COLOR PERCEPTION WITH BINOCULARLY FUSED ADAPTING FIELDS OF DIFFERENT WAVELENGTHS

RICHARD A. HUMANSKI and STEVEN K. SHEVELL
Department of Behavioral Sciences, The University of Chicago, 5848 S. University Avenue, Chicago, IL 60637, U.S.A.

(Received 12 February 1985; in revised form 20 June 1985)

Abstract—By presenting to one eye a small test superimposed on a background field, and to the other eye only a similar background field of a different wavelength (arranged so that the fused percept is the test centered upon a single fused background), the color appearance of the perceived background can be changed while keeping constant the light stimulating the test eye. Measurements demonstrate that the contralateral field clearly influences the color of the test, even when the left- and right-eye backgrounds are very different in wavelength and illuminance. This change in color appearance cannot be explained (a) by simple contribution of a color signal from the contralateral eye, (b) by the perceived color of the fused background, or (c) by combining the effects of contralateral adaptation (alone) and monocular adaptation (alone). Instead, the central-mechanism response depends on the particular pair of wavelengths that are fused. The results suggest chromatic coding of neural signals arriving at the central locus.

Chromatic adaptation Contralateral adaptation Color perception Binocular adaptation

INTRODUCTION

The color of a small patch of light that falls on a large chromatic background depends on the wavelength and retinal illuminance of the background field. The adaptation mechanisms affecting color appearance have been extensively explored in recent years (Jameson and Hurvich, 1972; Walraven, 1976, 1981; Cicerone et al., 1975; Shevell, 1978, 1982; Laramer, 1981; Shevell and Handte, 1983), and there now is general agreement that a background light has the effect both of selectively reducing receptor sensitivity and of reducing the influence of its own quanta that fall in the area of the small superimposed patch. While the magnitudes of these effects depend on the spectral composition and level of the background, the problem is simplified somewhat since lights that match perceptually (metamers) have equal adapting effects when lights are presented to a single eye. The other eye saw only a background light of a different wavelength (arranged so that the fused percept is the test centered upon a single fused background). The results suggest chromatic coding of neural signals arriving at the central locus.

Metamers have identical adapting effects when all lights stimulate one eye, but this property fails when the background results from binocular fusion of two lights, each presented to a different eye. It is well known that fused lights of different wavelengths can result in a homogeneous and stable mixture (Hecht, 1928; Prentice, 1948; Hurvich and Jameson, 1951; Hoffman, 1962; De Weert and Levelt, 1976). The perceived color of the fused field depends on the wavelengths and radiances of the lights; for example, results described later show that the fused percept of a left-eye 540 nm light and a right-eye 660 nm light changes from primarily greenish to yellowish-green to yellowish-red as the 660 nm field is raised from 0 to 90 td. However the adapting effect of a fused field is not a function only of the fused percept. As a simple example, consider the fused yellowish-red background mentioned above and a test patch presented to only one eye. Monocular effects of adaptation can predominate (Shevell and Humanski, 1984); thus a moderately intense test patch that appears yellow in the dark would be reddish if presented to the left eye, due to greater desensitization of middle-wavelength sensitive (MWS) cones, but greenish if presented to the right eye, due to greater desensitization of long-wavelength sensitive (LWS) cones. Further, if the fused left-eye 540 nm and right-eye 660 nm lights both were replaced with a single light metameric to the fused mixture, the color of the small patch would be still different. Clearly the appearance of a fused background field is not sufficient to specify its adapting effect.

That metameric mixtures cause identical adapting effects when lights are presented to a single eye is accounted for by first principles of receptor quantum absorption (see Brindley, 1970, for a thorough discussion); thus it is not surprising that the property fails for fused percepts that result from a combination of neural signals from the two eyes. At the same time, the failure reveals a method for changing a background's perceived color without changing light absorption in one eye. In the experiments reported here, a small test patch and a background were presented to one eye. The other eye saw only a background light that fused binocularly with the background in the test eye. By increasing the radiance of the background in the non-test eye, the perceived color of the fused
background could be varied without affecting light absorbed by receptors in the test eye. The changes in color appearance of the small patch caused by varying the level of the contralateral-eye background reveal the effect of a central mechanism. Red:green equilibrium measurements were used to quantify adapting effects of fused fields; these experiments extend previous results with backgrounds to the two eyes that were different in radiance but identical in wavelength (Shevell and Humanski, 1984).

