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Quantitative Studies of Single-Cell Properties in Monkey Striate Cortex. II. Orientation Specificity and Ocular Dominance

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SUMMARY AND CONCLUSIONS

1. Quantitative analyses of orientation specificity and ocular dominance were carried out in striate cortex of the rhesus monkey.

2. Sharpness of orientation selectivity was greater for simple (S type) than for complex (CX type) cells. CX-type cells became more broadly tuned in the deeper cortical layers: S-type cells were equally well tuned throughout the cortex.

3. Sharpness of orientation selectivity for S-type cells was similar at all retinal eccentricities studied ($0^\circ - 20^\circ$ from the fovea): in CX-type cells orientation selectivity decreased slightly with increasing eccentricity.

4. The orientation tuning of binocular cells was similar when mapped separately through each eye.

5. Orientation selectivity and direction selectivity are independent of each other, suggesting that separate neural mechanisms give rise to them.

6. More CX-type cells can be binocularly activated than S-type cells (88% versus 49%). The ocular dominance of S-type cells is similar in all cortical layers: for CX-type cells there is an increase in the number of cells in ocular-dominance category 4 in layers 5 and 6.

INTRODUCTION

One of the most distinctive features of striate cortex neurons is their selectivity for stimulus orientation (2, 3, 9, 10). The extent of this specificity has been studied in some detail in the cat by generating tuning curves with moving bars and gratings (4, 7, 8, 14). The results of these investigations suggest that the degree of orientation specificity varies over a relatively broad range among cortical cells and that in the cat simple cells are more sharply tuned than com-

plex ones (14). Quantitative work on the rhesus monkey has not been previously reported, although qualitative observations from several laboratories suggest that orientation specificity of cells in the striate cortex of the monkey is a less persuasive characteristic than it is in the cat (1, 13). Since in the previous paper several kinds of S-type (simple) cells were identified, not only is it of interest to determine the extent to which S-type and CX-type (complex) cells differ in orientation selectivity in the monkey, but also to find out to what degree this selectivity varies among the various subclasses of S-type cells.

Orientation specificity is most commonly determined with moving stimuli. Since direction specificity is also assessed in this manner, the difference between these two attributes is sometimes unclear. In this paper we will attempt to determine whether the same or different mechanisms are responsible for orientation and direction specificities in the monkey.

The second concern of this paper is the transformation which combines the inputs from the two eyes. The clear segregation of the LGN input from each of the eyes in layer 4 of monkey striate cortex, as demonstrated anatomically by the ocular-dominance columns (11), suggests that convergence of the inputs from the two eyes is delayed to a somewhat later stage than in the cat, where binocular cells are common already in layer 4. The lower percentage of binocular cells reported in the monkey cortex (10, 13) compared to that in the cat (3, 9) appears to be in consonance with this view. If S-type cells represent the first stage in information processing in the cortex, a greater proportion of these cells should be monocular than the CX-type cell population. Due to the small sample of such cells in previous work, this has not yet been established. Hubel and Wiesel (10) found all their simple cells in layer 4; these cells were, as one might expect,

mostly monocular. Since the studies of Poggio (13), Dow (5), and Schiller et al. (15) found simple cells in other layers as well, one might ask whether these cells outside layer 4 are also apt to be monocularly driven.

METHODS

The general methods and procedures were described in the previous paper. Data from two additional animals are included (total $N = 44$) in which cells representing the foveal area and regions representing 7° – 20° from the fovea were studied. Orientation and direction selectivities and ocular dominance were assessed as follows:

Orientation selectivity

Bars or edges moved under manual control served to approximate the optimal orientation for each cell. Then a bar, edge, or grating of appropriate length (0.25° – 10°) moving over a distance of 1° – 3° at the optimal velocity within the range of 0.5° – 5° /s were presented under computer control. Our convention was to call right to left movement on the screen, 0° ; up to down, 90° ; left to right, 180° ; and down to up, 270° . The use of gratings for those cells which responded to them afforded a more economical way of obtaining a reliable measure of orientation selectivity.

A randomized sequence of sweeps of the stimulus across the receptive field was initiated by typing the appropriate command on the computer Teletype. These commands specified 1) the range of orientations, 2) the number of different orientations, and 3) the number of repeated measures to be taken at each orientation. Most commonly a range of 120° was selected with 10° steps and 10 repeated measures at each step. For broadly tuned units the range was extended to 180° with 20° steps, and for sharply tuned units, the range was reduced with a corresponding reduction in the size of the steps. In some cells, sweeps were taken over the entire 360° range. An attempt was made on the basis of our manual plotting to place the optimal orientation in the center of the range chosen. After each stimulus sweep the shutter closed and a change in orientation occurred before a new sweep.

Once the sequence was initiated the program ran automatically: the sequence of orientations and repetitions was randomized by the computer.

On completion of the run, which generally would take a little less than 5 min, the data were graphically displayed on a Tektronix 611 storage oscilloscope, providing either total number of discharges, means, or means and standard deviations. An example of such a display is shown

in Fig. 1. On further command the means and standard deviations at each orientation could be typed out on the Teletype and could be stored on magnetic tape.

Direction selectivity

Selectivity for direction was assessed as already described in the previous paper of this series. A stimulus, such as a bar, spot, or edge, was moved back and forth across the receptive field, most commonly at the rate of 2° /s, for 30 repeated trials. An index of directionality was calculated by dividing the number of responses obtained to the optimal direction of stimulus motion into the number of responses obtained in the opposite direction.

Ocular dominance

The ocular dominance of each unit was determined qualitatively during the manual plotting of the fields. A number from 1 to 7 was assigned to the unit as described by Hubel and Wiesel (9), where 1 stands for a contralaterally driven monocular unit, 7 for a cell driven only by the ipsilateral eye, and 4 represents equal activation from the two eyes.

In addition, some cells were also studied quantitatively by sweeping a moving stimulus across the receptive fields in one or more orientations in both the left and the right eyes. The purpose of this procedure was to determine to what extent the basic receptive-field properties of cells described in the previous paper were similar in the two eyes.

RESULTS

The results are presented under three headings: orientation, ocular dominance, and histological analysis. The topic of orientation is further divided into three subsections dealing with 1) the sharpness of orientation selectivity of cortical neurons; 2) the relationship between orientation selectivity, receptive-field size, and retinal eccentricity; and 3) the relationship between orientation and direction selectivities. The topic of ocular dominance is also divided into three subdivisions dealing with: 1) the distribution of ocular dominance, 2) orientation selectivity in binocular cells, and 3) direction selectivity and receptive-field size in binocular cells. The histological analysis related to orientation and ocular dominance data appears under the third heading.

