



Published in final edited form as:

*Vision Res.* 2008 March ; 48(8): 1018–1026.

## Early Visual Mechanisms Do Not Contribute to Synesthetic Color Experience

**Sang Wook Hong and Randolph Blake**

*Departments of Psychology & Vanderbilt Vision Research Center, Vanderbilt University 301 Wilson Hall 111 21<sup>st</sup> Avenue South Nashville TN 37023 USA*

### Abstract

Color-graphemic synesthetes perceive colors when viewing alphanumeric characters. Theories of color-graphemic synesthesia posit that synesthetic color experience arises from activation of neural mechanisms also involved in ordinary color vision. To learn how early in visual processing those mechanisms exist, we performed several experiments. In one experiment, real colors were altered in appearance by the lightness of their backgrounds, but the appearance of synesthetic colors was immune to surrounding light levels. In the second experiment using a hue cancellation technique, adaptation to synesthetic color had no subsequent effect on the amount of canceling light to achieve equilibrium yellow, whereas adaptation to real colors did. In the third experiment, vivid synesthetic color had no influence on equilibrium yellow settings of the actual color of the characters evoking synesthesia. Because brightness contrast and chromatic adaptation are putatively mediated by neural mechanisms early in visual processing including retina and primary visual cortex, our results imply that neural events responsible for synesthetic color emerge subsequent to these early visual stages.

### Keywords

color-graphemic synesthesia; brightness contrast; chromatic adaptation

### INTRODUCTION

Individuals with color-graphemic synesthesia perceive vivid color when viewing alphanumeric characters. For example, L.R., a color synesthete who has participated in many of our studies, always sees the letter ‘A’ as a highly saturated red and ‘D’ as bright green regardless of the actual colors of the ink in which those letters are printed. L.R.’s synesthetic color experiences, like those of other color-graphemic synesthetes, are very specific and highly reliable in hue and brightness (Harrison & Baron-Cohen, 1997; Mattingley, Rich, Yelland & Bradshaw, 2001). This invariance of synesthetic color experience for a given individual makes it possible to study the impact of synesthetic colors on performance of perceptual/cognitive tasks. Indeed, on a variety of psychophysical tasks, including visual search (Ramachandran & Hubbard, 2001a; Smilek, Dixon, Cudahy & Merikel, 2001; Palmeri, Blake, Marois, Flanery & Whetsell, 2002)<sup>1</sup>, visual masking (Ramachandran & Hubbard, 2001b; Hubbard, Arman, Ramachandran

---

Please send correspondence to Sang Wook Hong, Departments of Psychology, Vanderbilt University, 301 Wilson Hall, 111 21<sup>st</sup> Avenue South, Nashville TN 37023, U.S.A., FAX: 1-615-322-5546, EMAIL: sang.w.hong@vanderbilt.edu.

**Publisher's Disclaimer:** This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

<sup>1</sup>Edquist, Rich, Brinkman & Mattingley (2006) failed to find an enhancement in visual search based on synesthetic color differences, and they speculate that selective attention may be required for synesthesia to be experienced.

& Boynton, 2005), and perceptual grouping (Kim, Blake & Palmeri, 2006; Ramachandran & Azoulay, 2006), synesthetic colors behave like real colors.

Complementing these findings are studies identifying brain areas activated during synesthetic color experiences. These studies show that synesthetic color experience is accompanied by neural activation in visual areas V4/V8 (Hubbard, Arman, Ramachandran & Boynton, 2005; Sperling, Prvulovic, Linden, Singer & Stirn, 2006), brain areas implicated in normal color vision (Zeki & Marini, 1998; Hadjikhani, Liu, Dale, Cavanagh & Tootell, 1998; Bartels & Zeki, 2000). It is uncertain, however, whether neural events earlier in the color processing stream contribute to color synesthesia. This possibility is not far-fetched, given the extensive feedback from higher visual areas including V4/V8 to primary visual cortex (Rockland, Saleem & Tanaka, 1994; Bullier, 2003) and, for that matter, from primary visual cortex to the lateral geniculate nucleus (Sillito & Jones, 2003). To address the possible involvement of early visual processes in color synesthesia, we have assessed the susceptibility of synesthetic color appearance to contextual influences attributable to neural circuitry in the very earliest stages of visual processing.

Besides being governed by the light reflected from object surfaces, color appearance is also influenced by the spatial and temporal context in which an object is viewed. Hue and brightness are affected by nearby light (chromatic/brightness induction) and by prior exposure to chromatic light (short-term chromatic adaptation). Neural mechanisms underlying these contextual influences on perception of hue (von Kries, 1905; Jameson & Hurvich, 1972; Walraven, 1976; Shevell, 1978; Jameson, Hurvich & Varner, 1979; Shevell, 1982) and brightness (Ratliff, 1965; Wyszecki, 1986; Shevell, 1986; Palmer, 1999; Boyaci, Fang, Murray & Kersten, 2007) can be traced to early stages of the visual pathway, including the retina and primary visual cortex. Do these mechanisms also influence the appearance of synesthetic colors?

## GENERAL METHODS

### Apparatus

All stimuli were generated using MATLAB (Mathworks, MA) in conjunction with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997), and presented on an accurately calibrated Mitsubishi color display (Diamond Pro 2020u). Spectral power distributions of the red (R), green (G) and blue (B) phosphors were measured using a spectroradiometer (Ocean Optics, Model OOIBase 32). The relative light level of each gun at every digital value (256;  $2^8$  levels) was measured with a Minolta colorimeter (model CA-100). These values were saved in a lookup table. The pixel resolution of the color CRT was 1024×768 pixel and its refresh rate was 120 Hz non-interlaced. In all experiments, observers viewed the monitor binocularly from a distance of 95 cm, with the head stabilized by a head-and-chin rest.

### Observers

Four individuals (L.R. and K.E.D. were female) with color-graphemic synesthesia participated in these experiments. All four individuals see their synesthetic colors on the surface of the inducing characters, not “in their mind’s eye.” This aspect of their synesthetic experience classifies them as “projectors” and not “associators” (Dixon, Smilek & Merikle, 2004). Repeated measurements using a computer-based, color-matching procedure (Eagleman, Kagan, Sagaram & Sarma, 2007) confirm that the synesthetic color experiences for each individual are highly consistent over time, with specific associations between colors and alphanumeric characters varying among the four. Two of the four observers (L.R. and W.O.) were confirmed trichromats, as evidenced by their performance on a modified version of the 100-hue test. The other two observers (K.E.D. and T.W) described experiencing no difficulties

with color discrimination, but we did not have an opportunity to evaluate their color vision formally. The consistency of their performance in experiments 2 and 3 (involving repeated settings of red/green values to achieve equilibrium yellow), strongly imply that they are not dichromats.

