Interactions between chromatic adaptation and contrast adaptation in color appearance

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Abstract

Color appearance depends on adaptation processes that adjust sensitivity both to the average color in the stimulus (through light or chromatic adaptation) and to the variations in color (through contrast adaptation). We explored how these different forms of adaptation interact, by examining how the state of chromatic adaptation depends on the time-varying color contrasts in the stimulus, and conversely, how adaptation to the mean determines the stimulus contrasts underlying contrast adaptation. Light adaptation levels remain very similar whether observers adapt to a static chromaticity or to large temporal modulations in cone excitation that vary at rates of 0.5 Hz or higher. This suggests that up to the sites of light adaptation, the response to moderate contrasts is effectively linear and that the adaptation effectively averages over several seconds of the stimulus. For slower flicker rates color is differentially biased by the last half-cycle of the flicker, and perceived contrast may be altered by response polarization. This polarization selectively saturates responses to moderate (but not low) contrasts along the color direction complementary to the mean color bias, implying that the response changes occur within multiple mechanisms tuned to different chromatic axes. Chromatic adaptation often adjusts only partially to the mean color of the stimulus, and thus leaves a residual bias in the color appearance of the field. Contrast adaptation reduces perceived contrast relative to this residual color, and not relative to the stimulus that appears achromatic. Similarly, contrast discrimination thresholds appear lower around the residual color than around the achromatic point. Thus under biased states of chromatic adaptation alternative measures of 'zero contrast' can be dissociated, suggesting that they do not depend on a common null point within the channels encoding chromatic contrast. © 2000 Published by Elsevier Science Ltd.

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1. Introduction

Adaptation effects on color appearance reflect distinct classes of sensitivity adjustment that operate at different levels of the visual system and adjust to different aspects of the stimulus. Light (chromatic) adaptation is primarily retinal (Hood, 1998), and adjusts to the average color in some local region of the image. These adjustments include both multiplicative gain changes in cone-specific pathways, that scale the cone signals to discount changes in the average color or lightness of scenes (von Kries adaptation; von Kries, 1970); and subtractive adjustments in post-receptoral pathways, that serve to discount the response to the average background (Walraven, Enroth-Cugell, Hood, MacLeod, & Schnapf, 1990). Contrast adaptation is instead cortical, and alters sensitivity to the spatial or temporal variations in color around the average, or to contrast (Webster, 1996). In natural viewing, both the mean color and the color contrast within and across images are constantly changing. Thus changes in the states of both chromatic adaptation and contrast adaptation must continuously regulate color appearance. In this study we explored interactions between these different classes of adaptation.

Webster and Mollon (1995, 1997) examined the combined effects of chromatic adaptation and contrast adaptation on color appearance, by measuring the changes in perceived color induced by adapting to

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distributions of colors that varied around different mean chromaticities. Fig. 1 shows an example of their results. The observer viewed an adapting field that had a fixed color or that flickered at 1 Hz along a bluish-yellowish (135 deg) or reddish-greenish (45 deg) direction within the chromatic plane, and then matched the perceived color of test stimuli presented within the adapting field. The four panels plot these matches when the adapting stimuli were centered at four different mean (DC) colors. In each case, chromatic adaptation to the mean color adjusted sensitivity so that the average color of the adapting field appeared almost achromatic, and produced corresponding color shifts in the appearance of each test color. For example, under neutral adaptation the test stimuli in the upper-left panel of Fig. 1 all appeared as varying shades of blue. Yet after adapting to the bluish DC they appeared centered near the achromatic point and thus took on a

full range of hues. These hue shifts occurred independently within the S-cone and L − M cone axes defining the stimulus plane, and approximate the sensitivity changes predicted by multiplicative, von Kries scaling in the L, M and S cone receptors. Thus the color changes induced under steady-state adaptation to the static DC color were consistent with peripheral, independent adjustments in cone-specific pathways. When the adapting stimulus instead flickered in color around the DC, test stimuli again showed the same average color shift. However, adaptation to the contrast now induced an additional color change, by affecting the perceived contrast (saturation) of the tests. For example, after adapting to the bluish-yellowish flicker, tests that fell along the color axis of the adapting flicker appeared less saturated. These selective changes in contrast sensitivity reflect interactions between the different cone axes, and thus reflect adjustments within post-re-
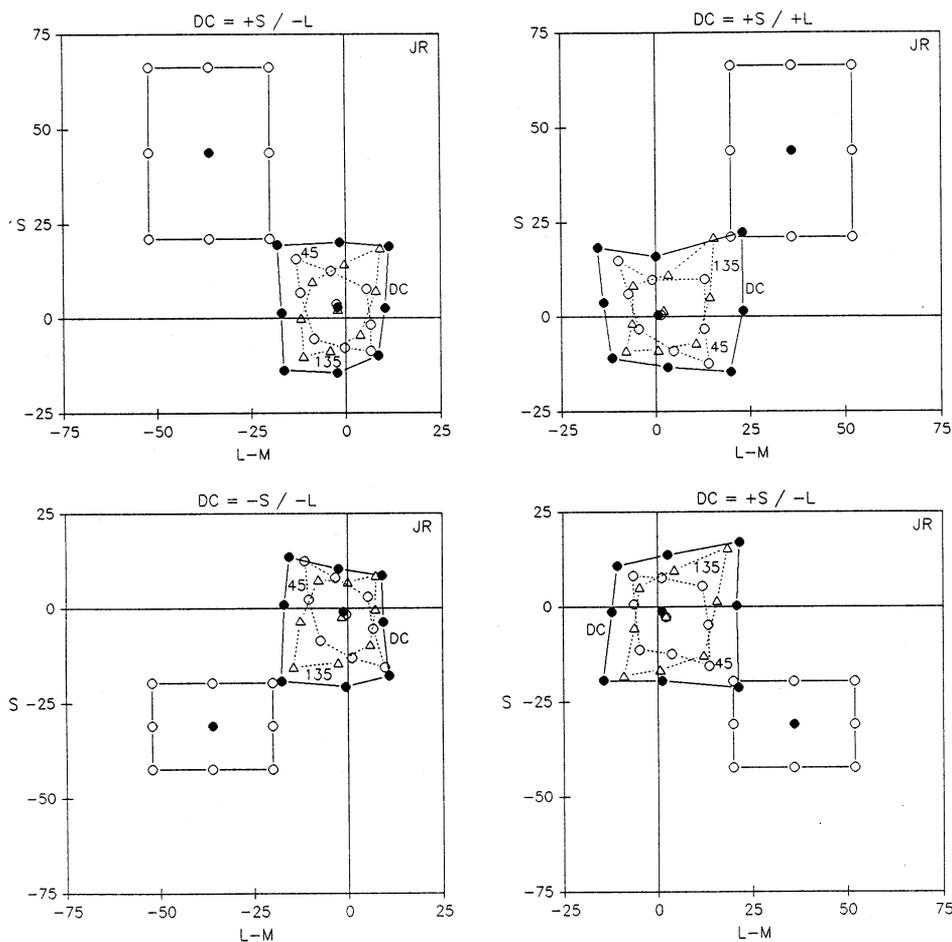

Fig. 1. Combined effects of light adaptation and contrast adaptation on color appearance, shown for one subject (JR) (from the study of Webster and Mollon, 1995). Plots show the matches made to a set of test stimuli (○, —) after adapting to a static chromaticity (● centered on tests) or 1 Hz sinusoidal modulations around this chromaticity along normalized axes of 45–225 or 135–315 deg within the L − M vs. S − (L + M) chromatic plane. Adaptation to the DC chromaticity shifted the appearance of the tests independently along the S and L − M axes so that they appeared nearly centered on white (●). Adaptation to the flickering fields induced the same mean color shift, and selectively reduced perceived contrasts along the 45–225 deg (○) or 135–315 deg (△) axes of the adapting flicker. The four panels show similar results for DC adapting colors in different quadrants of the chromatic plane. Similar results are shown for a second observer in Webster and Mollon (1995), Fig. 2.

ceptoral pathways that combine the cone signals (Webster & Mollon, 1995).

These results demonstrate that chromatic adaptation and contrast adaptation induce separate and distinct changes in color appearance, and are consistent with two distinct stages of sensitivity regulation that adjust to the mean or contrast in the stimulus. In this study, we asked how the initial stage of chromatic adaptation defines the stimulus contrasts available to the subsequent stage of contrast adaptation. Again, chromatic adaptation determines stimulus contrasts because it defines both the scaling of stimuli and the point of zero-contrast in the stimulus, and one goal of the work was to examine how this mean adaptation level is determined from the time-varying distribution of input signals. Such results are important for understanding light adaptation in natural viewing, since adaptation to the mean is thought to depend on sampling different regions of the image over time (D'Zmura & Lennie, 1986). A second goal was to ask how contrast adaptation influences color appearance when the adjustments of chromatic adaptation are incomplete, so that the mean chromaticity of the adapting field does not appear achromatic. In fact, adaptation is typically incomplete for stimuli with biased chromaticities (Fairchild, 1991). These conditions have important implications for understanding the nature of contrast coding. Under incomplete chromatic adaptation the mean chromaticity itself has a color contrast (relative to the achromatic point), and its perceived contrast could thus be modulated by contrast adaptation. Yet the measurements instead suggest that contrast adaptation adjusts contrast sensitivity relative to the mean perceived color (and not relative to the achromatic point). These results thus reveal a dissociation between alternative measures of 'zero contrast' — between the stimulus that appears achromatic and the stimulus that is the neutral point for color contrast adaptation. This dissociation suggests that the mechanisms encoding color contrast may not share a common neutral point.