The present experiments show the centrally mediated effect of chromatic adaptation depends critically on the wavelengths of the backgrounds presented to each eye. Specifically, the change in test-patch color appearance due to varying the radiance of a contralateral-eye 660 nm background is largest when a dim test-eye background is a different wavelength (540 nm), smallest when the test-eye background is the same wavelength (660 nm), and intermediate when there is no test-eye background light. This reveals that contralateral adaptation causes color-appearance changes that depend on the chromatic content (and not simply the level) of the background in the fellow eye.

**METHOD**

**Apparatus and stimuli**

The experiments were conducted using a six-channel, binocular Maxwellian-view optical system (three independent channels for each eye). Monochromatic stimuli were obtained from broadband light (tungsten-halogen sources) passed through Ditric Optic three-cavity interference filters. The annular test field, presented to the left eye, had an inner diameter of 1.0° and an outer diameter of 1.5°. It was composed of a mixture of 540 nm light (denoted $\Delta G$) and 660 nm light (denoted $\Delta R$). A 4.8° adapting field, concentric with the test, also could be presented to the left (test) eye. A 660 nm adapting field is denoted $R_t$, and a 540 nm field $G_t$, where the first letter indicates the dominant hue of the adapting light and the subscript $T$ denotes a field presented to the same eye as the annular test. In addition, a similar 4.8° adapting light could be presented to the right (contralateral) eye. A 660 nm (540 nm) contralateral-eye adapting light is denoted $R_c$ ($G_c$), where the first letter gives the hue of the light and the subscript $C$ indicates stimulation of the contralateral (nontest) eye.

In the center of each adapting field was a 30° diameter circle with two inward facing spokes. The circles and spokes, when properly fused, formed a “clock face” fixation point that aided binocular fusion and minimized fixation disparity. When properly fixated, the observer saw a single circle with spokes at 3, 6, 9 and 12 o’clock. Figure 1 shows a schematic drawing of the stimuli. All lights were presented steadily. A detailed description of the apparatus and calibration procedures is given elsewhere (Shevell and Humanski, 1984).

**Observers**

Two naive student volunteers and one of the authors served as observers: K.B. (female, age 20), M.E.M. (female, age 20), and R.H. (male, age 23). Subjects were screened for stereoscopic and color vision defects using the T.N.O. and Titmus stereo tests, the Farnsworth Panel D-15 test, and a Nagel anomaloscope. Reported measurements were collected following approximately ten hours of practice; each observer’s ability to replicate results from identical conditions on different days determined the end of practice sessions. Observers wore their prescription eyeglasses (if any).

**Procedure**

The measurements reported here were collected in two different sets. For one set, the test-eye adapting light was 660 nm and the contralateral-eye adapting light was 540 nm ($R_t G_c$ set). Within this set there were 19 adapting conditions: each of the levels of $R_t$ (OFF, 0.5, 1.0, and 1.9 log td) was paired with each level of $G_c$ (OFF, 0.7, 1.3, and 2.2 log td) and, in
addition, each $R_T$ light (0.5, 1.0, 1.9 log td) was paired with a contralateral-field retinal illuminance of $G_C$ that cancelled the redness in the background (in these conditions the fused background was, approximately, neither reddish nor greenish in hue). Initially, each of the 19 conditions was repeated twice (replications always on a different day). Two different conditions were run in a single session, with conditions randomly assigned to sessions. During replication, the order of the two conditions within a session was reversed so that order-within-session (first or second) was counterbalanced. If results from the two replications did not agree very closely, two additional replications were run using a similar randomized and counterbalanced design. Each reported measurement is the median of results from (2 or 4) separate days, where the value for each day is based on the average of five measurements within a session.

In the other set of 19 conditions, the test-eye adapting light was 540 nm and the contralateral-eye light was 660 nm ($G_T R_C$ set). Again, each $G_T$ level (OFF, 0.7, 1.4, and 2.0 log td) was paired with each $R_C$ level (OFF, 0.5, 1.3, and 1.9 log td) and, in addition, with an $R_C$ level that canceled the greenness in the background.

