight bias towards the right hemisphere. In parallel to frontal activity, parietal locations revealed significant differences in activity for intact compared to new conditions across the first three time intervals. This difference was maximal at superior electrode sites.
8.3.3.2 Deep encoding conditions

Besides the investigation of retrieval induced differences in ERP activity for shallowly encoded items, corresponding examinations were performed for stimuli studied under deep encoding conditions. Thus, differences in ERP activity associated with the factor of test were examined with an ANOVA including the factors of test (old, new), epoch (300-600ms, 600-900ms, 900-1200ms, 1200-2000ms), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior). Non-semantic stimuli revealed a range of significant interactions with the factor of test, including a test by epoch by location by hemisphere interaction \[F(1.9, 28.8)=5.3; p<0.01\]. Semantic conditions revealed a variety of significant interaction with the factor of test, including a test by epoch by location by hemisphere by site interaction \[F(3.2, 48.4)=2.8; p<0.05\]. These results indicate differences in the temporal and spatial occurrence of ERP old/new effects, for deeply encoded semantic and non-semantic stimuli.

Subsidiary analyses employed ANOVA with the factors of test (old, new), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior) across all four consecutive time windows. The resulting effects obtained for non-semantic and semantic stimulus conditions are presented now in turn.

8.3.3.2.1 Non-semantic stimuli

Non-semantic stimuli exhibited significant interactions with the factor of test from the second time window onwards (see Table 8-7). The second, third and fourth time windows reveal significant test by location by hemisphere interactions, suggesting that modulations in activity for intact vs. new conditions differs across location and hemisphere. An additional set of analyses separated the data across frontal and parietal locations and employed an ANOVA with the factors of test (old, new), hemisphere (left, right) and site (inferior, mid, superior).
Table 8-7 This table shows significant effects and interactions with the factor of test for non-semantic stimuli, which were previously studied under deep encoding conditions. The significant effects resulted from an ANOVA with the factors of test, location, hemisphere and site, which are displayed separately for all four epochs.

<table>
<thead>
<tr>
<th>Effects for non-semantic stim.</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deep encoding</td>
<td>300-600</td>
</tr>
<tr>
<td>test</td>
<td>-</td>
</tr>
<tr>
<td>test by loc.</td>
<td>-</td>
</tr>
<tr>
<td>test by hem</td>
<td>-</td>
</tr>
<tr>
<td>test by site</td>
<td>-</td>
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<tr>
<td>test by loc. by hem</td>
<td>-</td>
</tr>
</tbody>
</table>

Frontal locations elicited significant interactions involving the factor of test only in the third and fourth time window, in the form of a test by hemisphere interaction (see Table 8-8). Pair-wise comparisons at individual electrodes, however, failed to show any significant effects. Thus, the significant test by hemisphere interaction describes a change in the activity profile across hemispheres, which shows more positive activity for intact compared to new stimuli across the right hemisphere in the third time window, but a more negative deflection for intact compared to new conditions across the left hemisphere in the fourth time window (see Figure 8-6).

Table 8-8 This table shows significant effects and interactions with the factor of test for non-semantic stimuli, which were previously studied under deep encoding conditions. The significant effects resulted from an ANOVA with the factors of test, hemisphere and site, which are displayed separately for all four epochs.

<table>
<thead>
<tr>
<th>Effects for non-semantic stim.</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>at frontal locations</td>
<td>300-600</td>
</tr>
<tr>
<td>test by hem</td>
<td>-</td>
</tr>
</tbody>
</table>
Parietal locations disclose a significant effect of test and a test by site interaction, which is limited to the second time window (see Table 8-9) and reflects more positive going deflections for intact compared to new stimuli. Contrasts at individual electrodes showed significant differences in ERP activity at nearly all parietal electrode sites ($p<0.05$, for all cases with the exception of CP6). Consequently, the results show differences in intact vs. new activity that occurs in the second time window, with a slight, but non significant shift towards the left hemisphere.

Table 8-9 This table shows significant effects and interactions with the factor of test over parietal locations for non-semantic stimuli, which were previously studied under deep encoding conditions. The significant effects resulted from an ANOVA with the factors of test, hemisphere and site, which are displayed separately for all four epochs.

<table>
<thead>
<tr>
<th>Effects for non-semantic stim.</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>at parietal locations</td>
<td>300-600</td>
</tr>
<tr>
<td>test</td>
<td>-</td>
</tr>
<tr>
<td>test by site</td>
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</tbody>
</table>

Taken together, the electrical activity associated with recognition performance for non-semantic stimuli studied under deep encoding conditions failed to elicit significant difference in the first time window. The first significant difference between intact vs. new conditions appeared in the second time window over left parietal electrodes. This difference was limited to the second time window, as no further parietal modulations were obtained beyond 900ms. Within the third and fourth time window intact and new conditions elicited significant differences in activity over frontal electrodes across the left and right hemisphere, albeit it was not significant at any individual electrode sites.
8.3.3.2.2 Semantic stimuli

Finally, semantic stimuli studied under deep conditions were examined with an ANOVA including the factors of test (old, new), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior) across all four consecutive time windows. Significant interactions involving the factor of test were found across all time windows with the exception of the third one (see Table 8-10). While the first time window resulted simply in a main effect of test, the second and fourth time window revealed multiple interactions with location, hemisphere and site. Subsidiary analyses separated the data over frontal and parietal locations, employing an ANOVA with the factors of test (old, new), hemisphere (left, right) and site (inferior, mid, superior).

<table>
<thead>
<tr>
<th>Effects for semantic stim.</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deep encoding</td>
<td>300-600</td>
</tr>
<tr>
<td>test</td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td>test by loc.</td>
<td>-</td>
</tr>
<tr>
<td>test by hem</td>
<td>-</td>
</tr>
<tr>
<td>test by site</td>
<td>-</td>
</tr>
<tr>
<td>test by hem. by site</td>
<td>-</td>
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</tbody>
</table>

Table 8-10 This table shows significant effects and interactions with the factor of test for semantic stimuli, which were previously studied under deep encoding conditions. The significant effects resulted from an ANOVA with the factors of test, location, hemisphere and site, which are displayed separately for all four epochs.

Frontal locations revealed significant effects and interactions with the factor of test across all four time windows (see Table 8-11). The first time window displayed a main effect of test and a test by site interaction, while the second time window showed a main effect of test in combination with a test by hemisphere by site interaction. In contrast to the first two time windows, the third and fourth time window failed to reveal a main effect of test, but showed a test by hemisphere by site interactions.
interaction instead. All of these findings reflect a more positive going deflection for intact compared to new conditions. In the follow-up analyses, performed at individual electrodes, the first two time windows revealed significant differences at superior electrode sites. To be precise, significantly more positive activity for intact vs. new conditions were found in the first time window at electrode F1 (t(15)=2.3, p<0.05), F3 (t(15)=2.3, p<0.05) and F4 (t(15)=2.3, p<0.05), and in the second time window for electrode F1 (t(15)=2.1, p<0.05), F2 (t(15)=2.2, p<0.05) and F4 (t(15)=2.9, p<0.05). The third time window failed to elicit differences at single electrodes, while the fourth time window demonstrated significant differences at electrode F3 (t(15)=2.8, p<0.05) and F5 (t(15)=2.9, p<0.05), but this difference described more negative going deflections for intact compared to new items. Thus frontal locations show early onsetting mid-frontal differences in electrical activity which disappear after 900ms, while left frontal differences emerge in the last time window.

<table>
<thead>
<tr>
<th>Effects for semantic stim.</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>at frontal locations</td>
<td>300-600</td>
</tr>
<tr>
<td>test</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>test by hem</td>
<td>-</td>
</tr>
<tr>
<td>test by site</td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td>test by hem. by site</td>
<td>-</td>
</tr>
</tbody>
</table>

*Table 8-11* This table shows significant effects and interactions with the factor of test for semantic stimuli, which were previously studied under deep encoding conditions. The significant effects resulted from an ANOVA with the factors of test, hemisphere and site, which are displayed separately for all four epochs.

In the first two time windows parietal electrodes exhibit significant main effects of test without additional higher level interactions (see Table 8-12). Follow up comparisons at individual electrodes revealed significantly larger positive activity for intact vs. new conditions at all parietal electrode sites in the first as well as second time window (p<0.05, in all cases).
Retrieval of shallow and deep encoded classes of stimuli

Table 8-12 This table shows significant effects and interactions with the factor of test over parietal locations for semantic stimuli, which were previously studied under deep encoding conditions. The significant effects resulted from an ANOVA with the factors of test, hemisphere and site, which are displayed separately for all four epochs.

In sum, semantic stimuli studied under deep encoding conditions demonstrated, across the first and second time windows more positive going deflections for intact compared to new test conditions at frontal as well as parietal electrode sites. While frontal locations demonstrated within the third time window intact vs. new differences only across hemisphere and site, frontal differences re-emerged in the last time window, primarily with a focus over left frontal locations.

Differences for intact/new pairs, shallow encoding

Figure 8-10 Significant differences in ERP activity between correctly identified intact and new test conditions are illustrated for semantic and non-semantic stimuli previously studied under shallow encoding conditions. The cartoon shows the distribution of frontal and parietal differences across the four time windows.
Figure 8-11 Significant differences in ERP activity between correctly identified intact and new test conditions are illustrated for semantic and non-semantic stimuli previously studied under deep encoding conditions.

8.3.4 Magnitude analyses

So far the analyses have revealed frontal and parietal differences in ERP activity for intact and new conditions. Such results, however, do not indicate whether the effects vary in magnitude. It is possible that larger intact vs. new effects occur either at frontal or parietal locations. Furthermore, the effect size of frontal or parietal differences might be modulated across the type of stimuli and encoding conditions. Therefore, the following analysis explores quantitative differences in effect size by contrasting frontal and parietal activity within single time windows. Differences in effect size are assessed between semantic and non-semantic stimuli, and across shallow and deep encoding conditions, as well.

8.3.4.1 Shallow encoding condition

Potential differences in the size of intact vs. new effects were examined across frontal and parietal locations. Since shallowly encoded non-semantic stimuli revealed intact vs. new differences at frontal as well as parietal locations across all four time windows, magnitude analyses were employed at all four time windows. These comparisons were conducted on difference waveforms obtained by subtracting
new from intact ERP activity. Changes in effect size across location were statically assessed with ANOVA, including the factors of location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior).

While the first time window failed to elicit significant effects of location, the remaining three time windows revealed significant interactions between the factors of location and hemisphere or site. More specifically, the second time window elicited a significant effect of location \([F(1, 15)=7.8; p<0.05]\) and a location by site interaction \([F(1.7, 25.3)=10.0; p<0.01]\) (for illustration of the effect sizes see Figure 8-12). Follow up comparisons at single electrodes demonstrated significantly different effect sizes at electrode E3 \((t(15)=-4.1, p<0.01)\), E1 \((t(15)=-3.7, p<0.01)\) and E2 \((t(15)=-2.4, p<0.05)\). This indicates that parietal electrodes reveal significantly larger effect sizes than frontal locations, most prominently at superior sites.

![Figure 8-12](image)

**Figure 8-12** Differences in effect size across frontal (striped bar) and parietal (solid bar) electrode sites in the second time window (600-900ms) previously studied under shallow encoding conditions. Mean (and standard error) of the effect size of correctly identified intact and new conditions are compared across six frontal and parietal electrodes. Superior parietal electrodes reveal significantly larger effect sizes compared to frontal locations.

\(^{23}\) Note that this comparison is performed at a virtual electrode as differences in activity obtained at frontal locations are directly contrasted with activity obtained at parietal locations.
The third time window also revealed significant location by site [F(1.9, 28.9)=7.2; p<0.01] and location by hemisphere interactions [F(1, 15)=6.0; p<0.05] (see Figure 8-13). Subsidiary contrasts at the electrode level demonstrated significant differences at electrode E3 (t(15)=-3.2, p<0.01) and E1 (t(15)=-2.4, p<0.05). Similar to the second time window, parietal locations elicit effects that were significantly larger in size compared to frontal effects, specifically over the left hemisphere.

![Figure 8-13](image)

**Figure 8-13** Differences in effect size across frontal (striped bar) and parietal (solid bar) electrode sites in the third time window (900-1200ms) previously studied under shallow encoding conditions. Left lateralised parietal electrodes reveal significantly larger effect sizes compared to frontal locations.

Finally, magnitude differences in the fourth time interval were evident as significant location by hemisphere interaction [F(1, 15)=9.0; p<0.01] (see Figure 8-14). Significant differences at individual electrodes were once more present at E3 (t(15)=-2.9, p<0.05) and E1 (t(15)=-2.0, p<0.05), indicating significantly larger parietal than frontal effect sizes, primarily across the left hemisphere.
8 Retrieval of shallow and deep encoded classes of stimuli

Figure 8-14 Differences in effect size across frontal (striped bar) and parietal (solid bar) electrode sites in the fourth time window (1200-2000ms) previously studied under shallow encoding conditions. Left hemispheric parietal electrode sites reveal significantly larger effect sizes compared to frontal locations.

The magnitude analyses were also performed on differences waveforms for semantic stimuli. In this instance frontal and parietal intact vs. new effects only occurred in the first two time windows. Changes in effect sizes across locations were therefore assessed with an ANOVA employing the factors of location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior). However, neither the first nor the second time window revealed any significant effect or interaction with the factor of location. Thus, there is no indication that the magnitude of intact vs. new effects differs between frontal and parietal locations when semantic stimuli were tested.

Although no change in magnitude occurred for the semantic stimuli it is possible that modulations may occur between the types of stimuli. In other words, the magnitude of frontal and parietal differences may be influenced by whether shallow encoded stimuli were of semantic or non-semantic nature. This possibility was tested by submitting intact vs. new difference waveforms to an ANOVA with the factors of stimulus (semantic, non-semantic), hemisphere (left, right) and site (inferior, mid, superior) across the first two time windows at frontal locations, and the first three
time windows at parietal locations. Significant intact vs. new effects have previously been observed at these locations and time windows (compare Figure 8-10). However, none of these contrasts revealed any significant effect or interaction with the factor of stimulus, suggesting that no significant differences in effect size was present for shallowly encoded non-semantic compared to shallowly encoded semantic stimuli.

Nevertheless, it should be noted that these results by no means imply the absence of significant differences in the overall profile of intact vs. new effects, as the current comparison only focussed on existing intact vs. new effects present for semantic as well as non-semantic stimuli. Consequently, the results permit the conclusion that when both stimulus conditions do express significant intact vs. new effects, the size of such effects is not dependent on the specific type of stimuli.

8.3.5 Deep encoding condition

Differences in effect sizes were also assessed for deeply encoded items. The simultaneous occurrence of frontal and parietal differences was more limited under deep encoding conditions, as significant effects occurred for semantic stimuli only within the first two time windows (compare Figure 8-11). Potential magnitude differences were assessed with an ANOVA including the factors of location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior). Whilst the first time window failed to show any significant effects or interactions with location, the second time window revealed a main effect of location. Subsidiary analyses at individual electrodes confirmed significant differences at selective sites; E5 (t(15)=−2.1, p<0.05), E2 (t(15)=−2.0, p<0.05) and E6 (t(15)=−2.2, p<0.05), while other electrodes did not quite reach significance (for illustration see Figure 8-15). Nevertheless, parietal electrodes demonstrated an overall elevated level of effect size compared to frontal electrodes in the second time window.
Potential differences in effect size between semantic and non-semantic stimuli were also assessed under deep encoding. The only contrasts that qualified for this comparison were parietal effects elicited for semantic and non-semantic pairs in the second time window (see Figure 8-12). Nevertheless, an ANOVA including the factors of stimulus (semantic, non-semantic), hemisphere (left, right) and site (inferior, mid, superior) demonstrated no significant effect or interaction with the factor of stimulus. Hence, the obtained parietal effects did not differ in magnitude between deeply encoded semantic compared to non-semantic stimuli.

**8.3.5.1 Contrasts across shallow and deep encoding conditions**

Finally, in addition to differences in magnitude evoked by the type of stimuli, the present experiment also allowed investigations of potential magnitude differences between shallow and deep encoding conditions. The logic behind such contrasts is that the level to which an item was initially studied may influence subsequent retrieval. Intact vs. new difference waveforms were created for non-semantic and
semantic stimuli studied under deep and shallow encoding conditions, which were each submitted to an ANOVA including the factors of encoding (shallow, deep), hemisphere (left, right) and site (inferior, mid, superior). The contrast for non-semantic stimuli was limited to parietal effects emerging in the second time window. The outcome of this analysis revealed a significant effect of encoding \([F(1, 15)=10.7; p<0.01]\) for non-semantic stimuli. Secondary contrasts of effect sizes across individual parietal electrodes demonstrated significant differences at all tested sites \((p<0.05)\) with the exception of electrode CP5 \((p>0.05)\). Surprisingly, shallowly encoded non-semantic stimuli elicited larger differences in activity in comparison to deeply encoded non-semantic stimuli (see Figure 8-16 left panel). Thus, in the context of non-semantic material the type of encoding condition seems to influence electrical activity associated with successful retrieval across parietal locations between 600-900ms.

![Figure 8-16](image_url)

**Figure 8-16** Differences in effect size at parietal electrodes in the second time window (600-900ms) are shown for non-semantic stimuli (left panel) and semantic stimuli (right panel) encoded either under shallow or deep encoding conditions. Significantly larger effect sizes were present for shallow compared to deep encoding non-semantic stimuli.

Similarly, shallow and deep encoded semantic stimuli were tested in a subsequent analyses employing an ANOVA with the factors of encoding (shallow, deep), hemisphere (left, right) and site (inferior, mid, superior). For both encoding conditions, semantic stimuli revealed significant intact vs. new effects in the first two time windows at frontal as well as parietal locations. However, none of these effects
exhibited a significant difference in effect size across encoding conditions. In other words, no significant effect or interaction of encoding has been observed at frontal or parietal locations with respect to changes in effect size. Of course, like any null result, this result has to be interpreted with caution.

8.3.6 Topographical analyses

The previous section reported differences in parietal effect size elicited by non-words studied under shallow compared to deep encoding conditions. Unfortunately, it is not straightforward to disambiguate whether two independent or one common source of neuronal activity gave rise to these findings. While it is possible that the difference in magnitude is evoked by a single source that was engaged to a different extent between the two encoding conditions, the results are also compatible with an interpretation that two independent sources gave rise to the difference in magnitude.

Therefore, further analyses are necessary to determine whether the change in the parietal effect size reflects the engagement of qualitatively distinct neuronal generators across encoding conditions. This topographical analyses is performed on difference waveforms contrasting intact and new test conditions, and the data is rescaled prior to the analyses to avoid confounding effects of size.

An ANOVA including the factors of encoding (shallow, deep), hemisphere (left, right) and site (inferior, mid, superior) was employed to compare the parietal old/new differences obtained for non-semantic stimuli in the second time window. The results of the ANOVA revealed no significant effect of encoding, suggesting that the same neuronal source gave rise to parietal differences under deep and shallow encoding conditions.
8.3.7 Summary

8.3.7.1 Shallow encoding

ERP analyses revealed more positive going deflections under intact compared to new conditions for semantic and non-semantic stimuli. The specific pattern of activity was, however, dependent on whether shallow or deep encoding strategies were applied. With regards to shallow encoding conditions, both semantic and non-semantic stimuli elicited frontal and parietal ERP old/new effect in the first time window (300-600ms). Magnitude analyses, however, failed to reveal any significant difference in effect size between these frontal and parietal modulations within semantic or non-semantic conditions. Similarly, analyses comparing the magnitude of the old/new effects across semantic and non-semantic stimuli failed to reveal any significant modulation.

Analyses of ERP activity within the second time window (600-900ms) also demonstrated significant frontal and parietal old/new effects for non-semantic and semantic conditions. However, modulations in the effect size were obtained for non-semantic stimuli, which elicited larger parietal than frontal old/new effects. Nevertheless, magnitude analyses contrasting activity between stimuli revealed no significant change in effect size at frontal or parietal locations.

Within the third time window (900-1200ms) semantic stimuli demonstrated only parietal old/new effects. By comparison, non-semantic stimuli elicited significant old/new effects at frontal and parietal locations, which were associated with differences in magnitude and distribution. The parietal effect revealed thereby a larger effect size and a more bilateral distribution compared to the frontal effect, which occurred over the right hemisphere. Similar to the foregoing analyses, contrasts of old/new effects between stimulus conditions, performed for the common parietal old/new effect, revealed no significant difference in magnitude.

Finally, only non-semantic stimuli revealed old/new effects in the forth time window (1200-2000ms). These effects were obtained across frontal and parietal locations. In continuation of the results obtained in the third time window, the parietal old/new effect in the fourth time window was associated with larger amplitudes than the frontal old/new effect.
8.3.7.2 Deep encoding

Analyses assessing differences in activity under deep encoding conditions revealed, only for semantic word pairs, significant old/new effects in the first time window (300-600ms). Those old/new effects were present at frontal and parietal locations but revealed no difference in magnitude when compared with one another. This result is analogous to the profile of activity reported for semantic pairs studied under shallow encoding conditions.

The second time window (600-900ms) revealed, again for semantic word pairs significant frontal and parietal old/new effects, but now these effects exhibited magnitude differences in the form of significantly larger parietal modulations compared to frontal modulations. Non-semantic word pairs, by contrast, demonstrated significant old/new effects only at parietal electrodes. Hence, semantic and non-semantic stimuli elicited a profile of activity which shows enhanced old/new effects at parietal locations. Statistical comparisons across stimulus conditions, however, revealed no significant difference in magnitude at parietal locations.

While no ERP old/new effects were obtained in the third time window (900-1200ms), the fourth time window (1200-2000ms) indicated a significant left frontal difference for semantic conditions which was not present for non-semantic conditions. Overall, this section summarised the pattern of old/new effects obtained under deep and shallow encoding conditions respectively. Besides differences in activity between stimulus conditions, one question of interest in the present study concerns modulation in activity induced by different encoding strategies. Therefore, the subsequent section reports analyses assessing qualitative and quantitative difference in old/new effects between encoding conditions.

8.3.7.3 Analyses across encoding conditions

The comparison of activity elicited under deep and shallow encoding, non-semantic stimuli offered only one point of contrast to assess potential differences in topography: the parietal old/new effect in the second time window. This was the only effect present under shallow as well as deep encoding conditions. While magnitude
analyses indicated significantly stronger parietal effects for shallow compared to deep encoding conditions, topographical analyses failed to reveal any significant difference between encoding conditions, suggesting that the same neuronal source gave rise to parietal old/new effects obtained under shallow and deep encoding conditions.

Semantic stimuli, by contrast, offered multiple sites of comparisons, as frontal and parietal old/new effects were elicited under shallow and deep encoding conditions in the first two time windows. Nevertheless, no significant difference in magnitude was obtained between encoding conditions. Thus ERP old/new effects of similar temporal and spatial distribution elicited for semantic stimuli across deep and shallow encoding conditions demonstrate no quantitative or qualitative modulations in activity.

8.4 Discussion

The aim of the present study was to shed light on the operations that support episodic and semantic memory interactions. This experiment, in particular, investigated the inter-dependence of internal and external semantic manipulations by varying semantic encoding strategies and semantic stimulus organisation. Two distinct encoding condition embodying LOP manipulations were presented in the form of a shallow (word length judgement) and deep (semantic relatedness judgement) encoding task. Semantic stimulus organisation was altered by presenting word pairs describing either semantically congruent or incongruent exemplars of a category. The present study intended to discriminate between two possible scenarios, by which semantic stimulus organisation (i.e. external manipulation) and semantic encoding strategies (i.e. internal manipulation) exhibit either an independent or conditional influence on episodic and semantic memory interactions.
8.4.1 Behavioural Performance

The behavioural data reveal an influence of both external and internal semantic manipulations. The latter demonstrated, as predicted by the LOP theory (Craik & Lockhart, 1972), that deep encoding conditions evoked superior recognition performance compared to shallow encoding conditions. This finding was independent of stimulus type, occurring for semantic as well as non-semantic stimulus conditions. In addition, significant effects of external semantic manipulations (i.e. stimulus type) were also found in the behavioural data. Under deep encoding conditions, semantic compared to non-semantic stimuli elicited significantly more correct responses. This result is in good agreement with a previous study investigating manipulations of semantic-coherence on episodic retrieval (Greve et al., 2007). However, the current behavioural data suggest that this effect is limited to deep encoding and does not extend to shallow encoding conditions.

Experimental manipulations in the current study are based on the LOP theory, which proposes that memory traces are the product of analyses that were employed during the perception and comprehension of stimuli. Deeper or more semantically meaningful processing is thought to result in better memory traces. This view predicts that brain activity should differ as a function of depth of processing, which was tested in this study using ERP methods.

8.4.2 ERP results

The ERP data demonstrate significant old/new effects that reveal modulations in their magnitude and temporal-spatial occurrence dependent on the type of semantic manipulation employed. Importantly, the ERP data suggest, in agreement with the behavioural findings, that the influence of external semantic manipulations (i.e. stimulus type) is conditional on the type of internal semantic processing (i.e. encoding strategy). In other words, the degree to which semantic coherence of stimuli modulates episodic retrieval is dependent on the encoding strategy adopted. Modulations in ERP activity under deep encoding show that semantic stimuli elicit
retrieval of shallow and deep encoded classes of stimuli.

Both semantic and non-semantic stimuli revealed a parietal old/new effect between 600-900ms. These findings are in good agreement with the pattern of results reported in the previous chapter (see also Greve et al., 2007), replicating these findings. Nevertheless, the profile of old/new activity changed when participants were instructed to adopt a shallow (non-semantic) encoding strategy. The ERP data for shallowly encoded semantic and non-semantic stimuli revealed comparable results especially in the beginning of the recording epoch. A similar activity profile was observed in the first two time windows, during which the ERP correlates for familiarity and recollection are seen. The only difference across conditions occurred in the magnitude of the parietal old/new effect in the second time window. Non-semantic stimuli reveal a parietal old/new effect with larger amplitudes compared to the frontal old/new effect. This difference was not found for shallow encoded semantic stimuli. Nevertheless, it is noteworthy that the contrast between stimulus conditions exhibited no magnitude differences in the second time window. This may indicate a potential lack of power to statistically detect magnitude differences in semantic stimuli.

The similarity in ERP activity between shallowly encoded semantic and non-semantic conditions stands in contrast to the difference in ERP activity obtained under deep encoding conditions. In theory it is possible that the semantic organisation of stimulus content inherently influences information processing at a lexical level and would therefore be expected to impact episodic retrieval for stimuli studied under shallow encoding conditions. Alternatively, if semantic coherence does not have an automatic effect but is dependent on conceptual processing, semantic and non-semantic stimuli would be expected to exhibit no significant modulation in episodic retrieval under shallow but under deep encoding conditions. The latter prediction is in good agreement with the behavioural and ERP data presented here. Thus, the influence of semantically coherent stimuli seems to depend on the level of semantic processing employed.

A second important finding of this study concerns differences evoked by encoding manipulations. The behavioural data reveal very clearly an advantage in
retroire of shallow and deep encoded classes of stimuli. This finding is predicted by the LOP theory. Previous studies have shown that this advantage arises primarily due to increased recollection relative to familiarity (Yonelinas, 2002; Gardiner, Ramponi, & Richardson-Klavehn, 1999; Toth, 1996; Gardiner, Java, & Richardson-Klavehn, 1996). In the context of ERP data this would predict a significant change in the left parietal old/new effect from shallow to deep encoding conditions but no (or if at all a minor) modulation in the frontal old/new effect.

The data presented here are not in line with these predications. When focussing on non-semantic stimuli, the manipulation of processing depth is associated with a decrease in the frontal as well as parietal old/new effect. The semantic stimulus condition, by contrast, reveals no significant change in the frontal and parietal old/new effect across encoding conditions. Most striking in this pattern of results, though, is a decrease in the magnitude of the left parietal old/new effect from shallow to deep encoded non-words, a finding that is directly opposite to that predicted by LOP manipulations (which are thought to selectively increase recollection from shallow to deep encoding conditions).

Previous studies have investigated LOP theories using ERPs (Rugg et al., 2000; Rugg et al., 1998). One study, for instance, examined the influence of depth of processing by asking participants to either generate sentences that contained the to-be-remembered words, or to perform an alphabetic judgement task with those words. Subsequent recognition was shown to be higher for deep relative to shallow encoding conditions (Rugg et al., 1998). ERPs demonstrated only for deeply studied items parietal old/new effects at about 500ms post stimulus which was absent for shallow encoded stimuli. An earlier frontal old/new effect, by contrast, was obtained at about 300-500ms post stimulus, which did not differ across encoding conditions. A further study (Rugg et al., 2000) using a similar manipulation found comparable ERP result for deep but not shallow encoding conditions. Shallow encoding failed to elicit either parietal or frontal ERP old/new effects. Hence, the putative correlates of recollection and familiarity were modulated by the depth of processing in Rugg et al. (2000). Nonetheless, both studies demonstrated larger left parietal effects under deep
compared to shallow encoding conditions, in line with the prediction that depth of processing selectively alters recollection. These results stand in opposition to the data reported in the current study. Nevertheless, there are two potential explanations for this disparity.

First, fundamentally different types of memory were tested in the former compared to the current experiment. While previous studies have focused on item memory the current study investigates associative memory, which places higher demands on recollecting the precise combination of the studied word pairs. Consequently, the current memory test necessitates recollection and can not be performed solely on the basis of familiarity. This is likely to affect the parietal old/new effect and would predict differences in the patterns of results obtained in the current study compared to previous experiments reported in the literature.

A second and somewhat complementary issue concerns inferences about the magnitude differences of the left parietal effect. Such differences need to be interpreted with caution however, as is outlined below this can not be easily equated with increases in successful recollection. Topographic analyses of the current data demonstrated that the scalp distribution of parietal old/new effects elicited under shallow and deep encoding conditions were statistically equivalent, despite existing modulations in magnitude. Hence, there is no evidence that distinct neuronal sources were engaged across conditions. Comparable findings have been reported in previous studies (Wilding, 1999; Wilding & Rugg, 1996) which obtained parietal old/new effects of increased magnitude but the same topography for correct compared to incorrect source judgements. Those results were interpreted as indicating that recognition with and without retrieval of contextual information differs in quantity but not quality. Consequently, the magnitude of the parietal old/new effect is linked by this interpretation to the amount of retrieved information.

This view is consistent with the current findings obtained for non-semantic stimuli. Non-semantic pairs are associated with decreased hit rates for shallow compared to deep encoding conditions. Thus, participants had more difficulties recognising shallowly encoded non-words, possibly because the encoding task oriented them towards information (word length) that is not very diagnostic for
successful discrimination of novel from previously studied pairs at test. Since the shallow encoding task does not prohibit participants from processing the meaning of the stimuli, some pairs may be retrieved on the basis of their previously encoded morphology as well as semantic meaning. Such cases should have an advantage in terms of successful retrieval due to better encoding, but should also be associated with an increased amount of retrieved information. Stimuli studied under deep encoding conditions, by contrast, are oriented towards the word meaning at encoding which may be sufficient to allow subsequent retrieval. Importantly, in this case, the amount of retrieved information would primarily be based on semantic meaning, while recognition in the shallow encoding condition may rely on the morphology of the words pairs as well as semantic meaning.

Under the premise that the changes in the magnitude of the left parietal old/new effect reflect the amount of retrieved information, this interpretation is consistent with a larger parietal effect for shallow compared to deep encoded non-semantic pairs obtained in the present experiment. In fact, this interpretation of the left parietal old/new effect is not incompatible with the LOP principle, which predicts that more elaborative encoding leads to better retrieval since more contextual information is available to access the learned information. Nevertheless, this interpretation of the parietal old/new effect in the present experiment faces two principle questions.

