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Retinal Projections and Functional Architecture of Cortical Areas 17 and 18 in the Tyrosinase-negative Albino Cat[1]

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Abstract

The visual field representation and functional architecture of cortical areas 17 and 18 in albino cats were studied. In the same animals the distributions of ipsilaterally and contralaterally projecting retinal ganglion cells were determined by injecting horseradish peroxidase into the dorsal lateral geniculate nucleus or optic tract. All cats were tyrosinase-negative albinos (cc), not deaf white cats (*W*).

The proportion of ipsilaterally projecting ganglion cells in the temporal retina of the albino cat was found to be much smaller than in the normal cat or in the Siamese cat. In the albino cat less than 5% of ganglion cells in temporal retina project ipsilaterally.

Recordings from areas 17 and 18 provided evidence of a substantial representation of the ipsilateral hemifield in albino visual cortex; cells representing the contralateral and ipsilateral hemifields were often segregated into alternating zones in area 17 and were always segregated in area 18.

Cells recorded at the borders of zones representing the ipsilateral and contralateral hemifields often had abnormal properties. Some border cells had two receptive fields separated by as much as 60° of azimuth; one field subserved the contralateral hemifield (contralateral nasal retina) and the other subserved the mirror-symmetric part of ipsilateral hemifield (contralateral temporal retina). Receptive fields of cells subserving the two hemifields did not differ in size. The preferred orientations, preferred velocities, and other characteristics of the two fields were approximately the same; preferred orientation changed gradually and systematically across the borders of zones representing the two hemifields.

Our results indicate that afferents representing nasal and temporal regions of retina of the same eye can segregate and form "hemiretina" domains in albino visual cortex. These afferents can also converge upon individual cortical cells in a fashion reminiscent of convergence of afferents from the two eyes upon binocular cells in the normal cortex. The organization of albino visual cortex is therefore different from the organization of Siamese visual cortex. This may be because, in the albino cat but not the Siamese cat, nearly all cells in temporal retina project contralaterally; afferents representing contralateral temporal retina are not at a significant competitive disadvantage in the albino.

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In Siamese cats (Guillery, 1969) and in albino mammals in general (Lund, 1965; Sheridan, 1965; Creel, 1971a, b; Guillery et al., 1984), the normal patterns of retinal ganglion cell projection are disrupted. In particular, many of the ganglion cells in temporal retina which, in normal cats project to the ipsilateral hemisphere, project to the contralateral hemisphere in Siamese cats. As a result, the layers of the dorsal lateral geniculate nucleus (LGNd), which normally receive inputs exclusively from the ipsilateral temporal retina, receive a substantial projection from the contralateral temporal retina in Siamese cats (Guillery and Kaas, 1971).

In the normal cat, cortical areas 17 and 18 each contain representations of the *contralateral* visual hemifield; the vertical meridian is represented at the border between areas 17 and 18. In "Boston" Siamese cats, the 17/18 border region does not represent the zero vertical meridian. Instead, it contains a representation of up to 20° of the *ipsilateral* hemifield in order to accommodate the aberrant projection each hemisphere receives from the contralateral temporal retina (Hubel and Wiesel, 1971; Shatz, 1977; Cooper and Blasdel, 1980).

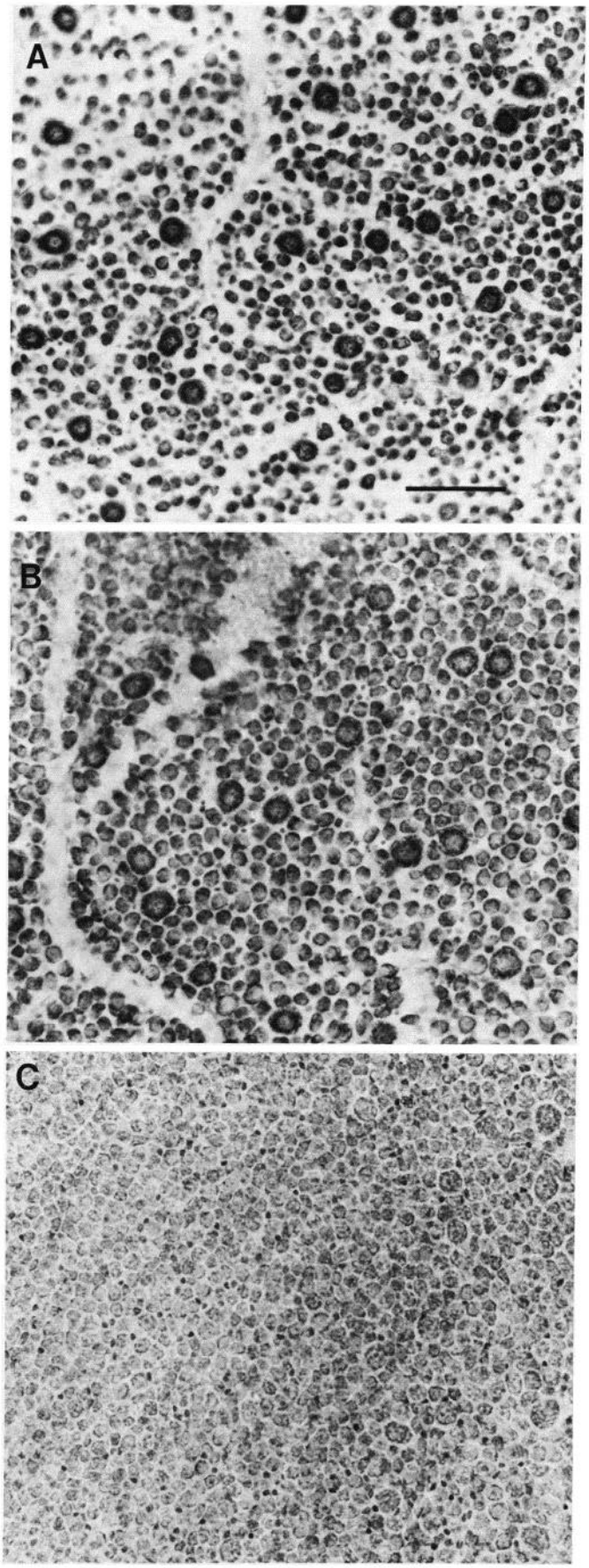
Unlike "Boston" Siamese cats, other Siamese cats, termed "Midwestern," do not have a sizable representation of the ipsilateral hemifield in the 17/18 border region (Kaas and Guillery, 1973; Shatz, 1977; Cooper and Blasdel, 1980). It has been hypothesized that the extent of the ipsilateral visual field represented in Siamese visual cortex is related to the extent of abnormality present in the lamination of the LGNd in different Siamese cats (Shatz, 1977).

Autoradiographic studies indicate that the LGNd is more abnormal in the tyrosinase-negative albino cat than in the Siamese cat (Creel et al., 1982). The retinal afferents to the albino LGNd nearly all arise from the contralateral eye. The purpose of this experiment, therefore, was to study the visual field representation in areas 17 and 18 of the albino cat in order to determine the manner in which the visual field is represented in the cortex of an animal with frontally placed eyes and almost no ipsilaterally projecting retinal ganglion cells.

Our results indicate that the dominant pattern of visual field representation in cortical areas 17 and 18 of the albino is different from the dominant patterns in "Boston" and "Midwestern" Siamese cats. We find that, beginning at the border between areas 17 and 18, afferents representing progressively more peripheral regions of contralateral nasal and contralateral temporal retina are usually grouped into alternating, retinotopically organized domains which are reminiscent of ocular dominance columns in the normal animal.

Materials and Methods

Subjects. Five tyrosinase-negative albino cats provided the data for this study. All of these animals exhibited a small amount of strabismus. A detailed description of the tests used to determine that these cats were truly tyrosinase-negative albinos has been published previously (Creel et al., 1982). These cats were obtained from the colony of albino cats kept at the Veterans Administration Hospital in Salt Lake City, Utah. In three animals cortical recordings were carried out for about 50 hr prior to injecting horseradish peroxidase (HRP) into the optic tract or LGNd. These animals were then



maintained about 24 hr prior to perfusion. One of the remaining two animals had HRP injected into its left optic tract; the other had its retinae stained with thionin.

Physiological recording procedures. Cats were prepared for electrophysiological recording as described previously (Leventhal and Hirsch, 1978, 1980). Under Fluothane anesthesia a cylindrical chamber was positioned over a craniotomy above areas 17 and 18, filled with a 4% solution of agar in saline, and sealed with wax. All pressure points and incisions were infiltrated with a long-acting local anesthetic. A mixture of *d*-tubocurarine (0.4 mg kg^{-1} hr^{-1}) and gallamine triethiodide (7 mg kg^{-1} hr^{-1}) was infused intravenously, and the animal was ventilated with a mixture of nitrous oxide (75%), oxygen (25%), and Fluothane as needed. Body temperature was maintained at 38°C and heart rate was monitored throughout the experiment. Expired CO_2 was maintained at approximately 4%. The eyes were protected from desiccation with contact lenses and, when necessary, spectacle lenses and artificial pupils (3 mm in diameter) were used to focus the eyes on a tangent screen positioned 114 cm from the cat. The projections of the optic discs were determined repeatedly during the course of each recording session and were used to infer the positions of the areae centrales (Fernald and Chase, 1971). In some instances the locations of the areae centrales were determined directly. Their locations did not differ significantly from those inferred from the projections of the optic discs.

