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J Neurophysiol 39:1288-1319, 1976. ;

Journal of Neurophysiology publishes original articles on the function of the nervous system. It is published 12 times a year (monthly) by the American Physiological Society, 9650 Rockville Pike, Bethesda MD 20814-3991. ISSN: 0022-3077, ESSN: 1522-1598. Visit our website at http://www.the-aps.org/.

JOURNAL OF NEUROPHYSIOLOGY
Vol. 39, No. 6, November 1976. *Printed in U.S.A.*

Quantitative Studies of Single-Cell Properties in Monkey Striate Cortex. I. Spatiotemporal Organization of Receptive Fields

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SUMMARY AND CONCLUSIONS

1. The properties of single cells in striate cortex of the rhesus monkey, representing the visual field 2°–5° from the fovea, were examined quantitatively with stationary and moving stimuli. Three distinct classes of cells were identified: S type, CX type, and T type.

2. S-type cells were defined as those oriented cells which to the optimal direction of movement in their receptive fields exhibited one or more spatially separate subfields within each of which a response was obtained to either a light or dark edge, but not to both. Several different types of S-cells were distinguished: *a*) S_1-type cells for which moving edges revealed a single excitatory area within which a response was elicited by either a light or a dark edge but not by both. Most of these cells were unidirectional. *b*) S_2-type cells for which moving edges revealed two spatially separate response areas, one of which was excited by a light edge and the other by a dark edge. Both regions responded to the same direction of movement. *c*) S_3-type cells which had two response areas, one of which was excited by a stimulus moving in one direction (at right angles to the axis of orientation) and the other, of opposite contrast, which responded in the opposite direction. *d*) S_4-type cells which to one direction of movement showed two spatially separate regions sensitive to a light and dark edge and which in the other direction of movement had only one responsive area (either light or dark). *e*) Cells which had multiple spatially separate subfields (S_{5-7} types).

3. CX-type cells were defined as those oriented cells which in their receptive fields exhibited no spatial separation for light- and dark-edge responses; they discharged to both edges in the same direction of movement and in the same spatial area. Flashing stimuli elicited both on and off responses throughout the receptive field. CX-type cells were predominantly of two types: those which were selective for direction of stimulus movement and those which were not.

4. A third class of cells (T-type) were those which were excited by only one sign of contrast change and responded in a sustained fashion even when there was no contour within the receptive field. These cells were poorly or not at all oriented; some of them were selective to wavelength.

5. Quantitative comparisons showed the following differences between S-type and CX-type cells: *a*) S-type cells had smaller receptive fields than CX-type cells but the populations overlapped considerably. Receptive-field size was smallest in layer 4c. In all other layers S-type cells had the same size fields. CX-type cells, by contrast, tended to have larger fields in layer 5–6 than 2–3. *b*) The spatial separation between light and dark response areas was the best criterion for distinguishing S-type and CX-type cells. The distribution of this measure disclosed two populations of cells with relatively limited overlap. *c*) In layers 2 and 3, both S-type and CX-type cells had low spontaneous activity. In layers 5 and 6, S-type cells retained this attribute. Most CX-type cells, however, showed significantly higher spontaneous activity in these bottom layers. Thus the criterion of spontaneous activity discriminated S-type and CX-type cells in layers 5 and 6 but failed to do so in the upper layers. *d*) S-type cells were found in all cortical layers. CX-type cells were absent in layer 4c.

6. The measure of inhibition along the axis of orientation, typically used to classify cells into the "hypercomplex" category, did not establish a distinct subcategory of cells. This property was observed in both S-type and CX-type cells

Received for publication December 22, 1975.

and was continuously distributed. However, this inhibition was more prevalent in the superficial layers than in the deep ones.

7. The results are suggestive of a hierarchy among S-type cells. Lowest in this hierarchy are those S-type cells which could be activated by only one kind of moving edge. From these, S-type cells with two or more subfields may be constructed.

INTRODUCTION

Following the pioneering work of Hubel and Wiesel (7, 8), striate cortex has been subjected to extensive analysis with single-unit recording techniques (1–5, 11–14). The input to this structure from the lateral geniculate nucleus (LGN) is transformed in five notable ways. The first of these produces specificity for the orientation of contours within the receptive field. The second transformation is that of direction selectivity. While in the LGN of the cat and monkey cells respond to stimuli moving in any direction, in cortex many cells are responsive to movement only in one direction. The third transformation involves the combination of responses to contrasts of opposite sign. Most LGN cells in the center of their receptive field are excited by either light increment or light decrement, but not by both. In cortex these attributes are combined so that many cells respond to both kinds of stimulus change within a single region. The fourth transformation unites the input from the two eyes, resulting in cells which can be binocularly activated. The fifth transformation alters the spatial frequency response of cells: in the striate cortex there is a sharply increased selectivity for spatial frequency when compared to what is found in the LGN (14). All five transformations may be seen in a single cell.

In this series of papers we will present the results of experiments in which we analyzed the visual cortex of the monkey in terms of these transformations. In the first paper we will examine the response properties of single neurons in striate cortex to direction of movement, contrast, and stimulus length, with special emphasis on simple cells. The second paper will present data regarding orientation selectivity and ocular dominance. The third paper will be concerned with selectivity for spatial frequency. The fourth paper will examine the properties of the corticotectal cells in area 17. In the last paper we will consider the relationship among the different measures we used and how these measures reflect on various models of visual cortex.

Work on the cat has disclosed several criteria whereby simple and complex cells can be distinguished (1, 8, 20). Simple cells have relatively small receptive fields. These fields can be plotted with stationary flashing spots of light; such a plot discloses spatially separate activating regions for the onset (on-response) and the turning off (off-response) of a flashing light. The response within a given region summates as the size of the stimulus increases. Moving stimuli may demonstrate either one such activating region or several spatially separate activating regions. Furthermore, simple cells have low spontaneous activity and show a preference for relatively slow velocities of stimulus movement. In the cat, cells with simple receptive fields are most numerous in layers 3, 4, and 6 of striate cortex (8).

Complex cells have larger fields and respond more poorly to flashes. The activating region shows no subdivision into spatially separate zones: when a cell responds to them, flashing stimuli elicit both on- and off-responses throughout the field; similarly, a response is obtained to both the light edge and the dark edge of moving stimuli within this one region. These cells are more often binocular, tend to have greater spontaneous activity, especially in cortical layers 5 and 6, and respond over a greater range of velocities.

In contrast to work on the cat, simple cells in the monkey have not been studied in detail, primarily because they have been encountered less frequently. Hubel and Wiesel (10) report that only about 8% (25 of 272) of the cells they have studied in the monkey fell into this category. Poggio (15) classified 7% (12 of 224) and Dow (5) 9% (21 of 234) of the cells as simple.

Considerable uncertainty exists regarding the location of these cells in monkey striate cortex. Hubel and Wiesel (10) found that of the 25 cells they classified as simple, 23 were in layer 4. By contrast, Poggio (15) reports only 1 of 12 in this layer. Dow (5) shows a relatively even distribution of simple cells among the cell layers. According to Hubel and Wiesel (10), complex cells in the monkey are least common in layers 4b and 4c. Poggio's data show them equally distributed.

Subsequent to their initial discoveries, a third class of cells has been identified by Hubel and Wiesel (9) in the cat; these cells were called hypercomplex, and it was suggested that they were formed by excitatory and inhibitory inputs from complex cells. The major criterion for placing the hypercomplex cells into a distinct class was the observation that their responses are inhibited by stimuli extended along the axis of orientation, thereby rendering them selective for stimulus length, an attribute absent in simple and complex cells. Several qualifications have been made subsequently regarding this cell type (3).

Further investigation disclosed several other

classes of cells in striate cortex. Prominent among these are unoriented cells, which may be further divisible into several subgroups (5, 10, 15).

One of the problems with these classifications is that few of the dimensions which have been used for assigning cells to categories have been studied quantitatively. Thus it is not known, especially in the monkey, to what extent the measurements used form distributions which justify the classificatory schemes. The assumption of classes can be inferred quantitatively when the measure on the basis of which the classification is made yields separate groupings as demonstrated, for example, by a bimodal distribution. If, however, a distribution is continuous, one cannot, of course, claim two distinct classes. An example in point is binocularity. Since the extent to which cortical cells are binocular forms a relatively continuous distribution, this property has been believed not to reflect two distinct classes of monocular and binocular cells. Thus, issues about binocularity are typically formulated in statistical terms asking, for instance, how the ocular dominance distribution is affected by such variables as brain site or environmental manipulation. The question may be raised: to what extent will the quantitative measures of single-cell receptive-field properties disclose distributions which justify the classificatory schemes hitherto proposed? In particular, we will examine distributions based on such measures as subfield separation, directionality, contrast independence, and spontaneous activity.

In addition to the problem of classification, the criteria which have been used to group cells in striate cortex into the simple, complex, and hypercomplex classes have been under some debate (3, 11). It appears that a portion of the cells considered as simple by some investigators may not have been so designated by Hubel and Wiesel (8) who were the first to describe and name these cells. Almost unavoidably, perhaps, each investigating group has developed its own set of criteria. Since we may too have done so, we decided to call cells in the monkey which we believed to be simple, S-type cells. Those which we thought analogous to complex cells we called CX-type cells. We found that the most reliable classification was achieved on the basis of the spatial location of responses to light increment and light decrement. For this reason we defined our S-type cells, as did Hubel and Wiesel (8), as those orientation-selective cells whose receptive fields had one or more distinct subfields within each of which a flashing stimulus or a stimulus moving in one direction elicited a response to either the increment or decrement of light, but not to both. CX-type cells were defined as those which within their activating region showed no spatial separation; the areas which responded to light increment and light decrement overlapped. Specificity for direction in these cells was similar for moving light edges (light increment) and dark edges (light decrement).

In what follows we present qualitative and quantitative data describing the properties of various types of cells found in monkey striate cortex as determined by moving edges and stationary, flashing stimuli. We will place special emphasis on S-type cells as here defined. Distributions of cells according to a variety of response measures will be used to scrutinize the validity of classificatory schemes. Finally, these data will be considered in terms of the anatomical distribution of cell types within the layers of striate cortex.

METHODS

Single-unit recording procedures

A total of 42 rhesus monkeys (*Macaca mulatta*) were used to obtain the data reported in this paper. All 42 were studied while the animals were anesthetized and paralyzed. In addition, two of these animals had also been recorded from while alert, with one eye surgically immobilized.

ANESTHETIZED ANIMALS. Surgical procedures were carried out under Pentothal anesthesia. After tracheotomy and vein cannulation, animals were placed in a Kopf stereotaxic apparatus with raised eye and ear bars. In 32 animals a closed chamber of 10 or 16 mm diameter was implanted over area 17 in a region where receptive fields were found 2°–5° from the fovea in the lower visual field.

The dura mater overlying the visual cortex was removed in approximately half the animals and was left intact in the others. We found that successive penetrations can be undertaken with greater ease, rapidity, and with fewer episodes of electrode breakage when dura is removed. This procedure also permits the use of finer electrodes. On the other hand, recordings are not quite as stable and cortex deteriorates more rapidly.

In 32 of the animals penetrations were made perpendicular to the surface of the brain. In 10 monkeys tangential penetrations were made which were between 10° and 25° to the surface of the brain, in a manner similar to that described by Hubel and Wiesel (12).

Animals were infused with Flaxedil (40 mg/h) dissolved in 5% dextrose in Ringer and were artificially respired. End-tidal CO_2 was monitored and maintained at 4.0–4.5%. Pentothal anesthesia was discontinued after the first 2–10 h

and subsequently animals were maintained on a 70%–30% mixture of N_2O and O_2.

Following application of hyoscine, contact lenses of proper curvature were applied to bring the eye in focus on a tangent screen 57.3 inches away. Using a reversible ophthalmoscope the fovea of each eye was projected onto the screen. In most experiments 3-mm artificial pupils were placed in front of the eyes.

Animals were typically studied over a period of 2 days. During the night contact lenses were removed for a few hours to reduce corneal clouding. Even so, in some animals slight opacity was observed by the end of the 2nd day of recording. When this occurred the corneal epithelium was removed by scraping, which resulted in clear optic media (18).

Single cells were recorded using glass-coated platinum-iridium microelectrodes (21).

ALERT MONKEYS. In two animals one eye was surgically immobilized by transection of the 3rd, 4th, and 6th cranial nerves. Skull screws and recording wells were implanted prior to recording as previously described (17). During recording sessions the head was restrained, permitting the study of cortical receptive fields via the immobilized eye. The prime purpose of this study was to determine whether or not the receptive-field properties of single cells in visual cortex of the alert animal in our situation were comparable to those of the paralyzed, anesthetized animals.

Stimulus delivery systems

Two separate stimulus delivery systems were used, one manual and one computer operated.

MANUAL SYSTEM. The manual system consisted of an optic bench, a control box, and assorted power supplies. The optic bench had the following elements: *a*) tungsten ribbon filament lamp; *b*) condenser; *c*) motor-driven aperture permitting adjustment of stimulus length, width, and orientation; *d*) projection lens; *e*) X-Y mirror galvanometer. The image was projected to a tangent screen 57.3 inches from the animal.

The control box contained a joy stick, which operated the X-Y galvanometers, and several switches which activated the aperture motors.

The manual system was used to localize the receptive field on the tangent screen and to determine qualitatively the basic attributes of receptive fields such as orientation, binocularity, directionality, and the location of subfields in the S-type cells.

COMPUTER-CONTROLLED SYSTEM. Stimulus delivery for detailed analysis was accomplished by a second optic bench. The elements on this bench were driven with stepping motors activated either manually or by a PDP-11/20 computer. The aperture in this case consisted of two sets of leaves driven by two stepping motors which could produce rectangular stimuli. Stimuli could be made to increase or decrease in size either symmetrically with respect to the center of the optical axis or asymmetrically by keeping one leaf fixed at the center of the optical axis.

The next element on the optic bench was the projection lens which was followed by a shutter. After the shutter a right-angle prism permitted the movement of the stimulus using either a galvanometer or a stepping motor. The galvanometer was used in conjunction with a waveform generator for smooth stimulus movement on the tangent screen. The stepping motor was used to place stimuli into various fixed positions on the screen. Following this was a dove prism which was rotated with a stepping motor to produce changes in stimulus orientation and direction of motion.

All the motor-driven elements in this system could be manipulated either manually or by computer. The PDP-11 was used and was programmed to allow the manipulation of each of several stimulus dimensions such as stimulus orientation, stimulus length, and stimulus width.

One of the major features of the computer program we used, which was developed by A. Polit, was that it enabled us to present stimulus conditions in randomized order. The determination of orientation specificity, for example, was accomplished by having a bar or edge move across the receptive field in a number of different orientations, all of which were presented automatically in a random order after specification of the range and number of trials. For some of our quantitative measures this feature was deemed essential due to the inherent response variability of single cells in visual cortex. Our data (16) show that the average short-term variability of cortical neurons to repeated presentations of an optimal stimulus is 35.4 using the formula: standard deviation/mean $\times$ 100.

On collecting the data for a given run, the results were displayed on a Tektronix 611 storage oscilloscope; total, mean, and standard deviation of the number of spikes obtained to each stimulus presentation could be displayed on command. These data could also be printed out on the Teletype or stored on DEC tape. The stimuli used were 0.8–1.6 log units above cell response threshold. Background illumination was 0.8–1.2 cd/m^2.

PROCEDURE

Each unit was first studied by manual operation of the first optic bench. The response

characteristics were subsequently assessed quantitatively with the computer-driven arrangement.

Manual assessment

When a single cell was clearly isolated and properly triggered by the Schmitt trigger, we began by determining: *1*) the location and size of the receptive field; *2*) the dominant eye; *3*) the best orientation; *4*) the optimal direction of movement; *5*) the responsiveness to light and dark edges or bars; *6*) the effect of different stimulus lengths and widths; and in some cases, *7*) the response to stimulus velocity within a range of 0.5–50°/s; and *8*) the response to colors using red, green, blue, and yellow filters. Some of these measures were again reassessed manually following the computer-operated sequence.

Computer-driven assessment

The following procedures were used to assess the response characteristics of single cells quantitatively. Each step described below was carried out as a single uninterrupted sequence, initiated by the necessary commands via a Teletype.

ORIENTATION. Most commonly we began the detailed study of a cell by initiating a computer command which resulted in having a bar or edge sweep across the receptive field in different orientations in a randomized sequence. The results obtained in this fashion will be described in detail in the second paper. On completion of an orientation sequence the data were stored and displayed on a 611 storage oscilloscope enabling us to see the optimal orientation and the sharpness of orientation tuning.