## EXPERIMENT 1

In the first experiment, brightness<sup>2</sup> of a synesthetic color was measured as a function of the light level of the surrounding context. Brightness of a visual stimulus is highly dependent on the light level of its surrounding context as well as light level of the stimulus itself. With a simple stimulus configuration (e.g. a small target patch within a large uniform surround), target brightness (within limits) is inversely related to the surround's light level, the induction effect known as brightness contrast. For years it was widely accepted that brightness contrast arose from lateral inhibition, perhaps embodied in center-surround receptive fields of neurons in early stages of visual processing (Ratliff, 1965; Wyszecki, 1986; De Valois, Webster, De Valois & Lingelbach, 1986; Shevell, 1986; Palmer, 1999). More recently, however, simultaneous contrast illusions dependent on global scene properties have challenged the view that low-level visual mechanisms alone determine perceived lightness/brightness (Adelson, 2000). Consequently, it is now acknowledged that the neural concomitants of these illusions arise from the combined operation of mechanisms at multiple levels of processing, including the retina and primary visual cortex. For our work, we used a very simple stimulus configuration devoid of 3D cues that support natural scene interpretations of the configuration (see Witthoft & Winawer, 2006, for possible influences on synesthesia of lightness illusions dependent on high-level scene interpretations).

### Stimuli and Procedure

The experimental design is illustrated in Fig. 1a. For each observer we selected two alphabetic characters that evoke highly saturated synesthetic colors. Then, we obtained the chromaticity values that were equivalent to the synesthetic colors for both of those characters using a conventional color matching procedure. For these measurements, the backgrounds for the test target (alphabetic character, 1-deg height, about 8-min line width) and for the matching target (a 1-deg circle) were identical; both backgrounds were 5 deg, uniform fields metameric to equal-energy-spectrum 'white' (EES,  $x = 0.33$  and  $y = 0.33$  in Judd (1951)) at 30 cd/m<sup>2</sup>. The test targets were also EES at 8 cd/m<sup>2</sup>. Observers used a game pad to adjust the hue, saturation and brightness of the matching target exactly matched the appearance of the synesthetic color of each of the two test targets, i.e., the alphabetic characters. These values, transformed to Judd CIE chromaticity values, are shown in Fig. 1b.

In one condition, the brightness of the synesthetic color for a given inducing letter was measured by asymmetric matching, in which the luminance of the background for the inducing letter (test target) was systematically varied from 10 to 30 cd/m<sup>2</sup> while the luminance of the background of the matching field was fixed at 30 cd/m<sup>2</sup>. The luminance of the inducing letter (EES) was fixed at 8 cd/m<sup>2</sup>. Because the letter itself appeared colored in virtue of synesthesia, we call this the synesthetic color condition.

In a control condition, brightness matches to real colored symbol (& for observer L.R., K.E.D. and W.O., \$ for observer T.W.) were obtained using exactly the same procedure as that described above. In this condition, a symbol was displayed with real color whose chromaticity value matched that associated with a given synesthetic color, as defined by the matching procedure.

<sup>2</sup>Here we use the term "brightness" rather than "lightness" because our experiments were performed on a video monitor where the test targets were defined by emitted light, not reflected light (Palmer, 1999; Adelson, 2000).

## Results and discussion

Average brightness settings for synesthetic color and real color as a function of background light level are shown in Fig. 2. In each panel, squares represent the matched luminance of synesthetic colors (letters displayed in EES 'gray') and circles represent the matched luminance of real colors (symbols displayed in real color). For all four observers, the matched luminance for real colors decreased with increasing luminance of the surrounding background. In contrast, matched luminance of synesthetic colors did not systematically vary with background luminance. The brightness of synesthetic color experiences, in other words, is immune to brightness contrast, implying that the neural events generating synesthetic color experience arise at a level of visual processing beyond that at which simultaneous contrast effects arise, at least for these relatively simple stimulus configurations.

Hubbard, Manohar & Ramachandran (2006) found that synesthetic color appearance changes when the actual contrast of the inducing letter is low. We did not observe appearance changes with contrast in our study, but our contrast levels are relatively high (the smallest being 22% Weber Contrast) compared to those found by Hubbard et al. (2006) to be dependent on contrast.

## EXPERIMENT 2

The second experiment tested whether exposure to synesthetic color subsequently affects perception of real color. It is well known that short periods of exposure to a chromatic light can alter perceived color, a phenomenon called short-term chromatic adaptation. For example, exposure to a light appearing reddish shifts the color appearance of subsequently presented light, the result being that a light appearing yellowish before adaptation appears more greenish. Appearance shifts produced by short-term chromatic adaptation are adequately explained by a two-process model (Jameson & Hurvich, 1972; Jameson, Hurvich & Varner, 1979) that incorporates gain changes in cone receptors and in opponent mechanisms. Can prolonged exposure to a synesthetic color induce a temporary shift in the perceived color of a real chromatic light? To answer this question we required observers to perform a visual search task in which they inspected an array of identical letters ("distractors") until they found and indicated the location of a different letter ("targete"). This search task continued for five minutes, allowing us to measure the effect on real color perception of exposure to a field of synesthetic color for an extended period of time. The influence of exposure to a synesthetic color on real color was measured using a modified 'hue cancellation' technique (Hurvich & Jameson, 1957; Malkoc, Kay & Webster, 2005).

### Stimuli and Procedure

To implement the hue cancellation technique, four physically identical, 1-deg squares were presented against a black background, equally spaced around a central fixation cross (Fig. 3a). The squares were composed of two chromatic lights, one that appeared reddish and another that appeared greenish. The luminance of the light appearing reddish was fixed at 6 cd/m<sup>2</sup> and observers adjusted the luminance of the light appearing greenish to make the squares appear neither reddish nor greenish (an appearance referred to equilibrium yellow). Observers were free to move their eyes while making a setting. Note that with this procedure overall luminance of the test squares will vary as the green component is varied, but other work shows that perception of unique yellow does not change depending on light level (Larimer, Krantz & Cicerone, 1974).

