Receptive field properties of V3 neurons in monkey

J. S. Baizer

Receptive field properties of cells deep in the posterior bank of lunate sulcus and on the annectant gyms (V3) were studied in the awake, fixating monkey. Properties of these cells were compared with those of a population of cells recorded in V2. Receptive fields of cells in V3 were larger than fields of V2 cells at comparable eccentricities. Cells were classified according to their sensitivity to the orientation and direction of motion of rectangular stimuli. Nonoriented cells were most common (39/75, 52%); the next largest class consisted of cells sensitive to stationary stimulus orientation (25/75, 33%); the third class consisted of directionally selective cells (11/75, 15%). No cells in V3 showed color-opponent responses. Comparison of the orientation-sensitive population in V3 and V2 showed V3 cells more broadly tuned for orientation than V2 cells. These results suggest that V3 and V2 serve different functions in the analysis of the visual world. Neither area, however, is devoted to the analysis of only one stimulus parameter. [INVEST OPHTHALMOL VIS SCI 23:87-95, 1982.]

Key words: monkey visual cortex, prestriate cortex, V3 neurons, visual receptive fields, behaving monkey

Recent anatomic and electrophysiologic experiments have shown that extrastriate visual cortex in primates is subdivided into multiple visual areas.1-9 The functional implications of this organization are not understood, but a promising approach to understanding function has been to compare response properties of cells in the different areas with each other and with cells in Area 17.

How might one expect these cortical areas to differ? Two ideas have been proposed. Extrapolation of the Hubel-Wiesel model of hierarchical processing in the visual pathways10, 11 leads to the prediction of "higher order" cells in the extrastriate regions. However, there is so far little support for the idea that extrastriate cell populations might be more highly specified than Area 17 cells. Most extrastriate neuron response properties have clear counterparts in Area 17.6, 9, 12, 13

A second idea postulates a functional differentiation of the multiple visual representations and suggests that each area might be concerned with the analysis of a different stimulus parameter (see refs. 6 and 9). These are not incompatible hypotheses; different areas might be devoted to "higher order analysis" of different stimulus parameters. There are some data in support of the idea of functional differences among areas. In rhesus monkey, reports of a preponderance of color cells in the anterior bank of the lunate sulcus (V4) and of directional cells in the posterior bank of the superior temporal sulcus (MT) led to the suggestion that V4 is an area specialized for the analysis of color, and MT for
analysis of movement. In the owl monkey, MT also seems specified for directionality, and another area, DL, for stimulus size. Other data, however, do not support the notion that each extrastriate area is concerned with only one stimulus parameter. In V2 we found cells with a variety of stimulus specificities, reminiscent of the diversity of cell types seen in Area 17. Recent reports also question whether the degree of color specificity in V4 is markedly greater than that in V1 or V2.

In this article we describe response properties of cells in a narrow strip of extrastriate cortex bordering V2. This region has been referred to as V3 และ Zeki has claimed that both V2 and V3 contain mainly cells sensitive to stimulus orientation. His data do not suggest functional differences between these regions. We have found, however, that V3 is distinguished by fewer cell types than found in V2 and, further, that stimulus orientation is not of concern to the majority of V3 cells. In addition, comparison of the orientation-sensitive cells in V2 and V3 shows differences between these subpopulations. Orientation cells in V3 are less tightly tuned for orientation and less sensitive to stimulus width than V2 orientation cells.

Materials and methods

Recordings were made from extrastriate cortex of five awake, trained rhesus monkeys. Procedures for training the animals, restraining their heads, and recording neuronal responses and eye movements were as previously described. Briefly, animals were fluid deprived and trained on a task requiring them to maintain fixation on a small spot of light projected on a tangent screen. The animals learned to depress a response lever mounted on the chair. This turned on a small spot of light, the fixation light, which remained on for a variable period of time, usually 1, 2, or 3 sec. The fixation light then dimmed for about 0.5 sec. If a monkey released the lever during the dim period, he received a reinforcement of a drop of water. After several weeks of pretraining, monkeys were surgically implanted, under aseptic conditions, with bolts for head fixation, silver-silver chloride pellet electro-oculogram electrodes, and a stainless steel microdrive base. The microdrive base was centered over the lunate sulcus and was angled so that penetrations could be made in parasagittal planes. Recordings were made from about 6 to 15 mm lateral to the midline. Penetrations were spaced 1 mm apart. Cell activity was recorded with glass-insulated platinum-iridium microelectrodes.