In a given adapting condition, the adapting light presented to each eye was fixed. In order to minimize possible centrally-mediated effects that might influence the relative contribution of each eye to the fused percept, both eyes first were dark adapted for seven minutes. The observer then viewed the adapting lights for seven minutes. In some conditions, an absolute threshold measurement was made prior to light adaptation. This measurement was a check for accurate positioning of the bite bar and optical components that had to be moved in order to accommodate different observers. Though these positions were set using calibrated scales with units of 0.5 mm or less, the threshold measurement provided additional confirmation of correct positioning. When another subject had used the apparatus since the last run, a threshold was measured and then 2 min of additional dark adaptation followed prior to light adaptation.

The observer’s task was always the same: adjust the admixture composing the annular test so that the test was neither reddish nor greenish. When the test-eye background was 660 nm, the experimenter controlled the level of 660 nm light in the test ($\Delta R$); the observer adjusted the retinal illuminance of the 540 nm test light ($\Delta G$) so that the annulus was neither reddish nor greenish. When the test-eye background was 540 nm, the experimenter controlled the level of 540 nm light $\Delta G$ and the observer adjusted 660 nm light $\Delta R$. This procedure gave the observer control of the light that cancels the test-eye-background hue, thereby allowing measurements in the presence of a background-field additive effect (Shevell, 1978, 1980). During the last two minutes of light adaptation, the annular test held was introduced at its lowest level (about 0.5 log td). The observer then approximated a neutral setting and viewed the test for the remainder of the adapting period. The observer then made a new setting that was recorded: repeated settings were made, with the observer-controlled level randomly perturbed by up to 0.2 log unit after each one. Five settings were obtained at each test level. The experimenter-controlled component of the test was increased in approximately 0.3 log unit steps up to a maximum of nearly 3.0 log td. Observers were allowed a rest period and were exposed to ordinary room light at the conclusion of the first condition within a session. Prior to the second condition, dark and light adaptation proceeded as described above, except that threshold measurements were excluded.

Variability of the reported measurements is small. For two of the observers, the average standard error of the mean (SEM) is 0.05 log td (90% of the SEMs at or below 0.09 log td). Corresponding values for the third observer (K.B.) are 0.07 and 0.15 log td.

RESULTS

Backgrounds that stimulate only one eye

When the perceived background results from fusing two lights, each presented to a different eye, chromatic adaptation affects both monocular (retinal and central) and binocular (central) mechanisms. We first consider the adapting effects of backgrounds presented only to one eye—either the same eye as the test patch or the opposite eye. These results provide a basis for examining the adapting effect from fused lights that is beyond those effects caused by adapting each eye alone.

Measurements with a 660 nm monochromatic background are shown in Fig. 2. The top panels show results with the 660 nm background presented to the right eye and the test to the left eye; each panel shows measurements for a different observer. Despite substantial differences among observers, it is clear that the 660 nm background generally reduces the amount of required reddish 660 nm light ($\Delta R$) in the opposite-eye test at every level of the test-patch. This is shown more clearly by the filled symbols (bottom of each panel), which plot for each condition the change in $\Delta R$ from its level under dark adaptation ($R_C$ off). Except perhaps for observer M.E.M., the effect of the contralateral background does not disappear as the radiance of the test increases. Therefore the background does not, in general, simply add a fixed amount of redness to the test. These measurements confirm earlier results from a slightly different paradigm (Shevell and Humanski, 1984).

The bottom panels show measurements for the same three observers with the 660 nm background presented to the same eye as the test. As expected from many similar experiments, increasing the background level generally reduces the amount of greenish light $\Delta G$ (or, equivalently, increases the amount of reddish test light $\Delta R$) required for an equilibrium yellow percept.
Fig. 2. Equilibrium yellow measurements for three observers. Top panels: open points are measurements under contralateral 660 nm adaptation; each point shows the retinal illuminance of the 660 nm light ($\Delta R$) as a function of the retinal illuminance of the 540 nm light ($\Delta G$) in the test field. Solid points show the change in $\Delta R$ retinal illuminance from the $\Delta R$ level with $R_c$ OFF. The change is shown as a function of $\Delta G$ retinal illuminance. Symbols indicate the level of the contralateral 660 nm adapting field $R_c$ (values of $R_c$ in log td). Solid points with error bars are mean values plus or minus one SEM. Bottom panels: measurements with the 660 nm adapting field and the test presented to the same eye. Each point shows the retinal illuminance of the 540 nm light ($\Delta G$) as a function of the 660 nm light ($\Delta R$) in the test field; symbols indicate the level of test-eye adapting light $R_t$ (values in log td).
binocularly fused adapting fields

