

Relating cone signals to color appearance: Failure of monotonicity in yellow/blue

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Abstract

Observers performed red–green and yellow–blue hue cancellation tasks for a 0.8-deg circular test field on a dark surround, by manipulating the excitation level of one cone class while the other two classes were held constant. The results of the red–green judgments conformed to classical opponent color theory in that both L- and S-cone excitation levels were antagonistic to M-cone signals. The yellow–blue judgments revealed a nonmonotonic nonlinearity in which the S-cone signal could act either antagonistically or synergistically with M- and L-cone signals. These results demonstrate that fixed hue sensations should not be associated with a given class of cone, even at the level of opponent neural coding.

Keywords: Cone signals, Hue cancellation, Color mechanisms

Introduction

How is color perception related to neural encoding of light? Three classes of cone photoreceptor provide the neural information required for color vision. Subsequent transformations of these signals result in the neural activity underlying the hues we perceive, such as red, green, and blue. At one time, a direct relation was assumed between the response of each type of cone and hue (Hecht, 1929) but the response from a single cone now is known to encode neither the wavelength nor the perceived hue of stimulating light (Rushton, 1972; Abramov & Gordon, 1994). While modern color theory dissociates the perception of hue from the response of any single type of cone, the relation between hue and the ensemble of cone activity remains an open question.

Two well-established properties of neural encoding of color are trichromacy and cone antagonism. *Trichromacy* is the empirical phenomenon that any isolated patch of light can be matched in color by a mixture of three primary lights (Maxwell, 1856; Helmholtz, 1911). In terms of neural coding, trichromacy implies a bottleneck that passes exactly three independent codes to represent color. Trichromacy is often associated with the three distinct classes of cone (labeled L, M, or S to indicate their peak sensitivity at the long, middle, or short wavelengths of the visible spectrum, respectively) but, more generally, it places a trivariate restriction on the neural representation for color. *Cone antagonism* characterizes the inhibitory interactions among signals from the various

classes of cone. Neural responses that carry chromatic information from the retina to the cortex have been described by a difference between signals from L and M cones, and a difference between S cones and the sum of L and M cones (De Valois, 1965; Wiesel & Hubel, 1966; Derrington et al., 1984; Kaplan et al., 1990; Dacey & Lee, 1994). Thus, the neural representation for trichromacy reaching the cortex is based on interactions among signals from the three types of cone, not individual cones' responses.

A fundamental unsolved problem in vision is to link neural signals to color perception. Hering (1920) proposed three neural responses to account for the hues of normal color vision. His red–green, yellow–blue, and white–black opponent mechanisms explained why we experience certain hue combinations and not others. Red and green are opposite poles of one bipolar neural response, and yellow and blue are poles of a second response. Each of these neural responses has a single value (toward red or toward green on one dimension, toward yellow or blue on the other) so, for example, redness and yellowness can occur simultaneously to give the hue orange, or greenness and blueness can occur together to give aqua. The bipolar dimensions, however, do not allow a hue that is simultaneously reddish and greenish, or simultaneously bluish and yellowish, in agreement with human color experience.

When a single patch of light is viewed in a dark, context-free environment, the hue perceived must follow from the ensemble of cone responses to the light. Prevailing theory holds that the signal from each type of cone can contribute to two perceptual hue components. In classical opponent-colors theory (Hurvich & Jameson, 1957; Jameson & Hurvich, 1968), for example, the bipolar red/green dimension results from the antagonistic difference between the signal from M cones and a sum of signals from L and S

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cones; and the bipolar yellow/blue dimension is the difference between the signal from S cones and the sum of signals from L and M cones. In comparison to the disproved idea that each cone encodes a single hue, opponent-colors theory holds that each cone can contribute to both bipolar dimensions so, for example, L-cone stimulation affects both redness and yellowness. While empirical evidence shows failures of a strictly linear combination of receptor responses, a fundamental principle of the classical opponent-colors model is preserved in nearly every nonlinear model proposed as a replacement (Larimer et al., 1975; Werner & Wooten, 1979; Elzinga & de Weert, 1984): a cone type can contribute to *either* red or green on the red/green dimension, and to *either* yellow or blue on the yellow/blue dimension. In fact, theoretical debate is framed by this principle, as in opposing views of whether M cones contribute to yellowness or to blueness (Jameson & Hurvich, 1968; Drum, 1989; De Valois et al., 1997).

