Luminance Coding of Briefly Presented Stimuli in Area 17 of the Rhesus Monkey

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SUMMARY AND CONCLUSIONS

1. Single cells in area 17 of the alert rhesus monkey were classified according to their sensitivity to variations in stimulus orientation, color, and direction of movement. The sensitivity of the cells to stimulus luminance was then tested using moving bars and large stationary spots presented for 500 ms. The luminance of the stimulus was varied over trials; background luminance was kept constant. Short stimulus durations and long intertrial intervals were chosen to minimize changes in light adaptation, and thus compare responses to briefly presented stimuli of different luminances at a constant mesopic adaptation level (0.15 ft-L). Moving bars were chosen so as to be of optimal orientation for orientation-specific cells.

2. Orientation-specific cells differ from cells without orientation specificity in the range of stimulus luminances over which they respond differentially. Generally, orientation-specific cells show response saturation at luminances 2–10 times the background luminance. Cells without orientation specificity respond differentially over a larger luminance range; some of these cells did not show response saturation within the range tested.

3. We conclude that under conditions of constant light adaptation, the luminance of a brief stimulus is more reliably coded by cells without orientation specificity, particularly at higher stimulus luminances.

INTRODUCTION

A goal of visual neurophysiology is to describe the manner in which successive neural structures preserve and transform information contained in the visual image. Visual information processing in a variety of animals has been shown to include groups of cells that are particularly sensitive to certain aspects of the image. This specialization is well developed at the level of striate cortex in the monkey, where cells show differential sensitivity to such stimulus parameters as orientation, form, color, disparity, and movement (9, 10, 12, 17–20, 22, 27). Somewhat surprisingly, sensitivity to pattern luminance has not been as extensively studied as sensitivity to these other stimulus dimensions. Psychophysical observations show that humans distinguish brightness differences in flashed stimuli over a wide range of stimulus luminances. The magnitude of the range is determined by adaptation level of the eye, since flashes with luminances more than 2 log units below the adapting level will be below threshold and not perceived. The upper limit of the range, however, seems independent of adapting luminance (21, 24) and appears under certain conditions to be unreached even at very intense luminance levels, corresponding to the luminance of the sun (≈10^8–10^9 ft-L) (21).

Given the many psychophysical similarities between vision of man and rhesus monkey (7, 8), it seems reasonable to expect that the monkey should experience brightness differences over an equally wide luminance range. It is therefore also reasonable to expect to find cells in the rhesus monkey visual system whose responses could account for the wide range of luminances that are perceptually distinguishable. Cells with relatively wide dynamic ranges have been described in the monkey lateral geniculate nucleus, where some cells have been found to show responses monotonically increasing
with stimulus luminance for flashed stimuli under dark-adapted conditions over a range exceeding 5 log units (2, 16).

There are a number of ways in which this information about stimulus luminance might be transmitted in the next stage of visual processing, striate cortex. Sensitivity to flashed stimulus luminance might be broadly distributed throughout the cell population. That is, all or most cells might vary their responses monotonically with variation in stimulus luminance, regardless of their other sensitivities. A second possibility is that incremental luminance coding is restricted to some subset of the striate cell population. Thus, only a certain percentage of striate cells might respond monotonically with increasing stimulus luminance. In addition, this subpopulation might or might not differ from the general population of striate cells in its sensitivity to other stimulus parameters.

We have studied the ability of striate cells to code luminance of brief stimuli. Our approach was to measure dynamic range (distance between the luminance that elicits a threshold response and that luminance at which response saturates) of a sample of striate cells, after we had determined the standard receptive-field sensitivities of these cells. Dynamic range was determined for two standard test stimuli, a moving bar and a large stationary spot. We found that cells lacked sensitivity to stimulus orientation, regardless of their other sensitivities. A preliminary report of these results has been presented (15).

**METHODS**

**Behavioral and recording procedures**

Two rhesus monkeys were fluid deprived and weighed daily. They had standard laboratory primate chow available ad libitum in their home cages. Animals were trained to climb into a primate chair for daily experimental sessions, and returned to their home cages each evening.

