J. Anat. (1966), 100, 1, pp. 5–33
With 21 *figures*
Printed in Great Britain

The retinal representation upon the optic tectum and isthmo-optic nucleus in the pigeon

By J. I. McGILL, T. P. S. POWELL and W. M. COWAN
Department of Human Anatomy, University of Oxford

INTRODUCTION

Previous studies of the avian visual system (Cowan, Adamson & Powell, 1961; Cowan & Powell, 1963) have demonstrated the site of origin, the course and the termination of the centrifugal fibres to the retina. These fibres arise in a well-defined cell mass in the midbrain, the isthmo-optic nucleus, and pass through the isthmo-optic tract and optic chiasma to end on the inner aspect of the bipolar cell layer (probably upon amacrine cells) of the contralateral retina. Although the functional significance of this centrifugal fibre system is not known it must be dependent upon the afferent influences acting upon the isthmo-optic nucleus. At present the only known source of afferents to the nucleus is the optic tectum, which is the major site of termination of optic nerve fibres, and such a connexion provides a direct link between the afferent fibres from the retina and the efferent fibres to the retina. Preliminary experiments have indicated that there is some degree of organization within this tectal projection upon the isthmo-optic nucleus, and in view of the known organization of the retino-tectal projection (Hamdi & Whitteridge, 1954) it has been suggested that each part of the retina may be reciprocally related, through the tectum, with that part of the isthmo-optic nucleus from which it receives its centrifugal afferent fibres (Cowan & Powell, 1963). In order to test this theory it is necessary to determine the representation of the retina upon the tectum, the organization of the projection of the tectum upon the isthmo-optic nucleus, and finally whether the cells of the isthmo-optic nucleus send their axons to different parts of the retina. The present study is concerned with the first and second of these problems. Although the representation of the retina upon the tectum has been determined with the evoked potential method (Hamdi & Whitteridge, 1954), for several reasons it was necessary to re-investigate the retinal projection using neurohistological techniques. First, it was essential to test the adequacy of our methods for placing localized lesions in the retina before using them to determine the distribution of centrifugal fibres to the retina; the most suitable control of their adequacy was to compare the pattern of degeneration in the tectum after such lesions with the results of the previous electrophysiological study. Secondly, it was considered necessary to map the retinal projection upon the tectum in brains which would be sectioned in the standard plane found to be most convenient for studying degeneration in the isthmo-optic nucleus. Thirdly, as the observations of Hamdi & Whitteridge (1954) were confined to the dorsal and ventral surfaces of the tectum it was considered necessary to map the retinal representation upon the rest of the surface of the tectum. The distribution of centrifugal fibres to the retina will be dealt with in a subsequent paper (McGill, Powell & Cowan, 1966).

MATERIAL AND METHODS

The operative procedures were performed under open ether anaesthesia; for the study of the retino-tectal projection thirty-one pigeons were used; the sclera was exposed either by widening the palpebral fissure or by incising the adjoining skin, and, where necessary, by removing the overlying bone. The retinal lesions were produced electrolytically by inserting needles through the layers of the eyeball. Two methods were used; in the first the electrode was directed through the vitreous to the chosen area on the retina; for the second, only the tip of the electrode entered the eyeball and it was then turned against the immediately adjacent retina. The animals were allowed to survive for between 8 and 14 days and were then killed by an overdose of ether. The brains were removed and fixed by immersion in 10 % formalin. For the orientation of the eyes a steel needle was inserted vertically through the eyeball while the animal's head was held in a stereotaxic apparatus. As the alignment of the eye is critical for a comparison of the results of different experiments the position of the head was the same in all animals with the upper beak on the same horizontal plane as the external auditory meatus. The needle was left *in situ* during fixation in 10 % formalin and the subsequent processing for histology. All the eyes were examined histologically, the majority having been embedded in low viscosity nitro-cellulose. 50 μ sections were cut in the vertical plane, and from each eye a 1 in 10 series was stained with haematoxylin and eosin. The site and extent of the lesions were accurately reconstructed at a magnification of $\times 10$ and subsequently transferred to a standard diagram of the retina.

All the brains were embedded in paraffin wax, and, in order to enable accurate comparison of the distribution of the degeneration in different brains, were sectioned in a standard horizontal plane. The plane which was found to be the most suitable was that parallel to a tangent to the postero-dorsal surfaces of both the cerebral and cerebellar hemispheres (Fig. 19B); with the brain in this position there is a considerable tilt of the tectum so that what we shall refer to as the horizontal and vertical axes of the tectum (corresponding to the lines *A–P* and *S–I* respectively) would lie obliquely across the tectum with the brain positioned as in the study of Hamdi & Whitteridge (1954) (Fig. 19A). These horizontal sections were cut at 15 μ and a 1 in 12 series was stained according to the Nauta & Gygax (1951) method. The distribution of the degeneration in each experiment was plotted on a series of standard diagrams of sections through the tectum and also upon orthogonal surface reconstructions of the tectum.

For the projection of the tectum upon the isthmo-optic nucleus, fourteen birds were used; a skin incision was made over the lateral aspect of the head, and in the majority the bone overlying the optic tectum was removed with a dental drill; in some birds, in order to obtain adequate exposure of the medial part of the anterior surface of the tectum, the greater part of the cerebral hemisphere was removed on one side. Superficial lesions of varying size were placed in different parts of the tectum using a fine needle. As it had been established previously that the tectal projection to the isthmo-optic nucleus is strictly unilateral, lesions were placed in the tectum of both sides in several animals. The survival periods and histological preparation of all but two of the brains were the same as for those brains used for the investigation of the projection of the retina upon the tectum; from each brain a regular 1 in 12 series of sections through the whole brain and a 1 in 2 series through the isthmo-optic nucleus were mounted and stained according to the original Nauta & Gygax (1951) method; an alternate series was mounted and stained with thionin. The other two brains were sectioned, one coronally and the other horizontally, on the freezing microtome at 25 μ and the sections were stained by the conventional Nauta (1957) technique and by the Glees (1946) method. For each experiment the site and extent of the lesion were plotted, first on tracings of horizontal sections through the tectum and then upon a standard series of outlines of the five surfaces of the tectum. The distribution of the degeneration within the isthmo-optic nucleus was first plotted on a series of projected outlines of the nucleus from each experiment and subsequently transferred to a standard series of tracings from a normal brain.

RESULTS

I. *The retinal projection upon the tectum*

Although the avian retina is known to project to several sites in the diencephalon and midbrain (Cowan *et al.* 1961), in the following account only the representation of the retina upon the tectum will be considered. That the techniques which have been used for the placement of retinal lesions are in fact adequate is borne out both by the discreteness of the retinal damage and by the precise localization of the terminal degeneration within the tectum. Indeed it has been surprising how, after a small lesion in the peripheral retina, the terminal degeneration is limited to a correspondingly low area of the tectum, and how sharply the affected zone can be delimited from the neighbouring areas. The most serious problem in the analysis and correlation of the different experiments has resulted from slight differences in the orientation of the eyes with respect to the horizontal and vertical axes through the fovea. Although considerable care was taken to align the eyes in a standard position, some degree of rotation is inevitable during the process of embedding and cutting. However, as in nearly all the sectioned eyes it was possible to identify the fovea (as well as the optic disc) it has been possible, in making the reconstruction of the retina, to correct for slight degrees of rotation. As anatomical techniques are, in general, less suitable than the evoked potential method for determining the projection of the central retina, we have concentrated on determining the essential quadrantic organization of the retino-tectal projection. Many of the lesions in the retina have involved the same, or similar, areas, and for this reason only a few representative experiments will be described.

In Expt. P101 there is a small triangular area of retinal damage at the extreme edge of the retina close to the vertical axis between the antero-superior and the postero-superior quadrants (Fig. 1). In the tectum of the contralateral side the degeneration resulting from this lesion is found in the outer part of the stratum griseum et fibrosum superficiale (Fig. 9 (5)) at, or close to, the postero-medial margin of the tectum over a little more than a third of its dorsal-ventral extent. In its lower part the degeneration is confined to a very small area along the postero-medial edge of the tectum, but dorsally it occupies a slightly greater area and is situated further laterally so that on the upper sections there is an unaffected zone between it and the postero-medial margin (Fig. 1).

The projection of the anterior inferior quadrant of the retina is illustrated by Expts. P20 and P140, in both of which there are small lesions along the periphery of this quadrant. In Expt. P20 the lesion is situated approximately midway

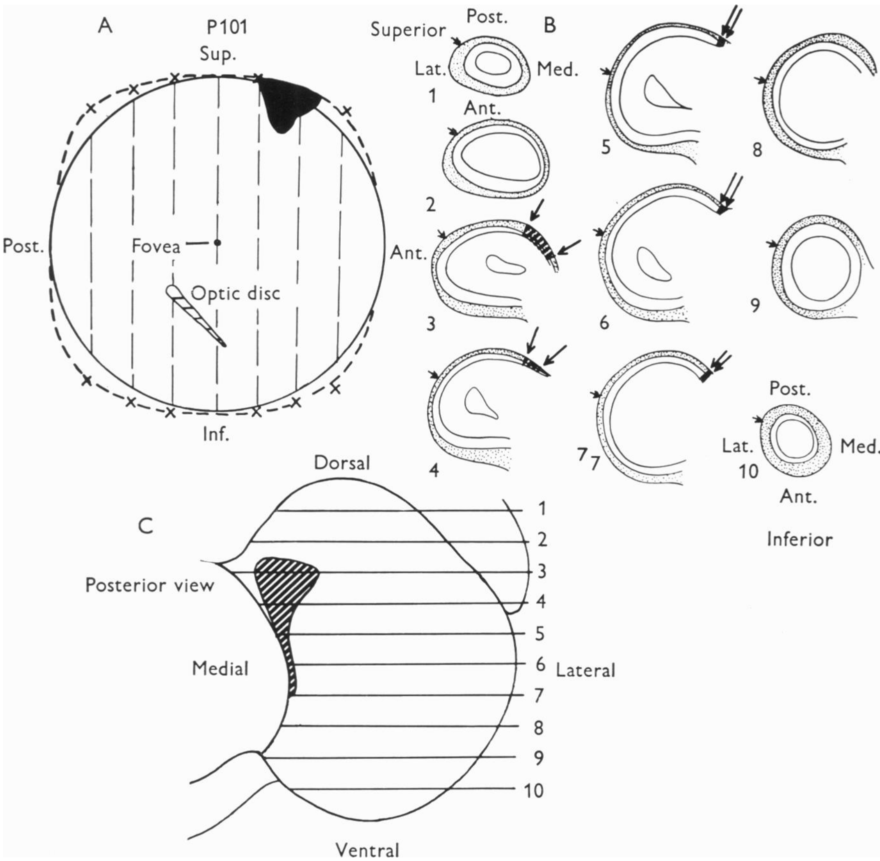


Fig. 1. The site and extent of the retinal lesion and the distribution of the resulting degeneration in the tectum in Expt. P101. In A the lesion is shown in solid black on a standard diagram of the right retina (continuous line) and on the reconstructed outline of the retina of this experiment (interrupted line). In B the degeneration is shown in hatching and delimited by large arrows on a standard series of outlines of horizontal sections through the dorso-ventral extent of the tectum. In this and the subsequent diagrams the middle of the circumference of the tectum is shown by a small arrow, and for the sake of convenience the degeneration is plotted in diagrams of the tectum of the *right* side. In C the extent of the degeneration is shown on a reconstruction of the posterior surface of the tectum.

between the horizontal and vertical axes and is in the form of a rather wide V, with the apex at the extreme edge of the retina. In P140 there is a small focus of destruction just in front of the vertical axis, and it has no doubt interrupted fibres from a small wedge-shaped area of this quadrant (Fig. 2). In the tectum of both these brains the degeneration is limited to a small area along its dorso-medial edge (Fig. 2). A comparison of these two experiments with P101 makes it clear that the antero-superior quadrant of the retina is represented upon the posterior aspect of the

