

Termination Patterns of Individual X- and Y-Cell Axons in the Visual Cortex of the Cat: Projections to Area 18, to the 17/18 Border Region, and to Both Areas 17 and 18

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ABSTRACT

Horseradish peroxidase was injected intracellularly into single, physiologically identified X- and Y-cell geniculocortical axons that projected to area 18, to the 17/18 border region, or to both areas 17 and 18 via branching axons. The axon terminal fields in cortex were labeled anterogradely, and the cell bodies of the axons in the A-laminae, lamina C, and the medial interlaminar nucleus (MIN) of the dorsal lateral geniculate nucleus (LGN) were labeled retrogradely.

The laminar projections in area 18 of eight Y-cells and one geniculate, non-Y-cell were analyzed. Most of the cells arborized densely within layer IVa and the lower 200 to 400 μm of layer III. Most provided little or no input to layer IVb or layer VI. Thus, the laminar projections of Y-cells to layer IV of area 18 were similar to those of their area 17 counterparts, although the input to layer III was greater and rose much higher in area 18 than in area 17. The terminal arbors in area 18 were two to three times larger in lateral extent than those in area 17. They spread over 2.0 to 2.8 mm^2 of layer IV and occupied proportionately much greater regions of area 18 than the Y-cell arbors in area 17. This may partially account for the large receptive fields of cortical cells in area 18, and it indicates that a small region of area 18 may receive converging inputs from a relatively wide retinotopic region of the LGN. The terminal arbors were also highly asymmetric, generally being two to four times longer anteroposteriorly than mediolaterally. These asymmetric arbors may form the structural basis for the anisotropic organization of the retinotopic map in area 18.

We recovered three cells (two Y, one X) whose axons arborized in the border zone between areas 17 and 18. One Y-cell axon had a receptive field located in the ipsilateral visual hemifield and it arborized in a small region restricted almost exclusively to the border zone. The other two cells had receptive fields on or adjacent to the vertical meridian, and they terminated on either side of the 17/18 border region as well as within it. Thus, geniculate afferents representing the ipsilateral hemifield or the vertical meridian appear to have different patterns of termination on and adjacent to the 17/18 border zone. Also, some X-cell input may invade area 18 in the region immediately adjacent to the border zone.

Some Y-cell axons bifurcated in the white matter to innervate areas 17 and 18, but the majority innervated one area or the other. The bifurcations occurred at the level of the lateral sulcus or higher in cortex, within 1 to 5

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mm of the termination zones in the gray matter. Of 12 well-labeled Y-cell axons arising from the A-laminae of the LGN, two branched to areas 17 and 18, nine projected to area 17 only, and one projected to area 18 only. Of four lamina C Y-cells, two branched and two projected only to area 18. Two Y-cells from the MIN projected to only area 18. Thus, within the A- and C-laminae there are substantial and dedicated populations of Y-cells that project to one cortical area or the other, as well as some that project to both areas via branching axons.

Finally, our data indicate little or no input of X-cells to area 18, except across the 17/18 border zone. Of 23 axons projecting to area 18, 22 were Y-cells and one was unclassified. Of 35 X-cell axons that were traced to their terminations, all projected to area 17 or the 17/18 border zone.

Key words: laminar terminations, soma locations, arbor extents, branching axons, retinotopic mapping

Like area 17, area 18 of the cat's visual cortex receives significant projections from three major divisions of the dorsal lateral geniculate nucleus (LGN)—the A laminae, the C laminae, and the medial interlaminar nucleus (MIN) (Garey and Powell, '67; Stone and Dreher, '73; Rosenquist et al., '74; LeVay and Gilbert, '76; Wilson et al., '76; Hollander and Vanegas, '77; Raczkowski and Rosenquist, '83). Many of the geniculate cells project to one cortical area or the other but some appear to project to both areas via branching axons (Garey and Powell, '67; Stone and Dreher, '73; Geisert, '80; Bullier et al., '84). In addition to some common geniculate input, areas 17 and 18 share a number of similarities, including (1) common receptive field types (i.e., simple and complex cells) with similar laminar distributions, (2) cells monosynaptically activated by geniculate afferents, (3) a functional architecture for ocular dominance and orientation, and (4) similar efferent projection systems arising from similar layers and projecting to common cortical and subcortical targets (Hubel and Wiesel, '65; Singer et al., '75; Tretter et al., '75; Harvey, '80a,b; Orban, '84). These similarities in inputs, properties, and projections led to the suggestion that areas 17 and 18 process visual information in a largely parallel fashion (see reviews by Stone et al., '79; Lennie, '80; Sherman and Spear, '82). This is further supported by the observation that area 17 removal or inactivation has remarkably little effect on neuronal response properties in area 18 (Donaldson and Nash, '75; Dreher and Cottee, '75; Sherk, '78).

In the previous paper (Humphrey et al., '85), we described the laminar and areal projection patterns of single geniculate cells to area 17. A similar study has never been done for area 18. Given the functional and structural similarity of these two areas it is important to determine whether the laminar projections of geniculate cells to these areas are similar. Exact correspondence was not expected since area 18 does not appear to get input from X-cells, but only from W- and Y-cells (Stone and Dreher, '73; Tretter et al., '75; Mitzdorf and Singer, '78; Harvey, '80a; Dreher et al., '80). Earlier tracer studies suggested that relay cells from the A- and the C-laminae project throughout layer IV of area 18 (Rosenquist et al., '74; LeVay and Gilbert, '76). It is possible, in light of the area 17 results (Humphrey et al., '85), that individual afferents might have different sublaminar projections in cortex depending upon their physiological properties or soma locations within the depth of the geniculate laminae. We also wanted to determine whether the lateral

spreads of the Y-cell axons in area 18 are similar to those in area 17. Finally, we wanted to directly visualize, and thus confirm the existence of, single axons that branch to innervate areas 17 and 18. To address these and other issues, we injected single, physiologically identified geniculate axons with horseradish peroxidase (HRP) to fill their terminal arbors in cortex and their somata in the lateral geniculate nucleus. Preliminary results of this work have appeared in abstract form (Humphrey et al., '82; Uhlrich and Humphrey, '84).

METHODS

The general methods used in this study were identical to those described in the previous paper (Humphrey et al., '85). Two variants noted below were our cytoarchitectonic divisions for area 18 and our matches of somata and axon arbors.

Cytoarchitectonics

Figure 1A shows the cytoarchitecture of area 18, which has been described by numerous authors (Otsuka and Hasler, '62; Sanides and Hoffmann, '69; Garey, '71; Harvey, '80a). In accord with Harvey's ('80a) description, we divided layer IV into dorsal (IVa) and ventral (IVb) tiers. The border between layers IVb and V occurs at the level of the apices of the most superficial pyramids comprising layer V. Layer IVb is conspicuous by its relatively small, moderately packed somata. This layer in area 18 is similar in appearance to layer IVb of area 17, although it contains more medium-sized cells and is not as densely packed (cf. Fig. 1 of Humphrey et al., '85). Layer IVa of area 18, compared to layer IVb, contains more loosely packed, slightly larger neurons and a greater proportion of pyramidal-shaped somata. The border between layers IVb and IVa is somewhat ambiguous. It involves a gradual transition between the smaller cells in layer IVb and the medium and larger sized, more loosely packed cells in layer IVa. The gradual transition to larger cells continues dorsally within layer IVa.

At the border with layer III, pyramidal morphology becomes dominant and occasional large pyramids are seen. These large pyramids occur less frequently than the analogous border pyramids in area 17, but their presence marks the base of layer III in both areas (arrow in Fig. 1A indicates a border pyramid). Above this point, there is a rapid increase in the number of large, loosely packed pyramids, which become most prevalent about 200 μm above the bor-

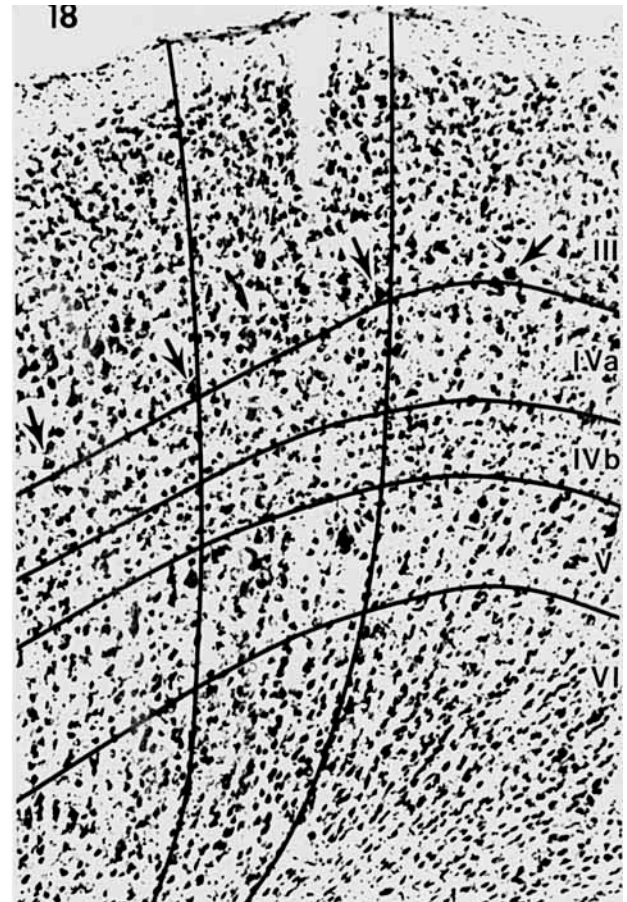


Fig. 1. Cytoarchitectonic criteria for areas 17 and 18. A. Photomicrograph of a Nissl-stained section of cat area 18 showing the laminar boundaries according to Harvey ('80a). Arrow indicates a large pyramid at the layer III/IV boundary. Scale: 100 μ m and applies to B. B. Photomicrograph

of a Nissl-stained section showing the border region between areas 17 and 18. Arrows point to large pyramids at the base of layer III. The border zone is cytoarchitecturally a transition region where these pyramids drop down to occupy a deeper position in cortex and layer IV narrows.

der between layers III and IV, but which are scattered throughout the lower half of layer III. The upper half of layer III primarily contains small and medium pyramidal-shaped somata. We have neither subdivided layer III (cf. Otsuka and Hassler, '62; Harvey, '80a) nor distinguished it from layer II in our reconstructions.

We could not sharply distinguish the border between areas 17 and 18 on the basis of cytoarchitecture. Instead, we have treated it as a transition zone roughly 200 to 400 μ m wide (Fig. 1B). Medially is area 17, where the large pyramids at the base of layer III sit relatively superficially in cortex and where layer IV is relatively wide. Laterally is area 18 where large pyramids at the base of layer III occupy a fairly deep position, making layer III wider and layer IV narrower than in area 17. As one moves from area 17 to area 18 in the transition zone, the large pyramids of layer III gradually descend and layer IV becomes narrower and descends.

The border between areas 18 and 19 was also treated cytoarchitecturally as a transition zone 200 to 400 μ m wide. Key cellular differences between the two areas are: (1) layer

V in area 19 contains noticeably fewer large ($> 40 \mu$ m) pyramids, and (2) layer III in area 19 also contains fewer large pyramids and thus appears more homogeneous in soma size relative to layer III of area 18 (Otsuka and Hassler, '62). The cytoarchitectonic criteria used to determine the 17/18 and 18/19 borders were found to match the known myeloarchitectonic features at these borders (Otsuka and Hassler, '62; Hubel and Wiesel, '65).

In the following reconstructions of axon arbors, the full extents of border zones were drawn when the arbors were located on or immediately adjacent to the 17/18 border. For arbors located farther from the 17/18 border, the boundaries of area 18, but not the transition zones, were indicated.

Identification of somata

Geniculate neurons retrogradely labeled with HRP were found in the A-laminae, the C-laminae, and the MIN. Somata in the A- and C-laminae could be matched to axons in cortex on the basis of ocular dominance and receptive field position, as noted in the previous paper (Humphrey et al., '85). All labeled cells in the C-laminae were driven from

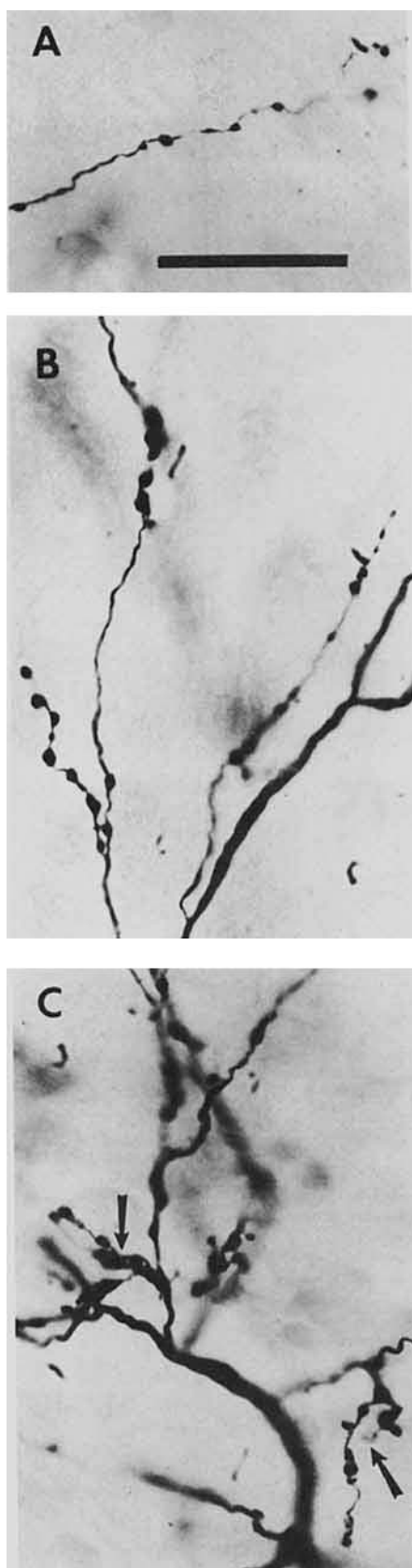
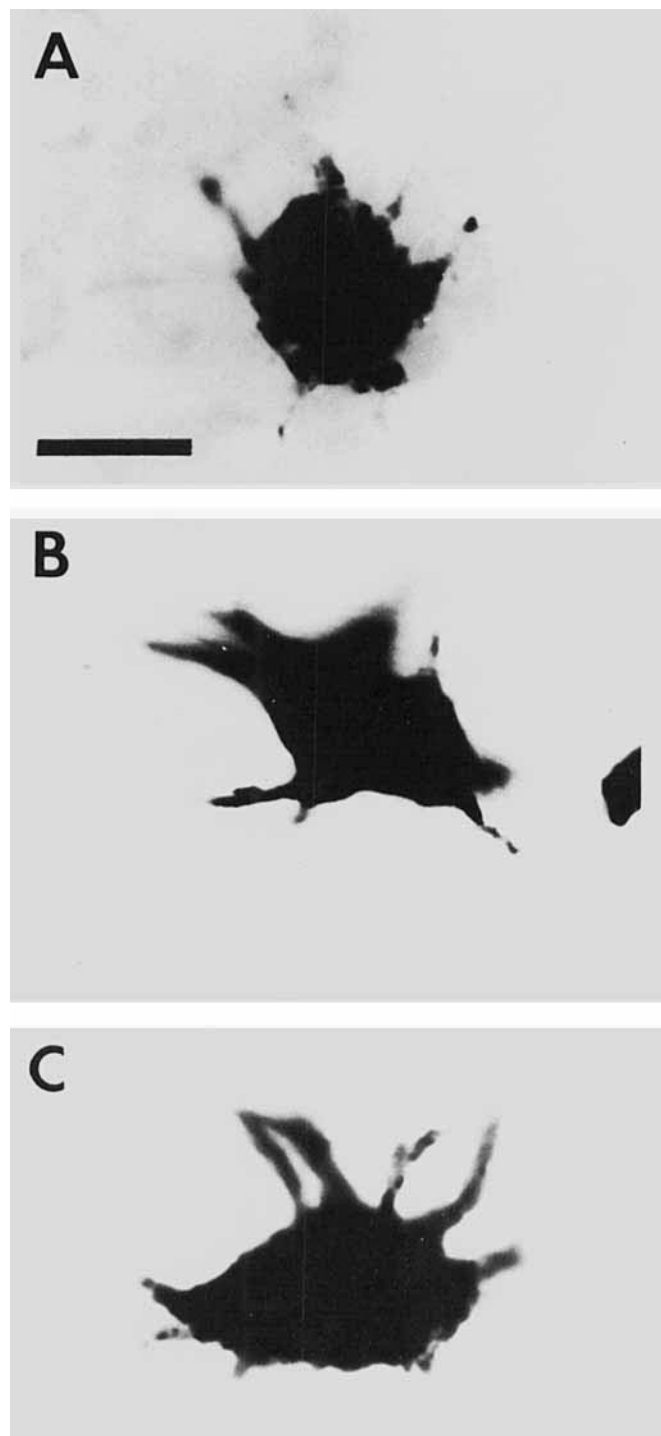


Fig. 2. High power photomicrographs showing Y-cell axon terminals in layers III and IV of area 18. A and B illustrate boutons distributed en passant. Note the variation in size between individual boutons. Scale in A



= 50 μm and applies to B,C. C. Arrows indicate two clusters of five to ten boutons each.

