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Exploring the functional nature of synaesthetic colour: Dissociations from colour perception and imagery

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ABSTRACT

Individuals with grapheme-colour synaesthesia experience anomalous colours when reading achromatic text. These unusual experiences have been said to resemble 'normal' colour perception or colour imagery, but studying the nature of synaesthesia remains difficult. In the present study, we report novel evidence that synaesthetic colour impacts conscious vision in a way that is different from both colour perception and imagery. Presenting 'normal' colour prior to binocular rivalry induces a location-dependent suppressive bias reflecting local habituation. By contrast, a grapheme that evokes synaesthetic colour induces a facilitatory bias reflecting priming that is not constrained to the inducing grapheme's location. This priming does not occur in non-synaesthetes and does not result from response bias. It is sensitive to diversion of visual attention away from the grapheme, but resistant to sensory perturbation, reflecting a reliance on cognitive rather than sensory mechanisms. Whereas colour imagery in non-synaesthetes causes local priming that relies on the locus of imagined colour, imagery in synaesthetes caused global priming not dependent on the locus of imagery. These data suggest a unique psychophysical profile of high-level colour processing in synaesthetes. Our novel findings and method will be critical to testing theories of synaesthesia and visual awareness.

1. Introduction

Studying colour perception epitomises the challenge of understanding the mechanisms that underpin the contents of consciousness – how is the subjective experience of colours created from variations in the wavelengths of light? Grapheme-colour synaesthesia provides a unique window into the mechanisms by which the brain creates colour. People with this unusual condition have involuntary colour experiences triggered by reading achromatic letters and numbers. The relationship of synaesthetic colour with 'normal' colour (triggered by relative wavelengths of light) and imagined colour (generated at will) is a topic of much neural and psychophysical research. Attempts to characterise the nature of synaesthetic colour have been faced with the classic difficulties of studying conscious experience. Most of the data come from subjective reports of perceptual judgements that are prone to post-perceptual cognitive strategies, contextual influences, or paradigms that do not have appropriate control conditions, which are confounded by decisional bias. Other 'proxy' measures of synaesthesia, such as the synaesthetic congruency/Stroop effect, reflect the involuntary nature of synaesthetic colour rather than its qualia *per se* (for review of relevant evidence, see Chiou & Rich, 2014; Mattingley, 2009).

Although synaesthetes readily differentiate different forms of colour experiences, many describe synaesthetic colour as vivid as 'normal' colour (Rich, Bradshaw, & Mattingley, 2005). This apparent resemblance between synaesthetic and actual colour has led to prominent hypotheses that synaesthetic colours involve a key functional cortical area for colour perception – the ventral occipitotemporal V4 (Hubbard, Brang, & Ramachandran, 2011; Hubbard & Ramachandran, 2005; Rouw, Scholte, & Colizoli, 2011). Some studies claim that synaesthetic colours trigger V4 activation (or *in the vicinity of* V4) in some synaesthetes (e.g., Brang, Hubbard, Coulson, Huang, & Ramachandran, 2010; Dovern et al., 2012; Hubbard, Arman, Ramachandran, & Boynton, 2005; Tomson, Narayan, Allen, & Eagleman, 2013; Van Leeuwen, Den Ouden, & Hagoort, 2011; van Praag, Garfinkel, Ward, Bor, & Seth, 2016), while others have failed to find similar effects (e.g., Hupé, Bordier, & Dojat, 2012; Rich et al., 2006). In light of the

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discrepancy, Rouw et al. (2011) conducted a review highlighting the variability between studies with fewer than half showing V4 activation in synaesthetes. Similarly, in a critical review, Hupé and Dojat (2015) challenged all V4 activation findings in the synaesthesia literature on the grounds of statistical power and liberal threshold, concluding that there is *no* evidence whatsoever for the involvement of V4. Thus, despite the ubiquity of claims that synaesthesia induces V4 activity, there are significant concerns regarding the robustness of evidence, creating doubt about whether synaesthesia does actually depend on the same areas as 'normal' colour perception.

In fact, behavioural research has demonstrated marked differences between synaesthetic and 'normal' colour. For example, 'normal' colour captures visual attention when it is the singly distinctive feature, leading to efficient visual search (pre-attentive pop-out: Treisman & Gelade, 1980). Although synaesthetic colour has been seen to bestow advantage for some synaesthetes in visual search (Laeng, Svartdal, & Oelmann, 2004; Laeng, 2009; Palmeri, Blake, Marois, Flanery, & Whetsell, 2002; Ramachandran & Hubbard, 2001), such advantage is not always replicated (Edquist, Rich, Brinkman, & Mattingley, 2006) and seems to reflect higher-level strategies (e.g., grouping) rather than pop-out (Rich & Karstoft, 2013; Ward, Jonas, Dienes, & Seth, 2010). Additionally, perceiving 'normal' colour is affected by its surroundings (chromatic contrast: Hurlbert & Wolf, 2004), but such contrast phenomena do not influence synaesthetic colour (Erskine, Mattingley, & Arnold, 2012; Nijboer, Gebuis, te Pas, & van der Smagt, 2011). Finally, Arnold, Wegener, Brown, and Mattingley (2012) found that adjusting a colour patch to match synaesthetic colour (induced by either visually or aurally presented letter or number) and recalled colour (perceptual memory of a colour seen earlier) were all less precise than matching to a 'normal' colour currently in view. These data suggest that synaesthesia is closer to *recollecting* colour than to *perceiving* colour, at least in precision.

