Do rod signals control stimulus field prevalence in binocular rivalry?

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We tested the hypothesis that rod signals mediate the effect of luminance on field prevalence in binocular rivalry. Results show that (1) field prevalence saturates at a luminance that is less than 0.001 that of the value reported for rod saturation, (2) the spectral sensitivity inferred from the prevalence-luminance relationship is not scotopic, and (3) the prevalence-luminance relationship does not behave univariantly under all chromatic conditions. We conclude that rod signals alone do not control field prevalence.

Key words: binocular rivalry, rod and color vision, eye dominance, stimulus field prevalence

The influence of luminance on the prevalence of the right (or left) stimulus field in binocular rivalry has been well known.[1-3] In particular, the systematic studies of Kakizaki[4] and Kaplan and Metlay[5] have demonstrated that when the luminance of the left field (for example) is fixed, the right field *prevalence* (as measured by the fraction of the viewing time that the right field is perceived) increases with the right field luminance over mesopic levels. At photopic levels, however, further increases in luminance result in little or no systematic change of the right field prevalence. The effect of luminance on field prevalence appears to saturate at photopic luminances.

Although the mechanism underlying the effect of luminance on field prevalence has not been thoroughly investigated, the studies of Aguilar and Stiles[6] and, more recently, of Alpern et al.[7-9] showed that the neural signals from rods also increase with luminance and saturate at some photopic level. We therefore speculated that rod signals alone control field prevalence in binocular rivalry.

To test the rod hypothesis, we examined three predictions: (1) that field prevalence would saturate at the same light level that rod signals saturate, i.e., at about 3000 scotopic trolands; (2) that the relationship between field prevalence and stimulus luminance is invariant with stimulus wavelength composition (as would be predicted by the principle of univariance of Naka and Rushton[10]); and (3) that the action spectrum underlying the prevalence-luminance relationship is scotopic. (The principle of univariance states that "each visual pigment can only signal the rate at which it is effectively catching quanta; it cannot also signal the wavelength associated with the quanta caught."[10] Thus, if field prevalence is mediated by a single pigment system, e.g., rods, then the function relating prevalence and luminance should have the same form regardless of whether the stimulus field is white, red, green, or blue.)

Our approach was to examine predictions 1

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and 3, assuming prediction 2 was true, and then, in a separate experiment, to examine prediction 2. We reasoned that if the rod hypothesis provides an adequate explanation, all three predictions would be confirmed.

Methods

The stimulus patterns used to induce binocular rivalry are shown in Fig. 1, top. The diameter of each disc subtends 7.73 degrees; the width of the dark bar subtends 12.4 minutes of visual angle. The purpose of having the bar at the 7 o'clock position was to help maintain binocular fusion. Each stimulus field was imaged in a Badal optical arrangement[11] and was viewed in Maxwellian view by each eye. The Badal optics permitted the observer to obtain optimal focus without changing the size of the stimulus fields.

The light source of the stimuli was a 250 W tungsten-halogen lamp that had a color temperature of about 3000 ° K. Monochromatic light conditions were produced by interposing 10 nm half-bandpass interference filters. Retinal intensity measurements for the achromatic condition were made with an S.E.I. photometer by the method of Westheimer.[12]

When the left and right stimulus field were fused binocularly, only the horizontal or vertical bar appeared complete at any given moment (Fig. 1, middle and bottom). When the right field prevailed (Fig. 1, middle), the observer depressed a key that activated a cumulative timer; when the left field prevailed, (Fig. 1, bottom), the observer released the key. Right field prevalence was calculated by dividing the time (in seconds) that the observer reported seeing the right field by 60 sec, the total viewing period. Left-field prevalence can be calculated by subtracting this fraction from unity. At the start of each experiment, the observer was given a brief trial period, after which he was required to respond during the 1 min viewing period.

Extensive measurements were made on one male observer (age 30 years) who had normal monocular and binocular vision as confirmed by the Titmus test and the Worth four-dot test.

Results

Assuming (for the sake of discussion) that the prevalence-luminance relationship in binocular rivalry behaves univariantly, we averaged the data from 19 experiments (Fig. 4) to derive an estimate of the actual relationship. The results are shown in Fig. 2. Each data point represents the mean (±2 S.E.M.) of the data scattered within a 0.50 log luminance interval. The solid line represents the general trend depicted by the mean and will serve as a template curve for the prevalence-luminance relationship.

