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Color shifts induced by S-cone patterns are mediated by a neural representation driven by multiple cone types

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Abstract

This study investigated chromatic induction from inhomogeneous background patterns. Previous work showed that a background pattern detected by only S cones induced strong color shifts in a nearby test area (Monnier & Shevell, 2003). In that work, the S-cone patterns were composed with constant L- and M-cone stimulation over the entire background; in terms of L and M cones, therefore, the background was uniform. S-cone stimulation was varied over space to produce S-cone-isolated background patterns. These S-cone patterns, however, established spatial structure (the pattern) at both the receptoral level (S-cone stimulation) and the postreceptoral level (S/(L+M)). Here, these two levels of pattern representation were unconfounded to determine whether color shifts induced by S-cone patterns were due to spatial structure within an S-cone-specific neural pathway versus a pathway that combines responses from S cones and other cone types (e.g. S/(L+M)). The results showed that the induced color shifts were mediated by signals within a pathway that combines responses from multiple cone types. These results are consistent with a $+s/-s$ spatially antagonistic neural receptive field, which is found in some neurons in V1 and V2.

Keywords: Chromatic induction, Chromatic assimilation, S cones, S-cone pathway

Introduction

The hue, saturation, and brightness of a light depend on the surrounding context in which the light is viewed. Chromatic induction from uniform backgrounds has been studied extensively (Chevreul, 1839; Jameson & Hurvich, 1961; Shevell, 2003), but induced color shifts caused by inhomogeneous background patterns have been investigated only recently. While induction from two-color patterns is described by Wright (1964) and his student Gindy (1963), the physiological mechanisms that mediate it were virtually ignored for 40 years.

Based on Gindy's work, Wright (1964) suggests "that scattered light in the eye, chromatic aberration of the optical system of the eye, simultaneous contrast, eye movements and local adaptation, all contribute to the effect (p. 49)." We now know that large hue shifts from chromatic patterns have a neural basis (Monnier & Shevell, 2003; Shevell & Monnier, 2005). Specifically, a background pattern detected by only the S cones can induce conspicuous color shifts. Further, the relation between the magnitude of color shift and the size of the chromatic elements within the background pattern is spatially bandpass, which implicates a neural receptive field with center-surround spatial antagonism.

Previous studies, however, fail to distinguish between a pattern represented within an S-cone-specific neural pathway *vs.* a pathway that combines responses from S cones and other cone types. In our earlier work, the background was uniform in L- and M-cone excitation (and thus also in luminance) in order to isolate the contribution from S cones. For L and M cones, the background was a uniform field, not a pattern. An S-cone isolated pattern at constant luminance establishes spatial structure at both the S-cone receptor level and at the S/(L+M) postreceptoral neural level. The present study determined whether the induction from S-cone patterns depends on a neural representation of only S-cone excitation *vs.* a representation that depends also on excitation of other cone types.

Materials and method

Apparatus

Stimuli were presented on a colorimetrically calibrated Sony 21-inch video display controlled by a Macintosh G4 computer with an auxiliary Radius video board (10 bits per gun). The resolution was 1360 × 1024 pixels, and the refresh rate was 75 Hz noninterlaced. The spectral energy distribution of each phosphor was measured with an Optronics 745 spectroradiometer, and absolute light levels were determined with a Minolta LS-100 photometer. The relative luminance of each phosphor at every digital gun value (0 to 1023)

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was measured with an International Light IL-1700 radiometer and stored in a look-up table.

Stimuli

Separate test and comparison fields were viewed simultaneously. The test field was composed of a circular test ring embedded within a background of concentric inducing circles (Fig. 1). Each ring had a width of 9 min, and so the background pattern had spatial frequency 3.3 cpd. Four inducing circles were on either side of the test ring which was judged in color. The central 1.8 deg was dark; the width of the complete test stimulus was 4.5 deg.

The comparison-field background was a circular achromatic disk metameric to equal-energy white (EEW) and of diameter 4.5 deg, also with a 1.8-deg dark center. A comparison ring, equal in size and relative position to the test ring, was adjusted by the observer in chromaticity and luminance to match the appearance of the test ring. Both the comparison and test fields were presented on a dark background.

