pattern of results was the same whether exclusive visibility for each eye was considered separately or (as in the figures) the two amounts were summed.

We conclude that it is possible to adapt the mechanism responsible for the frequently observed complete suppression or dominance of a rivalry target. Our results make it very unlikely that the increase in fragmentation is due to a criterion shift or other attitudinal change on the part of the subject, and they rule out the possibility that the drop in the completeness of rivalry results primarily from adaptation to the gratings per se. Although particular patterns of eye movements could almost certainly influence the course of rivalry—horizontal saccades might bring a vertical grating into prominence, for example—an explanation based on eye movements is hard to reconcile with the spatial frequency selectivity of the fatigue effect. The most reasonable interpretation of the data reported here is that binocular rivalry suppression is a cooperative phenomenon, with the occurrence of suppression in one region of a target normally facilitating the occurrence of suppression in adjacent regions. The fact that the process by which this cooperation is effected can be rendered temporarily ineffective provides a tool for dissecting the mechanisms underlying binocular rivalry suppression.

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REFERENCES


Behavioral enhancement of visual responses of prestriate neurons of the rhesus monkey.
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Neurons in the superior colliculus, striate cortex, frontal eye fields, and posterior parietal cortex of the monkey respond to visual stimuli. Many of these cells discharge more intensely to a stimulus when it is to be the target for a saccadic eye movement than when fixation is maintained. We have demonstrated that such enhancement of the visual response is also present for cells in prestriate cortex. The prestation effect is a modulation of the visual response and not a concomitant of oculomotor activity. It is present for eye movements away from as well as into the visual receptive field and is thus similar to that seen in striate cortex and different from that studied in the superior colliculus, frontal eye fields, and posterior parietal cortex. The visual responses of many prestriate cells habituate with repeated stimulation. When the monkey makes saccadic eye movements to a stimulus that is eliciting only a habituated response, the enhancement acts as a dishabituation which persists throughout the eye movement trials.

Visual stimuli continually excite the retinal receptors. In spite of this sensory bombardment, only a limited number of stimuli evoke a saccadic eye movement. Therefore the visual system must have mechanisms for selecting salient events. Previous investigations of the visual system of the monkey have attempted to determine the neural basis of such selection mechanisms.1-3

Neurons in the superior colliculus, frontal eye fields, and posterior parietal cortex respond more vigorously to stimuli in their receptive field if the animal subsequently makes a saccadic eye movement to the stimulus than if fixation is maintained.1-3 This “enhancement” of the visual response is selective; it is present for eye movements to the receptive field and is not demonstrable for eye movements to points distant from the receptive field. In contrast, the few cells in striate cortex that show enhanced visual responses
do not have limited enhancement fields but show this facilitation prior to saccades in all directions.\(^2\)

In an earlier study, we examined the visual response properties of cells in area 18 (V2), one of the prestriate areas in the rhesus monkey.\(^4\) The prestriate areas receive direct input from striate cortex\(^5\) and may also receive indirect afferents from the superior colliculus via the inferior pulvinar.\(^6\)\(^7\) We wondered whether prestriate neurons would show behavioral enhancement of visual responses either with restricted enhancement fields or associated with saccades in all directions.

**Materials and methods.** We recorded from five awake monkeys that were trained and prepared as described previously.\(^1\) The animals were taught to fixate a spot of light (fixation point) projected onto a tangent screen and to maintain fixation for as long as the spot remained on. While the monkey fixated, a second light (stimulus) was used to determine the receptive field location and response properties of single neurons. To test for enhancement, we changed the task. In this paradigm we turned off the fixation point and simultaneously turned on the stimulus light; the monkey made a saccadic eye movement to fixate the stimulus. We compared the responses of cells to the onset of the same visual stimulus in the two behavioral situations: one requiring maintained fixation (no-saccade condition) and the other requiring fixation followed by a saccadic eye movement (saccade condition).

