

Perceiving Opponent Hues in Color Induction Displays

Gennady Livitz¹, Arash Yazdanbakhsh^{1,2}, Rhea T. Eskew, Jr.³ and Ennio Mingolla^{1,*}

¹ Department of Cognitive and Neural Systems, Boston University, Boston, MA 02215, USA

² Neurobiology Department, Harvard Medical School, Boston, MA 02115, USA

³ Department of Psychology, 125-NI, Northeastern University, Boston, MA 02115, USA

Received 4 February 2010; accepted 9 November 2010

Abstract

According to Hering's color theory, certain hues (red vs green and blue vs yellow) are mutually exclusive as components of a single color; consequently a color cannot be perceived as reddish-green or bluish-yellow. The goal of our study is to test this key postulate of the opponent color theory. Using the method of adjustment, our observers determine the boundaries of chromatic zones in a red–green continuum. We demonstrate on two distinct stimulus sets, one formed using a chromatic grid and neon spreading and the other based on solid colored regions, that the chromatic contrast of a purple surround over a red figure results in perception of 'forbidden' reddish-green colors. The observed phenomenon can be understood as resulting from the construction of a virtual filter, a process that bypasses photoreceptor summation and permits forbidden color combinations. Showing that opponent hue combinations, previously reported only under artificial image stabilization, can be present in normal viewing conditions offers new approaches for the experimental study of the dimensionality and structure of perceptual color space.

© Koninklijke Brill NV, Leiden, 2011

Keywords

Color induction, color opponency, neon color spreading

1. Introduction

Human color perception is normally compatible with the classic opponent color theory of Hering (1872), which describes chromaticity in two dimensions formed by pairs of primary hues: red–green and blue–yellow. All other hues are perceived as mixtures of two primary dimensions. Opponent mixtures do not create chromatic combinations, as they fall inside the two-dimensional continuum of Newton's color circle. In an opponent color space, transitioning from a green color to red results in seeing mixtures of green and yellow followed by seeing mixtures of yellow and

* To whom correspondence should be addressed. E-mail: ennio@cns.bu.edu

red, with some color in between appearing as pure (unique) yellow. A great deal of psychophysical data fits within this framework (Kaiser and Boynton, 1996).

However, Crane and Piantanida (1983) and Billock *et al.* (2001) used retinally stabilized, equiluminant, bipartite images comprising opponent hues to produce forbidden (non-Hering) color mixtures by making opponent hues from two different spatial locations blend together into a single color *via* a filling-in process. Subjects reported colors with simultaneous red/green and blue/yellow components. Billock *et al.* (2001) and Billock and Tsou (2010) argued that the opponency of red and green or blue and yellow hues is not hard-wired but rather an emergent property of color perception. However, the retinal stabilization technique used in these studies necessitated a limited number of subjects, and the results were solely verbal descriptions. Our study explores the perception of ‘forbidden’ colors using conventional displays and psychophysical methods.

In Fig. 1(a) an illusory desaturated ‘neon’ red hue appears in the white areas between the red line segments that form the diamond figure (Da Pos and Bressan, 2003; van Tuijl, 1975). A chromatic outer grid induces a hue complementary to its own in the region of the central diamond figure (Bressan, 1995; van Tuijl, 1975), and thus the black diamond in Fig. 1(c) appears greenish when embedded within the purple outer grid. Combining the purple outer grid with red lines in the diamond (Fig. 1(b)) creates conditions for integration of the central figure’s red neon hue with a green hue induced by the purple surround.

Similar perceptual effects can be observed in displays where chromatic contrast is made by solid colors (Fig. 1(g)–(i)). A chromatic surround induces a hue complementary to its own in the region of a central diamond figure. For example, perception of a blue diamond against a purple surround (Fig. 1(h)) results in integration of the green hue induced by the purple surround (Fig. 1(g)) and the blue color of the diamond (Fig. 1(i)), so the color of the diamond in Fig. 1(h) is perceived as bluish-green.

The complementary chromatic induction demonstrated in Fig. 1 is a manifestation of the much-studied process of color constancy (Brenner and Cornelissen, 2002; Conway, 2001; D’Zmura and Lennie, 1986; Hurlbert and Wolf, 2004; Krauskopf *et al.*, 1986; Land and McCann, 1971; Walraven *et al.*, 1987), which asserts spectral properties of a particular spatial region as either pertaining to an illuminant or to a surface. Chromatic induction constitutes a failure of this fundamental process, since it leads the visual system to respond as if the color of the object is different from what it would have appeared against a neutral background. Brenner and Cornelissen (2002) pointed out that in the case of complementary chromatic induction, spectral properties of the surround are incorrectly inferred to be properties of the illuminant.

Da Pos and Bressan (2003) provide evidence that a chromatic shift associated with complementary chromatic induction amounts to an additive mixture of the induced color (complementary to the surround) and the color of the target; compare Fig. 1(a) with 1(b), 1(d) with 1(e). However, this additive mixing is different

from the additive mixing of lights stimulating the same retinal location, because it does not involve photoreceptor summation (absorption of quanta of different wavelengths by the photoreceptors), and thus may produce a different perceptual outcome if the induced hue and the hue of the target region are opponent. Using a purple surround creates distinct conditions for integration of red and green hues through complementary chromatic induction, because in order to be integrated with the red hue, the green hue can only be induced by a complementary surround (see Discussion).

In the present study we parametrically varied the luminances of the color within the diamond (the red line segments in the neon stimulus, or the red of the solid diamond) and in the outer purple inducer (the surround grid or solid region), thereby creating a continuum of colors between red and green. Any red–green continuum contains red and green perceptual zones: a subset of colors where red hue is perceived and a subset of colors where green hue is perceived. In the geometrical model adopted by the opponent color theory these zones do not overlap; they are instead separated by yellow colors. However, if the postulate of opponency between red and green hues is violated, then perception of both red and green as components of a single color would be reflected as an overlap between red and green perceptual zones. We used a task aimed at detecting the presence or absence of red or green in the color of the diamond (Fig. 2(b)).

