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Quantitative Studies of Single-Cell Properties in Monkey Striate Cortex. III. Spatial Frequency

PETER H. SCHILLER, BARBARA L. FINLAY, AND SUSAN F. VOLMAN

*Department of Psychology, Massachusetts Institute of Technology,
Cambridge, Massachusetts 02139*

SUMMARY AND CONCLUSIONS

1. The response properties of single cells in monkey striate cortex were examined using moving bars, square-wave gratings, and sine-wave gratings.

2. The majority of cells studied were not selective for bar width or for the spatial frequency of square-wave gratings.

3. Most cells responded selectively to the spatial frequency of sine-wave gratings.

4. The spatial frequency of the sine-wave grating eliciting the optimal response could not be predicted from the organization of the receptive field of each cell as determined by stationary or moving stimuli.

5. The sharpness of spatial-frequency selectivity is only slightly more pronounced in S-type cells than in CX-type cells.

6. S-type and CX-type cells differ significantly in the temporal modulation of their discharges to gratings. S-type cells discharge in sharp bursts to each cycle which traverses the receptive field. CX-type cells discharge in a rather continuous fashion. This measure can be used reliably to classify cells as S or CX type.

INTRODUCTION

In addition to the pronounced selectivity of neurons in striate cortex for stimulus orientation and directionality, they also show specificity for the spatial frequency of the stimulus. This attribute has been shown both with bars and gratings (1-7).

From the data presented in the literature it appears that cortical neurons show greater selectivity for the frequency of sine-wave gratings than for the width of single bars (1, 2, 6). The reasons for these apparent differences are difficult to identify because the responses of cells to bars and to gratings have not been directly compared. Furthermore, it is not known

how the spatial-frequency selectivity of the various classes of cortical cells, either to bars or to gratings, relates to their receptive-field properties as determined by standard mapping procedures.

How might the selectivity of cortical cells to the width of single bars be produced? The work of Bishop et al. (1) suggests that in simple cells this selectivity can be predicted from the spatial organization of the receptive field. Thus, if one encounters a double-field cell in which both subfields respond to the same direction of movement, with one region responsive to a dark edge and the other to a light edge (S_2 type), the optimal response of the cell should be obtained when a moving bar has a width which corresponds to the center-to-center separation of the two subfields. The two subregions would be excited simultaneously by the two bar edges of opposite contrasts and would, thus, produce discharges of a higher frequency than would a single edge. This kind of model predicts that selectivity for bar width depends on the spatial arrangement of subfields. The selectivity is produced by the spatiotemporal summation of excitatory responses.

Alternatively, or in addition, specificity for bar width might result from an inhibitory mechanism whereby the edges of nonoptimal stimuli which impinge on inhibitory regions prevent the cell from discharging.

These models make different quantitative predictions of cell response as the width of a stimulus is systematically varied. The first model predicts that the unit discharges obtained to single edges simply summate when the width of the bar corresponds to the separation of the subfields of simple (S type) cells. The model also predicts a relatively low degree of specificity since the response is unlikely to more than double (1). S-type cells with only a single subfield should show little or no specificity for bar width.

By contrast, the inhibitory model predicts that bars of certain widths exercise specific inhib-

itory effects. This kind of model can yield a far greater degree of specificity in that cells could be virtually unresponsive to stimuli significantly different from the optimal one. The best stimulus need not be derivable from the receptive-field map of the excitatory subregions as obtained by either flashing or moving stimuli.

Similar considerations might apply to specificity for spatial frequency when gratings are used. The question may be raised, however, whether selectivity for bar width is similar to selectivity for spatial frequency of square-wave and sine-wave gratings. Inhibitory mechanisms would seem to be necessary for generating the kind of sharp spatial-frequency selectivity with sine-wave gratings reported by Campbell et al. (2) and Maffei (6). Low-frequency gratings in these experiments may elicit no discernible discharge even though the rate of contrast change is kept constant for all frequencies.

The study of the spatial-frequency response of cortical neurons has also revealed that in the cat simple cells are more sharply tuned for spatial frequency than are complex cells (6). These observations, if confirmed, could have bearing on the hierarchic versus serial processing issue (8) in monkey striate cortex. If CX-type cells, which do not have demonstrable inhibitory sidebands (8), are as broadly tuned for spatial frequency as are lateral geniculate nucleus (LGN) cells, a direct input from the LGN would seem feasible. Sharp selectivity for spatial frequency in CX-type cells, on the other hand, would be difficult to reconcile with a direct input from the LGN and might, therefore, favor the hierarchic model.

Another notable difference between the two principal classes of cortical cells comes from the work to be reported here. We find that S-type and CX-type cells exhibit different temporal responses to moving gratings. S-type cells respond in clearly separated bursts as each cycle moves across the receptive field, while CX-type cells increase their firing in a relatively uniform manner. These differences, if sufficiently pronounced, could provide an additional criterion for classifying cells in visual cortex.

The aims of our study were, therefore, as follows: 1) To assess the spatial frequency selectivity of single cell responses in monkey striate cortex to single bars, square-wave gratings, and sinusoidal gratings. 2) To determine whether or not selectivity for spatial frequency can be related to the spatial organization of receptive fields. 3) To assess the extent of the differences between S-type and CX-type cells in response specificity to spatial frequency and in temporal modulation of responses.

METHODS

The methods used were similar to those described in the preceding papers. The data reported here are based on systematic variations of three kinds of stimuli: single bars, square-wave gratings, and sine-wave gratings.

Single bars

In order to assess the response specificity of cells to stimulus width, bars of different widths were moved across the receptive field. The bars were always in the optimal orientation and a sequence of single sweeps at the different widths was presented in random order. Most commonly, white bars on a dark background were presented. Stimulus width was varied by having a stepping motor operate one leaf or two leaves in the path of the light beam on the optic bench (8). Steps of 0.05° – 0.20° were used most frequently. Stimuli of six to eight different widths were presented in random order with 10 or 20 repeated measures for each width. The stimuli were moved at the rate of 1° – 4° /s over a range of 1.5° – 4.5° , and were presented 0.2–1.4 log units above threshold.

Square-wave gratings

Square-wave gratings were photographic negatives mounted on a disk driven by a stepping motor. For stimulus presentation this disk was mounted on the computer-driven optic bench. The rate of stimulus movement (about 2° /s) and the distance over which the stimulus pattern moved (1.5° – 4.5°) were kept constant for all frequencies. With this mode of presentation the number of cycles which traversed the center of the receptive field varied with the frequency of the stimulus, and the rate at which each edge moved across the field was constant. This mode of presentation was similar to that used with single bars.

The data collected were stored on magnetic computer tape for later analysis. The derived quantitative data were mostly of three sorts: *a*) total number of responses elicited by one full sweep; *b*) peak frequency response (spikes per second averaged over a time sample of 50–200 ms); *c*) extent to which cells modulated their responses in time to the moving gratings. This measure was obtained using a mean variation score ($(\sum(\chi - \bar{\chi})^2)/N\bar{\chi}^2$), where a value near 0 is equivalent to no modulation, meaning that the cell responded in a uniform, sustained manner to the stimulus, while a score of 1.0 or better represents a highly modulated response where a temporally distinct discharge was obtained to each cycle of the grating.

Sine-wave gratings

The sine-wave gratings were photographic negatives obtained from C. F. Stromeyer. They were mounted on the optic bench in the same manner as the square-wave gratings. The mode of presentation was different from that used with square-wave gratings in that the distance over which each stimulus moved varied in proportion to the spatial period of the stimulus while the time for the total stimulus sweep was held constant at 3 s. Therefore, the number of cycles moved across the center of the receptive field was held constant for all sine-wave gratings (at 3.33 cycles/s). This mode of presentation made the rate at which the contrast changed in the center of the field the same for all gratings. Prior to the experiment, the gratings were tested for uniformity and for similarity of temporal modulation by means of a photocell. All gratings produced similar spatiotemporal waveforms as measured by this photocell. Stimuli were presented 0.6–1.5 log units above response threshold. The peak-to-peak contrast ratios for bars, square-wave gratings, and sine-wave gratings were comparable.

RESULTS

The results will be presented in three parts: unit responses to bars, square-wave gratings, and sine-wave gratings.

Unit responses to bars of different widths

In Fig. 1 the responses of two photocells are shown when bars of different widths are moved across them. One photocell is set to respond to only the dark edge and the other to the light edge. In the third line of this figure, where the width of the bar is the same as that of the spatial separation between the two photocells, the two responses occur at the same time when the bar is moved from left to right. One might say that the response frequency is thereby doubled, although the total number of responses elicited remains the same.

