PERCEPTUAL INTERACTION BETWEEN REAL AND SYNESTHETIC COLORS

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ABSTRACT

People with color-graphemic synesthesia experience vivid, reliable color upon viewing achromatic alphanumeric characters. Recent evidence indicates that synesthetic color experiences are as perceptually real as actual colors are for non-synesthetic observers. To investigate possible interactions between real and synesthetic colors, we tested two adult color-graphemic synesthetes on a pair of perceptual grouping tasks. In Experiment 1, we employed a well-known phenomenon of motion perception, bistable apparent motion, to explore whether synesthetic colors interact with real colors in grouping over time. Two-frame apparent motion sequences were presented with both path lengths and colors systematically manipulated. Results showed that synesthetic colors of motion tokens interacted with matching real colors of the corresponding motion tokens, which could subsequently bias perceived direction of motion. In Experiment 2, we exploited binocular rivalry, a condition under which two dissimilar monocular images compete with each other and result in perceptual switches, to explore whether synesthetic colors interact with real colors in grouping over space. Pairs of rival images with two different characters were presented dichoptically with colors of characters manipulated. Results showed that synesthetic and real colors of characters tended to group together, which, in turn, promoted the perceived global dominance during binocular rivalry. Therefore, the present results identify substantial interaction between synesthetic colors and real colors in perceptual grouping.

Key words: color-graphemic synesthesia, apparent motion, binocular rivalry, perceptual grouping

INTRODUCTION

"If a husband and wife have names whose colors don't match, I don't usually like them. They just don't 'seem right'. My husband knows that I couldn't have married him if his name had been the 'wrong' color for me. We are, color-wise, perfectly compatible".

This beguiling quote comes from an email sent to us by a woman who "sees" colors when looking at letters, at words and at names. Termed color-graphemic synesthesia, her condition is as baffling as it is fascinating, at least to the vast majority of us who do not share these colorful experiences. The existence of synesthesia has been known for centuries, and the phenomenon can take many different forms including taste-triggered tactile experiences and sound-triggered visual associations. Being trained skeptics, scientists first learning about synesthesia tend to question whether these verbally described experiences are genuinely "sensory-perceptual" in nature. It is, after all, difficult for most of us to conceive what is meant, for example, by the musical note C# being colored "orange." Moreover, synesthetic descriptions have a certain metaphorical quality to them (e.g., perhaps an "orange C#" is comparable to being "green with envy"), which naturally leads those of us who are not synesthetic to wonder whether synesthetes are just using their sensory descriptions as figures of speech.

Based on recent work in a number of laboratories, however, it is now impossible to dispute that at least some forms of synesthesia entail mental experiences that have a genuine perceptual reality. We know, for example, that synesthetic colors can promote figure grouping, just as real colors do (Ramachandran and Hubbard, 2001), and that synesthetic colors can facilitate visual search for a target letter among a background of distractor letters (Palmeri et al., 2002; Laeng et al., 2004). Work in our laboratory has further shown that synesthetically colored letters organized to form horizontal contours and vertical contours can generate orientation-contingent color aftereffects (Blake et al., 2005), implying that the "colors" associated with the contours behave like real colors (McCollough, 1965). Considered together, these and other, related findings (Rich and Mattingley, 2005; Smilek et al., 2001) strongly imply that synesthetic colors triggered when viewing achromatic alphanumeric characters behave just like real colors do for non-synesthetic individuals. We further investigate such color-graphemic synesthesia in this paper.

Having convinced ourselves that synesthetic colors are perceptually real, it is natural to wonder how real colors interact with synesthetic colors. To the extent that both color experiences arise from common neural mechanisms, we would expect to observe pronounced interactions. Yet based on verbal descriptions provided by two color-

graphemic synesthetes whom we have worked with extensively, we were initially led to think that real and synesthetic colors might peacefully co-exist with little or no influence on one another. Thus, for example, when shown a letter printed in colored ink that does not match that letter's synesthetic color, both of these individuals readily report the "true" color of the letter (i.e., the color of the ink in which it is printed) and, at the same time, describe seeing their synesthetic color "overlaying" it. Thus, the letter "A" printed in green ink appears both "green" and "red" to one of our synesthetic observers, with the two colors occupying the same region of visual space. This "dual experience" implies that the two color impressions – genuine chromatic and synesthetic – are available to perception simultaneously.

At the same time, we knew from more indirect measures that the two forms of colors can interact. For example, synesthetic colors can interfere with the naming of real colors, an effect dubbed the "synesthetic Stroop effect" (Dixon et al., 2000; Mattingley et al., 2001; Palmeri et al., 2002). And, conversely, there are conditions where real background colors make it slightly more difficult to identify a letter whose synesthetic color matches the background (Smilek et al., 2001). Thus in our very recent work, we have pursued the interaction question by exploiting two well-known grouping phenomena in which real colors influence grouping over time (as evidenced in apparent motion) or over space (as evidenced by global dominance in binocular rivalry). This paper describes those studies and examines the implications of the results. In this work we have tested two adult color-graphemic synesthetes, WO (male) and LR (female). Both are classified as "projector" synesthetes (Dixon et al., 2004) – that is, they see vivid, reliable colors located directly on the achromatic alphanumeric characters, not in their "mind's eye." Both report having experienced colored characters since early childhood. The particular color-character associations differ for LR and WO, but both individuals show high test-retest reliability (meaning that their color associations are remarkably stable). Both individuals have normal trichromatic color vision, good acuity in both eyes, and normal stereopsis. (For more information about the synesthetic experiences of WO and LR, see Palmeri et al., 2002; Blake et al., 2004).

