A STUDY OF THE SUBCORTICAL CONNEXIONS OF THE OPTIC TRACT SYSTEM OF THE FERRET, WITH SPECIAL REFERENCE TO GONADAL ACTIVATION BY RETINAL STIMULATION

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INTRODUCTION

The occurrence of seasonal variations in both plants and animals is an observation as old as man, but not until comparatively modern times has any attempt been made to inquire into the precise mechanism of this rhythm. Throughout the nineteenth century it was believed that the important factor underlying this periodism was seasonal variation in temperature—a view derivative from Linnaeus, who published in 1793 what appears to have been the earliest investigation of the phenomenon (Rowan, quoting F. Smith, 1933). However, in 1920, the work of Garner and Allard showed conclusively that the important factor in the growth and maturation of various species of plants was rather the relative length of day to night. Five years later Rowan (1925) demonstrated that this was also true of birds; thus finches of the northern hemisphere, which normally only breed in spring, could be brought into full breeding condition in midwinter by daily subjection to gradually increasing periods of artificial illumination, additional to the normal hours of daylight. This response could only be attributed to retinal stimulation, since it was elicited in spite of exposure to intense cold (Canadian winter). Although this effect of visual stimulation was scientifically new, natural philosophy had long been aware of it, for it was apparently made use of empirically by both Dutch and Japanese bird-fanciers (Rowan, 1938*b*).

Research has now shown that gonadal activation follows retinal stimulation in other animal species; amongst mammals, the ferret has most commonly been used to demonstrate this. A brief historical review of the experimental work with the ferret may therefore be presented. Normally the female ferret is in the anoestrous phase between (approximately) September and the end of the following March. In 1932 Bissonette observed, however, that ferrets could be brought into full oestrus during this period by subjecting them daily—after the fall of darkness—to artificial illumination for 6–6½ hr. Male ferrets treated similarly showed well-developed accessory organs and readiness to copulate, but matings were sterile. Microscopical examination of the testes proved that, though the testicular interstitial tissue was fully developed, no spermatozoa, and only few spermatids, were present. Bissonette (1935) later found that normal spermatogenesis was induced in male ferrets, and fertile matings obtained, if short progressively increasing periods of illumination were substituted for his earlier method. Hill & Parkes (1933) confirmed the sexual response of the ferret to experimentally increased retinal stimulation, and demonstrated that it was completely abolished by hypophysectomy. This latter result has been corroborated in birds by various authors; the place of the anterior pituitary as an intermediary in gonadal activation is well established.

Conversely, the effect of reducing visual stimulation was also tested experimentally. Thus Hill & Parkes (1934) kept five female ferrets in darkness for 23½ hr. daily from the end of January onwards; they reported that, in spite of this, four animals showed the beginning of vulval swelling (indicative of oestrus) well within the normal range of time. They commented that "it was noticeable, however, that the time taken for the vulva to become enlarged fully was longer than normal". In the fifth animal, the recurrence of oestrus was undoubtedly delayed, since no signs of gonadal activity were observed until 16 May. Marshall & Bowden (1934) also subjected female ferrets to "incomplete" darkness between the middle of April and the middle of July. Of seven animals, "four were beginning to come on heat before they were put into the dark room. The darkened conditions did not prevent them from coming fully on (heat)...the other three which were anoestrous at the commencement remained so throughout." Similarly, Bissonette (1936) reported that the reappearance of oestrous phenomena was markedly delayed in normal ferrets, if they were provided with light-tight hoods covering their eyes. Other experiments yielded comparable results. Marshall & Bowden described a ferret blinded in both eyes by cataract, which never came on heat at any time between December 1932 and July 1935; this finding was confirmed by Bissonette (1936). Bissonette (1936) also reported that section of the optic nerves delayed oestrus in female ferrets. Le Gros Clark *et al.* (1939) found that, after section of the optic nerves in four animals, two never showed any gonadal activity; of the remaining two ferrets, one came into full heat at the normal time, whilst the other showed delay, since only very slight vulval swelling was observable at the time of autopsy (10 May).

Thus the existence of a relationship between retinal stimulation and gonadal activation has been conclusively proved in the ferret by two methods of approach: (*a*) by augmentation, and (*b*) by either diminution or complete elimination, of retinal stimulation.

Retinal stimulation is therefore important to the animal in a manner which might perhaps be additional to, and different from, the ordinary visual perception of objects. On the assumption that gonadal activation might be a special response, it became a matter of considerable interest and importance to discover whether there is a special pathway from the retina concerned in its mediation. The work of Le Gros Clark *et al.* (1939) was undertaken to determine what the route of such a pathway might be. None of their experiments led to conclusive evidence for the solution of this problem, but the results did suggest the possibility that "the normal response of the pituitary to retinal stimulation depends on impulses passing either to the ventral nucleus of the lateral geniculate body, or to the subthalamus by way of the accessory optic tracts". To this list may be added the so-called "dorsal hypothalamic root" of Frey.

The aim of the present study has therefore been to elucidate the anatomy of those pathways which might mediate the gonadal response of the ferret to retinal stimulation, and, in general, to provide a general survey of the anatomy of the optic tract system of this animal.

MATERIAL AND METHODS

The material made use of in the present investigation consisted of eighteen series of ferrets' brains; in addition there were available for comparison four series of rats' brains, and a single series of the rabbit. These preparations consisted of serial sections of the brain stem after removal of the cerebral hemisphere, extending from the optic chiasma rostrally to the inferior colliculus caudally. The plane of section was approximately parallel to the course of the optic tracts.

The rat and rabbit brains, as well as much of the ferret material used, were provided from earlier work of Prof. Le Gros Clark, who kindly placed them at my disposal.

The nature of the lesions and the staining techniques employed may most simply be presented in tabular form (Table 1). The nature of the lesion is indicated at the top of each column; the staining technique used in each case is shown in brackets after the animal's number.

Table 1

Normal control	Section of one optic nerve	Section of both optic nerves	Section of optic tracts	Midbrain lesion	Ablation of occipital lobes
F 85 (modified Ranson)	F 59 (Marchi)	F 25 (Bodian & Nissl)	F 16 (Weigert)	F 14 (Loyez)	F 23 (Nissl)
	F 64 (Marchi)		F 39 (Bodian)	F 15 (Loyez)	F 93 (Marchi)*
	F 60 (Sereni & Young)		F 20 (Loyez)		
	F 61 (Sereni & Young)		F 22 (Loyez)		
	F 91 (modified Ranson)		F 50 (Loyez)		
	F 92 (modified Ranson)		F 71 (Loyez)		
	Rat 10 (modified Ranson)				
	Rat 13 (modified Ranson)				
	Rat 14 (modified Ranson)				
	Rat 15 (modified Ranson)				
	Rabbit 2 (Marchi)				

* In F 93 only the right occipital lobe was removed.

The operative technique used in the ferret material has been described in detail elsewhere (Le Gros Clark *et al.* 1939), and no description of it is therefore necessary.

RESULTS

The optic chiasma

Special attention has been given in the present study to the form of the chiasma of the ferret, and to the disposition of fibres within it. It has been asserted (Frey, 1937) that, in the guinea-pig (Frey has also used human embryo material), there is a discrete "dorsal hypothalamic root" of the optic tract. According to Frey, this root arises from the dorsal part of the optic chiasma, and after a short course ends in the region of the supra-optic recess of the hypothalamus, caudal and dorsal to the chiasma. Some of the fibres in this root are said to decussate in the midline before passing into the hypothalamus; others, more laterally placed, to remain uncrossed. In addition to these fibre components of the hypothalamic optic root, Frey described a fine bundle of unmyelinated fibres, arising from the posterior margin of this hypothalamic root, which passes caudally on either side of the third ventricle to the median tuber nucleus of the hypothalamus.

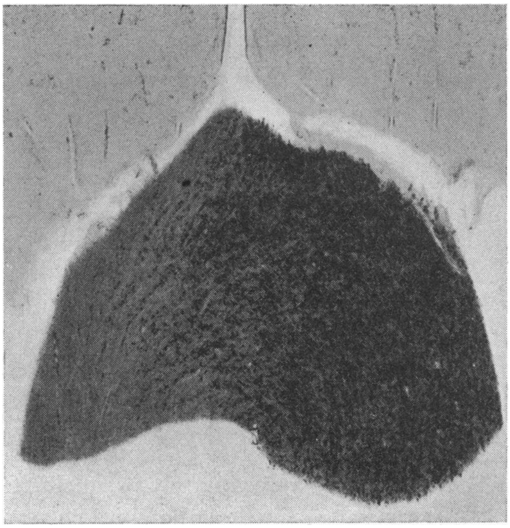
In order to test the accuracy of Frey's observations, two Marchi series of ferrets' brains, after section of the left optic nerve, have been studied.

In vertical frontal sections the chiasma of the ferret shows a characteristic dorsal hump. Oblique frontal section alters the apparent shape of the chiasma; thus, in sections taken in a plane approximately parallel with the course of the optic tracts across the cerebral peduncles, the chiasma appears crescentic or biconvex, in either case with its maximum convexity dorsally. As the obliquity of section increases, its plane more and more approaches that of a tangent to the dorsal hump of the chiasma. Thus, in some slides of the ferret's brain, where this tangential plane of section has been most nearly achieved, the chiasma appears unconnected with the optic tracts. Study of more caudal sections establishes, of course, the continuity of the optic tracts with this seeming "median" root.

Disposition of the fibres in the chiasma

In the ferret Marchi preparations, after section of one optic nerve, it is found that the osmic granulation of the crossed optic tract is much greater than that of the uncrossed tract; the relative degree of degeneration in the two sides indicates that approximately two-thirds of the fibres arising in one retina cross in the chiasma, to reach the optic centres of the contralateral side; the remaining one-third are uncrossed.

