The functional effects of color perception and color imagery

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Functional imaging research and studies of brain-damaged patients suggest the mechanisms of color perception and color imagery have some degree of overlap. Previous research into color imagery has focused on compound images consisting of both color and form, e.g., whole objects. Little is known regarding the characteristics of pure color imagery—color without form structure. Binocular rivalry has proven to be a successful method for assessing mental imagery indirectly, quantitatively, and reliably. Here, we utilized this technique to access pure color imagery. Experiment 1 consisted of three conditions, in which participants were instructed to either imagine pure colors according to a letter cue, imagine pure colors in the presence of background luminance, or passively view weak perceptual color patches. Subsequently, a brief rivalry display was presented. Results indicated that perceptual dominance during rivalry was significantly biased by the participants' prior color imagery and perception. However, for imagery, the addition of background luminance attenuated this priming effect. In Experiment 2, we tested whether color imagery was location-specific in retinotopic space. Color imagery was only found to prime subsequent rivalry when the imagery and rivalry stimuli occurred at the same retinotopic location. These results demonstrate that imagery of pure colors without form structure can influence subsequent color perception and can be localized in retinotopic space. These results are consistent with previous studies examining mental imagery of compound visual stimuli and demonstrate the potential of investigations into mental imagery of individual visual features.

Introduction

Color plays an important role in visual memories. Strong memories of color can develop for a wide range of objects or events through learning associations between visual features presented together within the environment. Recalling color memories can have a powerful influence on the concurrent perception of color (Hansen, Olkkonen, Walter, & Gegenfurtner, 2006; Hering, 1920; Pérez-Carpinell, de Fez, Baldoví, & Soriano, 1998). Unlike color constancy (D'Zmura & Lennie, 1986), color memory effects can be experienced if all objects in a scene are uniformly colored or if an object is presented in isolation (Hering, 1920). Although the existence of these kinds of perceptual color memories is generally agreed upon, their nature is not (for reviews see Barsalou, 2008; Bramão, Reis, Petersson, & Faisca, 2011). Regardless, previous research has clearly demonstrated that stored memories of color can influence color perception.

When asked to recall a particular color memory, people tend to use the sensory-based substrate of mental imagery to inspect the perceptual characteristics of that particular memory. Mental imagery is a perception-like experience based on memories with no concurrent sensory input. As such, a mental image can be generated without corresponding perceptual stimuli (Kosslyn, Ganis, & Thompson, 2001), allowing an individual to re-experience stimuli or simulate future events (Barsalou, 2009; Decety & Grèzes, 2006). Evidence suggests that mental imagery can be pictorial in nature as evidenced by research showing that early visual areas, which are known to represent information pictorially/retinotopically, tend to be active during visual mental imagery (Kosslyn, Thompson, Kim, & Alpert, 1995; Slotnick, Thompson, & Kosslyn, 2005). Perception can interfere with the ability to concurrently generate mental imagery (Keogh & Pearson, 2011; Pearson, Clifford, & Tong, 2008; Sherwood & Pearson,

2010), and imagery can influence subsequent perception in a manner specific to early visual cortex (Ishai & Sagi, 1995; Pearson et al., 2008). In these studies, imagery actually primes or facilitates subsequent perception in the same way as a weak or low-energy sensory stimulus. Additionally, imagery can be dissociated from visual attention in a number of ways (Pearson et al., 2008). Several studies have shown that there is a greater probability that a mental image will bias subsequent rivalry when the reported vividness of the mental image is higher (Pearson, Rademaker & Tong, 2011; Rademaker & Pearson, 2012). However, whether pure color information can be voluntarily represented in pictorial/retinotopic mental imagery is unknown.