When the stimulus moves from right to left the responses remain separate throughout. If, however, a black bar were moved over a light background the situation would also reverse: under such conditions the responses to one bar width would summate for right-to-left movement.

A further consideration is the directionality of the response. If in Fig. 1 the photocells were set to respond only to movement from left to right, the responses would be simultaneous for the appropriate stimulus width when a light bar is used. If, however, the photocells were set to respond only to right-toward-left movement, a dark bar would be needed to produce a simultaneous discharge from both edges.

If single cells in visual cortex were found to respond in this manner, one might suggest that

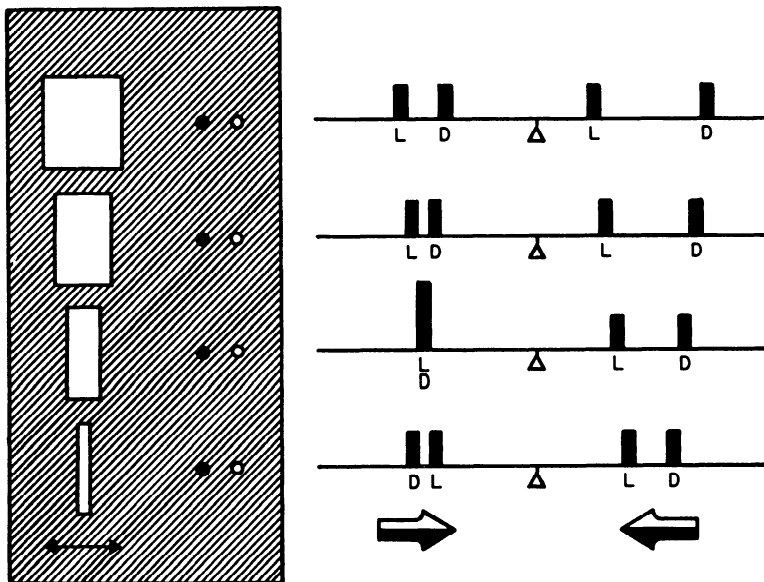


FIG. 1. Photocell responses to moving rectangles of different widths. Photocell depicted by filled circle is set to respond transiently to a dark edge; photocell depicted by circle responds to light edge. Arrows below histograms indicate direction of movement. L, light-edge response; D, dark-edge response.

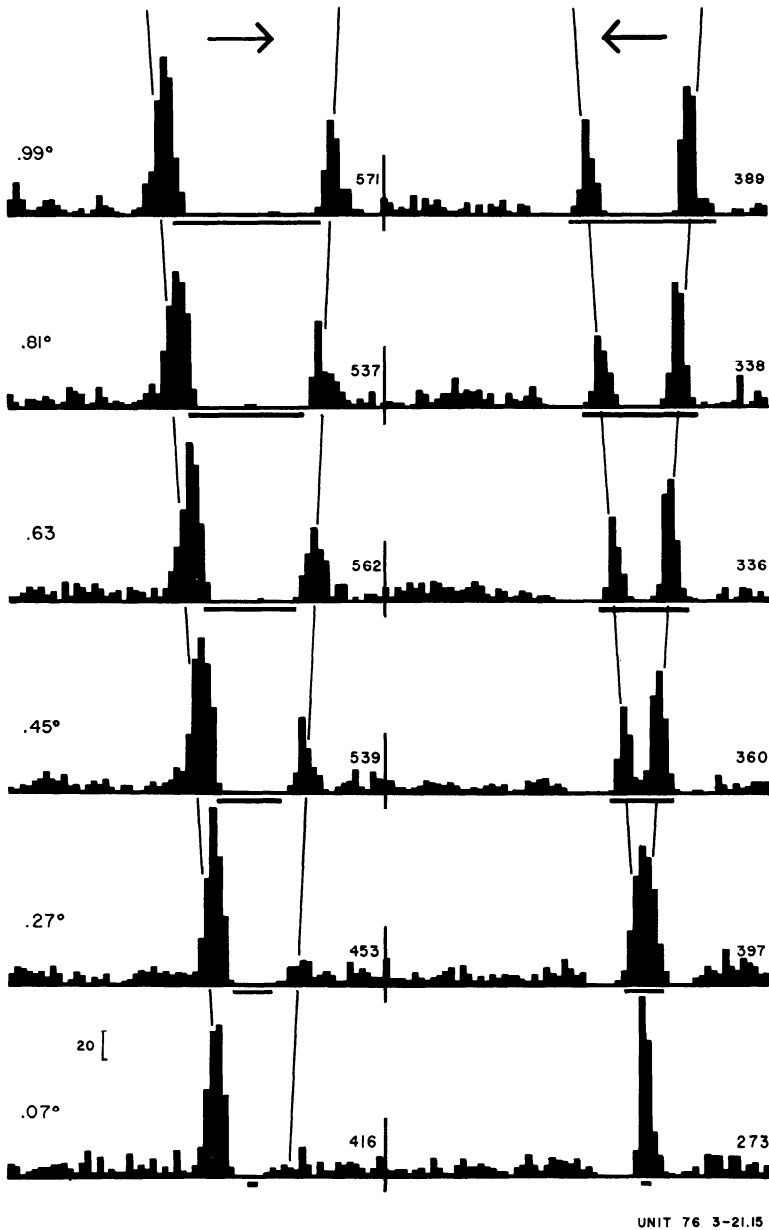


FIG. 2. Response of an S-type cell to bars of different widths. Numbers at left above each histogram indicate stimulus width in degrees. Horizontal bars below each set of responses also indicate stimulus width. Numbers to the right of each set of responses give the total number of spikes elicited in each direction. Arrows on top show direction of stimulus movement. Each histogram was compiled using 20 repeated trials, with the stimulus traversing 3° in each direction at the rate of $2^\circ/\text{s}$.

they act as a linear system working, in this case, by purely excitatory mechanisms.

Figure 2 shows the response properties of an S_5 -type cell to bars of different widths. The total number of responses elicited to each direction of movement appears to the right of each set of responses. These data also appear in Fig. 4B

where, in addition, the frequency responses are also plotted (spikes per second averaged over 94 ms). The following points are relevant: 1) For right-to-left movement the total number of responses for all widths, except for the 0.07° stimulus, is about the same. The maximum discharge frequency of the responses increases (Fig. 4B)

when the width of the stimulus is similar to the separation of the light and dark areas, thus activating both subregions at the same time. This suggests that in this cell the specificity of the response for stimulus width is brought about primarily by excitatory action by having the responses to the two excitatory subfields sum-

mate. However, this specificity is not very pronounced since the peak response frequency to the best width is only 41% greater than to a much wider bar. 2) Since this cell has relatively high spontaneous activity, one can see the inhibitory sidebands in the right-to-left direction. These bands appear on both sides of the light

