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Chromatic induction from S-cone patterns

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Abstract

Chromatic induction from patterned backgrounds depends on the spatial as well as the chromatic aspects of the background light. Color appearance with patterned and uniform backgrounds was compared using chromaticities distinguished by only the S cones; all backgrounds were equivalent to equal-energy white in terms of L-cone and M-cone stimulation. The measurements showed larger shifts in color appearance with a patterned chromatic background than with a uniform background at any chromaticity within the pattern. The measurements also showed that inducing light within different spatial regions could cause opposite shifts in color appearance: inducing light near a test field shifted appearance toward the inducing chromaticity (assimilation), while the same light some distance from the test shifted appearance away from the inducing chromaticity (simultaneous contrast). The shifts in color appearance were accounted for by a neural receptive field with S-cone spatial antagonism.

Keywords: Chromatic induction; Chromatic contrast; Chromatic assimilation; Receptive-field organization; Short-wavelength-sensitive (S) cones

1. Introduction

Chromatic induction is the influence of one light on the color appearance of another light. Traditionally, chromatic induction has been studied with relatively large uniform inducing backgrounds (Chichilnisky & Wandell, 1995; Shepherd, 1999; Shevell, 1982; Walraven, 1973; Wuerger, 1996) but studies that use more complex scenes show that induction depends also on the chromatic variation within the background (e.g., Barnes, Wei, & Shevell, 1999; Brown & MacLeod, 1997; Jenness & Shevell, 1995). An implication of this work is that color appearance in complex scenes cannot be fully understood by applying principles of induction developed with uniform backgrounds (e.g., Jameson & Hurvich, 1961; Ware & Cowan, 1982). A complete explanation of induction must take account of the spatial as well as the chromatic structure of the scene.

This study examines patterned chromatic backgrounds composed of concentric inducing circles that differ from each other in only S-cone stimulation. These patterned backgrounds can induce color shifts that are larger than the shifts from a uniform background at *any* chromaticity within the pattern. Compare, for example, the difference in appearance between the test rings in Fig. 1a and b to the difference between the test rings in Fig. 1c and d. All four test rings are physically identical. The neural substrate that mediates a larger difference with patterned backgrounds (Fig. 1c vs Fig. 1d) than with uniform backgrounds (Fig. 1a vs Fig. 1b) is the focus of this paper.

Previous work shows that optical factors cannot explain the larger induced color shifts from patterned than uniform backgrounds (Monnier & Shevell, 2003). The optics of the eye render a slightly blurred image on the retina but theory and calculation show that neither wavelength-independent spread light nor wavelength-dependent chromatic aberration offers an explanation. Moreover, introducing an achromatizing lens and 2mm artificial pupil does not diminish the color shifts from patterns. The experiments and analyses here demonstrate that cortical receptive-field organization can account for the large color shifts induced by S-cone patterns.

2. Methods

2.1. Apparatus and calibration

Stimuli were displayed on a 17″ calibrated color monitor (NEC FE750, 832 by 624 pixels, 75Hz

