

# The Mode of Innervation of the Dorsal Lateral Geniculate Nucleus and the Pulvinar of the Rabbit by Axons Arising from the Visual Cortex<sup>1</sup>

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**ABSTRACT** Sections prepared by the Nauta method were used to study the fiber degeneration in the dorsal lateral geniculate nucleus and the pulvinar of the rabbit after lesions in the visual cortex, and sections processed by the Golgi and the Cajal methods provided the material needed to study the normal fiber architecture of these nuclei.

Two distinct systems of fibers are recognizable in the dorsal lateral geniculate nucleus and in the pulvinar. One is a transverse system formed by the fiber bundles which run within these nuclei oriented in parallel with the optic tract; some of these bundles mingle with the fibers of the optic tract. The other is a longitudinal system whose fibers course perpendicularly to those of the transverse system. Lesions in the visual cortex produce degeneration within both of these fiber systems, in the geniculate nucleus as well as in the pulvinar. The degenerating transverse fibers are corticopretectal and corticotectal axons, and these send collateral branches into the longitudinal systems of these nuclei.

The degenerating longitudinal fibers are of two types. One type consists of fibers which are fine in caliber, give rise to numerous short terminal branches, and degenerate early (undegenerated fibers showing this same morphology are identified in the Golgi preparations). These longitudinal fibers are the collateral branches of the degenerating transverse fibers and at the same time they represent the terminal portions of the fibers which provide the visual cortical input to the geniculate nucleus and the pulvinar. It is noteworthy that within the geniculate nucleus these terminal fibers run along the lines of projection for individual points on the visual field.

The second type of degenerating longitudinal fibers is found in the dorsal lateral geniculate nucleus but not in the pulvinar. Its fibers are coarser and degenerate later than the longitudinal fibers described above, and they are probably geniculocortical axons undergoing retrograde degeneration.

Montero and Guillery ('68) have found that the fibers in the dorsal lateral geniculate nucleus of the rat are organized into two systems which they have designated as the transverse and longitudinal fiber systems. These investigators have demonstrated that the transverse system contains projectional fibers arising from the visual cortex whereas the longitudinal system contains the terminal portions of the corticogeniculate fibers; and they have further shown that these terminal fibers course along the lines of retinal projection de-

scribed in the geniculate nucleus of the rat by Montero, Brugge and Beitel ('68). The anatomical observations of Giolli and Guthrie ('71, see also Giolli and Pope, '71) have revealed that a similar organization is to be found in the dorsal lateral geniculate nucleus of the rabbit. However, the above mentioned studies have not been concerned primarily with the relationship between the transverse and the longitudinal fibers, and it is our intention in the present in-

<sup>1</sup> This study was supported by N.I.H. grant EY-00607 from the National Eye Institute.

vestigation to show to what extent the terminal portions of the corticogeniculate fibers are the direct continuations, or the collateral branches, of transverse fibers.

The morphology of the terminal portions of the corticogeniculate fibers in the cat has been carefully studied by Guillery ('66, '67). This investigator has shown that these terminal fibers are of fine caliber, give rise to numerous short side branches along their extent, and run along the lines of retinal projection demonstrated in the dorsal lateral geniculate nucleus of the cat (see Hubel and Wiesel, '61; Bishop et al., '62). As one of the primary goals of the present investigation we shall analyze the morphological organization of the corticogeniculate fibers in the rabbit, combining, as has Guillery ('66, '67), the study of normal brains prepared by the Golgi method with that of experimental brains processed according to the Nauta method.

In the rabbit, Giolli and Guthrie ('71) have found that the pulvinar receives a sizeable input from the visual cortex and contains the segments of visual cortical fibers which are oriented in essentially two different planes. In the present study we shall attempt to show (i) the anatomical relationship between the fibers oriented in the two different planes and (ii) the morphology of the fibers providing the visual cortical input to the pulvinar.

#### MATERIALS AND METHODS

A total of 16 adult albino rabbits of the New Zealand breed was used. Each of 11 rabbits was anesthetized with sodium pentobarbital and using electrocoagulation, a lesion was produced in the central portion of its right visual cortex.<sup>2</sup> After survival times ranging between 2 and 14 days (see table 1) the rabbits were again anesthetized with pentobarbital and then perfused through the ascending aorta with physiological saline followed by 10% formalin. The brains were subsequently removed and further fixed in 10% formalin for periods of from two to six weeks.

The posterior halves of the right hemispheres were sectioned at 40  $\mu$ . A one in eight series of each of these hemispheres was stained with cresyl violet, and the assembled series were used to determine the extent of the cortical lesions and the posi-

tions of these lesions in relation to the maps of visual cortical areas I and II of the rabbit is provided by Thompson, Woolsey and Talbot ('50). The diencephalon and midbrain were sectioned at 35  $\mu$  horizontally in ten of the cases, transverse in the remaining case (table 1). From each, a series consisting of every third section was stained with cresyl violet, and a series contiguous with this was prepared according to the methods of Nauta and Gyax ('54) and Fink and Heimer ('67) (table 1). Additional sections from eight of the brains were processed by the following modification of the Fink-Heimer method (table 1):

(1) After a brief rinse in distilled water, sections are immersed in 10% uranyl nitrate four minutes.