Animals were first trained on the fixation task developed by Wurtz (27). After pretraining, they were anesthetized with pentobarbital sodium and, under aseptic conditions, implanted with head-restraint bolts, a stainless steel microdrive base (Evarts-Narishige), and silver-silver chloride pellet electrodes (4). The bolts provided the base for a head holder, permanently attached to the head, constructed of four aluminum strips cemented to a vertical stainless steel sleeve. A metal rod was fixed to the chair and to the sleeve during recording sessions. Activity of single cells was recorded with glass-insulated platinum-iridium microelectrodes (26) using an Evarts- (11) style hydraulic microdrive (Narishige). The stainless steel base for the microdrive was implanted over parafocal striate cortex. Eye movements were recorded from the pellet electrodes implanted in the bone of the orbits. Unit signals were amplified and sent to a time-window discriminator, displayed on a Tektronix 565 oscilloscope, and sent to an audio monitor. Output pulses from the discriminator were sent to the computer.

Behavioral control and data analysis were accomplished by a DEC PDP 11/34 laboratory computer. The computer constructed rasters and histograms of selectable time base, trigger, etc. Only trials during which the monkey maintained fixation were used in the data analysis.

**Visual stimulation**

Visual stimuli were automatically presented during fixation periods.

Monkeys sat a distance of 114 cm from a large Polacoat screen. The screen was constantly illuminated at a luminance of 0.15 ft-L. Luminance was checked every few days with an Omega photometer. All surfaces within the monkey's field of view were painted a flat gray and the chamber was illuminated by a dim bulb. Visible-surface luminances ranged from 0.05 to 0.25 ft-L, keeping the state of light adaptation relatively stable no matter where the monkey looked between trials. Stimuli were presented through a Leitz projector fitted with a rectangular diaphragm, which permitted focusing of rectangular stimuli of different lengths, widths, and orientations on the screen. Shutters controlled stimulus onset and offset, a set of narrow-band color filters (Melles Griot) adjusted with Wratten neutral-density filters to be of equal transmittance could be inserted in the light path. Luminance was controlled by neutral-density filters and by a pair of Polaroid filters (Bausch & Lomb), one stationary, the other gear mounted and rotatable with a stepper motor. Stimulus position and movement were controlled with an X-Y mirror system. The image projected on the screen was intercepted by a beam splitter and focused on a table, allowing the experimenter to plot receptive-field position and boundaries. The stimulus used to plot receptive fields had a luminance of 2.7 ft-L. All testing was binocular.

**Experimental protocol**

Receptive-field boundaries and characteristics were determined with flashed or moving spots and bars, white and colored. The optimal stimulus was determined by evaluating audio output and by
looking at raster or histogram displays. Cells were classified according to their responses to bar and spot stimuli. Sensitivity to orientation, direction, and color were assessed qualitatively. Cells were classed as orientation specific if responses over some range of orientations were clearly stronger than responses to other orientations. Responses to a stimulus, spot or slit, moving in the direction giving the strongest response were compared with movement in the opposite direction. Cells for which movement in the two directions elicited approximately equal responses were classified as nondirectional; cells giving clearly asymmetrical responses to the two directions of movement were classified as directional. Responses to white and colored stimuli of equal luminance were compared. If responses to colored stimuli were markedly different than responses to white light, cells were classified as color specific.

Cells were then tested with two standard stimuli. One stimulus was a large 4° x 4° white stationary spot centered on the receptive field. It was presented for 500 ms during each fixation. The stimulus exceeded the boundaries of the largest receptive fields encountered. The second stimulus was a moving bar. For cells with orientation specificity, the orientation of the bar, as well as its direction, velocity, and width, were adjusted to give best responses. The bar, however, was always white. If the cell was not orientation specific, a bar was chosen with velocity and width within the standard range that drove the cell well.

The stimuli were always brighter than the background field. Stimuli were presented at a standardized set of luminances and these luminance conditions were presented in random order. The most commonly presented stimulus luminances were 0.16, 0.17, 0.20, 0.25, 0.35, 0.6, 2.85, 10.9 ft-L. These stimuli were created by projecting a stimulus image 0.01, 0.02, 0.05, 0.1, 0.2, 0.45, 2.7, or 10.8 ft-L on the background, which was always 0.15 ft-L.

