A STUDY OF THE SUBCORTICAL VISUAL PATHWAYS IN CAT

by

Mohammed Rafiullah, B.Sc.(Honours), M.B., B.S.

A THESIS

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I wish to extend my gratitude and sincere appreciation to Dr. William A. Stotler for his supervision of this project, and for his valuable attention, friendship, kindness and patient instructions given to me in the past few years.

INTRODUCTION

The visual pathways have been the subject of considerable study in the past century. Henschen (31) wrote on the subject of visual path and center, and felt that there was a point to point representation of the retina upon the lateral geniculate body and visual cortex. On the other hand it was von Monakow's (4,50) belief that the localization is not as exact as described by Henschen. Munk (51) and Schaffer (67) described the cortical representation of the retina on the basis of their pathoanatomic studies and speculated on the organization of this system.

Ronne (64,65) studied the papulomacular bundle in human material, and traced the course of these fibers through the optic nerve, chiasm and the lateral geniculate body. Falachi (57), Baquis (57), Usher and Dean (75), and Parsons (57) using experimental animals and more refined techniques of making small lesions in the retina, presented further data regarding the course and distribution of the retinal fibers. Similar lesions were made by Brouwer and Zeeman (11, 22), and Polyak (60). They arrived at similar conclusions. Barris, Ingram and Ransom (7) found that a greater number of optic fibers crossed in the chiasm in the cat. Marburg (46) found that all optic nerve fibers arose in the retina. Electrophysiological studies were carried out by Bishop and Clare (9) who described four different types of fibers depending on the speed of conduction and the various subcortical areas activated by stimulation of these fibers. More recently, Hoyat and Luis (37) using the Zeiss photocoagulator made discrete retinal lesions, and described the course of optic fibers in the optic nerve chiasm and tract of monkeys.

Minkowski (48,49) is credited by Polyak (60) as the first to discover that crossed and uncrossed fibers alternate in the cell lamina of the lateral geniculate body. Hechst (35) found a similar arrangement in humans. LeGros Clark and Penman (16) described transneuronal degeneration in the lateral geniculate body, identified its laminated structure, and confirmed the termination of crossed and uncrossed optic fibers in alternating layers in monkeys.

The cytoarchitecture of the lateral geniculate body in cat has been studied by Ramon y Cajal (14), Tello (72), Thuma (73), O'Leary (54), Rioch (63), Winkler and Potter (76), and others. Thuma (73) described five components of the lateral geniculate body in the cat. These layers are the pars dorsalis A, pars dorsalis A1, pars dorsalis B, pars ventralis, the mucelus perigeniculatus anterior and nucleus perigeniculatus posterior. Rioch (63) found a similar arrangement in dogs. Cohn (19) demonstrated the three layered electrical organization of this structure in the cat by microelectrode studies. More recent accounts of Hayhow (32) indicate a somewhat modified cytoarchitectural organization in the lateral geniculate body of the cat.

The fiber projections to the optic tectum have been studied by various techniques by Tsai (74) in opposum, Johnson (38) in mole, Cajal (14) in mouse, Lashley (42), Clark (18) and others in rat, Minkowski (49), Brouwer and Zeeman (10) and Overbosch (55) in rabbit. In the cat this area was investigated by Monakow (50), Probst (61), Cajal (14), Barris, Ingram and Ranson (7), Crosby, Voss and Henderson (20-21) and Bucher and Burgi (13). The optic tectum in monkey was studied by Brouwer and Zeeman (11), Polyak (60) and others, and in man by Juba (39). In a recent study Altman (1) dealt with the efferent connections of the superior colliculus in cat, using the Nauta-Gygax technique.

Polyak (60), Peele (58), Crosby (22), O'Leary (54) and others described the distribution of optic fibers by size. Bishop and Clare (9) described the electrophysiological organization of fibers in the optic tract of cat. Distribution of the small and large fibers in the lateral geniculate body of the cat was also studied by Hayhow (32) by the Nauta-Gygax staining technique. Glees (26) in cat and LeGros Clark (29) in monkey investigated the manner of termination of optic fibers, in the lateral geniculate body, by silver impregnation technique, and described terminal boutons establishing synaptic contact with the cells of this structure.

MATERIAL AND METHODS

Twenty adult cats were used in this investigation. Sections of the optic nerve, usually the left, were performed by two different routes, transorbitally through the lateral wall and roof of the orbit, or transcranially through a subfrontal approach, sectioning the nerve just caudal to its emergence from the optic foramen. By either method damage was avoided to any structures inside the optic globe, and each acted as a control for the other structure. Thus some damage to the olfactory tract and trigone area was noted in the animals where a transcranial approach had been used, but did not interfere with the study of the visual pathways, as it could be easily compared with similar lesions of the optic nerve produced extracranially. It was possible to carry out section of the optic nerve, either completely or in segments to study the segmental distribution and termination of retinal fibers.

All lesions were made under aseptic conditions. For anesthesia 50 mgm. per kilogram body weight of veterinary nembutal was used intraperitoneally. Complete or partial sections were performed with a sharp surgical knife. In two animals, sections of the optic chiasm in the mid sagittal plane were performed.

The animals were sacrificed with a lethal dose of nembutal after a survival period ranging from four days to one month. After intraperitoneal injection of 5cc of nembutal, immediate thoracotomy was performed and a transcardiac perfusion of the whole animal with fifteen per cent formalin solution was done. The brains were then removed en bloc with the optic nerves and the optic globes in continuity with the brain. These were further fixed in formalin for a period of up to six months. The optic nerve, chiasm and tracts were removed in continuity in four animals and sectioned separately. Appropriate blocks of tissue were made from all brains in the coronal or horizontal plane. The tissue was dehydrated in the usual manner and embedded in paraffin. Sections, twenty microns thick, were cut with a Spencer rotatory microtome. Every tenth section was then mounted and stained by the Stotler's intensified protorgal staining technique. Drawings were made of these areas and compared with the normal silver stained, Weigert and Nissl stained material for further orientation of laminae and planes.*

The criteria of degeneration were: 1. Swollen and fragmented axons which, with increasing survival, showed linear accumulation of argyrophilic material, and infiltration with microglial cells along the course of degenerating axons; 2. The perikaryon around the cells stained dully; 3. Loss of normal cell and/or fiber population; 5. Visualization of darkly staining degenerating preterminals and club shaped degenerating black boutons around the neurons. Repeated frequent comparison

*Horizontal and coronal sections of normal cat brains stained by Weigert, Nissl and Stotler silver impregnation techniques were kindly made available by Dr. William A. Stotler.

with similarly stained normal tissue was of great help in excluding artifacts.

RESULTS

A brief review of the anatomy of the subcortical visual pathways is in order at this point. The optic nerve is made of axons of ganglion cells of the retina, which converge on the optic papilla. Passing out of the cribriform area, most if not all of these become myelinated, and collect into bundles separated by septa. They have no neurolemma (60). The optic nerve thus formed proceeds caudually, enters the cranial cavity through the optic foramen and joins the chiasm. The chiasm in the cat is H-shaped (4). Posteriorly it is continuous with the optic tracts, which contains fibers from homolateral temporal and contralateral nasal retina. The optic tract curves around the lateral surface of the diencephalon, and upwards in a broad sweep around the cerebral peduncles, becoming almost vertical and very much broader as the lateral geniculate body is approached. At this point it bifurcates into medial and lateral rami which surround the lateral geniculate body (9, 58, 60).

The lateral geniculate body is divided into a pars dorsalis and a pars ventralis, the two being separated by a well defined fibrous septum. The pars dorsalis consists of three laminae, A, Al and B. Other components of the lateral geniculate body in the cat are the nucleus perigeniculatus anterior and the nucleus perigeniculatus posterior. The pars dorsalis A and Al are two gently sigmoid, cellular laminae of almost identical histological structure of fairly uniformly distributed small, medium and large cells. They are separated by a medullary lamina containing scattered large cells and called the A-Al interlaminar fiber plexus. The pars dorsalis B is a sigmoid lamina containing medium sized spindle-shaped cells. It lies between pars dorsalis Al dorsally and a layer of dispersing optic fibers ventrally. The two laminae are separated from each other by a cellular transitional zone characterized by presence of large deeply staining cells. The nucleus perigeniculatus anterior is an attenuated irregular layer of small cells forming a cap over the anterior and dorsal surface of the pars dorsalis A. The nucleus perigeniculatus posterior forms a cap of small cells over the posterior end of pars dorsalis Al and is in apparent continuity with pars dorsalis B. It is regarded as identical to pars dorsalis B. A diffuse cluster of cells similar to those found in the main mass of pars dorsalis is situated between the pars dorsalis laterally and the pulvinar medially, and is embraced by the lateral and medial rami of the optic tract dorsally and medially. This is called the nucleus interlaminaris medialis.

The pars ventralis is a small pyramidal mass of cells located between medial and lateral rami of the optic tract. It is composed predominantly of small cells and anteriorly becomes continuous with the nucleus perigeniculatus anterior.

The pretectal region is a rostral diencephalic extension of the superior colliculus. It receives a larger number of the retinal fibers as compared to the superior colliculus. These fibers reach the pretectal area mainly by way of the lateral division of the brachium of the superior colliculus laterally and through the optic tract in the ventromedial aspect of the lateral geniculate body. Some fibers also reach the pretectum, particularly its rostral part, by way of the medial division of the brachium of the superior colliculus. The majority of these fibers terminate on the large cells of the pretectal area while some penetrate the whole extent of the pretectum by way of the stratum opticum.

The superior colliculus receives more crossed than uncrossed fibers. These fibers arrive by way of the lateral division of the brachium of the superior colliculus after a short course over the dorsal edge of the lateral geniculate body. A few fibers reach the dorsomedial surface of the superior colliculus through the medial division of its brachium. The fibers are distributed through the stratum opticum and reach dorsally the stratum griseum superficiale and ventrally the stratum griseum mediale (1).

The present investigation was undertaken to study the course of the optic fibers in the cat by the silver impregnation technique. Most of the investigators in the past have relied on three main forms of staining techniques (32). The Nissl method employed by Minkowaski (49), Barris (6), and Cohn (19) is able to demonstrate the cellular structures well, but falls short in demonstrating degenerating axons. The Marchi technique, utilized by Minkowaski (48), Overbosch (55), and Barris, Ingram and Ransom (6), shows the myelinated degenerating axons only, and artifacts are an ever present problem. The special silver staining technique used by Glees (26) provides a method of studying optic tract fibers, and their termination by staining the degenerating axons, preterminal

Figure 1. A semidiagramatic drawing of the lateral geniculate body of the cat, in the coronal plane of section, to show the laminar arrangement and principle cytoarchitectural features.

Figure 2. A semidiagramatic drawing of the lateral geniculate body of the cat, in a horizontal plane of section, to show the laminar arrangement and the principle cytoarchitectural features.

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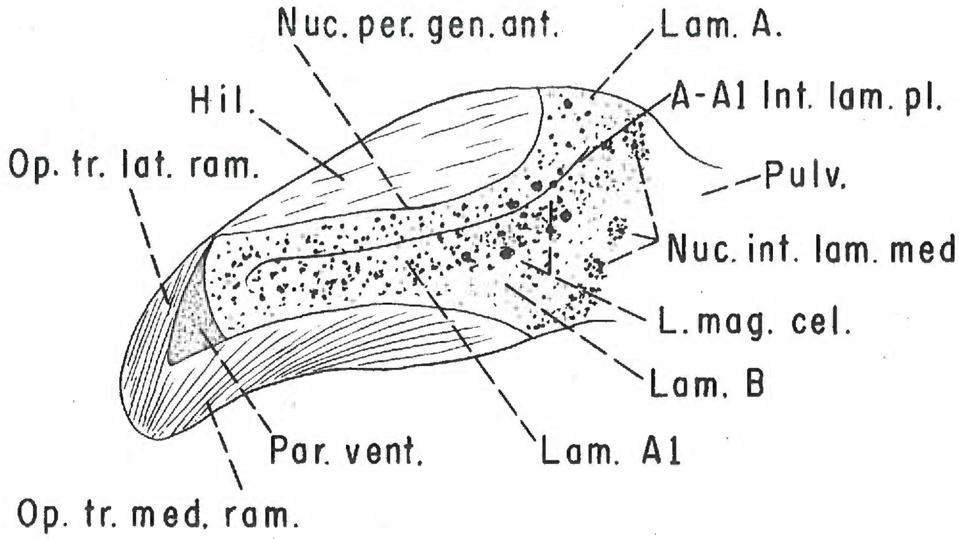
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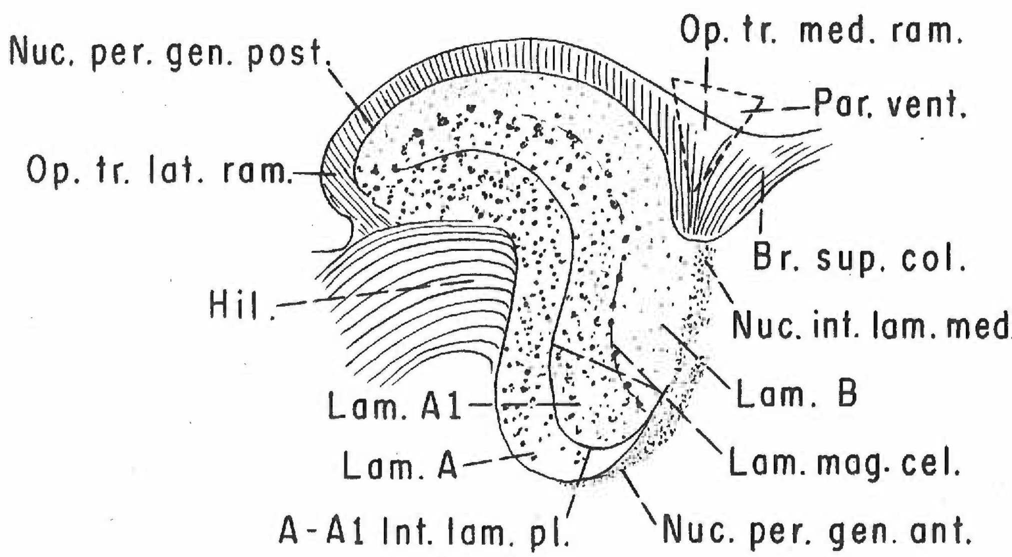
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Lam. A
A-A1 Int. lam. pl.
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Figure 3. A semidiagramatic drawing of a coronal section, of the brain stem in cat, to show the various strata at the level of the superior colliculus.

Figure 4. A semidiagramatic drawing of a horizontal section, of the brain stem in cat at the level of the superior colliculus and pretectal area, to show the appearance of the various strata of the visual tectum at this level.

Figure 5. A semidiagramatic drawing of a horizontal section of the brain stem in cat, at a level dorsal to Figure 4, to show the arrangement of the strata of the superior colliculus at this level.

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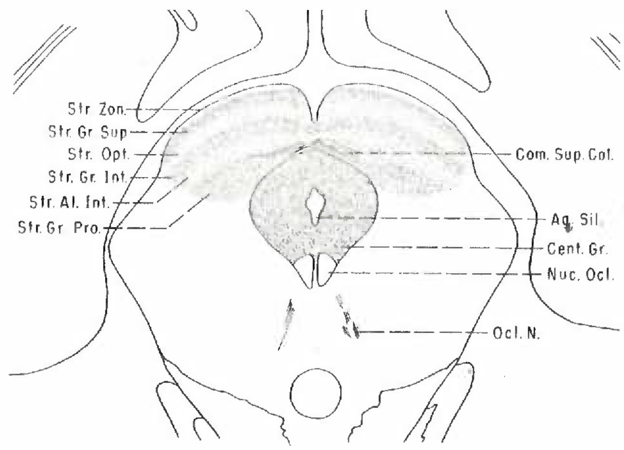
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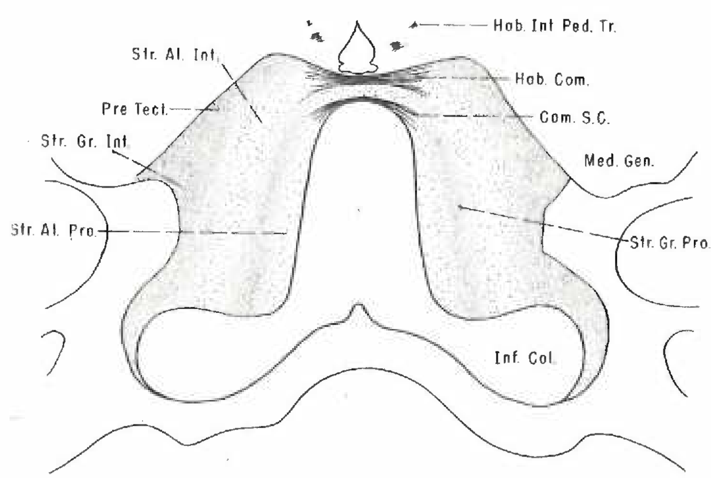
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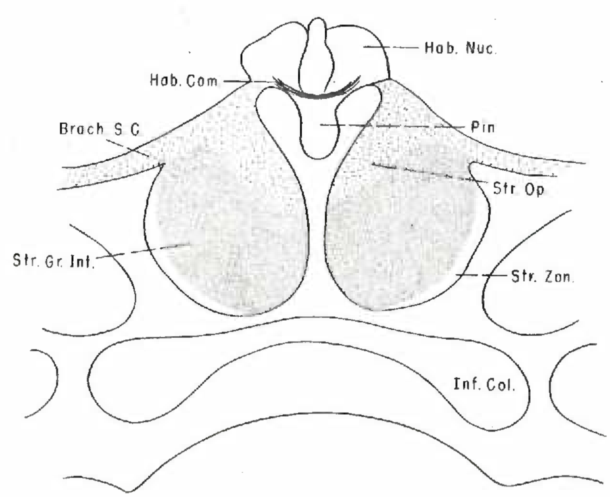
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Brach. S.C.
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Str. Op.
Str. Gr. Int.
Str. Zon.
Inf. Col.

fibers and boutons. By these silver impregnation techniques it is possible to study the myelinated and unmyelinated fibers as well as the cellular structures. Recently Hayhow (32), Altman (1), and Hoyat and Luis (37) have employed the Nauta-Gygax (53) method of silver impregnation. This, too, as pointed out by Hoyat and Luis (37), has its short comings. The main problem being non staining of some tissues and the difficulty of handling individual tiny frozen sections. In the present study the Stotler's (71) intensified protargal technique has been used. This method employes the standard paraffin sections. Non staining of tissue is unusual, and staining, in general, is found to be satisfactory. It is, however, not usually possible to distinguish the degenerated and undegenerated areas under the low power, recognition of the degenerating preterminals and boutons requiring higher powers of magnification.

This study also concerns itself with the determination of the segmental distribution of the retinal fibers in the optic chiasm, tract, lateral geniculate body, the pretectal area and the superior colliculus. No more recent study of such a nature was encountered in the literature than that of Brouwer (10), and Overbosch (55) in 1927. The approach is also different as the lesions are made in the optic nerve directly rather than in the retina.