EXPERIMENT 1

Apparent Motion

To study the role of synesthetic color grouping over time, we employed a well-known illusion of motion: bistable Apparent Motion (AM). When two static "frames" containing individual tokens located at different positions in the two frames are shown in rapid succession, motion of the tokens is readily perceived (Wertheimer, 1912). Historically, this perceptual experience of motion has been dubbed "apparent" since the figures do not actually change their positions smoothly and continuously over time. According to current thinking, however, apparent motion and "real" motion are thought to arise from stimulation of common neural mechanisms (Newsome et al., 1986), in part because apparent and real motion can be rendered entirely indistinguishable under appropriate viewing conditions.

Examine frames 1 and 2 of the AM sequence shown in the top panel of Figure 1. The brief presentation of frame 1 followed immediately by brief presentation of frame 2 produces compelling AM of the tokens, but the direction of AM is inherently ambiguous because a given token in frame 2 could correspond to either token in frame 1. Moreover, because the two alternative motion paths are equal in length in the top panel, either alternative is equally likely to be perceived over repeated presentations (Ramachandran and Anstis, 1983): observers sometimes see the two tokens moving in a clockwise (CW) direction and other times see them moving in a counterclockwise (CCW) direction. This bistability of AM can be reduced or eliminated when one potential correspondence match between the tokens implies a shorter path of motion than the alternative correspondence match (Shepard and Zare, 1982) – this situation is illustrated in the middle panel of Figure 1.

The ambiguity produced by equal-length motion paths (top panel) can be counteracted, however, by similarity of stimulus attributes between tokens in the two frames (Green, 1986). Color is one such attribute (Green, 1989). For example, when red tokens and green tokens are paired in frame 1, the red tokens are more likely to be perceived to move to the position of red tokens in frame 2 instead of the green tokens in frame 2, even if the path lengths are equal (bottom panel in Figure 1). It has been suggested that synesthetic colors can also affect a synesthete's perception of apparent motion (Ramachandran and Hubbard, 2003). Color's ability to influence perceptual grouping over time in bistable AM thus provide a means for studying possible interactions between real and synesthetic colors. In this experiment, we examined how real color and synesthetic color of tokens influenced the perceived direction of AM.

Methods

We tested WO and LR on two-frame AM displays in which we varied both the path length and the color (real and synesthetic) of the motion tokens. On each trial, the observer viewed a two-frame AM sequence and reported in which direction – CW or CCW – the pair of tokens
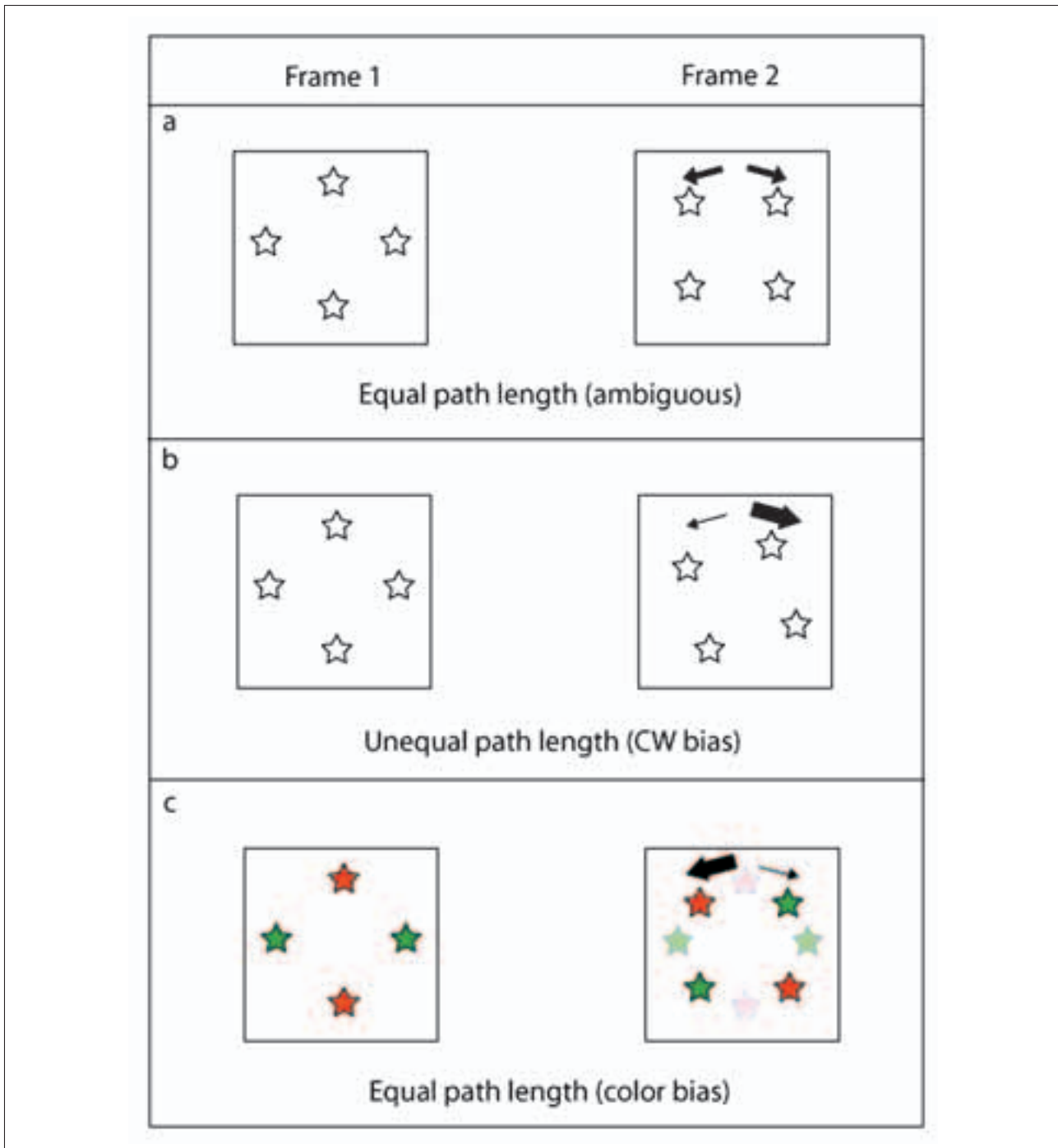
Fig. 1 – *Schematic diagrams of two-frame AM sequences. a) In this sequence the four "tokens" in frame 1 are located at the four corners of an imaginary diamond and the four tokens in frame 2 are located at positions 45 angular degrees away from the positions occupied in frame 1 (the frame 1 tokens are shown in light gray in frame 2, just to denote their original positions; in actual sequences, those 'ghost' tokens are not present). When displayed once in rapid succession, this sequence gives rise to the compelling impression of smooth motion, with the tokens moving as a group from one set of positions to the other. The direction of motion is ambiguous, meaning that the tokens could move either in a clockwise or a counterclockwise direction (denoted by two arrows in equal width); this ambiguity arises because the two possible paths of motion associated with CW and CCW are equal in length. When observers view repeated, discrete presentations of this two-frame sequence, they sometimes perceive CW motion and other times CCW motion. b) In this sequence, the position of tokens in frame 2 (relative to the position in frame 1) favors perception of CW motion (denoted by the bold arrow), because the path lengths associated with this alternative are shorter than those associated with CCW motion (as can be seen in relation to the 'ghost' tokens in frame 2). c) An equal path-length sequence in which the one pair of tokens is displayed on one color and the second pair in another color. Although completely ambiguous with respect to direction specified by path length, motion perception tends to favor the direction that maintains color matches from frame 1 to frame 2, which in this example is CCW (denoted by the bold arrow). Note: these were not the displays or colors used in our actual experiments.*

