The representation of the visual field on the optic tectum of the frog: evidence for the presence of an area centralis retinae.

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The representation of the visual field on the optic tectum of Rana temporaria was mapped by a method similar to that used by Gaze (1958a). The frog was fixed with its right eye covered and its left eye centred on the axis of an A.I.M. projection perimeter. A spot of light subtending an angle of 10' at the eye could be projected to any position in the frog's visual field. Action potentials evoked in response to the spot of light were recorded from the surface of the tectum with a steel micro-electrode (tip diameter about 5 μ) and amplified in the usual manner.

At each electrode position on the tectum there was a point in the visual field at which the stimulus evoked a maximal response. The determination of the position of maximal response was repeated with the electrode at successive positions spaced at 200 μ intervals on the tectum. Responses were obtained from 40 to 60 positions on the contralateral tectum and 10–20 positions on the ipsilateral tectum.

The results confirm the findings of Gaze (1958a, b) that there is a point-to-point projection of the visual field on to the optic tectum. There is a bilateral representation of the binocular part of the left visual field on the rostrolateral part of the right optic tectum and on the rostrolateral part of the left optic tectum, while the monocular part of the left visual field is represented only on the contralateral optic tectum.

The results show that the vertical and horizontal co-ordinates of the visual field undergo a geometrical transformation in the course of projection on to the tectum. It was possible to determine the number of microns of tectum devoted to one degree of visual field measured radially from the fixation point, the magnification factor (M) of Daniel & Whitteridge (1959). M does not decrease at the same rate along the vertical and horizontal meridians. Along the vertical meridian, M decreases from a maximum of 18.9 μ/degree, 20° below the fixation point, to a minimum of 7.7 μ/degree at the superior periphery of the vertical meridian. Along the horizontal meridian, M decreases from a maximum of 15.0 μ/degree 50° nasal to the fixation point, to a minimum of 10.7 μ/degree at the temporal periphery.

The region of the visual field which has the most magnified central representation forms a horizontal band stretching across the visual field just below the horizontal meridian. This corresponds with the position of the area centralis retinae in the frog described by Chievitz (1889).
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INTRODUCTION
INTRODUCTION

PREAMBLE

One of the main objectives of neurophysiology has been to seek for ever more accurate correspondences between the structure and functions of the nervous system. During the past century, as more refined techniques became available, the trend has been towards localization of specific functions in ever more limited regions of the brain.

At first, the very principle of functional localization in the nervous system was questioned. Before the development of refined histological techniques, and especially of the Marchi method of staining degenerating myelinated axons, evidence of localization was gained mainly by observing the functional deficits which were caused by crudely executed brain lesions. From the time of Flourens to that of Ferrier, the evidence was confused and the disputants were frequently inclined to adopt the view that best suited their personal philosophical preconceptions. The early brain mappers were in a position somewhat similar to that of the early cartographers, who could draw the outlines of uncharted territory, but had to await new means of exploration into the interior before they could erase the imaginary kingdoms and mythical monsters from the blank spaces on their maps. The announcement of each newly localized brain centre provoked acrimonious dispute from other physiologists who claimed to have located the same function elsewhere. Lashley (1929), in
summing up the work of that time, commented that "It is difficult to discover the truth in this record of contradictions."

The dispute has centred particularly around the problem of the spatial organization of the visual system, which "has become, in a sense, a battleground on which the opposing conceptions of the intrinsic organization of the brain have been tested" (Polyak, 1941, p. 437). However, during the past fifty years, with the improvement of histological techniques, sufficient anatomical evidence has accumulated to establish with certainty that the retina projects in a topographical manner onto the lateral geniculate body, the superior colliculus, and the striate cortex. Electrical recording from the visual centres has provided functional confirmation of the spatial organization of the visual system.

In the visual system, more than in any other, there is reason to suspect that the topographical organization is not only a macroscopic feature, but is found also in the dimensional relations of each cell to those that surround it in space. In the visual centres, the "sphere of influence" of each cell, depending on the size and shape of its dendritic field, may be as essential a functional property as the temporal pattern of nerve impulses that impinges on it. It may be that in the visual centres, cells with different shapes of dendritic fields, by being placed in different spatial relations to the afferent stream of impulses, may be preferentially excited by specific spatial elements, for example by angles or curves, in the stimulus configuration. Thus the geometrical properties of the cells in the visual centres may partly determine their functional properties. In this way it may be possible to explain the phenomenon of stimulus equivalence by extending the principle of geometrical organization.
from a macroscopic to a microscopic level in the visual centres, without having to invoke an electrical field theory.

The evidence that the visual centres are organized as a geometrical analogue of visual space has been fully discussed by Polyak (1941, 1957), who concluded that visual space sense is an inherent faculty due to the dimensional organization of the visual system. Whether or not any part of the sense of visual space is acquired by experience, has been keenly argued. Even in man, it seems probable that visual space sense is an innate faculty and that it is not acquired by learning or experience (Ogle, 1950; Tschermak, 1952). In the amphibians there is no doubt that the dimensional organization of the visual system is stable and is genetically determined by growth processes incapable of functional adjustment (Sperry, 1951a, b, c; 1955, 1956). After the optic nerve of a frog or a newt has been cut, and the eye rotated through $180^\circ$, the optic nerve regenerates and vision recovers (Matthey, 1926, 1927; Sperry, 1943, 1945; Stone, 1944, 1953). However the animal's sense of direction in visual space becomes confused, so that its efforts to capture a fly are misdirected to the side opposite to that of the prey. This maladaptive behaviour is never corrected by experience (Sperry, 1943; Stone, 1944).

In the submammalian vertebrates, the optic axons terminate in the optic tectum, which is the chief visual centre. All the modalities of visual perception, such as the sense of direction and location in space, the perception of patterns, and the perception of movement, are functions of the optic tectum. In keeping with its complex functions, the submammalian optic tectum has a structural complexity comparable with that of the mammalian visual cortex. In common with the visual cortex, the optic tectum has
been exhaustively studied with all the histological methods available during the past eighty years, without much advance towards understanding the functions of the strata or individual cells which histology has revealed. The beautiful cytoarchitectonic diagrams of the optic tectum appear to have about the same relationship to the structures they depict as a city plan has to the activities of its inhabitants.

The complexity of tectal architectonics has thwarted all attempts to follow individual axons from the retina to their tectal terminations, or to determine the number and the spatial distribution of the tectal neurons with which each optic axon makes contact. The only definite knowledge is that the optic axons terminate in a retinotopic order on the optic tectum and its mammalian homologue, the superior colliculus. The anatomical and physiological evidence for a point-to-point projection of the retina onto the optic tectum and superior colliculus is discussed more critically and in greater detail in the following two chapters.
ANATOMICAL STUDIES OF THE PROJECTION OF THE RETINA ONTO THE
OPTIC TECTUM AND SUPERIOR COLLICULUS

The anatomical work is frequently cited as evidence in favour of a point-to-point projection of the retina onto the optic tectum and superior colliculus. However, a critical survey of the literature reveals many gaps and inadequacies in the anatomical knowledge. The earlier workers were content to trace degeneration after enucleation of one eye, and so to establish that primary optic afferents reach the optic tectum or superior colliculus. In this way it was found that in the submammalian vertebrates the optic fibres decussate completely at the chiasma, and Marchi degeneration could be found only in the contralateral side (Bellonci, 1888; Mlassak, 1893; Ramon y Cajal, 1952-1955). Marchi studies in submammalian vertebrates have never revealed degenerating fibres on the ipsilateral side or in the intertectal commissure. Silver degeneration techniques have shown uncrossed optic fibres in a snake and a lizard (Armstrong, 1950; 1951) but they appear to terminate in the ipsilateral lateral geniculate body and not in the optic tectum. None of these studies was able to give any information about the detailed spatial organization of the visual pathways in the submammalian vertebrate orders.

In the mammals, optic fibres have been traced to the superior colliculus of the opossum (Tsai, 1925; Bodian, 1937); the ferret (Jefferson, 1940); the rabbit (Pavlov, 1900; Loepp, 1912; Minkowski, 1920; Brouwer, Zeeman and Houwer, 1923; Brouwer and Zeeman, 1925, 1926; Overbosch, 1927);
the rat (Lashley, 1934; Jefferson, 1940; Nauta and Van Straaten, 1947); the sheep (Nichterlein and Goldby, 1944); the goat (Minkowski, 1920); the cat (Probst, 1900; Minkowski, 1920; Barris and Ingram, 1934; Barris, Ingram and Ranson, 1935; Hoessly, 1947); the dog (Probst, 1900); monkeys and apes (Bernheimer, 1899; Minkowski, 1920; Brouwer and Zeeman, 1925, 1926; Crosby and Henderson, 1948); and man (v. Leonowa, 1896; Minkowski, 1920). Though the majority of retinocollicular fibres cross to the contralateral colliculus, uncrossed optic fibres have been traced to the ipsilateral superior colliculus in all the mammalian orders. However, the ease with which this can be achieved depends on the size of the uncrossed optic bundle. The termination of uncrossed optic fibres in the ipsilateral colliculus has been shown in the opossum (Bodian, 1937); the rabbit (Loepp, 1912); the rat (Nauta and van Straaten, 1947); the sheep (Nichterlein and Goldby, 1944); the goat (Minkowski, 1920); the cat (Probst, 1900; Minkowski, 1920; Barris, Ingram and Ranson, 1935); the dog (Probst, 1900); monkeys and apes (Bernheimer, 1899; Minkowski, 1920; Brouwer and Zeeman, 1925, 1926); and man (v. Leonowa, 1896). Following enucleation of one eye, the degeneration is always less in the ipsilateral colliculus than it is in the contralateral, and in the rodents, with a small percentage of uncrossed optic fibres, there have been reports of failure to find any Marchi degeneration granules in the ipsilateral colliculus, (Pavlov, 1900; Minkowski, 1920;
Lashley, 1934; Brouwer and Zeeman, 1925). The demonstration of Marchi degeneration in the uncrossed colliculus of the rabbit by Loepf (1912) may be discounted in the face of so many reports to the contrary. In the rat, the Marchi method revealed no ipsilateral projection to the superior colliculus (Lashley, 1934), whereas degeneration in the ipsilateral colliculus was found by Nauta and van Straaten (1947) using a silver degeneration technique. It is clearly unwise to accept negative evidence obtained with the Marchi technique. Another instance of this is the failure by Brouwer and Zeeman (1926) to find degeneration in either superior colliculus of the monkey after macular lesions.

The authors already cited gave no indication of whether there is any retinotopic organization of the optic fibres terminating in the superior colliculus; but they paved the way for Marchi studies following localized retinal lesions. This has been done in fish (Lubsen, 1921; Akert, 1949, a, b); in the rabbit (Brouwer, Zeeman and Houwer, 1923; Brouwer and Zeeman, 1925, 1926); in the rat (Lashley, 1934), in the opossum (Bodian, 1937). These authors are frequently cited, without any reservations, in support of the principle of a point-to-point projection of the retina onto the optic tectum and superior colliculus. Though it is true that they have succeeded in demonstrating a topographical projection of the retinal quadrants onto the optic tectum and superior colliculus, they have not been able to map the projection in
sufficient detail to prove that there is a point-to-point type of projection. In the following review it is therefore justifiable to draw attention to the limited number of species which have been investigated, and to some of the limitations of the anatomical techniques that have been used.

Most attention has been paid to the mammals, and for this reason they are dealt with first, in the order in which they were investigated rather than in phylogenetic order.

After making small retinal lesions in the rabbit, Brouwer, Zeeman and Houwer (1923), Brouwer and Zeeman (1925, 1926) and Overbosch (1927) were able to trace Marchi degeneration to localized regions of the contralateral superior colliculus. The uncrossed optic fibres were traced to the lateral geniculate body but could not be followed to the ipsilateral colliculus. They found that there was an orderly projection of retinal quadrants onto quadrants of the contralateral superior colliculus; the superior temporal retinal quadrant projects onto the rostrolateral part of the colliculus; the inferior temporal retinal quadrant projects onto the rostromedial part of the colliculus; the inferior nasal retinal quadrant projects onto the caudomedial part of the colliculus; and the superior nasal retinal quadrant projects onto the caudolateral part of the colliculus. The projection of the vertical meridian of the retina onto the colliculus is shown by Brouwer and Zeeman (1925, fig. 2) running from the midline obliquely caudolaterally across the summit of the colliculus at an angle of about 45 degrees to the midline.
The horizontal meridian bisects the vertical so that retinal quadrants are projected onto quadrants of about equal area on the colliculus. Brouwer and Zeeman were unable to map the projection in any more detail, though Overbosch (1927, quoted by Lashley, 1934) found that concentric circles of the retina from the optic papilla to the ora serrata projected onto concentric zones of the colliculus from its centre to its periphery.

Lashley (1934) made small retinal lesions in the rat and studied the resulting degeneration by means of the Marchi technique. He found that the quadrants of the retina were projected onto the quadrants of the contralateral superior colliculus in the manner already described in the rabbit by Brouwer and his colleagues. In the rat, the vertical meridian runs transversely and the horizontal meridian rostrocaudally across the summit of the colliculus parallel with the midline and not obliquely, as in the rabbit.

Though Lashley (1932) had been able to demonstrate an area centralis lying just above the horizontal meridian of the rat's retina, about 50° temporal to the optic papilla, he found no evidence of an increased amount of colliculus devoted to the projection of the area centralis (Lashley, 1934). Lashley traced Marchi degeneration to the ipsilateral geniculate body, but not as far as the ipsilateral colliculus. Nauta and van Straaten (1947) have found degeneration in the ipsilateral colliculus of the rat, but only by using the bouton degeneration technique after enucleation of one eye.
They were unable to localize the projection of the uncrossed optic fibres to a specific region of the ipsilateral superior colliculus.

The most complete study of the projection of the retina onto the superior colliculus is that of Bodian (1937) on the opossum (Didelphis virginiana). After making small retinal lesions, Bodian traced degeneration in Marchi series to localized regions of both contralateral and ipsilateral superior colliculi. The scheme of projection of the retinal quadrants onto the contralateral superior colliculus of the opossum was found to be the same as that already described in the rabbit and the rat. In addition, Bodian found that the temporal crescent of the retina projects to the rostral part of the ipsilateral superior colliculus, with the ventrodorsal sequence of retinal fibres projecting in mediolateral order onto the colliculus. Other workers (Probst, 1900; Minkowski, 1920; Brouwer and Zeeman, 1925, 1926; Neura and van Straaten, 1947; Hoessly, 1947) have been unable to localize the termination of uncrossed optic fibres to a specific region of the ipsilateral colliculus. Bodian has provided the only anatomical evidence of retinotopic projection of uncrossed optic fibres onto the ipsilateral superior colliculus, and the only demonstration that crossed and uncrossed fibres from the temporal homonymous retinal regions terminate in the same part of each superior colliculus.

There is some anatomical evidence for a topographical representation of the retina onto the superior colliculus of the
cat (Hoessly, 1947). However, only peripheral retinal lesions were made. Nasal retinal lesions resulted in Marchi degeneration in localized regions of the contralateral colliculus which conformed with the scheme described in other mammals. After temporal retinal lesions, the degeneration granules were scattered diffusely through out both colliculi without any evidence of localization. Though a larger projection from the area centralis is to be expected, a diffuse projection to the whole of both superior colliculi is difficult to reconcile with the demonstration, by means of evoked potentials, of a detailed point-to-point projection of the visual fields onto the superior colliculus of the cat (Apter, 1945). A similar problem has arisen in the course of all the Marchi studies. The dispersal of Marchi granules in the colliculus is usually so extensive that it is not possible to discriminate between small retinal lesions less than 30 to 40 degrees apart. One reason for this is that retinal lesions always interrupt fibres coming from the retina peripheral to the lesion. Another possibility is that there may be two systems of retino-collicular fibres; the thickest fibres forming a diffuse projection, the thinner fibres forming a retinotopically organised projection. Herrick found this in Amblystoma (Herrick, 1941; 1948), and Chang (1952) has suggested that the same may be true of mammals. If so, the Marchi technique, by selectively showing the thick fibres of the diffuse system, may mask the point-to-point projection.
Yet another possibility is that fibres from the peripheral retina form the primary retino-collicular system whose spatial organization is coarser than that of the macular fibres which may relay in the lateral geniculate body. Whitteridge (1960) has suggested this explanation of the failure of Brauer and Zeeman (1926) to find degeneration in the superior colliculus of the monkey after macular lesions.

The literature dealing with the projection of the retina onto the optic tectum of the submammalian vertebrates is less extensive, but not less controversial than that dealing with the mammals.