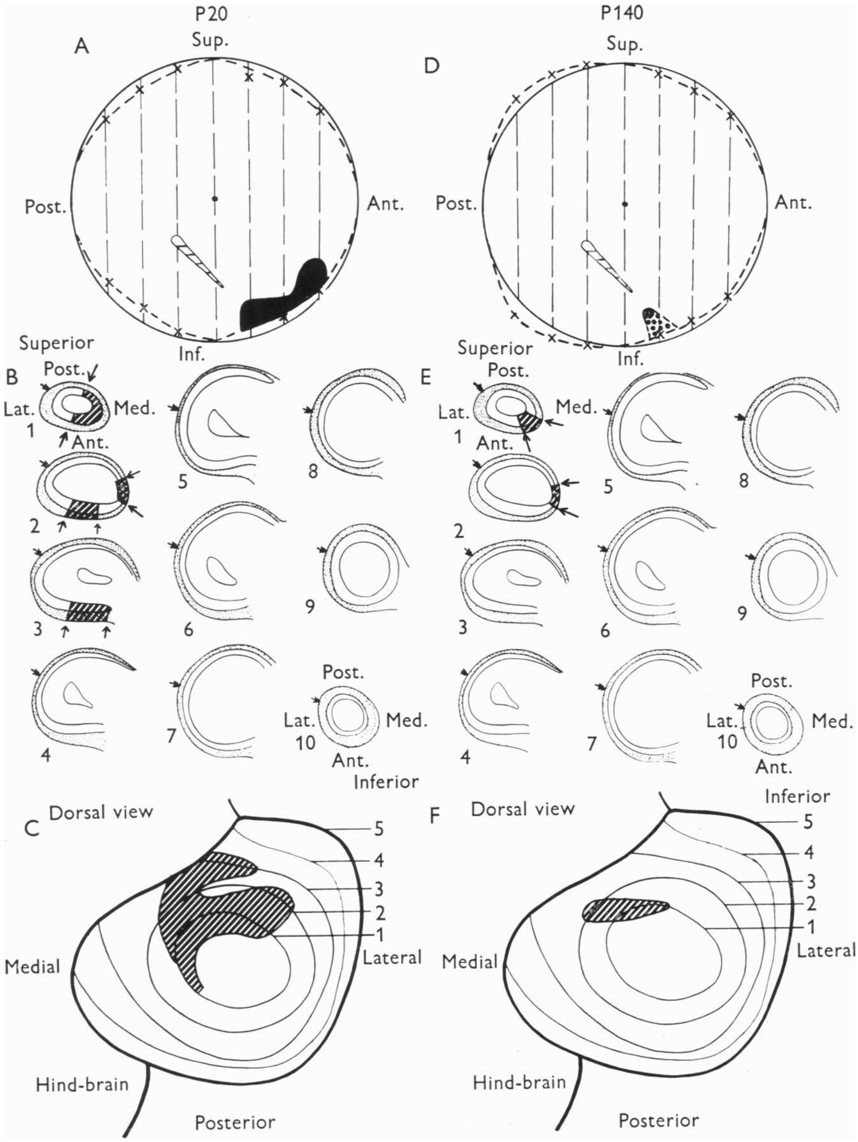


Fig. 2. The site and extent of the lesion in the retina and the distribution of the terminal degeneration in the tectum in Expt. P20 (A, B, C) and P140 (D, E, F).

tectum and the antero-inferior quadrant upon the dorsal surface. From this it would follow that as one moves from the upper to the lower part of the anterior half of the retina the representation in the tectum moves upwards along the posterior surface and then forwards along the dorsal aspect. That this is indeed so is shown by Expt. P114 in which the larger lesion more or less straddles the horizontal axis between the antero-superior and antero-inferior quadrants.

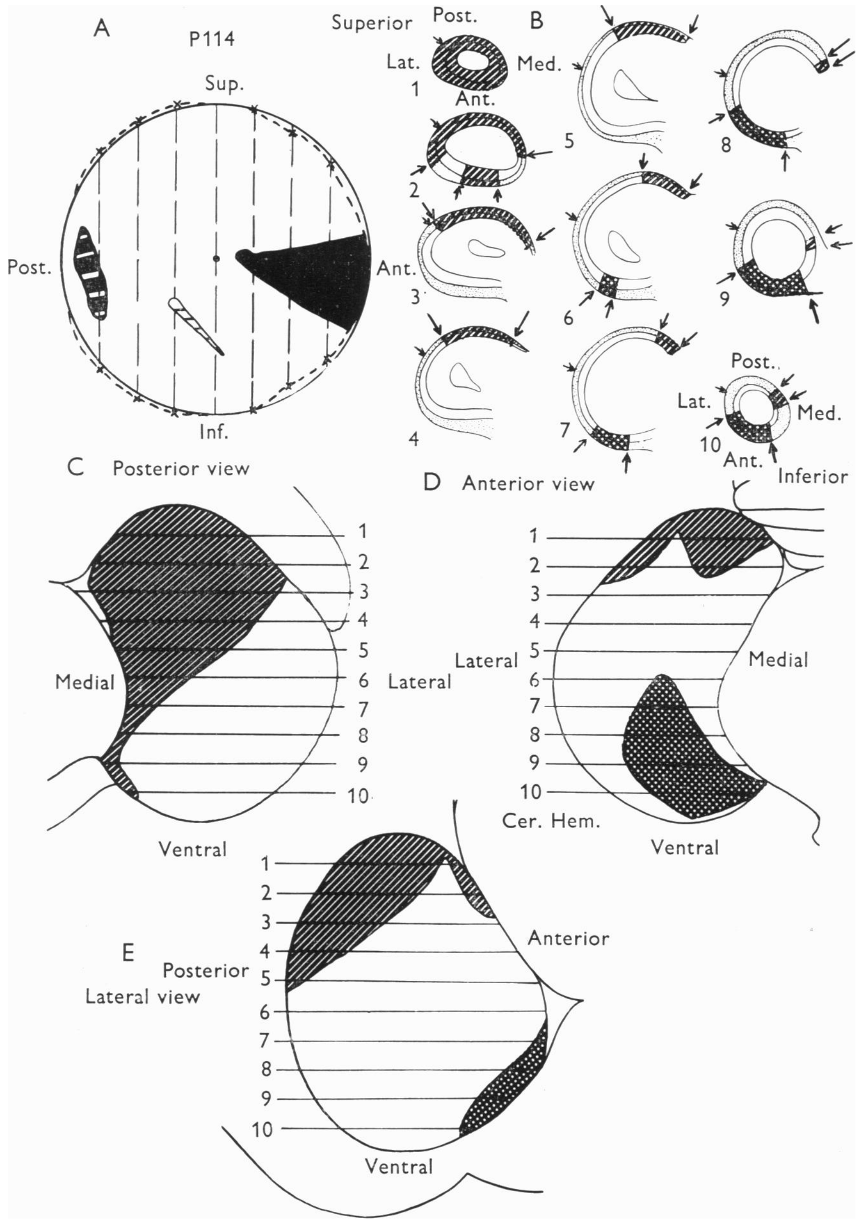


Fig. 3. The lesion and resulting degeneration in Expt. P114. The degeneration due to the large anterior lesion is shown in single hatching, and that in the anterior-ventral part of the tectum resulting from the smaller posterior lesion in cross-hatching.

In the retina of P114 two lesions were produced: one in the posterior half and a second in the junctional region between the antero-superior and antero-inferior quadrants. Only the latter will be dealt with here; the area of the retina which had been damaged by this lesion is large and roughly wedge-shaped, the apex of the wedge being directed centrally and reaching to about three-quarters of the distance

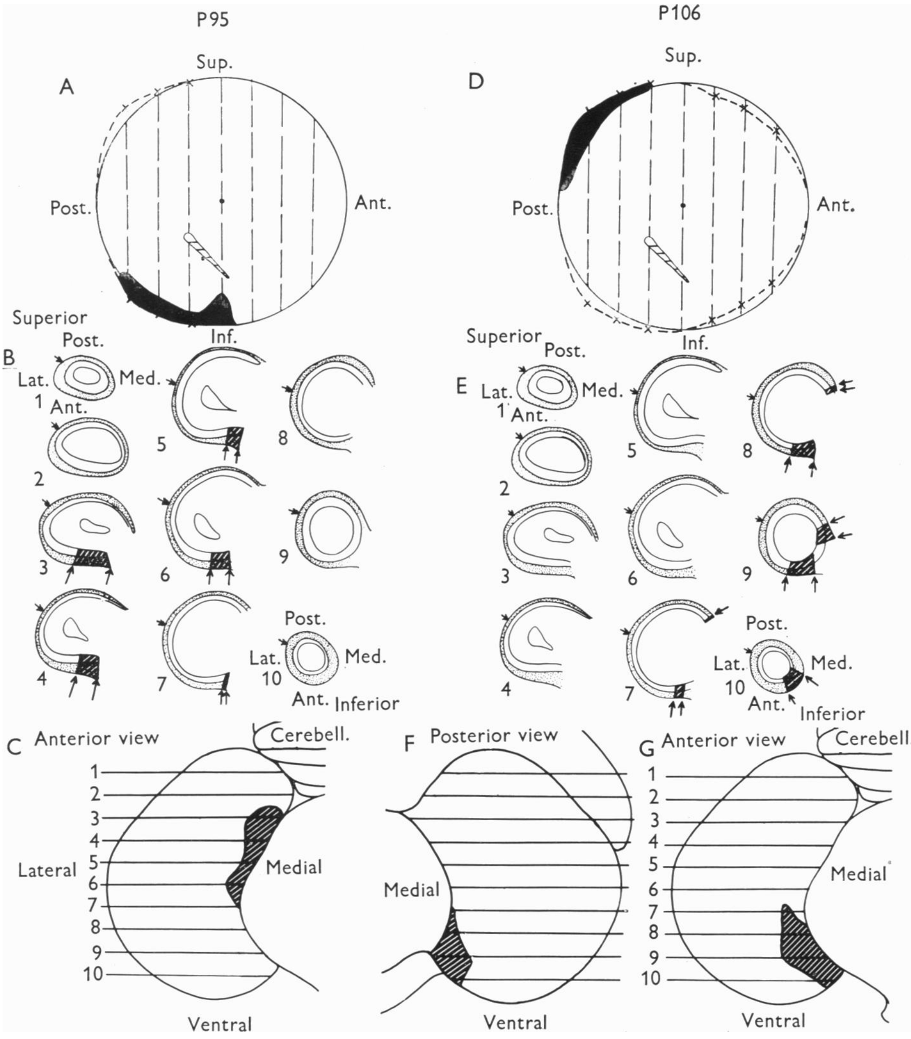


Fig. 4. The retinal lesion and resulting tectal degeneration in Expts. P95 (A, B, C) and P106 (D, E, F, G).

between the peripheral margin and the fovea (Fig. 3). In addition to the direct retinal destruction it is probable that a large number of fibres from the antero-superior quandrant have been interrupted in their course to the optic nerve. In the horizontal sections of the tectum there are two discontinuous areas of terminal degeneration; the relationship of these areas to the two lesions is easily determined both from the extent of the tectal surface involved and from what is already known about the organization of the retinal projection. The degeneration resulting from the larger lesion is found throughout almost the entire dorso-ventral extent of the tectum; in the lower half it occupies a very small area adjoining the postero-medial margin, but in the dorsal half it progressively increases in extent and is found more

