Color contrast and contextual influences on color appearance

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We used a hue-scaling task to examine changes in color perception resulting from adaptation or induction to color contrast in spatially-varying backgrounds. Observers judged the perceived color of tests after or while viewing backgrounds composed of color differences along selected axes in color space. Both contrast adaptation and contrast induction produced large and selective shifts in perceived hue angle, and interacted in similar ways when combined, suggesting that they had functionally similar influences on perceived hue. Both also consistently biased perceived hue away from the color axis of the background, implying response changes within multiple channels tuned to different directions in color space. Selective hue changes were also observed when the gamut of colors forming the backgrounds were drawn from natural color distributions. This suggests that color perception in different environments may be systematically biased by adaptation to the distributions of colors in those environments. However, we did not find these biases when the same test stimuli were judged after adapting to actual natural scenes.

Keywords: color, contrast, adaptation, induction, natural images

Introduction

A central question in color vision is how color appearance is affected by the context in which lights or surfaces are viewed. Answers to this question are important because they help to reveal the processes that shape color perception, and because they define the viewing conditions under which color may behave as a stable or variable property of objects. There are in fact many different contextual influences on color; for example, from light adaptation or spatial induction from different average colors, to influences that depend on interpretations of the three-dimensional viewing geometry of the scene (e.g., Adelson, 1993; Mausfeld, 1998; Webster, 1996). In this study we have explored the influence of color contrast, by measuring how the perceived hue of a stimulus is affected when the stimulus is presented after or during exposure to backgrounds defined by different distributions of colors.

In previous work we have examined how color is affected by color contrast adaptation to fields that vary in color over time. After adapting to a field that is temporally modulated in chromaticity or luminance, thresholds for detecting stimuli of similar color are selectively elevated, suggesting that adaptation reduces

sensitivity in channels tuned to the adapting color axis (Krauskopf, Williams, & Heeley, 1982; Krauskopf, Williams, Mandler, & Brown, 1986). These sensitivity changes alter color appearance by selectively reducing the perceived contrast or saturation of colors that are similar to the adapting axis, and by biasing the perceived color angle or hue of other stimuli away from the adapting axis, much as adaptation to a particular orientation or spatial frequency biases the appearance of other orientations or frequencies in figural aftereffects (Webster & Mollon, 1994). One goal of the present work was to explore whether comparable selective changes in color perception occur when observers are adapted to the complex spatial backgrounds that are characteristic of natural viewing contexts, rather than uniform fields. In spatially varying patterns temporal modulations of color will still arise because of eye movements, and adaptation to spatial color contrast can have a large and selective effect on threshold sensitivity for color contrast (Bradley, Switkes, & De Valois, 1988; Zaidi, Spehar, & DeBonet, 1998). We therefore expected that color appearance could be strongly affected by adaptation to patterned backgrounds.

On spatially-varying backgrounds a second factor that can influence color appearance is contrast induction or contrast gain control from the spatial surround (Brown &

MacLeod, 1997; Shevell & Wei, 1998; Singer & D'Zmura, 1994). Surrounds of high contrast can strongly reduce the perceived contrast within a central test region (Chubb, Sperling, & Solomon, 1989). A second goal of our study was to examine the relative influences of contrast adaptation and contrast induction, and how they interact to determine color appearance. While both modulate perceived contrast at a cortical locus (e.g., Shevell & Wei, 2000), they are likely to depend on different underlying processes with different properties. For example, contrast induction effects typically show less spatial selectivity than contrast adaptation (Blakemore & Campbell, 1969; Chubb et al., 1989; Solomon, Sperling, & Chubb, 1993). In the case of color, the induction is strongest when the surround and center contrasts vary along the same directions of color space, revealing color selectivity (Singer & D'Zmura, 1994; Brown & MacLeod, 1997). However, the induction has primarily been found to affect perceived contrast with little effect on perceived hue (D'Zmura & Singer, 1999; though in other contexts its effects are manifest by shifts in unique hues; Wesner & Shevell, 1992); and it is not well established whether the response changes can be selective for any arbitrary axes of color space. This differs from the marked hue shifts and selectivity observed with contrast adaptation (Webster & Mollon, 1994). In the present study we asked how these two processes combine to affect color appearance when observers are adapted to a background and then judge the color of stimuli presented on that background.

A final goal of our study was to examine the extent to which these contrast effects might be manifest for the patterns of color contrast that observers typically encounter in natural environments. The gamut of colors in different natural scenes can vary widely in both the range and direction of color variation, and we have found previously that adaptation to the biases in the color distributions of different scenes are sufficient to selectively bias color appearance (Webster & Mollon, 1997). These adaptation effects were assessed by adapting observers to a random temporal sequence of colors drawn from a given scene. Here we again asked whether comparable selective changes in color perception would occur when observers are exposed to natural color distributions presented with the spatial structure of natural scenes. Characterizing the actual contrast effects for natural viewing conditions is important for testing whether color vision might be shaped in different ways by different environments. To examine this we measured the adaptation effects both for synthetic "camouflage" patterns whose colors were taken from natural color distributions, and for actual calibrated images of outdoor scenes.