To begin a session, the synesthetic observer made five independent settings of equilibrium yellow; these provided baseline settings in the absence of any chromatic adaptation. Next, the observer experienced five minutes of adaptation to a synesthetic color or to a real color during which the observer performed a visual search task that used two alphabetic characters that

induced the same synesthetic experience; one character constituted the target letter and the comprised the array of distractor letters in which the target was embedded. So, for example, synesthetic observer LR searched for an M among arrays of G's: for LR both letters evoke the synesthetic experience of saturated red. For each observer we selected a pair of letters that appeared red (these target and distractor letters differed, of course, among observers because not all our observers have the same letter/color associations). The multiple distractor characters were distributed throughout four quadrants defined by thin vertical and horizontal lines, and the single target letter appeared randomly within one of those quadrants (Fig. 3b). The observer indicated which quadrant contained the target by pressing one of four pre-assigned buttons, performing the search task as quickly and accurately as possible.

Each of the four quadrants contained 16 distractor letters (width: 0.8 deg, height: 1.2 deg, line width: 8 min), producing a total of 64 distractors throughout the array; only one quadrant contained the target letter, and its dimensions were the same as the distractors. We created multiple exemplars of these arrays, with the target letter and the distractor letters varied in location. A new array of the letters was presented following the observer's button press, with a 0.3-second inter stimulus interval (ISI) during which only the lines dividing the screen into four quadrants were present. On average, observers took about 2 seconds per array to perform this task, which means they received on average about 4.3 minutes of adaptation for a given condition. Observers naturally moved their eyes around the four quadrants to locate the target, and this should minimize local color adaptation at specific retinal locations that could occur if eye fixation were steady.

In a pilot experiment performed on non-synesthetic observers searching through arrays of red-colored characters, we confirmed that performing the search task for five minutes using these arrays of colored letters was sufficient to produce pronounced shifts in the R/G setting yielding equilibrium yellow. For three non-synesthetic observers tested, the R/G settings for equilibrium yellow shifted, on average, 27% after adaptation. We are confident, therefore, that the conditions of adaptation experienced by our synesthetic observers are sufficient to produce adaptation if, in fact, the red associated with the target and distractors behaves like real red-colored letters.

In the synesthetic neutral condition, observers performed the search task with the achromatic target and distractor letters displayed in EES at 8 cd/m<sup>2</sup>. In the synesthetic congruent condition, those letters were actually colored reddish (pinkish for WO) to match their synesthetic color experience, as determined by the chromaticity values obtained in the previous experiment. In the synesthetic incongruent condition, the letters were actually colored green, with the particular value of green selected from their palette of synesthetic colors. Chromaticity values used for congruent and incongruent conditions are shown in Table 1. Following each condition the observer rested for at least 30 min to allow recovery from any lingering adaptation from the previous adaptation period. We confirmed recovery by always measuring equilibrium yellow settings before starting a new condition, requiring that those settings be equivalent to those measured in the baseline condition.

## Results and discussion

Shown in Figure 4 are the R/G ratios required to achieve equilibrium yellow (fixed R-value 6 cd/m<sup>2</sup> over G-value setting) in the baseline condition and in each of the adaptation conditions. Planned orthogonal contrasts were used to compare the various conditions. Chromatic adaptation was effective when observers were exposed to real colors during the adaptation period (Fig. 4a, replicating the findings obtained with non-synesthetic observers in our pilot experiment). For three observers (L.R., K.E.D. and T.W.), equilibrium yellow settings were significantly different between synesthetic congruent and incongruent conditions, indicating short-term chromatic adaptation to real color (obs. L.R.,  $F(1,16) = 21.33$ ,  $p < 0.001$ ; obs.

K.E.D.,  $F(1,16) = 27.28$ ,  $p < 0.001$ ; obs. T.W.,  $F(1,16) = 15.68$ ,  $p < 0.01$ ). Observer W.O. also showed differences in his settings for these conditions, but those differences failed to achieve statistical significance ( $F(1,16) = 1.17$ ,  $p > 0.05$ ) owing to the overall large variability in his settings.

Of particular relevance, none of the four observers showed a statistically significant difference in R/G ratios between the baseline condition and the synesthetic neutral condition (Fig. 4b, obs. L.R.,  $F(1,16) = 0.05$ ; obs. K.E.D.,  $F(1,16) = 0.92$ ; obs. W.O.,  $F(1,16) = 0.12$ ; obs. T.W.,  $F(1,16) = 0.31$ ). Adaptation to a synesthetic color did not alter the balance of neural activity produced by viewing real color mixtures, even though synesthetic color was presented in an adaptation regime that produced reliable shifts in color mixtures following adaptation to real colored items. We note that TW's R/G settings are considerably different from those of the other three observers, in a direction indicating that he requires less green light to achieve equilibrium yellow (this is also evident in TW's results in the next experiment). This suggests that TW might be an anomalous trichromat. We are confident that TW is not a dichromat because his R/G settings are highly consistent unlike the settings produced by dichromats (Kaiser & Boynton, 1996).

One could argue that color adaptation produced by prolonged exposure to an array of colored letters does not engage the same neural mechanisms as does adaptation produced by exposure to a uniform, colored field, the conventional stimulus used in chromatic adaptation experiments. Indeed, it is true that the spatial frequency content of these two kinds of displays is different, with the amplitude spectrum for a letter array being more complex than that for a uniform patch of color. While it is true that the magnitude of chromatic adaptation can vary with spatial frequency (Stromeyer, Kranda & Sternheim, 1978), there is no evidence that the mechanisms of chromatic adaptation are different – the cones and the neurons with chromatic opponency are still being stimulated by spectral light. Indeed, it would be peculiar from an ecological standpoint for visual scenes with complex spatial frequency spectra somehow to bypass mechanisms susceptible to chromatic adaptation in the retina and early stages of visual processing. We realize that the absolute magnitude of chromatic adaptation might be different had we not used arrays of colored letters, but it is still the case that real colored letters produce marked shifts in equilibrium yellow while synesthetically colored letters did not. The critical difference, we contend, is the absence of activation in chromatic visual mechanisms, presumably in early stages of vision, when synesthetic colors are being experienced.

From other work (Blake, Palmeri, Marois & Kim, 2005) we know that synesthetic colors can induce the McCollough effect (McCollough, 1965), an orientation-contingent color aftereffect. There is disagreement concerning the neural site of the McCollough effect, but there is no reason to believe it transpires as early in visual processing as color adaptation producing temporary shifts in the red/green null point. So our results are not inconsistent with the finding that synesthetic colors induce a McCollough effect.

