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VISUAL RESPONSES OF AREA 18 NEURONS IN THE AWAKE, BEHAVING MONK--ETC(U)
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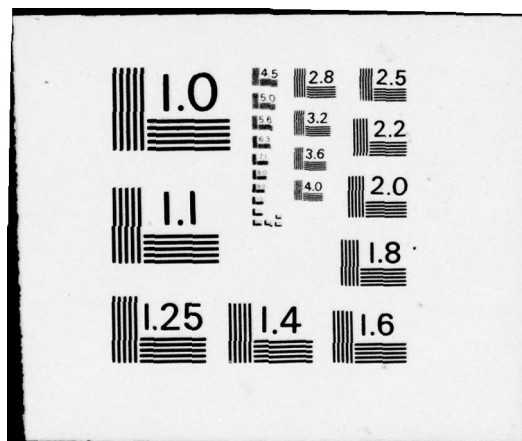
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VISUAL RESPONSES OF AREA 18 NEURONS IN THE AWAKE, BEHAVING MONKEY

J. S. Baizer
D. L. Robinson
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Research was conducted according to the principles outlined in the
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20. ABSTRACT (Continue on reverse side if necessary and identify by block number) The mechanisms underlying effects of ionizing radiation on visual-motor tasks in combat are not understood but definitely involve some disruption of visual perception. The degree of involvement is not known and must be studied and quantified in animal models. It is possible to identify those parts of the central nervous system necessary for visual perception. Once these areas have been identified, their sensitivity to irradiation can be studied more precisely. Visual responses		

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20. ABSTRACT (continued)

of area 18 neurons were studied in the awake, behaving monkey. Cells were divided into six different classes on the basis of their stimulus preferences and spatial characteristics. Orientation cells were sensitive to the orientation of elongated stimuli. Color cells had nonoriented receptive fields with spatially coextensive opponent color inputs. Direction cells preferred moving stimuli, giving the greatest response to movement in some direction and no response or inhibition to movement in the opposite direction. Spot cells preferred a properly positioned small spot of light and responded equally well to all directions of stimulus movement. Border cells responded best to a stimulus that filled an excitatory region without encroaching on a powerful suppressive flank. Light-inhibited cells had high maintained spontaneous activity that was reduced or abolished by light. Most cells responded equally well to monocular and binocular stimulation; some orientation cells greatly preferred binocular stimulation. In conclusion, independent classes of cells in area 18 perform qualitatively different analyses of incoming visual information. Our data suggest that area 18 is involved in visual perception. Since perceptual difficulties are included in the early transient incapacitation occurring postirradiation, these experiments suggest that area 18 should be very sensitive to ionizing radiation.

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SUMMARY

Visual responses of cells in the posterior bank of the lunate sulcus, area 18, were studied in the awake animal trained on a fixation task. During the course of studying many cells with a variety of stimuli we found that cells could be divided into six different receptive field classes. We gave each class a descriptive name: orientation, color, direction, spot, border, and light-inhibited.

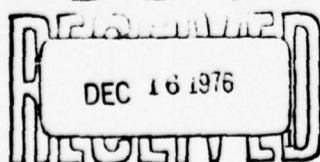
Orientation cells responded best to a properly oriented, elongated stimulus. Most preferred a slit that was narrow relative to the total width of the receptive field. They responded about equally well to both directions of movement of a properly oriented stimulus and were indifferent to color.

Color cells responded with excitation to some colors and inhibition to others. All gave spatially coextensive color opponent responses in a round or oval center. Some had suppressive surrounds which limited the size of a stimulus effective in eliciting one, or both, of the center responses.

Direction cells responded maximally to a spot or slit of light moving in a specified direction across their receptive fields. Movement in the opposite direction elicited either no response or inhibition. These cells were indifferent to color, contrast, and leading edge configuration of moving stimuli; some showed weaker responses to elongated stimuli.

Spot cells preferred a properly positioned small spot of light. Changing the position or increasing the size of an optimal stimulus weakened the response. The optimal stimulus was usually small relative to the total field extent. Spot cells responded equally well to different stimulus colors, and to all directions of movement.

Border cells responded best to a stimulus that filled an excitatory region without encroaching on a powerful suppressive flank. The excitatory region could be delimited by mapping with small spots. The presence of the flank was indicated by the decreased effectiveness of stimuli extending into that part of the field.



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Light-inhibited cells were distinguished by high, regular spontaneous activity which was reduced or abolished by light falling on their receptive fields. Field centers were round or oval; some fields had suppressive surrounds. These cells did not have color opponent properties.

Stimuli were always presented on the fixation plane. Most cells responded equally well to monocular and binocular stimulation. Some orientation cells responded much better to binocular than monocular stimulation.

There are six independent classes of cells in area 18. Separate classes perform qualitatively different analyses of incoming visual information. The most likely sources of input to these cells are cells in area 17 with similar properties.

PREFACE

Supported by postdoctoral fellowships from the National Institute of Neurological Diseases and Stroke (JSB); the National Institute of Mental Health (JSB); and the Foundations' Fund for Research In Psychiatry (DLR). We wish to express our appreciation and thanks to Dr. R. H. Wurtz for advice, encouragement and an unfailing sense of humor throughout these experiments. We also thank M. F. Roark, R. A. Sandlin, and J. L. Washington for technical assistance.

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INTRODUCTION

A major approach to understanding the neural basis of vision has been the analysis of receptive fields of cells at different sites along the visual pathways. The classic work on striate cortex (area 17) of cat and monkey^{24, 26} emphasized the role of this area in the analysis of form. Hubel and Wiesel described simple and complex, and, later, hypercomplex cells in area 17 of the cat. All preferred elongated stimuli, and all were sensitive to stimulus orientation. In area 17 of the monkey, the same authors identified the same basic cell types, as well as a population of units lacking orientation specificity.²⁶ Color specificity and directional selectivity were noted in some neurons, but were largely discussed as subsidiary properties of orientation sensitive simple, complex and hypercomplex cells. A few color-specific cells were reported to have receptive fields with inhibitory surrounds and no orientation specificity.

In an investigation of color processing in foveal area 17 of the monkey, Dow and Gouras¹⁴ reported a population of color cells with spatially coextensive color opponent center inputs and no surround inhibition. These cells were unlike either the orientation sensitive color cells or the nonoriented color cells described by Hubel and Wiesel²⁶ and seemed more concerned with color than with spatial information. Wurtz⁴⁰ studying the awake, behaving monkey reported that almost all directionally selective neurons came from a population of striate cells giving transient responses to stationary stimuli. Dow¹¹ subsequently noted that direction selective cells showed broader orientation tuning than another group of cells without direction selectivity. These findings prompted the suggestion^{11, 14} that different, independent populations of striate neurons were concerned with analysis of either orientation, color, or movement, the elaboration of orientation sensitive cells being then only one of several functions of striate cortex in monkey.

Striate cortex represents only the first stage in the cortical processing of visual information. There are several possibilities for the course of subsequent processing. The segregation of function by different cell groups might persist,

or even increase. Alternatively, fibers from cells of different types might converge, resulting in higher order cells with compound functions. We have explored these alternatives in one of the cortical regions that receives a direct projection from area 17, namely area 18 or VII.^{8,9,31,41} In monkey, unlike cat, area 18 does not receive a direct projection from the lateral geniculate nucleus.^{19,20,28,38} In this study our recordings have been restricted to the posterior bank of the lunate sulcus, which contains the representation of the lower, contralateral visual field. Previous reports^{4,27,29} have implicated some cells in area 18 of the monkey in the processing of binocular disparity information; Dow¹⁰ reported a population of nonoriented color cells in foveal area 18. There has, however, been no published comprehensive study of the visual responses of neurons in this region.

During the course of studying many cells with different sizes, shapes, orientations and colors of stationary and moving stimuli, we found we could divide cells into six different receptive field classes. Each class was uniquely defined by the combination of stimulus preferences and spatial characteristics of the cells included. Our results suggest that in area 18, as in area 17, different, independent, classes of cells are concerned with processing different kinds of visual information. Brief reports of some of these findings have been presented.^{1-3,12,13}

METHODS

Procedures for behavioral control, recording and receptive field analyses were similar to those previously described for the study of visual receptive fields in the awake monkey.^{21,40}

Behavioral procedures. Three rhesus monkeys (*Macaca mulatta*) were trained to press a bar to turn on a fixation light on a tangent screen 57 cm in front of them. The light stayed on for a randomly selected, variable time, between 0.5 and 3 sec; and then dimmed for about 0.5 sec. If the monkey released the bar during the dim period, it received a drop of liquid, either water

or fruit drink, as a reinforcement. Animals were trained to perform this task with both eyes open and also with either eye occluded.

Recording procedures. During recording sessions, the monkey's head was immobilized by bolts previously implanted in the skull. Direct current electro-oculograms were recorded with chronically implanted silver-silver chloride pellet electrodes as described previously.^{7,36}

Single cell recordings were obtained from glass insulated platinum-iridium microelectrodes³⁹ using the Evarts hydraulic closed chamber microdrive.¹⁸ The base of the microdrive was implanted over the lunate sulcus, in the stereotaxic vertical plane. Electrodes were lowered through striate cortex into the cortex in the infolded lunate sulcus.

To localize selected cells histologically, lesions were made in some penetrations by passing 10 μ A of cathodal current for 60 sec through the electrode tip. At the end of the experiment the monkey was anesthetized and perfused with saline and then Formalin. Parasagittal frozen sections 50 μ m thick were stained with cresyl violet. Precise localization information was available on relatively few of the total number of penetrations, thus recording sites on other penetrations were estimated from microdrive depth readings and penetration location in the recording chamber.

Receptive field analysis. While the monkey fixated the small point of light, a second light, the receptive field stimulus, was projected onto the screen. Receptive field stimuli were produced by tungsten projector lamps; white stimuli were 1.0 or 1.6 log units above the background screen illumination of 1 cd/m². Colored stimuli, produced by inserting broad band filters into the light path, were not matched for brightness and were yellow (Wratten #15), green (Wratten #61), red (Wratten #25), blue (Wratten #47b) in order of decreasing brightness. We compared responses to these stimuli with responses obtained by inserting only neutral density filters in the light path.

