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Complexity, specificity, and the timescales of developing expectations in visual perception

Nikos Gekas

Doctor of Philosophy
Institute for Adaptive and Neural Computation
School of Informatics
University of Edinburgh
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Abstract

Perception is strongly influenced by our expectations, especially under situations of uncertainty. A growing body of work suggests that perception is akin to Bayesian Inference in which expectations can be viewed as ‘prior’ beliefs that are combined via Bayes’ rule with sensory evidence to form the ‘posterior’ beliefs. In this thesis, I aim to answer open questions regarding the nature of expectations in perception, and, in particular, what the limits of complexity and specificity in developing expectations are, and how expectations of different temporal properties develop and interact.

First, I conducted a psychophysical experiment to investigate whether human observers are able to implicitly develop distinct expectations using colour as a distinguishing factor. I interleaved moving dot displays of two different colours, either red or green, with different motion direction distributions. Results showed that statistical information can transfer from one group of stimuli to another but observers are also able to learn two distinct priors under specific conditions. In a collaborative work, I implemented an online learning computational model, which showed that subjects’ behaviour was not in disagreement with a near-optimal Bayesian observer, and suggested that observers might prefer simple models which are consistent with the data over complex models. Next, I investigated experimentally whether selective manipulation of rewards can affect an observer’s perceptual performance in a similar manner to manipulating the statistical properties of stimuli. Results showed that manipulation of the reward scheme had similar effects on perception as statistical manipulations in trials where a stimulus was presented but not in the absence of stimulus. Finally, I used a novel visual search task to investigate how expectations of different timescales (from the last few trials to hours to long-term statistics of natural scenes) interact to alter perception. Results suggested that recent exposure to a stimulus resulted in significantly improved detection performance and significantly more visual ‘hallucinations’ but only at positions at which it was more probable that a stimulus would be presented.

These studies provide new insights into the approximations that neural systems must make to implement Bayesian inference. Complexity does not seem to necessarily be a prohibitive factor in learning but the system also factors the provided evidence and potential gain in regards to learning complex priors and applying them in distinct contexts. Further, what aspects of the statistics of the stimuli are learned and used, and how selective attention modulates learning can crucially depend on specific task properties such as the timeframe of exposure, complexity, or the observer’s current goals and beliefs about the task.
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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.

(Nikos Gekas)
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Chapter 1

Introduction

All living organisms have to function and survive in an ever changing environment using the information they can obtain from the environment through their senses. The accuracy and precision of that information can be crucial when looking for food or trying to avoid a predator. The accuracy is defined as the amount of bias in a perceptual estimate, whereas the precision is defined as the variability of that estimate (Mamasian and Landy 2010). However, perceptual systems are not perfect in obtaining and processing information and sometimes information from the environment can itself be very noisy. When driving during a foggy day, it is difficult to discern whether there is a car ahead of us but it is very important to identify the presence of one immediately and react accordingly. Can we use past information about our environment to help us in these situations? For example, we might know that the road we are currently driving in is usually quiet so it is unlikely that we will encounter many other cars. On the other hand, we might know that at the present time the road is expected to be busy with commuters. So, in order to make the best possible decision we need to use all available information but also combine it with all that we have managed to learn over time. The question then is how to best combine sensory information with our prior beliefs, or expectations, about the world especially under conditions in which sensory information is uncertain.

Bayesian statistics provides a systematic way of calculating an optimal estimate under conditions of uncertainty (Gelman et al. 2013). By using Bayes’ rule, we can calculate how likely each potential state of the environment $y$ is, based on observed stimuli $x$:

$$p(y|x) = rac{p(x|y)p(y)}{p(x)}$$  \hspace{1cm} (1.1)
The posterior probability $p(y|x)$ of different states of the environment is calculated by combining the prior belief about that state $p(y)$ with the likelihood of observing a stimulus in that state $p(x|y)$ divided by a normalisation constant $p(x)$, which ensures that the sum of the posterior probabilities over all states is equal to one. Following our previous example, we may be trying to estimate whether there is a car in front of us ($y = \text{‘car in front’}$) or coming from the opposite direction ($y = \text{‘car opposite’}$) given that we can hear the sound of a car engine ($x = \text{‘sound of car engine’}$) but it is difficult to see due to the heavy fog. If the likelihood of hearing the sound of a car engine when a car is in front is high ($p(x|y) = 90\%$), we find cars often in our lane ($p(y) = 60\%$), and the sound of car engines are generally frequent on the road ($p(x) = 75\%$), then there is a high chance that the car is in front ($p(y|x) = 90\% \times 60\% / 75\% = 72\%$). If we find cars in our lane less often ($p(y) = 20\%$), then it is less likely that the car is in front ($p(y|x) = 90\% \times 20\% / 75\% = 24\%$).

So, we have a belief about the state of the environment but it is time to make a decision; for example, should we brake or continue at the same speed? Bayesian Decision Theory provides the framework to answer this question. Suppose we observe stimulus $x$ and take action $a$. If the true state of the environment is $y$, we gain (or lose) a certain utility. We need to define a function $\lambda(a|y)$, often called the loss or cost function, that quantifies the utility associated with making different decisions. To choose the best action, we calculate the expected gain (or loss) for a given action, which is the gain (or loss) averaged across all possible states weighted by the posterior distribution of each state:

$$\text{expected gain}(a) = \sum_y \lambda(a|y) p(y|x) \quad (1.2)$$

We can now choose the action that has the maximum gain (or the minimum loss). The choice of an appropriate loss function is vital to making the best decision. In our example, the cost of braking and arriving at our destination later is significantly less than the cost of hitting the car in front. So, the loss function in this case would bias us towards reducing our speed even if the posterior probability was small. Figure 1.1 summarises all the steps of the process from observing a stimulus to deciding on an action.
1.1 Probabilistic inference and learning in the brain

A growing body of work suggests that the brain could be using such a strategy to infer the true state of the environment from noisy and incomplete data. This is called the Bayesian brain hypothesis (BBH) (Knill and Pouget, 2004; Ma et al., 2006; Vilares and Kording, 2011). According to the BBH, incoming sensory signals, for example visual stimuli, are combined with prior beliefs about the world using Bayes’ rule to infer the posterior probability of different states of the world. This information then propagates to higher cortical areas, where decisions are made and actions are taken in order to maximise the expected utility (Körding and Wolpert, 2006; Platt and Glimcher, 1999).

One area where this theory has been very successful is cue combination (Ernst and Banks, 2002). Imagine that we want to determine the exact form of the object shown in Figure 1.2 but we only have ambiguous haptic and visual input. There are a number of different three-dimensional shapes that would match our information about the object. Each source of information provides different degrees of support to the possible interpretations of the object’s identity. An optimal probabilistic estimate of the correct object is provided by combining each source of information according to their respective uncertainties. Probabilistically optimal integration has been demonstrated when the different sources are different sensory modalities but it has also been shown between sensory information and memory information (Kording and Wolpert, 2004).

In spite of the success of the BBH in describing multiple aspects of perceptual behaviour, a consensus has yet to be reached on how probabilistic inference and learning could be implemented in the brain. There are two main theoretical proposals of how probabilities can be represented in the brain (Fiser et al., 2010). In the first, it is as-
assumed that probabilistic beliefs can be described by a particular type of probability distribution, and neural activities represent parameters of the probability distribution describing uncertainty in sensory variables. In the second, it is assumed that beliefs can be described as a series of possible values (samples) for the variable of interest, such that if the histogram of these values was constructed, it would eventually trace out the actual probability distribution. In these schemes, neurons, or populations of neurons, themselves represent the sensory variables.

Probabilistic population codes (PPCs) are a primary example of parameter-based descriptions (Ma et al., 2006). Neural activities encode parameters of the probability distribution that results from probabilistic inference, and maintain a full probability distribution at any moment in time. Changes in neural activities encode dynamically changing distributions on continuously incoming stimuli. It has been shown that such representations can be used for optimal perceptual inference and decision making (Yang and Shadlen, 2007), and neurophysiological support in cortical areas for PPCs has been reported (Ma et al., 2008). However, it is not yet clear how learning could be implemented with such representations.

In sampling-based approaches, each neuron, or population of neurons, can encode the value of one of the variables of a multivariate Gaussian distribution, and its activity can represent a sample from that distribution at any time. Thus, the activities of
many neurons (or populations) can represent a sample from a high-dimensional distribution, and time is required for building up an increasingly reliable estimate of the represented distribution. Sampling models provide a natural explanation for neural variability (Hoyer and Hyvärinen 2003) and bistable perception (Moreno-Bote et al. 2011; Sundareswara and Schrater, 2008). Additionally, learning for such representations is shown to be possible, as classical statistical neural networks already use this scheme implicitly (Hinton et al. 1995), and statistical receptive field models (Karklin and Lewicki 2008) use approximate versions of that scheme. However, there is no direct electrophysiological evidence for sampling-based representations in the cortex at present.

Overall, it is important to consider that the techniques for doing inference are likely to be the same across domains (perception, decision-making, etc.), and understanding the neural basis of probabilistic inference might help in discovering general theories of neural computation (Pouget et al. 2013).

1.2 Overview of thesis

An important prediction of the BBH is that since our expectations are combined probabilistically with our sensory input according to Bayes’ rule, the more ambiguous or noisy the input is, the more our expectations will affect our perception and decision-making (Girshick et al. 2011; Stocker and Simoncelli 2006). By introducing different degrees of uncertainty in the sensory input, it is possible to study the role of expectations in perception in a quantitative manner. Equally important though to our understanding of perception is to study the process of developing expectations. Despite extensive experimental and theoretical work on expectations (discussed in depth in Chapter 2 of this thesis), many questions remain unsolved. What are the limits in the complexity of expectations that can be formed? Do expectations transfer to similar stimuli and tasks or are they specific and to what degree? How fast can expectations be formed and how do expectations of different temporal properties interact?

Answers to these questions are vital in identifying how probabilistic inference and learning are implemented in the brain. At the experimental level, the limits to the complexity and specificity of expectations that can be learned as well as the level of plasticity of expectations of different timescales might be able to reveal the biological constraints of probabilistic learning. At the theoretical level, investigating how expectations of different complexities and timescales develop from sensory data of varying
statistical properties could help us build better neurally-plausible implementations of models of probabilistic learning and inference.

With the purpose of providing answers to these open issues, in this thesis I examine the complexity, specificity, and timescales of developing expectations in visual perception. I use psychophysical experiments to identify the limits inherent in the formation of expectations, and I implement Bayesian models to investigate potential mechanisms of learning.

In Chapter 2, I review existing literature on the role of expectations in perception, and present in detail existing experimental and theoretical approaches to developing expectations in visual perception. Further, I discuss the motivation and aim of each experimental and theoretical work presented in this Thesis, though more details are also provided in the introductory section of each chapter when appropriate.

In Chapter 3, I describe a psychophysical experiment that investigates the complexity and specificity of developing statistical expectations by extending an existing motion perception paradigm. By modelling the results in a Bayesian framework, I investigate the degree of optimality in learning complex priors by human observers.

In Chapter 4, I present a collaborative theoretical and experimental project with Dr Kevin Lloyd from the University of Bristol in investigating the limitations on learnable priors as a Bayesian inference problem. I briefly describe the computational model, its simulations of the experimental results of Chapter 3, and its predictions on how learning of complex priors could be facilitated by changing aspects of the experimental procedure. Then, I describe a new experiment conducted to test these predictions.

In Chapter 5, I investigate experimentally how manipulation of expected reward affects visual motion perception, and I discuss how and why its effect may differ from manipulating statistical expectations.

In Chapter 6, I describe a novel visual search experimental paradigm developed in order to investigate the timescales of expectations. I present how priors developed over different timescales interact to affect perception, and I implement a simple Bayesian model to investigate the form of prior distribution that best explains the experimental findings in a Bayesian framework.

Finally, in Chapter 7, I discuss the implications of my experimental and theoretical work, its limitations, and its relation to existing work, and I propose future directions of research.
2.1 The role of expectations in perception

There is a plethora of evidence that perception is strongly influenced by expectations. Particularly in situations of high uncertainty, we rely not only on the information we can gather at the present moment but also on our knowledge of the world and our previous experience in it. Expectations can be formed automatically and continuously, on shorter or longer timescales, and have universal impact or apply only in specific situations. Based upon how expectations generalise across time and environment, they can be divided into two major categories; ‘structural’ and ‘contextual’ (Seriès and Seitz, 2013).

2.1.1 Structural and contextual expectations

Structural expectations are developed over long time frames based on implicit learning of the statistics of the natural environment, or they can be innate. They apply equally to already experienced situations and novel ones. They are not explicit to vision but can be found in a broad range of cognitive processes. For example, in speech perception, Cutler et al. (1987) showed that listeners use their knowledge of language to construct expectations about the phonological structure of words.

There are many examples of structural expectations in visual perception. The light-
Figure 2.1: Structural expectations. (A) The ‘light-from-above’ prior. All 2-dimensional shapes appear as 3-dimensional bumps with the exception of one which appears as a dimple because of the expectation that a light source is coming from above. (B) Expectations in figure-ground separation. In (I), the convex black region is seen as the foreground object, whereas, in (II), the horizontally symmetric white region is seen as the foreground object.

from-above prior has been well documented in humans (Adams et al., 2004; Sun and Perona, 1998) and in animals (Hershberger, 1970), and it influences how we perceive an object’s properties from its shading. For example, in Figure 2.1A, we perceive all two-dimensional circles as three-dimensional bumps except one, which we see as a dimple, because we assume a source of light coming from above. If we simply flip the page upside-down, we will perceive dimples with the exception of one bump. Massion and Landy (1998) has also found evidence of a viewpoint-from-above prior, which corresponds to a preference for a surface orientation consistent with the object being viewed from above. In figure-ground separation tasks, the expectation that objects tend to be convex rather than concave influences how we separate objects from the background (Kanizsa and Gerbino, 1976; Peterson and Salvagio, 2008). The same phenomenon can be seen for symmetry, area size, and region (Peterson and Skow-Grant, 2003; Vecera et al., 2002). Figure 2.1B shows that a convex black shape and a symmetrical white shape appear as objects over a white and black background respectively. Furthermore, Burge et al. (2010) showed that human observers perceived more depth between two surfaces when the near surface’s silhouette was convex rather than concave, and Langer and Bulthoff (2001) showed that observers are better at local shape discrimination when a surface is globally convex rather than concave. Finally, a well studied structural expectation is that objects in the environment are expected to move slowly or be stationary, the ‘slow speed prior’ (Hedges et al., 2011; Stocker and Simoncelli, 2006; Weiss et al., 2002).
Chapter 2. Experimental and theoretical approaches to developing expectations in visual perception

Figure 2.2: Contextual expectations. Rabbit-duck illusion. The ambiguous image in the middle can be seen as either a duck or a rabbit. Looking at the image on the left or the right helps the visual system to resolve the ambiguity towards the animal of the image.

Contextual expectations modulate perception in isolated temporal or spatial situations, and they can be manipulated explicitly or implicitly over short time frames through sensory cues, specific instructions, or the context in which a stimulus is shown (e.g. Haijiang et al., 2006; Posner, 1980; Sekuler and Ball, 1977; Sterzer et al., 2008). Consider the central image in Figure 2.2. It is an ambiguous image that can be seen as a duck or as a rabbit. By looking first at one of the images on the left or on the right, it is possible to influence the visual system to see the central image as a duck or a rabbit respectively. However, the context does not have to be visual; Brugger and Brugger (1993) found that it is more likely to perceive the image as a duck in October and as a rabbit on Easter. In contrast to structural expectations, contextual expectations are short-lived and do not typically transfer to different contexts. For example, after training, observers were able to selectively invoke different light priors in different contexts using colour as a cue (Kerrigan and Adams, 2013). This learning was found to be context-specific. Interestingly, this also indicates that contextual expectations can mask or replace structural expectations in a given context as suggested by Seriès and Seitz (2013).

2.1.2 How do expectations affect perception?

Expectations can affect perception in two different ways. First, they can affect perceptual performance by increasing observers’ speed and accuracy at detecting stimuli that are presented at an expected location (Chalk et al., 2010; Downing, 1988; Posner,
Figure 2.3: The aperture problem (adapted from Pei et al., 2008). The visible part of the line is only that inside the circular aperture (dashed circle). The red arrows show the true motion of the bar, while the blue arrow shows the motion of the bar as seen by a human observer. Only the line's corners provide information about the line's true direction of motion.

1980), or by facilitating the recognition of expected objects in a visual scene (Bar, 2004). Second, expectations can directly affect the perceived stimulus. An example of the influence of expectations on perception can be seen in the aperture problem, first observed by Hans Wallach in 1936 (republished in Wuerger and Shapley, 1996). When a line has no identifiable features on it (for example is hidden behind a circular aperture), perceptually it is always seen to move in the direction perpendicular to its orientation regardless of its true direction of motion (Figure 2.3). Wallach noted that the perpendicular direction corresponds to the slowest possible speed, which might suggest a preference of the visual system toward slow speeds. More recently, Stocker and Simoncelli (2006) found that observers tend to underestimate the speed of low-contrast stimuli. The slow speed prior has also been hypothesised of affecting tactile perception. Goldreich and Tong (2013) suggested that a learned expectation can explain tactile illusions including the cutaneous rabbit illusion in which taps delivered to as few as two skin positions appear to hop progressively from one position to the next, and even on intervening positions that were never stimulated.

It is important to note here that prior expectations are not the only valid explanation for these effects. For example, alternative approaches to solving the aperture problem
have focused on the spatiotemporal energy of local features (Wilson and Kim, 1994; Nowlan and Sejnowski, 1995; Bowns, 2002). Bayesian models, which assume a slow speed prior, can successfully explain the "Thompson effect" (Thompson, 1982), where low contrast stimuli appear to move more slowly than higher contrast similar stimuli at low speeds (≤ 8 Hz). However, they have difficulty explaining why these stimuli appear to move more quickly at higher speeds (16 Hz). Several authors have proposed alternative, non-Bayesian models to explain this effect (so-called "ratio models", see Thompson et al., 2006; Hassan and Hammett, 2015). The two approaches, however, are not incompatible. Sotiropoulos et al. (2014) incorporated the "ratio model" of Thompson et al. (2006) into the Bayesian model of Stocker and Simoncelli (2006) and the combined model provided better fits to experimental data than either the ratio model or the Bayesian model alone, even though it had the same number of free parameters as the Bayesian model.
2.2 How do we develop expectations?

2.2.1 Statistical learning

Human observers are able to learn from their environment by extracting regularities from seemingly random variability. This learning can be unconscious and unintentional so that observers are not even aware of the learning process. The study of the mechanisms of implicit learning encompasses diverse fields from language to motor learning. A form of well studied implicit learning is statistical learning. According to Turk-Browne et al. (2010), statistical learning can be defined as the process of extracting regularities from continuous environments where the only cues for segmentation are statistics of co-occurrence between specific stimuli. Statistical learning was first reported in studies of word learning where infants could discriminate between ‘words’ and ‘non-words’ based just on transitional probabilities after passively listening to ‘words’ in the form of unexpected repeated syllable sequences inside brief syllable streams (Saffran et al., 1996).

Several studies have found that such learning also occurs for visual regularities; spatial regularities (Baker et al., 2004; Chun and Jiang, 1998; Fiser and Aslin, 2001; Fiser and Aslin, 2002; Zhao et al., 2011), multi-element displays (Fiser and Aslin, 2005), shape-colour object pairs (Turk-Browne et al., 2005; Turk-Browne et al., 2008), and shape sequences (Bulf et al., 2011; Kirkham et al., 2002).

Statistical learning has been shown to be fast (Brady and Oliva, 2008) and automatic (Turk-Browne et al., 2005). However, Turk-Browne et al. (2005) showed that even though statistical learning does not require conscious effort, it can be modulated by attention. Subjects were required to monitor one of the colours of coloured streams of stimuli, and detect repetitions of sequentially presented shapes. Through a surprise forced choice familiarity test, it was shown that statistical learning was present within the attended colour and not in the unattended colour, and that participants were able to generalise the shapes into the correct patterns (in triplets) without colour affecting recognition. Recently, Musz et al. (2014) failed to reproduce those results in a series of experiments where they found that subjects learned as well from unattended as from attended coloured streams of stimuli. The authors suggested that their findings do not conclusively determine the role of selective attention in statistical learning but they demonstrate that modifications to the stimulus presentation can crucially affect the relevance of selective attention.

It is not yet fully understood how statistical learning relates to other types of learn-
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ing. While statistical learning has been studied primarily in humans, there is some evidence that it may not be unique to humans (Newport et al., 2004; Toro and Trobalón, 2005). This suggests that statistical learning may be a part of a more general learning mechanism. A way to distinguish statistical learning from other forms of learning such as classification learning or motor sequence learning is to consider that its output consists of stimulus-specific associations rather than abstract rules or motor programs. Turk-Browne et al. (2009) used functional magnetic resonance imaging (fMRI) in a statistical learning task in an effort to identify the neural basis of visual statistical learning and compare it with other forms of learning. The authors found strong activation of the right caudate and the hippocampus to structured sequences versus random sequences of stimuli.

Both brain areas are involved in many forms of implicit learning in humans (Seger and Cincotta, 2005) and animals (Packard and McGaugh, 1996), suggesting that statistical learning may be related to other forms of associative learning. Aslin and Newport (2012) argued that what we define as statistical learning and rule learning may represent different outcomes of the same learning mechanism. The outcome of this mechanism depends on the manner and consistency with which elements are patterned in the learner’s input and can therefore apply either to experienced elements or to generalisation beyond experienced elements.

We need to mention here that there is a long history of quantitative models of classical (Pavlovian) conditioning (‘associative learning models’, see Rescorla and Wagner, 1972; Le Pelley, 2004). In a classical conditioning experiment, neutral stimuli, referred to as ‘conditioned stimuli’ (e.g., the sound of a bell) are repeatedly paired with biologically significant reinforcers (‘unconditioned stimuli’, e.g., food). Subjects (typically animals) learn to predict various patterns of conditioned and unconditioned stimuli pairings. This prediction is assessed via ‘conditioned responses’ (e.g., salivation), which are assumed to directly reflect the expectation of an unconditioned stimulus. In typical associative learning models, each stimulus is assumed to have a weight, or ‘associative strength’, correlated to how strongly it predicts reinforcement.

The weights for the presented stimuli are updated based on the subsequent delivery or non-delivery of reinforcement. Some studies have looked at these experiments under a Bayesian framework and investigated classical conditioning in terms of hidden (latent) causes models (Courville et al., 2003; Courville et al., 2006; Gershman et al., 2010; Gershman and Niv, 2012). According to such models, subjects attempt to learn the hidden structure of the environment from their experience, and they employ this internal model of the environment to make predictions about unobserved or future variables.
While these models cannot yet fully describe all aspects of classical conditioning experiments, they suggest that different aspects of learning such as statistical learning and classical conditioning, which have usually been studied separately, might share similar underlying mechanisms.

### 2.2.2 Developing contextual expectations

A number of statistical learning studies show that contextual expectations can be developed quickly in experimental settings and have a significant effect on visual perception. Knill (2007a) investigated whether an observer’s learned expectations about stimulus shape affect her depth judgments. Subjects were asked to judge the planar orientation of random shaped ellipses and they exhibited a pre-existing expectation due to which they would perceive elliptical stimuli as circular stimuli presented at an oblique angle. However, after training with stereoscopic views of randomly shaped ellipses, subjects gave progressively lower weights to the circle interpretation of test stimuli and more weights to the stereoscopic cues.

Chalk et al. (2010) investigated whether expectations can be acquired through fast statistical learning and how these expectations affect the perception of simple stimuli. The experimental procedure can be seen in Figure 2.4. In each trial, subjects were presented with either a field of coherently moving white dots shown at low contrast or a blank screen. If they had detected a stimulus, they were asked to report the direction of motion of the dots by moving a central bar to match the direction of motion and click the mouse button to confirm their choice (estimation task). The stimulus presentation and estimation task lasted a maximum of 3 seconds. Then, they were asked to report whether they had perceived a stimulus or not (‘DOTS’ or ‘NO DOTS’, detection task). Subjects were given immediate feedback at the end of each trial but only about their detection performance (i.e. whether they had correctly detected the presence or absence of a stimulus). On the other hand, they were given block feedback on their average estimation performance over the previous 20 successful trials. This was done in order for subjects to remain motivated about the estimation task but not get corrective feedback on their estimation errors.

Unbeknownst to the subjects, 2 motion directions (-32° and +32° away from a randomised central direction) were presented more frequently than the other 7 directions (Figure 2.5A). After only minutes of exposure to these stimuli, subjects developed expectations for the frequent directions, and this affected their behaviour in three ways.
First, subjects were significantly more likely to detect stimuli that were moving at the expected directions (Figure 2.5B). Second, subjects tended to perceive motion directions as being more similar to the expected directions than they really were (attractive bias, Figure 2.5C). Finally, even when there was no stimulus presented on the screen, subjects tended to ‘hallucinate’ motion, significantly more in the expected directions (Figure 2.5D). This learning was implicit; when asked about the stimulus distribution after the experiment, subjects indicated no conscious knowledge that some directions had been presented more frequently than others.

2.2.3 How complex a prior can be learned?

The findings of Chalk et al. (2010) show that subjects were able to learn the stimulus distribution but they only learned an approximation of the true distribution with high
Figure 2.5: Experimental results in Chalk et al. (2010). (A) Probability distribution of presented motion directions. Two directions, 64° apart from each other, were presented in a larger number of trials than other directions. Motion direction is plotted relative to a reference direction at 0°, which was different for each subject. (B) The fraction of trials where subjects correctly detected a motion stimulus is plotted against presented motion direction. Data points from either side of the central motion direction have been averaged together so that the furthest left point corresponds to the central motion direction, and the vertical dashed line corresponds to data taken from the two most frequently presented motion directions (±32°). Results are averaged over all subjects and error bars represent within-subject standard error. (C) Subjects’ mean estimation bias is plotted against presented motion direction. (D) Probability distribution of subjects’ estimates of motion direction when no stimulus was presented. Response distributions are plotted for all trials (blue) as well as the subset of trials where subjects reported detecting a stimulus (gray) and trials where they did not (red).
variability between subjects. Is there a limit to the complexity of a distribution that can be learned? In a visuomotor task, Berniker et al. (2010) investigated whether subjects learn the mean and variance of a prior at the same or different rates. Subjects rapidly learned the mean of a new prior, whereas the variance was learned more slowly and with a variable learning rate. This finding was not unexpected as the variance of a distribution would require more samples for an accurate estimate than just the mean. Subjects were also slower to adapt as the experimental session progressed. This suggested that subjects might be growing more confident in their estimates of the prior due to accumulated evidence, and so become slower to react to changes.

Most experiments have looked at simple statistical learning tasks involving regularities in one dimension. How humans learn probability distributions integrating multiple features simultaneously is still unclear, but there is indication that statistics about more than one variable can be learned jointly. Seitz et al. (2007), for example, showed that it is possible for stimulus associations to form across modalities when there are statistical contingencies. They used a novel audio-visual procedure where subjects were passively exposed to a rapid serial presentation of audio-visual pairings and were later tested to report about the degree of familiarity of the stimuli. They found that subjects acquired knowledge of visual-visual, audio-audio, and audio-visual stimulus associations and that the learning of these types of associations occurred in an independent manner. Looking at vision alone, Turk-Browne et al. (2008) investigated how subjects learn regularities involving both shape and colour. They showed that visual statistical learning could be both object based and feature based in regard to how feature dimensions covary. When shapes covaried perfectly with a particular colour, statistical learning was object based: the expression of learning required the presence of both shapes and colours at test. However, when shape and colour were partially decoupled during learning, subjects showed robust statistical learning for each feature separately. Kok et al. (2013) manipulated human subjects’ prior expectations about visual motion stimuli using auditory cues to examine whether the learned priors would modify the visual stimulus representations. Subjects were asked to report the predominant motion direction of random dot motion patterns out of 5 possible directions. An auditory cue at the start of the trial indicated the distribution from which the visual stimulus would be drawn. For each cue (out of 2), one motion direction was more likely to be presented than the other 4. The results showed that the predictive cue induced a bias in the perception of the visual stimulus. Subjects were inclined to perceive motion as more similar to the direction predicted by the cue, and this effect was found
to strengthen over time. Moreover, subjects’ neural activity in early visual cortex areas, measured non-invasively using fMRI, was found to be equally affected by the auditory cue. Subjects’ sensory representations of the stimulus were significantly biased towards the direction predicted by the cue, and representations were more closely related to what subjects subjectively reported than to the actual presented stimulus.

Acerbi et al. (2012) asked human subjects to reproduce time intervals drawn from underlying temporal distributions of varying complexity, from uniform to bimodal while also varying the error mapping that determined the performance feedback. They found that subjects, facilitated by corrective feedback, were able to learn good approximations of unimodal distributions of time intervals, even for skewed distributions but struggled to learn multimodal distributions of timing intervals. In a subsequent study, Acerbi et al. (2014b) used a visuomotor task to examine the role of complexity of prior experience on decision making. Subjects were asked to find a specific target out of a number of potential targets and were given explicit knowledge about the prior probability of where the target might be. It was found that subjects’ performance was affected by statistical features of the priors but was largely independent of the class of the prior. The authors suggested that the statistical complexity of priors might affect the process of acquiring priors more than the process of computing with them.

### 2.2.4 How specific are learned priors?

Another open area of research concerning the learning of priors is that of specificity or transfer of the learning that is acquired. Is statistical learning very specific to the learned objects or do humans spontaneously transfer the acquired knowledge to similar objects? Using statistical learning of sequences of shapes, Turk-Browne and Scholl (2009) explored transfer across space and time and across temporal order. They found that learning of statistically defined temporal sequences could be expressed in static spatial configurations and that learning of statistically defined spatial configurations facilitated detection performance in temporal streams. Investigating the specificity of the prior for isotropy of shapes, Seydell et al. (2010) used two groups of stimulus shapes (diamonds and ellipses) with different distributions of aspect ratios, and two groups of stimulus with the same elliptical shape but different colours. Subjects were asked to judge the planar orientation of the stimulus (as in Knill, 2007a), and were able to learn distinct distributions of aspect ratios for each shape but failed to do so for the two colours.
Adams et al. (2004) showed that the ‘light-from-above prior’ can be temporarily modified with an active visual-haptic experience and that the resultant adaptation generalises to a different visual task. Furthermore, Adams (2007) measured subjects’ ‘light-from-above’ priors using visual search, shape perception, and reflectance-judgment tasks, and found that while there were substantial differences across subjects, the priors used by each subject for all three tasks were very similar. Kerrigan and Adams (2013) investigated whether subjects could learn two light priors differentiated by an illumination colour. Using the same visual-haptic experimental setup of Adams et al. (2004), subjects were trained to retain their baseline light prior distribution when illumination was red but shift their light prior 30° away when illumination was green (Figure 2.6). The results showed evidence of subjects learning two distinct priors for each colour cue. However, learning was not completely context-specific. The authors suggested that this might reflect robustness to temporary changes in cue contingencies as subjects would not have previously associated colour with illumination direction. This robustness could also explain the incomplete learning observed both in Kerrigan and Adams (2013) (10° instead of 30°) and in Adams et al. (2004) (11° instead of 30°). Finally, Adams et al. (2010) found that learned changes to subjects’ light priors after experimental training persisted several days after training despite exposure to a range of lighting conditions in every day activities. This suggests that learning was very context-specific. However, one of the authors, who participated in the experiment, observed transfer of learning across different experimental setups with various stimulus properties.

### 2.2.5 Can new relationships among variables be learned?

As we discussed, learning can be specific in the sense that it does not generalise to different stimulus positions or configurations, or to novel tasks. Michel and Jacobs (2007) investigated the notion that apparent limitations to learning can be explained by a failure of early perceptual processes to learn the underlying ‘structure’ of an environment or task. In particular, when viewed in a Bayesian network framework, their hypothesis was that early perceptual processes are capable of ‘parameter learning’, which translates to learning the prior and conditional probability distributions, but incapable of ‘structure learning’, which translates to learning the nodes and edges of the graphical structure in a Bayesian network. Figure 2.7 shows an example of a Bayesian network in the acquisition of new cue combination rules. The top node represents a scene vari-
Figure 2.6: Learning two light priors using illumination cues (adapted from Kerrigan and Adams, 2013). The shaded regions represent the fitted light priors, and the arrows represent the mean of each light prior. Baseline light prior: a subject’s proportion of responses that were convex as a function of shading orientation. Trained light priors: the coloured shaded regions indicate the range of stimulus shading orientations with convex haptic feedback during red and green visual-haptic training trials respectively. Final light priors: proportion of convex responses on red and green final test trials.
Figure 2.7: A Bayesian network representing the potential modifications in the acquisition of new cue combination rules (adapted from Michel and Jacobs, 2007). The reliability of Cue 1 is fixed, whereas the reliability of Cue 2 is decreasing. The dashed grey curve and solid black curve represent the conditional distribution for Cue 2 before and after learning respectively.
thereafter fixed in adulthood, and new structures are based on these original structures.

While it might be more difficult to learn associations between cues that are not normally codependent (Backus, 2011), it is not impossible (Ernst, 2007). Learning was observed even when the visual cue was ‘invisible’ to the observers (Di Luca et al., 2010). Kerrigan and Adams (2013) suggested that the visual system should represent the information that cues have been previously related in the environment but also unrelated. By doing so, the visual system avoids learning relationships with little ecological validity or learning becomes considerably slower. The authors further suggested that the divide between parameter and structural learning could be better approached as a continuum instead of a dichotomy.

The questions of the complexity and specificity of developing expectations are investigated experimentally in chapter 3 of this thesis. We modified the experimental paradigm of Chalk et al. (2010) by using differently coloured stimuli in order to present two distinct distributions of motion directions to subjects. The results of Chalk et al. (2010) showed that subjects were able to learn a single prior. Is it possible for subjects to learn two distinct priors? Is learning specific to each stimulus category or is there transfer between contexts? We expect that subjects will be able to use colour as a differentiation cue and learn two priors but learning is not expected to be completely context-specific. Also, colour and motion direction are not normally correlated in everyday environments. In what way will that affect learning?

### 2.2.6 What are the timescales of developing expectations?

Another related question that has been poorly explored is that of the timescales involved in developing expectations. The slow speed prior for example is hypothesised to develop over the course of the observer’s lifetime in an environment where objects are usually static and slow moving objects are more common than fast moving objects. Likewise, the ‘light-from-above’ prior develops over a lifetime exposure to sources of light, natural or artificial, coming almost exclusively from above the observer. On the other hand, we have already discussed many examples of learning contextual expectations in the time frame of an experimental session, from a few minutes to a few hours. In that sense, is a structural expectation just a contextual expectation applied continuously in ever more general situations until it becomes context-independent? In relation to this, it is important to understand how long expectations learned in an experimental setting persist over time. We have already discussed examples of learned expectations
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Persisting over days after training (Adams et al., 2010) and transferring to different tasks (Adams et al., 2004; Turk-Browne and Scholl, 2009).

Kim et al. (2009) investigated long-term statistical learning. They used a similar task to the one employed in Turk-Browne et al. (2005) and tested one group of subjects immediately after exposure to the stimulus and another group after an interval of approximately 24 hours. The results showed similar amounts of implicit learning in both groups, which suggested that statistical learning can persist at least over 1 day, even after only 5 minutes of exposure. Sotiropoulos et al. (2011a) investigated the potential plasticity of the slow speed prior in an experimental paradigm where no explicit feedback about motion directions was given. Subjects were shown a field of parallel lines moving in a direction that was either normal to the line or oblique to the line with equal chance, and were asked to report the direction of movement of the stimulus. One group of subjects was exposed to stimuli moving at high speeds, whereas a control group to stimuli of low speeds. At the start of the experiment both groups reported motion more often at normal directions for low contrast stimuli. After training over 5 successive days, the high speed group reported motion more often at oblique directions, while there was no change in the control group. An interesting aspect of the experimental results is that the high speed group showed two distinct phases of learning. A fast within-session learning component that was reset at the start of a new session, and a slow across-sessions learning component that persisted over successive days. There was evidence of limited 'fast' learning in the control group but absence of 'slow' learning. The authors suggested that the latter could be consistent with the need for a learning threshold to be exceeded for perceptual learning to occur (Seitz and Dinse, 2007). Perceptual learning refers to improvements in sensory abilities that occur with experience or after extensive training on a given task (Seitz and Watanabe, 2005). Perceptual learning can range from high-levels of visual processing, for example pattern recognition and visual search, to low-level processing of basic visual skills, for example contrast detection and orientation discrimination. An interesting idea proposed by Seriès and Seitz (2013) is that structural expectations could be understood in terms of changes in representations in perceptual areas (perceptual learning), whereas contextual expectations could correspond more to top-down influences from decision stages (statistical learning). These two aspects of learning could also mirror the different timescales involved in learning expectations from fast learning within a session that decays rapidly to slow learning that is preserved for several months to even years (Kami and Sagi, 1993).
Interestingly though there is evidence that there are differences in learning even looking specifically at short timescales. Chopin and Mamassian (2012) conducted two experiments using ambiguous test stimuli presented at regular intervals within a series of adapting gratings varying randomly between two orientations. In the first experiment, two test gratings were presented, one to each eye, and competed for perceptual dominance. Subjects had to report the dominant percept after exposure to non-rivalrous series of one to four gratings. A negative correlation effect was found at intervals of up to three minutes between preceding and test stimuli. However, the effect was reversed for longer intervals of 5 to 13 minutes. In the second experiment, a series of gratings of two possible orientations, separated by 40 degrees, were randomly presented, followed by a test patch, which subjects had to be report whether its orientation was closer to one of the two orientations. Unbeknownst to subjects, the orientation of the test grating was always exactly in-between the two presented orientations. Subjects were biased to perceive orientations away for recently presented stimuli (less than 2 minutes) and toward the orientations of stimuli presented further in the past (between 2 and 8 minutes). Raviv et al. (2012) used an auditory delayed comparison task to investigate how recent stimulus history affects perception. Subjects were asked to compare 2 sequential tones with frequencies drawn from a wide distribution and adapted using a staircase procedure to maintain similar accuracy across subjects. When both tones had higher pitches relative to past stimuli, subjects were more likely to report that the second tone was higher, while they were more likely to report the first tone when the two tones had lower pitches. This ‘contraction bias’, also found in a visual discrimination task (Ashourian and Loewenstein, 2011), was observed even when it was detrimental to performance. Moreover, it was found that only the most recent stimuli had an effect on performance. The authors argued that subjects might have not been able to compute the joint distribution of the stimuli or that the relatively small stimulus blocks (80 trials) might have not been enough to facilitate learning. It is unknown how the recent stimulus history would affect performance under longer exposure to distribution statistics.

Motor learning has been investigated extensively using error-based paradigms (Shadmehr et al., 2010). For example, an observer experiences a perturbation of her hand during a reaching movement due to a lateral displacement by a prism or a lateral force applied by a robot arm. In these paradigms, learning is well described by models that have identifiable learning and retention parameters (Smith et al., 2006). According to a normative Bayesian hypothesis, these parameters can change over time and in a
near-optimal manner (Kording and Wolpert, 2004). The optimisation algorithm that has been most investigated is the Kalman filter (Kalman, 1960), which computes a learning rate that depends on the variance of the prior estimate of the world relative to the variance of sensory observations of the world. Wei and Körding (2010) investigated whether learning rate data can be explained within the framework of Bayesian estimation. In a reaching task with adaptation to a visuomotor rotation, there was a reduction in learning rates when the position of a computer screen cursor, indicating hand position, was blurred, whereas learning rates increased when it was preceded by a block of trials with no visual feedback. For a Kalman filter, the learning rate should decrease as sensory noise increases and should increase after a period of no sensory information. Burge et al. (2008) also found that learning rates decreased and increased in a fashion predicted by measurement reliability and environmental statistics. Moreover, they found that responses to random perturbations were non-optimal for an environment with stationary statistics but could be for an environment with changing statistics. However, Krakauer and Mazzoni (2011) argued that there are examples where rates change even when they are not predicted by a Kalman filter (Krakauer et al., 2005), and suggested that alternative factors could be influencing learning rates in addition to uncertainty.