(2) Sections are rinsed and transferred to 20% silver nitrate five to ten minutes.

(3) Sections are rinsed and then immersed in the following solution three to five minutes.

1.5%	silver nitrate	20 ml
100%	ethanol	10 ml
27-39%	ammonium hydroxide	4 ml
2.5%	sodium hydroxide	1.5 ml

(4) Without rinsing sections are treated in the following solution one to two minutes.

Distilled water	910 ml
95% ethanol	90 ml
10% formalin	37 ml
1% citric acid	27 ml

(5) Sections are transferred to 0.5% sodium thiosulfate one minute.

(6) If desired, the background in the sections may be lightened by treating them in 0.05% potassium ferricyanide 10-20 seconds.

(7) Sections are rinsed well, dehydrated, cleared and mounted.

In our hands this procedure has proven useful for the study of the fiber degeneration resulting from lesions in the visual cortex of the rabbit. Degenerating axons including their fiber arborizations and bouton endings, appear heavily impregnated; and at the same time the entire procedure requires only 30-35 minutes.

<sup>2</sup>In our definition of the visual cortex we shall include both the first and the second visual areas of Thompson, Woolsey and Talbot ('50). The lesions produced in the present study involve the central region in the visual cortex and as such they include lateral portions of visual area I together with medial portions of visual area II.

LATERAL

Case	Postoperative survival	Data page
	days	
EAR 2	6	
EAR 3	4	
EAR 4	14	
EAR 6	5	
EAR 7	3	
EAR 8	4	
EAR 9	7	
EAR 10	2	
EAR 11	7	
EAR 14	8	
EAR 15	14	

In this column, the use of the Fink-Heimer method

In addition to the above sections from each of four of the brains were processed by the method (table 1) as modified by S. and the brains of five normal rabbits prepared by the Golgi-Romeis, '48).

#### RESULTS

##### 1. The normal fiber arc dorsal lateral geniculate the pulvinar as revealed by the Cajal method

The normal fiber organization of the dorsal lateral geniculate pulvinar has been studied in the present study (series EA, table 1), with the sides contralateral to the lesions b

TABLE 1  
Data pertaining to the experimental brain series

Brain number	Postoperative survival	Plane of section	Stains <sup>1</sup>	Illustrated in figures
	days			
EAR 2	6	Horizontal	Nauta-Gygax, Fink-Heimer, Cajal	Figs. 1A, 5, 11
EAR 3	4	Horizontal	Nauta-Gygax, Fink-Heimer, Cajal	
EAR 4	14	Transverse	Nauta-Gygax, Fink-Heimer, Cajal	
EAR 6	5	Horizontal	Fink-Heimer, present method	
EAR 7	3	Horizontal	Fink-Heimer, present method	Fig. 8
EAR 8	4	Horizontal	Fink-Heimer, present method	Fig. 1B
EAR 9	7	Horizontal	Fink-Heimer, present method	Fig. 9
EAR 10	2	Horizontal	Fink-Heimer, present method	
EAR 11	7	Horizontal	Fink-Heimer, present method	Figs. 2-4, 6, 7, 10, 12
EAR 14	8	Horizontal	Fink-Heimer, present method	
EAR 15	14	Horizontal	Nauta-Gygax, Fink-Heimer, present method, Cajal	Figs. 13, 14

<sup>1</sup> In this column, the use of the term *present method* indicates that sections were processed by the modification of the Fink-Heimer method described in the MATERIALS AND METHODS.

In addition to the above, selected sections from each of four of the experimental brains were processed by the Cajal method (table 1) as modified by Scalia et al. ('68) and the brains of five normal rabbits were prepared by the Golgi-Kopsch method (Romeis, '48).

#### RESULTS

##### I. The normal fiber architecture of the dorsal lateral geniculate nucleus and the pulvinar as revealed by the Cajal method<sup>3</sup>

The normal fiber organization of the dorsal lateral geniculate nucleus and the pulvinar has been studied in Cajal sections prepared from series EAR 2, 3, 4 and 15 (table 1), with the sides of the brains contralateral to the lesions being used for this

purpose. It has been found that the fibers in the geniculate nucleus, as well as those in the pulvinar, are organized into two discrete fiber systems. These systems are depicted in figure 1A and in accordance with the terminology previously devised for the dorsal lateral geniculate nucleus of the rat (Montero and Guillery, '68), they will be called the transverse and longitudinal fiber systems.

