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Relationship Between Preferred Orientation and Receptive Field Position of Neurons in Extrastriate Cortex (Area 19) in the Cat

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ABSTRACT

Orientation sensitivity is a characteristic of most retinal ganglion cells (Levick and Thibos, '82), most relay cells in the dorsal lateral geniculate nucleus (Vidyasagar and Urbas, '82), and most neurons in the visual cortex (Hubel and Wiesel, '62) in the cat. In the retina there is a systematic relationship between receptive field position (polar angle) and preferred orientation. Outside of the area centralis most retinal ganglion cells respond best to stimuli oriented radially, i.e., oriented parallel to the line connecting their receptive fields to the area centralis (Levick and Thibos, '82). This relationship is strongest along the horizontal meridian (the visual streak) and appears to reflect the innate, radial orientation of retinal ganglion cell dendritic fields (Leventhal and Schall, '83).

A relationship between preferred orientation and polar angle also exists in cat striate cortex; outside of the area centralis representation most cells respond best to lines oriented radially. This relationship is strongest for S-type cells, the most orientation-selective cells, and cells in regions representing the horizontal meridian (Leventhal, '83). To determine if similar relationships exist in cat extrastriate cortex, the preferred orientations and receptive field positions of 226 neurons in area 19 were studied. We find that, as in area 17, most area 19 cells outside of the representation of the area centralis respond best to lines oriented radially; this relationship is strongest for the cells having the narrowest receptive fields and in regions subserving the horizontal meridian. Unlike in striate cortex, in area 19 the relationship between preferred orientation and polar angle is not dependent upon cell type (S or C) or to the degree of orientation sensitivity exhibited. Also, in area 19, but not in area 17, the relationship between preferred orientation and polar angle fails for the cells having the widest receptive fields.

The results of this study show that the systematic relationship between preferred orientation and receptive field position which begins in the retina is largely preserved through extrastriate cortex. The functional architecture of orientation sensitive cells throughout the visual pathways may depend ultimately upon the innate, radial orientation of the dendritic fields of retinal ganglion cells.

Key words: **orientation sensitivity, radial orientation, visual field meridians, receptive field size, functional architecture**

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Neurons in the mammalian visual cortex respond preferentially to lines, bars, or edges of a particular orientation. A number of hypotheses have been proposed to account for the orientation-sensitive response of cortical cells (Hubel and Wiesel, '62, for example). Recent work indicates that ganglion cells in the retina and relay cells in the dorsal lateral geniculate nucleus (LGNd) providing the afferent input to visual cortex are themselves sensitive to stimulus orientation; preferred orientation is represented systematically across the retina (Levick and Thibos, '82). In the retina, orientation sensitivity apparently comes about because retinal ganglion cells have oriented dendritic fields; the dendritic fields of most ganglion cells are oriented radially, i.e., like the spokes of a wheel, having the area centralis at its hub (Leventhal and Schall, '83). As a result the orientation preferences of cat retinal ganglion cells are related to the positions (polar angles) of their receptive fields, and adjacent retinal ganglion cells exhibit similar orientation preferences (Levick and Thibos, '82).

In area 17 (striate cortex) of cats and monkeys preferred orientation is also represented in a systematic fashion (Hubel and Wiesel, '63), and most striate cortical cells in the cat respond best to lines oriented radially (Leventhal, '83). To determine if a relationship between preferred orientation and polar angle exists in cat extrastriate visual cortex, the preferred orientations and receptive field positions of single cells throughout area 19 were studied. The results provide evidence that, as in the retina, LGNd, and striate cortex, most cells in area 19 respond best to bars oriented radially, i.e., oriented parallel to the line connecting their receptive fields to the projection of the area centralis.

METHODS

Subjects

Eight adult cats provided the data for this study. Four of the animals were normal, and four were deprived of vision from birth by monocular lid suture (MD). Some of the subjects for this study also provided data for a previous study (Leventhal and Hirsch, '83). All recordings were done prior to the work of Leventhal and Schall, '83; and Leventhal, 1983; thus, the results of this study could not have been influenced by experimenter bias.

