

Structural Basis of Orientation Sensitivity of Cat Retinal Ganglion Cells

AUDIE G. LEVENTHAL AND JEFFREY D. SCHALL

Department of Anatomy, University of Utah School of Medicine, Salt Lake City, Utah 84132

ABSTRACT

We investigated the structural basis of the physiological orientation sensitivity of retinal ganglion cells (Levick and Thibos, '82). The dendritic fields of 840 retinal ganglion cells labeled by injections of horseradish peroxidase into the dorsal lateral geniculate nucleus (LGNd) or optic tracts of normal cats, Siamese cats, and cat deprived of patterned visual experience from birth by monocular lid-suture (MD) were studied. Mathematical techniques designed to analyze direction were used to find the dendritic field orientation of each cell. Statistical techniques designed for angular data were used to determine the relationship between dendritic field orientation and angular position on the retina (polar angle). Our results indicate that 88% of retinal ganglion cells have oriented dendritic fields and that dendritic field orientation is related systematically to retinal position. In all regions of retina more than 0.5 mm from the area centralis the dendritic fields of retinal ganglion cells are oriented radially, i.e., like the spokes of a wheel having the area centralis at its hub. This relationship was present in all animals and cell types studied and was strongest for cells located close to the horizontal meridian (visual streak) of the retina. Retinal ganglion cells appear to be sensitive to stimulus orientation because they have oriented dendritic fields.

Key words: dendritic field orientation, polar angle, area centralis, circular statistics, normal, Siamese and visually deprived cats

While orientation sensitivity is a distinctive feature of visual cortical cells (Hubel and Wiesel, '62, '77), recent evidence suggests that neurons in more peripheral parts of the visual pathways are also orientation sensitive. Most ganglion cells in cat retina (Levick and Thibos, '82) as well as most relay cells in the cat's dorsal lateral geniculate nucleus (LGNd) (Vidyasagar and Urbas, '82) are sensitive to stimulus orientation. There appears to be a systematic relationship between receptive field position and preferred orientation in the retina. Retinal ganglion cells respond best to stimuli oriented radially, i.e., oriented parallel to the line connecting them to the area centralis (Levick and Thibos, '82). A similar tendency has also been reported for the LGNd (Vidyasagar and Urbas, '82).

This study describes the possible structural basis of the orientation-sensitive response of cat retinal ganglion cells. We analyzed the dendritic fields and angular positions (polar angles) of retinal ganglion cells. We find that most retinal ganglion cells have oriented dendritic fields and that dendritic field orientation is highly correlated with retinal position. The dendritic fields of most retinal ganglion cells are oriented radially, i.e., like the spokes of a wheel having the area centralis at its hub.

MATERIALS AND METHODS

Subjects

Retinae from four normal adult cats, two adult Seal Point Siamese cats and two cats deprived of vision in one eye from birth until the day of the experiment by monocular lid-suture (MD), provided the data for this study. One of the MD cats was deprived until 10 weeks of age; the other was deprived until 7 months of age. Injections of horseradish peroxidase (HRP) were made into the LGNd of two normal cats, one Siamese cat, and the two MD cats. The optic tracts were injected in the rest of the animals.

Surgery

Nembutal was administered intraperitoneally to induce and intravenously to maintain anesthesia. The animal's head was positioned in a stereotaxic apparatus and the skin, bone, and dura mater covering the appropriate regions were removed. The cortex was covered by a 4% solution of agar in saline as protection. Body temperature was

Accepted June 21, 1983.

monitored continuously and maintained automatically at 37–38°C.

Neosynephrine was used to retract the nictitating membranes and atropine was employed to dilate the pupils. The corneas were protected from desiccation with zero-power contact lenses and the optic discs and areae centrales were projected onto a tangent screen located 1.14 m from the cat's retina.

Electrophysiological recording

Prior to all HRP injections electrode penetrations were made into the LGNd in order to locate the representation of predetermined parts of the visual field. Multiple- and single-unit activity was recorded with low impedance (1–3 megohm) microcapillary electrodes filled with 4 M NaCl. Neuronal responses were amplified conventionally, displayed on the oscilloscope, and monitored by ear. For all units and groups of units studied response fields (the area of the visual field within which a visual stimulus elicited a response) were determined and the distance from the center of each response field to the area centralis projection was measured. Since the animals were not paralyzed, each field was mapped twice and the areae centrales were plotted before and after each plot to verify that the eyes had not moved.

Multiple HRP injections (four to five) were made into the optic tract about 4 mm from the optic chiasm. In all cats injections were closely spaced and made across the entire width of the optic tract. Injections were started in the ventral part of the optic tract and withdrawn slowly, until, at the end of the injection, the electrode was in the dorsal portion of the optic tract. Multiple injections made in this fashion expose the entire optic tract to HRP and are necessary to label all types of ganglion cells since fibers of different diameters are reportedly segregated within the optic tract (Guillery et al., '82). In agreement with this we find that single injections into the optic tract do not randomly label cells of all types.

Electrophoretic injection

Once a satisfactory site 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 μ A (1.5 seconds on, 0.5 seconds off) for a period of 2–3 hours. The sites resulting from these injections appeared well localized and virtually black with HRP reaction product. This suggests that such long electrophoretic injections slowly deposit a high concentration of HRP over a small region. Shorter injections, regardless of the amount of HRP injected, did not give satisfactory labeling.

Histology and histochemistry

Animals were maintained for approximately 40 hours following HRP injections. They then were anesthetized and perfused through the heart with 700 ml of 35°C lactated Ringer's solution containing 0.1% heparin, followed by 1,000 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 2–4 days in a 30% sucrose solution and then frozen sectioned at 50 μ m. Sections were collected in 0.1 M TRIS-HCl buffer (pH 7.4), reacted for 20 minutes in 0.1 M TRIS buffer containing 0.03% p-phenyldiamine dihydrochloride, 0.06% pyrocatechol, and 0.02% H₂O₂ (PPD-PC reagent), and transferred back into 0.1 M TRIS-HCl buffer.

Whole retinæ were removed and reacted immediately after the perfusion. The best labeling was observed when the reaction was begun without delay. All retinæ were rinsed in 0.1 M TRIS buffer (pH 7.4) for 5 minutes, incubated in 1% cobalt chloride in TRIS buffer containing 0.5% DMSO for 20 minutes at 35°C, rinsed in TRIS buffer at 35°C for 5 minutes, rinsed in 0.1 M phosphate buffer (pH 7.4) at 35°C for 5 minutes, prereacted in PPD-PC reagent containing 0.5% DMSO (without H₂O₂) at 35°C for 15 minutes, reacted with fresh PPD-PC reagent containing 0.5% DMSO (with H₂O₂) at 35°C for 20 minutes, and rinsed in phosphate buffer for 30 minutes. Some of the animals in this study also provided data for two previous studies (Leventhal, '82; Leventhal and Hirsch, '83). Photomicrographs of retinal ganglion cells illustrating the type of staining obtained using the foregoing procedures are presented in these papers.