Information was also sought in this investigation as to the distribution of optic nerve fibers according to fiber size.

An attempt was made to study these fibers of small and large diameter in normal as well as in the experimental brains stained in a similar manner.

I. Complete Section of One Optic Nerve.
A. Coronal Sections.

Cat R-369

A complete section of the left optic nerve was performed transcranially. Figure on next page diagramatically represents selected sections to show the pattern of degeneration in this animal. The prechiasmatic portion of the left optic nerve shows complete degeneration. Although in one section some fine undegenerated fibers were seen, presence of such fibers could not be confirmed in the remaining sections. These are to be regarded as artifacts. No degeneration was found in the intact right optic nerve.

In the chiasm degenerating fibers from the nasal portion of the left optic nerve begin to cross in the anterior most chiasm and are intermingled with the intact fibers from the right optic nerve. The number of crossed fibers is greater than uncrossed fibers. The degenerated fibers from the temporal portion of the left nerve occupy the lateral aspect of the chiasm.

After crossing, the fibers lie in the medial posterior chiasm and pass into the contralateral tract. A considerable scattering of fibers takes place in the tract. Most of the right optic tract is occupied by degenerating fibers. There is increased concentration of these fibers in the medial and ventral portions of the right optic tract. The fibers from

Figure 6. A series of six drawings to illustrate representative coronal sections of Cat R-369 after complete section of one optic nerve. (1) Complete degeneration in one optic nerve (lines). (2) Degeneration in the chiasm (lines). Note the degeneration free area of chiasm occupied by the intact uncrossed fibers of the intact nerve. (3) Degeneration in the optic tracts (lines). Only areas where degenerating fibers are heavily concentrated are shown. Also, note the degeneration in the rostral portions of the lateral geniculate bodies (stipples). (4) Degeneration in laminae A and B of contralateral lateral geniculate body and lamina A1 of homolateral lateral geniculate body. (5) Degeneration in the hrachii of the superior colliculi (lines) and pretectal areas (stipples). (6) Extent of degeneration in the superior colliculi.

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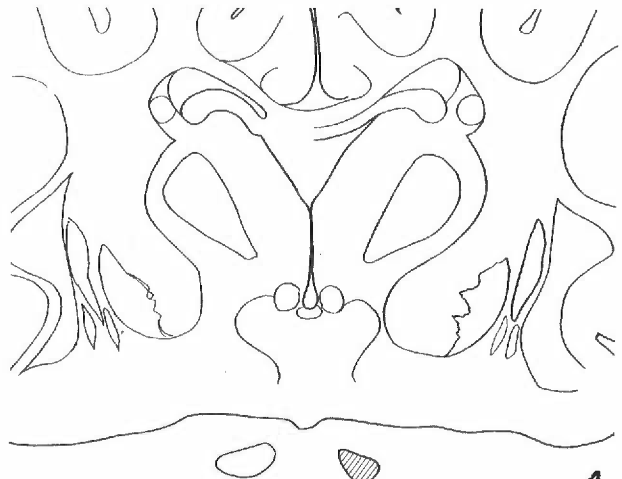

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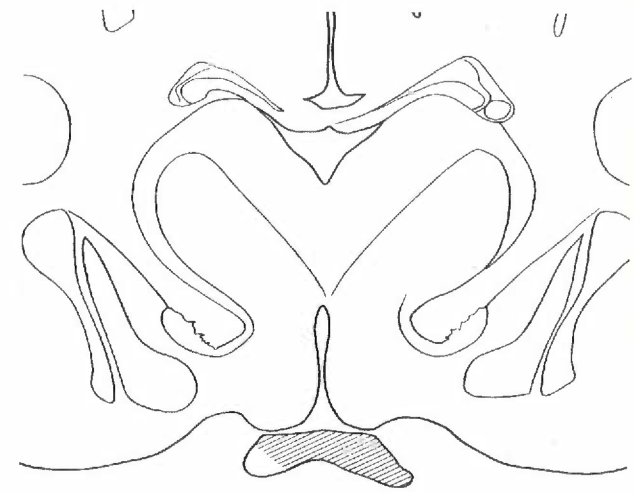

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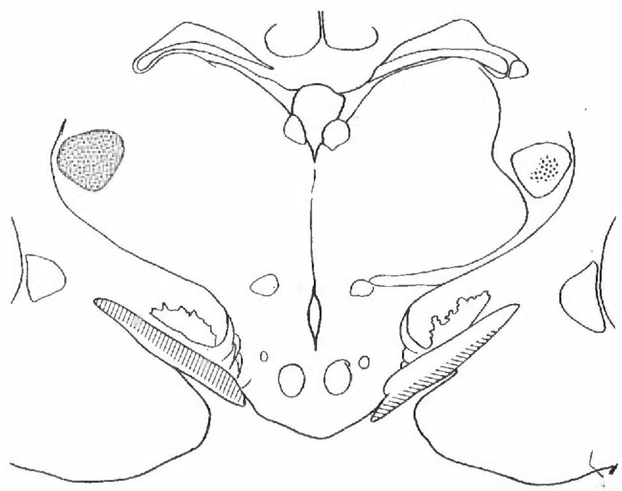

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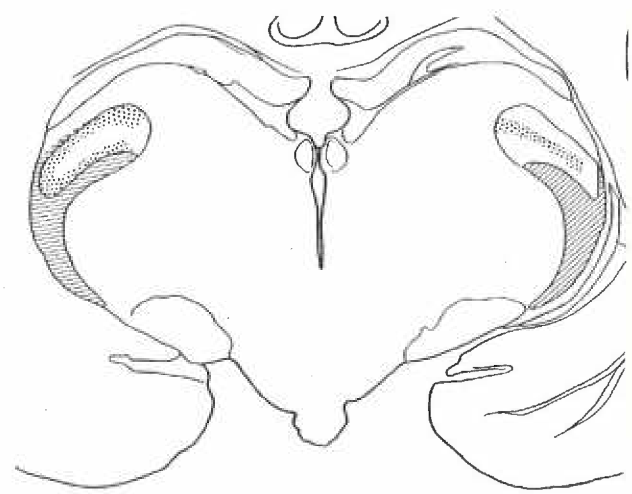

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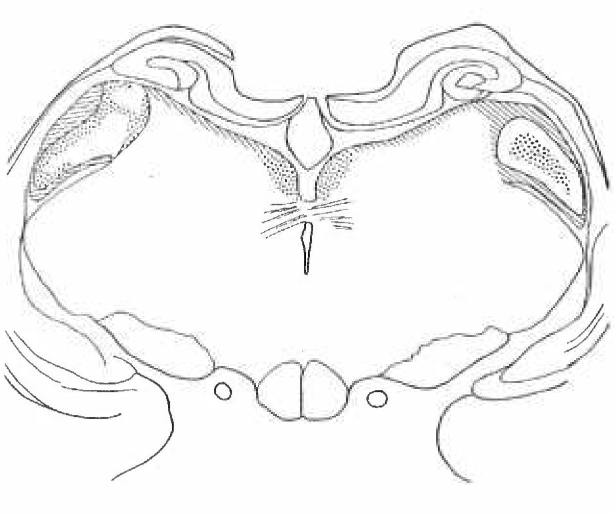

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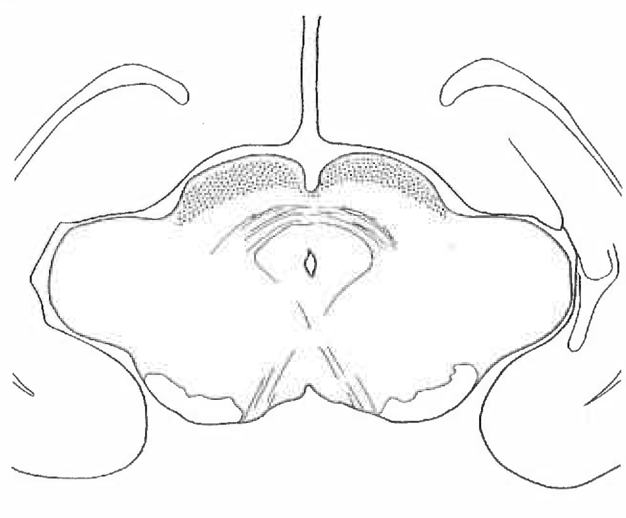


the lateral portion of the left optic nerve are scattered throughout the left optic tract. A much smaller number of degenerated fibers are noted in the left tract.

As the optic tracts are followed posteriorly they divide into a medial and lateral component. The two rami encircle the pars ventralis. A large number of degenerating fibers of passage are noted in the pars ventralis. Evidence of degeneration is present around a very few of the cells of the pars ventralis. The intensity of degeneration is greater on the right side.

Optic fibers enter the pars dorsalis from the lateral aspect progressively becoming oblique and then at right angles to the tract, as the main mass of the lateral geniculate body is reached. Degeneration is seen in a crescentic area over the lateral margin of the ventral portion of the right lateral geniculate body. A band like degeneration extends and forms a club shaped medial end. Another area of degeneration appears at the medial and superior margin of the lateral geniculate body, and gradually extends to encircle the entire periphery. Subsequent sections show degeneration in the ventral portions of pars dorsalis, and around its margin, leaving an inner crescent shaped, degeneration free area which gradually enlarges in size. As the hilum appears, the band of degeneration skirts the hilum. In the most dorsal portions of the pars dorsalis at this level, a small triangular shaped degeneration free area is seen. Medially a band of degeneration continuous with the main mass separates the pars dorsalis from the pulvinar. The dorsomedial margin of the pars dorsalis is free of degeneration. Caudally the entire geniculate body is peripherally encircled by a collar of degeneration with a degeneration free area located centrally. On the left side, the most rostral portions of the lateral geniculate body are free of degeneration. An area of degeneration, placed eccentrically in its dorsomedial aspect, appears and then splits into a small circular ventral and band like dorsal portions. The latter elongates mediolaterally, the ventral portion now lying medially curves into a horseshoe shape. The two ends then join to form an encircling band around a degeneration free area which in turn is surrounded peripherally by a degeneration free zone. Further posteriorly its central portion is occupied by process of degeneration and the marginal zone is completely free of degeneration.

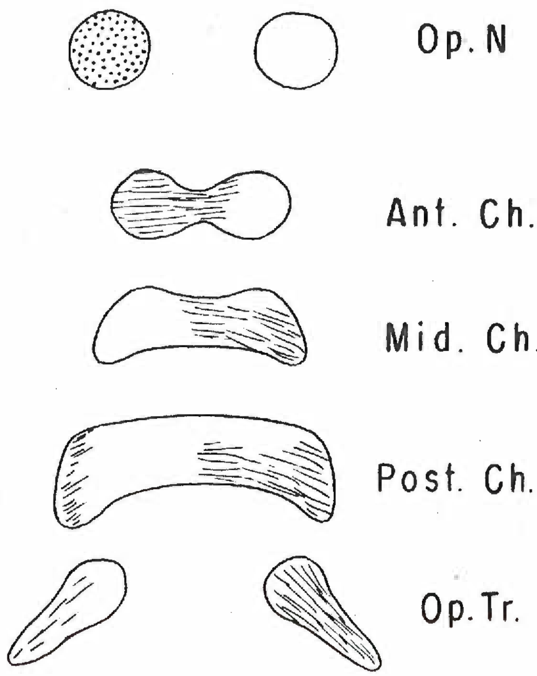
There are more degenerating fibers in the brachium of the superior colliculus, the pretectum and the superior colliculus of the right side. In the pretectal area evidence of degeneration is noted around the large cells of this area. In the superior colliculus degenerating axons are seen in the stratum opticum. Some of the degenerating fibers enter the stratum griseum intermediale, and others the stratum griseum superficiale and seem to terminate in these layers. None of the degenerating fibers penetrate any further than the above mentioned layers.

Some degeneration was noted in the anterior commissure and olfactory tract on the left side representing damage from retraction of frontal lobe in approaching the optic nerve.

Figure 7. A series of five drawings of the representative sections of the optic nerves chiasm and optic tracts from Cat R-370 to show the course of degenerating retinal fibers (lines) after a complete section of one optic nerve.

Figure 8. A diagramatic representation of the course of retinal fibers in the optic nerve, chiasm and optic tract in Cat R-370.

7.



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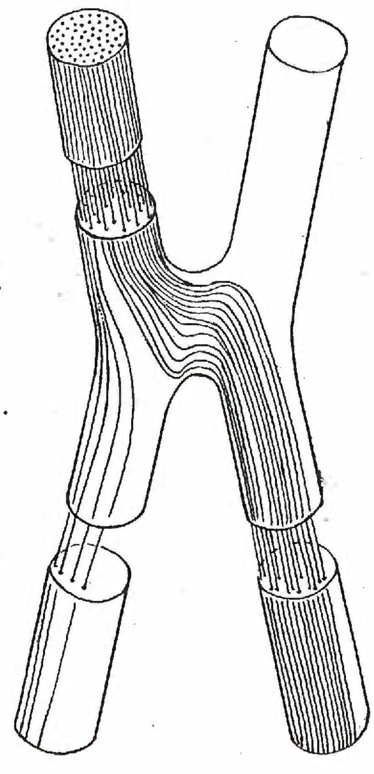


Cat R-370

The left optic nerve was transected through a transorbital approach. The prechiasmatic portion of the left optic nerve is completely degenerated. The right optic nerve shows no evidence of degeneration. The course and termination of degenerating fibers is essentially similar to that described above. Therefore, only additional points of information will be added.

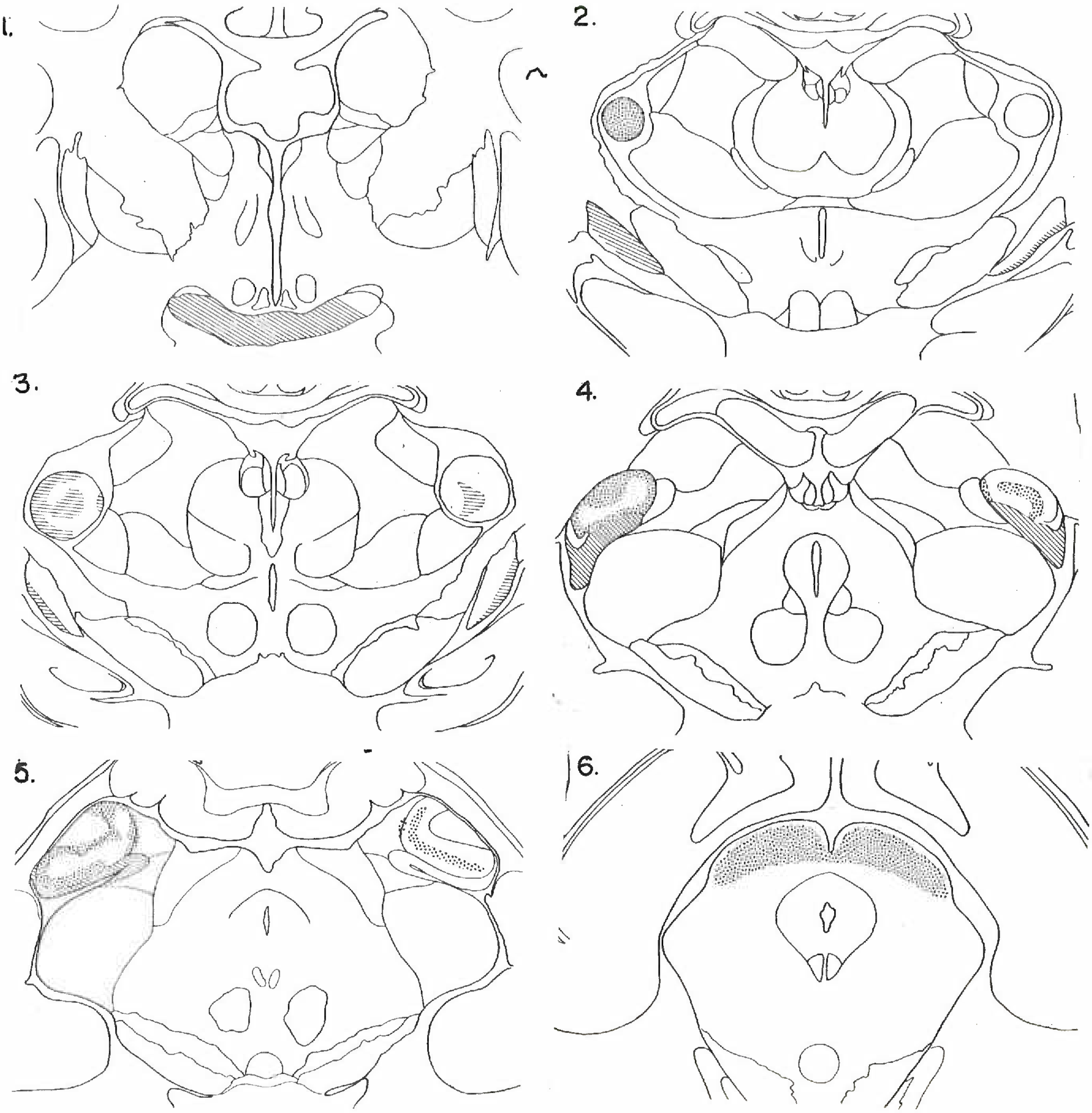
Crossing of optic fibers takes place mainly in the central chiasm. Some crossing degenerated fibers course through the hypothalamic area but do not end there.

Uncrossed fibers are located in the lateral chiasm, occupying a semilunar area. The number of uncrossed fibers is less than crossed fibers.

Both optic tracts are occupied by scattered degenerating axons of small and large diameter. The proportion of degenerating fibers is much greater in the right optic tract.

On the right side fine fibers are seen to end in the ventral layers of pars dorsalis while the large fibers with a few small fibers traverse through this layer and form a tangential plexus. In this plexus a few scattered large cells are embedded. Evidence of degeneration is present around some of these cells. The remaining fibers terminate in the two more dorsal layers. Degeneration is seen around cells scattered in the interlaminar plexus present between these two layers. In the left lateral geniculate body degeneration is present around cells scattered in the zone of transition between the two ventral layers.

Figure 9. A series of six drawings to illustrate representative sections of Cat R-370 after complete section of one optic nerve. (1) Position occupied by degenerating fibers from the sectioned optic nerve (lines). (2) Areas of maximum concentration of degenerating fibers in the optic tracts (lines), and degeneration in the rostral portion of the contralateral lateral geniculate body (stipples). (3-5) Pattern of degeneration in the contralateral and homolateral pars dorsalis. (6) Degeneration in the stratum griseum superficiale, stratum opticum and stratum griseum intermediale of the superior colliculi.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Most of the fibers in the brachium of superior colliculus are of small diameter, and only a few fibers are seen. Some of the fibers traversing through the brachium seem to be a continuation of the optic fibers which have given off collaterals to the lateral geniculate body.