In mental imagery research, color was initially treated as a "side issue" of little importance to the models of mental imagery under debate. More recently, color imagery has become an independent area of research in itself (Bramão et al., 2011). Functional imaging methods have been used in an attempt to show similar patterns of activity for color perception and color imagery; however, these results have been largely inconclusive. Some studies have found that color perception and color imagery involve activity within the same neural areas (Hsu, Frankland, & Thompson-Schill, 2012; Hsu, Kraemer, Oliver, Schlichting, & Thompson-Schill, 2011; Simmons et al., 2007), and other studies have shown that the two processes are largely independent (Bramão, Faisca, Forkstam, Reis, & Petersson, 2010; Chao & Martin, 1999; Lu et al., 2010; Miceli et al., 2001). Likewise, case studies of brain-damaged patients with acquired achromatopsia have produced conflicting evidence that color perception and color imagery are sometimes independent but can also overlap in function (e.g., Damasio, 1989; De Vreese, 1991; Goldenberg, Mullbacher, & Nowak, 1995; Shuren, Brott, Schefft, & Houston, 1996).

Various tasks have been employed to investigate color imagery. These tasks can be divided into two basic categories: "color naming," which requires participants to imagine an object and report the name of its color (e.g., Shuren et al., 1996) and "color comparison," which requires participants to imagine two objects and compare their colors (e.g., Howard et al., 1998). However, it is likely that both of these kinds of tasks can be performed using semantic object knowledge rather than visual imagery. In addition, these types of tasks are aimed at imagery of whole objects, such as the entire image of a raspberry, including shape, surface texture, luminance, and color. Hence, even though the task directly queries the color of the object, it remains unclear how separable the color information is from composite object representations. To conclusively show that color imagery is perceptual in nature, it is necessary to demonstrate that

it can influence perceptual color processing in a manner specific to retinotopic visual cortex.

A recent study by Pearson et al. (2008) provided some evidence regarding the perceptual nature of voluntary mental imagery involving color. Using imagery of red- and green-oriented Gabor patterns as stimuli, the authors demonstrated that such imagery could prime subsequent binocular rivalry in a manner specific to early visual cortex. In one experiment, participants were instructed to imagine red horizontal or green vertical Gabor patterns; however, the subsequent rivalry patterns were spatially rotated. The results showed that the imagery-priming effect decreased sharply as the angle between imagined and subsequent rivalry stimuli increased. In other words, visual imagery can be represented in an orientation-specific manner, a characteristic of early visual cortex (Hubel & Wiesel, 1968; Tootell et al., 1998b). However, although the color of the imagined and rivalry Gabor patterns were the same, the color information was seemingly not enough to drive the priming effect when the orientation differed. This lack of a color effect seems to indicate either that participants simply could not imagine the Gabor colors or that participants were focusing on the orientation of the Gabor patterns. Similar effects of orientation, but not color, have also recently been found when mental images of these kinds of colored Gabor patterns are used within an associative learning paradigm (Lewis, O'Reilly, Khuu, & Pearson, 2013). While these findings demonstrate the perceptual nature of visual imagery, they do not describe perceptual contents of mental imagery in detail. A slightly modified methodology might allow for a more direct investigation of individual visual features, such as color.

In the present study, we sought to determine if the voluntary generation of pure color imagery, without any specific object form structure, could bias the subsequent perception of color. To more directly investigate color imagery, we used a modified version of the binocular rivalry task, which has previously been used to measure visual imagery (Keogh & Pearson, 2011; Pearson et al., 2008; Pearson et al., 2011; Rademaker & Pearson, 2012; Sherwood & Pearson, 2010). Binocular rivalry has been demonstrated to be a reliable (Rademaker & Pearson, 2012) and indirect approach to mental imagery (Pearson et al., 2008). By replacing the colored Gabor patterns used in previous studies with pure Gaussian color patches, this task should assess a more pure form of color imagery because the only element in the stimulus is color.

In Experiment 1 we assessed to what extent voluntary color imagery can bias subsequent color perception in the form of color rivalry across three conditions. The first condition was conducted to determine if color imagery could occur in a dark

context. The second condition was conducted to determine if background luminance would interfere with color imagery generation as it has been shown to interfere with other kinds of compound mental imagery (Keogh & Pearson, 2011; Pearson et al., 2008; Sherwood & Pearson, 2010). The third condition sought to determine if a weak perceptual stimulus could have priming effects similar to that of color imagery on subsequent perception as has been previously suggested (Pearson et al., 2008).

In a second experiment, we sought to determine if color imagery was location-specific in visual space. Participants were instructed to imagine a color patch at a particular location in visual space; subsequently, the color rivalry stimulus would appear at the same or at a different spatial location. Differences in priming rates between the same and different location conditions would be indicative of location-specificity for color imagery and would suggest that the primary visual cortex, which is known to be retinotopic (Hubel & Wiesel, 1968), is involved in color imagery.