To probe color appearance we used a simple hue scaling task in which observers judged hue by rating the proportion of red, green, blue or yellow that appeared present in the stimulus. This had the advantage that appearance could be measured without a reference stimulus or unique point as in typical matching or nulling tasks, and thus lent itself well to the task of measuring a wide range of chromaticities on spatially extended backgrounds. The scaling also had the advantage of being an intuitively easy and natural visual judgment. Hue scaling results agree well with the red-green and blue-yellow variations defined by hue cancellation (Boynton, 1975), and like cancellation have been used to define the perceptual dimensions characterizing phenomenal color perception (Abramov, Gordon, & Chan, 1990; De Valois, De Valois, Switkes, & Mahon, 1997). In the following experiments we examine how these dimensions are biased by contrast adaptation and contrast induction.
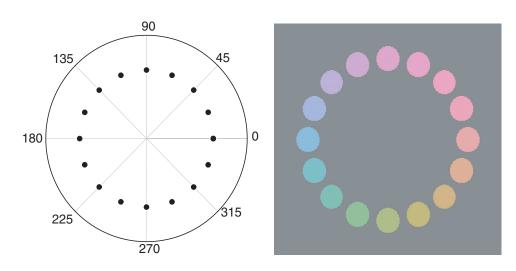
Methods

Stimuli

Patterns were displayed on a SONY 20SE color monitor. In most experiments the monitor was controlled through a Cambridge Research Systems VSG graphics card, which provided a color resolution of 12 bits per gun. For the final experiment with color images we instead used a standard PC and graphics card, with 8-bit color resolution. In both cases gun luminances were linearized through calibration tables measured with a PhotoResearch PR650 spectroradiometer, which was also used to measure the phosphor chromaticities.
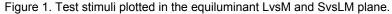
The test stimulus consisted of a 0.5-deg uniform circle presented on a 6- by 8-deg background. The chromaticity of the circle was defined according to a scaled version of the MacLeod-Boynton color space (Derrington, Krauskopf, & Lennie, 1984; MacLeod & Boynton, 1979). Within this equiluminant plane signals along the LvsM axis vary the ratio of signals in the L and M cones while holding S cones constant. Signals along the SvsLM axis instead vary the signals in the S cones (opposed by a constant sum of L and M cone signals). In our plane the origin corresponded to a chromaticity of Illuminant C and a luminance of 30 cd/m2, and the two axes were scaled based on previous measurements to approximately equate the adaptation effects for different color directions. The LvsM and SvsLM coordinates of the plane are related to the r and b coordinates of the MacLeod-Boynton space by:

$$LvsM = (r - 0.6568) * 1955$$

$$SvsLM = (b - 0.01825) * 5533$$

For test stimuli we used 16 saturated colors with a fixed contrast of 80 and varying at angles of 22.5 deg along a circle centered on the white point (Figure 1).The test circle was presented on a background formed by a dense random array of circles (each also 0.5 deg in diameter). This stimulus is similar to one developed by

Figure 1. Test stimuli plotted in the equiluminant LvsM and SvsLM plane.

Mausfeld (1998) to examine background influences on color appearance. In the first set of experiments we restricted the color of the background to a single axis of color space. To maximize contrast, the chromaticity of each circle was chosen at random from one of the two poles (+80 or –80) of the 8 axes defining the test stimuli. The circles also varied randomly in luminance by $\pm20\%$ around the 30 cd/m^2 mean. Figure 2 shows an example of a background with colors drawn from the LvsM axis. The superimposed test is a yellowish color with an angle of -45 deg in the cone-opponent space. The experiments were designed to examine whether the color of the test was biased by adaptation or induction from the color contrasts defining the background. These backgrounds all had the same achromatic mean chromaticity (equivalent to Illuminant C). Contrast adaptation does not bias the mean chromaticity, and instead biases perceived contrast relative to the mean (Webster & Wilson, 2000). We therefore assumed that the achromatic point would be unaffected by the backgrounds, and thus did not include measurements of the achromatic point.

In later experiments we used the color distributions from natural scenes to define the colors of the background elements. These distributions were measured in a previous study (Webster & Mollon, 1997) and are discussed in the Results section below. In these cases both the luminance contrast and chromaticity of each circle were selected at random from the distribution. In the final measurements the backgrounds shown were color images of outdoor scenes. These images were collected in Maharashtra, India as part of a separate study (Webster et al., 2002). The images were taken in a rural agricultural area during the monsoon or winter seasons, and were panoramic scenes of cultivated fields (primarily rice) and the surrounding hills, vegetation and sky (see Figure 12). The images were taken with a SONY DSC D770 digital camera. Each scene included a MacBeth color checker in the lower right corner. We used measurements of the

color checker taken with the PR650 to calibrate the RGB colors of the palette, and then used these to calibrate the RGB colors within the image. This was done by first correcting for the RGB values for the camera gamma function, and then by using the estimated shifts in the palette colors to adjust the color for each pixel through interpolation. Finally, to display the images on the screen, we generated corresponding images that were further corrected for the nonlinearities of the monitor.

Figure 2. An example of the stimulus background. Colors in the background vary between the two poles of the LvsM axis, and randomly vary in luminance. The yellowish test circle at center corresponded to a chromatic angle of -45 deg.

Procedure

To measure the perceived hue of the test stimuli, subjects rated the proportion of red, green, blue, or yellow with a 5-point rating scale, by pressing a series of buttons on a micropad (De Valois et al., 1997). The responses were designed to measure (out of a total of 5 "parts") how many parts of the color came from each primary hue component. However, observers could (and sometimes did) also use more than 5 button presses. For example, a reddish orange might be rated as 3-parts red and 2-parts yellow, while an orange that appeared as an equal red-yellow mixture could be rated as 3-red and 3-yellow. In a single run each test color was rated 5 times in

random order. Results reported are based on two runs for each condition, and thus show the average of 10 ratings for each test. As expected, on a single trial subjects never rated a test color as both red and green or both blue and yellow. Accordingly, we represent the perceived hue of each test by its angle within a red vs. green and blue vs. yellow perceptual opponent-color space. In this space the red-green axis lies at 0 and 180 deg and the blue-yellow axis at 90 and 270 deg. An orange rated as 3-red and 2-yellow has an angle of 326.3 deg. Standard deviations of the mean selected angles across sessions averaged 4-6 deg and were similar for different observers and conditions. To measure the effects of adaptation and induction, the test hues were rated under the following 5 conditions (see Figure 3).

