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Retinal Constraints on Orientation Specificity in Cat Visual Cortex

J. D. Schall,[1] D. J. Vitek, and A. G. Leventhal

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

Most retinal ganglion cells (Levick and Thibos, 1982) and cortical cells (Leventhal, 1983; Leventhal et al., 1984) subserving peripheral vision respond best to stimuli that are oriented radially, i.e., like the spokes of a wheel with the area centralis at the hub. We have extended this work by comparing directly the distributions of orientations represented in topographically corresponding regions of retina and visual cortex. Both central and peripheral regions were studied. The relations between the orientations of neighboring ganglion cells and the manner in which the overrepresentation of radial orientations is accommodated in the functional architecture of visual cortex were also studied. Our results are based on an analysis of the orientations of the dendritic fields of 1296 ganglion cells throughout the retina and the preferred orientations of 1389 cells located in retinotopically corresponding regions of cortical areas 17, 18, and 19 in the cat.

We find that horizontal and vertical orientations are overrepresented in regions of both retina and visual cortex subserving the central 5° of vision. The distributions of the orientations of retinal ganglion cells and cortical cells subserving the horizontal, vertical, and diagonal meridians outside the area centralis differ significantly. The distribution of the preferred orientations of the S (simple) cells in areas 17, 18, and 19 subserving a given part of the retina corresponds to the distribution of the dendritic field orientations of the ganglion cells in that part of retina. The distribution of the preferred orientations of C (complex) cells with narrow receptive fields in area 17 but not C cells with wide receptive fields in areas 17, 18, or 19 subserving a given part of the retina matches the distribution of the orientations of the ganglion cells in that part of retina.

The orientations of all of the α-cells in 5-9 mm^2 patches of retina along the horizontal, vertical, and oblique meridians were determined. A comparison of the orientations of neighboring cells indicates that other than a mutual tendency to be oriented radially, ganglion cells with similar orientations are not clustered in the retina.

Reconstructions of electrode penetrations into regions of visual cortex representing peripheral retina indicate that columns subserving radial orientations are wider than those subserving nonradial orientations.

Our results provide evidence that the distribution of the preferred orientations of simple cells in visual cortex subserving any region of the visual field matches the distribution of the orientations of the ganglion cells subserving the same region of the visual field. It may be that the preferred orientations of first-order cortical cells are specified during development by the orientations of the ganglion cells ultimately providing their inputs.

Orientation specificity is a distinctive property of neurons in the visual cortex (Hubel and Wiesel, 1962, 1977). Most explanations of cortical orientation selectivity assume that the afferents to the cortex are not orientation sensitive (e.g., Hubel and Wiesel, 1962; von der Malsburg, 1973). Recently, however, it has been reported that most retinal ganglion cells (Levick and Thibos, 1982) and dorsal lateral geniculate nucleus neurons (Daniels et al., 1977; Lee et al., 1979; Vidyasagar and Urbas, 1982) are orientation sensitive. It has been argued that the degree of orientation sensitivity exhibited by most retinal ganglion cells is sufficient to be meaningful functionally (Thibos and Levick, 1985). Thus, it is possible that the orientation sensitivity exhibited by dorsal lateral geniculate nucleus (LGNd) and cortical cells may be derived somehow from that in the retina.

If this were the case, then the distributions of the preferred orientations of LGNd cells and different types of cortical neurons should correspond to the distributions of the orientations of the ganglion cells that ultimately provide their excitatory input. Earlier work suggested that this might in fact be the case, since most ganglion cells outside the area centralis prefer stimuli that are oriented radially (Levick and Thibos, 1982); most cells in striate (Leventhal, 1983) and extrastriate cortex (Leventhal et al., 1984) subserving regions outside the area centralis also prefer radially oriented stimuli.

These previous studies, although suggestive, did not show whether the distributions of orientations represented by topographically corresponding regions of retina and visual cortex were the same. Accordingly, this study addresses for the first time whether the distribution of the preferred orientations of visual cortical cells ultimately receiving input from any spot of retina, from center to periphery, matches the distribution of the orientations of the ganglion cell dendritic fields in that spot of retina.

Also, we have investigated for the first time the relations between the orientations of neighboring dendritic fields in the ganglion cell mosaic and examined how the overrepresentation of radial orientations is accommodated into the functional architecture of visual cortex.

Materials and Methods

Single-unit recording procedures

Subjects

Neurons from area 17 were recorded from 18 cats. Eleven cats were used to study area 18; eight cats were used in studying area 19. Some of these animals provided data for earlier studies (Leventhal, 1983; Leventhal et al., 1984).

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Correspondence should be addressed to A. G. Leventhal.

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Preparation

Cats were prepared for electrophysiological recording and electrophoretic injections as described previously (Leventhal and Hirsch, 1978, 1980; Leventhal and Schall, 1983). Under Fluothane anesthesia a cylindrical chamber was positioned over a craniotomy above visual cortex and was 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 hr) and gallamine triethiodide (7 mg/kg hr) was infused intravenously, and the animal was ventilated with a mixture of nitrous oxide (75%) and oxygen (25%). Body temperature was maintained at 38°C, and heart rate was monitored throughout the experiment. Expired pCO_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 diameter) were used to focus the eyes on a tangent screen positioned 114 cm from the cat. The projections of the optic disks 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). The locations of the areae centrales were also determined directly. Their locations did not differ significantly from those inferred from the projections of the optic disks.

Action potentials of cortical cells were recorded with epoxy-coated tungsten microelectrodes or microcapillary electrodes containing a saturated solution of Fast green dye in 2 M NaCl. The electrode was advanced using a piezoelectric microdrive (Burleigh Instruments). Cells were recorded from the cortical projection of the area centralis and from the cortical representation of peripheral regions of the retina. Cells were sampled at intervals of 75–200 μm in each penetration in order to study large regions of cortex and reduce sampling bias.

Receptive field mapping

The receptive field of a cortical neuron was defined as the largest area in visual space within which visual stimulation elicited a response. Receptive fields were plotted using light bars and both light and dark edges. A detailed description of the procedures has been given previously (Leventhal and Hirsch, 1978, 1980). The *eccentricity* of a cell's receptive field was defined as the distance from the center of the receptive field to the projection of the area centralis of the unit's dominant eye. Since the receptive fields were plotted on a tangent screen, all distances were converted to degrees of visual angle. The *polar angle* of a cell's receptive field was defined as the angle of the center of the receptive field off of the horizontal meridian. A polar angle of 0° describes a receptive field on the horizontal meridian, and a polar angle of 90° describes a receptive field on the vertical meridian.

Orientation sensitivity

Five to ten stimulus presentations at each of 8–18 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 under investigation, and the optimal velocity and direction of movement for the unit were used to construct each orientation tuning curve. As a measure of a cell's orientation sensitivity, the range of orientations to which the cell responded (tuning width) was determined. The techniques employed to determine orientation preference and selectivity should be accurate to within 5°; thus, experimenter bias is unlikely to have influenced the present results.

Other receptive field properties

Whenever possible, the ocular dominance, cutoff velocity (the maximum stimulus velocity to which the cell responds), preferred stimulus velocity, direction selectivity, end-zone inhibition, spontaneous activity, and response to flashing stimuli were studied as described previously (Leventhal and Hirsch, 1978, 1980). All of the data were stored by computer for subsequent analysis. S cells in our sample had the narrowest receptive fields and/or spatially separated ON and OFF subregions; C cells had wider receptive fields and/or overlapping ON/OFF regions.

Electrode track reconstruction

When using metal electrodes, the localization of electrode tracts was facilitated by making small electrolytic lesions (3 μA for 3 sec) at sites of particular interest. Large currents (10 μA for 10–15 min) delivered through the microcapillary electrodes also resulted in a green dye spot and a small amount of gliosis and thus aided in the localization of electrode tracts. Penetrations were localized in Nissl-stained 50 μm frozen sections.

Morphometric analysis

Subjects

Reginal ganglion cells of all types were sampled randomly from the retinas of eight cats. Some of these cells were also involved in an earlier study (Leventhal and Schall, 1983). Complete patches of α-cells were drawn from the nasal retinas of three additional cats. Each patch was located on a different retinal meridian.

Electrophoretic injection

Prior to injecting horseradish peroxidase (HRP), 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 MΩ) microcapillary electrodes filled with 4 M NaCl. Neuronal responses were amplified conventionally, displayed on the oscilloscope and monitored by ear. The positions of the receptive fields of cells encountered in these penetrations directed the placement of the injection.

In some cats multiple HRP injections (3–5) were made into the optic tract about 4 mm from the optic chiasm. These injections were closely spaced and made across the entire width 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 segregated within the optic tract (Guillery et al., 1982).

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% dimethylsulfoxide (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 2–3 hr.