2. Methods

Stimuli were presented on a color monitor controlled by a Cambridge Research Systems VSG graphics card. The card allowed colors to be specified with a resolution of 12 bits per gun. Phosphor luminances were calibrated with a PhotoResearch PR650 spectroradiometer and linearized through look-up tables. The CIE, 1931 x, y chromaticities of the phosphors were measured to be 0.618, 0.344 (red), 0.281, 0.605 (green) and 0.150, 0.063 (blue).

Colors were represented within a variant of the MacLeod–Boynton (MacLeod & Boynton, 1979) chromaticity diagram, which defines chromaticities in terms of two cone-opponent axes corresponding to differences in L versus M cone activity at constant luminance (L − M), or S cone activity at constant luminance [S − (L + M)]. The space was scaled so that the origin corresponded to the chromaticity of Illuminant C (CIE, 1931 $x, y = 0.31, 0.316$), and so that signals along the two axes yielded color contrast adaptation effects of roughly comparable magnitude. The resulting L − M and S − (L + M) coordinates are related to the r, b coordinates of the MacLeod–Boynton space by the following equations:

$$L - M \text{ contrast} = (r_{mb} - 0.6568) \times 1955$$

$$S - (L + M) \text{ contrast} = (b_{mb} - 0.01825) \times 5533$$

where 0.6568,.01825 are the MacLeod–Boynton coordinates of Illuminant C, and 1955, 5533 are the constants that scale contrasts along the L–M and S − (L + M) axes, respectively. For most experiments stimulus luminance was fixed at 27.5 cd/m² for the Illuminant C reference chromaticity. Constant-luminance planes through this point were then determined empirically for individual observers based on minimum-motion settings (Cavanagh, MacLeod, & Anstis, 1987).

The effects of adaptation on color appearance were examined using an asymmetric matching task. Adapting and test stimuli were presented in a uniform 2-deg field centered 1.25 deg above a black fixation cross. The test stimuli were matched by adjusting the color of a comparison stimulus presented in a matching field centered 1.25 deg below fixation. Narrow black borders delimited the fields from a 6.4×8.4 deg uniform gray (Illuminant C, 27.5 cd/m²) background. (See Fig. 1 of Webster & Mollon, 1995.) Observers viewed the display binocularly in an otherwise dark room, from a distance of 250 cm. Adapting stimuli were static chromaticities (DC) or sinusoidal modulations of chromaticity that were centered at different mean chromaticities and varied along different directions in the color space (AC + DC). Observers initially adapted for 3–5 min. The adapting field then returned to the mean adapting chromaticity for 1 s, after which a fixed test color was presented for 0.5 s. The test was followed by 0.5-s of the DC and then by a period of readaptation to the modulation. This cycle repeated while subjects adjusted the chromaticity of the matching stimulus (presented at the same time as the test, but to a retinal region maintained under adaptation to the zero-contrast gray). During a single run matches were made for four to six different test colors. A daily session typically consisted of six runs restricted to a single adapting stimulus. Subjects included the authors and four additional observers who participated in different subsets of experiments, with two or three subjects tested per condition. Results for different subjects differed quantitatively (primarily with regard to the degree of adaptation), but

were consistent with regard to the principal features exhibited. Accordingly, these features have been illustrated below for single observers. All of the observers had normal color vision as assessed by standard color tests and normal or corrected-to-normal visual acuity.

3. Results

The color matches illustrated in Fig. 1 show that the visual system adjusts to both the mean and the variance of an adapting modulation. To examine interactions between these two adjustments, we focused on two specific questions: (1) how is the mean of the adapting stimulus determined from the time-varying set of stimulus levels?; and (2) how does this mean determine the variance — or contrasts — within the processes underlying contrast adaptation? These questions are examined in turn in the following sections.

3.1. Chromatic adaptation and the visual response to contrast

In the first set of experiments, we examined how the state of chromatic adaptation depends on the set of stimulus contrasts in the adapting stimulus. As illustrated in Fig. 1, contrast adaptation reduces the apparent contrast of stimuli relative to the mean color, but can have little effect on the apparent color of the mean stimulus itself. This suggests that the state of chromatic adaptation remains similar whether observers are adapted to the static mean chromaticity or to large modulations of color around the mean. In turn, this implies that the response to contrast up to the sites of chromatic adaptation may be approximately linear, or more generally, that any nonlinearities are approximately symmetric for increments or decrements about the mean. If the contrast response were instead asymmetric, then the mean of the responses to the modulation could differ substantially from the response to the DC, and thus should alter the state of chromatic adaptation. For example, a compressive nonlinearity (e.g. a log response to stimulus contrast) that preceded the locus of chromatic adaptation would give disproportionate weight to stimulus decrements. This should 'dark adapt' the observer relative to the linear mean, and thus should shift the appearance of the DC color (so that it appears as a contrast increment). Biases in the mean color might also arise if opposite poles of the contrast (increments and decrements) are encoded by different mechanisms that have different contrast response functions (Chichilnisky & Wandell, 1999; Krauskopf, Williams, & Heeley, 1982; Mausfeld & Niederee, 1993; Whittle, 1994). However, note that contrast adaptation itself might obscure the presence of

such distortions, since it reduces sensitivity to contrast and thus would reduce the perceived contrast of an increment. It is thus uncertain how large a distortion might actually be introduced by the modulated stimulus, or in other words, how asymmetric the response to contrast would have to be before the modulated stimulus leads to measurable changes in the appearance of the DC color.

To examine this, an actual bias was introduced into the mean of the adapting modulation, and then we measured sensitivity to this bias. Fig. 2a illustrates the stimulus used. Adaptation was to a 1 Hz sinusoidal modulation that varied over a range of ± 64 units along either the $L - M$ or $S - (L + M)$ axis. Test stimuli included the zero-contrast field and an incremental or decremental contrast of ± 16 units. For each, matches were measured as a function of the magnitude of the mean bias in the adapting modulation. Results are shown in Fig. 2b and c for modulations along the $L - M$ or $S - (L + M)$ axes, respectively. In both cases the matches are closely centered on the linear mean when the adapting stimuli are unbiased, and shift steadily as the mean chromaticity of the adapting flicker is increased or decreased. As expected, the matches also reveal a substantial contrast adaptation effect, since the tests of ± 16 contrast units are matched by stimuli with less than half this contrast.

The size of the mean drifts in the settings effectively rule out some possible asymmetric nonlinearities, since these predict biases in the DC matches that are larger than the biases observed. For example, Fig. 2c shows that a log response to the S-cone signals should introduce a mean change of roughly -11 units for the ± 64-unit modulation, yet a bias of this magnitude should have measurably altered the matches. On the other hand, the shifts in the settings are too gradual to preclude the presence of modest nonlinearities (e.g. that introduce a distortion of 4 units or less, or $\sim 3\%$ of the modulation range). Again, the results also do not rule out nonlinearities that are symmetric for increments and decrements (e.g. a sigmoidal response to contrast), since the mean response for these would not differ from the response to the DC.

