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Adaptation of the binocular rivalry mechanism. MARK HOLLINS AND KEN HUDNELL.

The completeness of binocular rivalry suppression was measured by recording the fraction of a trial during which targets were perceived as alternating in their entirety, rather than blending together into a composite. It was found that the completeness of rivalry declines with prolonged stimulation. A control condition in which subjects saw the same grating targets, but without rivalry, resulted in no decrement. The phenomenon was spatial-frequency specific. The results suggest that binocular rivalry suppression is mediated by a cooperative mechanism which is susceptible to adaptation.

In a number of perceptual phenomena, there are alternative ways in which the visual system can process information coming from particular regions of the field of view. In stereopsis, for example, a given stimulus element seen by one eye can often be fused with any of several elements seen by the other eye. Julesz¹ has shown that a choice among these alternatives is typically made in a "cooperative" way, meaning that the choice made in one spot will influence the making of choices in adjacent regions.

The question considered in the present study is whether binocular rivalry—the perceptual alternations which occur when very different stimuli are presented to corresponding regions of the two retinas—is also a cooperative phenomenon. When two targets rival, there are periods when they alternate crisply and in their entirety, while at other moments portions of both are seen at once.² Total suppression is not simply a coincidence, occurring when the small elements comprising a target hap-

pen to be suppressed simultaneously, because the amount of perceptual fragmentation is profoundly influenced by changes in the color,^{3, 4} contrast,⁵ and alignment of target elements,⁶ even when those changes do not selectively favor one target or the other. This is not in itself evidence of cooperation, however; uncontrolled factors such as eye movements might be influenced by stimulus properties and in turn influence the amount of rivalry fragmentation.⁶ We reasoned that if the often unitary nature of rivalry suppression were due to an active, cooperative process, then this process might be susceptible to adaptation. Experiments reported here show that such adaptation does occur.

From a distance of just over 1 m, subjects with normal binocular vision viewed sinusoidal gratings produced by standard methods⁷ on oscilloscope screens. Both eyes viewed the same screen in the first set of experiments, whereas separate oscilloscopes were used for the two eyes in the experiment of Fig. 2. Differently oriented Dove prisms positioned close to the two eyes caused the grating to be vertical in the left eye, horizontal in the right. The stimulus filled a 1° square which was surrounded by darkness except for bars of diffuse light to aid in fusion. There were four such bars, each paralleling one side of the square, from which they were separated by 14 min arc; they were 1° in length and 9 min arc wide and had a luminance of 1 cd/m².

Subjects fixated the approximate center of the grating, moving their line of sight slightly from time to time to minimize the formation of an after-image. A three-position response key allowed them to report continuously whether they perceived the vertical or the horizontal grating, or a composite of the two. Between trials the gratings were replaced by a uniform square of the same space-averaged luminance (1.4 cd/m²), which was inspected throughout rest periods of less than 5 min and for the last 5 min of longer rests.

The first experiments began with 5 min of light adaptation to the uniform square, followed by two baseline rivalry trials separated by a 100 sec interval. After another interval of 100 sec, the rivalry adaptation period began. This consisted of 15 trials separated from one another by 20 sec rest periods. Finally, during the recovery period, rivalry was measured at more widely spaced intervals. All trials were 100 sec in duration.

The results are reported in terms of the number of seconds per trial which were free of blending and fragmentation of the targets, i.e., the time for which the left eye's target was seen exclusively

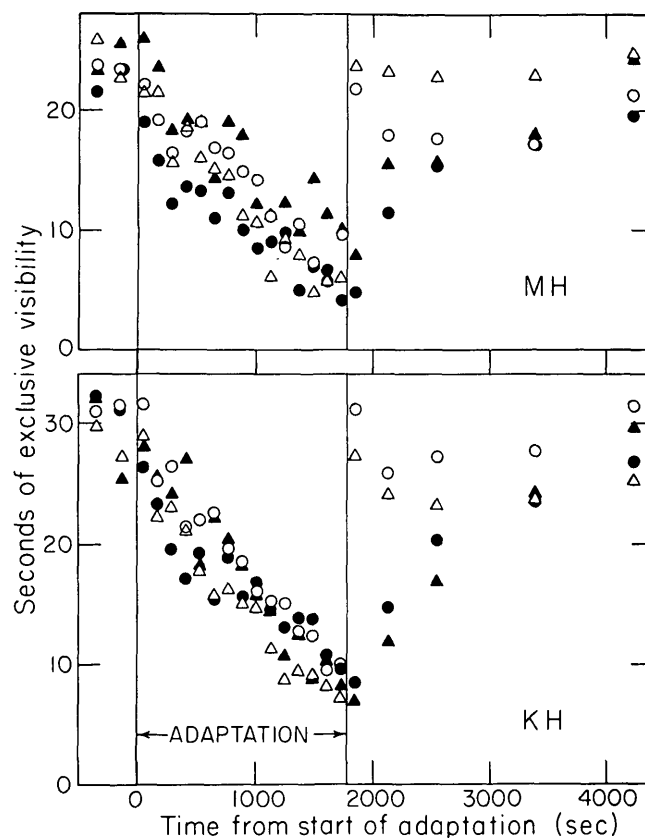


Fig. 1. Number of seconds of exclusive visibility (complete dominance) within each 100 sec trial is plotted for a baseline period, an adaptation period when the trials occurred in close succession, and a subsequent recovery period in which they were more widely spaced. In some experiments, the spatial frequency of the targets was either 1.54 cy/deg (*filled triangles*) or 9 cy/deg (*filled circles*) throughout; *unfilled symbols*, spatial frequency during adaptation was different from that used during the pretest and recovery periods: either 1.54 cy/deg during adaptation and 9 cy/deg during pretest and recovery (*circles*), or the converse (*triangles*). Symbols are positioned horizontally at the midpoint of the trials they represent. Each point is the median of five determinations. The authors served as subjects.