The earliest study of the degeneration resulting from localized retinal lesions was that of Lubsen (1921) on a teleost fish (Leuciscus rutilus) and his findings have been confirmed by Akert (1949 a, b) on another teleost (Salmo irideus). Lubsen and Akert were able to show that quadratic retinal lesions result in Marchi degeneration localized to specific regions of the contralateral optic tectum. No degeneration was found in the ipsilateral tectum. They found that the superior temporal retinal quadrant projects to the caudolateral part of the contralateral optic tectum; the inferior temporal retinal quadrant projects to the rostrolateral part of the tectum; the inferior nasal retinal quadrant projects to the rostromedial part of the tectum; and the superior nasal retinal quadrant projects to the caudomedial part of the tectum. In these studies only a gross projection of retinal quadrants onto the tectum could be demonstrated, as the retinal lesions were
not sufficiently small to show a more detailed point-to-point type of projection. These are the only reliable anatomical studies which have shown a topographical projection of the retina onto the optic tectum of the submammalian vertebrates.

The observations of Stroer (1939, 1940), though frequently cited, have serious defects. Using silver impregnated material, Stroer described two fascicles of optic nerve fibres which he followed from the retina to the tectum of a fish (Salmo salar) and a newt (Triturus taeniatus). One fascicle originated in the anterodorsal half of the retina and terminated in the ventrolateral part of the tectum; the other fascicle originated in the posteroverentral half of the retina and terminated in the dorsomedial part of the tectum. This order of projection does not conform with that found by Lubsen and Akert in related species of fish. Herrick (1941b, c), also using silver impregnated material, was unable to find any evidence of retinotopic projection onto the optic tectum of a urodele (Necturus) or the catfish (Ameiurus nebulosus). In Necturus (Herrick, 1941 b, c) and Amblystoma (Herrick, 1942, 1943) it was not possible to trace discrete fascicles of optic nerve fibres all the way from retina to tectum, as Stroer had described. The optic fibres in amphibians retain a fasciculation according to retinal quadrants for a very short distance proximal to the optic papilla, but become randomly interlaced in the optic nerve, and appear to terminate randomly in the tectal neuropil (Herrick, 1942, 1943; Maturana, 1958). Silver-impregnated material is quite
inappropriate for determining whether or not there is a point-to-point projection from retina to tectum. Though a more suitable degeneration technique might show such a projection in some submammals with highly developed visual capacities, the evidence now available is limited to two species of teleosts; and it is conceivable that some fish and amphibians, especially the urodeles, may have only a gross projection of retinal quadrants onto quadrants of the tectum. The species studied by Herrick have poorly developed vision, and Buser and Dusardier (1953), using the evoked potential technique, were also unable to find a point-to-point projection of the visual fields onto the optic tectum of the catfish, though they were successful in showing it in the carp and tench (see p. 16).

Probably there are species differences in the detail with which the retina projects onto the optic tectum in the various submammalian orders. This may be inferred from the differences which have been observed in retinal structure (Walls, 1942; Rochon-Duvigneaud, 1943), in the number of optic nerve fibres (Bruesch and Arey, 1942), and in the degree of structural complexity of the optic tectum (Kappers, Huber and Crosby, 1936; Ramon y Cajal 1952-1955). A comparative study of the anatomical organization of the visual pathway of the submammalian vertebrates and a correlation of this with the visual function of the different species remains a task for the future. No anatomical evidence has been produced for bilateral representation of the parts of the retinas concerned with binocular vision;
nor is there a hint of the manner of representation of the area centralis or the fovea in those submammals which possess those retinal structures. The anatomical evidence for a topographical projection of the retina onto the tectum is limited to two species of teleost fish, and requires to be extended to the amphibians, reptiles and birds.
PHYSIOLOGICAL EVIDENCE OF TOPOGRAPHICAL PROJECTION OF THE RETINA ONTO THE OPTIC TECTUM AND SUPERIOR COLLICULUS

The initial studies of the electrical activity in the superior colliculus were not concerned with localisation, as the potentials were evoked in response to illumination of the whole retina (Wang, 1934; Bernhard, 1940), or electrical stimulation of the optic nerve (Bishop and O'Leary, 1941, 1942).

Talbot and Marshall (1941) introduced the technique of mapping the central representation of the visual fields by recording, from a determined position on the visual cortex action potentials evoked in response to a small light in the visual field. Their method was used by Apter (1945) to map the projection of the visual fields on the superior colliculi of the cat. By means of a similar technique it has been shown that there is a topographical representation of the visual fields on the optic tectum of the carp and the tench (Buser and Dusardier, 1953); the frog (Gaze, 1958 a, b); and the pigeon (Hamdi and Whitteridge, 1953-1954); and on the superior colliculus of the rabbit (Hamdi and Whitteridge, 1953); and the goat (Cooper, Daniel and Whitteridge, 1953; Hamdi and Whitteridge, 1953). These papers are discussed below in the order of their publication.

Buser and Dusardier (1953) stimulated the retina with bipolar electrodes 1 mm apart and recorded potentials evoked in the contralateral optic tectum of the cat-fish, tench and
carp. In the cat-fish, their technique and the small size of the retina permitted them to distinguish a separated projection only for the nasal and temporal hemiretinas. In the carp and the tench, they found a separate projection of the retinal quadrants which conformed with the scheme of representation found in other bony fish by Lubsen (1921) and Akert (1949a, b) with the Marchi method. It is debatable whether their inability to show a detailed projection of the retina onto the optic tectum of the cat-fish was due to the inadequacies of their technique, or whether it can be correlated with the poor visual capacities of the cat-fish, an animal which has small eyes, and lives in murky water.

The technique employed by Apter (1945) was an advance over that used by Buser and Dusardier. Apter recorded action potentials with a wet-thread electrode on the surface of the superior colliculus of the cat, using as a stimulus a spot of light subtending an angle of 4.2° in the visual field. She found that for any position of the electrode, the evoked response was of minimum latency and maximum amplitude only at a localized position of the light in the visual field. In this sense there is a point-to-point projection of the visual field onto the colliculus, and Apter was able to map the projection in detail. However, with the light at a fixed position in the visual field, action potentials of diminished amplitude and increased latency were recorded from the whole surface of both superior colliculi. This was considered by Apter to have been due mainly to intraocular dispersal of light (Bartley, 1935;
Fry and Bartley, 1935). In the cat the tapetum is the main source of intraocular reflection (Weale, 1953; Dodt and Walther, 1958). It would, therefore, be interesting to compare the extent of lateral spread of the collicular potentials evoked from intratapetal and extratapetal regions of the retina.

Other causes of widespread evoked activity may be found in the histological structure of the superior colliculus. Lateral spread of the evoked potential may occur through the rich terminal arborizations (the "arborisations supérieures", and "arborisations inférieures" of Ramon y Cajal, 1952-1955) by means of which each optic afferent makes contact with many cells; through the optic afferents that pass obliquely through the strata of the colliculus; and through the wide lateral connections of horizontal dendrites. The contribution of the latter to tangential spread of slow wave responses in the tectum has been emphasised by Cragg, Evans and Hamlyn (1954) and Buser (1956).

Marshall and Talbot (1942) have shown that extensive reciprocal overlap and lateral interaction need not be incompatible with, and may enhance, topographical localization. The peaked distribution of activated units in the colliculus, found by Apter, is that which is most likely to satisfy the requirements of Marshall's and Talbot's theory. The finding of widespread activity in the colliculus in response to focal stimulation of the retina is thus not necessarily incompatible with a point-to-point projection.

Apter was able to map the representation of the visual
fields on the superior colliculi of the cat in more detail than had been accomplished in any other animal. The vertical meridian splits the field so that the nasal half is represented on the contralateral superior colliculus and the temporal half is represented ipsilaterally. The vertical meridian is represented along the rostral margin of the colliculus and the horizontal meridian runs rostrocaudally, and slightly obliquely, across its summit. The fixation point is represented at the rostral pole, and the peripheral part of the field at the caudal pole of the colliculus; while the upper field is represented on its medial, and the lower field on its lateral part.

Apter found that on each superior colliculus the representation of the ipsilateral temporal half-field and of the contra-lateral nasal half-field are superimposed in such a manner that corresponding points in the homonymous half-fields are in register. Details are not given of the procedure adopted in the single experiment in which the latter result was obtained. The main difficulty would have been to immobilize the eyes, or if that were not done, to make frequent checks on the position of the optic axes during the course of the experiment. This could have been done by repeated checking of the position at which a stimulus in the visual field gave a maximum response at an electrode fixed in position on each superior colliculus. Any deviation of the optic axis could be measured from the deviation of the stimulus from its expected position.
If the retinal projection onto the colliculus can be mapped in sufficient detail, it should be possible to determine the number of millimetres of colliculus representing a degree of visual field measured radially from the fixation point. Similar determinations of the magnification factor have been made on the visual cortex of primates (Talbot and Marshall, 1941; Marshall and Talbot, 1942; Daniel and Whitteridge, 1959). Measurements made from Apter's data (1945, fig. 3) show that the magnification factor diminishes by a factor of approximately 5 from the fixation point to the horizontal periphery of the visual field. It also appears as if the magnification factor does not decrease symmetrically about the fixation point, but diminishes about twice as steeply along the vertical as along the horizontal meridian.

Apter found a 29 msec latency of the response in the contralateral superior colliculus and a 33 msec latency of the ipsilateral collicular response. As variations in latency were not reported, the significance of the difference cannot be determined. The difference might be less than the variations in latency caused by uncontrolled experimental variables.

An additional difficulty in the interpretation of Apter's latency measurements arises from the finding of Ingvar and Hunter (1955) that, in the cat, the latency of the photically evoked collicular response was increased from 14 to 24 msec to 15 to 29 msec by removal of the striate cortex. They suggested that the latency of the earliest component of the photically evoked response on the superior colliculi may be shortened by corticofugal volleys through striato-tectal
pathways. If this is so, the 4 msec increase in latency of the evoked response in the ipsilateral colliculus, reported by Apter, may have been the result of functional impairment of the visual cortex caused by retraction of the cerebral hemispheres.

Hamdi and Whitteridge (1953, 1954) determined the representation of the visual fields on the optic tectum of the pigeon. They used a steel microelectrode on the tectum to record responses evoked by a neon flash subtending an angle of 0.5° in the contralateral visual field. They found that the superior half of the visual field is represented on the dorsal surface of the tectum and the inferior half-field on the ventrolateral surface, which could be reached only by passing the electrode through the tectum. Responses obtained from one needle track from dorsal and ventral surfaces of the tectum were evoked from positions in the upper and lower halves of the visual field approximately symmetrical about the horizontal meridian. The representation of the horizontal meridian runs rostro-caudally over the summit of the tectum, which has become tilted laterally in the pigeon, so that the horizontal meridian runs along the lateral edge of the tectum as seen from above. The vertical meridian runs transversely across the tectum, with the nasal half-field represented rostrally, and the temporal half-field caudally. There was no evidence of a larger area of tectum representing the centre of the visual field, but more recent experiments have shown that
the magnification factors for the fovea and peripheral retina differ by a factor of about 6 (Whitteridge, personal communication). It still remains to be seen whether there is any visual representation on the ipsilateral optic tectum of the pigeon. The pigeon's retina connects with both sides of its brain since it is capable of interocular transfer of visually learned habits (Levine, 1945), and has a consensual pupillary light reflex.

With the evoked potential technique, Hamdi and Whitteridge (1953) mapped the representation of the retinal quadrants on the superior colliculus of the rabbit. Their map conforms with, but does not add to, that which had already been described from Marchi series by Brouwer and his associates (Brouwer, Zeeman and Houwer, 1923; Brouwer and Zeeman, 1925, 1926). It should now be possible to discover whether any uncrossed optic fibres reach the rabbit's colliculus, or whether, as is more probable, the uncrossed fibres are confined to the geniculostriate pathway.

Cooper, Daniel and Whitteridge (1953) and Hamdi and Whitteridge (1953) found that the retinal quadrants project onto the goat's superior colliculus in the same order as that already described in other animals. The projection of the area centralis and other details of the retino-collicular projection in the goat, still remain uncharted. In the goat, as in many other ungulates, some birds, and some species of anuran amphibians, the area centralis retinae is in the form of an horizontal band (Chievitz, 1889, 1891; Slonaker, 1897;
Walls, 1942). The visual central representation of the goat may have geometrical properties in common with that of other animals with an horizontal bandlike area centralis. From the present evidence it is not possible to derive a function for the geometrical transformation involved in the projection of the retina onto the tectum of the frog or the goat.

Gaze (1958 a, b) established that there is a point-to-point projection of the visual fields onto the optic tectum of the frog, similar to that already described in the fish, pigeon, and rabbit. The unicovalar fixation point (the optic axis) is represented on the summit of the contralateral optic tectum. Concentric circles of visual field from the fixation point to the periphery are represented on concentric zones of tectum from its centre to its margin. The naso-superior, naso-inferior, temporo-inferior, and temporo-superior quadrants of the visual field are represented on the rostralateral, caudolateral, caudomedial, and rostromedial quadrants of the optic tectum. No evidence was obtained of a larger area of tectum representing the area centralis, but this might well have been due to the procedure of arranging the electrode positions in one or two straight rows across the summit of the tectum, rather than in a regular grid covering the whole tectal surface. The frog's area centralis was described by Chievitz (1889, 1891) as a band above the horizontal meridian of the retina, and is therefore expected to be projected onto the lateral edge of the tectum as seen from above. This part of the tectum is unlikely to be included in one or two rows of electrode positions, and in addition, it is frequently covered by a large venous sinu, the tractus venosus cerebralis dorsalis (Hofmann, 1901).
RECOVERY OF VISION AFTER REGENERATION OF THE OPTIC NERVE

In fishes and in larval and adult amphibians the visual tract has an amazing capacity to regenerate. The subject has already been exhaustively reviewed (Sperry, 1951 a,b,c; 1955; Stone, 1953; Gaze, 1960), and hence the following section is limited to a brief summary of the main findings and unsolved problems.

Regeneration of the visual tract will occur in immature and adult fishes and amphibians but not in any of the other vertebrate orders. The optic nerve can regenerate after simple section in fishes (Sperry, 1948); urodele amphibians (Matthey, 1926, 1927; Stone and Chace, 1941; Sperry, 1943); and anuran amphibians (Sperry, 1944; Maturana, 1958; Gaze, 1959; Maturana, Lettvin, McGulloch and Pitts, 1959). In adult frogs, regeneration of the optic nerve into the optic tectum on the same side occurs after excision of the optic chiasma and uncrossing of the optic nerves (Sperry, 1955).

In urodeles, the visual tract regenerates after transplantation of an eye to the opposite orbit (Stone, 1930; Stone, 1941; Stone and Cole, 1943); after transplantation of an eye to the orbit of another urodele of the same species (Stone, 1930, 1941; Stone and Zaur, 1940) or after transplantation of an eye to the orbit of a urodele of a different species (Stone, 1930; Stone and Ellison, 1940).

The optokinetic and pursuit reactions that have been used to demonstrate recovery of vision after regeneration of the optic nerve are tests of two major modalities of visual
perception - the ability to detect the position of an object in the visual field and its direction of movement. The simplest and most probable explanation of the recovery of these visual capacities is that the retinotopic projection onto the optic tectum has been restored after regeneration of the optic nerve. The most direct evidence of this is the demonstration by means of electrophysiological mapping that the normal retinotopic projection onto the optic tectum is restored after regeneration of the optic nerve (Gaze, 1959; Gaze and Jacobson, 1959; Maturana, Lettvin, McCulloch and Pitts, 1959).

Following inversion of the eye, the optokinetic and pursuit reactions are inverted to a similar extent. For example, when vision returns following 180° rotation of the eye plus section of the optic nerve (the other eye having been removed), the amphibian will follow a series of vertical stripes moving in a naso-temporal direction across the visual field, whereas optokinetic responses are normally evoked only to movement in a temporo-nasal direction. If a lure is waved in the naso-superior quadrant of the visual field the amphibian will attempt to capture the lure with snapping movements directed at the temporo-inferior visual field quadrant. These maladaptive responses have never been known to be corrected by experience (Sper, 1943; 1945, 1951a; Stone, 1944, 1953). In one newt maladaptive visuomotor responses were observed for 42 years following rotation of the eye, but readjustment of the optokinetic response and
accurate localization of a lure occurred immediately after the eye was rotated back to its normal position (Stone, 1953).

The conclusions drawn from these and other experiments were that the normal topographical representation of the retina on the optic tectum is restored irrespective of whether the retina is upright or upside down or whether the optic tract is connected to the ipsilateral or contralateral optic lobe. In addition, the regenerating optic nerve fibres become chaotically scrambled at the site of section of the optic nerve (Sperry, 1944; Maturana, 1958). It therefore appears necessary to postulate a mechanism which ensures that each optic nerve fibre connects with its correct tectal locus.

