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**Color processing in synesthesia: What synesthesia can and cannot tell us
about mechanisms of color processing.**

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Abstract

Synesthetic experiences of color have been traditionally conceptualized as a perceptual phenomenon. However, recent evidence suggests a role of higher order cognition in the formation of synesthetic experiences. Here we discuss how synesthetic experiences of color differ from and influence veridical color processing, and how non-perceptual processes such as imagery and color memory might play a role in eliciting synesthetic color experience.

Introduction

Synesthetes experience everyday life very differently to typical individuals. For them, words can have distinctive flavors, colors can accompany sounds, or days of the week can be represented in intricate spatial arrangements (Ward, 2013). Synesthesia is defined as a condition where stimulation of one sensory modality elicits involuntary additional percepts within the same or different modality (Sagiv, 2004). For instance, in grapheme-color synesthesia achromatic letters or numbers (inducers) trigger secondary color experiences (concurrents). While many types of synesthesia have been identified so far (e.g. Simner, Mayo, & Spiller, 2009; Ward, Banissy, & Jonas, 2008; Simner & Ward, 2003), grapheme-color is one of the most common forms of synesthesia (Ward, 2013), therefore much of our discussion will involve findings concerning this synesthetic sub-type.

Although many prominent theories of synesthesia advocate it to be a perceptual phenomenon elicited by sensory input (Ramachandran & Hubbard, 2001b; Grossenbacher & Lovelace, 2001), several findings support the notion that construing synesthesia in purely perceptual terms cannot fully describe the nature of this condition. Here we discuss this evidence to further elucidate to what extent synesthetic color experiences are perceptually based. Specifically, we first discuss different theoretical models of synesthesia as well as the mechanisms underlying aspects of synesthetic and veridical color processing. Subsequently we examine the nature of synesthetic inducers and how non-perceptual processes such as imagery and color memory might play

a role in eliciting synesthetic color experiences. We then discuss how synesthetic color can inform our knowledge on typical color processing.

1. Neural basis of synesthesia for color

Three influential hypotheses of the mechanisms underlying synesthesia are the cross-activation (Ramachandran & Hubbard, 2001b), cortical disinhibition (Grossenbacher & Lovelace, 2001; Cohen Kadosh & Walsh, 2008) and the re-entrant feedback theory (Smilek, Dixon, Cudahy & Merikle, 2001). The cross-activation model states that increased connections between neighboring brain areas such as the visual word form area (VWFA) and color sensitive regions of the brain (e.g. hV4) provide the basis for synesthetic experiences. Recent cross-activation accounts also highlight an important role of attentional processes located in the parietal lobe, which allow for binding information from these two areas into one coherent percept (Hubbard, Brang, & Ramachandran, 2011).

Disinhibition accounts advocate that a lack of inhibition from multisensory (Grossenbacher & Lovelace, 2001) or executive control regions (Cohen Kadosh, Henik, Catena, Walsh, & Fuentes, 2009) to unisensory brain areas is the source of synesthesia. In a related context it has also been suggested that synesthesia arises as a consequence of local differences in cortical excitation through mechanisms akin to perceptual unmasking (Cohen Kadosh & Henik, 2007; Cohen Kadosh & Walsh, 2008).

The re-entrant feedback model (Smilek, Dixon, Cudahy & Merikle, 2001) suggests a crosstalk between form and color sensitive brain regions but at the same time highlights the importance of top-down processes exerted by feedback connections from brain regions involved in conceptual representation to those involved in color processing, thus emphasizing the essential role of the activation of the conceptual representation of the inducer (grapheme) in the elicitation of the synesthetic experience of color concurrent.