1. *Neutral adaptation and induction.* In this baseline condition the background was achromatic (all elements with the chromaticity of Illuminant C). The background elements still varied in luminance so that luminance contrast was constant across all conditions.

2. *Contrast adaptation.* To isolate the influence of prior adaptation, the test was shown on an achromatic background after subjects adapted to a background with color contrast.

3. *Contrast induction.* Conversely, to measure the effects of induction alone, the adapting pattern was achromatic while the test was shown on a background with color contrast.

4. *Contrast adaptation and contrast induction.* In this case a background with the same color contrast was shown both before and during the test, to examine the combined influence of adaptation and induction.

5. *Adaptation and orthogonal induction.* Finally, to further examine how the two influences might combine, we pitted them against each other by adapting to one color axis (e.g., LvsM) and then presenting the test on an orthogonal axis (e.g., SvsLM).

In all cases the test was shown at the center of the display for 500 ms. Subjects first adapted to the background for 300 sec. During this time the background filling the screen was randomly changed every 250 ms, in order to avoid local differences in light adaptation and to simulate the pattern of stimulation that might arise from rapid and random eye movements. The series of test colors were then shown interleaved with 6-sec periods of re-adaptation, with the field blanked for 250 ms before and after the test. These gaps were added to help separate the inducing background from the adapting background, though control measurements without them yielded similar results.

Observers viewed the display binocularly from a distance of 250 cm in an otherwise dark room. The subjects included authors MW, GM, and AB. All three

had normal or corrected-to-normal acuity. MW and GM have normal color vision. AB is mildly deuteranomalous. He behaves normally on standard color screening tests (e.g., Ishihara plates and Farnsworth-Munsell) but exhibits shifted Rayleigh matches.
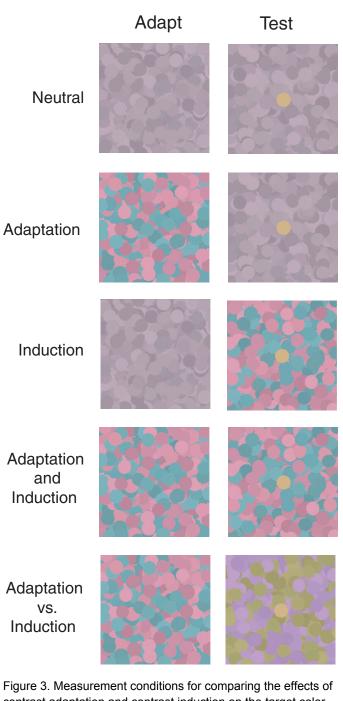

Figure 3. Measurement conditions for comparing the effects of contrast adaptation and contrast induction on the target color. Observers judged the hue of the test after adaptation to a background, in the presence of the background, or both. Effects were assessed relative to the ratings in the neutral condition.

Results

Backgrounds Varying Along a Single Color Axis

Figure 4 shows examples of the hue ratings for the three observers. Specifically, the figures show how color appearance (plotted along the y axis as angle within the red-green and blue-yellow axes of perceptual color space) varies as a function of stimulus angle within the LvsM and SvsLM axes of cone-opponent space. The conspicuous bend away from the diagonal results from the well-established observation that stimulus variations along the cone-opponent axes do not correspond to pure red-green and blue-yellow sensations. For example, the color patches to the right show the angles corresponding to unique red, blue, green, and yellow—the cardinal directions of the perceptual space. Pure blue, green, and yellow all occur at angles in-between the SvsLM and LvsM cardinal axes of cone-opponent space. However, consistent with previous results, unique red was very close to the +L pole of the LvsM axis (Webster, Miyahara, Malkoc, & Raker, 2000b).

The unfilled symbols show the settings when observers were adapted to a chromatic background and then judged the test in the presence of the same chromatic background. Results along the left column were for an SvsLM background, while the right column shows settings for an LvsM background. In both cases the effect of the background was to strongly bias the perceived hue of the stimuli, for some tests by more than 30 degrees. Note that these biases were in the opposite direction for the two backgrounds. For example, the 45-deg test (a reddish-blue) appeared bluer with the LvsM background and appeared redder with the SvsLM background. Thus in both cases the hue changes were strongly selective for the background color axis.

To better capture the effects of the different backgrounds we plotted for each condition the difference between the hue settings on the chromatic background and the neutral background. Examples of these plots are shown in Figure 5 for observer MW. In this case the 8 panels show the results for 8 different background axes, while the 4 curves within each panel plot the changes resulting from the 4 combinations of adaptation and induction. The undulations in the curves are similar for the different conditions. That is, the biases in perceived hue were qualitatively similar whether they resulted from prior adaptation or simultaneous induction from the background axis. The main exception was when the adapting and inducing backgrounds fell along different color directions, which resulted in only weak effects. The variations also show a similar though phase-shifted

pattern across the different background axes. That is, in each case the color is generally biased away from the chromatic angle of the background, consistent with a color change that is selective for each background axis.

