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Morphology of Physiologically Identified Retinogeniculate X- and Y-Axons in the Cat

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SUMMARY AND CONCLUSIONS

1. We studied the morphology of individual, physiologically identified retinogeniculate axons in normal adult cats. The axons were recorded in the lateral geniculate nucleus or in the subjacent optic tract, characterized as X or Y by physiological criteria, penetrated, and injected with horseradish peroxidase. With subsequent application of appropriate histochemistry, the enzyme provides a complete label of the terminal arbors and parent trunks for morphological analysis. We have recovered for such analysis 26 X- and 25 Y-axons; of these, 14 X- and 12 Y-axons were studied in detail.

2. Within the optic tract, the parent trunk of every X-axon is located closer to the lateral geniculate nucleus and thus further from the pial surface than that of every Y-axon. This probably reflects the earlier development of X- than of Y-axons. Furthermore, the parent axon trunks of the X-axons are noticeably thinner than are those of the Y-axons. Every retinogeniculate X- and Y-axon in our sample branches within the optic tract. One of these branches heads dorsally to innervate the lateral geniculate nucleus and one heads medially and rostrally toward the midbrain, although none of these labeled axons were traced to a terminal arbor beyond the lateral geniculate nucleus. For Y-axons, all branches are of comparable diameter, but for X-axons, the branch heading toward the lateral geniculate nucleus is always noticeably thicker than is the branch directed toward the midbrain.

3. Every retinogeniculate X- and Y-axon produces the greatest portion of its terminal arbor in lamina A (if from the contralateral retina) or A1 (if from the ipsilateral retina). These arbors typically extend across most of the lamina along a projection line. Not a single terminal bouton from any axon was found in the inappropriate lamina A or A1 (i.e., in lamina A for ipsilaterally projecting axons or in lamina A1 for contralaterally projecting ones). Occasionally, an X-axon also innervates the medial interlaminar nucleus, and even more rarely does an X-axon innervate the C-laminae. In contrast, nearly all Y-axons from the contralateral retina branch to innervate part of the C-laminae (probably lamina C), and most from either retina also innervate the medial interlaminar nucleus. Although these details imply considerable variation in the overall pattern of retinogeniculate innervation for both X- and Y-axons, we found no physiological properties to correlate with this variation.

4. Within lamina A or A1, certain differences were noted between X- and Y-axon arbors. Compared with Y-arbors on average, the X-arbors are half as wide in the mediolateral direction (150 μm vs. 300 μm) and one-quarter the volume, and they produce only about half as many terminal boutons (500–600 vs. 1,000). Although a wide range of bouton sizes (2–6 μm diam) is evident for each arbor, Y-axons contain a wider range of sizes with many more of the larger ones than do X-axons. Finally, the boutons in X-arbors are found on short stalks in prominent clumps, whereas those in Y-arbors are more diffusely distributed en passant along the preterminal axon branches.

5. In addition to forming more boutons than do X-axons in laminae A and A1, Y-axons also form many boutons elsewhere in the lateral geniculate nucleus, whereas such

boutons beyond the A-laminae are rare for X-axons. Each Y-axon thus seems able to innervate more geniculate neurons, which may represent the morphological basis for previously published evidence that the X-to-Y cell ratio is considerably lower in the lateral geniculate nucleus than in the retina. A similar difference between X- and Y-axons has already been described for geniculocortical innervation. This pattern of greater synaptic numbers for individual Y- than for X-axons may serve to explain in part how the Y pathway, which is so small at its retinal origin, can become so important at the level of visual cortex.

INTRODUCTION

The cat's retina contains several morphologically and physiologically distinct classes of ganglion cell (for reviews, see Refs. 48, 49, 54, 55, 59). Two of these, the X- and Y-cells, represent the point of departure for two parallel neuronal streams conveying retinal information through the lateral geniculate nucleus to the visual cortex. Geniculate X- and Y-cells are generally innervated by one or a few retinal axons of the same class (i.e., X- or Y-cell, on or off center), with the result that the receptive-field properties of these geniculate neurons are virtually the same as those of their retinal afferents (7, 9, 26, 30, 56). Although there thus seems to be relatively little convergence in retinogeniculate circuitry, there must be considerable divergence, since the postsynaptic geniculate neurons outnumber their retinal afferents by a factor of roughly 5 (16, 50). Furthermore, since the geniculate X-to-Y cell ratio seems to be considerably lower than the analogous ratio among retinal ganglion cells, this divergence factor seems to be greater for retinogeniculate Y-axons than for X-axons (16).

Given the obvious importance of retinogeniculate connections in the relay of visual information to cortex (reviewed in Ref. 54), we reasoned that it would be most useful to understand the morphological basis for these connections. In particular, we wished to elucidate the central projections and termination patterns of individual retinogeniculate X- and Y-axons. This not only would provide us with a basic morphological framework for understanding the parallel X and Y pathways, but it would also address specific questions, such as the morphological basis for the apparently greater divergence of the retinogeniculate Y-axons compared with those of X-axons.

We employed the technique of physiologically characterizing a retinogeniculate axon and intracellularly injecting it with horseradish peroxidase (HRP). The subsequent Golgi-like HRP labeling permits a complete morphological reconstruction of the axon's terminal arbor in the lateral geniculate nucleus. We found a number of similarities and differences in the terminal arbors of X- and Y-axons. Among the differences is the noticeably larger terminal arbors with more terminal boutons of the Y-axons compared with the X-axons, a presumed morphological concomitant of the greater divergence of the retinogeniculate projection for the former axons than for the latter. Our data confirm and extend many of our previous observations (61) and those of Bowling and Michael (3, 4). Some of our results have been published in abstract form (12, 58).

METHODS

Our methods are only briefly outlined here, because further details can be found elsewhere (16, 18, 19, 61).

Normal adult cats were anesthetized, paralyzed, and artificially ventilated. Various vital signs (expired CO_2, body temperature, heart rate, etc.) were monitored and maintained at physiological levels. We made craniotomies both for the stimulating electrodes placed across the optic chiasm and for the recording micropipettes. We used a low-impedance (ca. 5 MΩ at 100 Hz) micropipette filled with 3 M KCl for the first recording penetration. This facilitated the recording and receptive-field plotting of neuronal activity within the lateral geniculate nucleus. This, in association with Sanderson's (51) retinotopic maps of the lateral geniculate nucleus and our informal reconstructions of the shape of the optic tract, provided a ready guide to future electrode placement for optic tract recording. These latter electrode penetrations passed through the anterior and lateral regions of the lateral geniculate nucleus, because the subjacent optic tract is relatively thick there. Furthermore, it is easier there to locate parent trunks of retinogeniculate axons before they branch, which also facilitates recording and impalement for HRP injections. The micropipettes used for recording and injection were filled with 5–10% HRP (Sigma type VI) in 0.2 M KCl and 0.05M Tris (pH 7.6), and they were beveled to a final impedance of 90–120 MΩ at 100 Hz. We estimate the final tip diameters to be 0.2–0.5 μm (16).

We recorded extracellularly from a retinofugal axon, plotted its receptive field, noted the eye that drove it, and determined various receptive-field characteristics, such as the center type (i.e., on or off), the linearity of spatial and temporal summation in response to a sinusoidal grating stimulus, the strength of the surround response and antagonism, the tonicity of the center response, and the responsiveness to large, fast-moving targets. The axon's response latency to optic chiasm stimulation was also measured. These various response properties were used to identify each axon as X or Y (6, 9, 11, 26, 35, 48, 49, 54, 55).

After we classified an axon extracellularly, we attempted to impale it as follows. We advanced the electrode in 1- to 2-μm steps until the extracellularly recorded spike amplitude was 2–3 mV. We then either passed brief 1- to 3-nA pulses of depolarizing current through the electrode or advanced the electrode in short, rapid steps to achieve penetration. A sharp drop in the DC resting potential (25–50 mV) and an increase in recorded spike amplitude (usually >20 mV) signified successful impalement. Key physiological properties were quickly rechecked to ensure that we were inside the same axon that was studied extracellularly, and HRP was iontophoresed into the axon using depolarizing current pulses up to 20 nA in amplitude at 4–20 Hz. We monitored the axon's resting potential at frequent intervals to ensure integrity of the impalement. After 2–5 min of injection, or if the resting potential began to decay appreciably, we discontinued iontophoresis and withdrew the electrode. We made certain that the receptive-field locations of injected axons were suitably separated so that there was no ambiguity in assigning recovered axonal arbors in the lateral geniculate nucleus to specific axons from which electrophysiological data were obtained (see below). After we completed each electrode penetration, we rechecked the projected optic disk positions to compensate for small eye movements.

After a survival time of at least 3 h following the last HRP injection, we deeply anesthetized the cat with barbiturate and transcardially perfused it with saline followed by fixatives. Following removal from the cranium and storage in sucrose overnight, the brain was sectioned coronally or parasagittally at 100 μm on a freezing microtome. We reacted every section with 3-3′ diaminobenzidine intensified with cobaltous chloride (1). Selected sections containing

TABLE 1. *Physiological features of the retinogeniculate X- and Y-axons described in detail in the text plus the figures in which they are illustrated*

Axon Class	Eye of Origin	Center Type	Center Size, deg	Optic Chiasm Latency, ms	Eccentricity, deg	Figure(s)
X	C	On	0.6	0.8	23	2,4,7*D*
Y	C	On	2.7	0.6	32	3,12,15*A*
X	C	On	0.8	1.1	25	5
X	C	On	1.3	1.0	4	6,8*B*
X	C	On	0.5	0.9	9	7*A*
X	C	On	0.5	1.0	12	7*B*
X	C	On	0.7	0.7	8	7*C*
X	C	On	1.7	0.7	8	8*A*
X	C	On	1.5	1.0	37	8*C*
X	C	Off	1.0	1.1	18	9*A*
X	C	Off	0.9	1.1	23	9*B*
X	C	Off	0.5	0.7	6	9*C*
X	I	On	1.0	0.6	13	10
X	I	Off	1.1	0.6	29	11*A*
X	I	Off	3.0	0.8	38	11*B*
X	I	Off	2.2	0.7	10	11*C*
Y	I	Off	2.8	0.5	22	13,12,15*A*
Y	I	On	1.7	0.3	16	14,17*B*
Y	C	On	1.1	0.5	45	15*B*
Y	C	Off	1.2	0.4	12	16*A*
Y	C	Off	4.2	0.6	14	16*B*
Y	C	Off	2.3	0.6	56	16*C*
Y	I	On	1.7	0.6	32	17*A*
Y	I	On	2.2	0.5	27	17*C*
Y	I	On	9.0	*	60	17*D*
Y	I	On	2.0	0.4	18	17*E*
Y	I	Off	3.7	0.4	8	18*B*

C, contralateral; I, ipsilateral. * Not driven by electrical stimulation of optic chiasm.

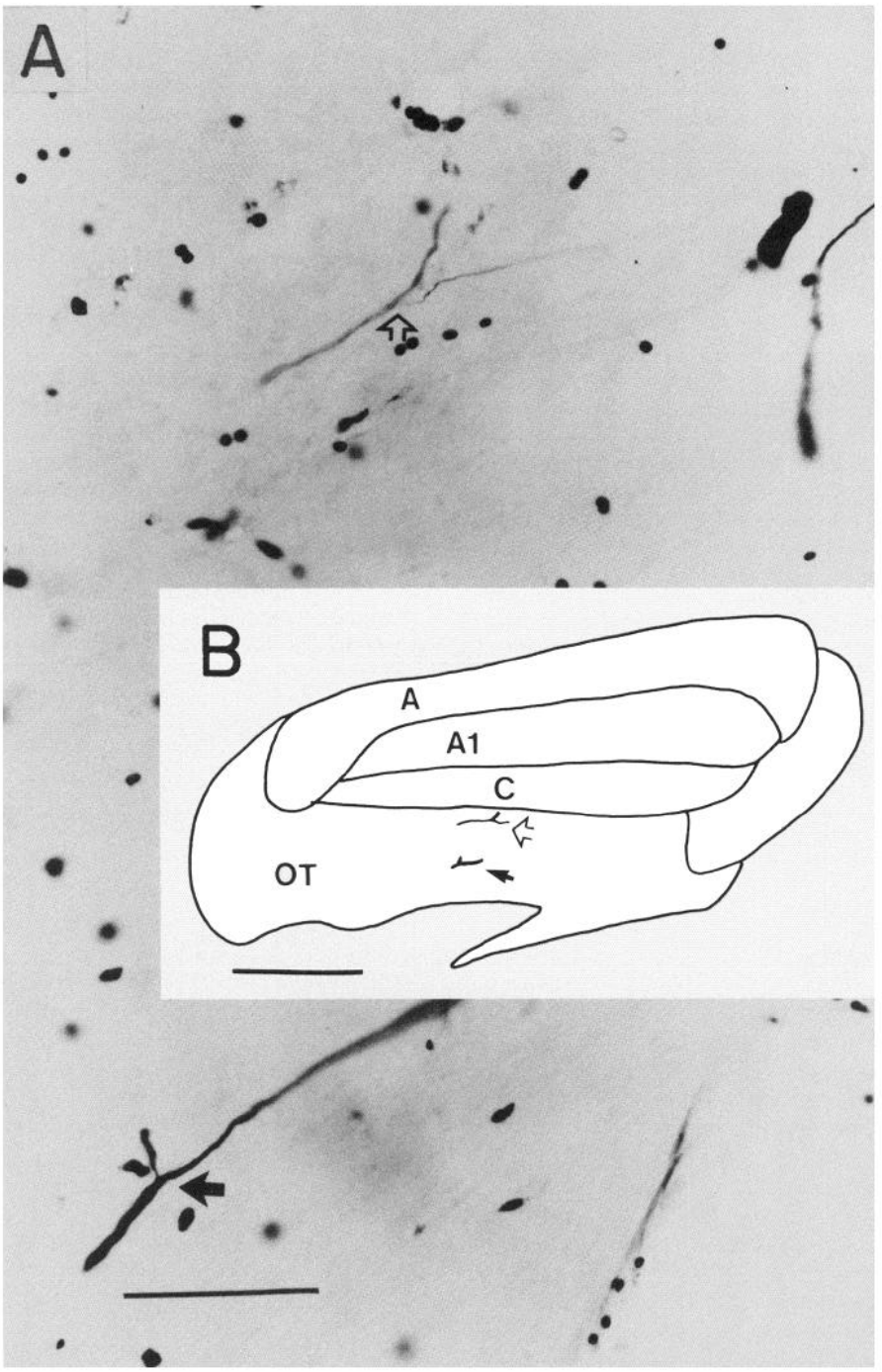


FIG. 1. Appearance of HRP-labeled X and Y retinogeniculate axons in the optic tract subjacent to the lateral geniculate nucleus. *A*: photomicrograph of an X-axon (*open arrow*) and a Y-axon (*solid arrow*) in the same coronal section through the optic tract. The *arrows* indicate the first branch point of each axon. One branch of each heads dorsally into the lateral geniculate nucleus, and the other branch heads toward the right en route to the brachium of the superior colliculus. Note that the parent fiber is thicker for the Y-axon than for the X-axon. Note also that, while both branches of the Y-axon are comparable in diameter, the X-axon forms a geniculate branch that is clearly thicker than is the brachium branch. Scale, 100 μm. *B*: *inset* showing the locations of these axons within the optic tract (*OT*)

