

Cite as: Brogaard, B. (2013). "Synesthetic Binding and the Reactivation Model of Memory", in O. Deroy and M. Nudds (eds.), *Sensory Blendings: New Essays on Synaesthesia*, Oxford University Press. In Press.

Synesthetic Binding and the Reactivation Model of Memory

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December 31, 2012

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Abstract

Despite the recent surge in research on, and interest in, synesthesia, the mechanism underlying this condition is still unknown. Feedforward mechanisms involving overlapping receptive fields of sensory neurons as well as feedback mechanisms involving a lack of signal disinhibition have been proposed. Here I show that a broad range of studies of developmental synesthesia indicate that the mechanism underlying the phenomenon may involve reinstatement of brain activity in different sensory or cognitive streams in a way that is similar to what happens during memory retrieval of semantically associated items. In the paper's final sections I look at the relevance of synesthesia research, given the memory model, to our understanding of multisensory perception and common mapping patterns.

Keywords: cross-modal integration, grapheme-color synesthesia, high-level properties, long term potentiation, mechanism underlying synesthesia, memory associations, model of perception, multisensory perception, reactivation model of memory, semantic memory, sensory recruitment model

1. Introduction

Synesthesia is an unusual way of perceiving the world, in which internal or external stimuli provoke atypical sensations or thoughts (Baron-Cohen, et al., 1987; Cytowic, 1989; Ramachandran, et al., 2001; Grossenbacher and Lovelace 2001; Emrich et al., 2002; Rich and Mattingley, 2002; Hubbard and Ramachandran 2005; Sperling, et al., 2005; Hubbard and Ramachandran 2005; Hubert et al. 2005; Ward, et al., 2006; Hubbard 2007; Brogaard 2013). For example, seeing the number 3 printed in black ink may lead to a sensation of cobber green, hearing the word “kiss” may flood the mouth with the flavor of tomato soup and hearing the key of C# minor may elicit a slowly expanding purple spiral.

In grapheme-color synesthesia, one of the most common forms of synesthesia, perceiving or thinking about an achromatic grapheme (also known as the ‘inducer’) gives rise to the sensation or thought (also known as the ‘concurrent’) that the grapheme has a specific color with a highly specific hue, brightness and saturation (Simner, et al. 2006). The concurrent images are either projected onto the external world (projector synesthesia) or perceived in the mind's eye (associator synesthesia) (Dixon, et al., 2004). In projector synesthesia, the projected concurrent may be seen as instantiated like non-synesthetic colors, as floating above its inducer or as an “afterimage” that floats close to the subject’s eyes. In associator synesthesia, the concurrent image is seen internally, much like a visual image retrieved from memory or generated by imagination.

Most cases of synesthesia are developmental. Subjects report having had the condition for as long as they can remember, and the condition appears to run in families. While most cases of synesthesia are developmental, acquired cases have also been reported, for example following stroke (Beauchamp and Ro, 2008), optic nerve chiasm (Afra et al, 2009), extensive use of a sensory substitution device (Ward and Meijer 2010), post-hypnotic suggestion (Kadosh et al., 2009) and traumatic brain injury (Brogaard, et al. 2011). Synesthesia also occurs during intoxication resulting from exposure to psychedelic drugs, such as psilocybin, LSD, mescaline, peyote cactus and DMT (Sinke et al., 2012). Drug-induced synesthesia differs from the other forms in being transient and less inducer-specific. Anecdotal evidence suggests that, under intoxication, the same concurrent images can have a wide variety of inducers that happen to be present in the subject’s environment.

Up until the twenty first century, the key evidence suggesting that synesthesia is a special condition that is fundamentally distinct from ordinary memory associations came from introspective reports. The idea that introspective reports can serve as evidence has been heavily criticized by behaviorists for almost a century, and introspective reports are still regarded as highly unreliable by most philosophers and scientists (Switzgebel 2008; Hurlburt & Schwitzgebel 2007). The widespread skepticism of

phenomena that could not be subjected to objective testing, which accompanied the twentieth century behaviorist movement, resulted in a lack of scientific interest in synesthesia during most of that century. The two main developments triggering in spark in research interest in synesthesia was the recent considerable progress in the area of neuroimaging as well as the development of the Synesthesia Battery, an automated online battery of tests that allows for rigorous testing for a range of different types of synesthesia (www.synaesthete.org; Eagleman et al., 2007).

The Synesthesia Battery consists of two sections: a color-identification task and a color retrieval task. In the first task, the subject is presented with an inducer and must choose the concurrent she experiences among numerous options. When the concurrent is a color, the subject must choose a specific hue, brightness and saturation from a color palette representing over 17.6 million distinct choices. The subject repeats the exercise three times for each inducer, which in the case of grapheme-color synesthesia amounts to 108 trials for graphemes A-Z and 0-9. The software then calculates the geometric distance among the subject's answers in red, green and blue (RGB) color space. If the geometric distance in RGB color space is less than 1, that is strong evidence that the subject is a synesthete for that grapheme. In the second task, the subject is presented with randomly ordered inducers one at a time together with a possible concurrent. The subject must determine whether the inducer elicits the concurrent in question as quickly as possible. A score higher than 90 percent further validates the results of the first task.

The online software tests for the presence of two features commonly regarded as diagnostic of synesthesia (Eagleman et al., 2007; Baron-Cohen et al., 1987). One is the specificity of inducer-concurrent pairs. The other is the automatic (and hence fast) associations between inducers and concurrents. If re-administered, the Battery can also be used to measure the stability of synesthetic connections over time, a third feature commonly regarded as diagnostic of synesthesia.