The fibers which form the transverse system are oriented caudomedially (fig. 1A) and dorsally as they course within the geniculate nucleus and the pulvinar. These fibers are disposed into bundles that are scattered throughout the full extent of

<sup>3</sup> For descriptions of the cytoarchitecture of the dorsal lateral geniculate nucleus and the pulvinar of the rabbit it is recommended that the interested reader consult the articles of Rose ('42) and Giolli and Guthrie ('69, '71).

these nuclei, and some of the more superficial of these bundles are intermingled with the fibers of the optic tract. In figure 1A the transverse fiber system in the geniculate nucleus and in the pulvinar is shown in a horizontal section passing approximately midway through these nuclei.

The fibers comprising the longitudinal system of the geniculate nucleus and the pulvinar run perpendicularly to the transverse fibers and are not grouped into bundles (fig. 1A). As figure 1A shows, local differences exist in the density of the longitudinal system. Thus, the longitudinal fibers are uniformly distributed in each of the geniculate subdivisions, the alpha and the beta sectors, but their density is greater in the beta sector than in the alpha sector; and the longitudinal fibers are distributed more densely to the half of the pulvinar nearest to, as compared with the half farthest from, the geniculate nucleus.

## II. Fiber degeneration in the dorsal lateral geniculate nucleus and the pulvinar as revealed by the Nauta method<sup>4</sup>

The findings presented below are concerned with the distribution of the fiber degeneration produced by lesions involving the central region of the visual cortex, i.e., the zone of cortex encompassing the lateral part of visual area I and the medial part of visual area II.

### 1. Degenerating fibers in the transverse system of the dorsal lateral geniculate nucleus and the pulvinar

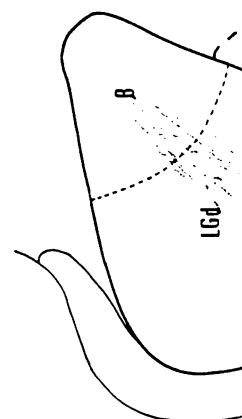
Degenerating fibers leave the lesion sites in the visual cortex and descend ipsilaterally through the internal capsule. The majority of these fibers diverge from the internal capsule to project caudomedially and dorsally through the lateral thalamus and to continue caudally into the pretectum and the superior colliculus. These fibers contribute to the transverse system found in the geniculate nucleus and in the pulvinar (compare figs. 1A, B). These observations have been consistently made in all of the experimental cases except EAR 10, which had a postoperative survival time of only two days and lacked signs of degeneration subcortically.

Figure 1B serves to illustrate the distribution of the transverse fiber degeneration as it has generally been seen in the geniculate nucleus and the pulvinar in the experimental material. As noted, this fiber degeneration is particularly dense in the bundles lying within the beta sector of the geniculate nucleus, it is moderately dense in the bundles situated in the outer portion of the pulvinar, and it is sparse in the remaining portions of these nuclei. Further, some of the degenerating transverse fibers are shown to mingle with the fibers of the optic tract.

Our study of the Nauta sections reveals that a substantial number of the degenerating transverse fibers bifurcate and that in so doing these fibers give rise to branches which either pass into, or are directed toward, the zones of pericellular fiber degeneration present in the geniculate nucleus (figs. 2-4) and in the pulvinar (figs. 5, 6). These bifurcations are demonstrated frequently in the beta sector of the geniculate nucleus (figs. 2-4), the outer portion of the pulvinar (fig. 6), and the strip of the optic tract adjacent to the pulvinar

<sup>4</sup> The term *Nauta method* as it is used throughout this report refers collectively to the Nauta-Gygax method ('54), the Fink-Heimer method ('67), and the modification of the latter method as described in the MATERIALS AND METHODS.

Fig. 1 The fiber organization in the dorsal lateral geniculate nucleus and in the pulvinar illustrated in drawings of horizontal sections passing approximately midway (dorsoventrally) through these nuclei. Arrows t and l denote the general orientation of the fibers comprising the transverse and longitudinal fiber systems as described in the text. (A) Cajal preparation from series EAR 2 in which the fiber populations of the nuclei are seen to be organized into transverse and longitudinal systems. (B) Nauta preparation from series EAR 8 (4 days survival after cortical lesion) showing the patterns of fiber degeneration within the two nuclei. Degenerating fibers (depicted by line segments) are seen to course in both the transverse and longitudinal systems, and the degenerating longitudinal fibers are shown to be confined to the columns of pericellular fiber degeneration (indicated by stipple pattern). (C) Golgi preparation in which zone of fibers belonging to the longitudinal system of each nucleus is impregnated. In each of these three drawings an interrupted line separates the alpha and beta sectors of the dorsal lateral geniculate nucleus; in figure 1C a similar line depicts a border of the pulvinar which is difficult to delineate.  $\beta$ , beta sector of the dorsal lateral geniculate nucleus; LGd, alpha sector of this nucleus; OT, optic tract; Pul, pulvinar.