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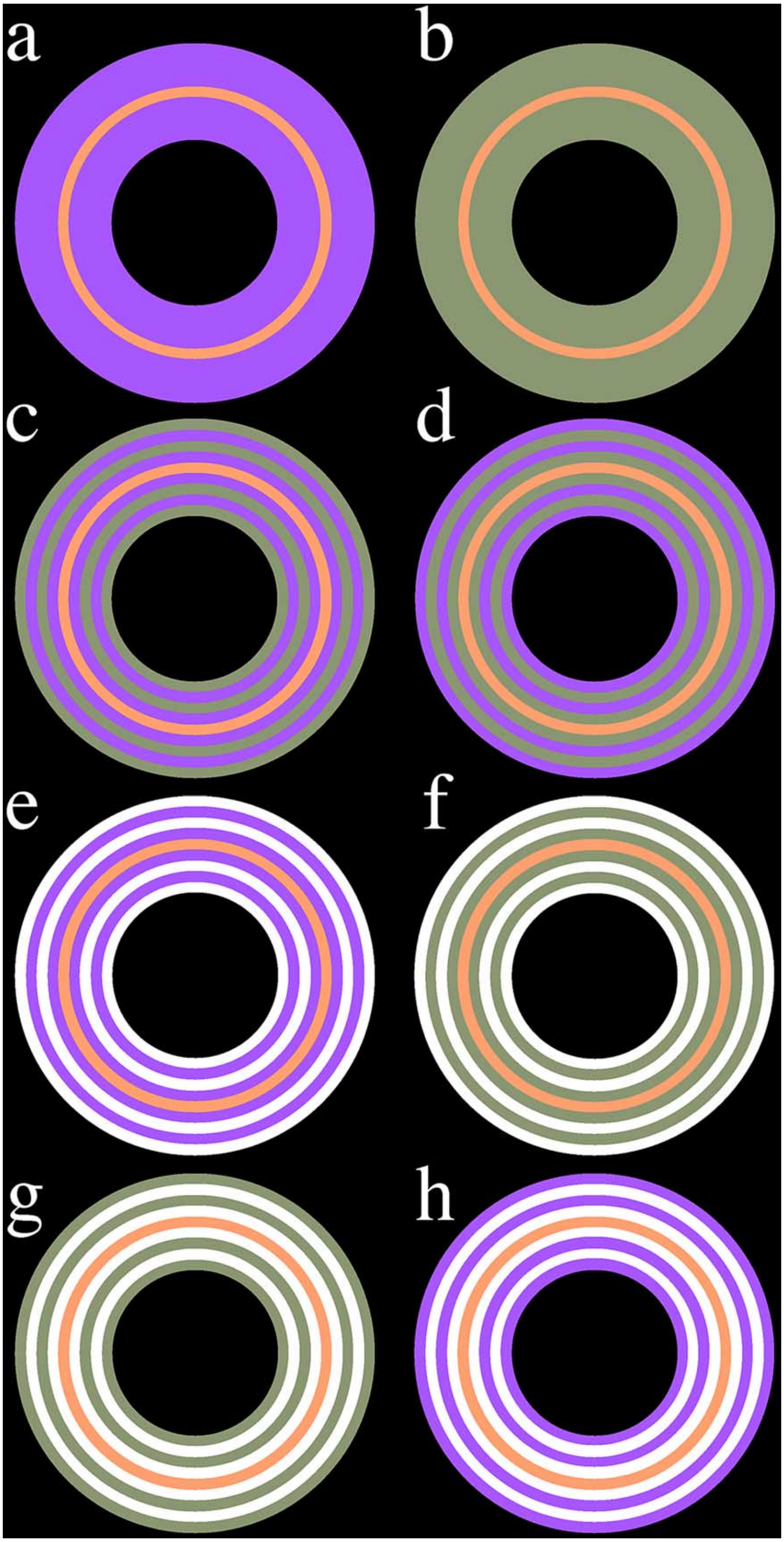

Fig. 1. Patterns composed of concentric circles alternating between two chromaticities (c and d) cause larger shifts in color appearance than uniform backgrounds (a and b) at either component chromaticity in the pattern. (e–h) Backgrounds with chromatic light removed from a uniform chromatic field to form patterns with chromatic light and white (see text).

non-interlaced) controlled by a Macintosh G4 computer with a Radius Thunder 30/1600 auxiliary video board (10-bits per gun). The spectral power distributions of the R, G, and B guns were measured using an Optronics 754 spectroradiometer. Gamma correction of each gun was provided by a look-up table based on measurements of the gun's output luminance at each of the 1024 (2^{10}) digital input values. Absolute luminance and the stability of the calibration were measured frequently with a Minolta LS-100 photometer.

Stimuli were specified in a cone-based chromaticity space (MacLeod & Boynton, 1979). In this space, the x-axis represents relative L- to M-cone stimulation [$l = \mathrm{L}/(\mathrm{L+M})$], and the y-axis represents relative S-cone stimulation [$s = \mathrm{S}/(\mathrm{L+M})$]. The unit of s is arbitrary and normalized here to 1.0 for equal-energy white (EEW).

