COLOR PERCEPTION UNDER CHROMATIC ADAPTATION: RED/GREEN EQUILIBRIA WITH ADAPTED SHORT-WAVELENGTH-SENSITIVE CONES

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Abstract—Chromatic adaptation can dramatically alter the color appearance of a light. The specific effect of adapting short-wavelength-sensitive (SWS) cones is examined by using two adapting wavelengths that lie on a tritanopic confusion line. The change in color appearance caused by signals from adapted SWS cones is isolated by restricting the wavelengths of the test light to 550 nm or longer. Thus the test negligibly stimulates SWS cones, so their sensitivity does not affect the test's appearance. The results show that adapted SWS cones contribute redness to the appearance of a superimposed test light, while not affecting sensitivity of MWS and LWS cones. Quantitatively, the redness from SWS cones illuminated by a large adapting field approaches physical admixture of test and adapting lights. This is very different from an adapting field that stimulates only MWS and LWS cones which, due to a postreceptoral process, contributes much less redness to a small superimposed test than expected from admixture. The difference between the adapted SWS-cone and the adapted MWS/LWS-cone contributions to the color of a small test explains a surprising result: a bluish-green (491 nm) adapting field contributes redness to a superimposed test light.

INTRODUCTION

The color appearance of a light is difficult to predict. Quantal absorption by each of the three types of cone is an important factor, but the percepts of hue, saturation and brightness depend on many other aspects of a complete stimulus configuration.

Adaptation to other lights can cause dramatic shifts in color perception. A chromatic background can alter the color of a small superimposed patch of light by at least two processes: (1) desensitization of photoreceptors, which varies in degree for the three types of cone; and (2) a neural process that minimizes, but usually does not eliminate, the influence of background light that falls in the retinal area of the small patch. The two processes, operating together, account for color appearance under a wide range of adapting conditions (Hurvich and Jameson, 1958; Jameson and Hurvich, 1972; Walraven, 1976; Shevell, 1978, 1982; Adelson, 1981; Drum, 1981; Larimer, 1981; Ware and Cowan, 1982; Werner and Walraven, 1982; Shevell and Handte, 1983).

The second process explains the surprisingly small effect of quanta from a background field that add physically with a superimposed patch. Consider, for example, a small patch that is a mixture of 540 and 660 nm lights, set at levels so the mixture appears yellow. Superimposing the patch on a large 660 nm background field increases the 660 nm light in the area of the patch by the amount of light in the background. The redness of the patch, however, increases much less than expected from physical admixture of patch and background lights. A neural process, which incorporates information about light surrounding the patch, compensates in part for the added 660 nm background light. Thus quanta from the background field affect the appearance of the superimposed patch less than quanta composing the patch itself. This phenomenon is called "discounting" the background.

Though receptoral desensitization and the neural discounting process occur simultaneously, desensitization often dominates the color we perceive, particularly when the small patch is much brighter than the background. For example, a small patch that appears bright yellow in the dark becomes greenish when superimposed on a large, moderate long-wavelength ("reddish") field. This occurs despite the long-wavelength background light that falls in the area of the patch, which increases the quantal catch of long-wavelength-sensitive (LWS) cones predominantly and thus tends to shift the appearance of the patch toward red-
ness, not greenness. The neural discounting process, however, minimizes the influence of added background quanta, so receptoral desensitization is the dominant mechanism by which the background affects the color of the patch. Because the long-wavelength background field causes relatively more desensitization of LWS than MWS photoreceptors, the patch that is yellow in the dark appears greenish on the long-wavelength background. In many experimental paradigms, the dominant influence of receptoral desensitization masks other processes of adaptation.