Histology and histochemistry

Animals were maintained for approximately 48 hr after HRP injections. They were then deeply 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, 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 d 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 20 min in 0.1 M Tris buffer containing 0.03% *p*-phenylenediamine dihydrochloride, 0.06% pyrocatechol, and 0.02% H_2O_2 (PPD-PC reagent), and transferred back into 0.1 M Tris-HCl buffer.

Whole retinas were removed and processed immediately after the perfusion. All retinas 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 for 5 min at 35°C, rinsed in 0.1 M phosphate buffer (pH 7.4) for 5 min at 35°C, prereacted in 0.1 M Tris buffer containing PPD-PC reagent with 0.5% DMSO without H_2O_2 for 15 min at 35°C, reacted with fresh PPD-PC reagent containing 0.5% DMSO with H_2O_2 for 20 min at 35°C, and finally rinsed in phosphate buffer for 30 min. Photomicrographs of retinal ganglion cells illustrating the quality of staining obtained using these procedures have been published (Leventhal, 1982; Leventhal and Hirsch, 1983).

Dendritic field orientation analysis

Cells were drawn under the camera lucida using a 40× or 100× oil immersion objective. Drawings of each cell were traced onto a digitizing tablet interfaced to a PDP 11/23 computer. The high resolution of the digitizing tablet (0.005 in., Houston Instruments) allowed a very accurate representation of the dendritic field. Only that part of the dendritic field ramifying in its specific sublamina of the inner plexiform layer (IPL) was considered in the analysis of orientation. The cell body and proximal trunk of the dendrites were excluded, since electron-microscopic studies indicate that these support virtually no synapses (Kolb, 1979; Stevens et al., 1980).

Using the Cartesian coordinates representing the arborization in the

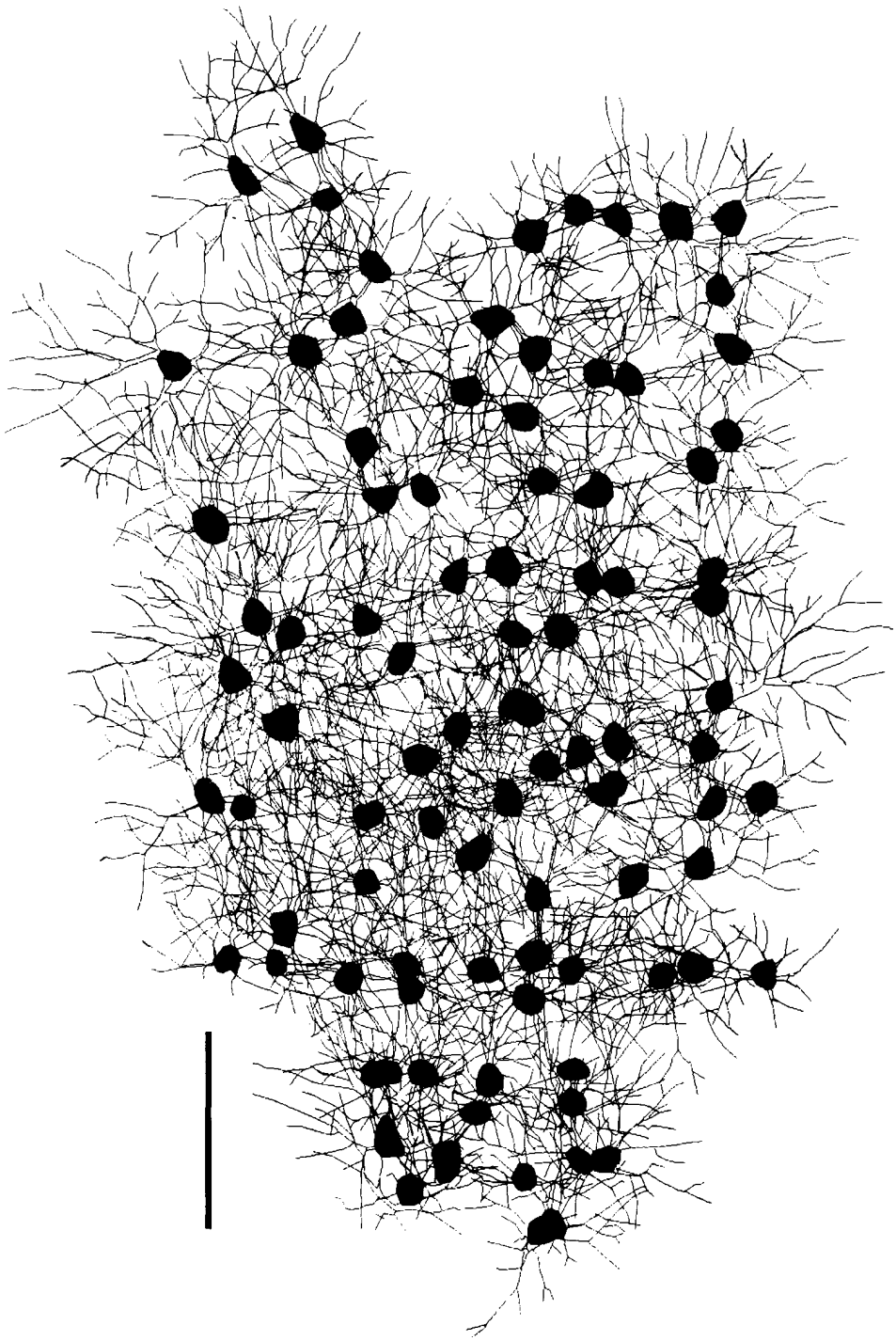

Figure 1. Computer-generated drawing of all of the α-cells in a patch of retina. Scale bar is 0.25 mm long and oriented vertically, parallel to the nasotemporal division.

IPL, the center of the dendritic field was computed. Vectors were drawn from that center to each point comprising the dendritic field. The angle of each vector was defined relative to the vertical meridian of the retina. The vertical meridian was determined from the nasotemporal distribution of labeled ganglion cells resulting from HRP injections into the LGNd or optic tract. Since we were calculating orientation and not direction, we considered angles across the circle, e.g., 10° and 190°, equivalent. The vectors were then added; the angle of the resultant vector gave the orientation of the dendritic field. The length of the resultant vector, termed *orientation bias,* provided a quantitative measure of how oriented the dendritic field was. Orientation biases range from 0 to 1, with 0 being completely unoriented.

Our measure of dendritic field orientation bias is analogous to the one used by Levick and Thibos (1982) in their study of the physiological orientation sensitivity of retinal ganglion cells. We have shown previously (Leventhal and Schall, 1983) that the distributions of the elongations and morphological orientation biases of retinal ganglion cell dendritic fields match the distributions of their receptive field elongations (Hammond, 1974) and physiological orientation biases (Levick and Thibos, 1982). The shape of an individual ganglion cell receptive field matches the shape of the cell's dendritic field (Peichl and Wässle, 1983). Thus, the structure of a ganglion cell's dendritic field appears to confer on the cell its physiological orientation preference and sensitivity.

Alpha-cell patches

All of the α-cells in selected regions of three retinas were drawn under camera lucida. In our material, reducing the condensor setting on the

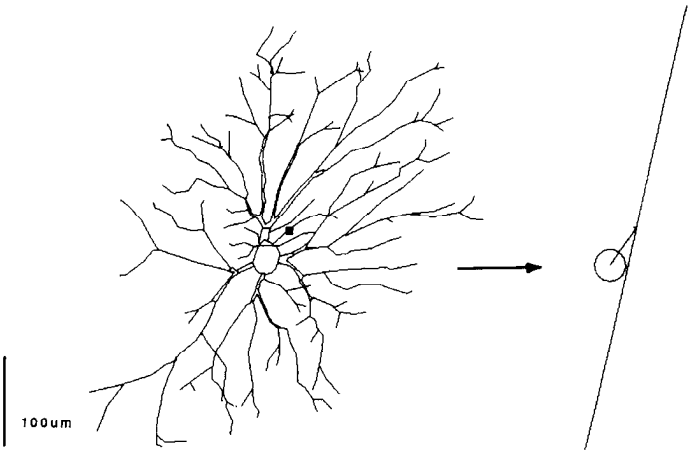

Figure 2. Computer drawing of an α-cell and its stick figure representation. *Solid square* marks the center of the dendritic field. Scale bar is oriented vertically. This dendritic field had an orientation bias of 0.19 and an orientation of 78°. The polar angle of this cell was 79°, so this is an example of a radially oriented dendritic field. The stick figure was drawn as follows: A circle was drawn at the position of the cell body. A short line was drawn from the center of the cell body to the center of the dendritic field; this line connects to a long line, which is drawn at the orientation of the dendritic field.

microscope allows the outlines of cell bodies not filled with HRP to be visualized (Leventhal, 1982). Since α-cell bodies are larger than any others in the ganglion cell layer, they could be identified unambiguously. Only regions containing no unlabeled α-cells were chosen for this analysis.