First, if more contextual information is present for the retrieval of shallowly encoded non-semantic stimuli, does this imply that more elaborative encoding was present in the shallow compared to the deep encoding condition? Second, if successful recognition of shallowly encoded stimuli relies on the retrieval of morphological and semantic information, reflected in the increased parietal old/new effect, why were no magnitude differences obtained for shallowly vs. deeply encoded semantic stimuli?

In order to deal with the first question it is important to keep in mind that, although the LOP theory has been very influential in memory research (Craik, 2002), it has not been free of criticism. In particular, conceptual criticism of the LOP theory has been directed to the circularity of the theory, i.e. recall depends on the depth of
processing and depth of processing is inferred from the level of recall. This highlights the lack of a principled metric for assessing depth of processing independently. Furthermore, empirical limitations of the LOP theory have been put forward by studies investigating orienting procedures (Roediger III & Gallo, 2001). For example, positive responses to an orienting question are associated with better recall than negative responses (for review see Roediger & Gallo, 2001). Such criticism emphasises that the level of processing is not the definitive (or only) manipulation affecting recognition performance, suggesting that the level of stored contextual information can be changed by factors other than level of processing.

With regards to the second question, as to why no magnitude differences were obtained for shallow vs. deep encoded semantic stimuli, it must be stressed that null results have to be interpreted with caution. It is possible that insufficient power in the data has lead to such a null result (compare left and right panel in Figure 8-16). An indication that his may have been the case in the current experiment comes from magnitude analyses contrasting the parietal old/new effect (present at 600-900ms) within encoding conditions. The analyses failed to show any significant differences between the parietal old/new effects when contrasting shallowly encoded semantic and non-semantic stimuli. Equally, no difference was obtained between deeply encoded semantic and non-semantic stimuli. If the reported magnitude differences of the parietal old/new effect between shallow and deep encoding conditions were selective to non-semantic stimuli, this should result in magnitude differences when contrasting non-semantic and semantic stimuli under shallow encoding conditions.
8.5 Conclusion

External semantic manipulations (i.e. the coherence) of stimuli have been shown to influence episodic and semantic memory interactions. The current experiment investigated whether this influence is conditional on internal semantic manipulations (i.e. encoding strategy). This study raises two important points. First, behavioural and ERP data show that external semantic manipulations are encoding dependent. The data demonstrate that modulations in the semantic coherence of stimuli are only effective when deep encoding strategies were employed to orient participants towards elaborative processing of word meaning. Second, this study examined depth of processing manipulations for associative recognition instead of item recognition (as in most previous studies). Although behavioural performance was consistent with the classic LOP prediction, ERP data suggest that this performance is supported by a different contribution of familiarity and recollection. Increased recollection of contextual information may be needed under shallow encoding conditions to allow successful performance of the associative recognition task.
9 Encoding of semantic and non-semantic stimuli

9.1 Introduction

Written language is based on strings of letters formed into words that index knowledge about the world. In order for language comprehension to take place the perceptual representation of a word has to be mapped to its associated semantic knowledge. Such mapping occurs in the course of semantic processing, which has been examined in previous experiments presented in this thesis. The previous experiments, for instance, manipulated semantic processing demands by employing different encoding tasks (Chapters 5 and 6). One task required thereby the word meaning to be accessed to enable a semantic relatedness judgement, while a second task only required access to perceptual information to allow discrimination of word length. A limitation of this approach is that these encoding tasks may differ in aspects other than semantic processing demands. For example, semantic encoding tasks may place greater demands on mechanisms involved in memory search, selection and decision processes than non-semantic tasks (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). As the intention of this thesis is to investigate the interplay between semantic processes and memory performance, it is important to establish that changes in memory performance can be attributed specifically to changes in semantic processing.

A solution to this problem is the contrast of different classes of stimuli that vary in their engagement of semantic processing. The underlying premise of such a comparison is that, if cognitive task demands are held as constant as possible, differences in brain activity should reflect changes in semantic processing induced by the stimuli. The first experiment reported in this thesis described one such contrast by investigating electrical activity elicited for semantically related compared to semantically unrelated word pairs. Nevertheless, both stimulus conditions were based on words referencing known objects and were therefore associated with lexical and semantic representation in our memory system. The difference between the stimulus conditions employed in the first experiment was defined by the feature overlap
between the two words presented in a pair. Semantically related pairs, for example, exhibited a larger feature overlap, as both words were members of the same category. Although that first experiment was likely to engage semantic processes to differing degrees, it does not provide a complete account of semantic processing per se. The present study, therefore, aims to investigate the differences in neuronal activation evoked by the presence and absence of lexical and semantic features, while holding processing demands constant. Neuronal correlates reflecting the access to semantic word information were isolated by contrasting electrical activity elicited for pairs of words and non-words, the latter being meaningless but phonologically legal structures.

To minimize the difference in processing strategy and demands between the stimulus types, words and non-words were presented in a random order and participants were asked to pronounce the words aloud. In contrast to previous experiments, subjects were not asked to perform a lexical decision task because words and non-words differ along several dimensions that could influence performance. For instance, a lexical decision for non-words might be performed solely on the basis of orthographic familiarity or through further access to phonological or lexical information (James, 1975). Thus a lexical decision task can be performed in multiple ways. By contrast, the pronunciation task forces participants to engage orthographical, phonological and for real words even semantic processing. In general, the comparison of neuronal activity obtained for words and non-words should enable the identification of stimulus specific semantic processing.

9.2 Material and Methods

9.2.1 Participants

All participants were right-handed native English speakers, ranging from 18 to 35 years in age, with normal or corrected-to-normal vision and no known neurological problems. Informed consent was required, and payment provided at a rate of £5 per hour. Twenty five participants performed the ERP study but four of
them had to be excluded due to technical failure. The remaining 21 (15 female) subjects had an average age of 20 years.

9.2.2 Materials

Study and test lists were created according to the same principle outline in previous chapters (Sections 5.2.2 and 7.2.2). Different types of stimuli were presented in the current study as pairs based on words or non-words were presented. Word pairs were constructed from 480 nouns, 4-6 letters in length, with a frequency between 10 and 30 occurrences per million (Kucera & Francis, 1967). The words forming a pair contained no particular semantic organisation (i.e. were not exemplars of the same category), and are therefore comparable to the ‘non-semantic’ stimulus conditions described in previous chapters. Similarly, pairs of pronounceable non-words were constructed from 480 non-words, matching the length and number of phonemes of the nouns.

Stimuli were created for 6 blocks, each containing a single study list of 32 pairs of words and 32 pairs of non-words (randomly intermixed), matched with a corresponding test list of 24 pairs of words and 24 pairs of non-words. Test lists were created for each condition (words, non-words) in the following way: 8 studied pairs were re-presented at test in the same pairings as at study, providing 8 intact word pairs. 16 pairs shown at study were rearranged to create 8 rearranged word pairs by taking one word from each of two study pairs (maintaining word position in each case) and discarding the other member of each study pair. To be clear, rearranged study word pairs A-B and C-D were rearranged to form A-D, discarding B and C. The first word and second words of a study pair were discarded equally often. The remaining 8 pairs were used to create 8 new word pairs, by combing the first member of each pair (always discarding the second member of the pair) with a previously unstudied word. The resulting pairs of words and non-words for each of the intact, rearranged and new conditions were randomly intermixed within each test list.
9 Encoding of semantic and non-semantic stimuli

9.2.3 Procedures

The experiment was implemented in the same way as outlined in previous chapters (Sections 5.2.3 and 7.2.3). The trial structure was slightly altered so that only the word pairs but not category words were presented (Figure 9-1 illustrates the design). The factors of stimulus (words, non-words) and pairing (intact, rearranged, new) were fully crossed within participants.

Each study trial started with a fixation cross (+) displayed for 500ms in the centre of the screen, followed by a blank screen for 250ms. A word pair was then presented for 2000ms, followed by a blank screen presented for 1000ms. Participants were instructed to read the word pair presented on the screen, pause for 1000ms while the blank screen was presented and then pronounce the presented word pairs aloud. An auditory record was taken of their performance. This study task had the purpose of ensuring that subjects attended to the presented word pairs. Once the word pair was spoken, subjects were instructed to press a button which caused the

Figure 9-1 Experimental design and materials. In the study phase each trial presented either a pair of words or non-words. During the test phase the same trial procedure was employed and three types of word pairs were presented: intact pairs, which were previously presented at study, rearranged pairs, which were constructed by recombining words from two study pairs, and new pairs, which were constructed by combining a member of a studied pair with an unstudied word. Intact, rearranged and new word pairs were constructed separately for the class of words and non-words.
screen to go blank for 250ms, and the next trial to begin. Participants were informed that their memory for the studied stimuli would be tested subsequently.

Each test trial started with an initial 500ms fixation cross, followed by a 250ms blank screen, after which a word pair was presented for 2000ms, followed by a blank screen shown for 2000ms. Participants were instructed to indicate by button press (within 4000ms of word pair onset) whether each word pair was a target (respond: old) or a non-target (respond: new). Targets were defined as intact word pairs; non-target as rearranged and new word pairs. Once a response was made, the screen went blank for 250ms and the next trial began. Participants were asked to respond as quickly and accurately as possible, and the mapping of buttons to old and new responses was counterbalanced across participants.

9.2.4 ERP recordings and analysis

Scalp EEG was recorded in precisely the same form as described in the previous studies (Sections 5.2.4 and 7.2.4). ERP waveforms were formed separately for pairs of words and non-words. ERP analyses were designed to investigate possible differences in encoding activity and subsequent memory effects evoked by the different classes of stimuli. On the basis of visual inspection of the waveforms, data at study were analysed over 3 consecutive time windows (300-600ms, 600-1000ms, 1000-1800ms). These time windows are selected because they capture the effects of interest in the current data most appropriately, and furthermore represent analogous time windows used in previous experiments (Sections 5.2.4 and 7.2.4).

9.3 Results at study

The first part of the analyses concentrated on encoding differences recorded during study between words and non-words. The study task required subjects to read the word and non-word pairs aloud to ensure that the stimulus material was attended to. Subjects performed the task accurately on all trials. As no further behavioural measures were recorded the following report will begin with an account of the obtained ERP activity.
9.3.1 ERP data

Grand average ERP waveforms elicited for pairs of words and non-words are shown in Figure 9-2. The mean number of trials that contributed to the average waveforms was 96 for words and 118 for non-words.

![Figure 9-2](image)

**Figure 9-2** Grand average ERPs elicited for pairs of words (red) and non-words (blue) during study. ERP waveforms are shown here (and in all following figures of similar kinds) for 61 electrodes, displayed as if looking down onto the top of the head. Differences between the waveforms emerge over centro-parietal locations, indicating changes in neuronal activity when different classes of stimuli are encoded.

ERP activity elicited during study diverges for words and non-words over centro-parietal electrodes. This difference onsets at about 600ms and remains present until the end of the recording epoch (see Figure 9-3 for an enlarged view). Non-words reveal a more positive going deflection relative to words. For statistical analyses average voltages were calculated over three consecutive epochs (300-600ms, 600-1000ms, 1000-1800ms) across each class of stimuli.
9 Encoding of semantic and non-semantic stimuli

![Figure 9-3](image)

**Figure 9-3** Grand average ERPs elicited for pairs of words (red) and non-words (blue) during encoding. This and all subsequent figures of similar kind display ERP waveforms at 3 frontal (F1, Fz, F2) and 3 parietal (CP1, CPz, CP2) electrodes, whose locations are highlighted in green on the schematic top down view of the head. Frontal electrodes show no clear differences in encoding activity between the two classes of stimuli. Parietal electrodes, however, exhibit a positive deflection for non-words compared to words which onsets at about 600-1000ms post stimulus.

### 9.3.2 ERP analysis

ERP activity elicited for words and non-words during study was contrasted over frontal and parietal locations with an ANOVA including the factors of stimulus (words, non-words), epoch (300-600ms, 600-1000ms, 1000-1800ms), hemisphere (left, right) and site (inferior, mid, superior). The results revealed at frontal locations no significant difference between the two types of word pairs. Parietal location, in contrast, gave rise to a significant stimulus by epoch by site interaction \([F(1.8,36.4)=10.1, p<0.01]\), in addition to a main effect of stimulus \([F(1,20)=8.8, p<0.01]\) and a stimulus by site interaction \([F(1.2,23.1)=8, p<0.01]\). Hence, stimulus induced ERP differences were limited to parietal locations and changed across time.

Follow-up analyses focussed on parietal locations and investigated individual epochs with an ANOVA including the factors of stimulus (words, non-words),
Encoding of semantic and non-semantic stimuli

The first time window (300-600ms) revealed a significant stimulus by site interaction [F(1.1,22)=4.2, p<0.05], which reflects more positive deflections for non-words compared to words at electrodes site CP1 (t(20)=2.3, p<0.05) and CP2 (t(20)=2.1, p<0.05), see also Figure 9-4. The topography of this effect was investigated more closely to determine whether this modulation might resemble an N400 effect. Word and non-words were therefore contrasted on six virtual midline electrodes (F,FC,C,CP,P,O) each representing electrical activity of a central electrode collapsed together with one left and right neighbouring electrode (i.e. F represents the mean activity of F1, Fz, F2). The data revealed in the first epoch significant differences between words and non-words at the PC (t(20)=2.4, p<0.05) and P electrode (t(20)=3.8, p<0.01) and a marginally significant effect at electrode O (t(20)=2.0, p=0.058). The second epoch failed to reveal any differences at all. Thus, the effect exhibits a centro-parietal distribution that is limited to the first time window.

Figure 9-4 The magnitude of encoding activity for words (red) and non-words (blue) are displayed for the first epoch (300-600ms) over six parietal electrodes. Three electrodes were located over the left (CP5, CP3, CP1) and right hemispheres (CP2, CP4, CP6). The displayed mean (and standard error) of the encoding activity reveals more positive going ERP activity for non-words compared to words over the two centro-parietal electrodes: CP1 and CP2.
The second epoch (600-1000ms) failed to show any significant effects or interactions with the factor of stimulus. The third epoch (1000-1800ms) exhibited a stimulus by site interaction $[F(1.2,23.7)=16.8, \ p<0.001]$, indicating significantly different activity between stimuli at electrode CP3 ($t(20)=2.4, \ p<0.05$), CP1 ($t(20)=3.8, \ p<0.05$), CP2 ($t(20)=3.2, \ p<0.05$) and a marginally significant differences at electrode CP4 ($t(20)=2, \ p=0.06$) (see Figure 9-5).

![Figure 9-5](image)

**Figure 9-5** The magnitude of encoding activity for words (red) and non-words (blue) are displayed for the third epoch (1000-1800ms) over six parietal electrodes. Three electrodes were located over the left (CP5, CP3, CP1) and right hemispheres (CP2, CP4, CP6). The displayed mean (and standard error) of the encoding activity clearly demonstrates more positive going ERP activity for non-words compared to words over four centro-parietal electrodes: CP3, CP1, CP2 and CP4.

### 9.3.3 Summary

Parietal electrodes exhibited more positive going deflections for non-words relative to words in the first (300-600ms) and third epoch (1000-1800). These results confirm that encoding activity differs as a function of pre-existing semantic representations. Such encoding differences might affect the way information is subsequently stored and remembered. To test for modulations in encoding efficiency,
electrical activity that is predictive for successful memory performance was examined with the subsequent memory paradigm.

### 9.4 Subsequent memory effects

The subsequent memory paradigm is dependent on recognition performance, which might limit the number of subjects that qualify for this type of test (due to insufficient numbers of trials). In the present study 15 (10 female) subjects (with an average age of 20 years) qualified for the subsequent memory analysis by exhibiting at least 16 artefact free trials for every condition.

#### 9.4.1 Behavioural data

The subsequent memory paradigm investigates study data as a function of later recognition success. The behavioural results for correct recognition are presented in the next chapter of this thesis (Chapter 10) and will therefore not be discussed any further at this point. The following section investigates ERP differences at study that predict subsequent memory performance. Such examination could be based on memory performance obtained for intact or rearranged test conditions. The following analyses collapses across theses two conditions, so that intact as well as rearranged test performance defined correct and incorrect responses.

#### 9.4.2 ERP data contrasting classes of words and non-words

Grand average ERPs recorded during the study of non-words were formed and contrasted with respect to subsequent memory effects. The mean number of trials contributing to the averages was 60 for subsequent correctly and 44 for subsequent incorrectly recognised trials.
9 Encoding of semantic and non-semantic stimuli

More positive going activity for subsequent incorrectly compared to correctly identified items seem to be present from about 1000ms onwards (see Figure 9-7 for an enlarged view). This pattern of activity is opposing typically reported subsequent memory effects, which demonstrate stronger positive deflections for subsequent correctly compared to incorrectly recognised stimuli. A comparable discrepancy has been reported earlier in this thesis which was shown to be a consequence of the target and non-target definition between intact and rearranged conditions. The present results might be open to a similar explanation which is followed up in later analyses.
Figure 9-7 Grand average ERPs elicited for subsequent correctly (blue) and incorrectly (black) remembered pairs of non-words. This close up view highlights differences in electrical activity between correctly and incorrectly recognised non-words over frontal locations.

Grand average ERP waveforms recorded during the study of words were formed and contrasted with respect to subsequent memory performance. The corresponding ERP waveforms are displayed in Figure 9-8, based on an average of 60 trials of subsequent correctly and 32 trials of subsequent incorrectly recognised word pairs.
9 Encoding of semantic and non-semantic stimuli

Figure 9-8 Grand average ERPs elicited for subsequent correctly (red) and incorrectly (black) remembered pairs of words. This general view suggests that no differences in electrical activity emerge and consequently no subsequent memory effects are obtained for words pairs.

Figure 9-9 Grand average ERPs elicited for subsequent correctly (red) and incorrectly (black) remembered pairs of words. The inspection of the enlarged electrodes suggests no differences in electrical activity between correctly and incorrectly recognised non-words over at the selected frontal and parietal electrode sites.
Figure 9-8 reveals no apparent difference in ERP activity over frontal or parietal locations (see Figure 9-9 for enlarged view). Thus, the grand average ERP waveforms indicate no difference in subsequent memory effects for pairs of words across the entire recording epoch.

Differences in ERP activity were examined statistically by contrasting mean voltages formed again over three consecutive epochs (300-600ms, 600-1000ms, 1000-1800ms).

9.4.3 ERP analysis

ERP activity for subsequent memory performance was examined by contrasting non-words and words across individual locations and epochs with an ANOVA including the factor of response (correct, incorrect), hemisphere (left, right) and site (inferior, mid, superior). Non-words exhibited only one significant effect of response \([F(1,14)=5.24, p<0.05]\) in the third time window, over frontal locations. This effect reflects significant differences over two left frontal electrodes: F5 \((t(14)=-2.63, p<0.05)\) and F3 \((t(14)=-2.25, p<0.05)\); and marginally significant differences occurred across two left-central electrodes: F1 \((t(14)=-2, p=0.06)\) and Fz \((t(14)=-2.1, p=0.055)\). Thus, subsequent memory effects for non-words seem to appear with a late onset over frontal locations.

Words, by contrast, revealed only one significant interaction including the factor of response with hemisphere and site over parietal locations in the second time window \([F(1.9,26.5)=4.97, p<0.05]\). This effect was not strong enough to elicit significant differences over any of the six parietal electrodes (CP1, CP2, CP3, CP4, CP5, CP6) \([p>0.05, \text{in all cases}]\) see Figure 9-11.
9 Encoding of semantic and non-semantic stimuli

Figure 9-10 The magnitude of encoding activity for subsequent correctly (blue) and incorrectly (black) recognised non-words is displayed for the third epoch (1000-1800ms) over six frontal electrodes. Three electrodes were located over the left (F5, F3, F1) and right hemispheres (F2, F4, F6). The displayed mean (and standard error) of the encoding activity reveals significant differences (as indicated by stars) and marginally significant differences (as indicated by stars in brackets) over the left hemisphere, showing a stronger positive deflection for incorrectly compared to correctly recognised non-words.

Figure 9-11 The magnitude of encoding activity for subsequent correctly (red) and incorrectly (black) recognised words is displayed for the second epoch (600-1000ms) over six parietal electrodes. Three electrodes were located over the left (CP5, CP3, CP1) and further three over the right hemisphere (CP2, CP4, CP6). The displayed mean (and standard error) of the encoding activity demonstrates no significant differences in encoding activity for subsequent correctly and incorrectly recognised words.
In general, the analysis reported here shows that non-words elicit late onsetting (at about 1000ms) frontal subsequent memory effects, while words indicate earlier onsetting (at about 600ms) parietal subsequent memory effects. The latter, however, failed to reach significance at individual electrodes. The obtained differences were of reversed polarity to typical subsequent memory effects. This may be caused by the altered target and non-targets definitions between intact and rearranged test conditions, which were collapsed together in the current analyses. The following set of analyses tested this account by separating subsequent memory analysis for intact and rearranged test conditions.

**9.4.4 ERP data contrasting intact and rearranged test conditions**

Grand average ERPs at study recorded for subsequent correctly and incorrectly recognised items were split across intact and rearranged test conditions. The analysis of the associated subsequent memory effects will first be reported for non-words followed by words.

**9.4.4.1 Class of stimuli comprising non-words**

Figure 9-12 and Figure 9-13 show the study activity for subsequent correctly and incorrectly remembered non-words assessed under intact test conditions, while Figure 9-14 and Figure 9-15 illustrates the corresponding study activity for non-words tested under rearranged conditions. The mean number of trials that contributed to the subsequent memory analysis for correct and incorrect non-words was 41 and 32 for intact, and 22 and 17 for rearranged test conditions, respectively. Figure 9-12 demonstrated that ERP activity for intact test conditions is more positive going for correctly compared to incorrectly identified non-words from around 400ms onwards over frontal locations. This difference seems to be biased towards the left hemisphere (see Figure 9-13 for an illustration of selective electrode sites).
9 Encoding of semantic and non-semantic stimuli

Figure 9-12 Grand average ERP activity reveals subsequent memory effects for correctly (blue) and incorrectly (black) identified non-words tested under intact conditions. Items that are subsequently correctly remembered are associated with more positive going ERP waveforms over frontal locations during encoding.

Figure 9-13 Grand average ERPs illustrating subsequent memory effect for correctly (blue) and incorrectly (black) identified non-words tested under intact conditions. Subsequent correctly compared to incorrectly identified items are more positive going over frontal electrodes. This effect demonstrates a long lasting positivity which onsets at about 400ms post stimulus.
Rearranged conditions, by contrast, show more positive going ERP activity for incorrectly compared to correctly identified non-words over frontal locations, which onsets at about 1000ms (see Figure 9-15 for an enlarged view). The described differences for intact and rearranged test conditions were examined statistically using average voltages calculated for each condition over three consecutive epochs (300-600ms, 600-1000ms, 1000-1800ms).

Figure 9-14 Grand average ERPs demonstrate subsequent memory effects for correctly (blue) and incorrectly (black) identified non-words tested under rearranged conditions. In contrast to intact test conditions, items tested in rearranged pairs reveal far more positive going activity for subsequent incorrectly compared to correctly classified items over frontal locations during encoding.
9.4.4.1.1 ERP analysis

ERP activity for non-words tested under intact conditions was assessed over individual locations by employing an ANOVA with the factors of response (correct, incorrect), epoch (300-600ms, 600-1000ms, 1000-1800ms), hemisphere (left, right) and site (inferior, mid, superior).

Frontal locations exhibited a significant response by epoch by hemisphere interaction \([F(1.9,27.5)=4.7, p<0.05]\). Surprisingly, parietal locations also revealed an interaction involving the factors of response, epoch, hemisphere and site \([F(1.27,17.9)=3.9, p<0.05]\). However, when electrical activity was contrasted within each time window, no main effect or interactions involving the factor of response reached significance over frontal or parietal locations. Even contrasts of individual electrode sites within each epoch failed to reveal any significant differences in electrical activity between response conditions. Thus, differences in subsequent memory activity obtained by visual inspection and higher level analyses were not robust enough to reach statistical significance in subsidiary analysis and are therefore
Regarded as unreliable. Consequently, no significant subsequent memory effects were obtained for non-words tested under intact conditions.

Non-words tested under rearranged conditions were submitted to analyses analogous to those performed for intact conditions. The ANOVA testing the factor of response (correct, incorrect), epoch (300-600ms, 600-1000ms, 1000-1800ms), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior) elicited a significant response by epoch \([F(1.3,18)=4.4, p<0.05]\) and response by epoch by location interaction \([F(1.8,24.5)=4.4, p<0.05]\). This pattern of results suggests subsequent memory effects that differ with time and across locations.

Changes across location were examined with a subsidiary ANOVA performed separately over frontal and parietal locations, including the factors of response (correct, incorrect), epoch (300-600ms, 600-1000ms, 1000-1800ms), hemisphere (left, right) and site (inferior, mid, superior). This analysis resulted in a response by epoch interaction over frontal locations \([F(1.3,18.3)=5.9, p<0.05]\), but revealed no main effect or interaction with response over parietal locations. Further contrasts were performed over frontal locations at each individual epoch by employing an ANOVA including the factor of response (correct, incorrect), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid, superior). The results revealed only for the third epoch a significant effect of response \([F(1,14)=8.35, p<0.05]\). This effect was present at all six frontal electrode sites (F6, F5, F4, F3, F2, F1) as individual t-tests confirm in all cases \([p<0.05]\). This subsequent memory effect was characterised by more positive going electrical activity for subsequent incorrectly compared to correctly remember items (see Figure 9-16).
9.4.4.2 Class of stimuli comprising words

Analyses for words were limited to rearranged conditions as intact conditions failed to elicit sufficient numbers of trial for incorrectly recognised word pairs. Study activity for subsequent correctly and incorrectly remembered word pairs tested under rearranged conditions is shown in Figure 9-17 and Figure 9-18. The mean number of trials that contributed to the subsequent memory analysis was 37 for correctly and 28 for incorrectly recognised words pairs. Visual inspection of the electrical activity suggests more positive going ERP waveforms for incorrectly compared to correctly identified word pairs from around 400ms onwards over parietal locations. This seems to be biased towards the left hemisphere (see Figure 9-18 for enlarged illustration). Similar to previous analyses, statistical test were performed on average voltages calculated for each condition over three consecutive epochs (300-600ms, 600-1000ms, 1000-1800ms).
Figure 9-17 Grand average ERPs demonstrate subsequent memory effects for correctly (red) and incorrectly (black) identified words tested under rearranged conditions. The waveforms reveal far more positive going activity during encoding for subsequent incorrectly compared to correctly classified items over parietal locations.

Figure 9-18 Grand average ERPs showing subsequent memory effect for correctly (red) and incorrectly (black) identified words tested under rearranged conditions. This enlarged display illustrates more positive going ERP activity for subsequent incorrectly compared to correctly classified items over parietal location when tested under rearranged pairing.
9.4.4.2.1 ERP analysis

ERP analyses for words tested under rearranged conditions were performed separately across frontal and parietal locations by using an ANOVA with the factor of response (correct, incorrect), epoch (300-600ms, 600-1000ms, 1000-1800ms), hemisphere (left, right) and site (inferior, mid, superior). However, no significant effects or interactions involving response were obtained. Even comparisons within individual time windows failed to reveal any significant differences in electrical activity between response conditions. Hence, differences in electrical activity, although obtained by visual inspection, are not robust enough to reach statistical significance across individual locations. Thus, no reliable subsequent memory effects were obtained for words tested under rearranged conditions.

9.4.5 Summary

First, analyses of subsequent memory effects were performed for individual classes of words and non-words without separating individual test conditions. No reliable subsequent memory effects were obtained for pairs of words. Non-words, however, revealed frontally located subsequent memory effects. This effect was of reversed polarity compared to typical subsequent memory effects (see Section 4.1.1). This reversal might resemble the fact that subsequent memory contrasts included performance for intact and rearranged conditions.

This was examined with a second set of analysis, which tested subsequent memory performance for intact and rearranged test conditions separately. Non-words tested under rearranged conditions elicited a subsequent memory effect over frontal locations, revealing positive going deflection for incorrectly compared to correctly recognised non-words. This difference was not observed for non-words tested under intact conditions. To the contrary, a more positive going deflection for correct compared to incorrect conditions were obtained, which however did not reach statistical significance at individual electrodes. These results suggest that the rearranged test condition is largely responsible for the more positive going ERP deflection for incorrectly vs. correctly recognised non-words.
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Word pairs permitted statistical analyses only for rearranged but not intact test conditions due to insufficient number of trials. Grand average ERPs suggest more positive going ERP waveforms for incorrectly relative to correctly identified words over parietal locations. Interestingly, this pattern of results is in accordance with the reversal of the subsequent memory effects reported in the first experiment presented in this thesis (Section 5.4). The condition referred to as ‘non-semantic’ contained two words that shared no categorical relation representing effectively the same experimental manipulation as the condition ‘words’ in the current experiment. The non-semantic conditions in the first experiment also displayed a more positive going deflection for incorrectly compared to correctly recognised pairs when tested under rearranged conditions. Yet, the parietal difference in the present experiment failed to reach statistical significance, most likely due to a lack of power caused by the greatly reduced number of trials.

In general, the analyses demonstrated differences in subsequent memory effects for stimuli based on words which contain semantic representation stored in our memory compared to stimuli that contain no direct representation in our semantic memory system. This suggests that effective encoding is modulated by stimulus material that either is or is not associated with an existing semantic memory representation.

9.5 Discussion

In this chapter, Event-Related Potentials were used to examine the differential engagement of semantic processes during encoding of words and pronounceable non-words. The previous studies reported in this thesis revealed that pre-existing semantic knowledge of to-be-encoded stimuli influences not only the encoding processes but also elicits differences in encoding activity predictive for successful retrieval. It has further been shown that such encoding effects depend on the processing strategy employed at encoding. Nevertheless, the previous investigations had all employed stimuli that reference lexical and semantic features. The main question of the current investigation was whether the observed differences would
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generalise to semantic manipulations that extend to stimuli that differ in their lexical/semantic nature, as for example normal words and pronounceable non-words. As in the previous study, the analyses presented here were conducted in two different stages. The first stage investigated general changes in electrical activity elicited during encoding, while the second stage employed the subsequent memory paradigm to examine effective encoding. The discussion will consider these findings in turn.

9.5.1 Differences at encoding

The results at encoding indicate a significant difference in the way words and non-words are processed by the brain. The main findings revealed robust difference in electrical activity during encoding over centro-parietal locations for words relative to non-words even when the task demand was held constant.

![Study effect](image)

**Figure 9-19** Significant differences in ERP activity between different classes of stimuli (words and non-words) are illustrated in this cartoon. Modulations in study activity occur in the first (300-600ms) and third time window (1000-1800ms) reflecting more positive activity for non-words compared to words over parietal locations.

The experiment was designed to encourage stimulus induced differences in semantic encoding, as only real words had access to existing semantic and lexical representations stored in semantic memory. Before elaborating on possible explanation of these experimental results prior findings from studies of visual word recognition are worth considering.
Central to most theories of visual word recognition is the idea that processing of words and non-words engages multiple, distinct representations or codes (Carr & Pollatsek, 1985). For example, the code describes orthographic, phonologic, or semantic representations. Although activation of these various codes appears to be mostly automatic, some strategic processing (e.g. induced by the encoding task) can control the extent to which these codes are accessed (Grainger & Jacobs, 1996; Posner & Carr, 1992; Seidenberg & McClelland, 1989). A lexical decision task, for instance, might intuitively seem to require access to specific semantic knowledge of the word. However, as mentioned earlier lexical decision experiments may not engage phonological or semantic codes if words and non-words are orthographically distinguishable (Waters & Seidenberg, 1985; Shulman, Hornak, & Sanders, 1978; James, 1975). In the present study subjects were asked to read words and non-words aloud, requiring access to orthographic and phonological processes, and most likely enabling semantic access for real words only. Therefore, it might be hypothesised that differences in encoding activity should reflect semantic processing for words compared to non-words. The current results reveal more negative ERP deflection for words compared to non-words in the first (300-600ms) and third epoch (1000-1800ms) over centro-parietal locations. This raises the question: what functional significance does this difference in electrical activity reflect.