The present experiments examine color perception under adapting conditions that do not change the sensitivities of the receptors detecting the test. Two adapting-field wavelengths are selected that differ in the light absorbed by SWS cones (by about 30-fold), but not in the light absorbed by MWS and LWS cones. At the same time, the spectral composition of the small test patch is restricted to wavelengths that negligibly stimulate SWS cones. Therefore SWS photoreceptors absorb quanta from only the background field, allowing direct assessment of the effect of signals from adapted SWS cones on the redness/greenness of a test patch detected only by MWS and LWS cones.

This design has two features that distinguish it from the many previous studies of chromatic adaptation. First, as mentioned above, color appearance measurements are made with two specific adapting wavelengths that differ only in SWS-cone quanta absorption (the two adapting lights are on a tritanopic confusion line; v. Boynton and Kambe, 1980). Thus the experiments isolate the specific effect of adapting SWS cones. In most earlier research on red/green equilibrium colors (that is, lights that appear neither reddish nor greenish), the adapting light appreciably stimulated only MWS and LWS cones. The few experiments conducted with short-wavelength fields investigated the adapting effect of equilibrium blue (Cicerone et al., 1975; Ingling, 1977; Ikeda and Ayama, 1980; Ejima and Takahashi, 1985; Takahashi et al., 1985), the present measurements with tritanopic metamer s should eliminate any dwindling skepticism.

METHOD

Apparatus

Measurements were made using a five-channel Maxwellian-view optical system (Fig. 1). Four channels share a single light source $S_{1,2,3,4}$ (24V, 150 W tungsten–halogen GE DZE lamp connected to a Power-one F-24-12A regulated d.c. power supply, underrun at about 22.5 V) and are identical in design and path length from the source to the observer’s pupil ($P$). In each channel, lenses image the filament on an aperture stop (A) which is adjacent on one side to an Inconel neutral density wedge ($W$) and on the other side to a Uniblitz electronic shutter (Sh). An additional lens collimates the light prior to a filter box (FB) which contains Inconel neutral density filters and a Ditric Optics three-cavity interference filter (manufactured to block transmission of wavelengths outside the bandpass to below 0.01%). Light from channels 1 and 2 (3 and 4) is combined by mixing cube $C_{1,2,3,4}$ prior to a field stop (FS) located near the rear focal plane of final lens $FL$. Light from the four channels is combined by cube $C_{1,2,3,4}$. A fifth channel with its own source ($S_5$) is similar in design. Mixing cube $C_{1,2,3,4,5}$ combines light from all five channels. For safety, an infrared filter (IR) is mounted between the source and each aperture stop. A permanently mounted laser is used to maintain alignment of the optics. The observer’s head is held steady by a bite bar mounted in a three-dimensional positioning device. Light levels are calibrated with an EG&G 550 radiometer/photometer using corrections for the spectral characteristics of our particular instrument.

The optical system is connected to an IBM PC XT microcomputer that controls shutter timing and, via stepping motors, the positions of the Inconel wedges. The light level of each channel is set with a wedge, controlled by a joystick. Measurements are recorded by the
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Observers
All observers except R.H. (an author) were paid undergraduate volunteers. Each was screened for color defects by Rayleigh-match measurements. Observers wore their normal prescription lenses (if any).

Procedures
In each experiment a small incremental test field is superimposed upon a background light. The test is a thin annulus (1.2–1.8") centered upon a 5.8° circular adapting field (Fig. 2).

Two adapting wavelengths are used: 441 and 491 nm (in one experiment, a 440 and 490 nm pair is used instead). The two wavelengths fall approximately on a tritanopic confusion line. All lights on a tritanopic confusion line share the same ratio of MWS-to-LWS cone stimulation. A control experiment (below) shows the two wavelengths within a pair adequately match MWS: LWS stimulation.

The two adapting wavelengths must be matched in luminosity as well if the lights are to be distinguishable only by SWS cones. Luminosity matches were made separately by each observer using heterochromatic flicker photometry. Each wavelength was matched to tungsten white at four retinal illuminances covering a range from about 1 to 30 td. The four matches for a given observer were very close (the range never exceeded 0.12 log unit, which is near the spread of identical measurements repeated on different days), so the average of the four flicker matches was used.