A rectangular diaphragm was used to produce rectangular stimuli of different lengths, widths and orientations. Moving stimuli were generated either

manually by moving the projector on its tripod mount or electronically by oscillating a mirror mounted on a galvanometer. Visual stimuli were usually flashed on 500 msec after the fixation point, and off at the end of that trial. When it was desirable to look at the effects of stimulus offset, we turned the stimulus off before the animal broke fixation. We have, wherever possible, mapped receptive fields with small, stationary spots of light in order to determine the configuration of excitatory and inhibitory areas.

Most cells in the awake animal are spontaneously active. Our criterion for excitation was an increase in activity above the spontaneous level. Inhibition could usually be seen as a decrease in activity below the spontaneous level; we have relied on this decrease in activity rather than off responses as an indication of inhibition. We have also found it useful to distinguish suppressive areas, regions which do not give evidence of an independent inhibitory input when explored with small spots, but which limit the extent of effective excitatory or inhibitory stimuli. We have used a qualitative definition of summation: a cell shows summation if increasing the size of a stimulus within an excitatory or inhibitory area renders it more effective.

RESULTS

Our recordings were limited to the posterior bank of the lunate sulcus. Figure 1A shows a lateral view of the brain and the sites of three penetrations indicating the approximate mediolateral extent of the region explored. Figure 1B-D show sagittal sections through striate and prestriate cortex at the different locations. The shaded region in each section indicates the approximate limits of recording for the different lateralities. The vertical lines represent electrode penetrations. The circles along the tracks represent electrolytic lesions made at the sites of specific cells, or at the end of a penetration. At the beginning of each penetration we noted the receptive field location, in area 17, usually from multiple unit recordings. Cells in underlying area 18 had slightly more eccentric receptive fields (see Figure 1 legend). Cells with still more lateral

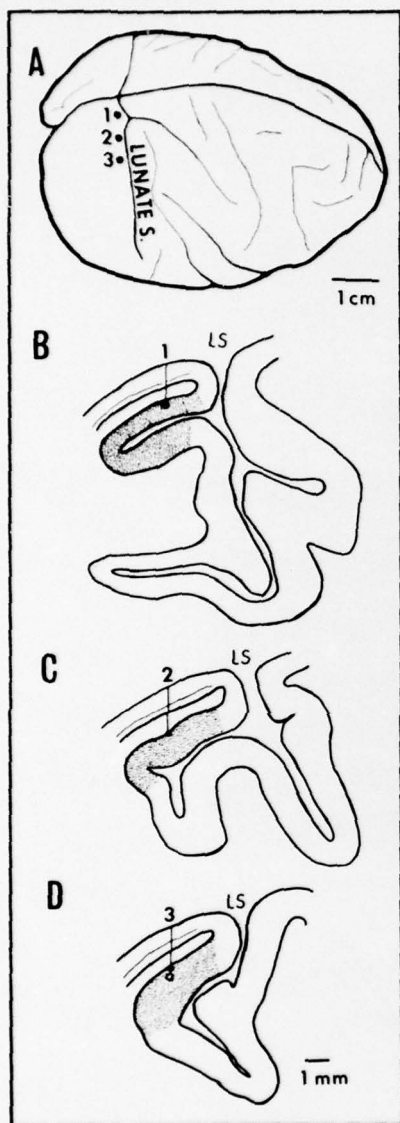


Figure 1.

Area 18 recording sites. A is a lateral view of a rhesus monkey brain. The numbers 1, 2, 3 mark the sites of entry of three different electrode penetrations. B, C and D show sagittal sections through the brain at the lateralities of each of the numbered penetrations. In each section, area 17 (striate cortex) is indicated schematically by a line parallel to the cortical surface representing the granule cell layer. The shaded areas correspond to the approximate extent of the lunate sulcus from which recordings were made at each laterality. Reconstructed penetrations are represented as vertical lines in B, C, and D. Lesions are represented as circles. In penetration 1 the receptive fields in striate cortex, as determined by multiunit recording, were at 1° lateral, 4° down. The lesion marks the approximate recording sites of several orientation cells with receptive field centers at 3° lateral, 4° down. In penetration 2 the area 17 fields were at $1-1/2^{\circ}$ lateral, 3° down. The lesion was made at the recording site of a spot cell with field center at 4° lateral, $1-1/2^{\circ}$ down. In penetration 3 the striate multiunit field was at $1/2^{\circ}$ lateral, $1-1/2^{\circ}$ down; the upper lesion was made at the recording site of a color cell (Figures 9B and 10) with field center at 1° lateral, 2° down. Figure 2 shows a photomicrograph of part of the section from which D was drawn.

receptive fields were encountered in the lower lunate fold included in the shaded area in Figure 1B. Figure 2 is a photomicrograph of part of the section from which Figure 1D was drawn. The superior of the two lesions was made at the site of a color cell whose properties are described in Figures 9B and 10. The second lesion was made to aid in identifying the penetration.



Figure 2. Photomicrograph showing recording site of an area 18 color cell. Same penetration as in Figure 1D. The upper lesion marks the recording site. The color cell, AR195, is described in Figures 9B, and 10. The lower lesion was made to aid in identifying the penetration.

Results are based on recordings from a total of 645 cells. Of these, 333 were visually driven but not studied long enough to allow classification, and 61 (61/645, 9 percent) were not driven during the period they were held. Two hundred fifty-one cells were thoroughly studied and subdivided into six classes. We have given each receptive field class a name descriptive of the stimulus preferences of the cells included: orientation, color, direction, spot, border, and light-inhibited.

Orientation cells. Of the 251 classified cells, 85 (34 percent) were orientation cells. The defining characteristic of cells in this class was their sensitivity to the orientation of elongated stimuli. Figures 3-6 illustrate the properties of one cell in this class. Figure 3C shows the responses to an optimally

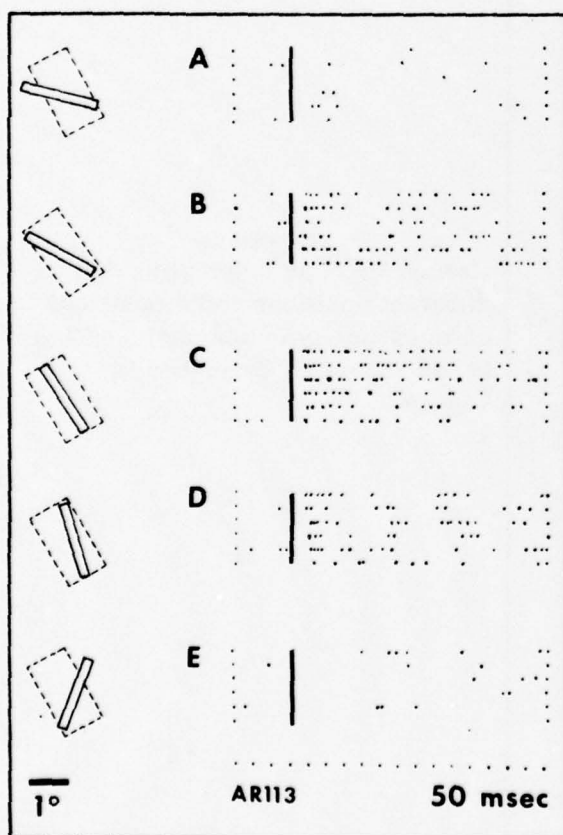


Figure 3.
Responses of an orientation cell to variations in stimulus orientation. Receptive field was 5° from the vertical meridian and $2-1/2^{\circ}$ below the horizontal meridian, and is indicated by the dashed line. Stimuli are represented by solid lines. The vertical bar at the left of each raster indicates stimulus onset as calibrated with a photocell; on most trials the stimulus remains on for the full duration of the raster. Testing was with binocular presentation of stationary, flashed stimuli. Monkey (AR) and unit number (113) are indicated below the rasters on the left. Spacing of dots beneath the rasters is 50 msec. (These conventions will be followed throughout unless otherwise noted.)

positioned and oriented narrow slit. Tilting the slit by about 20° (Figure 3B, D) weakens the responses; at 45° from the optimal orientation the cell no longer responds (Figure 3A, E).

Figure 4 shows the responses of this cell to different positions and dimensions of an optimally oriented stimulus. The best responses occur when the slit is at positions C or D. Placing it at position B weakens the response. At positions A and E the slit is ineffective. The receptive field for this, and other cells in this class, is defined as the area in which an optimally oriented appropriate

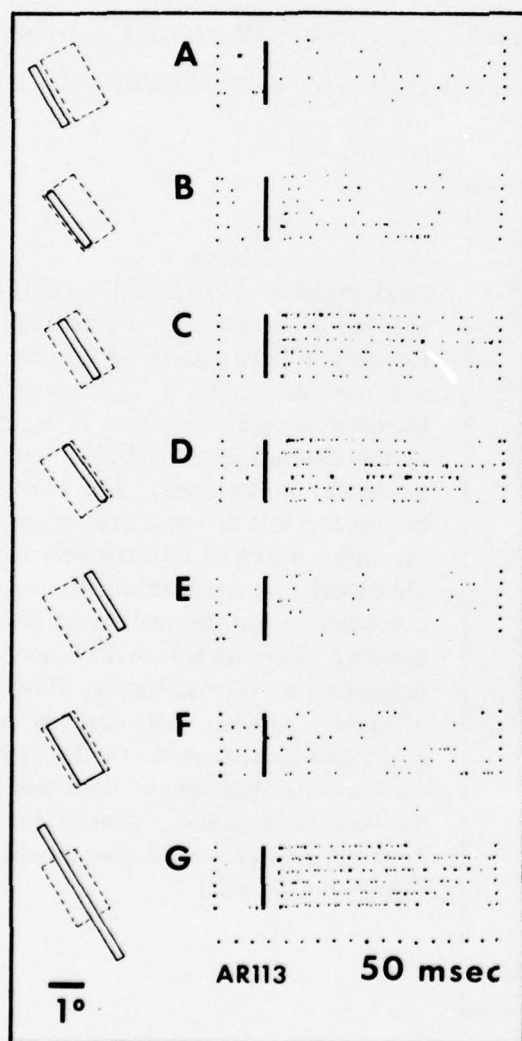


Figure 4.
Responses of an orientation cell to different positions and dimensions of an optimally oriented slit. This is the same cell described in Figure 3.