STIMULUS LENGTH. For this series the stimulus was set to the orientation which provided the best response during the orientation sequence described above. The length of the stimulus was varied in a random order, typically over eight steps using stimuli of fixed widths and varying lengths of 0.1, 0.2, 0.4, 0.8, 1.6, 3.2, 6.4°, with 10 or 20 measures in all at each step. Included in this series was a "no stimulus" condition used to obtain a measure of the response rate in the absence of a visual stimulus.

MOVING EDGES. To assess the response of units to light (light increment) and dark (light decrement) edges, to determine the spatial location of the response areas, and to assess degree of directionality, single edges or rectangles were swept across the receptive field. Commonly 1° by 1° stimuli were used and most units were tested with both a light square on a dark background and a dark square on a light background. These stimuli were moved back and forth across the receptive field in the optimal orientation, usually over a range of 3° at a velocity of 2°/s, for 30 repeated trials. For units with large fields or complicated responses, single edges were used and for strongly "stopped" cells, stimuli with lengths shorter than 1° were introduced.

During data collection the responses were displayed as they occurred on the 611 storage oscilloscope in the form of a raster, with each response generating one dot and successive stimulus sweeps appearing on successive lines of the oscilloscope. At the termination of the sequence the data were stored and displayed in the form of a cumulative-response histogram; 256 bins were used, which for 3° back-and-forth movement at 2°/s meant 11.7 ms/bin or 0.023° spatial resolution per bin.

STATIONARY FLASHES. The responses of cells to stationary flashes were studied using two procedures. One was a single sequence of 30 repeated flashes of an optimal stimulus in the best location with a 1.5 s on and a 1.5 s off cycle. For the second method, several spatially separate sites were flashed. The stimulus was typically a 0.09°-wide bar in the optimal orientation of the receptive field. Stimuli were flashed over a range of either 0.8° or 1.6°, depending on receptive-field size, using eight different equally spaced positions; 20 trials, with a 1 s on, 1 s off cycle, were obtained for each position in random order.

RESULTS

The results reported in this section are divided into five parts. In the first we will describe the response of various kinds of cells in monkey striate cortex to stationary and moving edges. The second section will deal with the size and shape of receptive fields. In the third section the distributions of cells according to a variety of quantitative measures will be presented. In the fourth section the relationship between unit responses and the site of recording in the cortical layers will be analyzed. The last section briefly describes results obtained in alert animals.

Examples of cell properties assessed by responses to stationary and moving stimuli

We defined S-type cells as those oriented cells whose receptive fields had one or more spatially distinct regions within each of which a moving-edge or a flashing stimulus elicited a response to either light increment or light decrement. By contrast, CX-type cells were defined as those oriented cells which to either moving edges or stationary flashes of light responded to both light increment and light decrement throughout their

receptive fields. For these cells, direction selectivity was not affected by the contrast of the moving stimulus.

The results described in this section were obtained by *1*) sweeping light and dark rectangles or single edges across the receptive field, and *2*) flashing stationary targets into various parts of this field. The use of both light figures on a dark background and dark figures on a light background was considered an important reciprocal control for moving stimuli, and the data shown always include examples of both. In most cells a close correspondence was found between receptive-field maps obtained with small stationary, flashing spots and with moving stimuli.

As an introduction to the data obtained with moving rectangles, the first figure describes what such responses would look like when the stimuli are swept across photocells attached to the tangent screen where the receptive fields of cells were to be studied.

When a single photocell responds transiently to any sudden change in illumination, a light or dark rectangle sweeping across it will generate four pulses in a histogram (Fig. 1*A*), two in each direction of movement, one for the light edge and the other for the dark edge. If the photocell circuit is arranged to produce a pulse to light increment alone, only those peaks will be seen which are labeled L. If, furthermore, we have the photocell respond to only one direction of movement, only one peak would be seen.

Not so obvious is what happens when we place two photocells side by side with some spatial separation between them and have the first respond transiently only to light increment and the second only to light decrement. The responses elicited by moving white and black rectangles traversing the two photocells are shown in Fig. 1*B* and *C*. As can be seen the pulses are now asymmetrically displaced with opposite asymmetries for the light and dark squares. If response latency and the total distance traversed by the moving stimuli are known, the relative location of the response areas can be calculated on the basis of the temporal separation between the pulses (1).

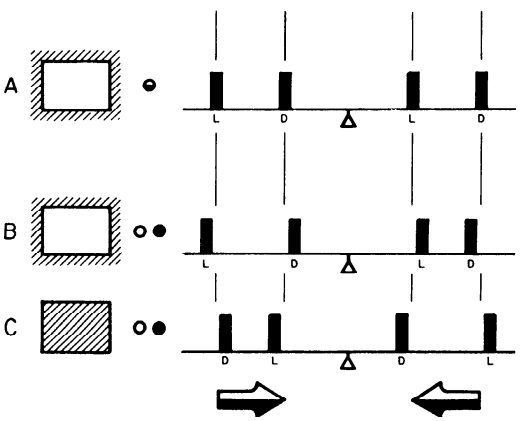

FIG. 1. Photocell responses to the light and dark edges of moving rectangles. *A*: light rectangle on dark background, single photocell responding to both light and dark edges. *B*: light rectangle on dark background, two spatially displaced photocells, one responding to the light edge and the other to the dark edge. *C*: dark rectangle on light background, photocell arrangement same as *B*. Direction of movement across photocells is shown by arrows; turnaround point is indicated by triangle. L, response to light edge; D, response to dark edge. Time is left to right throughout. To facilitate comparisons, thin vertical lines are drawn for each edge centered on responses appearing in the first histogram.

S-TYPE CELLS. Our findings suggest that S-type cells with a variety of response characteristics can be distinguished in area 17 of the monkey. From the nature of their responses several inferences may be made regarding the organization of visual cortex. Qualitatively we could discern seven distinct cell types from our total sample of 245 S-type cells. An example of each cell type will be shown.

Figure 2 shows the simplest response we obtained to moving stimuli from S-type cells. This cell discharged only to a dark edge traversing the field and did so only in response to one direction of movement. The stimulus was moved at right angles to the axis of orientation so as to elicit the optimal response. Figure 2,1 shows the response to a white, 1° square. In Fig. 2,2, stimulus contrast is reversed; a black 1° square is swept across the receptive field. In both cases response occurs to light decrement, that is, to the dark edge only. In the drawing of this figure and subsequent ones, the original 256 bins in the computer display were reduced to 128 by combining adjacent pairs of bins.

In Fig. 2,3 the response property of this cell to moving stimuli is drawn in schematic manner. It shows the approximate size of the field and the kind of response elicited. The arrow indicates that the response was unidirectional. This unit may be described then as a unidirectional S-type cell, sensitive to a dark edge. This cell responded vigorously to the turning off of a thin rectangular light bar flashing in the center of the field, as shown in Fig. 3,1. Flashing this stimulus anywhere but in the center of the field produced no response at all. A large rectangle centered on the field, when flashed, also failed to elicit any response. However, when the center-activating region was continuously illuminated, the superimposed flashing of a large rectangle did evoke a response to its onset. These observa-

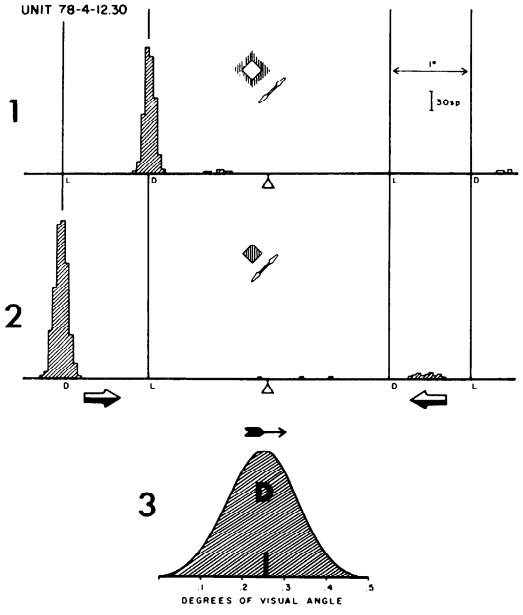

FIG. 2. Unidirectional S_1-type cell located 3° from the center of the fovea which, with moving stimuli, responds only to a dark edge. 1: response to a 1° light square. 2: response to a 1° dark square. Arrows indicate direction of movement across receptive field. Extent of stimulus movement: 3° in each direction, turnaround point indicated by triangle. Velocity: 2°/s. Histogram time is left to right throughout. Vertical lines indicate position on the histogram of the response that a single photocell would give to each edge. The position of these lines has been adjusted for unit response latency. The total number of bins across equals 128, reduced from the original 256 by adding adjacent bins. Number of trials per histogram, 30. L, light-edge response; D, dark-edge response; sp, spikes. 3: schematic drawing showing size and approximate spatiotemporal response properties of the receptive field. Arrow indicates direction of movement across field: the upper part of this figure depicts response to movement in one direction and the lower part response to movement in the opposite direction.

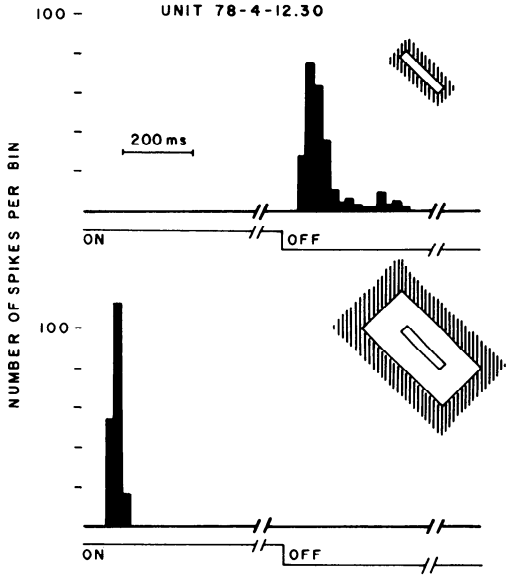

FIG. 3. Flash response of unit in Fig. 2. Top histogram shows response to a thin bar flashed in the center of the receptive field. Bottom histogram shows response to a large rectangle which was flashed while the center was continuously illuminated. Flashing of this same large rectangle without the small rectangle tonically illuminating the center did not elicit a single response in 30 trials.

tions suggest that the cell has a surround which is opposite in sign to the center. This surround region, however, is unresponsive to moving stimuli and to small stationary flashing spots. This cell is similar to LGN cells in that it has an antagonistic center-surround organization; the surround can be potentiated by illuminating the center region. It is also similar to LGN units in that in its central activating region it responds only to one sign of contrast. However, in contrast to units in the LGN, this S-type cell is orientation and direction selective, has low spontaneous activity, and discharges to moving stimuli only while a dark edge moves across the activating region of the field. Cells of this sort are common in area 17 of the monkey, and their counterpart, cells responding to a light edge only, are equally numerous. Of the 245 S-type cells studied, 67 were of this type; 34 had light fields and 33 had dark fields. Over 80% of them were unidirectional. We called these S_1 or single-contrast cells.

Figure 4 shows the response properties of another cell. It responded to both a light edge and a dark edge. The responses were elicited from two different regions in the field, as is evident from the different locations of the peaks in Fig. 4,1 and 4,2. Had they been in the same place, the responses would have centered on the vertical lines which show where a photocell located in the center of the field would have responded to each edge of the stimulus (Fig. 1A).

Figure 4,3 shows the schematic organization of this cell to a moving stimulus, demonstrating spatially separate light- and dark-activating regions. Both of these regions appear to be excitatory since contrast reversal does not alter the response to each edge. Only the temporal sequence of events changes because of the way the stimulus edges of opposite contrast move across the two subregions (see Fig. 1). The centers of the two regions are 0.29° apart. When stationary

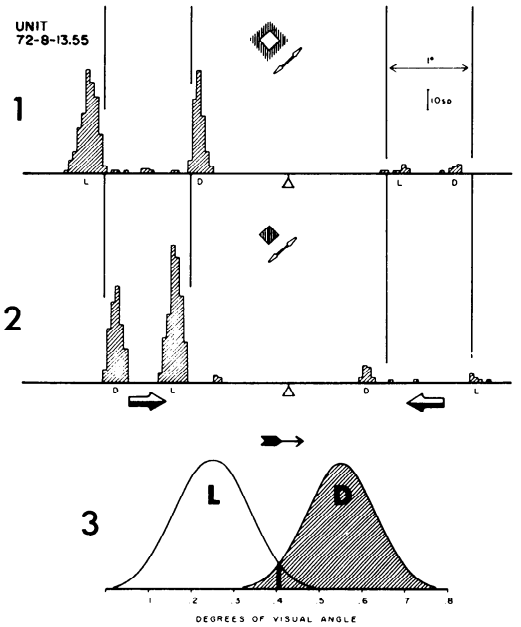

FIG. 4. Unidirectional S_2-type cell with separate subfields for light- and dark-edge responses. 1: response to a 1° light square. 2: response to a 1° dark square. 3: schematic drawing of receptive field showing size, separation, and directionality of the two subfields. The two subfields responding to opposite contrast respond to the same direction of movement (all parameters as in Fig. 2).

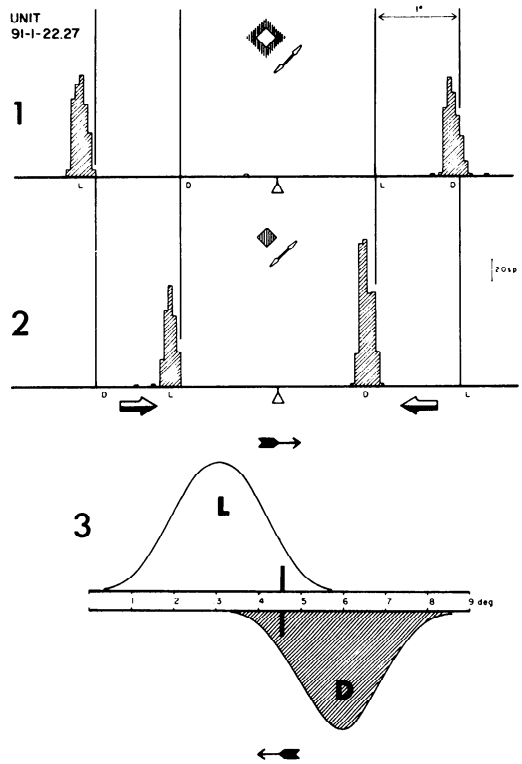

FIG. 5. S_3-type cell demonstrating interaction between contrast and direction. 1 and 2: responses to 1° light and dark squares. 3: schematic drawing of spatiotemporal response. The two subfields responding to opposite contrast also respond to opposite directions of movement.

flashes are used a similar spatial separation of the light region (on-response) and dark region (off-response) is revealed. The cell is essentially unidirectional. We called these S_2 or double-field cells; 47 units in our sample had this property.

The cell in Fig. 5 shows another commonly occurring property in the cell population of area 17 of the monkey. This cell responds to both light and dark edges, but the direction of the response is affected by contrast. Both the light and the dark edge responses are unidirectional, but they are specific for opposite directions of motion. The locations of these responses are spatially separate, as shown in the schematic spatiotemporal drawing in Fig. 5,3, where the upper part of the figure shows response to movement in one direction and the lower part, response to movement in the other direction. The spatial separation between the two regions can be derived two ways. It can, first of all, be determined by hand plotting using slowly moving edges or small stationary flashing spots. Second, it can be calculated. This calculation, however, must take into account the response latency of the discharge. This we typically obtained by measuring response latency to flashing stimuli of equal intensity. In some cells latency was calculated from responses obtained to different stimulus velocities, as described by Bishop, Coombs, and Henry (1).

For this cell, then, the light region is activated by one direction of movement and the dark region by the other. Reversing the sign of contrast between the stimulus-background does not alter this relationship. We called these S_3 or interaction cells because they demonstrate an interaction between direction and contrast. Such units may be thought of as responding best to a single edge moving back and forth across the field which, for this cell, has the light region on the left and the dark region on the right side. When the contrast is reversed, moving the edge within the field elicits no response. When tested in this fashion this is exactly what happens; 36 cells in our sample had this kind of interaction between contrast and direction.