Retinal illuminance values stated below are calibrated levels for 441 nm (or 440 nm) light; the 491 nm (or 490 nm) level was set according to the subject's luminosity match. Quantal absorption by SWS cones stimulated with 441 nm light is about 30 times the level achieved with a luminosity-matched 491 nm field. The level of

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**Fig. 1. Schematic diagram of the apparatus.**

**Fig. 2. Spatial representation of the stimuli.**
the adapting light was varied between sessions from 1 to 25 td.

The test is an admixture of 550 nm light (denoted $\Delta_{550}$) and 660 nm light (denoted $\Delta_{660}$). These wavelengths negligibly stimulate SWS cones. The retinal illuminance of the 660 nm test component, $\Delta_{660}$, is held fixed while the observer adjusts the level of the 550 nm light, $\Delta_{550}$, so that the thin annular test field appears neither reddish nor greenish. Five settings are made at each level of $\Delta_{660}$: prior to each setting the previous one is randomly offset by up to 0.2 log td. The average of the five settings is taken as the measurement for the day.

At the beginning of each session the observer dark adapts for 7 min, after which the 660 nm absolute threshold is measured as a check on observer alignment. The observer then adapts to the background light for the session; after 5 min, increment threshold for the 660 nm test light is determined to check whether any levels of the 660 nm test component planned for the session cannot be detected. The first equilibrium-color measurement is made after 2 min of additional adaptation. The level of $\Delta_{660}$ is incremented in steps of about 0.3 log unit.

Each condition is repeated on at least two separate days; standard errors are based on the variability of a measurement over days. Measurement variability is small: in the first experiment, for example, the median (90th percentile) standard error of the mean for observers C.C., M.E.M. and R.H. is 0.04 (0.10), 0.03 (0.07), and 0.03 (0.09) log td, respectively. Variability in the other experiments is comparable.

**RESULTS**

The adapted state of short-wavelength-sensitive cones strongly affects the color appearance of a light that does not stimulate them. This is clearly demonstrated in both the main experimental conditions and the control conditions.

The change in color appearance caused by adapting SWS cones is established by comparing two sets of red/green equilibrium-color measurements: measurements with a 441 nm (or 440 nm) adapting field, and measurements with a luminosity-equated 491 nm (or 490 nm) field. The rate of quanta1 absorption by SWS cones is about 30 times higher at the shorter wavelength. Because quanta1 absorption by the two other types of cone is equivalent for these two wave- lengths, the difference between 441 and 491 nm adaptation is due to SWS cones alone.

Results from the first experiment, in which a steadily presented test is superimposed on a large adapting field, show the main conclusion: a signal from adapted SWS cones contributes a fixed amount of redness to a test detected only by MWS and LWS cones. Later experiments eliminate alternative explanations, the most important of which is signals from rods stimulated by the large adapting field, and show the conclusion is the same whether the test field is steadily presented or briefly flashed.

**Test field presented steadily**

Typical results with a steadily presented test are shown in Fig. 3. The adapting level is 8 td. The level of 660 nm light in the test mixture, $\Delta_{660}$, is on the horizontal axis; the amount of 550 nm light in the test mixture, $\Delta_{550}$, which is set by the observer so the test appears neither reddish nor greenish, is on the vertical axis. Open squares are results with 440 nm adaptation; filled squares are values with a luminosity-equated 490 nm field. Circles are dark adapted measurements, included here to show the magnitude of shift caused by the adapting light. Error bars indicate ±1 SEM (the SEM is smaller than the plotted symbol where no error bar is visible).

The main result is that more 550 nm "greenish" test light is needed with 440 than with 490 nm adaptation (open squares above filled squares at left of plot). This means a light that appears neither reddish nor greenish on the 490 nm adapting field is reddish on the 440 nm adapting field. The additional redness from the 440 nm field must be due to SWS cones, because MWS and LWS cones cannot detect a difference between the 440 and 490 nm lights.