While these different theoretical models can explain the mechanisms underlying synesthesia construed as a perceptual condition, their ability to account for the conceptual phenomena of synesthetic experiences is not uniform. The cross-activation theory (Ramachandran & Hubbard, 2001b) acknowledges the involvement of top down mechanisms in the binding of the inducer and concurrent, however it does not regard this process to play a role in evoking synesthetic experiences. Similarly, the disinhibited feedback theory does not consider the possibility of purely concept driven synesthetic concurrents (Grossenbacher & Lovelace, 2001). On the other hand, the re-entrant model postulates that top down processes such as categorization of an inducer play an essential part in the elicitation of the synesthetic experiences (Smilek, Dixon, Cudahy & Merikle, 2001) and as such can accommodate the findings of conceptually induced synesthesia.

To examine these models, one stream of research has investigated if synesthesia is associated with structural brain differences in color relevant brain areas. Using diffusion tensor imaging technique (DTI) Rouw and Scholte

(2007) found synesthesia to be linked with increased structural connectivity in the right inferior temporal cortex. Others, however, failed to find similar results (e.g. Jancke, Beeli, Eulig, & Hanggi, 2009; Hupé, Bordier, & Dojat, 2012). A similar pattern has emerged from studies using voxel-based-morphometry (VBM) to examine gray matter differences between synesthetic who experience color as their evoked sensation; with some (Jancke et al., 2009; Weiss & Fink, 2009; Banissy, Stewart, Griffiths, Muggleton, Walsh, Ward, & Kanai, 2012), but not all (e.g. Hupé et al., 2012; Rouw & Scholte, 2010) studies reporting synesthesia to be associated with increased gray matter volume in brain areas linked to veridical color processing in typical adults. Notably, in the studies that do report gray matter differences in neural regions close to those previously associated with veridical color processing, the regions responding to color were not functionally localized in their subjects; given inter-individual variability in cortical color responsiveness it is therefore difficult to disentangle the exact relationship between brain structure and function.

The findings of functional neuroimaging studies are also inconsistent. Some fMRI studies report hV4 activation in response to both colored and achromatic stimuli inducing synesthetic color experiences (Hubbard, Arman, Ramachandran, & Boynton, 2005; Sperling, Prvulovic, Linden, Singer & Stirn, 2006). Hubbard and colleagues (2005) also found that the strength of hV4 activation to achromatic inducers in grapheme-color synesthetic was mediated by their performance on a visual crowding task where participants were required to identify an achromatic target grapheme presented in the

visual periphery and surrounded by other graphemes printed in black ink (the greater the activation, the better the performance; suggesting that real and synesthetic color processing might be driven by the same mechanisms). However, other studies failed to replicate these findings, putting in question the idea that these processes are analogous (Sinke, Neufeld, Emrich, Dillo, Bleich, Zedler & Szycik, 2012; Hupe et al., 2012; Rouw and Scholte, 2010). Indeed, recently the reliability of the findings suggesting that synesthetic color is handled by color-sensitive brain regions has been further undermined by Hupe and colleagues (2012) who pointed out that studies reporting functional neural activity in regions of the brain linked to color processing during the experience of synesthesia tended to apply liberal statistical thresholds. In their own fMRI study, Hupe and colleagues (2012) investigated whether the brain regions responsive to real color and those activated by synesthetic color overlapped in a group of grapheme-color synesthetes. Their findings indicated that none of the areas recruited in veridical color processing, which were individually identified for each of the participants by means of full retinotopic mapping, were activated by a synesthetic color; suggesting that it is unlikely that synesthetic and real color share identical neural mechanisms. In this regard, neuroimaging has struggled to clarify the extent to which synesthetic and veridical color processing rely on common or distinct mechanisms.

2. Is real color processing and synesthetic color the same thing?

Aside from neuroimaging, psychophysical studies have also been employed to investigate whether synesthetic color has the properties of the real color. A

number of psychophysical studies have demonstrated that synesthetic color does not produce the color constancy effect (Erskine, Mattingley, & Arnold, 2012), simultaneous color contrast (Nijboer, Gebuis, Te Pas, & Van Der Smagt, 2011) or chromatic adaptation (Hong & Blake, 2008). Some reports have, however, indicated that synesthetic color and real color share common characteristics such as the ability to produce the watercolor illusion (Kim & Blake, 2005) or to influence bistable apparent motion (Kim, Blake, & Palmeri, 2006). Nevertheless, these results have been questioned on their methodological basis (Chiou & Rich, 2014) and thus need to be treated with caution.

