Contours and Contrast: Responses of Monkey Lateral Geniculate Nucleus Cells to Luminance and Color Figures

Abstract. *The responses of single units in the monkey lateral geniculate nucleus to different portions of figures which differed from their backgrounds in color and brightness were examined. Border enhancement was found in the response to luminance figures but not in the response to color figures. In addition, cells showed border enhancement only in the case of a figure which produced an increment (as opposed to a decrement) in their firing rates. In situations in which very striking brightness contrast is seen perceptually, the cells do not show the corresponding changes in firing rate across the whole pattern. The lateral inhibitory mechanisms found in the retina and geniculate can thus account for luminance border enhancement, but not entirely for simultaneous brightness or color contrast, for which other cortical processes of some sort must be responsible.*

It has long been known that spatial contours are very important in visual perception. To a large extent, the importance of a spatial contour is that it provides a temporal change as the eye sweeps or oscillates across it: experiments in which the retinal image is stabilized show that spatial contours in the absence of temporal change cannot maintain vision of forms for more than a few seconds (*1*). Nonetheless, spatial contours by themselves also play an important role.

A century ago, Mach (*2*) postulated the presence of lateral interactions in the visual system to account for the bright or dark lines (since known as Mach bands) seen at discontinuities in certain types of visual figures. He further postulated that such lateral interactions could account for brightness and color contrast. Ratliff and Hartline (*3*) have shown that eccentric cells in the *Limulus* eye show the neural equivalent of Mach bands in enhanced firing rates at luminance discontinuities in a figure, and that this can be explained by the presence of an excitatory-center, inhibitory-surround organization in the cells' receptive fields much like that postulated by Mach. Retinal ganglion cells in the cat have a similar although more complicated center-surround arrangement of the receptive field and also display enhanced firing at the borders of figures composed of luminance differences (*4*).

In higher primates there is the additional complication that visual figures can be distinguished from their backgrounds not only on the basis of luminance or brightness differences, but also on the basis of color differences. Figures of these two types may very well be analyzed quite differently by the visual system. In fact, although Mach bands at the contours of some types of black-white figures are very obvious, there has been considerable disagreement on whether pure color borders produce Mach bands at all (*5*). It is also by no means clear whether such border phenomena as Mach bands, which reflect local interactions, and brightness contrast, which operates over vast retinal distances, can be accounted for by the same process. For all these reasons, it appeared useful to examine how the cells in the monkey lateral geniculate nucleus respond to the borders and to the central regions of various types of visual figures presented to the eye.

We have shown (*6*) that different classes of cells in the primate visual system are involved in the processing of achromatic and chromatic information. Spectrally opponent cells, which respond with excitation to some wavelengths and with inhibition to others, are responsive to color differences; spectrally nonopponent cells carry information about the achromatic (black-white) dimension. These latter cells are very responsive to differences in luminance; spectrally opponent cells, for the most part, especially the red-green cells, respond to luminance differences to a considerably lesser extent. In the experiment reported here we examined how the cells of these various types respond to both luminance and color borders.

Ideally, one would like to present a figure to the eye while recording responses from cells whose receptive fields were at all possible locations with respect to the figure: outside it, right at the border, and inside it. One cannot perform such an experiment because of the impossibility of finding the appropriate cells and recording from them all simultaneously. However, the same goal can be attained by recording from one cell while successively positioning the figure at each of these various locations with respect to its receptive field. This was the approach used by Ratliff and Hartline (*3*), and it is the one we employed.