What is the mechanism by which the adapted SWS cones contribute to color perception? A suggestion comes from the relation between test level and the effect of adapting wavelength. The additional amount of 550 nm test light ($\Delta_{550}$) required with the 440 nm field is large at low test levels but is much smaller or negligible at higher test levels. The open and filled squares in Fig. 3 converge as $\Delta_{660}$ is increased toward 3.2 log td. This pattern of results is consistent with SWS cones contributing a fixed amount of redness to the test while not affecting the sensitivity of MWS and LWS photoreceptors. The redness from SWS cones is substantial compared with the redness from low levels of the long-
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Fig. 3. Red-green equilibrium measurements with an 8 td adapting field. The retinal illuminance of the 660 nm test component is on the horizontal axis; the amount of 550 nm test light, set by the observer for a neither reddish nor greenish percept, is on the vertical axis. Results with a 5.8' 440 nm and a 5.8' 490 nm adapting field are shown by open and solid squares, respectively. Dark adapted measurements are shown as circles. Error bars indicate ± 1 SEM.

wavelength test light, \( \Delta_{660} \), but declines in relative significance as the level (and thus redness) of \( \Delta_{660} \) is increased.

If adapting SWS cones had not affected the color of a light that does not stimulate them, the measurements with 440 nm adaptation would be indistinguishable from results with 490 nm adaptation. No effect from SWS cones is predicted by complete discounting of the background (Walraven, 1976), which specifies background light falling in the same retinal area as the test will not change the appearance of the test. (The appearance of the test here is not affected by desensitization of SWS cones because the test is not detected by them.) The data in Fig. 3 refute the complete-discounting hypothesis for the case of an 8 td field. The measurements in Fig. 4 extend this conclusion to a wide range of adapting illuminances.

Results with 1-, 2.5-, 8-, and 25-td adapting fields are shown in Fig. 4. Each panel contains data from a different observer. The axes and symbols are the same as in Fig. 3 (half-filled squares in Fig. 4 are explained in the next subsection). At low test levels (\( \Delta_{660} \) less than about 1.5 log td) the open and filled squares always are separated. Even with a dim 1-td adapting field, raising SWS-cone adaptation by using 440 rather than 490 nm light increases the required amount of 550 nm test light: at low test levels the increase is a factor of 5 (0.7 log unit) for 2 of the 3 observers. With a 25-td adapting field, the increase in \( \Delta_{550} \) is 10 fold (1 log unit) or more.

The complete set of measurements can be accounted for by adapted SWS cones contributing redness to the appearance of the test. The magnitude of the contribution depends on the level of the adapting light. In theory, a large SWS-cone contribution could dominate the redness of even the brightest 660 nm test light, so that varying the level of \( \Delta_{660} \) would have little effect. In this case the measurements would fall near a horizontal line, which is, in fact, what is found at the highest 440 nm adapting level (open squares at right of each panel in Fig. 4).

Receptoral sensitivity changes and an additive contribution to the redness/greenness of a test light are the components of the two-process model of chromatic adaptation. The model is quantitatively assessed in a later section.

The symbols with arrows pointing to the horizontal axis are increment threshold measurements (where no measurement is shown the threshold value is below 0.0 log td). They show the 660 nm test component, \( \Delta_{660} \), is never below detection threshold at lower levels of the adapting light. At more intense adapting levels the
Fig. 4. Red-green equilibrium measurements at four adapting levels (1, 2.5, 8 and 25 td). Axes as in Fig. 3. Results with a 5.8° 440 nm, 5.8° 490 nm, and 1.2°-1.8° 440 nm adapting field are shown by open, solid and half-solid squares, respectively. Symbols with arrows pointing to the horizontal axis are increment thresholds for a 660 nm test upon the given adapting field. Dark adapted measurements are shown as circles. Error bars indicate ± 1 SEM. Each panel shows results for a different observer.

dimmest 660 nm test lights cannot be detected by some observers, but in general the 660 nm test field is clearly visible over most of its range.