2.2. Stimuli and procedure

Color appearance was measured by asymmetric color matching. A comparison pattern and a test pattern were presented side by side at a viewing distance of 1 meter (Fig. 2a). The comparison background consisted of a uniform achromatic field approximately metameric to EEW (l, s, Y of 0.66, 0.98, 15 cd/m^2). The test background was either uniform in chromaticity (Fig. 1a and b) or composed of concentric circles alternating between two chromaticities (e.g., Fig. 1c and d). The inducing chromaticities were on a tritanopic line in color space so they differed in only S-cone stimulation: l, s, Y of 0.66, 2.00, 15 cd/m^2 appeared 'purple' on a dark background; l, s, Y of 0.66, 0.16, 15 cd/m^2 appeared 'lime' on a dark background (squares, Fig. 2b). Induction was measured for three test-ring chromaticities (crosses, Fig. 2b), which differed in only l chromaticity (l, s, Y values 0.62, 0.98, 20 cd/m^2; 0.66, 0.98, 20 cd/m^2; and 0.70, 0.98, 20 cd/m^2). The width of the comparison and test rings as well as the concentric inducing circles was about 9 min of visual angle, resulting in a spatial frequency of 3.3 cycles/deg. The comparison and test fields were 1.8 and 4.5 deg in inner- and outer-diameter, respectively, and were separated by 6.4 deg center to center. The stimuli were presented on an otherwise dark background in a dark room.

A session began with two minutes of dark adaptation followed by five matches at each of the three test chromaticities, for a total of 15 matches per session. Observers were instructed to adjust the hue, saturation, and brightness of the comparison ring to match the appearance of the test ring, using buttons on a Gravis gamepad sensed by the computer.The computer randomly selected the comparison-ring's starting chromaticity and luminance. The matching procedure was self-paced and fixation was not enforced. Each condition was repeated three times, on different days. The three test chromaticities were ordered randomly within a session. A mean matching chromaticity was calculated for the replications within a day. Graphs show the average of the three mean matches, and error bars are standard errors of the mean computed from the three daily means.

Isoluminance was determined for each observer using the method of minimum motion (Anstis & Cavanagh, 1983). Each observer, therefore, was presented with slightly different chromaticities, based on his or her isoluminant setting for each of the R, G, and B guns. S-cone isolation was confirmed using the minimally-distinct-border technique (Tansley & Boynton, 1978).

2.3. Observers

Three observers took part in the study. All had normal or corrected acuity (20/20) and normal color vision as assessed with the Ishihara plates and Rayleigh

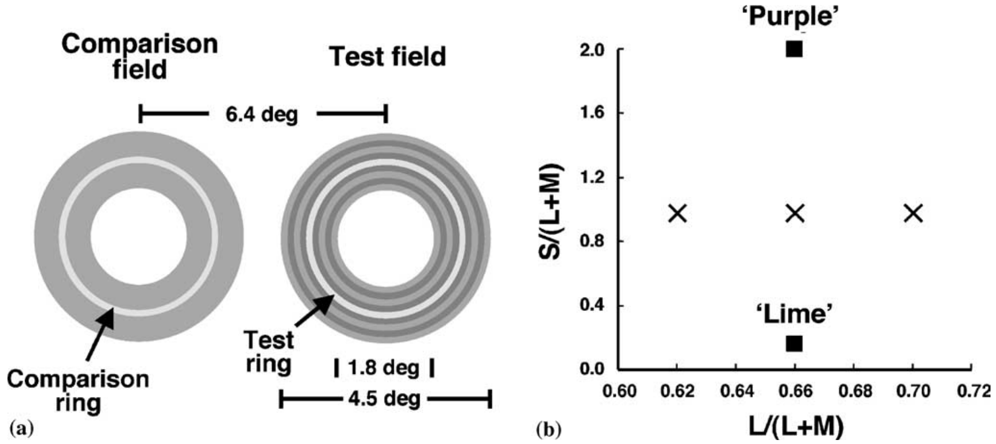

Fig. 2. (a) The experimental stimulus was composed of a uniform EEW comparison background and a test background. The observer adjusted the comparison ring to match the test ring. (b) Inducing chromaticities (squares) and test-ring chromaticities (crosses) plotted in a modified MacLeod and Boynton (1979) chromaticity space.

matches. Observers completed practice sessions to familiarize themselves with the task before data collection was initiated. Observers AZ and MC were naïve as to the purpose of the study. Observer PM is an author. Each subject gave informed consent. This study was approved by an Institutional Review Board at the University of Chicago.

3. Results

3.1. Chromatic patterns

Chromatic induction was measured with uniform purple and lime backgrounds (Fig. 1a and b) and with patterned backgrounds composed of concentric circles alternating between purple and lime (Fig. 1c and d). Matching chromaticities are shown in Fig. 3 for one observer (measurements for two other observers are in Monnier & Shevell, 2003). Isomeric matches (circles), for which both the comparison and test backgrounds were identical uniform fields, fell close to the physical test ring chromaticities (crosses). The color appearance of the test ring shifted modestly when presented within the uniform purple or uniform lime background (open squares and diamonds, respectively). The uniform purple background shifted the matches to lower *s*, compared to the shifts from the uniform lime background (squares below diamonds).