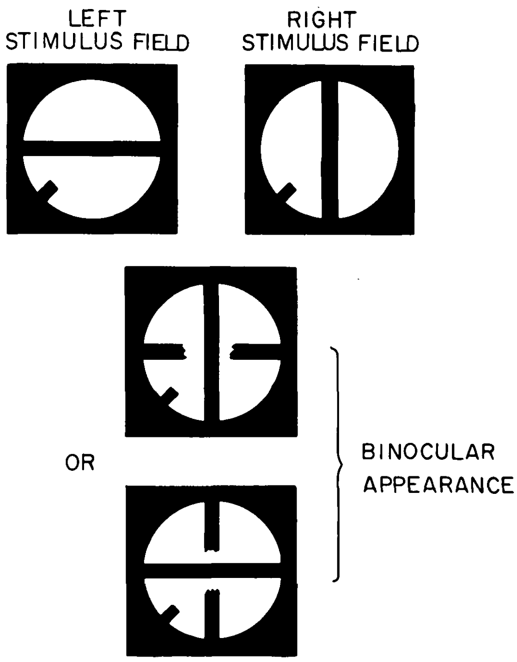

Fig. 1. *Top,* Stimulus patterns used to induce binocular rivalry. *Middle,* Binocular appearance of stimuli when right stimulus field prevails. *Bottom,* Binocular appearance when left stimulus field prevails.

In order to estimate the stimulus intensity required to saturate the prevalence of the right field, the intensity of the left stimulus field was held constant at 2.44 log photopic trolands, and the right field prevalence was determined as a function of right field intensity. Both right and left fields were achromatic. The results are shown in Fig. 3. The circles are the data points; the solid curve is the template curve that was displaced horizontally for best fit to the data. These results indicate that the major change in field prevalence occurs within a 30-fold intensity range from about −2.50 to −1.00 log photopic trolands. Retinal intensities greater than −1.00 photopic trolands (i.e. −0.82 log scotopic tro-

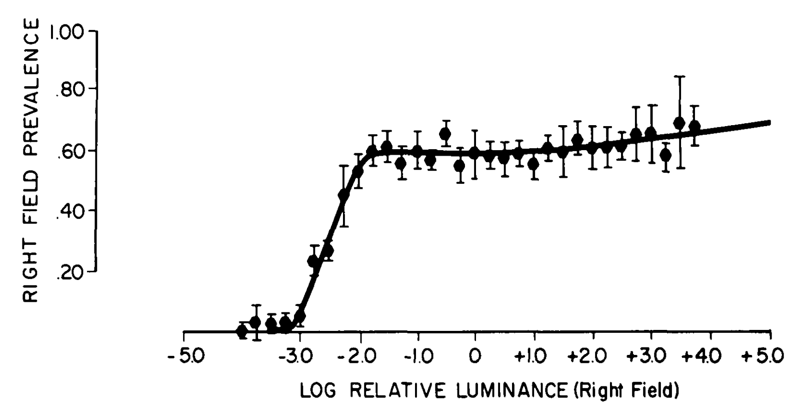

Fig. 2. Mean right field prevalence (±2 S.E.M.) plotted as a function of relative log luminance.

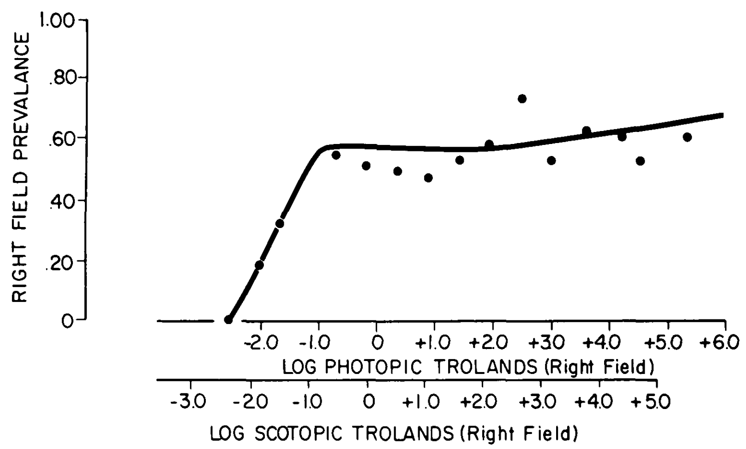

Fig. 3. Data from an experiment in which both left and right fields were achromatic.

lands) have little additional influence on field prevalence.