Annular adapting field. A possible explanation for the results is that SWS cones contribute to color appearance only because the total light in the retinal area of the test is the sum of test and adapting-field lights. Because the annular test field is superimposed upon the background, the photoreceptors in the area of the test absorb quanta from the adapting light as well as from the test light. Perhaps the redness from SWS cones is just the redness expected from a physical admixture of test and adapting wavelengths. On this hypothesis there is no discounting of adapting-field quanta that fall in the area of the test and stimulate SWS cones. While this is contrary to earlier results with middle- and long-wavelength fields (Walraven, 1976; Shevell, 1978, 1982; Humanski and Shevell, 1985), it may be that signals from SWS cones are qualitatively different. The physical-admixture hypothesis was tested by replacing the 5.8° circular field with a 1.2°-1.8° adapting field, which is the same size as the test. The "adapting light" is now a true component of the test field, as it cannot be
distinguished spatially. Under the admixture hypothesis, the results with a 440 nm annular adapting field should be the same as with a 440 nm 5.8° field, except perhaps for differences in MWS and LWS sensitivity, which might depend on signals from MWS and LWS cones outside the area of the test annulus. The experimental procedure is the same as before, except that the adapting field is now an annulus coincident with the test.

Results for two observers (C. C. and R. H.) are shown by the half-filled squares in Fig. 4. The half-filled squares tend to fall above the open squares at lower adapting levels, which shows the redness from adapted SWS cones is not precisely the same as the redness from adding adapting light and test light. Thus there is some discounting of background light absorbed by SWS cones. The 5.8° adapting field, however, is nearly as effective as the annular adapting field, demonstrating there is much less discounting of background light absorbed by SWS cones. The 5.8° adapting field, however, is nearly as effective as the annular adapting field, demonstrating there is much less discounting of background light absorbed by SWS cones than by MWS and LWS cones (Shevell, 1982). At higher adapting levels there is very little difference between the annular adapting light and the large 5.8° adapting field.

The close convergence of half-filled and open squares at higher levels of ΔL indicates receptor sensitivity is not appreciably different under the two adapting conditions, which is consistent with previous results with long-wavelength fields (Shevell, 1981).

Controls

Luminosity mismatch. Lights on a tritanopic confusion line produce the same ratio of MWS-to-LWS quanta absorption but they must be equated in luminosity as well in order to be identical in their stimulation of MWS and LWS cones. Luminosity matches, established by heterochromatic flicker photometry as discussed above, showed little day-to-day variability but still might be considered a potential source of artifact because a deviation of 0.1 log unit corresponds to a mismatch of 25%. Figure 5 shows results with a 10 td, 441 nm adapting field and a luminosity-matched 491 nm field; also shown are measurements with the 491 nm light offset from the luminosity match by ±0.1 log unit (left panel) and ±0.2 log unit (right panel). The luminance of the 491 nm light has some effect, as expected, but the qualitative difference between 441 and 491 nm adaptation is always maintained. Thus small errors in luminosity matching will not affect the conclusions.

Rods. A 441 nm or 491 nm, 5.8° adapting field will stimulate rods. While cones are the receptors primarily responsible for color vision, rods can affect color perception of both normal and color defective observers (McCann and Benton, 1969; Trezona, 1973; Smith and Pokorny, 1977). To eliminate the possibility that rods account for the results, some measurements were repeated in a control experiment that exploits the different recovery times of rods and cones.