Action potentials of cortical cells were recorded with epoxy-coated tungsten microelectrodes or microcapillary electrodes containing 4 M NaCl. The electrode was advanced using a piezoelectric microdrive (Burleigh Instruments) and was moved 75 to 150 μm between units to reduce sampling bias and to record from a large region of cortex in each cat. Cells were recorded from the cortical representation of the area centralis and from the cortical representations of more peripheral regions of the visual field.

Receptive field mapping. The receptive field of a cortical neuron was defined as the largest area in visual space within which a visual stimulus elicited a response. Response fields were plotted by using light bars and both light and dark edges. A detailed description of the procedure has been given previously (Leventhal and Hirsch, 1978, 1980).

Receptive field eccentricity. The eccentricity of a cell's receptive field was defined as the distance from the center of the receptive field (determined by presenting stimuli to the dominant eye) to the projection of the area centralis for that eye. For all units studied, the most recent determinations of the projections of the optic discs were used to infer the locations of the areae centrales. Since receptive fields were plotted on a tangent screen, appropriate corrections were made for all receptive fields to convert distance from the projections of the areae centrales to degrees of visual angle.

Orientation sensitivity. Five to 10 stimulus presentations at each of 8 to 12 orientations were used to compile an orientation tuning curve for each unit. Responses were monitored first by ear and subsequently with a gated counter which provided a quantitative measure of response frequency and total number of responses. Moving bars of light were presented to the eye that elicited the strongest response from the unit. The stimulus was moved in one of the two directions orthogonal to its long axis; the particular direction employed was the one that initially was judged to be the more effective. Similarly, the velocity employed was the one judged to be optimal.

Other receptive field properties. For most units, ocular dominance, cutoff velocity (the maximum stimulus velocity to which the cell responds), direction selectivity, end-zone inhibition, and spontaneous activity were also studied. Cells were identified as being S or C type based upon their responses to flashing stimuli (Leventhal and Hirsch, 1978). S cells exhibit pure on and/or pure off responses to flashing stimuli; C cells exhibit mixed on/off responses to flashing stimuli. All data collected were stored in the laboratory PDP 11/23 computer system for subsequent analysis. A detailed description of our receptive field mapping procedures has been given previously (Leventhal and Hirsch, 1978, 1980).

Electrode track reconstruction. When using metal electrodes, the localization of electrode tracks was facilitated by making small electrolyte lesions (3 μA for 3 sec) at sites of particular interest. Large currents (10 μA for 10 to 15 min) delivered through the microcapillary electrodes also resulted in a small amount of gliosis and thus aided in the localization of electrode tracks. Electrode tracks were reconstructed from Nissl-stained 50-μm frozen sections.

Figure 1. Photomicrographs of the area centralis in albino (*A*) Siamese (*B*), and normal (*C*) cat. All retinae are stained with thionin. *Scale bar* = 100 μm. Notice that in the Siamese (*B*) and especially in the albino (*A*) cat the density of ganglion cells is abnormally low within the area centralis. Also notice that many large ganglion cells are present throughout the area centralis in the albino and Siamese cat, but not in the normal cat.

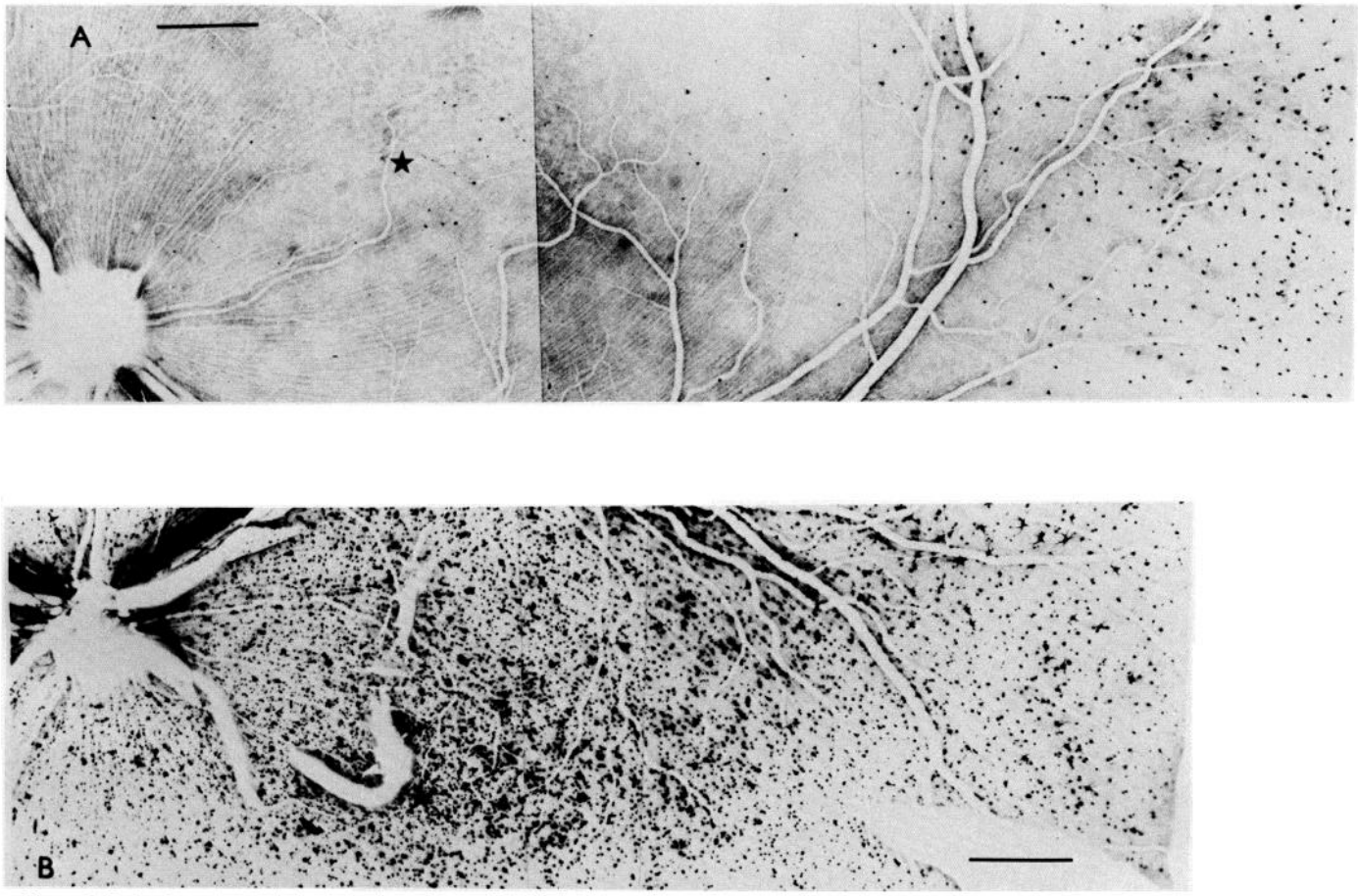


Figure 2. Retinal ganglion cells in the ipsilateral temporal (*A*) and contralateral temporal (*B*) retinae of an albino cat that received multiple HRP injections into the optic tract. *Scale bar* = 1 mm. Notice that the great majority of the ganglion cells in the temporal retina of the albino cat project contralaterally. The *star* indicates the approximate center of the area centralis.

Electrophoretic injection. Once a satisfactory site in the visual cortex, LGNd, or optic tract was located, the electrode was removed, and a microcapillary electrode filled with 10% HRP in Tris-HCl buffer (pH 8.6) containing 1% dimethyl sulfoxide (DMSO) was lowered into the appropriate region. The correct position was confirmed by recording with this electrode prior to the injection. HRP was injected using currents of 3 μA (1.5 sec on, 0.5 sec off) for a period of 2 to 3 hr (Leventhal, 1982). An attempt was made to expose a large region of the LGNd to HRP by making four or five closely spaced small injections across the mediolateral extent of the nucleus at the approximate level of the horizontal meridian (Leventhal, 1982). Similarly, four or five injections were made across the width of the optic tract in order to expose fibers of all calibers (Guillery et al., 1982) to HRP. Optic tract injections were made about 3 mm from the optic chiasm. In one animal a single injection into the visual cortex was made with a recording microelectrode in order to restrict the injection site to a few hundred micrometers (Leventhal, 1979).

Histology and histochemistry. All cats were anesthetized and perfused through the heart with 700 ml of 35°C lactated Ringer's solution containing 0.1% heparin, followed by 1000 ml of a 35°C solution of 1% paraformaldehyde and 2.5% glutaraldehyde in 0.1 M phosphate buffer at pH 7.4, followed by 600 ml of 35°C lactated Ringer's solution containing 5% dextrose. Brains were removed, and the portions containing the injection sites were blocked and stored for 2 to 4 days in a 30% sucrose solution and then frozen sectioned at 50 μm. Sections were collected in 0.1 M Tris-HCl buffer (pH 7.4), reacted for HRP for 20 min in 0.1 M Tris buffer containing 0.03% *p*-phenylendiamine dihydrochloride, 0.06% pyrocatechol, and 0.02% H_2O_2 (PPD-PC reagent), and transferred back into 0.1 M Tris-HCl buffer. After the HRP reaction was completed, all sections were mounted on gelatinized slides and stained with thionin.