### EXPERIMENT 3

This final experiment tested three of our synesthetic observers on a task designed to learn whether the presence of synesthetic color affects perception of real color as revealed in equilibrium yellow settings; observer K.E.D. was not available to participate in this final experiment. Hue cancellation, the procedure described in Experiment 2, was used to measure real color appearance in the presence of letters that evoke synesthetic colors. Instead of the four-square target used in Experiment 2, the target was one of three characters presented against a black background: an alphabetic character that evoked a reddish color, an alphabetic character that evoked a greenish color, and a non-alphanumeric symbol that did not evoke any synesthetic color experience. The size of the letter (symbol) was 4 deg by 4 deg, with various line width

depending on the letter (font: Arial Black). As in the previous experiment, observers adjusted the R/G ratio until the character appeared neither reddish nor greenish. If synesthetic color affects perception of real color, the equilibrium yellow settings for the letter evoking reddish synesthetic color should differ from the neutral settings for the letter evoking greenish synesthetic color. Based on color opponency, we would predict that the R/G ratio for the letter evoking synesthetic red would be lower than the ratio for the letter evoking synesthetic green because the former, with synesthetic red, should require more light that appears greenish to achieve equilibrium yellow than the latter with synesthetic green.

The R/G ratios producing equilibrium yellow are shown in Figure 5. The horizontal axis represents the target letter used for the equilibrium yellow settings (“Symbol” refers to a non-alphanumeric character that does not induce synesthetic color experience; “RED” refers to a letter that induces a reddish synesthetic experience; “GREEN” refers to a letter that induces a greenish synesthetic experience.) For none of the three observers were the R/G settings with the synesthetic color ‘red’ significantly different from the R/G settings with the synesthetic color ‘green’. Moreover, the variances associated with these settings were comparable, suggesting that any adaptation occurring during individual trials was minimal and constant across conditions. It is unlikely, for example, that observers were differentially adapted to red or to green during the course of the equilibrium setting. Moreover, all individual trials started with the R/G values set close to equilibrium yellow, such that observers spent relatively little time viewing the displays while making their adjustments.

Evidently, then, synesthetic color experience has no influence on real color perception. This result does not necessarily imply that synesthetic colors are not organized in a color-opponent fashion and, indeed, there is some evidence for such a conclusion (Nikolić, Lichti & Singer, 2007). Our results do indicate, however, that any opponency in the mechanisms evoking synesthetic colors must arise after the neural site at which equilibrium yellow, as determined by the R/G value, is represented.

Observer L.R. showed a significant difference in the R/G ratio when there was no synesthetic color (symbol target) compared to when there was synesthetic color (letter targets). This result, however, cannot be accounted for by opponent color mechanisms because the R/G ratio with no synesthetic color was lower than the R/G ratio with both synesthetic color ‘red’ and ‘green’. Settings of equilibrium yellow were not significantly different among the three conditions for the other two observers (obs. W.O.,  $F(2,12) = 0.18$ ; obs. T.W.,  $F(2,12) = 1.49$ ). It is interesting to note that the pattern of individual differences in R/G values is identical to that observed in Experiment 2 (compare neutral conditions for LR, WO and TW in Figure 4 and Figure 5) even though the two experiments employed rather different stimuli for the R/G settings (four squares in one case and one large letter in the other).

## DISCUSSION

Much of the recent work on color-graphemic synesthesia, including work out of our laboratory, has focused on the perceptual equivalence of real and synesthetic colors. Results from that work has led to the quite reasonable conclusion that synesthetic colors are evoked by neural mechanisms that are also involved in real color perception, a conclusion substantiated by brain imaging studies (Hubbard, 2007). Of course, synesthetic colors arise consequent to the presence of alphanumeric characters and not other spatial forms, implying the existence of connections between higher brain areas involved in orthographic processing and color processing mechanisms. There are different accounts of how those interconnections come to exist and how they trigger synesthetic colors (see Hubbard, 2007, for a nice overview of those alternative positions). All, however, appeal to activity within brain structures involved in the analysis of color, structures present in all color-normal individuals.

Surely, however, those chromatic mechanisms activated by the appearance of letters do not stretch back to the earliest stages of vision. No one believes, for example, that patterns of activity in the three cone types of a synesthetic individual vary systematically when that individual views different achromatic letters, even though those letters evoke dramatically different color impressions. Nor does it seem plausible that midget ganglion cells in the retina, an important substrate in color perception, carry signals that relate directly to synesthetic experiences – there are no known feedback pathways from higher visual stages to the retina to support such a role. So, how far up the hierarchy of areas comprising the visual pathways must we travel before encountering neural events associated with synesthesia?

Our results do not directly answer that question, but they do place lower boundaries on candidate structures. Specifically, we now know that the brightness of synesthetic colors, unlike real colors, are immune to effects of the surround light level, as indicated by the absence of simultaneous brightness contrast, and we know that previous and simultaneous exposure to synesthetic colors, unlike real colors, does not affect the perception of real color. These negative results were found despite the fact that the synesthetic colors evoked in each of our three experiments were quite vivid; indeed, using real colors matched in quality to the synesthetic colors produced strong brightness contrast and potent color adaptation. We conclude, therefore, that the earliest neural concomitants of color experiences associated with viewing alphanumeric characters are to be found in extra-striate visual areas, beyond the early processing stages generally thought to mediate contrast and adaptation effects in color vision. This tentative conclusion is based, of course, on studies of people whose synesthetic experiences are projected onto the stimuli that evoke those experiences. It may well be that other classes of chromatic synesthesia, including those who see colors in their mind's eye, possess a different neural nexus triggering the experience of colors. Indeed, very recent work using anatomical tracing techniques points to significant differences in connectivity patterns between synesthetes who see their colors in the world compared to those who see colors in their mind's eye only (Rouw & Scholte, 2007). Whatever those connectivity patterns may be, our results make it unlikely that those connections stretch back to primary visual cortex.

