Brown Induction and Red/Green Hue Shifts

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Abstract

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This body of work details a number of experiments relating to brown induction (the change of appearance of a stimulus from yellow to brown) and shifts in red/green hue balance (the balance point of stimuli across the yellow-blue spectrum where they appear neither reddish nor greenish). These experiment involve variations of targets and their surrounding stimuli in the dimensions of luminance, saturation, and hue, as well as variations in the manner of their optical presentation (monocular [stimulus only in one eye], binocular [same stimulus both eyes], or dichoptic [different stimuli in each eye] presentations). It was found that brown induction is strongest for stimuli that are sufficiently darker than their surround and slightly desaturated. Although brown stimuli show a systematic shift in their red/green balance compared to yellow stimuli this appears to be controlled by a separate mechanism that is present for all targets that vary along the yellow-

blue spectrum (including achromatic gray targets) when they are darker than their surrounds. It was also found that brown induction can occur both prior to and after the cortical combination of signals from the two eyes (in both monocular and binocular pathways, respectively), showing an enhancement from perceptually contiguous bright surrounds presented in either the same or opposite eye as a target. No similar effect was observed for red/green balances, which appear to be influenced only in monocular pathways and have a different relationship with surround contiguity. There are also differences in the effects of target and surround size on brown induction compared to red/green balance shifts. Brown represents a categorical hue change from yellow that is usually accompanied by a red/green balance shift, but such red/green balance shifts can also occur independently of a categorical hue changes as seen with achromatic gray stimuli. These many differences between brown induction and red/green balance shifts suggest that they are two separate phenomena that can co-occur but are not directly related, suggesting different neural mechanisms for each. In addition to academic significance, understanding and accurately modeling these effects is increasingly important for issues related to both human and machine vision.

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I. INTRODUCTION

Research on the perception of brown colors has been a rarity throughout the history of color research despite its ubiquity as a color category in human languages. Although there are some older papers published in German (Kiesow, 1930; Oesterreich, 1928), the earliest English language research was presented by Bartleson (1976). Bartleson used a set of paper Munsell chromatic color chips to make a number of observations about stimuli that appear brown. These observations were Bartleson's own (although he points out he used some outside observers for verification, he expected there to be variation in reports from other observers) and relied on him scaling three relative attributes of the Munsell chips. These attributes were lightness (with 0% representing black and 100% representing white), hue (percentage of red, green, blue, and/or yellow for a total of 100%), and what he called "strength" (the percentage of chromatic content to achromatic content). He points out that what he calls strength is not equivalent to saturation as he says "strength" can vary with hue even without changes in saturation. He scaled a set of chips using these criteria before performing a modified version of the experiment. In the modified experiment, he replaced the four hue categories with two relating to brown (the percent of brown versus not brown). His results showed that the strength of brown was maximal for stimuli of Munsell hue 5 YR ("orange"), and low value (roughly "lightness") and moderate chroma (roughly "saturation"). Importantly, across a range of yellow-red Munsell hues (2.5Y to 7.5 R), strong perception of brown was associated with dark samples, while orange was associated with samples of higher lightness.

Subsequent research focused primarily on whether or not brown was an elemental or unique hue percept rather than studying the nature of brown stimuli themselves (Fuld et al., 1983; Quinn et al., 1998). The question of if something is an elemental hue (a basic building block from which all other hue categories are constructed) is named in parallel to the chemical elements which compose all substances (Mollon & Jordan, 1996). The search for a biological basis for elemental hues is undertaken by many approaches and is a major aspect of linguistics research as well (Stoughton & Conway, 2008). The possibility of brown belonging to this category has yet to be resolved within the literature by subsequent research and will not be explored in this dissertation, though we will address issues that are relevant to those interested in exploring this issue further.

Uchikawa, Uchikawa, and Boynton (1989) returned to research on the factors that influence the perception of brown, showing that nearness of a higher luminance surround relative to a stimulus had a great influence on whether it was perceived as brown or orange. They looked at both bright and dark colors and varied the location of the bright surround in relation to the colored targets allowing for contiguous and non-contiguous surrounds. They found a bright, contiguous surround, even if it was only 1/16 the size of the target stimulus, greatly increased the likelihood a subject would call the stimulus brown instead of orange. Their study was limited by the available technology and they did not systematically vary the luminance or size of either the target stimulus or surround. Although they were able to conclude the effect of surround contiguity was powerful when it came to inducing brownness, they were unable to quantify the size of these effects using their methodology. I subsequently developed a method for measuring strength of brown by using what we have come to call the brown boundary (the highest light level at which brown is perceived with no trace of yellow). This technique has allowed us to measure relative brown strength under a wide variety of surround conditions in order to better understand the nature of brown induction.

One of the primary foci of this dissertation will be examining red/green balance and how it is both separate from and related to the perception of brown stimuli. Red/green balance is present for both yellow/brown and blue stimuli and it represents a point at which a stimulus looks neither reddish nor greenish. Bartleson described this change in red/green balance from brown versus yellow by noting the strong browns produced by darkening orange colors. This leads to a question if brown as a category has a shifted balance as a function of its appearance or if the red/green balance shift is due to the darkening of stimuli as a whole, regardless of color category. This is the primary question I will be addressing in this dissertation. We have gathered a large amount of red/green balance data across a wide variety of conditions. Some of these are gathered simultaneously with brown boundary data and some of them are gathered independently of brown boundary data. We have also developed a model for explaining how red/green balance shifts operate and have gathered physiological and psychophysical data in support of red/green balance shifts occurring outside of the retina. Our current explanation for shifts in red/green balance perception is based on a cognitive model using higher level visual areas of the brain. This dissertation will begin by focusing on brown boundary data and developing plausible neural mechanisms that could underlie brown induction and then shift to the change in red/green balance that is also observed with brown stimuli. Finally we will reach a conclusion about how these effects are and are not related on various properties related to their induction.

II. STUDIES OF BROWN INDUCTION

In order to investigate quantitatively the effects of target stimulus and surround parameters, we allowed subjects to adjust the luminance of a constant-chromaticity target stimulus that appeared peach (yellow-orange) at high luminance and brown at low luminance, using a CRT display. Subjects adjusted the luminance level of the target stimulus to the threshold for perceiving only brown (termed the upper boundary of brown perception) as well as the threshold where brown is last perceptible (termed the lower boundary of brown perception). Based on the qualitative data discussed previously, we hypothesized that the luminance level at which subjects could perceive brown would be highest in the presence of a high luminance surround contiguous with the target stimulus, but that brown would still be perceived under conditions where there was a high luminance surround present in the visual field, but not contiguous with the stimulus. This type of hypothesis is consistent with both a global contrast mechanism and a local contrast mechanism working simultaneously. If only a global contrast mechanism is being used we will not see any change between bright contiguous and non-contiguous surrounds. However if a local contrast mechanism also exists it will enhance brown induction for bright contiguous surrounds. We also hypothesized that under conditions where there was no high luminance surround present subjects would be unable to perceive the stimulus as brown as it is considered a contrast color and therefore requires a luminance contrast. In all conditions, we hypothesized that both the upper and lower thresholds would shift together as the range of stimuli that appear brown should be derived from their relative contrast. These hypotheses are derived from what Bartleson (1976) considered to be the strongest brown stimuli and the surround induction effects noted by Uchikawa et al., (1989).

Additionally, we conducted a set of experiments where we varied the size of both the target stimulus and the contiguous surround in order to test for size influences. If luminance anchoring is primarily responsible for these effects we should see little effect of size variations of the surround. However if perceived saturation of the target is important as well, as noted by Bartleson, changes in target size could impact the size of the brown induction effect due to the relationship between target size and saturation (McKeefry, Murray & Parry, 2007).

A. EXPERIMENT 1 - SURROUND LOCATION EFFECTS

Methods

Apparatus: A ViewSonic G90fB CRT monitor, with a frame-rate of 75Hz, was used for stimulus display. The monitor's light output was measured with a Photo Research SpectraScan PR-702. A subject's head was supported by a chin and forehead rest at a distance of 63cm, causing the full screen to subtend 33° by 25°. A black foam-board enclosure surrounded all apparatus components and the observer's head, so that when room lights were off, nothing was visible beyond the monitor screen. This apparatus was used for Experiments 1-5 without any changes to the arrangement of the display from what is listed here.

Subjects: Subjects were 9 University of Washington undergraduates (ages 20-25) who completed the studies in exchange for course credit and who were assessed as having normal color vision by the Ishihara Pseudoisochromatic Plate test. Some were native speakers of American English, while some were not. All procedures and consent forms were approved by the appropriate Institutional Review Board at the University of Washington. These color vision testing methods and IRB approvals applied to all studies in this paper.

Stimuli and Procedures: In Experiment 1, subjects adjusted the luminance of a constant-chromaticity 4°-diameter foveal target stimulus to set both upper (the highest light level at which brown is perceived with no trace of yellow) and lower (the lowest light level at which brown is perceived) boundaries of brown perception. Above the upper boundary, the hue of the target appeared to be a mixture of brown and yellow or red. Below the lower boundary, the target appeared achromatic black (see Figure 1). Subjects were tested with the room lights off, but were kept room-light adapted by switching the lights on between conditions. Subjects were specifically instructed to set their upper boundary "at the highest light level at which the target appears exclusively brown with no trace of yellow" and their lower boundary "at the lowest light level at which the target still appears brown rather than black". The upper boundary lies along the border of a yellow/brown mixture (butterscotch) and a stimulus that appears brown without any remaining element of yellow. Similarly, the lower boundary lies along the border between achromatic (black) and a stimulus that still appears brown with no trace of yellow. These boundary categories and instructions were chosen for their ease of allowing consistent judgments by subjects that are externally valid with how we judge colors in the real world. The chromaticity of the target (CIE 1964: x=.44, y=.46) was selected to appear "peach" (yellow-orange) at high luminance and brown at low luminance.

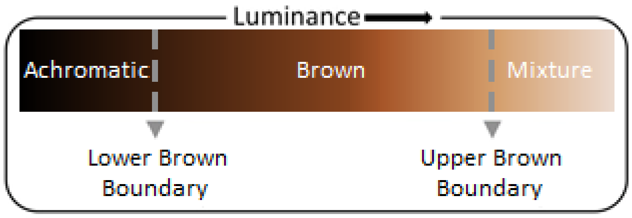


Figure 1. Perceptual Hue Categories as Luminance Changes.
This is a schematic representation of the change of hue of a target from a brown/yellow mixture (right) through brown (middle) to achromatic (left), as target luminance decreases. Observers can adjust the luminance of the target to their perceptual boundaries of the brightest brown that has no trace of yellow (upper brown boundary) or the dimmest brown (lower brown boundary).

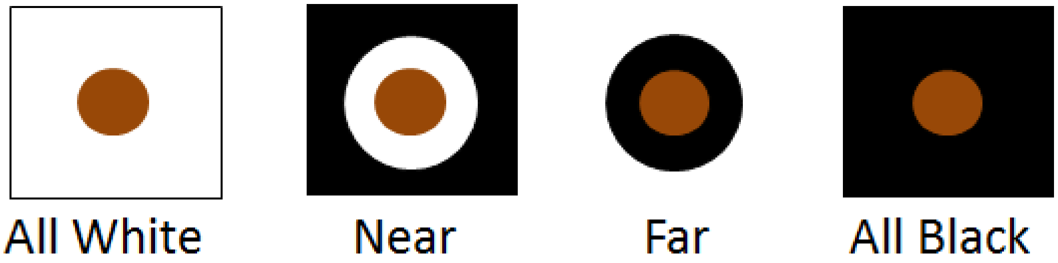


Figure 2. Spatial Configurations of Target Stimulus and Surround in Experiment 1.
The Near condition was a white annulus of 2° width contiguous with the 4° target stimulus with a black background. The Far condition was an otherwise identical black annulus on a white background. The All Black and All White conditions feature full screen backgrounds with no annuli.

The 4°-diameter target stimulus appeared with either a white or black annulus of 2° width immediately surrounding it (near surround). There was also a white or black annulus (far surround) extending from the edge of the near surround to the monitor screen’s terminus (see Figure 2). The white surround was 142 cd/m^2 (CIE 1964, x, y = .29, .30) and black surround was <0.001 cd/m^2. The target appeared for 1 second before turning off (replaced by whatever the near surround color was for that condition) for 3 seconds. This was done to prevent adaptation to the target.

Subjects viewed stimuli with the right eye, while the left eye was patched. Subjects adjusted the luminance of the target stimulus using a keyboard and were free to increase or decrease the luminance over a range of 85 equally spaced luminance values (.98 cd/m^2 to 83.3 cd/m^2) until they could make a judgment on the upper or lower boundary. Subjects then pressed a key to accept the boundary luminance value. The subjects made a total of five such settings, each starting at a randomly selected luminance, before moving on to the next surround condition. Subjects completed four sessions for each condition and only completed a maximum of one session per day. Conditions were counter-balanced across sessions to control for order effects.

Results

Figure 3 shows upper and lower boundaries for perceiving brown (upper and lower ends of the thick bars) for the different stimulus surround configurations averaged across all subjects, with the thin error bars showing ±1 standard deviation. Results indicated that subjects perceived the target stimulus as brown at significantly higher light levels for both the upper and lower boundaries in the presence of a white near surround than in its absence. Subjects perceived brown at significantly lower light levels in the presence of a white far surround with a black near surround when compared to conditions with a white near surround. If no white near or far surround was present most subjects did not consistently perceive brown alone at any light level (for this reason that condition was excluded from analysis). The upper and lower boundaries shifted in the same direction between stimulus configurations (white/black near/far surrounds), such that if one (upper or lower) increased or decreased in comparison to another configuration the other behaved likewise.

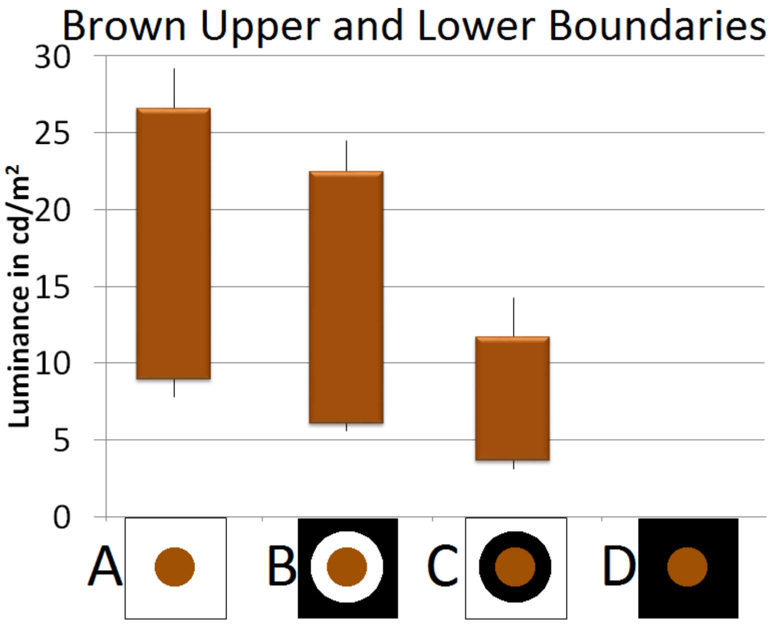


Figure 3. Brown Boundaries as a Function of Surround Configuration, Experiment 1. Upper and lower boundaries of luminance levels at which the target appeared brown, averaged across subjects for the four possible spatial configurations in Experiment 1. Error bars show the standard errors of subject means. A is a white far and near surround. B is a black far surround and white near surround. C is a white far surround and black near surround. D is a black near and far surround. No subjects consistently saw the target stimulus as brown in the D condition.

A repeated measures ANOVA was performed for the spatial configuration (white/black near/far surround conditions) and boundary (upper/lower). Significant effects were found for the spatial configuration of the stimulus ($F(3,8)=72.433$, $p<.001$, $\eta^2=.901$), the upper versus lower boundary of the target stimulus ($F(1,8)=60.043$, $p<.001$, $\eta^2=.882$), and the interaction between the spatial configuration and the boundary (upper/lower) ($F(3,8)=16.612$, $p=.001$, $\eta^2=.675$). Every pairwise comparison between stimulus configurations at both upper and lower boundaries was significant at the $p<.01$ level. All subjects showed the same general pattern of results between conditions.

B. EXPERIMENT 2 – TARGET SIZE EFFECTS

Methods

In Experiment 2, 5 observers completed a set of trials with an otherwise identical 2°, 3°, 4°, 5°, 6°, or 7°-diameter foveal target stimulus with a 8° outer-diameter white near surround and black far surround. All other methodology is identical to that utilized in Experiment 1, meaning these conditions are variations on the stimulus arrangement B (Near) from Experiment 1.

Results

The results from Experiment 2 indicated that both the upper and lower thresholds for perceiving brown decreased as target stimulus size increased. Figure 4 shows upper and lower thresholds, expressed in cd/m^2, for the different stimulus sizes for perceiving brown for each near/far surround configuration (upper and lower ends of bars) averaged across all observers, with error bars of ±1 standard deviation.

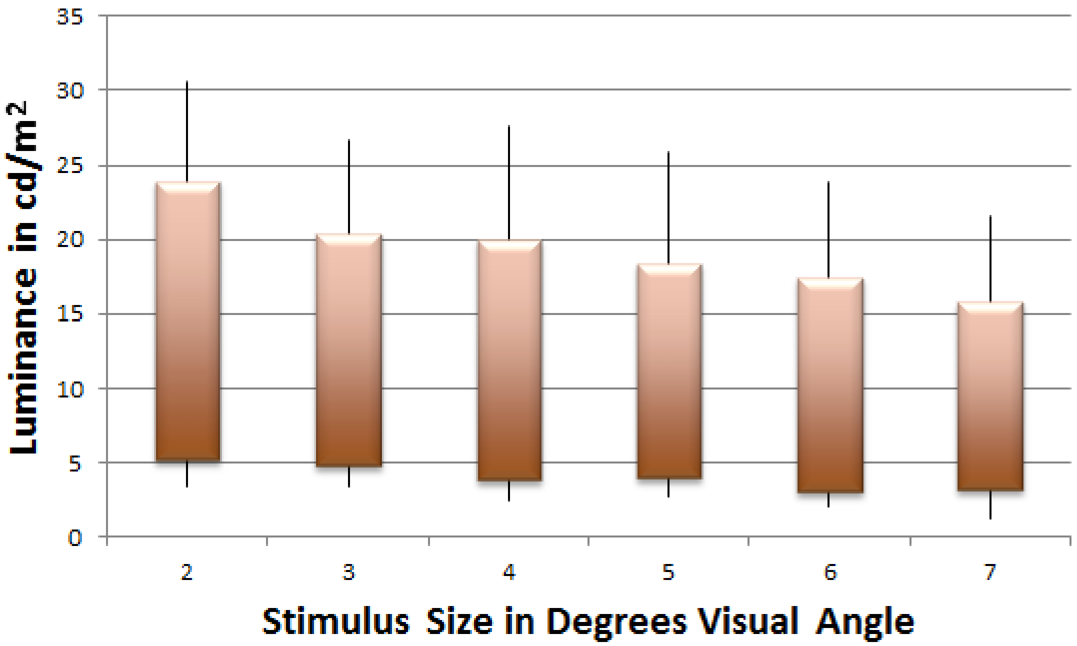


Figure 4. Brown Boundaries with Variation of Target Size, Experiment 2.
The upper and lower thresholds of brown perception for the six tested stimulus sizes in Experiment 2 are pictured here with standard deviations represented by the error bars. The stimulus parameter is otherwise identical to condition B from Experiment 1, but with an 8° contiguous surround diameter.

A repeated-measures ANOVA showed significant main effects for the size of the stimulus ($p<.01$, $F=11.512$, $\eta^2=.742$), and the threshold (upper/lower) of the stimulus ($p<.01$, $F=32.064$, $\eta^2=.889$), but the interaction was not significant ($p=.063$, $F=1.657$ $\eta^2=.515$).

C. EXPERIMENT 3 – SURROUND SIZE EFFECTS

Methods

In Experiment 3, 3 observers completed a set of trials with an otherwise identical constant 4°-diameter foveal stimulus and either a 6°, 12°, 18°, or 24° outer-diameter white near surround and black far surround, or a full-screen white surround. All other methodology is identical to that utilized in Experiment 1, meaning these conditions are replication of the stimulus arrangements B (Near, 6°) to A (All White, full-screen white) from Experiment 1 with the addition of 3 surround sizes in-between (12°, 18°, or 24°).

Results

The results from Experiment 3 indicated that the surround size had a significant effect on subjects' thresholds for perceiving brown. Figure 5 shows upper and lower thresholds, expressed in cd/m^2, for the different stimulus sizes for perceiving brown for each near/far surround configuration (upper and lower ends of bars) averaged across all observers, with error bars of ±1 standard deviation.

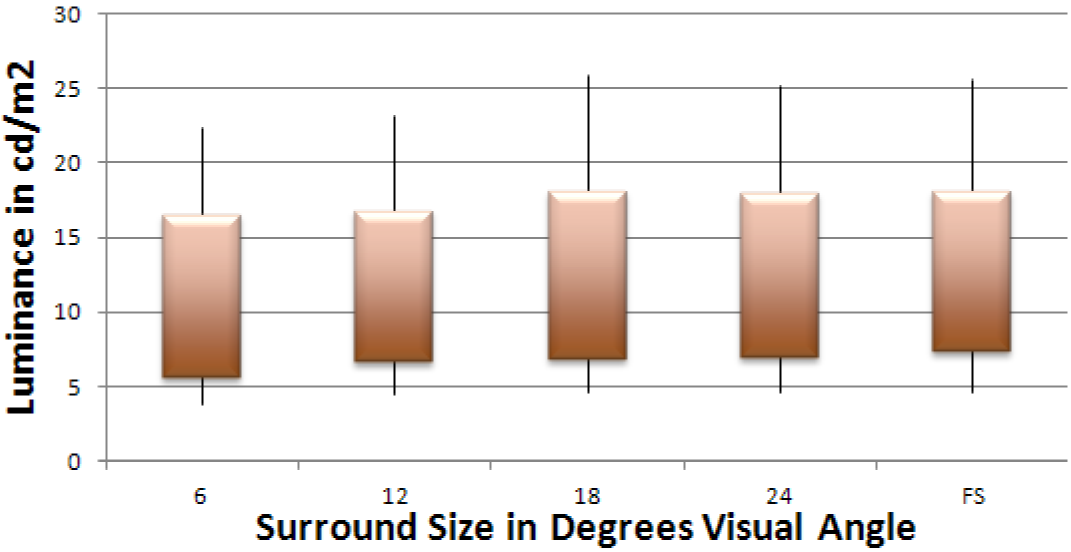


Figure 5. Brown Boundaries with Variation of Surround Size, Experiment 3.
The upper and lower thresholds of brown perception for the five tested surround sizes in Experiment 3 are pictured here with standard deviations represented by the error bars. The stimulus parameters are similar to condition C from Experiment 1 (identical for 6°) except for FS, which is identical to condition D.

A repeated-measures ANOVA showed significant main effects for size of the surround ($p<.05$, $F=4.674$, $\eta^2=.438$), and the threshold (upper/lower) of the stimulus ($p<.01$, $F=19.030$, $\eta^2=.760$), but the interaction was not significant ($p=.626$, $F=.540$ $\eta^2=.083$). None of the pairwise comparisons for surround size were significant for individual sizes.

Discussion for Experiment 1-3

The presence of a high luminance surround area in the visual field appears to be a key determinant of the perception of brown. When there is no high luminance surround in the observer's visual field that is sufficiently brighter than the target stimulus they could not consistently set a threshold for perceiving brown. The only conditions where it was possible to perceive brown on a black background required extremely low light levels and dark adaptation, but this effect still did not persist across the majority of observers (DeLawyer, Foote, Kwong, Lin, Short, Suh, & Buck, 2012).

Our results from the near-and far-surround spatial configurations taken together with the results from the variable near-surround configuration show that the location of high-luminance stimulation has a significant effect on brown perception, but the size of the surround has little effect, at least over the range we tested beyond 6° as seen in Experiment 3. It is possible smaller surrounds will have smaller effects, as the smallest surround we utilized is still relatively large (this is explored further in Buck, Shelton, Stoehr, Hadyanto, Tang, Morimoto, & DeLawyer, 2016). It is still the case that the surround presented in the contiguous condition B of Experiment 1 is many times smaller than the non-contiguous surround of condition C, leading us to conclude that a small high-luminance surround that is contiguous with a stimulus will allow brown perception at much higher light levels than a far larger high-luminance surround that is not contiguous with the stimulus.

These results suggest the neural mechanism for perceiving brown takes into account luminance of all objects in the visual field, but gives greater weighting to objects immediately surrounding the stimuli, and is not influenced greatly by the size of the high luminance surround area. It is possible two mechanisms exist, one at the level of the retina that takes into account contiguous surround luminance (possibly mediated by parasol ganglion cells) and another in higher cortical areas that is responsible for an anchoring effect that moderates the perception of luminance which is responsible for the effects observed when there is a black surround contiguous with the target stimulus. These mechanisms could be similar to those involved in blackness induction by which the presence of high luminance contrast induces blackness into a contiguous stimulus (Bimler, Paramei, & Izmailov, 2009). Some subsequent research in our lab has been mixed in regard to this, suggesting at least partial independence of blackness induction and brown induction (Vincent, 2017).

In addition to the importance of high luminance surrounds that are located near the target stimulus in producing brown perception, the size of the target stimulus also appears to be an important factor. As the size of the stimulus increases, the luminance level at which brown can be perceived decreases. One possible objection to this interpretation is the presence of the constant 8° surround with changing stimulus size. Thus, the near surround width shrank as the target stimulus size increased. Although the results of Experiment 3 suggest surround area doesn't have a large influence on these conditions, it is possible that it is exaggerating the effect of stimulus size. However, we can reject this possible alternative interpretation because we have replicated this condition with a full field white near and far surround and shown similar results as we will see in Experiment 4.

Although all subjects showed a significant difference in luminance between upper and lower thresholds, one thing to note is the relatively large amount of variance between where individual subjects' set their upper and lower thresholds. While within-subject variability was very low, the large variance between subjects in all conditions makes it hard to determine where a given individual from the general population's thresholds may lie. This means for a given observer they may require a high luminance surround to be anywhere from 5 to 14 times brighter than a stimulus in order for it to be perceived as brown. This large variation suggests the categorical perception of brown does not have well defined borders and could be influenced by a variety of cognitive factors beyond our control. Individuals' language, culture, profession, and other experiences likely influence the boundaries at which they perceive a stimulus as brown.
Question: how similar/different is the inter-individual variability for the perception of other colors?

Consistently across conditions, lower thresholds of brown perception show smaller effects sizes and less variability. This suggests compared to the upper threshold the lower threshold is less variable, and remains fairly stable despite changes in the surround configuration. Despite this, the same pattern of effects is observed for both upper and lower thresholds. Taken together, upper thresholds are preferred for experimental methodology due to the increased power they provide. Subsequent studies from our lab measuring the perception of brown focus exclusively on upper thresholds for this reason. The lower thresholds are also noteworthy in that they shift in the same directions as upper thresholds, but not to as large of a degree. This means that even though an increase in a subject's upper threshold will allow them to perceive a stimulus as brown across a wider range of light levels, they will still lose the ability to perceive a stimulus as brown at some lower light levels perhaps due to overlapping blackness induction mechanisms.

