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Organized Arrangement of Orientation-Sensitive Relay Cells in the Cat's Dorsal Lateral Geniculate Nucleus

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We studied the physiological orientation biases of over 700 relay cells in the cat's dorsal lateral geniculate nucleus (LGNd). Relay cells were sampled at regular intervals along horizontally as well as vertically oriented electrode penetrations in a fashion analogous to that used previously in studies of visual cortex (Hubel and Wiesel, 1962). The strengths of the orientation biases and the distributions of the preferred orientations were determined for different classes of relay cells, relay cells in different layers of the LGNd, and relay cells subserving different parts of the visual field.

We find that, at the population level, LGNd cells exhibit about the same degree of orientation bias as do the retinal ganglion cells providing their inputs (see also Soodak et al., 1987). Also, as in the retina (Levick and Thibos, 1982; Leventhal and Schall, 1983), most LGNd cells tend to prefer stimuli oriented radially, i.e., parallel to the line connecting their receptive fields to the area centralis projection. However, the radial bias in the LGNd is weaker than in the retina. Moreover, there is a relative overrepresentation of cells preferring tangentially oriented stimuli in the LGNd but not in the retina. As a result of the overrepresentation of cells preferring radial and tangential stimuli, the overall distribution of preferred orientations varies in regions of the LGNd subserving different parts of the visual field.

Reconstructions of our electrode penetrations provide evidence that, unlike in the retina, cells having similar preferred orientations are clustered in the LGNd. This clustering is apparent for all cell types and in all parts of laminae A and A1. The tendency to cluster according to preferred orientation is evident for cells preferring radially, intermediately, and tangentially oriented stimuli and thus is not simply a reflection of the radial bias evident among retinal ganglion cells at the population level.

It is already known that cells having inputs from different eyes, on-center, off-center, X-, Y-, W-type, and color-sensitive ganglion cells are distributed nonrandomly in the LGNd of cats and monkeys (for review, see Rodieck, 1979; Stone et al., 1979; Lennie, 1981; Stone, 1983). The finding that relay cells having similar preferred orientations are also distributed nonrandomly suggests that the initial sorting of virtually all properties segregated in visual cortex may begin in the LGNd.

Most cells in mammalian visual cortex are sensitive to stimulus orientation. Orientation-sensitive cortical cells are arranged in a systematic fashion. Cells having similar preferred orientations are grouped into columns extending from the pial surface to the white matter; preferred orientation changes gradually and systematically from one orientation column to the next (Hubel and Wiesel, 1962). The genesis of cortical orientation sensitivity has been the subject of intense speculation for decades. To date, the mechanisms mediating the development of this property remain unclear.

Recently, it has been reported that retinal ganglion cells are also weakly orientation sensitive (Levick and Thibos, 1982), probably as a result of the elliptical shape of their dendritic fields (Leventhal and Schall, 1983). The orientation-sensitive response of relay cells in the lateral geniculate nucleus (LGNd) has also been studied (Daniels et al., 1977; Lee et al., 1979; Vidyasagar and Urbas, 1982; Albus et al., 1983; Shou et al., 1986; Soodak et al., 1987), although the degree of sensitivity of the different LGNd relay cell types, the distribution of their preferred orientations and how orientation sensitivity of relay cells varies in different parts of the LGNd are controversial issues and merit additional study. This information is needed in order to determine if cortical orientation sensitivity is dependent upon the orientation sensitivity of cells in the retinogeniculate pathway.

We present the results of a quantitative study of the orientation sensitivity of over 700 LGNd relay cells. Single cells were sampled at regular intervals along electrode penetrations through the LGNd. The orientation sensitivity of different relay cell types, relay cells in different layers of the LGNd, relay cells subserving different eccentricities, and relay cells subserving different retinal meridians were analyzed quantitatively. The relationship between the preferred orientations of successively recorded cells was also analyzed in detail. Some of these results have appeared in abstract form (Shou and Leventhal, 1988).

Materials and Methods

Physiological recording procedures. Cats were prepared for electrophysiological recording as described previously (Leventhal and Hirsch, 1978; Leventhal and Schall, 1983). Subjects were anesthetized with Fluothane. Intravenous and tracheal cannulae were inserted. Animals were placed in a stereotaxic apparatus, and all pressure points and incisions were infiltrated with a long-acting anesthetic (1% lidocaine HCl, Elkins-Sinn). A mixture of *d*-turbocurarine (0.4 mg/kg/hr) and gallamine triethiodide

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(7 mg/kg/hr) was infused intravenously to induce and maintain paralysis. Animals were ventilated continuously with a mixture of nitrous oxide (75%) and oxygen (25%) and halothane as needed. Body temperature was maintained at 38°C. The ECG and EEG were monitored throughout the experiment. Expired pCO_2 was maintained at approximately 4%.

The eyes were protected from desiccation with contact lenses. The optic disks were projected upon a tangent screen positioned 114 cm from the retina. These projections 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). Locations of the areae centrales were also determined directly using the method of Pettigrew et al. (1979) to assure that their locations did not differ significantly from those inferred from the projections of the optic disks. The clarity of the optics was checked repeatedly during all experiments. Artificial pupils were used routinely. Spectacle lenses were used for correction when needed.

Action potentials of LGNd cells were recorded with an extracellular amplifier (Dagan Corp.) and high-impedance (~4 MΩ) microcapillary electrodes containing 4 M NaCl and HRP. The electrode was advanced using a piezoelectric microdrive (Burleigh Instruments) and was moved at least 50 μm between units to reduce sampling bias. Electrode tracts were reconstructed in Nissl-stained, 50 μm frozen sections (Fig. 1).

Receptive field mapping procedures. The responses of single cells to drifting high and low spatial frequency sinusoidal gratings as well as to alternating gratings were used to determine whether the cell summated linearly or nonlinearly. The spatial resolution, receptive field size, tonicity of response, response to rapid stimulus motion, and sluggishness of response were also studied. Units were identified as X- or Y-type (Enroth-Cugell and Robson, 1966; Cleland and Levick, 1974; Stone and Fukuda, 1974; Hochstein and Shapley, 1976). The responses of cells to visual stimulation were studied quantitatively with an Innisfree "Picasso" oscilloscope-based (Tektronix 608) optical display and a PDP 11/23-based computer system. We recently developed an apparatus which allows the oscilloscope display to be moved to any point in the animal's visual field while at the same time maintaining a fixed distance between the display and the animal's retina. At each visual field position the center of the display screen was exactly 57 cm from the animal's retina. Thus, we were able to accurately study cells subserving all parts of the visual field without distortion.

The eccentricity of each 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 disks (Fernald and Chase, 1971) and areae centrales (Pettigrew et al., 1979) were used to determine eccentricity. Since receptive fields were plotted on a tangent screen, appropriate corrections were made for all receptive fields to convert receptive field size and distance from the projections of the areae centrales to degrees of retinal angle. The calibrations on our optical display apparatus also provided a means of determining each unit's eccentricity directly.

Orientation sensitivity. The stimulus used to study orientation sensitivity in LGNd, as well as retina, is critical (Levick and Thibos, 1982; Soodak et al., 1987). In this study, the physiological orientation biases of LGNd cells were studied using sinusoidal gratings drifting across the receptive field (Levick and Thibos, 1982; Soodak et al., 1987). Twenty to 40 presentations of moving gratings (temporal frequency, 2–4 Hz) at each of 24–36 orientations were used to compile orientation tuning curves for the cells studied. The spatial frequency employed was just below the high spatial frequency limit of the unit determined at the nonoptimal orientation. The stimulus used was at least 3 times larger than the receptive field center of the cell. The velocity employed was the one judged to be optimal for the unit. These procedures are like those employed by Levick and Thibos (1982) in their study of retinal ganglion cells.

The responses of each cell to the different orientations presented were stored in the computer as a series of vectors (Fig. 2). The angle of each vector was defined relative to the vertical meridian of the retina with vertical defined as 90° and horizontal defined as 0° or 180°. The vectors were added and divided by the sum of the absolute values of the vectors. The angle of the resultant vector gave the preferred orientation of the cell. The length of the resultant vector, termed orientation bias, provided a quantitative measure of the orientation sensitivity of the cell. Orientation biases range from 0 to 1, with 0 being completely unoriented. The measure of "orientation bias" used in this study is analogous to that used by Levick and Thibos (1982) in their study of the physiological orientation sensitivity of retinal ganglion cells.

In order to provide a second measure of orientation sensitivity, an ellipse was computed based upon the responses of the cells to the orientations presented (Batschelet, 1981; Fig. 2). The ratio of the long to the short axis of the ellipse provided a second measure of orientation sensitivity termed "ellipse axis ratio," or ellipticity. This method is similar to the one used by Soodak et al. (1987) in their study of the orientation sensitivity of LGNd relay cells.

Since virtually all LGNd cells respond to all stimulus orientations, we thought it necessary to test whether the preferred orientations of the cells studied could be determined accurately and consistently over time. To this end we studied most cells for 1 hr or more and compiled multiple orientation tuning curves for many of the cells studied. We find that using the quantitative techniques and statistical analyses described above, the preferred orientations of relay cells can be determined repeatedly to within 5°–10° over a range of spatial frequencies and that the degree of orientation bias varies very little between trials for a given spatial frequency. However, as reported previously (Levick and Thibos, 1982; Soodak et al., 1987), we find that the magnitude of orientation bias is dependent upon spatial frequency. The orientation biases of most LGNd cells are relatively low for spatial frequencies near the optimal and can be quite pronounced for spatial frequencies near the high-frequency limit of the cell. In fact, for some cells, a spatial frequency could be found which would elicit a visual response only at or around the cell's preferred orientation. It is for this reason that the spatial frequency chosen to compare cells was always below the high-frequency cutoff at the nonpreferred orientation.

Electrophoretic injection of HRP. HRP injections were made into the LGN using microcapillary electrodes filled with 10% HRP in Tris-HCl buffer (pH 8.6) containing 1% dimethyl sulfoxide (DMSO). HRP was injected using currents of 3 μA (1.5 sec on, 0.5 sec off) for a period of 2–3 hr (Leventhal and Schall, 1983).

Histology and histochemistry. Animals were maintained for approximately 24 hr following HRP injections. They were then deeply anesthetized and perfused through the heart with 700 ml of lactated Ringer's solution containing 0.1% heparin, followed by 1000 ml of 1% paraformaldehyde and 2.5% glutaraldehyde in 0.1 M phosphate buffer at pH 7.4, followed by 600 ml of 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 buffer containing 0.03% *p*-phenylendiamine dihydrochloride, 0.06% pyrocatechol, and 0.02% H_2O_2 (PPD-PC reagent) and transferred back into 0.1 M Tris-HCl buffer. Sections were mounted on gelatinized slides, counterstained with Thionin, and coverslipped.

Whole retinae were removed and processed immediately after the perfusion. All retinae were rinsed in 0.1 M Tris buffer (pH 7.4) for 5 min, incubated in 1% cobalt chloride in Tris buffer containing 0.5% DMSO for 20 min at 35°C, rinsed in Tris buffer 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. Retinae were then flat-mounted on gelatinized slides.