We used these well-studied diamond-shaped stimuli (Da Pos and Bressan, 2003; Grossberg and Mingolla, 1985; van Tuijl, 1975) in order to place our results in the context of the ongoing discussion related to the mechanisms and interpretation of the perceptual outcome of chromatic induction effects. We used both neon and solid color stimuli in order to analyze the strong connection between simultaneous chromatic contrast and perceptual transparency suggested by multiple studies and widely discussed in the literature (Anderson, 1997; Da Pos and Bressan, 2003; Ekroll and Faul, 2002; Grossberg and Mingolla, 1985; Nakayama *et al.*, 1990; Wollschläger and Anderson, 2009).

2. Methods

In Experiment 1 subjects were asked to vary colors, as described below, to find bounds on when they first (or no longer) saw ‘redness’ or ‘greenness’ in a diamond figure (Fig. 1(a)). Each subject was shown two stimulus sets, both using neon color displays. The RGC set (Fig. 2(a)) had an achromatic outer grid and inner line segments with a hue that varied from green to red, with yellow near the middle. Subjects could adjust the intensity of the red monitor primary (R) from minimum to maximum while the intensity of the green primary (G) was kept at maximum, and then adjust the intensity G from maximum to minimum while the intensity R was kept at maximum. In the second stimulus set, called RGC*, the purple outer grid made the inner diamond region look greenish by chromatic induction (Fig. 2(b), left). Subjects could adjust the intensity of the red primary for the line segments in

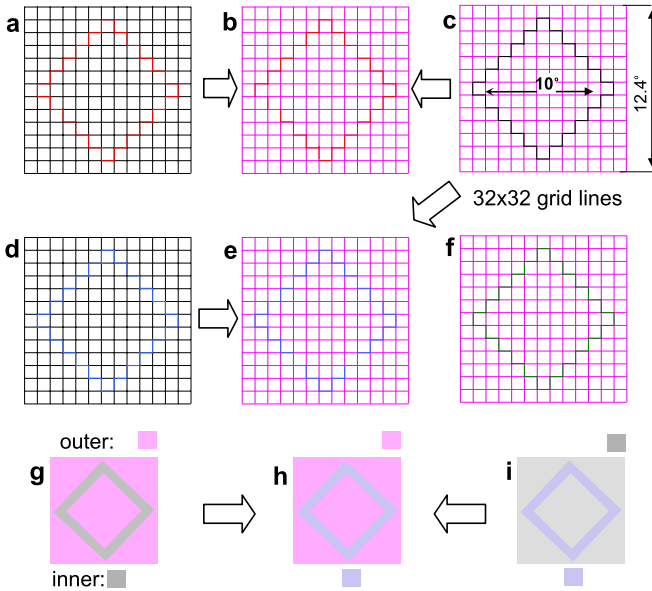


Figure 1. Neon color spreading: integration of colors in the diamond figure produced by varying the color of the inner line segments and the outer grid region. (a) Red inner segments in a black grid produce red neon color in the diamond; (d) blue inner segments in a black grid produce blue neon color; (c) purple grid segments induce a greenish color in the diamond composed of black inner segments; (b) red over green diamond, produced by superposing the red inner segments from (a) and the purple grid from (c); (e) blue over green figure produced by superposing the blue inner segments from (d) and the purple grid from (c); (f) purple grid induces green over green inner segments.

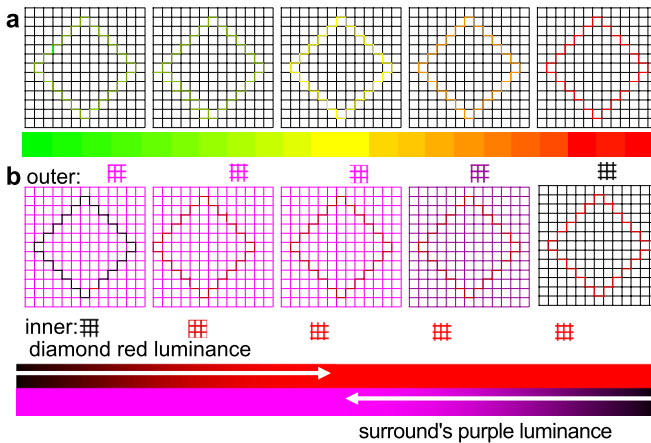


Figure 2. Neon color stimuli and color continua. (a) No chromatic induction: hue of inner segments is varied from green through yellow to red. (b) Chromatic induction: induction of green hue, produced by various amounts of purple in the outer grid, over illusory diamond figure formed by various amounts of red in the inner line segments of the diamond figure.

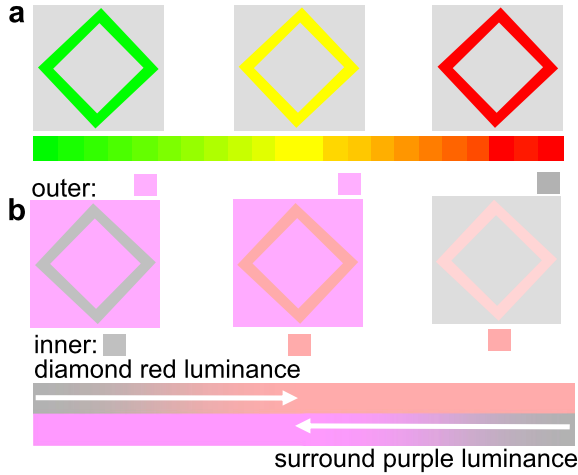


Figure 3. Solid stimuli. (a) No chromatic induction: hue of figure is varied from green through yellow to red. (b) Chromatic induction: induction of green hue, produced by various amounts of purple in the surround over the diamond, which contains various amounts of red.

the diamond from zero to maximum, with the outer grid segments kept purple. Further variation was achieved by varying the red and blue primaries (B) together in the outer grid segments, thereby decreasing the induced green. The ratio of luminances of the R and B primaries was fixed in the grid, and was fixed (at the minimum) for the G primary in the inner segments. As a result, the neon coloration of the diamond figure varied from green to red. The purpose of producing this continuum was to evaluate color experiences between two unambiguous extremes.