To summarize the results of the first three experiments, target stimuli that have a contiguous high luminance surround present will be perceived as brown at higher light levels than those that have a higher luminance surround elsewhere in the field, regardless of surround size. The size of the stimulus appears to play a role in that larger stimuli are perceived as brown at lower light levels than smaller stimuli. Interestingly, on a fully black background some subjects can perceive the stimulus as brown and one possible explanation is that the categorization of brown is variable between observers, such that some may have a broader spectrum of colors they view as exclusively brown. Other research (Buck & DeLawyer, 2014) suggests that brown differs from bright colors not just in the requirement of high luminance surrounds, but also in its red/green "balance" point and the effect of rods on that balance point, which will be explored more thoroughly in later sections. Though it is worth noting that even if a brown is reddish or greenish (different shades of brown) these types of boundaries can still be readily set by subjects.

D. EXPERIMENT 4 - VARIATIONS IN SPECTRAL PURITY

Early research by Bartleson (1976) established some of the qualitative properties of brown. Among these was the observation that the best browns are produced by long-wavelength stimuli that look yellow-orange when bright, relative to their surrounding stimuli.

Bartleson also observed that desaturated stimuli appear browner than saturated stimuli. I was interested in quantitatively studying the effects of saturation on the perception of brown stimuli. To study these effects, I varied the size of the target stimulus presented both foveally and extra-foveally with both higher and lower spectral purity. Lower purity stimuli are usually perceived as less saturated when compared to an otherwise identical high spectral purity stimulus; therefore, manipulations of spectral purity should also manipulate perceived saturation. Previous research by McKeefry et al., (2007) also suggests larger stimuli appear more saturated whereas extra-foveal stimuli appear less saturated, meaning we can manipulate the perceived saturation of a target stimulus simply by changing its size or eccentricity without changes to the spectral composition of the stimulus. I hypothesized that these three indirect manipulations of perceived saturation (low spectral purity, increased size, and increased eccentricity from the fovea) would all allow subjects to perceive brown at higher light levels in accordance with Bartleson's descriptions of the strongest browns.

Methods

In this experiment eight observers completed a set of trials with a 2°, 3°, 4°, 5°, 6°, and 7°-diameter foveal and extra-foveal target stimuli displayed on a full-field white background. The extra-foveal condition presented the target stimulus at 7° eccentricity with the size of the stimulus adjusted to account for the optics of the retina (the physical size of a 2° target stimulus at foveal presentation needs to be increased as it moves along a flat surface toward the periphery of the retina in order to subtend the same amount of retinal space). A black fixation cross was always present for the extra-foveal conditions. These conditions were also completed with a target stimulus for which purity was reduced by addition of blue phosphor to the previously target stimulus that was composed exclusively of red and green phosphor.

The observers adjusted the luminance of the stimulus using a keyboard until they found the highest light level at which the stimulus appeared exclusively brown (the upper threshold of brown perception).

The high purity stimulus was selected to appear "peach" (yellow-orange) at high luminance and brown at low luminance and was produced using only the red and green phosphors on the CRT (CIE 1964: x=.44, y=.46). The low purity stimulus was produced by adding blue phosphor (CIE 1964: x=.36, y=.36) giving it a "pastel yellow" appearance at high light levels and a "dark tan" appearance at low light levels. The white surround was 111.06 cd/m^2 and covered the entire surface of the monitor (subtending 33° by 25°).

Results and Discussion

A Repeated Measures ANOVA was run to analyze the dataset. Significant main effects were found for stimulus size ($p <.01$, $\eta2 =.447$), eccentricity ($p <.05$, $\eta2 =.376$), and spectral purity ($p <.01$, $\eta2 =.674$). As the size of the stimulus decreased subjects set their thresholds at significantly higher light levels. Extra-foveal stimuli were set as brown at significantly higher light levels than foveal stimuli and low purity stimuli were set as brown at significantly higher light levels than high purity stimuli. Between subject variability was high with standard deviations across conditions between 14 and 22 cd/m^2; however within subject variability was very low with standard deviations between .5 and 4 cd/m^2. The average data across subjects can be seen in Figure 6.

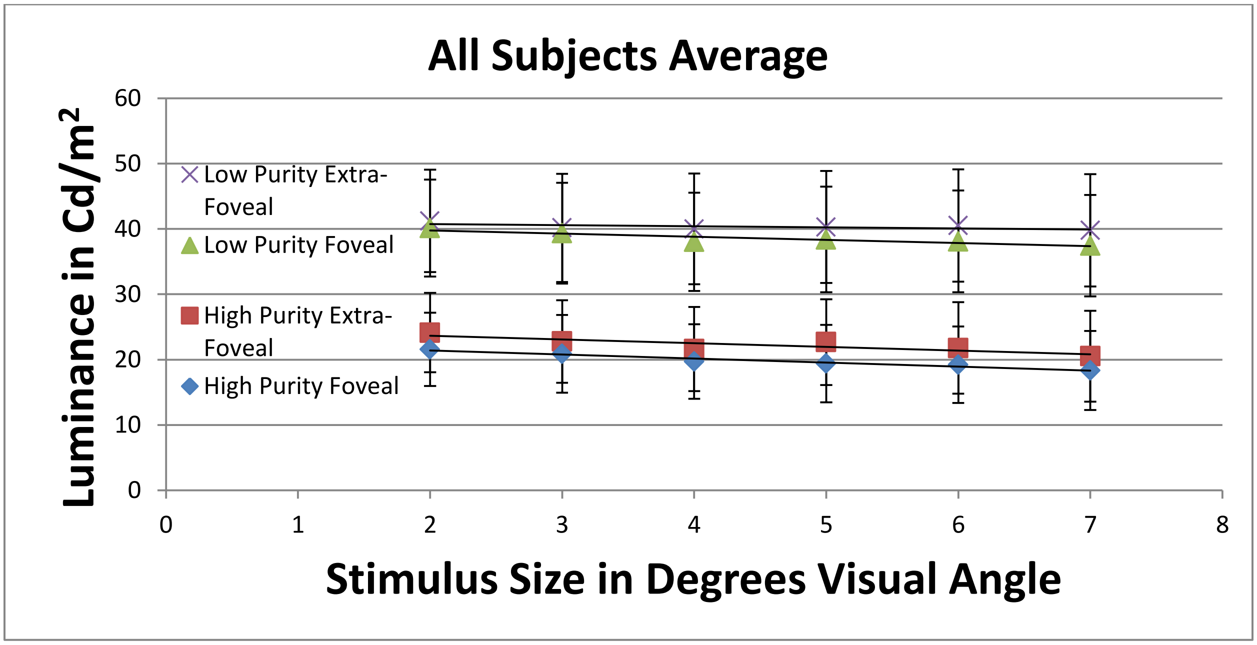


Figure 6. Brown Boundaries for Indirect Saturation Manipulation, Experiment 4. The upper and lower thresholds of brown perception for the six tested stimulus sizes for both low and high spectral purity stimuli presented both foveally and extra-foveally in the spectral purity experiment are pictured here. Error bars represent the standard error of individual subject means.

These data support our past research that suggested the size of target stimuli have significant effects on the luminance at which stimuli can be perceived as brown. In addition these were full-field white backgrounds which controls for a potential confound in earlier data that used variable sized contiguous white rings (Experiment 2). Smaller stimuli will be perceived as brown at significantly higher light levels than larger stimuli regardless of spatial configuration provided there is a high luminance contrast white surround present. Additionally, extra-foveal stimuli also appear brown at significantly higher light levels than foveal stimuli. This suggests that the location of a stimulus in the visual field will influence its perceived color category. Our less spectrally pure stimuli had the largest effect size on brown perception. If our assumption is that all of these manipulations were varying the perceived saturation of the stimulus, then this is to be expected, as manipulating spectral purity impacts perceived saturation a great deal when compared to size and location (McKeefry et al., 2007). Although we did not have subjects rate the perceived saturation of the target stimuli, these data suggest a strong association between desaturated stimuli and the perception of stimuli as brown (the less saturated a stimulus is, the easier it becomes to perceive it as brown) as every effect went in the predicted direction of a saturation manipulation. This is in contrast to the traditional “unique hues” of red, green, blue, and yellow where individuals tend to perceive more saturated stimuli as being more categorically red, green, blue, or yellow. This may suggest that the visual system categorizes brown in a way fundamentally different than red, green, blue, and yellow. It is worth noting that the saturation effect must fall off at some point as the stimulus would eventually become achromatic. Where that point is and what a saturation/brownness curve may look like is a question to be addressed in a future experiment.

E. EXPERIMENT 5 - TEMPORAL DEPENDENCE

Note: Experiment 5 has been previously published as Buck, Morimoto & DeLawyer (2016), to which Buck and DeLawyer made equal contributions and were exclusively responsible for the design, analysis and writing.

Brown has often been described as a dark yellow (a combination of yellow and black). In this study we looked at some aspects of darkness (blackness) induction to see how they were similar to or different from brownness induction. Research on darkness (blackness) induction has suggested it is highly dependent on surround proximity. Distal surrounds can induce darkness induction, but more localized surrounds show a larger induction effect (Reid & Shapley, 1988). These spatial aspects of darkness induction are similar to those we have observed for brownness induction, in that while distal surrounds are sufficient for brownness induction, more localized surrounds have a greater effect. Early research showed brightness induction to be a slow process (Rossi & Paradiso, 1996), but more recent research has shown it can happen very quickly (Blakeslee & McCourt, 2008). In this experiment we hoped to address in detail not only the previously established spatial dependence, but the as of yet unknown temporal aspects of brown induction.

Methods

In order to test for the effect of stimulus onset timing on brown induction we used a task similar to those in the previous experiments with an added variable of stimulus duration. All previous experiments had a set timing of 1 second on followed by 3 seconds off. Stimuli could either appear for 27-ms or for 1 s and were adjusted to their upper brown boundary under a variety of surround configurations. Additionally the stimuli in these experiments were set to a red/green balance to achieve a perceptual null (additional details of this procedure are discussed in the section on red/green balance). Subjects were free to adjust this red/green balance at any point, as changes in luminance affect perception of red/green balance. Aside from this aspect the task was identical to that discussed previously, stimuli are adjusted to their upper brown boundary (the highest light level at which a stimulus looks exclusively brown). There was also one other minor change to methodology compared to the previously mentioned experiments. Subjects no longer received a completely randomized stimulus after each trial. Instead their previous red/green setting was carried over into the next trial with only luminance being randomized. Although this may have reduced the independence of red/green settings from trial to trial, it allowed the subjects to save time, as the red/green balance adjustments combined with the luminance settings adds a considerable amount of time to the completion of a given trial.

These conditions used different background configurations. Three had a white background (the 0° gap condition, 0.25°, and 1°) separated by a black annulus, or gap, that was either 0°, 0.25°, or 1° in width. The 0° condition has a full screen white background, identical to the all-white conditions from previous experiments. The 0.25°, and 1° conditions are similar in their spatial relationship to the white "Far" surround conditions from previous experiments, varying only in the size of the gap between the stimulus and the white surround. The fourth condition is labeled "black", and features a full screen black background, identical to the all-black conditions in previous experiments.

Results and Discussion

Note: The following section incorporates some text from Buck, Morimoto & DeLawyer (2016).

Figures 7(a) and 7(b) show the luminance levels of brown boundary settings, below which the target appeared brown with no trace of yellow, for each observer and surround configuration separately for (a) 27-ms and (b) 1 s stimulus presentations. With the target presented alone against the all-black surround, observers only rarely saw the target as pure brown, even at the 1 cd/m^2 minimum setting of the display. Thus, the mean values for those conditions cluster tightly at 1 cd/m^2 in Figure 7(c).

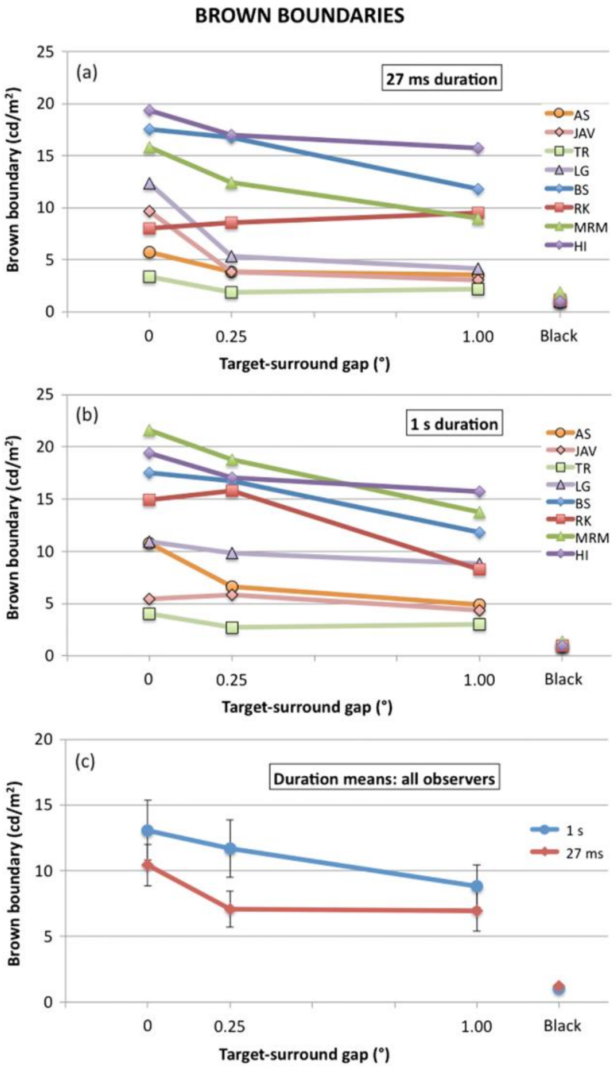


Figure 7. Duration and Target-Surround Gap Size Effect on Brown Boundaries, Experiment 5.

Brown-boundary luminance levels as a function of gap between the target and ring surround (0°, 0.25°, 1°) or with no ring (black) surround, for individual observers with (a) 27-ms stimulus presentation and (b) 1 s stimulus presentation. (c) Means and ±1 sE across all observers for 27-ms and 1 s stimulus presentations.

However, all of the bright ring surrounds raised the brown boundary to higher luminance levels for both stimulus durations. Thus, even the brief 27-ms stimulus presentation was sufficient to induce brown.

There was considerable variation among observers in the luminance level of brown boundaries, with up to 5-fold variation and a span of 15–20 cd/m^2 across observers. This variation appears to reflect true differences among observers because the average within-observer standard error (SE) is much smaller, 0.7 cd/m^2 for both 27-ms and 1 s stimulus durations. Discussion with each individual observer assured that each understood the criterion for the brown boundary.

As noted above, the bright ring surround produced higher brown and yellow boundaries when it was contiguous with the target than when a black gap separated the surround and target. Pairwise-comparison tests (with Bonferroni correction) showed significant differences between the 0° gap condition and both the 0.25° and 1° gap conditions for brown boundaries (p<0.01) but, for yellow boundaries, only between 0° and 1° gap conditions (p<0.05) and not between 0° and 0.25° gap conditions (p=0.079).

The effect of surround proximity can be quantified as the arithmetic difference between the boundary (either brown or yellow) for the contiguous 0° gap condition and that for either the 0.25° gap condition or the 1° gap condition. The two calculations, 0°–0.25° and 0°–1°, characterize surround proximity effects over narrower and wider spatial scales, respectively. We computed these proximity effects separately for each individual observer to factor out the large interobserver differences in brown and yellow boundary levels. The results are shown in

Figures 7(a) and 7(b), which display the average size of individual observers' proximity effects for brown and yellow boundaries. The overall sizes of the proximity effects are small but are at least 2 SE greater than zero for all but one condition (yellow, 1 s, 0.25° gap), where the effect is >0 but not by at least 2 SE.

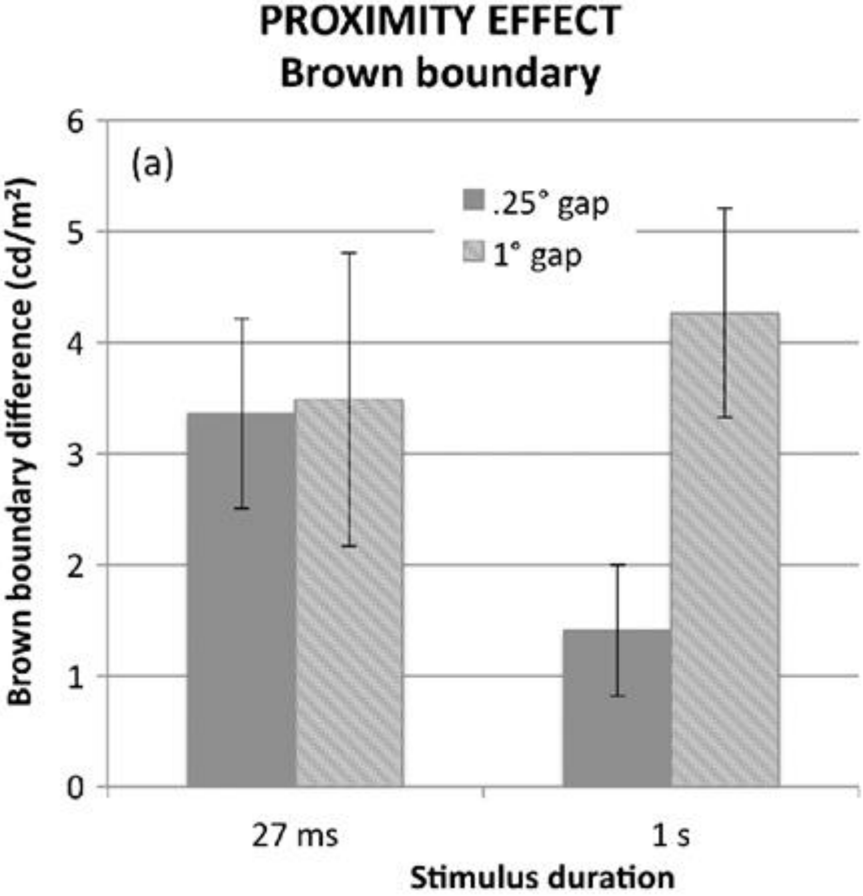


Figure 8. Proximity Effects for Brown Induction, Experiment 5.
These data show the effect of the size of the gap between the target and surround on brown boundaries for the 27ms and 1s time courses. There is no effect for gap size during the shorter 27ms time course, but for the longer time course it shows a large difference. Error bars represent the standard error of individual subject means.

Figure 8 reveals a trend that proximity effects differ in spatial scale between the 27-ms and 1 s conditions, for both brown and yellow boundaries. At the brief 27-ms stimulus duration, the full decline of brown and yellow boundaries is confined entirely to within 0.25° of the target: there is no additional decline with the larger 1° gap size. However, at the longer 1 s duration, the proximity effect has a broader spatial scale: Figure 7(a) reveals that the brown boundary drops somewhat over the 0.25° area around the target but keeps dropping at least out to 1° away from the target. Thus, the magnitude of the overall proximity effect is comparable for both stimulus durations but it is essentially complete within 0.25° of the target for the 27-ms duration and changes over greater distances for the 1 s duration.

The results from this experiment helped to establish brown induction as a process that can occur quickly, but appears to occur in stages. One stage occurs within 27-ms of stimulus onset, implicating early cortical processes and is driven by the immediate surround, showing invariance to the overall size of a surround. The second stage occurs later, within 1 s of stimulus onset, which suggests a slower filling in-process that could implicate latter cortical areas that are engaged in top-down processes. This two-stage model of brown induction will continue to be discussed in the next study, which attempts to separate cortical processes from retinal processes involved in brown induction.

F. EXPERIMENT 6 - DICHOPTIC STIMULUS PRESENTATION

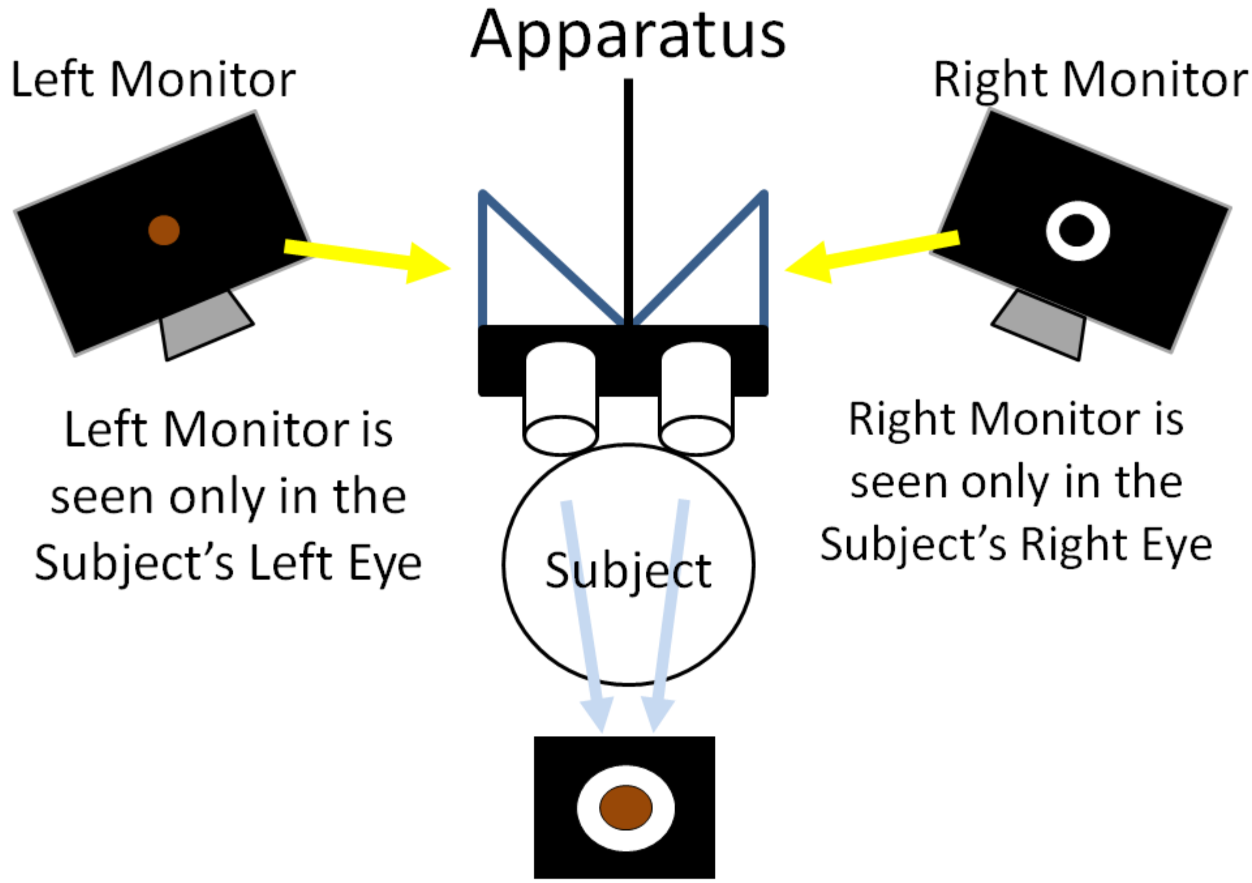
Note: Experiment 6 has been previously published as DeLawyer, Morimoto, and Buck (2016), to which DeLawyer made the principal contributions.

Experiment 1 had suggested that there are two or more separable mechanisms of brown induction that operate over different spatial scales. This was further supported by the spatial and temporal (stimulus duration) data in Experiment 5. In order to learn more about the potential loci of these two mechanisms for brown induction, we performed the following experiment using a dichoptic viewing apparatus that allowed presentation of surround and target stimuli in either the same or different eyes. This allowed us to explore the dependence of brown induction on processing in monocular pathways beginning in the same retina (with target and surround presented to the same eyes) or on cortical pathways after the convergence of signals from the two eyes (with target and surround presented to different eyes). In both cases, the stimuli appeared as perceptually single view of a target surrounded by the concentric surround elements.

Methods

Note: The following Methods and Results and Discussion sections incorporate text from DeLawyer, Morimoto, and Buck (2016).

Two Dell U2412M LCD monitors with frame-rates of 75Hz, were used for stimulus display. The monitors' light output was measured with a Photo Research SpectraScan PR-702. Subjects viewed stimuli with both eyes through a binocular viewing apparatus composed of prisms that would redirect the light from one monitor to the corresponding eye. A chin and forehead rest was attached to the binocular viewing apparatus to ensure the subject had a consistent viewing angle. The monitors were viewed through the apparatus at a distance of 58 centimeters. A black foam-board barrier prevented the light from the other monitor from entering the viewing apparatus on the opposite side. This ensured that the light from each monitor was only visible by one eye.



Subject's Perception is a fusion of the Left and Right Monitor stimuli

Figure 9. **Dichoptic Apparatus used in Experiment 6.**
The dichoptic apparatus made use of prisms to redirect the light into a binocular viewing apparatus such that each monitor was only visible to one eye.

Nine subjects (ages 20-31) were all University of Washington undergraduates who met the specified criteria for Experiment 1 in addition to demonstrating normal stereoscopic vision on Julesz (1972) random-dot stereogram tests.

Subjects adjusted the luminance of a constant-chromaticity 4°-diameter foveal target stimulus to set just the upper boundaries (the highest light level at which brown is perceived with no trace of yellow) of brown perception. Above the upper boundary, the hue of the target appeared to be a mixture of brown and yellow or red (see Figure 9). Subjects were tested with the room lights off, but were kept room-light adapted by switching the lights on between conditions. Subjects were specifically instructed to set their upper boundary "at the highest light level at which the target appears exclusively brown with no trace of yellow". The chromaticity of the target (CIE 1964: x=.44, y=.46) was selected to appear "peach" (yellow-orange) at high luminance and brown at low luminance.