A further factor playing a role in the increased scientific interest in synesthesia over the last few decades has been the realization that synesthesia can be informative in ways similar to other conditions that result from brain abnormalities. By studying how brain abnormalities affect normal perception, cognition and action, we can gain insight into how these processes work in neurotypical individuals. One well-known hypothesis that has been validated by studies of lesions is the two visual stream hypothesis (Goodale et al. 1991, Goodale and Milner 1992, Milner and Goodale 1995, 2008). Research on subjects with lesions to the ventral stream but with intact dorsal systems as well as subjects with lesions to the dorsal stream but with intact ventral streams has led to a better understanding of how vision for perception and vision for action work as independent pathways (Brogaard 2011). Though most forms of synesthesia do not result from brain lesions, but are the result of early developmental deviations in regions

of the brain involved in perception and cognition, researchers believe that synesthesia can help elucidate models of perception, cognition and action in neurotypical individuals. A good model of perception or cognition should be able to explain synesthesia by showing which processes or pathways in these models lead to the aberrant blending of sensory experiences.

It is still widely debated which models we should expect to be the best explanatory models of synesthesia. Typical early-perceptual models suggest that synesthesia is the result of interaction between brain regions via feedforward mechanisms. Typical late-perceptual and cognitive models suggest that synesthesia is the result of both feedforward and feedback mechanisms. In the first type of model the phenomenon is explained by unusual bottom-up interaction, for example, between adjacent color and form areas. In the second type, the phenomenon is explained by unusual signal feedback from higher brain regions.

Earlier research on grapheme-color synesthesia has suggested that the phenomenon arises as a result of feed-forward perceptual processes. Results from visual search tasks have indicated that when synesthetic inducers are hidden among distractors, this can lead to a pop-out effect and faster response times (Ramachandran and Hubbard 2001; Edquist et al., 2006; Rothen and Meier 2009). As features processed in the early visual system are believed to be processed prior to a selection process facilitated by selective attention, these pop-out effects provides evidence that grapheme-color binding is an early visual phenomenon (Treisman, 1982). The claim that grapheme-color binding is an early visual phenomenon remains the subject of great controversy, however. The location of inducers relative to distractors appears to influence response time, suggesting that selective attention may be needed for synesthetic colors to reach consciousness (Laeng et al.'s 2004)

There are other aspects of synesthesia that are difficult for the early-perceptual models to explain. Though there is some degree of idiosyncrasy in which concurrent experiences are elicited by inducers, synesthetic connections are not completely arbitrary (Simner et al., 2005). A range of unrelated factors contribute to the formation of patterns across the concurrents experienced by synesthetes, including normal tendencies to associate certain items (e.g., high pitch and lighter colors) (Mondloch & Maurer 2004), the visual or spectral shape of the inducer (Brang et al. 2011), contextual frequency of the inducer (Simner et al. 2005; Beeli et al. (2007) and exposure to the inducer-concurrent connection during early learning processes (Blake et al. 2005; Hancock, 2006; Witthoft & Winawer, 2006, 2013). In a recent study, Witthoft & Winawer (2013) looked at the letter-color associations in 11 grapheme-color synesthetes whose letter-color connections were remarkably similar. On the basis of battery tests, subjective reports and market investigations, the researchers were able to provide

strong evidence that the 11 subjects acquired their synesthesia while learning the alphabet using refrigerator magnets.

It is important to note that Witthoft and Winawer's results do not show that synesthesia just is a memory association, similar to the association between sadness and the color blue, that we are all prone to make (Deroy & Spence 2013). There are significant differences between stereotypical ties between two concepts and synesthetic binding. Unlike stereotypical memory associations, synesthetic connections are automatic, immediate, specific and stable over time. Synesthetic associations also tend to have a different phenomenology compared to other types of associations. Many grapheme-color synesthetes, for example, see letters and numerals printed in black as having a specific color. But Witthoft and Winawer's results do suggest that semantic memory may be importantly involved in generating the atypical, tightly interwoven connections that characterize the phenomenon. This, in turn, provides evidence that grapheme-color synesthesia is not an early-perceptual phenomenon but rather involves neurological processes occurring late in the perceptual and cognitive system.

The theory that semantic memory may underlie synesthetic connections should not be taken to suggest that synesthesia is best explained by models of cognition as opposed to models of perception. Recent models of memory suggests that there is considerable overlap between neural correlates of retrieved or actively maintained memories and those of sensory perception. Retrieved and actively maintained memories originate in reinstated cortical representations of perceptual and semantic features.

In what follows I review the evidence for thinking that synesthetic connections should be understood as semantic memory associations. In the subsequent section I briefly review the most recent results of memory research and show how this research can shed light on the mechanism underlying synesthesia. Finally, I argue that synesthesia understood as involving a reinstatement of activity in sensory brain regions can inform models of multisensory perception.

2. Evidence for Semantic Memory Associations in Synesthesia

The main evidence motivating local cross-activation as the mechanism underlying synesthesia has come from visual search tasks demonstrating inducer pop-out effects and quicker than normal response time (see **Fig 1**). Synesthetes must experience inducers as having synesthetic colors prior to explicitly identifying them for them to have a pop-out effect. So the initial results of visual search tasks suggested that synesthetic experience was the result of a pre-attentive bottom-up binding of inducer and concurrent and hence was an early perceptual phenomenon (Ramachandran and Hubbard 2001; Treisman, 1982).