We estimated how selective the color changes were by fitting a simple model to the results. The model assumed that adaptation or induction reduces sensitivity to the background axis more than to the orthogonal axis, consistent with previous findings. We modeled the relative sensitivity loss by rescaling the signals along the adapting axis, and then calculating the resulting change in hue angle. For example, a sensitivity loss that was twice as strong along the LvsM axis compared to the SvsLM axis would halve the relative LvsM component of any test. This would have no effect on the perceived hue of tests along the LvsM and SvsLM axes, but would rotate all other tests away from the LvsM axis and toward the SvsLM axis (see Figure 6). To fit the observed results we varied the magnitude of the sensitivity change along the background axis to find the least-squares fit of the predicted to the observed hue angles. Note that we use this model only to measure the size of the hue shifts, and not the size of any contrast changes (which the ratings do not measure). As far as the fitting is concerned, a two-fold loss in sensitivity to the LvsM axis is equivalent to a two-fold increase in sensitivity to the SvsLM axis. As noted above, we also assumed that because the backgrounds all had the same mean chromaticity and luminance, differences in the background conditions would not lead to differences in the overall mean hue of the tests. That is, we assumed that the state of light adaptation remained constant and thus, for example, assumed that there were no differential effects of von Kries adaptation.

A question arises as to what the relevant color space is for these predictions. Previous work has shown that contrast adaptation alters sensitivity in color channels organized in terms of orthogonal LvsM and SvsLM axes (Krauskopf et al., 1982; Webster & Mollon, 1994). However, the hue shifts are instead measured by the change in the perceptual color space, in which red-green and blue-yellow are orthogonal. To address this, we assumed sensitivity changes along the axes of cone-opponent space, but then fit these either directly to the observed hue angles, or to the angles transformed back into the cone-opponent space. This was done by first fitting a polynomial curve to the neutral hue settings of Figure 4, to define the transformation between the two spaces. The observed changes in perceptual hue angles could then be converted to the equivalent angle change in the cone-opponent space. However, it turned out that this did not strongly influence the selectivity estimates. Errors in the fits to MW and GM's results were modestly improved by the conversion, while AB's did not clearly change. Thus the estimates do not depend critically on the choice of axes.
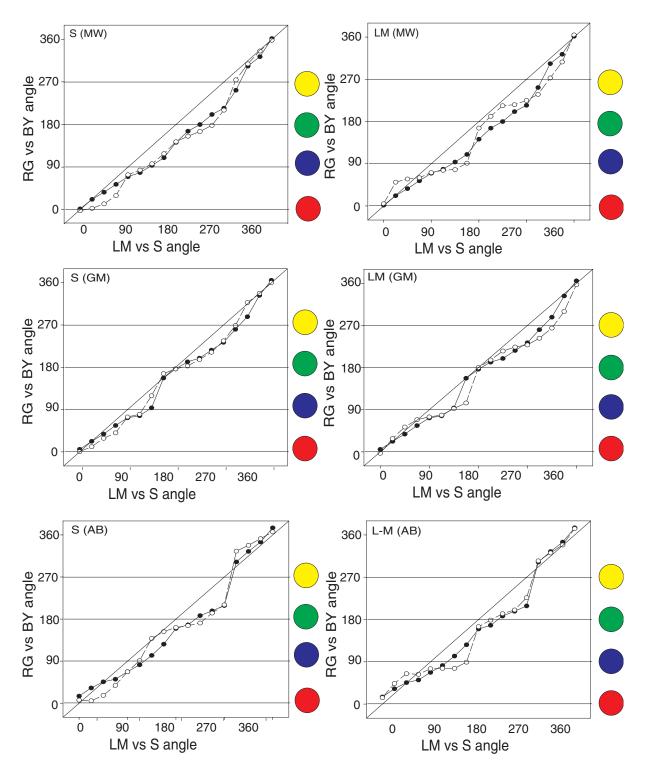
Figure 4. Perceived color of the targets plotted as a function of their angle in the cone-opponent space (x axis). The perceived color is represented by the angle within a perceptual red vs. green and blue vs. yellow space (y axis). Angles corresponding to pure red (0 deg), green (180 deg), blue (90 deg), or yellow (270 deg) are indicated by the color circles at the right of each panel. Filled symbols—mean ratings for the neutral background. Unfilled symbols—mean ratings under both adaptation and induction from the background. Left panels show results for 3 observers for the SvsLM background. Right panels show corresponding results for the LvsM background.
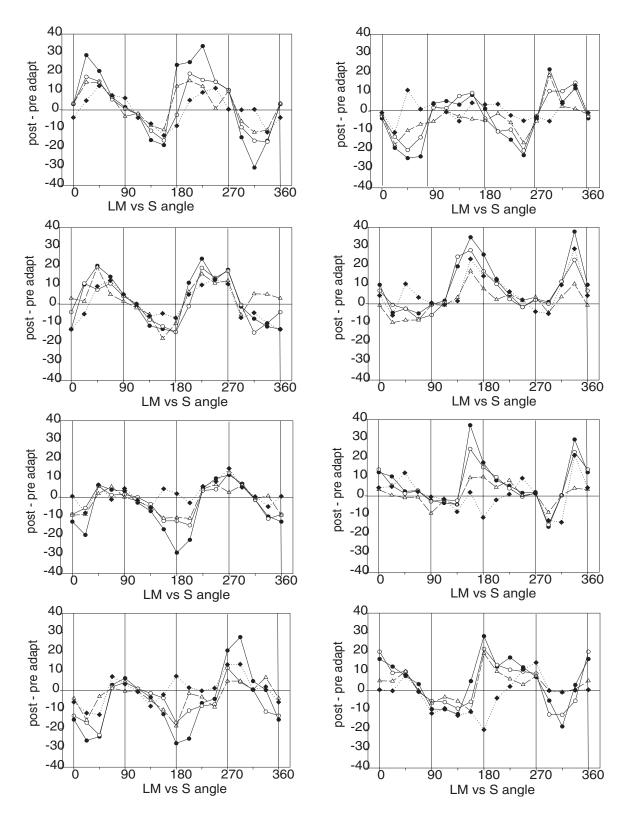
Figure 5. Changes in the hue ratings for adaptation or induction. Points plot the difference between the angles rated on the color backgrounds and the neutral background, as a function of the target's cone-opponent angle. Unfilled circles—adaptation alone. Unfilled triangles—induction alone. Filled circles—adaptation and induction to the same background color. Filled diamonds—adaptation and induction to orthogonal background colors. Each panel plots the settings for one background axis for one observer (MW). Left column: background axes of 0-180, 22.5-202.5, 45-225, or 67.5-247.5. Right column: background axes of 90-270, 112.5-292.5, 135-315, or 157.5-337.5.
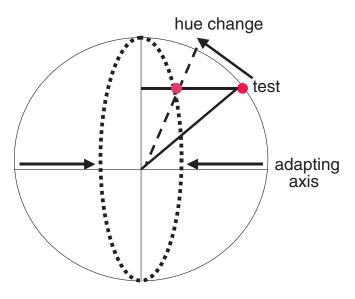
Figure 6. Biases in perceived hue predicted by a selective loss in sensitivity to the adapting axis. Sensitivity losses along the LvsM axis bias perceived hue toward the SvsLM axis.