In chapter 6 of this thesis, we present an experimental investigation of how expectations of different timescales (from the last few trials to hours to long-term statistics of natural scenes) interact to alter perception. Using a novel visual search experimental paradigm, we compared the effect of expectations developed over a long sequence of trials, with exposure to stimuli in the very last few trials. We presented human observers with brief displays of low contrast stimuli and asked them to report the presence and exact position of the stimuli, while manipulating their expectations by presenting stimuli in some positions more frequently than others. We expected that observers would learn the statistics of the stimuli and improve their detection performance at the more probable stimulus positions, while they would also improve their performance at positions where a stimulus was very recently presented. We hypothesised that they would integrate the learned expectations with the very recent exposure in a near-optimal way in order to further enhance their performance. Consequently, we hypothesised that this would also lead to significantly more false detections at these positions.
Figure 2.8: Example of an experimental task and its generative model (adapted from Ma, 2012). Task: An observer is asked to detect a rightward tilted grating among leftward tilted distractors. Observation: The noisy observation $x_i$ follows a Gaussian distribution around the true orientation $s_i$ with standard deviation $\sigma_i$. Generative model: $c_1,...,c_N$ corresponds to whether a target is present or not for each position 1,...,$N$. An observer infers $c$ from observations $x_1,...,x_N$, which are dependent from true orientations $s_1,...,s_N$ in turn dependent from whether a target is shown in $c_1,...,c_N$.

2.3 Theoretical models of developing expectations

2.3.1 Probabilistic inference and learning

As we discussed in chapter 1, a Bayesian observer calculates the posterior probability about a state of the environment by combining the observed likelihood with her prior beliefs using Bayes’ rule (Figure 1.1). The joint distribution of observations and states that captures the statistical properties of the environment is also called the generative model. To maximise the potential gain (or minimise the potential loss), the observer should pick the state with the highest posterior probability. This is called maximum-a-posteriori (MAP) estimation. An example of a task and its generative model can be seen in Figure 2.8 (adapted from Ma, 2012). An observer has to detect a rightward tilted grating (target, oriented at $2^\circ$) among leftward tilted grating (distractors, oriented at $-2^\circ$). All inputs signals can have varying contrasts. The probability that a target is present is 50% and, if present, it is equally likely to be at any of the four possible positions. At position $i$, a noisy observation $x_i$ of the true orientation $s_i$ is drawn from a Gaussian distribution with standard deviation $\sigma_i$, which corresponds to the contrast of the stimulus.

The observer infers the presence or absence of a target by evaluating the noisy
measurements at each position. To accomplish that, the observer has to choose a decision rule, i.e. the function that connects the observations to an appropriate action. The observer can choose from a variety of different decision rules. Ma (2012) explores in great detail how different models of perception can range from probabilistic to non-probabilistic and from optimal to suboptimal, and how that affects the decision rule. In the visual search example, an optimal observer knows the level of uncertainty in each observation through the standard deviations in the measurements, and, so, can use an optimal probabilistic decision rule to report whether a target is present or not. The optimal decision rule can be computed analytically (see Ma et al., 2011). For $N$ stimuli, the observer reports that a target is present if:

$$\frac{1}{N} \sum_{i=1}^{N} \frac{4x_i}{\sigma_i^2} > 1$$  \hspace{1cm} (2.1)$$

otherwise, the observer reports that a target is absent. Every measurement $x_i$ is weighted by its inverse variance $\sigma_i$. Thus, noisier signals have a smaller effect on the decision than less noisy signals. However, if the observer believed incorrectly that all measurements were equally noisy, the rule would change to $\frac{1}{N} \sum_{i=1}^{N} \frac{4x_i}{\sigma^2} > 1$, where $\sigma_i$ is replaced by a common $\sigma$ for all stimuli. Thus, the decision rule is still probabilistic but now it is suboptimal and should lead to worse performance than the optimal rule.

Humans have been found to perform near-optimal probabilistic computations in many perceptual tasks from estimating a stimulus’ orientation (Girshick et al., 2011), speed (Weiss et al., 2002), or direction of motion (Chalk et al., 2010), to visual search (Ma et al., 2011) and movement planning (Hudson et al., 2007). Other examples of probabilistic inference can be seen in contour grouping mechanisms that link local edge elements into global contours (Geisler et al., 2001), in mechanisms of encoding complex scenes from lower-level visual features (Orbán et al., 2008), in causal learning in toddlers (Gopnik et al., 2004), and even in everyday cognition judgments such as predicting human life spans and movie run times (Griffiths and Tenenbaum, 2006).

2.3.2 Is the process of developing expectations optimal?

Bayesian probabilistic inference can often be optimal but not always. A Bayesian MAP estimation based on incorrect assumptions can be sub-optimal. Returning to the example of Figure 2.8, if the observer incorrectly assumed that a target is present in only 25% of trials (instead of 50%), the sensory evidence required to report the presence of a target would increase ($\frac{1}{N} \sum_{i=1}^{N} \frac{4x_i}{\sigma_i^2} > 3$). This would result in the observer
missing targets that otherwise would be correctly reported. Thus, the observer would behave sub-optimally even though she still accounted for varying standard deviations for each measurement ($\sigma_i$). Bias in human observers can be seen when the statistics of a task do not match the long term statistics of the environment. For example, the McGurk effect (McGurk and MacDonald, 1976) illustrates that introducing a small conflict between simultaneous auditory and visual speech cues can result in observers perceiving a third cue. The observer’s ‘default’ prior, obtained from the statistics of the natural environment, expects that synchronous audio and video originate from the same speech but that leads to biased percepts in the experiment. However, an observer’s use of such priors is typically regarded as optimal since natural statistics are unarguably more fundamental than experimental ones.

Sub-optimality in human behaviour can occur when the true prior distribution is difficult to learn. Eckstein et al. (2004) employed a perceptual learning paradigm to compare learning in human observers with that of an ideal Bayesian observer. Subjects were presented with an image containing one of 4 possible targets in one of 8 potential locations. The experiment was divided in blocks of 4 trials each. On each block, the target remained the same but the target’s location was randomised for each trial. On the first 3 trials, subjects were asked to report only the location of the target, and on the last trial of the block (4th trial) to also identify the target. At the end of the trial, subjects received feedback only about the target’s location until the end of the block where they were also told the identity of the target. The experimental results showed evidence of learning even within the timeframe of 4 trials (less than 1 minute), and subjects improved most from the 1st to 2nd trial in each block in agreement with an optimal observer. However, subjects’ learning was found to be slower than that of an optimal observer. For example, there was complete lack of learning on the 2nd trial when subjects’ answer to the 1st trial within a block was incorrect. This suggested that subjects might have been unable to use the location feedback to update their priors due to an inability to remember the input at the missed location. Thus, subjects exhibited imperfect visual memory (Luck and Vogel, 1997) in contrast to an optimal observer’s perfect visual memory. However, subjects still used the feedback in a positive manner by not updating their priors using incorrect information, and they resumed learning in the subsequent trials of the block. Overall, the modelling work suggested that human observers in contrast to an optimal observer relied more heavily on previous decisions than on the feedback.

As we discussed in 2.2.5, Raviv et al. (2012) used a two-tone comparison task to in-
vestigate how recent stimulus history affects perception and found that subjects failed to learn the joint distribution of the stimulus. The authors implemented two models to describe subjects’ performance: a Bayesian model that utilised a full prior distribution based on the stationary statistics of the experiment, and a simple ‘implicit memory’ model that utilised a single scalar to represent past stimuli. This scalar \( M \) is an exponentially weighted sum of the current and past stimuli and their respective encoding noises. According to the model, in trial \( t+1 \) after being presented with the first tone \( f_1 \), the subject updates the value of \( M(t) \) such that \( M(t+1) \) is a linear combination of the past value of \( M(t) \) with the present stimulus: 

\[
M(t+1) = (1 - \eta)(\log(f_1)) + n + \eta M(t),
\]

where \( \eta \) is the weight given to past stimuli and \( n \) is the noise associated with the encodings of \( f_1 \). The subject then instead of comparing \( f_1 \) with the second tone \( f_2 \), compares \( M(t+1) \) with \( f_2 \) and responds accordingly. This means that past values of \( f_2 \) do not contribute to \( M \), which reflects the dominance of past values of \( f_1 \) in the experimental data. The ‘implicit memory’ model provided comparably good fits to the experimental data as the full Bayesian model but it also matched the skewed contribution of very recent trials to performance found in the experimental data. The authors argued that the ‘implicit memory’ model provides a good compromise between signal detection theory (SDT) approaches, where no learning takes place, and a full Bayesian model, where all trials are equally informative, and shows how the system may incorporate expectations when unable to learn the underlying statistics of the environment or assumes that those are highly volatile.

Signal detection theory (SDT) ([Green and Swets, 1966](#)) involves treating detection of a stimulus as a decision-making process, determined in part by the nature of the stimulus, by how sensitive an observer is to the stimulus, and by cognitive factors. It has been a powerful approach with which to model simple detection or discrimination tasks, and SDT and Bayesian models can be quite similar in some of their properties. According to [Ma (2012)](#), we could distinguish SDT models from Bayesian models by investigating the notion of probabilistic computation. While SDT models are equivalent to optimal Bayesian models for simple detection and discrimination tasks, they tend to use non-probabilistic decision rules in more complex tasks. A non-probabilistic decision rule used extensively in SDT models is the maximum-of-outputs or max rule ([Verghese, 2001](#)). In the example visual search task, this decision rule corresponds to 

\[
\max_i x_i > k,
\]

where \( k \) is a constant criterion and \( x \) the observation. However, the rule has been shown to fail when uncertainty varies unpredictably ([Ma et al., 2011](#)). As [Ma (2012)](#) suggests, a probabilistic version of the max rule in this example could be
max_i(\frac{x_i}{\sigma_i}) > k, thus representing the level of uncertainty associated with the measurement. It is important to note here that the brain will eventually have to make crude approximations to perform inference when confronted with increasingly complex tasks. This could lead to a suboptimal model describing behavioural data better than the optimal one (e.g., in [Landy et al., 2007]). However, [Ma, 2010, p. 2318] speculates that "no task exists in which a suboptimal, non-probabilistic model outperforms an optimal, probabilistic one, because in realistic situations, taking into account uncertainty is a crucial element of good behavioral performance". Conducting experiments with tasks of greater complexity could be an important tool in investigating how prevalent probabilistic computation is in perception, and help disentangle between the SDT and Bayesian approaches.

Acerbi et al. (2014b) examined the role of complexity of the prior distribution in suboptimal decision making. Instead of subjects having to learn complex priors, the prior information was given to them explicitly. The authors systematically explored the sources of sub-optimality and variability in subjects’ performance by generating and comparing a set of models which assumed different sources of sub-optimality using a technique called factorial model comparison, introduced by [van den Berg et al., 2014]. They found that experimental results were best described by a Bayesian observer with a slightly mismatched representation of the likelihoods, a noisy estimation of the parameters of the prior, and a stochastic representation of the posterior. The complexity of the prior distribution did not significantly affect performance. However, reconstructed subjects’ priors generated by the models showed certain tendencies of subjects when using priors of different complexity. For example, non-Gaussian, narrow-peaked distributions induced worse performance than broad and smooth distributions, and subjects overestimated the width of the narrower distributions. These findings again indicate that the characteristics of sensory input can produce subtle differences between the behaviour of a human observer and that of an optimal observer even when they are not significantly affecting the observer’s performance.

Chalk et al. (2010) constructed a simple Bayesian model that provided a good fit of subjects’ estimation biases. The model assumed that, on each trial, subjects probabilistically combined their sensory evidence, which had the form of a noisy measurement of motion direction, with a learned prior distribution of expected motion directions (Figure 2.9). The shape of subjects’ learned prior was found to be qualitatively similar to the distribution of the presented stimulus. The model also provided correct predictions for subjects’ behaviour when no stimulus was presented. The authors argued that
Chapter 2. Experimental and theoretical approaches to developing expectations in visual perception

### Figure 2.9: Bayesian model of Chalk et al. (2010)

An observer makes a noisy observation ($\theta_{obs}$) of the true stimulus motion direction $\theta$. The posterior distribution is calculated by combining the noisy observation with the prior belief about likely motion directions probabilistically. The mean of the posterior distribution provides a perceptual estimate ($\theta_{perc}$). The final response of the observer is affected by additional ‘motor noise’ ($\theta_{est}$).

While ‘hallucinating’ motion in the absence of stimulus is not ‘ideal’ in everyday interactions with the environment (Seitz et al., 2005), such behaviour is expected from an Bayesian observer who seeks to minimise her estimation error in the context of the psychophysical experiment. The model is described in detail in section 3.4.1 of this thesis.

An extension of this Bayesian model is implemented in chapter 3 to investigate the optimality of subjects’ learning in the psychophysical experiment of two motion distributions differentiated by colour. We test a series of models with different priors and show how closely they fit the experimental results. Then, we compare them to a model of a near-optimal Bayesian observer and discuss the degree in which the best matching models differ from the near-optimal one. In chapter 4, an online learning Bayesian computational model is used to investigate in more detail the connection between the complexity of the experimental task and the sub-optimality in the results. In particular, whether subjects were in fact behaving sub-optimally or whether their behaviour can be explained given the specific parameters of the task and the two distribution that subjects had to learn. The model was used to predict changes to the experimental procedure that would facilitate subjects’ learning of the complex priors, and this predictions were tested in a new experiment.

2.3.3 Neural substrate of expectations

While Bayesian models have been successful in describing psychophysical experimental results, there is a difficulty in translating these models into potential neurobiological...
mechanisms (Colombo and Seriès, 2012). Likewise, even though studies have investigated how learning affects cortical representations (Buonomano and Merzenich, 1998; Gilbert et al., 2009), there is little direct electrophysiological evidence that learning is statistically optimal. Finally, there is no wide consensus on the neural substrate of expectations.

One proposal is that expectations correspond to an increase in the activity of neurons. Electrophysiological studies have examined short-term learning of expectations in regards to its effect on neural activity. Carpenter et al. (1995) conducted an experiment in which human observers would make eye movements to peripheral visual stimuli during blocks of trials. During each block, the probability that a stimulus would appear in any trial was kept constant, from very unlikely to very likely. Subjects’ response times were much shorter in the likely trials in comparison to the unlikely trials. Researchers in several laboratories recorded the activity levels of single neurons in monkeys performing the same experiment (Basso and Wurtz, 1997; Dorris and Munoz, 1998; Platt and Glimcher, 1999) and found that the activity level of neurons was enhanced for stimuli or saccades with higher prior probability in the superior colliculus (Basso and Wurtz, 1997) and lateral intraparietal (LIP) areas (Platt and Glimcher, 1999). That was true even before the stimulus was presented (Dorris and Munoz, 1998) or even before the subject received an explicit instruction on which of two possible stimuli was the target (Platt and Glimcher, 1999). However, whether these effects would also be observed at earlier cortical areas, such as in the media-temporal (MT) area, has not yet been confirmed.

A different approach suggest that expectations can lead to suppression of neural activity. Summerfield et al. (2008) were the first to suggest that repetition suppression, a phenomenon in which repeated presentations of a stimulus elicit weaker neural activity (Grill-Spector et al., 2006), could be explained by expectation suppression. Using fMRI, the authors found that expected repetitions of faces elicited stronger suppression than unexpected repetitions. This finding has been replicated in a number of studies and different modalities (e.g., auditory tones, Todorovic et al., 2011), however, it was not replicated by Kaliukhovich and Vogels (2011) using fractal patterns and natural stimuli, which suggests that the effect might not generalise over all stimuli.

While the increase in activity of single neurons and the decrease of activity over large populations of neurons during expected stimuli might seem contradictory, a simple explanation for these observations is that neurons selective to expected stimuli might become more sensitive and active, whereas neurons selective to unexpected stim-
uli might produce dampened responses. Inhibition can in fact ‘sharpen’ the tuning of cortical neurons to preferred stimuli (Isaacson and Scanziani [2011]), something that would also explain the reduced overall neural activity. In agreement to this, [Kok et al. (2012)] found that when an auditory cue predicted the orientation of an upcoming grating, neural response amplitudes in V1 were reduced but stimulus representation, as measured by multivariate pattern analysis (MPVA), was improved. Finally, [de Lange et al. (2013)] used magneto-encephalography (MEG) in human observers to measure neural activity in the visual and motor cortices when deciding over the direction of motion in moving random-dot displays. Subjects had to report the direction of motion (left or right) by using the index finger of their respective hand. The authors induced contextual expectations by providing 3 types of probabilistic cues about the motion direction of the stimulus; predictive, non-predictive (neutral), and counter-predictive. They found that expectations strongly altered the state of both visual and motor cortices before stimulus presentation. On the subset of trials where the cue was non-predictive, the authors found spontaneous biases in the motor cortex that could partly predict subjects’ decisions. Interestingly, these biases were in part affected by the choice a subject made in the preceding trial; the direction chosen in the last trial would bias the decision in the current trial towards the same direction. Moreover, these biases decreased linearly with increasing motion coherence, and were not present when conditioning on the previous cue. The latter suggests that the bias originates from the previous decision rather than the previous cue.

An interesting notion proposed by [Fiser et al. (2010)] is that background patterns of neuronal activity might represent prior information learned over lifetime experience. As we discussed, the posterior distribution is the combination of observed stimuli and prior beliefs. In the absence of stimulus though, the posterior is just the prior, which is represented by the spontaneous activity of the system. [Berkes et al. (2011)] compared spontaneous neural activity in the primary visual cortex of awake ferrets at different stages of development, and observed an increasing similarity between that activity and activity evoked by natural images. However, it is yet unclear whether spontaneous activity is mostly shaped by visual experience or by developmental processes, and whether experimentally induced changes to structural expectations, as for example in [Sotiropoulos et al. (2011a)], or contextual expectations can also be observed in spontaneous activity.
2.3.4 Attention and expectation

Superficially, the goals of attention and expectations appear to be similar. Selective attention prioritises sensory inputs according to their relevance to current goals (Desimone and Duncan, 1995). It is not yet commonly accepted how the terms ‘attention’ and ‘expectation’ exactly differ and it is not unusual for both be used to express the same behavioural effects. However, a way to distinguish between the two is to consider expectations in terms of the statistical properties of stimuli, and attention in terms of the relevance of stimuli to current goals. Summerfield and de Lange (2014) argue that a stimulus might be probable or improbable irrespective of its relevancy to behaviour. In section 2.2.1, we already discussed how statistical learning does not require attention but can be modulated by it. On the other hand, probabilistic cues have been used to direct attention to a location that a stimulus is expected (Posner, 1980). Thus, expectations can guide attention but attention is not a prerequisite for expectations to affect perception.

It might be particularly useful to distinguish the two in their role in optimising the visual system’s internal model. Chalk et al. (2013) proposed a Bayesian model in which goal-oriented attention and expectations refer to adaptation of priors to changes in reward statistics and stimulus statistics respectively. According to the model, the brain learns a probabilistic model that predicts how both the sensory input and reward received for performing different actions are determined by a common set of hidden causes (Sahani, 2004). The authors employed a simple visual detection task (Figure 2.10) to show how experimentally observed attention-dependent changes to visual neuron responses can be defined as a consequence of optimal adaptation towards a given task. An observer is presented with one or more stimuli at various locations and has to report whether a stimulus is present at a single target location. Correct responses are followed by a reward, whereas incorrect responses receive no reward. Stimuli are equally likely to be presented at all locations. The observer learns the target location by using the received feedback and updating her reward model, and directs attention towards the target by updating her sensory model.

The model predicts that attention-dependent changes to the perceptual prior will induce an estimation bias toward task-relevant stimulus features. Thus, estimation biases observed in Chalk et al. (2010) due to expectations induced by manipulating the stimuli statistics, should be replicated by changes to the behavioural task alone.

In chapter 5, we describe a project that aims to investigate whether selective manip-
Figure 2.10: Schematic of the detection task in Chalk et al. (2013). An observer is presented with one or more stimuli at various locations and has to report whether a stimulus is present at a single target location. The observer gives a response indicating whether a stimulus is present at a target location, based on her noisy sensory input and learned model of reward. Correct responses are followed by a reward.

ulation of rewards can affect an observer’s perceptual performance in a similar manner to manipulating the statistical properties of the presented stimulus. We modify the experimental paradigm of Chalk et al. (2010) so that subjects get rewarded on their accuracy in the estimation task. While stimuli are equally likely to be presented at all directions, some directions are rewarded more than others. We expect subjects to develop an internal model of the sensory input and reward scheme and exhibit an attractive bias towards the more rewarded directions in their estimation performance.
Chapter 3

Complexity and specificity of experimentally induced expectations in motion perception

3.1 Introduction

In this chapter, we use a variation of the experimental paradigm in Chalk et al. (2010) to investigate the complexity and specificity of the priors that can be learned. Instead of using one colour for the dots and one distribution for the motion directions, we now use two colours for the dots (green and red) corresponding to two different distributions of motion directions. We tested 2 different pairs of distributions over 2 experiments. In Experiment 1, one distribution was uniform over 9 possible motion direction, while in the other distribution 2 directions were much more frequent than the remaining 7. The combined distribution of all stimuli was bimodal. In Experiment 2, in one distribution again 2 direction were more likely to be presented (but to a lesser extent than in Experiment 1), while the other distribution was complementary to the first one, so that the combined distribution for all stimuli was uniform over all directions.

We ask whether subjects are able to form distinct expectations for the two different colours or whether subjects can form only a colour nonspecific prior. Colour information is mostly processed through the ventral stream while motion information is processed primarily through the dorsal stream. Our hypothesis is that a suboptimal integration of the two information streams may provide insight on the mechanisms underlying the formation of priors and their constraints. This work has been published in Gekas et al. (2013). One of the reviewers of the paper argued that the results of Exper-
iment 2 were messy and could be clarified by using more discriminable distributions. An additional psychophysical experiment was conducted to address that but the results of this experiment were inconclusive regarding the specificity of learning, so it was not included in the final submission. A description of this experiment and its results can be found in Appendix A. Supplementary figures not included in the Chapter can be found in Appendix B.

3.2 Methods

3.2.1 Stimuli & subjects

The motion stimuli consisted of a field of coloured dots, either red or green, with a density of 2 dots/°², moving coherently at a speed of 9°/sec within a circular annulus that had a minimum and a maximum diameter of 2.2° and 7°, respectively. They were generated using the Matlab programming language with the psychophysics toolbox (Brainard, 1997; Pelli, 1997) and displayed on a Mitsubishi DiamondPro 750SB monitor with a resolution of 1024 x 768 at 100 Hz. Subjects viewed the display in a darkened room at a viewing distance of 70 cm. The display luminance was calibrated and linearised with a Cambridge Research Systems Colorimeter separately for each colour. The background luminance was set to 5 cd/m².

22 naive subjects with normal colour acuity and normal or corrected vision were recruited from the University of Edinburgh for Experiment 1 and 23 subjects for Experiment 2. All subjects gave informed written consent in accordance with the University of Edinburgh School of Informatics Ethics Panel and the Declaration of Helsinki and received monetary compensation.

3.2.2 Procedure

At the beginning of each trial, a central white dot (0.15° diameter) was presented as a fixation point (Figure 3.1). Then, the field of dots was presented in an annulus around the fixation point along with a grey bar that projected out from the central dot. The initial angle of the bar was randomised for each trial. Subjects reported the direction of motion by rotating the bar using a mouse (estimation task). The display cleared when either the subject clicked on the mouse button, validating her choice, or when a period of 3000 ms passed. After the estimation response, there was a 200 ms delay before the detection response screen was shown. The screen was divided into three equal parts.
by three lines originating from the center of the screen and ending at the borders of
the screen, resulting in an upper right, a lower right, and a left compartment, which
displayed the text RED DOTS, GREEN DOTS, and NO DOTS, respectively. Subjects
moved a cursor to the appropriate compartment on the screen to indicate their choice
and validated with a mouse click. The cursor then flashed green or red for a correct
or an incorrect choice, respectively. After the detection task was complete the screen
was cleared, and the next trial began after a 400 ms delay. Subjects were presented
with block feedback on the estimation task every 20 trials: a message was shown on
the screen indicating their average performance in terms of their estimation error in the
previous 20 trials.

3.2.3 Design

The experiment consisted of two sessions, lasting around 1 hr each, with each session
comprising 765 trials. The two sessions were taken over successive days. The stim-
uli were presented at four different contrast levels and two colours (red and green),
all randomly interleaved. There were 225 trials for each colour where the contrast
was determined using 3/1 staircases on detection performance (one staircase for each
colour). Additionally, there were 45 trials for each colour where the stimuli had the
highest contrast level (high contrast) and 225 trials where no stimulus was presented
(zero contrast). For the two staircased contrast levels, the direction of motion could be
0°, ±8°, ±16°, ±32°, ±48°, or ±64°, with respect to a central reference angle. At the
highest contrast level, the dots were given random directions, even outside the nine di-
rections mentioned, in order to emphasise that the estimation task is continuous rather
than a categorical decision out of nine alternative directions.

3.2.3.1 Stimulus distributions of Experiment 1

Depending on their colour, the dots could move according to one of two different di-
rection distributions: uniform or bimodal. In the uniform condition, all nine directions
were equally likely to be presented in each session or 25 trials per direction per session,
whereas in the bimodal condition, there were 95 trials per session with direction -32°
and +32° and five trials per session for each of the other directions of motion (Figure
3.2A). The combined distribution was identical to the one used by [Chalk et al. (2010)]
with the difference that the total number of trials was slightly lower. The distributions
of the two colours were counterbalanced between subjects in order to avoid any biases
Figure 3.1: Experimental procedure. Subjects were presented with a fixation point followed by the motion stimulus and the response bar, which they rotated to indicate their perceived direction of motion. After a period of 3 seconds or the press of the mouse button, the screen was cleared and divided into three separate sections. Subjects clicked in the appropriate section to indicate their choice.
caused by colour selection or colour sensitivity.

### 3.2.3.2 Stimulus distributions of Experiment 2

The stimulus distributions of Experiment 2 were chosen so that the combined distribution over both colours was uniform. The first distribution was bimodal, similar to the one used in Experiment 1, while the second distribution was complementary to the first one, having its peaks shifted by 32° (Figure 3.2B). For convenience, we refer to the latter distribution as *trimodal*. The trimodal distribution had 40 trials per session for directions 0° and ±64°, four trials per session for directions ±32°, and 24 trials per session for each of the other directions. The bimodal distribution had 44 trials per session for directions ±32°, eight trials per session for directions 0° and ±64°, and 24 trials per session for each of the other directions. The distributions of the two colours were counterbalanced between subjects in order to avoid any biases caused by colour selection or colour sensitivity.

### 3.2.4 Data analysis

As detailed above, the presented directions were symmetrical around a central motion angle randomly chosen for each subject. This symmetry allowed us to average the results for stimuli moving to either side of the central motion direction. Unfolded versions of the data can be found in Appendix B of this thesis (Appendix B, Figures B.2 and B.6).

The first 200 trials from each session were excluded from the analysis in order to allow the staircases to reach stable contrast levels (Appendix B, Figure B.1). Subjects’ performance was evaluated after their first session to eliminate those that could not perform adequately in the estimation task. Out of the original 22 subjects of Experiment 1, 4 failed to have a mean absolute estimation error less than 30° in the highest contrast trials, and they were not asked back for a second session. The remaining 18 subjects passed that criteria for two sessions, and their data were analysed. Responses to the highest contrast stimuli were disregarded from the analysis, and they were used only as a performance benchmark.

Subjects were significantly better than chance in reporting the colour of the stimulus even at low contrast (82% correct on average). However, they still made an error about colour in a significant number of trials. Because those cases were ambiguous in terms of our hypothesis regarding colour-specific expectations (i.e., whether subjects...
Figure 3.2: (A) Probability distributions of motion directions for Experiment 1. In the uniform condition, all directions were equally presented, while in the bimodal condition, two directions, 32° away from the central direction, were presented in a larger number of trials than other directions. The combined distribution was identical to the one used in Chalk et al. (2010). (B) Probability distributions of presented motion directions for Experiment 2. In the trimodal condition, three directions, the central direction along with directions 64° away from it, were presented in a larger number of trials than other directions, while in the bimodal condition there were two directions, 32° away from the central direction, more frequently presented. The combined distribution was uniform. For both experiments, the distributions of the two colours were counterbalanced between subjects and the central motion direction was randomised for each subject.
would be using expectations corresponding to the stimulus colour or to the reported colour), these trials were removed from our analysis.

In the estimation task, the variance of subjects’ direction estimates was large. Similarly to Chalk et al., we hypothesised that this was due to the fact that in some trials subjects made completely random estimates, thus increasing the variance of motion direction estimates quite substantially. To account for this, we fitted the estimation responses of each subject to the distribution $(1 - a) \cdot V(\mu, \kappa) + a/2\pi$, where $a$ is the proportion of trials where the subject makes random estimates, and $V(\mu, \kappa)$ is a von Mises (circular normal) distribution with mean $\mu$ and width $1/\kappa$, given by:

$$V(\mu, \kappa) = \exp(\kappa \cos(\theta - \mu)/(2\pi I_0(\kappa)))$$

We first convert the angle difference values (angle reported - angle of stimulus presentation) from degrees to radians, and we use the arctangent function to constrain the range to $(-\pi, \pi]$. The parameters were chosen by maximising the likelihood of generating the data from the distribution. Subjects’ estimation mean and standard deviation were taken as the circular mean and standard deviation of the von Mises distribution. The use of this approach allows for more consistent and significantly smaller variances across subjects, motion directions, and contrasts than merely averaging over trials without compromising the qualitative aspect of the results.

In trials where no stimulus was presented, we aggregated all subjects’ responses and fit the population estimation performance using a linear combination of 6 circular normal distributions. The mean (peak) and variance (width) of each distribution were fit by maximising the log likelihood of generating the data from the combined distribution. The use of a small number of distributions (2-3) was rejected in order to not bias the combined distribution towards a bimodal or trimodal distribution. A large number of distributions (e.g., 15) was also rejected in order to avoid over-fitting due to the small number of reported stimuli by some subjects. The final number (6) was chosen as a middle ground between avoiding over-fitting and not biasing towards a specific combined distribution. We did not observe any difference when we used 7 distributions and we did not expect any qualitative difference for numbers from 5 to 8. However, a more appropriate procedure to select the number of distributions would have been to use a cross-validation technique such as leave-one-out cross-validation (Arlot et al., 2010). This procedure makes a more efficient use of the available data but it can be very time consuming to implement.

For 11 subjects of Experiment 1, the motion direction of the red dots followed the uniform distribution and the directions of green dots the bimodal one, whereas for
seven subjects this was reversed. There was no significant effect of colour on the estimation bias, given a particular distribution ($p = 0.37$ and $p = 0.52$) for the uniform and bimodal distributions, respectively, one-way analysis of variance (ANOVA), so the data was combined across all subjects. Additionally, there was no significant interaction between experimental session and motion direction on the bias and standard deviation ($p = 0.65$ and $p = 0.46$, respectively, four-way within-subjects ANOVA), so the data across sessions was combined as well.

We performed the same analysis for Experiment 2. 23 observers participated in the first session of Experiment 2. 2 of them were excluded from the second session, as their estimation error in high contrast trials was greater than 30° (our pre hoc criterion), and 3 of them ignored the estimation task completely. The remaining 18 subjects returned for the second session, and their data were used in the results.

For 9 subjects of Experiment 2, the motion direction of the red dots followed the trimodal distribution and the directions of the green dots the bimodal one, whereas for 9 other subjects this was reversed. There was no significant effect of the colour presented on the estimation bias ($p = 0.73$ and $p = 0.6$ for the trimodal and bimodal distributions, respectively, one-way ANOVA), so the data was combined across all subjects. Additionally, there was no significant interaction between the experimental session and motion direction on the bias and standard deviation ($p = 0.4$ and $p = 0.55$, respectively, four-way within-subjects ANOVA), so the data across sessions were combined as well.

### 3.3 Results

#### 3.3.1 Motion direction estimates when a stimulus was presented

##### 3.3.1.1 Experiment 1

We asked whether the more frequently presented directions of the bimodal distribution would bias the subjects’ estimation performance and whether that bias would be present only in the bimodal condition or in both conditions. We first analysed the estimation responses obtained by averaging over all trials irrespective of the colour condition. These results showed a distinctive pattern very similar to the one reported by Chalk et al. (2010) (Figure 2.5C), which is expected if subjects are biased towards perceiving motion directions as being more similar to the most frequent directions than they really are (Figure 3.3A). Estimates of the central motion direction were largely unbiased, whereas estimates of ±16° and ±48° were positively and negatively biased,
respectively. This indicates an attractive bias, which, however, is not centered on ±32° (the most frequent directions) but slightly shifted (to around ±40°). Finally, estimation responses for stimuli moving at ±64°, which lies at the largest distance from the most frequent directions, were significantly biased towards more central directions.

There was a significant effect of motion direction on the estimation bias \((p < 0.001,\) two-way within-subjects ANOVA between motion direction and subjects), and the estimation bias of subjects at ±16° and ±48° was significantly larger and smaller, respectively, than the bias at ±32° \((p = 0.043\) and \(p = 0.001,\) signed rank test). This verified that subjects made estimates that were closer to the most frequently presented directions than the actual directions of the stimulus.

We next explored whether the bias towards the most frequently presented motion directions was found in both uniform and bimodal conditions or whether subjects behaved differently for the two conditions. The results showed that the estimation bias for the uniform condition closely resembles the bias for the bimodal condition (Figure 2b). Figure 2b (inset) shows the estimation biases predicted by an ideal observer that has learned the true statistics of the stimuli. There was a significant effect of motion
direction on the estimation bias for both conditions ($p < 0.001$ for both conditions, two way within-subjects ANOVA), and direct comparison of the estimation biases between the two conditions showed that there was no significant difference between them ($p = 0.1$, three-way within-subject ANOVA between motion direction, colour condition, and subjects). Additionally, for the uniform condition, the estimation bias of subjects at $\pm 16^\circ$ was significantly larger than the bias at $\pm 32^\circ$ ($p = 0.012$, signed rank test), and the bias at $\pm 48^\circ$ was significantly smaller than the bias at $\pm 32^\circ$ ($p = 0.047$, signed rank test). This suggests that subjects tended to perceive motion direction as being more similar to $\pm 32^\circ$ than it really was independently of the colour of the dots. There appears to be a large positive bias in the bimodal condition at $0^\circ$. However, the number of trials is very small for this condition and bootstrap analysis indicates that the difference between biases at $0^\circ$ between the two conditions is in fact not significant (Appendix B, Figure B.3A).

In accordance with [Chalk et al. (2010)], in Experiment 1, the standard deviation at the most frequently presented directions was lower than at other directions (Figure 3.4B). Overall, there was a significant effect of motion direction on the estimation standard deviation ($p = 0.017$, two-way within-subjects ANOVA between standard deviation and subjects). The standard deviations showed no significant difference between the two conditions ($p = 0.08$, three-way within-subjects ANOVA between standard deviation, colour condition, and subjects).

### 3.3.1.2 Experiment 2

Looking at the results of Experiment 2, when a stimulus was presented and the data was pooled across colour conditions, we found that, on average, subjects’ motion estimation performances did not vary significantly with motion direction (Figure 3.5A, $p = 0.29$, two-way within-subjects ANOVA between motion direction and subjects). This was not unexpected; because the combined distribution of the stimuli was uniform, potential biases in the estimation of each colour condition might have cancelled each other out when averaged. There was no significant effect of motion direction on the estimation bias for both conditions ($p = 0.12$ and $p = 0.15$ for the trimodal and bimodal, respectively, two-way within-subjects ANOVA), but there was a significant difference between the estimation biases for the two colour conditions ($p = 0.046$, three-way within-subjects ANOVA between motion direction, colour condition, and subjects, Figure 3.5B). However, these biases were weaker than in Experiment 1. The largest difference between the conditions was at $\pm 48^\circ$, where, on average, estimates
were positively biased for the trimodal condition and slightly negatively biased (or unbiased) for the bimodal condition. Additionally, at ±64°, estimates were largely unbiased for the trimodal condition but negatively biased for the bimodal condition. In contrast, at 0° (respectively ±16°), subjects’ estimates were negatively biased (resp. unbiased) for both conditions. Figure 3.5B (inset) shows the estimation biases predicted by an ideal observer who has learned the true statistics of the stimulus. These results suggest that the subjects’ motion direction estimates were approximately biased towards the most frequent directions for each colour condition for outwards angles (i.e., 32° and 64°, respectively with an outwards shift for the bimodal condition) but dominated by an attraction towards the central direction for small angles, independently of the colour condition.

In Experiment 2, there was a significant effect of motion direction on the estimation standard deviation (Figure 3.4B, \( p < 0.001 \), two-way within-subjects ANOVA between standard deviation and subjects). The highest values were at ±16° while the lowest were at ±64°. On average, stimuli closer to the central direction produced larger standard deviations than those further away. There was no significant difference between the standard deviations for the two colour conditions (\( p = 0.23 \), three-way ANOVA).
Figure 3.5: (A) Subjects’ mean estimation bias for Experiment 2 is plotted against presented motion direction. (B) Subjects’ mean estimation biases for Experiment 2 separated for the trimodal and bimodal conditions are plotted against presented motion direction. Inset: expected biases if subjects use a prior that approximates the stimulus statistics. Here, the prior has modes centered on the most frequent directions, and the widths of the prior distributions and of the sensory likelihoods correspond to the average values across subjects. The red and green vertical dashed lines correspond to the most frequently presented motion directions for the red and green conditions (0° and ±64°) and ±32°, respectively. Results are averaged over all subjects and error bars show within-subject standard error.

within-subjects ANOVA between standard deviation, colour condition, and subjects).

3.3.2 Motion direction estimates when a stimulus was not presented

3.3.2.1 Experiment 1

In Experiment 1, on average, subjects reported seeing a stimulus in 8.53% ± 3.95% of the trials when no stimulus was presented. When subjects reported detecting a stimulus, they reported the colour of the uniform condition in 46.4% of the trials and the colours of the bimodal condition in 53.6% of the trials. We divided all subjects’ estimation responses into three sets: trials where they reported detecting stimulus of the uniform condition, trials where they reported detecting a stimulus of the bimodal condition, and trials where they reported detecting no stimulus. We fit a linear combination of six circular normal distributions to each data set and for all the combined data. We show the data along with the fitted distributions for the sets where subjects reported detecting a stimulus of each condition (Figures 3.6A & 3.6B). Detailed de-
scriptions of the distributions can be found in Appendix B (Figure B.6). In order to compare statistics of the distributions, we used a Bootstrapping analysis. The data for each condition were resampled with replacement and distributions were fit to each data set. The process was repeated 10,000 times, and 95% percentile confidence intervals were calculated for each condition. A direct comparison of the folded distributions can be seen in Figure 3.6C.

The results suggest that subjects were strongly biased to report motion in the most frequently presented directions when no stimulus was presented but they reported detecting a stimulus. A possible explanation for this behaviour could be that subjects automatically moved the estimation bar towards one of the two most frequently presented directions, irrespective of their response in the detection task. However, such a response bias could be ruled out: subjects were not significantly more likely to move the estimation bar close to the frequent directions on trials where they reported seeing no stimulus. There was no significant difference between the subjects’ estimation behaviour when reporting different colours, and the peaks of the combined distributions for both conditions were close to the frequently presented directions (±32°) but shifted slightly outwards, closer to ±36°, to a greater degree for the uniform condition. These results largely replicate those of Chalk et al. (2010) but seem to suggest that the learned perceptual biases may be largely colour invariant.

3.3.2.2 Experiment 2

In Experiment 2, on average, subjects reported seeing a stimulus in 10.34% ± 9.1% of trials when no stimulus was presented. Subjects reported seeing the colour corresponding to the trimodal condition in 49.9% of the trials and the colour corresponding to the bimodal condition in 50.1% of the trials. We divided all subjects’ estimation responses into three sets: trials where they reported detecting stimulus of the trimodal condition, trials where they reported detecting stimulus of the bimodal condition, and trials where they reported detecting no stimulus. We fit a linear combination of six circular normal distributions to the estimation performances for each data set and for all the combined data. Figure 3.7 presents the data along with the fitted distributions for the sets where subjects reported detecting a stimulus of each condition (Figures 3.7A & 3.7B). Detailed descriptions of the distributions can be found in Appendix B (Figure B.6). As in Experiment 1, we used a Bootstrapping analysis to compare the statistics of the distributions. A direct comparison of the folded distributions can be seen in Figure 3.7C.
Figure 3.6: Subjects’ responses in trials where no stimulus was presented but they reported detecting a stimulus of the (A) uniform condition or (B) bimodal condition for Experiment 1. The vertical grey lines correspond to all the data points (estimation response) pooled across subjects and the solid coloured lines to fitted distributions. (C) Fitted response distributions for trials of Experiment 1 where subjects reported the colour of the uniform distribution (red), the colour of the bimodal distribution (green), trials where they did not detect a stimulus (black), and for all trials (blue). The vertical dotted line corresponds to the two most frequently presented motion directions (±32°). Error bars show 95% confidence intervals.
The results suggest that subjects were strongly biased to report motion around \( \pm 54^\circ \) when no stimulus was presented but they reported detecting a stimulus. As in Experiment 1, subjects were not significantly more likely to move the estimation bar close to those directions on trials for which they reported seeing no stimulus. Here though, there are differences between the subjects’ estimates depending on the colour they reported. The trimodal and bimodal shapes of the distributions resemble the stimulus distributions for the two conditions. It was significantly more likely for subjects to report the colour of the trimodal condition at 0\(^\circ\) and non-significantly at \( \pm 64^\circ \), while it was significantly more likely for them to report the colour of the bimodal condition at \( \pm 32^\circ \). This suggests that when no stimulus was presented but subjects reported perceiving one, they were biased to make direction estimates consistent with the most frequent directions of the colour condition they reported. However, the peaks of the fitted distributions were not exactly centered at the frequent directions but shifted (\( \pm 59^\circ \) for the trimodal and \( \pm 44^\circ \) for the bimodal condition), consistent with the estimation biases when a stimulus was presented. The probability of reporting the stimulus of the trimodal condition at 0\(^\circ\) was lower than the probability at \( \pm 64^\circ \).