#### ACKNOWLEDGEMENT

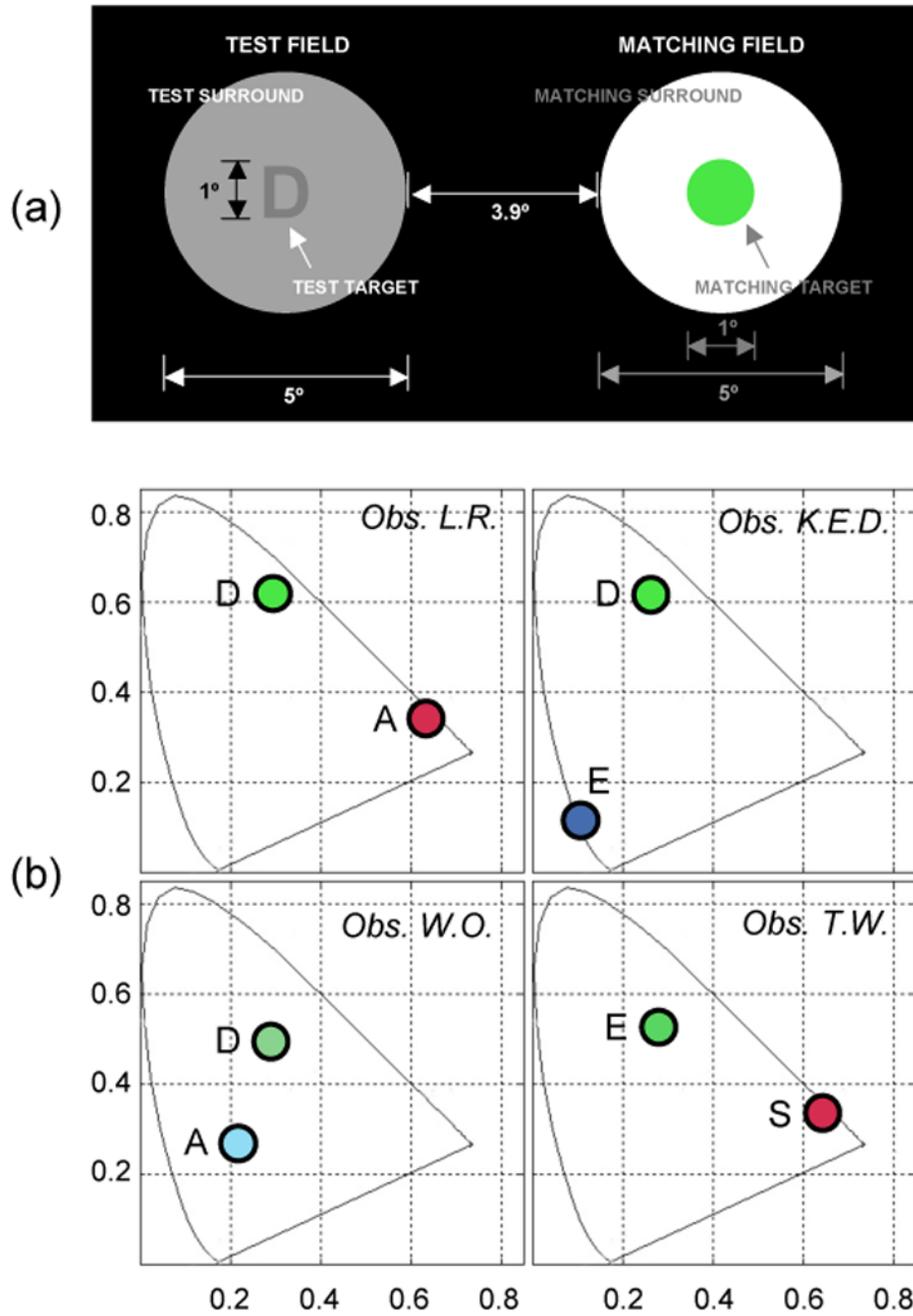
We thank Steven Shevell, Chai-Youn Kim and Edward Hubbard for helpful comments on the manuscript. This research was supported by NIH grant EY-13358.

#### REFERENCES

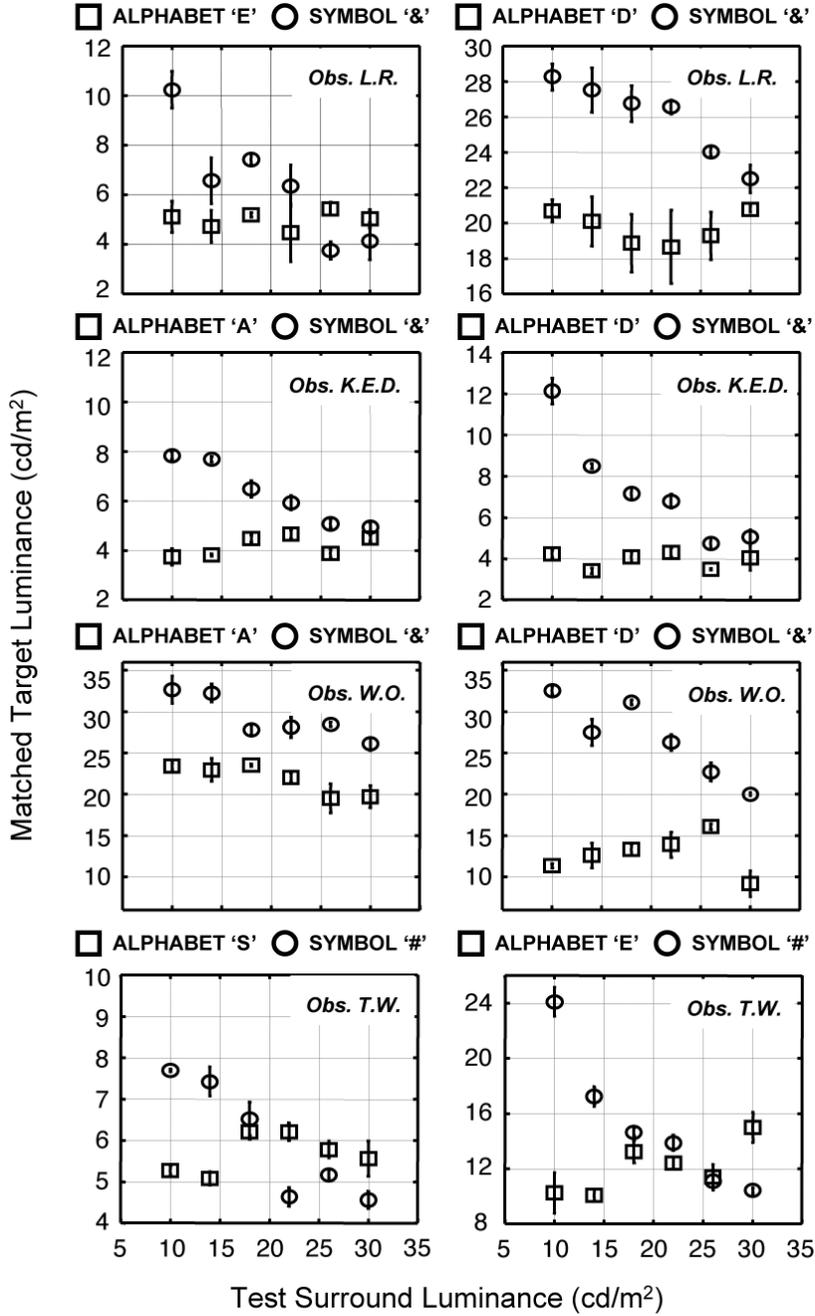
- Adelson, EH. Lightness Perception and Lightness Illusions. In: M. Gazzaniga, MS., editor. *The New Cognitive Neurosciences*. 2nd Ed.. Cambridge, MA: MIT Press; 2000. p. 339-351.
- Bartels A, Zeki S. The architecture of the colour centre in the human visual brain: new results and a review. *European Journal of Neuroscience* 2000;12:172–193. [PubMed: 10651872]
- Blake, R.; Palmeri, T.; Marois, R.; Kim, C-Y. On the perceptual reality of synesthetic color. In: Robertson, LC.; Sagiv, N., editors. *Synesthesia*. New York, NY: Oxford University Press; 2005. p. 47-73.
- Bullier, J. Communication between cortical areas of the visual system. In: Chalupa, LM.; Werner, JS., editors. *The Visual Neurosciences*. Cambridge, MA: MIT Press; 2003. p. 522-540.
- Boyaci H, Fang F, Murray SO, Kersten D. Responses to lightness variations in early human visual cortex. *Current Biology* 2007;17:989–993. [PubMed: 17540572]
- Brainard DH. The Psychophysics Toolbox. *Spatial Vision* 1997;10:433–436. [PubMed: 9176952]
- de Valois RL, Webster MA, de Valois KK, Lingelbach B. Temporal properties of brightness and color induction. *Vision Research* 1986;26:887–897. [PubMed: 3750872]
- Dixon MJ, Smilek D, Merikle PM. Not all synaesthetes are created equal: projector versus associator synaesthetes. *Cognitive, Affective, and Behavioral Neuroscience* 2004;4:335–343.
- Eagleman DM, Kagan AD, Sagaram D, Sarma AK. A standardized test battery for the study of Synesthesia. *Journal of Neuroscience Methods* 2007;15:139–145. [PubMed: 16919755]