Figure 7 plots the estimates of color selectivity. In this figure a value of 1.0 corresponds to a nonselective hue change, while values less than 1.0 correspond to a bias in perceived hue away from the background axis, and thus imply a selective loss in sensitivity to the background axis. Though variable, these estimates point to a consistent pattern of how the color-varying backgrounds influenced appearance. One important feature of this pattern is that the biases induced by the background were often strongly selective, in some cases approaching a two-fold change in relative sensitivity to the adapting axis (i.e., approaching a selectivity index of 0.5). A second feature is that selective changes occurred for all (observer MW) or most (GM and AB) adapting angles. The results thus reinforce evidence from studies of temporal contrast adaptation in pointing to a central color organization based on channels that can be tuned to directions intermediate to the LvsM and SvsLM axes (Krauskopf et al., 1986; Webster & Mollon, 1994). A further important property is that selective hue changes occurred not only for adaptation but also for induction. For the specific conditions we examined, adaptation to the background had a more selective effect on a subsequently presented test than did induction from the concurrent background, yet hue changes with induction were also evident. Moreover, when combined the two influences tended to reinforce each other when they shared a common color axis and interfere when they were defined by opposing axes. Specifically, the most selective changes occurred when the adapting and inducing background both varied along the same color direction, while the weakest hue shifts occurred when they varied along orthogonal directions. These interactions are summarized by the histograms in Figure 8, which show the selectivity of the changes for each of the 4 context conditions averaged across the 8 different color directions.
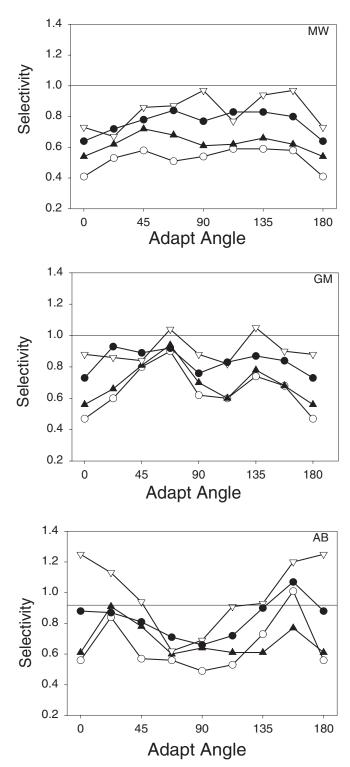

Figure 7. Change in relative sensitivity to the background axis for the 4 background conditions. Note a value of 1.0 corresponds to a nonselective color change, while lower values correspond to a larger relative sensitivity change (i.e., greater selectivity). Filled triangles—adaptation alone. Filled circles—induction alone. Unfilled circles—adaptation and induction to the same background color. Unfilled inverted triangles—adaptation and induction to orthogonal background colors. The 3 panels plot the estimates for each observer.
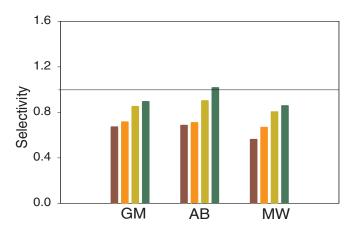
Figure 8. Changes in relative sensitivity averaged across the 8 background color axes. Bars from left to right show the relative sensitivity change for conditions of adaptation and induction (dark red), adaptation alone (orange), induction alone (light green), and adaptation vs. induction (dark green). A lower bar represents a greater relative sensitivity change and thus greater selectivity.

Despite individual differences, these features were evident in the results for all 3 observers, including AB, who we noted is mildly deuteranomalous. Because his two longwave cone spectra are similar, he might be expected to have weaker sensitivity to the LvsM axis (Shevell et al., 1998), highlighting the fact that a fixed cone-opponent space cannot capture the properties of individual observers (Webster, Miyahara, Malkoc, & Raker, 2000a). On the other hand, color sensitivity may not be tightly coupled to the cone pigment spectra in anomalous trichromats if the gain of postreceptoral mechanisms is matched to the range of available inputs (Regan & Mollon, 1997; MacLeod, in press). In either case, the general ways in which his color judgments were modulated by the backgrounds appeared similar to the other observers.

