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A Summary of Current Ideas on Synesthesia

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Abstract

Synesthesia is a condition in which stimulation of one sensory modality causes unusual experiences in a second, unstimulated modality. Commonly synesthetes are graphemic-chromatic, perceiving specific colors when exposed to specific letters or numerals. Other synesthetes perceive color for phonemes, color for music and tones, tactile perceptions of shapes for taste, and taste sensations for phonemes. Several neural models have been developed to explain the occurence of synesthesia, the most common theory suggesting that synesthetic percepts are the result of crossactivation between brain regions, such as the visual word form area in the inferior temporal lobe and V4, perhaps as a result of insufficient neural pruning. Characteristics of grapheme-color synesthesia and implications for the involvement of V4 and the posterior parietal cortex in this form of synesthesia are discussed. Case studies of music-color, and lexical-gustatory synesthetes are also presented. Findings strongly suggest that synesthetes are a heterogeneous group, differing in the kinds of information (perceptual and conceptual) that elicit their synesthetic concurrents and also in the experience of their synesthetic percepts.

A Summary of Current Ideas on Synesthesia

Synesthesia is a condition in which stimulation of one sensory modality causes unusual experiences in a second, unstimulated modality. Synesthetic percepts are involuntary and consistent across time (Mills, Boteler, & Larcombe, 2003). Most commonly, synesthetes are graphemic-chromatic, meaning they consistently perceive specific colors when exposed to specific letters or numerals. Other synesthetes perceive color for phonemes or units of speech sounds, color for music and tones, tactile perceptions of shapes for taste, and taste sensations for phonemes. A compilation of over 400 synesthetes revealed that 68 percent are graphemic-chromatic, while only 10 percent are phonemic-chromatic. (Day, 2005, as sited in Hubbard, Arman, Ramachandran, & Boynton, 2005). Other forms of synesthesia are less common. Synesthesia has been a phenomenon of interest for centuries. Pythagoras acknowledged the existence of some sensory inter-relations in the sixth century BCE, when he set out to assign colors to musical notes (Ione & Tyler, 2004). However, Pythagoras's idea has almost always been seen as neurologically abnormal. It contradicted the idea that we have five distinct senses and was at odds with Mueller's Law of Specific Nerve Energies, which stated that each sensory modality has a characteristic sensory quality and that the nature of a sensory perception is defined by the pathway that the information is carried through (i.e. information traveling from the optic nerve will always be experienced visually). Despite its long history, synesthesia was not formally documented until 1812, when the medical doctor G.T.L Sachs reported on the grapheme and phoneme-color synesthetic perceptions in himself and his sister. Later, Gustav Fechner used the scientific method to study color-sound interactions and document the color associations to tones of 347 people. Five years after Fechner's work, psychiatrist Eugen Bleuler studied 600

people and found that 12 percent reported color associations to vowels. Several nineteenth and twentieth century artists are also well known for having synesthetic abilities. Composers Alexander Scriabin and Nikolai Rimsky-Korsokoff perceived colors for musical notes, writer Vladamir Nabokov perceived colors and textures for different phonemes, and painter Vassily Kandinsky experienced color and other visual sensations for music. Synethesia was studied less after the rise of behaviorism because there was a reduced interest in studying subjective, non-observable perceptions for knowledge; however, it has returned as a subject worthy of study with the increased interest in consciousness and its neural basis. (Hubbard et al., 2005).

Several neural models have been developed to explain the occurence of synesthesia. The predominant neural model, local crossactivation theory, was developed around the finding that the visual word form area in the temporal lobe, the region of the brain important in the recognition of digits and letters, lies adjacent to V4 in the visual cortex, the region critical for color perception. This might suggest that for grapheme-color synesthetes, synesthetic percepts are the result of crossactivation between these two regions. Hubbard & Ramachandran (2005) note that it might have a neural basis similar to phantom limb sensations in amputees, which are thought to arise from cortical reorganization. Several amputees reported having experienced sensation in their missing limbs with stimulation of their facial-nerves. The novel percepts were involuntary and reproducible because the cortical area designated for processing of information from facial nerves had grown into the area designated for processing information from the nerves of the missing limbs. Evidence supporting the idea of local crossactivation comes from the finding that in fetal macaques, 70 to 90 percent of connections to V4 comes from higher brain structures, while only 20 to 30 percent of connections to V4 in the adult macaque come from higher brain areas. Prior to neural pruning it appears that there are an abundance of connections

from the visual word form area in the inferior temporal lobe to V4. These connections could persist into adulthood as a result of a genetic mutation influencing neural pruning, leading to synesthetic experiences of color for digits and letters.