Physiological recording procedures

Cats were prepared for electrophysiological recording as described previously (Leventhal and Hirsch, '78, '80). Under Fluothane anesthesia a cylindrical chamber was positioned over a craniotomy above area 19 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^{-1} $hour^{-1}$) and gallamine triethiodide (7 mg kg^{-1} $hour^{-1}$) was infused intravenously and the animal was ventilated with a mixture of nitrous oxide (75%), oxygen (25%), and Fluothane as needed. Body temperature was maintained at 38°C and heart rate was monitored throughout the experiment. Expired 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 discs were determined repeatedly during the course of each recording session and were used to infer the positions of the areae centrales (Fernald and Chase '71). In some instances the locations of the areae centrales were determined directly. Their locations did not differ significantly from those inferred from the projections of the optic discs.

Action potentials of cortical cells were recorded with epoxy-coated tungsten microelectrodes or microcapillary electrodes containing a saturated solution of fast green dye in 2 M NaCl. The electrode was advanced using a piezoelectric microdrive (Burleigh Instruments) and was moved 75–150 μm between units to reduce sampling bias and to record from a large region of cortex in each cat. Cells were recorded from the cortical projection of the area centralis and from the cortical representations of more peripheral regions of the visual field.

Receptive-field mapping

The receptive field of a cortical neuron was defined as the largest area in visual space within which a visual stimulus elicited a response. Response fields were plotted by using light bars and both light and dark edges. A detailed description of the procedure has been given previously (Leventhal and Hirsch, '78, '80).

Receptive-field eccentricity

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

Orientation sensitivity

Five to 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. The stimulus was moved in one of the two directions orthogonal to its long axis; the particular direction employed was the one that was determined initially to be the more effective. Similarly, the velocity employed was also the one judged to be optimal. As a measure of a cell's orientation sensitivity, the range of orientations to which the cell responded (tuning width) was obtained.

Other receptive-field properties

For most units, ocular dominance, cutoff velocity (the maximum stimulus velocity to which the cell responds), direction selectivity, end-zone inhibition, and spontaneous activity were also studied. Cells were identified as being S or C type based upon their responses to flashing stimuli (Leventhal and Hirsch, '78; Duysens et al., '82). S cells exhibit pure on- and/or pure off-responses to flashing stimuli; C cells exhibit mixed on/off-responses to flashing stimuli. All data collected were stored in the laboratory PDP 11/23 computer system for subsequent analysis. A detailed description of our receptive-field mapping procedures has been given previously (Leventhal and Hirsch, '78, '80; Hirsch et al., '83).

Electrode track reconstruction

When using metal electrodes, the localization of electrode tracks was facilitated by making small electrolytic lesions (3 μA for 3 seconds) at sites of particular interest. Large currents (10 μA for 10–15 minutes) delivered through the microcapillary electrodes also resulted in a green spot and a small amount of gliosis and thus aided in the localization of electrode tracks. All penetrations were localized in Nissl-stained 50-μm frozen sections, and all units studied were in area 19.

Statistical analyses

Statistical techniques designed to analyze distributions of angles (circular statistics) were used to determine the relationship between the preferred orientations and receptive-field positions of cortical cells. First, circular symmetry was eliminated, since we were interested in orientation, not direction, and for our purposes angles of 0° and 180°, for example, are equivalent. Next, the angle of the cell's receptive field relative to the vertical meridian (90°) of the visual field was subtracted from the preferred orientation of the cell. The resulting value, termed *angle difference,* ranges from 0° for a cell responding best to lines oriented radially, that is, parallel to the line connecting its receptive field to the area centralis projection, to 90° for a cell responding best to lines oriented tangentially, that is, orthogonal to the line connecting its receptive field to the area centralis projection. It should also be explained that according to our conventions a cell in the inferior quadrant of the right visual hemifield with a preferred orientation of 150° (30° off horizontal) and a polar angle of 320 (140)° (40° off horizontal) has a preferred orientation that is 10° more horizontal than its polar angle. This cell has an angle difference of +10 according to our conventions, since preferred orientation (150)° − polar angle (140)° = +10°. A cell subserving the superior quadrant of the right visual hemifield with a preferred orientation of 30° (30° off horizontal) and a polar angle of 40° (40° off horizontal) would have an angle difference of 30° − 40° or −10°. Hence, according to our conventions, cells subserving the superior, left visual hemifield and inferior, right hemifield exhibit *positive* angle differences if their preferred orientations are closer to horizontal than their polar angles. Cells subserving the inferior, left hemifield and superior, right hemifield exhibit *negative* angle differences if their preferred orientations are closer to horizontal than their polar angles.