Orientation

ORIENTATION SELECTIVITY AS DETERMINED BY BARS OR EDGES. Orientation selectivity was tested for a total of 654 units using bars or single

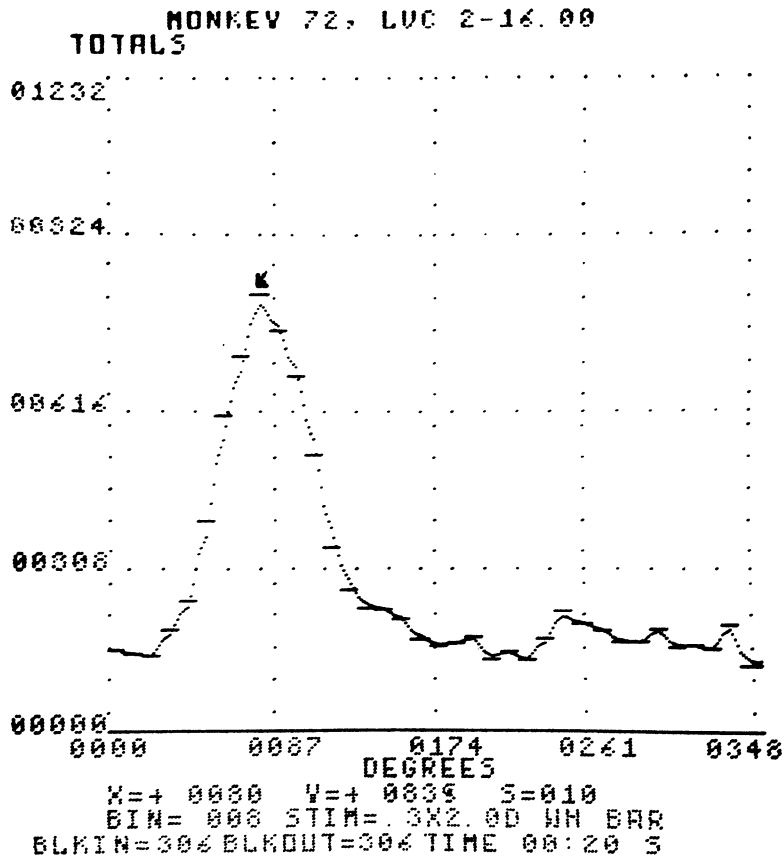


FIG. 1. Computer-generated display of data secured from one oriented, direction-selective cell in monkey striate cortex. Abscissa: total number of discharges. Ordinate: stimulus orientation. Data were gathered for 36 different orientations with 10 repeated measures at each using a randomized order of stimulus presentations. Short horizontal lines represent data points. Interconnecting dots show the moving boxcar-average function. Stimulus: $0.3^\circ \times 2.0^\circ$ white bar.

edges. An additional 95 cells were studied with gratings. An example of a computer display showing data obtained from a CX-type cell appears in Fig. 1. A $2^\circ \times 0.3^\circ$ bar was swept across the receptive field at a rate of $2^\circ/\text{s}$ in 36 different orientations, each orientation being presented 10 times. The 360 stimulus trials were randomized. The 36 short horizontal lines on the graph show the total number of responses elicited at each of the orientations. The data points are connected using a moving boxcar-average function. This CX-type cell is rather broadly tuned with its maximum response at 80° . The cell is unidirectional: movement of the stimulus upward at 260° did not produce a comparable peak. With bidirectional cells tested under analogous conditions, two peaks 180° apart are observed.

The orientation tuning selectivity of each cell was automatically computed by measuring the width of the smoothed response curve. This width was measured at a level equal to maximal

response/ $\sqrt{2}$. This region contains approximately 60% of the response area.

Figure 2 shows a sample of 20 representative orientation tuning curves. The first column (A–J) shows results obtained from S-type cells; the second (L–V) are from CX-type cells. The number at the right end of each curve is the tuning width value of each cell. These data show a broad range of orientation specificities.

Figure 3 shows the distribution for orientation tuning specificity for the 654 cells studied with bars or edges. The 151 S-type and 201 CX-type cells in this sample are also shown separately. The remaining 302 cells include T-type cells ($N = 20$), unoriented cells ($N = 59$), and unclassified cells ($N = 223$). The relatively high percentage of unclassified cells in this sample is in part due to the loss of cells subsequent to assessment of orientation selectivity, thereby, not permitting us to secure the data required for cell classification. T-type cells are those poorly

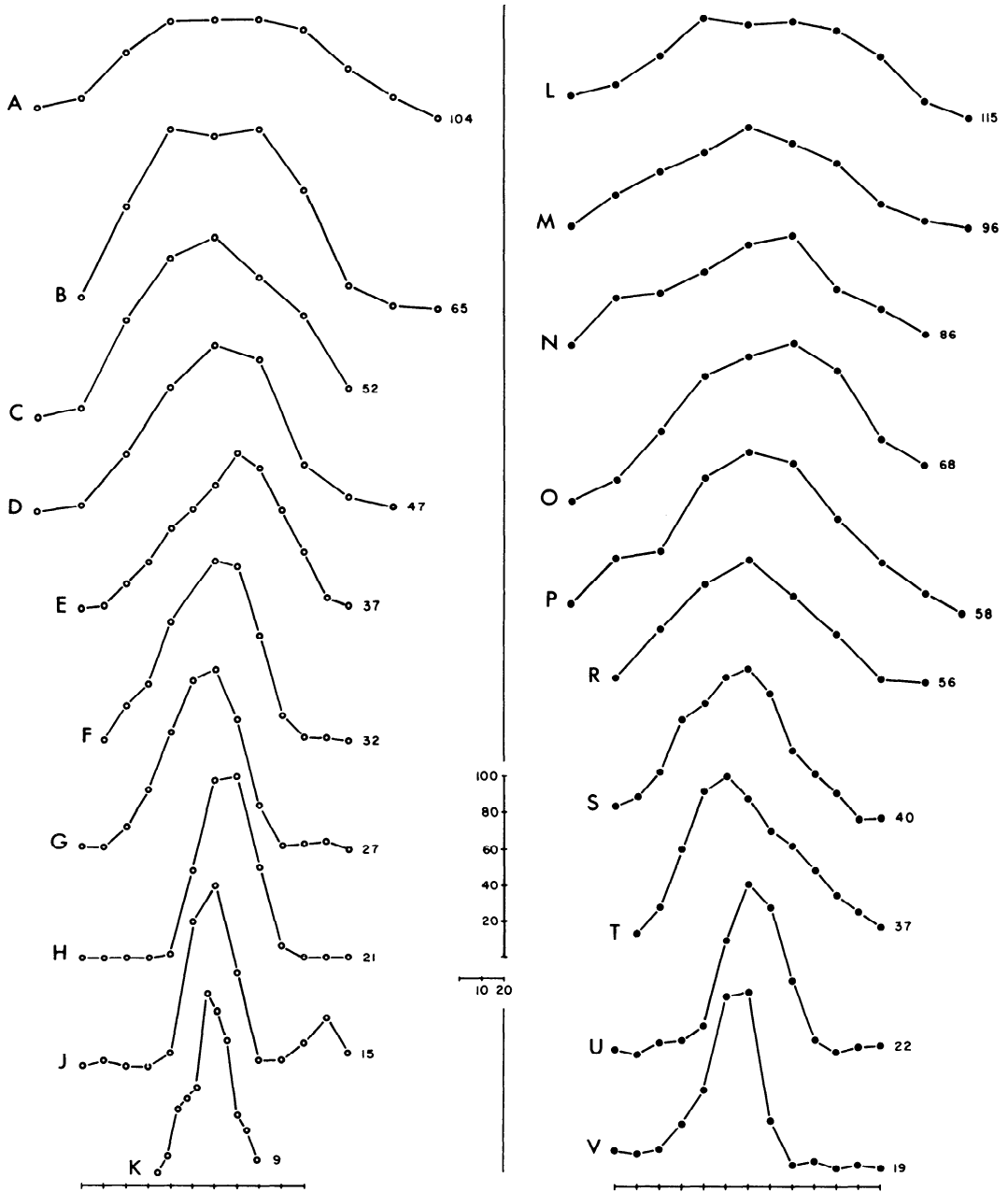


FIG. 2. Orientation tuning curves for 10 S-type (left-hand column, A–J) and 10 CX-type (right-hand column, L–V) cells. Responses have been normalized. Each point represents 10 repeated measures obtained in a randomized sequence. Ordinate: number of discharges. Abscissa: stimulus orientation in 10° steps. Number at right of each graph is the orientation tuning selectivity score, as described in the text.