A link is often suggested or assumed between the cone antagonism in hue perception and the antagonism of retino-geniculate coding. The agreement, however, is only qualitative at best (Mollon & Cavonius, 1987). For example, the cell types that signal differences between L and M responses are often cited as the substrate for a red/green pathway (e.g. Dacey, 2000), but such a pathway fails to account for redness from S-cone signals (Wooten & Werner, 1979; Shevell, 1992). Another difference is the degree of nonlinearity found perceptually for yellow/blue equilibria (Larimer et al., 1975; Burns et al., 1984; Chichilnisky & Wandell, 1999), which is not characteristic of cells in the retina or lateral geniculate nucleus (LGN) with S-cone input (Derrington et al., 1984; Chichilnisky & Baylor, 1999; De Valois et al., 2000). In sum, no known neural signals correspond to perceived hues.

While several studies have aimed to infer the relation between cone excitation and color appearance, none has measured color perception of an isolated patch of light while varying stimulation of only a single class of cone. Here, we measure hue while varying the excitation of only a single cone type, in a patch of light seen on a dark background. This approach allows direct measurement of each cone's contribution to hue, and implicitly tests the principle that each type of cone contributes to a single hue on each bipolar dimension. Surprisingly, the measurements refute this principle under some conditions. These results imply that a cone type (L, M, or S) should not be rigidly associated with particular hues, even at the level of neural combinations of receptor responses.

Methods

Apparatus and calibration

Chromatic stimuli were presented on a high-resolution Radius Pressview 17-inch color video display (832 × 624 pixel resolution, 75-Hz frame rate noninterlaced). The experiments were controlled by a Macintosh 7600/132 computer with an auxiliary video board (Radius ThunderPower 30/1600). Judd (1951) chromaticities of the phosphors were determined with a calibrated scanning spectroradiometer, and the phosphors were linearized with look-up tables. These tables were created by measuring the relative luminance from the video display at each of the 10-bit levels for each phosphor (additional details of the calibration are in Shevell & Wei, 1998). A chin rest was used to maintain a stable head position.

Stimuli were specified in relative L, M, and S trolands. L and M trolands were scaled relative to each other so that L+M gave relative luminance. Scaling of S trolands is arbitrary (MacLeod & Boynton, 1979). Pupil size was not measured (thus *relative* tro-

lands) but did not change significantly within any experiment because luminance varied by less than 0.1 log unit, except in Fig. 1 below. In Fig. 1, luminance could vary by 0.3 log unit but pupil size had no practical consequence because those measurements were almost perfectly linear.

Procedure

Prior to the main experiments, the radiances of the phosphors for isoluminance were determined individually for each observer, using heterochromatic motion photometry (Anstis & Cavanagh, 1983). S-cone isolation was established for each observer with the minimally distinct border technique at isoluminance (Tansley & Boynton, 1978). Excitations of the L, M, and S cones were calculated from the Smith and Pokorny (1975) cone fundamentals.

The experiments were run in a dark room. Each experimental session began with 5 min of dark adaptation. The only stimulus was a 0.8-deg circular test field presented for 200 ms every 2 s (no fixation point).

The hue cancellation technique was used. Observers set the test field to appear neither reddish nor greenish or, in separate sessions, to appear neither yellowish nor bluish. Within a session, stimulation of one cone type was held fixed; stimulation of a second cone type was set to a different level in each block of the session. The observer adjusted the excitation of the third cone type, using a joystick, to achieve the criterial color appearance. The procedure and computerized presentation of stimuli were identical in experiments to measure either red/green or yellow/blue equilibrium colors. The only difference was the instruction at the beginning of the session, to make settings that appeared neither reddish nor greenish, or settings that appeared neither yellowish nor bluish.