Morphological analysis. Retinal ganglion cells in topographically appropriate regions of retina were drawn under camera lucida using a Nikon orthoplan microscope system with either a 40× or 100× oil-immersion objective. Some of these cells provided data for a previous study (Schall et al., 1986b). Drawings of each cell were traced onto a digitizing tablet (Houston Instruments) interfaced to a PDP 11/23 computer (Digital Equipment Corp.). The high resolution of the digitizing tablet allowed for a very accurate representation of the cell. The cartesian coordinates comprising the drawing were stored on a DSD 880 Winchester disk (Data Systems Design), and the dendritic field orientations of all cells were analyzed quantitatively as described previously (Leventhal and Schall, 1983; Schall et al., 1986b).

Data analysis. Several statistical techniques designed specifically to analyze distributions of angles (circular statistics) were used to help us to interpret 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

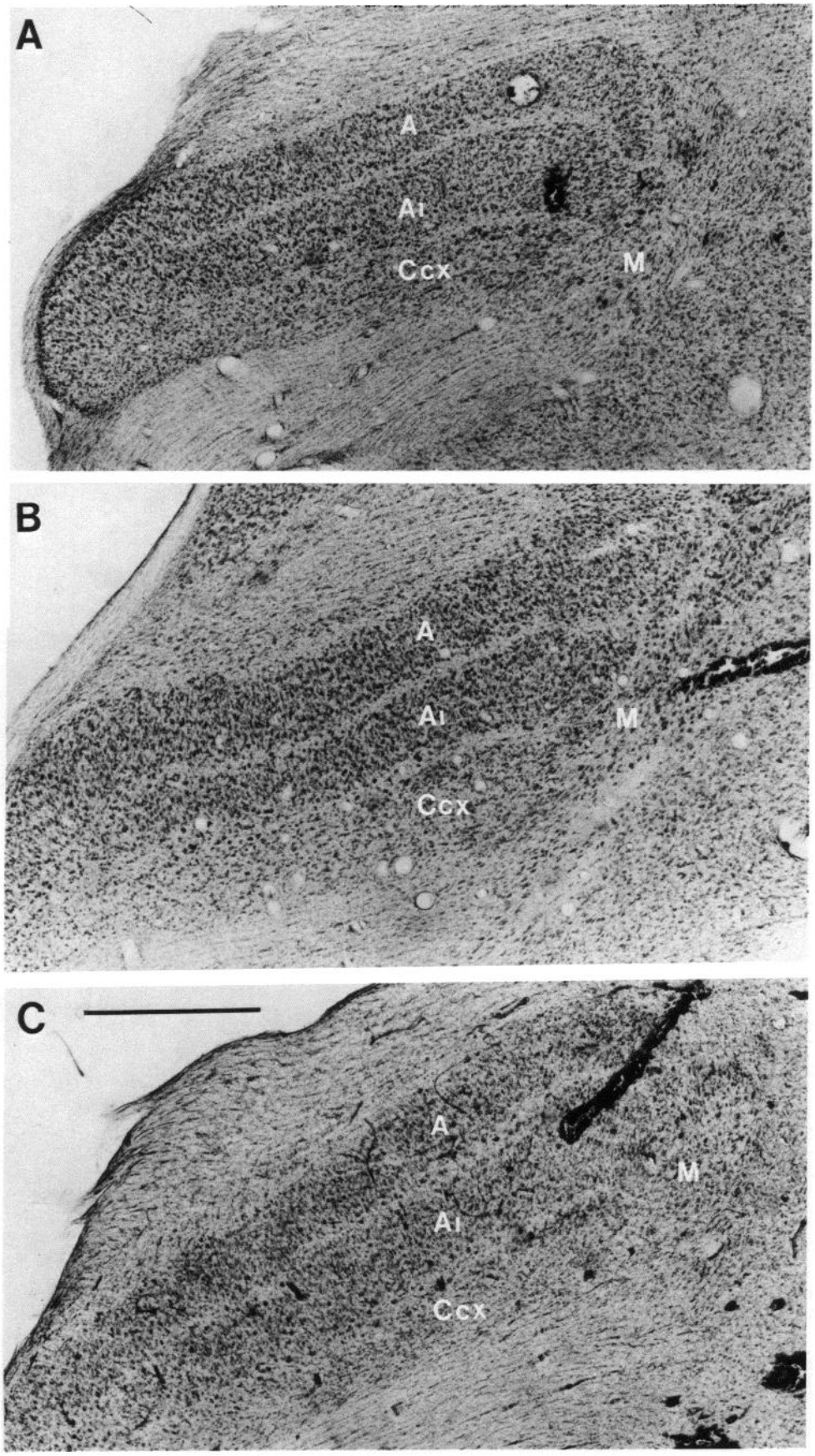

Figure 1. Photomicrographs of Nissl-stained coronal sections through the LGNd of 3 of the cats studied. In *A*, the dark spot illustrates the end point of an electrode penetration made roughly perpendicular to the border between laminae A and A1. In *B* and *C*, the dark lines (*arrows*) illustrate the angles of approach of electrodes which entered the A laminae from the opposite hemisphere. In *B*, the penetration was approximately parallel to the border between laminae A and A1. In *C*, the penetration was oriented somewhat obliquely to the border. Camera lucida drawings of reconstructions of the different types of penetrations made through the LGNd in this study are shown in Figures 11–16.

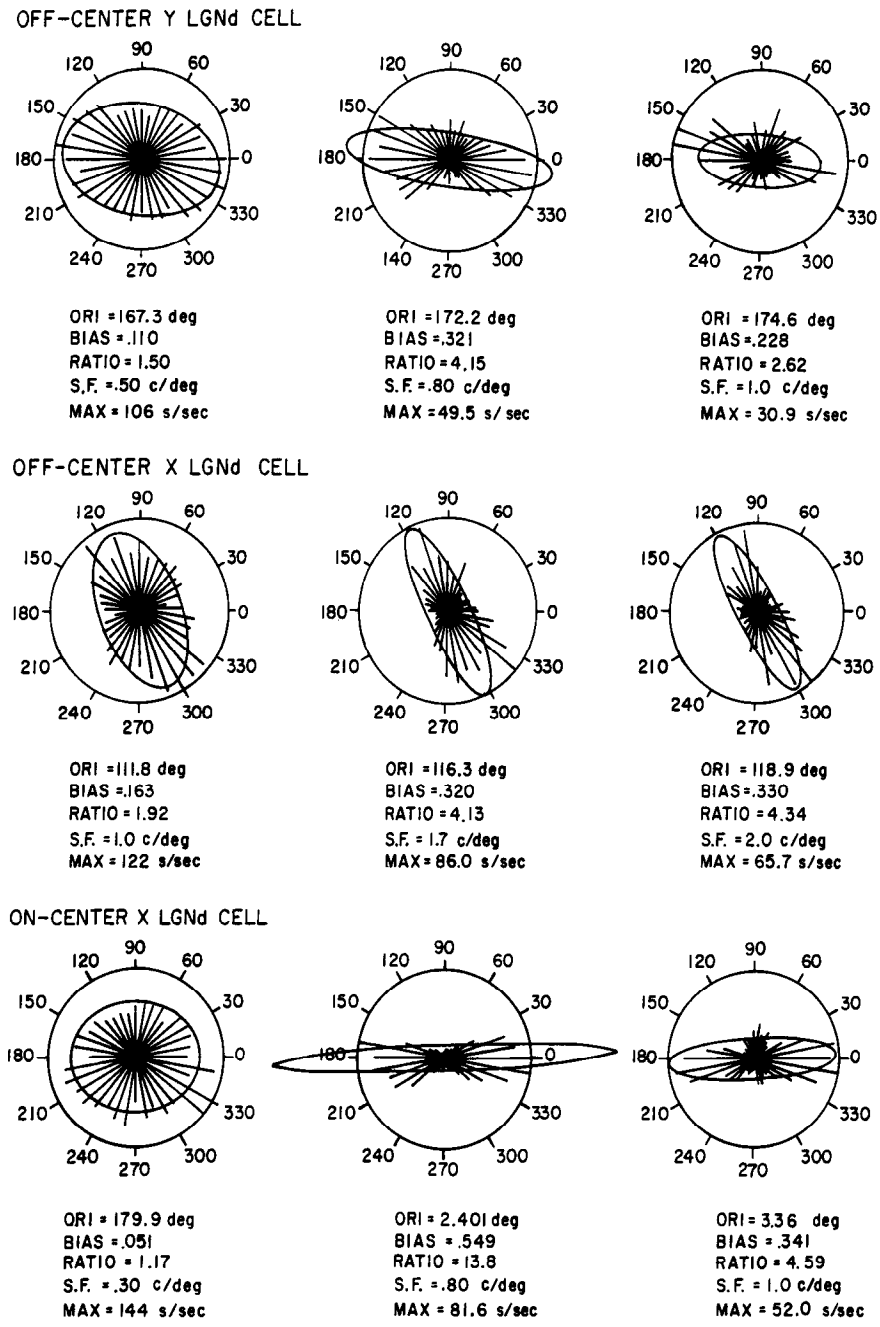

Figure 2. Computer-generated orientation tuning curves (circular histograms) for 3 of the more highly orientation biased LGNd relay cells studied. The longest line in each circular histogram was made to equal the radius of the circle and reflects the strongest response elicited. All shorter lines were made proportional in length to the responses at the other orientations. For all cells studied the magnitude of orientation sensitivity was determined in 2 ways. The first is termed orientation bias, and the second is termed the ellipse axis ratio (ellipticity). Orientation bias ranges from 0 to 1, with 0 being completely unoriented. Ellipse axis ratios range from 1 to infinity, with 1 being a circle (unoriented; see Materials and Methods). For each tuning curve shown the type of cell is indicated as is the orientation bias (BIAS), the ellipse axis ratio (RATIO), the preferred orientation (ORI), the peak response (MAX), and the spatial frequency of the test grating (S.F.). For most of the cells studied, multiple tuning curves were compiled over a 1–2 hr period. Using these quantitative mapping techniques and statistical analyses, orientation sensitivity can be determined reliably from one trial to the next (see text). Note that some high-bias cells had "butterfly-shaped" tuning curves, not elliptical ones (*bottom middle*). These cells responded very weakly to stimuli oriented roughly orthogonal to the preferred orientation. Some cells exhibited "butterfly-shaped" tuning curves even when tested with gratings having spatial frequencies significantly below the cells' high spatial frequency limit. At high spatial frequencies, the orientation tuning curves of some of these cells exhibited secondary peaks orthogonal to the cell's preferred orientation (*bottom right*).