We also assessed the tendency for subjects to make estimates close to the most frequent directions relative to other directions by multiplying the probability of estimation within 8\(^\circ\) of 0\(^\circ\) and of \( \pm 64^\circ \) for the trimodal distribution and of \( \pm 32^\circ \) for the bimodal distribution by the total number of 16\(^\circ\) bins. This probability ratio \( p_{rel} \) would be equal to 1 if estimation was equally likely between the most frequently presented directions and other 16\(^\circ\) bins. It is possible to investigate how quickly these biases developed by calculating the probability ratio for individual subjects every 100 trials for both sessions (including all responses up to that point, Appendix B, Figure B.9). For the bimodal condition, the median value of \( p_{rel} \) was significantly larger than 1 at the most frequently presented directions of that distribution (\( \pm 32^\circ \)) after only 200 trials of the first session. On the other hand, for the trimodal condition it took approximately 400 and 900 trials for the probability ratio to become significantly larger than 1 for the most frequently presented directions of that distribution (0\(^\circ\) and 0\(^\circ\) and \( \pm 64^\circ \), respectively), suggesting that it may have taken longer to learn the trimodal distribution. Also, the probability ratios for the most frequently presented directions of the opposite distribution (\( \pm 32^\circ \) for the trimodal and 0\(^\circ\) and \( \pm 64^\circ \) for the bimodal) were never significantly larger than one.

These results suggest that colour information was used when learning the direction distributions and support the postulate that the lack of colour specificity found in
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Figure 3.7: Subjects’ responses in trials where no stimulus was presented but they reported detecting a stimulus of the (A) trimodal condition or (B) bimodal condition for Experiment 2. The vertical grey lines correspond to all the data points (estimation response) pooled across subjects and the solid coloured lines to fitted distributions. (C) Fitted response distributions for trials of Experiment 2 where subjects reported the colour of the trimodal distribution (red), the colour of the bimodal distribution (green), where they did not detect a stimulus (black), and for all trials (blue). The red and green vertical dotted lines corresponds to the most frequently presented motion directions for the trimodal and bimodal distributions (0° and ±64°) and (±32°), respectively. Error bars show 95% confidence intervals.

Experiment 1 was due to a transfer of information between the colours rather than an inability for the system to use the colour information when present. To better understand these results we applied several models to the data.

3.4 Modelling

Chalk et al. (2010) used two classes of models to understand how subjects’ expectations may be combined with the presented stimulus to produce the observed behaviour. The first class assumed that subjects developed response strategies unrelated to perceptual changes, while the second class assumed that subjects used a Bayesian strategy in
which they combined a learned prior of the stimulus statistics with their sensory evidence in a probabilistic way (Figure 2.8).

The models were assessed with the use of a metric called the Bayesian information criterion (BIC), which is defined as \( \text{BIC} = -2 \cdot \ln(L) + k \cdot \ln(n) \), where \( L \) is the likelihood of generating the experimental data from the model, \( k \) is the number of parameters in the model, and \( n \) is the number of data points available. The first term quantifies the error between the data and the model predictions, while the second term penalises increasing model complexity, and the model with the lower value of BIC should be preferred when comparing two models (Schwarz, 1978). The Bayesian model in Chalk et al. (2010) was found to exhibit significantly smaller BIC values than all other models and produced fits for the estimation bias and the standard deviation that were at least on par with the first class of models despite having fewer free parameters. This suggests that a Bayesian strategy was the best description of the subjects’ behaviour.

Here, we implemented both the simple Bayesian model and the response strategy models, and we again found that the Bayesian model was able to fit the data accurately and exhibited significantly better BIC values than the other models (Appendix B, Figure B.5). Next, we evaluated several extended versions of the simple Bayesian model that took into account the statistical information of the two coloured conditions and compared them to the simple model. We will briefly describe the Bayesian models before reporting their performances.

### 3.4.1 The simple Bayesian model

The simple Bayesian model assumed that subjects combined their sensory evidence with a learned prior of the stimulus directions in a probabilistic manner. Subjects were assumed to make noisy observations \( (\theta_{obs}) \) of the stimulus motion direction \( (\theta) \) with a probability \( p_l(\theta_{obs}|\theta) = V(\theta, \kappa_l) \), where \( V(\theta, \kappa_l) \) is a circular normal distribution with width \( 1/\kappa_l \). The posterior probability that the stimulus is moving in a particular direction \( \theta \), using Bayes’ rule, is given by multiplying the likelihood function \( p_l(\theta_{obs}|\theta) \) with the prior probability \( p_{prior}(\theta) \):

\[
p(\theta|\theta_{obs}) \propto p_{prior}(\theta) \cdot p_l(\theta_{obs}|\theta)
\]  

(3.1)

It was hypothesised that subjects could not access the true prior, \( p_{prior}(\theta) \), so they learned an approximation of this distribution, \( p_{exp}(\theta) \). This approximation was defined as the sum of two circular normal distributions, each with width determined by \( 1/\kappa_{exp} \).
and centered on motion directions $\theta_{\text{exp}}$ and $\theta_{\text{exp}}$, respectively:

$$p_{\text{exp}}(\theta) = \frac{1}{2}[V(-\theta_{\text{exp}}, \kappa_{\text{exp}}) + V(\theta_{\text{exp}}, \kappa_{\text{exp}})]$$  \hspace{1cm} (3.2)

By allowing the means of the two von Mises to vary, we were able to better fit the prior that each individual subject learned. For example, the prior could be centered further away from the frequent directions (as hinted by the averaged estimation biases of Experiment 1, Fig. 3.3), or could potentially be a unimodal distribution over the whole window of presentation ($128^\circ$). Further, it is easier to parametrise and has a shape similar to what we found in subjects’ hallucinations. Subjects were assumed to make perceptual estimates of motion direction $\theta_{\text{exp}}$ by choosing the mean of the posterior distribution:

$$\theta_{\text{perc}} = \frac{1}{Z} \int \theta \cdot p_{\text{exp}}(\theta) \cdot p_l(\theta_{\text{obs}}|\theta) \cdot d\theta$$  \hspace{1cm} (3.3)

where $Z$ is a normalisation constant. We chose the mean of the posterior distribution in order to be consistent with the model of Chalk et al. (2010). Similar to that study, we did not expect to find a difference by using the maximum of the posterior. Finally, it was hypothesised that there is a certain amount of noise associated with moving the mouse to indicate the direction the stimulus is moving and that the subjects make completely random estimates in a fraction of trials $\alpha$. The estimation response $\theta_{\text{est}}$ given the perceptual estimate $\theta_{\text{perc}}$ is then:

$$p(\theta_{\text{est}}|\theta_{\text{perc}}) = (1 - \alpha) \cdot V(\theta_{\text{perc}}, \kappa_{\text{m}}) + \frac{\alpha}{2\pi}$$  \hspace{1cm} (3.4)

where the magnitude of the motor noise is determined by $1/\kappa_{\text{m}}$. We assumed that the perceptual uncertainty at the highest contrast was close to zero ($1/\kappa_{\text{m}} \sim 0$). So, by substituting $\theta_{\text{exp}} = \theta$ and using Equation 3.4 we fit subjects’ estimation distributions at high contrast in order to approximate the width of the motor noise ($1/\kappa_{\text{m}}$) for each subject for all models.

In total, the free parameters that were fitted to the estimation data for each subject were the center and width of the expected distribution ($\theta_{\text{exp}}$ and $1/\kappa_{\text{exp}}$, respectively), the width of the subjects’ sensory likelihood ($1/\kappa_{l}$), and the fraction of trials where they made completely random estimations ($\alpha$).
3.4.2 Extended models of Experiment 1

In Experiment 1, the simple Bayesian model that assumes a single bimodal prior corresponding to the combined distribution of the stimuli is a suboptimal model, as it is blind to stimulus colour. We will refer to this model as 1Bimodal.

Five different model variations of the simple model were proposed (Table 3.1). The first two variations, Uni+Bi and Gaus+Bi, also assumed that subjects form a unique prior used in all trials irrespective of the colour of the dots. Uni+Bi assumed that subjects learn a linear combination of the two different motion distributions used to construct the stimuli, a uniform and a bimodal distribution. These distributions are combined to create the final prior \( p_{\text{prior}}(\theta) \) in the following way:

\[
p_{\text{prior}}(\theta) = c_{pr} \cdot p_{\text{bimodal}}(\theta) + (1 - c_{pr}) \cdot p_{\text{uniform}}.
\]  

(3.5)

where \( c_{pr} \) is a free parameter fitted for each subject, \( p_{\text{uniform}} \) is a uniform distribution identical to the distribution of the uniform stimuli (Figure 3.2A), and \( p_{\text{bimodal}}(\theta) \) is equal to Equation 3.2. The model had a total of five free parameters (\( \theta_{\text{exp}}, \kappa_{\text{exp}}, \kappa_l, \alpha, \) and \( c_{pr} \)). The model Gaus+Bi assumed that subjects develop a Gaussian prior instead of a uniform one, which was of the form \( p_{\text{gaussian}}(\theta) = \mathcal{N}(\theta_u, \kappa_u) \). This model was inspired by data inspection showing that subjects tend to exhibit an attraction towards the central direction. This model required two additional free parameters (\( \theta_u, \kappa_u \)).

The other three variations correspond to the hypothesis that subjects may form distinct priors for the two colour conditions. The data was split between the two colour conditions which were fit separately. The model Split_UniBi assumed that subjects correctly learn a uniform prior for the uniform condition and a bimodal prior for the bimodal condition. This model corresponds to the optimal observer model. The model Split_GausBi assumed that subjects learn a Gaussian prior for the uniform condition and a bimodal prior for the bimodal condition. The form of the Gaussian prior was the same as in Gaus+Bi, so it required two additional free parameters. Finally, the model Split_2Bimodal assumed that subjects learn two different bimodal priors for each condition. This model required two additional free parameters for the center and width of the additional bimodal prior.

All five extended models were implemented and assessed. We compared all extended models with the simple model, 1Bimodal, which assumed subjects only learned the combined colourblind distribution of the motion directions. The BIC values obtained for each model were subtracted by the BIC value obtained for the 1Bimodal.
Table 3.1: Names and descriptions of the models proposed to describe the subjects’
behaviour in Experiment 1 are provided along with the number of free parameters re-
quired by each model and example priors.

<table>
<thead>
<tr>
<th>Model Name</th>
<th>Description</th>
<th>Free parameters</th>
<th>Example priors</th>
</tr>
</thead>
<tbody>
<tr>
<td>1Bimodal</td>
<td>A single Bimodal prior is applied in both conditions.</td>
<td>4</td>
<td>Both conditions</td>
</tr>
<tr>
<td>Uni+Bi</td>
<td>A Uniform and a Bimodal prior are combined in a single prior applied in both conditions.</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Gaus+Bi</td>
<td>A Gaussian and a Bimodal prior are combined in a single prior applied in both conditions.</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Split_UniBi</td>
<td>A Uniform prior is applied in the uniform condition, while a Bimodal prior is applied in the bimodal condition.</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Split_GausBi</td>
<td>A Gaussian prior is applied in the uniform condition, while a Bimodal prior is applied in the bimodal condition.</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Split_2Bimodal</td>
<td>Two distinct Bimodal priors are applied in the uniform and bimodal conditions.</td>
<td>6</td>
<td></td>
</tr>
</tbody>
</table>

model (Figure 3.8B). The results show that all BIC values were significantly greater than those obtained with the 1Bimodal model ($p = 0.006$ for Uni+Bi, $p = 0.001$ for Gaus+Bi, and $p < 0.001$ for Split_UniBi, Split_GausBi, and Split_2Bimodal, signed rank test). The single prior models performed better than the Split models, and the bimodal prior dominated over the uniform and Gaussian priors with averaged $c_{pr}$ values of $0.87 \pm 0.14$ and $0.8 \pm 0.22$, respectively. The best performing Uni+Bi model was still significantly worse than the simple 1Bimodal model.

Among the Split models, the BIC values exhibited by the theoretically optimal Split_UniBi model were not significantly better than the values of the other Split models despite having two free parameters less than the other two models. This strongly suggests that subjects did not learn a uniform prior for the uniform condition. Moreover, the Split_2Bimodal model exhibited significantly better values than the other two models ($p = 0.02$ and $p = 0.002$ compared to Split_UniBi and Split_GausBi, respectively) which indicates that subjects learned bimodal priors for both the uniform and bimodal conditions. However, the values were significantly worse compared to the values of the simple 1Bimodal model.

In addition to the BIC, the models were evaluated with the Akaike information
Figure 3.8: Model comparison. The (A) Akaike information criterion (AIC) and (B) Bayesian information criterion (BIC) values of each model subtracted by the AIC and BIC values of the 1Bimodal model are plotted for each subject (black dots), along with median values (red lines) and the 25th and 75th percentiles (blue lines). Here, $p$ values indicate whether the median was significantly different from zero for each model (signed rank test).
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Figure 3.9: Predicted (A) averaged estimation biases and (B) standard deviations for each model. Predictions for the Split_UniBi (green), the Split_2Bimodal (blue), and the 1Bimodal models (black) are plotted with the experimental data (red). Results are averaged over all subjects and error bars represent within-subject standard error.

criterion (AIC), which is defined as $AIC = 2 \cdot k - 2 \cdot \ln(L) + (2 \cdot k \cdot (k + 1)/n - k - 1)$, where $L$ is the likelihood of generating the experimental data from the model, $k$ is the number of parameters in the model, and $n$ is the number of data points available. The AIC penalises the number of parameters less strongly than the BIC. Even so, the extended models perform worse than the 1Bimodal model, non-significantly for the single prior models and significantly for the Split models (Figure 3.8A).

While most of the extended models had more free parameters than the 1Bimodal model, they did not produce significantly better fits for the subjects’ estimation biases and standard deviations (Figures 3.9A & 3.9B). To predict subject’s estimation biases and standard deviations from the models, we run each model with its inferred parameters to generate 1 million estimates for each motion direction. From these estimates, we use the same equation as with the experimental estimates (page 42) to calculate subjects’ bias, standard deviation, and $\alpha$. The Split_2Bimodal model had almost identical results to the 1Bimodal model ($p = 0.45$, three-way within-subjects ANOVA between motion direction, model, and subjects), further suggesting that subjects did not form two independent priors for the two colour conditions. Additionally, while the Split_UniBi predictions were not significantly different compared to 1Bimodal predictions ($p = 0.14$, three-way within-subjects ANOVA), they exhibited a larger mean absolute error (3.258 compared to 1.878 for the 1Bimodal model and 1.858 for the Split_2Bimodal).
3.4.3 Extended models of Experiment 2

Subjects’ behaviour in Experiment 2 was more difficult to quantify, as the estimation performances varied greatly on a subject-by-subject basis. We first assessed whether the data could be described using a simple model called Uniform that assumed that subjects only learned the combined statistics of the stimuli. The prior distribution was defined as a uniform distribution identical to the combined distribution over both colours, and the model required only two free parameters ($\kappa_l$ and $\alpha$). The model’s predictions on the estimation biases differed highly from subjects’ estimation biases with a mean absolute error of 6.028, suggesting that subjects formed nonuniform priors.

We next implemented models with more complex priors, assuming that the same prior was used for both colour conditions (Table 3.2); in the 2Circ model the prior is defined as the sum of two pairs of circular normal distributions, and in the 3Circ model the prior is defined as the sum of three pairs of circular normal distributions. The former model requires six free parameters ($\theta_{\text{exp}}$, $\kappa_{\text{exp}}$, $\theta_{2\text{exp}}$, $\kappa_{2\text{exp}}$, $\kappa_l$, and $\alpha$) and the later eight (adding $\theta_{3\text{exp}}$, $\kappa_{3\text{exp}}$). The predictions of these models were significantly more accurate than the predictions of the Uniform model with mean absolute errors of 5.89° and 5.76°, respectively ($p < 0.0001$ for both, signed ranked test, Figure 3.10A). The prior distributions predicted by the models differed extensively between subjects. The standard deviation predicted by the models was larger than the experimental results (Figure 3.10C). However, the qualitative trend for the standard deviation to decrease away from the central direction displayed by all models (but the Uniform) was consistent with the data.

We next tried models that assumed distinct priors depending on the colour condition. The model Split_TriBi assumes that subjects correctly developed a trimodal prior for the trimodal condition and a bimodal prior for the bimodal condition. The center of the trimodal distribution was fixed at 0°, while the other peaks were fit to the data. The Split_TriBi model requires six free parameters ($\theta_{\text{tri}}$, $\kappa_{\text{tri}}$, $\theta_{\text{bim}}$, $\kappa_{\text{bim}}$, $\kappa_l$, and $\alpha$) and corresponds to a model of the optimal observer. The models Split_2Circ and Split_3Circ are similar to 2Circ and 3Circ defined above but now with two distinct priors for each condition, requiring 10 and 14 free parameters, respectively. As can be expected from the models’ increased complexity, the estimation biases predicted by the Split models were closer to the experimental results with mean absolute errors of 5.72°, 5.66°, and 5.67°, respectively. The models predict different biases for the two colour conditions (Figures 3.10B1 and 3.10B2). The Split_TriBi model provides very
Table 3.2: Names and descriptions of the models proposed to describe the subjects’ behaviour in Experiment 2 are provided along with the number of free parameters required by each model and example priors.

Accurate predictions for both conditions at ±48° and at ±64° but fails at ±16°. This suggests that the subjects’ estimation performances were more weakly biased towards the central direction for the trimodal condition than expected and that this attractive bias possibly transferred to the bimodal condition. The predicted standard deviations of these models did not differ much from those predicted by the single prior models (Figure 3.10D).

We computed the AIC and BIC values to evaluate the models’ goodness of fit for the estimation performances. The simple Uniform model performed significantly worse than all the other models, so we selected the optimal Split_TriBi model as the reference for comparison. The BIC results (Figure 3.11B) showed that the 2Circ model was the only one that performed significantly better than the Split_TriBi model, whereas the Split_3Circ model performed significantly worse. In terms of AIC, the Uniform model was non-significantly worse, while again only the 2Circ model was significantly better (Figure 3.11A). The fact that more complex models provided significantly better results suggests that subjects learned complicated priors even though the combined distribution was uniform. Moreover, it is interesting that while, on av-
Figure 3.10: (A) Comparison between the predicted averaged estimation biases for the 3Circ (blue), the 2Circ (green), and the Uniform models (black) and the experimental data (red). (B) Predicted averaged estimation biases for the Split_3Circ (blue), the Split_2Circ (green), and the Split_TriBi models (black) and experimental data (red) of the trimodal condition (B1) and of the bimodal condition (B2). (C) Predicted averaged estimation standard deviations for the 3Circ (blue), the 2Circ (green), and the Uniform models (black) and the experimental data (red). (D) Predicted averaged estimation standard deviations for the Split_3Circ (blue), the Split_2Circ (green), and the Split_TriBi models (black) and the experimental data (red). Results are averaged over all subjects and error areas show within-subject standard error. The red and green vertical dotted lines correspond to the most frequently presented motion directions for the trimodal and bimodal distributions (0° and ±64°) and (±32°), respectively.

average, the Split_TriBi model was significantly worse than 2Circ, it performed better for one third of the subjects. This suggests that, for these subjects, estimation performances were better explained by assuming distinct priors for the two colour conditions.

We compared the centers of the circular normal distributions predicted by the models 2Circ, 3Circ, Split_2Circ, and Split_3Circ with the most frequently presented directions by measuring the minimum absolute difference between the model \( \theta_{\text{exp}} \) values and \( 0^\circ, 32^\circ, \) and \( 64^\circ \). We found that the \( \theta_{\text{exp}} \) values were distributed in a similar way across all models. We calculated the ratios of \( \theta_{\text{exp}} \) values based on their proximity to each direction for each of the four models; the percentage of \( \theta_{\text{exp}} \) values (averaged over all models) which fall closest to one of the most frequent directions (than to
Figure 3.11: Model comparison. The (A) Akaike information criterion (AIC) and (B) Bayesian information criterion (BIC) values of each model subtracted by the AIC and BIC values of the Split_TriBi model are plotted for each subject (black dots), along with median values (red lines) and the 25th and 75th percentiles (blue lines). Here, p values indicate whether the median was significantly different from zero for each model (signed rank test).
the other two directions) were 46.4% ± 5.2% for ±64°, 37% ± 4.5% for ±32°, and 16.6% ± 4.7% for 0°. The average minimum absolute difference was 8.45° ± 2.6° from the frequently presented directions (averaged over all models). This suggests that, on average, subjects do learn a distribution with peaks located around the most frequent directions. However, it seems that the representation of the central direction is suppressed compared to the other directions (±32° and ±64°).

3.5 Discussion

3.5.1 Summary

The results of Experiment 1 showed that subjects quickly developed expectations for the most frequently presented directions over all trials, irrespective of the colour of the dots. They exhibited estimation biases towards those directions similarly for both the uniform and bimodal colour conditions. On trials where no stimulus was presented but subjects reported seeing a stimulus, they were strongly biased to make estimates in the most frequently presented motion directions regardless of the colour reported. Subjects’ estimation behaviour in Experiment 1 was described successfully by a probabilistic model that assumed they used a suboptimal Bayesian strategy. The model combined their sensory evidence with a unique learned prior of the combined stimulus statistics applied to both colour conditions in a probabilistic way. The model could accurately predict the subjects’ behaviour when no stimulus was presented and performed better than response strategy models, which assumed that subjects developed response strategies unrelated to perceptual changes. Several variations of the Bayesian model were proposed that took into account the colour information of the stimuli presented. The models assumed that subjects formed a single prior by linearly combining two different distributions or that they used two different priors to estimate the motion direction of the two colour conditions. While the new models provided slightly more accurate fits to the data, they performed significantly worse in terms of the BIC and AIC criteria compared to the simple Bayesian model. This suggests that subjects developed a single bimodal prior that was used for all stimuli independent of colour.

In Experiment 2, subjects’ estimation performances on trials where a stimulus was presented were significantly different between the two colour conditions, but the induced biases were comparably weaker than and not as clear as in Experiment 1. Subjects’ estimation performances on trials where no stimulus was presented but where
subjects reported seeing a stimulus were significantly different depending on the colour they reported, and there were indications that subjects increasingly perceived the most frequently presented directions of the colour condition they reported as the sessions progressed. Subjects’ estimation behaviour in Experiment 2 was described more effectively by a model that assumed that subjects learned a complex combination of both distributions and applied it to both conditions. The model provided significantly better fits to the experimental data than a simple model that assumed that subjects learned only the combined statistics of the stimuli (a uniform prior) and had a smaller AIC and BIC, despite having a larger number of free parameters. Finally, a model that assumed subjects learned and applied a distinct prior for each colour condition, which matched the distribution of each condition was significantly better than the uniform model but worse than the complex prior model.

3.5.2 Optimality

In general, it is not easy to distinguish between biases that occur at the perceptual or decision-making level (Schneider and Komlos [2008]). However, the modelling results in the current work showed that subjects combined their expectations with sensory observations, not by following different strategies on each trial but by using both in a probabilistic way. At the end of the second session in Experiments 1 and 2, we questioned the subjects as to whether they had identified directions that were presented more frequently and whether they had noticed a difference between the directions of the two colour conditions (the questionnaire can be seen in Appendix C). In Experiment 1, the majority (13 out of 18 subjects) reported that there were equal number of stimuli moving in all directions, and even more subjects (15 out of 18) reported that they did not notice any difference between the motion directions of the two coloured stimuli. In Experiment 2, 12 out of 18 subjects thought that there were an equal number of stimuli moving in all directions, and 14 out of 18 thought that the red and green dots had the same distribution. The subjects who reported noticing one or two directions being more frequent (5 out of 18 in Experiment 1 and 6 out of 18 in Experiment 2) were only able to give an approximate estimate of the quadrant of motion directions. The subjects who reported noticing a difference between the two distributions (3 out of 18 in Experiment 1 and 4 out of 18 in Experiment 2) failed to report the correct frequent directions of each distribution, and their estimation performance was not in accordance with their conscious estimates.
In both experiments and when stimulus was and was not presented, there is evidence that, on average, the priors used by the subjects are slightly shifted compared to the stimulus distribution. A similar shift was also present in Chalk et al. (2010). That subjects would learn only an approximation of the stimulus distribution with slight variability in its peaks was not unexpected. However, it is possible that this shift reflects more than interindividual variability. In this case, we can only speculate about its potential origin. A possible explanation is that it would reflect a perceptual repulsion from the main reference direction, which in this case is the central direction (Rauber and Treue, 1998) or an apparent repulsion between the two modes of the motion distributions (Treue et al., 2000).

The Bayesian model in Chalk et al. (2010) showed that subjects behaved similarly to an optimal Bayesian observer. Here, in Experiment 1, subjects failed to behave optimally, as they did not incorporate the information provided by the colour condition to make more accurate estimates of the motion directions of the stimuli. This suboptimal behaviour could have resulted from either ignoring the colour of the dots in the estimation task (since it was not directly relevant to this task) and learning only the overall combined distribution of the motion directions or from learning only the distribution of the bimodal condition and using it also for the uniform condition. The results of Experiment 1 could not disentangle between these two explanations. Experiment 2, on the contrary, was designed so that those two explanations would lead to different predictions. The results of Experiment 2 showed that subjects didn’t ignore colour information but tried to learn the statistical properties of the stimuli for each condition.

That only one motion distribution was learned in Experiment 1 is intriguing. A possible explanation is that neural mechanisms might exist that restrict the formation of multiple priors in order to reduce extensive plasticity in sensory cortex or that force competition between different sensory adaptations. In Experiment 1, learning of the bimodal prior seemed to have dominated over the uniform prior. This might be related to a compromise between plasticity and performance cost for the task at hand. Indeed, one can argue that, in Experiment 1, the benefit of learning about the uniform distribution is not as large as that of learning about the bimodal distribution or about each of the two distributions in Experiment 2, in terms of the detection task performances. As discussed in section 2.2.4, Kerrigan and Adams (2013) also found incomplete learning using colour as a distinguishing factor, and suggested that this might reflect robustness to temporary changes in cue contingencies as subjects might have not previously associated colour with illumination direction. Likewise, subjects are unlikely to have
previously associated colour with motion direction and this might have affected their behaviour in our experiments.

Another reason for suboptimality in these tasks might be found in the classically postulated separation of the motion and colour pathways in the visual cortex. One may wonder whether there is a single representation of the joint colour-motion statistics (and if so, where in the brain?), or whether there is a representation of the motion statistics, e.g., in middle temporal cortex (MT), that would be further integrated with colour information. The relationship between the neural processing of colour and motion information has been a debated issue in visual neuroscience. However, there is evidence that chromatic information influences the responses in MT and that this cortical area is an important component of the neuronal substrate of colour-based motion processing (Dobkins and Albright, 1998; Thiele et al., 2001). It has also been shown that colour signals in MT of the macaque monkey influence behaviour in speed judgment tasks (Seidemann et al., 1999) and, similarly, that the colour sensitivity of motion-selective cortex MT+ in humans follows the colour sensitivity of psychophysical observers in making speed judgments (Wandell et al., 1999).

Gegenfurtner and Hawken (1996) suggested the existence of two distinct pathways that differ mostly in their temporal properties. A ‘slow’ channel has a high sensitivity for colour contrast but does not encode speed in a contrast-invariant manner and it is more suitable for assigning surface characteristics such as colour to slow moving objects. A ‘fast’ channel can accurately represent the speed of moving stimuli and has a high sensitivity to the luminance of stimuli but processes colour differences as luminance variations without colour-specificity. The best candidate for the ‘slow’ channel is the pathway via V3 and V4, and for the ‘fast’ channel the pathway via V3 and MT. While luminance differences between red and green stimuli were not negligible (Appendix B, Figure B.1), it is possible that the small differences in luminance between coloured stimuli in addition to the potential colour-nonspecificity of the ‘fast’ channel are responsible for the transfer between colour modalities.

3.5.3 Attention

The experimental and modelling results suggested that subjects’ estimation performances did not vary depending on the colour condition in Experiment 1 and only moderately so in Experiment 2. Subjects identified the correct colour in 82% and 79.6% of the trials on average for Experiments 1 and 2, respectively, which indicates
that they paid attention to the colour as well as the motion direction of the stimuli. Additionally, there was no preference for one colour condition over the other as the errors on colour were evenly balanced in both experiments (51% false green and 49% false red with 13% standard deviation in Experiment 1 and 53% false green and 47% false red with 16% standard deviation in Experiment 2). While on average there was no colour preference, some subjects exhibited a tendency towards reporting one colour more than the other. However, there was no indication that this preference was affecting their estimation behaviour (i.e., reporting a particular colour at a specific direction as a response strategy when uncertain about the stimulus).

Selective attention towards one colour at a time could possibly explain the results in Experiment 2. Subjects could have attended more to one colour for a certain amount of time and then switched to the other colour and so on. This behaviour should result in learning being spread between the two colour conditions and in subjects forming priors that would be a combination of the statistical properties of the two distributions. In order to evaluate this hypothesis, we implemented two models that assumed subjects developed such priors; a linear combination of the stimuli distributions, i.e., a trimodal and a bimodal distribution (Appendix B, Figure B.8). The weight of each distribution was a free parameter that could take any value from zero to one. The first model assumed a single prior and the second assumed two distinct priors for each colour condition. The performances of both models were worse than the optimal Bayesian model in fitting the experimental data and in the AIC and BIC. Moreover, closer examination of the subjects’ performances in terms of colour reported showed that colour errors and hallucinations were evenly spread over time between the two colours, which is inconsistent with the selective attention hypothesis.

In the original paradigm of Chalk et al. (2010), subjects were not required to identify any other characteristic of the stimulus than its direction of motion. Here, the fact that subjects were additionally asked to report on stimulus colour can be argued to introduce a processing component associated with the ventral stream, while the original task was associated only with the dorsal stream. This might have affected how attentional processes were deployed, particularly if attention serves to combine information from the ventral and dorsal streams (Van Der Velde and De Kamps, 2001).

This might explain the performance differences we observe with some aspects of the original study. In particular, in Experiment 1, while there was a clear estimation bias towards the frequently presented directions, the detection rates and reaction times did not show a marked difference for those directions as found in Chalk et al. (2010).
On the contrary, in both experiments, detection rates were higher near the central direction and decreased away from it (Appendix B, Figure B.4).

### 3.5.4 Neural encoding

A lot of research has been devoted to modelling how visual neurons could encode information about sensory stimuli in the form of probability distributions, from the population level (Ma et al. 2006) to a single neuron (Deneve 2008). While many studies have shown that selective attention increases the sensitivity of neurons (Treue 2001; Treue and Maunsell 1996; Wolfe and Horowitz 2004), direct evidence for neural encoding of the prior is still scarce (Summerfield and Koechlin 2008). It is unclear whether learned priors are encoded directly by gain changes in sensory neurons as has been observed with attention and how these changes reach higher cortical areas to affect perceptual behaviour. Furthermore, the current study raises the question of whether features that are processed by different cortical pathways integrate and affect perceptual biases and whether multiple priors can be encoded simultaneously from different sensory features.

The experimental results showed that the brain is endowed with mechanisms that adapt efficiently to different statistical properties of sensory information and that, given enough time, can learn increasingly complex statistical structures or close approximations. The two models that best described subjects’ behaviour in the two experiments differed extensively. However, in theory, there should exist a single unifying model that could explain both behaviours and their dependency on the stimulus distributions. The exact form of this model and how it relates to existing theories of how probability distributions are encoded in the brain will be a matter of further investigation.
Chapter 4

Limitations on learnable priors as a Bayesian inference problem

In this chapter, we describe a collaborative work with Dr Kevin Lloyd and Professor David Leslie, both at the University of Bristol at the time, in developing an online learning Bayesian model of the ‘colour motion perception experiments’, which were described in the previous chapter and published in Gekas et al. (2013), and conducting a new psychophysics experiment based on the predictions of the model. Our main motivation was to investigate the source of sub-optimality in subjects’ performance and whether specific changes to the design of the experiment, as predicted by the model, would allow observers to learn the two distributions. First, we briefly describe the computational model, the outcomes of the simulations of the original experiments, and the predictions of the model and, then, present the methods and results of the new psychophysical experiment.

The computational model as well as the simulations of the experiments of Chapter 3 were conceived and implemented by Dr Kevin Lloyd, whereas the psychophysical experiment and analysis were conducted by the author of this thesis. Further changes to the model and investigation of the model’s predictions for different experimental designs were conducted by both. Some parts of this work also appear in Kevin’s doctoral thesis.

4.1 Introduction

An important aspect of perceptual processing that we have briefly discussed in this thesis is causal inference, i.e. the process of inferring whether or not an event A is caused
by another event B (Shams and Beierholm, 2010). The observer of the experimental task in Figure 2.7 infers that there is a hidden variable (true orientation of the grating) based on an observed variable (noisy measurement). Several studies have suggested computational solutions to the problem of causal inference in perception (Beierholm et al., 2009; Bresciani et al., 2006; Knill, 2007b; Stocker and Simoncelli, 2008; Wozny et al., 2008). For example, Körding et al. (2007) implemented a hierarchical Bayesian model, which explicitly performed causal inference, and was shown to predict subjects’ unity judgments and stimulus estimates in an auditory-visual spatial localisation task.

As we discussed in the previous chapter, the experimental findings of the colour experiments suggested that subjects of Experiment 1 failed to learn distinct, colour-specific priors, while some but not all subjects of Experiment 2 showed learning of two distinct priors for differently coloured stimuli. The modelling work in Chapter 3 reinforced the belief that subjects of Experiment 1 behaved in disagreement with a near-optimal observer by learning colour-nonspecific priors. However, that work did not explore the possibility that subjects were actually consistent with a Bayesian observer given the properties of the chosen distributions and the experimental procedure and design. In order to examine the validity of this idea, we constructed an online learning Bayesian model of the task and assessed the degree to which a process of inference, as implemented in this model, leads to results in agreement with subjects’ performance.

We worked with a simple generative model called a Gaussian mixture model. We made the assumption that component distributions were Gaussian but also that the number of mixture components was initially unknown. Thus, the inference problem was directed at the number of underlying causes, or ‘clusters’, and their associated parameterisations in regards to the sensory data. In this case, inference is required both at the level of model structure (the number of underlying causes) and model parameters (the Gaussian means and variances) (Orbán et al., 2006). We used a Bayesian non-parametric approach to mixture models called Dirichlet process mixture models (DPMMs), first introduced by Ferguson (1973). An advantage of using a Bayesian non-parametric model is that model complexity is determined mostly by the data itself. As we assume that the number of components is unknown, it is desirable that this number is able to change depending on the nature of the data.

Another important issue that we wanted to explore is the process of learning and how it might be affected by the specifics of the experimental design. For example,
the order of presentation of the stimulus (blocked, interleaved, high or low contrast) could have a significant effect on how subjects infer the underlying causes of the stimuli. Thus, we used an approach based on the particle filter for inference in DPMMs (Fearnhead, 2004). The advantage of this approach is that particle filters can be used to analyse dynamic problems in ‘real-time’. Gershman and Niv (2013) used a similar model in a study of how human observers categorise visual stimuli. Subjects were presented with coloured circles, and were asked to report the number of the circles, which was drawn from colour-specific distributions. When the distributions of each colour overlapped considerably, subjects were found to ignore the stimulus’ colour and group different-coloured stimuli into one perceptual category. On the other hand, when the distributions overlapped to a small degree, subjects gave estimates closer to the true means of each colour distribution. These findings suggested that human observers may use an ‘Occam’s razor’ approach in perception. According to this approach, they assign visual stimuli, which originate from overlapping distributions, to one category despite them having different colours. However, observers are able to develop more complex models when the presented sensory evidence is sufficient.

4.2 Computational model

The model can be considered as having two components. The first component embodies beliefs that we ascribe to subjects about how the experimental stimuli are generated (i.e., a ‘generative model’; Dayan and Abbott, 2001). The second component comprises a method for performing Bayesian inference based on observations, i.e. a way of ‘inverting’ the generative model. A full description of the model along with a more detailed mathematical description can be found in Kevin Lloyd’s doctoral thesis.

4.2.1 Generative model

Stimuli are assumed to be generated by some unknown number of hidden causes or ‘clusters’, and each cluster generates stimuli with directions and colours according to an associated set of parameters. On a given trial, a single cluster is assumed to be responsible for generating the stimulus. It is also assumed that the direction and colour sensed by the subject only imperfectly reflect the true stimuli, and that the accuracy of this sensory representation depends on stimulus contrast. Thus, the lower the contrast, the less reliable the sensory data and the greater the subject’s uncertainty regarding the
true stimulus.

It is assumed that on each trial $t$, the presented direction $X_t \in [-180, 180)$ and colour $C_t \in \{ \text{red, green} \}$ are generated by cluster $k$, as indicated by auxiliary variable $Z_t = k$, with associated parameters $(\mu_k, \sigma^2_k, \theta_k)$ characterising the stimuli which it generates. A convenient prior distribution for how prolific clusters are in generating stimuli in the present case is provided by the Chinese Restaurant Process (CRP) (Pitman, 2006), with conditional distributions of the form

$$p(Z_t = k \mid Z_{1:t-1}) \propto \begin{cases} a & \text{if } k \text{ new cluster} \\ n_k & \text{if } k \text{ old cluster} \end{cases}$$

(4.1)

where $\alpha$ is the associated concentration parameter (effectively controlling prior expectations about the number of clusters), and $n_k$ is the number of observations up to $t - 1$ allocated to cluster $k$. The CRP therefore places greater prior probability mass on clusters which have been more active in the past, but always allows for the possibility of a new cluster becoming active.

Each cluster $k$ is assumed to generate normally-distributed stimulus directions

$$X_t \sim \text{Normal}(\mu_k, \sigma^2_k)$$

(4.2)

and to generate colours according to

$$C_t \sim \text{Bernoulli}(\theta_k)$$

(4.3)

Thus, cluster parameters $(\mu_k, \sigma^2_k)$ characterise the central tendency and spread of directions generated by component $k$, while $\theta_k$ captures its tendency to produce stimuli which are mainly red ($\theta_k \approx 0$), green ($\theta_k \approx 1$), or a mixture of both ($\theta_k \approx 0.5$).

For convenience, cluster parameters are given conjugate Normal-Inverse-Gamma and Beta priors:

$$\sigma^2_k \sim \text{IG}(\alpha_0, \text{rate} = b_0)$$

$$\mu_k \sim \text{Normal}(\mu_0, \sigma^2_k / \lambda_0)$$

$$\theta_k \sim \text{Beta}(c_0, d_0).$$

(4.4)

Since directions have a natural scale due to restriction to the interval $[-180, 180)$ we took the variance of a uniform distribution on this interval ($\approx 10^4$) as a guide to forming a non-informative prior on $\sigma^2_k$. In particular, shape $\alpha_0$ and rate $b_0$ were chosen so that $E[\sigma^2] = b_0 / (\alpha_0 - 1) = 10^4$. Fixing $\alpha_0 = 2$, and therefore setting $b_0 = 10^4$, yields a suitably diffuse prior. As it is common in studies using mixtures (e.g., Rasmussen).
we also considered the weakly informative prior $\sigma^2_k \sim IG(\alpha_0 = 2, b_0 = \sigma^2_{data})$, with $\sigma^2_{data}$ the variance of the presented stimulus directions ($\approx 2000$ for all data sets). The effect of reducing rate $b_0$ further was also explored. The prior on cluster locations was simply set to the central direction $\mu_0 = 0$ with inverse-scale $\lambda_0 = 1$. Finally, $\theta_k$ was given the uniform Beta prior $\theta_k \sim Beta(1, 1)$.