appeared to move. In all conditions, each frame had four tokens located at the corners of an imaginary square (a pair of tokens in opposite corners of the square were the identical character).

From trial to trial, the path length between tokens was varied randomly to bias the perceived direction of motion. This was accomplished by rotating the imaginary square from frame 1 to frame 2 by 75°
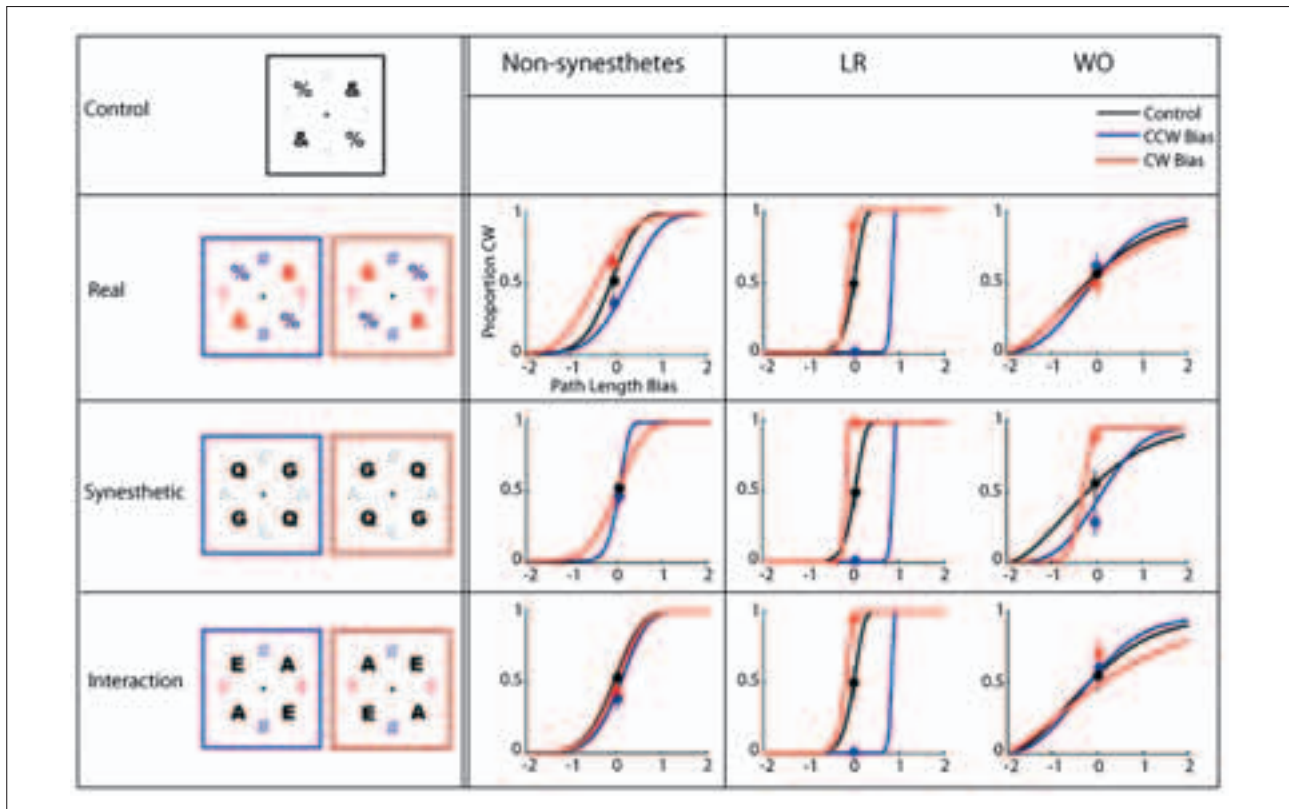
Fig. 2 – *Apparent motion perception for non-synesthetic observers (middle column) and synesthetic observers LR and WO (right column), for four conditions of apparent motion. In each graph the incidence of CW motion is plotted as the function of the path length of motion tokens from frame 1 to frame 2 (with negative values denoting paths favoring CCW motion, positive numbers paths favoring CW motion and zero denoting equal path lengths for the two alternative directions of motion). Psychometric functions were fitted using the psignifit toolbox version 2.5.41 for Matlab (http://bootstrap-software.org/psignifit/) which implements the maximum-likelihood method (Wichmann and Hill, 2001). Red curves represent the results from CW color bias, and blue curves represent the results from CCW bias for the real [top; for non-synesthetic observers, Threshold = − .381, Slope = .607 (CW), Threshold = .250, Slope = .617 (CCW), for LR, Threshold = − .092, Slope = 3.243 (CW), Threshold = .849, Slope = 2.832 (CCW), for WO, Threshold = − .168, Slope = .367 (CW), Threshold = − .117, Slope = .444 (CCW)], synesthetic [middle; for non-synesthetic observers, Threshold for .5-level CW perception = − .017, Slope = .756, Threshold for .5-level CCW perception = .008, Slope = 2.033, for LR, Threshold = − .180, Slope = 8.188 (CW), Threshold = .821, Slope = 8.294 (CCW), for WO, Threshold = − .276, Slope = 2.048 (CW), Threshold = .128, Slope = .526 (CCW)], and the interaction [bottom; for non-synesthetic observers, Threshold = .038, Slope = .888 (CW), Threshold = .099, Slope = .752 (CCW), for LR, Threshold = − .125, Slope = 3.424 (CW), Threshold = .821, Slope = 8.294 (CCW), for WO, Threshold = .010, Slope = .233 (CW), Threshold = − .234, Slope = .423 (CCW)] conditions. Black curve showing the results from the control condition was superimposed on each graph for comparison (for non-synesthetic observers, Threshold = − .017, Slope = 0.756, for LR, Threshold = − .005, Slope = 2.015, for WO, Threshold = − .248, Slope = .346). Filled circles denote the mean proportion of CW responses for the conditions with no path length bias. Error bars denote one standard error. The left column schematically shows the two-frame AM stimulus arrays used for four conditions with no path length bias, when the colors of tokens were manipulated to bias observers' perception of motion to either CCW (blue square) or CW (red square) direction.*

