

Color shifts from S-cone patterned backgrounds: contrast sensitivity and spatial frequency selectivity

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Abstract

Patterned backgrounds that selectively stimulate the S-cones cause conspicuous color shifts. These shifts are accounted for by an S-cone antagonistic (+S/–S) center-surround receptive field [Monnier, P., & Shevell, S. K. (2004). Chromatic induction from S-cone patterns. *Vision Research*, 44, 849–856]. The present study tested two additional implications of the S-cone receptive field for color shifts: (1) proportionality of the shifts with respect to S-cone contrast within the inducing pattern and (2) bandpass selectivity of the shifts with respect to the spatial frequency of the inducing pattern. Measurements showed that the magnitude of the color shift was linear with S-cone contrast and that the largest color shift was observed with inducing patterns at an intermediate spatial frequency. These results further support an S-cone spatially antagonistic receptive field as the neural substrate mediating the large color shifts from S-cone patterns.

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1. Introduction

The color appearance of a light is not exclusively determined by its physical spectral power distribution. Two surfaces reflecting the identical light can appear quite different in color, depending on the context in which the surfaces are viewed. Shifts in color appearance caused by context are referred to as chromatic induction and have been studied extensively (e.g., Chevreul, 1839; Jameson & Hurvich, 1961; Helson, 1963; Shevell, 2003).

Recent research aims to understand color appearance with complex backgrounds (Barnes, Wei, & Shevell, 1999; Bäuml, 1995; Brown & MacLeod, 1997; Delahunt & Brainard, 2000; Fach & Sharpe, 1986; Jenness & Shevell, 1995; Singer & D’Zmura, 1994). This work shows that induction from complex backgrounds con-

sisting of multiple chromatic surfaces is not equivalent to induction from a uniform field at the backgrounds’ space-average chromaticity. Furthermore, and surprisingly, induction from patterned backgrounds composed of two chromaticities can be substantially larger than from a uniform background at either chromaticity in the pattern (Monnier & Shevell, 2003).

Patterned backgrounds composed of concentric inducing circles alternating between two chromaticities that differentially stimulate the S-cones induce large shifts in color appearance. On a qualitative level, these color shifts are consistent with contrast and assimilation acting simultaneously, either synergistically with patterned backgrounds to produce large shifts or antagonistically with uniform backgrounds to produce weak shifts. On a neural level, modeling shows that an S-cone antagonistic center-surround (+S/–S) receptive-field accounts for these color shifts (Monnier & Shevell, 2004). While no such neuron is found in the retina (Calkins,

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2001; Dacey, 1996, 2000), recent physiology reveals cortical neurons with S-cone center-surround antagonistic organization (Conway, 2001; Solomon, Peirce, & Lennie, 2004).

A +S/–S receptive field would affect color appearance by its excitatory S-cone center, causing assimilation, and inhibitory S-cone surround, causing contrast. If the size of the receptive field is such that the test area and a portion of the adjacent inducing light fall within its center, the response reflects a weighted sum of the test and adjacent chromaticity. This center component of the receptive field, therefore, accounts for chromatic assimilation, which is a shift in the direction of the inducing chromaticity. The antagonistic surround of that receptive field responds in an inhibitory fashion to light some distance away from the test. This component alone, therefore, causes simultaneous contrast. With patterned backgrounds, the excitatory and inhibitory components can be synergistic so, for example, a contiguous ‘purple’ high S-cone chromaticity and more distant ‘lime’ low S-cone chromaticity result in a relatively large overall response and therefore a large predicted color shift. With uniform backgrounds, excitation and inhibition to the same S-cone chromaticity tend to be counterbalancing, resulting in a relatively small predicted shift (see Monnier & Shevell, 2004 for details).

The S-cone center-surround receptive field that accounts for color shifts from S-cone patterns has additional, testable properties. First, it implies that the magnitude of color shift should increase linearly with S-cone contrast within the inducing pattern. Second, an S-cone center-surround receptive field of fixed size (i.e., fixed spatial-frequency tuning) implies that the largest shift in color appearance occurs at an intermediate spatial frequency of inducing pattern. This prediction follows from the bandpass characteristic of a spatially antagonistic receptive field.