Fig. 3. Photomicrographs of three retrogradely labeled cells in the lateral geniculate nucleus whose axons were injected in cortex and found to arborize in area 18. Note the dense filling of the large cell bodies and the stout primary dendrites. A. Soma located in lamina A. Its size is 445 μm^2 ; the complete outline of the cell and its arbor in cortex are shown in Figure 4. Scale = 20 μm and applies to B, C. B. Soma (442 μm^2) located in the medial interlaminar nucleus. C. Soma (679 μm^2) located in lamina C. Its complete outline and terminal arbor are shown in Figure 6.

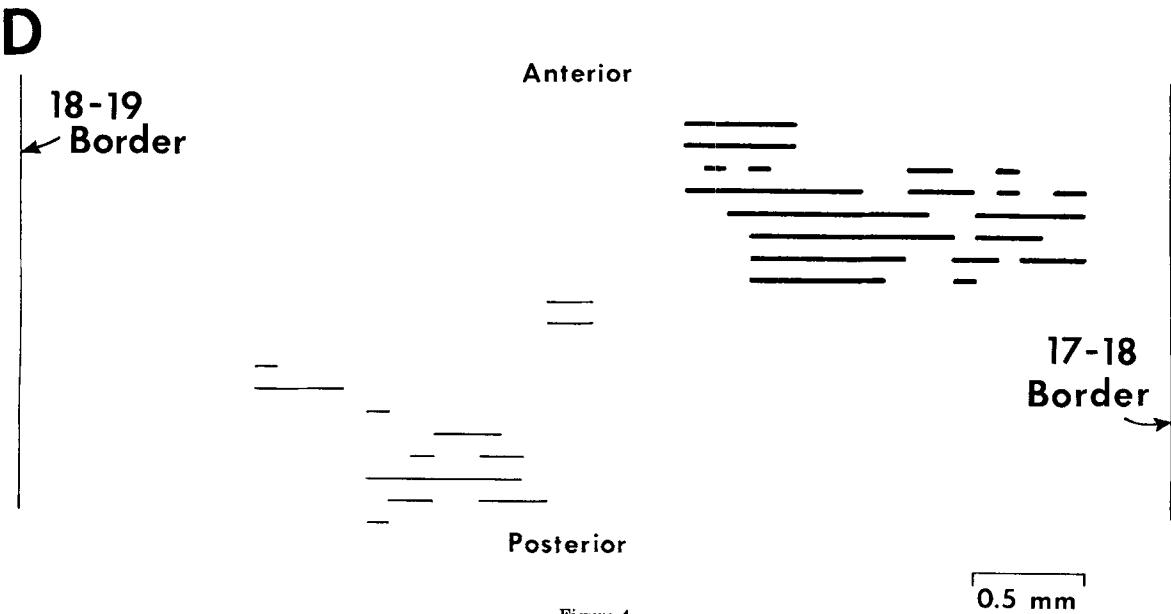
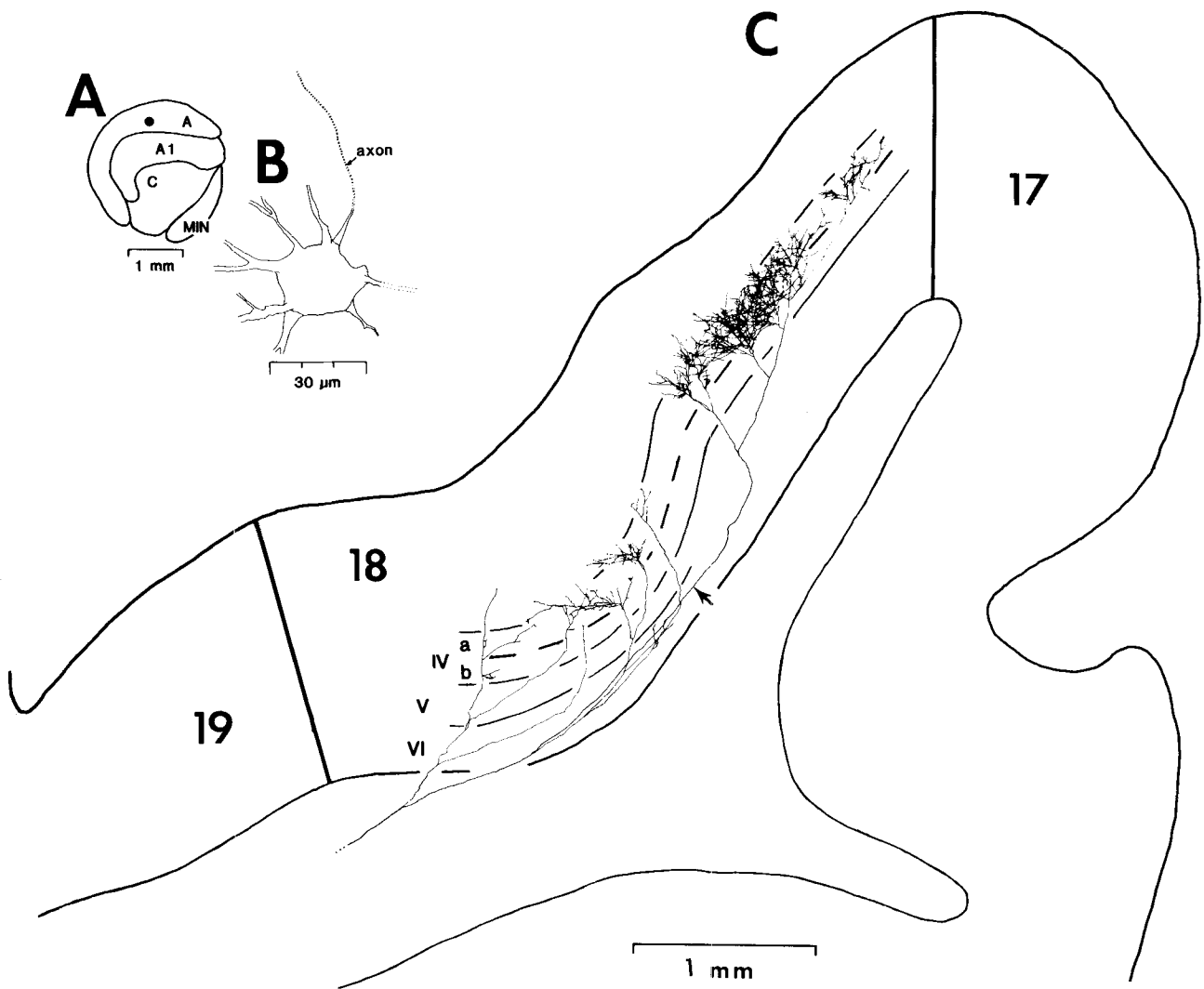


Figure 4

the contralateral eye and were thus attributed to lamina C (Wilson et al., '76). We matched labeled cells in the MIN to their axons in cortex on the basis of receptive field position (e.g., Sanderson, '71; Guillery et al., '80; Lee et al., '84) only after accounting for all labeled somata in the A- and C-laminae.

RESULTS

Our axon sample falls into three major groups, including those that project to area 18, those that project to and across the 17/18 border zone, and those that project to areas 17 and 18 via collaterals. Our sample of axons in each projection group is generally smaller than that for the axons projecting to only area 17 (see the previous paper, Humphrey et al., '85), and we are not confident that we have seen the complete variety of projection patterns. We shall thus restrict our descriptions largely to the general features of these axonal projections and not provide as much quantitative detail as in the previous paper.

Five major features of the geniculate projections have particularly impressed us. First, most of the terminal fields in area 18 were considerably larger in lateral extent than those in area 17. Second, there was a significant degree of sublaminar segregation among geniculate afferents to layer IV in area 18. Third, the Y-cell projection to layer III was much more extensive and rose much higher in the layer within area 18 than within area 17. Fourth, we found evidence for possible X-cell input to area 18, although if present at all, this appears to be a minor pathway. Fifth, most of the Y-cell axons from the A-laminae innervated area 17 only; a minority branched in the white matter to innervate area 18 as well; only rare Y-cells from the A-laminae exclusively innervated area 18.

Overview of somata and terminal arbors

Figure 2 shows photomicrographs of typical HRP-filled Y-cell terminal arbors in area 18. At this level, the arbors were virtually indistinguishable from the X- and Y-cell arbors in area 17. The fine axon collaterals containing the boutons were generally less than $0.5\ \mu\text{m}$ in diameter. The boutons were 0.5 to $2.5\ \mu\text{m}$ in diameter (with an average of

$1.0\ \mu\text{m}$) and were distributed mainly en passant along the widely spreading processes, each of which also terminated in a bouton.

Figure 3 shows photomicrographs of typical Y-cell somata in the LGN that were labeled retrogradely by injecting their axons in cortex. Most of the Y-cells projecting to area 18 possessed large somata and well-labeled, stout, radiating primary dendrites. These class 1 morphological features (Guillery, '66) are characteristic of geniculate Y-cells (Friedlander et al., '81).

Projections to area 18

Axons of 20 Y-cells and one neuron identified as not a Y-cell were injected and traced to area 18. Eight of the Y-cells were labeled sufficiently to analyze their laminar projections. These axons arose from somata in the A-laminae (three cells), lamina C (four cells), and the MIN (one cell). The non-Y-cell arose from a soma in lamina C.

Y-cell projections from the A-laminae. The projection of a geniculate Y-cell from lamina A to area 18 is shown in Figure 4. (For this and most of the following cells, each cell's physiological properties are summarized in the figure legends). Its axon arose from a large ($445\ \mu\text{m}^2$) soma that had stout, radiating primary dendrites (Fig. 4B). The axon was injected within a primary collateral about 2 mm distal to the first visible bifurcation point, thus densely labeling the right-hand portion of the terminal field but poorly and incompletely labeling the left-hand portion (Fig. 4C). The well-labeled right-hand portion of the arbor contained over 1,100 boutons, nearly all of which were located in layer IVa and lower layer III. There was virtually no input into layer IVb, and there was little or no input to layer VI. A similar laminar pattern appeared to hold for the poorly labeled left-hand portion of the field.

It is noteworthy that this axon's boutons avoided layer IVb and terminated only above it. We have recovered two other well-filled Y-cell axons that arose from the A-laminae of the LGN (not illustrated). While a few boutons were present in layer IVb, the vast majority of their arbors ($> 90\%$) were distributed to layers IVa and lower layer III. Thus, it appears that, for area 18 as well as area 17, Y-cells located in the A-laminae of the lateral geniculate nucleus may project predominantly to the upper half of layer IV and to the bottom of layer III.

Despite the incomplete filling of the terminal arbor illustrated in Figure 4, it is clear that the axon terminated throughout most (72%) of the mediolateral extent of this region of area 18. This is further revealed in a surface view of the terminal field in layer IV (Fig. 4D), which shows two to three clumps of boutons, each of which may have been aligned within an ocular dominance column. The surface area of the terminal fields, not including the intervening terminal free gaps, was about $1.0\ \text{mm}^2$. This value was clearly underestimated given the incomplete filling of the left-hand portion of the arbor. Note also that, while the cell's receptive field center was 6° from the vertical meridian, the axon terminated within about $500\ \mu\text{m}$ of the 17/18 border zone. This region of area 18 maps visual space on or very near the vertical meridian (Hubel and Wiesel, '65; Bilge et al., '65; Woolsey, '71). Likewise, the left portion of the arbor terminated within about 1 mm of the 18/19 border. Receptive fields of cortical neurons near this border were likely to be more peripheral than that of the Y-cell axon, although variability in the retinotopic map in area

Fig. 4. Reconstruction of a Y-cell from lamina A that projected to area 18. The cell had an off-center receptive field, 2° in center diameter, that was driven through the contralateral eye and was located 6° from the vertical meridian and 9° below the horizontal zero parallel. It responded nonlinearly to gratings and was activated from the optic chiasm at a latency of 1.7 msec. Optic radiation electrodes were not implanted. A, B. Drawing of the retrogradely filled cell ($445\ \mu\text{m}^2$) and its geniculate location in lamina A (filled circle). Note the cell's straight, stout, radiating primary and secondary dendrites. A photomicrograph of the cell is shown in Figure 3A. C. Complete reconstruction of the portions of the terminal field that were labeled. The more densely labeled right half of the arbor terminated almost exclusively in layer IVa and lower layer III. A similar pattern existed in the poorly labeled left portion. Note the broad expanse of the arbor. Arrow points to injection site. The parent axon diameter was $2.0\ \mu\text{m}$. In this and subsequent figures where a single line marks the border of area 18, it represents the area 18 side of the transition zone with area 17 or area 19 (See Methods). D. Surface view of the extent of the terminal arbor relative to the areas 17/18 and 18/19 borders (see Humphrey et al., '85, for methods of surface view reconstructions). Two to three separate clumps of the terminals were visible. The upper right clump (thick lines) corresponds to the well-filled portion of the arbor and was $1.4\ \text{mm}^2$ in extent. The middle and lower left clumps correspond to the poorly and incompletely filled portions, which were probably larger than that which was visualized. The scales for all of the surface view outlines in this and the preceding paper (Humphrey et al., '85) are identical, allowing direct comparison of shapes and extents of arbors in area 18 and area 17.