Figure 6 shows another common S-type cell. It is one which discharges to a dark edge in both

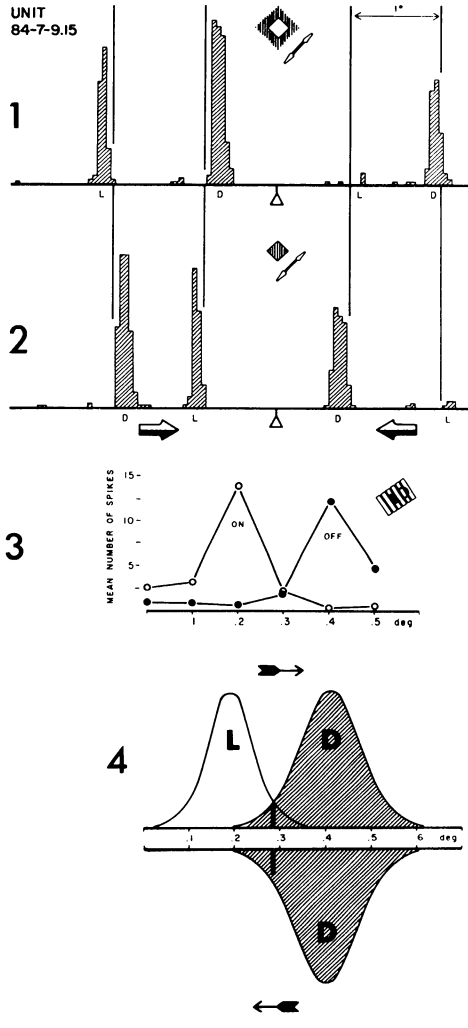

FIG. 6. S_4-type cell with unidirectional light edge and bidirectional dark-edge responses. 1 and 2: responses to light and dark 1° squares. 3: response to a 0.09° bar flashed in different locations. Open circles are response to onset of light; closed circles show off-response. 4: schematic drawing of receptive field.

directions but to the light edge in only one direction. This occurred in the same manner whether one moved a light square on a dark background (6,1) or a dark square on a light background (6,2) across the field.

Figure 6,3 shows the results of flashing a stationary 0.09° light bar in various parts of the receptive field. The light bar was flashed in six different locations 20 times each in random order. The mean number of responses are plotted for the first 250 ms after the light is turned on and off. These data clearly show the separate spatial locations of the light (on) and dark (off) response fields. The cells shown in Figs. 4, 5, and 6 have similar spatial arrangements. The directionality of the response among these cells is quite different, however, and is not predictable from the maps obtained with the stationary flashing stimuli.

The schematic diagram shows the spatial arrangement and relative response amplitudes of the regions of this field. The light area is unidirectional. The dark area may be thought of as a single bidirectional subregion or as two subregions, one responding in one direction and the other responding in the opposite direction. Complementary cells which have bidirectional light and unidirectional dark areas are also common. We have a total of 31 such asymmetric cells in our sample, 14 bidirectional for light and 17 bidirectional for dark. These were called S_4 or U-B cells, where U stands for unidirectionality for one contrast and B for bidirectionality for the other contrast.

Figure 7 shows a cell which produces a bidirectional response for both light and dark edges. Both of the light areas and both of the dark areas appear to be in the same location for the two opposite directions of movement; 21

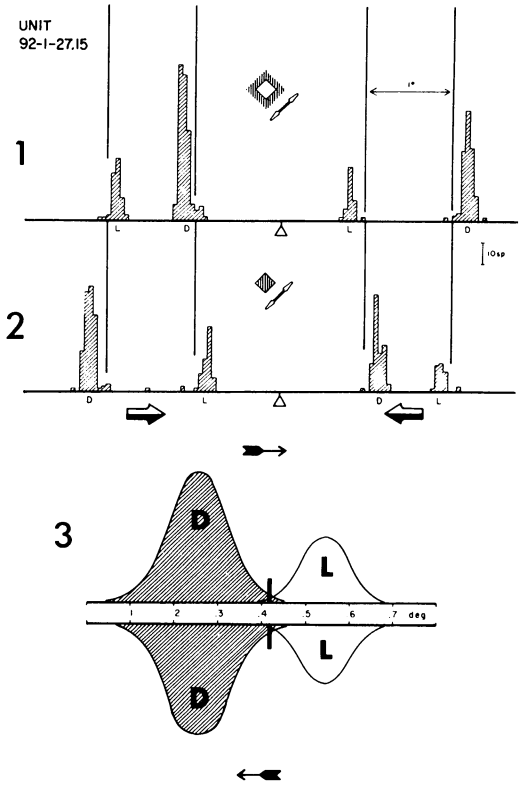

FIG. 7. S_5-type cell with bidirectional light and dark responses.

S-type cells had this characteristic with some variability in the location of the fields as a function of direction of movement, and were called S_5 or B-B cells.

The cells shown so far are relatively common in area 17 of the monkey.

Figure 8 shows a less common cell type with rather interesting properties. Because of the complexities of the response and the size of the receptive field, the data shown were obtained by moving only a single edge across the field, with the contrast of the light and dark regions reversed for Fig. 8,1 and 8,2. The field was also carefully hand plotted to verify the relationship between the light- and dark-activating regions.

The schematic drawing in Fig. 8,3 shows two sets of light and dark regions which are located in different places depending on the direction of movement. Five cells of this type were observed in our sample, and were called S_6 or double interaction cells because of the two regions of interaction between direction and contrast. Most cells with this kind of spatial arrangement produce both on- and off-responses to flashing spots throughout their receptive fields. For this reason, if they were mapped only with stationary stimuli they could be mistaken for CX-type cells.

Using single edges again, Fig. 9 shows a cell in area 17 with a bidirectional response, which, in both directions, shows three activating regions; a central dark edge region flanked by light regions. The first subfield responds well to left-right movement; in the opposite direction this region is barely observable; 17 cells in our sample had multifield properties of this sort, and were called S_7 or flanked-field cells. The subfields of some of these cells could not be activated with both directions of movement. Thus some cells had a tripartite field in one direction and only a bipartite field in the opposite direction.

The cells we have considered up to now had relatively distinct properties. It would be misleading, however, to claim that all S-type cells were as well defined as these. We have found a minority of S-type cells with intermediate characteristics, suggesting that the various S-type cells, inasmuch as they fall into groups, do not form unique categories. Two examples of such cells appear in Fig. 10. The first (Fig. 10A)

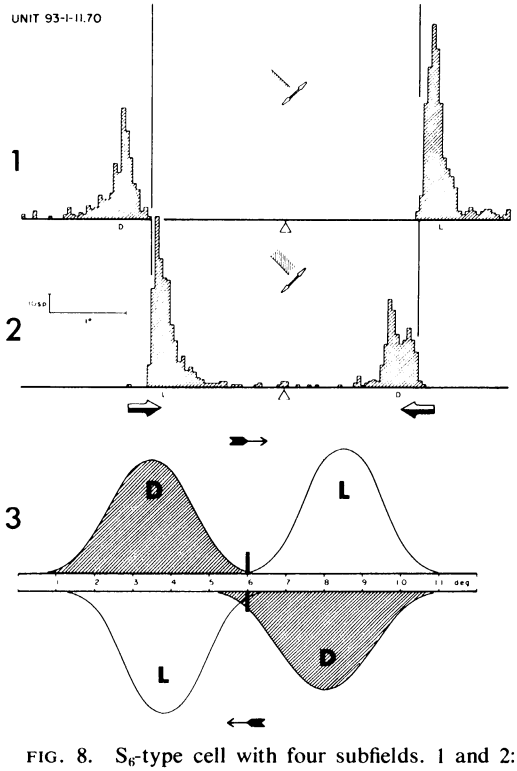

FIG. 8. S_6-type cell with four subfields. 1 and 2: responses to moving single edges. 3: schematic drawing showing that light and dark edge subfields are in different locations for opposite directions of movement.

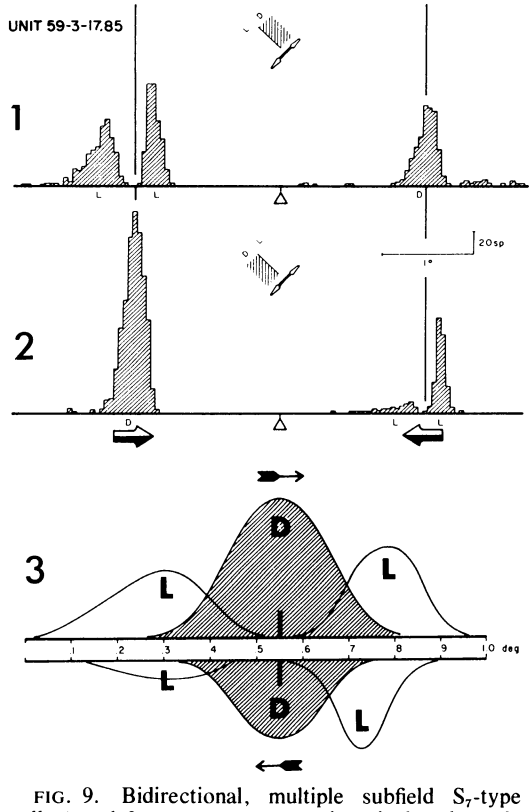

FIG. 9. Bidirectional, multiple subfield S_7-type cell. 1 and 2: responses to moving single edges. 3: schematic drawing of receptive field.

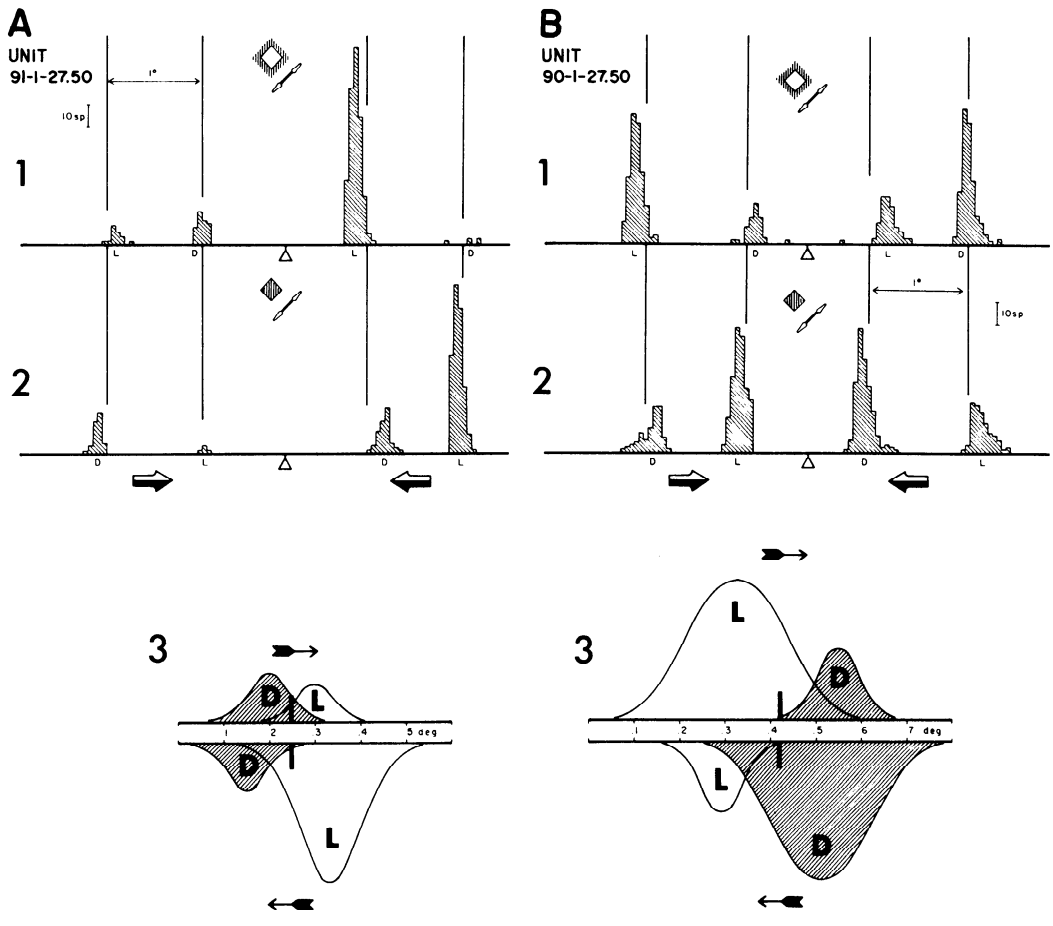

FIG. 10. Two examples of S-type cells with properties which fell in between some of those previously shown.

is one which responds predominantly to one edge; additional fields are evident, however, placing it in between a single-field S_1-type cell (Fig. 2) and an S_5-type cell (Fig. 7).

In Fig. 10*B* an example is given of a cell whose properties fall between an interaction (S_3) cell and a cell responsive to both light and dark edges in both directions (S_5).

For none of the S-type cells we studied was it possible to predict the directionality of the response reliably on the basis of the receptive-field map obtained with stationary flashing spots.

CX-TYPE CELLS. Cells which responded to both light and dark edges throughout their activating region and showed no interaction between direction of movement and stimulus contrast were classified as CX type. There were 342 CX-type cells in our total sample of 1,125 units.

Figure 11 shows a unidirectional CX-type cell. It has a relatively large receptive field as shown both with moving edges and with flashing stationary targets (Fig. 11,3). The data and the schematic drawing demonstrate overlapping light and dark regions.

Figure 12 shows a similar cell although with low spontaneous activity and a smaller field. This unit is bidirectional with superimposed light and dark regions in both directions.

The two cells in Figs. 11 and 12 conform to the typical complex cells so far described. The majority of CX-type cells are of this sort. We have found, however, that a number of these cells had rather small fields. Such a cell is shown in Fig. 13. By our criteria this is a CX-type cell, yet its field is no larger than that of S-type cells in the same region of the visual field. A small degree of interaction between contrast and direction, typical of S_3-type (interaction) cells, is also evident in this figure.

INHIBITORY RESPONSES OF S-TYPE AND CX-TYPE CELLS. In the cells described so far the schematic drawings were derived from the prin-

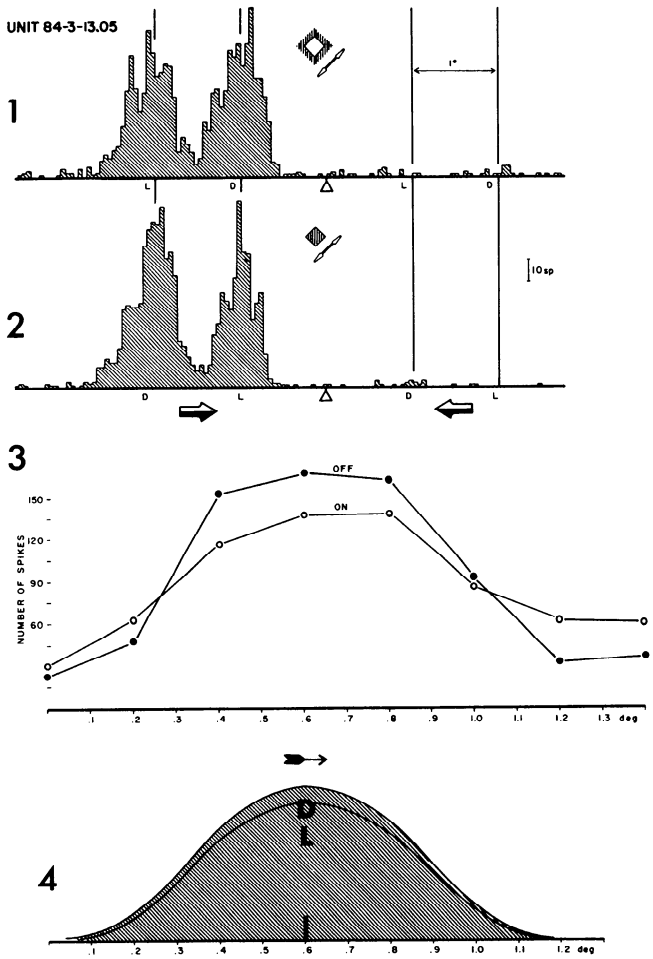

FIG. 11. Unidirectional CX-type cell.

cipal excitatory responses to increase or decrease in energy level produced by either moving edges or stationary flashing stimuli. In this section we will deal with the inhibitory responses in S-type and CX-type cells as observed on the basis of a decrease in responsiveness, which presumably reflects inhibitory action.