The observer made five settings for each block during each session. The average of these settings was recorded as the mea-

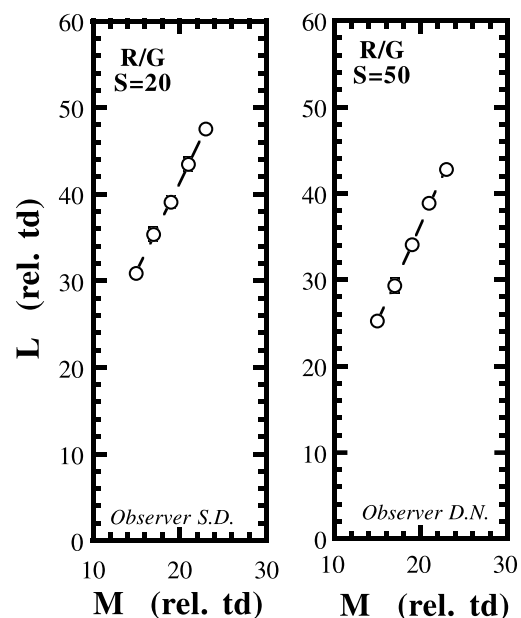


Fig. 1. Relative L-cone excitation required as a function of M-cone excitation to obtain an appearance that is neither reddish nor greenish. Each graph represents data from a different observer. In the left graph, the S-cone level is set to 40% of that of the right graph. Standard errors are within the size of the symbols.

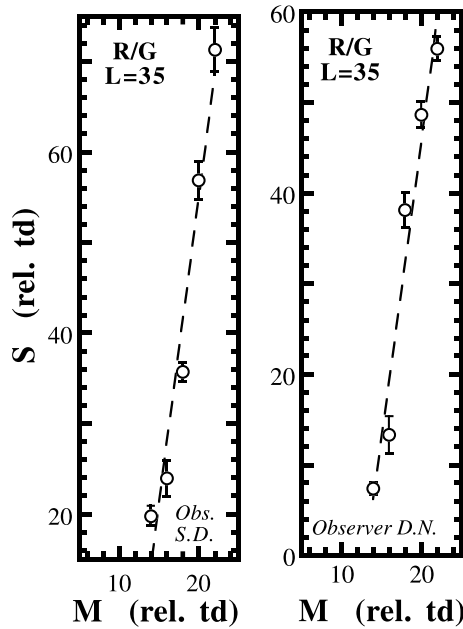


Fig. 2. Relative S-cone excitation required as a function of M-cone excitation to obtain an appearance that is neither reddish nor greenish.

surement for the block on that day. Measurements were repeated on 4–5 days. The daily block means were averaged to give an overall mean, and were used to compute standard errors of the mean (S.E.M.). These 4–5 sessions formed a ‘set’ of measurements. Every observer completed each set twice.

The reliability of the measurements was good for both red/green and yellow/blue judgments. For example, when observers adjusted S-cone stimulation to obtain red–green equilibrium (Figs. 2 and 3), the average S.E.M. was 1.76 S units, which is less than 4% of measurement range (90th percentile S.E.M. was 2.83). The

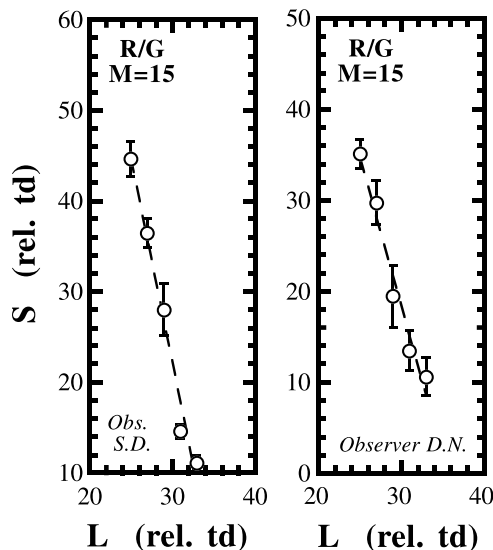


Fig. 3. Relative S-cone excitation required as a function of L-cone excitation to obtain an appearance that is neither reddish nor greenish.