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 differs significantly from an expected angle, the confidence intervals given by Batschelet (1981, p. 86) are used. Watson's U^2 test compares 2 distributions of angles (unimodal or multimodal) in order to determine whether the 2 samples differ significantly. High U^2 values result if the 2 distributions are different. These techniques have been described previously (Mardia, 1972; Zar, 1974) and have been used to study anatomical and physiological orientation sensitivity in the retina (Levick and Thibos, 1982; Leventhal and Schall, 1983).

Results

There is currently disagreement concerning the degree of orientation sensitivity of LGNd relay cells (Vidyasagar and Urbas, 1982; Soodak et al., 1987; see Discussion). Thus, one of the aims of this study was to provide a quantitative description of the orientation sensitivity of a large number of cells sampled from different parts of the LGNd. To this end, over 700 X- and Y-type relay cells in the A laminae in 20 cats were studied. A small sample (n = 12) of MIN cells were also studied. The eccentricities of the cells studied ranged from 0°–36°. Cells subserving the vertical, oblique, and horizontal retinal meridians were included in the sample. Overall, our results are in reasonable agreement with those of previous studies of the retina and LGNd. The mean bias for our total sample of 705 LGNd cells in laminae A and A1 was 0.143 and the mean ellipse axis ratio was 1.27. These values are consistent with the physiological results of Levick and Thibos (1982), who reported a mean orientation bias of 0.16 and a mean ellipse axis ratio of 1.3 for retinal ganglion cells, and with those of Soodak et al. (1987), who reported a mean ellipse axis ratio of 1.26 for LGNd cells.

We should point out that our methods were similar to those employed by Levick and Thibos (1982). Thus, our results can

be compared with theirs. However, Soodak et al. (1987) employed somewhat different techniques, and thus, our results are not directly comparable to theirs. It is also noteworthy that some of the LGNd cells in our sample exhibiting strong orientation biases had "butterfly-shaped," not elliptical, response profiles. These cells could be X- or Y-type and exhibited a clear response minimum approximately orthogonal to the cells' preferred orientation (Fig. 2, bottom middle). For some of these cells a response minimum was evident over a range of spatial frequencies and secondary peaks appeared orthogonal to the preferred orientation at high spatial frequencies (Fig. 2, bottom right; see also Soodak et al., 1985, 1987). Thus, their response profiles cannot be accounted for simply on the basis of the spatial frequency dependence of the orientation sensitivity of LGNd cells (see also Soodak et al., 1985a, b, 1987; Soodak, 1986, 1987).

The distributions of the orientation biases of X- and Y-type relay cells and on- and off-center cells are shown separately in Figure 3, *A–D*. The distributions of the orientation biases of cells subserving central and peripheral regions of retina are shown in Figure 3, *E–H*. None of the histograms differs significantly (Watson test, $p > 0.20$). The distributions of orientation biases of cells subserving the horizontal, vertical and oblique retinal meridians were also analyzed separately. As in the retina (Leventhal and Schall, 1983), there was a tendency for cells subserving the horizontal meridian to be more biased (mean bias = 0.153) than the rest (mean bias = 0.138). Also, relay cells having preferred orientations within 20° of radial exhibited stronger orientation biases (mean bias = 0.153) than did those having preferred orientations with 20° of tangential (mean bias = 0.135) (see also Schall and Leventhal, 1987).

During our experiments we also recorded from a small sample ($n = 12$) of cells in the medial interlaminar nucleus (MIN). The mean orientation bias of the MIN cells studied was 0.143. This value does not differ from the mean (0.143) of our overall sample.

Even though it is beyond the scope of this paper, it is worth noting that we have recently studied the orientation biases of cells in the LGNd of the Old World monkey *Macaca fascicularis*. We find that many of the cells in both the magnocellular and parvocellular laminae (including color-opponent cells; Wiesel and Hubel, 1966) of the monkey LGNd are clearly orientation biased (A. G. Leventhal, Y. Zhou, and K. Thompson, unpublished observations).

Relationship between preferred orientation and receptive field position (polar angle)

In the retina (Levick and Thibos, 1982; Leventhal and Schall, 1983) and LGNd (Vidyasagar and Urbas, 1982; Shou et al., 1986), it has been reported that there is a tendency for cells to prefer stimuli oriented radially, i.e., oriented parallel to the line connecting their receptive fields to the area centralis projection. In this study we analyzed the relationship between the preferred orientations and receptive field positions (polar angles) of LGNd cells in detail. Unless otherwise specified, in the following analyses we included only cells having orientation biases of 0.05 or greater (ellipse axis ratios greater than 1.1) (Fig. 2). These cells accounted for about 90% of our sample. Cells having lower biases are not significantly oriented so their preferred orientations are meaningless. Also, the results for cells having receptive fields less than 10° from the area centralis projection should be interpreted cautiously. There can be a 1°–2° error in localizing

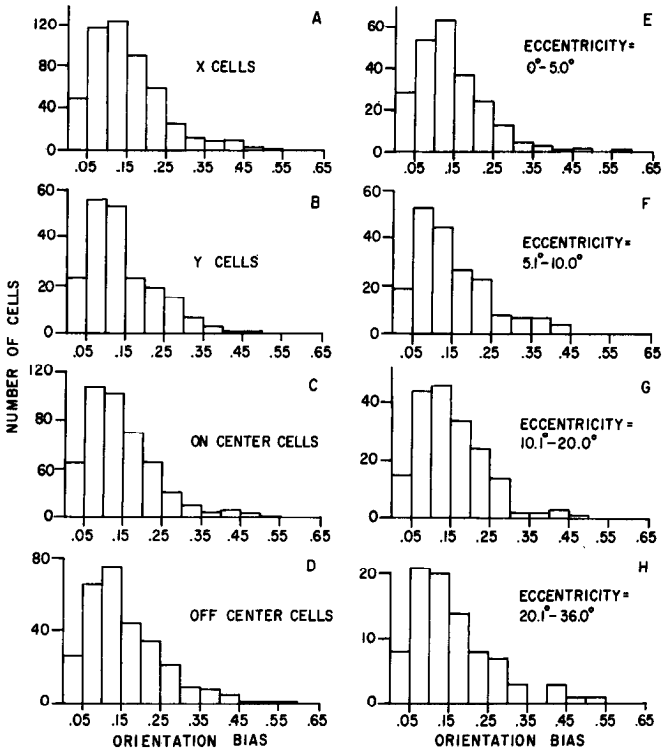

Figure 3. Physiological orientation biases of different types of LGNd cells (*A–D*), as well as of cells subserving different eccentricities (*E–H*). Note that the distributions do not differ significantly.

the polar angles of cells subserving central retina cannot be determined precisely. Nevertheless, since we plotted the area centralis projection directly (Pettigrew et al., 1979), the error in this study is likely to be no more than 1°, and thus, our results for cells subserving regions more than 4°–5° from the area centralis should be accurate.

We refer to the difference between a cell's preferred orientation and its polar angle as its "angle difference." A cell preferring exactly horizontal stimuli (0° or 180°) having a receptive field exactly on the horizontal meridian (polar angle of 0° or 180°) has an angle difference of 0° and thus is oriented radially. A cell preferring exactly vertical stimuli (90°) having a receptive field exactly on the horizontal meridian (0° or 180°) has an angle difference of 90° and thus is oriented tangentially. A negative or positive value indicates whether a cell's preferred orientation deviates from the polar angle of its receptive field in a clockwise or counterclockwise direction, respectively. Thus, angle differences range from −90° to +90°.

The distribution of the angle differences of all LGNd cells studied is shown in Figure 4. For comparison, a matched sample of retinal ganglion cells studied morphologically located in regions of retina projecting to topographically appropriate regions of the LGNd is also shown. Notice that both of the distributions are clearly peaked (Rayleigh test, $p < 0.001$) and the means of the distributions do not differ significantly from 0° (V test, $p < 0.005$). Thus, as reported previously, most retinal ganglion cells and LGNd relay cells prefer stimuli oriented radially (Levick and Thibos, 1982; Vidyasagar and Urbas, 1982; Leventhal and Schall, 1983; Schall and Leventhal, 1987; Shou et al., 1986). One difference we noted, however, was that the tendency to be oriented radially was clearly stronger among retinal ganglion

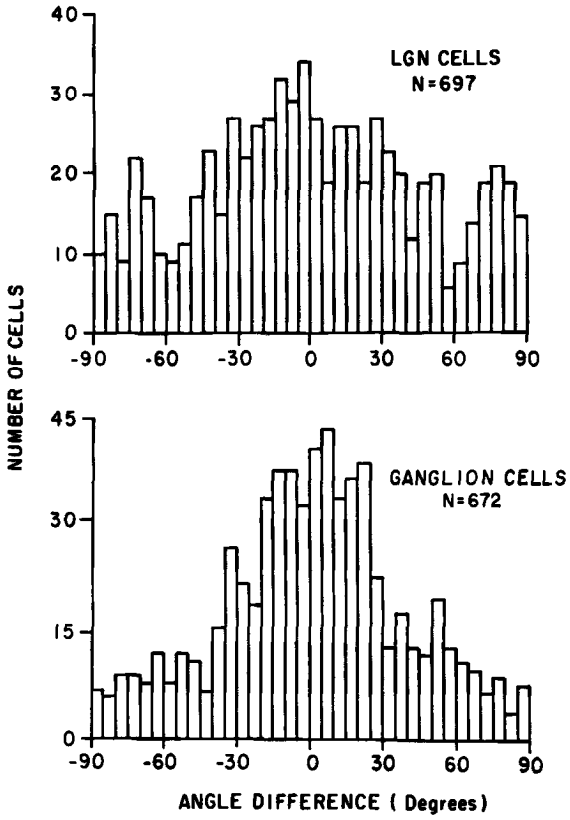

Figure 4. Angle differences between the preferred orientations and receptive field positions (polar angles) of all LGNd cells studied (*top*). For comparison, the angle differences, determined anatomically (Leventhal and Schall, 1983), of a sample of retinal ganglion cells located in regions of retina projecting to the regions of the LGNd studied are also shown. An angle difference of zero for LGNd cells indicates that the cell responded best to radially oriented stimuli, i.e., oriented parallel to the line connecting the cell's receptive field to the center of the area centralis projection. For retinal ganglion cells, an angle difference of zero indicates that the cell's dendritic field is oriented parallel to the line connecting it to the center of the area centralis. Note that a clear radial bias is evident in the retina and the LGNd (Rayleigh test, $p < 0.001$; V test, $p < 0.0005$). However, the tendency to prefer radial stimuli is stronger in the retina than in the LGNd (Watson test, $p < 0.001$) and there is a relative overrepresentation of cells preferring tangential stimuli (angle difference of $+60°$ to $+90°$ and $-60°$ to $-90°$) in the LGNd but not in the retina.