- Edquist J, Rich AN, Brinkman C, Mattingley JB. Do synesthetic colours act as unique features in visual search? *Cortex* 2006;42:222–231. [PubMed: 16683496]
- Hadjikhani N, Liu AK, Dale AM, Cavanagh P, Tootell RBH. Retinotopy and color sensitivity in human visual cortical area V8. *Nature Neuroscience* 1998;1:235–241.
- Harrison, JE.; Baron-Cohen, S. Synaesthesia: A review of psychological theories. In: Baron-Cohen, S.; Harrison, JE., editors. *Synaesthesia: Classic and contemporary readings*. Malden, MA: Blackwell Publishers Inc; 1997.
- Hubbard EM. Neurophysiology of synesthesia. *Current Psychiatry Reports* 2007;9:193–199. [PubMed: 17521514]
- Hubbard EM, Manohar S, Ramachandran VS. Contrast affects the strength of synesthetic colors. *Cortex* 2006;42:184–194. [PubMed: 16683492]
- Hubbard EM, Arman AC, Ramachandran VS, Boynton GM. Individual differences among grapheme-color synesthetes: brain-behavior correlations. *Neuron* 2005;45:975–995. [PubMed: 15797557]
- Hurvich LM, Jameson D. An opponent-process theory of color vision. *Psychological Review* 1957;6:384–404. [PubMed: 13505974]
- Jameson, D.; Hurvich, LM. Color adaptation: sensitivity control, contrast, after-images. In: Jameson, D.; Hurvich, LM., editors. *Handbook of Sensory Physiology*. vol. VII/4. Berlin: Springer-Verlag; 1972. p. 568–581.
- Jameson D, Hurvich LM, Varner D. Receptor and postreceptor visual processes in recovery from chromatic adaptation. *Proceedings of the National Academy of Science* 1979;76:3034–3038.
- Judd, DB. *Proceedings of the CIE 1, part 7*. (Stockholm). Paris: Bureau Central CIE; 1951. Report of US Secretariat, Committee on Colorimetry and Artificial Daylight; p. 11
- Kaiser, RK.; Boynton, RM. *Human Color Vision*. Washington DC: Optical Society of America; 1996.
- Kim C-Y, Blake R, Palmeri T. Perceptual interaction between real and synesthetic colors. *Cortex* 2006;42:195–203. [PubMed: 16683493]
- Larimer J, Krantz DH, Cicerone CM. Opponent-process additivity: I. Red/green equilibria. *Vision Research* 1974;14:1127–1140. [PubMed: 4428619]
- McCollough C. Color adaptation of edge-detectors in the human visual system. *Science* 1965;149:1115–1116. [PubMed: 17737844]
- Malkoc G, Kay P, Webster MA. Variations in normal color vision. IV. Binary hues and hue scaling. *Journal of Optical Society America A* 2005;22:2154–2168.
- Mattingley JB, Rich AN, Yelland G, Bradshaw JL. Unconscious priming eliminates automatic binding of colour and alphanumeric form in synaesthesia. *Nature* 2001;410:580–582. [PubMed: 11279495]
- Nikolić D, Lichti P, Singer W. Color opponency in synaesthetic experience. *Psychological Science* 2007;18:481–486. [PubMed: 17576258]
- Palmer, SE. *Vision science: Photons to phenomenology*. Cambridge MA: Bradford/MIT Press; 1999.
- Palmeri TJ, Blake R, Marois R, Flanery MA, Whetsell W. The perceptual reality of synesthetic colors. *Proceedings of the National Academy of Science* 2002;99:4127–4131.
- Pelli DG. The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision* 1997;10:437–442. [PubMed: 9176953]
- Ramachandran VS, Azoulay S. Synesthetically induced colors evoke apparent-motion perception. *Perception* 2006;35:1567–1560.
- Ramachandran VS, Hubbard EM. Psychophysical investigations into the neural basis of synaesthesia. *Proceedings of the Royal Society of London B* 2001a;268:979–983.
- Ramachandran VS, Hubbard EM. Synaesthesia : A window into perception, thought and language. *Journal of Consciousness Studies* 2001b;8:3–34.
- Ratliff, R. *Mach bands: Quantitative studies on neural networks involved in the retina*. San Francisco: Holden Day; 1965.
- Rockland KS, Saleem KS, Tanaka K. Divergent feedback connections from areas V4 and TEO in the macaque. *Visual Neuroscience* 1994;11:579–600. [PubMed: 8038130]
- Rouw R, Scholte HS. Increased structural connectivity in grapheme-color synesthesia. *Nature Neuroscience* 2007;10:792–797.