(strong CCW bias), 60º (weak CCW bias), 45º (no bias, bistable), 30º (weak CW bias), or 15º (strong CW bias).

In the *control condition*, frame 1 consisted of two pairs of identical characters ("#" and "?") and frame 2 consisted of two other pairs of identical characters ("%" and "&") rotated to new positions. These characters were selected because none of the four induced synesthetic colors for either LR or WO. For this control condition, the characters appeared in black against a white background. In the *synesthetic condition*, frames 1 and 2 contained two pairs of achromatic alphabetic characters, and in each frame one pair of characters induced one synesthetic color (red) and the other pair induced a different synesthetic color (blue). The specific letter pairs were different from frame 1 to frame 2 (to minimize matching based on form similarity). The specific letters used for each synethete were

different because they generally perceive different colors for the same letter. In the *interaction condition*, two pairs of physically colored 'non-inducing' characters were presented in frame 1 and two different pairs of achromatic 'inducing' characters with matching synesthetic colors were presented in frame 2. In the *real condition*, two pairs of physically colored, non-inducing characters were presented in frame 1 (each pair with a different color) and two different pairs of physically colored non-inducing characters were presented in frame 2 (see the left-hand panel in Figure 2). Stimuli were presented on a 17-inch Apple Studio Display (1024 × 768 resolution) under the control of a Macintosh G4 computer. An individual character within a frame subtended 0.75 × 0.75 degree of visual angle from a viewing distance of 60 cm, and each character was equally spaced (1.9 degree) from the center dot. Three non-

synesthetic observers were also tested for comparison; one of three non-synesthetic observers was tested using the stimulus display for WO and the other two were tested using the stimulus display for LR.

The observer initiated a trial by pressing a key that triggered presentation of frame 1 for 1 sec followed immediately by frame 2 for 1 sec. This stimulus sequence always produced a vivid experience of AM in one of two rotational directions. Following each trial, the observer reported the perceived direction of motion (CW or CCW) by pressing one of two buttons. The four conditions were run in blocks. Within a block, path length value varied randomly from trial to trial (with the stipulation that each path length value was presented for a total of 10 trials). Each block consisted of a total of 350 trials and the observer completed two blocks.

All aspects of this study were approved by Vanderbilt University Institutional Review Board, with written consent obtained from all the observers tested.

Results

Figure 2 plots the proportion of CW judgments as the function of path length for each of the four conditions (control, real, synesthetic, and interaction). Both non-synesthetic observers and the two synesthetic observers, WO and LR, showed the characteristic dependence of perceived AM on path length. For non-synesthetic observers, ambiguous AM biased by color was only found in the in *real* condition. For LR, ambiguous AM was biased by real color, as evidenced by the shift (relative to *control*) in the *real* color graph in favor of CW motion when the colored tokens in frames 1 and 2 were located at positions consistent with CW motion and the shift in favor of CCW motion when the colored tokens were consistent with CCW motion. We are baffled by the failure of *real* color to affect WO's perception of bistable AM, particularly given his performance on the synesthetic and interaction conditions described next.

For *synesthetic* trials, both LR and WO tended to see ambiguous motion in the direction consistent with a correspondence-match based on synesthetic color, even though the tokens were achromatic on the video screen. Non-synesthetic observers viewing these animations show no such bias. As expected, the most pronounced influence of synesthetic color matches occurred for equal path lengths. For both LR and WO, ambiguous AM was biased by synesthetic color, as evidenced by the shift in the *synesthetic* color graph in favor of CW motion when the tokens of the same synesthetic colors in frames 1 and 2 were located at positions consistent with CW motion and the shift in favor of CCW motion when the tokens of the same synesthetic colors were consistent with CCW

motion. This finding provides yet another example where synesthetic colors behave for synesthetic observers like real colors do for non-synesthetic observers, lending further credence to the notion that synesthetic colors are genuinely perceptual in nature.