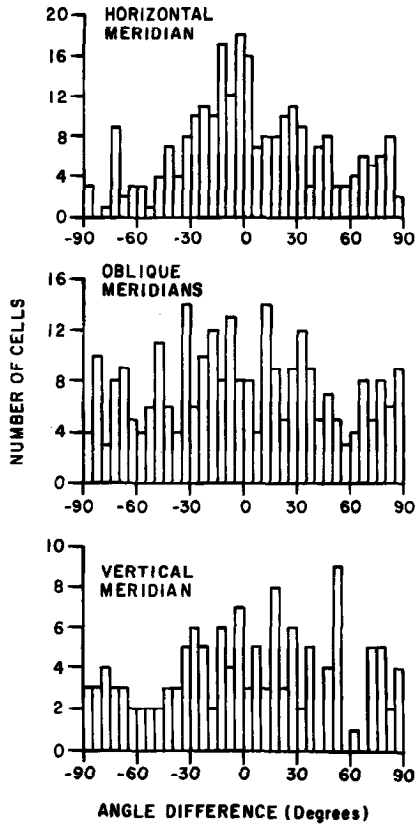

Figure 5. Angle differences for cells subserving the horizontal, oblique, and vertical meridians. Note that the tendency to prefer radial stimuli is strongest for cells subserving the horizontal meridian. Also note that, in addition to the radial bias, there is a general tendency for cells preferring tangential stimuli to be overrepresented.

cells studied anatomically (Fig. 4) as well as physiologically (see fig. 8 of Levick and Thibos, 1982) than among LGNd cells (Watson test, $p < 0.001$).

In fact, the LGNd distribution but not the retinal distribution was multimodal (Watson test, $p < 0.001$) as a result of a relative overrepresentation of cells preferring tangentially oriented (angle differences of $-60°$ to $-90°$ and $+60°$ to $+90°$) stimuli (Figs. 4–6). It should be pointed out that there is a greater error in localizing the center of the area centralis in physiological than in anatomical studies. This could make the radial bias appear weaker in the LGNd. However, an error in locating the area centralis projection would not result in the multimodal distributions which were observed for cells throughout the LGNd (Figs. 4–6).

Because of the large sample of cells in this study, it was possible for the first time to analyze separately the distributions of the angle differences of cells subserving different eccentricities, different retinal meridians, cells exhibiting different degrees of orientation bias, X cells, Y cells, on-center cells, off-center cells, and cells in laminae A and A1 (Figs. 5, 6). We found that none of the distributions was uniform (Rayleigh test, $p < 0.001$) and that relative overrepresentations of cells preferring radial and tangential stimuli were typically observed.

As described above, there was a general tendency for cells preferring radial and tangential stimuli to be overrepresented throughout the LGNd. However, the strength of this tendency clearly differed for different cell types and in different parts of the LGNd. For example, cells subserving central vision (eccentrities $< 10°$) exhibited a weaker tendency to prefer radial stimuli than did cells preferring peripheral vision (eccentricities $\geq 10°$) (Watson test, $p < 0.005$). Also, the tendency to prefer radial stimuli was clearly stronger for cells subserving the horizontal meridian than for cells subserving the vertical or oblique meridians (Watson test, $p < 0.001$) (Fig. 5). Moreover, unlike in the retina (Levick and Thibos, 1982; Leventhal and Schall, 1983), the tendency to prefer radial stimuli, although significant, was much weaker for Y cells than for X cells (Watson test, $p < 0.05$) (Fig. 6). In fact, a radial bias was evident only among Y cells having receptive fields more than $10°$ from the area centralis and a relative overrepresentation of cells preferring tangential stimuli was especially marked among Y cells (Fig. 6).

Distribution of preferred orientations

A number of studies indicate that cells preferring horizontal and vertical orientations are overrepresented in the LGNd (Daniels

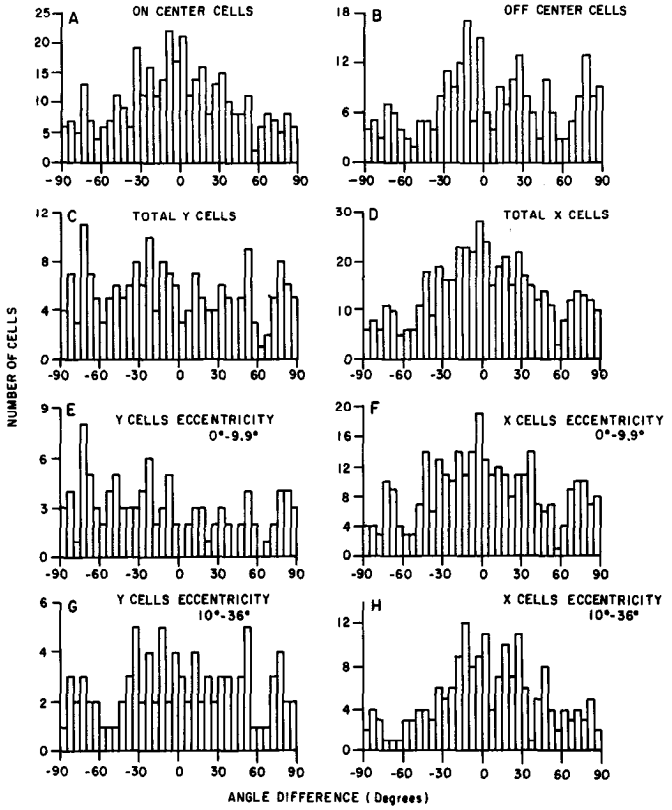

Figure 6. Angle differences for on-center cells (*A*) and off-center cells (*B*), as well as for X- and Y-type relay cells subserving different eccentricities (*C–H*). Note that the tendency to prefer radial stimuli is weaker among Y-cells than among X-cells (Watson test, $p < 0.001$). Also note that in addition to a radial bias, a tangential bias in the distribution of angle differences is evident regardless of cell type.

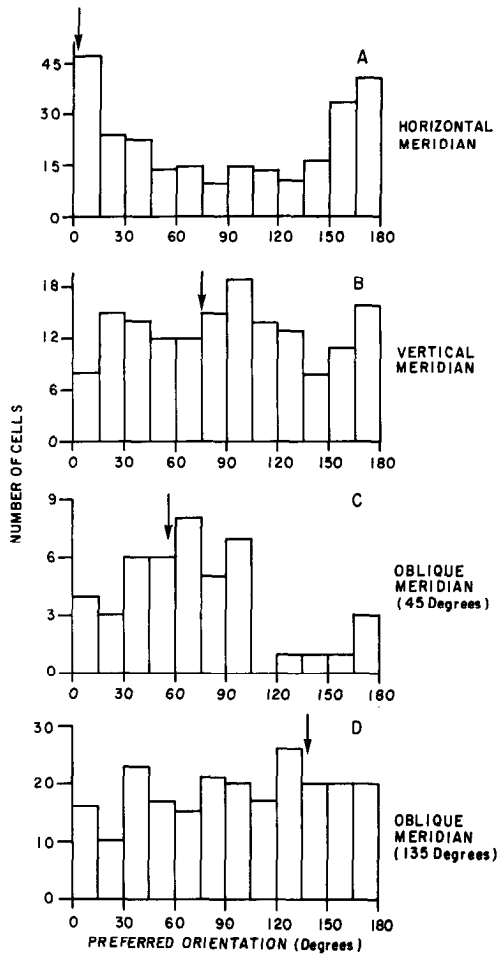

Figure 7. Distribution of preferred orientations of cells. Subserving the horizontal (0°), vertical (90°), and oblique (45° and 135°) meridian. The *arrows* indicate the average orientation for each distribution. Note the distributions of the preferred orientation of relay cells differs in different parts of the LGNd. The distribution is most anisotropic for cells subserving the horizontal meridian where the radial bias is strongest.

et al., 1977; Vidyasagar and Urbas, 1982). The distributions of the preferred orientations of the cells we studied are presented in Figure 7. Notice that the distribution of the preferred orientations of cells in different parts of the LGNd varied. The average orientations of the populations of cells subserving regions of retina within 22.5° of the 0°, 45°, 90°, and 135° retinal meridians were 1°, 57°, 75°, and 137°, respectively (Fig. 7). These differences do not support a general overrepresentation of horizontal and vertical orientations per se. Rather, they presumably reflect the radial and tangential biases described above. For example, the radial bias is most evident for cells subserving the horizontal meridian (Fig. 5*A*); there were clearly more cells preferring horizontal orientations in regions of the LGNd subserving the horizontal meridian (Fig. 7*A*). On the other hand, the radial bias is relatively weak among cells subserving the vertical and oblique meridians (Fig. 5, *B, C*). This combined with the finding that tangential orientations are overrepresented results in a much more uniform distribution of preferred orientations in regions of the LGNd subserving these meridians (Fig. 7, *B–D*).

Relationship between the preferred orientations of neighboring cells

In cat visual cortex, cells having similar orientations are grouped into columns extending from the pial surface to the white matter; the preferred orientations of successively recorded cells change gradually and systematically as the electrode is advanced parallel to the cortical surface (Hubel and Wiesel, 1962; Albus, 1975). Evidence has been presented that, in the visual cortex of the cat, columns subserving radial orientations are larger than those preferring nonradial orientations (Schall et al., 1986b). An organized arrangement of orientation-sensitive cells is not present in the retina, where there is a tendency for ganglion cells to prefer radial stimuli at the population level but no tendency for adjacent cells to prefer similar orientations or to be clustered according to preferred orientation (Schall et al., 1986b).

In this study we analyzed the preferred orientations of successively recorded LGNd relay cells as has been done previously in studies of visual cortex (Hubel and Wiesel, 1974; Albus, 1975). In some animals, the cells studied were recorded along vertical penetrations made roughly perpendicular to the border between laminae A and A1 (Figs. 1*A*, 14–16). In others, the cells studied were recorded along penetrations made roughly parallel to the border between laminae A and A1 (horizontal penetrations) by approaching the LGNd through the opposite hemisphere (Bowling and Wieniawa-Narkiewicz, 1986) (Figs. 1, *B, C*; 11–13).

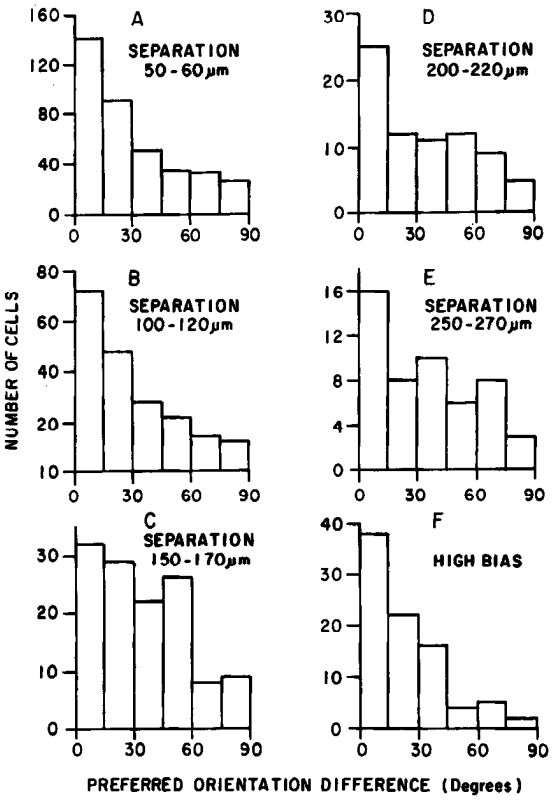

Figure 8. Differences in the preferred orientations of successively recorded LGNd cells having overlapping receptive fields. A preferred orientation difference of zero indicates that the successively recorded cells preferred exactly the same orientation. A preferred orientation difference of 90° indicates that the successively recorded cells preferred orthogonal orientations. Preferred orientation differences for successively recorded cells separated by different distances are shown in *A–E*. Note that the tendency for cells to prefer similar orientations is weaker for cells separated by greater distances (150–170, 200–220, and 250–270 μm) than it is for neighboring cells (50–60 and 100–120 μm). The preferred orientation differences of successively recorded cells separated by 50–60 μm having high biases (>0.20) are shown in *F*. These cells show a strong tendency to be clustered according to preferred orientation.

