Chromatic and contrast selectivity in color contrast adaptation

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Abstract

We used color contrast adaptation to examine the chromatic and contrast selectivity of central color mechanisms. Adaptation to a field whose color varies along a single axis of color space induces a selective loss in sensitivity to the adapting axis. The resulting changes in color appearance are consistent with mechanisms formed by different linear combinations of the cone signals. We asked whether the visual system could also adjust to higher-order variations in the adapting stimulus, by adapting observers to interleaved variations along both the L versus M and the S versus LM cardinal axes. The perceived hue of test stimuli was then measured with an asymmetric matching task. Frequency analysis of the hue shifts revealed weak but systematic hue rotations away from each cardinal axis and toward the diagonal intermediate axes. Such shifts could arise if the adapted channels include mechanisms with narrow chromatic selectivity, as some physiological recordings suggest, but could also reflect how adaptation alters the contrast response function. In either case they imply the presence of more than two mechanisms within the chromatic plane. In a second set of measurements, we adapted to either the L versus M or the S versus LM axis alone and tested whether the changes in hue could be accounted for by changes in relative contrast along the two axes. For high contrasts the hue biases are larger than the contrast changes predict. This dissociation implies that the contrast and hue changes are not carried by a common underlying signal, and could arise if the contrast along a single color direction is encoded by more than one mechanism with different contrast sensitivities or if different subsets of channels encode contrast and hue. Such variations in contrast sensitivity are also consistent with physiological recordings of cortical neurons.

Keywords: Contrast adaptation, Chromatic channels

Introduction

Adaptation to contrast (to temporal or spatial modulations of color) is thought to induce sensitivity changes in cortical mechanisms, and thus has been used to examine properties of color coding in the cortex (Webster, 1996). Viewing a field that flickers in color along a single axis in color space produces a selective loss in sensitivity to the adapting axis (Krauskopf et al., 1982). This alters color appearance by reducing perceived contrast along the adapting axis, and by rotating perceived hue away from the adapting axis (Webster & Mollon, 1994). The pattern of these color changes is roughly consistent with sensitivity changes in mechanisms defined by different linear combinations of the cone signals, and thus in mechanisms that can be broadly tuned to many different directions in color space. By this account changes in perceived contrast result because adaptation reduces the response of the mechanisms, while changes in perceived hue occur because these response changes are selective and consequently alter the distribution of responses across the set of mechanisms.

However, a number of questions remains about the properties of the mechanisms implied by adaptation. First, it remains uncertain whether the selectivity of the adaptation for any color direction reflects the presence of multiple mechanisms each tuned to a different direction or a small number of mechanisms that can interact to alter their tuning (Krauskopf et al., 1986; Atick et al., 1993; Zaidi & Shapiro, 1993; Lennie, 1999; Webster & Mollon, 1994). Second, there is evidence from both physiology and psychophysics pointing to mechanisms that are narrowly tuned for color and thus combine the cone signals nonlinearly (Kiper et al., 1999; DeValois et al., 2000b; Webster & Wilson, 2000; Goda & Fujii, 2001; Clifford et al., 2003). Third, it is unclear whether changes in contrast and changes in hue can be accounted for by the same underlying response change. In the present study, we used simple variants of color contrast adaptation to explore each of these properties.

Model

To test the number and selectivity of the adapted mechanisms, we adapted to variations along two directions in color space instead of one. Specifically, observers adapted to interleaved random signals along the LM and S cardinal axes. If the sensitivity changes are comparable along the two axes, this would remove most of the hue

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shifts resulting from linear mechanisms, and thus might reveal more directly any residual hue shifts owing to (possibly additional) narrowband mechanisms. These hue shifts also constrain possible models of the number of color mechanisms. Fig. 1 shows the hue changes predicted by four different models following equal and independent adaptation to the LM and S axes. The models differ in the number of chromatic channels (two cardinal mechanisms or a continuous distribution), the form of the response changes (multiplicative or subtractive) which bracket the actual response changes and the chromatic selectivity of each mechanism (Webster & Mollon, 1994). For a linear mechanism, sensitivity varies as the cosine of the preferred color angle in the LM and S plane. We simulated more narrow tuning by raising the cosine response to a power greater than 1 (see DeValois et al., 2000a).