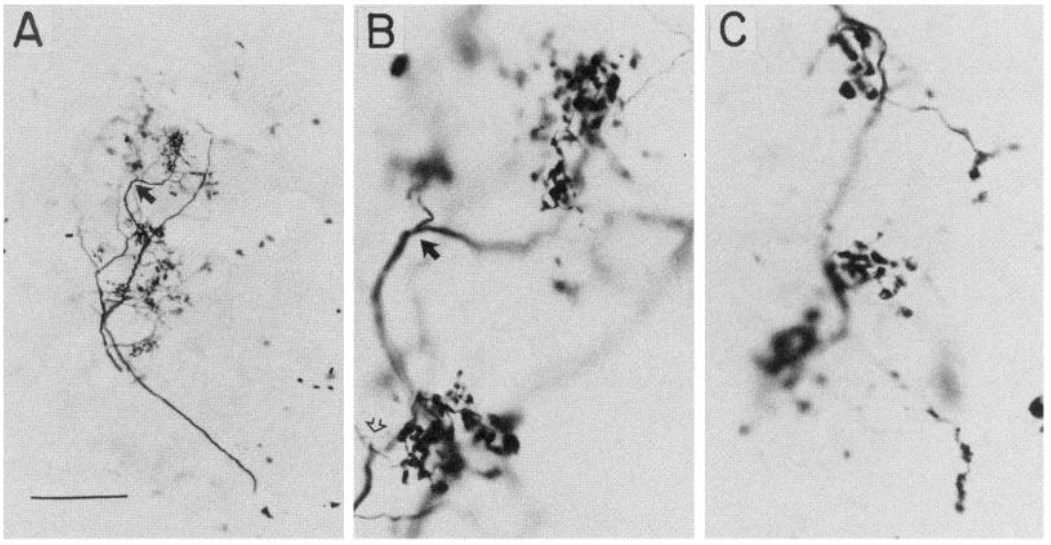


FIG. 2. Photomicrographs of a sagittal section through the terminal arbor of an HRP-labeled retinogeniculate X-axon. The axon derives from the contralateral eye, and the terminal arbor is completely confined to lamina A. This is the same axon that is reconstructed in Fig. 4. The scale in *A* represents 100 μm for *A* and 25 μm for *B* and *C*. *A*: lower-power view showing the clustering of terminal boutons. The *filled arrow* points to the same axonal branch point as does the *filled arrow* in *B*. *B*: higher-power view of terminal boutons shown in *A*. The *open arrows* depicts a fine, long process connecting a cluster of terminal boutons to the preterminal axon. *C*: higher power of another portion of the terminal arbor from a section adjacent to that illustrated in *A* and *B*.

terminal arbors were later stained with cresyl violet for identification of geniculate laminar borders.

Two procedures were used to match labeled retinogeniculate axons to their electrophysiological responses. First, the receptive-field location and eye dominance was matched to the location of the terminal arbor by using Sanderson's (51) retinotopic maps of the lateral geniculate nucleus plus knowledge of the different ocular input to each lamina (cf. Ref. 24). Our care in injecting axons with well-separated receptive fields (see above) simplified this process. Second, we reconstructed electrode tracks and could often match an obvious injection site with the depth of the electrode tip during the HRP iontophoresis.

Labeled axon terminal arbors were reconstructed from serial sections with the use of a drawing tube attachment on a microscope. We did not correct for tissue shrinkage, since we were primarily interested in the relative features of X- and Y-axons. We reasoned that constant shrinkage would not affect such relative measures. We obtained several measures of each terminal arbor in the lateral geniculate nucleus. Terminal boutons, which are readily visible in this material, were counted through the light microscope from serial sections. We also measured the diameters of selected samples of boutons; for elongated boutons, we took as the diameter the mean length of the longest and shortest axes. Finally, we estimated the volume of each terminal arbor by drawing an outline enclosing the outermost boutons in each section and measuring the enclosed area; we converted this to volume by treating each section as a 100-μm-thick slab (see Ref. 19). Where wide gaps separated zones of terminal arbors, such as the laminae A and C terminal zones of a single Y-axon, we measured the volume of each zone separately and summed them later.

Wherever possible, we traced each labeled axon arbor back to its parent trunk in the optic tract. For these, we made two additional measurements. First, we measured the diameter of the parent axon at three points separated by 100 μm; we took the mean of these measurements to the nearest 0.5 μm for the parent axon's diameter. Second, we estimated the relative location within the optic tract of the parent axon by measuring the ratio of its distance from the border of the optic tract with the C-laminae

relative to the main laminae (*A*, *A1*, and *C*) of the lateral geniculate nucleus. The X-axon (*open arrow*) is located more dorsally within the optic tract (i.e., closer to the lateral geniculate nucleus) than is the Y-axon (*solid arrow*). Scale, 1 mm.

to the overall thickness of the optic tract in the same sections.

Unless stated otherwise, we used the Mann-Whitney *U* test for all statistical comparisons.

RESULTS

We obtained electrophysiological data from 139 retinofugal axons, 41 X- and 98 Y-axons, recorded either within the lateral geniculate nucleus or in the subjacent optic tract. Of these, we injected with HRP and recovered 26 X- and 25 Y-axons. Our descriptions of axon caliber and site within the optic tract plus the general region and laminar location of axonal terminations are drawn from this sample. The terminal arbors of a subpopulation of 14 X- and 12 Y-axons were particularly well labeled, and this represents our database for detailed analysis of retinogeniculate X- and Y-axon arbors. Table 1 summarizes many features of these 14 X- and 12 Y-axons; one extra X-axon (the 2nd X-axon in the Table) is also included, because it is separately illustrated, even though we have not done a detailed analysis of its arbor due to faint staining.

Physiology of retinogeniculate X- and Y-axons

Because the recording electrodes passed through the lateral geniculate nucleus and because retinogeniculate axons were recorded in the nucleus as well as in the optic tract, it was important to distinguish between recordings from retinogeniculate axons and those from geniculate neurons. The success of our ability to make this distinction, which proved fairly straightforward, is demonstrated by the fact that we commonly recovered labeled retinogeniculate axons, but never geniculate neu-

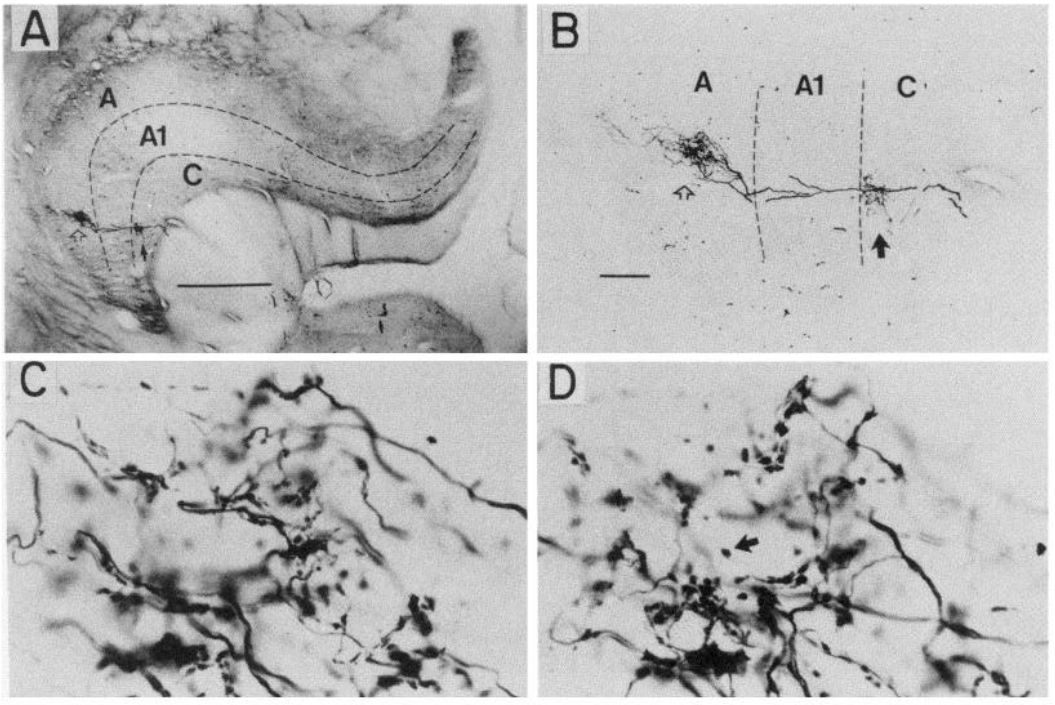


FIG. 3. Photomicrographs of a sagittal section through the terminal arbor of an HRP-labeled retinogeniculate Y-axon. Anterior is the *left* and dorsal to the *top* in each *panel*. The axon derives from the contralateral eye, and, at this level, it innervates both the C-laminae and lamina A. This is the same axon that is reconstructed in Fig. 12. *A*: low-power view of the labeled axon in relationship to the laminae (*A*, *A1*, and *C*) of the lateral geniculate nucleus. The *filled arrow* points to the arbor within the C-laminae, and the *open arrow* points to the arbor within lamina A. Notice the absolute lack of boutons formed in lamina A1. Scale, 0.5 mm. *B*: medium-power view of the labeled axon. As in *A*, the *arrows* point to the separate terminal arbors in the C-laminae and lamina A. The scale in *B* represents 100 μm for *B* and 10 μm for *C* and *D*. *C* and *D*: two different focal planes of the same high-power views of part of the terminal arbor located in lamina A. The *arrow* in *D* depicts a single bouton at the end of a long, thin axonal process.

rons, after we injected a unit deemed to be an axon. Our distinction was based on five criteria. First, retinogeniculate axons respond with shorter latencies to optic chiasm stimulation than do geniculate neurons, because responses of the latter are delayed by additional axonal transmission time and synaptic delay (7, 26, 56). Second, compared with geniculate neurons, retinogeniculate axons can follow higher rates of optic chiasm stimulation (>100 Hz) without failure, and they exhibit much less variation in their orthodromic spike latency (<0.1 ms). Third, retinogeniculate axons have monophasic action potentials with fast rise times and long "tails" without prominent afterhyperpolarizations, whereas geniculate neurons exhibit faster repolarization after the action potential as well as afterhyperpolarizations (cf. Ref. 28). The characteristic shapes of these potentials are readily apparent in DC-coupled oscilloscope traces produced via a DC amplifier, particularly during intracellular recording. The difference between retinogeniculate axons and geniculate neurons in action potential shape presumably reflects the lack in myelinated vertebrate axons of a repolarizing outward potassium current consequent to the sodium spike, an outward current common to somata (8, 28, 29). Fourth, during intracellular recording, optic tract axons do not exhibit slow waves or apparent postsynaptic potentials, whereas geniculate neurons always exhibit such activity (cf. Ref. 16). Fifth, and finally, retinogeniculate axons typically display much

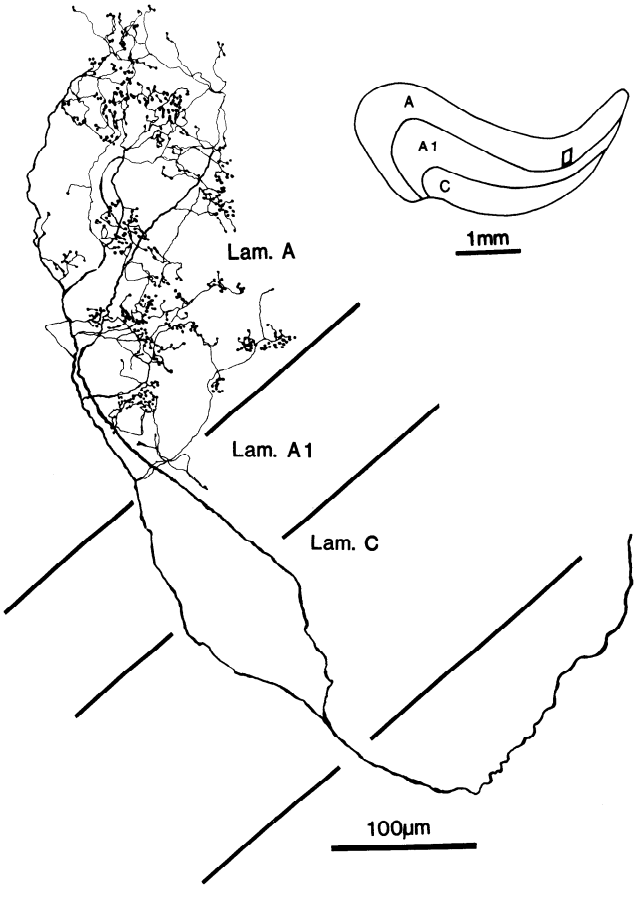


FIG. 4. Sagittal view of reconstruction of X-axon from left retina innervating the right lateral geniculate nucleus. Although only lamina A is innervated in the lateral geniculate nucleus, a branch of the axon (not illustrated) continues medially to enter the brachium of the superior colliculus. The box in the *inset* drawing of the lateral geniculate nucleus shows the location of the axon's terminal arbor. As is the case for all axon arbors reconstructed, the physiological properties of this axon are shown in Table 1.

higher rates of spontaneous activity than do geniculate cells (7).

We reliably identified and distinguished between retinogeniculate X- and Y-axons with our battery of physiological tests. X-axons exhibited longer response latencies to electrical activation of the optic chiasm than did Y-axons. The latency range for the population of X-axons was 0.6–1.2 ms, with a mean of 0.8 ms; the range and mean for the Y-axons were, respectively, 0.3–0.7 ms and 0.5 ms. Receptive-field center diameter was consistently smaller for X- than for Y-axons at matched eccentricities from the area centralis. The range for the X-axons was 0.5–3.3° over an eccentricity range of 1–56°; for Y-axons, the center diameters were 0.5–12.1° over an eccentricity range of 3–87°. The mean center diameter for X-axons was 1.1° at a mean eccentricity of 15°, and for Y-axons, these respective values were 2.8 and 31°. Every X-axon exhibited linear summation in response to visual stimuli, whereas every Y-axon exhibited nonlinear summation.

Our subpopulation of X- and Y-axons with well-labeled terminal arbors was physiologically representative of our total population of recorded axons (see Table 1). Among this subpopulation, the 14 X-axons exhibited response latencies to optic chiasm stimulation of 0.6–1.1 ms with a mean of 0.8 ms, and latencies of the 12 Y-axons were 0.3–0.7 ms with a mean of 0.5 ms. The X-axons had receptive-field center diameters of 0.5–3.0° at eccentricities of 4–38°, with a mean diameter of 1.2° at a mean eccentricity of 17°. The Y-axons had center diameters of 1.1–10.0° at eccentricities of 8–60°, with a mean diameter of 3.0° at a mean eccentricity of 29°.