For each histogram in Figures 1–4 we then employed two separate statistical tests. The first of these, the Rayleigh test, indicates whether or not a circular distribution is uniform or peaked significantly, that is, biased toward one angle. The second test, the V-test, is a more powerful test of nonuniformity and indicates whether a circular distribution is peaked significantly when a particular angle, for example 0° in this study, is expected. More complete descriptions of these techniques can be found in Mardia, '72; Zar, '74; Batschalet, '78; Levick and Thibos, '82; Hirsch et al., '83; and Leventhal and Schall, '83.

RESULTS

The orientation preferences and the positions in the visual field of the receptive fields of 226 neurons in area 19 were studied. Two-thirds of the cells studied had receptive fields on or below the horizontal meridian of the visual field. One hundred fifteen cells were sampled from normal cats and the rest were sampled from monocularly deprived (MD) cats. Receptive fields studied ranged in eccentricity from 0° to 30° from the area centralis projection. All of the analyses described in this paper were carried out separately on cells sampled from normal and MD cats, and no differences were observed. Ninety-nine percent of the cells studied in normal cats were activated binocularly; all orientation-sensitive cells studied in MD cats could only be activated by the nondeprived eye (Leventhal and Hirsch, '83).

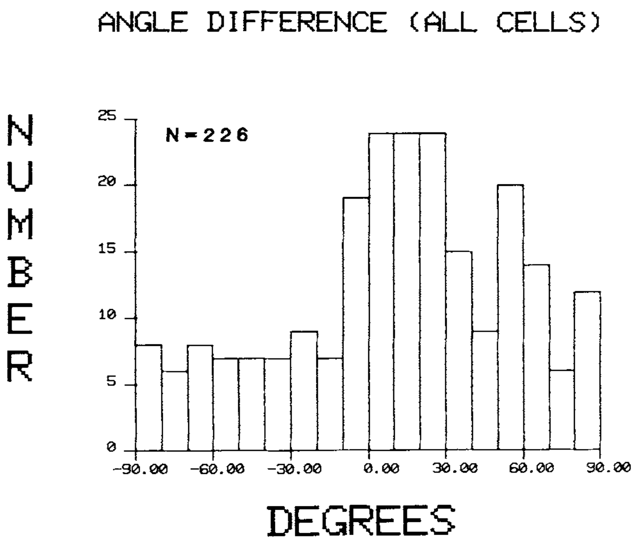

Fig. 1. Differences between the preferred orientations and polar angles (angle differences) of receptive fields of cells in extrastriate cortex (area 19). An angle difference of 0° indicates that the cell responded best to lines oriented radially, i.e., parallel to the line connecting the cell's receptive field to the area centralis projection. Most cortical cells exhibit small angle differences, indicating a systematic relationship between preferred orientation and polar angle in area 19. In this and the following histograms there is a tendency for positive angle differences to be overrepresented. This has resulted since we have not sampled equal numbers of cells from all four quadrants of the visual field. Specifically, cells in the retina, area 17, and area 19 that subserve the diagonal and vertical meridians prefer lines oriented somewhat more horizontally than their polar angles predict. According to our conventions a cell in the inferior quadrant of the right visual hemifield with a preferred orientation of 150° (30° off horizontal) and a polar angle of 320 (140)° (40° off horizontal) has a preferred orientation that is 10° more horizontal than its polar angle. This cell has an angle difference of +10 according to our conventions, since preferred orientation (150)° − polar angle (140)° = +10°. A corresponding cell subserving the superior quadrant of the right visual hemifield would have a negative angle difference. That is, a cell with a preferred orientation of 30° (30° off horizontal) and a polar angle of 40° (40° degrees off horizontal) would have an angle difference of 30° − 40° or −10°. Thus, according to our conventions, cells subserving the superior, left visual hemifield and inferior, right hemifield exhibit positive angle differences if their preferred orientations are closer to horizontal than their polar angles. Cells subserving the inferior, left hemifield and superior, right hemifield exhibit negative angle differences if their preferred orientations are closer to horizontal than their polar angles.