The procedures used in analysis of visual response properties were as previously described and are briefly summarized below. Visual stimuli were automatically presented during fixation periods and were white or colored spots or bars of light. A rectangular diaphragm was used to adjust stimulus length, width, size, and orientation. White stimuli were 1.0 or 1.6 log units above background illumination of 1 cd/m². Colored stimuli were obtained by inserting broad-band Wratten filters into the light path, giving red (Wratten 25), blue (Wratten 47 B), green (Wratten 61), or yellow (Wratten 15) stimuli. Response properties for most cells were first determined with white stimuli. When the optimal spatial configuration had been determined, the color of the stimulus was varied. Responses to colored stimuli were then compared with responses elicited with only neutral density filters in the light path. No attempt was made to quantify responses as a function of wavelength. This testing procedure can reveal color opponent or strongly color biased cells, but more subtle differential sensitivity to wavelength might well be undetected.

Both stationary and moving stimuli were used. Stationary stimuli were usually flashed on 500 msec after the onset of the fixation point and turned off at the end of the trial. Thus stimulus duration varied from trial to trial, from 0.5 to 2.5 sec as a function of fixation duration. When we wished to examine responses to stimulus offset, we turned the stimulus off during the trial, before the animal broke fixation. Moving stimuli were generated with a mirror-galvanometer system, and velocities were in the range of 2° to 20°/sec. They were swept through the receptive field during fixations. We did not systematically vary velocity but chose speeds that elicited strong responses from a cell. Binocular interactions were assessed by comparing responses to the same stimulus presented to both eyes together and to either eye alone. A cell was considered to show binocular interaction if responses to monocular stimulation differed greatly from responses to binocular stimulation with a particular stimulus.

The locations of recording sites of interest were "marked" by passing 15 μAmp of current through
Fig. 1. Diagram showing three penetrations, 1 mm apart (B) down the posterior bank of the lunate sulcus at the level of section shown in A. Recording sites 1 to 6 are numbered in increasing order as they move from the V1-V2 border toward the anterior border of V2. C, Progression of receptive-field centers, plotted for single cells or small clusters of cells. Recording sites 7 and 8 are in V3. Receptive-field centers begin moving away from the horizontal meridian. B also illustrates receptive-field sizes for two V2 cells recorded at sites 5 and 6 and two V3 cells recorded at sites 7 and 8. The V3 receptive fields are larger. The photomicrograph inset shows the three marking lesions 1 mm apart used to reconstruct penetration III.

the recording electrode for 10 sec. Different numbers and patterns of lesions were used on different penetrations in the same hemisphere. After recording from an animal, it was deeply anesthetized and perfused through the heart with saline and then formalin. The brain was removed and allowed to sink in sucrose formalin. Thirty-five micrometer frozen parasagittal sections were cut and stained with cresyl violet. Marked penetrations were reconstructed whenever possible and drawn onto tracings of the appropriate sections. Recording sites on other penetrations were localized on the basis of penetration position relative to marked penetrations, depth of electrode, and recording "landmarks" such as multiunit receptive-field location and size, and were drawn onto tracings of representative sections.

Results

Cells were recorded from five monkeys. The results are based on 75 cells recorded in V3. Comparisons with V2 were made on the basis of data reported earlier, supplemented by some additional V2 recordings. Cells in V3 were encountered beyond the anterior border
Fig. 2. Responses of a V3 nonoriented cell to different configurations of stationary stimuli. Dashed line, Receptive field of the cell, as plotted with small stationary spots; solid lines, visual stimuli. Scale is shown at the bottom left. Data are shown in raster format; action potentials are represented by dots. A column of dots indicates beginning and end of each line. Each line of the raster corresponds to one stimulus presentation. The vertical line at the left indicates stimulus onset. Stimulus duration varied from trial to trial. The row of dots below the raster shows the time base (50 msec between dots). These conventions are followed throughout. The cell responded best to the small spot in B. Changing the position (A, C, and D) or increasing the length (E), width (F), or overall size of the stimulus (G) decreased the response. Enlarging the stimulus beyond the receptive field boundaries (H) decreased the response still further, suggesting a suppressive surround mechanism.

of V2, the representation of the horizontal meridian, which lies deep in the posterior bank of the lunate more medially, or in the annectant gyrus more laterally.

Entry of the electrode into V3 was signaled by a reversal of progression of receptive fields, which move toward the horizontal meridian as the anterior border of V2 is approached and then away from the horizontal meridian as the electrode enters and traverses V3. This is illustrated in Fig. 1, which shows data from three penetrations at a relatively medial level. In penetrations I and II, recording sites were from V2. In penetration III, the electrode entered V3 between recording sites 6 and 7. Receptive fields then shifted away from the horizontal meridian.