THE HYPOTHESIS OF BIOCHEMICAL SPECIFICITIES DETERMINING THE ORDERLY CENTRAL CONNECTIONS OF OPTIC NERVE FIBRES

It is clear that the processes which determine the selective central connections of optic nerve fibres cannot be modified by experience and learning. However, none of the experiments so far devised gives any further insight into the nature of these processes. Sperry has devised a hypothesis for this purpose, according to which each optic nerve fibre has a unique biochemical specificity and is able to establish functional connections in the tectum only with cells having the same specificity. Sperry's own summary of this concept leaves one in little doubt that
He envisages an unscrambling process in the tectum as the essential mechanism for ensuring a correct spatial distribution of afferent optic terminations:

"How does a fibre find its way to its destination? There is good reason to believe that the regenerating fibres employ a shotgun approach. Each fibre puts forth many branches as it grows into the brain, and the brain cells likewise have widespread branches. Thus the chances are exceedingly good that a given fibre will eventually make contact with its partner cells. We can picture the advancing tip of a fibre making a host of contacts, the great majority of which come to nothing; but eventually the growing tip encounters a type of cell surface for which it has specific chemical affinity and to which it adheres." (Sperry, 1956)

This image of the axon tip 'begging from door to door like Blake's earthworm, is attractive, but there are at least two experimental observations which cast doubt on its validity. The first of these has been provided by Sperry himself, when he showed that recovery of vision occurred after excision of the chiasma, ipsilateral union of the stumps, and regeneration of the optic nerve into the optic tectum on the same side (Sperry, 1945). For this result to be consistent with the specificity hypothesis, it is necessary for a mirror image pattern of identical biochemical specificities to exist in each tectum. This is not impossible, but it introduces an unlikely elaboration on a hypothesis which already has no direct evidence in its favour.

The second objection to Sperry's hypothesis arises from the observation that eyes transplanted between different species of Salamanders are able to establish normal functional
connections with the optic tectum of the host (Stone, 1930; Stone and Ellison, 1940). This occurs even when the size of the eye and the visual capacity of the host differs from that of the donor (Twitty and Schwind, 1931; Stone and Ellison, 1940). For example, an eye from Amblystoma tigrinum can be exchanged for the much larger eye of Amblystoma punctatum, or a small eye from Triturus viridescens can be grafted in place of the large eye of Amblystoma punctatum. Most important of all, the size of the optic tectum becomes adapted to the size of the transplanted eye. Thus replacement of a normal eye by one of greater size results in enlargement of the contralateral optic tectum of the host, and substitution of an eye from a smaller species results in shrinkage of the contralateral optic tectum (Harrison, 1929; Twitty, 1932). It is most unlikely that an identical pattern of biochemical specificities is found in the retina and optic tectum of all species of urodèles. These observations can only be consistent with Sperry's hypothesis if in these cases the essential functional adequacy was restored in spite of considerable deviation from the normal pattern of nerve connections. This would introduce yet another point of controversy into Sperry's hypotheses, namely the issue of the latitude allowed to developmental and regenerative processes.

Rather than hedge Sperry's hypothesis with numerous qualifications, it was considered reasonable to formulate an alternative hypothesis which not only would be consistent with all the known data, but which could be tested experimentally.
THE HYPOTHESIS OF DIFFERENTIAL GROWTH RATES OF OPTIC NERVE FIBRES DETERMINING THE ORDERLY PROJECTION OF THE RETINA ON THE OPTIC TECTUM

The alternative hypothesis is that different rates of growth of axons from different parts of the retina determine the orderly point-to-point retinal projection onto the optic tectum. This possibility has not, as far as I am aware, been previously suggested. Although there is no direct evidence to support it, there is some indirect evidence in its favour, and the hypothesis appears to be quite consistent with all that is known. The following evidence seems to be relevant:

In amphibians, differentiation of the optic tectum does not occur simultaneously in all regions, but begins at the anterior pole, and maturation proceeds in an anteroposterior direction. Thus stratification is first seen in the anterior pole of the tectum and extends posteriorly as optic fibres grow into the tectum (Herrick, 1942, 1948; Kollros, 1953). Acetylcholinesterase develops first at the anterior pole of the tectum, and during development there is a gradient of ChE concentration from anterior to posterior pole (Boell, Greenfield and Shen, 1955). The first afferent fibres to grow into the tectum are those of the optic tract. In Amblystoma these grow into the tectum from its anterior pole (Herrick, 1942, 1948) and subsequent fibres appear to follow the same route.
It is reasonably certain from the work of Crelin (1952) and Wiemer (1955) that the optic tectum does not become functionally polarized before optic fibres grow into it. Thus 180° rotation of the tectum at any larval stage before its connection with the retina results in reconstitution of the tectum with recovery of normal vision. However, rotation of the tectum during the period when it is being invaded by optic nerve fibres results in progressive impairment of vision. Crelin (1952) concluded from these experiments that "the differential properties possessed by the optic axons from the different retinal loci are believed to have served as an organizing influence on the formation of the synaptic connections within the rotated tectum". Crelin believed that these differential properties were biochemical specificities carried by each optic fibre into the tectum. With equal validity, differential growth rates of optic axons could explain these results. In any case, there does not appear to be any pattern of biochemical specificities in the tectum before optic axons grow into it. On the other hand, all the evidence shows that the polarity of the whole visual system is determined by a field differentiation of the retina (Stone, 1944, 1946). Stone showed that before larval stage 34, when the optic fibres start sprouting from the retina, the optic cup of Amblystoma can be transplanted and rotated without affecting normal vision. The retina is said to be functionally unpolarized. However, rotation of the eye during stages 34 to 36 results in progressive confusion of
visuomotor responses; and rotation of the eye after stage 36 invariably results in reversal of visuomotor responses.

Since the optic axons only start invading the tectum during stage 38, it is clear that the polarity of the retina is fully expressed in both DV and AP axes before the eye is connected with the optic tectum. It is of interest that there is a stage during which retinal polarity is not completely determined, since rotation of the eye at that stage does not invariably result in reversal of visuomotor responses (Stone, 1943).

It has been shown that there is an interval between the determination of retinal polarity in the AP axis which occurs prior to its determination in the DV axis (Sato, 1933; Barden, 1942; Stone, 1948; Szekely, 1954, 1957). This might mean that the functional polarization of the retina is independently determined by two growth gradients, one acting in the AP and the other in the DV axis of the eye.

Bearing the above evidence in mind, I shall attempt to expand the hypothesis as broadly as possible without doing violence to the facts:

During development, as well as during regeneration, the optic nerve fibres growing from the retinal ganglion cells into the brain do not all have the same rate of growth. If all the fibres have to traverse a pathway of the same length, they will arrive at their terminations in a sequence which will depend on their relative rates of growth. If, in addition, the growth rates of optic nerve fibres is specific for different parts of the retina, the arrival of the fibres in the tectum
will occur in a succession which will have validity in terms of retinal area. In brief, differential growth rates provide a means whereby retinal spatial specificity becomes translated into tectal spatial specificity.

One can conceive of successive waves of optic fibres entering the anterior pole of the tectum. The tectum prior to its invasion by optic fibres is in a pluripotential state of neuronal organisation. At this stage in embryonic development, the tectum is unstratified and is divided only into outer undifferentiated white and inner undifferentiated grey. As the first optic nerve fibres enter the anterior pole of the tectum, cells migrate out of the tectal grey and establish contact with the optic afferents near the surface of the tectal white. The exact forces which determine the configuration of these linkages is an unsolved problem of growth and development generally, with which this hypothesis is not particularly concerned. The important point is that the fastest growing optic fibres, arriving first in the tectum, make their connections nearest to their point of entrance into the tectum, and therefore constrain the next wave of optic fibres to connect more posteriorly. In this way, successive waves of optic fibres are excluded from the anterior regions of the tectum and forced to make their connections more posteriorly.

It is necessary for each retinal and tectal locus to be specified in at least two co-ordinates. This necessity can be satisfied by means of differential growth rates if the rate
of growth of any retinal ganglion cell is determined by two growth gradients, one in the DV, and the other in the AP axis of the eye. If each of these gradients determined the time of maturation and sprouting of retinal ganglion cells, every ganglion cell will have a uniquely specified growth rate, and as a result of the timing of arrival of its axon in the tectum, it will acquire a unique tectal spatial specificity corresponding with its retinal spatial specificity.

An interesting analogy is that of two-dimensional paper chromatography, by means of which a mixture of substances can be spatially separated as a result of their different rates of movement in two electric fields acting in directions at right angles to each other. It is possible that the growing axon tips are subjected to bi-axial growth-promoting fields continuously or at several points along the visual tract. It is known that in amphibians the optic fibres are tangled in the optic nerve but become segregated into thick and thin fibres at the chiasma and there is some evidence of retinotopic organization of the fibres in the optic tract. The gradual increase of dimensional organization of the visual tract along its long axis is consistent with an organizing force exerting a summative effect along the axis of the tract.

Sperry seems to have regarded the problem of scrambling of optic fibres during regeneration as a serious reason for believing that "the tangle of regenerating fibres is sorted out in the brain so as to restore the orderly maplike projection of the retina on the optic lobes" (Sperry, 1956). It is
worth noting that, however randomly interwoven optic nerve fibres become during regeneration, provided that their individual growth rates are unaffected, the spatial relations of their tectal terminations will remain undisturbed.

One of the attractions of this hypothesis is that it might be possible to test its validity experimentally. Histological methods appear to be distinctly limited for this purpose, not only because of anatomical complexity, but also because there is no certain histological way of detecting whether the structure being examined is functional or not.

The evidence required to test this hypothesis might be gained by the use of the evoked potential technique to map the visual fields on the tectum at progressive stages during the regeneration of an optic nerve, and thus to establish when, where, and how the first optic fibres make their connections in the tectum.

Some of the questions which may receive an answer are:—

How soon after section of the optic nerve does function return to the tectum? In what region of the tectum is function first re-established. Does function return to the whole tectum simultaneously, or to a small region of the tectum, for example the anterior pole, and subsequently extend to the rest of the tectum? If so, in which direction does the extension occur? How precisely is point-to-point representation re-established? Is the projection initially a diffuse one, later becoming clarified into a more precise point-to-point projection?
Is the projection point-to-point at the time that the first optic fibres grow into the tectum? If so, is the projection at first only from one region of the visual field, with the visual field extending its projection when more fibres grow into the tectum? If this is so, in what order does the projection evolve?

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Neural organization has always been the dominating theme of neurogenesis, and there has been a gradual convergence of approaches to this subject from the neuro-embryologists and the neurophysiologists. Already in 1929, Lashley had appreciated the necessity for this convergence of interests, when he wrote: "In the process of growth and regeneration we meet the same problems of determination of specific reactions (differentiation) by the interrelations of parts and by the total mass of tissue, the establishment of equilibrated systems, and the limitation of complexity of differentiation by the mass of tissue. The parallel is so close that, I believe, we may turn to the phenomena of morphogenesis for a clue to neural organization." The discoveries of Weiss and Sperry and of their collaborators have vindicated this belief. It has taken a long time for the disciplines of neurophysiology and neuroembryology to establish a common field of inquiry. The confirmation by Gaze (1959) of Sperry's hypothesis, that regenerating optic axons re-establish their topographical projection onto the optic tectum of the frog, has been the first fruit of this union of disciplines.
The experiments to be described in this thesis were inspired by the success with which the evoked potential technique had been able to throw new light on a problem central both to neuro-embryology and to neurophysiology. The experiments are of two kinds: mapping the projection of the visual fields onto the tectum of normal frogs; and mapping the projection of the visual fields onto the tectum of frogs at successive stages during the course of regeneration of the optic nerve. These experiments were performed with the hope that they might result in a further understanding of the way in which the geometry of visual space is reflected in the organization of the visual system.
**EXPERIMENTAL METHODS**

**METHOD OF MAPPING THE PROJECTION OF THE VISUAL FIELDS ONTO THE OPTIC LOBES**

Adult Rana temporaria and Bufo vulgaris were used to map the visual field on the optic tectum. The animal was anaesthetised in an atmosphere of ether. The optic lobes and cerebral hemispheres were exposed by removing the parietal and frontal bones. After decerebration, 0.3 mg. tubocurarine was injected intramuscularly. The optic lobes were kept moist in a pool of liquid paraffin and the meninges were removed. The optic lobes were photographed.

The right eye of the frog was either removed or covered. The frog was positioned on the platform of a micromanipulator, with its left eye centered on an A.I.M. projection perimeter with a radius of 33 cm. (fig. 1). By means of this perimeter, a spot of light of variable diameter and intensity could be projected to any position in the frog's visual field. The optic axis of the eye was aligned with the axis of the perimeter in the following manner:

A narrow beam of light was projected from the centre of the perimeter through a hole in the centre of a plane mirror lying on the axis of the perimeter and inclined at 45° to it. The position of the eye was adjusted so that the light beam entered the eye and was reflected back and could be seen
reflected in the mirror as a red glow emerging from the pupil. Since a tapetum is absent from the frog's eye, the reflection is faint, and rotation of the eye by only a few degrees from the axis of the perimeter caused the glow to fade and disappear. The head of the frog was rotated about the interocular axis so that the long axis of the horizontal oval pupil corresponded with a thin nylon thread stretching between the arms of the perimeter in the horizontal meridian.

A centimeter grid was drawn on a fifty-times enlarged photograph of the optic tectum (See figs. 2 and 3). There is a pattern of melanophores on the surface of the tectum, and an electrode could be positioned with reference to these and the grid on the photograph. Under vision through a dissecting microscope, a steel microelectrode could be guided by means of a micromanipulator to each of the positions on the tectum corresponding to the intersects of the grid on the photograph. The electrode was lowered onto the surface of the tectum until electrical contact was made.

Action potentials in the tectum, evoked in response to a spot of light in the visual field, were recorded between the microelectrode on the tectum and an electrode on one of the frog's hindlimbs or in its mouth. Evoked potentials were amplified by an RC amplifier with a time constant of about 10 msec., displayed on an oscilloscope and monitored with a loudspeaker. The position of the light was adjusted to give the maximum response. This procedure was repeated with the
micro-electrode at 200 micron intervals on the tectal grid.
In this way it was possible to obtain responses from 40 to 60 positions on the right (Contralateral) half of the tectum, and 10 to 20 positions on the left (ipsilateral) half of the tectum.

In four experiments the accuracy with which the electrodes were placed was checked histologically (fig. 6). At each electrode position, after recording from the dorsal surface of the tectum, the electrode was driven 500 microns down into the tectum. The electrode tracks could subsequently be seen in silver-impregnated serial sections of the brain, and a check could be made of the accuracy with which the electrodes had been positioned.

Only the dorsal surface of the optic tectum is visible from above. The ventrolateral third of the tectum is not directly accessible, and in some experiments, the electrode was passed through the dorsal surface of the tectum, until contact was made with the ventrolateral surface.

The stimulus was a circular spot of light of approximately uniform brightness, 1 mm in diameter, subtending 10' of arc at the eye. The light was projected onto the arc of the perimeter from a 12v 36w precentered tungsten filament lamp through an optical system containing a neutral density filter. The experiment was performed in dim light, with the intensity of stimulus light adjusted to about 0.65 cd/m.

No special attention was paid to the duration of the stimulus, but it was of the order of 1 second. The interval between stimuli was of the order of 1 minute. With this duration and frequency of stimulation, the localization of the position of maximal response did not appear to be affected by retinal adaptation.

The electrodes used were electropolished steel needles,
with a tip diameter of from 3 to 10 microns, insulated except at the tip.

TRANSECTION OF THE OPTIC NERVE.

Transection of the left optic nerve was performed in seventy-one frogs. After the frog had been anaesthetized with ether, the optic chiasma was exposed through the roof of the mouth by lifting a small flap of the left sphenopalatine bone. With iridectomy scissors, the left optic nerve was transected close to the chiasma. The flap of bone was replaced, and the cut edges of the palatal mucosa were approximated by pinching them together with forceps.

METHOD OF TESTING FOR THE RETURN OF OPTOKINETIC RESPONSES FOLLOWING TRANSECTION OF THE LEFT OPTIC NERVE.

After its left optic nerve had been cut, each frog was tested daily for the return of the optokinetic response from left to right, which is normally mediated through the left eye, and which was absent following the optic nerve section.

