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## **The Long-Term Potentiation Model for Grapheme-Color Binding in Synesthesia**

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### **Abstract**

The phenomenon of synesthesia has undergone an invigoration of research interest and empirical progress over the past decade. Studies investigating the cognitive mechanisms underlying synesthesia have yielded insight into neural processes behind such cognitive operations as attention, memory, spatial phenomenology and inter-modal processes. However, the structural and functional mechanisms underlying synesthesia still remain contentious and hypothetical. The first section of the present paper reviews recent research on grapheme-color synesthesia, one of the most common forms of synesthesia, and addresses the ongoing debate concerning the role of selective attention in eliciting synesthetic experience. Drawing on conclusions of the first half, the paper's second half examines the various models proposed to explain the cognitive mechanisms behind grapheme-color synesthesia, and discusses the explanatory virtues of a new model suggesting that grapheme-color synesthesia is grounded in memory. The last section offers an examination of some of the broader philosophical implications of synesthesia.

### **Introduction**

Synesthesia is a condition in which input from one sensory or cognitive stream gives rise to experience in another sensory or cognitive stream, characterized by atypical binding of objects and properties (Rich and Mattingley, 2002; Brogaard, 2012). The most common forms of synesthesia involve associations between graphemes or words and visual experience, commonly known as grapheme-color synesthesia (Simner et al., 2006). In grapheme-color synesthesia, looking at or thinking about an achromatic letter or numeral gives rise to the sensation or thought that the numeral has a specific color with a highly specific hue, brightness and saturation. Synesthetic visual experiences, however, can take many forms, and some synesthetes may have visual experiences unique to their individual cases, such as experiences of complex geometrical patterns in response to mathematical formulas (Brogaard et al., 2012). In another common form of synesthesia, certain concepts can give rise to associated spatial phenomenology. An example would be synesthetes reporting days of the week as exhibiting a particular spatial arrangement across their perceptual field. Even further, although the most common forms of synesthesia elicit visual experiences, other variations can involve different

sensory modalities. For example, some synesthetes report the occurrence of touch sensations or gustatory experiences in response to auditory input.

Within the literature and study of synesthesia, the stimulus that gives rise to a synesthetic experience is known as the 'inducer' while the synesthetic experience itself is called the 'concurrent' (Grossenbacher and Lovelace, 2001). For each individual case of synesthesia, concurrents either may be projected out into space or merely associated with the inducer. Projection is experienced much like veridical perception, that is, the concurrents are experienced as located in the visual scene outside of the synesthete's mind (Dixon et al., 2004). While some synesthete who experience projection report seeing concurrents that float above their inducers, others describe experiences similar to seeing afterimages or phosphenes. Projection may also be experienced through other sensory modalities than vision. Some music-touch synesthetes experience touch sensations localized to specific regions of the body in response to music, and some motion-sound synesthetes experience sounds in response to visual motion.

Synesthetes who merely associate concurrents with their inducers describe seeing or feeling synesthetic concurrents with their "mind's eye" or simply "knowing" that inducers are strongly connected to or associated with their concurrents (Dixon et al., 2004). For example, grapheme-color synesthetes might view a black letter 'A' yet describe it as having the quality of the color red, even though they do not actually have the perceptual experience of seeing a red 'A'. Association between an inducer and its concurrent is analogous to the connection between smell and memory in non-synesthetic perceptual experience. In neurotypical individuals, a smell may elicit vivid visual imagery that is associated with that smell in memory. For example, the smell of a particular perfume may trigger a particular memory of a former friend who wore that perfume. The main difference between synesthesia and neurotypical memory association is that associations formed in synesthetes are idiosyncratic (Baron-Cohen et al., 1993). A synesthete typically has no explanation for why a concurrent becomes associated with a particular inducer.

A key characteristic of synesthesia regardless of its associator or projector form is that the synesthetic experiences are automatic, that is, synesthetes cannot suppress the association between an inducer and its concurrent. Just as the smell of fresh baked cookies would bring on thoughts of the cookies themselves, synesthetes cannot help but experience a synesthetic concurrent when an inducer is presented to them. The synesthetic association of inducers to concurrents also is stable over time (see **Fig. 1**) (Baron-Cohen et al., 1987). Although the color attributed to a particular grapheme in grapheme-color synesthesia may vary among synesthetes, within-synesthete measurements of test-retest reliability show that the particular grapheme-color associations are highly stable and consistent in over 80% of cases (Mattingley et al., 2001).

		Grapheme									
		0	1	2	3	4	5	6	7	8	9
Age (in years)	3	/	B	Y	G	P	R	Bl	W	Br	R
	4	/	B	Y	G	P	R	Bl	W	Br	R
	5	Go	B	Y	G	P	R	DBr	W	Br	R
	6	Go	B	Y	G	P	R	DBr	W	Br	R
	7	B	B	Y	G	P	R	Br	W	Br	R
	8	B	B	Y	G	P	R	Bl	W	Br	R
	9	B	B	Y	G	P	R	Bl	W	Br	R

**Figure 1:** Example of test-retest reliability of synesthetic experience in an associator grapheme-color synesthete from age 3 to 9 (B = blue, Bl = black, Br = brown, DBr = dark brown, G = green, Go = gold, P = purple, R = red, W = white, Y = yellow).

For cases of grapheme-color synesthesia, the Synesthesia Battery, an automated online test, allows for rigorous phenotyping of grapheme-color synesthetes along with many of the other forms of the condition ([www.synaesthete.org](http://www.synaesthete.org); Eagleman et al., 2007). Data generated within the test is used to determine whether a participant meets a certain threshold purported to indicate a high likelihood of synesthetic experience occurring in a subject. Since it is possible that some subjects who have genuine synesthetic experiences will fall below the threshold, the battery is not ultimately diagnostic, yet the difficulty of reaching the threshold ensures that only genuine synesthetes are identified as such for research purposes.

The Synesthesia Battery is made up of two sections: a color-choosing task and a color recall task. For the first task, a subject is presented with a grapheme for which she must choose a specific hue, brightness and saturation from a color palette representing over 17.6 million distinct choices. After the subject repeats the exercise three times for each grapheme (108 trials; graphemes A-Z and 0-9), a computer then calculates the geometric distance among the subject's answers in red, green and blue (RGB) color space. If the range of chosen RGB values for a grapheme is less than 1, the subject is scored as a synesthete for that grapheme. For the second task, the subject is presented with randomly ordered graphemes printed in the specific colors the subject chose. The subject must then quickly determine whether the grapheme has the color in question. Synesthetes tend to have no trouble answering correctly 90 percent of the time, and thus a score in excess of 90 percent further validates the score achieved in the prior color choosing task.

Even with the breadth of recent research and interest in synesthesia, the mechanism behind it is still currently unknown. Any accurate neural mechanism for synesthesia should accommodate at least two factors: whether the connection between an inducer and concurrent is direct or indirect and whether this connection is structural or functional (Bargary and Mitchell, 2008; Ward,

2013). The first factor is concerned with whether unimodal brain regions interact by feed-forward mechanisms alone (direct) or whether they influence regions that influence other brain areas through feedback (indirect) (Ward, 2013). Both types of mechanisms exist in the neurotypical brain, but in synesthesia they are aberrant compared to normal (Driver and Noesselt, 2008; Ward, 2013). The second factor turns on whether neural networks that give rise to synesthetic experiences have additional synaptic connections (structural) or merely exhibit excessive disinhibition or hyperexcitement of neurotypical connections through a change in neurotransmitters (functional) (Ward, 2013).