The basic finding of this study is that most cells in area 19 respond best to lines oriented radially, that is, oriented parallel to the line connecting their receptive fields to the projection of the area centralis. A histogram supporting this is shown in Figure 1. For each cell in Figure 1 the difference between the preferred orientation of the cell and the angle of the cell's receptive field relative to the vertical meridian (polar angle) has been computed. For example, a

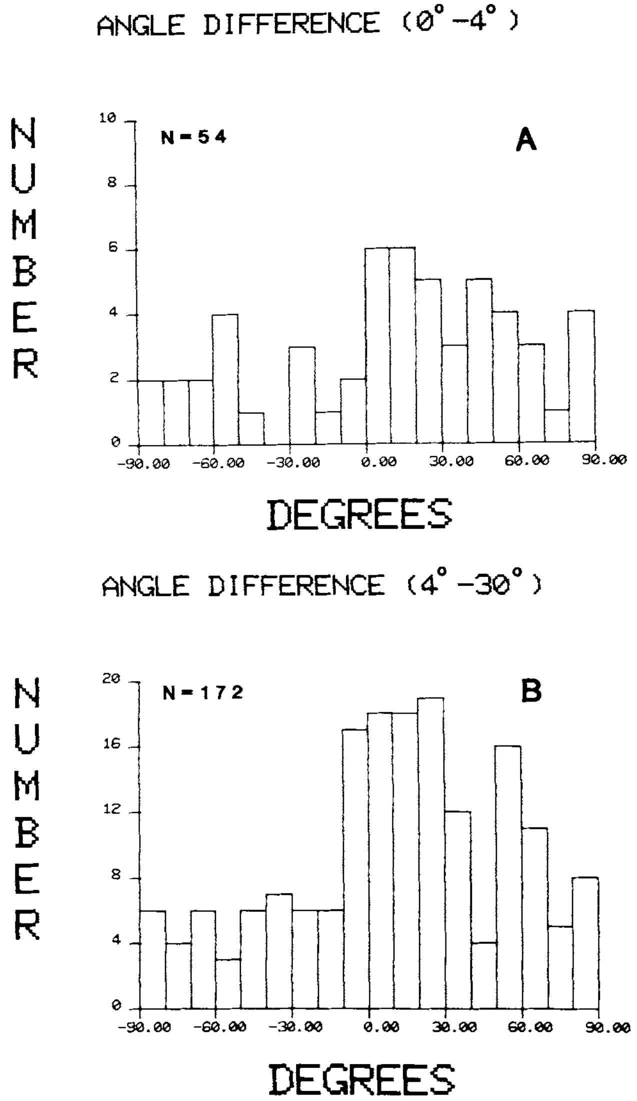

Fig. 2. Differences between preferred orientations and polar angles of area 19 cells subserving the central 4° of retina (A) and cells subserving regions of retina 4–30° from the area centralis (B). There is a very weak relationship (if any) between preferred orientation and polar angle in regions of area 19 subserving the central 4° of retina. In regions of area 19 from 4° to 30° from the area centralis projection there is a pronounced relationship between preferred orientation and polar angle.