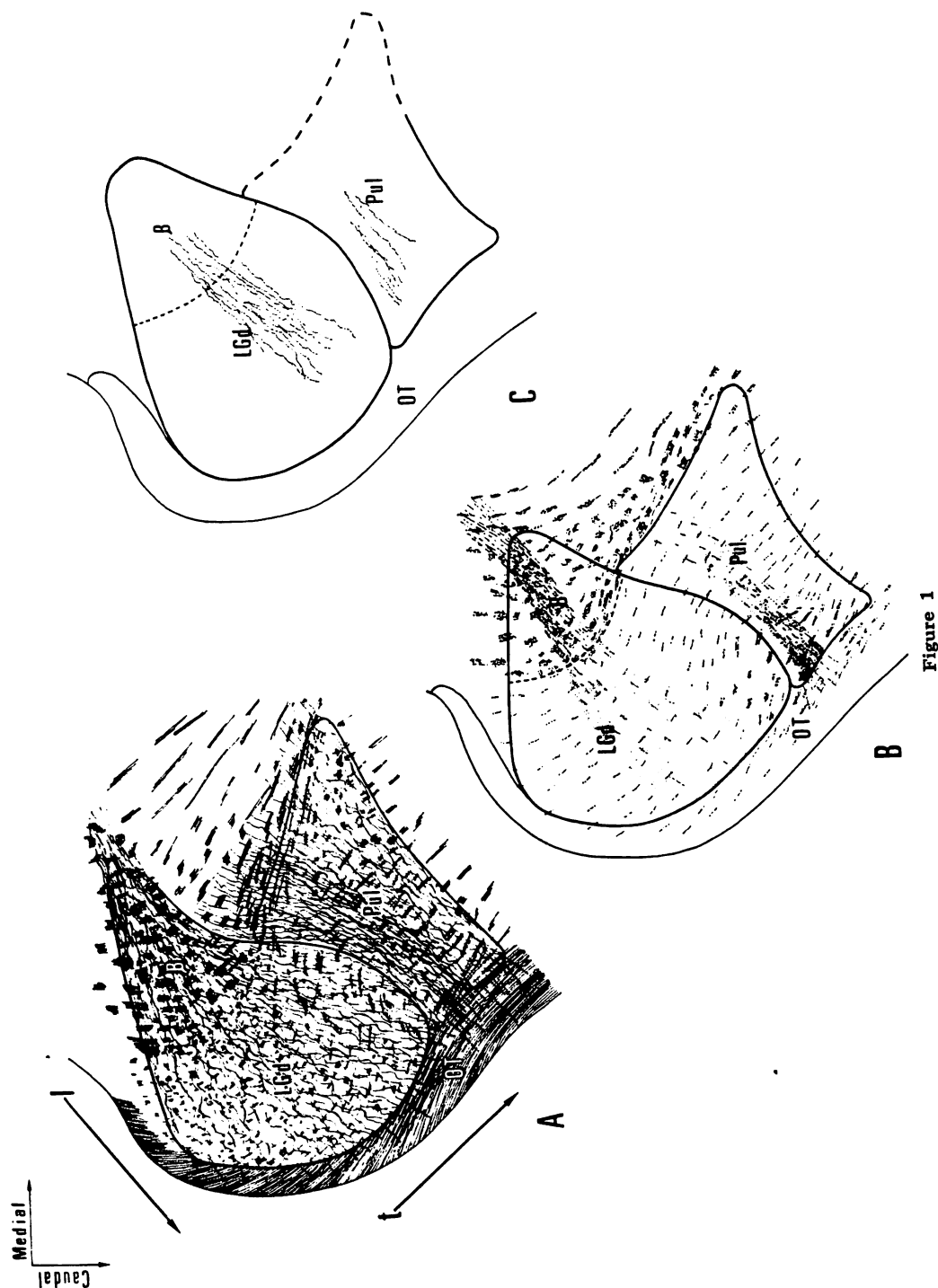


Figure 1

(fig. 5). They are seen only occasionally in the other parts of these nuclei and in the strip of the optic tract adjacent to the geniculate nucleus.

## 2. Degenerating fibers in the longitudinal system

Degenerating fibers have been observed within the longitudinal system of the dorsal lateral geniculate nucleus and the pulvinar in all of the experimental cases with survival times ranging from 3 to 14 days. Such fibers could not be identified in series EAR 10 with a survival time of two days.

*a. Dorsal lateral geniculate nucleus.* Figure 1B illustrates the general pattern of fiber degeneration which has been found in the geniculate nucleus. As shown, the longitudinal fiber degeneration is restricted to the column of pericellular fiber degeneration. Within this column the degeneration is particularly dense in the beta sector and becomes substantially reduced in amount in passing outward through the alpha sector.