Empirical investigation on grapheme-color synesthesia has led to three different hypotheses accounting for the atypical binding that is characteristic of synesthesia. The local cross-activation hypothesis proposes that synesthesia results from a cross-activation between neural networks in adjacent brain regions. In explaining grapheme-color synesthesia, for example, the local cross-activation hypothesis proposes that the color areas in the visual cortex and the physiologically adjacent word form area interact to produce a synesthetic concurrent (Ramachandran and Hubbard, 2001a, 2001b; Hubbard et al., 2005b). Another hypothesis, the disinhibited feedback model, holds that synesthesia occurs due to disinhibition of an area of the brain that binds information from different senses, causing information from one sensory modality to trigger another (Grossenbacher, 1997; Armel and Ramachandran, 1999; Grossenbacher and Lovelace, 2001). The third hypothesis, called the aberrant re-entrant processing hypothesis, holds that high-level information re-enters low-level color areas, leading to the experience of synesthetic colors in response to a grapheme stimulus (Smilek et al., 2001; Myles et al., 2003). While there are a few different studies that individually support these three hypotheses, recent research has brought each of them into question (Bor et al. 2007; Cytowic and Eagleman, 2009: 75, 217-218; Brogaard et al., 2012; Brogaard, 2013).

In the present paper we first discuss the ramifications of the Long Term Potentiation (LTP) model for synesthesia, first introduced by Brogaard (2013). Based on what we call the 'reactivation model of memory', the model proposes that, in cases of grapheme-color synesthesia, the hippocampus binds together information from color areas with information from grapheme areas by associations made in long-term memory, simultaneously giving rise to conscious color experience. The LTP model is therefore an indirect one, however, more research is needed to determine whether it emerges via structural or functional changes in brain structure. The comparative explanatory strength of the LTP model lies in its ability to accommodate conclusions from recent synesthesia research. Not only does the LTP model explain why synesthetic experience must occur after attention is directed at its inducer, it can also account for cases in which there is not a true binding of graphemes and colors. From this discussion, we then examine the possible cognitive advantages of synesthesia, such as heightened mathematical or artistic ability. Finally, we assess how the cross-modal nature of synesthesia makes the condition relevant to classical debates in philosophy of mind, including the modularity and cognitive impenetrability hypotheses and the binding problem.

## Selective Attention and Color-Binding

The automaticity of synesthesia has been taken by some to provide evidence that synesthetic experience is much like normal veridical perception. Prior research has shown perceptual features that attract attention and lead to segregation must be processed early in the visual system (Beck, 1966; Treisman, 1982); therefore many studies have attempted to determine whether selective attention is required to bind inducing graphemes with their synesthetic colors (Mattingley et al., 2001; Ramachandran and Hubbard, 2001a, 2001b; Rich and Mattingley, 2002, 2003; Robertson, 2003; Smilek et al., 2003; Mattingley and Rich, 2004). The idea is that if synesthetic inducers attract attention and lead to segregation like perceptual features do, then the synesthetic inducers must be processed early in the visual system.

Automaticity is supported by research showing that synesthetes are susceptible to Stroop effects. A Stroop effect is a type of reaction time interference in certain perceptual tasks (Stroop, 1935). The most common Stroop task demonstrates that neurotypical individuals take significantly longer to name the color in which a color word is printed if the color referred to by the word is incongruent with the printed color (see **Fig. 2**) (MacLeod, 1991). Likewise, synesthetes take significantly longer to name the printed color of a grapheme if the synesthetic color induced by the grapheme is incongruent with the printed color (Wollen and Ruggiero, 1983; Mills et al., 1999; O'dgaard et al., 1999; Mattingley et al., 2001, 2006). A Stroop effect also has been demonstrated in music-taste (Beeli et al., 2005) and music-color synesthesia (Ward et al. 2006) as well as synesthesia which gives rise to spatial phenomenology (Sagiv et al., 2006; Smilek et al., 2006). Although neurotypical controls can be trained to exhibit responses that are seemingly automatic, functional magnetic resonance imaging (fMRI) has shown differences in brain activation for synesthetes, indicating that synesthetes and trained neurotypical controls may have different experiences for these associations (Elias et al., 2003).



Red  
Red

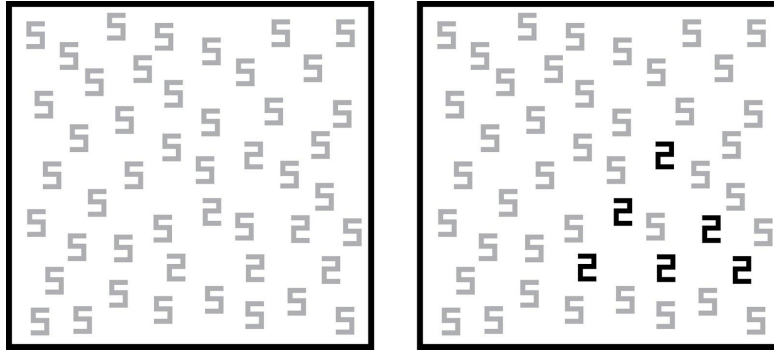
**Figure 2:** The word 'red' is here displayed in the color black (top) and the color green (bottom). It takes longer for subjects to read the word 'red' when it is printed in green than when it is printed in black or red.

Automaticity, however, should not be construed as an indication that synesthetic experience occurs prior to attention directed at its inducers. In other synesthetic Stroop tasks, no significant differences in response times were observed between congruent and incongruent target colors when the letter-primes were masked from conscious recognition (Mattingley et al. 2001). If the color experience in grapheme-color synesthesia occurs prior to conscious recognition, then, regardless of whether the letter prime is masked or visible, synesthetes should have slower response times when identifying incongruent colored targets. The study's results indicate that synesthetic primes elicit color experiences only after they reach consciousness.

Response time also may be affected by attentional load during the presentation of letter primes (Mattingley et al., 2006). The effect of letter-prime congruency was still present when tasks placed low demands on attention during the presentation of letter-primes, but the influence of priming diminished as attentional tasks became difficult. The finding that synesthetic experience may be altered by the degree of attentional load suggests that attention at least plays some role in grapheme-color synesthesia. However, it cannot be determined whether the manipulation of attentional load affected the cognitive process of linking the letter-prime to its synesthetic color or whether it merely influenced the perceptual representation of the letter-prime (Myles et al., 2003; Mattingley et al., 2006). Given its limitations, one cannot conclude based on this study that synesthetic experience is post-attentional.

Research involving visual search tasks has also provided further ground for debate on whether synesthesia is an early visual phenomenon. In studies involving neurotypical subjects, visual search tasks typically present a subject with a target hidden among other objects or features (distractors). In these tasks, a subject is instructed to find a target as quickly as possible while computer measures the time it takes for the target to be identified. Visual search tasks have also been used to study the role of attention in perceptual experience. For example, reaction time tends to be quicker when the color of the target is incongruent with distractors, causing a phenomenon known as 'pop-out'. In the case of grapheme-color synesthesia, if selective attention is not required to elicit color-associations then a digit's synesthetic color should capture attention much like it would if the digit were actually colored differently from distractors. This would lead to a highly efficient identification of the target grapheme in visual search tasks. However, if selective attention is required to induce the synesthetic grapheme-color association, then identification should be inefficient since the grapheme would still have to be located amongst the distractors prior to the elicitation of the synesthetic color (Edquist et al., 2006).

Ramachandran and Hubbard (2001) investigated this question on the role of selective attention in grapheme-color synesthesia. They conducted a visual search task that presented synesthetes (only two synesthetes participated) and neurotypical controls with an array of synesthetic color-inducing graphemes. Within each array, a group of the graphemes were arranged so that they could be grouped together into shapes (see **Fig. 2**). Participants were presented with the stimuli for a duration of one second, and then asked to name the formed shape from a group of four alternatives. Their findings showed that although synesthetes are not remarkably better than neurotypical controls at finding the target shapes hidden amongst distractors, they do appear to have a slight advantage evidenced by marginally quicker reaction times (Ramachandran and Hubbard, 2001). The synesthetes outperformance of the controls was taken to be due to a pop-out effect that pre-attentively directed the synesthetes in locating the grouped target graphemes more efficiently than controls. Based upon this observed pop-out effect it was argued that synesthesia is a early visual phenomenon that is induced prior to selective attention (Ramachandran and Hubbard, 2001, 2003).