oriented or unoriented cells which are excited by only one sign of contrast change and which respond in a relatively sustained fashion. These results are summarized as follows: *a)* The distributions are skewed. *b)* Approximately 13% (N = 82) of the cells were poorly or not at all

oriented (greater than 120°). Of these cells, 4 were classified as S-type cells, 7 as CX-type cells, and 12 as T-type cells: of the remaining 61 cells in this sample, 46 responded to both signs of contrast within the receptive field. It is our impression, therefore, that unoriented cells do

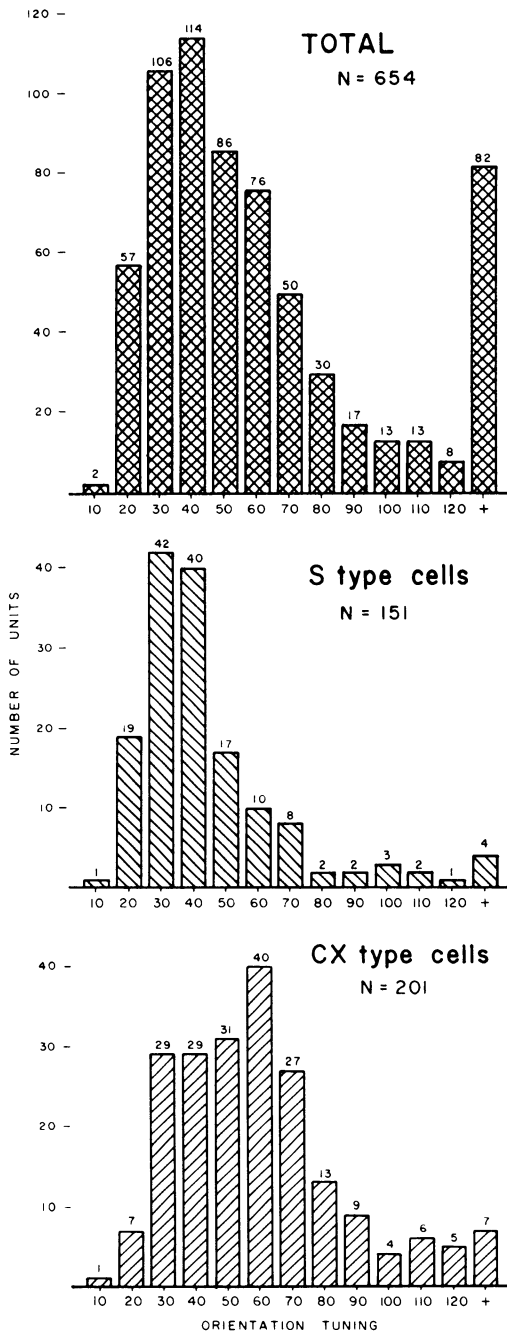


FIG. 3. Distribution of orientation tuning selectivity for all cells combined, for S-type cells, and for CX-type cells.

not comprise a single class of cells. In fact, there may be several different subclasses of un-oriented cells. The percentage of cell types in this sample should not be construed as an actual indication of the relative percentage of such cells

in striate cortex. Considerable variations in such percentages have been reported in the literature (10, 13) and they undoubtedly reflect on the recording methods rather than on the actual cell distributions in the brain. c) S-type cells are more sharply tuned than CX-type cells. This difference is statistically significant ($P < 0.001$). An orientation tuning score of 40 or better was obtained for 68% of the S-type cells, but only 33% of the CX-type cells were so well tuned.

According to the Hubel-Wiesel model, specificity for orientation in simple cells is produced as a result of two factors. The first is that the fields are elongated along the axis of orientation by virtue of the input from a line of LGN cells. The second factor is that the spatially adjacent subfields of simple cells are assumed to be mutually inhibitory. Thus, if both regions are stimulated at the same time, as is the case when a bar at 90° to the axis of orientation is presented, little or no response is obtained. This then limits the cell's response to bars and edges oriented in such a fashion that the two regions are not activated simultaneously by the same contrast change.

If such interaction between the adjacent regions of S-type cells and the length of the activating regions are crucial for the sharpness of orientation selectivity, the following considerations might apply: 1) Cells with weak flanks, such as the single-field S-type cells described in the previous paper, should be more broadly tuned than cells with strong flanks. 2) Orientation specificity of cells with bipartite fields should be dependent on *a*) the spatial separation between the subfields, and *b*) the length of the subfields along the axis of orientation. When the two regions are close to each other and are elongated their tuning should be sharp. When the subfields are separated by a greater distance and are short, tuning should be broad. 3) Cells with tripartite fields might be expected to be sharply tuned since they have two well-defined flanking zones.

Figure 4 shows the tuning specificity of the various subclasses of S-type cells. Figure 4A is a distribution of S-type cells with only single fields (S₁ as described in the first paper); cells with two spatially separate excitatory subfields appear in Fig. 4B; cells with interaction between direction and contrast are shown in Fig. 4C; cells with multiple subfields are shown in Fig. 4D. These data suggest that the tuning specificity of single-field cells is comparable to those in the other categories. The most poorly tuned cells appear to be those with multiple fields. It must be noted, however, that the number of cells in this group is small.

To assess the relationship among subfield sep-

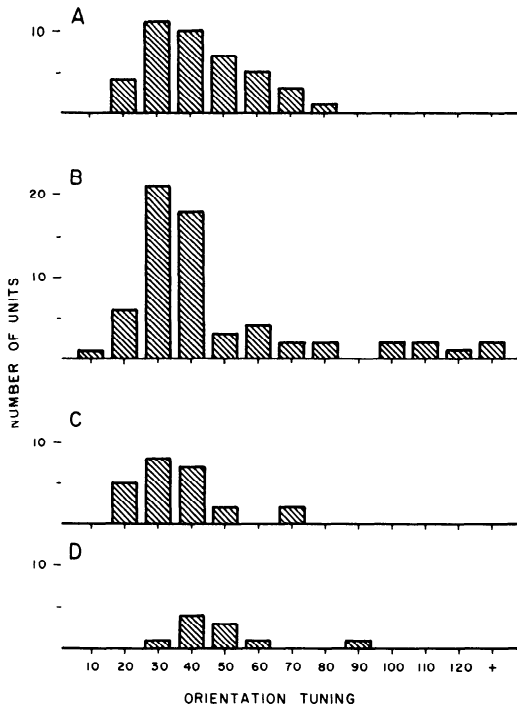


FIG. 4. Distribution of orientation tuning selectivity for different subclasses of S-type cells. *A*: S-type cells with only one field. *B*: S-type cells with two spatially separate fields. *C*: cells with interaction between contrast and direction. *D*: cells with multiple subfields.

eration, field length, and orientation selectivity, we correlated the tuning score of each cell with the separation between subfields and receptive-field length as described in the first paper of this series (Figs. 20 and 25 of ref 15). The measure for receptive-field length was obtained by plotting the number of discharges relative to stimulus length. The value on the curve for each unit

at which 80% of the maximal response was obtained was taken as the length of the receptive field. For each unit center-to-center separation was divided by receptive-field length. When this value was correlated with orientation tuning, the correlation coefficient was only 0.29. Correlation of orientation tuning with center-to-center subregion separation alone yielded a value of $r = 0.03$. Correlation of orientation tuning with length alone yielded a value of $r = -0.25$. These correlations are not statistically significant.