It has been possible to distinguish two types of degenerating longitudinal fibers in the experimental material. One of these types consists of fibers which are fine in caliber ( $0.3$  to  $0.75 \mu$ ), degenerate as early as three days after cortical lesions, and give origin to numerous short terminal branches along their extent (figs. 7-10). We conclude that many, perhaps most, of these fibers represent the collateral branches of axons originating from the visual cortex and, further, that these fibers provide much, if not most, of the visual cortical input to the geniculate nucleus. Three of our observations support these conclusions. First, we find that degenerating transverse fibers bifurcate within, or immediately adjacent to, the zones of degenerating longitudinal fibers and that in so doing these transverse fibers send branches into the longitudinal fiber system (figs. 2-4); second, we note that the degenerating longitudinal fibers give rise to numerous short processes (figs. 7-10) which lie within the columns of pericellular fiber degeneration and which we regard as the actual endings of the corticogeniculate fibers; and third, we are unable to demonstrate degenerating fibers that pass

from the transverse to the longitudinal system without branching.

Compared to the above, the second type of degenerating longitudinal fibers to be recognized in the geniculate nucleus are coarse ( $0.75$ - $1.5 \mu$ ), degenerate at 14 days after cortical lesions (figs. 13, 14) but not at the shorter survival times used, and lack any large number of side branches (figs. 13, 14). Principally because of their slow rate of degeneration, we consider these fibers to be geniculocortical axons undergoing retrograde degeneration.

We find that a significant number of both the fine and the coarse longitudinal fibers to be impregnated in the columns of pericellular fiber degeneration look undegenerated even as late as the fourteenth day after cortical lesions. These fibers probably represent the distal segments of retinogeniculate axons as described in the rabbit by Giolli and Guthrie ('69).

*b. Pulvinar.* The longitudinal fiber degeneration within the pulvinar consistently shows the arrangement depicted in figure 1B. As this figure illustrates, this degeneration is limited to the column of pericellular fiber degeneration where its density ranges from a high next to the optic tract to a low at the inner margin of the pulvinar.

Morphologically, all of the degenerating longitudinal fibers fit into one category: they are always fine in caliber ( $0.3$ - $0.75 \mu$ ), they degenerate early (3-4 days postoperatively), and they give rise to numerous short terminal branches along their length (figs. 11, 12). Also, the bifurcations of degenerating transverse fibers run in the longitudinal fiber system of the pulvinar just as they do in the dorsal lateral geniculate nucleus. For these reasons, we consider the degenerating longitudinal fibers found in the pulvinar to be the collateral branches of visual cortical axons and, in addition, we regard these fibers as the primary source of the visual cortical input to this nucleus.

## 3. Pericellular fiber degeneration.

A detailed description of this degeneration has been given previously by Giolli and Guthrie ('71) and Giolli and Pope ('71). In the present report it is necessary only to point out that after survival periods

ranging from 3 to 14 days, columnar pericellular fiber degeneration has been consistently found in the dorsal lateral geniculate nucleus and in the pulvinar. Columns of such columns are shown in figure 1C.

## III Fiber impregnation in the lateral geniculate nucleus and pulvinar as revealed by the Golgi-Kopsch method

Figure 1C shows the fiber pattern in the lateral geniculate nucleus and the pulvinar in the brain as revealed by the Golgi-Kopsch method. As this figure illustrates, the fiber impregnation is limited to segments of these nuclei (one segment is shown in each of the nuclei), and within these segments the staining is limited to fine longitudinal fibers. The vast majority of longitudinal fibers, regardless of their caliber, are fine in caliber ( $0.3$ - $0.75 \mu$ ) and give origin to numerous short terminal branches along their extent (figs. 15-18). Based upon their origin in the different segments of the visual cortex and their morphology these fibers appear to be the fine-caliber longitudinal fibers which are degenerating in the Nauta preparations (compare figs. 7-12 with figs. 15-18).

## DISCUSSION

The study of Nauta preparations has provided three basic findings: first, the manner in which the dorsal lateral geniculate nucleus and the pulvinar are innervated by axons originating from the visual cortex. First, it has been shown that the geniculate nucleus, as the pulvinar, receives a large portion of its visual cortical input through the collateral branches of axons originating from a transverse fiber system. Second, it has been shown that the collateral fibers for these inputs are fine in caliber and run along to a longitudinal fiber system within each of the nuclei. Third, it has been revealed that these collateral fibers are fine-caliber longitudinal fibers which give rise to numerous short terminal branches along their extent. From the study of Nauta preparations it has been pointed out that in normal brains, the visual cortical input to the lateral geniculate nucleus and the pulvinar is primarily derived from the fine-caliber longitudinal fibers which in the Nauta preparations

ranging from 3 to 14 days, columns of pericellular fiber degeneration have been consistently found in the dorsal lateral geniculate nucleus and in the pulvinar. Examples of such columns are shown in figure 1B.