But of most relevance for our present purposes are the results from the *interaction* condition. Here we see that both LR and WO perceived motion more frequently in the direction corresponding to a color match, where color match in this situation refers to a match between the real colors of tokens in frame 1 and the synesthetic colors of tokens in frame 2. Here again, the most pronounced influence of synesthetic color matches occurred for equal path lengths. For LR, ambiguous AM was biased by the interaction between real and synesthetic colors, as evidenced by the shift in the *interaction* graph in favor of CW motion when the colored tokens in frame 1 and the tokens of the matching synesthetic colors in frames 2 were located at positions consistent with CW motion and the shift in favor of CCW motion when the tokens of the "same" colors were consistent with CCW motion. For LR, the tendency to match real and synesthetic colors (*interaction* condition) was just as strong as that found for matches between synesthetic colors (*synesthetic* condition) or matches between actual colors (*real* condition). For WO, the most pronounced effect of color was obtained for the *synesthetic* condition. However, the shift (relative to *control*) in the *interaction* condition in favor of CW motion also showed an interaction between real and synesthetic colors, leading to a bias in otherwise bistable AM.

Experiment 2

Binocular Rivalry

Experiment 2 explored how real and synesthetic colors interact over space through grouping by color during binocular rivalry. When two dissimilar images are presented to corresponding regions of the two eyes, these images compete for perceptual dominance rather than merge smoothly into a single percept (Blake and Logothetis, 2002). During this visual competition – called *binocular rivalry* – observers not only experience perceptual switches between the two monocular images but also see blends, or mosaics, of the images occasionally – an outcome termed *mixed dominance*.

Beginning with an initial observation in the early 20th century (Diaz-Caneja, 1928), a number of studies have shown that similar image features distributed over space or between the two eyes tend to group together during rivalry (Kovács et al., 1996; also see review by Papathomas et al., 2005). In these studies, color often covaried with pattern coherence, making it impossible to
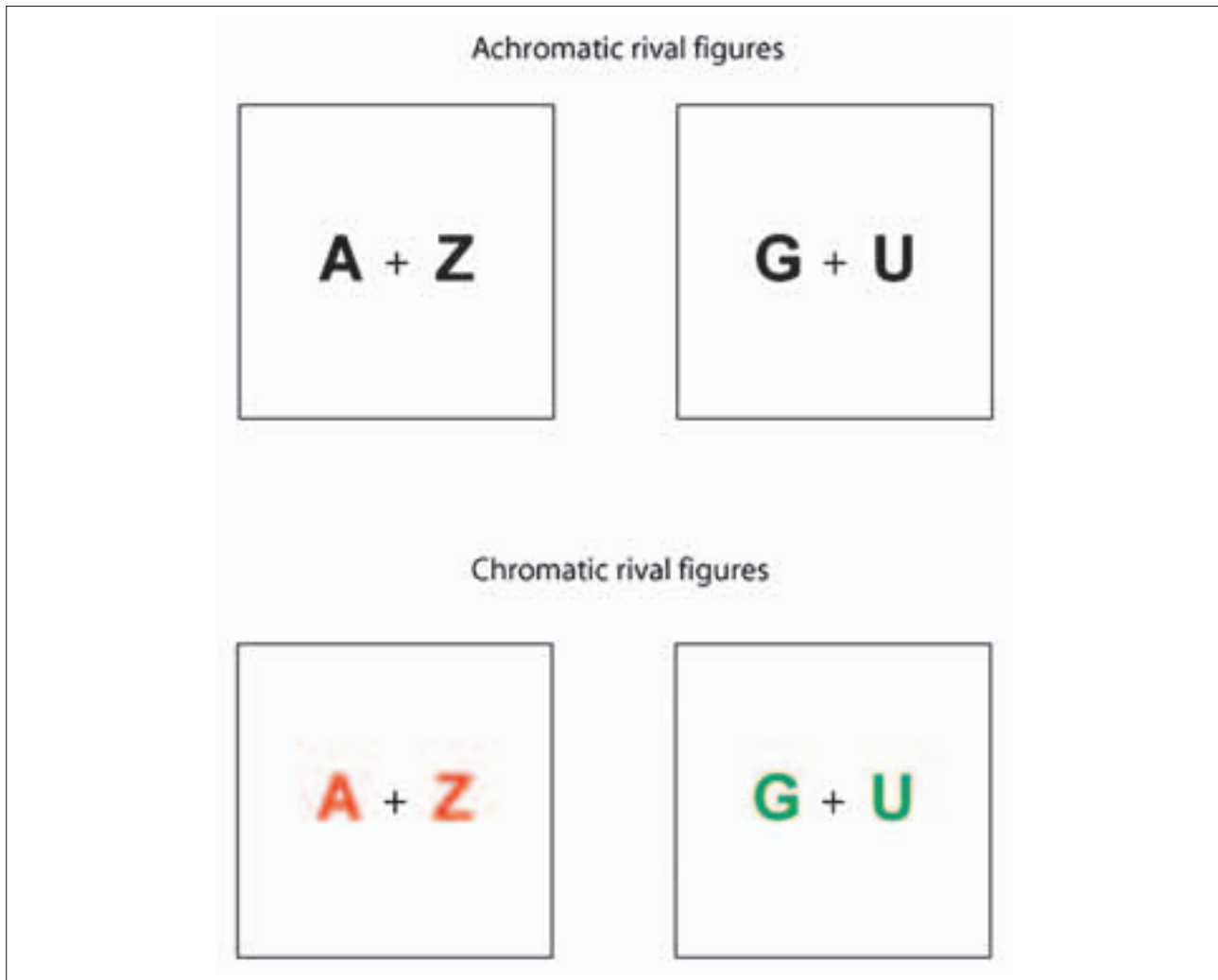
Achromatic rival figures