Some insight into this question may be gained from ERP studies focussing on the precise time course of visual word recognition. This may allow to pinpoint the exact processing stage at which words and non-words diverged in the present study. Previous studies have examined the processing stages engaged during word recognition by comparing ERP responses across various types of orthographic stimuli, such as words, pronounceable non-words and unpronounceable letter strings. These studies report an early divergence in electrical activity between letter strings compared to words and non-words. This difference in lexicality (word-like vs. not word-like properties) was reported to occur between 100-200ms post stimulus onset (Proverbio, Vecchi, & Zani, 2004; Sereno, Rayner, & Posner, 1998; Dehaene, 1995; Compton, Grossenbacher, Posner, & Tucker, 1991). These results show that orthographic regularity affects linguistic processing at a very early processing stage,
which is reflected in a centro-parietal positivity for words and non-words compared to letter strings.

Additional differences between letter strings and pronounceable non-words have been reported between 250 and 350ms bilaterally over mid-temporal locations (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999). This modulation is thought to reflect the access of phonological representations (Proverbio et al., 2004) and grapheme-phoneme conversion mechanisms (Simon, Bernard, Largy, Lalonde, & Rebai, 2004). Besides this modulation a large number of studies have further reported a component that is especially sensitive to semantic properties, marked by a negative-going potential that peaks around 400ms post stimulus, the so-called N400 component (for a comprehensive review see Section 4.2.1 or Kutas & Federmeier, 2000; Kutas & Van Petten, 1994).

In general, these previous findings suggest that the reading of letters activates visual modules that detect orthographic material 100-200ms before any deeper linguistic processes occur. Furthermore, orthographic stimuli that allow phonological processing engage language specific analysis between 250-350ms before additional semantic processing occurs 350-450ms. As the present study reports a divergence in ERP activity with the earliest maximum occurring at around 400ms, it is likely that this difference reflects semantic rather than phonological processing. This is also supported by the topography of the observed difference, which exhibits a centro-parietal scalp distribution (whereas differences in phonological processing have been reported to occur over mid-temporal regions). The modulation in electrical activity between words and non-words was obtained in two epochs. The first modulation revealed a negative deflection for words compared to non-words at 300-600ms over centro-parietal electrode sites, resembling an N400 component. Consequently, the functional significance of this electrical difference indicates semantic processing associated with larger analysis costs for words compared to non-words. Since non-words are unlikely to engage semantic processing mechanisms it seems plausible that unrelated but real words place higher demands on semantic processing.

The second modulation between words and non-words occurred at 1000-1800ms and was characterised by a sustained positivity for non-words compared to
words. Given the late onset of this effect it is likely that this difference reflects
cognitive processes following the word recognition stage. The experimental design
required participants to read the word pairs presented on the screen silently and keep
them in mind. After the word pair disappeared a black screen was presented for
1000ms before subjects were instructed to pronounce the presented pairs aloud. This
experimental procedure is likely to engage working memory processes in order to
keep a representation of the presented word pairs active in memory up to the point
when those word pairs have to be reproduced aloud. It is, therefore conceivable that
the late onsetting electrical difference between words and non-words may reflect
differences in working memory engagement.

In fact, previous studies have reported modulations in brain activity
associated with short-term retention of words and non-words (Ruchkin et al., 1999).
For example, Ruchkin and colleagues (1999) used words and non-words to
investigate how brain activity associated with verbal working memory varied as a
function of lexical/semantic processing. Differences were observed over central scalp
regions constituting more positive going deflections for non-words compared to
words. The present findings suggest in this context that lexical or semantic
information directly influences retention processes. Non-words seem to be associated
with higher working memory loads than real words. The active maintenance of non-
words is thought to primarily rely on a verbal rehearsal process (the phonological
loop; Baddeley, 1986). Real words, by contrast, are sustained in working memory via
an enhanced activation of the words’ representation in long-term memory (Saffran &
Martin, 1990). This interpretation may account for the obtained late positive shift in
activity for non-words compared to real words.

Taken together, the results of the present experiment provide evidence that
stimuli that differ in their lexical and semantic information content can modulate the
brain processes during encoding. Whether these stimuli evoked modulations that
were further predictive for successful retrieval was tested in a second set of analysis
employing the subsequent memory paradigm.
9.5.2 Differences in subsequent memory

A second set of analyses aimed to clarify whether the encoding of stimuli that do or do not contain lexical/semantic representations would alter brain activity that is predictive for subsequent memory performance.

The initial comparison of encoding activity for words and non-words (collapsed across test conditions) showed no reliable subsequent memory effects for words, but revealed frontally distributed modulations for non-words at 1000-1800ms. However, this modulation was of reversed polarity compared to commonly reported subsequent memory effects. Since this analysis was collapsed across intact and rearranged test conditions it is possible that the different target and non-target definition may have evoked this alleged reversal. Memory retrieval engaged for rearranged pairs which results in an incorrect target response may have evoked the more positive going deflection.

![Subsequent memory effects](image)

**Figure 9-20** Significant differences in subsequent memory effects are illustrated for the class of words and non-words. Differences in electrical activity occur only in the late time window (1000-1800ms) for non-word conditions. This effect is characterised by more positive going activity for subsequent incorrectly compared to correctly recognised items.

Analyses split across intact and rearranged conditions showed that non-words elicited under rearranged conditions a subsequent memory effect over frontal locations at 1000-1800ms, revealing a more positive going deflection for incorrectly
compared to correctly recognised non-words. Non-words tested under intact conditions, however, did not reveal such differences. Hence, these results suggest that the rearranged condition is largely responsible for the more positive going ERP deflection for incorrectly vs. correctly recognised non-words. This effect concurs with typically reported subsequent memory effects, although it appears disguised by the particular target definition for rearranged pairs.

![Subsequent memory effects](image)

*Figure 9-21* Significant differences in electrical activity for subsequent correctly and incorrectly remembered items occurred for non-words only under rearranged test conditions. This difference in subsequent memory performance occurred in the late time window (1000-1800ms) and reveals more positive going activity for subsequent incorrectly compared to correctly recognised items.

Besides non-words, real words were also examined with analyses separating intact and rearranged test conditions. However, only rearranged conditions qualified for this analysis, which showed more positive going parietal ERP activity for incorrectly compared to correctly identified words. This pattern of activity is similar to the subsequent memory effect reported for non-semantic conditions in the first experiment. The current findings, however, failed to reach statistical significance, most likely due to a lack of statistical power caused by the greatly reduced number of trials. Thus, it is concluded that statistically robust subsequent memory effects occurred only for non-words over frontal locations.
Finally, the discussion will now focus on the nature of information that was retrieved for non-words in rearranged conditions and gave rise to the subsequent memory effect. As outlined earlier, the difference in electrical activity is driven by incorrect ‘old’ responses to rearranged pairs, probably reflecting recognition of individual items without contextual retrieval of the precise pairing. According to dual process theories, this type of retrieval is regarded as familiarity (Yonelinas, 2002). When interpreting these findings in the spirit of dual-process accounts, incorrectly recognised non-words tested under rearranged conditions are supported by familiarity-based retrieval. As no obvious lexical or semantic features were available for non-words, such familiarity processes must have operated primarily on phonological or orthographical levels. It should be noted that occasionally semantic codes may have been attached to some of the non-words, for example primed by orthographical or phonological similarities. Nevertheless, the electrical activity obtained during study suggests categorical differences in semantic processing between words and non-words reflected in the modulation of the N400. This indicates that if such associations between semantic codes and non-words appeared at all, it must have remained an exception. Consequently, the present study suggests that frontally located subsequent memory effects support encoding processes that lead to familiarity based retrieval which are primarily related to the processing of phonological or visual/orthographic features.

This conclusion might be challenged by the fact that words and non-words show no behavioural differences in familiarity driven false alarms to rearranged pairs. Frontal subsequent memory effects, however, were only present for non-words but not words. Although, this null result (i.e. no frontal difference for words) has to be interpreted with caution, it is unlikely that a lack of statistical power is responsible for the absence of frontal modulations, as a greater number of trials contributed to words compared to non-words. By contrast, words revealed subsequent memory effects at parietal locations, which were not statistically robust. Nevertheless, a comparable parietally distributed subsequent memory effect was obtained for stimuli containing semantic features in a previous experiment. This subsequent memory
effect was interpreted as reflecting effective encoding processes that support familiarity driven retrieval based on semantic features.

In general, the results from the present and previous experiment suggest that encoding mechanisms associated with familiarity based retrieval are modulated by lexical and semantic features. Encoding activity supporting familiarity processes primarily based on visual/orthographic features appear to be located over the frontal scalp regions. By contrast, encoding mechanisms supporting subsequent familiarity based on semantic features may be hypothesised to occur over parietal scalp regions. Thus, effective encoding is modulated depending on whether to-be-remembered stimuli relate to existing semantic representations stored in our memory system.
9.6 Summary and Conclusion

The present study investigated whether the availability of lexical and semantic information influences encoding processes and whether it amends encoding processes associated with successful retrieval in particular. In general, ERP patterns exhibited at encoding a divergence in electrical activity indexing semantic processing via a centro-parietally located N400. This divergence was followed by a sustained positivity for non-words over centro-parietal locations but with a late onset at about 1000ms post stimulus. This late positivity was interpreted to reflect an increased working memory load for non-words as the experimental paradigm required the active maintenance of the presented stimuli for a short period of time.

The results suggest that lexical and semantic features do alter encoding processes. Such differences might account for behavioural differences, as significantly more correct responses were obtained for words compared to non-words. Consequently, the current findings advocate a stimulus driven involvement of semantic processing in episodic memory by providing evidence that words and non-words diverge in their engagement of semantic processing activity during episodic encoding.

Thus, the subsequent memory paradigm was employed to investigate the neuronal activity associated with subsequent correctly and incorrectly recognised stimuli. Differences in electrical activity were obtained at about 1000-1800ms over frontal locations for non-words, while no such deviation was found for words. The functional role of this frontal dissociation was interpreted to reflect encoding activity for familiarity based retrieval directed towards visual/orthographic features. Conversely, in combination with a previous experiments presented in this thesis it may be hypothesised that encoding activity for familiarity based retrieval focussing on semantic features appears over parietal scalp regions.

In general it is not straight forward to relate the findings of the subsequent memory paradigm to the general encoding differences observed for words and non-words, as the former comparison focuses on a between-item contrast, whereas the latter describes within-item comparisons. Nevertheless, both comparisons reveal alterations in electrical brain activity between words and non-words, providing
evidence that not only information processing at encoding is modulated by differences in lexical/semantic features, but that this difference in semantic knowledge effects the way successfully retrieved information is encoded. Overall these findings indicate that non-words tend to engage encoding processes that deviate from those engaged for words, which has implications for the subsequent episodic retrieval of those items.
10 Retrieval of semantic and non-semantic stimuli

10.1 Introduction

The previous chapter revealed altered encoding processes for stimuli that do and do not permitted lexical or semantic processing. Such stimulus driven encoding differences are likely to affect retrieval, which is the focus of the present investigation. The central topic of this thesis concerns potential interactions between the semantic and episodic memory system. Earlier chapters have reported experiments, which manipulated the semantic coherence of to-be-encoded stimuli and showed evidence that such semantic manipulations influence episodic memory. Unclear, however, is whether semantic memory access itself affects episodic retrieval. The present experiment addresses this question by manipulating the semantic vs. non-semantic content of stimuli within an episodic memory paradigm.

The memory literature reports differences between words and non-words primarily in the context of lexical decision tasks. The premise of those tasks is that response speed and accuracy indicate how well word representations can be activated and retrieved from memory. Several variables are shown to influence lexical decisions including word frequency (Malmberg, Holden, & Shiffrin, 2004; Glanzer, Adams, Iverson, & Kim, 1993) and repetition priming (Hintzman & Curran, 1997; Scarborough, Cortese, & Scarborough, 1977). The latter has a longer lasting (Grant & Logan, 1993) and stronger effect on words compared to non-words (Forster & Davis, 1984). In the attempt to explain these effects, several theoretical accounts have been developed, either based on automatic processing such as spreading activation or on controlled processing such as semantic integration or expectation (for overview see Chwilla et al., 1998; Ruz, Madrid, Lupianez, & Tudela, 2003; Chwilla, Kolk, & Mulder, 2000; Weisbrod et al., 1999).

While words strongly benefit from repetition priming, the influence on non-words is less clearly understood. Although repetition priming effects for non-words are rarely as strong as for words, some studies have revealed robust priming effects for non-words under certain conditions (McKone, 1995; Smith & Oscar-Berman, 1990). These findings suggest that not only lexical but also non-lexical sources
contribute to repetition priming, which consequently has to act beyond the level of semantic representations.

Memory processes for words and non-words other than repetition priming and lexical decision tasks are less well studied. Nevertheless, differences in retrieval processes elicited by non-words and words are of great importance when investigating semantic and episodic memory interactions. It may well be that lexical access is critical for effective encoding and retrieval of new episodic associations. Alternatively, pre-existing semantic knowledge could only be one of several different sources episodic memory traces are based on, such as phonological or orthographical information. In that case it would be of interest how such different sources of semantic vs. non-semantic features influence the process of episodic retrieval.

For instance, as discussed in chapter 9.5, the processing of different types of information occur at temporally distinct stages. While orthographic regularities affect processing at a very early stage (100-200ms post stimulus onset), differences between letter strings and pronounceable non-words emerge between 250-350ms, followed by processing of semantic expectancy at around 400ms post stimulus. Yet, it remains unknown whether different study-test lags amend the influence of these different sources on retrieval. It is possible that the long term storage of pre-existing semantic knowledge allows episodic traces based on such semantic knowledge to endure a long study-test lag. Phonological or orthographical sources, by contrast, may be less effective in maintaining information for a longer period of time. Therefore, the present study investigates whether lexical manipulations using words vs. non-words evoke episodic and semantic memory interactions and if so whether such interactions vary as a function of study-test lag. The functional significance of dissociations between words and non-words were tested with ERP old/new effect that index familiarity and recollection based retrieval (see Chapter 9).

A previous ERP study examined intentional vs. incidental memory retrieval for words and non-words (Curran, 1999) by employing either a recognition or a lexical decision task. The recognition test demonstrated no difference in the early frontal ERP old/new effect for words compared to non-words. The later parietal old/new effect, however, was larger for words compared to non-words. Therefore, this study
concluded that words vs. non-words differentially engage recollection based retrieval. Curran’s study, however, was limited to item memory and did not extend to associative recognition. Thus, it remains unclear whether and what kind of retrieval differences occur when new associations were formed between words or non-words. The following study addresses this question by testing recognition performance for newly formed pairs of words and non-words either after short or long study-test lags.

10.2 Material and Methods

10.2.1 Participants

The very same group of participants reported in chapter 9 performed the recognition test presented here. However, only a subgroup of 11 (7 females) subjects with an average age of 20 provided a sufficient number of trials in all experimental cells to qualify for subsequent analyses.

10.2.2 Material

This experiment was conducted with exactly the same stimulus material as reported in chapter 9 (Section 9.2.2). This experiment tested studied pairs of words and non-words under intact (same as study), rearranged (studied pairs were recombined to new pairs) and new test conditions (studied items are presented with novel items). Rearranged test conditions were presented to prevent strategic responses and are therefore not analysed or reported in the result section.

10.2.3 Procedures

The procedure described in section 9.2.3 was employed in this experiment. Twelve study and test blocks were presented in a random order to each participant. Half of the test blocks were shown immediately following the study block (short lag condition), while the other half were presented after a 5 minute break between study
and test (long lag condition), during which participants were presented with short movie clips to prevent active rehearsal.

**10.2.4 ERP recordings and analysis**

Scalp EEG was recorded in exactly the same procedure as described in section 9.2.4. ERP waveforms were formed separately for correctly identified pairs of words and non-words. A minimum of 12 artefact-free trials was required from each participant, in each condition, to create average ERP waveforms. The displayed grand average ERP data were smoothed with a 5 points window for presentation purposes only. The ERP analyses were designed to investigate possible differences in retrieval activity evoked by correctly identified intact (previously studied) and new (not previously studied) pairs of words and non-words. Based on visual inspection and consistent with previous analyses, the data at test were analysed over 4 consecutive time windows (300-600ms, 600-900ms, 900-1200ms, 1200-2000ms).

**10.3 Results at retrieval**

**10.3.1 Behavioural data**

Figure 10-1 displays the likelihood of correct task performance for previously studied (intact) and new (new) pairs of words and non-words tested either under short or long lag conditions. An ANOVA with the factors of lag (short, long), stimulus (words, non-words) and test (intact, new) showed a significant main effect of stimulus \([F(1,10)=38.0; p<0.001]\) and test \([F(1,10)=9.2; p<0.05]\) as well as an interaction between lag and stimulus \([F(1,10)=4.7; p<0.05]\). The latter interaction reflects decreased recognition accuracy for non-words tested under long compared to short lag conditions, which reached significance in follow-up analyses only in intact test conditions \((t(10)=2.4, p<0.05)\). Words, by contrast, indicate the opposite trend of increased recognition accuracy for long compared to short lags, which did not reach significance in follow-up analyses.

The main effect of test describes an overall higher level of correct responses to new compared to intact test conditions. Pair-wise contrasts showed with exception
of the ‘long lag–word’ condition, for all remaining ‘long lag–non-word’, ‘short lag–word’ and ‘short lag–non-word’ conditions significantly more correct responses to new compared to intact pairs (t(10)=2.7, p<0.05; t(10)=2.6, p<0.05; t(10)=2.1, p<0.05; respectively).

Overall, words compared to non-words attracted higher proportions of correct responses. Follow-up comparisons show only after long lags significantly increased accuracy for words relative to non-words under intact as well as new conditions (t(10)=4.7, p<0.01; t(10)=2.8, p<0.05; respectively).

The data reveal that participants were in principle able to discriminate between intact and new word pairs. Pair-wise contrasts of hits (intact correct) vs. false alarms (new incorrect) exhibited significant differences for words and non-words under short (t(10)=15.9, p<0.001; t(10)=10.0, p<0.001; respectively) as well as long lag conditions (t(10)=17.8, p<0.001; t(10)=6.9, p<0.001; respectively).

The discrimination accuracy [Pr=hit – false alarm] and response biases [Br=false alarm/(1-Pr)] were computed for words and non-words tested under short and
long lag conditions. The discrimination accuracy under short lag conditions was significantly better for words (0.66) compared to non-words (0.48) \((t(10)=3.2, p<0.01)\). A comparable result was obtained for long lag conditions as a significantly better discrimination accuracy was obtained for words (0.69) compared to non-words (0.36) \((t(10)=6.0, p<0.001)\). Furthermore, the results reveal a significant decrease in discrimination accuracy between short and long lag conditions for non-words only \((t(10)=3.7, p<0.01)\).

The analyses of response bias revealed no significant differences between words (0.29) and non-words (0.38) under short lag conditions and equally no difference between words (0.29) and non-words (0.38) under long lag conditions. Furthermore, contrasts across short and long lag conditions also failed to elicit significant differences in response bias. Thus, although both words and non-words consistently demonstrate a conservative response bias across short and long lag conditions, difference in behavioural performance or ERP activity between words and non-words can not be explained by response bias as no significant difference in bias is obtained.

![Figure 10-2](image)

*Figure 10-2* Behavioural data showing reaction times (RT) for correctly recognised intact and new pairs. Mean (and standard error) reaction times are displayed for words and non-words tested under short and long lag conditions. Correct responses to intact word conditions are made significantly faster than to intact non-words across both short and long lag conditions.
Finally, the speed at which accurate responses were given was investigated with an ANOVA including the factor of lag (short, long), stimulus (words, non-words) and test (intact, new). This analysis resulted in a main effect of stimulus \( [F(1,10)=15.0; \ p<0.01] \) which reflects faster responses to words compared to non-words particularly under intact test conditions (see Figure 10-2). Pair-wise contrasts of word vs. non-words showed significant differences for intact pairs when tested under short as well as long lag conditions \( (t(10)=2.5, \ p<0.05; \ t(10)=2.3, \ p<0.05; \) respectively). This pattern of results suggest that participants required more time to make an accurate judgement to intact non-words compared to intact words.

In general, the statistical analysis of the behavioural data suggests that participants were able to successfully discriminate intact from new pairs, that is, to recognise previously studied pairs of words and non-words. Recognition accuracy, however, was modulated for non-words across lag conditions, with significantly fewer items being correctly recognised under long lag compared to short lag conditions. This effect was limited to non-words. Although, the discrimination ability was significantly higher for words compared to non-words, both stimulus conditions revealed the same conservative response bias. Finally, reaction time analyses indicate that non-words required significantly more time to be correctly recognised compared to words.

### 10.3.2 ERP data

Grand average ERPs elicited for correctly recognised intact and correctly rejected new pairs of non-words tested under short lag conditions are shown in Figure 10-3. The mean number of trials contributing to the average waveforms is 14 for intact, and 15 for new pairs.
Figure 10-3 Grand average ERPs elicited for correctly recognised intact pairs of non-words (blue) and correctly rejected new pairs of non-words (black) tested under short lag conditions. Unless stated otherwise, ERP waveforms are shown here and in subsequent graphs of this kind for 61 electrodes, displayed as if looking down onto the top of the head. Differences between the waveforms emerge over frontal and parietal locations, signifying modulations in neuronal activity for successfully recognised stimuli.

Figure 10-4 Grand average ERPs elicited for correctly identified non-words for intact (blue) and new conditions (black) tested under short lags. Here, and in all corresponding subsequent graphs, ERP waveforms are displayed at 3 frontal (F1, Fz, F2) and 3 parietal (CP1, CPz, CP2) electrodes, whose locations are highlighted in green on the schematic top down view of the head. The frontal electrodes show more positive going deflections for intact compared to new pairs of non-words, onsetting at about 300ms post stimulus. Parietal electrodes also reveal more positive going activity for intact compared to new stimuli, onsetting at about 800ms post stimulus.
ERP activity elicited for intact and new pairs exhibited a small divergence in activity over anterior right frontal locations onsetting at about 300ms post stimulus (see Figure 10-4 for enlarged illustration). Intact conditions exhibited more positive going deflections relative to new conditions. Parietal locations also revealed a more positive going deflection for intact compared to new conditions from about 500ms onwards. While modulations over parietal locations disappeared at about 1200ms, right frontal electrodes continue to exhibit small differences in encoding activity until the end of the recording epoch.

Grand average ERPs elicited for correctly identified intact and new words tested under short lag conditions are shown in Figure 10-5. The mean number of trials contributing to the average waveforms is 14 for intact, and 16 for new pairs.

![Figure 10-5](image)

**Figure 10-5** Grand average ERPs elicited for correctly identified words for intact (red) and new conditions (black) tested under short lag conditions. Differences between the waveforms emerge over frontal, central and parietal locations, indicating differences in neuronal activity for successfully recognised and rejected stimuli.
Similar to non-words, retrieval of words evoked differences in activity between correctly identified intact and new word pairs over frontal locations at about 300ms post stimulus (see Figure 10-6 for a more detailed illustration of selected electrode sites). More positive going waveforms for intact compared to new words pairs emerged bilaterally over frontal electrodes and remained present over a long period of time. At about 600ms post stimulus, parietal activity starts to diverge in concert with the persisting frontal difference. Both frontal and parietal electrodes show more positive going ERP activity for intact compared to new word pairs, which is present until the end of the recording epoch.

![Figure 10-6](image)

**Figure 10-6** Grand average ERPs for correctly recognised intact pairs of words (red) and correctly rejected new pairs of words (black) tested under short lag conditions. The frontal electrodes show more positive going deflections for intact compared to new words at about 300ms post stimulus. These frontal differences are sustained until the end of the recording epoch. Parietal electrodes also reveal more positive going activity for intact compared to new stimuli, onsetting at about 800ms post stimulus which persists equally to frontal activity until the end of the recording epoch.

Grand average ERPs elicited for correctly identified intact and new non-words presented after long lags are shown in Figure 10-7. The mean number of trials contributing to the average waveforms is 14 for intact, and 15 for new pairs.
Figure 10-7 Grand average ERPs for correctly recognised intact non-words (blue) and correctly rejected new non-words (black) tested under long lag conditions. Differences between the waveforms seem only to occur over right frontal locations, indicating differences in neuronal activity for successfully recognised and rejected stimuli.

ERP waveforms show a late onsetting (about 800ms post stimulus) right frontal modulation (see Figure 10-8 for enlarged view), reflecting more positive going activity for intact compared to new conditions. Although parietal locations also reveal fluctuations in ERP activity between intact and new conditions, they do not appear to be particularly robust.
Figure 10-8 Grand average ERPs for correctly recognised intact (blue) and correctly rejected new pairs of non-words (black) tested under long lag conditions. The frontal electrodes reveal a clear positivity for intact compared to new pairs of non-words, onsetting at about 800ms post stimulus. These frontal differences are sustained until the end of the recording epoch. Parietal electrodes, however, show no clear divergence in electrical activity.

Finally, grand average ERPs for correctly identified intact and new pairs of words, tested after long lag conditions, are shown in Figure 10-9. The mean number of trials contributing to the average waveforms is 14 for intact, and 16 for new pairs.

ERP waveforms exhibit a clear difference in activity over frontal locations from about 300ms onwards (see Figure 10-10 for enlarged view) revealing a more positive going ERP activity for intact compared to new word pairs. The same pattern of activity was obtained at parietal locations form about 600ms onwards. While parietal differences disappear around 1200ms, right frontal locations continue to exhibit small differences in encoding activity until the end of the entire recording interval.
10 Retrieval of semantic and non-semantic stimuli

Figure 10-9 Grand average ERPs for correctly recognised intact (red) and correctly rejected new non-words (black) tested under long lag conditions. Clear differences in ERP activity are present over frontal and parietal locations, indexing the neuronal activity associated with successful recognition and rejection of stimuli.

Figure 10-10 Grand average ERPs for correctly recognised intact (red) and correctly rejected new words (black) tested under long lag conditions. The frontal electrodes reveal a clear positive deflection for intact compared to new stimuli, which onsets at about 300ms post stimulus. Parietal electrodes reveal also more positive going ERP activity for correctly identified intact compared to new stimuli, but with a later onset at about 800ms post stimulus.
Statistical tests were performed on average voltages calculated over four consecutive epochs (300-600ms, 600-900ms, 900-1200ms, 1200-2000ms). These epochs are in line with time windows employed in studies reported earlier in this thesis (see Sections 5.2.4 and 7.2.4) and capture the present changes in electrical activity.

### 10.3.3 ERP analyses

Differences in ERP activity between intact and new test conditions across the two classes of stimuli were assessed with an ANOVA employing the factors of test (intact, new), epoch (300-600ms, 600-900ms, 900-1200ms, 1200-2000ms), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid superior). Most lag and stimulus contrasts revealed a significant interaction between the factors of test, epoch, location and hemisphere (see Table 10-1), which exception of non-words studied under short lag conditions, which resulted in a significant test by epoch by hemisphere \([F(2.2,22.3)=5.8; p<0.01]\) and test by epoch by location by site \([F(3.3,32,6)=4.0; p<0.01]\) interaction. These results suggest the presence of ‘old/new effects’, which appear to change across time and location.

<table>
<thead>
<tr>
<th>test - epoch - loc. - hem. interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>short lag cond., words</td>
<td>3.4</td>
<td>2.4</td>
<td>24.2</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>long lag cond., non-words</td>
<td>4.09</td>
<td>1.8</td>
<td>17.8</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>long lag cond., words</td>
<td>3.23</td>
<td>2.7</td>
<td>26.8</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

*Table 10-1* This table shows the statistical parameters for the significant interactions between the factors of test, epoch, location and hemisphere when words and non-words were tested under short and long lag conditions.

Subsequent analyses explored the pattern of temporal and spatial modulation with an ANOVA including the factors of test (intact, new), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid superior) across the four consecutive time windows. The resulting effects obtained for short and long lag conditions will be presented in turn.
10.3.3.1 Short lag conditions

Non-words tested under short lag conditions revealed significant interactions including the factor of test in the first, third and fourth time window (see Table 10-2), suggesting that intact vs. new ERP old/new effects are modulated across location and time. A subsidiary set of analysis separated the data over frontal and parietal locations, and employing an ANOVA with the factors of test (intact, new), hemisphere (left, right) and site (inferior, mid superior) across individual time windows.

<table>
<thead>
<tr>
<th>Effects for non-words</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>under short lag</td>
<td>300-600</td>
</tr>
<tr>
<td>test by ep. by hem</td>
<td>-</td>
</tr>
<tr>
<td>test by loc. by hem.</td>
<td>-</td>
</tr>
<tr>
<td>test by loc. by hem. by site</td>
<td>p&lt;0.01</td>
</tr>
</tbody>
</table>

Table 10-2 This table shows significant effects and interactions with the factor of test (intact, new) when non-words were tested under short lag conditions. The significant effects resulting from an ANOVA with the factors of test, location, hemisphere and site are displayed separately for all four epochs.

Frontal locations failed to elicit significant effects or interactions with the factor of test across the first three time windows. The fourth time window (1200-2000ms) however, revealed a significant interaction between the factor of test and hemisphere [F(1,10)=7.4; p<0.05], as well as a marginally significant interaction between test, hemisphere and site [F(2,20)=3.2; p=0.06]. These interactions reflect more positive going activity for intact compared to new non-word pairs over the right hemisphere. Nevertheless, pair-wise comparisons of ERP activity between intact and new conditions failed to reveal any significant differences at individual electrode sites.

By contrast, at parietal locations significantly more positive activity was obtained for intact compared to new conditions over the left hemisphere at electrode site CP5 (t(10)=2.3, p<0.05) and CP3 (t(10)=2.2, p<0.05) between 900-1200ms. All
other time windows (300-600ms, 600-900ms, 1200-2000ms) failed to elicit significant differences between intact and new test conditions.

In sum, non-words tested under short lag conditions revealed a significant left parietal difference between intact and new conditions at about 900-1200ms, followed by a late right frontal modulation in activity which was only observed in opposition to left frontal activity i.e. as an interaction with hemisphere.

The analyses for words demonstrated significant effects of test and test by site interactions in all four time windows (see Table 10-3), indicating modulations in ERP activity for intact and new test conditions that differ for location and individual electrodes.

<table>
<thead>
<tr>
<th>Effects for words under short lag</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>300-600</td>
</tr>
<tr>
<td>test</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>test by site</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>test by loc. by hem. by site</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 10-3 This table shows significant effects and interactions with the factor of test (intact, new) when words were tested under short lag conditions. The significant effects resulting from an ANOVA with the factor of test, location, hemisphere and site are displayed separately for all four epochs.

Follow-up comparisons employed an ANOVA with the factor of test (intact, new), hemisphere (left, right) and site (inferior, mid superior). While frontal locations revealed no significant effect or interaction with test in the first epoch (300-600ms), parietal locations elicited a main effect of test \([F(1,10)=9.3; \ p<0.01]\) and a test by site interaction \([F(1.3,12.7)=4.7; \ p<0.05]\). This finding seems surprising as the grand average ERP data (see Figure 10-6) suggest a divergence in electrical activity over parietal locations at about 600ms but not 300ms.

This motivated a more thorough comparison of the pattern of activity within the 300-600ms time interval by dissecting this interval into three 100ms sub-epochs (300-400ms, 400-500ms, 500-600ms). The very same ANOVA including the factors of test (intact, new), hemisphere (left, right) and site (inferior, mid superior) was
performed over these sub-epochs across frontal and parietal locations. In accordance
with the previous analysis, frontal electrodes did not reveal any significant effects or
interactions with the factor of test. Parietal locations, however, revealed a significant
effect of test \([F(1,10)=9.3; \ p<0.01]\) in the third sub-epoch (500-600ms). This
suggests that parietal differences arise slightly before 600ms at about 500ms post
stimulus.