In experiments where the left field was achromatic and the right was monochromatic (Fig. 4), the prevalence of the right field again increased with low intensities and then saturated at higher intensities. (Note that the curves for different wavelengths were displaced along the horizontal axis by arbitrary amounts for clarity.) To determine the spectral sensitivity of the field prevalence response, we plotted the reciprocal of the intensity (calculated on a quantal basis) necessary to shift each curve into superposition. (This procedure is described in Naka and Rushton.[10]) The derived action spectrum is shown in Fig. 5. Of main importance, Fig. 5 shows that the peak sensitivity is at 540 nm and that, as a whole, the data do not conform to the C.I.E. scotopic efficiency curve (solid line). On the other hand, the photopic luminosity curve obtained by flicker photometry for the same observer (dash line) seems to provide a satisfactory fit to the data over the middle- and long-wavelength portions of the spectrum.

To pursue the question of univariance, prevalence luminance curves were compared when the left field was 650 nm and the right field either 440 or 570 nm. The results are illustrated in Fig. 6. Note that the relative positions of the two curves on the abscissa

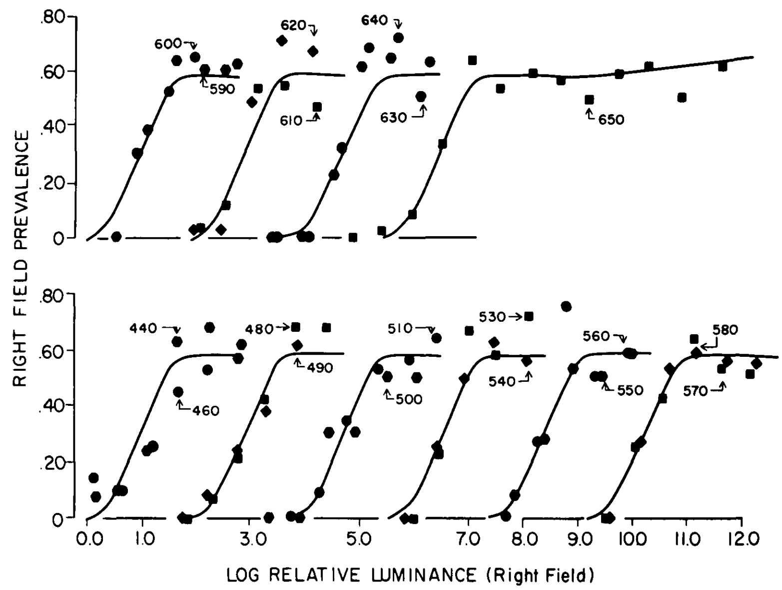

Fig. 4. Prevalence-luminance curves when the left field was achromatic and the right field was monochromatic.