Targets of retinogeniculate X- and Y-axons

Each of the axons of the present study produces a terminal arbor in the lateral geniculate

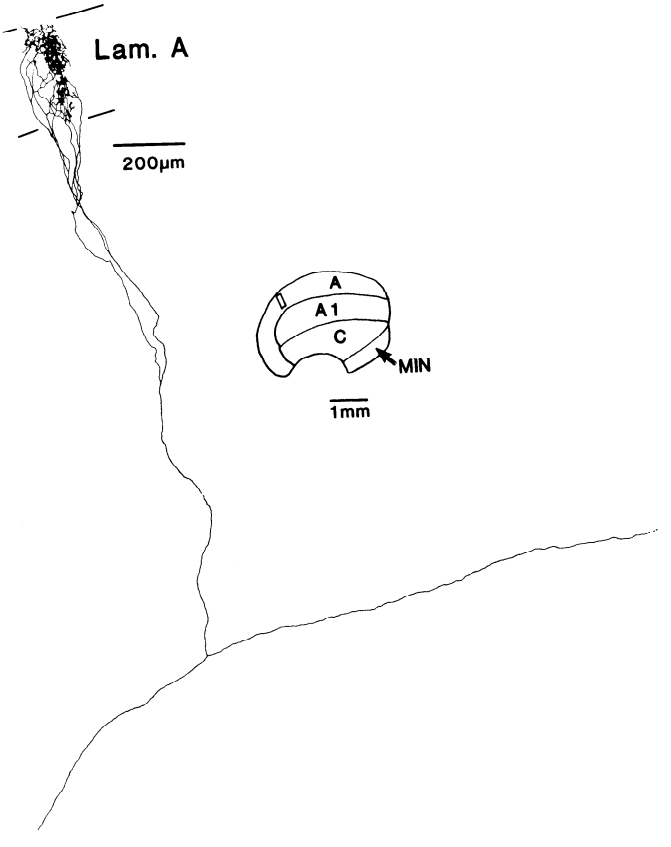


FIG. 5. Coronal view of reconstruction of X-axon from right retina innervating the left lateral geniculate nucleus; conventions as in Fig. 4. The dorsal branch terminates in lamina A, and the medial branch enters the brachium of the superior colliculus.

nucleus. These arbors are characterized by repeated axonal branching, and they contain numerous swellings that can be readily detected with the light microscope. These swellings, or terminal boutons, have been unambiguously identified with the electron microscope as the sites of retinogeniculate synapses (22, 47). The following paragraphs describe the general regions of termination of these boutons. The terminal arbors of these retinogeniculate axons are more completely described below under the section entitled *Qualitative observations of retinogeniculate axon arbors.*

X-AXONS. Of our total sample of 26 labeled X-axons, 19 derive from the contralateral retina and 7 from the ipsilateral retina. Each of these terminate most densely in lamina A or

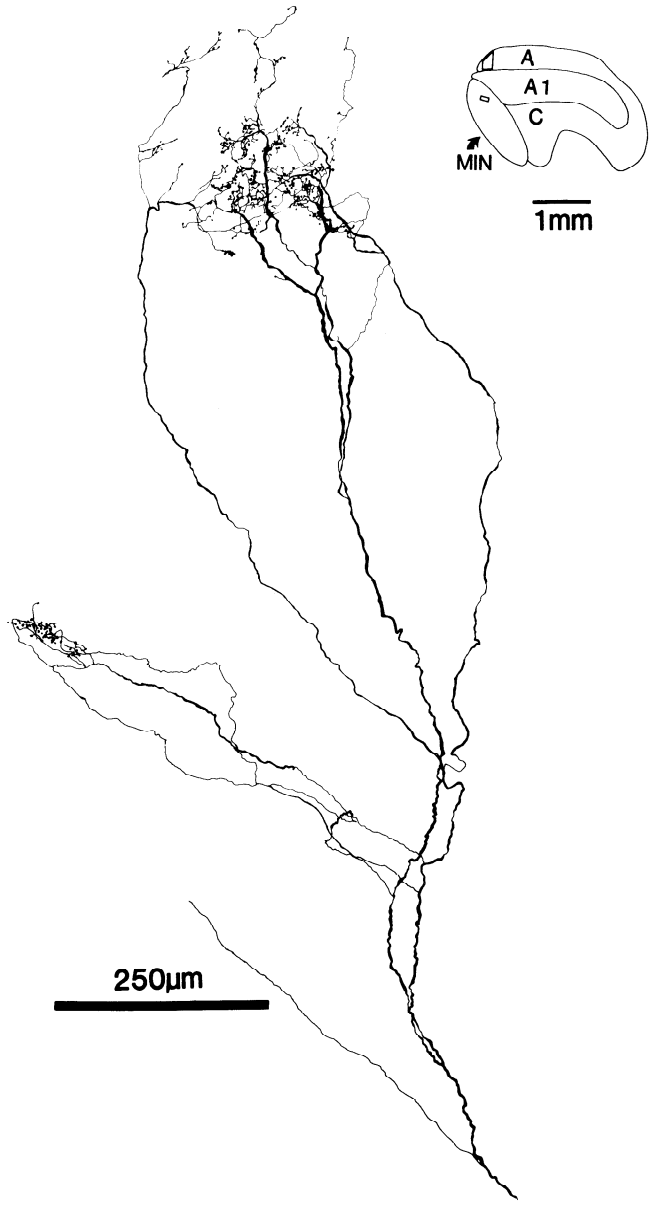


FIG. 6. Coronal view of reconstruction of X-axon from left retina innervating the right lateral geniculate nucleus; conventions as in Fig. 4. The major, dorsal branch innervates lamina A and the medial interlaminar nucleus, and the minor, ventral branch enters the brachium of the superior colliculus.

A1, and for most, this represents the only geniculate zone of termination. Two contralaterally projecting axons (i.e., originating in the contralateral retina) provide a small number of boutons to the dorsal portion of the C-laminae, a portion that is probably limited to lamina C. Every one of the seven ipsilaterally projecting X-axons (i.e., originating in the ipsilateral retina) terminates exclusively and densely in lamina A1. We traced 17 of the X-axons (13 contralaterally and 4 ipsilaterally projecting) well into the optic tract, where each of these axons branches. The conspicuously thicker branch progresses dorsally to innervate lamina A or A1, whereas the thinner branch heads medially and posteriorly (see Fig. 1). We followed 12 of these fine branches (11 contralaterally and one ipsilaterally projecting) through the optic tract beneath the medial interlaminar nucleus and into the brachium of the superior colliculus, but we could not trace any of these to a terminal zone beyond the thalamus. Five of these fine branches, all from the contralateral retina, issue another fine branch beneath the medial interlaminar nucleus that heads dorsally to innervate that nucleus with a few boutons. One X-axon terminates medially in lamina A, and, as the axon ascends through the lateral geniculate nucleus, it emits a medially directed branch that innervates the medial interlaminar nucleus with more boutons than any other X-axon in our sample (see also below). We detected no differences in physiological properties between the majority of X-axons that innervate only lamina A or A1 and the minority that also sparsely innervate other geniculate regions.

Y-AXONS. The parent branches of the Y-axons are conspicuously thicker than are those of the X-axons (see also below). As do the X-axons, each of the Y-axons densely innervates lamina A or A1. In addition, all but one of the 13 contralaterally projecting Y-axons innervates the C-laminae, in a zone probably limited to lamina C. None of our sample of ipsilaterally projecting Y-axons innervates the C-laminae, although Bowling and Michael (4) have reported that a small minority of such axons innervate lamina C1 as well as lamina A1. As is the case for X-axons, every Y-axon in our sample exhibits branching in the optic tract, with one branch directed dorsally toward the lateral geniculate nucleus and one directed medially and posteriorly toward the brachium of the superior colliculus (see Fig. 1). However,

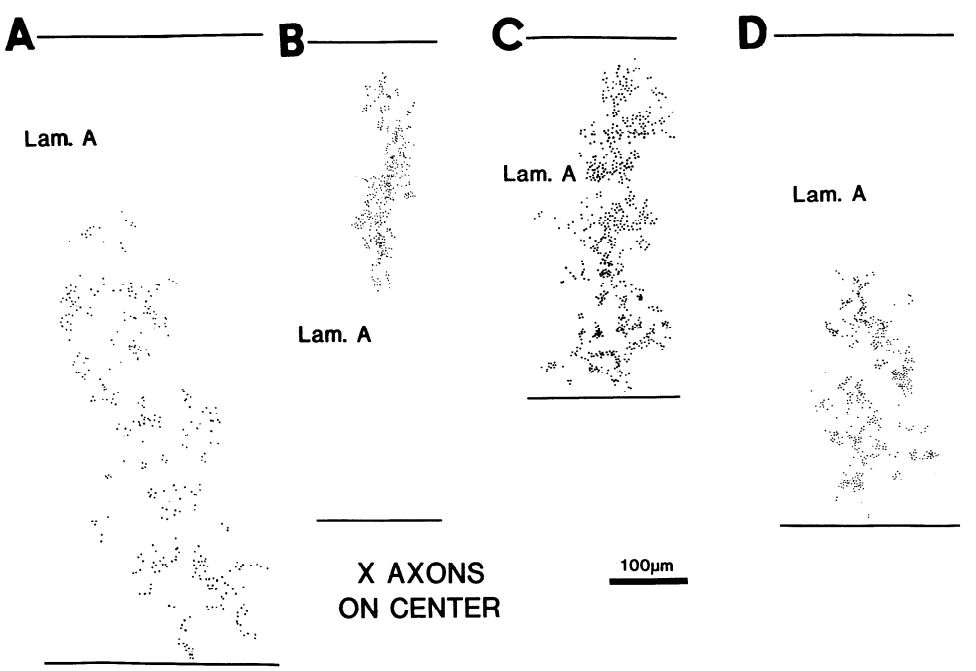


FIG. 7. Summary of terminal boutons in lamina A from 4 contralaterally projecting, on-center retinogeniculate X-axons. Each terminal bouton is represented by a *dot*. The *horizontal lines* mark the dorsal and ventral borders of lamina A.

unlike the X-axons, which project a branch toward lamina A or A1 that is considerably thicker than that directed medially toward the brachium, the Y-axons produces branches of roughly equal diameter. For the Y-axons, we did not trace any of these latter branches much beyond the lateral geniculate nucleus. Most of the Y-axons also branch more medially in the optic tract to innervate the medial interlaminar nucleus.

Because we found it difficult in sagittally sectioned material to reconstruct the terminal arbors of single Y-axons in the medial interlaminar nucleus and the A- and C-laminae, we limited our further analysis of the medial interlaminar nucleus terminations to 13 Y-axons reconstructed from coronally sectioned material. Of these, eight axons (4 contralaterally projecting and 4 ipsilaterally projecting) innervate the medial interlaminar nucleus. The terminal zones of Y-axons in the C-laminae and medial interlaminar nucleus are strikingly denser with many more boutons than seen for any X-axon (see below).

Qualitative observations of retinogeniculate axon arbors

The photomicrographs illustrated in Figs. 2 and 3 document many of the morphological features seen in the terminal arbors of retinogeniculate X- and Y-axons. As noted above, these arbors consist of dense preterminal axon

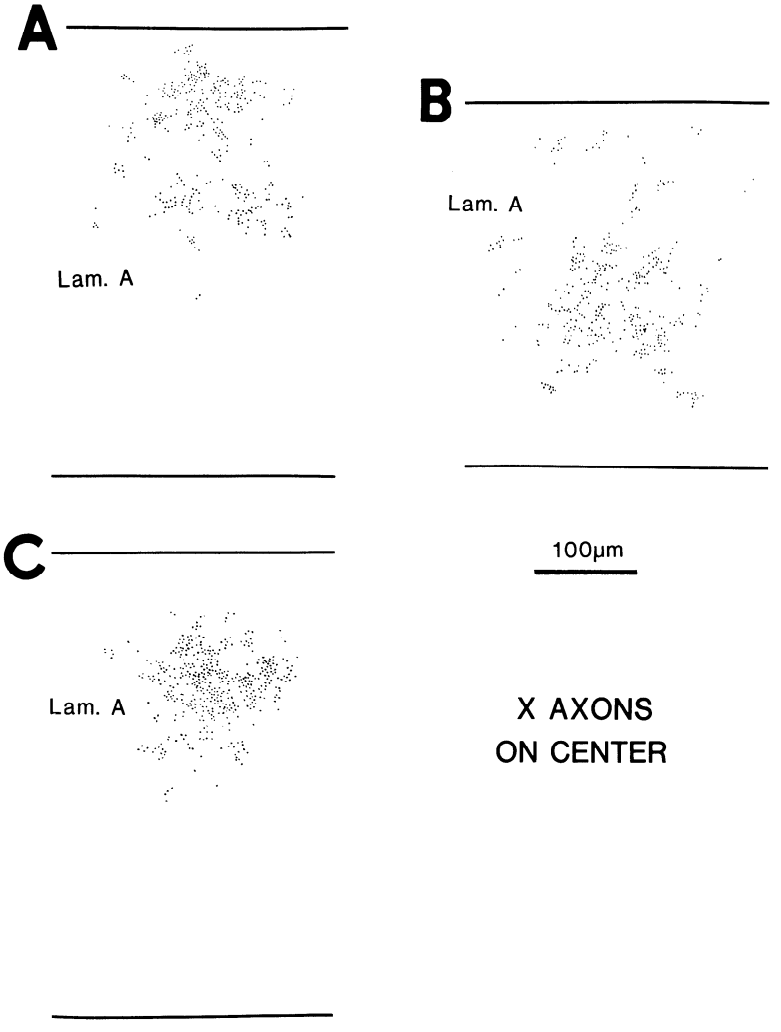


FIG. 8. Summary of terminal boutons in lamina A from 3 other contralaterally projecting, on-center retinogeniculate X-axons; conventions as in Fig. 7.

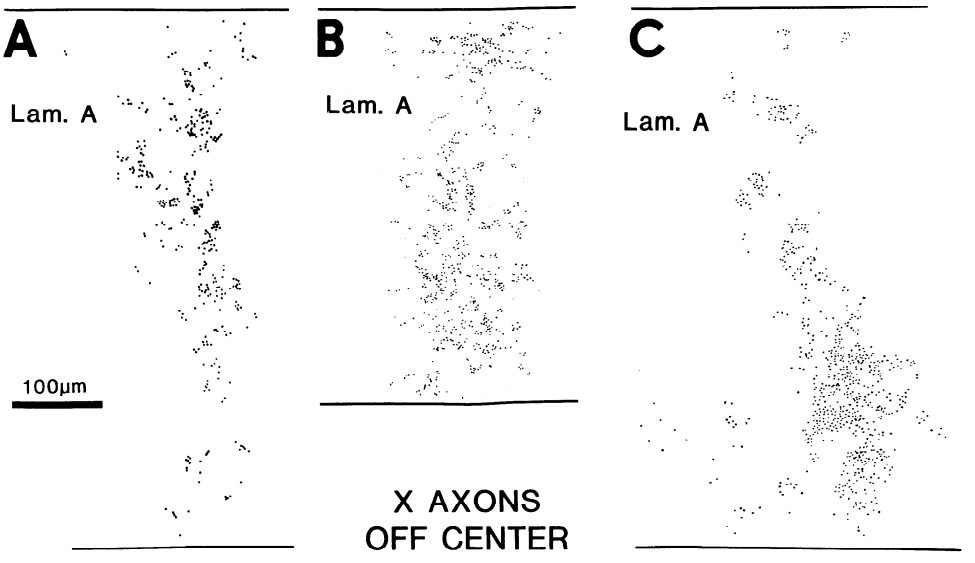


FIG. 9. Summary of terminal boutons in lamina A from 3 contralaterally projecting, off-center retinogeniculate X-axons; conventions as in Fig. 7.

branches and contain many terminal boutons. Some of the preterminal branches leading to boutons or bouton clusters are exceedingly fine (e.g., Fig. 3*C*). The terminal boutons of each axon are concentrated near a single retinotopic focus and are limited to laminae appropriate to the retina of the axon's origin (e.g., lamina A but not lamina A1 for axons from the contralateral retina, and the converse for axons from the ipsilateral retina). So striking is this laminar segregation that not a single bouton was found in a lamina inappropriate for the retina of origin.