Similarly, although initial reports suggested that synesthetic color might pop-out of a display of achromatic graphemes and thus facilitate the visual search just like real color does (Ramachandran & Hubbard, 2001a), subsequent studies failed to replicate this finding. While some found synesthetes to be better than controls on the visual search tasks (Palmeri, Blake, Marois, Flanery, & Whetsell, 2002; Laeng, Svartdal, & Oelmann, 2004; Ward, Jonas, Dienes, & Seth, 2010; Rich and Karstoft, 2013), their results indicated an involvement of attentional resources in this process thus refuting the possibility that synesthetic color is a result of low-level, pre-attentive processes and can pop-out like real color (Treisman and Gelade, 1980). It has also been suggested that implicit processing of visual stimuli is not sufficient for synesthetic concurrents to occur, and that only by consciously identifying the inducers it is possible to elicit them (Mattingley, Rich, Yelland, &

Bradshaw, 2001). Based on these findings it appears that the mechanisms underlying synesthetic and real color are not identical.

3. Percept or concept? - characteristics of an inducer

In order to further examine whether synesthetic color is a perceptual phenomenon other studies have sought to determine if physical characteristics of inducers would impact on synesthetic experiences of color. A number of studies reported that low-level physical features of inducers can influence synesthetic color experiences. For instance, high frequency fonts give rise to greater intensity of synesthetic colors compared to low frequency fonts (Ramachandran & Hubbard, 2003; Witthoft & Winawer, 2006). Similarly, upper case letters can produce more vivid color experiences than those printed in lower case (A vs a) (Witthoft & Winawer, 2006). It has also been shown that graphemes that are similar in shape (e.g., E, 3) compared to those which are not (e.g., E, X) can be colored in a similar fashion (Eagleman, 2010; Brang, Rouw, Ramachandran, & Coulson, 2011).

Although these reports suggest that visual properties of inducers might influence synesthetic experiences, other findings indicate that the appearance of inducers has little impact on synesthetic colors. For instance, an inducer typically elicits different synesthetic colors depending on its context, e.g. whether it is perceived as a letter or a digit like in case of the grapheme 'l' (Dixon, Smilek, Duffy, Zanna, & Merikle, 2006). Similarly, different physical variants of the same letter (e.g., a, **a**, *ℒ*, **ℒ**) tend to consistently produce the

same synesthetic color (Grossenbacher & Lovelace, 2001). Additionally, although with some exceptions (e.g. see Arnold, Wegener, Brown & Mattingley, 2012; Simner, 2012) commonly the modality of the inducer does not seem to play an important role as synesthetic report color concurs irrespective of whether the inducer is heard, read, or merely thought about (Rich, Bradshaw & Mattingley, 2005).

These findings demonstrate that while occasionally purely perceptual features of an inducer might influence concurrents, for a number of synesthetes it is higher level cognitive constructs that elicit color experiences; leading some to suggest that synesthesia is in fact a form of 'ideasthesia' (Jürgens & Nikolic, 2012)

4. Can a color concurrent be experienced in the absence of an inducer?

The aforementioned studies suggest that it is the conceptual rather than perceptual dimension of the inducing stimulus that triggers synesthetic experiences of color. This idea has been addressed in a number of different studies that sought to determine if it is necessary for the inducer to be physically present in order to produce synesthetic experiences.