Subjects do not have direct access to the true direction and colour of the presented stimulus, but rather form a sensory representation comprising what we call the ‘sensed’ direction $Y_t = y_t$ and ‘sensed’ colour $O_t = o_t$. These variables are assumed to depend both on the true stimuli and associated uncertainty levels:

$$Y_t \sim Normal(X_t, \sigma^2_t),$$

$$O_t \sim \begin{cases} c_t \text{ w.p. } \rho_t \\ \neg c_t \text{ w.p. } (1 - \rho_t) \end{cases}$$

where known parameters ($\sigma_t, \rho_t$) respectively characterise the subject’s uncertainty regarding direction and colour on the current trial, and are assumed to depend deterministically on the stimulus contrast (lower contrast entailing greater uncertainty). For high contrast trials, we assumed that direction uncertainty was low (we simply set $\nu_t = \nu_{HC} = 1$) and colour uncertainty non-existent ($\rho_t = 1$). For staircase trials, we set $\rho_t = 0.8$ to reflect the proportion of trials on which colour was correctly reported ($82\%$), and explored the effect of varying $\nu_t = \nu_{ST}$.

To explore the fact that subjects sometimes reported perceiving a stimulus on trials in which no stimulus was presented, we also assumed sensory representations of direction and colour on such trials but attached to them very high levels of uncertainty. In particular, sensed directions were sampled uniformly $y_t \sim Uniform[-180, 180]$ and $\nu_t$ was simply set to a large value ($\nu_t = \nu_{ZC} = 100$) to reflect the presumably large amount of uncertainty on such trials. Setting $\nu_{ZC}$ large means that prior expectations will drive estimated direction on these trials, producing an essentially ‘internally-generated’ percept on these trials. Regarding colour uncertainty, we set $\rho_t = 0.5$ to reflect the fact that subjects were equally likely to report detecting red or green stimuli on no stimulus trials.

The form of the model is summarised by the graphical model in Figure 4.1.
Figure 4.1: Generative model of the ‘colour experiment’. On each trial, the sensed direction $Y_t$ and colour $O_t$ are assumed to be imperfect reflections of the true direction $X_t$ and colour $C_t$, respectively. The respective amount of uncertainty regarding true direction and colour is controlled by contrast-dependent parameters $\nu_t$ and $\rho_t$. On a given trial, stimuli are assumed to be generated by underlying cluster $Z_t = k$ with associated parameters $\{\mu_k, \sigma_k^2, \theta_k\}$ characterising its direction- and colour-generating tendencies. Shaded nodes indicate observed variables, unshaded nodes indicate latent variables, and shaded squares indicate fixed parameters. The symbol $\infty$ indicates that the number of clusters underlying the data are unknown and potentially unbounded.
4.2.2 Inference

Even in problems of modest complexity, exact Bayesian inference is generally not possible. In the model considered here, exact inference is intractable due to the exponentially increasing number of possible partitions $Z_{1:t}$ of the observations. The number of partitions corresponds to the Bell number so it increases very quickly with $t$. Approximate inference must be incremental, since subjects are asked to make estimates trial by trial, and preferably with guarantees on the quality of the approximation in the limit. Sequential Monte Carlo (SMC), or ‘particle filtering’, methods are therefore well suited to the task (Griffiths et al., 2012).

The aim of SMC methods (Doucet, 2001) is to approximate a sequence of distributions of interest with a set of samples, or ‘particles’, drawn according to those distributions. This is achieved by generating samples from a sequence of simpler distributions, then re-weighting (and re-sampling) these samples so that the target distribution is characterised by this weighted set.

In our case, the inference problem can be characterised as approximating the sequence of distributions $\{p(Z_{1:t}, X_{1:t}, C_{1:t} | y_{1:t}, o_{1:t})\}_{t=1}^T$. Accordingly, on each trial, we firstly propose sample values for variables $\{Z_t, X_t, C_t\}$, and re-weight these samples so that they reflect the distribution of interest. Secondly, having proposed and re-weighted samples, estimates of direction and colour for the current trial are generated. We do this by sampling a single particle with probability proportional to its weight, then simply setting the estimates equal to that particle’s values. Finally, particles are selectively replicated or discarded (‘re-sampling’) with probabilities based on their normalised weights to create a new, equally-weighted particle set. All steps are then repeated. A large number of particles ($L = 5000$) was used to avoid potential issues with sample degeneracy, though we obtained similar results for lower numbers (e.g. $L = 1000$).

The procedure is summarised in pseudocode form in Algorithm 1.

4.2.3 Simulations of the experiments of Chapter 3

To explore the behaviour of the model, the effect of varying parameters one at a time was measured. To align with the collected data from the original experiments, the algorithm was run 18 times (corresponding to 18 ‘subjects’) and average behaviour reported. For each simulation, observed stimulus values $(y_{1:t}, o_{1:t})$ were generated from the stimulus values presented experimentally. In particular, a random realisation $(y_{1:t}, o_{1:t})$ was generated from the presented values $(x_{1:t}, c_{1:t})$ by drawing from the
Chapter 4. Limitations on learnable priors as a Bayesian inference problem

Algorithm 1 Particle filter pseudocode

1: for trial $t = 1 : T$ do
2:     for particle $l = 1 : L$ do
3:         for cluster $k = 1, 2, \ldots$ do
4:             Sample a direction $x^{(l,k)}_t \sim p(X_t | z_t^{(l)}, x_{t-1}^{(l)}, y_t)$
5:             Sample a colour $c^{(l,k)}_t \sim p(C_t | z_t^{(l)}, y_t = k, c_{t-1}, o_t)$
6:             Compute particle weight $w_t^{(l,k)}$
7:         end for
8:     end for
9:     Set estimate to $(x_t^{(l,k)}, c_t^{(l,k)})$ with probability $\propto w_t^{(l,k)}$
10:    Resample independently, with replacement, $L$ times with probabilities $\propto w_t$
11: end for

Distributions described in Equations (4.5) and (4.6) using the appropriate values of $\nu_t$ (direction uncertainty) and $\rho_t$ (colour uncertainty) for staircase and high contrast trials. ‘Observations’ of direction and colour in no stimulus trials were generated by drawing from a uniform distribution on [-180, 180) and by the flip of a fair coin respectively. Patterns of bias for stimuli of different colours were used to measure model behaviour in response to different parameter values.

4.2.3.1 Experiment 1

We explored model behaviour for Experiment 1 under different parameterisations, with inputs designed to mimic the stimuli faced by subjects (full results can be found in Kevin’s doctoral thesis). The result of most interest for current purposes was that, as in the behavioural results, estimation biases for red and green stimuli tended to be very similar, with both sets of biases consistent with an expectation for bimodally distributed stimuli (Figure 4.2). This result was observed under the default weakly informative prior ($\sigma_k^2 \sim IG(\alpha_0 = 2, b_0 = \sigma^2_{data})$) and proved relatively robust to variations in parameters.

One way to gain insight into what the model has inferred is to consider the clusterings of particles with the highest posterior (MAP) probability and, in particular, 2 summary measurements of these: the number of inferred clusters $K$, and a measure of the extent to which clusters tend to contain stimuli of just one colour or both. In most parameter settings, the model infers a small number of clusters that are colour-nonspecific and follow a bimodal distribution. Even in parameter settings in which
biases were slightly different between colours (e.g., decreasing the rate of the prior $b_0$), there was substantial mixing of colours within clusters. The only difference was that expectations for green stimuli were increasingly ‘peakier’ than for red stimuli with decreasing $b_0$.

While the model captures the main results in Chapter 3’s data for Experiment 1, we note the following discrepancies. Firstly, estimates generated by the model center exactly on the most frequent directions, $\pm 32^\circ$, while the center of attraction for subjects is slightly shifted to more extreme values ($\approx \pm 40^\circ$) (Figures 4.2A & 4.2D). This shifting of bias has been reported previously in [Chalk et al. (2010)] and possibly reflects perceptual repulsion effects. Secondly, subjects’ estimates are clearly more variable than the model, as indicated by the difference in error bars. Finally, the average standard deviation from simulations is slightly lower ($\approx 2^\circ$) than that of subjects (Figures 4.2C & 4.2F). This is not surprising considering the additional sources of variability in the real experiment not modelled here (e.g. variability induced by the short time subjects have to indicate their estimates, or varying levels of motor noise between subjects).
4.2.3.2 Experiment 2

Unlike in Experiment 1, there was evidence in the results of Chapter 3’s Experiment 2 that at least one third of subjects developed distinct expectations for red and green stimuli, and in a manner somewhat consistent with the respective distributions of those stimuli. This was supported by differences in estimation behaviour both when stimuli were presented and when no stimulus was actually presented but subjects reported a stimulus. The results were not, however, clear cut. Notably, the colour-specific patterns of bias deviated from what would be expected from an ideal observer informed of stimulus statistics, showing rather similar biases at smaller angles as well as positive biases at ±32°.

With regard to simulations (Figure 4.3), we found that biases under most model parameterisations did not notably differ for red versus green stimuli (Figures 4.3E). The inferred clusters were colour-nonspecific and followed a unimodal distribution over the presented stimuli directions. Consistent with our findings for Experiment 1, only when the prior rate $b_0$ was decreased did clear differences in bias appear. This was corroborated by differences in predictive distributions at lower levels of $b_0$. A clear difference in predictive densities was not observed until the rate was reduced to $b_0 = 250$, at which point one could discern a tendency to trimodal distributions for a new red stimulus, and bimodal distributions for a new green stimulus. However, even then, red and green observations tended to be assigned to the same clusters.

4.2.4 Insights on the experimental paradigm

Overall, the simulations of the model showed that the experimental procedure and design did not facilitate learning of two different priors in either experiment. The model had a tendency to infer ‘colour-blind’ clusters and only under specific parameter settings clusters were more colour-specific. A number of reasons could explain such results. First, the stimulus distributions might not be distinct enough in either experiment. As we discussed, subjects of Gershman and Niv (2013) could not differentiate between differently coloured stimuli of which distributions overlapped considerably. Moreover, the uncertainty in both colour and motion direction information due to the stimulus low contrast might occasionally provide contradicting information to the model (e.g., when the colour of a stimulus is misjudged).

We also speculated on the effect of the order of stimulus presentation on learning. At the early stages of the model, simulations showed that blocking of trials with stimuli
Figure 4.3: Average estimation biases and standard deviations of subjects (A-C) and model (D-F) as a function of presented motion direction for Experiment 2. (A,D) Mean estimation biases for all trials. (B,E) Mean estimation biases separated for trimodal (red) and bimodal (green) conditions. Inset: Expected bias if subjects had prior expectations approximating the true stimulus statistics. (C,F) Mean standard deviations of all estimates. Error bars indicate within-subject standard errors. In each plot, the vertical dashed lines indicate the most frequently presented directions (0°, ±32°, ±64°).

of the same colour appeared the produce better separation between the two distributions of Experiment 1. In particular, presentation of the bimodal distribution before the uniform distribution produced good separation in learning, whereas presentation in the opposite order (uniform-bimodal) did not. This finding was surprising as it has been shown that interleaving of trials can facilitate learning versus blocking of trials in many different types of category learning (see Rohrer [2012] for a review) but also in perceptual learning (Mitchell et al. [2008], Wang and Mitchell [2011]). However, simulations with the final computational model, which incorporated no stimulus trials and colour uncertainty, failed to reproduce the initial findings.

We suggested that certain adjustments to the experimental paradigm may be particularly helpful in clarifying effects and guiding model development. One useful outcome of our approach has been to highlight aspects of the task especially likely to make it difficult for subjects to learn that colour is a relevant cue, thus suggesting experimental manipulations that may be of most interest.

First, stimuli of high-contrast, staircase, and no stimulus trials were interleaved
throughout the experiments. To see why this might be problematic, consider that the staircase trials can be seen to be playing two roles. One role is to provide the (intended) uncertainty necessary for expectations to play a role in estimating direction (i.e. to generate bias). Thus, estimates on staircase trials provide evidence of subjects’ learned expectations. However, staircase trials also necessarily play a second role here, which is as data for the inference process. Due to their very uncertainty, however, these trials may have had the unintended effect of weakening the evidence that red and green stimuli are drawn from distinct distributions. A possibly more satisfactory procedure would be to initially present only high-contrast stimuli, providing evidence about stimulus structure, and only later introduce lower contrast stimuli to test what has been learned. Such a ‘training’ vs. ‘test’ distinction is somewhat artificial, but may lead to clearer results. Indeed, it is a prediction of the model that such a manipulation would lead to greater differences between biases for red and green stimuli (model’s predictions are shown in the following section).

A second, related, issue is that reducing contrast induces uncertainty not only about direction but also about colour (subjects misreported the colour of staircase trials on approximately 80% of such trials in the original experiments). It was observed in simulations for Experiment 1 that eradicating colour uncertainty (by setting $\rho_t=1$ in the model) led to greater differences between colour-specific biases. An experimental paradigm that allowed direction and colour uncertainty to be manipulated independently would at least be desirable to disentangle these sources of uncertainty, and eradicating colour uncertainty may lead to different behaviour as predicted by the model. This could be achieved by presenting all stimuli at high contrast while using different motion coherences to induce different levels of uncertainty about direction. However, such an approach would drastically alter the experimental procedure and, thus, make direct comparison with the original results questionable.

### 4.2.5 Model’s predictions

Simulations using the insights on the experimental paradigm produced interesting results. We eliminated colour uncertainty (by setting $\rho_t=1$ for all trials and not just high contrast trials), and changed the order of presented stimuli so that in the first 240 trials the contrast was high ($\nu_t = 1$). In the remaining trials, stimuli were shown at staircase contrast ($\nu_t = \nu_{ST}$). Figure 4.4 shows the model’s predictions for Experiment 1 (4.4A) and Experiment 2 (4.4B). While the prediction of Experiment 1 shows no significant
Figure 4.4: Model's predictions. Predictions of estimation biases for Experiment 1 (A) and Experiment 2 (B) where the largest differentiation in learning was observed. However, in order to obtain these results, extensive tweaking of the parameters were required, which weakened the overall reliability of the results. Insets: Expected biases if subjects had prior expectations approximating the true stimulus statistics for each Experiment.

colour and direction interaction, it shows smaller biases for the Uniform condition and better separation with the biases of the Bimodal condition. On the other hand, the prediction of Experiment 2 shows even better separation between the two conditions (especially for directions $\pm 16^\circ$ and $\pm 48^\circ$) and a significant colour and motion direction interaction.

Unfortunately, results as clear as the ones in Figure 4.4B were found to be very sensitive to the settings of the prior ($b_0$ and $\lambda_0$). We found difficult to produce these results with a degree of robustness that we would be comfortable with and we considered that more data were required to identify aspects of the model that deviated from the experimental results. To that end, we believed worthwhile to test these predictions in a new experiment using the distributions of Experiment 1. Our hypothesis was that by eliminating colour uncertainty and by allowing subjects to learn the distributions initially with stimuli of high contrast, we would observe a decrease in bias levels for stimuli of the Uniform distribution, and qualitatively different behaviours between conditions in the ‘no-stimulus’ trials. Further, the large number of trials with high contrast stimuli would provide us with the opportunity to observe subjects’ behaviour when presented with unambiguous stimuli. We were unable to do that with the results of Chalk et al. (2010) and Chapter 3 for two reasons: first, there was a comparatively small number of high contrast trials, and, second, motion directions of high contrast stimuli were chosen
randomly across all possible directions even outside the 9 main directions. Subjects’
behaviour with unambiguous stimuli presented at the main 9 directions could be used
as a ‘baseline’ against which behaviour in the low contrast trials might be compared.

4.3 Experiment

We conducted a new experiment to test the predictions of the model and, in particular,
the two themes discussed in 4.2.4. A larger number of high contrast trials were shown
separately before the staircase contrast trials and colour uncertainty was reduced to 0
for all stimuli. The methodology and experimental setup was identical to the one used
in Chapter 3, but there were major changes to the experimental design. We briefly
describe the methods and, then, the results of the psychophysical experiment.

4.3.1 Methods

Seventeen naive subjects with normal colour acuity were recruited from the Univer-
sity of Edinburgh. All subjects gave informed written consent in accordance with the
University Of Edinburgh, School Of Informatics Ethics Panel and the Declaration of
Helsinki, and received monetary compensation.

The motion stimuli were identical to the ones used in Chapter 3. The experimental
procedure was identical to Chapter 3 (Figure 3.1), except for one crucial change. The
fixation dot matched the colour of the stimuli and subjects were explicitly informed of
that at the beginning of the experiment. When no stimulus was presented, the fixation
don was randomly shown as either red or green. This eliminated the uncertainty of
the colour of the stimulus without affecting the uncertainty of its presence and motion
direction. Another minor alteration to the procedure was that, at the end of each trial,
the cursor indicating a correct or incorrect response was changed from a green or red
dot to a ‘check’ mark or an ‘x’ mark for a correct or an incorrect choice respectively.
This was done to prevent any confusion between the colours of the distributions and
feedback to subject’s responses.

The experiment consisted of 2 sessions over successive days, lasting around 1 hour
each, with each session comprising of 840 trials. During the first 240 trials, stimuli
were presented in high contrast. For 90 trials of red stimulus, the distribution of mo-
tion directions was uniform, and for 90 trials of green stimulus the distribution was
bimodal. For 40 (20 red & 20 green) trials, stimuli motion directions were random in-
side a window of -70° to 70° from the central direction, and for 20 (10 red & 10 green) trials, stimuli were given completely random directions even outside this window. The remaining 600 trials of the session were divided into 270 trials of red stimulus where the stimuli motion directions distribution was uniform, 270 trials of green stimulus where the distribution was bimodal, and 60 trials where no stimulus was presented. The contrast for the stimuli in the uniform and bimodal distributions was determined using 3-1 staircases on detection performance with one staircase for each distribution. The distributions of the two colours were counter-balanced between subjects in order to avoid any biases caused by colour selection or colour sensitivity.

Similar to the original experiments, subjects’ performance was evaluated after their first session to eliminate those that could not perform adequately in the estimation task. Out of the original 17 subjects, 2 failed to have a mean absolute estimation error less than 30° in the high contrast trials, and they were not asked back for a second session. From the remaining 15 subjects who passed that criteria for 2 sessions, 3 subjects failed to perform correctly in the staircase trials. In particular, they continuously reported detecting targets at very low contrasts, even when the staircase contrast was very close to zero. However, their answers were more often than not counted as correct due to the limited number of trials without stimulus. Thus, their data for the staircase trials were not included in the analysis. Out of the final 12 subjects, for 6 subjects, the motion direction of the red dots followed the uniform distribution and the directions of green dots the bimodal one, whereas for 6 subjects this was reversed. Responses to the high contrast stimuli were analysed for all 15 subjects.

In the estimation task, similarly to Chapter 3, we hypothesised that in some trials subjects made completely random estimates. To account for this, we fitted the estimation responses of each subject to the distribution \( (1 - a) \cdot V(\mu, \kappa) + a/2\pi, \) where \( a \) is the proportion of trials where the subject makes random estimates, and \( V(\mu, \kappa) \) is a von Mises distribution with mean \( \mu \) and width \( 1/\kappa \), given by: \( V(\mu, \kappa) = exp(\kappa \cos(\theta - \mu)/(2\pi I_0(\kappa))). \) The parameters were chosen by maximising the likelihood of generating the data from the distribution. In trials where no stimulus was presented, we aggregated all subjects’ responses and fit the population estimation performance using a linear combination of 6 circular normal distributions. The mean and variance of each distribution were fit by maximising the log likelihood of generating the data from the combined distribution.
4.3.2 Results

4.3.2.1 Motion direction estimates when a stimulus was presented

The first 45 trials of each staircase from each session were excluded from the analysis in order to allow contrast to reach stable levels. We analysed the estimation responses obtained from the uniform and bimodal conditions. Estimation biases for both conditions do not follow the trends we observed in the original experiment. In regards to the uniform condition, estimations were unbiased for all angles, except for $\pm 64^\circ$, where they were negatively biased (Figure 4.5A, ‘red line’). This suggests that, on average, subjects did not perceive motion direction as being closer to the most frequently presented directions. The negative bias at $\pm 64^\circ$ could be the result of an attraction towards the $128^\circ$ window in which stimuli were primarily shown during the experiment.

Regarding the bimodal condition (Figure 4.5A, ‘green dashed line’), subjects’ behaviour was closer to the one observed in the original experiment with estimations at the most frequently presented directions being unbiased, at $\pm 48^\circ$ slightly negatively biased, and at $\pm 64^\circ$ largely negatively biased. However, biases at $\pm 16^\circ$ were negative instead of positive. This suggests an attraction towards the central direction even for the stimuli of the bimodal condition which overpowered the attraction towards the most frequently presented directions.

Standard deviations also differed from the original experiment. For the uniform condition, where the data is more accurate, the highest values were observed at $\pm 16^\circ$ instead of at $0^\circ$ (Figure 4.5C), which suggests a slight attraction towards the central direction. Moreover, standard deviations at $\pm 32^\circ$, $\pm 48^\circ$ and $\pm 64^\circ$ were more or less equal suggesting that subjects made estimations with the same consistency over these directions. Standard deviations for the bimodal condition were slightly more similar to those of the original experiment at least for the outwards directions ($\pm 48^\circ$ and $\pm 64^\circ$).

In contrast to the original experiment, the large number of high contrast trials in this experimental design allowed us to analyse subjects’ behaviour in those trials. Subjects exhibited similar behaviour for both conditions (Figure 4.5B). At $0^\circ$ and $\pm 16^\circ$ estimations were unbiased or slightly negatively biased, and estimations at $\pm 32^\circ$ were unbiased. Interestingly, estimations at $\pm 48^\circ$ and $\pm 64^\circ$ were positively biased suggesting a repulsion from the most frequently presented directions. Surprisingly, estimations further away from the frequent directions appear more biased than closer estimations. As can be expected, standard deviations in high contrast trials were significantly lower than those in the staircase trials, and not significantly different across motion directions.
Figure 4.5: Effect of expectations on estimation biases and standard deviations. Subjects’ mean estimation biases in the staircase trials (A) and in the high contrast trials (B) separated for the uniform and bimodal conditions are plotted against presented motion direction. The standard deviation in subjects’ estimation in the staircase trials (C) and in the high contrast trials (D) separated for the two conditions is plotted against presented motion direction. Results are averaged over all subjects and error bars show within-subject standard error. The vertical dotted line corresponds to the most frequently presented motion directions (±32°)
4.3.2.2 Evolution of estimation biases over the course of each session

The large difference of estimation biases between the staircase and high contrast trials prompted us to investigate how biases might change over the course of each session. We looked at subjects’ estimation biases for three different timeframes of the staircase contrast level; the initial 100 trials, which we previously discarded and where contrast is still relatively high, the first half of the staircase trials for each session, and the last half of the staircase trials for each session.

For the first 100 trials, biases were similar to the ones we saw in the high contrast trials for both conditions, and more so for the uniform condition (Figure 4.6A & 4.6B, black lines). In the first half of each session, estimations at the most frequently presented directions remained unbiased but biases at the outward directions ($\pm 48^\circ$ and $\pm 64^\circ$) reversed from positive to negative (Figure 4.6A & 4.6B, blue dashed and orange dotted lines), with absolute biases larger on later trials compared to earlier trials. It is reasonable to assume that as the session progressed, the stimulus contrast decreased but the difference in average stimulus contrast between the first and second half of each session might have not been extensive since contrast fluctuates around threshold levels. Figure 4.7A shows the stimulus luminance value difference from background luminance for one subject during his first experimental session. The vertical dotted lines indicate the division between the 3 different timeframes (initial 100 trials, first half of the session, and second half). Stimulus contrast in the first half of the session is slightly higher overall than in the second half but the difference is not large.

Thus, a better approach to see how changes in stimulus contrast affected subjects’ estimation behaviour is to divide responses for each subject into two subsets; trials where stimulus contrast was larger than a ‘threshold contrast’ and trials where stimulus contrast was smaller. To calculate the ‘threshold’ for each subject, we followed the same approach used in Chalk et al. (2010). We fitted psychometric curves to each subject’s responses with the function $p_{detect}(c) = \gamma + F(c)(1 - \gamma)$, where $p_{detect}(c)$ is the probability that a subject detected a stimulus at contrast $c$, $\gamma$ is the probability that a subjects reported a stimulus when none was presented, and $F(c)$ is a cumulative normal distribution. We set $\gamma$ to the fraction of trials where each subject reported a stimulus when none was presented, and $F(c)$ is a cumulative normal distribution. We selected a ‘threshold contrast’ $c_{thresh}$ for each subject
Figure 4.6: Effect of expectations on estimation biases over different timeframes of the experimental sessions. Subjects’ mean estimation biases in the initial 100 trials of the sessions (black line), first half of the sessions (blue line) and last half of the sessions (orange line) are plotted against presented motion direction for the (A) uniform and (B) bimodal conditions. Results are averaged over all subjects and error bars show within-subject standard error. The vertical dotted line corresponds to the most frequently presented motion directions ($\pm 32^\circ$).

where $F(c) = 0.75$, and divided subjects’ responses (in the staircase trials) into trials where the contrast was larger than the the threshold and trials where it was smaller.

In Figure 4.7A, the coloured vertical lines indicate the ‘threshold contrast’ for that subject for each colour condition. In Figures 4.7B and 4.7C, we plot subjects’ estimation biases for ‘below threshold trials’ (black dashed line) and ‘above threshold trials’ (blue solid line) for the two conditions. Biases in the ‘above threshold trials’ are almost flat for both conditions whereas in the ‘below threshold trials’, for stimuli moving away from the central motion direction ($\pm 48^\circ$ and $\pm 64^\circ$) they are much larger, more so for the bimodal condition. However, even in the ‘below threshold trials’, we do not observe a positive bias at $\pm 16^\circ$ found in both [Chalk et al. (2010)] and the experiments of Chapter 3. Overall, stimulus contrast seemed to have an effect on subjects’ estimation biases but it was not significant ($p = 0.37$ and $p = 0.11$ for the uniform and bimodal conditions respectively, three-way within-subjects ANOVA).

### 4.3.2.3 Motion direction estimates when a stimulus was not presented

On average, subjects reported detecting a stimulus in $26.8\% \pm 16\%$ of the trials where no stimulus was presented. They reported the colour of the uniform condition in $54.3\%$
Figure 4.7: Estimation biases at different contrast levels. (A) Luminance values above background luminance of red and green stimuli plotted against trial number of session 1 for subject #4. The vertical dotted lines indicate the division between the 3 different timeframes of Figure 4.6. The horizontal red and green dotted lines indicate the 'threshold contrast' values for each condition. (B, C)Subjects' mean estimation biases for trials with stimulus contrast above (blue solid line) and below (black dashed line) the 'threshold contrast' are plotted against presented motion direction for the (B) uniform and (C) bimodal conditions. Results are averaged over all subjects and error bars show within-subject standard error. The vertical dotted line corresponds to the most frequently presented motion directions (±32°).
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Figure 4.8: Subjects’ responses in trials where no stimulus was presented but they reported detecting a stimulus of the (A) uniform condition or (B) bimodal condition and fitted distributions. The vertical grey lines correspond to all the data points (estimation response) pooled across subjects. Fitted response distributions for trials where subjects reported the colour of the uniform distribution (red), the colour of the bimodal distribution (green), and trials where they did not detect a stimulus (black). The vertical dotted line corresponds to the most frequently presented directions (±32°). Error bars show 95% confidence intervals.

We show the data along with the fitted distributions for the trials where subjects reported detecting a stimulus of each condition (Figure 4.8A & 4.8B). We used a Bootstrapping analysis to compare statistics of the distributions (Figure 4.8C). The results suggest that subjects were more likely to report stimuli in the most frequently presented directions when reporting stimulus of the bimodal condition and slightly outwards of those directions when reporting stimulus of the uniform condition. However, there is no significant difference between the two conditions. A difference with the results of the original experiment is subjects’ behaviour on trials where they did not report detecting a stimulus. Subjects tended to move the estimation bar inside the area between the central direction and the most frequently presented directions with increased frequency even when they reported no stimulus. This could be explained due to the increased expectation of a stimulus being present but also suggests that subjects were consciously aware to a larger extent than before of the specific area where stimulus was more likely to appear. In fact, when asked after the experiment whether they have noticed anything about the distribution of motion directions, 10 out of 15 subjects were...
able to describe fairly accurate the window in which stimulus was shown, and 5 out of 15 noticed that there was a difference between the distribution of red and green stimuli, though they were not completely accurate in their guesses of the specifics of that difference.

### 4.4 Discussion

#### 4.4.1 Summary

In this work, we hypothesised that the seemingly sub-optimal subjects’ performance in Experiment 1 of Chapter 3 could be consistent with a Bayesian observer. In other words, the tendency for subjects to treat stimuli of different colours similarly might be normatively determined by a combination of reasonable prior beliefs and the provided visual evidence. We implemented an online learning Bayesian model of the task to test this hypothesis. Simulation results only partially supported the hypothesis. While simulations of Experiment 1 replicated the tendency to learn a colour-nonspecific prior and apply it to both colour conditions, simulations of Experiment 2 also showed that learning was colour-nonspecific. However, tweaking of parameter settings produced examples in which the model showed distinguishable colour-specific biases more so for Experiment 2. Furthermore, the model predicted better separation in learning by applying changes to the experimental design; namely, elimination of colour uncertainty and dividing sessions into a ‘training’ phase of high contrast stimuli and a ‘test’ phase of low contrast stimuli.

An additional psychophysical experiment was conducted using the distributions of Experiment 1 and applying changes to the experimental design. The results were mixed. While estimation biases for the Uniform condition were significantly subdued in comparison to the original results, subjects’ behaviour in trials where no stimulus was presented but they reported a stimulus was similar across conditions. Moreover, subjects, on average, exhibited a strong tendency to move the estimation bar towards the window of presentation and particularly inside $\pm 32^\circ$ from the central direction. Interestingly, we found a repulsion from the frequently presented directions in trials where stimuli contrast was high, and estimation biases appeared to reverse from repulsion to attraction as stimuli contrast decreased over the course of each session.
4.4.2 Reference repulsion

A finding from the original experiments that was not replicated by the model was the slight positive biases at ±32° in both Experiments. A possible explanation for this behaviour is the reference repulsion effect, discussed in 3.5.2, according to which directions close to some reference direction (in this case the frequently presented directions) are perceived as further away from the reference than they actually are. The model, representing an ideal observer, exhibited zero biases at those directions.

The origin of reference repulsion effects is not yet clearly understood. In their original study, Rauber and Treue (1998) conducted two experiments. In experiment 1, observers were asked to indicate whether a random dot display had drifted clockwise or counterclockwise of a subsequently presented comparison line. The authors found that the observers were consistently biased away from the nearest cardinal direction. In their experiment 2, the comparison line was presented together with the random dot display, and, in this case, observers were found to be biased away from the nearest horizontal directions but not the vertical. The authors suggested that this implied that observers only apply a horizontal cardinal bias at simultaneous judgments. Wiescô and Wenderoth (2008) sought to reproduce these findings in an exact replication of the original experiments. However, they observed no consistent pattern in their data. In experiment 1, they found a repulsion effect in only one quadrant of presentation (between 0° and 90° where 0° indicates the vertical upward cardinal and angles are measured clockwise) but not in any other quadrant. In experiment 2, the results were closer to the original ones with a repulsion effect found in all but one quadrant (180° - 270°).

The authors did not offer an explanation for the differences between experiments 1 and 2 but argued that the observed biases are more likely to correspond to specific judgments affected by the experimental procedure than any inherent biases regarding motion direction judgments. The authors also compared several studies of direction judgments with moving dots and found that errors in estimates can vary greatly in magnitude and direction. Even in two experiments where the ‘baseline’ conditions were identical, two different groups of subjects exhibited very different biases in their estimates. These results suggest that without a well understood framework of what these ‘baseline’ biases are (inherent biases or products of the experimental procedure) and where they originate, it can be misleading to make specific claims about them across different experiments and groups of subjects.

The altered design of this chapter’s experiment provided the opportunity to mea-
sure for the first time subjects’ ‘baseline’ behaviour in our experimental task (i.e., subjects’ behaviour to unambiguous stimuli). The ‘training’ phase of the experiment employed a large number of high contrast stimuli moving at the 9 directions used in both Chalk et al. (2010) and Chapter 3. We found that subjects were unbiased for stimuli moving in the more inwards directions (0°, ±16° and ±32°) but strongly biased for outwards directions (±48° and ±64°). More surprisingly, these biases were away from the most frequently presented directions and actually increased for directions further away. However, when stimulus contrast was low these biases reversed from positive to negative indicating a reversal from ‘repulsion’ to ‘attraction’ towards the most frequently presented directions. It is not clear why subjects exhibited a repulsion when presented with high contrast stimuli and why this was later changed. A similar observation was made by Jazayeri and Movshon (2007) in a task requiring fine discrimination of motion direction. Observers viewed a field of randomly moving dots and reported whether the direction of motion was clockwise or counterclockwise of a decision boundary. In 30% of the trials, they also estimated the direction of motion by aligning a bar to the direction they have perceived. Subjects were consistently biased away from the discrimination boundary in their estimations. In a second experiment, subjects had an easier task of discriminating movement towards or away from a decision boundary. Their estimations were then biased towards the boundary. The authors argued that these biases could be the result of ‘decoding’ strategies adopted by the subjects in order to optimise their perceptual judgments, and, thus, the direction of bias depended on the subject’s task; a fine discrimination task led to repulsion biases, whereas a coarse discrimination task led to attraction biases. In our experiment, subjects might have perceived the most frequently presented directions as the reference. So, when stimulus contrast was high and direction judgments could be more accurate, they exhibited a repulsion away from the reference. On the other hand, when contrast was low and judgments became more difficult, subjects exhibited an attraction towards the reference.

It is surprising that biases for directions further away from the reference are larger than biases for directions closer. Interestingly, in Rauber and Treue (1998), biases are strongest not near the cardinals but in directions between the obliques and the cardinals (i.e., between 15° and 35° away from the cardinals). The presented outwards directions were 16° and 32° away from the reference. However, the opposite was found by Jazayeri and Movshon (2007), where biases were larger near the boundary than further away from it. This suggests that our findings and reference repulsion effects
cannot be solely accounted for by the decoding strategy proposed by Jazayeri and Movshon (2007). Further, the high inter-individual variability even at high contrast trials (and in Rauber and Treue, 1998 and Wieseö and Wenderoth, 2008) suggests that these biases are not a result of a common ‘decoding’ strategy and more complex processes might be at work.

The reference repulsion effect could arise from subjects’ implicit discrimination against available internal or external references. However, this line of reasoning introduces a potential problem. The reference repulsion away from the cardinal directions observed in Rauber and Treue (1998) could in reality be a reference attraction towards the oblique directions. In fact, there is some evidence supporting this hypothesis in the complementary ‘colour’ experiment shown in Appendix A. So, it is important to be accurate about defining references in any experimental task. In our experiment, it is reasonable to assume that the frequently presented motion directions are acting as a reference, which is used by subjects when making their estimates. This would explain the strong biases at the outwards directions. However, we saw that estimates were unbiased at $0^\circ$ and $\pm 16^\circ$. This suggests that the central direction could have also been used as a reference by the subjects. Further, the lack of positive bias at $\pm 16^\circ$ even at low contrast stimuli and the high standard deviations at $\pm 16^\circ$ suggest an attraction towards the central direction. It is not clear whether this is a result of the initial high contrast stimulus presentation. Future investigation on how unexpected reference effects emerge in psychophysical tasks could help disambiguate those effects from experimental perceptual manipulations in present and future studies.

### 4.4.3 Subjects’ behaviour in the absence of stimulus

An interesting aspect of the computational model we have not discussed yet is its prediction about subjects’ performance in trials were no stimulus was shown but they reported a stimulus. In the model, estimates on these trials were generated by sampling a particle with probability proportional to its weight and using the value of that particle to set the ‘estimated’ direction. This kind of probability matching rule (Mamassian et al., 2002) has been proposed in previous studies on perception (Mamassian and Landy, 1998, Wozny et al., 2010) and provides a good approximation of subjects’ behaviour in the no stimulus trials.

Simulations of Experiments 1 and 2 produced similar results with the already discussed simulations of estimation biases. In Experiment 1, the estimates predicted by
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Figure 4.9: (A) Fitted response distributions to simulated estimates for Experiment 1 in no stimulus trials. The vertical dotted line corresponds to the most frequently presented directions (±32°). (B) Fitted response distributions to simulated estimates for Experiment 2 in no stimulus trials. Default values are used (b₀ = σ²_data, λ₀ = 1). (C) Simulated data with b₀ = 500 and λ₀ = b₀/σ²_data. The vertical dashed lines indicate the most frequently presented directions (0°, ±32°, ±64°). Error bars show 95% confidence intervals.

The model followed a bimodal distribution irrespective of colour (Figure 4.9A), and in Experiment 2, the estimates followed an almost uniform distribution again irrespective of colour (Figure 4.9B). However, manipulating the settings of the prior can produce estimations much closer to the original results of Chapter 3 but only for Experiment 2 (Figure 4.9C). We set the rate of the prior b₀=500 and the inverse scale of cluster means λ₀ = b₀/σ²_data. The finding that the behaviour predicted by the model can change so drastically by manipulating the prior is intriguing. A default high value of b₀ matching the variance of the presented stimulus produces no differentiations between the two colour conditions. However, if the value of b₀ is decreased and λ₀ is decreased in step with b₀, the model predicts a very clear separation between the colour conditions. Moreover, the model also predicts a shift of the trimodal peak from ±64° to around ±48°. A similar but weaker shift was observed in the original results.

There is a strong correlation between the value of b₀ and the number of clusters...
that the model infers. Lower values of $b_0$ produce higher number of clusters but also more colour-specific clusters. This provides an insight on the role of subjects’ own expectations about the task and their behaviour. For example, subjects who appeared to learn two distinct priors in Experiment 2, could have a prior expectation towards a more complex model of the task (e.g., stimuli of different colours are likely to move in different directions), which corresponds to smaller values of $b_0$ in the model. On the other hand, subjects who developed a single colour-nonspecific prior and applied it to both conditions, could have a prior expectation towards a simple model of the task (e.g., that colour is independent of the direction of motion of a stimulus), which corresponds to higher values of $b_0$ in the model.

In conclusion, we hypothesised that apparent limitations on subjects’ perceptual learning capabilities could be explained by the usual workings of Bayesian inference. On the one hand, the model plausibly replicated subjects’ tendency to treat all stimuli similarly in Experiment 1, regardless of colour. These findings, along with the results of the additional experiment described in this chapter, provide strong evidence that subjects’ behaviour in the original Experiment 1 was not sub-optimal but consistent with a near-optimal observer who has not enough evidence to assume that stimuli of different colour are generated from distinct distributions. On the other hand, in Experiment 2, exploration of parameter space showed settings under which the model expressed distinguishable colour-specific biases. This finding provides an explanation as to why some subjects of the original Experiment 2 showed robust learning of 2 distinct priors but, on average, subjects appeared to learn a complex colour-nonspecific prior and apply it all stimuli.

The experimental results failed to match the model’s predictions. One possible explanation is that the model did not predict certain effects of the initial high contrast stimuli presentation on subjects’ behaviour. In particular, it did not predict the response biases towards the central directions observed in subjects’ estimates when they reported ‘No Dots’, and the repulsion away from the frequent directions when estimating the direction of unambiguous stimuli. Regarding the response biases, subjects quickly learned the window of stimulus presentation and, because of the speeded nature of the estimation task, proactively moved the bar towards the center of that window. The model does not account for the time aspect of the task. A time penalty to longer estimates could be implemented in the model so as to bias estimates towards the window of presentation even when no stimulus is reported. Regarding the repulsion biases, it is not clear what the origin of the biases is and, so, how it could be implemented
in the model. A potential approach would be to add a contrast-dependent adaptation mechanism. It would be interesting to see whether simulations of an extended model would match the lack of biases at $\pm 16^\circ$ in the experimental results, and the differences in estimation biases between high and staircase stimuli.
Chapter 5

Manipulating reward to induce perceptual biases in visual motion perception

In this chapter, we describe a project in which we investigated whether selective manipulation of rewards can affect an observer’s perceptual performance in a similar manner to manipulating the statistical properties of the presented stimulus (as seen in Chalk et al., 2010, the experiments of Chapter 3). This project was carried out in collaboration with Cyril Ng Lung Kit, who was supervised by Peggy Seriès and co-supervised by the author of this thesis, and parts of it appear also in Cyril’s Master’s thesis (Kit, 2014). Cyril originally run the pilot studies and 10 subjects with the bimodal reward scheme. However, due to an undetected bug in the code of the psychophysical experiment, the reward scheme used for these 10 subjects was actually uniform. So the data from the subjects run by Cyril have been incorporated in the results of the ‘control’ experiment where the reward for each motion direction was uniform.