Whole retinae were removed and reacted for HRP immediately after the perfusion. The best labeling was observed when the reaction was begun without delay. Retinae were rinsed in 0.1 M Tris buffer (pH 7.4) for 5 min, incubated in 1% cobalt chloride in Tris buffer containing 0.5% DMSO for 20 min at 35°C, rinsed in Tris buffer at 35°C for 5 min, rinsed in 0.1 M phosphate buffer (pH 7.4) at 35°C for 5 min, prereacted in the PPD-PC reagent containing 0.5% DMSO (without H_2O_2) at 35°C for 15 min, reacted with fresh PPD-PC reagent containing 0.5% DMSO (with H_2O_2) at 35°C for 20 min, and rinsed in phosphate buffer for 30 min. Retinae were fixed onto gelatinized slides by placing them in formalin vapor for 2 hr. They were then dehydrated and coverslipped.

Results

Retinal abnormalities in the albino cat. All of the morphological types of retinal ganglion cells observed in studies of normal and Siamese cats (Boycott and Wassle, 1974; Leventhal, 1982) were present in albino cats. Outside of the area centralis, the relative numbers of the different cell types in albino retina were normal; there were no obvious morphological differences between corresponding classes of ganglion cells in albino and normal cats.

There were a number of retinal abnormalities evident in Nissl-stained albino retinae. Compared to normal animals, albino cats had a weakly developed area centralis. The density of retinal ganglion cells was abnormally low within the albino area centralis; the cell bodies and dendritic fields of retinal ganglion cells within the albino area centralis were abnormally large (Fig. 1). Also, sizable blood vessels often ran through the area centralis in the albino. This disrupted the vascular "wreathing" normally seen in the area centralis. The abnormalities noted above were more severe than, but qualitatively similar to, those observed in the retinae of Siamese cats (Stone et al., 1978a; Leventhal, 1982).

The nasotemporal division in the albino cat. The relative numbers of ipsilaterally and contralaterally projecting retinal ganglion cells in an albino cat can be seen in Figure 2, *a* and *b*. This animal received multiple HRP injections into the optic tract about 3 mm from the

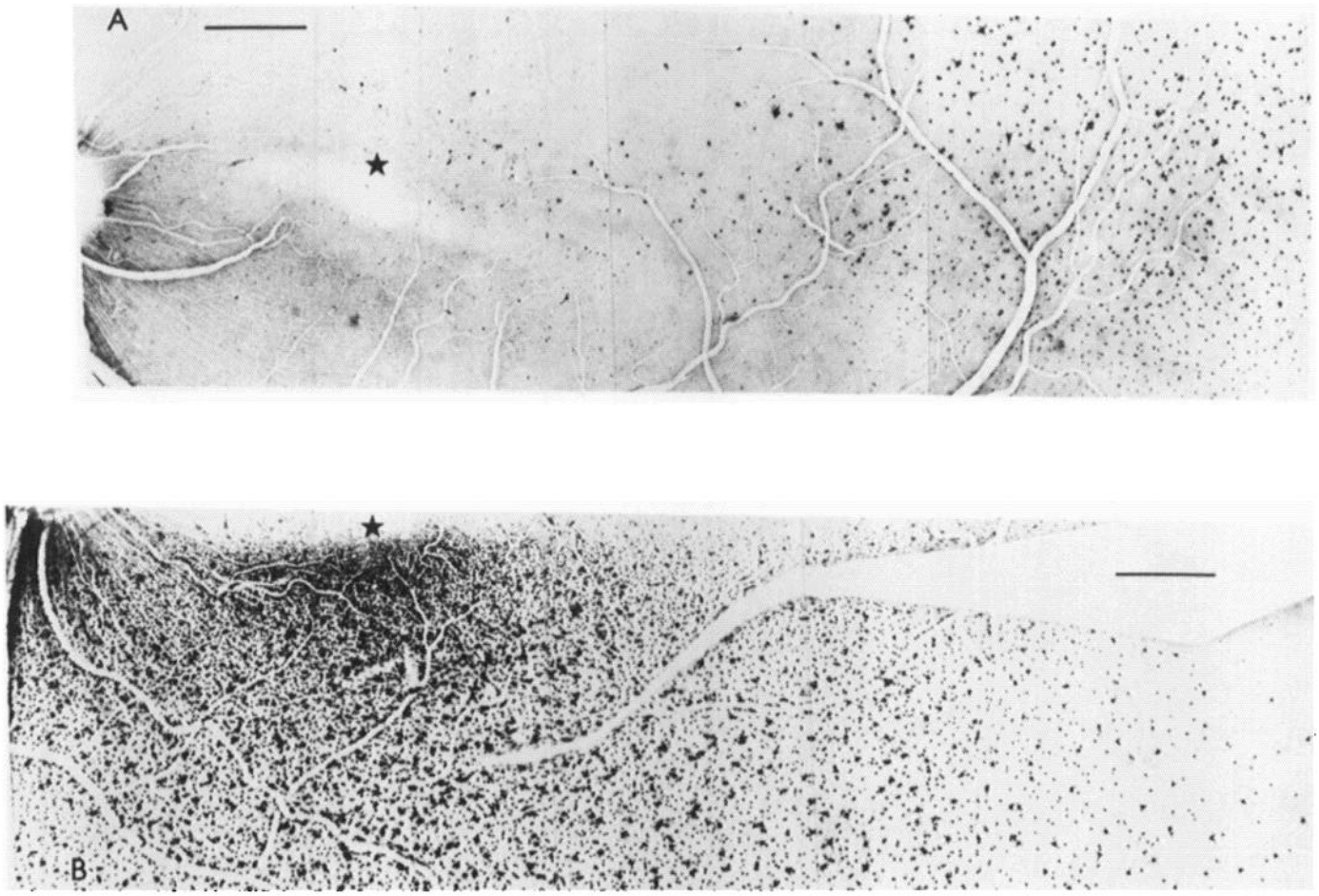


Figure 3. Retinal ganglion cells in the ipsilateral temporal (*A*) and contralateral temporal (*B*) retinae of an albino cat (albino 4) that received multiple HRP injections into the A laminae of the LGNd. *Scale bar* = 1 mm. The physiological results shown in Figures 7 to 11 were also obtained from this animal. The *star* indicates the approximate center of the area centralis.

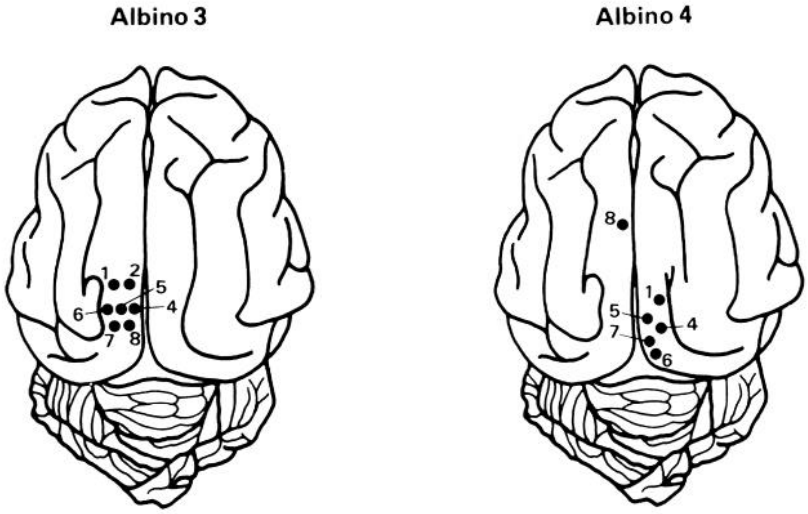


Figure 4. Dorsal view of cat brain showing the positions (*1* to *8*) of the electrode penetrations reconstructed in the following figures.

optic chiasm. Notice that the great majority of cells in temporal retina projected contralaterally in this cat. The ratio of labeled cells in the contralateral temporal and ipsilateral temporal retinae was greater than 20:1. This is never the case in the normal cat and rarely, if ever, the case in the Siamese cat (Cooper and Pettigrew, 1979; Leventhal, 1982). Nevertheless, in all three groups of animals, ipsilaterally projecting cells are found throughout temporal retina. Thus, although the nasotemporal division seems to be quantitatively more abnormal in the albino than in the Siamese cat, the pattern of misrouting is qualitatively similar. In both cases, there is a decrease in the number of ipsilaterally projecting ganglion cells throughout temporal retina, not just a shift in the line of decussation.