A second hypothesis, Disinhibited Feedback theory, suggests that synesthetic percepts might be due to disinhibited feedback from regions of the brain that facilitate multisensory integration. Proponents suggest that it could be related to functioning of the temporo-parietal-occipital junction. The fact that some people on psychedelic drugs report synesthetic experiences might support this theory. Other evidence suggestive of disinhibition comes from a case study, PH, who became blind in adulthood due to disease. Several years later he reported that tactile stimulation produced the impression of "seeing" visual movement. Further, greater tactile sensation was necessary to elicit the visual perceptions of movement when PH's hand was in front of his face than when it was behind his face. This might suggest the involvement of top-down processing by multisensory structures in synesthesia.

A third theory also based on disinhibition is known as re-entrant processing. This theory suggests that grapheme-color synesthesia might be related to feedback from higher areas, like the inferior temporal areas, to lower structures, like V4. It suggests that there is retrograde feedback from higher structures to lower structures in addition to the upward transfer of information from V1 to V4 and then from the posterior inferior temporal region (containing the visual word form area) to the anterior inferior temporal region (important for attaching meaning to graphemes and words).

A study conducted by Simner et al. (2005), comparing grapheme-color synesthetes to non-synesthetes, highlights characteristics of synesthesia. Data was collected from 70 grapheme-color synesthetes and 317 non-synesthetes, both predominately female. Synesthetic participants

were given a written questionnaire asking them to describe color associations for the 26 letters of the alphabet as well as for the digits zero through nine. Non-synesthetes were broken up into forced and free choice groups. The free choice group was also given the aforementioned questionnaire and was instructed to note color associations if they easily came to mind for a letter or digit, but they were not forced to generate grapheme-color associations if they were not salient. The forced choice group, upon being given the questionnaire, was instructed to write down the first color association that came to mind for all 26 letters and digits zero through nine. They were forced to make an association for every grapheme. Thirty-five participants from this group served as controls for a test of genuineness; they and all 70 synesthetes were retested on their grapheme-color associations after a pre-determined time interval. For synesthetes this time interval was 2-6 months and for controls it was 1-3 weeks. Results of this test indicate that synesthetes' associations remain very constant over time (92 percent consistent for letters and 93 percent constant for numbers) while the control participants showed a great deal of variance over time ((35 percent consistent for letters and 36 percent constant for numbers)35 and 36 percent consistency for letters and numbers respectively).

Results from a comparison of the initial association questionnaires also indicate that synesthetes produced a greater range of color descriptions in their associations than non-synesthetes. This might suggest that the grapheme-color associations for synesthetes are more actual or more vivid than those of controls. Further, colors most frequently produced by controls tended to be those that rank highest for ease of generation and typicality (according to a Battig and Montague ranking scale). The easiest colors to generate were associated with letters closer to the beginning of the alphabet. This was not the case for synesthetes, suggesting that their associations are genuine and durable rather than something spontaneously generated. For

example, the most commonly associated colors for synesthetes were brown, yellow, and grey

while the most commmonly associated colors for controls were yellow, green, and blue. While

synesthetes did not pair high frequency graphemes with colors based on typicality or the colors'

ease of generation, grapheme-color frequencies were correlated, such that high frequency

graphemes were often paired with high frequency color terms. More specifically, the highest

frequency graphemes were paired with fundamental color distinctions that were made the

earliest, perhaps suggesting that persistent associations reflect early learning. Both synesthetes

and controls were influenced by linguistic priming, that is they were more likely to attribute a

color to a grapheme if the color's name began with the grapheme of interest (for example *b* and

the color blue). This effect was less prominent among synesthetes than controls. For controls,

however, this effect was cognitive rather than perceptual as for synesthetes.