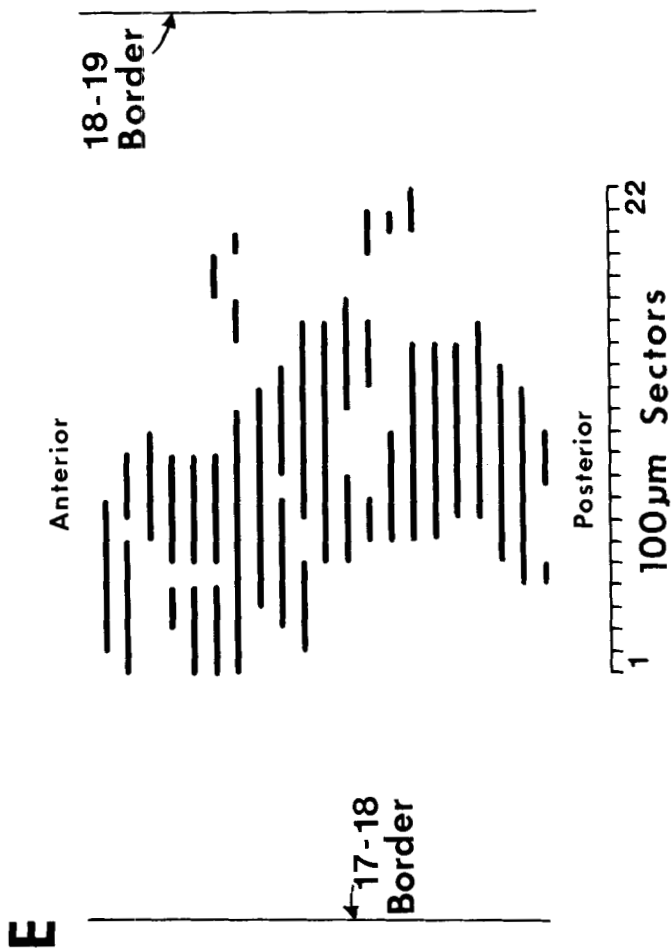
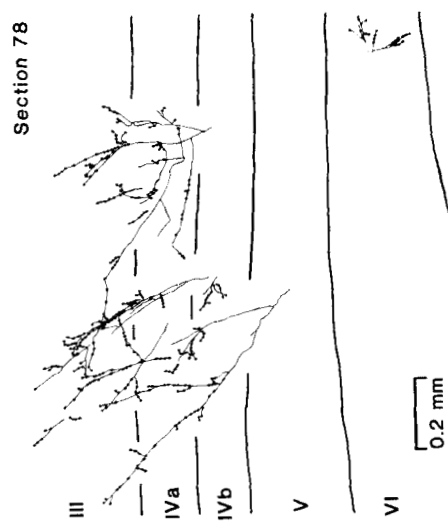
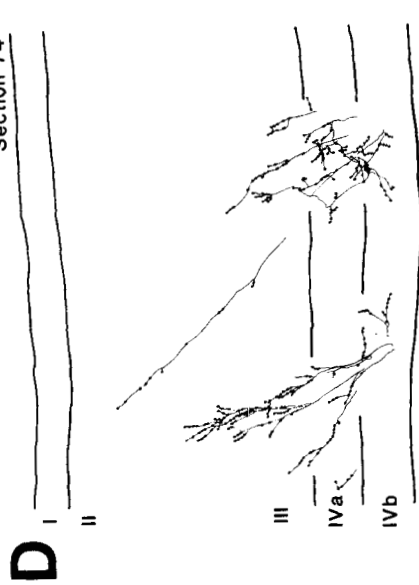
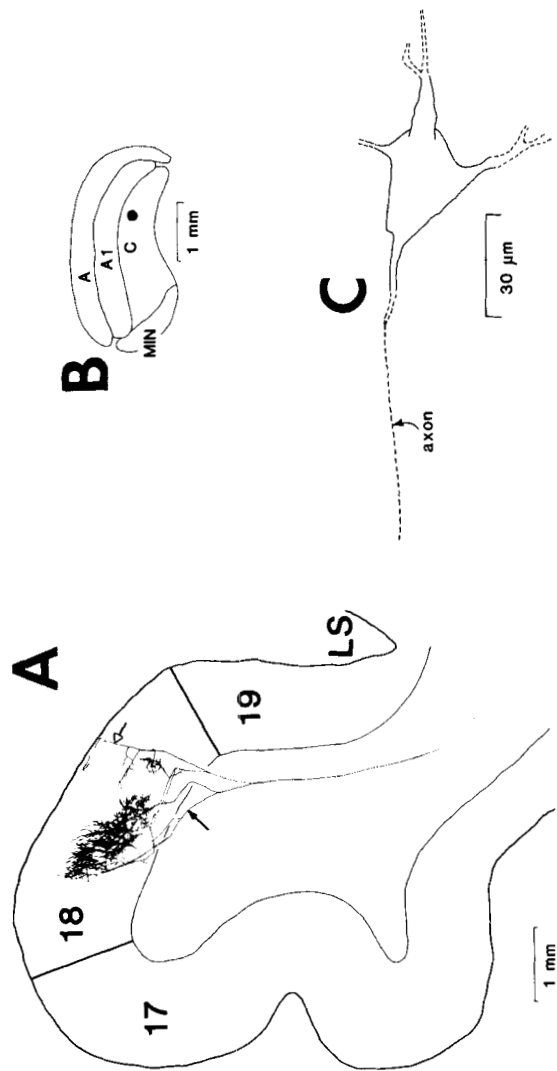


Figure 5

18 (Donaldson and Whitteridge, '77; Tusa et al., '79; Albus and Beckmann, '80) renders this conclusion uncertain. Nonetheless, it is clear that this Y-cell arbor diverged to a remarkable degree and presumably provided input to cells distributed over a broad expanse of area 18. Such broad divergence could partly account for the large receptive fields that are found among area 18 cells (Hubel and Wiesel, '65; Treter et al., '75; Dreher and Cottee, '75; Orban and Calens, '77).

Y-cell projections from lamina C. We retrieved four well-labeled Y-cell axons that arose from lamina C and projected to area 18. One such cell is illustrated in Figure 5. Its large soma ($498 \mu\text{m}^2$) was located in lamina C (Figure 5B,C). Although the axon was injected in a second order collateral (arrow in Fig. 5A), the terminal fields of all of the main collaterals were well-labeled. The laminar projections, seen in three representative sections through the field, are reconstructed in Fig. 5D. The field contained over 3,800 boutons. Roughly 90% of them were distributed to the upper half of layer IV and throughout most of the lower half of layer III. A few collaterals encroached into the upper half of layer III (e.g., section #74, Fig. 5D). The projection onto layer IVb was small (5 to 10%) and in most cases was restricted to the upper half of layer IVb (Fig. 5D). Thus, like the A-lamina Y-cell illustrated in Figure 4, this C-lamina cell largely avoided the zone of small cells that comprises layer IVb. Likewise, its input to layer VI was quite small (less than 0.5%).

Most interestingly, this axon also distributed nine boutons to the upper half of layer I (Fig. 5A). We may have underestimated the size and extent of this layer I projection because the ascending axon collateral was very lightly labeled. This cell's soma location in the LGN is congruent with previous anatomical observations that C-laminae cells project to layer I. It has been suggested that the layer I input derives primarily from W-cells (Leventhal, '79). Our results demonstrate that Y-cells in lamina C also can project to layer I. This is the only example we have seen of such a projection, and the strength of the Y-cell input to layer I relative to that of W-cells remains to be determined. We have not yet seen any Y-cell projections to layer I deriving from other regions of the LGN.

As illustrated in Figure 5E, the terminal arbor in layer IV occupied approximately one-third of the mediolateral extent of area 18. Also, the layer IV arbor was longer in anteroposterior extent (2.1 mm) than in mediolateral extent (about 1.3 mm). The axon's total surface area, including the few terminal free gaps, was about 2.4 mm^2 . Though not visible in this surface view, examination of consecutive

sections through the field revealed three anteroposteriorly separated regions of high bouton density, separated by zones of much lower density. This may represent clumping into adjacent ocular dominance columns for the contralateral eye.

Another example of a lamina C Y-cell projection to area 18 is illustrated in Fig. 6. Its large soma ($679 \mu\text{m}^2$) and thick primary dendrites were quite well-labeled and typical of Y-cells in the LGN (Fig. 6D). The cell's axon innervated two separate regions adjacent to the 17/18 border (Fig. 6A,B). The field contained 4,551 boutons whose laminar distribution is illustrated in reconstructions of four representative sections (Fig. 6E). About 4,100 (roughly 90%) boutons were distributed to the upper half of layer IV and the lower 250 μm of layer III. Figure 7 shows photomicrographs of terminal processes in layer IVa and lower layer III. The projection to layer IVb was small, accounting for less than 400 (< 10%) of the total terminals, and was restricted to the upper half of the sublayer. About 80 (2%) terminals were distributed to the upper two-thirds of layer VI, and these were seen only in the far rostral end of the field (Fig. 6A). There was no visible projection to layer I.

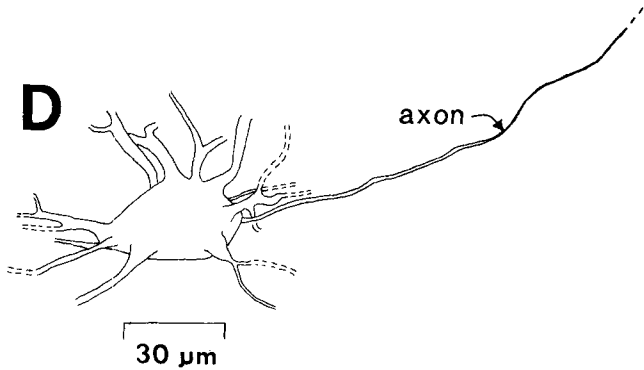
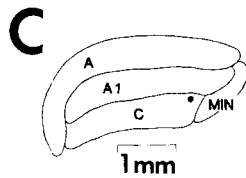
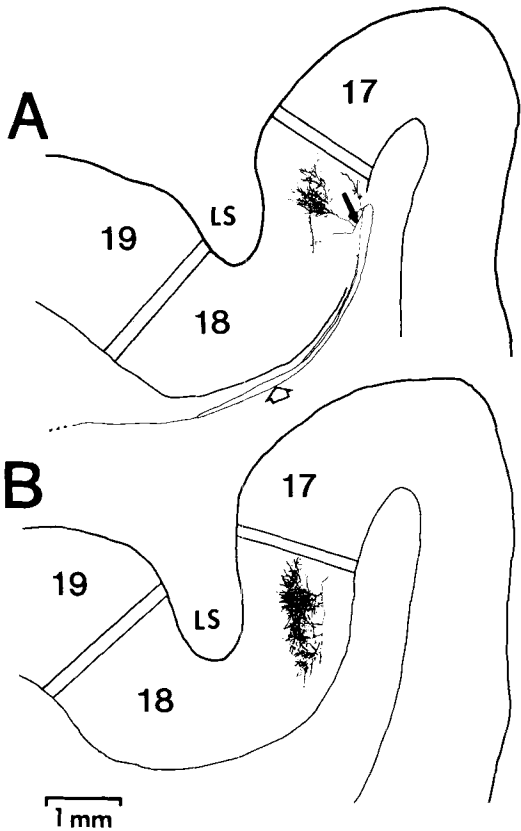
A surface view of the outline of the layer IV arbor (Fig. 8) clearly reveals that the axon formed a long (3.2 mm) and narrow (about 0.8 mm) field that abutted the 17/18 border all along its length. There was a 300 to 400 μm gap between the smaller, anterior and larger, posterior portions of the field. Comparison among single sections through the large, posterior portion yielded no further evidence of separate clumps of boutons. Thus the posterior portion formed a continuous field, about 2 mm long, that ran parallel, rather than perpendicular, to the 17/18 border. The surface area of the whole field, not including the terminal free gaps, was 1.5 mm^2 ; including the gaps, it occupied about 2.0 mm^2 .

Y-cell projection from MIN. We recovered one well-labeled axon from a Y-cell in the MIN (Fig. 9). Its laminar projections were more widely distributed than the axons we have seen from the A- or C-laminae cells. The cell's soma, $357 \mu\text{m}^2$ in area, was located in the dorsal and lateral half of the MIN (Fig. 9B) and was elongated in shape with stout primary dendrites originating mainly from either end (Fig. 9C). Its shape is typical of MIN Y-cells recently described by Raczkowski and Sherman ('83). The axon was injected near the first bifurcation point, and the terminal arbor was heavily labeled. The parent axon was traced 3 mm back in the white matter with no further bifurcations seen (Fig. 9A). We thus are reasonably confident that the entire arbor in area 18 has been visualized.

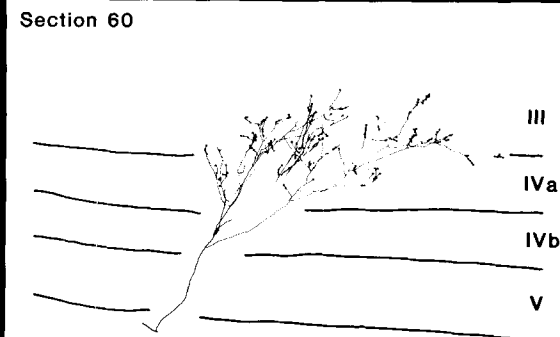
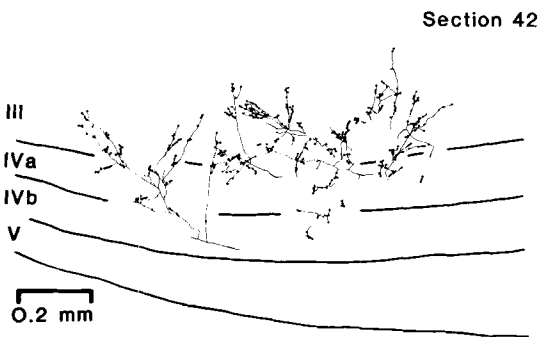
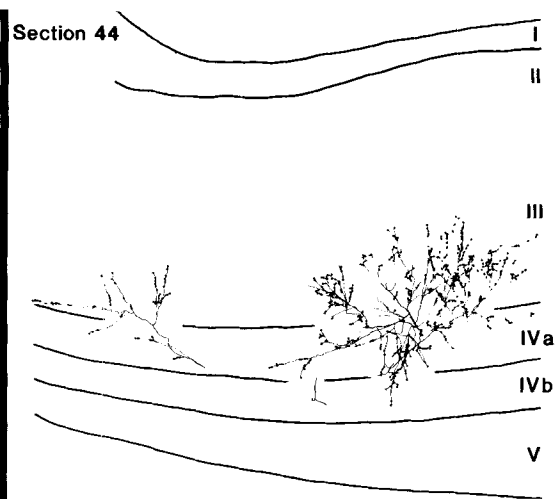
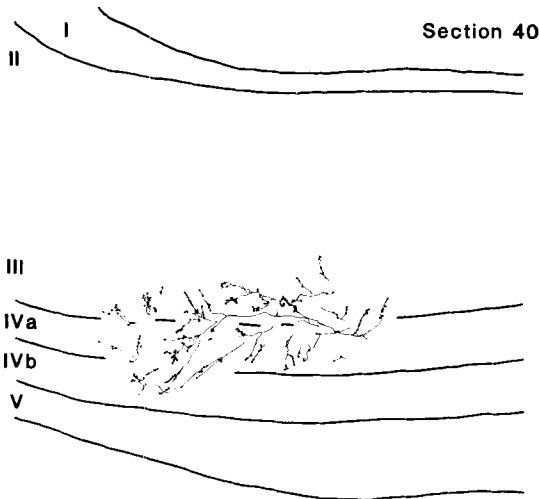
Figure 9D shows the laminar projections of the axon in reconstructions of four typical sections. The arbor contained 2,140 boutons, 92% (1,960 boutons) of which were distributed throughout both divisions of layer IV and lower layer III. In layer IV, the projections were greatest in the upper division (IVa). In layer III the axon frequently rose 400 to 600 μm above the III/IV border. There was a small input throughout the depth of layers VI and V which accounted for only 8% (185 boutons) of the terminal arbor.

The surface view reconstruction of the layer IV arbor (Fig. 10) reveals that the Y-cell axon terminated in two distinct clumps, with an intervening terminal free gap of 800 μm . As with many other Y-cell axons in area 18, the arbor was asymmetrically distributed, being about 4 mm long (in the A-P plane) and about 1.0 mm wide. It occupied a large expanse of area 18, having a surface area of 1.7 mm^2 . The

Fig. 5. Reconstruction of a Y-cell from lamina C that projected to area 18. The cell had an off-center receptive field, 7° in center diameter, was activated through the contralateral eye, and was located 24° from the vertical meridian and 13° below the horizontal zero parallel. It responded nonlinearly to gratings and had a latency of 1.7 msec to stimulation of the optic chiasm (no radiation electrodes were used). A. Lower power reconstruction of the terminal arbor in area 18. In addition to the dense, widely spreading arbor, note the small collateral (open arrow) projecting to layer I. The filled arrow points to the injection site, and the parent axon diameter was 1.5 μm . LS, lateral sulcus. B, C. Drawing of the lateral geniculate nucleus and retrogradely filled cell body ($498 \mu\text{m}^2$) located in lamina C. D. Higher power reconstructions of the laminar projections in three sections within the terminal field. Note the small number of terminals in layer IVb compared to those in layers IVa and III. E. Surface view outline of the terminal arbor. The arbor occupied a large expanse of area 18 (2.4 mm^2 , including gaps) and was distributed more along the anteroposterior axis than along the mediolateral axis. Conventions as in Figure 4D.