For this neon color continuum, the minimum values for R, G and B monitor primaries were *zero*. In the sRGB color coding system (Stokes *et al.*, 1996) this continuum can be described as two joined sets:

- (1) Grid segments: $R = 1, G = 0, B = 1$ combined with diamond segments: $R = 0:1, G = 0, B = 0$ ($a:b$ designates range from a to b);
- (2) Grid segments: $R = 1:0, G = 0, B = 1:0$ combined with diamond segments: $R = 1, G = 0, B = 0$.

Similarly, in Experiment 2, we designed two alternative red–green stimulus sets using solid surrounds and diamonds. In the RGC set (Fig. 3(a)), the hue of the central diamond figure, presented on a grey surround, was varied from green to red, while in the RGC* set (Fig. 3(b)), the hue of the diamond was produced by complementary chromatic induction, in the same way as for the neon stimuli (Fig. 2(b)). The minimum value for R, G, and B primaries for this continuum was set to the midpoint of each primary’s range, desaturating all the stimuli.

The geometrical proportions of the stimuli in both stimulus sets for both solid and neon color spreading configurations were the same: 12.4° — for the diagonal of the outer diamond boundary and 10° — for the inner diamond boundary (Fig. 1(c)).

2.1. Apparatus and Calibration

Subjects sat on a chair in a dark room, 584 mm from the monitor screen in a chin and forehead rest. Stimuli were presented on a Dell 3007WFPt 30" LCD monitor (406 × 650 mm) with resolution of 2560 × 1600 pixels. The monitor was calibrated *in situ* with a Photo Research PR-650 spectrophotometer using standard procedures (Brainard, 1989) with its three input–output relationships linearized by means of software lookup tables (Watson *et al.*, 1986). Viewing was binocular. The CIE 1931 chromaticity coordinates (x , y) and maximum luminances of the key colors used to construct the stimuli were green (0.214, 0.661, 65.7 cd/m²), yellow (0.426, 0.499, 95.1 cd/m²), red (0.655, 0.323, 29.6 cd/m²), magenta (0.376, 0.185, 37.5 cd/m²) and white (0.319, 0.342, 103 cd/m²). Most of the monitor was kept black, with a gray square off to the side displaying instructions (see below).

2.2. Subjects

Twenty-one and ten subjects participated in Experiment 1 and Experiment 2, respectively. All but one subject in both experiments were naïve. That subject, who alone participated in both experiments, was an author (RTE); he is a highly-experienced subject in color vision experiments, yet his results were very similar to the majority of naïve subjects. In both experiments, subjects performed 10 blocks of each of four different hue boundary tasks, on both the RGC and RGC* stimulus sets.

2.3. Experimental Protocol and Data Analysis

The hue boundary task was described in text displayed on the left side of the computer monitor. The instructions encouraged subjects to explore the continuum of colors until they felt confident with the outcome of their selection. The procedure for measuring individual red and green zones consisted of four consecutive tasks, each resulting in a position along the green–red continuum, arbitrarily denoted from 0 (green) to 1 (red). Because the measurements were expected to show some hysteresis, four different tasks were used. The four tasks and four resulting hue boundaries GR1–GR4 (Fig. 4(a) and 4(b)) were, in the order performed:

Starting from the extreme green position, while moving from green to red, report the *first* color where greenness is no longer perceived (GR1).

Starting from the extreme red position, while moving from red to green, report the first color where redness is no longer perceived (GR2).

Starting from the extreme green position, while moving from green to red, report the first color where redness is first perceived (GR3).

Starting from the extreme red position, while moving from red to green, report the first color where greenness is first perceived (GR4).

While performing these tasks, subjects were not explicitly asked to report simultaneous presence of redness and greenness in a single color. Using a variation of the method of adjustment, subjects were instructed to move back and forth along the

continuum, which typically involved multiple iterations converging to a color consistent with the goal of one of the hue boundary tasks. Depending on the task, that color would mark the location on the red–green continuum before which (or after which) redness (or greenness) is perceived. Thus, in each response subjects were asked to report either presence or absence of a *single* color quale (either redness or greenness). Subjects were never given any instructions about whether the color zones should, or should not, overlap, nor did they have any way to compare their responses across different trials or tasks.

Continuous perception of the same color quale while performing a hue boundary task could result in a bias either towards the presence or the absence of the color quale in question. This potential bias could cause hysteresis in the settings. Averaging the two mean settings (GR1 and GR4 or GR2 and GR3) should cancel the bias effects.

In Experiment 1 the neon stimuli were displayed while a subject performed a hue boundary task. In Experiment 2, in order to reduce the effects of retinal adaptation to the solid chromatic surrounds, the stimulus was presented for one second followed by a uniform midpoint grey square covering the stimulus region, presented for at least 1.5 s before the next stimulus was displayed.

The boundaries of the green and red zones were defined in a red–green continuum $[0, G]$ and $[R, 1]$. The values of GR1, GR2, GR3 and GR4 were averaged over 10 task repetitions performed for each subject, for RGC and RGC* stimulus sets.