By way of preview, the results of Experiment 1 indicate that color imagery biases or primes the dominance of a subsequent color rivalry display. This result is replicated using weak perceptual stimuli, which has been previously shown to affect perception in a manner similar to that of mental imagery (Pearson et al., 2008). However, we do not find any significant priming effects of voluntary imagery in the presence of background luminance. In Experiment 2, we show that pure color imagery can be location-specific when assessed using color rivalry.

Method

Participants

Ten participants (two females) were recruited for this study ($n_{Experiment\ 1} = 9$; $n_{Experiment\ 2} = 6$). Authors SC and DL and three other participants completed both experiments. All participants had normal or corrected-to-normal vision and provided written informed consent. This experiment was approved by the UNSW Human Research Ethics Advisory Panel for Psychology.

Stimuli and apparatus

Stimuli were displayed on a linearized Sony Trinitron G520 CRT monitor with 1280 × 960 resolution and a 75-Hz refresh rate. Stimuli were generated using Matlab 7.9.0 (R2009b) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) running on an iMac

computer with an Nvidia GeForce GT120 graphics chip. Luminance and CIE values of colors were measured using a Konica Minolta CS-100 photometer. In both experiments, a circular bull's-eye fixation mark (diameter = 0.3° visual angle) was used to help participants maintain fixation.

In Experiment 1, the stimuli consisted of six different colored Gaussian blobs (standard deviation ≈ 1°) presented at fixation. The CIE color values of the Gaussians were as follows: red: x = 0.633, y = 0.340, max luminance = 2.22 cd/m^2, min luminance = 0.97 cd/m^2; cyan: x = 0.208, y = 0.326, max luminance = 7.24 cd/m^2, min luminance = 1.18 cd/m^2; green: x = 0.274, y = 0.406, max luminance = 7.58 cd/m^2, min luminance = 2.06 cd/m^2; violet: x = 0.293, y = 0.157, max luminance = 2.88 cd/m^2, min luminance = 1.06 cd/m^2; blue: x = 0.142, y = 0.075, max luminance = 1.01 cd/m^2, min luminance = 0.50 cd/m^2; yellow: x = 0.387, y = 0.521, max luminance = 9.66 cd/m^2, min luminance = 1.27 cd/m^2. These Gaussian patches were split into three separate pairs of stimuli: red/cyan, green/violet, blue/yellow. The luminance values of the two colors in each pair were adjusted for each participant using an eye-dominance test adapted from previous studies to ensure that they were perceptually balanced (Keogh & Pearson, 2011; Pearson et al., 2008; Pearson et al., 2011; Rademaker & Pearson, 2012; Sherwood & Pearson, 2010). The procedure used for this perceptual balancing is described in greater detail within the "procedure" section. In the weak perception condition, the weak perceptual color stimuli were presented at 30% of the luminance of the rivalry stimuli.

In Experiment 2, only the red and cyan Gaussians were used. These Gaussians were made smaller (mean diameter ≈ 2.7°) and presented either 2.6° to the left or right of fixation. Additionally, a weak (low luminance) circle outline (diameter = 3°) was presented either to the left or right of fixation during the mental-imagery interval in order to indicate the spatial location in which participants should generate their mental image. During this interval, the circular fixation mark was replaced with a triangular one of equal size, which pointed toward the chosen spatial location.

Procedure

For both experiments, participants were seated in a darkened room with their heads stabilized using a mirror stereoscope and chin rest. An eye-dominance test was conducted for each color pair. Relative luminance of the two colored Gaussians was adjusted during this test in order to minimize potential eye bias. For each eye-dominance trial, the two colored Gaussians were briefly presented in a binocular rivalry display, and participants were required to indicate the

dominant color by pressing different numbered keys. Then, that same color (the previously dominant one) was presented to one eye for 4 s, after which the rivalry pair was presented again. If adapting to the previously dominant color did not induce a change in rivalry dominance across the two presentations, the relative luminance was adjusted accordingly. There were 30 trials in each eye-dominance session. The eye-dominance test was repeated until the two eyes were balanced (the adaptation period led to a change in rivalry dominance on 90% of trials). This method of adjusting the stimuli is based upon previous research (for a detailed explanation of the eye-dominance test, refer to Pearson et al., 2008).