Backgrounds Defined by Natural Color Distributions

We next examined whether changes in perceived hue could be induced by color distributions that are more characteristic of natural scenes. As noted above, Webster and Mollon (1997) tested this by adapting to a temporal sequence of colors drawn from distributions measured for outdoor scenes. They found large changes in the contrast and hue of their test stimuli, and these were clearly selective for the principal axes of the adapting distributions. We used the same color distributions to test for comparable effects on hue scaling after adapting to spatially patterned backgrounds.

Figure 9 shows a plot of chromatic contrasts for the two color distributions we tested and examples of the backgrounds defined by each. The two distributions roughly bracket the range of color axes reported by

Webster and Mollon (1997). The meadow distribution was taken from a scene of a Sierra meadow backed by mountains and sky. It is typical of arid, panoramic scenes in exhibiting a strong bias in color contrast along bluish-yellowish axes. The second distribution was measured within a forest in India, and is representative of more lush environments in showing a color bias along the SvsLM axis. Unlike the preceding stimuli, the two scenes also had a bias in their average color, which was shifted toward yellow or green for the meadow or forest, respectively. In this case, we therefore rescaled the set of test stimuli so that they were centered around the average chromaticity of each scene, by calculating the equivalent test contrasts after assuming von Kries adaptation to each distribution.
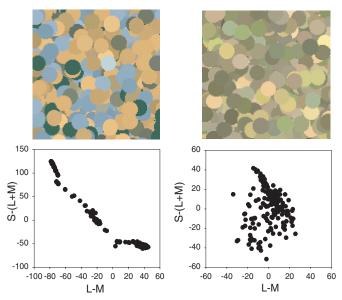

Figure 9. Backgrounds defined by natural color distributions measured in a meadow (left column) or forest (right column). Lower panels plot the distribution of chromaticities in the LsvM and SvsLM space.

The backgrounds were formed by selecting the color at random from the distribution as each circle was drawn. Hue settings were then measured for the condition in which subjects first adapted to the background and then rated the hues in the presence of the background. This corresponds most closely to the context observers would be in if they were actually judging the color of an object in the scene. Figure 10 shows an example of the hue angles for one observer (AB). The neutral settings (on the new mean background) remained similar to those we measured previously, while the settings for the color-varying background show systematic but modest biases.

We again fit the differences in the angles to estimate the magnitude of the selective color change, this time by varying sensitivity along angles of -55 or –87 deg, the principal axis of the meadow and forest distribution. The best fitting values are plotted in Figure 11. For all three observers the bluish-yellowish scene induced a relative

sensitivity change of roughly 20% along the adapting axis. Changes for the forest distribution were less consistent but still selective for two observers. This difference is consistent with the results of Webster and Mollon (1997), and with the fact that the contrast biases are substantially weaker in the forest scene. The overall effects agree with our previous results in suggesting that adaptation to the color biases characteristic of different environments may induce characteristic differences in color appearance.
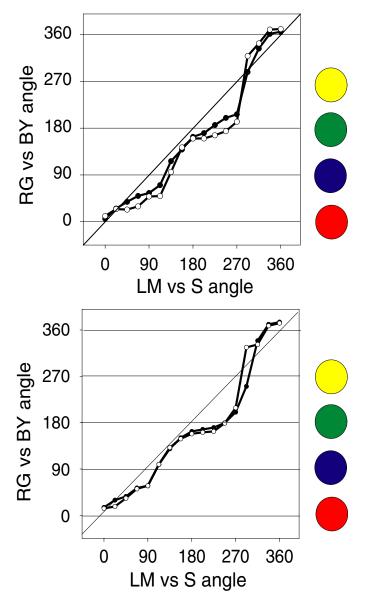

Figure 10. Hue settings for the natural color backgrounds. Filled circles: neutral background; unfilled circles: settings under adaptation and induction to the background. The two panels plot the results for observer AB for the meadow (top) or forest (bottom) distribution.

Adaptation to Natural Images

Clearly, there are many ways in which the backgrounds shown in Figure 9 fail to simulate actual

natural scenes. One of the most obvious is that by coloring the elements at random, we scrambled the original color locations and thus, for example, mixed regions of meadow and sky. In an attempt to explore these effects for more representative stimuli, in the final experiment we measured color appearance for backgrounds formed by actual images of scenes. D'Zmura (1998) has modeled the large changes in image contrasts predicted by contrast induction in natural scenes. We empirically examined the changes in color appearance resulting from adaptation to scenes. Figure 12 shows two pairs of scenes from the collection of images we used. The images in each pair were views of the same valley, yet the color differences are dramatic because of the large seasonal changes in precipitation and thus in the vegetation. In fact, differences in illumination across the two sets of images were trivial compared to the mean color differences resulting from the changes in the scenes' surfaces, consistent with the general violation of the "gray world" assumption in natural images (Brown, 1994; Webster & Mollon, 1997).
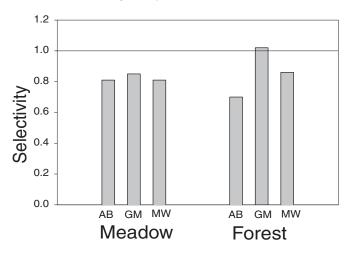

Figure 11. Estimated change in relative sensitivity to the principal axis of the color distributions.