Bishop, Coombs, and Henry (2) have shown that the inhibitory side bands of simple cells in cat's visual cortex, in contrast to the excitatory regions, can be mapped when the base-line response of these cells is increased by repeated stimulation of the excitatory field(s), while at the same time a moving stimulus is swept across the entire receptive field. This second stimulus inhibits the response of the cell when it crosses the inhibitory regions. Similar results have been obtained by Watkins et al. (20) who, instead of stimulating in the center of the field, increased the base line firing rate of these normally silent cells by injecting potassium ions near the cell.

The easiest way to observe such inhibitory responses is to take advantage of the relatively high degree of naturally occurring spontaneous activity that one can occasionally find in these cells. One S-type cell of this sort is shown in Fig. 14*A*. This cell had two excitatory subfields for each direction of movement (S_5 type), similar to the cell shown in Fig. 7. Stimulus-response histograms are shown to two different stimuli. In Fig. 14*A*,1 the response was elicited with 0.63° wide bar moving across the field at 2°/s in one direction. Two excitatory responses can be seen, one to the light and the other to the dark edge. Inhibition is evident before and after each response. In Fig. 14*A*,2 the bar was reduced to 0.27° in width, resulting in a summation of the light and dark edge responses. The inhibition to

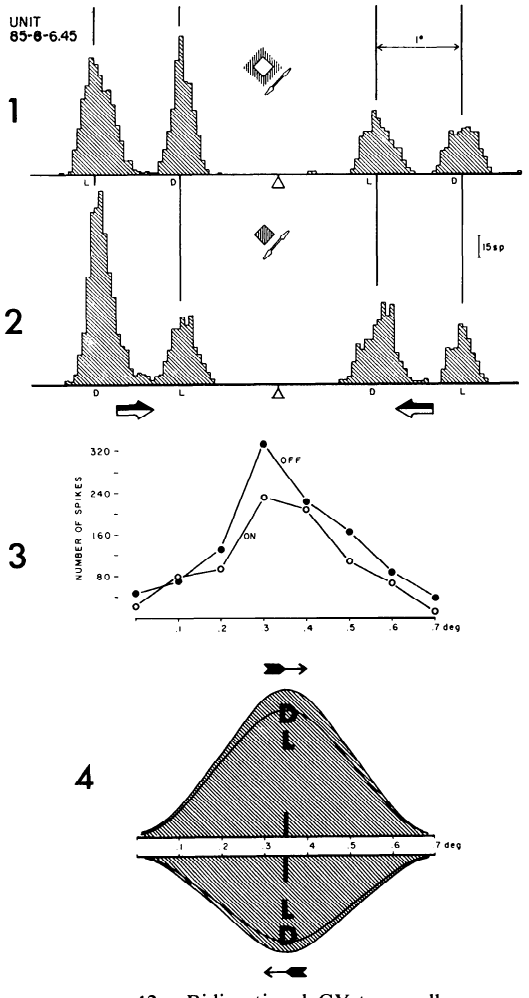

FIG. 12. Bidirectional CX-type cell.

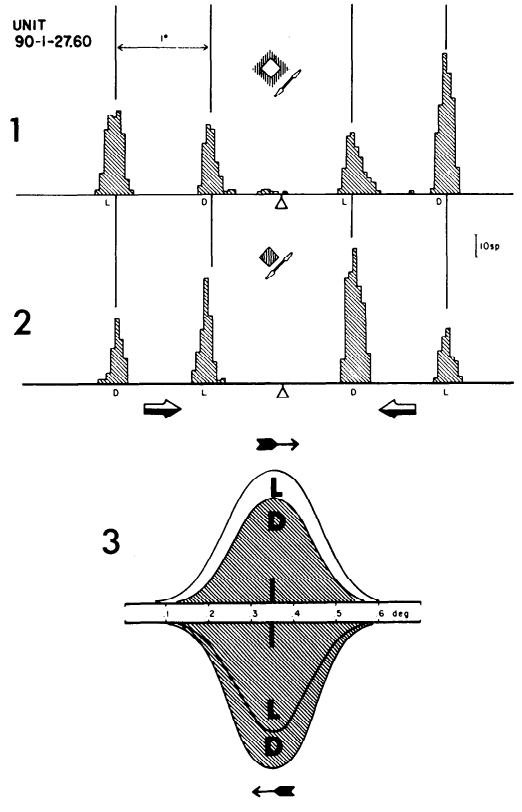

FIG. 13. Bidirectional CX-type cell with small spatially overlapping light and dark subfields showing a small degree of interaction between direction and contrast.

either side of the excitatory areas is even more pronounced.

A detailed study of this cell, using various stimuli, yielded the schematic drawing shown in Fig. 14*A*,3. It appears that each region has its own inhibitory side bands. While it was clear that the excitatory light and dark areas were not in the same place for the two directions of movement, it was not really possible to determine whether this was also true for the inhibitory side bands. In the S-type cells which we tested in this manner or with Bishop's method (2), such inhibitory regions were frequently evident.

Similar examination of CX-type cells failed to disclose analogous inhibitory side bands. Figure 14*B* shows a direction-selective CX-type cell with moderate spontaneous activity. Movement from left to right, as represented in this figure, shows only excitation to light and dark edges. In the opposite direction, however, a small degree of inhibition is evident when the stimulus moves over the center of the field. This kind of inhibition was seen in many directional CX-type cells.

TONIC CELLS. Another group of cells, which we believe forms a rather distinct third class in monkey striate cortex, comprises those neurons which are excited by one sign of contrast and are inhibited by its opposite. These cells, which were called T-type cells, respond to changes in illumination in a relatively sustained (tonic) fashion and the response is not contingent on having a contour within the receptive field. Typically they are poorly or not at all oriented, and some fire preferentially to colors without being sharply selective. They appear to be similar to LGN cells, but some of them are binocular.

Two examples are shown in Fig. 15. The first of these (15*A*) is excited by light and inhibited by dark. The opposite is true for the second cell

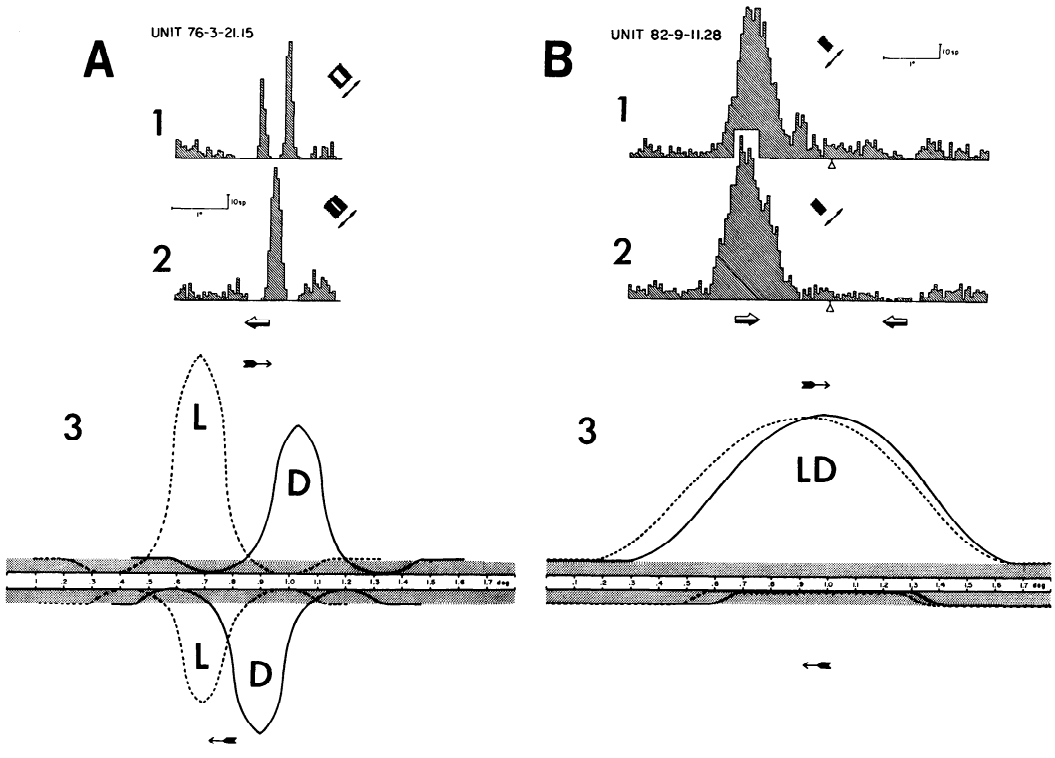

FIG. 14. Excitatory and inhibitory responses of an S-type and a CX-type cell. *A*: bidirectional S-type cell with two subfields in each direction. A,1: response for one direction of movement to a 0.63° wide bar. A,2: response to a 0.27° bar showing a summation of excitatory light and dark regions. *A*,3: schematic drawing of receptive field. Stipled area shows maintained activity. The response profile of subfields to light and dark edges is shown for both directions of movement. *B:* unidirectional CX-type cell. *B*,1 and 2; responses to single edges in both directions of movement, *B*,3: schematic drawing of receptive field.

(Fig. 15*B*); 49 cells in our sample were of this type.

COLOR SELECTIVITY. Only a small percentage of the cortical units in our sample were color selective. The characteristics of such cells were similar to those described recently by Dow (5) and earlier by Hubel and Wiesel (10), and hence were not studied in detail. Most of them could be classified as S-, CX-, or T-type cells, although color-coded S-type cells were especially rare. It was our impression that color-selective cells occur in batches; when we found one in a penetration, succeeding cells were similarly color selective. It is, therefore, possible that color is represented in a columnar fashion in striate cortex.

Shape of receptive field and response to stimuli of various lengths

We employed a variety of methods to assess the size of single-cell receptive fields. When stationary flashing spots were used, the majority of cells, including S type, yielded roughly circular or elliptical fields, the long axis of which did not necessarily fall along the axis of orientation.

Receptive-field size can also be plotted with moving stimuli. This works well with movement at right angles to the axis of orientation. If the stimulus moves at less than about 3°/s, the cell will fire as long as the edge is within the activating region. Hence the size of the response is a good index of receptive-field size along this dimension, which we will refer to as the width of the field.

Plotting the size of the field along the axis of orientation, which will be referred to as its length, is more difficult with moving stimuli. This may be done by moving an optimally oriented edge (at right angles to the axis of orientation) progressively toward the center of the field from the periphery. Under these conditions it is not uncommon that the edge has to be moved beyond the center of the field from either side. Thus one may find that having marked the

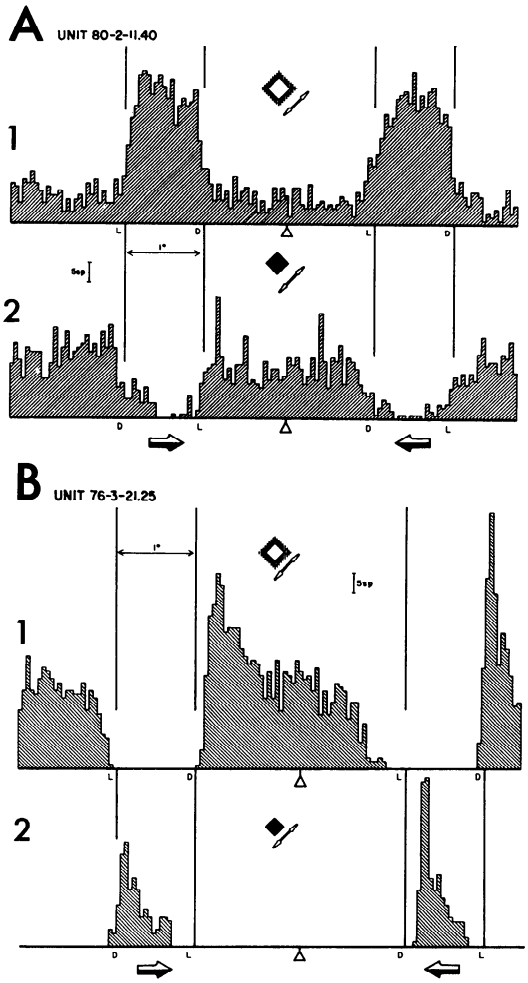

FIG. 15. Two T-type cells. *A*: excitation to light increment. *B*: excitation to light decrement.

location of the upper border of the field on the tangent screen as the stimulus was advanced beyond the marked point, creating what might be called a "negative field." What this probably means is that a certain degree of summation is required along the axis of orientation of the field before a response can be elicited (3).

Another approach for measuring the length of the receptive field is to increase the length of a stimulus centered in the field in small steps until the response asymptotes or begins to decline. The size of the stimulus at this point should be equivalent to the length of the activating region. This method also allows one to determine to what extent a unit might be inhibited as the length of the stimulus is progressively increased. Such a measure has often been used to place cells in the hypercomplex category (9). In the cat's and monkey's visual cortex these cells have been shown to have inhibitory regions along the axis of orientation so that once a stimulus had been increased beyond a certain length the response is attenuated. Units with such "end stopping" are classed as hypercomplex cells. Simple and complex cells in the cat are not inhibited in this manner (9), but their summation properties to stimuli of increasing lengths appear to be different. Simple cells have been shown to summate while complex cells are less apt to do so.

In order to obtain a measure of receptive-field length, summation, and end stopping, we moved optimally oriented slits of various lengths across the receptive fields of single cells. Most commonly the stimulus lengths used were 0, 0.1, 0.2, 0.4, 0.8, 1.6, 3.2, and 6.4° of visual angle, the first being a control no stimulus condition. These stimuli were swept across the receptive field in a randomized order for 10 or 20 trials per stimulus condition utilizing our computer-driven optic display. Stimulus velocity was typically around 2°/s.

The results for a strongly stopped unit are shown in Fig. 16 in the form of a set of histograms and a curve for one direction of stimulus movement. This unit had low spontaneous activity. Responses rapidly summated with increasing stimulus length reaching a maximum with the 0.8° stimulus. With further increases in stimulus length, the response declined so that the 6.4°-long stimulus elicited only 15% of the maximum response. This ratio can be used as an index of end stoppage for each cell:

$$\text{stopping index} = 100 - \frac{\text{6.4° stimulus response}}{\text{best response}} \times 100$$

Figure 17 shows a representative sample of nine S-type and nine CX-type cells studied in this fashion from a sample of 572 units. All the cells shown in the left-hand column of this figure had spatially separate light and dark regions and were, therefore, classified as S-type cells. Cells classified as CX type had overlapping light and dark regions. We wish to make the following points about this figure: *1*) The slopes of summation among both S-type and CX-type cells are highly variable and show no consistent differences for the two types. Thus, these cells in the monkey do not seem to differ dramatically in terms of summation. *2*) There is considerable variation in the extent to which cells are stopped (index of stoppage at right extreme of each graph). S-type and CX-type cells do not differ in this respect. The relatively continuous variation in the degree of inhibition among these cells suggests that the criterion of end stopping may

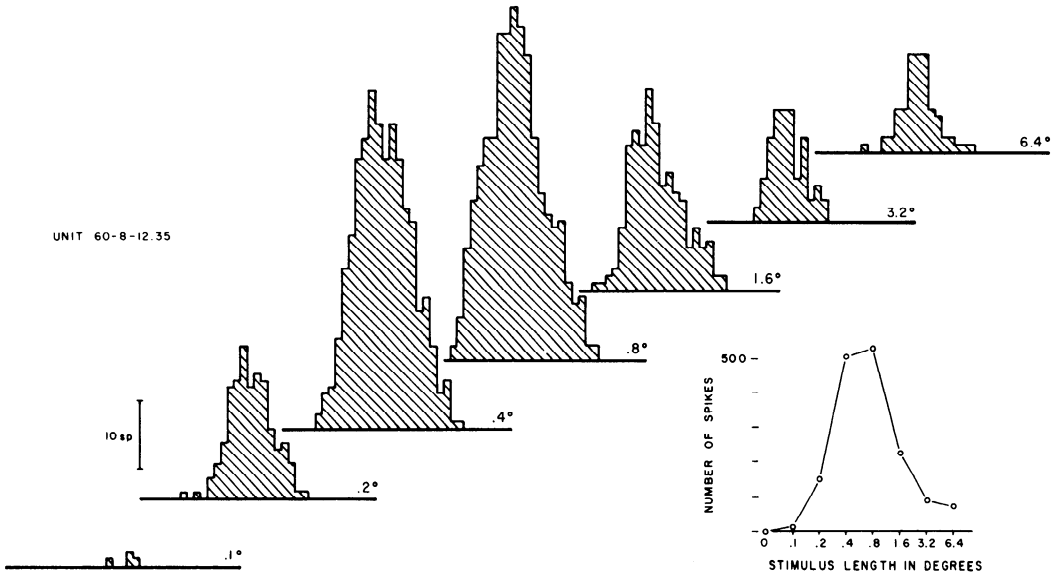

FIG. 16. Response of a strongly stopped CX-type unit with a receptive-field width of 1° to stimuli of increasing length. Histograms are for one direction of movement, reduced from 128 to 32 bins.

not adequately distinguish a separate class of hypercomplex cells in the monkey striate cortex. We will examine this question in more detail in the next section. *3*) The maximum response occurs anywhere from 0.2° to 6.4°. This would suggest that the length of the receptive field is often indeed greater than its width, a finding which does not correspond with that obtained using other indexes of receptive-field length.