Consider two alternative models that relate the magnitude of the color shift to the spatial frequency of the inducing pattern (Fig. 1). Positive values in these plots

are shifts in appearance toward the chromaticity of the inducing circle adjacent to the test (assimilation) while negative values are shifts away from the adjacent inducing chromaticity (simultaneous contrast). Fig. 1a shows how color appearance is affected by the spatial frequency of an inducing pattern if appearance is mediated by an S-cone center-surround receptive field. The receptive field model predicts the largest shift at an intermediate inducing-pattern spatial frequency. The three lines in each panel show the color shift for different widths of test ring (e.g., see any row in Fig. 4). The largest overall color shifts are predicted to occur with the smallest test-ring width.

Fig. 1b shows the predicted magnitude of color shifts as a function of spatial frequency assuming only retinal defocus caused by optical factors. Optical factors alone predict that the largest color shift occurs at the lowest inducing-pattern spatial frequency, and with the smallest test-ring width.

2. Methods

2.1. Apparatus and calibration

Stimuli were displayed on a 21" calibrated color monitor (Sony GDM-F520, 1360 × 1024 pixels, 75 Hz non-interlaced) controlled by a Macintosh G4 computer with a Radius Thunder 30/1600 auxiliary video board (10-bits per gun). The guns' spectral characteristics were measured using an Optronics 754 spectroradiometer. The gun outputs were gamma-corrected by storing in a look-up table the luminance measured at each of the 1024 (2^{10}) digital gun values. A Minolta LS-100 photometer was used to measure absolute luminance levels as well as the stability of the calibration during the course of the experiments.

Chromaticities were specified in a cone-based chromaticity space (MacLeod & Boynton, 1979) where the x-axis represented relative L-to-M-cone stimulation

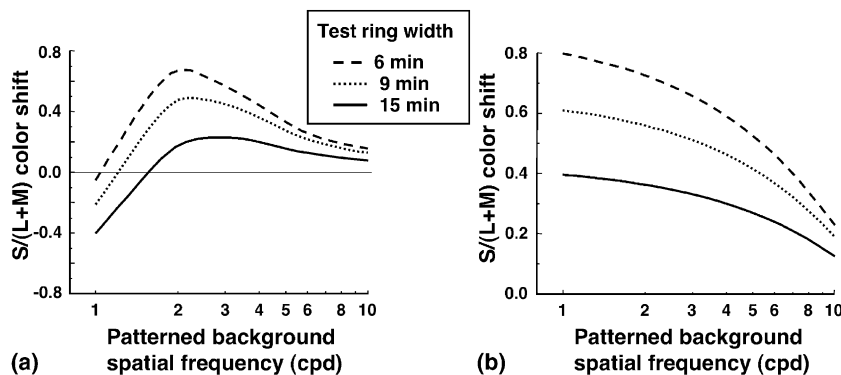


Fig. 1. Two sets of color-shift predictions as a function of the spatial frequency of the inducing pattern: (a) for an S-cone center-surround receptive field and (b) for only optical defocus. The three curves in each panel are for different widths of test ring (see legend).

$[l = L/(L + M)]$ and the y -axis represented S-cone stimulation [$s = S/(L + M)$]. The unit of s was normalized here to 1.0 for light metameric to equal-energy white (EEW), a chromaticity that appears approximately achromatic when viewed in isolation.