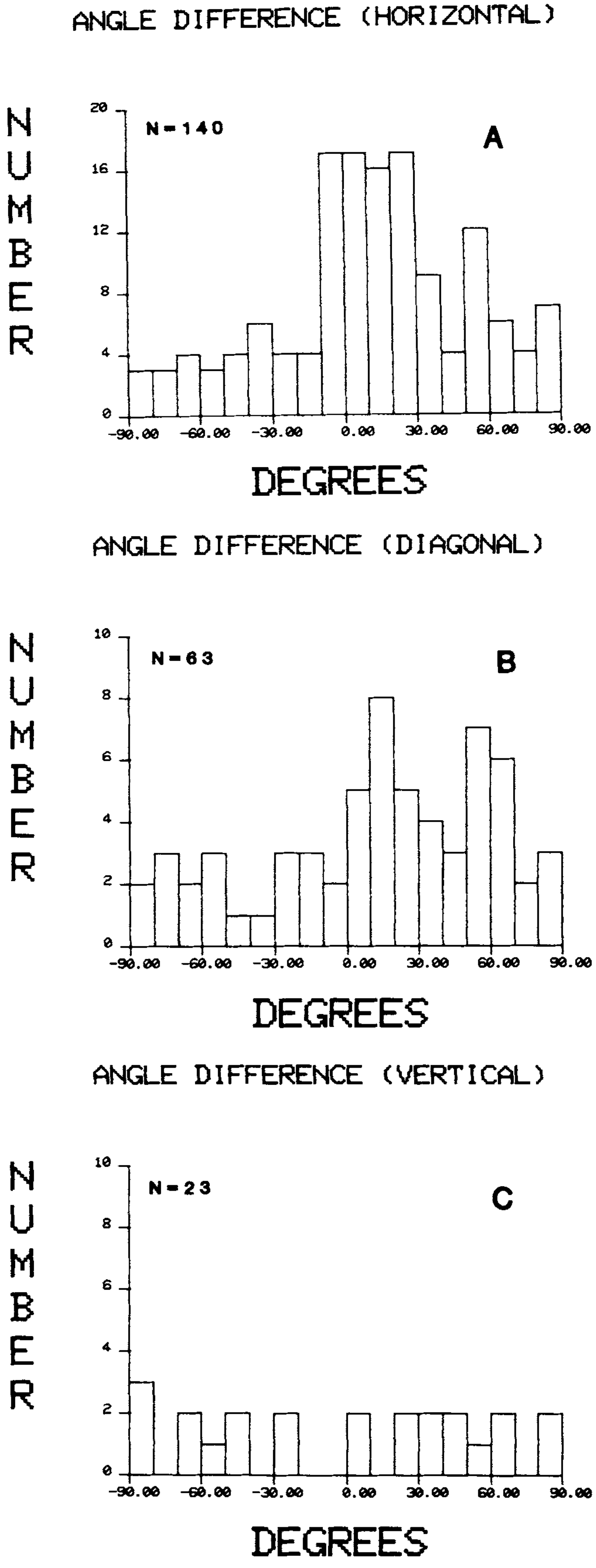

Fig. 3. Angle differences for area 19 cells subserving regions of retina within 22.5° of the horizontal (0°) (A), diagonal (45° and 135° (B) and vertical (90°) (C) meridians. The relationship between preferred orientation and polar angle is strongest in regions of area 19 cortex subserving the horizontal meridian.