Distributions based on quantitative measures

The data described so far have been primarily in the form of individual examples of cell responses. In order to assess the validity of classificatory schemes and to obtain a general picture of single-cell function in visual cortex of the monkey, we examined the distribution of these cell properties in a large sample.

Table 1 gives an overall account of the number of cells studied and the gross categories into which they were placed. The criteria used for classification of S-type cells appear in the legend of this table. These criteria permitted us to classify all but 21 S-type cells. This suggests that the cells we distinguished do not form continuous distributions in their properties as already noted.

We will next turn to a number of quantitative measures to determine to what extent the basic criteria which had been used in classifying cells might be applicable for single cells in monkey striate cortex.

RECEPTIVE-FIELD WIDTH. Our recordings were undertaken in an area representing a relatively narrow range of the visual field, spanning 2°–5° from the fovea. Figure 18 shows the distribution of overall receptive-field widths in this region. The width of the field was obtained with stimuli moving at right angles to the axis of orientation. The duration of the moving edge response was measured at the half-height point between the base line and the peak of the response (area containing approximately 75% of the response). For cells having spatially separate response regions, field width was measured to include the entire area these regions covered.

To assess the validity of this method we compared the receptive-field width of 50 units using two different measures; the one just described and one derived on the basis of flashing a 0.09° bar in various parts of the receptive field using the computer-driven display. These two measures yielded similar results, showing a correlation of +0.69. This relationship would probably have been even better had we been able to activate the field reliably with thinner bars, thereby increasing the sensitivity of the flash measure. The receptive-field sizes derived using moving stimuli also corresponded closely with our hand plots.

The data in Fig. 18, obtained from 589 cells, show a skewed distribution of sizes which vary over almost a 20-fold range. Only a relatively small fraction of this range is due to variation in retinal eccentricity. Even in a vertical penetration, where receptive fields scatter only over a small area, field size can vary over a large range, with the receptive fields of cells in layer 4 being

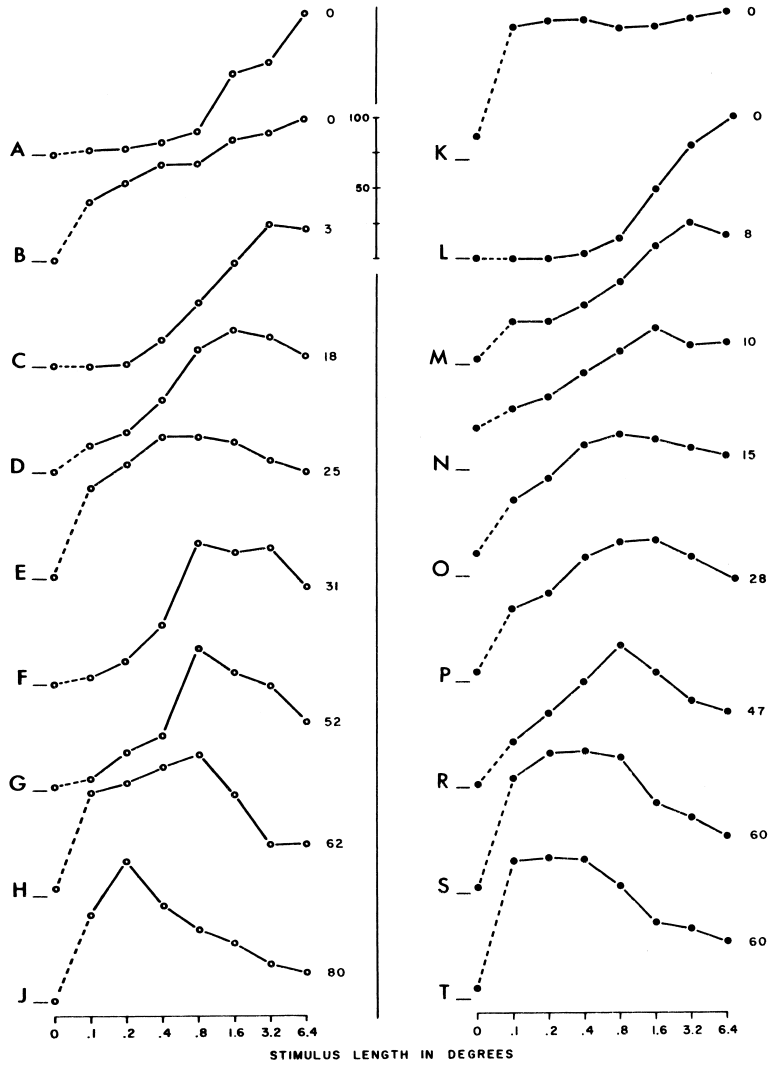

FIG. 17. Length tuning curves. Left-hand column (*A–J*): S-type cells with spatially separate light and dark regions; right-hand column (*K–T*): CX-type cells. Responses have been normalized. Numbers at right of each curve are stopping index derived by the formula: 100 − (6.4° stimulus response/best response) × 100. Horizontal lines at left show the starting point for each graph.

small and those in layers 5 and 6 often being very large (10, 13).

Figure 18 also shows that CX-type cells, on the whole, have larger receptive fields than do S-type cells. This difference is statistically significant ($F > 0.001$), although there is clearly considerable overlap in these populations. This is due, in part, to the fact that the measure of overall receptive-field size for S-type cells includes the light and dark regions as well as the separation between them. Thus, while each of the subfields may be quite small, the overall field, by virtue of the spatial separation of these subfields, might be considerable. We therefore assessed the size of one subfield for both types of cells. The field responding to the light edge was used for this measure except where the dark field responded more vigorously, in which case the size of the latter was measured. In Fig. 19 the results of this analysis, based on 144 S-type cells and 258 CX-type cells, show a clear-cut difference between them. Of the S-type cells, 88% had subfields 0.3° and smaller; only 11% of the CX-type cells had subfields this small. The overall distribution of the CX-type cells is similar to that given in the previous figure.

Quantitative data of this sort allow one to obtain an estimate of the adequacy with which

TABLE 1. *Account of cells studied*

Total distribution	
1. S-type cells	245
2. CX-type cells	342
3. T-type cells	49
4. Unoriented cells	62
5. Unresponsive cells	130
6. Unclassified	297
Total	1,125
S cell breakdown	
1. Response to one edge	
a. Unidirectional, L only	28
b. Unidirectional, D only	28
c. Bidirectional, L only	6
d. Bidirectional, D only	5
2. Response to two edges	
a. Unidirectional	47
b. Bidirectional	21
c. L in one direction, D in other	36
d. L in both directions, D in one	14
e. D in both directions, L in one	17
3. Multiple responses	
a. Three fields	17
b. Two opposite direction fields	5
4. Uncategorized	21
Total	245

Criteria for S-type cell classification (calculations for these criteria are described in RESULTS, *Distribution based on quantitative measures*. 1: contrast measure is less than 15 (response to dark edge only) or more than 85 (response to light edge only) (S_1 type). 2a: two separate subfields where $15 < C < 85$, interaction index is greater than 10, overall directionality is less than 50, and the difference between directionality for the light edge (D_L) and that for the dark edge (D_D) is less than 50 (S_2 type). 2b: Two separate subfields, $15 < C < 85$, $I > 10$, overall directionality more than 50, and $|D_L - D_D| < 50$. (S_5 type). 2c: $I \leq 10$, $15 < C < 85$, D_L and D_D are both ≤ 30 in opposite directions (S_3 type). 2d, e: $15 < C < 85$, $I > 10$ and $|D_L - D_D| \geq 50$ or $D_L(D_D) > 30$ if $D_D(D_L) < 10$ (S_4 type). 3a: Three subfields alternating light and dark in at least one direction (S_7 type). 3b: Two separate subfields where each meets the criteria for 2c (S_6 type). Unclassified: not enough data to classify but enough separation of subfields to be called S-type cells.

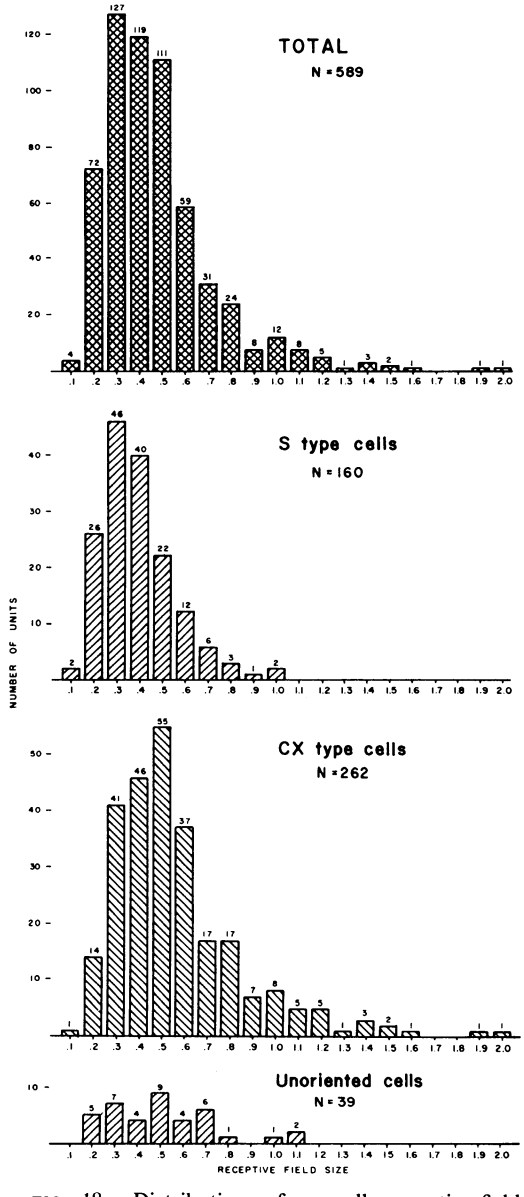

FIG. 18. Distribution of overall receptive-field width.

S-type and CX-type cells can be differentiated. This can be expressed in terms of a potential misclassification between these classes. Choosing the best criterion to differentiate S-type from CX-type cells on the basis of subfield size results in a misclassification of 18% of the population. Using the same criterion for overall receptive-field size, 34% of the cells are misclassified.

SPATIAL SEPARATION BETWEEN SUBFIELDS. CX-type cells and many S-type cells respond to both light and dark edges. By definition, the prime distinction between these classes of cells is that the subfields of S-type cells are spatially separate, while those of CX-type cells are spatially superimposed. To check on the validity and the classificatory power of this distinction we compared the extent of spatial overlap between the light and dark subfields in S-type cells with bipartite fields and in CX-type cells. This was done by using the measure of receptive-field size and the center to center spatial separation between the subfields. The follow-

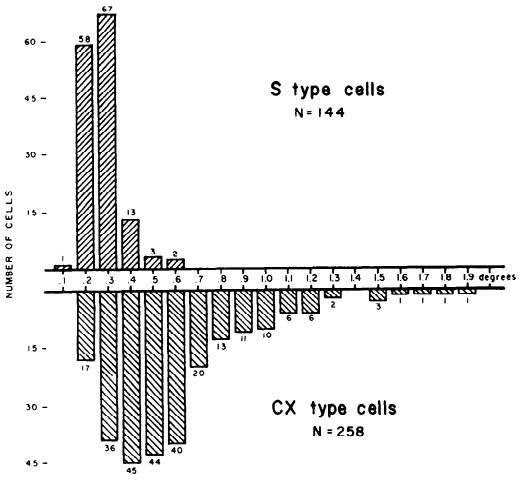

FIG. 19. Distribution of subfield widths for S-type and CX-type cells. The light-edge receptive field was used unless the dark-edge response was better.

ing formula was used to determine the extent of separation or overlap between the subfields:

$$\text{overlap} = \frac{1/2L + 1/2D + \text{center-to-center field separation}}{1/2L + 1/2D - \text{center-to-center field separation}}$$

where L stands for the receptive-field size of the light-edge response region and D stands for the receptive-field size of the dark-edge region. A value of 100 obtained this way is equivalent to a 100% overlap between the light and dark fields. A value of 0 indicates that the two subregions are immediately adjacent without overlapping. A negative value indicates a space between the subfields as determined by this measure.

Figure 20*A* shows the comparison between S-type cells with bipartite fields and CX-type cells. These data show that our criterion successfully discriminates these two types of cells, with only a few falling into a common area. A few S-type cells had subfields with an unresponsive region between them. This is somewhat exaggerated in Fig. 20 because receptive-field size was measured so as to include only 75% of the response area. For example, the value for the cell in Fig. 4 was −18 although it is clear that there is indeed a small degree of overlap between the subfields. By changing the receptive-field size criterion to the less reliable but more encompassing level of 90% of the response area, one would effectively shift the 0 point for S-type cells to the −20 region on the figure. This still leaves a number of cells which show an unresponsive area between the subfields.

These data suggest that the prime criterion used in differentiating S-type and CX-type cells is an effective one. Our analysis shows that choosing the best criterion to differentiate S-type from CX-type cells on the basis of subfield separation results in misclassification of only 4% of the

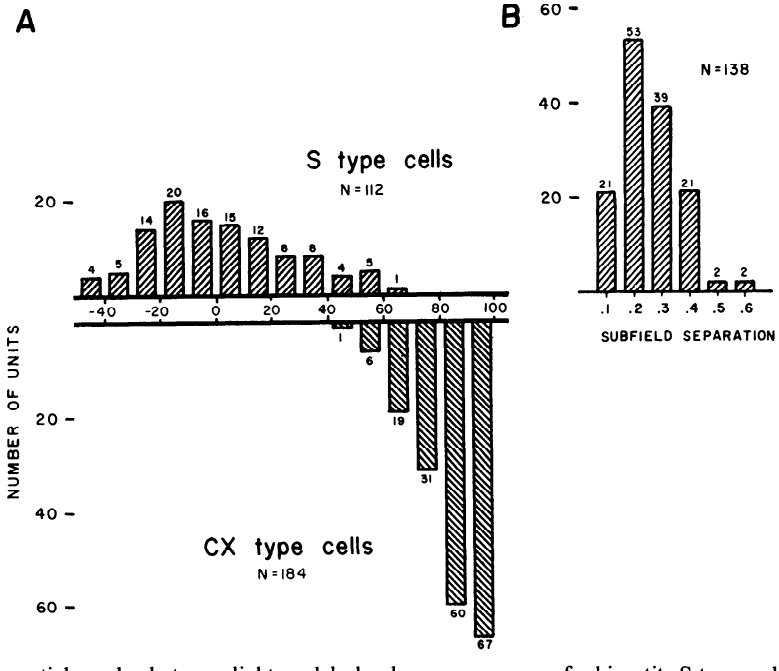

FIG. 20. *A*: spatial overlap between light- and dark-edge response areas for bipartite S-type and CX-type cells. *B*: center-to-center separation of subfields of bipartite S-type cells.

population. The overall differentiation of these two classes of cells may actually be even better, since this sample does not include the easily categorized single-contrast, S_1-type cells.

In Fig. 20*B* we plotted the center-to-center subfield separation of S-type cells in degrees. The majority of cells had 0.2–0.3° of center-to-center separation. The average spatial separation is about as great as the average receptive-field size of each subregion (see Fig. 19). CX-type cells are not shown in Fig. 20 because, with the exception of three cells, they would all fall into the 0–0.1 column.

We were also interested in determining for S-type cells the relationship between the size of the subfields and the degree of center-to-center separation between them (measured in degrees of visual angle). A correlation performed between these two measures using 135 S-type cells did not show a significant relationship ($r = 0.15$). Thus it appears that in our sample, which was restricted to a region 2°–5° from the fovea, the size of the subfields in bipartite field S-type cells and their spatial separations vary independently of each other.