Synesthesthetic associations are over 90 percent consistent over time (Hubbard &

Ramachandran, 2005; Simner et al., 2005). Further, synesthetes seem to produce color-

grapheme associations through different mechanisms than non-synesthetes, and their associations

are perceptual rather than cognitive in nature (Simner et al., 2005). A study conducted by

Hubbard et al. (2005) also indicates that synesthetic experiences are qualtitatively different from

the cognitive associations made by non-synesthetes. Synesthetic percepts are shown to facilitate

texture segregation as well as the effects of crowding. In an embedded figures task, six

grapheme-color synesthetes and 40 controls per synesthete were shown displays of 44 to 48

black graphemes on a white background, in which a form (a square, diamond, triangle, or

rectangle) composed of six to eight graphemes was embedded in a matrix of distractor

graphemes (one distinct letter). Graphemes that composed the embedded figures elicited either

red, green, blue, or yellow percepts for synesthetes. Participants were to identify the embedded

shape.

   Results indicate that the synesthetes were significantly better than their respective controls at identifying the embedded shapes. Furthermore, when controls were shown displays in which the embedded figure was displayed in the synesthete's corresponding color, they performed better than the synesthetes. This suggests that synesthetic color percepts are not as effective as real colors in improving performance and perhaps less salient. This experiment did not show synesthetic participants embedded figures in color (neither in their corresponding or non-corresponding colors). Perhaps if the experiment had used this manipulation, synesthetes would have performed better than controls.

   In a second experiment, particpants were asked to complete a crowding task, in which a cross of five graphemes (with the target grapheme at the center) was presented to the periphery. As in the first experiment, the target graphemes elicited percepts of red, green, blue, or yellow in synesthetic particpants. Results indicate that three of the synesthetes performed significantly better than their respective controls, while three did not. As might be expected, when controls were shown the target in color, they performed significantly better than the synesthetes. The effect of real color seems to be greater than the effect of synesthetic color percepts.

   These experiements were followed by a third experiment that measured the brain activity of the same six synesthetes and six non-synesthete controls in four functional magnetic resonnance imaging (fMRI) sessions. Participants viewed graphemes while in the scanner and were asked to identify them as standard, upright, or italicized. Overall, results indicated that synesthetes showed more activation across all areas than non-synesthetes. However, individual comparisons reveal that the only area that produced significantly greater activation in synesthetes than nonsynesthetes was area V4, the region of the brain thought to code for color. Also,

magnitude of activity in area V4 corrlated with behavioral performance on the crowding task.

Degree of activity in V4 is thought to relate directly to the strength of synesthetic colored

percepts. Activity in regions of the brain important in grapheme idenfication was no different for

synesthetes than for non-synesthetes. Hubbard et al. (2005) also found greater neural actvity in

early visual areas of synesthetes in comparison to control non-synesthetes. Activity in these

regions was highly variable among synesthetes, with some synesthetes showing greater

individual activty of V1 in response to graphemes than in response to other nonlinguistic

symbols. Variable activity was also noted in the parietal lobe, particularly the intraparietal sulcus;

however, there was no clear difference in activity between synesthetes and non-synesthetes.

Hubbard et al. were hesistant to make claims regarding this activity because intraparietal sulcus

has been implicated in a number of processes.

Results of this study suggest that synesthetic colors lead to improved behavioral

performance in search tasks similarly to real colors, and that they activate the same color

selective region in the brain as real colors. Results from the crowding task in which only three of

the six synesthetes performed signficantly better than controls are thought to be related to a

division of abilities among synesthetes. Two subtypes of synesthesia have been defined. For

some grapheme-color synesthetes, it is the alphabetical or numerical concepts that elicit color

percepts. For others, it is the perception of the physical graphemes that elicit color percepts. The

former have been referred to as higher or associator synesthetes while the latter have been

referred to as lower or projector synesthetes (Hubbard et al., 2005; Smilek & Dixon, 2002, as

cited in Hubbard et al., 2005). One synesthete commented that while performing the crowding

task, he could not identify the target grapheme but he could identify it based on the perception of

its synesthetic color. A second synesthete who did not show an advantage on either the crowding

or embedded figure task,commented that she did not experience her synesthetic colors until she had identified graphemes (and in the case of the behavioral testing, the target graphemes). Therefore, her synesthetic percepts could not aid her performance on either task.