The second time window (600-900ms), revealed significant effects of test
across both frontal \([F(1,10)=8.7; \ p<0.05]\) and parietal locations \([F(1,10)=22.2;
\ p<0.001]\). Moreover, interactions between the factor of test and site were also present
at frontal \([F(1.1,11.4)=11.6; \ p<0.01]\) and parietal locations \([F(1.9,18.6)=12.3;
\ p<0.001]\). Modulations seem to be larger at parietal relative to frontal locations, but
statistical analyses failed to reveal significant differences (see Figure 10-11 for
illustration). The pattern of activity obtained in the second time window (600-900ms)
was sustained in the third time window (900-1200ms), where frontal and parietal
sites exhibited a significant main effect of test \([F(1,10)=6.8; \ p<0.05; F(1,10)=19.26;
\ p<0.001, \text{ respectively}]\) and a test by site interactions \([F(1.1,11.4)=8.7; \ p<0.05;
F(1.8,18.4)=5.2; \ p<0.05, \text{ respectively}]\). Pair-wise comparisons revealed the same
profile of activity across the second and third time interval. Frontal locations elicited
significant differences over all electrodes except F6, while all parietal sites exhibited
significant differences in activity.

![Figure 10-11](image)

**Figure 10-11** Differences in effect size between intact vs. new conditions are shown for frontal
(solid bar) and parietal (striped bar) words tested under short lag conditions. Mean (and standard
error) of the effect size are compared across six different electrode sites. Although the effect size
appears larger over parietal locations, this difference did not reach statistical significance.
Finally, both frontal and parietal locations show a main effect of test in the last time window (1200-2000ms) \([F(1,10)=11.2; \ p<0.01; \ F(1,10)=14.1; \ p<0.01,\) respectively]. Pair-wise contrasts at individual electrodes suggest a shift in the frontal activity from bi-lateral towards more right frontal distributions, as all electrodes except F5 exhibit significant differences in activity. Follow up contrasts over parietal sites reveal once more significant differences across all individual electrodes.

Taken together, the statistical analyses for words tested under short lag conditions provide no evidence for early frontal differences, while parietal modulations occur slightly before 600ms (at 500ms) and remain present across the remaining recording interval. Frontal differences co-occurred with parietal differences across the final 3 time windows (600-900ms, 900-1200ms, 1200-2000ms). These findings are compatible with the view that strong parietal differences arise from about 500ms onwards, whose activity spreads over frontal electrode sites. In addition to this parietal difference, a late right frontal effect emerges in the final time window and elicits a more right lateralised modulation in activity. The following section will first describe the statistical results obtained for words and non-words tested under long lag conditions.

**Figure 10-12** Significant differences in ERP activity between intact and new test conditions are illustrated for words and non-words, tested under short lag conditions. The cartoon shows the distribution of frontal and parietal differences across the four time windows.
10 Retrieval of semantic and non-semantic stimuli

10.3.3.2 Long lag condition

Analogous to short lag conditions, modulations in ERP activity for stimuli tested under long lag conditions were examined by employing an ANOVA with the factors of test (intact, new), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid superior) over every individual time window. For non-words, this analysis revealed significant effects and interactions involving the factor of test (see Table 10-4), highlighting modulations in ERP activity between intact and new test conditions across location and hemisphere. Supplementary analyses separating the data over frontal and parietal locations and employing an ANOVA with the factors of test (intact, new), hemisphere (left, right) and site (inferior, mid superior).

<table>
<thead>
<tr>
<th>Effects for non-words</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>under long lag</td>
<td>300-600</td>
</tr>
<tr>
<td>test</td>
<td>-</td>
</tr>
<tr>
<td>test by loc. by hem.</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 10-4 This table shows significant effects and interactions with the factor of test (intact, new) when non-words were tested under long lag conditions. The significant effects resulting from an ANOVA with the factors of test, location, hemisphere and site are displayed separately for all four epochs.

The first time window (300-600ms) failed to elicit significant effects or interactions with the factor of test at frontal and parietal locations. The second time window (600-900ms), however, demonstrated a significant effect of test over frontal electrodes [F(1,10)=6.2; p<0.05] and a test by hemisphere interaction over parietal electrodes [F(1,10)=4.3; p=0.06]. Pair-wise contrast showed that frontal activity was dominant over right frontal sites, since only electrode F6 (t(10)=2.9, p<0.05), F4 (t(10)=2.7, p<0.05) and F2 (t(10)=2.4, p<0.05) revealed significant differences. Parietal activity, however, was more focused over the left hemisphere, as only electrode CP5 (t(10)=2.3, p<0.05) revealed a significant difference in electrical activity between intact and new non-words.
Parietal differences were restricted to the second epoch. Frontal locations, by comparison, revealed a main effect of test and a test by hemisphere interaction in the third epoch (900-1200ms) [F(1,10)=8.2; p<0.05; F(1,10)=6.0; p<0.05, respectively] and the fourth epoch (1200-2000ms) [F(1,10)=7.2; p<0.05; F(1,10)=23.3; p<0.001, respectively]. These effects reflect more positive going deflections for intact compared to new non-word pairs over the right hemisphere. Additional comparisons confirmed this by revealing significant effects at electrode F6 (t(10)=3.9, p<0.01), F4 (t(10)=3.6, p<0.01) and F2 (t(10)=2.8, p<0.05) in the third epoch and for electrode F6 (t(10)=4.9, p<0.001), F4 (t(10)=3.6, p<0.01) and F2 (t(10)=2.9, p<0.05) in the fourth epoch.

In sum, non-words tested after long lag conditions failed to elicit early differences across frontal and parietal locations. The first significant difference occurred in the second epoch (600-900ms) over parietal and frontal locations (with opposite hemispheric dominance). While parietal differences emerged primarily over the left hemisphere, frontal differences were prominent over the right hemisphere. Non-words demonstrated a clear divergence in electrical activity across right frontal locations in the two later time windows (900-1200ms, 1200-2000ms) by showing more positive going deflections for intact compared to new non-words. Thus, these findings are consistent with the view that intact and new conditions diverge over left parietal sites between 600 and 900ms, followed by later right frontal difference, whose onset partially overlaps with the parietal effect.

Finally, pairs of words were tested after long lag conditions by employing an ANOVA with the factors of test (intact, new), location (frontal, parietal), hemisphere (left, right) and site (inferior, mid superior) over every individual time window. The results demonstrated significant main effects of test and a variety of significant interactions with test (see Table 10-5), suggesting differences in activity across time and location. Subsidiary tests separated the data over frontal and parietal locations by employing an ANOVA with the factors of test (intact, new), hemisphere (left, right) and site (inferior, mid superior).
This analysis demonstrated in the first time window (300-600ms) a significant effect of test \([F(1,10)=17.5; p<0.01]\) and a test by site interaction over frontal locations \([F(1.2,12.4)=4.8; p<0.05]\). Parietal locations failed to reveal effects or interactions with the factor of test. The test by site interactions at frontal locations reflects a stronger positive deflection for intact pairs over superior than inferior sites, but significant differences were obtained at all individual electrode site \((p<0.05, \text{ in all cases})\).

The second time window (600-900ms) demonstrated a significant effect of test \([F(1,10)=24.1; p<0.001; F(1,10)=26.1; p<0.001, \text{ respectively}]\) and a test by site interaction across frontal as well as parietal locations \([F(1.2,12.1)=16.1; p<0.001; F(1,10)=18.2; p<0.001, \text{ respectively}]\). These test by site interactions indicate for frontal and parietal electrodes more positive going activity to intact relative to new pairs over superior compared to inferior sites. Contrast performed at individual electrodes revealed significant differences in activity at all frontal and parietal sites \((p<0.05, \text{ in all cases})\). Although it is possible that for instance the parietal activity reflects only spreading activation from frontal sources, a direct comparison of the effect size across frontal and parietal locations revealed no significant differences in the second time window (600-900ms) (see Figure 10-13 for illustration).

<table>
<thead>
<tr>
<th>Effects for words</th>
<th>time window in ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>under long lag</td>
<td>300-600</td>
</tr>
<tr>
<td>test</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>test by loc.</td>
<td>p=0.06</td>
</tr>
<tr>
<td>test by site</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>test by loc. by site</td>
<td>-</td>
</tr>
<tr>
<td>test by loc. by hem. by site</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 10-5  This table shows significant effects and interactions with the factor of test (intact, new) when words were tested under long lag conditions. The significant effects resulting from an ANOVA with the factors of test, location, hemisphere and site are displayed separately for all four epochs.
Analyses across the third time window resulted over frontal locations in a significant effect of test \([F(1,10)=10.7; \ p<0.01]\) and a test by site interaction \([F(1.7,17.4)=17.0; \ p<0.001]\). This interaction reflects a more positive going activity for intact compared to new pairs at mid and superior but not inferior electrodes sides, since significant effects were only obtained at electrodes F4 (\(t(10)=3.9, \ p<0.01\)), F3 (\(t(10)=2.6, \ p<0.05\)), F2 (\(t(10)=3.8, \ p<0.01\)) and F1 (\(t(10)=3.9, \ p<0.01\)). Parietal locations also revealed a significant effect of test \([F(1,10)=7.1, \ p<0.01]\), which reached significance at all electrode sites except CP6 (\(t(10)=2.0, \ p>0.05\)), indicating a slightly left hemispheric distribution of the effect.

Finally, the last time window (1200-2000ms) revealed a significant effect of test \([F(1,10)=9.6; \ p<0.01]\) and a test by site interaction \([F(1.9,18.8)=14.8; \ p<0.001]\) over frontal electrodes. This interaction describes more positive deflections for intact compared to new pairs primarily over right frontal locations, since significant differences were only obtained at electrode F4 (\(t(10)=3.9, \ p<0.01\)), F2 (\(t(10)=2.6, \ p<0.05\)) and F1 (\(t(10)=3.8, \ p<0.01\)). Parietal locations, however, failed to reveal any significant effects or interactions with the factor of test.

Figure 10-13 Differences in effect size of the intact vs. new contrast are compared across frontal (solid bar) and parietal (striped bar) electrodes for words that were tested under long lag conditions in the second epoch (600-900ms). Mean (and standard error) of the effect size are compared across six different electrode sites. No systematic overall differences emerge between frontal and parietal electrode sites.
In general, word pairs tested after long lag conditions demonstrate frontal but not parietal modulations in the first time window (see Figure 10-14). The second (600-900ms) and third time window (900-1200ms), however, exhibited frontal and parietal differences between intact and new test conditions, maximal over superior sites. The fourth time window sustains this difference but only at right frontal electrodes.

![Differences for intact/new pairs under long lag](image_url)

**Figure 10-14** Significant differences in ERP activity between intact and new test conditions are illustrated for words and non-words when tested under long lag conditions. The cartoon shows the distribution of frontal and parietal differences across the four time windows.

### 10.3.4 Magnitude analyses

The following analyses assess qualitative differences of ERP effects elicited for words and non-words. First, parietal effects obtained under short lag conditions were contrasted in the third (900-1200ms) and fourth time window (1200-2000ms). Changes in effect size were assessed via difference waveforms, formed by subtracting new from intact ERP waveforms. An ANOVA employing the factor of stimulus (words, non-word), hemisphere (left, right), and site (inferior, mid superior) failed to reveal significant main effects or interactions with the factor of stimulus. Thus there is no evidence that words and non-words tested under short lag conditions elicit ERP effects of different size.
Effects occurring under long lag conditions were contrasted at frontal and parietal locations in the second time window (600-900ms). An ANOVA testing the factor of stimulus (words, non-word), hemisphere (left, right) and site (inferior, mid superior) revealed a significant stimulus effect at parietal [F(1,10)=8.9; p<0.05] and frontal locations [F(1,10)=6.9; p<0.05], indicating an increased effect size for words than non-words. Frontal locations revealed an additional stimulus by site interaction [F(1.5,15.1)=20.9; p<0.01], reflecting significantly larger effects for words compared to non-words at electrode F2 (t(10)=3.2, p<0.01), F1 (t(10)=4.5, p<0.01) and F3 (t(10)=2.8, p<0.05) (compare Figure 10-15).

![Figure 10-15](image)

*Figure 10-15* Differences in effect size at frontal electrodes in the second time window (600-900ms) between words (red bar) and non-words (blue bar) tested under long lag conditions. Mean (and standard error) of the effect size are compared across six frontal electrodes. Words show significantly larger effects compared to non-words across superior electrode sites.

If non-words are thought to exhibit temporally delayed frontal effects, it might be more appropriate to contrast frontal effects elicited for non-words in the second epoch with those elicited for words in the first epoch. This analysis also revealed by a main effect of stimulus [F(1,10)=16.8; p<0.01] indicating a significantly larger effect size for words than non-words at electrode F2 (t(10)=4.3, p<0.01), F1 (t(10)=3.6, p<0.01) and F3 (t(10)=5.8, p<0.001).
Parietal locations, by comparison, demonstrated significantly larger effects for words compared to non-words at all parietal electrodes ($t<0.05$; in all cases) with the exception of CP5 (see Figure 10-16).

Figure 10-16 Differences in effect size at parietal electrodes in the second time window (600-900ms) between words (red bar) and non-words (blue bar) tested under short lag conditions. Mean (and standard error) of the effect size are compared across six parietal electrodes. Words reveal thereby significantly larger effects across all electrodes, with the exception of CP5.

Further, equivalent ANOVAs performed over frontal locations revealed a significant stimulus by site interaction [$F(1.4,13.9)=9.5; p<0.01$] in the third time window (900-1200ms), showing significantly larger effects for words compared to non-words only at electrode site F6 ($t(10)=3.3$, $p<0.05$). Also the fourth time window (1200-2000ms) elicited significant stimulus by hemisphere [$F(1.4,13.9)=9.5; p<0.01$] and stimulus by site interaction [$F(1,10)=5.8; p<0.05$], driven by significantly larger effects for words compared to non-words that reach significance at electrode F6 ($t(10)=2.6$, $p<0.05$).

Taken together, the magnitude analyses reveal no quantitative differences in the size of the ERP effects for words and non-words when tested under short lag conditions. Long lag conditions, by contrast, evoked stronger effects for words compared to non-words across frontal and parietal locations, indicating quantitative differences in retrieval activity.
10 Retrieval of semantic and non-semantic stimuli

10.3.5 Summary

In general, the behavioural data demonstrated that subjects could successfully discriminate intact from new pairs in both word and non-word conditions. Enhanced recognition accuracy was obtained for words compared to non-words, but without any significant change in response bias. In addition, the significantly faster reaction times for words compared to non-words supports the view that recognition memory for words was superior compared to non-words.

Electrophysiological analyses were used to elaborate on the precise mechanisms supporting this enhanced recognition performance for words compared to non-words. Under short lag conditions, both words and non-words evoked frontal and parietal differences in activity for correctly identified intact and new pairs. Frontal and parietal effects, though, elicited an earlier onset and a broader distribution for words compared to non-words. Nevertheless, no significant modulations in magnitude were obtained when frontal and parietal effects were compared between words and non-words in the short lag condition.

Comparisons in effect sizes demonstrated for long lag conditions significantly larger amplitudes for words compared to non-words, particularly at right frontal electrodes.

10.4 Discussion

The present study investigates stimulus induced differences in associative recognition by contrasting pairs of items that do or do not permit lexical and semantic processing. The aim of this investigation was to determine whether semantic access modulates episodic and semantic memory interactions. Furthermore, the study addressed whether such potential interactions are a function of study-test lags.

It was predicted that if associative recognition depends on lexical and semantic processing, retrieval differences should be obtained for pairs of words and non-words. However, if not semantic access but only semantic coherence and encoding of stimuli are critical for episodic retrieval, the current study should reveal no changes
in recognition performance between words and non-words. The following discussion first the behavioural results followed by the ERP findings.

10.4.1 Behavioural Performance

Short and long lag conditions revealed significantly faster reaction times for words relative to non-words. Based on previous findings, such increased RTs for non-words might be attributed to an exhaustive search in the mental lexicon (Forster, 1976). Alternatively, non-words may be inhibited by other items with stronger lexical components such as words that are very similar to the presented non-words and therefore take up more processing time (Marslen-Wilson, 1978; Elman and McClelland, 1984).

Significantly better recognition for non-words tested under short lag compared to long lag conditions indicates that memory for this type of stimuli deteriorate with increased study-test lag. Such an effect of lag was not observed for words. This temporal dependence of the recognition ability for non-words is also reflected in the significantly decreased recognition accuracy for non-words vs. words tested under long lag conditions, while no significant difference was obtained under short lag conditions. Thus, the present behavioural data support the argument that associative recognition benefits from lexical and semantic information. This benefit, however, is not constant, but increases with lag between study and test. Unfortunately, these behavioural data give very little insight into the underlying retrieval processes that are susceptible to the status of lexical and semantic information content of the stimuli. Therefore, electrophysiological activity was recorded during the recognition test performed for words and non-words after short and long lag conditions. These conditions will now be discussed in turn.
10.4.2 ERP results after short lag

ERP data reveal more positive going deflections for intact compared to new waveforms, which describe so called ERP old/new effects. After short study-test lags, non-words revealed late onsetting old/new effects over left parietal locations (900-1200ms) followed by differences at right frontal locations (1200-2000ms). Words, by contrast, elicited earlier onsetting and more broadly distributed old/new effects, which occurred at parietal and frontal locations from about 500ms onwards and were sustained until the end of the recording epoch.

Previous studies have linked parietal old/new effect (at 500-800ms) to recollection based retrieval. In the context of the present experiment this functional interpretation suggests that recollection appears later for non-words compared to words. This interpretation is in agreement with the significantly prolonged reaction times for non-words compared to words. Magnitude comparisons of the parietal old/new effect revealed no significant difference between words and non-words, suggesting that both classed of stimuli engaged recollection to the same extent. This is consistent with the reported behavioural performance, which indicates no significant difference in recognition accuracy between words and non-words.

According to dual process theories, recognition memory is not only supported by recollection but also familiarity. The putative ERP correlate of familiarity is a bilaterally distributed early frontal old/new effect emerging at about 300-500ms post stimulus. No such ERP difference was obtained for word or non-words tested under short lag conditions. There may be many reasons why no such frontal component was observed, including a lack of statistical power. Alternatively, it is possible that retrieval of words and non-words was supported by a strong memory trace, which is in line with the high level of accurate behavioural performance. Such strong memory traces may have evoked recollection without engaging familiarity. This account is consistent with most types of dual process models, which assume that recollection and familiarity function independently at the time of retrieval (for review see Yonelinas, 2002).

Finally, a late right frontal ERP old/new effect of comparable size was elicited for words and non-words. Although the functional interpretation of this
effect is currently still debated it is hypothesised to index post-retrieval monitoring processes. The data of the present experiment do not contradict with this functional interpretation but provide no compelling evidence to support it either. Regardless of the functional interpretation the later right frontal effect is not modulated between words or non-words.

Overall, the ERP data obtained under short lag conditions suggest that recognition performance was primarily driven by recollection. Although no quantitative differences in effect sizes were obtained, temporal modulations in the engagement of the recollection process occurred. The parietal effect emerged later for non-words compared to words, suggesting that the absence of lexical and semantic representations evoke temporal delayed retrieval processes.

### 10.4.3 ERP results after long lag

Long study-test lags exhibited in the first time window (300-600ms) early frontal old/new effects for words but not non-words. This frontal effect has been linked to familiarity based retrieval and may suggest that familiarity was engaged for words but not for non-words. Nevertheless, as discussed for recollection related activity under short lag conditions it is possible that non-words compared to words require more time to engage a specific retrieval processes.

The second time window (600-900ms) revealed indeed such frontal differences for non-words as well as for words, suggesting that frontal old/new effects occur for both classes of stimuli but are temporally delayed for non-words. Furthermore, words revealed larger frontal effects relative to non-words in the second epoch (600-900ms) but also when frontal activity elicited for non-words in the second epoch (600-900ms) was contrasted with activity elicited for words in the first epoch (300-600ms). Hence, stronger frontal old/new effects were obtained for words relative to non-words, suggesting a stronger engagement of familiarity based retrieval for words.

Magnitude analyses were also conducted for parietal old/new effects which emerged for words and non-words in the second time window (600-900ms). Similar to the frontal differences, larger parietal old/new effects were obtained for words
relative to non-words, which indicates stronger recollection based retrieval for words.

Furthermore, stronger right lateralisated late frontal old/new effects emerged for words compared to non-words in the third (900-1200ms) and fourth time window (1200-2000ms). Analogous to short lag conditions, the account of the frontal effect to index post-retrieval monitoring processes does not contradict with the current data. It may well be that more post-retrieval monitoring processes are engaged, when recognition becomes more difficult.

Overall, recognition after long lag conditions appears more difficult for non-words compared to words. The level of correct recognition performance is significantly smaller for non-words compared to words and the neuronal correlates of familiarity and recollection reveal a reduced effect size for non-words relative to words.

10.4.4 General discussion

The encoding of words is likely to feature semantic information activated from long-term representations, such as images, associations or even autobiographical references. These details are cued when words are presented again at test and enhance retrieval of the studied information. In contrast, the encoding of non-words do not access lexical or semantic representations but are more likely to feature phonological and orthographic information, which may be less diagnostic of a prior presentation of the material.

The intention of the present study was to elucidate whether episodic and semantic memory interactions are modulated by stimuli that do or do not permit semantic access. Previous studies reported in this thesis have suggested that the semantic coherence of stimuli fosters familiarity driven interactions between episodic and semantic memory. Furthermore, manipulations in encoding strategies revealed that the semantic coherence of stimuli influences episodic retrieval only when the encoding task directs processing towards the meaning of the stimuli. The current study investigated whether stimulus driven changes only occur for semantically coherent stimuli or whether semantic access is an equally important factor. If the
latter is the case it was of question whether qualitatively different episodic and semantic memory interactions would occur. This study also addressed the temporal dynamic of such potential interactions by testing different study-test lags.

First, the data show very clearly that semantic access modulates interaction between episodic and semantic memory. Stronger familiarity as well as recollection based retrieval was engaged for words compared to non-words after long study-test lags, resulting in better recognition performance for words relative to non-words. Furthermore, retrieval for non-words was temporally delayed, as longer RTs and later onsetting old/new effects were obtained. This suggest that stimulus driven episodic and semantic memory interactions are not limited to semantically coherent stimuli but do also occur for stimuli that differ in lexical and semantic access.

Secondly, the obtained interactions after long study-test lags were qualitatively different from those reported for manipulations of semantic coherence. The current study demonstrated increased familiarity as well as recollection based retrieval for words compared to non-words. Manipulations of semantic coherence, by comparison, selectively altered familiarity but not recollection based retrieval.

Finally, episodic and semantic memory interactions reported in the current study depend on the study-test lag. The former two conclusions are based on findings obtained under long lag conditions. Short lag conditions, by contrast, exhibited temporally delayed retrieval processes for non-semantic compared to words, without revealing further qualitative or quantitative differences. Nevertheless, the data obtained under short lag suggest in line with the results form the long-lag condition that semantic access influences episodic and semantic interactions and this interaction is qualitatively different from the previously reported modulation evoked by semantic coherence.
10.5 Conclusion

The present study suggests that semantic-lexical manipulations do influence retrieval processing. This influence is modulated by the temporal distance between study and test. For short lag conditions, semantic-lexical manipulations prolong the temporal onset of retrieval for non-words compared to words, but exhibit no quantitative or qualitative influence regarding the retrieval processes engaged. By contrast, after long study-test lags semantic-lexical manipulations evoke quantitative changes in retrieval processes exhibiting larger familiarity and recollections components in response to words compared to non-words. Hence, semantic-lexical manipulation tap into different types of interactions between episodic and semantic memory compared to semantic-organisational manipulations, which causes a familiarity specific modulation in episodic retrieval. These results show that the nature of episodic and semantic memory interactions do not only depend on the type of semantic organisation (i.e. semantic congruent, semantic incongruent), but also the semantic/lexical source of the stimulus representation (i.e. semantic, phonological, orthographical). Furthermore, manipulations of semantic coherence and semantic access engage types of interactions, which demonstrates that semantic memory is able to influence episodic retrieval in multiple ways.
11 Computational model of familiarity and recollection

11.1 Introduction

Memory theories have increasingly focused on the retrieval mechanisms supporting episodic memory, in particular by addressing the question of whether single process or dual process models characterise episodic retrieval more appropriately. This chapter presents a novel computational model of episodic memory that operates on the basis of a single memory representation and is capable of performing true episodic (one-shot) learning, but which nonetheless supports two distinct retrieval processes. Before introducing the model current single and dual process accounts will be briefly reviewed, along with empirical findings that support a dual process account, contrasting this account with existing (largely single process) computational models of episodic memory.

Single process models support the view that episodic recognition is based on a global index of memory strength, typically called familiarity, which operates as a signal-detection process (Green & Swets, 1966). Retrieval from episodic memory is therefore determined by only a single parameter $d'$ (d-prime, defined as the distance between the old and new familiarity distributions), which can be used to identify studied (old) items as more familiar than unstudied (new) items. Recent data, however, indicate that a single retrieval parameter can not fully account for all memory findings (Yonelinas, 2002; Clark & Gronlund, 1996), encouraging the proposal of ‘dual-process models’ in which episodic retrieval is supported by two component processes, familiarity and recollection (Mandler, 1980; Jacoby & Kelley, 1992; Yonelinas, 1994; Yonelinas, 2002).

Dual process models currently dominate memory research, and behavioural findings are largely interpreted within, and viewed as in agreement with, dual-process models. Consequently, attention has turned to investigating the neural basis of episodic retrieval. To date, however, there is little consensus as to which anatomical brain structures support familiarity and recollection. Neuropsychological
studies, for instance, suggest that extensive lesions of the medial temporal lobe (MTL), including impairments to the hippocampus, parahippocampal, and perirhinal cortices, cause severe deficits in both familiarity and recollection (Hamann & Squire, 1997; Yonelinas, 2002). By contrast, case studies report that patients with focal hippocampal lesions suffer from impaired recall (i.e. actively retrieving information) but retain relatively spared recognition memory (i.e. discriminating previously learned from novel information)24 (Aggleton & Brown, 1999; Aggleton et al., 2005; Mayes et al., 2001; Holdstock et al., 2002). Furthermore, single unit recordings in monkeys and rats have identified cells, primarily located in the perirhinal cortex, which selectively respond to the novelty of visual stimuli (Brown et al., 1987; Miller, Li, & Desimone, 1993; Li, Miller, & Desimone, 1993; Xiang & Brown, 1998; Brown & Bashir, 2002). Taken together, this evidence supports the dual process hypothesis and suggests that familiarity and recollection depend on distinct brain regions, possibly with recollection being linked to the hippocampus, while familiarity is associated with the perirhinal cortex.

Although there is substantial evidence that recall and recognition processes engage distinct brain regions, some cases of selective hippocampal damage exhibit severe deficits in both episodic recall and recognition (Reed & Squire, 1997; Manns & Squire, 1999; Manns, Hopkins, Reed, Kitchener, & Squire, 2003), supporting the conclusion that familiarity and recollection depend on the same anatomical brain region. In addition, a recent study examining patients with limited hippocampal lesions using receiver operating characteristics (ROC curves plotting hit rates versus false alarm rates across different decision criteria) found evidence that both

24 Note the subtle change in terminology which is adopted here to summarise the findings consistent with the reports given in the reviewed literature. While recognition memory is supported by familiarity and recollection processes, recall is often described as a process that bears some resemblance to recollection. Thus, cases that show impaired recall but intact recognition memory are usually interpreted to rely on familiarity driven retrieval.
familiarity and recollection are supported by the hippocampus (Wais, Wixted, Hopkins, & Squire, 2006). The asymmetry of ROC curves have been interpreted as reflecting the degree to which recollection and familiarity are involved during episodic recognition. Wais et al. (2006) have shown that after correcting for differences in memory strength the ROC curves of these patients matched the ROC curves of the control group, suggesting that recollection and familiarity are similarly impaired after hippocampal damage.

Generally, although it is known that the MTL plays a critical role in episodic memory it remains unresolved whether the hippocampus and other MTL areas make distinct contributions to episodic retrieval, and if so, what these contributions are. In practice, the finding that familiarity and recollection are associated with activity in two distinct brain regions can be interpreted in more than one way. On the one hand it is possible that these two brain areas store two distinct memory traces for the same event. By this view, during retrieval the recollection and familiarity process each activate information stored in these distinct traces, which leads to activation of the corresponding brain areas. Alternatively, familiarity and recollection could both operate on information stored in a single memory trace, with the subsequent retrieval output of the two processes leading to activation within different brain areas. One important corollary of this second interpretation is that it does not necessitate the storage of two distinct memory traces – activity in different brain areas reflects the product of familiarity and recollection processing acting upon a single memory trace. There is currently no evidence that discriminates between these competing viewpoints.

This chapter introduces a computational model to explore this issue. Most biologically inspired computational models concentrate on the role that the hippocampus plays in recollection (Marr, 1971; McNaughton & Morris, 1987; Treves & Rolls, 1994; McClelland & Goddard, 1996; Burgess & O'Keefe, 1996; Hasselmo & Wyble, 1997). Although these models differ in their specific details, they are in overall agreement as to how the hippocampus supports episodic retrieval: it forms a compact code of non-overlapping representations in a recurrently connected network. The recurrent network facilitates binding of different features
into a single episode and enables a partial cue to evoke retrieval of the complete episode.

In contrast to hippocampal models of recollection, only a few neocortical models attempt to simulate familiarity based retrieval (Bogacz & Brown, 2003; Sohal & Hasselmo, 2000; Norman & O'Reilly, 2003). While some models propose a specialized network for familiarity discrimination, others advocate that familiarity emerges from a feature extraction process (Norman & O'Reilly, 2003). Although such feature extraction based models have been widely accepted as providing an account of familiarity, it is important to note that they necessarily rely upon multiple encoding episodes to produce familiarity, which is in conflict with true episodic memory retrieval (which, by definition, occurs on the basis of one-shot learning).

Existing computational models of recollection and familiarity have provided important insight into the neuronal basis for these memory processes, producing biologically plausible accounts of episodic retrieval. Surprisingly few attempts have been made to formalise dual process theories of episodic memory within a single computational model. In practice it is difficult to evaluate the performance of separate familiarity and recollection models by comparing them to experimental findings, because assuming that the dual-process view is correct, performance is typically supported by a mixture of familiarity and recollection. Thus, there is the need for models that specify episodic retrieval as the combined outcome of familiarity and recollection processing.

The present model implements familiarity and recollection within a single network, delineating two separate retrieval processes that act upon a single representation, but provide to two distinct outputs (i.e., assessments from memory). This proposal follows the dual-process tradition; recognition memory is still supported by two distinct retrieval processes even though they operate within a single network. Modelling familiarity and recollection within a single network has the advantage that no distinct representations and encoding processes are required. Thus, the network proposed here is a simple and parsimonious model of episodic memory retrieval. Moreover, this model emphasizes an important distinction
between a neuronal process and the neural representation upon which that process operates.

This chapter starts with a description of familiarity and recollection processes that are implemented within a single Hopfield network, outlining the output measures that result from the models operation and dynamics. The model shows that both retrieval processes are able to discriminate novel from previously studied patterns, and demonstrate that this discrimination remains successful under more biologically realistic coding schemes like sparse coding. Furthermore, the model is evaluated as to whether the putative familiarity and recollection processes operate as empirical findings suggest they should, considering the time course of retrieval, the capacity of the retrieval processes and the shape of the ROC curves that they produce. Finally, the performance of the model is tested by employing experiments which parallel empirical studies to assess the overall performance of the model in relation to recent findings in associative recognition.