No degeneration is seen in stratum zonale, or layers deeper than stratum griseum intermediale. None reach the central gray or oculomotor nuclear complex.

Cat R-383

The left optic nerve was sectioned completely transorbitally. Besides the findings described for Cat R-369 and R-370, the following points were noted.

In the right pars dorsalis degeneration in lamina A and B is seen. A sharp line of demarcation between lamina B and A1 cannot be identified. There is, however, a reduction of degenerating preterminals in the region of transition. Degenerating preterminals extend into the A-A1 interlaminar plexus.

In the left pars dorsalis the process of degeneration shows its maximal intensity ventral to A-A1 interlaminar plexus in the lamina A1. An overlapping of degeneration into the A-A1 interlaminar plexus was not noted. The A1-B transitional zone contains evidence of degeneration around its cells.

B. Horizontal Series

Cat R-379

The pattern of degeneration in this animal is shown diagramatically in the accompanying figure. The left optic nerve

Figure 10. A series of four drawings illustrating representative horizontal sections of Cat R-379 to show the pattern of degeneration after complete section of one optic nerve. (1) Degeneration in the contralateral lateral geniculate body, both pretectal areas and both strati opticum (stipples). (2) Degeneration in laminae A and B in the contralateral pars dorsalis and in lamina A1 of the homolateral pars dorsalis (stipples). Degenerating fibers are present in the brachii of superior colliculus (lines). Also, note the degeneration in the pretectal areas (stipples). (3) Degeneration in laminae A and B contralaterally and in lamina A1 homolaterally (stipples). Degenerating fibers in the brachii bilaterally (lines), and degeneration in the stratum griseum intermediale (stipples) are also indicated. (4) Degeneration in the lateral geniculate body and the stratum griseum superficiale (stipples). Note the absence of degeneration from the stratum zonale.

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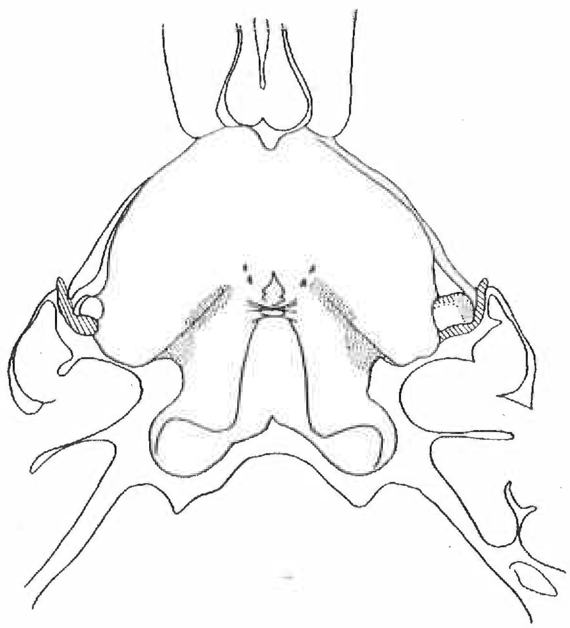

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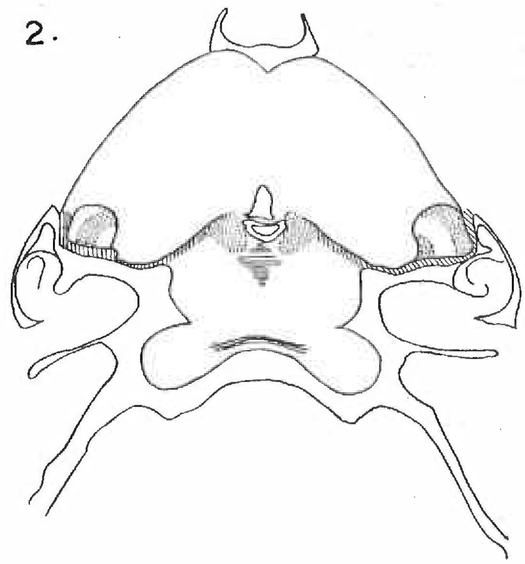

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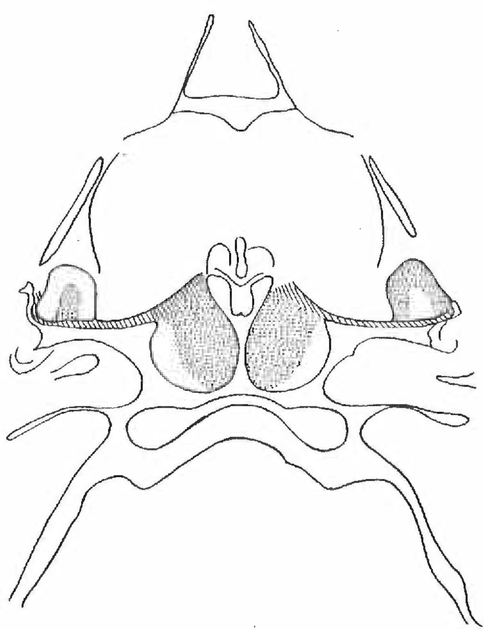

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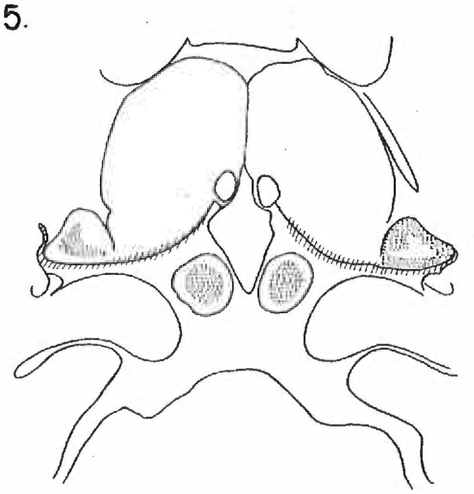

has been sectioned completely and degeneration is present throughout its extent. The right nerve is completely free of degeneration, except for the medial tip of its most proximal end just before it joins the chiasm. Here a few degenerated crossed fibers loop into the intact nerve. Crossing takes place mainly in the central portion of the chiasm, the crossed fibers then enter the optic tract where they are diffusely scattered, but show a heavier concentration in the medial portion of the tract.

A few degenerating fibers course through the suprachiasmatic area of the hypothalamus but no evidence of these fibers ending in the hypothalamic area is found. Some of them are seen to rejoin the posterior chiasm or optic tract.

The uncrossed fibers enter the left optic tract where they are scattered and become difficult to identify as a separate bundle. They, however, seem to maintain a preponderance in the lateral aspects of the tract.

The optic tract divides to enclose the pars ventralis which contains many degenerating fibers of passage. These fibers of passage are more on the right side than on the left.

On the right side the pars dorsalis makes its appearance as a circular area of degeneration medial to the pars ventralis and separated from it by a well defined fibrous septum. An area free of degeneration appears and surrounds the area of degeneration. Another band of degeneration appears medially to the degeneration free area. The two areas of degeneration then join to enclose an area free of degeneration. In the middle sections the trilaminar appearance and the S-shaped laminae are apparent.

Segments of A-Al interlamina plexus are recognizable in various sections. The transition between Al and B is marked by a layer of sparsely scattered large cells of the lamina magnacellularis. The area between the A-Al interlaminar plexus and lamina magnacellularis is completely free of degeneration. Process of degeneration is encroached onto A-Al interlaminar area, and the transitional zone between Al and B.

On the left side the part of the pars dorsalis first appearing medial to the pars ventralis is completely free of degeneration. A band of degeneration appears medially to the former and partially envelopes it. This in turn is skirted in its medial and rostral aspects by another area free of degeneration. The two degeneration free areas join to surround the central area of degeneration. An S-shaped configuration of the three laminae is noticable. Overlapping of degeneration is only seen in the zone of transition between lamina Al and lamina B.

The brachium of the superior colliculus is formed by fibers converging medially from the medial and lateral rami of the optic tract. Both brachia of superior colliculus contain degenerating fibers, but the right contains a greater number. A greater number of these fibers turn medially and rostrally and end around cells of the pretectal area. Other fibers turn caudally and enter the stratum opticum of the superior colliculus from its medial rostral aspect. Degenerating preterminals are also seen in the stratum griseum intermediale.

In the optic nerve chiasm the small and large fibers are

Figure 11. A series of four drawings illustrating representative horizontal sections of Cat R-377 to show pattern of degeneration in the lateral geniculate bodies and visual tectum after complete section of one optic nerve.
(1) Degeneration in the contralateral laminae A and B (stippled). (2) Degeneration in the homolateral lamina A1 (stipples). Note the characteristic S-shaped configuration of the laminae and segregation of crossed and uncrossed fibers in alternate laminae. (3-4) Degeneration in the pretectal and collicular areas (stipples).

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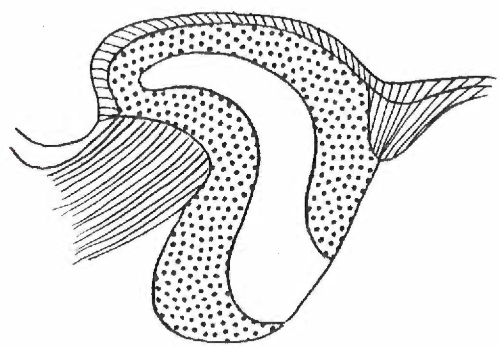

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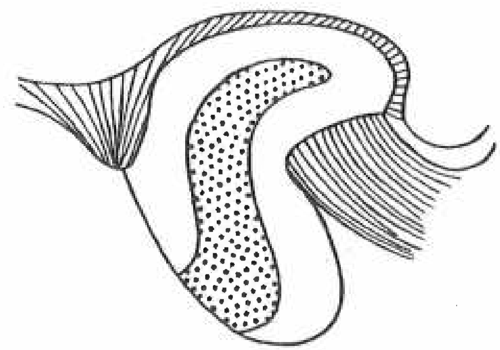

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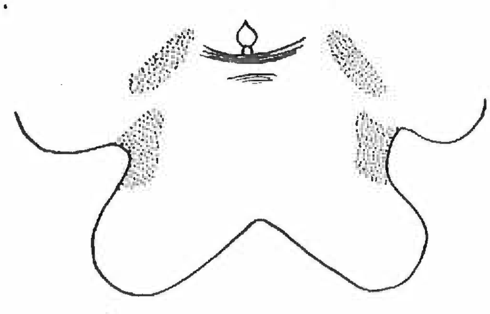

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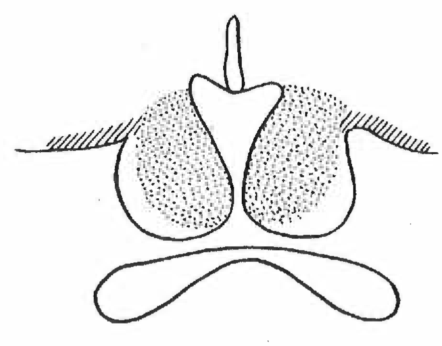

intermixed and do not show any definite grouping according to fiber size. As they approach the tract they start to group according to size. The small fibers move medially, the large fibers remaining lateral. This grouping is maintained throughout the tract. Their distribution in the pars ventralis, pars dorsalis, brachium of superior colliculus, pretectal area and tectum is similar to that described in coronal sections after complete section of one optic nerve.

Cat R-377

The left optic nerve has been sectioned completely. The survival period in this animal is one month. Findings are similar to those described for Cat R-379. The degeneration pattern in the contralateral and homolateral side differs very little, slight variation being due to different plane of section, and the longer period of survival. At this stage no degenerating preterminals or boutons are identified.

Cats R-376, 380 and 399.

The findings are similar to those described above. No significant change in pattern of degeneration is noted to justify a detailed account.

II. Lesions Involving the Medial Optic Nerve Fibers.

A. Coronal Sections.

Cat R-368

An attempt was made to section the medial portion of the left optic nerve transcranially. The lesion involves the medial portion of the nerve closer to the mid line in the lower quadrant than in the upper quadrant.

The degenerated fibers start crossing in the anterior chiasm and interdigitate with the intact fibers from the right optic nerve. More degenerating fibers are seen in the ventral aspect of the chiasm.

In the right optic tract, these degenerating fibers are scattered considerably. More of these fibers enter the medial ramus of the optic tract, from there they gradually pass into the ventral portion of the lateral geniculate body. No degenerating fibers are seen in the left optic tract.

In the right lateral geniculate body greatest density of degeneration is present in the peripheral dorsal and ventral layers of pars dorsalis. It does not quite extend to the medial boundary of the lateral geniculate body. Other findings are similar to those described for the contralateral geniculate body in animals with complete sections of one nerve. No degeneration is noted in the left lateral geniculate body.

Fibers reach the right pretectal area mainly through the lateral branch of the brachium of superior colliculus, and terminate around cells of this area. No degenerating axons were seen in the left brachium or pretectal area.

A smaller number of degenerating fibers reach the right superior colliculus, mainly through the lateral branch of the brachium of superior colliculus. Entering the stratum opticum some end around cells in this area. Some degeneration is also seen around cells of the second and fourth layers of the superior colliculus. Concentration of degeneration is heaviest in the medial and rostral medial portion of the superior colliculus.

B. Horizontal Sections

Cat R-384

A mid sagittal section of the optic chiasm was performed transcranially.

The central portion of the chiasm has been destroyed by the lesion. Both optic tracts are occupied heavily by degenerating fibers. A few intact fibers representing the uncrossed fibers are also scattered in the tracts.

The lateral geniculate body on both sides shows extensive degeneration. It is quite similar to that described for the contralateral geniculate body in animals with complete sections of one nerve.

An equal number of degenerating fibers are seen in both brachia of superior colliculus. A larger proportion reaches the pretectal area. The pretectum also receives some fibers by way of medial ramus of the optic tract.

The superior colliculus receives a comparatively smaller contribution mainly through the lateral division of the brachium of superior colliculus, a few fibers arriving by way of the medial division. The distribution in the second, third and fourth layer is similar to that described previously.

III. Lesion of Temporal Portion of One optic Nerve.
A. Coronal Sections

Cat R-378

Through transcranial approach a lesion was made in the temporal portion of the left optic nerve. The lesion involves the left temporal upper quadrant mainly and the left lower quadrant partly.

Degeneration is seen mainly in the lower portion of the prechiasmatic part of the left optic nerve. These fibers course through the lateral ventral aspect of the chiasm and then become scattered in the left optic tract.

Few fibers of passage are seen to pass through the pars ventralis. No terminal degeneration was found in this area.

The central portion of the left pars dorsalis shows degeneration in its lateral and ventral portions mainly. Degeneration overlaps, and extends into the zone of transition between the two ventral laminae and the cells of lamina magna cellularis in this zone of transition. No degeneration is seen in the right lateral geniculate body.

A few degenerating fibers are seen in the lateral branch of the brachium of superior colliculus on the left side. These are more in its rostral portion. Some of these fibers are seen to enter the left pretectal area while the left superior colliculus receives a very small number of degenerating fibers. No degenerating axons are seen in the comparable areas on the right side.

B. Horizontal Sections.

Cat 398

In this animal a lesion was made in the lateral portion of the right optic nerve transorbitally.

The lateral portion of the right optic nerve shows degenerating fibers. These fibers run into the lateral portion of the chiasm and enter the right optic tract laterally. In the tract

Figure 12. A series of five drawings of representative sections of optic nerves, chiasm and optic tracts, in Cat R-382, to show course of degenerating retinal fibers from the superior quadrants (lines). Stipples indicate the extent of the lesion in the nerve.

Figure 13. A diagramatic representation of the course of retinal fibers from the superior quadrants in Cat R-382 through the optic nerve chiasm and optic tracts.

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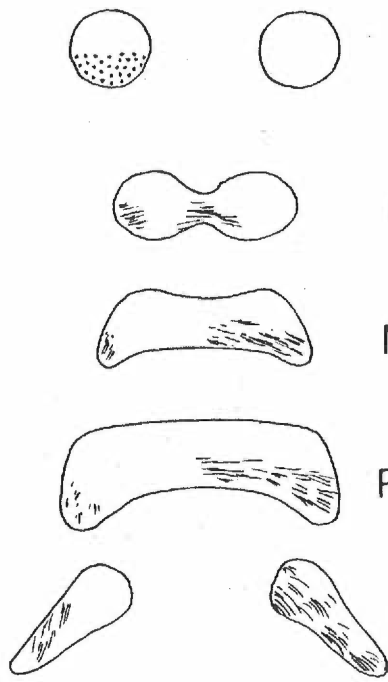

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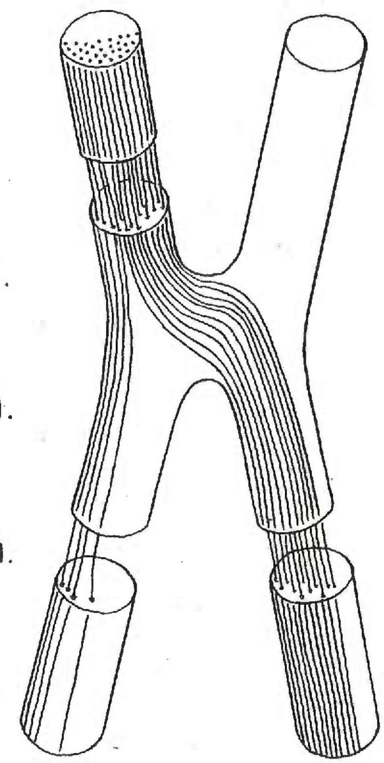


they are scattered but show some degree of concentration in the lateral aspect.

No degeneration is seen in the left lateral geniculate body. On the right side the pattern of degeneration is similar to that described for the homolateral side in animals with complete section of one nerve.

A few degenerating axons are noted in the left brachium of superior colliculus. The right brachium is free of degenerating axons. Some degeneration is also seen in the left pretectum and superior colliculus.