Optokinetic responses consist of the movement of the frog's head, and sometimes of its whole body, in the direction of movement of a series of vertical stripes passing horizontally across the frog's visual field. The optokinetic stimulus
is effective when moving only in a temporo-nasal direction across the visual field of either eye, and therefore optokinetic responses from left to right and from right to left are mediated separately through the left and the right eye.

The frog was placed on a stationary platform in the centre of a drum, 40 cm in diameter, which could be rotated horizontally round the frog. Painted on the inside of the drum, facing the frog, were alternate black and white vertical stripes 4 cm broad. The drum was manually rotated at a variety of speeds between 10 and 20 cm/sec. After the left optic nerve had been cut, optokinetic responses were elicited by rotation of the drum from right to left, but not by rotation from left to right. Each frog was tested daily after optic nerve section until the optokinetic response from left to right returned. This occurred in 23 frogs which were then used for mapping the projection of the left visual field onto the optic tectum. In 17 frogs the mapping was performed before the return of optokinetic responses.
METHOD OF MAPPING THE PROJECTION OF THE LEFT VISUAL FIELD ON THE OPTIC LOBES FOLLOWING REGENERATION OF THE LEFT OPTIC NERVE

The frogs were kept for periods ranging from 21 to 125 days after transection of the optic nerve (Tables 7 and 8). The projection of the visual field of the operated eye onto the tectum was then mapped in the manner already described for normal animals.

In these experiments, the additional precaution was taken of using the normal eye as a control to show that lack of response through the operated eye was not due to any defect in the preparation.

While the projection of the operated eye was being mapped on the tectum, the normal eye was carefully covered with an opaque shield. If no response could be evoked through the operated eye the shield was removed, and responses evoked through the normal eye were used to check whether the preparation was still active.

If responses were obtained through the operated eye, a comparison was made of the position in the visual field of the stimulus which evoked a response through each eye, at the same electrode position.

After completing the experiment, the brain was fixed, embedded in paraffin wax, and cut into transverse serial sections 15 microns thick, which were silver impregnated by Holmes' method.
EXPERIMENTAL RESULTS
RESULTS OF MAPPING THE PROJECTION OF THE VISUAL FIELDS

ONTO THE OPTIC LOBES OF NORMAL FROGS AND TOADS

For each electrode position on the tectum there was an area 10° to 30° in diameter in the visual field, from within which the stimulus evoked a response. Within this receptive field there was a position at which the response was clearly maximal. The position of maximal response was determined partly by viewing the oscilloscope trace, but mainly by subjective evaluation of the loudness of the audio-amplified response. In many cases, especially with the stimulus at the periphery of a receptive field, responses which were not visible were clearly audible.

In these experiments, records were made only of the position of the stimulus in the visual field. The response, which occurred after a latency of the order of 200 to 500 milliseconds, consisted of a group of action potentials from many units. No attention was paid to latency, amplitude, or duration of the responses, and the recording conditions did not permit the detection of slow wave responses.

The representation of the visual field on the optic tectum was successfully mapped in 14 frogs and in 6 toads. In 7 frogs and 4 toads only the representation of the left visual field on the right optic tectum was mapped. In 4 frogs, a map was made of the representation of the left visual field on the left optic tectum, and in 3 frogs and 2 toads, a map was made of the representation of the left visual field on the ipsilateral and the contralateral optic tectum.

Projection of the left visual field onto the right optic tectum

In figs. 2 and 3, the positions of maximum response in the
left visual field are shown corresponding with the positions of the electrode on the surface of the right optic tectum. Each point in the left visual field is represented by a point on the right optic tectum, so that the horizontal and vertical dimensions of the frog's uniconal visual field are projected as a two-dimensional map onto the surface of the contralateral optic tectum. The projection of this map in the third dimension of the tectum was not explored. However, by passing the electrode through the tectum for its full thickness (about 0.5 mm) and recording from different depths, it was always found that, provided the needle track was normal to the surface, the position remained unchanged at which the stimulus evoked a maximum response.

Only the dorsal surface of the optic tectum, onto which the upper three-fifths of the visual field project, is directly accessible from above. The lower two-fifths and the peripheral nasal part of the visual field project onto the ventrolateral surface of the optic lobe. By passing the electrode through the dorsal surface of the tectum, until contact was made with the ventral surface, it was possible to obtain responses with the stimulus in the lower two-fifths of the visual field. These stimulus positions are marked with crosses in the visual field diagram of fig. 3. As it was not possible to determine the exact position on the ventral surface of the tectum from which these responses were recorded, the map could not be extended from the dorsal onto the ventral surface of the tectum.
The method of plotting the map of the meridians and parallels of the left visual field onto the right optic tectum can be seen from figs. 2 and 3. By measuring the relative distances of a pair of stimulus positions to the meridian or parallel that passes between them in the visual field, the projection of the meridian or parallel can be plotted at the same relative distances from the corresponding pair of electrode positions on the photograph of the tectum. By repeating the measurements for all pairs of stimulus and electrode positions, the projection of the left visual field onto the right tectum can be plotted (figs. 2 and 3).

The topographical scheme of this projection is as follows: The vertical meridian of the visual field is represented running backward and laterally across the summit of the tectum, and dividing it into a rostro-lateral half onto which the nasal half-field is represented, and a caudo-medial half on which the temporal half-field is represented. The nasal end of the horizontal meridian is represented at the rostrolateral pole of the tectum. The representation of the horizontal meridian runs backwards and medially across the summit of the tectum, and its temporal end projects onto the caudo-medial pole of the tectum. The superior half of the visual field is projected onto the dorso-medial part of the tectum, and the inferior half-field onto its ventrolateral part. The uniocular fixation point is projected onto the summit of the contralateral optic tectum and concentric circles from the fixation point to
the periphery of the visual field are projected onto concentric zones of the tectum from its summit to its margins.

It is immediately evident from figs. 2 and 3 that certain parts of the visual field have relatively larger areas of tectal representation than others. This can be expressed quantitatively by determining the number of microns of tectum devoted to the representation of one degree measured radially on any meridian of the visual field. This was done by measuring the distance along a meridian between two parallels 10° apart in the projection of the visual field drawn on the enlarged photograph of the optic tectum.

The magnification factors for every 10° along the vertical and horizontal meridians have been calculated from the results of five experiments on Rana temporaria (Tables 1, 2, 3) and from five experiments on Bufo vulgaris (Tables 4, 5, 6). In these ten experiments, responses were obtained from a sufficient number of tectal electrode positions to allow the construction of a detailed map of the projection of the visual field onto the contralateral optic tectum.

In figs. 6 and 7, the means and limits of the magnification factors have been plotted against visual field eccentricity. It can be seen that the magnification factor (M) does not decrease at the same rate along the vertical and horizontal meridians. In Rana temporaria, M decreases from a maximum of 19 microns/degree, 20° below the fixation point, to a minimum of 8 microns/degree at the superior periphery of the
vertical meridian (Table 3). In Bufo vulgaris, M decreases from a maximum of 22 microns/degree, 10° below the fixation point, to a minimum of 7 microns/degree at the superior periphery of the vertical meridian (Table 6). Along the horizontal meridian, in Rana temporaria, M increases from a minimum of 11 microns/degree at the temporal periphery, to a maximum of 15 microns/degree 50° nasal to the fixation point (Tables 2 and 3). Along the horizontal meridian, in Bufo vulgaris, M increases from a minimum of 10 microns/degree at the temporal periphery, to 13 microns/degree 50° nasal to the fixation point. However, this peak at the fixation point for the value of M in Bufo is not significantly different from the value of M at the fixation point in Rana. An analysis of variance shows that there are no significant differences between the magnification factors for Rana and Bufo.

The region of the visual field which has the most magnified central representation lies 10° to 20° below the fixation point, and is projected onto the lateral edge and latero-ventral part of the contralateral optic tectum. However, this is the part of the tectum onto which it is most difficult to place electrodes with any degree of accuracy because of the curvature of the lateral part of the tectum, whereas the dorsal surface of the tectum is almost flat. This can be seen in the transverse sections of the tectum shown in Figs. 8 and 10 to 16. For this reason it is not possible to extend the map to include the whole of the region of the visual field which has the
greatest central representation. However, it appears as if the region of the visual field which has the most magnified central representation forms a horizontal band just below the horizontal meridian. Along the upper part of this band, along the horizontal meridian, M increases by a factor of only 1.4 from the temporal to the nasal periphery of the visual field, whereas along the vertical meridian, M increases by a factor of 2.5 to 3 from the superior periphery to 10° below the fixation point.

Projection of the binocular visual field onto both optic lobes

A light in the binocular visual field evoked a response through either eye on the rostrolateral part of both optic lobes. Since the scheme of projection of the binocular visual field onto the ipsilateral and contralateral optic lobes was the same for Rana and Bufo, only the results of an experiment on Bufo have been illustrated (Figs. 4 and 5, Experiment B7).

In fig. 4, the upper diagram shows the outline of both optic lobes with the positions of the electrode from which potentials were recorded in response to a flash of light in the visual field. The different symbols distinguish between the electrode positions from which responses were obtained through the left eye only, and those from which responses were obtained through both the left and right eyes.

Responses were obtained through the left eye at all the electrode positions on the right optic tectum, and at the electrode positions marked with circles on the rostrolateral part of the left optic tectum.
Responses were obtained through both eyes at the electrode positions marked with triangles on the rostrolateral part of the right optic tectum and at the electrode positions marked with circles on the rostrolateral part of the left optic tectum. Thus, referring to fig. 4, a stimulus at position 13 in the visual field evoked a response through either eye at electrode position 13 on the right optic tectum and at position P on the left optic tectum.

The part of the binocular visual field which has the greatest central representation forms a band 15° to 20° below the horizontal meridian passing through the optic axes. In fig. 5 the meridians of the binocular visual field have been drawn through a point on the toad’s sagittal plane 20° below the horizontal meridian passing through the optic axes. As the frog and toad do not converge their eyes in fixation, the term "binocular fixation point" is not appropriate, and this point will simply be called the binocular point.

The binocular point is projected onto symmetrical points on the rostrolateral pole of each optic lobe. The projection of the vertical meridian of the binocular visual field runs medially and parallel with the rostral margin of each optic lobe. The projection of the horizontal meridian of the binocular visual field runs along the lateral edge of each optic lobe.

In experiment B7 (figs. 4 and 5), the angle of divergence of the optic axes was 116°, and the optic axes were 58° lateral and 20° superior to the binocular point. The extent of the binocular visual field was 90° horizontally and 70° vertically. Measurements
of the extent of the binocular visual field in four frogs and two
toads were as follows, with the angle between the optic axes
given in brackets:

- Frog N2: 90° horizontal, 85° vertical (118°)
- Frog N3: 75°, 70° (123°)
- Frog LL: 80°, 70° (120°)
- Frog NLL: 75°, 70° (122°)
- Toad B4: 100°, 85° (115°)
- Toad B7: 90°, 70° (116°)

RESULTS OF MAPPING THE VISUAL FIELD ON THE OPTIC LOBES

FOLLOWING REGENERATION OF THE OPTIC NERVE

The left optic nerve was transected in seventy-one frogs. Seventeen of these died before they could be used for mapping. Another fourteen died of haemorrhage soon after they had been prepared for mapping, or early in the course of mapping. These have not been included with the other results.

The remaining forty frogs may be divided into three groups, according to the time which was allowed to elapse between section of the left optic nerve and mapping the projection of the left visual field onto the tectum. (Tables 7 and 8).

Group one consisted of eighteen frogs which had been kept for between twenty and forty days after section of the optic
nerve. Group Two consisted of twelve frogs which had been kept for between forty and sixty days. Group Three consisted of ten frogs which had been kept for between sixty and one hundred and twenty days.

Three types of results were obtained from mapping the projection of the visual field of the operated eye onto the tectum:

1) No responses were obtained through the operated eye. (9 frogs)
2) Responses were obtained, but the pattern of projection was not normal (15 frogs).
3) An essentially normal pattern of projection was found (16 frogs).

The frequency with which each of these results was found in the three groups mentioned above is shown in Tables 7 and 8.

1) In 9 frogs (six in Group 1; one in Group 2; and two in Group 3), no responses were obtained from the operated eye. In all these animals, responses were obtained from the normal eye, which was used as a control to test whether the preparation was functioning normally.

2) In 15 frogs (seven in Group 1; five in Group 2; and three in Group 3), responses were obtained from the visual field of the operated eye, but these responses were in several respects unlike those found in normal frogs.

The responses were obtained from only one or two small regions of the visual field. The usual pattern, which was found in eight animals, was that there was one region in the nasal half of the visual field from which responses could be evoked, and another responsive region in the temporal half of
the visual field (Figs. 18 to 23). Both responsive regions usually lay on, or just above, the horizontal meridian of the visual field. In seven frogs, only one of these responsive regions could be found. In five of these it was in the nasal part (Fig. 24), and in the other two cases in the temporal part of the visual field (Fig. 25).

Each of these regions of response on the visual field was found to project to only one half of the tectum. The nasal region projected to the lateral half of the tectum; the temporal region to its medial half. A fairly sharp boundary could be drawn on the tectum between the projection of the two responsive fields, but there were usually several electrode position on or close to this boundary, at which responses could be evoked from both nasal and temporal fields. These are shown enclosed in blocks in figs. 18 to 21. The two responsive regions of the visual field were thus found to project to the appropriate halves of the tectum, but a more detailed point-to-point projection was not apparent.

At any electrode position on the tectum, a response could be obtained from the whole extent of the appropriate one of these responsive fields, each of which was 40° to 80° in diameter. Although there was usually a smaller region of maximum response, the stimulus position usually could not be localised more precisely than to somewhere within an area of the visual field 50° or more in diameter. In figs. 18 to 26, the determination of each position in the visual field corresponding with one of the numbered positions on the tectum was subject
to an error of 50 or more degrees, and the exact placing of each number within an irregular constellation of stimulus positions is somewhat arbitrary.

In all twelve frogs, which were found to conform with the pattern of projection described above, the projection was to the contralateral optic lobe only. In no cases were ipsilateral responses obtained, though special attention was given to their detection.

3) In sixteen frogs, at varying times after transection of the left optic nerve, an essentially normal map was obtained of the projection of the left visual field onto the tectum. This result was obtained in five frogs from Group 1 (20–40 days postoperatively); in six frogs from Group 2 (40–60 days postoperatively); and in five frogs from Group 3 (60–125 days postoperatively).

In all these cases there was an area-to-point projection of the left visual field onto the contralateral tectum, which conformed in its essentials with the normal map. In the regenerated animals, the quadrants of the visual field projected to their usual parts of the tectum, and the projections of the centre, and of the meridians and parallels of the visual field, were found to be approximately in the same positions as they have consistently been found in normal animals. However, in the regenerated animals, there was considerable distortion of the map as compared with the normal.
A conspicuous and consistent finding in these animals was the wide area in the visual field from which responses were obtained from any position of the electrode on the tectum. These receptive fields were usually two to four times the diameter of comparable fields in normal animals. In regenerated animals, an electrode at one position on the tectum could record responses from an area in the visual field 50° or 60° in diameter, and it was frequently not possible to find a precise point of maximum response within this large area of field. Moreover, there is considerable overlap of the receptive fields of tectal electrode positions 200 microns apart.

After having localised the position of a stimulus in the left visual field which evoked a response in the right tectum, the opaque shield was transferred from the right eye to the left eye. A determination was then made of the position of a stimulus in the right visual field which evoked a response at the same electrode position. When the two eyes were tested separately, the positions of the two stimuli were very rarely found to coincide, as they always do in normal frogs. There was usually a disparity of 30° to 45° between the two stimulus positions. The problem arose as to whether this constituted evidence that the regenerated optic axons had not connected with their correct tectal loci. However, this disparity appeared to be due to the large receptive field within which a stimulus would evoke a response through the operated eye at a single tectal electrode position. There are two reasons in support
of this. Firstly, the disparity was never greater than the size of this receptive field, which was usually 50 or more degrees in diameter. Secondly, if the position at which a stimulus evoked response in an electrode on the right tectum was first localized through the normal right eye, it was found that a stimulus at the same position also evoked a response through the left eye. Tested in this way, it was possible to confirm the finding of Gaze (1959) that, after regeneration, corresponding retinal points projected to the same position in the tectum. This was regarded as evidence that the normal projection had been restored, and that the apparent distortion of the regenerated map was due to the error inherent in subjective placing of the maximum stimulus position within a very large receptive field.
DISCUSSION
This study is concerned with only a limited aspect of the function of the visual system; the nervous organization concerned with the localization of a visual stimulus in space.