### 11.2 Design and Implementation

![Diagram](image)

**Figure 11-1** Overview of the network used in this simulation. The pattern $x_i$ provides input to the network. The connecting weights ($w_{ij}$) recurrently link one node of the network to all the other neurons except itself. The training phase changes the connection weights ($w_{ij}$) so that learned patterns are associated with themselves. When a partial input ($x_i$) of a trained pattern is presented in the test phase, the network should be able to fully recover the trained representation as output ($x_j$). The Network provides a familiarity output based on the energy level of the test pattern at time zero, and a recollection output measuring the distance between the test pattern at time zero and the final settling time.
The network is a standard Hopfield type network with $N=1000$ binary nodes. The nodes are recurrently connected in an ‘all-to-all’ fashion, but without self-connections. During the training phase (memory encoding) a set of patterns $x_{\mu}$ is presented to the network (henceforth, $\mu$ indicates the patterns). The patterns are stored by training the connection weights between neurons via Hebbian learning:

$$w_{ij} = \frac{1}{N} \sum_{\mu=1}^{p} x_{i}^{\mu} x_{j}^{\mu} (1 - \delta_{ij}) \tag{1}$$

The strength of the connection ($w_{ij}$) between neuron $i$ and $j$ is determined by the outer product of the patterns summed across the total number ($p$) of stored patterns. During the test phase (memory retrieval) both learned and new patterns are presented to the network and a variety of readouts are measured. As is common in these models, the weights are kept fixed during the testing phase.

Within the Hopfield network it is possible that many nodes are simultaneously active for a single representation; within brain systems however the mean activity is low, and only a limited number of neurons are active at any one time. Such sparseness is incorporated in the model by decreasing the probability of a node being in the active (+1) state compared to the inactive (-1) state. The memory patterns ($x_{\mu}$) are generated from the following probability:

$$p(x_{\mu}) = \prod_{i=1}^{n} p(x_{i}^{\mu}) \quad \text{with} \quad p(x_{i}^{\mu}) = \frac{1+a}{2} \delta(x_{i}^{\mu}-1) + \frac{1-a}{2} \delta(x_{i}^{\mu}+1) \tag{2}$$

The parameter ‘$a$’ indicates the average activity of a pattern $x_{\mu}$. In the simulations presented in this chapter, sparse patterns are created by randomly generating patterns which contain an average of 1% active and 99% silent units, corresponding to $a = -0.98$. Note however that the actual number of active and silent units across patterns does vary around the mean level of sparseness. It is known that for sparse patterns the covariance rule (Tsodyks and Feigel’man, 1988) provides a
better storage capacity than the previously introduced Hebbian learning rule (shown as [1]). The covariance rule reads:

$$w_{ij} = \frac{1}{N} \sum_{\mu=1}^{p} (x_i^{\mu}-a)(x_j^{\mu}-a)-c$$  \hspace{1cm} [3]

Global inhibition is implemented in the model by subtracting a constant (c) from the weight matrix. This constant (c) represents a term that keeps the retrieval sparseness of the network identical to the input sparseness; its value was determined from simulations. Equating input and output sparseness is essential for maintaining storage capacity at low values of ‘a’, but does not affect the familiarity measure.

### 11.2.1 Familiarity process

The key aspect of this model is to demonstrate that two independent retrieval processes can differentially access representations stored in a single Hopfield network and perform familiarity- and recollection-based retrieval. The following outlines the definition and implementation of the familiarity and recollection process. A familiarity process is initiated with the presentation of a test pattern to the network. At time ‘t=0’ familiarity is assessed; the output value is dependent on the energy function of the attractor network as a whole, which is defined by:

$$E^f = -\frac{1}{2} \sum_{i=1}^{n} \sum_{j=1}^{n} x_i^f x_j^f w_{ij}$$  \hspace{1cm} [4]

As soon as a pattern is presented to the network this function computes the associated energy, which will result in low values for previously stored patterns and high energy values for new patterns. This characterisation of familiarity has been previously used by Bogacz et al. (2001). It is worth noting however that for this type of familiarity discrimination the Hopfield network is engaged very differently from its typical application. The network does not undergo a relaxation process which
would allow the pattern to settle into an attractor state. Instead, the energy (familiarity) is evaluated at the very first time step.

11.2.2 Recollection process

A recollection process is initiated with the presentation of a test pattern to the network. At time $t=0$ the activity of the network state vector ‘$s$’ is set to the input pattern $x^n$. Next, the state of the network is asynchronously updated according to:

$$s_i(t+1) = \text{sign} \left( \sum_{j=1}^{n} w_{ij} s_j(t) \right) \tag{5}$$

until a stable state (attractor) is reached. Dependent on how closely the attractor state resembles the initial pattern, the test pattern will either be classified as a previously stored or new pattern.

It is proposed that the recollection process takes into account the settling dynamics of a test pattern (see Results 11.3). The recollection measure calculates the amount of change the state undergoes when it is presented initially to the network compared to when it is relaxed into a final attractor state. If a previously studied item is presented to the network, the stored attractor state should be identical to the presented test item. Therefore, the pattern (or state vector ‘$s$’) will undergo no or few changes when settling into its corresponding attractor state. However, tested with a new item, the network will settle into an attractor state that is quite different from the initial test pattern and the state will change significantly in the course of settling to an attractor state. A distance measure captures this change by calculating the normalised dot product,

$$d(\vec{a}, \vec{b}) = \frac{1}{2} \left( 1 - \frac{\vec{a} \cdot \vec{b}}{\|\vec{a}\| \|\vec{b}\|} \right) \quad \text{with} \quad \vec{a} = s(t=0), \quad \vec{b} = \lim_{t \to \infty} s(t) \tag{6}$$
If the test pattern has been learned previously, the distance measure \( d \) should be close to zero. If an unlearned pattern is presented, the attractor state is likely to diverge significantly from the presented pattern, resulting in a distance measure larger than zero.

### 11.2.3 Thresholds and Signal to Noise Ratios

Given the definitions of the familiarity and recollection processes it is necessary to set an appropriate threshold that can be used to differentiate between studied items and new items. Here the thresholds for both the recollection based discrimination and the familiarity detection were set such that the total error (false positives plus false negatives) was minimal. Note that although the same principle is used to set the thresholds for each process, the absolute values are not the same.

The quality of the separation between response to old and new patterns can be quantified with the Signal-to-Noise ratio (SNR):

\[
\text{SNR} = 2 \frac{(\mu_{\text{old}} - \mu_{\text{new}})^2}{(\text{var}_{\text{old}} + \text{var}_{\text{new}})}
\]  

[7]

The SNR for both the familiarity and recollection process is used to characterise performance of the network.
11.2.4 ROC curves

Receiver Operating Characteristics (ROC) curves provide more information about discrimination performance than the Signal-to-Noise ratio. ROC curves are constructed by plotting hit rates (correctly identified old items) relative to false alarm rates (incorrectly classified new items). This proportion of hits and false alarms can be expressed in a single measure of sensitivity $d'$ (called ‘dee prime’, which is distinct from the distance measure $d$ introduced above):

$$d' = \text{hits} - \text{false alarms} \quad [8]$$

ROC curves are generated by computing $d'$ for different sampling points along the underlying distributions. The shape of ROC curves is informative for the type and level of discrimination. When discrimination performance is at chance ($d'=0$), the ROC curve is the major diagonal where hit and false alarm rates are equal (see Section 2.6.1.4.2 for more detailed information about ROC curves). When performance increases the ROC curve shifts towards the upper left corner, where discrimination is perfect (hit rate = 1 and false alarm rate =0).

A different representation of ROC curves, which is sensitive to changes in hit rates relative to changes in false alarm rates, is given by z-transformed ROC or z-ROC curves. The slope of the linear z-ROC curve quantifies the symmetry of ROC curves, and is informative about the underlying distribution of old and new signals. Those z-ROC curves which have a slope of one (i.e. are symmetrical around the minor diagonal), are defined by:

$$d' (1-\text{hit}, 1-\text{false alarm}) = d' (\text{hit}, \text{false alarm}) \quad [9]$$

For example, z-ROC curves have a slope equal to 1 if hits and false alarms describe two Gaussian distributions with identical variances. If the slope of the z-ROC curves does not equal 1, the discrimination changes along the decision axis. Asymmetric ROC curves can be generated in a number of different ways. For example, the variance of the underlying old and new distributions may not be equal.
Alternatively, threshold theories assume that the decision space is characterised by discrete states. While some states reflect decisions purely based on hits, others show a proportional contribution of hits and false alarms. This also results in asymmetric ROC curves.

11.2.5 Correlated and mixed patterns

In order to examine the network model with scenarios analogous to manipulations employed in the early empirical investigations (chapters 5, 7, and 9), the model was tested with highly correlated patterns. The logic of this assessment rests on the assumption that semantically related words contain overlapping neuronal representation (Warrington & McCarthy, 1987; Warrington & Shallice, 1984; Warrington, 1975). Hence, whether familiarity and recollection based discrimination is modulated by semantically related items was tested via highly correlated pattern. These patterns share a number of units with identical activation. The correlated test patterns were generated by randomly duplicating 80% of the units from a studied pattern combined with 20% randomly generated units (according to the given sparseness level).

The networks performance for mixed patterns was also assessed. Mixed patterns were formed by combining the first half of one vector with the second half of another vector. This way two classes of mixed pattern were created. One class represents a recombination of two studied patterns (old-old), while the second class is mixing a half of a studied with a half of a new pattern (old-new) (see Figure 11-2). The network’s performance is tested for these two classes of mixed patterns and compared to performance for completely new patterns (new-new).
11.3 Results

This chapter presents a memory model of episodic retrieval, incorporating the distinction between familiarity and recollection. The aim of this model is to investigate whether a single memory trace could be differentially accessed by the two distinct retrieval processes of familiarity and recollection. The model is based on the architecture of a Hopfield network, in which binary units are connected through trainable weights (Hopfield, 1982)(see Section 11.2).

The network was assessed with tests that simulate an associative recognition memory task. In such tasks one presents lists of word pairs (or other stimulus pairs) in the study phase. Memory for these pairs is subsequently tested with lists containing intermixed studied and new word pairs. The participants are asked to discriminate studied from unstudied pairs, typically leading to familiarity or recollection based retrieval.
### 11.3.1 Familiarity and Recollection process

The familiarity process implemented in the current network computes an energy value as soon as a test pattern is presented to the network. This account of familiarity is illustrated in Figure 11-1, and was originally proposed by Bogacz and colleagues (Bogacz R., Brown M.W., & Giraud-Carrier C., 2001). If the network has been previously trained with the test pattern, the energy will have a low value, whereas untrained or new patterns evoke high energy values. The energy is obtained in the very first time step, so that no dynamical process is engaged (note that this is not how Hopfield networks are typically used), consistent with the rapid discrimination performance associated with familiarity. The continuum of low to high energy values signals familiarity. A suitable threshold is then used to enable discrimination between old and new items.

In contrast to familiarity, the recollection process does engage the dynamical evolution of the network once a test pattern is presented. As time evolves a Hopfield network will always settle into a memory state (although this may be a spurious memory state). Interestingly, there is no established method to distinguish true from false memories, i.e. to determine whether the retrieved state is a true memory state or whether the retrieved state is irrelevant to the cue. A procedure that allows discrimination between learned and spurious states in a Hopfield Network has been proposed by Robins et al. (2004). Their approach is based on the ‘energy ratio’ which is the energy of the three lowest energy units of a pattern divided by the energy of the 3 highest energy units. This energy ratio is able to discriminate whether a given attractor state is learned or spurious. However, as new patterns can converge to attractor states which are either learned or spurious, this measure does not translate into a suitable recollection measure that can reliably discriminate previously learned from unlearned patterns.

The proposed recollection process takes advantage of the different settling dynamics between previously studied and new patterns. The recollection measure reflects the amount of change a state undergoes when it is presented initially to the network compared to when it is relaxed into a final attractor state (see Figure 11-1). The basic idea of this approach is that if a previously studied item is presented to the
network, the final attractor state should be identical to the presented test item. Thus, the state or pattern will undergo few changes when settling into the learned attractor state. However, if a new item is presented at test, the network will settle into an attractor state that is likely to deviate from the initial state. This can be characterised by the number of changes. An appropriate threshold for these changes can then be used to discriminate recollected from not recollected items.

To evaluate the proposed model the network is trained with randomly generated input patterns (using the standard covariance learning rule, see Section 11.2). In a subsequent test session previously trained patterns were presented, together with randomly generated new patterns. The signal to noise ratio (SNR), which relates to the ratio of hits (correctly identified old items) to false alarms (incorrectly identified new items), is employed to assess the performance of familiarity and recollection (see Figure 11-3). A larger SNR corresponds to better discrimination. An SNR of one corresponds to 30% false positives and false negatives, which although poor, still supports above chance performance.

![Figure 11-3](image)

**Figure 11-3** The left panel displays the decline in the Signal to Noise Ratio (SNR) for the Familiarity (blue line) and Recollection (black line) in a network of 1000 nodes trained and tested with an increasing number of patterns. The x-axis indicates the amount of stored patterns in proportion to the number of nodes in the network. The patterns contain active and inactive units with equal probability. The right panel shows the fraction of misclassified patterns (false positives and false negatives) when the threshold for discriminating old or new patterns is set to the point of minimum error i.e. the point where the old and new distributions intersect. Dense (a=0), uncorrelated patterns.
Figure 11-3 (left panel) illustrates the SNR values plotted as a function of the number of patterns learned. Both familiarity and recollection are able to successfully discriminate ‘old’ from ‘new’ patterns, and the SNR is much larger than one when only a few patterns were stored. Overall discrimination ability decreases when the number of trained and tested patterns increases. In particular, the SNR for recollection declines notably at the point where the number of trained patterns reaches about 15 per cent of the number of nodes. Within Hopfield networks this point is known as ‘the storage capacity’, indicating the maximum number of stored patterns that can be recalled without significant errors (Hertz et al., 1991). Above this capacity limit, the attractor deforms and the activity is caught in spurious attractors.

Despite the noticeable drop in SNR for recollection beyond the capacity limit, the recollection measure is still able to distinguish old from new patterns. As is illustrated in Figure 11-3 (right panel) an assessment of error rates indicates that recollection continues to be effective as increasing numbers of patterns are learned. For comparison, recall error rates (where successful recall is defined by less than 1% error between trained and recalled patterns) are also shown. Even when the magnitude of test patterns exceeds recall capacity, evident in the striking increase in recall errors, recollection is still able to accurately discriminate between old and new patterns.

Although a comparison of recall and recollection is not the primary aim of the current analyses, the greater capacity for recollection compared to recall is noteworthy and highlights the importance of distinguishing between the two. Both processes depend on the final attractor state. However, the outcome of the attractor state is evaluated differently in each case. Accurate recall requires the attractor state to be identical to the learned patterns. In contrast, correct recollection can occur even when only parts of the attractor states are identical to the learned pattern. For correct recollection it is simply critical that the distance between the initial and final state is smaller for learned than new patterns. Note that if this behaviour was observed with a human subject completing a memory test, the subject would correctly identify studied items but would make errors on free or cued recall.
Figure 11-3 also illustrated that the capacity for familiarity discrimination is much greater than either the recollection or recall capacity. Familiarity discrimination has a capacity of order \( N^2 \) which is proportional to the number of synapses rather than the number of neurons as was derived by Bogacz (2001). Instead of recalling the whole pattern familiarity has to perform only a binary decision: stimulus is familiar or new. The difference in capacity for familiarity and recollection discrimination is illustrated in Figure 11-4, a rescaled and extended version of the data in the right panel of Figure 11-3, showing a much larger range of trained patterns. Three features of the data are evident in Figure 11-4; i) errors arise to a greater degree for recollection compared to familiarity overall, ii) recollection errors increase rapidly, and ultimately approach complete failure of memory, similar to the failure of recall at much lower levels (as discussed above and shown in Figure 11-3 right panel), and iii) errors occur for familiarity as the number of trained patterns becomes large (no errors are evident for familiarity at the low number of trained patterns shown in the right panel of Figure 11-3).

![Figure 11-4](image)

**Figure 11-4** The percentage of errors (y-axis) obtained for familiarity and recollection discrimination are displayed for simulations that train and test a very large proportion of patterns (x-axis is in log scale). The error measured for familiarity and recollection describes the amount of misclassification (false positives and false negatives) when the threshold for discriminating old or new patterns is set to the point of minimum error i.e. the point where the old and new distributions intersect.

The difference in storage capacity between familiarity and recollection is also reflected in their underlying old/new distribution across increased numbers of
training and test patterns. Figure 11-5 illustrates such changes in the joint distribution of familiarity and recollections values as the number of trained patterns increases from 100 to 250.

![Figure 11-5](image)

**Figure 11-5** The distribution of familiarity (i.e. energy values) and recollection (i.e. distance values) associated with 100 different patterns (left panel). The old distribution (black) and new distribution (blue) are well separated (left panel). However, when an increasing number of patterns are learned and tested (right panel) the recollection measure shows an increasingly overlapping distributions for old (black) and new (blue) patterns. This can be seen in the decreased separation between these distributions along the y-axis. Nevertheless, the familiarity distributions remain virtually unchanged and display the same distance along the x-axis.

The old/new distributions related to both familiarity and recollection show a clear separation when using 100 patterns (left panel). If the number of patterns is increased to 250 patterns, the recollection measure shows a decreased separation between the old and new distribution, while the familiarity measure shows no significant changes (Figure 11-5 right panel).

These results demonstrate that both familiarity and recollection, operating within a single memory network, are able to discriminate between previously studied and new items. Familiarity and recollection discrimination are more robust and of higher capacity compared to recall. In addition, familiarity reveals a higher storage capacity in contrast to recollection, which is in good agreement with empirical findings. Standing (1973), for instance, showed that people show familiarity for up to 10,000 previously studied pictures.
11.3.2 Constrained recollection

Recollection is defined as an iterative process that occurs over multiple cycles. The retrieval dynamics associated with recollection are illustrated in Figure 11-6, which plots the recollection value (i.e., distance) as a function of the number of cycles, shown separately for different numbers of learned patterns. As noted in the methods, a threshold is required, above which recollection is said not to have occurred. During recollection the state of the network can always converge to an attractor state no matter what the input was. If one assumes that the final attractor state is the retrieval outcome, this function of the network could be undesirable, because a true failure to recollect would not be possible. To be clear, empirically, a failure in recollection can occur in which no information is recovered (i.e., is not associated with a retrieval product).

To allow this to occur in the network the retrieval mechanism was designed to terminate as soon as the recollection processes failed to classify an item as old (i.e. if a state changed significantly above threshold during the settling process). Given this constraint, an attractor state only provides a retrieval output when test items are recollected as previously studied, and new items can be rejected without reaching a final attractor state. As is evident from the retrieval dynamics shown in Figure 11-6, one consequence of this is that terminating the recollection process during the settling phase produces temporal differences in retrieval duration – the correct rejection of new patterns (retrieval failure) can occur more rapidly than successful retrieval of old patterns (retrieval success).
Figure 11-6 The evolution of the distance measure (y-axis) while old and new patterns settle over multiple update cycles (x-axis) into their final attractor state. Different numbers of study and test patterns are used ($\alpha$ indicates the test patterns by network size ratio). The simulation shows that the distance measure can discriminate between old and new patterns during the dynamic settling process. Old patterns (red lines) are associated with systematically lower distances compared to new patterns (black lines), even when a recall limit is reached.

Repeated simulation of the model with an increased number of patterns demonstrates that new patterns reach the critical recollection threshold of 0.4, which discriminates old and new patterns, fairly earlier in the settling process (see Figure 11-6). Within the first 5000 updates, new patterns exceed the recollection threshold, even though some of the old items have not yet settled into their final attractor state. This suggests that the retrieval distance can gate the recollection output so that only old but not new patterns are associated with the retrieval of an item. Furthermore in the simulation the temporal dynamics differ. In particular under high memory load ($\alpha > 0.2$) new items will be identified long before the final retrieval state of an old item is reached.

11.3.3 Sparse coding

So far it has been established that the recollection and familiarity process can discriminate between old and new items. This section examines how performance is affected when more biologically plausible sparse coding is used. The network was trained and tested with the covariance rule using patterns containing 1% active and 99% inactive units, while the learning rule was modified to optimally store sparse patterns.
Figure 11-7 The left panel shows a decline in the Signal to Noise Ratio (SNR) for the Familiarity and Recollection measure, when the Network is trained and tested with an increased number of sparse patterns. The x-axis shows the amount of stored patterns in proportion to the number of nodes in the network. The patterns contain at average 1% active and 99% inactive units. The Error (right panel) describes the amount of misclassification (false positives and false negatives) when the threshold for discriminating old or new patterns is set to the point of minimum error (i.e. the point where the old and new distributions overlap).

The data presented in Figure 11-7 show that familiarity- and recollection-based retrieval can successfully discriminate between sparsely coded old and new patterns, but performance is less than in the non-sparse case. It is known that familiarity performance decreases for sparse patterns (Bogacz & Brown, 2002). Even though sparse coding is generally associated with decreased SNR compared to non-sparse patterns, the overall pattern of higher SNR for familiarity compared to recollection is preserved in sparse pattern (although the relative difference is less). The distributions associated with old and new patterns are shown in Figure 11-8.
11 Computational model of familiarity and recollection

Figure 11-8 The left panel shows the familiarity and recollection distribution resulting from a network trained with 100 sparsely coded patterns (1% active units). In comparison to non-sparse patterns (see Figure 6) the familiarity distribution shows less separated (left panel). However, when an increasing number of patterns is learned and tested (right panel) the recollection measure shows progressively overlapping old (black) and new (blue) distributions, while the old/new distributions associated with familiarity do not undergo significant changes.

In comparison to non-sparse patterns (see Figure 11-5), the familiarity and recollection measure for sparse patterns reveals a greater overlap between the old and new distributions (see Figure 11-8). In particular, an increase in the number of trained patterns affects recollection discrimination as it evokes a greater overlap between the old and new distribution whilst the distributions associated with familiarity are not significantly altered. In sum, sparse coding decreases the discrimination performance of these processes. Nevertheless, the same patterns of results have been observed as in simulations with non-sparse coding.
### 11.3.4 Receiver Operating Characteristics

![ROC curves](image)

**Figure 11-9** The distributions for old and new items are displayed for the familiarity and recollection measure together with their resulting ROC curves. The ROC curves are simulated with a network of 500 nodes with sparse coding (1% active units). The first row shows a lower proportion of study and test patterns ($\alpha=0.1$) compared to the second row ($\alpha=0.25$).

Both the recollection and familiarity measure used above require setting a threshold to separate new from old patterns. Errors due to the overlap in the distributions of familiarity and recollection can either occur in form of false positives or false negatives. The threshold for the error analysis presented above was set so that the total number of error was minimal.

Interestingly, the familiarity and recollection process differ in the shape of the old and new distributions. While the familiarity process exhibits Gaussian distributions for both old and new items, the recollection process reveals a bimodal distribution for old items but a Gaussian distribution for new items (see Figure 11-9, top row). The bimodal distribution for recollected old items indicates two possible classes of attractor states for trained patterns. One class of attractors reflects the vector of studied patterns, so that the patterns presented at test show zero distance when settling into their final attractor state during recollection. The second class of
attractors does not entirely represent the state vector of the trained patterns but are slightly altered in the training process, depending on the parameters of the network and the total number of trained patterns. Patterns associated with the second class of attractors show at test a distribution of distances different from zero when settling into their final attractor state. Thus, the recollection process, which is based on Gaussian distributions for the new items that overlap with part of the bimodal distribution for old items, acts effectively as a threshold process. However, the Familiarity process is based on old and new items that have Gaussian distributions of similar width. The difference between familiarity and recollection is more pronounced when smaller proportions of old and new items are studied but gradually decreases when more and more patterns are studied and tested.

Empirical memory experiments do not provide the old and new distribution familiarity and recollection discrimination is based upon. Nevertheless, receiver operating characteristics (ROCs) can be used to probe the underlying distributions by exploring false positives (false alarms) versus true positive (hits) at different thresholds. As described in the method section 11.2.4, the shape and symmetry of ROC curves is indicative of the process underlying a discrimination performance and have been used to distinguish between familiarity and recollection processes (Fortin, Wright, & Eichenbaum, 2004; Kelley & Wixted, 2001; Yonelinas, 1999; Yonelinas, 1994).

As expected from the above simulations, the ROC curves generated by the familiarity process show a near-to-perfect discrimination performance, as familiarity distributions for old and new items barely overlap (see Figure 11-9). In contrast to familiarity, the recollection process evokes old and new distributions that overlap to a greater extent and a poorer discriminability.

Empirical recognition performance has been reported to predominantly exhibit asymmetric ROC curves. These are interpreted as reflecting components of two independent processes: a symmetric, curvilinear component associated with familiarity and an asymmetrical, linear component reflecting recollection. The two components are assumed to reflect qualitatively distinct processes. While the familiarity process is hypothesised to rely on a signal detection process recollection
is believed to be supported by a threshold process. Distinct forms of ROC curves associated with different episodic retrieval processes have also been reported in non-human species. A study by Fortin and colleagues (2004) demonstrated asymmetrical and curvilinear components in ROC curves in rats, which were interpreted as evidence for recollection and familiarity processes. Selective damage to the hippocampus caused the ROC curves to become entirely symmetrical and curvilinear, supporting the view that recollection is selectively supported by the hippocampus. These studies are in agreement with the result of the current model demonstrating differently shaped ROC curves for familiarity and recollection reflecting qualitatively distinct processes of retrieval.

11.3.5 Overlapping Patterns

As the investigations up to this point have all focused on uncorrelated patterns, the following section will examine the network’s performance for correlated patterns. In accordance with human memory tests, the network is tested with items that were similar but not identical to previously studied items. Several empirical studies have contrasted recognition memory for studied items with highly similar but non-studied items (Nessler et al., 2001; Curran, 2000; Roediger & McDermott, 1995). For example, subjects were presented with a list of singular and plural words (e.g. table, cup) and were tested with studied words (table) and similar lures presented in the opposite plurality of the studied word (cup) (Curran, 2000). The results of this line of research suggest that false alarm rates are based on the high overlap between studied items and lures that yield a feeling of familiarity, while correct recognition is primarily associated with recollection of detailed information of the studied event. In the same spirit, the model is tested with a mixture of old patterns and patterns that were new but similar to previously studied patterns. Similarity between old and new patterns is modelled by constructing a part of the new pattern as identical or overlapping with the activity of an old pattern, while the remaining part of the new pattern is randomly generated (see Section 11.2). The model is trained with a set of randomly constructed patterns. In the test phase, those previously studied old items were presented together with a set of new items which
contained a certain overlap or similarity to the old items. The ability of the familiarity and recollection process to discriminate between old and similar new items was tested with non-sparse and sparse patterns (specifying the number of active units within the network).

Figure 11-10 The Signal to Noise Ratio (SNR) for overlapping patterns is shown for Familiarity (blue line) and Recollection (black line) in a Network trained and tested with an increasing number of non-sparse patterns (left panel) and sparse patterns of 1% active units (right panel). The x-axis shows the amount of stored patterns in proportion to the number of nodes in the network. The test patterns are 80% overlapping with the study patterns. The graph shows that SNR for familiarity is highly sensitive to such an overlap and in contrast to non-overlapping patterns (see Figure 11-3) it declines below the SNR for recollection.

For non-sparse items, recollection demonstrates comparable SNRs for overlapping and non-overlapping patterns. This is in contrast with familiarity which reveals a considerably reduced SNR for overlapping patterns (compare left panel of Figure 11-10 with left panel of Figure 11-3). Hence, the SNR for familiarity is smaller than the SNR for recollection when tested with overlapping patterns, while the opposite pattern of results was found for non-overlapping patterns (see Figure 11-3). The decrease in familiarity SNR is driven by a decline in $d'$ (the mean distance between the old and new distribution) between non-overlapping compared to overlapping patterns. Generally, familiarity and recollection show a reversal in SNR between non-overlapping and overlapping patterns only when the magnitude of studied and tested items remains below the well established critical recall capacity (0.15 times the number of network nodes; Hertz, Krogh, & Palmer, 1991). If the number of trained and tested items exceeds the critical recall capacity, the SNR for
recollection decreases dramatically in overlapping patterns and becomes smaller than the SNR for familiarity.

It is interesting to note that the reduced performance of the familiarity detector to correlated patterns was already pointed out by Bogacz (2001), who then went on to design a familiarity detector based on Long Term Depression (LTD) that had good performance also for correlated patterns. Here, because familiarity and recollection are both implemented in the same network, no change in network can be introduced.

This decrease in the SNR for recollection at the point of recall capacity is driven by a diminished correspondence between the retrieved attractor states and trained patterns. This causes an overall increase in the recollection measure for old and new items but a decrease in the relative difference (d’) of the recollection values for old and new items. This is the source of the reduced SNR for recollection under increased test patterns. The familiarity measure, by contrast, is not modulated by the number of test patterns. The familiarity values for old and new patterns are largely constant and consequently the relative difference between old and new familiarity values remains invariant.

When tested with overlapping and also sparse pattern the SNR for recollection equally exceeds the SNR for familiarity (right panel Figure 11-10). Such sparse coding decreases the overall level of active units while the overlap between a previously studied item and a similar test item is not affected. In general, it is known that the recall capacity increases under sparse coding (Tsodyks & Feigel'man, 1988). However, similar to non-overlapping patterns overlapping patterns demonstrate a decrease in SNR for familiarity and recollection from non-sparse to sparsely coded patterns. Interestingly, comparisons of non-overlapping with overlapping patterns demonstrate a striking increase in SNR for recollection under sparse coding (compare right panel of Figure 11-10 with left panel of Figure 11-7). This increase in SNR is largely caused by increased recollection values for new items for overlapping compared to non-overlapping patterns (see Figure 11-11).
11 Computational model of familiarity and recollection

Figure 11-11 The mean and variance for Familiarity (top row) and Recollection (bottom row) are shown for non-overlapping (left side) and 80% overlapping patterns (right side). The test patterns included old and new items. While the familiarity measure shows not clear modulation for non-overlapping and overlapping test patterns, the recollection measure reveals a significant increase in the mean distance for new items.

11.3.6 Item and associative Recognition

Finally, the performance of the network is examined with a protocol that resembles item recognition and associative recognition. This examination intends to assess whether the network’s performance is compatible with empirical observations reported previously. In empirical studies item recognition usually requires the discrimination between studied and non-studied items, while associative recognition involves discrimination about the specific configurations of studied items. For example if pairs of items are presented at study, the decision whether individual items embedded in test pair have been previously studied is supported by item
recognition. However, identifying whether the pairs presented at test were studied in exactly the same arrangement or pairing at study engages associative recognition.

The ability of the familiarity and recollection process to perform such item and associative recognition will now be assessed. The network was presented with a set of single input pattern, which were taken to reflect item pairs. The first and second half of the input patterns described individual parts of that item pair. The test phase recombines previously studied pairs to create so-called mixed pairs, which were tested together against pairs that were identical to the studied patterns. There were two types of mixed pairs: One type represents a re-configuration of two items that were previously studied in different pairs (old-old). The second type merges a previously studied item with a new item (old-new) (see Section 11.2). Finally, the network was also tested with a set of inputs representing completely new pairs.

Figure 11-12 shows the SNR associated with familiarity and recollection for sparsely coded patterns. The SNR for familiarity indicates that the network is unable to discriminate between previously studied pairs and new mixed pairs. The mixed pairs were produced by either combining two different learned patterns (old-old), a learned with a new pattern (old-new) or completely new patterns (new-new). Mixing patterns has a stronger impact on the familiarity measure compared to the recollection measure.

Figure 11-12 shows the SNR associated with familiarity and recollection for sparsely coded patterns. The SNR for familiarity indicates that the network is unable to discriminate between previously studied and recombined old-old patterns, and also between previously studied and recombined old-new patterns. These findings indicate that the familiarity process fails to disambiguate the specific configuration of studied items as new, i.e. whether the two items were studied in separate pairs. By contrast, the recollection process shows no differences in the SNR between the old-
old, old-new or new-new items (see Figure 12, right chart). This indicates that the recollection process is able to discriminate new patterns from those that were studied in a different configuration. These results suggest that successful associative recognition in this model is predominantly supported by recollection.