Note that the 660 nm background is an effective adapting stimulus. When presented to the contralateral eye at any level from 3 to 80 td (0.5–1.9 log td), the average amount of reddish light in the test, ΔR, is significantly less than in the dark at every adapting level for each observer. In one case (observer K.B., 80 td background), the average decrease is nearly 0.3 log unit (solid circle with error bars). When an 80 td, 660 nm background is presented to the test eye, it causes at higher test-patch illuminances a ΔG reduction of more than 0.5 log unit below dark adapted levels.

Measurements with the background wavelength changed to 540 nm are shown in Fig. 3. When the 540 nm background is presented contralaterally (top panels), its average effect at any level is less than 0.15 log unit and often near zero (see solid symbols). Even when stimulating the test eye (bottom panels), the 540 nm background field has a smaller effect than the 660 nm field. Clearly, a 540 nm background presented alone to either eye is a less effective adapting stimulus than a 660 nm field of the same retinal illuminance. This is not surprising, since the difference between MWS and LWS cone sensitivity is much smaller at 540 nm than at 660 nm and, further, in the dark 1 td of 660 nm light is canceled by 2–6 td (depending on observer) of 540 nm light for equilibrium yellow. The observed relative effectiveness of illuminance-equated 540 and 660 nm adapting lights will be useful for interpreting measurements with binocularly fused fields.

Binocularly fused background lights of different wavelengths

Long-wavelength test-eye and middle-wavelength contralateral-eye backgrounds: Figure 4 shows results with a 660 nm background presented to the test eye and a fused 540 nm background to the other eye. The perceived color of the fused binocular mixture depends on the relative radiances of the two backgrounds: in some cases it is very reddish, in others very greenish, and in still others (approximately) neither reddish nor greenish. The color appearance of each fused background is indicated within parentheses in the symbol legend of each panel. These informal reports were made after the observer adapted to the fused fields for five minutes and before any measurements were taken. It is important to stress the informality of the color naming data; subjects were given no formal training in the use of color names and saw only those stimuli presented in the course of the experiments (e.g. they never saw a unique green). The letters G, Y, and R stand for green, yellow, and red, respectively. When there are two letters, the upper case letter refers to the more dominant hue and the lower case letter to the less dominant hue (e.g. YE is greenish-yellow). If the fused field appeared desaturated, this also is noted.

The main purpose of these measurements is to determine the effect of the contralateral-eye background, and the results in Fig. 4 are plotted to assess this directly. In each panel, the test-eye adapting light is fixed; different symbols represent distinct levels of the opposite-eye background. Each plotted point indicates the retinal illuminance of the greenish (540 nm) light in the annular test patch. ΔG, required to cancel redness at the given retinal illuminance of the 660 nm test-patch light ΔR. Solid symbols at the bottom of each panel are changes in ΔG from the identical test-eye condition with no contralateral background.

The most striking result is the very minimal effect of adding the contralateral background field. This is shown most clearly by the solid symbols in each panel that fall very close to zero (dashed line). There is a clear effect due to the test-eye background. Since the general shape of the curves through the open symbols changes with RF, retinal illuminance (e.g. compare the top and bottom panels for each observer). However, the solid symbols with error bars show the average effect-size due to adding a contralateral 540 nm field usually is less than 0.1 log unit.

Average effect-size is plotted as a function of contralateral-field retinal illuminance in Fig. 3 (left panel) to show another clear result from this experiment: there are substantial differences among the three observers. Each subject’s results are indicated by a different symbol. As an example, consider measurements with a fairly dim test-eye background (RF = 0.5 log td, top part of left panel in Fig. 5); when the level of the opposite-eye field (G1) is increased from 0.7 to 2.2 log td, the test-patch color (and thus required amount of canceling ΔG) clearly changes for observer K.B. (solid circles), but for observer R.H. (solid squares) the effect is much closer to zero and in the opposite direction. The middle section (RF = 1.0) and bottom section (RF = 1.9) of the left panel show similar differences among the observers. Though the effect of the contralateral field is statistically significant in some cases (standard errors for these points range from 0.07 to 0.08 log td), in general the effects are rather small and, more importantly, qualitatively dissimilar for different observers. Increasing the level of the opposite-eye 540 nm field does not consistently raise or lower the required amount of greenish test-patch light ΔG.