We limited our study to striate cortex and the underlying prestriate cortex in the posterior bank of the lunate sulcus, which includes areas V2, V3, and V3A as defined by Zeki,\(^8\)\(^9\) Zeki and Sandeman,\(^9\) and Van Essen and Zeki.\(^10\)

**Results.** We compared responses in the two behavioral conditions for a total of 214 visual cortical neurons. We distinguished recordings in striate and prestriate cortices on the basis of recording depth in the brain, receptive field location, receptive field size, cylinder coordinates, and subsequent histological reconstructions of penetration tracks marked by electrolytic lesions.\(^4\) We found enhancement in 40% (54/136) of prestriate cells and in 24% (19/78) of striate cells. The difference in frequency of enhancement between these striate and prestriate samples was statistically significant (\(p < 0.005\), chi square).

Fig. 1 is an example of enhancement of the visual response in a cell recorded in prestriate cortex. In no-saccade condition (A), stimulus was flashed onto receptive field while monkey fixated throughout trial. In saccade condition (B), same stimulus was used as target for eye movement that began about 200 msec after light onset. Return to no-saccade condition is illustrated in C. Response of the cell is more vigorous in B than in A or C. Receptive field center was 7° lateral, 2° down; stimulus was a 1.5° by 3.5° rectangle. End of each line. Each horizontal row constitutes a single trial. The solid vertical bar depicts the time of stimulus onset. Fig. 1, B, shows the discharge of this cell to the same stimulus when it was the target for a saccadic eye movement. Approxi- mately 200 msec after the stimulus onset in Fig. 1, B, the monkey made a saccadic eye movement to fixate the stimulus. The burst of firing occurred before any change in retinal stimulation caused by the eye movement. The visual response of the cell was clearly more vigorous in the saccade condition in Fig. 1, B: the discharge onset was more regular, and the subsequent firing slightly more prolonged. Fig. 1, C, shows the transition trials from the saccade condition to the no-saccade condition. The enhancement was readily reversible.

When the monkey made saccadic eye movements spontaneously in light and dark, there was
no associated activity for enhanced cells, presumably because an adequate visual stimulus was not present. The prestriate enhancement effect is thus a modulation of the visual response and not a concomitant of oculomotor activity. We found no cells that discharged with spontaneous eye movement in light or dark.

For 13 cells that had an enhanced response, we tested whether the effect was selective only for eye movements into the visual receptive field. In these experiments when the fixation point was turned off, target lights came on simultaneously in the receptive field and in the opposite visual hemifield. The animal could make an eye movement to either target light. For all 13 cells tested (three cells in striate cortex, 10 cells in prestriate cortex), the enhancement was present for those eye movements away from the visual receptive field as well as those into the receptive field. The enhancement was therefore not selective for spatial position. We conclude that in regard to enhancement, these prestriate areas were qualitatively similar to striate cortex and different from the superior colliculus, frontal eye fields, and posterior parietal cortex.

We previously described six classes of cells in area 18: orientation cells, direction cells, color cells, spot cells, border cells, and inhibited-by-light cells. We have seen clear cases of enhancement in all cell types in area 18 except those inhibited by light, which were not tested. Wurtz and Mohler also found enhancement in all cell classes tested in striate cortex.

While characterizing the visual responses of neurons using the fixation task, we occasionally observed that the discharge to a stimulus would diminish with repeated presentations. This response habituation was observed mostly with stimuli that elicited submaximal responses, and it was seldom seen with optimal stimuli. We saw clear evidence of habituation in 29 of 146 (19%) prestriate neurons studied.

Changing from the fixation to the saccade condition could reestablish the original strong discharge after habituation had begun. Fig. 2, A, shows the prolonged response of a prestriate cell to the first presentation of a stimulus, with subsequent habituation so that only a brief burst was evident on later trials. Fig. 2, B, shows activity in the saccade condition, with the cell giving a prolonged response that persisted without habituation for many trials. Upon return to the no-saccade condition (Fig. 2, C), the habituation recurred. Enhancement and habituation could be intro-
duced and eliminated repeatedly by switching between the saccade and no-saccade conditions (Fig. 2, C and D). Similar results were obtained on 13 of 14 prestriate cells tested in this manner.

Discussion. The enhancement found in striate and prestriate cortices occurs prior to all saccadic eye movements and thus differs from that found in posterior parietal cortex, the superior colliculus, and frontal eye fields. The underlying mechanism remains uncertain, although there are two possibilities: (1) it may reflect the influences of general arousal or (2) it may reflect a more specific activation that is used to prepare perceptual areas of the brain for an impending eye movement. In the pulvinar the latter mechanism appears to be present.

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REFERENCES