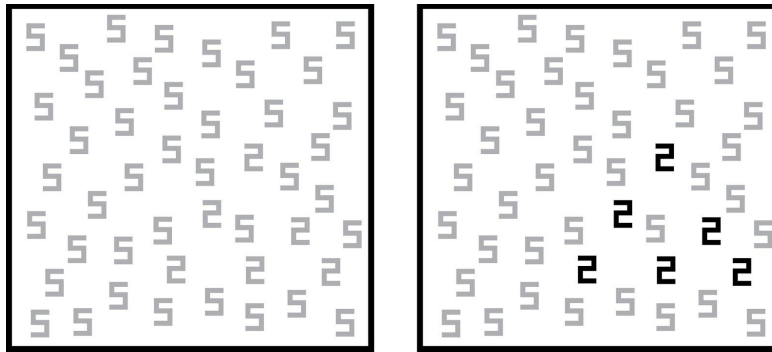


Figure 1 When normal subjects are presented with the figure on the left, it takes them several seconds to identify the hidden shape. Some grapheme-color synesthetes instantly see the triangular shape because they experience the 2s and the 5s as having different colors.

The pop-out effects in grapheme-color synesthesia, however, have been questioned. Cytowic and Eagleman (2009) suggest that the observed pop-out effects may not be due to pre-attentive bottom-up binding. Instead, when synesthetes pay attention to a grapheme during a visual search, the post-attentive synesthetic color experience may enhance their memory of the location of identified graphemes. The combined effect of the post-attentive synesthetic experiences of color-inducing graphemes organized in a particular pattern may be felt as the pop-out of a shape.

Later studies have argued that synesthetes are not more efficient than controls in visual search tasks (Edquist et al. 2006; Rothen and Meier 2009). Edquist et al. (2006), for example, conducted a study involving 14 grapheme-color synesthetes and 14 controls completing visual-search tasks. The targets had a unique display color (e.g., red targets against a background of black distractors) in some trials. In other trials the targets were specifically chosen to induce colors in the synesthetes. Synesthetes and controls identified the targets equally efficiently when the target had a unique display color, but the two groups were equally inefficient when the target induced a synesthetic color. This study indicates that synesthetic experiences do not form as a result of pre-attentive bottom-up perceptual mechanisms but, like higher-level perceptual phenomena, depend on selective attention. Though there is still extensive debate about pop-out effects and search efficiency in grapheme-color synesthesia, the combined results of recent research indicate that the mechanism underlying synesthesia does not merely involve local cross-activation in feed-forward processing.

Studies of cross-modal illusions also provide evidence against the early-sensory models of synesthesia. Bargary et al. (2009) studied the effect of the McGurk illusion on synesthetic experience. The McGurk effect is an illusion that occurs when one sound is

played while a person is shown uttering a different sound. For example, the speaker is mouthing the word /ba-ba/ while the audio is dubbed as /ga-ga/. What you end up hearing is /da-da/. The researchers tested the reactions of nine word-color synesthetes to a version of the McGurk illusion. The auditory stimuli were recordings of words such as /bay/, /cup/ and /cap/. The visual inputs were recordings of a person mouthing words such as /gay/, /con/ and /can/. When the auditory and visual stimuli are played simultaneously, subjects will normally hear entirely different words, for example, /day/, /cot/ and /cat/. The participants were presented with three videos: One in which the visuals were scrambled, so only the audio could be perceived, a second in which the sound was off, so only the visual could be perceived, and one where the audio and the visual were played simultaneously. After seeing the videos, the synesthetes clicked on a color in a large color array on a separate monitor. The researchers found that the synesthetes experienced significantly different colors depending on whether or not the McGurk illusion was present. For example, they would experience one color when hearing the word /bay/ in the scrambled video, a second color when seeing someone mouth the word /guy/ in the video with the sound off and a third color when exposed to the combined output normally giving rise to a perception of the word /day/. As the McGurk effect results from integrating inputs from multiple senses, it occurs relatively late in the perceptual process. Because the illusions affected the color experienced by the synesthetes, this suggests that synesthetic experience is driven by late, multi-perceptual processing, rather than early, unisensory processing.

A different type of factor that counts against the early-perceptual models of synesthesia is the lack of complete idiosyncrasy in grapheme-color associations in grapheme-color synesthesia. There is greater agreement on letter-color associations among grapheme-color synesthetes than would be expected by chance (Barnett et al. 2008a, Rich et al. 2005, Simner et al. 2005). Letter shape, grapheme frequency and color names can explain a good deal of these patterns. Brang et al. (2011) observed that graphemes that have similar shapes tend to elicit the same concurrents in grapheme-color synesthetes. Simner et al. (2005) found that frequently occurring letters tend to have common colors such as red, blue and yellow, whereas less frequently occurring letters have more unusual colors such as purple or brown. They also found that letters more often give rise to a concurrent whose expression in English starts with that letter than expected by chance. Beeli et al. (2007) found inverse correlations between grapheme frequency and saturation and lightness in color space. Less frequent letters tend to be darker and less saturated than more frequent letters. While the shape-concurrent correlations observed by Brang et al. (2011) are consistent with theory that grapheme-color binding occurs via interactions between color and shape areas in feed-forward preattentive mechanisms, the findings showing correlations between letter frequency and color or colors and color names count against the this possibility.