As noted above, the measurements are insensitive to small asymmetries in part because the contrast adaptation depresses sensitivity to the contrasts they introduce. For example, the filled triangles in Fig. 2c show the matches to the zero-contrast test after adapting to the static DC bias (i.e. without the flickering component). These matches show that the DC component on its own introduced large and complementary color shifts into the test, yet in the flickering stimulus these after-images were very strongly desaturated by contrast adaptation (filled circles).
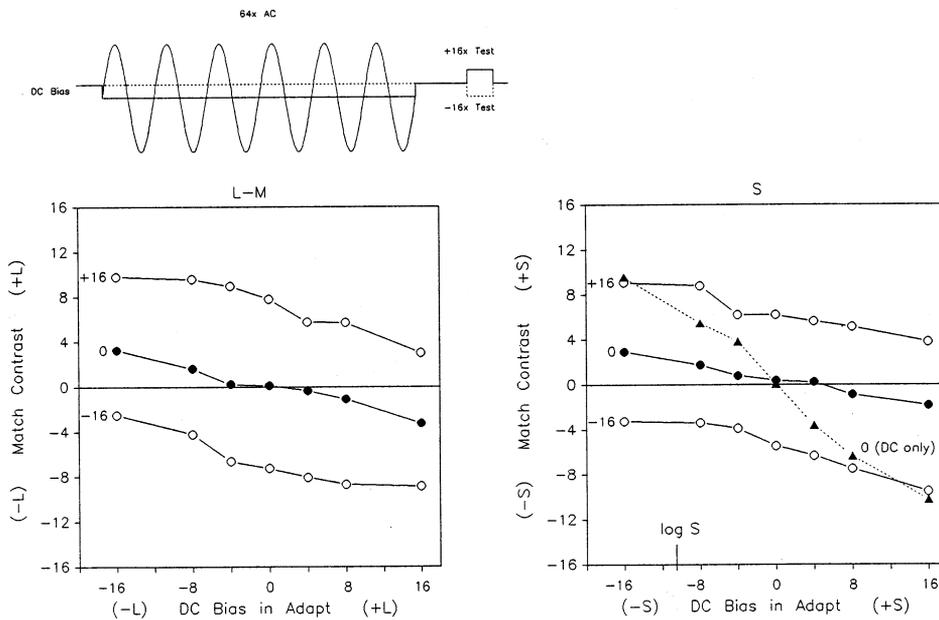
Fig. 2. Adaptation to flickering fields with a mean color bias along the L − M (left panel) or S (right panel) axis. Points plotted are the contrast matches made to the neutral, zero-contrast field (●) or tests of ± 16 units (○), as a function of the mean chromatic bias in the adapting flicker. (▲) show the matches to the zero-contrast field after adapting to a static field with a color bias along the S axis. For both axes the matches show the least bias when the adapting stimulus is unbiased, consistent with a linear response to contrast. The 'log S' value indicated in the right panel shows the mean bias that would have to be added to the adapting stimulus to produce unbiased matches for a log response to contrast. Similar results (biases evident for offsets of 8 or more) were confirmed in a second observer tested only along the S axis.

3.2. Time course of chromatic and contrast adaptation

The preceding results suggest that for the sinusoidally flickering stimulus the state of light adaptation depends on the linear average of the color signals, but obviously this average must be accumulated over time. To examine the time course of these adjustments we measured how the adaptation effects depend on the temporal frequency and phase of the adapting flicker. Specifically, we asked how rapidly the adapting stimulus must flicker in order to maintain a constant state of chromatic adaptation. Fig. 3a illustrates the stimulus for these experiments. If the flicker rate is fast relative to the time course of the adaptation (e.g. so that the state of adaptation depends on the color signals integrated over many cycles of the stimulus) then the state of chromatic adaptation should remain relatively stable and should be independent of the flicker phase. However, as the flicker rate is reduced, the chromatic adaptation should begin to vary in time with the adapting modulation, and color appearance during the test interval should depend on which half-cycle of the flicker (e.g. + S or − S) was presented last. We therefore tested for phase-dependence in the color matches following adaptation to different temporal frequencies. These measurements were also of interest in order to assess the range of temporal frequencies over which contrast adaptation arises, since again, this adaptation depends on responses to the variations in signals rela-

tive to the mean, and thus on the time-varying state of chromatic adaptation.

Observers adapted to sinusoidal flicker at temporal frequencies ranging from 0.0625 to 17.5 Hz. The readaptation interval between each test was 16-s, corresponding to one complete cycle for the lowest frequency. The flicker varied over a range of ± 64 units along the L − M or S − (L + M) axes. Test stimuli again included contrast of ± 16 units or the zero-contrast field. Fig. 3b and c illustrate the resulting matches. For temporal frequencies of 0.5 Hz or more the matches were independent of the phase of the adapting flicker and were centered on the mean chromaticity of the stimulus. However, at lower frequencies the matches for the two adapting phases begin to diverge (each shifting away from the polarity of the last half-cycle of the flicker) indicating that the chromatic adaptation was differentially biased by the last half-cycle of the adapting stimulus. These biases were symmetric for opposite phases of the L − M axis but for two of the three observers were noticeably asymmetric for the S axis, which showed stronger biases for − S (yellow-green) adaptation than + S (purple) adaptation.

These results suggest that during 'steady-state' flicker the effective integration time for chromatic adaptation is on the order of several seconds. However, note again that contrast adaptation to the flicker reduces sensitivity to the test contrasts, and thus could have masked phase-dependent variations in chromatic adaptation at

the higher frequencies. Fig. 3 shows that these sensitivity losses were pronounced at all but the highest temporal frequency (17.5 Hz) tested, and surprisingly, remained strong even at the lowest frequency (which had a period of 16 s/cycle). This implies that the range of temporal variations that can lead to contrast adaptation is very broad. However, at lower frequencies an additional factor that comes in to play is response polarization, owing to the changing state of chromatic adaptation. For example, adapting to the $-S$ phase of the S-axis flicker and then switching to the neutral reference is analogous to the stimulus conditions that are conventionally used to induce transient tritanopia (in which thresholds are elevated for detecting a short-wavelength light after extinguishing a long-wavelength adapting field; Mollon & Polden, 1975). These sensitivity losses are thought to reflect response compression resulting from polarizing an opponent site (Pugh & Mollon, 1979). Thus the sensitivity losses during the recovery of adaptation to the color-biased field may themselves partially underlie the perceived contrast changes for the low-temporal-frequency adaptation.

3.3. Transitions in the state of chromatic adaptation

To explore contrast coding during a change in the state of chromatic adaptation, observers adapted to a static color, and then matched tests that were presented after the adapting field was returned to gray for varying intervals. The color-biased field was initially presented for 3 min, and then for 8.5 s between each 500 ms presentation of the test color. The gray intervals preceding each test varied from 0 to 4 s. This sequence is similar to adapting conditions tested by Webster and Mollon (Webster & Mollon, 1994), who found a strong compression of perceived contrast along the S axis when matches were made on gray fields 1-s after adapting to an S-color bias in the field. The experiment is also similar to conditions examined by Krauskopf, Williams, Mandler, and Brown (1986), who measured thresholds for chromatic tests presented 200 ms after a 1-s chromatic adapting pulse.

The aim was to track the mean perceived color and any contrast compression during the recovery of adaptation to the neutral field. Surprisingly, the effects on perceived contrast were large even when there was no intervening gap between the adapting color and the 0.5-s tests. An example of this effect is illustrated in Fig. 4, which shows matches following adaptation to a steady green field (filled diamond). The left panel plots
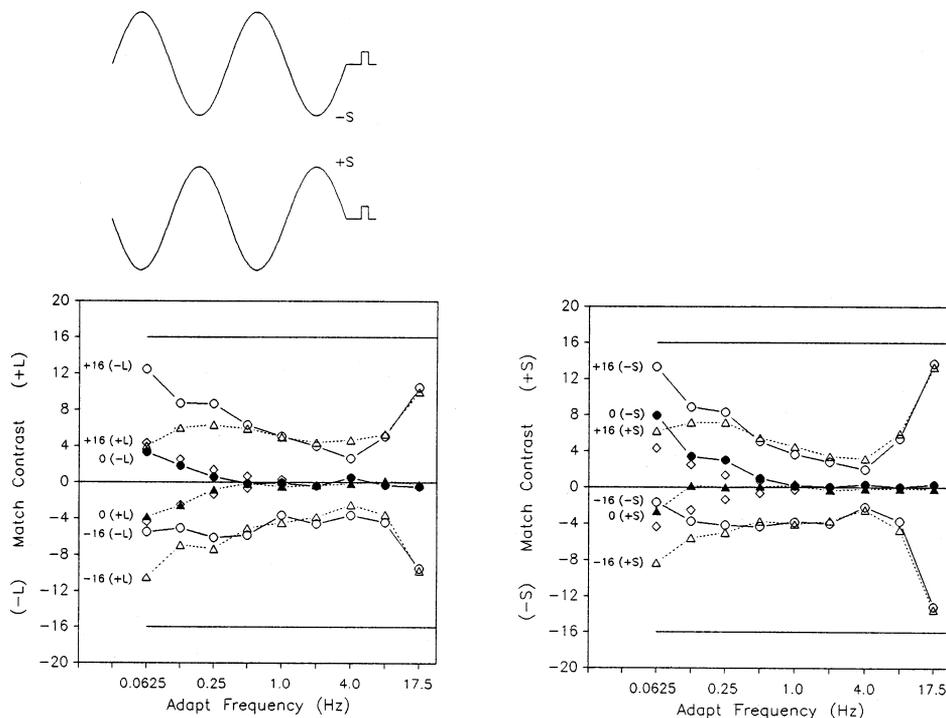