In Figure 1 we present a computer generated replication of all of the α-cells in a region of retina near the vertical meridian. In a display of this fashion, it is difficult to glean much useful information about the orientations of individual cells. To represent the orientations and positions of the dendritic fields in each patch in a more meaningful fashion, all of the cells were reduced to appropriately oriented stick figures. Figure 2 shows an example of a computer drawing of an α-cell with its stick figure representation.

Nearest neighbor analysis

Figure 3 illustrates a composite of the stick figure representations of all of the cells in three patches of retina. All of the cells were positioned at their correct retinal coordinates. The positions of the dendritic field centers were considered rather than the cell bodies for determining each cell's nearest neighbor, since the center of the dendritic field is the functional center of the ganglion cell receptive field (Peichl and Wässle, 1983). Moreover, we find that the centers of the dendritic fields of retinal ganglion cells are distributed in a more precise mosaic than are their cell bodies (J. D. Schall and A. G. Leventhal, unpublished observations).

Ganglion cells whose dendritic fields ramify in the inner sublamina of the IPL (ON-center cells) are distributed in a mosaic that is independent of the ganglion cells ramifying in the outer sublamina of the IPL (OFF-center cells) (Wässle et al., 1981). In retinal whole mounts it is possible to distinguish the depth of ramification of overlapping dendritic fields. Therefore, each dendritic field in the patches was assigned to either the ON or OFF sublamina.

In each patch more cells were drawn than are illustrated. If the nearest neighbor of a cell located on the border of a patch was not in the patch, then that cell was not included in the illustration or in any of the nearest neighbor analyses. The dendritic field orientations of these cells, however, were included in the distributions of orientations since there was no reason to exclude them.

Statistical analyses

Specific statistical tests have been devised to analyze distributions of angles. Several such tests were used to analyze our data; a short description of each test is given below. A complete account of circular statistics can be found in Batschelet (1981). The *Rayleigh test* determines if a distribution of angles differs significantly from a random distribution, i.e., whether the angles are clustered about some value. If a certain angle is expected, then the V *test* is a more powerful test of whether a distribution of angles is peaked about the expected value. To determine if the mean of the sample of angles is different from the expected angle, the confidence intervals given by Batschelet (1981, p. 86) were used. *Watson's* U^2 *test* compares two distributions of angles in order to determine whether the two samples differ significantly. High U^2 values result if the two distributions are different.

Results

Retinal distribution of preferred orientation

As a first step in our analysis it was necessary to determine accurately the distributions of the orientations of retinal ganglion cells in different parts of the retina.[2] Consequently, the dendritic fields of all of the α-cells in three large (5–9 mm^2) patches of retina were drawn. One patch was in the nasal visual streak, just superior to the horizontal meridian; one was on a nasal oblique meridian, and one was just nasal to the superior vertical meridian (Fig. 3). The distributions of the orientations of all of the cells in each patch were then compared with the distributions of the orientations of α-cells sampled randomly from corresponding regions of retina. In this fashion it was possible to determine whether our random sampling procedure accurately reflects the overall distribution of retinal ganglion cell orientations.

The distributions of the orientations of the α-cell dendritic fields in different parts of the retina are illustrated in Figure 4. The orientations of all the α-cells in each patch are shown on the right. The orientations of α-cells sampled randomly from within 22.5° of the horizontal, diagonal, and vertical meridians are displayed on the left. Comparing the histograms vertically in the figure, it is evident that they are different. The distributions of orientations of cells in each patch differ significantly from one another (e.g., $U^2 = 1.36$, $p < 0.001$ comparing the horizontal and vertical patches).

The distributions of the orientations of the α-cells in each patch do not differ significantly from the distributions of the orientations of the α-cells sampled randomly from exactly corresponding regions of the retina.[3] Moreover, the distribution of the *orientation biases* of the dendritic fields in each patch corresponds to what was found in the random samples. Thus, we did not selectively draw only well-oriented dendritic fields or dendritic fields of any particular orientation. It can be concluded that the sample of α-cell dendritic field orientations acquired randomly is representative of the total population of α-cells. Since our sampling procedure was the same for all cell types and no error was introduced into the α-cell sample, our samples of β- and other ganglion cell types are also likely to be representative of their total respective populations.

[2] We believe that incomplete staining of some of the cells in our sample had no significant effect on our reported results for the following reasons: (1) Many of the dendritic fields included in our analysis appeared comparable to published drawings of Golgi-stained and Lucifer yellow filled ganglion cells (Boycott and Wässle, 1974; Kolb et al., 1981; Saito, 1983). These cells were analyzed separately and the results did not differ from those obtained from the entire population studied. (2) The degrees of elongation and orientation biases exhibited by the ganglion cell dendritic fields in the patches analyzed corresponded to the elongations (Hammond, 1974) and physiological orientation biases (Levick and Thibos, 1982) of ganglion cell receptive fields. If our results were not accurate due to incomplete filling, this correspondence would be unlikely. (3) The observed significant radial relation between dendritic field orientation and polar angle could only have arisen artifactually if HRP selectively fills radially extended dendrites. This possibility seems unlikely.

[3] It must be pointed out that the diagonal patch was centered on a polar angle of 65°. This was 20° further from the horizontal meridian than was the mean polar angle for diagonal meridian group of cells. Consequently, there are more vertically oriented cells in the diagonal patch than in the diagonal meridian group of cells.

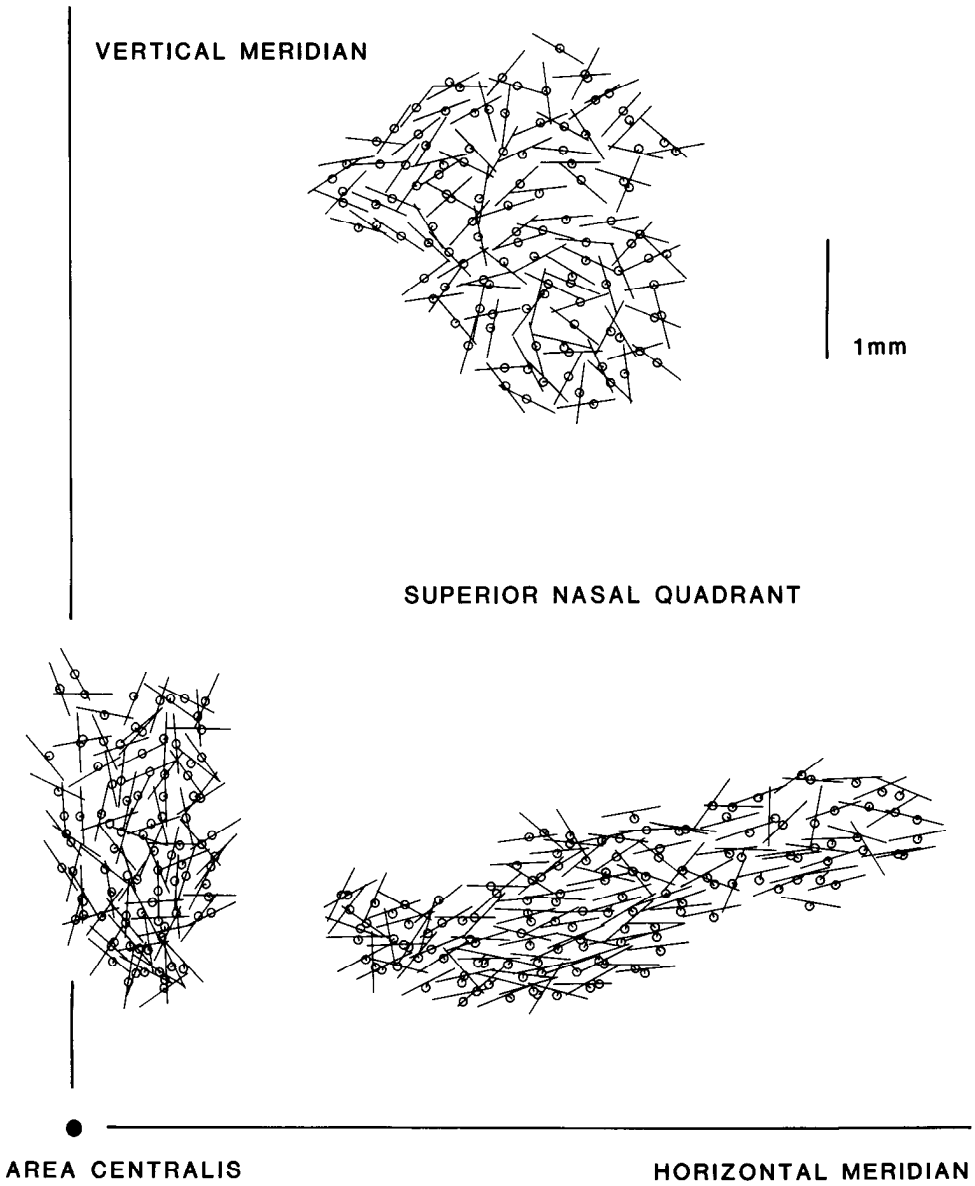

Figure 3. Stick figure representations of all of the α-cells in three patches of retina. All of the patches were in superior nasal retina. The radial tendency of the dendritic field orientations is obvious in this display, especially along the horizontal meridian.