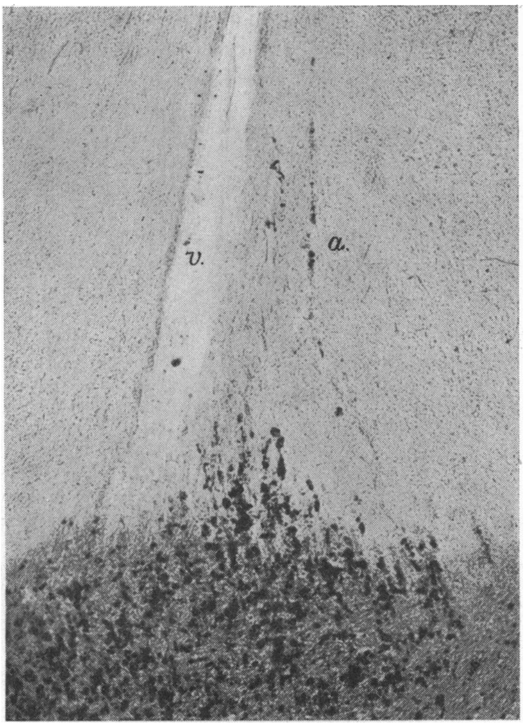
In oblique frontal sections of the chiasma, fibres showing degeneration are seen running upwards towards the convex dorsal hump (Text-fig. 1). In Text-fig. 1 it is quite clear that the greater number of these fibres, having run upwards, then loop down into the optic tract of the opposite side. Since this section is approximately parallel with the course of the optic tract, i.e. oblique to the axis of the brain stem, the U-shaped loop formed by decussating retinal fibres must have its convexity directed not only upwards but also backwards. Other fibres can be seen in Text-fig. 1 in the more dorsal part of the chiasma, which give the appearance of running directly towards the wall of the supra-optic recess. Study of serial sections shows that they do not end in this region, and that more caudally they pass down into the optic tract of the opposite side. The loop formed by these fibres, therefore, has its apex more caudally, as well as more dorsally, than that of the majority of fibres which have been described above.



Text-fig. 1. F 64. Marchi. Magnification ×28. Frontal section through chiasma, after section of the left optic nerve. Degenerated fibres may be seen crossing in the chiasma. Dorsally, many fibres appear to run directly to the wall of the supra-optic recess.

In addition, in sections through the chiasma farther caudally than that illustrated in Text-fig. 1, fibres showing the Marchi reaction can be traced from the chiasma into the hypothalamus in close relation to the wall of the third ventricle (Text-fig. 2). Careful study, in Marchi sections, of these retinal fibres establishes the fact that they are really aberrant fibres of the optic decussation which eventually rejoin the crossed optic tract. For, in Marchi series after section of the left optic nerve, in sections in which they first appear, these fibres are limited to the hypothalamus to the left of the midline (Text-fig. 2). In more caudal sections, they are seen more or less symmetrically arranged on both sides of the midline. Still farther caudally, degenerated fibres are found in the ventral hypothalamic substance only to the right of the midline.

Since in this experiment only the left optic nerve was severed, degenerated fibres showing the Marchi reaction can only have had their origin in the left retina. It is clear therefore that these aberrant fibres do not really have a hypothalamic destination, but having made this detour rejoin the crossed optic tract.

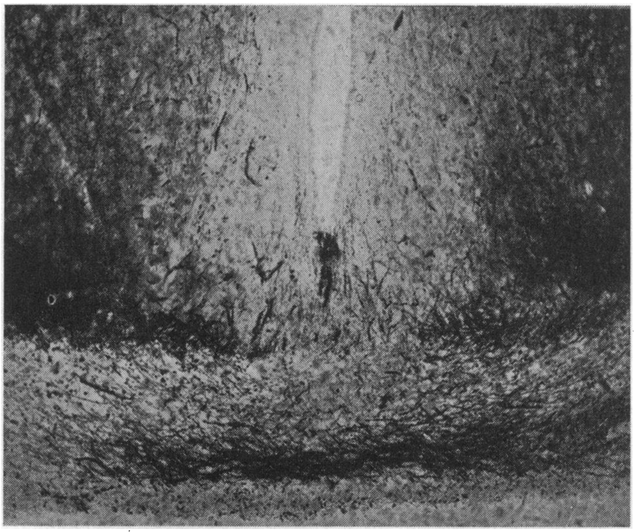


Text-fig. 2. F 64. Marchi. Magnification ×111. Frontal section through chiasma at a more caudal level than that illustrated in Text-fig. 1. To the right of the third ventricle (*v.*), degenerated fibres leave the chiasma and pass dorsally into the substance of the hypothalamus. After an intrahypothalamic excursion these fibres rejoin the crossed optic tract. Pseudo-Marchi reaction along blood vessels is shown at *a*.

In a Weigert-Pal preparation of the ferret brain after section of both optic nerves, numerous short, undegenerated, myelinated fibres are seen running vertically in the ventral hypothalamus just dorsal to the posterior half of the chiasma (Text-fig. 3). These fibres, which run for short distances, are presumably short internuclear hypothalamic neurons; at all events, they can have no connexion with the retina. In normal material they might easily be mistaken for myelinated fibres of retinal origin which leave the chiasma; for this reason, they should be noted as a possible source of error in the interpretation of normal material.

Discussion. It is now possible to attempt some correlation of our findings with those of Frey.

It has been made clear that the chiasma of the ferret is characterized by a dorsal hump, and that more or less tangential section of this hump alters the apparent shape of the chiasma, so that it may even appear as an isolated median root. In the brain of the guinea-pig the dorsal hump of the chiasma is even larger than that of the ferret. It is obvious that the discrete median "dorsale hypothalamische Wurzel" of Frey (who used the guinea-pig) must be an illusion, produced by tangential section of the dorsal chiasmatic hump.



Text-fig. 3. F 16. Weigert-Pal. Magnification ×70. Frontal section through caudal part of chiasma in a ferret after section of both optic nerves; all retinal fibres have disappeared. Numerous short myelinated fibres are seen dorsal to the chiasma in the hypothalamic substance. In normal material these fibres might be mistaken for optic components. The commissure of v. Gudden is seen decussating in the ventral part of the degenerated chiasma.

This thesis is supported by the fact that the legends under the illustrations in Frey's paper, in which the "dorsal hypothalamic root" is shown, give the plane of sections as "horizontal". Such sections would undoubtedly be tangential to the dorsum of the chiasma.

The existence of a "hypothalamic optic root" as a discrete anatomical entity may therefore be dismissed. Frey described in his hypothalamic optic root myelinated fibres of retinal origin, which end in relation with nuclear masses of cells in the borders of the supra-optic recess, and with cells of the ependymal wall of the recess. These fibres are, according to Frey, partly crossed and partly uncrossed. In the ferret, it has not been possible to confirm this statement. An explanation of this observation of Frey may be provided by our findings in the ferret. It has been noted that those fibres seen in Text-fig. 1

in the dorsal part of the chiasma, which seem to run to the wall of the supra-optic recess, are found, more caudally, to pass down into the optic tract of the opposite side. It seems probable that Frey's claims for crossed and uncrossed fibres, which end in relation to cells in the neighbourhood of the wall of the supra-optic recess, are based upon a false conception of the course of fibres similar to those which we have described in the ferret. Frey also states that from the posterior border of his "dorsal hypothalamic root", fibres pass caudalwards as fine bundles on either side of the third ventricle towards the median tuber nuclei. These fibres are particularly well illustrated in Figs. 37 and 38 of his paper. It is possible that these fibres are homologous with the retinal fibres in the ferret which, in decussating, pursue an aberrant intra-hypothalamic course. Against this view, however, are two facts: first, these fibres are unmyelinated, and secondly, the plane of the section is horizontal and the fibres appear to run, without any inclination dorsalwards, directly caudally for some distance—so far, in fact, that they could not possibly rejoin the optic chiasma. On the other hand, it is extremely probable that these fibres do not belong to the optic system at all; possibly they are analogous with those myelinated fibres seen in the ferret, dorsal to the chiasma, after section of both optic nerves, when of course all fibres with retinal connexions have degenerated.

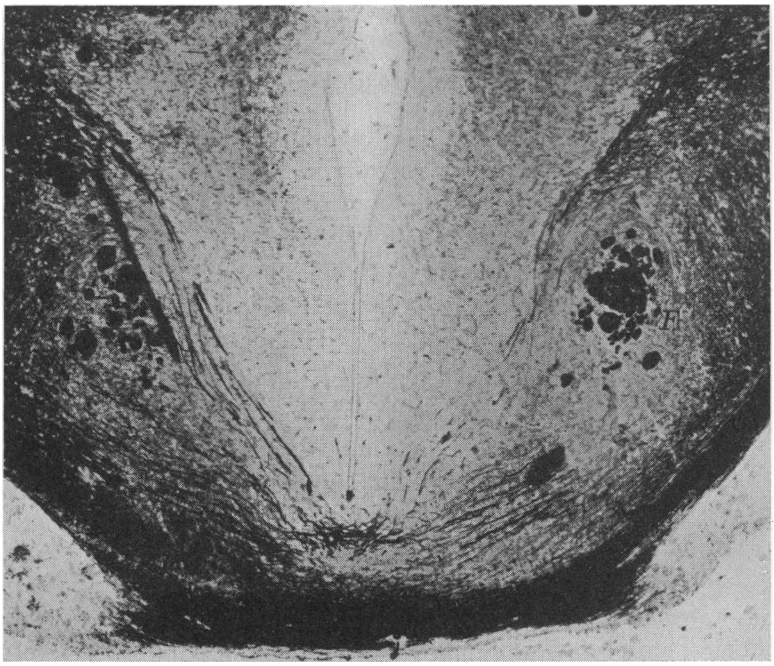
The supra-optic commissure systems

Three commissural systems are included under this head; they are the commissures of Ganser, Meynert and van Gudden, respectively. Their importance lies in the very intimate relationship they bear to the chiasma, and also to the anterior accessory optic tract of Bochenek.