Fig. 3. Contrast matches as a function of the temporal frequency of the adapting flicker. The two panels again plot results for the $L-M$ (left) or S (right) axes, for tests of zero contrast (filled symbols) or ± 16 units (unfilled symbols). Triangles show the matches when the last half-cycle of the flicker had $+L$ or $+S$ contrast. Circles plot the matches for the opposite flicker phase. For both axes matches at the two phases begin to diverge ~ 0.5 Hz, indicating that the light adaptation is varying with the flicker and thus is unstable for lower frequencies. A similar time course was observed for two further subjects. Unfilled diamonds show the mean biases in the matches predicted by the rate of recovery in chromatic adaptation implied by the results of Fig. 6.
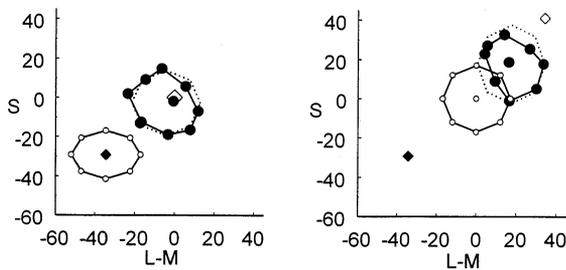
Fig. 4. Matches to test stimuli after adapting to a static green field. In the left panel matches (●) were to low-contrast tests (○) centered on the adapting chromaticity (◆). The matches are nearly centered on the white point (◇) and coincide roughly with the predictions for von Kries scaling (···). In the right panel the tests were instead centered on the neutral chromaticity. The shift in color appearance falls short of complete von Kries scaling (◇), and deviates from the von Kries prediction for the equivalent mean color shift (···) by being selectively compressed along the 45-deg axis complementary to the adapting color.

matches to low-contrast test stimuli (open circles) centered on the adapting chromaticity. Like Fig. 1, these matches are centered near the white point, and approximate the color changes predicted by von Kries adaptation (dotted line). Thus changes in the appearance of the low contrast tests were again consistent with a nearly complete adjustment to the background that rescaled the cone signals. However, the right panel shows results for an identical adapting sequence, but this time for tests centered on the neutral point. In this case the mean color shift is only 60–70% of the shift predicted by complete von Kries scaling (unfilled diamond), and the matches are compressed along the positive diagonal defining the adapting color direction. Thus for these higher-contrast tests there appeared to be substantial response saturation. It is unlikely that this effect resulted from adaptation to the different sets of test stimuli themselves, since similar contrasts (relative to the steady background) were present in the matching field, and the match settings can only reflect the differences in adaptation between the matching and test fields. It is also unlikely that the differences reflect differences in contrast adaptation to the chromatic contrast presented by the adapting background, since this adaptation should have induced larger changes in the appearance of the low contrast tests than the high contrast tests (Webster, 1996).

Fig. 5 shows for a second observer the effect of varying the duration of the neutral interval. The mean biases in the perceived color of the tests steadily diminishes with increasing periods of re-adaptation to the neutral field. Yet a strong selective compression along the 45–225 deg axis persists largely unabated over the 4-s range tested, consistent with the sluggish rate of recovery reported for second-site chromatic adaptation (Augenstein & Pugh, 1977; Mollon & Polden, 1977; Loomis, 1980). To estimate the time course of the mean

color change, the L, M and S cone responses for the mean of the matches were calculated, and these were compared to the mean response predicted for complete von Kries adaptation either to the green adapting chromaticity or to the neutral gray chromaticity. These were then expressed as the percent of re-adaptation to the neutral reference. These percentages are shown in Fig. 6. A value of zero corresponds to complete adaptation to the green DC, while a value of 1 represents complete recovery to the gray reference. The dashed lines plot the fraction of adaptation to the neutral field based directly on the matches. Note that because of the presumed response saturation these means overestimate the rate
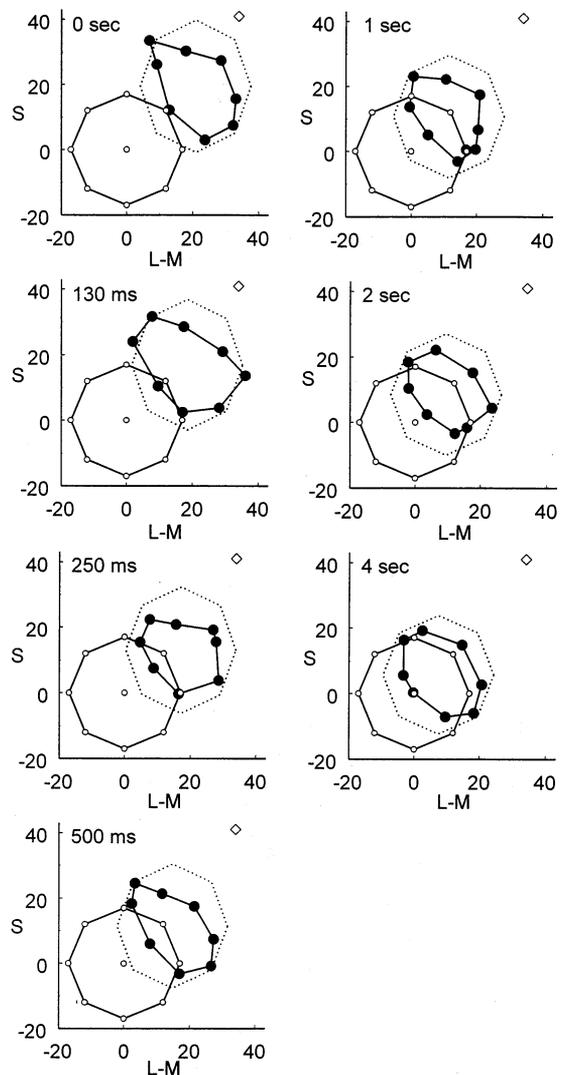

Fig. 5. Matches (●) to test stimuli (○) after adapting to a static green field (as in Fig. 4). The upper left panel shows results similar to Fig. 4b for a different observer. The remaining panels plot the matches as a function of the delay introduced between the adapting and test stimulus. Mean biases in the matches steadily diminish with increasing delay, while the compression along the adapting color axis persists over the 4-s range of delays tested.
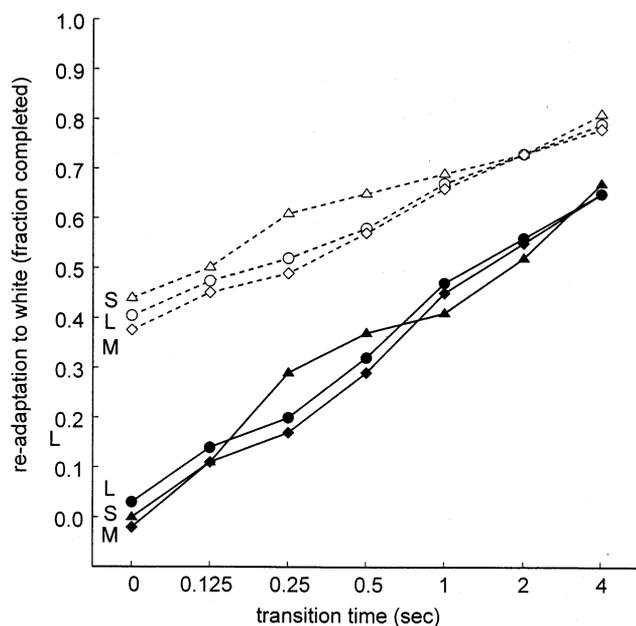
Fig. 6. Time course of the recovery of light adaptation, based on the mean biases in the matches of Fig. 5. Points plotted give the percent by which each cone class was readjusted to the neutral chromaticity relative to the adapting chromaticity. A value of 1.0 indicates complete recovery to the neutral stimulus while a value of 0 corresponds to complete adaptation to the initial adapting color. Unfilled symbols show the rate of recovery estimated directly from the mean matches. Filled symbols plot the rates after adjusting for the shortfall in the mean bias for the zero-delay.

of recovery. For example, as Fig. 4 showed, the nearly complete desaturation of the adapting field was not matched by a corresponding shift in the appearance of the gray reference. As an alternative measure, an equivalent adapting stimulus was therefore calculated (i.e. the weaker DC chromaticity that would have been consistent with the size of the mean color shift in the tests), and was used to adjust the adaptation rates. For this observer the equivalent stimulus had a value of $L - M = -22.8$, $S = -17.1$, compared to $L - M$, S coordinates of -34.5, -29 for the adapting chromaticity. (For the second observer the value was $L - M = -17.4$, $S = -14.9$.) The solid lines in Fig. 6 show the transition in adaptation adjusted for this stimulus. For these conditions re-adaptation to the white was 50% complete after approximately 2 s and approached two-thirds complete at the longest tested interval of 4 s.

The rate of recovery is indistinguishable for the S or the L and M cones, and is approximated by an exponential function of the form $r = 0.64 \exp[-0.23(t + 0.25)]$, where t is the duration (in s) of the intervening neutral gap. (For the second observer estimated values were $r = 0.54 \exp[-0.16(t + 0.25)]$.) The constant of 0.25 was added to the gap duration to reflect the time at the center of the 0.5 s test. This exponential decay rate was used to estimate the phase-dependence of chromatic adaptation at different temporal frequencies,

as measured in Fig. 3. The predicted shifts are shown by the unfilled diamonds in Fig. 3, and fall very close to the actual biases measured for the $L - M$ axis. In fact, this close correspondence is deceptive, because as noted the observed shifts also reflect the desaturating effects of contrast adaptation and/or response compression, and thus underestimate the magnitude of the mean change in chromatic adaptation. Nevertheless, the two different measures agree in suggesting that the state of chromatic adaptation remains stable for flicker rates of 0.5 Hz or higher.