**Figure 2** When normal subjects are presented with the figure on the left, it takes them several seconds to identify the hidden shape. Some grapheme-color synesthetes instantly see the triangular shape because they experience the 2s and the 5s as having different colors.

Cytowic and Eagleman (2009), however, offered an alternative explanation of the greater efficiency in synesthetes' search tasks compared to controls. Cytowic and Eagleman argued that the additional identifier provided by the synesthetic color of target graphemes may only be assisting synesthetes in remembering the location of previously discovered targets or rejected distractors. Although synesthetes may scan a matrix for targets in the same way as non-synesthetes, the additional post-attentional cue of the synesthetic colors of the target graphemes may reduce the time necessary for the grouped graphemes to break into conscious awareness (Cytowic and Eagleman, 2009). With this counter explanation on the table, it cannot be concluded that the quicker reaction times of synesthetes observed in Ramachandran and Hubbard (2001) are due to the graphemes eliciting vivid color experience prior to selective attention. Even subsequent research (Hubbard et al., 2005; Ward et al., 2010) that has replicated Ramachandran and Hubbard's (2001) original findings is still subject to the critique that the synesthetic colors may only be facilitating the perceptual grouping of the graphemes, and that a quicker reaction time is not necessarily indicative of a pop-out effect.

If grapheme-color associations occur prior to selective attention, then true color-based pop-out should capture attention at the same rate regardless of the number of distractors in an array, much like it would if the targets were actually colored. However, other studies have found that increasing the number of target and distractor elements in visual search tasks causes a corresponding increase in reaction time for synesthetes (Palmeri et al., 2002). This increase in reaction time could be indicative of a limitation on the speed by which graphemes are processed after selective attention, further supporting the hypothesis that synesthetic color associations merely speed up the visual search.

It has also been argued that grapheme-color synesthetes are more efficient in visual search tasks than neurotypical controls due to an implicit bias in visual search paradigms. Laeng et al.'s (2004) case study with subject PM observed that PM quickly identified graphemes only when the color-inducing target graphemes were close to PM's initial focus of attention in the visual search task. Another team led by Edquist et al. (2006) carried out a group study involving 14 grapheme-color synesthetes and 14 controls. Each subject performed a visual search task in which a target digit differed from the distractor digits in terms of its synesthetic color or its

display color. Both synesthetes and controls identified the target digit efficiently when the target had a unique display color, but the two groups were equally inefficient when the target had a unique synesthetic color.

The body of research continues to grow in support of the hypothesis that for most grapheme-color synesthetes, graphemes elicit a synesthetic color only once the subject attends to them. Evidence, however, is still limited in its conclusiveness on the question of selective attention in grapheme-color synesthesia. Thus far, only theoretical, alternative explanations have been offered to explain synesthetes' more efficient visual searches as originally observed in Ramachandran and Hubbard (2001) and replicated in subsequent studies (Hubbard et al, 2005; Ward et al. 2010).

We recently conducted our own study utilizing a novel visual search task that overcomes the limitations described above (Brogaard et al. *forthcoming*). In order to examine whether synesthetic colors guide a subject's attention to the location of a target, we compared the speed at which synesthetes and controls were able to identify the location of graphemes heavily camouflaged within flicker images. Grapheme-color synesthetes and non-synesthetic controls were presented with a series of Graphics Interchange Format (GIF) images created to alternate between images of a forest scene with and without a target '2' grapheme. The target grapheme was colored red, blue or green (camouflaged) (see **Figs. 3 a,b**). A control condition was also included wherein only a small change in the forest scene alternated between images. Participants were tasked with, and timed on, searching for the target change. Given the difficulty of finding the camouflaged green '2' grapheme, we suspected that any true pop-out effect induced by the number '2' should significantly reduce reaction time.



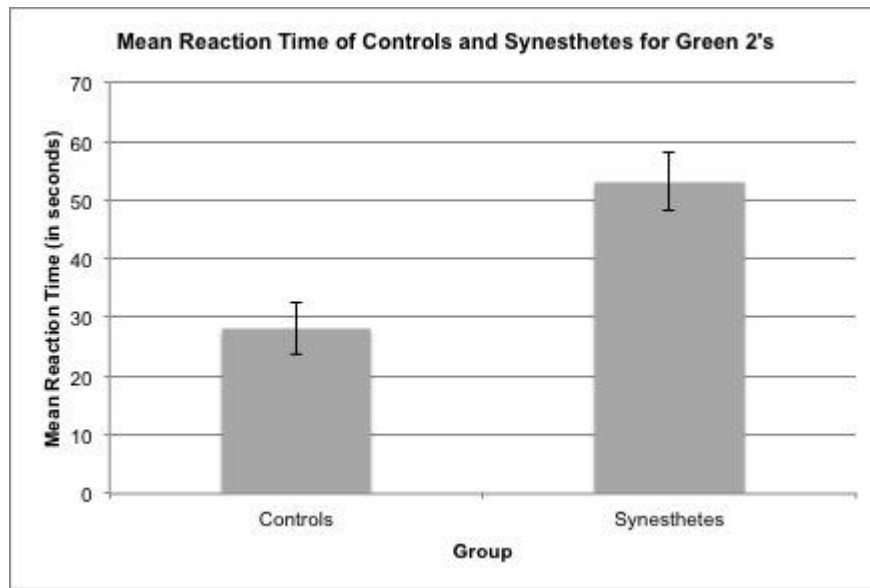




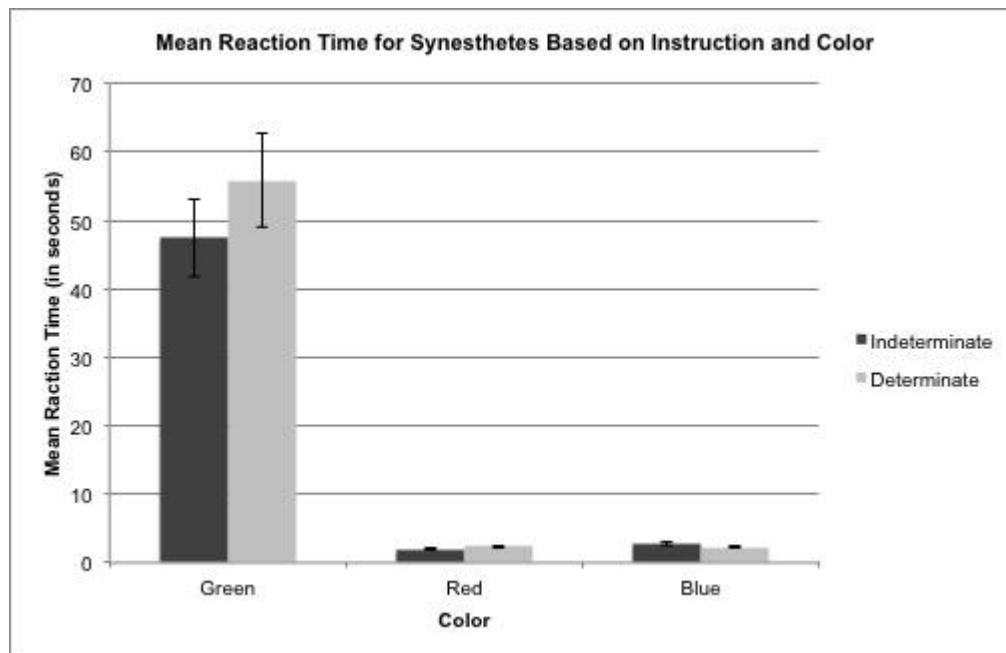
**Figures 3a and b:** Example of GIF image with and without target superimposed over a forest scene. The '2' grapheme has been circled to better assist the reader in noticing the change.