11.4 Discussion

A fundamental but controversial issue of episodic retrieval is whether familiarity and recollection describe two distinct processes that access a single memory trace or whether familiarity and recollection are based on two separate memory traces. This chapter introduces a recognition memory model which shows that two different retrieval processes, such as familiarity and recollection, can indeed operate upon a single memory trace while generating distinct types of retrieval outputs. Thus, the current model demonstrates that such an account is feasible and, therefore acts as a proof of concept.

The familiarity process in the proposed model discriminates previously studied items from new items by computing the energy as soon as test items are presented to the network (as proposed by Bogacz et al., 2001). This means that familiarity is obtained in the very first time step before any dynamical process is engaged. In accordance with the Bogacz network, familiarity in this model has a high storage capacity which enables appropriate discrimination for a large number of study and test items. Such great storage capacity parallels empirical findings which report that humans have for example an immense recognition capacity for pictures (Standing, 1973).

In addition to familiarity, the model also contains a recollection process which is believed to be governed by the difference in settling dynamics between previously studied and new patterns. More precisely, the recollection measure reflects the amount of change a pattern undergoes when relaxing from an initial state into a final attractor state. Consequently, familiarity and recollection operate on different time scales: familiarity of items is retrieved very early on whereas recollection requires additional settling time. This is in accordance with empirical
findings, which suggest that the process of familiarity acts faster compared to recollection (Yonelinas & Jacoby, 1994; Mandler, 1980; Benjamin & Craik, 2001).

Combining familiarity and recollection in this model so that they act on the same memory trace yields testable predictions. In particular, when familiarity is based on the Hopfield network rather than on the LTD network (Bogacz & Brown, 2003), familiarity performance becomes sensitive to the correlation in the patterns, which is in line with empirical observations. Hintzman and Curran (1994), for example, investigated experimentally how correlated patterns affect retrieval by asking subjects to study lists of singular and plural words (e.g. jar, cats). A subsequent memory test presented subjects with a list of the previously studied words combined with completely new words and highly similar words that changed plurality from study to test (e.g. jars, cat). In a test condition where only familiarity was likely to be engaged (e.g. after very short retrieval times), subjects were able to discriminate new items from studied and similar items. However, subjects failed to separate studied from similar items. Only with increased retrieval time, which was likely to recruit additional recollection processes, were subjects able to discriminate previously studied items from correlated or similar non-studied items. Consequently, these results suggest that recollection compared to familiarity can more appropriately discriminate previously studied from highly correlated but non-studied items.

A good test of the current model would be to measure how well familiarity and recollection can separate old from new patterns when their overlap is systematically varied. The results reveal better discrimination performance for old and overlapping new patterns when retrieval is based on recollection compared to familiarity, as indicated by a larger SNR. This pattern of results was observed for sparse and non-sparse items with exception of non-sparse items that exceeded the critical recall capacity. Discrimination based on recollection in that case diminished below familiarity. Nevertheless, overall these results are compatible with the empirical findings suggesting that familiarity is more susceptible to overlapping patterns.

Distinct engagements of familiarity and recollection with respect to specific memory tasks as for example item or associative recognition are well established in
the empirical literature. While familiarity is thought to be sufficient to support recognition of single items, recollection has to be engaged for associative recognition involving pairs of items (Yonelinas, 1997). Most direct evidence for this comes from associative recognition tests requiring subjects to discriminate between previously presented word pairs, newly combined (rearranged) pairs and entirely new word pairs (Donaldson & Rugg, 1998). The account of distinct retrieval engagement put forward in this chapter yields the prediction that associative recognition is less successful if retrieval is solely based on familiarity compared to recollection. Although it is difficult to test this prediction empirically, the current model is able to explicitly investigate this question by comparing discrimination performance based on either familiarity or recollection in the context of an associative recognition memory test. Thus, this prediction can be tested by probing the models associative recognition for re-configurations of studied pairs e.g. two items that were previously studied in a different configuration (old-old) or one previously studied item combined with a non-studied item (old-new). The results demonstrate that recollection, in contrast to familiarity, can successfully discriminate previously studied from re-configured items confirming the prediction that recollection but not familiarity predominantly contributes to successful associative recognition.

Familiarity and recollection differ qualitatively with regards to characteristics of their old and new distributions. While familiarity reveals two Gaussian distributions for old and new items, the recollection measure for old items displays a bimodal distribution while new items exhibit a Gaussian distribution. Thus, in line with hypotheses from empirical ROC findings (Fortin et al., 2004; Kelley & Wixted, 2001; Yonelinas, 1997), the recollection process in the model may be interpreted to effectively act like a threshold process, whereas familiarity may be seen to operate more like a signal detection process.

An alternative episodic memory model based on the Complementary Learning System (CLS) has been proposed by Norman and O’Reilly (2003). This model rests on the assumption that two separate brain areas contribute to familiarity and recollection and proposes, in agreement with Aggleton and Brown (1999) that the hippocampus contributes to recall of studied details, whereas the medial temporal
lobe cortex (MTLC) extracts a familiarity signal. In contrast to the model introduced in this chapter, the CLS approach portrays familiarity and recollection not as two retrieval processes accessing a single episodic memory representation, but as two different memory representations with separate encoding and retrieval mechanisms. In particular, familiarity in the MTLC is framed as a general feature extraction process operating across repeatedly presented inputs. Nevertheless, a familiarity mechanism that relies on multiple stimulus presentations conflicts with empirical findings showing rapid memory acquisition and retrieval after a single stimulus presentation (one shot learning).

A further contentious feature of the MTLC is that familiarity is modelled as a function of representational “sharpness” i.e. how well known the item is. If subjects are exposed within an episode to stimuli associated with sharp representations (i.e. well known items) an additional episodic exposure will barely alter that sharpness, while significant changes arise for non-sharp representations (i.e. unknown items). Consequently, studied but unknown items will appear indistinguishable or potentially even less familiar than non-studied but well known items. Hence, the MTLC model describes memories that depend on the amount of previous exposure which seems to relate more to semantic memory than episodic familiarity.

By comparison, the model presented in this chapter is in line with the one-shot learning principle of episodic memory. Furthermore, the model emphasizes the existence of two episodic retrieval processes does not necessitate the proposal of two distinct memory representations. In fact, the current model demonstrates that two retrieval processes may describe two distinct ways of accessing different parts of information stored in a single memory representation.
11.5 Conclusion

This chapter presented a computational model that uses a single neuronal network to store memory traces, with two distinct and independent retrieval processes accessing the memory store. The model is capable of performing familiarity and recollection based discrimination between old and new items after a single exposure. This demonstrates that dual-process models can be implemented that act upon a single memory trace. Furthermore, the putative familiarity and recollection processes exhibit distinct characteristics in the model, for example, diverging in capacity and sensitivity to sparse and convoluted patterns and exhibit ROC curves analogous to those found in empirical data. By demonstrating that a dual-process single-trace model can account for a range of empirical findings, this work highlights the importance of distinguishing between neuronal processes and the neuronal representations upon which they operate.
11 Computational model of familiarity and recollection
12 Discussion

This thesis reported a series of studies investigating the factors and mechanisms that mediate potential interactions between episodic and semantic memory. These investigations attempted to answer three main questions. First, is episodic memory sensitive to the mapping between existing semantic knowledge and the content of to-be-encoded stimuli? Second, does the organisation of the semantic stimuli (e.g. categorical relationships) and semantic encoding strategy (e.g. depth of processing) exhibit an independent or conditional influence on episodic and semantic interactions? Finally, are semantic and episodic interactions limited to stimuli that permit lexical access or do modulations in lexical/semantic factors also evoke episodic and semantic memory interactions?

These questions were addressed by manipulating semantic factors that target semantic memory either directly or indirectly. Direct manipulations vary the semantic content of the stimuli whilst indirect manipulations employ episodic encoding strategies that gate the processing or availability of semantic information with specific encoding tasks. The investigation of the first question requires a direct semantic manipulation of the stimulus organisation by contrasting coherent (categorical) vs. incoherent (non-categorical) material. The second question relates to an indirect semantic manipulation targeting the episodic encoding strategy (deep vs. shallow encoding, i.e. the degree of lexical access) in addition to the direct semantic manipulation of the stimulus organisation. Thus, the second question also addresses the potential crossover of direct and indirect semantic manipulations. The final question focuses on a direct semantic manipulation of lexicality by contrasting meaningful (lexical) vs. non-meaningful (non-lexical) stimuli.

The influence of these experimental manipulations (i.e. stimulus organisation, encoding strategy, and lexical access) was assessed at different stages of memory processing: encoding, subsequent memory and retrieval processes. The intention of this investigation was not only to characterise the circumstances under which episodic and semantic memory interact, but also to identify the mechanisms supporting such interactions. Modulations in ERP effects were used to pinpoint the
precise mechanisms implicated in episodic and semantic memory interactions. The most prominent ERP effects will be briefly outlined in this section before their modulation is discussed in the context of the experiments conducted.

The ERP data reported in this thesis demonstrated two prominent ERP effects in response to semantic modulations during encoding: the N400 and a parietal positivity or P600. While the N400 reveals a negative deflection over fronto-central location between 300-500ms, the P600 elicits a positive deflection over parietal locations between 600-800ms. As reviewed in the first part of this thesis (Chapter 4), the N400 seems to be functionally associated with cognitive operations that process stimulus information in relation to the preceding semantic context (Kutas & Federmeier, 2000). The P600, by contrast, is thought to index the successful integration of a stimulus into a given context (Section 5.5.2).

With regards to ERP effects elicited for processes that predict subsequent retrieval, this thesis repeatedly reported the engagement of parietal and frontal Dm effects. These effects onset as early as 300ms and were long lasting, often spanning the entire recording epoch. The characteristics and functional significance of Dm effects have been outlined earlier in this thesis (Section 4.1.1). Although the precise timing and scalp distribution varies across studies and experimental manipulations, frontal Dm effects are typically associated with intentional encoding, while incidental encoding elicit predominantly parietal Dm effects (Paller, 1990; Friedman, 1990). This thesis proposes a potential link between Dm effects specific for different retrieval processes. Parietal Dm effects seem to index encoding processes leading to familiarity based retrieval of semantic features (Chapters 5, 7, and 9). By comparison, frontal Dm effects seem to support encoding processes linked to familiarity based retrieval of visual/orthographic features (Chapter 9). Frontal Dm effects have further been reported for elaborative encoding potentially supporting recollection based retrieval (Chapter 5).

At retrieval, the empirical data in this thesis identified modulations in two distinct ERP effects: the early frontal old/new effect and a left parietal old/new effect. Early frontal old/new effects exhibit a more positive deflection for old relative to new stimuli across frontal locations between 300-600ms. Parietal old/new effects
elicit a similar pattern of activity, with more positive going deflections for old relative to new items over parietal locations between 600-800ms. A large body of previous research suggests that the left parietal old/new effect is a putative correlate of recollection and there is some evidence that the frontal old/new effect is associated with familiarity driven retrieval (see Section 4.1.2.2.2 for detailed review).

The ERP effects summarised above will now be discussed with regards to the empirical manipulations used: stimulus organisation, encoding strategy and lexical access. This discussion focuses on the potential of these factors to modulate episodic and semantic memory interactions and uses the pattern of ERP effects to infer the underlying mechanisms supporting such interactions at the different stages of memory processing.

12.1 Stimulus organisation

The first experiment investigated the factor of stimulus organisation by testing whether the mapping between existing semantic knowledge and the content of to-be-encoded stimuli alter the actual process of encoding and retrieval. Neuropsychological and neuroimaging studies suggest that semantic knowledge is organised as categorical representations (Okada et al., 2000; for a review see Capitani, Laiacona, Mahon, & Caramazza, 2003). As noted previously, this type of organisation is observable neuroanatomically (Warrington & McCarthy, 1983; Laiacona, Barbarotto, & Capitani, 1998) and affects psychological processing, as demonstrated in semantic priming experiments (Collins & Loftus, 1975). The first experiment, thus investigates whether stimuli congruent or incongruent with this organisation of semantic knowledge has a significant impact on the normal functioning of episodic memory. The obtained results provide evidence that this is indeed the case.

The encoding of semantically congruent information was dissociated from the encoding of semantically incongruent information by the N400. Larger N400 deflections were observed for incongruent compared to congruent information. This suggests that the operations that process stimuli are modulated by the preceding
semantic context. Subsequent contextual integration operations were more effective for congruent information, which elicited larger parietal ERP effects (at about 600ms). Thus, not only semantic processing but also semantic integration operations were altered by the semantic organisation of the stimulus.

What was not known was whether such differences in encoding would change later memory processes. Subsequent memory analyses examined this question and demonstrated differences in parietal Dm effects for familiarity-based subsequent memory elicited under rearranged test conditions. This Dm effect was stronger for congruent compared to incongruent pairs. Intact test conditions, by contrast, revealed frontally located Dm effects for congruent and incongruent pairs, which might index elaborative encoding, potentially related to recollection-based retrieval processes. Thus, subsequent memory effects suggest that encoding activity is modulated by the stimulus organisation, but only in terms of the parietal Dm effects. These could, potentially be interpreted as indexing familiarity-based processing.

It is of interest whether Dm effects can link encoding differences reflected in the N400 or P600 to subsequent memory performance. The topography of the parietal Dm effect makes the P600 (which exhibits a similar parietal topography) a prime candidate to forecast modulations in retrieval performance for different stimulus material. Nevertheless, it is not straightforward to link subsequent memory effects to encoding effects, as they are based on different contrasts. While subsequent memory effects reflect activity elicited by the same class of items, encoding effects describe changes in activity between different classes of items. Thus, any potential functional relations between the P600 and parietal Dm effects have to be established through careful and systematic manipulations of encoding and subsequent memory effects.

At retrieval, recognition performance is enhanced for semantically congruent relative to incongruent information. This confirms that the semantic organisation of the stimulus effects retrieval processes. Further investigation established whether this interaction between episodic and semantic memory was associated with changes in familiarity or recollection. The putative ERP correlate of familiarity, the early frontal old/new effect, was selectively engaged for congruent but not incongruent
information. The ERP correlate for recollection, the left parietal old/new effect, was present but did not differ for congruent or incongruent material. Thus, the data suggest that semantic memory modulates familiarity based retrieval, leaving recollection relatively unaffected. Independent PDP estimates provided converging behavioural evidence for this conclusion by revealing larger familiarity estimates for congruent relative to incongruent stimuli, but similar estimates for recollection. This account is also consistent with the obtained encoding data, since congruent and incongruent stimuli elicited a selective modulation in Dm activity that is thought to support familiarity-driven retrieval. Overall, these experimental findings provide novel evidence for an interaction between semantic and episodic memory, demonstrating that the semantic organisation of information influences the engagement of episodic memory by modulating familiarity based retrieval.

These findings, however, stand in striking contrast to results from LOP studies, which typically reveal an interaction between episodic and semantic memory that is driven largely by the differential engagement of recollection. For example, Rugg et al., (Rugg et al., 1998); see also (Rugg, Allan, & Birch, 2000) measured ERP old/new effects during an LOP study (sentence generation vs. alphabetic judgement), and revealed a modulation of the left parietal effect but no change in the mid-frontal ERP old/new effect. The discrepancy between LOP studies and the current findings might be related to the kind of semantic manipulations employed. While LOP studies alter the semantic encoding strategy without changing the encoding material, the present study manipulated the semantic coherence of the encoding material without changing the encoding strategy. This leads to the hypothesis that semantic encoding strategies may evoke semantic and episodic memory interactions supported by modulations in recollection-based retrieval, while semantic coherence of the encoding material results in interactions that modulate familiarity-based retrieval. This suggests that the way in which semantic memory is manipulated has a critical impact on the interaction between episodic and semantic memory.
12.2 Encoding strategy

The goal of the second experimental was to examine whether stimulus induced modulations in encoding activity are dependent on different encoding strategies. More precisely, this investigation tested whether encoding of information that is congruent or incongruent with pre-existing semantic knowledge is modulated by depth of processing. The results suggest that encoding processes depend on the semantic nature of the stimuli (coherent vs. incoherent) as well as the semantic processing demands of the encoding task (shallow vs. deep). While shallow encoding conditions failed to elicit any changes in encoding activity between the different classes of stimuli, deep encoding conditions elicited stimulus driven modulations in the N400 and P600, analogous to the pattern of results obtained in the previous experiment. Thus, operations that process stimuli in relation to a preceding semantic context differ only for congruent and incongruent information, when a semantic encoding strategy is employed. The same is true for subsequent contextual integration operations during encoding (indexed by the P600), which are more effective for congruent information, but only under semantic encoding strategies. These results suggest a dependency of the factor of semantic organisation on the semantic encoding strategy.

With regards to effective encoding, subsequent memory analyses revealed two distinct Dm effects under intact test conditions which were dependent on the nature of the encoding task and stimulus organisation. Deep encoding conditions revealed, similar to the previous study, frontal Dm effects for congruent stimuli. Shallow encoding conditions, by contrast, elicited parietal Dm effects for congruent stimuli. These findings strongly suggest that the set of cognitive processes used to facilitate subsequent memory for semantically congruent stimuli are not engaged for incongruent stimuli. Thus, processes of successful encoding are sensitive to existing semantic knowledge. These results are in line with the findings reported in the previous study. The previous findings are extended by demonstrating that congruent stimuli evoke different subsequent memory effects under deep and shallow encoding conditions. While deep encoding elicited a frontal subsequent memory effect, shallow encoding resulted in parietal subsequent memory effects. With regards to the
proposed functional interpretation of frontal and parietal Dm effects, these results suggest that deep encoding conditions support elaborative encoding in relation to recollection based retrieval, while shallow encoding evoke encoding leads to familiarity-based retrieval. Overall, the data reveal that semantic stimuli alter encoding processes dependent on the particular encoding strategy engaged.

An additional set of analyses were used to examine how semantic encoding strategies and stimulus organisation impact retrieval processes. The behavioural and ERP data show that stimulus driven modulations in episodic retrieval are conditional on the type of encoding task. The degree to which semantic coherence of stimuli modulates episodic retrieval is dependent on the encoding strategy adopted. Deep encoding conditions modulate the early frontal old/new effect, thought to index familiarity, but reveal no change in the parietal old/new effect, the putative correlate of recollection. These findings are in good agreement with the retrieval data obtained in the previous experiment. The profile of old/new activity changed when participants were instructed to adopt a shallow (non-semantic) encoding strategy. The ERP data for shallow encoded congruent and incongruent stimuli revealed no modulation in the early frontal old/new effect, suggesting no selective engagement of familiarity. Both semantic and non-semantic stimuli elicited parietal old/new effects of similar magnitude, indicating no change in recollection.

Although it has to be acknowledged that a lack of statistical power may have prevented the detection of magnitude differences, the obtained similarity in ERP activity between shallow encoded congruent and incongruent stimuli stands in contrast to the modulations in activity obtained under deep encoding conditions. This difference holds important information regarding the impact of semantic encoding manipulations on different types of stimuli. In theory it can be hypothesised that the semantic organisation of stimuli influences information processing already at a pre-lexical level and would therefore be expected to modulate episodic retrieval under shallow and deep encoding conditions. Alternatively, if semantic coherence is not processed automatically but is dependent on conceptual or lexical processing, semantic and non-semantic stimuli should exhibit no significant modulation in episodic retrieval under shallow encoding conditions. The latter prediction is in clear
agreement with the behavioural and ERP data obtained. The results demonstrate that
tasks that limit encoding to pre-lexical processing stages fail to show differences in
encoding activity for semantically congruent or incongruent material. Thus, the
influence of the semantic coherence of stimuli is dependent on the level of semantic
processing. This indicates that the way in which semantic memory is manipulated
has a critical impact on the interaction between episodic and semantic memory.
Although, this study demonstrates that lexical encoding strategies are necessary to
evoke stimulus driven interactions between episodic and semantic memory, it
remains to be seen whether the same is true for the stimulus material per se. In other
words, given that the previous experiments employed stimuli that contained lexical
and semantic features, it is of interest whether the stimulus driven effects on episodic
and semantic interactions would generalise to stimuli that differ in their
lexical/semantic nature, as for example pairs of pronounceable non-words.

12.3 Lexical access

The third experiment tested whether varying the lexicality of the to-be-encoded
stimuli has a qualitatively or quantitatively different effect on the interactions
between semantic and episodic memory compared to manipulating the semantic
congruency of the stimuli. Pre-lexical (pronounceable non-words) and lexical stimuli
(words) were studied by reading them out loud. This encoding task does not actively
require semantic access but is likely to evoke it if lexical information is available.
The encoding activity revealed modulations in the N400 and P600 effect, suggesting
that pre-lexical and lexical features alter encoding processes. The modulation of the
N400 was stronger for words compared to non-words, indicating that pre-lexical and
lexical stimuli differ in their engagement of operations that process stimuli in a
particular semantic context. In fact, the N400 deflection is known to elicit stronger
negative deflections if a word is incongruent with a semantic context (Kutas &
Hillyard, 1980). The reduced N400 deflection for non-words reflects the absence of
any semantic context and, therefore failure to detect any incongruency. Lexicality
also modulated the P600, which revealed a larger positive deflection for non-words.
relative to words. Although this effect is difficult to reconcile with the functional interpretation of contextual integration operations, this pattern of activity is consistent with the implied relation to working memory processes, since the retention of non-words between reading and saying them aloud demands a higher working memory load compared to words.

Analysis of subsequent memory effects revealed, under rearranged conditions, late onsetting frontal difference for non-words but not words. This effect might reflect encoding activity supporting familiarity based retrieval of visual/orthographic features. In combination with the Dm effect reported in the previous study these data are open to the interpretation that familiarity based encoding differs for visual/orthographical and lexical features. Encoding activity supporting familiarity of visual/orthographic features occurs over the frontal locations (see Section 9.4), while encoding mechanisms supporting familiarity of semantic features is located over parietal scalp regions (see Sections 5.4). Overall, these findings suggest that stimulus driven lexical/semantic features influence the way successfully retrieved information is encoded.

Retrieval processes were also examined to see whether episodic and semantic memory interactions only occur for semantically congruent stimuli or whether semantic access also creates such changes. Furthermore, the temporal dynamics of such potential interactions were addressed by testing different study-test lags.

The data show very clearly that lexical access modulates the interaction between episodic and semantic memory. Stronger familiarity as well as recollection based retrieval was engaged for words compared to non-words after long study-test lags, resulting in better recognition performance for words relative to non-words. Furthermore, retrieval for non-words was temporally delayed. This suggest that stimulus driven episodic and semantic memory interactions are not limited to semantically congruent stimuli but also occur for stimuli that differ in lexical and semantic access. The interactions obtained for long study-test lags were qualitatively different from those reported for manipulations of semantic coherence. Increased familiarity as well as recollection based retrieval was present for words compared to
non-words. Semantic coherence manipulations, by comparison, selectively altered familiarity but not recollection-based retrieval.

Finally, episodic and semantic memory interactions seem to depend on the study-test lag. Short lag conditions exhibited temporally delayed retrieval processes for non-words compared to words, without revealing further qualitative or quantitative differences. Nevertheless, the data obtained under short lag suggest, in line with the results form the long-lag condition, that semantic access influences episodic and semantic interactions and these interactions are qualitatively different from the previously reported modulation evoked by semantic coherence.

These results suggest that lexical access does influence retrieval processing. This influence is modulated by the temporal distance between study and test. Lexical manipulations tap into different types of interactions between episodic and semantic memory compared to the familiarity specific modulation in episodic retrieval caused by manipulations of stimuli’s semantic organisation. These results show that the nature of episodic and semantic memory interactions do not only depend on the type of semantic organisation (i.e. semantic congruent, semantic incongruent), but also the semantic/lexical source of the stimulus representation (i.e. semantic, phonological, orthographical). Overall, manipulations of semantic coherence and semantic access engage different types of interactions between semantic and episodic memory. This demonstrates that semantic memory is able to influence episodic retrieval in multiple ways.

In order to understand why episodic retrieval processes are implicated differentially for distinct semantic manipulations, it is necessary to understand the precise mechanisms underlying familiarity- and recollection-based retrieval. Such a formalisation was provided by developing a computational model of recognition memory.
12.4 A model of episodic retrieval

Insight into the processes by which semantic memory influences episodic retrieval can be gained by understanding the mechanisms underlying and supporting episodic memory. Therefore, this thesis proposes a recognition memory model which specifies familiarity- and recollection-based retrieval. More precisely, familiarity and recollection are modelled as two separate retrieval processes that act upon a single representation, but provide two different outputs. This proposal follows the dual-process tradition as recognition memory is supported by two distinct retrieval processes even though they operate within a single network. Modelling familiarity and recollection within a single network has the advantage that no distinct representations and encoding processes are required.

Examinations of the model confirmed that both retrieval processes are able to discriminate novel from previously studied patterns even under biologically realistic coding schemes such as sparse coding. Furthermore, familiarity and recollection exhibit, in accordance with empirical findings different characteristics in processing speed, retrieval capacity and ROC curves. More importantly, the performance of the model was tested using an approximation of empirical manipulations presented in this thesis. The results revealed a differential modulation of familiarity in response to changes in the overlap and specific configuration of patterns. If semantic coherence is operationalised as pattern overlap the modelling data can be seen to be in agreement with the behavioural finding that familiarity processes are modulated by the degree of semantic coherence (pattern overlap). By demonstrating that the proposed dual-process single-trace model can account for a range of empirical findings, this work highlights the importance of distinguishing between neuronal processes and the neuronal representations upon which they operate.

12.5 Episodic and semantic memory interactions

The results of the empirical investigations summarised above demonstrate that episodic memory processes are sensitive to the type of semantic information inherent to an episode and the type of semantic encoding strategy employed. Such episodic
and semantic memory interactions are expressed at different processing stages, including encoding and retrieval. Modulations in encoding activity appear only when lexical information is available. Non-lexical stimulus material or encoding strategies failed to elicit an N400 or P600 effect, which confirms a direct link between these effects and lexical/semantic processing. Nevertheless, Dm effects are modulated by the semantic organisation of stimuli as well as factors of semantic/lexical access granted by encoding processes and stimulus material. Semantic congruent stimuli elicit Dm effects under deep as well as shallow encoding conditions. This may suggest a close relationship between Dm effects and the semantic organisation of stimuli. Nevertheless, non-lexical stimuli also revealed Dm effects indicating that these effects do not exclusively occur for stimuli containing semantic information.

The results presented in this thesis also demonstrate that semantic memory is able to influence episodic retrieval in multiple ways. Coherent stimulus organisation has a selective effect on familiarity-based retrieval, which suggests that this process is susceptible to whether the content of to-be-encoded stimuli maps onto existing semantic knowledge. This susceptibility, however, is dependent on the employed encoding strategy. Level of processing manipulations demonstrate that the stimulus organisation exhibits only a selective influence on retrieval processes under deep (semantic/lexical) but not shallow (non-lexical) encoding conditions. However, the precise stimulus organisation is not the only influence semantic memory has on episodic retrieval. Further investigations have elucidated that lexical compared to non-lexical stimuli are associated with enhanced familiarity as well as recollection processes. This finding highlights that, in addition to familiarity, recollection-based retrieval is also modulated by semantic factors. More precisely, by the lexicality of the stimulus material. Interestingly, these findings parallel predictions from the LOP theory, which concern lexical vs. non-lexical encoding strategies.

These findings lead to an overall account of episodic and semantic memory interactions in which lexical access provided by stimulus material and encoding strategies influence episodic retrieval via modulating recollection in concert with familiarity. Once lexical access is granted on the basis of appropriate stimulus material and encoding strategies, the organisation of the stimulus materials in
relation to pre-existing semantic knowledge exhibits a further, qualitatively distinct level of episodic and semantic memory interaction. This interaction selectively modulates familiarity-based retrieval, which is enhanced when the content of to-be-encoded stimuli maps onto pre-existing semantic knowledge.

12.6 Current findings in the context of the SPI model

This thesis began with an introduction of the memory research that has led to the proposal of multiple memory systems. Memory taxonomies subdivide declarative memory into episodic and semantic memory systems (see Section 2.7.2). These systems are usually investigated in isolation leading to an isolation of the theories and models of the episodic and semantic memory systems. This raises the question of whether potential functional relations or interactions exist between the two systems. A model that proposes relations between episodic and semantic memory has been suggested by Tulving (Tulving, 1995; Tulving & Markowitsch, 1998). The central idea of the so-called SPI model is that episodic and semantic memory perform ‘Serial encoding’ (S), ‘Parallel storage’ (P) and ‘Independent retrieval’ (I).

The serial encoding system proposes that perceptual information is first processed by the semantic system before it is passed on to the episodic system. The ERP data obtained during encoding elicit semantic processing as early as 400ms but are further engaged at around 600ms post stimulus. As there is no specific ERP effect known to index episodic encoding, it is difficult to assess whether the semantic and episodic systems exhibit a serial engagement during encoding. Although the current findings are, in principle, consistent with a serial account, it seems likely that episodic encoding is engaged before 600ms post stimulus and therefore overlaps at least in part with semantic processing. The storage process in the SPI model assumes that different aspects of information become consolidated separately in different systems. The current data provide no direct insight into the storage process of episodic and semantic memories and therefore can not speak to the question of separate consolidation processes.
Finally, the retrieval process in the SPI model is proposed to be independent. This is in line with the assumption of parallel storage. Information retrieved from the semantic systems has no influence on retrieval of information from the episodic system. Although information from different systems might equally contribute to the access of a specific situation, their contribution is regarded as additive and independent. This prediction of the SPI model seems to contradict the data reported in this thesis. Semantic manipulations very clearly evoked modulations in the processes supporting episodic retrieval. In fact, different types of semantic manipulations (i.e. lexical access and semantic coherence of stimuli) are shown to exhibit a differential influence on episodic retrieval processes. Admittedly, it is difficult to determine whether such changes are based on the influence of semantic factors at the time of retrieval or whether semantic factors modulate the type of information stored in memory which, in turn mediates changes in retrieval processes. Either way, the data suggest that episodic retrieval is amended under the influence of the semantic memory system.

Manipulations of encoding strategies employed in this thesis have shown that shallow encoding fails to elicit differences between semantic coherent vs. incoherent stimuli. Interestingly, differences were not only absent during encoding but also retrieval, whereas deep encoding conditions exhibited differences at encoding as well as retrieval. This suggests that the interaction between episodic and semantic memory obtained at retrieval might be a consequence of the processes engaged during encoding. Since the same recognition test was employed to items that were previously studied under shallow or deep encoding conditions, it might be expected that if semantic memory influences episodic memory at retrieval, this should result in similar retrieval interactions regardless of the previous encoding history. Nevertheless, this is not necessarily the case as the episodic memory trace is likely to differ dependent on the shallow and deep encoding history, which might affect the interaction between episodic and semantic memory at the time of retrieval.
12.7 Familiarity and semantic memory

The data in this thesis highlights a close link between the organisation of semantic memory and familiarity based retrieval processes. Semantic memory is thought to store knowledge about the world without maintaining contextual information of when and where this information was acquired. Familiarity, by comparison, is defined as an episodic retrieval process that evokes the feeling of knowing, which is not accompanied by specific contextual details. Beside the fact that semantic memory and familiarity based retrieval both lack contextual information the present study suggests that familiarity is sensitive to semantic organisation of stimuli. Semantically coherent stimuli appear more familiar than incoherent stimuli. This suggests that familiarity processing is shaped by properties inherent to semantically organised representations. What precisely defines such properties remains to be seen, but semantically coherent representations (i.e. items that belong to the same category) are likely to have more features in common compared to incoherent representations. It is possible that such an overlap in features evokes the sense of familiarity.