For multiplicative adaptation in only two channels, equal LM and S adaptation lead to a nonselective response change regardless of the chromatic bandwidth, and thus no residual hue shifts are predicted (Fig. 1a). If the two mechanisms instead show a subtractive response change, then this will have proportionately larger effect on the less sensitive channel, shifting intermediate hues *toward* the closer adapting axis (Fig. 1b). For multiple channels, multiplicative adaptation is again nonselective for linear mechanisms, but results in hue shifts *away* from the cardinal axes as the tuning narrows (Fig. 1c). Finally, the corresponding subtractive changes again predict weak shifts away from the LM and S axes even if the preadapt sensitivity is linear (Fig. 1d). Clearly, the specific hue changes will depend on specific assumptions in the models, yet the direction of the residual hue shifts is qualitatively different for the different models.

Materials and methods

Stimuli were presented on a SONY Multiscan 20se monitor. They consisted of 2-deg squares with narrow black borders, and were vertically separated by a 0.35-deg gap. Adapting stimuli were presented in the upper field and consisted of a continuous stream of chromatic pulses (250 ms each) that varied randomly along either cardinal axis over a range of ± 40 or 80 in a scaled version of the LM and S equiluminant plane (Webster & Mollon, 1994). The mean luminance (20 cd/m^2) and chromaticity (equal to illuminant C) remained the same in both the upper and lower fields and the surround. We have found previously that this adaptation does not alter the mean perceived color of the test field (Webster & Mollon, 1994; Webster & Wilson, 2000).

While fixating between the fields, observers first adapted for 5 min. Test stimuli were then presented for 500 ms in the adapting field interleaved with 6 s readaptation intervals. Observers matched the color appearance of the test by adjusting both hue and contrast of a matching stimulus presented simultaneously with the test in the lower field. This procedure was repeated for 16 test stimuli spanning the hue circle in 22.5-deg steps. In experiment 1, observers adapted to stimuli of contrast 80 along the L-M (80-0) or S-LM (0-80) cardinal axis or both axes (80-80) and matched tests of contrast 80. In experiment 2, observers adapted to stimuli modu-
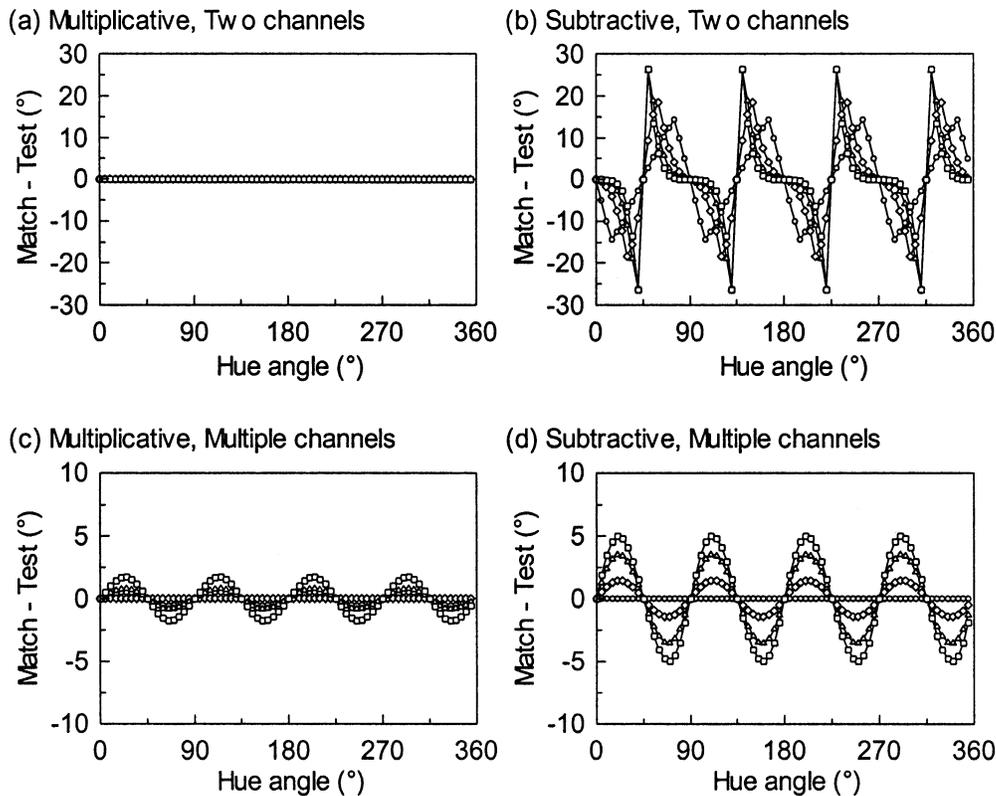

Fig. 1. Hue changes predicted by four different models. (a) Multiplicative adaptation in two cardinal channels. (b) Subtractive adaptation in two cardinal channels. (c) Multiplicative adaptation in multiple channels. (d) Subtractive adaptation in multiple channels. Contrast losses of 75% for both adapting axes were simulated in multiplicative adaptation and 25% for subtractive adaptation. Circle, diamond, triangle, and square show predictions for cosine tuning functions raised to exponents of 1 (linear), 2, 3, and 4, respectively.

lating over a contrast of ±40 along either the L-M (40-0) or S-LM (0-40) cardinal axis and then again matched tests with a contrast of 80. Results reported are the mean of two settings for each adapt and test condition.