Results showed that both synesthetes and controls demonstrated highly efficient searches in locating red and blue numerals. In searching for the camouflaged green '2' grapheme, however, synesthetes took significantly longer than controls in their visual searches. It was also found that within synesthete results showed significantly longer search times in locating the green camouflaged grapheme '2' than either the red or blue '2' graphemes (see **Figs. 4, 5**). These findings indicate that no pre-attentive pop-effect occurred for synesthetes prior to selective attention, since such an effect should have made synesthetes' searches (particularly in the case of locating the green camouflaged '2' graphemes) more efficient than neurotypical controls.

Another intriguing finding from our study is that there appeared to be some interference caused by the synesthetic condition in identifying the green camouflaged '2' graphemes. This interference is inferred from the fact that synesthetes and controls did not differ in their abilities to detect more general changes in the scenery, yet synesthetes had significantly slower detection times for the camouflaged graphemes. This suggests that the greater inefficiency in locating the camouflaged graphemes for synesthetes is due to the synesthetic condition. This slower reaction may be the result of a unique Stroop effect on visual search for the synesthetes. Participant synesthetes in the study were subjected to an elimination criteria that excluded synesthetes who had green color-association to the '2' grapheme. Since participant synesthetes experienced non-green color concurrents to the grapheme '2', some interference could be occurring between the top down feedback of the synesthetic color association and the different bottom up visual information. Such an occurrence could account for the slower reaction times for synesthetes when compared to controls in locating the camouflaged green '2' graphemes.



**Figure 4:** Synesthetes take significantly longer than controls to find green '2' graphemes.



**Figure 5:** Synesthetes take significantly longer to find green '2' graphemes than either red or blue '2' graphemes but exhibit no difference in reaction time between determinate and indeterminate conditions for green '2' graphemes.

## Mechanism

While the precise neural mechanism underlying grapheme-color synesthesia is unknown, several hypotheses have been offered (Baron-Cohen, Harrison, Goldstein, and Wyke, 1993; Grossenbacher, 2001; Ramachandran and Hubbard, 2001; Nunn et al., 2002; Zilles and Fink,

2005; Hubbard and Ramachandran, 2005; Hubbard, Arman, Ramachandran, and Boyman, 2005; Rouw and Scholte, 2007; Weiss, Cytowic, and Eagleman, 2009). The different proposed mechanisms underlying developmental grapheme-color synesthesia can be divided into groups based on two factors: whether the mechanism suggests a direct or indirect binding of grapheme and color and whether the mechanism suggests structural or functional differences from the neurotypical brain (Bargary & Mitchell 2008; Ward 2013). In regard to the first factor, the direct mechanisms take unusual connectivity to be the result of an atypical feed-forward connection between form processing areas and color areas, whereas the indirect mechanisms suggest that the connectivity issues from aberrant feedback from number or word processing areas to color areas. In regard to the second factor, structural mechanisms take the cause for unusual connectivity to be the underlying brain structure whereas functional mechanisms take the cause to be a difference in how an otherwise neurotypically-structured brain processes perceptual information.

An influential hypothesis of the direct structural type is the local cross-activation hypothesis, according to which grapheme-color synesthesia arises due to cross-activation between color areas in the visual cortex and the adjacent visual word form area (Ramachandran and Hubbard, 2001a, 2001b; Hubbard et al., 2005b). This suggestion is inspired by the observation that local crossover phenomena can explain other illusory and hallucinatory experiences, such as phantom limb sensations. This hypothesis has several limitations. One is that it doesn't explain why processing of the visual form of a grapheme should elicit processing of unique brightness in striate cortex and unique hue in the V4/V8 color complex in visual cortex. Another is that it doesn't generalize to other forms of color synesthesia (e.g., sound-color and emotion-color). It is, of course, plausible that different forms of color synesthesia proceed via different mechanisms. Cases of color synesthesia have been reported in which the visual cortex is not involved in generating synesthetic colors (Bor et al. 2007, Brogaard et al., 2012).

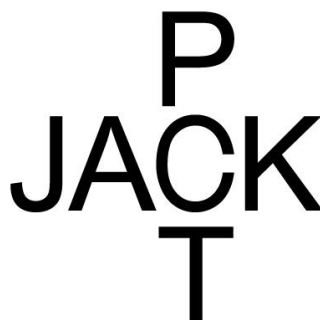
The best known hypothesis of the direct functional type posits that the unusual crosstalk originates in feedback processes as a result of disinhibited feedback from an area of the brain that binds information from different senses (Armel and Ramachandran, 1999; Grossenbacher, 1997; Grossenbacher and Lovelace, 2001). The main piece of evidence cited in favor of this hypothesis comes from an analogous case in which a patient PH reported seeing visual movement in response to tactile stimuli following acquired blindness (Armel and Ramachandran, 1999). As PH was blind, he could not have received the information via standard visual pathways. It is plausible that the misperception was a result of disinhibited feedback from brain regions that receives information from other senses.

The observation that the synesthetic effect of psychedelic substances, such as LSD or psilocybin, like is due to a disinhibition of feedback from areas of information binding provides further evidence for the disinhibited feedback hypothesis (Shanon, 2002; Sinke et al., 2012). It is unknown, however, whether drug-induced synesthesia and developmental synesthesia have the same underlying mechanism, as the former differs from the latter in nearly every respect. Even the very experience of drug-induced synesthesia at the time at which it occurs appears notably different from most cases of developmental synesthesia. Though music and sounds are the

most frequent inducers of synesthesia during drug intoxication, all sorts of sensory input, including olfactory, gustatory, haptic, pain and emotional stimuli, can induce synesthetic experience. Drug-induced synesthesia also may fail to exhibit the test-retest reliability that is characteristic of other forms of synesthesia, though the judge is still out.

A second hypothesis posits that the unusual crosstalk originates in feedback processes, but takes synesthetic experience to be the result of an indirect mechanism. The atypical re-entrant processing hypothesis, similar to the disinhibited feedback hypothesis, suggests specifically that high-level information re-enters color areas in the visual cortex and that it is this form of re-entrant information processing that leads to the experience of synesthetic colors (Smilek et al., 2001; Myles et al., 2003).

This model would explain why visual context and meaning typically influence the phenomenal quality of synesthetic experience (Myles et al., 2003; Dixon and Smilek, 2005). In **figure 7**, for instance, grapheme-color synesthetes assign different colors to the shared letter depending on whether they interpret the string of letters as spelling the word 'pot' or the word 'Jack'. For example, one of our child subjects, a seventeen-year old female, experiences the shared letter as bitter lemon (O) when she reads the word 'pot' and as bright pink (C) when she reads the word 'Jack'. This suggests that it is not the shape of the letter that gives rise to the color experience but the category or concept associated with the letter (Cytowic & Eagleman 2009: 75).



**Figure 7:** Synesthetes interpret the middle letter as a C when it occurs in 'Jack' and as an O when it occurs in 'pot'. The color of their synesthetic experience will depend on which word the grapheme is considered a part of.

The observation that the very same grapheme can elicit different color experiences in synesthetes depending on the context in which it occurs suggests that synesthetes need to interpret what they visually experience prior to having a synesthetic experience. Though Ramachandran and Hubbard (2003) argue that grapheme-color synesthesia is a form of low-level perception (a 'sensory phenomenon'), they grant that linguistic context can affect synesthetic experience. They presented the sentence 'Finished files are the result of years of scientific study combined with the experienced number of years' to a subject and asked her to count the number of 'f's' in it. Most normal subjects count only three 'f's' because they disregard the high-frequency word 'of', and even though the synesthete eventually spotted six 'f's', she initially responded the way normal subjects do.