These systems have been studied in the ferret brain, using material which had been stained by the Weigert-Pal method after section of both optic nerves. Several Loyez series, after bilateral section of the optic tracts, were also studied; but, since the results were substantially the same as in the Weigert material, detailed reference will be made only to the latter series.

The commissure of Ganser (Text-fig. 4). This commissure lies below the floor of the third ventricle and above the optic chiasma. Fibres belonging to the system show clearly in Weigert sections as thick myelinated fibres which do not run in compact bundles. From their decussation below the floor of the third ventricle they can be traced laterally and dorsally; chiefly they pass medial to the columna fornicis to reach the region of the subthalamus. Beyond this point they cannot be followed. Some fibres of this commissure, however, take a different course, running inferior to the columna fornicis to enter the medial forebrain bundle. There are indications that they pass through the medial forebrain bundle to join the system of fibres traversing the lateral surface of the cerebral peduncle.

The exact connexions of Ganser's commissure in our ferret material cannot be clearly defined; it probably constitutes a link between the subthalamic regions of opposite sides. This is in agreement with the suggested role of this commissure in the opossum (Tsai, 1925). It may be mentioned that Gurdjian (1927) traced fibres of Ganser's commissure in the rat into the medial forebrain bundle, and, through it, into the subthalamic area. It was not possible, in the ferret brains available, to verify this. Gurdjian believed the function of this commissure to be in connecting the subthalami of opposite sides. In addition, he noted, in Cox-Golgi preparations of the rat brain, that a scattered group of cells lying in the ventral hypothalamus, through which fibres of Ganser's commissure pass, contribute axons to the commissure. In the rat at least, this system may therefore play some part in connecting the hypothalamus with the subthalamus.



Text-fig. 4. F 16. Weigert-Pal. Magnification ×30. Frontal section through the brain stem just caudal to the chiasma. The thick myelinated fibres of Ganser's commissure are clearly shown, passing dorso-medially to the columna fornicis (*F*), after decussating in the floor of the third ventricle. The commissure of Meynert is seen more ventrally. The degenerated optic tracts lie ventro-laterally on either side of the brain stem.

The commissure of Meynert (Text-fig. 4). Meynert's commissure lies slightly caudal and dorsal to the optic chiasma, and ventral to the commissure of Ganser. It consists of finer myelinated fibres than the latter; the fibres composing this system in the ferret are very numerous and closely packed. From its decussation it may be traced laterally and dorsally, lying to the medial side of the optic tract. It penetrates the medial forebrain bundle, in which many of its fibres appear to bend dorsally and medially to come into relation with the region of the subthalamic nucleus. Other fibres, however, continue over the ventral surface of the cerebral peduncle, medial to the optic tract. At least some of these fibres appear to pass through the septa of the cerebral peduncle to reach the zona incerta. In addition to the fibres of this commissure which pass to the subthalamus, Gurdjian traced (in the rat brain) fibres which join with the cortico-tectal fibres to run to the tectum, and other fibres which are intimately connected with the ventral nucleus of the lateral geniculate body. These findings may apply also to the ferret; in the Weigert series after section of both optic nerves, many normal fibres running in the so-called "optic tract" can be seen, but they clearly have no retinal connexions at all. It is difficult to assign these fibres to one commissural system rather than another; they must belong to the commissures of Meynert and Gudden, but it is impossible to make out their exact connexions or destinations.

Tsai has stressed the close relation of the anterior accessory optic tract and the commissure of Meynert. Observations on Marchi ferret preparations after section of one optic nerve, demonstrate that fibres of retinal origin showing the Marchi reaction are seen in the position occupied by the commissure of Meynert (as identified in Weigert and Loyez series of the ferret's brain). Whether these degenerated fibres are, in fact, the fascicles of the anterior accessory optic tract or not will be discussed below. In any case, the classical description of the anterior accessory optic tract shows that it must be very closely related topographically to the commissure of Meynert.

The commissure of Gudden (Text-fig. 3). In a Weigert series after section of both optic nerves, the fibres of the commissure of Gudden may be seen decussating in the ventral and posterior part of the chiasma. Posteriorly, it is impossible to distinguish the commissure of Gudden from the anterior portion of Meynert's commissure. From its decussation, the fibres of Gudden's commissure run dorso-laterally in the posterior part of the optic tract, apparently directly to its lateral side. It has been mentioned above that, even after bilateral section of the optic nerves resulting in degeneration of the optic tracts proper, so many undegenerated fibres remain that the picture presented is confusing. The connexions of Gudden's commissure in the ferret cannot be distinguished in the material available. Gudden's commissure is generally believed to connect the medial geniculate bodies of opposite sides, and perhaps also the inferior colliculi.

The anterior accessory optic tract of Bochenek

This small fascicle is generally described as arising from the optic tract just distal to the chiasma; it then runs dorso-laterally on the medial side of the optic tract in close relation with the commissure of Meynert. As it crosses the lateral surface of the cerebral peduncle, it turns dorso-medially and penetrates the peduncle to reach the corpus Luysii (subthalamic nucleus). A number of fibres of this tract may also pass over the dorsal surface of the peduncle to reach the corpus Luysii. This tract was first stated to be derived from the main optic tract by Stilling in 1878. Its existence as an optic pathway was not, however, generally accepted till the work of Bochenek (1908) thirty years later. Bochenek made use of the Marchi technique, after removal of one eye, in several mammalian species. This work was confirmed by Pavlov (1900) and Loepp (1912). Both these workers used the rabbit for their experiments. Loepp gave the name "radix Luysii" to this optic component.

There is no evidence for the existence of this tract in the ferret. In two Marchi series, after section of the left optic nerve, no degeneration could be found which corresponds in its relations to the anterior accessory optic tract. Immediately distal to the chiasma a few fibres, showing the Marchi reaction, can be observed running in the ventral hypothalamus, medial to the main optic tract. They occupy a position amongst the fibres of Meynert's commissure (as identified in Weigert and Loyez series). If these degenerated fibres are followed in serial sections, they are found, rostrally, to arise from the chiasma, and caudally, to rejoin the main optic tract ventral to the cerebral peduncle. There is no degeneration which can be followed in serial sections either through the peduncle to the subthalamic nucleus or dorsally over the peduncle and thus down to the nucleus. Some slight pseudo-Marchi granulation is scattered irrelevantly through the peduncle, and also along blood vessels penetrating the latter, but this appears to be without significance.

From a review of the literature, it seems that the evidence for the existence of the anterior accessory optic tract is more or less confined to the rabbit and the rat. Thus, in the rabbit, it has been described by Pavlov (1900), Bochenek (1908) and Loepp (1912). Amongst our own material was a single Marchi series of a rabbit's brain after enucleation of the left eye. This series extends from the middle of the chiasma anteriorly, to about the middle of the superior colliculus posteriorly. Approximately three-quarters of the fibres from one retina cross in the chiasma, the remainder being uncrossed. There is a considerable amount of pseudo-Marchi reaction scattered in the internal capsule, the cerebral peduncle, the region of the subthalamus and the ventral hypothalamus. This appearance is found on both sides, though more markedly on the right (i.e. contralateral) side. The slides are therefore of little value, except for two points: (i) There is no sign of fibres penetrating the peduncle to reach the subthalamic nucleus, the whole picture being entirely unlike that figured by Loepp (1912). (ii) On the dorsum of the peduncle, many fibres bend medially, and run as if about to circle downwards on the medial aspect of the peduncle. Such a course for fibres of the anterior accessory optic tract has been described (see above). In our rabbit material, however, the fibres which at first give this impression are found, when followed caudally in serial sections, always to bend upwards again to run through the ventral nucleus of the lateral geniculate body. The sigmoid course of these fibres may have misled earlier workers. This material, however, does not provide sufficient evidence to disprove the existence of the anterior accessory tract, which has been recognized in the rabbit by many other workers.

After enucleation of one eye in the rat, Kosaka & Hiraiwa (1915; quoted by Lashley, 1934) were unable to trace the anterior accessory tract into the cerebral peduncle; they regarded it as an aberrant bundle of optic fibres, which later rejoined the main optic tract. Le Gros Clark (1931) stated that the anterior accessory optic tract was clearly demonstrable in the rat in Marchi preparations; he was able, however, to follow it only as far as the ventral surface of the peduncle; no degenerated fibres were seen penetrating the peduncle.

The findings of these authors in the rat, therefore, seem to agree closely with our observations in the ferret, i.e. that the so-called anterior accessory tract is composed of aberrant fibres, which leave the tract just behind the chiasma, run amongst the fibres of commissure of Meynert and later rejoin the main optic tract.

On the other hand, Lashley (1934) and Chang (1936) have identified this tract in Marchi preparations of the rat's brain after unilateral enucleation; they found Marchi degeneration only in the crossed accessory tract. According to Lashley, the course of the anterior accessory tract was as follows. The fibres, having left the chiasma, travel at first in the substance of the hypothalamus with the commissure of Meynert as far as the inferior margin of the peduncle. At this point the tract divides into superior and inferior branches. The superior branch rejoins the main optic tract, and a few of its fibres may be traced between the fasciculi of the peduncle, but they cannot be followed into the corpus Luysii. The inferior branch, which contains the greater number of fibres, joins the posterior accessory optic tract, and terminates with it in the nucleus opticus tegmenti. It is interesting to note that Overbosch (1927; quoted by Bodian, 1937) found in the rabbit that retinal lesions, which caused degeneration to appear in the anterior accessory tract, always caused degeneration also in the posterior accessory tract, and conversely. He suggested that the anterior accessory optic tract might be merely an aberrant part of the posterior tract. Lashley's observation in the rat seems to lend support to this view. It seems, therefore, that the existence of the anterior accessory optic tract in the rat is equivocal.