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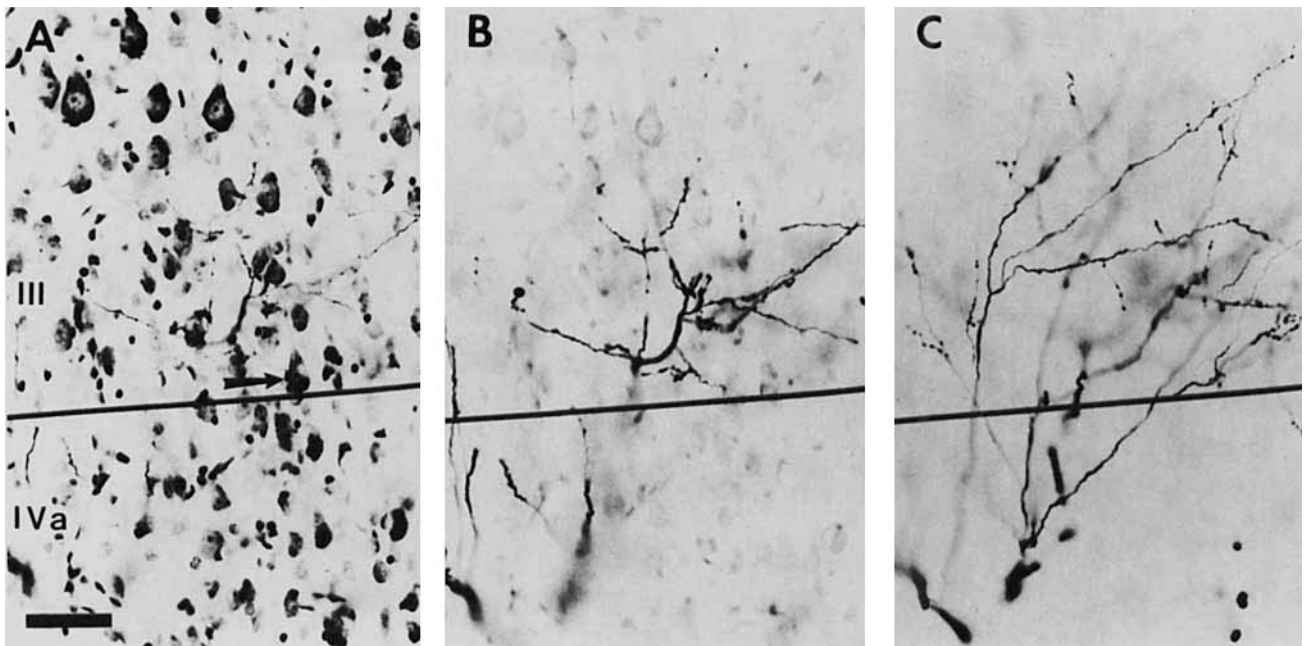


Fig. 7. Photomicrographs of some terminal processes of the Y-cell arbor illustrated in Figure 6. A, Nissl-stained cell bodies illustrating the laminar border between layers IVa and III. The arrow points to a large pyramid at the III/IV border. Scale = 50 μm and applies to B, C. B, The same field of

view and focal plane as in A but filtered to reveal more clearly the terminal arbor of the axon. C, Same field of view as in A, but different focal plane, revealing bouton-studded processes in layer IVa and lower layer III.

total surface area was 2.8 mm^2 when the terminal-free gaps were included.

X- or W-cell projection. We recovered one LGN axon projecting to area 18 that was not a Y-cell but which seemed to be an X- or W-cell. The response properties, although typical of many X-cells, did not permit us to rule out a W-cell identification. The axon responded briskly to visual stimuli and displayed center/surround antagonism and linear summation. It had an on-center receptive field, with a center diameter of 1° , that was activated through the contralateral eye. Latency to optic chiasm stimulation was 2.6 msec; no radiation electrodes were used in this animal. Although these features are consistent with X-cell proper-

Fig. 6. Reconstruction of another Y-cell from lamina C that projected to area 18. The nonlinear cell had an off-center receptive field, 7° in center diameter, was driven through the contralateral eye and was located on the vertical meridian and 2° below the horizontal zero parallel. It had an (OX - OR) latency of 1.0 msec. A, B, Lower power views of the two separate regions formed by the terminal arbor. The filled arrow in A indicates the injection site. The parent axon (2.5 μm in diameter) collateralized twice deep in the white matter (A). One of these collaterals, labeled by the open arrow, gave rise to the anterior portion of the arbor, illustrated in A. It also collateralized and traveled posteriorly to give rise to the larger arbor illustrated in B. The total terminal arbor was reconstructed from over 29 serial sections. The other (unmarked) collateral off the parent axon was too poorly labeled with HRP to visualize all of its terminal arbor. The border regions separating area 18 from areas 17 and 19 are indicated in A and B as zones roughly 200 μm wide. LS, lateral sulcus. C, D, The retrogradely filled cell body (679 μm^2) was located in lamina C of the lateral geniculate nucleus. The cell contained numerous, large, radiating primary dendrites that are typical of Y-cells. A photomicrograph of the cell is shown in Figure 3C. E, Higher power reconstructions of the terminal arbor in four representative sections. Sections 40, 42, and 44 were from the posterior portion of the arbor. Section 60 was from the anterior portion. The axon's termination was largely in layer IVa and lower layer III as well as layers V and VI (not illustrated). There was a relatively small input to the upper half of layer IVb.

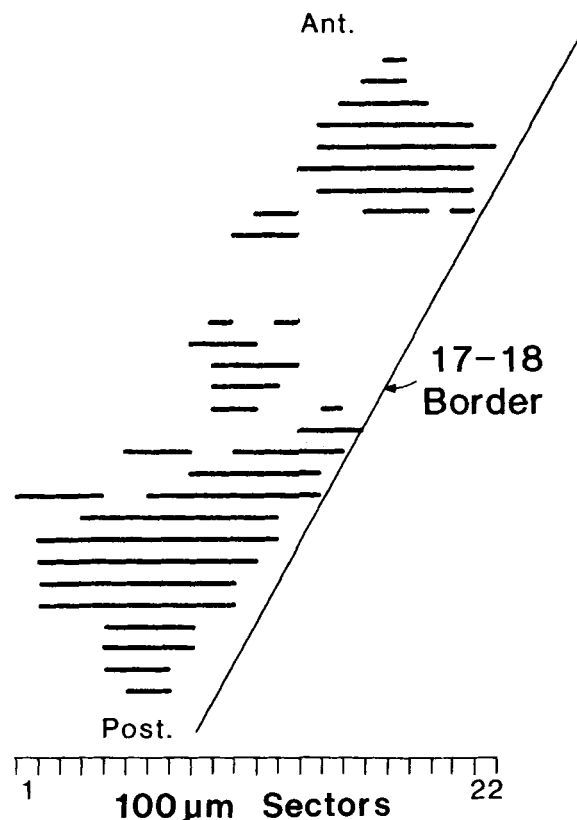


Fig. 8. Surface view reconstruction of the layer III and IV terminal arbor from the axon in Figure 6. The axon arborized over a long, narrow region adjacent to the 17/18 border and covered an area of 2.0 mm^2 , including terminal-free gaps. Ant., anterior, Post., posterior. Conventions as in Figure 4D.

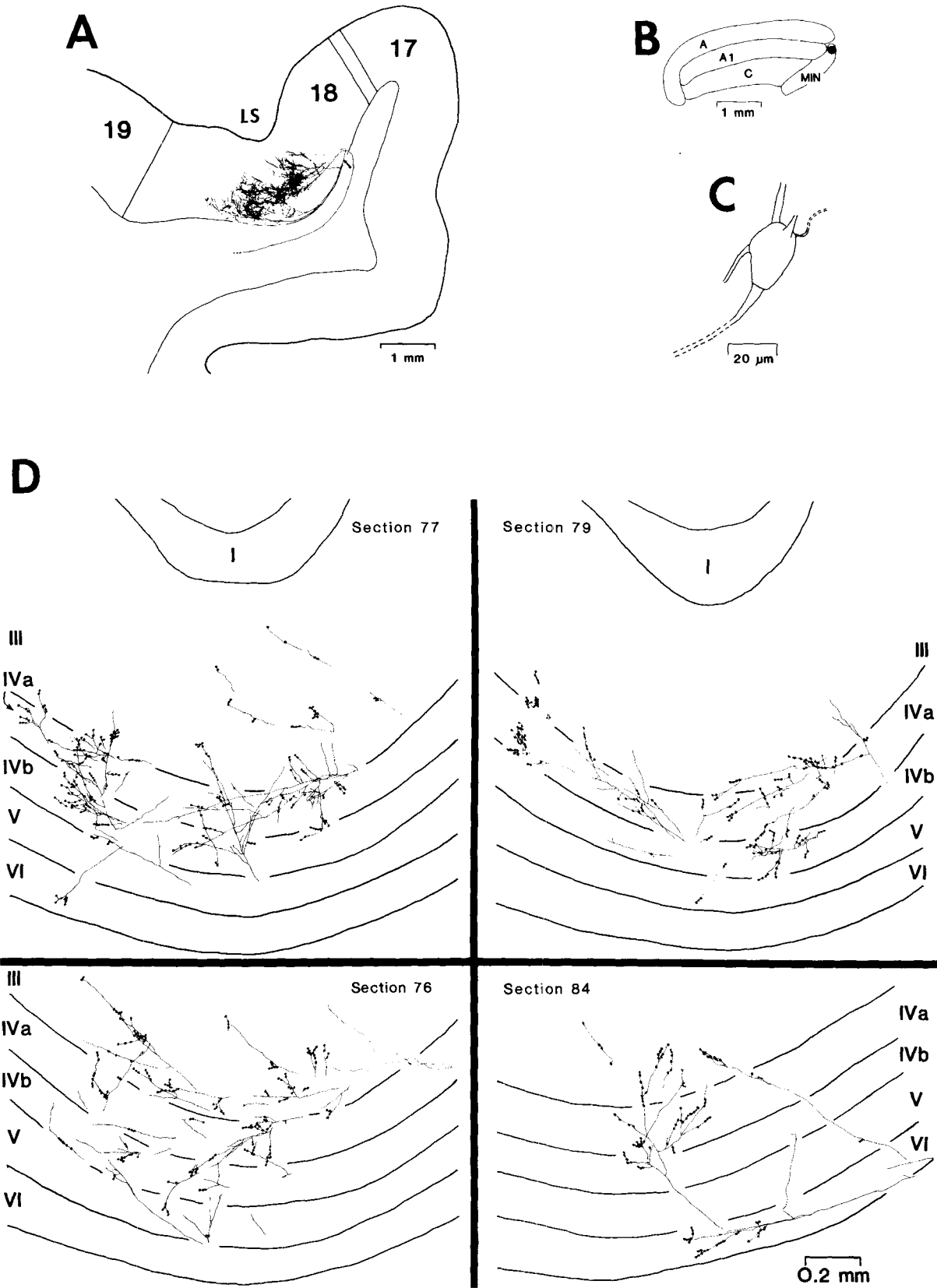


Figure 9

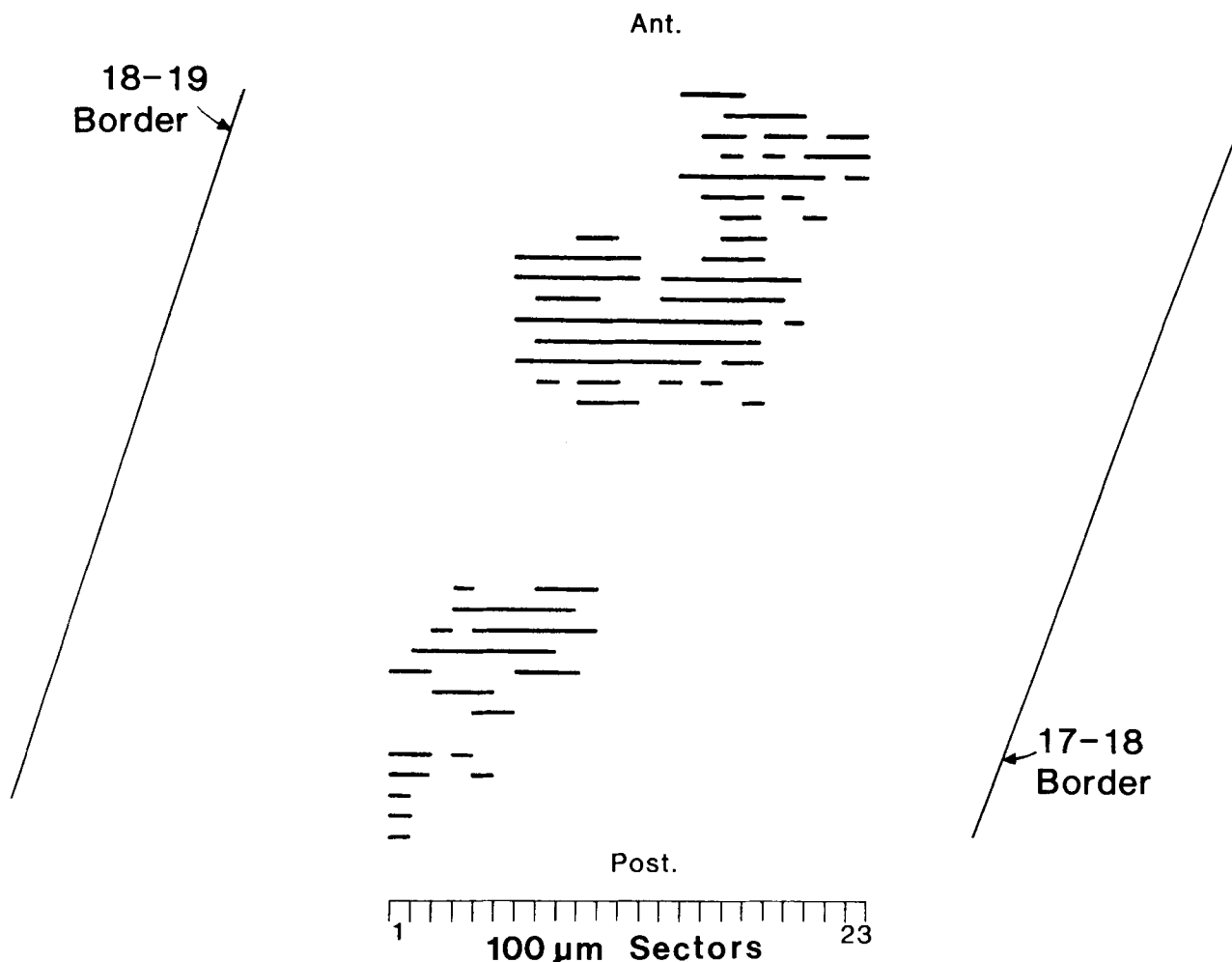


Fig. 10. Surface view plot of the layer III and IV arbor of the axon in Figure 9. Note the marked elongation of the field anteroposteriorly and the two separate clumps (total surface area, including gaps, was 2.8 mm^2). Conventions as in Figure 4D.

ties (and not Y-cells), the axon arose from a cell in the dorsal, magnocellular division of lamina C and projected only to area 18 (Fig. 11). Since X-cells are rare in the C-laminae and the above properties are clearly within the range of W-cells (Wilson et al. '76; Stanford et al., '83), we cannot unambiguously identify this axon's physiological class.