A 5.4 log scot. td (5.6 log phot. td) broadband bleaching light was viewed for 7 min. The light, produced with a 530 nm long-pass filter, excluded short wavelengths to avoid the possibility of eye damage. This light strongly bleaches the rods at a level of about 90% (Alpern, 1971). During the bleaching period,

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Fig. 5. Red-green equilibrium measurements with the 491 nm adapting field offset from the measured luminosity match. Axes as in Fig. 3. Open and solid squares are results with luminosity-equated 441 and 491 nm fields, respectively. Circles and diamonds are measurements with the 491 nm field mismatched by 0.1 log unit (left panel) or 0.2 log unit (right panel). Error bars indicate ±1 SEM.
One of the usual short-wavelength adapting fields was presented as well. When the bleaching light was extinguished, the short-wavelength field remained on; in addition, the long-wavelength test component, \( \Delta_{\lambda_{660}} \), was introduced at a fixed level. During recovery the observer continually adjusted the 550 nm test light, \( \Delta_{\lambda_{550}} \), to maintain a neither reddish nor greenish color appearance of the annular test.

If rods do not affect the color-appearance results, measurements following cone recovery, taken a few minutes after the bleach, should correspond to measurements when rods recover completely, about 40 min after the bleach. Figure 6 shows measurements made 3, 6, 8, 12 and 40 min after offset of the bleaching light. The short-wavelength adapting level is 10 (phot.) td; in different runs, the level of the 660 nm test component, \( \Delta_{\lambda_{660}} \), was 0.2, 1.1 or 2.0 log td. The effect of the bleach on cones is still evident after three minutes, as shown by the circles which lie above the other symbols. Results at 6, 8, and 12 min are overlapping, indicating these values were taken on the cone plateau. After 40 min of recovery (inverted triangles), the measurements are similar to those on the cone plateau: with 441 nm adaptation there is no difference between values at 6, 8, 12 and 40 min, while at 491 nm the measurement after 40 min tends to be slightly higher (\( P < 0.01 \)). This suggests rods affect the results at 491 nm by about 0.1 log unit, a relatively slight effect compared to the difference between 441 and 491 nm adaptation (0.6 log unit or more at lower test levels in Fig. 6). Note that the difference between 441 and 491 nm adaptation is larger on the cone plateau than after rod recovery, indicating rods reduce rather than contribute to the effect of adapting wavelength observed in other experiments.

The small change in color due to rods is towards redness. The few measurements taken suggest the effect of rods (on a logarithmic scale) is about the same at each test level, unlike the redness from SWS cones.

**Wavelengths of a tritanopic pair.** Wavelengths forming a tritanopic pair were determined from theoretical cone fundamentals (Smith andPokorny, 1975). While they are unlikely to be precisely correct for each individual observer, the deviations from exact tritanopic wavelengths cannot account for the results. This follows from three separate arguments.

First, with moderate adapting fields the measurements with either adapting wavelength con-
verge toward a common asymptote at higher test levels (Figs 3 and 4). This is the region where the additive redness contribution from the background becomes insignificant compared to the redness in the $\Delta_{560}$ test component, so measurements reflect only the sensitivities of the MWS and LWS receptors. If MWS- and LWS-cone stimulation were significantly different for the two adapting wavelengths, the MWS and LWS sensitivities also would be different, in which case the measurements for the two adapting wavelengths would not converge to a common asymptote; but this is contrary to the data.

Second, an additive contribution from the adapting light resulting from MWS and LWS cones (alone) would cause the test field to shift toward greenness rather than redness. At the short-wavelengths used here, relative MWS-to-LWS sensitivity is considerably higher than at middle-wavelengths that appear greenish; for example, relative MWS-to-LWS sensitivity at 491 nm (and at 441 nm, by definition of a tritan pair) is about 40% higher than at 540 nm (Smith and Pokorny, 1975). Thus a redness/greenness contribution from the adapting light due only to MWS and LWS cones would be greenish. The measurements, however, show a 441 nm adapting light always contributes redness. Thus, the results cannot be due only to the two adapting wavelengths being mismatched in relative MWS-to-LWS stimulation because such a mismatch would vary contributed greenness, while the measurements show a contribution of redness.