The luminance of the test ring was fixed at 20 cd/m^2. Three different test-ring chromaticities were used. They were specified in MacLeod and Boynton (1979) l, s chromaticity space: (0.66, 1.0), which was nearly metameric to EEW; (0.62, 1.0), which appeared aqua; and (0.70, 1.0), which appeared pinkish. The unit of s was arbitrary and scaled here to 1.0 for EEW.

The luminance of the inducing circles was varied in different conditions in order to assess the neural representation that mediates the color shifts induced by the background patterns (see below). Inducing-circle chromaticity was either (0.66, 0.5), which appeared lime (labeled $-s$), or (0.66, 1.5), which appeared purplish (labeled $+s$).

Experimental design

The study included 13 background conditions. Ten patterned-background conditions are shown schematically in Fig. 2. The first column shows two conditions that replicated previous studies (e.g., Monnier & Shevell, 2003) with a background pattern at constant luminance. The patterns in these two conditions are represented at both the S-cone receptoral level (S, which is quantified by (S/(L+M) × luminance)) and at the level that includes responses from other cone types (S/(L+M)); the two patterns differ with respect to which chromaticity of inducing circle is contiguous with the test ring. The labeling convention here puts first (second) the adjacent (more distant) chromaticity, and so, for example, the top left pattern labeled "$+s/-s$ *BOTH*" is a background with purplish (lime) appearing background circles contiguous with (more distant from) the test ring. "*BOTH*" indicates this background pattern is represented at BOTH neural levels (S-cone values of 21 and 7, S/(L+M) values of 1.5 and 0.5; see numbers below each pattern in Fig. 2).

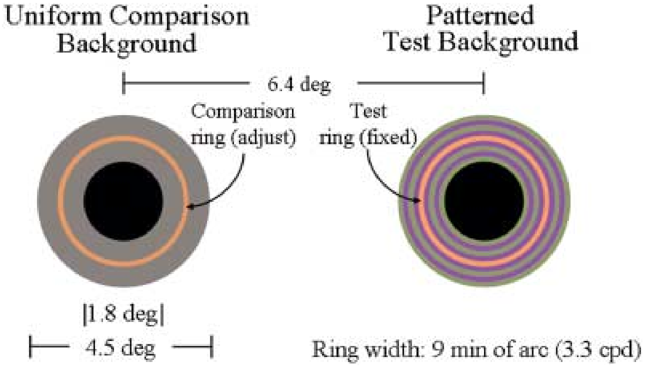

Fig. 1. Schematic of the stimuli used for asymmetric matching.

The next two columns show four conditions with the background pattern represented at only the S-cone-specific neural level. Note that S-cone stimulation *within* each background varies from 21 to 7, as in the first column; S/(L+M), however, is constant within each background pattern.

The last two columns are conditions with the pattern represented at only the S/(L+M) level. S-cone stimulation *within* each pattern is constant (at either 21 or 7), while the level of S/(L+M) in the concentric circles of each background alternates between 0.5 and 1.5.

Note that the four S-cone-only patterns (in columns 2 and 3) and also the four S/(L+M)-only patterns (in columns 4 and 5) have luminance variation within each background pattern. The experimental design, however, controls for the luminance variation within a background pattern by including identical luminance patterns in the S-cone-only and S/(L+M)-only conditions. Consider columns 2 and 5. If patterns in luminance mediated the color shifts, then the results from patterns in columns 2 and 5 would be the same (similarly, columns 3 and 4 have the same luminance patterns). Thus, luminance variation is not a confound. The color shifts induced by patterns in columns 2 and 3 (S-cone-only patterns) *vs.* shifts from patterns in columns 4 and 5 (S/(L+M)-only patterns) distinguish between a neural representation that is S-cone-specific *vs.* one that includes an influence from additional cone types.

Three further conditions were also tested. Two were baseline conditions with a uniform background field at a chromaticity and luminance used within the patterns in column 1 (specifically, a uniform $+s$ and a uniform $-s$ background, both at 14 cd/m). In addition, a uniform EEW background identical to the comparison background was tested as an isomeric control. (Four additional conditions with patterned or uniform backgrounds were interleaved with the conditions described above. These four conditions are not discussed here.)

Procedure

The appearance of the test ring within the inducing circles was measured by asymmetric matching. Following 3 min of dark adaptation, the observer adjusted the hue, saturation, and luminance of the comparison ring to match the color appearance of the test. Adjustments were made *via* a multibutton game pad sensed by the computer. At the beginning of each trial, the comparison ring was assigned a random starting chromaticity and luminance.