Since cells in the primate geniculate respond almost exclusively to stimulus transients, it would not be sensible merely to position a figure at various locations and record the steady-state activity. Rather, provision must be made for suddenly presenting the stimulus at different loci. This was accomplished by use of the four-beam optical system diagrammed in Fig. 1. Beam D, which remained on throughout the experiment, subtended 20° of visual angle and provided the background. In the center of this beam was a black square 2° on a side. Each of the other three beams just filled this black square. Beam A provided light of a color and luminance matched to that of the background. The background light plus beam A thus produced a homogeneous surface. To present a figure, beam A was switched off and either beam B or beam C was simultaneously switched on. Beam B came from a monochromator and provided light of some wavelength matched in luminance with beam A and the background. A switch from beam A to beam B would thus present a figure differing from the background in color but not in luminance, with a pure color border. Beam C was of the same color as beam A and the background, but was 0.8 logarithmic unit higher or lower in luminance. A switch from beam A to beam C thus presented a figure that was either brighter or darker than the background but of the same color, thus with a luminance but not a color contour. In the experiments reported here, beams A and C and the background were all white lights of approximately 5000°K. The luminance figures thus appeared perceptually as a white or a black square on a gray background, and the color figures as a colored square on the same background.

The entire optical system was located on a carriage that could be rolled laterally on a table before a translucent diffusing screen which the animal viewed from the opposite side. The animal's eyes were refracted retinoscopically, and contact lenses that were appropriate to the animal's refractive error and the screen distance were fitted.

We made the unit recordings from cells in the lateral geniculate nucleus of the *Macaca irus* monkey, using conventional recording techniques. The eyes of the lightly anesthetized monkey

were immobilized with Flaxedil. We find that it is often possible to immobilize the eyes without attaining a level of paralysis which necessitates artificial respiration by the use of direct retrobulbar infusion of the Flaxedil. When a cell was isolated, its receptive field was located on the screen. The animal observed the screen through a double mirror system (see Fig. 1), the top mirror of which could be rotated to position the receptive field in the same horizontal plane as the optical system. Once this was done, the carriage was moved laterally so that the figure would first be presented some distance away from the center of the receptive field. In successive 1-second stimulus presentations the figure was moved systematically across the receptive field. The homogeneous background remained on during the 10-second intervals between stimulus presentations to maintain a constant adaptation level. In any single traverse, white, black, and color figures would be presented.

The results from a sample of more than 50 cells of the various response types indicate a considerable difference between the responses to color and to luminance borders, and between the responses to white and black luminance borders. Figures composed of luminance differences consistently produce border enhancement from those cells that show excitatory responses to them: such cells show more firing when the receptive field is at the border of the figure than when it is in the center of the figure. The cells show this firing pattern despite the fact that there is actually slightly more light in the center of a bright figure, as a result of stray light. As mentioned above, it is mainly but not exclusively spectrally nonopponent cells that are responsive to such figures. On the other hand, figures that differ from the background only in color usually do not show border enhancement: maximum firing occurs in central region of the 2° figure rather than at the borders. Only the spectrally opponent cells respond to such figures, and this conclusion is based on their responses.

The difference between the responses to color and luminance borders is seen most dramatically in the case of those spectrally opponent cells that respond to both types of figures. A particularly good example of this difference is seen in Fig. 2, in which the responses of a green-excitatory, red-inhibitory (+G −R) cell are plotted. A traverse was made with a green figure on a gray background and with a white figure on the same background. As can be seen in Fig. 2, the cell gave its maximum responses at the borders in the case of the white figure, but in the central region in the case of the green figure. Border enhancement is thus shown by this cell only to the luminance contour. Such a difference is consistent across the various cell types.

Lateral geniculate cells have a spontaneous activity rate and respond to some stimuli with an increase and to others with a decrease from this spontaneous rate. A cell such as that illustrated in Fig. 2, which shows excitation to a white figure, responds with inhibition to a black figure. In this case, however, it did not show enhanced responsiveness (that is, maximum inhibition) at the border regions, as it did to the incremental luminance figure. This was a general finding: cells that responded to a figure, whether white or black, with inhibition did not show border enhancement.