Experiments in which a stationary spot of light had been used as the stimulus have been criticized for not taking into account those functions of the visual system which are concerned with attributes of the visual stimulus other than its position in space. The M.I.T. group have criticized the results of experiments of the kind presented in this thesis, on the grounds that they present a naively simple "nineteenth century view of visual space." However, their results (Lettvin and Maturana, 1959; Lettvin et al., 1959) have shown that the use of a complex stimulus situation leads to an essentially similar view. They have mapped the projection of the visual field onto the tectum of Rana pipiens, using as a stimulus a small dark object which could be moved about against a lighter background. They concluded that there are four groups of fibres projecting from the retina to the tectum. Each set of fibres carries a different kind of information about the visual stimulus, namely, about dimming, contrast, curvature of edges and movement of edges. They concluded that each set of fibres projected as a map of the visual field onto a different stratus of the optic tectum, with the four maps in register. Therefore, the experiments in which a variety of complex stimuli were used, and the experiments of the kind
described in this thesis demonstrate the same principles: that
the geometrical properties of visual space have their analogues
in the geometrical organization of the visual anatomy.

The results of the experiments reported in this essay do
not preclude the possibility that there might be dual or
multiple systems of projection, each conveying information about
a different attribute of the visual stimulus, from the retina
to the tectum. However, it is most probable that the stable
spatial organization of the visual system is the essential
framework within which the processing of information about the
attributes of the visual stimulus is conducted.

Another criticism of these experiments is that the
structures in the tectum from which the responses were
recorded, could not be identified. This defect was
particularly serious when mapping the projection of the visual
field onto the tectum after regeneration of the optic nerve,
and imposed a severe limitation on the interpretation of the
results of the regeneration experiments.

These defects in the experimental design are admitted.
Nevertheless, there is a pragmatic justification for the
methods that have been adopted. In spite of their defects,
they have permitted some new insight into the organisation
of the visual system in amphibians. In particular, it has
been possible to confirm that there is an area centralis in
the frog's retina; further knowledge has been obtained of the
central representation of the binocular visual field; and some
more insight has been gained into the way in which the optic axons
regenerate.
THE EVIDENCE FOR AN AREA CENTRALIS RETINAE

IN THE FROG

According to Polyak (1941), "Whether the amphibia possess
a central area or fovea is as yet uncertain", and his opinion
has been generally accepted, and has influenced the
interpretation of much of the work on the frog's visual system.
For example, Hartline (1940 a, b) and Barlow (1953 a, b) in
their microelectrode studies of the receptive fields of ganglion
cells in the frog's retina, did not consider the possibility
of regional variations in the sizes of receptive fields. In
fact, they even neglected to mention the regions of the retina
from which responses were recorded.

Several authorities (Walls, 1942; Detwiler, 1943;
Rochon-Duvigneaud, 1943) briefly refer to an area centralis
in the frog's retina, but consider it to be of little
significance. This view has been summarized by Walls (1942,
p. 305) as follows: "Frogs have an area centralis, but this is
a large vaguely defined horizontal crescent, whose superiority
in resolving power over the remainder of the retina is
extremely slight".

This view appeared to receive support from the mapping
experiments of Gaze (1953a), who was unable to find any
evidence for an area of acute vision in Rana temporaria. This
failure was probably due to the procedure which was adopted
of placing the electrode positions in one or two rows, rather
than in a regular grid covering the whole tectum.
It is curious that the papers of Chievitz (1889; 1891) have been overlooked, which contain a careful description of the frog's area centralis. According to Chievitz (1889), the area centralis of Rana esculenta "geht als ein ca. 1-1.5 mm breites (hohes) Band quer durch die ganze Retina dicht oberhalb des Opticus eintrittes, von welcher seine Mitte etwa 1 mm entfernt ist, und erstreckt sich sowohl vorn wie hinten bis fast an die Ora retinae; seine Grenzen gegen die übrige Netzhaut sind nicht scharf." In Bufo vulgaris, Chievitz (1891) described the area centralis as follows: "In der Schnittreihe wird eine Area aufgefunden; dieselbe liegt dicht nach oben vom Opticus, ist von langgestreckter Form, nasotemporal gerichtet und hat ihre stärkste Entwicklung im hinteren Theile, wo auch eine schwache Andeutung von einer Fovea erkennbar ist". These descriptions have been confirmed by Gaupp (1896) and Slonaker (1897).

The shape and position of the area of greatest magnification factor coincides so well with the shape and position of the area centralis, that it is reasonable to assume that they are closely related.

According to the evidence already presented, the area centralis in the frog and the toad is in the form of an horizontal band above the horizontal meridian of the retina (below the horizontal meridian of the visual field). It projects onto the lateral part of the optic tectum, and has a magnification factor nearly three times that of the lower peripheral retina. The full extent of the central
representation of the area centralis could not be mapped because the upper and temporal limits of the area centralis are represented on the inaccessible lateral and ventral surfaces of the tectum.

It is not possible to sustain the objection that the differences of magnification factor for different regions of the visual field may be an artefact due to the method of treating the curved surface of the tectum as a plane surface on a photograph. Electrode positions apparently spaced at equal intervals on the photograph, are really spaced at increasing intervals as the curvature of the tectum becomes steeper in its lateral part onto which the area centralis projects. The transverse section of the tectum shown in fig. 8 illustrates that it is justifiable to ignore the slight curvature of the dorsal surface of the tectum without affecting the accuracy of spacing of electrode tracks 200 microns apart. The error increases greatly in the steeply curved lateral part of the tectum, and the lateral pair of electrode tracks are 225 microns apart. The effect of this error is that the experimentally determined magnification factor for the area centralis has less than its true value.

There is some evidence that the anatomical basis of the magnification factor is the size of a retinal unit. In fig. 9, the ratios of outer nuclei to ganglion cells in the frog's retina (Chievitz, 1889) and the reciprocal of the magnification factors along the vertical meridian are plotted against retinal eccentricity. Both ratios are linear functions of
retinal eccentricity with approximately the same gradient.

It is interesting that, in the human eye, the minimal angle of resolution (the reciprocal of visual acuity) is a linear function of retinal eccentricity (Weymouth, 1958). This applies only under photopic conditions, and in the human eye, is true for only the central 20° or 30°. Weymouth concluded that the anatomical basis for this linear relationship was probably a gradient of ganglion cells representing sensory units consisting of increasing numbers of cones with increasing eccentricity. In the frog, there may be a similar anatomical basis for the linear relationship between 1/M and retinal eccentricity.

As Chievitz (1839) counted the average number of retinal elements along a line 40 microns long, it is convenient and fairly accurate to consider 40 microns equal to 1° of retina measured linearly along the vertical meridian of the retina. In the area centralis, there are an average of 17 retinal receptors per degree, which converge onto 6 ganglion cells, and which project onto 20 microns of the tectum. Forty degrees peripheral to the area centralis, there are on the average 10 retinal receptors per degree, which converge onto 2 ganglion cells and which project onto about 10 microns measured linearly on the tectum. In contrast to the expansion of the visual pathway from retina to striate cortex of mammals, in the frog and toad there appears to be a convergence from retina to tectum by about 2 times linearly or 4 times in area for the area centralis, and about 4 times
linearly or 16 times in area for the peripheral retina. However, these calculations do not take the volume of the tectum into account, nor the possibility that a high density of packing of the tectal cells may compensate for the small size of the tectum relative to that of the retina. Even considering these factors, it is improbable that there is much expansion in the pathway from retina to the tectum of amphibians.

Unlike the striate cortex which appears to have a uniform thickness (except where it is distorted by the convolutions), the tectum is clearly thicker and contains more cells in the lateral part on which the area centralis is represented. This is fairly evident in fig. 8, but is much more marked in more rostral transverse sections which cut across the region of greatest magnification on the lateral part of the tectum and the region of least magnification on its medial part. It may well be that an increased packing density of tectal cells is an additional mechanism for increasing the functional capacity of the part of the tectum devoted to the representation of the area centralis retinae. Unfortunately, this possibility cannot be tested directly by counting all the tectal cells, as probably fewer than half the cells in the tectum have visual functions (Kollros, 1953) and it is not yet possible to distinguish the cells which have optic connections from those which have not.
WHAT IS THE PATHWAY FOR THE RETINAL PROJECTION ONTO THE
IPSILATERAL OPTIC TECTUM?

The idea that semidecussation of the optic nerves is a
necessary condition for binocular vision, and that animals with
total decussation of the optic nerves have panoramic vision, was
originally proposed by Isaac Newton in the 15th query to
his Opticks:

"Are not the Species of Objects seen with both Eyes united
where the optic Nerves meet before they come into the
Brain, the fibres on the right side of both Nerves uniting
there, and after union going thence into the Brain in
the Nerve which is on the right side of the Head, and the
fibres on the left side of both Nerves uniting in the same
place, and after union going into the Brain in the Nerve
which is on the left side of the Head, and these two
Nerves meeting in the Brain in such a manner that their
fibres make but one entire Species or Picture, half of
which on the right side of the Sensorium comes from the
right side of both Eyes through the right side of both
optic Nerves to the place where the Nerves meet, and
from thence on the right side of the Head into the Brain,
and the other half on the left side of the Sensorium comes
in like manner from the left side of both Eyes. For the
optic Nerves of such Animals as look the same way with
both Eyes (as of Men, Dogs, Sheep, Oxen, etc.) meet before
they come into the Brain, but the optic Nerves of such
Animals as do not look the same way with both Eyes (as of
Fishes and of the Chameleon), do not meet, if I am rightly
inform'd."

That the degree of binocularity in mammals is correlated with
the number of non-decussating optic nerve fibres was established
mainly by Gudden and by Ramón y Cajal, and has met with general
approval. The corollary, that animals with total decussation
of the optic nerves are incapable of binocular stereopsis, has
recently been questioned, and there are several reasons for
believing that the Newton-Gudden rule does not apply to the submammalian vertebrates. Walls (1944) and Polyak (1957) have collated the very numerous observations which show that many of the lower vertebrates have extensive binocular visual fields: that in feeding they behave as if they enjoy binocular vision; and that many species of fish, reptiles, and birds have foveate retinas with convergent lines of vision.

Interocular transfer of monocularly learned habits has been demonstrated in animals with total decussation of the optic nerves. In a teleost fish (Bathygobius seoperator), monocularly learned patterns are recognised by the eye which was covered during training (Sperry and Clark, 1949). Interocular transfer of monocularly learned habits occurs only if, during monocular training, the stimulus is placed in the pigeon's binocular visual field (Levine, 1945). The conclusion drawn from these experiments is that there are pathways which connect each eye with both sides of the brain. This is certainly the case in frogs, since photic stimulation of one eye evokes action potentials in both ipsilateral and contralateral optic tecta (Rensch, 1955; Zagorul'ko, 1957; Gaze, 1958b).

There can be no doubt that in the frog, and probably in several species of fish, reptiles and birds, the retina projects to both optic tecta. However, the anatomical pathway to the ipsilateral tectum remains undiscovered.

That the optic nerves decussate completely in the lower vertebrates is apparent from degeneration studies. The only
exceptions so far discovered are in a snake (Natrix) and a lizard (Lacerta) in which Armstrong (1950, 1951) found uncrossed optic fibres by means of a bouton degeneration technique. The uncrossed fibres are said to terminate in the ipsilateral lateral geniculate body, and could not be traced to the optic tectum. These observations, though limited to two species of reptile, are sufficient to reopen the question of whether there are uncrossed fibres in the optic chiasma of submammalian vertebrates. The question is one which the electron microscope may answer.

After enucleation of one eye of the frog, all the conventional histological methods show that degeneration is confined to the contralateral optic tract (Bellonci, 1891; Wassek, 1893; Myers, 1901; Harris, 1904; Herrick, 1925). There is reason to question these authorities, since electron microscopy of the optic nerve of the frog shows that half the optic nerve fibres have diameters too small to enable them to be seen with the histological methods used by the earlier workers (Maturana, 1958a, b, 1959). The possibility remains that some of the optic nerve fibres with diameters less than the resolving power of the light microscope, do not decussate in the optic chiasma.

Another possibility is that some optic fibres recross to the ipsilateral tectum, and the most probable position for this decussation is in the intertectal commissure which has been described in all the vertebrate orders. This commissure is known as the lamina commissuralis tecti in fishes; the
the commissura tecti mesencephali in amphibians; the commissura colliculi superioris in reptiles; the dorsal part of the commissura posterior in birds; and the commissura colliculi superioris in mammals (Kappers, Huber, and Crosby, 1936).

The functions of the intertectal commissure are entirely unknown. There are several reasons to doubt whether primary optic afferents cross in it. For example, after enucleation of one eye, degenerating fibres have never been found in the intertectal commissure. In two species of blind fish whose optic tracts are rudimentary, Charlton (1933) found that the intertectal commissure was normal in appearance. The intertectal commissure appears to arise and terminate almost entirely in the stratum album centrale of the submammalian tectum, and in the stratum lemnisci of the superior colliculus. Primary optic afferents do not appear to enter these strata (Huber and Crosby, 1943; Herrick, 1948; Ramón y Cajal, 1952-1955). It may be concluded that primary optic afferents, unless they are very fine, do not cross in the intertectal commissure, but there is still the possibility that secondary optic afferents run in it from the contralateral to the ipsilateral optic tectum.

Secondary optic axons would not degenerate after removal of an eye, but may degenerate after suitably placed lesions in the tectum. This has not been tried in submammals. In mammals, experimental lesions in one superior colliculus result in degeneration in the intercollicular commissure in rats (Papez and Freeman, 1930), and in cats (Marburg and Warner, 1947; Hess, Burgi, and Bucher, 1950). From these studies
it is impossible to know whether the degenerating fibres are optic, and in mammals it is most unlikely that optic fibres cross in the midbrain commissures - an arrangement which would appear to cancel the effect of partial decussation at the chiasma. However, in submammalian vertebrates, which have total crossing of the optic nerves, there is more reason to suspect the existence of a suprachiasmatic decussation.

There are several ways, each with its own limitations, of discovering whether this decussation runs in the intertectal commissure.

One method consists of making a small lesion in one optic tectum and following the resulting degeneration with the Marchi technique. Studies of this kind done on mammals (Papez and Freeman, 1930; Marburg and Warner, 1947; Hess, Burgi and Bucher, 1950) exemplify the limitations of this method. The difficulties of making an accurately localized lesion have been emphasised by Carpenter and Whittier (1952). The Marchi method is at its most fickle when applied to amphibian brain, and is in any case unable to show degeneration in unmyelinated axons or to allow fibres to be traced to their terminations. The silver impregnation techniques for showing preterminal and terminal degeneration have numerous advantages over the Marchi method (Evans and Hamlyn, 1956; Nauta, 1957; Bowsher, Brodal and Walberg, 1960), and may prove more reliable for showing degeneration in the frog's brain. However, even if a punctate lesion in one optic tectum results in degeneration of fibres which can be followed through the intertectal commissure into the opposite optic tectum, the
degenerated fibres need not necessarily be optic, since the
tectum has other function apart from its visual ones.

Another way of localizing the pathway of the ipsilateral
tectal response is to make localized lesions in the visual
pathway followed immediately by mapping of both visual fields
on both optic lobes. It may then be possible to correlate
the functional deficit with the histological appearance of the
lesion. Zagorul'ko (1957) reported that midline section
through the posterior part of the diencephalon, the midbrain,
cerebellum and medulla, or complete division of the midbrain
between the optic lobes was without any effect on contralateral
and ipsilateral tectal responses. He did not check the
extent of the lesion histologically and he was unable to localize
the pathway to the ipsilateral optic tectum.

The results of the experiments reported in this thesis
do not entirely agree with those of Zagorul'ko. In the two
experiments (L5, fig. 16; L6) in which the lesion was made
in the ventrolateral wall of the diencephalon on the left
side, stimulation of the left eye evoked normal responses in
both optic lobes, whereas no responses were obtained in either
optic lobe to stimulation of the right eye. Histologically
the lesion appeared to have divided the left optic tract
completely. It was concluded from this that fibres mediating
both ipsilateral and contralateral responses decussate completely
at the chiasma.

In experiments L7 (fig. 10, L8 (fig. 11), L9 (fig. 12)
and L10 (fig. 14), responses continued to be recorded in both
optic lobes after dorsal midsaggital cuts had been made in the
diencephalon or mesencephalon; whereas in experiments B6 (fig. 13)
and B7 (fig. 15), the ipsilateral response from either eye was
abolished while the contralateral responses were unaffected.