One condition was run within each session. Five repeated measurements were taken within a session. Each condition was repeated in three separate sessions on different days. The order of sessions was randomized. Standard errors were calculated using the mean value for each condition from each of the three sessions.

Observers

Three observers participated in the study. Two were naive regarding the design and purpose of the experiments, and one was author

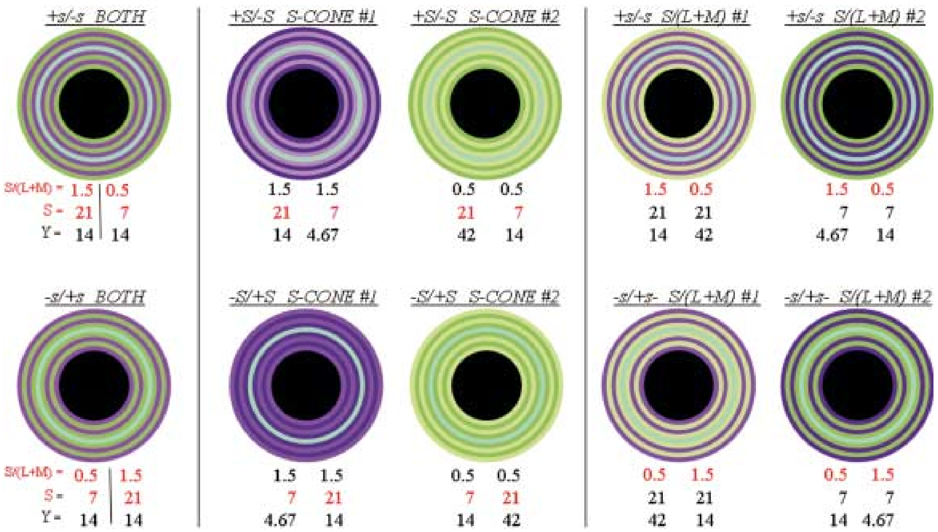

Fig. 2. Ten patterned background conditions used in the experiments. Patterns were represented (i) at both the S-cone-specific and the S/(L+M) levels (leftmost column), (ii) at only the S-cone-specific level (two center columns), or (iii) at only the S/(L+M) level (two rightmost columns). The numbers under each pattern quantify the magnitude of S/(L+M), which depends on responses from all three types of cone; S, which is S-cone-specific; and luminance Y (in cd/m^2). By definition, the value of S is luminance × S/(L+M). The two patterns within each column have the same pair of inducing-circle chromaticities but in opposite phase.

P.M. All observers had normal color vision as determined by Rayleigh matching. They signed an informed consent form before participating in the experiments, which were approved by an institutional review board at the University of Chicago.

Results

Observers matched the color appearance of the test-within-inducing-circles by adjusting the chromaticity and luminance of the comparison ring on its achromatic background (Fig. 1). The settings for the patterned isoluminant S-cone backgrounds (column 1, Fig. 2) replicated previous studies (two-color triangles in Fig. 3, which shows results for one observer). Measurements with the purple/lime ($+s/-s$) background are shown by purple triangles outlined in lime; results with the lime/purple ($-s/+s$) background are shown by lime triangles outlined in purple. Measurements are shown also for the uniform lime and uniform purple backgrounds (solid lime and purple triangles, respectively). Each column of measurements in Fig. 3 shows values for a different chromaticity of test ring, which is indicated by an X.

The color shifts induced by these patterned backgrounds were large and were almost entirely in the S/(L+M) direction. For a given test chromaticity, the vertical difference in Fig. 3 between the purple/lime and lime/purple conditions was taken as a measure of the magnitude of color shift resulting from the S-cone patterned backgrounds. This difference is called the *pattern-induced shift* (see Fig. 3). The color shifts induced by the same chromaticities in these patterns but in uniform fields were much smaller (see *uniform-induced shift*, Fig. 3). The uniform-induced shift is a useful baseline with which to compare the pattern-induced shift. A larger pattern-induced shift than uniform-induced shift reveals a neural representation of the pattern that increased