As noted above, Krauskopf et al. (1986) examined similar polarization effects for detecting chromatic pulses presented on a neutral field after adapting to a static chromatic field. The sensitivity changes they found were selective for the color direction defining the adapting field, and thus reinforced evidence from their habituation (contrast adaptation) experiments pointing to multiple chromatic channels tuned to different color directions. (If the sensitivity changes instead depended on independent adjustments along the $L - M$ and $S - (L + M)$ axes, then they should show selectivity only for these two axes.) The results of Figs. 4 and 5 similarly support this conclusion because the changes in perceived contrast are selective for an axis intermediate to the $L - M$ and $S - (L + M)$ axis. To verify that these changes in color appearance could be selective for different axes, the measurements were repeated for eight different adapting chromaticities within the chromatic plane. Observers again adapted to the static chromaticity for 3 min and then matched the same set of tests presented after a 1-s interval of the neutral chromaticity. The matches for each direction are shown in Fig. 7, again compared to the matches predicted by von Kries scaling. There is a consistent trend for the deviations from the von Kries predictions to be along the color direction of the adapting field, confirming that the response changes occur within mechanisms that can be tuned to a variety of axes within the chromatic plane. The clearest exception to this is in the case of the $+ S$ adapting field, paralleling the asymmetry noted above in the results for the flickering adapting fields (Fig. 3). A similar asymmetry between $+ S$ and $- S$ adaptation was also found in the study of Krauskopf et al. (1986).

3.4. Contrast adaptation under incomplete chromatic adaptation

The preceding results examined how variations in the level of the adapting stimulus are integrated over time to define the state of chromatic adaptation. In the present experiments we examined the converse question — how does the state of chromatic adaptation determine the effective variations in the stimulus? If chromatic adaptation adjusted completely to the mean of

the adapting stimulus, then the mean should appear achromatic and variations in the stimulus should be determined by their contrast relative to the achromatic point. However, for the conditions which have been examined the adaptation instead only partially discounted the background color. For example, Fig. 1 shows that while adaptation caused each DC chromaticity to appear desaturated, even after prolonged viewing a weak residual color remained. Again, this incomplete adaptation may be the norm for chromatically biased fields (Fairchild, 1991). How is this residual chromatic contrast affected by the subsequent adjust-

Fig. 8. Matches to test stimuli (●) following adaptation to a +S (left panel) or −S (right panel) DC color (○) or to modulations around the DC along the S axis (▲). Unfilled and filled diamonds plot the mean of the DC or DC + AC matches, respectively. Contrast adaptation to the DC + AC stimulus selectively reduces perceived contrasts along the S axis but has little effect on the mean perceived color of the test stimuli relative to the DC-only matches. The collapse of perceived contrast around the DC is similar to the results of Fig. 1, but more apparent for this observer because the DC adaptation is less complete.

ments of contrast adaptation? The AC + DC matches of Fig. 1 suggest that there is in fact little effect, for the matches in these conditions continue to appear centered on the DC match and thus show a similar residual color bias. However, the color biases in this case are so small that any changes with contrast adaptation are difficult to assess. We therefore examined more closely how contrast adaptation influences apparent contrast when incomplete chromatic adaptation leaves a mean color contrast in the stimulus.

Fig. 8 shows the matches for an observer who exhibited weaker chromatic adaptation. The two panels plot the matches made to tests after adapting to purple or yellow-green fields that were biased in color along the S axis. Settings were again made after adapting to the DC color or to 1 Hz modulations around the DC color along the S axis (over a range of ± 48 units adjusted for the differences in the mean S-cone level). As was found previously, matches for the DC adaptation alone are shifted along the S axis toward the achromatic point, while matches following AC + DC adaptation are in addition compressed along the S axis. For this observer a mean color bias remained that was several-times threshold, yet again there was little shift apparent in this bias with contrast adaptation. For example, the mean of the DC and AC + DC matches are shown by the diamonds in the figure and remain very similar (and several times threshold) for the two adapting conditions. These results thus suggest that adaptation collapses perceived contrast relative to the residual mean color, and not relative to the stimulus that appears
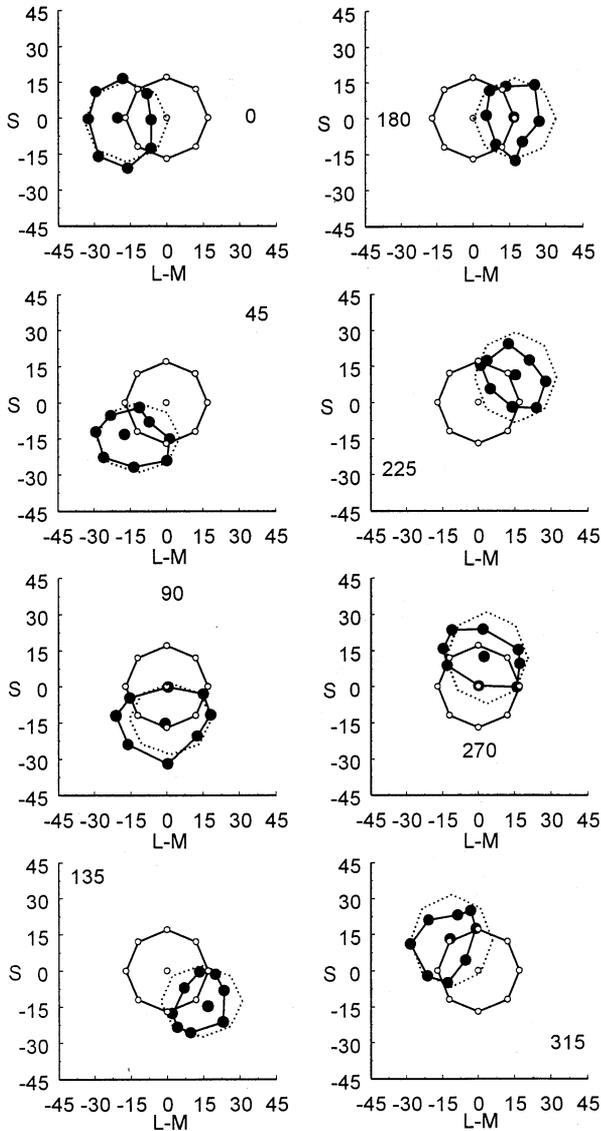

Fig. 7. Matches to test stimuli after adapting to static colors at different directions in the chromatic plane. The matches (●) were made to tests (○) presented 1-s after extinguishing the color of the adapting field. Each panel plots the matches for a different adapting color with coordinates indicated by the number in the figure (which corresponds to the hue angle within the plane). For both observers tested the matches tended to be compressed along the color axis complementary to the adapting color.
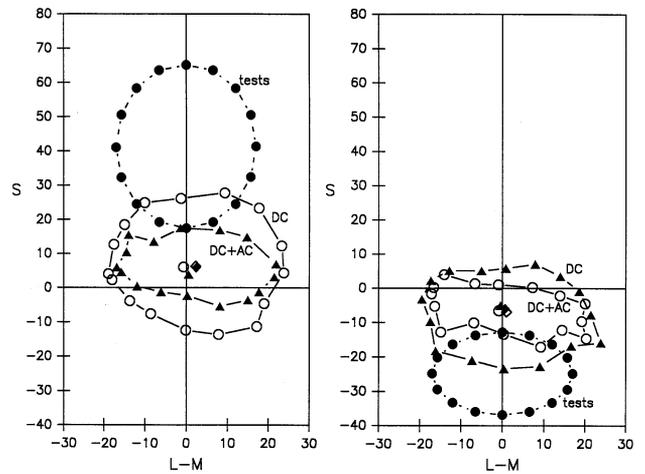
achromatic. To verify this, the AC + DC matches were fitted by scaling sensitivity to the DC-alone matches. Multiplicative scaling was applied independently to the L − M and S axes, and was based on scaling contrast relative to either the mean of the DC matches or the achromatic point. Fig. 9 shows the predictions based on either neutral point compared to the observed matches. Scaling relative to the DC (unfilled circles) provided a good account of the AC + DC matches, while adjustments relative to the achromatic point (unfilled squares) gave a consistently poorer fit (resulting in a 2-fold increase in the ssq error for the predicted S coordinates). In particular, assuming that contrast is adjusted around the achromatic point introduced large errors in the predicted matches for test colors that were complementary to the DC chromaticity. These errors occurred because contrast adaptation shifted the matches for these tests close to or possibly even past the achromatic point (e.g. from purple to yellow-green or vice versa), while contrast sensitivity losses based on the achromatic point predict only a proportional shift from the DC match toward the achromatic point.

As an additional test of the neutral point for contrast adaptation, changes in apparent contrast for different stimulus levels along the S axis were examined. Observers again adapted to fields that had a DC bias and AC modulations along the S axis, but now made contrast matches (rather than both saturation and hue matches) for test stimuli restricted to the S axis. The upper-left panel of Fig. 10 shows an example of these matches. Test stimuli are shown by the column of filled circles at the left. These bracketed the purple DC color, which corresponded to a + 0.15 log unit increase in S-cone excitation relative to the background. After adapting to the DC color the matches to these tests are shifted toward the achromatic point (unfilled circles), while matches following contrast adaptation are compressed

together (filled triangles), reflecting large losses in apparent contrast.