After intensive search of Marchi sections of the opossum's brain, Bodian (1937) failed to discover any degenerated fibres which might be called the anterior accessory optic tract. Bodian also studied the normal Weigert material of the opossum, which had been used by Tsai (1925); he was not convinced that the fibres labelled in Tsai's figures as the anterior accessory optic tract were, in point of fact, of retinal origin.

Barris *et al.* (1935) found no sign of the tract of Bochenek in Marchi series of the cat's brain after either unilateral or bilateral section of the optic nerves. They quote several other observers who had not been able to see this tract in the cat's brain (Probst, 1900; Kosaka & Hiraiwa, 1915; Brouwer *et al.* 1925). Barris *et al.* are of the opinion that the anterior accessory optic tract does not exist in higher mammals.

To summarize the position: the anterior accessory optic tract does not exist in the opossum, ferret or cat. It must be believed to exist in the rabbit. The existence of the tract in the rat is more questionable. It seems legitimate to suppose that findings in the rat correspond largely with our observations in the ferret. That is, the fibres seen in the rat do not agree with the classical description of the orientation of the anterior accessory tract, because they cannot be followed to the corpus Luysii through the peduncle (but cp. Chang, 1936, who claimed that fibres showing Marchi degeneration do reach this nucleus in the rat). The presumption is, therefore, that the fibres described under the heading of the anterior accessory optic tract by workers with the rat are homologous with those which we have described in the ferret as aberrant fascicles of the main optic tract.

It is also possible that considerable individual variation occurs, even in animals in which this tract has been shown conclusively to exist.

The posterior accessory optic tract

Typically the posterior accessory optic tract is described as a small bundle of fibres arising from the main optic tract just proximal to the lateral geniculate body. This accessory fascicle then passes caudally and ventrally over the cerebral peduncle to the interpeduncular space. Just anterior to the superficial origin of the oculomotor nerve it enters, and terminates in, the nucleus opticus tegmenti; this nucleus lies between the mammillary body medially and the cerebral peduncle laterally.

The tract was first recognized as part of the optic system by van Gudden (1870), who observed degeneration in the tract after removal of the opposite eye. Gudden gave the name of "tractus peduncularis transversus" to this bundle of fibres of retinal origin. The existence of this accessory optic path was confirmed by the experimental work of Pavlov (1900) and Loepp (1912) in the rabbit. These authors traced Marchi degeneration in the crossed tract after unilateral enucleation. Bochenek (1908) also found Marchi degeneration in this tract after similar procedures in a variety of mammals; he named the tract "fasciculus accessorius opticus posterior".

In the ferret brain a small and circumscribed bundle of fibres can usually be seen crossing obliquely over the lateral surface of the cerebral peduncle, occupying the topographical position of the tractus peduncularis transversus of other mammals. Attention was drawn to this by Le Gros Clark *et al.* (1939), and it was assumed that, as is the case in rodents, it represents a posterior accessory optic tract; but a further study of sixteen ferret brains makes it doubtful if this is the case, for the fascicle appears macroscopically not to rise from the main optic tract, but rather to be split off the brachium of the inferior colliculus. If this is so, it clearly cannot be a posterior accessory optic tract.

In Marchi sections of the ferret's brain, after section of one optic nerve, no fibres are seen which follow the course described as that of the posterior accessory optic tract, nor is any Marchi granulation seen either in the contralateral or the ipsilateral nucleus opticus tegmenti. This experimental evidence shows therefore that, in the ferret, the posterior accessory optic tract probably does not exist (at least so far as myelinated fibres are concerned).

Recent work with the rat, the guinea-pig, and the opossum has, however, established the presence of this tract in these animals. Thus, in Marchi preparations of the rat's brain, degeneration in the tract has been observed after removal of the opposite eye (Le Gros Clark, 1931; Lashley, 1934; Chang, 1936). Tsang (1937) has noted atrophy of the tract in rat Weigert material after unilateral and bilateral enucleation. Frey (1937) has identified this bundle in Marchi preparations of the guinea-pig after removal of one eye; this confirms the earlier observations of Wallenberg (1904) and Castaldi (1923) in the same animal. Frey has given this tract in the guinea-pig the name of "basale optische Wurzel" (basal optic root), on the presumed homology (Marburg, 1903) of the posterior accessory optic tract and its nucleus with the basal optic root and ganglion ectomammillare of reptiles and birds.

In the opossum, Tsai (1925) described the course of the posterior accessory optic tract as seen in Weigert sections of the normal brain. Bodian (1937) found Marchi degeneration following the path described by Tsai as that of the posterior accessory tract, after enucleation of the opposite eye in the opossum.

Barris *et al.* (1935) were unable to find the posterior accessory optic tract in Marchi series of cats' brains after either one or both eyes had been removed. They conclude, from a review of the literature, that the evidence for its existence seems to be limited to the rodents and lower mammals. The absence of the posterior accessory optic tract in the ferret is in agreement with this thesis. Furthermore, if the anterior accessory optic tract is merely an aberrant portion of the posterior tract (see above: Overbosch, 1927), the absence of the anterior accessory optic tract in the ferret would not be surprising.

The lateral geniculate body

Anatomy of the ventral nucleus of the lateral geniculate body. In two Marchi series of the ferret's brain after removal of the left eye, degeneration is present in the ventral nucleus of the lateral geniculate of both sides; it is greater in the contralateral than in the ipsilateral nucleus. The Marchi reaction however appears very largely to be limited to bundles of fibres of retinal origin which run through the ventral nucleus on their way to the dorsal nucleus of the lateral geniculate body. Marchi granulation outside these fibres in the substance of the ventral nucleus is very slight: the appearance is therefore totally unlike that of the dorsal nucleus (see below), and is consistent with the view that this granulation seen in the ventral nucleus is related only to fibres of passage. The possibility remains however that unmyelinated fibres or the unmyelinated collaterals of myelinated optic fibres of passage of course may end in this nucleus. Our ferret material does not provide positive evidence on this point.

Cajal (1911) and Kappers (1921) both believed that collaterals of optic tract fibres ended in the ventral nucleus; Pavlov (1900), Loepp (1912) and Brouwer (1923), from study of Marchi preparations after unilateral enucleation in the rabbit, stated that fibres of the optic tract ended in the ventral nucleus of the lateral geniculate. In Marchi sections of one rabbit's brain which was at our disposal, the appearance of the degeneration is very similar to that described above for the ferret; certainly no positive evidence is presented that optic fibres end in the ventral nucleus.

Amongst recent workers the view that the optic tract makes no connexions either by direct fibres or by collaterals with the ventral nucleus of the lateral geniculate is widely held (Gurdjian, 1927; Lashley, 1934 (rat); Tsai, 1925; Bodian, 1937 (opossum); Barris *et al.* 1935 (cat)). The work of Tsang (1937) in the rat is also in support of this view. He observed that after either unilateral or bilateral extirpation of the eyes there is never atrophy of the cells of the ventral nucleus of the lateral geniculate, however long the period of degeneration. On the other hand after similar operative procedures the cells of the dorsal nucleus become shrunken, rounded and embryonic in form, with fewer processes than normal. Tsang believes this to be an example of atrophy from disuse. In the rat, therefore, it seems that there can be no close relation between the optic tract and the ventral nucleus of the lateral geniculate, either by myelinated or by unmyelinated fibres; for if there were, an atrophy of the ventral nucleus comparable with that of the dorsal nucleus might perhaps be expected.

In a Weigert preparation of the ferret's brain after section of both optic nerves, with the consequent complete degeneration of the optic tracts, numerous myelinated fibres are still present in the ventral nucleus of the lateral geniculate (see Pl. 1, fig. 1), which in normal preparations may easily be mistaken for component fibres of the optic tract. Many of these fibres appear to pass straight through the ventral nucleus and over the lateral aspect of the dorsal nucleus towards the tectum. The picture presented is somewhat confusing. These fibres probably belong chiefly to the commissures of Meynert and v. Gudden. Fibres have however been described running from the ventral nucleus of the geniculate to the tectum; e.g. Barris *et al.* (1935) observed a "tractus geniculatus ascendens" in the cat, which passes up dorso-laterally over the dorsal nucleus of the lateral geniculate. They suggested that this tract consists of fibres going only in one direction, i.e. towards the tectum. Rioch (1929) described geniculo-tectal fibres in the dog which arise in the ventral nucleus, and join with the retino-tectal fibres to pass superficially over the dorsal nucleus of the lateral geniculate to the midbrain. Le Gros Clark also has described geniculo-tectal fibres in the rat (1931). It is therefore probable that in the ferret a number of the fibres, seen in the ventral nucleus of the lateral geniculate and also passing over the superficial aspect of the dorsal nucleus, belong to this geniculo-tectal tract; it is however impossible in our Weigert material to make out this tract as a discrete bundle, distinct from the other fibres. In Weigert preparations of the ferret's brain, many finely myelinated fibres are seen running from the ventral nucleus ventro-medially to the zona incerta. These constitute the geniculo-incertal tract which has been observed by many authors (Gurdjian (1927) in the rat; Barris *et al.* (1935) in the cat—these latter authors gave the name of "tractus geniculatus descendens" to the geniculo-incertal connexions; Rioch (1929) in the dog; Le Gros Clark (1930) in *Tarsius*). The incertal connexions of the corpus griseum pregeniculatum—the primate homologue of the ventral nucleus—have also been described in man and other primates (Balado & Franke, 1937).

Study of a Nissl preparation of the ferret's brain after bilateral ablation of the occipital lobes demonstrates that, whereas the cells of the dorsal nucleus undergo complete degeneration, the cells of the ventral nucleus remain apparently unchanged. The ventral nucleus of the lateral geniculate therefore has no connexions with the striate cortex.

Briefly, it is clear that the ventral nucleus of the lateral geniculate body of the ferret is connected with the zona incerta and probably also with the tectum; it has no connexions with the cortex. Its connexions with the optic tract have not been demonstrable in the material available; it seems legitimate to assume that they do not exist.