It was concluded that the ipsilateral pathway had been
interrupted in experiments B6 and B7, but had escaped damage
in experiments L7, L8, L9, and L10. In the former two
experiments, but not in the latter four, the knife had cut
through the commissura tecti mesencephali. In B6 the
lesion, apart from involving the commissura tecti mesencephali,
extended into the pretectal region and dorsal thalamus; but
in B7, it was fairly localized to the dorsal part of the
midbrain between the optic lobes. Therefore, although it was
not possible to make a lesion confined to the commissura
tecti mesencephali, it appears probable that the optic fibres
to the ipsilateral tectum run in that commissure.

However it is appreciated that mechanical lesions of the
kind made in these experiments are unpredictable in size and
shape. Due to extravasation of blood and interruption of the
blood supply, the damage was almost certainly more extensive
than it appeared on histological sections. For these reasons
one is reluctant to accept evidence of functional localization
obtained by means of relatively crudely executed brain lesions.
**BINOCULAR VISION IN ANURANS**

Illumination of one eye of the frog evokes electrical activity in the ipsilateral as well as in the contralateral optic tectum (Rensch, 1955; Zagorul'ko, 1957; Gaze, 1958b). The earlier workers used large electrodes and diffuse illumination of the retina, whereas Gaze used a steel microelectrode and a light subtending an angle of 15° at the eye. Because of these technical refinements, he was able to show that corresponding retinal points project to the same position on each optic lobe. Gaze's observations have been confirmed, and it has been possible to extend them by making a more detailed map of the binocular projection. The projection of the binocular visual field onto both optic lobes of the toad is shown in fig. 5, and this has already been described.

The frog is an ideal animal in which to investigate the central representation of corresponding retinal points because its eyes are fixed in a position of symmetrical divergence. Eye movements, apart from retraction, have never been observed in frogs (Walls, 1942, p. 305; Rochon-Duvigneaud, 1943, p. 692). Even electrical stimulation of the frog's optic tectum does not result in any ocular movements except retraction of the eyeball (Abbie and Adie, 1950; Goodman, 1958). In contrast, stimulation of the optic tectum of a number of species of fish resulted in conjugate and convergent eye movements (Chauchard and Chauchard, 1927; Akert, 1949), and the same has been found
in the cat (Hess, Burgi and Bucher, 1945; Apter, 1946; Hoessly, 1947). One might wonder why the extra-ocular muscles of frogs are fully developed, and why they have not become vestigial during the course of evolution. It is most probable that they have been retained for the essential function of producing the fine ocular movements which serve to enhance visual acuity (Marshall and Talbot, 1942) and without which vision cannot be sustained (Riggs et al., 1953; Ditchburn, 1956).

Walls (1942) believed that because the frog's vision was equally poor in all directions, eye movements were not necessary to fixate the image onto the retinal region of greatest acuity. He considered that a system of corresponding retinal points did not exist in the frog or in any of the submammals with little or no ocular movements, and suggested that a system of corresponding points only evolved in mammals in association with partial decussation of the optic nerves and conjugate eye movements (Walls, 1942, p. 325). Walls regarded the system of corresponding points primarily as a motor system, and took the view that, for visual sensation, "the whole matter of corresponding points is a purely psychological one, and not anatomic in any way." (Walls, 1942, p. 325). The results of these experiments support the opposite view that, in the frog, the visual system is organized as a geometrical analogue of visual space. The two dimensional organization of the retinal receptors is projected as a two dimensional map onto the optic tectum. Projection
of the third dimension of visual space is probably achieved by intertectal connections linking corresponding points. The system of corresponding points thus evolved in the pre-mammalian stage of vertebrate evolution. Even in the Anura, there is a far more elaborate dimensional organization of the visual system than had hitherto been suspected.

Each of the frog's eyes has a panoramic field of acute vision extending horizontally across the visual field and overlapping in the nasal 75° to 90° with the field of acute vision of the other eye. The image of any object in the binocular visual field falls on corresponding retinal points which project from each eye to the same two tectal points — one on the contralateral and the other on the ipsilateral optic tectum. As is evident in fig. 5, only the binocular point and the vertical meridian of the binocular visual field are projected from each eye onto symmetrical positions on the two optic lobes. All other points in the binocular visual field are projected from each eye onto one point on the contralateral optic tectum, and onto an asymmetrical point on the ipsilateral tectum. The more lateral an object is from the vertical meridian through the binocular point (and therefore from the best position of the frog's tongue to strike it), the greater will be the asymmetry between its points of projection onto the two optic lobes. The train of events culminating in the frog's striking at a fly directly in front of its mouth may be initiated when the image of the
fly on the two retinas sets up symmetrical patterns of activity on both optic lobes. The tectum may function as a comparator which obtains the difference between the retinal images on the two eyes, and initiates a pursuit reaction only when the difference between the evoked pattern on the two optic lobes is zero.

In the frog, the lack of ocular movements may be an adaptation to achieve speed in predicting the future positions of an insect at the moment when the frog’s tongue will meet it in flight. The appropriate motor response can occur without the delay involved in converging the eyes onto the target. This may be illustrated by a comparison of the fly-catching behaviour of the frog and the chameleon. The chameleon very deliberately stalks a resting insect, slowly converges its eyes on the target, and then suddenly shoots out its tongue. Because it cannot converge its eyes with sufficient speed, it cannot capture an insect flying across its visual field, as the frog is able to do.
RETURN OF OPTOKINETIC RESPONSES FOLLOWING REGENERATION OF THE OPTIC NERVE

One of the interesting results of these experiments was that optokinetic responses were present in 10 of the 15 frogs with the incomplete types of regeneration shown in Figs. 18 to 26. Optokinetic responses had also returned in those cases (Figs. 24 and 25) in which tectal responses could be evoked from only a small region of the visual field. It appears as if optokinetic responses can return despite a considerable deviation from the normal pattern of retino-tectal connections. It can therefore be concluded that the return of optokinetic responses after section of the optic nerve does not necessarily indicate full restoration of the normal projection of the retina onto the tectum.

Presumably a certain minimal number of correct linkages have to be formed by the regenerated optic axons in order that the frog should recover some degree of visuomotor coordination. It is probable that the quality of the response improves as more correct central connections are formed. The ability of the frog to follow a series of stripes moving across its visual field, or to locate and pursue a moving lure, are not all-or-none phenomena. Maturana (1958 a, b) found that the capacity of toads to perform these visual tasks slowly improved for up to 150 days after the first signs of visual recovery following regeneration of the optic nerve. However,
these simple behavioural tests permitted him to make only a rough correlation between the quality of functional recovery and the degree of regeneration and myelination of the optic nerve and tract as they appeared in silver impregnated sections and electron photomicrographs. Maturana's studies indicated some of the causes of the wide variations in the times reported for recovery of vision in amphibians after regeneration of the optic nerve. Apart from difference due to species, age and temperature, the main factor influencing the recovery time was the amount of scarring at the site of transection of the nerve. "In extreme cases of incomplete or slow recovery, a neuroma was found in the region of section of the nerve, and the functional delay was accompanied by an anatomical delay in regeneration" (Maturana, personal communication).

The reports of the time taken for recovery of vision after optic nerve section in amphibians, illustrate how difficult it is, using behavioural tests, to establish a correlation between the duration of regeneration and the degree of functional recovery. In Triton cristatus, recovery of vision returned 3 to 5 months after optic nerve section (Matthey, 1926; 1927). In Triturus viridescens, a closely related species of newt, Stone and Chace (1941) observed visual recovery in 2 to 3 months, whereas Sperry (1943) reported that these newts reacted to visual stimuli as early as 10 days, and usually within 30 days of optic nerve section. Sperry (1944) observed the return of optokinetic and pursuit reactions
21 to 33 days after having cut the optic nerve in several species of adult Anurans (Rana, Bufo and Hyla). In adult Bufo americanus, Maturana (1958 a, b) found that vision returned gradually, starting about 50 days after optic nerve section, and continuing to improve for up to 150 days. The results of the present experiments agree with those of Sperry (1944). Optokinetic responses returned 12 to 51 days (mean 29 days, SD = 13.4) after section of the optic nerve.

All observers have reported that, after section of the optic nerve in amphibians, the optokinetic responses return several days to weeks before the recovery of pursuit reactions. The restoration of a detailed retinotopic projection onto the optic tectum is probably necessary before the animal is able accurately to localize a small object in its visual field, whereas it is probable that optokinetic responses may occur once a "functionally adequate" number of correct retino-tectal connections have been made. This is indicated by those frogs in which optokinetic responses had returned, and which were later shown to have only a partial restoration of the projection of the retina onto that tectum. (Experiments 10c; 12c; 13b, fig. 24; 13c; 15b, fig. 25; 22b, fig. 23; 23b, fig. 18; 26d, fig. 19; 27a, fig. 20; 27b).

Optokinetic responses returned in 13 of the 16 frogs with complete regeneration of the optic nerve, and in 10 of the 15 frogs with incomplete regeneration, but did not return in all 9 frogs in which regeneration failed to occur. Therefore,
optokinetic responses were useful for detecting whether some retino-tectal connections had been established, but could not be used to distinguish between partial and total restoration of the normal pattern of retinal projection onto the optic tectum.
RESTITUTION OF THE RETINO-TECTAL PROJECTION AFTER
REGENERATION OF THE OPTIC NERVE

There is, at present, only the theory propounded by Sperry to account for the selectivity with which optic nerve fibres, either during normal development or during regeneration, form their central connections. Sperry (1951a, b, c, 1955, 1956) has summarised the great variety of experiments that support his hypothesis that the restoration of spatial relations in the visual system is achieved as a result of growth processes which cannot be modified by function and experience. However, none of these experiments gives an answer to the question of exactly what the growth processes are, which determine the selective central connections of optic nerve fibres. No analytic experiments have been devised which give an answer to this question.

The evidence obtained by Gaze (1959) and by Maturana, Lettvin, McCulloch and Pitts (1959) that the normal projection from retina to optic tectum is restored following regeneration of the optic nerve, confirms Sperry's hypothesis but does not throw any more light on the process of regeneration and selective central connection.

Apart from confirming that the normal retinotopic map on the tectum is completely restored following regeneration of the optic nerve, these experiments provide the first evidence of an incomplete type of regeneration. Fifteen of a total
of 40 frogs showed the incomplete types of regeneration illustrated in Figs. 18 to 26. Whether these are stages in the transition to an orderly retino-tectal projection, or whether they are aberrant types of regeneration which would never have developed into a normal map, will be discussed later. All these experiments have a common type of pattern. There were one or two small regions in the visual field, either in the nasal or the temporal field, or in both, from within which electrical responses could be evoked in the tectum. This was particularly marked in experiments 23b (Fig. 18), 26d (Fig. 19), 13b (Fig. 24), and 15b (Fig. 25). In experiments 23b and 26d, there were two small constellations of stimulus positions, one in a small region close to the temporal pole of the visual field, and another in a small region close to the nasal pole of the field. The nasal constellation projected onto the lateral half of the tectum and the temporal constellation onto its medial half. In experiment 13b (Fig. 24), responses were evoked only in the lateral half of the tectum by the stimulus in a small region in the nasal half of the visual field. In experiment 15b (Fig. 25), responses were evoked only in the medial half of the tectum by the stimulus in a small region in the temporal half of the visual field. In the other 11 experiments in which similar patterns of stimulus positions were found, the stimulus positions were more scattered, but were still grouped into nasal and temporal constellations, each projecting to its appropriate half of the tectum (Figs. 20 to 23). The only exception is illustrated
by Fig. 26 (experiment 21c), in which responses were recorded from the whole dorsal surface of the tectum when the stimulus was in a small area in the nasal half of the visual field.

Without definite knowledge of the tectal structures from which the responses were led, it is only possible to speculate on the meaning of this result and of the other results in which responses were evoked in a large part of the tectum by a stimulus in a small region of the visual field. It is not improbable that the regenerated optic axons initially have terminal arborizations which spread laterally over a wide area of the tectum, and that at a later stage the area of tectum with which each optic axon connects, shrinks to that of its correct retinotopic locus.

The results illustrated by Figs. 13 to 25 appear to indicate that optic axons do not regenerate into the tectum simultaneously from all regions of the retina. It appears rather as if there are two regions of the retina, one in the nasal hemi-retina, the other in the temporal hemi-retina, which give origin to the first axons to regenerate into the tectum.

A similar pattern of growth occurs during the development of the retina (Schaper and Cohen, 1905; Jokl, 1918; 1921). The most active mitosis is seen in two localised regions at the nasal and temporal poles of the optic cup. Addition of new cells to the optic cup continues from these growth centres until the retina is fully differentiated.

There is also evidence that these regions of the retina retain their growth capacity in adult amphibians. In
urodeles, after transplantation of the eye, the retina usually degenerates and a new retina regenerates from the ciliary margin at the anterior and posterior poles of the eye (Stone, 1944; 1948).

For some unknown reason, the potential for regeneration appears to be most marked at the nasal and temporal poles of the retina. Moreover, these experiments indicate that each of these halves of the retina sends optic axons into its own specific half of the tectum. The nasal retinal growth centre projects to the medial part of the tectum and the temporal retinal growth centre to the lateral part of the tectum (Figs. 18 to 25). Lettvin et al. (1959) have also reported, without further comment, that "in one frog, after 90 days, the fibres had grown back best at the entrance of the two brachia to the colliculus, and least at the center ..."

The optic axons from different parts of the retina of the normal frog appear to be randomly intertwined in the optic nerve (Maturana, 1958b). Sperry (1944) and Maturana (1958a,b) have reported that the regenerating axons are completely scrambled at the site of optic nerve section, and these experiments have confirmed their observations. The question therefore arises as to where in the course of regeneration the segregation occurs of fibres destined for the medial and those destined for the lateral parts of the tectum. Sperry envisaged an unscrambling process in the tectum, as the essential mechanism ensuring a correct spatial distribution of neuronal
connections. This may be so once the fibres enter the tectum, but a consideration of the anatomy of the optic tracts leads one to conclude that the initial segregation occurs before the regenerating fibres reach the tectum.

The anatomy of the optic tracts in amphibians has been described by several authors, notably by Wlassak (1893), Herrick (1925) and Rothig (1927) in the frog; and by Herrick (1925, 1948) in Amblystoma.

There are three main divisions of the optic tract in amphibians. The basal optic tract passes caudalwards along the periphery of the hypothalamus to terminate in a nucleus which lies in the tegmentum just rostral to the nucleus of the third nerve. The axial optic tract passes medial to the marginal optic tract, to end in the lateral geniculate body, mainly in its ventral nucleus. The marginal optic tract passes dorso-caudally round the side of the diencephalon, and reaches the di-mesencephalic junction just rostral to the optic tectum. Here it splits into two divisions; a medial and a lateral. The lateral division passes caudally along the lateral margin of the optic tectum, sending fibres into its lateral half. The medial division passes medially, parallel to the rostral margin of the optic tectum, and then turns caudalwards, sending its fibres into the medial half of the tectum.

The selective regrowth of optic axons into their appropriate division of the optic tract, has been accepted as a necessity for which no explanation is yet available. These
experiments provide the first demonstration of this phenomenon. A reasonable interpretation of the experimental results illustrated in figs. 18 to 25 is that the optic axons from the nasal and temporal halves of the retina segregate from one another at the di-mesencephalic junction, and regenerate along different paths into the tectum. The axons from the nasal half of the retina pass into the medial division of the marginal optic tract, and terminate in the medial half of the tectum. The axons from the temporal half of the retina pass into the lateral division of the marginal optic tract and terminate in the lateral half of the tectum.

The exact forces which determine this selective growth remain a mystery, and so do the mechanisms which determine that each optic axon terminations at its appropriate place in the tectum.

By mapping the projection of the retina onto the optic tectum in a series of frogs at different times during the course of regeneration of the optic nerve, it seemed possible to find successive stages in the reconstitution of a topographically organized projection. This hope was not realised. Although 15 of a total of 40 frogs proved to have the incomplete types of regeneration illustrated in figs. 18 to 26, it was not possible to arrange these in a series showing progressive stages in the recovery of an orderly retino-tectal projection. It remains to be shown whether these results represent stages in the transition to an orderly retinotopic projection, or
whether they are aberrant types of regeneration which would never have evolved into a normal map. To settle this point will require a larger series of experiments, including a series on frogs up to a year after section of the optic nerve, to allow sufficient time for maximal regeneration to occur.

In the present experiments, the main interest was in the early stages of regeneration, in order to discover the temporal and spatial sequence with which the first regenerating axons entered the tectum. Consequently the majority of frogs were mapped within 70 days of optic nerve section (tables 7 and 8). It is quite probable that insufficient time had been allowed to elapse for complete regeneration to have occurred. It has been reported that after the optic nerve of Bufo americanus had been cut, the first signs of visual recovery occurred in about 50 days, and improvement of vision continued for about 150 days (Maturana, 1958a). It is therefore essential to supplement the present experiments with another series at a longer period after section of the optic nerve. A comparison of the results of these two sets of experiments may show whether the incomplete type of regeneration is aberrant or whether it is part of the normal process of recovery.