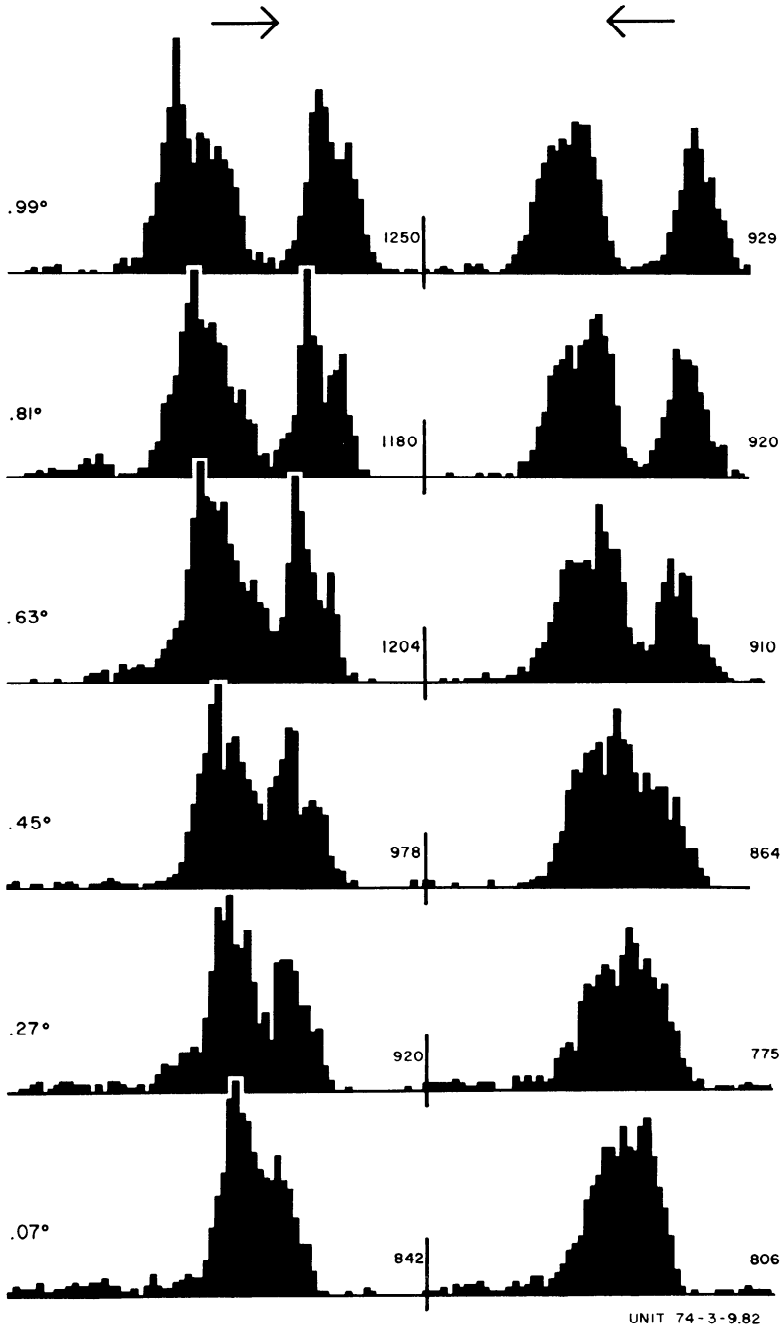


FIG. 3. Response of a CX-type cell to bars of different widths.

and dark response areas, but do not seem to play a significant role in specifying stimulus width.

Figure 3 shows the responses of a typical CX-type cell to stimuli of different widths. The cell responds well to all the stimuli, although with decreasing width the number of responses to the light and dark edges do not summate quite as well as those of the S-type cell. We conclude that this cell is not specific for stimulus width.

Figure 4 shows representative responses for six S-type cells and six CX-type cells. The

curves for the cell shown in Fig. 2 appear in Fig. 4B. The disks show the normalized data for the total number of spikes elicited by each width. The circles represent the response frequencies. These data were normalized for each cell relative to the widest stimulus. The total number of responses of these cells show little specificity for stimulus width, but the frequency of firing shows a somewhat greater effect for some cells. All S-type cells shown in this figure had bipartite light and dark fields. Of the CX-type cells pre-

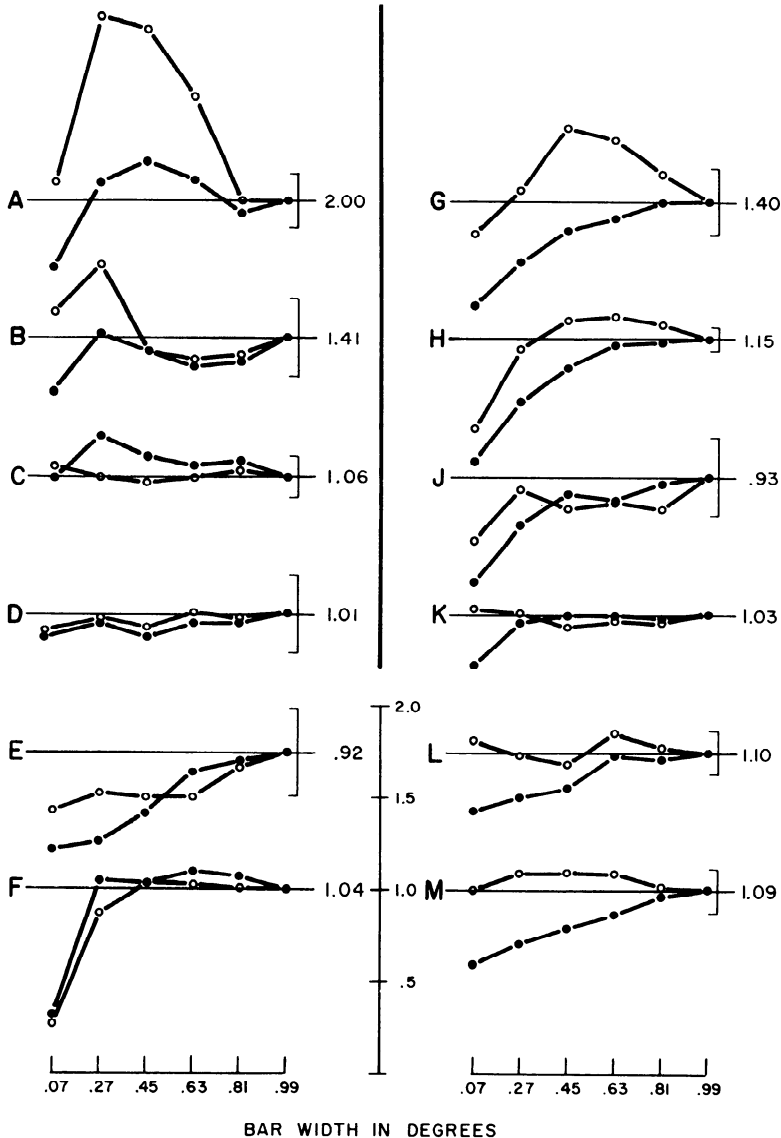


FIG. 4. Representative sample of unit responses to bars of different widths. A-F are S-type cells; G-M are CX-type cells. Filled circles: mean number of discharges; circles: frequency response. All data are normalized relative to the widest stimulus. Number to the right of each curve gives the ratio of frequency responses between the best bar and the widest bar. Brackets show ± 3 SE.

sented in this figure, only the first one (Fig. 4G) shows specificity for width; all the others appear to be unselective. The number to the right of each figure is the index of width specificity for frequency. This value was calculated by dividing the response elicited by the widest stimulus, which was wider than the size of the receptive field, into the response obtained by the optimal stimulus. The bracketed line to the right of the last data point for 10 of the 12 curves represents ± 3 standard errors.

A total of 144 cells were studied with bars of different widths in this manner, of which 47 were classified as S type and 97 as CX type. The index of width specificity for each cell was computed in two ways, by using the mean number of responses elicited by each stimulus and by using the frequency of the response. These data are presented in Fig. 5. The values for the entire sample of S-type and CX-type cells appear separately. Using either measure, one sees that most of the units studied were rather unselective for stimulus width. Using the number of responses, only 3 of 144 (2%) had more than twice as many responses to any specific width. Using response frequency, 10 of 144 cells (7%) showed this degree of specificity.

These results suggest that in monkey cortex, cells show little specificity for the width of a bar moved across the receptive field. Edges are extremely potent stimuli and can drive cells well regardless of the separation between light and dark edges. This lack of specificity for width is not merely a simple saturation effect caused by

using too intense stimuli, for when we reduced the response by decreasing stimulus contrast, cells tested did not show any greater specificity for width.

Square-wave gratings

Square-wave gratings of various frequencies were presented in a fashion similar to the presentation of bars; the rate of stimulus movement was constant for all frequencies. A total of 97 cells were studied, of which 47 were S and 50 CX in type.

Figure 6 shows representative responses of an S-type and a CX-type cell to gratings of different frequencies. The following points are noteworthy: *a*) Neither cell type shows a high degree of selectivity for any one frequency. A small degree of specificity is evident, however, in the S-type cell (Fig. 6A) in that higher frequency bursts were obtained to each cycle of the 2.4-Hz grating than to the 0.5- and 4.7-Hz gratings. The maximum frequency response to each grating was obtained using a time sample of 50 ms. From these data a peak frequency ratio (PFR) was calculated by dividing the peak frequency response obtained for the lowest frequency grating (0.5 Hz) into the peak frequency response of every other histogram in the set. The PFR score appears in the second right-hand column of numbers next to each histogram. For the S-type cell in Fig. 6A, this column shows that the 2.4-Hz grating elicited a peak frequency response 1.43 times greater than the 0.5-Hz grat-

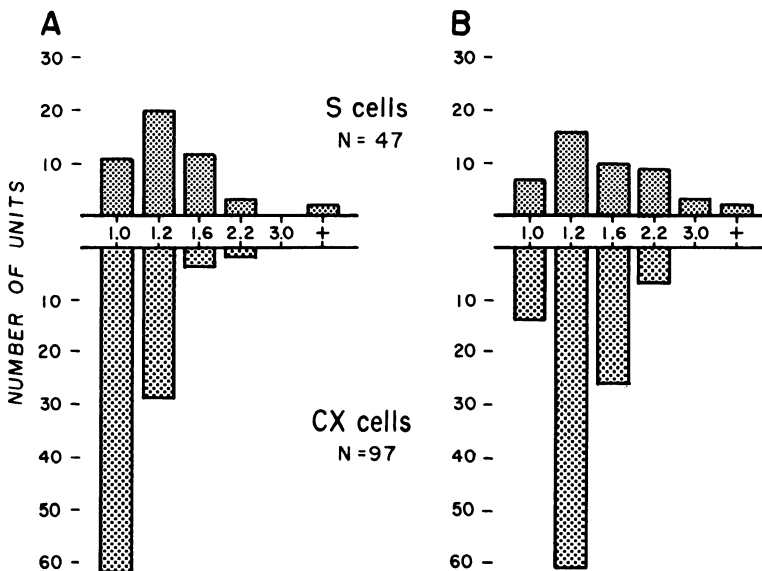


FIG. 5. Distribution of width specificity. A: number of discharges; B: response frequency. The ratio score represents the response to the best width divided by the response to the widest stimulus.