Since 660 nm light is a more effective adapting stimulus than 540 nm light and because test-eye stimulation in general tends to cause larger adapting effects than opposite-eye stimulation, these stimulus conditions may exacerbate observer differences in binocular processing since the opposite-eye signal is relatively weak. If this is correct, then exchanging the background wavelengths presented to the two eyes should give larger contralateral-eye adapting effects and better agreement among observers. With a 540 nm background presented to the test eye and a fused 660 nm background to the contralateral eye, the relative weakness of opposite-eye effects is offset.
Fig. 3. Equilibrium yellow measurements for three observers. Top panels: open points are measurements under contralateral 540 nm adaptation, each point shows the retinal illuminance of the 540 nm light ($\Delta G$) as a function of the retinal illuminance of the 690 nm light ($\Delta R$) in the test field; solid points show the change in $\Delta G$ retinal illuminance from the $\Delta G$ level with $G_T$ OFF. The change is shown as a function of $\Delta R$ retinal illuminance. Symbols indicate the level of the contralateral 540 nm adapting field $G_T$ (values of $G_T$ in log td). Solid points with error bars are mean values plus or minus one SEM. Bottom panels: measurements with the 540 nm adapting field and the test presented to the same eye. Each point shows the retinal illuminance of the 690 nm light ($\Delta R$) as function of the 540 nm light ($\Delta G$) in the test field; symbols indicate the level of test-eye adapting light $G_T$ (values in log td).
somewhat by the relative strength of the 660 nm adapting wavelength.

**Middle-wavelength test-eye and long-wavelength contralateral-eye backgrounds.** Measurements with the background wavelengths reversed are shown in Fig. 6. As in Fig. 4, results are plotted to show explicitly the effect of the contralateral background. The 540 nm test-eye background is fixed in each panel; symbols indicate the level of the 660 nm opposite-eye field. Each plotted point shows the illuminance of the reddish (660 nm) test-patch light, \( \Delta R \), as a function of the illuminance of the greenish test-patch light, \( \Delta G \), for given levels of test- and opposite-eye backgrounds. Solid symbols show the change in \( \Delta R \) from the identical test-eye condition with no contralateral background. As before, there are substantial differences among the three observers, but in general the effect of contralateral adaptation is larger than in Fig. 4 and, more importantly, is qualitatively consistent across subjects. Observer
Fig. 5. **Left panel:** effect (averaged over all test-patch levels) of the contralateral 540 nm field ($G_c$) when fused with a 660 nm test-eye background ($R_e$), plotted as a function of contralateral-field retinal illuminance. Results are shown separately for each level of the test-eye background $R_e$ (top section: 0.5 log td; middle section: 1.0 log td; bottom section: 1.9 log td). Each observer is represented by a different symbol. Open symbols indicate contralateral-field levels resulting in a fused background that is neither reddish nor greenish. **Right panel:** effect (averaged over all test-patch levels) of the contralateral 660 nm field ($R_c$) when fused with a 540 nm test-eye background ($G_e$), plotted as a function of contralateral-field retinal illuminance. Results are shown separately for each level of the test-eye background $G_e$ (top section: 0.7 log td; middle section: 1.4 log td; bottom section: 2.0 log td). Symbols as in left panel. Each arrow points to the effect-size for the same condition as the symbol to which it is attached, except that the average is taken only over the four dimmest test-patch levels (see text).

K.B. shows the largest effect from the contralateral background (well over 0.5 log unit with the most intense opposite-eye 660 nm light [solid circles, left panels]); any contralateral 660 nm field causes the test to appear more reddish, regardless of the level of 540 nm test-eye background. Further, for K.B. the size of the effect clearly increases with the level of contralateral light. Observers R.H. and M.E.M. show qualitatively similar though smaller effects, as described below.