The computational model presented in this thesis provides further insight into this question. The proposed model defines familiarity as a function of the energy of the network, which is larger for novel and smaller for old stimuli. The energy associated with a stimulus depends on how closely that stimulus resembles a stored attractor state. A stimulus that is similar but not identical to a stored attractor state will evoke a lower energy than stimuli that greatly deviate from the stored attractor states. This suggests that higher levels of agreement in the activation pattern (or features) between stimulus and attractor state evoke increased familiarity. Thus, it might be possible that the increased feature overlap is the critical link between familiarity and semantic memory.
12.8 Future Work

Although the present thesis clearly demonstrates interactions between episodic and semantic memory, further work is need to elucidate the precise conditions and mechanisms that support these interactions. This thesis focussed on examining effects of semantic manipulation on episodic memory, but did not address how episodic manipulations may influence semantic memories. It is important to also investigate this reversed influence in order to gain a complete account of how episodic and semantic memories interact with each other. Investigating the influence of episodic manipulations on semantic memory is problematic as it is difficult to ensure that existing semantic memories are identical across subjects. A further complication lies in the fact that the formation of semantic memories are expected to be long lasting and it becomes difficult to control behaviours or experiences of different subjects in their everyday lifes that might interfere with such processes in the meantime. Nevertheless, further research, which tackles such problems and systematically investigates the influence of episodic factors on semantic memory, is needed. It is difficult to predict what kind of effects episodic factors such as temporal, spatial or contextual manipulations might have on semantic memory. If the semantic memory system is expected to reflect regularities in the environment, episodic events that present items in constant co-occurrence with each other should be stored as such in semantic memory. Besides pure correlational co-occurrences, items that have a functional, causal or contextual relationship should equally be stored in semantic memory. It would be of interest to determine precisely how semantic memories differ along such dimensions. In addition it would be interesting to see whether the resulting semantic representations evoke modulations in familiarity or recollection when retrieved in an episodic context.

A second important path for future research relates to the principle by which semantic memories are organised. Neuropsychological research reports patients who reveal semantic impairments restricted to categories of natural items (Warrington & Shallice, 1984). These category specific deficits have been interpreted to reflect a category specific organisation of memory. Nevertheless, it is possible that the organisational principle of semantic memory is not based on categories per se, but
resembles the difference in knowledge associated with the distinct categories. For example, the defining attributes of natural items are more likely to be visual compared to human-made items, which are better characterised by functional attributes. This distinction leads to the hypothesis that semantic memory might be organised by the different kinds of semantic domains. Knowledge about concepts might be distributed across a variety of distinct memory stores. Future research is needed to dissociate these organisation principles of semantic memory.

The experimental manipulations (e.g. lexicality, semantic organisation, LOP) should be investigated further in future research. For example, the frequency of occurrence of stimuli or amount of information associated with semantic material might be important variables influencing the interaction between episodic and semantic memory.

The computational model would benefit from future research and work which aims to implement an additional semantic memory system. The current model represents semantic memory as a function of the input patterns. Semantically related items are modelled as patterns with overlapping representations. It appears difficult, however, to represent different levels of lexicality with that approach. Therefore, a more sophisticated semantic model is needed to represent the different aspects of semantic memory. Furthermore, the formalisation and computational implementation of theories about the structure and processes involved in the episodic and semantic memory systems would be beneficial, as this allows these theories to be tested. The outcomes of such tests can then be compared with behavioural and neuroimaging evidence to provide informed modification of the theories and, ultimately, the computational models. Such models provide the basis for integrating the contribution of episodic and semantic memory to declarative memory, which will give insight into the mechanisms underlying episodic and semantic memory interactions.

Finally, it is of importance to consider the limitation of the employed research methods. It is possible that ERP methods are only sensitive to a particular aspect of episodic and semantic interaction. Therefore, converging evidence from neuroimaging, neuropsychological and behavioural data are needed to gain a more complete account of episodic and semantic memory interactions.
13 Conclusion

This thesis demonstrates that episodic memory is influenced by how well the stimulus material maps onto the organisation of semantic memory, i.e. category membership. Chapter 5 reports efficient relational processing and enhanced contextual integration at encoding for semantically congruent compared to incongruent stimuli (section 5.3). Encoding differences that predict subsequent retrieval based on familiarity are more prominent for congruent than incongruent stimuli (section 5.4). Chapter 6 demonstrates that semantically congruent stimuli also lead to enhanced recognition performance compared to incongruent stimuli. Behavioural PDP estimates (section 6.3.3) and electrophysiological ERP correlates (section 6.3.2) reveal converging evidence that this enhancement is driven by familiarity. These findings provide novel evidence that semantic memory interacts with episodic memory through the process of familiarity-based retrieval.

To further understand the stimulus induced interactions between episodic and semantic memory this thesis continues to investigate the impact of different encoding strategies. Chapter 7 reveals that in addition to the semantic nature of the stimuli (coherent vs. incoherent) episodic encoding depends also on the semantic processing demands of the encoding task (deep vs. shallow). Differences in relational processing and contextual integration between semantically congruent and incongruent stimuli appear only when a semantic encoding strategy is employed (section 7.3). Equally, differences in successful encoding depend on the nature of the encoding task (section 7.4). These findings provide a more comprehensive account of episodic and semantic memory interactions by highlighting that semantic stimuli alter episodic encoding dependent on the specific encoding task engaged. A similar conclusion is reached in Chapter 8, which examines the dependency of episodic retrieval on semantic stimulus coherence and encoding manipulations. The results clearly show that the effect of semantic coherence on episodic retrieval is conditional on the type of semantic encoding strategy (section 8.3). These results extend the novel findings of familiarity-driven semantic and episodic memory interactions by providing
additional insight that such interactions are conditional on the level of semantic encoding strategies.

In addition, the lexicality of words is manipulated across the stimulus material with the intention to establish whether the resulting episodic and semantic memory interactions are qualitatively or quantitatively distinct from those elicited by semantic coherence manipulations. Chapter 9 indicates differences in relational processing and contextual integration for lexical and non-lexical stimuli during encoding (section 9.3). Similarly, differences in successful encoding are dependent on the lexicality of the stimuli (section 9.4). These findings verify that semantic memory influences episodic encoding not only at the level of coherence but also lexicality. More importantly, the retrieval data reported in Chapter 10 reveal that lexicality elicits interactions between episodic and semantic memory (section 10.3), which are qualitatively distinct from those elicited by semantic coherence manipulations. These data demonstrate increased familiarity- as well as recollection-based retrieval for lexical compared to non-lexical stimuli. Thus, the results suggest that semantic coherence and semantic lexicality probe different types of interactions between episodic and semantic memory. Overall, the findings of this thesis give novel insight into the processes underlying episodic and semantic memory interactions and show that such interactions can occur in multiple different ways.

Finally, Chapter 11 outlines a computational memory model with the aim to gain a deeper understanding of the mechanisms by which semantic memory influences episodic retrieval. In this model familiarity and recollection operate within a single network. When semantic coherence is operationalised as a pattern overlap, the model exhibits differences in familiarity processing when semantic coherence (the pattern overlap) is modified. By demonstrating that the proposed model can account for a range of empirical findings (section 11.3), this model highlights the important distinction between neuronal processes and neuronal representations upon which they operate.

Overall, the empirical data presented in this thesis provide novel evidence that episodic and semantic memory interact in different ways on multiple levels. This finding yields useful information for situations in everyday life. In some
circumstances it is desirable to improve episodic memory, for example, in order to remember what was discussed in an important meeting or which arguments were encountered when reading a specific article. The presented work suggests that a coherent organisation of the to-be-encoded material will be beneficial in those situations and enhances episodic memory via familiarity based retrieval. Nevertheless, a coherent organisation of the stimulus material is not sufficient but needs to be combined with an appropriate encoding strategy. For instance, to encourage retrieval success it is not enough to simply structure study material in a coherent fashion since the material has to be processed at a semantic level to evoke an enhanced episodic memory. Thus, elaborating on the relational character of the to-be-encoded material provides enhanced episodic retrieval. Furthermore, the recognition of non-lexical material is enhanced on the basis of familiarity and recollection, when lexical meaning is defined and attached to this material.

Overall, the data presented in this thesis provides clear evidence for different levels of episodic and semantic memory interactions. If lexical access is encouraged by the encoding strategy and the to-be-encoded material matches existing semantic knowledge there will be increased recognition of the material. This advantage occurs due to a selective enhancement of familiarity driven retrieval. However, stimulus material that differs in lexical access reveals interactions between episodic and semantic memory on the basis of familiarity and recollection based retrieval. The computational memory model suggests, that these different processes by which semantic manipulations influence episodic retrieval might echo the sensitivity of the two episodic retrieval process to representational characteristics evoked by the semantic modulations. Thus, this thesis provides novel evidence for different types of episodic and semantic memory interactions dependent on the kind of semantic manipulation and offers an account of the mediating mechanisms leading to such interactions.
13 Conclusion
14 Bibliography


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15 Appendix A: Data

15.1 Chapter 5: details of analyses

The tables in this section show significant effects and interactions with the factor of condition resulting from an ANOVA testing the factor of condition (non-semantic, semantic-one, semantic-two), hemisphere (left, right) and site (inferior, mid, superior), across all three individual time windows (1. = 300-600ms, 2. = 600-1000ms, 3. = 1000-1800ms).

15.1.1 Frontal locations

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<th>$F$</th>
<th>$df_1$</th>
<th>$df_2$</th>
<th>$p$</th>
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<td>not sign.</td>
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<tr>
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<td>48.0</td>
<td>p&lt;0.001</td>
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<td>cond. by hem. by site</td>
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Table 6. First epoch (300-600ms).

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Table 7. Second epoch (600-1000ms).

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<th>$df_2$</th>
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<td>cond.</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cond. by hem.</td>
<td>5.3</td>
<td>1.5</td>
<td>27.4</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>cond. by site</td>
<td>not sign.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cond. by hem. by site</td>
<td>not sign.</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
15 Appendix A: Data

Table 8. Third epoch (1000-1800ms).

15.1.2 Parietal locations

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>cond.</td>
<td>14.4</td>
<td>1.8</td>
<td>32.2</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>cond. by hem.</td>
<td></td>
<td></td>
<td></td>
<td>not sign.</td>
</tr>
<tr>
<td>cond. by site</td>
<td>4.1</td>
<td>2.4</td>
<td>43.9</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>cond. by hem. by site</td>
<td>3.0</td>
<td>2.8</td>
<td>51.0</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

Table 9. First epoch (300-600ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>cond.</td>
<td>26.0</td>
<td>1.9</td>
<td>34.5</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>cond. by hem.</td>
<td></td>
<td></td>
<td></td>
<td>not sign.</td>
</tr>
<tr>
<td>cond. by site</td>
<td>5.1</td>
<td>2.5</td>
<td>44.1</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>cond. by hem. by site</td>
<td></td>
<td></td>
<td></td>
<td>not sign.</td>
</tr>
</tbody>
</table>

Table 10. Second epoch (600-1000ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>cond.</td>
<td></td>
<td></td>
<td></td>
<td>not sign.</td>
</tr>
<tr>
<td>cond. by hem.</td>
<td></td>
<td></td>
<td></td>
<td>not sign.</td>
</tr>
<tr>
<td>cond. by site</td>
<td></td>
<td></td>
<td></td>
<td>not sign.</td>
</tr>
<tr>
<td>cond. by hem. by site</td>
<td></td>
<td></td>
<td></td>
<td>not sign.</td>
</tr>
</tbody>
</table>

Table 11. Third epoch (1000-1800ms).
15.2 Chapter 7: details to analyses

15.3 Comparison of stimulus conditions

The tables in this section show significant effects and interactions with the factor of stimulus resulting from an ANOVA testing the factor of stimulus (non-semantic, semantic-one, semantic-two), hemisphere (left, right) and site (inferior, mid, superior), across all three individual time windows (1. = 300-500ms, 2. = 500-800ms, 3. = 800-1800ms).

15.3.1 Deep encoding frontal location

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>stim.</td>
<td>8.3</td>
<td>2</td>
<td>30</td>
<td>p=0.001</td>
</tr>
<tr>
<td>stim. by hem.</td>
<td>4.7</td>
<td>2</td>
<td>30</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

**Table 12** First epoch (300-500ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>stim.</td>
<td>10.0</td>
<td>2</td>
<td>30</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>stim. by hem.</td>
<td>7.2</td>
<td>2</td>
<td>30</td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td>stim. by hem. by site</td>
<td>3.5</td>
<td>2.1</td>
<td>31.1</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

**Table 13** Second epoch (500-800ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>stim.</td>
<td>4.1</td>
<td>1.3</td>
<td>20.0</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>stim. by hem.</td>
<td>4.2</td>
<td>2</td>
<td>30</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>stim. by hem. by site</td>
<td>3.6</td>
<td>4</td>
<td>60</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

**Table 14** Third epoch (800-1800ms).
15.3.2 Deep encoding parietal locations

The first epoch failed to reveal any significant effects or interactions with stimulus.

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>stim.</td>
<td>16.8</td>
<td>2</td>
<td>30</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>stim. by site</td>
<td>5.6</td>
<td>2</td>
<td>30.3</td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td>stim. by hem. by site</td>
<td>2.7</td>
<td>4</td>
<td>60</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

Table 15 Second epoch (500-800ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>stim.</td>
<td>6.9</td>
<td>1.5</td>
<td>22.0</td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td>stim. by hem.</td>
<td>3.7</td>
<td>2</td>
<td>30.3</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>stim. by hem. by site</td>
<td>5.0</td>
<td>2.2</td>
<td>33.5</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

Table 16 Third epoch (800-1800ms).
15 Appendix A: Data

15.4 Comparison of the two encoding conditions

The tables in this section show significant effects and interactions with the factor of encoding resulting from an ANOVA employing the factor of encoding (shallow, deep), hemisphere (left, right) and site (inferior, mid, superior), across all three individual time windows (1. = 300-500ms, 2. = 500-800ms, 3. = 800-1800ms).

15.4.1 Frontal locations

15.4.1.1 Non-semantic pairs

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc</td>
<td>13.7</td>
<td>1</td>
<td>15</td>
<td>p&lt;0.01</td>
</tr>
</tbody>
</table>

Table 17 First epoch (300-500ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc</td>
<td>17.7</td>
<td>1</td>
<td>15</td>
<td>p=0.001</td>
</tr>
<tr>
<td>enc by hem by site</td>
<td>4.4</td>
<td>1.5</td>
<td>21.8</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

Table 18 Second epoch (500-800ms).

The third epoch (800-1800ms) failed to reveal any significant effects or interaction with the factor of encoding.

15.4.1.2 Semantic-one pairs

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc</td>
<td>13.1</td>
<td>1</td>
<td>15</td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td>enc by site</td>
<td>7.1</td>
<td>1.1</td>
<td>17.0</td>
<td>p=0.01</td>
</tr>
</tbody>
</table>

Table 19 First epoch (300-500ms).
15.4.1.3 Semantic-two pairs

The semantic-two pairs failed to reveal any significant effects or interactions with factor encoding.

15.4.2 Parietal locations

15.4.2.1 Non-semantic pairs

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc</td>
<td>5.9</td>
<td>1</td>
<td>15</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>enc. by hem. by site</td>
<td>5.9</td>
<td>1.3</td>
<td>19.8</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

Table 20 Second epoch (500-800ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc. by hem.</td>
<td>5.1</td>
<td>1</td>
<td>15</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>enc by hem. by site</td>
<td>9.4</td>
<td>1.7</td>
<td>25.8</td>
<td>p&lt;0.01</td>
</tr>
</tbody>
</table>

Table 21 Third epoch (800-1800ms).

<table>
<thead>
<tr>
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<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc</td>
<td>29.0</td>
<td>1</td>
<td>15</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>enc by site.</td>
<td>14.7</td>
<td>1.1</td>
<td>16.2</td>
<td>p&lt;0.001</td>
</tr>
</tbody>
</table>

Table 22 First epoch (300-500ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc</td>
<td>34.8</td>
<td>1</td>
<td>15</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>enc. by site</td>
<td>17.9</td>
<td>1.1</td>
<td>16.6</td>
<td>p&lt;0.001</td>
</tr>
<tr>
<td>enc. by hem by site</td>
<td>4.4</td>
<td>1.5</td>
<td>21.8</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

Table 23 Second epoch (500-800ms).
### Table 24 Third epoch (800-1800ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc</td>
<td>6.2</td>
<td>1</td>
<td>15</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>enc. by hem.</td>
<td>8.6</td>
<td>1</td>
<td>15</td>
<td>p=0.01</td>
</tr>
<tr>
<td>enc. by site</td>
<td>7.4</td>
<td>1.2</td>
<td>18.4</td>
<td>p=0.01</td>
</tr>
<tr>
<td>enc. by hem by site</td>
<td>13.2</td>
<td>2</td>
<td>30</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

### Table 25 First epoch (300-500ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc</td>
<td>15.5</td>
<td>1</td>
<td>15</td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td>enc by site</td>
<td>12.5</td>
<td>1.1</td>
<td>16.5</td>
<td>p&lt;0.01</td>
</tr>
</tbody>
</table>

### Table 26 Second epoch (500-800ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc</td>
<td>15.9</td>
<td>1</td>
<td>15</td>
<td>p=0.001</td>
</tr>
<tr>
<td>enc. by hem.</td>
<td>4.4</td>
<td>1</td>
<td>4.7</td>
<td>p=0.05</td>
</tr>
<tr>
<td>enc. by site</td>
<td>12.7</td>
<td>1.1</td>
<td>16.5</td>
<td>p&lt;0.01</td>
</tr>
</tbody>
</table>

### Table 27 Third epoch (800-1800ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc. by site</td>
<td>3.4</td>
<td>1.4</td>
<td>1.4</td>
<td>p=0.05</td>
</tr>
</tbody>
</table>
## 15.4.2.3 Semantic-two pairs

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc.</td>
<td>6.1</td>
<td>1</td>
<td>15</td>
<td>p&lt;0.05</td>
</tr>
<tr>
<td>enc. by site.</td>
<td>4.4</td>
<td>1.1</td>
<td>16.2</td>
<td>p=0.05</td>
</tr>
<tr>
<td>enc. by hem. by site</td>
<td>5.0</td>
<td>1.5</td>
<td>22.0</td>
<td>p&lt;0.05</td>
</tr>
</tbody>
</table>

*Table 28* First epoch (300-500ms).

<table>
<thead>
<tr>
<th>Interaction</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>enc</td>
<td>4.4</td>
<td>1</td>
<td>15</td>
<td>p=0.05</td>
</tr>
</tbody>
</table>

*Table 29* Second epoch (500-800ms).

The third epoch (800-1800ms) failed to reveal any significant effects or interaction with the factor of encoding.
Investigating the functional interaction between semantic and episodic memory: Convergent behavioral and electrophysiological evidence for the role of familiarity

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Received 20 January 2006; revised 21 July 2006; accepted 24 July 2006

Throughout our lives we acquire general knowledge about the world (semantic memory) while also retaining memories of specific events (episodic memory). Although these two forms of memory have been dissociated on the basis of neuropsychological data, it is clear that they typically function together during normal cognition. The goal of the present study was to investigate this interaction. One influence of semantic memory on episodic retrieval is “Levels Of Processing”; recognition is enhanced when stimuli are processed in a semantically meaningful way. Studies examining this processing advantage have largely concluded that semantic memory augments episodic retrieval primarily by enhancing recollection. The present study provides strong evidence for an alternative relationship between semantic and episodic memory. We employed a manipulation of the semantic coherence of to-be-remembered information (semantically related vs. unrelated word pairs) during an associative recognition memory test. Results revealed that associative recognition was significantly enhanced for semantically coherent material, and behavioral estimates (using the process dissociation procedure) demonstrated concomitant changes in the contribution of familiarity to retrieval. Neuroimaging data (event-related potentials recorded at test) also revealed a significant increase in familiarity based retrieval. The electrophysiological correlate of familiarity (the mid-frontal ERP old/new effect) was larger for semantically related compared to unrelated word pairs, but no difference was present in the electrophysiological correlate of recollection (the left parietal old/new effect). We conclude that semantic memory and episodic memory do indeed interact in normal functioning, and not only by modulating recollection, but also by enhancing familiarity.

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Keywords: Episodic memory; Semantic memory; Recollection; Familiarity; ERP; PDP

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Available online on ScienceDirect (www.sciencedirect.com).
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doi:10.1016/j.neuroimage.2006.07.043
Similarly, several well established neuropsychological tests (e.g., the California Verbal Learning Test, Delis et al., 1987) assess the tendency to utilize semantic information inherent in the material that is studied and tested within an episodic memory paradigm. What is less clear, however, is exactly how semantic memory interacts with episodic retrieval. Dual-process models of episodic memory describe retrieval as contingent upon familiarity and recollection (Yonelinas, 2002). Familiarity refers to a fast acting process that reflects a quantitative assessment of memory strength, while recollection is the retrieval of qualitative contextual information about a previous event. Thus, our question is whether semantic memory influences episodic retrieval in terms of familiarity or recollection.

Event-related potentials (ERPs) provide an ideal method to investigate the engagement of retrieval processes during episodic memory tests because distinct ERP old/new effects (contrasting hits and correct rejections) have been identified as indexes of familiarity and recollection (see Johnson, 1995; Rugg, 1995; Donaldson et al., 2002, for reviews). Familiarity is reflected by an early mid-frontal ERP old/new effect, elicited around 300-500 ms post-stimulus onset, with maximum amplitude over frontal scalp sites (Curran, 2000; Nessler et al., 2001; although see Tsivilis et al., 2001). While debate continues as to whether the mid-frontal ERP old/new effect reflects familiarity when non-verbal stimuli are employed (e.g., faces, see Voyer and Paller, 2004), the effect has been widely used as a reliable index of familiarity in experiments using verbal stimuli (e.g., in studies of the revelation effect, see Azrani-Man-Fardin and Wilding, 2004). Recollection is indexed by the left parietal old/new effect, elicited around 500-800 ms post-stimulus onset, with maximum amplitude over the left temporo-parietal region (Paller and Kutas, 1992; Wilding et al., 1995; Rugg et al., 1998; for reviews see Allan et al., 1998; Curran, 1999). Although these two ERP old/new effects are well characterized, ERP research has not directly investigated the question of how semantic memory influences successful episodic retrieval.

Current behavioral findings, most notably from Levels of Processing (LOP) studies (Craik and Lockhart, 1972), suggest that manipulations of semantic memory influence episodic retrieval largely by modulating recollection. The LOP theory states that episodic memory retrieval is influenced by semantic memory processing at encoding, with enhanced encoding for deep, semantically meaningful encoding (e.g., semantic categorization) compared to shallow non-semantic encoding (e.g., letter discrimination). Evidence suggests that deep encoding leads to recognition based on familiarity and recollection, while shallow encoding leads to recognition based primarily on familiarity (Mulligan and Handman, 1995; Toth, 1996; for review see Yonelinas, 2002).

Thus, LOP strongly supports an interaction between episodic and semantic memory which influences recollection to a greater extent than familiarity.

Further evidence that it is mainly recollection that is susceptible to semantic and episodic interactions is provided by Deese–Roediger–McDermott (DRM) false memory studies (for reviews, see Roediger and Bergman, 1998; Schacter, 1999). The DRM paradigm presents participants with a list of words, all unambiguously associated with a particular concept. In a subsequent recognition memory test, false alarm rates for unstudied words are much higher for words that are semantically associated than unassociated with the target concept. More importantly, these false alarm rates contain higher levels of false recollection compared to familiarity (Roediger and McDermott, 1995; Norman and Schacter, 1997). Although behavioral evidence strongly suggests that recollection is the source of false memories during the DRM paradigm, a recent ERP study by Nessler et al. (2001) suggests a possible role for familiarity. Specifically, Nessler et al. found that differences between true and false memory are influenced by strategic processes engaged during encoding (such as processing conceptual features of the stimuli), and that this is reflected primarily in the ERP correlates of familiarity. False memory data are, therefore, somewhat difficult to reconcile with the ERP findings—apparently sitting at odds with behavioral findings.

While behavioral evidence from both LOP and DRM studies suggests that it is primarily recollection that mediates the interaction between semantic and episodic memory, other evidence suggests that familiarity may also play a role. For example, the Speed–Accuracy Trade-off (SAT) method has been used to test recognition for semantically related and unrelated word pairs, revealing a maximum false-alarm rate to semantically related lures at short retrieval deadlines (Dodier, 1984). Whereas retrieval based on recollection is relatively slow, familiarity is regarded as a fast acting process, suggesting that the false alarms to semantically related pairs were due to familiarity. This finding suggests, therefore, that familiarity, but not recollection, might be more affected by manipulations of semantic memory.

In general, previous studies do not provide a conclusive account as to which episodic retrieval process (familiarity or recollection) mediates the interaction between semantic and episodic memory. The present study is designed to directly investigate this question, examining the functional and neural correlates of successful episodic retrieval. To examine the interaction between episodic and semantic memory we manipulated the semantic coherence of to-be-remembered information, requiring the retrieval of categorically related vs unrelated word pairs during an associative recognition test. We employed neuroimaging (event-related potentials) and behavioral (process dissociation procedure) measures to provide convergent evidence that semantic memory does indeed influence episodic retrieval. We predicted that episodic retrieval would be enhanced for semantically coherent word pairs, and based largely on LOP theory, that the increase in performance would primarily be associated with greater recollection.

Materials and methods

Participants

All participants were right-handed native English speakers, ranging from 18 to 35 years in age, with normal or corrected-to-normal vision and no known neurological problems. Informed consent was required, and payment provided at a rate of $5 per hour. Twenty-two participants performed the ERP study; seven were excluded due to either technical failure or EEG artifact, and the remaining 15 (6 female) had an average age of 24 years. An additional 12 participants (8 females, mean age 21) performed a follow-up behavioral study using the process dissociation procedure.

Materials

Stimuli consisted of the presentation of a category name followed by a word pair. Each word pair was chosen as being
either semantic (one or both words were category exemplars) or non-semantic (both words were completely unrelated to the category) as shown in Fig. 1. Word pairs were constructed from 864 nouns, 4-6 letters in length, with a frequency between 10 and 30 occurrences per million (Kucera and Francis, 1967). A third (288) of the nouns were category exemplars (12 nouns for each of 24 categories), the remainder (576) were unrelated to the categories.

Stimuli were created for 6 blocks, each containing a single study list of 32 semantic and 32 non-semantic word pairs (truncation interspersed), matched with a corresponding test list of 24 semantic and 24 non-semantic word pairs. Test lists were created for each condition (semantic and non-semantic) in the following way: 8 pairs were re-presented at test in the same pairings as at study, providing 8 intact word pairs; 16 pairs shown at study were recombined to create 8 rearranged word pairs by taking one word from each of two study pairs (maintaining word position in each case) and discarding the other member of each study pair. To be clear, rearranged study word pairs A-B and C-D would be recombined to form A-D, discarding B and C (i.e., the first word and second words of a study pair were discarded equally often). The remaining 8 pairs were used to create 8 new word pairs, by combining the first member of each pair (always discarding the second member of the pair) with a previously unstudied word. The resulting semantic and non-semantic word pairs for each of the intact, impaired and new conditions were randomly intermixed within each test list.

**Procedures**

The experiment was implemented using E-Prime and a PST Serial Response Box. All stimuli were displayed in white, using upper case Courier New 18 point font, against a black background. Category names were displayed in central vision, and word pairs were displayed one above the other, slightly above and below central fixation. The category name associated with an individual word was always the same at study and test (thus when pairs were rearranged this was performed within each category). At the viewing distance of approximately 1 m, the stimuli subtended a maximum visual angle of 3.7° horizontally and 1.4° vertically. The 6 study-test blocks were presented in a random order for each participant. An additional practice list was always shown first to familiarize participants with the procedure. Fig. 1 illustrates the design. The factors of relationship (semantic, non-semantic) and pairing (intact, impaired, new) were fully crossed within participants.

Each study trial started with a fixation cross (+) displayed for 750 ms in the center of the screen, followed by a blank screen for 250 ms. The category name was then presented for 1500 ms before being replaced by a word pair for 2000 ms. Participants were instructed to indicate by button press (within 1500 ms of word pair onset) whether each word pair was a target (respond: old) or a non-target (respond: new). Targets were defined as intact word pairs; non-target as rearranged and new word pairs. Once a response was made, a short (250 ms) delay occurred, and participants were then prompted to rate their response confidence by button press on a five point scale (1 = guess, 2 = unsure, 3 = think so, 4 = pretty sure, 5 = certain). Once a confidence response was made, the screen went blank for 250 ms, and the next trial began. Participants were then informed that their memory would be tested.

Each test trial started with an initial 750 ms fixation cross, followed by a 250 ms blank screen, a 1500 ms category name and then a word pair for 2000 ms. Category names were re-presented at test, ensuring that the semantic coherence of the stimuli remained salient, and therefore augmenting the influence of the category on performance. Participants were instructed to indicate by button press (within 1500 ms of word pair onset) whether each word pair was a target (respond: old) or a non-target (respond: new). Targets were defined as intact word pairs; non-target as rearranged and new word pairs. Once a response was made, a short (250 ms) delay occurred, and participants were then prompted to rate their response confidence by button press on a five point scale (1 = guess, 2 = unsure, 3 = think so, 4 = pretty sure, 5 = certain). Once a confidence response was made, the screen went blank for 250 ms, and the next trial began. Participants were asked to respond as quickly and accurately as possible, and the mapping of buttons to old and new responses was counterbalanced across participants.

The initial ERP study was followed by a behavioral study based on the process dissociation procedure (Jacoby, 1991), which allows estimates of the contributions of familiarity and recollection to be calculated based on differences in performance in ‘exclusion’ and ‘inclusion’ tests. The ERP study outlined above is an exclusion test, whereby rearranged pairs had to be excluded as non-targets. The inclusion test is identical to the exclusion test with exception of the task instructions given to participants. In the inclusion version, an ‘old’ response is required for intact and rearranged word pairs (target trials) while a ‘new’ response is required only for new word pairs (non-target trials). By comparing performance on exclusion and inclusion tasks the process dissociation procedure (PDP) provides estimates of the contribution of recollection and familiarity. PDP estimates are based on the assumption that an ‘old’ response to recombinated pairs is given in the inclusion task when either the pair was recollected (R) or when the pair was familiar (F) in the absence of recollection (1 - R), i.e., P (old inclusion) = R + (1 - R) F. In contrast, an ‘old’ response to recombinated pairs in the exclusion task should only be evoked by familiarity (F) in the absence of recollection (1 - R), i.e., P (old exclusion) = (1 - R) F. Recollection of the precise pairing in the exclusion task would lead to a correct rejection of the recombinated pair. These processing differences for inclusion and exclusion responses allow the derivation of the following estimates for familiarity and recollection:

Recollection = \( P(\text{old inclusion}) - P(\text{old exclusion}) \)

Familiarity = \( P(\text{old exclusion}) / (1 - R) \).

Inclusion and exclusion experiments are typically performed within participants, to avoid differences in response bias across tasks and to allow statistical analysis of the resulting estimates. We therefore carried out an additional behavioral experiment to obtain PDP estimates of familiarity and recollection using the same stimuli as in the ERP study. Only two changes were made from the original paradigm. First, subjects performed both inclusion and exclusion versions of the experiment, as outlined above; task order was counterbalanced across participants. Second, because two
Fig. 1. The experimental design and materials. During the study phase each trial involved the presentation of a category name followed by a word pair. Either one or both of the words were semantically related to the category (semantic), or neither of the words contained a semantic relation to the category (non-semantic). During the test phase the same trial procedure was employed and three types of word pairs were presented: intact pairs, which were previously presented at study; rearranged pairs, which were constituted by rearranging words from intact study pairs and new pairs, which were constituted by combining a member of a studied pair with an unstudied word. Intact, rearranged and new word pairs were constructed separately for the semantic and non-semantic conditions.