2.2. Stimuli and procedure

Color appearance was measured by asymmetric color matching. Comparison and test fields were presented side by side at a viewing distance of 1.5 m (Fig. 2). The comparison-field background was uniform and approximately metameric to EEW (l, s, Y of 0.66, 1.00, 15 cd/m²). The test background was composed of either a uniform chromatic background or concentric circles alternating between two chromaticities selected from a tritanopic confusion line. The inducing chromaticities, therefore, differentially stimulated only the S cones. Observers adjusted the hue, saturation and brightness of the comparison ring to match the appearance of the test ring, using buttons on a Gravis gamepad. Steady fixation was not enforced. Induction was measured for three test-ring chromaticities, which differed in only l chromaticity (l, s, Y values 0.62, 1.00, 20 cd/m²; 0.66, 1.00, 20 cd/m²; and 0.70, 1.00, 20 cd/m²). The luminance of the test chromaticities (20 cd/m²) was set higher than the luminance of the inducing chromaticities (15 cd/m²) to minimize the influence of spread light and chromatic aberration. Matches in each condition were considered relative to an isomeric match with the background in both the comparison and test fields at the EEW chromaticity (l, s, Y of 0.66, 1.00, 15 cd/m²).

Each session began with 2 min of dark adaptation. A session was composed of five matches for each of the three test ring chromaticities, for a total of 15 matches per session. All factors except test chromaticity were

fixed within a session. Each condition was repeated three times on separate days.

Isoluminance was measured for each observer using the method of minimum motion (Anstis & Cavanagh, 1983), and S-cone isolation was confirmed using the minimally-distinct-border technique (Tansley & Boynton, 1978).

2.3. Observers

Two observers completed each experiment (J.W. and M.L. in Experiment 1, M.L. and P.M. in Experiment 2). Partial results from J.W. for Experiment 2 were generally consistent with the two other observers but incomplete (data not shown). All observers had normal or corrected acuity (20/20) and had normal color vision as assessed with the Ishihara plates and Rayleigh matches. Observers completed practice sessions before data collection was initiated. Observers J.W. and M.L. were naïve as to the purpose of the study. Observer P.M. is an author. Each subject gave informed consent. This research was approved by an Institutional Review Board at the University of Chicago.

3. Results

3.1. Experiment 1: S-cone contrast sensitivity

Induction was measured as a function of the S-cone contrast between the two inducing chromaticities. Michelson contrast values between 0.10 and 0.86 were tested (Table 1). Inducing chromaticities with s values higher than 1.0 appeared purple and mainly increased in saturation with increasing s . Chromaticities with s values lower than 1.0 had a lime appearance and mainly increased in saturation with decreasing s . The space-average s chromaticity of all patterns was near 1.0. The l chromaticity was fixed at 0.66 for all inducing chromaticities.

The width of the comparison and test rings as well as the width of the concentric inducing circles was 9 min of visual angle, resulting in a pattern spatial frequency of 3.3 cycles per degree. The comparison and test fields

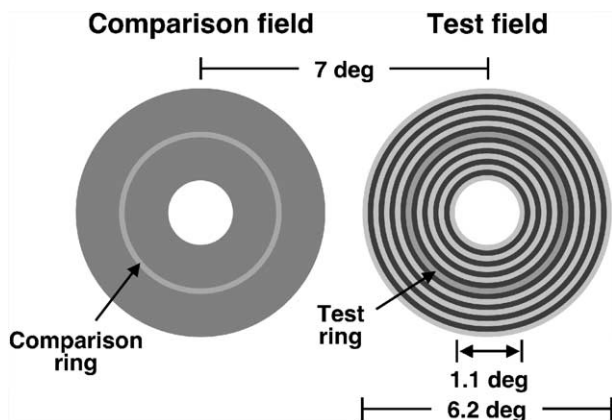


Fig. 2. The stimulus display consisted of a comparison and test field. The task was to adjust the comparison ring's hue, saturation, and brightness to match the test ring. In Experiment 2, the concentric inducing circles' spatial frequency and the test-ring's width were varied.

Table 1

S-cone Michelson contrast of the inducing patterns used in Experiment 1

Michelson contrast	'Purple' $S/(L + M)$	'Lime' $S/(L + M)$
0.10	1.10	0.90
0.20	1.20	0.80
0.30	1.30	0.70
0.50	1.50	0.50
0.70	1.70	0.30
0.80	1.80	0.20
0.86	1.86	0.14

subtended 1.1° – 6.2° in inner- and outer-diameter, respectively, and were separated by 7° center to center (Fig. 2). The stimuli were presented on a dark background in a dark room.

