Color Vision Is Altered During the Suppression Phase of Binocular Rivalry

Abstract. *Increment-threshold spectral sensitivity functions were determined during the dominance and suppression phases of binocular rivalry. The shapes of the functions obtained during the dominance phase exhibited three maxima at approximately 440, 530, and 610 nanometers and resembled functions obtained for nonrivalrous control conditions. However, the functions measured during suppression had a single broad peak near 555 nanometers and were adequately described by functions measured with flicker methods during nonrivalrous conditions. The results indicate that binocular rivalry differentially attenuates opponent-color information relative to achromatic information.*

Binocular rivalry is the alternating phenomenal suppression of visual information from each eye that occurs when the two eyes receive dissimilar images that cannot be fused into a single percept. Although dichoptic viewing conditions are usually required to observe the compelling effectiveness of suppression, binocular rivalry may help eliminate ambiguities occurring under normal viewing conditions and, therefore, play an important role in normal single binocular vision (*1*).

In order to better understand the apparent inhibitory interactions responsible for binocular rivalry, investigators have used a variety of test probes to compare the sensitivity of the eye during suppression and dominance. Results have suggested that during suppression, the sensitivity of the eye to all types of visual stimuli is generally reduced. For example, thresholds are elevated for a diversity of tasks including form recognition, movement detection, and the detection of luminance increments. Since performance on such a wide variety of tasks is impaired, suppression is generally considered to be nonselective (all types of information are suppressed) (*2, 3*). However, rivalrous stimuli differing in both color and form often produce types of percepts suggesting that suppression may be selective for certain spectral aspects of a stimulus (*4, 5*). A basic aspect of the decrease in sensitivity associated with suppression that has not (to our knowledge) been previously investigated is the relation between the color (dominant wavelength) of a test probe and the detection threshold (the spectral sensitivity of the eye). Therefore, we measured the spectral sensitivity of the eye during the dominance and suppression phases of binocular rivalry and found that the decrease in sensitivity was dependent on wavelength. Furthermore, the alterations in the shape of the spectral sensitivity curve indicate that binocular rivalry selectively altered the sensitivity of specific mechanisms that process opponent-color information.

Two experienced psychophysical observers with normal visual acuity, color perception, and binocular vision viewed the rivalry-inducing stimuli in a Brewster stereoscope. The rivalry stimuli were high-contrast square-wave gratings (fundamental spatial frequency, 2.8 cycles per degree) presented separately to the two eyes at orthogonal orientations of 45° to the left and right of vertical. The rivalry fields were limited by a 0.5° dark border to subtend 5.7° squares with a space-averaged mean luminance of 5.9 cd/m^2. An optical system—consisting of a heat-filtered 250W tungsten-halogen light source, a monochromator (10-nanometer bandpass), an electronic shutter, neutral density wedges, and the appropriate focusing lenses—was used to produce spectral test-probe stimuli for measuring detection thresholds (*6*). With this system, a rectangular test stimulus (0.4° by 0.8°) was projected as 20-msec flashes on the center of the rivalry field seen by the left eye. The observer triggered the onset of the stimulus by depressing a button.

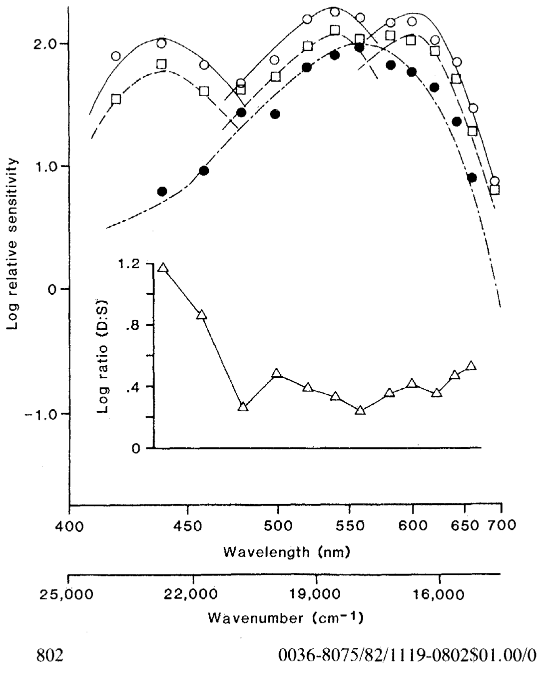

Fig. 1. Mean increment threshold spectral sensitivity of subject E.S. for the nonrivalry viewing condition (□) and the dominance (○) and suppression phases (●) of binocular rivalry. The standard errors of the mean were smaller than the symbol size. The lower inset shows the log ratio of the sensitivities obtained during the dominance and suppression phases of binocular rivalry.