Fig. 9. Reconstruction of a Y-cell from the MIN that projected to area 18. The cell's nonlinear, off-center receptive field was 2° in center diameter, was driven through the contralateral eye, and was located 18° from the vertical meridian and 2° below the horizontal zero parallel. It had an (OX - OR) latency of 1.0 msec. A. Lower power drawing of the terminal field in the middle of area 18. The filled arrow points to the injection site, and the axon diameter was $2.0 \mu\text{m}$. Due to the great anteroposterior expanse of the terminal arbor, the reconstruction does not accurately show the height and location of all portions of the arbor relative to the pial surface. LS, lateral sulcus. B, C. Drawing of the lateral geniculate nucleus and backfilled cell ($357 \mu\text{m}^2$). Cell location in the MIN is indicated by the filled circle. D. Higher power reconstructions of the terminal arbor in four representative sections. Sections 76, 77, and 79 were from the posterior portion of the field. Section 84 was from the anterior portion. The axon terminated throughout layers IVb, IVa, and lower III and sparsely in layers V and VI.

Despite the classification problem, the cell's laminar projections offer an interesting comparison with the Y-cell projections to area 18. The axon was injected at a secondary collateral about 3 mm distal to the first branch point, and only the right-hand portion of the terminal field was well filled (Fig. 11A). Although weakly labeled collaterals emanating from the first branch point were traced to the lateral border of area 18, their boutons were not labeled (Fig. 11A). The well-labeled portion had the same laminar projections as the Y-cells located in laminae A and C. Of the 940 visible boutons, 890 (95%) were distributed to layer IVa and lower layer III. Only 50 boutons (5%) were found in layer IVb, and these were restricted to the upper half of that division. There was no visible input to layer VI. Like X- and Y-cell axons in areas 17 and 18, the boutons were strung along the finer processes that coursed horizontally and obliquely through the layers. Despite incomplete labeling of the left-hand portion of the arbor, it is clear that this axon, like the Y-cell axons in area 18, terminated over a very broad expanse of visual cortex and approached to within 1 mm of the 17/18 border. Thus visual information from this cell's

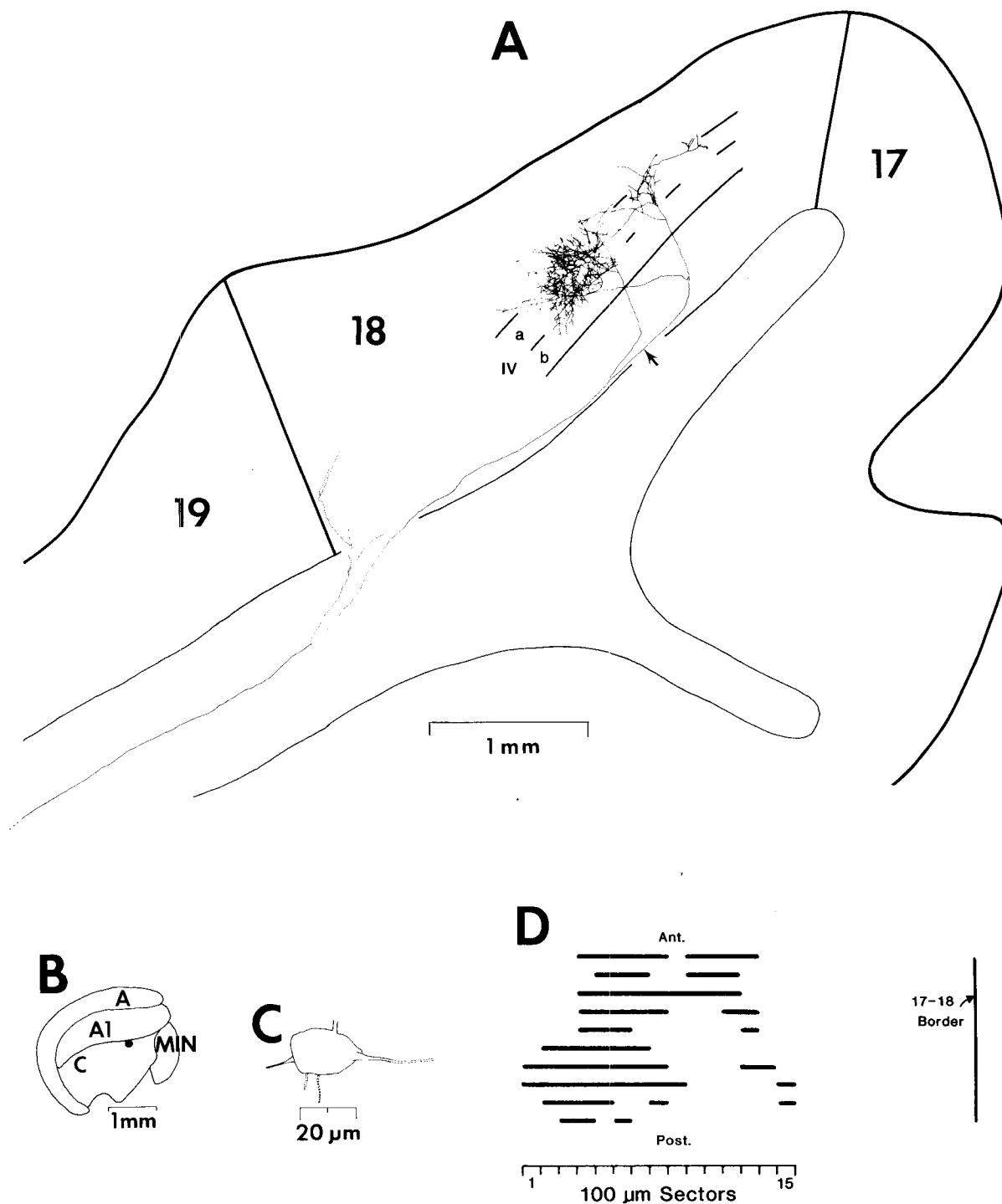


Fig. 11. Reconstruction of an unclassified, non-Y-cell in lamina C that projected to area 18. The cell had an on-center receptive field, 1° in center diameter, was driven through the contralateral eye, and was located 11° from the vertical meridian and 9° below the horizontal zero parallel. It responded linearly to counterphased sine wave gratings and was electrically activated from the optic chiasm at a latency of 2.6 msec (no radiation electrodes were used). A. Reconstruction of the axon and labeled portions of the terminal arbor. The well-labeled terminals in the medial half of area 18 were distributed primarily to layer IVa and lower layer III, with only a

small input to layer IVb. Another collateral, given off deep in white matter, innervated cortex at the lateral edge of area 18 but was too poorly labeled to follow further. The arrow points to the injection site in a secondary axon collateral and the parent axon diameter was $1.0 \mu\text{m}$. B, C. Drawing of the lateral geniculate nucleus and retrogradely filled cell body ($291 \mu\text{m}^2$), which was located near the dorsal edge of lamina C (filled circle in B). D. Surface view outline of the well-labeled, right-hand portion of the terminal arbor shown in A (about 0.7 mm^2 in area). Conventions as in Figure 4D.

small receptive field located 11° from the vertical meridian was distributed very widely in area 18. A surface view of the right-hand portion of the layer IV arbor is shown in Figure 11D. Its area was about 0.7 mm^2 .

Soma sizes, axon diameters, and numbers of boutons.

Figure 12 shows the size distribution of geniculate somata projecting to area 18, including other area-18-projecting Y-somata whose axons were not well-enough-labeled to analyze the sublaminar distribution of their boutons. Figure 12 also includes somata whose axons branched to innervate both areas 18 and 17. Soma sizes of the six Y-cells from laminae A and A1 ranged from 416 to $658 \mu\text{m}^2$ with a median of $610 \mu\text{m}^2$ (Fig. 12A). As noted in the previous paper (Fig. 20C of Humphrey et al., '85), these cells were significantly larger than the Y-cells projecting to area 17. Soma sizes of the C-lamina Y-cells ranged from 310 to $679 \mu\text{m}^2$ with a median of $450 \mu\text{m}^2$ (Fig. 12B) while those from the MIN ranged from 280 to $512 \mu\text{m}^2$ with a median of $420 \mu\text{m}^2$ (Fig. 12C).

As shown in the previous paper (Humphrey et al. '85), the diameter of the parent axons of Y-cells projecting to area 18 ranged from 1.5 to $2.5 \mu\text{m}$. This range completely overlapped those of the Y-cells projecting to area 17. The previous paper also revealed that, on average, the latency differences between optic chiasm and radiation stimuli were shorter for Y-cells that projected to area 18 than for those that projected to area 17. However, our present sample of well-labeled Y-cell parent axons is too small to determine whether those projecting to area 18 were, on average, larger than those projecting to 17.

Finally, the terminal arbors of Y-cell axons projecting to area 18 possessed 2,000 to 5,000 boutons, which was similar to the arbors of some X- and Y-cell axons in area 17. However, given the different arbor extents, the density of boutons/ mm^3 was significantly less in area 18 than in area 17.

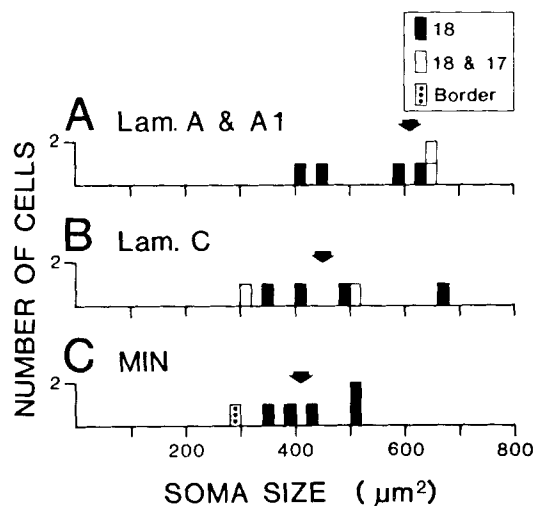


Fig. 12. Frequency histograms of the soma sizes of 18 retrogradely filled Y-cells that projected to area 18, to 17 and 18 by branching axons, or to the 17/18 border region. A. Six Y-cells from laminae A and A1. The open arrow indicates the median soma size of $610 \mu\text{m}^2$. This histogram is reproduced from Figure 20D of the previous paper. B. Six Y-cells from lamina C; median soma size was $450 \mu\text{m}^2$. C. Six Y-cells from the MIN; median soma size was $420 \mu\text{m}^2$.

Projections to and across the 17/18 border region

In the cat, the border between areas 17 and 18 is difficult to delineate sharply by cytoarchitectonic criteria. In the present study we have treated it as a transition zone about 200 to $400 \mu\text{m}$ wide (see Methods). Retinotopically, the zone represents the vertical meridian of the visual field plus a few degrees of the ipsilateral visual hemifield (Hubel and Wiesel, '65; Blakemore, '69; Innocenti, '80; Harvey, '80b; Tusa et al., '79; Albus and Beckmann, '80). This ipsilateral representation may derive from LGN input, since some LGN cells map the ipsilateral hemifield (Sanderson, '71; Lee et al., '84 and/or input from the opposite hemisphere which arrives through the corpus callosum (Hubel and Wiesel, '67; Innocenti, '80).

We recovered three well-labeled cells (two Y-cells, one X-cell) whose axons arborized in the 17/18 border zone. One Y-cell axon, which had a receptive field in the ipsilateral hemifield, terminated almost exclusively within the border zone. It was different from the other arbors we have seen either in area 18 or in area 17. The other two axons had receptive fields on the vertical meridian and in the contralateral hemifield and formed more characteristic, widespread arbors, and these arbors crossed the 17/18 border zone.

Projection to the 17/18 border zone. The projection of a Y-cell from lamina A to the 17/18 border zone is shown in Figure 13. The neuron's nonlinear, off-center receptive field had a center diameter of 0.8° and was located 7° in the ipsilateral visual hemifield. Its soma was $306 \mu\text{m}^2$ in area and was located near the dorsal, medial edge of lamina A (Fig. 13C,D). The fact that it was not located on the very medial border of the lamina is not inconsistent with the retinotopic maps of the LGN (Sanderson, '71; Lee et al., '84). The cell's axon was injected in a primary collateral that was darkly labeled (Fig. 13A). The other collateral was traced into layer IV, but it was too poorly labeled to see all of its boutons. Both collaterals arborized almost exclusively within the narrow region of the 17/18 border zone. Here they distributed about 830 boutons, primarily to layer IV and lower layer III (Fig. 13B). Layer IVb contained 165 boutons (20%), layer IVa 304 boutons (37%), and layer III 333 boutons (40%). There were also small inputs to layer V (15 boutons, 1.5%) and to layer VI (14 boutons, 1.5%). The axon's limited lateral spread is revealed more clearly in the surface view reconstruction of the layer IV arbor (Fig. 13E). It was $900 \mu\text{m}$ wide by $900 \mu\text{m}$ long and covered a total area of 0.4 mm^2 .

Projections across the 17/18 border zone. We recovered one X- and one Y-cell axon that arborized in and to either side of the 17/18 border zone. A reconstruction of the X-cell is shown in Figure 14. The linear cell had an off-center receptive field located on the vertical meridian. The axon was injected in a primary collateral (Fig. 14A), whose terminal field was well-labeled. Three other collaterals (not shown) were visible in the white matter but could not be traced into the gray matter. The injected collateral arborized within the 17/18 border zone (dashed lines in Fig. 14A) and 600 to $700 \mu\text{m}$ into the adjacent cortical areas. In all three of these regions, it terminated throughout layer IV and lower layer III as well as most of layer VI. A surface view of the layer IV arbor (Fig. 14D) reveals its shape and location more clearly. The single collateral gave rise to a relatively continuous field, about 1.2 mm^2 in area that, interestingly, ran more parallel than perpendicular to the