A + Z   G + U

Chromatic rival figures

A + Z   G + U

Fig. 3 – *The two images were presented separately to the two eyes. Dissimilar half images that produce binocular rivalry: the pair of dissimilar letters to the left of the central fixation cross compete for dominance while, at the same time, the pair to the right of fixation also compete for dominance. Over time observers experience different combinations of dominance between left- and right-side letters. When the two of the rival targets share the same color, the incidence of their conjoint predominance is greater than would be expected on the basis of chance alone. Readers capable of free-fusion may verify this tendency by comparing rivalry with the upper pair of rival targets ('achromatic') to rivalry with the lower pair of rivalry targets ('chromatic'). Note: these are not the specific characters or colors used in our experiment; these half-images are for demonstration purposes only.*

document color's unique contribution to grouping. Recently, Pearson and Clifford (2004) showed that color tends to stabilize perception during rivalry when rival stimuli are intermittently presented, so long as those stimuli are not also swapped between the eyes. In their study, color coherence had a larger influence on rivalry than did orientation coherence. Recent work in our laboratory, using figures similar to those shown in Figure 3, has confirmed that color alone can boost the joint dominance of two spatially separated rival targets (Kim and Blake, 2004). Moreover, we have also found that even orientation-dependent color aftereffects (McCollough, 1965) can promote global dominance during rivalry (Kim and Blake, 2004); objects of the same color are more likely to be dominant simultaneously than two objects of different colors, even when one of those "colors" is produced by the McCollough effect.

Knowing that color promotes perceptual grouping over space in binocular rivalry, we investigated the possible interactions between real and synesthetic colors to promote grouping in rivalry.

Methods

We tested WO and LR on four conditions of binocular rivalry in which we systematically varied the colors (real and synesthetic) of two component objects in rival images presented to the two eyes. On each trial, the observer dichoptically viewed a pair of rival images through a mirror stereoscope and pressed and held a button whenever the two perceptually dominant component objects were the same color (in the *synesthetic*, *interaction*, and *real* conditions) or comprised either of the two specified pairs (in the *control* condition) thus providing duration measures of conjoint dominance. Each rival target image consisted of two different
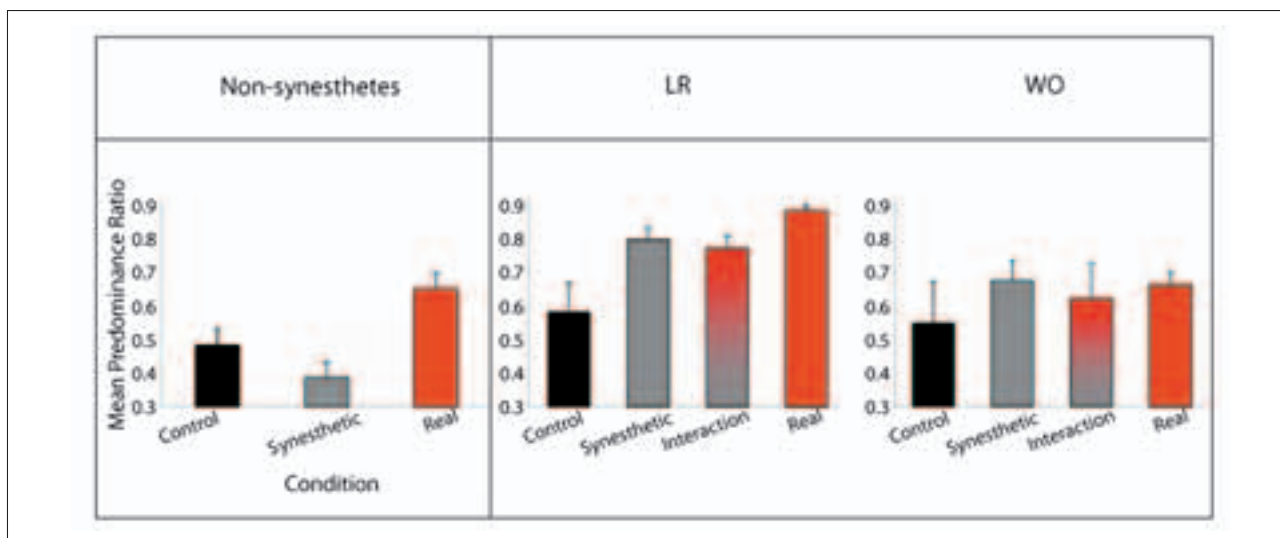
characters (the component objects) presented side by side with a central fixation cross midway between the two component objects.

In the *control* condition, one of two rival images consisted of two non-inducing characters ("?" and "&") and the other consisted of two other non-inducing characters ("#" and "$"). For this control condition, the characters appeared in dark gray against a light gray background. In the *synesthetic* condition, each of the two rival target images contained a pair of achromatic inducing characters of the same synesthetic color; the synesthetic color of the letter pair in one rival target image was different from that in the other rival target image. For example, achromatic "A" and "R" (dark blue for WO) were presented to the one eye and "B" and "M" (pink for WO) were presented to the other eye of WO. In the *interaction* condition, the two rival target images were each composed of a physically colored non-inducing character and an achromatic inducing character with a matching synesthetic color; each rival target image had different (real and synesthetic) colors. For example, blue "#" and achromatic "A" were presented to the one eye and pink "&" and achromatic "B" were presented to the other eye of WO. In the *real* condition, each of the two rival target images was composed of a pair of non-inducing characters of the same color. For example, blue "?" and "&" were presented to the one eye and pink "#" and "$" were presented to the other eye of WO. Stimuli were presented on a 21-inch NEC monitor (1024 × 768 resolution, 75 Hz frame rate) under the control of a Macintosh G4 computer. An individual character within a rival target image subtended 0.5 × 0.5 degree of visual angle from a viewing distance of 90 cm, and each character was equally spaced (0.16 degree) from

the central cross. Two non-synesthetic observers were also tested for comparison; one of two non-synesthetic observers was tested using the stimulus display for WO and the other was tested using the stimulus display for LR.