Orientations of cells in retina and cortex subserving central vision

In regions of striate cortex subserving central vision, most S (simple) cells prefer stimuli that are oriented horizontally or vertically (Leventhal and Hirsch, 1980; Mansfield, 1974; Mansfield and Ronner, 1978; Orban and Kennedy, 1981; Pettigrew et al., 1968). A similar anisotropy is present in the LGNd (Vidyasagar and Urbas, 1982). In order to see if this anisotropy is present in the retina, the distributions of the orientations of α- and β-cells within the central 1 mm of the retina were compared with the distribution of the preferred orientations of area 17 S cells subserving this region.

Histograms of the three distributions are shown in Figure 5. The distribution of the preferred orientations of area 17 S cells is not flat (Rayleigh test; $Z = 13.9$, $p < 0.001$); more cells respond preferentially to horizontal and vertical orientations than to oblique orientations. Similarly, in central retina 61% of the β-cells are oriented either horizontally or vertically. The distribution of the orientations of central β-cells does not differ significantly from the distribution of the preferred orientations of S cells subserving the area centralis. Most α-cells in central retina are also oriented horizontally or vertically; horizontal orientations appear overrepresented among central α-cells (Rayleigh test; $Z = 4.49$, $p < 0.02$). The distribution of the orientations of α-cells in central retina is not statistically distinguishable from the distribution of the preferred orientations of S cells in area 17 subserving central vision.

Orientations of cells in retina and cortex subserving peripheral vision

X cells, which probably correspond to β-type ganglion cells (Boycott and Wässle, 1974; Cleland and Levick, 1974), give rise to the major source of input to striate cortex in the cat (Dreher et al., 1980; Singer et al., 1975; Stone and Dreher, 1973). Y cells, which correspond to α-cells (Boycott and Wässle, 1974; Cleland and Levick, 1974; Cleland et al., 1975), initiate the primary afferent pathway to area 18 but also provide substantial input to area 17 in the cat (Dreher et al., 1980; Stone and Dreher, 1973; Tretter et al., 1975). W cells are likely to correspond to epsilon, g1 and g2 ganglion cells (Leventhal, 1982; Leventhal et al., 1984) and ultimately supply the major source of geniculocortical input to area 19 (Dreher et al., 1980). Accordingly,

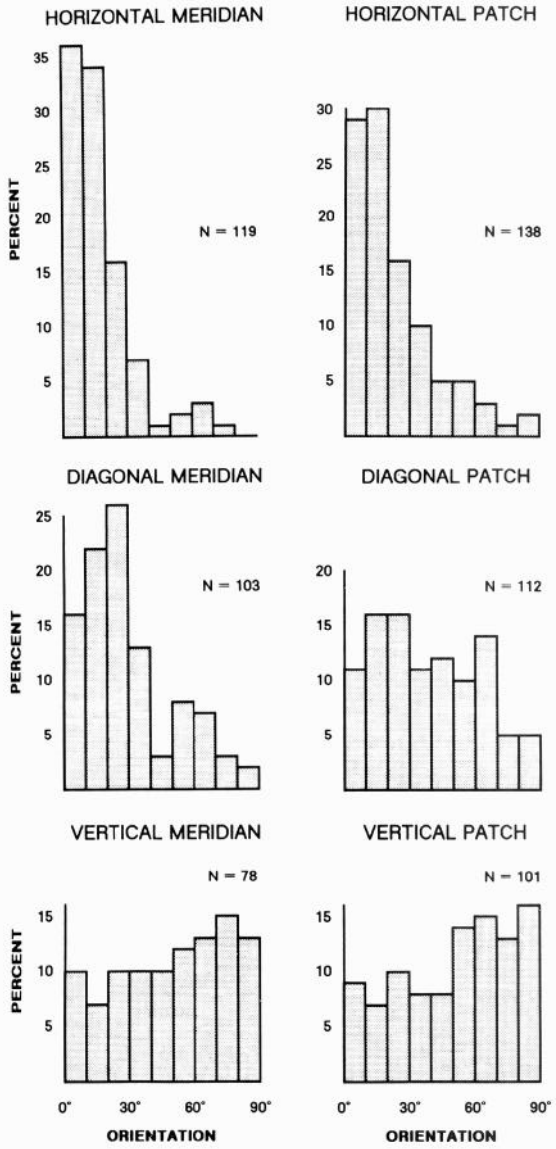

Figure 4. Distributions of the dendritic field orientations of all of the α-cells in the three patches (*right*) and of α-cells sampled randomly along each meridian (*left*). All cells were more than 1 mm from the center of the area centralis. Notice that the distributions for cells on each meridian are significantly different, while the distributions are similar for both sampling procedures. Orientations of 0° and 90° represent cells oriented horizontally and vertically, respectively. Cells with orientations near 45° and 135° were assigned to the same bin. This folding was for the purposes of illustration; the Watson U^2 statistical test is nonparametric, and the actual orientation of each cell was used in the statistical analysis.

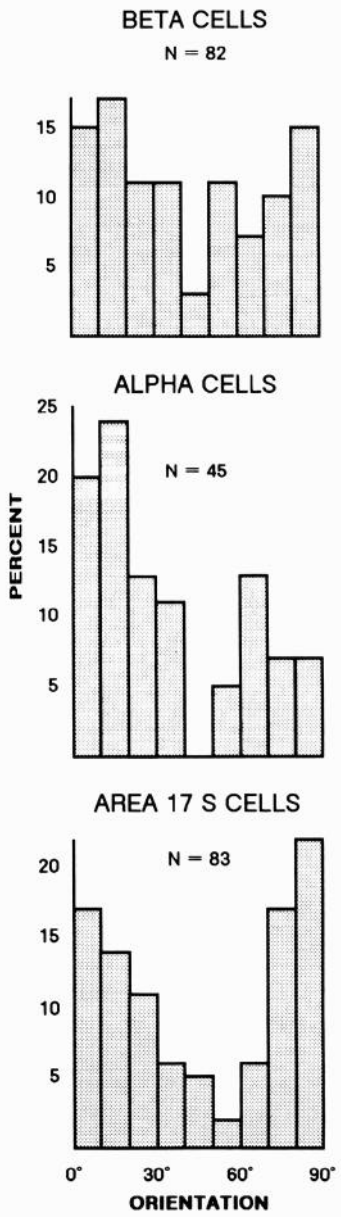

Figure 5. Dendritic field orientations of α and β ganglion cells and preferred orientations of area 17 S cells subserving central vision. The α- and β-cells used in this analysis were located in the central 1 mm of the retina and the S cells subserved eccentricities of less than 4°. The distribution of the preferred orientations of area 17 S cells subserving central vision is not significantly different from the distribution of the orientations of the β- or α-cell dendritic fields in the area centralis. All of the distributions reveal an overrepresentation of horizontal and vertical orientations.

we compared the orientations represented by cells in area 17 and α- and β-ganglion cells, between area 18 and α-cells, and between cells in area 19 and the other ganglion cells.

Figure 6 shows the distributions of the dendritic field orientations of β-cells subserving different retinal meridians and the preferred orientations of S and C type cells in retinotopically corresponding regions of area 17. In Figure 7 are shown the distributions of orientations represented by α-type ganglion cells and cortical neurons in area 18. Notice that for both ganglion cells and cortical cells there is a preponderance of horizontal orientations on the horizontal meridian, diagonal orientations on the diagonal meridians, and vertical orientations on the vertical meridian. These differences across meridians are significant for β-cells (e.g., $U^2 = 0.35$, $p < 0.005$ for the horizontal versus the vertical meridian distributions), α-cells ($U^2 = 0.49$, $p < 0.001$), and other ganglion cells (ϵ, g1, g2) ($U^2 = 0.39$, $p < 0.001$), as well as for S cells in area 17 ($U^2 = 0.33$, $p < 0.005$) and area 18 ($U^2 = 0.26$, $p < 0.02$). Notice that in all cases in the retina and cortex the percentage of cells preferring horizontal orientations on the horizontal meridian is greater than the percentage of cells on the vertical meridian perferring vertical orientations.