The relative numbers of retinal ganglion cells labeled in the ipsilateral and contralateral retinae of an albino cat that received multiple injections of HRP into the LGNd can be seen in Figure 3. HRP reaction product extended throughout all layers of the LGNs in this animal. The optic tract was probably not involved significantly since it was not in the primary injection site, the electrode was not lowered deep enough to damage any fibers, and very few small ganglion cells (Leventhal, 1982) were labeled by the injection. Once

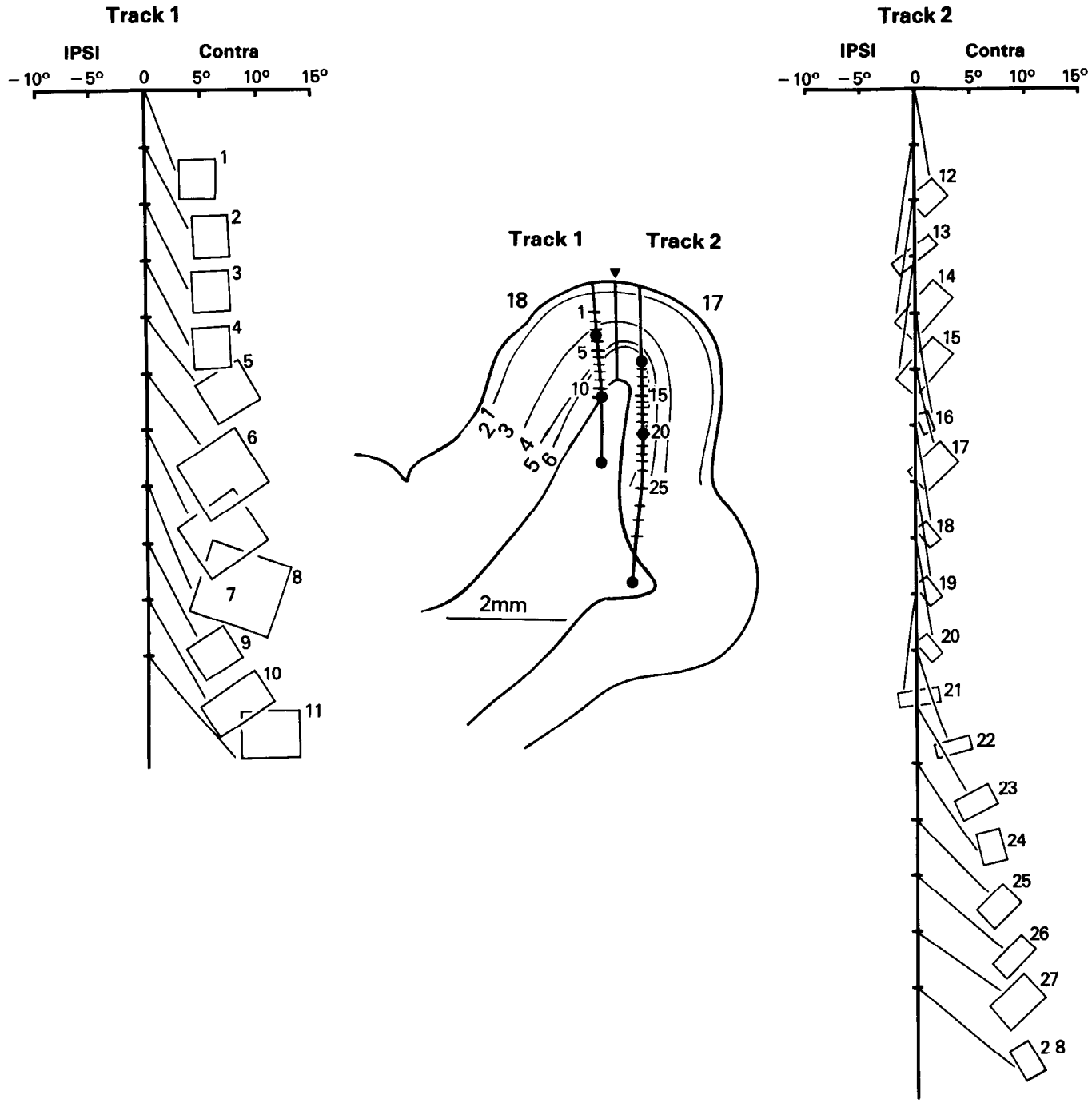


Figure 5. Receptive field positions (*1* to *11*) of units recorded along electrode penetrations through areas 17 and 18 of albino cat 3. The positions of each receptive field in this and the following are shown relative to the area centralis projection. Mean elevations of receptive fields in *tracks 1* and *2* were 8° and 9° below the horizontal meridian, respectively. Receptive field positions and positions in cortex of units studied are indicated by corresponding numbers.

again, notice that the great majority of ganglion cells in temporal retina projected to the contralateral LGNd in this albino. We find that, overall, more than 20 times as many ganglion cells are labeled in the contralateral temporal retina as in the ipsilateral temporal retina as a result of this type of injection. In fact, within 7 mm of the area centralis in albino temporal retina, the number of alpha type ganglion cells projecting to the ipsilateral LGNd is so small that no more than 2 or 3 cells/mm^2 were ever labeled by our injections. The cells which were labeled in the ipsilateral temporal retina were mostly beta cells.

Visual field representation in albino area 17. There were two different patterns of visual field representation evident in area 17 of the albino cats studied (Fig. 4). Both patterns were evident in each animal. The first was reminiscent of the representation of the visual field in area 17 of the "Midwestern" Siamese cat (Kaas and Guillery, 1973) in that there was virtually no representation of the ipsilateral hemifield in the 17/18 border region. *Track 2* in Figure 5, *track 8* in Figure 6, and *track 7* in Figure 7 illustrate this pattern. These penetrations provided no evidence for a sizable representation of the ipsilateral hemifield in area 17; as the electrode was advanced down the medial bank of the postlateral gyrus, receptive fields of successive units moved progressively further into the contralateral hemifield. None of the units encountered had receptive fields more than a few degrees into the ipsilateral hemifield. It must be noted, however, that some of the penetrations into area 17, such as *track 8* in Figure 6 and *track 7* in Figure 7, did not sample cells within a millimeter or so of the 17/18 border. Thus, we cannot rule out the

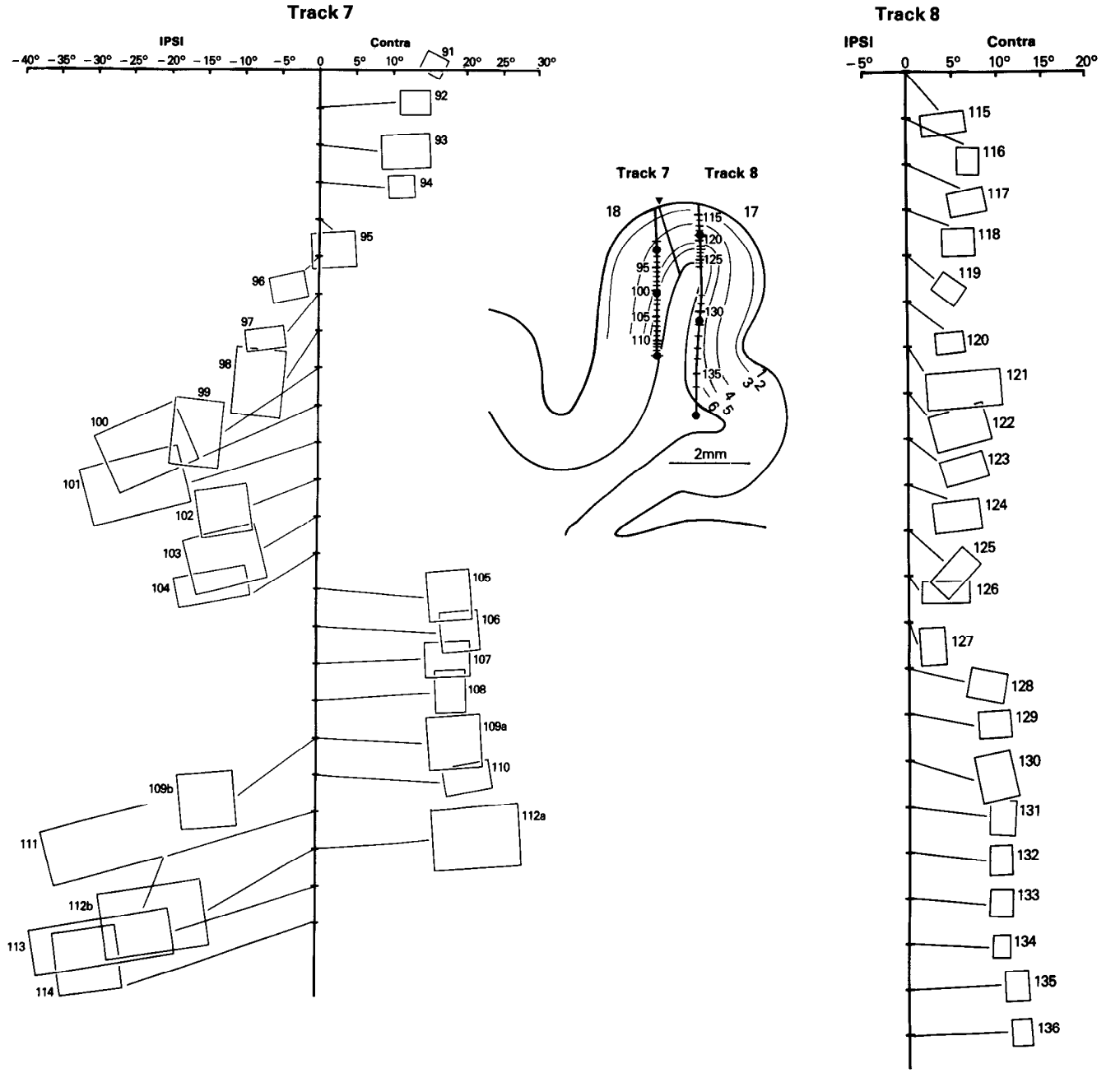


Figure 6. Receptive field positions of units recorded along two additional electrode penetrations through areas 17 and 18 of albino cat 3. The mean elevations of fields in *tracks 7* and *8* were 5° and 3° below the horizontal meridian, respectively.

possibility that part of the ipsilateral hemifield was represented near the 17/18 border in these cases.