IV. Sections of Superior Half of One Optic Nerve.
A. Coronal Sections.

Cat R-382

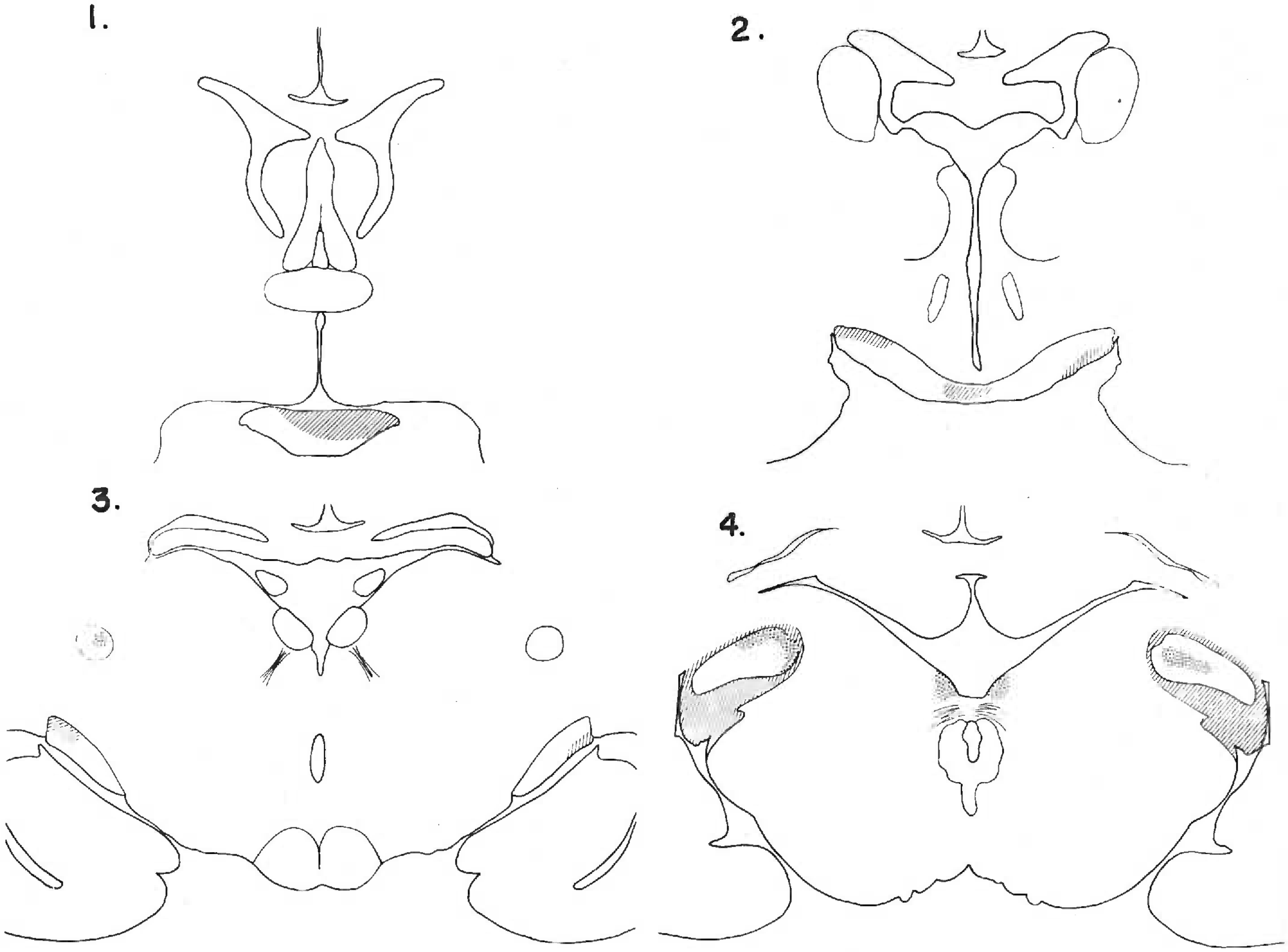
Representative diagramatic sections from this animal are shown in the figure on the next page. The superior portion of the right optic tract was sectioned transorbitally.

The degenerating fibers from the superior portion of the right optic nerve enter the chiasm superiorly. The nasal fibers cross in the superior portion of the chiasm, the temporal fibers remaining laterally and somewhat ventrally.

The crossed fibers enter the dorsomedial part of the left optic tract, then scatter to a considerable extent. There is, however, some increased concentration in the dorsomedial portions of the tract.

The uncrossed fibers enter the right optic tract dorsoventrally where they undergo considerable scattering, but show some degree of preponderance in the dorsolateral portions of the tract.

Figure 14. A series of four drawings to illustrate representative sections of Cat R-382 to show the distribution of fibers from the superior quadrants of one optic nerve.
(1and 2) The dorsal location of the superior quadrant fibers in the chiasm and optic tracts (lines). (3) Degeneration in the dorsal portions of the optic tracts (lines) and the rostral portion of the contralateral lateral geniculate body (stipples). (4) Degeneration of the medial portions of laminae A and B contralaterally and lamina A1 homolaterally. Also, note the degeneration in the pretectal areas. (stipples).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B. Horizontal Sections.

Cat R-393

The major portion of the lesion involves the superior half of the left optic nerve. The disposition of the degenerating superior quadrant fibers in the optic nerve, chiasm and tract is similar to that described for Cat R-382. Crossing of these fibers is noted to be maximum in the posterior chiasm.

The pars ventralis contains numerous degenerating fibers bilaterally, but more on the right.

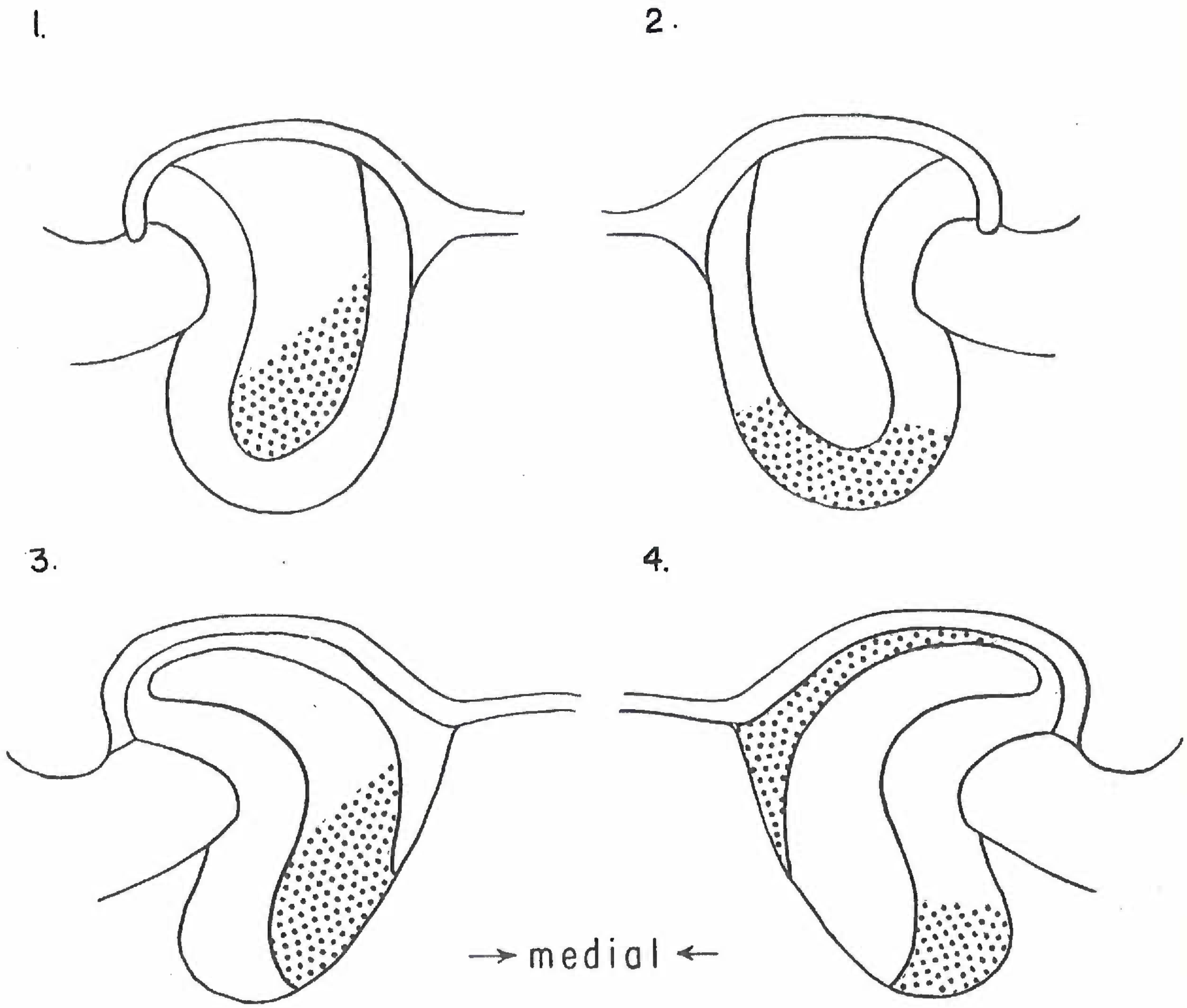
In the right pars dorsalis, degeneration occupies the medial and caudal aspects of the periphery identified as the medial and caudal aspects of lamina A and B. This distribution is noted in the more dorsal sections of the series.

On the left side degeneration is present in the middle layer, identified as lamina A1. The process of degeneration shows its maximum concentration in the caudal and medial portions, and is more pronounced in the more dorsal sections. The most dorsal and most ventral sections being free of degeneration.

Degenerating fibers are seen in the right pretectal area and are distributed evenly. No definite segmental arrangement can be established. Evidence of degeneration was very scanty in the left pretectal area.

In the right superior colliculus the heaviest concentration of degeneration is located in the caudal and lateral portions. It is present in the stratum opticum, stratum griseum intermediale and the stratum superficiale. Degeneration in the left superior

Figure 15. A series of four drawings to illustrate representative horizontal sections of the contralateral and homolateral lateral geniculate bodies of Cat R-396 to show areas of degeneration in the pars dorsalis after section of the superior fibers of one optic nerve. (1-2) Degeneration in the rostral and medial portions of the homolateral lamina A1 (stipples). (3-4) Degeneration in the rostral and medial portions of laminae A and B.



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→ medial ←

colliculus is very sparse.

Cat R-396

The superior portion of the left optic tract was sectioned transcranially. The distribution of these superior temporal and nasal fibers is similar to that described for Cat R-393. Figure on the next page shows the distribution of the superior quadrant fibers diagramatically.

V. Distribution of Fibers by Size in Normal Brains.

A. Coronal Sections.

Cat 253

In the prechiasmatic portion of optic nerve, small and large fibers are intermingled with some tendency of the large fibers to be in the peripheral zone. The number of small fibers is much larger than the large fibers.

In the chiasm the small and large fibers are intermingled and show no definite separation in bundles according to size. Very few of the large fibers cross in the chiasm.

The fibers organize according to size in the optic tract. The small fibers form a tightly packed aggregation of fibers in the dorsal portion of the tract. The large fibers are loosely packed and are located in the ventral part of the tract. In the more caudal sections, the large fibers move into a ventrolateral and then a lateral position, and the small fibers come to lie medially.

The majority of the fibers of the optic tract enter the medial ramus where the large and small fibers are intermixed. They enter the lateral aspect of the ventral portion of the pars dorsalis at right angles to the medial ramus. Further medially they take a progressively oblique course, the most medial fibers entering horizontally.

The lateral ramus receives a much smaller share of fibers from the optic tract. Almost all of these fibers are of small size. Very few of these enter the pars dorsalis.

Only small fibers are seen entering pars ventralis. Multiple branching fibers and terminal boutons are visible around the small cells of pars ventralis.

In the pars dorsalis large and small fibers branch several times. The termination seems to be by way of boutons which are seen to lie as club-shaped structures around the cell body.

The brachium contains small fibers mainly, although an occasional large fiber is seen. In the pretectal area all fibers are of small size and terminate by means of boutons around cells of this area.

In the superior colliculus the majority of fibers are of small diameter, but a few large fibers are also seen.

B. Horizontal Sections.

Cat 263

The fibers are grouped by size in the optic tract. The small fibers are located rosteromedially, occupying a larger part of the tract. The large fibers are found in the caudolateral portion of the tract, occupying a smaller area. The small fibers are tightly packed while the large fibers are loosely arranged.

As the two rami of the optic tract are formed, a larger proportion of fibers enter the medial ramus. At this point the small tightly packed fibers occupy the inner portion of the tract, the large loosely packed fibers lying peripherally.

A considerable number of fibers enter the pars ventralis. They are all of small size. Termination is similar to that described for Cat 253.

Large and small fibers enter the pars dorsalis mainly through the medial ramus of the optic tract. Multiple branching fibers are seen around the cells of pars dorsalis. They end by means of terminal boutons which lie in close proximity to the cell body. Most of the large fibers and some of the small fibers pass through lamina B and enter the lamina A1 and A.

In the brachium of superior colliculus, pretectal area and superior colliculus, the distribution by fiber size is similar to that described for Cat 253.

DISCUSSION

The visual pathways, in general, have been the subject of considerable study in the past. Henschen (31) divided the visual system into frontal, middle and occipital portions, and felt that there was a discrete point-to-point representation in this system. Polyak (60) divides it into infranuclear, intermediate, and supranuclear portions. This study is concerned with the first two divisions of these authors. The infrageniculate pathways include the optic nerve, chiasm and tract. In the intermediate portion are included the lateral geniculate body, the pretectal area and the superior colliculus.

The Infrageniculate Division.

Wilbrand and Sanger (78) found that the fibers from different quadrants lie in separate bundles, and recognized a compact papillomacular bundle in the ventrolateral aspect of the optic nerve. Ronne's (64,65) studies on human material revealed that the ganglion cell degeneration in the retina corresponded to the scotoma for color. He traced the course of the papillomacular bundle in the infrageniculate division of visual pathways.

Optic Nerve

In an attempt to outline the disposition of optic fibers circumscribed retinal lesions were made by Falachi (57), Baquis (57, and Pick (57). The degenerating fibers were then traced to determine their disposition. Discrete retinal lesions, with a knife or electrocautery, were made by Usher and Dean (75), Parsons (57), and Polyak (60) in rabbits and monkeys. Using the

Marchi technique for study of the resultant degeneration, they found that degeneration in the nerve corresponded to the retinal lesions and maintained the same relationship throughout the nerve. Parsons (57) in monkeys, found that the nearer the lesion was to the optic papilla the greater was the extent of degeneration and described rotation of the nasal fibers ventrally and temporal fibers dorsally in the posterior portion of the nerve near the chiasm. Such a rotation in the prechiasmatic portion of the optic nerve of primates has been denied by Hoyat and Luis (37) recently. Neither was such a rotation found in the cat in the present study.

Usher and Dean (75) had found some evidence of degeneration in the opposite optic nerve, but considered this to be an artifact. Parsons (57) on the other hand, interpreted similar findings to be genuine in nature. He felt that these fibers in the opposite intact nerve belonged to some form of inter-retinal fibers or collaterals distributed to physiologically corresponding parts of the opposite retina. In his opinion these possibly induced chemical changes in the visual system or movement in the cells so that visual impulses could subserve a modified type of binocular vision. Kellerman (57) attributed similar findings in pathological human material to compression of these fibers by the crossing of the opposite side undergoing atrophic process in the chiasm. These findings have not been reduplicated by subsequent, more sophisticated, histoanatomical methods and Polyak (60) feels that no commissural fibers directly link the two eyes. In the present study, some degenerating fibers were found in the most proximal and medial portion of the intact opposite optic nerve. However, these degenerating fibers belong to the sectioned optic nerve. These are the medial most nasal fibers which take the longest course and loop into the most proximal and medial portion of the opposite optic nerve just before its junction with the chiasm. It is also noted that the nasal fibers are longer than the temporal fibers due to the fact that they have to cross the transverse extent of the chiasm during the process of decussation, the looping adding further to their length.

Brouwer and Zeeman (11) found the macular bundle to be gathered chiefly in the temporal area of the optic nerve in monkeys. Polyak (60) stated that these fibers were located temporally only in the three-fourths of the post bulbar stretch of the optic nerve and assumed a central position in its proximal fourth where they became surrounded by peripheral retinal fibers. Hoyat and Luis (37) could not find an exclusive macular bundle in the most distal portion of the nerve in monkeys.

Polyak (60) agreed with Brouwer and Zeeman that the organization of fibers in the optic nerve was in a quadrantic fashion representative of the respective quadrants in the retina. Wolff and Penman (79), and Hoyat and Luis (37) point out that the peripheral retinal fibers course peripherally in the optic nerve in the primates. This statement cannot be corroborated from the present investigation since the nature of the lesion was such that a definite retinal quadrant was not directly involved, but rather an attempt was made to make a partial lesion of the optic nerve itself.

<u>Optic Chiasm</u>

The number of crossed fibers increases progressively with the development of binocular vision. In the cat. according to Barris, Ingram and Ranson (7), the greater part of the optic nerve fibers cross. According to Glees (26,28) they constitute a third of the total number of optic fibers in this animal.

Ronne (64,65) found that the crossed and uncrossed fibers separate in the intracranial portion of the nerve, crossing in the middle and posterior portions of dorsal chiasm in human material.

A mixing of lower crossed and both uncrossed fibers in the lateral borders of the chiasm was found by Hoyat and Luis (37) in the primates. They found the peripheral nasal retinal fibers in the dorsal as well as the ventral area of the chiasm, and a free intermixture of macular fibers with peripheral quadrant projections. The superior retinal fibers were found dorsally and the inferior retinal fibers ventrally in the chiasm by Brouwer and Zeeman (11), and Polyak (60) in monkeys.

In the present investigation separation of the crossed and uncrossed fibers was found to take place in the most proximal portion of the optic nerve at its junction with the chiasm. The majority of the fibers from the medial portion of the nerve cross to the opposite sides. The crossing takes place throughout the chiasm, but mainly in the central portion.

Polyak (60) states that some chiasmal fibers loop in the opposite optic nerve in the cat, and that such a detouring is more enhanced in man and monkey. This is confirmed in the present study. A loop of the medial most portion of the nasal fibers reaches into the most proximal medial portion of the opposite optic nerve.

The crossing fibers from the two sides intermingle in the chiasm and no definite separation exists between the fibers of the two sides.

The fibers from the superior portion of the optic nerve remain dorsally and those from the inferior portion of the nerve ventrally. The upper nasal fibers cross predominantly in the dorsal portion of the chiasm. The decussation being maximum in the posterior portion of the chiasm. After crossing they lie in the superior medial portion of the posterior chiasm just before entering the contralateral optic tract. The upper temporal fibers remain in a lateral position throughout the extent of the chiasm. The lower quadrants occupy a ventral position in the chiasm. Some of the most lateral of the crossing fibers have a tendency to loop into the medial aspect of the ipsilateral optic tract, just at the junction of the chiasm and the tract.

According to Polyak (60) the supraoptic commissure and other similar decussating fiber systems of the adjacent region of the hypothalamus have no direct connection with the visual system except topographically. Hoyat and Luis (37) found degenerating optic fibers of passage in the hypothalamic region with no evidence of terminal arborization in monkeys.

In the present study a few degenerating fibers were seen intermingled with the undegenerated fibers of the supraoptic commissure in the hypothalamic region. This portion of the hypothalamus is in direct contact with the optic chiasm. However, there was no evidence of these fibers terminating in this area and they are considered as fibers of passage which run a slightly aberrant course into the ventral portion of the hypothalamus.

Optic Tract

In the optic tract a considerable intermingling of fibers is found. The crossed and uncrossed fibers spread out uniformally and intermingle in the optic tract (60). The conclusions in the present study based on the predominant concentration of these fibers, indicate that the uncrossed fibers are concentrated mainly in a small crescentic area over the lateral aspect of the tract while the larger remaining portion of the tract is occupied predominantly by crossed fibers.