stimulus could drive the cell. Although the wide slit in Figure 4F is still clearly within the receptive field, there is almost no response to it. One edge of either contrast centered in the field also elicited a very weak response. This cell shows a preference for narrow slits centered in its receptive field. Increasing the length of an effective stimulus does not diminish the response to it (Figure 4G). The same cell is vigorously driven by a moving stimulus (Figure 5),

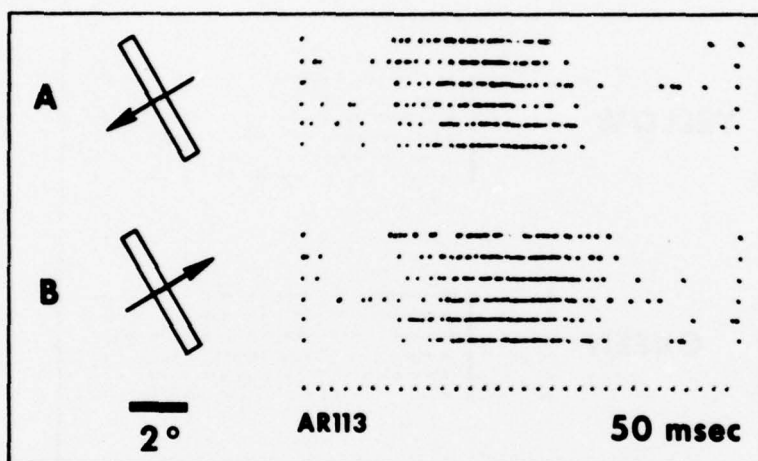


Figure 5. Responses of an orientation cell to movement of an optimally oriented slit. Arrows show direction of movement, velocity $3^\circ/\text{sec}$. This is the same cell as in Figures 3 and 4.

with responses about equal to the two directions. Figure 6 shows the responses of this cell to variations of the color of an optimal stationary stimulus. Responses to red, yellow, green and blue are about equal.

Figure 7 summarizes data from 36 orientation cells, showing the range of stimulus orientations effective in eliciting some excitatory response. The narrowest range was about 15° , the broadest about 95° , with 40° to 60° the most common. Most of the cells in this class (35/48 tested) showed a preference for narrow slits. There was some variation in width of preferred stimulus and in the degree to which an increase in width would affect the response. A few cells responded as well to edges as to slits (8/48), and a few others preferred

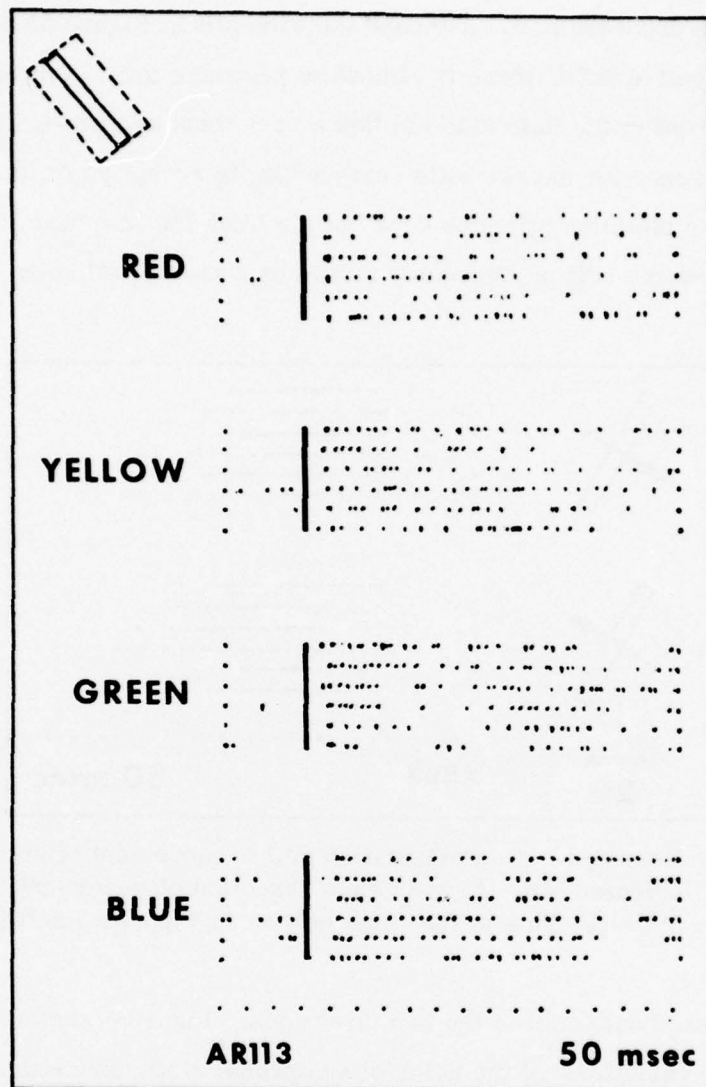


Figure 6. Responses of an orientation cell to different colors of an optimally positioned and oriented narrow slit. Other properties of this cell described in Figures 3-5.

edges to slits (5/48). Almost all cells in this class responded similarly to increases in stimulus length. They required an elongated stimulus, not responding at all until some minimum length was reached. They then showed response improvement until the stimulus extended the full length of the receptive

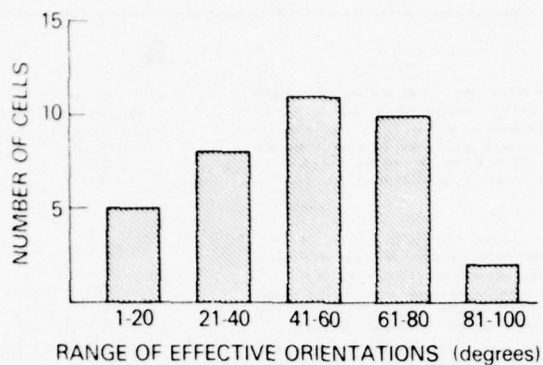


Figure 7. Orientation specificity of 36 orientation cells in area 18. Cells are grouped according to the total range of orientations eliciting excitation. Testing was with stationary stimuli.

field. Further length increases had no effect. The sole exception was one cell that was end-stopped at one end. Almost all orientation cells were driven by both stationary and moving stimuli; a few preferred one or the other. All 58 cells tested with moving stimuli responded about equally well to both directions of movement of an optimally oriented stimulus. The 39 orientation cells tested were similarly unaffected by variations in stimulus color.

Hubel and Wiesel^{27,29} reported finding "binocular depth cells" in monkey in the posterior bank of the lunate sulcus and in the annectant gyrus. Some cells required the same simultaneous input from both eyes, others required a specific disparity between stimulus locations for the two eyes. We studied cells by first finding the best stimulus for the cell binocularly, then testing through either eye alone. The fixation point and visual stimuli were always presented on the tangent screen 57 cm from the monkey. Some orientation cells responded about equally well to monocular and binocular stimulation (Figure 8A). Other cells responded much better binocularly than monocularly (Figure 8B). A third group (not illustrated) responded better to monocular than binocular stimulation. Of the 14 orientation cells tested monocularly, 7 showed some sign of interaction between the two eyes.

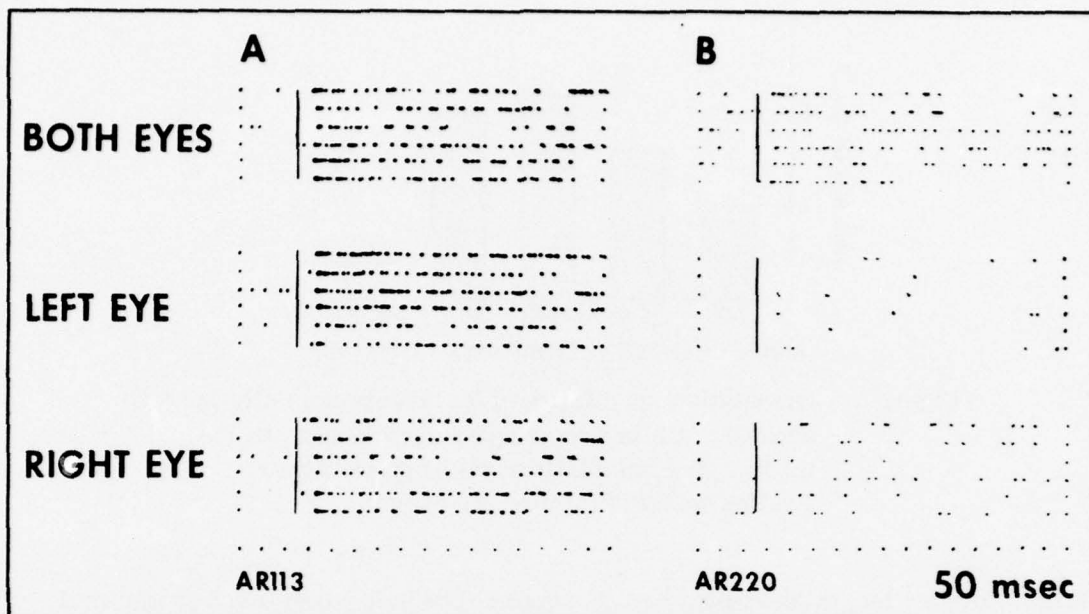


Figure 8. Monocular and binocular stimulus presentation for two orientation neurons. The stimulus in all three conditions for both cells was an optimally positioned and oriented white slit. The cell in A is also described in Figures 3-6. Receptive field center for the cell in B was $3\frac{1}{2}^{\circ}$ lateral, 3° down.