The second pattern of visual field representation in area 17 is illustrated in *track 5* in Figure 8. Of nine penetrations made into area 17 in three albino cats, five (56%) showed this pattern. The first units encountered in this penetration had receptive fields close to the vertical meridian; as the electrode was advanced through area 17, receptive fields of successive units moved gradually into the contralateral hemifield. Between fields 62 and 63 there was an abrupt shift in receptive field position. The shift represented a change in azimuth of about 20° and placed field 63 and 10° into the ipsilateral hemifield. As the electrode was advanced further, receptive fields moved progressively further into the ipsilateral hemifield until, between fields 72 and 73a, there was again an abrupt shift in receptive field position. This shift represented a change in azimuth of about 30° and placed the receptive field of unit 73a in the roughly mirror-symmetric position in the contralateral hemifield. As the electrode was advanced, receptive fields moved progressively further into the contralateral hemifield; after a few hundred micrometers, receptive fields again shifted to the roughly mirror-symmetric position in the ipsilateral hemifield. Shifts of this type were evident all along this penetration; the final shift, between fields 83 and 84a, represented a change in azimuth of over 60° and resulted from a movement of the electrode of less than 100 μm (Fig. 8). The center of field 84b was 37° into the ipsilateral hemifield. Smaller shifts of the type described above have been observed in the visual cortex of Siamese cats (Hubel and Wiesel, 1971; Kaas and Guillery, 1973; Shatz, 1977).

We interpret the shifts of the type observed along this and similar penetrations (*track 8* in Fig. 9) as evidence that, in some parts of areas 17 of the albino, neurons subserving the ipsilateral and contralateral hemifields are segregated into zones or domains. These

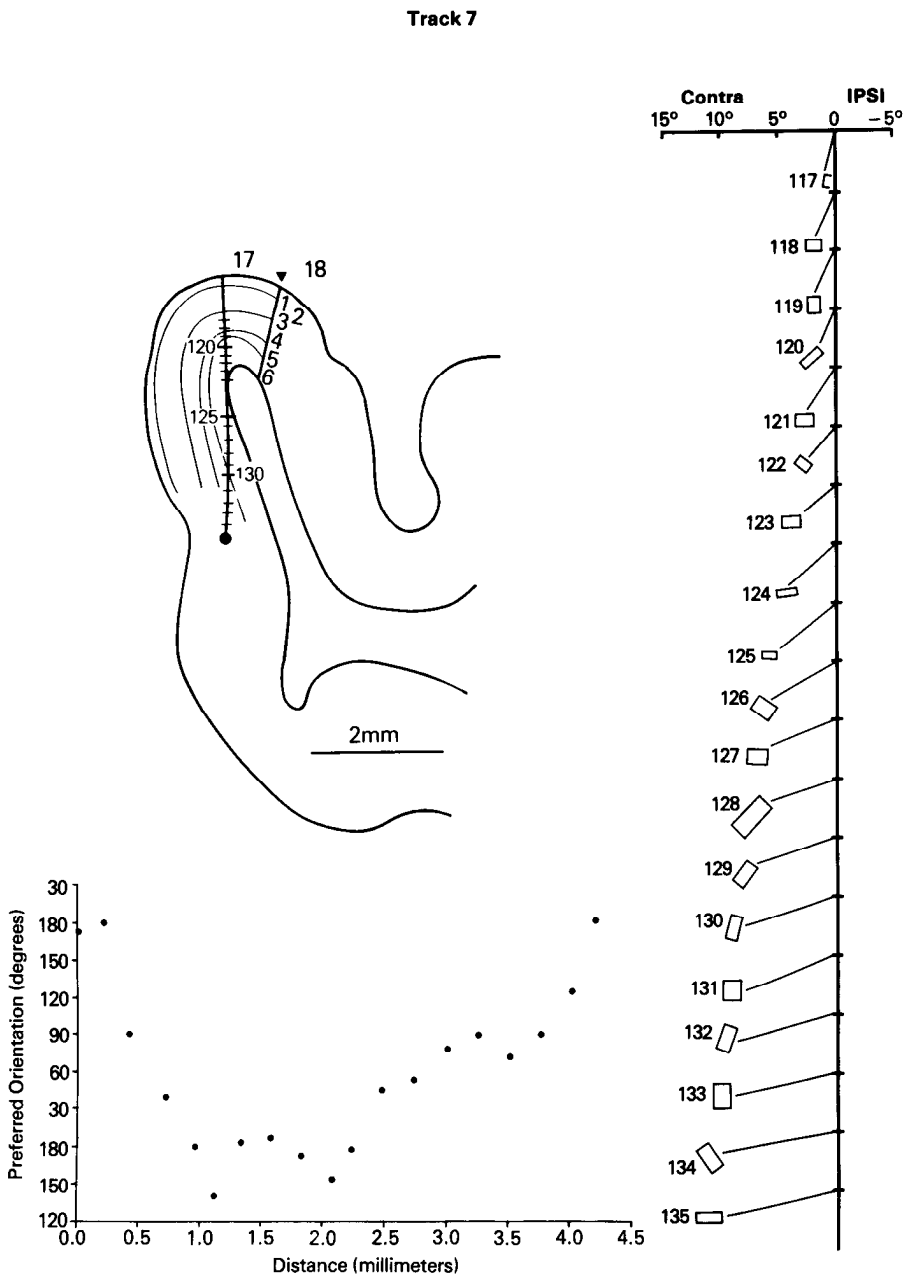


Figure 7. Receptive field positions and preferred orientations of units recorded along an electrode penetration through area 17 of albino cat 4. The mean elevation of fields in this track was 3° below the horizontal meridian. Anatomical results shown in Figure 3 were also obtained from this animal.

"hemiretina" domains are superimposed upon an orderly, albeit "schizophrenic," representation of the visual field. We have inferred the width of these domains from penetrations such as penetrations 5 in Figure 8. On average, domains in area 17 appear to be about 700 μm wide; when present, domains representing the two hemifields did not differ in width. It should be noted that statements about domain width must be interpreted cautiously since we do not know the angle of our electrodes relative to the borders of domains.

Visual field representation in area 18. All penetrations into area 18 of three albino cats which were oriented obliquely relative to the cortical surface (7 of 7) provided evidence that cells subserving contralateral and ipsilateral hemifields were segregated into alternating domains. A number of such penetrations into area 18 are illustrated in Figures 6, 10, and 11. In all oblique penetrations there were abrupt shifts in receptive field azimuth as the electrode was advanced down the lateral bank of the postlateral gyrus. The size of the shifts always increased as the receptive fields of units moved more peripherally; units at the borders of columns representing the two hemifields had receptive fields in roughly mirror-symmetric positions in the ipsilateral and contralateral hemifields. Hemiretina domains in area 18 tended to be somewhat wider than in area 17. On average, domains in area 18 were about 1 mm wide. A penetration into area 18 which was made perpendicular to the cortical surface provided evidence that hemiretina domains extended from the pial surface to the white matter. In the penetration of this type no abrupt shifts in receptive field positions were observed (*track 1* in Fig. 5).

The LGNd relay cell projection to albino area 18. Evidence that LGNd afferents representing contralateral nasal and contralateral temporal retina are segregated in albino area 18 was obtained in one animal by injecting HRP electrophoretically into a region adjacent to the 17/18 border that subserved the contralateral hemifield. As a result of this injection, many labeled relay cells were evident in the retinotopically appropriate parts of lamina A, lamina C, and the medial interlaminar nucleus (MIN) (Fig. 12). The region of lamina A_1 between these clusters of labeled cells was virtually devoid of labeled cells. Such a pattern is to be expected if afferents representing the ipsilateral and contralateral hemifields are segregated in visual cortex. It is noteworthy that a similar injection in the visual cortex of a "Boston" Siamese cat should produce identical results (Kaas and Guillery, 1973).