DIRECTIONALITY. To determine the distribution of direction specificity, for each cell a count was made of the total number of responses elicited by moving edges in each direction to both signs of contrast based on 60 trials. An index of direction specificity was calculated by the following formula:

$$\text{index of directionality} = \frac{L\rightarrow + D\rightarrow}{L\leftarrow + D\leftarrow} \times 100$$

where the smaller number was always placed in the numerator. This measure does not reflect anything about absolute direction in the visual field but, instead, specifies the directionality of a cell to opposite directions of movement at right angles to the axis of orientation. A small value reflects a tendency for the cell to respond only in one direction of movement; such cells are thus considered predominantly unidirectional. A high value, such as 90–100, indicates that the cell responded equally well to both directions and, hence, could be called a bidirectional cell.

Figure 21 shows the distribution of direction specificity for 762 cells, of which 220 were classified as S type and 313 as CX type. The CX-type cells show a roughly bimodal distribution, suggesting that unidirectional and bidirectional cells may be considered as two separate subpopulations of CX-type cells. The distribution for S-type cells is skewed, strongly favoring unidirectionality. Since this sample includes cells which show an interaction between response to direction and to contrast (S_3 type), we attempted

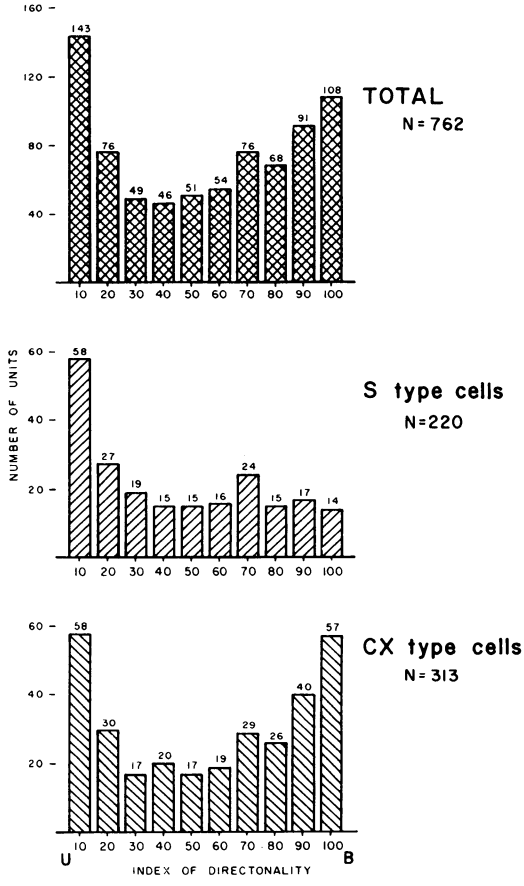

FIG. 21. Distribution of directionality. The index of directionality is 100 times the total response in the worse direction divided by the total response in the better direction. An index of 100 indicates a bidirectional cell; an index of 0 indicates a unidirectional cell.

to analyze the extent of directionality by reducing this confounding variable. We did this in two ways. First, we analyzed all single-contrast, S_1-type cells separately. Figure 22*A* shows this analysis from which it is clear that these cells are predominantly unidirectional. Second, we determined for all S-type cells the extent to which either a light or dark edge alone elicits a unidirectional response. The distribution derived in this manner is given in Fig. 22*B*. It shows that when the interaction between contrast and direction is reduced as a variable, the unidirectional properties of S-type cells are more apparent. This kind of analysis does not affect the distibution of complex cells as given in the previous figure because these cells (see also Fig. 24) show no interaction between contrast and direction.

CONTRAST. To assess the overall selectivity of striate cells for contrast, we counted the number

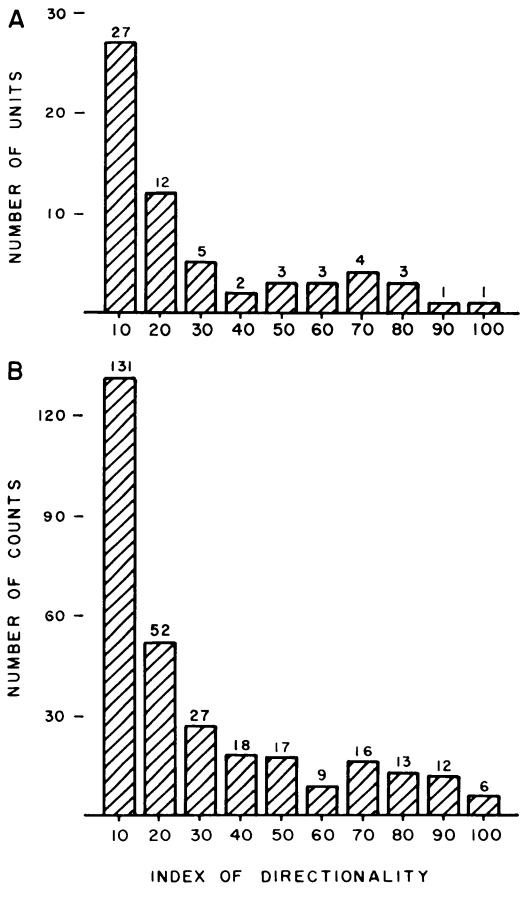

FIG. 22. Index of directionality for S-type cell subfields. *A*: units which respond to only one sign of contrast. *B*: directionality index distribution of single contrast subfields considered separately. The proportion of unidirectional fields increases when light and dark response subfields are considered separately.

of responses elicited by the light and dark edges separately, independent of direction of motion. These data were obtained, as described earlier (Figs. 1–13), by moving rectangular stimuli or single edges across the receptive field at right angles to the axis of orientation. An index of the contrast specificity of a cell was derived by the following formula:

$$\text{contrast specificity} = \frac{\Sigma L}{\Sigma L + \Sigma D} \times 100$$

where L and D stand for the responses elicited by the light and dark edges. An index value of 10 or less means that the cell responded almost exclusively to a light edge, while a value of 90 or more indicates a strong preference for dark edges. A score of 50 indicates an equal response strength to light and dark edges.

In Fig. 23 the data based on 654 cells show

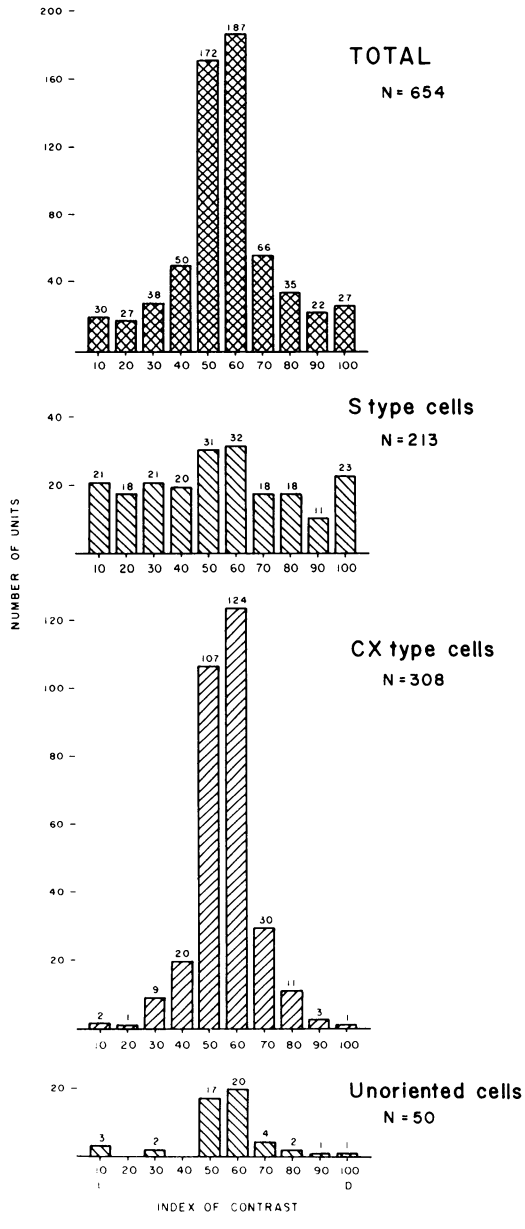

FIG. 23. Distribution of contrast dependency for total, S-type, CX-type, and unoriented units. The index of contrast = (response to light edge/response to both edges) × 100. An index of 100 indicates response to light only; a unit responding equally to light and dark has an index of 50; a dark response only gives an index of 0.

that the majority of cells in our sample responded fairly equally to light and dark edges. CX-type cells as well as unoriented cells show this tendency most strongly. By contrast, S-type cells are evenly distributed on the scale, with

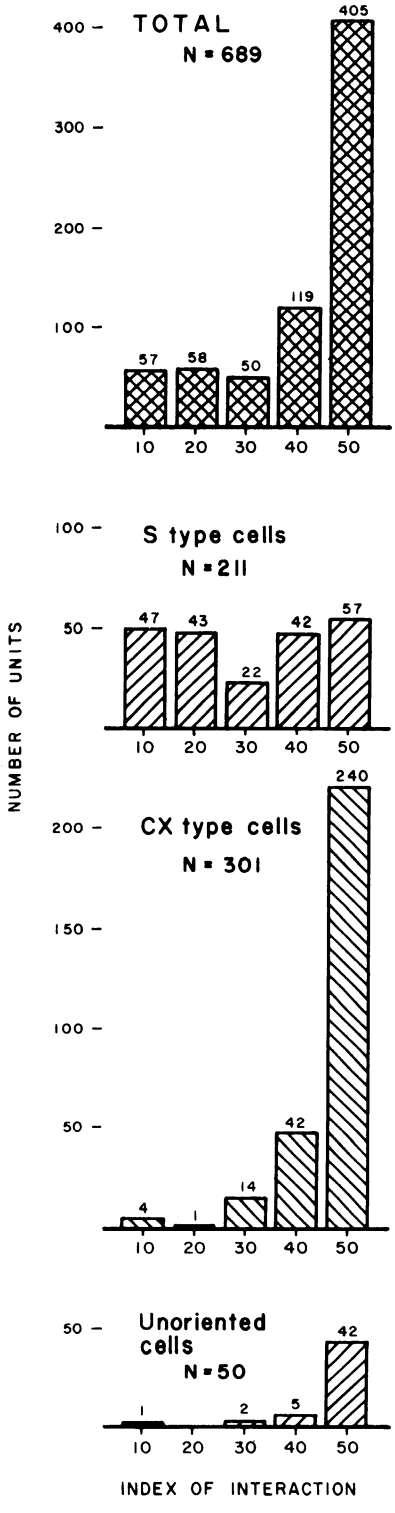

FIG. 24. Distribution of interaction between contrast dependence and directionality. The index of interaction (I) = (L→ + D← or L← + D→/total L + D) × 100. An I of 50 shows no interaction; a unit with an I of 0 responds to light and dark edges in opposite directions.

many cells responding only to one sign of contrast. Not included in this sample are the tonic cells, all of which respond in an excitatory fashion to only one sign of contrast.

INTERACTION BETWEEN CONTRAST AND DIRECTION. We have shown that some S_3-type cells exhibit a strong interaction between contrast and direction. To measure the distribution of this interaction, the same data, obtained by moving light and dark edges over the receptive field, were reanalyzed to obtain an index of interaction. This was computed for each unit using the following formula:

$$\text{interaction} = \frac{[L\rightarrow + D\leftarrow] \text{ or } [L\leftarrow + D\rightarrow]}{\text{total } L + D} \times 100$$

The smaller combination was used in the numerator. This measure ranges from 0 to 50, where a value near 0 reflects very strong interaction of the sort shown for unit *91-1-22.27* in Fig. 5, while a value near 50 would indicate no interaction.

Figure 24 shows the distribution of interaction values for 689 cells, of which 211 were classified as S-type, 301 as CX-type, and 50 as unoriented cells. These data show that CX-type cells, as stipulated, do not have a significant degree of interaction. S-type cells show some bimodality in their distribution, which is indicative of two subgroups, one showing a low and the other a high degree of interaction.

INHIBITION WITH INCREASING STIMULUS LENGTH. The measure for inhibition along the axis of orientation was obtained by sweeping bars of different lengths across the receptive field, as already described. Stopping index (stimulus length-response ratio) was calculated by dividing the response obtained with the longest stimulus (6.4°) by the optimal response. This fraction was multiplied by 100 and this value was subtracted from 100. If the cell's maximum response was elicited by the 6.4° stimulus, a value of 0 was assigned to that unit. Thus, a low value on this scale indicates an unstopped unit, that is, one which responds without being inhibited by increasing the length of the stimulus. A value near 100 indicates a cell which is strongly inhibited by stimulation of regions along the axis of orientation away from the receptive-field center.

The distribution for end stoppage shown in Fig. 25 was determined from the analysis of 572 cells, of which 129 were S-type, 226-CX-type, 78

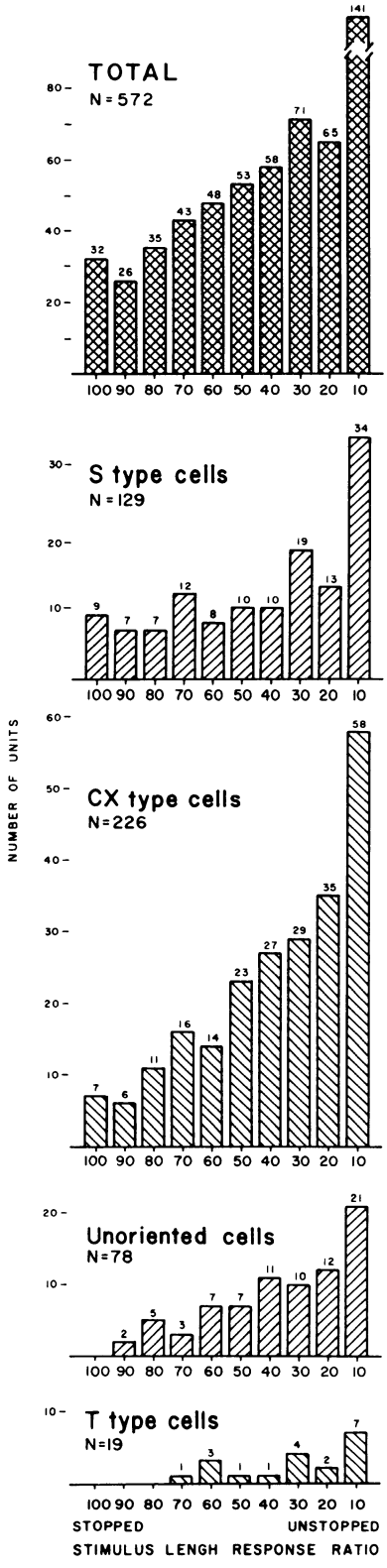

FIG. 25. Degree of inhibition as a function of increasing stimulus length. The measure of end stoppage (stimulus-length response ratio) was obtained by sweeping the receptive field with bars or edges of various lengths and applying the following formula: 100 − (response to best length/response to longest bar) × 100. Large values indicate strongly stopped cells.

were unoriented, and 19 were T-type cells. The distribution appears to be primarily unimodal with no clear difference between the classes. It is our impression on the basis of these data that this measure cannot be used to separate cells reliably into a hypercomplex category in the monkey.

In order to obtain an idea about the extent to which an analogue to end stopping is observable in the LGN, we also studied 16 cells in the same 2°–5° area of the visual field using similar methods. The index of stoppage for these cells was 15, 21, 22, 23, 27, 33, 38, 39, 43, 45, 49, 63, 65, 74, 75, and 100. It may be said that most LGN cells using this method show pronounced surround inhibition and, hence, demonstrate strong end stopping. In what sense end stopping represents a cortical transformation then is a problem. We will consider this question in the DISCUSSION.

SPONTANEOUS ACTIVITY. The last distributional measure deals with spontaneous activity, which in previous work has been shown to be lower for simple cells than for complex ones in the cat (1).

The mean number of discharges occurring with no stimulus in the receptive field was measured during the testing of various stimulus lengths. A 1-s time period was sampled randomly during these trials.

The distribution for spontaneous activity is given in Fig. 26. It shows that S-type cells have lower spontaneous activity than CX-type cells (mean for S = 1.2, for CX = 4.9). Yet there is a considerable overlap in population. Particularly evident is the fact that there are many CX-type cells which have low spontaneous firing rates. Choosing the best criterion to differentiate S-type from CX-type cells on the basis of spontaneous activity results in misclassification of 27% of the population.