Dendritic field analysis

Retinal ganglion cells of all types (see Leventhal, '82, for description) were drawn using a Nikon orthoplan microscope system, a $\times 40$ or $\times 100$ oil immersion objective, and a camera lucida. Cells were sampled from all regions of retina containing satisfactory labeling using a $\times 10$ objective. At this magnification much of the dendritic field was not visible, so the experimenter could not have affected the sampling by favoring cells elongated in a particular direction. Drawings of all cells were traced onto a digitizing tablet (Houston Instruments) interfaced to the laboratory PDP 11/23 (Digital Equipment) computer system. The cells shown in Figures 1 and 2 were drawn on a Prism 80 (Integral Data Systems) graphics printer. Each cell is comprised of 1,000–2,000 points. Since the accuracy of the digitizing tablet used to transfer the cell into Cartesian coordinates is 0.005 inches we were able to represent the cells in our sample very accurately. The Cartesian coordinates comprising the drawing were stored on a DSD 880 Winchester disc (Data Systems Design) and the dendritic fields of all cells were analyzed quantitatively as described below.

First, the Cartesian coordinates comprising the cell were combined algebraically to find the geometric center of each dendritic field (solid squares in Figs. 1A,C, 2A,C). The analyses were based only on those coordinates which represented parts of dendrites in the sublamina of the inner plexiform layer in which the cell arborized. The cell body and stem dendrites were excluded from the analysis since electron microscopic studies (Stevens et al., '80) indicate that these make virtually no synapses.

Once the center of the dendritic field was found, a line was computed between the center and each of the 1,000–2,000 points comprising the cell. These lines were defined as vectors of unit length. The angles between each of these vectors and the vertical meridian as defined by the nasotemporal division of the retina were then computed. The nasotemporal division was determined in all retinæ from the distribution of labeled ganglion cells resulting from HRP injections into the LGNd or optic tract. Next, circu-

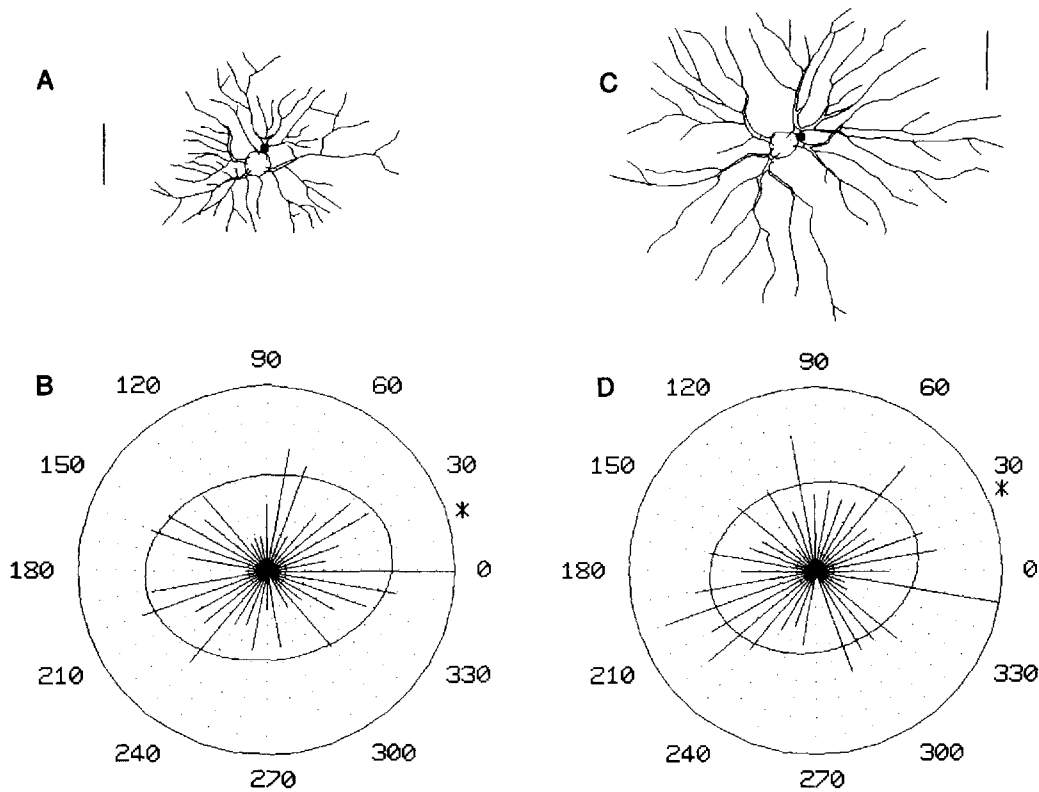


Fig. 1. Computer representations of HRP-stained alpha cells. The cells in A and C were, respectively, 1 mm and 5 mm from the area centralis. The scale bars in A and C correspond to 80 μ m and are aligned parallel to the vertical meridian of the retina. The circular histograms in B and D were based on the cells shown in A and C, respectively. In each histogram 90 refers to 90° and represents vertical as defined by the nasotemporal division of the retina. The center of the histogram corresponds to the geometric center of the cells dendritic field; the center of the dendritic fields of the cells in A and C are marked by solid squares. The length of the lines emanating

from the center of the circular histogram is proportional to the amount of dendritic coverage in each 10° segment within the dendritic field. The asterisks in B and D mark the orientations of the dendritic fields of the cells in A and C. These were computed as described in Methods. The ratio of the long and short axes of the ellipses in B and D provide a measure of dendritic field elongation; the angle of the long axis of each ellipse provides a second measure of dendritic field orientation. The alpha cell shown in A had an orientation bias of 0.13 and an ellipse axes ratio of 1.2. The alpha cell shown in C had an orientation bias of 0.16 and an ellipse axes ratio of 1.3

lar symmetry was eliminated since we were interested in orientation not direction, and for our purposes angles of 0° and 180°, for example, were equivalent. The sum of vectors was then divided by the number of vectors, yielding a vector having a particular angle and length. The angle of this resultant vector gave the orientation of the dendritic field. The length of the resultant vector, termed the *orientation bias*, provided a measure of how oriented the dendritic field was. Orientation biases range from 0 to 1 with 0 being completely unoriented. Our measure of orientation bias is analogous to the one used recently by Levick and Thibos ('82) in their physiological study of the orientation sensitivity of cat retinal ganglion cells.

The circular histograms in Figures 1B,D and 2B,D are based upon the cells shown in Figures 1A,C and 2A,C, respectively. In each histogram 90 refers to 90° and has been made to correspond to the nasotemporal division. The asterisk indicates the orientation of the dendritic field. The center of the circular histogram corresponds to the geometric center of the dendritic field; the length of the lines emanating from the center is proportional to the amount of dendritic coverage at the respective angle within the dendritic field. The ellipse in each polar plot was

fitted to all points representing dendrites in the inner plexiform layer (Batschalet, '78). The ratio of the long to short axes of the ellipse provides a measure of how elongated each dendritic field is; a cell's *ellipse axes ratio* is related linearly to its orientation bias. The ellipse axes ratio is useful in relating dendritic field shape to receptive field shape (Hammond, '74). The inclination of the major axis of the ellipse provides a second measure of the orientation of the dendritic field. More complete descriptions of the mathematical and statistical techniques employed can be found in Mardia ('72), Zar ('74), and Batschalet ('78).

RESULTS

Overall, we quantified the dendritic fields of 840 retinal ganglion cells. All morphological classes of cells were studied. Cells were sampled from regions of nasal and temporal retina ranging from 0 to 16 mm and 0 to 11 mm from the area centralis, respectively.