5.1 Introduction

Simple operant conditioning experiments have shown that rewards can strongly affect behaviour. For example, Skinner (1963) showed that rewards increase the frequency of a behaviour (the frequency at which a rat will press a lever), while punishments can reduce the occurrence of a behaviour. In a cued-choice task (Bendiksby and Platt, 2006), monkeys would receive an initial cue for the direction of a target followed by two peripheral cues one of which would flash after a delay to alert the monkey to make
the saccade in order to obtain a reward. The monkeys would receive different rewards depending on which of the peripheral cues flashed. It was found that an increased reward would lead to a higher rate of correct detections and faster response times for responses to that cue.

Reward and attention are closely related concepts (Maunsell, 2004), and manipulation of reward has been extensively used to study attention (Della Libera and Chelazzi, 2006). Several studies have also demonstrated that differential reward in relation to different spatial locations or objects can strongly guide attention (see Chelazzi et al., 2013). On a behavioural level, it is difficult to distinguish between the effects of expectations and attention, and it not uncommon for both to be used interchangeably to describe the same effects on perception. Further, it is unclear whether learning works differently for attention and expectations. Della Libera and Chelazzi (2009) investigated whether highly rewarded attentional selections can affect behaviour in the long term. They used an experimental paradigm that included a training phase in which correct attentional selection of specific visual shapes provided differential rewards, and a non-rewarded test phase, delayed for several days, in which the history of rewards on selection was evaluated. Visual items associated with high rewards became more difficult to reject when they functioned as distractors and easier to select as targets during the test phase, whereas items associated with low rewards where easier to reject as distractors and more difficult to select as targets. Likewise, when the rejection of a distractor was highly rewarded, its rejection was easier as distractor and its selection harder as target, whereas the opposite was found for less rewarded distractor shapes. Further, this learning was found to generalise to a different test task suggesting that learning did not reflect a specific strategy during training but attentional learning in relation to specific stimuli.

As we discussed in section 2.3.4, Chalk et al. (2013) suggested that expectations and attention might share underlying mechanisms or even correspond to two sides of the same mechanism. They proposed that the visual system learns a probabilistic model for the expected stimulus and the reward, and is constantly trying to optimise this internal model in order to predict how sensory input and reward are generated by hidden causes. According to the model, expectations reflect changes in stimulus statistics, and goal-driven attention reflects changes to task relevant reward. Indeed, the model predicts that estimation biases, induced by changes to the presented stimulus statistics, should also be induced by changes to the behavioural task alone.

This hypothesis was initially tested by a previous preliminary study which sought to
investigate the effect of reward manipulation on statistical learning (Papasavvas, 2012). In his Master’s dissertation, Papasavvas used a protocol similar to Chalk et al. (2010) in which stimuli were equally probable to be presented at 8 possible directions. However, 2 of the directions provided an increased reward based on whether subjects were able to correctly identify the presence of dots moving at these directions. The results of that work were inconclusive (Figure 5.1). Although there seemed to be some evidence of a bias in subjects’ estimations in the absence of stimulus (Figure 5.1C), there was no evidence for any estimation bias when a stimulus was presented. A potential flaw with the paradigm was that the estimation task was of very little importance to subjects. Estimation performance did not affect the received reward. Thus, subjects were found to exhibit a pronounced estimation bias towards the central motion direction.

The results of that study suggested that the reward scheme did not have any effect on subjects performance. Was that due to a flaw in the experimental design or was there an effect that was not identified properly? In a Bayesian framework, it is not clear whether the reward scheme would induce changes just in the observer’s loss function, or loss function and prior. A number of studies have investigated the extent to which human observers represent uncertainty about the potential risk or reward of their actions in order to optimise decision-making (see Körding, 2007). Whiteley and Sahani (2008) investigated whether human observers can optimally integrate an externally imposed loss function with an estimate of their internal uncertainty about a visual stimulus. Subjects were asked to perform a simple discrimination task in which they were asked to detect whether the lower of 2 Gabor patches was offset to the left or right, and were rewarded for a correct answer and punished for an incorrect one. Feed-
back was given only periodically (every 15 trials), and, crucially, the loss function was asymmetric; correct responses were given equal points for ‘left’ or ‘right’ but penalties for incorrect responses could differ for answering ‘left’ or ‘right’. The experimental results and comparisons with the model of a Bayesian observer suggested that subjects near-optimally used an internal model of sensory uncertainty in decision-making, and that this model was available even under block feedback. Interestingly, [Landy et al. (2007)] used a similar loss function in an unspeeded visual orientation estimation task and found evidence of optimality but also of sub-optimality under specific conditions. In particular, when stimulus variability was high and changed unpredictably from trial to trial, there was high inter-subject variability, and subjects were found to adopt a variety of suboptimal strategies (e.g. an avoid-the-penalty strategy). On the other hand, [Navalpakkam et al. (2010)] showed experimentally that decisions are affected by both value and saliency of a stimulus, and both sources of information are combined within each trial in a manner consistent with the predictions of an ideal Bayesian observer.

Is it possible that the subjects of Papasavvas (2012) combined a learned unimodal prior of motion directions (centred at the central direction and with width the window of stimulus presentation) with a simple loss function of ‘avoid-the-penalty’? According to the reward scheme, false alarms were heavily penalised (-4 points) whereas correct detections were highly rewarded only for 2 directions (+5 points but +1 points for the remaining 6 directions). Correct rejections and misses were given +1 and -1 points respectively. While this guaranteed a balanced reward scheme, subjects might have overestimated the false alarm penalty and have tried to avoid false alarms as a priority. Further, the fact that the estimation task was irrelevant to the given reward meant that subjects’ estimates were uncorrelated with their loss function.

In this work, we hypothesised that in order for subjects’ perception of the stimulus to be affected by the reward scheme, the reward scheme would need to be correlated with the estimation task. Similarly to the experiment of Papasavvas (2012), stimuli were equally likely to be presented at 8 possible motion directions, and 2 motion directions were more rewarded than other directions. However, in contrast to Papasavvas (2012), reward was depended on subjects’ estimation performance and not on their detection performance. We speculated that this would shift subjects’ attention from the detection task to the estimation task, and we expected to find an attractive bias towards the more rewarded directions in subjects’ estimation performance. A novel experimental paradigm was designed based on the paradigm established in Chalk et al. (2010).
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5.2 Methods

5.2.1 Experimental design

45 naive subjects (15 of them female; 19-35 years of age) with normal or corrected vision were recruited from the University of Edinburgh. All subjects gave informed written consent in accordance with the University of Edinburgh School of Informatics Ethics Panel and the Declaration of Helsinki, and received monetary compensation for their participation. 21 subjects took part in the main experiment where the reward scheme was manipulated and 24 subjects in the control experiment where the reward scheme was uniform.

Subjects took part in 2 sessions, which lasted approximately 1 hour and consisted of 800 trials each. The stimulus was identical to the one used in [Chalk et al. (2010)], and was presented in 8 discrete motion directions. The motion directions were selected in equal 16 degree spacings (+56°, +40°, +24°, +8°, -8°, -24°, -40°, -56° degrees) around a randomly chosen central orientation. Each motion direction was equally likely to be presented in order to avoid any frequency biases.

The dots were displayed at 4 different contrast categories; ‘high contrast’ in which stimuli were presented at 1 cd/m² above background luminance, ‘zero contrast’ in which no stimuli were presented, and two intermediate contrasts in which stimulus contrast was calculated by an upper 4/1 and lower 2/1 staircase. The upper staircase begins at a luminance above threshold, while the lower staircase begins below threshold. So, as the session progresses, the contrast for the upper and lower staircases should converge towards the threshold of detection [García-Pérez, 1998]. The number of trials at each contrast level were distributed as such: 10% high contrast, 20% zero contrast, 20% lower staircase, and 50% upper staircase.

5.2.2 Experimental procedure and feedback

The experimental procedure up to the end of the detection task was identical to the one in [Chalk et al. (2010)] (Figure 2.4). After the detection task, subjects were given feedback based on their performance in the trial. The performance criterion was the estimation error. Feedback was given in two forms; visually displayed on screen combined with an auditory sound effect. The number of points that the subject achieved in the trial is based on the reward scheme (Section 5.1.3), and was shown on the screen in coloured text (‘red’ for negative points, ‘green’ for positive points, and ‘yellow’ for 0.
Figure 5.2: Four examples of visual feedback of the reward provided to subjects after each trial.

points). A few examples of the visual feedback can be seen in Figure 5.2. Block feedback was given every 20 trials in the form of a motivational message to keep subjects engaged in the task and inform them of their average speed and detection performance. For example, if they were correct at detection but slow they would receive a message such as "In the last set of trials...You correctly identified DOTS or NO DOTS in 18/20 trials. Great work! Your average reaction times could be better. You earned 37.0 points and now have 102.0 points."

Sound effects were used to motivate subjects to take note of the scoring system. Correct answers were accompanied by either 1, 2, or 3 correct ‘ding’ sounds depending on the number of points scored. Larger numbers of ‘dings’ denote a higher score. The thresholds were as follows; scores higher than 6 received three dings; scores between 4 and 6, two dings; and scores between 0 and 3, one ding. Incorrect answers, which scored negative points, were accompanied by an incorrect ‘buzzer’ sound. The sound effects were modified to ensure that the duration of each sound was approximately the same.
5.2.3 Reward scheme

The reward scheme is based on estimation performance and is manipulated to emphasise particular directions over others. The scores that subjects achieve depend both on their estimation error (i.e., the distance of their estimate from the actual motion direction) and the direction of motion. The directions were split into 3 categories; the preferred directions (±40°), the central directions (±8°) and the remaining 4 ‘normal’ directions (±24°, ±56°). Thus, the highest number of points is achieved with a small error and with dots moving in the preferred direction.

Table 5.1 shows the reward scheme according to the estimation error and the category of direction. The preferred directions have an increased score compared to the ‘normal’ and central directions. The scores for each estimation bracket in the preferred direction were doubled relative to the scores for the ‘normal’ directions. As discussed earlier, in Papasavvas (2012) subjects showed a strong bias toward the central direction. As a result, the central directions are given a lower score in order to reduce this central bias.

The error thresholds for each reward level were chosen by looking at subjects’ estimation errors in the experiments of Chapter 3. We created a histogram of all subjects’ estimation errors and measured the error at the 20th (4.1°), 40th (8.9°), 60th (14.5°) and 80th (23.8°) percentiles. We used each percentile’s error as a threshold; errors of less than 4.1° receive maximum points, errors of less than 8.9° receive less points and so on. We assumed that subjects’ estimation errors would follow a similar distribution, given that we used the exact same experimental equipment and setup as in Chapter 3. Thus, we expected a reasonable spread across the possible scores. Incorrect estimations (where the estimation error was over 23.8°) were given a penalty score of -4. This score value was chosen as it is approximately the negative mean of the possible positive scores. A negative score is used to help discourage a strategy of choosing the same estimation direction as a response strategy.

A potential problem that arises from rewarding the estimation performance is that subjects may choose to take longer in the estimation task to increase the accuracy of their estimate. The duration of stimulus exposure is 3 seconds, however, in that time subjects are required to both detect the presence or absence of dots and move the estimation bar to match the direction of motion. Thus, there is a speed vs accuracy trade-off which could lead to additional variability in the results as different subjects could operate under different strategies. For example, some subjects might
spend more time to move the estimation bar more precisely and receive more points, whereas other subjects could make fast but crude estimates and receive less points and, possibly, an incorrect notion of the reward scheme. To avoid this potential problem and to promote a more consistent speed-accuracy trade-off strategy across subjects, a speed penalty factor was implemented. A threshold was chosen at the median (1.9s) of subjects’ reaction times in Chapter 3. Estimations that occurred after this time threshold were penalised by 50% and subjects were warned that their estimation was slow. This penalty was applied only on positive scores. If subjects did not click the mouse to make an estimation within the time limit of stimulus exposure (3s), the response was considered incorrect and resulted in a -4 point penalty.

In trials where no stimulus was presented, subjects were given a random reward independent of their estimation and detection choices. They would receive 0 points in 66% of trials and a random number from a selection of scores (1, 1, 1, 2, 3, -4, -4) in the rest of the trials. The scores were selected so that their sum would be zero. The randomised reward on hallucinations was chosen because we did not want to penalise hallucinations too strongly but we also wanted to discourage subjects from developing response strategies of reporting seeing stimulus even when they had not seen one.

Table 5.1: Original reward scheme based on the category of the motion direction and the estimation performance of the subject when a stimulus was presented.

<table>
<thead>
<tr>
<th>Error</th>
<th>&lt; 4.1°</th>
<th>&lt; 8.9°</th>
<th>&lt; 14.5°</th>
<th>&lt; 23.8°</th>
<th>&gt; 23.8°</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preferred</td>
<td>12</td>
<td>8</td>
<td>4</td>
<td>0</td>
<td>-4</td>
</tr>
<tr>
<td>Normal</td>
<td>6</td>
<td>4</td>
<td>2</td>
<td>0</td>
<td>-4</td>
</tr>
<tr>
<td>Central</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>-4</td>
</tr>
</tbody>
</table>

5.2.4 Data analysis

Some subjects who did not meet the detection performance criteria were excluded from the analysis. Data from 1 subject of the main experiment and 4 subjects of the control experiment were removed from the final analysis because they failed to perform adequately in the detection task. In particular, they would consistently report seeing dots even when the stimulus contrast was the same as the background contrast.

The first 100 trials from each session are excluded from the analysis in order to give the contrast staircases time to settle to stable levels. Data from both staircase levels
were combined. The score function and the distribution of the stimuli was designed to be symmetrical around the central motion direction. This allows the data to be folded around the central orientation in order to dramatically increase the number of data points for analysis. For example the +8° and -8° motion directions are combined so that the angles are the absolute angle of the motion direction relative to the central direction.

Subjects’ detection performance is calculated by examining the ratio of subjects’ correct detection responses for each of the presented directions of motion. Estimation biases are calculated in the same way as in Chalk et al. (2010) and Chapter 3, and described in section 3.2.4 of this thesis.

For trials where no stimulus was presented, we calculated the probability density function of subjects’ estimation performance using a kernel comprised of a normal distribution with an automatically computed optimal sigma (Silverman, 1986) adapted for circular data. The probability density function will be examined separately for trials where subjects reported ‘Dots’ and for trials where subjects reported ‘No Dots’. The same method can be used to also analyse subjects’ performance in trials where stimulus was shown, and, as in this experiment the distribution of the presented stimulus was uniform, we utilise it in the results section in order to directly compare subjects’ behaviour in the absence or presence of stimulus.

5.2.5 Pilot studies and resulting alterations to the experimental design

As previously mentioned, Cyril conducted a pilot study in order to collect preliminary data and to test the suitability of the experimental paradigm. Volunteers performed one session of trials (800) under experimental conditions using a complete version of the experiment. Questionnaires were given to the subjects afterwards in order to receive feedback on their experiences (see Appendix C). The data were analysed in order to see whether any trends were discernible.

One concern that arose from the questionnaires and the feedback was that the score function was confusing and sometimes seemed random. It was thought that the variations between the different score criteria could make it difficult for the subjects to recognise how the score they received was affected by their estimation. As a result the score function was simplified by removing the slow speed penalty, i.e. the score which subjects received was not penalised by 50% if their reaction time was above the
Table 5.2: Updated reward scheme based on the category of the motion direction and the estimation performance of the subject when a stimulus was presented. The scores for estimations in the ‘< 23.8°’ bin were adjusted from ‘0’ across all motion directions to ‘2’ and ‘1’ for the preferred and normal direction respectively. This change was implemented in order to further emphasise the reward differences between motion directions.

reaction time threshold. However, if subjects did not make an estimation inside the maximum allowed time of 3 seconds, they still received a penalty. A simple examination of the feedback and data suggested that the reaction time ‘slow’ message was sufficient to encourage suitably speedy responses.

The error thresholds appeared to be suitably chosen such that estimations were distributed across all bins. However, the scores for estimations in the ‘< 23.8°’ bin were adjusted in order to further emphasise the different direction categories. While the score was previously ‘0’ across all categories, the scores for the preferred and normal categories was changed to ‘2’ and ‘1’ points respectively. The main reason for this change was to eliminate any ambiguity that an identical score across all three categories might have produced. The penalties were kept constant. After making these adjustments a few more pilot subjects were run in order to have a better look at the data. 3 subjects undertook the study for 2 sessions each, and the data appeared to show some promising results. Thus, the decision was made to continue using this adjusted experimental paradigm in order to run the main stage of the study.

5.3 Results

We first present the results of the main experiment in which the bimodal reward scheme was used along with the results of the control experiment in which a uniform reward scheme was used. Then, we present subjects’ answers to the post-experimental questionnaire. Finally, we present an analysis based on subjects’ detection performance in the task which shows more clearly the correlations between subjects’ behaviour in the different aspects of the experiment and the effects of the reward scheme on each one.
Figure 5.3: Effect of reward scheme on estimation biases. (A) Subjects’ mean estimation bias and (B) mean standard deviations in subjects’ estimations averaged over all trials are plotted against presented motion direction for subjects presented with the uniform reward scheme (black dashed line) and the bimodal reward scheme (purple solid lines). The vertical dashed line corresponds to the two more rewarded motion directions (±40°). Results are averaged over all subjects and error bars show within-subject standard error.

5.3.1 Estimation performance

First, we asked whether the more rewarded motion directions would bias subjects’ estimation performance. The results show a distinctive pattern very similar to the one reported by Chalk et al. (2010) (Figure 2.5C), which is expected if subjects are biased towards perceiving motion directions as being more similar to the more rewarded directions than they really are (Figure 5.3A, purple solid line). Estimates of the more rewarded directions (±40°) were slightly negatively biased while estimates of ±24° and ±56° were positively and largely negatively biased, respectively. Estimates of motion directions closer to the central motion direction (±8°) were unbiased on average. Overall, there was a significant effect of motion direction on the estimation bias (p < 0.001, two-way within-subjects ANOVA between motion direction and subjects). Similar to the findings of Chalk et al. (2010), the averaged standard deviation at the more rewarded directions was lower than at other directions (Figure 5.3B). Overall, there was a significant effect of motion direction on the estimation standard deviation (p = 0.017, two-way within-subjects ANOVA between standard deviation and subjects).

Figure 5.4 plots individual subjects’ estimation biases for stimuli moving at ±24° (red dots) and ±56° (black dots) versus their estimation bias at ±40°. Estimation
Figure 5.4: Scatter plot of estimation biases at rewarded versus nearby ‘normal’ motion directions. The estimation bias for stimuli moving at ±24° (red) and ±56° (black) from the central motion direction plotted against the estimation bias at the more rewarded ±40° for each subject. The red and black crosses mark the population mean with the length of the lines on the crosses equal to standard error.

Biases at ±24° were significantly larger (p = 0.015) than biases at ±40°, and biases at ±56° were significantly smaller (p = 0.001). This finding shows that the pattern of subjects’ estimation biases that was observed by Chalk et al. (2010) by manipulating the statistical distribution of the stimulus can also be induced through manipulation of reward.

We considered important to verify that the observed estimation biases were not a product of the experimental procedure or pre-existing biases. Thus, we conducted a control experiment in which all presented motion directions were rewarded with the same number of points (the ‘Normal’ scores in Table 5.2). Estimation biases (Figure 5.3A, black dashed line) were more or less equally negative for all presented motion directions, however, they were not significantly different from 0 (p = 0.06, 0.09, 0.85, and 0.2 for directions ±8°, ±24°, ±40°, and ±56° respectively). Overall, there was no significant effect of motion direction on the estimation bias (p = 0.5, two-way within-subjects ANOVA between motion direction and subjects). This suggests that there was an attraction towards the central direction for stimuli moving at all directions but this attraction was on average weak as absolute biases were small and not significantly
different from 0. The averaged standard deviation was highest at motion directions closer to the central direction and decreased at directions further away from it (Figure 5.3B), and there was a significant effect of motion direction on the estimation standard deviation ($p = 0.03$, two-way within-subjects ANOVA between standard deviation and subjects).

The similarities and differences in subjects’ performance between the 2 reward schemes can be seen more clearly by comparing the results directly. While estimation biases are similar for stimuli moving at directions ±8° and ±40°, there is a significant difference between biases at directions ±16° ($p = 0.02$, Wilcoxon rank sum test) and a non-significant difference at ±56° ($p = 0.1$). The differences suggest that the attraction bias towards the more rewarded directions is a result of the reward scheme and not a pre-existing bias.

### 5.3.2 Detection performance

We next looked at the effect of the bimodal reward scheme on subjects’ detection performance. Figure 5.5A plots the fraction of trials where subjects correctly detected stimuli as a function of motion direction. In contrast to the results of Chalk et al. (2010), subjects were not more likely to detect stimuli that were moving at the more rewarded directions (79.4 ± 0.9% detected at ±40° versus 79.7 ± 0.4% over all other directions). There was a significant effect of motion direction on the fraction detected ($p = 0.015$, two-way within-subjects ANOVA) but, on average, subjects were more likely to detect stimuli moving closer to the central direction than stimuli moving further away from the central direction. In fact, subjects were significantly less likely to detect stimuli moving at the most outward directions (±56°, $p = 0.023$, signed rank test) in comparison to all other directions.

Figure 5.6A plots individual subjects’ detection performance for stimuli moving at the more rewarded directions (±40°) versus their mean detection performance at all other directions. While the population mean (black cross) is almost on the identity line, individual data points indicate that subjects’ detection behaviour was highly varied. Most of individual subject data points are further away from the identity line. This suggests that for at least some of the subjects the reward scheme had a strong effect on their detection performance, whereas other subjects were significantly worse at the more rewarded directions in comparison to more central directions.

Averaged reaction times were not different for stimuli moving at the more rewarded
Figure 5.5: Effect of reward scheme on detection rates and reaction times. (A) The fraction of trials where subjects correctly detected a motion stimulus and (B) time taken for subjects to click on the mouse during stimulus presentation are plotted against presented motion direction for subjects presented with the uniform reward scheme (black dashed line) and the bimodal reward scheme (purple solid lines). The vertical dashed line corresponds to the two more rewarded motion directions ($\pm 40^\circ$). Results are averaged over all subjects and error bars show within-subject standard error.

Looking at the results of the uniform reward scheme, there was no significant effect of motion direction on the fraction detected ($p = 0.3$, two-way within-subjects ANOVA). Averaged reaction times were very similar for stimuli moving at all directions and there was no significant effect of motion direction on reaction times ($p = 0.15$).

The cause of the observed difference of subjects’ detection performances between the two experiments is less clear than the cause of the difference of their estimation
performances. While we would expect detection rates to be higher at central directions for the uniform reward scheme (as it is the center of the window of stimulus presentation), detection rates are unaffected by motion direction. Moreover, detection rates at the more rewarded directions ($\pm 40^\circ$) are very similar for both groups of subjects ($p = 0.47$, Wilcoxon rank sum test). However, there are significant differences in the detection rates at $\pm 24^\circ$ and $\pm 56^\circ$ ($p = 0.02$ and $p = 0.036$ respectively). It is not clear whether this is an effect of the reward scheme or subjects consciously followed different strategies in order to improve their detection performance and if so why. A detailed analysis based on subjects’ detection behaviour in a later section will provide some insight on this issue.

### 5.3.3 Behaviour in the absence of stimulus

On average, subjects presented with the bimodal reward scheme reported detecting a stimulus in $26.67\% \pm 17.2\%$ of the trials where no stimulus was presented. The average number of reported visual hallucinations was considerably higher than the one reported in [Chalk et al.](2010), where subjects reported detecting a stimulus in
Figure 5.7: Effect of reward scheme on estimation responses in the absence and presence of a stimulus. (A) Probability density functions of subjects’ estimates of motion direction in trials where no stimulus was presented but they reported detecting a stimulus for subjects presented with the uniform reward scheme (black dashed line) and the bimodal reward scheme (purple solid line), as well as when they did not report detecting a stimulus (red dashed line and blue solid line, respectively). The vertical dotted line corresponds to the two more rewarded motion directions ($\pm 40^\circ$). Results are averaged over all subjects and error bars show within-subject standard error. (B) Corresponding probability density functions for trials in which a stimulus was presented.

10.8% $\pm$ 2% of trials. Figure 5.7A plots the averaged probability density functions of subjects’ estimates of motion direction in trials where no stimulus was presented but they reported detecting a stimulus (purple solid line). Subjects were biased to report motion close to the more rewarded directions but not significantly more in comparison to less rewarded inward directions. This suggest that, in contrast to the findings of Chalk et al. (2010), the reward scheme did not have a significant effect on subjects estimation behaviour in trials where no stimulus was presented but they reported seeing a stimulus. Another interesting point of the plot is that the probability of subjects reporting movement at the most outward directions ($\pm 56^\circ$) was significantly lower in comparison with the mean probability for all other presented directions ($p = 0.005$, signed rank test). This, in conjunction with the significantly worse detection rates and reaction times, suggest a strong inward ‘compression’ effect on stimuli moving at the most outwards directions.

Subjects, on average, also appear to have a response strategy in trials where no stimulus was presented and they did not report a stimulus (blue solid line, Figure
5.7A). They were strongly biased to move the estimation bar towards the central direction. The same behaviour can be seen in trials where a stimulus was presented (Figure 5.7B). Subjects were strongly biased to move the estimation bar towards the central direction at the start of the trial even when they reported that they have not seen the presented stimulus. This behaviour could be explained by the speeded nature of the task. Subjects were instructed to respond as fast as possible, so most of them would move the estimation bar toward the center of the area where stimuli were presented at the start of the trial in order to report the possible presence of a stimulus as fast as possible. This behaviour was not observed in Chalk et al. (2010), where fast responses were explicitly asked from subjects during initial instructions but reaction times did not have any direct effect on immediate or block performance feedback.

Interestingly, subjects presented with the bimodal reward scheme were also biased to report motion in the more rewarded directions even though they were not more likely to detect stimuli moving at these directions (purple solid line, Figure 5.7B). On the other hand, they were less likely to report motion close to the central direction even though they were more likely to detect stimuli at central directions. These findings provide more evidence towards the existence of an attractive bias towards the more rewarded directions on presented stimuli. However, this bias does not seem to have affected subjects’ visual hallucinations.

Looking at the results of the uniform reward scheme, on average, subjects reported detecting a stimulus in 25.22% ± 19.4% of the trials where no stimulus was presented. Subjects were more likely to report motion close to directions ±40° away from the central direction but variability in their performance was high. They were also less likely to report motion in the most outward directions in comparison to all other directions but not significantly (p = 0.19, signed rank test). This could explain the small increase at the ±40° directions. Subjects used the response strategy of moving the estimation bar toward the central direction even in trials where they did not report detecting a stimulus. More interestingly, subjects were more likely to report the direction of a presented stimulus exactly at the central direction than other directions (black dashed line, Figure 5.7B), even though the central direction was never presented and the detection performance was worse at the more central directions (±8°). Overall, the uniform reward scheme appears to have no strong effect on subjects’ estimation performance in the presence or absence of stimulus.

Directly comparing subjects’ responses during hallucinations, there is no significant difference between the responses of the two groups of subjects. Both groups of
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Subjects appear to be equally likely to report any motion direction inside the presented window of directions with the exception of the most outward directions (±56°). Subjects’ responses in trials where a stimulus was presented are more distinct but there is no significant difference. This is not unexpected on account of stimuli being equally likely to be presented at all 8 discrete motion directions.

5.3.4 Signal detection analysis

At this point, it would be worthwhile to analyse subjects’ behaviour using Signal Detection Theory (SDT) measures and, in particular, calculate subjects’ sensitivity and response bias. Suppose that a subject is using a decision variable to distinguish between stimulus presence or absence. The decision variable has a range of different values across signal trials (presence of stimulus) and across noise trials (absence). The distribution of values in signal trials is the signal distribution and in noise trials is the noise distribution. Sensitivity is the degree of overlap between the signal and noise distributions, while the response bias is the general tendency of the subject to report the presence or absence of a stimulus (Stanislaw and Todorov, 1999). This analysis will provide us with a more clear picture of whether sensitivity to a stimulus differs between presented motion directions (e.g., whether there was a difference between central and outwards directions) and whether the bimodal reward scheme had any effect on subjects’ response biases.

A way to calculate sensitivity is to find \( d' \), which measures the distance between the signal and noise means in standard deviation units. It is calculated as follows:

\[
d' = \Phi^{-1}(H) - \Phi^{-1}(F)
\]

where \( \Phi^{-1} \) is the ‘inverse phi’ function, \( H \) is the hit rate (the percentage of correct stimulus detections) and \( F \) is the false alarm rate (the percentage of false positives per noise trials). In our experiment, the hit rate is easy to calculate but the false alarm rate is less straightforward. We grouped all estimations in trials where no stimulus was shown in 16° bins around the presented motion directions, and calculated the percentage of total estimations for each bin to the total number of no stimulus trials. That percentage is the false alarm rate for each motion direction. Larger values of \( d' \) indicate a greater ability to distinguish signals from noise.

A way to calculate response bias is to find \( \beta \), which assumes that responses are based on a likelihood ratio. If the decision variable corresponds to a value \( x \) on a given
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trial, the numerator for the ratio is the likelihood of obtaining a value $x$ on a signal trial (i.e., the height of the signal distribution at $x$), whereas the denominator for the ratio is the likelihood of obtaining $x$ on a noise trial (i.e., the height of the noise distribution at $x$). Subjects report ‘Dots’ if the likelihood ratio exceeds $\beta$ or ‘No dots’ otherwise. It is also convenient to calculate the natural logarithm of $\beta$. In that case, negative values of $\ln(\beta)$ signify bias in favour of ‘Dots’ responses, whereas positive values of $\ln(\beta)$ signify bias in favour of ‘No dots’ responses. The natural logarithm of $\beta$ is calculated as follows:

$$\ln(\beta) = \frac{[\Phi^{-1}(F)]^2 - [\Phi^{-1}(H)]^2}{2}$$

(5.2)

We calculated both metrics for all subjects of each of the reward schemes and the results can be seen in Figure 5.8. Sensitivity at each direction appears to be similar across experiments; it is higher at the central directions and lowest at directions $\pm 40^\circ$. In fact, sensitivity at $\pm 40^\circ$ was significantly lower than sensitivity at all other directions for both experiments ($p = 0.01$ and 0.03 for bimodal and uniform respectively). We find similar results in subjects’ response biases. Subjects are on average significantly more likely to respond ‘Dots’ at directions $\pm 40^\circ$ in comparison to all other directions for both experiments ($p = 0.025$ and 0.01 for bimodal and uniform respectively).

These findings suggest that the reward scheme did not affect subjects’ sensitivity or response bias. Instead, subjects, on average, appear to be less able to distinguish signal from noise near the $\pm 40^\circ$ directions. A possible explanation for such a behaviour is that subjects follow 2 distinct conscious (or unconscious) strategies when trying to detect a stimulus; either guide their attention to the central direction or discriminate between clockwise and anticlockwise from the central direction and search for the stimulus in the outwards directions around the edges of the window of stimulus presentation. Both of these strategies would lead to lower sensitivities at $\pm 40^\circ$ because these directions are always in-between the central and most outwards directions.

The original work of [Chalk et al. (2010)] did not include a SDT analysis, so, for the purpose of comparing our findings with theirs, we measured the sensitivity and response bias of subjects in [Chalk et al. (2010)] using the same procedure (Figures 5.8C & 5.8D). Subjects’ average sensitivity was lower at the ‘middle’ directions ($\pm 32^\circ$ and especially at $\pm 48^\circ$), which is in agreement with our findings in this work. We can speculate that subjects’ sensitivity at $\pm 32^\circ$ would actually be even lower if these directions were not frequently presented. Subjects’ response biases appear to have been affected by the stimulus distribution, as they are lowest (i.e., subjects have a
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Figure 5.8: Effect of reward scheme on subjects' sensitivity and response bias. (A) Subjects' mean sensitivity and (B) response bias averaged over all trials is plotted against presented motion direction for subjects presented with the uniform reward scheme (black dashed line) and the bimodal reward scheme (purple lines). Results are averaged over all subjects and error bars show within-subject standard error. The vertical dashed line corresponds to the two more rewarded presented motion directions ($\pm 40^\circ$) of the bimodal reward scheme. (C) Subjects' mean sensitivity and (D) response bias averaged over all trials is plotted against presented motion direction for the 12 subjects of [Chalk et al. (2010)](#). The vertical dotted line corresponds to the two more frequently presented directions ($\pm 32^\circ$).
greater tendency to report ‘Dots’) at the most frequently presented directions (±32°). Overall, subjects of Chalk et al. (2010) were less likely to report ‘Dots’ in comparison to subjects in our experiments.

5.3.5 Experimental feedback

After finishing the experimental sessions, subjects were asked to complete a questionnaire (Appendix C). The percentage of subjects who answered positively to some of the more interesting questions are summarised in Figure 5.9. The most surprising finding from the questionnaires was that only 55% of the subjects (11 out of 20) who did the bimodal reward scheme experiment answered that they thought that some directions were rewarded more than others, while the same answer was given by 40% of the subjects (8 out of 20) who did the uniform reward scheme experiment. 85% and 95% of subjects for each experiment (bimodal and uniform respectively) agreed that gaining points in the task was important for them. Finally, the vast majority of subjects correctly thought that estimation performance was a criterion for allocating points (90% bimodal, 75% uniform) but the majority also thought incorrectly that correct detection was also a criterion (70% bimodal, 75% uniform) and so was speed of response (60% bimodal, 55% uniform).

These findings suggest that the reward scheme was engaging to subjects and motivated them to maximise their score. At the same time, it was not transparent enough for subjects to develop response strategies to improve their scores. For example, from the 10 subjects with the highest scores of the bimodal experiment, only 3 subjects reported that some directions were more rewarded than others. The high number of subjects of the uniform experiment who thought some directions were more rewarded also suggests that subjects would try to understand the reward scheme, potentially developing incorrect assumptions about it. However, most subjects acknowledged that estimation accuracy played a role in gaining more points, and subjects with higher scores exhibited significantly smaller standard deviations in their estimations and, consequently, longer reaction times on average.

3 subjects noted that they were more engaged by the sound feedback than the visual (number of points) feedback. 5 subjects also thought that the penalties were high and that the punishment sound could become annoying. Interestingly, 4 subjects complained that the feedback given was sometimes incorrect as they were certain of the presence of a stimulus (during a hallucination) or the absence of a stimulus (when a
stimulus was presented but the contrast was very low). Finally, the visual instruction to respond faster after ‘slow’ responses was enough to motivate subjects to perform faster even though there was no penalty to score from a ‘slow’ response.

5.3.6 Analysis based on subjects’ detection performance

Lastly, we investigated why subjects of the two experiments appeared to have similar performance in some metrics (detection and hallucinations) but different in others (estimation). We used subjects’ detection performance as a starting point. We divided the subjects presented with the bimodal reward scheme into 2 groups based on their detection performance at the more rewarded directions. One group (rewarded, n = 10) had better detection rates at the more rewarded directions compared to the average of all other directions (corresponding to the data points to the right of the identity line in Figure 5.6A), while the other group had worse (inwards, n = 10, left of the identity line). The purpose of the split of subjects into the two groups is not to suggest that subjects can be classified into two groups of distinct behaviour but to make easier to identify the correlations between the different performance metrics. Figure 5.10 compares the

Figure 5.9: Summary of subjects’ answers to the post-session questionnaire. The percentage of subjects of the bimodal (purple) and uniform (grey) experiments who answered positively to each question.
Bimodal reward scheme - Divided by detection performance

**Rewarded (n = 10), Inwards (n = 10)**

Figure 5.10: Performance comparison of subjects who exhibited high detection rates at the more rewarded directions (±40°) with subjects who had low detection rates at the more rewarded directions. (A) (Left) Detection rates and (right) reaction times, (B) (left) estimation biases and (right) standard deviations, (C) hallucinations, and (D) (left) sensitivity and (right) response bias. Error bars show within-subject standard error. The vertical dashed line corresponds to the two more rewarded motion directions (±40°).

We performed a similar split for subjects presented with the uniform reward scheme. One group (outwards, n = 12) had better average detection rates at the 4 more outwards directions (±40° & ±56°) compared to the average at the inward directions (±8° & ±20°), and vice versa for the other group (Inwards, n = 8). Figure 5.11 shows the

Performance of each group in each of the metrics we have presented so far. Detection performance seems to be strongly predictive of subjects’ visual hallucinations (5.10C) and reaction times (5.10A right). However, estimation biases and standard deviations (Figure 5.10B) are very similar for both groups. The familiar shape that indicates attraction towards the more rewarded directions can be seen for both groups, while standard deviations are smallest at those directions. The attractive bias is significant for the rewarded group (p = 0.01 between ±20° and ±40°, and p = 0.002 between ±56° and ±40°) and non-significant for the inwards group (p = 0.4 and p = 0.08 respectively).
Uniform reward scheme - Divided by detection performance

Outwards ($n = 12$), Inwards ($n = 8$)

Figure 5.11: Performance comparison of subjects who exhibited high detection rates at the more outward directions ($\pm 40^\circ$ & $\pm 56^\circ$) with subjects who had high detection rates at the more inward directions ($\pm 8^\circ$ & $\pm 20^\circ$); (A) (left) Detection rates and (right) reaction times, (B) (left) estimation biases and (right) standard deviations, (C) hallucinations, and (D) (left) sensitivity and (right) response bias. Error bars show within-subject standard error.

performance metrics of each group. As before, detection performance is strongly predictive of subjects’ visual hallucinations and reaction times. However, estimation biases are very different to the ones exhibited by subjects of the bimodal reward scheme. Subjects of the *outwards* group are mostly unbiased across directions, whereas subjects of the *inwards* group are negatively biased and show an attraction towards the central direction (though the effect is not significant). Standard deviations also differ with subjects of the *outwards* group being more consistent at outwards directions while subjects of the *inwards* group at the more inward directions.

Subjects’ behaviour across both experiments suggest that detection behaviour is strongly related with reaction time and behaviour in the absence of stimulus. A possible explanation is that subjects either focused their attention towards the central direction and responded faster and more accurately for stimuli moving at inward directions.
or focused towards the outwards directions and responded significantly slower. These potential strategies do not appear to be related to the reward scheme because they seem to be employed by subjects across both experiments. However, independent of detection performance, the reward scheme seems to have an effect on subjects’ estimates of presented stimuli. Subjects of the uniform reward scheme are largely unbiased, whereas subjects of the bimodal reward scheme are biased towards the more rewarded directions even when they perform better at ‘inwards’ directions. The difference in the number of subjects classified into the two groups in each experiment (10 vs 10 in the main experiment and 12 vs 8 in the control experiment) could explain the differences we identified in subjects’ averaged detection rates between experiments (Figure 5.5A).

We investigated whether such correlations between metrics were also present in the performance of the subjects in Chalk et al. (2010). We split subjects into 2 groups based on their detection performance. As almost all subjects were more successful in detecting a stimulus moving at the frequently presented directions, we compared detection rates at the 3 inward directions (0° & ±16°) with rates at the 4 outwards directions (±48° & ±64°). Out of a total of 12 subjects, 5 subjects had comparatively higher rates at the outward directions (outwards group), whereas 7 subjects at the inward directions (inwards group). Figure 5.12 shows the performance of each group. In agreement with our results of the bimodal reward scheme, reaction times for the outwards group are significantly higher than the inwards group, and estimation biases and standard deviations are similar for both groups. Interestingly, the visual hallucinations are also quite similar between both groups, and, more importantly, subjects of the inwards group are not likely to report a stimulus near the central directions in contrast to our results. Likewise for subjects’ response biases (Figure 5.12D right), independent of their detection performance, subjects show similar response biases across all motion directions, which mirrors their visual hallucinations. In our results, subjects’ response biases were correlated with their detection performance regardless of the reward scheme. Overall, this analysis suggests that while the bimodal reward scheme had an effect on subjects’ estimates in the presence of stimulus, it did not have an effect on subjects’ detection rates and estimates in the absence of stimulus in contrast to the bimodal distribution of motion directions in Chalk et al. (2010) which affected all aspects of subjects’ performance.
Chapter 5. Manipulating reward to induce perceptual biases in visual motion perception

Chalk et al. (2010) - Divided by detection performance

Outwards ($n = 5$), Inwards ($n = 7$)

![Graphs showing detection rates, reaction times, and biases for outwards and inwards directions.]

