

# Large shifts in color appearance from patterned chromatic backgrounds

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**The perceived color of a light varies with the background on which it is seen. In the present study, patterned backgrounds composed of two different chromaticities caused larger shifts in perceived color than did a uniform background at either chromaticity within the pattern. Cortical receptive-field organization, but not optical factors or known retinal neurons, can account for the color shifts from patterned backgrounds.**

Human color perception depends on the neural representation of the spectral properties of light reaching the eye. While a single wavelength has a characteristic color when seen against a dark background, the same wavelength can appear a different color when part of a complete scene.

The four orange rings in Fig. 1a–d are physically identical, but appear different in color. Although background context is known to affect color appearance<sup>1,2</sup>, the large difference between Fig. 1a and b is not explained by color contrast from the immediate surround or by diminished spatial resolution due to optics of the eye or neural processes<sup>3,4</sup>. Each of these explanations implies a difference in appearance between a uniform ‘purple’ versus a uniform ‘lime’ background (Fig. 1c,d) at least as large as the difference between patterned backgrounds composed of alternating purple and lime circles (Fig. 1a,b). Laboratory measurements showed the opposite: a larger color difference between patterned than between uniform backgrounds at the chromaticities composing the patterns. We refer to this as ‘enhanced color shifts from patterns.’

How can a background of concentric circles, half purple and half lime, induce a larger color shift than either a purple or lime uniform field? Here we examined whether the cause was the optics of the eye or neural processes. The appearance of a test ring on a chromatic background was determined using an asymmetric matching technique in which an observer also viewed a separate comparison ring on its own achromatic (white) background. Stimuli were presented on a calibrated video display. The observer adjusted the comparison ring in hue, saturation and brightness to match the appearance of the test. The matching measurements are plotted in Fig. 2 along axes that represent light caught by the three types of cone photoreceptor, L, M and S.

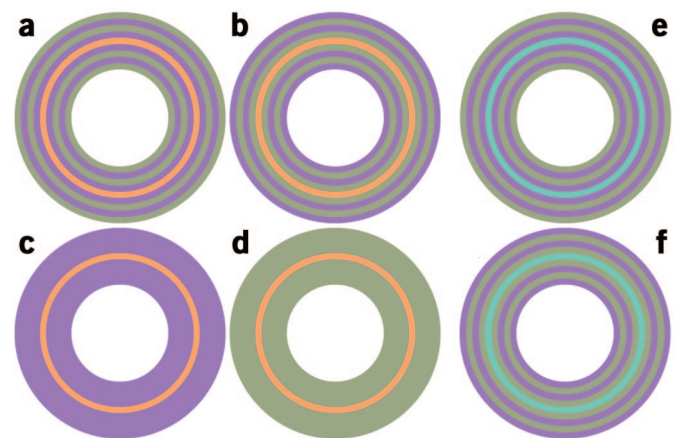
Three different chromaticities of test ring were used (Fig. 2, ×); one chromaticity is shown in Fig. 1a,b and another in Fig. 1e,f (printed figures approximate chromaticities). When the test ring was on a uniform ‘white’ background, an isomeric control, the matches (Fig. 2, ●) fell close to the true chromaticity of the rings (×s) as expected. A uniform lime or uniform purple background (squares) caused the test ring’s appearance to shift modestly, but patterned backgrounds (triangles) composed of

alternating lime and purple concentric circles at 3.3 c.p.d. caused far larger shifts.