Another observation worth mentioning is that, in regenerated frogs, the area of visual field from which a response could be evoked at a single tectal electrode position, was two to three times the diameter of the normals. This observation has already been reported by Gaze (1959) and by Lettvin et al. (1955).
It is mentioned here with the reservation that the method used in these experiments did not permit a sufficiently exact determination of the size of the responsive fields to warrant a quantitative comparison of normal and regenerated animals. However, the difference in the sizes of receptive fields in regenerated as compared with normal frogs is so large, and occurs with such regularity, that it is worth reinvestigating with intracellular micropipettes and more rigorously controlled stimulus conditions. Until that is done, there is little to be gained from a discussion of the possible causes of the phenomenon.

In conclusion, it must be admitted that the forces which determine the selective growth and central connection of optic axons are still completely mysterious. Differential growth rates cannot account for the selective way in which regenerating optic axons enter their appropriate division of the optic tract. Some kind of specificity seems to be involved. Possibly, the regenerating axon tips can be identified and guided by the appropriate glial cells. Possibly, each optic axon, once it has entered the tectum, establishes connections only with a group of cells with which it has a unique chemical affinity (Sperry, 1950). These images of miniscule processes of neuronal organisation are irritatingly artificial, and yet at the same time sufficiently probable, to make them worth retaining.
SUMMARY.

The representation of the visual field on the optic tectum of Rana Temporaria and Bufo vulgaris was mapped by using a steel micro-electrode on the tectum to record action potentials evoked in response to a punctate light stimulus in the visual field. At each electrode position, the stimulus evoked a response from a localized area of the visual field, 10° to 30° in diameter, within which there was a point of maximal response. The determination of the position of maximal response was repeated with the electrode at 40 to 60 positions spaced at 200 micron intervals on the contralateral tectum, and at 10 to 20 positions on the ipsilateral tectum.

It was possible to draw a detailed map of the retinotectal projection in 5 frogs and 5 toads, and to measure the number of microns of tectum devoted to the representation of 1° of visual field measured radially from the fixation point — the magnification factor (M). M is nearly three times as great for a band just below the horizontal meridian of the visual field, as it is for the superior peripheral field. This correlates with the horizontal bandlike area centralis retinæ described in the frog and the toad by Chievitz (1889).

The binocular visual field is represented on both optic lobes in such a manner that corresponding retinal points are represented at the same locus on each optic lobe.

In order to localize the visual pathway to the ipsilateral optic tectum, it was seen whether acute brain lesions abolished the ipsilateral response. In 6 frogs and 2 toads the extent of the lesions was determined from serial sections of their brains. The results are not regarded as conclusive, but indicate that the fibres to the ipsilateral tectum decussate in the optic chiasma and recross at a higher
level, probably in the commissura tecti mesencephali.

The return of visual function after regeneration of the optic nerve was studied by determining the time for the return of optokinetic responses, and by mapping the representation of the visual field on the optic tectum in a series of frogs at different times after section of the optic nerve.

In 40 frogs there was a wide variation in the time taken for the return of optokinetic responses (12 to 51 days, Mean 29 days, SD = 13). Optokinetic tests were useful for showing whether some fibres had regenerated, but were not able to discriminate between partial and total recovery since the electrophysiological method showed that there was an incomplete map in 10 frogs in which the optokinetic responses were normal.

Regeneration of the optic nerve with restoration of the normal retinotectal projection occurred in 16 frogs, and in 15 frogs the regeneration was incomplete. In the cases of incomplete regeneration, optic nerve fibres from a small zone in the temporal hemiretina had made connections in the lateral half of the contralateral tectum, and fibres regenerating from a small zone in the nasal hemiretina had connected with the medial half of the tectum. It was concluded that there had been selective regeneration of the temporal retinal fibres into the lateral division of the optic tract, and of the nasal retinal fibres into the medial division of the optic tract.
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REFERENCES


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**Table 1**
TABLE 2.

Magnification factors (microns tectum / degree visual field) calculated for 10° intervals along the nasal horizontal meridian of the visual field. (Rana temporaria).

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**Table 3:** Magnification factors (μm/°) for intervals along the superior and inferior vertical meridians of the visual field. (Best temporal)
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<td>9.5</td>
<td>13.5</td>
<td>0.0</td>
<td>13.0</td>
<td>14.0</td>
<td>15.5</td>
<td>7.5</td>
<td>12.0</td>
<td>11.0</td>
<td>10.0</td>
</tr>
<tr>
<td>24°</td>
<td>10.8</td>
<td>8.0</td>
<td>9.5</td>
<td>13.5</td>
<td>0.0</td>
<td>13.0</td>
<td>14.0</td>
<td>15.5</td>
<td>7.5</td>
<td>12.0</td>
<td>11.0</td>
<td>10.0</td>
</tr>
<tr>
<td>30°</td>
<td>10.8</td>
<td>8.0</td>
<td>9.5</td>
<td>13.5</td>
<td>0.0</td>
<td>13.0</td>
<td>14.0</td>
<td>15.5</td>
<td>7.5</td>
<td>12.0</td>
<td>11.0</td>
<td>10.0</td>
</tr>
</tbody>
</table>

Table 4: Calculations of factors (microsphere) for the results of the visual field in the frog Bufo vulgaris.
TABLE 5.

Magnification factors (microns tectum / degree visual field) calculated for 10° intervals along the nasal horizontal meridian of the visual field, from the results of five experiments on Bufo vulgaris.

<table>
<thead>
<tr>
<th></th>
<th>0°-10°</th>
<th>10°-20°</th>
<th>20°-30°</th>
<th>30°-40°</th>
<th>40°-50°</th>
<th>50°-60°</th>
</tr>
</thead>
<tbody>
<tr>
<td>B 1</td>
<td>14.5</td>
<td>14.0</td>
<td>13.5</td>
<td>15.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B 4</td>
<td>19.0</td>
<td>10.5</td>
<td>13.5</td>
<td>10.0</td>
<td>15.0</td>
<td>15.0</td>
</tr>
<tr>
<td>B 5</td>
<td>12.5</td>
<td>13.0</td>
<td>12.5</td>
<td>16.5</td>
<td>10.0</td>
<td>11.5</td>
</tr>
<tr>
<td>B 6</td>
<td>15.0</td>
<td>12.0</td>
<td>11.0</td>
<td>13.0</td>
<td>10.5</td>
<td>10.0</td>
</tr>
<tr>
<td>B 7</td>
<td>14.5</td>
<td>13.0</td>
<td>15.0</td>
<td>14.0</td>
<td>13.0</td>
<td>15.0</td>
</tr>
<tr>
<td>TOTAL</td>
<td>75.5</td>
<td>62.5</td>
<td>65.5</td>
<td>68.5</td>
<td>48.5</td>
<td>51.5</td>
</tr>
<tr>
<td>MEAN</td>
<td>15.1</td>
<td>12.5</td>
<td>13.1</td>
<td>13.7</td>
<td>12.1</td>
<td>12.9</td>
</tr>
<tr>
<td>1/M</td>
<td>.066</td>
<td>.080</td>
<td>.076</td>
<td>.073</td>
<td>.083</td>
<td>.077</td>
</tr>
</tbody>
</table>
TABLE 6.

| Magnification factors (microns tectum/degree visu.) calculated for 10° intervals along the superior vertical meridian (90°-10°) and inferior vertical meridian (0°-10°) of the visual field. 

<table>
<thead>
<tr>
<th>T/M</th>
<th>0°</th>
<th>10°</th>
<th>20°</th>
<th>30°</th>
<th>40°</th>
<th>50°</th>
<th>60°</th>
<th>70°</th>
<th>80°</th>
<th>90°-10°</th>
</tr>
</thead>
<tbody>
<tr>
<td>0°</td>
<td>1.53</td>
<td>13.0</td>
<td>11.4</td>
<td>11.6</td>
<td>0.91</td>
<td>0.74</td>
<td>0.77</td>
<td>0.79</td>
<td>0.95</td>
<td>0.059</td>
</tr>
<tr>
<td>10°</td>
<td>8.0</td>
<td>7.0</td>
<td>8.5</td>
<td>8.0</td>
<td>12.0</td>
<td>6.0</td>
<td>4.0</td>
<td>3.0</td>
<td>2.0</td>
<td>1.5</td>
</tr>
<tr>
<td>20°</td>
<td>6.0</td>
<td>1.0</td>
<td>9.0</td>
<td>8.0</td>
<td>7.0</td>
<td>6.0</td>
<td>5.0</td>
<td>4.0</td>
<td>3.0</td>
<td>2.0</td>
</tr>
<tr>
<td>30°</td>
<td>6.0</td>
<td>5.0</td>
<td>4.0</td>
<td>3.0</td>
<td>2.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

From the results of five experiments on Bufo vulgaris.
TABLE 7.

RESULTS OF MAPPING THE PROJECTION OF THE LEFT VISUAL FIELD
ONTO THE OPTIC LOBES, FOLLOWING TRANSECTION OF THE LEFT
OPTIC NERVE

<table>
<thead>
<tr>
<th>Days after section of optic nerve</th>
<th>No response</th>
<th>Abnormal</th>
<th>Essentially normal</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>GROUP 1 20-40 days</td>
<td>6</td>
<td>7</td>
<td>5</td>
<td>18</td>
</tr>
<tr>
<td>GROUP 2 40-60 days</td>
<td>1</td>
<td>5</td>
<td>6</td>
<td>12</td>
</tr>
<tr>
<td>GROUP 3 60-125 days</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>TOTAL</td>
<td>9 frogs</td>
<td>15 frogs</td>
<td>16 frogs</td>
<td>40 frogs</td>
</tr>
</tbody>
</table>
Summary of the results of regeneration experiments, showing the time for return of optokinetic responses after section of the optic nerve, and the results of mapping the representation of the left visual field on the right optic tectum in 40 frogs at different times after section of the left optic nerve.

**Key:**

NORMAL = Normal representation of the left visual field on the right optic tectum following regeneration of the left optic nerve.

NO RESPONSES = No potentials could be recorded in the right optic tectum in response to illumination of the left visual field.

NL = Responses were evoked only from the nasal visual field at positions on the lateral part of the optic tectum (Fig. 24).

TM = Responses were evoked only from the temporal visual field at positions on the medial part of the optic tectum (Fig. 25).

NL + TM = A combination of the two previous kinds of results (Figs. 18 to 23).

0 = Optokinetic responses failed to return.
<table>
<thead>
<tr>
<th>Days after section of the left optic tectum</th>
<th>Result of mapping projection of left visual field onto right optic tectum</th>
<th>Experiment number</th>
<th>Histology number</th>
<th>Days for return of optokinetic responses</th>
</tr>
</thead>
<tbody>
<tr>
<td>21</td>
<td>NL</td>
<td>27b</td>
<td>CR7</td>
<td>18</td>
</tr>
<tr>
<td>23</td>
<td>see Fig. 26</td>
<td>21e</td>
<td>GN9</td>
<td>0</td>
</tr>
<tr>
<td>26</td>
<td>NO RESPONSES</td>
<td>29a</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>28</td>
<td>NO RESPONSES</td>
<td>29c</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>29</td>
<td>NL + TM (fig. 21)</td>
<td>21b</td>
<td>GN8</td>
<td>0</td>
</tr>
<tr>
<td>30</td>
<td>NL + TM (fig. 23)</td>
<td>22b</td>
<td>CP3</td>
<td>21</td>
</tr>
<tr>
<td>31</td>
<td>NO RESPONSES</td>
<td>11e</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>33</td>
<td>NO RESPONSES</td>
<td>23a</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>33</td>
<td>NO RESPONSES</td>
<td>25c</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>33</td>
<td>NL (fig. 24)</td>
<td>13b</td>
<td>GJ9</td>
<td>20</td>
</tr>
<tr>
<td>33</td>
<td>NORMAL</td>
<td>16d</td>
<td>CK6</td>
<td>23</td>
</tr>
<tr>
<td>34</td>
<td>NO RESPONSES</td>
<td>10d</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>34</td>
<td>NL</td>
<td>13e</td>
<td>CK1</td>
<td>20</td>
</tr>
<tr>
<td>34</td>
<td>NORMAL</td>
<td>11e</td>
<td>GJ7</td>
<td>20</td>
</tr>
<tr>
<td>35</td>
<td>NL + TM</td>
<td>10a</td>
<td>GJ2</td>
<td>0</td>
</tr>
<tr>
<td>35</td>
<td>NORMAL</td>
<td>11d</td>
<td>GJ8</td>
<td>25</td>
</tr>
<tr>
<td>36</td>
<td>NORMAL</td>
<td>8e</td>
<td>-</td>
<td>34</td>
</tr>
<tr>
<td>37</td>
<td>NORMAL</td>
<td>10b</td>
<td>GJ3</td>
<td>0</td>
</tr>
<tr>
<td>40</td>
<td>NL</td>
<td>12e</td>
<td>CK3</td>
<td>19</td>
</tr>
<tr>
<td>41</td>
<td>NORMAL</td>
<td>15a</td>
<td>CK9</td>
<td>12</td>
</tr>
<tr>
<td>Days after section of left optic nerve</td>
<td>Result of mapping projection of left visual field onto right optic lobe</td>
<td>Experiment number</td>
<td>Histology number</td>
<td>Days for return of optokinetic responses</td>
</tr>
<tr>
<td>--------------------------------------</td>
<td>---------------------------------------------------------------</td>
<td>-------------------</td>
<td>-----------------</td>
<td>-----------------------------------------</td>
</tr>
<tr>
<td>42 NO RESPONSES</td>
<td></td>
<td>8a</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>43 TM (fig. 25)</td>
<td></td>
<td>15b</td>
<td>CL1</td>
<td>15</td>
</tr>
<tr>
<td>44 NORMAL</td>
<td></td>
<td>12c</td>
<td>CK7</td>
<td>17</td>
</tr>
<tr>
<td>45 NORMAL</td>
<td></td>
<td>12b</td>
<td>CK8</td>
<td>19</td>
</tr>
<tr>
<td>47 NORMAL</td>
<td></td>
<td>15c</td>
<td>CL2</td>
<td>29</td>
</tr>
<tr>
<td>48 NL</td>
<td></td>
<td>18b</td>
<td>CN1</td>
<td>0</td>
</tr>
<tr>
<td>48 NORMAL</td>
<td></td>
<td>15d</td>
<td>CL3</td>
<td>16</td>
</tr>
<tr>
<td>51 NL + TM (fig. 19)</td>
<td></td>
<td>26d</td>
<td>CR1</td>
<td>51</td>
</tr>
<tr>
<td>52 TM</td>
<td></td>
<td>10c</td>
<td>CJ6</td>
<td>50</td>
</tr>
<tr>
<td>56 NORMAL</td>
<td></td>
<td>18d</td>
<td>CN2</td>
<td>43</td>
</tr>
<tr>
<td>60 NO RESPONSES</td>
<td></td>
<td>28b</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>60 NORMAL</td>
<td></td>
<td>18f</td>
<td>-</td>
<td>35</td>
</tr>
<tr>
<td>62 NO RESPONSES</td>
<td></td>
<td>26c</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>68 NL + TM (fig. 18)</td>
<td></td>
<td>23b</td>
<td>CO9</td>
<td>48</td>
</tr>
<tr>
<td>68 NORMAL</td>
<td></td>
<td>18c</td>
<td>-</td>
<td>48</td>
</tr>
<tr>
<td>70 NORMAL</td>
<td></td>
<td>17a</td>
<td>CM3</td>
<td>0</td>
</tr>
<tr>
<td>83 NORMAL</td>
<td></td>
<td>25d</td>
<td>CR6</td>
<td>46</td>
</tr>
<tr>
<td>90 NL + TM (fig. 22)</td>
<td></td>
<td>17e</td>
<td>CM9</td>
<td>0</td>
</tr>
<tr>
<td>91 NL + TM (fig. 20)</td>
<td></td>
<td>27a</td>
<td>-</td>
<td>24</td>
</tr>
<tr>
<td>125 NORMAL</td>
<td></td>
<td>18k</td>
<td>-</td>
<td>0</td>
</tr>
</tbody>
</table>
FIGURES
Fig. 1.

Photograph of the apparatus showing the projection perimeter on the left. The microscope on the right could be swung into position so that the tip of the electrode could be seen as it was driven by the micromanipulator to the correct position on the optic tectum. The frog, with its left eye centred on the perimeter, was pinned to the platform of the micromanipulator.
Projection of the left visual field onto the right optic tectum of Rana temporaria. (Experiment NL 3).