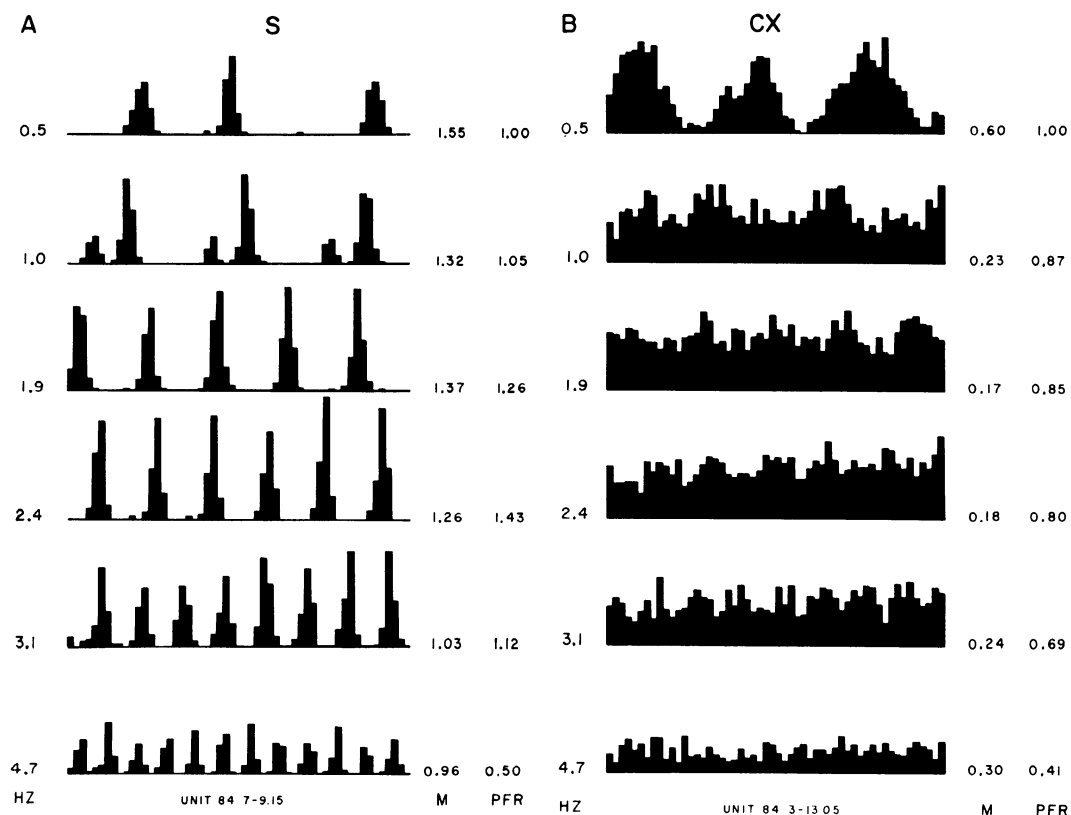


FIG. 6. Response histograms to square-wave gratings of different widths based on 20 repeated trials per histogram. *A*: S-type cell; *B*: CX-type cell. Hz, frequency of grating; M, temporal modulation score; PFR, peak frequency ratio. The spontaneous activity of the cell shown in *A* was 1.3 spikes/s, and for the cell in *B*, 3.9 spikes/s. The highest peak appearing in the 2.4-Hz histogram in *A* is equal to 76 discharges.

ing. *b*) The S-type cell responds distinctly to each edge at low frequencies and to pairs of edges at higher frequencies. The unequal spatial separation at low frequencies is a result of the spatial separation of the light and dark subfields. These responses summate with frequencies approximately the spatial separation between subfields and continue to do so with stimuli of higher frequency. *c*) The CX-type cell responds in a relatively uniform manner to the moving grating without modulating its response to each edge. In order to obtain a quantitative measure of the degree to which gratings elicited distinct bursts to each grating cycle, a mean variation score was calculated for each histogram. This value was termed the temporal modulation score, M, and appears in the first number column to the right of each histogram.

The cumulative data for all cells tested for spatial-frequency selectivity to square waves appear in Fig. 7. The data shown here were calculated in a manner similar to that used for the bars depicted in Fig. 5. Only measures of

response frequency are shown because with square waves the number of edges traversing the field and, therefore, the total number of responses, varied with frequency. These results indicate that for square waves, as for bars, there is little specificity for spatial frequency using these conditions of presentation.

In order to examine quantitatively the striking difference between the S-type and CX-type cells shown in Fig. 6 in the temporal modulation of their response, an index of modulation was determined for each cell. This was calculated for each histogram by obtaining the difference between the number of responses in each bin of the histogram and the mean overall response (index of modulation = $(\sum(\chi - \bar{\chi})^2)/N\bar{\chi}^2$). Large values indicate a high degree of modulation. For a comparison between S-type and CX-type cells we used the histogram for each cell which represented the response to the highest frequency grating at which the response exceeded 4 times the spontaneous activity. The distribution of grating frequencies used to obtain these data was

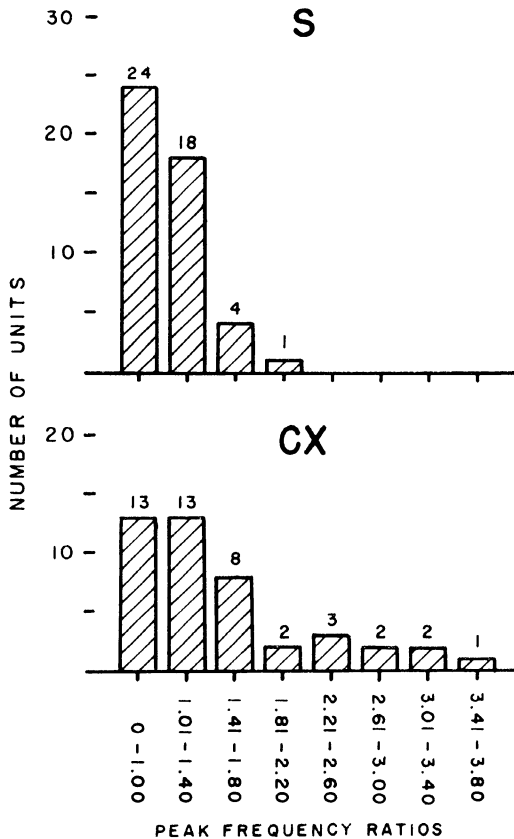


FIG. 7. Distribution of peak frequency ratios for square waves in S-type cells and CX-type cells.

the same for S-type and CX-type cells. All the data were obtained at between 2° and 5° from the fovea. Figure 8 depicts the results of this analysis. Also shown in this figure are the peak response frequencies to the square-wave gratings for S-type and CX-type cells.

The results indicate that S-type and CX-type cells differ significantly; the response of S-type cells is strongly modulated while that of CX-type cells is poorly modulated. Two factors appear to contribute to this difference. First, CX-type cells, on the average, have larger receptive fields than S-type cells, within which an edge of either contrast elicits a response as long as the stimulus is moving through the field (5). Second, at higher frequencies the number of bursts in the response of S-type cells is equal to half the number of edges crossing the field. For S-type cells with only one subfield this is always the case since only one change in sign of contrast produces a response. For S-type cells with bipartite fields the light and dark responses to high spatial frequency gratings summate.

These data suggest that the different re-

sponses of S-type and CX-type cells to grating stimuli can be used as a means of distinguishing these two populations.

Sine-wave gratings

SELECTIVITY FOR SPATIAL FREQUENCY. Sine-wave gratings were presented so that the number of cycles traversing a point on the tangent screen per unit time was constant for all frequencies. The advantage of sine-wave gratings is that this mode of presentation also keeps the rate of contrast change constant at any one point on the screen.

We studied a total of 142 cells with sine-wave gratings, of which 56 were S-type and 72 were CX-type cells.