Again, we asked at which level of the S axis contrasts were being compressed relative to. To assess this, in Fig. 10B the matches have been replotted as a function of the test contrast. These are well fit by straight lines (and thus show little response saturation, consistent with the low test-contrast matches of Figs. 1 and 4a). Chromatic adaptation effects in the matches are reflected in the slopes of the lines and the shifts in the x-intercepts toward the DC chromaticity (vertical line). These shifts are large but remain several units short of the DC, again indicating that the chromatic adaptation was incomplete. Contrast adaptation is reflected by the different slopes for the DC and AC + DC matches. The slopes for the DC-only matches are close to the values predicted by incomplete von Kries scaling, but are substantially shallower for AC + DC adaptation because of the losses in perceived contrast.

The critical feature of these plots is where the two lines intersect, for this defines the level around which perceived contrast is modulated by the contrast adaptation. This point of intersection is close to the match to the DC level (vertical line), but clearly deviates from the level that appeared achromatic (horizontal line). Similar results were obtained for the two further DC adapting conditions tested, as shown in Fig. 10C and D. Thus these results again confirm that contrast adaptation does not reflect changes in perceived contrast per se, but rather changes in the perceived magnitude of stimuli relative to the DC stimulus. In fact, Fig. 10 suggests that in some cases contrast adaptation may paradoxically increase the perceived contrast of stimuli by reducing their contrast relative to the background color. For example, tests of − 19 (Fig. 10C) or − 42 (Fig. 10D), appeared almost achromatic following the DC adaptation, but after AC + DC adaptation were matched by
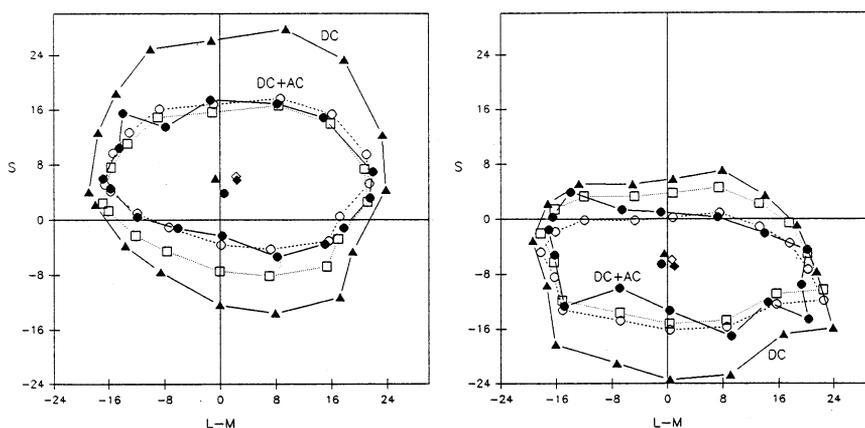

Fig. 9. Matches following contrast adaptation from Fig. 8, compared to the matches predicted by defining zero-contrast as the achromatic point or as the perceived DC color. In each case the DC matches (▲) were scaled independently along the S and L − M axes to give the best fit to the DC + AC matches (●). Fits were substantially better when contrasts were scaled relative to the DC match (○; ssq error = 43 and 92 for + S and − S) than the achromatic point (□; ssq error = 134 and 131).
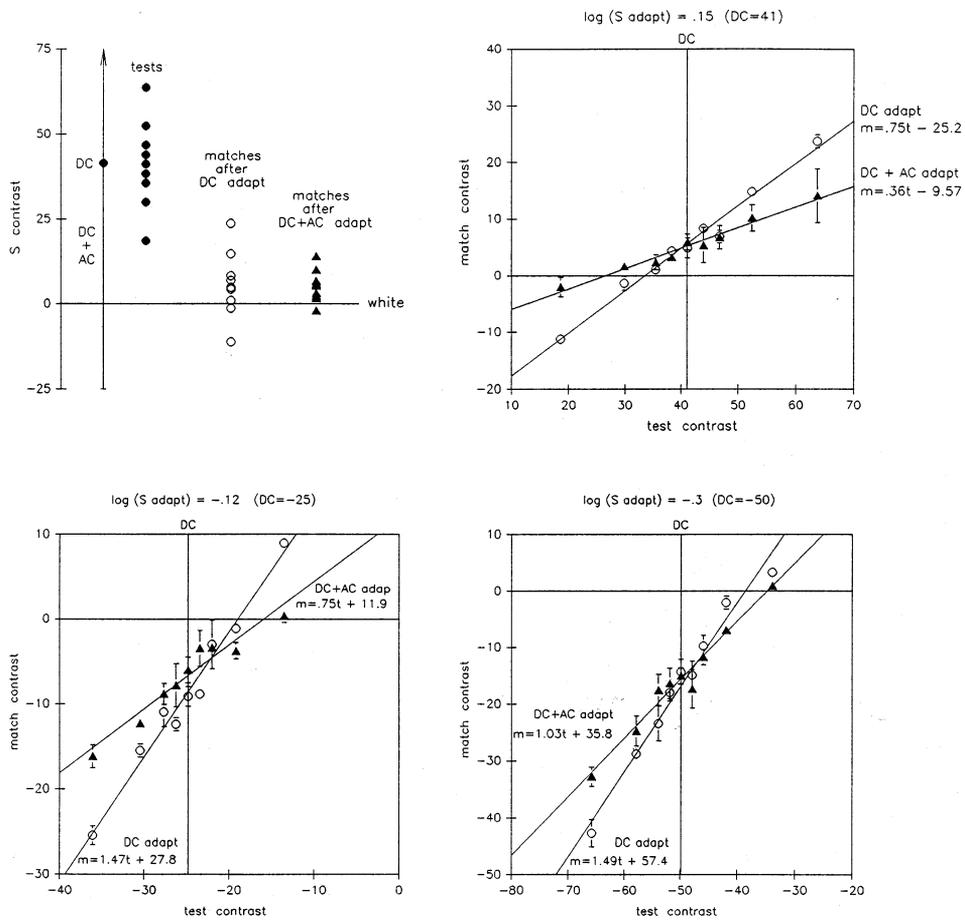
Fig. 10. Contrast matches for test and adapting stimuli varying along different levels of the S axis. The upper left panel shows matches to tests (●) following adaptation to a +S DC (○) or to 1 Hz flicker around the DC along the S axis (▲). In the upper right panel, the matching contrasts are plotted as a function of the test contrasts. Lower panels show corresponding results following adaptation to DC chromaticities representing a −0.12 or −0.3 log decrement in the S cone signals relative to the neutral point. Lines fitted to the DC and the DC + AC matches cross more consistently near the DC match (vertical line) than the achromatic point (horizontal line), indicating that the DC match more accurately predicts the zero-contrast point around which contrast collapses.

more saturated colors that were shifted toward the perceived saturation of the DC chromaticity.

3.5. Chromatic discrimination

In the final experiment we examined whether similar dissociations between the effective and the perceived chromatic contrast may occur when the task is contrast discrimination, rather than contrast adaptation. Sensitivity to color differences is highest around the adaptation point and poorer around points far removed from the adapting chromaticity (Krauskopf & Gegenfurtner, 1992). Similarly, studies of color contrast discrimination have shown that sensitivity to a contrast increment is highest on near-threshold pedestals but falls progressively as the pedestal contrast increases (Switkes, Bradley, & De Valois, 1988; Cole, Stromeyer, & Kronauer, 1990). We again asked whether the point of zero-contrast defined by these discrimination measures is better described by the mean chromaticity of the adapting

field or by the chromaticity that appears achromatic and thus has the lowest apparent color contrast. Observers adapted to a static yellow-green field (S contrast = −50) chosen to decrease S-cone signals by 0.3 log units relative to the gray background. The field was again 2-deg but was centrally fixated. A temporal 2AFC QUEST procedure (Watson & Pelli, 1983) was used to measure the threshold for detecting which of two presented pedestals had a difference in contrast between the upper and lower halves of the field. Thresholds were set for a range of different pedestal contrasts corresponding to different levels along the S axis. The two pedestals were separated by an interval of 250 ms and were each presented at full contrast for 500 ms. The field was otherwise maintained at the adapting chromaticity.

Fig. 11a plots the contrast thresholds as a function of the pedestal contrast. These show a minimum that falls near the background chromaticity but is shifted relative to the chromaticity that appeared white. The achro-

matic point was estimated by varying the pedestal contrast in a staircase while the observer responded whether the presented pedestal appeared 'too greenish' or 'too purplish'. The resulting psychometric function is shown in Fig. 11b, and shows that the pedestal that appeared achromatic had a +S contrast of approximately 8 units (relative to the DC), again indicating incomplete adaptation to the −S DC stimulus. Discrimination thresholds varied only gradually with pedestal contrast, but again point to a minimum that is closer to the DC color than the +8 pedestal. Two further observers' results were also consistent with a minimum near the DC value, though for both the minimum was broader and thus more poorly defined. However, taken together these results suggest that in contrast discrimination — like contrast adaptation — the effective chromatic contrast is more closely tied to the DC chromaticity than the chromaticity that appears achromatic.