S.E.M.s were even smaller when S cones were adjusted for yellow–blue equilibrium (Fig. 4): the average S.E.M. was 1.11 (90th percentile: 2.25). Note that the S.E.M.s were smaller for yellow–blue than for red–green settings, which demonstrates that these yellow–blue measurements are no less reliable than those for red–green. When subjects adjusted L rather than S (Figs. 1 and 5), the average S.E.M. for red–green was 0.57 L units (90th percentile: 0.74). For yellow–blue, corresponding S.E.M.s were 1.35 L units (90th percentile: 1.97). Overall, these are quite small measurement errors.

Observers

Three university undergraduates served as paid volunteer observers. Data are shown for two of them who completed similar conditions. The third observer completed all red–green conditions and one for yellow–blue. Her results were similar to those of the other two. The observers were naïve concerning the purpose of the experiments. They practiced making hue judgments in preliminary sessions until they achieved good repeatability over days.

Results

Red/green equilibria

First consider experiments in which observers were instructed to adjust the test field to appear neither reddish nor greenish. For the measurements in Fig. 1, the observer controlled the level of L-cone excitation (vertical axis) at each level of M-cone excitation (horizontal axis). The level of S was fixed for each panel of the figure. The results show that an increase in M requires a proportional increase in L to maintain a percept that is neither reddish nor greenish (that is, a color in red–green equilibrium). The measurements are fit well by a straight line with positive slope, which

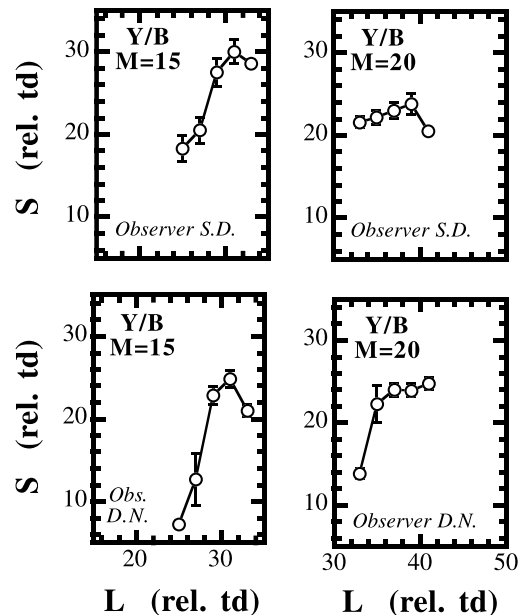


Fig. 4. Relative S-cone excitation required as a function of L-cone excitation to obtain an appearance that is neither yellowish nor bluish. Data from two observers are shown for each of two levels of M-cone excitation.

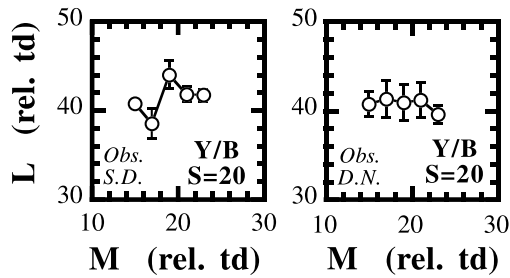


Fig. 5. Relative L-cone excitation required as a function of M-cone excitation to obtain an appearance that is neither yellowish nor bluish.

indicates the L and M cones contribute with opposite polarity to these red–green hue judgments. Similarly, the slope is positive when the observer adjusts the level of S-cone excitation to cancel the sensation evoked by increasing M-cone excitation (Fig. 2). These results imply that both L cones and S cones are antagonistic to M cones in the determination of red–green equilibria. They are consistent with an opponent-colors model in which both L- and S-cone signals contribute redness, and are antagonistic to M-cone signals which evoke greenness.

Such a model accounts also for measurements where the observer adjusts S-cone excitation to compensate changes in L-cone excitation, with M fixed (Fig. 3). Now, the slope is negative, indicating that an increase in L-cone excitation is compensated by a proportional decrease in S.