As a first step in our analysis it was necessary to determine whether or not retinal ganglion cells have oriented dendritic fields. Histograms illustrating the ellipse axes ratios and orientation biases of all 840 retinal ganglion cells analyzed are shown in Figure 3A,B. These histo-

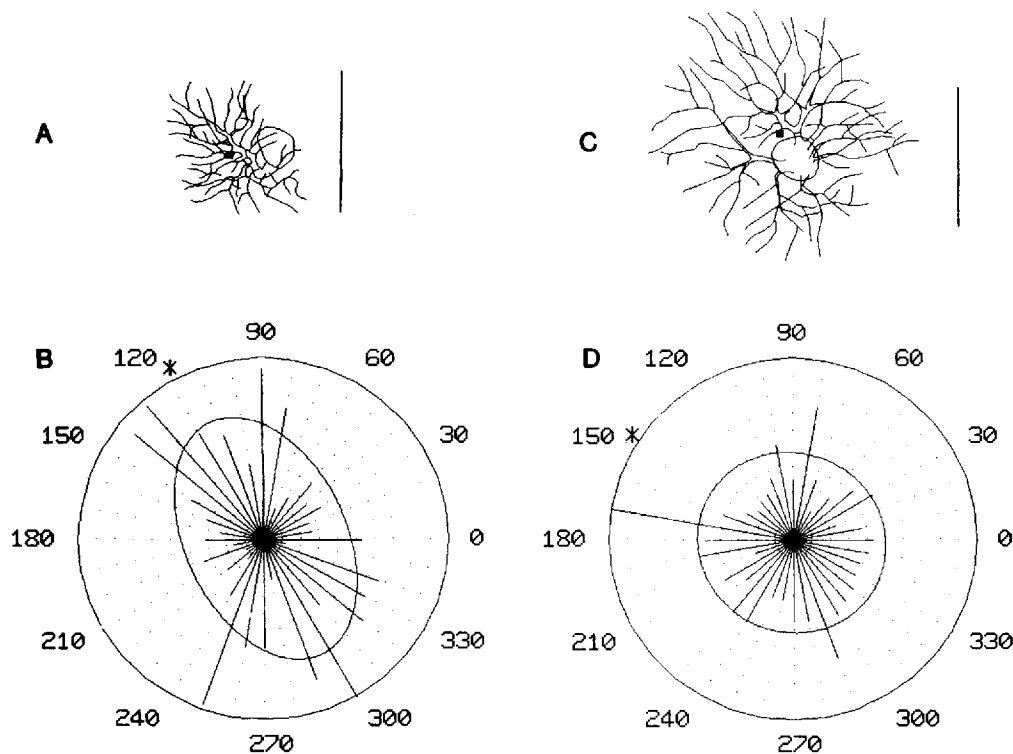


Fig. 2. Computer representations of HRP-stained beta cells. The cells in A and C were, respectively, 1 mm and 5 mm from the area centralis. Scale bars correspond to $80 \mu\text{m}$ and are aligned parallel to the vertical meridian of the retina. The analyses illustrated in B and D were carried out on the cells

shown in A and C, respectively. Conventions are as in Figure 1. The beta cell shown in A had an orientation bias of 0.27 and an ellipse axes ratio of 1.6. The beta cell shown in C had an orientation bias of 0.01 and an ellipse axes ratio of 1.0.

grams show that the dendritic fields of virtually all retinal ganglion cells exhibit some degree of elongation and orientation bias. It thus becomes a problem to determine what degree of asymmetry is significant. Since, as described in the methods, the orientation bias of each dendritic field is based upon many hundreds of points, a value of about 0.1 indicates significance at the 0.01 level (Zar, '74). It is not strictly legitimate, however, to conclude that dendritic fields with bias values of greater than 0.1 are significantly oriented since points along the same dendrite cannot be considered independent; the results of this sort of analysis must be interpreted cautiously. Additional evidence described in the next section supports the suggestion that a cell must have an orientation bias of 0.1 or greater to be considered oriented.

Relationship between dendritic field orientation and retinal position

The basic finding of this study is that the dendritic fields of cat retinal ganglion cells are oriented radially, that is, like the spokes of a wheel having the area centralis at its hub. A histogram supporting this, which includes all cells studied, is shown in Figure 4. For each cell we have computed the difference between the dendritic field orientation of the cell and the angle of the cell on the retina (polar angle). For instance, a cell having a dendritic field orientation of 0° and a polar angle of 0° (the horizontal meridian of the retina) is oriented exactly radially. This cell has an "angle difference" of 0 in Figure 4. At the other extreme a cell

with a dendritic field orientation of 0° and a polar angle of 90° (the vertical meridian of the retina) has an angle difference of -90° . Similarly, a cell with a dendritic field orientation of 180° (horizontal) and a polar angle of 90° has an angle difference of 90° . The latter two cells are oriented tangentially, that is, perpendicular to the line connecting them to the area centralis.

If the dendritic field orientations of retinal ganglion cells are unrelated to polar angle, then the histogram in Figure 4 should be flat and range from -90° to $+90^\circ$. If, on the other hand, retinal ganglion cells tend to be oriented radially, then the distribution should be unimodal and peak at 0° . Our statistical analysis indicates that the latter is clearly the case. The Rayleigh test and the V test both show the distribution is not flat ($z = 142.0$, $P < 0.0000001$) and the Watson test indicates that the mean of the distribution (-2°) is not significantly different from 0° ($P < 0.001$). In this and all of the following analyses significance values of less than 0.0000001 are presented as $P < 0.0000001$. The actual z values (Rayleigh test) and u values (V test) upon which the significance values are based are presented in the text.

Although the foregoing analysis shows that the dendritic fields of most retinal ganglion cells are oriented radially, it is clear from Figure 4 that the orientations of many cells do not match their polar angle. The histograms in Figure 5 explain some of this variability and provide additional evidence that an orientation bias of 0.1 is a reasonable point at which to separate oriented from unoriented dendritic fields.

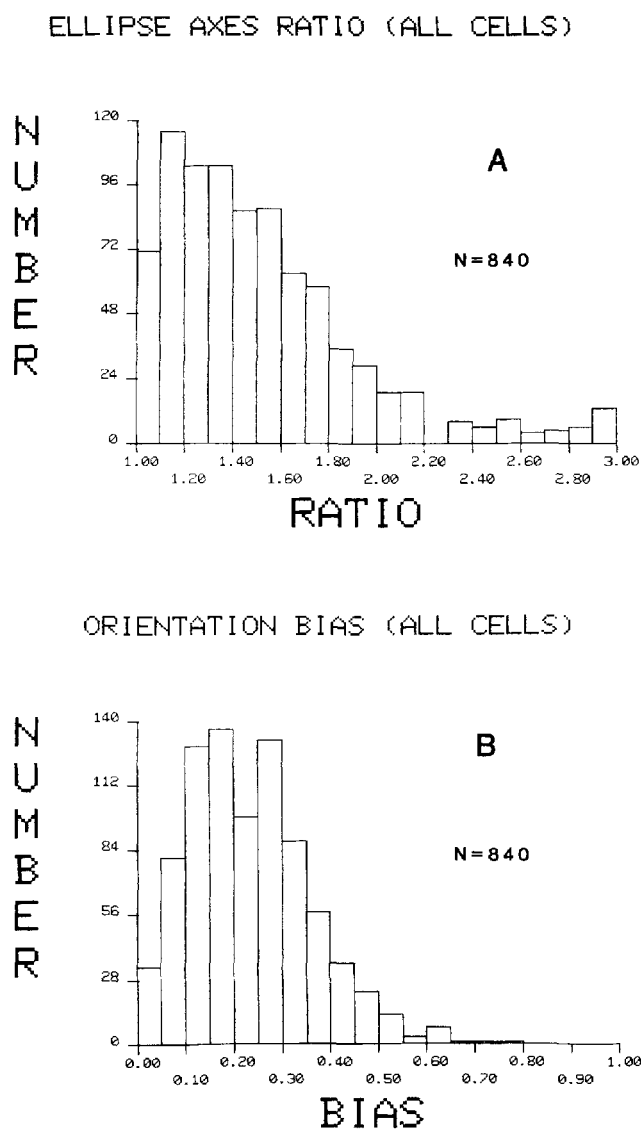


Fig. 3. Ellipse axis ratios (A) and orientation biases (B) of all cells analyzed. An ellipse axes ratio of 1.0 indicate that a cell has a perfectly circular dendritic field; progressively higher ratios indicate increasing elongation. Orientation biases (described in Methods) range from 0 to 1 with 0 being completely unoriented. Notice that most retinal ganglion cells have asymmetric dendritic fields. An orientation bias of 0.1 seems to be a reasonable point at which to separate oriented from unoriented cells.