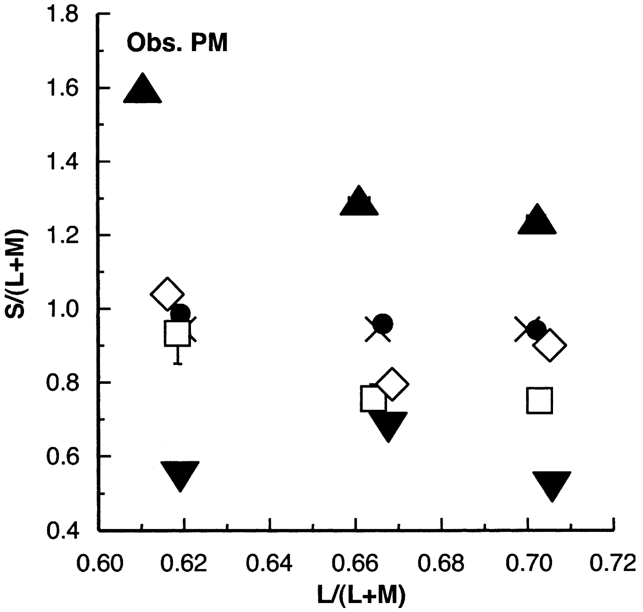

Fig. 3. Matches with purple and lime uniform and patterned backgrounds: test-ring chromaticities (Xs), isomeric matches (circles), uniform purple and uniform lime backgrounds as in Fig. 1a and b (squares and diamonds, respectively), the purple and lime pattern as in Fig. 1c (up-pointing triangles), and the lime and purple pattern as in Fig. 1d (down-pointing triangles).

The patterned backgrounds composed of purple and lime concentric circles (Fig. 1c and d) caused much larger shifts in color appearance, as reported previously (Monnier & Shevell, 2003). The pattern composed of purple/lime circles, in which the test ring was flanked by purple inducing circles (Fig. 1c), shifted matches to higher levels of *s* (filled up-pointing triangles), compared to either a uniform purple or uniform lime background (squares or diamonds). On the other hand, the lime/purple pattern, in which the test ring was flanked by lime circles (Fig. 1d), shifted color appearance to a lower *s* than with either uniform background (filled down-pointing triangles). The patterned backgrounds caused larger shifts in color appearance than either uniform background at the chromaticities in the pattern.

The shifts in color appearance were predominantly in the *s* direction, even though observers were free to adjust the matching field in hue and saturation. This is not surprising because all patterned and uniform backgrounds were identical to the achromatic comparison background with respect to L- and M-cone stimulation.

Note that the large shifts caused by the patterned backgrounds cannot be explained by local physical contrast between the test ring and the inducing background. If local contrast were the primary determinant of color appearance, backgrounds with the same local physical contrast (Fig. 1a and c, or Fig. 1b and d) would cause similar shifts in appearance. The measurements show this is not the case.

Color appearance in complex scenes is sometimes accounted for by the space-average chromaticity of the scene (Fairchild & Lennie, 1992; Valberg & Lange-Malecki, 1990) but the space-average of the patterned backgrounds cannot account for the color shifts observed here. The difference in space-average chromaticity for the two patterned backgrounds (Fig. 1c and d) is much smaller than the difference between the uniform purple and uniform lime backgrounds. Thus, induction from a space-average chromaticity predicts a larger difference in color appearance between the two uniform backgrounds than between the two patterned backgrounds, which is contrary to the measurements.

3.2. Patterns with white

Patterns with 'white' circles assessed specific contributions from the purple or lime inducing light within the patterned backgrounds. New patterns were constructed in which one of the inducing chromaticities (either purple or lime) was replaced with equal-energy white (l, s, Y of 0.66, 0.98, 15 cd/m^2). These patterns, therefore, were concentric inducing circles alternating between purple and white, or between lime and white (Fig. 1e–h). Recall that the comparison background always was white, so purple and white patterns (Fig. 1e and h) or lime and white patterns (Fig. 1f and g) were more similar to the comparison background than a uniform purple or uniform lime background. One might expect, therefore, that these patterns would cause weaker shifts than the uniform purple or uniform lime fields. If spatial structure, however, is a critical aspect of chromatic induction, then the purple and white or lime and white patterns may induce larger shifts than either a uniform purple or uniform lime background.