Ramachandran and Hubbard (2003) suggest that these contextual effects can be explained by top-down influences. Whether this is right in cases of grapheme-color synesthesia, however, will depend on whether color experience processed in early visual areas is indeed affected by high-level contextual information and interpretive processes. If it is not, then strong top-down influences cannot explain the contextual effects. A better explanation of contextual influence then may be that interpretation of low-level perceptual information is required for synesthetic experience.

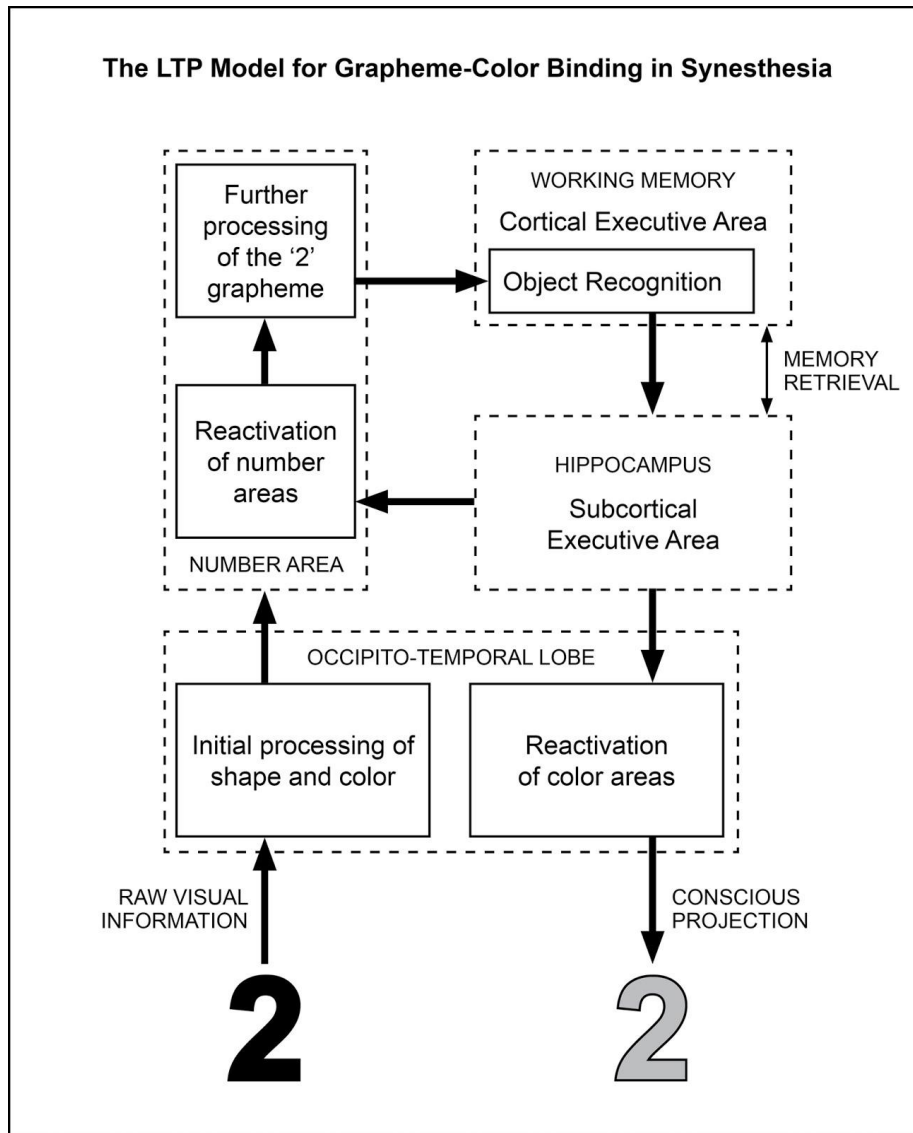
The lack of pop-out effects as described in Edquist et al. (2006) and Brogaard, et al (2013) do, however, lend support to the reentrant processing model. The absence of preattentive pop-out in synesthetes' searches indicates that top-down attention is needed to elicit the synesthetic experience. From this, it could be understood that the reentrant processing of higher level attentional information to lower level color areas is responsible for inducing the synesthetic color experience from the attended grapheme inducer. The reentrant processing theory can also explain why synesthetes may have significantly slower reaction times for locating inducers compared to controls (Brogaard, et al. forthcoming). If high-level information reenters lower-level color areas, then there could be cognitive interference caused by a clashing between the top-down synesthetic color association differing from bottom-up visual information of the grapheme. For example, under the reentrant processing model, a black letter 'A' is processed bottom-up as achromatic and then is attentionally perceived as red by the grapheme-color synesthete. The top-down reentrant processing of the red association would then conflict with the bottom up visual information of the achromatic grapheme, creating cognitive interference that impedes target recognition. Such an account could possibly explain synesthetes' slower search times when compared to controls as observed in Brogaard, et al. (forthcoming).

There are also models that suggest that grapheme-color synesthesia consists in special kinds of automatized memory associations. Brogaard (2013) proposes that the automatic association between graphemes and colors in grapheme-color synesthesia is akin to the automatic association between smell and memories. For example, the smell of chlorine may automatically induce visual images of a particular pool party. In the case of smell, the tight association presumably is formed immediately as a result of the negative value of the event. Presumably hyperactivation of the amygdala leads to the formation of connections between the adjacent olfactory bulb and visual areas. Affect is unlikely to be a factor that influences information binding in developmental synesthesia. The association presumably forms automatically because of its advantage in the learning process. Because of the indirect character of memory processes, the memory model is best understood as depicting one of the indirect mechanisms.

According to a recent model of memory, which we might call the 'reactivation model', the hippocampus is not a storage space for information but a subcortical executive region in charge of maintaining connections between neural networks located in different areas of the brain (Eichenbaum 2004; Serences, et al. 2009; Rissman and Wagner 2012). Working memory in the prefrontal cortex and hippocampus work in tandem. The hippocampus guides the depositing of proteins at the synapses of neurons in areas that originally processed the information to be

remembered. Together with neighboring hippocampal areas it also keeps track of the relative order of events and binds together events that belong together. Memory retrieval by working memory reactivates the original areas of information processing by interaction with the executive hippocampus.

On the memory model, synesthesia is the result of an indirect mechanism. The hippocampus would at some point have bound together long term potentiation (LTP) in visual color areas as well as in grapheme areas. Exposure to achromatic grapheme-stimuli would trigger both recognition of the grapheme as a particular grapheme (e.g., the numeral '2') and memory retrieval of synesthetic colors to executive areas of the brain. The renewed activity in the color areas taking place in order for memory retrieval of synesthetic color information to occur may simultaneously give rise to a conscious projection of synesthetic color from visual color areas. In synesthetes in which graphemes and colors truly are bound together to the extent that graphemes literally are seen as having colors, hippocampus may be treating the distinct neural networks the way it normally would with form and color that belong together (e.g., tomato and red). In cases in which grapheme and color are not tightly bound together, the hippocampus must be treating the neural networks more like involuntary quick associations, such as the association between the striking of a match and its being lit.



The LTP model is supported by the lack of pop-out effects described in Edquist et al. (2006) and Brogaard, et al (2013). On the LTP model, conscious projection of synesthetic color is subsequent to memory retrieval of synesthetic colors from visual color areas in response to exposure to graphemes. For conscious projection to occur, the synesthete must first spot the grapheme and interpret it, which would rule out any pop-out of graphemes. The LTP model can also account for the slower reaction times among synesthetes in searching for green inducer targets in Brogaard, et al. (forthcoming). The processing of green in visual areas may have slowed down the retrieval of the non-green synesthetic color information and the projection of the synesthetic color onto the '2's after reactivation of color areas.