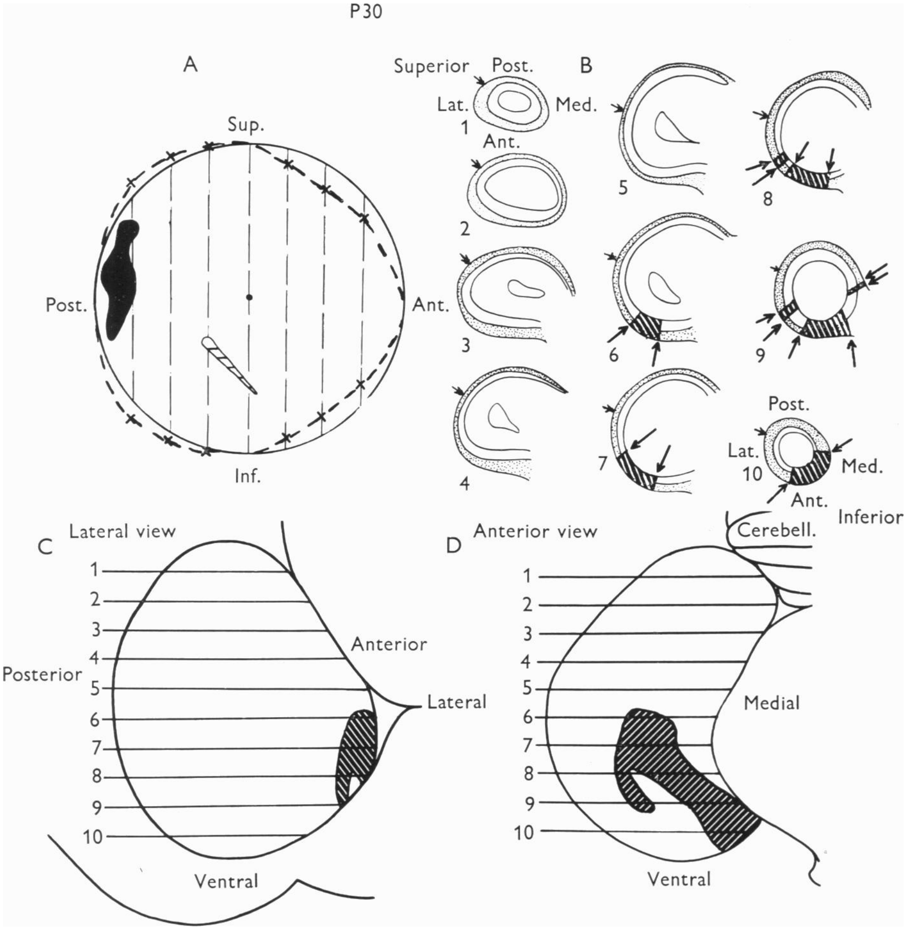


Fig. 5. The site of the lesion and the degeneration in Expt. P30.

laterally so that there is a small unaffected area of the tectum along the postero-medial edge. At the dorsal surface of the tectum the degeneration attains its maximum extent reaching on to the anterior surface of the tectum and coming to occupy the entire circumference. The distribution of the degeneration as seen on the surface of the tectum is shown in Fig. 3, from which it is clear that the degeneration resulting from the lesion described in this experiment overlaps that found after lesions in the antero-superior quadrant and that resulting from lesions in the lower part of the antero-inferior quadrant.

As an example of experiments with lesions in the postero-inferior quadrant of the retina, Expt. P95 will be presented. The definitive lesion is in the form of a narrow strip along the extreme peripheral edge of the retina and although it extends backwards for some distance from the junction of the antero-inferior and postero-inferior quadrants, the total area of retinal damage is quite small as may be judged from Fig. 4. The area of degeneration due to this lesion is found in the horizontal

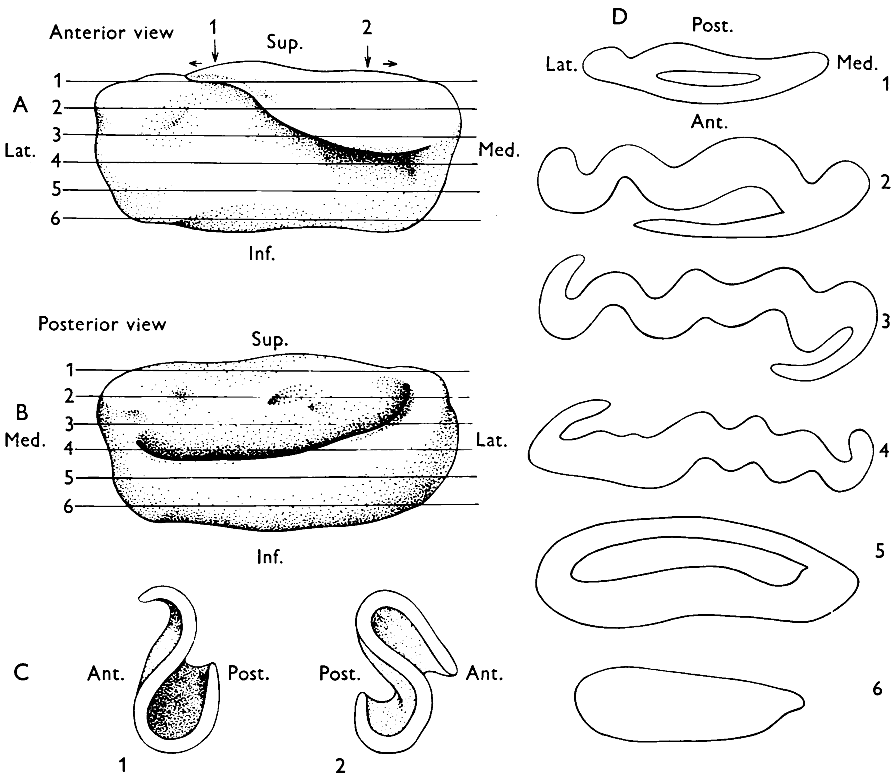


Fig. 6. The normal morphology of the isthmo-optic nucleus. A and B are anterior and posterior views of a reconstruction of the whole nucleus made from the horizontal sections (D) taken at regular intervals through the dorso-ventral extent of the nucleus; the numbers 1–6 correspond to the levels shown on the reconstruction. In C are shown diagrammatic views of sagittal sections of the nucleus at the relevant positions marked by arrows in the reconstruction shown in A. Section C1 is drawn as seen from the medial aspect looking laterally and C2 from the lateral aspect.

sections of the tectum only on its anterior surface where it is seen to occupy a narrow band close to the antero-medial margin of the tectum. In a surface reconstruction of the tectum this area forms a narrow strip over approximately the middle third of the dorso-ventral extent of the antero-medial aspect of the tectum. From this it may be inferred that the periphery of the postero-inferior quadrant of the retina projects to the anterior part of the tectum, and by deduction it would follow that the peripheral part of the postero-superior quadrant is related to the ventral part of the tectum. That this is so is directly confirmed by the findings in Expt. P106.

In Expt. P106 there are again two lesions; a very small anterior lesion at the point where the electrode was inserted horizontally through the eyeball and a larger definitive lesion which has destroyed the peripheral part of the retina over nearly the whole postero-superior quadrant (Fig. 4). The form of the smaller lesion and the degeneration resulting from it will not be described as it is so similar to the previous experiments with lesions in this quadrant. Consequent to the posterior lesion

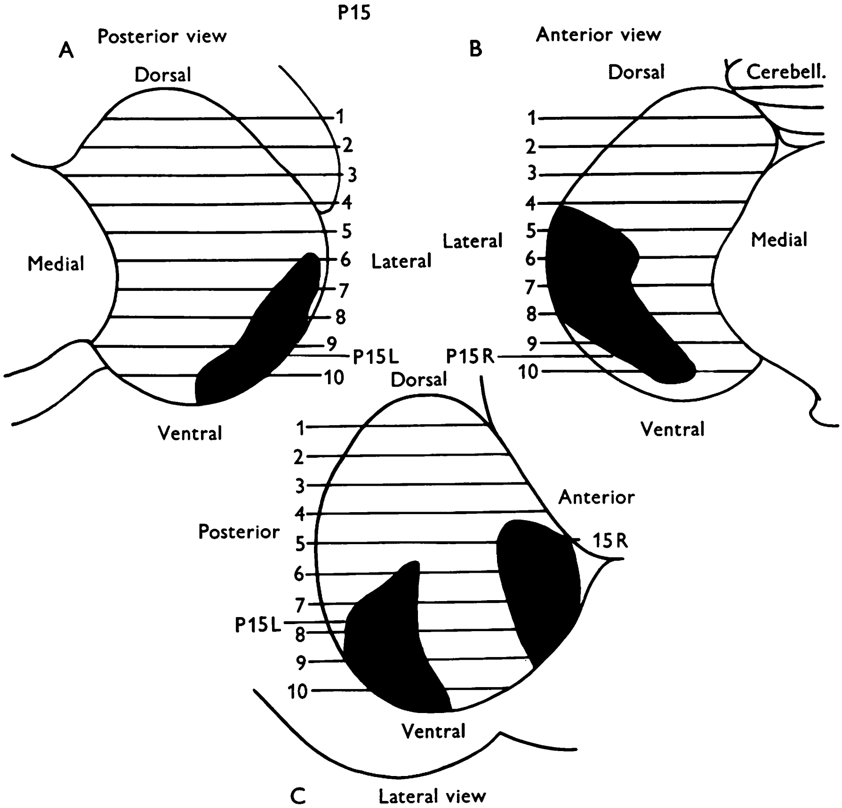


Fig. 7. The site and extent of the lesion in Expt. P15 on surface reconstructions of the tectum. In this and the subsequent figures the lesions are all depicted on diagrams of the *right* tectum.

terminal degeneration is restricted to the ventral third of the tectum and in the horizontal sections over this region the area of degeneration is seen to occupy the medial half of the most ventral sections and at more dorsal levels the antero-medial and postero-medial margins of the tectum. The width of the affected zone progressively diminishes dorsally, and a surface reconstruction of the degenerated area shows it to lie along the medial edge of the ventral surface of the tectum from its anterior to its posterior end. The lesion in P30 (Fig. 5) and the smaller lesion in Expt. P114 which is similar to it in size are good examples of lesions overlapping the boundary between the postero-inferior and postero-superior quadrants of the retina. Both lesions are approximately rectangular in shape and extend upwards and downwards from the horizontal axis of the retina so that the long axes of the lesion are roughly vertical. In the horizontal sections through these brains terminal degeneration is seen only in the ventral half of the contralateral tectum. In both cases it occupies the middle two-thirds of the antero-lateral aspect of the tectum, and when plotted on the surface it appears as a broad strip in the lower part of the tectum overlapping the anterior and lateral surfaces. Together, these experiments confirm the pattern of representation of the posterior retina upon the tectum seen in P95 and P106, and it may be stated in conclusion that to pass from superior to inferior along the posterior margin of the retina is equivalent to passing from the ventral to the anterior surfaces of the tectum as these are orientated in our material.