The photograph of the dorsal surface of the right optic tectum shows 60 electrode positions at which action potentials were evoked in response to a light stimulus in the left visual field at the positions shown on the perimeter chart. At each electrode position on the tectum, a maximal response was evoked by the stimulus at a position indicated by a dot in the upper two-thirds of the visual field.

The figure illustrates the method of plotting the projection of the meridians and parallels of the visual field onto the photograph of the optic tectum.
Fig. 2
Fig. 3.

Projection of the left visual field onto the right optic tectum of Rana temporaria. (Experiment NL 10)

The upper left diagram of the outline of the right optic tectum shows the electrode positions at which action potentials were evoked in response to a light stimulus at the positions in the left visual field shown in the upper right diagram.

At each electrode position on the dorsal surface of the optic tectum, a maximal response was evoked by the stimulus at a position indicated by a dot in the upper two-thirds of the visual field. After recording from the dorsal surface of the tectum, the electrode was lowered through the tectum at positions 14, 15, and 49 to 53, until contact was made with the ventral surface of the tectum. Responses were recorded from the ventral surface of the tectum when the stimulus was at the positions marked by crosses in the lower half of the visual field.

The lower diagram shows the representation of the meridians and parallels of the left visual field on the right optic tectum.
Fig. 4.

Projection of the left visual field onto the optic tectum

(Experiment E7)

The upper diagram of the outline of the optic lobes shows the electrode positions at which responses were evoked to a light stimulus in the visual field.

The position in the visual field at which the stimulus evoked the maximum response at each electrode position is shown in the middle diagram.

At each electrode position marked with a triangle or a circle, a response was evoked through both eyes from the same position in the visual field. At the electrode positions marked with dots, responses were evoked through the left eye only.

The lower diagram shows the projection of the left visual field onto both optic lobes.
**Fig. 5.**

**Projection of the binocular visual field onto the optic tectum (Experiment B7).**

The upper diagram of the outline of the optic lobes shows the positions at which electrodes were placed in order to record action potentials evoked in response to a light stimulus in the visual field.

At the electrode positions marked with triangles and circles, responses were obtained through both eyes, with a light at the positions in the visual field shown in the middle diagram. The electrode positions marked with dots on the right optic lobe gave responses through the left eye only.

The lower diagram shows the projection of the meridians and parallels of the binocular visual field onto both optic lobes.
RIGHT OPTIC TECTUM

caudal

LEFT OPTIC TECTUM

rostral

200μ

43 - 45
36
29
21
13
6
1

A
D
H
L
Q
C
G
K
P
U

SUPERIOR
90

INFERIOR
270

RIGHT
0

LEFT
180

BINOCULAR VISUAL FIELD

caudal

rostral

200μ

180°

90°

0°

90°
Graph of the variation of magnification factor with eccentricity along the vertical meridian of the visual field.

The dots indicate the means of the results of 5 experiments on Rana temporaria (see table 3).

The triangles indicate the means of the results of 5 experiments on Bufo vulgaris (see table 6).

The range of each set of 5 results is shown by a vertical line.
Graph of the variation of magnification factor with eccentricity along the horizontal meridian of the visual field.

The dots indicate the means of the results of 5 experiments on Rana temporaria (see tables 1 and 2). The triangles indicate the means of the results of 5 experiments on Bufo vulgaris (see tables 4 and 5). The range of each set of 5 results is shown by a vertical line.
Fig. 8.

Photomicrograph of a transverse section through the midbrain of Bufo vulgaris (Experiment B6) just caudal to the exit of the oculomotor nerves (the section has been cut slightly obliquely, with the left side more rostral, and the left oculomotor nerve has been included in the section).

Six electrode tracks are visible in the right optic tectum. In this experiment the electrode positions were spaced at 200 micron intervals, and after each recording had been made with the electrode on the tectal surface, the electrode position was marked by driving it 500 microns into the tectum. (Scale: 1 cm = 200 microns).
Fig. 2.

Graph showing that the reciprocal of the magnification factor \((1/m)\) is a linear function of retinal eccentricity along the inferior vertical meridian and the central 20° of the superior vertical meridian of the retina. The results are shown of five experiments on Rana temporaria (circles), and five experiments on Bufo vulgaris (dots).

The triangles show that the ratio of outer nuclei to ganglion cells in the frog's retina is a linear function of retinal eccentricity along the superior vertical meridian of the retina. These values were obtained by Chievitz (1889).
The following seven figures are camera lucida drawings of every tenth transverse serial section of the brains of seven Anurans in which observations had been made of the effects of brain lesions on the ipsilateral tectal response.

The following abbreviations have been used:

C  Cerebrum.
CB  Cerebellum.
CP  Commissura posterior.
CTM  Commissura tecti mesencephali.
DO  Dorsal division of the marginal optic tract.
H  Nucleus habenulae.
LG  Lateral geniculate body.
LT  Left optic tectum
NB  Nucleus of Bellonci.
NI  Nucleus isthmi.
ON  Optic nerve.
OT  Optic tract.
RT  Right optic tectum.
TS  Torus semicircularis.
VO  Ventral division of the marginal optic tract.
A superficial cut was made in the midline between the optic lobes. This did not affect the normal responses in the ipsilateral or contralateral optic lobes evoked by stimulating either eye with a light.

The frog's brain was cut into transverse serial sections 15 microns thick, and a drawing of every tenth section in the region of the lesion is shown in the figure.

There is a rostro-caudal cut between the caudal parts of the optic lobes. At its rostral extremity the cut passes through the sulcus between the optic lobes into the ventricle, but not through into the tegmentum. More caudally the cut inclines to the right into the torus semicircularis. The lesion undercuts the posterior pole of the right optic lobe, passes close to the rostral tip of the cerebellum into the right nucleus isthmi.

The optic tracts and the optic tectum are normal in appearance. The commissura posterior and the commissura tecti mesencephali have not been affected by the lesion.
A cut was made between the caudal parts of the optic lobes. This did not affect the normal responses in the ipsilateral or contralateral optic lobes evoked by stimulating either eye with a light.

The frog's brain was cut into transverse serial sections 15 microns thick, and a drawing of every tenth section in the region of the lesion is shown in the figure.

There is a right dorsal parasagittal cut in the caudal half of the midbrain and the rostral part of the medulla. The rostral end of the cut passes through the dorsal division of the right marginal optic tract, through the right optic tectum and into the right torus semicircularis. The lesion extends caudally into the right nucleus isthmi.

The left optic tectum, the optic tracts, and the commissures in the dorsal part of the midbrain have not been damaged by the lesion.
A deep midsaggital cut was made in the diencephalon extending from the pineal organ to the diencephalothalamic junction. Immediately afterwards, normal evoked potentials were recorded from both optic lobes in response to a flash of light in either eye.

The frog's brain was cut into transverse serial sections 15 microns thick, and a drawing of every tenth section in the region of the lesion is shewn in the figure.

The cut extends from the pineal organ caudally through the left habenular nucleus, the dorsal thalamus on the left side, the pretectal region, and as far as the posterior commissure. The lesion reaches close to the left optic tract as it passes round the dorsolateral margin of the diencephalon. More caudally, the lesion involves the dorsal division of the right marginal optic tract, and the caudal end of the lesion passes through some fibres of the posterior commissure. The bulk of the posterior commissure appears not to be damaged, and the cut does not extend as far caudally as the commissura tecti mesencephali. The optic tectum appears to have escaped damage.

The dorso-ventral extent of the cut is as follows: At its rostral end, the cut passes through the third ventricle into the right supraoptic nucleus. The cut does not extend to the base of the brain, and the supra-optic commissure and the optic chiasma have not been damaged. In the posterior diencephalon, the cut passes through the aquaduct and divides the commissura tuberculum posterius and the other commissures in the floor of the midbrain. There are several areas of damage in the periaqueductal region.
A dorsal left parasagittal cut was made in the diencephalon and midbrain. Following this, stimulation of either eye with a light evoked a response in the contralateral but not in the ipsilateral optic lobe.

The toad's brain was cut into transverse serial sections 15 microns thick, and a drawing of every tenth section is shown in the figure.

The cut commences about 1 mm to the left of the pineal organ close to the most dorsal fibres of the left marginal optic tract. The rostral end of the cut comes close to the left lateral geniculate body and nucleus of Bellonci. The lesion extends caudally through the dorsal thalamus into the pretectal region and completely divides the commissura posterior and the comm. tecti mesencephali. At the level of the rostral poles of the optic lobes the lesion has damaged some fibres of the dorsal division of the left optic tract.

A dorsal sagittal cut was made between the caudal parts of the optic lobes. Immediately afterwards, evoked potentials were recorded from both optic lobes in response to a flash of light in either eye.

The frog's brain was cut into transverse serial sections 15 microns thick, and a drawing of every tenth section in the region of the lesion is shown in the figure.

There is a sagittal cut in the sulcus between the optic lobes. The cut starts immediately caudal to the commissura tecti mesencephali and extends to the caudal end of the midbrain. At its ends the cut is about 1 mm deep in the sulcus between the optic lobes, but in its middle third the lesion extends through the optic ventricles, between the tori semicirculares, through the aqueduct and to the base of the brain. The optic tracts, optic tectum, and the commissures in the rostro-dorsal part of the midbrain do not appear to have been damaged by the lesion.
EXPERIMENT B 7.

A shallow midsagittal cut was made in the sulcus between the optic lobes. Immediately afterwards photic stimulation of either eye evoked a response in the contralateral but not in the ipsilateral optic lobe.

The toad's brain was cut into transverse serial sections 15 microns thick, and a camera lucida drawing of every tenth section is shown in the figure.

There is a cut in the sulcus between the anterior halves of the optic lobes. The cut passes from the dorsal surface through into the ventricle of the optic lobes, but does not extend into the ventral part of the midbrain. The caudal part of the commissura posterior has been damaged, and the commissura tecti mesencephali has been completely divided. The damage appears to be localized to midline dorsal structures, and the rest of the brain appears to have escaped injury.
The optic chiasma and ventral diencephalon were exposed by removing a flap of the left sphenopalatine bone. A cut was made in the ventro-lateral part of the diencephalon on the left side just caudal to the optic chiasma. Following this, photic stimulation of the left eye evoked responses in both optic lobes, while stimulation of the right eye failed to evoke responses in either optic lobe.

The frog's brain was cut into transverse serial sections 15 microns thick, and a camera lucida drawing of every tenth section is shown in the figure.

There is an area of damage in the ventro-lateral wall of the diencephalon on the left side. The lesion extends for about 0.5mm caudal to the optic chiasma, and appears to have divided most of the fibres of the left optic tract, though the most medial fibres may have escaped injury.
Photomicrographs of silver impregnated transverse sections of the left optic nerve of a frog, 35 days after the nerve had been transected at the position indicated by the arrow. The photomicrographs are of different sections of the same optic nerve and illustrate the differences which are frequently seen between different parts of the same nerve.

The upper photomicrograph (aprox. X 1000), shows a number of fairly discrete fascicles of optic nerve fibres regenerating into the proximal stump of the optic nerve.

The lower photomicrograph (aprox. X 500), shows the typical scrambling of optic nerve fibres at the site of transection. Similar scrambling occurred in all the experiments, even in those cases in which a normal pattern of retino-tectal connections had been restored after regeneration of the optic nerve.
Fig. 18.

The projection of the left visual field onto the right optic tectum, 68 days after transection of the left optic nerve (Experiment 21b)

The upper diagram of the outline of the right optic tectum shows the electrode positions at which action potentials were evoked in response to a light in the visual field, shown in the lower diagram.

There are two constellations of stimulus positions. Stimuli in the constellation in the nasal half of the visual field evoked responses in the lateral half of the optic tectum; while stimuli in the temporal half of the visual field evoked responses in the medial half of the optic tectum. Responses were evoked from both the nasal and the temporal constellations at the electrode positions enclosed in the blocks.
The projection of the left visual field onto the right optic tectum, 51 days after transection of the left optic nerve (Experiment 26d).

The upper diagram of the outline of the right optic lobe shows the electrode positions at which action potentials were evoked in response to a light in the visual field, shown in the lower diagram.

There are two constellations of stimulus positions. Stimuli in the constellation in the nasal half of the visual field evoked responses in the lateral half of the optic tectum; while stimuli in the temporal half of the visual field evoked responses in the medial half of the tectum. Responses were evoked from both the nasal and the temporal constellations at the electrode positions enclosed in the block.
Fig. 20.

The projection of the left visual field onto the right optic tectum, 91 days after transection of the left optic nerve. (Experiment 27a)

The upper diagram of the outline of the right optic tectum shows the electrode positions at which action potentials were evoked in response to a light in the visual field at the positions shown in the lower diagram.

No responses were recorded from the electrode positions marked o.

There are three groups of stimulus positions, two in the nasal half of the visual field, and one in the temporal half-field. Stimuli in the nasal half-field evoked responses in the lateral part of the optic tectum, while stimuli in the temporal half-field evoked responses in the medial part of the optic tectum. At the electrode positions enclosed in blocks responses were evoked from both halves of the visual field.
Fig. 21.

The projection of the left visual field onto the right optic tectum, 29 days after transection of the left optic nerve. (Experiment 21b).

The upper diagram of the outline of the right optic tectum shows the electrode positions at which potentials were evoked in response to a light in the visual field shown in the lower diagram.

Stimulus positions in the nasal half of the visual field evoked responses in the lateral part of the tectum, while stimulus positions in the temporal half-field evoked responses in the medial part of the tectum. The dotted line on the tectum indicates the boundary between the lateral and medial parts of the tectum. The electrode positions in the blocks were those at which responses were recorded from both nasal and temporal half-fields.
Fig. 22.

The projection of the left visual field onto the right optic tectum, 90 days after transection of the left optic nerve. (Experiment 17a).

The upper diagram of the outline of the right optic tectum shows the electrode positions at which action potentials were evoked in response to a light in the visual field at the positions shown in the lower diagram.

Stimulus positions in the nasal half of the visual field evoked responses in the lateral part of the tectum, while stimulus positions in the temporal half-field evoked responses in the medial part of the tectum. The dividing line between the medial and lateral parts of the tectum is shown as a dotted line in the upper diagram.
The projection of the left visual field onto the right optic tectum, 30 days after transection of the left optic nerve (Experiment 22b)

The upper diagram of the outline of the right optic tectum shows the electrode positions at which action potentials were evoked in response to a light in the visual field at the positions shown in the lower diagram.

At electrode positions 9, 15, 16, 22, 23, in the rostromedial corner of the tectum, action potentials were evoked from positions 9, 15, 16, 22, 23, in a small area in the superior temporal visual field. At all the other electrode positions potentials were evoked from stimulus positions in the nasal periphery of the visual field. No responses were recorded from the electrode positions marked 0.
RIGHT OPTIC TECTUM

caudal

midline

lateral

rostral

superior

nasal

temporal

in inferior

LEFT VISUAL FIELD
The projection of the left visual field onto the right optic tectum, 33 days after transection of the left optic nerve. (Experiment 13b).

The upper diagram of the outline of the right optic tectum shown the electrode positions at which action potentials were evoked in response to a light in the visual field at the positions shown in the lower diagram.

No responses were recorded from the electrode positions marked 0.

Responses were evoked at electrode positions in the lateral part of the tectum by the stimulus in a small area in the nasal half of the visual field close to the horizontal meridian and 30° to 60° from the fixation point. From anywhere within this small area of visual field responses could be evoked at any of the electrode positions 1 to 11 on the lateral part of the tectum.
The projection of the left visual field onto the right optic tectum, 43 days after transection of the left optic nerve. (Experiment 15b).

The upper diagram of the outline of the right optic tectum shown the electrode positions at which action potentials were evoked in response to a light in the visual field at the positions shown in the lower diagram.

No responses were recorded from the electrode positions marked 0.

Responses were evoked from a small area in the superior temporal visual field at electrode positions in the rostromedial corner of the tectum. From anywhere within this small area of visual field responses could be evoked at any of the electrode positions 1 to 10, but the numbers indicate the positions of maximum response.
The projection of the left visual field onto the right optic tectum, 23 days after transection of the left optic nerve. (Experiment 21c).

The upper diagram of the outline of the right optic tectum shows the electrode positions at which action potentials were evoked in response to a light stimulus in the visual field at the positions shown in the lower diagram.

No responses were recorded from the electrode positions marked o.

Responses were evoked from a small area in the visual field at electrode positions distributed over most of the dorsal surface of the tectum. From anywhere within this small area of visual field, responses could be evoked at any of the electrode positions, but the numbers indicate the positions of maximum response.
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