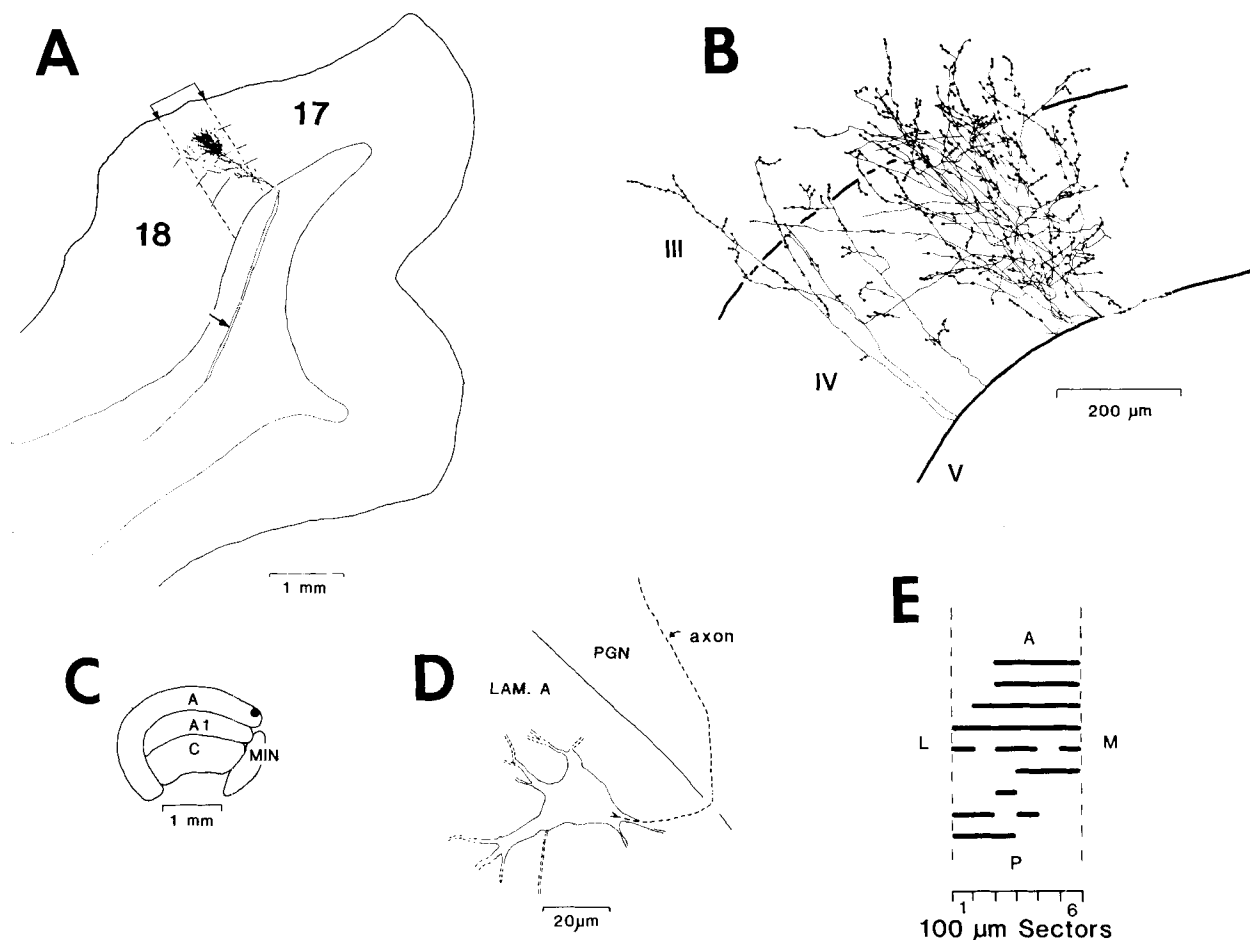


Fig. 13. Reconstruction of a Y-cell that had a receptive field in the ipsilateral visual hemifield and that projected to the 17/18 border region. The cell had a nonlinear, off-center receptive field, 0.8° in center diameter, was driven through the contralateral eye, and was located 7° ipsilateral to the vertical meridian and 8° below the horizontal zero parallel. It was activated from the optic chiasm at a latency of 1.9 msec. No radiation electrodes were used. A. Lower power drawing of the axon and the terminal field within the 17/18 border region (dashed lines). The filled arrow points to the injection site in a primary axon collateral, and the parent axon diameter

was $1.5 \mu\text{m}$. B. Higher power drawing of the terminals in layers IV and III. Note that the axon terminated throughout layer IV and lower layer III. Drawings of the axon collaterals were not extended into layer V. C, D. Drawing of the retrogradely labeled cell body ($306 \mu\text{m}^2$) and its location near the medial edge of lamina A (filled circle in C). Short portions of the cell's axon and primary and secondary dendrites were also labeled. E. Surface view outline of the cell's small arbor, 0.4 mm^2 in area, restricted to the border region (dashed lines). A, anterior, P, posterior, M, medial, L, lateral. Conventions as in Figure 4D.

17/18 border. The cell's soma was located in the upper one-third of lamina A (Fig. 14B). It was surprisingly large ($587 \mu\text{m}^2$) and had stout primary dendrites, suggestive of class 1 geniculate cell morphology. These features have previously been associated exclusively with Y-cells in the normal LGN of the cat. This suggests that this axon may be an unusual example of X-cell innervation, since none of the X-cell somata reported by Friedlander et al ('81) were this large.

A second example of a projection across the 17/18 border is illustrated in Figure 15. This was a Y-cell with a receptive field located 1° from the vertical meridian. The axon arose from a large ($642 \mu\text{m}^2$) soma in lamina A1 (Fig. 15B,C). Figure 15D shows three consecutive sections through the center of the arbor. In area 18, the axon terminated heavily within about $750 \mu\text{m}$ of the border zone. Its boutons were distributed throughout layer VI (not illustrated), layer IVa, and the lower half of layer III. A few boutons were distributed to the upper half of layer IVb, but for the most part the axon largely avoided layer IVb. Its

sublaminar projections in area 18 were similar to the axon from lamina A shown in Fig. 4. The axon then crossed medially through the 17/18 border zone and extended into area 17 for about $500 \mu\text{m}$. Here again the arbor was largely restricted to layers IVa and lower III, although it encroached deeper into layer IVb. The layer VI projection was present only in area 18. A surface view of the layer IV arbor (Fig. 15E) shows that the axon arborized over a relatively small region, 0.9 mm^2 in total area, and its long axis was roughly perpendicular to the 17/18 border. Note also that it narrowed in extent within the border region.

Projections via branching axons to areas 17 and 18

As shown above (Figs. 14,15), geniculate cells with receptive fields on or very near the vertical meridian have axon terminal fields that extend across the 17/18 border zone and innervate both areas 17 and 18. There is compelling anatomical and physiological evidence to suggest that some geniculate Y-cells with receptive fields farther from the

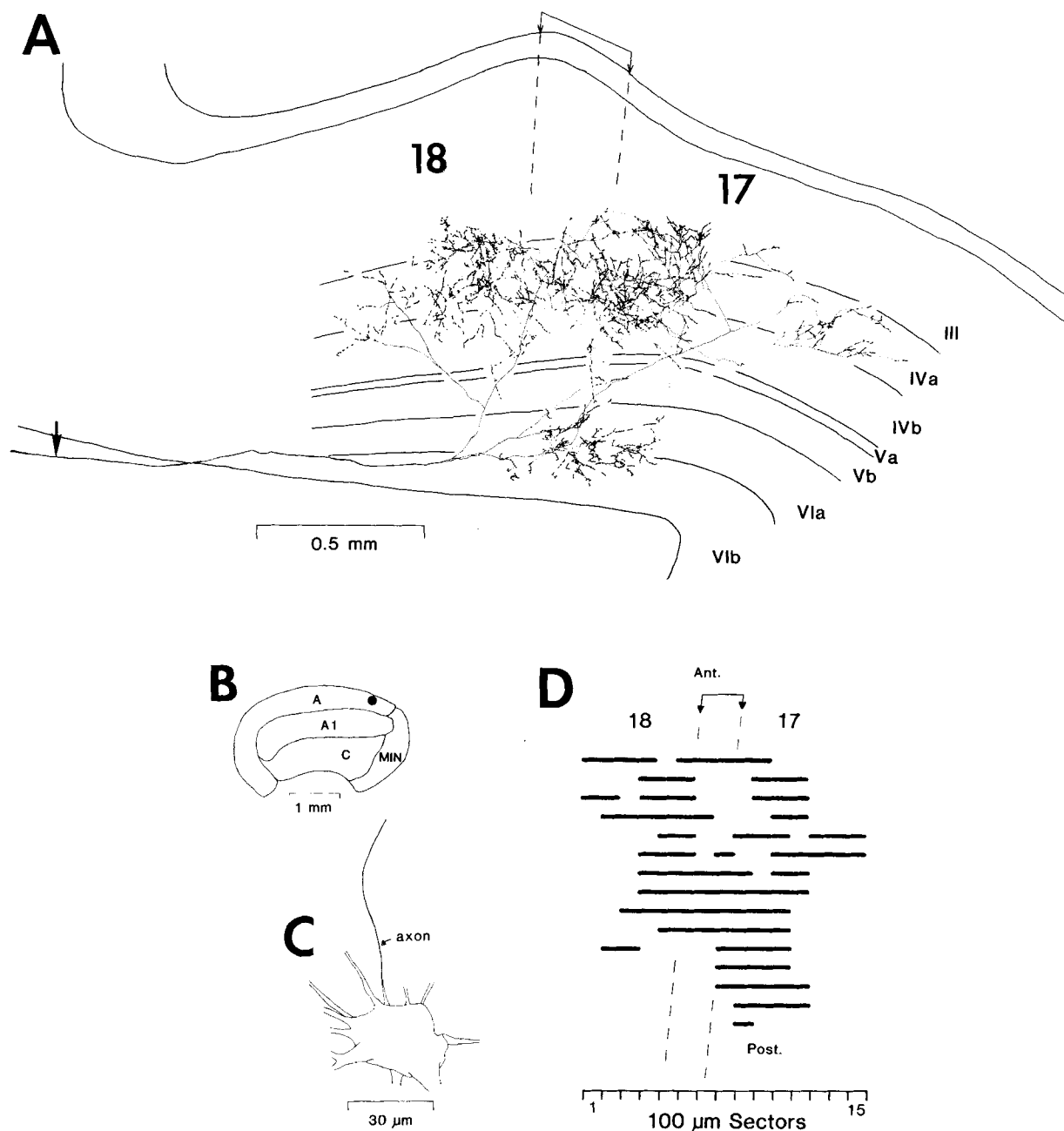


Fig. 14. Reconstruction of an X-cell that projected to areas 17 and 18 by crossing the border zone. The cell had a linear, off-center receptive field, 0.6° in center diameter, was driven through the contralateral eye, and was located on the vertical meridian 4° below the horizontal zero parallel. Its axon was activated from the optic chiasm with a latency of 2.6 msec. No radiation latency was obtained. A. Reconstruction of the portion of the terminal arbor that was labeled. The filled arrow in white matter points to the injection site in an axon collateral. The border region between areas 17

and 18 is indicated by the dashed lines enclosed by the arrows. The axon terminated throughout layer IV, lower layer III, and layer VI. Note the termination in area 18, area 17, and the border region. B, C. Drawing of the lateral geniculate nucleus and the large ($587 \mu\text{m}^2$), retrogradely filled cell body, located in lamina A (filled circle in B). D. Surface view outline of the layer III and IV terminal arbor, which was 1.2 mm^2 in area. The 17/18 border region is indicated by the dashed lines and brackets. Conventions as in Figure 4D.

vertical meridian project to areas 17 and 18 in separate, retinotopically homonymous zones via axons that branch (Stone and Dreher, '73; Geisert, '80; Bullier et al., '84). Thus, we expected to find a number of such axons distributing collaterals to both cortical regions, and we hoped to determine where in the white matter the branching occurs.

Figure 16 illustrates the bifurcating projection of one such Y-cell axon with a receptive field that was located 7°

from the vertical meridian. It was injected (filled arrow in Fig. 16) in a secondary collateral in the white matter and was not sufficiently well-filled to see the terminal fields in any detail. Despite this, a few bouton-laden collaterals are clearly visible in area 18 (open arrow) and in the dorsal, medial bank of area 17. The bifurcation point (asterisk) giving rise to the two different projections was about 1.5 mm ventral to the injection site, but still relatively high in

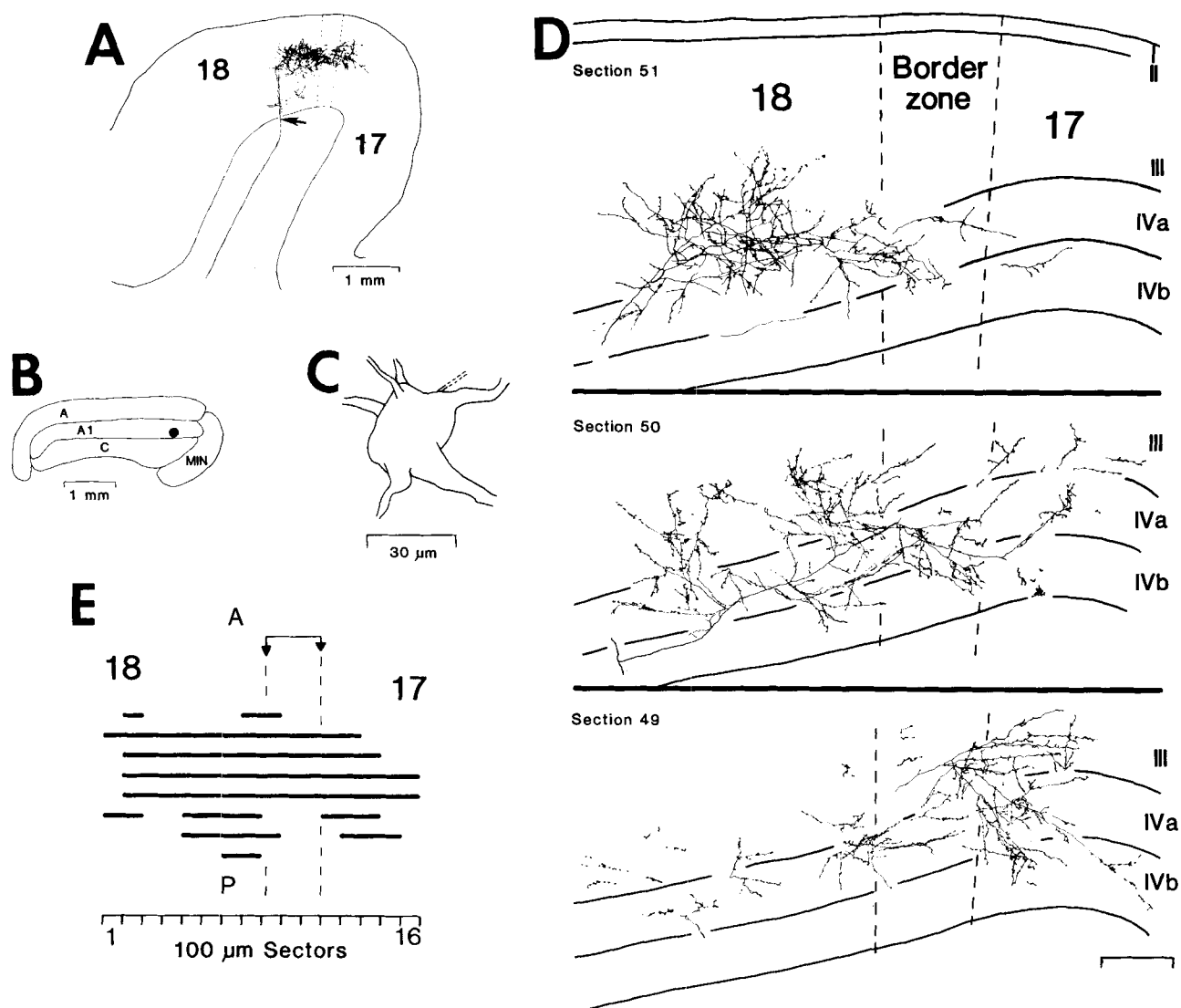


Fig. 15. Reconstruction of a Y-cell that projected to areas 17 and 18 by crossing the border region. The cell had a nonlinear, on-center receptive field, 0.8° in center diameter, was driven through the ipsilateral eye, and was located 1° from the vertical meridian and 3° below the horizontal zero parallel. Its (OX - OR) latency was 1.5 msec. A. Lower power drawing of the axon and terminal arbor. The axon diameter was $1.5 \mu\text{m}$, and the injection site is indicated by the arrow. Dashed lines indicate the 17/18 border region. The parent axon innervated area 18, terminating densely there, and then crossed medially to terminate in the border region and in area 17. B, C. Drawing of the lateral geniculate nucleus and retrogradely

filled cell body ($642 \mu\text{m}^2$) in lamina A1. D. Higher power reconstruction of three consecutive sections through the densest portion of the terminal arbor. The axon terminated primarily in layer IVa and the lower half of layer III, but also distributed some terminals in layer IVb, particularly in the border region and in area 17. Scale bar = $200 \mu\text{m}$. E. Surface view of the layer III and IV terminal arbor. Dashed lines bracketed by arrows mark the 17/18 border region. The arbor was distributed perpendicular to the border. Note that the arbor narrowed within the border region. The total surface area was 0.9 mm^2 . A, anterior, P, posterior. Conventions as in Figure 4D.

the white matter between areas 17 and 18. There was also another, deeper branch point about 4 mm farther down in the white matter, but one of its processes could not be followed into cortex. This cell's soma was not retrieved. We are confident the axon was from an LGN Y-cell due to its briskly responsive, concentric receptive field and its (OX - OR) latency of 1.1 msec (see Fig. 2 in Humphrey et al., '85).