Distribution of receptive-field properties of cells in cortical layers

Using lesions to mark electrode tracks, we identified the location of 201 cells in striate cortex.

Figure 27 depicts the reconstruction of part of a tangential penetration between two marker lesions in which 18 isolated single cells were recorded. Two cells were not held long enough to

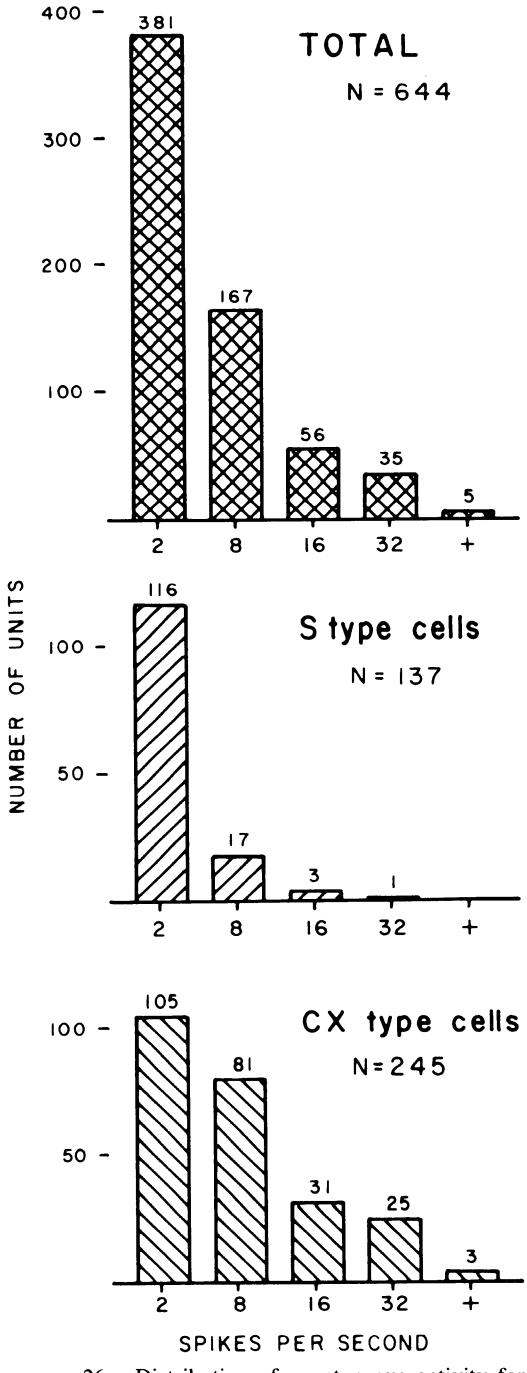

FIG. 26. Distribution of spontaneous activity for total, S-type, and CX-type cells.

be identified. Two were classified as tonic types (T), five as S type (*6, 7, 9, 15, 16*), and eight as CX type. The receptive-field organization of these cells in terms of optimal orientation, directionality, receptive-field size, and light-dark edge response is represented in the schematic drawings. The short, heavy line in the center of each schematic drawing represents the axis of orientation. The stimuli used to generate the data from which the drawings were derived were moved across the receptive field at right angles to the axis of orientation, as described earlier. The markings are in 0.1° steps. The main points to be considered about this figure are the following: *1*) Both S-type and CX-type cells can be found in layer 6. This is also true for T-type cells. *2*) Receptive-field size varies over a broad range among the cells in the two layers sampled in this pass. *3*) Nearby cells have similar orientations (12) but their directions can be 180° reversed. This is especially evident for the cells numbered 15 and 16. These two cells were recorded from simultaneously. *4*) The double-field S_2-type cell (7) has a small center-to-center separation, which with stationary, flashing stimuli might not have been discernible. This cell is only marginally different from a small CX-type cell. This cell falls into the overlapping region of Fig. 20. *5*) In this penetration there are four single-contrast, S_1-type cells in layer 6 (numbers *6, 9, 15,* and *16*).

Figure 28 shows the overall distribution of cell types in the cortical layers (11). S-type cells were found in all layers, and in layer 4c most of the isolated cells recorded were S type. This layer contains practically no CX-type cells, which are numerous in all other layers.

The sample in Fig. 28 is based on only 201 cells and does not include data from a number of penetrations, not reconstructed histologically, in which we estimated the location of the cells in cortex by noting when the electrode touched brain and when it entered white matter. The relative thickness of layers in striate cortex is quite constant, with layers 1, 2, and 3 constituting the top 35% of tissue, layers 4a, b, and c, the next 30%, and layers 5 and 6, the remaining 25% of gray matter. We could, therefore, assign cells with a reasonable degree of accuracy to these three subdivisions. The locations of 295 cells were determined in this way giving a total of 496 cells whose approximate positions in cortex were known. The number of S-type cells in layers 1–3, 4, and 5–6 were 29, 36, and 35, respectively; there were 62, 48, and 50 CX-type cells in these subdivisions of cortex. Of the single-contrast, S_1-type cells there were 8 in layers 1–3, 8 in layer 4, and 7 in layers 5–6. T-type cells had the following distribution: layers 1–3, 3; layer 4, 7; layers 5–6, 7.

In Fig. 29 distributions among the cortical layers are shown for receptive-field size, inhibition along the axis orientation, and spontaneous activity.

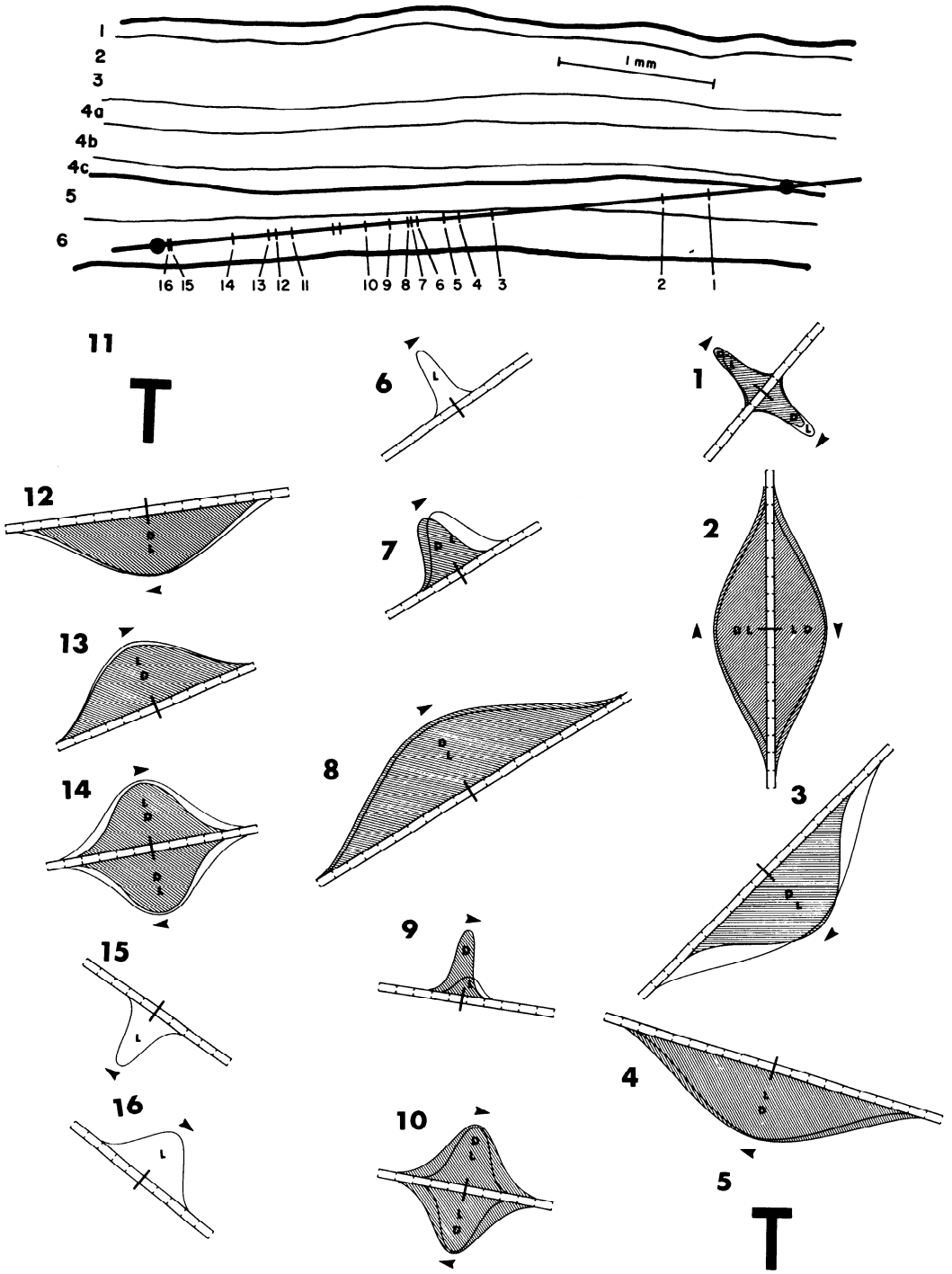

FIG. 27. Tangential penetration reconstruction (layers 5 and 6). Filled circles show position of marker lesions. Receptive fields were mapped with moving edges or squares and are shown schematically marked in 0.1° steps; the short, heavy lines are the axes of orientation. Cells number *6, 7, 9, 15,* and *16* are S type; *5* and *11,* T type; all others are CX type. The two units between *10* and *11* were not held long enough to classify.

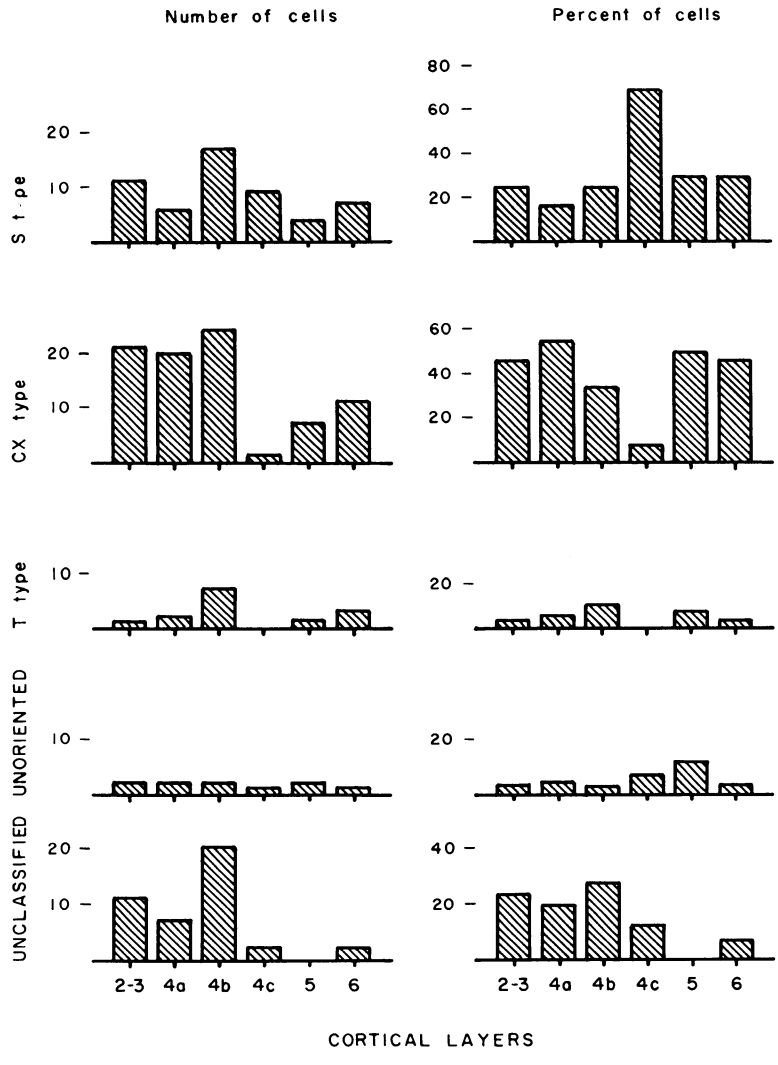

FIG. 28. Distribution of cell types in cortical layers. Locations of 201 cells were determined from histological reconstructions. Graphs at left show numbers of each type cell found in the various layers. Graphs at right show the percentage of cells in each layer classified into the various cell types.

These results indicate that: *1*) The receptive-field size of S-type cells is the same in all the layers, except for layer 4c (not shown separately in Fig. 29 for which 4a, b, and c were combined), where all the cells had fields smaller than 0.2°. Receptive fields of CX-type cells are smallest in layers 1–3, and get progressively larger in deeper layers. *2*) The degree to which cells are inhibited along the axis of orientation varies considerably with depth. Cells in layers 1–3 tend to be more strongly stopped than cells in layers 5 and 6, where most cells are unstopped, while layer 4 falls between these extremes. The differences between S-type and CX-type cells are small. *3*) S-type cells have low spontaneous activity in all layers of cortex. CX-type cells also show low spontaneous activity in layers 1–3, but tend to have higher rates of maintained firing in layers 5–6. This measure seems reasonably effective in discriminating between S-type and CX-type cells in layers 5 and 6, but is ineffective in the other layers. In contrast to the overall misclassification of 27%, in layers 5–6 only 11% of the cells are misclassified using spontaneous activity as a criterion.

Alert monkeys

We were concerned in the course of our recordings that the state of the animal, including anesthesia, might produce sufficiently pro-

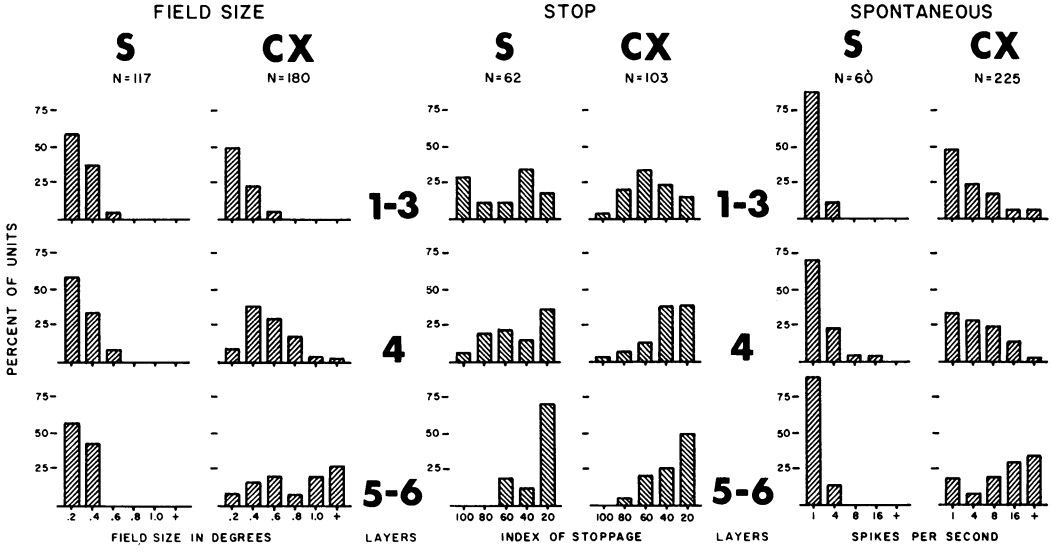

FIG. 29. Field size, inhibition along axis of orientation, and spontaneous activity as a function of depth for S-type and CX-type cells. Depths were obtained from reconstructions and the estimation method described in the text. CX-type cells become larger, less stopped, and more spontaneously active with increasing depth; S-type cells show a change only in their stopping index.

nounced changes in striate cortex to render the properties of single cells in our situation different from those of the alert, normally behaving monkey.

Our paralyzed animals were anesthetized initially by Pentothal and subsequently by N_2O. We did not see any striking differences in the properties of cells using these two agents. The spontaneous activity and responsiveness of cells was somewhat less with Pentothal, but this was most evident only for the first 5–10 min following readministration.

Irrespective of the anesthetic agent used, the responsiveness of cells in the superficial layers (but not in layers 4, 5, and 6) tended to decrease with time, especially during the latter part of the second day of recording.