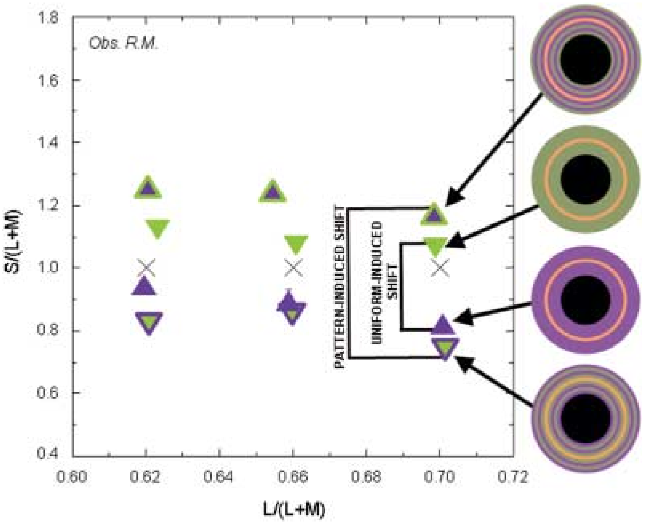

Fig. 3. Asymmetric matches to the appearance of the test ring within patterned backgrounds represented at both the S-cone-specific and the S/(L+M) levels (column 1, Fig. 2), for observer R.M. Measurements with the purple/lime (lime/purple) pattern are shown by purple triangles outlined in lime (lime triangles outlined in purple). Measurements with a uniform purple or lime background are shown by solid purple or lime triangles, respectively. Results are shown for three test-ring chromaticities (shown by Xs); measurements for a single test chromaticity are nearly aligned vertically as the color shifts primarily were in S/(L+M). For a given test chromaticity, the difference between the S/(L+M) settings with the two patterned backgrounds is defined as the *pattern-induced shift*; the difference between the S/(L+M) settings with the two uniform backgrounds is defined as the *uniform-induced shift* (see text). Error bars indicate the standard error of the mean, but nearly all are smaller than the plotted symbols.

the induced color change beyond that caused by adaptation to a single chromaticity.

Recall that the results in Fig. 3 are for patterned backgrounds represented at both the S-cone-specific and S/(L+M) levels. The neural representation mediating these induced color shifts can be assessed by eliminating from these patterns either the S/(L+M) spatial variation (columns 2 & 3, Fig. 2) or the S-cone spatial variation (columns 4 & 5, Fig. 2), and then comparing the pattern-induced shift from these backgrounds to the uniform-induced shift in Fig. 3.

This comparison is shown in Fig. 4 (averaged over the three test-ring chromaticity). Each panel shows results for a different observer. Consider the top panel (observer R.M.). The leftmost bar shows the uniform-induced shift, to which other conditions were compared. As discussed above, the isoluminant pattern, which was represented at both the S-cone-specific and S/(L+M) levels, had a pattern-induced shift (second bar from left) substantially larger than the uniform-induced shift. The next two bars show the pattern-induced shift with patterns represented at only the S-cone-specific level. These pattern-induced shifts were weaker than with the isoluminant patterns and comparable to the uniform-induced shift. The two rightmost bars are for patterns represented at the S/(L+M) level but not the S-cone-specific level. These pattern-induced shifts, on average, were comparable to those found with the isoluminant patterns (second bar from left) and larger than the uniform-induced shift. The measurements, therefore, showed that large induced color shifts from S-cone patterns depended on a neural representation incorporating responses from more than one type of cone (i.e. S/(L+M)), not on a neural representation of only S-cone excitation.

Similar results are shown in the other panels for two additional observers. S-cone patterns represented at the S-cone-specific level but not the S/(L+M) level (two middle bars in each panel of Fig. 4) had far weaker pattern-induced shifts than patterns represented at only the S/(L+M) level (two rightmost bars). Further, in most cases a pattern represented at only the S-cone-specific level caused weak pattern-induced shifts comparable in magnitude to the uniform-induced shift.