While inter-observer differences are troublesome for a general model of chromatic adaptation with fused adapting stimuli, these differences may be turned to advantage in considering the measurements of Fig. 6. The right panel of Fig. 5 (solid symbols) summarizes these measurements for each observer; each point is the average over all test-patch levels of the $\Delta R$ difference caused by adding a contralateral 660 nm background. Despite considerable observer differences, these average effect-size results reveal a
consistent pattern: Increasing the level of the contralateral 660 nm background reduces the required amount of canceling 660 nm test-patch light, $\Delta R$, for each observer at every test-eye background illuminance. Further, the magnitude of the contralateral effect is not systematically different at lower test-patch levels. This is shown by the arrow attached to points in Fig. 5 (right panel), whose tip indicates the average $\Delta R$ difference for the four dimmest test-patch levels (in contrast to the plotted point, which is the average over all test-patch levels). If the contralateral adapting effect were dependent on test-patch level, then these arrows should point systematically to smaller or larger effects. In fact, there is no such pattern; of the 27 connected points in the right panel of Fig. 5, for 11 the magnitude of the contralateral adapting effect is smaller for dimmer test patches, for 9 the magnitude is larger, and for 7 the magnitude is
nearly the same (the difference is smaller than the size of the plotted point). Of the last 7, for 4 the magnitude is slightly smaller and for 3 the magnitude is slightly larger: thus of all 27, for 15 the magnitude is smaller and for 12 the magnitude is larger, which is far from significant by a sign test \( (P > 0.50) \). This confirms that a contralateral 660 nm background does not simply add redness to the test patch, since added redness would have a much larger effect on low than high illuminance test patches (note the trend, while not significant, is in the opposite direction).

Analyses of variance, computed separately for each observer, further support the view that the effect of a contralateral field \( (R_c) \) is not dependent on test-patch level \( (\Delta G) \). In a three-way factorial design (test-eye-background level \( \times \) contralateral-eye-background level \( \times \) experimenter-controlled-test-component level —i.e. \( G_T \times R_c \times \Delta G \)) with observer-controlled-test-component logarithmic retinal illuminance \( (\Delta R) \) as dependent variable, the effects of \( G_T \times R_c \times \Delta G \) and \( G_T \times \Delta G \) were highly significant, but the contralateral-eye-background \( \times \) experimenter-controlled-test-component interaction \( (R_c \times \Delta G) \) and the three-way interaction never approached significance \( (P > 0.30 \text{ in every case}) \).

Fused adapting fields that are neutral (neither reddish nor greenish)

No mention of the adapting conditions with fused fields that are neither reddish nor greenish has been made because these conditions are entirely unremarkable: a contralateral background radiance selected to cancel the redness or greenness of a test-eye background had an effect predicted by its radiance alone. In most cases the canceling level of contralateral light fell near or between levels tested in other conditions (in the range 0.5–2.2 log unit). The measurements showed that the effect of a canceling contralateral field similarly tended to fall between the effects of the nearby levels tested in other conditions. Occasional exceptions were not consistent across observers. Results with fused backgrounds that are neither reddish nor greenish are summarized by the open symbols in Fig. 5.

The neutral conditions were included to consider two hypotheses. The first hypothesis is that fused backgrounds resulting in a neither-reddish-nor-greenish percept have no effect on the test-field admixture. This means the results should be the same as dark-adapted measurements, as indeed is the case with a moderate neither-reddish-nor-greenish monocular adapting field that does not stimulate SWS cones (self-invariance of equilibrium yellow; Cicerone et al., 1975). Since 540 nm adaptation of the test-eye alone tends to reduce the required amount of \( \Delta R \) (bottom panels, Fig. 3), this hypothesis implies that adding the appropriate amount of fused 660 nm contralateral light should require more \( \Delta R \), since the fused percept would be neither reddish nor greenish and thus should give dark-adapted results. However, adding any amount of contralateral 660 nm light reduces \( \Delta R \), contrary to hypothesis. This result emphasizes the point made in the introduction: fused adapting lights have effects that cannot be accounted for by the fused percept.

The second hypothesis is that a fused background that is neither reddish nor greenish has the same central effect as a monocular (test-eye only) adapting field. A central chromatic mechanism that requires binocular stimulation might be in a neutral state both (1) when only the test-eye is stimulated or (2) when the fused percept is chromatically neutral. Clearly there is no support for this hypothesis, since it implies every open symbol in Fig. 5 should fall along the dashed zero-line.