Because of these observations we undertook to record from two alert monkeys which had one eye surgically immobilized as described in the METHODS section. Only qualitative data were obtained in these animals. Our recordings from 109 cells suggest that the properties of units in these animals were quite similar to those of the paralyzed, anesthetized animals. In the superficial layers many cells responded erratically and tended to habituate, while the cells in layers 4, 5, and 6 discharged consistently to visual stimuli. The majority of cells were oriented although this sample seemed to contain a somewhat greater percentage of unoriented cells. We also found fewer S-type cells, which may have been due to the fact that the recording stability and time spent in a given region was less than in the paralyzed animals. In general, our qualitative observations suggest that the properties of single cells in anesthetized, paralyzed animals are representative of the alert monkey's visual cortex.

DISCUSSION

This section discusses the various types of cells described in the RESULTS and the significance of the distributional measures. Possible models for cortical cells will be considered briefly.

Characteristics of single cells in striate cortex

S-TYPE CELLS. The results suggest that a variety of S-type cells may be distinguished in the striate cortex of the monkey; their properties are summarized schematically in Fig. 30. The single-contrast, S_1-type cell in this figure shows the simplest type of oriented cell, which exhibits a single excitatory region to moving edges, within which it responds only to one sign of contrast change. In some of these cells it is possible to demonstrate an antagonistic surround by placing a stationary stimulus in the center while flashing a large, superimposed stimulus. These cells are striking in that practically all of them are unidirectional.

The second notable group is the double-field, S_2 cell, in which one subfield is excited by a light edge and the other by a dark edge. Both fields

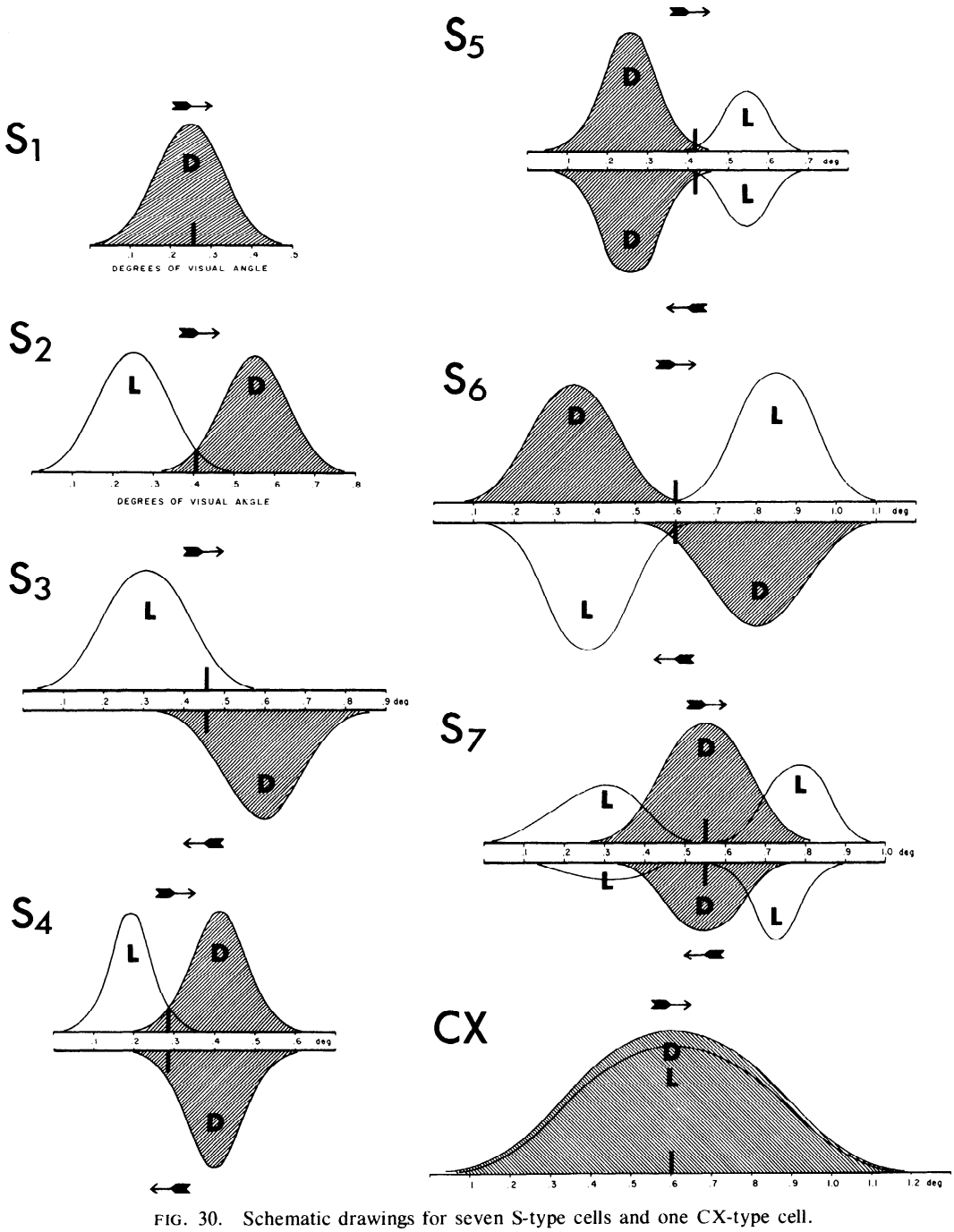

FIG. 30. Schematic drawings for seven S-type cells and one CX-type cell.

respond to movement in the same direction, and two-thirds of such cells in our sample were completely unidirectional.

The third group are cells which show an interaction between contrast and direction of movement (S_3). They have two subfields, and each responds only to one direction of movement, but in opposite directions to each other.

The fourth group of commonly observed S-type cells are those in which one contrast edge elicits responses for both directions of movement, while the other contrast edge elicits a re-

sponse only for one direction of movement. These cells were called U-B or S_4 cells.

More complicated arrangements are observed in S-type cells which have several subfields (S_5, S_6, and S_7). Some of these cells may have three distinct areas with, typically, a center region responding to one sign of contrast change flanked by two regions responsive to the opposite contrast (S_7). In some cases these cells are completely bidirectional, while others may demonstrate unidirectionality for some regions and bidirectionality for others.

The properties of the various S-type cells we discussed are similar to the simple cells described by Bishop, Coombs, and Henry (1) in area 17 of the cat. In Fig. 10 of their paper these investigators show a variety of spatial arrangements of simple-cell subfields. We have seen cells similar to almost all of these. It is rather interesting that this similarity in cat and monkey cells extends, in part, to the percentage of each cell type; in the sample of Bishop et al., 9 of 43 cells responded only to a single edge, and all of these cells were unidirectional. Of the cells responding to 2 edges, 22 were unidirectional and 7 bidirectional, again a ratio rather similar to the one we obtained in the monkey. However, we have seen more cells showing interaction between direction and contrast (S_3) of which Bishop, Coombs, and Henry report two. The U-B cells (S_4) were also more common in our sample.

How might the more elaborate receptive-field arrangements of S-type cells be derived from their inputs? While a variety of possibilities exist, the array of S-type cells described might well be understood by assuming a hierarchic relationship among them. Lowest in the hierarchy are the single-contrast, S_1 cells, which may be thought of as being first-order S-type cells. Assuming such a hierarchy, the initial transformation of LGN input in visual cortex involves not only orientation, but also direction selectivity: it appears that at this early stage a conversion occurs which renders almost all cells unidirectional.

S-type cells with more complicated properties may be constructed by convergent excitatory input from the first-order S_1 cells. Thus a double-field, S_2 cell may result from two single-contrast, S_1 cells of opposite contrast response, but with the same orientation and direction. An S_3 cell may be constructed in the same manner, but the two single-contrast, S_1 cells would have direction preferences 180° in opposition. Cells with multiple subfields may be made from a variety of combinations. In favor of such a hierarchic relationship among S-type cells is the fact that the receptive-field width of these cells increases with increasing complexity. This is especially clear when one compares the S_1- and S_2-type cells. The mean receptive field of the single-contrast, S_1 cells in our sample is 0.20° (SD = 0.09); that of the double-field, S_2 cells is 0.40 (SD = 0.10).

The proposed combinations do not go contrary to the known cytoarchitecture of cortex: while orientation is strictly maintained in a columnar fashion, no such organization is evident for direction; within a column reversals of preferred direction are common. Furthermore, one can, on occasion record from two single-contrast, S_1-type cells simultaneously, as already noted, which have spatially separate fields and are sensitive to opposite directions of movement.

The problem with any sort of hierarchic concept is that recordings from S-type cells, including S_1-type, are obtained in all cortical layers. One must, however, consider the possibility that the order of cell types in these layers is greater than revealed by extracellular recording methods. If single-unit records were obtained not only from cell bodies, but to some extent also from axons and dendrites, such order would be significantly obscured. In this respect it is interesting that progressive changes in receptive-field properties as a function of recording depth in cortex are found only in CX-type cells. If unit signals are indeed recordable at sites other than near the cell body, the probability of this would be higher for S-type cells provided they have the profuse axonal terminations within striate cortex postulated by the Hubel-Wiesel (8) hierarchic model.

The proposed hierarchy is only one possible way of conceptualizing the various S-type cells since models of cells can also be constructed assuming no such hierarchy. A more detailed discussion of models of visual cortex will be deferred until the fifth paper in this series.

Irrespective of the manner in which these cells are constructed, the question remains as to how a single cell can have spatially separate excitatory subfields of the sort described. Since input from the LGN seems highly ordered topographically (12), one possibility is that inputs converge from spatially separate cortical areas, from one or two hypercolumns away where cells of the same orientation but of a slightly different spatial location reside. The other possibility is that the different layers of the LGN, consisting of repeated representations of the visual field project into visual cortex with some misalignment. These projections form multiple layers of terminal fields (6) and thus could be the source of the spatially separate subfields observed in S-type cells. If this is the case one might expect that in some cases the subfields have their origin in different layers of the LGN.

This notion does not explain one interesting problem, namely that there are potential combi-

nations of subfields in S-type cells which do not appear. For instance, cells in our sample which have two or more spatially separate fields responding to the same sign of contrast are extremely rare or nonexistent, although it is true that such combinations might be difficult to recognize. In spite of this, it is fair to say that some combinations have a high probability of occurrence while others have a low probability.

CX-TYPE CELLS. We defined CX-type cells as those oriented cells which have a unified activating region within which a response can be elicited to both light increment and light decrement. The receptive fields of these cells tend to be larger than those of S-type cells, although there is some overlap in the distribution obtained. The measure of direction selectivity suggests that these cells constitute two subgroups: unidirectional and bidirectional cells.

T-TYPE CELLS. The T-type cells, which appear to form a distinct group, are characterized by the fact that they respond to visual stimuli in a relatively sustained fashion and are excited by only one sign of contrast. They are generally poorly oriented, or not oriented at all, and a higher percentage of them are color specific than S-type and CX-type cells. These cells may be analogous to the class I cells reported by Dow (5). Since their properties are somewhat similar to LGN cells, they do not appear to transform the geniculate input greatly. Therefore, it is likely that these cells are driven primarily by geniculocortical afferents.

Quantitative measures

The basic criteria which have been used in earlier studies to distinguish among cells types in cat visual cortex are the following: *1*) Simple cells have one or more spatially distinct activating regions which can be plotted with stationary flashes. Complex cells do not show such separation. *2*) The responses within each area summate with increasing stimulus length in simple cells but not in complex. *3*) Low spontaneous activity is a property of simple cells. *4*) Simple cells are most numerous in layer 4, while complex cells are found primarily above and below this layer. *5*) Simple cells have relatively small receptive fields in comparison with complex cells. *6*) Hypercomplex cells form a separate class distinguished from others by virtue of the fact that they are strongly stopped for stimulus length along the axis of orientation.

The distribution of cell properties and the histological data make evident the following points: *1*) The measure of subfield overlap (Fig. 20) shows a bimodal distribution suggesting two classes of cells. Only 36 cells appear in an area common to both classes. *2*) Summation for stimulus length, as shown in Fig. 17, does not differentiate S-type from CX-type cells. *3*) The distribution of cells according to spontaneous activity is unimodal. Cells classified as S type and CX type show a considerable overlap so that this measure discriminates these two classes only in layers 5 and 6. *4*) There is extensive intermingling of S-type and CX-type cells in almost all layers of cortex. *5*) Receptive-field width shows a broad distribution, which appears to be unimodal. CX-type cells have, on the whole, larger overall receptive fields than S-type cells, but there is an overlap of field size for a considerable portion of the two populations. A better differentiation between these classes is obtained, however, when subfield size to one sign of contrast change is compared.

These observations suggest that with the measures detailed, S-type and CX-type cells can best be distinguished on the basis of the spatial separation of the light and dark response areas. This measure does not, however, establish unique classes.

Our qualitative observations confirm that S-type cells have inhibitory sidebands while CX-type cells lack this property. S-type cells with more than one excitatory subfield seem to have inhibitory sidebands for each of their subfields. Since mapping of these regions is difficult, it cannot be used as an efficient means of classifying cells into the S and CX categories. We have not studied the inhibitory property in sufficient detail to make quantitative and distributional statements about it.

The major problem we encountered in our classification was with the third member of the hierarchy as originally proposed by Hubel and Wiesel (9): the hypercomplex cell. While it is clear that examples of cells with hypercomplex properties can be found in area 17 in the monkey, the strength of end stopping does not seem to provide a satisfactory criterion for classifying cells in the monkey. The extent to which one can observe inhibition along the axis of orientation forms a unimodal, skewed distribution. Many, although not all, of the moderately and even strongly stopped cells could be clearly classified as S or CX type. End stopping, however, is not evenly distributed in the cortical layers. Significantly more cells are stopped in layers 1-3 than in layers 5–6. This is an agreement with the reports by Hubel and Wiesel (10) and Poggio (15). On the basis of this one might suggest that the hypercomplex attribute is the product of a general inhibitory network, the effectiveness of which diminishes for progressively deeper cells in cortical gray matter.

The extent to which end stopping represents a transformation of the LGN input to visual cortex is a knotty problem. It appears that the majority of cells in the LGN are strongly inhibited by their surrounds when long bars or edges are used, more so than the population of cortical cells we studied. On the basis of this one might consider the possibility that the significant cortical transformation produces a lack of end stopping rather than its opposite. This may be produced, as suggested by Hubel and Wiesel (8), as a result of a great deal of convergence of LGN cells on cortical cells. Strongly stopped cells in cortex may be produced either by a sparse input from the LGN or by a special inhibitory circuit in cortex. A more thorough study is needed to assess the nature of this transformation.

Finally, we might pose the question of what the functional significance of the various cell types might be. Why, for example, are so many S-type cells comprised of bipartite or multipartite excitatory fields? Does this arrangement permit a specific form of analysis of visual information? Assuming a hierarchy, with S-type cells providing the input to CX-type cells, why should this property be promptly lost in CX-type cells? Perhaps S-type cells are involved in the analysis of spatial frequency or some other parameter and send this information to another structure for further analysis. On the other hand, it is also possible that the spatially separate subregions observed in these cells serve no specific function, and may be an outcome of a relatively sparse input from the slightly misaligned regions of the multilayered LGN terminal fields. Further pooling of S-type cell outputs would eventually get rid of this defect.

If it could be shown that *1*) S-type cells perform a specific analysis of the visual input and *2*) that they selectively project to other brain sites, one could perhaps better understand their function. In the subsequent papers we will attempt to contribute to the first question. Assessment of the second awaits further work.

The major findings in this study and the inferences drawn from them may be summarized as follows: *a*) Several different types of S-type cells may be discerned in monkey striate cortex. The subfields of these cells appear to be produced by excitatory action. *b*) A hierarchy may exist among S-type cells. *c*) S-type cells are predominantly unidirectional, which suggests that the cortical transformation for directionality may occur at an early stage in striate cortex. *d*) S-type units, including the single contrast, S_1 cells are found in all cortical layers. *e*) The only measures used in this study which yield well-separated distributions for S-type and CX-type cells are those which specify the spatial organization of the light- and dark-response areas of the receptive field. *f*) Unidirectional and bidirectional CX-type cells represent two distinct classes. *g*) Tonic cells, which are excited by only one sign of contrast change, form a third class of cells. *h*) The measure of the inhibition along the axis of orientation forms a continuous distribution which, therefore, does not yield a separate class of hypercomplex cells in the monkey's striate cortex.

ACKNOWLEDGMENTS

The authors thank Andres Polit, Cynthia Richmond, Kathy Anderson, and Louis Porter for their help on this project.

This research was supported in part by grants from National Institutes of Health (EY00676) and the Alfred P. Sloan Foundation (72-4-1).

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