These observations suggest that orientation specificity depends only minimally on the spatial location of the light and dark excitatory regions of S-type cells and on the length of the receptive fields. It appears that the subfields mapped with stationary or moving stimuli are not analogous to the inhibition which gives rise to orientation specificity. Special techniques may be necessary to assess the inhibitory regions of receptive fields (2, 15).

RECEPTIVE-FIELD SIZE, RETINAL ECCENTRICITY, AND SELECTIVITY FOR ORIENTATION. The data in Fig. 3 suggest that the orientation-tuning selectivity of S-type cells is sharper than that of CX-type cells. Since CX-type cells tend to have larger receptive fields than S-type cells, the effect reported could in part be due to receptive-field size.

Figure 5A is a plot of the relationship between receptive-field size and orientation tuning for 62 cells. For these cells, gratings were used to assess orientation selectivity. These results show that among S-type cells there is no orderly relationship between overall receptive-field size and selectivity for orientation. On the other hand, among CX-type cells there appears to be a relationship, although not a very pronounced one ($r = 0.56$). CX-type cells with large receptive fields are more poorly tuned than those with small receptive fields.

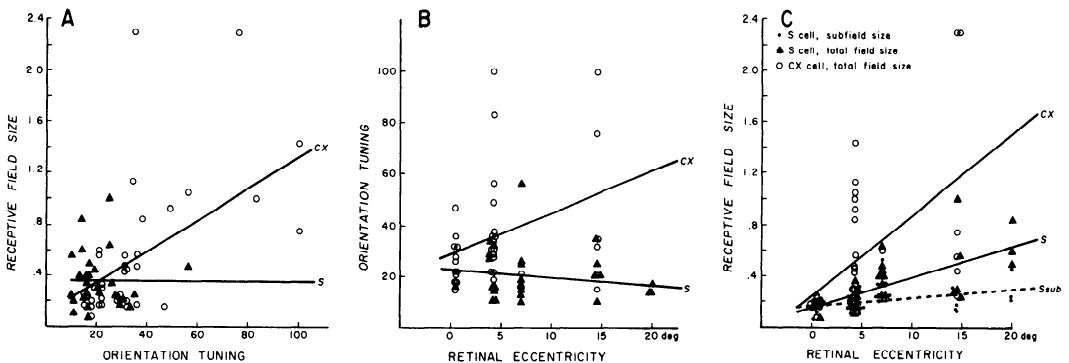


FIG. 5. Plots of *A*: orientation tuning and receptive-field size; *B*: orientation tuning and retinal eccentricity; and *C*: receptive-field size and retinal eccentricity. In *C* two plots appear for S-type cells, one is for total receptive-field size (triangles), and the other for the size of one subfield (small spots).

We also examined how orientation tuning varies as a function of retinal eccentricity. This relationship is shown in Fig. 5B. Figure 5C shows a plot of receptive-field size and retinal eccentricity. The following conclusions are drawn: *a*) There is an increase in overall receptive-field size with increasing retinal eccentricity. S-type cells yielded a correlation coefficient of 0.66 and CX-type cells an r of 0.57. The total field size of S-type cells increases at a slightly faster rate with retinal eccentricity than does S-type cell subfield size. *b*) For S-type cells sharpness of orientation tuning is not affected by retinal eccentricity ($r = -0.15$). For CX-type cells sharpness of orientation decreases somewhat with increasing retinal eccentricity ($r = 0.31$). *c*) Orientation selectivity decreases with increasing receptive-field size for CX-type cells ($r = 0.56$). This is not the case for S-type cells ($r = 0.003$).

These data suggest that the mechanism for orientation-tuning selectivity for S-type cells is the same in different regions of area 17 and that it is not linked to the overall size of the activating region(s) of these cells. The correlation in CX-type cells between receptive-field size and sharpness of orientation selectivity may be interpreted in agreement with the Hubel-Wiesel (9) hierarchic model. If CX-type cells have large receptive fields by virtue of a convergent input from S-type cells, their input is likely to come from several adjacent orientation columns. Such convergent input should reduce orientation tuning and increase receptive field size.

ORIENTATION TUNING AND DIRECTIONALITY. In the previous paper we reported that the direction selectivity of S-type cells cannot be derived on the basis of the receptive-field properties of these cells as determined by moving or flashing stimuli. It appears that orientation selectivity cannot be derived from such maps either. Our study further suggests that selectivity for orientation and direction are produced by separate neural mechanisms.

Four arguments will be advanced in support of this view:

Columnar organization and directionality. Hubel and Wiesel (11, 12) have shown recently that both ocular dominance and orientation specificity are arranged in an orderly, columnar fashion in cortex. When viewed on the cortical surface, regions representing the right and left eyes are laid out in adjacent strips in layer 4c; each is approximately 400–500 μm wide. Hubel and Wiesel have also demonstrated that when an electrode in cortex travels parallel with the surface of the brain and at right angles to the orientation columns, successive changes

in the orientation of cells occurs with 10° shifts approximately every 50 μm (12). A complete, 180° shift occurs over a distance of approximately 1 mm. Because of the columnar organization of orientation specificity, a penetration at right angles to the surface of the cortex, progressing down a column, produces little or no change in the orientation of successively recorded cells. Although the evidence is fragmentary on this point, Hubel and Wiesel (11) have suggested that orientation strips run at right angles to the ocular-dominance columns.

Given the orderly arrangement of orientation specificity and ocular dominance, the question may be raised whether directionality is organized in a similar fashion. Our results suggest that directionality is not arranged in a columnar fashion. Within a single penetration at right angles to the cortical surface in which the orientation specificity of successively isolated cells remains essentially unaltered, it is common to find cells adjacent to each other which are selective for opposite directions of movement. It is not uncommon to record from two cells simultaneously with such opposing selectivity. An example of this appears in Fig. 6 which shows that the direction selectivity of these simultaneously recorded S-type cells was opposite. The cells had the same orientation specificity.

Use of moving and stationary stimuli in assessing directionality and orientation. Because direction selectivity is defined using moving stimuli, this property has both spatial and temporal components. Thus, if the response is contingent on movement in a given direction, a cell is considered to have directional properties.