In Experiment 1, each experimental session was divided into three blocks, one for each color pair: red/cyan, green/violet, blue/yellow. Each block consisted of a total of 63 trials, split evenly into three conditions: imagery, background-luminance, and perception in a random order. Participants were told which color pair would be presented before each section began and were allowed to take breaks between the three sections. All participants completed a total of four experimental sessions.

As can be seen in Figure 1A, at the start of each trial of the imagery condition, a word cue was presented at fixation for 1 s. This cue indicated which color the participant should imagine during the subsequent 9 s imagery interval. In the imagery condition, the background remained black, but during the background luminance condition, the luminance of the background ramped over a period of 2 s, remained at full brightness for 5 s, and then ramped off for 2 s. After the imagery interval, a colored rivalry stimulus was presented for 1 s followed by a 1 s interval. Hence, there was a 2 s response window for each trial. Participants were required to report the dominant color by pressing the corresponding numbered keys on the keyboard within the response window: "1" stood for red, green, or blue, depending on the block being tested; "3" stood for cyan, violet, or yellow, depending on the block being tested; "2" stood for an equal mixture of the two colors. Rivalry alternations do not typically occur with brief presentations. However, in the event that they did, participants were instructed to report a temporal average (i.e., if the dominance duration was the same for red and green, participants were asked to report this as a mixed percept). Once a key was pressed or no key was pressed within the response window, the response window ended, and the 2 s intertrial interval would start.

In the weak perception condition, the word cue presented at fixation was "FOCUS." This word cue indicated to the participants that they should not attempt to generate any mental imagery during the imagery period. During this interval, a perceptual

Gaussian was presented at fixation. The Gaussian was ramped on for approximately 1 s, remained at full brightness for 7 s, and was then ramped off for about 1 s. All other procedures were the same as the other two conditions.

As can be seen in Figure 2A, for Experiment 2 the same basic procedure was used with the following exceptions: only the red/cyan color pair and the imagery condition of Experiment 1 were used. The imagery cues were immediately followed by direction cues (a triangular fixation mark and circle outline) that indicated whether the participant should attempt to localize their color imagery at either 2.6° visual angle to the left or right of fixation. This imagery interval was 9 s. During the following binocular rivalry presentation, the rivaling color pair was presented in either the same location as the previous mental imagery or in the opposite location with equal probability. A binocular rivalry stimulus was presented for 1 s, followed by a 1 s blank screen. The participants were allowed to make their responses either during the binocular rivalry or while the screen was blank (response window = 2 s). All four combinations of imagery location and binocular rivalry location were tested an equal number of times during each experimental session. All other procedures were identical to Experiment 1.

Mock rivalry trials were included in both Experiments 1 and 2 to determine if the participants were influenced by a non-perceptual, cue-related bias. Such a nonperceptual bias would become apparent if participants indicated one color being dominant in the fake rivalry (non-rivalrous) stimulus in which both colors were of equal strength and were not undergoing binocular rivalry. Mock rivalry stimuli were created by combining the two colors together, so that the left half of the mock stimulus was one color and the right half was the other color. This mock stimulus was presented simultaneously to both eyes, ensuring that the two colors were perfectly balanced and no actual rivalry could occur.