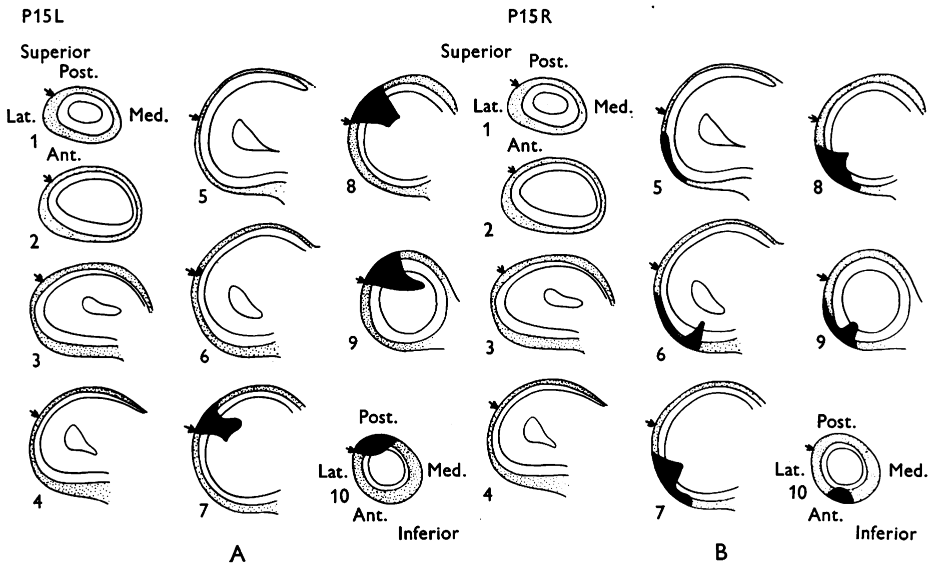
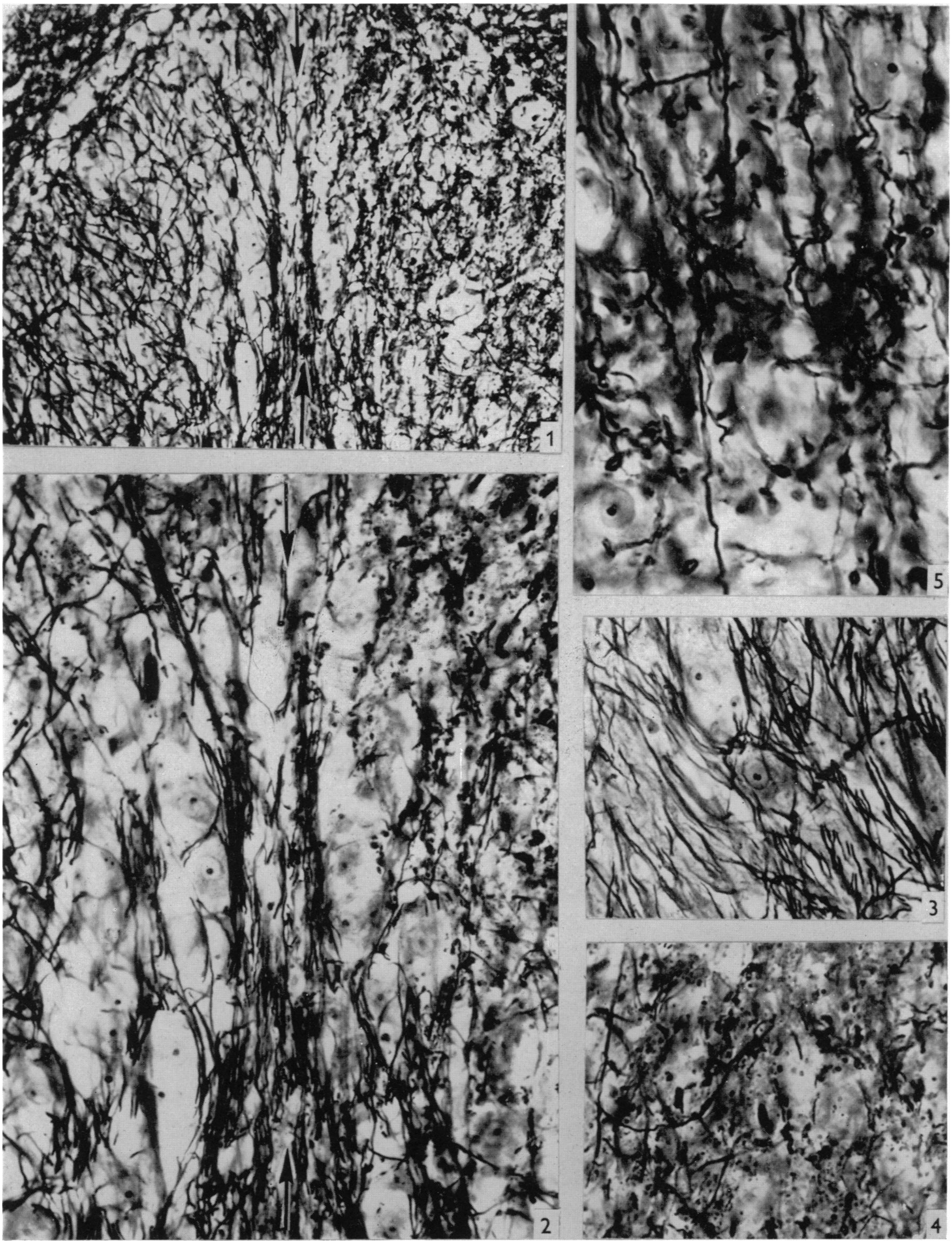


Fig. 8. Diagram of lesions in Expt. P15 on a standard series of horizontal sections through the dorso-ventral extent of the tectum. Again, for comparison, both lesions are shown on sections of the *right* tectum.

II. *The projection of the tectum upon the isthmo-optic nucleus*

Because of the highly complex form of the isthmo-optic nucleus, a description of its normal morphology will be given, before presenting the experimental findings.

As may be seen from the outlines of horizontal sections taken at regular intervals through the dorso-ventral extent of the isthmo-optic nucleus (Fig. 6D) the nucleus is really a highly convoluted lamina which, over most of its extent, consists of two layers of cells separated by a narrow fibre layer. Whether, in fact, it should be regarded as a single lamina, two cells in thickness, or as a double lamina, is difficult to determine, but as it will be shown that the afferents to any part af the nucleus are always distributed to both layers, and both layers send their efferents to the same part of the retina (McGill *et al.* 1966) we shall consider the two layers as forming a single lamina. Sagittal sections show that the nucleus has undergone an S-shaped folding so that the superior border is bent forwards and downwards and its inferior


1
5
3
2
4

border backwards and upwards (Fig. 6C). Fig. 6A and B are drawings of a reconstruction of the nucleus as seen from its anterior and posterior aspect, respectively, and it is apparent that the foldings of the superior and inferior borders are not uniform over their medio-lateral extent. The superior border is prolonged much farther ventrally along the medial edge of the nucleus, while the inferior border is folded over the whole of its medio-lateral extent but the folding along the lateral margin reaches farther dorsally than that on the medial side. The effect of this folding is that in horizontal sections the nucleus appears to have superiorly an 'antero-medial limb', and inferiorly, 'postero-medial' and 'postero-lateral limbs' (Fig. 6D). A plasticine reconstruction of the nucleus, when unfolded to form a flat sheet, is found to be more or less circular or oval in outline.

The first experiment to be described, P15, illustrates the basic antero-posterior organization of the tecto-isthmo-optic projection. Two large lesions were placed in this brain, one in the antero-inferior part of the tectum of the right side and the second in the postero-inferior portion of the left tectum (Fig. 7). The lower limit of the lesion on the right side is close to the ventral surface of the tectum on its antero-lateral aspect. Extending more or less vertically upwards it remains of uniform width over the lower two-thirds of its extent where it occupies approximately one-fifth of the circumference of the tectum. In its upper third, which extends above the middle of the dorso-ventral aspect of the tectum, it is rather wider and covers nearly one-third of the circumference of the tectum. The lower and upper parts of the lesion are very superficial being confined to the stratum opticum and the stratum griseum et fibrosum superficiale, but for the greater part of its dorso-ventral extent it penetrates through the stratum griseum centrale into the underlying white matter (Fig. 8). Thus, with the exception of its extreme dorsal part, it is essentially a lesion of the antero-inferior quadrant of the tectum in which it is situated approximately equidistant from the anterior border and the middle of the lateral surface. The lesion on the left side is smaller and occupies rather less than the anterior half of the posterior-inferior quadrant of the tectum (Fig. 7). From the inferior surface of the tectum the area of damage reaches dorsally almost to the midpoint of the dorso-ventral extent of the tectum, and its anterior border coincides with the middle of the lateral surface; over almost the whole of its extent, it has penetrated into the stratum album centrale (Fig. 8).

From the deep aspect of both lesions degenerating fibres can be seen passing through the stratum album centrale of the tectum and around the posterior angle of the ventricle to enter the isthmo-tectal tract. This tract approaches the antero-ventral part of the isthmo-optic nucleus, and on both sides terminal degeneration can be seen over a restricted area of the nucleus. On the right side this area of

Fig. 9. Paraffin section stained by method of Nauta & Gygax (1951). (1) The demarcation of the terminal degeneration in the isthmo-optic nucleus after a lesion in the tectum of Expt. P15. The arrow points to the limit between the degeneration (on the right) and the unaffected part of the nucleus (on the left). ×210. (2) The same region of the isthmo-optic nucleus as in (1). ×480. (3, 4) Normal area in the isthmo-optic nucleus (3) and an area of degeneration in the affected part of the nucleus (4) in Expt. P15. ×480. (5) Terminal degeneration in the outer part of the stratum griseum et fibrosum superficiale of the tectum after a small lesion in the retina of the contralateral eye in Expt. P18. ×1360.

terminal degeneration is confined to the ventral third of the nucleus and to the medial third of its cross-sectional area, chiefly in the junctional region between the body of the nucleus and its small postero-medial limb (Fig. 10A, C). On the left side both the density and the extent of the terminal degeneration are appreciably greater than on the right being found in all but the more ventral sections of the nucleus. In the lower part of its extent the degeneration occupies approximately

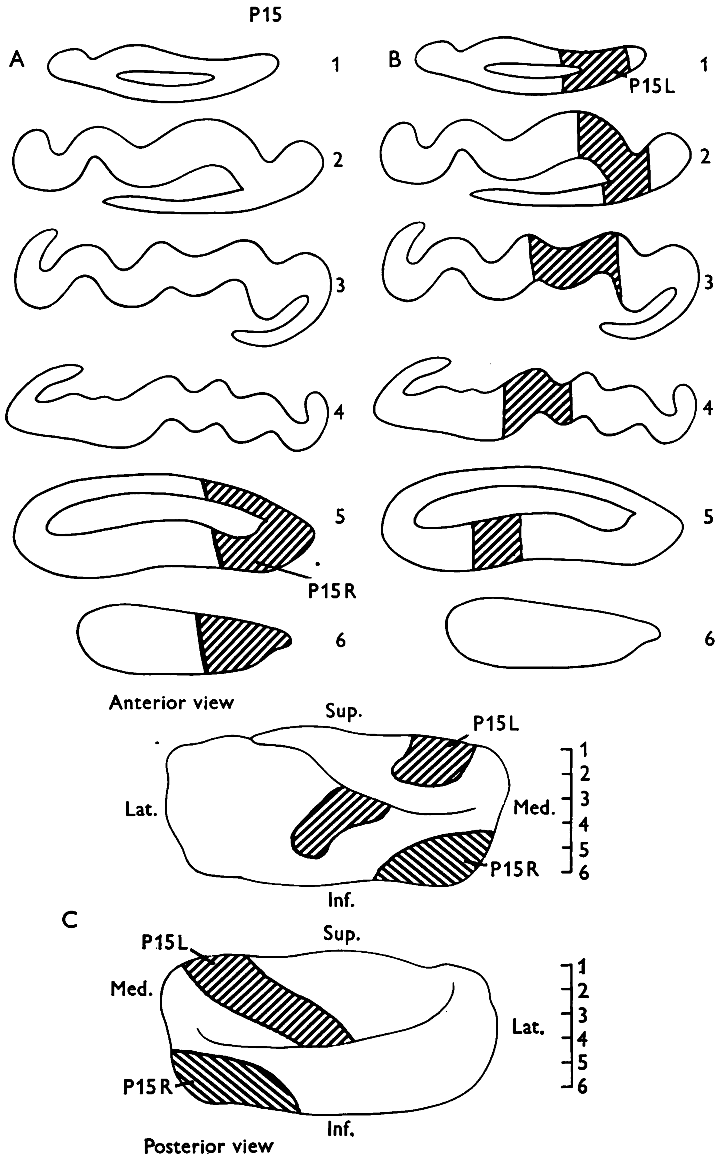


Fig. 10. The distribution of the terminal degeneration (hatching) in horizontal sections and on a reconstruction of the isthmo-optic nucleus in Expt. P15. In this and the subsequent figures the degeneration in the nucleus is shown as though on the *right* side.

the central fifth of the cross-sectional area, but in the dorsal third it is found progressively more medially and comes to occupy the medial edge of the nucleus including the junctional region between its body and antero-medial limb (Fig. 10B, C). A comparison of the extent of the degeneration in the nuclei of the two sides makes it clear that the smaller and more posterior lesion of the left side has resulted in a much more extensive area of degeneration in the nucleus; the probable