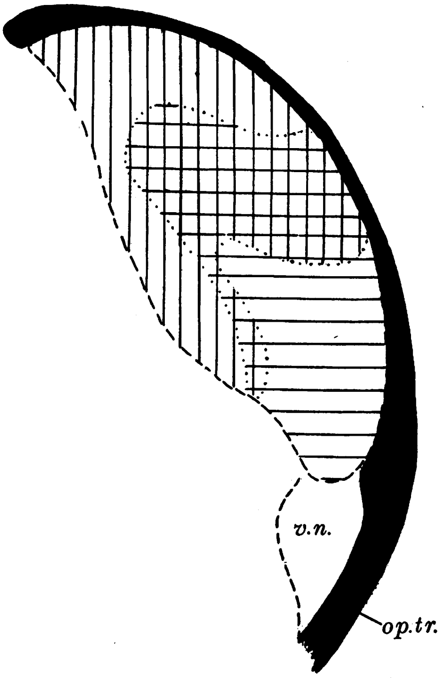
Anatomy of the dorsal nucleus of the lateral geniculate body. It was suggested towards the end of last century, on the basis of clinical and pathological studies, that there is a point-for-point representation of the retina on the striate cortex (Henschen, 1893; Wilbrand, 1890). If such a relationship between the retina and the visual cortex obtains, it is clear that "segregation" of the fibres from the various parts of the retina must exist throughout the visual system. Thus if there is in fact a complete cortical representation of the retina, it is to be expected that the dorsal nucleus of the lateral geniculate will also show a "projection" of retinal points, in so far as this nucleus functions as a relay centre for optic impulses to the cortex. From a study of human clinical material, Henschen concluded that the dorsal quadrants of the retina were projected dorsally, and the ventral quadrants ventrally, in the dorsal nucleus of the lateral geniculate. It has been shown however by more recent work that this view is incorrect, though representation of the retina in the dorsal nucleus is indeed present. Such a relationship between the retina and the dorsal nucleus has now been found to exist in a number of mammals, e.g. opossum, rabbit, rat, and cat, as well as in primates including man; representation most closely approximates to a point-for-point projection in primates. It is probable therefore that in the ferret localization of retinal points exists in the lateral geniculate. Such results as we have obtained support this hypothesis, and may be compared with the more detailed observations of other workers.

Study of two Marchi preparations of ferrets' brains after section of one optic nerve shows that there is much Marchi granulation present as a fine "dust" in the dorsal nucleus of both crossed and uncrossed sides. These granules are scattered through the substance of the nucleus, and for the most part are not arranged in rows as if along some definitive pathway: i.e. the granulation appears to represent the terminal portions of myelinated optic fibres ending in relation to cells of the dorsal nucleus, and does not give the impression of being limited merely to the course of bundles of fibres of passage. This is in contradistinction to the picture presented by the ventral nucleus after similar operative procedures. The Marchi reaction in the crossed dorsal nucleus is seen to be both more dense and more widely distributed than in the uncrossed nucleus. Further, the distribution of degeneration is not identical on the two sides. In the uncrossed dorsal nucleus the distribution is as follows: in frontal sections through the rostral end of the dorsal nucleus, the greatest diameter of the nucleus is approximately horizontal, and in this portion of the nucleus the Marchi degeneration is seen to be limited to the medial one-third. Slightly more caudally the greatest diameter shifts so that it becomes more or less vertical. Granulation is now seen in the dorsal pole and upper two-thirds of the medial part of the nucleus. Further caudally, degeneration is limited to a horseshoe-shaped cap in the dorsal part of the nucleus; the medial limb of the horseshoe reaches considerably more ventrally than the lateral limb (see Pl. 2, fig. 4). In the caudal end of the nucleus the area of Marchi granulation is confined to a comparatively small oval, situated at the middle of the medial portion of the nucleus. At levels through the crossed nucleus corresponding to those described in the uncrossed nucleus, the areas of Marchi granulation are as follows: anteriorly where the longest diameter is horizontal, degeneration occupies the lateral three-quarters. When the long axis has shifted to become vertical, degeneration is seen throughout the nucleus except in its dorsal pole and medial one-third. Farther posteriorly, degeneration is again present throughout the nucleus, except for a narrow horseshoe-shaped band which has its apex dorsally and the medial limb of which extends much farther ventrally than the lateral (see Pl. 2, fig. 3). At the caudal end of the nucleus, Marchi granulation is limited to the ventral half of the nucleus. In the most caudal part of the crossed nucleus, Marchi degeneration is seen arranged in rows parallel with the greatest diameter of the nucleus; this appearance indicates degenerated fibres of passage belonging to the mesencephalic root of the optic tract which run through the dorsal nucleus to join the brachium of the superior colliculus.

To summarize these observations: it is seen that retinal fibres end everywhere in the crossed nucleus except in its dorsal pole and its most medial part. Conversely retinal fibres end in the dorsal pole and medial portion of the uncrossed nucleus. This segregation in the lateral geniculate of crossed and uncrossed fibres is not complete, so that a partial overlap occurs; this can readily be seen in Text-fig. 5; in this figure it is clear that the area occupied by Marchi granulation in the uncrossed dorsal nucleus is considerably larger than the area which shows no granulation in the crossed dorsal nucleus of the lateral geniculate body.

The projection of crossed and uncrossed optic fibres in the dorsal nucleus of the ferret thus appears comparable with the projection described in other mammals, e.g. opossum, rabbit, rat and cat (Minkowski, 1920; Brouwer, 1923; Brouwer & Zeeman, 1926; Putnam & Putnam, 1926; Overbosch, 1927; Lashley, 1934; Chang, 1936; Bodian, 1937).

In addition, in the above-mentioned animals, the localization of the retinal quadrants in the dorsal nucleus of the lateral geniculate has been worked out.



Text-fig. 5. Diagram illustrating the overlapping projection of the crossed and uncrossed retinal fields in the dorsal nucleus of the lateral geniculate body (prepared from photomicrographs in Pl. 2). The crossed projection field is represented by horizontal lines, and the uncrossed by vertical lines. *op.tr.* optic tract; *v.n.* ventral nucleus of the lateral geniculate body.

It is found that the ventral half of the contralateral retina is projected dorsally—the nasal quadrant being lateral and the temporal quadrant medial; similarly the dorsal half of the retina is projected ventrally—the nasal quadrant again being lateral and the temporal quadrant medial. The uncrossed portions of the temporal quadrants are projected most medially in the dorsal nucleus, partially overlapping the crossed temporal fields; the ventral half of the uncrossed temporal retina is projected dorsally in this area, and the dorsal half ventrally.

It seems probable that research on the projection of the retinal quadrants on the dorsal nucleus of the ferret will reveal similar relations.

Some correlation might exist between the cytoarchitectural structure of the dorsal nucleus of the ferret lateral geniculate and those areas which receive respectively crossed and uncrossed optic fibres. A study of a Nissl preparation of the ferret's brain was therefore made: the dorsal nucleus shows some lamination, but its pattern is complex and cannot be readily analysed. It is impossible to integrate it with the localization of crossed and uncrossed retinal fibres as worked out in Marchi sections after unilateral enucleation. Two reasons for this failure may be offered. First, the findings in the ferret as to the representation of the retina in the dorsal nucleus are only of a gross nature, i.e. they are limited to observations on the projection of the *whole* of the crossed, and the *whole* of the uncrossed, retinal fields. Perhaps a more detailed analysis of the projection of the retinal quadrants might reveal a correlation. Secondly, Rioch (1929) has described in the dog the laminar structure of the dorsal nucleus: he states that though in frontal sections the picture presented is confusing, paramedian sagittal sections clearly demonstrate that there are four laminae which are arranged in sigmoid curves. Possibly parasagittal sections of ferret Nissl preparations would demonstrate a clear and simple lamination of this kind, which might then be correlated with observations on the projection of retinal quadrants in the dorsal nucleus. Further research along these lines is indicated.

The superior colliculus

The superior colliculus has been shown in a variety of mammals to have a laminated structure (Cajal, 1911; Tsai, 1925; Tsang, 1937; and others). This lamination is also present in the colliculus of the ferret, being clearly demonstrable in Nissl and Weigert preparations. In the enumeration of the layers, the nomenclature of Tsang (1937) has been followed:

Layer I: Stratum zonale: a thin superficial layer consisting of small marginal cells, and a number of fine myelinated fibres.

Layer II: Stratum griseum superficiale: a much thicker layer, which consists of comparatively scattered cells mostly rather smaller than those of the deeper layers.

Layer III: Stratum opticum: in this layer run the fibres of the mesencephalic root of the optic tract, and a deeper fibre component which arises in the cerebral cortex. This layer also contains medium-sized cells.

Layer IV: Stratum lemnisci: the fibres composing this layer belong to the lemniscal systems and to the brachium of the superior colliculus. The cells found in this layer are small and scattered, though a few are giant cells.

Layer V: Stratum album profundum: this layer contains small scattered cells and the efferent fibres of cells in the more superficial layers, e.g. the fibres of the commissure of the superior colliculus and of the radiation of Meynert.

Layer VI: Stratum griseum centrale: this is the grey matter surrounding the aqueduct of Sylvius.

The significance of the collicular stratification. Since the classic work of Cajal (1911), it has been generally recognized that only the more superficial layers of the colliculi are concerned with the reception of optic fibres.

Cajal described the fibres of the mesencephalic root of the optic tract passing first in the superficial layer of the stratum opticum. According to this author, some optic fibres terminate in this part of their course: these he termed "arborisations inférieures". Other fibres continue obliquely or sinuously towards the periphery of the colliculus, and end at varying levels in the stratum griseum superficiale almost to the plane of the stratum zonale. Fibres ending in this manner were called by Cajal "arborisations supérieures". In Golgi preparations he demonstrated that the terminal arborizations of optic fibres are rich and complex, especially those of the fibres which terminate more superficially. By means of these large arborizations, a single retinal fibre makes synaptic connexions with many cells.