Matches with patterns in which chromatic light (purple or lime) was adjacent to the test ring but alternating inducing circles were EEW (Fig. 1e and f) revealed color shifts as large or larger than with a uniform purple or lime background (Fig. 4). Replacing chromatic light with EEW light never reduced chromatic induction and usually increased it (compare left-pointing and right-pointing triangles to open symbols). Further, compared to the isomeric matches (circles), the direction of the shifts with the purple and white pattern (left-pointing triangles) and with the lime and white pattern (right-pointing triangles) always was *toward* the adjacent chromaticity (chromatic assimilation).

Chromatic induction was also measured with patterns in which chromatic light adjacent to the test ring was replaced with EEW (Fig. 1g and h). Again, these

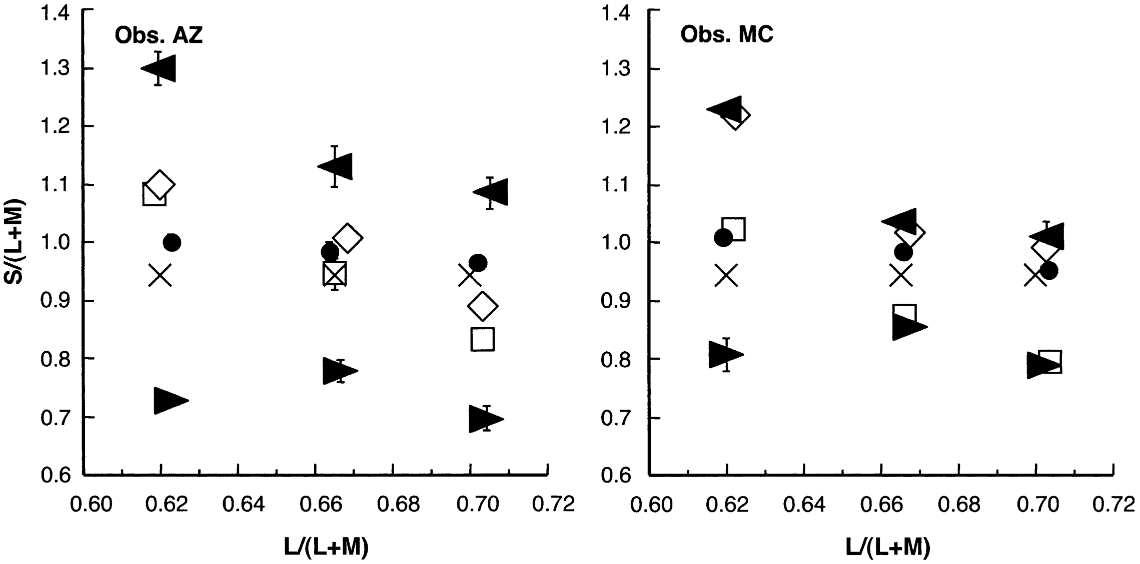

Fig. 4. Matches with patterns having chromatic circles adjacent to the test, and alternating with white concentric circles (Fig. 1e and f). Crosses, circles, squares and diamonds are as in Fig. 3. Left-pointing and right-pointing triangles are matches for the purple/white (Fig. 1e) and lime/white (Fig. 1f) patterns, respectively.