In contrast to the results obtained with bars and square-wave gratings, the majority of cortical neurons in the monkey were highly selective for the spatial frequency of sine waves. This is shown for an S-type cell and a CX-type cell in Fig. 9. The S-type cell responds only to three of the frequencies tested and may be said to be sharply tuned. The CX-type cell is somewhat more broadly tuned, responding to four of the frequencies tested. As with the square-wave gratings, the S-type cell response is modulated sharply while the CX-type cell is poorly modulated.

Figure 10 gives a representative series of tuning curves (indicated by heavy lines) for spatial frequency. The cells in the first column are S type (A-E) while those in the second column are CX type (F-K). These cells were also studied with bars of different widths as described in the first section of the results. These data are also shown in this graph by the circles and thin-line curves. The peak-to-peak contrast ratios for the bars and gratings were comparable. The following points are worth noting: *a*) both the S-type and CX-type cells show selectivity for spatial frequency, with S-type cells somewhat more sharply tuned than CX-type cells; *b*) these cells are not selective for the width of bar stimuli; *c*) The optimal spatial frequency response is not always elicited with a grating whose half-period corresponds to the size of the receptive field of the cell. The receptive-field size of each cell, converted to spatial frequency, is shown by the open arrows.

Previous work on the cat has indicated that simple cells tend to be more sharply tuned for spatial frequency than are complex cells (6). We examined this in the monkey for those cells which were located 2° - 5° from the fovea. These data are shown in Fig. 11. Sharpness of tuning was determined for each cell by first normalizing the curve according to the best response, and

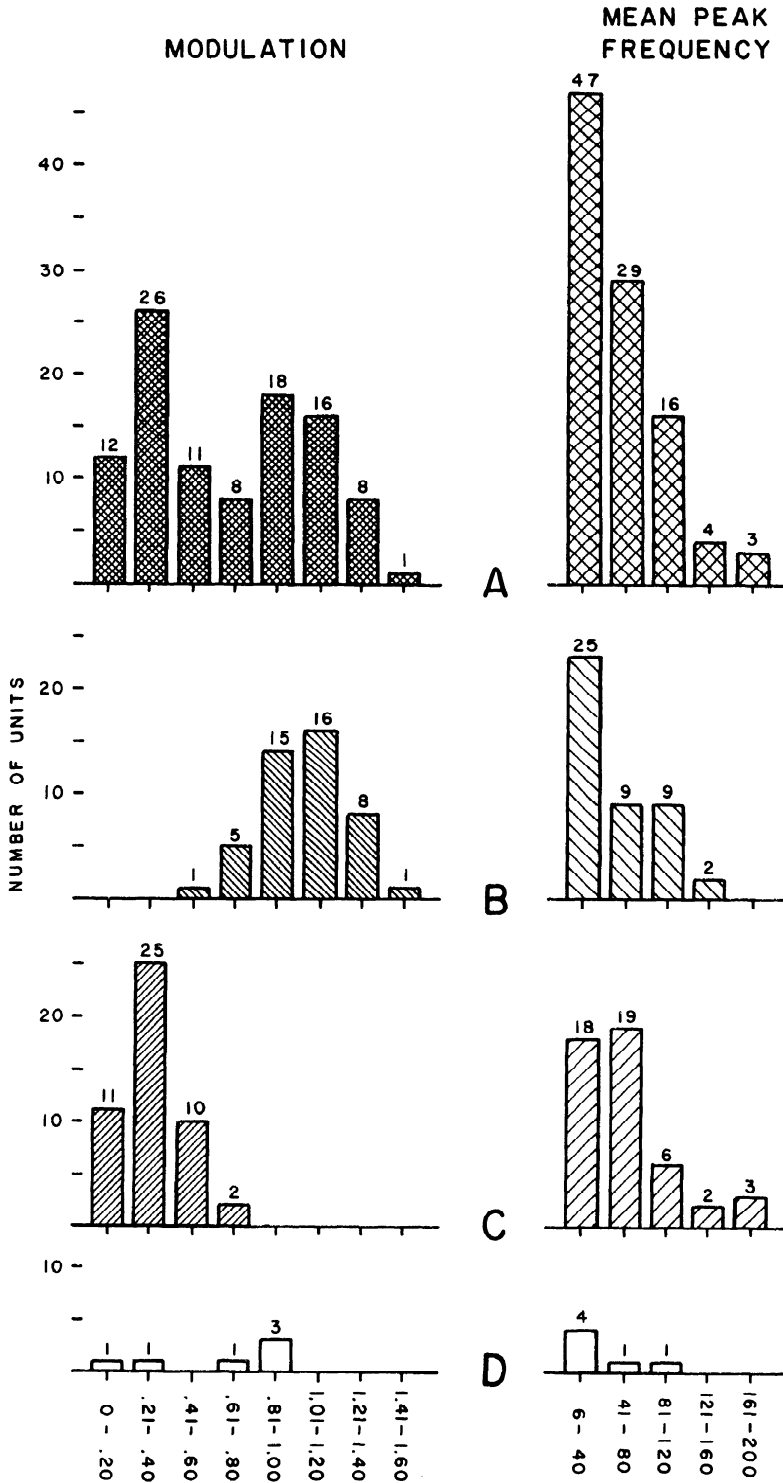


FIG. 8. Temporal modulation of response to square waves. *A*: total number of cells; *B*: S-type cells; *C*: CX-type cells; *D*: unclassified cells. First column shows distribution of response modulation score ($M = (\sum(\chi - \bar{\chi})^2) / N\bar{\chi}^2$), where χ represents the number of responses in each 23.5 ms duration bin. Second column shows distribution of the peak response frequency (spikes per second).

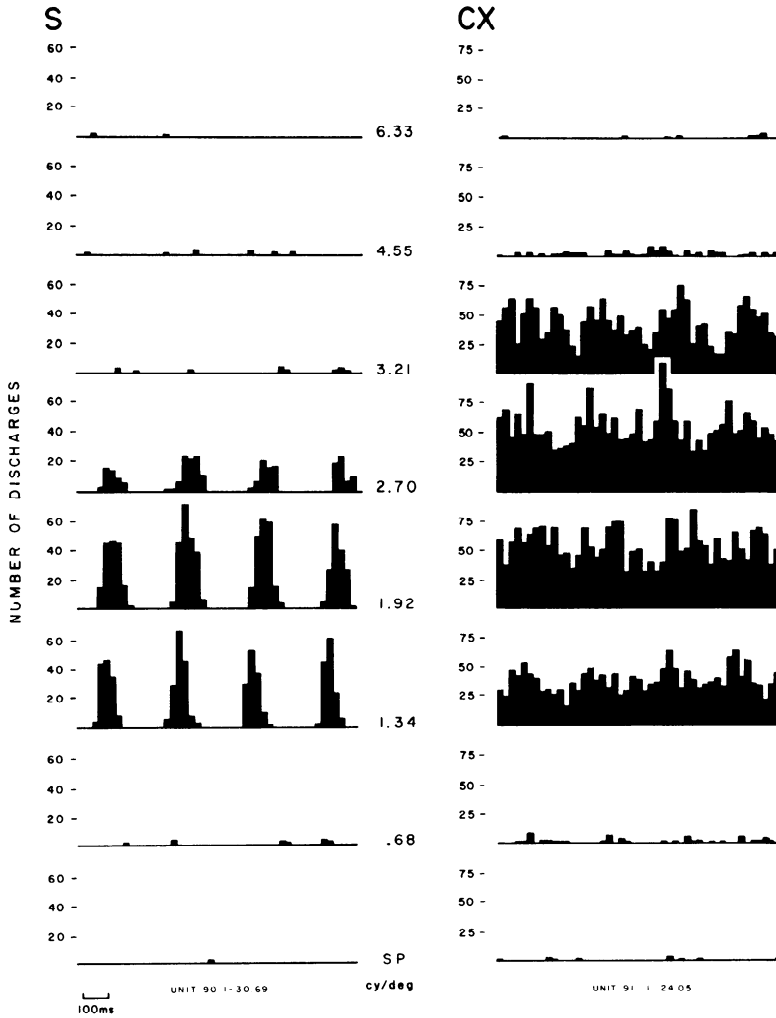


FIG. 9. Response of an S-type (S) and a CX-type (CX) cell to sine-wave gratings of different frequencies.

then measuring the points where the low- and high-frequency slopes crossed the 71% level (which is equivalent to maximum response/ $\sqrt{2}$). The tuning function of each cell is obtained by dividing the frequency at which the curve intersects the 71% level at the high-frequency end into the value where the intersection occurs at the low-frequency end. This score is multiplied by 100. Sharply tuned units have a high number and poorly tuned units, a low number. A score of 50 represents the 1-octave range of this measure. Cells whose responses to low-frequency gratings did not decline and were, therefore, considered unselective for spatial frequency appear offset at the right end of the histogram. These results show only a moderate difference between S-type and CX-type cells.