Third, measurements with an adapting wavelength displaced from the theoretical tritanopic match show the same qualitative results as above. The filled circles in Fig. 7 are measurements with a 10-td 480 nm adapting light, an 11 nm mismatch from the 491 nm theoretical tritanopic wavelength. Comparing these results with measurements using a 491 nm field (filled squares) reveals a small quantitative difference at lower test levels. Results at 480 and 491 nm are qualitatively equivalent, however, in comparison with 441 nm adaptation: at lower test levels they show a large difference from 441 nm measurements, with 441 nm adapting light contributing more redness to the annular test; while at higher test levels the results for all three adapting wavelengths converge. Therefore the conclusions do not depend critically on the exact adapting wavelengths used, and thus differences between individual observers’ exact tritanopic wavelengths and the theoretical tritanopic values are not a concern.

**Flashed test field**

The previous experiments were conducted with a small, steadily presented test superimposed upon a larger adapting field. An implicit assumption is that the much larger adapting field establishes the state of adaptation. The visual system, however, also is adapting to the continuously viewed test. To determine whether adaptation to the test itself is an important factor (v. Vimal et al., 1987), the first experiment was repeated using a flashed test field. The flashed test was presented for 600 msec once every 7 sec. Measurements for two observers are in Fig. 8; the adapting levels are 2.5, 8, and 25 td (filled symbols). For comparison, results with a steady test are shown as well (open symbols). The steady-test data supplement those of the first experiment; observer R. H. repeated the steady-test conditions, some months later, so the steady and flashed runs could be interleaved randomly among the sessions.

The pattern of results with a flashed test is the same as with a steady test. At lower test levels, the 441 nm adapting wavelength requires significantly more 550 nm test light, $\Delta_{550}$, to achieve a percept that is neither reddish nor greenish. At higher test levels the measurements for the two adapting wavelengths converge.

While none of the earlier conclusions can be explained by adaptation to the test field itself, there is a small quantitative difference between
Fig. 8. Red-green equilibrium measurements at three adapting levels (2.5, 8 and 25 td). Axes as in Fig. 3. Filled symbols are results with a 600 msec test flash presented once every 7 sec; open symbols are results with a steadily presented test field. Circles, squares and triangles indicate 5.8' 441 nm adaptation, 5.8' 491 nm adaptation, and dark adaptation, respectively. Error bars show ±1 SEM. Results for each observer are in a separate panel.

flashed and steady fields (compare filled and open symbols). Modeling (below) shows the difference is consistent for the two subjects.

DISCUSSION

Adapting short-wavelength-sensitive cones with a large background field alters the color appearance of a small superimposed patch of light that is not detected by the SWS photoreceptors. This is shown by comparing the effect of two luminosity-equated adapting wavelengths that fall on a tritanopic confusion line. The conclusion is the same whether the small patch is briefly flashed of steadily viewed.

The measurements are explained qualitatively by adapted SWS cones contributing a fixed amount of redness to the color appearance of the superimposed patch. The amount of redness is nearly as much as the redness from physically mixing the adapting wavelength with the test field. This indicates there is relatively little "discounting" of background light that stimulates SWS cones in the retinal area of the small test patch. This finding is qualitatively different from the effect of background light absorbed by MWS and LWS receptors, from which contributed redness is a small fraction (often less than 20%) of the redness added by physically mixing the background wavelength with the test field.

Adapting SWS cones had no measurable effect on the sensitivity of MWS and LWS cones.