We compared the distributions of the orientations of α-, β-, and other ganglion cell types on different meridians with the distributions of the preferred orientations of retinotopically corresponding narrow field S cells in areas 17, 18, and 19. The

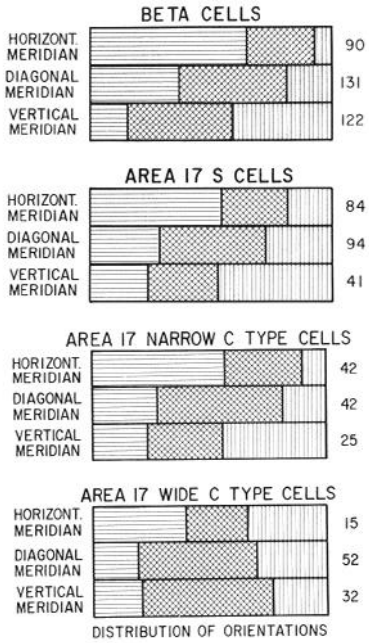

Figure 6. Orientations of β-cells and preferred orientation of area 17 S- and C-type cells subserving different meridians. The β-cells were more than 1 mm from the center of the area centralis; cortical cells had receptive fields more than 4° from the area centralis projection. Each band represents cells subserving the given meridian; the number of cells sampled is noted at right. Each band is partitioned according to the percentages of cells preferring orientations within 22.5° of horizontal (0°), diagonal (both 45° and 135°), and vertical (90°). The expanse of each band covers 100%. The orientation of the *crosshatching* signifies the orientation represented. Notice that the distribution of the preferred orientations of area 17 S cells subserving each meridian matches the distribution of the dendritic field orientations of β-cells on the corresponding meridian. The area 17 S cell preferred orientations are also not different from the orientations of the topographically corresponding α-cells shown in Figure 7. The distributions of the preferred orientations of narrow field C cells but not wide field C cells match the distributions of the orientations of β- and α-cells.

ganglion cell distributions match each other, and none differed from the S cell distributions. Thus, the distribution of the preferred orientation represented by S cells in the visual cortex can be predicted from the distribution of the orientations of the ganglion cells in the topographically corresponding region of retina.

C cells in striate cortex can be divided into two groups according to their receptive field properties. Differences in receptive field properties reflect laminar location (Gilbert, 1977; Leventhal and Hirsch, 1978). Most C cells in the supragranular layers have narrow receptive fields, and many C cells in the deeper layers have wider receptive fields. We analyzed C cells having wide and narrow receptive fields separately; wide field C cells were those with receptive fields more than 3° wide and constituted about half of the C cells sampled from regions outside of the area centralis representation. The distributions of the preferred orientations of cells from the two groups are shown in Figure 6.

The distributions of the preferred orientations of narrow field C cells in area 17 vary with meridian ($U^2 = 0.23$, $p < 0.05$ for horizontal versus vertical). Moreover, the distributions of the preferred orientations of narrow field C cells subserving the different meridians do not differ significantly from the distributions of orientations of α- or β-cells on corresponding meridians. The distributions of the preferred orientations of wide field C cells in striate cortex neither vary across meridians nor match the ganglion cell distribution.

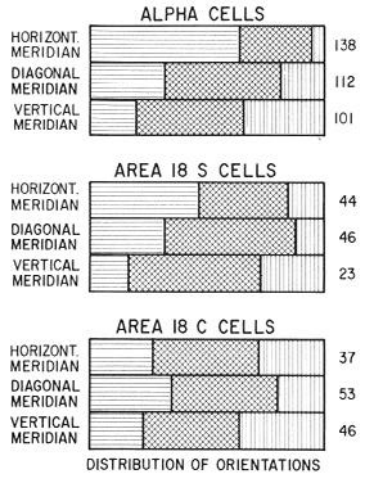

Figure 7. Orientations of α-cells and preferred orientations of area 18 S and C cells. The conventions are as in Figure 6. The α-cells were located more than 1 mm from the center of the area centralis; the same distributions were illustrated on the left in Figure 4. The cortical cells subserved eccentricities greater than 4°. Notice that the distributions of the preferred orientations of area 18 S cells but not C cells subserving each meridian match the orientations of α-cells on the corresponding meridian.

The distributions of the preferred orientations of area 18 and 19 C cells were compared with the distributions of the orientation of ganglion cells. We did not distinguish two populations of C cells in area 18 or 19 since C cells in extrastriate cortex generally tend to have wide receptive fields. Overall, the distributions of the preferred orientations of C cells in areas 18 and 19 are different from the distributions of the orientations of α- and other types of ganglion cells in retinotopically corresponding regions of retina ($U^2 = 0.27$, $p < 0.01$).

Lack of clustering of orientations in retina

Cells preferring similar orientations are grouped into columns in cat visual cortex (Albus, 1975; Hubel and Wiesel, 1963). The strong tendency for retinal ganglion cells to be oriented radially causes most cells, especially along the horizontal meridian, to be aligned nearly parallel to each other (Fig. 3). In order to see if, in addition to this radial proclivity, there is a clustering of orientations in the retina, the differences in orientation between neighboring retinal ganglion cells were calculated.

Figure 8 illustrates the differences in orientation between neighboring α-cells that arborize in the ON and OFF sublamina of the IPL in all of the patches. The results for ON-center and OFF-center cells did not differ; the values for the two groups are combined in Figure 8, *A* and *B*. Figure 8*A* shows the differences for cells oriented within 30° of radial. The distribution is peaked at 0° ($Z = 18.0$, $p < 0.001$). Thus, most radially oriented α-cells have nearest neighbors of like type that are also oriented radially. Figure 8*B* shows the differences in orientation between nonradially oriented α-cells and their nearest neighbors of like type. This distribution does not differ from a random one and does not peak at 0°, as would be expected if nonradially oriented α-cells were clustered in the retina. We conclude, therefore, that nonradial orientations are not clustered in the retina.

The varying widths of orientation columns in visual cortex

The foregoing results indicate that, other than the tendency for most cells to be oriented radially, a retinal ganglion cell's orientation is independent of its neighbor's; ganglion cells that prefer nonradially oriented stimuli are not clustered in the retina. On the other hand, cortical neurons that prefer nonradially

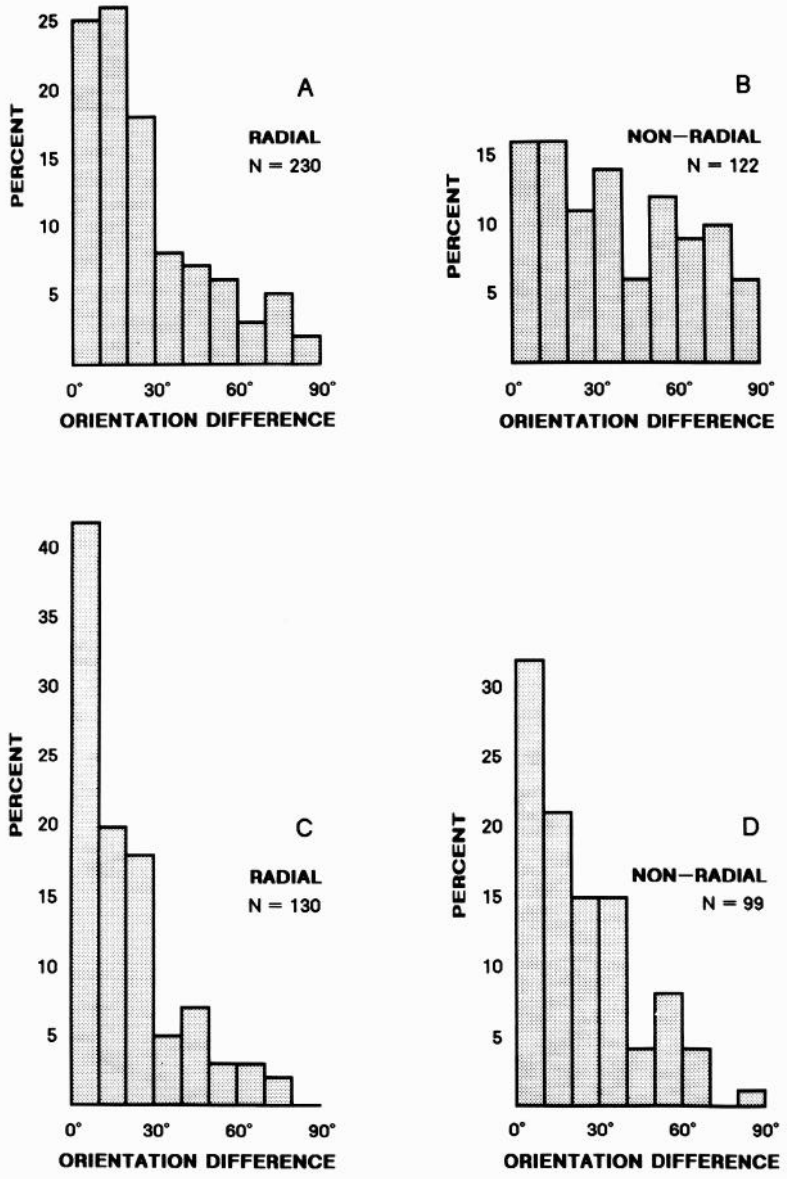

Figure 8. Differences in orientation between neighboring α-cells of like type (*A* and *B*) and differences in preferred orientation between successively recorded cells in area 17 (*C* and *D*). Cortical cells were more than 75 but less than 200 μm apart. ON-center and OFF-center cells were analyzed separately. The results are combined in the histograms of *A* and *B*, since the distributions obtained for the two groups did not differ. A difference of 0° indicates that nearest neighbors had the same preferred orientation. Notice that in area 17, but not in the retina, cells preferring nonradial orientations are clustered.

oriented stimuli are clustered; i.e., there are nonradial orientation columns (Fig. 8*D*).