In summary, orientation cells responded best to elongated stimuli of the correct orientation; changing the orientation of a stimulus within the receptive field greatly affected the responses of these cells. Most of these cells preferred stimuli that were narrow relative to total field width. None of these cells showed either color specificity or directional selectivity. Some had specific binocular requirements. Most, if not all, of the cells in this class fit the definition of "complex cells" originally proposed by Hubel and Wiesel.²⁴

Color cells. Cells in this class (39/251, 15 percent) showed excitation or inhibition to a single stimulus configuration depending on its color. The cell in Figure 9A is excited by blue, gives a brief on-response followed by sustained inhibition to yellow, and gives mixed responses to red and green. The cell in Figure 9B is excited by red, inhibited by blue and green, and gives mixed

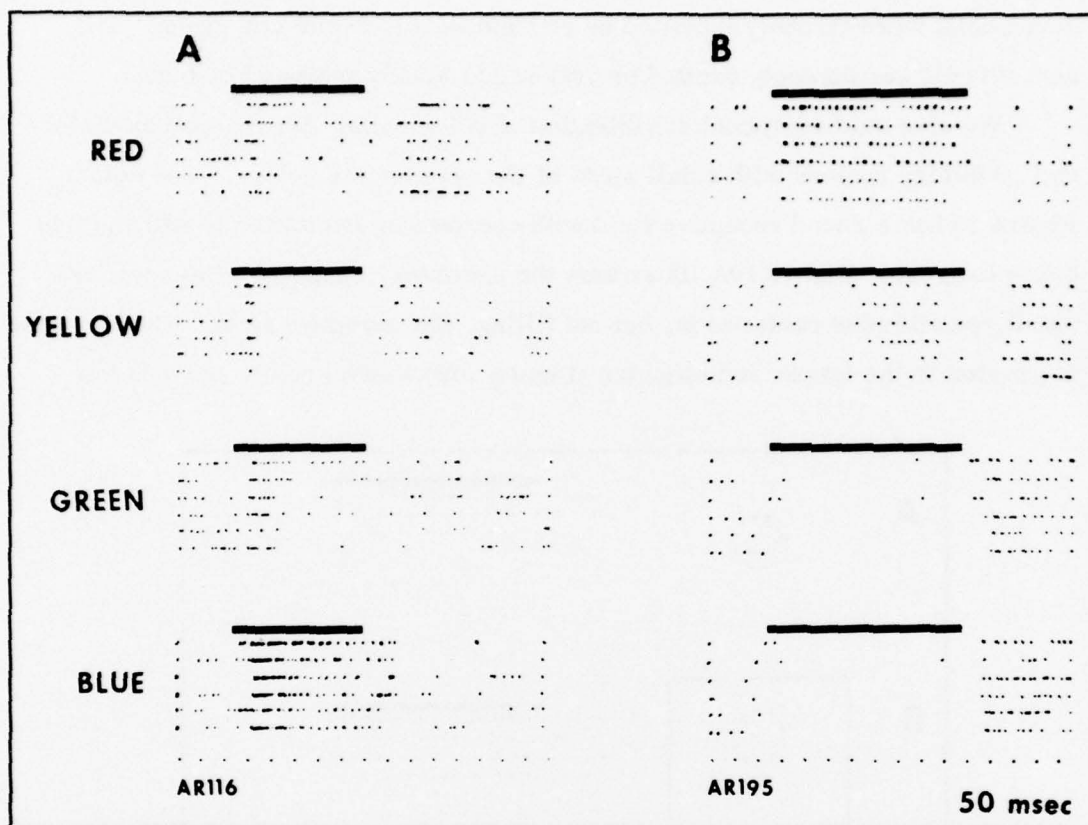


Figure 9. Responses of two color cells to variations in stimulus color. In A the stimulus was a $2^\circ \times 2^\circ$ square centered on the receptive field at 5° lateral, 2° down. In B the stimulus was a $3\text{-}1/2^\circ \times 3\text{-}1/2^\circ$ square centered on the receptive field at $1\text{-}1/2^\circ$ lateral, 2° down. Horizontal bar above each raster indicates stimulus onset and duration, in this and all figures of similar format.

responses to yellow. Twenty-four cells showed similar opponent properties when tested with these four colors and white: 13 were excited by red and inhibited by green; 3 were excited by green and inhibited by red; 5 were excited by blue and inhibited by yellow, and 3 were excited by yellow and inhibited by blue. In the remaining 15 cells at least one color was more effective than white in either exciting or inhibiting the cell. In seven of these, a colored background was useful in demonstrating a second weaker, opponent color input.¹⁴ Six of the

seven cells were strongly inhibited by red and weakly excited by green. The seventh cell was strongly excited by yellow and weakly inhibited by blue.

We also studied spatial organization of color cells. We mapped excitatory and inhibitory regions with small spots of the appropriate colors. The cell in Figure 10 had a round receptive field with coextensive excitation to red and inhibition to green. Figure 10A illustrates the excitatory response of the cell to a small red stimulus centered in, but not filling, the receptive field. The response is greater to the larger red stimulus (Figure 10B) which greatly exceeds the

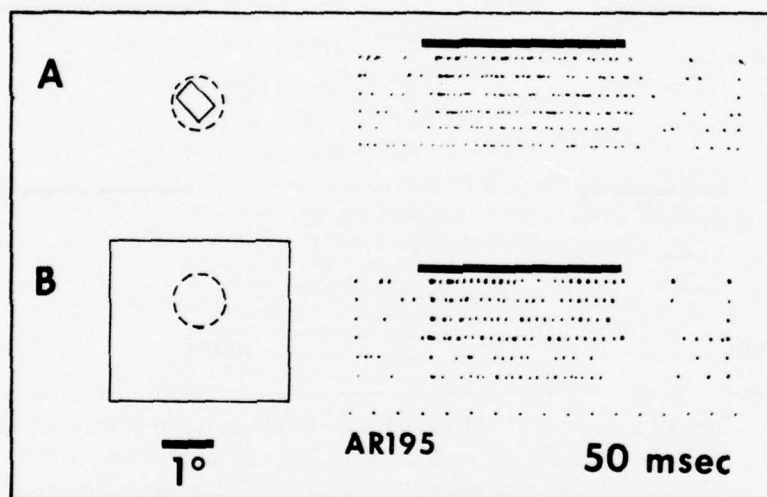


Figure 10. Responses of a color cell to two different stimulus configurations. This is the same cell whose color properties were illustrated in Figure 9B. Testing is with red. The recording site of this cell is shown in Figures 1 and 2.

mapped center. A large green stimulus (Figure 9B) is highly effective in inhibiting the cell. There was no evidence of a suppressive surround affecting either of the opponent color inputs. Of 19 color cells tested with stimuli of different sizes 12 were like this cell, with no sign of any suppressive surround. A lesion made at the site of this cell is illustrated in Figures 1D and 2.

Other color cells had suppressive surrounds affecting both excitatory and inhibitory inputs. The cell in Figure 11 was excited by blue and inhibited by

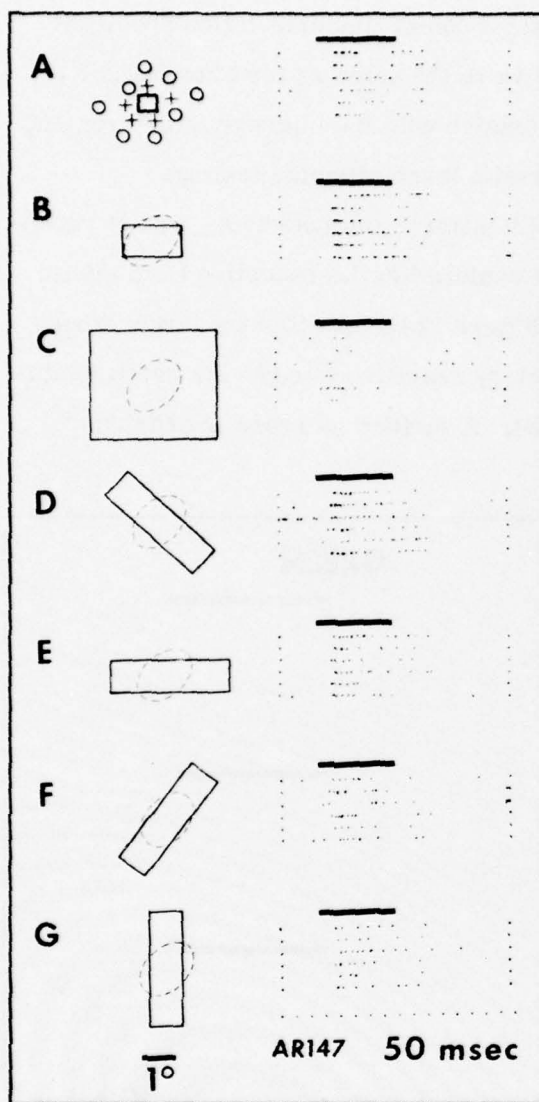


Figure 11.
Effect of changes in stimulus configuration on the responses of a color cell. All stimuli were blue. The receptive field was mapped with the small square shown in A. The +'s indicate other locations where that stimulus was effective; o's indicate ineffective locations. The raster in A shows responses to the square illustrated. The dashed line in B-G encloses the area where small blue spots drove the cell. Receptive field center was at $2\frac{1}{2}^{\circ}$ lateral, 3° down.

yellow. Figure 11A shows the responses to a small blue spot, and the receptive field map obtained with that spot. Enlarging the stimulus to cover more of the excitatory region results in a stronger response (Figure 11B), indicating summation within the center. Enlarging the stimulus still further, however, reduces the response (Figure 11C), revealing the presence of a suppressive surround. Wide bars covering most of the receptive field center and extending into different parts of the surround (Figure 11D-G) elicit roughly equal responses, suggesting

that the surround is symmetrical: it does not confer any orientation specificity on the cell. Spatial properties for yellow were the same as for blue, namely, there was a yellow inhibitory region coextensive with the blue excitatory region, and a suppressive surround apparent only with large stimulus testing.