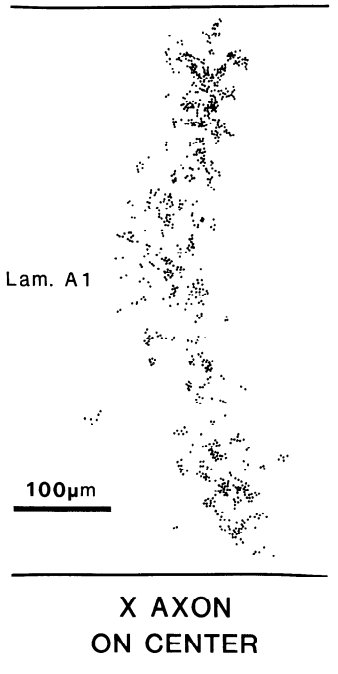


FIG. 10. Summary of terminal boutons in lamina A1 from an ipsilaterally projecting, on-center retinogeniculate X-axon; conventions as in Fig. 7.

FINE STRUCTURE OF TERMINAL ARBORS. As can be appreciated from the photomicrographs of Figs. 2 and 3, the terminal arbors of retinogeniculate X- and Y-axons can be distinguished from one another on the basis of the morphology of their terminal boutons and bouton clusters. For X-axons, the boutons tend to be relatively spherical in shape and tend to occur in clusters appended to the preterminal axon by a fine, short stalk. For Y-axons, the boutons are less regular in shape and size, and they tend to occur en passant along the axon branches, although many individual boutons are found at the end of fine stalks. The boutons for Y-axons are also more randomly dispersed within the terminal arbor than is the case for boutons of X-axons. When bouton clustering is seen for Y-axons, the boutons are invariably located en passant. Thus the relatively less frequent accumulations of boutons for Y-axons takes the appearance of a short string of pearls, whereas the more pronounced bouton clumping of X-axons looks like bunches of grapes.

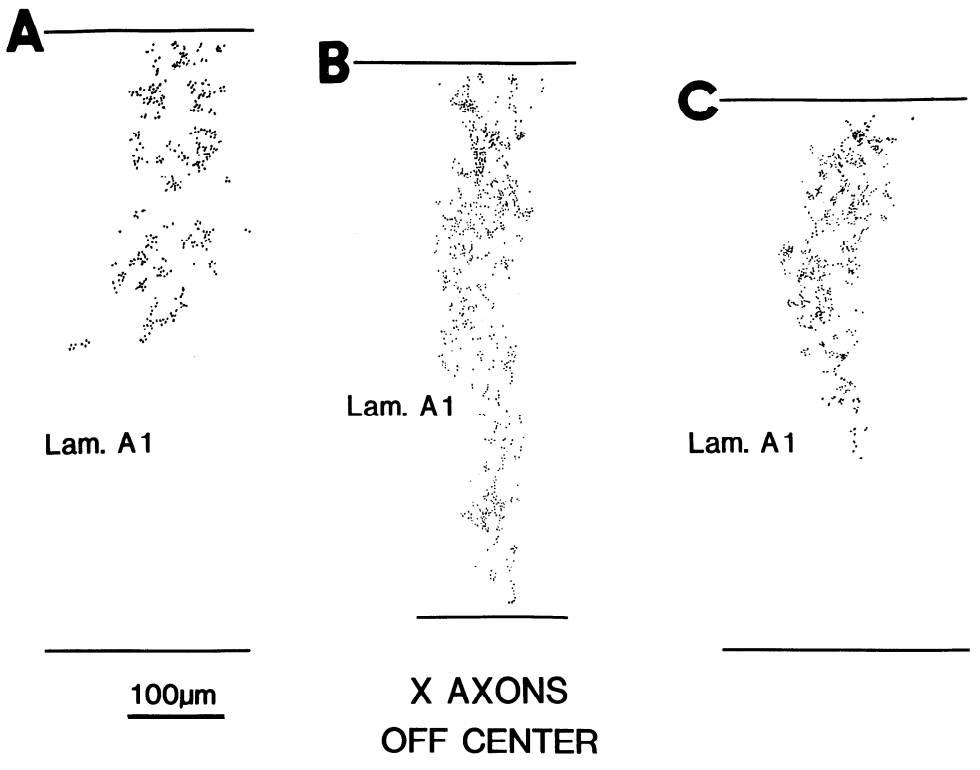


FIG. 11. Summary of terminal boutons in lamina A1 from 3 ipsilaterally projecting, off-center retinogeniculate X-axons; conventions as in Fig. 7.

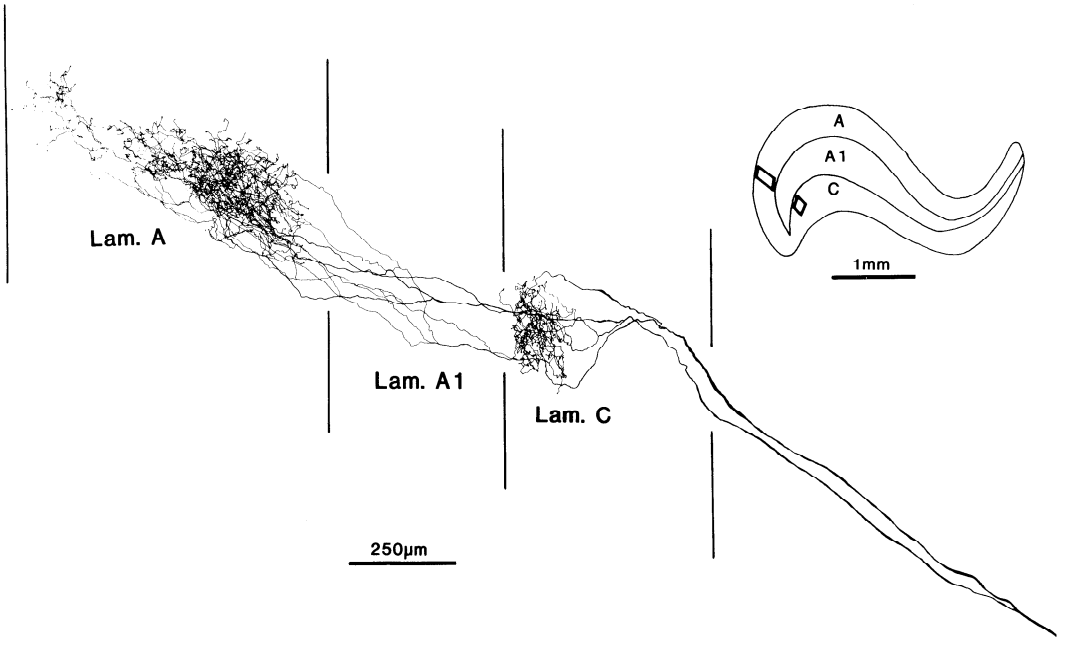


FIG. 12. Sagittal view of reconstruction of Y-axon from right retina innervating the left lateral geniculate nucleus; conventions as in Fig. 4. The axon terminates both in lamina A and in the C-laminae, with no boutons in lamina A1. A branch of the axon in the optic tract (not illustrated) courses medially and could not be followed; it may innervate the medial interlaminar nucleus and/or enter the brachium of the superior colliculus.

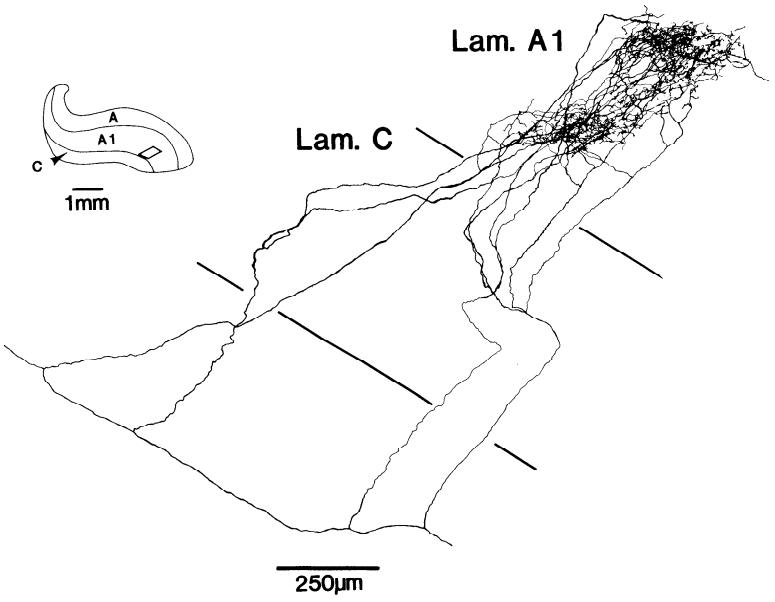


FIG. 13. Sagittal view of reconstruction of Y-axon from right retina innervating the right lateral geniculate nucleus; conventions as in Fig. 4. Note that several distant branch points of the parent axon in the optic tract give rise to branches that converge to the terminal arbor in lamina A1.

GROSS GEOMETRY OF TERMINAL ARBORS. *X-axons.* Figure 4 illustrates the complete reconstruction of the X-axon arbor from which the photomicrographs of Fig. 2 were derived. Figure 5 shows the reconstruction of another typical X-axon arbor. Both of these X-axons issue from the contralateral retina, and their terminal boutons are strictly limited to lamina A in relatively small zones. Figure 6 shows a reconstruction of another contralaterally projecting X-axon that provides a scant input to the medial interlaminar nucleus in addition to its major terminus in lamina A. Note also that Figs. 5 and 6, which represent coronal

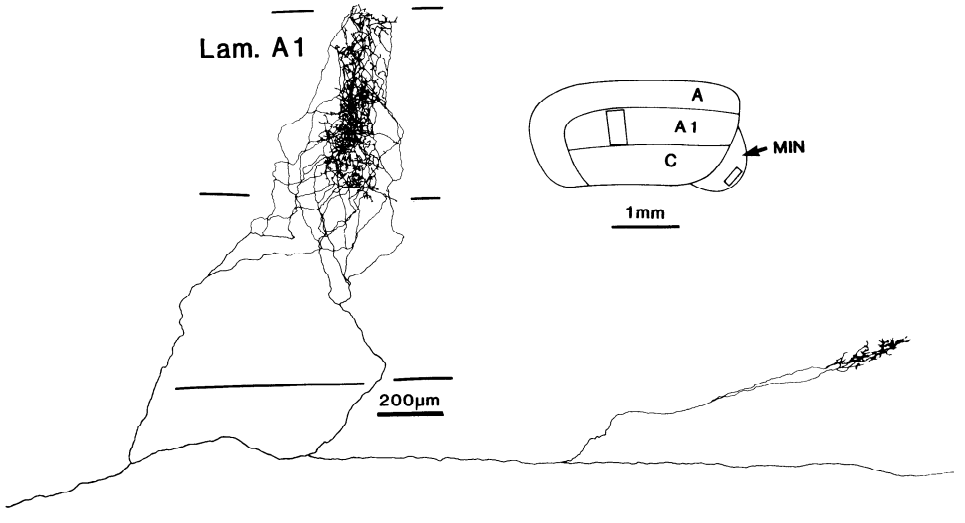


FIG. 14. Coronal view of reconstruction of Y-axon from left retina innervating the left lateral geniculate nucleus; conventions as in Fig. 4. The axon innervates both lamina A1 and the medial interlaminar nucleus, and a branch continues medially to enter the brachium of the superior colliculus.

views, show the abovementioned branching of the axon in the optic tract.

Each of the axons illustrated in Figs. 4–6 had an on-center receptive field. Figures 7–9 represent a larger sample of contralaterally projecting X-axons with on-center (Figs. 7 and 8) or off-center (Fig. 9) receptive fields. For simplicity, instead of complete reconstructions of the axonal arbors, Figs. 7–9 represent only the locations of terminal boutons, with each bouton represented by a small dot. We see no obvious morphological differences between these on- and off-center axons, including no evidence of a sublaminar organization of their inputs. Too few ipsilaterally projecting X-axons were analyzed in detail, to be as confident that no such differences exist for lamina A1, but the terminal arbors of these axons are not noticeably different in morphology from those of contralaterally projecting X-axons, except, of course, for the different laminar terminus. Figures 10 and 11 show examples of ipsilaterally projecting X-axons, including one with an on-center receptive field (Fig. 10) and three with off-center fields (Fig. 11). In general, then, the X-axons tend to innervate lamina A or A1 in relatively small zones with no hint of a sublaminar organization of boutons within these laminae.

Y-axons. Figure 12 shows the reconstruction of the contralaterally projecting retinogeniculate Y-axon that was previously illustrated with photomicrographs in Fig. 3. Note the dense terminal arbor in both lamina A and the C-laminae and the complete absence of boutons in lamina A1. Figure 13 illustrates a

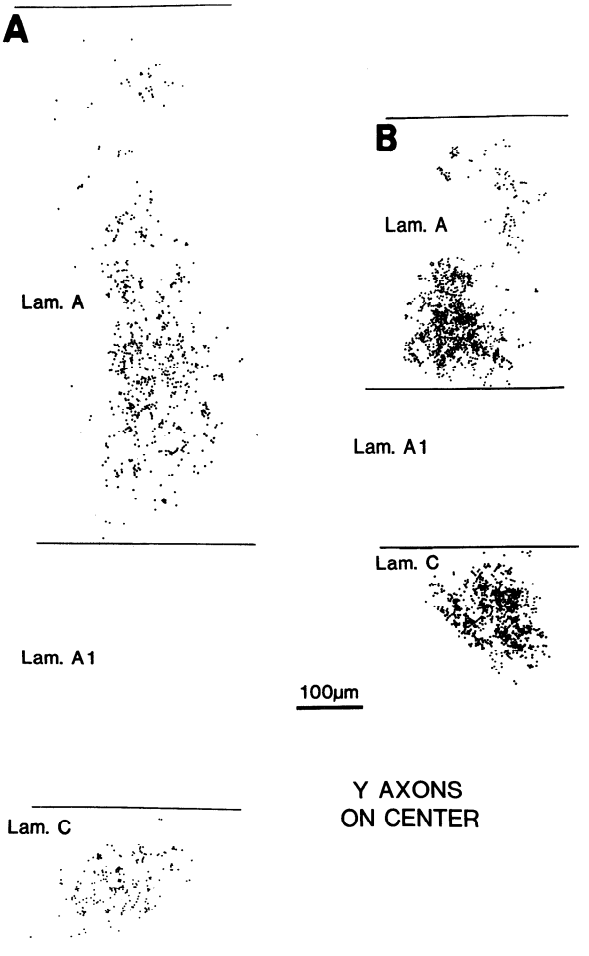


FIG. 15. Summary of terminal boutons in lamina A and the C-laminae from 2 contralaterally projecting, on-center retinogeniculate Y-axons; conventions as in Fig. 7. Note complete absence of boutons in lamina A1.

reconstruction of an ipsilaterally projecting Y-axon that densely innervates lamina A1 but provides no boutons for lamina A or the C-laminae. Because the axons shown in Figs. 12 and 13 were reconstructed from sagittal sections, branches from them that probably innervate the medial interlaminar nucleus could not be traced with confidence, and thus no terminal arbors are shown for that geniculate division. Figure 14 represents the reconstruction from coronal sections of an ipsilaterally projecting Y-axon that densely innervates both lamina A1 and the medial interlaminar nucleus. For each of the axons illustrated in Figs. 13 and 14, the terminal arbor in lamina A1 derives from several branches of the parent axon in the optic tract; these branches are often quite distant from each other and they markedly converge toward the focused zone of termination. Such a pattern was quite common for our sample of Y-axons.