After conducting the perceptual zone measurements, we asked each subject to verbally identify all the perceived hue components along the red–green continua where individual perceptual zones were measured. The subjects were limited to using only red, green, blue, and yellow as color names, but were not limited in a number of components describing a single color. Thus, in this part of the experiment, the subjects were not limited by reporting a single color quale, but were asked to name all perceived qualia. All but one subject were naïve and were not told about hypothetical perception of forbidden hue combinations.

3. Results

Subjects' judgments mark two zones in the red–green continua: a zone where a green hue is perceived and a zone where a red hue is perceived. Overlapping red and green zones mark the forbidden region wherein red and green hues coexist perceptually. Disjoint red and green zones correspond to yellow colors wherein red and green hues are mutually exclusive.

Figure 4(a) and 4(b) shows the results of two subjects who are typical of the majority of our subjects. The diamonds at the end of the red and green bars represent boundaries determined in tasks GR1–GR4 (bars labeled 1 to 4). The top two panels refer to neon stimuli (Experiment 1), the bottom two to solid stimuli (Experiment 2). For both stimulus types, the red and green zones overlap for the RGC* stimulus set, representing colors seen as both red and green, but are disjoint in the RGC stimulus

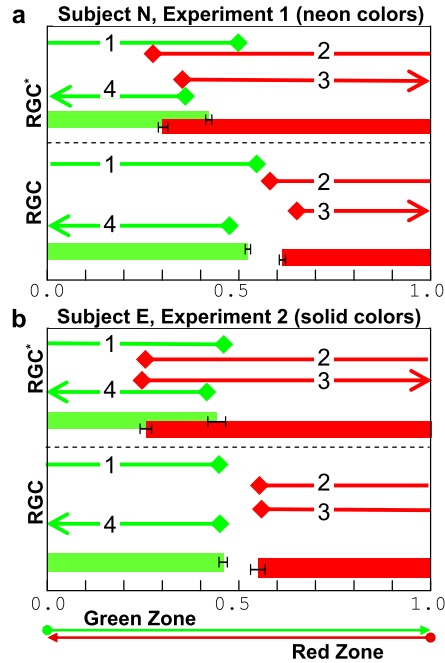


Figure 4. Results of measurement of red and green perceptual zones for two subjects using two color continua to illustrate data analysis. (a) Shows a subject from the neon stimulus experiment, (b) shows a subject from the solid stimulus experiment. RGC: colors formed without chromatic induction, as in Figs 2(a) and 3(a). RGC*: colors formed using purple surround to produce induction of green over a diamond figure, as in Figs 2(b) and 3(b). The color continua are arbitrarily denoted on a scale from 0 to 1 for both RGC and RGC*. Diamonds indicate the measured color boundary (e.g. in the bar labeled ‘1’, the diamond indicates the mean position where green is no longer to be seen, starting from extreme green). See Methods for full explanation. Both subjects show overlapping red and green zones for the RGC* continua but no overlap for the RGC continua, instead showing a gap indicating a distinct yellow zone.

set, consistent with yellow colors that are neither red nor green. Hysteresis (e.g., the difference between 1 and 4 in Fig. 4(a), top) is found for both RGC and RGC* in both neon and solid stimulus configurations.

The histograms in Fig. 5 show the extent of the overlap/gap between red and green zones measured in experiments with neon (panel a) and solid stimuli (panel b). A gap, predicted by opponent color theory, is shown as a negative overlap. The RGC* data reveal that perception of reddish-green colors is common for both neon and solid stimuli. Overlap is observed in about 70% of subjects. In contrast, a clear gap between red and green zones exists for almost all subjects in the RGC data sets for both neon and solid stimuli.

Using median values for GR1–GR4 yields essentially the same results with respect to an overlap between red and green perceptual zone. The overlap was observed for the RGC* stimulus set in about 77% of the subjects.

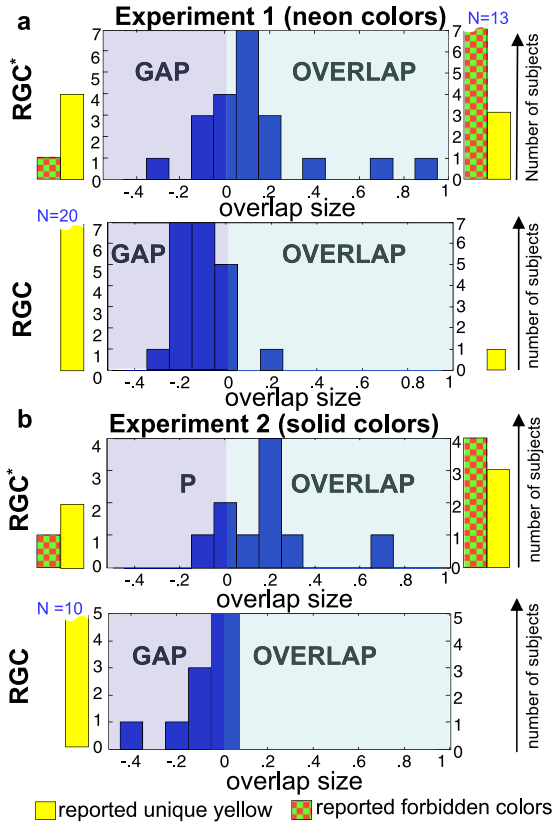


Figure 5. Histograms of red and green zone overlap/gap, with bin widths = 0.1. (a) Represents data with neon stimuli (Experiment 1), (b) represents data with solid stimuli (Experiment 2). In both experiments, most subjects show an overlap (positive value) between red and green zones with the RGC* continua, and a gap (negative value) with the RGC continua. Yellow and red–green checkered bars on the sides of (a) and (b) show the number of subjects verbally reporting only yellow or forbidden red–green colors correspondingly, separately for subjects showing the gap (at left) and the overlap (at right).