The mean color biases in these images were in fact so large that they dominated the color settings. Figure 13 shows measurements made for the collection of monsoon scenes for two sets of test stimuli. (Effects for the winter scenes were similar but shifted according to their different average color.) In one case the tests were centered on the average illuminant for each set. In the second case the tests were recentered on the mean background color and rescaled assuming von Kries adaptation to the background. Observers adapted either to the uniform background chromaticity or to a random series of scenes taken from a set of 12 images from each season. Each scene was zoomed to an "effective" field size of 12 by 16 deg, and viewed through the monitor field size of 6 by 8 deg. The specific image displayed and its position relative to the screen window was changed randomly every 250 ms. Tests were presented on a uniform background of the
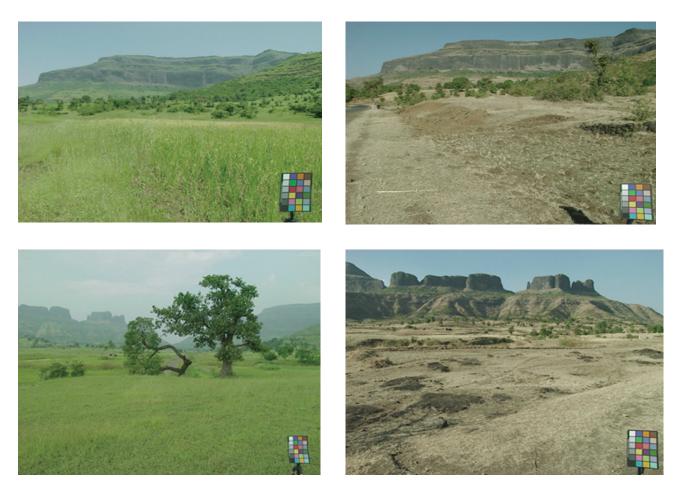
Figure 12. Examples of adapting images, taken in the same area during the monsoon (left) or winter (right) seasons.

mean adapting chromaticity, and thus were shown under the "adaptation-alone" condition. (Presenting the tests on the actual images produced highly variable results because of the random variations in the local color and brightness of the background.)

Chromatic adaptation to the scenes was pronounced, and thus strongly biased perceived hue (Figure 13, top two panels). On the other hand, the average color differences were so large that adaptation only partially adjusted to the mean background. This is evident in the settings when the tests were rescaled for the adapting background (Figure 13, bottom two panels). This rescaling required the SvsLM contrasts to be reduced in proportion to the reduction in S cone excitation for the backgrounds. Yet because adaptation did not adjust completely to the lower mean S cone level, the rescaled contrasts were too low and thus the hue angles are biased toward the LvsM axis. The residual color of the background also meant that the hue settings were influenced by simple chromatic induction from the greenish or yellowish surrounds. For both test conditions, there was relatively little difference in color appearance whether observers adapted to the mean color or to the actual images. Thus for these images there was little

evidence for color contrast adaptation from the spatially-varying backgrounds.

Discussion

Two limitations of our dependent measure bear emphasis. First, the rating scale we used is only a crude index of color appearance, especially when compared to the sensitivity provided by methods like matching or nulling. Subtle changes in hue may often have been insufficient to change the relative ratings for different hue categories. On the other hand, the fact that we could reliably measure hue rotations with this scale indicates that the changes induced by the backgrounds were large and salient. The second limitation is that the ratings measure only the hue of the test color and not its saturation. Consequently our estimates of the underlying sensitivity changes reflect only the *selectivity* of the change and not its overall magnitude. For example, the results do not reveal whether stronger response changes resulted from adaptation or induction, because they are insensitive to any component of the color change that is nonselective.

With this in mind, the hue shifts we found were consistently more selective following contrast adaptation

to the background than from contrast induction to the background. This parallels the results of a number of studies in suggesting that the processes underlying contrast gain control show less stimulus selectivity, and is one source of evidence that the adaptation and gain control are in fact distinct sensitivity adjustments (Heeger, 1992). However, disentangling the two putative processes is complicated. For example, contrast adaptation effects themselves may include very rapid adjustments (Muller, Metha, Krauskopf, & Lennie, 1999), and therefore the state of adaptation may have changed substantially during the 500 ms presentation of the test. Moreover, our results do not reveal whether any differences in selectivity are merely a consequence of differences in the magnitude of the sensitivity changes. In any case, the present results suggest that for the conditions we examined, the adaptation and induction influenced color appearance in functionally similar ways. In both cases perceived hue was selectively biased away from the adapting axis, consistent with response changes in multiple color-selective channels, and consistent with the response changes resulting from temporal contrast adaptation. Moreover, the influence of both factors combined in similar ways. As a result, pronounced color biases occurred when observers first adapted to the backgrounds and then judged colors on those backgrounds. As noted above, this would be typical of natural viewing contexts, and suggests that in natural viewing the joint influences of contrast adaptation and contrast induction could strongly modulate color appearance.