Although the cell in Fig. 2 responded to the black square with inhibition of firing from the spontaneous level, other cells responded to such a figure with excitation. The most responsive of these are those cells that we have previously termed inhibitory nonopponent cells (and which might better be termed black-excitatory, white-inhibitory cells). They showed maximum firing at the border regions of the black figure, but the border enhancement in this case was over a broader area and slightly farther from the border than it was in the case of those cells that gave corresponding excitatory responses to white figures. We thus found narrow, sharply defined border enhancement to white figures, broader enhancement of border regions

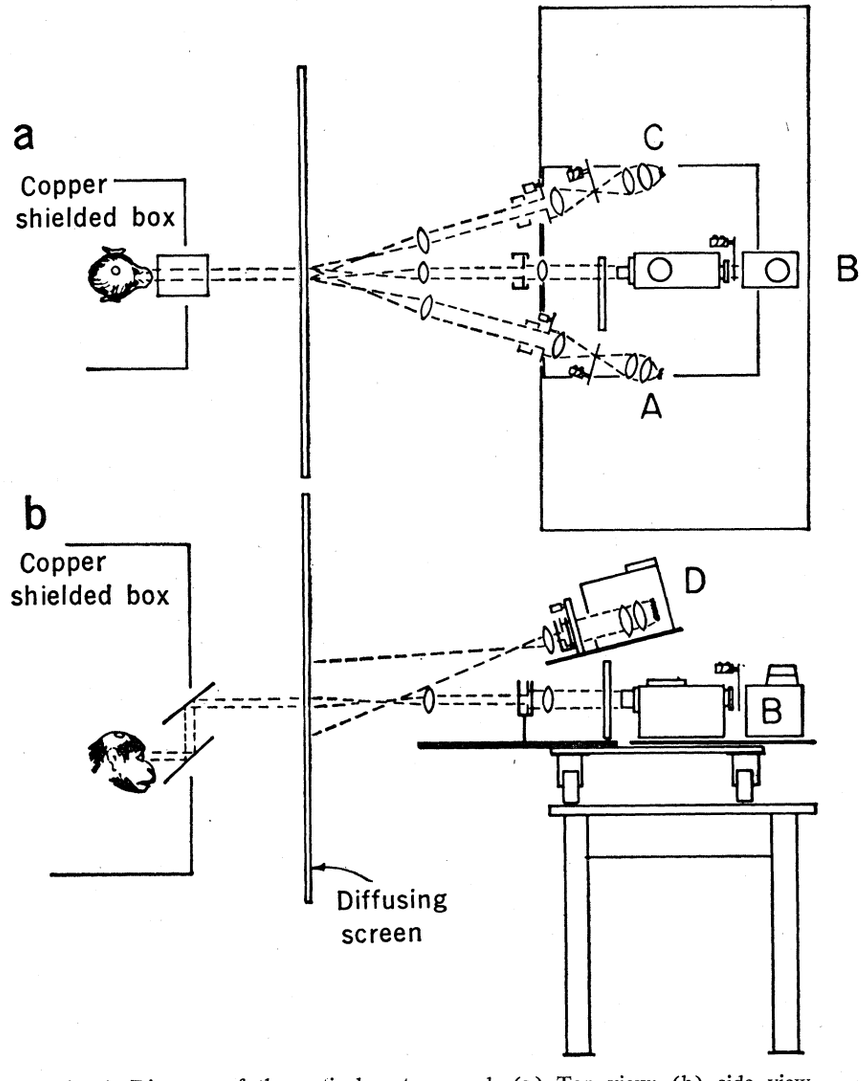

Fig. 1. Diagram of the optical system used. (a) Top view; (b) side view.