Figure 12 illustrates a color cell with a third, intermediate, type of receptive field organization. A small stimulus centered in the receptive field elicits excitation to red and inhibition to green (Figure 12A). A stimulus larger than the mapped center evokes a briefer excitatory response to red; the green inhibition, however, is not affected (Figure 12B). A further increase in stimulus

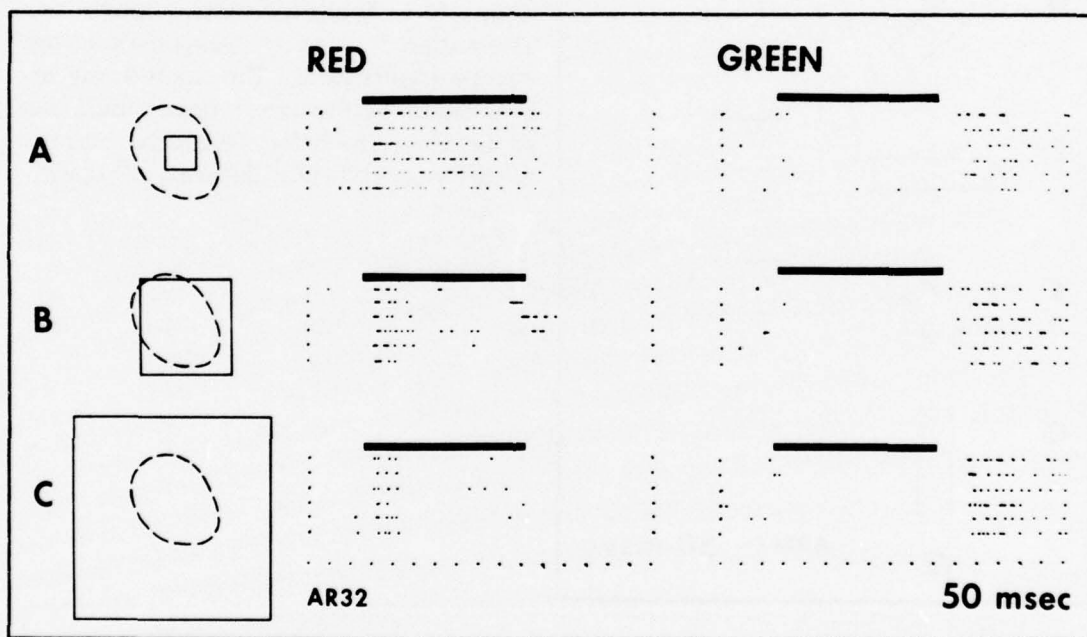


Figure 12. Responses of a color cell to different stimulus colors and sizes. The receptive field center was at 2° lateral, 3° down. The dashed line encloses the area where small red spots excited the cell and green inhibited it.

size (Figure 12C) decreases the excitatory response to red even more, and again leaves the inhibition to green unaffected. This color cell, then, had a suppressive surround affecting only one of the center mechanisms.

Seven of nineteen color cells tested showed weaker excitatory and/or inhibitory responses to stimuli that exceeded the center (Figures 11, 12). Three additional cells gave responses suggesting spatially separate color opponent inputs. Testing of these cells was not thorough enough to allow adequate description of either their color or spatial properties.

Responses to stimulation through either eye alone and binocularly were about equal for all eight color cells tested (Figure 13). Responses to moving

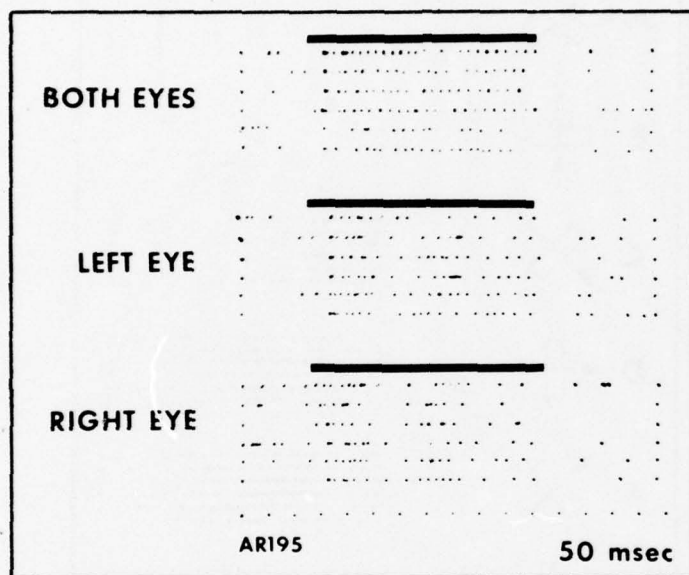


Figure 13. Ocularity testing for a color cell. The stimulus was the red square as illustrated for the same cell in Figure 9B.

colored stimuli were predictable from stationary field properties; cells responded about equally well to all directions of movement (10 cells tested).

In summary, color cells had spatially coextensive opponent color inputs that could be mapped with small spots. Each opponent mechanism showed summation within a round or oval center. Narrow, oriented stimuli were less effective in driving the cells than larger, nonoriented stimuli which filled the centers. Some cells had suppressive surrounds affecting one or both inputs; in these cells a large stimulus was less effective in eliciting excitation or inhibition than

a smaller stimulus of the same color. Color cells showed little specificity for stimulus orientation or direction of movement, and received binocular inputs.

Direction cells. The best stimulus for a direction cell (35/251, 14 per-cent) was a spot or slit of light moving through the receptive field in a given direction. Figure 14 illustrates the responses of one cell in this group to a mov-ing slit. The cell responds best to the stimulus in E, and continues to respond,

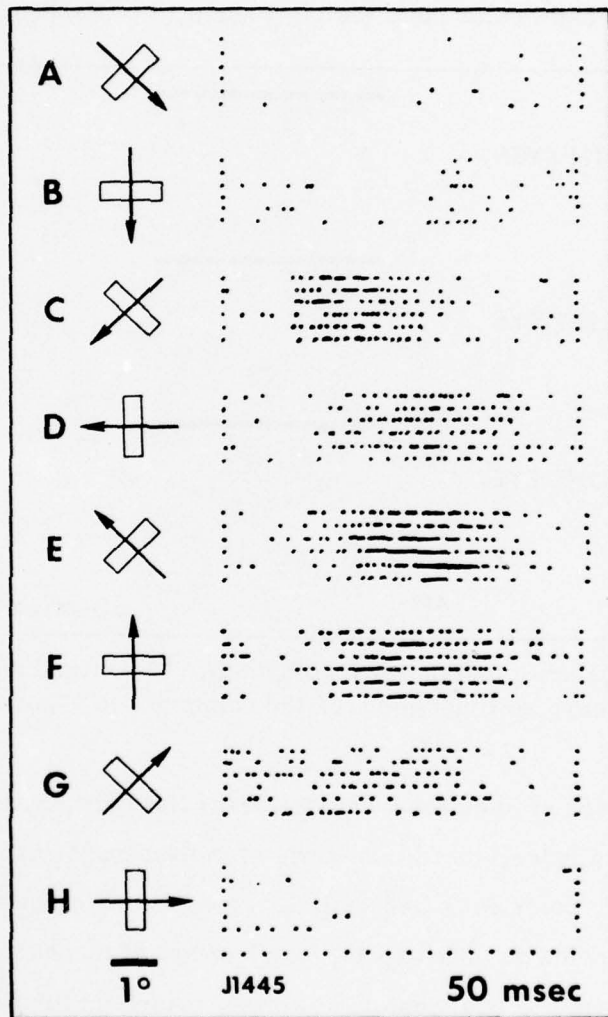


Figure 14. Responses of a direction cell to moving stimuli. The stimulus was $1\frac{1}{2}^{\circ} \times \frac{1}{2}^{\circ}$; velocity was $10^{\circ}/\text{sec}$; arrows indicate di-rection of movement. The receptive field center was at 8° lateral, $3\frac{1}{2}^{\circ}$ down.

though less strongly, when the direction of movement is changed by first 45° (D, F) and then 90° (C, G) on either side of the optimal direction. Movement in the opposite direction (A) is not only ineffective in driving the cell but seems to decrease the cell's activity below the spontaneous level. This cell, then, gives its best response to movement in a "preferred" direction, and is inhibited by movement in the opposite, or "null" direction. It responds through a total range of directions of about 225° . Direction cells showed either inhibition or no response to movement in the direction opposite to the preferred. Range of effective directions varied from about 45° to about 270° . We did not see any tendency for any direction to predominate as preferred.

Orientation and direction are confounded when a moving slit is used as a test stimulus. We therefore tested direction cell responses to moving stimuli of various shapes. Figure 15 shows responses of another direction cell to

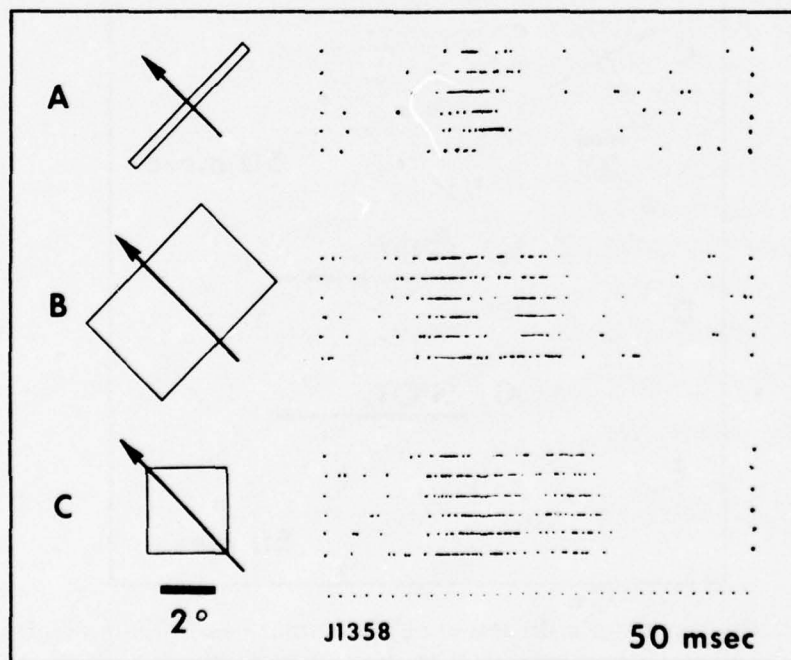


Figure 15. Responses of a direction cell to stimuli of different shapes moving in the preferred direction. Stimulus velocity was $10^{\circ}/\text{sec}$, field center at 2° lateral, 3° down.

narrow and wide slits and a square turned at an angle so that the leading edge was a corner. The cell responds well to the wider stimuli, with responses to both the leading and trailing edges. The response is thus contrast independent. The cell responds as well to the corner as to the straight edges. All cells in this group were similarly indifferent to the configuration of the leading and trailing edges of stimuli moved through the field.