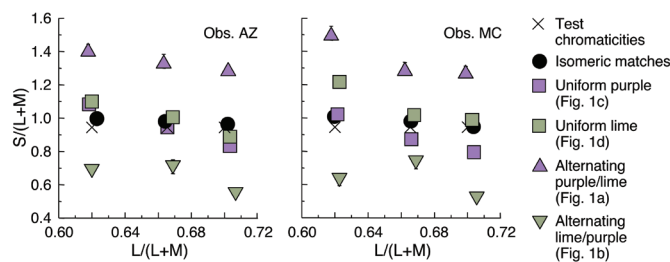
The lime and purple background chromaticities differed only in S-cone stimulation, with L and M fixed at the ratio that results from a spectral power distribution of all visible wavelengths at equal energy (equal-energy white). Thus, backgrounds composed of lime and purple concentric circles were patterns defined by only S-cone variation. With these chromaticities, the shifts in appearance caused by the patterned backgrounds were in only the S-cone direction (each set of points along a nearly vertical line in Fig. 2).

Two classes of optical factors that defocus the retinal image might mediate the induced color differences in Fig. 2: wavelength-independent spread light and wavelength-dependent chromatic aberration<sup>5</sup>. Wavelength-independent spread light was ruled out by the enhanced color shifts from patterns. Light spread into the test area from any background is simply the sum of spread light from each point within the background. The uniform purple and uniform lime backgrounds (Fig. 1c,d), therefore, established the extremes of light spread into the test area; the spread light from alternating purple and lime concentric circles (Fig. 1a,b) must be within these extremes. The enhanced color shifts from patterns were contrary to these magnitudes of spread light.

Theoretical and experimental results showed that the measurements could not be explained by chromatic aberration, which causes wavelength-dependent defocus. The retinal light distribution due to chromatic aberration, estimated using a well-known method<sup>5</sup>, would cause larger color shifts with the uniform lime and uniform purple back-



**Figure 1** Shifts in color appearance caused by nearby light. (a–d) A constant object (test ring in each of a–d) within a patterned background composed from two chromaticities (a,b) can appear outside the range of colors perceived with a uniform background at either chromaticity in the patterns (c,d). (e,f) Patterns as in a and b, but with a different test-ring chromaticity.

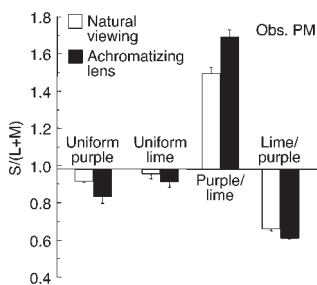


**Figure 2** Color matches to a test ring within a patterned or uniform chromatic background. The horizontal axis shows L-cone stimulation, whereas the vertical axis shows S-cone stimulation; both axes are normalized to the luminance of the ring (L+M). Each panel shows measurements for a different observer. Error bars are standard errors from measurements repeated on 3 days. The spatial frequency of the concentric circles in **Fig. 1a,b,e** and **f** was 3.3 c.p.d.; inner and outer diameters of the backgrounds were 1.8 and 4.5°, respectively. Stimuli were presented on an otherwise dark field. The three test-ring chromaticities, in MacLeod-Boynton<sup>13</sup> coordinates (*l,s*) and luminance (*Y*), were (0.62, 0.98, 20 cd/m<sup>2</sup>), (0.66, 0.98, 20 cd/m<sup>2</sup>) and (0.70, 0.98, 20 cd/m<sup>2</sup>). Purple, lime and white background chromaticities were, respectively, (0.66, 2.0, 15 cd/m<sup>2</sup>), (0.66, 0.16, 15 cd/m<sup>2</sup>) and (0.66, 0.98, 15 cd/m<sup>2</sup>). The unit of S/(L+M) is arbitrary and normalized here to 1.0 for equal-energy white. The experiments were approved by the University of Chicago Institutional Review Board. Informed consent was obtained from each observer.

grounds than with either the purple/lime or lime/purple concentric circles (7% more S-cone stimulation in the test area from uniform purple (**Fig. 1c**) than from purple/lime circles (**Fig. 1a**); 12% less S-cone stimulation from uniform lime (**Fig. 1d**) than from lime/purple circles (**Fig. 1b**)). This was inconsistent with the measurements from each observer at every test-ring chromaticity. Also, an independent analysis<sup>6</sup> using an alternative method<sup>7</sup> showed that chromatic aberration was not an important factor affecting color induction from a 4 c.p.d. grating. Experimentally, an achromatizing lens and 2 mm artificial pupil introduced immediately in front of the eye greatly reduced chromatic aberration<sup>8</sup> but did not reduce the enhanced color shifts from patterns (**Fig. 3**).