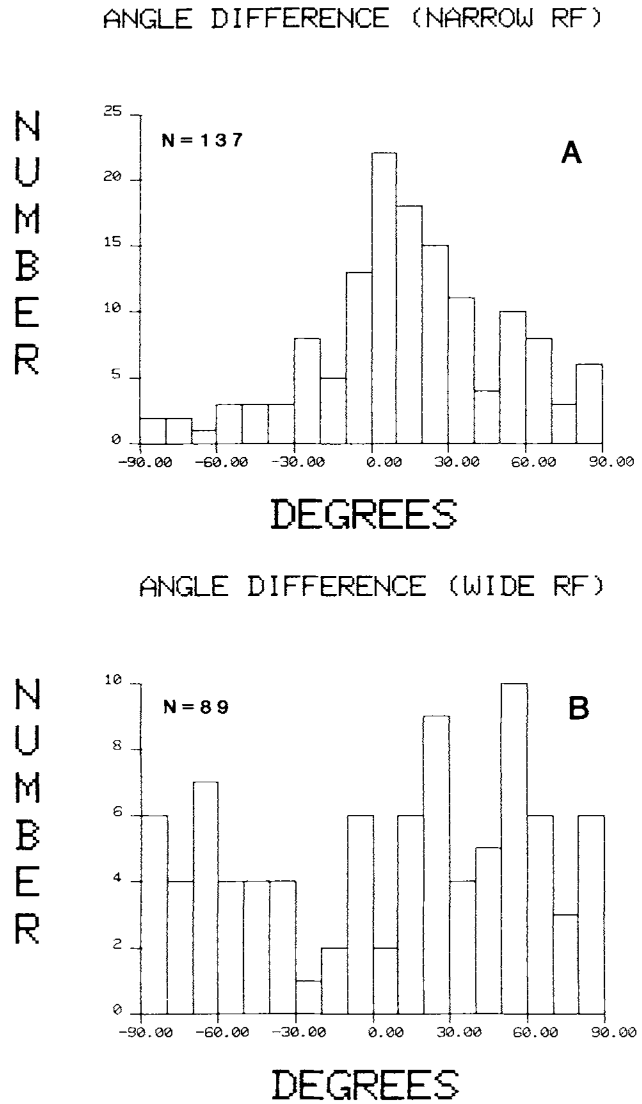

Fig. 4. Angle differences for area 19 cells having receptive fields less than (A) and greater than (B) 2° wide. A relationship between preferred orientation and polar angle is only evident among area 19 cells having narrow receptive fields.

cell having a preferred orientation of 0° or 180° (horizontal) and a polar angle of 0° or 180° (receptive field on the horizontal meridian) has an "angle difference" of 0 in Figure 1. This cell responds best to lines oriented radially. At the other extreme, a cell with a preferred orientation of 0° and a polar angle of 90° (receptive field on the vertical meridian) has an angle difference of −90. Similarly, a cell with a preferred orientation of 180° and a polar angle of 90° has an angle difference of 90°. The latter two cells prefer lines oriented tangentially, i.e., oriented perpendicular to the line connecting their receptive fields to the area centralis projection. If the preferred orientations of cells in area 19 are unrelated to polar angle, the histogram in Figure 1 should be flat and range from −90° to 90°. If, on the other hand, most area 19 cells prefer lines oriented radially, then the distribution should be unimodal and peak at 0. The results presented in Figure 1 have been analyzed statistically and the results of the Rayleigh test ($z = 18.5$, $P < 0.0000001$) and V-test ($u = 5.6$; $P < 0.0000001$) indicate that the distribution is not flat; it is obvious that the peak is close to 0. Thus, most cells in area 19 prefer lines oriented approximately parallel to the line connecting their receptive fields to the area centralis projection. It is noteworthy that the distribution does not peak exactly at 0. This is because as in the retina and area 17, cells in area 19 having receptive fields off of the horizontal meridian tend to prefer lines oriented somewhat more horizontally than the polar angles of their receptive fields predict. This has resulted in an overrepresentation of positive (0–+90) angle differences in our sample (Fig. 1) because we have not sampled equal numbers of cells from all four quadrants of the visual field. This point is explained in the methods and in the legend to Figure 1. The relationships between preferred orientation and polar angle in area 19 are described in more detail in the following sections. In the foregoing and all 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.

Differences related to receptive field eccentricity

To determine if the relationship between polar angle and preferred orientation was present throughout area 19, cells subserving different retinal eccentricities were analyzed separately. Figure 2 illustrates that the relationship between preferred orientation and polar angle in parts of area 19 representing the area centralis (eccentricity of 0–4°) is very weak or absent ($z = 3.2$, $P < 0.05$, Rayleigh test; $u = 2.1$, $P < 0.02$, V-test) (Fig. 2A). In regions of area 19 subserving parts of the retina between 4° and 30° from the area centralis, there is a pronounced relationship between preferred orientation and polar angle ($z = 16.0$, $P < 0.0000001$, Rayleigh test; $u = 5.3$, $P < 0.0000001$, V-test) Fig. 2B).