Some direction cells (12/30) preferred shorter to longer stimuli. The cell in Figure 16 responds about equally well to the two short slits (A,B), and less

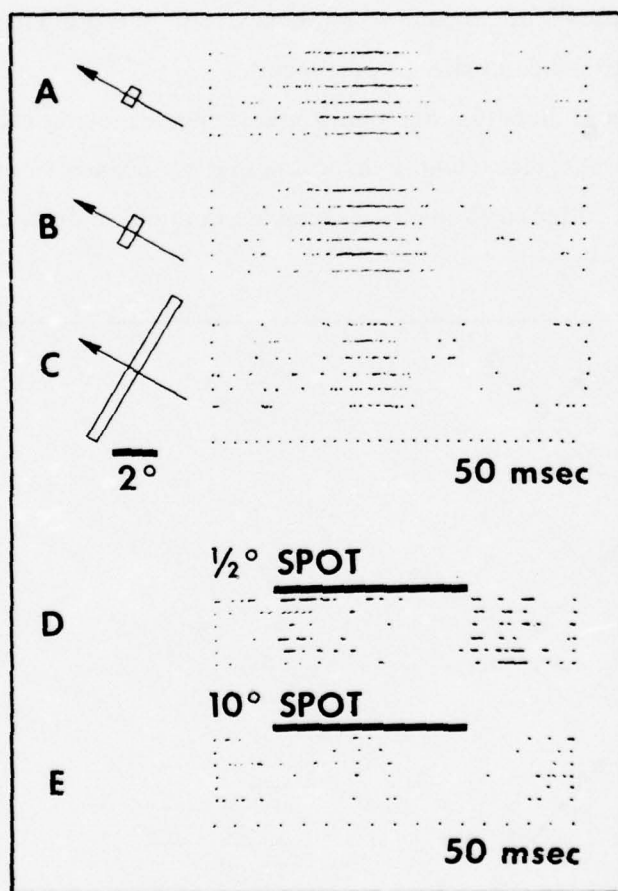


Figure 16. Responses of a direction cell to variations in the size of moving and stationary stimuli. Movement in A-C was $10^\circ/\text{sec}$. Stationary stimuli in D and E were centered on the receptive field. The responses of this cell to different directions of movement of stimulus B are shown in Figure 14.

well to the long slit (C). We did not test systematically to determine if the length restriction was imposed at one or at both ends. Figure 16D,E show the responses of the same cell to flashed stimuli of different sizes. The cell responds transiently at on and off of a small, centered stimulus (D), and more weakly to the larger stationary stimulus (E) indicating the action of a suppressive surround. There were no responses to small spots outside the field center. About one-quarter of all direction cells did not respond to stationary stimuli; transient on and off responses to flashed stimuli were characteristic of those cells that did respond. Where stationary stimuli were effective, fields mapped with spots were round or oval. There was no preference for oriented stimuli within the excitatory region, and no summation to stimuli of increasing size confined to the excitatory area. The responses of direction cells to moving stimuli were not predictable from receptive field maps obtained with stationary stimuli.

Direction cells could be classified as "complex" or "hypercomplex".^{24,25} The differences among cells in sensitivity to stimulus length, however, seemed far less significant than the strong sensitivity to direction of movement common to all the cells in this group. Furthermore direction cells have the following properties which distinguish them from orientation cells: (1) weak or no responses to stationary stimuli and no orientation specificity, (2) directional selectivity, with the strongest response to movement in the preferred direction and no response to movement in the opposite direction, (3) broad range of effective directions of moving stimuli, and (4) good response to, and sometimes a definite preference for, short stimuli. The distinction between orientation and direction cells in both area 17 and area 18 is also supported by the findings of Dow (manuscript in preparation) in anesthetized, paralyzed animals.

For six cells tested with colored stimuli, no color specificity was evident. Monocular presentation of an appropriate stimulus moving in the preferred direction was about as effective as binocular presentation (five cells tested).

In summary, direction cells were concerned with direction of movement through their receptive fields. They were indifferent to stimulus contrast, color

and configuration; some were sensitive to stimulus length, preferring shorter stimuli. They showed weak responses and little specificity to stationary stimuli.

Spot cells. The optimal stationary stimulus for these cells (33/251, 13 percent) was a properly positioned small spot; changing the position of a small stimulus, or increasing the size of a properly positioned spot, resulted in weaker responses. In Figure 17 the best position is 2; positions 3 and 1 give

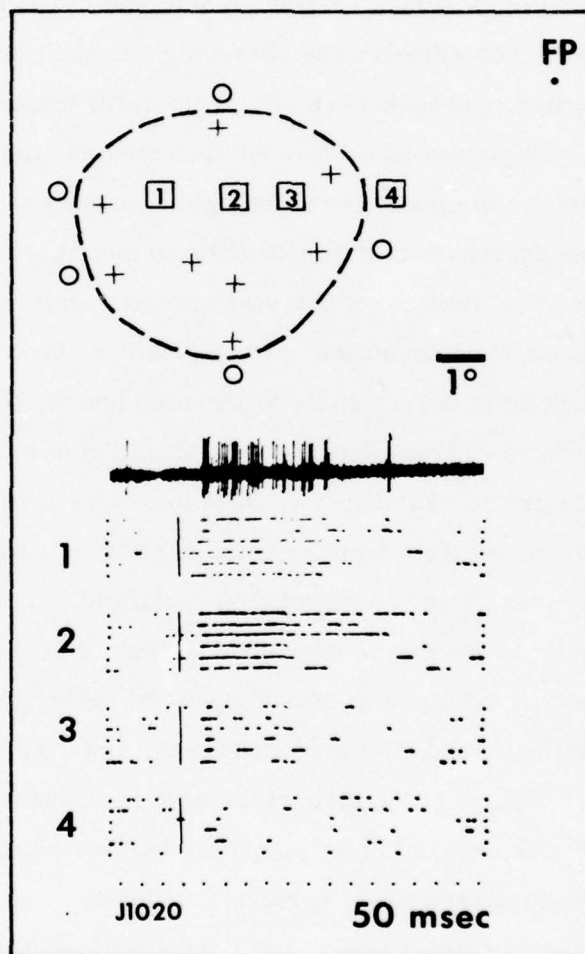


Figure 17. Responses of a spot cell to small stimuli at different positions. 1, 2, 3, 4 refer to positions of the spot which evoked the responses shown in the rasters below. The dashed line encloses the total area in which a spot was an effective stimulus. FP shows the location of the fixation point. The microelectrode recording trace corresponds to the top line of raster 1.

weaker responses, and position 4 gives almost no response. Increasing the length (Figure 18B) or the width (Figure 18C) or both length and width (Figure 18D) of an optimal stimulus results in a less sustained excitatory response.

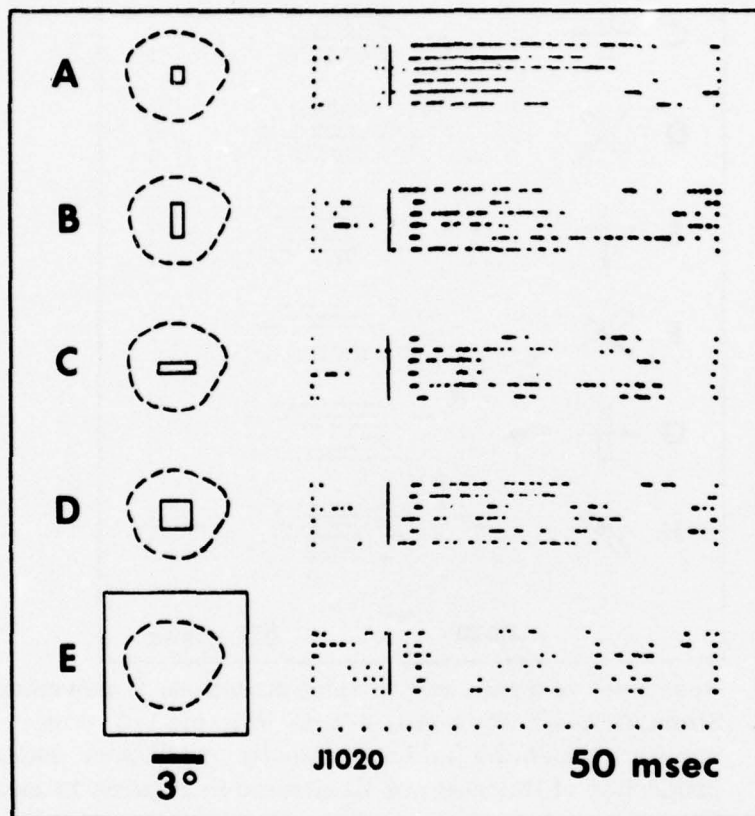


Figure 18. Responses of a spot cell to variations in stimulus size and orientation. This is the same cell described in Figure 17.

Extending the stimulus well beyond the receptive field borders (Figure 18E) weakens the response still further. This cell responded well to all directions of stimulus movement tested (Figure 19).