An ascending method of limits was used to estimate the detection thresholds. For a given ascending series, the initial intensity of the stimulus was set well below the observer's threshold, and it was incremented in 0.1 log unit steps after trials in which the observer failed to detect the test stimulus. The lowest flash intensity the observer detected was taken as threshold. In each experimental session, threshold determinations were made at consecutive 20-nm intervals from 420 to 680 nm and then from 680 to 420 nm for each of the following three viewing conditions: monocular nonrivalry viewing (the right eye was occluded with a black patch); binocular rivalry, left-eye dominance phase; and binocular rivalry, left-eye suppression phase. The log of the reciprocal of the number of quanta associated with the geometrical mean of the six threshold estimates determined over three experimental sessions was plotted against the wave number of the test stimulus to produce spectral sensitivity functions for each of the three viewing conditions (Fig. 1).

The functions determined for the nonrivalry control condition and the dominance phase of binocular rivalry are similar in shape, with maxima of sensitivity at about 440, 530, and 610 nm. The smooth curves drawn through the data were derived from the linear subtractive-interaction model of spectral sensitivity developed by Sperling and Harwerth (*7*). Accordingly, the peak at 440 nm was fit by the absorption spectrum of the cones sensitive to short wavelengths ("blue" cones), whereas the maxima at 530 and 610 nm were fit by a linear difference function of the absorption spectra of cones sensitive to the middle ("green")

Table 1. The d' scores derived for a 50 percent a priori probability during the dominance and suppression phases of binocular rivalry.

Subject	460 nm		540 nm		640 nm	
	Dominance	Suppression	Dominance	Suppression	Dominance	Suppression
E.S.	> 7.56*	1.63	3.60	1.25	> 7.56*	1.63
D.L.	> 7.56*	1.12	2.72	.84	> 11.0*	.94
Combined ± S.D.	4.63 ± 0.57	1.36 ± 0.28	2.97 ± 0.26	1.04 ± 0.27	4.91 ± 0.61	1.10 ± 0.27

*The value of d' could not be determined precisely because the hit rate was 100 percent. It was assumed that the subjects missed one-half trial.

and long ("red") wavelengths. Although the sensitivity at each wavelength obtained during the dominance phase of binocular rivalry was slightly higher than that for the nonrivalry condition (*8*), both sets of data are adequately described by the same function. However, in comparison with the nonrivalry or the dominance phase function, the spectral sensitivity function determined during the suppression phase of binocular rivalry exhibited a single broad peak near 555 nm and a substantial relative reduction in sensitivity (> 1.0 log unit at 440 nm) in the blue region of the spectrum. The inset in the lower part of Fig. 1 shows the difference between dominance and suppression phase thresholds as a function of wavelength. The curve fit to data of the suppression phase is the mean spectral sensitivity function determined by a flicker method under nonrivalry conditions for normal observers (*9*). The spectral sensitivity functions determined for the second observer qualitatively resembled those shown in Fig. 1.

With respect to the shapes of the spectral sensitivity functions, King-Smith (*10*) has shown that the spectral sensitivity for the detection of a test flash can be analyzed in terms of two parallel but independent mechanisms (a luminance or achromatic channel and an opponent-color or chromatic channel) and that the exact shape of the spectral sensitivity function for absolute detection is the upper envelope of the spectral sensitivities of these two mechanisms. Furthermore, he demonstrated that when detection is mediated exclusively by opponent-color mechanisms, the spectral sensitivity function has three peaks at about 440, 530, and 610 nm and conforms to the subtractive-interaction model of Sperling and Harwerth (*7*). In contrast, when the luminance channel dominates detection, the spectral sensitivity function has a single broad peak at approximately 555 nm and conforms to data obtained by a flicker method. Therefore, the shapes of the spectral sensitivity functions in Fig. 1 indicate that for the nonrivalry and dominance phase viewing conditions, the threshold for the opponent-color system was lower than that for the luminance system; thus, detection was mediated by the chromatic channel. This was not unexpected, since a white background selectively depresses the sensitivity of the luminance system relative to the opponent-color system. The change in the shape of the spectral sensitivity function found for the suppression phase of binocular rivalry indicates that for this viewing condition, the luminance system dominated detection; hence, the process of binocular rivalry suppression differentially reduced the sensitivity of the opponent-color system relative to the luminance system. In agreement with this interpretation, the observers reported that they could perceive the color of threshold stimuli during dominance but not during suppression.