Meridional differences

In cat retina the relationship between dendritic field orientation and polar angle is strongest for ganglion cells located along the horizontal meridian (Leventhal and Schall, '83). A corresponding meridional difference exists in cat striate cortex (Leventhal, '83); we also find this meridional difference in area 19. The histograms in Figure 3 illustrate angle differences for area 19 cells having receptive fields within 22.5° of the horizontal (0°), diagonal (45° and 135°) and vertical (90°) meridians. In parts of area 19 from 4° to 30° from the area centralis projection, there is a strong tendency for cells subserving the horizontal meridian to prefer lines oriented radially ($z = 18.3$, $P < 0.0000001$, Rayleigh test; $u = 5.8$, $P < 0.0000001$, V-test) (Fig. 3A). In regions of cortex subserving the diagonal meridians there is a weaker relationship between preferred orientation and polar angle ($z = 4.3$, $P < 0.01$, Rayleigh test; $u = 2.4$ $P < 0.01$, V-test) (Fig. 3B). In regions subserving the vertical meridian, our small sample of cells provided no evidence for a relationship between preferred orientation and polar angle ($z = 0.57$, $P < 0.5$, Rayleigh test; $u = 0.4$, $P < 0.5$, V-test) (Fig. 3C).

Differences related to receptive field size

In order to see if area 19 cells having receptive fields of different sizes show the same relationship between preferred orientation and polar angle, cells having narrow and wide receptive fields were analyzed separately. The results of this analysis indicate that the relationship between preferred orientation and polar angle holds only for cells in area 19 (both S and C type) having receptive fields less than 2° wide ($z = 27.4$, $P < 0.0000001$, Rayleigh test; $u = 7.1$, $P < 0.0000001$, V-test) (Fig. 4A). Cells having wider receptive fields do not show a tendency to respond best to lines oriented radially (Fig. 4B). In fact, more wide-field cells (both S and C type) in area 19 prefer lines oriented tangentially or nearly tangentially than radially. In regions of area 19 from 4° to 30° from the area centralis projection about 60% of wide-field cells exhibit angle differences greater than 45°.

Differences related to other receptive field properties

In area 17 the relationship between preferred orientation and polar angle is related to the degree of orientation selectivity the cell exhibits (tuning width) and to the cell's response to flashing stimuli (whether the cell is S type or C type) (Leventhal, '83). S-type and C-type area 19 cells were analyzed separately and, unlike in area 17, the preferred orientations of S-type area 19 cells did not appear to relate more to polar angle than those of C-type cells. We also analyzed strongly and weakly orientation-sensitive area 19 cells separately and found, unlike in area 17, there is no tendency for the preferred orientations of the most orientation-sensitive area 19 cells to be the most strongly related to polar angle.

DISCUSSION

The results of this study indicate that the preferred orientations and receptive field positions of cells in area 19 are related. Outside of the area centralis representation, most area 19 cells having narrow receptive fields respond best to lines oriented radially, i.e., parallel to the line connecting their receptive fields to the area centralis projection. Also, in area 19, as in the retina and area 17 (Leventhal and Schall, '83; Leventhal '83), the relationship between preferred orientation and polar angle is strongest in regions subserving the horizontal meridian. As a result, there are relatively few cells in regions of area 19 subserving the horizontal meridian that prefer diagonal or vertical contours while there are significant numbers of area 19 cells subserving the diagonal and vertical meridians that prefer horizontal contours. The net result of this is that, as in the retina and area 17, there is an overrepresentation of horizontal preferred orientations in area 19. This overrepresentation is compounded by the overrepresentation of the horizontal meridian of the retina (the visual streak) in area 19 (Tusa et al., '79).