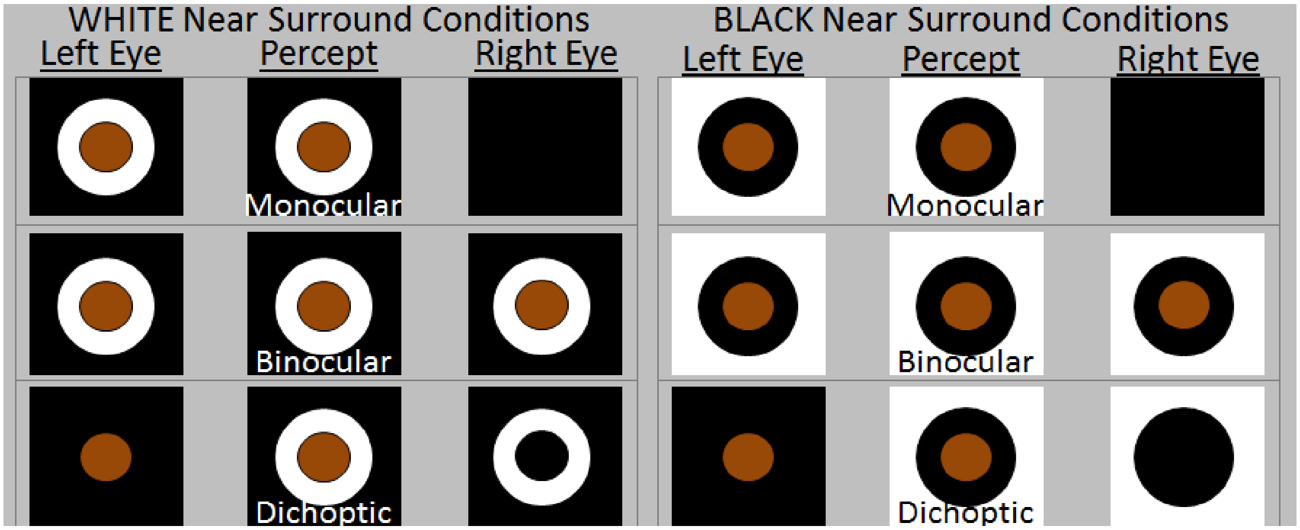


Figure 10. Target Stimulus and Surround Configurations for Experiment 6.
Spatial configurations used for Experiment 6. The combinations are all variations of the white near surround/black far surround and black near surround/white far surround conditions from Experiment 1. They were presented either monocularly (both target and surround to only one eye), binocularly (both target and surround to both eyes) or dichoptically (target stimulus to one eye, surround to the other eye).

The 4°-diameter target stimulus appeared with either a white or black contiguous *near surround* annulus of 2° width and a white or black *far surround* annulus extending from the edge of the near surround to the edge of the monitor screen. The near and far surrounds were either white or black but always opposite (see Figure 10). The white surround was 81 cd/m^2 (CIE 1964, x, y = .27, .26) and black surround was 0.0601 cd/m^2. To minimize adaptation effects, the target appeared for 1 s before turning off for 3 s while being replaced by the near surround color for that condition. All stimuli were viewed through the dichoptic apparatus and all light measurements were made through the optics of the apparatus.

As depicted in Figure 10, the target and surrounds were either presented together to a single eye (monocular condition) or to both eyes simultaneously (binocular condition) or to separate eyes (dichoptic condition). The precise placement of the monitors and alignment of the optics was arranged so that, in the dichoptic condition, the subject saw a single stereoscopic view of the target and concentric surrounds.

Results and Discussion

Figure 11 shows the average upper brown boundaries for white-near-surround conditions (right panel) and the black-near-surround conditions (left panel) for the *binocular*, *dichoptic*, and *monocular* presentation conditions. A Repeated Measures ANOVA found a significant effect of presentation type ($F(2,8)=18.347$, $p<.001$, $\eta^2=.787$), but there was no significant effect for white versus black near surround (p=.114). The pairwise comparisons showed the dichoptic boundaries were significantly lower than binocular (p<.01) or monocular (p<.01) boundaries, but there was no significant difference between the binocular and monocular presentation boundaries (p=1.0). There was also a significant interaction between the background (black/white) and presentation type ($F(2,8)=11.402$, $p<.01$, $\eta^2=.588$) with the white background facilitating increased thresholds for binocular and monocular conditions, but not dichoptic conditions. All subjects showed the same pattern of results between the significant conditions.

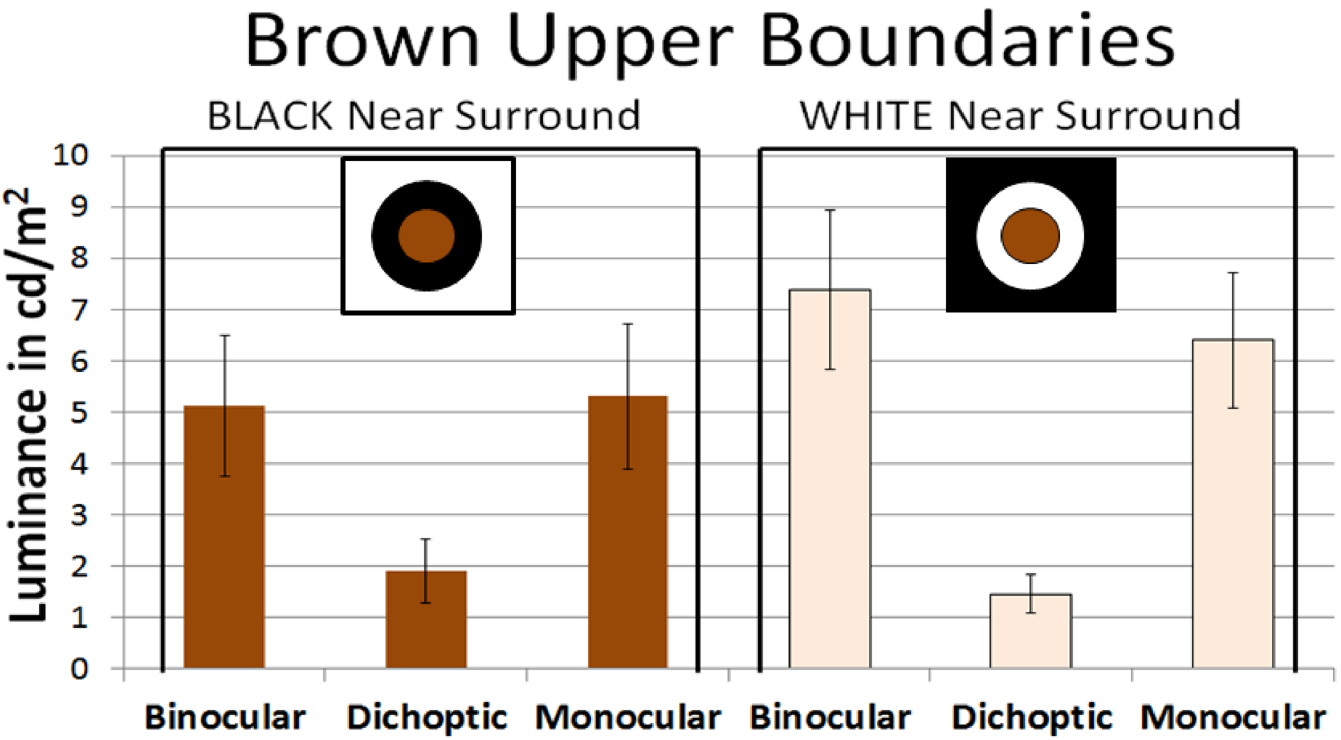


Figure 11. Brown Boundaries for the three Viewing Conditions in Experiment 6. Upper boundaries of brown perception averaged across subjects for the six possible spatial configurations in Experiment 6. Error bars show the standard errors of subject means. BLACK Near Surround is the black near surround, white far surround condition set. WHITE Near Surround is the white near surround black far surround condition set. Error bars represent the standard error of individual subject means.

The results provide further evidence that separate mechanisms are involved in the Near and Far surround effects observed in Experiment 1. As expected, there was no significant difference between binocular and monocular presentations, showing that two-eyed viewing alone does not enhance or diminish brown induction. However, there was a very large decrease in brown upper boundaries for dichoptic viewing. The dichoptic condition had a comparatively small effect on inducing brown compared to the effect of the binocular and monocular conditions.

Importantly, the dichoptic effect was not just smaller, but it also showed a different effect of surround stimulation in the region contiguous with the target. In both experiments, a white surround contiguous with the target produced significantly higher brown boundaries in monocular or binocular conditions than did a black contiguous surround. However, in the dichoptic condition, the black contiguous surround (Far) raised brown boundaries slightly more than the white contiguous surround (Near).

This suggests that different mechanisms control the elevation of brown boundaries under dichoptic conditions compared to monocular and binocular conditions. While the dichoptic brown boundaries are low, they are reliable and consistent across observers, in stark contrast to the absence of consistent brown boundaries found in Experiment 1 for the All-Black surround. Thus, monocular pathways may be a powerful inducer of brown, but other pathways are sufficient for brown induction.

G. GENERAL DISCUSSION OF BROWN INDUCTION MECHANISMS

The results from these experiments provide evidence for at least two separate mechanisms for brown induction. One mechanism is dependent on physically contiguous contrast and operates in monocular pathways and operates quickly. The neural substrate for this mechanism could reside in the retina, possibly in the influence of localized lateral interactions mediated by horizontal or amacrine-cell circuits. Some or all of the neural processing contributing to this mechanism could also operate in monocular cortical pathways.

Another mechanism responds to high luminance contrast anywhere in the visual field and can operate after convergence of signals from the two eyes, anywhere from area V1 onward. It is also possible that there are additional mechanisms of brown induction operating in one or both experiments. This mechanism by its nature would be expected to be slower, and could be responsible for the slower filling in-effect observed in Experiment 5.

Past research looking at the influence of near and far surrounds on inducing brightness/darkness in achromatic stimuli in dichoptic presentation has found similar results to those observed here for induction of brown, showing that an advantage of contiguous near surrounds over distal far surrounds for inducing brightness/darkness disappears under dichoptic viewing (Shevell Holliday, & Whittle, 1992). Additionally, the mechanisms responsible for the induction of blackness into a contiguous chromatic target by a brightness contrast have been shown to cause hue and saturation shifts (Bimler et al., 2009). Although we have not measured brightness in the studies presented here, we have shown shifts in brown perception related to variations in saturation as seen in Experiment 4 and red/green balance (Buck & DeLawyer, 2014), suggesting these shifts in hue and saturation could be similar to those observed in blackness induction.

Taken together, these findings suggest that the mechanisms responsible for darkness and/or blackness induction appear to operate in similar ways to those observed here for brown induction. Nevertheless, recent and ongoing work from our laboratory has shown that the relationship between brown induction and brightness/darkness induction is complex and still incompletely understood. For example, we have not yet found evidence in brown induction (Morimoto, Slezak, & Buck, 2016) of the surround articulation effects that have been shown by some brightness (Zemach & Rudd, 2007; Schirillo, & Shevell, 1996; Shirillo, 1999 a, b, 1996; 1999; Kanari & Kaneko, 2014) and chromatic (Shevell & Wei, 1998; 2000) induction studies.

Also, the magnitude of darkness induction produced by contiguous and distant surround features does not predict the magnitude of brown induction produced by the same features (Buck et al., 2016). Thus, brown induction appears not to be simply a manifestation of darkness induction. Additional work will be needed to clarify the relationship between brown induction and brightness induction and their underlying neural substrates.

III. RED/GREEN BALANCE OF BROWN AND YELLOW

The first section of this dissertation focused largely on the brown boundary and conditions that induced brownness into a stimulus. However, another important aspect of brown stimuli that Bartleson (1976) discussed in his original paper concerns the perception of red/green balance. Bartleson said the best browns were made from darkening bright orange stimuli, which suggests that brown stimuli have a red/green balance that is shifted in the red direction compared to yellow in order to overcome a green bias (as the stimulus becomes darker, greenness seems to be induced, requiring the addition of red to create a balanced stimulus). A perceptually balanced yellow would therefore make a greenish brown (and therefore a perceptually balanced brown would make a reddish-yellow [orange]). However, this change in red/green balance may not reflect a unique property of brown. It is possible that dark colors themselves exhibit a balance shift. It is possible that the shift in red/green balance occurs independently of brownness induction and is mediated by partially overlapping or fully independent mechanisms. The primary purpose of this section will be to focus on the factors that influence red/green balance and how they are related to, or differ from, those seen in brown induction. Another purpose (which will be explored in more depth in the next section) is to propose possible neural loci to mediate these effects, and a way these effects can be successfully modeled.

Note: Experiments 7 and 8 have been previously published as Buck & DeLawyer (2014), to which Buck and DeLawyer made equal contributions.

A. EXPERIMENT 7 – RED/GREEN BALANCES ON BLACK OR WHITE SURROUNDS

This experiment represented our first attempt to quantify what Bartleson had described qualitatively: That the ideal perceptual brown stimuli are shifted in the red direction compared to those that are perceived as yellow. As we can empirically determine using cone trolands (a measure of the relative excitation of the cone photoreceptors in the retina) the quantitative difference between colored lights, we are able to come up with a more objective measure of the difference between brown and yellow stimuli's red/green balance. Subjects can set a balance to an equilibrium point on a bright or dark hue which we can then compare with the equivalent dark or bright hue. These differences represent the degree to which a subject perceives a stimulus as biased in one direction or another. If a subject requires more L-cone activity relative to M-cone activity to create an equilibrium hue from some standard, than (then) that suggests the original hue had a green bias. Based on the Bartleson's paper, we would expect a red bias for yellow stimuli and a green bias for brown stimuli, which predicts more L-cone activity relative to M-cone activity for equilibrium brown stimuli than equilibrium yellow stimuli.

In order to test if red/green balance shifts are a property unique to brown and yellow stimuli we first tested for red/green balance shifts for both brown and yellow stimuli as well as dark and bright blue stimuli which are also a red/green balance. We also looked at the equivalent blue/yellow balance for dark and bright red and green stimuli. This allows us to see if these balance shifts are unique to brown and yellow or a property shared by all dark colors. Whether it is being controlled by a unique mechanism or by a shared universal mechanism is important for establishing a plausible neural model. Since previous research (Fuld, 1983) did not suggest equivalent properties in dark blue, red, or green, we did not predict to see an equilibrium hue shift of equivalent proportion for these hues.

Note: The following Methods and Results and Discussion sections incorporate some text from Buck & DeLawyer (2014).

Methods

Observers: Eleven observers served in subsets of the present conditions. All observers were students or faculty at the University of Washington and were assessed as having normal color vision by Nagel anomaloscope and Ishihara Pseudoisochromatic Plate tests. The eight female and three male student observers ranged in age from 20 to 30 years. The male faculty observer was 63. All procedures and consent forms were approved by the appropriate Institutional Review Board at the University of Washington.

Apparatus and Stimuli: All stimuli were presented on a conventional ViewSonic G90fB CRT display at a frame rate of 75 Hz. The light output of each display phosphor was measured with a Photo Research SpectraScan PR-705 spectral radiometer and linearized by an ATI Radeon HD 4870 video card. The observer's head was positioned by means of a chin and forehead rest so that the full screen subtended 33° by 25° (w x h) at a distance of 63 cm. A black foam-board enclosure surrounded all apparatus components and the observer's head, so that when room lights were off, nothing was visible beyond the monitor screen.

The observer viewed the display monocularly through the natural pupil of the right eye, while wearing an opaque patch on the left eye. For mesopic conditions, a filter holder was positioned in front of the observer's right eye, so that inserted neutral-density filters covered a field of view that extended beyond the full monitor screen, thus dimming all display stimuli equally. For photopic conditions, the filter holder was removed and the observer viewed the screen directly.

All conditions used a 2°-diameter foveal test stimulus that was centered inside a square fixation array of 0.5°-diameter white dots, spaced 4° apart on a side. During a condition, the test stimulus square-wave cycled continuously, 1 s on and 3 s off. Test luminance was kept constant at 21 cd/m^2 for photopic conditions and 0.2 cd/m^2 for mesopic conditions (both specified in CIE 1964 units (Wyszecki & Stiles, 1982). The chromaticity of the test stimulus could be varied at constant luminance in 494 steps around the perimeter of the triangle formed by the RGB phosphors. The fixation array was presented only during the interval between test-stimulus presentations and was set to 50% of the test-stimulus luminance. The remainder of the display was either black (about 10–5 cd/m^2 below test-stimulus luminance) or white (x=29, y=29, 141 cd/m^2 photopic or 1.4 cd/m^2 mesopic, specified in CIE 1964 units), thus creating either black or white test-stimulus surrounds. When either the test stimulus or the fixation stimuli were absent, that portion of the screen was filled with the surround light for that condition. When either the test or fixation stimuli were present, they replaced their portion of the surround. Thus, the surround did not serve as a pedestal or background on which the test was superimposed.

<u>Procedures</u>: The observer's task was to adjust the chromaticity of the test stimulus to null or balance either red–green appearance for the yellow, brown, and blue test conditions or blue–yellow appearance for the red and green test conditions. Observers were instructed to adjust the hue balance of the test until neither opponent-hue percept (e.g., red–green) was present or until they were equally likely to describe the test hue by either opponent-hue name. (Note that all test lights were presented at a constant luminance, so total L+M excitation remained constant while

the observer varied either L/(L+M) or S-cone troland value.) The observer controlled the direction of chromaticity change and signaled the final setting by means of presses on a keyboard, following an adaptive adjustment procedure. At the start of a condition, test-stimulus chromaticity was assigned randomly from a wide range of steps bracketing the given unique-hue range. The observer could change the chromaticity in either direction at any time. Observers were instructed to make their judgments on the basis of the hue seen at the conclusion of the 1 s test-stimulus presentation.

For each separate stimulus/adaptation condition, observers made five test-stimulus settings back to back. The starting chromaticity for each setting was random within the given step range and independent of any prior settings. After five settings, the computer signaled the end of the condition with a dark screen. Unless otherwise indicated, all sessions were repeated four times, with orders of stimulus conditions counterbalanced or varied as much as possible across sessions and results reported as means and standard errors computed across session means. For rod-influence measurements, a given stimulus condition was always tested under both adaptation conditions in the same session, and the order of adaptation conditions was counterbalanced across sessions.

Cone troland values were calculated from the color-step measurements using the Smith–Pokorny cone fundamentals (Smith & Pokorny, 1975), the 1964 CIE $V\lambda$, and a nominal pupil diameter for all observers of 6 mm. S-cone trolands, which are arbitrarily related to L- and M-cone trolands, were calculated using the scaling factor suggested by Smith and Pokorny (2003).

Results and Discussion

Figure 12 shows how red–green balances shifted for a constant-luminance 21 cd/m^2 foveal target stimulus presented on a black surround (diamonds) or on a white surround (squares). Each of the 8 observers required a higher proportion of R phosphor (hence, more L-cone excitation) in the equiluminant mixture to achieve the red–green balance when the test was surrounded by white than when the same test was surrounded by black. The average difference across observers was 0.021. Individual observer differences are also shown in Figure 13.

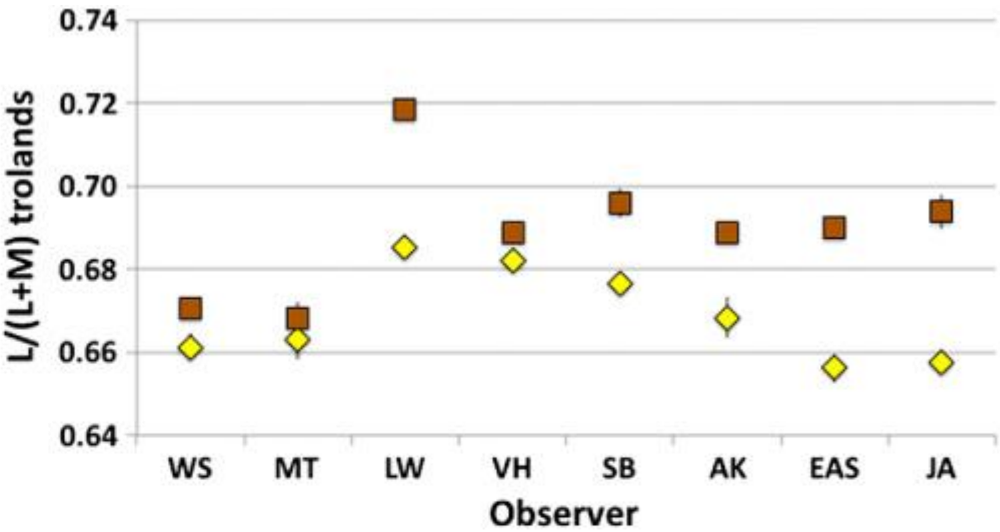


Figure 12. Red/Green Balances for Individual Observers in Experiment 7.
Equilibrium red–green balances (expressed as L/(L+M) trolands) for the same photopic target stimulus when it appeared yellow (diamonds) surrounded by black and when it appeared brown (squares) surrounded by white, for each of eight observers. For all observers, the balance required more R and less G phosphor when the test appeared brown than when it appeared yellow. Error bars represent ±1 standard error of the four session means.

Figure 13A shows a comparison of the shifts of red–green balance [expressed as L/(L+M) cone trolands] associated with yellow/brown and bright/dark blue under photopic conditions for individual observers (solid bars, presented in the same left–right order as in Figure 12). Hatched bars represent the overall means across observers. All eight observers showed shifts between yellow and brown (left panel) that are in the direction of increased L/(L+M) and greater than one standard error. In comparison, only four observers showed such shifts between bright/dark blue (right panel), but all four (marked by asterisks) showed shifts for bright/dark blue that were roughly equal to or greater than those for yellow/brown. One other observer showed a shift in the opposite direction, and the three remaining observers showed shifts that were not greater than one standard error of the four session means for that condition for that observer.

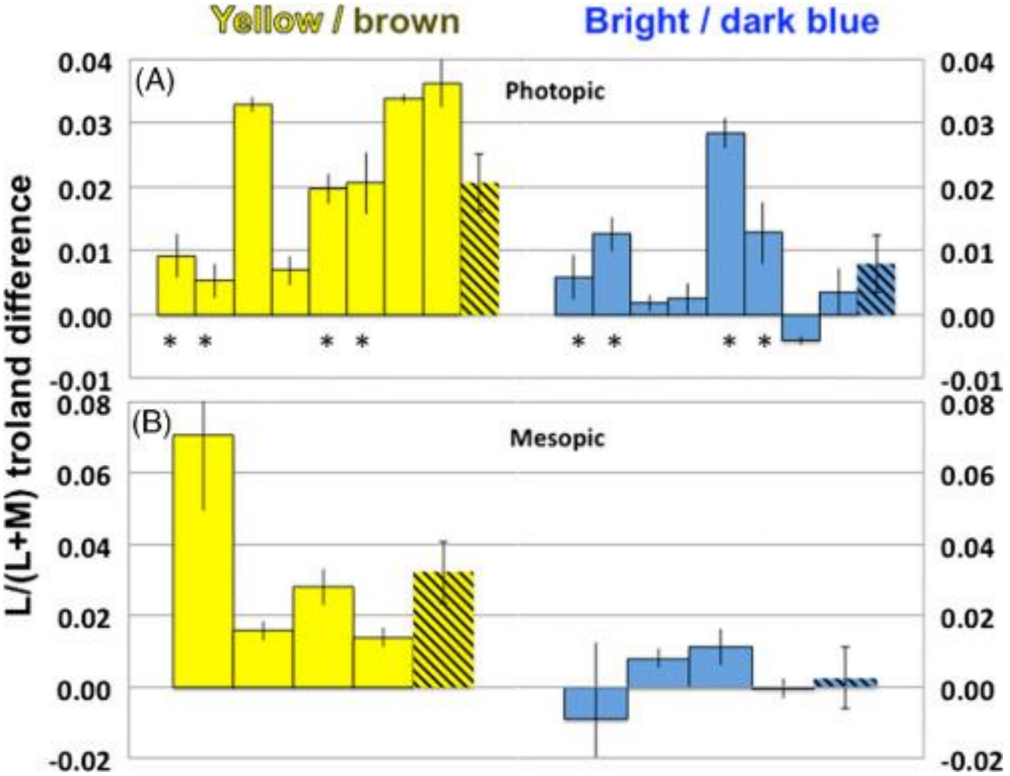


Figure 13. Red/Green Balances for Yellow and Blue Targets in Experiment 7.
Shift of equilibrium red–green balance from yellow to brown (left) and from bright to dark blue (right). **A**, photopic conditions: solid bars show shifts for individual observers, in the same order on left and right. Stippled bars show group means. Positive values denote greater equilibrium L/(L+M) troland values for brown or dark blue than for yellow or bright blue. Asterisks mark four observers who showed substantial hue shift for both yellow/brown and bright/dark blue. Error bars are ±1 s.e. of four session means. **B**, mesopic conditions: solid bars show shifts for same individual observers shown leftmost in **A**. Note scale difference between **A** and **B**.

We also conducted a control experiment to rule out simultaneous color contrast as an explanation for the red/green hue shift seen on the bright surround. In theory, if the “white” surround were actually reddish, it could induce green into the target stimulus (simultaneous color contrast), which would require more R phosphor to cancel. This potential explanation seemed unlikely because every observer accepted the white surround as a red–green balance (although the surround did have a slight bluish cast, as is common on CRT displays). However, to be sure, we progressively “green-biased” the surround by reducing the amount of R phosphor in the surround (horizontal axis) and remeasured the red–green balance. The surround looked unambiguously greenish with a 69% reduction of the luminance of the R phosphor, but Figure 14 shows that this did not shift the red–green balance down to the level obtained on the black surround for either photopic (A) or mesopic bleached (B) conditions. Similar results were obtained for two other observers. The reduction of the R phosphor needed to match the black-surround red–green balance for one observer (not shown) was found to be 43% of the full white level. Thus, it appears implausible that a small, undetected red bias in our original full white surround could have caused the observed differences in red–green balance between white- and black-surround conditions.

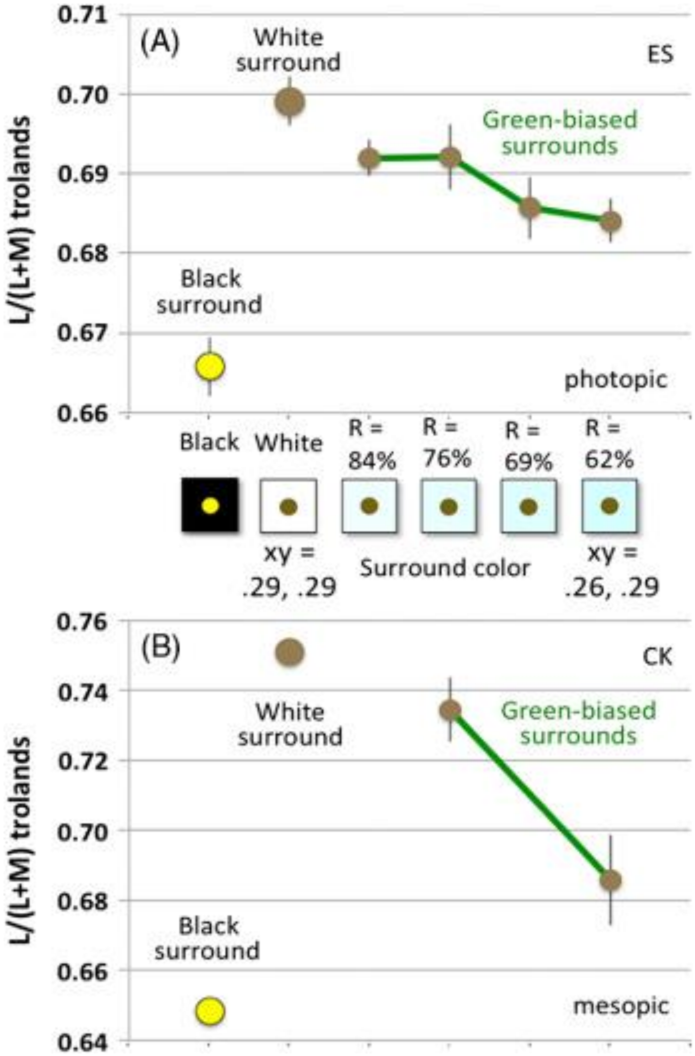


Figure 14. Red/Green Balances for Green-Biased Surrounds in Experiment 7.
Red–green balance (expressed as L/(L+M) trolands) of (A) photopic or (B) mesopic yellow or brown test with black, white, and green-biased surrounds. The green-biased surrounds were formed by reducing the R phosphor by the percentages shown. CIE 1964 chromaticity coordinates are shown for full white and 62% R surrounds. Green-biased surrounds still produced a red–green shift compared to the black surround. Error bars are ±1 s.e. of four session means.