A second study conducted with 13 auditory word-color synesthetes (and 27 controls) also confirmed activity of V4 with synesthetic color percepts. Nunn et al. (2002) used positron emission tomography (PET) scans to identify areas active in the brains of word-color synesthetes as they listened to words and tones. They found that words elicited activity in language areas similarly in controls and synesthetes. However, synesthetes also showed activity in the color selective region of the left fusiform gyrus, which corresponds to left V4. Although V4 was only active in the left hemisphere of the brain, synesthetic colors were not exclusively experienced in the right visual field, possibly suggesting that area V4 is not strictly contralateral. Area V4 became active without any indication of activity in V1 or V2, which would normally be active in response to seeing colors. In a second experiment, Nunn et al. (2002) used PET scans to measure brain activity of the same synesthetes and controls in response to chromatic mondrians. Right hemispheric activity of V4 was similar between controls and synesthetes. However, controls showed corresponding activity of left V4. There was no indication of left V4 activity in the synesthetic participants in response to seeing colors. This affirmed that the left lateralized response of V4 to hearing words cannot be attributed to greater overall sensitivity of V4 to stimuli. In a third experiment, control participants learned and practiced eight word-color associations and were asked to visualize the corresponding colors when words were auditorally presented through headphones. However, even under these conditions, control participants failed to show any V4 activity. This is an indication that synesthetic color percepts are more closely related to true color perceptions than to color imagery.

There are several implications that can be drawn from the results of the Nunn et al. (2002) study. The first is related to the finding of V4 activity in synesthetes without activity of the primary visual cortex and V2. This is evidence that the brain is capable of generating visual percepts without activity of the primary visual cortex and it suggests that the primary visual cortex might not be sufficient or possibly even necessary for conscious visual experience. A second implication is related to the finding that synesthetic perceptions were facilitated by activity in the left V4 of word-color synesthetes, though this area (active in controls) remained inactive while they viewed chromatic mondrians' colors. It seems that synesthetic color perception might reduce the availability of the left V4 for normal processing of colors. The significance of synesthetic color percepts' relation to activity in left V4 is that the left hemisphere is also the primary site of language processing. Synesthetic percepts could be related to left-lateralized direct projections, neural connections from speech areas to V4.

Several studies have also indicated the parietal lobe to be a region of interest in synesthetes. Rich et al. (2003, as sited in Esterman, Verynen, Ivry, & Robertson, 2006) found activity in the posterior parietal cortex during grapheme-induced colored percepts. This region has been implicated in normal binding of color and shape, as in conjunction with visual search tasks (Donner et al., 2002, as sited in Esterman et al., 2006). More specifically, the intraparietal sulcus has been associated with color-grapheme synesthesia, both in the left hemisphere and bilaterally (Esterman, 2006). In the aforementioned study of color-grapheme synesthetes, Hubbard et al. (2005) also noted increased activity in the intraparietal sulcus, although they were hesitant to claim that there were significant differences in regional activity between synesthetes and controls while performing psychophysical search tasks.

Esterman et al. (2006) examined the role of the parietal lobe and parietal binding

mechanisms in two color-grapheme synesthetes who could be classified as "projectors" since they experience their photisms mapped in the external world. The method was fairly explicit. Trials involved the presentation of a colored letter in one of three colors. The color was either congruent or incongruent with participants' synesthetic photisms. In congruent conditions, synthetic facilitation was expected to occur where reaction times for color identification are faster than baseline reaction time (reaction time for identifying the color of graphemes that do not induce synesthetic percepts). Incongruent conditions were expected to produce synesthetic interference, in which discrepancy between the physical color of the grapheme and the graphemes corresponding synesthetic photism causes reaction times to be slower than baseline. Participants engaged in the color-naming task following transcranial magnetic stimulation of the left or right posterior intraparietal sulcus. Results indicate that following transcranial magentic stimulation of the right parietal region of interest, both synesthetes showed significant attenuation of synesthetic interference, suggesting that the right parietal cortex plays a greater role in color-form binding than the left. Stimulation of the right posterior parietal cortex seemed to disrupt synesthetic color-form binding. This could indicate that the intraparietal sulcus is important for color-form binding when color is elicited by shape as well as physical properties. This study supports the disinhibited feedback theory of synesthesia, in which a multimodal association region is the basis of synesthetic percepts. Esterman et al. concluded that these findings might not generalize to all to synesthetes and might be particularly related to projector synesthetes and those whose percepts are highly connected to spatial features of inducing graphemes.

A wealth of research has been conducted on grapheme-color synesthesia; it is the most common form of this intersensory phenomenon. While it has thus far been the focus of this

paper, other less common types of synesthesia will also be discussed. A second kind of

synesthesia is lexical-gustatory, in which speech sounds induce involuntary taste sensations.