Track 5

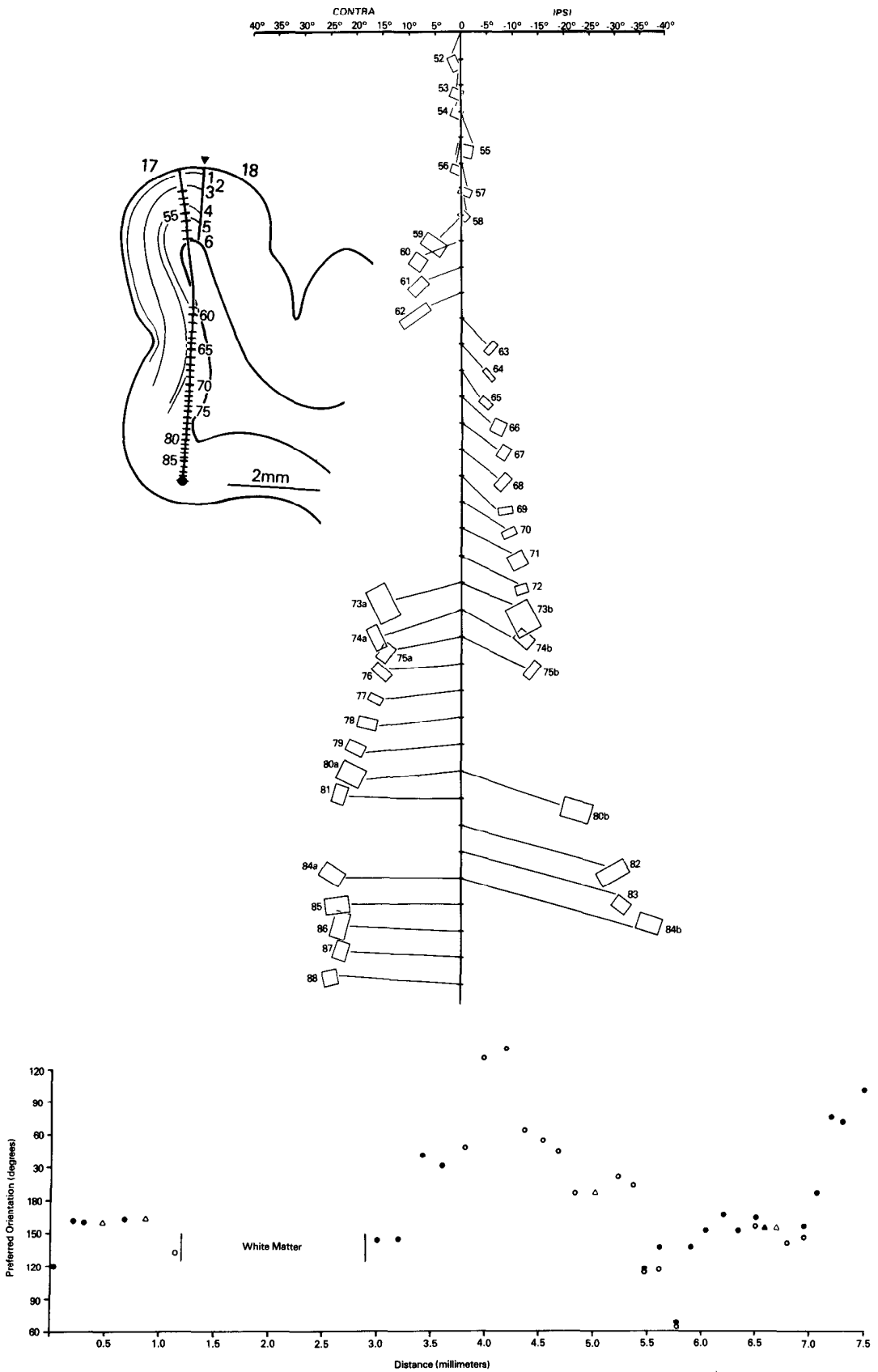
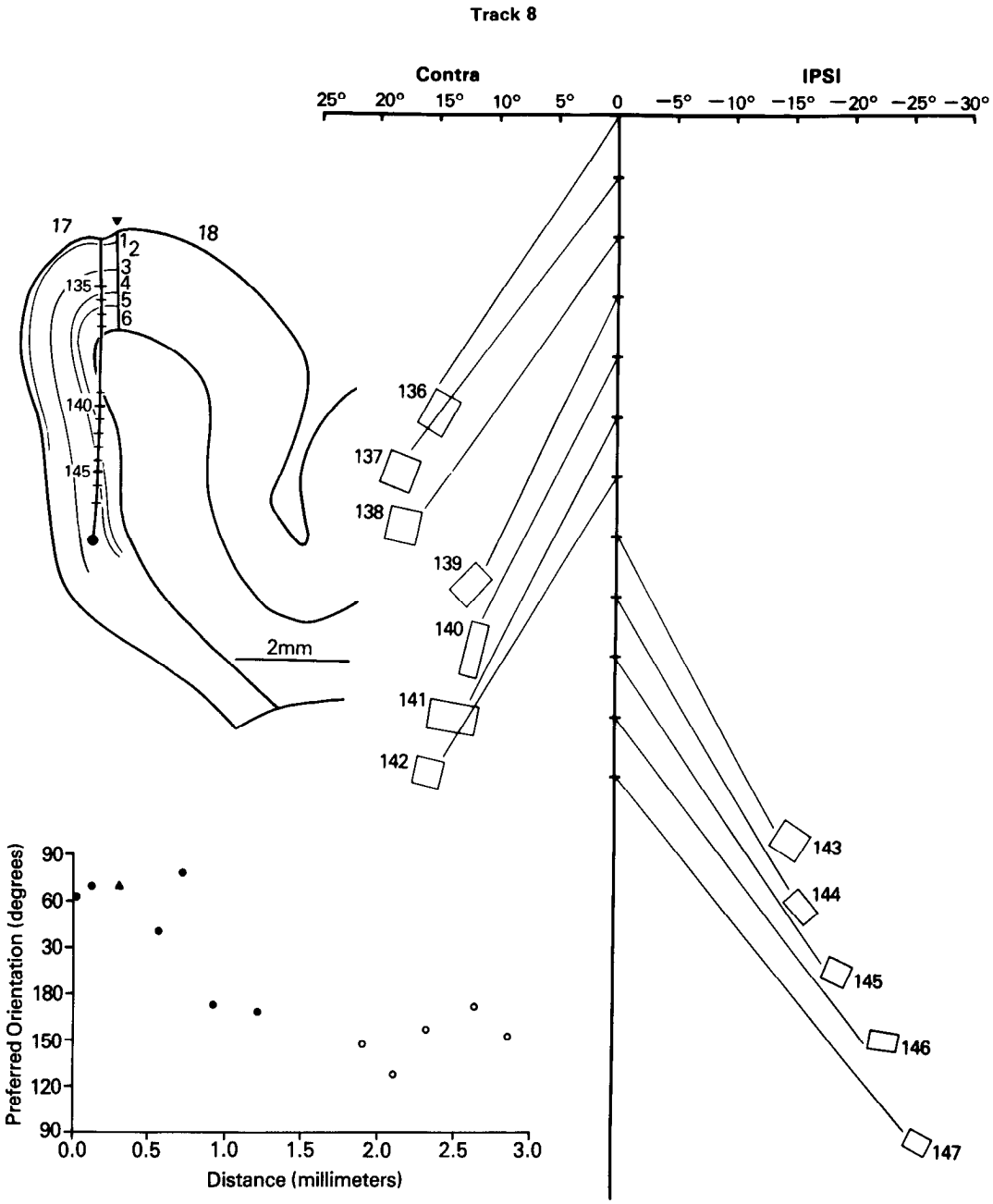


Figure 8. Receptive field positions and preferred orientations of units recorded along another electrode penetrations through area 17 of albino cat 4. *Solid and open circles (bottom graph) indicate the preferred orientations of cells having receptive fields in the contralateral and ipsilateral hemifields, respectively. Triangles* indicate nonselective cells. Notice that some cells at the borders of domains representing the two hemiretina have two receptive fields in roughly mirror-symmetric positions. The mean elevations of fields in this track were 4° below the horizontal meridian.



Figures 9 to 11. Receptive field positions and preferred orientations of units recorded along other electrode penetrations through areas 17 and 18 of albino cat 4. Conventions are as in Figure 8. The mean elevations of fields in tracks 8, 1, and 4 were 25°, 6°, and 3° below the horizontal meridian, respectively.

Receptive field properties of cells in areas 17 and 18 of the albino cat. The receptive field properties of most cells in albino visual cortex were unremarkable except that all cells studied were activated only by the contralateal eye. Nearly all cells studied in areas 17 and 18 were orientation sensitive and many were direction sensitive. In both areas receptive field size increased with distance from the projection of the area centralis; this was true whether the cell's receptive field was in the contralateral hemifield or in the ipsilateral hemifield (Fig. 8). Finally, area 18 cells tended to have larger receptive fields and higher cutoff velocities than did area 17 cells (Figs. 5 and 6). Interestingly, in the albino cat the receptive fields of cells subserving the ipsilateral hemifield were not larger than those subserving the contralateral hemifield (Figs. 8 to 11), as they are in the Siamese cat (Hubel and Wiesel, 1971).

Some cells in areas 17 and 18 of the albino had abnormal properties. These cells were always located at the borders between zones representing the ipsilateral and contralateral hemifields. Border cells fell into three groups. Cells in the first group had normal properties and need not be discussed further. Cells in the second group were abnormal in that they had two distinct receptive fields: one field subserved the ipsilateral hemifield and the other subserved the roughly corresponding part of the contralateral hemifield (Figs. 6, 8, and 10). In one case, the two fields of the same cell (*cell 84* in Fig. 8) were separated by more than 60°. In every case, when the two fields were mapped separately, the cell exhibited similar receptive field properties; in no case did preferred orientation, velocity selectivity, or other factors differ significantly for the two fields. Cells of this type were observed 50% of the time the electrode crossed a hemiretina domain's border. Although they are extremely rare, cells of this type have also been observed in the visual cortex of the Siamese cat (Hubel and Wiesel, 1971).