For example, in a study carried out by Dixon, Smilek, Cudahy and Merikle (2000) a synesthete was visually presented with a simple arithmetic task such as e.g. '2+5 =' followed by a color patch. The task was to first name the color patch and to subsequently give a solution to the problem. The authors

reported that the synesthete was quicker at naming the color patch when it was congruent with the synesthetic color of the solution and slower when these colors did not match. These results have been subsequently replicated in the auditory domain in a study carried out by Jansari, Spiller and Redfern (2006), where participants heard rather than saw examples such as '2+5 = yellow'. These findings suggest that it is the concept of the inducer rather than physical properties that triggers synesthetic experiences of color.

Additionally, implicit bidirectionality has been demonstrated in many studies. For instance, Brugger et al., (2004) reported that digit-color synesthetes compared to controls had faster left-hand responses to colors associated with small digits and faster right-hand responses for colors representing large numbers, suggesting that these synesthetes could access numerical magnitude information through their color associations. Similar results have been found in the domain of lexical processing. For example, Weiss et al. (2009) asked grapheme-color synesthetes and controls to perform a word completion task where either high or low-frequency words could be generated by inserting a different first letter. A color patch consistent with the individual synesthetes' color concurrents replaced the space where first letter would appear, biasing them to generate low-frequency words significantly more often than the control participants. This was interpreted as evidence for implicit bidirectional priming. Behavioral data demonstrating bidirectional nature of synesthetic experience has also been supported by neuroimaging evidence which suggested that color can activate the number form area of the fusiform gyrus in a grapheme-color synesthete, for whom synesthesia

typically manifests itself in a uni-directional fashion i.e. digits elicit color concurrents (Cohen Kadosh, Cohen Kadosh & Henik, 2007). Recently bidirectional priming in synesthesia has also been demonstrated across different sensory modalities (vision and audition; Paffen, Van der Smagt and Nijboer, 2015), further supporting the claim that although subjective synesthetic experiences are typically reported to follow the unidirectional path from the inducer to the concurrent, it is possible to induce priming in the opposite direction. More importantly, these findings suggest that synesthesia relies on higher-order representations rather than low-level sensory processing.'

Further evidence in support of the idea that it is possible to elicit synesthetic concurrents in the absence of a sensory inducer has been provided by Nikolić, Juergens, Rothen, Meier, and Mroczko (2011), and Rothen et al. (2013), who reported a new form of synesthesia where swimming styles evoke color concurrents. Their findings suggest that the proprioceptive input associated with different swimming styles is not essential to elicit synesthetic colors, instead the mere concept of it, induced with photographs (Nikolić et al., 2011) or pictograms of different swimming styles (Rothen et al., 2013) is sufficient to evoke color concurrents.

Grapheme-color synesthesia might also be elicited in even more extreme circumstances. For instance, synesthetes who have lost their sight and thus have no means of visually processing the graphemes still report very vivid color experiences triggered by letters, numbers, words or Braille characters

(Steven & Blakemore, 2004). Neuroimaging studies using fMRI have further validated these subjective reports by demonstrating that listening to words inducing synesthetic color experiences in blind synesthetes is associated with activity in color sensitive brain areas (Steven, Hansen, & Blakemore, 2006; Niccolai, van Leeuwen, Blakemore, Stoerig, 2012). However, as the experimenters were not able to localize these brain regions there is no guarantee that the reported activation in color areas is actually related to veridical color processing. Although these findings were interpreted by Steven and colleagues (2006) as evidence for perceptual nature of synesthetic colors, others (Niccolai et al., 2012) suggested an alternative explanation, namely that synesthesia resembles object color knowledge and imagery.