4. Discussion

4.1. Light adaptation and contrast adaptation

The properties of light adaptation and contrast adaptation are fundamental to vision and have been studied extensively (Webster, 1996). However, few studies have explored the interactions between them (e.g. Graham, 1972; Webster & Mollon, 1995). It is well recognized

that to a first approximation the two forms of adaptation can be readily isolated. For example, in studies of pattern-selective after-effects, it is routine procedure to vary the position of the stimulus or ask the observer to vary their fixation point in order to control for local differences in light adaptation and thus isolate the effects of the contrast adaptation. Similarly, it is common to interpose delays between adapting and testing in order to allow the effects of light adaptation to the adapting stimulus to dissipate. Notably, less attention is typically given to controlling the converse interaction. That is, studies of light adaptation have rarely been explicitly designed to control for the possibility of contrast adaptation to the adapting stimulus, even though the adapting field often presents a very large spatial and (through eye movements) temporal contrast. However, for the static DC adapting fields the matches for low-contrasts test appear well-approximated by von Kries scaling, suggesting that at least under these conditions there was not measurable contrast adaptation to the static and steadily fixated stimuli.

In part, this study was designed to examine more formally the conditions under which light adaptation and contrast adaptation could be separated. It is striking that large modulations in color (e.g. over more than a 4-fold range of S-cone excitation) can yield states of light adaptation that are indistinguishable from the static mean chromaticity. As discussed above, this implies that under a steady state of light adaptation the
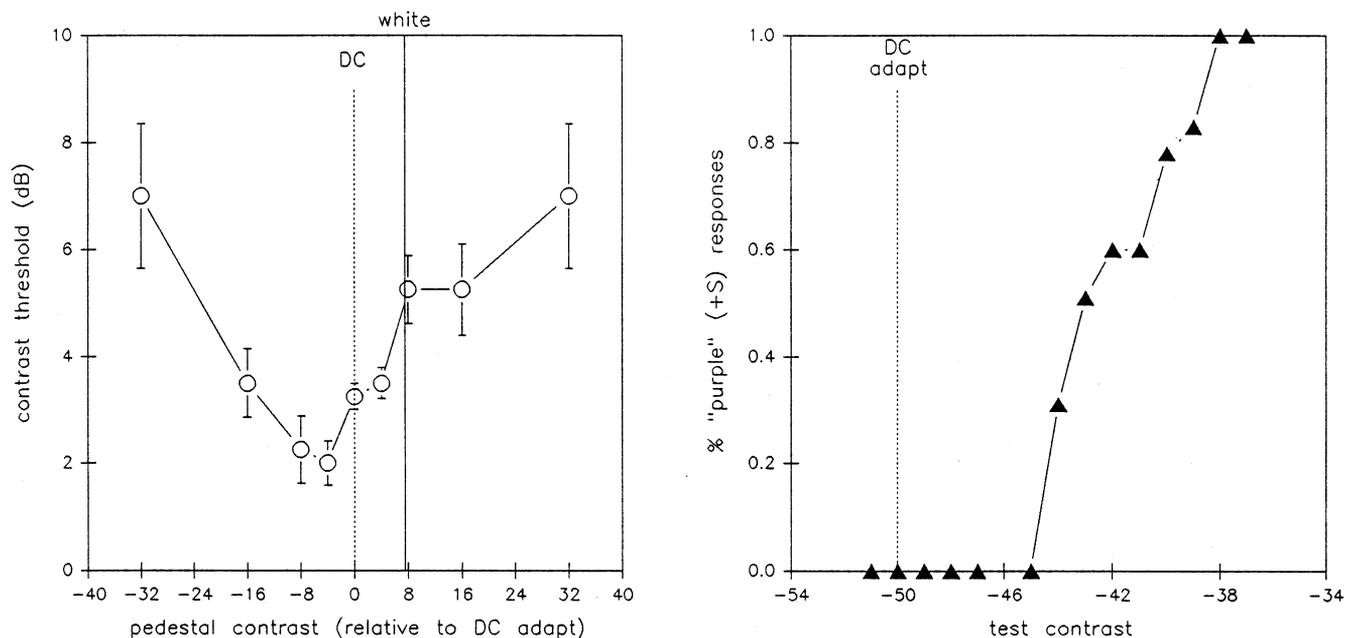

Fig. 11. Chromatic contrast discrimination on a yellow-green (−S) adapting field. The DC adapting color was a −0.3 log unit change in S-cone activity relative to the neutral point. The left panel plots the thresholds for detecting a change in S contrast as a function of the S pedestal contrast. Thresholds show a minimum near the DC chromaticity but are removed from the contrast that appeared achromatic, as estimated from the psychometric function for judging the appearance (too green vs. too purple) of different pedestal contrasts (right panel).

visual response to moderate contrasts is effectively linear, though again, the results are also consistent with nonlinearities that are symmetric for increments and decrements. A possible test for symmetric nonlinearities would be to measure the light adaptation state for flickering stimuli that have the same mean chromaticity but vary in their duty cycle, so that increments and decrements have different durations and amplitudes. However, the current results are consistent with the linearity for moderate signals observed in psychophysical studies of increment thresholds and single-unit studies of the responses of retinal cells (Hood, 1998). Of course for large modulations, response compression results from the limited dynamic range of visual cells, and is the primary reason why processes of light adaptation are so important. The results are not consistent with a strongly asymmetric compression, such as a log response to contrast. A log transform provides a powerful metric for describing many properties of color vision, yet this power lies more in equating the scaling changes induced by different adaptation levels than in describing the visual response to different stimulus levels under a fixed state of light adaptation (Whittle, in press).

In natural viewing, the state of light adaptation to a scene depends on how the observer samples different regions of the image over time. For typical scenes composed of multiple objects, this sampling necessarily introduces the temporal contrasts in the stimulus that can lead to contrast adaptation. Thus in natural viewing conditions both forms of adaptation may play a prominent role in color perception. A large number of studies have examined the time course of chromatic adaptation (e.g. Hayhoe & Wenderoth, 1991; Fairchild & Reniff, 1995) and contrast adaptation (e.g. Greenlee, Georgeson, Magnussen, & Harris, 1991; Hammett, Snowden, & Smith, 1994) typically by measuring the build-up of adaptation when a stimulus is presented or the recovery of sensitivity after the adapting stimulus is removed. The present experiments examined the temporal patterns of adaptation that might result from sampling the same stimulus distribution over time, by examining how both light adaptation and contrast adaptation varied depending on the temporal frequency of the adapting modulation. For the conditions that were examined, modulation rates of 0.5 Hz or higher maintained effectively stable states of light adaptation, indicating that under steady viewing conditions (i.e. for a fixed distribution) the current state of light adaptation is effectively determined by signals integrated over the preceding several seconds.

The results also show that large changes in contrast sensitivity can be induced over a broad range of temporal frequencies. This suggests that the processes underlying contrast adaptation are sensitive to a wide range of temporal variations (see also Pantle, 1971). However,

the interpretation of the present results is complicated by several factors. At low temporal frequencies biases are introduced in chromatic adaptation and these can lead to response saturation, mimicking the effects of contrast adaptation on the appearance of test stimuli. This response saturation was substantial even when the 500 ms tests were presented immediately after a static adapting field. In previous studies testing similar conditions, Webster and Mollon (1995, 1997) found that the effects of light adaptation on the appearance of low-contrast stimuli closely approximated simple von Kries scaling of the cone signals. However, the present results show that this scaling breaks down for high contrast stimuli that are complementary to the adapting color direction. That this response saturation was consistently selective for the complementary axis suggests that it depends on mechanisms that can be tuned to multiple color directions, as noted previously by Krauskopf et al. (1986).

Contrast adaptation effects are more safely isolated at medium or high temporal frequencies, at which light adaptation to the flicker remains stable. Changes in sensitivity were large for medium temporal frequencies and were substantially weaker only at the highest modulation rate examined (17.5 Hz). At this frequency the perceived contrast of the chromatic flicker is greatly reduced. However, we do not know whether the high-frequency fall-off of the adaptation resulted from the weaker effective contrast of the flicker, or because these high frequencies were primarily affecting different temporal channels than the test stimulus. Studies of luminance contrast suggest that temporal frequency is encoded by two to three broadly tuned channels that can adapt somewhat independently (Watson, 1986). In the experiments the test was always a 500 ms square pulse. If the perceived contrast of this pulse depended on a low temporal-frequency chromatic channel then the measures might fail to reveal the magnitude of the adaptation for high-frequency flicker.