Luria's patient S. is an example of a synesthete who experiences taste percepts; however, his

were induced by tones of varying pitches and volumes (Ward & Simner, 2003). Patient JIW

(studied by Ward & Simner, 2003) experiences tastes in response to speech sounds. He notes that

while his mother does not have synesthesia, his sister reports associating words with smells and

colors. This might suggest a genetic link. Like S., JIW also reports having eidetic imagery, a

capacity previously linked to synesthesia (Cytowic & Wood, 1982b, as sited in Ward and Simner,

2003). Like most true synesthetes, he can describe his synesthetic percepts in great detail. For

example, he reports that the word *this* tastes of "bread soaked in tomato soup", and *safety* tastes

of "lightly buttered toast". He was shown to be 94 percent consistent across time in his lexical-

gustatory associations. Most of his synesthetic taste sensations are of edible items (all food

groups including drinks and sweets); however, a small percent of percepts can be categorized as

bodily inedibles (such as vomit and fingernails) and synthetic inedibles (wax candles, for

example). Across testing, JIW was asked to describe the taste of 671 words, although 44 percent

elicited no taste at all. Another 524 word-taste associations were compiled by JIW in response to

interactions with his daily environment. Similar to the way grapheme-color synesthetes display

activity in the color selective brain region V4 in response to graphemes, JIW shows bilateral

activity of the primary gustatory cortex when listening to words but not to tones.

Ward and Simner sought out determinants of JIW's synesthetic tastes and found tastes to

be reliably associated with phonemes. Of 64 tastes described by JIW, 60 were significantly

associated with the presence of one or more phonemes. Further, certain phonological sounds

taste alike regardless of whether they are expressed the same orthographically. For example, the

taste of eggs is evoked with the phoneme /k/ whether it appears as a *c* as in *accept*, as a *ck* as in *chuck*, as an *x* as in *sex*, or as a *k* as in *York*. Similarly the phoneme /g/ (as in *begin*) tastes of yogurt; when *x* takes on the phonological sound of /g/ it also tastes of yogurt. This finding indicates that trigger of taste percepts are phonological rather than orthographical in nature. JIW's synesthetic responses also seem to be dependent on the order of phonemes in a word. When given 24 pairs of words that contain the same phonemes only which are reversed in order (fox and scoff, for example), none of the similar pairs produced identical or similar synesthetic tastes, although 72 percent of words did elicit a synesthetic percept. It was also discovered that in many of JIW's synesthetic associations, the phoneme that triggers a certain taste is present in some subset in the phonemes that form the name of the concurrent taste percept. For example, *Barbara* tastes of rhubarb, *April* tastes of apricots, and *Virginia* tastes of vinegar. His pairings of 436 pairs of inducer words to [words for] concurrent tastes experienced contained significantly greater phonological overlap than those found on a randomized control list.

In addition to phonological links between inducer words and subsequent taste experiences, semantic relationships are also present. For example, blue tastes "inky". Further, *shop* (which bares phonological resemblance to the word *chop*) tastes of lamb, which could be semantically associated to the word *chop*. Further, *union* tastes of the phonologically similar percept of onion, however, words semantically related to union (society and united, for example) also produce the same taste sensation. Many food words also taste of themselves (such as *cabbage* and *bacon*), although their phonological components could be expected to elicit other taste experiences. This indicates that lexical-conceptual information can override correspondences made at the phonological level. Further evidence of this can be derrived from the fact that when tested on 36 pairs of homophones (such as *sea* and *see*), JIW experienced

corresponding tastes percepts only 41 percent of the time. This percentage is significantly lower than the consistency reported for words identical in phonology and semantics.

Through learning of food-related vocabulary, it is thought that some phonemes become associated with certain gustatory experiences; words that share phonemes with these food-related words also come to elicit the same gustatory responses. This might imply the crosstalk theory, in which neural connections persist into adulthood instead of being pruned away; phoneme and taste centers in the brain are also geographically close to one another like the grapheme recognition and color areas proposed as the root of grapheme-color synesthesia. However, this does not account for semantic lexical-gustatory associations. Instead, it could be that lexical-gustatory synesthesia might be related to disinhibited feedback from brain regions important for conceptual knowledge related to food, and food names to areas responsible for taste generation. (Ward & Simner, 2003).