To confirm that two different mechanisms were involved in detecting the test stimulus and that the changes in the shape of the spectral sensitivity function did not simply reflect a change in the observers' criterion, d' scores were determined at selected wavelengths (460, 540, and 640 nm) for both the dominance and suppression phases of viewing. (The d' scores represent a criterion-free measure of stimulus detectability.) The d' scores were determined in yes-no experiments (100 trials per viewing condition) according to the procedures outlined by Green and Swets (*11*). For all three stimuli, the flash intensity was set approximately 0.1 log units below the suppression phase threshold determined by the method of limits. The test stimulus was presented randomly on 50 percent of the trials for the 460- and 640-nm test probes and at three different a priori probabilities (25, 50, and 75 percent) for the 540-nm test stimuli.

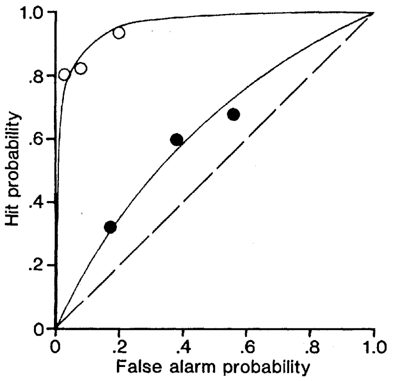

Fig. 2. Receiver-operating-characteristic curves obtained for subject E.S. with a 540-nm stimulus adjusted 0.2 log units below the suppression phase threshold illustrated in Fig. 1. The functions associated with each set of data were derived from the mean d' scores for a priori probabilities of 25, 50, and 75 percent. Symbols: (○), Dominance phase; (●), suppression phase.

In every case the d' scores measured during the dominance phase of binocular rivalry were substantially larger than those obtained during the suppression phase (Table 1). For the false-alarm rates obtained during suppression, a d' score of 1.0 would indicate that the stimulus was correctly detected approximately 50 percent of the time and a d' score of 4.0 would indicate that it was almost perfectly detected (> 99 percent of the time). The ROC curves (Fig. 2) also show performance differences between the dominance and suppression phases. Moreover, the combined data reveal a wavelength-dependent difference ($P < .05$, t-test) in detectability between suppression and dominance phases of rivalry. These results support the hypothesis that the changes in the shape of the spectral sensitivity function during binocular rivalry reflect a change in the mechanism mediating detection and not a change in the observers' criterion for threshold.

Our results agree with those of a number of previous studies (*2, 3*) showing that the suppression phase of binocular rivalry is nonselective. In this instance the term "nonselective" indicates that elevations in threshold are not restricted to test probes similar to the rivalry stimuli (in this case, grating patterns). However, the alternations in color vision we observed demonstrate that the inhibitory interactions associated with suppression differentially attenuate opponent-color and luminance information.

This selective aspect of binocular rivalry may help explain a number of old as well as more recent observations in the field of binocular vision. For instance, in 1899 Breese (*4*) described a percept produced by viewing rivalry stimuli differing in color, form, and temporal characteristics. To one eye Breese presented a stationary grating pattern on a green background, and to the other, an orthogonally oriented, moving grating pattern on a red background. When the eye viewing the red field was suppressed, Breese reported that the moving grating from that eye was perceived in conjunction with the pattern and color of the dominant eye. (The color information from the suppressed eye was lost but not the contour information.) It seems reasonable that the loss of color information from the suppressed eye reflected the inhibitory actions of binocular rivalry on the opponent-color mechanisms originating in the suppressed eye and that the perception of the moving contours reflected the activity of luminance mechanisms that respond well to stimulation at high temporal frequencies (*12*) and whose sensitivity is relatively unaffected by binocular rivalry.

With respect to more current investigations of binocular rivalry, it also seems likely that the differential attenuation of opponent-color information contributed to the rivalry-induced alterations in perceived hue, purity, and brightness of binocular color mixtures recently quantified by Makous and Pulos (*5*).