B. EXPERIMENT 8 – BLUE/YELLOW BALANCES ON BLACK OR WHITE SURROUNDS

The white surround changed the appearance of the target stimulus from bright and yellow to dark and brown. The white surround produces no analogous categorical hue change for the other three bright chromatic Hering unique hues—blue, red, or green—but it does make them turn dark. We next addressed what changes of hue balance might also accompany the change from bright to dark appearance.

Methods

This experiment used the same subjects and overall methodology of the previous experiment, but with a key difference in the judgment during the hue-balance task. For these stimuli the balance is a blue/yellow balance, not a red/green balance. Subjects set stimuli to a red or green that looks neither blueish nor yellowish.

Results and Discussion

Figure 15 shows the shifts in hue balance for all four Hering unique hues between black (triangles) and white (circles) surround conditions in a modified MacLeod–Boynton (1979) chromaticity diagram showing excitation of L/(L+M) cones on the horizontal axis and S cones on the vertical axis. The triangle shows the hue-balance steps available to the observer from paired combinations of the RGB phosphors. The previously described average shift of red–green balance between bright yellow and dark brown target stimuli encompasses about 10% of the total difference in L/(L+M) between the G and R phosphors. In contrast, there are much smaller average differences in hue balance between bright and dark versions of blue, green, and red, which are examined in detail in the following two figures.

Figure 15 shows that shifts of blue–yellow hue balance (expressed as change of S-cone trolands for the constant-luminance target stimulus) for bright/dark green (left panel) and bright/dark red (right panel) may be small (see Figure 16), but on this expanded ordinate are mostly in the direction of needing increased S phosphor and S-cone excitation when the target stimulus looks dark in the presence of a white surround. This direction of effect is consistent with what would be predicted by simultaneous color contrast with the somewhat bluish color of the white surround. Unlike the analogous case for the red–green balance of yellow/brown (Figure 14), control studies (not shown) were not able to rule out this simultaneous color contrast as an explanation for the bright/dark differences in blue–yellow balance shown by most observers for green and red conditions. It remains unclear whether different stimulus conditions might produce blue–yellow hue shifts between bright and dark stimuli for most observers, independent of simultaneous color contrast.

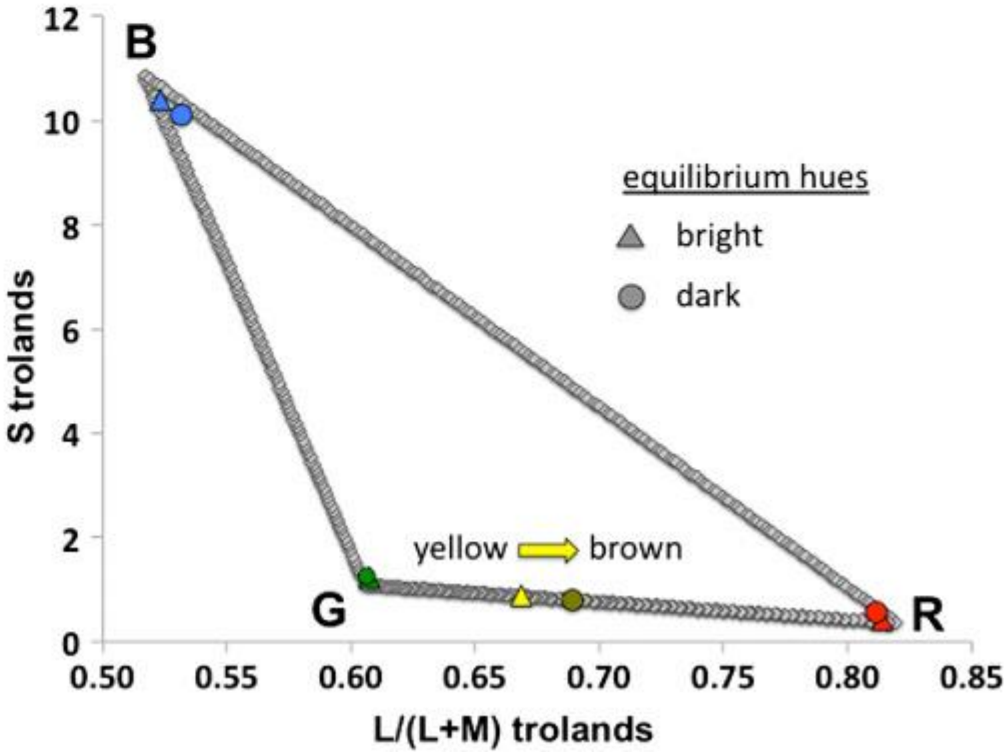


Figure 15. Balance Data Plotted in MacLeod-Boynton Space for Experiment 7.
Shifts in photopic hue balance for bright (triangles) and dark (circles) versions of all four unique hues, plotted in a modified MacLeod–Boynton chromaticity diagram. Data points for bright/dark red and green overlap in this plot. Values are the means for all eight observers. Only partially resolvable are the 494 equiluminant color steps available to the observers.

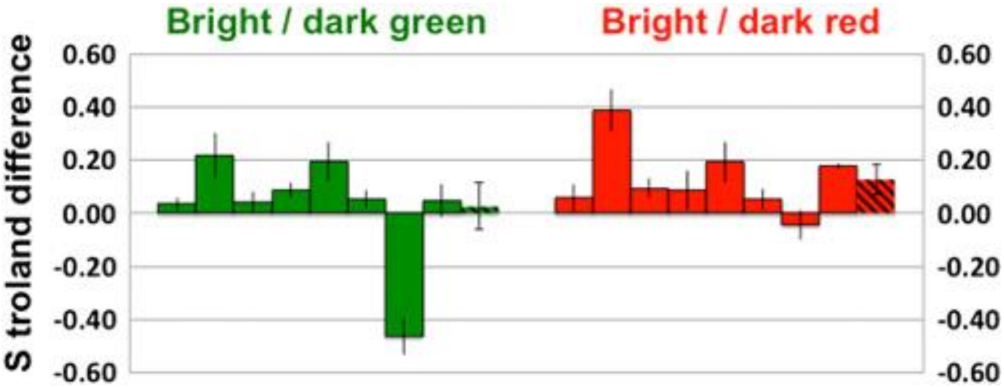


Figure 16. Blue/Yellow Balances for Individual Observers in Experiment 7.
Shift of photopic equilibrium blue–yellow balance from bright to dark green (left) and from bright to dark red (right). Format details are the same as in Figure 13. Positive values denote greater equilibrium S-cone troland values for dark green or red than for bright green or red. Error bars are ±1 s.e. of four session means.

To summarize all of the results of Experiments 7 and 8, Figure 16 shows the shifts in hue balance for all four Hering unique hues between black (triangles) and white (circles) surround conditions in a modified MacLeod–Boynton chromaticity diagram showing excitation of L/(L+M) cones on the horizontal axis and S cones on the vertical axis. The triangle shows the hue-balance steps available to the observer from paired combinations of the RGB phosphors. The previously described average shift of red–green balance between bright yellow and dark brown target stimuli encompasses about 10% of the total difference in L/(L+M) between the G and R phosphors. In contrast, there are much smaller average differences in hue balance between bright and dark versions of green and red, which can be seen in the Figure 15 by the nearly overlapping icons in MacLeod-Boynton space. There was also a very small difference between bright and dark blue (which is also shown in Figure 15), the cause of which will be examined in more detail in another section of this work.

C. DISCUSSION OF RED/GREEN BALANCE OF BROWN AND YELLOW

These experiments suggested the possibility that red/green balances of brown and yellow share a unique relationship not seen among red/green balances of dark and bright blue and that there is no parallel blue/yellow-balance shift between dark and bright red or green. That this shift appears unique to brown and yellow provides yet more evidence that these two colors are not merely dark and bright equivalents, but distinct hue categories. This suggested that there could be a single underlying mechanism or set of mechanisms for both red/green balance and brown induction. Similarly, then, we could see a red/green balance mechanism that is present at the level of the retina, operating in midget-cell pathways (which receive input primarily from L and M cones). This possibility was tested specifically in research utilizing primate retinal physiology and we did not find any evidence to support this possibility (Buck, Rieke, & DeLawyer, 2018).

There is also the possibility of a cortical mechanism that, as evidence for brown induction also suggested, operates after binocular fusion occurs and takes into account the luminance of all elements of the visual field. This possibility will be explored further in the next two sections of this dissertation.

The present study also limited its analysis to saturated hues (the highest spectral purity the CRT monitor could produce). These are the most perceptually “colorful” representations of their hue categories and as such may show a different pattern than stimuli that are less spectrally pure. A color-category based hue shift that does not take spectral purity into account would suggest high-level cognitive processes that also contribute to color naming and hue boundaries. If we find that spectral purity does influence these results it could suggest either perceived saturation is an additional contributor to red/green balance shifts in addition to perceived hue, or that the activation of S-cones in the retina is a primary driver of this shift (as yellow/brown stimuli have little S-cone activation compared to blue stimuli which maximally activate S-cones). It is important to note that S-cones largely contribute to the signals of small-bistratified ganglion cells and these signals are processed in the koniocellular sublayers of the LGN and do not integrate with the signals originating from midget ganglion cells until the visual cortex (Hendry & Reid, 2000). This means that whether perceptual saturation or S-cone activity drive these differences between yellow and blue stimuli the effects will be cortically mediated. The difference would be early cortex (S-cone activity regardless of hue category) or late cortex (perceived hue category and perceived saturation). The question of the role of saturation is one we will return to in the last section of this dissertation.

IV. SPATIAL AND LUMINANCE DEPENDENCE OF RED/GREEN HUE SHIFTS

One of the first tasks when looking at red/green balances was to determine if they showed a similar spatial and luminance dependence to those we saw for brown induction. For brown stimuli both the location of and ratio of surround luminance to target luminance greatly influenced the strength of the brown percept. At the time these experiments were performed we hypothesized a similar dependence of red/green balance on surround proximity as that seen for brown boundary. We expected contiguous surrounds to contribute to greenness induction to a greater degree than those of non-contiguous surrounds. As brown stimuli require more red to achieve a perceptual balance, it can be inferred that inducing factors that make a stimulus appear browner will also cause the same stimulus to appear greener. This set of experiments features a variety of spatial manipulations and luminance manipulations that are designed to test red/green balances under conditions similar to those tested for brown as well as additional manipulations to further understand the aspects of red/green balances that are similar to or different from those involved in brown induction.

A. EXPERIMENT 9 – VARIABLE TEST LUMINANCE EXPERIMENT

One of the defining features of brown induction appears to be its dependence on high luminance contrasts. To see a stimulus as brown it must have a sufficiently bright surround somewhere in the visual field. It was similarly observed in previous experiments that on bright backgrounds a target stimulus that is brought to a red/green balance will be balanced toward greater L/(L+M) cone excitations than an identical target presented on a dark background. This effect suggested bright backgrounds induce greenness into a target for which subjects compensate by increasing the amount of L-cone excitation relative to M-cone excitation. In order to observe if this effect would vary linearly with changes in the surround luminance, we utilized a variety of luminance values for the target itself.

Methods

The conditions for this experiment used a variable luminance target, almost identical to those used in the brown boundary surround location effects experiment (Experiment 1). As such, Figure 2 shows the exact spatial relationship of target and surround used in this experiment.

A 2°-diameter target stimulus appeared with either a white (near) or black (far) annulus of 2° width immediately surrounding it. Near and Far conditions had a white or black 2°-width annulus surrounding the stimulus with the rest of the screen reversed. All Black and All White conditions had homogeneous full-screen surrounds. In those conditions the background covered the entirety of the screen and there is no annulus present. The white surround varied between 5.4-87.2 cd/m^2 (CIE 1964, x, y = .32, .33) and the black surround was <0.001 cd/m^2. The target appeared for 1 second before turning off (replaced by whatever the background color was for that condition) for 3 seconds. This was done to prevent adaptation to the target.

Subjects viewed stimuli with both eyes and were instructed to fixate on the target stimulus, though no fixation cross was present in the absence of the target stimulus. Using a keyboard, subjects freely adjusted the ratio of Red and Green gun outputs on a CRT monitor (and thus the relative activation of L and M cones) for the target stimulus to yield a red/green null (appearing neither reddish nor greenish). Subjects then pressed a key to accept the red/green balance point. The subjects made a total of five such settings, each starting at a randomly selected red/green balance, before moving on to the next surround condition. Subjects completed four sessions for each condition and only completed a maximum of one session per day. Conditions were counter-balanced across sessions to control for order effects.

Additionally, the test was varied between 5.4, 10.9, 16.3, 21.7, 27.1, and 32.6 cd/m^2 while in the presence of a constant 87.2 cd/m^2 surround. This variation was counter-balanced such that no two conditions followed each other more than once and each condition appeared a total of five times.

Results

A Repeated Measures ANOVA was run to analyze the dataset. A significant main effect was found for background condition ($p < .001$, $\eta 2 = .518$), and there was a significant main effect for test luminance ($p < .001$, $\eta 2 = .835$). There also was a significant interaction between the background condition and light level ($p < .05$, $\eta 2 = .221$). The surround condition pairwise comparisons show that although every other condition is significantly different when compared to the All Black ($p < .05$) condition, they are not significantly different from each other. The light level effect pairwise comparison shows every test luminance being significantly different from every other test luminance ($p < .05$) other than 27.1 cd/m^2 compared to 32.6 cd/m^2 ($p = .724$). The interaction shows a significant change in the slope of the test luminance effect for the All

Black condition compared to the other conditions. The average data across subjects can be seen in Figure 17.

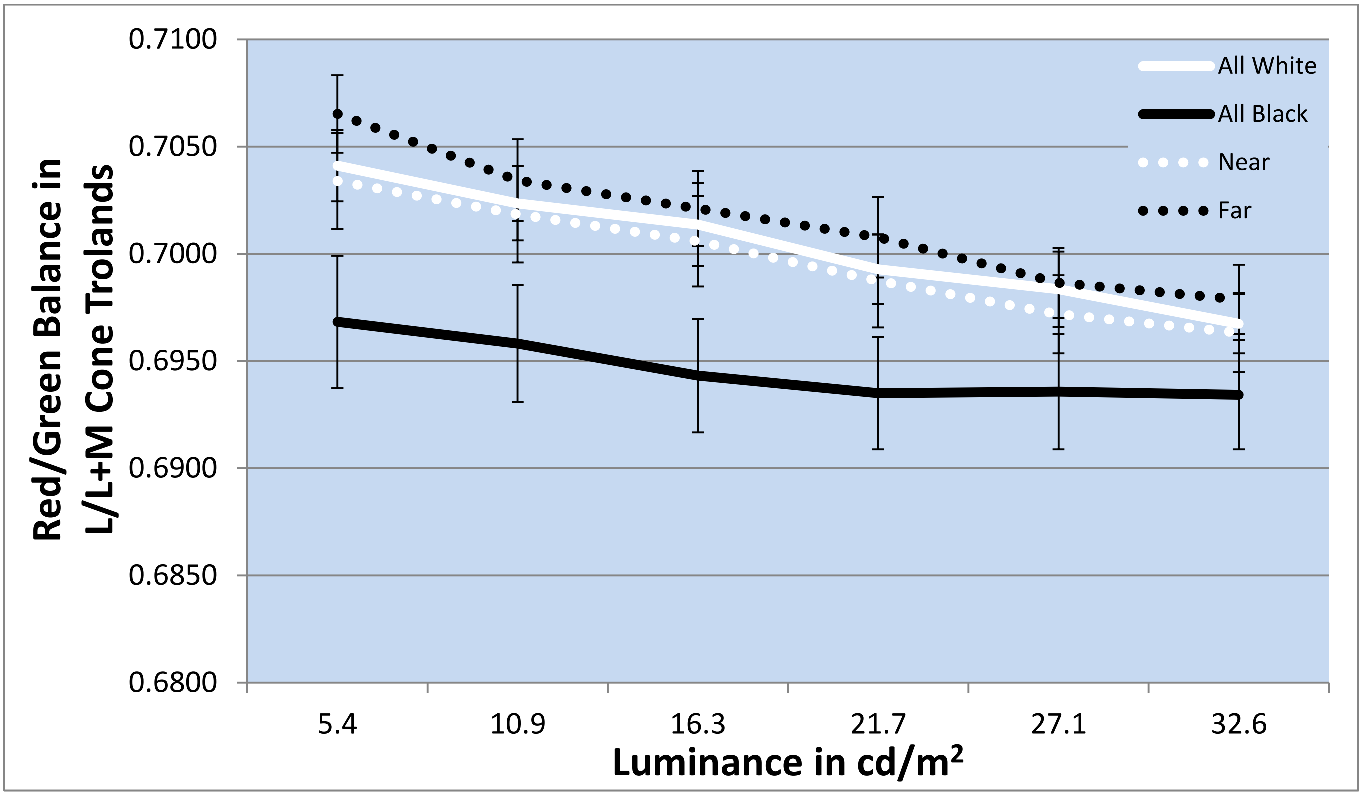


Figure 17. Red/Green Balance as a Function of Surround Configuration, Experiment 9. The Experiment 9 results showing red/green balances for the four background conditions of All White (solid white line), All Black (solid black line), Near (white dotted line), and Far (black dotted line) for each of the six light levels. The error bars depict the standard error of individual subject means.

Discussion

These results are in contrast to the expected results based on the brown boundary experiments. We hypothesized a similar pattern to the brown boundary experiments, such that contiguous surrounds would induce more green into the stimulus. However, the actual results suggest that contiguity is not a sufficient explanation. The Far condition, which has a non-contiguous surround, induced a statistically identical amount of green into the stimulus as the Near condition which did have a contiguous surround. The Near condition should be inducing more green into the stimulus if the pattern we found for brown boundaries held true for red/green balance. As such, alternative explanations such as flux or edge integration needed to be tested to determine the cause of this effect. This was also the first major set of data to suggest brown induction and red/green balance are separable effects that are not governed by a shared set of inducers.

B. EXPERIMENT 10 – VARIABLE SURROUND LUMINANCE EXPERIMENT

The purpose of this experiment was to vary the surround luminance instead of the test itself to test for the possibility of a flux explanation for the previous experiment. It could be that the total amount of light (flux) is the reason for the observed difference between the Near and Far conditions in the previous experiment. The Far conditions has a far greater amount of flux than the Near condition, as the remaining screen space is much larger than the annulus and thus puts off far more light. For this experiment, we simply replicated the near and Far conditions of the previous experiment, but we made two important adjustments. The first adjustment is that the Far condition’s bright surround now occupies the same amount of screen space (in area) as the Near condition and both conditions exist in small and large variations that double the amount of screen area (and thus flux) they use. The second adjustment is that the surround varies in luminance while the test stays constant. This allows us to test a much wider range of ratios of surround to luminance as we no longer are constrained by the limits of using colored stimuli on the monitor. The Green gun of a CRT monitor produces a larger portion of the total luminance than the Red gun, making it difficult to produce bright stimuli that can be adjusted along their red/green balance. By simply adjusting the brightness of the achromatic surround we can achieve a much larger amount of surround ratios. It also allows us to create conditions where the stimulus is brighter than the surround, but the surround is still brighter than the black background.

Methods

In this experiment we varied the luminance of the surround in the presence of a constant luminance test. The surround varied between 2.7 and 87.2 cd/m^2 with a constant 10.9 cd/m^2 test in each of the four configurations in Figure 18.

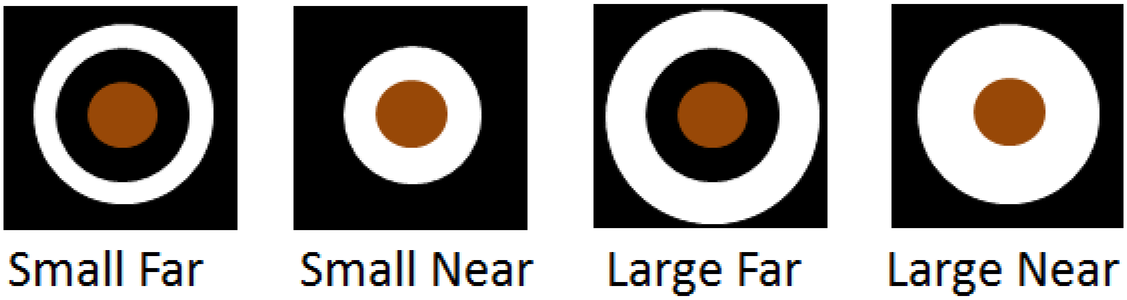


Figure 18. Surround Configuration for Variable Surround Luminance, Experiment 10. *The four spatial configurations used in the conditions for Experiment 10. The Near condition was a white annulus of 2° width contiguous with the 2°-diameter target stimulus with a black background. The Far condition was an otherwise identical black annulus on a white background. The all black and all white conditions feature full screen backgrounds with no annuli. The large surrounds are twice the area in cm^2 as the small surrounds.*

A 2°-width (target outer edge to annulus outer edge) white or black annulus surrounded the target stimulus. A second surrounding annulus had either the same or twice the physical area (cm^2) of the 2°-width annulus, thus creating twice the total flux coming from the annulus. The background was always black.

Results

A Repeated Measures ANOVA was run to analyze the dataset. No significant main effect was found for the size of the surround (p = .515, η2 =.043) or location of the surround (p = .551, η2 =.037), but there was a significant main effect for surround luminance (p <.001, η2 =.742). There was only one significant interaction, the interaction between the location of the surround (near or far) and the luminance of the surround (p < .01, η2 =.434). The average data across subjects can be seen in Figure 19. As the luminance of the surround increased subjects set their red/green balances at both lower (10.9 cd/m^2) and higher (43.6 cd/m^2 and 87.2 cd/m^2) L/(L+M) cone excitations in the Near conditions compared to the Far conditions. This interaction can be seen more clearly in Figure 20.

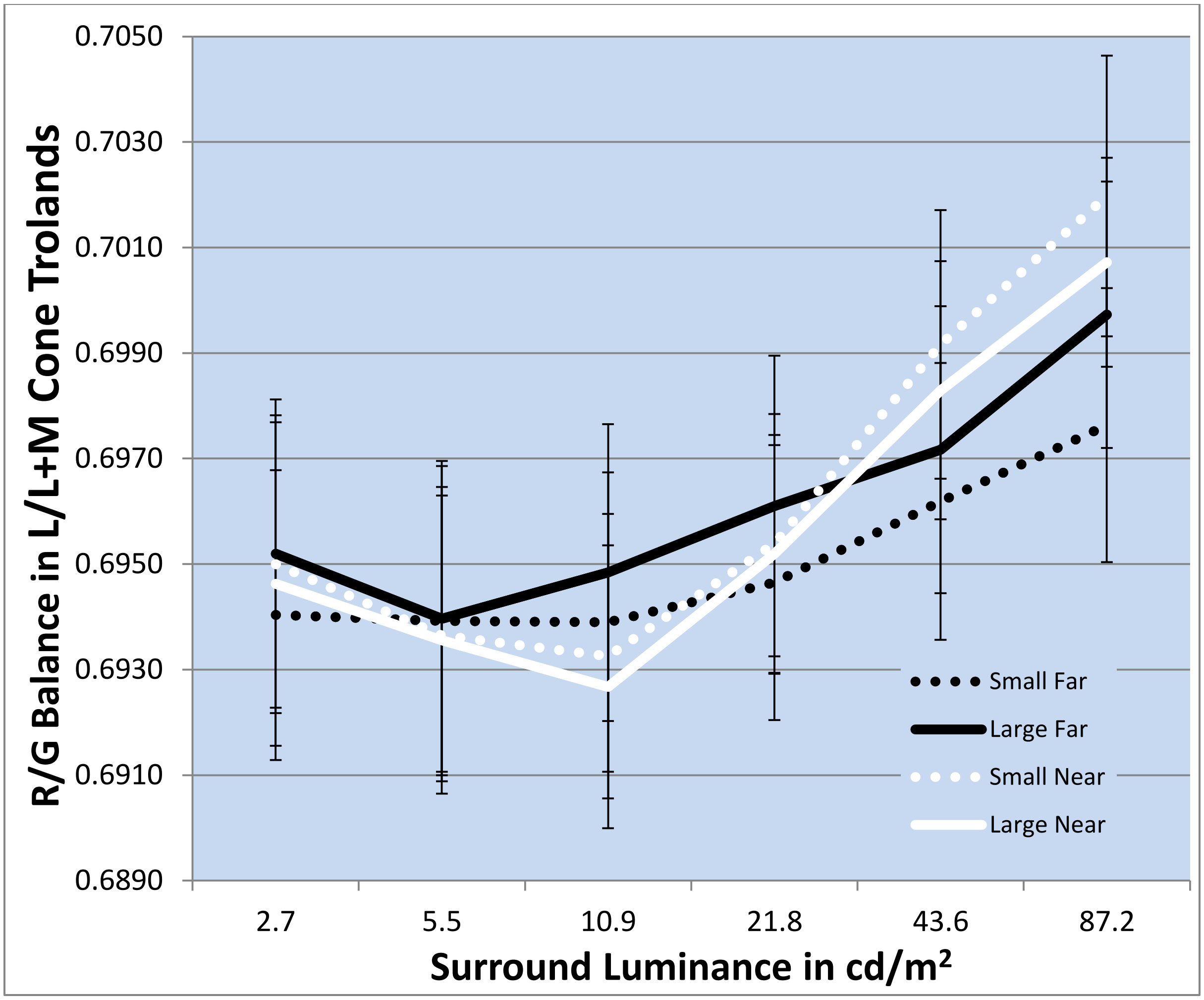


Figure 19. Red/Green Balances for Variable Surround Luminance, Experiment 10. This figure shows the red/green balances of Experiment 10 where the target stimulus was kept constant at 10.9 cd/m^2 while the surround luminance varied each trial. The small surrounds (dashed lines) are 2°-width and the large surrounds (solid lines) are twice the area (flux). Near surrounds (white lines) are contiguous and far (black lines) have a black 2°-width gap after the target stimulus. The error bars depict the standard error of individual subject means.