SPATIAL-FREQUENCY SELECTIVITY AND RECEPTIVE-FIELD ORGANIZATION. What is the attribute of receptive-field organization which is responsible for cortical cell selectivity for spatial frequency? Two ideas have been advanced to account for spatial-frequency selectivity in terms of other receptive-field characteristics. One idea is that a cell responds optimally to a grating whose period is twice the size of the excitatory region of the cell's receptive field (2, 6). This hypothesis assumes that the selectivity results from an interaction between the excitatory area and surrounding inhibitory flanks. The flanking inhibition would seem to be essential for producing this selectivity. This hypothesis makes no clear prediction about CX-type cells, for which inhibitory flanks cannot be found (8).

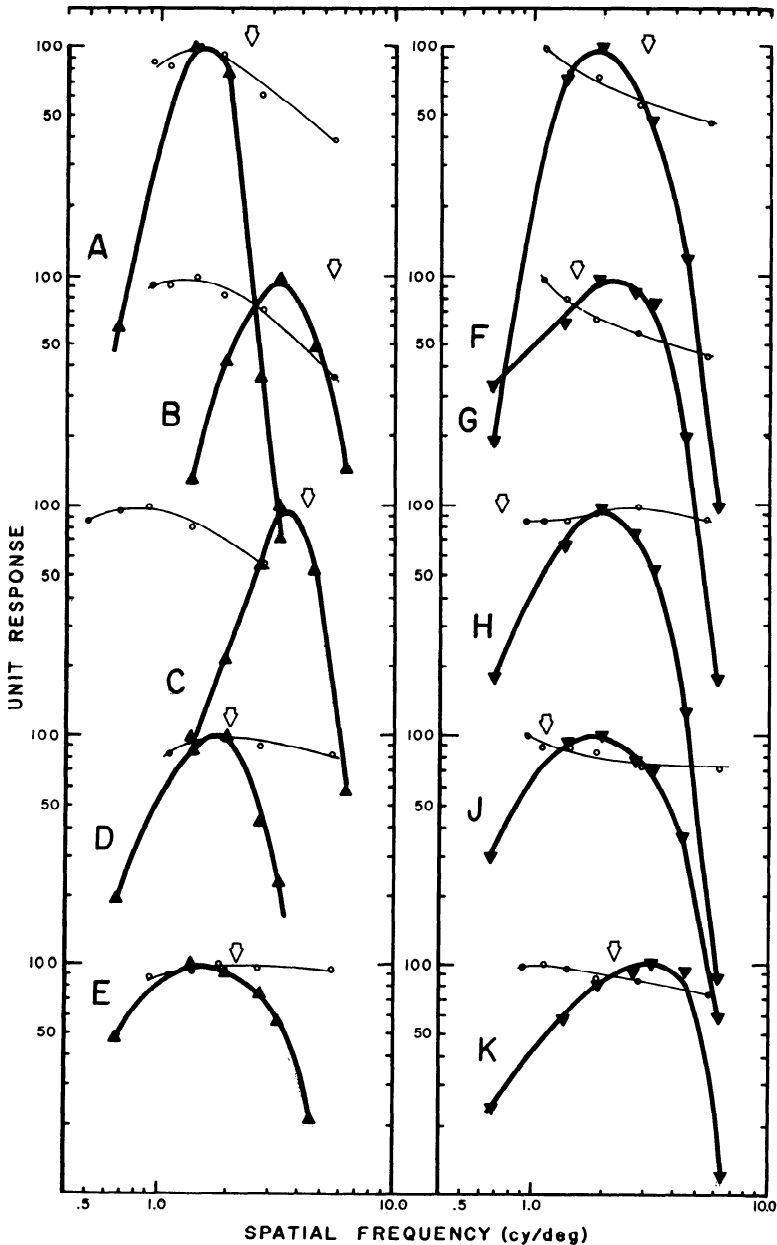


FIG. 10. Representative sample of response curves to sine-wave gratings. A-E: S-type cells; F-K: CX-type cells. Triangles show total number of responses to gratings of different frequencies normalized to the best response. Circles show response of same cells to bars of different widths. Receptive-field size expressed in frequency terms.

The second hypothesis suggests that in S-type cells the optimal response should be elicited when the distance between subfields and the half-cycle width of the grating are matched. The optimal grating would be the one which stimulates the light and dark subfields simultaneously. The problem with this hypothesis is that the

subfields of S-type cells, when mapped by standard procedures, often appear to be excitatory. That being the case, the maximal grating should elicit approximately twice the responses per unit time from the cell than any other grating. This is not the case; cells are clearly more selective than this. If, on the other hand, inhibitory areas pro-

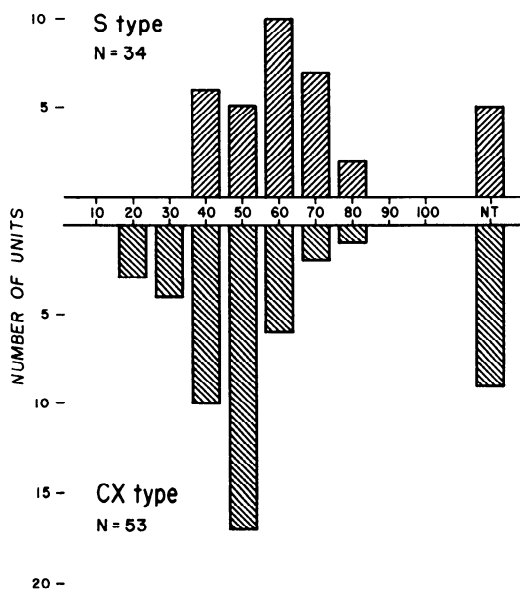


FIG. 11. Distribution of spatial-frequency selectivity. Abscissa: index of selectivity obtained by dividing the frequency score at the high crossover of the curve at the 71% response level into the low crossover at the same level and multiplying this value by 100. A score of 50 represents a specificity of 1 octave. NT, units not selective for spatial frequency.

duce the selectivity, one might expect only a marginal relation between the spatial separation of subfields and the optimal grating.

Figure 12 plots the relationship between cycle width of the optimal sine-wave grating and receptive-field size. The data indicate a poor relationship between these two variables for

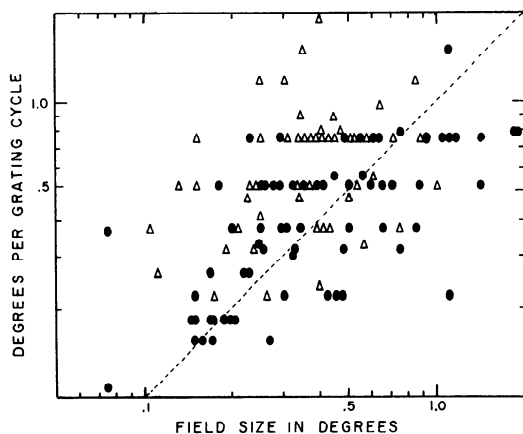


FIG. 12. Relationship between receptive-field size and optimal spatial-frequency response. Δ , S-type cells; \bullet , CX-type cells. A close relationship between these measures would require that points be distributed along the dotted line.

S-type and CX-type cells. The correlations we performed yielded coefficients (r) of 0.43 for S-type cells and 0.62 for CX-type cells (log-log correlations). When retinal eccentricity was reduced as a variable by taking only those cells which were 2° – 5° from the fovea ($N = 81$), the correlation was only 0.38 and 0.26 for S-type and CX-type cells, respectively. The receptive-field size of 90% of the CX-type cells was larger than the half-cycle width of the optimal grating.

Figure 13 shows the relationship between the optimal grating and the center-to-center separation between the subfields of S-type cells. These data also reveal a poor relationship. The center-to-center separation of 74% of the S-type cells was smaller than the half-cycle width of the optimal grating.

These data suggest that spatial-frequency selectivity is not predictable from those properties of receptive-field organization which can be derived directly from the excitatory responses of the cell.

SPATIAL-FREQUENCY SELECTIVITY AND RETINAL ECCENTRICITY. We have shown that only a marginal relationship exists between receptive-field size and the frequency of the optimal sine-wave grating when cells are sampled 2° – 5° from the fovea. The other variable which may influence the frequency response is retinal eccentricity. The relationship between these two variables is plotted in Fig. 14. This figure demonstrates a moderate decrease in the optimal spatial frequency of sine-wave gratings with increasing retinal eccentricity, but also shows a great deal of scatter (r for S type, 0.33; for CX type, 0.63).