The subsequent verbal response of most of the subjects was consistent with the presence of an overlap between the red and green zone in their responses during the hue boundary experiment. About two-thirds of the subjects who set overlapping hue boundaries described the RGC* colors in the middle of the overlap as either reddish-green or reddish-yellowish-green (Fig. 5(a) and 5(b), checkered bars at right). In contrast, almost all of the subjects whose response was characterized by disjoint red and green zones described either RGC or RGC* colors in the ‘neither red nor green zone’ as yellow (Fig. 5(a) and 5(b), yellow bars at left).

Thus, many subjects explicitly identified colors on the trajectory from green to red for the RGC* stimuli — but not for the RGC stimuli — as a mixture of red, green, and yellow hues. The subjects’ unprompted hue naming using forbidden

color combinations is further evidence of the inadequacy of opponent color theory to describe their perceptual experience.

4. Discussion

One question that arises is the degree to which our method of producing ‘forbidden’ colors depends upon the particular color scheme we used — a purple surround, and the red–green dimension. Red and green are opponent but not complementary: their sum is not white, but yellow. Therefore, the green induced by the purple surround could combine with the red central color, without completely desaturating it. Although a cyan surround could be used to induce red over a green target, in our experience this induction is not as perceptually salient as the induction of green by a purple surround. Using the same principle of chromatic contrast for creating blue-and-yellow integration conditions is not feasible, because blue and yellow are both complementary and opponent, and therefore their combination lacks chromatic contrast either between the inducing region and the target or between the induced hue and the target. For example, a yellow surround inducing a blue hue over a blue target fails to create an opponent hue combination. Similarly, a blue surround inducing a yellow hue over a yellow target could not produce an opponent mixture. Thus, using opponent but not complementary colors is a critical element for creating conditions for integration of opponent hues as components of a single color through additive mixing. We see this as an intrinsic property of our method of constructing opponent mixtures that can be used to invoke perception of forbidden colors along the red–green dimension.

One explanation for our results is based on the evidence that chromatic induction stimuli can generate a dual color percept (Ekroll and Faul, 2002). One percept results from a transparent layer, the other from a background layer. Here, the red and green sensations we measured would be attributed to these two layers, rather than to a forbidden color combination. Such an interpretation is consistent with perceptual hue opponency. It is difficult to definitively rule this explanation out based upon our data: further experiments may be required. But in what follows, we argue that this explanation would require not one, but two transparent layers to account for our data, and that there is no evidence for that third layer. Central to our account is the perceived color of the background as discussed in the following paragraphs.

Neon color spreading is known to cause a sense of transparency (Anderson, 1997; Ekroll and Faul, 2002; Grossberg and Mingolla, 1985; Nakayama *et al.*, 1990), and red and green hues might be perceived as belonging to two separate surfaces on two different planes. In neon configurations similar to ours, neon color has been reported to appear on a transparent layer in front of a grid (Anderson, 1997; Da Pos and Bressan, 2003; Grossberg and Mingolla, 1985). Alternative explanations of chromatic effects in neon color spreading as phenomenal scission (Anderson, 1997; Ekroll and Faul, 2002) or assimilation of chromatically induced color (Da Pos and Bressan, 2003) have important implication for interpretation of the results of our experiments as either dual chromatic impressions pertaining to two different layers

or opponent mixtures within a single layer. According to Anderson (1997), phenomenal scission amounts to a perceptual decomposition of a low contrast region along the aligned contours into a near transparent layer and a distant layer. Scission is sufficient to explain perceptual effects in classical neon color spreading displays similar to the stimuli in Fig. 1(a) and 1(d), by which the chromaticity of the inner segments is assigned to the near transparent layer perceived in front of the achromatic grid.

Thus, the scission idea implies that the distal layer must have a lightness (or, to explain color scission, chromaticity) that is consistent with it being a continuation of the surround in which a target is embedded (Anderson, 1997; Ekroll and Faul, 2002). As Anderson (Anderson, 1997, p. 429) notes, without this ‘critical aspect of the present theory’ the predictions of scission would be ambiguous. Strict application of the scission concept implies that subjects should perceive a transparent green layer — a green filter — in front of a purplish plane in Fig. 1(c), due to phenomenal scission of the achromatic layer (the diamond) into complementary colors green and magenta. In informal observations using naive subjects, however, all of them report perceiving a black grid within the greenish diamond region of Fig. 1(c), not a continuation of the purple grid.

Applying the scission concept to chromatic contrast configurations brings up another problem pointed out by Da Pos and Bressan (2003). For example, having green segments embedded in a purple outer grid leads to perception of a transparent green layer in front of green segments within the diamond (Fig. 1(f)), which is hard to reconcile with the notion of green split into green and magenta — a logical prediction of the chromatic extension of the scission theory to this neon configuration. It is easy to verify that a physical green filter held in front of the purple grid produces a percept of a green region in front of a purplish grid, consistent with scission, but not with the perception of Fig. 1(f). These inconsistencies were pointed out and discussed in detail in Da Pos and Bressan (2003).

Bressan (1993) offered an alternative explanation of neon color spreading based on chromatic induction and subsequent assimilation of the induced color in the target region. Bressan’s concept extended Grossberg and Mingolla’s (1985) original explanation of neon color spreading. Da Pos and Bressan (2003) demonstrated that in configurations similar to the ones shown in Fig. 1, the neon color resides in a single transparent layer the hue of which can be described as an additive mixture of a hue of the line segments in the figure and a hue complementary to the hue of the surround. For example, a blue diamond (Fig. 1(d)) on a purple surround (Fig. 1(c)) looks blue–green (Fig. 1(e)) forming a single transparent blue–green neon color layer. Interpretation of this pattern as having two different transparent blue and green layers, both seen in front of a white background, seems exotic and unnecessary. By the same line of reasoning, the neon color of the diamond in Fig. 1(b) can be parsimoniously interpreted as a single transparent layer, whose hue results from integration of the green hue induced by the surround and the red hue of the figure, and not as two different transparent red and green layers in front of a purple

background. Thus, although neon displays may indeed generate transparency, for that transparency to explain a violation of red–green opponency would require not one transparent layer but two, and there is no evidence for such.