Results

Data from Experiment 1 are shown in Figure 1B. This figure illustrates the average perceptual bias for the three conditions with 0.5 being chance-level performance given the two randomized imagery cues. Percentages of equal mixed-color responses were very low (mean 0.5% of trials), and these responses were excluded from the data analysis. Priming for imagery trials with a dark background was significantly greater than chance (0.5), $t(8) = 3.46$, $p = 0.0086$ (far left bar, Figure 1B). However, imagery with an illuminated background was not found to produce a bias signifi-
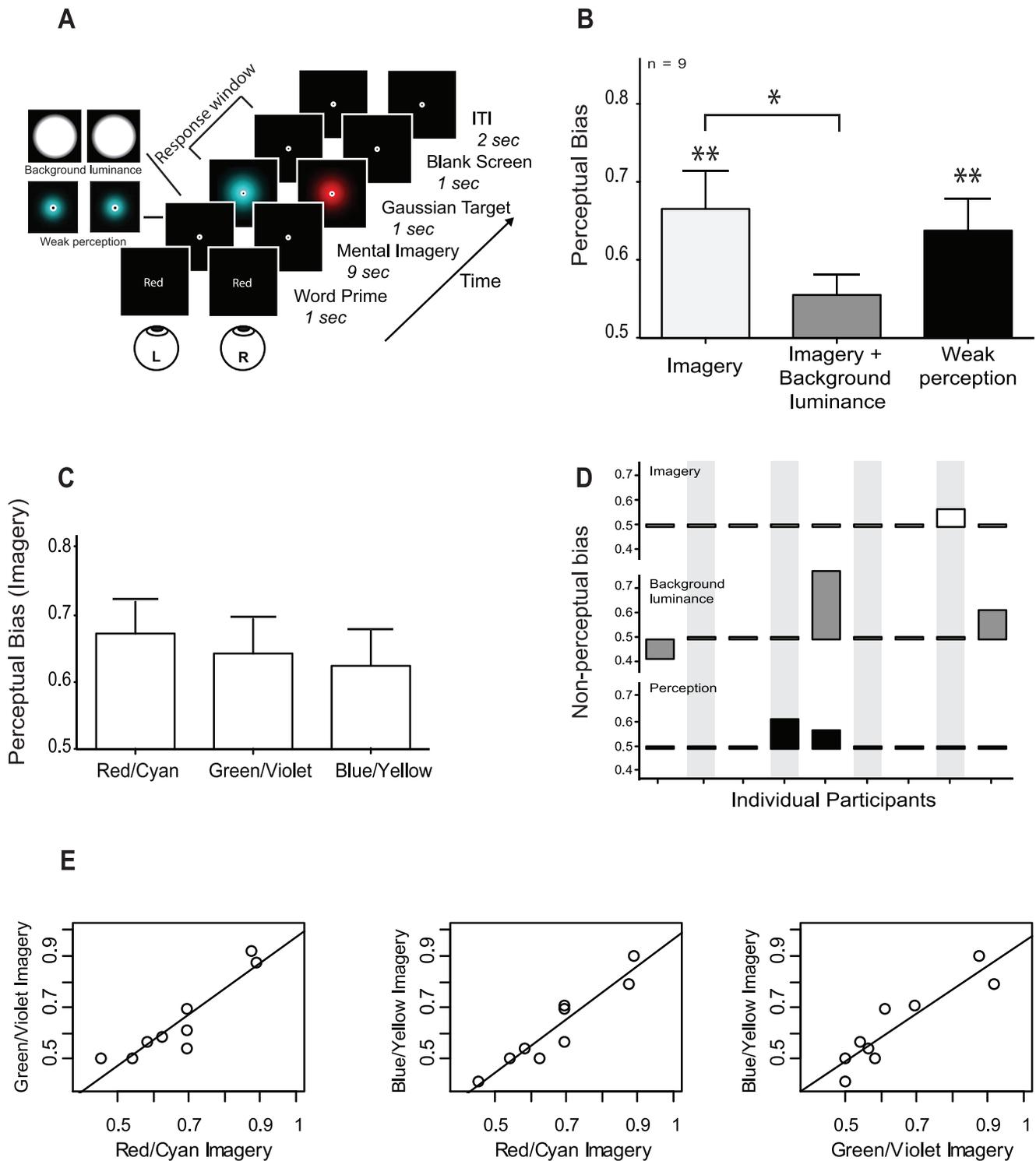
Figure 1. A: Individual trial timeline for Experiment 1. B: Average perceptual biases for the three conditions. The mean values of the three conditions were $M_{imagery} = 0.66$, $M_{background\ luminance} = 0.56$, $M_{weak\ perception} = 0.64$. C: Average perceptual biases of the three color pairs, $M_{red/cyan} = 0.67$, $M_{green/violet} = 0.64$, $M_{blue/yellow} = 0.62$. All error bars show +1 *SEM*. D: Average non-perceptual bias for each individual participant within each experimental condition. Averages different from 0.5 are indicative of possible bias. E: Correlations between the perceptual biases for the imagery conditions of the three color pairs in Experiment 1.*$p < 0.05$, ** $p < 0.001$
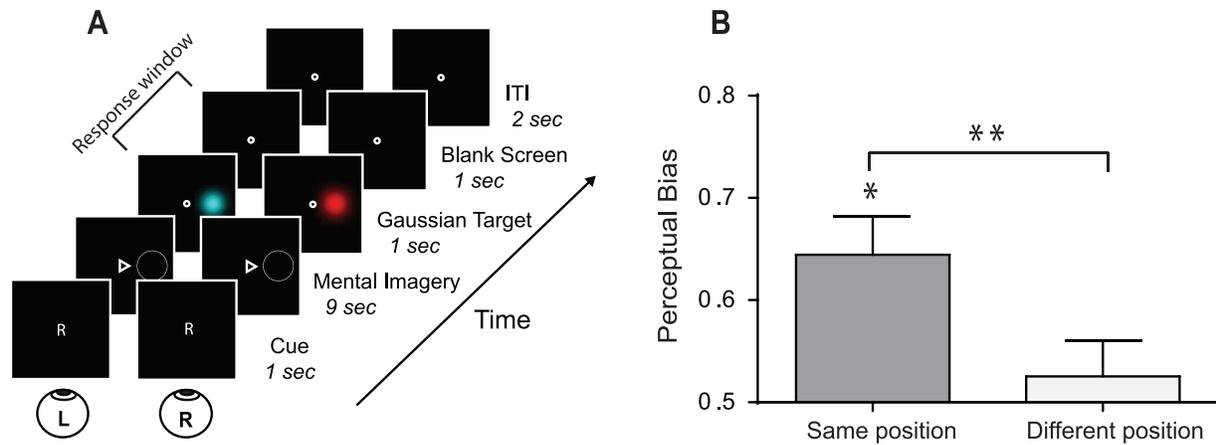
A