If a dendritic field is not oriented significantly, then the dendritic field orientation computed for that cell is a random value and should not be related systematically to polar angle. The histogram in Figure 5A shows that for dendritic fields with orientation biases of less than 0.08 there is no relationship between dendritic field orientation and polar angle. The distribution must be considered flat ($z = 0.2$, $P < 0.5$, Rayleigh test; $u = 0.7$, $P < 0.25$, V test) and the mean of the distribution cannot be considered zero. Similarly, the dendritic fields of cells with biases between 0.08 and 0.1 show only a weak tendency to be oriented radially ($z = 3.1$, $P < 0.05$, Rayleigh test; $u = 2.5$, $P < 0.01$, V

ANGLE DIFFERENCE FOR ALL CELLS

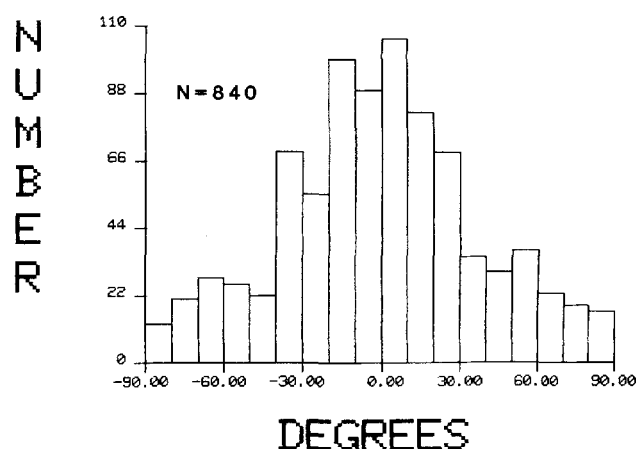


Fig. 4. Differences between dendritic field orientation and polar angle for all 840 retinal ganglion cells studied. An angle difference of 0 indicates that the dendritic field of a cell is oriented radially, that is, oriented parallel to the line connecting it to the area centralis. Angle differences of -90° and $+90^\circ$ indicate that the cell was oriented tangentially, i.e., oriented perpendicular to the line connecting it to the area centralis. Notice that retinal ganglion cells tend to be oriented radially.

test; Fig. 5B). On the other hand, the dendritic fields of cells with biases over 0.1 show an impressive tendency to be oriented radially ($z = 132.0$, $P < 0.0000001$, Rayleigh test; $u = 16.2$, $P < 0.0000001$, V test; Fig. 5C,D). These results support the suggestion that a dendritic field must have a bias of 0.1 or greater to be considered oriented. Accordingly, we consider the cells shown in Figures 1A,C and 2A to have oriented dendritic fields (biases 0.13, 0.16, and 0.27, respectively) while the cell shown in Figure 2C must be considered unoriented (bias 0.01). It is noteworthy that the results of Levick and Thibos ('82) also indicate that, in general, only retinal ganglion cells with physiologically determined orientation biases of 0.1 or greater exhibit meaningful orientation sensitivity. Thus, we will only deal with retinal ganglion cells exhibiting biases of 0.1 or greater in the following sections. These cells constitute 88% of our sample.

Differences related to abnormal visual experience and central projection

In this study ganglion cells were sampled from the retinae of normal cats, the deprived retinae of MD cats, and the contralateral temporal retinae of Siamese cats. All of the analyses described in this paper were carried out separately on cells sampled from the three groups of animals. Our results indicate that a systematic relationship between dendritic field orientation and polar angle is present in all of these groups of animals. The histograms in Figure 6 show separately the angle differences for the three groups. In all groups dendritic fields are oriented radially ($z = 33.0$, $P < 0.0000001$, Rayleigh test; $u = 8.0$, $P < 0.0000001$, V test; worst case). Since one of the MD cats was deprived for a much longer period (7 months) than the other (10 weeks), we analyzed the results for the two cats