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Rotational Invariance in Visual Pattern Recognition by Pigeons and Humans

Abstract. *Pigeons and humans chose which one of two alternative visual forms was identical to, or a mirror image of, a previously presented sample form. The two comparison forms were presented in various orientations with respect to the sample. The two species yielded similar accuracies, but although human reaction times depended linearly on the angular disparities, those of the pigeon did not. Humans appeared to apply a well-known, thoughtlike, mental rotation procedure to the problem, whereas pigeons seemed to rely on a more efficient automatic process that humans can use only in simpler rotational invariance tasks. Mirror-image forms may be better discriminated by the pigeon's visual system than by the human one.*

The visual recognition of objects regardless of their relative spatial orientation is a competence that humans use constantly. Research on this capability has accordingly a long history (*1*), and individual proficiency in it is assessed by several intelligence and aptitude tests (*2*). Certain feats of rotational invariance are believed to implicate cognitive skills and to involve mental imagery (*3*). Although casual observations of higher animals dealing with objects force one to assume that they are capable of visual rotational invariance, a formal demonstration seems to be lacking (*4*). An animal model would be useful for the study of the mechanisms underlying these operations, which even robot engineers find cumbersome to implement (*5*). We now report that pigeons are more efficient than humans at recognizing certain two-dimensional visual patterns regardless of their orientation in the frontal plane.

Ten adult homing pigeons (*Columba livia*) were maintained at 85 percent of their normal weight throughout the experiment. A Skinner box with three keys was used. Stimuli were presented by projector, the display on the individual keys being controlled by shutters. The forms appeared as white 10-mm by 10-mm patterns on a dark background 25-mm in diameter. A computer controlled events within the experimental sessions and recorded the data on a printer (Fig. 1A).

The subjects were trained to master the matching-to-sample discrimination task. Only the final stage of the procedure is described (*6*). A trial began with the projection of a sample stimulus on the center key. After 15 pecks on it, two comparison stimuli were displayed on the side keys. One comparison form was identical to the sample, and the other was always its mirror image. Half of the subjects were rewarded with a 3-second access to food as soon as they pecked the side key bearing the identical match-

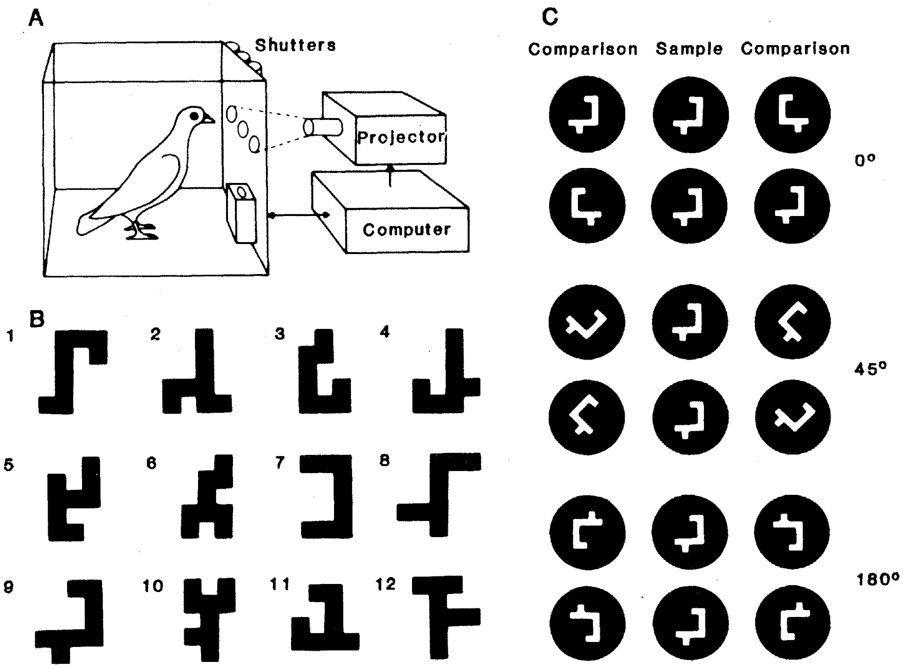

Fig. 1. (A) Experimental apparatus as used with pigeons. (B) Visual forms used. (C) Examples of stimulus sets used for rotational invariance test.