Figure 5.12: Comparing the behaviour of subjects of Chalk et al. (2010) who exhibited high detection rates at the more outward directions ($\pm 48^\circ$ & $\pm 64^\circ$, blue group) with subjects who had high detection rates at the more inward directions ($0^\circ$ & $\pm 16^\circ$, green group); (A) (left) Detection rates and (right) reaction times, (B) (left) estimation biases and (right) standard deviations, (C) hallucinations, and (D) (left) sensitivity and (right) response bias. Error bars show within-subject standard error. The vertical dotted line corresponds to the two more frequently presented motion directions ($\pm 32^\circ$)

5.4 Discussion

5.4.1 Summary

The results of the main experiment in which the bimodal reward scheme was used showed that subjects developed an attractive bias towards the more rewarded motion directions. This bias affected subjects’ estimates of presented stimuli so that subjects perceived motion directions as being more similar to the more rewarded directions than they really were. However, this attractive bias was not observed in subjects’ average detection performance or in trials where no stimulus was presented but they reported seeing a stimulus.
The results of the control experiment in which the uniform reward scheme was used showed that subjects developed a very small attractive bias towards the central direction for all presented motion directions. Subjects’ average detection performance was unaffected by the presented motion direction and they were not more likely to report any specific direction in trials where no stimulus was presented but they reported seeing a stimulus.

Subjects of both experiments, on average, exhibited a response strategy in trials where they reported not seeing a stimulus. More often than not, they would move the estimation bar towards the central direction at the start of a trial. Further, in both experiments, estimations made for stimuli moving at the most outward directions were biased towards the window of presentation and this behaviour appeared to transfer to visual hallucinations. Finally, an exploratory analysis based on subjects’ detection performance across both experiments indicated that there might be a correlation between subjects’ detection performance, reaction times, and visual hallucinations but not estimation performance.

5.4.2 Effects of reward manipulation on stimulus perception

In our main experiment, we found evidence that subjects developed expectations for the more rewarded directions and these expectations had a significant effect on their estimation performance. This effect on subjects’ estimation behaviour replicates our findings from [Chalk et al. (2010)] and Chapter 3 where the statistical properties of presented stimuli were manipulated. Subjects’ average detection performance was not better at the more rewarded directions as it was found in [Chalk et al. (2010)]. However, a similar result to the one here was found in Experiment 1 of Chapter 3 where subjects exhibited better performance at the central directions while still exhibiting an estimation attractive bias towards the more frequently presented directions.

The biggest departure from the previous experiments can be found at subjects’ behaviour in trials where no stimulus was presented but they reported seeing a stimulus. In all previous experiments using the same experimental paradigm, subjects’ were found to be significantly more likely to report a stimulus at the more frequently presented directions. Even in the additional experiment of Chapter 3 (presented in Appendix A) where motion directions were spread across 360° and estimation biases might have been ‘masked’ by strong pre-existing biases, there was evidence of subjects learning the statistical properties of the stimuli in visual hallucinations. The results of
Papasavvas (2012) hinted towards an effect of the reward scheme in hallucinations. However the limited number of subjects and the possible ‘compression’ effect of the most outward directions, which was also observed here in our uniform reward scheme experiment, make such claim difficult to substantiate. Further evidence toward this ‘compression’ effect can be seen in subjects standard deviations of estimates. Average standard deviations across both experiments are lower for motion directions further away from the central direction. Based on subjects’ responses even when they reported not seeing a stimulus, subjects were able to easily identify the window of presented stimuli. It is highly probable then that subjects were able to identify the extremes of the window ($\pm 56^\circ$) and, thus, be less likely to estimate movement outside of this window.

5.4.3 Reward and attentional optimisation

We introduced a reward scheme to the experimental paradigm of Chalk et al. (2010), and we hypothesised that manipulation of the reward scheme alone, without manipulation of the stimulus statistics, would induce estimation biases similar to the ones induced by manipulating the stimulus statistics. Within the framework proposed by Chalk et al. (2013), when there is a mismatch between the internal model of the observer and the external environment, behavioural demands should alter visual processing. Attention should alter visual processing to improve predictions of the received reward at the cost of learning a worse model of the sensory inputs. This is exactly what we found in this work. The manipulated reward scheme, which rewarded some directions more than others, induced estimation biases that are very similar to the biases observed by manipulating the statistics of the stimuli even though in this case the stimulus distribution was uniform over the discrete motion directions. These attractive biases were not found in the results of the uniform reward scheme experiment where subjects’ estimates were on average unbiased. This suggests that the origin of the attractive biases was the manipulation of the reward scheme and not the changes to the experimental procedure and design. However, manipulation of any reward scheme does not necessarily induces the same perceptual effects. In the results of Papasavvas (2012), where a different reward scheme that did not include the estimation task was manipulated, no attractive biases were found. This indicates that reward manipulation should induce biases only if it is behaviourally relevant.

It is not exactly clear whether these biases indicate a change in the subjects’ prior
or loss function. We can speculate that certain aspects of subjects’ performance are more closely linked to changes in perception and behaviour. For example, estimation biases are more likely to represent a change in the perception of the stimulus, whereas the response bias of moving the estimation bar at the start of the trial represents a change in behaviour. Interestingly, in the experiments of this chapter, we found that subjects’ biases were not present in detection and visual hallucinations in contrast to the findings of Chalk et al. (2010). The exploratory analysis based on subjects’ detection performance suggested a potential explanation of subjects following different detection strategies. Another explanation could be the interaction of the prior with the loss function. We could argue that if estimation biases were caused solely by changes to the prior, we would also observe clear biases on detection performance and hallucinations (as in Chalk et al. 2010). Thus, subjects could have developed a unimodal or bimodal prior, which affected their detection performance accordingly, and a bimodal loss function, which affected their estimation performance. However, there is no evidence to verify this hypothesis. Modelling of the task would be necessary in identifying subjects’ priors and loss functions, and it would be an interesting direction for future work.

It would be interesting to investigate whether the effect of the reward scheme was induced more from the association with the reward sounds than the visual feedback of exact scores. The former did not require the immediate attention of subjects, whereas the latter required explicit reading of the score and comparison with previous rewards. Future replications of the experiment using only sound feedback or only visual feedback as a reward cue could potentially clarify this issue.

We already discussed potential reasons as to why subjects’ visual hallucinations between our results and the results of Chalk et al. (2010) differed. Another possibility is that relatively small changes to the experimental paradigm, for example the lack of trial-by-trial feedback on detection performance, might have significantly affected subjects’ behaviour in the absence of stimulus. Subjects were significantly more likely to report a hallucination than in Chalk et al. (2010) (and this is reflected also in their response biases), which suggests that the threshold of a false alarm could have been lower for all motion directions. Thus, subjects would be more likely to report a hallucination across all directions and not just the more rewarded ones, and this could ‘hide’ the effect of the reward scheme on hallucinations. It is not surprising then to find hallucinations correlated with subjects’ more attended outwards or inwards directions even when the reward scheme was uniform.
Chapter 6

Expectations developed over multiple timescales facilitate visual search performance

In this chapter, we describe a psychophysics experiment that was conducted to explore how expectations of different time scales (from the last few trials to hours to long-term statistics of natural scenes) interact to alter perception.

6.1 Introduction

Expectations can be developed over long time frames (hours, days, or years). For example, [Stocker and Simoncelli] provided evidence towards the hypothesis that the visual system expects objects to be static or move slowly, and this prior expectation can explain perceptual phenomena such as the aperture problem and why speed perception can differ between high and low contrast stimuli (Stone and Thompson, 1992). While this slow-speed prior is thought to develop over the lifetime, recent research shows that experience within an hour long experimental session, and across days of exposure, with quickly moving stimuli can alter this prior towards an expectation of more quickly moving speeds (Sotiropoulos et al., 2011a). Expectations can also be developed over very short time frames (seconds or minutes). When we search for a target with a particular feature (shape, orientation, colour etc.), it is easier to detect or discriminate that target or one of its features if we have seen it or interacted with it in the immediate past. This effect is formalised as perceptual priming and suggests that an implicit memory system strongly influences how visual attention is allocated.
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Perceptual priming in visual search has been studied for a variety of features including orientation (Olivers and Meeter, 2006), motion direction (Kristjánsson, 2009), shape (Fecteau, 2007), and colour (Maljkovic and Nakayama, 1994). Many studies have also shown that repetition of trials with a target in the same location can improve search performance significantly (e.g., Geng and Behrmann, 2005; Maljkovic and Nakayama, 1996; Miller, 1988), and this improvement can be very location specific. For example, Le Dantec and Seitz (2012) showed that repeatedly performing a visual search task to find a subtly different line orientation led to long-lasting performance improvements in a large number of independent locations that incompletely transferred to neighbouring locations as close as 1.5 degrees of visual angle. While these studies have shown that the statistical predictability of a target’s location due to repetition can facilitate performance, a study by Druker and Anderson (2010) found that the statistical properties of a target’s location can influence the observer’s performance even outside of priming effects. In order to dissociate the effect of a high-probability location from a simple location repetition, they used continuous probability distributions that included a very large number of possible locations in contrast to typical visual search experiments that use a limited number of possible locations. They found that subjects learned the distribution of the stimulus implicitly and their performance was improved more than what would account to priming effects given the distance to recently presented targets. Together, these results suggest that people are continuously integrating the statistics of the environment and using this information to update their expectations of future experiences.

Visual search provides a useful framework in which to investigate the formation of expectations. While mainly signal detection approaches have been used in accounting for visual search phenomena (Verghese, 2001), studies have also used a Bayesian framework to successfully model human visual search behaviour and investigate how it compares to that of a Bayesian optimal observer (Eckstein et al., 2004; Eckstein et al., 2009; Elazary and Itti, 2010; Ma et al., 2011). Droll et al. (2009) compared the performance of learning the statistics of cue validity by human observers in a visual search task to that of an ideal Bayesian observer. The authors found that human observers were able to learn the statistics in a single experimental session but learning was slower compared to that of an ideal observer even using supervised feedback. Recently, Vincent (2011) investigated whether better performance in a visual search task is achieved by combining visual evidence and prior beliefs in a Bayesian optimal way. Observers’ prior expectations were manipulated in two experiments via periph-
eral cuing and via explicit information about the stimulus spatial probabilities. It was found that observers improved their detection rates by optimally combining slightly biased priors with sensory evidence irrespective of how expectations were manipulated. Interestingly, counter-predictive peripheral cues (i.e., cues that indicated that a location was less likely than average to contain a target) increased choice reaction times, whereas counter-predictive spatial probabilities slightly decreased reaction times. This suggested that counter-predictive cues guided observers’ attention involuntarily and unavoidably to the less probable cued locations.

These results suggest a link between perceptual priming and expectation formation and that these may both be parsimoniously described within a Bayesian model. One possibility is that perceptual priming influences how attention shifts to repeated stimulus features or locations. Sigurdardottir et al. (2008) showed that priming improved detection performance for a target but did not facilitate acuity judgments for the same target. This suggests that priming might influence the speed of attentional shifts rather than stimulus sensitivity directly. Also, in an experiment where eye movements were analysed, Becker (2008) found that the accuracy and time course of the first saccade within a trial was modulated by priming effects. Observers would saccade faster and more accurately when the same target was repeated than when it changed between trials. At the same time, many studies have manipulated contextual expectations so as to direct attention to particular locations or features. For example, Posner (1980) developed a task in which a cue explicitly predicts the location of a subsequent target with a certain probability. Subjects were found to process the target stimuli faster and more accurately on correctly cued trials than on incorrectly cued trials, and the difference has been shown to increase with cue validity (e.g., Downing, 1988). In that sense, priming may be considered as a form of contextual expectation in a very short timescale. This outstanding issue naturally extends to the question of what is the distinction between attention and expectations. The focus of spatial attention has been successfully compared to a spotlight (Posner, 1980) as well as to a zoom lens (Eriksen and Yeh, 1985). A more rare Bayesian account for attention was described by Eckstein et al. (2006), in a study where subjects looked at pictures with targets at expected or unexpected locations, or targets completely absent. A differential weighting Bayesian model was consistent with subjects’ pattern of first saccades toward probable locations in target absent images. Both attention and expectations are thought to be controlled by similar cognitive processes (Corbetta and Shulman, 2002), and, on a behavioural level, both can have superficially identical effects on performance. However, the exact
mechanisms that produce these effects remain unclear, as is the exact nature of the interaction between attention and expectations (Summerfield and Egner, 2009).

In this study, we addressed these issues by investigating the form in which perceptual priming acts in a statistical learning experimental paradigm, and how it interacts with expectations formed over longer timescales. We do this through a novel visual search paradigm (though with some similarities with the task in Droll et al. (2009)) in which we presented human observers with brief displays of low contrast stimuli and asked them to report the presence of a stimulus (yes/no task) as well as the exact location of the stimulus (localisation task) at the same time. We manipulated their expectations by presenting stimuli in some locations more frequently than others. This task provides an interesting glimpse into the impact of priors in perceptual judgments as we are able to track a number of separate, but likely related, types of errors; mislocalisations are errors in detection where the location of an item reported is incorrect, false alarms are errors in detection where stimuli are detected when none were present, positional-errors refer to small but systematic biases in localisation estimates within the neighbourhood of a target location. We hypothesised that subjects would learn the stimulus distribution and use that information to improve their performance in the task, and that consistent with prior work (Chalk et al., 2010; Chapter 3), to observe biases in subjects’ localisation performance towards the more frequently presented locations (positional-errors), and increased false detections in the absence of stimulus (false alarms and mislocalisations) matching the probability distribution of the actual stimuli. In addition to these effects, we investigated the form of interaction between the rapidly learned expectations of the stimulus distribution and priming from very recent stimulus presentations. Our hypothesis was that subjects would integrate both sources of information, which would facilitate their detection performance in the more probable stimulus locations but also induce more false alarms in the process.

6.2 Methods

6.2.1 Stimuli & subjects

28 naive subjects (17 of them female; 19-33 years of age) with normal or corrected vision were recruited from the University of California, Riverside. All subjects gave informed written consent in accordance with the University of California, Riverside Human Research Review Board and the Declaration of Helsinki, and received course
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The stimuli consisted of 1, 2, or 3 white dots (0.5\(^\circ\) in diameter) at 12 possible locations equally spaced on a circle at 4\(^\circ\) of visual angle from the center of the screen. They were generated using the Matlab programming language with the psychophysics toolbox (Brainard, 1997; Pelli, 1997) and displayed on a CRT monitor with a resolution of 1400 x 1050 at 100 Hz. Subjects viewed the display in a darkened room at a viewing distance of 70 cm. A chin rest was used to maintain a constant head location and viewing distance. The display luminance was calibrated and linearised with a Cambridge Research Systems Colorimeter and the background luminance was set to 5.05 cd/m\(^2\).

6.2.2 Procedure

At the beginning of each trial, a central white cross was presented as a fixation point (Figure 6.1A). Then, the stimulus was presented for 100 ms. The display cleared and subjects were presented with a central circle and a cursor, which they could move freely with a mouse. Subjects were instructed to click inside the circle to finish the trial if no stimulus was perceived. On the other hand, they were instructed to move the cursor outside the circle if they had perceived one or more stimuli. Then, a white dot appeared at the same eccentricity as the stimulus, and moved in conjunction with the mouse cursor. Its function was to help subjects make an accurate localisation of where they had perceived a stimulus. Subjects were instructed to move the cursor to the location they detected a stimulus and click to validate their decision. At the same time, a bar extended from the center of the screen to the point of the cursor. Subjects used the bar to indicate their confidence level of the stimulus being present. The longer the length of the bar the more confident they were of their choice. After clicking, a small blue dot and a blue bar remained on screen. Subjects were free to report as many stimuli as they wanted. To finish the trial, they had to return the cursor inside the central circle and click. No immediate feedback was given after each trial. However, block feedback was given every 50 trials in the form of detection performance in 10% steps (e.g., ‘Your performance rate was between 60% - 70%’) along with a motivation message.
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Figure 6.1: Experimental procedure. (A) Subjects were presented with a fixation point followed by the stimulus for a brief 100ms. After the screen was cleared, subjects were presented with a circle and a cursor, which they could freely move. If they had not perceived a stimulus, they were instructed to click inside and finish the trial. If they had perceived a stimulus, they were instructed to move the cursor outside of the circle, and a dot similar to the stimulus would appear to allow them to indicate the exact location of the target. Simultaneously, they could extend a bar away from the circle to indicate their confidence level of seeing a stimulus at that location. (B) There were 12 possible stimulus locations, at 4° of visual angle, equally spaced on a circle, 15°, 45°, and 75° away from the horizontal cardinal. (C) Probability distributions of presented stimulus locations for the control (black dots) and bimodal (blue dots) groups of subjects. In the control group, all locations were equally presented, while in the bimodal group, 4 locations were 2 times more likely to be presented, and 2 locations were 3 times more likely to be presented.
6.2.3 Design

The experiment consisted of 2, 1 hour, sessions (conducted on successive days) of 900 trials each. The stimuli were presented in 3 different contrast levels; in 60% of trials contrast was determined using a 2/1 staircase on detection performance (staircase contrast), in 10% of trials contrast was high (1.05 cd/m\(^2\) above the background luminance) and stimuli were easily visible (high contrast), and in 30% of trials there was no stimulus presented at all (zero contrast). High contrast trials were used as a metric of subjects’ confidence and localisation performance. Since stimuli were easily detected in those trials, subjects should, on average, be very confident of their choice and also be fairly accurate in the localisation of the stimulus. Thus, performance in the high contrast trials allowed us to calculate a baseline behaviour for each subject regarding their confidence and localisation error when reporting a stimulus and compare it to their behaviour in the staircase and zero contrast trials. In the staircase and high contrast levels, up to 3 stimuli could be presented in the same trial; 1 stimulus was presented in 73.33% of trials, 2 stimuli in 20%, and 3 stimuli in 6.67%. We used multiple stimuli in some trials in order to encourage more false alarms during the experiment. If subjects were uncertain about the exact number of stimuli presented in each trial, they would be more likely to report a false alarm even in trials where they had already reported a presented stimulus.

Stimuli could appear at 12 possible locations (Figure 6.1B). The probability that a stimulus would appear at a given location depended upon the subject’s group. In the control group (\(n=12\)), stimuli were equally likely to appear at all locations (Figure 6.1C). In the bimodal group (\(n=16\)), stimuli were more likely to appear at locations in quadrants II and IV than at locations in quadrants I and III; in particular, stimuli were twice more likely to appear at locations 15\(^\circ\) (locations 3 & 9) and 75\(^\circ\) (locations 5 & 11) away from the horizontal cardinal, and 3 times more likely at locations 45\(^\circ\) away from the horizontal cardinal (locations 4 & 10). This grid was rotated for each subject such that the location on the circle for location 1 was located at one of 4 possible orientations (45, 135, 225, 315). As the bimodal distribution is symmetrical, this created 2 possible subgroups of frequent versus non-frequent locations that were counter-balanced between subjects (8 subjects in each subgroup) in order to cancel out any existing biases.
6.2.4 Data analysis

The first 150 trials from each session were excluded from the analysis in order for the staircase to reach stable levels. No significant differences were observed in subjects’ behaviour across the 2 experimental sessions (Appendix D, Figure D.1). Thus, we combined data across both sessions. High contrast trials were excluded from the analysis.

As discussed in the experimental procedure, subjects were free to make an exact localisation of a stimulus they reported. In order to count correctly detected stimuli, we divided all possible angles in 12 30° bins. The center of each bin was the exact angle of each presented location. We then assumed that subjects correctly identified the location of a stimulus, classified as a correct detection, when they localised inside the respective 30° bin of each location, otherwise the response was classified as a mislocalization. During our analysis, it became clear that subjects’ detection performance was significantly affected by the absolute location of a stimulus and, in particular, by the distance from the horizontal cardinal. In order to show more clearly any underlying effects of the stimulus distribution, we present the stimulus locations in 3 categories based on the distance from the horizontal cardinal. Thus, locations were grouped into horizontal (15° away from the cardinal; absolute locations 2, 3, 8, and 9 in Figure 6.1B), intermediate (45° away; locations 1, 4, 7, and 10), and vertical locations (75° away; locations 5, 6, 11, and 12). In the results section, we will present subjects’ performance over the different location categories in a within-subjects analysis. However, all statistical analyses regarding the effect of frequency of a location have been done on all 12 locations, and not on the 3 location groups.

Subjects would sometimes report that they had perceived one or more stimuli in trials where no stimulus was presented (zero contrast trials). They did so in approximately 2% of trials for the control and the bimodal groups. However, that frequency was not large enough to allow for a within-subjects analysis. Instead, we resample each subject’s data with replacement for all 12 locations and then aggregate all false alarms from all subjects. We repeat the process 100,000 times and calculate 95% confidence intervals. As we discussed in the Introduction, we will refer to these responses as false alarms. The aforementioned mislocalizations were more frequent than false alarms consistently across all subjects (in approximately 10% of trials for the control and 8% for the bimodal group) allowing us to do an analysis similar to the detection performance (within-subjects).
6.3 Results

6.3.1 Stimulus distribution effects on detection performance

First, we investigated whether the stimulus distribution had an effect on subjects’ detection performance and the probability that subjects would make a mislocalization (e.g., reporting the wrong stimulus location when a stimulus was present). As discussed previously, we separated stimuli locations into three categories by their distance from the horizontal cardinal: horizontal, intermediate, and vertical (Figure 6.2). Further, we separated the locations of stimuli presented to the bimodal group by the probability of a stimulus to appear at a location, into frequent and non-frequent locations. Figure 6.2A shows the probability distribution of each location category for the control group and for the two conditions of the bimodal group. It was twice as likely for a stimulus to appear at a frequent horizontal or vertical location than at a non-frequent similar location, and three times more likely for a frequent intermediate location than a non-frequent intermediate location. If there is a strong effect of the stimulus distribution on performance, we expect to find a significant difference between the detection performance of frequent and non-frequent locations as well as significantly more false alarms at frequent than non-frequent locations.

Looking at the fraction of correctly detected stimuli (i.e., the fraction of correct detections over total stimuli presentations, Figure 6.2B), there is a significant effect of absolute stimulus location on performance. Subjects were significantly better at detecting a stimulus at locations that were closer to the horizontal cardinal, and increasingly worse at locations away from that cardinal ($p < 0.0001$, one-way within-subjects ANOVA for all groups). Regarding the effect of the stimulus distribution, detection rates were consistently higher for stimuli presented at the frequent locations than at the non-frequent locations, and there was a significant effect of a location being frequent on the detection performance ($F(1,160) = 9.81$, $p = 0.007$, two-way within-subjects ANOVA between frequency and subjects). It is not surprising that the average detection performance is very similar between the control group and the frequent condition of the bimodal group, since its upper bound is set dynamically by the 2/1 staircase procedure on correct detection. Overall, subjects of the bimodal group appeared to have learned the stimulus distribution and that facilitated their performance at the frequently presented locations but at the cost of reduced performance at the non-frequently presented locations.

Looking at subjects’ mislocalizations, there was a significant effect of absolute
Figure 6.2: Effect of stimulus distribution on detection performance. (A) (Left) Dividing stimulus locations by their distance from the horizontal cardinal. (Right) Probability distributions of stimulus locations divided by their distance from the horizontal cardinal for the control group (black solid line), and for the frequent (red dashed line) and non-frequent (green dashed-dotted line) conditions of the bimodal group. (B) The fractions of correctly detected stimuli are plotted against presented stimulus location. (C) Relative frequencies of subjects’ mislocalizations and (D) false alarms are plotted against stimulus location. (E) Subjects’ mean sensitivity and (F) response bias are plotted against stimulus location. Results are averaged over all subjects and error bars show within-subject standard error, except for (D) false alarms where results are summed over all subjects and error bars show 95% confidence intervals.
stimulus location on their relative frequencies ($p = 0.02, p = 0.0001, \text{ and } p = 0.01$ one-way within-subjects ANOVA for control, frequent, and non-frequent respectively, Figure 6.2C). The frequency of mislocalizations was calculated out of the total number of trials where a stimulus was presented at a different location to the mislocalization. The total number of trials where a stimulus was presented at a frequent location was larger than at a non-frequent location, so it was important to calculate relative frequencies and not just absolute frequencies. In contrast to detection rates, subjects were significantly more likely to report a stimulus in the intermediate or vertical locations than in the horizontal locations. There was no significant effect of a location’s condition (frequent or non-frequent) on the relative frequency of mislocalizations ($F(1, 160) = 1.46, p = 0.24$, two-way within subjects ANOVA between frequency and subjects). Overall, it was more likely, but non-significantly so ($p = 0.18$, two-way between subjects ANOVA), for subjects of the control group to make an incorrect response than for subjects of the bimodal group.

We also found that subjects reported false alarms in no stimulus trials (Figure 6.2D), and, were consistently more likely to report a stimulus at a frequent location than at a non-frequent one, but the difference was noticeable only at intermediate locations. This observation is consistent with prior work where false alarms were shown to be consistent with perceptual hallucinations of motion (Seitz et al., 2005; Chalk et al., 2010, Chapter 3). The average frequency that subjects of the bimodal group would report false alarms was almost identical to subjects of the control group for horizontal locations. However, it was more likely for subjects of the bimodal group to report a false alarm at a frequent location than subjects of the control group for vertical and intermediate locations. This suggests that the stimulus distribution had a strong effect not only between locations (frequent versus non-frequent intermediate locations) but induced more overall false alarms in the most frequently presented locations (frequent intermediate). Like in our previous work, the close similarity between subjects’ false alarm distributions and the distribution of the stimulus suggests that false alarms might directly reflect the prior beliefs of subjects in the task. In summary, the results suggest that the stimulus distribution facilitated detection performance but also increased subjects’ false alarms at the frequent stimulus locations.

Finally, we computed subjects’ sensitivity (Figure 6.2E) and response bias (Figure 6.2F). The hit rate at each location was defined as the number of correct detections divided by the total number of trials in which a stimulus was presented at that location, and the false positive rate was defined as the sum of mislocalizations and false alarms
divided by the total number of trials in which a stimulus was not presented at that location. Because the number of false alarms was low, we used a loglinear approach before calculating the hit and false positive rates, which involves adding 0.5 to both the number of hits and false positives and adding 1 to both numbers of trials (Stanislaw and Todorov [1999]). For sensitivity we computed $d'$ and for response bias the natural logarithm of $\beta$. Not surprisingly, sensitivity significantly decreased for locations away from the horizontal cardinal ($p = 0.008$ & $p < 0.0001$ for subjects of the control and bimodal groups respectively, one-way within-subjects ANOVA). Looking at the subjects of the bimodal group, there was no significant effect of frequency on sensitivity ($F(1, 160) = 0.81$, $p = 0.38$, two-way within-subjects ANOVA). The opposite was found regarding subjects’ response biases. There was a significant effect of frequency on response bias ($F(1, 160) = 7.04$, $p = 0.018$). The difference between conditions was smallest at horizontal locations and largest at the intermediate locations. Interestingly, subjects of the control group were more likely to report a stimulus at the intermediate locations but there was no significant effect of location of response bias ($p = 0.35$, one-way within-subjects ANOVA). Overall, the signal detection theory analysis highlights the significant sensitivity differences between locations closer and further away from the horizontal cardinal, and the effect of the stimulus distribution on subjects’ bias to report the presence of a stimulus.

### 6.3.2 Stimulus distribution effects on localisation performance

Absolute stimulus location and location frequency had a significant effect on detection performance. We next looked at whether these properties had an effect on subjects’ positional estimates of presented stimulus. We expect that if there was a strong effect, subjects’ positional-errors in reporting the target locations, on average, would be biased towards the frequently presented locations. Figure 6.3A shows the averaged positional-error biases for staircase contrast and high contrast trials. A positive bias indicates systematic positional-errors away from the horizontal cardinal, while a negative bias systematic positional-errors towards the horizontal cardinal. Subjects of both the control and bimodal groups appear to be biased away from the horizontal cardinal at horizontal and intermediate locations both in staircase and high contrast stimuli. In vertical locations, they were slightly biased or unbiased in staircase contrast stimuli but negatively biased in high contrast stimuli. There was no significant difference between subjects’ positional-error biases at frequent and non-frequent locations in staircase or
high contrast trials ($F(1, 160) = 0.37, p = 0.55$ and $F(1, 160) = 1.04, p = 0.32$ respectively) but there was a significant effect of absolute position on positional-error biases ($p < 0.0001$). The similarity of biases for both low (staircase) and high contrast stimuli at frequent and non-frequent locations suggest that these biases are preexisting and largely unaffected by presented contrast or stimulus distribution.

However, we still expect position estimates in high contrast trials to be more consistent across locations and subjects in comparison to staircase contrast trials. Figure 6.3B plots the averaged standard deviations of position estimates for staircase contrast and high contrast trials. Indeed, standard deviations in high contrast trials were significantly smaller than in staircase contrast trials across all data ($p = 0.041$, $p = 0.011$, $p = 0.016$ three-way within-subjects ANOVA for control, frequent, and non-frequent respectively). There is also a strong effect of the stimulus distribution; standard deviations of position estimates at frequent locations were significantly smaller than at non-frequent locations in staircase contrast trials ($F(1, 160) = 9.82, p = 0.007$), and the smallest deviations were exhibited at the most frequently presented intermediate locations. However, across all data, there was no significant effect of absolute stimulus location on the standard deviation. These results suggest that the stimulus distribution had no effect on the direction of positional-errors but had a significant effect on the consistency of position estimates.

### 6.3.3 Confidence levels over correct detections, mislocalisations, and false alarms

Subjects were more likely to detect a stimulus and more consistent in reporting the actual location of that stimulus when it was presented at a frequent location. We then asked whether subjects were also more confident when they detected a stimulus at a frequent location. We used the high contrast trials as a benchmark for confidence levels reported by subjects when they had detected a stimulus. Figure 6.3C shows box plots (along with data points for each subject) of the differences in confidence level reported by subjects of the control group between high contrast trials and trials where they detected a stimulus (left), reported a mislocalization (center), and a false alarm (right). The median lines are significantly smaller than 0 for correct detections and mislocalizations (with 95% confidence) but not for false alarms. Moreover, confidence levels were significantly higher in false alarms than in mislocalizations. Interestingly, some subjects were more confident in their false alarms than in their average confi-
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Figure 6.3: Effect of stimulus distribution on localisation performance and confidence. 

(A) Subjects’ mean positional-error biases are plotted against stimulus location for (left) staircase contrast stimuli and (right) high contrast stimuli. A positive bias indicates localisations away from the horizontal cardinal (0° angle), while a negative bias indicates localisations towards the horizontal cardinal. 

(B) Standard deviations in subjects’ position estimates distributions are plotted against stimulus location for (left) staircase contrast stimuli and (right) high contrast stimuli. Results are averaged over all subjects and error bars show within-subject standard error. 

(C) Box plots, along with individual subject data, of the differences in confidence level reported by subjects of the (C1) control group and of the (C2) bimodal group (divided into frequent and non-frequent conditions) between high contrast trials and correct detections of a stimulus (left), mislocalizations (center), and false alarms (right). Dots indicate values for each subject. Each box shows the inter-quartile range, the horizontal line within the box shows the median, and the notches show 95% confidence intervals on the median.
dence in successful high contrast trials at the same stimulus location. It is worthwhile to remind the reader here that subjects did not receive any immediate feedback for their reports during the task. Thus, one could argue that subjects could have reported a stimulus as a response strategy when uncertain about the presence of a stimulus, and they would never be directly penalised for using such a strategy. However, we saw that false alarms were rare (Figure 6.2D). This, in conjunction with the high, on average, confidence suggests that subjects may have felt quite certain when they chose to report a false alarm and provides some additional evidence towards the argument that subjects may have actually ‘perceived’ these stimuli.

A similar behaviour was exhibited by subjects of the bimodal group. Subjects’ reported confidence for false alarms across locations and for correct detections at frequent locations were not significantly different from confidence for high contrast correct detections. Subjects’ median confidence in frequent locations was higher than in non-frequent locations for correct detections and false alarms but neither effect was significant. In contrast to subjects of the control group, we saw a much larger variation in the bimodal group, with some subjects being very uncertain about their mislocalizations and false alarms. Overall, there was no strong effect of the stimulus distribution on subjects’ confidence at detecting a stimulus.

### 6.3.4 Presented stimulus proximity influences subjects’ mislocalisations

As seen in Figures 6.2 and 6.3, mislocalizations were more frequent than false alarms but with largely reduced confidence on average. That hints to a qualitative difference between mislocalizations and false alarms. We investigated whether we could distinguish between mislocalizations that represented genuine false alarms and those that represented just extreme errors in position estimates. Figure 6.4A shows the proportion of mislocalizations as a function of the distance from the nearest presented stimulus in the same trial. The distance ranges from 1 to 6. In the vast majority of mislocalizations across all data (≈80%), a stimulus was presented at a nearby location in the same trial (distance = 1). It is more likely that such responses correspond to large errors (localizations outside the 30° window which defines a correct detection), rather than to false alarms unrelated to the stimulus. If so, the presented stimulus would be scored as undetected. Indeed, only a small fraction of these stimuli were scored as detected (Figure 6.4B). This might explain the significantly reduced reported confidence of mislocal-
izations (Figure 6.3C). These data are consistent with the idea that mislocalizations are aptly termed and reflect cases where stimuli were detected but the location of the stimuli were not well encoded or recalled.

Another way to visualise subjects’ behaviour in these mislocalizations is to plot a histogram of subjects’ position estimates. Figure 6.4C shows histograms of subjects’ (of the bimodal group) position estimates when a stimulus was presented at a nearby location (distance = 1, grey bars) and at locations further away (distance > 1, blue bars). Position estimates are grouped into $3^\circ$ bins. Because the stimulus distribution is symmetrical (Figure 6.1C), it is possible to fold the 12 presented locations around the horizontal cardinal into 6. For example, we can combine the results from the two frequent horizontal locations (locations 3 & 9 in Figure 1), and so on. In Figure 6.4C, $0^\circ$ angle indicates the horizontal cardinal, positive angles indicate frequent locations, and negative angles indicate non-frequent locations. When mislocalizations were at a distance of 1 from a stimulus, most position estimates were made at the boundaries between locations (vertical dotted black lines) and very few happened close to the stimulus locations (red and green vertical dashed lines). When mislocalizations were at a distance larger than 1 from an actual stimulus, position estimates were less frequent but more evenly distributed across the visual space. These larger mislocalizations, are most consistent with false alarms than misjudgments of the stimulus position because it would have to be an error of at least $45^\circ$. However, we cannot say with complete certainty whether these responses represent very large errors or genuine false alarms. Overall, subjects’ mislocalizations appear to be significantly affected by the proximity to a presented stimulus, and, so, are very difficult to correctly classify as errors in position estimates or false alarms. For that reason, we do not include mislocalizations in our following analysis regarding recency effects, and our modelling of subjects’ behaviour in the task.

Figure 6.4D plots a zoomed in version of the behaviour in mislocalizations when distance > 1 along with subjects’ position estimates of false alarms. For both sets of data, most position estimates were made around the area $+45^\circ$ away from the horizontal cardinal where the most frequent intermediate stimuli were presented. This effect was more pronounced for false alarms. We calculated the probability density function for the false alarms data using a kernel comprised of a normal distribution with an automatically computed optimal sigma (Silverman, 1986) adapted for circular data. The probability density function matches the stimulus distribution; subjects were 2.4 times more likely to report a false alarm at $+45^\circ$ (frequent intermediate location) than at -
Figure 6.4: Effect of stimulus proximity on mislocalizations. (A) Proportions of subjects’ mislocalizations as a function of the distance from the nearest presented stimulus in the same trial for the control group (black squares), and for the frequent (red circles) and non-frequent (green diamonds) conditions of the bimodal group. (B) The fraction of correctly detected stimuli, which were presented at a nearby location (distance = 1) to a mislocalization in the same trial. Results are averaged over all subjects and error bars show within-subject standard error. (C) Histograms bimodal group’s position estimates when they made a mislocalization. Grey bars indicate mislocalizations with a distance of 1 from the nearest stimulus and blue bars indicate a distance larger than 1. Vertical red and green dashed lines indicate frequent and non-frequent locations respectively, and vertical dotted black lines indicate the boundaries between locations. The 0° angle indicates the horizontal cardinal. (D) Histograms of bimodal group’s position estimates when they made a mislocalization with a distance larger than 1 from the nearest stimulus (blue), and when they reported a false alarm (yellow).
45° (non-frequent intermediate), 1.4 times at +15° (frequent horizontal) than at -15° (non-frequent horizontal), and 1.5 times at +75° (frequent vertical) than at -75° (non-frequent vertical). This result agrees with our previous findings regarding false alarms matching the stimulus distribution (Chalk et al., 2010; Chapter 3), and along with the high, on average, confidence levels reported on false alarms suggests that subjects were certain of their reports of the presence and location of these false alarms.

### 6.3.5 Effect of stimulus presentation at the same location $n$-trials back

So far, we showed that the stimulus distribution had a strong effect on subjects’ detection performance, positional-errors, and false alarms. Finally, we investigated the effect of location priming on subjects’ behaviour and whether there was an interaction with the stimulus distribution. Figure 6.5A shows subjects’ detection performance as a function of whether a stimulus was presented at the same location $n$-trials back for the control group, and the frequent and non-frequent conditions of the bimodal group. In this analysis, we did not divide locations based on their distance to the horizontal cardinal in order to have as many data points as possible. For the control group and the frequent condition of the bimodal group, there is a strong effect on detection performance for stimuli presented at the same location in the preceding trial, but the effect steadily weakens when exposure is further in the past. Overall, there was a significant effect of recent exposure to the same stimulus location for both control group and frequent condition ($p = 0.009$ and $p = 0.005$ respectively, one-way within-subjects ANOVA). However, we see an important difference in subjects’ performance between the frequent and non-frequent conditions. There was no significant effect of recent stimulus exposure to detection rates for non-frequent locations ($p = 0.73$) and there was a significant effect of a location being frequent on the detection performance ($p = 0.0325$, three-way within-subjects ANOVA). With the exception of when $n = 5$ (i.e., a stimulus was presented at the same location in the 5th preceding trial), detection rates are consistently higher at frequent locations than at non-frequent, and there is only a marginal improvement for the non-frequent locations even when a stimulus was presented at the same location in the preceding trial ($n = 1$). A possible explanation would be that the same stimulus being presented in two consequent trials is very rare for the non-frequent locations (Appendix D, Figure D.2, green bars) and that subjects might ‘learn’ that a stimulus repeat at a non-frequent location was highly unlikely. However,
Figure 6.5: Effect of stimulus presentation at the same location $n$-trials back. (A) The fraction of correctly detected stimuli as a function of whether a stimulus was presented at the same location $n$-trials back for the control group (black square), and for the frequent (red circles) and non-frequent (green diamonds) conditions of the bimodal group. Results are averaged over all subjects and error bars show within-subject standard error. Dashed lines indicate the best fitting linear functions. (B) Relative frequencies of subjects’ false alarms in the absence of stimulus as a function of whether a stimulus was presented at the same location $n$-trials back. Dashed curves indicate the best fitting quadratic functions. Response probabilities are calculated out of the total number of trials subjects could make an incorrect response.
a stimulus repeat was equally unlikely for subjects of the control group (Figure D.2, black bars) but there is still a very strong effect of a stimulus repeat on detection performance for that group. Even when a stimulus was not presented at the same location in the last 9 trials \( n = 10+ \), which accounts for the majority of trials in each session, detection rates were higher at the frequent than at the non-frequent locations, though non-significantly \( p = 0.18 \), signed rank test).

We next looked at the effect of location priming on false alarms. Figure 6.5B shows the relative frequencies that subjects would report a false alarm as a function of whether a stimulus was presented at the same location \( n \)-trials back. Again, exposure to a stimulus in the most recent 3 trials had a strong effect only for the control group and the frequent condition of the bimodal group but not for the non-frequent condition. It was only marginally more likely than average for subjects to report a false alarm at a non-frequent location even after a stimulus was presented at the same location in the preceding trial. Stimulus exposure further in the past seem to have very little effect for any group. The difference can be seen also by fitting the data to a quadratic function (dashed curves). It is interesting to note that the fits for the control and frequent data are very similar even though they represent the behaviour of two different groups of subjects. In summary, location priming had a significant effect on subjects’ detection performance and probability of reporting false alarms for all subjects regardless of the stimulus distribution. However, when the stimulus distribution was bimodal, this effect only extended to locations at which it was more likely that a stimulus would be presented.