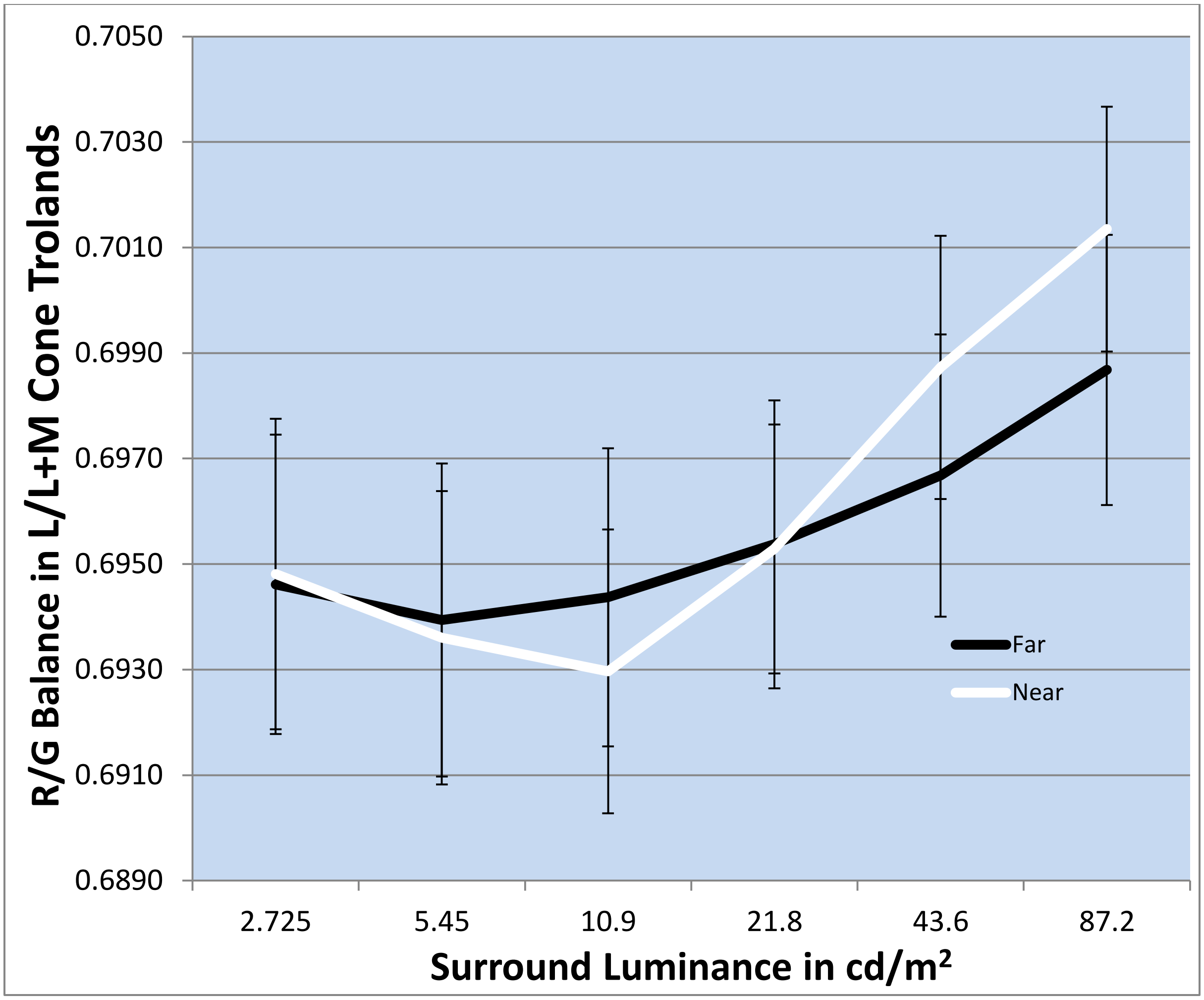


Figure 20. Replotted Variable Surround Luminance Data, Experiment 10.
This shows the same data as Figure 19, but with the Far and Near conditions combined into one in order to better show the significant interaction. The Near conditions show a greater variation in comparison to the far conditions. The error bars depict the standard error of individual subject means.

Discussion

These results showed that the Far conditions were relatively stable across the full range of surround light levels. Although the Far conditions trend upward as we increase the brightness of the surround they never reach the same heights as the Near conditions. However, the Near conditions also go much lower than the Far conditions, suggesting it increases the size of the effect in general, both toward red and toward green. Additionally, we observe a small trend to slightly elevated L/(L+M) activity at the lowest light levels, which is elaborated on further in the next experiment. The lowest L/(L+M) activities are observed when the stimulus and the contiguous surround (Near conditions) are the same luminance (10.9 cd/m^2) suggesting that there is some additional effect that only occurs at this light level. If we eliminated this data point from the curve it would look like there was no substantial change in L/(L+M) balance at all from 2.725 to 21.8 cd/m^2. One possibility is that at the point in the Near conditions where the stimulus and surround are equal there is a form of brightness assimilation occurring. Although there is a perceptual color border between the stimulus and the surround, luminance and potentially perceived brightness, is identical. This may suggest that if there is no luminance contrast the contiguous surround simply acts as an expanded border and shifts the contiguous contrast to the edge with the background. This would make these conditions equivalent to the All Black condition of the previous experiment which have consistently shown the smallest L/(L+M) activity in their balances.

The lack of any significant difference between Small and Large conditions rules out flux as major explanation of red/green balance differences. These data further support the idea that the ratio of test/surround matters, especially for conditions with a contiguous surround. If flux was a significant factor we would expect a doubling of flux to produce a noticeable difference, but the trend was actually for smaller changes in the Large conditions compared to the Small.

C. EXPERIMENT 11 – GRAY RING VARIABLE SURROUND LUMINANCE

In the this experiment we varied the luminance of the surround in the presence of a constant luminance test with a fixed white ring surrounding a variable gray ring on a black background. This experiment was designed to address the strange effect of the white near conditions where they shifted toward a great L/(L+M) cone ratio as the light level of the surround decreased below the target stimulus luminance. By using a gray ring between the target stimulus and a constant white surround we are able to create a stimulus set that should cause a similar effect if we assume it is due to the presence of a contiguous dim surround. The different sizes allow us to see if there is a spatial component to this effect.

Methods

In this experiment we used a target stimulus that was 2° in diameter with a spatially, ¼, ½, ¾, or 1°-width gray annulus surrounding the target stimulus. This gray surround varied between 2.275 and 87.2 cd/m^2 with a constant 10.9 cd/m^2 test in the configuration in Figure 21. The outer annulus was a constant 2°-width, and was fixed at 87.2 cd/m^2. This second annulus was surrounded by a black background. A representation of this stimulus is shown in Figure 21. A total of 10 observers completed these conditions in four sessions that were run on separate days with 5 trials per surround light level per gray ring size (20 trials total for each light level with each gray ring size).

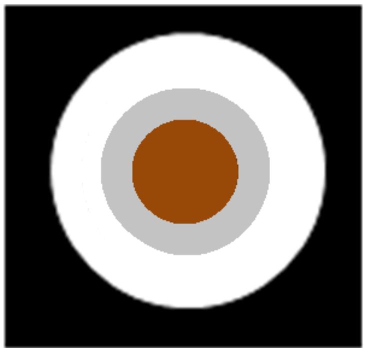


Figure 21. Stimulus Configuration for Gray Rings in Experiment 11.
This is a representation of the stimulus arrangement used in the Gray Ring Variable Surround Luminance experiment.

Results

A Repeated Measures ANOVA was run to analyze the dataset collected from the 10 observers. No significant main effect was found for the size of the gray ring ($p = .193$, $\eta2 = .172$), but there was a significant main effect for surround luminance ($p < .05$, $\eta2 = .314$). There was also a significant interaction between the size of the gray ring and surround luminance ($p < .05$, $\eta2 = .203$). The significance that was shown here is completely driven by the 10.9 cd/m^2 surround luminance condition. It is the only condition that showed a significant pairwise comparison for surround luminance and also shows an interaction where the L/(L+M) excitation significantly decreases as the size of the gray ring increases. The average red/green balances across subjects are shown in Figure 22. The gray ring results demonstrated that as the size of the gray annulus increased the effect of the annulus increased logarithmically to a potential asymptote at 1°.

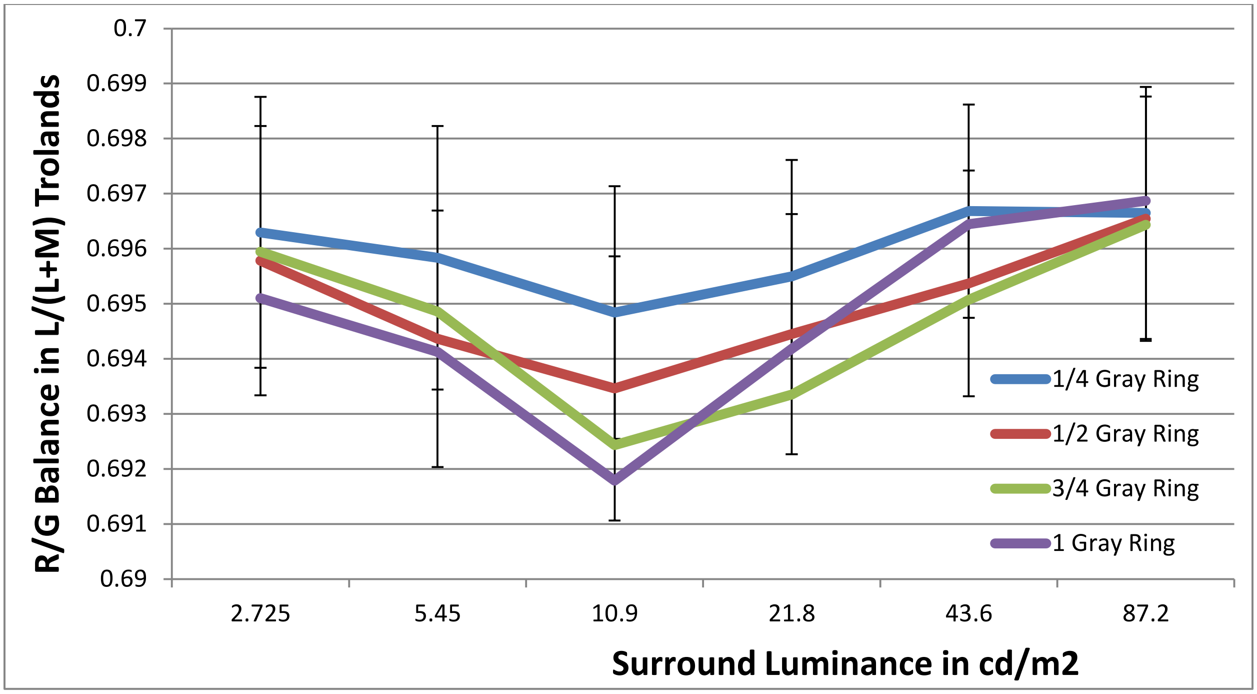


Figure 22. Red/Green Balances for Gray Rings in Experiment 11.
These are the red/green balances from the gray rings experiment with the six luminance values of the target stimulus plotted on the x-axis and the four sizes of the gray ring represented by the different colored lines. The error bars depict the standard error of individual subject means.

Discussion

These results suggest that the dim surround does cause a significant increase in the amount of L/(L+M) cone activity required for setting a red/green balance. It also shows there is a spatial dependence, such that smaller rings (less than ¾°) will reduce the size of the effect. This effect appeared to reach an asymptote at 1°, which would agree with our earlier research that suggest these ring size or gap effects dissipate rapidly for brown stimuli. As a whole, these data strongly suggest that the shift observed in Experiment 10 (the Variable Surround Luminance Experiment) toward lower L/(L+M) trolands, where the test was equivalent to the contiguous surround in luminance (at 10.9 cd/m^2), is a real effect that can be replicated even if there is a white surround instead of a black surround after the contiguous surround. One possibility suggested earlier is that, in these conditions, the initial surround is actually treated as an extension of the stimulus itself (brightness assimilation) and simply expands the luminance contrast to the outer edge of the gray annulus. However, in this experiment, that new first edge (the white annulus) is brighter than the stimulus, not darker. This would predict an increase in L/(L+M) trolands, not a decrease, as it would induce greenness into the stimulus. Additionally, if brightness assimilation is occurring, it suggests that either the target and/or surround size have an effect on red/green (R/G) balance (as the assimilated target/surround is now larger). We tested this possibility in the next experiment.

D. EXPERIMENT 12 - VARIATIONS IN TARGET AND SURROUND SIZE

One possibility raised by Experiment 11 is that, when the target and surround are the same luminance, brightness assimilation occurs such that the target and luminance are now treated as one object for the purpose of R/G balance. However, if this assimilation of brightness between target and surround is occurring then there needs to be an explanation for why it does not behave in the predicted direction. In both Experiments 10 and 11, a similar effect was observed under conditions where a target and contiguous surround were equiluminant, which was a reduction in L/(L+M) activity at an observer’s R/G balance point (suggesting redness induction). However these two experiments actually have opposite surround polarities with their outer surround (the surround immediately after the contiguous surround) at these equiluminant points. In Experiment 10 the outer surround was darker (black background), but in Experiment 11 it was brighter (maximally bright white annulus). This suggests that if luminance assimilation is occurring there must be an effect of surround and/or test size. This is something we found in the past for brown induction (Experiment 2 and 3) and it is possible this is also a factor for R/G induction. In order to test both these possibilities we utilized a target and surround that are the same total size (target alone or target and surround together) and equiluminant to simulate brightness assimilation. If the target and surround are acting as a single stimulus then changes to the size of the target or surround should have the same effect. Additionally, we had conditions with targets and surrounds that are twice their original size to see if there is an overall size effect. Finally we varied the light level of the target and surround in order to see if this assimilation effect occurs at multiple light levels as we previously only tested it at one light level.

Methods

This experiment utilized a set of stimuli very similar to those in previous experiments. In the target size conditions a target that was either 4° or 8° in diameter was presented on a black background. For the surround size conditions a 2°-diameter target with an equiluminant contiguous surround that was either 2° or 6° in diameter (from the outside of the target to the outside of the surround). A visual representation of these four conditions is seen in Figure 23. The target also varied between 3, 6, 11.9, 23.7, and 47.5 cd/m^2. The contiguous surround was always the same luminance as the target (replicating the gray ring from the previous Experiment 10). Seven observers completed these trials in a total of four sessions that were run on separate days with 5 trials per target light level per stimulus arrangement (20 trials total for each light level on each stimulus arrangement).

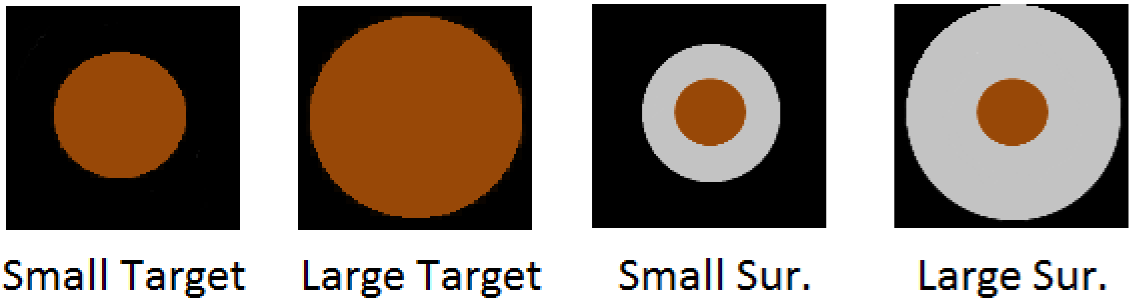

Small Target Large Target Small Sur. Large Sur.

Figure 23. Stimulus Arrangements for Targets and Surrounds in Experiment 12.
These four arrangements represent the target and surround sizes used in this experiment. The small sizes are 4° and the large sizes are 8° in total (surround conditions are 2° stimulus with a 2° or 6° surround.

Results

A Repeated Measures ANOVA was run to analyze the dataset collected from the 7 observers. No significant main effect was found for size of the target or surround (p = .661, η2 =.034), but there was a significant main effect for the surround conditions compared to target conditions (p <.01, η2 =.858). The effect of target light level was also significant (p <.001, η2 =.796). None of the interactions were significant. The average data across subjects can be seen in Figure 24. The significant effect of the surround and target conditions, is a replication of the same luminance surround effect seen in previous experiments and can be seen clearly in Figure 25.

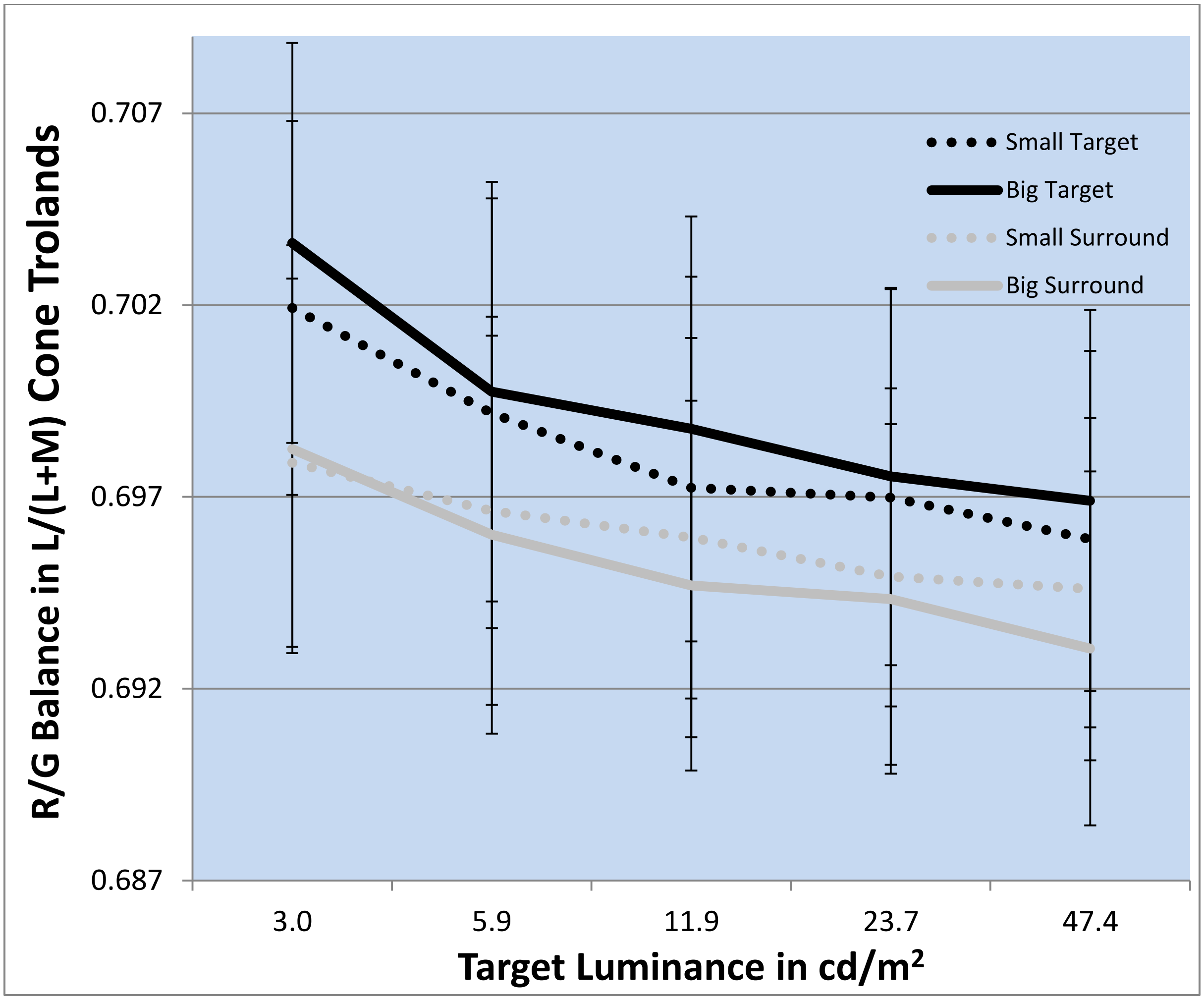


Figure 24. Red/Green Balances for Variable Target and Surround Size in Experiment 12. These are the red/green balances of 7 observers averaged together for the four stimulus configurations. There is an effect between target and surround, but not for size. Additionally, as target luminance increases in either condition, it moves towards lower L/(L+M) ratios. The error bars depict the standard error of individual subject means.

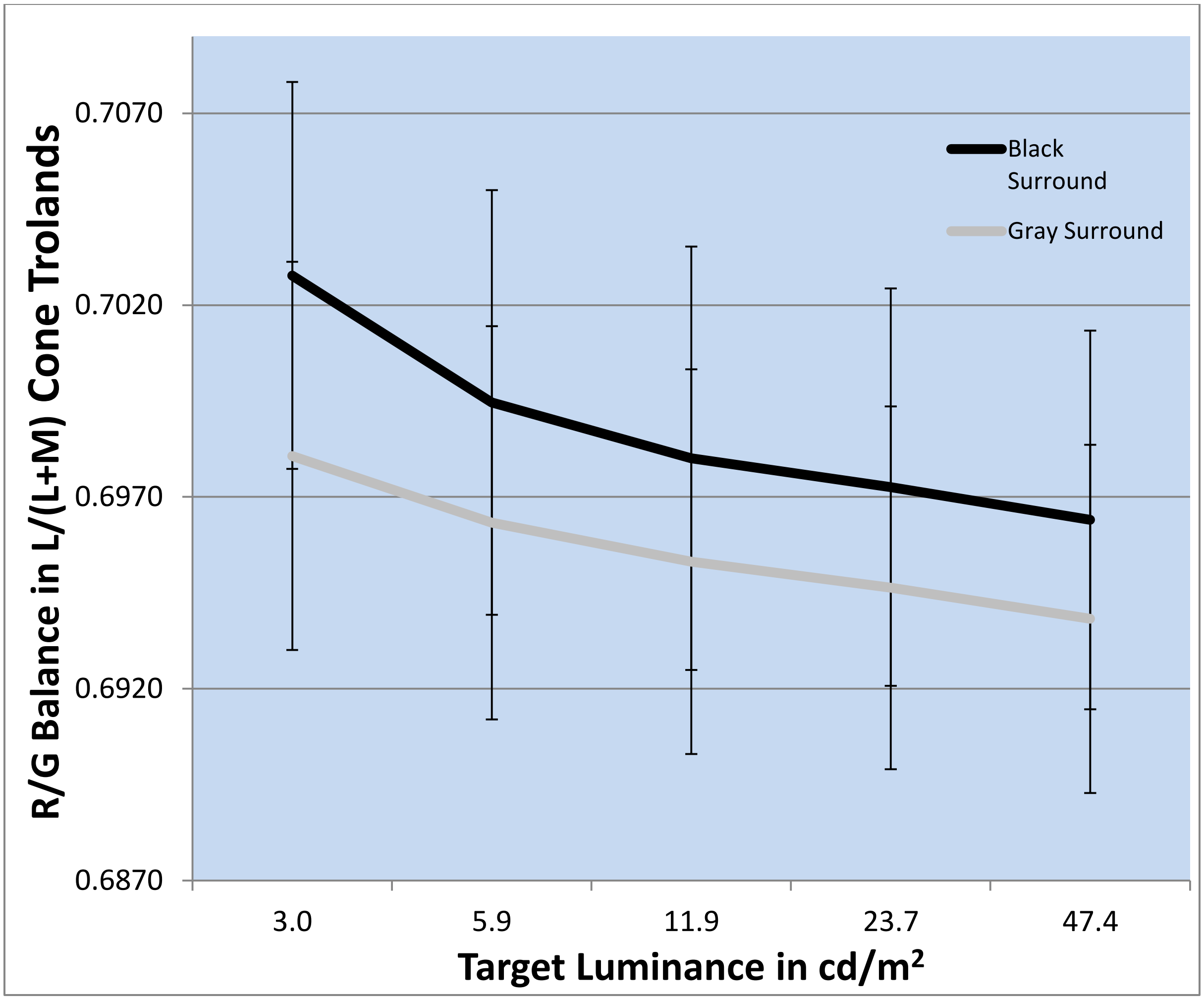


Figure 25. Replotted Red/Green Balances for Surround Configurations in Experiment 12. This graphs the same data but with the size conditions combined (small and big target are black while small and big surround are white) to show the effect between the target and surround size variations is due to the surround luminance. The error bars depict the standard error of individual subject means.

Discussion

These results showed no significant effect of size for either target or surround on red/green balances. This is yet another difference between red/green balances and brown induction, as brown induction showed significant effects of size manipulations on both target and surround. This also suggests that the results in Experiments 10 and 11 are not due to changes in the perceived size of the target or surround due to brightness integration. These data, when taken in addition to the previous data, suggests that brightness integration is a poor explanation of the phenomenon that occurs when a target and surround have identical luminance. Their outer surrounds should behave similarly to the contiguous inner surround of a target that has a different luminance than its surround, but instead they show a consistent effect of reducing L/(L+M) excitation at the R/G balance point. The previous explanation of a possible effect of size is not supported by the data from this experiment. Although we cannot rule out the possibility of target or surround size having some effect on R/G balance, the data presented here suggests it is not sufficient to explain the effect equiluminant surrounds have on R/G balance. This equiluminant surround effect also occurred at every light level tested, which included the highest and lowest luminance levels possible on our display.

Another effect observed here that was not observed previously is the effect of target light level independent of surround light level. Other than in the Experiment 9 All Black condition, we always had light level of a test varying in the presence of a bright surround somewhere on the screen. As we predict R/G balance to be determined by the ratio of the target's luminance to the luminance of the surround this is an unexpected effect. When the surround is either the same or darker than the test, the direction of change with increasing target light level is the same, toward lower L/(L+M) ratios. This trend could be observed in Experiment 9 in the All Black condition for the lower target light levels, but here it is demonstrated more clearly across the full range of test light levels and is also demonstrated for conditions where a surround is the same light level as the target. The relative contribution of target luminance and the ratio of target luminance to surround luminance will be explored further in Experiment 14.

E. EXPERIMENT 13 – MULTIPLE RING SURROUNDS

Experiments 10 and 11 suggested the possibility that the amount of rings present influences the type of effect surrounds will have on a stimulus on a stimulus. The amount of contrasting edges could have a cumulative effect and drive the red/green balance in one direction or the other depending on the nature of the extra edges (luminance increments or decrements). In order to test for these effects we utilized an experiment that largely mimicked the previous Variable Surround Luminance Experiment (Experiment 10) with the addition of extra rings that take up the same amount of total area and therefore the same total flux. We hypothesized that there would be a non-linear increase in the size of the effect as we added more rings (3) to the stimulus as a result of the increased number of contrasting edges. We would expect the 3 ring Near conditions to move more in the direction of greater L/(L+M) excitation and Far conditions to move more in the direction of less L/(L+M) excitation.

Methods

Using same stimuli set from the Variable Surround Luminance Experiment (Experiment 10) we varied the luminance of the surround in the presence of a constant luminance test with the addition of a 3 ring (annuli) conditions in which extra rings where added to the outside of the first annulus. This results in 3 visible white rings in the Near conditions and two visible white rings in the Far conditions. Both the Small and Large sizes of the surrounds in Experiment 10 were maintained in this experiment. In the three ring conditions the size (in cm^2) was equally distributed between the three visible or two visible white rings in order to maintain total flux.