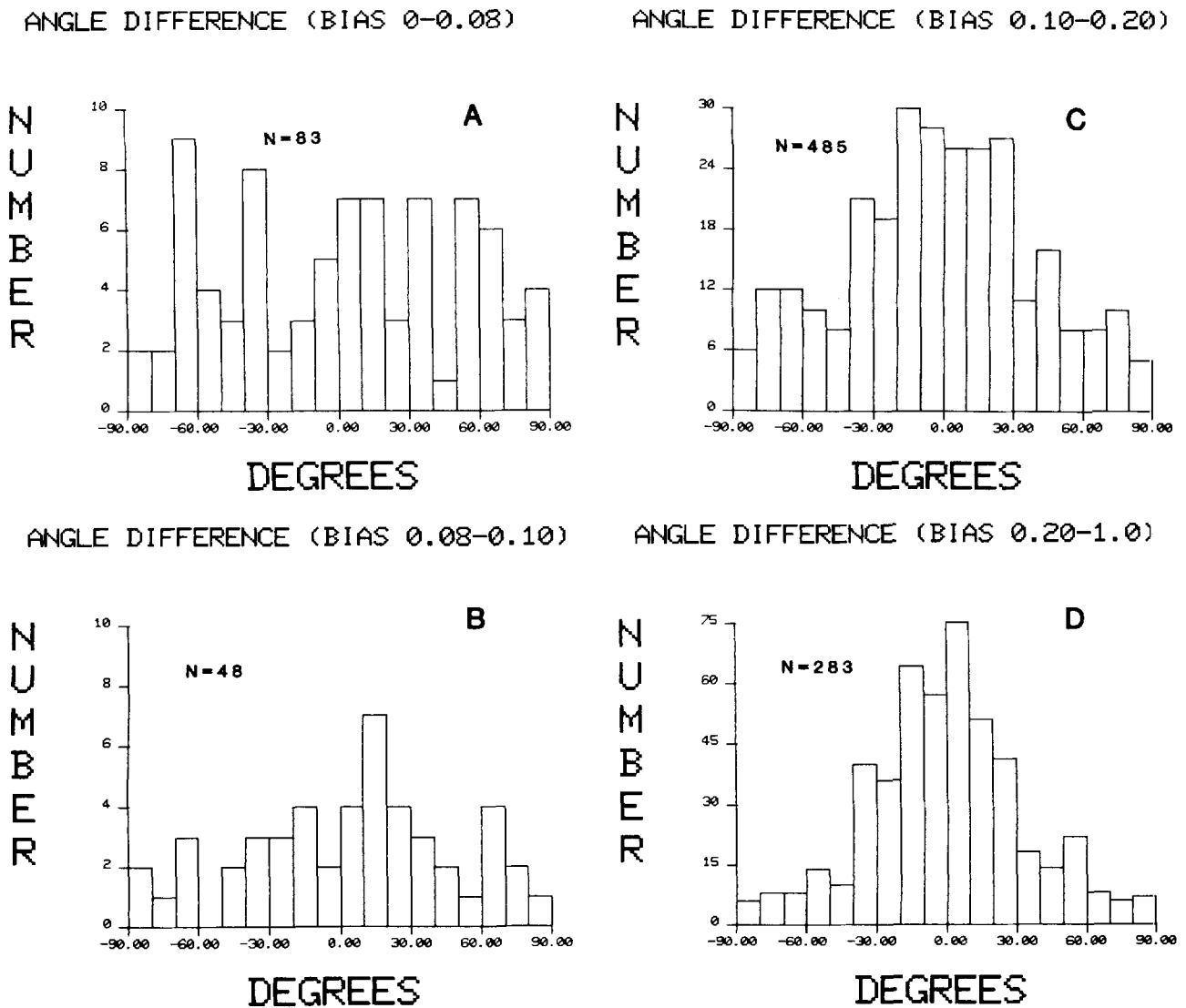


Fig. 5. Angle differences for retinal ganglion cells exhibiting different degrees of orientation bias. The range of biases represented in each histogram is indicated. The ranges are inclusive so cells with biases of 0.08, 0.1, and 0.2 are represented in more than one histogram. The numbers of cells included in each histogram are also shown. Conventions are as in Figure 4. Notice that there is no relationship between polar angle and dendritic field orientation for cells with orientation biases less than 0.1.

separately. No differences were observed. It appears, therefore, that dendritic field orientation is not affected by the absence of normal pattern vision and that retinal ganglion cells have normally oriented dendritic fields at 10 weeks after birth. Since cells in the contralateral temporal retinae of Siamese cats have normally oriented dendritic fields it seems that most retinal ganglion cells are oriented radially whether or not their axons are misrouted at the optic chiasm.

Differences related to ganglion cell class

All of the analyses described in this paper were carried out separately on each of the different morphological classes of retinal ganglion cells. We observed no differ-

ences related to ganglion cell class. The histograms in Figure 7 show separately the results for alpha cells, beta cells, and "other types" of cells. The dendritic fields of all cell types appear to be oriented radially ($z = 34.0, P < 0.0000001$, Rayleigh test; $u = 8.0, P < 0.0000001$, V test; worst case). Since the histogram representing "other types" of cells includes gamma, epsilon, g1, and g2 cells (Leventhal, '82), we analyzed these types separately; no differences were evident. It appears that dendritic field orientation and polar angle are related for all classes of retinal ganglion cells.

Differences related to retinal eccentricity

In order to determine if there are any differences in dendritic field orientation related to distance from the area

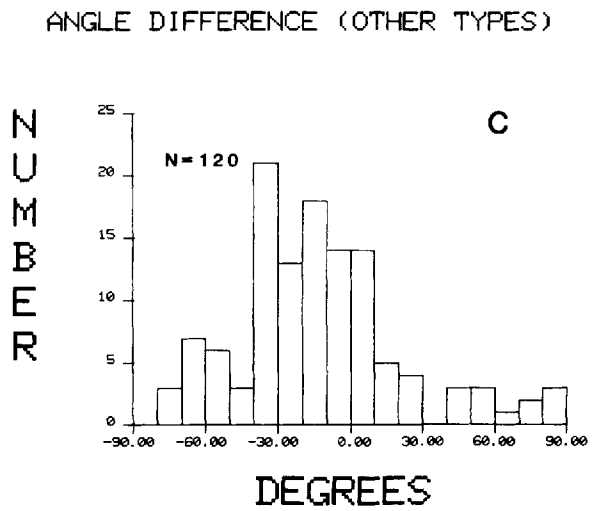
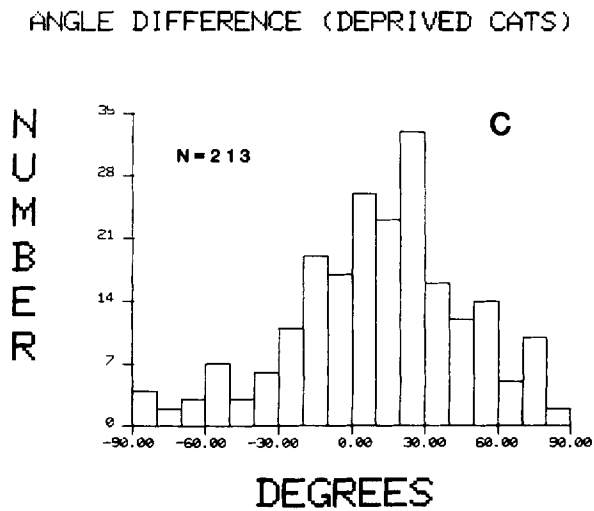
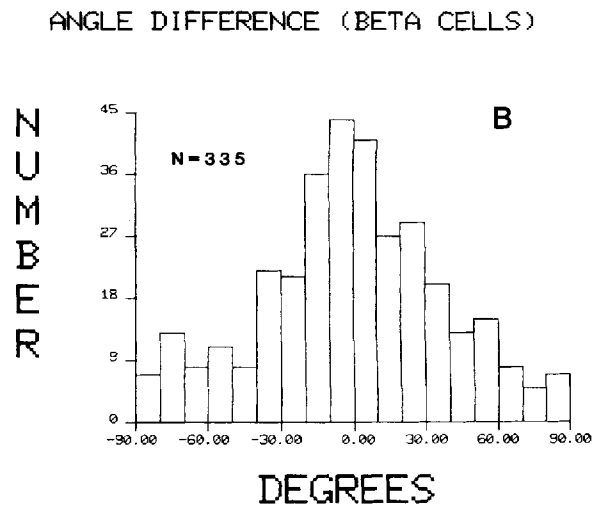
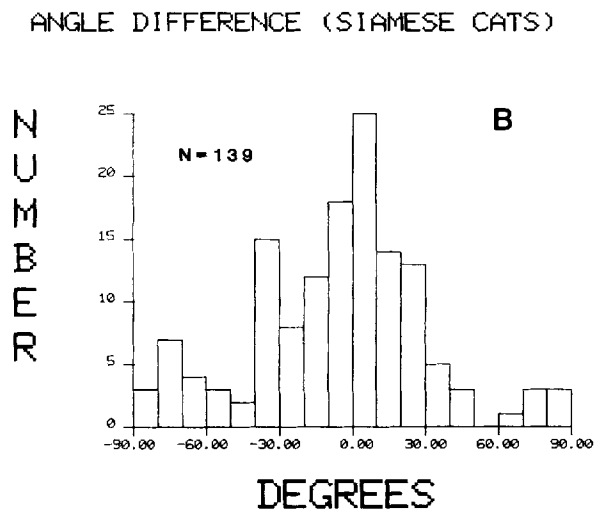
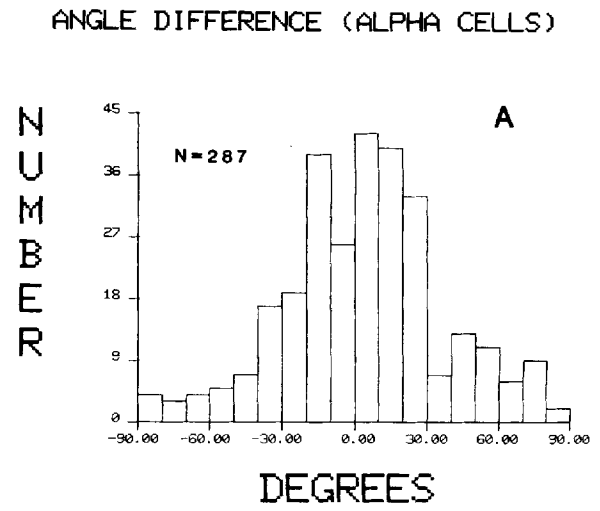
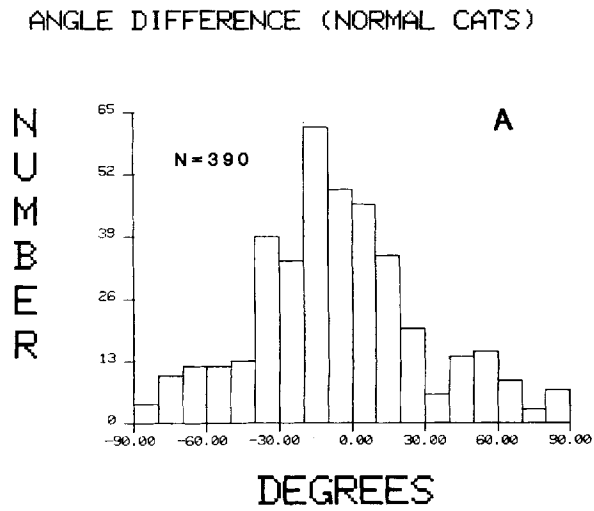