Cells were recorded at 50–60 μm intervals along each penetration, and cell body recordings were differentiated from recordings from axons and dendrites using the waveform criteria of Bishop et al. (1962). For each penetration the differences in the preferred orientations (preferred orientation difference) of successively recorded cells having overlapping receptive fields (cell pairs) were determined (Hubel and Wiesel, 1962; Albus, 1975; Schall et al., 1986b). Preferred orientation differences ranged from 0° for successively recorded cells having exactly the same preferred orientation to 90° for successively recorded cells having orthogonal preferred orientations.

The preferred orientation differences between successively recorded cells having overlapping receptive fields (cell pairs) are shown in Figures 8–10. Clearly, there is an overall tendency for relay cells separated by 50–60 μm to prefer similar orientations. The mean differences in the preferred orientations of successively recorded cells separated by 50–60 μm was 29° (Fig. 8*A*). The distribution was significantly peaked (Rayleigh test, $p < 0.001$) in the 0°–30° range (69% of cells as opposed to the 30% expected by chance).

We analyzed separately the preferred orientation differences of successively recorded cells subserving the horizontal, oblique, and vertical retinal meridians. Cells subserving central and peripheral regions were also analyzed separately. All of them peaked significantly (Rayleigh test, $p < 0.001$) in the 0°–30° range. Thus, regardless of the polar angle and retinal eccentricity of their receptive fields, neighboring LGNd cells tend to prefer similar orientations.

As a control and in order to see if the grouping of LGNd cells according to preferred orientation was related to the magnitude of their orientation sensitivity, we analyzed separately the preferred orientation differences of the cell pairs in our sample which exhibited the greatest orientation biases (>0.2). These cells accounted for about one-fifth of our sample, and their relatively strong biases made errors in the determinations of their preferred orientations unlikely. The histogram in Figure 8*F* shows that strongly selective, successively recorded cells exhibited a very clear tendency to prefer similar orientations (Rayleigh test, $p < 0.0005$). The mean difference in preferred orientation between successively recorded high-bias cells was only 24°; 70% of the high-bias cells had neighbors with preferred orientations differing by <30°. This suggests that experimenter bias and/or errors in the determination of preferred orientation cannot account for our results. In fact, the foregoing analysis suggests the opposite; the tendency for neighboring LGNd cells to have similar preferred orientations may be even stronger than our results indicate; the inaccurate determination of preferred orientation caused, for example, by slight optical distortions or response variability may result in larger differences than actually exist. Alternatively, or in addition, the most selective LGNd cells may actually show the greatest tendency to be clustered according to preferred orientation.

We also compared the preferred orientations of cells having overlapping receptive fields and separated by different distances. Cells separated by 50–60, 100–120, 150–170, 200–220, and 250–270 μm are shown in Figure 8. For cells separated by 50–60 and 100–120 μm, the distributions were clearly peaked (Rayleigh test, $p < 0.001$) in the 0°–30° range (69 and 67% of cells, respectively). We note, however, that the tendency to prefer similar orientations was much weaker for more widely separated cells (Fig. 8, *C–E*) than for cells separated by 120 μm or less (Fig. 8, *A, B*). Nonetheless, even cells separated by 150–170, 200–220, and 250–270 μm showed weak tendencies (49, 49, and 47% in 0°–30° range, respectively) to prefer similar orientations (discussed below).

We were also interested to know whether the tendency of adjacent cells to prefer similar orientations was related to the cells' preferred orientation. Thus, we analyzed separately cells subserving different retinal meridians preferring stimuli oriented radially (angle differences of 0°–29.9°), cells with intermediate angle differences (30°–59.9°), and cells preferring stimuli oriented tangentially (angle differences of 60°–90°). Histograms illustrating the results of these analyses are shown in Figure 9. All distributions peaked significantly in the 0°–30° range (Rayleigh test, $p < 0.001$). However, for cells having tangential angle differences (Fig. 9, *I–L*), the tendency for adjacent cells to prefer similar orientations was somewhat weaker than for cells having radial (Fig. 9, *A–D*) or intermediate (Fig. 9, *E–H*) angle differences.

It should be emphasized that the finding that cells having intermediate preferred orientations are clustered argues against the possibility that the clustering observed is an artifact of the overrepresentations of cells preferring radial and tangential

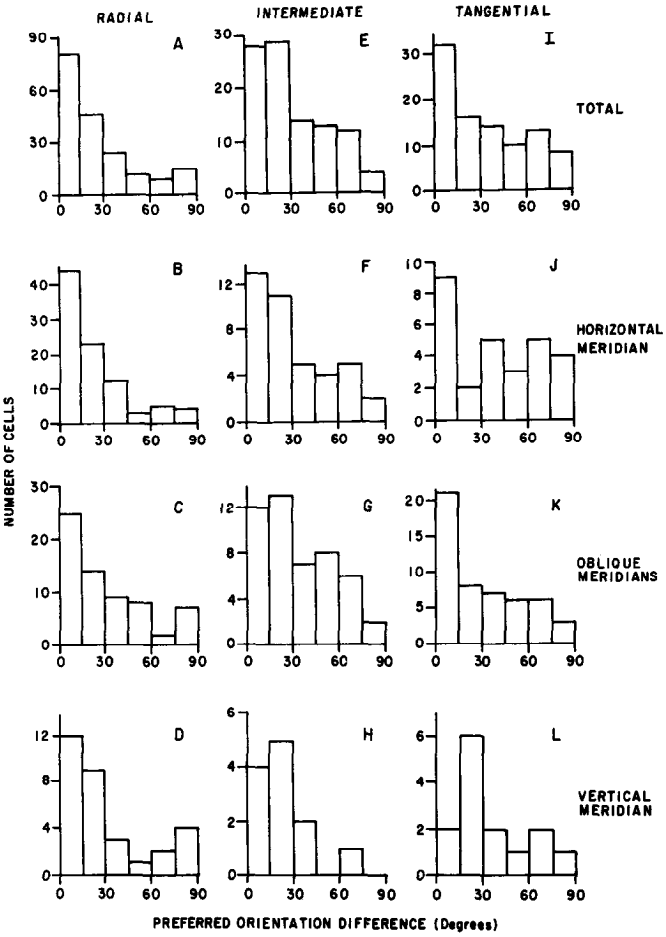

Figure 9. Preferred orientation differences for successively recorded cells (separated by 50–60 μm) preferring radial (*A–D*), intermediate (*E–H*), and tangential (*I–L*) orientations. Cells subserving the horizontal (*B, F, J*), oblique (*C, G, K*), and vertical (*D, H, L*) meridians are shown separately. Cell pairs were grouped according to the preferred orientation of the first cell recorded in the pair. Note that if a cell is encountered which prefers radial or intermediate orientations, there is a strong tendency for the next cell encountered to prefer a similar orientation. If a cell having a tangential angle difference is encountered, then the tendency for the next cell to prefer the same orientation is weaker.

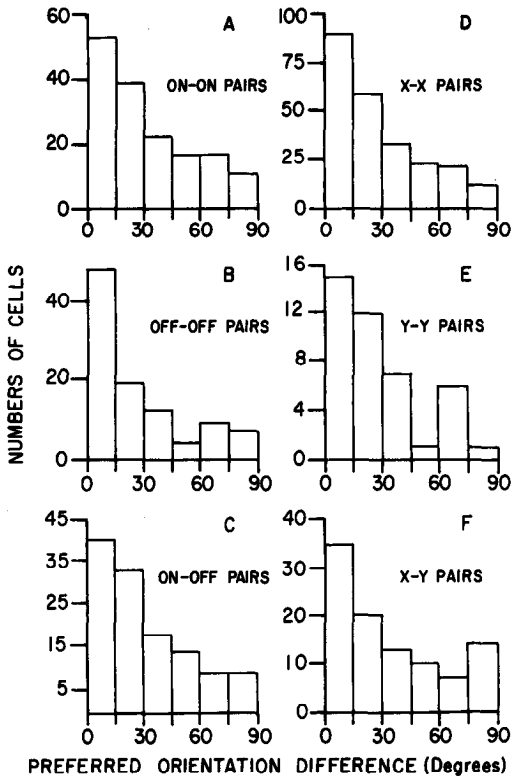

Figure 10. Preferred orientation differences for successively recorded cells of different types (cell pairs separated by 50–60 μm) having overlapping receptive fields. Note that all distributions are significantly peaked (Rayleigh test, $p < 0.001$) in the 0°–30° range. Thus, successively recorded cells tend to prefer similar orientations (Watson test, $p > 0.20$) regardless of whether both cells are on-center (*A*), both cells are off-center (*B*), one cell is on-center and the other is off-center (*C*), both cells are X-cells (*D*), both cells are Y-cells (*E*), or one cell is X-type and the other is Y-type (*F*).

stimuli. If this were the case, then the histograms shown in Figure 9, *E–H* would peak at 45°, not 0°, because cells with intermediate angle differences would tend to be surrounded by cells preferring radially or tangentially oriented stimuli.

Finally, we wanted to determine whether the tendency for nearby cells to prefer similar orientations was related to the cells' other receptive field properties. To this end, the preferred orientation differences for successively recorded cells were determined separately in cases (1) when both cells were on-center, (2) when both cells were off-center, (3) when one cell was on-center and the other was off-center, (4) when both cells were X-cells, (5) when both cells were Y-cells, and (6) when one cell was an X-cell and the other was a Y-cell.

Histograms illustrating the results of these analyses are shown in Figure 10. In all cases, successively recorded cells tended to prefer similar orientations, and all histograms were significantly peaked (Rayleigh test, $p < 0.001$) in the 0°–30° range. Thus, as in cat visual cortex (Hubel and Wiesel, 1962), nearby LGNd cells have similar preferred orientations and this tendency is independent of the cells' other receptive field properties.