### 6.4 Computational model

In previous work [Chalk et al., 2010, Chapter 3], we described subjects’ performance in a motion estimation and detection task by using models that assumed subjects used a Bayesian strategy in which they combined a learned prior of the stimulus statistics with their sensory evidence in a probabilistic way. These models were shown to outperform models that assumed subjects developed response strategies unrelated to perceptual changes. Moreover, they successfully fit the experimental data, and predicted subjects’ behaviour in trials where no stimulus was presented but subjects reported a stimulus. Here, we describe a simple Bayesian model of the experimental task and implement it in order to investigate the form of the prior distribution that would predict subjects’ behaviour in the experiment. In particular, we were interested in understanding why
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There were strong recency effects at frequently presented locations but weaker effects at non-frequently presented locations. The model replicates the behaviour of a sub-optimal Bayesian observer performing the experimental task. The observer combines a learned prior of the stimulus statistics with her sensory evidence in a probabilistic manner. Trial-by-trial variability is driven by noise in the sensory likelihood (which in turn generates false alarms in the absence of stimulus), while recency effects are driven by a dynamically changing prior of recent stimulus history. We did not explicitly fit the model to the data; however, we did a systematic exploration of parameter space in order to find values under which the model approximated subjects’ average performance in the task.

According to the model (Figure 6.6, Bayesian model), on each trial, the observer computes the posterior probability of a stimulus’ presence at each of the 12 possible stimulus locations given the sensory input at all locations \( (x) \). The posterior probability \( \text{post}_i(s|x_i) \) of a stimulus being present \( (s) \) at the \( i \)th location is the combination of the likelihood \( \text{like}_i(x_i|s) \) of the input given stimulus presence at the \( i \)th location with the prior probability \( \text{prior}_i(s) \) of a stimulus being present at the \( i \)th location, using Bayes’ rule:

\[
\text{post}_i(s|x_i) \propto \text{like}_i(x_i|s) \cdot \text{prior}_i(s)
\]

On each trial, up to 3 stimuli \( j \) combine linearly to generate the sensory input received by the observer at each location \( (x_i) \). The probability of observing a stimulus at the \( i \)th location is calculated according to:

\[
\text{like}_i(x_i|s) = c \cdot \sum_j V(x_j, \kappa_j) + \gamma_i
\]

where \( c \) is the stimulus contrast, \( V(x_j, \kappa_j) \) is a von Mises (circular normal) distribution centered on the stimulus location \( \mu_j \) and with width \( 1/\kappa_j \), and \( \gamma_i \) is a Gaussian noise variable. The term \( c \) has as a multiplicative effect on the likelihood of a stimulus being observed at a location and can take values ranging from 0, when no stimulus is presented, to 1, when a stimulus is presented with high contrast. We assume that the width \( 1/\kappa_j \) varies with the stimulus location so that it is narrower at locations closer to the horizontal cardinal and wider at locations further away. The variance of the noise term \( \gamma \) does not vary with absolute stimulus location.

The observer then makes perceptual estimates by comparing the posterior at each location with the posterior distribution \( \text{post}_i(n|x_i) \) of the stimulus being absent \( (n) \)
given the observation. This is calculated similarly so that \( \text{post}_i(n|x_i) \propto \text{like}_i(x_i|n) \cdot \text{prior}_i(n) \). If the ratio of \( \text{post}_i(s|x_i)/\text{post}_i(n|x_i) \) is greater than 1, the observer reports that a stimulus was present at the location, otherwise that it was absent. For simplicity, in the model, the observer detects a stimulus at the \( i \)th location when the posterior \( \text{post}_i(s|x_i) \) is larger than a threshold level \( \alpha \), otherwise the stimulus is not detected.

The model follows the same staircase procedure in regard to the stimulus’ contrast as in the experiment. If the observer successfully detects all presented stimuli in a trial, the stimulus’ contrast is decreased, whereas if the observer fails to detect any of the stimuli, the contrast is increased. However, if the observer detects at least one of the stimuli (if more than one was presented) but not all, the contrast remains the same. The starting value for \( c \) is 0.5, and changes in steps of 0.005. When \( c \) is equal to 0, only random noise affects the observer’s likelihood. This allows the model to generate false alarms in trials where no stimulus is shown. For each of the possible 12 locations, if the posterior is larger than the threshold \( \alpha \), the observer reports a false alarm at that location.

We run simulations of 16 ‘observers’ presented with the same set of stimuli as each of the 16 experimental subjects of the bimodal group. The result for each observer is obtained after 1000 simulations, and we average the results over all observers (16000 simulations in total). The model requires 5 free parameters: the widths of the likelihood for each location in relation to its distance from the horizontal cardinal (\( \kappa_{\text{horizontal}}, \kappa_{\text{intermediate}}, \kappa_{\text{vertical}} \)), threshold \( \alpha \), and the variance of the gaussian noise \( \sigma_{\text{noise}} \). We adjusted the values of the free parameters to approximate the average detection performance of subjects in the experiment (in regard to the performance gap between horizontal and vertical locations) as well as their frequency of false alarms in the no stimulus trials. We did not fit the free parameters to the experimental data, instead we used values that provided a good qualitative fit with subjects’ average performance. We leave the fitting of individual subjects’ performances to future work.

Using the computational model, we can compare the effect of different priors on the observer’s behaviour. We consider 3 different types of priors: a recent stimulus distribution, a statistical expectation of the stimulus distribution, and a combination of the two (Figure 6.6, Model of the prior). The recent stimulus distribution is a weighted sum of the stimuli \( j \) \( n \)-trials back defined as:

\[
\text{recent\_stimulus\_distribution} = U + \sum_{j,n} w_n \cdot V(x_k, \kappa_j)
\]  \hspace{1cm} (6.3)
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Figure 6.6: Bayesian model. The sensory evidence based on a noisy observation of the stimulus is combined with the prior to form the posterior distribution. A perceptual estimate is made by taking the mean of the posterior and a response is made of the presence and position of the stimulus. Model of the prior distribution. The recent stimulus distribution is a weighted scalar of the stimuli shown in $n$-back trials. The statistical expectation is an approximation of the true stimulus distribution implicitly learned after hundreds of trials. The prior distribution before each new trial is constructed by combining the recent stimulus distribution with the statistical expectation. When the expectation is uniform (e.g. for the control group), the prior distribution is just the recent stimulus distribution.

where $U$ is a uniform prior over each location, and $w_n$ is the weight given to stimuli of the $n$-trial defined as $w_n = w_1 \cdot \exp[-\lambda(n - 1)]$, with $w_1$ the weight of the stimuli 1-trial back and $\lambda$ the rate of the weight’s decrease over time. Importantly, only stimuli detected by the observer are considered when calculating the recent stimulus distribution. For the simulations of the model we defined $n = 10$, so that the observer has a memory of the last 10 trials.

The statistical expectation is defined as an approximation of the true stimulus distribution presented to the bimodal group formalized as the sum of two circular normal distributions centered on the most frequently presented locations ($45^\circ$ & $225^\circ$). The widths of the distributions can vary in order to manipulate the degree of the effect of the prior. Finally, the combined prior distribution is obtained by multiplying the recent stimulus distribution with the expectation. The two distributions are combined equally.
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Figure 6.7: Example run of 3 successive trials. For each trial, we show the recent stimulus history and compare the different prior distributions before the new stimulus is presented. The recent stimulus history shows the stimuli presented in the last 3 trials, which are used to calculate the recent stimulus distribution (black solid line). The vertical solid lines indicate the exact recent stimuli angle of presentation and the width of the line indicates the weight of the stimulus on the prior. The recent stimulus distribution is combined with the Bimodal expectation (blue dashed line) to form the combined prior distribution (orange dashed-dotted line). The vertical dashed coloured lines indicate the exact angle of presentation. Red stimuli indicate frequent locations, while green stimuli indicate non-frequent locations. When a frequent location is primed (Trial 3), the combined prior distribution is strongly skewed towards that location. When a non-frequent location is primed (Trial 1), the combined prior is less affected as the peak of the distribution is still closer to the nearby frequent locations.
The different models of the prior make distinct predictions regarding recency effects for frequent and non-frequent locations. Figure 6.7 shows 3 successive example trials of the task and the prior distribution before the presentation of a new stimulus for each trial. In Trial 1, a stimulus is presented at the same location as in the preceding trial at a non-frequent location. The recent stimulus distribution (black solid line) is strongly biased towards that location (vertical green dotted line). However, because the location is non-frequent, the combined prior (dashed orange line) is biased towards the nearby frequent locations and not as much on the presented primed non-frequent location. Thus, under equal noise levels, an observer utilising only the recent stimulus distribution as a prior is more likely to correctly detect and report the stimulus than an observer utilising the combined prior. In Trial 3, a stimulus is presented at the same location as in the preceding trial but now at a frequent location. The recent stimulus distribution is biased towards that location (vertical red dotted line) but not very strongly because of the recent presentation of stimuli at other locations. However, the combined prior is strongly biased towards the location. Thus, an observer utilising the combined prior is more likely now to correctly detect and report the stimulus than an observer utilising just the recent stimulus distribution.

The combined model of the prior offers a parsimonious explanation for the recency effects on subjects’ detection performance at frequent locations, and also the weaker evidence of such effects at the non-frequent locations. Additionally, it can provide an explanation for subjects’ false alarms. In a trial where no stimulus is presented, the posterior collapses to the prior distributions. If we imagine that no stimulus was presented in Trial 1 and the observer reports a false alarm, the observer is more likely to report it at a nearby frequent location and not at the primed non-frequent location. In contrast, in Trial 3, the observer is even more likely to report a false alarm at the primed frequent location.

All simulations of the model use the same values for $\kappa_{\text{horizontal}}, \kappa_{\text{intermediate}}, \kappa_{\text{vertical}}, \alpha$, and noise variance $\sigma_{\text{noise}}$. Figure D.3 in Appendix D shows the behaviour of the model using a flat prior: $\text{prior}_i(s) = b \cdot (1/12)$ for each location, where $b$ is the fraction of trials in which a stimulus is presented ($b = 0.7$). As can be expected, in this case, there are no performance differences between frequent and non-frequent locations and no recency effects. We run simulations using the 3 different priors. We set the parameters of the priors so that the overall number of false alarms is very similar between the 3 simulations and the experimental data. Figure 6.8 shows the results of the simulations along with the experimental data for detection performance and false
Figure 6.8: Comparison between experimental data and model. (A) Experimental data. (Left) The fraction of correctly detected stimuli as a function of whether a stimulus was presented at the same location \(n\)-trials back, and plotted against presented location. Dashed lines indicate the best fitting linear functions. (Right) Relative frequencies of subjects’ false alarms as a function of whether a stimulus was presented at the same location \(n\)-trials back, and plotted against presented location. Dashed curves indicate the best fitting quadratic functions. (B) Simulations of 16 observers presented with the same stimuli as the experimental subjects using 3 distinct priors: statistical expectation of the stimulus distribution, recent stimulus distribution, and the combined distribution of the former two. Insets show the root mean square error of each simulation with the experimental data. The simulations of the combined prior more successfully match the experimental data than the simulations of the other prior distributions.
alarms. We calculated the root mean square error (RMSE) between the linear and quadratic fits of the simulations and the experimental data. When the prior is limited to the statistical expectation, the model does not reproduce any recency effects, resulting in an overall root mean square error of 7.73% in the fractions of correctly detected stimuli, and 0.31% in the relative frequencies of false alarms (number of false alarms divided by the total number of no stimulus trials). On the other hand, when the prior is limited to the recent stimulus distribution, the model predicts strong recency effects but for both conditions resulting in a larger overall error in both detection (7.81%) and false alarms (0.32%) in comparison to the statistical expectation. The simulations using the combined prior are the closest to the experimental results with the smallest overall error (5.74% and 0.3%). While recency effects are observed in both conditions, they are stronger at frequent locations than at non-frequent locations. Further, detection performance is different between the two conditions even when a stimulus was presented at the same location 10 or more trials in the past.

While the combined prior offers a possible explanation for subjects’ performance in the task, there might be a simpler explanation requiring the use of only one prior. We run simulations with a single prior, which starts as a uniform distribution over all locations and is updated with the presented stimuli of each trial. The weight given to past stimuli is determined by a single parameter $\eta$ so that at trial $i$: $prior_i \propto \eta prior_{i-1} + (1 - \eta) like_i$. The simulations can be seen in Figure D.4. The RMSE between the linear and quadratic fits of the simulations and the experimental data is very similar to that of the combined prior, as are the trends in both detection rates and false alarms. These results suggest that subjects are very likely to combine accumulated knowledge of the stimulus statistics with an overestimation of recent stimulus history but the exact manner of how they approximate that procedure (a single vs. two priors) will require further and closer investigation.

The Bayesian model presented here can successfully, albeit simplistically, describe our experimental results. However, it is important to note that the model does not correspond to an optimal Bayesian model of the task. For example, it does not take into account the statistics of the number of stimuli presented in each trial or the motor noise in the localisation task. A more complete model would have to take into account the aforementioned issues as well as the mislocalizations of presented stimuli, how multiple stimuli presented in the same trial combine (e.g., a non-linear integration of stimuli information), and the preexisting biases we observed in subjects’ localisation performance at different absolute stimulus locations. The implementation of such a model
could help explain certain deviations between model and data, such as the prediction of a large detection performance gap between frequent and non-frequent intermediate locations, which was not observed experimentally. That model will be the focus of future work.

6.5 Discussion

6.5.1 Summary

Both perceptual priming and statistically driven expectations have been shown to have a strong influence on visual perception. In the current study, we investigated their interaction in a visual search task. Our results showed that both priming and expectations had a significant effect on visual perception by facilitating detection performance and by inducing more false alarms in the absence of stimulus (false alarms). However, recency effects were subdued or even non-existent at locations at which it was less likely that a stimulus would be presented. We also found that subjects’ detection and localisation performance were significantly affected by absolute stimulus location and that statistically driven expectations had a strong effect on subjects’ localisation consistency and the probability distribution of false alarms.

6.5.2 Cardinal effects on performance

Visual search performance has been shown to vary across the visual field even at equal eccentricities. A horizontal-vertical anisotropy in which performance is better on the horizontal than the vertical meridian is well documented \cite{Carrasco1995, Rijndijk1980}, as is a vertical asymmetry in which performance is better in the lower than the upper visual field \cite{Edgar1990, Rubin1996}. The horizontal-vertical anisotropy has also been shown to lead to more saccades to the upper and lower visual fields during visual search \cite{Najemnik2008}. Physiological studies in human and non-human primates have found that along the vertical meridian of the retina there are lower densities of ganglion cells \cite{Perry1985} and cones \cite{Curcio1987} than along the horizontal meridian, while similar asymmetries have been found in LGN \cite{Connolly1984} and V1 \cite{Tootell1988} of macaque monkeys.

\cite{Carrasco2001} investigated whether covert attention affects these performance asymmetries in discrimination, detection and localisation tasks and found that
attentional manipulations did not have an effect on performance asymmetries. Our results agree with these findings. Subjects showed significantly better detection performance at locations closer to the horizontal cardinal and increasingly worse away from it. This performance gap was unaffected by the stimulus distribution; even though detection performance was on average better at frequent locations, performance at frequent vertical locations was still worse than performance at non-frequent intermediate locations and so on. This suggests that subjects preexisting horizontal-vertical anisotropy, which may be considered a structural expectation, provides a strong constraint on subjects’ performance that was minimally impacted by our relatively brief intervention.

While there was a strong effect of the absolute stimulus location on detection performance, the same was not observed for accuracy in localisation performance. Subjects’ localisations at horizontal locations were not significantly more accurate than localisations at other locations. However, subjects exhibited systematic positional-error biases away from the horizontal cardinal and towards locations between the intermediate and vertical locations (between 45° and 75° away from the horizontal cardinal), and these biases appear to be unaffected by the stimulus distribution. We have observed similar biases towards oblique (45° away from the cardinals) locations in a previous statistical learning experiment (unpublished) where low contrast coherent motion stimuli were shown at multiple motion directions, which were not restricted to a part of the visual field but encompassed the whole circular annulus. We found that subjects’ estimates of the presented stimuli motion directions were strongly biased towards the oblique directions, and that this bias seemed to mask the possible influence of the stimulus distribution on estimation behaviour.

These findings relate to the ongoing discussion on whether structural expectations match the statistics of the environment and whether they are continuously updated over the observer’s lifetime. Recent studies have successfully managed to measure observers’ biases of visual stimuli and compare it to the environment’s statistics. For example, Girshick et al. (2011) investigated subjects’ performance on comparing different orientations of uncertain stimuli and found that it was strongly biased toward the cardinal axes. These biases were shown to match the distribution of local orientations in a dataset of photographs. So, if these biases are learned over very long term exposure, can they be quickly updated in an experimental task? In Sotiropoulos et al. (2011b), we showed that the structural prior on slow speeds of moving stimuli is not fixed and can change through experimental training. Interestingly, this change
occurred inside the experimental session but also carried over incompletely between different sessions. Our experimental findings in the current task suggest that there are structural expectations that affect subjects’ perception of the stimulus location, which were largely unaffected by exposure to the stimulus distribution during our task. The exact nature of these expectations is unknown, and further work will be needed to identify their origin. Further, it would be interesting to investigate whether they can be modulated by a longer lasting perceptual learning experiment. An alternate explanation for this behaviour unrelated to perceptual priors could be that subjects used the physical structure of the monitor as a reference with which they could improve their localisation performance. While we cannot rule out this possibility, we suspect it unlikely given that the distance of stimulus presentation to the monitor edges was large (12.5° visual angle to the top and 21.6° to the sides of the monitor).

6.5.3 Developing expectations of different timescales

A growing body of work shows that expectations can be quickly developed in experimental settings (e.g., [Adams et al., 2004]). In previous work (Chalk et al., 2010, Chapter 3), we found that, after a few minutes of presenting low contrast coherent moving stimuli to subjects, they perceived new stimuli as moving in directions closer to the most frequently presented directions than they actually were. Additionally, we found that subjects were more consistent in their estimations at the most frequently presented directions, that they were better at detecting stimuli that were moving in these directions, and that they were more likely to report motion in these direction in trials where no stimulus was presented but they reported seeing a stimulus. In the current study, we found that the stimulus distribution had the same effects on subjects’ behaviour (with the exception of positional-error biases) inside of a similar timeframe (around 5 to 8 minutes of stimulus presentation).

Interestingly, we found that perceptual priming had similar effects as the manipulated stimulus distribution on the behaviour of subjects of the control group for which the stimulus distribution was uniform. In our task, priming significantly facilitated detection performance and induced significantly more false alarms. Notably, all forms of priming are not the same and we do not suggest that all forms of priming involve the same underlying mechanisms; priming in visual search has been shown for many different forms of stimulus characteristics, from easy pop-out search tasks to more difficult conjunction search tasks, and, importantly, it has been shown that the level of
priming can be affected by the stimuli used to test the priming effects (e.g. McBride et al., 2009). In our study, priming seems to act as a form of very short-term expectation that changes dynamically over time. When the average statistics of the stimuli were uniform, statistical regularities over a few recent trials induced identical results as statistical regularities that would need much longer exposure to be learned by subjects. This suggests that the updating process of expectations works continuously from the very short timescale of a few trials to the medium timescale of an experimental session and the long timescales of structural expectations formed over an observer’s lifetime.

However, statistical regularities over the last few trials still affected subject’s performance even when the average statistics of the stimuli were bimodal. Thus expectations of different timescales appear to interact depending on the properties of the task and the environment. In our results, priming, as a form of short-term expectation, interacts with the longer-term expectation formed by the group of subjects that were presented with the bimodal stimulus distribution, which in turn interacts with the longer-term expectation of a horizontal-vertical anisotropy. While the role of expectations and their effect on perception are increasingly being studied, the interactions of different types of expectations have earned less attention from the scientific community. A synergistic effect between spatial and temporal expectations was observed by Doherty et al. (2005) in an EEG experiment, and this effect was recently shown to enhance visual discrimination (Rohenkohl et al., 2014); temporal expectations significantly increased the effectiveness of spatial expectations but they did not facilitate performance at locations that were unattended. Likewise, Kingstone (1992) found a synergistic interaction between location and form expectations. However, response times were lower when a cued form appeared at an uncued location or when an uncued form appeared at a cued location. Our findings are in agreement with these studies. If we consider priming as a form of short-term expectation, it has a positive interaction with the longer-term expectation of the stimulus distribution when the primed location is a more probable location but a neutral interaction when the primed location is a less probable location. It is also worthwhile to note that priming does not have a negative interaction in that it does not divert attention from a more probable location towards a less probable location. In contrast to counter-predictive external cues in Vincent (2011), priming did not reflexively draw attention to the primed non-frequent location. Otherwise, we would expect to see increased detection performance and more false alarms at primed non-frequent locations in comparison to non-primed non-frequent locations.
6.5.4 Mechanisms of developing expectations

The timescale over which expectations are developed and/or updated is not yet clearly understood. In sensorimotor tasks, for example, it has been shown that observers combine prior knowledge obtained over short timescales and uncertain sensory information in a near-optimal way (Kording and Wolpert, 2004; Tassinari et al., 2006). However, some studies have suggested that this process might be sub-optimal (Eckstein et al., 2006; Raviv et al., 2012). Raviv et al. (2012) showed that subjects exhibited biases in a 2-tones discrimination task that matched the stimulus distribution. These biases were strongly skewed toward the most recent trials and deviated from biases of an optimal Bayesian observer. They suggested that subjects did not learn a close approximation of the true stimulus distribution and that their behaviour could be better described by an ‘implicit memory’ model in which the representation of past stimuli is a continuously updating single scalar. An interpretation of this finding is that subjects assumed that the statistics of the stimuli in the experiment were highly volatile and only the very recent stimulus history was informative. However, the task was purposely brief consisting of tens of trials, so it is possible that subjects could not form a complete picture of the prior in that time frame. In our study, on the other hand, subjects had abundant exposure to the statistics of the stimuli and we find that subjects learned the (static) bimodal statistics of the stimuli, while also being affected by the recent stimulus history for the frequent locations. Compared to the study of Raviv et al. (2012), this suggests that what aspects of the statistics of the stimuli are learned and used could depend on specific task properties (e.g., timeframe of exposure, complexity, initial instructions, etc). Complex recency effects can arise even in simple two-alternative forced choice (2AFC) tasks. For example, in a speeded 2AFC task, Jones et al. (2013) define as a "first-degree recency effect" the reduction in response time due to a physical match between a current stimulus and past stimuli on recent trials. They also define as a "second-degree recency effect" the reduction in response time in a repetition trial (i.e., the current trial matches the previous one) when recent trials were repetitions, and in an alternation trial (i.e., the current trial mismatches the previous one) when recent trials were alternations. They propose two simple learning mechanisms that can explain these recency effects; learning the base rate, which is the proportion of trials on which each stimulus occurs, and learning the repetition rate, which is the proportion of trials that repeat the previous trial. However, it is the interaction of these two mechanisms that can explain specific phenomena such as the alternation advantage that were not
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predicted by previous models of sequential effects (Wilder et al., 2009; Angela and Cohen, 2009). More work will be needed to identify how these learning processes differ in different task situations and whether such differences could be explained in terms of the system trying to optimise its task performance.

A number of questions regarding the underlying mechanisms of expectations remain open. For example, how expectations developed over short (minutes) or medium (hours) time frames persist over time and, eventually, become structural expectations. Contextual expectations can persist for long periods (e.g., Sotiropoulos et al., 2011b) or even transfer to different tasks (e.g., Turk-Browne and Scholl, 2009), so the same mechanisms that are responsible for the formation of these short-term expectations should to some extent be used for the formation of long-term structural expectations.

Another important question is how expectations are encoded in the properties of populations of sensory neurons. While Bayesian models provides us with mechanisms to successfully describe behavioural performance, they usually fail to be predictive at the neural level (Colombo and Seriès, 2012; O’Reilly et al., 2012). Unfortunately, it is still unknown how probability distributions are neurally implemented and it is generally difficult to propose experimental setups that would distinguish between different models of neurally plausible probabilistic inference. Nonetheless, our findings and modelling work suggest some of the constraints that such models should adhere to. We show that a prior of the very recent stimulus history is constantly updated and interacts directly with priors formed further in the past in a synergistic way. Moreover, we show that priors can dynamically change over very short timescales (seconds to a few minutes), whereas the formation of a longer-term prior requires at least 5 to 10 minutes of stimulus exposure. Similar time-scales were reported by Chopin and Massian (2012) in a visual adaptation task. They showed that visual adaptation could lead to negative correlation of the current percept with visual events presented recently (up to 3 minutes) and a positive correlation with a reference window of stimuli further into the past (5 to 10 minutes). This result seems to contradict our findings at first glance. However, we should note that the negative correlation arises after repeated presentation of the same stimulus. It was unlikely that we would observe negative correlations in our experiment, as the same stimulus was never presented at the same location for more than 2 consecutive trials.

In the current study, we described a Bayesian model in which the prior is a combination of a continuously updating distribution of the recently presented stimuli and an expectation of the average stimuli statistics developed over hundreds of trials. We
believe that this model of the prior distribution offers a parsimonious explanation for our experimental results. However, the model is unable to predict whether the final prior is indeed a combination of two separate processes of different timescales or one single process extended over time. In fact, simulations with a single updating prior, which used fewer free parameters, were comparable with the simulations of the combined prior. On the other hand, neither prior is able to perfectly capture all trends of the experimental results, and we did not try to fit each subject’s individual performance. Will the single prior be equally successful in a more complete model? Otherwise, how could we distinguish between the two alternatives? More physiology and imaging studies investigating the neural loci of expectations could help us answer that question.

Finally, the current study replicates our previous findings that statistically driven expectations can induce increased false alarms in the absence of stimulus (false alarms) and that the probability distribution of these false alarms matches the distribution of the presented stimuli. Fiser et al. (2010) argued the interesting notion that, in the absence of sensory inputs, the prior distribution might be reflected on the spontaneous activity of neurons. This notion accounts for the observed similarity between spontaneous activity and evoked activity. For example, Berkes et al. (2011) found that the spontaneous activity of awake ferrets in primary visual cortex at different stages of development is similar to the averaged evoked activity, and that this similarity increased with age and was specific to responses evoked by natural scenes. Moreover, it has been found that spontaneous activity is sufficient to evoke firing in some cells without sensory input (Tsodyks et al., 1999). We believe that the link between spontaneous activity and the prior distribution is a promising direction for future research, as do alternative approaches such as the top-down modulation of sensory signals or the shift in the selectivity of neurons. However, more theoretical and experimental work is needed to answer the outstanding questions regarding the potential neurobiological mechanisms of priors.

In conclusion, our results show that human observers are able to probabilistically combine their noisy observations with a learned expectation of likely stimulus locations. Furthermore, learned expectations over a large number of trials are combined with recent exposure to a stimulus, which facilitates correct detection of stimuli but at the cost of increased false detections (mislocalizations and false alarms). Our work suggests that prior expectations may develop simultaneously over different timescales, potentially through multiple mechanisms, and interact synergistically depending on the demands of the behavioural task. These findings may help in the effort of understand-
ing how probabilistic inference could be implemented in the cortex.
Chapter 7

Discussion

In this chapter, I summarise the experimental and theoretical work that was presented in this thesis, and discuss its relation to other work. Further, I discuss its limitations and propose future directions that would address these limitations and facilitate research in the field of expectations.

7.1 Limitations

7.1.1 Colour experiments

A strong limitation of the experimental paradigm introduced in [Chalk et al. (2010)] is the lack of a control experiment where stimuli are equally likely to be presented at all motion directions. Such an experiment would provide a useful baseline so that results from experiments with manipulated statistics can be compared. While a replication of the original study using a uniform distribution is not available, there are several experiments where the distribution of motion directions was uniform (the ‘control’ experiment presented in Chapter 5 and the ones in [Papasavvas, 2012]). In these experiments, subjects appear to have a bias towards the central direction. However, we cannot say with complete certainty whether this bias mirrors learning of a unimodal prior over the window of presentation because the reward scheme could have affected subjects’ estimation performance.

A potential problem with the experiments of Chapters 3 and 4 was the use of colour as a distinguishing factor in this particular experimental paradigm. Due to the low contrast of the stimulus, colour information was not always correctly registered by the observers. As it was discussed in Chapter 4, this introduced more uncertainty to the
inference process, and might have hindered learning of the association between colour
and motion direction. In the experiment of Chapter 4, the colour of the stimulus was
explicitly presented to subjects at the same time as the stimulus presentation. However,
the results were inconclusive as to whether that change affected the learning process in
a positive way.

Alternative visual cues that could be used instead of colour could be the speed or
the size of the stimulus. I conducted a pilot study using grey stimuli moving at either a
‘slow’ or a ‘high’ speed. High contrast stimuli were easily discernible, however, in low
contrast stimuli, the ‘speed prior’ discussed in Chapter 2 affected subjects’ perception
significantly so that they assumed that the vast majority of the stimuli were moving at
the ‘slow’ speed. Thus, speed could not be used in the current experimental design.
While I did not experimentally examined the validity of size as a factor, it is likely
that at low contrast, it would be difficult for subjects to discern the stimulus’ size. At
near-threshold stimulus contrast, subjects focus on the center of the screen and use
their peripheral vision to detect motion because peripheral vision is better at detecting
motion than central vision. However, peripheral vision is worse at distinguishing stim-
ulus properties such as shape and colour. This might also explain why subjects were
not completely accurate when reporting the correct colour of the stimulus.

Regarding the experiment of Chapter 4, in hindsight, it might have been better to
conduct an experiment using the distributions of the second experiment, as the pre-
dictions of the model were better for these distributions and we might have observed
more evidence of colour-specific learning. A number of different distributions were
also tested with the model and some were found to lead to clearer priors. However, a
decision was made to not change the distributions so that the new experimental results
could be directly comparable to the original ones.

7.1.2 Reward experiments

A potential issue with the experimental design of Chapter 5 was the required accuracy
in the estimates and its relation to the reward. We chose the reward estimation bins
based on the spread of estimation errors in previous experiments with the same experi-
mental procedure. However, the relatively large estimation window that was rewarded
with a positive score (47.6°) around each motion direction could be a reason why sub-
jects developed two distinct detection strategies. A successful detection close to the
central direction would be by default rewarded for the 2 inward directions (±8°) and
possibly for the ±24° directions. On the other hand, a successful detection at around ±40° from the central direction would be rewarded for any of the 3 directions (24°, 40°, and 56°) provided that the observer correctly discriminated clockwise or anticlockwise from the central direction. It is not surprising then that we found subjects following both strategies regardless of the reward scheme. A simple way to counter this issue would be to decrease the estimation bins so that higher accuracy will be required in order to gain a positive score. This should eliminate the simple response strategies of guessing in the center or discriminating clockwise and anticlockwise, and we might observe a closer relation between the attractive bias and subjects’ detection performance and hallucinations. However, this could also lead to significantly more zero or negative scores making the task more frustrating for subjects who might lose interest in the task if they find it too difficult.

It is difficult to predict whether this change would also affect subjects’ visual hallucinations. We saw that subjects were more likely to report a hallucination in comparison to subjects of Chalk et al. (2010). The most likely suspect for this behaviour is the absence of trial-by-trial feedback on detection performance. It would be difficult to introduce such feedback without affecting the reward scheme, and potentially its effect on estimation performance.

### 7.1.3 Visual search experiments

We have discussed some of the limitations of the Chalk et al. (2010) experimental paradigm regarding the colour experiments. I investigated ways to improve on the experimental procedure used in the colour experiments in order to avoid certain limitations: specifically the problematic interaction of colour and motion in the paradigm due to the contrast of the stimulus, and the estimation procedure, which renders the experiment too difficult and tiresome for some subjects and produces extensive motor noise in the estimates of all subjects.

One idea to alter the experimental paradigm was to change the main task from a motion detection task to a visual search task in which subjects have to identify the presence of a low-contrast target amongst distractors at 1 location out of 12 discrete locations. This would eliminate motor noise and visual fatigue allowing for more trials in a session, while maintaining the uncertainty of stimulus presence and location. Moreover, it would facilitate the introduction of more complex stimulus properties (e.g., colour, reward, priming effects). A first run of experiments using a bimodal dis-
tribution in which targets were presented at some locations more frequently than others (mirroring the original Chalk et al. experiment) produced disappointing results. There were strong biases towards the horizontal locations and there was no apparent effect of the frequently presented stimuli on perception. Changes to the experimental design (allowing multiple target reports, removing trial-by-trial feedback) produced clearer results in a second run of experiments. However, it became apparent that the learned expectations of frequent locations had a reverse effect on perception: subjects were less likely to detect a target at a frequent location and report a hallucination at those locations. A third run of experiment where the distractors were completely removed and subjects were allowed to freely report the location of the target produced encouraging results and this paradigm was used in the experiments presented in Chapter 6. While the initial aim was to investigate the complexity and specificity of developing expectations using the new paradigm by employing stimuli of different colours, the results of the pilot experiment using just a uniform distribution revealed an interesting correlation between recent exposure to a stimulus and increased hallucinations at the same location. This interaction, viewed from a Bayesian perspective, hinted to a dynamic short term prior affecting subjects performance. Thus, the new experimental paradigm allowed for an investigation of how expectations develop over time and how expectations of different timescales (from the last few trials to hours to long-term statistics of natural scenes) interact to affect perception.

A limitation with the paradigm was the measurement of confidence on each trial. While confidence data provided some interesting insights on the difference between false alarms and mislocalisations, it was too noisy to be used on a trial-by-trial basis. A possible workaround would be to initially train subjects to be consistent in their responses on a large number of trials. However, this could have the drawback of subjects becoming tired during the rest of the experiment and lose motivation as the experiment becomes more difficult.

Paraphrasing William James’ aphorism about attention, Jeremy Wolfe asserts that everyone knows what visual search tasks are because every one does them all the time (Wolfe, 1996). Visual search tasks are those where one looks for something, and are typically about discriminating a target from competing distractors according to differences in one or more features. By that definition, the experimental paradigm of Chapter 6 is not a typical visual search task. Observers have to report whether there are one or more targets during a brief stimulus presentation. This is more similar to a detection task than a visual search task. However, the target(s) can appear in one of a
number of locations and the observer has to search for it (or for them). This is different from a pure detection task where observers know the single (or very small number) of locations that they attend to.

In Chapter 6, the experiment and its findings have been discussed in the context of visual search literature. This could be problematic considering that the task is not a typical visual search task. Mechanisms that have been proposed in visual search tasks might not generalise to our task. To that end, we caution the reader to not draw direct parallels between our task and classical visual search tasks. However, we think that it is still worth discussing our experiment in that context. In particular, the extensive work done on recency effects in visual search tasks should not be ignored when looking at recency effects on different kinds of tasks and the potential mechanisms that explain those effects.

### 7.2 Relation to other work

#### 7.2.1 The limits of learning

In Chapter 3, I presented two psychophysical experiments in which the ability of human observers to learn complex priors using colour as a distinguishing factor was examined. Subjects were presented with moving dot displays of two different colours, either red or green, with different motion direction distributions. When one distribution was bimodal while the other was uniform, I found that subjects learned a single bimodal prior for all stimuli. In contrast, when one distribution was bimodal while the other was complementary of the first, I found evidence for the formation of two distinct priors. Modelling work suggested that subjects of the first experiment learned a single colour-nonspecific prior and applied it to all stimuli, whereas subjects of the second experiment, on average, learned a complex combination of the two distributions and applied it to both conditions.

The source of sub-optimality of subjects’ behaviour in the colour experiments was explored in Chapter 4. A online learning Bayesian model was implemented in collaboration with Dr Kevin Lloyd in order to compare subjects’ behaviour with that of an optimal observer presented with the same stimuli in the same procedure. Extensive simulations of the model showed that an optimal observer would still develop a single colour-nonspecific prior when presented with the stimuli of the first colour experiment and only develop two distinct priors for the stimuli of the second experiment when the
model’s prior assumptions regarding clusters were manipulated. The experimental results suggested that subjects not only failed to learn the shapes of the stimulus motion distributions but also to learn the structure of the task, i.e. that stimuli were drawn from 2 distinct distributions depending on their colour. However, the simulations indicated that subjects were not presented with enough evidence to infer the true structure of the task, and their behaviour should not be considered suboptimal per se.

So, returning to the question posed at the beginning of this thesis, have we identified the limits in the complexity of expectations that can be formed? Overall, complexity does appear to be a limiting factor in the process of learning two distinct priors but not in a way that is immediately apparent. The distributions used in the second colour experiment were more complicated that the distributions of the first experiment. However, subjects of the second experiment showed some evidence of learning while subjects of the first did not. As suggested by Gershman and Niv (2013), human observers could be using a ‘Bayesian razor’ approach to model selection in that they have a tendency to prefer simple models which are consistent with the data over complex models. Observers might employ a meta-prior learned over a lifetime of ‘generating’ models of the environment, which assumes that models are usually simple, and complex models should be used only when there is strong enough evidence to support them. A reason for this behaviour could be to reserve resources as developing complex models presumably requires extensive strengthening or weakening of neural connections. Another reason might be that observers want to avoid ‘overfitting’ to the environment so that they are able to adapt more quickly to changes in it.

Even in Chalk et al. (2010), where the stimulus distribution was easier to learn than in the colour experiments, inter-individual variability was large and subjects learned approximations to the true stimulus distribution. However, bimodal distributions can be difficult to learn in the first place (Kording and Wolpert, 2004; Acerbi et al., 2012). In contrast to the more clear results of Kerrigan and Adams (2013) and Kok et al. (2013), the experiments of Chapter 3 showed that it is possible to learn the joint statistics of two simultaneous complex distributions within the visual modality but only under specific conditions. The fact that colour and motion direction are normally uncorrelated in everyday environments could have made learning more difficult. Haijiang et al. (2006) trained observers to perceive a perceptually bistable stimulus as having a certain rotation direction using depth cues. At the same time, another signal was added contingent on rotation direction. On test trials, only the new signal was present and not the depth cues. The authors found reliable changes in the perception of the
stimulus when the signal was the screen position of the stimulus and its translational motion but not when it was a sound cue. Moreover, in a similar task, Jain et al. (2010) found that extrinsic signal, i.e., signals not conveyed by the same image elements as the stimulus itself, did not change perception of the stimulus. As extrinsic cues have been shown to have effect on perception (the aforementioned McGurk effect), the authors speculated that certain conditions must be met for the effect to take hold (e.g., the age of the observer or the amount of exposure to the correlation). They suggested that statistical congruence between separate objects may not be a sufficient condition to modify the system’s default preconception that individual objects in the environment are independent, even when presented evidence is very reliable.

It is a reasonable assumption that the amount of exposure to a correlation influences the learning of that correlation. An interesting point to discuss here is whether learning in the experiment of Chapter 3 would be facilitated if subjects were allowed to do more experimental sessions. Complexity might not completely limit learning but it is highly likely to slow it down. In Experiment 2 of Chapter 3, subjects appeared to learn the stimulus statistics (measured from their probability of reporting a ‘hallucination’ at a frequent direction, Figure B.8) after a large number of trials, larger than the number reported by Chalk et al. (2010) in their experiment, especially for the ‘trimodal’ distribution. We did not observe any significant differences between the two experimental sessions but it would not be surprising to find, after more sessions, a significant effect across sessions similar to the one observed by Sotiropoulos et al. (2011a). Differences in how fast learning was acquired by different subjects could also explain why some subjects’ performance was better described by two distinct priors. If some subjects suspected a possible correlation between colour and motion direction, they could potentially learn that correlation faster. As we discussed in Chapter 2, learning rates are expected to decrease with decreasing stimulus reliability. So after the initial exposure to relatively high contrast stimuli, it might become more difficult for subjects to learn the stimulus statistics. This issue is directly connected with another question posed in the beginning of the thesis on how fast expectations are formed and how expectations of different temporal properties interact.

In Chapter 6, I presented a series of experiments where human observers were presented with low contrast white dots at twelve possible locations equally spaced on a circle, and were asked to identify the presence and location of the dots. Their expectations were manipulated by presenting stimuli at some locations more frequently than others. The effect of expectations developed over a long sequence of trials was com-
pared with the effect of exposure to stimuli in the very few last trials. Subjects quickly learned about the stimulus distribution which improved their detection performance but caused increased visual hallucinations at the most frequently presented stimulus locations. Very recent exposure to a stimulus had a significant effect on an observer’s detection performance and behaviour in the absence of stimulus but only at locations at which a stimulus was more probable or at least equally probable (in the control experiment) to be presented.