Matching measurements are shown in Fig. 3 for the two observers who participated in this experiment. The shifts in s , relative to the isomeric match, are plotted as a function of the S-cone contrast in the inducing pattern (shifts along l were negligible). Open and solid symbols are matches for patterns with the test flanked by purple or lime inducing circles, respectively. The circles, squares, and triangles in the plots are matches for the three test ring chromaticities (l of 0.62, 0.66, and 0.70, respectively, with s and Y fixed at 1.0 and 20 cd/m^2). Each match represents the mean of three measurements made on separate days. Standard errors of the mean are smaller than the plotted symbols.

The matches shifted to higher (lower) s levels when the test ring was flanked by adjacent purple and non-contiguous lime (adjacent lime and non-contiguous purple) inducing circles. These shifts in color appearance show assimilation to the adjacent and contrast from the non-adjacent inducing chromaticity, as found previously (Monnier & Shevell, 2003, 2004).

The magnitude of the shifts increased with S-cone contrast for both types of patterns. The measurements are monotonic and nearly linear. The magnitude of the s shifts was generally independent of the l chromaticity of the test. All of these results are consistent with an S-cone antagonistic receptive field.

3.2. Experiment 2: Spatial frequency selectivity

The spatial frequency of the concentric inducing circles and the width of the test ring were varied indepen-

dently. Spatial frequencies between 1 cpd and 10 cpd and ring widths of 15 min (2 cpd), 9 min (3.3 cpd), and 6 min (5 cpd) were tested. The width of the comparison ring always was the same as the width of the test ring. One set of inducing patterns, for the purple/lime condition (i.e., test ring adjacent to purple inducing circles), is shown in Fig. 4. Matches were measured also with inducing patterns having the test ring adjacent to lime inducing circles (the lime/purple condition, not shown in Fig. 4). Induction from uniform backgrounds (uniform purple or uniform lime) also was measured. We opted to keep the overall size of the test pattern roughly constant as opposed to keeping the number of inducing circles, or number of cycles, constant. As a result, as the spatial frequency of the inducing pattern increased, the number of inducing-circle cycles increased as well. The 1, 2, 3.3, 5, and 10 cpd patterns contained one, two, four, six, and twelve cycles on either side of the test ring, respectively (see Fig. 4).

As in Experiment 1, the two inducing chromaticities were selected from a tritan line (l , s , Y of 0.66, 1.86, 15 cd/m^2 ; and 0.66, 0.14, 15 cd/m^2). In this experiment, the S-cone Michelson contrast was fixed at 0.86. Induction was measured for the same three test ring chromaticities (l , s , Y values 0.62, 1.00, 20 cd/m^2 ; 0.66, 1.00, 20 cd/m^2 ; and 0.70, 1.00, 20 cd/m^2).

Matching measurements are shown in Fig. 5 by the plotted symbols, for two observers (a third observer did not finish this experiment). The solid lines are model fits described in the discussion. Shifts in s , relative to the isomeric match, are plotted as a function of the spatial frequency of the inducing pattern. Shifts along l were again negligible so measurements for the three test chromaticities were averaged. Open or solid circles are