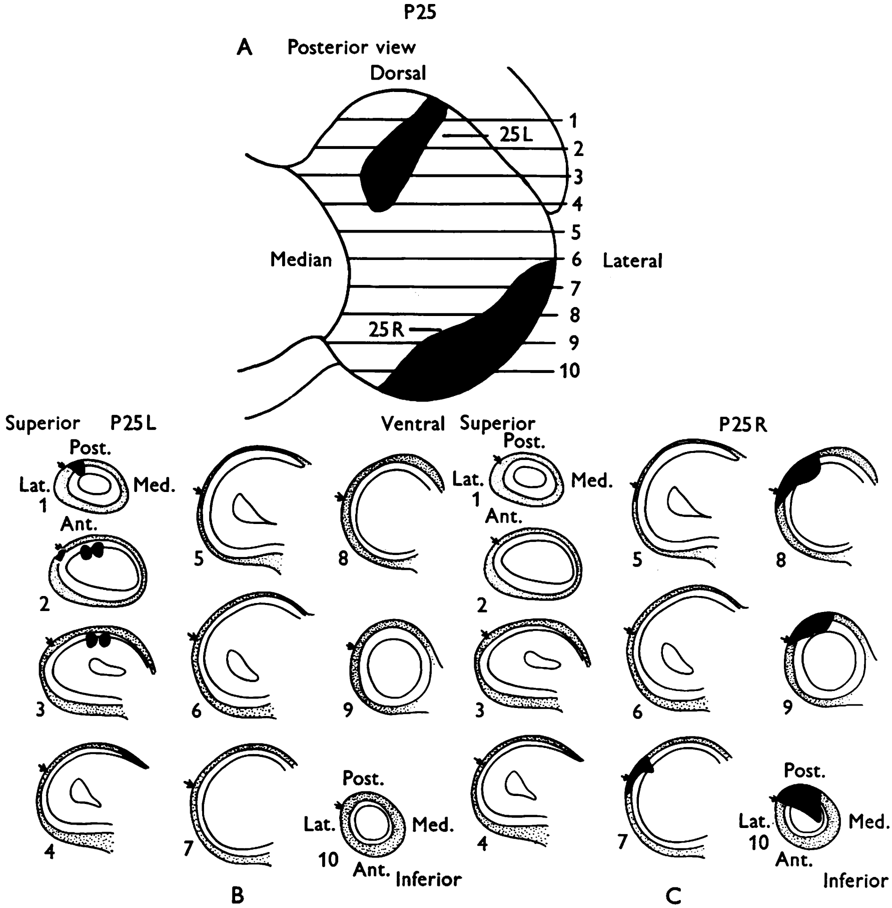


Fig. 11. The site and extent of the two lesions in Expt. P25.

explanation for this is that the lesion on this side is considerably deeper than that on the right and in consequence has interrupted fibres from more anterior parts of the tectum. That this is so is further suggested by the fact that there is some overlap in the distribution of the degeneration on the two sides. Together, these two lesions indicate that there is an antero-posterior organization in the projection of the tectum upon the isthmo-optic nucleus, such that anterior parts of the tectum are represented ventrally in the nucleus and posterior areas of the tectum more dorsally. That there is a comparable dorso-ventral organization in this projection is shown in the following experiment.

In Expt. P25 there are again two lesions: that on the right side is the larger, is oval in outline, and is obliquely placed across the lower part of the central portion of the tectum, extending upwards from the inferior surface almost to the middle of the tectum. By far the greater part of the lesion lies in the postero-inferior quadrant

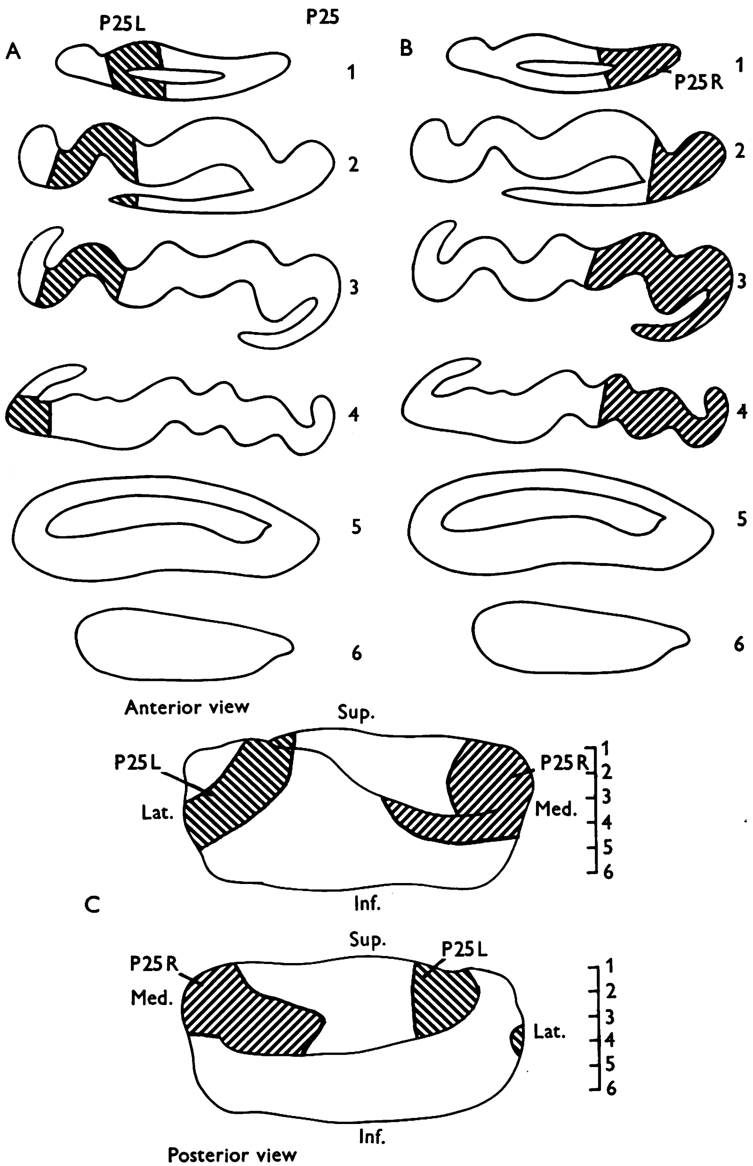


Fig. 12. The distribution of the degeneration in the isthmo-optic nucleus resulting from the two lesions in Expt. P25.

of the tectum, but rather less than a third of its extent overlaps into the antero-inferior quadrant. Except for that part which lies on the inferior surface of the tectum, in which there is considerable involvement of the deep white matter, the damage is essentially limited to the stratum opticum and the stratum griseum et fibrosum superficiale (Fig. 11). The lesion on the left side is in the form of an obliquely placed strip along its postero-superior aspect, involving only a narrow band in the dorsal two-thirds of its posterior half. Over the greater part of its dorso-ventral extent there is some involvement of the stratum album centrale as well as the more superficial layers, but at no point does it reach the ventricle (Fig. 11). In the isthmo-optic nucleus on the right side the area of terminal degeneration is confined to the upper two-thirds of the medial half of the body of the nucleus together with the junctional region between the body and the antero-medial limb. The greater part of the limb, however, is free of degeneration (Fig. 12B, C). The degeneration on the left side covers the same dorso-ventral extent of the nucleus, but it is confined to the lateral third of the nucleus and occupies an appreciably smaller extent of its cross-sectional area. Over the lower part of its extent the degeneration fills approximately the lateral quarter of the body of the nucleus and its junction with the postero-lateral limb, but without actually extending into the latter. In its upper half the affected area is rather more medially placed leaving the extreme lateral part of the body unaffected, but there is a small zone of degeneration in the extreme tip of the antero-medial limb (Fig. 12A, C). This apparent discontinuity in the areas showing degeneration over the dorsal part of the nucleus is readily explained when the degeneration is plotted on the three-dimensional reconstruction of the nucleus (see later). A comparison of the two sides of this brain makes it clear that superior and inferior lesions in the posterior half of the tectum respectively cause degeneration in the lateral and medial halves of the nucleus, which indicates that the dorso-ventral dimension of the tectum is represented along the medio-lateral axis of the nucleus. As the degeneration on both sides is confined to the dorsal part of the nucleus the conclusion drawn from the first experiment is substantiated.

An additional point which emerges from a comparison of these two brains is that the two lesions involving the postero-inferior quadrant (P15L, P25R) are almost identical, the only difference being that the lesion on the right side of P25 extends farther downwards into the antero-inferior quadrant. As can be seen in Figs. 10B and 11B the distribution of the degeneration in the isthmo-optic nucleus is similar in the two experiments, but extends rather more medially (into the antero-medial limb) in P25. Taken together, the four lesions in these two experiments have involved all but the antero-superior quadrant of the tectum. Two representative experiments with damage of this part of the tectum will now be described.

In Expts. P11R and P24L there are strip-like lesions in this region, and although the two lesions are similar in their general form that in P24L (Fig. 14) is smaller but appreciably deeper (and extends into the underlying white matter) than that in P11R (Fig. 13). The degeneration of the isthmo-optic nucleus in P11R is restricted to the ventral third of the nucleus, and is found only in the postero-medial and the postero-lateral limbs, both of which are almost completely filled in the most ventral sections. As a result of the deeper lesion in P24L the degeneration in the isthmo-optic nucleus of this brain occupies the whole of the postero-medial and the tip of the postero-lateral limb over a greater dorso-ventral extent, covering the ventral half of the nucleus: on the most ventral sections the degeneration extends anteriorly to involve the middle of the body (Fig. 14). Again, these experiments confirm the basic organization of the tectum upon the isthmo-optic nucleus, the antero-superior quadrant being related to the ventral part of the nucleus.

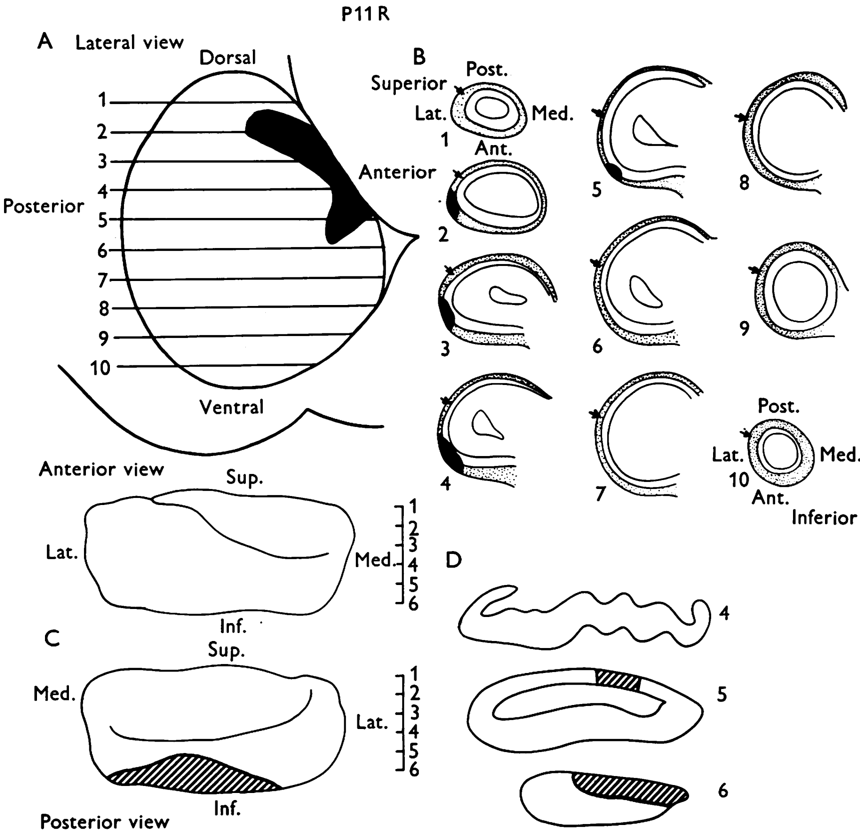


Fig. 13. The extent of the lesion in the tectum and the resulting degeneration in the isthmo-optic nucleus in Expt. P11R. Only three sections through the ventral part of the nucleus are shown in D.

The lesions which have been described all lie essentially within one or other quadrant of the tectum, leaving its central part unaffected. In Expt. P124L there is a large superficial area of damage in this region extending across the surface from the part involved in P11R and P24L on the one hand and P25R and P15L on the other. It involves an irregular area running obliquely downwards and backwards, crossing the centre of the tectum (Fig. 15). The terminal degeneration in the isthmo-optic nucleus is confined to the junctional region between its body and postero-lateral limb in the ventral quarter of the nucleus. Just as the four lesions of the first two experiments established the antero-posterior and dorso-ventral organization of the tecto-isthmo-optic projection, so the lesion of the last experiment, lying as it does between all the lesions described earlier, can be used to determine the representation of the oblique axes of the tectum upon the nucleus. The details of this relationship will be discussed later.