Orientation specificity is not defined in terms

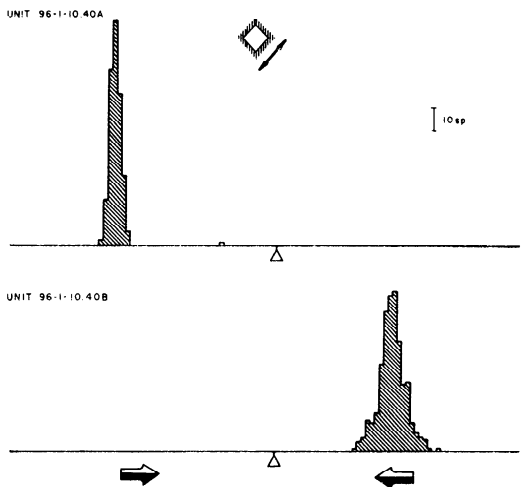


FIG. 6. Two S-type cells recorded from simultaneously, which were responsive to opposite directions of movement.

of movement, although typically, moving stimuli are used to assess it. This can be a source of confusion when a cell is direction selective since, under such conditions, it is difficult to know whether the results obtained with moving stimuli are due solely to direction of movement or to orientation as well. This is less of a problem when a cell is not directional; if under such conditions a cell is tuned for a certain stimulus axis irrespective of direction, this fact might suggest orientation selectivity.

Since direction selectivity is contingent on stimulus movement, the easiest way to circumvent the confusion is to flash stationary stimuli in different orientations. Generally cells which show orientation specificity as measured with moving stimuli also show this to stationary flashing stimuli. This fact suggests that directionality and orientation may be produced by two separate mechanisms, one which involves primarily a spatial code, and the other which involves a spatiotemporal code.

Orientation and direction specificity with short and long stimuli. Another way to assess possible differences in orientation and direction selectivity is to vary the length of the stimulus used. It has been observed by several investigators recording from the cat visual cortex that an extended stimulus, such as a bar or a long edge, provides the best orientation-tuning data for a cortical cell as well as eliciting the strongest response. When a short stimulus is used, many cells respond to it irrespective of its orientation. This observation suggested to Henry and Bishop (6) that it is the inhibitory surround and its particular spatial organization which is responsible for orientation specificity. The question may be raised then to what extent directionality is affected by such stimulus manipulation.

We investigated this question in 65 cells by obtaining both orientation tuning and direction selectivity with both extended and small moving stimuli. In the case of the small stimuli, the size was made equal to or less than the width of the activating region of the cell, typically 0.1° – 0.3° . The long stimulus always had the same width as the small stimulus.

An example of a cell studied with both short and long stimuli is shown in Fig. 7A. The orientation tuning of this cell was much broader for the short stimulus (labeled spot) than for the long one (labeled bar).

The overall difference in selectivity for 65 units with bars and short stimuli is shown in Fig. 7B. This demonstrates a sizable decrement in orientation specificity as one goes from bars to spots (mean decrease in tuning is 32°), although cells varied considerably in the extent to which they were affected.

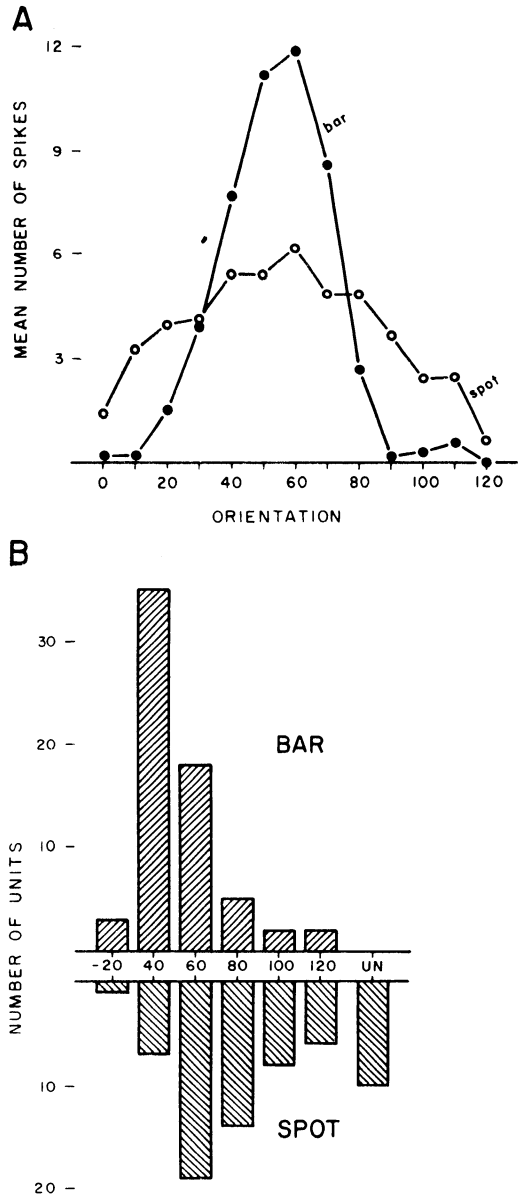


FIG. 7. A: comparison of selectivity for orientation with a moving bar and a moving spot. B: distribution of selectivity for orientation with bars and spots. The cell population for each distribution is the same.

Results for direction selectivity for long and short stimuli are shown in Fig. 8. Figure 8A shows the mean responses of two cells when short and long stimuli were swept across their receptive fields in both directions at the optimal orientation. The directionality of the response was similar with the small and long stimuli. The directionality ratio was calculated for the two stimuli as follows: (response in worse direction

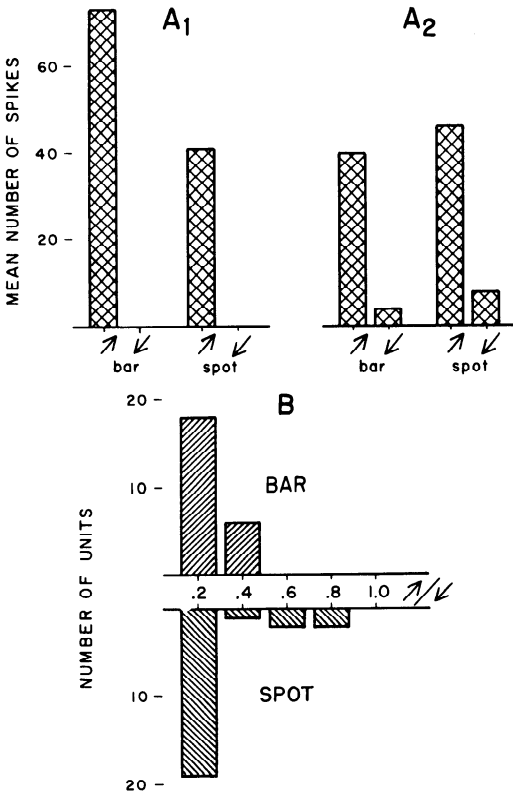


FIG. 8. *A*: total number of responses elicited in each of two cells for two directions of movement for a bar and for a spot. Data points are based on 30 repeated trials. *B*: directionality ratio obtained with bars and spots for 26 direction-selective cells.

– spontaneous activity)/(response in best direction – spontaneous activity). Figure 8*B* shows the distributions of these ratios for 24 directional units for long (bar) and short (spot) stimuli. This figure shows that changing stimulus length has little effect on the attribute of directionality.