All cells in this class had round or oval receptive fields. None showed orientation specificity. Preferred stimulus size was typically small relative to total field size. Cells varied in optimal stimulus size and in the degree to which

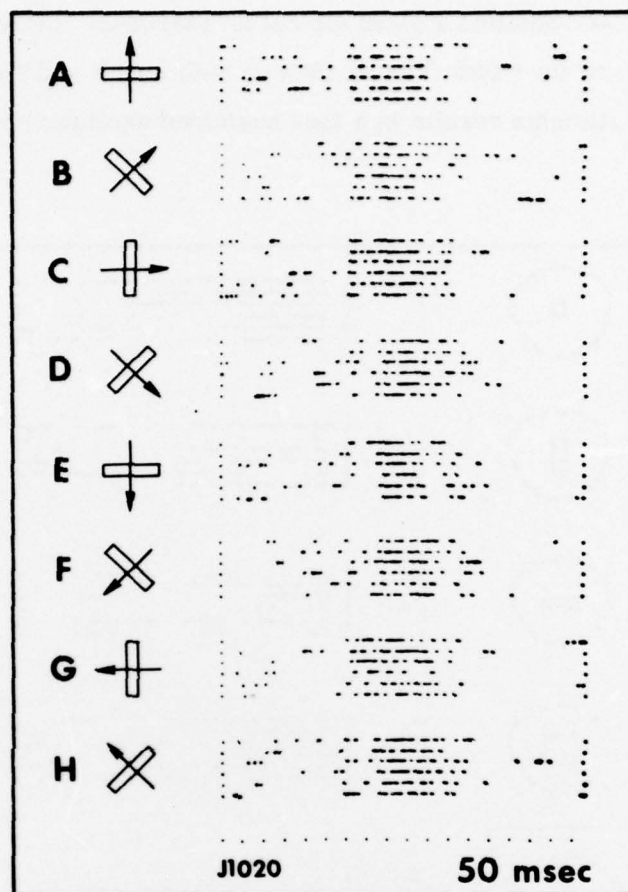


Figure 19. Responses of a spot cell to eight directions of movement. Stimulus was a white slit, $2\frac{1}{2}^{\circ}$ long and $1\frac{1}{2}^{\circ}$ wide, moving through the field at a velocity of $14^{\circ}/\text{sec}$. Other properties of this cell are illustrated in Figures 17 and 18.

an increase in stimulus size would affect the response. The cell illustrated in Figures 17-19 had one of the largest fields seen; other spot cells at the same eccentricity had receptive fields as small as 1° in diameter. Most spot cells responded well to moving stimuli. All 23 cells tested were nondirectional in their responses to moving stimuli. The eight cells tested monocularly responded through either eye alone; we did not do enough monocular testing to determine

if details of field organization were the same in the two eyes. There was no evidence of color opponency in any of the 17 cells tested.

Border cells. Border cells (33/251, 13 percent) responded optimally to a stimulus which filled an excitatory region as long as it did not encroach on a powerful suppressive flank. Figure 20A shows the response of a border cell to a small spot centered in the excitatory area. Filling this region (Figure 20B)

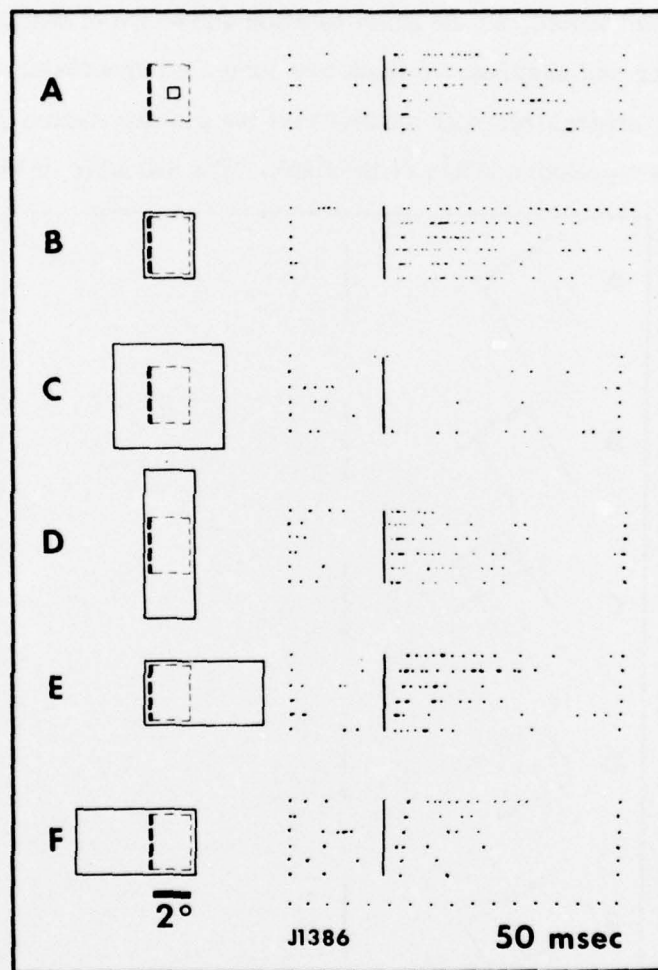


Figure 20. Responses of a border cell to different stimulus configurations. The excitatory part of the cell's receptive field is indicated by the dashed line; the heavier dashed line at the left is the approximate location of the border between excitatory and suppressive areas. The receptive field center was at $2\frac{1}{2}^{\circ}$ lateral, 4° down.

gave a stronger response, indicating summation within the area. Increasing the size of the stimulus further (Figure 20C) completely eliminated the response. Extending the stimulus above and below (Figure 20D) or to the right (Figure 20E) in the field had little effect on the cell's response, whereas extending the stimulus to the left (Figure 20F) reduced the response considerably. The border for this cell was drawn therefore at the left edge of the field. Stimuli extending obliquely were not tested, so the exact location and shape of the border between excitatory center and suppressive flank are somewhat uncertain.

Figure 21 emphasizes with another cell the precise nature of the border and the strong suppressive effect of the flank. The stimulus in Figure 21A is

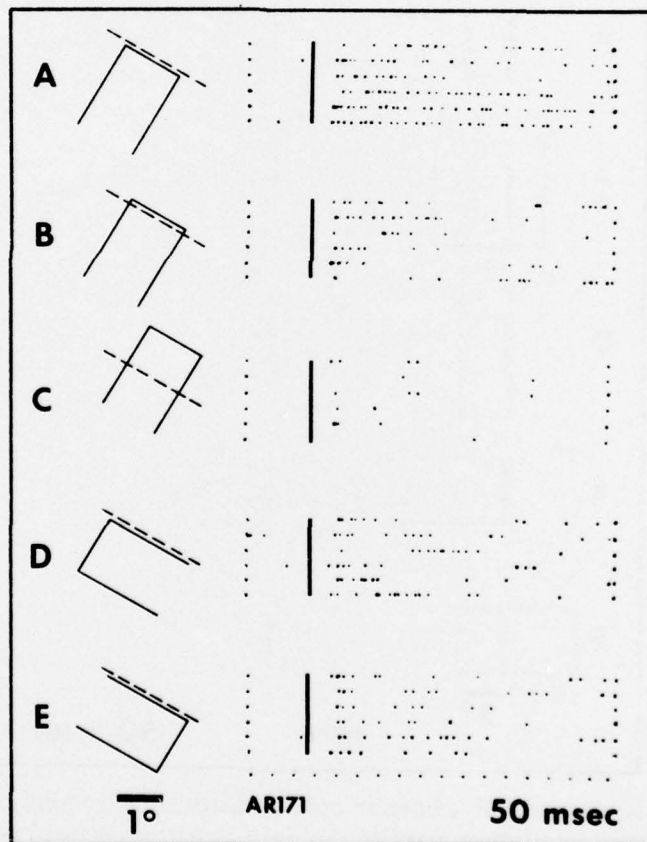


Figure 21. Responses of a border cell to different positions of a stimulus relative to the border. The dashed line indicates the border, with the excitatory region below and the suppressive flank above. Field center was at 1° lateral, 2° down.

quite effective in driving the cell. If that stimulus extends across the border by a fraction of a degree (Figure 21B) the response is considerably weaker. If the stimulus extends across the border still further (Figure 21C) the response is nearly abolished. Figure 21D, E again show the highly asymmetrical arrangement of the suppression; stimuli extending along the border just below it weaken the response less than stimuli crossing the border. We have drawn the borders for these cells as straight lines. For some cells, the best stimulus was a tongue or corner, suggesting that the border was more complicated than a straight line. None of the 10 border cells tested showed color opponency. Most responded well to all directions of movement of a small spot through the excitatory part of the receptive field. Larger moving stimuli were effective as long as they did not encroach on the flank. Four cells tested responded well monocularly.

Border cells resemble hypercomplex cells^{15, 25} in having a suppressive region which delimits the extent of an effective stimulus. However, neither the activating nor the suppressive region of border cells displayed much sensitivity to orientation. Further, the summation properties of border cells were more characteristic of simple than of complex cells²⁴ suggesting that inputs to border cells probably do not come from orientation sensitive complex cells. We therefore rejected the designation "hypercomplex"; these cells may well, however, represent a further stage in the processing of form.

Border cells, then, have an excitatory field limited in extent by a suppressive flank. Their responses may be predicted from the principles of summation within, and antagonism between, the two regions.

Light-inhibited cells. Cells in this class (26/251, 10 percent) were distinguished by high, maintained spontaneous activity which was decreased or abolished by light falling in their receptive fields. It was frequently possible to plot receptive fields with spots of light; fields were round or oval, and showed summation. A few cells required a stimulus as large as the total receptive field extent. Figure 22 shows the increased effectiveness of a stimulus filling the field center (Figure 22B) compared to a smaller spot in the field (Figure 22A).

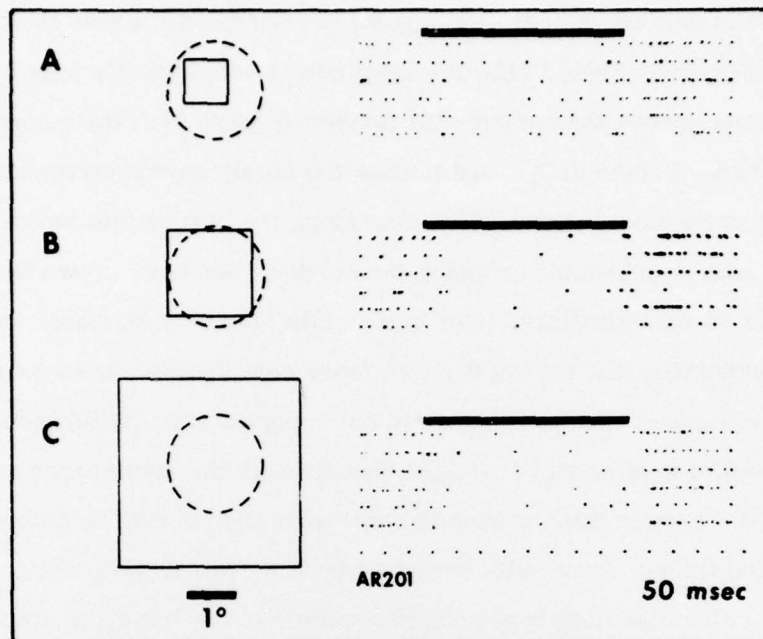


Figure 22. Responses of a light-inhibited cell to stimuli of different sizes. Receptive field center $3\frac{1}{2}^{\circ}$ lateral, $3\frac{1}{2}^{\circ}$ down.