Fig. 6. Angle differences for cells sampled from normal cats (A), the contralateral temporal retinae of Siamese cats (B), and the deprived retinae of monocularly deprived cats (C). Conventions are as in Figure 4. Notice that in all three groups retinal ganglion cells tend to be oriented radially.

Fig. 7. Angle differences for alpha (A), beta (B), and other types (C; gamma, epsilon, g1, and g2) of cat retinal ganglion cells. Conventions are as in Figure 4. Notice that all morphological types of retinal ganglion cells tend to be oriented radially.

centralis, all analyses described in this paper were carried out separately on cells located at different retinal eccentricities. Within 3 mm of the area centralis, 0.5-mm intervals were analyzed separately; in more peripheral regions 1-mm intervals were analyzed separately. The results of these analyses are summarized in Figure 8. Our findings indicate that, for cells located less than 0.5 mm from the center of the area centralis, dendritic field orientation is unrelated to polar angle ($z = 1.6, P < 0.2$, Rayleigh test; $u = 1.8, P < 0.05$, V test; Fig. 8A). In contrast, in all regions of retina between 0.5 and 8 mm from the area centralis there is a very strong relationship between dendritic field orientation and polar angle ($z = 129.0, P < 0.0000001$, Rayleigh test; $u = 16.0, P < 0.0000001$, V test; Fig. 8B). A

similar relationship is evident out to the rim of the retina (Fig. 8D). However, a somewhat higher proportion of cells are oriented tangentially (perpendicular to the line connecting the cell to the area centralis) at the margin of the retina (Fig. 8D; cf. Kock and Reuter, '78; Kock, '82). This appears to be due more to the cell's location near the rim of the retina than to its greater distance from the area centralis. More cells are oriented tangentially at the margins of temporal and nasal retina (8-11 mm and 13-16 mm from the area centralis, respectively; $z = 10.0, P < 0.0001$, Rayleigh test; $u = 4.3, P < 0.0001$, V test; Fig. 8D) than between 8-13 mm from the area centralis in nasal retina ($z = 30.0, P < .0000001$, Rayleigh test; $u = 7.6, P < .0000001$, V test; Fig. 8C). Thus, it appears that dendritic field orien-

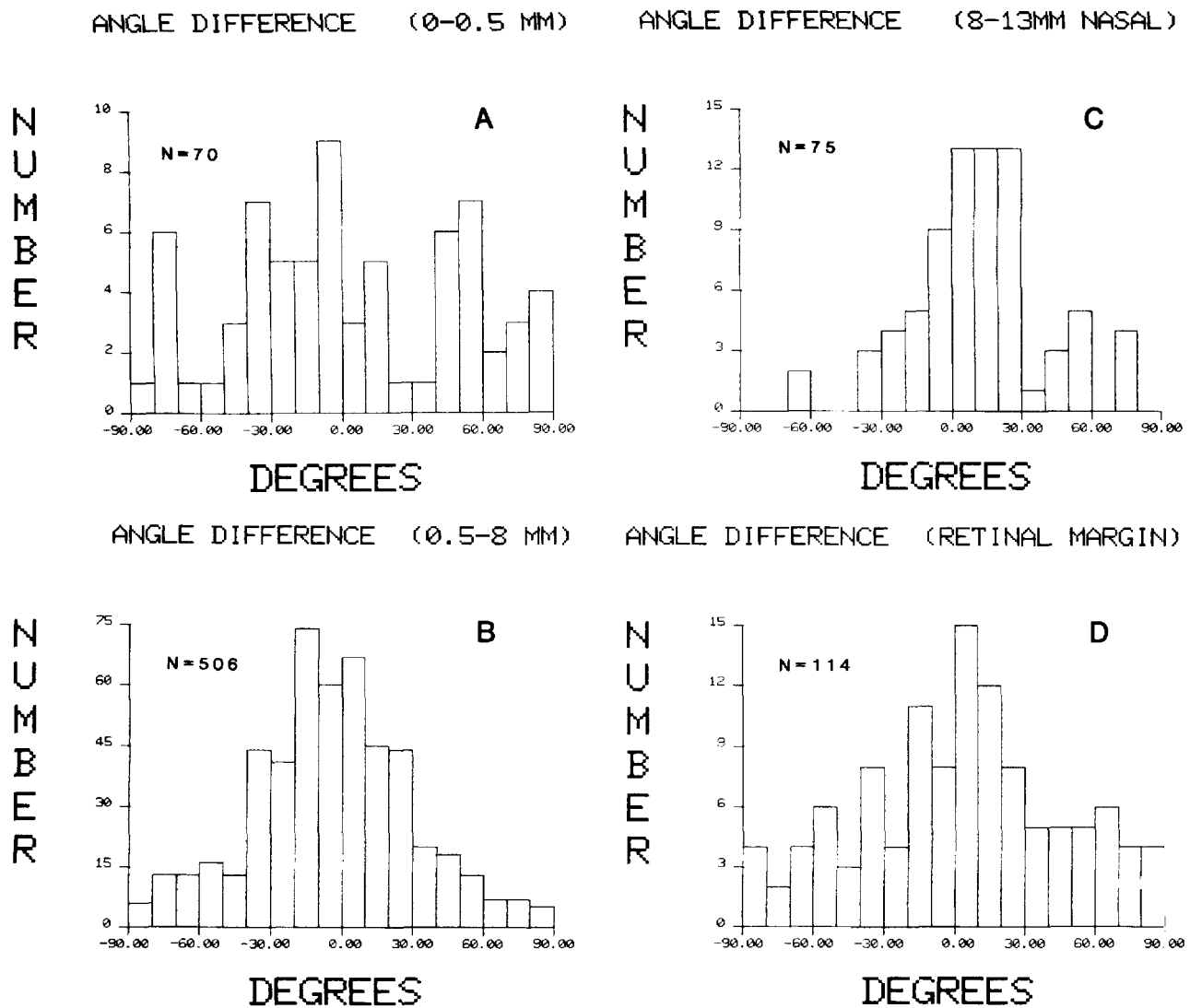


Fig. 8. Angle differences for cells located at different distances from the area centralis. Conventions are as in Figure 4. The regions of retina upon which the histograms are based are indicated. Retinal margin refers to the outermost 3 mm of the retina. This is 8-11 mm from the area centralis temporally and 13-16 mm from the area centralis nasally. Cells sampled from

the margins of nasal and temporal retina were analyzed separately and no differences were observed. All cells sampled from the nasal and temporal retinal margin are combined in D. Notice that cells in all regions of retina (B-D) except the central 0.5 mm (A) tend to be oriented radially.

tation is related to polar angle in all parts of cat retina outside of the area centralis; however, at the retinal margin this relationship is somewhat weaker.