Discussion

Many physiological processes affect the perceived color of a light viewed within a complex context. These include the optics of the eye forming the retinal image, photoreceptor sensitivity change, and postreceptoral neural processes in retina and cortex. The experiments here specifically examined the large color shifts induced by a pattern detected by only S cones to determine whether the shifts were mediated by an S-cone-specific neural representation of the pattern or a neural representation that also incorporates responses from other cone types. Two general results were (i) that a pattern represented at only an S-cone-specific level caused weak color shifts, which were comparable in magnitude to shifts caused by a uniform background at one of the chromaticities within the pattern, and (ii) that much larger color shifts could be induced even when receptoral S-cone excitation was uniform across the background (i.e. no S-cone-detected pattern), as long as the pattern was represented postreceptorally in a pathway incorporating responses from other cone types (S/(L+M)). These findings showed that the conspicuous color shifts induced by S-cone patterned backgrounds resulted from a neural representation that depends also on signals from another type of cone.

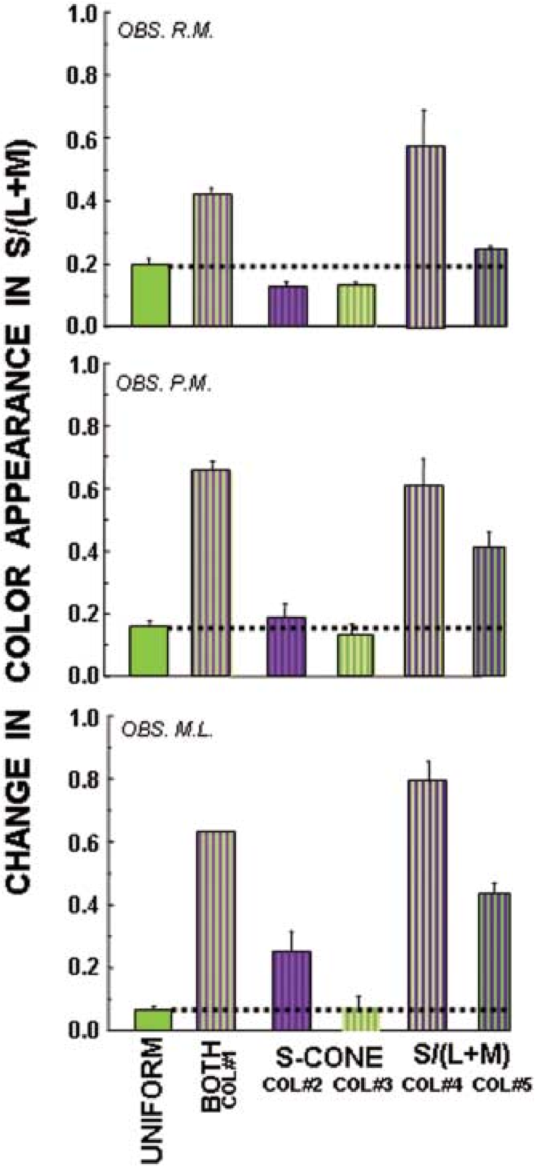

Fig. 4. The uniform-induced shift (leftmost bar) and pattern-induced shifts for the conditions shown in Fig. 2. Each panel shows results for a different observer. The pattern-induced shift is shown for patterns represented at both the S-cone-specific and S/(L+M) levels (second bar from left), patterns represented at only the S-cone-specific level (two middle bars), and patterns represented at only the S/(L+M) level (two rightmost bars). The labels on the horizontal axis refer to columns 1–5 in Fig. 2. Error bars indicate the standard error of the mean.

A common practice in vision research is to measure the perceptual or physiological response to a light detected by only S cones (e.g. Conway, 2001; Solomon et al., 2004). Modulating quantal absorption in only S cones has the further advantage of keeping luminance fixed because only L and M cones contribute to luminance. Such S-cone isolating stimuli, however, may falsely suggest that varying S-cone photoreceptor excitation in space or time directly mediates a particular response. Alternatively, the response may be due to a neural signal driven by a response from S cones *relative* to the responses from other cone types. In this case, the perceptual or physiological effect (here, the large color shifts induced by S-cone patterns) can be caused by a postreceptoral neural representation even when there is no time- or space-varying signal from the S cones themselves (e.g. columns 4 & 5, Fig. 2).

The color shifts induced by S-cone patterns are accounted for by a cortical receptive field with S-cone center-surround spatial antagonism (Shevell & Monnier, 2005). Previous work does not distinguish between receptive-field antagonism of S-cone-specific signals or S/(L+M) neural responses. The measurements here support the latter: receptive-field center-surround antagonism between neural signals that combine responses from different types of cone.

Acknowledgments

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