B

Figure 2. A: Individual trial timeline of Experiment 2. B: Average perceptual biases for the two conditions in Experiment 2. Error bars show +1 *SEM*.** $p < 0.001$

cantly different from chance (0.5), $t(8) = 2.23$, $p = 0.056$, and was significantly different from the dark background condition $t(8) = 2.59$, $p = 0.032$. For the weak perception condition, similar to the non-illuminated condition, priming was also greater than chance, $t(8) = 3.48$, $p = 0.0073$ (Figure 1B; far right bar). Here, as in previous publications, voluntary mental images prime or facilitate subsequent perception, much like weak sensory stimuli.

These results suggest that mental imagery of pure colors can have a priming effect on subsequent binocular rivalry, and the weak perception of color has similar effects to that of mental imagery. Adding passive luminance to the background only during the imagery-generation period and not during the rivalry display attenuated the imagery-priming effect. These results suggest that perceptual processes occurring during the imagery-generation period are responsible for the observed priming effect on subsequent rivalry. In all conditions, as in previous studies (Keogh & Pearson, 2011; Pearson et al., 2008; Pearson et al., 2011; Sherwood & Pearson, 2010), there were an equal number of both imagery cues, which were shuffled across each block of trials. Such randomized cues give us a measure of imagery strength unbiased by any effects of intermittent rivalry stabilization (Pearson & Brascamp, 2008) or any eye/luminance imbalance as well as eliminating potential systematic influences of afterimages from binocular rivalry.

Figure 1C shows the perceptual bias for imagery separated into the three color pairs of the rivalry stimuli. The perceptual biases are all significantly greater than chance level ($ps < 0.05$). In addition, there is no significant difference in the magnitude of the color priming effects between the three color pairs ($F = 2.854$, $p = 0.09$). We also looked at rivalry dominance independent of the imagery cues. No significant difference was found between different colors ($F =$

1.804, $p = 0.19$). These results indicate that there was no bias for dominance of a specific color.