SPATIAL-FREQUENCY SELECTIVITY, DIRECTIONALITY, AND ORIENTATION TUNING. In the previous paper we suggested that orientation and direction selectivities are produced by separate mechanisms. In order to determine whether or

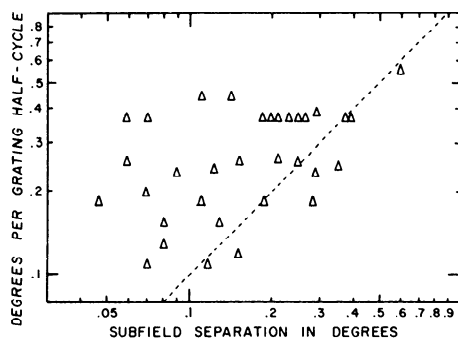


FIG. 13. Relationship between the optimal spatial-frequency response and the subfield separation of S-type cells.

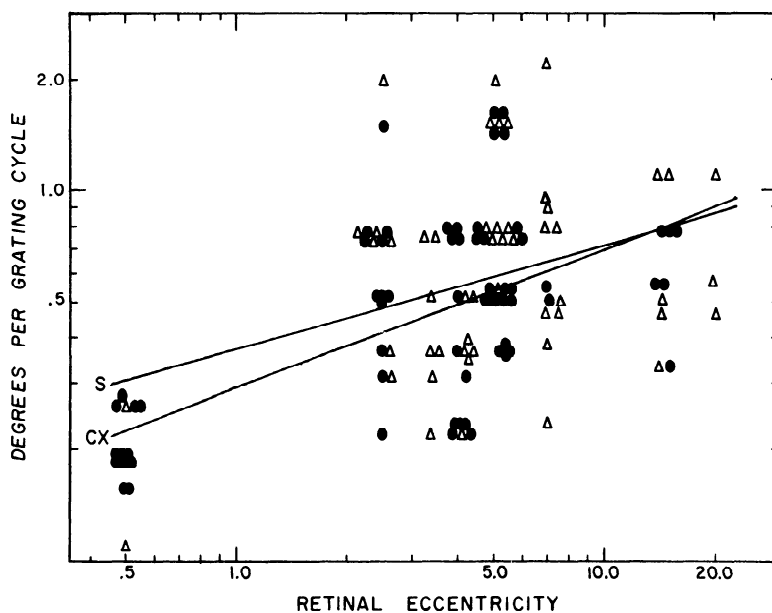


FIG. 14. Optimal spatial-frequency response and retinal eccentricity. Δ , S-type cells; \bullet , CX-type cells. Regression lines are fitted for both S-type and CX-type cells.

not spatial-frequency selectivity can be linked to either of these mechanisms we examined our data for a relationship among these attributes.

To examine the relationship between spatial frequency and direction selectivity, we compared directional and nondirectional cells (dividing cells into two groups, one above and the other below 50 on the index of directionality). These two groups of cells had distributions for spatial-frequency selectivity which were almost identical. It appears then that the mechanism responsible for directionality is not directly contributory to spatial-frequency selectivity.

Establishing a lawful relationship between spatial-frequency selectivity and orientation tuning is a more difficult task. If inhibitory regions flanking the excitatory portion of the receptive field generate orientation tuning, the same mechanism might also determine spatial-frequency selectivity. However, the schematic receptive fields drawn in Fig. 15 demonstrate that although the same inhibitory mechanism might be responsible for both orientation and spatial-frequency selectivity, the correlation between these measures might still be poor. In Fig. 15A and B the length of the inhibitory areas parallel to the axis of orientation is the same, but the spatial separation between them is different. As a result of this, orientation tuning (OT) is broader for the field in Fig. 15B. One might conjecture that the response to spatial frequency is also defined by this spatial separation, where

one cycle of the optimal grating frequency corresponds to the center-to-center separation of these inhibitory flanks. If this were the only consideration, one should obtain a high correlation between the degree of selectivity for orientation and the frequency of the optimal sine wave. However, we obtained a correlation of only 0.13 for S-type cells and 0.47 for CX-type cells. The problem is that orientation specificity, according to this scheme, is determined not only by the spatial separation of the inhibitory regions, but also by their length in the direction parallel to the axis of orientation. In Fig. 15C the center-to-center separation of the inhibitory flanks is the same as in Fig. 15A, but the length of these regions is different. This difference alters the orientation tuning but not the spatial-frequency response. According to this scheme, then, one needs to obtain data for both the separation and length of the hypothetical inhibitory flanks in order to establish a relationship between orientation tuning and spatial-frequency selectivity. Unfortunately, this information cannot be derived from our data.

RESPONSE MODULATION OF S-TYPE AND CX-TYPE CELLS TO SINE-WAVE GRATINGS. The temporal modulation of response obtained with sine-wave gratings was similar to that found for square-wave gratings. The response of S-type cells was strongly modulated and that of CX-type cells was weakly modulated. For the sine-wave grat-

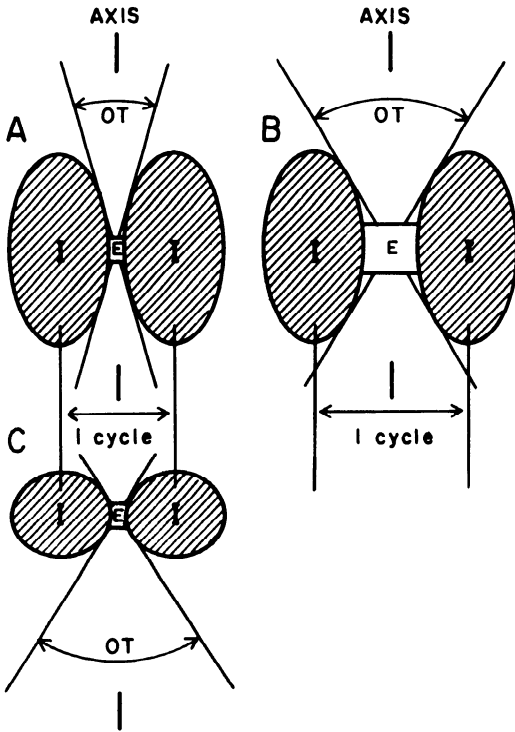


FIG. 15. Hypothesized relationship between orientation tuning and spatial-frequency selectivity. I, inhibitory areas; E, excitatory center; OT, orientation tuning; axis, axis of orientation. A and B: inhibitory flanks have same length but differ in extent of spatial separation; A and C: inhibitory flanks have same separation but differ in length.

ings the index of modulation was calculated for each cell using the data secured with the optimal-frequency grating. These results appear in Fig. 16. Also included is a similar analysis made on 44 LGN cells whose receptive fields were in the same area of the visual field. It can be seen that the S-type cell population shows more modulation of response than the LGN population.

These data are consistent with the results using square-wave gratings. S-type and CX-type cells differ significantly in their temporal modulation.

To obtain the data presented here we studied primarily those cells which could be easily classified as S or CX type. Not evident is the fact that many cells responded poorly to sine-wave gratings even when bars or edges elicited good responses from them. Most of the cells which did not respond or responded weakly to sine-wave gratings were found in the upper layers of cortex (above layer 4). We estimate that approximately one-third of the cells we en-

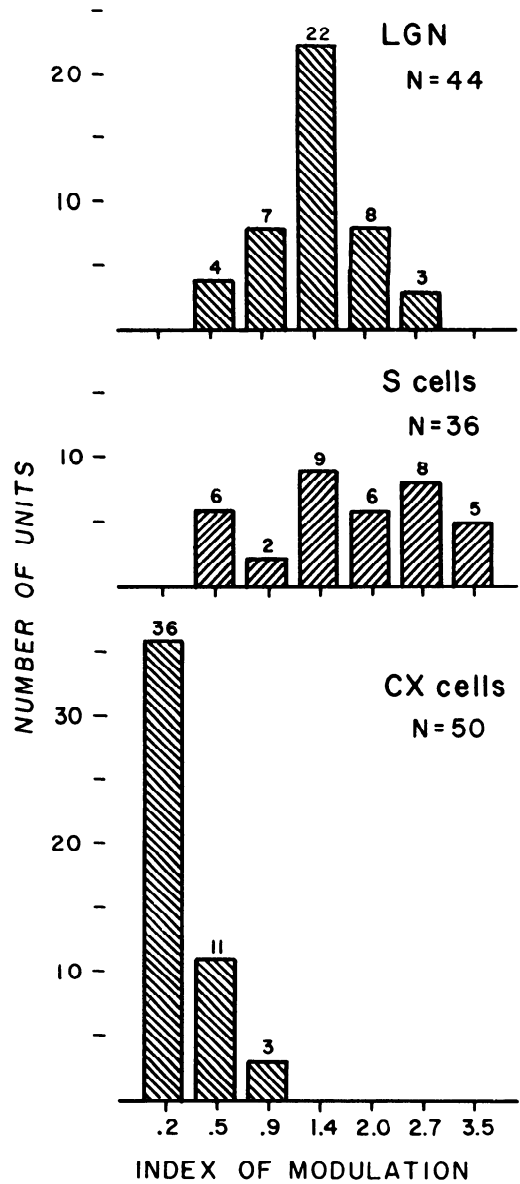


FIG. 16. Temporal response modulation to sine-wave gratings. LGN, lateral geniculate nucleus cells. The modulation score of each cell was obtained with the grating frequency eliciting the optimal response.

countered with the intent of obtaining data using sine-wave gratings could not be driven effectively with these stimuli.