5. Is synesthetic color imagined?

Synesthetes have previously been found to show enhanced self-reported imagery vividness measured with the Vividness of Visual Imagery Questionnaire (VVIQ) (Barnett & Newell, 2008). There is also evidence showing that high scores on VVIQ are associated with greater activation within the early visual system during mental imagery tasks (Cui, Jeter, Yang, Montague, & Eagleman, 2007). In a neuroimaging study conducted by Rich, Williams, Puce, Syngeniotis, Howard, Mcglone and Mattingley (2006) grapheme-color synesthetes and controls were asked to perform a voluntary color imagery task which required participants to make color judgements about objects in grey scale photographs. Participants were also shown letters inducing synesthetic colors and asked to perform a localization task. The aim

of this study was to examine neural mechanisms underlying color experiences arising in the absence of veridical color input. Their results indicated that voluntary color imagery was associated with hV4 activation both in synesthetes and non-synesthetes, while synesthetic color was linked to neural activity in the left medial lingual gyrus. These findings suggest that synesthetic and imagined color may be supported by different brain structures. Interestingly, in view of this others (e.g. Mattingley, 2009); Chiou and Rich, 2014) have suggested that previous reports of enhanced hV4 activation in synesthesia might in fact reflect mental imagery rather than a perceptual process. Further support for the idea of V4 activity being linked to imagery was provided by Sinke and colleagues (2012) who found no difference between synesthetes and controls in hV4 activation in response to colored and black letters and pseudo-letters, when both groups were matched in terms of scores on VVIQ. These findings suggest that synesthetic color is a separate phenomenon from real color perception, although it probably entails much more than mere imagination.

6. Is synesthetic color a memory?

The suggestion that synesthesia is a form of color memory is consistent with previous findings demonstrating that synesthetes are better than controls on tests of color recognition memory as well as memory tests inducing synesthetic experiences (Yaro & Ward, 2007; Mills, Innis, Westendorf, Owsianiecki, & McDonald, 2006; Rothen & Meier, 2010). There is also some evidence suggesting that grapheme-color synesthetes have enhanced

memory for stimuli that do not trigger their synesthesia (Ward, Hovard, Jones, & Rothen, 2013; Rothen, Meier, & Ward, 2012).

Results of structural neuroimaging studies using voxel-based morphometry also suggest that grapheme-color synesthetes, at least those classified as associators, have greater gray matter volume in the hippocampus and parahippocampal gyri, which are brain regions involved in memory processes. Functional imaging results confirmed these results by showing increased activity in these areas in the same group of synesthetes (Rouw & Scholte, 2010).

Rouw and Scholte (2010) found projector synesthetes to have structural differences in other brain regions (e.g. increased gray matter volume in V1) than those classified as associators, suggesting that experiencing internal vs external concurrents differs in terms of underlying neural substrates. Van Leeuwen, den Ouden and Hagoort (2011) reported bottom-up activation in projector synesthetes and top-down influences in associators determined using dynamic causal modelling, providing further evidence for the claim that differences in phenomenal experiences between projector and associator synesthetes are reflected in different neural mechanisms. Taking into account these individual differences, it is possible that the potential involvement of memory would appear more crucial to associator synesthetes.

The hypothesis that synesthesia involves recollection of color rather than actual color perception was directly tested in a study carried out by Arnold and

colleagues (2012). The authors recruited grapheme—color synesthetes who only experienced colors for read, but not heard inducers. In this experiment participants were presented both with printed and spoken graphemes. Using a color picker they had to adjust the color of the graphemes that triggered, or in case of the auditory condition, that would normally trigger synesthetic experiences if seen. Their results indicated no difference in the precision of the color matching between the two conditions, which was interpreted by the authors as evidence for the idea that automatically induced synesthetic color resembles color recalled from memory. In addition, they ran a control experiment which indicated that the precision of matching real visible colors was much greater to recollected colors. Their findings are consistent with previous reports indicating that the precision of color memory is much lower compared to real-time color perception (Knill & Richards, 1996). Taken together these results suggest that if triggered in real time or recalled from memory synesthetic color is subject to greater variability and less precision than real color perception. Therefore, synesthetic color appears to behave more like color memory than real color perception.