### III. *Fiber impregnation in the dorsal lateral geniculate nucleus and the pulvinar as revealed by the Golgi-Kopsch method*

Figure 1C shows the fiber picture which is generally seen in the geniculate nucleus and the pulvinar in the brains processed by the Golgi-Kopsch method. As this figure illustrates, the fiber impregnation is confined to segments of these nuclei (in fig. 1C one segment is shown impregnated in each of the nuclei), and within these segments the staining is limited to longitudinal fibers. The vast majority of these longitudinal fibers, regardless of their locations in these nuclei, are fine in caliber ( $0.3-0.75 \mu$ ) and give origin to many short terminal branches along their extent (figs. 15-18). Based upon their orientation within the different segments of these nuclei, their fine caliber, and their overall morphology these fibers appear to correspond to the fine-caliber longitudinal fibers found degenerating in the Nauta preparations (compare figs. 7-12 with 15-18).

### DISCUSSION

The study of Nauta preparations has provided three basic findings regarding the manner in which the dorsal lateral geniculate nucleus and the pulvinar of the rabbit are innervated by axons originating from the visual cortex. First, this study has shown that the geniculate nucleus, as well as the pulvinar, receives a large portion of its visual cortical input through the collateral branches of axons which form part of a transverse fiber system. Second, it has shown that the collateral fibers responsible for these inputs are fine in caliber and belong to a longitudinal fiber system present within each of the nuclei. Third, it has revealed that these collateral fibers (the fine-caliber longitudinal fibers) give rise to numerous short terminal branches along their extent. From the study of the Golgi preparations it has been possible to identify in normal brains, the fiber component which in the Nauta preparations is rep-

resented by the fine-caliber longitudinal fibers undergoing degeneration.

Previous studies which have utilized the Nauta method in the rat (Montero and Guillery, '68), the rabbit (Gioli and Guthrie, '71) and the cat (Guillery, '67) have suggested that some of the axons which originate in the visual cortex and descend into the thalamus give rise to collateral branches that terminate in the dorsal lateral geniculate nucleus. The present study has now shown that much, and perhaps most, of the visual cortical innervation of the geniculate nucleus in the rabbit is supplied by the collateral branches of axons which are projecting caudally into the pulvinar and the pretectal nuclei. This latter conclusion is supported by four of the present findings. First, the presence of degenerating transverse fibers (representing projectional fibers from the visual cortex) which branch within or closely adjacent to the zones of degenerating longitudinal fibers. Second, the common orientation of the branches of these transverse fibers and the fine-caliber degenerating longitudinal fibers suggesting that the two represent parts of the same fibers. Third, the morphology of the degenerating longitudinal fibers of fine-caliber which indicates that they are the terminal portions of the corticogeniculate fibers. Fourth, our failure to demonstrate degenerating transverse fibers which pass directly into the longitudinal fiber system.

Other data concerning the mode of visual cortical innervation of the dorsal lateral geniculate nucleus are lacking. However, the subject of the collateral innervation of the geniculate nucleus has received some attention in electrophysiological studies which have dealt with the retinal input to this nucleus and to the superior colliculus. In this respect, Sefton ('68) has shown that a large proportion of the optic nerve fibers which in the rat respond to stimulation of either the geniculate nucleus or the superior colliculus are refractory to the prior stimulation of the other nucleus, and she has concluded that in the rat, most or all of the retinal axons terminating in one of these nuclei also end in the other nucleus. Similarly, Hayashi, Sumitomo and Iwama ('67) have found that the antidromic responses recorded in the cat's optic

chiasma to stimulation of the geniculate nucleus and superior colliculus interact, and on this basis these investigators have reached the same conclusion as has Sefton.

Bouwer ('23) produced discrete lesions on the retinas of rabbits and subsequently examined the retinogeniculate projection using the Marchi method. He was able to show that the different retinal quadrants project sharply to localized regions in the dorsal lateral geniculate nucleus, but he was unable to define more precisely the geniculate zones receiving the inputs from smaller retinal sectors. The projection of small retinal sectors onto the geniculate nucleus in the rabbit has recently been investigated by Hughes ('71) and Stewart, Chow and Masland ('71) who have shown that the cells responsive to spot stimulation of the retina lie in columns extending horizontally through the thickness of this nucleus.

The visuotopic organization within the dorsal lateral geniculate nucleus of the rabbit has also been studied by producing small lesions in the visual cortex, relating these lesions to the retinotopic maps of visual areas I and II provided by Thompson, Woolsey and Talbot ('50), and then studying the fiber degeneration present in the geniculate nucleus. In this way, Giolli and Guthrie ('71) have demonstrated that the retinotopic organization found in the visual cortex is preserved in the cortical projection to the geniculate nucleus, and they have further shown that the geniculate inputs from different sectors of the visual cortex are in the form of discrete columns which are oriented in parallel with the lines of projection for single points on the visual field as described by Hughes ('71). The present findings have substantiated the latter observation of Giolli and Guthrie ('71) and have in addition revealed that the terminal portions of the individual corticogeniculate fibers are themselves directed along these lines of projection. The above data bear particular functional importance because they indicate that the same group of geniculate cells which receives an input from a small locus on the visual cortex must also be related to a single point on the visual field.