To complete the evidence for the topographical arrangement of the projection of the tectum, two experiments with lesions situated along its periphery will be described. The first of these, P48, has a strip-like lesion along the antero-medial edge of the upper half of the tectum (Fig. 16). To expose this area it was necessary

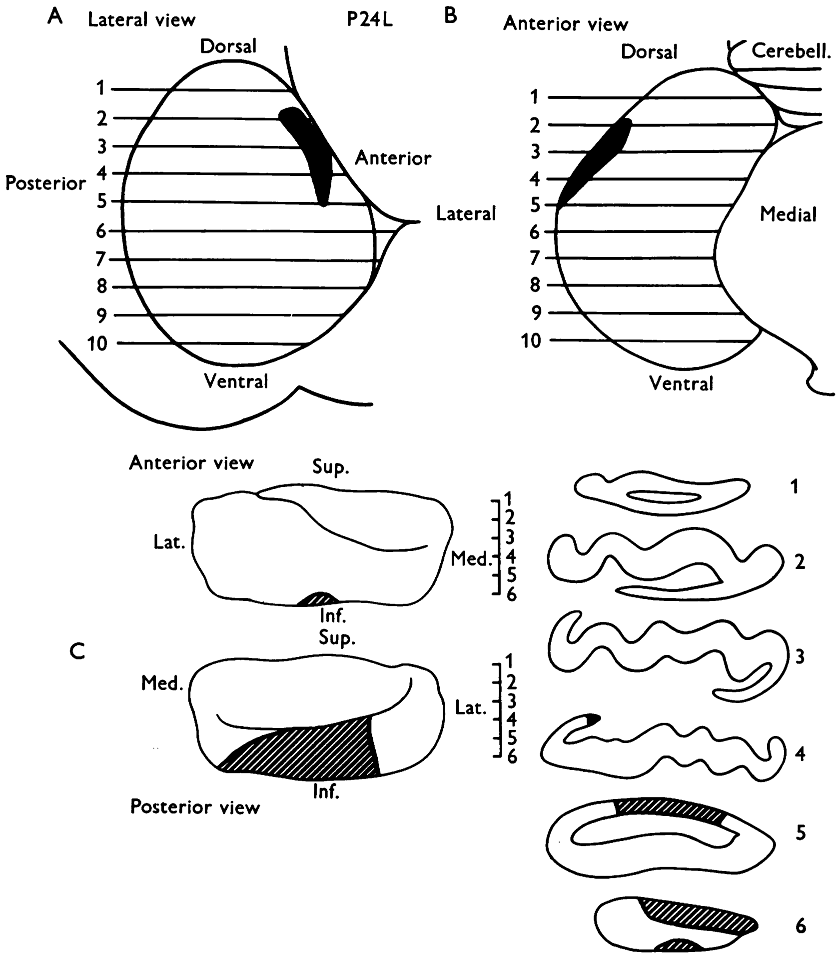


Fig. 14. The lesion and degeneration in Expt. P24L.

to remove completely the cerebral hemisphere on this side; the interpretation of the findings in this experiment has not been complicated by this concomitant removal of the hemisphere, however, as control experiments, in which only the hemisphere was removed, have not shown degeneration in the isthmo-optic nucleus. For the greater part of its extent the lesion in the tectum has extended deeply into the underlying white matter, and has interrupted the isthmo-optic tract as it passes downwards on the anterior surface of the tectum. The terminal degeneration in the isthmo-optic nucleus is found only in the postero-medial and postero-lateral limbs in approximately the lower half of the nucleus. In this experiment, in which the brain was cut by the frozen method, sections stained by the Glees (1946) technique show many degenerated end-bulbs and fragmented fibres throughout the part of the nucleus in which degenerating fibres are seen in the Nauta-stained sections. In addition to the

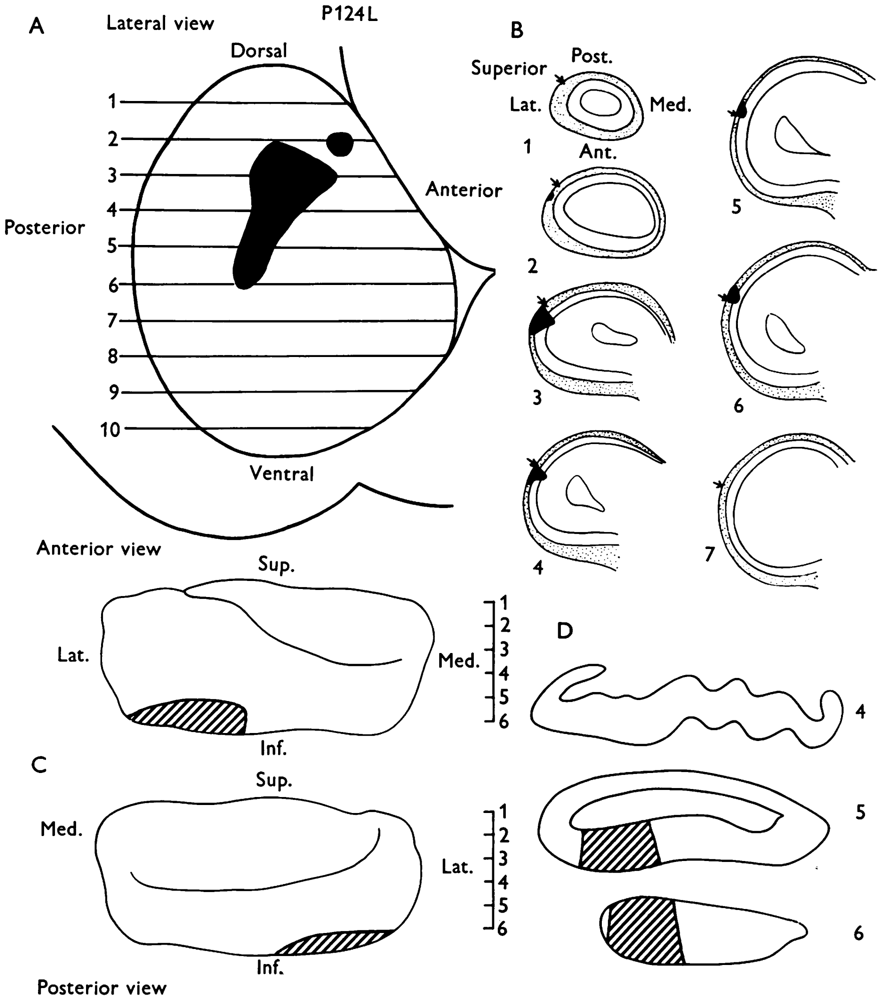


Fig. 15. The lesion and resulting degeneration in the isthmo-optic nucleus in Expt. P 124L.

terminal degeneration found actually within the nucleus the sections stained by the Nauta (1957) method show increased argyrophilia and some fibre fragmentation in the proximal part of the isthmo-optic tract. This appearance is indicative of early retrograde fibre degeneration due to interruption of the tract at the level of the lesion. Although this degeneration extends back to, and surrounds, the dorsal aspect of the nucleus it can be distinguished quite clearly from the orthograde tecto-isthmo-optic degeneration within the ventral part of the nucleus (Cowan & Powell, 1963). The second experiment with a peripheral lesion of the tectum is P54R, in which there is a small, rectangular lesion of the tectum along the postero-superior quadrant. For the greater part of its extent the damage is confined to the

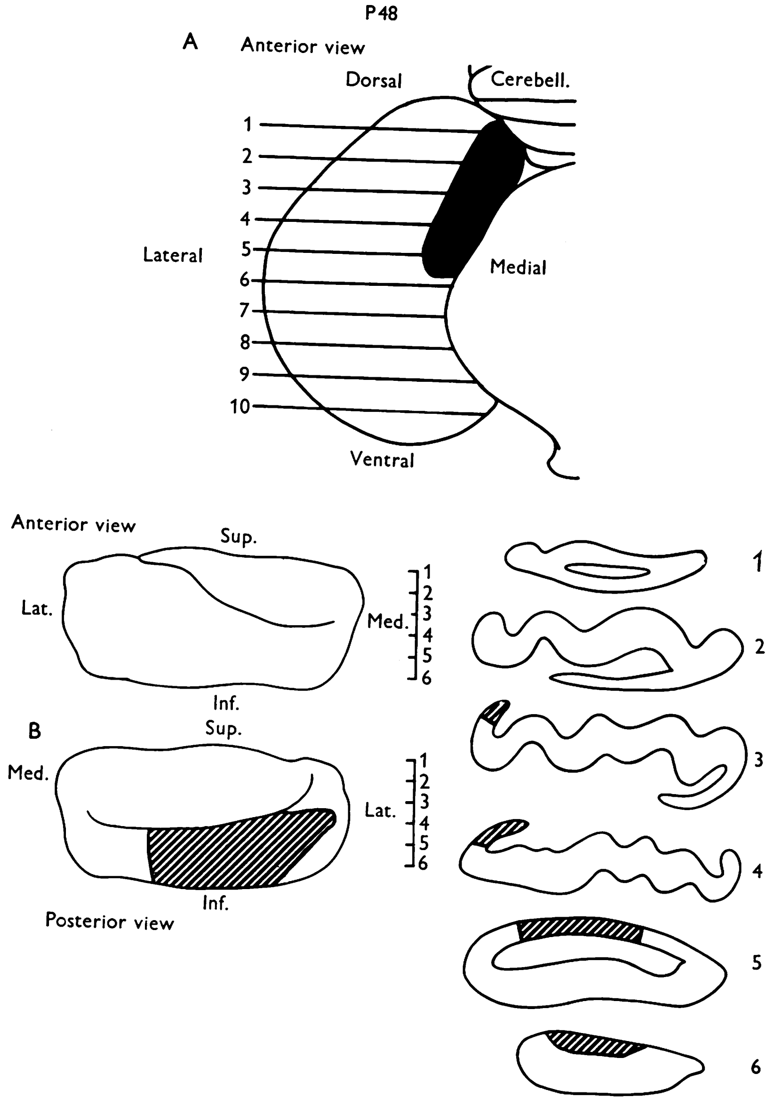


Fig. 16. The surface extent of the lesion in the tectum and the fibre degeneration in the isthmo-optic nucleus in Expt. P48.

superficial layers, but near its anterior end there is an extension into the underlying white matter. This is one of the few lesions which has been cut in the coronal plane, and this plane of cutting has given a particularly clear indication of the mode of entry of the fibres of the isthmo-tectal tract into the nucleus. The fibres approach the nucleus from its antero-ventral aspect and pass dorsally in front of the lateral part of the body, and, on more caudal sections between the body and the postero-lateral limb. Terminal degeneration can be clearly recognized, being finer and having a pericellular arrangement, only in the dorsal part of the body where it adjoins the postero-lateral limb (Fig. 17). Both the lesion and the extent of the ensuing degeneration in this experiment are smaller than in any of the other experiments