Meridional differences

Our results indicate that most retinal ganglion cells, regardless of their polar angles, are oriented parallel to the line connecting them to the area centralis. Angle differences for cells located within 22.5° of the horizontal, diagonal, and vertical meridians are shown separately in Figure 9. We find that along all retinal meridians, most cells are oriented radially ($z = 22.0$, $P < 0.0000001$, Rayleigh test; $u = 7.0$, $P < 0.0000001$, V test; worst case).

The relationship between dendritic field orientation and retinal position is strongest in and near the visual streak (horizontal meridian) of the retina. Only 20% of ganglion cells within 22.5° of horizontal exhibited angle differences greater than 30° (Fig. 9A). 39% of cells within 22.5° of the diagonal meridian (Fig. 9B) and 46% of cells within 22.5° of the vertical meridian (Fig. 9C) were oriented more than 30° off their respective polar angles.

Overall in cat retina, ganglion cell dendritic fields were oriented somewhat more horizontally than their polar angles predicted. This was true in all regions except within 5° of vertical meridian and (obviously) close to the horizontal meridian (Fig. 10). Consequently, very few cells near the horizontal meridian were oriented diagonally or vertically while significant numbers of cells outside of the visual streak were oriented horizontally. As a result there is an overrepresentation of horizontal dendritic fields in cat retina: 34% of cells sampled were within 22.5° of the horizontal meridian but 45% of cells sampled had dendritic fields oriented within 22.5° of horizontal. It appears that dendritic field orientation is influenced by both major retinal specializations—the area centralis and the visual streak.

DISCUSSION

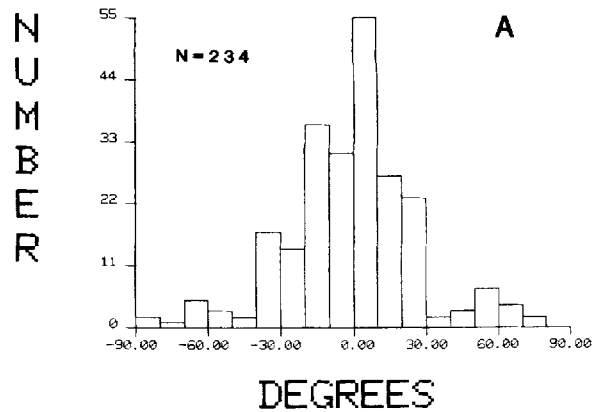
This study provides evidence that most alpha, beta, and other types of ganglion cells in cat retina have radially oriented dendritic fields. The relationship between dendritic field orientation and polar angle is evident in all parts of cat retina other than the central 0.5 mm and is strongest in and around the visual streak. Neither the abnormal visual experience produced by monocular lid-suture nor the chiasmatic misrouting of retinal ganglion cells in Siamese cats affects this relationship.

Relation to physiological studies

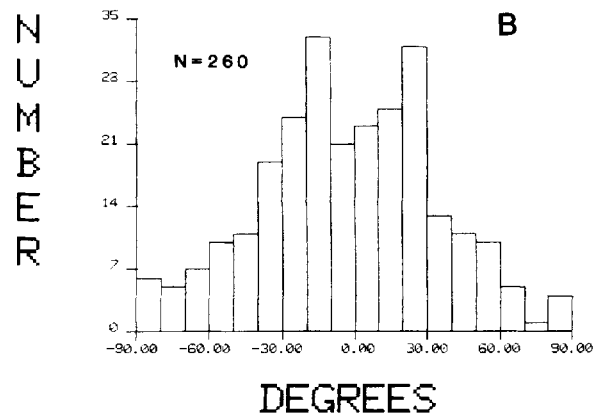
There are two physiological studies of cat retinal ganglion cells which relate to the present anatomical one. Hammond ('74) studied the shape of the receptive fields of ganglion cells in cat retina and found most to be elliptical with major to minor axes ratios ranging from 1.0 to 1.8. There was an overrepresentation of horizontal receptive fields in Hammond's sample. Our anatomical results indicate that most retinal ganglion cells have elongated dendritic fields. Most of the cells in our sample had ellipse axes ratios between 1.0 to 1.8; we also found an overrepresentation of horizontal dendritic fields. It appears, therefore, that there is a correspondence between the dendritic field shape and the receptive field shape of cat retinal ganglion cells.

It is important to note that Hammond ('74) studied receptive field shape, not the orientation sensitivity of cat

ANGLE DIFFERENCE (HORIZONTAL)



ANGLE DIFFERENCE (DIAGONAL)



ANGLE DIFFERENCE (VERTICAL)

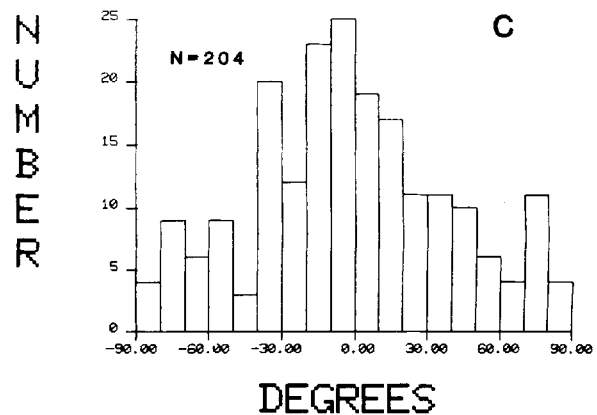


Fig. 9. Angle differences for cells located within 22.5° of the horizontal (0°), diagonal (45 and 135°), and vertical (90°) meridians of the retina. Conventions are as in Figure 4. Notice that most retinal ganglion cells, regardless of retinal angle, tend to be oriented radially. However, this relationship is strongest for cells close to the horizontal meridian (A) of the retina.

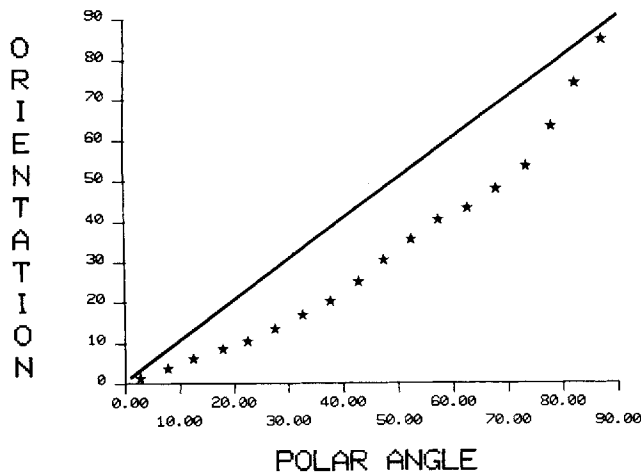


Fig. 10. Dendritic field orientation as a function of polar angle. This figure is based upon cells having orientation biases greater than 0.1 located more than 0.5 mm from the area centralis. Stars indicate the mean of the dendritic field orientations of cells located in 5° increments off the horizontal meridian. All means would fall along the solid line if dendritic fields throughout cat retina were simply oriented radially. However, all points fall below the solid line, suggesting that dendritic fields in cat retina tend to be oriented somewhat more horizontally than their polar angles predict.

retinal ganglion cells. A recent report by Levick and Thibos ('82) has described in detail the orientation sensitivity of retinal ganglion cells. Their results indicate that about 70% of cat retinal ganglion cells exhibit orientation preferences. Most of the cells in their sample exhibited orientation biases between 0.1 and 0.3. Levick and Thibos ('82) also found that in all regions of retina studied other than the central 2° most retinal ganglion cells responded best to lines oriented radially. Levick and Thibos ('82) concluded that the center mechanism of ganglion cell receptive fields is elongated along the line joining the cell to the area centralis.