We note for completeness that the level of the contralateral adapting light could be changed only with neutral density filters and therefore was varied in steps of about 0.1 log unit. While this may have forced observers to accept a setting that was not perfectly neutral, it is extremely unlikely to affect the conclusions.

**DISCUSSION**

Our results show that the color of a small test patch superimposed on a background and presented to only one eye can be changed by a background light presented to the opposite eye, even when test- and opposite-eye backgrounds are quite different from each other in wavelength and retinal illuminance. While this holds for each of the observers tested, clearly there are large differences among the subjects; agreement among observers is qualitative, not quantitative. These differences cannot be attributed to measurement error since the variability of measurements is far too small. Further, differences among observers are consistent in various stimulus conditions (e.g. observer K.B. always showed the largest effect of contralateral long-wavelength adaptation). We here made no attempt to explain these differences among subjects, but instead used them to determine those experimental results that reflect features of the visual system common across natural variation.

**Chromatic coding of centrally mediated adaptation signals**

The measurements show that the effect of a contralateral field cannot be explained simply by addition of a hue signal from the contralateral eye. This hypothesis already was rejected for test- and opposite-eye backgrounds of the same wavelength (Shevell and Humanski, 1984). The present results extend this conclusion to fused backgrounds that differ in wavelength, and further allow more explicit characterization of the central mechanism that receives information regarding the state of chromatic adaptation in each eye.

Consider the effect of increasing the radiance of a contralateral adapting light of some fixed wave-
length. If the size of this effect depends strongly on the wavelength (but not radiance) of the background in the test eye, this would be evidence that the central mechanism is affected by the chromatic content of the components contributing to the fused background field. Consider specifically the effect of increasing a contralateral 660 nm background from 0.5 to 1.9 log td (a 25 fold increase). How does the size of this effect depend on the background wavelength in the test eye? First, examine the baseline case of no test-eye background; here, of course, there is no influence of test-eye-background wavelength since the test-eye background is absent. We previously showed (Shevell and Humanski, 1984; also replicated here) that increasing the illuminance of a long-wavelength contralateral field increases the $\Delta G/\Delta R$ ratio for equilibrium yellow (equivalently, shortens the equilibrium yellow wavelength). Further, we found that adding a fused test-eye background of the same wavelength as the contralateral light reduces the change in $\Delta G/\Delta R$ ratio caused by raising the 660 nm background.

A simple explanation is that when the test-eye sees only the small test (no background), the large contralateral-eye field acts as a kind of chromatic reference standard. Normally both eyes view the same visual scene, so each eye would have its own "reference" information for the complete scene; reference signals from the other eye would be of little value. The effect of contralateral adaptation then would be a consequence of the unnatural haploscopic stimulus presentation. Without being specific about how the reference standard might affect color perception, a clear prediction of this hypothesis is that any test-eye background, even a very dim one, should reduce the influence of the contralateral field. This is exactly what was found with 660 nm adapting lights presented to both eyes (Shevell and Humanski, 1984).

The measurements in Figs 2 and 6 show this hypothesis is wrong. For every observer, adding a 540 nm test-eye background increases the change in $\Delta G/\Delta R$ ratio caused by raising the 660 nm field, a result opposite to the prediction of a contralateral chromatic reference standard. This is shown explicitly in Fig. 7 where the change in $\Delta G/\Delta R$ ratio, averaged over test-patch level, is plotted; each connected set of points shows measurements for a different observer. The left panel shows results with 660 nm test-eye background (based on Figs 3, 4 and 5 in Shevell and Humanski, 1984); in the right panel the test-eye background is 540 nm (measurements from Figs 2 and 6 here). Adding a 660 nm test-eye background (left panel) reduces the change in $\Delta G/\Delta R$ ratio (equivalently, reduces the change in equilibrium yellow wavelength), but adding instead a 540 nm test-eye background (right panel) increases it ($P < 0.01$ for each observer by a posteriori Scheffe procedure). Note that the influence of the 660 nm test-eye background is similar even when it approaches photopic threshold (0.0 log td). Therefore
the effect of test-eye-background wavelength cannot be attributed to the differential adapting effectiveness of luminance-equated 540 and 660 nm lights.