Relation to studies of area 17 (striate cortex)

Outside of the area centralis representation in area 17, most cells prefer lines oriented radially. This relationship is strongest for S-type cells, cells exhibiting the highest degree of orientation sensitivity and cells in regions subserving the horizontal meridian (Leventhal, '83). Outside of the area centralis representation in area 19, there is also a relationship between preferred orientation and polar angle; this relationship is also strongest in regions subserving the horizontal meridian.

There are three differences between the results of this study and studies of area 17. First, in striate cortex but not in area 19 the relationship between preferred orientation and polar angle appears to be markedly stronger for S cells than for C cells. Second, in striate cortex but not in area 19 the most orientation-selective cells show the strongest relationship between preferred orientation and polar angle. Finally, in area 19 but not in area 17 the orientation preferences of the cells having the widest receptive fields are not related to polar angle.

Mechanisms mediating orientation selectivity in visual cortex

All of the differences between areas 17 and 19 mentioned above may be related to the manner in which orientation sensitivity is generated in these two areas. The orientation preferences of S cells in area 17 may be strongly related to polar angle because most of these cells have their orientation preferences *specified* by orientation sensitive excitatory afferents they receive from the LGNd. The orientation tuning of S cells is much sharper than the tuning of retinal ganglion cells and thus the orientation preferences of S cells are likely to be *enhanced* by intracortical inhibition (Blakemore and Tobin, '72). The relationship between preferred orientation and polar angle appears weaker for C-type than S-type cells in area 17. Therefore, it may be that many C-type cells in area 17 have their orientation preferences specified as well as enhanced by intracortical inhibitory connections (Sillito, '75).

In area 19 narrow-field cells (both S and C type) but not wide-field cells prefer lines oriented radially. Wide-field cells (both S and C type) in area 19 tend to respond best to lines oriented more tangentially. This suggests that narrow-field cells in area 19 have their orientation preferences specified by orientation-sensitive excitatory afferents from narrow field cells in area 17 or from the LGNd while the orientation preferences of wide-field cells subserving the same part of the visual field are specified by inhibitory inputs from narrow-field cells in areas 17 or 19.

Laminar differences in preferred orientation

We have not yet undertaken a detailed laminar analysis of preferred orientation in areas 17 and 19. However, limited evidence based upon recording depth and the cells we have been able to localize indicates that the relationship between polar angle and preferred orientation in areas 17 and 19 is strongest in layer 4 and weakest in the deeper layers. This finding must be regarded as preliminary until a proper laminar analysis is carried out. Nevertheless, the finding that the relationship between preferred orientation and polar angle is strongest among S cells in area 17 and narrow-field cells in area 19 is consistent with this observation, since these cell types concentrate in layer 4, while wide-field cells concentrate in the deeper layers (Gilbert, '77; Leventhal and Hirsch, '78). It is interesting to note that shifts in preferred orientation between layers 4 and 5 have been reported in both cat (Bauer, '82) and monkey (Bauer et al., '80) striate cortex. Such shifts are to be expected if cells in layer 4 have their orientation preferences specified by their excitatory LGNd afferents, while many cells in layers 5 and 6 have their orientation preference specified by intracortical inhibitory connections.

CONCLUSION

This study provides evidence that the systematic relationship between preferred orientation and receptive-field position which begins in the retina due to the innate, radial orientation, of ganglion cell dendritic fields (Leventhal and Schall, '83) is largely preserved through extrastriate cortex. The radial orientation of retinal ganglion cell dendritic fields may thus provide an intrinsic structural framework for the "functional architecture" (Hubel and Wiesel, '62, '65) of orientation-sensitive neurons throughout the visual system.

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NOTE ADDED IN PROOF

We have recently studied the orientation sensitivity of cells having receptive fields 0° to 40° from the area centralis projection in area 18 of cat visual cortex. We find that, as in areas 17 and 19, most area 18 cells having receptive fields more than 4 degrees from the area centralis projection respond best to lines oriented radially. (Schall, J.D., Leventhal, A.G. and Vitek, D., in preparation).