Results

Fig. 2a compares the hue changes for one observer (YM) following adaptation to the LM or S axes or both axes. In the LM (80-0) or S (0-80) conditions, sensitivity losses are largest along the adapted axis and hue is biased toward the orthogonal axis, consistent with previous studies. These hue biases are shown in Fig. 2b by plotting the difference between the match and test angles. For joint adaptation (80-80), sensitivity instead decreased more uniformly. The hue changes are much smaller compared to single-axis adaptation, but still appear systematic. To characterize them, we calculated the Fourier transform of the hue shifts (Krauskopf et al., 1986). The amplitude spectra are peaked at 2 cycles/360 deg following single-axis adaptation, consistent with hue shifts away from the adapting axis. Alternatively, joint adaptation shows a stronger peak at 4 cycles/360 deg, suggesting that hue shifts relative to both adapting axes. As shown in the right panel of

Fig. 2c, the phase of this component was close to 0 deg, indicating that the shifts were away from each cardinal axis and toward diagonal axes. Results were similar for two further observers (Fig. 3), even though the magnitudes of the contrast changes were very different. The pattern was also confirmed for a second condition in which 500-ms achromatic gaps were interleaved with each adapting pulse, in order to more clearly separate the signals along the two axes. Once again the frequency analysis shows that perceived hue shifted away from each cardinal axis and toward the two diagonal axes (Figs. 2b & 2c). Thus, the residual hue shifts follow the predictions for multiple and possibly more narrowly tuned mechanisms.

In the next experiment, we tested whether the magnitude of the hue shifts could be predicted from the magnitude of the contrast changes. The two appear closely coupled in the case of high contrast adaptation and low contrast tests (Webster & Mollon, 1994). We therefore instead tested for dissociations in the converse case of higher contrast tests, where adaptation has little affect on perceived contrast (Webster & Mollon, 1994). Fig. 4 shows the results for three observers following adaptation to the LM (a) or S (b) axis. Each subject shows small hue shifts away from the adapting axis. We used these to predict the corresponding changes in perceived contrast, by finding the relative sensitivity loss along
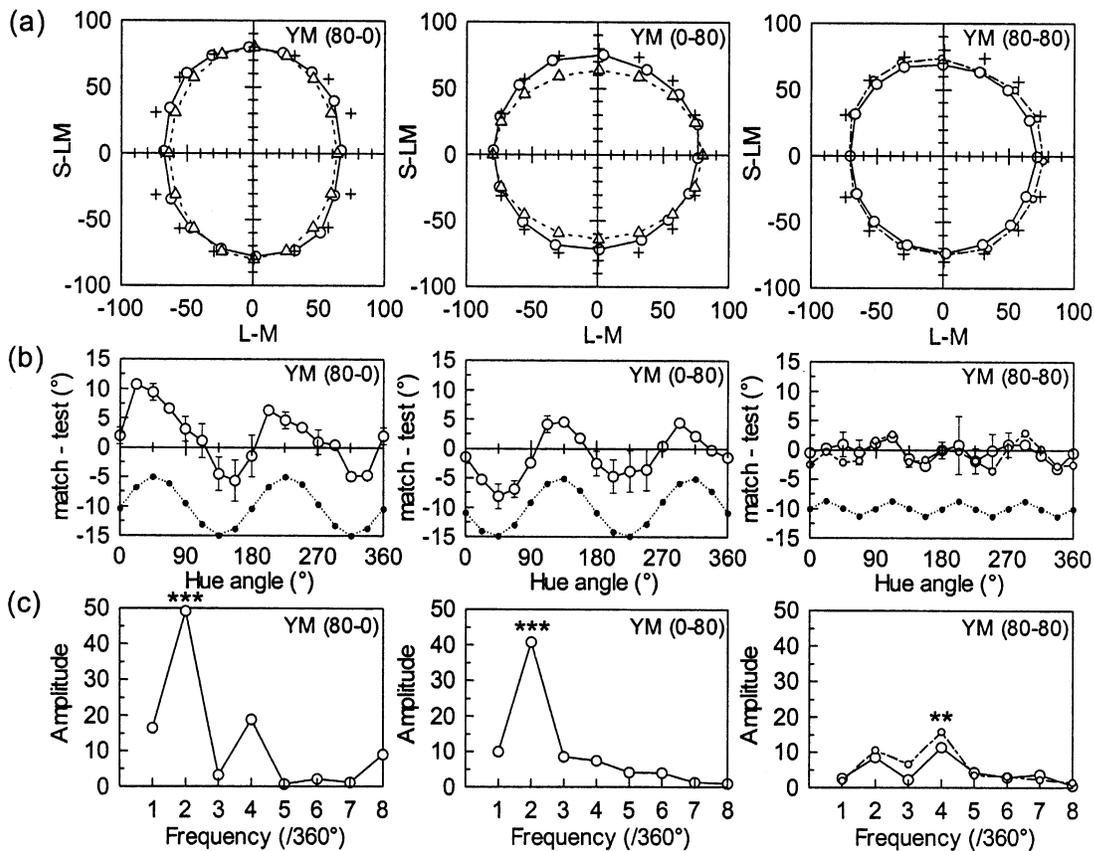