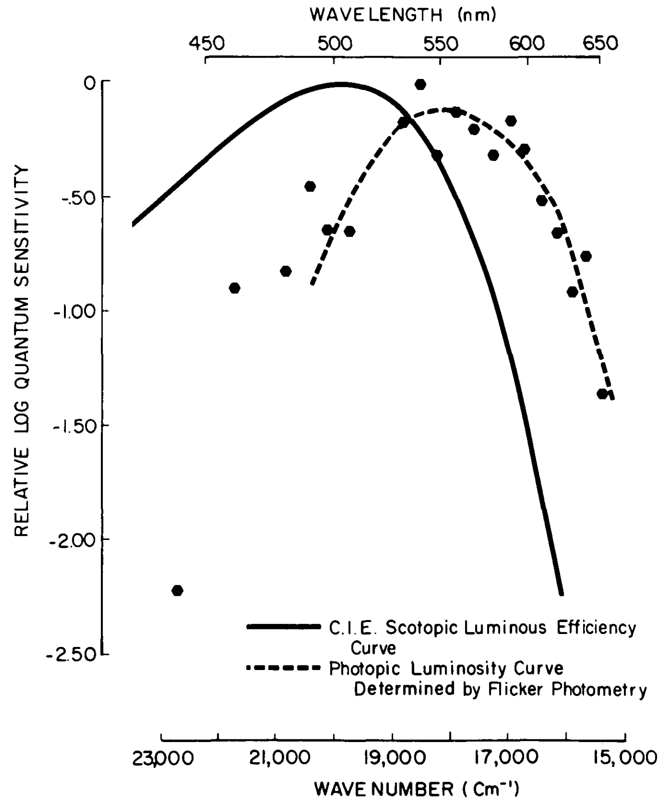

Fig. 5. Quantum spectral sensitivity derived from data shown in Fig. 4.

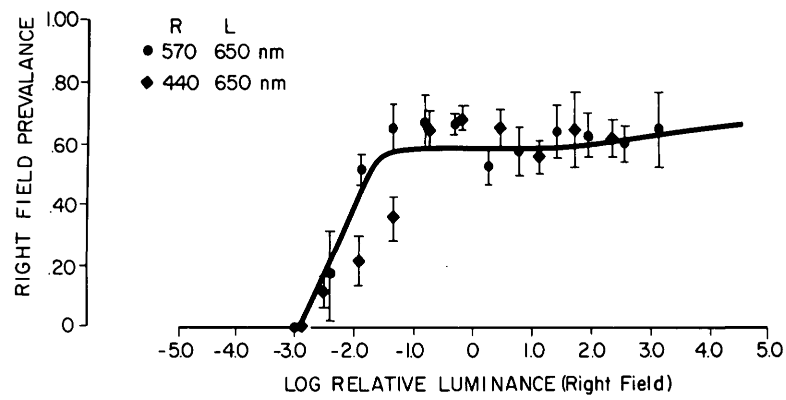

Fig. 6. Prevalence-luminance relationship when the left field was 650 nm and the right field was either 440 or 570 nm.

were corrected for the sensitivity difference to the 440 and 570 nm stimulus. (The correction was determined from the data shown in Fig. 5 but calculated for energy rather than for quanta.) Each data point represents the mean (±2 S.E.M.) of five replications. The results indicate a small but consistent difference between the two chromatic conditions, suggesting that the prevalence-luminance relationship is not perfectly univariant.

Discussion

Assuming that the prevalence-luminance relationship behaves univariantly (as would be predicted on the basis of rod-mediated signals), we infer from our results that field prevalence saturated (see Fig. 3) at a retinal intensity less than 0.001 that of the low estimates for rod saturation reported for Fuortes et al.[13] and that the spectral sensitivity was not scotopic (Fig. 5). The two inferences are contrary to our predictions 1 and 3. In addition, when the left field was red and the right field was either green or blue, we found evidence suggesting that the prevalence-luminance relationship was not perfectly univariant (prediction 2). Thus the results of our experiments are contrary to at least one of the three predictions. We therefore conclude that rod signals alone do not mediate the effect that luminance has on field prevalence in binocular rivalry.

On the basis of the spectral sensitivity data (Fig. 5), it might be inferred that cone—not rod—signals control field prevalence. However, cone signals do not saturate under steady illumination conditions.[14] Thus the cone hypothesis cannot explain why field prevalence seems to plateau as a function of luminances greater than −1.00 photopic trolands.

Kaplan and Metlay[5] suggested that field prevalence was related to improvements of the visual resolution capability of the eye with higher luminations. They noted that visual resolution also reaches a plateau at photopic luminances. However, if the visual resolution hypothesis were correct, we would predict from our data that visual resolution should show major improvements over a 30-fold range of illumination and should plateau at about −1.00 photopic trolands. Instead, Hecht and Mintz,[15] using conditions similar to those in our study, reported that visual acuity showed continuous improvements over a one million–fold range of illumination; the photopic system accounting for more than a 10,000-fold range of illumination. According to Shlaer's[16] results, the improvement of visual acuity plateaus at about 3.5 log trolands (for the Landolt C) and at about 2.0 log trolands (for gratings).

In summary, the results of our study cannot be adequately explained by any of the obvious "monocular" hypotheses. Could the effect of luminance on field prevalence be a cortical manifestation?

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