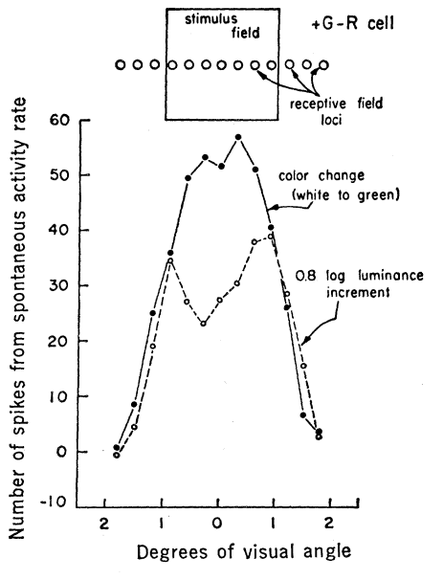

Fig. 2. Plot of the responses (spikes per second) of a +G—R cell to two different figures, each presented in different loci with respect to its receptive field. The relative locations of the receptive field and the figure for each data point are indicated in the drawing above the graph. The cell gave its maximum responses to the luminance figure when its receptive field was at the borders of the figure, whereas the largest responses to the color figure occurred when the figure was centered on the receptive field.

to black figures, and no border enhancement to colored figures.

Simultaneous brightness contrast is a very striking perceptual phenomenon: if a gray figure on a black background is compared to the same gray figure on a white background, it appears in the first case white and in the second black (the common textbook illustrations of this phenomenon give only a feeble indication of the strength of brightness contrast, because of the limited intensity range of the printed figures). This changed appearance of a figure depending on its background extends over the whole figure, not to just the border regions, and over retinal areas of many degrees of extent.

The same lateral inhibitory systems that are invoked to explain Mach bands have been assumed also to account for brightness contrast. A cell with an excitatory center and an inhibitory surround should indeed give a larger response to a gray figure on a black background than to the same gray figure on a white background (which would stimulate the inhibitory surround and thus diminish the response). But this response would hold only for figures that are roughly the size of the center of the cells' receptive fields. Although we find some variation in the size of the receptive field, such as that postulated by those who suggest the presence of different size-specific channels (*7*), none of the cells in this sample and none of the cells among many others we have examined in other experiments have receptive fields nearly large enough to account for brightness contrast over large areas. The cells receiving their inputs from the center of the eye have receptive fields whose centers are from about 1 to 30 minutes of arc, whereas brightness contrast operates over areas of 20° or more.

Despite the common assumption that a center-surround receptive field organization provides the mechanism for brightness contrast, there is no report in the literature of an examination of the responses of visual units under conditions in which the presence of contrast, as opposed to border enhancement, can be assessed. We did that with the cells in this study. In the experiment reported above we examined the responses to black and white squares on the same gray background; in this second experiment we recorded the responses to a gray square on either a white or a black background when the square was centered on the receptive field of the cell.

In no case did we find brightness contrast to be operating. A cell that fires to a white square, for instance, does not show a larger response to the gray square on a black background (which appears white by contrast) than to the gray square on a white background (which appears black). The responses to these two gray squares were always either the same or slightly different in the direction opposite to that expected from simultaneous contrast (as one would expect from stray light). Tests of spectrally opponent cells for color contrast (with a gray square on a red versus green background, for instance) also produced no evidence for contrast.

The center-surround organization of the cells' receptive fields should, we believe, be considered as a contour-enhancing mechanism. Except perhaps for very small visual objects, it does not produce brightness (or color) contrast. For that effect some other presumably cortical process must operate upon the border information.

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Visual Attention in the Tree Shrew: An Ablation Study of the Striate and Extrastriate Visual Cortex

Abstract. *Removal of the striate area in tree shrews results in increased distractibility, which prevents the animals from learning to discriminate form when hue is an irrelevant and distracting cue. Removal of the extrastriate visual cortex results in the reciprocal deficit: an increase in perseveration manifested by an inability to shift attention when irrelevant dimensions are made relevant.*

The tree shrew (*Tupaia glis*) possesses two visual projections to the cortex: in the first, the lateral geniculate nucleus relays optic tract impulses to the striate area; in the second, the pulvinar nucleus relays superior colliculus impulses to the temporal area (*1*). Inasmuch as neither cortical area is the *sole* link in the chain connecting visual impulses to the other, the two systems are anatomically independent. We have obtained evidence (*2*) for some functional independence of the extrastriate visual area and the striate area as well. With-