The surround varied between 2.275 and 87.2 cd/m^2 with a constant 10.9 cd/m^2 test in each of the four configurations in Figure 26.

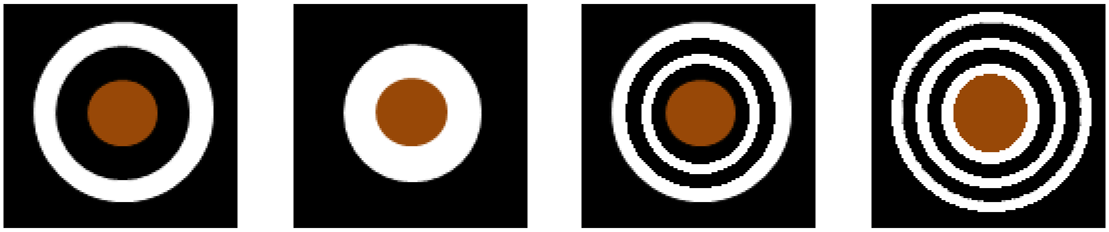


Figure 26. Target Stimulus and Surround Configurations for Multiple Rings, Experiment 13.
These are representations of the ring stimuli used in the two multiple ring experiments. The first two are the 1 ring Far and Near conditions. The second two are the 3 ring Far and Near conditions (the third black ring blends into the background and is not visible).

Results

A Repeated Measures ANOVA was run to analyze the dataset for the Far Rings conditions. No significant main effect was found for amount or size of rings (p = .386, η2 =.111), but there was a significant main effect for surround luminance (p <.01, η2 =.691). There was no significant interaction between ring number or size and surround luminance (p = .185, η2 =.174). As the luminance of the surround increased subjects set their red/green balances at statistically identical points until the surround luminance reached levels above 10.9 cd/m^2 at which point they set their balances toward greater L/(L+M) excitation. The average data across subjects can be seen in Figure 27.

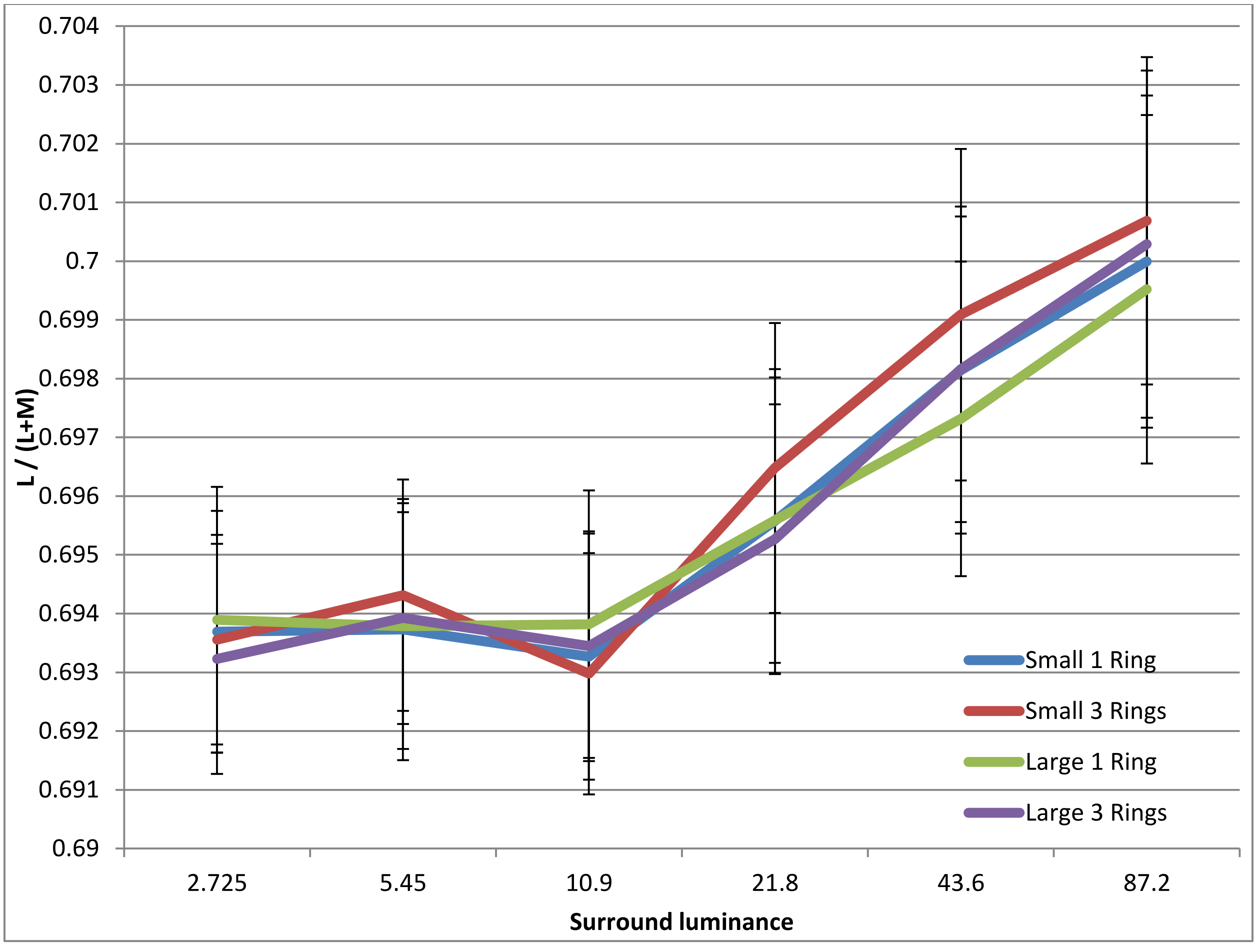


Figure 27. Red/Green Balances for Far-Ring Conditions in Experiment 13. These are the red/green balances from the Far Rings of the multiple rings experiment featuring a black contiguous ring with a white non-contiguous ring. 3 rings conditions also feature 2 extra rings. The error bars depict the standard error of individual subject means.

A Repeated Measures ANOVA was run to analyze the dataset for the Near Rings conditions. No significant main effect was found for amount or size of rings ($p = .547$, $\eta 2 = .074$), but there was a significant main effect for surround luminance ($p < .001$, $\eta 2 = .849$). There was no significant interaction between ring number or size and surround luminance ($p = .206$, $\eta 2 = .141$). As the luminance of the surround increased subjects set their red/green balances at statistically identical points until the surround luminance reached levels above 10.9 cd/m^2 at which point they set their balances toward greater L/(L+M) excitation. The average data across subjects can be seen in Figure 28.

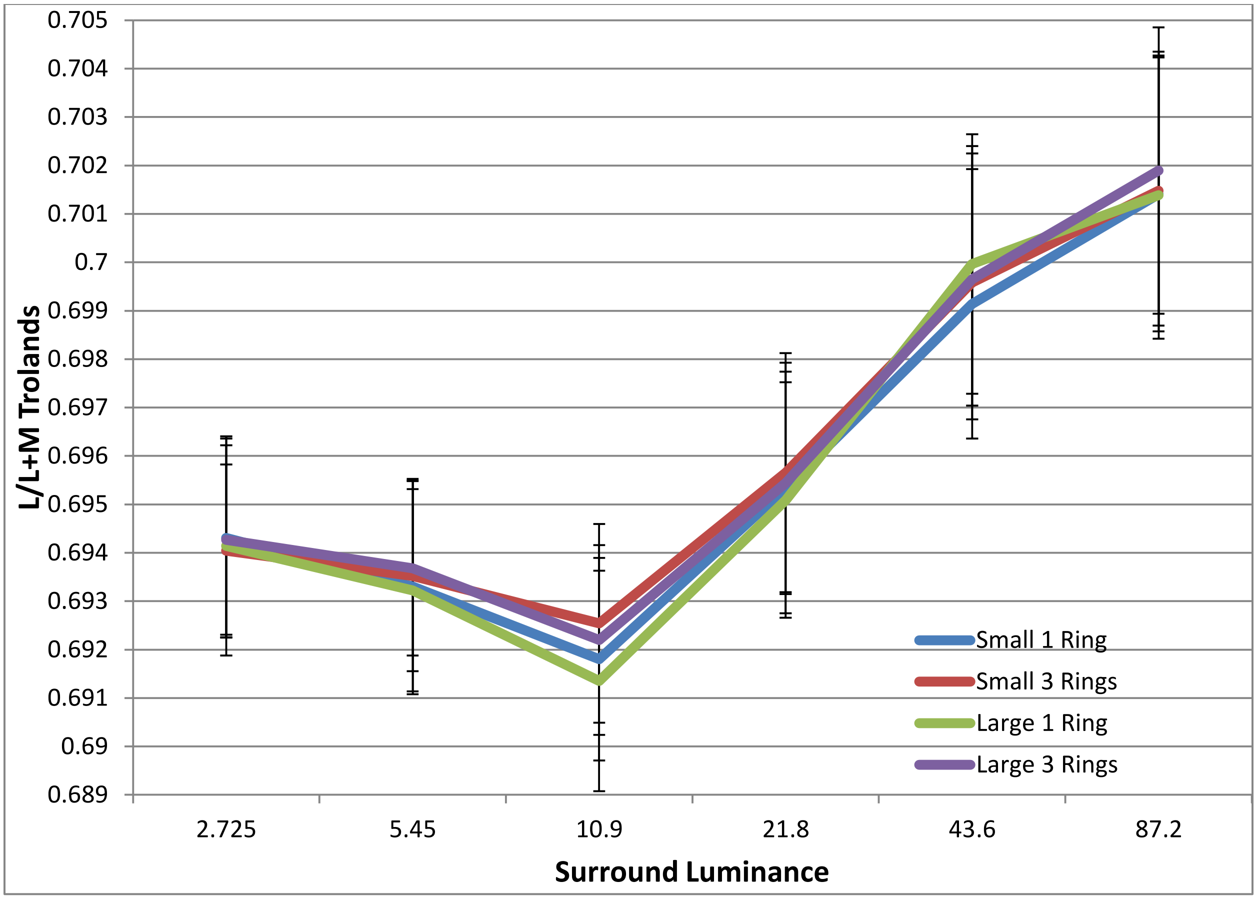


Figure 28. Red/Green Balances for Near-Ring Conditions in Experiment 13.
These are the red/green balances from the Near Rings of the multiple rings experiment featuring a white contiguous ring with a black non-contiguous ring. 3 rings conditions also feature 2 extra rings. The error bars depict the standard error of individual subject means.

A Repeated Measures ANOVA was run on this combined data set to test for an interaction similar to that observed in the previous Variable Surround Luminance Experiment (Experiment 10) between the Near and Far conditions. The interaction between near and far with surround luminance was significant ($p < .01$, $\eta 2 = .447$). This is the same interaction as observed previously. Near conditions have greater variability than seen in Far conditions and show a noticeable dip when the surround and test are the same luminance. The combined data sets can be seen in Figure 29.

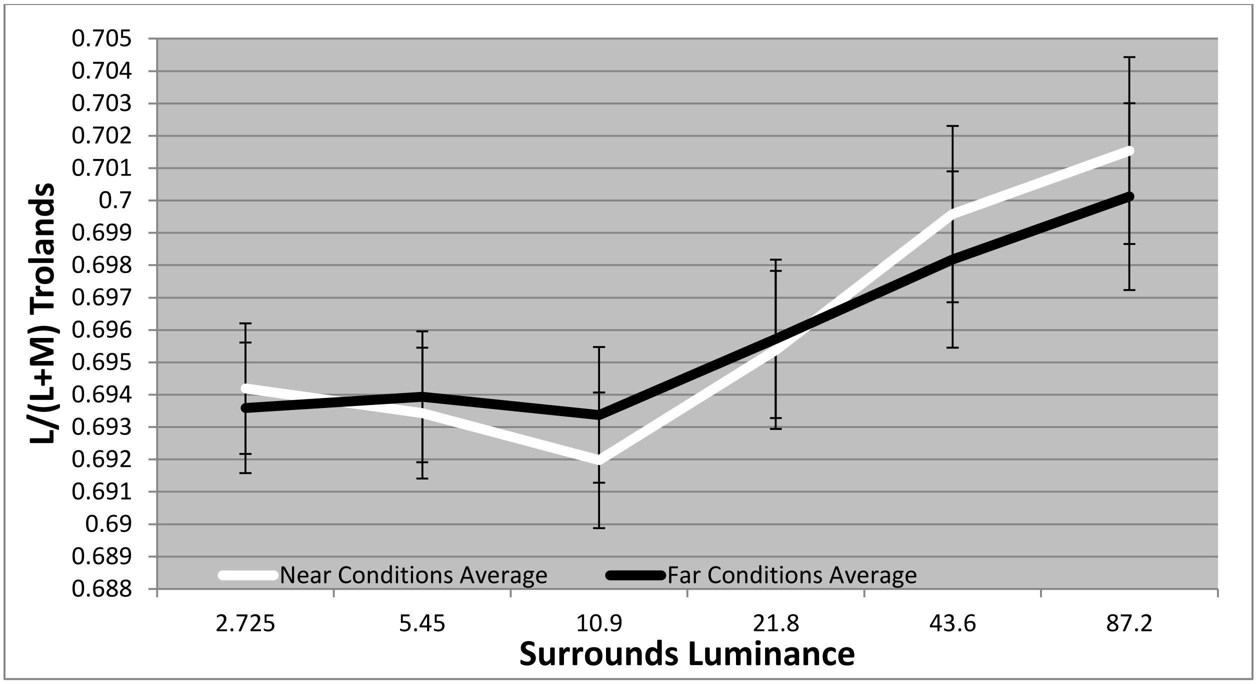


Figure 29. Combined Ring Data for Experiment 13.
Here we combine the four ring conditions (which did not differ significantly from each other) into one average set of data for both the Near and Far conditions in order to observe the interaction of surround location and surround luminance. The error bars depict the standard error of individual subject means.

Discussion

There is no significant effect of adding more rings, beyond what was previously observed in Experiment 10 (Variable Surround Luminance Experiment). This suggests the effect is most prominently predicted by the immediate surround and the next contiguous ring. There is no significant effect of subsequent contrasting edges. The lack of any synergistic effect from adding additional contrast edges in either condition suggests that there may be two effects similar to those we saw with brown induction, one that is mediated by local (contiguous) surrounds and another by more distal surrounds. However, we again see a dip for contiguous surrounds when they are identical in luminance to the target stimulus, adding to the large body of evidence of a unique equiluminant surround effect.

F. EXPERIMENT 14 – LIGHT LEVEL AND RED/GREEN BALANCE

In this experiment, we tested is if the overall light level of the target, independent of the ratio of target to surround luminance has an effect on red/green balance. Experiment 12 demonstrated that the light level of the target alone can have a significant effect on R/G balances. In order to test the relative contribution of this effect we created a set of stimuli which varied in their overall light level, but the ratio of the targets to their surround luminance was kept constant within the limitations of the monitor. This allows us to perform a multiple linear regression to determine the relative contributions of target luminance, surround luminance, and the ratio of surround luminance to target luminance.

Methods

We created a set of stimuli of various surround to target ratios with four different target stimuli luminance levels, 10, 15, 20, and 25 cd/m^2. These target stimuli were 2°-diameter and presented with a background that could be 2-10 times brighter than the target stimulus. Not all ratios could be tested for every target stimulus brightness level due to limitations of the monitor (it cannot go above 87.2 cd/m^2). A total of 10 observers completed these conditions in four sessions that were run on separate days with 5 trials per stimulus configuration.

Results

As we could not test all ratios for the purpose of doing a repeated measure ANOVA, we instead performed a multiple linear regression analysis in order to determine the best predictor of L/M Ratio between target luminance, surround luminance, and the ratio of surround/target. From this the best predictor variable was surround/target ratio which predicted 88% of the variance, with none of the other predictor variables contributing any additional predictive power when added to surround/target ratio. When looked at alone, target luminance predicted 20% of the variance and surround luminance predicted 35% of the variance. The collected red/green balance data is shown in Figure 30.

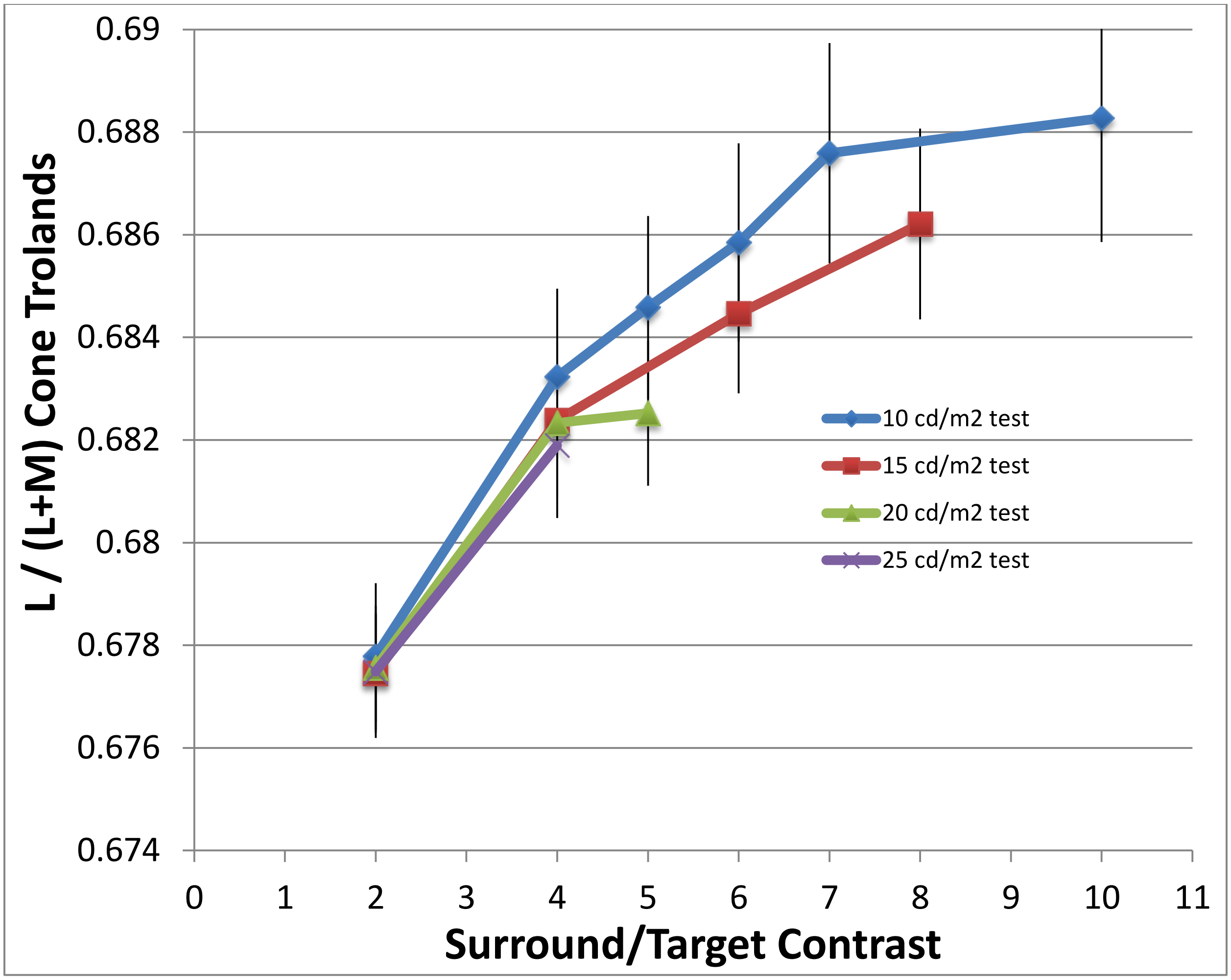


Figure 30. Red/Green Balances with Surround and Target Light Level Variations in Experiment 14

These are the average red/green balances from the 10 observers. The four colored lines show the four target light levels used in this experiment, with the ratio of the target to its surround shown on the x-axis. Not all target light levels could be tested at all ratios due to monitor limitations. The error bars depict the standard error of individual subject means.

Discussion

These results show that the overall target light level does not make a major contribution to red/green balance beyond what is contributed by the ratio of the target to the surround. Surround light level was actually a better predictor than target light level under these conditions. That is red/green balance appears to be controlled strictly by surround/target ratio independent of the overall light level of the test when the test is dimmer than its surround. The surround/target ratio is a very powerful predictor, accounting for 88% of the variance, suggesting the mechanism behind red/green balance is largely controlled by the physical properties of stimuli and not simply their perceptual category. Stimuli in this experiment could appear brown to a varying degree, but the red/green balance varied systematically with the ratio. One of the major limitations of this experiment was the inability to test some of the light levels at higher ratios. This is due to the physical limitations of the monitor. It is also worth noting we previously observed the effect of target light level under a condition where it was brighter than its surround. All of the conditions here feature surround bright than the target. It could be the case that in those conditions where the target is brighter than the surround, target light level is a larger contributor to this effect.

G. EXPERIMENT 15 – DICHOPTIC RED/GREEN BALANCE

Based on the previous research that supports both a local (contiguous) surround effect and a distal surround effect for brown induction (Experiment 6) we suspected we may find a similar dichoptic effect for red/green balance. This would suggest the possibility of a potential retinally mediated pathway for red/green balance effects (responsible for the contiguous surround effect) in addition to a cortically mediated pathway (for the distal surround effect). As the previous data in this section show, contiguous surrounds have a different pattern of effect than the distal surrounds. Red/green balance shifts could be primarily driven by monocular pathways, which would show an enhanced effect for monocularly presented contiguous surrounds, but as we saw with brown induction, it is also possible a second mechanism can operate for perceptually contiguous surrounds that are processed in dichoptic pathways. To test these possibilities experimentally, a dichoptic apparatus was utilized to check for the presence of a systematic red/green dichoptic effect based on target and surround contrast variation.

Methods

This experiment made use of a dichoptic viewing apparatus that divided the screen in half through the use of mirrors such that one eye would only see one half of the screen and the other eye would only see the other half of the screen. This apparatus reduced the light levels such that the white surrounds were 49.94 cd/m^2. Four observers made judgments on either an all-white or an all-black surround presented to both eyes (binocular presentation). In addition, two sets of surrounds were used where one eye had a white surround and the other a black surround (dichoptic presentation). When the eye that had the target had the white surround this was referred to as Ipsilateral White, and if the white surround was in the eye not viewing the target it was called Contralateral White. These conditions are similar to those utilized in Experiment 6, but differ in that a single monitor with a split screen was used for stimulus display, rather than two monitors. An additional variable, that would not be possible in brown induction experiments, is that of the target light level. We varied the target luminance between 1.6, 3.19, 6.37, 12.75, and 25.5 cd/m^2. This was the maximum extent possible due to the apparatus reducing the total amount of light reaching the observers’ retinas. A total of 4 observers completed these conditions in four sessions that were run on separate days with 5 trials per stimulus configuration.

Results

A Repeated Measures ANOVA was run on this combined data set to test for an effect of presentation type. There was a significant difference in presentation type (p <.05, η2 =.683) with the pairwise comparisons showing that the White and Ipsilateral White conditions differed significantly from the Contralateral White and Black conditions, but not from each other. The effect of target light level was not significant (=.525, η2 =.219). The average data across subjects can be seen in Figure 31.

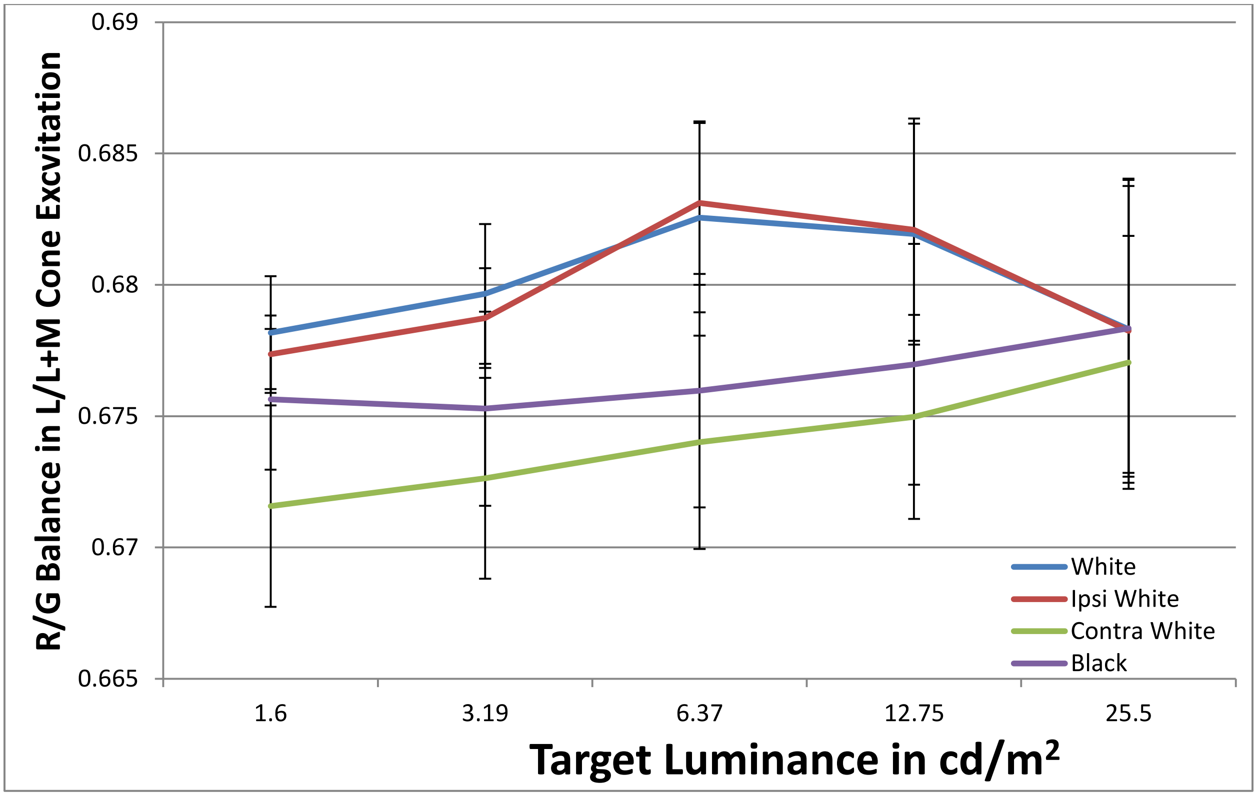


Figure 31. Red/Green Balances for Dichoptic Conditions in Experiment 15
This shows the red/green balances from the dichoptic experiment. There is no dichoptic effect as the White and Ipsi(lateral) White lines as well as the Black and Contra(lateral) White lines largely overlap. The error bars depict the standard error of individual subject means.

Discussion

Although these results suggest no significant effect of dichoptic presentation, we used a small sample size of 4 observers and the data was rather noisy. This effect is revisited in another form in the next section (Experiment 19) which provides stronger evidence for a lack of a dichoptic effect for red/green balance.