The results of this study are compatible with the conclusions of Levick and Thibos ('82). We have found that most ganglion cell dendritic fields have orientation biases between 0.1 and 0.3. Moreover, in all regions of cat retina except the central 0.5 mm (the central 2°) the dendritic fields of most cells are oriented radially. In view of the foregoing correspondences it seems reasonable to conclude that cat retinal ganglion cells are sensitive to stimulus orientation because they have oriented dendritic fields.

Technical considerations

Problems with the interpretation of this study could result if a large number of the cells analyzed were incompletely stained by the HRP procedures employed. We feel that incomplete staining of retinal ganglion cells can be eliminated as a problem for a number of reasons. First, the staining of nearly all of the alpha cells and most of the beta cells in our sample appear comparable to the published drawings of Golgi-stained alpha and beta cells (Boycott and Wassle, '74; Kolb et al., '81). We analyzed alpha and beta cells with this appearance separately and found no differences between the results for these and the remaining cells. Second, both the ellipse axes ratios and the orientation biases of the dendritic fields in our sample were

comparable to the ellipse axes ratios (Hammond, '74) and orientation biases (Levick and Thibos, '82) of retinal ganglion cell receptive fields. Such correspondences would be unlikely if our cells were incompletely stained. Finally, the relationship between dendritic field orientation and polar angle we have observed could only have resulted from incomplete staining if HRP selectively fills those dendrites parallel to the line joining the cell to the area centralis. This possibility seems extremely unlikely. We conclude that incomplete staining of cells in our sample had no significant effect upon our results.

Developmental implications

In the cat most cortical neurons are not orientation sensitive at birth. The proportion of orientation-sensitive cortical cells increases dramatically during the first weeks of life (Pettigrew, '74; Fregnac and Imbert, '78). The dendritic fields and receptive fields of cat retinal ganglion cells are also immature at birth; at 3 weeks of age the dendritic fields of kitten retinal ganglion cells have not yet reached their adult dimensions (Rusoff and Dubin, '78). Since the dendritic fields of retinal ganglion cells are still developing during the period when cortical cells are becoming orientation sensitive, it is possible that the development of orientation sensitivity in the retina must precede the development of orientation sensitivity in the visual cortex. A study of the development of dendritic field orientation in kitten retina should provide more information concerning the mechanisms mediating the development of orientation sensitivity in the visual pathways.

We have provided evidence that retinal ganglion cells are orientation sensitive because they have oriented dendritic fields. It is possible that the development of orientation sensitivity in cat retina is prerequisite to the development of orientation sensitivity in visual cortex. In the following paper (Leventhal, '83) evidence is provided that, as in the retina, cells in striate cortex tend to respond best to lines oriented radially, i.e., oriented parallel to the line connecting their receptive fields to the area centralis projection.

ACKNOWLEDGMENTS

Support was provided by UPHS grant EY03427. We are grateful to E. Steck for secretarial assistance and W. Wallace for skillful, tireless technical assistance. Dr. H.V.B. Hirsch provided valuable discussion and comments on the manuscript.

LITERATURE CITED

- Batschalet, E. (1978) Second order statistical analysis of directions. In: K. Schmidt-Koenig and W.T. Keeton (eds): *Animal Migration, Navigation and Homing*. Berlin: Springer-Verlag, pp. 3-24.
- Boycott, B.B., and H. Wassle (1974) The morphological types of ganglion cells of the domestic cat's retina. *J. Physiol. (Lond.)* 240:397-419.
- Fregnac, Y., and M. Imbert (1978) Early development of visual cortical cells in normal and dark-reared kittens: Relationship between orientation selectivity and ocular dominance. *J. Physiol. (Lond.)* 278:27-44.
- Guillery, R.W., E.H. Polley, and F. Torrealba (1982) The arrangement of axons according to fiber diameter in the optic tract of the cat. *J. Neurosci.* 6:714-721.
- Hammond, P. (1974) Cat retinal ganglion cells: Size and shape of receptive field centres. *J. Physiol. (Lond.)* 242:99-118.
- Hubel, D.H., and T.N. Wiesel (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol. (Lond.)* 160:106-154.

- Hubel, D.H., and T.N. Wiesel (1977) Ferrier lecture. Functional architecture of macaque monkey visual cortex. *Proc. R. Soc. Lond. [Biol.]* 198: 1-59.
- Kock, J.H. (1982) Dendritic tree structure and dendritic hypertrophy during growth of the Crucian carp eye. *J. Comp. Neurol.* 209:275-286.
- Kock, J.H., and T. Reuter (1978) Retinal ganglion cells in the Crucian carp (*Carassius carassius*). II. Overlap, shape and tangential orientation of dendritic trees. *J. Comp. Neurol.* 179:549-562.
- Kolb, H., R. Nelson, and A. Mariani (1981) Amacrine cells, bipolar cells and ganglion cells of the cat retina: A Golgi study. *Vision Res.* 21:1081-1114.
- Leventhal, A.G. (1982) Morphology and distribution of retinal ganglion cells projecting to different layers of the dorsal lateral geniculate nucleus in normal and Siamese cats. *J. Neurosci.* 2:1024-1042.
- Leventhal, A.G. (1983) Relationship between preferred orientation and receptive field position of neurons in cat striate cortex. *J. Comp. Neurol.* 220:476-483.
- Leventhal, A.G., and H.V.B. Hirsch (1983) Effects of visual deprivation upon the morphology of retinal ganglion cells projecting to the dorsal lateral geniculate nucleus of the cat. *J. Neurosci.* 3:332-344.
- Levick, W.R., and L.N. Thibos (1982) Analysis of orientation bias in cat retina. *J. Physiol. (Lond.)* 329:243-261.
- Mardia, K.V. (1972) *Statistics of Directional Data*. London: Academic Press.
- Pettigrew, J.D. (1974) The effect of visual experience on the development of stimulus specificity by kitten cortical neurones. *J. Physiol. (Lond.)* 237: 49-74.
- Rusoff, A.C., and M.W. Dubin (1978) Kitten ganglion cells: dendritic field size at 3 weeks of age and correlation with receptive field size. *Invest. Ophthalmol. Vis. Sci.* 17:819-821.
- Stevens, J.K., T.L. Davis, N. Friedman, and P. Sterling (1980) A systematic approach to reconstructing microcircuitry by electron microscopy of serial sections. *Brain Res. Rev.* 2:265-293.
- Vidyasagar, T.R., and J.V. Urbas (1982) Orientation sensitivity of cat LGN neurones with and without inputs from visual cortical areas 17 and 18. *Exp. Brain Res.* 46:157-169.
- Zar, J.H. (1974) *Circular distributions*. In: *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall, Inc.