Wollschläger and Anderson (2009) argue that chromatic induction in displays in which transparency is perceived may be understood as an attempt to attribute to a near transparent layer a chromaticity that would account for its apparent transformation of the surround color. According to this concept, in Fig. 1(b) the visual system should assign a yellowish hue to the diamond-shaped filter to account for the purple grid appearing red in that region. The continuum of stimuli in Fig. 2(b) would correspond to a set of illusory or virtual diamond-shaped filters with chromaticities ranging from green to red passing through yellow. As illustrated in Fig. 6, the spec-

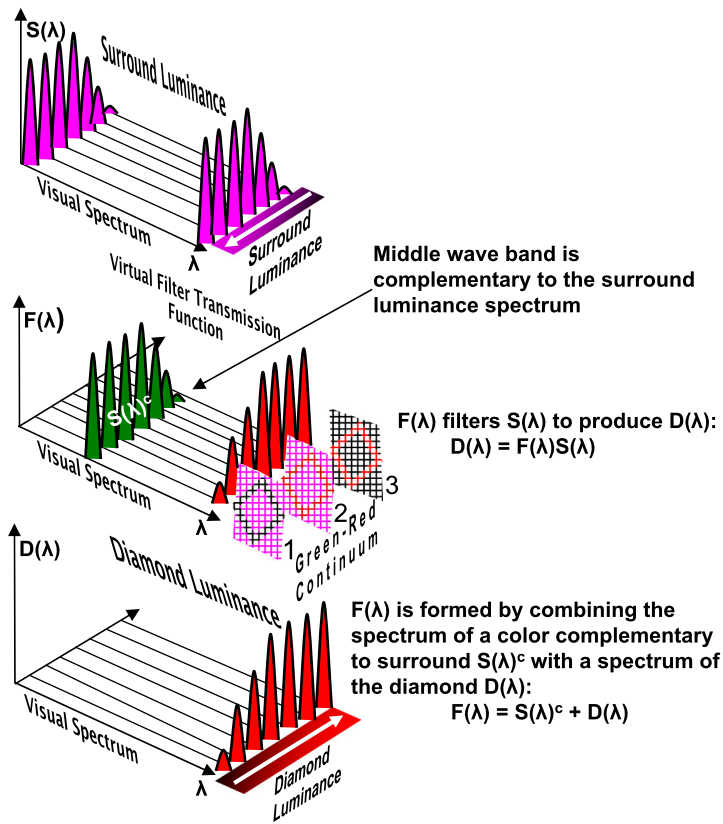


Figure 6. Formation of chromaticity of the diamond-shaped virtual filter by integration of the spectral properties of the diamond segments and a color complementary to the surround grid. The top and bottom panels schematically represent physical stimuli that are metameric to our monitor chromaticities; the middle panel represents the virtual filter (see text). The precise shapes of the wavelength bands are not important. The middle panel shows how the spectral transmittance of the virtual filter changes as the red luminance of the diamond segments increases from minimum to maximum (bottom panel), and as the purple luminance of the outer grid segments increases from minimum to maximum (top panel).

tral characteristics of this set of filters would have a band in the middle wavelength region, to account for the green end of this continuum, with a second band in the long wavelength region of increasing height across the continuum (going from '1' to '2', middle panel), so that in the middle of the continuum (at '2') there would be a double-peaked spectral distribution. The second half of the continuum (going from '2' to '3') would imply a decrease in transmittance of the middle wavelength band, so that the continuum's red end ('3') would correspond to a filter with a single long wave peak. Formation of the spectral properties of these illusory or virtual filters can be interpreted as integration of the spectral properties of the color complementary to the surround (green, for the red–green continuum in Fig. 2(b)) and those of the diamond segments (red, for the red–green continuum in Fig. 2(b)), consistent with the results of Da Pos and Bressan (2003). Thus our results are completely compatible with scission of the stimulus into a background and a transparent layer, and with Da Pos and Bressan's results, in that the virtual filters seen in our neon stimuli are formed by the visual system to produce an additive mixture of the color complementary to the surround and the color of the target. Whereas a *real* filter with the passbands shown at '2' in Fig. 6 (middle) would have produced a percept of yellow when placed over the white background, due to additive color mixture of the long- and middle-wave bands at the level of the photoreceptors, construction of the virtual filter bypasses photoreceptor summation and permits the percept of the forbidden hue combinations of reddish-green or reddish-yellowish-green. The idea is that forbidden hues would be seen in the middle of the continuum, where the middle- and long-wave bands of the virtual filter are simultaneously of maximum height.

Data from Experiment 2 illustrate that forbidden hues are not peculiar to neon color stimuli. The virtual spectral transmittance (Fig. 6) is consistent with the results obtained in Experiment 2 as well as Experiment 1, assuming the solid diamond is interpreted as a transparent layer in front of the solid background, so the virtual filter explanation described for neon displays is also completely consistent with the scission hypothesis applied to solid stimuli. Unlike the neon stimuli, however, chromatic induction in the solid stimuli also readily admits of a second interpretation, with a uniform filter or illuminant that is discounted (color constancy). As discussed next, mechanisms of color constancy would produce the same results in our experiment as the scission mechanism.