In order to determine how the visual cortex accommodates the overrepresentation of radial orientations into its functional architecture, the changes in preferred orientation between successively recorded single units were calculated. The results indicate that the change in preferred orientation between nearby cells in area 17 increases as the preferred orientation deviates from radial ($n = 329$; correlation coefficient, $r = 0.26$; $p < 0.0005$). For cells preferring radial (Fig. 8*C*) and nonradial (Fig. 8*D*) orientations the differences in preferred orientation between successively recorded cells averaged 17° and 26°, respectively. To be certain that this was not a sampling artifact, i.e., that the electrode was not advanced further between cells with nonradial than between cells with radial preferred orientations, the change in orientation per micrometer between cells was also calculated. This analysis also indicates that the change in orientation increases as preferred orientation deviates from radial ($n = 329$, $r = 0.20$, $p < 0.005$). The change in orientation between successively recorded units in area 18 also increases as the preferred orientation deviates from radial ($n = 301$, $r = 0.11$, $p < 0.05$).

The foregoing analysis implies that columns in areas 17 and 18 subserving radial are wider than those subserving nonradial orientations. To look at this issue more directly, the preferred orientations of cells in individual penetrations into peripheral regions of visual cortex were plotted as a function of their position. Figure 9 shows an example of a penetration into the representation of the peripheral horizontal meridian in area 17. Each spot in the figure is situated at the value of a single cell's preferred orientation; each arrow is drawn to the value of the polar angle of the cell's receptive field. Cells that prefer stimuli oriented radially have short arrows; the shorter the arrow, the more radial the preferred orientation. It is clear that more cells were encountered that preferred stimuli oriented radially. Notice that all orientations were represented in approximately 1 mm but that the slope of the plot is flatter (the change in orientation less) when the preferred orientations are near radial and steeper when the orientations are off radial. Thus, the rate of change in preferred orientation as a function of distance depends on whether the preferred orientation is radial.

Figures 10 and 11 illustrate the results for penetrations into regions of area 17 subserving the oblique and vertical meridians, respectively. In both cases the change in preferred orientation between neighboring cells is less if their orientations match the

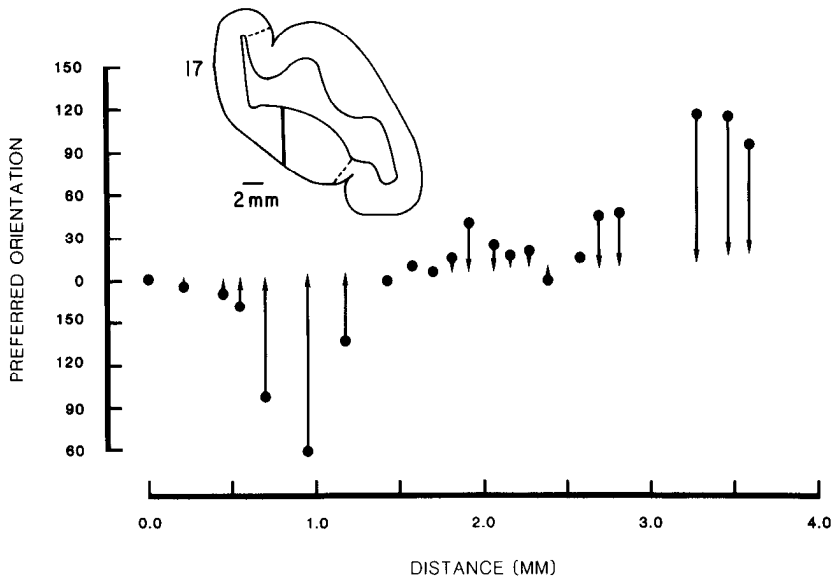

Figure 9. Plot of preferred orientation versus distance in a penetration into striate cortex subserving the peripheral horizontal meridian. The receptive fields of units encountered ranged in eccentricity from 48° to 36° from the area centralis and in polar angle from 0° to 20° off of the horizontal meridian. *Inset*: Coronal section shows the position of the electrode track. The preferred orientation of each unit is marked by a *circle*, and each *arrow* points to the polar angle of the cell's receptive field. Cells preferring radially oriented stimuli have *short arrows*. Most cells preferred radial orientations. The sequence of orientations changes smoothly, with only occasional reversals. The rate of change of orientation depends on whether the orientation is radial, i.e., the slope is steepest when the orientations are nonradial. This indicates that columns subserving radial orientations are wider than columns subserving nonradial orientations.

polar angles of their receptive fields. It appears that in parts of area 17 representing peripheral retina, columns representing radial orientations are wider than columns representing nonradial orientations.

Discussion

Our results can be summarized as follows:

1. The distribution of the preferred orientations of S cells in areas 17, 18, and 19 subserving a spot of retina outside the area centralis is not different from the distribution of the orientations of the ganglion cell dendritic fields in that spot of retina. This is true in regions of cortex and retina where radial orientations are heavily overrepresented, the horizontal meridian, as well as for regions where radial orientations are not so heavily overrepresented, the oblique and vertical meridians. Earlier studies of area 17 (Leventhal, 1983) and area 19 (Leventhal et al., 1984) only showed that radial orientations are overrepresented. This report is the first to compare the orientations represented in corresponding regions of retina and visual cortex directly.

2. The overrepresentation of horizontal and vertical orientations subserving central vision, first noted in striate cortex and later in the LGNd, is present also in the dendritic fields of ganglion cells in central retina.

3. The orientations represented by C cells with narrow receptive fields in area 17 match the orientations represented by topographically corresponding S-type cortical cells and retinal ganglion cells. The preferred orientations of C cells with wide receptive fields in areas 17, 18, and 19 subserving an area of the visual field are not the same as the orientations represented by cortical S cells and ganglion cells subserving the same part of the visual field.

4. The width of the column or slab of neurons representing a given orientation varies with the visual field representation over the cortex such that more space is devoted to radial orientations than to nonradial. The organized arrangement of orientation-sensitive cells in visual cortex has no correlate in the retina, since other than a mutual tendency to be oriented radially, ganglion cells with similar orientations are not clustered in the retina.

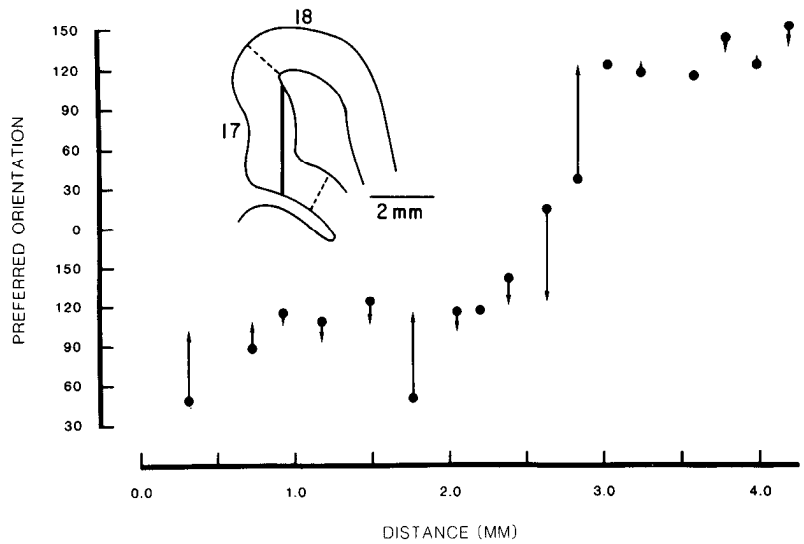

Figure 10. Plot of preferred orientation versus distance in a penetration into striate cortex subserving an oblique meridian. The conventions are as in Figure 9. The receptive fields of cells in this penetration ranged in eccentricity from 30° to 45°, and in polar angle from 80° to 50° off of the horizontal meridian in the lower visual field. Notice that most of the cells encountered preferred radial orientations (*short arrows*), and the cycle passed through nonradial orientations quickly.