A rotation of the superior and inferior quadrant fibers in the optic tract has been reported by Hoyat and Luis (37) in the Macaque, but such a rotation was not found in the cat in the present study.

The crossed superior quadrant fibers enter the dorsal medial portion of the opposite optic tract, and then disperse throughout the dorsal portion of the tract. The uncrossed upper quadrant fibers enter the dorsolateral part of the homolateral optic tract where they are scattered diffusely. A much smaller number of the optic fibers enter the homolateral optic tract, the larger portion entering the contralateral tract.

<u>Fiber Size Distribution</u>

Polyak (60) stated that the optic fibers vary in thickness. Some distance from the eyeball, the coarsest fibers are located peripherally in a zone not exceeding one-tenth to one-eigth of the nerve diameter. The thin fibers in the immediate vicinity of the eyeball are found along the temporal margin of the nerve, but some distance from the eyeball they are located centrally. This position has been shown to be occupied by macular fibers by Brouwer and Zeeman (11), Polyak (60), Hoyat and Luis (37) and others, indicating that the majority of macular fibers are of small size.

In the present investigation the optic nerves were found to contain smaller fibers in greater number than large fibers. Some tendency of the large fibers to remain peripherally and the small fibers centrally was noted. However, a considerable amount of dispersion and intermingling was found. In the chiasm, the majority of crossing fibers were found to be of small size.

The thick fibers were found in the wedge shaped ventral medial end of the tract, and thin fibers near the surface of the bulkier, club-shaped dorsolateral extremity of the tract in monkey by Polyak (60). Hayhow (32) found the large and small fibers to be closely intermingled in the cat. In the present studies these fibers are seen to undergo reorganization. The fine fibers come to lie medially as a tightly packed group in the medial aspect of the tract, and appear to be in greater number than the large fibers. The large fibers are loosely packed and lie lateral to the fine fibers. This arrangement was established in the normal as well as in the experimental material.

Different sizes of the fibers and their organization indicates that they probably subserve different functions. Electrophysiologically these fibers were classified by Bishop and Clare (9) and Bishop, Jermy and Lance (8) according to their speed of conduction. They pointed out that the phylogenetically more recently developed areas are served by the larger and faster conducting fibers.

Crosby, et al, states that each thick optic fiber gives a fine collateral before entering the lateral geniculate body. Although a very few such collaterals were seen, the fact that the number of fine fibers was considerably increased in the proximal portion of the tract is in favor of this view.

THE INTERMEDIATE DIVISION

The Lateral Geniculate Body

The lateral geniculate body which is present in all mammals, was first divided into dorsal and ventral portions by Kollikar according to LeGros Clark (15). These portions were identified by Tsai (74) in oppossum, Winckler and Potter (76), Brouwer and Zeeman (11), and others in rodents. A lobulodorsal and lobuloredundo was described by Cajal(14) in cats. Gilbert (25) considered the lateral geniculate body to functionally belong to the ventral thalamus.

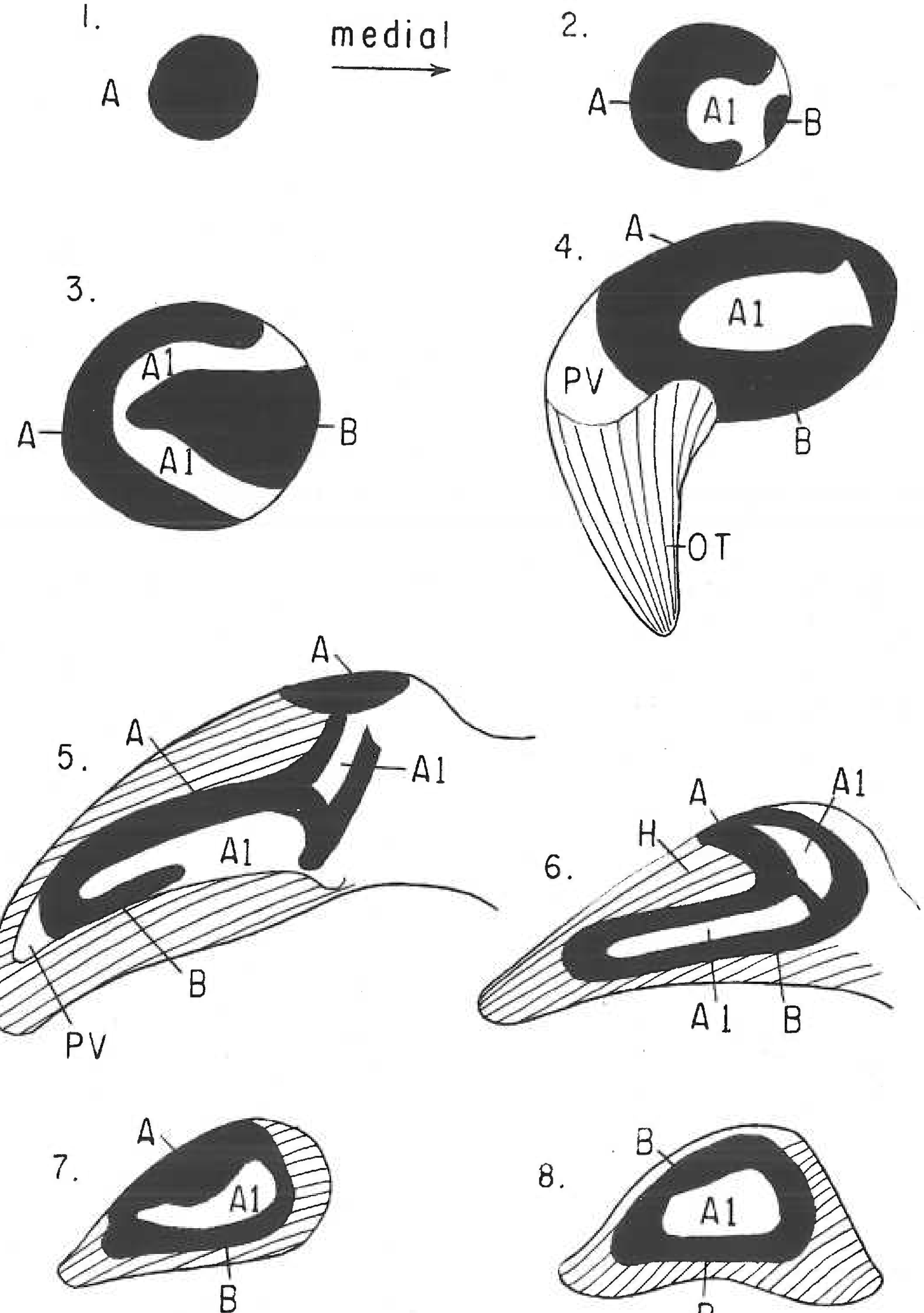
Tello (72) noted the trilaminar arrangement of the lateral geniculate body, and the characteristic S-shaped lamina in the cat. Thuma (73) reconstructed the lateral geniculate body in the horizontal plane from his coronal sections in the cat. His schematic drawing closely resembles, in appearance, the shape of the lateral geniculate body found in horizontal sections in this study. The difference is probably due to the strict dorsoventral plane of section in this investigation as compared to his theoretical plane of section which is inclined towards the mid line at an angle of thirty degrees from the vertical. An S-shaped configuration of the laminae was found to be present in the horizontal sections in this study.

Minkowski (48) described degeneration in alternating laminae of lateral geniculate body after ennucleation of one eye in cat. Evidence of termination in alternate cell layers was found by LeGros Clark (17) in monkeys and by Orlando (4), Hechst (35) and others in man. Hayhow (32) recently provided proof of such termination within the pars dorsalis of cat, using silver staining techniques. He is in agreement with Minkowski's findings, based on the Marchi technique, of segregation of crossed and uncrossed fibers in the pars dorsalis. This segregation was not established by the Marchi studies of Brouwer and Zeeman (11) and Overbosch (55). Cohn (19), by microelectrode studies arrived at similar conclusions so that lamina A and B were found to be activated by light from the contralateral eye, and the lamina A1 by light from homolateral eye. The present study confirms the conclusions of earlier investigators that the crossed and uncrossed fibers terminate in alternate layers. The crossed fibers ending in lamina A and B, and the uncrossed fibers in lamina A1 of pars dorsalis.

Thuma (73) describes the pars dorsalis A and A1 as making up the main body of the S-shaped lateral geniculate nucleus, in longitudinal sections, separated by a medullary lamina. O'Leary (54) described it as an interlaminar fiber plexus much thinner dorsally then ventrally. He found two main types of cells in the laminae. The principle cells are medium or large sized oval shaped cells, whose axons enter the optic radiation, and short axon cells which are medium or small size cells whose axons arborize in the mediate vicinity.

A description of the appearance of the homolateral and contralateral geniculate bodies after section of one nerve, in coronal and saggital sections, has been given by Hayhow (32)

Figure 16. A series of eight drawings of the contralateral lateral geniculate body, in coronal section, representing a complete picture of the distribution of the degenerating preterminal fibers and boutons in cats in which one optic nerve was sectioned completely. These drawings represent a rostromedial series.
(1) Degeneration in rostral most portion of lamina A. (2-4) Lamina A1 interposed between lamina A laterally and lamina B medially.
(6) The hilum is skirted by lamina A. Note a medial band of degeneration separating the lamina A1 from the pulvinar. (6-8) Progressive changes in the pattern of degeneration as the caudal portions of the pars dorsalis are approached.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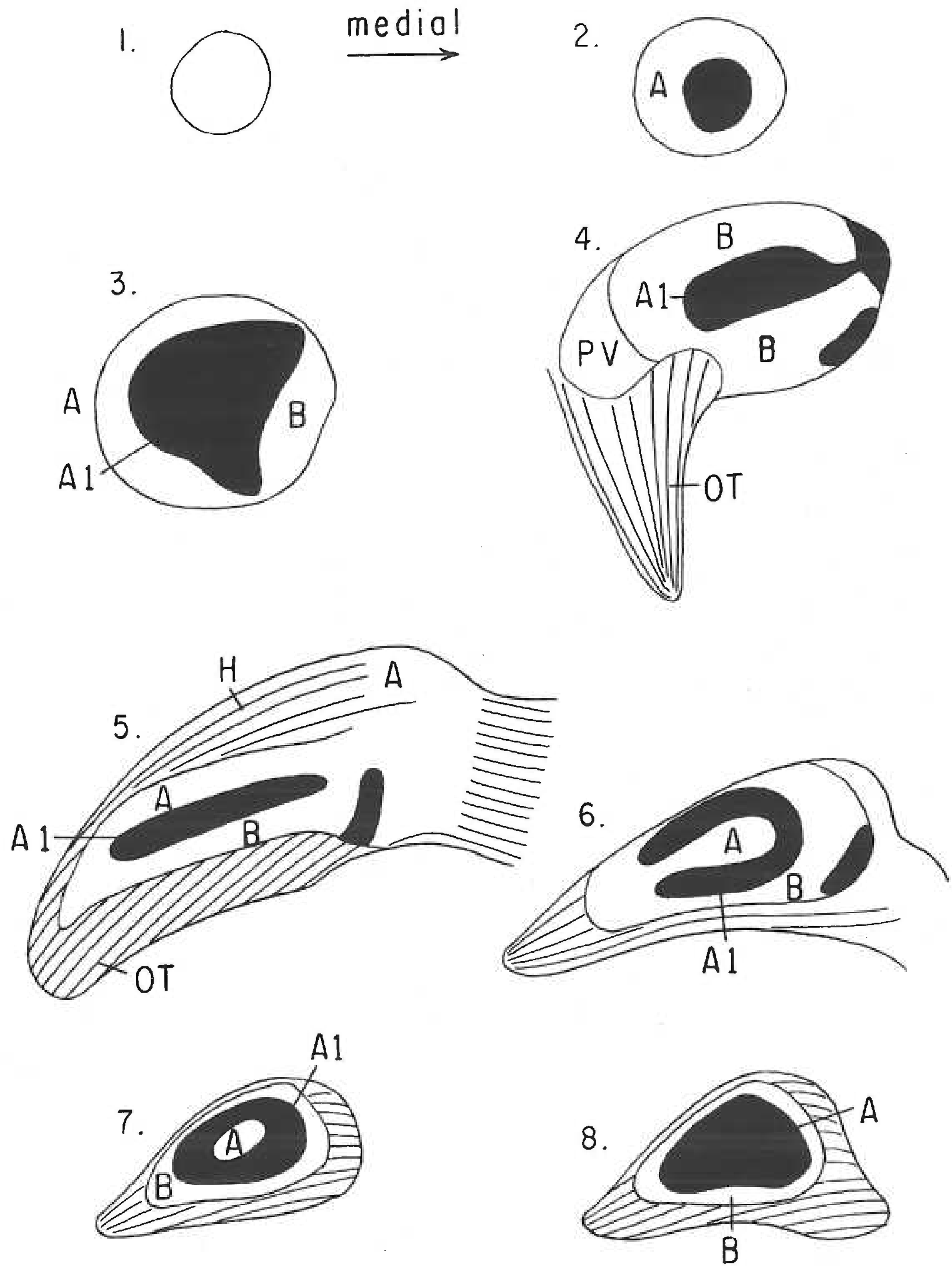
A1
B

recently. The degeneration patterns in coronal sections obtained in the present study are quite similar to those obtained by Hayhow. The slight difference is due to the different staining technique. With the silver impregnation technique used in this study it is not always possible to distinguish the degenerated and the degeneration free areas under the low power. The characteristic preterminal fibers and axonal degeneration can only be seen under the higher magnifications. In some preparations, however, a distinction could be made under the lower power.

The accompanying diagrams show the distribution of degeneration in the contralateral and homolateral pars dorsalis. These are representative sections, and show the' changing shapes of the laminae proceeding from a rostral to caudal direction. Following Hayhow's (32) example fibers of passage have not been marked, only the areas where evidence of terminal degeneration is present being represented in black. Although the intensity of degeneration is variable, it has not been represented for the sake of clarity.

In coronal sections the lamina A is seen most anteriorly. Lamina A1 appears medial to lamina A as a circular area situated somewhat eccentrically. It gradually expands to meet the medial border of the lateral geniculate body, and ventrally and dorsally to enclose the small rostral portion of lamina B. The later remains in contact with the medial margin of the pars dorsalis, and expands laterally so that the lamina A and A1

Figure 17. A series of eight drawings of homolateral lateral geniculate body in the coronal section, representing a composite picture of the distribution of degenerating preterminal fibers and boutons in cats in which one optic nerve was sectioned completely. These drawings represent a rosteromedial series.
(1) Degeneration free rostral portion of lamina A. (2) Rostral portion of lamina A1 (black) surrounded by lamina A. (3) Appearance of lamina B medial to lamina A1. (4-5) Note the appearance of a band of degeneration between lamina B and the pulvinar. (6-8) Progressive changes in the pattern of degeneration as the caudal pole of the lateral geniculate body is approached.


1.
medial
2.
A
3.
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B
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PV
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B
A1
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A1
A
B
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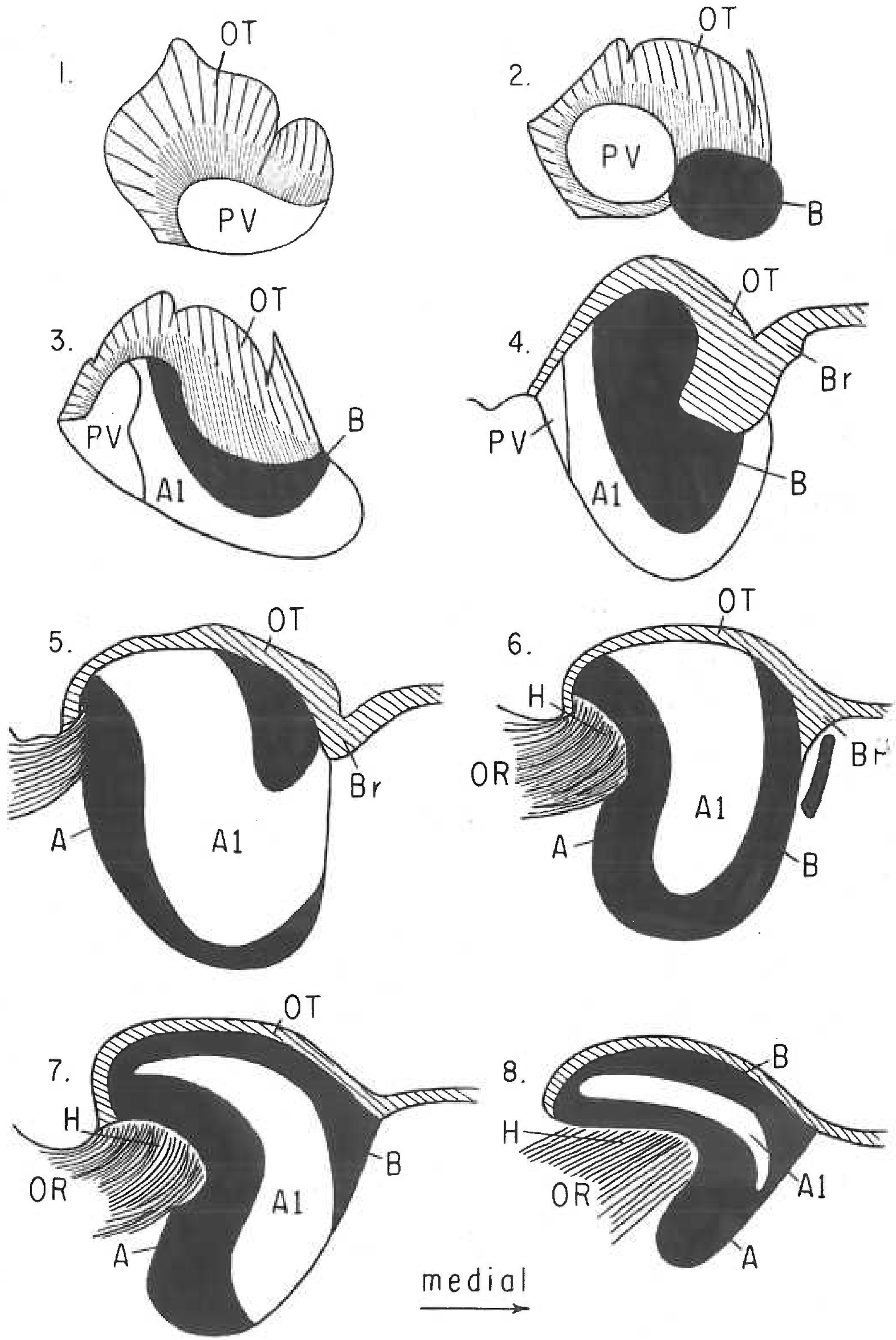
A
B

acquire a horseshoe shape. The lateral geniculate body itself, gradually changing its shape, becomes elongated in a mediolateral direction. The three laminae elongate with it in a transverse plane so that lamina A and B come to lie dorsally and ventrally respectively and enclose the lamina A1 completely on all sides. The hilum appears dorsal to the lamina A, indenting the latter ventrally, leaving a portion of its mediodorsal aspect dorsally. This dorsal component of the lamina A remains in contact with the main lamina by a narrow band. The lamina B is interrupted in its ventromedial aspect by lamina A1. The lamina A1 is interrupted in its medial aspect by the ventrally curving portion of the lamina A. Another portion of the lamina A lies medial to the dorsal and ventral limbs of lamina A. On the medial aspect of this portion of lamina A1, is an area of overlapping degeneration, separating the pars dorsalis from the pulvinar medially. This probably represents the medial homolateral and contralateral degeneration components of Hayhow (32), or the nucleus interlaminaris medialis of Thuma (73). Lamina B then completely surrounds the main mass of the lamina A1 except for a small portion of the lamina A1 which lies medial to lamina A. The hilum gradually diminishes in size until the lamina A has completely replaced it. The lamina A in turn disappears and only the lamina B remains to encircle the lamina A1.