Arrangement of orientation-sensitive cells

The foregoing results are consistent with the idea that cells preferring different orientations are clustered separately in the LGNd. In order to examine the arrangement of orientation-sensitive cells in more detail, we reconstructed our electrode penetrations in order to determine how preferred orientation changed with distance in the LGNd. Some representative penetrations are presented in Figures 11–16. Note that in most penetrations oriented approximately parallel to the border between laminae A and A1 (Figs. 11–13) there seemed to be a systematic (or at least nonrandom) change in preferred orientation as the electrode was advanced over long distances. In contrast, most cells encountered along penetrations oriented approximately perpendicular to the border between laminae A and A1 had similar preferred orientations (Figs. 14–16). Cells preferring radial stimuli (squares) were clearly clustered (Figs. 11–14), as were cells preferring tangential orientations (circles) (Figs. 12, 13, 15). In some penetrations, however, significant scatter was evident (for example, Fig. 16). In others, there were occasional, abrupt changes (Fig. 12). Some, but not all, of the time changes in orientation were observed at the border between laminae A and A1 (Fig. 15). Finally, in many penetrations, preferred orientation varied little over distances large enough to result in significant shifts

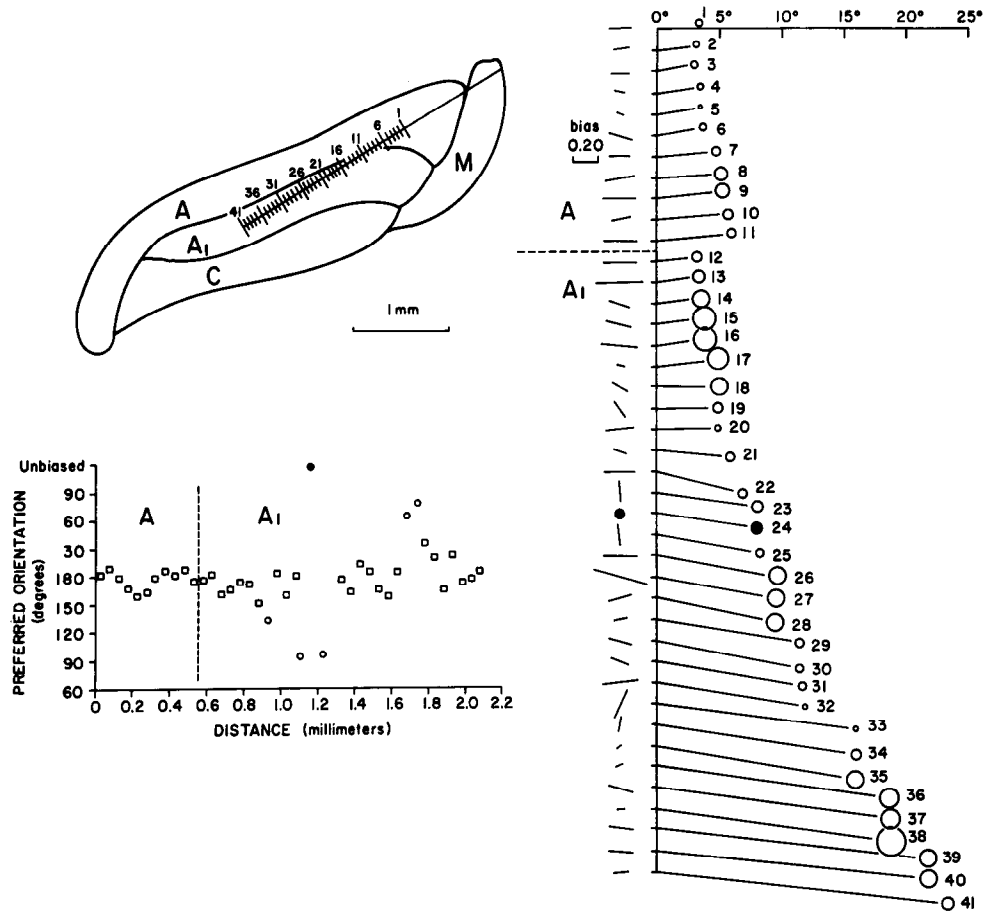

Figure 11. Reconstruction of an electrode penetration through laminae A and A1 of the cat's LGNd. The electrode was advanced through the right hemisphere into the left LGNd and was oriented almost parallel to the border between laminae A and A1. *M* refers to the MIN, and *C* refers to the C layers (C, C1, C2, C3). The positions of each of the units recorded along the penetration are indicated by the *short lines.* The preferred orientations of each of the units recorded along the penetration are shown in the scatterplot (*bottom left*). *Squares* indicate cells having preferred orientations within 45° of radial, and *circles* indicate cells having preferred orientations within 45° of tangential. *Solid circles* indicate unoriented cells. The sizes and positions of the receptive fields of the cells recorded along the penetration are shown at *right.* The *abscissa* indicates azimuth, and the *ordinate* indicates elevation. The *tick marks* on the ordinate indicate the relative position of the origin for each cell. For each receptive field the preferred orientation is indicated at the *left-hand side* of the ordinate. The length of the line indicating the cell's preferred orientation is proportional to the cell's orientation bias. The length of the scale bar indicates a bias of 0.20. The *dashed lines* indicate the border between laminae A and A1. Note that most cells recorded along this penetration subserved the horizontal meridian and most preferred horizontal (180°) orientations. However, regardless of preferred orientation, successively recorded cells preferred similar orientations, and the change in preferred orientation with distance along the penetration was clearly nonrandom.

in receptive field position (Figs. 11, 12). This was most often true in regions where cells preferring radial orientations were clustered (Fig. 11) and can account for our finding (presented above) that even widely separated cells exhibited a weak tendency to prefer similar orientations.

It should be emphasized that it is more difficult in studies of the LGNd than in studies of striate cortex (Hubel and Wiesel, 1962, 1974; Albus, 1975) to interpret the changes in the preferred orientations of cells recorded along long electrode penetrations. First, the LGNd is shaped irregularly and is much smaller than striate cortex. Second, the visual field is represented in 3 dimensions in the LGNd (Sanderson, 1971). Third, making penetrations exactly parallel to or perpendicular to laminae borders is extremely difficult and can only be done at coronal levels subserving the horizontal meridian where the A laminae are relatively "flat" (Sanderson, 1971; Fig. 11). Thus, long penetrations, both vertical and horizontal, invariably encounter cells subserving different parts of the retina.

Discussion

This study demonstrates that the large majority of relay cells throughout the A laminae of the LGNd of the cat are sensitive to stimulus orientation; orientation sensitivity is not a rarely encountered property of relay cells. The results indicate that the different classes of relay cells, cells subserving different retinal eccentricities, and cells in laminae A, A1 and the MIN exhibit similar degrees of orientation sensitivity. This report also provides evidence that at the population level the distributions of the preferred orientations of relay cells varies in different parts of the LGNd and does not strictly reflect the distributions of the preferred orientations of the ganglion cells providing their afferent inputs. At the population level in both the retina and the LGNd, there is a clear tendency for most cells to prefer stimuli oriented radially. However, this tendency is weaker in the LGNd, especially among Y-cells, than in the retina. Also, in the regions of the LGNd studied but not in the corresponding

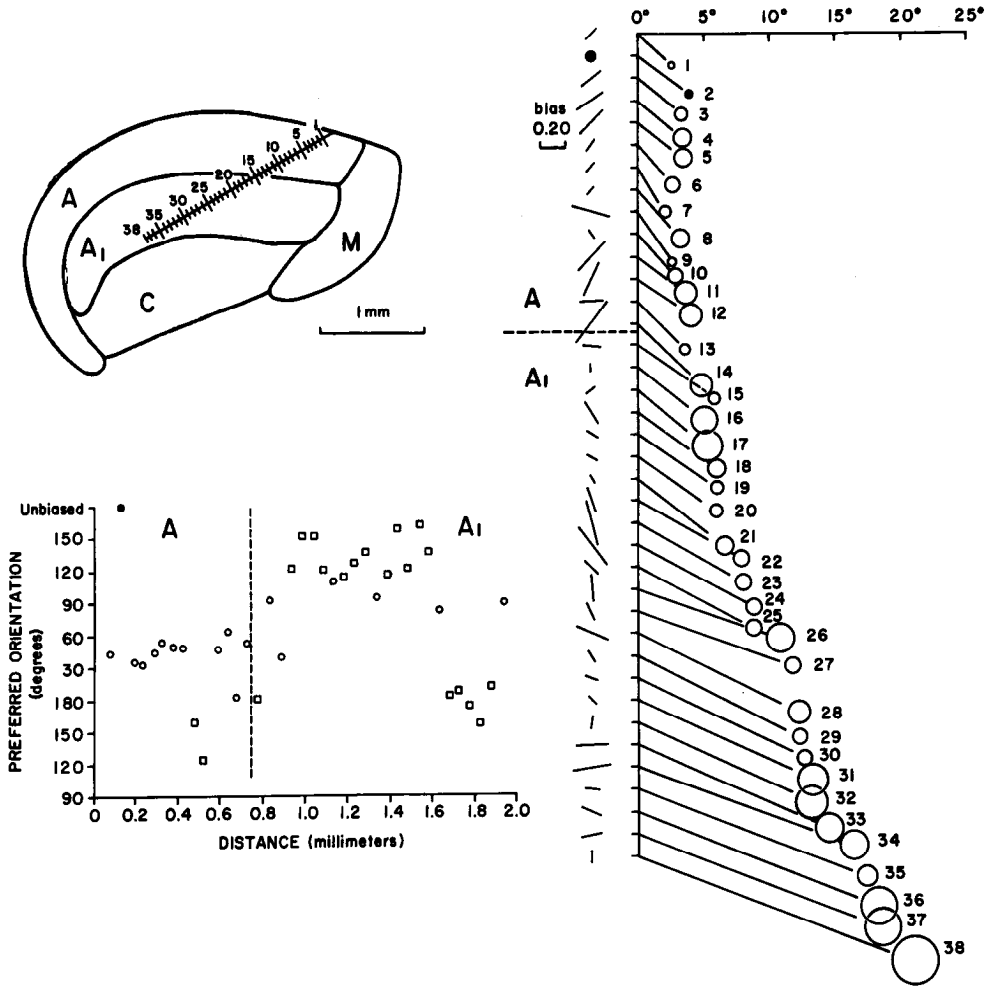

Figure 12. Reconstruction of an electrode penetration through laminae A and A1 of the cat's LGNd. The electrode was oriented obliquely relative to the border between laminae A and A1. Conventions are as in Figure 11. Note that successively recorded cells preferred similar orientations. The change in preferred orientation with distance along the penetration appeared systematic. Also note that cells preferring radial as well as tangential stimuli were clustered. Thus, the clustering of cells having similar preferred orientations cannot be accounted for by the overall tendency of LGNd cells to prefer radial stimuli.

regions of retina, there is an overrepresentation of cells preferring tangentially oriented stimuli.

The present results also provide the first evidence that cells having similar preferred orientations are clustered in the LGNd. This is very different from the situation in the retina, where it has been demonstrated that cells are not clustered according to preferred orientation (Schall et al., 1986b). In the retina there is a tendency for cells to prefer radial stimuli at the population level, but, otherwise, ganglion cells preferring different orientations are distributed randomly (Schall et al., 1986b).