As noted above for the X-axons, we detected no morphological differences for the Y-axon arbors that could be correlated with their on- or off-center receptive fields. Figures 12 and 14 represent Y-axons with on-center fields, whereas Fig. 13 represents a Y-axon with an off-center field. Further examples of terminal arbors of on and off are illustrated for the A- and C-laminae in Figs. 15–18.

Quantitative analysis of retinogeniculate axons

AXON DIAMETER. To verify the abovementioned difference in thickness between X- and Y-axons, we measured the diameters of 17 X-

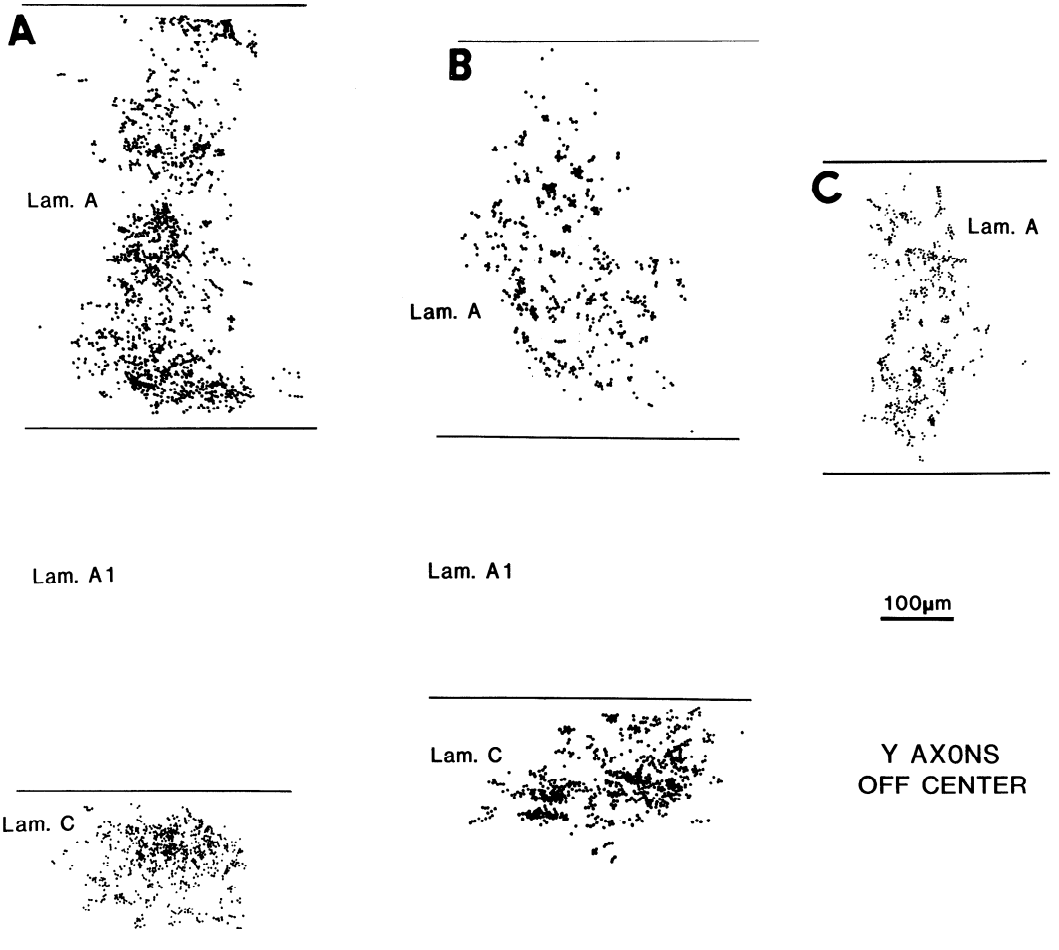


FIG. 16. Summary of terminal boutons in lamina A and the C-laminae from 3 contralaterally projecting, off-center retinogeniculate Y-axons; conventions as in Fig. 7. Note complete absence of boutons in lamina A1.

and 17 Y-axons in the optic tract proximal to any branching (see METHODS). Figure 19 depicts the distribution of axon diameters. The X-axons are 1.0–2.5 μm in diameter with a mean diameter of 2.0 μm, and the Y-axons are 2.0–4.5 μm in diameter with a mean diameter of 3.0 μm. The difference in diameter between X- and Y-axons is statistically significant ($P < 0.001$).

AXON LOCATION. We used the following protocol to estimate the relative position of each labeled axon within the optic tract. We first located a segment of the axon just prior to its initial branching. We then measured the overall thickness of the optic tract at that point by determining the distance between the pial surface and the border between the optic tract and ventral laminae of the lateral geniculate nucleus along a line running roughly parallel to those laminae. We arbitrarily denoted the lateral geniculate nucleus and the pial surface as the optic tract's dorsal and ventral borders, respectively. Finally, we determined the distance from the dorsal border of the optic tract at which the labeled axon was located and divided this distance by the overall thickness of the optic tract. This provides a normalized value of relative dorsoventral position of each optic tract axon. Figure 20 shows that, with this measure, every X-axon lies dorsal to every Y-axon. The X-axons generally occupy the dorsal quarter of the optic tract, and most Y-axons are found in the ventral two-thirds. We found no major shift in these locations for axons located subjacent to the lateral geniculate nucleus. Six examples of labeled retinogeniculate axons were traced for roughly 2 mm

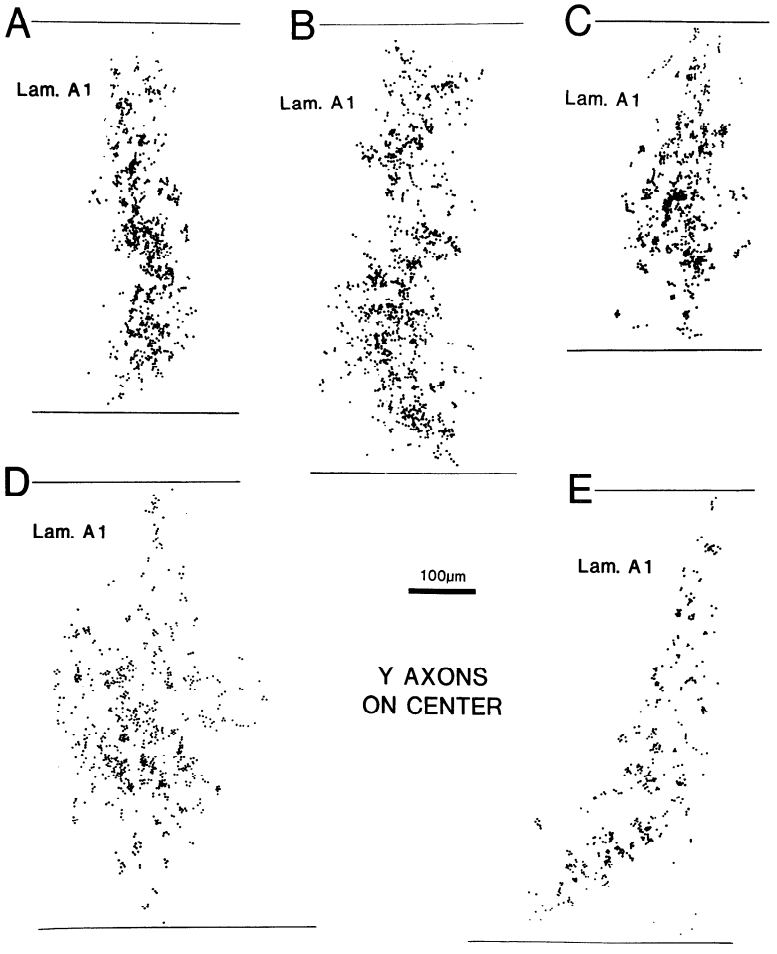


FIG. 17. Summary of terminal boutons in lamina A1 from 5 ipsilaterally projecting, on-center retinogeniculate Y-axons; conventions as in Fig. 7.

proximal to their first branch point. In each of these, there was essentially no change in the relative dorsoventral location of the parent axon within the optic tract.

TERMINAL ARBORS IN LAMINA A OR A1. Most of our detailed analysis of the labeled terminal arbors was limited to lamina A or A1, because every X- and Y-axon of our sample innervated one of these laminae.

Size of individual boutons. We measured a bouton's diameter with an oil-immersion objective (NA 1.3) on a light microscope. Figure 21*A* shows our analysis for every bouton found in lamina A or A1 in a single section each for one X- and one Y-axon. The sections were through the middle of the terminal arbor in these laminae. Although each axon has a wide range of bouton diameters (from 1 to >4 μm), only the Y-axon has boutons larger than 5 μm, and the X-axon tends to have many more smaller boutons than does the Y-axon. The population of boutons is significantly larger for the Y-axon ($P < 0.001$), and the Y-axon displays a greater size range of boutons ($P < 0.001$ on a Moses test for dispersion).

Although it is clear from Fig. 21*A* that individual axons can differ with regard to the

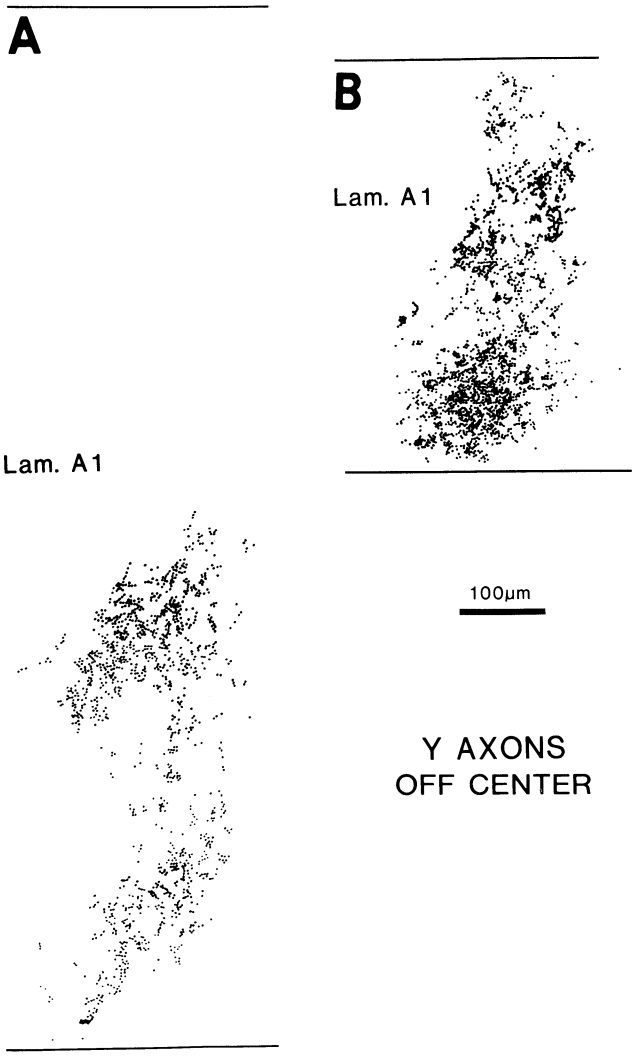


FIG. 18. Summary of terminal boutons in lamina A1 from 2 ipsilaterally projecting, off-center retinogeniculate Y-axons; conventions as in Fig. 7.

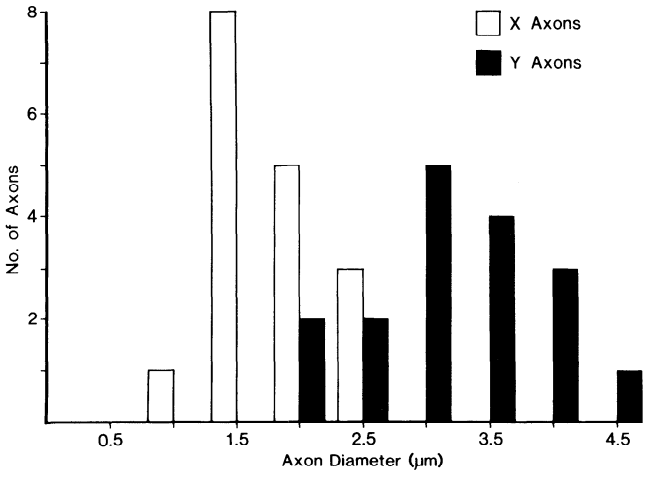


FIG. 19. Frequency histogram of diameter of retinogeniculate X- and Y-axons in the optic tract subjacent to the lateral geniculate nucleus. The measurements were made from the parent trunks before branching occurred.

size distribution of their boutons, a larger sample is needed to determine the extent to which such differences are reliably found between X- and Y-axons. We thus chose 13 X- and 12 Y-axon arbors for further analysis. For each of these, we measured the diameter of 50 boutons randomly selected near the center of the terminal arbor in lamina A or A1. For each axon, Fig. 21*B* plots both the bouton diameter (mean ± SE from the 50 measurements) on the ordinate as well as the total number of boutons in lamina A or A1 on the abscissa. Our analysis indicates that the mean bouton diameter for the Y-axons is larger than that for the X-axons (2.6 μm vs. 2.0 μm; $P < 0.001$) and that the range of bouton sizes as derived from the standard error bars is greater for Y- than for X-axons ($P < 0.001$). Thus the observation seen in a fairly complete analysis of one X- and one Y-axon (Fig. 21*A*) is confirmed by a less complete analysis of a larger sample of axons (Fig. 21*B*). Finally, we found no correlation between mean bouton size and the total number of boutons for either X-axons ($r = +0.08$; $P > 0.1$) or Y-axons ($r = -0.29$; $P > 0.1$). There is thus no tendency for larger boutons to be found in arbors with fewer boutons.