The arguments above reject optical factors that affect S-cone stimulation within the test area. Chromatic aberration also may disrupt perfect L- and M-cone uniformity within the background. The calculated estimate<sup>5</sup> of the L/(L+M) variation due to chromatic aberration was small: a range of 0.656–0.664 rather than constant 0.660. Moreover, measurements with a concentric-circle background at chromaticities with much larger L/(L+M) variation (0.70 and 0.62, with uniform S/(L+M) at the level for EEW) did not affect the matching results for S/(L+M): 1.01 with a uniform equal-energy white background (isomeric match) compared to 1.00 with alternating 0.70/0.62 (pink/aqua) concentric circles. In comparison, with purple/lime concentric circles tested in the same set of experimental runs, the S/(L+M) match was 1.35, which replicated results in **Fig. 2** (purple triangles). Thus, the slight background inhomogeneity

**Figure 3** Color-match settings for the S/(L+M) direction. L/(L+M) shifts were negligible. An achromatizing lens did not reduce the color shifts from patterns. Test-ring chromaticity (*l,s*, *Y*) was (0.66, 0.98, 20 cd/m<sup>2</sup>).



in L/(L+M) caused by chromatic aberration could not explain the enhanced color shifts from patterns.

The negligible S/(L+M) shift induced by 0.70/0.62 variation in L/(L+M) implies also that known retinal ganglion cells cannot explain these shifts in appearance. The shifts must depend on signals from S cones, which are carried at the retinal level by small bistratified ganglion cells<sup>9</sup>. Small bistratified cells are characterized by S-cone excitation and L- and M-cone inhibition, but for these backgrounds, only the S excitation altered the cell's response (with fixed excitation of L and M cones, the receptive field was spatially low-pass for S-cone stimulation). The uniform purple and lime backgrounds (**Fig. 1c,d**) were the most different from each other in overall S-cone stimulation, and thus resulted in the largest difference in response from the small bistratified cells, which was not in accord with the measurements. Recently, a second class of retinal ganglion cell carrying S-cone signals was found in macaque (D.M. Dacey, personal communication). These monostратified S-OFF cells have about twice the diameter of the bistratified S-ON neurons, but no S-cone spatial antagonism. A central neural combination of retinotopically corresponding S-ON and S-OFF cells could mediate the S-cone-specific spatial antagonism discussed below.

The enhanced color shifts from patterns were inconsistent also with a weighted sum of independent chromatic contrast from each point within the surround<sup>10</sup> and with theories of color constancy that rely on only an enumeration of chromaticities in a background<sup>11</sup>.

The color shifts from patterns can be explained by a neural receptive field with S-cone spatial antagonism (for example, +S center and -S surround). Modeling showed this type of receptive field accounted quantitatively for the measurements in **Fig. 2**. No known retinal neuron has +S/-S antagonism, so the model implicitly posits a class of neuron in visual cortex. Such neurons are plausible. V1 cells in alert macaque<sup>12</sup> show S-cone spatial antagonism in double-opponent cells, which also have L- and M-cone antagonism. In experiments here, L- and M-cone stimulation was constant so these cells would be modulated by only S-cone spatial antagonism.

In sum, color appearance depended strongly on the spatial structure of chromatic context. An important implication is that background context composed of a chromatic pattern, as in natural viewing, cannot be understood using explanations for color shifts from uniform backgrounds at each chromaticity in the pattern. We suggest the color shifts from patterns here are due to a cortical cell class with S-cone spatial antagonism.

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**COMPETING INTERESTS STATEMENT**

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