In order to assess orientation and direction specificity further as a function of stimulus length we examined the correlation between the value for the orientation tuning given by long and short stimuli and a similar correlation for directionality. This comparison yielded a correlation coefficient of 0.34 for orientation and a coefficient of 0.79 for directionality. Thus the degree of direction selectivity is altered only to a small extent by varying the stimulus length. By contrast, orientation selectivity is altered significantly.

Sharpness of orientation selectivity and directionality. If there were a dependent relationship between direction selectivity and orientation tuning, one might expect that selectivity for orientation of directional cells would be different

from those of nondirectional ones. We examined this separately in 128 S-type and 226 CX-type cells. These data appear in Fig. 9. Cells were called directional if their ratio of directionality (see Fig. 21 of ref 15) was less than 0.50; non-directional cells were those with a ratio of more than 0.50. For S-type cells directionality was determined separately for light and dark edges.

These data show that directional and non-directional cells do not differ in terms of orientation tuning. Since S-type cells are predominantly unidirectional, only a small sample of bidirectional cells is available. CX-type cells, however, are equally represented in the two subgroups.

These four considerations suggest that orientation and direction selectivities are accomplished by two relatively independent mechanisms. They appear to be yoked, however, since directionality is typically at right angles to the axis of orientation.

Ocular dominance and receptive-field organization

DISTRIBUTION OF OCULAR DOMINANCE. The extent to which single cells in striate cortex get an input from both eyes varies considerably from species to species. In mammals with a large overlap in the visual fields of the two eyes, many cells in area 17 are binocular. For the cat the estimated proportion of binocular cells is between 80 and 85%. In the monkey, however,

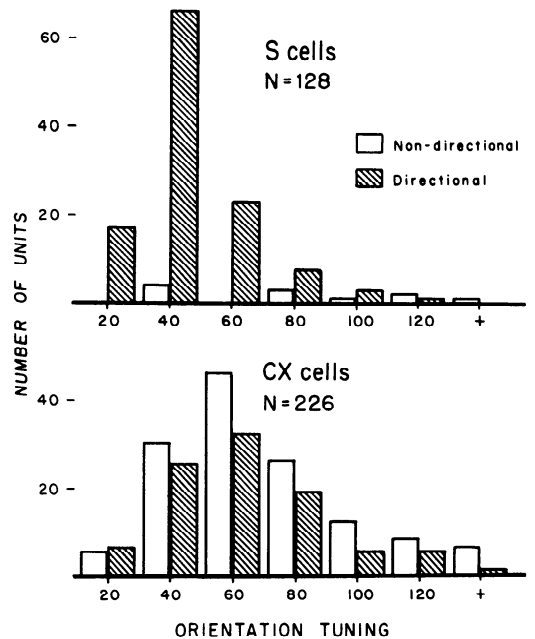


FIG. 9. Comparison of orientation tuning selectivity for directional and nondirectional cells.

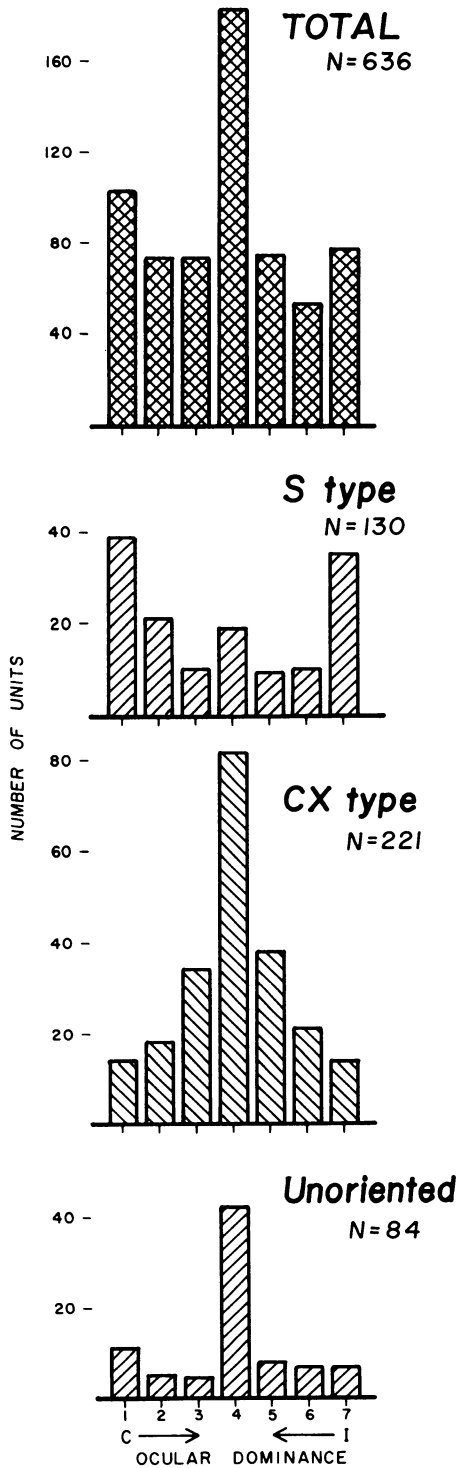


FIG. 10. Ocular-dominance distribution of total, S-type, CX-type, and unoriented cells.

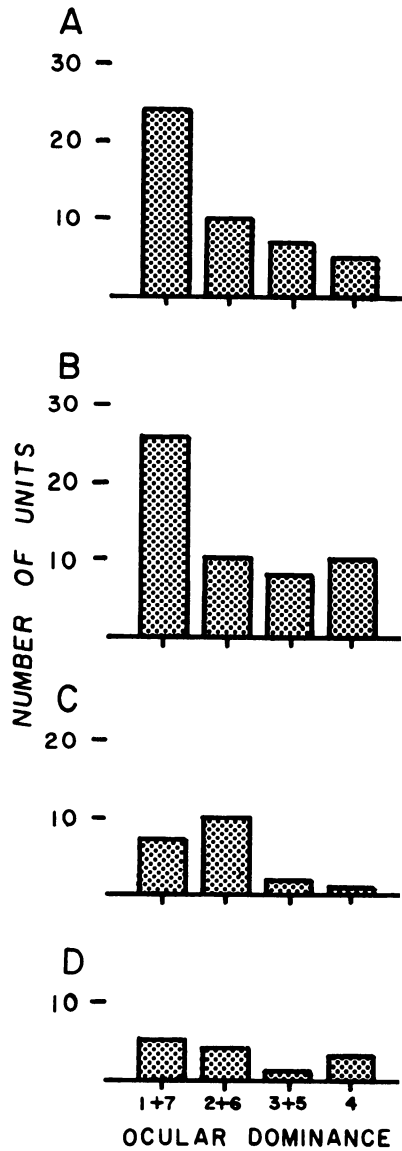


FIG. 11. Ocular-dominance distribution of the different subclasses of S-type cells. A: S-type cells with only one field. B: S-type cells with two spatially separate fields. C: cells which show strong interaction between contrast and direction. D: cells with three spatially separate subfields.

fewer cells appear to be binocular. Hubel and Wiesel (9) found that approximately 60% of the cells they studied received excitatory input from both eyes, while Poggio (13) found that only 43% of the cells he sampled had binocular responses. Hubel and Wiesel (9) also reported that of the 25 simple cells they studied, 22 were monocular (12% binocularity). By contrast, 65% of the complex cells were binocular.