Yellow/blue equilibria

In contrast to the linear results above for red/green equilibria, cone signals interact in a complex way to establish hues that appear neither yellowish nor bluish. Fig. 4 shows some of these measurements from the same two observers conducting the same experiment as before except that the criterion is a hue that appears neither yellowish nor bluish. Measurements for two different fixed levels of M are shown in separate columns. When the observers adjust the level of S-cone excitation to compensate changes in L, S-cone excitation initially increases with L. This indicates that S and L cones contribute in an antagonistic fashion to yellow–blue equilibrium hues, in accord with prevailing models. At a certain level of L, however, this relation reverses for three of the four curves: the observers reduce S-cone excitation to compensate further increases in L. The interaction between S and L cones in achieving a yellow–blue equilibrium, therefore, changes from antagonism (L opposing S) to synergism (L bolstering S). In terms of cones' contributions to hues, these results contradict the usual assumption that raising S-cone excitation contributes additional blueness, and raising L-cone excitation adds yellowness.

Fig. 5 shows the interaction between L and M cones, with S fixed. For one observer, the level of L-cone excitation is nearly unchanged as M-cone excitation increases (right panel); for the other observer, a more complex nonlinear relation is found for the level of L-cone excitation required to compensate increases in M (left panel). Compare this change in L as a function of M to results in the left panel of Fig. 1, which is the identical experiment except that the criterion is a red/green equilibrium hue.

The measurements of yellowness/blueness in Figs. 4 and 5 are inconsistent, of course, with classical, linear opponent-colors theory.

More importantly, they reveal *nonmonotonicity*, not simply nonlinearity.

Discussion

The major conclusion from this study is that the hue associated with a given cone type is not invariant. For example, increasing stimulation of L cones may require *either* an increase or a decrease in S excitation to reestablish yellow/blue equilibrium, depending on the level of L and M. Hue cancellation, therefore, is a *non-monotonic* function of the photon catch by a particular cone type. This implies that there is not a fixed hue sensation associated with increasing the response of a single class of cone, even for the simple stimulus configuration of a uniform field on a dark background.

The nonmonotonicity was found only for yellow–blue judgments. Our results for red–green equilibrium hues are consistent with a linear opponent-colors model, in that L- and S-cone signals contribute redness that is antagonistic to greenness contributed by M-cone signals. While nonlinear red/green measurements have been reported (Burns et al., 1984; Ayama et al., 1985), the linear results here (Figs. 1–3) are not inconsistent with them. The limited color gamut of the video display does not extend to the parts of the red/green equilibrium locus that exhibit nonlinearity. The linear results, here, are in striking contrast to the nonlinearity of our yellow–blue measurements.

While rods can affect hue under some conditions, the 0.8-deg, foveal stimulus used here was imaged on a part of the retina with few if any rods. Studies that have demonstrated rod influences on color appearance have used much larger, peripherally viewed fields (reviewed in Buck, 2001).

Yellow/blue nonlinearity is well known (Valberg, 1971; Larimer et al., 1975; Werner & Wooten, 1979; Burns et al., 1984; Elzinga & de Weert, 1984; Chichilnisky & Wandell, 1999), but the nonmonotonicity revealed in this study is a qualitative violation of most previous models. Our procedure of varying the stimulation of one cone class independently brings out this nonmonotonicity but corroborative evidence is implicit in a previous study. Fig. 6 shows the yellow–blue equilibrium locus for one of the observers studied by Burns et al. (1984, Fig. 4), replotted in the MacLeod and

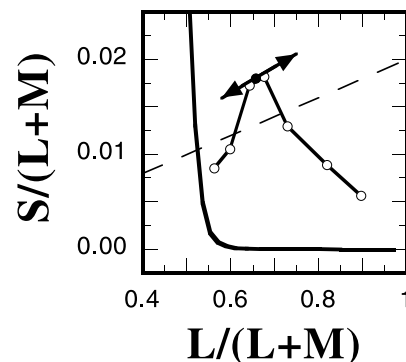


Fig. 6. Equilibrium yellow/blue locus obtained by Burns et al. (1984) for one of their observers, plotted in the MacLeod and Boynton cone excitation diagram (unfilled circles). The solid curve is the spectrum locus. The dashed line is a deuteranopic confusion line. The filled circle indicates the coordinates of illuminant C and the double-headed arrow through it is along a deuteranopic confusion line.