Relation to previous work

It has been reported previously that LGNd relay cells are orientation sensitive (Daniels et al., 1977; Creutzfeldt and Northdurft, 1979; Vidyasagar and Urbas, 1982; Albus et al., 1983; Vidyasagar, 1984; Shou et al., 1986; Soodak et al., 1987). There has, however, been a renewed interest in this area in recent years, and there is currently disagreement in the literature concerning LGNd orientation sensitivity. The points of contention seem to focus upon the degree of selectivity of LGNd cells, the distribution of their preferred orientations, how LGNd orientation sensitivity is generated, and whether it is functionally meaningful.

Some reports indicate that LGNd neurons are more sensitive to stimulus orientation than are the retinal ganglion cells providing their inputs (Vidyasagar and Urbas, 1982; Vidyasagar, 1984). These authors find a preponderance of LGNd cells preferring horizontal and vertical stimuli and suggest that cortical afferents are involved in the generation of LGNd orientation sensitivity (see also Daniels et al., 1977). Other authors report that the orientation biases of LGNd relay cells strictly reflect those of their retinal afferents (Soodak et al., 1987). These authors favor the idea that the orientation sensitivity of LGNd relay cells originates in the retina and reflects the anatomically generated (Leventhal and Schall, 1983), linear, orientation-sensitive response (Levick and Thibos, 1982) of the retinal ganglion cells providing their afferents.

The present study is arguably the most exhaustive to date. We believe that some of the disagreements described above are more apparent than real and may have resulted because previous studies included only relatively small samples of cells and, thus, differences in laminar location, eccentricity, polar angle, cell type could not be adequately controlled. For example, our findings that relay cells preferring different orientations are clustered and that radial and tangential orientations are overrepresented makes claims regarding the overall distribution of preferred orientations based upon small samples of cells especially hard to interpret. For example, if cells are recorded mainly from regions of the LGNd subserving the horizontal and vertical meridians, then an apparent preponderance of these orientations should result. Our finding that the radial bias is strongest in regions of the LGNd subserving the horizontal meridian further complicates matters.

It should be noted that our results are generally consistent

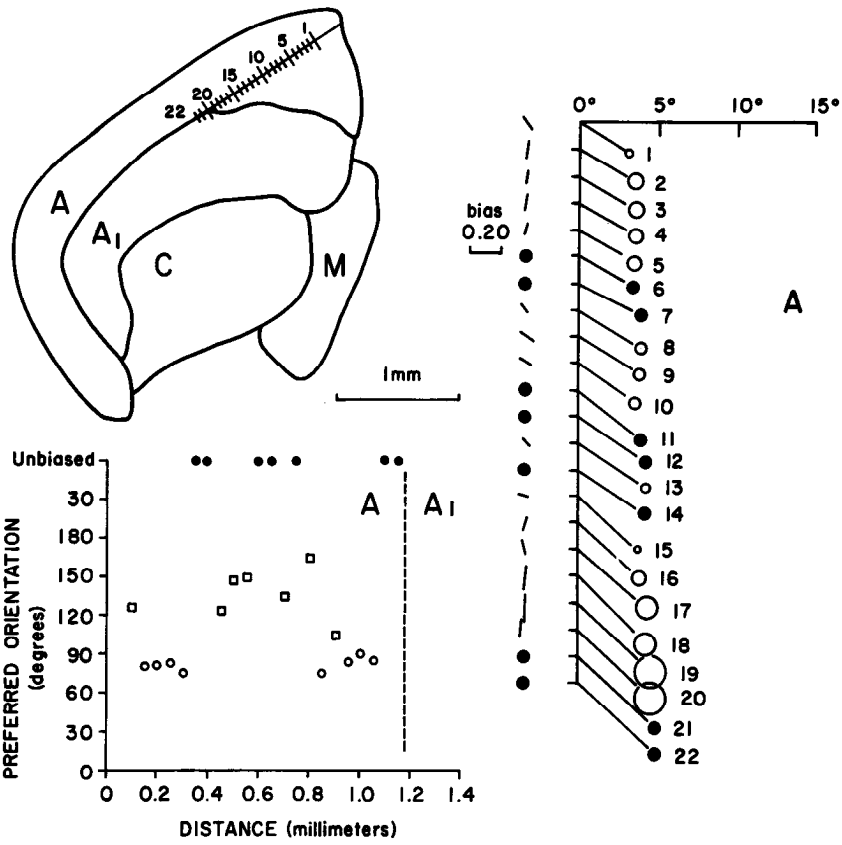

Figure 13. Reconstruction of another penetration through lamina A of the LGNd. This penetration was oriented obliquely relative to the border between laminae A and A1. A significant number of unoriented cells were encountered along this penetration. Nevertheless, neighboring cells tended to prefer similar orientations, and the change in preferred orientation with distance appeared systematic. Again note that clusters of cells preferring radial as well as tangential stimuli were evident.

with the idea that the orientation-sensitive response of most LGNd cells is a direct reflection of their retinal inputs (Soodak et al., 1987). Evidence for this stems from our finding that the overall distributions of the orientation biases of LGNd cells are similar to those reported previously for retinal ganglion cells (Levick and Thibos, 1982; Leventhal and Schall, 1983) and that the receptive fields of most of the cells we studied were consistent with the model proposed by Soodak et al. (1987). Our results do not support the idea (Vidyasagar and Urbas, 1982; Vidyasagar, 1984) that LGNd relay cells are much more orientation

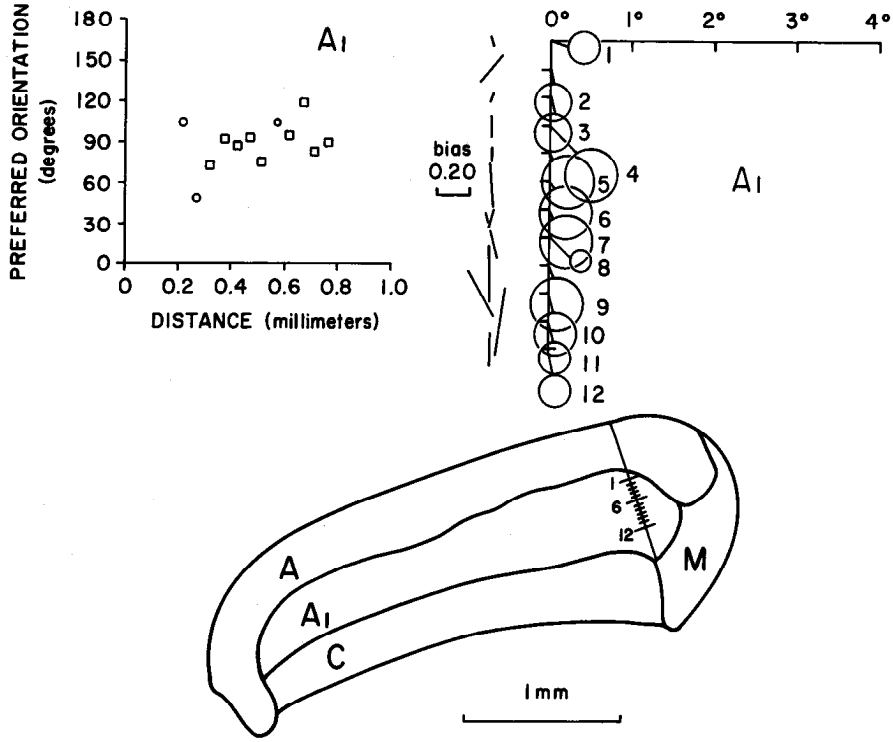

Figure 14. Reconstruction of an electrode penetration through lamina A1 of the cat's LGNd. The electrode was oriented roughly perpendicular to the border between laminae A and A1. Note that nearly all cells preferred radial (90°) orientations.

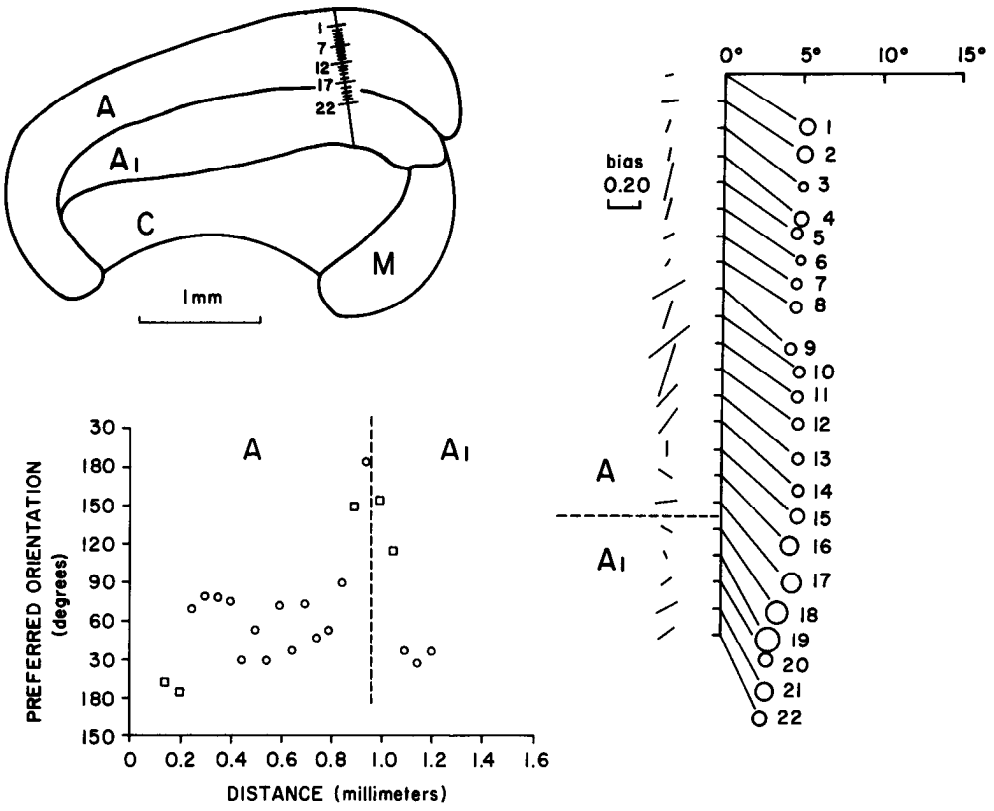

Figure 15. Reconstruction of an electrode penetration through laminae A and A1 of the cat's LGNd. The electrode was oriented roughly perpendicular to the border between laminae A and A1. Note that most cells recorded preferred tangential orientations (about 60°). There was, however, a systematic change in preferred orientation in the region of the border between laminae A and A1. Discontinuities in the border region were seen in some penetrations (see also Fig. 12) but not in others (Fig. 11).

sensitive than their retinal imputs. However, it should be noted that some of the most orientation-sensitive cells we studied exhibited "butterfly-shaped" orientation tuning curves even at relatively low spatial frequencies. A number of these cells actually exhibited multimodal tuning curves at very high spatial frequencies (see also Soodak et al., 1985b, 1987). The orientation sensitivity of these cells cannot be easily explained solely on the basis of direct retinal inputs and an elliptical center/surround receptive field arrangement (Soodak et al., 1987). However, the responses of these cells can be explained on the basis of their retinal inputs if their afferent ganglion cells exhibit orientation-dependent, multimodal spatial frequency tuning curves (see Thibos and Levick, 1983; Soodak, 1986, 1987; Soodak et al., 1987). The subunit structure of retinal ganglion cell receptive fields could result in such responses (Soodak, 1986; Soodak et al., 1987).