It is not clear why subjects behaved as such. An ideal Bayesian observer would over the course of the session learn that repeats of stimuli are actually quite rare and it would be advantageous to reduce the prior expectation of a presented stimuli in the very next trial. Can then the behaviour of subjects in the experiment be characterised as suboptimal? It might not be when we consider that computational resources are limited in the cortex because of the metabolic costs of cortical computation (Lennie, 2003) and the limited (even if very large) number of available neurons. If we assume that finding a stimulus repeatedly at the same location requires reduced computational resources, it would be economically sensible for an observer to spent less resources and try to detect a stimulus at the same location that she had very recently detected one. In contrast, it would be less economically sensible for the observer to ignore the repetition and spent more resources to try and detect a stimulus at different locations. While this behaviour might be considered suboptimal inside the constraints of the task, it is more efficient in the long term and in general situations. Interestingly, subjects did not exhibit that behaviour at the less probable locations. This suggests that the system still factors in the statistical properties of the stimulus and behaves in an efficient manner by ignoring repeats of the less probable stimuli even if statistically they have the exact same probability of reappearing in the next (or after next) trial as the stimuli of the control (uniform) distribution. It would be a worthwhile future project to investigate whether after extensive training subjects would be able to suppress that behaviour even at more probable locations.

Regarding the specificity of expectations, in Chapter 3, we observed complete transfer between the statistical properties of the 2 distributions in Experiment 1, and significant transfer in Experiment 2. It is difficult to define a cost function in our experimental task. However, we may assume that subjects are likely to want to maximise their performance in the detection task given that they receive immediate feedback for their detection responses. In Experiment 1 where the combined stimulus distribution was bimodal, subjects can still improve their detection performance even if they
do not learn colour-specific priors but only a bimodal colour-nonspecific prior. Naturally, detection performance would be further improved by learning 2 distinct priors, however, the small extra benefit in performance might not justify the cost of learning. Thus, learning specificity is not encouraged by the stimulus distributions. In Experiment 2, subjects can improve their detection performance only if they learn that stimuli of certain colours are more likely to be presented at certain directions and not in others. However, the limitations of the experimental paradigm (i.e., the uncertainty about colour in some trials and the inference process from ambiguous stimuli) could have prevented complete specificity in learning. This might explain why subjects on average developed a complex colour-nonspecific prior and applied it to all stimuli.

Looking further into the specificity of developing expectations, there is the question of specificity of these contextual expectations in relation to structural expectations. We have discussed examples in which the same light-from-above prior is used in various tasks (Adams et al., 2004; Adams, 2007), and also an example of a learned light prior persisting over days after training (Adams et al., 2010). However, the latter learned prior did not seem to interfere with everyday tasks and remained specific to the experimental environment. Likewise, the subjects of our colour experiments would not reasonably expect red or green dots to move in particular directions in an non-experimental environment. These learned priors do not seem to ‘overwrite’ existing long-term priors, and even when they do in an experimental setting (e.g., in Adams et al., 2004 or in Sotiropoulos et al., 2011a), they do not appear to replace it in general situations. This suggest that the system is able to learn multiple variations of priors and apply them in specific tasks or environments without losing the generality required to function in an ever-changing environment. It is not clear how the system decides when to use a ‘default’ generic prior or to develop a more specific expectation. Does the decision depend solely on the statistics of the stimulus? Our results suggest that task properties, such as the order of presentation, can have a significant effect on learning on par with the stimulus statistics.

### 7.2.2 Expectations and Bayesian inference

In this thesis, we considered perception as a form of Bayesian inference. We have paid more attention to the prior but the behaviour of a Bayesian observer does not depend only on the prior. There are three distributions of interest: the prior, the likelihood, and the loss function, and distinct combinations of the distributions can lead to identi-
cal behavioural results (Mamassian and Landy, 2010). Studies on Bayesian inference have used different approaches to influence one or more of the distributions so that the other(s) can be identified correctly. For example, provide explicit knowledge of the prior (Acerbi et al. 2014b) or measure the likelihood function by determining a subject’s ability to discriminate similar stimuli (Knill and Saunders, 2003).

Several studies have shown that prolonged exposure to a visual stimulus results in sensory adaptation (Levinson and Sekuler 1976; Seriès et al. 2009; Schwartz et al. 2007). This adaptation causes subsequently presented stimuli to be perceived as less similar to the overexposed stimulus. As mentioned in section 6.5.4, Chopin and Mamassian (2012) showed that different timeframes of exposure to a stimulus can produce qualitatively different types of biases. Visual adaptation leads to repulsion for stimuli presented recently (up to 3 minutes) and attraction for stimuli further into the past (5 to 10 minutes). A possible explanation for this phenomenon is that observers might be able to change their likelihood of incoming sensory input faster than they are able to change their prior expectations. Thus, in the short-term, changes to the likelihood can lead to repulsion biases, whereas, in the long-term, changes to prior expectations can lead to attractive biases.

We also observed such a reversal from repulsion to attraction in the experiment of Chapter 4. Repulsion biases for stimuli of high contrast at the beginning of the experimental session changed to attractive biases for stimuli of low contrast later in the session. More so, we found that the reversal was gradual as the contrast of the stimulus was steadily decreased through the staircase procedure. These findings fit nicely into a Bayesian framework. The posterior distribution is the combination of the likelihood and the prior. For stimuli of high contrast, the posterior is influenced significantly more by the likelihood than by the prior. So, prolonged exposure to the frequently presented motion directions induced repulsion biases. However, when stimulus contrast decreases, the influence of the prior on the posterior increases, and, at near-threshold levels of detection, it should supersede the influence of the likelihood. Thus, repulsion biases turn into attractive biases, even though the same motion directions are still more frequently presented. It is interesting that this effect is not related only to the timeframe of exposure. It is reasonable to expect that if there was another block of high contrast stimuli after the end of each session, subjects would again exhibit repulsion biases. So, it is important to consider all factors that might be influencing a behavioural task when studying perceptual biases.

In Chapter 5, I presented a collaborative work with Cyril Ng Lung Kit in which we
investigated whether selective manipulation of rewards can affect an observer’s perceptual behaviour in the same manner as manipulating the statistical properties of the stimulus. We used the experimental procedure of [Chalk et al. (2010)] but made changes to the experimental design. In our experiment, stimuli were equally likely to be presented at all 8 discrete motion directions, and subjects received points based on their estimation performance. Estimates closer to the presented motion direction were rewarded higher scores, whereas estimates away from the direction were rewarded lower scores or were even penalised. In order to manipulate subjects’ expectations, accurate estimates of 2 directions were rewarded more points than other directions. We found that subjects developed an attractive bias towards the more rewarded motion directions. However, this bias was observed only in trials where a stimulus was presented and not in trials where no stimulus was presented but subjects reported seeing a stimulus. An attractive bias was not observed in the behaviour of subjects who were presented with a uniform reward scheme in which estimates across all motion directions were rewarded the same number of points.

In this experiment, we imposed a specific loss function and we hypothesised that it would induce perceptual biases. We have not modelled these results and one question is whether the source of the bias should be modelled as originating from the prior or the loss function. The divergence of some of the experimental metrics (detection, ‘hallucinations’) with previous experiments (Chalk et al. (2010), Chapter 3) can also be explained through multiple hypotheses that are difficult to disprove without more experiments or modelling work. The practice of fitting Bayesian observer models to the data, though successful, has been questioned (Jones and Love, 2011). This extends to the approach employed in this thesis. For example, in Chapter 3 we reconstructed subjects’ priors from the experimental data but we did not consider the potential influence of subjects’ loss functions in our models. Recently, [Acerbi et al. (2014a)] proposed a framework that allows a modeller to perform a systematic a priori investigation of identifiability, i.e. the ability to reliably recover the parameters of interest, for a chosen Bayesian observer model. The framework has been tested on two case studies by the authors, and it can be extended to more complex tasks, e.g. to allow multiple cues in order to analyse cue-integration tasks (as in Chapter 3). Further, the framework can be used to compare identifiability within distinct ideal experimental setups, and, so, improve experimental design. The experimental design of Chapter 5 would have benefited greatly from such a framework.

The computational work of Chapter 6, while incomplete, may provide further ev-
idence towards a Bayesian understanding of developing expectations. A dynamically changing prior, which is updated trial-by-trial, can successfully predict the recency effects in subjects’ behaviour regardless of the overall stimulus statistics (uniform or bimodal). This suggests that a very rapid learning mechanism is always active even when the long term stimulus statistics are known to the observer (e.g., after hundreds of trials). It is not clear whether these are 2 separate mechanisms that function over different timescales or 2 different aspects of the same mechanism. The simulations of a single updating prior seems to point to the latter hypothesis. As exact Bayesian inference is intractable, it is expected that approximations are necessary especially in complex environments. Bayesian explanations of aspects of perception are becoming increasingly more popular but it is important that researchers have the ability to properly construct and test the limits of such explanations. That can be accomplished by both accessible (Vincent 2015) and in depth (Lewandowsky and Farrell 2010) examinations of Bayesian methods. If we accept the Bayesian brain hypothesis, the more difficult question is then how these probabilities are encoded in the brain.

In conclusion, the work in this thesis sought to investigate the limits of what can be learned in visual perception. The process of learning is a dynamic and adaptive process; expectations are continually updated through exposure to environmental statistics. The complexity of these statistics appears to make acquisition of learning more difficult and time consuming but not impossible per se. The system might have a preference for being as economical as possible when building associations between features of the environment, and shows robustness to change when presented with associations that were previously negative or have not been encountered before. We are beginning to form a better idea of the timescales of these process (from fast statistical learning to slow perceptual learning), of how expectations developed over a lifetime combine with very recently learned statistical regularities in a synergistic way, and how these recent regularities eventually develop into long-term expectations. It is my hope that this work will stimulate further interest into this research topics, and inspire further investigations into understanding the process of learning in the brain.

7.3 Future work suggestions

The work presented in this thesis could be used as a starting point for further experimental and modelling work in the study of expectations and their development. I suggest some directions, which are by no means exhaustive.
An open question relating to the colour experiments is whether we can propose new methods to further facilitate the investigation of complexity and specificity of expectations. While the experimental paradigm of Chalk et al. (2010) works well for colourless stimuli, it might not be an ideal choice for investigating complex expectations using colour as a distinguishing factor. A way to solve this issue is to alter the experimental paradigm so that the estimation and discrimination tasks are ‘reversed’. The new procedure will be as follows: subjects will be presented with unambiguous stimuli moving coherently at one of 2 possible motion directions (leftwards or rightwards). However, the colour of the stimulus will be chosen from a Gaussian distribution (ranging from red to grey to green) depending on the motion direction (Figure 7.1). We will ask subjects to report the colour of the stimulus and its direction of motion. Subjects will have to report the exact colour of the stimulus from a continuous scale from red to grey to green (estimation task), and the direction of motion as a two-alternative forced choice (discrimination task). We expect subjects to develop expectations about colour and motion direction, and these expectations to induce biases in the colour estimation of grey stimuli. Further, by varying the distance between the means of the two colour distributions ($\Delta\mu$) or the variances of the distributions, we will be able to quantify how learning specificity is affected by the stimulus statistics. For example, whether there is a threshold of $\Delta\mu$ over which subjects always learn two distinct distributions and below which only one distribution, or whether learning specificity increases in step with $\Delta\mu$. If the experimental paradigm proves successful, it would be easy to introduce a third colour and motion direction, thus enabling further investigation on how human observers learn increasingly complex statistical properties.

As proposed by Chalk et al. (2013), the role of goal-orientated attention might be to reshape the observers’ internal model in order to improve their predictions of the received reward at the potential cost of learning a worse internal model of the received sensory inputs. The bimodal reward scheme induced attraction biases towards the more rewarded motion directions even though the distribution of directions was uniform. However, what kind of internal model would an observer learn if presented with two different distributions for stimulus statistics and reward? It would be easy to conduct the same experiment using the bimodal reward scheme but with a non-uniform distribution of motion directions. In particular, an inverse distribution of the reward scheme so that the average reward would be equal across directions (Figure 7.2). How would that affect the observer’s perception of the stimulus? It is possible that the effects will cancel out and we will fail to notice any significant biases. On the
Section 7. Discussion

![Motion direction and colour distributions](image)

**Colour estimation task**

**Motion direction discrimination task**

Figure 7.1: Proposed 'reversed' colour experiment. Unambiguous stimuli move coherently in one of 2 discrete motion directions. The colour of the stimulus is chosen out of a Gaussian distribution (from red to grey to green) depending on the motion direction. Subjects are asked to report the colour of the stimulus from a continuous scale (estimation task) and the direction of motion (discrimination task).

On the other hand, we might observe reward and expectations having different effects on behaviour: for example, reward affecting estimation biases while statistical expectations affecting detection performance and visual hallucinations. The implementation of such an experiment might help in identifying important differences between attention and expectations in behaviour and, in turn, possible differences in their neural mechanisms.

An interesting approach to extend the experiments of Chapter 6 would be to manipulate the stimulus statistics over the course of a session. For the first half of the session, the distribution of locations will follow the same bimodal distribution. At the beginning of the second half of the session, unbeknownst to subjects the distribution will shift 90 degrees, so that frequent locations will become non-frequent and vice versa. After a limited number of trials $n$ (e.g., 150), the stimulus distribution will change to a
uniform distribution over all locations. If subjects develop a long term expectation over the first half of the session, it is unlikely that the presentation of the shifted distribution for a limited duration will significantly affect that expectation, and subjects will remain biased towards the original frequent locations when presented with the uniformly distributed stimuli. However, if subjects use a continuously updating prior of the last $n$ trials, we expect them to be biased towards the alternate frequent locations when presented with the uniformly distributed stimuli. Conducting such an experiment will allow the implementation of an even more accurate computational model, and identifying the exact mechanisms of the formation of priors may be crucial in formulating successful theories of probabilistic inference in the cortex.
Appendix A

Complimentary colour experiment

Here I present an additional psychophysical experiment conducted after suggestion from one of the reviewers of the work presented in Chapter 3 (Gekas et al., 2013). The results of this experiment were inconclusive regarding the specificity of learning but an interesting finding was that some subjects estimation behaviour appeared to be influenced by pre-existing biases towards oblique motion directions (or away from cardinal motion directions).

One of the reviewers argued that the results of Experiment 2 of Chapter 3 were messy, and asked for a complimentary experiment were the distributions might be more discriminable. The major issue with trying to implement such a setup is that subjects could be consciously aware of the differences between the distributions, and resort to response strategies (e.g., report red dots when the stimulus appears on the left and green dots on the right). Response biases would then be impossible to distinguish from perceptual biases.

We introduced a new experimental paradigm where motion directions shown to subjects were not restricted inside a 128° window, but were evenly distributed across the whole 360°. Potential biases towards the central motion direction could be avoided and differences between the two colour distributions could be accentuated. Thus, for 90% of the trials of the staircase contrast levels, 8 directions 45° apart were shown (Figures A.1A & A.1B). For the Red distribution, two motion directions 180° apart were presented more frequently than the others, while, for the Green distribution, the most frequently presented directions were shifted 90° away from the Red. The combined distribution of the stimuli was uniform. In the rest 10% of trials, dots were moving in random directions in order to hinder subjects’ conscious acknowledgment of the 8 directions, and to identify potential response biases towards the frequent directions.
Appendix A. Complimentary colour experiment

We did not find any notable estimation biases towards the more frequently presented motion directions when a stimulus was presented independent of stimulus colour (Figures A.1C & A.1D). Interestingly however, and consistent with the results of Experiment 2, we found that when no stimulus was presented but subjects reported detecting a stimulus, they were more likely to report detecting a stimulus at the frequent directions and to report the colour of the corresponding condition (Figure A.1E). While these results largely replicate those of Experiment 2, we chose not to include these results in the revised manuscript, as they did not add significantly to the clarity of the manuscript.

A possible explanation for the lack of estimation biases towards the more frequently presented directions when a stimulus was presented is that subjects’ estimations may have been strongly biased towards the oblique directions (or away from the cardinal directions), and this strong bias could have ‘masked’ any effect of learned priors on estimation behaviour. Unfortunately, we are unable to show average estimation biases in comparison to actual cardinal and oblique motion directions because the central motion direction for each subject was randomised. Thus, the distance of a presented motion direction from a cardinal or oblique direction was different for each subject. The only way to observe whether subjects exhibited these kind of biases is to plot the estimation biases for each subject individually (Figure A.2). While such biases are not found consistently across all subjects, they can be seen very clearly in a number of subjects (e.g., subjects #8, #11, #13, #14, and #15). Positive biases indicate biases towards larger values of direction (rightwards in the figure), while negative biases indicate biases towards smaller values of direction (leftwards in the figure). As we discuss in section 4.4.2 (reference repulsion), it is not clear whether these biases indicate a repulsion from the cardinal directions or an attraction towards the oblique directions. Moreover, a new experiment in which all subjects would be assigned the same central motion direction will be necessary in order to conclusively state whether these biases are indeed present and not just noise in the data.
Figure A.1: Complimentary experiment not included in Chapter 3. (A). Probability distributions of presented motion directions for the ‘Full circle’ experiment. (B). Presented motion directions plotted as actual directions shown to subjects. Red and green lines correspond to the most frequent directions of each condition, and black lines correspond to directions with equal number of trials for both conditions. The central motion direction was randomized for each subject. (C). Subjects’ mean estimation biases are plotted against presented motion direction. (D). Subjects’ mean estimation biases separated for the Red and Green conditions are plotted against presented motion direction. (E). The fitted combined distributions for each colour condition in trials were no stimulus was presented but they reported detecting a stimulus are plotted against motion direction. The red and green vertical dotted lines correspond to the most frequently presented motion directions for the Red and Green distributions (0° and ±180°) and (±90°) respectively.
Figure A.2: Individual subjects’ estimation biases for the ‘Full-circle’ experiment are plotted against presented motion direction. The black vertical dashed lines correspond to actual cardinal directions, while the blue vertical dotted-dashed lines correspond to actual oblique directions.
Appendix B

Supplementary materials of Chapter 3

B.1 Luminance levels

For each session of the experiments, the staircases reached stable luminance levels after approximately 60 trials of each staircase (Figure B.1). A slow luminance descent was used to allow bigger variations in subjects’ performance and colour sensitivity, as a few subjects had significantly higher threshold levels than the average. For each staircase step, the luminance was decreased by 0.0318 cd/m$^2$ for the red dots and by 0.0321 cd/m$^2$ for the green dots. The threshold values between 0.4 and 0.5 cd/m$^2$ are in accordance with threshold values in Chalk et al. (2010), albeit slightly lower. This could be due to the slightly lower background luminance in our experiment (5 cd/m$^2$ instead of 5.2 cd/m$^2$ in Chalk et al.).

B.2 Unfolded plots of estimation performance

In the main text we averaged data from both sides of the central motion direction. Here we present versions of the plots where this has not been done. Figures B.2A and B.2B plot subjects average estimation bias for all stimuli and for each colour condition respectively for Experiment 1, while figures B.2C and B.2D plot the corresponding data for Experiment 2.
Figure B.1: (A) Subjects’ averaged stimulus luminance, in relation to background luminance, for the 3/1 Red and Green staircases plotted against trial number for each staircase. Data is shown only for the first experimental session of Experiment 1. Coloured areas show within-subjects standard error. (B) Fraction of stimuli detected at each of the 4 different contrast levels for Experiment 1. In both plots, results are averaged over all subjects, and the standard deviation is denoted by shaded curves and error bars, respectively.
Figure B.2: (A) Experiment 1. Subjects’ mean estimation bias is plotted against presented motion direction, averaging over the two colour conditions. (B) Subjects’ mean estimation biases against motion direction, isolating the unimodal (red curve) and bimodal (green curve) conditions. The vertical dashed lines correspond to the two most frequently presented motion directions ($\pm 32^\circ$). (C) Experiment 2: Subjects’ mean estimation bias is plotted against presented motion direction. (D) Subjects’ mean estimation biases isolating the trimodal (red curve) and bimodal (green curve) conditions. Results are averaged over all subjects and error bars represent within-subject standard error. The red and green vertical dashed lines correspond to the most frequently presented motion directions for the trimodal and bimodal distributions ($0^\circ$ and $\pm 64^\circ$) and $\pm 32^\circ$ respectively.
Appendix B. Supplementary materials of Chapter 3

B.3 Bootstrap analysis

Because of the structure of the stimuli distributions (uniform, bimodal, or trimodal), the number of trials for each colour condition can vary significantly with motion direction. In order to address this issue when looking at statistical differences between conditions, we used a Bootstrap analysis.

The estimation data of all subjects for each direction and condition for the two conditions were collected. Then, the data corresponding to each direction and condition were re-sampled with replacement. The estimation biases were then fit to the distribution 

\[ (1 - \alpha) \cdot V(\mu, \kappa) + \alpha/2\pi, \]  

where \( \alpha \) is the proportion of trials where the subject makes random estimates, and \( V(\mu, \kappa) \) is a von Mises (circular normal) distribution with mean \( \mu \) and width \( 1/\kappa \), given by:

\[ V(\mu, \kappa) = \exp(\kappa \cos(\theta - \mu)/(2\pi I_0(\kappa))). \]

The mean (bias), width (standard deviation), and alpha values were stored and the process was repeated 10,000 times. From these data sets, 95% percentile confidence intervals were calculated for each direction and colour condition.

The results for the estimation biases did not differ extensively from the results using the within-subjects analysis in the main text for Experiment 1 (Figure B.3A). The differences between conditions in Experiment 2 (Figure B.3B) are no longer significant, but this can be attributed to pooling all the subjects’ estimates. In contrast, in the main text, we calculated the biases on a subject-by-subject basis and, in this case, the differences between conditions are significant \((p = 0.046, \) three-way within-subject ANOVA between motion direction, colour condition, and subjects). The differences in standard deviations are not significant for either experiments (Figure B.3C & B.3D). There were no significant difference for the values of \( \alpha \) between the conditions in Experiment 2 (Figure B.3F), but there was a significant difference for the values of \( \alpha \) at directions \( \pm 16^o \) and \( \pm 64^o \) in Experiment 1 (Figure B.3E), suggesting that, on average, subjects were more likely to make random estimations for the uniform condition at these directions.
Figure B.3: Subjects’ estimation biases separated for the two colour conditions as a function of motion direction for (A) Experiment 1 and (B) for Experiment 2. Subjects’ standard deviations separated for the two colour conditions as a function of motion direction for (C) Experiment 1 and (D) Experiment 2. Alpha values corresponding to subjects’ random estimates separated for the two colour conditions as a function of motion direction for (E) Experiment 1 and (F) Experiment 2. The vertical dotted lines correspond to the two most frequently presented motion directions (±32°) in Experiment 1. The red and green vertical dotted lines correspond to the most frequently presented motion directions for the trimodal and bimodal distributions (0° and ±64°) and (±32°) respectively in Experiment 2. Error bars show 95% confidence intervals
B.4 Detection performance and reaction times

After the staircase had converged to stable luminance levels, we measured the fraction of trials where subjects both detected a stimulus and clicked on the mouse during stimulus presentation, as a function of motion direction. The detection rates in high contrast trials were close to perfect and these trials were not included in the analysis. In Experiment 1, there was significant effect of motion direction on the detection rate ($p = 0.02$, three-way within-subjects ANOVA, Figure B.4A), but it was not more likely for the subjects to detect a stimulus at the most frequently presented directions ($p = 0.74$, signed rank test). In Experiment 2, there was a significant effect of motion direction on the detection rate ($p = 0.02$, three-way within-subjects ANOVA, Figure B.4C). However, the only difference was a lower detection rate at $\pm 64^\circ$ ($p = 0.01$, signed rank test).

We measured subjects’ reaction time in clicking the mouse from trials where they detected a stimulus. In Experiment 1, there was no significant effect of motion direction on the reaction time ($p = 0.19$, three-way within-subjects ANOVA, Figure B.4B), and the subjects’ reaction time was not reduced for stimuli at the most frequently presented directions. Likewise in Experiment 2, there was no significant effect of motion direction on the reaction time ($p = 0.18$, three-way within-subjects ANOVA, Figure B.4D).
Figure B.4: (A) Experiment 1. The fraction of trials where subjects correctly detected a motion stimulus is plotted against presented motion direction. (B) Time taken for subjects to click on the mouse and during stimulus presentation, measured from the initial presentation time. The vertical dashed lines correspond to the two most frequently presented motion directions ($\pm 32^\circ$). (C) Experiment 2. The fraction of trials where subjects correctly detected a motion stimulus is plotted against presented motion direction. (D) Time taken for subjects to click on the mouse and during stimulus presentation, measured from the initial presentation time. The red and green vertical dashed lines corresponds to the most frequently presented motion directions for the trimodal and bimodal distributions ($0^\circ$ and $\pm 64^\circ$) and ($\pm 32^\circ$), respectively. Error bars show within-subject standard error.
B.5 Response strategy models in Experiment 1

As in Chalk et al. (2010), the ‘response strategy’ models assumed that subjects followed different strategies on different trials; i.e. making an unbiased estimate of motion direction on a fraction of the trials and estimating one of the most frequently presented motion directions on other trials. In the simpler ‘ADD1’ model, when subjects were unsure about the motion direction, they made an estimate that was close to one of the two most frequently presented motion directions. In the more complex ‘ADD2’ model, when subjects were unsure, they made estimates that were preferentially sampled from different proportions of their ‘expected’ distribution, which depended on the actual stimulus motion direction.

The models that we compared include the already mentioned ‘ADD1’ and ‘ADD2’, as well as two variations of these models ‘ADD1_mode’ and ‘ADD2_mode’, which had one less free parameter by setting $1/\kappa_{\text{exp}}$ equal to zero. The number of free parameters varied extensively between models; ADD1 and ADD2 required 9 and 14 free parameters respectively, with the variations at 8 and 13 respectively, while the ‘1Bimodal’ model required only 4 free parameters (see section 3.4 of this thesis).

The BIC value obtained for the ‘1Bimodal’ model was subtracted from the BIC values obtained for each response strategy model (Figure B.5A). The results show that the BIC values obtained for each model were significantly greater than the BIC values obtained with the ‘1Bimodal’ model ($p < 0.001$ for ADD1, ADD2, ADD1_mode, ADD2_mode, signed rank test). The ‘1Bimodal’ also produced significantly better AIC values than any other model (Figure B.5B), and it was able to provide a good fit for the averaged estimation biases (Figure B.5C) and standard deviations (Figure B.5D).

B.6 Fit distributions to ‘no-stimulus’ data

The data of all subjects for each condition were fit to a linear combination of 6 circular normal distributions. Starting from random values, the mean (peak) and variance (width) of each distribution were fit to the data. Figures B.6A and B.6B show the combined distributions for each condition for Experiment 1 and Experiment 2 respectively. Figures B.6C & B.6E show the 6 distributions that make up the combined distributions of each condition for Experiment 1, and Figures B.6D & B.6F for Experiment 2.
Figure B.5: Response strategy model comparison for Experiment 1. The (A) Bayesian information criterion (BIC) and (B) the Akaike Information Criterion (AIC) values of each response strategy model minus the AIC and BIC values of the ‘1Bimodal’ model for each subject (black dots), along with median values (red lines), and the 25th and 75th percentiles (blue lines). p-values indicate whether the median was significantly different from zero for each model (signed rank test). Predicted averaged estimation biases (C) and standard deviations (D) for each model. Predictions for the ‘ADD1_mode’ (green), the ‘ADD2_mode’ (blue), and the ‘1Bimodal’ models (black) are plotted with the experimental data (red). Results are averaged over all subjects and error bars represent within-subject standard error. The vertical dashed lines correspond to the two most frequently presented motion directions (±32°).
Figure B.6: The fitted combined distributions for each colour condition against motion direction unfolded (A) for Experiment 1 and (B) for Experiment 2. The 6 circular normal distributions fitted to all subject data on trials where no stimulus was shown but they reported detecting a stimulus of the (C) Uniform condition and (E) Bimodal condition in Experiment 1. The 6 circular normal distributions fitted to all subject data on trials where no stimulus was shown but they reported detecting a stimulus of the (D) Trimodal condition and the (F) Bimodal condition in Experiment 2. The black vertical dotted lines correspond to the two most frequently presented motion directions (±32°) in Experiment 1. The red and green vertical dotted lines correspond to the most frequently presented motion directions for the trimodal and bimodal distributions (0° and ±64°) and (±32°) respectively in Experiment 2.
B.7 Individual priors predicted by the ‘1Bimodal’ model in Experiment 1

Figure B.7 plots the distributions of individual subjects’ ‘learned prior’, as predicted by the ‘1Bimodal’ model to fit the experimental data. On average, the peak of the distribution lies at $\pm 37^\circ$, shifted slightly outwards, compared to the most frequently presented directions ($\pm 32^\circ$), suggesting that subjects learned a close approximation of the ‘true’ prior.

Figure B.7: Subjects’ prior distributions of presented motion directions as predicted by the ‘1Bimodal’ model in Experiment 1. Data points from either side of the central motion direction have been averaged together. The vertical dotted lines correspond to the two most frequently presented motion directions ($\pm 32^\circ$).
B.8 Development of ‘no-stimulus’ estimation bias in Experiment 2

On trials where no stimulus was presented, but where subjects reported detecting a stimulus, they were more likely to report motion directions close to the most frequently presented directions of the colour condition they reported (see Chapter 3). In order to investigate how quickly these biases developed, we calculated the probability ratio of giving an estimate within $8^\circ$ of each motion direction for individual subjects every 100 trials, including all responses up to that point. For subjects who had not reported detecting stimuli on any trials where none was presented, the probability ratio was undefined and these data points were not included in the plot.

After only 200 trials of the first session, the median probability ratio was significantly larger than 1 at the most frequently presented directions of the bimodal condition ($\pm 32^\circ$), but only when subjects reported the colour of that condition (Figure B.8B). It took approximately 400 and 900 trials for the probability ratio to become significantly larger than 1 for the most frequent presented directions of the trimodal condition ($0^\circ$ and $\pm 64^\circ$ respectively, Figure B.8A).

B.9 Linear combination models in Experiment 2

We implemented two additional models that assumed that subjects formed priors, which were a linear combination of the Trimodal and the Bimodal distributions. The ‘Combined’ model had 2 free parameters, non-negative weights $w_{tri}$ and $w_{bi}$, that measured the influence of the distributions on a single prior applied to both conditions. The ‘Split_Combined’ model assumed that subjects learned two distinct priors for each condition of the stimuli, each prior being described as a linear combination of the two distributions and requiring 4 free parameters. In total, the ‘Combined’ model required 5 free parameters and the ‘Split_Combined’ model 8 free parameters.

We compared the BIC values of the two models against the optimal ‘Split_TriBi’ model (Figure B.9A). The ‘Split_TriBi’ model was significantly better than both models ($p = 0.053$ for ‘Combined’, and $p < 0.001$ for ‘Split_Combined’, signed rank test). The ‘Split_TriBi’ model produced also significantly better AIC values ($p = 0.005$ for ‘Combined’ and ‘Split_Combined’, signed rank test, Figure B.9B), and provided better fits to subjects’ estimation biases (Figure B.9C) and standard deviations (Figure B.9D) than the other two models.
Figure B.8: Probability ratio that subjects gave an estimate within 8º from the most frequently presented motion directions (0º, 32º, and 64º) relative to other 16º windows, for trials where no stimulus was presented, but where they reported detecting a stimulus with the colour of (A) the Trimodal condition or (b) the Bimodal condition. This probability ratio is calculated for each subject after every 100 trials, and takes into account data from all trials up to that point. Data points represent the median values. The vertical dashed line corresponds to the end of session 1 and the beginning of session 2.
Figure B.9: Model comparison of linear combination models for Experiment 2. The (A) BIC and the (B) AIC values of each model subtracted by the BIC and AIC values of the ‘Split_TriBi’ model are plotted for each subject (black dots), along with median values (red lines), and the 25th and 75th percentiles (blue lines). *p*-values indicate whether the median was significantly different from zero for each model (signed rank test). Predicted averaged estimation biases (C) and standard deviations (D) for each model. Predictions for the ‘Combined’ (green), the ‘Split_Combined’ (blue), and the ‘Split_TriBi’ models (black) are plotted with the experimental data (red). Results are averaged over all subjects and error bars represent within-subject standard error. The red and green vertical dashed lines corresponds to the most frequently presented motion directions for the trimodal and bimodal distributions (0° and ±64°) and (±32°) respectively.
Appendix C

Experimental questionnaires

The questionnaires used to get feedback from subjects after each experiment are presented in succession; colour experiments (chapters 3 & 4), reward experiment (chapter 5) and visual search experiment (chapter 6) respectively.
Thanks for taking part in my experiment. I would appreciate it if you could also fill out this short questionnaire.

1. Did you find the first or second easier, or were they both the same? (please circle as appropriate)
   - 1st session easier
   - 2nd session easier
   - about the same

2. Did you notice anything unusual about the number of motion stimuli that were moving in each direction? For example, were some directions shown more than others? If yes, please describe in more detail what you saw.

3. If you filled in the last question, then was this the same in both sessions? (circle as appropriate)
   - Yes
   - No
   - Don’t know

4. How many directions of motion do you think there were? (please circle as appropriate)
   - 1,
   - 2,
   - 3,
   - between 4 and 10,
   - more than 10,
   - don’t know

5. Did you ever think you saw moving dots, and then it turned out there were none there?
   - Yes
   - No
   - Don’t know

6. Do you think that one color of the dots was more frequent than the other, or were they both the same? (please circle as appropriate)
   - Red
   - Green
   - about the same
7. Which of the following descriptions best describes the distribution of motion directions that you saw? (tick statement that you most agree with)

(a) There were equal numbers of stimuli moving in all directions.
(b) Most of the stimuli were centered around one central direction of motion.
(c) Most of the stimuli were centered around 2 different directions of motion.
(d) There were only two possible directions of motion.
(e) Don’t know.

8. If in the last question you selected (b), (c) or (d), can you draw a line (or lines) from the centre of this diagram out to the edge, indicating the direction(s) that were most frequently presented?

9. Do you think that the color of the dots affected the distribution of motion directions that you saw? (tick statement that you most agree with)

(a) The red and green dots had the same distribution
(b) The red dots had some directions more frequently presented than the green dots
(c) The green dots had some directions more frequently presented than the red dots
(d) The red and green dots had completely different distributions
(e) Don’t know
10. If in the last question you selected (b), (c) or (d) can you draw a line (or lines) from the centre of this diagram out to the edge, indicating the direction(s) that were most frequently presented for the appropriate color?
Questionnaire of reward experiment

Feedback Questionnaire

Thanks for taking part in my experiment. I would be grateful if you could also fill out this short questionnaire about your experience.

1. Did you think that the initial instructions were clear?

________________________________________________________________

2. Did you understand what you were expected to do in the experiment?

________________________________________________________________

3. Did you understand the criteria for allocation of points? (Tick all applicable)
   a. Based on estimating the direction of motion accurately ☐
   b. Based on the speed of your response ☐
   c. Based on correct identification of dots (detection) ☐
   d. It seemed random ☐
   e. Comments: _______________________________________________________

4. Did you feel as if the points system was fair? (Tick all applicable)
   a. Points were easy to get ☐
   b. The penalties seemed high ☐
   c. The points system seemed reasonable ☐
   d. The points system seemed random ☐
   e. Comments: _______________________________________________________

5. Approximately how many different directions of motion did you think there were?
   a. 1-5 ☐
   b. 5-10 ☐
   c. 10-15 ☐
   d. 15-20 ☐
   e. 20+ ☐
   f. Don't know ☐

6. Did you think that movement in some directions were rewarded more than others?
   a. Yes ☐
   b. No ☐
7. If you answered ‘Yes’ for the previous question, could you sketch the directions which you thought resulted in a higher number of points:

8. In the estimation task were you ever told that you were too slow?
   a. Yes ☐
   b. No ☐

9. Did you think that the speed expected for each trial was:
   a. Too Fast ☐
   b. Challenging but ok ☐
   c. Not a problem ☐

10. Did you feel as if gaining points was important to you?
    a. Strongly agree ☐
    b. Somewhat agree ☐
    c. Somewhat disagree ☐
    d. Strongly disagree ☐

11. What strategies were you using to maximise your score?
    ________________________________________________________________
    ________________________________________________________________

12. Do you have any other comments or suggestions?

Name:

Date:
Questionnaire of visual search experiment

1. Did you notice anything unusual about the experiment? If yes, please describe in more detail what you noticed.

2. Did you find the second session easier than the first one, or were they all approximately the same in difficulty? (please circle as appropriate)

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<thead>
<tr>
<th>Equal</th>
<th>First session was easier</th>
<th>Second session was easier</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

3. Do you think that there were an equal number of trials with target(s) present and not present? (please circle as appropriate)

<table>
<thead>
<tr>
<th>Equal</th>
<th>More trials with targets</th>
<th>More trials without targets</th>
<th>Don’t know</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

4. When you were uncertain about a target being present, what did you do MORE OFTEN? (please circle as appropriate)

<table>
<thead>
<tr>
<th>Chose that there were targets in the trial</th>
<th>Chose that there were NO targets in the trial</th>
<th>Did not choose a particular answer more often</th>
<th>Don’t know</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

5. In trials where there were targets, how many targets do you think there were MORE OFTEN?

<table>
<thead>
<tr>
<th>1</th>
<th>2</th>
<th>3</th>
<th>More than 3</th>
<th>Don’t know</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

6. Did you ever think you saw more than 3 targets on the same trial?

<table>
<thead>
<tr>
<th>Yes</th>
<th>No</th>
<th>Don’t know</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

   If you answered ‘Yes’, do you think that there were actually more than 3 targets or you just thought that you saw more because of the low contrast?

<table>
<thead>
<tr>
<th>There were actually more than 3 targets</th>
<th>It was because of the low contrast</th>
<th>Don’t know</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

7. Did you notice anything unusual about the number of targets in the positions they were shown? For example, were there more targets in some positions than in others? If yes, please circle in which session did first you notice that.

<table>
<thead>
<tr>
<th>No</th>
<th>1st session</th>
<th>2nd session</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
8. Which of the following statements do you most agree with? (please circle as appropriate)
(a) There were equal numbers of targets in all positions.
(b) Most of the targets were presented in a specific position.
(c) Most of the targets were presented in 2 specific positions.
(d) Most of the targets were presented in more than 2 specific positions.
(e) Don’t know.

9. If in the last question you selected (b), (c) or (d), can you identify the position(s) were targets were more frequently presented?

10. When you were uncertain about a target being present, did you choose to select a position that you knew a target might be present because of previous trials?

    Yes    No    Don’t know

If you answered ‘Yes’, did you choose the position(s) that you identified as frequently presented in 9?

    Yes    No    Don’t know

Name

Signature

Date
Appendix D

Supplementary materials of Chapter 6

We investigated whether subjects’ detection performance was different between the first and second sessions of the experiment. Regarding subjects of the control group, we conducted a three-way within-subjects ANOVA of subjects’ detection performance between location, session, and subjects (Figure D1.A). There was no significant effect of session on detection performance ($p = 0.49$) and no significant interaction of location*session ($p = 0.76$).

Regarding subjects of the bimodal group, we conducted a four-way within-subjects ANOVA between stimulus location, session, frequency of location, and subjects (Figure D1.B). There was no significant effect of session on detection performance ($p = 0.64$) and no significant interaction of location*session ($p = 0.81$) or session*frequency ($p = 0.06$), but there was a significant effect of frequency ($p = 0.007$, see main text).
Figure D.1: Detection performance comparison between experimental sessions. (A) The fractions of correctly detected stimuli are plotted against presented stimulus location for the control group in the first experimental section (black solid line) and in the second experimental session (black dashed line). (B) The fractions of correctly detected stimuli are plotted against presented stimulus location for the frequent and non-frequent conditions of the bimodal group in the first experimental section (red and green solid lines respectively) and in the second experimental session (red and green dashed lines). Results are averaged over all subjects and error bars show within-subject standard error.
Figure D.2: Frequency of a stimulus presentation at the same location n-trials back. The number of times a stimulus was presented at the same location in the current trial and in the n-trial back for the control group (black), and for frequent (red) and non-frequent (green) conditions of the bimodal group. Results are averaged over all subjects and error bars show within-subject standard error.
Figure D.3: Simulations of 16 observers presented with the same stimuli as the experimental subjects using a uniform prior over all presented locations: for each location $i$, \[ \text{priori}(s) = b \times \frac{1}{12}, \] where $b$ is the fraction of trials in which a stimulus is presented ($b = 0.7$).
Figure D.4: Simulations of 16 observers presented with the same stimuli as the experimental subjects using a single updating prior.