Montero and Guillery ('68) have reported that only a few of the longitudinal

fibers found in the zones of pericellular fiber degeneration in the dorsal lateral geniculate nucleus of the rat appear to be normal 13 days after lesions of the visual cortex. By contrast, the present observations on the rabbit indicate that a substantial number of the equivalent fibers present a normal appearance as late as 14 days after similar lesions. If the great number of fibers in the rabbit is not attributable to geniculocortical or corticogeniculate fibers which have managed to retain a normal appearance 14 days after cortical lesions it must be concluded that there is a basic difference in the composition of the longitudinal fiber system in the rat and rabbit. This conclusion is in actual harmony with other findings which indicate that the longitudinal fiber system in the rabbit (Giolli and Guthrie, '69), but not in the rat (Montero and Guillery, '68), contains a substantial number of retinogeniculate fibers.<sup>5</sup>

The present study has revealed a striking similarity in the manner in which the fibers of visual cortical origin provide input to the dorsal lateral geniculate nucleus and the pulvinar. In both of these nuclei, the visual cortical input is supplied by the collateral branches of transverse fibers which are projecting caudally into the pretectum and the superior colliculus. In addition these collateral branches run within the longitudinal fiber system of each of these nuclei and they are all fine in caliber and give off numerous short branches along their length. The significance of the parallel organization as demonstrated within these two nuclei is not clear, and it remains for further experimentation to show whether the fibers providing the visual cortical inputs to other nuclei, e.g., the ventral lateral geniculate nucleus and the anterior and posterior pretectal nuclei (Giolli and Guthrie, '71), are similarly organized.

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<sup>5</sup> As with Montero and Guillery ('68) and Giolli and Guthrie ('69), Giolli and Creel ('72) have utilized the Nauta method after ocular enucleation, and these latter workers have found that in guinea pigs, as in rabbits but not in rats, the retinogeniculate axons contribute substantially to the longitudinal fiber system of the dorsal lateral geniculate nucleus.

typing the manuscript. We wish to express our sincere appreciation to Professor R. W. Guillery of the Department of Anatomy at the University of Toronto for his continued interest in this research.

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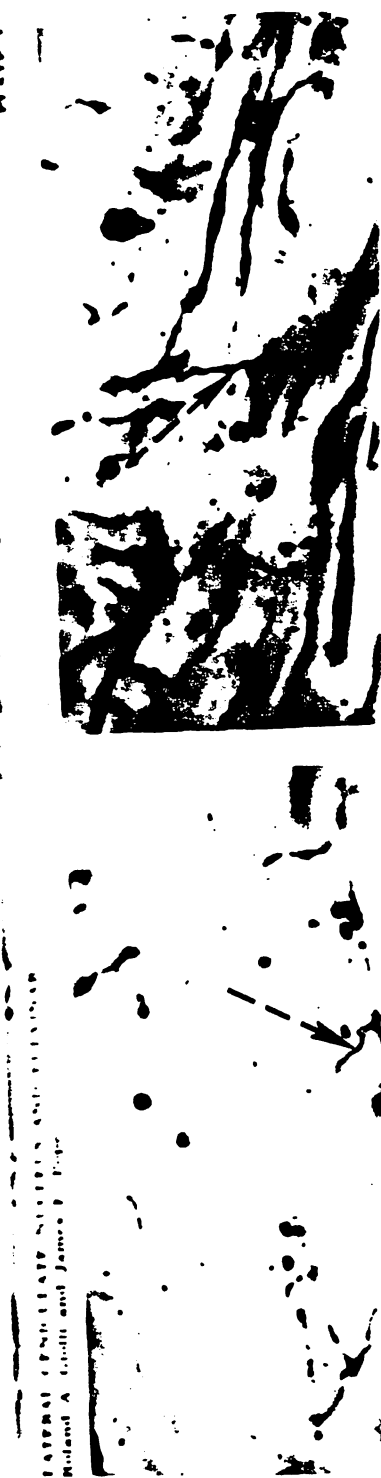
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## PLATE 1

## EXPLANATION OF FIGURES

- 2-4 In each of these figures a broken arrow points to the collateral branch being given off by a degenerating transverse fiber which is situated within the beta sector of the dorsal lateral geniculate nucleus and is oriented in the plane indicated by a solid arrow. In figures 3 and 4, a few degenerating fibers of the transverse and longitudinal fiber systems have been impregnated (the transverse fibers are directed in the planes of the solid arrows and the longitudinal fibers are oriented perpendicularly to these arrows). (EAR 11, 7 days survival), modification of the Fink-Heimer method.  $\times 1660$ .
- 5 A broken arrow points to a collateral branch shown leaving a degenerating transverse fiber located within the optic tract adjacent to the pulvinar (a solid arrow reveals the plane of the transverse fiber). The collateral branch is directed toward a column of pericellular fiber degeneration situated in the pulvinar but not illustrated in this figure. EAR 2, 6 days survival, Nauta-Gygax method,  $\times 830$ .
- 6 A broken arrow points to a collateral branch which is seen to arise from a degenerating transverse fiber (plane indicated by a solid arrow) located within the outer part of the pulvinar. A few degenerating transverse fibers have been impregnated and these are oriented in line with the solid arrow. EAR 11, 7 days survival), modification of the Fink-Heimer method,  $\times 1660$ .