Finally, we found that cells preferring tangential orientations are overrepresented in the regions of the LGNd studied but not in the corresponding regions of retina. This suggests that some sort of cortical influence, intrageniculate inhibition, or convergence of retinal afferents may be involved in the generation of the orientation sensitivity of some LGNd cells.

In fact, it has been reported previously that some classes of cortical cells (especially C-cells in the infragranular layers) respond best to tangentially, not radially oriented stimuli (Leventhal, 1983; Leventhal et al., 1984; Schall et al., 1986b; Bauer and Dow, 1987). Cells in these layers are known to project to the LGNd (Gilbert and Kelly, 1975). It has been suggested that the preferred orientations of these cells are likely to be specified by intracortical mechanisms (Leventhal, 1983; Leventhal et al., 1984). The present findings raise the possibility that the preferred orientations of the cells comprising the cortico-geniculate projection are responsible for the tangential bias evident among cat LGNd cells as well as for the orientation sensitivity of color-opponent cells in the parvocellular laminae of the monkey's LGNd (see Results) which are unlikely to derive their orientation sensitivity from their retinal inputs (see Schall et al., 1986a, for discussion). Recordings from the LGNd in cats and monkeys in which visual cortex has been ablated or inactivated should determine whether this hypothesis is correct.

Do the orientation-sensitive responses of cortical and subcortical cells differ qualitatively?

The orientation biases of retinal ganglion cells and LGNd relay cells are weak compared with those of cortical cells. Virtually all retinal and LGNd cells respond to all orientations; most cortical cells do not. Thus, there is no question that cortical and subcortical orientation sensitivities differ quantitatively. Whether there are also qualitative differences is a much more difficult question to answer.

Some evidence for qualitative differences comes from the observation that the orientation biases of subcortical cells but not cortical cells virtually disappear at spatial frequencies close to the optimal (Levick and Thibos, 1982). Also, as already noted, the orientation-sensitive responses of most, but not all (see above), LGNd cells, but not cortical cells, can be modeled by an elliptical center/surround receptive field (Soodak et al., 1987).

On the other hand, there are also some qualitative similarities in the orientation-sensitive responses of cortical and subcortical cells. For example, it has been demonstrated that, like cortical cells, retinal ganglion cells and LGNd cells are sensitive to orientation when tested with moving bars (Daniels et al., 1977; Lee et al., 1979; Albus et al., 1983), as well as with moving gratings (Levick and Thibos, 1982; Shou et al., 1986; Soodak

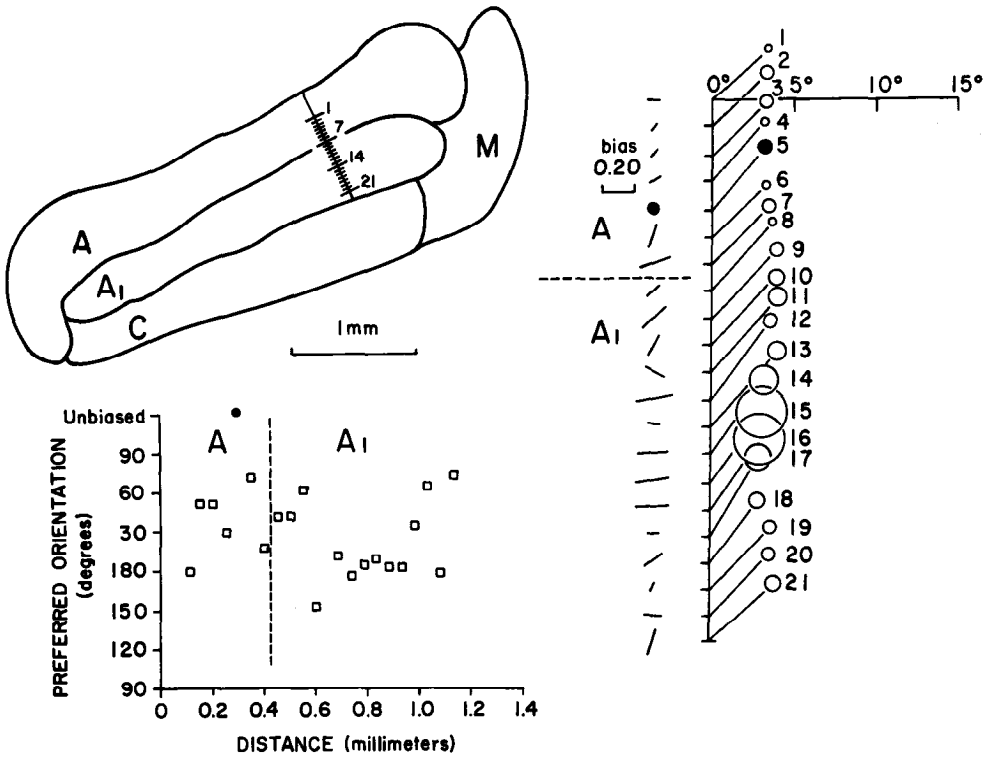

Figure 16. Reconstruction of another penetration through laminae A and A1 of the cat's LGNd. The penetration was oriented roughly perpendicular to the border between laminae A and A1. Most cells recorded along this penetration preferred similar orientations (about 30°). However, there was significant scatter in the preferred orientations of successively recorded units at a number of positions.

et al., 1987). A radial bias in the distribution of preferred orientations has been found in the visual cortex of cat and monkey (Leventhal, 1983; Schall et al., 1986b; Bauer and Dow, 1987), as well as in the retina and LGNd of these species. Also, in the retina, LGNd, and visual cortex the radial bias is strongest in regions subserving the horizontal meridian (Leventhal and Schall, 1983; Schall et al., 1986b). Finally, as already noted, a tangential bias has also been reported for some cell types in cat visual cortex. Thus, while there may be qualitative differences in the orientation sensitivity of cortical and LGNd cells, this is currently an open question.

Distribution of orientation-sensitive cells in the retina and LGNd

Our results indicate that there are differences in the distributions of orientation-sensitive cells in the retina and LGNd. In cat retina, different morphological cell types, as well as on- and off-center cells, are arranged into precise, independent mosaics (Wässle et al., 1981a–c; Schall and Leventhal, 1987). As a result, each spot of retina is "covered" by the entire complement of cell types. Also, it has been demonstrated that each region of retina contains a complete complement of cells preferring different orientations (Leventhal and Schall, 1983; Schall et al., 1986b); and in the retina there is no tendency for retinal ganglion cells to be clustered according to preferred orientation (Schall et al., 1986b).

It would thus seem that the LGNd is the first level in the visual pathways at which cells begin to sort according to preferred orientation. Since we have found that successively recorded cells tend to prefer similar orientations regardless of cell type (X or Y), center polarity (on or off), or preferred orientation (radial, intermediate, or tangential), it is likely that the clustering in the LGNd is not simply a result of the fact that retinal ganglion cells have large axonal arborizations and thus contact many adjacent relay cells. If this were the case, then adjacent on- and off-center relay cells, as well as adjacent X- and Y-type relay cells, would not necessarily tend to prefer similar orientations; the ganglion cells providing the afferents to these cells show no such organization according to preferred orientation (Schall et al., 1986b). In fact, since different cell types are distributed across the retina in independent mosaics (Wässle et al., 1981a–c) yet project to nearby relay cells preferring similar orientations, it may be that during development a process of sorting according to preferred orientation is occurring at the level of the LGNd.

It is important to note that in regions of retina outside of the central area the density of retinal ganglion cells is not high enough to permit all orientations to be represented by each ganglion cell type, separately. For example, the coverage factor for Y-cells is only 5–6 in most regions (Wässle et al., 1981c; Leventhal, 1982). Thus, it would seem that a complete range of orientations cannot be represented by each cell type in most parts of the LGNd; any sorting according to preferred orientation must be constrained by the topographic organization and magnification factors in the LGNd.

Is there a "columnar organization" of orientation-sensitive relay cells?

The segregation of LGNd relay cells according to ocular dominance, cell type (W, X, Y), and center type (on or off) has been well documented in both cat and monkey (see Rodieck, 1979; Stone et al., 1979; Lennie, 1981; Stone, 1983). This study provides the first evidence that relay cells having similar preferred orientations are also segregated (clustered) in the LGNd. This study has not, however, provided compelling evidence for a systematic organization of orientation-sensitive relay cells as precise as the one reported over the years for cells in visual cortex (Hubel and Wiesel, 1962, 1974).

There are, in fact, a number of reasons why intracortical

mechanisms must be contributing to the arrangement of orientation-sensitive cells in visual cortex. As already noted, there are not enough retinal ganglion cells of different types at most retinal locations to allow for a complete range of orientations to be represented independently by each cell type. Since "orientation scotomas" do not seem to exist in visual cortex, the preferred orientations of some cells are likely to be specified by intracortical mechanisms. Further evidence for this comes from the finding that the tendency to prefer radial stimuli is weaker in the visual cortex (Leventhal, 1983; Payne and Berman, 1983) than in the LGNd and retina. Finally, in some of our penetrations (see Figs. 11 and 12, for example), preferred orientation remained relatively constant over distances so large that the receptive field positions of the units encountered shifted dramatically. Since this is not the case in visual cortex (Hubel and Wiesel, 1962, 1974), it appears that significant transformations are occurring in the geniculocortical pathway. There are many more cells subserving different parts of the retina in visual cortex than in the LGNd. This magnification, combined with the intracortical generation of the preferred orientations of some cells (see also Vidyasagar and Urbas, 1982; Leventhal, 1983; Leventhal et al., 1984), may be required for all orientations to be repeatedly represented in regions of visual cortex subserving different retinal loci.

Conclusion

We have studied the orientation sensitivity of a large sample of relay cells distributed throughout the A laminae of the LGNd. The results indicate that orientation sensitivity is a common and probably functionally significant property of LGNd cells in the cat and monkey. Cells preferring radial and tangential orientations are overrepresented; relay cells preferring similar orientations are clustered. Numerous hypotheses and models have been put forth to explain how orientation sensitivity and the organized arrangement of orientation-sensitive cells develops in visual cortex. We will not complicate matters further by proposing another. It is sufficient to say that models put forth to explain how an organized system of orientation-sensitive cells develops in visual cortex should be simplified, not complicated, by the finding that most LGNd cells are orientation sensitive and that cells having similar preferred orientations are distributed nonrandomly in the LGNd.

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