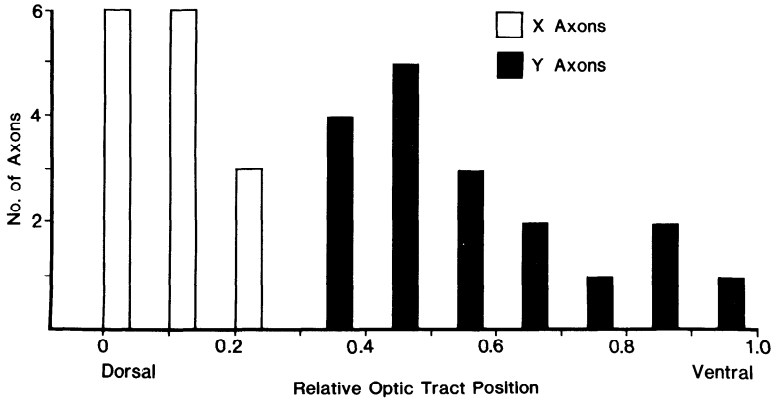
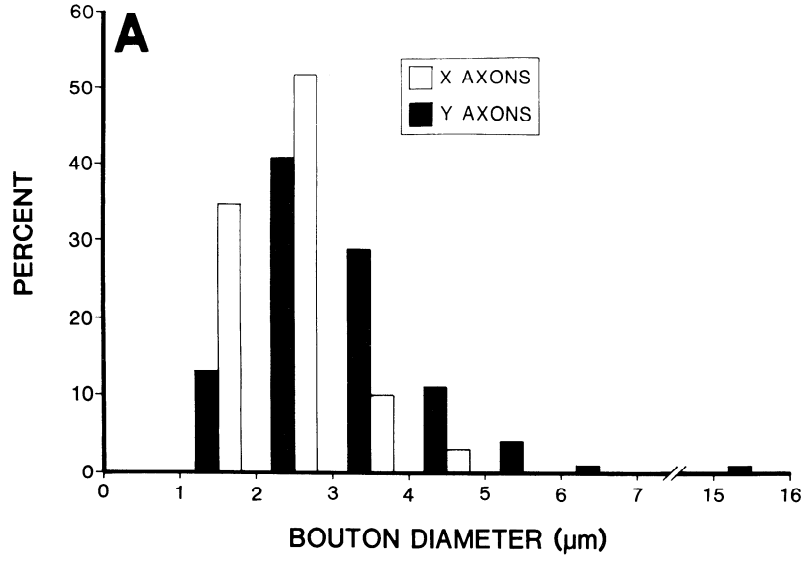


FIG. 20. Frequency histogram of relative position subjacent to the lateral geniculate nucleus and within the optic tract of retinogeniculate X- and Y-axons. The positions are plotted for parent trunks before branching. The optic tract was divided into 10 sectors from dorsal (sector 0 at the border with the C-laminae) to ventral (sector 10 at the border with the pia).



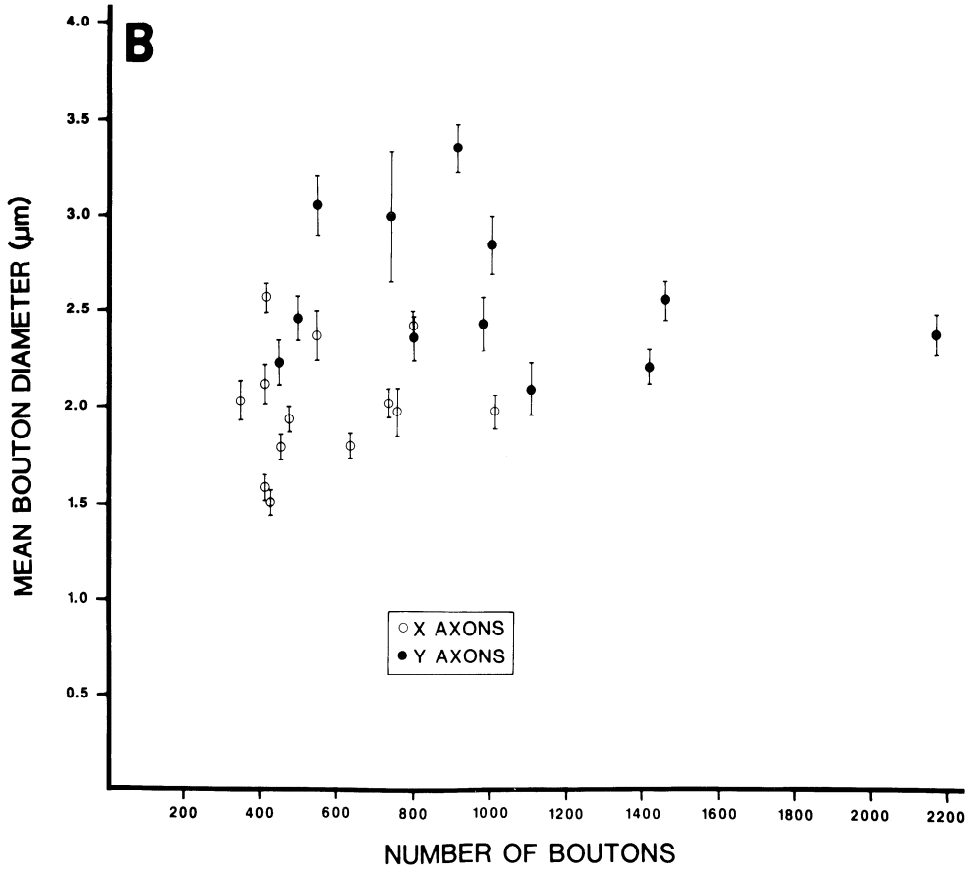


FIG. 21. Distribution of bouton diameters within laminae A and A1 for retinogeniculate X- and Y-axons. *A*: frequency histogram of bouton diameters for every bouton found in one X- and one Y-axon arbor. The X-arbor, located in lamina A, has 115 boutons, and the portion of the Y-arbor, also located in lamina A, has 157 boutons. *B*: plot of bouton diameter (mean ± SE) vs. number of boutons in the terminal arbor within lamina A or A1 for individual retinogeniculate X- and Y-axons. The diameter measurements were made from 50 randomly selected boutons for each axon.

Extent of arbors. As can be seen in Figs. 4–18, the terminal arbors of retinogeniculate Y-axons, when compared with those of X-axons, are larger and contain many more boutons. This is evident even if the analysis is limited to lamina A or A1, which represents practically all of the terminal arbor for X-axons but only part of that for Y-axons. Within these laminae, X-axon arbors are considerably narrower in mediolateral extent than are Y-arbors. The X-arbors measure 90–175 μm across, whereas the Y-arbors are all larger, with diameters of 190–410 μm. This difference is statistically significant ($P < 0.001$).

Figure 22 summarizes additional details for terminal arbors located in lamina A or A1, showing for each axon the number of boutons and the volume estimated for the terminal arbor (see METHODS). The X-arbors contain 359–1,017 boutons within volumes of 1.1–3.9 $\times$ 10^{-3} mm^3; the mean values are 584 boutons in an arbor volume of 2.4 $\times$ 10^{-3} mm^3, yielding an average bouton density of 2.4 $\times$ 10^5 boutons/mm^3. The Y-arbors contain 434–2,175 boutons and occupy volumes of 3.8–12.7 $\times$ 10^{-3} mm^3; the mean values are 1,011 boutons in an arbor volume of 8.7 $\times$ 10^{-3} mm^3, yielding an average bouton density of 1.1 $\times$ 10^5 boutons/mm^3. The mean volume of Y-axon arbors is larger than that of X-arbors ($P < 0.001$), and the Y-arbors contain more boutons ($P < 0.01$). However, the bouton density is greater within the X-arbors than within the Y-arbors ($P < 0.001$), so that the differences between X- and Y-arbors is more dramatic for their volume than for the number of boutons they contain. Finally, for both axonal classes, bouton number increases with terminal arbor volume (for X-axons: $r = +0.57$, $P < 0.05$; for Y-axons: $r = +0.67$, $P < 0.01$), with the result that bouton density remains fairly constant for each axon class.

We noticed a difference between X- and Y-axons with regard to the location of boutons within laminae A and A1. The boutons of X-axons tend to be evenly distributed throughout these laminae, whereas Y-axons tend to produce more boutons in the ventral half of each

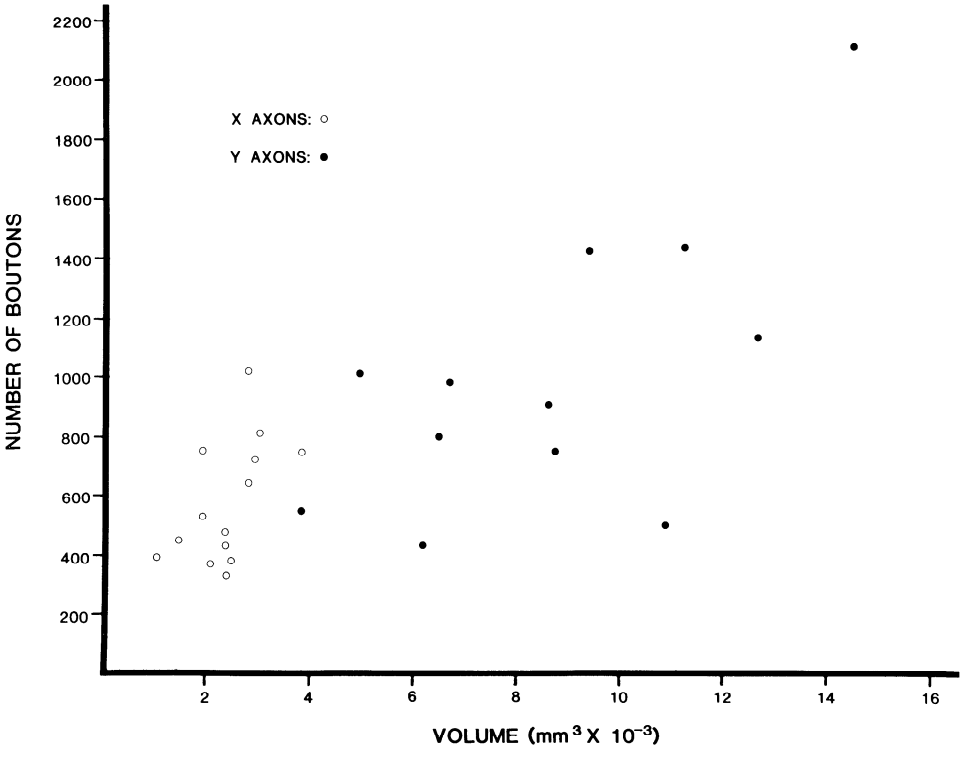
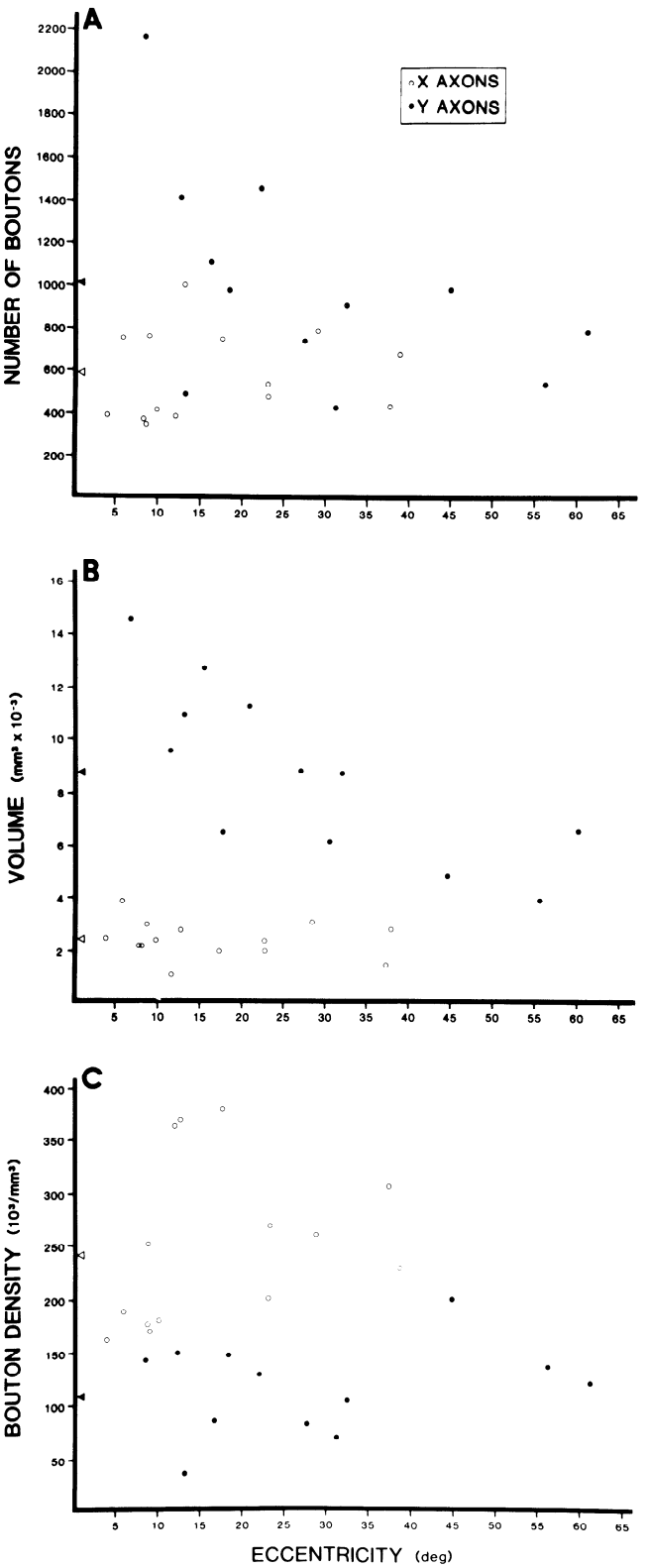


FIG. 22. Plot of number of boutons vs. volume of the terminal arbors within lamina A or A1 for retinogeniculate X- and Y-axons. Each point represents data from a single axon.


A
X AXONS
Y AXONS
NUMBER OF BOUTONS
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
5 10 15 20 25 30 35 40 45 50 55 60 65
B
VOLUME (mm³ x 10⁻³)
16
14
12
10
8
6
4
2
5 10 15 20 25 30 35 40 45 50 55 60 65
C
BOUTON DENSITY (10³/mm³)
400
350
300
250
200
150
100
50
5 10 15 20 25 30 35 40 45 50 55 60 65
ECCENTRICITY (deg)

lamina than in the dorsal half. To verify this difference, we divided each lamina A or A1 into ventral and dorsal halves and simply noted the number of boutons formed by each axon in each half. In this analysis, we saw no difference in the location of boutons between lamina A and lamina A1. One of the 14 X-axons was located too far anteriorly to be certain of the dorsal and ventral halves of its termination in lamina A given the coronal plane of section used, so our analysis here was based on 13 X-axons. For these, 56% of the boutons are in the dorsal halves of the laminae; eight of the axons have more boutons dorsally and five do so ventrally. Neither of these differences between dorsal and ventral halves is statistically significant ($P > 0.1$ on both a Mann-Whitney U test and on a sign test). For the 12 Y-axons, only 28% of the boutons are formed in the upper halves of the laminae; 11 of the axons have more boutons ventrally, and only 1 has more dorsally. This tendency of boutons from Y-axons to concentrate ventrally in laminae A and A1 is statistically significant ($P < 0.001$ on a Mann-Whitney U test and $P < 0.006$ on a sign test). Furthermore, the percentage of boutons found in the ventral half of laminae A and A1 is significantly greater for Y- than for X-axon arbors ($P < 0.02$).