Each stimulus condition was presented in a block of 8 or 12 trials. If eight trials were chosen, all conditions were generally run twice, giving 16 stimulus presentations per condition. The number of presentation of different luminances was random. Intertrial interval (ITI) was 5 s. With this intertrial interval, there was no sign of habituation over consecutive trials for the great majority of cells. A few cells, however, showed habituation under these conditions. For these cells, we continued to use a 5-s ITI, but presented the stimulus on only about half the trials. In subsequent analysis, we included only those cells on which we had done sufficient testing to determine their responses across a broad range of luminances.

Data analysis

To determine dynamic range we examined two measures of response, peak firing rate and total number of spikes. For moving bars, these two measures give similar results with regard to luminance variation. For stationary flashed spots, total number of spikes tends to saturate at lower luminance values than peak firing rate.

Dynamic range was determined in the following manner. Response threshold was reasonably easy to determine by comparing total number of spikes in the 500 ms preceding the stimulus with the 500 ms during which the stimulus was present, and assigning threshold to the luminance level at which the spike increment during stimulus presentation just exceeded the spontaneous rate, or interpolating this point if it fell between presented conditions. Saturation is more difficult to determine precisely. We assigned saturation values in the following manner. We first determined the conditions over which the response rate averaged over trials was clearly increasing with stimulus luminance. The response rate at saturation was chosen as the largest response seen for any condition. We then computed a regression line and correlation coefficient for the set of points lying on the increasing portion of the function. Saturation was calculated to be that luminance where the regression line intersected a line drawn with \( y = \text{maximum response rate}, \) and slope \( = 0. \)

We examined two regression models, both linear response rate and logarithmic response rate as a function of logarithmic luminance. In general, the correlations were good for both functions, but there was a slight superiority of the logarithmic function (linear response rate) over the power function. The logarithmic function is of course insensitive to the presence or absence of subtractive corrections for spontaneous rate in the data. Only cell profiles for which the regression calculation (logarithmic function) was statistically significant \( (P < 0.05) \) were included in dynamic range calculations. There was one exception to this latter consideration. A few cells, with small dynamic ranges, did not include enough points in the increasing portion of the function to allow the above procedure. Since eliminating these cells would have been an obvious sampling bias, a saturation point was determined by a best-fitting line on semilog coordinates, and statistical considerations were ignored. We used peak firing rate within a 15-ms window to determine the dynamic range of these cells. Response profiles were well fitted by logarithmic functions with the majority of correlation coefficients in excess of 0.9 and significant at \( P < 0.01. \) The slight superiority of logarithmic over power functions for such data has been noted before (25).

Histology

At the conclusion of recording from an animal, it was deeply anesthetized with pentobarbital sodium and perfused with saline and then formalin. The brain was removed and prepared for histo-
logical analysis; 35-μm frozen or celloidin sections were stained with cresyl violet for cells or Weil stain for fibers. We did not attempt to reconstruct each penetration, but did verify recording sites to be in striate cortex.

RESULTS

We recorded from 187 cells in three hemispheres of two monkeys. All cells had receptive-field centers from 1 to 5° from the fixation point, which presumably falls on central fovea.

In pilot work, examining the relation of receptive-field properties, particularly directionality, to luminance coding, we soon found that directionality and color sensitivity appeared to be related to the magnitude of dynamic range of cells only to the extent that these properties were correlated with the presence or absence of orientation specificity. Correlations with other properties could, however, certainly be present and simply missed with our sample sizes.

Our major finding was that orientation-specific cells and cells without orientation specificity differ in their dynamic ranges. Nonoriented cells in general are capable of encoding a much wider range of luminances than are orientation-sensitive cells. We shall describe responses of orientation-sensitive cells and cells without orientation specificity separately.