While the re-entrant processing model may also explain arbitrary associations between inducers and their concurrents, only the LTP model explains non-arbitrary associations that may occur in certain types of synesthesia. In lexical-gustatory synesthesia, a word that denote foods typically

gives rise to the taste of the food it denotes (Ward and Simner, 2003). The non-arbitrariness of associations between words and tastes indicate that the mechanism responsible for the creation of associations must be related to memory. Under the LTP model, association between words and tastes may occur in neurotypical memory formation. In cases of synesthesia, the connections between food words and tastes become strong enough as to produce gustatory experiences.

A further virtue of the LTP model is that it straightforwardly can account for cases in which there is not a true binding of graphemes and colors. Some grapheme-color synesthetes report that graphemes merely are felt as inducers of colors either projected out into the world or seen in the mind's eye. On the LTP model, information stored in memory about graphemes and their synesthetic colors need not as tightly connected as characteristic features of objects (e.g., red hearts). There are also synesthetes that merely know the color of graphemes but have no corresponding visual experience associated with the grapheme. Ward (2013) suggests that the visual experience may have faded over the years. The LTP model offers a simple explanation of this type of fading. Memories tend to fade in their vividness over time. So, if synesthetic binding is stored in memory, we should expect it to fade over time.

Sound symbolism, the idea that phonemes carry meaning, indicates that synesthetic associations arise from similar cognitive structure. In the English language, nouns and verbs have distinct phonological properties (Farmer et al., 2006). Studies have shown that neurotypical individuals can use phonemes to correctly determine the meaning of a word in the absence of any other clues. For example, one study showed that subjects consistently preferred the non-words 'baluma' to denote a rounded shape and 'takete' to denote a pointed shape (Köhler 1929). Other studies have shown similar consistency for other phoneme-object pairs (Davis, 1961; Ramachandran and Hubbard, 2001b; Maurer et al., 2006). The phenomenon of sound symbolism has also been demonstrated across languages. In one study, native English speakers were able to correctly guess which phonemes denoted birds when presented with both bird and fish phonemes (Berlin, 1994).

The similarity between phoneme-object association in neurotypical perception and inducer-concurrent association in synesthesia indicates is that the neurotypical brain is primed to make seemingly arbitrary associations between stimuli and concurrents. In the case of synesthesia, inducer-concurrent associations are much stronger, leading to the distinct phenomenology that characterizes the condition. Under the LTP model, it is possible that neurotypical individuals forms the same sort of associations as synesthetes without actually experiencing synesthetic phenomenology. Synesthetic phenomenology might only appear above a certain threshold for activation due to the abnormally strong degree of association between inducers and their concurrents.

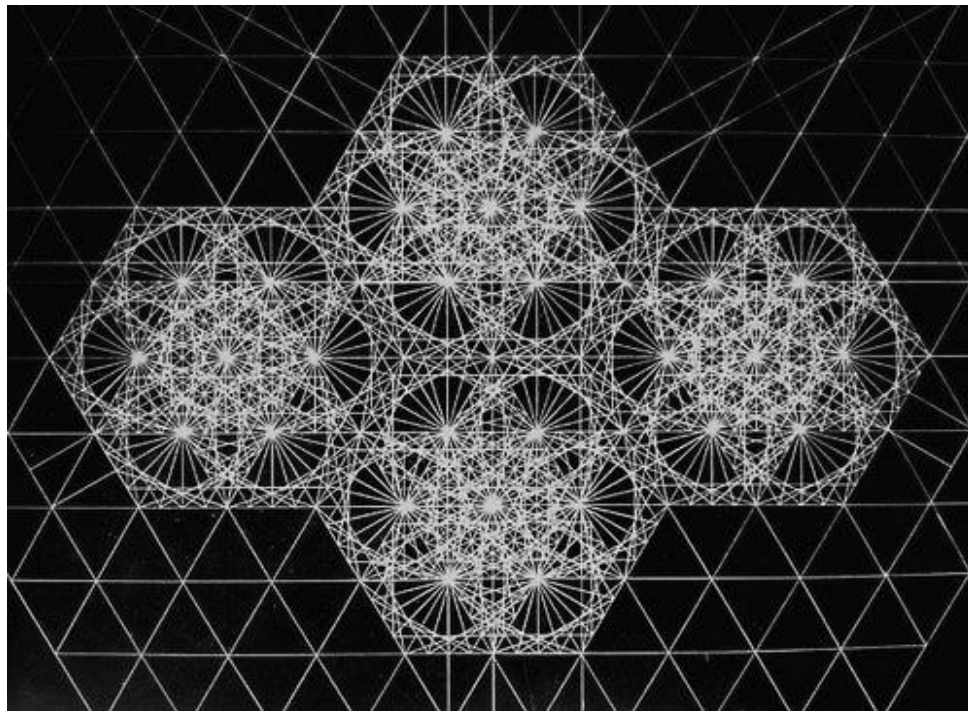


## Cognitive Advantages of Grapheme-Color Synesthesia

If pop-out effects require top-down attention to the synesthetic inducers, grapheme-color synesthesia is unlikely to give subjects much of a cognitive advantage in visual search tests. However, there may nonetheless be other cognitive advantages associated with color synesthesia. For example, some of our recent pilot studies suggest that grapheme-color synesthetes may have greater recall ability for digits and written names when compared to non-synesthetes, though it is yet to be seen whether our initial results hold up in larger studies.

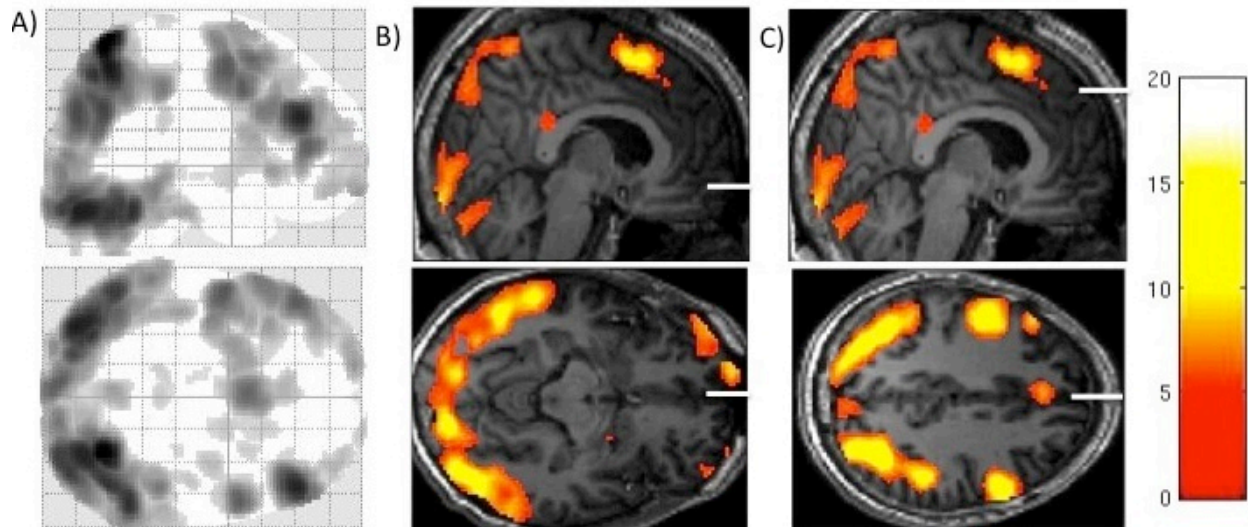
There have also been rare cases where color synesthesia has been associated with extreme mathematical skills. Subject DT, for example, sees numbers as three-dimensional colored, textured forms (Bor et. al, 2007), and he reports his synesthesia as giving him the ability to multiply high digits very rapidly. As DT describes it, the product of multiplying two numbers is the number that corresponds to the shape that fits between the shapes corresponding to the multiplied numbers. Subject DT's color synesthesia also gives rise to extreme mnemonic skills. DT currently holds the European record in reciting the decimal points of the number pi. An fMRI study comparing DT to controls while attempting to locate patterns in number sequences indicated that DT's synesthetic color experiences occur as a result of information processing in non-visual brain regions, including temporal, parietal and frontal areas.