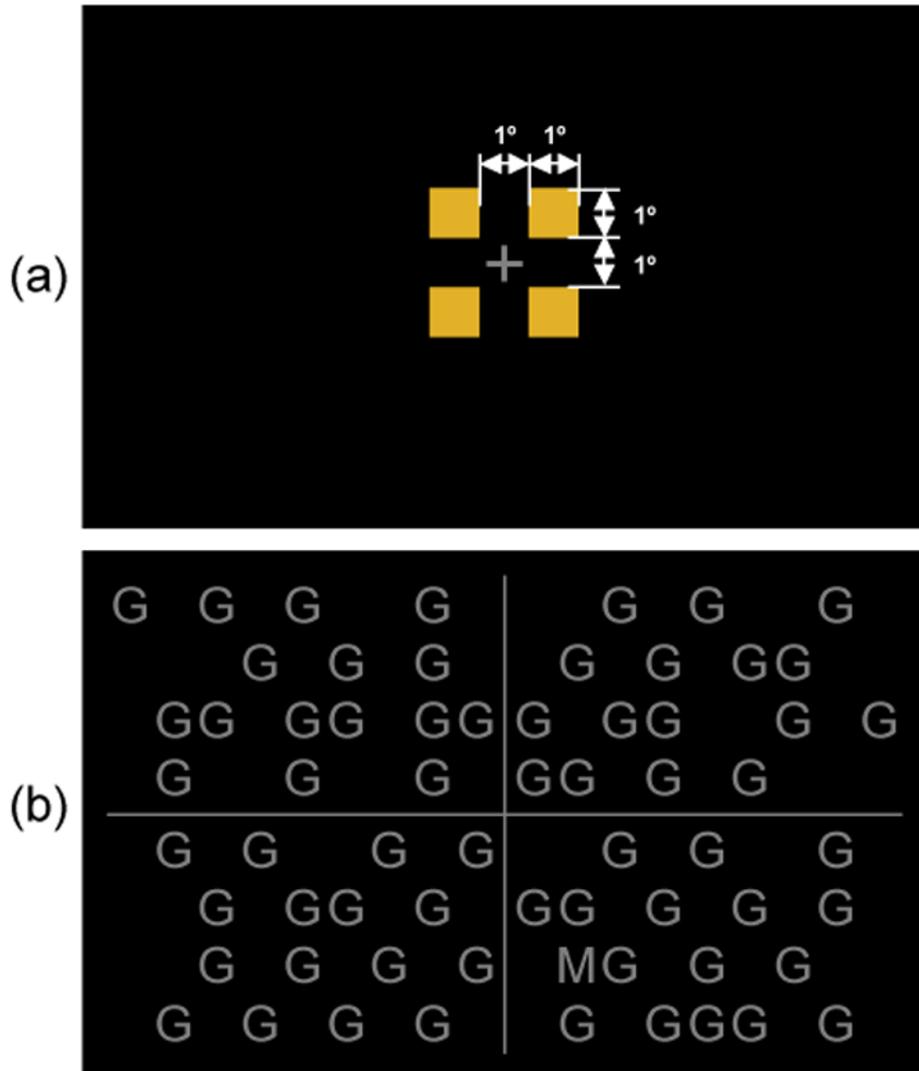
- Shevell SK. The dual role of chromatic backgrounds in color perception. *Vision Research* 1978;18:1649–1661. [PubMed: 726318]
- Shevell SK. Color perception under chromatic adaptation: equilibrium yellow and long-wavelength adaptation. *Vision Research* 1982;22:279–292. [PubMed: 7101764]
- Shevell SK. On neural signals that mediate brightness. *Vision Research* 1986;26:1195–1208. [PubMed: 3798754]
- Sillito, AM.; Jones, HE. Feedback system in visual processing. In: Chalupa, LM.; Werner, JS., editors. *The Visual Neurosciences*. Cambridge, MA: MIT Press; 2003. p. 609-624.
- Smilek D, Dixon MJ, Cudahy C, Merikle PM. Synaesthetic photisms influence visual perception. *Journal of Cognitive Neuroscience* 2001;13:930–936. [PubMed: 11595096]
- Sperling JM, Prvulovic D, Linden DEJ, Singer W, Stirn A. Neuronal correlates of colour-graphemic synaesthesia: A fMIR study. *Cortex* 2006;42:295–303. [PubMed: 16683504]
- Stromeyer CF, Kranda K, Sternheim CE. Selective chromatic adaptation at different spatial frequencies. *Vision Research* 1978;18:427–437. [PubMed: 664322]
- von Kris, J. Influence of adaptation on the effects produced by luminous stimuli. In: MacAdam, DL., editor. *Sources of Color Science* (1970). Cambridge, MA: MIT Press; 1905. p. 120-126.
- Walraven J. Discounting the background – the missing link in the explanation of chromatic induction. *Vision Research* 1976;16:289–295. [PubMed: 1266073]
- Witthoft N, Winawer J. Synesthetic colors determined by having colored refrigerator magnets in childhood. *Cortex* 2006;42:175–183. [PubMed: 16683491]
- Wyszecki, G. Color Appearance. In: Boff, KR.; Kaufman, L.; Thomas, JP., editors. *Handbook of Perception and Human Performance*. Vol. I: Sensory Processes and Perception. New York: John Wiley and Sons; 1986.
- Zeki S, Marini L. Three cortical stages of colour processing in the human brain. *Brain* 1998;121:1669–1685. [PubMed: 9762956]