In the horizontal sections the pars ventralis makes its appearance between the lateral and medial rami of the optic tract. Lamina B appears as a disk shaped mass on the medial

Figure 18. A series of eight drawings of the contralateral lateral geniculate body, in horizontal section, representing a composite picture of distribution of the degenerating preterminal fibers and boutons after complete section of one optic nerve in several cats. The drawings form a ventrodorsal series.

(1) Although a few degenerating boutons were present in the pars ventralis, it was occupied mainly by fibers of passage and is shown as a clear area. (2) Appearance of ventral most portion of lamina B (black), medial to pars ventralis. (3-4) The degeneration free lamina A1 is interposed between pars ventralis and lamina B. (5-6) Note the appearance of the hilum and a band of degeneration between lamina B and the pulvinar. (7-8) Progressive encircling of the degeneration free lamina A1 by laminae A and B (black).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6.
OT
H
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OT
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OR
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A
B
8.
B
H
OR
A1
A
medial

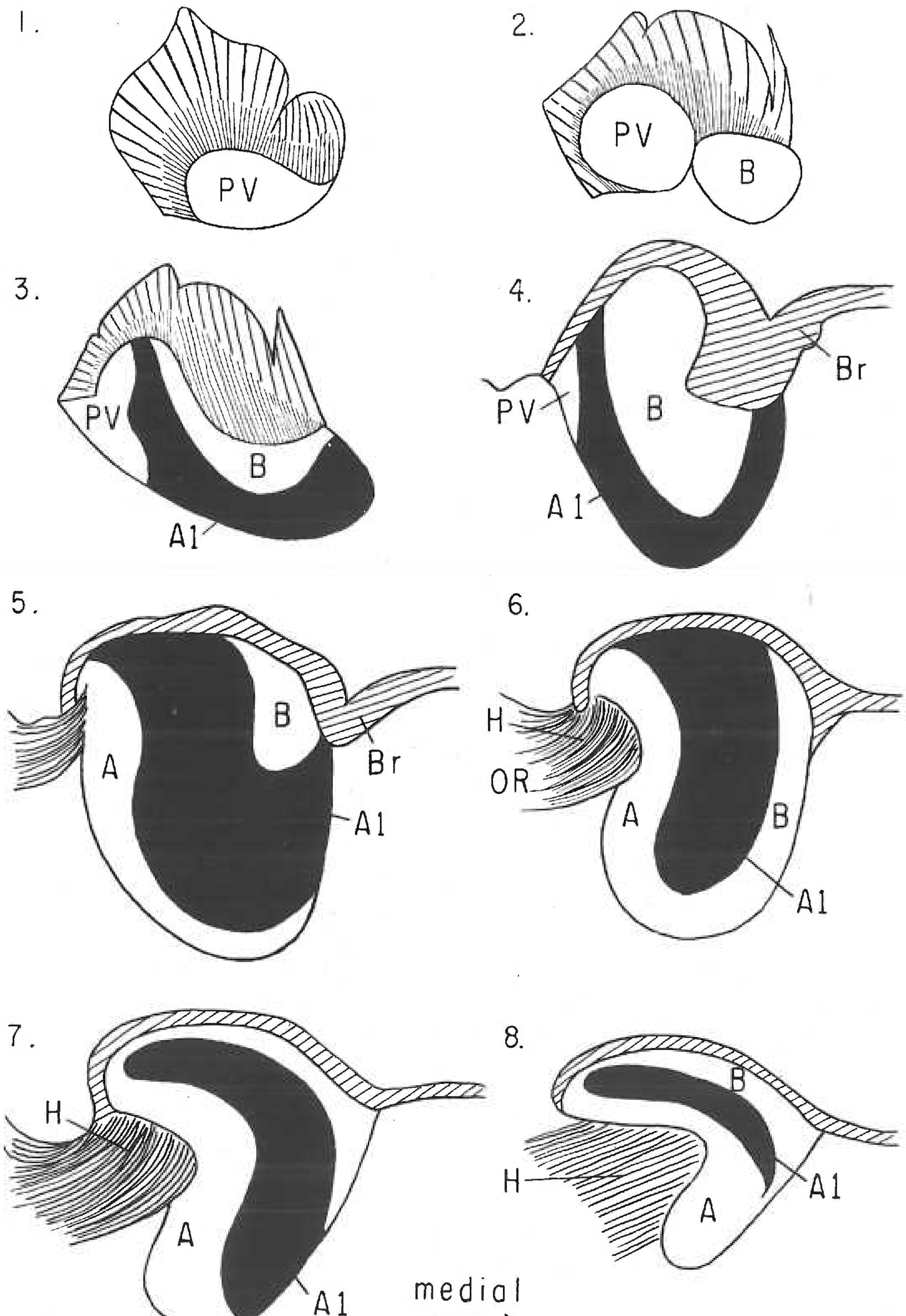
aspect of the pars ventralis from which it is separated by a well defined fiber lamina. The ventralis then shifts laterally and occupies a triangular area. The lamina A1 appears between the pars ventralis and lamina B, and gradually surrounds the medial caudal and lateral aspects of lamina B. The rostral portion of lamina B remains in contact with the optic tract. The brachium of the superior colliculus is well formed at this level. Lamina A appears at the lateral aspect of lamina A1, and follows the contour of the latter. At this stage the hilum and optic radiation are visible. All the laminae in the mid section have an S-shaped configuration. The laminae A and B establish continuity and surround the lateral and medial aspects of lamina A1. A median bar of degeneration is seen over the medial aspect of lamina B between the lamina B and pulvinar and probably represents the medial contralateral and homolateral components of degeneration of Hayhow (32) or the nucelus interlaminaris medialis of Thuma (73). Finally lamina A1 becomes transversally oriented and is completely surrounded by lamina A and B.

A sharp line of demarcation exists between lamina A and A1 by means of the identifiable portions of A-A1 interlaminar plexus. On the other hand it is not possible to distinguish a discrete demarcation between lamina B and A1. The differentiation here is made by the decrease in density of degenerating preterminals in the zone of transition between lamina A1 and B.

Marchi studies of Brouwer and Zeeman (11) had indicated that the crossed and uncrossed optic fibers from binocular fields

Figure 19. A series of eight drawings of the homolateral lateral geniculate body, in horizontal section, representing a composite picture of the distribution of degenerating preterminals and boutons, after complete section of one optic nerve, in several cats. These drawings form a ventrodorsal series.

(1) The pars ventralis is shown as a clear area although a few degenerating boutons were noted in this area. (2) Appearance of degeneration free lamina B. (3-4) Interposition of degenerating lamina A1 (black) between pars ventralis and lamina B, and appearance of the brachium of superior colliculus. (5-6) The pars ventralis has disappeared and the lamina A seen lateral to lamina A1 is free of degeneration. Note the characteristic S-shaped configuration of the laminae. (7-8) The progressive encircling of degenerating lamina A1 by degeneration free lamina A and B.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medial

of vision are intermingled in the pars dorsalis in monkeys. This was not confirmed by the silver impregnation studies of Glees and LeGros Clark (29), while Packer (56) was able to produce evidence of such an overlap in phalanger. Similar overlap was found by Nauta and Van Stratten (52) in rat. Hayhow (32) feels that the zone of cellular intermingling in cat is interlaminar rather than of laminar nature. He was able to demonstrate the existence of overlapping supply from both crossed and uncrossed optic fibers in the cat. This, according to him, occurs in the nucleus interlaminaris centralis and the nucelus interlaminaris medialis which are interlaminar in position and separate areas of charateristic cellular structure which received preterminal fibers derived entirely from crossed or uncrossed fibers respectively, but which in turn are supplied with preterminals from each of the two areas they so separate. According to Hayhow (32) the region of the nucleus interlaminaris medialis is constituted by three poorly defined, approximately verticaly oriented bars of cells which are continuous with the main portions of lamina A, A1 and B. He considers the nucleus interlaminaris medialis as the medial representative of the nucelus interlaminaris centralis of the main cellular mass of the pars dorsalis, representing a relatively independent accessory pars dorsalis whose cellular laminae are oriented in a manner approximately perpendicular to those of the adjacent main pars dorsalis. He felt that two of the laminae are supplied by crossed fibers and the central lamina by uncrossed fibers, thus providing an anatomical basis for some degree of binocular interaction. Such an intermingling was found in the monkeys by LeGros Clark (17).

Silva (69) also using the Nauta-Gygax staining technique was able to confirm the interlaminar segregation of fibers within the pars dorsalis, but did not elaborate on the interlaminar region. He suggested occurrence of electrical interaction between the layers on the basis of simple contact of, or proximity of fibers. Hayhow (32) felt that the lamination of pars dorsalis is more complex than has been suspected due to the presence of both concealed lamination and areas of overlap. He postulates one to five or probably nine strata in the different regions of the nucleus. According to him at most levels interlaminar cells which are supplied with preterminal fibers of both crossed and uncrossed origin alternate with laminar cells which are supplied exclusively with preterminal fibers of either crossed or uncrossed origin. These later strata alternate with each other.

Glees (28), discussing this concept of Hayhow, of overlapping of optic fibers in the interlaminar zones, feels that if such is the case, it could not be very significant. For the interlaminar zone would account for the behavior of a small proportion of optic fibers, compared with the considerable projection areas within the layers themselves. He suggests the possibility of ipsilateral and contralateral impulses propogating through straying of dendrites of the geniculate cells into adjoining cells and thus picking up impulses from the other eye.

In the present investigation an overlapping of degenerating preterminals was found in the A-A1 interlaminar plexus and the large cells of the transitional zone between lamina A1 and B, in the contralateral pars dorsalis, and in the large cells of lamina magnocellularis in the transitional zone between A1 and B in the homolateral pars dorsalis. Degeneration in the region of the nucleus medialis interlaminaris was found on both sides. These findings are in agreement with those of Hayhow (32). However, as Glees states, this overlapping is insufficient toprovide an explanation for the extensive interaction of optic impulses which would be necessary to take place for binocular vision. An anatomical evidence of a more extensive overlap than that discussed above is not forthcoming. Perhaps the interaction is more on a physiological basis as suggested by Glees (28) and others.

The Retinal Quadrants in the Lateral Geniculate Body

Brouwer and Zeeman (11), and Brouwer (10) reported that in the cat the upper retinal quadrants lie a little more frontal than the lower retinal quadrants. In monkeys they found the upper quadrants represented medially and the lower retinal quadrants laterally. In the humans the lower peripheral retina is represented in the lateral horn, the upper peripheral retina in the rostral one-third of the mucelus, and the central retina as an inverted pyramidal shaped area with its convex base dorsally and apex ventrally. According to Polyak (60) and Crosby, et al (22), the binocular area is located at the anterior margin of the nucleus. In the present investigation fibers from the superior half of the nerve were found to terminate superiorly and medially. The uncrossed temporal fibers reaching the medial and rostral aspects of lamina A1 of the homolateral pars dorsalis and the crossed fibers terminating in the medial and rostral aspects of the lamina A and B of the contralateral pars dorsalis.

The Pars Ventralis

According to Thuma (73) the pars ventralis, located ventrolateral to pars dorsalis, and separated from it by intermedullary lamina, is mainly composed of small pale cells. Brouwer (10) in rabbit and Packer (56) in phalanger had found evidence of termination of optic fibers in the pars ventralis from their Marchi studies. On the other hand, Lashley (42) in rat and Barris, et al (57) in cat, also using the Marchi technique, failed to find enough evidence of such a termination. Glees (26) and Nauta and Stratten (52), using the silver impregnation techniques, were able to establish such a termination in the cat and rat respectively. Hayhow (32) with Nauta-Gugax method was able to prove that both crossed and uncrossed optic fibers terminate in the pars ventralis of the lateral geniculate body, but felt that the pars ventralis was supplied predominantly by fibers other than those of the optic system. The present investigation is in conformity with the findings of Hayhow. Although some evidence of terminal degeneration was found in the pars ventralis of both sides, it receives a very scanty supply of retinal fibers. In the experiments which involve lesions of part of the optic nerves it was not possible to establish a definite segmental representation in the pars ventralis due to paucity of degeneration.

O'Leary (54) described collaterals from small optic fibers arborizing in the pars ventralis, but none arising from the large fibers. In the present study, although a large number of degenerating fibers were seen to course through the pars ventralis, no large fibers were found in this structure.

<u>Fiber Size Distribution and Termination in Pars Dorsalis</u>

According to Peele (58, in humans, eighty per cent of fibers from the optic nerve, and practically all thick ones, go to the dorsal portion of the lateral geniculate body. The remaining predominantly thin ones go to the perigeniculate nucleus, pretectal area and superior colliculus. Polyak (60) states that in monkey the thick fibers branch into thick and thin branches. The thick branches end in the lateral geniculate body and are mainly crossed. He states that the thick and thin crossed and uncrossed fibers from binocular homonomous halves of the retina distribute according to their topographical relationship, and thin macular fibers end in the posterior extremity of the lateral geniculate body after traversing its entire posterior extent. The thicker fibers end more proximaly near the hilum.

Crosby, Humphrey and Lauer (22) stressed that each thick optic fiber gives a fine collateral branch before entering the lateral geniculate body. Collaterals are also given out by thick main branches before they form terminal arborization.

O'Leary (54), on the basis of his Golgi studies, stated that the large fibers divide into thick and thin branches in the dorsal nucleus entry zone. The thick branches penetrate the pars dorsalis first while the thin ones are the last of the dispersing optic fibers which sheath the dorsal and caudal surface of the pars dorsalis. He felt that the large fibers terminated in pars dorsalis B and the thin fibers entering the pars dorsalis B did not terminate there. Hayhow's (32) investigations show that within the pars dorsalis the small fibers undergo terminal arborization predominantly in the relation to medium sized cells of contralateral lamina B, which is supplied exclusively by small fibers. According to him, the large fibers of both homolateral and contralateral origin together with a few small fibers form a prominent tangentially oriented plexus which embraces the cells of the entire nucleus interlaminaris ventralis after which the large fibers undergo terminal arborization in homolateral lamina A1 and contralateral lamina A. In the present study it is noted that a large number of small fibers terminate in lamina B though a considerable number of large fibers are seen passing through it, and the cells of lamina A and A1 are supplied by large fibers as well as small fibers.

<u>Mode of Termination of Optic Fibers in the Lateral Geniculate Body</u>

LeGros Clark (17) found that in monkeys the crossed and uncrossed fibers are not separated until after they have penetrated the lateral geniculate body and that approximately sixty per cent of the fibers arriving in the lateral geniculate body are crossed and forty per cent uncrossed. Glees (26), on the basis of silver stains, stated that each optic fiber divides into five or six branches in the cat. Each of these branches ends by means of terminal boutons which in turn establish contact with the dendrites and perikaryon of geniculate cells. There are more axodendritic contacts than the axosomatic contacts. He estimated that about forty synaptic contacts are made by optic terminals with one principle cell, and one optic fiber covers about ten cells so that there is an extensive overlap, the same region receiving supply from more than one optic nerve fiber.

The findings in the present study are similar to those of previous investigators. The optic fibers branch repeatedly inside the lateral geniculate body. Their termination is by means of fine terminal rings or boutons as described by Glees (54) and Glees and Clark (29). Considerable overlapping supply of each individual cell is present, terminal endings of more than one optic fiber reaching each cell, and each fiber supplying multiple cells.

<u>The Pretectal and Tectal Areas</u>

Polyak (60), Altman (1) and others found that in the cat some retinal fibers reach the pretectum and the superior colliculus. According to Crosby, Voss and Henderson (20) the superior colliculus forms the main terminal station for direct optic fascicles. The fiber projection to this area has been studied by Tsal (74) and Bodian (4) in oppossum, Parsons (57) in monkey, Cajal (14) in mouse, Lashley, LeGros Clark (18), Bucher and Burgi (13), and others in rat, Monokaow (50), Probst (61), Cajal (11), Barris, Ingram and Ranson (7) in cat, Brouwer and Zeeman (11,12), and Crosby and Henderson (20,21) in monkeys, and Juba (39) in man. Barris, Ingram and Ranson (7) stated that in cat the superior colliculus received much larger contribution of the crossed retinal fibers as compared to the uncrossed fibers, Altman (1) confirmed this by recording evoked potentials simultaneously from both superior colliculi. Polyak (60) states that the number of retinal fibers to the superior colliculus is much smaller than the retinogeniculate fibers. This represents a greater corticalization in the cat as compared to some of the lower mammals. It has also been established by many of these previous investigators that more fibers reach the contralateral pretectal and tectal areas, through the contralateral brachium mainly, as compared to the homolateral prectal and tectal areas. The superior colliculus in cat receives a much smaller number of direct retinal fibers compared to the pretectal area.

Cajal (11) described two types of fiber terminations, one group entering the stratum opticum turning ventrally and ending in the same layer, the other turning dorsally and ending in the stratum griseum superficiale. Brouwer and Zeeman (11,12), Altman (1) and others did not find any fibers terminating in the stratum zonale.

The present study confirms the above findings. The number of retinotectal fibers is much less than the retinogeniculate fibers. More fibers arrive in the contralateral than in the homolateral tectal and pretectal areas and that in the cat more fibers reach the pretectum than the superior colliculus.

The termination of these fibers is similar to that described recently by Altman (1) and previously by Cajal (11). The fibers enter in the stratum opticum. Some of them terminate on cells of this layer while others turn ventrally and dorsally. The fibers turning ventrally enter the stratum griseum intermediale and show evidence of termination around cells of this layer. The dorsally turning fibers enter the stratum griseum superficiale but do not reach the stratum zonale. There is some evidence of these fibers undergoing preterminal arborization in the stratum griseum superficiale. None of these fibers directly reach the third nerve nuclear complex or the central gray, nor is there any crossing of these fibers in the posterior commissure or the commissure of the superior colliculus. Any such connections that might exist are probably in the nature of multiple internuncial chains.