Recent testing of patterns in grapheme-color binding suggest that synesthetic binding may be partially facilitated by semantic memory of graphemes and their colors. Witthoft and Winawer (2013) matched the data from 11 grapheme-color synesthetes who had completed the Synesthesia Battery. 10 of the 11 subjects reported having owned one of three sets of refrigerator magnets with the same color scheme sold by Fisher-Price between 1972 and 1989. The researchers found a remarkable similarity of letter-color associations among the synesthetes. The fewest matches among the synesthetes was 14 letters. The probability of finding 14 or more letter matches in 26 chances is less than 1 in 1 billion, which strongly supports the hypothesis that the subjects acquired their letter-colors associations from the Fisher-Price toys. Witthoft and Winawer's results indicate that learning and memory may be involved in at least some instances of grapheme-color synesthesia.

Though learning and memory may be involved in synesthetic binding, attempts to train normal subjects to become synesthetes indicate that mere exposure to grapheme-color connections is not sufficient for inducing synesthesia. Several researchers have shown that training non-synesthetes can induce Stroop interference of the kind seen in synesthesia (Colizoli et al. 2012; Nunn et al. 2002; Meier & Rothen, 2009; Proulx, 2010). A Stroop effect is a reaction time interference in 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 (MacLeod 1991). The Stroop effect has been found in grapheme-color synesthetes. They can name the printed color of a grapheme much faster if the synesthetic color induced by the grapheme is congruent with the printed color (Mills et al., 1999; O'dgaard et al., 1999; Mattingley et al., 2001, 2006; Wollen and Ruggiero, 1983).

Although neurotypical controls trained to make semantic memory connections that mirror synesthetic connections are also subjects to Stroop interference, this does not show that the trainees have acquired genuine synesthesia, as over-learned associations produce a Stroop effect. Neuroimaging also indicates a difference between synesthetes and trainees. Nunn et al. (2002) trained 28 non-synesthetes to associate words and colors and measured brain activation using functional magnetic resonance imaging (fMRI). The non-synesthetes developed a condition similar to synesthesia but the trainees didn't have the same brain activation patterns as the synesthetes they were trained to mirror. This indicates that Stroop interference is an indicator, not of synesthesia, but of semantic memory connections that are tightly interwoven and automatic. As Stroop interference is an aspect of synesthesia, these results point to a possible shared mechanism in synesthetes and trainees.

Together the results of recent research suggest that synesthesia is not an early-perceptual phenomenon but is rather a type of late, perceptual processing that involves semantic memory and reinstatement of activity in sensory areas.

3. The Reactivation Model of Memory

One of the reasons that synesthesia researchers have been reluctant to consider semantic memory associations an important aspect of the mechanism underlying synesthesia is that synesthesia has a perceptual phenomenology and has been associated with neural activity in sensory areas of the brain (Nunn, et al. 2002; Sperling, et al. 2006; Paulesu et al. 1995; Elias et al. 2003), whereas memory is thought to be distinctly non-sensory.

However, this sort of argument contrasting ideational associations and sensory perception rests on an outdated understanding of memory. On this older conception, short-term maintenance as well as the storage of semantic information and personal episodes involves the transfer of relevant stimulus representations to one or more dedicated storage regions in prefrontal/parietal cortices or hippocampus (Baddeley 1992). Actively maintained or stored neural representations of stimuli are thought to be distinct from those encoded during sensory perception or proprioception.

Recent studies of memory, however, have found that the contents of our memories and the processes involved in the formation, storage, and retrieval of these memories are distributed across a wide range of neural assemblies in the brain that were active during encoding (e.g., Fuster 2009; Eichenbaum & Cohen 2001; Jonides et al. 2008, Martin & Chao 2001, McClelland & Rogers 2003, Schacter et al. 2007, Simons & Spiers 2003; Danker and Anderson 2010).

Working memory maintains behaviorally relevant representations of stimuli that were just experienced or retrieved over short time intervals (Rissman & Wagner 2012). According to a model of working memory that has been dubbed 'the sensory recruitment model' (Serences et al. 2009), working memory does not engage special working memory neural ensembles but consists in a maintenance of brain regions that were just activated. Areas in the prefrontal cortex allows for this activation maintenance through top-down modulatory control (D'Esposito 2007; Postle 2006; Fuster 2009; Gazzaley et al. 2004). Top-down attentional processes also facilitate the generation and maintenance of mental images. Mental imagery activates many of same cortical regions that are involved in sensory perception (Kosslyn 2005; Stokes et al 2009, 2011). One of the main differences between sensory perception and stimulus maintenance turns on the lateralization of the activity. During initial stimulus processing from one eye, only contralateral visual areas are implicated. During the activity maintenance that is crucial

to working memory, however, both hemispheres may become involved. This strongly suggests that stimulus maintenance in short-term memory goes beyond the retinotopic representation of the stimulus.

There is also solid evidence that long-term storage of episodic memories involves the formation of neural networks in distributed neural assemblies that were originally activated during a given episode (Kahn et al. 2004; Polyn, et al. 2005; Danker & Anderson 2010; Rissman & Wagner 2012). The brain regions involved in long-term memory are widely distributed, extending from sensory cortical areas to prefrontal cortex. Memory retrieval and recollection-based recognition involve a reactivation of these brain regions through coordination processes in hippocampus. The process of retrieval begins with a reactivation of neural pathways associated with features of the event. These features are then contextualized by reinstating neural assemblies associated with contextual information. Which aspects of an event are retrieved will depend on attentional processes that can render one aspect of the event more relevant than others.

