Neuroanatomical bases for synesthesia and their implications for perception and consciousness

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Keywords: synesthesia, synesthetes, neuroscience, perception, consciousness, grapheme-color, semantics, cross-modal mechanisms

Abstract

Synesthesia is a condition that affects an individual's conscious perception of the world. Individuals with this disorder vary greatly, but have in common the phenomenon of cross-modal perceptions. For example, grapheme-color synesthetes perceive color when presented with graphemes, such as letters and numbers. In this review, we investigate this phenomenon further in order to evaluate the plausibility of currently proposed mechanisms. There is some debate about whether synesthetic mechanisms are primarily perceptual or are primarily concept-driven. There are also important questions about the relationship of attention and consciousness to synesthesia, and here we examine specific studies that shed light on this issue. We will show that the evidence suggests a wide heterogeneity between synesthetic subjects. We will also demonstrate that *both* perceptual *and* concept driven hypotheses are crucial to the understanding of the inner neural mechanisms of synesthesia. By achieving said understanding, we may be able to gain valuable information about how conscious experience is produced through neural mechanisms.

Introduction

Synesthesia is a phenomenon in which an individual's experience includes phenomenological qualities associated with one sensory modality when presented with stimuli associated with a different sensory modality. More simply, it is when sensory perceptions get "mixed-up," such that one's experience may include the taste of a color, or the color of a sight or sound. One specific example discussed here is "grapheme-color synesthesia," in which viewing letters and numbers induces a concurrent perception of color [1]. Reports of synesthesia's prevalence vary widely, but one study by Simner et. al reports a prevalence of 4.4% [2]. This is higher than many previously proposed prevalence rates and heightens the imperative to understand how exactly this phenomenon occurs. Synesthesial mechanisms are thought by some to be linked to mechanisms vital to concept-formation, language, and the formation of subjective experience [3].

One hypothesis to explain the mechanism of synesthesia is the "cross-activation" model, according to which neural modal networks associated with one processing center in the brain are aberrantly connected with another one, resulting in cross-activation. This model was proposed on the basis of fMRI studies in grapheme-color synesthetes. Findings showed co-activation of the posterior temporal grapheme area (PTGA) and color processing centers (V4) [4]. According to this hypothesis, the nature of synesthetic experience will be highly dependent on where in the system the crossing-over event occurs. This is consistent with the evidence that the population of synesthetes is extremely heterogeneous [5]. Synesthesia is a naturally occurring phenomenon, but it has also been reported in case of drug use such as LSD or psilocybin. However, it is unclear whether drug-induced synesthesia operates via the same mechanisms as congenital synesthesia [6].

It is not clear that synesthesia is associated with any behavioral or medicinal deficit; if anything, synesthetes are associated with *improved* abilities for things like visual search tasks and artistic endeavors [7]. However, the study of synesthesia is relevant to scientific study for many reasons. To begin with, increased knowledge about sensory anomalies also increases knowledge about normal perception and enables the scientific community to develop a more complete understanding of the complex human brain. Further, many scientific endeavors are performed in the pursuit of knowledge for the sake of itself. A piece of knowledge that has no medicinal utility still has value *in itself* simply because it increases our body of knowledge.

In addition, learning about synesthesia has vital implications for philosophy and consciousness studies. Consciousness itself is difficult to study scientifically because of its inherently subjective nature. While we can study the neural processes responsible for producing subjective experiences, there seems to be an *explanatory gap* between these neural mechanisms and the qualitative features of *experience* itself. A particularly mysterious aspect of consciousness concerns semantics and language. What does it mean for a term to have "meaning"? Is there a difference between being able to give all the synonyms for a word, and actually *understanding* what the word means? What does it mean for a thought to have "content," and how do thoughts obtain content? It is difficult to see the empirical applicability of philosophical questions such as these. However, one cannot deny that both consciousness and semantics exist in the universe: though they are subjective in nature, they are also objectively real and deserving of study. A study of synesthesia may be able to provide this link between neurochemistry and semantics [8]. This is because in addition to perceptual mechanisms proposed for synesthesia, conceptually driven mechanisms are also implicated. One study discussed here explores this notion and attempts to disentangle these mechanisms from the perceptual ones [9].

This review will focus on four distinct studies of synesthetic patients in order to examine its mechanisms, effects, and implications for the rest of us [5,9,10,11]. We will look specifically at grapheme-color synesthesia as well as sound-color synesthesia to determine whether different synesthetic forms are mediated by similar mechanisms. We will explore the plausibility of the cross-activation hypothesis and examine the similarities of this mechanism to mechanisms present neonatally and in non-synesthetic adult experience. Some evidence suggests that all neonates are endowed with synesthetic ability and that this ability is lost for most individuals during development [10]. If this is true, the study of synesthesia might have vital implications for neonatal development. Finally, we will examine the credibility of proposed "semantic" mechanisms and discuss their applicability to broader philosophical and scientific issues.