Brogaard, et al. (2012) describe a case of a subject, JP, who has exceptional abilities to draw complex geometrical images by hand (see **Fig 8**) and a form of acquired synesthesia for mathematical formulas and moving objects, which he perceives as colored, complex geometrical figures.



**Figure 8:** Image hand-drawn by subject JP

JP's synesthesia began in the wake of a brutal assault that led to unspecified brain injury. An fMRI study contrasting activity resulting from exposure to image-inducing formulas and non-inducing formulas indicated that JP's colored synesthetic images arise as a result of activation in areas in the temporal, parietal and frontal cortices in the left hemisphere. The image-inducing formulas as contrasted with the non-inducing formulas induced no activation in the visual cortex or the right hemisphere (see **Fig 9**).



**Figure 9:** Sagittal slices. Activation induced by the image-inducing formula contrasted to non-inducing formulas. The SPM(T) maps were thresholded at family-wise-error-corrected p-value 0.01 and overlaid on JP's structural T1-weighted MRI which was standardized into MNI-space using SPM8.

These two unusual case studies suggest that at least some forms of color synesthesia can give rise to cognitive advantages in the area of mathematics. As the visual cortex does not appear to be directly involved in generating the synesthetic images in either subject, however, the two cases also suggest that at least some forms of color synesthesia are best characterized as forms of high-level perception that proceeds via a non-standard mechanism.

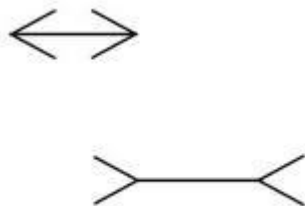
Cases of acquired synesthesia suggest a yet unexplored theory: the condition may be a window to unconscious brain processes. In the neurotypical brain, much information is processed unconsciously. One such type of information consists of calculations made in the dorsal visual stream. According to the two-streams hypothesis, visual information is split into two streams in the visual cortex. The ventral stream runs sideways through the temporal lobe and ends in the prefrontal cortex, whereas the dorsal stream runs upward through the parietal cortex and ends in motor-sensory cortex. The ventral pathway is specialized for vision for object recognition and the dorsal pathway is specialized for vision for action (Goodale and Milner, 1992; Milner and Goodale, 1996, 1998; Brogaard, 2011). The dorsal stream is highly sophisticated, responsible for the complex calculations necessary to perform actions directed at moving stimuli in real time. But despite their sophistication, dorsal stream processes do not correlate with visual awareness

(Brogaard 2011). Other high-level cognitive information, such as simple mathematical calculations, may be processed unconsciously as well. At least one recent study showed that abstract, symbolic and rule forming computations can be processed unconsciously (Sklar et al., 2012).

It is possible that synesthetic phenomenology is a conscious representation of the output of unconscious processes. The representational nature of some synesthetic phenomenology is evidenced by DT's case: the ability to consciously report the results of multiplication relies on visual phenomenology, but the synesthetic shapes used in multiplication correspond to real numbers. DT lacks conscious awareness of the method used to generate the imagery, yet the imagery is representative of the correct result. The representational ability of synesthesia need not be limited to developmental cases. Traumatic brain injury and subsequent anatomical or functional reorganization sometimes lead to the arbitrary associations of high-order concepts with perceptual representations. These associations may then become bound into a conscious experience when triggered. JP's case lends credibility to this theory. As JP learned new mathematical concepts following the injury, corresponding synesthetic imagery must have evolved over time before becoming stable.

## Modularity

It is often said that synesthesia research has few, or no, interesting implications for classical debates in philosophy of mind. Research on synesthetic phenomena, however, has been recognized to have had profound influences on the modularity of mind hypothesis, which claims that systems involved in producing particular mental states or abilities are modular (Fodor 1983, Sperber, 1994, 2002, Pinker, 1997, Carruthers 2006). Beyond the core premise of modularly describing what different regions of the brain do, the modularity hypothesis also holds that certain kinds of information are encapsulated from influences from other regions. (Fodor 1983). For example, the Müller-Lyer illusion illustrates that perceptual information is encapsulated from belief influence (see **Fig 10**). Though people familiar with the illusion believe that the line segments have the same length, they perceptually experience the line segments as having different lengths.



**Figure 10** In the Müller-Lyer illusion you believe the lines are of the same lengths but no matter how long you look, you continue to experience them as having different lengths. This illustrates a case in which perceptual information is encapsulated from belief influence.

For information to be encapsulated it does not suffice that there are no top-down influences on producing it; it must also be free of influences from other modules. So the Muller-Lyer illusion does not demonstrate that perception is modular under a strict interpretation of 'modularity'.

The modularity of mind hypothesis was rejected long before synesthesia research took off as a serious field of study, but the theory has persisted in a limited form with respect to color perception. Synesthesia evidently provides a challenge even for those who restrict modularity to systems of color. If grapheme-color synesthesia is a type of perceptual experience or a perceptual experience enriched by a mental image (Deroy 2012), then grapheme-color synesthesia undermines the idea that the system that produces color perception is not free of influences from other modules.<sup>1</sup>

There are further cases of synesthesia that challenge the modularity hypothesis even when restricted to perception. In the cases discussed above, subjects JP and DT report having internal, colorful visual imagery in response to formulas or numerals. fMRIs show in both cases that the visual cortex is not a source of the imagery. On the assumption that JP and DT's synesthetic experiences are perceptual experiences enriched by visual imagery, as argued by Deroy (2012), these cases challenge even a very modest form of modularity. A very modest form of modularity states that perceptual systems computing color are regionally defined and encapsulated. For example, defenders of the modularity claim could hold that, in the human brain, these systems are restricted to the V4/V8 color complex in the visual cortex, and that these systems are free of outside influences. The visual cortex, however, is not involved at all in producing the colors of the synesthetic experiences of JP and DT.

The cases of JP and DT also challenge later more radical defenses of modularity that hold that modules are, as Carruthers puts it, 'isolable function-specific processing systems,' which are all or almost all domain specific, and 'whose operations aren't subject to the will, (and) are associated with specific neural structures (albeit sometimes spatially dispersed ones)... whose internal operations may be inaccessible to the remainder of cognition'. (Carruthers, 2006, p. 12). This variant, too, would be undermined by cases in which color experiences synesthetically are associated with colored numerals or geometrical equations, which seem to be produced by structures in the parietal cortex or the temporal gyri rather than in the visual cortex.

### **Cognitive Impenetrability**

The implications of synesthesia research do not end with the modularity hypothesis, however. Another related, but distinct, classical debate turns on to what extent visual experience is penetrable by cognitive factors, such as belief and familiarity (Pylyshyn 1984). This concept of impenetrability should not be understood in the same way as encapsulation. Whereas

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<sup>1</sup> This only holds if the mechanism underlying grapheme-color synesthesia is of the feedback type as opposed to the feed-forward type. However, we already offered several reasons for thinking the mechanism underlying grapheme-color synesthesia is of the feedback type and not the forward type.

encapsulation concerns all influences on a mental state, cognitive penetration merely concerns top-down influences on perceptual experience.