The visual system could either interpret the solid stimuli in the Experiment 2 as diamond-shaped filters seen in front of a purple plane, similar to the neon case, or as diamond shapes viewed through a rectangular purple filter or purple illuminant that covers the whole stimulus. Let us designate these interpretations as the scission hypothesis and the color constancy hypothesis (because this interpretation involves discounting the filter or illuminant), respectively. Since our subjects were asked to evaluate the color of the diamond, their answers should refer either to the color of the diamond object (according to the color constancy hypothesis) or to the color of the diamond filter (according to the scission hypothesis). If the stimulus

sequence (Fig. 3(b)) causes any sense of transparency, the green end of the continuum should either be interpreted as a green shape seen through a rectangular purple filter or a diamond-shaped green filter in front of a purple plane. However, none of our subjects reported any redness at this end of the continuum, whether in their chromatic boundary settings or their verbal report — the only color name used was ‘green’ here. Therefore, we can conclude that, to the extent transparency was involved at all, our subjects could effectively discount the purple color of the rectangular filter (if they perceive this stimulus as a green diamond viewed through a purple filter) or the purple color of the plane behind the filter (if they perceive this stimulus as viewed through a diamond-shaped green filter). This conclusion is consistent with perceptual experience one would get viewing a physical green diamond shape through a physical purple filter covering the whole stimulus, or viewing a purple surface through a green diamond-shaped filter. In fact, this observation is a reflection of color constancy.

Thus, reporting of stimuli in the middle of this red–green continuum as reddish-green or reddish-yellow-green refers either to the color of the diamond filter, or to the color of the diamond shape seen through a filter — in either case, to a single surface. The fact that perception of red and green hues in our solid stimuli belongs to a single surface is more evident if we compare the image in the middle of the red–green continuum in Fig. 3(b) with the image in Fig. 1(h) made by the purple surround and the blue diamond figure. The fact that the bluish-green color of the diamond is an additive mixture of the color of the diamond (blue) and the induced color (green) is quite evident there. There is no evidence for judging it as belonging to two separate transparent surfaces. Parsimoniously we should apply the same interpretation to the stimulus formed by a red diamond on the purple surround.

To summarize our interpretation, we suggest that our subjects effectively discount the color of the surround, whether they perceive a rectangular filter in front of the diamond or a diamond-shaped filter. The effect on the diamond’s color caused by complementary chromatic induction in configurations with solid stimuli (Fig. 3(b)) is the same as in neon color configurations (Fig. 2(b)). The resulting hue amounts to a mixture of a hue of the elements forming a central figure and a hue complementary to the elements of a surround. Whether this induced color is seen in a transparent layer is not relevant to our main point, as it is perceptually attributed to a single surface in either the neon or solid stimuli.

Ekroll and colleagues (2002, 2004) did not directly challenge hue opponency. However, their findings do suggest a general inadequacy of classical three-dimensional color space based on hue-saturation-brightness attributes to perception of simultaneous chromatic contrast (MacLeod, 2003). Vladusich *et al.* (2006) pointed out that the ‘peculiar nature of chromatic contrast’ (Ekroll *et al.*, 2004) could be a basis for an interpretation of red, green, blue, and yellow qualia as independent non-opponent chromatic dimensions. Vladusich *et al.* (2007) demonstrated that redness and greenness fail to cancel each other in certain chromatic contrast configurations and suggested a six-dimensional unipolar color space.

Our results also support a revision of the opponent structure of perceptual color space. Unlike classical opponent color space which permits at most two hue components in a single color (e.g. reddish-yellow or greenish-yellow), a non-opponent color space does not forbid perception of opponent hues together and subsequently opens the possibility of perception of colors with three and even four primary hue components. Not only do the chromatic border results of Experiment 1 and Experiment 2 imply perception of opponent red–green mixtures, but also red–green–yellow mixtures were verbally reported by most of our subjects. The red–green colors reported with stabilized retinal images (Billock *et al.*, 2001; Crane and Piantanida, 1983) are also consistent with a non-opponent color space.

Our results strongly support the idea of unipolar mechanisms associated with red, green, blue, and yellow hues. This idea was an important part of the model of De Valois and De Valois (1993), in which half-wave rectified LGN inputs feed into cortical mechanisms to provide perceptual hue opponency. Psychophysical evidence in support of rectified color encoding has been described by Billock *et al.* (1994), Eskew (2008), Miyahara *et al.* (2001), Sankeralli and Mullen (2001), and Smith and Pokorny (1996).

5. Conclusions

In classical opponent color space, hue is two-dimensional; it admits combinations of no more than two unique hues. In effect, opponent hues represent positive and negative values of a single chromatic dimension. However, the results of our study are incompatible with such a geometry. A color space with a two-dimensional hue structure cannot account for overlapping red and green zones. Our study helps to further explore the dimensionality of perceptual color space and provides experimental evidence, supporting the idea of independent dimensions encoding perceptual color qualia: red, green, blue and yellow.

Acknowledgements

G. L., E. M. and A. Y. were supported in part by CELEST, an NSF Science of Learning Center (SBE-0354378 and OMA-0835976) at Boston University. A. Y. was also supported by NIH grant EY13135 to the Neurobiology Department (Livingstone Lab), Harvard Medical School, USA.

References

- Anderson, B. L. (1997). A theory of illusory lightness and transparency in monocular and binocular images: the role of contour junctions, *Perception* **26**, 419–453.
- Billock, V. A. and Tsou, B. H. (2010). Seeing forbidden colors, *Scientific American* **302**, 72–77.
- Billock, V. A., Vingrys, A. J. and King-Smith, P. E. (1994). Opponent color detection threshold asymmetries may result from reduction of ganglion cell subpopulations, *Vis. Neurosci.* **11**, 99–109.