Fig. 2. (a) Results of experiment 1 (80-0, 0-80, and 80-80 adapting condition, 80 contrast test) for observer YM shown by open circles connected by solid lines on threshold-scaled cone-opponent spaces. Crosses indicate the coordinates of test stimuli. Triangles with dashed lines show the predicted contrast from hue shifts (see Fig. 4). (b) Differences of angles between matched hue and test hue as a function of the hue angle. Error bars are ±1 standard deviation. Small solid circle/dotted line indicates the best-fitting sine waves. The predictions are shifted down (to −10) to aid viewing. (c) Amplitude spectra of the hue shifts. Small circles connected by dash-dotted lines (right panels) indicate the results of 80-80 adapting condition with added white gaps (see text). Asterisks indicate significant coefficients (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$).
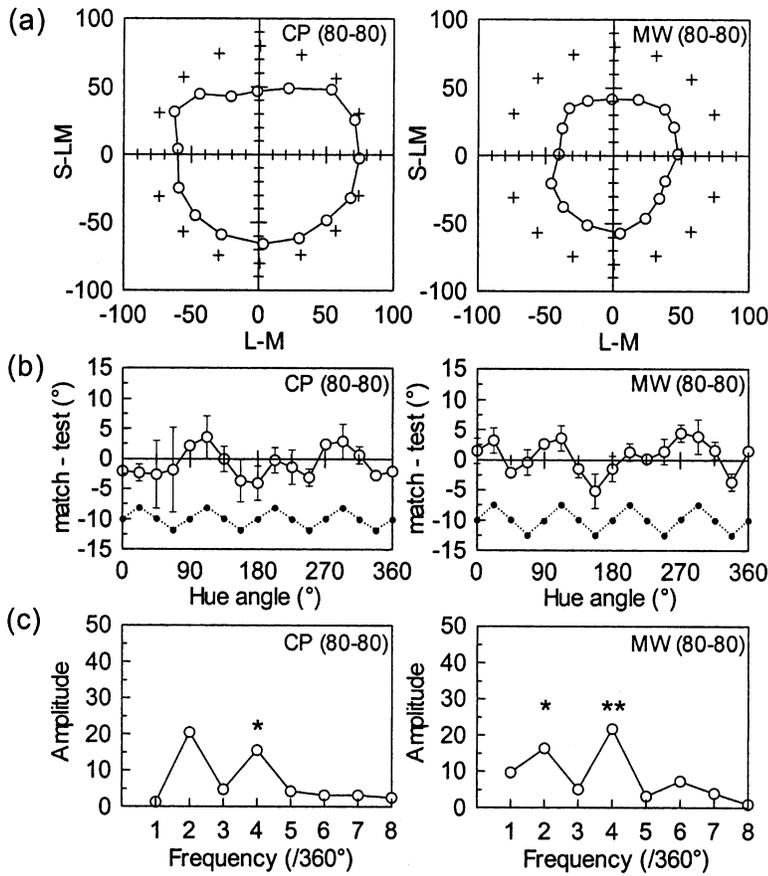
Fig. 3. Results of 80-80 adapting condition for observer MW and CP shown by open circles on threshold-scaled cone-opponent spaces (a). (b) Differences of angles between matched hue and test hue. Small solid circle/dotted line indicates the best-fitting sine waves (shifted to -10). (c) Amplitude spectra of the hue shifts.
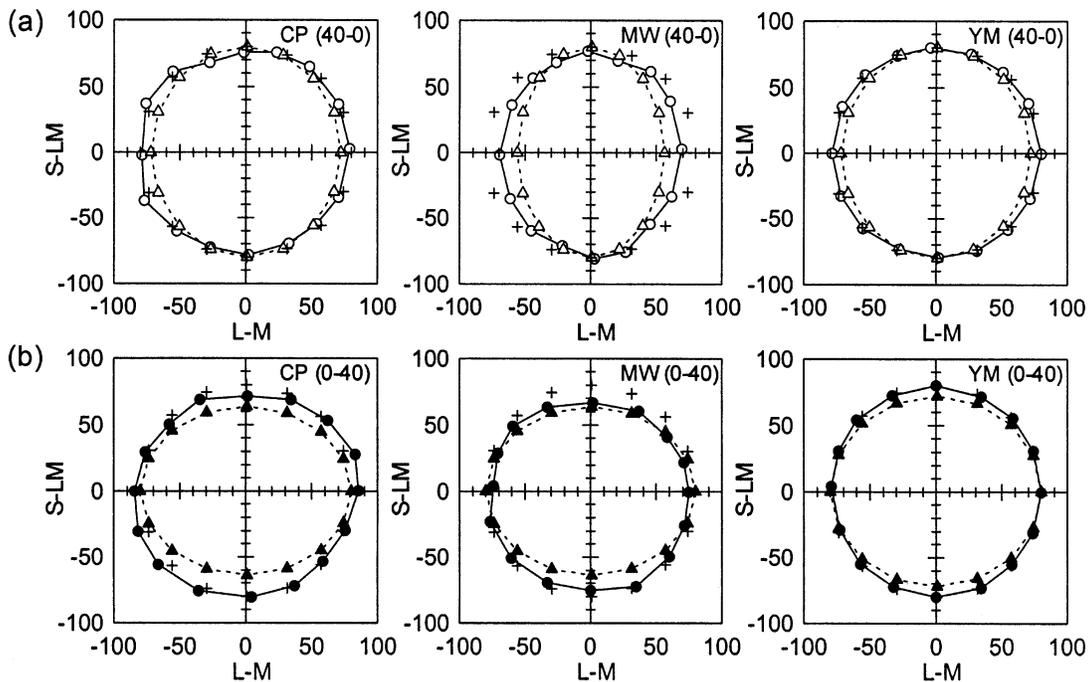