There was a dramatic increase in the sizes of receptive fields encountered in V3 compared with those in V2. This can be seen in Fig. 1, which compares receptive field sizes at recording sites 5 and 6 in V2 and at sites 7 and 8 in V3. This was true for all V3 cells, regardless of stimulus specificity. Mean receptive field size for 55 V2 cells, whose receptive field centers were between 6° and 12° from the fovea, was 1.8°, S.D. 0.46. For 51 V3 cells over the same eccentricities, the mean size was 3.9°, S.D. 0.70. Receptive field size was calculated as the square root of the product of length times width.

All V3 cells had receptive fields in the lower, contralateral visual quadrant, with centers from 4° to 13° from the fixation point. As in V2, cells in V3 were visually responsive and could be driven with relatively simple stimuli such as spots or bars of light. Most cells responded well to stationary, flashed stimuli. Cells were first evaluated for sensitivity to the orientation of stationary stimuli, bars, and edges of light, and to direction of motion. We divided cells into three major groups on the basis of their orientation and direction sensitivity.

The majority of cells encountered lacked sensitivity both to orientation of stationary stimuli and to the direction of motion; we classified these as "nonoriented cells." Other cells were sensitive to the orientation of sta-
tionary stimuli; these are referred to as "orientation cells," and were similar to V2 orientation cells. A third group of cells was indifferent to the orientation of stationary stimuli but selective for the direction of motion; these cells were similar to V2 "direction cells." These three classes of cells will be described separately.

**Nonoriented cells (39/75, 52%).** The largest single class of cells lacked sensitivity to stimulus orientation and direction but responded optimally to spots. These cells varied considerably in the size of the optimal stimulus relative to total field size. For 26 cells, a measure of size preference (S) was calculated as the ratio of preferred stimulus size to total receptive-field size. About one third of the cells (9/26, 35%) preferred a small stimulus (S = 0.1 to 0.3). These cells were qualitatively similar to area 18 "spot" cells; both receptive-field and optimal stimulus sizes, however, were larger. Fig. 2 shows responses of one such cell (S = 0.2). The best response was to a small spot in the position shown in Fig. 2, B. Changing the position of the spot (A, C, and D) or increasing its length (E), width (F), or overall size (G and H) resulted in weaker responses. Seven cells (7/26, 27%) preferred stimuli of intermediate size (S = 0.3 to 0.6), and eight (8/26, 31%) preferred a large stimulus (S = 0.6 to 1.0). For all cells, increasing the size of the stimulus beyond the optimal rendered it less effective.

Nonoriented cells also varied in response pattern. Some, like the cell in Fig. 2, gave a sustained response to the optimal stimulus (13/39, 33%). Others gave only a brief burst, usually at both stimulus onset and offset (26/39, 67%). There was some slight but not significant tendency for the more sustained cells to prefer smaller stimuli; 75% (9/12) of the sustained cells preferred a stimulus less than half the size of the receptive field; whereas only 46% (6/13) of the more transient cells preferred a stimulus that small.

In V2, cells giving opponent-color responses were 16% of the population. These V2 color cells lacked orientation and direction selectivity. We tested 30 V3 nonoriented cells with colored spots by the same procedures as used in V2. All responded about equally well to colored and white stimuli; none gave color-opponent responses.

**Orientation cells (25/75, 33%).** The defining characteristic of cells in this class was sensitivity to the orientation of elongated stimuli. They were qualitatively similar to orientation cells in V2 but differed in several quantitative respects. These cells tended to respond to a wider range of orientations than V2 cells, often responding, although weakly, to the orientation perpendicular to the preferred. Fig. 3 shows responses to different orientations for one V3 cell. Fig. 4 compares orientation tuning for the V2 and V3 populations studied.
A number of V3 orientation cells were also insensitive to stimulus width (Fig. 5), some (7/11 tested) responding almost as well to an edge as to a narrow bar of light (Fig. 6).

Directional selectivity was tested in 20 orientation cells. A slit of optimal orientation was moved through the receptive field perpendicular to its long axis, and responses to the two directions of movement were compared. Most (19/20) responded about equally well to both directions of movement. Orientation cells responded quite well to white light. All of the orientation cells tested (19/19) gave about equal responses to white and colored stimuli.

**Directional selectivity** (11/15, 73%). Cells in this class preferred moving stimuli and were directionally selective. They gave their best responses to movement in some direction, and gave no response, or inhibition, to movement in the opposite direction (Fig. 7). In those cells tested, 2/2 responses to moving stimuli were independent of stimulus color. A few cells (3/8) responded better to a spot than to a slit moving in the preferred direction. These cells were indifferent to the orientation of stationary bars of light (5/5).