7. Can synesthetic color tell us anything about real color processing?

While synesthetic experiences might involve visual imagery or color memory, grapheme-color synesthesia has been shown to be linked to broader differences in perceptual processing. For example, psychophysical studies examining color processing of stimuli that do not evoke synesthesia have reported superior processing of color in synesthetes who experience color

concurrents (Banissy, Walsh, & Ward, 2009; Banissy, Tester, Muggleton, Janik, Davenport, Franklin, Walsh, & Ward, 2013; Yaro & Ward 2007; Arnold et al., 2012). For example, we have shown that color synesthetes outperform non-synesthetes on a visual search paradigm in which targets and distractors differ in a single color dimension (hue, saturation, or luminance), but do not differ when discriminating line orientation (Banissy et al., 2013).

Further, EEG findings suggest that synesthetes who experience color as their evoked sensation show perceptual processing differences to stimuli that bias parvocellular pathways (Barnett, Fox, Molholm, Kelly, Shalgi, Mitchell & Newell, 2008). In that study, Barnett and colleagues examined neural responses of linguistic-color synesthetes to Gabor patches varying in spatial frequency and stimuli of various luminance contrasts. Their results indicated that stimuli, which do not induce synesthesia, but selectively bias parvocellular pathways of the visual system (Derrington & Lennie, 1984; Kaplan, 1991), were associated with enhanced cortical responsiveness. These findings would appear to fit with evidence that synesthetes who experience color show heightened perceptual processing of color, however it is of note that the perceptual advantage in color processing shown by color synesthetes has been shown to be present for dimensions of hue, luminance, and saturation (Banissy et al., 2013); implying that synesthetes show perceptual processing advantages for stimuli that do not rely solely upon parvocellular projections (e.g.-Lee, Pokorny, Smith, Martin, & Valberg, 1990).

Another broader perceptual difference that we have recently observed in synesthetes who experience color as their evoked sensation are elevated motion coherence thresholds (i.e. a reduction in motion processing abilities; Banissy et al., 2013). Using a different group of participants from those that were found to differ on the color visual search task described above, we compared color synesthetes' and non-synesthetes' abilities to detect global motion direction using random-dot kinematograms. We observed reduced performance in synesthetes relative to non-synesthetes. We interpreted these findings in the context of principles that govern interactions between color and motion in non-synesthetes. Moreover, non-invasive brain stimulation experiments suggest that brain regions involved in motion and color processing (e.g. hV5 / MT and hV4) can mutually inhibit one another (Ellison, Battelli, Cowey, & Walsh, 2003; Walsh, Ellison, Battelli, & Cowey, 1998). For example, transcranial magnetic stimulation (TMS) to hV5 / MT results in enhanced color and form perception and simultaneous suppression of motion processing (Ellison et al., 2003; Walsh et al., 1998). This has been interpreted in the context of a competition for resources between motion and color areas in the visual system (Ellison et al., 2003; Walsh et al., 1998). We suggest that a bias towards color processing in synesthesia may mediate this interaction leading to heightened color, but reduced motion perception in synesthetes who experience color as their evoked sensation.

In this context, synesthesia may be useful to help inform us about principles that govern typical perceptual interactions. For example, the findings of increased color, but reduced motion processing in synesthetes who

experience color as their evoked sensation raises the question of the extent to which the perceptual profile that we observed in synesthetes is present in non-synesthetes. That is to say, if an individual has elevated color processing does this come at a cost for motion processing or vice versa? If so, this would suggest a clear way in which synesthesia may help to inform studies on typical visual processing (see McCarthy & Caplovitz, 2014 for a similar discussion).

Concluding remarks

While recent evidence suggest that the mechanisms involved in synesthetic colors resemble those involved in imagery and recollections of color, rather than those recruited when seeing real color, they by no means question the reality of synesthesia. There is an abundance of evidence suggesting that synesthesia is a percept-like, authentic, involuntary and automatic experience (Sagiv & Ward, 2006; Ward, 2013), however existing theories need to be refined in order to accommodate recent findings indicating that the mechanisms underlying this intriguing phenomenon extend beyond mechanisms of perceptual processing.

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