Interestingly, other studies looking at individual data have suggested that synaesthetic colours interact with 'normal' colours to influence perception. Most relevant to the current study, Kim, Blake, and Palmeri (2006) tested two synaesthetes using a binocular rivalry task that tested whether synaesthetic colour might enable grouping of separate elements into a unified global percept, similar to 'normal' colour stimuli that form a conjoint entity and prolong perceptual predominance. While undergoing binocular rivalry, their two synaesthetes viewed graphemic stimuli and reported their dominant percept. The authors found that both synaesthetic and 'normal' colour seemed to increase the amount of perceptual grouping and concluded that synaesthetic colours can behave like 'normal' colours. In the present study, we build on this intriguing finding with a novel rigorous approach that allows us to explore the nature of the synaesthetic colour and compare it to the effects of 'normal' and voluntarily imagined colour.

We present evidence that synaesthetic colour impacts conscious vision in a manner unlike perceiving 'normal' colour and with intriguing differences from non-synaesthetes performing voluntary colour imagery. We devised a paradigm to assess the influences of synaesthetic colour on vision during binocular rivalry. Our novel method allowed us to gauge whether the impact is facilitatory or suppressive, whether the effect occurs locally at the inducer (letter) location or spreads globally to other parts of the visual field, and whether it differs from perception and imagery. Specifically, we know that 'normal' colour experiences are strongly constrained to the patch of colour reflecting those wavelengths of light. Thus, we anticipate its effect on binocular rivalry should occur within the area where the 'normal' colour stimulus is located. However, it is unclear whether synaesthetic colour would be analogously confined to the location at which the inducing grapheme is located or whether it would show a 'spillover' effect to other locations. Thus, there may be crucial differences in terms of their reliance on location. In Experiment 1, we find that synaesthetic and normal colours have qualitatively different influences on subsequent conscious perception. In Experiment 2, we replicate our synaesthetic effect, and additionally show that controls do not show the same effects from achromatic graphemes, demonstrating it is specific to synaesthetes. In Experiment 3, we find that, unlike voluntary colour imagery, the synaesthetic effect on subsequent binocular rivalry is not disrupted by sensory luminance-level perturbation. In Experiments 4A and 4B, we find that attenuating synaesthesia through high-level cognitive interference during the elicitation of synaesthetic colour reduces its effect on subsequent binocular rivalry, consistent with previous reports about the importance of attention for evoking synaesthesia (e.g., Rich & Mattingley, 2010). Finally, in Experiment 5, we find that synaesthetes show qualitatively different effects when doing a voluntary colour imagery version of the binocular rivalry task, relative to controls performing the same task and from previous reports of voluntary colour imagery. This may reflect anomalous imagery in the synaesthesia group, or the combination of normal voluntary imagery with additional synaesthetic experiences.

2. General method

2.1. Participants

We tested 14 participants with grapheme-colour synaesthesia (mean age ± SD: 32 ± 14 years, 11 females, 12 native speakers of English, 2 native speakers of Mandarin; Experiment 1, $n = 6$; Experiment 2, $n = 10$; Experiment 3, $n = 8$; Experiments 4A & 4B, $n = 10$; Experiment 5, $n = 6$). Some synaesthetes participated in more than one experiment, summarised in Table S1 of the online supplemental information (SI); also see SI for discussion regarding the categorisation of synaesthetes into subgroups based on subjective descriptions. The number of participants varies somewhat across the experiments due to availability at the time of recruitment. Previous imagery studies using the same techniques as ours ranged in sample size between 5 and 20 participants (e.g., Chang, Lewis, & Pearson, 2013; Pearson, Clifford, & Tong, 2008; Pearson, Rademaker, & Tong, 2011; Sherwood & Pearson, 2010), suggesting our sample sizes, albeit small, give a reasonable chance of detecting effects. All synaesthetes completed a standard questionnaire, used in previous studies (Mattingley, Rich, Yelland, & Bradshaw, 2001; Rich & Karstoft, 2013; Rich et al., 2005), that covers personal and demographic details and experiences of synaesthesia. We also tested non-synaesthetic controls in Experiments 2 and 5. In Experiment 2, we compared 10 controls with 10 synaesthetes; the two groups were matched on sex, age, and native language (controls' age: 31 ± 12 years old, 8 females, 8/2 native speakers of English/Mandarin). In Experiment 5, we matched controls to 6 synaesthetes using two different sets of criteria. In our demographic-match group, 12 controls (2 for each of the 6 synaesthetes) were matched on demographic details (controls' age: 34 ± 4 years, 10 females, all native speakers of English). In our imagery-match group (non-overlapping with the demographic controls), we selected 12 controls from a larger sample of 30 participants based on the magnitude of their imagery priming in one specific condition of the voluntary mental imagery experiment (for details, see the Methods of Experiment 5). All participants were naïve to the purpose of the study and reported having normal or corrected-to-normal visual acuity and colour perception. All synaesthetes were recruited via the database of Synaethesia Participant Register of Macquarie University; all controls were recruited from the community/network of the University of New South Wales. We checked with all controls that they had no synaesthetic experiences. All gave informed consent before participating and received payment for their participation. The study was approved by the local advisory panel for human research ethics.

2.2. Synaesthetic colour matching and assessment of consistency

All synaesthetes completed a grapheme-colour matching task to reveal their idiosyncratic grapheme-colour associations and were retested at a later point, allowing us to gauge the consistency of their