The large hue shifts we observed for contrast induction are surprising in light of previous reports of minimal hue shifts (D'Zmura & Singer, 1999). One possible difference is that the test stimuli we used were highly saturated. However, hue shifts in such stimuli are further surprising because both adaptation and induction tend to have weaker effects on higher-contrast targets (Georgeson, 1985; Singer & D'Zmura, 1995; Webster & Mollon, 1994), and the contrast changes that do persist tend to be nonselective (Snowden & Hammett, 1992). This is problematic for models that assume that stimulus dimensions like hue are coded by the distribution of channel responses, while contrast is instead encoded by the size of the responses. By such models we should be able to predict the rotations in perceived hue by the changes in perceived contrast or vice versa. Yet the observed rotations imply a selective contrast loss of up to 50% (or more if perceived contrast also decreased along the orthogonal axis), while such large contrast changes were not subjectively evident during the experiment. Moreover, in matching tasks where both components were measured, we have observed significant hue and lightness aftereffects in test stimuli that are little changed in perceived contrast (see Webster & Malkoc, 2000, Figure 1). This raises the possibility that contrast, like hue angle, is represented by a distribution of activity across channels (Webster & Wilson, 2000).
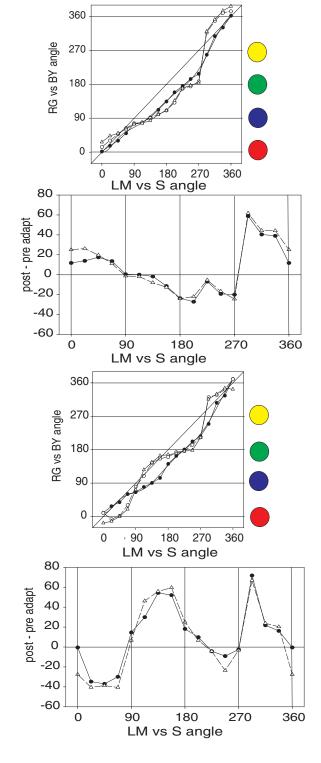

Figure 13. 1st and 3rd panels: Perceived hue after adapting to the sequence of monsoon images (unfilled triangles) or the equivalent average color (unfilled circles), compared to settings for the test stimuli in the neutral achromatic, condition (filled circles). In the 1st set the test chromaticities were centered on the grayish average illuminant color, while in the 3rd they were centered on the green average image color. 2nd and 4th panels show changes from the neutral settings after adapting to the background (filled circles) or the images (unfilled triangles).
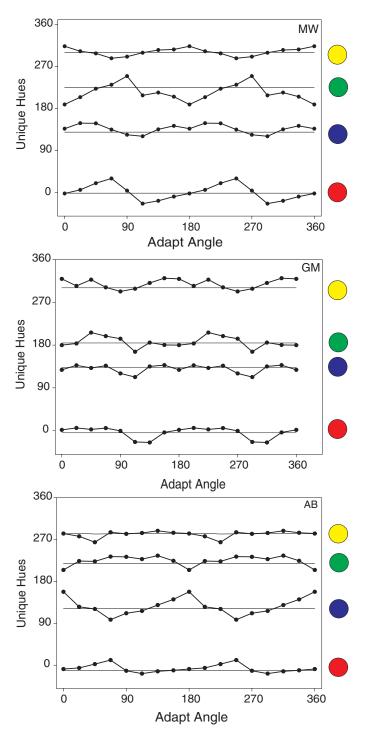
Figure 14. Estimates of the stimuli that would appear pure red, blue, green, or yellow under adaptation and induction to each background color axis. Horizontal lines plot the pure hues estimated from the neutral settings. Note that the adapting axes and points repeat after 180 deg.

It is interesting to also consider how adaptation or induction might change the perceived hue of test stimuli that were even more saturated than those we used. The test stimuli in our experiments correspond to different ratios of SvsLM and LvsM contrast. This ratio could be biased by changing sensitivity to either cardinal axis. For

example, a unique yellow could be shifted toward red or green by adapting to the SvsLM or LvsM axis, respectively. However, a monochromatic yellow falls at a wavelength too long to significantly excite the S cones. Such stimuli might therefore reveal a different pattern of influences (Webster et al., 2000b).

We were led to these experiments in part by the question of the role that contrast adaptation and contrast induction might play in shaping color vision within different environments. That is, would different color environments hold their inhabitants under different states of adaptation, thus leading them to perceive the same color signals in different ways? These effects could potentially be large. For example, Figure 14 plots the angles corresponding to the unique hues on the 8 different background axes. The angles were estimated by interpolating between the measured hue angles to find the cone opponent angles that would be rated as pure red, blue, green, or yellow. These stimuli are often measured as the principal directions defining color experience, but as the curves show, they could in theory be strongly influenced by adaptation to a strong bias in the color environment (at least for the moderately saturated stimuli we tested).

However, our attempts to simulate natural viewing provided only partial evidence for color contrast adaptation. When we used natural color distributions to define the spatially random images, the backgrounds induced systematic changes in hue that were consistent with the color variations in the adapting distributions. On the other hand, the present results failed to reveal a contrast adaptation effect when observers adapted to digital images of scenes, even though the color contrast biases in the two cases were comparable. Notably, we also failed to observe evidence for contrast effects when color appearance measurements were made literally within the actual environments while the scenes were being recorded. As part of a different study, two of the authors (MW and SW) judged unique hues in printed palettes in different outdoor settings that included the valley in which the images we used here were taken (Webster et al., 2002). Even after being immersed in these environments for long periods, their hue settings remained stable. The rich context of actual scenes adds many cues to the nature and origin of color signals, and these cues may mitigate the effects of low-level adjustments of the kind we have considered (MacLeod, in press; Mausfeld, 1998). It is also possible that the large average color biases in the scenes (and lack of complete adaptation to this average) reduced the effective contrast variations in the images, or that the test stimuli and backgrounds were somehow mismatched for the natural scenes in ways that prevented their interaction. For example, in the random patterns the test and background elements were chosen to have identical spatial properties, while the circular test differed from the spatial structure of the images of real scenes, which had broad regions of common color, and color variations that

were not randomly distributed across the image. Spatial-selectivity of the adaptation or cues to the spatial structure of the scenes might therefore have reduced an influence of the scenes on the color of the test target. Many perceptual judgments of natural scenes can be strongly influenced by contrast adaptation to the patterns in the image (Webster, in press), and it would be surprising if color were an exception.

Acknowledgments

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