The observer initiated a trial by pressing a key that triggered presentation of the two rival targets for 60 sec. During each trial, the observer tracked the duration of color grouping by holding down a button when he or she perceived two characters of the same color (real or synesthetic) exclusively in the *synesthetic*, *interaction*, and *real* conditions; the button was released otherwise. In the *control* condition, the observer held down a button when he or she perceived a "?"/"&" pair or a "#"/ "$" pair exclusively. The observer underwent practice trials until he or she got used to the tracking task in the control condition and performed as easily as they tracked based on colors in the other three conditions. For each condition we ran a block of 60-sec trials, with the order of trials randomized. Within a block, the position of each component object (left or right of the fixation cross) in rival target images varied randomly from trial to trial, and each rival target image was presented an equal number of times to the left and to the right eyes. Each condition was presented for a total of 8 trials.

Results

The graphs in Figure 4 plot the mean predominance ratio of color grouping for real colors, synesthetic colors, and interactions between real and synesthetic colors, compared with the mean predominance ratio of grouping unaccompanied by any colors (*control* condition). Predominance ratio is defined as the total duration of global dominance duration divided by the entire

trial duration; ratio values can range from 0 (no grouping) to 1.0 (grouping exclusively). Non-synesthetic observers showed enhanced grouping only for real color (Mean Predominance Ratio = .655 ± .043 (one standard error)). For these observers, the *synesthetic* condition was not different from the *control* condition in that no color experience was involved. By contrast, both LR *and* WO showed enhanced grouping by both *real* and *synesthetic* colors. For LR, grouping for real color (Mean Predominance Ratio = .885 ± .017) was slightly stronger than grouping for synesthetic color (Mean Predominance Ratio = .797 ± .038). Both *real* and *synesthetic* colors of the component objects in rival images, however, greatly enhanced grouping compared with achromatic component objects in the *control* condition (Mean Predominance Ratio = .585 ± .083) For WO, the strength of color grouping was literally the same for both real color (Mean Predominance Ratio = .663 ± .039) and synesthetic color (Mean Predominance Ratio = .676 ± .060), which again directly demonstrates the perceptual reality of synesthetic colors. For WO, grouping effects in both *real* and *synesthetic* conditions were also stronger than grouping effect in the *control* condition (Mean Predominance Ratio = .553 ± .050).

But of most relevance of our present purposes are the results from the *interaction* condition. Here we see that both LR *and* WO perceived two characters with the same color (the real color of one non-inducing character and the synesthetic color of the other inducing character in a rival target) as grouped for a longer total duration of time during binocular rivalry (For LR, Mean Predominance Ratio = .772 ± .037, and for WO, Mean Predominance Ratio = .624 ± .104). Furthermore, for both synesthetic observers, the tendency to group real and synesthetic colors over space (interaction condition) was comparable to that found for grouping between synesthetic colors (synesthetic condition) or matches between actual colors (real condition).

DISCUSSION

Overall, the present results point to substantial interaction between synesthetic colors and real colors, at least when it comes to perceptual grouping. There were idiosyncratic differences on some conditions between LR and WO, and we have no ready explanation for those differences. As we and others continue to study people with synesthesia it is reasonable to expect that the particulars of this condition may vary considerably among synesthetic observers. Such individual differences will complicate our efforts to generate a unified account of this fascinating condition, although in the long run these differences may work to our advantage once we get to the point of

identifying the neural concomitants of color-graphemic synesthesia.

What are the implications of the results found in the present studies? For one thing, the interactions between real and synesthetic colors further substantiate the emerging view that synesthetic colors are genuinely perceptual in nature. It is difficult to imagine how metaphorical associations could combine with real colors to influence apparent motion or binocular rivalry. Moreover, our results imply that synesthetic colors can be as robust perceptually as real colors, as evidenced by the strong grouping effects obtained in the conditions where all elements in the apparent motion display (Experiment 1) or the binocular rivalry display (Experiment 2) were achromatic but synesthetically colored. Most importantly, our results imply that real and synesthetic colors cooperatively interact to specify motion perception (Experiment 1) and figural grouping (Experiment 2). Whatever processes underlie these color grouping phenomena, those processes evidently receive inputs from neural mechanisms registering real object color and synesthetic object color. Does this conclusion, in turn, mean that real and synesthetic colors arise from the same neural mechanisms? We remain agnostic, but somewhat skeptical, about this possibility for the following reason.

First, let us clarify what we mean by neural "mechanisms" of color experience. In our usage this notion refers to a population of neurons, perhaps anatomically distributed, whose patterns of activity uniquely represent perceived color; this does not necessarily mean that color is produced by neural activity in one "special" brain region (e.g., V4). So starting with this notion, we also know that at least some synesthetic observers report being able simultaneously to perceive the real color of a letter (e.g., "red") as well as the synesthetic color of that letter (e.g., "green"). But how can two different colors located at the same region of the visual field arise simultaneously within a common mechanism? This would require two distinct patterns of activity to be maintained simultaneously within the same neural population, a logical impossibility.