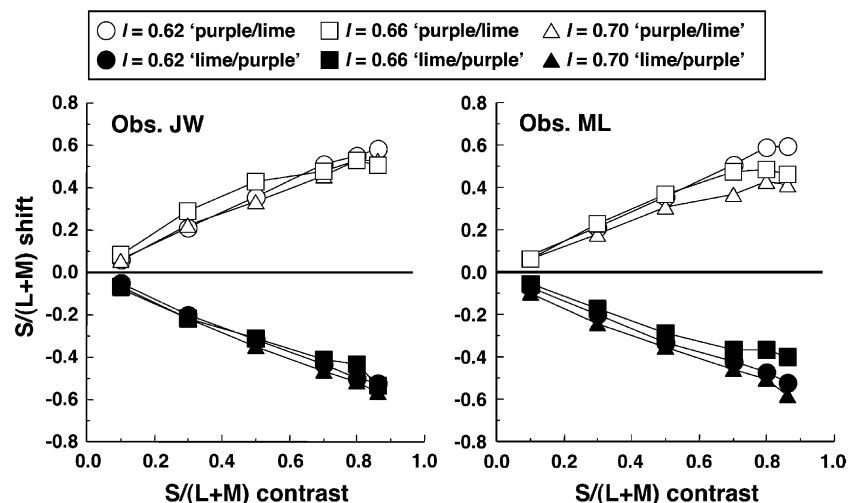


Fig. 3. Shifts in color appearance from an isomeric match, along the $S/(L+M)$ dimension, plotted as a function of the S-cone contrast within the inducing pattern. Open and solid symbols are matches with the test presented with purple/lime or lime/purple inducing circles, respectively. The three different symbols are matches for different chromaticities of the test ring (varied along only the $L/(L+M)$ axis). Each match is based on the mean of three measurements. Standard errors of the mean are smaller than the plotted symbols. Each panel shows results for a different observer.