DISCUSSION

This study yielded six basic findings: 1) Most cells in monkey striate cortex showed little selectivity for the width of single bars and for the spatial frequency of square-wave gratings. 2)

The responses of double-field, S_2 cells tend to summate when stimulated by bars of decreasing widths. Thus, simultaneous activation of each subfield produces about the same number of responses as the sum of the responses obtained from each field separately. This observation further supports our belief that the responses elicited from each of the subfields of S-type cells are produced by excitatory action. The responses of CX-type cells under similar conditions tend to show less summation. 3) The majority of S-type and CX-type cells we studied were selective for the spatial frequency of sine waves. 4) Receptive-field attributes such as size of activating field, spatial separation between excitatory subfields, orientation tuning, and directionality were not sufficient to predict the spatial-frequency specificity of these cells for sine-wave gratings. 5) S-type cells were only slightly more selective for the spatial frequency of sine-wave gratings than were CX-type cells. 6) Moving sine-wave and square-wave gratings elicited responses with sharp temporal modulation in S-type cells. The responses of CX-type cells, on the other hand, were poorly modulated. The degree of temporal modulation is a good measure for distinguishing S-type and CX-type cells.

The results pose two general questions: *a)* Why is it that cells exhibit spatial-frequency selectivity with sine-wave gratings but fail to do so with bars and square-wave gratings? *b)* What mechanism is responsible for spatial-frequency selectivity?

We suggest that the lack of spatial-frequency selectivity with single bars and square-wave gratings may be attributed to the fact that sharp edges are extremely potent stimuli. Excitatory regions of receptive fields can readily be driven by them. The hypothetical inhibitory regions under these conditions are relatively ineffective. It may be said that with sharply defined edges the responses of cells to edges parallel to the axis of orientation are defined almost entirely by the excitatory regions of the field.

By contrast, with sine-wave gratings which, in general, are less potent excitatory stimuli, it is possible that inhibitory mechanisms become more effective. Nonoptimal spatial frequencies in the low-frequency range activate inhibitory regions which, under these conditions, are much more effective than with sharp-edge stimuli.

We did not succeed in answering the further question: what inhibitory mechanism of cortical cells is responsible for spatial-frequency selectivity? Our data suggest that the circuitry giving rise to directionality is not involved in spatial-frequency selectivity. The possibility remains,

however, that the neuronal mechanisms involved in orientation selectivity may also be the ones which are responsible for spatial-frequency selectivity. Further work is required to determine this.

Since spatial-frequency selectivity is not evident in cortical cells when patterned stimuli with sharp contours are viewed with the lens optimally imaging them on the retina, one may question the role of this selectivity in perception. It appears that spatial-frequency analysis becomes operational only when stimuli lack sharp contours or are degraded by being out of focus. Under such conditions, these stimuli are similar to sine-wave gratings.

In the everyday viewing of images, the majority of them are out of focus. It is possible that the selectivity revealed with sine-wave gratings reflects a means whereby stimuli, even when they are out of focus, can be analyzed, perhaps rather crudely, in terms of such an attribute as spatial frequency. This is also true, of course, for stimuli which physically lack sharp contours, such as the gradations in light intensity one observes when viewing the waves on the ocean or the clouds in the sky.

These observations suggest that two mechanisms of pattern perception could be present at the level of visual cortex. Orientation selectivity of cortical cells could represent one of the early stages in this dual analysis. The other mechanism, that of spatial frequency, might become operative only when stimuli have poorly defined contours brought about either physically by the nature of the reflecting surfaces and conditions of light reflection or by the degradation of the image on the retina as a result of an out-of-focus lens and wide pupil.

The results presented here fail to relate the mechanism responsible for spatial-frequency selectivity to other attributes of receptive-field organization. Inhibitory processes appear to be necessary, but since our methods do not permit a delineation of the spatial organization of these inhibitory regions in S-type cells, we did not succeed in specifying the hypothetical role of regional inhibition.

Our results appear to favor a hierarchic relationship between S-type and CX-type cells. If one were to assume that CX-type cells receive their input exclusively from LGN cells, it would be difficult to explain their spatial frequency selectivity since 1) LGN cells show only a small degree of selectivity for spatial frequency, 2) CX-type cells have no demonstrable inhibitory flanks, and 3) the optimal frequency grating (expressed in half-cycle width) is often much smaller than the receptive-field size of CX-type cells.

On the other hand, S-type cells' convergence on CX-type cells could yield the kind of selectivity for spatial frequency we have obtained.

Finally, our results indicate that S-type and CX-type cells differ significantly in the degree to which their responses to gratings are temporally modulated. This is true even when the optimal sine wave is used to stimulate their receptive field (Fig. 15). These data imply that by using modulation as a way of classifying cells as S and CX type, one would misclassify only 10% of the cells. With square-wave gratings this value drops even lower to 3%. These values compare favorably with the other indexes we described in the first two papers of this series (8, 9).

Three questions may be posed regarding these data: *a*) What accounts for the difference in modulation between S-type and CX-type cells? *b*) What makes S-type cells better modulated than LGN cells (Fig. 16)? *c*) Does temporal modulation, as observed here, serve a useful analytic function in vision?

With respect to the first question it would appear that the difference in receptive-field size between S-type and CX-type cells cannot fully explain the temporal modulation effect since receptive-field size and optimal spatial-frequency response do not correlate (Fig. 12).

Modulation does appear to be strongly influenced, however, by the spatial arrangements of the (sub)fields of cortical cells. S-type cells respond to optimal sine-wave gratings with the same number of bursts as there are cycles traversing the field in spite of the fact that each cycle represents two contrast changes, one associated with light increment and the other with light decrement. S-type cells with only a single field do so because they are sensitive to only one sign of contrast change. S-type cells with two (or more) subfields do so because the responses summate when the subfields are activated at the same time, one being driven by light increment and the other by light decrement. However, the relationship between the spatial separation of subfields and the optimal grating is not pronounced (Fig. 13), probably because summation between the subfields occurs over a considerable range of spatial frequencies (see Fig. 6 and 9).

CX-type cells which have overlapping light and dark response areas might produce sustained responses for two reasons. One is that the overlapping light and dark subfields of CX-type

cells tend to produce two temporally separate responses to each cycle, one to light increment and the other to light decrement. The second, perhaps less important, reason is field size. With larger fields each response is extended in time as the stimulus traverses the field. It is indeed true that among CX-type cells, the ones with the largest fields are most poorly modulated. These considerations regarding temporal modulation are consistent with the view that CX-type cells receive a convergent input from S-type cells.

The second question of why some S-type cells are better modulated than LGN cells can perhaps be answered on the basis of two facts: *a*) S-type cells produce more transient responses than do LGN cells (8); and *b*) in S-type cells with more than one subfield, the subfield responses summate. These facts would appear to be sufficient for the size of the observed effect.

The possible significance of the temporal modulation effect in visual analysis cannot readily be answered. While this method of analysis is a useful aid for cell classification, one can only speculate about the possible adaptive significance of this difference in the temporal modulation of cortical cells. In alert, behaving animals these patterns of neural discharge would most commonly occur when a moving object is tracked against a stationary background. Thus, for example, while one watches a dog making its way through a grassy meadow, a repetitive pattern will drift across the observer's retina in the direction opposite to eye movement. Under such conditions, perifoveal S-type cells would presumably discharge in bursts and CX-type cells would discharge in a relatively sustained fashion. The S-type cells under such conditions may be carrying more information about the subunits of the background, thereby producing detailed pattern vision in the periphery. CX-type cells under such conditions would seem to yield primarily generalized information about the overall spatial frequency of the stimulus array. Further work is needed to determine whether or not and how this information is utilized.

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