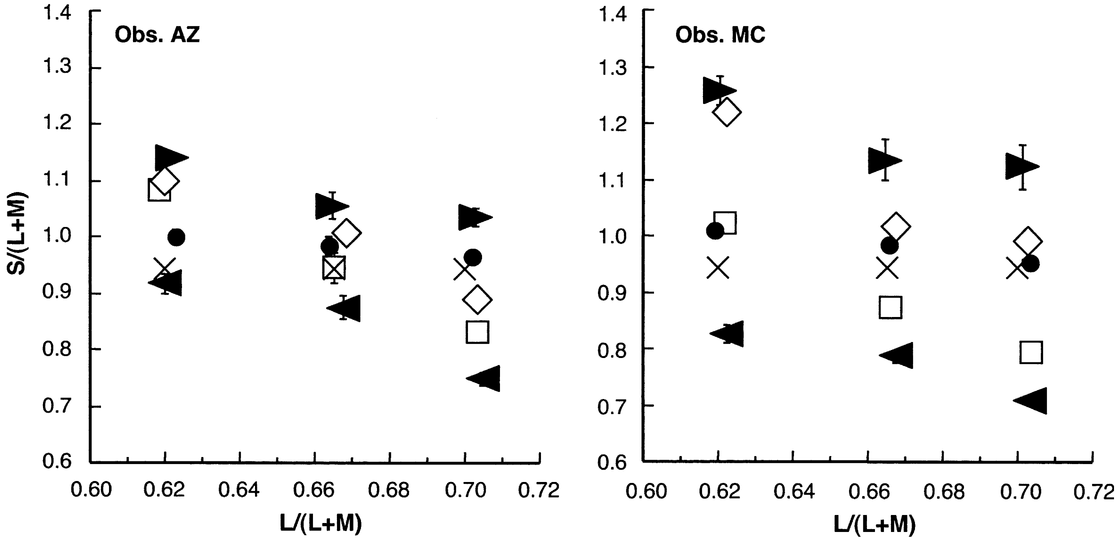

Fig. 5. Matches with patterns having chromatic circles not adjacent to the test, and alternating with white concentric circles (Fig. 1g and h). Crosses, squares and diamonds are replotted from Fig. 4. The right-pointing and left-pointing triangles are the matches for the white/lime (Fig. 1g) and white/purple (Fig. 1h) patterns, respectively.

patterns with EEW generally caused larger shifts than uniform purple or uniform lime backgrounds (Fig. 5; compare left-pointing and right-pointing triangles to open symbols). Now, however, with chromatic inducing light *not* adjacent to the test ring, the shifts were in the direction of simultaneous contrast, *away* from the inducing chromaticity (that is, lower s settings with the white and purple pattern [left-pointing triangles] than with the white and lime pattern [right-pointing triangles]). The spatial location of the chromatic inducing light, therefore, critically determined whether the color shift was toward or away from the inducing chromaticity.

The large shifts observed with the patterned backgrounds composed of alternating purple and lime circles (Fig. 3) are consistent with simultaneous and cumulative shifts toward the adjacent chromaticity and away from the non-adjacent chromaticity. For example, purple/lime circles in Fig. 1c would cause a $+s$ shift toward purple and, in addition, a further $+s$ shift away from lime. This framework also can explain the weak shifts with the uniform backgrounds because the shifts from adjacent and more distant light of the same chromaticity tend to counteract each other (e.g., with the uniform purple background, a $+s$ shift from adjacent purple and a $-s$ shift from more remote light). This qualitative framework suggests center-surround receptive field organization, which is considered quantitatively below.

4. Discussion

The experiments here demonstrate the importance of spatial structure on chromatic induction. Uniform chromatic backgrounds produced weak shifts in color appearance compared to the shifts caused by patterned backgrounds. The larger shifts from patterns could not be explained by local contrast between the test ring and contiguous inducing light, or by induction from an equivalent space-average chromaticity. Wavelength-independent spread light and wavelength-dependent chromatic aberration (Marimont & Wandell, 1994) have been ruled out as explanations (Monnier & Shevell, 2003). The measurements with the white inducing rings suggest that contrast and assimilation may act simultaneously, either synergistically with the purple/green patterns or antagonistically with a uniform background. We propose a cortical receptive-field model, which implicitly has these properties and which quantitatively accounts for the measured color shifts.

A neural receptive field with S-cone spatial antagonism is consistent with the color shifts. Conceptually, the response from this type of receptive field increases with S-cone stimulation near the test ring (accounting for assimilation to the adjacent inducing circles) and decreases with S-cone stimulation some distance away from the test (accounting for simultaneous contrast from the non-adjacent circles). With appropriate spatial-frequency tuning, this receptive field responds more extremely to a patterned S-cone background than to a uniform background at either chromaticity in the pattern, because with a uniform background center excitation and surround inhibition tend to cancel each other. Neurons with S-cone spatial antagonism have not been found in the retina (Dacey, 2000) but recent reports indicate they exist in visual cortex (Conway, 2001; Solomon, Peirce, Krauskopf, & Lennie, 2003).

The measurements here were compared to the response from a receptive field with a +S center and −S surround. The computational model also included retinal blurring due to spread light, ranging from minimal to extreme (modeled by a Gaussian with up to 10-min width at half height). This receptive-field model depends on only S-cone stimulation and therefore predicts shifts in only s but this is sufficient here because the observed shifts were along the s direction.