Reactivation of neural assemblies engaged during initial stimulus processing also occurs during familiarity-based recognition and recollection-based recognition involved in semantic memory (Brown and Aggleton 2001; Gonsalves et al. 2005, Norman & O'Reilly 2003; Yonelina, et al 2005; Johnson et al. 2009; Chang, et al. 2011). Whereas recollection-based recognition depends on pattern completion, familiarity-based recognition depends on pattern matching between retrieval cues and stored representations. Semantic memory of stimuli from discrete visual object categories, such as faces, houses and chairs, may be more likely to be associated with specific cortical regions rather than others, viz ventral temporal cortex (Aguirre et al. 1998, Epstein & Kanwisher 1998, Kanwisher et al. 1997). But even memories of specific object categories are not highly modular. Most memory content is distributed across larger neural areas, and the brain regions encoding the contents of distinct memories may be overlapping (Haxby, et al. 2001; Ishai, et al. 1999, 2000). Memory of stimuli from discrete visual object categories, such as faces, houses and chairs, is stored in a distributed pattern involving a weighing of features. The distributed activation pattern that reflects the mean feature weightings for stimuli from the category is also sometimes called a 'neural signature' (Rissman and Wagner 2012; Haxby and colleagues 2001). Each category has its own neural signature insofar as exemplars within a category share more features with each other than they do with exemplars from different categories. So, even if the brain regions associated with memories of stimuli from, say, chairs and tables overlap, the memories of stimuli from the two object categories will have distinct neural signatures (Williams et al. 2007; Haushofer et al. 2008; Weber et al. 2009; Walther et al. 2009; Hsieh et al. 2010; Nyberg et al., 2000; Wheeler et al., 2000; Wheeler et al., 2006).

Together the results of recent studies of memory strongly indicate that short-term memory maintenance as well as the retrieval of long-term episodic and semantic information involve a reinstatement of activity in brain regions initially activated during stimulus processing. Sensory perception and memory retrieval thus are not entirely distinct phenomena on the neurological level, even though there is a clear difference in phenomenology between the events of perceiving and remembering.

4. The Memory Model of Synesthesia

The main studies suggesting that synesthesia involves memory associations can be explained on the hypothesis that synesthetic experience is a form of recollection-based recognition, which involves the hippocampus as an organizational unit. The hippocampus and its subregions are thought to be involved in the formation of relational information including association between arbitrary stimuli (Eichenbaum and Cohen, 2001; Squire, et al. 2004; Brown and Aggleton 2001). If we understand grapheme-color synesthesia along these lines, perceiving a grapheme printed in black ink elicits the reinstatement of activity in the brain's color areas via hippocampal organizational control. During learning processes the hippocampus would bind together neural networks in visual color areas and grapheme areas. Once a strong association has been formed, exposure to achromatic grapheme-stimuli would trigger recognition of the grapheme as a particular grapheme (e.g., the numeral '3') and memory retrieval of synesthetic color (e.g., a particular shade of green). Retrieval by the inferior frontal gyrus (IFG) would reinstantiate neural activity in the color areas, yielding a synesthetic experience. The renewed activity in the color areas may simultaneously give rise to a conscious color projection. Let's call this the 'Long-Term Potentiation Model of grapheme-color synesthesia'.

The suggestion that semantic memory plays an important role in synesthesia raises the question of why some people acquire synesthesia while others do not, and why some synesthetes experience more intense projections of concurrents than others. While specific episodes in a child's life, for example, playing with refrigerator magnets, may contribute to the development of synesthesia, the inheritability of synesthesia suggests that specific episodes in early life are unlikely to be the only factor. There are likely a multiplicity of factors involved in developing synesthesia. One may have to do with an increased sensitivity in neural regions that process the synesthetic concurrent. One type of research supporting this explanation has looked at the abilities of synesthetes to process stimuli that trigger their concurrent experiences without themselves triggering synesthesia. Yaro and Ward (2007) showed that in spite of the unidirectionality of grapheme-color synesthesia, grapheme-color synesthetes show superior perceptual

discrimination of color compared to non-synaesthetes. Banissy et al. (2009) looked at tactile and color discrimination in three groups of synesthetes with mirror-touch synesthesia and/or color synesthesia and a group of non-synesthetes. To test for discrimination they subjected the participants to color and tactile discrimination tests using the Farnsworth–Munsell Colour Hue Test and the Gratings Orientation Test. They found that color synesthetes have enhanced color sensitivity, whereas synesthetes who experience touch have enhanced tactile sensitivity. These results suggest that synesthetes have an increased sensitivity in neural regions that process the concurrent experiences.

A related kind of increased sensitivity was found in a recent study conducted by Terhune and colleagues (2012). The team looked at whether grapheme-color synesthesia involves increased cortical excitability in primary visual cortex. Using transcranial magnetic stimulation to stimulate the primary visual cortex, a technique known to induce phosphenes spanning the visual field of normal subjects, they found that synesthetes experience phosphenes at a three-fold lower phosphene thresholds compared to controls. They further showed that synesthetic experiences can be enhanced magnetically, indicating that the hyperexcitability of the primary visual cortex in synesthetes helps strengthen neural activation in the primary visual cortex to the threshold of consciousness.

Together with the reactivation model, these results indicate that whether a person becomes a synesthete or not and how intense of a project the synesthesia results in may depend on the degrees of hyperexcitability and reactivation of neurons in the primary visual cortex. Synesthetes may exhibit more hyperexcitability and reactivation of neural assemblies in visual areas than non-synesthetes, and projectors may exhibit more hyperexcitability and reactivation than associators.