Finally, we used an analysis similar to that described in the above paragraph to search both for intralaminar differences between axons with on-center receptive fields versus those with off-center fields as well as for interlaminar differences between terminal arbors in lamina A versus those in lamina A1. Our analysis provided no evidence that, for either X- or Y-axons, those with on-center fields differ in any noticeable morphological manner from those with off-center fields ($P > 0.1$ on all comparisons). In particular, we saw no tendency for axons with on-center fields to produce terminal arbors located more dorsally than those with off-center fields (cf. Ref. 4). There was, however, a tendency for terminal arbors in lamina A1 to contain slightly more boutons than those in lamina A. This difference only approaches statistical significance for X-axons ($P < 0.05$) and is not significantly different for Y-axons ($P > 0.1$). However, because contralaterally projecting Y-axons also provide input to the C-laminae, the average combined number of boutons in lamina A and the C-laminae for these axons slightly exceeds the average number of boutons found in lamina A1 for the ipsilaterally projecting Y-axons, but this difference is not significant ($P > 0.1$).

Changes with eccentricity. Figure 23 illustrates the changes in the terminal arbors with the eccentricity of the axons' receptive-field locations within the visual field. The terminal arbors of X-axons exhibit a remarkable degree of consistency in number of boutons, volume, and density of boutons over a wide range of eccentricities, which in our sample covers 4–38°. We found no evidence of a trend for any of the three measures (for number of boutons: $r = +0.12$, $P > 0.1$; for volume: $r = -0.18$, $P > 0.1$; for bouton density: $r = +0.3$, $P > 0.1$). In contrast, the Y-axon arbors within lamina A or A1 show decreases with eccentricity for both bouton numbers ($r = -0.52$, $P < 0.05$) and terminal arbor volume ($r = -0.79$, $P < 0.01$). Because these decreases are fairly well matched, these axons exhibit no change in bouton density with eccentricity ($r = +0.24$, $P > 0.1$). Figure 23 implies that the relative differences between X- and Y-axon arbors in terms of their volumes and bouton numbers are more pronounced for central vision than for peripheral vision. Also, because the Y-axons in our sample are, on average, more eccentric in receptive-field location than are the X-axons (a mean eccentricity of 31° for the Y-axons vs. 15° for the X-axons), we may have slightly underestimated the relatively larger volumes and bouton numbers of the Y-axon arbors.

Correlations among conduction velocity, axon diameter, and bouton number. Figures 24 and 25 represent the relationships among conduction velocity, axon diameter, and bou-

FIG. 23. Plots of various parameters of terminal arbors in lamina A or A1 vs. receptive-field eccentricity for retinogeniculate X- and Y-axons. Each point represents data from a single axon. *A*: plot of number of boutons vs. receptive-field eccentricity. The *triangles* on the *ordinate* represent the mean number of boutons for X-axons (*open triangle*) and Y-axons (*closed triangle*). *B*: plot of volume of the terminal arbor vs. eccentricity; conventions for *triangles* on *ordinate* as in *A*. *C*: plot of bouton density vs. eccentricity; conventions for *triangles* on *ordinate* as in *A*.

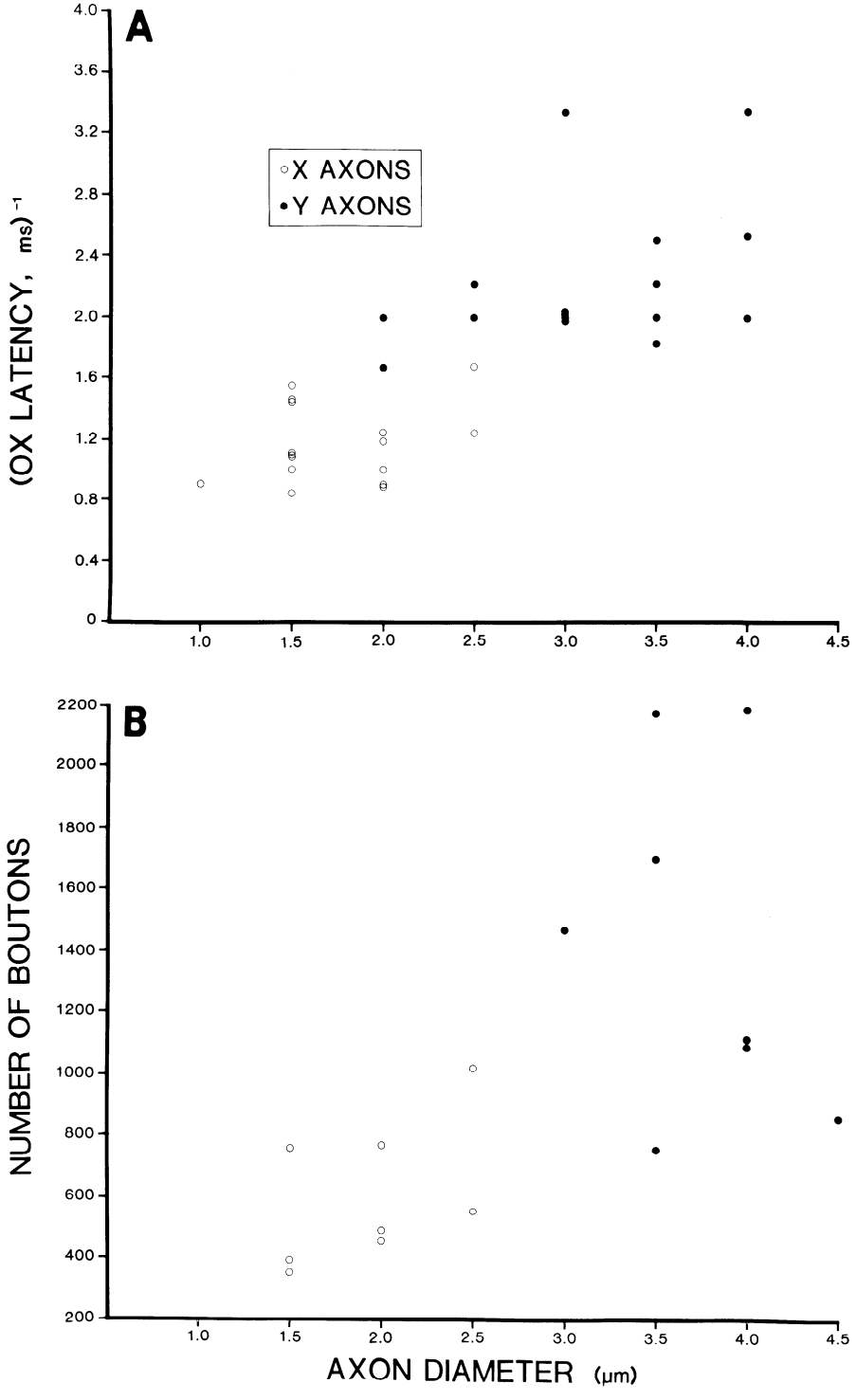


FIG. 24. Relationship between axon diameter and other parameters for retinogeniculate X- and Y-axons. Each point represents data from a single axon. *A*: plot of relative conduction velocity (taken as the inverse of the response latency to electrical activation of the optic chiasm) vs. axon diameter. *B*: plot of axon diameter vs. number of boutons either in laminae A and C or in lamina A1. The different sample size for *A* and *B* reflects the fact that for some axons we derived good measures of diameter and optic chiasm latency, and for others we could measure diameter and bouton numbers; these two populations are not identical.

ton number. For these relationships, conduction velocity is taken to be proportional to the inverse of the response latency to optic chiasm stimulation; bouton numbers here include any that occur in the C-laminae as well as those in lamina A or A1. For neither axon class do any pair of these variables display a significant correlation. This is illustrated by Fig. 24*A* for conduction velocity versus axon diameter (for X-axons: $r = +0.28$, $P > 0.1$; for Y-axons: $r = +0.25$, $P > 0.1$), by Fig. 24*B* for the number of boutons versus axon diameter (for X-axons: $r = +0.49$, $P > 0.1$; for Y-axons: $r = -0.30$, $P > 0.1$), and by Fig. 25 for the number of boutons versus conduction velocity (for X-axons: $r = +0.41$, $P > 0.1$; for Y-axons: $r = +0.32$, $P > 0.1$). However, when the data from X- and Y-axons are pooled, all three relationships are significantly correlated (for Fig. 24*A*: $r = +0.73$, $P < 0.001$; for Fig. 24*B*: $r = +0.62$, $P < 0.01$; and for Fig. 25: $r = +0.63$, $P < 0.001$). These correlations probably result only because the values for Y-axons are larger than are those for X-axons for each of these relationships; the correlations are thus not very meaningful.

ANALYSIS OF PORTIONS OF TERMINAL ARBORS OUTSIDE OF LAMINAE A AND A1. *Terminations in the medial interlaminar nucleus.* As noted above, 5 of 12 retinogeniculate X-axons that could be traced into the brachium of the superior colliculus also provide sparse input to the medial interlaminar nucleus. The number of terminal boutons formed in these zones ranges from 7 to 71, with a mean of 26. Of the 13 Y-axons traced into the brachium of the superior colliculus, 8 provide 90–156 boutons, with a mean of 118, to the medial interlaminar nucleus. The greater bouton numbers for Y-axons innervating the medial interlaminar nucleus is statistically significant ($P < 0.01$).

We could find no physiological or other morphological differences between those X- and Y-axons innervating the medial interlam-

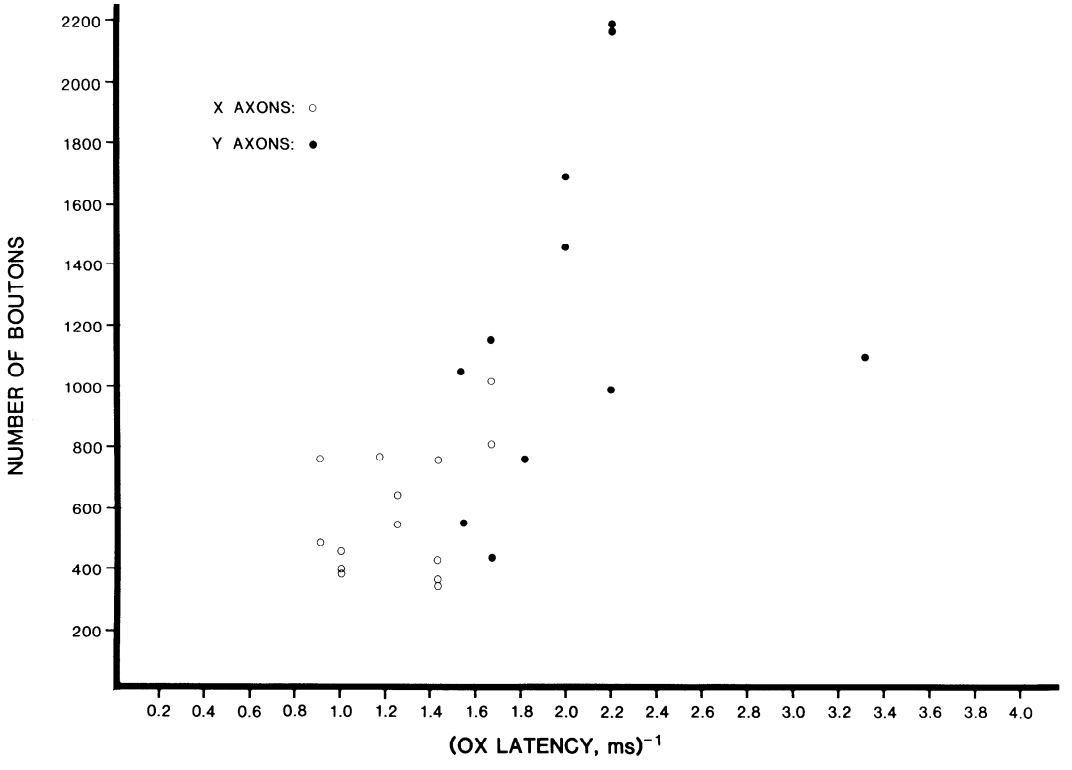


FIG. 25. Plot of relative conduction velocity vs. number of boutons either in laminae A and C or in lamina A1 (see legend for Fig. 24*A*) for retinogeniculate X- and Y-axons. Each point represents data from a single axon. Only 11 Y-axons are shown, because we were unable to activate one Y-axon from optic chiasm stimulation (see Table 1).

inar nucleus and those that do not. This applies to optic chiasm latency, diameter of the parent axon in the optic tract, and receptive-field center size. Furthermore, the X-axons included three with on-center receptive fields and two with off-center fields, and the respective numbers for the Y-axons are six and two. It has recently been suggested that only retinal ganglion cells with receptive fields corresponding to the tapetal region of the cat's retina actually innervate the medial interlaminar nucleus (34). By plotting retinal landmarks on the same tangent screen used for plotting receptive fields, a procedure we followed in every experiment, we readily determined which axons had receptive fields in the tapetal region. Only one Y-axon from our sample of the X- and Y-axons that could be traced past the medial interlaminar nucleus into the brachium of the superior colliculus did not have a receptive field in the tapetal region, and that Y-axon does not innervate the medial interlaminar nucleus. The remaining X- and Y-axons had receptive fields within the tapetum, and some of these innervate the medial interlaminar nucleus while others do not.

Relationship among different retinogeniculate terminal zones. It is of interest to consider the extent to which the number of boutons formed in lamina A or A1 of one of these axons tends to correlate with the number in the C-laminae or the medial interlaminar nucleus. Only a subset of our sample (6 X-axons and 9 Y-axons) was analyzed in lamina A or A1 plus the C-laminae and the medial interlaminar nucleus. For these, we found no evidence of correlations in numbers of boutons among the different terminal zones ($P > 0.1$ for all pairwise correlations).

Total extent of retinogeniculate arbors. We have made the point earlier that, within lamina A or A1, the Y-axon arbors are considerably larger and contain more boutons than is the case for X-axon arbors. We emphasize that this underestimates these differences between axon classes, because X-axons project fewer than 5% of their boutons to geniculate regions outside of lamina A or A1, whereas Y-axons commonly innervate the C-laminae and/or the medial interlaminar nucleus as well. We did not systematically and quantitatively analyze these other zones of termination for every Y-axon, largely because the frequent sagittal plane of section precluded reconstruction of most zones in the medial interlaminar nucleus. However, we did analyze for nine Y-axons the terminal arbors in the C-laminae and/or the medial interlaminar nucleus, and we conclude for these that up to one-third of their terminal boutons lie outside of lamina A or A1. This is, however, only a rough and tentative estimate, and a more systematic analysis of the complete terminal arbors of these axons is needed for a more confident estimate of their total extent within the lateral geniculate nucleus.