These results suggest that neural signals arriving at the central mechanism are chromatically coded. This would account for the relation between test-eye-background wavelength and the change in $\Delta G/\Delta R$ ratio: Relative to the no-test-eye-background condition, the change reverses direction when the test-eye-background wavelength (but not radiance) is varied. A fused test-eye background of 540 nm increases the change, while a similar 660 nm field reduces it.

However, there is a possible alternative to chromatic coding of signals carrying information about each eye's adapting field. Each signal arriving at the central mechanism could depend exclusively on responses originating within receptors of a single type, with the central mechanism itself transforming these signals into chromatic responses. The results here cannot distinguish this from chromatic coding of relevant signals from each eye.

**What is the role of centrally mediated adaptation?**

These experiments represent an initial attempt to determine the function and nature of central mechanisms of chromatic adaptation. They indicate that the response of the central mechanism depends on the relation between the wavelength stimulating the left eye and the wavelength stimulating the right eye. The effects of a fused background cannot be explained by combining the effects of monocular adaptation (alone) and contralateral adaptation (alone). Instead, color-appearance shifts caused by contralateral adaptation depend on the adapting wavelength in the other eye.

The central visual system usually is not confronted with signals from the two eyes as different as those here. However the signals from the two eyes are seldom, if ever, the same, even when both eyes view the same stimuli. The differences may be due to prereceptoral factors, small differences in the photopigments or orientation of receptors, and neural mechanisms that are not precisely identical in each eye. Psychophysical measurements show clear differences between an observer's left and right eyes. Color matches for the two eyes usually are not identical (V. C. Smith, personal communication) and interocular brightness matching often reveals differences between an observer's eyes of up to 0.3 log unit (Wright, 1946; Heintzmann, 1955; Stevens and Diamond, 1965; Whittle and Challands, 1969).

The results here suggest a central mechanism that tends toward color constancy when the two eyes are in different states of chromatic adaptation. One way this central mechanism could adjust for differences between the eyes is to set the "color balance" in each eye by comparing the color signals from that eye's background to the color signals of the fused background. For example, if the right eye is adapted to a long-wavelength "red" field and the left eye is dark adapted, the right eye alone suffers a sensitivity loss for long-wavelength light. Comparison of signals from the dark adapted eye with signals for the fused reddish percept could result in an increase of relative gain for LWS-cone signals (or perhaps some transformation of a chromatically coded response) for the dark-adapted eye, so that the fused mixture of a test stimulus seen by both eyes would have a color appearance closer to the totally dark adapted percept. This would account for the increase in $\Delta G/\Delta R$ ratio under contralateral long-wavelength adaptation, as seen in Fig. 2, since such compensation in the test eye would require equilibrium yellow to shift to a shorter wavelength.

This qualitative model also can account for the contrasting influences of 540 nm and 660 nm test-eye backgrounds on color appearance changes caused by increasing a contralateral long-wavelength field. When both eyes see a 660 nm background, the color signals for the fused percept differ less from the signals for each eye than in the case where only the contralateral eye is adapted; therefore the relative change in balance induced in the test-eye by contralateral adaptation is smaller. Precisely the opposite occurs when the test-eye views a 540 nm background, in which case the difference between the color of the test-eye background and the color of the fused percept can be larger than when there is no test-eye background; here the effect of changing from a relatively dim to a relatively intense opposite-eye 660 nm background causes a large change in the color of the fused field and consequently causes a large change in centrally mediated test-eye long-wavelength relative sensitivity (or chromatically coded response).

Note that this posited central mechanism seeks to keep the two eyes in balance but does not defeat the normal processes of adaptation; specifically it has little effect when both eyes are adapted equally and further does not overcome retinal (or central but purely monocular) adaptation even when each eye is adapted to very different lights. For example, a 540 nm test-eye background, which increases relative sensitivity to long-wavelength light when presented alone, causes in the presence of a 660 nm contralateral field a centrally mediated effect described by still greater long-wavelength relative sensitivity.

The specific characteristics of the hypothesized central mechanism are vague. What monocular color signals and fused color signals are compared? Given these signals, how are they compared? How is the result of the comparison process related to observed changes in color appearance? Though these questions require further investigation, the qualitative implications of the posited central mechanism provide a consistent account for the complete set of color perception measurements.

**Acknowledgement**—Supported by the National Science Foundation (BNS-8303765) and the National Institutes of Health (EY-04802).
REFERENCES