H. OVERALL DISCUSSION OF EXPERIMENTS 9-15

Taken together, these experiments suggest that red/green balance is primarily controlled by the ratio of the luminance of a target stimulus to the luminance of a bright surround somewhere in the visual field. In the absence of a bright surround, red/green balance shifts toward lower L/(L+M) excitation compared to conditions where a bright surround is presented somewhere is the visual field. This means that the target appears reddish on a black surround compared to a physically identical target presented with a bright white surround. If a bright surround is contiguous with the target stimulus it does not provide an enhanced effect compared to non-contiguous surrounds. This lack of enhancement suggests that retinal pathways are unlikely to be potential candidates for these effects (a hypothesis we will test using primate physiology later), and instead points to a more cortically based global mechanism that is not controlled by simple center-surround mechanisms at the level of the retina. However, this cortical mechanism does not appear to integrate edges and instead seems to be making a single comparison to the brightest target stimulus in the visual field.

It is also worth noting that Experiment 12 suggests that target luminance appears to be a strong driver of this effect in the absence of a bright surround. This would suggest the presence of two mechanisms which work in the same direction. Making a stimulus dark will increase the amount of L excitation an observer needs to achieve a balance as will increasing the ratio of the surround luminance to the target luminance. Both of these have an effect on the perceived brightness of a stimulus suggesting that brightness mechanisms could underlie this effect. Brightness modeling is an area we are currently exploring and hope to determine to what degree brightness induction and R/G balance are related.

The gray-ring surround data from Experiment 11 seems to provide a contrast to brightness as an explanation based on the consistent shift toward lower L/(L+M) excitation in the presence of a contiguous surround that is the same luminance as the test. This effect is supported by data from every experiment we have performed where the target stimulus and the surround were identical. The lowest L/(L+M) excitation for a balance point is always the point at which the stimulus and surround are contiguous and identical in luminance, and making the surround brighter or dimmer than the target stimulus will raise the L/(L+M) excitation for the balance point. This occurs whether the outer surround is a bright white (therefore making the stimulus appear relatively dim) or dark black (making the stimulus appear relatively bright). We initially thought it was possible that when the surround and the target stimulus are the same luminance the visual system assimilates them and treats them as no longer having an edge (as the edge between them is strictly chromatic) for the calculation of red/green balance; thus making it a single stimulus composed of both the target stimulus and it's same luminance contiguous surround. However, Experiment 12 shows this size effect explanation is insufficient and the consistent direction of effect on R/G balance of the gray inner surround with a bright outer surround in Experiment 11 and the dark black outer surround from the Near conditions in Experiment 10. Taken together, this strongly suggests there is a fundamental difference in a contiguous surround that is of the same luminance as the target stimulus and any other type of surround configuration. One possible explanation comes from the data in Experiment 13 where the number and polarity (bright or dark) of outer rings appeared to have no effect on R/G balance. It could be that only the immediate contiguous ring affects R/G balance, but this is contradicted by the difference in the All Black condition of Experiment 9 and the Far condition which features a non-contiguous bright surround. This is also supported by the difference observed in Experiment 12.

V. RED/GREEN BALANCE ACROSS THE YELLOW-BLUE SPECTRUM

Note: Experiments 16-19 have been published as DeLawyer, Tayon, Yu, and Buck (2018).

Both brown and yellow can exist in a pure, unitary (or unique) state, can be mixed perceptually with either red or green, and can be canceled by blue. Brown and yellow may therefore be considered analogs in opponent-color theory for dark and bright colors, respectively. Yet early research by Bartleson (1976) suggested the strongest browns are made by darkening stimuli that look orange, rather than yellow. From this, we have shown that a key difference between brown and yellow is the conditions needed to achieve a red/green balance (Buck & DeLawyer, 2012). Balanced browns need more L-cone excitation to achieve a red/green balance than do balanced yellows for most observers. At issue, though, is whether the red/green balance shift is specific to yellow-brown (long-wavelength biased) targets or is also found for blue (short-wavelength biased) and achromatic gray (broad-band) targets, all of which can be red/green balanced. The outcome has implications for the mechanisms of red/green hue shifts. In the former case, the shift may be determined by mechanisms that are specific to long-wavelength biased targets. In the latter case, the hue shift may be determined by mechanisms involved in perceptual representation of red and green, regardless of target appearance. Our previous research did not show a consistent shift of observers' balances for blue targets (Experiment 8). Specifically, a target that appeared bright blue when presented on a black surround, and the same target that appeared dark blue target when presented on a bright white surround, had similar red/green balances for half the observers, while the other half showed shifts of comparable size for both yellow/brown and blue targets. This inconsistency across observers of a shift for short-wavelength targets is reminiscent of results reported by Bimler et al., (2009) for spectral lights that found green shifts for yellow targets but not blue targets as surround luminance increased. Both of these studies employed targets having high spectral purity and saturation, leaving the generality of the red/green hue shift across less spectrally pure stimuli unsettled.

Bartleson (1976) showed that the strongest browns are seen for stimuli that were somewhat desaturated. We too have observed that desaturated stimuli can produce brown perceptions at higher light levels than more saturated stimuli, suggesting this aspect of Bartleson's observations can also be shown quantitatively. This raises the question whether desaturated brown stimuli will also show a stronger red/green hue shift than more saturated stimuli.

To address these issues and compare red/green hue shifts seen for blue and desaturated/achromatic targets to those seen for yellow/brown targets, we varied the spectral composition of a target so that it systematically varied in appearance from saturated yellow/brown, to desaturated yellow/brown, to gray, to desaturated blue, to saturated blue. We compared the red/green balance points of each of these targets when presented on black or white surrounds in order to quantify red/green hue shift for each target. We expected to observe red/green balance shifts only along the yellow/brown range with some enlargement of the effect for desaturated yellow/brown stimuli.

We also investigated the possible role of S-cone signals from the bright surround in driving target red/green hue shifts. We previously showed that the red/green hue shift between yellow and brown could not be explained on the basis of reddishness in the bright surround (which could make the target look greenish by simultaneous color contrast). However, the bright white surround certainly provides strong S-cone stimulation that is absent for the black surround. Although the bright surround was red/green balanced, S-cone signals were presumably contributing along with L-cone signals to the “red side” of that balance. Perhaps this S-cone contribution to the surround might inhibit redness in the contiguous target or in some other way induce greenness into the target. If true, we would expect a shift of target red/green balance toward needing greater L-cone excitation when a target is presented on a surround with high S-cone excitation in order to compensate for the induction of greenness into the target predicted by simultaneous color contrast. If surround S-cone stimulation does indeed drive the red/green hue shifts seen between bright white and black surround conditions, then we would expect the variation of surround S-cone excitation to display the same pattern of effects on yellow/brown, blue, and achromatic targets that we find in the first set of experiments using bright-white and black surrounds. If we were to instead find a different pattern of red/green hue shifts across the spectrally different targets, then some other factor(s) must also influence red/green hue shifts that occur between bright-white and black surround conditions.

Finally, we sought to characterize the nature of the neural pathways in which these red/green hue shifts occur by comparing conditions in which both target and surround were presented to the same eye (monocular condition) and conditions in which target and surround were presented to different eyes (dichoptic condition). In the latter condition, target and surround were aligned and fused by the observer to produce the same perception as in the monocular condition, even though target and surround were not presented to the same eye. If the red/green hue shift occurs later in visual pathways, after convergence of signals from the two eyes, then the perception of a contiguous surround (whether from monocular or dichoptic conditions) should be sufficient to drive the shift. Or, if the red/green hue shift occurs earlier in visual pathways, before the site of binocular convergence, then only the actual physical contiguity of target and surround in the monocular condition would drive the shift. We previously showed that this sort of dichoptic presentation induced brown into yellow targets in Experiment 6, so the present study provides another test of possible parallels between brown induction and red/green hue shift.

A. GENERAL METHODS

A Hewlett-Packard CRT monitor, with a frame-rate of 85Hz, and a resolution of 1600x1200 was used for stimulus display. The monitor's light output was measured with a Photo Research SpectraScan PR-702. A subject's head was supported by a chin and forehead rest at a distance of 63cm, causing the full screen to subtend 33° by 25°. A black foam-board enclosure surrounded all apparatus components and the observer's head, so that when room lights were off, nothing was visible beyond the monitor screen. The CRT monitor features 3 separate phosphors - R, G, and B - that can be adjusted in output between 0 (off) and 255 (maximum) individually. The maximum gun outputs in luminance were 27.3 cd/m^2 for Red, 60.9 cd/m^2 for Green, and 11.1 cd/m^2 for Blue (all measurements are in CIE 10°). Using a MATLAB gamma correction table, we linearized the values from 1-255 such that each step represents a near equal difference in luminance and therefore troland value (1/255 of the maximum value seen in Table 1). The measured combined output (which produced the white observers saw in the white surround conditions) was 99.6 cd/m^2. The black level of the monitor (which produced the black observers saw in the black surround conditions) was less than .1 cd/m^2.

Table 1. Cone Trolands at Maximum Luminance Output for the three CRT Phosphors

	Red Phosphor	Green Phosphor	Blue Phosphor
L Trolands	625.8	1050.7	158.2
M Trolands	138.7	674.4	152.2
S Trolands	0.4	2.7	5.7

All observers were University of Washington undergraduates (ages 19-25) who completed the studies in exchange for course credit and who were assessed as having normal color vision by the Ishihara Pseudoisochromatic Plate test. Some were native speakers of American English, while some were not. All procedures and consent forms were approved by the appropriate Institutional Review Board at the University of Washington. Not all subjects completed all conditions, but the subjects used for each experiment after Experiment 16 had completed all previous experiments.

Subjects freely adjusted the ratio of Red and Green phosphor outputs on a CRT monitor (and thus the relative activation of L and M cones) for a 2°-diameter target stimulus to yield a red/green null (appearing neither reddish nor greenish).

For a total of 9 different combinations, fixed, preset levels of Blue phosphor (Table 2 displays the S-troland values for the corresponding levels of Blue phosphor) were added to the target stimuli, which were composed of varying amounts of Red and Green phosphor, as controlled by the observer using a keyboard. This created a set of yellow/brown, grey (achromatic), and blue stimuli varying in their spectral purity. In the yellow/brown range (from Blue phosphor levels 0-16 for all conditions except the high luminance conditions in Experiment 2 where it is 0-32) subjects were likely to perceive the target as appearing yellowish on a black surround and brownish on a white surround; the target appeared less saturated as the Blue phosphor level increased. In the gray range (Blue phosphor level 32 for all conditions except the high luminance conditions in Experiment 2 where it is 64) subjects were likely to perceive the target as achromatic once balanced regardless of the surround color. In the blue range (all remaining levels not mentioned previously) subjects were likely to perceive the target as appearing blue regardless of the surround color, but the target appeared less saturated as the Blue phosphor level decreased.

In Experiment 16, the luminance of the test target was allowed to vary with increases of Blue phosphor. In Experiments 2 and 3, luminance (and therefore L/M activity) was kept constant by scaling it relative to the increasing amounts of Blue phosphor activation. This allowed us to increase S-cone activity while keeping total L and M cone activity relatively stable as observers adjusted the ratio of L and M cone excitation to a balance. Experiment 4 used identical surrounds and targets as those in Experiment 2, but they were presented using a dichoptic apparatus.

The data from all experiments were analyzed in SPSS for Windows 10 using a Repeated Measures ANOVA with a Greenhouse-Geisser correction for sphericity and Bonferroni correction for multiple comparisons.

Table 2. Average S-Cone Trolands and Luminance for each level of Blue Phosphor in Exps. 1-3 when added to the Red and Green Phosphor Levels at the Observers' Average Red/Green Balance Points.

Blue Phosphor Level	S Trolands	Luminance in cd/m^2
0	0.60	11.5
2	0.65	11.6
4	0.69	11.7
8	0.80	11.9
16	1.01	12.3
32	1.4	13.1
64	2.31	14.5
128	3.95	17.3
256	7.06	22.6

B. EXPERIMENT 16 – VARIABLE TARGET S-CONE EXCITATIONS, VARIABLE LUMINANCE

Methods

This experiment measured red/green balance on white and black surrounds for targets that varied in amount of Blue phosphor that was added to Red and Green phosphors. Target appearance ranged from saturated yellow/brown (no Blue phosphor) to desaturated yellow/brown to achromatic to desaturated blue to saturated blue (maximum Blue phosphor) in 9 steps. The average S-cone trolands varied between and .6 and 7.06 and the average luminance varied between 11.5 and 22.6 cd/m^2 over these 9 conditions because of the variation in the Blue phosphor content (Table 2). Sixteen observers adjusted a target to a red/green balance (perceptual null) 5 times at each level of the Blue phosphor levels per session for both white and black surrounds and repeated this on 4 separate days for a grand total of 20 settings per condition. The contribution of L+M cone excitation from the Blue phosphor was not controlled for. This means that there was a slight increase, which proportionally favored M-cone trolands, as the Blue phosphor was added to the target

Results and Discussion

Figure 31 shows that white surrounds lead to consistently higher L/(L+M) ratios at the red/green balance point of the target when compared to black surrounds, at all target Blue phosphor levels, but the intensity of this difference decreases as the amount of Blue phosphor in the target increases. This is consistent with induction of greenness into the target by the bright white surround, and the resulting need for observers to add proportionately more Red phosphor to restore the target's red/green balance. As Blue phosphor level increases two things happen. Firstly, the L/(L+M) ratios for red/green balance become significantly lower. This is expected from opponent-color theory because proportionately more Green phosphor, and resulting M-cone excitation, is needed to balance the redness contributed by the added S-cone stimulation from the Blue phosphor [9]. Secondly the difference in L/(L+M) ratios for red/green balance between white and black surrounds decreases until they become virtually identical when the target is maximally blue (though they are still significant according to the pairwise comparison).

Both the main effects of the surround and the Blue phosphor level of the target, as well as the interaction between the two main effects were significant at the $p<.001$ level (see Table 3). All pairwise comparisons for Blue phosphor level of the target were significant at the $p<.05$ level. The data, averaged across the 16 observers, is graphed in Figure 32.

These data partially support our earlier results in Experiment 7 that did not show a consistent shift in red/green balance for blue targets on white versus black surrounds. In that experiment, our blue targets were highly saturated, which the present results show produces only a very small difference in red/green balance on white vs. black surrounds. These results are also consistent with work by Bimler and colleagues (2009), who found little hue shift for blue targets having high spectral purity but who did find hue shifts for yellow targets in the same direction shown here.

The present data suggest an effect of luminance contrast between the target and its surround (luminance contrast effect) that varies in magnitude based on the level of S-cone excitation in the target. In this way, S-cone activity would act as a moderating variable for the luminance contrast effect, causing the size of the luminance contrast effect to decrease as S-cone activity in the target increases. However, the increase of Blue-Phosphor level in this experiment also increased target luminance (Table 2), which would change the ratio of the target's luminance to its surround and therefore change the size of the luminance contrast effect. In order to control for this possibility another experiment was performed.

Table 3. Repeated Measured ANOVA for Experiment 16

Experiment 1 ANOVA	Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
White versus Black Surround	.011	1.000	.011	99.401	<.001	.869
Error(Surround)	.002	15.000	.000			
Amount of Blue Phosphor	.417	1.266	.330	744.657	<.001	.980
Error(BluePhos)	.008	18.991	.000			
Surround * BluePhos Interaction	.003	2.037	.002	51.045	<.001	.773
Error(Surround*BluePhos)	.001	30.552	.000			

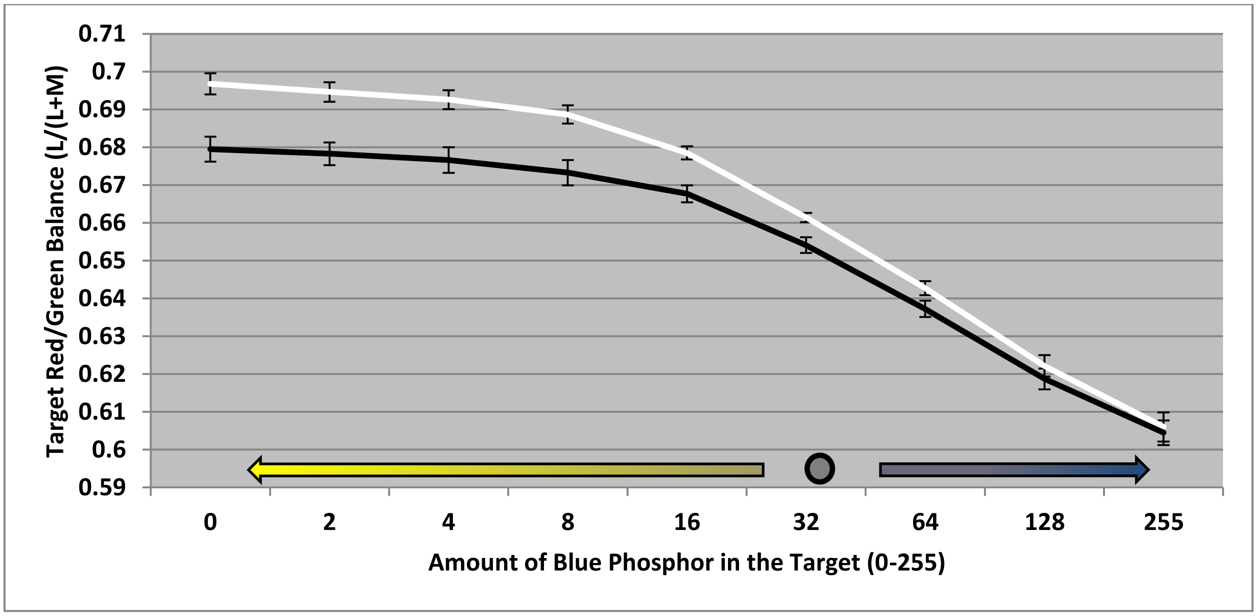


Figure 32. Red/Green Balances as a Function of Target Blue Phosphor Levels in Experiment 16.

The red/green balanced target appeared achromatic at 32, increasingly saturated yellow at lower values, and increasingly saturated blue at higher values. Contrast-dependent red/green hue shift is seen as the distance between bright-white-surround (white line) and black-surround (black line) conditions. In Experiment 1, as the Blue phosphor increased the total luminance from the red and Green phosphors stayed the same, but luminance increased from the addition of Blue phosphor. Error bars represent the standard error of individual subject means.

C. EXPERIMENT 17 – VARIABLE TARGET S-CONE EXCITATIONS, CONSTANT LUMINANCE

Methods

In this experiment, observers set red/green balances for two target stimuli, one that averaged 22.6 cd/m^2 (low luminance) and another that averaged 45.2 cd/m^2 (high luminance), for 9 levels of Blue phosphor content of the target. The judgments were made on either an all-white surround (87.2 cd/m^2) or an all-black surround (<.01 cd/m^2).

For the lower luminance targets, 13 observers adjusted the target to a red/green balance (perceptual null) for each condition. Twelve of the 13 observers also made the same judgments for the higher luminance targets. The remaining observer was no longer available.

Unlike Experiment 16, target luminance was kept constant as Blue phosphor was added. This was achieved by scaling the Red and Green phosphors to compensate for the increase in L and M cone activity provided by the Blue phosphor. As the Blue phosphor increased, the Red and Green phosphors decreased by an appropriate amount to keep the luminance constant.

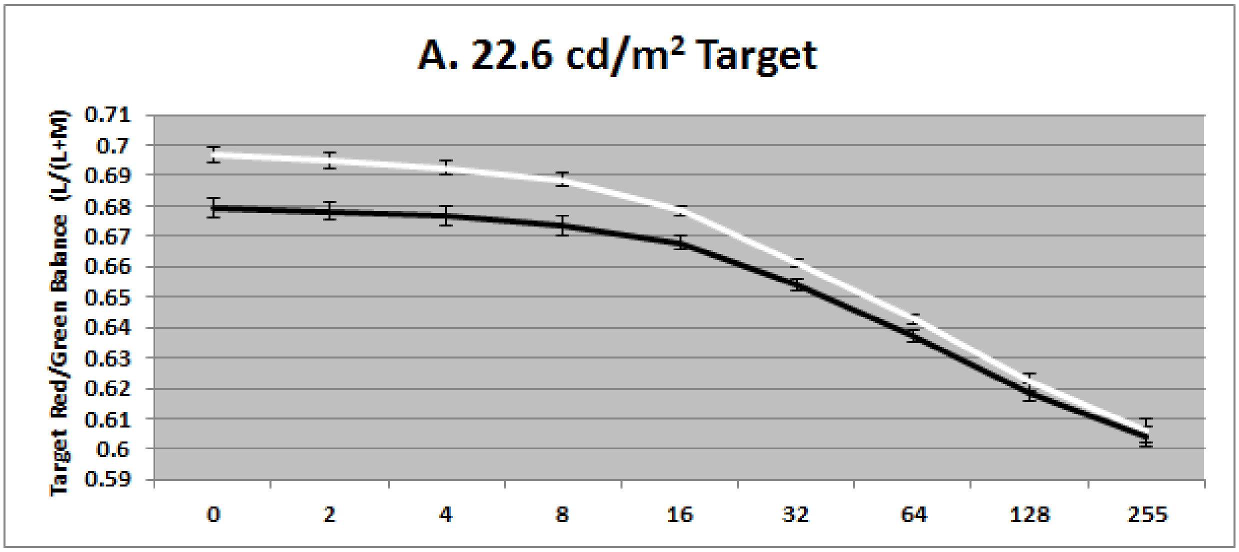
Results and Discussion

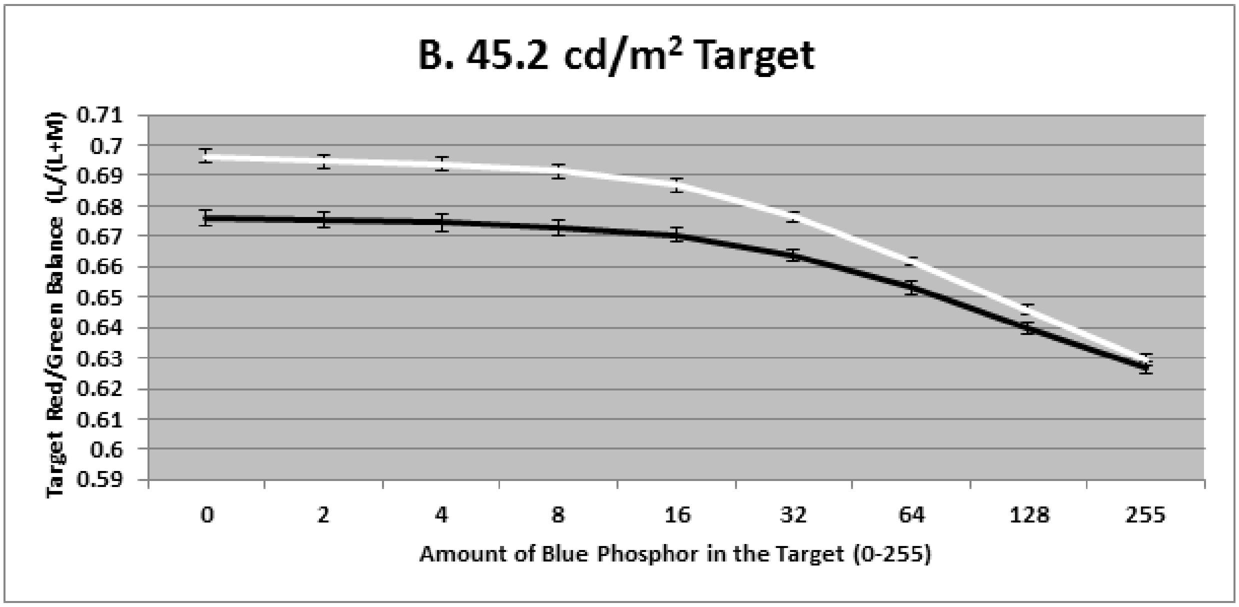
Figure 32 shows that the results replicate all principal effects shown in Experiment 16, for both lower (A) and higher (B) luminance targets. There was a comparable shift to higher L/(L+M) trolands for targets on white surrounds compared to black surrounds. There was also the same overall gradual decrease in L/(L+M) trolands as target Blue phosphor increase that was shown in the previous experiment. Additionally, the same interaction effect observed in Experiment 16 was shown here as well, with the size of the difference between white and black backgrounds decreasing as the Blue phosphor level of the target increases. The similarity of the results in Experiments 16 and 17 showed that variation of target luminance was not responsible for the pattern of results in Experiment 16. Both the main effects of the surround and the Blue phosphor level of the target, as well as the interaction between the two main effects were significant at the p<.001 level (see Table 4). All pairwise comparisons for Blue phosphor level of the target were significant at the p<.05 level. The data averaged from across the 13 observers for the low luminance target and 12 observers for the high luminance target is graphed in Figure 33 (A and B).

Table 4. Repeated Measures ANOVAs for Experiment 17

Low Luminance Target ANOVA	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**Sig.**	**Partial Eta Squared**
White versus Black Surround	**.006**	**1.000**	**.006**	**25.777**	**<.001**	**.682**
Error(Surround)	**.003**	**12.000**	**.000**			
Amount of Blue Phosphor	**.200**	**1.118**	**.178**	**229.978**	**<.001**	**.950**
Error(BluePhos)	**.010**	**13.421**	**.001**			
Surround * BluePhos Interaction	**.002**	**1.270**	**.002**	**18.762**	**<.001**	**.610**
Error(Surround*BluePhos)	**.001**	**15.236**	**.000**			
High Luminance Target ANOVA						
White versus Black Surround	**.010**	**1.000**	**.010**	**48.110**	**<.001**	**.814**
Error(Surround)	**.002**	**11.000**	**.000**			
Amount of Blue Phosphor	**.084**	**1.178**	**.072**	**312.114**	**<.001**	**.966**
Error(BluePhos)	**.003**	**12.957**	**.000**			
Surround * BluePhos Interaction	**.002**	**1.632**	**.001**	**33.033**	**<.001**	**.750**
Error(Surround*BluePhos)	**.001**	**17.954**	**.000**			

Although the results for the two target luminance levels are generally similar (Figures 33A and 33B), there is smaller shift of red/green balance as Blue phosphor is added for the higher luminance target. Such a shift would be expected if a mechanism that uses the ratio of S-cone activity to L+M cone activity determines target red/green balance. As the amount of Blue phosphor is identical for both target luminance levels, but the amount of Red and Green phosphor for high-luminance targets is twice that for low-luminance targets, one might predict that the effect of the addition of Blue phosphor would be half as strong. This is shown visually in Figure 33C, which depicts the ratio of Blue phosphor (0, 2, 4, 8, 16, 32, 64, 128, or 255) divided by the average amount of Red and Green phosphor (32 for the low luminance target and 64 for the high luminance target). When viewed in this way, these data suggest that a ratio of S-cone to L+M-cone activity determines the size of the luminance contrast effect.