Orientation cells: responses to moving bars

We were able to determine dynamic range of 17 orientation-specific cells. Of the 17 cells, 10 showed neither color nor directional specificity, 5 showed directional and not color specificity, 1 showed color and not directional specificity, and 1 was selective for both color and direction. Stimulus widths varied from 0.08 to 0.5° velocities from 3 to 20°/s. In general, responses of these cells saturated at relatively low stimulus luminances. Figure 1 shows the response profile of one such cell. The example is typical. The median dynamic range for all orientation cells using peak response as the response measure and the logarithmic model to determine saturation luminance was 1.4 log units. In addition, the greatest stimulus saturation luminance measured for an orientation-specific cell was 1.4 log units above background level. Thus orientation-specific cells are differentially sensitive to only a restricted range of stimulus luminances. At higher luminances, further luminance increases either have no effect or, for a number of cells, cause some decrease in response.

We were aware of a possible complication of our testing procedure, namely that increasing stimulus luminance might increase the effective width of the stimulus by increasing stray light on the screen and in the eye. Thus, an optimal stimulus might become increasingly nonoptimal as stimulus luminance was raised. For this reason, we tested a number of cells with a second bar stimulus twice as wide as the first. We found no consistent changes in the response profiles of cells tested with the stimulus save for a small tendency toward lower thresholds. In general, doubling stimulus width had only small effects on the peak firing rate of the cell. This relative insensitivity to width of moving-bar stimuli in striate cortex has been noted elsewhere.

Cells without orientation specificity: responses to moving bars

We were able to determine the dynamic range of 21 cells without orientation specificity with moving bars. Most of these cells had receptive fields with centers excited by light onset and inhibitory surrounds. Some (4/21) had uniform fields giving on-off responses throughout and preferring a stimulus smaller than the total receptive-field extent. Others (4/21) exhibited some type of color opponency. A few (3/21) showed directional specificity to a moving stimulus. These were tested with bars moving in the optimal direction. Of the 21 cells, 5 also responded to large spot onset in an excitatory manner.

These cells clearly had wider dynamic ranges than the orientation-specific cells, with a median range value of 2.4 units (an example is given in Fig. 2). As with the orientation-specific sample, the logarithmic functions matched the data closely with the vast majority of correlation coefficients in excess of 0.9. Figure 3 shows the distribution of dynamic range across the luminance continuum for both orientation-specific and nonoriented cells. The differences between the two groups are easily seen, the larger dy-
The difference in dynamic range between orientation-specific and nonoriented cells was statistically tested using the Mann-Whitney U test, a nonparametric test that makes no assumptions about the underlying distribution of dynamic range. The test showed differences between the two samples to be significant (Z = 2.24, P < 0.05).

The nonoriented cell population showed a wide distribution of dynamic ranges (Fig. 3). We did not find receptive-field organization or color specificity to be predictive of dynamic range in these cells. Cells with center-surround receptive-field organization were found with the smallest and the largest dynamic ranges encountered. Similarly, both
color and noncolor cells were found with wide and narrow dynamic ranges.

**Orientation cells: responses to large spot**

Most orientation cells (15/16) tested responded weakly, if at all, to this stimulus. Only one orientation cell, a complex cell with no directional or color specificity, was excited by this stimulus. The response showed a high threshold and decreased at higher intensities.

**Nonoriented cells: responses to large spot**

In contrast to orientation-sensitive cells, many (21/61) nonoriented cells were excited by the large spot stimulus. Some (12/61) showed inhibition below spontaneous level. Eighteen were unresponsive. The remaining 10 cells showed unique or complex responses, such as inhibition at high intensities and excitation at low intensities.

We were able to hold 13 of the 21 excited cells for a time sufficient to determine re-
Fig. 3. Threshold, saturation, and dynamic-range values of 21 nonoriented and 19 oriented cells tested with a moving-bar stimulus. Nonoriented cells are above the axis and orientation specific cells below the axis. Each bar represents a single cell, cells have been ordered according to their response thresholds. Luminance is expressed logarithmically as proportional increments to background. 0 on scale represents 0.15 ft-L.

responses to a broad range of luminances. Most of these cells had receptive fields with concentric antagonistic center-surround organization. Two were color opponent, and three were of the uniform variety. Table 1 provides threshold and saturation values for these cells as well as the results of the regression analysis performed on the averaged data. As with the moving-bar data, the logarithmic function is a slightly better fit than

<table>
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<th>Cell No.</th>
<th>Threshold</th>
<th>Log Slope Spikes/Log, ft-L</th>
<th>Log Saturation</th>
<th>r</th>
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Values based on responses of cells to 500-ms flashes of a 4° x 4° spot stimulus.
the power function, particularly for the measure of total spikes. The peak and total spike measures also yield different estimates of saturation. Some cells show no saturation of the peak response measure. Nonetheless it is clear, particularly where peak response measure is considered, that many of these cells have dynamic ranges in excess of 3 log units and that they encode luminance information differentially throughout the range tested. Figure 4 shows the response of one such cell.