The distribution of fibers by size was also studied in the visual tectum. It was found that the brachium of the superior colliculus was mainly formed by small fibers. Large fibers were noted in the brachium, in the normal sections, but degeneration of these fibers was not found in the experimental animals.

The pretectal area was found to receive and contain small fibers only. In the superior colliculus a few large fibers were noted in the normal brains. In the animals with a lesion of the optic nerve, none of them were found degenerated.

These findings indicate that the pretectal area and superior colliculus receive only small fibers of retinal origin.

Apter (2) using evoked potentials and strychnization studies to determine the projection of the retina on the superior colliculus found that each colliculus causes movements towards the contralateral visual field and regulates reflex conjugate eye movements in cat. Keller and Stewart (40) and Ranson and Magoun (62) in cat, and Ferrier and Turner (23) in monkey have demonstrated that the superior colliculus plays no part in the mediation of the light reflex. Magoun and Ranson (44) felt that the efferent pathway of light reflex turns centrally in the optic tract and brachium of the superior colliculus to the pretectal region, then swings ventrally around the central gray to reach the occulomotor nucleus undergoing partial crossing in the posterior commissure and another crossing somewhere ventrally to the central gray. These findings were based on electrophysiological studies in cat. They felt that no part of the superior colliculus is concerned with the pupillary light reflex, but if the pretectal region was completely destroyed on both sides along with some damge to the rostral medial portion of the superior colliculus, the light reflex was completely or permanently abolished. It was, therefore, concluded by these investigators that the greater part of the light reflex is mediated through the pretectal region.

The quadrantic distribution of the retinotectal fibers has formed a part of this study. LeGros Clark (18) found that the lower temporal fibers occupy an intermediate, the upper temporal an anterolateral, the inferior nasal a posteriomedial, and the superior nasal, a lateral position. Crosby, Humphrey and Lauer (22) state that the medial and rostral medial parts of the superior colliculus receives fibers from inferior retinal quadrants and the lateral and caudolateral part from the superior retinal quadrants. Brouwer (10) found the upper nasal and temporal fibers represented laterally and caudally in the superior colliculus of the cat.

This investigation reveals that the fibers from the superior quadrants are represented in the lateral and caudolateral portions of the stratum opticum, the stratum griseum intermediale and stratum griseum superficiale of the superior colliculus. The contribution of the contralateral pretectum and the superior colliculus was found to be greater than to the homolateral tectal and pretectal areas.

A quadrantic distribution in the pretectum could not be established and it is to be assumed that it is similar to that of the superior colliculus, as the pretectum represents a rostral diencephalic extension of the superior colliculus.

SUMMARY AND CONCLUSIONS

The projection of retinal fibers to the visual centers in the brainstem in the cat has been studied by experimental histologic methods. Complete and partial sections of the optic nerve and chiasm were made. The animals were sacrificied after a survival period of from five days to one month, and paraffin sections were prepared and stained by the Stotler intensified protargol method.

1. In the optic nerve of the cat there is segregation of fibers as to the point of retinal origin. Slightly more than half of these fibers form the crossed component of the chiasm.

2. Sections of the nasal quadrant of the optic nerve produce degeneration of the crossed components of the chiasm, while no degenerating fibers could be followed contralaterally following lesions of the temporal halves of the optic nerve.

3. In the optic tract the crossed and uncrossed fibers become intermingled, however, the crossed fibers concentrate medially and the uncrossed fibers in a lateral position.

4. The superior retinal quadrants are represented dorsally in the optic nerve and chiasm, and while scattering of these fibers takes place in the tract most of them remain in the dorsal position.

5. There is no segregation of fibers by size in the optic nerve and chiasm, however, in the optic tract the small fibers are located in a compact group medial to the loosely

packed large fiber segment. Near the termination of the tract in the lateral geniculate body, these small fibers form a wedge-shaped segment adjacent to this nucleus.

6. The pars ventralis of the lateral geniculate body contains a large number of optic fibers, very few of which terminate in this area, most of them being fibers of passage. These optic fibers are made up exclusively of the small diameter component. A majority of these fibers of passage are of contralateral origin.

7. The pattern of degeneration in the lateral geniculate body after complete or partial section of the optic nerve and chiasm has been described as it appears in coronal and horizontal sections.

8. The crossed optic fibers terminate in the contralateral laminae A and B and the uncrossed fibers in the homolateral lamina A1 of the lateral geniculate body.

9. The superior crossed retinal fiber component terminates in the medial, rostral and dorsal portions of the contralateral laminae A and B, while the uncrossed retinal fiber component terminates in the medial, rostral and dorsal portion of homolateral lamina A1 of the lateral geniculate body.

10. Evidence of overlapping innervation of the cells of interlaminar zones by both crossed and uncrossed retinal fibers has been found.

11. The optic fibers after entering the pars dorsalis of the lateral geniculate body, branch repeatedly and then terminate around the cells of various laminae by means of terminal boutons.

12. The large fibers entering the pars dorsalis course through the lamina B and terminate predominantly in the lamina A, lamina A1, and the interlaminar zones of the pars dorsalis while most of the small fibers terminate in lamina B. The remaining small fibers terminate in areas of pars dorsalis dorsal to lamina B.

13. The direct optic fibers reach the pretectum and superior colliculus by way of the lateral division of the brachium of the superior colliculus. A smaller component is derived from the medial division of the brachium of the superior colliculus and the medial ramus of the optic tract.

14. After section of one optic nerve and after section of the chiasm, only small fiber component of the brachium of the superior colliculus showed degeneration. The origin of sources of large fibers in the brachium remains undetermined.

15. A greater number of optic fibers reach the contralateral optic tectum than those reaching homolaterally. The pattern of degeneration in the optic tectum has been described in coronal and horizontal sections.

16. A greater number of direct optic fibers reach the pretectal area than the collicular area. This area receives termination of only the small fiber component of the optic tract.

17. Direct optic fibers of retinal origin pass into the stratum opticum and are then distributed to the stratum griseum superficiale and stratum griseum intermediale of the superior colliculus. None of these fibers of retinal origin reach the stratum zonale, the nuclear complex of the third nerve or the central gray, and none of these fibers cross in the posterior commissure or the commissure of the superior colliculus.

18. While these experiments have shown that the medial halves of the optic nerve cross completely and no degeneration could be followed contralaterally after section of the lateral segments, the area of the lateral geniculate body (laminae A and B), which receives contralateral projection, is considerably larger than the homolateral projection area (lamina A1). This indicates a less well developed thalamic substrate for binocular vision than is found in primates. Termination of retinal fibers in the midbrain centers is bilateral but here again contralateral dominance is found.

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TABLE OF ABBREVIATIONS

A	Lamina A of pars dorsalis of the lateral geniculate body
A1	Lamina A1 of pars dorsalis of the lateral geniculate body
A-A1	Interlaminar plexus between lamina A and A1
A-A1 int lam pl	Interlaminar plexus between lamina A and A1
Ant ch	Anterior chiasm
Aq Sil	Aquiduct of Silvius
B	Lamina B of pars dorsalis of the lateral geniculate body
Br	Brachium of superior colliculus
Br Sup Col	Brachium of the superior colliculus
Brach S C	Brachium of the superior colliculus
C	Chiasm
Cent Gr	Central gray
Com Sup Col	Commissure of the superior colliculus
D	Degenerating optic nerve
H	Hilum of the lateral geniculate body
Hab com	Habenular commissure
Hab Int Ped Tr	Habenulinterpeduncular tract
Hab	Habenular nucleus
Hab Nuc	Habenular nucleus
Hil	Hilum of the lateral geniculate body

Inf Col	Inferior colliculus
L	Large fibers
Lam A	Lamina A of pars dorsalis of the lateral geniculate body
Lam A1	Lamina A1 of pars dorsalis of the lateral geniculate body
Lam B	Lamina B of pars dorsalis of the lateral geniculate body
L Mag Cel	Lamina magnocellularis of pars dorsalis of the lateral geniculate body
LO	Looping optic fibers
S	Small fibers
Str Al Int	Stratum album intermediale of the superior colliculus
Str Al Pro	Stratum album profundum of the superior colliculus
Str Gr Int	Stratum griseum intermediale of the superior colliculus
Str Gr Pro	Stratum griseum profundum of the superior colliculus
Str Gr Sup	Stratum griseum superficiale of the superior colliculus
Str Op	Stratum opticum of the superior colliculus
Str Zon	Stratum zonale of the superior colliculus

PLATE I.

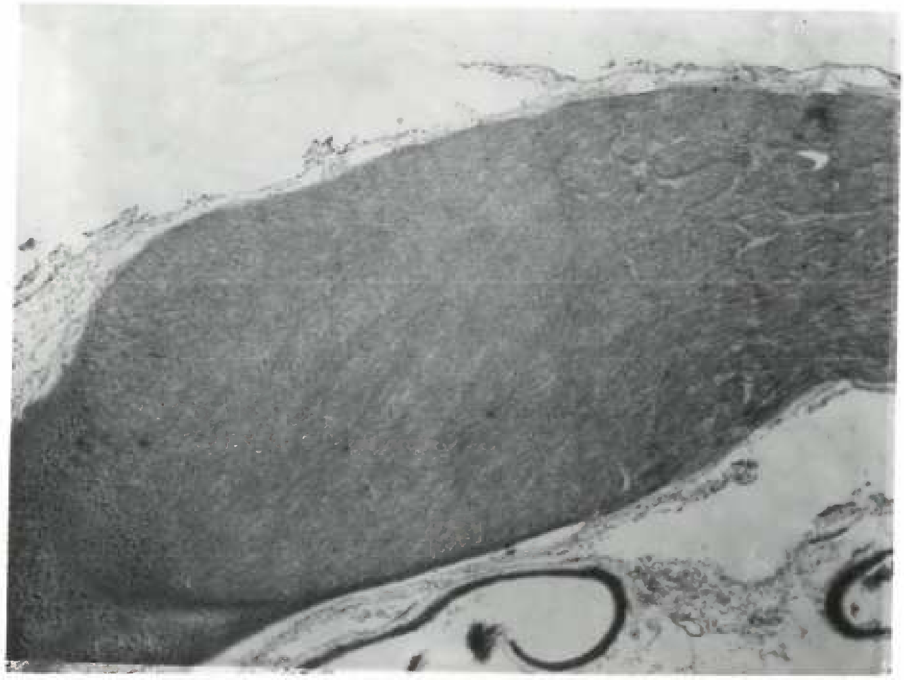
Figure 20

Cat R-380. Photomicrograph of the intact optic nerve showing the intermixture of small and large fibers. Low power. Intensified protargal stain.

Figure 21

Cat R-380. Photomicrograph of the intact optic nerve showing the intermixture of small and large fibers and lack of organization according to size. High power. Intensified protargal stain.

20



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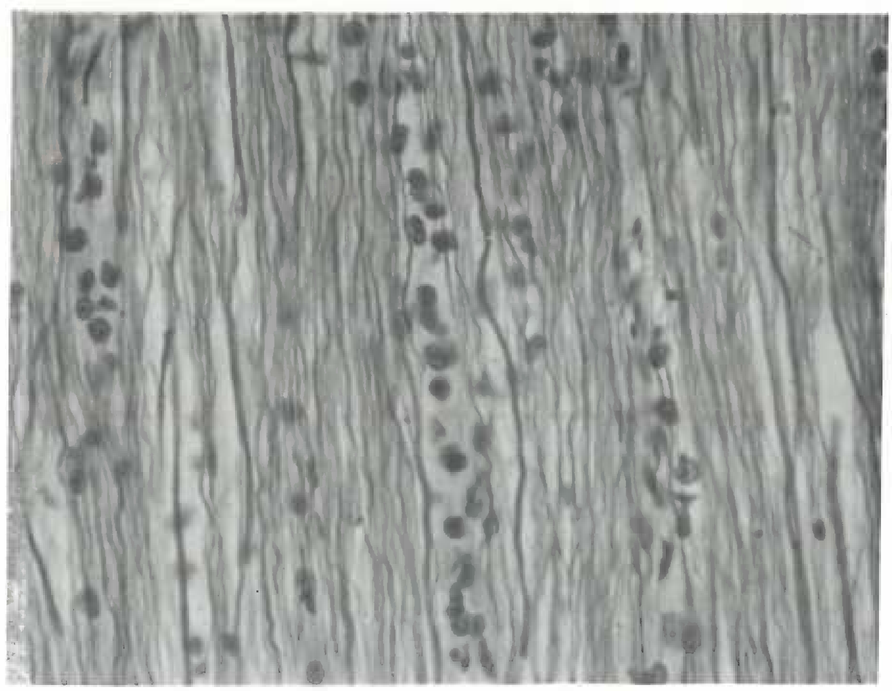

PLATE II

Figure 22

<u>Cat 263</u>. Photomicrograph of intact optic tract showing small fibers (S) aggregated in a wedge shaped segment of the tract, medial to the loosely packed large fibers (L). Low power. Intensified protargol stain.

Figure 23

Cat 263. Photomicrograph of intact optic tract showing closely packed fibers (S) located medial to the loosely packed large fibers (L). Low power. Intensified protargol stain.

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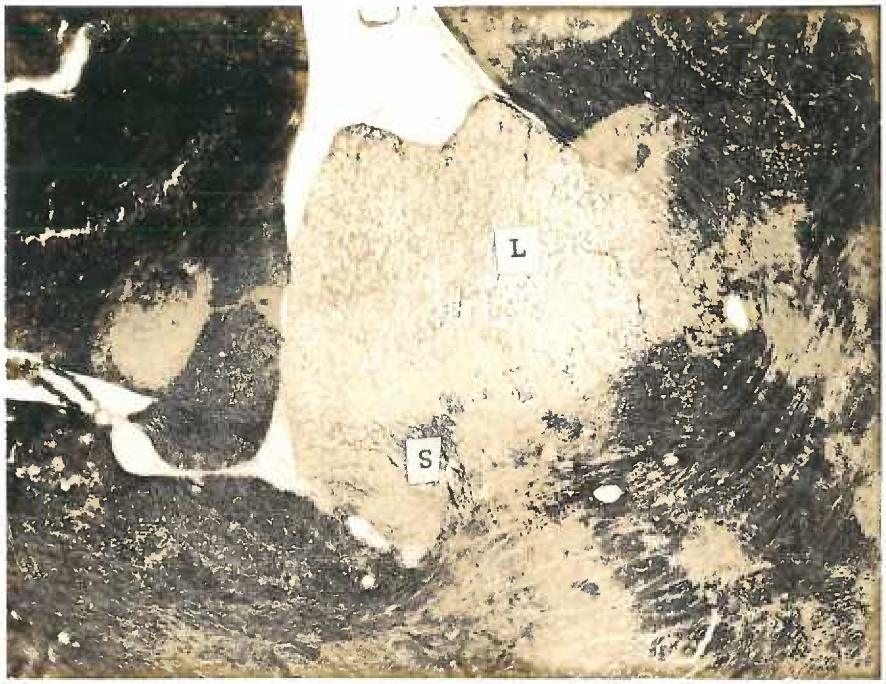

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PLATE III

Figure 24

Cat 263. Photomicrograph of intact optic tract showing the arrangement of small and large fibers. The small fibers (S) are grouped together in a compact group medial to the loosely packed large fibers (L). High Power. Intensified protargal stain.

Figure 25

Cat R-370. Photomicrograph of the completely sectioned degenerating optic nerve. Low power. Intensified protargal stain.

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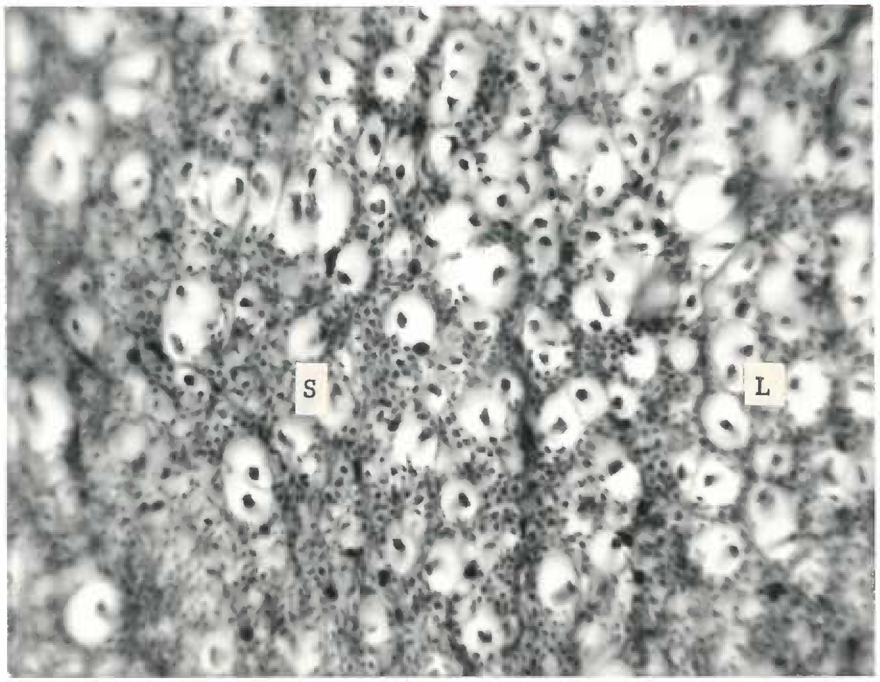

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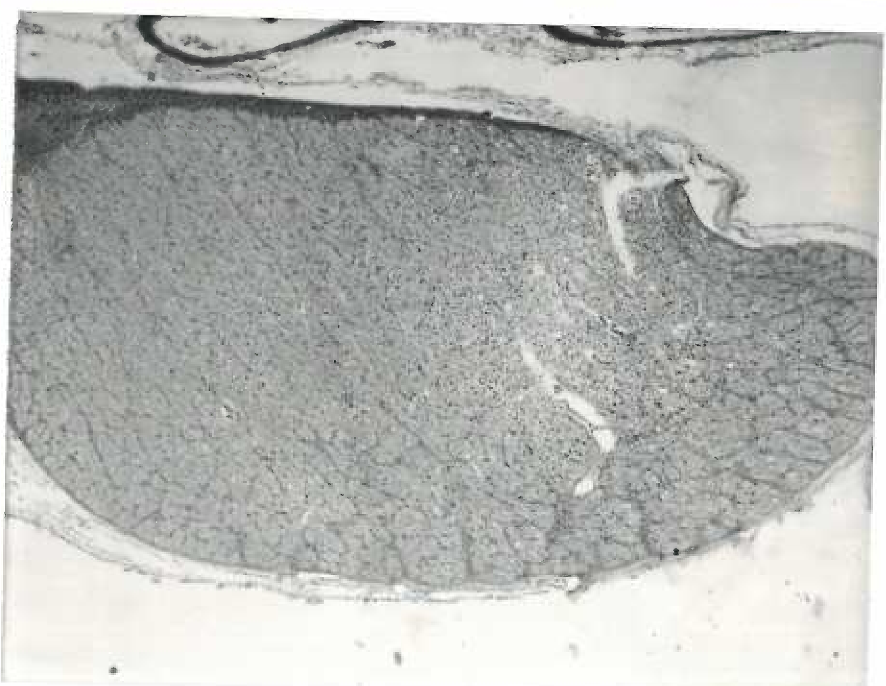

PLATE IV

Figure 26

<u>Cat R-370.</u> Photomicrograph of the degenerating sectioned optic nerve. Degeneration is seen in both the small and large fiber component. Low power. Intensified protargal stain.