Fig. 4. Results of experiment 2 (40-0, 0-40 adapting condition, 80 contrast test) for observer CP, MW, and YM. Open circles (upper) are the results of 40-0 adaptation and solid circles (lower) are 0-40 adaptation. Triangles with dashed lines show the contrasts predicted by the hue shifts.

the adapting axis that best fit the hue changes. In all cases these fits predict more elliptical matching contours than were observed. That is, the hue changes imply a larger and more selective change in perceived contrast than the contrast matches indicate. This was further confirmed by similar analyses of the matches for single-axis adaptation in the preceding experiment (Fig. 2a). Therefore, under these conditions the contrast and hue changes do not appear to be carried by a common underlying signal.

Discussion

The representation of color is thought to undergo major transformations between the geniculate and cortex, though the number and nature of these changes are still poorly defined (Lennie, 1999; Gegenfurtner, 2003). Our results provide further hints about this organization and point to some of the possible "higher-order" properties of these higher-order mechanisms. The hue shifts we found for joint adaptation are consistent with more than two adaptable mechanisms within the equiluminant plane. The selectivity of single-axis adaptation does not necessarily require multiple mechanisms because similar predictions can be made by assuming decorrelating interactions between only two channels. However, the joint-axis adaptation we tested already leaves the two cardinal axes uncorrelated, and thus the residual hue shifts are not readily predicted by simple decorrelation. Our results are also consistent with the narrower chromatic tuning suggested by many recent studies, since the adaptation is able to selectively adjust to higher-order variations in the stimulus. However, as Fig. 1 showed, such results are not conclusive because they might also be accounted for by how adaptation alters the contrast response function. Finally, for the high-contrast test conditions we examined, changes in perceived hue occurred without corresponding changes in perceived contrast. Such results suggest that hue and contrast are not carried by a common underlying signal, and could possibly arise if contrast along a single color direction is also encoded by multiple mechanisms coding different contrast ranges (Webster & Wilson, 2000). This organization has also been suggested from the limited dynamic range for contrast in cortical cells (Albrecht & Hamilton, 1982). An alternative possibility is that hue and contrast might be carried by different subsets of channels with different properties.

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