The highest temporal frequency to which the visual system can adapt remains an intriguing question. Cells in the retina and geniculate can follow high rates of luminance and chromatic flicker (Gielen, Van Gisbergen, & Vendrik, 1982; Derrington, Krauskopf, & Lennie, 1984; Stockman, MacLeod, & DePriest, 1991). This suggests that the large differences in temporal resolution for luminance and color (Regan & Tyler, 1971; Kelly, 1983) must be limited in the cortex. As noted, contrast adaptation also has a cortical locus, but the relative loci of these two processes remains unclear. If the site of adaptation preceded the cortical temporal filtering, then observers might adapt to flicker rates that are too high to perceive. Such effects are suggested for very high spatial frequencies (Smallman, MacLeod, He, & Kentridge, 1996), but not for high-frequency luminance flicker (Pantle, 1971). We did not attempt to test

neutral adaptation　　　white

incomplete DC adaptation　　DC
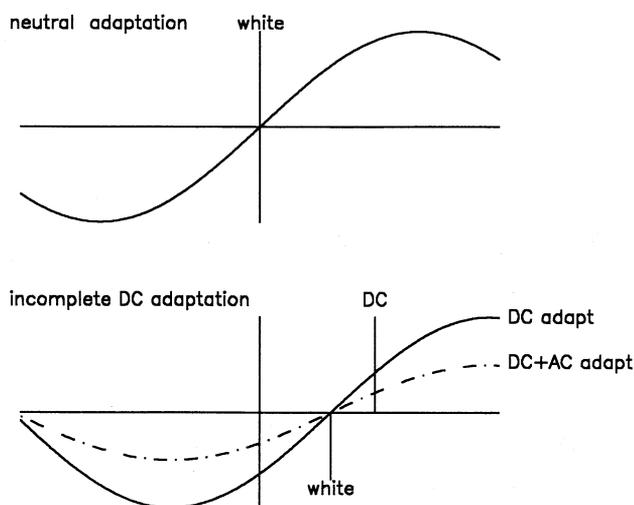
DC adapt

DC+AC adapt

white

Fig. 12. Adaptation effects predicted by a single-channel model of contrast coding. The upper figure shows the spectral sensitivity of a conventional color-opponent channel, which has a null point corresponding to white under neutral adaptation. Light adaptation to a DC color shifts the null toward the DC, but if the adaptation is incomplete then a difference remains between the DC and the stimulus that appears achromatic (lower figure). Contrast adaptation scales the sensitivity of the channel relative to the null point, and should therefore reduce any residual perceived contrast in the DC.

for contrast adaptation to very high temporal frequencies, in part because the matching field is also flickering at the monitor framerate, and thus would potentially also be susceptible to the adaptation. As an alternative, we instead compared for one observer the temporal frequency tuning of the contrast adaptation for luminance and chromatic contrast. If the adaptation preceded the locus of the filtering limiting the perception of chromatic flicker, then the temporal-frequency dependence of the contrast adaptation might be similar for luminance and color, despite differences in apparent contrast. In fact, consistent with this we did not observe a clear difference in the adaptation results for luminance or chromatic flicker. However, these results are inconclusive because they could also depend on differences in the selectivity of luminance and chromatic channels for temporal contrast.

4.2. Contrast adaptation under incomplete light adaptation

The effects of light adaptation on color appearance are well recognized — by adjusting to the average color in the scene, light adaptation tends to remove the mean color biases in the stimulus and thus passes on to subsequent levels only the local color differences or contrasts in the image. In this study the nature of these contrast signals was explored, by asking how they are influenced by contrast adaptation. Under complete light adaptation the mean color appears achromatic,

and contrast adaptation collapses perceived color around this point. Yet under incomplete light adaptation — when a residual color bias remains in the stimulus — contrast adaptation instead alters perceived contrast relative to this residual color. Thus the effective stimulus contrasts determining both contrast adaptation and contrast discrimination appear to be the differences relative to the DC stimulus. That contrast should depend on the stimulus transients relative to the steady background is not surprising, but is unexpected in light of the phenomenal appearance, or perceived contrast, of the transients. Under incomplete light adaptation the achromatic point is itself a contrast relative to the DC, and thus like other contrasts could be shifted in appearance by contrast adaptation. Consequently under incomplete light adaptation the achromatic point no longer has a special status.

The adaptation effects which were observed show that alternative definitions of chromatic contrast are not equivalent, because they become dissociated under biased states of adaptation. Webster and Mollon (1993) previously demonstrated analogous dissociations in luminance contrast, by showing that contrast adaptation induces different biases in equiluminance settings determined by different tasks and stimulus parameters. They argued that these dissociations arise because different tasks tap mechanisms with different chromatic properties that can therefore be biased by adaptation in different ways. Similarly, in the present study it has been found that different measures of zero chromatic contrast (specifically, as defined by perceived saturation or by the stimulus difference relative to the DC chromaticity) can be biased in different ways by adaptation. Again, this implies that these measures reflect either different properties or different subsets of the mechanisms encoding color appearance.

Fig. 12 illustrates why these dissociations are difficult to reconcile with contrast coding in a single mechanism. The figure shows the spectral sensitivity of a conventional opponent channel and how this sensitivity should be biased by adaptation, based on standard assumptions about post-receptoral color coding. The null or equilibrium point for this mechanism defines zero contrast and is the stimulus that should appear white. Chromatic adaptation (e.g. to a red field) biases the cone inputs to this mechanism and thus should shift the null point toward the DC adapting color. If this adaptation is incomplete then the shift in the zero-crossing falls short of the DC, accounting for the residual color of the DC. Contrast adaptation is instead assumed to adjust the gain of the channel. This should reduce the response of the channel to all stimuli except the equilibrium stimulus. Consequently the contrast adaptation should further reduce the perceived saturation of the DC stimulus, while the appearance of the achromatic stimulus should remain unaltered. Yet this predicts the

opposite of the color changes observed — for it is the DC stimulus, and not the achromatic stimulus, that appears unaffected by adaptation. Thus the observed color changes are inconsistent with a common neutral point defining zero-contrast and the achromatic point.

What sort of color organization could predict these changes? One possibility is that the color appearance of the adapting field depends on the combined responses of different mechanisms with different null points. For example, suppose that the mechanisms that signal the appearance of the static DC differ from the mechanisms encoding the transients. If only the latter mechanisms were affected by contrast adaptation (and if these mechanisms adjusted completely to the DC stimulus so that they signal only the transients), then the changes in color appearance with contrast adaptation would appear to collapse around the perceived DC color (as carried by the former mechanisms). The results do not provide any independent evidence for this arrangement. However, it is possible that a number of qualitatively different processes contribute to the perceived color of the fields — including direct responses to the field chromaticity and responses that spread or are filled in from signals at the field's edges (e.g. Broerse, Vladusich, & O'Shea, 1999). As suggested to the authors by a reviewer, the dissociations observed could also reflect functional differences between color appearance systems designed to extract different types of information about the image — for example about the illumination or surfaces in the scene — with contrast adaptation primarily affecting the surface representation. To probe such mechanisms it would be instructive to test interactions between chromatic adaptation and contrast adaptation in more complex and naturalistic images, for they may be only weakly engaged by the types of simple stimuli we used (Mausfeld, 1998).

A second general possibility is that the notion of a null response in contrast coding is in error. As Fig. 12 illustrates, conventional models of post-receptoral color coding assume that achromatic stimuli reflect the absence of activity within color channels, while saturation depends on the magnitude of activity. However, this assumes that the channels share a single common null point in their spectral sensitivities. Parvocellular cells in the lateral geniculate vary widely in their cross points, so that no single stimulus could silence the population (De Valois, Abramov, & Jacobs, 1966; Zrenner, 1983; Derrington et al., 1984). This suggests that the achromatic point may correspond to a particular distribution of activity, and more generally, that contrast is coded as much by which cells are responding as it is by the size of their responses. A population code for luminance contrast was proposed by Albrecht and Hamilton (1982), based on their measurements showing that cortical cells have limited dynamic ranges that span different contrast levels. Thus any given stimulus con-

trast might be encoded by different groups of cells. Georgeson (1985) subsequently noted that changes in this distribution with contrast adaptation could account for the way in which the adaptation alters apparent contrast. With regard to color, the light–dark achromatic axis does not reflect a fixed null axis for chromatic channels, because it can be biased by selective adaptation to different color-luminance combinations. For example, adaptation to a modulation between bright-red and dark-green causes a bright gray to appear greenish and a dark gray to appear reddish (Webster & Mollon, 1991, 1994; Webster & Malkoc, 1999). One interpretation of these after-effects is that the achromatic axis depends on the distribution of activity across multiple channels sensitive to different combinations of luminance and chromatic contrast — to different directions in color space. Adaptation to a specific color-luminance direction can bias this distribution and thus tilt the appearance of the achromatic axis, in the same way that adapting to an oblique line biases the distribution of responses encoding vertical lines (Webster, 1996). The dissociations found in the present results — between the achromatic point and the null contrast for adaptation — could similarly arise if color channels are distributed not only along different axes in color space but also along different levels of these axes (e.g. so that the S axis itself is encoded by a distribution of S vs. LM mechanisms that differ in the relative strength of the S and LM inputs). If white is determined not by the absence of activity, but by a distribution of activity (much as the unique hues may be; Webster & Mollon, 1991), then it is no longer tied in a necessary way to alternative measures of chromatic contrast.

Acknowledgements

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