DISCUSSION

We used the technique of intracellular injection of HRP into single, physiologically characterized, retinogeniculate X- and Y-axons to define their morphological features, many of which are schematically summarized by Fig. 26. We found that each of these axons densely innervates geniculate lamina A or A1; each also projects a branch beyond the lateral geniculate nucleus toward the midbrain, although this branch is especially thin for the X-axons (see also below). Not a single bouton from any retinogeniculate axon was found in a lamina innapropriate for the retina of origin. This contrasts sharply both to the situation in embryonic development, during which time the immature axons produce numerous synaptic contacts in inappropriate laminae (reviewed in Ref. 53) and also to the situation in cats reared with monocular enucleation, in which retinogeniculate Y-axons innervate the inappropriate, previously denervated geniculate laminae (18–20). We also cataloged a variety of clear differences between the X- and Y-axons. Y-axons are thicker and they form larger arbors with more boutons. Y-axons extensively innervate geniculate regions outside laminae A and A1, whereas X-axons do not. Finally, the boutons of X-axons tend to occur in prominent clusters appended to short stalks with gaps between clusters; Y-boutons occur en passant along the preterminal axon branches, and they tend to be more evenly distributed within the arbor. Many of these morphological features were noted previously by us (61) and by Bowling and Michael (3, 4) for retinogeniculate X- and Y-axons. Some of these features as well as detailed comparisons between the present study and that of Bowling

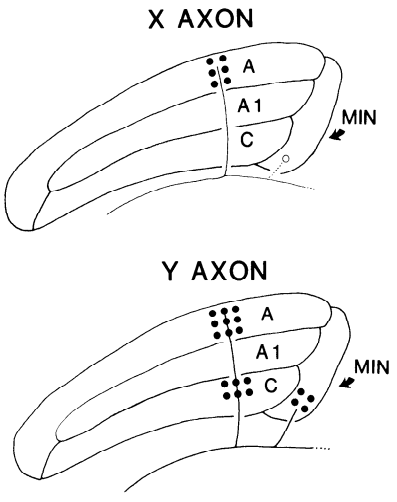


FIG. 26. Schematic illustration of some major differences between retinogeniculate X- and Y-axons and their terminal arbors. *Upper*: X-axons have relatively thin parent trunks that branch in the optic tract. A thicker branch innervates lamina A (shown) or A1 (not shown) in a relatively small terminal arbor. A thinner branch enters the brachium of the superior colliculus, and occasionally a fine branch innervates the medial interlaminar nucleus with a few boutons. *Lower*: Y-axons have relatively thick parent trunks that also branch in the optic tract, but all branches are of comparable diameter. Typically, if from the contralateral retina (shown), the axon innervates lamina A, the C-laminae, and the medial interlaminar nucleus; if from the ipsilateral retina (not shown), the axon innervates lamina A1 and the medial interlaminar nucleus. Y-axon arbors in these geniculate regions are relatively large. Finally, one branch enters the brachium of the superior colliculus. See text for details.

and Michael (3, 4) are discussed more fully in the sections below.

Zones of termination of retinofugal axons

TARGETS BEYOND THE LATERAL GENICULATE NUCLEUS. Virtually all of the retinogeniculate axons in this study produce a branch that enters the brachium of the superior colliculus. For the Y-axons, this is not surprising in view of much prior evidence that every retinal ganglion Y-cell innervates both the lateral geniculate nucleus and the midbrain via a branching axon (3, 4, 32, 39, 70). However, both morphological studies of labeled retinal ganglion cells following retrograde transport of HRP injected into the midbrain as well as electrophysiological studies of the antidromic activation of retinal ganglion cells from midbrain suggest that only a small proportion of retinofugal X-axons project beyond the lateral geniculate nucleus to the midbrain (10, 17, 25, 32, 39, 52, 70). Furthermore, although Bowling and Michael (3, 4) note that every Y-axon branches to innervate the midbrain, they described only a fraction of their X-axons as sending branches beyond the lateral geniculate nucleus.

Obviously, more data will be needed to settle the issue of the extent of the retinofugal X-innervation of the midbrain. We should emphasize that, although every X-axon in our sample branches to enter the brachium of the superior colliculus, none could be followed to a terminal arbor, and we cannot rule out the possibility that many of these end blindly. It is also worth reiterating our observation for X-axons that the branch entering the brachium of the superior colliculus is always noticeably thinner than the branch innervating the lateral geniculate nucleus. Perhaps this signifies a small terminal arbor for the midbrain-projecting branch. In any case, the small arbor and/or the thin branch may retard both the retrograde transport of HRP as well as the antidromic transmission of an action potential to the cell body.

Our evidence that most or all X-axons in adults innervate regions beyond the lateral geniculate nucleus might help to explain certain phenomena resulting from removal of visual cortex. If this is done in young kittens, retinal ganglion X-cells disappear, whereas Y-cells remain (44, 64). It has been suggested (44, 64) that, to survive, retinal ganglion cells need some sort of substance retrogradely transported from their terminal arbors. Since retinofugal X-axons innervate only the lateral geniculate nucleus, which undergoes massive retrograde degeneration following removal of visual cortex, their parent ganglion cells can no longer obtain this substance; they eventually die in a form of retrograde transneuronal degeneration. Retinal ganglion Y-cells are spared this fate, because their axons have sustaining collaterals to midbrain. In adult cats, cortical removal does not cause a massive loss of X-cells from retina (64), although such a lesion does appear to produce a loss of geniculate innervation by retinofugal X-axons (41). Thus both the adult and infant lesions result in a loss of the retinogeniculate X-pathway, yet only the latter leads to a loss of X-cells from retina. The different effects of infant and adult lesions would be easily explained if: *1*)

the branches of retinofugal X-axons directed toward the midbrain of adults represent sustaining collaterals; and *2*) such branches develop late enough postnatally to account for the observation that cortical lesions only during an early postnatal period cause losses of retinal ganglion X-cells. It is thus interesting that the only retinofugal X-axon fully documented for young kittens (i.e., Fig. 1*A* of Ref. 63) shows no collateral directed toward the midbrain. In this context, further comparisons between the projection patterns of these X-axons in kittens and adult cats could be most illuminating.

TARGETS WITHIN THE LATERAL GENICULATE NUCLEUS. Retinogeniculate X-axons terminate nearly exclusively in lamina A or A1, an observation also made by Bowling and Michael (4). Like us, these other authors reported only rare X-axon terminations in the medial interlaminar nucleus, but unlike us, they found no X-axon inputs to the C-laminae; given the relatively small sample in each study, minor differences such as this are not surprising. In any case, this pattern of retinogeniculate X-axon innervation seems consistent with electrophysiological evidence that few if any geniculate X-cells are found outside laminae A and A1 (13, 33, 46, 57, 62, 73).

In our sample, all retinogeniculate Y-axons terminate in lamina A or A1 and most also innervate the medial interlaminar nucleus; those that fail to innervate the medial interlaminar nucleus do not differ physiologically in any obvious way from those that innervate this region. Our sample of contralaterally projecting Y-axons also innervate the C-laminae, although none of our ipsilaterally projecting Y-axons do so. This pattern is remarkably similar to that reported by Bowling and Michael (3, 4), except that they note rare ipsilaterally projecting Y-axons that innervate lamina C1. As noted above, small differences in projection patterns of some axons between studies is not surprising. An implication of these projection patterns for the Y-axons is that the same individual retinogeniculate axons typically innervate Y-cells in all regions of the lateral geniculate nucleus. Evidence of receptive-field differences among different geniculate Y-cell populations (e.g., that those in laminae A and A1 have smaller receptive fields and lower temporal resolution than Y-cells in the C-laminae or the medial interlaminar nucleus; see Refs. 13, 15, 33, 43) thus cannot be attributed to different populations of afferent input from retina.

ZONES OF INPUT WITHIN LAMINA A AND A1. We found that Y-axons tend to concentrate their terminal boutons in the ventral halves of laminae A and A1, an observation first reported by Bowling and Michael (4). This is consistent with prior electrophysiological data from laminae A and A1 suggesting that synapses from retinogeniculate Y-axons occur ventral to those from X-axons (42). Indeed, there may be a general trend for geniculate Y-cells to lie ventral to X-cells, which is consistent with the observation of many Y-cells, but few, if any, X-cells in the C-laminae. It is interesting in this context that the monkey's lateral geniculate nucleus contains two prominent cell types: one in the magnocellular laminae lying ventral to the other in the parvocellular laminae, and that it has been suggested that the parvocellular and magnocellular cells are homologous, respectively, to the cat's X- and Y-cells (48, 54; but see Ref. 31). Perhaps the process of segregation of geniculate X- and Y-cells is less complete in the cat than in the monkey.

Bowling and Michael (4) reported that, within laminae A and A1, retinogeniculate Y-axons with off-center receptive fields have conical terminal arbors, broader ventrally, whereas those with on-center receptive fields have hourglass-shaped terminal arbors, although even the latter produced more boutons ventrally than dorsally within the A-laminae. We were unable to confirm this slight difference between Y-axons with on- and off-center receptive fields. In fact, we detected no morphological differences whatsoever for any of our X- and Y-axons that could be related to their receptive-field properties. An analogous discrepancy exists for the distribution of neurons in laminae A and A1: Humphrey et al. (27) failed to observe any difference that could be related to on- or off-center type, whereas Bowling and Wienawa-Narkiewicz (5) found a slight tendency for on-center cells to be located more dorsally than off-center cells. The discrepancy is, in any case, slight, since the claimed tendency for a differential distribution based on-center type is a minor one (4, 5).

Differences in bouton morphology

In their innervation of the laminae A and A1, retinogeniculate X- and Y-axons display a curious difference in their detailed morphological patterns. X-axons terminate in clustered boutons, whereas Y-axons terminate in diffusely distributed boutons, most of which are located en passant. This may relate to the nature of their specific connections with their postsynaptic targets. Geniculate X-cells tend to possess prominent clusters of dendritic appendages (16), and these appendages are the specific sites at which most retinal terminals form their synapses (72). For X-axons, therefore, the clustered boutons may simply correspond to the clustered dendritic appendages found in their targets. Evidence for such a relationship has been gathered from electron-microscopic analysis of a single, HRP-labeled retinogeniculate X-axon (22). In contrast, geniculate Y-cells tend to have smooth dendrites and they receive retinal synapses on their proximal dendritic shafts (72). This lack of a postsynaptic analog for bouton clustering in geniculate Y-cells may explain the lack of such clustering among the boutons of retinogeniculate Y-axons.

It is not yet clear what significance, if any, to attach to the observation that the mean bouton size is larger for Y- than for X-axon arbors. However, it was recently observed among boutons from a single retinogeniculate axon that larger boutons made more synaptic contacts (22), and this raises the possibility that each bouton from a Y-axon may tend to form more synaptic contacts than does its counterpart from an X axon. This possibility will have to be pursued with electron-microscopic techniques.

Location of X- and Y-axons within the optic tract

We observed that, as they course through the optic tract before branching to innervate the lateral geniculate nucleus, Y-axons always lie closer to the pial surface and thus farther from the lateral geniculate nucleus than do X-axons. This is consistent with Mastronarde's earlier physiological observations (40), although he noted a limited amount of overlap in terms of distance from the pial surface between the X- and Y-populations. Perhaps our sample was too small to detect such a small overlap, or perhaps Mastronarde (40) detected such overlap only because of imprecise knowledge of the actual recording position or because some Y-axons were recorded after they branched and began to ascend toward the lateral geniculate nucleus.

Our observations are also consistent with and extend prior morphological studies of the cat's optic tract (2, 21, 65), which indicate a location further from the pial surface for medium caliber, or X-, axons than for large caliber, or Y-, axons. This seems to have a developmental significance: the first axons to enter the optic tract seem to lie furthest from the pia, because the more recent arrivals are laid down next to the pia (21, 65–67). This suggests that X-axons develop before Y-axons do, a conclusion that, in turn, is consistent with evidence from three related lines of enquiry. First, among retinal ganglion cells, X-cells complete their final mitotic divisions before Y-cells do (68, 69). Second, retinogeniculate X-axons appear to innervate the lateral geniculate nucleus before Y-axons do so, and this early innervation of X-axons is accomplished via exuberant arbors that are pruned during the later growth of the Y-arbors (63). Third, the later developing retinogeniculate Y-axons are much more susceptible to effects of visual deprivation and lesions than are the earlier developing X-axons (18, 19, 60).

Extent of input to the lateral geniculate nucleus

It is clear from the present study as well as from prior ones (4, 61) that individual retinogeniculate Y-axons have many more terminal boutons, and thus form more synapses than do individual X-axons. Within the A-laminae alone, each Y-axon produces roughly twice as many boutons as does each X-axon. When innervation of the C-laminae and the medial interlaminar nucleus is also considered, we estimate that each Y-axon on average produces perhaps three times as many boutons in the lateral geniculate nucleus as does each X-axon, although our estimates for bouton numbers outside the A-laminae are based on a small sample of axons.

The relative extents of these retinogeniculate X- and Y-arbors probably relate to differences in X-to-Y ratios between retinal ganglion cells and geniculate relay neurons. This ratio in retina is roughly 10 to 1 (17, 38, 44, 71), whereas the geniculate ratio falls between 2 to

1 and 1 to 1 (16, 36; this issue is reviewed in Ref. 54). Studies of geniculate neurons indicate that X and Y relay cells receive roughly equal numbers of synapses from retinal axons (72); also, many of the inputs from retinogeniculate X-axons but not Y-axons innervate interneurons (16, 22, 23), which represent 20–30% of cells in laminae A and A1 (14, 37). Given these factors, the difference in bouton numbers between retinogeniculate X- and Y-axons can explain, at least partially, the dramatic change in the X-to-Y cell ratios between the retina and the lateral geniculate nucleus. Furthermore, as is summarized in Fig. 23, Y-arbors representing the central visual field are larger than those representing peripheral vision, which suggests that the difference in X-to-Y cell ratios between retina and the lateral geniculate nucleus may be greater for central than for peripheral vision. This, in turn, suggests that the decrease with eccentricity in the X-to-Y cell ratio (e.g., Refs. 17, 26, 36, 38, 44, 71) may be steeper for retina than for the lateral geniculate nucleus.

A similar conclusion could be drawn from an analysis of individual geniculocortical axons. That is, each Y-axon produces many more boutons in visual cortex than does each X-axon (27). Since Y-axons are roughly equal in number to X-axons in the geniculocortical projection (see above paragraph), it seems likely that Y-cell inputs to cortex are dominant relative to the X-cell inputs. This is the reverse of the conclusion that might be reached from inspection of the relative numbers of retinal ganglion X- and Y-cells. Sherman (54) has discussed the significance of this in a recent review. He suggests that the Y-pathway, which is more sensitive to lower spatial frequencies, is essential to the basic analysis of visual forms and that the X-pathway, which is more sensitive to higher spatial frequencies, is used for special functions, such as raised acuity, stereopsis, etc. The Y-pathway need not be densely represented in the retina, since encoding of lower spatial frequencies requires only a coarse grain, but the importance of the Y-pathway to form vision requires its extensive representation in cortex. Conversely, the X-pathway requires a dense retinal grain to encode the higher spatial frequencies, but being less important to basic form vision, it is less extensively represented in cortex (see Ref. 54 for details).

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