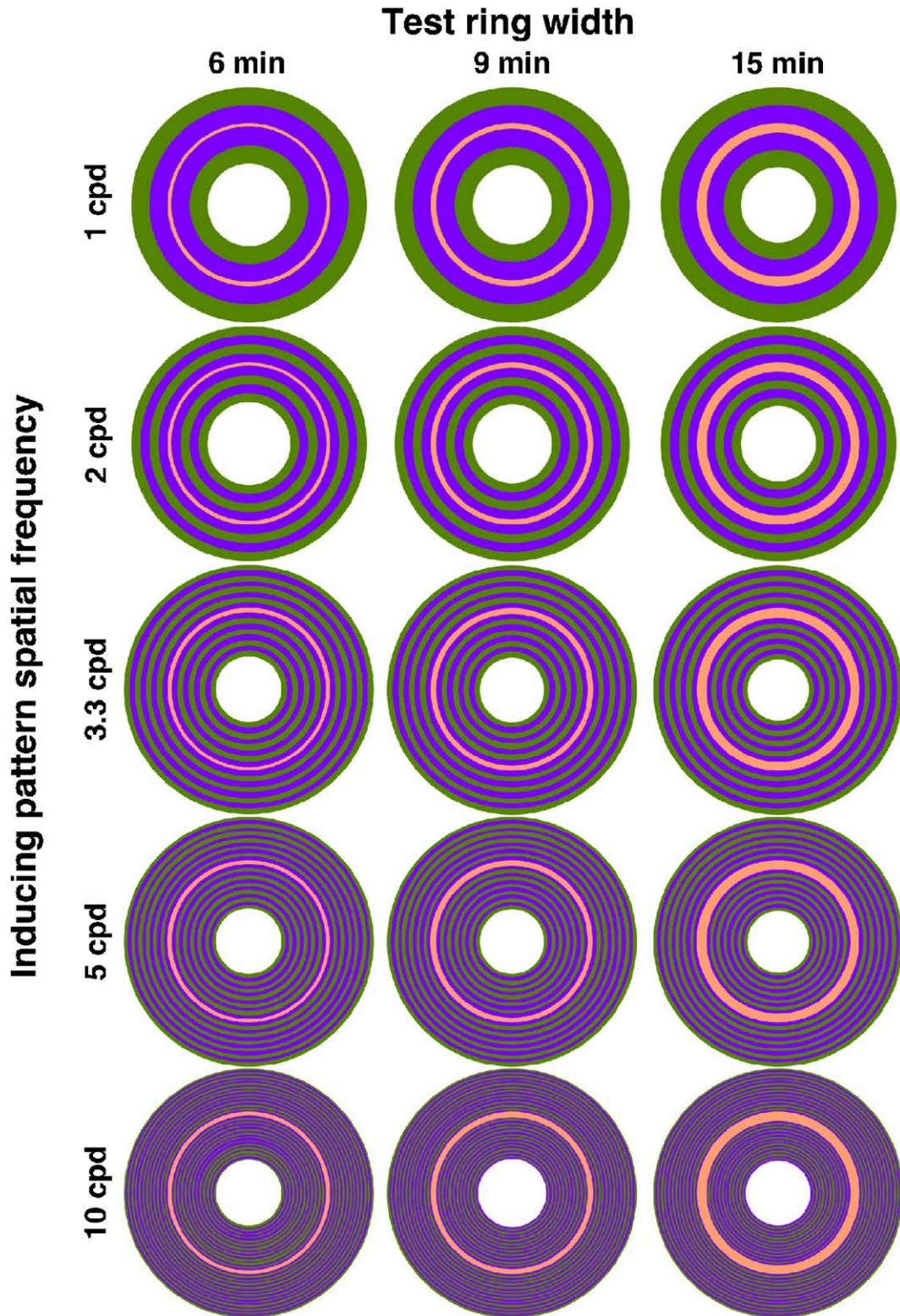


Fig. 4. A subset of the test patterns used in Experiment 2. The spatial frequency of the inducing pattern (rows) and the width of the test ring (columns) were varied.

matches for patterns with the test ring flanked by purple or lime inducing circles, respectively. The symbol size indicates the test-ring width (6, 9, or 15 min). Where vis-

ible, error bars show the standard errors of the mean; other standard errors were smaller than the plotted symbols.

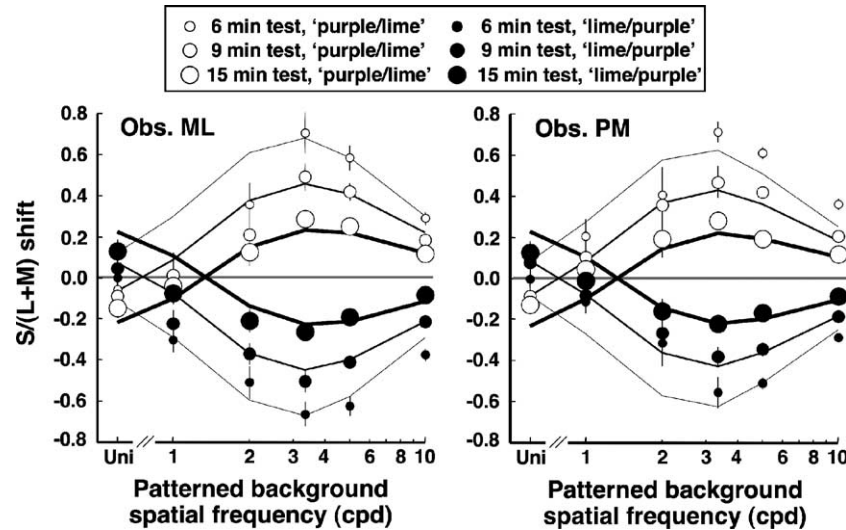


Fig. 5. $S/(L+M)$ shifts in color appearance as a function of the spatial frequency of the inducing pattern. Measurements for the three test-ring chromaticities were averaged. Open and solid circles are matches with the test presented with purple/lime or lime/purple inducing circles, respectively. The test-ring width is indicated by the symbol size (6, 9, or 15 min). Error bars where visible indicate standard errors of the mean. The largest shifts were observed at an intermediate spatial frequency (3.3 cpd), consistent with the shifts being mediated by an S-cone antagonistic center-surround receptive field. The solid lines are fits to a specific receptive-field model (see Discussion). Each panel shows results for a different observer.

Uniform inducing backgrounds (left-most symbols on each plot) generally caused shifts in appearance away from the inducing chromaticity, in the direction of chromatic contrast (Fig. 5). The magnitude of the color shift initially increased with the spatial frequency of the inducing pattern, then peaked at an intermediate spatial frequency, and finally decreased at higher spatial frequencies. A single-peaked function was observed for *each* test-ring width. These bandpass functions are consistent with an S-cone antagonistic center-surround receptive field (Fig. 1a). Note further that the largest color shift occurred at the same inducing-pattern spatial frequency (3.3 cpd) regardless of the test-ring width. This is consistent with shifts mediated by a single size of receptive field with maximal sensitivity at a relatively low spatial frequency. All of these properties are consistent with an S-cone center-surround receptive field.