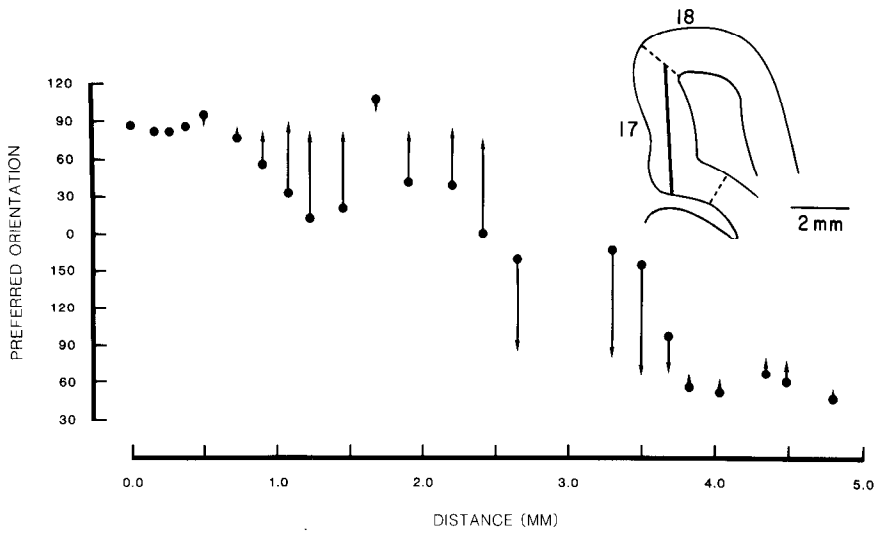

Figure 11. Graph of preferred orientation versus distance in a penetration into striate cortex subserving the vertical meridian. The conventions are as in Figure 9. Cells in this penetration had receptive fields with eccentricities from 30° to 35° and polar angles from 90° to 60° in the lower visual field. Once again the slope of the plot is steepest when the orientations are not radial.

Relation to previous work

Most narrow field C cells reside in the supragranular layers, and many wide field C cells are encountered in the infragranular layers (Gilbert, 1977; Leventhal and Hirsch, 1978). The finding that the orientations represented by these two groups of cortical cells are different is consistent with reports that the orientation represented in a vertical column of neurons in striate cortex often changes abruptly at the border of layers 4 and 5 (Bauer, 1982; Bauer et al., 1983; Krüger and Bach, 1982; but see Murphy and Sillito, 1984). Since it appears that the distribution of orientations represented by various groups of cells can differ, the identification and classification of neurons is critical in any analysis of the orientations represented in the visual cortex.

Payne and Berman (1983) have also studied the relationship between the preferred orientations and receptive field positions of cells in cat striate cortex. They report that most cells subserving the horizontal meridian prefer vertical orientations; most subserving the oblique meridians prefer horizontal, and most subserving the vertical meridian prefer horizontal. This overall overrepresentation of horizontal orientations is generally consistent with our results. Payne and Berman also reported that most of their simple I-type cells prefer stimuli that are oriented either radially or tangentially. We have found that the radial tendency is only observed for simple cells with receptive fields outside the central 4°. Payne and Berman apparently did not control for eccentricity in their analysis. Furthermore, few of their total sample of cells subserved regions more than 15° from the projection of the area centralis, which is where the radial tendency is most obvious. It also seems likely that we would consider many of the neurons that Payne and Berman sampled wide field C cells, possibly in the infragranular layers, since most of the complex cells they illustrated preferred tangentially oriented stimuli. Since Payne and Berman did not analyze their data according to cell type and eccentricity as we did, it is difficult to compare further their results with ours; we believe, however, that any inconsistency is more apparent than real.

It should be noted that in an earlier exploration of the peripheral visual field representation in cat striate cortex, Kalia and Whitteridge (1973) found that most cells with receptive fields 50°–90° from the projection of the area centralis on the horizontal meridian (in the monocular segment) preferred stimuli that were oriented horizontally, i.e., radially.

We have provided evidence that the width of orientation columns varies in regions of areas 17 and 18 subserving peripheral vision, and columns representing radial orientations are wider than those representing nonradial. The arrangement of orientation columns in cat visual cortex must be considered in interpreting these findings. Singer (1981) reported that iso-orientation slabs run predominantly dorsoventrally in the lateral gyrus of the cat. However, Albus and Sieber (1984) report that this dorsoventral arrangement is not very pronounced. When a microelectrode advances parallel to an iso-orientation slab, the change in orientation with distance is less than when the electrode advances across orientation columns (Hubel and Wiesel, 1974; Humphrey and Norton, 1980). The possibility must therefore be considered that we observed variability in the rate of change of orientation with distance because the electrode was passing parallel to iso-orientation slabs in some cases and not others.

This sort of artifact cannot account for the finding that the change in orientation with distance is less when the preferred orientations are radial. Such an explanation requires that of the 29 penetrations into area 17 and 48 penetrations into area 18 included in our results, the electrodes selectively encountered cells preferring radial orientations when advancing parallel to iso-orientation slabs. This is extremely unlikely, since our electrode penetrations were all oriented similarly relative to the cortical surface, and we sampled wide regions of cortex by advancing the electrode at least 75 μm between units.

The finding that the functional architecture of orientation-specific cells can vary is interesting in light of the recent observation that the width of ocular dominance columns varies over monkey striate cortex (LeVay et al., 1985). Using deoxyglucose, it may be possible to confirm whether the columns representing radial orientations are in fact wider than those representing nonradial. Such a study requires that both the orientation and visual field position of the stimulus be controlled; no study to date has controlled for both of these variables (Albus, 1979; Albus and Sieber, 1984; Hubel et al., 1978; Humphrey et al., 1980; Singer, 1981).

Perceptual correlates

Using central vision, humans are able to detect horizontal and vertical better than oblique orientations (see Appelle, 1972, for a review). This "oblique effect" seems to be innate (Leehey et al., 1975). Most LGNd relay cells (Vidyasagar and Urbas, 1982) and area 17 S cells subserving central vision have horizontal and vertical preferred orientations; this anisotropy has been suggested to provide the physiological basis for the oblique effect (Leventhal and Hirsch, 1980; Mansfield, 1974; Mansfield and Ronner, 1978; Orban et al., 1984). The oblique effect has been demonstrated in the cat (Bonds, 1982), and the degree to which a cat detects horizontal and vertical better than diagonal corresponds to the proportion of cells in visual cortex that have

horizontal, vertical, and diagonal preferred orientations (Vandenbussche and Orban, 1983).

Our results suggest that central vision's predilection toward horizontal and vertical may originate in the retina; the distribution of the orientations of ganglion cells in central retina also tends toward horizontal and vertical. The overrepresentation of horizontal and vertical orientations in central retina may simply reflect the fact that most ganglion cells about the area centralis are oriented radially (Leventhal and Schall, 1983). Since the density of ganglion cells is greatest along the horizontal and vertical meridians (Stone, 1978), most cells within a circular region about the area centralis should be oriented horizontally or vertically.

The oblique effect vanishes in the peripheral visual field (Berkeley et al., 1975) and gives way to a tendency to see radially oriented stimuli better than nonradially oriented stimuli (Fahle and Braitenberg, 1983; Rovamo et al., 1982; Temme et al., 1984). In peripheral regions of retina, most ganglion cells are oriented radially in the cat, the monkey (Schall et al., 1985), and the human (Rodieck et al., 1985). Hence, the perception of contours in the peripheral visual field is also predicted by the distribution of retinal ganglion cell orientations.

Neuronal interactions mediating orientation preference and sensitivity

Cortical neurons in the adult are much more selective for stimulus orientation than are LGNd cells, which are in turn somewhat more orientation-sensitive than retinal ganglion cells. Cortical cells exhibit orientation selectivity for short bars, but the degree of selectivity increases with bar length (Henry et al., 1974a, b). Longer bars are required to detect the weaker orientation sensitivity of LGNd neurons. LGNd cells show the sharpest orientation sensitivity to drifting sinusoidal gratings (Vidyasagar and Urbas, 1982), which is the stimulus required to detect the orientation sensitivity of retinal ganglion cells (Levick and Thibos, 1982).