Of course, it is premature to draw firm conclusions based solely on phenomenological reports, for it is possible that WO and LR are, in fact, rapidly switching between the two color "modes". In addition, there is reason to believe that attention can modulate synesthetic experiences (Palmeri et al., 2002), and this also could be a factor in the putative co-existence of real and synesthetic colors. In general, this issue of "co-existence" deserves further, careful psychophysical investigation using indirect techniques such as those devised by Smilek et al. (2001). Moreover, we may be able to utilize brain imaging techniques to learn the extent to which activations associated with perception of real and synesthetic colors overlap

anatomically. Not surprisingly, several laboratories have tackled this question but, unfortunately, the results lead to seemingly conflicting conclusions (Aleman et al., 2001; Blake et al., 2004; Nunn et al., 2002; Weiss et al., 2001). Note, too, that none of the current imaging techniques could reveal detailed spatial patterns of activity within a given color-sensitive brain area, which will be required to test definitively the hypothesis that real and synesthetic colors arise from common spatio-temporal patterns of neural activation.

REFERENCES

ALEMAN A, RUTTEN GJM, SITSKOORN MM, DAUTZENBERG G and RAMSEY NF. Activation of striate cortex in the absence of visual stimulation: An fMRI study of synesthesia. *Neuroreport, 12:* 2827-2830, 2001.

BLAKE R and LOGOTHETIS NK. Visual Competition. *Nature Reviews Neuroscience, 3:* 1-11, 2002.

BLAKE R, PALMERI TJ, MAROIS R and KIM C-Y. On the perceptual reality of synesthetic color. In L Robertson and N Sagiv (Eds), *Synesthesia: Perspectives from Cognitive Neuroscience.* Oxford: University Press, 2005.

DIAZ-CANEJA E. Sur l'alternance binoculaire [On binocular alternation]. *Annales d'Oculistique, 165:* 721-731, 1928.

DIXON MJ, SMILEK D, CUHADY C and MERIKLE PM. Five plus two equals yellow. *Nature, 406:* 365, 2000.

DIXON MJ, SMILEK D and MERIKLE PM. Not all synaesthetes are created equal: Distinguishing between projector and associator synaesthetes. *Cognitive, Affective and Behavioral Neuroscience, 4:* 335-343, 2004.

GREEN M. What determines correspondence strength in apparent motion? *Vision Research, 26:* 599-607, 1986.

GREEN M. Color correspondence in apparent motion. *Perception and Psychophysics, 62:* 15-20, 1989.

KIM C-Y and BLAKE R. Color promotes interocular grouping during binocular rivalry. Paper presented at the 4th Annual Meeting of the Vision Sciences Society, Sarasota, FL, USA, 2004.

KOVÁCS I, PAPATHOMAS TV, YANG M and FEHÉR A. When the brain changes its mind: Interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences, 93:* 15508-15511, 1996.

LAENG B, SVARTDAL F and OELMANN H. Does color synesthesia pose a paradox for early-selection theories of attention? *Psychological Science, 15:* 277-281, 2004.

MATTINGLEY JB, RICH AN, YELLAND G and BRADSHAW JL. Unconscious priming eliminates automatic binding of colour and alphanumeric form in synesthesia. *Nature, 410:* 580-582, 2001.

McCOLLOUGH C. Color adaptation of edge detectors in the human visual system. *Science, 149:* 1115-1116, 1965.

NEWSOME W, MIKAMI A and WURTZ RH. Motion selectivity in macaque visual cortex: III. Psychophysics and physiology of apparent motion. *Journal of Neurophysiology, 55:* 1340-1351, 1986.

NUNN JA, GREGORY LJ, BRAMMER M, WILLIAMS SCR, PARSLOW DM, MORGAN MJ, MORRIS RG, BULLMORE ET, BARON-COHEN S and GRAY JA. Functional magnetic resonance imaging of synesthesia: Activation of V4/V8 by spoken words. *Nature Neuroscience, 5:* 371-375, 2002.

PALMERI TJ, BLAKE R, MAROIS R, FLANERY MA and WHETSELL JR. The perceptual reality of synesthetic colors. *Proceedings of the National Academy of Sciences, 99:* 4127-4131, 2002.

PAPATHOMAS TV, KOVACS I and CONWAY T. Interocular grouping in binocular rivalry: Basic attributes and combinations. In D Alais and R Blake (Eds), *Binocular rivalry.* MIT Press, 2004.

PEARSON J and CLIFFORD CWG. Determinants of visual awareness following interruptions during rivalry. *Journal of Vision, 4:* 196-202, 2004.

RAMACHANDRAN VS, GINSBURG A and ANSTIS S. Low spatial frequencies dominate apparent motion. *Perception, 12:* 457-461, 1983.

RAMACHANDRAN VS and HUBBARD EM. Psychophysical investigations into the neural basis of synesthesia. *Journal of Consciousness Studies, 10:* 49-57, 2001.

RAMACHANDRAN VS and HUBBARD EM. The Phenomenology of Synesthesia. *Proceedings of the Royal Society of London, 268:* 979-983, 2003.

RICH AN and MATTINGLEY JB. Can attention modulate colour-graphemic synesthesia? In L Robertson and N Sagiv (Eds), *Synesthesia: Perspectives from Cognitive Neuroscience.* Oxford: University Press, 2005.

SHEPARD RN and ZARE SL. Path-guided apparent motion. *Science, 220:* 632-634, 1982.

SMILEK D, DIXON MJ, CUDAHY C and MERIKLE PM. Synesthetic photisms influence visual perception. *Journal of Cognitive Neuroscience, 13:* 930-936, 2001.

WEISS PH, SHAN NJ, TONI I, ZILLES K and FIINK GR. Associating colours with people: A case of chromatic-lexical synaesthesia. *Cortex, 37:* 750-753, 2001.

WERTHEIMER M. Experimentelle Studien über das Sehen von Bewegung. *Zeitschrift für Psychologie, 61:* 161-265, 1912.

WICHMANN FA and HILL NJ. The psychometric function: I. Fitting, sampling and goodness-of-fit. *Perception and Psychophysics, 63:* 1293-1313, 2001.

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