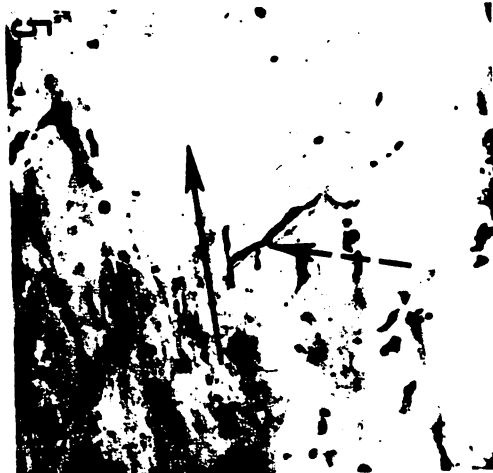
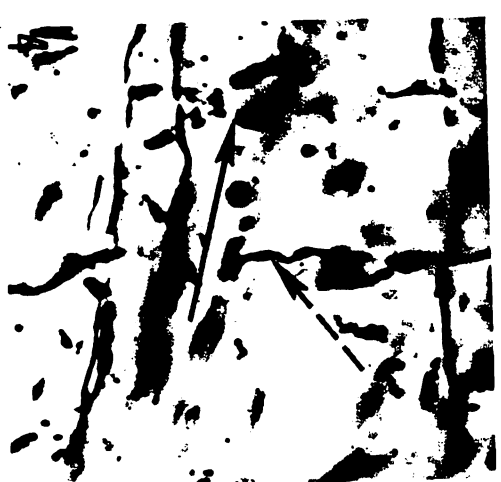


PLATE 2

EXPLANATION OF FIGURES

- 7 This photomicrographic montage shows a group of three fine-caliber, degenerating longitudinal fibers (i.e., the terminal portions of three corticogeniculate fibers) located in the alpha sector of the dorsal lateral geniculate nucleus. The small arrows point to the short terminal branches arising along the extent of these fibers. (EAR 11, 7 days survival), modification of the Fink-Heimer method,  $\times 1000$ .
- 8-9 Each photomicrographic montage pictures a fine-caliber, degenerating longitudinal fiber (i.e., the terminal portion of a corticogeniculate fiber) lying in the beta sector of the dorsal lateral geniculate nucleus. Small arrows depict the short terminal branches along the length of these fibers. (fig. 8: EAR 7, 3 days survival,  $\times 1660$ ; fig. 9: EAR 9, 7 days survival,  $\times 1250$ ), Fink-Heimer method.
- 10 A fine-caliber, degenerating longitudinal fiber (the terminal segment of a corticogeniculate fiber) located in the alpha sector of the dorsal lateral geniculate nucleus is shown in this photomicrographic montage. The short terminal branches arising for this fiber are indicated by small arrows. (EAR 11, 7 days survival), modification of the Fink-Heimer method,  $\times 1000$ .
- 11-12 Each figure shows a fine-caliber degenerating longitudinal fiber situated within the outer part of the pulvinar. The small arrows denote the short terminal branches given off by these fibers. (fig. 11: EAR 2, 6 days survival, Nauta-Gygax method,  $\times 1300$ ; fig. 12: EAR 11, 7 days survival, modification of the Fink-Heimer method,  $\times 1660$ ).





PLATE 3

EXPLANATION OF FIGURES

- 13-14 Each of these montages illustrates a coarse, degenerating longitudinal fiber (probably a geniculocortical fiber) located within the beta sector of the dorsal lateral geniculate nucleus. (EAR 15, 14 days survival) modification of the Fink-Heimer method,  $\times 1550$ .
- 15-17 Photomicrograph montages of Golgi-Kopsch preparations show fine-caliber longitudinal fibers within the alpha sector of the dorsal lateral geniculate nucleus. Each of the small arrows points to one of the many short terminal branches given off by these fibers. Figures 15 and 16:  $\times 1250$ , figure 17:  $\times 1550$ .
- 18 A photomicrographic montage illustrates a fine-caliber longitudinal fiber as seen within the outer part of the pulvinar in a Golgi-Kopsch preparation. The short terminal branches arising from this fiber are indicated by small arrows,  $\times 1550$ .