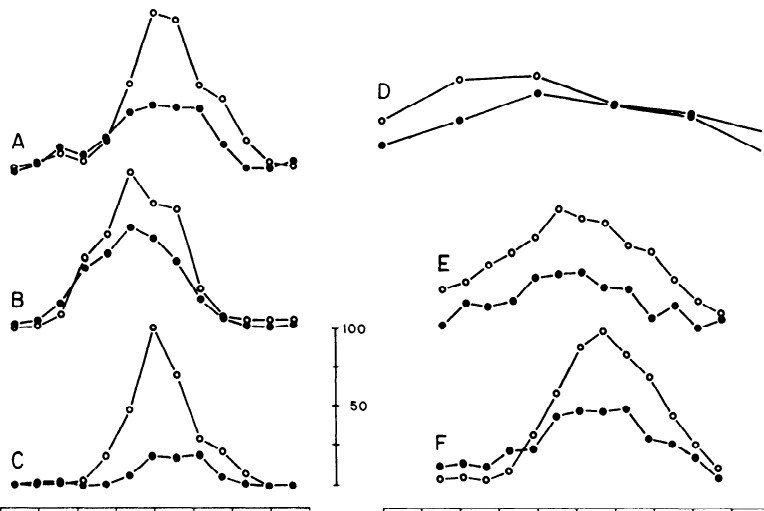


FIG. 12. Orientation tuning of three S-type (A–C) and three CX-type (D–F) cells as determined through each eye separately.

The ocular-dominance distribution of our sample is shown in Fig. 10. Of the 636 units, 72% were binocularly activated (groups 2–6). Fewer S-type cells were binocular than CX-type cells (49% versus 88%). This difference was most striking when one compared the percentage of cells in category 4. Only 14% of the S-type cells were equally sensitive to stimulation through both eyes, while 40% of the CX-type cells could be so activated.

We also examined the ocular dominance distribution of the various subclasses of S-type cells. The results of this analysis appear in Fig. 11. In this figure categories 1 and 7, 2 and 6, and 3 and 5 were combined. There is no marked difference among the various S-type cells. It is noteworthy that almost half of the single-field S-type cells (Fig. 11A) can be binocularly activated. These cells, therefore, must receive similar excitatory input from both eyes, with light-field cells presumably being driven only by on-center LGN cells and dark-field cells only by off-center ones.

ORIENTATION SELECTIVITY IN BINOCULAR CELLS. If sharpness of orientation selectivity were a direct function of the LGN input, one might expect to get different orientation tuning from the two eyes for those cortical cells, particularly S-type cells, which can be activated significantly better through one of the eyes. This might be expected since the hypothesized row of spatially aligned fields necessary for orientation tuning would more likely be provided by an extensive LGN input.

We examined this question in a few units quantitatively ($N = 18$) by obtaining orientation

tuning curves via each eye separately. A representative sample is shown in Fig. 12.

Orientation tuning appears to be similar for a given cell irrespective of the eye used to obtain its response. This is true even when the two eyes differ significantly in the extent to which they drive the cell.

These findings could be interpreted as an indication that orientation tuning is produced by an intracortical mechanism already present at the level of the S-type cells. This mechanism does not seem to depend directly on the extent of the excitatory input to the cell.

DIRECTION SELECTIVITY AND RECEPTIVE-FIELD SIZE IN BINOCULAR CELLS. Almost all cells which can be binocularly driven show similar receptive-field properties for the two eyes. This is true for cell type, inhibition along the axis of orientation, and directionality. The major difference between responses in the two eyes is in the sensitivity of the neurons, as reflected in the ocular-dominance measures. Figure 13 shows the response of three cells when stimulated via the left and right eyes, respectively. The first two cells are typical examples. The third cell responded to opposite directions of movement in the two eyes. This is one of two cells in our entire sample which showed this property. Except for the number of responses elicited, the responses of all other cells were strikingly similar when mapped through either eye.

Histological analysis

Combining histological data and estimation of depth as described in the preceding paper (15), we compared layers 1–3, 4, and 5–6 for orienta-

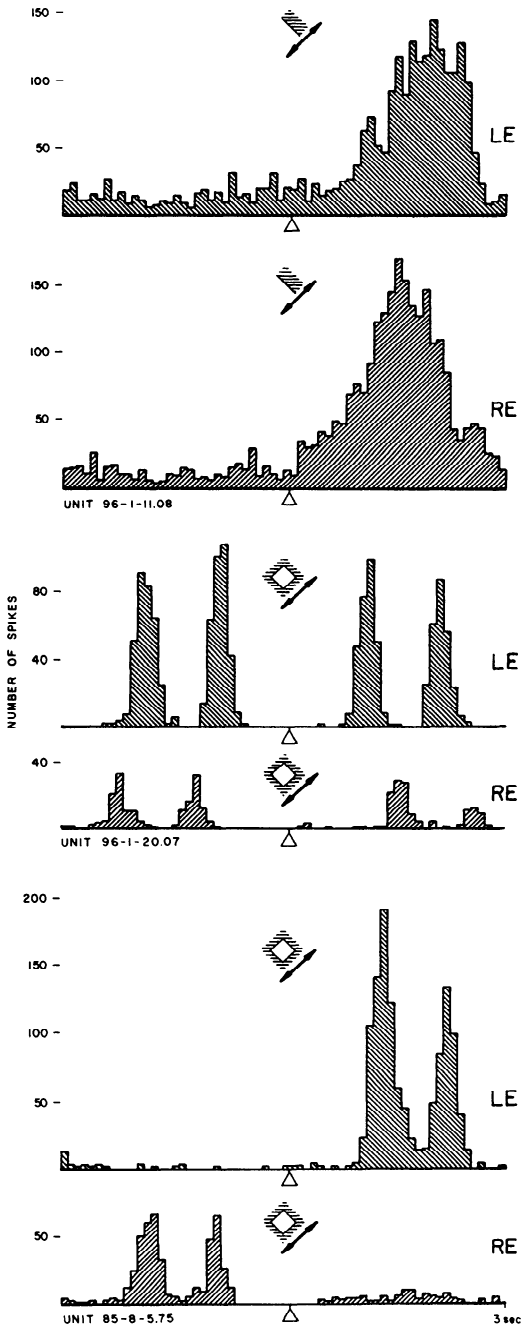


FIG. 13. Response of three cells to moving stimuli as determined through each eye separately.

tion selectivity and ocular dominance. These data are shown in Fig. 14. The orientation tuning of S-type cells does not change significantly as a function of depth although it appears that a broader distribution exists in layer 4. CX-type cells become progressively more broadly tuned as one advances through the cortical layers.

Our small sample of unoriented cells was not restricted to any one layer of cortex. To what extent the relatively even distribution of these cells in cortex and their percentage in our total sample are representative is unclear. The unresolved background activity in parts of layer 4, particularly layer 4c, is frequently unoriented, and could represent either small cells or geniculocortical afferents. Occasionally one can isolate units in this region which appear to be geniculate afferents based on such observations as *a*) LGN-type receptive fields, *b*) monocular activation, *c*) loss of unit with small electrode advance which is not accompanied by injury discharge (waveform is not a reliable index in area 17 in our experience). Most commonly, however, when we succeeded in isolating a unit in this region it was an oriented, S-type cell.