**Binocular interactions.** Hubel and Wiesel studied binocular interactions in macaque extrastriate cortex. They reported a population of "binocular depth cells" in the lunate sulcus and on the annectant gyrus; some of these cells were thus probably in V3. We initially studied each cell with binocular stimulation, and most cells responded quite well under these conditions. Twenty-eight cells were tested for binocular interactions; we did not vary disparity but compared monocular and binocular responses to a given stimulus configuration. Of the cells tested, 19 cells (68%) responded about equally to stimulation through each eye alone as to both eyes together. Nine cells (32%) responded differently to monocular and binocular stimulation; four showed binocular facilitation. Five responded most strongly to stimulation of one eye; these might well be the disparity-sensitive cells of Hubel and Wiesel.

**Discussion**

We found that the analysis of the visual world in V3 was both simpler and cruder than in V2 in all respects that we tested. When analyzing responses to the same stimuli, using the same procedures, we found fewer cell classes in V3 than in V2. We found three cell classes in V3 and six in V2. Although both areas contained orientation-sensitive cells, directional cells, and nonoriented cells, no color, border, or light-inhibited cells were found in V3; these cells constitute major classes in V2. These results agree with those of Zeki in the absence of color-opponent cells in V3. We have found a somewhat lesser number of binocular cells in V3 than in V2; this is consistent with the findings of Hubel and Wiesel.
Fig. 6. Responses of a V3 orientation cell to a stationary bar and edges of appropriate orientation. The response to edges of either contrast (B and C) was weaker than the response to the bar (A) but was still strong.

higher percentage of color-opponent cells in V2 than he has reported (16%12 compared with 8%9).

We agree with Zeki8 and Gattas et al.18,19 that receptive fields are larger in V3 than in V2. Thus a single cell in V3 carries less precise information about location of a stimulus in the visual field than does a V2 cell receiving information from the same part of the retina. Similarly, an orientation cell in V3 on the average carries less information both about stimulus orientation and stimulus width than does an orientation cell in V2.

Zeki8 has reported that 88% of his V3 sample was orientation specific. Using the same criterion for orientation sensitivity, namely differential responses to a bar moving in different directions, we would include only 48% of the V3 population; both orientation (25/75) and direction (11/75) cells would respond differentially to oriented bars moving in different directions. There are several possible reasons for this discrepancy. Our recordings were made in awake, trained animals, whereas his were made in the anesthetized, paralyzed animal. Nonoriented cells may well be more responsive in the latter preparation. Furthermore, our results are based on well-isolated cells; Zeki used both single and multiunit recordings.

Fig. 7. Responses of a V3 directional cell to different directions of movement of a spot. The cell gave its best response to the range of directions in C, D, and E. The response fell off as direction was changed still further (B and F). The cell was unresponsive to directions shown in A, G, and H. Velocity was 3°/sec.

The results do not support the notion of more complex feature detection by extrastriate cells; indeed, greater specificity is evident in striate cortex10,13 than in either V2 or V3. A color-specific simple cell13 has rather
stringent stimulus requirements; the stimulus must be precisely positioned, precisely oriented, and of the right wavelength to elicit maximal response. V3 cells, by contrast, are considerably lenient about position and form and are indifferent to color. Our studies in extrastriate cortex support the idea that the different extrastriate areas differ from each other and from primary visual cortex. V3 and V2 clearly differ in their analysis of pontine nuclei; this pathway is most likely parts of extrastriate cortex to inferotemporal between areas.

response properties so far have been studied parameter. It is worth noting that extrastriate however, is likely to be understood as de-voted to the analysis of only one stimulus pa-rameter. It is worth noting that extrastriate response properties so far have been studied only with relatively simple stimuli. It is possible that the use of more complex stimuli might reveal even more dramatic differences between areas.

It is also important to consider the possibility that not all extrastriate areas may be concerned with stimulus analysis per se. Diff-ferent areas might be extracting different kinds of visual information for rather different functions. There are anatomic data in support of this idea. There are projections from some parts of extrastriate cortex to inferotemporal cortex, an area clearly involved in visual learning.21,22 There are projections from different regions of extrastriate cortex to the pontine nuclei; this pathway is most likely involved in the visual guidance of move ment.23 Information useful for control of vi-sually guided movement may well differ from that needed for learning about critical features of the environment. The number of vi-sual areas and the properties of neurons in each thus may reflect the various ways in which visual information is used by the nervous system.

I thank Susan Wolf for secretarial assistance, Julie Lakatos for graphics and photography, and David Bender and William Maguire for helpful comments on the manuscript.

REFERENCES


20. Hubel DH and Wiesel TN: Cells sensitive to binocu-