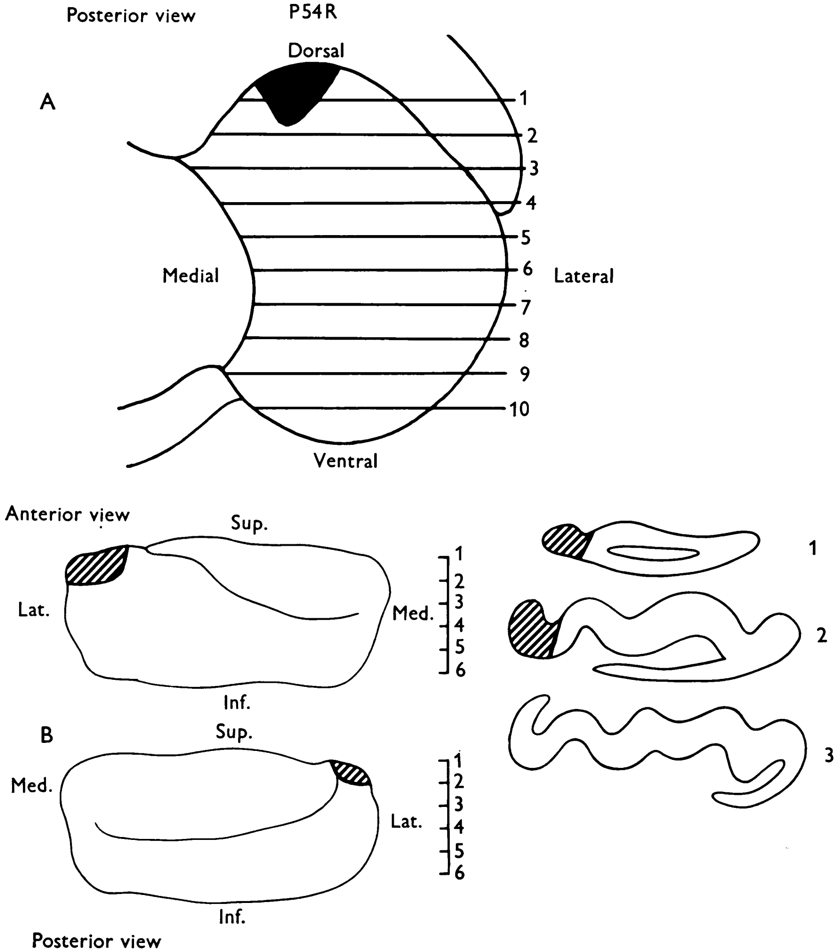


Fig. 17. The lesion and resulting degeneration in Expt. P54R.

which have been described, and to complete the evidence showing how precise the tecto-isthmo-optic projection is one further brain with two very small, closely related lesions will be described.

In the antero-superior quadrant of the tectum of the two sides of Expt. P123 very small and superficial lesions were made (Fig. 18); at no point does the damage penetrate more deeply than the stratum griseum et fibrosum superficiale on either side. In the isthmo-optic nucleus of both sides there is a small, but unequivocal amount of terminal degeneration in their ventral parts close to the junction between the body and the postero-lateral limb. The extent of the degeneration in the nucleus of the left side (resulting from the larger lesion) is unexpectedly rather less than on the right, but no satisfactory explanation can be given to account for this finding.

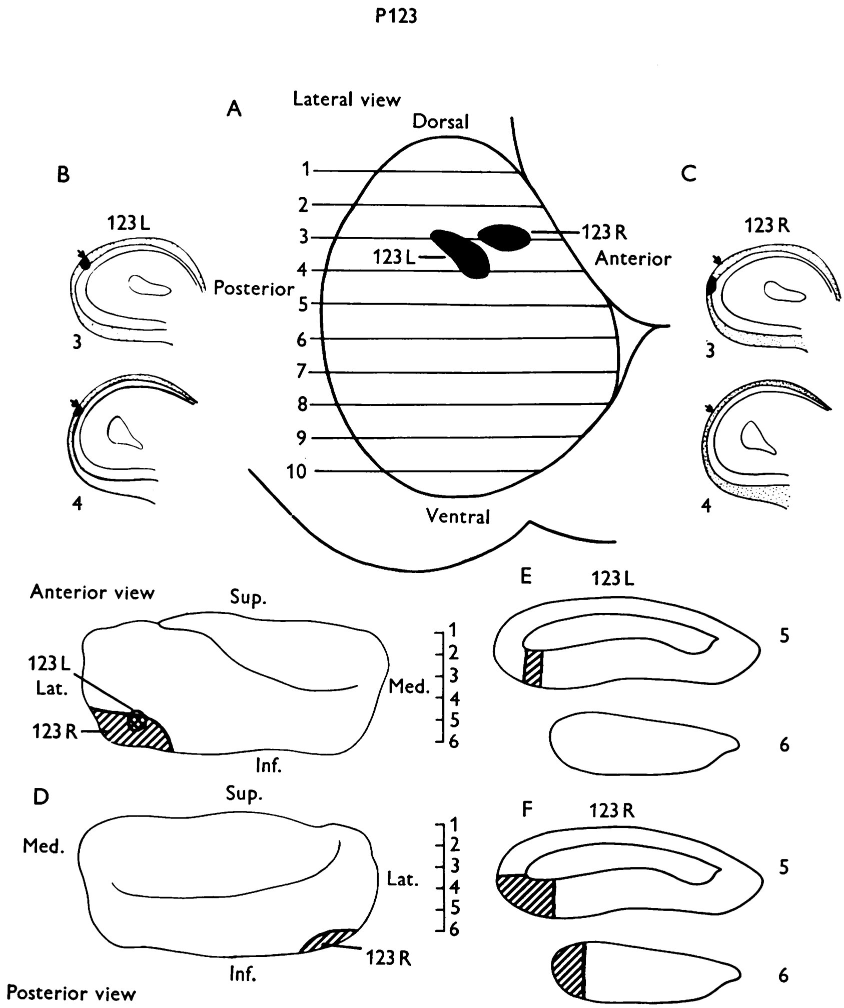


Fig. 18. The position of the two lesions in Expt. P123, together with the ensuing degeneration in the isthmo-optic nucleus.

DISCUSSION

The primary purpose of this study was to determine the projection of the retina upon the tectal surface in terms of its quadrantic organization in such a way that the results could be applied directly to the subsequent studies of the relationship between the tectum and the nucleus of origin of the centrifugal fibres to the retina. Because of the difficulties inherent in the methods used, and in particular because central retinal lesions inevitably interrupt fibres from more peripheral areas, no attempt has been made to determine the details of the representation of the fovea or the precise disposition on the tectal surface of the vertical and horizontal axes of the retina. Figs. 19C, E, which summarize the findings in the first group of experiments, show that with the brains aligned in the position used in this and the subsequent study the superior half of the retina is represented

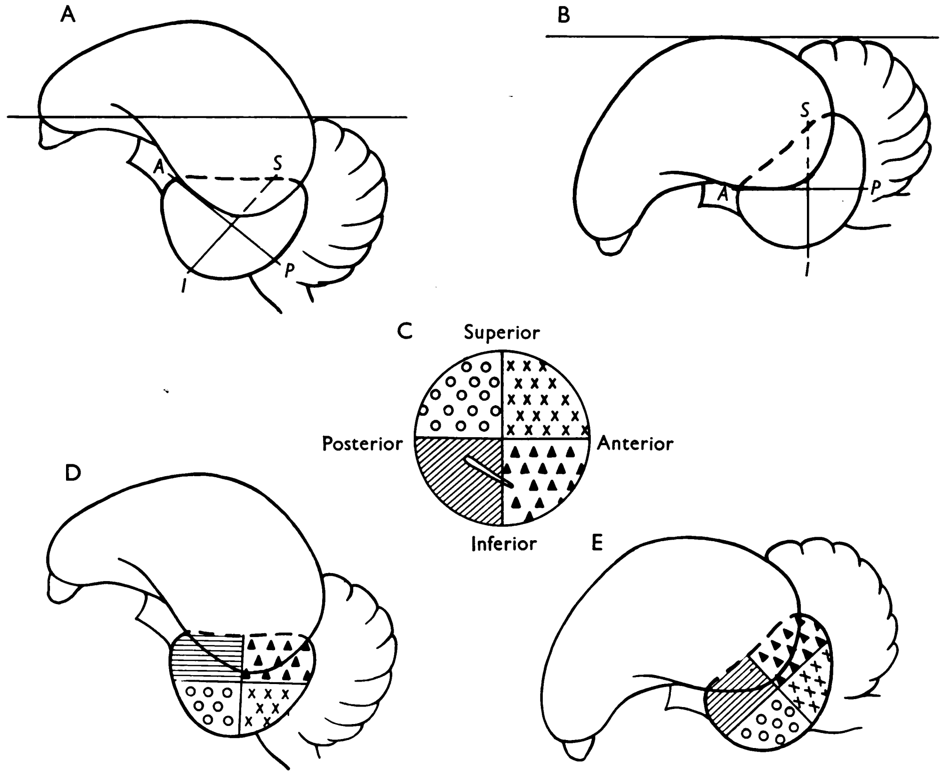


Fig. 19. A and B show the position of the brain in the study of Hamdi & Whitteridge (1954) and the standard position used throughout the present study respectively. The lines *A–P* and *S–I* correspond to what we have termed the horizontal and vertical axes of the tectum. C the quadrants of the *right* retina, and their representation upon the left optic tectum in the position used by Hamdi & Whitteridge (1954) (D), and in that of the present study (E).

postero-ventrally in the tectum and the anterior quadrants in the posterior and dorsal parts. These conclusions appear to be at variance with the representation of the visual fields upon the superior and inferior surfaces of the tectum described by Hamdi & Whitteridge (1954). According to these authors, the superior retina is represented upon the inferior surface of the tectum and the inferior retina on the superior tectal surface, with the vertical axis of the retina running transversely around the middle of the tectum in the coronal plane.

Hamdi & Whitteridge (1954) maintained the head in an approximately horizontal position, whereas in the present study it was considered necessary to section all the brains in a standard position with the postero-dorsal surfaces of the cerebral and cerebellar hemispheres in the same horizontal plane. As has been mentioned, with the brains in this position, the forward tilt of the tectum is such that what we have termed 'the horizontal and vertical axes of the tectum' lie obliquely across the tectal surface with the brain in the position used by Hamdi & Whitteridge (1954). In Fig. 19 the retinal representation upon the tectum is illustrated with the brain in the positions used in the two studies, and it is apparent that if allowance is made for this difference in the position of the brain the two maps of the retinal projection upon the tectum, are in fact identical.

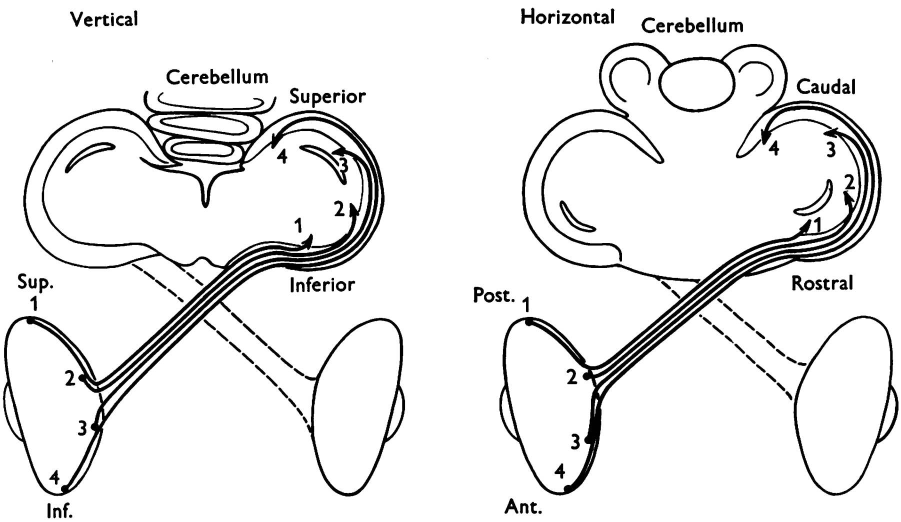


Fig. 20. The orderly arrangement of the fibres from the retina to the tectum of both the vertical (coronal) and horizontal dimensions.