Figure 27

<u>Cat R-380</u>. Photomicrograph of the degenerating small and large fibers in the completely sectioned optic nerve. High power. Intensified protargal stain.

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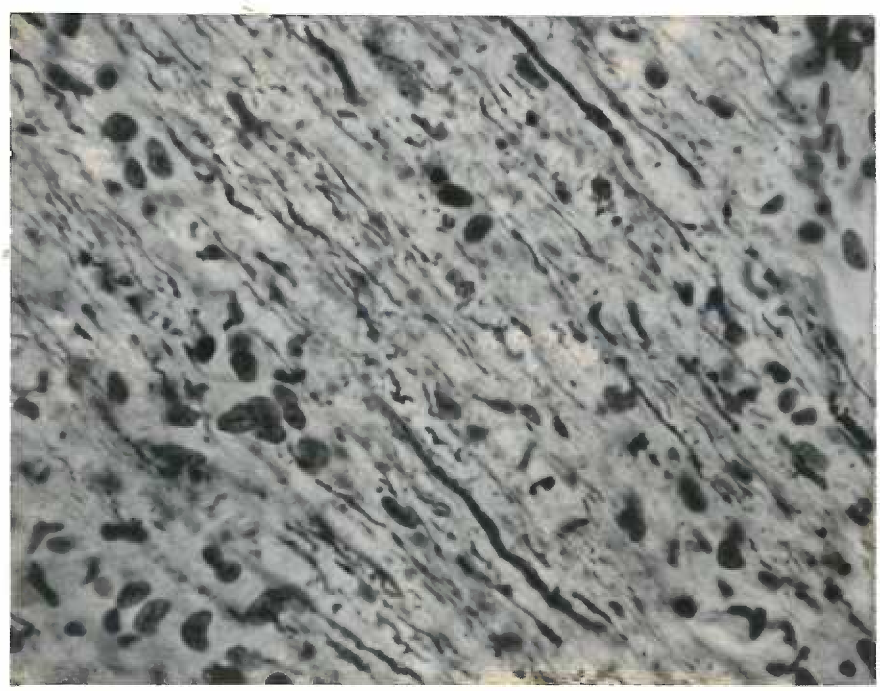

PLATE V

Figure 28

Cat R-380. Photomicrograph of the chiasm and adjacent hypothalamic area showing degenerating fibers of passage (P) extending into the hypothalamus. Low power. Intensified protargal stain.

Figure 29

Cat R-380. Photomicrograph showing looping of intact optic fibers (LO) in the proximal nasal portion of the degenerating optic nerve (D). Note the intermixture of degenerating and intact fibers on the chiasm (C). Low power. Intensified protargal stain.

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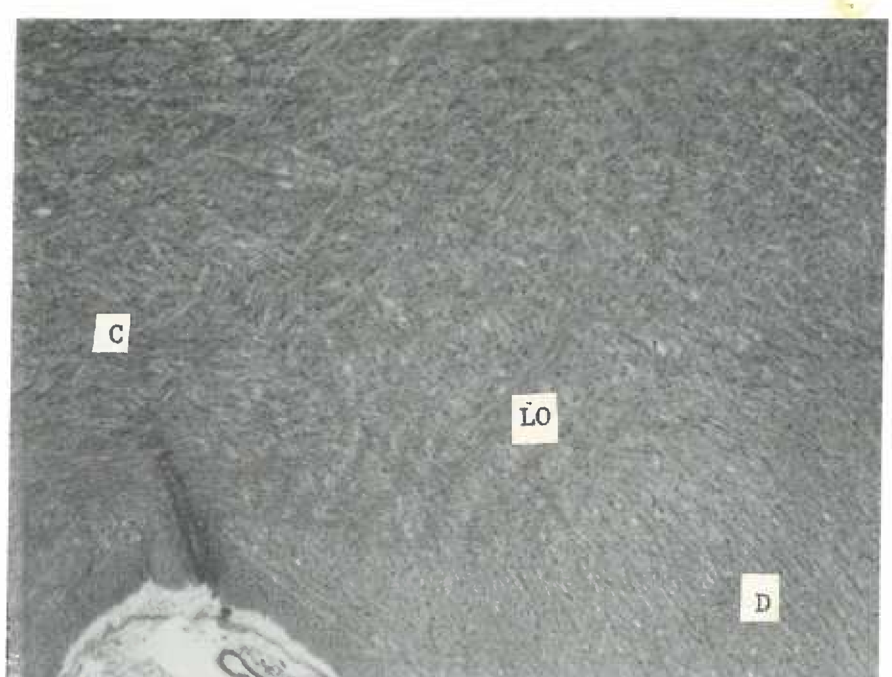

PLATE VI

Figure 30

Cat R-380. Photomicrograph of contralateral optic tract showing degenerating fibers dispersed throughout the cross section of the tract. Degenerating fibers are present in the small fiber component (S), as well as the large fiber component (L) of the optic tract. There is some increased concentration of degenerating fibers in the medial portion of the tract. Low power. Intensified protargal stain.

Figure 31

Cat R-380. Photomicrograph of the homolateral optic tract showing heavier concentration of degenerating fibers in its lateral portion (Lat). Low power. Intensified protargal stain.

al-). Low Power

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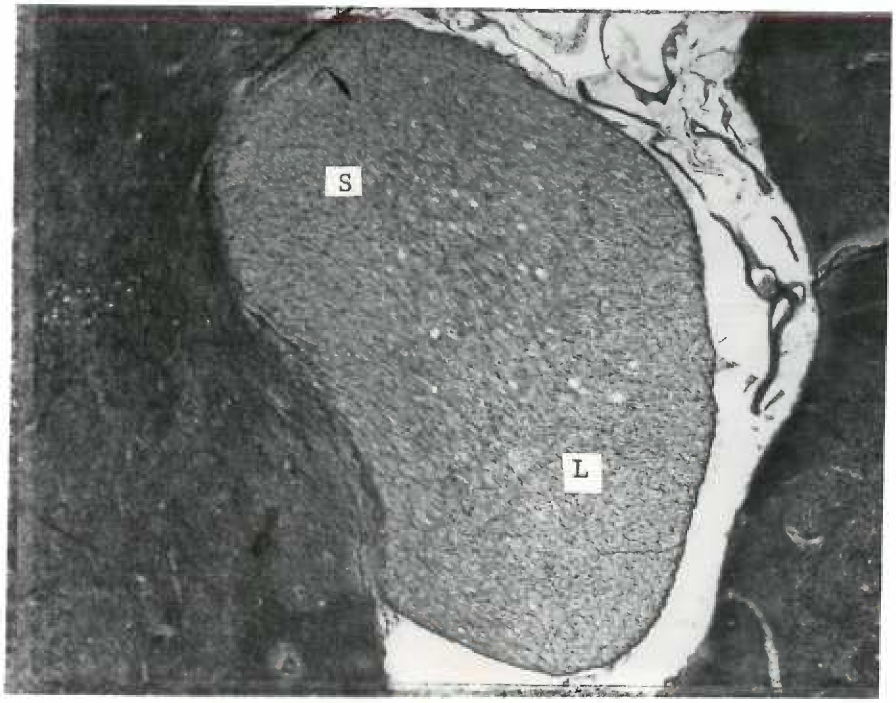

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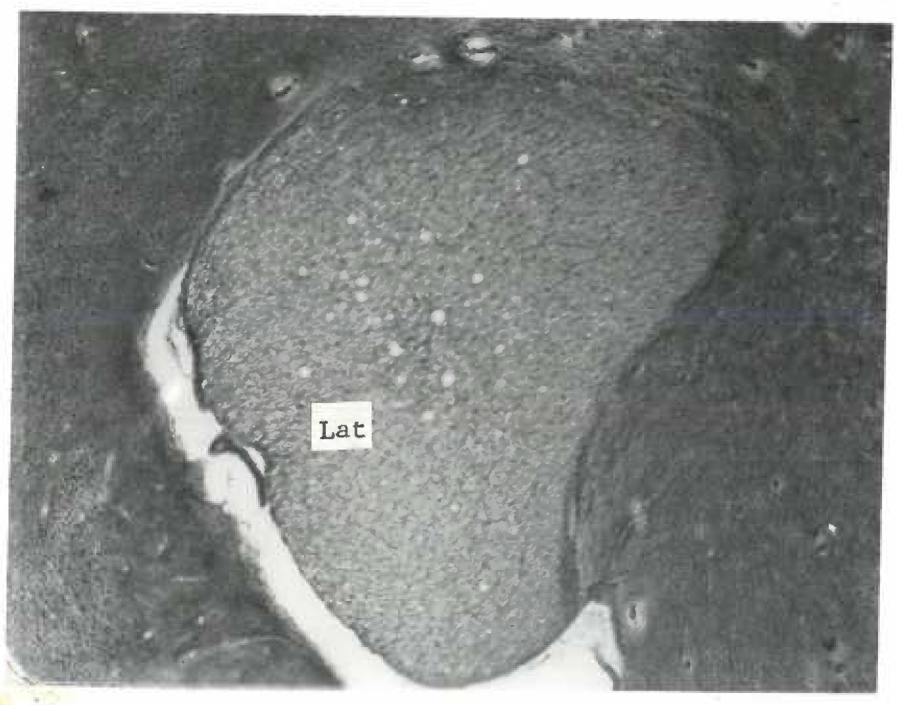


PLATE VII

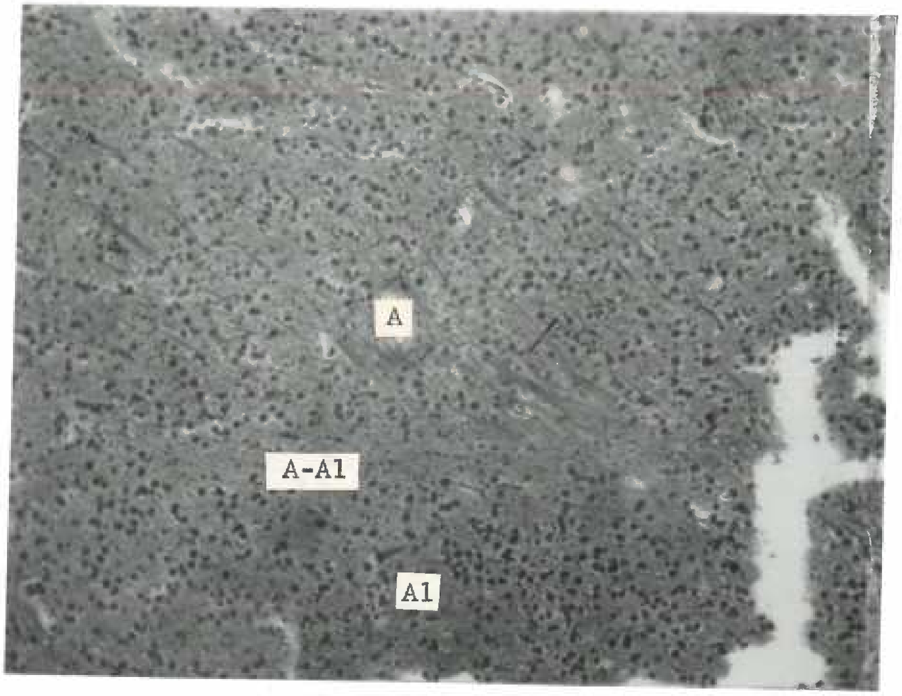
Figure 32

<u>Cat R-369.</u> Photomicrograph of the contralateral lateral geniculate body showing degeneration in lamina A (A) and the A-A1 interlaminar plexus (A-A1). The lamina A1 (A1) is free of degeneration. Low power. Intensified protargal stain.

Figure 33

<u>Cat R-393.</u> Photomicrograph of contralateral lamina A showing degenerating optic fibers, loss of cellular detail and degenerating terminal boutons. High power. Intensified protargal stain.

32



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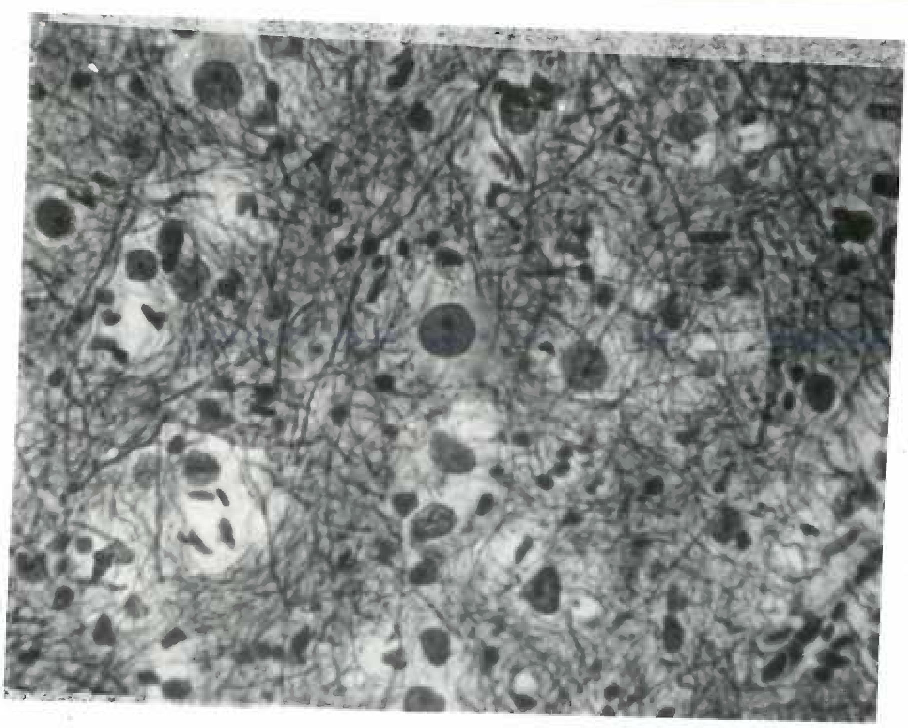


PLATE VIII

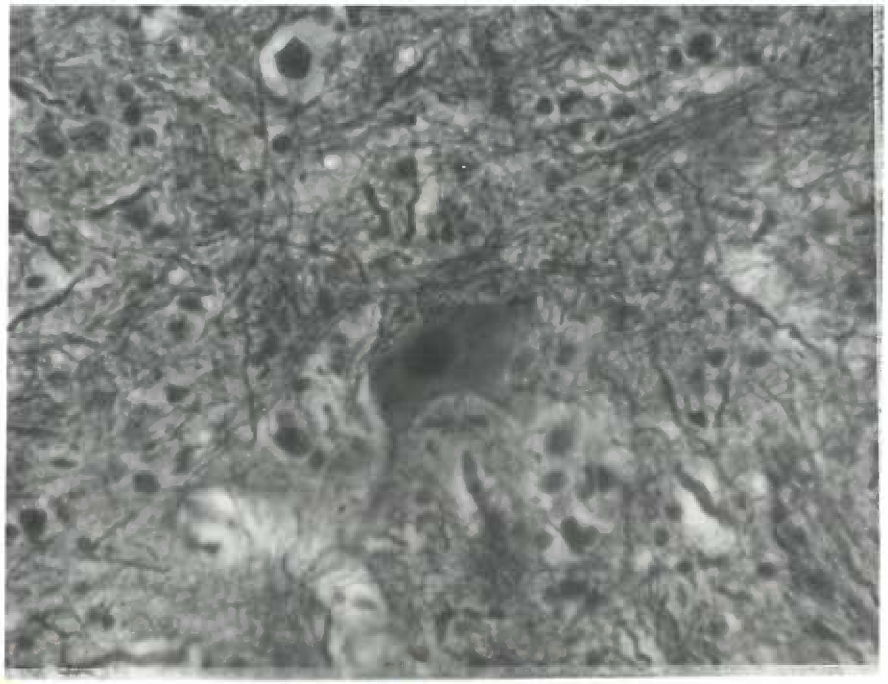
Figure 34

Cat R-377. Photomicrograph of the contralateral pretectal area showing degenerating fibers and terminal boutons. Oil immersion. Intensified protargal stain.

Figure 35

Cat R-393. Photomicrograph of the contralateral stratum griseum intermediale showing degenerating small optic fibers and loss of cellular detail. intensified protargal stain.

34



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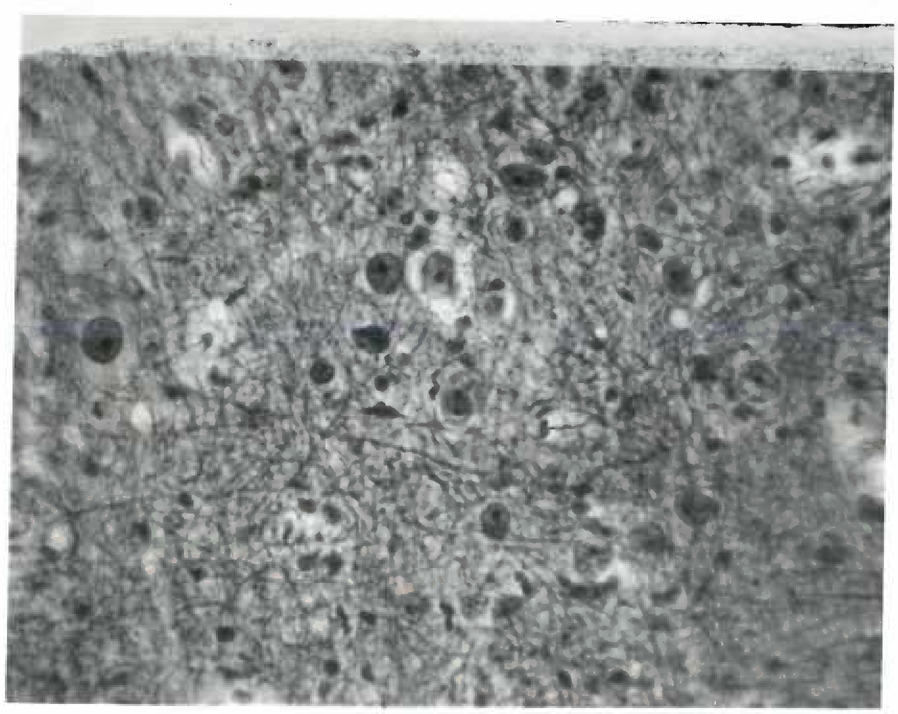

Plate IX

Figure 36

Cat R-393. Photomicrograph of the contralateral stratum griseum superficiale, showing degenerating terminal boutons. Oil immersion. Intensified protargal stain.

36