Two other Y-cell axons, one from lamina A and one from lamina C, bifurcated to innervate areas 17 and 18 (not illustrated). For both axons, the major branch points occurred in the white matter within 1–3 mm of their terminal arbors. Thus, from our series of intra-axonal injections near

areas 17 and 18, only a minority of Y-cells appeared to innervate areas 17 and 18 via branching axons.

The above results indicated that the sites at which axons branch to innervate area 17 and 18 can occur relatively near their termination arbors. However, the possibility remained that other Y-cell axons might bifurcate much deeper in the white matter, or close to the LGN, and that these bifurcations may have been missed in the majority of our injected axons. Two experiments were performed to investigate these possibilities. In one, we injected nine axons 2 to 3 mm deeper than usual in the white matter beneath areas 17 and 18 and used a more sensitive chromagen (O-

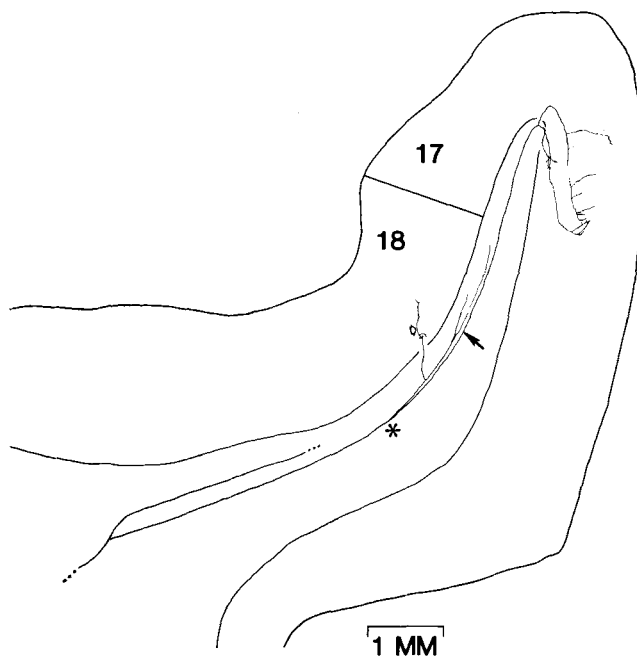


Fig. 16. Reconstruction of the visible portions of a Y-cell axon that bifurcated in the white matter to arborize in areas 17 and 18. The axon had an off-center receptive field, 0.9° in center diameter, was driven through the ipsilateral eye, and was located 7° from the vertical meridian and 5° below the horizontal zero parallel. It responded nonlinearly to counterphased gratings and had an (OX - OR) latency of 1.15 msec. Note that the bifurcation giving rise to the separate terminal arbors occurred relatively close to the area 18 arbor. The filled arrow indicates the location of the injection site, and the open arrow indicates small, bouton-laden collateral in area 18.

dianisidine; de Olmos, '77) to visualize the parent axons over greater distances than is generally possible using diaminobenzidine (DAB). Five of the axons were sufficiently well-labeled to follow them dorsally to their terminations in cortex and ventrally very deep in the white matter, from the region lateral and below the lateral sulcus to the region below the suprasylvian sulcus. This corresponds to a total retrograde distance of 6 to 16 mm. No axon was ever observed to bifurcate below the region directly beneath the base of the lateral sulcus. Three axons arose from somata in the A-laminae and projected only to area 17. One axon from the MIN projected only to area 18. Only one additional axon, from lamina C, projected to both cortical areas and its major bifurcation points occurred relatively high in cortex. Figure 17 shows a reconstruction of this Y-cell axon whose center diameter was located 22° from the vertical meridian. Its soma ($310 \mu\text{m}^2$ in area) is illustrated in Figure 17C. The first bifurcation point occurred near the injection site (filled arrow in Fig. 17A). (We followed the retrogradely filled parent axon for roughly 16 mm below the injection site to near the base of the suprasylvian sulcus, and we observed no further branching). At the first branch point (ventral asterisk) a thick collateral (about $2.5 \mu\text{m}$ in diameter) traveled dorsally toward the lateral portion of area 18 while the other collateral, about half that diameter, projected medially to innervate area 17 in the appropriate retinotopic location (Tusa et al., '78). Two other bifurcations occurred closer to area 18 (two dorsal asterisks), with their major projections being to the lateral portion of area 18. However, one of the collaterals proceeded dorsomedially in

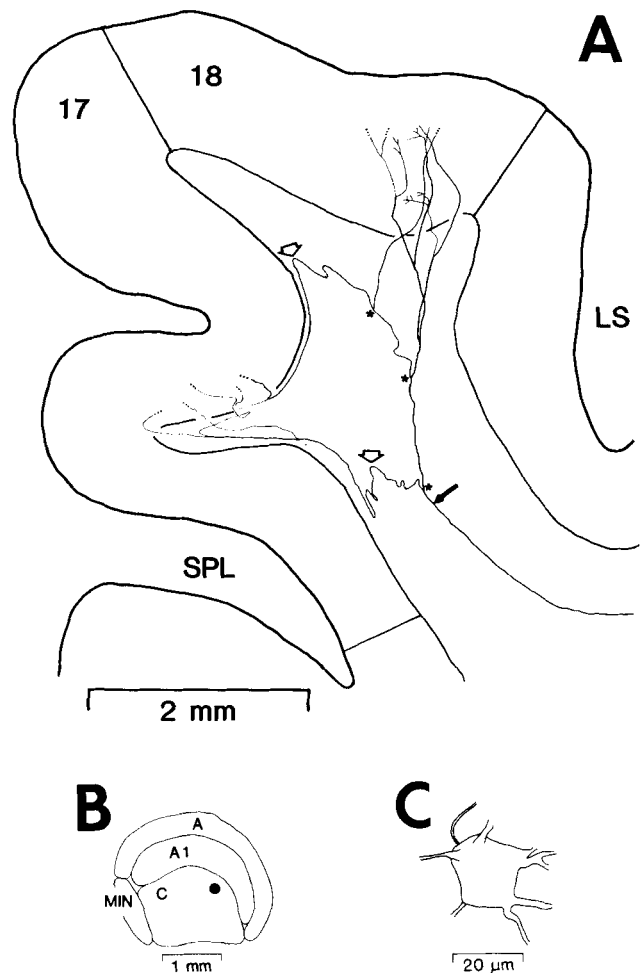


Fig. 17. Reconstruction of a Y-cell axon that bifurcated in the white matter to project to areas 17 and 18. The cell had an off-center diameter receptive field, 4.5° in center diameter, was driven through the contralateral eye and was located 22° from the vertical meridian and 23° below the horizontal zero parallel. Its axon was activated from the optic chiasm with a latency of 1.4 msec. No radiation electrodes were used. A. Reconstruction of the axon. The filled arrow points to the injection site just ventral to the first bifurcation point (lowest asterisk). The two dorsal asterisks indicate two additional bifurcation points. The upper open arrow notes the location where a collateral beneath area 17 reversed its trajectory and traveled ventrally to innervate area 17 deep on the medial bank. The lower open arrow indicates the other major collateral which projected to area 17. Note the highly circuitous routes taken by both major collaterals projecting to area 17. The terminal fields in cortex were not labeled sufficiently well to determine their laminar projections, although the overall projection to area 18 appeared to be larger than that to area 17 (not illustrated in detail). LS, lateral sulcus, SPL, splenial sulcus. B, C. Location and drawing of the retrogradely filled soma ($310 \mu\text{m}^2$) in lamina C of the lateral geniculate nucleus.

the white matter and crossed over to the area 17 side. Here it reversed direction (upper open arrow), and traveled ventrally for over 1 mm, just beneath layer VI, to finally arborize in the same region as the other major collateral to area 17.

Figure 17 illustrates two important points. First, for this Y-cell, the major branch points for the collaterals that projected to areas 17 and 18 occur high in the white matter, clearly above the level of the lateral sulcus and within 2 to 3 mm of their terminal arbors. The second point, which is

of some developmental interest, is that both major collaterals that project to area 17 took a tortuous, circuitous route to their final destinations. As with the Y-cell axon illustrated in Figure 8A of the previous paper (Humphrey et al., '85), we interpret these curious axon trajectories in the adult as evidence of target-finding behavior in the developing axons as they grew into cortex.

In the second experiment, we injected 7 Y-cell axons at a point 1 to 4 mm above the LGN and reacted the tissue with O-dianisidine to determine whether major bifurcations occur near the LGN. These included four neurons from the A-laminae, two from lamina C, and one from the MIN. Three of these (two from lamina A1 and one from lamina C) were traced at least up to the level of the middle suprasylvian sulcus in cortex, 10 to 12 mm from the LGN. When corrected for tissue shrinkage, which we estimate to be about 15%, this represents a total anterograde distance of up to 14 mm. Other than the fine, bouton-laden collaterals which arborized in the perigeniculate nucleus, we never observed any bifurcations of these axons in or near the LGN or in the internal capsule. However, for one of these Y-cells,

shown in Figure 18, a bifurcation occurred in cortex. The cell's soma was located in lower lamina A1 (Fig. 18C). Its axon rose dorsally through the LGN and crossed medially above lamina A, giving off numerous fine collaterals that were restricted to the perigeniculate nucleus (Fig. 18C). The parent axon then traveled without further branching through the internal capsule (Fig. 18B) and up to the base of the lateral sulcus (Fig. 18A). Here, the axon branched in the white matter (open arrow in Fig. 18A), with one collateral projecting toward area 17 and the other projecting toward area 18. Unfortunately by this point the collaterals were too poorly labeled to trace them further and we cannot be sure that they actually terminated in different cortical areas. Given the location of the soma (in lamina A1), the likely termination site is area 17 and/or area 18. Further, a comparison of the location of the branch point with the published maps of areas 17 and 18 indicates that the branch point was located within 5 mm of the axon's termination site(s) in cortex. We are confident that we did not miss any other collaterals in the better-labeled portions of the axon located deeper in the white matter. No bifurcations were seen in the other two Y-cell axons that were traced nearly this far into cortex.

The two experiments in which we actively searched for bifurcating Y-cell axons, coupled with the results of all of our previous injections, suggest the following two conclusions. First, some Y-cells project to areas 17 and 18 by axons that branch (Stone and Dreher, '73; Geisert, '80; Bullier et al., '84). Second, the branch points occur in the white matter beneath areas 17 and 18 at a point directly below the base of the lateral sulcus or higher. The branch points probably do not occur below this level. With knowledge of the locations of these branch points, we compared the number of bifurcating and nonbifurcating Y-cell axons in this

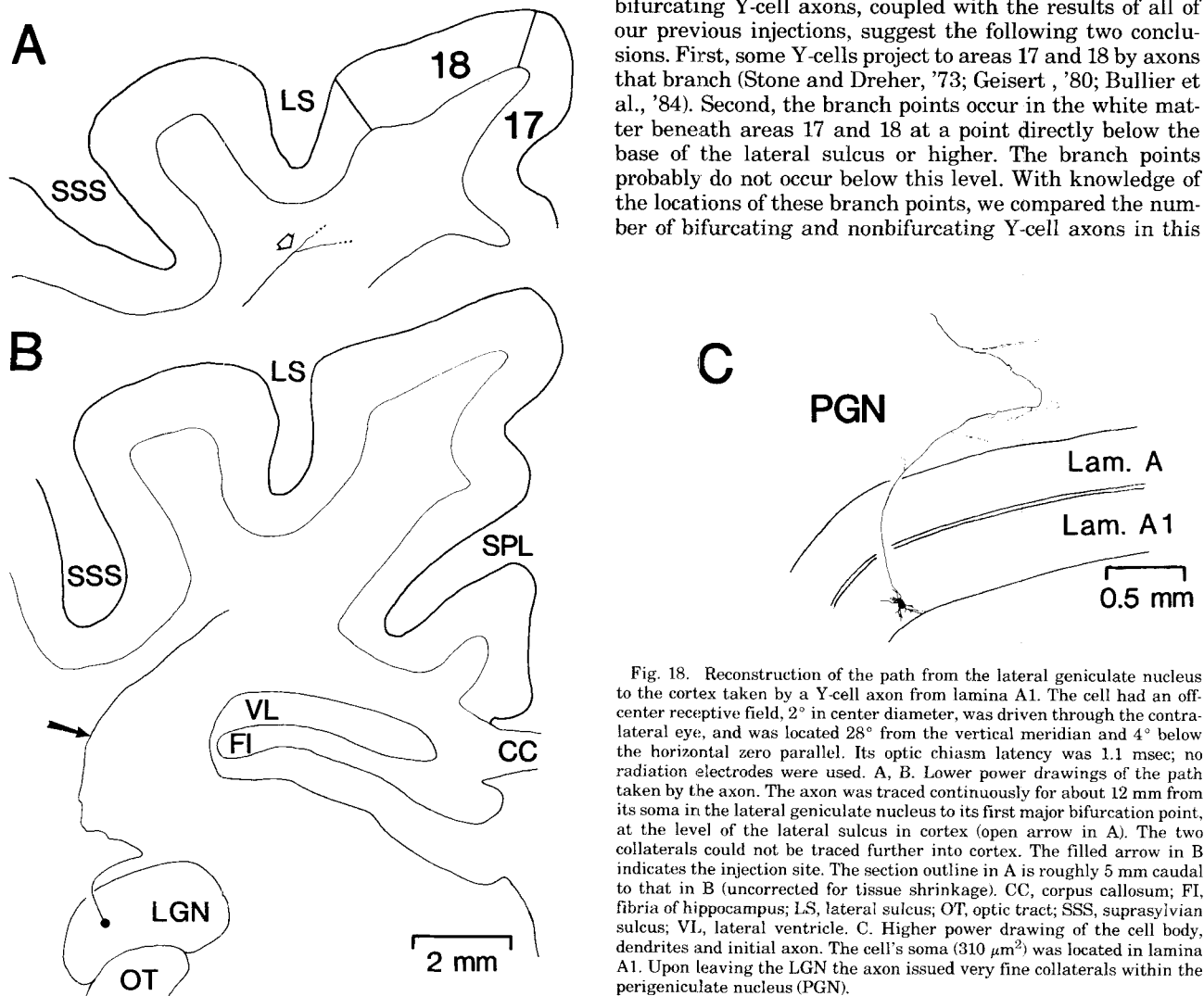


Fig. 18. Reconstruction of the path from the lateral geniculate nucleus to the cortex taken by a Y-cell axon from lamina A1. The cell had an off-center receptive field, 2° in center diameter, was driven through the contralateral eye, and was located 28° from the vertical meridian and 4° below the horizontal zero parallel. Its optic chiasm latency was 1.1 msec; no radiation electrodes were used. A, B. Lower power drawings of the path taken by the axon. The axon was traced continuously for about 12 mm from its soma in the lateral geniculate nucleus to its first major bifurcation point, at the level of the lateral sulcus in cortex (open arrow in A). The two collaterals could not be traced further into cortex. The filled arrow in B indicates the injection site. The section outline in A is roughly 5 mm caudal to that in B (uncorrected for tissue shrinkage). CC, corpus callosum; FI, fibria of hippocampus; LS, lateral sulcus; OT, optic tract; SSS, suprasylvian sulcus; VL, lateral ventricle. C. Higher power drawing of the cell body, dendrites and initial axon. The cell's soma ($310 \mu\text{m}^2$) was located in lamina A1. Upon leaving the LGN the axon issued very fine collaterals within the perigeniculate nucleus (PGN).

and in the previous study using only those Y-cells whose parent axons could be traced at least back to the level of the lateral sulcus. Of the 54 Y-cell axons traced to area 17 or 18, 18 axons could be traced retrogradely this far. Among the 12 Y-cell axons with somata in laminae A or A1, two projected via bifurcating collaterals to areas 17 and 18, nine projected to area 17 alone, and one projected only to area 18. Two axons out of four well-filled lamina C axons projected to both cortical areas; the other two projected only to area 18. Each of two MIN Y-cell axons projected only to area 18.