These qualitative observations can be examined more rigorously by comparing the measurements to the quantitative predictions of the two-process model of chromatic adaptation.
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Two-process model

The two-process model accounts well for equilibrium color percepts under long-wavelength adaptation, as discussed earlier. The model is easily extended to the measurements here with short-wavelength adapting fields. According to the model, the two processes by which an adapting field affects the appearance of a light are (1) an additive redness contribution and (2) receptoral sensitivity changes. Quantitative estimates of both processes are implicit in the data above. The estimates are derived from the empirical implication of the two processes, expressed as

\[ \Delta_{\text{test}} = (\Delta_{\text{red}} + f) g, \]

or equivalently

\[ \log_{10}(\Delta_{\text{test}}) = \log_{10}(\Delta_{\text{red}} + f) + \log_{10}(g). \]  

In equation (1) \( \Delta_{\text{test}} \) and \( \Delta_{\text{red}} \) are levels of the test components; \( f \) is proportional to the amount of redness (or greenness) contributed by an adapting field (by convention, positive for redness and negative for greenness); and \( g \) reflects relative LWS-to-MWS sensitivity (Shevell, 1978).

If adapting SWS cones affects color appearance only by an additive redness contribution, then (1) the amount of the redness contribution, expressed by \( f \), should be higher with 441 nm than with luminosity-equated 491 nm adaptation, and (2) the relative sensitivity of LWS:MWS cones, expressed by \( g \), should be the same for the two adapting wavelengths. The estimated values of \( f \) and \( g \), determined by fitting equation (1) to the data in Fig. 8, are given in Figs 9 and 10 in logarithmic form. \( \log_{10}(f) \) can be interpreted as the logarithm of the amount (in trolands) by which the 660 nm test light is reduced because of additive redness contributed by the short-wavelength adapting field; as expected, the redness contribution \( f \) at any given adapting level is much larger with 441 nm than with 491 nm adaptation (Fig. 9). \( \log_{10}(g) \) is the logarithmic asymptotic ratio \( \log_{10}(\Delta_{\text{test}}/\Delta_{\text{660}}) \) for an intense test field; its value does not depend on adapting wavelength (Fig. 10). As the model fits the data quite well (median deviation of 0.07 log unit, 90% of deviations less than 0.1 log unit), this is strong evidence that signals from adapted SWS cones contribute redness to the superimposed test but do not affect the relative sensitivities of MWS and LWS receptors.

Figures 9 and 10 also allow comparison of steady and flashed test fields. They show the redness contribution \( f \) is larger and LWS:MWS relative sensitivity \( g \) is lower with steady tests (compare corresponding open and filled symbols). These trends are consistent for the two observers, and with the smaller additive redness contribution from long-wavelength adapting fields when the test is flashed rather than steady (Shevell, 1978).

Redness contribution from 491 nm adapting light

The measurements assess color appearance of the small test annulus, but of course the larger adapting field is seen as well. An interesting result is that both adapting wavelengths, when sufficiently intense, contribute redness to the test. This is expected from the 441 nm field because it appears reddish-blue, but 491 nm light is greenish-blue. One might expect a 491 nm background to contribute greenness to
the test, or perhaps have no additive influence, but the data show a redness contribution.

Contributed redness from a large 491 nm background actually is predicted from results above. The measurements here show very little discounting of background light falling in the test-patch area and absorbed by SWS cones. The redness from SWS cones approaches the level obtained by physically adding short-wavelength light to only the small annular test field. On the other hand, MWS and LWS cones stimulated by a large adapting field provide a much smaller additive contribution to the test than expected from physical admixture (Walraven, 1976; Shevell, 1978, 1982). This implies for a 491 nm adapting field that the greenness from stimulated MWS and LWS cones tends to be discounted, while the redness from the SWS-cone pathway approaches the level of admixture of 491, 550 and 660 nm lights. Thus the signal from the SWS-cone pathway dominates, resulting in a net redness contribution from a 491 nm adapting field.

More generally, the color appearance of a light can be a misleading indicator of the adapting effect of the light. In at least some cases, signals from SWS cones have a more dominant influence on the state of chromatic adaptation than on the color appearance of the adapting light itself.

Acknowledgements—We thank John Mollon and Charles Stromeyer for comments on an earlier draft. Supported by PHS grant EY-04802.

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