A. 22.6 cd/m² Target
Target Red/Green Balance (L/(L+M))
0.71
0.7
0.69
0.68
0.67
0.66
0.65
0.64
0.63
0.62
0.61
0.6
0.59
0
2
4
8
16
32
64
128
255


B. 45.2 cd/m² Target
Target Red/Green Balance (L/(L+M))
0.71
0.7
0.69
0.68
0.67
0.66
0.65
0.64
0.63
0.62
0.61
0.6
0.59
0
2
4
8
16
32
64
128
255
Amount of Blue Phosphor in the Target (0-255)

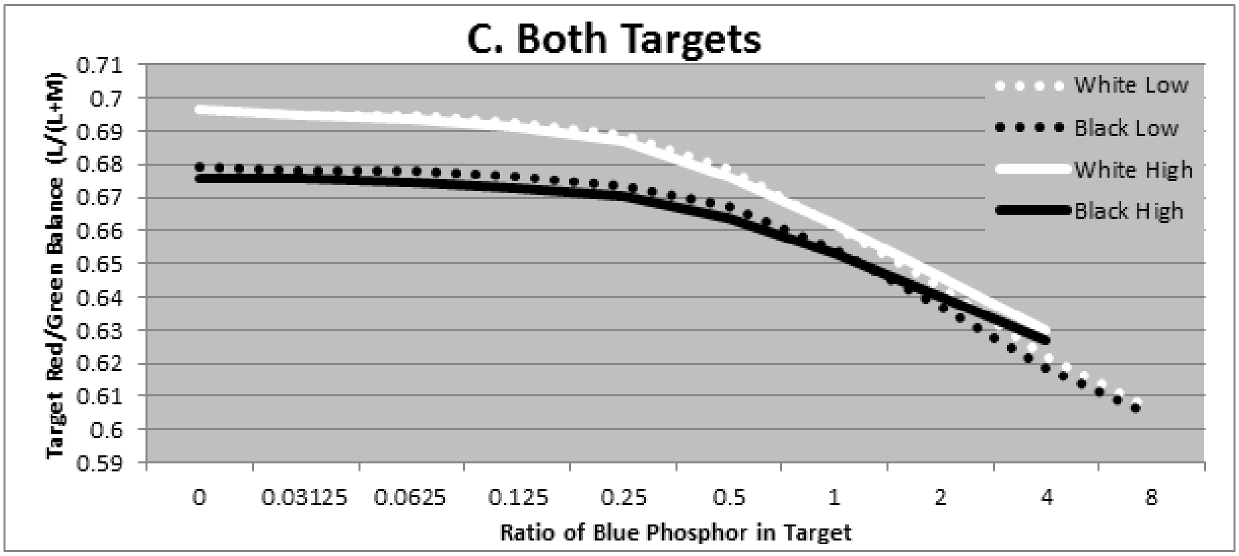

C. Both Targets
Target Red/Green Balance (L/(L+M))
0.71
0.7
0.69
0.68
0.67
0.66
0.65
0.64
0.63
0.62
0.61
0.6
0.59
White Low
Black Low
White High
Black High
0
0.03125
0.0625
0.125
0.25
0.5
1
2
4
8
Ratio of Blue Phosphor in Target

Figure 33. Red/Green Balances as a Function of Target Blue Phosphor Levels in Experiment 17.
In this experiment the amounts of Red and Green phosphors were adjusted to keep luminance constant with increases in Blue phosphor. (**A**), (**B**) Labeling conventions are the same as in Figure 32. Target was either (A) low luminance (22.6 cd/m^2), as in Experiment 1, or (**B**) high luminance (45.2 cd/m^2). **C**: This shows both low and high target luminance data overlapped and plotted as a ratio of the Blue phosphor divided by the average amount of Red and Green phosphor. Error bars represent the standard error of individual subject means.

D. EXPERIMENT 18 – SURROUND ACTIVATION OF S CONES

One possible explanation for the red/green balance shift produced by bright surrounds is that the substantial S-cone excitation provided by the bright white surround might induce greenness into the target, which would then require an increase of Red phosphor in the target to maintain a red/green balance. Because S-cone stimulation directly enhances redness (or decreases greenness), it might also induce contrasting greenness into the adjacent target. The black surround provides no such S-cone excitation, so there would be no greenness induced into the target. This explanation addresses the observed red/green-balance shifts in general but does not address why bluish targets show reduced shifts compared to yellowish targets.

If this explanation is correct, we would expect that variation of S-cone excitation provided by the surround would produce variation in red/green hue balance of the target. A high S-cone activity surround should show an effect similar to that seen for a white surround when compared to a low S-cone activity surround that is otherwise identical to the white surround. This experiment is designed to test this hypothesis. If the biased surrounds produce the same interaction seen in previous experiments (the difference between the surrounds on target red/green balance decreases as Blue phosphor levels increase) then it is a plausible explanation for the difference between white and black surrounds. Previous research has shown that a surround biased in terms of L or M-cone activity is not sufficient to explain these effects, but we have not explored the influence of S-cone activation by the surround.

Methods

In this experiment, a target that averaged 22.7 cd/m^2 was set to a red/green balance on 9 conditions varying in their Blue phosphor content. These target stimuli were identical to those used in the low-luminance condition of Experiment 2.

The judgments were made by 7 returning observers on either a full-screen blueish surround or a full-screen yellowish surround. These surrounds were constructed to have identical L/(L+M) cone troland balances (.67) and luminance (54.9 cd/m^2), varying only in their S-cone activity (1.94 S-cone trolands for yellow and 7.32 S-cone trolands for blue). As a result of fixing L and M-cone activity while varying S-cone activity, the surrounds are not perceptually red/green balanced. The blue surround appeared purplish and the yellow surround appeared greenish-yellow.

Results and Discussion

The results from the 7 observers, shown in Figure 34, look quite different from those seen in the previous experiments. Although we see the same lowering of L/(L+M) ratios with increases of target Blue phosphor level, the difference between the yellow and blue backgrounds is largely constant (ranging from 0.010 to 0.015) along the entire spectrum of targets from yellow to gray to blue. This contrasts with the decreasing difference (ranging from .001 to .017) observed between white and black surrounds as the Blue phosphor level in the target increased in Experiments 16 and 17.

The results of the Repeated Measures ANOVA for Experiment 18 show a significant main effect for surround (blue versus yellow) p<.01 and amount of Blue phosphor in the target (every level differs significantly from every other level) p<.001. The interaction between surround and Blue phosphor level was not significant (see Table 5). The two surrounds show a statistically identical difference in red/green balance at every Blue phosphor level of the target. These differences support the hypothesis that the effect observed previously cannot be explained by chromatic contrast (as it is of the same size for each condition), but is instead a result of the white or black surrounds themselves.

Table 5. Repeated Measures ANOVA for Experiment 18

Colored Surround ANOVA	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**Sig.**	**Partial Eta Squared**
Blue versus Yellow Surround	**.004**	**1.000**	**.004**	**15.038**	**.008**	**.715**
Error(Surround)	**.002**	**6.000**	**.000**			
Amount of Blue Phosphor	**.091**	**1.089**	**.083**	**175.444**	**<.001**	**.967**
Error(BluePhos)	**.003**	**6.533**	**.000**			
Surround * BluePhos Interaction	**.000**	**1.308**	**.000**	**1.093**	**.349**	**.154**
Error(Surround*BluePhos)	**.000**	**7.847**	**.000**			

Although S-cone excitation by a bright surround can increase target greenness, it does so equally for the full range of targets varying from yellow/brown to achromatic to blue. Thus, some additional factor(s) must mediate the variation in red/green hue shift seen in Experiments 16 and 17 that varied in size with the change of target spectral composition (the interaction effect). These data are instead consistent with a constant color contrast effect. One potential drawback of Experiment 18 is that the blue and yellow surrounds were not perceptually red/green balanced. The same yellow surround was used by all observers, so it may have appeared slightly greenish. The blue surround used by all observers was noticeably reddish to all observers because the increased S-cone excitation of the blue surround also contributed redness to that surround. This was a necessary consequence of holding constant both the ratio of L/M cone excitations and luminance between the yellow and blue surround conditions but it means that the effects on target red/green hue shift of surround hue and surround S-cone excitation cannot be separated. Thus, the shift in target red/green balance observed between yellow- and blue-surround conditions could have been a color-induction effect from the redness of the blue surround, as has been often demonstrated in studies of chromatic adaptation (Loomis & Berger, 1979; Fairchild & Reniff, 1995; Rinner & Gegenfurtner, 2000). Whether S-cone signals from the surround could have played some role in target hue shifts beyond just contributing redness to the surround remains unclear.

In any case, it is clear that surround-color contrast effects cannot explain the red/green hue shift caused by the luminance contrast effect, because those white surrounds were red/green balanced for each observer. While S-cone signals from the surround may play a role in the red/green hue shifts under white- and black-surround conditions, other presently unknown factors must also be involved because of the differential hue shifts seen for spectrally different targets in those conditions (the interaction effect on Experiments 16 and 17); that were not observed for the blue and yellow surround conditions in this experiment (the lack of an interaction effect).

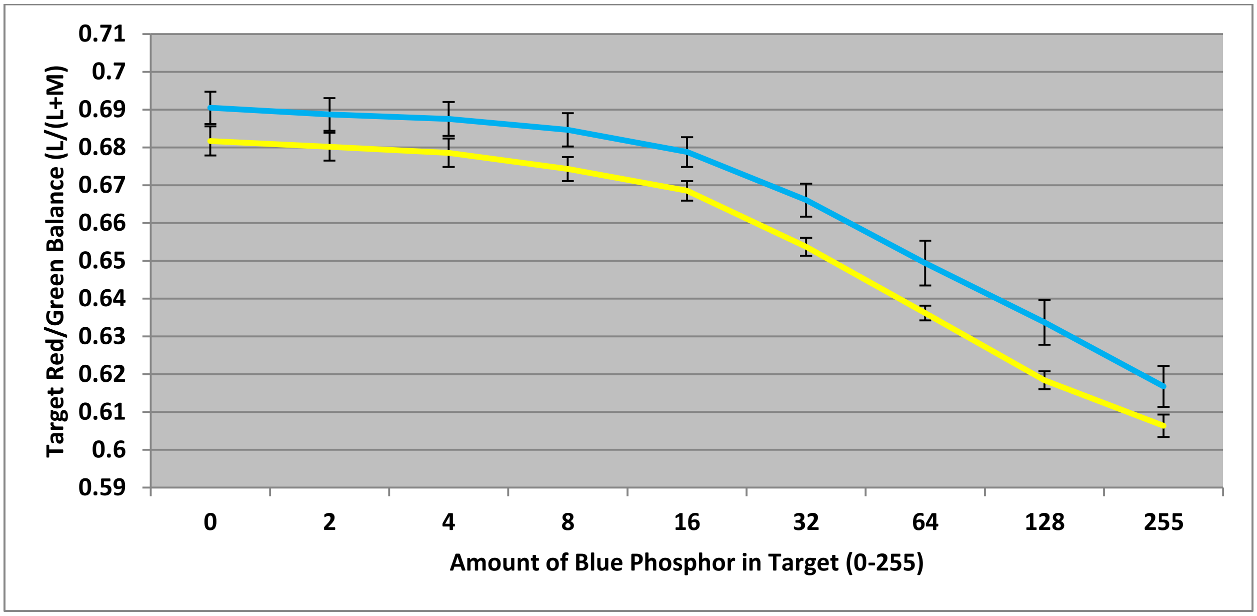


Figure 34. Red/Green Balances for High and Low S-troland Surrounds as a Function of Target Blue Phosphor Levels in Experiment 18

These data show a lack of systematic change in the size of the bright and dark surround using surrounds that differ only in their S-cone excitation (no significant interaction between Blue phosphor and surround color). The blue bar represents the high S-cone excitation surround, and the yellow bar represents the low S-cone excitation surround. Error bars represent the standard error of individual subject means.

E. EXPERIMENT 19 – DICHOPTIC VIEWING

Methods

This experiment made use of a dichoptic viewing apparatus that divided the screen in half through the use of mirrors such that one eye would only see one half of the screen and the other eye would only see the other half of the screen. This apparatus reduced the light levels such that the target averaged 10.29 cd/m^2 and white surrounds were 49.94 cd/m^2.

Four observers made judgments on either an all-white or an all-black surround presented to both eyes (binocular presentation). In addition, two sets of surrounds were used where one eye had a white surround and the other a black surround (dichoptic presentation). When the eye that had the target had the white surround this was referred to as Ipsilateral White, and if the white surround was in the eye not viewing the target it was called Contralateral White.
The construction of these surrounds was most similar to Experiment 17 in that their luminance remained constant as Blue phosphor was added.

Results and Discussion

The results were similar to those of Experiments 16 and 17 when surround and target were presented to the same eye. In all the ways that the white- and black-surround hue balances differed in Experiments 16 and 17, binocular-white and ipsilateral-white hue balances differ from binocular-black and contralateral white (in which there is an ipsilateral black surround) hue balances. Importantly, dichoptic presentation of test and surround produced neither an enhancement nor a reduction of the hue shift compared to the binocular presentations, meaning binocular-white and ipsilateral-white, as well as binocular-black and contralateral white, are statistically identical. The results for Experiment 19 show a significant main effect for presentation type (white, ipsilateral white, contralateral white, and black) with only the white and ipsilateral white differing significantly from the contralateral white and black presentation types

(Table 6). The amount of Blue phosphor in the target also showed a significant effect with every level differing significantly from every other level. The interaction between presentation type and Blue phosphor level was significant. These results are shown visually in Figure 35. These results show a similar pattern to those seen in Experiments 16 and 17; with no apparent effect of dichoptic presentation.

These data suggest that contrast-dependent red/green hue shifts are mediated by monocular pathways because information in the contralateral eye neither enhances nor diminishes the red/green balance shift from white to black surrounds. However, we have not found evidence for a retinal basis in monocular pathways based on primate retinal physiology, suggesting that the red/green hue shift may be mediated by early cortical, monocular pathways (Buck et al., 2018).

Table 6. Repeated Measures ANOVA for Experiment 19

Dichoptic ANOVA	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**Sig.**	**Partial Eta Squared**
Presentation Type	**.001**	**1.114**	**.001**	**27.144**	**.010**	**.900**
Error(Surround)	**.000**	**3.342**	**.000**			
Amount of Blue Phosphor	**.056**	**1.347**	**.042**	**171.951**	**<.001**	**.983**
Error(BluePhos)	**.001**	**4.042**	**.000**			
Surround * BluePhos Interaction	**.001**	**2.248**	**.000**	**36.190**	**<.001**	**.923**
Error(Surround*BluePhos)	**.000**	**6.743**	**.000**			

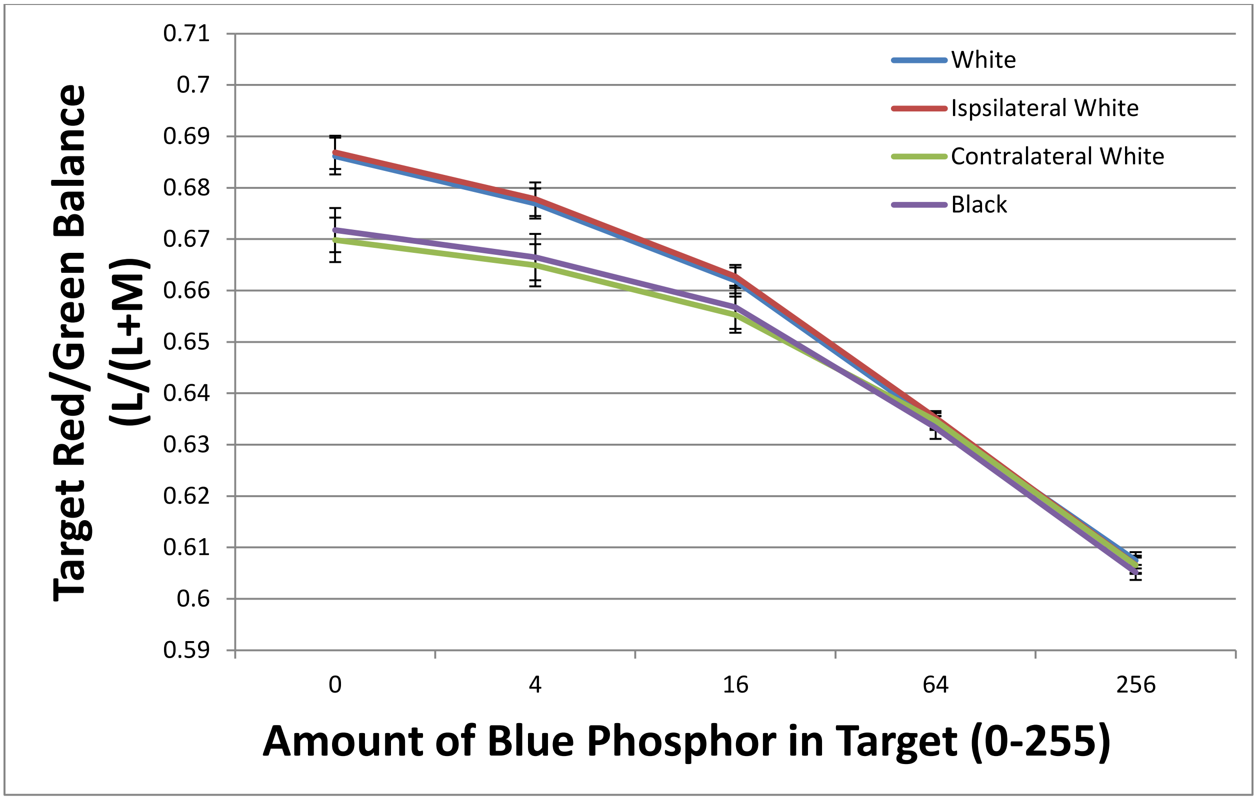


Figure 35. Red/Green Balances for all Four Viewing Conditions of Experiment 19
The data show that both target and surround must be presented to the same eye to produce a red/green hue shift. The White (both eyes) and Ipsilateral White are statistically identical as are the Black (both eyes) and Contralateral White. The effect observed effect follows the effect that would be predicted by the surround that is present in the same eye as the target, regardless of the surround that is present in the contralateral eye. Error bars represent the standard error of individual subject means.

F. GENERAL DISCUSSION OF RED/GREEN BALANCE ACROSS THE YELLOW-BLUE SPECTRUM

The present studies show that a loss of red/green hue shift between dark and bright surrounds is gradual, correlated with increases in target S-cone excitation, and not dependent on categorical hue differences among yellow/brown, bright/dark gray, and bright/dark blue targets. This was shown in Experiments 16, 17, and 19 where the magnitude of red/green hue shift seen between white and black surround conditions (luminance contrast effect) is modulated by the ratio of

S/(L+M) cone excitation of the target. When we take into account the results of Experiment 18, these results point to a luminance contrast effect on red/green balance shifts that is dependent on level of S-cone activity in a target; as well as pointing to a separate red/green balance shift mediated by color contrast that occurs independently of S-cone activity in a target (the size of the effect is identical for all stimuli along the yellow-blue spectrum).

But what perceptual and neural processes are involved with contrast-dependent red/green hue shift? One possibility is that the hue shift is driven by the same processes that induce brown into an initially yellow target. This was in fact the context in which we first observed the hue shift. Perhaps there is something about the categorical hue shift from yellow to brown targets that occasions the red/green hue shift, as some suggest brown is a separate elemental hue from yellow (Buck, 2015 and Fuld, 1983). However, the present results make clear that the red/green hue shift is not specific to yellow/brown targets. Rather, the hue shift can be observed (albeit in reduced magnitude) for achromatic and blue targets and the magnitude of the hue shift is related continuously to the degree of S-cone excitation by the target. Although there is some literature suggesting categorical color changes in Japanese (Kuriki, Lange, Muto, Brown, Fukuda, Tokunaga, Lindsey, Uchikawa, & Shioiri, 2017) and Russian (Paramei, 2005) for bright and dark blue stimuli there is no equivalent for brighter and darker achromatic gray targets; suggesting the relation between color categorization and contrast dependent red/green balance shifts is weak since we see a stronger effect for gray achromatic targets than we do for blue targets.

Another explanation that is not supported by the current data is that these changes are driven by target saturation. Our past data shows a strong role for saturation in brown induction as seen in

Experiment 4, which we thought might also play a role in red/green balance. Again, though, the present results have shown otherwise, with both the largest and smallest hue shifts associated with highly saturated targets, yellow/brown and blue respectively, and no overall advantage of desaturated targets and no discontinuity in magnitude of red/green balance shift for achromatic targets. Past studies of the Abney effect show that changes in saturation can cause changes in hue (Kurtenbach, Sternheim, & Spillmann 1984), but the luminance contrast effect observed here does not show the shifts predicted by the Abney effect alone. Additionally, some studies of the Abney effect and the Bezold–Brucke hue shift have demonstrated that low purity brown stimuli produced through luminance contrast would appear more reddish (Pridmore, 2007), which agrees with the reduction of L/(L+M) as yellow/brown stimuli are desaturated in our studies. But we also show that the shift still appears for achromatic stimuli which have no associated change in saturation (only brightness). Although we cannot rule out the potential contribution of saturation based effects on our data, we can safely say they are not a sufficient explanation for the pattern of results shown in the present study as these present results show a consistent correlation with S-cone activity in the target regardless of the targets spectral purity.

Past research in our lab has attempted to relate these red/green balance shifts to statistical regularities present in the natural world (Vincent, Kale, & Buck, 2016). When analyzing photos of natural scenes, bright and dark portions are found to contain different mean ratios of L/M cone excitation. On average, images that contained a significant amount of sky show a negative correlation between luminance and L/(L+M) ratios: As luminance increased, the relative amount of M-cone activity increased, compared to L-cone activity. A further analysis of natural scenes may suggest that the S-cone activity in a scene can act as yet another predictor variable of L/M excitation, as the parts of the scene with high luminance (sky) will presumably also have high S-cone activity.

Going forward, attempts to understand and model the processes contributing to luminance contrast-dependent red/green hue shift will have to consider the role of target S-cone excitation independent of color category and saturation based effects (such as Bezold–Brucke and Abney effects) that have been previously observed. Further research will also be needed to separate the potential of either (or both) chromatic contrast and S-cone excitation of surrounds contributing to the observed effects. Varying backgrounds systematically in perceptual hue balance, S-cone activity, and brightness may allow us to isolate the relative contributions they make to contrast-dependent red/green hue shift.

VI. CONCLUSION

Throughout this paper, we have looked at a variety of factors that affect both the perception of stimuli as categorically brown or yellow and the red/green balance point of those stimuli. At first, our hypothesis followed that of Bartleson and other earlier researchers that the change we saw in red/green balance from yellow to brown was mediated by the shift in categorical hue perception from yellow to brown, that the color category was the determining factor for red/green balance. However the factors that affect brown induction and change red/green balance are rarely overlapping and often operate in distinct ways.

Brown induction is primarily driven by the presence of a bright surround anywhere in the visual field (Experiment 1) and is facilitated by contiguous bright surrounds that appear to operate through by fast-acting monocular pathways (Experiment 5). There is also an enhancement of brown induction by the presence of a bright surround in the opposite eye as in dichoptic arrangements as seen in Experiment 6, which suggests a slower-acting cortical mechanism also plays a role. The strength of this brown induction can be modulated by changing the size of the stimulus, the size of the surround, and by the spectral purity of the stimulus (Experiment 2, 3, and 4). Therefore, the strongest browns are produced by small, desaturated stimuli with large, bright, contiguous surrounds presented in the same eye as the target (physically contiguous surrounds). Additionally, the categorical hue shift of (bright) yellow to (dark) brown does not appear to be present for bright and dark versions of the other basic colors (blue, red, green), which do not shift color categories, at least in English speaking populations (Lindsey and Brown, 2014).

In contrast, red/green balance is driven by the presence of bright surrounds anywhere in the visual field (Experiments 9 and 10), which induce greenness into a target forcing subjects to move to greater L/(L+M) excitation levels to achieve a perceptual red/green balance. The ratio of the luminance of a target to its surround is the best predictor of the R/G balance of a target as shown in Experiment 14, predicting 88% of the variability in R/G balance, though Experiment 12 also suggests a role for target luminance alone when a target is brighter than or equiluminant with its surround. However, when presented with a surround that is equiluinant with the target (as shown in Experiments 10, 11, 12, and 13), the overall effect is in the opposite direction, to induce redness into the target, requiring a decrease of L/(L+M) excitation to maintain a red/green balance. These experiments showed that the equiluminant surround effect is even stronger than the effect of a dimmer surround in terms of inducing greenness. The effect of equiluminant surrounds is not explainable by luminance/brightness integration, as Experiment 11 and 12 have outer surrounds that are opposite in polarity (white and black) yet show the same direction of effect to lower L/(L+M) excitation. This shift of red/green balance between bright and dark backgrounds also cannot be related to size of the test or surround, as both were manipulated in Experiment 12 and did not produce a significant difference. Red/green balance shifts also occur across nearly the entire range of yellow-blue stimuli, even with bright and dark gray targets (Experiments 16, 17, 18, and 19), though these effects weaken as a stimulus moves toward the blue spectrum. There is strong evidence that this shift is driven largely by low activation of S-cones in comparison to L and M-cones. As S-cone activity increases relative to L and M-cones the size of the effect is reduced and eventually disappears for most observers when viewing highly saturated blue targets. This is in contrast to the enhancement of brown induction in the presence of a slight elevation in S-cone activity (as seen in the less spectrally pure stimuli). Additionally, red/green balance shifts appear to be largely invariant of the size of both the test and the surround, unlike the size dependence observed for brown induction.

In terms of cortical pathways mediating these effects, we have strong evidence that red/green shifts cannot be mediated by retinal circuitry (Buck et al., 2018), but we also do not see evidence for enhancement of red/green hue shifts in binocular pathways (see Experiments 15 and 19). This suggests that red/green shifts are mediated by low-level visual processing beyond that of the retina, such as the double opponent cells found in area V1. In contrast, the light level at which brown replaces yellow appears to be controlled by at least two separate mechanisms: one that occurs with physically (but not perceptually) contiguous surrounds and could be plausibly mediated at the level of the retina by center-surround receptive fields, and another that occurs after binocular fusion and responds to bright surrounds anywhere in the visual field. This, of course, doesn’t explain why or how yellow is perceptually replaced by brown, just the light levels at which that transition occurs. This is a question that we are still far off from answering in detail.

The evidence presented here leads us to conclude that the processes controlling brown boundaries and red/green balances are actually largely distinct from each other, and that there is little correlation between the underlying mechanisms behind them. A stimulus that appears in the opposite eye may influence the perception of the brownness of a target without influencing its red/green balance. A change in saturation may influence the red/green balance of a target toward being more categorically red while also making it appear more categorically brown, which is what suggested originally that they could be controlled by the same mechanism. However, that both the categorical hue shift from yellow to brown and the red/green balance changes when we shift from a black background to a white background could be largely coincidental. As we can cause a shift in one, without shifting the other (with dichoptic presentation), and as we can cause shifts in opposite directions (with saturation manipulations) it suggests their effects occur simultaneously only under a subset of stimulus presentations.

I intend to continue to pursue research on red/green balances and on brown induction in order to further clarify their distinctions and commonalities. There still remain unanswered questions in regards to language, real-world perception, and neural mechanisms, for both phenomena, that I hope to address with research in the near future in collaboration with Keizo Shinomori at Kochi University of Technology.

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