A third kind of synesthesia is music-color synesthesia. As previously noted, several famous composers have been identified as having synesthetic percepts of color and shape for different tones and sounds. Patient GS, a 22 year old female who experiences colors, textures, and, most saliently, shapes for musical notes, was studied by Mills, Boteler, and Larcombe (2003). She also experiences synesthetic percepts for spoken digits, voices, emotions, smells, bodily sensations, and environmental noises. In one experiment, GS listened to individual notes (five notes in each of eight octaves played in the sounds of four instruments: the oboe, piano, guitar, and french horn) played on a keyboard that had used recordings of a variety of actual instruments to produce sounds. GS then described her photisms in an open-ended fashion and they were recorded by experimenters. In some instances she drew her photisms in order to supplement what she described. Results indicate that GS perceived darker colors for lower

octaves, while the upper two octaves were whites, and the middle octave of varying colors.

Further, higher notes seemed to be represented by smaller photisms. Marks (1974) found similar

positive pitch-brightness associations in non-synesthetic research participants who were asked to

find pure tones to match grey sufaces of varying luminance. This might be an indication that

some forms of synesthesia stem from neurological mechanisms common to everyone.

A second experiment presented in Mills, Boteler, and Larcombe (2003) looked at the

effect of contrast on GS's perceptions of middle notes played after a much higher or a much

lower note. It was hypothesized that a darker color would be experienced for a middle note

played after a very high note than for the same middle note played after a very low note. This

hypothesis was supported. GS did perceive a lighter colored photism for a middle note played

after a low note than for a middle note played after a high note. This implies that synesthetic

percepts can be influenced by context.

A further experiment which played three notes from octaves starting at middle C from

eighteen instruments indicated that GS's photisms for the same notes varied considerably when

played by different instruments, and that notes played by families of instruments produced

photisms similar in shape. It was apparent that color was elicited by pitch while photisms of

shape were elicited by the timbre of a sound.

The most prominent conclusion that can be drawn from these studies and case studies is

that synesthetes may constitute a highly heterogeneous group. Some experience synesthetic

percepts at the conceptual level while others experience synesthesia at the perceptual level.

Perceptual synesthetes seem to have the capacity to use their synesthesia as an aid in

psychophysical search tasks; for them synesthesia is evoked early in visual processing (Hubbard

et al., 2005). Synesthetes also differ in their synesthetic experience, some grapheme-color

synesthetes experience colors projected onto external stimuli while others simply see it in their "mind's eye." Further, it seems the mechanisms inducing synesthesia in grapheme-color and lexical-gustatory synesthetes differ. Case study JIW provided evidence that there is a strong semantic component to lexical-gustatory synesthesia (for example, spoken food words tend to taste of themselves) that is not present in grapheme-color synesthesia (the word red, does not necessarily elicit percepts of the color red).

There is also some dispute about the neurological structures involved in synesthesia. For grapheme-color synesthesia both the posterior parietal cortex and visual area V4 have been implicated. Also, the lack of left V4 activity in synesthetes in response to presentation of colored stimuli in the Nunn et al. (2002) study suggests that synesthesia may have the effect of reducing visual areas available for normal color processing. It is also possible that color processing is simply more efficient and therefore is more localized in some synesthetes. The music-color synesthete GS provided evidence that context can influence synesthetic percepts. She experienced a darker colored percept for a middle tone following a high tone than for the same middle tone following a low tone. This might also be support for conceptual versus perceptual synesthesia. Finally, there is evidence that synesthesia has a genetic component. Historically, Sachs documented similar color synesthesia in both himself and his sister, and lexical-gustatory case JIW reported that his sister experiences synesthetic colored percepts and smells for words. Researchers conducting a study comparing grapheme-color and lexical-gustatory synesthetes also found that 6 of their 14 synesthetes reported having relatives with synesthesia (Ward, Simner, & Auyeung, 2003).

There are several implications for normal populations that can be drawn from studying synesthetes, including the finding that the primary visual cortex might not be necessary for

experiencing conscious visual percepts. However, it does not seem that the normal population has the ability to activate later visual structures without activity of V1 and V2. A second implication might be that visual imagery does not necessarily activate visual structures in the normal population. Nunn et al. (2002) demonstrated that controls asked to visualize colors that they had learned to associate with graphemes failed to produce activity in the color selective region V4. This study also indicated that some hearing-color synesthetes only show V4 activity in the left hemisphere when they experience colored percepts. This finding could indicate that V4 is not strictly contralateral. Finally the similarity in pitch-luminance perception between music-color synesthete GS and the non-synesthetic population studied by Marks (1974) is evidence that the normal population also has some capacity for intersensory percepts.

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