Tasks were being performed by each participant rather than one, the number of inhouse and exclusive trials was reduced by half (leaving the total number of trials the same).

**ERP recording and analysis**

Scalp EEG was recorded from 61 Silver-Silver-Chloride electrodes embedded in a cap based on an extended version of the international 10-20 system (Jasper, 1958); Fz, FCz, Cz, CPz, F3, F4, P7, P8, O1, O2, FP1, FP2, AF7, AF8, AF3, AF4, F7, F8, F3, F4, F1, F2, FT7, FT8, FC5, FC6, FC1, FC2, T7, T8, C5, C6, C3, C4, C1, C2, T3, T4, CP5, CP6, CP3, CP4, CP1, CP2, P7, P8, P5, P6, P3, P4, P1, P2, P7, P8, PO4, PO3, PO1, PO2. Data were recorded and processed using Neuroscan 4.2 software. EEG was recorded using a left mastoid reference, but EEG was also recorded from the right mastoid, allowing re-referencing off-line to recreate linked mastoid recording. EOG electrodes were located above and below the left eye for monitoring eye blinks and the exophthalmi of both eyes to monitor lateral eye movements. Electrode impedances were adjusted below 5kΩ, and all data were recorded with a bandpass filter of 0.1–40 Hz and digitized (16 bit) at a rate of 8 ms per point.

Eye-blink artifacts were removed using a regression procedure (Neuroscan Ocular Artifact Reduction), calculating an average blink from a minimum of 32 blinks for each participant, and removing the contribution of the blink from all other channels on a point-by-point basis.

Continuous EEG data were separated into 2000 ms epochs, beginning 200 ms before the onset of each word pair. Individual epochs were baseline corrected and smoothed over 5 points. Epochs were excluded (average 9%, ranging from 4% to 19%) when eye movements were present (horizontal electrooculogram (EOG) effects greater than 100 μV), when any channel became saturated (exceeding ±495 μV) or when baseline drift (absolute difference in amplitude between the first and last data point of each individual epoch) was greater than 75 μV on any EEG channel. A minimum of 16 artifact-free trials were required from each participant in each condition to ensure an acceptable signal-to-noise ratio. To minimize EEG artifacts, participants were asked to relax, minimize body, head and eye movements, and to fixate on the center of the screen.

As noted above, the experiment was designed to examine the ERP old/new effects associated with the retrieval of semantic and non-semantic word pairs, thus ERPs were formed for correct responses to intact and new word pairs. ERP analyses were designed to investigate the pattern of old/new effects in the semantic and non-semantic conditions, revealing any differences in the engagement of the generators of the left parietal and mid-frontal ERP old/new effects. ERPs to rearranged pairs were not examined because there were insufficient artifact free trials in this condition. Based on previous findings and visual inspection of the waveforms, data were analyzed over 4 consecutive time windows (300–600 ms, 600–900 ms, 900–1200 ms and 1200–2000 ms). The first two time windows capture the ERP correlates of familiarity and recollection, the mid-frontal and left parietal old/new effects. As other late-emerging old/new effects have been reported, the latter time windows were also included in the analysis.

All statistical tests were conducted with a significance level of 0.05. Analysis of ERP data employed the Greenhouse-Geisser correction for non-sphericity, and corrected t and p values are reported as appropriate. All topographical analyses were performed on difference scores (subtracting the ERPs for new word pairs from those for intact word pairs) and these effects were normalized prior to analysis using the Max-Min method (McCarthy and Wood, 1985).

**Results**

**Behavioral data**

Fig. 2 shows the probability of a correct response (bars) for intact, rearranged and new word pairs, along with associated reaction times (lines). The data are shown separately for semantic and non-semantic word pairs, demonstrating a clear improvement in recognition performance for semantically related compared to unrelated pairs. Importantly, analysis revealed that participants were able to discriminate between the different types of word pairs.
in both conditions (paired t-tests comparing hits (intact) vs. false alarms (rearranged), and hits (intact) vs. false alarms (new) were significant, p<0.001 in all comparisons).

Old/new discrimination accuracy [Pr=Hit−FA] and response biases [BR=FA/(1−Pr)] were computed for semantic and non-semantic conditions, whereby Hit is the probability of ‘old’ response to an intact pair, and FA is the probability of an ‘old’ response to a new pair. Discrimination accuracy was significantly better for the semantic (0.680) than non-semantic (0.295) conditions (t(14)=4.68, p<0.001). Similarly, response bias was significantly higher for the semantic (0.56) than non-semantic (0.41) conditions (t(14)=3.77, p<0.005). We considered that the possibility that the two threshold model might not provide a suitable fit for the target/new discrimination and calculated the response bias based on detection theory. Nevertheless, the pattern of results remained the same as a more liberal response bias was found for the semantic condition. Whether this difference in performance for semantic and non-semantic pairs is reflected in the ERP data will be discussed later.

The statistical analysis of the behavioral data was performed with ANOVA including the factors of condition (semantic, non-semantic) and pairing (intact, impaired, new). Results revealed a significant main effect of pairing [F(2.28)=21.31, p<0.001], no main effect of relationship [p>0.05], but a significant interaction between relationship and pairing [F(2.28)=33.82, p<0.001]. As Fig. 2 shows, intact pairs were better remembered when semantically related (t(14)=7.56, p<0.001). By contrast, rearranged pairs were more difficult to reject when semantically unrelated (t(14)=4.38, p=0.001), and new pairs were equally well rejected in the semantic and non-semantic conditions (p>0.05).

Reaction time data in Fig. 2 (lines) reveal no clear influence of the manipulation of semantic relationship. ANOVA with the factors of relationship (semantic, non-semantic) and pairing (intact, impaired, new) revealed no significant main effects or interactions [p>0.05 in all cases]. Nonetheless, the behavioral results clearly demonstrate that semantically related word pairs were better remembered than unrelated pairs.

Confidence ratings for the semantic and non-semantic pairs were compared. The analysis tested whether the memory advantage for semantic vs. non-semantic intact pairs is carried solely by the ‘high confidence old’ ratings, which are expected to reflect recollection in addition to familiarity, or by ‘middle range confidence old’ (i.e., 2 to 4) ratings, which indicate the contribution of familiarity. The probability of confidence ratings for all semantic hits was contrasted with the probability of confidence ratings for all non-semantic hits. The ANOVA with the factors of condition (semantic, non-semantic) and confidence rating (1–5) for correctly identified intact pairs revealed a main effect of condition [F(1,14)=36.76, p<0.001], a main effect of confidence [F(4,56)=11.23, p<0.001] and an interaction between confidence and condition [F(4,56)=16.60, p<0.001], suggesting that the pattern of confidence ratings did vary across conditions. Importantly, a t-test confirmed that there was indeed an increase in confidence for the semantic compared to the non-semantic condition at the middle range confidence category 4 (t(14)=2.43, p=0.029). This difference did not reach significance for confidence ratings 2 and 3, but given the increase in confidence seen in category 4 ratings, it is likely that there was less opportunity for ratings at categories 2 and 3. Nonetheless, this suggests that semantic pairs did attract more ratings in the middle range, particularly at higher confidence levels, reflecting stronger familiarity for semantic pairs. Finally, a t-test contrasting the ‘high confidence ratings’ also reveals increased confidence ratings for semantic pairs (t(14)=6.32, p<0.001). Since familiarity as well as recollection is likely to contribute to ‘high confidence ratings’ it is difficult to determine which process is accountable for this difference. Nevertheless, stronger familiarity for semantic pairs is associated with a shift in confidence ratings towards higher values and would predict the observed increase in high confidence ratings.

Electrophysiological data

Grand average ERPs for correct responses to intact and new word pairs are shown for the semantic condition in Fig. 3, and for the non-semantic condition in Fig. 4. The mean number of trials contributing to the intact and new waveforms were 32 and 29 for semantic, and 24 and 31 for non-semantic. Figs. 3 and 4 show that the ERPs evoked in both semantic and non-semantic conditions are more positive-going for intact compared to new word pairs from around 300 ms. The old/new effects are initially bilaterally distributed and largest over frontal electrodes for the semantic condition, with a more central focus for the non-semantic condition. From around 600 ms, however, the positive shift for intact pairs exhibits a clear left parietal maximum in both conditions. The intact and new waveforms converge around 900 ms, but differences appear to remerge from around 1200 ms onwards. To characterize the pattern of old/new effects for each condition, average voltages were calculated over four consecutive epochs (300–600 ms, 600–900 ms, 900–1200 ms, 1200–2000 ms), at 4 separate locations, representing average activity over 3 electrodes: left-frontal (LF: F3, F1, F5), right-frontal (RF: F2, F4, F6), left-parietal (LP: CP1, CP3, CP5) and right-parietal (RP: CP2, CP4, CP6), as illustrated in Fig. 5A.

Initial high-level analyses were designed to identify whether old/new effects varied across conditions and epochs, using ANOVA with the factors of condition (semantic, non-semantic), epoch (300–600 ms, 600–900 ms, 900–1200 ms, 1200–2000 ms), old/new (intact, new), location (frontal, parietal) and hemisphere (left, right). Results revealed significant ERP old/new effects; a main effect of old/new [F(1,14)=8.41, p<0.01], a two-way interaction between old/new and location [F(2,67,37.5)=7.5, p<0.001] and three three-way interactions between condition, epoch and old/new [F(2,18,30.5)=5.91, p=0.011], epoch, old/new
Fig. 3. Grand average ERPs for semantic word pairs. ERP waveforms are shown from 22 electrodes, displayed as if looking down onto the top of the head. ERPs are shown for correct responses to intact (thin) and new (thick) word pairs, differences between the waveforms revealing a characteristic pattern of ERP old/new effects, with an anterior ERP effect followed by a smaller, left parietal effect.

and location \(F(2.50,34.93) = 4.3, p = 0.016\) and old/new, location and hemisphere \(F(1.41) = 7.95, p = 0.047\). The presence of significant old/new interactions involving factors of both epoch and location strongly suggests that a changing pattern of old/new effects exists over the four epochs, varying across the semantic and non-semantic conditions, and varying across frontal and parietal locations.

To further investigate the pattern of old/new effects, a second level of analysis was performed on the data from each epoch, using ANOVA with the factors of old/new (intact, new), location (frontal, parietal) and hemisphere (left, right). This analysis aimed to demonstrate whether old/new effects were present within each epoch. The results are shown in Table 1; significant effects involving the factor of old/new are present during the 300–600 ms

Fig. 4. Grand average ERPs for non-semantic word pairs. ERP waveforms are shown from 22 electrodes, displayed as if looking down onto the top of the head. ERPs are shown for correct responses to intact (thin) and new (thick) word pairs, exhibiting a different pattern of ERP old/new effects compared to those seen for semantic word pairs. While a clear left parietal effect is present, there is little evidence of an early mid-frontal ERP effect.
and $600-900$ ms epochs, but not for the later two time windows. As Table 1 shows, in both of the early epochs the factor of old/new interacts with location (albeit marginally significant for the first epoch), suggesting that the pattern of old/new effects varies at frontal and parietal electrodes. This pattern of results is consistent with the presence of an early effect over frontal scalp, and a later effect (which varies by hemisphere) over parietal scalp. To demonstrate that this is indeed the case, and to investigate whether these old/new effects differ across semantic and non-semantic conditions, a final set of analysis was performed separately at frontal and parietal locations during the $300-600$ ms and $600-900$ ms epochs. These data are highlighted in Table 1.

Analysis of the data from $300-600$ ms employed ANOVA with the factors of condition (semantic, non-semantic), old/new (intact, new) and hemisphere (left, right). Analysis at frontal electrodes revealed a significant main effect of old/new $[F(1,14) = 20.32, p < 0.001]$, and an interaction between old/new and condition $[F(1,14) = 6.30, p = 0.025]$. As Fig. 6 shows, old/new effects are present over frontal scalp sites from $300$ to $600$ ms, and these effects are significantly larger for the semantic condition. This result was confirmed with an additional focused analysis (collapsed across frontal electrodes) that directly compared the magnitude of the old/new difference across conditions ($[14] = 2.45, p < 0.028$).

By contrast, analysis at parietal electrodes revealed a significant effect of old/new $[F(1,14) = 33.57, p < 0.001]$ but no interactions. This pattern of results is important; it reveals differences in the old/new effects exhibited by semantic and non-semantic conditions only at frontal electrodes. The topographic distribution of the old/new effects is illustrated in Fig. 7, highlighting a bilaterally distributed old/new effect over frontal scalp for the semantic condition only, and a more posterior effect that is present for both the semantic and non-semantic conditions.

Analysis of the data from $300-600$ ms revealed significant old/new differences at centro-parietal locations, though these effects did not differ in the semantic and non-semantic conditions. This old/new difference is particularly visible in Fig. 7 for the non-semantic condition, where there is little sign of additional overlapping frontally distributed effects. Examination of the waveforms (see Fig. 4) suggests that, in this case, the difference appears to be restricted to a window from $300-500$ ms and is largest over central electrodes. This pattern of old/new differences is consistent with a modulation of the N400 component, a negative going peak (maximal over central–parietal electrodes between $300$ and $500$ ms post-stimulus) which is known to vary with the ease with which the meaning of words can be integrated into a given context (see Kutas and Van Petten, 1994). To be clear, we distinguish here between the N400 component (the negative going peak) and the N400 old/new effect (a modulation of the N400 component).

Given the pattern of data shown in Figs. 6 and 7, it seems likely that the small frontally distributed old/new differences seen for the non-semantic condition most likely reflects residual spread of activity from the N400 old/new effects seen for intact pairs (where the words have already been integrated) compared to new pairs (where integration is required).

Based on the pattern of effects seen at central and frontal electrodes, two possible interpretations of the data exist. First, both the semantic and non-semantic conditions are associated with activity over frontal electrodes that reflect spread of activity from the N400 old/new effects, and the increased old/new effect at frontal electrodes in the semantic condition simply results from a spread of a stronger N400 old/new component, with no additional purely mid-frontal activation present.

To discriminate between the two possibilities outlined above, additional analyses were performed on data from $300-500$ ms, over two rings of electrodes that capture the distribution of the N400 component (see Fig. 5B). ANOVA was performed with factors of condition (semantic, non-semantic), old/new (intact, new), ring (inner, outer) and site (FCZ, C2, CP2, PZ, CP1, C1, FC1 and FZ, F4, C4, P4, PZ, P3, C3, F3). Analysis revealed a significant effect of old/new $[F(1,14) = 28.95, p < 0.001]$, a two-way interaction between old/new and ring $[F(1,14) = 27.51, p < 0.001]$ and a three-way interaction between old/new and condition $[F(1,14) = 27.51, p < 0.001]$.
null
observed in the ERP experiment. ANOVA including the factors of relationship (semantic, non-semantic) and pairing (intact, impaired, new) revealed a significant main effect of pairing \(F(2,22)=18.87, p<0.001\), no main effect of relationship \(p=0.05\), but a significant interaction between relationship and pairing \(F(2,22)=14.22, p<0.001\). As was the case for the ERP experiment, intact pairs were better remembered when semantically related \((t(11)=2.79, p=0.018)\) whereas rearranged pairs were more difficult to reject when semantically related \((t(11)=3.97, p<0.002)\).

The inclusion task also revealed differences in recognition performances for semantic and non-semantic word pairs. ANOVA with the factors of relationship (semantic, non-semantic) and pairing (intact, impaired, new) revealed a significant main effect of relationship \(F(1,11)=5.32, p=0.041\) and a significant interaction between relationship and pairing \(F(1,7.77)=4.41, p=0.075\). Intact pairs were better remembered when semantically related \((t(11)=2.11, p=0.05)\) whereas rearranged pairs were associated with better performance for semantically related compared to unrelated pairs \((t(11)=3.91, p<0.002)\), as would be expected given the changes in task instruction.

**PDP estimates**

Based on the combined performance from the exclusion and inclusion studies, the process dissociation procedure (PDP) can be used to provide an estimate of the contribution of familiarity and recollection to performance. These data are illustrated in Fig. 8, showing that familiarity increased from 0.53 to 0.72 for non-semantic compared to semantic pairs, while estimates for recollection remained stable at 0.26 and 0.24 for non-semantic and semantic pairs. Clearly, the PDP data exhibit a considerable increase in familiarity from non-semantic to semantic conditions (0.19) but only a small difference in recollection (0.02). The PDP estimates were subjected to statistical analysis and an ANOVA with the factors of condition (semantic vs. non-semantic) and estimate (familiarity vs. recollection), revealing a main effect of condition \(F(1,11)=7.35, p=0.02\), a main effect of estimate \(F(1,11)=14.62, p=0.01\) and a significant interaction between condition and estimate \(F(1,11)=14.23, p=0.01\). Subsidiary analysis confirmed a statistically significant increase in familiarity from non-semantic to semantic conditions \((t(11)=6.13, p<0.001)\) and no significant difference in recollection \((t(11)=0.48, p>0.05)\). Thus, consistent
with the pattern of ERP effects, behavioral estimates suggest that episodic retrieval is modulated by the manipulation of semantic vs. non-semantic word pairs, and that this is driven primarily by changes in familiarity rather than recollection.

Discussion

We investigated the functional and neural interaction between episodic and semantic memory in normal cognition. By manipulating whether word pairs were categorically related, we demonstrated that associative recognition memory is enhanced for semantically coherent information. Second, we asked if this interaction produced changes in recollection or familiarity. To our surprise, the data revealed that the influence of semantic memory was to modulate the extent of familiarity-based retrieval, leaving recollection relatively unaffected. In short, our data provide novel evidence for an interaction between semantic and episodic memory, demonstrating that the semantic organization of information influences the engagement of episodic memory by modulating familiarity-based retrieval.

Convergent evidence that manipulating semantic memory modulates familiarity

Our results are particularly compelling because they reflect convergent behavioral and electrophysiological evidence. Estimates derived from the process dissociation procedure (Jacoby, 1991) revealed a considerable increase in familiarity, alongside a negligible change in recollection. While the behavioral findings are indirect, the neuroimaging data provide a direct record of the underlying neural activity associated with performance. As would be expected on the basis of previous findings (Donaldson and Rugg, 1999), our data provide clear evidence of significant left parietal old/new effects during associative recognition memory (see Figs. 6 and 7). Importantly, however, there was no evidence for a significant difference in the left parietal old/new effect elicited by semantic and non-semantic word pairs; consistent with the behavioral data, ERPs revealed comparable levels of recollection. By contrast, the semantic and non-semantic conditions were dissociable on the basis of the mid-frontal ERP old/new effect, which was only present for the semantic condition. The ERP findings are particularly clear; the semantic and non-semantic conditions exhibited a selective modulation of the mid-frontal ERP old/new effect, suggesting that recognition of the semantic word pairs was enhanced due to an increase in familiarity.

Although the PDP and ERP findings both point towards the conclusion that semantic coherence influences familiarity rather than recollection, it is important to recognize that the reasons for reaching this conclusion are quite different in each case. While the ERP findings are restricted to analysis of the intact pairs, the PDP estimates stem primarily from performance on the rearranged pairs (the likelihood of hits and false alarms to this class of stimuli during the inclusion and exclusion tasks, respectively). In some respects, the difference between these two measures is a strength; the two findings provide genuinely independent (yet convergent) evidence using methods that rely on very different assumptions. Nonetheless, drawing any direct correspondence between the ERP and PDP data relies on a strong assumption, namely that the selective familiarity advantage for rearranged pairs from the semantic vs. non-semantic condition seen in the PDP data also holds for the intact pairs in the ERP data.

To address this issue and provide a more direct link between the behavioral and electrophysiological evidence, we carried out an additional examination of the confidence judgements made during the ERP task. Recollection is associated mostly with high confidence judgements, whereas familiarity typically covers a range of confidence judgements (Vossoughi, 1997; Vossoughi, 2001). If, as we believe, familiarity shows an increased contribution to intact semantic pairs compared to non-semantic pairs, this should be reflected in the pattern of confidence judgements. Consistent with this view, analysis of the confidence ratings revealed differences between semantic and non-semantic pairs for confidence ratings which are typically assumed to reflect responses based on familiarity. This finding adds weight to our conclusion, providing additional behavioral evidence that the putative change in familiarity-based responding is evident for both the rearranged and intact pairs. Given this confidence analysis, the ERP findings alone provide strong evidence for an increase in familiarity for the semantic, compared to non-semantic, condition.

Utilization, bias and task difficulty

One potential objection to our findings is that, traditionally, associative recognition tests are thought to require recollection (Atkinson and Juola, 1974; Mandler, 1980, 1991), with familiarity playing little or no role in performance. Recent evidence suggests, however, that this is not always the case; familiarity can sometimes contribute to associative recognition. For example, Yonelinas et al. (1999) demonstrated that familiarity can play a significant role in associative recognition if the separate elements of a stimulus are united into a single larger representation (e.g., complex stimuli such as faces can be familiar when processed as a whole, but not when processed in parts). Our findings are consistent with this view; enhanced performance and increased familiarity for the semantically coherent stimulus may reflect the benefits of utilization. We are cautious about interpreting our data in this way, however, because the extent and limits of utilization are not well understood to date. For example, it is unclear what kinds of stimulus relationships support united representations, or whether a brief learning phase (as employed in the present experiment) would allow utilization of item-item associations to occur (see Mayes et al., 2004, for argument that utilization is sufficient but not essential for an engagement of familiarity in associative recognition). Finally, we note that a utilization account need not sit in opposition to our interpretation of the data; rather, the utilization hypothesis may offer an explanation of the way in which semantic memory influences episodic retrieval.

Our data are, of course, open to alternative interpretations. Here we consider the possibility that the findings reflect little more than changes in either task difficulty or response bias. Were the lower levels of performance in the non-semantic condition, and thus the lower estimates of familiarity, simply due to increased task difficulty? Task difficulty is notoriously hard to define a priori, and is typically introduced as an ad hoc explanation of changes in performance. In the present case, although performance is poorer in the non-semantic condition overall (consistent with a change in difficulty), reaction times are not significantly different in the semantic and non-semantic conditions (suggesting no overall change in difficulty). More importantly, both the behavioral and ERP findings suggest that the manipulation of semantic coherence had a selective effect; unlike familiarity, recollection did not vary across condition. By contrast, a task difficulty account would
predict changes in both familiarity and recollection, and not a
selective change in familiarity.

An alternative interpretation of our data is that the ERP findings
reflect little more than the influence of response bias. As reported
above, the behavioral data reveal a high response bias for semantic
pairs and a low response bias for non-semantic pairs. How might bias
influence the ERPs measured at retrieval? Perhaps the most
straightforward view would be that changes in bias should directly
influence the probability of responding old on the basis of familiarity
(a more liberal bias leading to an increased likelihood of items being
accepted as old on the basis of a lower level of familiarity). Our data
do, superficially, fit such a simple bias account; the more liberal bias
found for the semantic condition was associated with better
performance and an increase in familiarity. Thus, assuming that
changes in response bias exhibit more influence on familiarity than
recollection, encountering a semantic relationship between the
category name and word pair may have resulted in a reduced criterion
for responding ‘old’ overall, producing a change in the size of the mid-frontal old/new effect. From this perspective, the semantic
condition is seen as being associated with increased familiarity
based responding (as indexed by the mid-frontal old/new effect), but
this is simply a consequence of changes in response bias.

While a response bias account is plausible, we find it difficult to
sustain. Our data do not reveal a change in bias alone; the
behavioral results show both a change in bias and a change in
discriminability, with significantly higher discrimination in the
semantic compared to non-semantic condition. Moreover, the
behavioral results for the semantic and non-semantic conditions
show no significant differences in false alarm rate. A full account of
our data would therefore require an explanation that goes
beyond response bias. Moreover, it is clear from previous
findings that ERPs are sensitive to changes in response bias at
frontal recording sites, but that the neural correlates of response
bias may be distinct from those of familiarity, with the former
seen only in responses to new items (cf. Johansson et al., 2004),
or occurring in opposite directions for old and new items (cf.
Windmann et al., 2002). In the present case, careful examination
of the data reveals that the change in the pattern of mid-frontal
old/new effects across semantic and non-semantic conditions is
driven by the old conditions (see Fig. 6). Additional analysis
comparing the magnitude of activity across the two correct
rejection waveforms from 300 to 600 ms at frontal electrodes
revealed no significant difference between the semantic and non-
semantic conditions (means of −2.1 μV and −1.9 μV, respect-
ively; F(1,14)=0.13, p=0.70). If the mid-frontal old/new effect
was modulated by bias, this would be expected to be evident in
the ERPs to correct rejections. Thus, although differences in bias
are present across conditions, and this could theoretically underlie
the change in familiarity that is seen, we do not favor a bias
account. Finally, we note that this does not matter a great deal for
our central conclusion, which is that the change from semantic to
non-semantic conditions is associated with an increase in
familiarity, rather than recollection. Whether this turns out to
be associated with changes in utilization, bias, task difficulty, or
other factors, remains an interesting question.

Dissociating the mid-frontal ERP old/new effect and N400 old/new
effect

One important aspect of our data is the clear dissociation
between the mid-frontal ERP old/new effect and the N400 old/new
effect. The N400 component is typically seen in studies of
language comprehension, and reflects the difficulty with which the
meaning of words can be integrated with the current context (for
review see Kutas and Van Petten, 1994). Given our manipulation,
overall differences in the N400 component are to be expected in
the semantic and non-semantic conditions (with a larger N400 for
non-semantic compared to semantic pairs). Of more concern was
the possibility that differences in the old/new effects across
condition might simply have reflected a change in the pattern of
N400 old/new effects. Modulation of the N400 component elicited
by intact and new pairs (i.e., N400 old/new effects) are reasonable,
as semantic integration for intact pairs (where words have already
been integrated during study) is easier compared to new pairs
(where additional integration is required). It was, therefore, critical
that the observed N400 old/new effect did not vary across the
semantic and non-semantic conditions. Any such difference would
have suggested that our manipulation merely influenced the ease of
semantic integration and not episodic retrieval itself.

The present findings are, consequently, significant in ruling out
interpretations of the mid-frontal ERP old/new effect as nothing
more than a reduction of the N400 component (e.g., as suggested
by Yovel and Paller, 2004). In the present data, changes in the
N400 component (i.e., N400 old/new effects) occurred in both
semantic and non-semantic conditions, exhibiting a temporal
overlap with the mid-frontal ERP old/new effect. The mid-frontal
ERP old/new effect was, however, only present in the semantic
condition, and thus cannot reflect a modulation of the N400
component per se. By contrast, the ERP data are, in principle,
consistent with the possibility that the mid-frontal ERP old/new
effect reflects summation of the N400 old/new effect with an
anterior fronto-polar effect (cf. Carr and Den, 2003). This
anterior fronto-polar effect is, however, associated with visual
(perceptual) priming, and there seems little reason to expect
differences in visual priming across our semantic and non-semantic
conditions. Regardless, the present data clearly suggest that the
mid-frontal ERP old/new effect is driven by a different neural
source than that which underlies the N400 component.

While we interpret the mid-frontal ERP old/new effect as
reflecting familiarity, others have suggested that it reflects
cueing priming. One source of support for this view is the
idea discussed above, that the mid-frontal ERP old/new effect is
actually produced by an N400 reduction (Yovel and Paller, 2004),
which our data clearly militate against. In addition, in the current
context, a conceptual priming account would predict differences in
the magnitude of the mid-frontal old/new effect between the
semantic and non-semantic new pairs—the former are preceded by
a semantically related category cue, but the later are not.
Examination of the ERPs for correctly rejected new pairs revealed
no differences over mid-frontal electrodes however, suggesting that
the mid-frontal old/new effect is not elicited by conceptual
priming. Moreover, evidence from normal (Wolk et al., 2004)
and amnesic (Olichney et al., 2000) participants suggests that
conceptual priming modulates the N400 component, separate from
the mid-frontal ERP old/new effect. There are also clear examples
of dissociations between conceptual priming and episodic memory
retrieval using other neuroimaging methods (Donaldson et al.,
2001) and neuropsychological data (Levy et al., 2004). We
therefore favor the view that, at least for verbal material, the
conscious experience of familiarity and the unconscious activation
associated with conceptual priming are both functionally and
neurally distinct.
Multiple interactions between semantic and episodic memory

Our findings stand in striking contrast to results from Levels Of Processing studies, which typically reveal an interaction between episodic and semantic memory that is driven largely by a modulation of recollection. For example, Rugg et al. (1999) and also Rugg et al. (2000) measured ERP old/new effects during an LOP study (sentence generation vs. alphabetic judgement), and revealed a modulation of the left parietal effect but no change in the mid-frontal ERP old/new effect. In LOP studies the way in which information is processed is manipulated during learning. In contrast, here we manipulated the type of information that had to be remembered, while holding processing demands constant. Thus, while changes in semantic processing during learning lead to a modulation of recollection, it appears that changes in the semantic coherence of material results in a modulation of familiarity. Whether this result extends to other manipulations of semantic memory will be of considerable interest. Regardless, it is clear that the way in which semantic memory is manipulated has a critical impact on the interaction between episodic and semantic memory.

Neuropsychological and neuroimaging studies suggest that semantic knowledge is organized as categorical representations (Okado et al., 2000; for a review see Capitani et al., 2003) and if this type of organization is observable neurophysiologically (Warrington and McCarthy, 1983; Laiacona et al., 1998) and affects psychological processing, as demonstrated in semantic priming experiments (Collins and Loftus, 1975). Our findings suggest that this organization of semantic knowledge has a significant impact on the normal functioning of episodic memory retrieval. Our data go further, however, to suggest a mechanism that underlies this interaction in healthy subjects, namely familiarity. In general, familiarity can be interpreted as a consequence of the functional overlap amongst representations. We believe that familiarity arises when subjects become exposed to an item that matches (or largely overlaps with) previously stored representations. As mentioned above, semantic memory is categorically organized and items belonging to the same category are thought to share overlapping representations. By this view, it is plausible that the process of familiarity is particularly sensitive to the presence or absence of semantic relations between stimuli per se; whether it is the specific cueing of semantic categories employed here is that critical remains to be seen.

Finally, we suggest that future studies should examine the consequences that different types of manipulation of semantic memory have on behavior. We distinguish between manipulations of semantic content, which are inherent to the stimulus material and their representations, and manipulation of semantic content, which are dependent on the way stimuli are processed. In general, this difference might explain why processing manipulations in LOP studies (semantic deep vs. shallow encoding process) lead to recollection based interactions, while changes in material as applied in the current study (categorically related vs. unrelated word pairs) facilitate familiarity based interactions. We believe that these findings have important practical implications, for example, in relation to alleviating the memory impairments associated with aging. Processing manipulations require the active and intentional use of internal mental strategies, whereas material manipulations are external and independent from the engagement of strategies. As old people exhibit particular difficulty in strategic processing, manipulate the semantic organization of to-be-remembered material might prove a more effective way to enhance their episodic remembering.

Conclusion

In real life, when required to remember an important piece of information, one may strategically engage in elaborate thought to increase the likelihood of recollecting the information later. More often, however, memory operates without such intent. In this case, one of the important factors in determining whether information is remembered or forgotten is the characteristics of the information itself. Some of the information that we are required to remember maps onto our semantic knowledge about the world; it is coherently organized around a semantic theme or category. Alternatively, information can be relatively incoherent, without obvious relationship to existing knowledge, or any clear theme or category structure. As we have shown here, the nature of to-be-remembered information is important for how we remember; when information contains a coherent semantic structure, we are better able to remember it. Unlike changing the way in which information is processed, however, making information more semantically coherent simply causes it to become more familiar.

Acknowledgments

Thanks to Jim Bednar and anonymous reviewers for helpful comments. A.G. is supported by a DTC studentship funded by the EPSRC. D.I.D. is supported by a grant from the HBSRC.

References


Appendix B: Publication


Yonelinas, A.P., 2001. Components of episodic memory: the contribution of...