4. Discussion

4.1. S-cone antagonistic center-surround receptive field

The experiments here were motivated by two predictions from a neural receptive field with S-cone (+S/−S) center-surround antagonism (Monnier & Shevell, 2004). First, the neural model predicts that the magnitude of the shift in color appearance is linear with S-cone contrast within the inducing pattern. This follows from a simple model of the receptive field without non-linearities. The measurements supported this prediction (Fig. 3).

The second implication of the +S/−S receptive field is that the maximal shift in color appearance should occur at an intermediate, modest spatial frequency of S-cone variation within the inducing pattern. This prediction follows from the center-surround antagonistic organization of a receptive field of fixed size (that is, fixed spatial-frequency tuning), which accounts for previously published results (Monnier & Shevell, 2004). As the center and surround regions are antagonistic in terms of their S-cone inputs, the spatial modulation transfer function of the receptive field is bandpass. The measurements here are consistent with this property of the receptive field as well. The maximal shift in color appearance occurred at an intermediate spatial frequency for all three test-ring widths (Fig. 5).

A third prediction made by the spatial structure of the receptive field is that the magnitude of the color shift should vary with the width of the test ring. The receptive field implies the largest shift occurs with the smallest test-ring width. This is because the chromaticity directly adjacent to the test will be weighted more strongly in the excitatory center of the receptive field with a narrow test ring, compared to a wider one. The measurements indeed showed larger shifts in color appearance with the smallest test-ring width (Fig. 5).

Optical factors, such as spread light and chromatic aberration, also predict that the largest shifts in color appearance occur with the smallest test-ring width. A fixed amount of light spreading into the test-ring region will be relatively larger as the size of the test ring is made smaller. Optical factors alone, however, cannot accommodate the largest magnitude of color shift at an intermediate inducing-pattern spatial frequency (see Fig. 1).

Also, spread light and chromatic aberration predict the largest difference between the test-ring widths occurs at the lowest spatial frequency; in fact, the maximum shift would occur with uniform backgrounds because more inducing light of a single chromaticity is spread into the test-ring area. The measurements are contrary to the predictions for optical factors (see Monnier & Shevell, 2003, for further evidence against spread light and chromatic aberration as major factors affecting these color shifts).

A relatively simple neural receptive field with S-cone center-surround antagonism accounts for all the measurements. There is, however, one aspect of the measurements that the neural model presented previously (Monnier & Shevell, 2004) does not explain with quantitative precision: the bandwidth (or shape) of the spatial frequency functions. The model fits shown in Fig. 5 (solid lines) are for a +S/–S receptive field that differs in detail from the previous model in terms of (i) the width of the surround and (ii) the relative weight of the S-cone center and surround. Both parameters were optimized to fit the color shifts in Fig. 5. The optimal width of the surround is nearly 5 times the center's width (compare to the original model with surround width fixed at twice that of the center), and the center is weighted about 1.8 times the surround (compare to the original model with fixed, equally weighted center and surround). The peak spatial frequency of the new receptive field when optimally fit to each observer's measurements (solid lines in Fig. 5) is 1.0 and 1.1 cpd for M.L. and P.M., respectively. The quality of the fits is good overall, though less so for the thinnest (6 min wide) test ring with uniform backgrounds or low-spatial-frequency (1–2 cpd) inducing patterns. An additional receptive field with different size tuning may be required for those cases (cf. Humanski & Wilson, 1993). Recall that all 36 conditions were fit with only three parameters (center width, surround width, and center/surround weighting).