- Billock, V. A., Gleason, G. A. and Tsou, B. H. (2001). Perception of forbidden colors in retinally stabilized equiluminant images: an indication of soft-wired cortical color opponency? *J. Optic. Soc. Amer. A* **18**, 2398–2403.
- Brainard, D. H. (1989). Calibration of a computer controlled color monitor, *Color Res. Appl.* **14**, 23–34.
- Brenner, E. and Cornelissen, F. W. (2002). The influence of chromatic and achromatic variability on chromatic induction and perceived colour, *Perception* **31**, 225–232.
- Bressan, P. (1993). Revisitation of the luminance conditions for the occurrence of the achromatic neon color spreading illusion, *Percept. Psychophys.* **54**, 55–64.
- Bressan, P. (1995). A closer look at the dependence of neon color spreading on wavelength and luminance, *Vision Research* **35**, 375–379.
- Conway, B. R. (2001). Spatial structure of cone inputs to color cells in alert macaque primary visual cortex (V-1), *J. Neurosci.* **2**, 2768–2783.
- Crane, H. D. and Piantanida, T. P. (1983). On seeing reddish green and yellowish blue, *Science* **221**, 1078–1080.
- Da Pos, O. and Bressan, P. (2003). Chromatic induction in neon colour spreading, *Vision Research* **43**, 697–706.
- De Valois, R. L. and De Valois, K. K. (1993). A multi-stage color mode, *Vision Research* **33**, 1053–1065.
- De Valois, R. L., Abramov, I. and Jacobs, G. H. (1966). Analysis of response patterns of LGN cells, *J. Optic. Soc. Amer.* **56**, 966–977.
- D’Zmura, M. and Lennie, P. (1986). Mechanisms of color constancy, *J. Optic. Soc. Amer. A* **3**, 662–672.
- Ekroll, V. and Faul, F. (2002). Perceptual transparency in neon color spreading displays, *Percept. Psychophys.* **64**, 945–955.
- Ekroll, V., Faul, F. and Niederée, R. (2004). The peculiar nature of simultaneous colour contrast in uniform surrounds, *Vision Research* **44**, 1765–1786.
- Ekroll, V., Faul, F., Niederée, R. and Richter, E. (2002). The natural center of chromaticity space is not always achromatic: a new look at color induction, *Proc. Nat. Acad. Sci. USA* **99**, 13352–13356.
- Eskew, R. T., Jr. (2008). Chromatic detection and discrimination, in: *The Senses: A Comprehensive Reference*, R. H. Masland and T. D. Albright (Eds), Vol. 2: Vision II, pp. 101–117. Academic Press, New York, USA.
- Grossberg, S. and Mingolla, E. (1985). Neural dynamics of form perception, boundary completion, illusory figures, and neon color spreading, *Psycholog. Rev.* **92**, 173–211.
- Hering, E. (1872). *Outlines of a Theory of the Light Sense*. Harvard University Press, Cambridge, Mass., USA (1964).
- Hurlbert, A. and Wolf, K. (2004). Color contrast: a contributory mechanism to color constancy, *Prog. Brain Res.* **144**, 147–160.
- Kaiser, P. and Boynton, R. M. (1996). *Human Colour Vision*. Optical Society of America, Washington, DC, USA.
- Krauskopf, J., Zaidi, Q. and Mandler, M. B. (1986). Mechanisms of simultaneous color induction, *J. Optic. Soc. Amer. A* **3**, 1752–1757.
- Land, E. H. and McCann, J. (1971). Lightness and retinex theory, *J. Optic. Soc. Amer.* **61**, 1–11.
- MacLeod, D. (2003). New dimensions in color perceptions, *Trends Cogn. Sci.* **7**, 97–99.
- Metelli, F., Da Pos, O. and Cavedon, A. (1985). Balanced and unbalanced, complete and partial transparency, *Percept. Psychophys.* **38**, 354–366.

- Miyahara, E., Smith, V. C. and Pokorny, J. (2001). The consequences of opponent rectification: the effect of surround size and luminance on color appearance, *Vision Research* **41**, 859–871.
- Nakayama, K., Shimojo, S. and Ramachandran, V. S. (1990). Transparency: relation to depth, subjective contours, and neon color spreading, *Perception* **19**, 497–513.
- Sankeralli, M. J. and Mullen, K. T. (2001). Bipolar or rectified chromatic detection mechanisms? *Vis. Neurosci.* **18**, 127–135.
- Smith, V. C. and Pokorny, J. (1996). Color contrast under controlled chromatic adaptation reveals opponent rectification, *Vision Research* **36**, 3087–3105.
- Stokes, M., Anderson, M., Chandrasekar, S. and Motta, R. (1996). A standard default color space for the internet sRGB, <http://www.color.org/contrib/sRGB.html>, November 1996.
- van Tuijl, H. F. J. M. (1975). A new visual illusion: neonlike color spreading and complementary color induction between subjective contours, *Acta Psychologica* **39**, 441–445.
- Vladusich, T., Lucassen, M. P. and Cornelissen, F. W. (2006). Edge integration and the perception of brightness and darkness, *J. Vision* **6**, 1126–1147.
- Vladusich, T., Lucassen, M. P. and Cornelissen, F. W. (2007). Brightness and darkness as perceptual dimensions, *PLoS Comput. Biol.* **3**, e179.
- Walraven, J., Benzschawel, T. L. and Rogowitz, B. E. (1987). Color-constancy interpretation of chromatic induction, *Die Farbe* **34**, 269–273.
- Watson, A. B., Nielsen, K. R. K., Poirson, A., Fitzhugh, A., Bilson, A., Nguyen, K. and Ahumada, A. J., Jr. (1986). Use of a raster framebuffer in vision research, *Behav. Res. Methods, Instruments Computers* **8**, 587–594.
- Wollschläger, D. and Anderson, B. L. (2009). The role of layered scene representations in color appearance, *Curr. Biol.* **19**, 430–435.