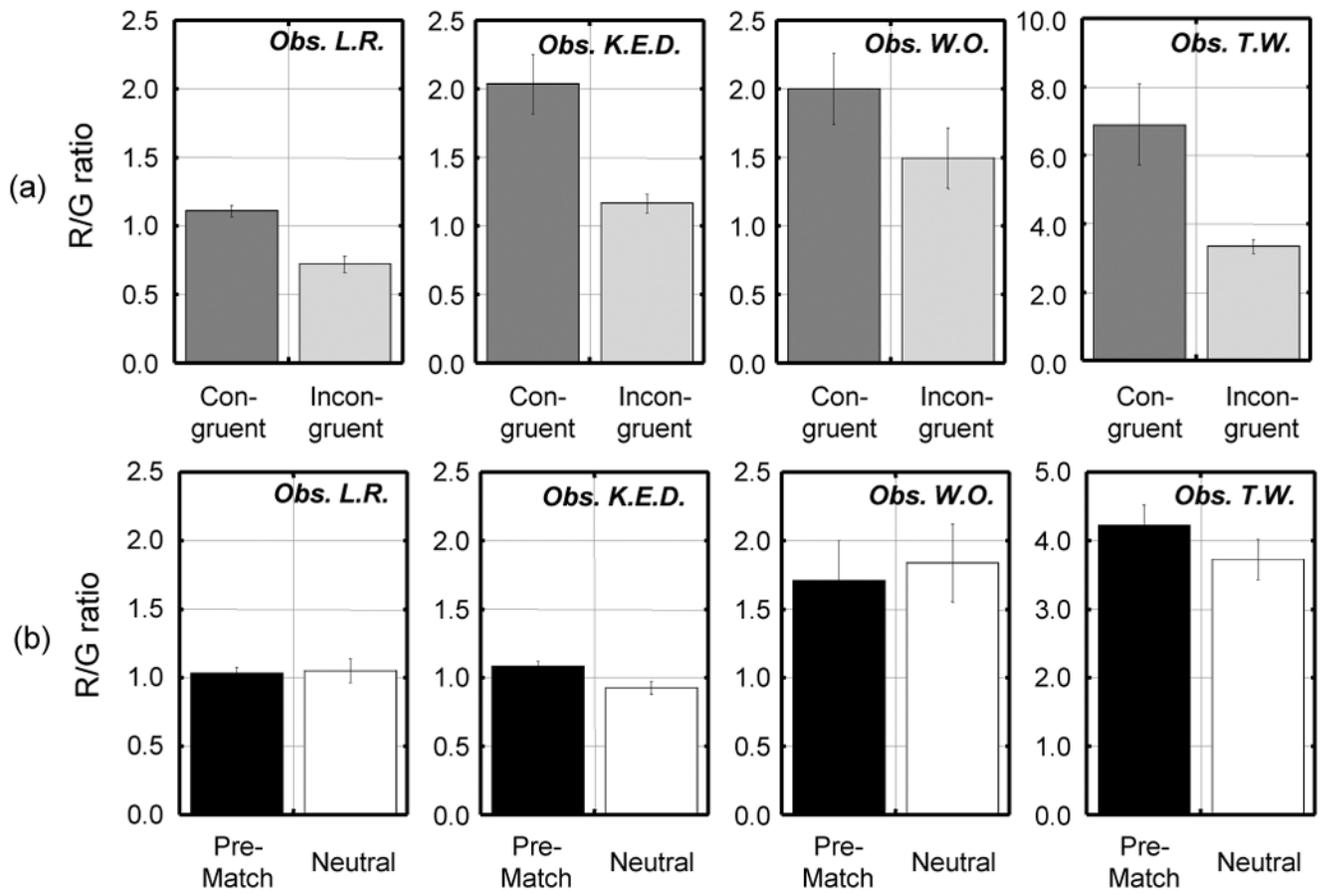
**Figure 1.** (a) An example of stimulus configuration for asymmetric color matching. (b) Chromaticity values (Judd, 1951), measured by color matching, for each character used in Experiment 1.



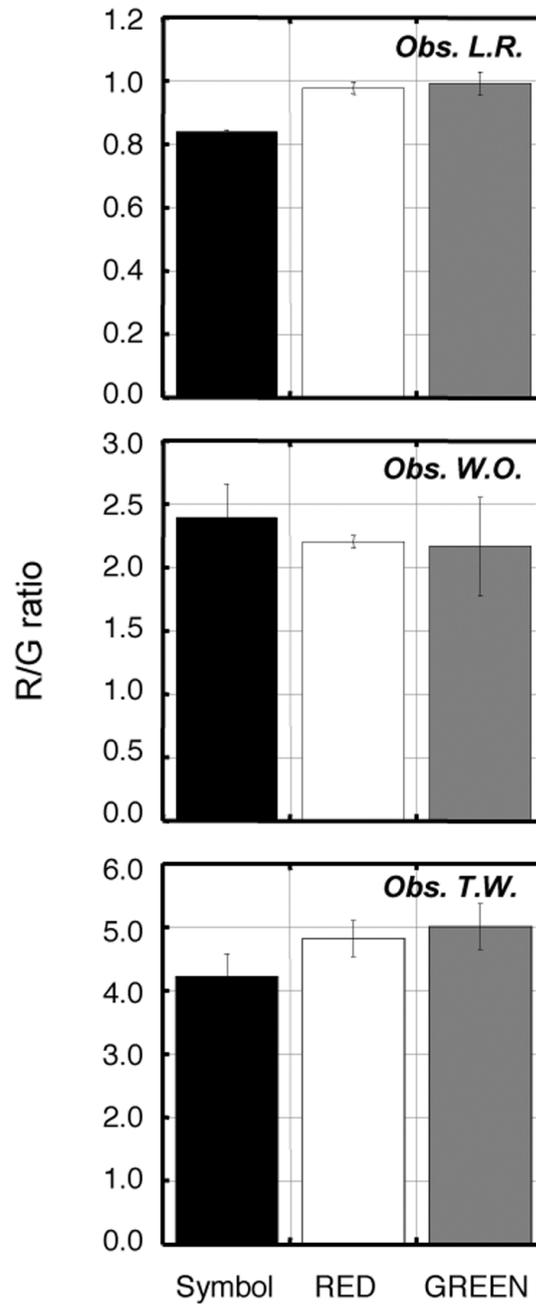
**Figure 2.** Matched target luminance as a function of surround luminance. Horizontal axis represents the luminance of the EES surround and the vertical axis represents the matched luminance of the target. Squares represent the brightness of the targets inducing synesthetic color experience (letters). Circles represent the brightness of the targets that do not induce synesthetic color experience (symbols).



**Figure 3.** (a) A schematic of stimulus configuration for hue cancellation (Experiment 2). (b) An example of stimulus configuration for adaptation to synesthetic colors (see text).



**Figure 4.** R/G ratio to achieve equilibrium yellow. (a) R/G ratio for equilibrium yellow after adaptation to a synesthetic color written in real color. In congruent condition (dark gray bar), the letters were written in reddish color, and in incongruent condition (light gray bar), the letters were written in greenish color. (b) R/G ratio for equilibrium yellow before adaptation (Pre-Match, black bar) and after adaptation to a synesthetic color written in EES gray (Neutral, white bar).



**Figure 5.** R/G ratio to achieve equilibrium yellow for the targets that induced no synesthetic color (Symbol, black bar), induced synesthetic color 'red' (RED, white bar) and induced synesthetic color 'green' (GREEN, gray bar).

**Table 1**

Chromaticity values used in Experiment 2.

Observer	Congruent Color	Incongruent Color
L.R.	$x = 0.62, y = 0.35$	$x = 0.29, y = 0.61$
K.E.D.	$x = 0.62, y = 0.35$	$x = 0.29, y = 0.61$
W.O.	$x = 0.35, y = 0.19$	$x = 0.28, y = 0.49$
T.W.	$x = 0.62, y = 0.35$	$x = 0.27, y = 0.53$