Measuring color shifts with different background spatial frequencies and test-ring widths (Experiment 2) better constrained the receptive-field properties than previous experiments (Monnier & Shevell, 2004), which were conducted with all inducing and test rings 9-min wide. In the previous work, eight background conditions were tested: uniform purple, uniform lime, purple/lime, lime/purple (these 4 conditions were repeated here), white/purple, white/lime, purple/white and lime/white ('white' indicates EEW achromatic light replaced one of the chromaticities). The receptive-field properties that fit the spatial-frequency conditions (Fig. 5) should also be consistent with the conditions tested previously. Fig. 6 shows they are. The bars show the color shifts here, averaged over observers and test chromaticities, for the uniform purple, uniform lime, purple/lime, and lime/purple backgrounds at 3.3 cpd, which were tested in both the previous study and this one. The symbols

show the receptive-field predictions, which are nearly identical for both observers M.L. and P.M. A critical condition in the previous work used concentric, alternating white and chromatic inducing circles, which were shown to cause a stronger color shift than a uniform chromatic surround (for example, alternating purple and white concentric circles induced larger shifts than a uniform purple surround). Also, a concentric-circles background with white caused a weaker color shift than a two-chromaticity background (e.g., purple/white versus purple/green). The plotted symbols in Fig. 6 show the new receptive-field model indeed predicts the largest color shifts from two-chromaticity backgrounds, intermediate shifts from patterns with white inducing circles, and the weakest shifts from uniform chromatic backgrounds.

In sum, the measurements here and in previous work (Monnier & Shevell, 2003, 2004) are consistent with a receptive field having S-cone (+S/–S) center-surround antagonism, a surround about 5 times wider than the center, and a center weighted about 1.8 times more than the surround. This type of neuron is physiologically plausible. Conway (2001) reports neurons that have a substantially larger surround than center, and that have a stronger response from center than surround.

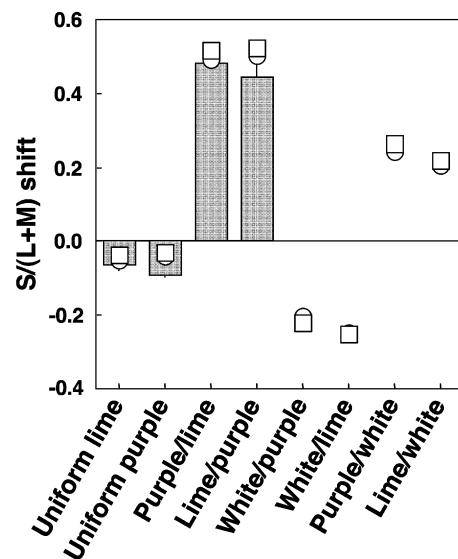


Fig. 6. (Bars) Color shifts averaged over test-ring chromaticities and observers (M.L. and P.M.) for uniform lime, uniform purple, purple/lime and lime/purple backgrounds (9-min inducing circles and test rings). Negative (positive) values are shifts away from (towards) the chromaticity nearest the test (the nearest chromaticity is listed first in each condition shown on the horizontal axis). (Squares and circles) Responses of the receptive field fit to spatial frequency results in Fig. 5 (see text) for observers M.L. and P.M., respectively. The optimal receptive-field parameters for relative surround-to-center width and relative center-to-surround weighting were 4.9x and 1.9x for M.L. and 4.5x and 1.8x for P.M. The symbols plotted for white/purple, white/lime, purple/white and lime/white show the receptive field is consistent with color shifts induced by backgrounds with white concentric circles, as used by Monnier and Shevell (2004) (see text).

The fits in Fig. 5 show the receptive-field model overestimates the magnitude of the color shifts with thin test rings (6 min) and low spatial frequency inducing patterns. This discrepancy may suggest more than one spatial-frequency filter mediates the appearance of S-cone patterns. Multiple filters would be consistent with related work. Using an adaptation paradigm that isolates the S-cones, Humanski and Wilson (1993) report that detection of spatial patterns is mediated by as many as three distinct spatial-frequency mechanisms. Overall, however, a single center-surround S-cone receptive field accounts well for the color shifts from S-cone patterns.

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