A further factor that may explain why some synesthetes develop memory associations that are more tightly interwoven than normal memory associations and mnemonic associations acquired to aid memory may turn on the cognitive benefits of multisensory connections. Psychophysical studies of multisensory perception suggests that the integration of stimuli presented in different sensory modalities provide complementary information, leading to improved immediate performance (Doehrmann & Naumer 2008). Laurienti and colleagues (2004), for example, found quicker response times for congruent audio and visual stimuli compared to unimodal stimulation but there was no improvement when the congruent stimuli were both visual. The response time for incongruent stimulations was significantly slower in both multisensory and intra-modal contexts. The integration of stimuli from different sensory modalities can also lead to enhanced memory performance over time. Murray et al. (2004) showed that subjects had enhanced recognition abilities when shown repeated line drawings of common

objects that were initially accompanied by semantically congruent sounds in comparison to an initial presentation of semantically incongruent sounds, sounds with no semantic content or no sound.

On the basis of these considerations it is plausible to think that tightly interwoven, multisensory synesthetic connections prove to be particularly advantageous, both early on in learning processes involving the inducer and later on in memory retrievals involving inducer, concurrent or both. This hypothesis has been validated by several recent studies.

Smilek et al (2002) presented a grapheme-color synesthete with a random selection of letters which were either randomly colored or colored in a manner consistent with their synesthesia and asked the subject to remember the letter selection. They subsequently tested the subject's recall of the letter selections and found that the selections that were consistent with the synesthesia were more accurately retrieved.

Jarick et al. (2009) tested the experiences of a time-space synesthete L, who experiences the time of day and the months of the year as located in a imaginary space around her body in an order that depends on the particular perspective she takes in that space. Subject L and controls were exposed to a spatial cueing paradigm in which a visual month cue was presented to the subject followed by a square to the left or right. As subject L perceives some of the months to the left in her mental space and some to the right, the researchers predicted that the visual month cues would cause her to pay special attention to the left or right of the cue and would lead to a faster detection of squares in the regions she pays attention to compared to controls. These predictions were confirmed.

Simner et al. (2009) compared the performance of 10 time-space synesthetes on eight memory tasks to controls. Tasks included tests of semantic and episodic retrieval of the dates of various events, non-verbal visual short-term memory, the manipulation and rotation of objects in three-dimensional space and the recognition of 3D objects from 2D silhouettes. The synesthetes outperformed the non-synesthetes on all eight memory tasks.

The observations that synesthesia provide enhanced discriminatory abilities with respect to concurrent-related stimuli as well as superior performance on memory tasks suggest that a factor in the explanation of why some people develop synesthetic connections is enhanced cognition. Though this factor is likely to play a greater role in explaining how the synesthesia gene has survived the obstacles of evolution (Brang & Ramachandran 2011), it may also yield insight into the mystery of why particularly tight memory associations are actually formed in people with the genetic disposition.

5. Synesthesia as a Model of Multisensory Perception

Though synesthesia always involves a blending of sensory or cognitive streams (perhaps within the same sensory modality), synesthesia is different from online interaction between different sensory modalities. Multisensory binding of incoming signals from different sensory channels occurs spontaneously when the spatial and temporal attributes of the signals match. For example, in the absence of evidence to the contrary, the brain assumes that simultaneous signals come from the same source (Stein and Meredith, 1993). This spontaneous, temporary binding of signals can be overridden if the semantic contents of the (largely) unimodal signals do not match relative to the individual's learning history, for example, if you are viewing a cat but are hearing the sound of a dog (Doehrmann & Naumer 2008). Both high-level sensory integration and low-level, spontaneous integration involves binding two incoming sensory stimuli. In synesthesia, a unimodal sensory or cognitive input triggers a concurrent experience, which makes synesthetic binding different from multisensory integration.

However, several authors have proposed that other forms of multisensory perception involving common mapping patterns are examples of synesthetic experience that is common to all of us (Bien, et al 2012; Martino & Marks, 2001). Bien, et al (2012) argue that the presence of a mental number line, a spatial distribution of small and large numerical values across horizontal mental space, could be considered a very common form of synesthesia. Mondloch and Maurer (2004) report on a study in which children consistently attribute high pitched tone to a small sized or light coloured ball, which might be attributable to a synesthetic connection between high pitch and small size/light colors. Stevenson and Boakes (2004) point to the case of taste perception induced by odor as an example of widespread synesthesia. And Auvray and Spence (2008) consider, but ultimately reject, the idea, that flavor perception (particularly sweetness enhancement) is a synesthetic experience induced by smell and taste (and perhaps visuals).

Regardless of how we decide on the categorical relationship between synesthesia and common mapping patterns across sensory modalities or pathways, the mechanisms underlying synesthesia and certain types of multisensory phenomena no doubt overlap considerably. As synesthesia offers the possibility of strict control of inducer and concurrent and it shares aspects of its mechanism with certain multisensory phenomena, synesthesia may be a good model in which to study these types of multisensory phenomena.