Boynton (1979) cone excitation diagram as unfilled circles. This chromaticity diagram is appropriate because their data were obtained at constant luminance, and the diagram represents an equiluminant plane. On any vertical line in this diagram, the ratio of L- to M-cone excitation is fixed so at constant luminance a vertical line represents changes in only S-cone excitation. On any horizontal line, the level of S is fixed while the L- to M-cone excitation ratio increases from left to right (recall the constant luminance constraint, that L+M is a fixed value).

This plot of the Burns et al. data shows that the level of S-cone excitation (vertical axis) varies nonmonotonically with increasing L/(L+M), which is in accord with our measurements. The relation between L- and M-cone excitation is more difficult to visualize but some insight can be obtained by considering the projection of an M-cone isolation line in this diagram (dashed line). (Again, the sum of L and M cones is constant at equiluminance; the dashed line is a projection of a line that is out of the plane of the diagram.) The projection of the M-cone isolation line intersects the yellow–blue equilibrium locus twice. Assuming the inverted V-shaped form of the locus extends out of the equiluminance plane, there will be M isolation axes that intersect the equilibrium-hue surface twice. Thus, by increasing M-cone activity, the hue passes from blue to yellow and then again to blue. V-shaped ridges in the equilibrium surface, as in Fig. 6, have been predicted (Mausfeld & Niederée, 1993) and observed (Chichilnisky & Wandell, 1999) in equilibrium yellow–blue judgments. Thus, increasing M-cone signals can be associated with either increasing yellowness or increasing blueness, depending on the excitation of the three classes of cones.

This diagram also may account for an interesting observation by De Valois et al. (1997). The subjects in their study named the hues associated with increments and decrements on cone isolating axes. The hues observed along the M-cone isolating axis were seen as bluish for both increments and decrements. Their study was performed on a background metameric to Illuminant C, which is usually described as slightly bluish. In the diagram of Fig. 6, the position of Illuminant C is plotted as a solid circle just above the summit point of the equilibrium locus, on the bluish side. Because the equilibrium locus is concave down, both increments and decrements along an M-cone line through Illuminant C (shown by a double-headed arrow) remain on the blue side of the equilibrium locus, in accord with their measurements.

While our results dissociate fixed hue appearances from cone signals, the data are consistent with sums and differences of cone signals that subsequently pass through a nonlinearity characterized by rectification, prior to the neural representation of yellowness and blueness. Such a model was suggested to explain the yellow–blue equilibrium locus (Pokorny et al., 1981) and was shown to account for equilibrium hue judgments on backgrounds of different chromaticities (Chichilnisky & Wandell, 1999). Models with this structure have been proposed to account also for hue scaling (Valberg et al., 1986b; De Valois & De Valois, 1993), though the nonmonotonic relation between cone signals and opponent hues was not recognized.

An alternative model that predicts nonmonotonicity in the relation between cone signals and hue equilibria allows L/M cone signals to alter the gain of the S-cone pathway prior to the antagonistic combination of cone signals. Such interactions are already incorporated into models of the S-cone pathway to account for phenomena such as transient tritanopia (Pugh & Mollon, 1979). In the present circumstances, L-cone stimulation would need to enhance the S-cone gain. The gain change would result in

increased blueness from the S-cone pathway, due to greater L-cone stimulation. A similar mechanism has, in fact, been suggested to account for simultaneous color contrast mediated by S-cone signals (Shevell & Barnes, 2001).

Finally, if the S-(L+M) cells described in the retina and LGN participate in the pathway mediating yellow/blue equilibrium hues, then they must interact with other cell types, such as the occasionally cited S-off cells (Valberg et al., 1986a), or cells that difference L and M cones, or perhaps cell types as yet undescribed (Calkins & Sterling, 1999). Therefore, the color names “red/green” and “yellow/blue” often given to retino-geniculate neural pathways are as misleading as the color names used in the past century to label cones.

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