Figure 1D shows the mock rivalry data for each individual participant in Experiment 1. The mock rivalry stimuli are non-ambiguous, stable stimuli; hence, there is no way that imagery can have a suprathreshold perceptual effect on them. As the mock stimuli consist of equal parts of each color, the correct response from a subject is the "mixed" key. Any bias to report the mock stimuli as unitary, e.g., red, might suggest a nonperceptual or criterion bias. We analyzed this nonperceptual bias by coding veridical "mixed" responses to the mock trials as 0.5, and responses that matched the cued pattern were coded as 1, and responses opposite to the cued grating were coded as 0. While a few participants did report some bias for the stable, non-rivalrous mock trials, overall, the decisional or criterion biases ($M_{imagery} = 0.51$, $M_{luminance} = 0.53$, $M_{perception} = 0.52$) were not statistically significant (t tests: $ps > 0.05$). This result remains the same when the two authors' data are excluded. These results suggest that a decisional or criterion bias is not responsible for the data in Experiment 1 and confirmed that the priming effect in binocular rivalry is due to color imagery.

Figure 1E shows scatter plots of perceptual bias for imagery of the three color pairs. Analysis shows that all three correlations were significant ($ps < 0.001$). This indicates that individual imagery strength seems consistent across the different color pairs.

In Experiment 2, we examined whether color imagery had similar location-specificity to that previously demonstrated with compound colored Gabor stimuli (Pearson et al., 2008). Figure 2B shows the data for imagery priming when imagery and subsequent rivalry are at the same and different locations. Priming for the same location was significantly greater than chance, $t(5) = 3.94$, $p = 0.011$, replicating the results of

Experiment 1 in the periphery. However, when the imagery and test stimuli were presented to different locations, the perceptual bias was not significantly different from chance, $t(5) = 0.75$, $p = 0.49$, and a significant difference was also found between the two conditions, $t(5) = 4.23$, $p < 0.01$. These results indicate that voluntarily generated pure color imagery can be location-specific over a distance of $\sim 5°$ of visual space.

Discussion

The results demonstrate that voluntary mental imagery of pure color can bias subsequent perceptual dominance in binocular rivalry. Increasing the luminance of the background during the imagery-generation period or displaying the rivalry stimulus at a different visual location greatly attenuated this bias. These data suggest that the perceptual bias effect on subsequent rivalry is specifically due to low-level sensory processes occurring during the imagery period and not due to other factors, such as voluntary control of the rivalry alternations. In addition, weak perceptual stimuli displayed bias-priming effects on subsequent rivalry much the same as voluntary imagery. The current results suggest that color imagery and color perception involve largely similar mental processing. These data are consistent with previous findings using compound multi-feature imagery stimuli (Lewis et al., 2013; Pearson et al., 2008).

In previous research, mental imagery has mostly been treated as a general trait-like, cognitive/perceptual process or ability, but potential differences between distinctive imagery features have largely been ignored. In the current study, we investigated one specific feature of visual imagery in isolation: color. Previous studies on color imagery used tasks such as color naming and color comparison in order to assess a participant's color imagery (Howard et al., 1998; Shuren et al., 1996). It could be argued that in these experiments the mental imagery generated by the participants contained all the same sensory information as the physical objects, such as shape, orientation, texture, and luminance. However, whether color information was a part of the mental image could not be confirmed as these kinds of tasks could also be based entirely on semantic knowledge (McNorgan, 2012). For example, Howard et al. (1998) used a color-comparison task but did not find activation in area V4, a brain area thought to be involved in color imagery (McNorgan, 2012). This lack of a response in area V4 could be, in part, due to participants performing the task using semantic object knowledge rather than a voluntary sensory representation.

Using the binocular rivalry method, color could be treated as an independent perceptual element of visual imagery rather than one integrated with other features. The use of binocular rivalry to study mental imagery was first employed by Pearson et al. (2008) to assess the perceptual nature of mental imagery. However, the stimuli used in this study and others (Keogh & Pearson, 2011; Pearson et al., 2011; Rademaker & Pearson, 2012; Sherwood & Pearson, 2010) consisted of Gabor patches that had multiple visual features, including color, orientation, and spatial frequency. In the current study, binocular rivalry stimuli only differed in color. By measuring the priming effects on perceptual dominance during binocular rivalry, we have shown that it is possible to not only generate mental imagery for color but that this imagery can also influence color perception.