plus the time for which the right eye's target was seen exclusively. Results with 9 cy/deg gratings having a contrast [defined as $(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$] of 0.6 are shown by the filled circles in Fig. 1, where the number of seconds of exclusive visibility⁴ is plotted for each trial. It can be seen that the completeness of rivalry declined steadily during the adaptation period but returned approximately to the baseline level when longer rest periods were given between the trials.

We repeated the measurements with a lower spatial frequency (1.54 cy/deg) and contrast (0.2), conditions which produced an initial level of exclusive visibility comparable to that in the first experiment. The filled triangles in Fig. 1 show that the results with these coarse gratings were

similar to those found at the higher spatial frequency. If, however, the spatial frequency was changed at the end of the adaptation period, there was an abrupt return of exclusive visibility to its baseline level (unfilled symbols). Clearly the decline in the completeness of rivalry is spatial-frequency selective.

For these measurements, subjects viewed the targets with the natural pupil. Additional data obtained on Subject M. H., with the pupil dilated and accommodation paralyzed by the installation of 2 drops of 1% cyclopentolate hydrochloride in each eye, were very similar to those plotted in Fig. 1.

Because long exposure to gratings can reduce their apparent contrast,^{8,9} we considered the pos-

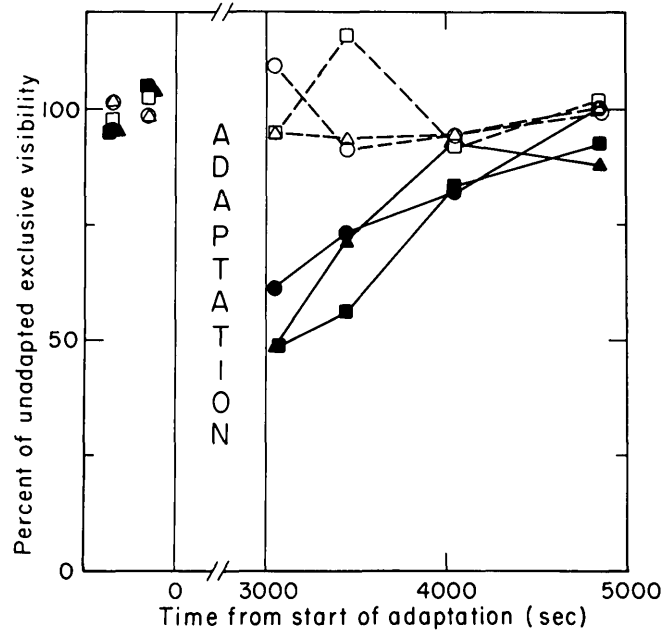


Fig. 2. Amount of exclusive visibility relative to the preadaptation level is plotted for experiments in which subjects were exposed to rivalrous stimuli during adaptation (*solid symbols*) and for experiments in which they received comparable exposure to gratings but did not experience rivalry (*unfilled symbols*). The grating was vertical in the left eye and horizontal in the right. The spatial frequency was 3 cy/deg, and the contrast was 0.4 throughout. In addition to the authors, a naive observer (*squares*) participated. Each point is the median of five determinations. Before being normalized, the results of this experiment were subjected to Mann-Whitney U tests, using an 0.01 level of significance. In the trial begun immediately after adaptation, the simultaneous condition data were significantly below the successive condition data for all three subjects; at 450 sec after adaptation, for two of the subjects; at 1050 sec after adaptation, for one subject; and by 1850 sec after adaptation, for none of the subjects. The effect of rivalry adaptation here is less than in the experiment of Fig. 1, presumably because of the longer intertrial intervals employed.

sibility that the adaptation effect studied here was simply a concomitant of changes in perceived contrast rather than a change in the rivalry mechanism itself. This possibility was investigated in an additional experiment using a naive observer as well as the authors. The general procedure was similar to that in the first set of experiments. During the adaptation period, however, the left- and right-eye targets were presented either simultaneously or successively to the two eyes. In the *simultaneous* condition, 100 sec rivalry periods alternated with 100 sec rests during which both eyes viewed a uniform square; in the *successive* condition, 100 sec periods in which the right eye viewed its target while the left eye viewed a uniform square alternated with periods of the same length during which the left eye viewed its target while the right eye viewed the uniform square. Thus,

from the point of view of either eye alone, the two 50 min adaptation conditions were closely comparable. Only in the simultaneous condition, however, did rivalry occur during the adaptation period. No measurements were made during the adaptation period itself; to do so would have required more vigilance during the simultaneous than during the successive condition, thus reducing their comparability.

The results of this experiment are shown in Fig. 2, where, for each subject and condition, the amount of exclusive visibility is plotted relative to that obtained during the preadaptation trials. It can be seen that exclusive visibility was approximately halved as a result of the rivalry adaptation but showed little or no change after alternating monocular exposure to the gratings. Hence rivalry itself can cause exclusive visibility to decline. The

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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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 prestriate 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