It seems certain that significant selectivity for stimulus orientation is achieved through intrageniculate and intracortical mechanisms. Mutual inhibition between cells with different orientation preferences can enhance the sensitivity of a neuron (Blakemore and Tobin, 1972; Creutzfeldt et al., 1974; Morrone et al., 1982) as can convergence along the line of optimal orientation (Hubel and Wiesel, 1962). GABAergic inhibition is reported to enhance the orientation sensitivity of LGNd cells (Vidyasagar, 1984) and cortical cells (Sillito, 1975, 1979; Sillito et al., 1980; Tsumoto et al., 1979). The experiments in which GABAergic inhibition is reduced, interestingly, reveal that the orientation preference of a neuron does not change with the degree of local inhibition (e.g., Sillito et al., 1980). It may be that the mechanism that is responsible for *enhancing orientation selectivity* is not also responsible for *specifying orientation preference.*

This study provides evidence that the distribution of the preferred orientations of first-order cortical cells receiving input from any spot of retina matches the distribution of the orientations of the ganglion cell dendritic fields in that spot of retina. The distribution of the preferred orientations of cells in the LGNd also appear to correspond to their retinal input (Vidyasagar and Urbas, 1982). Thus, the LGNd and visual cortex are either preserving the anisotropic pattern of orientation preferences delivered by the retinotopic projection or are, in some unknown way, duplicating the same biased distribution. It seems extravagant to suggest that the LGNd and cortex are both generating *de novo* a radial bias in the peripheral and horizontal–vertical bias in the central representation when these biases are already present in the retina. A more parsimonious explanation is that the anisotropies are observed because the orientation preferences of LGNd relay cells and, subsequently, first-order cortical cells (Bullier and Henry, 1979a, b; Henry et al., 1979; Singer et al., 1975; Toyama et al., 1977) are specified during development by their orientation sensitive, excitatory afferents.[4] Once the mature connectivity is achieved, the retinal orientation bias may or may not be necessary for continued cortical orientation selectivity, which, as discussed above, is derived largely through intracortical mechanisms.

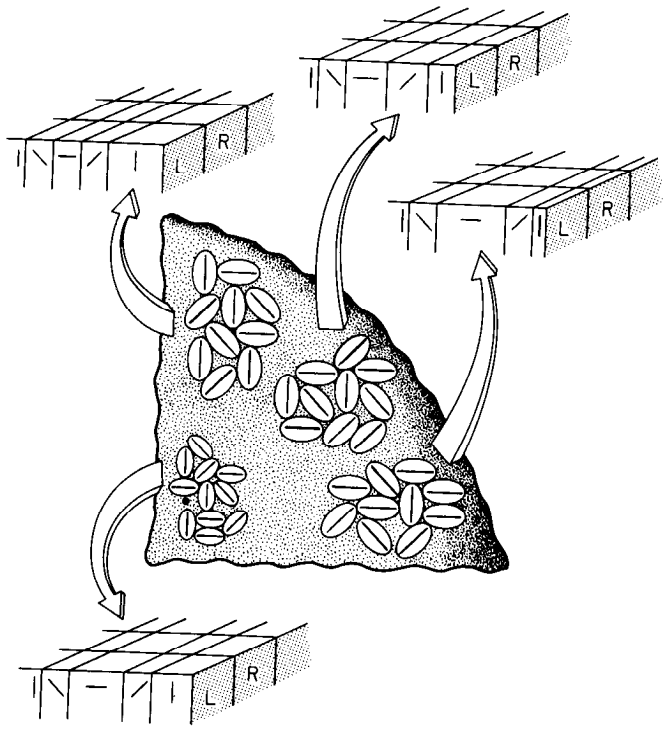

Figure 12. Summary of the results and hypotheses of this study. The *ellipses* represent the elongated dendritic fields of retinal ganglion cells in a quadrant of retina; the *lines through the ellipses* denote the orientations of the cells that have been restricted to 0°, 45°, 90°, 135° for the illustration. *Clusters of cells* located on the peripheral horizontal, diagonal, and vertical meridians, as well at the area centralis (marked by *circle*), are shown. The proportions of cells of different orientations in each cluster reflect our results for the respective regions of retina. Similarly, the widths of the orientation columns included in each idealized hypercolumn reflect the values obtained during our cortical recordings. Note that in the hypercolumn subserving central vision the columns subserving vertical and especially horizontal orientations are widest, while the columns subserving radial orientations occupy the most space in hypercolumns subserving the periphery. We hypothesize that retinal orientation sensitivity is necessary for the development of cortical orientation specificity. The preferred orientations of first-order cortical cells may be specified during development by the preferred orientations of their excitatory geniculocortical afferents, whose orientation preferences are in turn specified by the orientations of the retinal ganglion cells providing their inputs. In the adult the orientation selectivity of cortical neurons is enhanced by intracortical, probably inhibitory, connections. Whether retinal orientation sensitivity is necessary for cortical orientation sensitivity once mature connectivity is achieved remains to be determined.

Are horizontal and vertical orientations special?

A number of studies suggest that S-type cortical cells preferring horizontal and vertical orientations are the first to develop their

[4] It has been claimed that the excitatory input to first-order, simple type cortical cells is not orientation sensitive (e.g., Sillito et al., 1980). It must be noted, as described above, however, that the degree of orientation sensitivity measured depends on the stimulus used. To date, no study of the excitatory input to cortical cells has applied the type of stimulus and quantitative techniques necessary to detect the weak orientation sensitivity of retinal ganglion cells and LGNd relay cells.

orientation selectivity (Blakemore and Van Sluyters, 1975; Fregnac and Imbert, 1978; Leventhal and Hirsch, 1977, 1980). These studies have concentrated on central vision, where horizontal and vertical orientations predominate even in the retina. Our present findings suggest that studies of kittens and dark-reared cats must be repeated with an emphasis on the periphery. Such studies will determine whether the horizontal–vertical bias is initially present in all regions of the visual cortex. One recent study of the development of orientation selectivity in kitten visual cortex (Albus and Wolf, 1984) did not stress central vision, and the results of this study did not indicate a horizontal–vertical anisotropy. Thus, it may be that the distribution of the preferred orientations of cells in visually inexperienced animals actually reflects the retinal distribution, and there is nothing special about horizontal and vertical orientations *per se.*

Development of orientation sensitivity

Vertical columns of cells with similar response properties are found throughout the cerebral cortex. In general, the properties that define columns are established in the periphery and are delivered by the thalamic afferents. For example, in rodent primary somatosensory cortex, each facial vibrissa is represented by a vertical barrel of cells (Woolsey and Van der Loos, 1970), and the development of these barrels is directed by the arrangement of the afferent thalamic axons (Killackey and Belford, 1979). The properties subserved by columns in cat and monkey somatosensory cortex also originate at the receptor and are transmitted via the thalamocortical projection (Jones et al., 1982; Landry and Deschênes, 1981; Mountcastle, 1957; Sretavan and Dykes, 1983; Sur et al., 1984). Similarly, the representation of preferred frequency in primary auditory cortex (Abeles and Goldstein, 1970; Merzenich et al., 1975) is understood as a mapping of the cochlea onto the cortex through isofrequency bands in the medial geniculate body (Colwell and Merzenich, 1975). Finally, mammalian visual cortex contains a number of columnar systems; ocular dominance (Hubel and Wiesel, 1972), color (Michael, 1981), and spatial frequency (Thompson and Tolhurst, 1980a, b; Tootell et al., 1981) represent properties that originate in the retina.

Thus, it may be a rule in sensory cortex that the properties subserved by columnar systems arrive in the afferents; the job of cortex is not to create the property, but rather to organize and somehow process and pass it along. Orientation columns since their discovery, however, have been enigmatic. They have been conceived of as fundamentally different from all the rest, an intracortical, functional segregation of a property actually generated in the cortex during development. If cortical orientation selectivity has its origins in the retina, then this incongruity may be resolved, and orientation columns can be understood on the same terms as all the rest.

At present it is not known when retinal ganglion cells achieve their mature orientation sensitivity. Retinal ganglion cells in central cat retina undergo their most extensive differentiation prenatally (Rapaport and Stone, 1983), and adult size β-cell dendritic fields are found in central cat retina by 3 weeks of age (Rusoff and Dubin, 1978). Ganglion cell dendritic field orientation develops independently of visual experience (Leventhal and Schall, 1983; Thibos and Levick, 1982). Relay cells in kitten LGNd develop their orientation sensitivity by the first postnatal week, without visual experience (Albus et al., 1983). Thus, innate orientation sensitivity is established in the peripheral visual system well before cortical orientation selectivity has developed fully in the cat (Fregnac and Imbert, 1978; Pettigrew 1974). This time course is consistent with the idea that retinal orientation sensitivity is prerequisite for the development of cortical orientation selectivity.

Conclusion

Most retinal ganglion cells are orientation biased, but cortical neurons are orientation selective; hence, the lion's share of orientation sensitivity appears to be derived through intracortical mechanisms. Nevertheless, the preferred orientations of presumed first-order cortical neurons match the orientations of the retinal ganglion cells, ultimately providing their input. We suggest, therefore, that afferent orientation sensitivity is necessary for the specification of the orientation preferences of cortical cells during development. The results and hypotheses presented are reviewed diagrammatically in Figure 12.

The foregoing suggestions remain to be tested; the mechanisms underlying cortical orientation sensitivity are not yet understood. Still, it would seem that we have an easier problem than we had 20 years ago, when it was thought that cortical neurons had to derive orientation sensitivity exclusively from unoriented inputs.

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