Human brightness sensation as a function of stimulus luminance under mesopic conditions has been described by the equation $\psi = K(L - L_0)^\gamma$. Plotted on logarithmic coordinates this function is negatively accelerating at low luminances, becoming a straight line at high luminances. The exponent under mesopic conditions is approximately 0.4. In Fig. 5 we have plotted the variation in firing rate with luminance increments for the on-type nonoriented cells for both the peak response and total spikes measures. For each curve spontaneous activity was subtracted out. The curve reconstructed from peak response rates is a somewhat better match to the psychophysical data than the total spikes
FIG. 5. Average responses, based on pooled data from 13 on-type nonoriented cells. Open circles represent peak firing rate based on a 15-ms-wide window. Filled circles represent average firing rate during the time the stimulus was on. For both curves, the spontaneous rate has been subtracted.

measure. At the lower luminance levels, the curve resembles very much the psychophysical data, however, it tends to flatten out and deviate from linearity at the higher luminances. The possibility exists, however, that cells with very high thresholds for the spot stimulus may have been classified as unresponsive. The presence of such cells might lead to a steeper slope at high luminance levels than we found.

DISCUSSION

We have found that information about stimulus luminance of a moving bar or large flashed spot is more effectively coded by the nonoriented striate cell population than in the population tuned to the geometric properties of the bar. There appears, then, to be a subclass of striate units particularly suited for the transfer of information about stimulus luminance and relatively insensitive to stimulus orientation. Some of these cells are also sensitive to wavelength.

Coding of stimulus luminance has also been studied in the retina and lateral geniculate nucleus (LGN). Boynton and Whitten (5) showed that the late receptor potential increased with intensity of a flashed light over many log units under various conditions of light adaptation. Over most of the range the curve approximated a power function with exponent 0.7. The search for neural analogues to the wide response range more centrally in the visual system has been less successful. In the cat, those retinal ganglion cells and lateral geniculate cells studied have rather narrow dynamic ranges (6, 25).

In the monkey, an early study by Jacobs (13) using large diffuse-field stimulation revealed narrow, 1-log unit response ranges for LGN units. Two subsequent studies in the rhesus monkey LGN, however, were more successful in discovering cells with wide dynamic ranges. Marocco (16) found that 10% of his LGN sample showed dynamic ranges of 5 log units in the dark-adapted monkey with brief stimuli filling receptive field centers. Recently, Barlow et al. (2) using ganzfeld flashes found units in the LGN with 5-log unit ranges.

It would appear then that this wide range of flash-luminance information is carried by striate cortex cells unselective for orientation. Color specificity also appears to be more common in cells without orientation selectivity than orientation-specific cells (9, 10, 22); however, all types of orientation-specific cells have been shown to have color-selective representatives, and this selectivity is particularly high among simple cells (22). In the present study we found 47% of cells without orientation specificities to have color specificities, while this was true of only 20% of the orientation-specific cells. There appears to be an equivalent clustering of directional specificity into the largely orientation-specific cell class. In this regard the partition of cells into orientation-specific/nonspecific groups seen in striate cortex may not reflect differences between two stages in a hierarchy as much as a functional separation of extensive and intensive qualities of the visual scene (9, 10). Recently, Kayama et al. (14), have described the correlation between another intensive quality of the visual array, the ambient illumination, and specificity for orientation. Luxotonic units (units that alter maintained discharge with changes in ambient illumination) generally also lack orientation specificity.

In area V2, one also finds that cells without orientation specificity carry more color information than cells with orientation specificity (1). We are presently looking at lu-
REFERENCES


2. BARLOW, H. B., NOEL, W. M., AND SNODDERLY, D. M. Intensive information is similar there. Whether the separation of extensive and intensive information is similar there.