The striking simplicity of the arrangement of the afferent fibres from the contralateral eye is in marked contrast to the complex intrinsic structure of the tectum. As the upper half of the retina projects to the ventral half of the contralateral tectum, and the anterior half of the retina is related to the posterior part of the contralateral tectum the optic nerve fibres must be distributed in an orderly manner over the surface of the tectum in the manner shown in Fig. 20. Whatever the morphogenetic factors responsible for this may be, and the most plausible hypothesis at present is that of Gaze (1960) who has suggested that the critical factor is the time sequence of events during the ingrowth of the optic nerve fibres, the net result of this retinotopic organization is that the retinal image is inverted both from side to side and from above downwards. Young (1962) has discussed the significance of this type of organization, and has put forward the interesting suggestion that inversion of the image in the vertical dimension is related to gravity while side to side inversion provides for continuity in a panoramic field (Cajal, 1911). The anatomical features of the retino-tectal relationship in the avian brain could be considered as evidence in support of this view, especially as gravitational factors and panoramic vision play such an important part in the life of birds. An essentially similar retino-tectal projection has been found in other submammalian vertebrates (Buser & Dussardier, 1953; Gaze, 1958; Maturana, Lettvin, McCulloch & Pitts, 1960) and in mammals (Bodian, 1937; Lashley, 1934; Apter, 1945; Hamdi & Whitteridge, 1953), but in none of these animals does the degree of development of the tectum approach that found in birds.

The results of the experiments described in the second part of this study have confirmed and extended the earlier findings (Cowan & Powell, 1963) that the isthmo-tectal tract is an important source of afferents to the cells of origin of the centrifugal fibres to the retina, and they also show that within this projection of the tectum upon the isthmo-optic nucleus there is a definite topical organization. It would appear that all areas of the surface of the tectum contribute to this projection, and conversely that the whole of the isthmo-optic nucleus is in receipt of fibres from the tectum. Having determined the pattern of representation of the retina upon the surfaces of the tectum when the brain is aligned in the most suitable plane for studying the connexions of the isthmo-optic nucleus it is now possible to discuss the findings on the organization of the projection of the tectum upon this nucleus in terms of the retinal quadrants.

Before doing so it might be helpful to comment, first, upon the apparently complex structure of the nucleus, and, secondly, to analyse the topographical arrangment of the projection of the tectum upon it. No clear concept of the nucleus can be obtained from the examination of individual sections in any plane, and for this reason the three-dimensional reconstruction of the nucleus has been invaluable in showing that it is, in fact, a highly folded lamina of cells. When unfolded, this sheet is found to be approximately oval or circular in shape, and the manner of the folding is consistent in different brains. The general morphology of the isthmo-optic nucleus is very reminiscent of the inferior olive of mammals, and, as has been shown by Brodal (1954), this nucleus has a similar highly organized arrangement of its afferent and efferent connexions. Because the isthmo-optic nucleus is such a sheet of cells it is clear that within those parts of the visual pathway which are relevant to this study, the essentially two-dimensional retina is represented upon the two-dimensional tectal surface and this in turn projects upon a basically two-dimensional nucleus. The first experiments which were described readily showed that each topographical quadrant of the tectum projects upon a different part of the nucleus, the anterior quadrants being related to its ventral half while the superior half of the tectum sends its efferent fibres to the lateral part of the nucleus. Careful comparison of all the experiments has shown that the vertical axis through the tectum (with the brain in the standard position used throughout this study) may be represented in the nucleus by a line passing from its infero-lateral to its supero-medial corner. When plotted on the standard reconstruction of the nucleus as shown in Fig. 21 C, this line can be seen to commence near the infero-lateral angle of the posterior limb, and to proceed around the inferior border of the nucleus, obliquely across the body and over the superior border into the anterior limb. The horizontal axis through the centre of the tectum would similarly be represented by an oblique line passing from the infero-medial to the supero-lateral corner of the nucleus. The point of intersection of these two lines corresponds approximately to the 'centre' of the nucleus, but from the anterior aspect appears to be nearer its ventral border on account of the size of the posterior limbs of the nucleus.

Reference to the findings in the first part of this study makes it possible to express the organization of this projection of the tectum upon the nucleus in terms of the representation of the retinal quadrants. Figure 21 illustrates the sequence of this analysis. With the brain aligned in the standard plane the superior retinal quadrants are represented posteriorly and ventrally in the tectum and the anterior quadrants posteriorly and dorsally. The horizontal axis through the tectum thus passes backwards through the projection field of the postero-inferior quadrant into that of the antero-superior retinal quadrant (Fig. 21B). As we have seen, a line

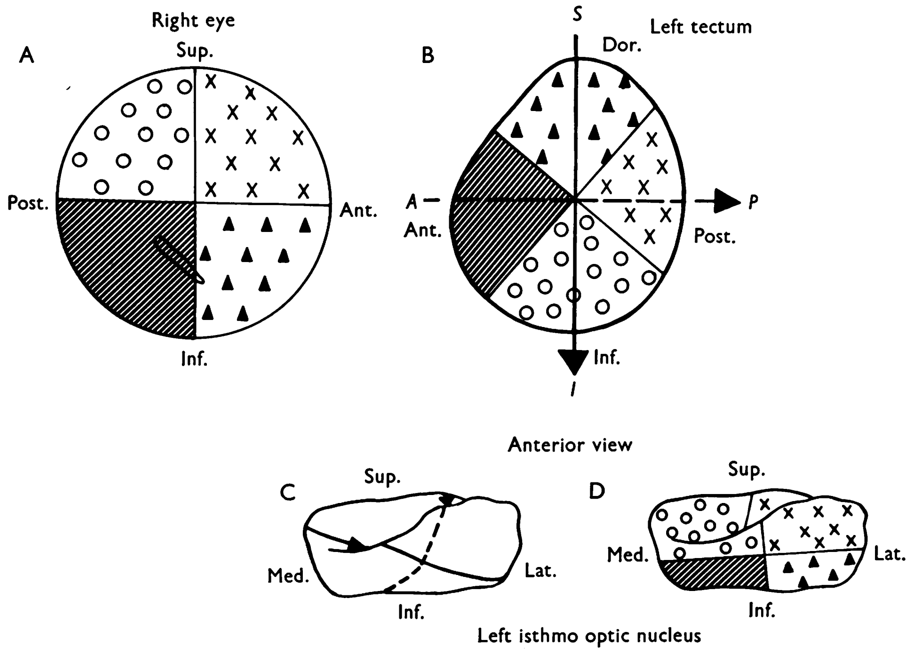


Fig. 21. The sequence in the analysis of the representation of the retina upon the isthmo-optic nucleus. B shows the projection of the retinal quadrants upon the tectum with the brain in the standard position used in the present study, together with what we have termed the vertical *S–I* and horizontal *A–P* axes. C shows the representation of these axes in the isthmo-optic nucleus, and D the representation of the retinal quadrants in the nucleus.

corresponding to this axis passes obliquely through the isthmo-optic nucleus from infero-medial to supero-lateral, and it therefore follows that the postero-inferior and the antero-superior quadrants of the retina must be related to the infero-medial and supero-lateral parts of the nucleus respectively (Fig. 21D).

The last group of experiments with small lesions on the surface of the tectum have demonstrated the precise nature of this projection, and in Expt. P123, for example, removal of only about 1% of the surface extent of the tectum has resulted in readily detectable degeneration in the nucleus. An additional point which emerges from this group of experiments is that the fibres of the isthmo-tectal tract appear to have their origin in the stratum griseum et fibrosum superficiale, because in the last two experiments the damage did not extend deep to this layer. This layer is not homogeneous and has been subdivided into ten laminae (Jungherr, 1945), to the superficial six of which optic nerve terminals have been traced (Cowan *et al.* 1961), and from which short-latency responses to visual stimuli have been recorded (Hamdi & Whitteridge, 1954). The other connexions of this layer and of the stratum griseum et fibrosum centrale, the large cells of which are generally regarded as the major source of efferents from the tectum, will not be dealt with here although there is abundant evidence in the present material for such connexions. Similarly, no systematic attempt has been made to investigate other sources of afferent fibres to the isthmo-optic nucleus, but it can be stated with confidence that it receives no fibres from the cerebral hemispheres. It seems likely that there are other important afferents to the nucleus, however, as virtually complete removal of the tectum does not result in transneuronal cell degeneration in the nucleus even after survival periods of several months.

SUMMARY

The projection of the retina upon the tectum and of the tectum upon the isthmo-optic nucleus has been studied in the pigeon using the Nauta method. Attention has only been paid to the quadrantic organization within the retinal organization, and it has been shown that with the head in an approximately horizontal position the superior retinal quadrants are represented inferiorly in the tectum and the anterior quadrants posteriorly.

With localized lesions of the tectum degeneration can be followed through the isthmo-tectal tract to restricted parts of the isthmo-optic nucleus, and it has been possible to demonstrate a well-defined topical organization within this projection. Reconstruction of the normal isthmo-optic nucleus has shown it to be a highly convoluted lamina of cells, the upper and lower margins of which are folded anteriorly and posteriorly respectively. With the brain aligned in a standard plane, the anterior part of the tectum is connected with the ventral part of the nucleus and the superior half of the tectum to its lateral part.

As the retina is accurately represented on the tectal surface it follows that each retinal quadrant is represented in a different part of the isthmo-optic nucleus. In these terms, the anterior retinal quadrants are related to the lateral half of the nucleus while the superior quadrants are represented superiorly in the nucleus.

This work was supported by a grant from the Medical Research Council.

REFERENCES

APTER, J. T. (1945). Projection of the retina on superior colliculus of cats. *J. Neurophysiol.* 8, 123–136.

BODIAN, D. (1937). An experimental study of the optic tracts and retinal projection of the Virginia oppossum. *J. comp. Neurol.* 66, 133–144.

BRODAL, A. (1954). Afferent cerebellar connections. In *Aspects of Cerebellar Anatomy*. Ed. J. Jansen and A. Brodal. Oslo: Forlagt Av Johan Grundt Tanum.

BUSER, P. & DUSSARDIER, M. (1953). Organisation des projections de la rétine sur le lobe optique, étudiée chez quelques Téléostéens. *J. Physiol., Paris*, 45, 57–60.

CAJAL, S. RAMON Y. (1911). *Histologie du système nerveux de l'homme et des vertébrés.* 2. Paris: Maloine.

Cowan, W. M., Adamson, L. & Powell, T. P. S. (1961). An experimental study of the avian visual system. *J. Anat.* **95**, 545–563.

Cowan, W. M. & Powell, T. P. S. (1963). Centrifugal fibres in the avian visual system. *Proc. R. Soc.* B, **158**, 232–252.

Gaze, R. M. (1958). The representation of the retina on the optic lobe of the frog. *Quart. J. exp. Physiol.* **43**, 209–214.

Gaze, R. M. (1960). Regeneration of the optic nerve in amphibia. *Int. Rev. Neurobiol.* **2**, 1–40.

Glees, P. (1946). Terminal degeneration within the central nervous system as studied by a new method. *J. Neuropath. exp. Neurol.* **5**, 54–59.

Hamdi, F. A. & Whitteridge, D. (1953). The representation of the retina on the optic lobe of the pigeon and the superior colliculus of the rabbit and goat. *J. Physiol., Lond.*, **121**, 44*P*.

Hamdi, F. A. & Whitteridge, D. (1954). The representation of the retina on the optic tectum of the pigeon. *Q. Jl exp. Physiol.* **39**, 111–119.

Jungherr, E. (1945). Certain nuclear groups of the avian mesencephalon. *J. comp. Neurol.* **82**, 55–76.

Lashley, K. S. (1934). The mechanism of vision: VII. The projection of the retina upon the primary optic centers in the rat. *J. comp. Neurol.* **59**, 341–573.

Maturana, H. R., Lettvin, J. Y., McCulloch, W. S. & Pitts, W. H. (1960). Anatomy and physiology of vision in the frog (*Rana pipiens*). *J. gen. Physiol.* **43**, 129–175.

McGill, J. I., Powell, T. P. S. & Cowan, W. M. (1966). The organization of the projection of the centrifugal fibres to the retina in the pigeon. *J. Anat.* **100**, 35–49.

Nauta, W. J. H. (1957). In *New Research Techniques of Neuroanatomy*. Ed. W. F. Windle. Springfield, Ill.: C. C. Thomas.

Nauta, W. J. H. & Gygax, P. A. (1951). Silver impregnation of degenerating axon terminals in the central nervous system: 1. Technique, 2. Chemical notes. *Stain Technol.* **26**, 5–11.

Young, J. Z. (1962). Why do we have two brains? In *Interhemispheric Relations and Cerebral Dominance*. Ed. V. B. Mountcastle. Baltimore: Johns Hopkins Press.