Cells in the third group were only encountered twice. These cells

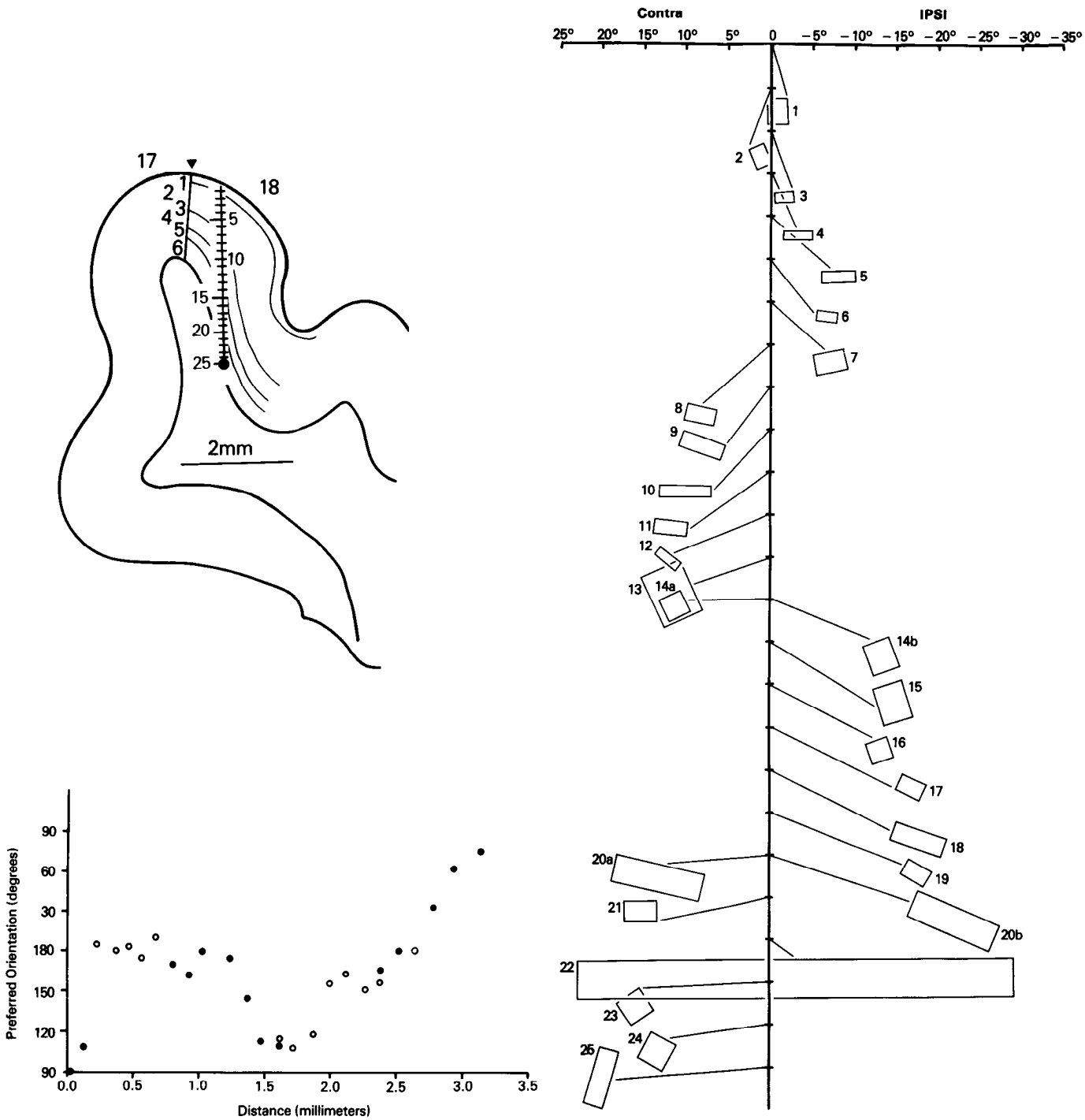


Figure 10

were similar to those in the second group in that they responded to stimulation of corresponding parts of the ipsilateral and contralateral hemifields. However, the two fields of cells in group 3 were not distinct. Rather, they were connected by a region which responded weakly to visual stimulation. Thus, these cells actually had one long narrow field with "hot spots" at both ends. The receptive fields of these cells could extend far across the vertical meridian (e.g., field *22* in Fig. 10).

Distribution of orientation-sensitive cells in albino visual cortex. Preferred orientation changes gradually and systematically, both within and across ocular dominance columns in the visual cortex of the normal cat (Hubel and Wiesel, 1963). As already noted, most cells studied in areas 17 and 18 of the albino cat were sensitive to stimulus orientation. It was of interest, therefore, to determine whether preferred orientation changed gradually and systematically across zones representing the ipsilateral and contralateral hemifields in the albino.

The preferred orientations of units recorded successively along a number of penetrations into areas 17 and 18 of albino visual cortex are presented in Figures 7 to 11. Reconstructions of these penetra-

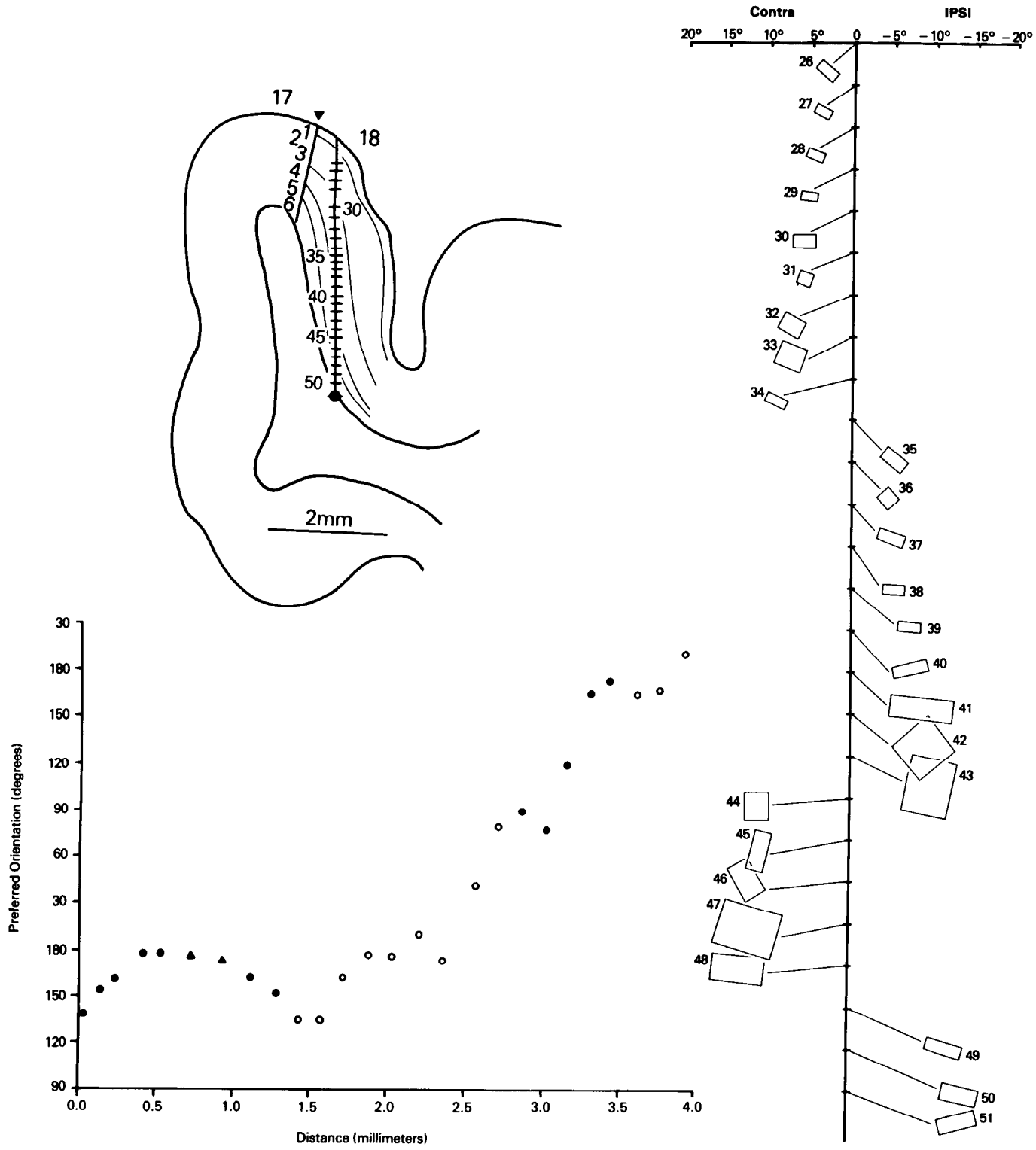


Figure 11

tions are also shown. It is evident that, in most penetrations, cells having similar preferred orientations were grouped together, and that preferred orientation changed gradually and systematically as the electrode moved parallel to the surface of the cortex. These gradual changes in preferred orientation appeared independent of the marked changes in receptive field position which occurred at the borders of domains representing the ipsilateral and contralateral hemifields (Figs. 8 to 11). As in normal cats, abrupt changes in preferred orientation were sometimes observed in albino visual cortex. Abrupt changes in preferred orientation were as common within hemiretina domains as at the borders of domains.