Early investigators believed that the stratum zonale received fibres of retinal origin. Cajal stated that after enucleation of one eye in the mouse, Marchi sections of its brain showed no evidence that retinal fibres reached this layer of the superior colliculus. From a study of Golgi material, he concluded that the stratum zonale is made up of the axons of cells in the stratum griseum superficiale.

As a result of his exhaustive observations on the microscopical anatomy of the superior colliculus, Cajal regarded the stratum griseum superficiale, and to a lesser extent the stratum opticum, as the site of termination of the mesencephalic root of the optic tract. He was of the opinion that no fibres of retinal origin turn down into the deeper layers to end in them: and that no optic fibres end in the stratum zonale.

The work of Tsai (1925) in the opossum led to similar conclusions: optic fibres, as seen in Weigert preparations of normal brains, ended in the stratum opticum of the superior colliculus. In silver-stained material some of these fibres could be followed turning outwards to end in the stratum griseum superficiale. Using the Marchi technique after unilateral enucleation of the eye, other workers (Loepp, 1912; Brouwer *et al.* 1923; Overbosch, 1927; Bodian, 1937) have followed degenerated retinal fibres both in the stratum opticum and in the stratum griseum superficiale. In such preparations no optic fibres have been traced into the stratum zonale. The Marchi granulation is always only to be seen in the contralateral colliculus. On the other hand, Bodian (1937) has described retinal fibres ending in the anterior half of the ipsilateral colliculus of the opossum. These fibres are much less numerous than those to the contralateral colliculus, and Bodian believes that they are entirely derived from the temporal part of the retina. In addition he traced fibres showing Marchi degeneration into the stratum zonale of both colliculi, but more especially that of the ipsilateral colliculus.

Tsang (1937), with an entirely different technique, obtained comparable results in rat material. He examined microscopically the superior colliculus in Weigert sections, and by means of a screw micrometer measured the depth of the various layers. He compared normal sections with those from rats which had been deprived of one eye in infancy, and found shrinkage of the outer three layers of the contralateral colliculus in the operated animals. In animals killed seven months after operation the depth of the stratum zonale plus the stratum griseum superficiale was 12–15 % of the total depth of the colliculus (control 19 %); similarly the depth of the stratum opticum was 20–22 % of the total (control 26 %). There was no apparent change in the depth of these layers in the ipsilateral colliculus. In the contralateral colliculus, the cells in the stratum griseum superficiale showed pronounced atrophy 7 months after operation; they were "roundish, granular, with fewer processes than normal, and with poorly stained cytoplasm". There were no recognizable changes in the cells of the stratum opticum, nor in the cells of the deeper layers. The fibres of the stratum lemnisci and stratum profundum appeared perfectly normal: the optic fibres of the stratum opticum, however, had completely vanished, though the deeper non-optic component remained intact.

The termination of optic fibres in the superior colliculus of the ferret was studied in Marchi preparations. Marchi reaction is limited to the contralateral colliculus, and is present only in the stratum opticum and to a lesser extent in the stratum griseum superficiale. No osmic acid granules are seen in the stratum zonale.

This finding is therefore in complete agreement with the observations of most other workers, but there is some reason for doubting that it is the whole truth.

A number of years ago, Prof. Le Gros Clark had cut the left optic nerve in a series of four rats in order to study early degenerative changes in the terminal fibres of the optic tract system; the animals were killed respectively 1, 2, 3 and 4 days after operation. After removal the brains were stained by a silver technique (modified Ranson method): on examination it was found that there were large granulations in the contralateral colliculus of the animals killed 2, 3 and 4 days after operation (see Pl. 1, fig. 2). These granulations represent the degenerated terminals of optic fibres: they were best shown by the rats killed 3 and 4 days after operation, and were absent in the animal killed only 1 day after operation, where the period allowed for degeneration was not sufficiently long. They are limited to the stratum opticum, the stratum griseum superficiale, and the stratum zonale: they are most prominent in the stratum griseum superficiale. The neuropil of the stratum lemnisci is more dense; however, if such granulations were present in this layer, they could not escape observation because of their large size. The contrast between the crossed and uncrossed colliculi is marked, the latter being innocent of degeneration granules. In contradistinction to the picture presented by Marchi sections this silver-stained material demonstrates conclusively that retinal fibres terminate in the stratum zonale. They are presumably the terminal branches or collaterals of myelinated fibres after the latter have lost their sheaths.

It was hoped that this phenomenon might be shown in the superior colliculus (and perhaps also in the lateral geniculate body and pretectal region) of the ferret. To this end the brains of two ferrets, after removal of the left eye, were stained by the silver method described by Sereni & Young (1932). As it had not been possible in the rat series to demonstrate degenerated terminals in the lateral geniculate because of the great density of the neuropil, the ferret brains were sectioned at 5μ in the hope of overcoming this difficulty. The results of this experiment were disappointing, for, with the characteristic capriciousness of silver stains, the fibres of the optic tract remained unstained, although the cell-bodies and dendrites of cells in the superior colliculi and lateral geniculate bodies were well impregnated. Despite this failure it seems probable that the termination of optic fibres in the contralateral superior colliculus of the ferret is similar to that obtaining in the rat; this point must however be decided upon the result of further research.

The dual origin of the stratum opticum has been briefly referred to above. Cajal (1911) observed that, after enucleation of one eye in the cat, Marchi granulation was limited strictly to the superficial fibres of the stratum opticum. He advanced the view that the fibres of the inferior component were of cortical origin ("voie cortico-bigeminale"), and demonstrated that they ended partly in the stratum opticum itself but largely by turning downwards into the stratum lemnisci ("zone ganglionaire" of Cajal).

Barris *et al.* (1935) found that, after lesions in the striate and parastriate cortex of the cat, Marchi granules were present in the stratum opticum of the ipsilateral colliculus. In the ferret confirmation of this observation has been obtained. After removal of the occipital pole of the right side in one ferret, Marchi reaction was seen in the stratum opticum of the ipsilateral colliculus. It was not possible, however, in this preparation to determine the exact site of termination of these fibres: it appears to be similar to that of the optic component (as seen in Marchi series), i.e. in the stratum opticum itself and in the stratum griseum superficiale. The non-optic component of the stratum opticum therefore contains fibres which are derived from the visual area of the cortex: but this does not preclude there being other fibres which take origin elsewhere in the cortex.

The pretectal region

The pretectal region may be regarded as belonging to the transition zone between the diencephalon and the mesencephalon. It has been described as being composed of two nuclei, which have been designated by a variety of names by different authors. Following the nomenclature of Le Gros Clark (1932*b*), they will be called respectively the pretectal nucleus and the large-celled nucleus of the optic tract.

The pretectal nucleus. This nucleus, which may be distinguished in the brains of many small mammals as an oval mass composed of small rounded or pyramidal cells, is situated just medial to the pars posterior of the lateral nucleus of the thalamus. Caudally it enlarges and extends in a ventral direction to the medial aspect of the medial geniculate body. It corresponds to the prebigeminal (bigeminal or posterior) nucleus of Cajal (1911), the posterior thalamic nucleus of d'Hollander (1913), Kappers (1921), and Gurdjian (1927), and the pretectal nucleus of Tsai (1925). The fibre connexions of the pretectal nucleus are many. It appears to be related by numerous short fibres to adjacent thalamic nuclei: particular attention may be drawn to its connexions with the lateral geniculate body. By way of the brachium, it is connected to the superior colliculus, and fibres from the medial lemniscus end in it. Tsai (1925) has also described fibres running to the substantia nigra (tractus pretecto-nigralis). It is traversed by fibres of passage belonging to the tecto-thalamic and cortico-tectal systems and to the mesencephalic root of the optic tract.

The large-celled nucleus of the optic tract. Along the anterior and lateral margins of the superior colliculus, dorsal and largely medial to the pretectal nucleus, is to be found the large-celled nucleus of the optic tract. Le Gros Clark (1932*b*) has homologized this nucleus with the "noyau de la voie optique" of Cajal (1911), and the nucleus parageniculatus of Lewandowsky (quoted by Loepp, 1912). It corresponds also with the rabbit "thalamus opticus" of Brouwer (1923) and the pretectal area of Gurdjian (1927). After passing over the pars posterior of the lateral thalamic nucleus, the mesencephalic root of the optic tract lies in close relation to this nucleus.

The pretectal region and the optic tract. Both the pretectal nucleus and the large-celled nucleus are in close topographical relation to fibres of the optic tract; the possibility therefore exists that optic fibres may end in them. According to the observations of Tsai, Weigert or silver preparations of the opossum's brain show optic fibres belonging to the mesencephalic root ending in the pretectal nucleus. He suggested also that fibres of the diencephalic root might reach it through the dorsal nucleus of the lateral geniculate body. Bodian (1937), in his experimental study of the optic tracts of the opossum, however, found no fibres showing Marchi degeneration in any of his material (after either unilateral or bilateral extirpation of the eye), which could be traced to the pretectal nucleus. Gurdjian (1927) believed that in the rat retinal fibres ended in the pretectal nucleus, and Lashley (1934) observed fine and rather sparse Marchi granulation in the dorsal one-third of the pretectal nucleus of the crossed side after injury to the temporal retina or after enucleation of one eye in the rat. Lashley was uncertain whether this represented terminal axons or scattered fibres passing to the colliculus.

In the rat a few degenerated optic fibres have been demonstrated by the Marchi technique passing to the large-celled nucleus (Le Gros Clark, 1931). Loepp (1912) had shown that in the rabbit optic fibres end in this region, and Brouwer (1923), experimenting on the rabbit and cat, made similar observations. Gurdjian (1927) stated that fibres of the mesencephalic root of the optic tract of the rat end in the "pretectal area" (=large-celled nucleus), and Lashley (1934) obtained fine Marchi granulation in the nucleus after unilateral enucleation of the eye in the rat, but was uncertain of its significance see above).