Predicted color shifts were determined by first convolving the comparison and test patterns with a Gaussian to simulate retinal blurring. The 'blurred' images were then convolved with an S-cone center-surround filter (difference of Gaussians, DOG). A predicted color shift was determined from the difference between the resulting responses to the test pattern and comparison pattern.

The fitting procedure determined the spatial tuning of the receptive field that minimized the difference between the empirical s matches and the responses from the receptive field. The +S center and −S surround were modeled as a DOG with the standard deviation of the surround twice that of the center. Center and surround were balanced in volume, which constrained the response to zero for a uniform field (but not, of course, for a test ring within a uniform surround). The only free parameter in the model was the width of the central Gaussian. For each observer, the measurements from all eight background conditions (Fig. 1) were fit simultaneously.

The fit of the +S/−S receptive-field model is compared to the measurements in Fig. 6. Each observed value, shown by a bar, is the difference between the s match for a particular background (as in Figs. 3–5) and the s setting for the isomeric match (s matches for the three test-ring chromaticities were averaged). Negative differences are shifts *away* from the chromatic inducing light closest to the test (simultaneous contrast); positive differences are shifts *toward* the chromatic inducing light closest to the test (assimilation). The smallest circles show predicted matches assuming no retinal blurring, and the largest circles are predictions assuming five times the typical light spread from pre-retinal factors (Westheimer, 1986). Other circles are predicted matches with

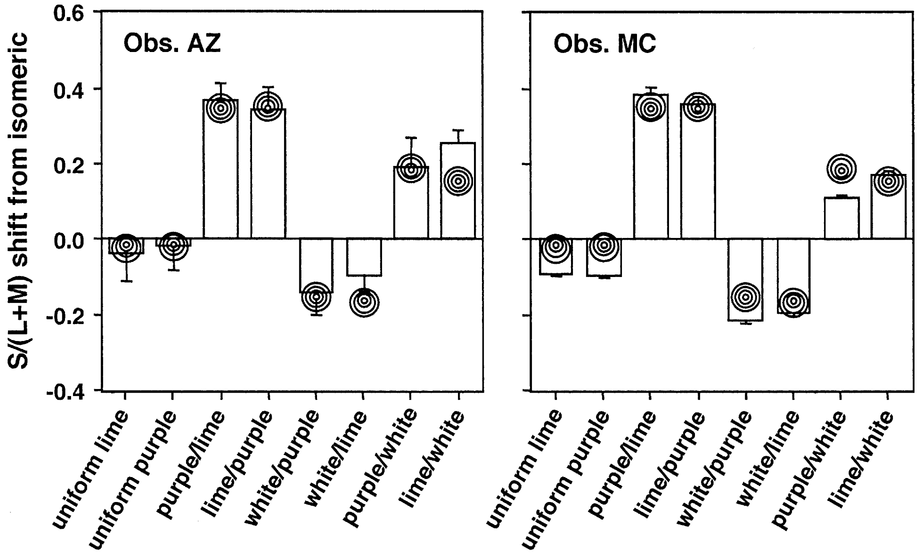

Fig. 6. Measurements are shown by bars as the difference between the match in each condition and the isomeric match, in the *s* chromatic direction. *s* matches for the three test-ring chromaticities were averaged. Negative (positive) values are shifts *away from* (*toward*) the chromaticity of the nearest chromatic inducing light. Small circles are predictions with no spread light (no retinal blurring); large circles are predictions with extremely high spread light (Gaussian with 10-min width at half height). Intermediate-size circles are predictions with more typical estimates of spread light (2-min or 4-min width at half height).

intermediate amounts of spread light (see figure caption). The +S/−S receptive-field model fits the measurements well, with virtually identical values for any spread-light assumption. This corroborates that spread light does not significantly contribute to the color shifts. The best-fitting spatial tuning of the +S/−S receptive field for every observer had peak sensitivity within a narrow range from 0.7–1.2 cpd, which is in good agreement with psychophysical estimates of spatial-frequency tuned mechanisms that mediate S-cone isolated vision (Humanski & Wilson, 1993).

In sum, these experiments demonstrate that color appearance depends critically on the spatial structure of the light in view. Simplified explanations that consider only local physical contrast or the space-average chromaticity of a background cannot explain color appearance in complex scenes. Neither optical factors nor known retinal neurons can explain color appearance with the patterns used here. We posit a cortical neuron with S-cone-specific spatial antagonism, which accounts for the measurements parsimoniously and has been reported in electrophysiological studies of visual cortex.

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