DISCUSSION

Four major conclusions arise from this study. First, Y-cells that project to area 18 arborize largely in layers III and IVa and appear to have very little input to layer IVb. Second, their terminal fields spread widely and asymmetrically over broad expanses of area 18. Third, only a minority of geniculate Y-cell axons project to both areas 17 and 18 by branching axons; when these branches occur, they are within a few millimeters of their termination sites in these two cortical areas. Fourth, as prior physiological studies have argued, area 18 receives little or no X-cell input, and X-cells project exclusively to area 17 or the 17/18 border region. The significance of each conclusion will be discussed below.

Laminar projections to area 18

We were surprised to find that the Y-cell projections from the A-laminae and lamina C largely avoided layer IVb and layer VI and terminated extensively throughout layer IVa and much of the lower half of layer III. Previous anatomical studies using transport of radioactive labels (Rosenquist et al., '74; LeVay and Gilbert, '76) concluded that cells in these geniculate laminae terminate throughout layer IV and rise only into the bottom (100 μ m) of layer III, much as many A-laminae cells do in area 17. The difference between our results, based on single afferents, and the earlier results, based on large groups of afferents, is not due to differences in assigning laminar borders in cortex (see Methods).

Within area 17, we found that Y-cells located near the outer edges of the A-laminae projected almost exclusively to layer IVa and the bottom of layer III while those located near the centers of the A-laminae projected extensively into layer IVb as well. Although our sample of area 18 projecting Y-cells from the A-laminae is small, all three Y-cell axons that projected mainly to layer IVa and lower layer III arose from somata in the ventral one-third of lamina A. Their projections are thus consistent with the area 17 projections of Y-cells. A larger sample is now needed to determine the laminar projections in area 18 of Y-cells located in the central one-third of the A-laminae. Our one MIN cell did project extensively throughout layer IV and the lower half of layer III, but a larger sample is needed to determine how representative this is of the MIN Y-cell projections. To our knowledge, there have been no degeneration or transport studies restricted to the MIN that reveal the sublaminar projections of MIN cells in area 18. It is also possible that the primary input to layer IVb of area 18 arises from W-cells in the parvocellular C-laminae but the axons of W-cells seem to be too small for our electrodes to record and impale. LeVay and Gilbert ('76) injected ^3H -proline into the C-laminae and reported label throughout both divisions of layer IV (and the upper half of layer I). Perhaps layers IVa and IVb receive their C-laminae projections from the mag-

nocellular and parvocellular divisions, respectively. Additional studies are necessary to test this possibility.

Our results reveal that Y-cells in all divisions of the LGN have substantial projections to the lower half of layer III. This projection is denser and rises higher (up to 400 μ m or more) into the layer than previously suspected. Also, it is far greater than the projection from A-laminae Y-cells to layer III of area 17; that projection generally rises no higher than 200 μ m into layer III. These anatomical data are consistent with the physiological data of Harvey ('80a), who reported that more than half of the cells recorded extracellularly in layers IVa and lower III (IIIb) of area 18 were monosynaptically activated via fast-conducting (i.e., Y-cell) geniculate axons, and the majority of these had S-type receptive fields. Harvey ('80a) also reported that less than 40% of the cells recorded in layer IVb were monosynaptically activated. The majority of the layer IVb cells were di- or polysynaptically activated and had larger, C-type receptive fields. These physiological findings reinforce our evidence that layer IVb of area 18 has a different source, or pattern, of geniculate input than do layers IVa and lower III.

The geniculate input to layer VI is much less in area 18 than in area 17. Less than 5% of each Y-cell's boutons in area 18 were distributed in layer VI, whereas up to 25% of the Y-cell boutons in area 17 occupied this layer. In addition, no region of the lateral geniculate nucleus (viz., A- vs. C-laminae) had a higher proportion of input to layer VI than any other. Our findings confirm, at the single cell level, previous tracer studies that reported a smaller projection to layer VI of area 18 than to area 17 (Rosenquist et al., '74; LeVay and Gilbert, '76). Since the corticogeniculate pathways originate in layer VI, this difference in geniculocortical input parallels the weaker corticogeniculate projection arising from area 18 than from area 17 (Gilbert and Kelly, '75; Updyke, '75).

Lateral spread of area 18 arbors

The extents of Y-cell terminal arbors in area 18 were quite large, two to three times those of X- and Y-cell arbors in area 17. Including terminal-free gaps within the arbors, the layer IV surface areas of our well-labeled axons averaged about 2.4 mm², ranging from 2.0 to 2.8 mm². There seem to be no major differences in the extents of the arbors arising from cells in different portions of the lateral geniculate nucleus (viz., A- vs. C-laminae), but our small sample makes this conclusion tentative.

While the absolute sizes of the arbors were large compared to those in area 17, their breadth relative to the smaller extent of area 18 was even greater. For instance, one axon's arbor occupied 70% of the mediolateral extent of area 18 (Fig. 4D). The others spread over similar absolute distances anteroposteriorly. This may have significant implications for the divergence and convergence of visual information onto cells in area 18. Information about a stimulus located within a small area of visual space (i.e., a geniculate cell's receptive field) is distributed across a large region of area 18 and thus to a large number of widely separated cells. Furthermore, cells within a small (e.g., 100 μ m) region of cortex probably receive converging information from a relatively large region of the visual field. Unfortunately, the size of this visual region cannot be estimated easily, since it depends on determining the degree to which the axon's receptive field and terminal arbor are out of register with the local retinotopic map in cortex. We did not

determine the retinotopic map in each of our animals, and substantial variability in the map in area 18 (Donaldson and Whitteridge, '77; Tusa et al., '79; Albus and Beckmann, '80) makes it difficult to predict. Also, there have been no published accounts of a detailed survey of receptive field scatter among neighboring neurons in area 18. We were able to show that the large size of arbors was actually consistent with this scatter for area 17 (see preceding paper: Humphrey et al., '85), but we cannot do the same for the area 18 arbors. However, given the large receptive fields in area 18 compared to those in area 17, the scatter, and thus the size of the "spatial subunit" (Albus, '75), must be substantially greater in area 18.

Many of these terminal arbors were highly asymmetric, with an anteroposterior axis that was two to four times longer than the mediolateral axis (Figs. 5E, 8, 10). These asymmetries may be due partly to the arbors skipping across ocular dominance columns which apparently run mediolaterally across area 18 (Shatz et al., '77). However, even when the gaps that may reflect this skipping are removed, clear asymmetries remain. These strong asymmetries among single axons have a correlate in the anisotropic organization of the retinotopic map in area 18. Fine-grain retinotopic mapping techniques (Cynader et al., '83) have revealed that iso-elevation contour lines in area 18 are spread about twice as far apart as are iso-azimuth lines for equal degrees of distance in the visual field. Since the elevation lines run roughly mediolaterally across cortex near the representation of the vertical meridian, there is a "stretching" of the cortical magnification in the anteroposterior dimension. This strong anisotropy is also visible in portions of other published maps of area 18 (Tusa et al., '79; Albus and Beckmann, '80). A less accentuated anisotropy emphasizing elevation is also visible in the lateral geniculate nucleus (Fig. 8 of Sanderson, '71).

Since these anisotropies in area 18 may be a reflection of Y-cell input, one might expect to see a correlate of this in the density distribution of alpha cells (i.e., Y-cells) in the retina. That is, one might expect to find a greater alpha cell density along the vertical meridian than along the horizontal midline of the retina. The opposite seems to be the case (e.g., see Fig. 16 of Hughes, '81). However, Bowling and Michael ('84) showed that retinal Y-cell axons innervate the A-laminae in elliptically shaped terminal arbors that are about 1.3 times longer along the anteroposterior axis than along the mediolateral axis. This may compensate for the alpha ganglion cell distribution in the retina and slightly accentuate the mapping of elevations in the visual field. We have shown that similar asymmetries in Y-cell terminal arbors are present in area 18. Thus, the strong magnification of visual field elevations in portions of area 18 may reflect the concatenated effects of asymmetric terminal arbors in the lateral geniculate nucleus and in area 18. Interestingly, the anisotropies in the retinotopic maps of these two areas are not obvious in the maps of area 17 (Tusa et al., '79), and we do not see any strong asymmetries in the terminal arbors of X- and Y-cell axons there (Humphrey et al., '85). This lends further support to our conclusion that the area 18 map reflects the anisotropic Y-cell arbors that innervate it. Thus, the retinotopic maps of various cortical areas may be dependent not only upon differences in the spatial density distributions in the retina of the functional cell classes but also in the shapes and extents of the geniculate afferents innervating each cortical area. In area 18, the geniculate terminal arbors may be much

more important than the retinal ganglion cell distribution in establishing the retinotopic map.

Bifurcating projections to areas 17 and 18

Garey and Powell ('67) by using degeneration techniques, were the first to provide anatomical evidence that some cells in the LGN project to areas 17 and 18 by branching axons. Stone and Dreher ('73) subsequently determined that these were Y-cells on the basis of electrophysiological criteria. Geisert ('80) and Bullier et al. ('84) used retrograde tracers to directly visualize the somata of these cells. We have confirmed the existence of Y-cells with branching axons by directly visualizing the branch points and the terminal fields in the separate cortical areas. Further, we conclude that most or all of these branch points occur beneath areas 17 and 18 within a few (1 to 5) mm of their terminal arbors and at or above the level of the base of the lateral sulcus.

An important question concerns the proportion of Y-cells that projects to area 17 only, to area 18 only, or to both areas. Stone and Dreher ('73) concluded that most, or all, Y-cells in the A-laminae project to both areas by branching axons, a conclusion our data do not support. Geisert ('80) estimated that 70% of the A-laminae neurons, both X- and Y-cells, project to area 17 only, less than 1% project to area 18 only, and 10% project to both areas. If nearly every A-laminae Y-cell projected to both areas (Stone and Dreher, '73), then Geisert's data suggest that only about 15% of the A-laminae neurons are Y-cells and that perhaps 65 to 70% are X-cells. However, other data (LeVay and Ferster, '77; Friedlander et al., '81) suggest that the A-laminae include an X- to Y-cell ratio of no more than 2 to 1, depending on the number of interneurons present. If Geisert's ('80) data are interpreted in the context of Y-cells representing one-third to one-half of the A-laminae relay neurons, then two-thirds to three-fourths of the Y-cells project to area 17 only. Our results and those of Bullier et al. ('84) are in general agreement with this interpretation. Thus, area 17 not only receives X-cell input but also a substantial and dedicated Y-cell input that does not project to other cortical areas. It is not yet clear how many Y-cells from the A-laminae project by branching axons to areas 17 and 18 and how many project only to area 18. Geisert concluded that up to 90% of the cells projecting to area 18 also branched to innervate area 17. Bullier et al. ('84) estimated that only about 50% of such cells did so. Our sample of area-18-projecting axons is too small to resolve this issue. Finally, some (two out of four) of our Y-cells in lamina C also projected to both 17 and 18 via branching axons. This is in agreement with other studies (Geisert, '80; Bullier et al., '84) which demonstrated higher proportions of bifurcating Y-cells in lamina C than in the A-laminae.

Lack of X-cell input to area 18

Prior physiological studies have demonstrated that X-cell inputs are largely limited to area 17, whereas Y-cell inputs are distributed to areas 17 and 18 (Stone and Dreher, '73; Mitzdorf and Singer, '78; Harvey, '80a; and many others). Our data from this and the prior paper (Humphrey et al., '85) offer morphological support for this. Excluding the 17/18 border zone, which receives some X-cell input that spills across into areas 17 and 18, we found no unambiguous evidence of X-cell inputs to area 18. Of the 23 axons innervating area 18 (including 21 where diaminobenzidine was used as the chromogen and two where O-dianisidine was

used), 22 were Y-cells. Only one unclassified axon could possibly have been an X-cell, but it arose from a soma in the C-laminae and could have been a W-cell. On the other hand, every one of the 35 X-cell axons from this and the preceding paper (Humphrey et al., '85) that could be traced into the gray matter innervated area 17 or the 17/18 border region. It seems reasonable to conclude that geniculocortical X-cell input is focused to area 17, whereas Y-cell input is not so limited in cortical extent.

Relative extent of the X- and Y-cell pathways

The relative size of the X- and Y-cell pathways seems to vary dramatically with various levels of the pathways. For instance, in retina the X- to Y-cell ratio is generally greater than 10:1, depending on eccentricity (Fukuda and Stone, '74; Cleland et al., '75; Levick, '75; Wässle et al., '75; Stone, '78), but in the lateral geniculate nucleus it is closer to 1:1 when all geniculate divisions are considered (LeVay and Ferster, '77; Friedlander et al., '81). This amplification of Y-cells relative to X-cells between retina and lateral geniculate nucleus seems to result from differences in the sizes of retinogeniculate arbors (Bowling and Michael, '80, '84; Sur and Sherman, '82).

Our data suggest a similar relative amplification of the Y-cell pathway to cortex. Within area 17, Y-cell arbors are larger and typically contain more boutons than do X-cell arbors. Furthermore, the number of synapses per bouton appears to be higher for Y- than for X-cell arbors (Winfield and Powell, '83). The X- to Y-cell ratio in the A-laminae is 1:1 or 2:1 (depending upon what percentage of the smaller neurons, which are all X-cells, are interneurons (cf. LeVay and Ferster, '77; Friedlander et al., '81). This implies that there are as many or more Y-cell synapses innervating area 17 as there are X-cell synapses.

Some of the Y-cell axons innervating area 17 branch to innervate area 18 as well, but axons of X-cells produce little or no extrastriate projection. Thus, in terms of the extent of geniculocortical innervation patterns, it follows that visual cortex is relatively dominated by the Y-cell pathway compared to the X-cell pathway.

This interpretation of the structural organization of the X- and Y-cell pathways leads to a surprising consequence. The majority of retinal ganglion cells involved in geniculocortical innervation are the X-cells. They have access through geniculocortical inputs to a relatively small volume of cortical tissue (i.e., some of the cells of area 17). The small minority of Y-cells in the retina come to dominate the geniculocortical projection. We argue that this is achieved because Y-cell arbors, both retinogeniculate and geniculocortical, are considerably larger than are the X-cell arbors.

The functional significance of this organization may be the following (reviewed in Sherman, '84). On the one hand, the Y-cell pathway seems mostly involved in the analysis of lower spatial frequencies (Lehmkuhle et al., '80; So and Shapley, '81; Troy, '83), which seem particularly important to basic spatial vision (Ginsburg, '78; Hess and Howell, '78; Hess and Woo, '78; Lehmkuhle et al., '82). To encode the lower spatial frequencies requires fewer peripheral elements, and thus the Y-cell pathway peripherally (i.e., in retina) is relatively small. However, the importance of this to pattern vision implies that considerable cortex must be devoted to the analysis of these lower frequencies. On the other hand, the X-cell pathway seems largely involved in the analysis of higher spatial frequencies (Lehmkuhle et al., '80; So and Shapley, '81; Troy, '83), which are important in maximizing spatial acuity but are less important in basic

form analysis (Ginsburg, '78; Hess and Howell, '78; Hess and Woo, '78; Lehmkuhle et al., '82). To encode the higher frequencies requires proportionately more peripheral (i.e., retinal) elements, but the secondary importance of higher frequencies to pattern vision implies that less cortex need be devoted to their analysis.

The above is an hypothesis to be tested of the organization of the X- and Y-cell pathways and of the functional significance of this organization. The data present in this and the previous paper (Humphrey et al., '85), which include evidence that geniculocortical Y-cell arbors contain more boutons and synapses than do X-cell arbors, are consistent with this model. Clearly, however, much more data, including an analysis of the relative numbers and functional properties of cortical neurons innervated by the X- and Y-cells, are needed to understand the functional implications of differences between X- and Y-cell innervation patterns within cortex.

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