One piece of evidence in favor of the cognitive penetrability hypothesis comes from studies investigating the effect of belief on color experience and the effects of cognitive factors on grapheme-color experience. For example, an early study completed by John L. Delk and Samuel Fillenbaum (1965) indicated that our beliefs about the characteristic color of an object may affect the color we experience that object as having. In the study, experimenters cut out shapes from uniformly colored pieces of paper. Some shapes represented objects that are characteristically red (for example, an apple, a heart, a pair of lips), while other shapes depicted objects that are not characteristically red (for example, a circle, a square, an oval, a bell, a mushroom). Each cutout shape was placed in front of a colored background that could be changed from yellow through orange to red. Subjects were asked adjust the background until the color was the same as the shape in front. The researchers found that when the object represented by a shape had a characteristically red color, the subjects selected a background color that was redder than the color they selected when the shape was of an object that was not characteristically red. Based on these types of observations, philosophers have argued our beliefs about the colors of objects penetrate our color experiences (Macpherson 2012). The question still remains, however, whether subjects were reporting on their visual experiences or on higher cognitive states based on interpretations of their visual experiences. If it's the latter that is true, then cognitive penetrability is unsurprising.

Synesthesia sheds some light on this uncertainty. Grapheme-color synesthesia has traditionally been characterized as experiential (low-level visual experience). Ramachandran and Hubbard (2003), for example, characterize synesthesia as a genuine experiential, or “sensory,” phenomenon. As they put it:

Work in our laboratory has shown that synaesthesia is a genuine sensory phenomenon ... The subject is not just ‘imagining the colour’, nor is the effect simply a memory association (e.g. from having played with coloured refrigerator magnets in childhood). (2003: 51)

Ramachandran and Hubbard grant that cognitive factors can influence synesthetic experience, but they maintain that this phenomenon can be explained by cognitive penetration of visual experiences. If Ramachandran and Hubbard were right, then we would have some vindication of the hypothesis that visual experience is penetrable by cognitive factors. As we have shown in the present paper, however, research into the dependence of synesthesia on focal attention suggests that grapheme-color synesthesia is not a low-level visual phenomenon. High-level cognitive mechanisms seem required to elicit synesthetic experience, indicating that what's cognitively penetrable is interpreted visual experience (e.g., the interpretation of a shape as a numeral) rather than visual experience as such. These findings thus undermine one of the main pieces of evidence in favor of the cognitive penetrability hypothesis, viz. the claim that synesthetic experience in grapheme-color synesthesia is cognitively penetrable. Even further, the evidence from synesthesia research suggests that what we previously took to be cognitive

penetrability may just be the subjects' beliefs penetrating higher-order cognitive states that depend on the interpretation of low-level color experience.

### **The Role of Attention in Feature Binding**

Synesthesia research can also shed light on philosophical debates about attention and the binding problem. Many cases of synesthetic experience are atypical in binding unusual features: Graphemes are in some cases literally consciously seen as colored. Despite this atypicality, recent research into the mechanism underlying synesthesia may give us some insights into the nature of attention and the role played by attention in feature integration. On the LTP model, the hippocampus binds together neural networks in distinct brain regions, viz. grapheme areas and color areas. Attention to an achromatic grapheme elicits both recognition of a shape as a particular grapheme and retrieval of the color information in visual areas.

In cases of normal perception, attention may consist in a selection of a target by selecting among features entering the system. The selection of features cannot proceed completely on the personal level, as some features appear inseparable (e.g., color and form). But one of the lessons from synesthesia is that selecting features is not the only role of attention. In grapheme-color synesthesia, selective attention facilitates recognition of a grapheme, which then elicits synesthetic color.

Wayne Wu (2011) argues that conscious selective attention consists in more than perceptually locking on to a specific object. According to Wu, it also involves a way of demonstratively locking on to it (e.g., attending to *that* women). Declan Smithies (2011) goes one step further and argues that attention is what makes information fully accessible for use in rational thought and action.

The lessons drawn in this paper about the dependence of synesthesia on attention is in broad agreement with Wu's and Smithies' views. However, our studies suggest that prior to being able to lock onto an object demonstratively or gain full access to information about a particular object that suffices for acting and reporting, we must be able to consciously *recognize* the thing attended to as a specific object. You can, perhaps in poor visual conditions, attend to a blob in the environment without recognizing it as a specific object and even without being able to see precisely where the blob begins or ends. Attention itself, however, is essential to conscious recognition.

In line with the LTP model for synesthesia, attention to a target presumably causes the hippocampus (or neighboring hippocampal areas) to re-activate neurons in distinct areas of the brain (e.g., color and form areas) (Brogaard 2013). When this information is retrieved by working memory in a bound form together with novel target information, this may result in conscious recognition of the object. It is at this point that one can demonstratively lock on to the object as a specific object with well-defined boundaries. On the view proposed here, then, one

function of selective attention is to select a target; another is to ensure that recognition can take place by initiating memory retrieval of bound features.

Initial integration of features of novel stimuli likely takes place earlier in the sensory systems. But initial feature integration probably does not correlate with consciousness. Blindsight patients are able to predict several features of a target located among distractors, despite being unable to consciously perceive them (Brogaard 2011). As blindsight patients have lesions to the primary visual cortex, there is reason to think that some features are found in early parts of the visual system, perhaps in LGN. Studies have shown that blindsighters can attend to targets they are not aware of, but this requires cues that indicate the location of the target (Kentridge 2011; Kentridge, et al. 1999). It is unlikely that focused attention is always required for feature integration to take place in blindsight.

On the feature integration theory of attention, first proposed by Anne Treisman (1980, 2003), conscious perception is preceded by a preattentive stage during which different features of objects (e.g., shape, color, orientation, depth) are processed by different brain regions. This is then followed by an attentive stage where the features are combined by focused attention to a specific object, resulting in a conscious experience of the object. Treisman and Schmidt (1982) showed in a masking study that subjects who are only briefly exposed to different objects often combine features of distinct objects, for example, mistakenly attributing a shape of one object to a different objects. Similar kinds of conjunctive illusions have been found in people with Balint's syndrome, a condition in which damage to parietal cortex prevents focused attention on individual objects (Friedman-Hill, et al. 1995). This model of attention, however, probably is too radical. Aside from the evidence from blindsight studies, there is evidence to suggest that initial feature integration does not depend on focused attention. For example, there are no known perceptual illusions where colors spill out of objects. This suggests that color and boundary integration is preattentive.

## **Conclusion**

The recent invigoration in synesthetic research over the past two decades has inspired novel empirical and theoretical approaches to studying and understanding the human mind. As a phenomenon, synesthesia has compelled profound reconsiderations on many once salient philosophical perspectives concerning a multitude of cognitive mechanisms such as memory, attention, and reentrant processing. This paper offered a reassessment of these mechanisms through the lens of grapheme-color synesthesia research and the related debate concerning the role of selective attention in the phenomenon. Out of this review and discussion, we presented new and compelling research contesting the theory of a pop-out effect aiding synesthetes in their visual searches for target graphemes amongst distractors. These findings, however, not only showed that grapheme-color synesthesia does not provide an advantage in complicated visual search tasks, it also appears to incur a slight disadvantage. Such an observation lends credence to either the re-entrant processing hypothesis or the LTP model for grapheme-color synesthesia.

Along with these new observations, we further argued that the LTP model has greater explanatory power than competitors. We contend that the superior explanatory power can be attributed to the fact that the LTP model can account both for the arbitrary associations between synesthetic inducers and concurrents and the non-arbitrary synesthetic associations that may arise in cases of synesthesia. Although grapheme-color synesthesia may not provide an advantage in visual search tests, there are independent reasons to think that color synesthesia can provide cognitive advantages in areas such as memory retrieval of words and digits. Continued research into the mechanisms of synesthesia will help reveal the cognitive idiosyncrasies and mental processes behind synesthetes as well as advance our understanding into the workings of the neurotypical brain. Through a litany of potentials, synesthesia offers modern cognitive research a new doorway into unlocking the secrets of the human mind.

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