A review of the literature therefore establishes the fact that the large-celled nucleus receives retinal connexions, though the position of the pretectal nucleus as an optic end-station has been somewhat equivocal.

In Nissl sections of the ferret's brain, the pretectal region appears as an undifferentiated mass of grey matter; it is not possible to distinguish any discrete groups of cells which might be called the pretectal or large-celled nuclei. In silver sections the neuropil in the pretectal region is very dense. Study of such sections shows that fibres of the brachium of the superior colliculus (which is largely formed by the mesencephalic root of the optic tract) burrow ventrally, in a loop, into the medial part of the pars posterior of the lateral thalamic nucleus, and especially into that part of the pretectal region which in other species is occupied by the large-celled nucleus. In addition, a general impression is gained from silver-stained material of fibres running ventrally from the more superficial part of the pretectal region towards the region corresponding to the site of the pretectal nucleus in other animals, and also towards the nucleus of the posterior commissure. It is however impossible to trace the course of individual fibres because of the great richness of the neuropil. (It may be noted that many fibres belonging to the cortico-tectal system, after passing up along the medial aspect of the lateral geniculate, and through the pars posterior of the lateral thalamic nucleus, join with retinal fibres in the pretectal region before running up to the superior colliculus. This is clearly demonstrated by a Marchi series of the brain of one ferret from which the occipital pole had been removed.)

In two Marchi preparations of the ferrets' brains after section of one optic nerve, degenerated optic fibres are seen making a ventral loop into the pretectal region of the contralateral side before passing upwards into the stratum opticum of the superior colliculus. Marchi granulation appears mostly to be limited to the course of optic fibres of passage. No fibres showing the Marchi reaction are seen running ventrally into the deeper parts of the pretectal region, or towards the nucleus of the posterior commissure. It is impossible to state definitively whether any retinal fibres terminate in the pretectal region simply on the evidence presented by these two ferrets' brains. Because of the intimate relation of the optic tract to the region of the presumptive large-celled nucleus, and in spite of the apparent limitation of Marchi granulation to the course of optic fibres of passage, it is possible that retinal fibres—either directly or by collaterals—end in this region; on the other hand there seems to be little reason on the basis of this material for assigning to the pretectal nucleus any primary optic connexions. It should be mentioned, however, that in recent years it has been abundantly proved by two independent lines of research (S. W. Ranson and his school on the pupillo-constrictor reflex; K. S. Lashley and others on the mechanism of vision) that the pretectal region must be regarded as a primary optic end-station. Detailed account of this work lies beyond the scope of the present paper, but the appropriate sources of information will be found in the references.

DISCUSSION

Le Gros Clark *et al.* (1939) observed that gonadal activation invariably followed retinal stimulation in ferrets, even after bilateral section of the optic tracts had been attempted at the ventral border of the dorsal nucleus of the lateral geniculate body. Microscopical examination of the brains of these animals showed that some fibres of the optic tract, of one side or the other, had always escaped division, and were left in communication either with the midbrain (pretectal region and superior colliculus) or with the dorsal nucleus of the lateral geniculate body. In two animals, F 22 and F 50, these connexions were very slender; in F 22, a fine strand of fibres belonging to the left mesencephalic root remained intact, whilst in F 50, intact diencephalic fibres passed to a narrow ventrally-placed strip of the dorsal nucleus of the right lateral geniculate body (the rest of the nucleus having been destroyed by the lesion itself). Neither of these animals responded to illuminated moving objects; thus it appeared that the intact fibre connexions were non-functional so far as *ordinary* visual reactions were concerned, and it was suggested that the persistence of the gonadal response might perhaps depend upon its mediation by direct pathways proximal to, and undamaged by, the lesions.

In the present anatomical study, however, no evidence has been found to support the existence of such pathways; it seems that the ferret does not possess either dorsal hypothalamic root or accessory optic tracts, nor does the ventral nucleus of its lateral geniculate body appear to receive any optic connexions. In experiments F 22 and F 50 of Le Gros Clark *et al.*, the gonadal response of these two animals, therefore, may only have been brought about *via* the intact fibre connexions of the optic tracts. Also, since the response was obtained equally after interruption of all but mesencephalic fibres (F 22) or all but diencephalic fibres (F 50), the conception of a single special pathway may have to be abandoned.[1]

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[1] It is important to record that a further series of experiments (unpublished) were carried out at Oxford during 1938–9 by Le Gros Clark *et al.*, in which attempts were again made completely to interrupt the optic tracts of the ferret, the operative technique being identical with that already described by Le Gros Clark *et al.* (1939). These experiments differed, however, from the earlier series, in that a conditioned response to light was established in the animals before operation. They were tested post-operatively for retention of the habit and retrained. At present it is only pertinent to note that amongst these ferrets was one (F 71) in which division of the optic tracts was almost complete. Microscopically, the picture presented was very similar to that of F 50; thus on the left, the lesion had successfully divided all optic tract fibres; on the right, the lesion was slightly more dorsally placed, leaving a small ventral portion of the dorsal nucleus of the lateral geniculate body (receiving diencephalic fibres) intact, though all the fibres of the mesencephalic root were cut. Gonadal activation followed retinal stimulation, though the animal appeared to be blind (as tested by methods similar to those used in F 22 and F 50). In this respect, F 71 resembled F 50. It was found, however, that the capacity of the animal to react to light by a conditioned reflex had not been abolished by the operation. In experiment F 71, therefore, it cannot be maintained that the intact fibre connexions of the optic tracts were functionless so far as other visual reactions were concerned, whilst remaining functional for the gonadal response. Hence it is open to question whether such a contention can be supported in the two earlier experiments, since it appears probable that F 50 was not completely "blind", and at least possible that F 22 was not either (though this is a more equivocal point).

One is led to further speculations on the relationship between gonadal activity and retinal stimulation. Reflexion shows that a conception may be put forward which does not demand the presence of a special pathway for the mediation of the sexual response of the ferret. It is permissible to think of the various ways in which an animal responds to retinal stimulation as different aspects of a single phenomenon, which is change of the animal's total activity induced by the stimulation. This change of total activity is a "generic" response, which may be termed "generic" visual perception.[1]

Thus differentiation of the unit phenomenon of "generic" visual perception into sharply defined categories may be necessary for descriptive purposes, but it should not be allowed to obtrude itself upon the conceptual approach to the problem. It may be stressed that this conception does not deny the existence of difference between responses to retinal stimulation, but simply affirms the unity of the underlying process, of which these differentiable responses are aspects. Gonadal recrudescence brought about by retinal stimulation may be regarded as a single aspect of "generic" visual perception (i.e. of change of total activity).

If this be so, it is not necessary to postulate that anatomical subdivision (in the sense of a special pathway) should exist; indeed, in the present paper, it has been shown that there is no direct anatomical evidence of such a pathway mediating the gonadal response of the ferret to retinal stimulation. It seems possible that gonadal recrudescence is not primarily produced by retinal stimulation, but secondarily induced by the change of total activity which follows such stimulation; in this connexion it may be noted that differentiation between stimulus and response should not be too rigidly enforced, in so far as every response itself constitutes a further stimulus.

This conception may be applied equally to stimulation of peripheral receptor groups other than retinal. Change of total activity ("generic" sensory perception) will be similarly induced by stimulation of any such group, and will become observable as a set of responses, which also need not be conceived of as belonging to entirely different categories. Grossly similar change of total activity may be obtained by stimulation of any single group, or any combination of groups, of peripheral receptors, provided that the stimulation is of sufficient intensity. It is therefore to be expected that gonadal activation (of the sexually quiescent animal) may follow stimulation of any kind. In this light, the observations of Rowan become immediately comprehensible. Reference has been made in the introduction to the early work of this author (1925) on the induction of the breeding condition in finches by retinal stimulation. He later showed (1929, 1937) that comparable development occurred in these birds if their motor activity was enhanced by a mechanical device.[2]

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[1] The presence or absence of perception in an animal is judged in terms of response to stimulus: it is clear that we are not here concerned with the introspective qualities of visual perception.

[2] In these experiments the finches were placed in a cage, illuminated only by a "dim glow", which was fitted with a motor-driven travelling bar. This apparatus was turned on each evening

He also (1938*a*) published observations on precocious gonadal development in London starlings, where the operative stimulus appeared to be largely, and perhaps entirely, auditory. It may be postulated that the appearance of sexual phenomena in the ferret could be induced by substitution of some other type of stimulation for retinal stimulation. Demonstration of this would fit in with the conception outlined in this paper.[1]

It also becomes possible to understand the equivocal observations of various workers on the appearance or non-appearance of oestrus in female ferrets which had been either blinded by section of the optic nerves or kept in darkness. The potentiality for retinal stimulation in such animals is thus either completely eliminated or very markedly decreased, and this sensory loss must be reflected in their total activity (which is of course "total" in a new sense, taking into account their artificially limited potentiality for stimulation). Whether oestrus will appear in a ferret treated in either manner now depends upon the intensity of other stimulation to which the animal is exposed, which may or may not produce such a change of total activity that one aspect of the latter becomes observable as gonadal activity.

In addition to the part played by sensory stimulation (of all kinds) in the evocation of the sexual response of the ferret, other factors in its environment must be involved. For example, seasonal changes in the biochemical composition of the food, which the intact captive animal eats, must influence its total activity.[2]

Further, whether an animal is isolated from, or in contact with, its fellows must constitute another factor.

In fine, it may be concluded that any aspect of an animal's environment, if treated for experimental purposes as an isolated factor and artificially augmented to a sufficient degree, may produce changes in the animal comparable with those brought about in Nature by its environment as a whole.

SUMMARY

1. A description is given of the subcortical connexions of the optic tracts of the ferret.

2. It appears that the ferret does not possess a "dorsal hypothalamic root", or either of the accessory optic tracts.

3. In the present investigation there is no evidence that the ventral nucleus of the lateral geniculate body receives any optic connexions.