One less frequently discussed type of multisensory perception that may be anchored in mechanisms similar to those underlying synesthesia is auditory object recognition that proceeds via interpretation of indexical sounds. Unlike symbolic sounds (e.g., words and narrative music), indexical sounds--when accurately interpreted--have meanings that are causally connected to the sound source, for example the sounds a dog makes when it is barking. The meaning of indexical sounds consists of low-level and high-level auditory features. Attributes such as pitch, spectral shape (pattern of amplitudes), temporal quality (continuous, oscillating, discrete serial units), transitions, on- and offset and rhythm are examples of low-level auditory properties, whereas a dog barking, a ball bouncing, water dripping, your colleague passing by outside the office door and the secretary getting ready to put on a fresh pot of coffee are examples of high-level auditory features.

Perceivers make use of memory associations between acoustic signals and the acoustic effects of the physical properties of objects on sound production to identify auditory objects from acoustic signals. Evidence from imaging studies suggests that retrieval of information about the acoustic effects of the physical properties of objects on sound production involves reinstatement of visual areas. Several studies have shown functional activation of visual areas by auditory stimulation in the blind (Buchel et al 1998; Weeks, et al, 2000; Arno, et al. 2001; Roder et al., 2002; Gougoux et al. 2005; Burton & McLaren 2006; Garg, et al. 2007, Voss, et al. 2008). Though auditory occipital activations have been absent in a vast number of neuroimaging studies of audition in sighted individuals, activation of visual areas has been observed in numerous brain imaging studies, including studies of music discrimination (Platel, et al. 1997; Janata, et al. 2002), word perception (Specht and Reul 2003), sentence interpretation (von Kriegstein 2003), auditory sound discrimination (Eisenberg, et al. 2005; Maeder, et al. 2001) and auditory spatial attention (Wu, et al. 2007). Cate et al. (2009) have shown that auditory occipital activations occur only when auditory stimuli are attended to in the active discrimination of sounds. The magnitudes of occipital activation does not depend on sound frequency or location but is probably a representation of the high-level meaning content of the sound. Because acoustic signals lead to visual representations in the perception of attended sounds, perception of attended sounds is thus multisensory, involving both the auditory and the occipital cortex. The cross-modal interactions in the perception of attended sounds likely are akin to the cross-modal interactions in synesthesia.

A, related, multisensory phenomenon that likely proceeds via mechanisms similar to those underlying synesthesia is language perception. The perception of language involves sound- or grapheme-imagery associations, either arbitrary associations or patterns unique to the individual. Language perception thus involves interactions between two sensory streams, e.g. the auditory and visual systems. Recent

neuroimaging studies confirm the multisensory nature of language perception (for discussion see Willems and Casasanto 2011). Action-related sentences which describe actions with different effectors, such as *I grasp the knife*, *I bite an apple* and *I kick the ball*, activate the premotor cortex in an effector-specific manner (Willems et al., 2010; Aziz-Zadeh et al., 2006; Tettamanti et al. 2005). Action-related nouns and verbs, such as *bookend*, *clock*, *door*, *cup* and *hammer*, also activate premotor and inferior parietal areas, and the amount of action associated with an object word is reflected in the activation of the motor system during word reading (Rueschemeyer et al. 2010). Bookends, clocks, cups, and hammers differ in how much action is needed to use the object effectively. Objects like hammers and cups that need active manipulation. give rise to higher levels of activation than objects like bookends and clocks that can be used without actively manipulating them. Similar observations have been made for action verbs, such as *kick*, *jump* and *run* (see Kemmerer and Gonzalez-Castillo, 2008 for discussion) and action sentences, such as *the wild horse crossed the barren field* (Saygin et al. 2010).

Language perception also has been found to involve a reinstatement of activity in perceptual areas. For example, object words followed by a word for a feature that typically belongs to the object reinstates activation in the area that would process the feature when it's perceived through a sensory modality (Simmons et al. 2007; Beauchamp and Martin 2007). For example, if *cucumber* were followed by *green*, it would give rise to increased activation in extrastriate color areas compared to if it were followed by *blue*. Aziz-Zadeh et al. (2008) found that listening to sentences describing faces (e.g., *The girl has freckles on her cheeks*) or places (e.g., *The house has a futon near the fireplace*) reinstates activity in the fusiform face area and the parahippocampal place area.

These data indicating that perceptual and cortical motor systems can be selectively activated during auditory object recognition and language perception suggests that these types of perception are multisensory in the same way as synesthetic experiences. All three phenomena involve reinstatement of activity in separate cognitive or sensory pathways.

6. Understanding Common Mapping Patterns

Besides serving as a potential model of certain forms of multisensory perception, synesthesia research can also potentially shed light on the function of common mapping patterns and the conditions under which they disserve us. The main function of common mapping patterns appears to be to allow for quick and reliable recall. In many cases of paired associate learning, the memory associations that are formed are arbitrary and only weakly encoded in neural networks. Because weakly encoded memory

associations are highly unstable, they are often lost, resulting in us forgetting things we were supposed to remember.

Mnemonic strategies effectively improve semantic memory for specific content even in individuals with mild cognitive impairment (Verhaeghen et al 1992; Hampstead, et al. 2008, 2012; Craik et al., 2007; Oswald et al., 1996; Willis et al., 2006; Brooks, et al. 1993) For example, a commonly used face-name mnemonic creates a relevant connection between a prominent facial feature and the meaning of a transformation of a person's name. As an example, to pair a face with the name *Bryant*, an individual might choose large eyebrows as the prominent facial feature, select the words *bride and ant* as the name transformation, and create a visual image in which an ant in a bridal gown takes part in a wedding ceremony in the grassy eyebrows. Another well known mnemonic technique is the method of loci. In the method of loci, sequential information is associated with particular places in a real or imagined environment such that by mentally walking through this space and visiting particular locations, a subject can sequentially recall the memories "stored" there. Mnemonic techniques are effective because they help strengthen connections formed as a result of paired associate learning. They are intended to generate relevant and more strongly encoded memory associations, which will increase the stability of the connection over time. Mnemonic techniques thus help generate semantic memory associations that more closely resemble the strong and stable connections observed in synesthesia.