A still larger stimulus is slightly less effective (Figure 22C), suggesting the presence of a suppressive surround. Six of seventeen cells tested likewise showed evidence of a suppressive surround. Seven cells tested with moving stimuli were all inhibited while the stimulus was on the receptive field regardless of its direction of movement. We found no evidence of opponent color inputs to these cells. Two cells were tested monocularly as well as binocularly; both responded about equally under the three conditions.

Cells in this class were inhibited by light falling on a certain region of the visual field. They lacked sensitivity to orientation and direction of movement, and did not show color opponency. Some had antagonistic surrounds limiting the size of a stimulus that would elicit the inhibition.

DISCUSSION

Classification of cells. The major finding to emerge from this study is that different cells are specialized to perform qualitatively different analyses of incoming visual information. We have identified six distinct kinds of analysis, each performed by a separate class of cells. Each class is named for the stimulus parameter to which the cells included are most sensitive, the parameter whose variation elicits the greatest modulation in the response of the cells.

One class of cells is most sensitive to the orientation of elongated stimuli, a second class to stimulus color, and a third class to direction of stimulus movement. Of the remaining three classes, spot cells are sensitive to the size and position of small stimuli in their receptive fields, border cells are sensitive to the position of stimuli relative to their "borders", and light-inhibited cells are sensitive to the presence of light in their receptive fields. In addition to differences in stimulus sensitivity among classes, there are also differences in receptive field organization. Orientation cells and spot cells tend to prefer stimuli that are small relative to receptive field size. Color cells and light-inhibited cells have nonoriented fields with summation through the centers; some cells in those two classes have suppressive surrounds. Border cells show summation within, and antagonism between, excitatory and suppressive regions. Direction cells respond weakly to stationary stimuli; some have suppressive surrounds.

Figure 23 summarizes the results, showing the distribution into six classes of 251 cells recorded from three monkeys. Orientation cells form the largest class. The remaining cells are about equally divided into the other five classes.

Information processing in areas 17 and 18. On the basis of their pioneering studies of receptive fields in areas 17 and 18 of the cat, Hubel and Wiesel^{24,25} proposed a serial model of cortical visual processing. The model suggested that lateral geniculate axons converge on cells with simple properties; simple cell outputs then combine to form complex cells, and complex converge to hypercomplex. Any cell encountered in striate cortex could theoretically be

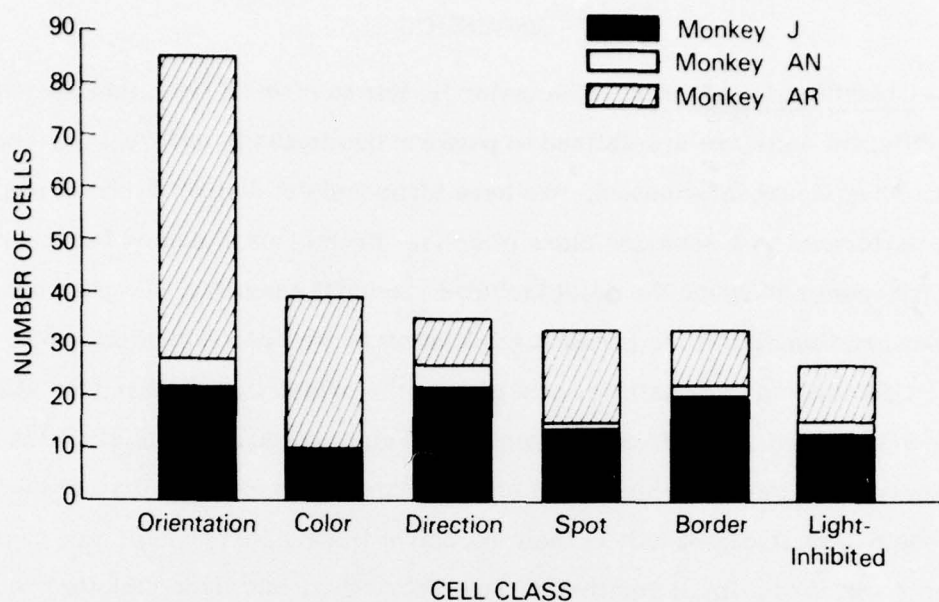


Figure 23. Receptive field classes of 251 cells recorded in area 18 in three monkeys: orientation 85/251, 34 percent; color 39/251, 15 percent; direction 35/251, 14 percent; spot 33/251, 13 percent; border 33/251, 13 percent; light-inhibited 26/251, 10 percent. Each class is divided to show number of cells from each monkey. Monkey J was studied first, AN second, and AR third.

placed somewhere in this hierarchical chain. There have been several challenges to this model.^{11,15,23,32,37} Dow¹¹ proposed a model whereby cells with different properties, such as orientation cells, color cells, and direction cells would constitute independent neuron chains all present in striate cortex. Our data lend support to this notion of multiple processing chains in area 17.

Five of the six cell classes seen in area 18 have clear predecessors in area 17: orientation, color, direction, spot and light-inhibited. Orientation cells in area 18 could receive inputs from orientation sensitive cells in striate cortex.^{11,14,26,35,40} Color cells in area 18 which lack surrounds could receive input from color cells in area 17 with the same properties.^{14,35} Color cells with surrounds might receive fibers from nonoriented area 17 double

opponent cells,^{22,26,34} or be built up from single opponent color cells located in either area 17 or area 18. Area 18 direction cells could receive afferents from directionally selective cells in area 17^{11,40} (also Dow, in preparation). Spot cells could receive inputs from nonoriented cells lacking color specificity in area 17.^{11,26,35} Light-inhibited cells might receive inputs from nonoriented striate neurons more active in dark than in light.^{5,30,40} Although this scheme could explain the formation of area 18 receptive fields solely from striate afferents, recent anatomical evidence indicates that area 18 of the rhesus monkey receives an input from the inferior pulvinar.⁶ Some properties of area 18 neurons might reflect this input.

Because of the striking dissimilarities among cells in the different classes in sensitivity to stimulus parameters such as color, orientation, and direction of movement, and in the spatial organization of their receptive fields, it seems unlikely that cells in one class serve as building blocks for cells in any of the other classes. Rather, the data suggest that cells in separate classes process different kinds of visual information independently of each other.

Zeki has studied the visual responses of cells in two other prestriate areas of the monkey. He reported a preponderance of color coded cells in one area on the anterior bank of the lunate sulcus,⁴² and of movement sensitive cells in another area on the posterior bank of the superior temporal sulcus.^{16,43} His data suggest that cells with different functional properties may eventually be segregated into separate prestriate areas. In contrast, we find several functional cell types in area 18. Possibly cells in these separate groups in area 18 send their outputs to different prestriate visual areas.

Cells with compound specificities such as color orientation or color direction have been described in area 17.^{11,14,22,26,34,35} The transition from area 17 to area 18 is not marked by the development of more cells with compound specificities. Such compound cells in area 17 might project to cortical regions other than 18, or might contribute inputs to area 18 direction or orientation cells without preserving the color specificity.¹³

There are many monocular cells in area 17;^{26,35} all of the cells we tested in area 18 were binocular. Clearly, the transition from area 17 to area 18 entails convergence of inputs from the two eyes onto single cells. Some area 18 cells have specific binocular requirements; others simply receive inputs from both eyes.

Implications for the neural basis of vision. The finding that different populations of cells in areas 17 and 18 are maximally sensitive to different stimulus parameters implies that, at least at this stage in visual processing, the neural representation of visual stimuli is accomplished through the simultaneous activity of cells in different groups, some responding, for example, in relation to form, others to color, and others to movement, rather than through the activity of single cells with compound specificities. We have described cells in terms of optimal stimulus requirements. For each class we have attempted to describe not only the stimulus parameter of greatest relevance, but all subsidiary stimulus parameters that must be specified to elicit the maximal excursion above and below base line from a given cell. While the optimal stimulus must be rather well specified, for any cell there are a great number of stimulus configurations that can elicit a given submaximal response. If one accepts the proposition that submaximal firing to suboptimal stimuli represents signal and not noise,^{17,33} it is clear that the neural specification of even one aspect of a complex stimulus also requires the activity of multiple cells, all within the relevant class. Consider just the analysis of form, as performed by orientation cells. For an orientation cell, the optimal stimulus must first be in the correct place in the visual field. It must also be of the correct orientation, of some minimal length and some specified width. Changing any of the parameters could result in decreased effectiveness of the stimulus, and a variety of different stimuli could thus have the same effect on the cell; one could, for example, change the position of the stimulus, tilt it off the correct orientation by either clockwise or counterclockwise rotation, decrease the length, or increase the width, and obtain equivalent submaximal responses to physically very different, suboptimal stimuli. It would

also be possible to alter the optimal stimulus in ways that have no effect on the cell's response, e.g., by increasing the length. A given suboptimal firing rate of one of these cells is not, then, unambiguously related to some external visual stimulus.

While the result of these various manipulations might be the same to the cell under immediate consideration, they would have different effects on other cells, increasing the effectiveness of the stimulus for some, decreasing it for others. Unambiguous representation of a stimulus could then come about through consideration of the pattern of activity across all cells affected. Most "real", complex visual stimuli would be optimal for few cells, and effective in activating a rather large number of cells, in several classes, at a submaximal level. Stimuli would, therefore, be "detected" through the activity of many cells rather than by single, highly specified feature detectors.

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