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after dark for progressively increasing periods. By this means the birds were forced to move every 20 sec. The results obtained support the hypothesis—suggested above—that gonadal activation may be a response to a response; clearly in these experiments, the primary response to this method of stimulation is motor activity.

[1] Change of total activity might alternatively be shown by determination of the basal metabolic rate of the animal before and after experimental stimulation, since metabolic rate may be regarded as one facet of total activity.

[2] This is probably so, even if under laboratory conditions an attempt is made to keep the animal on a standardized diet.

4. Some evidence is presented that projection of the retina exists in the dorsal nucleus of the lateral geniculate body of the ferret, which is comparable with that described in other species.

5. It is conclusively demonstrated that, in the rat, retinal fibres end in the stratum zonale of the superior colliculus, in addition to terminating in the stratum griseum superficiale and stratum opticum; it is presumed that a similar arrangement exists in the superior colliculus of the ferret.

6. It seems probable that optic fibres end in the pretectal region, although these terminations are not demonstrable in the ferret material available.

7. The question of gonadal activation of the ferret by retinal stimulation is discussed. It is suggested that there may be no special pathway mediating this response, and that the latter may be an indirect response to the changes in total bodily activity of the animal, which are primarily induced by such stimulation.

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(Other references quoted are to be found in the bibliographies of the works listed above.)

EXPLANATION OF PLATES 1 AND 2

Plate 1

Fig. 1. F 16. Weigert-Pal. Magnification ×40. Frontal section through the thalamus of a ferret after section of both optic nerves, showing the right lateral geniculate body. This photograph illustrates well the number of undegenerated myelinated fibres (*a*) remaining in the so-called optic tracts even after bilateral section of the optic nerves. Many such fibres are present in the ventral nucleus (*v.n.*) of the lateral geniculate body; others can be seen passing over the dorso-lateral surface of the dorsal nucleus (*d.n.*). The optic tracts should not therefore be regarded as a purely retinal system. The main degenerated optic tract is seen below (*op.tr.*).

Fig. 2. Rat 15. Modified Ranson. Magnification ×740. Frontal section through the contiguous borders of the two superior colliculi of a rat killed 72 hr. after section of one optic nerve. To the left of the middle line large black granulations are seen in the colliculus of this side. They are absent in the other colliculus. These granulations represent the degenerated terminals of crossed retinal fibres, and are present even in the stratum zonale.

Plate 2

Figs. 3, 4. F 59. Marchi. Magnification ×29. Frontal sections through the middle of the right (contralateral) and left (ipsilateral) lateral geniculate bodies; Marchi reaction appears in both the ventral and dorsal nuclei, but in the former it is confined to fibres of passage. For interpretation, see text.

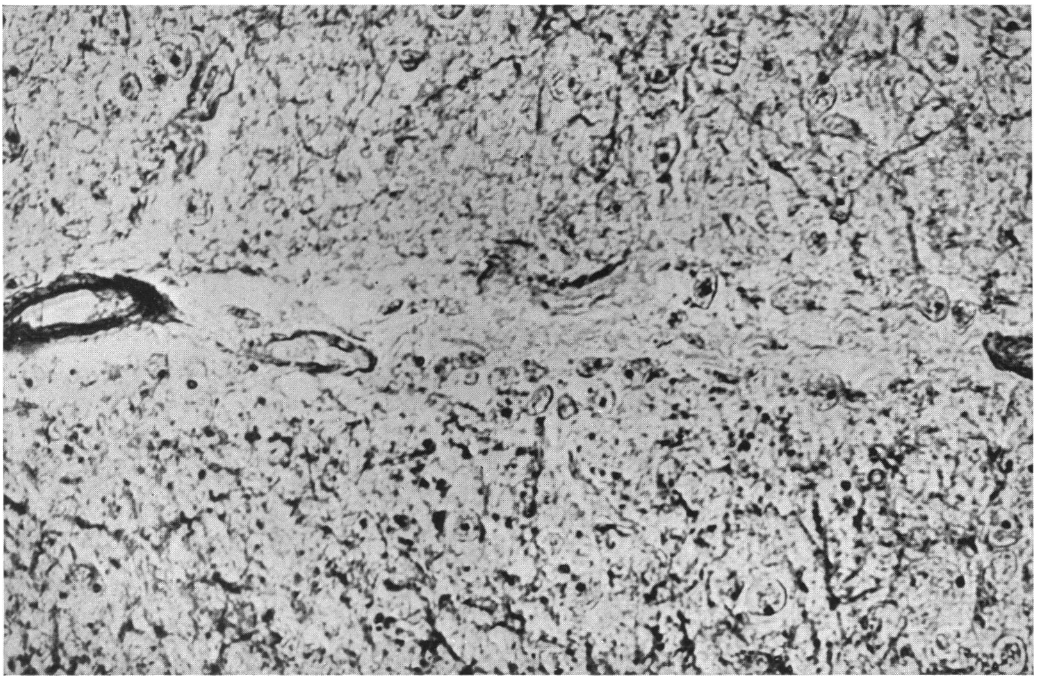

Fig. 2.

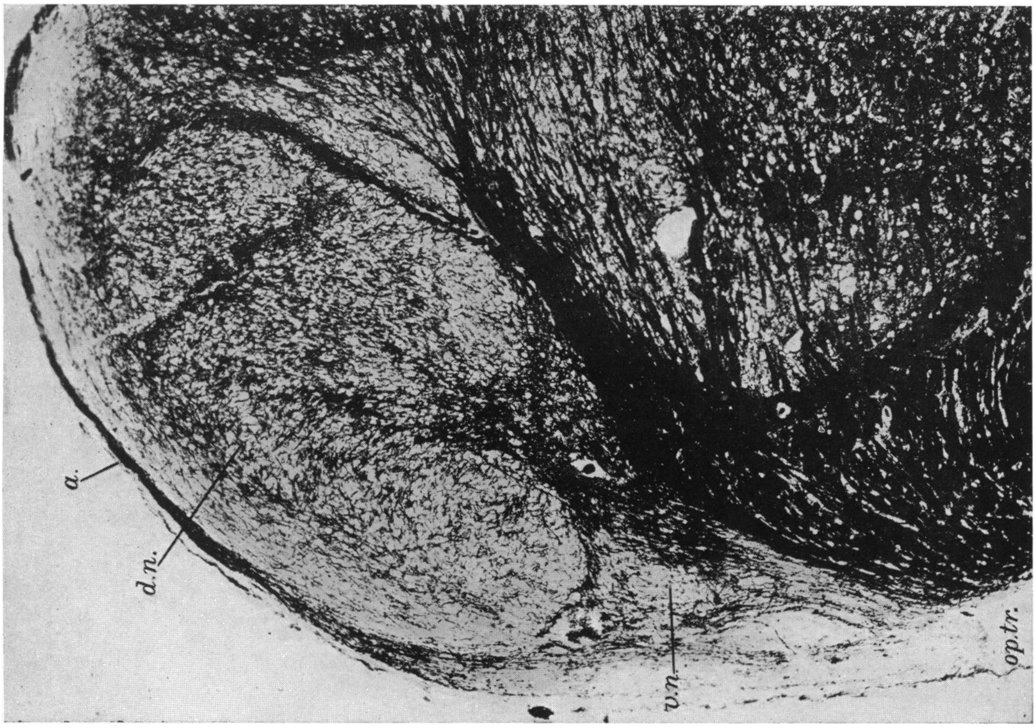

Fig. 1.

JEFFERSON—OPTIC TRACT SYSTEM

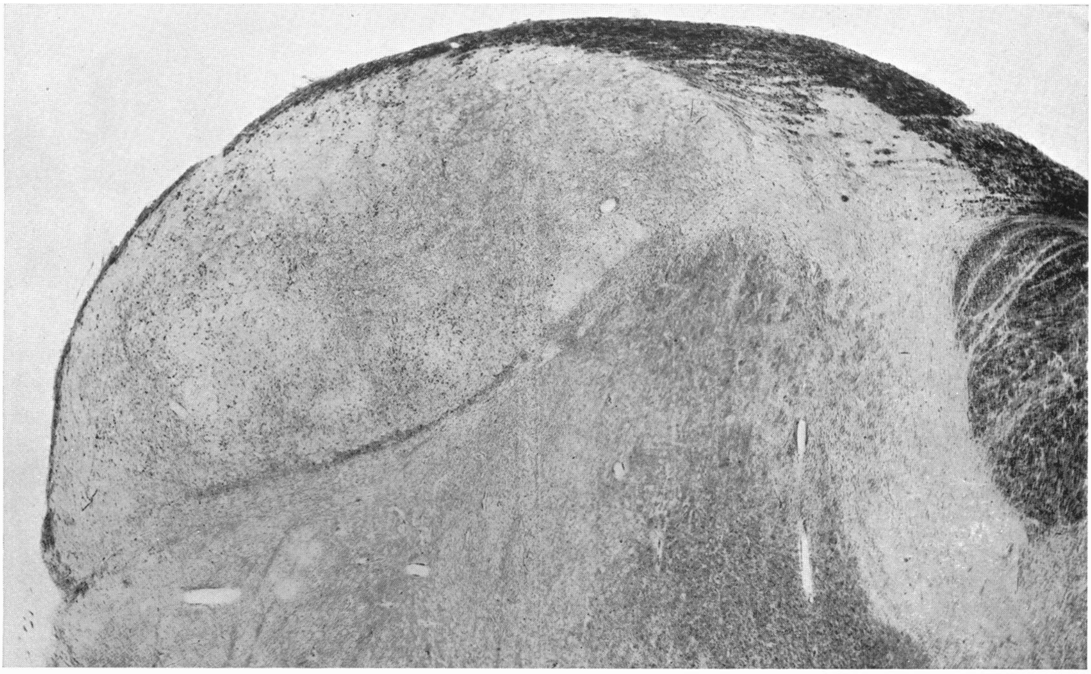

Fig. 4.

Fig. 3.

JEFFERSON—Optic tract system