Similar to color imagery, the passive perception of weak (low-luminance) colored Gaussians was found to bias perceptual dominance of subsequent binocular rivalry. Previous work has shown that this perceptual priming of subsequent rivalry is contingent on the contrast and luminance of the prior stimulus (Brascamp, Knapen, Kanai, van Ee, & van den Berg, 2007; Pearson et al., 2008). As the visual energy of the prior stimulus is increased, the facilitative priming effect turns into the opposite suppressive effect on subsequent rivalry—the other pattern is dominant. These data suggest that voluntary imagery on the whole is acting much like weak or low-energy perceptual stimuli. How does weak perception and imagery facilitate or prime subsequent perception? This is an interesting question that gets at the core of priming, a phenomenon documented across a huge range of stimuli and situations (Koutstaal et al., 2001; Pearson & Brascamp, 2008; Pearson et al., 2008; Schacter, Dobbins & Schnyer, 2004). What is interesting here is that we are measuring what seems to be a form of perceptual priming without any relevant afferent perceptual stimulation.

To rule out the possibility that the observed effects were caused by the presentation of the word cues at the beginning of each test trial (Burt, 1994; McClain, 1983), a background luminance condition and mock trials were included. When the background luminance was present during the imagery-generation period only, the bias effect on subsequent rivalry was greatly diminished. As the luminance only increased during the actual imagery-generation period, and not during the rivalry presentation, this finding suggests the priming effects we observed transpired specifically during this imagery-generation period. Previous work has demonstrated that attentional effects on subsequent rivalry are immune to background luminance. Hence, the attenuation of priming due to background luminance here suggests these effects are not driven by visual

attention. In addition, our non-rivalrous mock trials did not show any significant priming/decisional bias. This suggests that the criterion for reporting dominance in rivalry was not strongly driven by the word cues.

The perceptual biases in Experiment 1 showed large individual differences in imagery strength (see Figure 1E), which indicates that participants probably differ in their color imagery strength. Because of the method employed in previous color imagery studies, it was not possible to quantitatively evaluate mental imagery strength, and hence, individual differences could not be analyzed. In the current data, the strength of color imagery does seem fairly stable between the different color pairs. This suggests that one common mechanism was used to generate imagery for all color pairs. However, because we only tested color imagery in set pairs and not individually, it remains difficult to draw strong conclusions about mechanistic differences between imagery of different colors.

Experiment 1 confirmed that individuals could generate a form of pure color imagery. So why didn't the data in Pearson et al. (2008) show evidence of an effect of color imagery? One answer could be that when color is combined with orientation in an imagined or perceptual stimulus, such as a colored Gabor pattern, the effect of orientation is simply stronger than color. Hence, in a compound configuration, orientation information will "win" over color. Future work should carefully investigate any differences in voluntary imagery across the different visual features.

Experiment 2 revealed that color imagery is location-specific in a similar manner to visual perception. The perceptual bias observed in Experiment 1 was replicated in this experiment when the imagery and rivalry stimuli were presented at the same location, but the bias was lost when they were presented to different visual locations. The behavioral finding is also in line with findings from brain-imaging studies. Tootell, Hadjikhani, Mendola, Marrett, & Dale (1998a) used fMRI to show that early retinotopic visual cortex involving areas V2 and V3 are recruited during a mental imagery task. Other studies have shown that primary visual cortex (V1) is involved in visual imagery (Kosslyn et al., 1999; Kosslyn & Thompson, 2003). McNorgan (2012), in a meta-analysis, concluded that V4 is the most likely candidate area responsible for the generation of color imagery. Based on these brain-imaging data, we conclude that it may well be the retinotopic property of these visual areas that leads to the location-specificity we see for color imagery.

In conclusion, the current study replicates the findings of previous studies of mental imagery that used compound visual stimuli (Pearson et al., 2008; Pearson et al., 2011; Sherwood & Pearson, 2010) by using pure color stimuli. These results demonstrate that imagery of pure colors (without form structure) can influence subsequent color perception locally in retinotopic space. Like other forms of visual imagery, it appears that mental imagery of color can be pictorial/retinotopic in nature. It will be interesting for future research to utilize this method with other visual features in order to probe the unitary versus compound nature of visual imagery.

Acknowledgements

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