However, sometimes strong mapping patterns is the cause of illusions. Jamie Ward (2013) has argued that we should 'distinguish synesthesia from seemingly similar phenomena such as illusions (in which the inducer is, in some sense, misperceived) and hallucinations (a concurrent without an inducer).' (p. 50) In synesthesia, unlike in ordinary illusions and hallucinations, the inducer is frequently perceived correctly, even if it also gives rise to a concurrent experience. However, while it is true that synesthesia typically differs from more well known illusions and hallucinations, synesthesia satisfies the normal philosophical characterization of these phenomena. What we call an 'illusion' is not simply a failure of the perceptual system to precisely mirror the stimulus, as the perceptual system never completely mirrors the stimulus. Rather, it's an *aberrant* (conscious) misperception of a trait of an actual object defined relative to normal veridical experiences of neurotypical perceivers. A hallucination, on the other hand, is an aberrant (conscious) misperception of an object that isn't there. A grapheme-color synesthete who perceives a grapheme printed in black as black but also perceives it as green is misperceiving a trait of the grapheme in a way that is unusual compared to the general population. So her experience is illusory. A synesthete who experiences the time of day and the months of the year as being in a space around her body, on the other hand, is experiencing a space that doesn't exist. So her experience is hallucinatory. Whether we choose to call synesthetic experiences 'illusory' or

'hallucinatory' or something else is a verbal issue. What matters here is that these experiences have something in common with ordinary illusions and hallucinations: they are a type of aberrant misperceptions that result from strong cognitive mapping patterns.

It is important to bear in mind that illusory (pre-conscious) perception is an integral part of the perceptual processes that lead to perceptual experience. When a person is approaching, the retinal image of the person grows in size, yet we don't experience approaching objects as getting bigger.

Well known optical illusions that we are all prone to experience exploit standard cues to color, brightness, size and shape constancies as well as monocular cues to depth perception. For example, light and shape provides a monocular cue about depth. By using the shadowing effect, one can create the illusion that an object is concave or convex (**Fig. 2**).

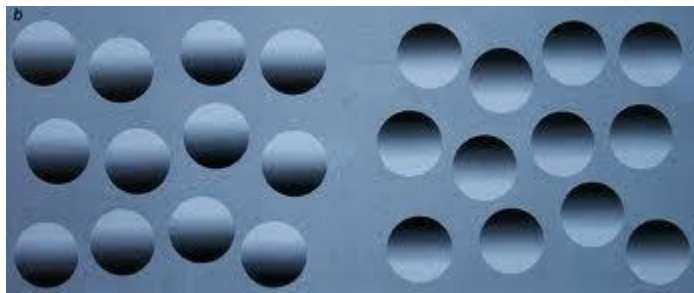


Fig 2: The shadows indicate that the circles on the left are convex and that the circles on the right are concave

Illusions that do not meddle with cues to depth perception or perceptual constancies are based on late-perceptual stream processes. Illusions of this kind are well-known in philosophical thought experiments. The philosophical literature is spawned with examples of misperceptions of spurious entities, such as sheep-shaped rocks, cleverly disguised mules, fake papier-mâché barns, lifelike robot cats and eerie doppelgangers. Though philosophical thought experiments can seem fanciful, these types of illusions are probably rather common in everyday life. You walk into a bar to meet your friend but walk up to and greet the wrong person. For a second you mistakenly experience someone with a slight resemblance to your friend as being your friend. Or you are sitting in the theater watching *Death Becomes Her* with Meryl Streep. In some of the scenes you misperceive Catherine Bell, Streep's body double, as Streep. Or you misperceive fish-flavored spherified watermelon as real caviar. These types of illusory perceptual appearances, represent high-level properties, such as being a sheep, being Meryl Streep and being real caviar. Presumably certain kinds of low-level perceptual experiences automatically trigger concepts of a particular kind via memory. When these concepts do not correctly apply to the object perceived, the result is an illusory

perceptual seeming (a type of high-level perception). These illusions can thus be understood in terms of automatic common mapping patterns similar to those found in synesthesia.

7. Conclusion

The idea that memory underlies synesthetic binding has been discredited by numerous synesthesia researchers because it has been thought that memory is a conceptual phenomenon entirely distinct from perception, whereas synesthesia typically has a perceptual phenomenology associated with neural activation of sensory brain areas. Recent research on memory, however, suggests that maintenance of working memory and the retrieval of semantic and episodic memory involve the reinstatement of neural processes in sensory (or other) areas activated during the original perceptual, emotional or cognitive sensory processes. The findings suggest that memory can have a perceptual phenomenology and neural activation profile very similar to what has been found in the case of synesthesia. When the results from synesthesia research and studies of memory are put side by side, it becomes apparent that synesthetic connections likely are a special case of common mapping patterns. The main differences between ordinary mapping patterns and synesthetic associations may consist simply in the tightness and stability of the association as well as the sensitivity of sensory neurons that process the concurrent. The suggestion that synesthesia is best understood as tightly interwoven semantic memory associations makes the phenomenon particularly suitable as a model of the types of multisensory perception that likewise consist in common mapping patterns.

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