Discussion

The present study provides evidence that about 95% of ganglion cells in temporal retina project contralaterally in the albino cat; albino visual cortex contains a representation of greater than 37° of the

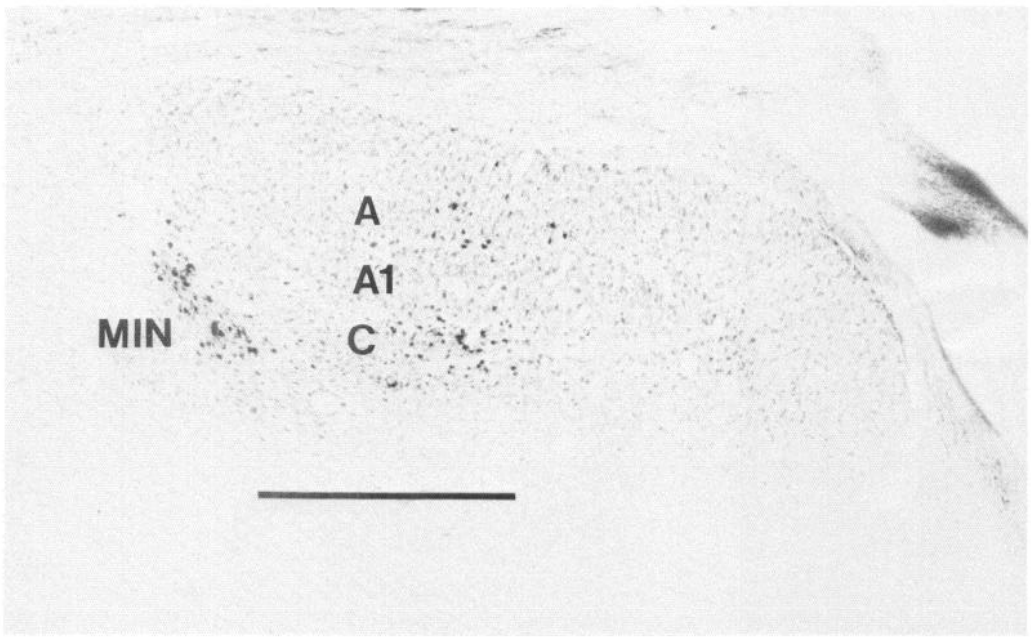


Figure 12. Labeled relay cells in the LGNd of an albino cat that received a small electrophoretic injection of HRP into a domain in area 18 that subserved the contralateral hemifield. Notice that cells in retinotopically corresponding parts of laminae A and C are labeled. These cells presumably subserve the contralateral hemifield. There are no labeled cells in lamina A1, suggesting that afferents subserving the ipsilateral hemifield did not project to the injection site. This indicates that afferents representing the two hemifields are segregated in albino visual cortex. *MIN*, medial interlaminar nucleus.

ipsilateral hemifield. In areas 17 and 18, cells representing the ipsilateral and contralateral hemifields are often grouped into alternating, retinotopically organized domains. These "hemiretina" domains are independent of the organized system of orientation columns in albino visual cortex.

Relation to previous work. A significant degree of variability has been observed in the manner in which the visual field is represented in Siamese visual cortex; it has been suggested that differences among Siamese cats may have been observed in some cases because different regions of areas 17 and 18 were studied by different investigators. Recordings from parts of the 17/18 border subserving different elevations in the same Siamese cat suggest that portions of the 17/18 border which represent the lower visual field often contain a representation of about 20° of the ipsilateral hemifield, the "Boston" pattern (Hubel and Wiesel, 1971; Shatz, 1977), whereas less than 5° of the ipsilateral hemifield, the "Midwestern" pattern (Kaas and Guillery, 1973; Shatz, 1977), are often found in regions of the 17/18 border which represent the upper visual field (Cooper and Blasdel, 1980). To date, no study of Siamese visual cortex provides evidence that, in areas 17 and 18, cells representing the two hemifields are grouped into a system of alternating, retinotopically organized domains.

In contrast, in this study 56% of the penetrations into area 17 and all of the penetrations into area 18 provided evidence for alternating, retinotopically organized domains representing the two hemifields. All of the animals we studied showed this pattern; variability among animals was slight. A similar arrangement may exist in the visual cortex of the albino monkey (Guillery et al., 1984). Thus, the dominant pattern of organization of visual cortex is different in the tyrosinase-negative albino and in the Siamese cat.

Mechanisms mediating column formation in areas 17 and 18. The effects of albinism appear to differ somewhat in areas 17 and 18 in the cat. Alternating zones representing the ipsilateral and contralateral hemifields were evident during all penetrations into area 18 but not all penetrations into area 17. When present, zones representing the two hemiretina were about the same width as ocular dominance columns in areas 17 and 18 of the normally pigmented cat (Shatz et al., 1977).

In the albino cat virtually all Y cells in temporal retina project to the contralateral LGNd; there were never more than 3 or 4 alpha (Y) cells/mm^2 labeled in the ipsilateral temporal retina as a result of multiple large HRP injections into the LGNd. Most of the labeled cells in the ipsilateral temporal retina observed following our injections were beta (X) cells.

In the cat, area 18 receives its LGNd projection almost exclusively from Y cells; area 17 receives its major projections from X cells with minor projections from Y cells and W cells (see Stone et al., 1979, for review). It may be that the formation of domains representing the ipsilateral and contralateral hemifields in visual cortex depends upon competitive interactions between *balanced* numbers of LGNd afferents representing nasal and temporal retina. Such interactions occur in the normal cat, and ocular dominance columns develop since each hemisphere receives a sizable projection from the temporal retina of the ipsilateral eye and from the nasal retina of the contralateral eye. Similar interactions occur during development in the albino cat, and domains representing nasal and temporal retina develop throughout area 18 since virtually all LGNd Y cells in nasal and temporal retina project contralaterally. Interactions of this type may not occur in all parts of area 17 in the albino since area 17 receives predominantly X cell afferents and most of the cells in temporal retina which project ipsilaterally in albinos are beta (X) cells. Thus, the number of LGNd X cell afferents representing contralateral temporal retina may be too low in some regions of area 17 to balance the number of LGNd X cell afferents representing contralateral nasal retina. In such regions, hemiretina domains may not develop since LGNd afferents representing nasal retina predominate. In these regions the representation of the ipsilateral hemifield may be suppressed as in "Midwestern" Siamese cats (Kaas and Guillery, 1973).

Many more ganglion cells in temporal retina project ipsilaterally in the Siamese cat than in the albino cat (Stone et al., 1978b; Cooper and Pettigrew, 1979; Leventhal, 1982). As a result, the visual cortex of Siamese cats does not receive balanced inputs from LGNd afferents representing contralateral nasal and contralateral temporal retina; this may explain why alternating domains representing the contralateral and ipsilateral hemifields are usually not found in visual cortex of Siamese cats. As already noted, however, limited evidence for such a pattern was found by Hubel and Wiesel (1971) in two of the Siamese cats they studied, as well as by Kaas and Guillery (1973) and Shatz (1977) in some of their animals. It may be that a sizable representation of the ipsilateral hemifield is found only near the 17/18 border in the "Boston" Siamese cat because this region normally represents the vertical meridian; in "Boston" Siamese cats it is only near the vertical meridian of the retina that there is a reasonable balance between the numbers of ganglion cells in nasal

and temporal retina which project contralaterally (Stone et al., 1978b; Cooper and Pettigrew, 1979; Leventhal, 1982).

Receptive field properties of cells in albino visual cortex. In areas 17 and 18 of the normal cat, most cells are binocular and have two receptive fields. One field is in the *ipsilateral temporal* retina; the other is in the corresponding part of the *contralateral nasal* retina. In the normal cat, the receptive field properties of the fields in the two eyes do not differ.

In the albino cat, abnormal cells are common at the borders of zones subserving the two hemifields. These cells have two receptive fields, one in *contralateral temporal* retina and the other in the roughly corresponding part of *contralateral nasal* retina. The receptive field properties of the two fields of these cells do not differ in the albino cat or in the Siamese cat (Hubel and Wiesel, 1971). These border cells, as Hubel and Wiesel (1971) have noted, are strikingly similar to binocular cells in the normal cat; in both cases afferents representing nasal and temporal retina converge upon individual cells without disrupting other aspects of the functional architecture of visual cortex such as the organized arrangement of orientation columns.

Relation to clinical observations. As noted above, our findings suggest that competitive interactions between nasal and temporal regions of the retina of one eye are sufficient for the development of dominance domains in visual cortex. A number of clinical observations such as the commonly observed "faulty nasal projection" led Jampolsky (1970) to hypothesize "that the interactions between the two half-retinas, stably housed in a common mobile eye, are as important to the study of visual dominances as are the studies of the right-left eye interactions in two less stably related mobile organs." The present results lend support to Jampolsky's (1970) hypothesis.

Conclusion. In areas 17 and 18 of the normal cat, LGNd afferents representing nasal and temporal regions of the two eyes are able to segregate into columns in visual cortex. Most cells within these ocular dominance columns are binocular; they have receptive fields in corresponding parts of contralateral nasal and ipsilateral temporal retina. In many respects, albino visual cortex has a similar organization. In areas 17 and 18 in the albino, LGNd afferents representing nasal and temporal retina are also segregated; some cells in albino cortex also have two receptive fields, one in the nasal and the other in the corresponding part of the temporal retina. In light of this, it is tempting to speculate that the ontogenetic mechanisms which guide the formation of normal ocular dominance columns depend upon competitive interactions between LGNd relay cells representing nasal and temporal regions of retina; it does not matter whether these afferents originate from one eye or two. It may be that differences between ganglion cells in nasal and temporal regions of the retina (Stone et al., 1980) guide the formation of laminae in the LGNd and ocular dominance columns in visual cortex.

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