Finally, S-type cells do not seem to have different ocular-dominance characteristics in the various cortical layers. A higher proportion of CX-type cells is binocular in layers 5-6 than in the other layers, and this is especially true for cells of category 4.

DISCUSSION

The first conclusion we derive from our data is that orientation and direction specificities are produced by separate neural mechanisms. This inference is based on four observations: 1) Orientation is organized in a columnar fashion while directionality is not. Within one orientation column successive cells commonly show preferences for opposite directions of movement. 2) Orientation specificity is evident with stationary stimuli. 3) The degree of directionality is independent of stimulus length. By contrast, orientation specificity is markedly reduced when short stimuli are used. 4) Cells with and without direction selectivity do not differ in their selectivity for orientation.

The second conclusion we draw from this work is that orientation and direction selectivities are not produced exclusively by the geometry of the geniculate input but as a result of intracortical circuitry. The evidence for this is based on four observations: 1) The sharpness of orientation tuning of S-type cells cannot be derived from the spatial arrangement of the receptive field as mapped by either flashing or moving stimuli. The subfields of S-type cells as derived by our methods seem to represent excitatory inputs (see first and third papers in this series, (15, 16)) and are not analogous to the inhibitory regions producing orientation selectivity. 2) S-type cells representing progressively more eccentric regions of the visual field show an increase in overall receptive-field size and subfield separation without a concomitant change in

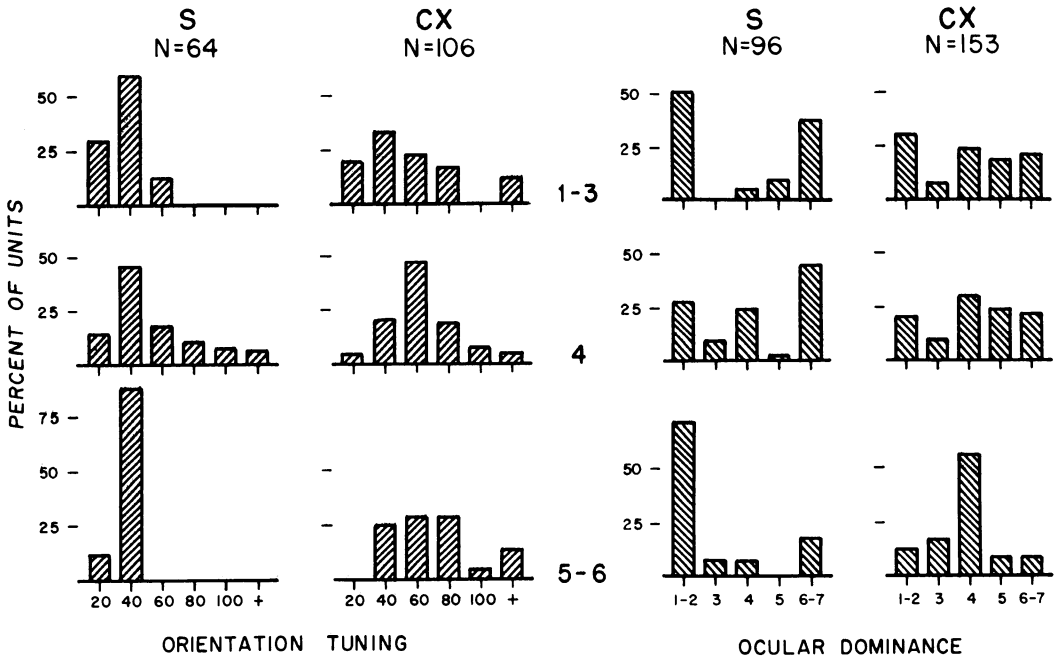


FIG. 14. Distribution of orientation tuning and ocular dominance in various cortical layers.

orientation tuning. 3) In binocular cells the degree of orientation tuning is similar when determined through either eye, even when the input from one of the eyes is strongly favored. 4) Recent reports indicate that the LGN input to cortex is excitatory (17), requiring cortical interneurons to produce inhibition.

The evidence for intracortical circuitry for directionality comes from similar observations; from the receptive-field map one can predict neither the presence nor absence of directionality in S-type cells nor the preferred direction. Selectivity for direction cannot be produced with only an excitatory LGN input.

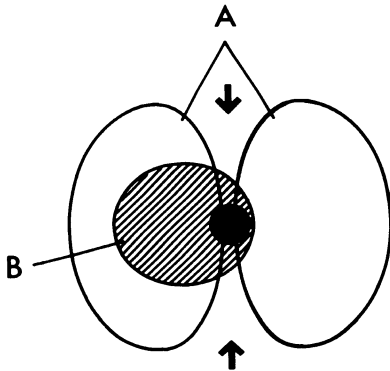


FIG. 15. Hypothesized dendritic fields of a directional and oriented cortical cell. A: apical dendritic field; B: basal dendritic field.

If directionality and orientation are achieved by separate, intracortical mechanisms, one might speculate how this is achieved. We propose that two separate layers of inhibitory interneurons in cortex give rise to directionality and to orientation selectivity. One of these layers connects with the basal dendritic field of S_1 -type pyramidal cells; the other connects with the apical dendritic field of these cells. The inhibitory connections to the dendritic fields are selective to provide the kind of spatial organization depicted in Fig. 15, which represents the effective dendritic fields of an S_1 -type cell in cortex viewed at right angles to the cortical surface. The black central disk represents the cell body and the site of the excitatory input to the cell. The cross-hatched oval (B) represents the effective basal dendritic field which is hypothesized to be involved in direction selectivity, while the bilobed ovals (A) represent the effective apical fields responsible for orientation selectivity. Stimuli moving from left to right fail to activate the cell due to inhibition from B. Edges or bars having orientations notably different from the projection line between the two arrows produce inhibition from A. Therefore, the cell responds best to a stimulus bar or edge which moves from right to left and is oriented parallel with the arrows.

The effective connections giving rise to the above configuration may actually be mirrored by the dendritic fields of the S_1 -type pyramidal

cells. If this were the case, Golgi-stained sections cut parallel to the surface of the cortex could reveal such organization. A second possibility is that the effective connections are produced not by the geometry of the dendrites themselves but by the relative distributions of inhibitory connections on them. This could be reflected in the relative number of dendritic spines in various regions of these fields in Golgi preparations. The third possibility, which is less amenable to histological analysis, is that the connections to these cells are determined by the geometry of the axons of the interneurons.

The ocular dominance distribution of cortical cells in our sample is somewhat different from those reported by Poggio (13) and Hubel and Wiesel (10). In our overall sample there were more binocular cells, and the S-type cells in particular showed a higher percentage of them sensitive to input from both eyes (49%) than did Hubel and Wiesel's (12%). The source of these differences is unclear. Part of the explanation

may be that we obtained a larger proportion of our cell sample in the deeper layers than did Hubel and Wiesel (10). Our data (see Fig. 14) suggest that this would increase the number of binocular CX-type cells. On the other hand, the ocular dominance of S-type cells should not be affected. It is also possible that our criteria of binocularity were more generous in categorizing cells into ocular dominance groups 2 and 6. Indeed, if one considers only groups 3, 4, and 5, S-type cells would show a 28% binocularity. This would also bring the overall assessment into closer agreement by yielding a 52% binocularity for the overall sample.

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