Study 1

The first thing that must be assessed is whether the behavioral differences in synesthetic subjects correlate with specific neurochemical activation. Using behavioral and fMRI studies, Hubbard et al (2005) attempted to do just that. They tested six grapheme-color synesthetes with two different experimental tasks and compared them with control groups. They subsequently performed similar tasks under fMRI in order to determine activated brain region in synesthetes vs. controls. In addition to comparing synesthetes with the control group, they also compared synesthetes with each-other in order to assess the heterogeneity of the condition [5].

The first experiment was the "Embedded Figures Task," which was designed to determine if synesthesia aids in texture segregation. Subjects were presented with stimuli on a screen that included one of four random shapes composed of target graphemes embedded within distractor graphemes. Graphemes are the unit used, such as a number, to invoke photisms, or synesthetic color experience. Participants were asked to identify the shape composed by the target grapheme. Since texture segregation is thought to be an early perceptual process, this experiment was able to demonstrate whether synesthetic colors are perceptual [12]. The results, indicated by % correct, were compared between synesthetes, a control group receiving the same display, and a control group using a colored display. The synesthetes performed significantly better than the control group, suggesting synesthetic colors are indeed perceptual. They also performed significantly worse than the colored-display control group, suggesting that synesthetic colors are not as effective as real colors in improving performance [5].

The next task was the "Crowding Task." Researchers used the crowding effect to examine whether synesthetic colors are useful in the identification of crowded graphemes. The crowding effect is an observed phenomenon in which subjects are worse at identification of a grapheme when there are more graphemes around it, but this effect is lessened if the target grapheme is displayed in a different color than the surrounding ones. The hypothesis to explain the crowding effect is that there are limitations in later stages of processing such as attention. Because of this, the researchers reasoned that if synesthetic colors lead to improvements in identification of crowded graphemes in the periphery, then synesthesia may arise prior to these attentional mechanisms. This is because if synesthesia was purely post attentional, the crowding effect would occur whether or not synesthesia was present. While statistical analyses showed no main affect between colorless control group and synesthetics, there were significant differences within individuals. These results may indicate the heterogeneity of synesthetes as a whole.

Perhaps certain synesthetic processes take place post attentionally, while others take place early in perception. It is also important to note that those synesthetes that did perform better than controls on this task also trend toward better performance in experiment one. This may indicate that the two tasks assess the same underlying psychological process in these synesthetes [5].

Finally, Hubbard et. al performed fMRI measurements in order to test the cross-activation model. They specifically were looking for activation in color-selective area hV4 when displayed graphemes vs. when displayed non-linguistic symbols. They compared data from six synesthetes and six nonsynesthetic control subjects, expecting to find hV4 activation in the synesthetic group when displayed graphemes only, but little to no activation in control subjects and when non-linguistic symbols were displayed. The expected results were obtained; activation was present in both the grapheme ROI and hV4 for the synesthetes, but only in the grapheme ROI for control groups. These three tests taken together imply that synesthetic colors are similar to real colors not only in their behavioral effects but also in their neural activation. Finally, these experiments provide strong support for the thesis that hV4 is the neural locus of the color perception experienced by grapheme-color synesthetes. The researchers also take their data to support preattentional mechanisms for synesthesia, but these results are unclear and also suggest that there is a high degree of variability between synesthetes when it comes to the modulation of synesthetic mechanisms [5].

Study 2

The next study further expanded on this idea of heterogeneity of synesthetic mechanisms. Jansari et. al studied individuals with number-color synesthesia in order to further elucidate its mechanisms as well as its behavioral effects and heterogeneity. They also investigated whether synesthesia can occur at the conceptual level without physical experience of an inducer and found that it can. This directly challenges the result proposed in the previous study that synaesthesia is mediated by purely perceptual processes, yet it *is* consistent with the above neuroimaging data and the cross-activation model, suggesting a pathway exists between the visual cortex and the grapheme-processing module [11].

The paradigm used for this experiment was an extension of a model used by Dixon et. al called "2 plus 5 equals yellow" [13]. The initial step is to verify that the participants genuinely have synesthesia. One way to do this is by utilizing the Stroop effect. The Stroop effect is observed when individuals are told to read a color word, such as GREEN, written in an incongruent color, such as red. It is shown that reaction time is much slower when the color is written in an incongruent color compared to when it is written in its own color [14]. In synesthetes, a similar effect is observed when a grapheme is displayed in a congruent vs. incongruent color with its photism [9]. Instead of the Stroop test, this study verified synesthesia by administering surveys to subjects asking about their photisms, and then they readministered the test three months later to verify that responses remained consistent [11].

Then, they wanted to see whether synesthetic color can be presented without physical presentation of the digit itself. To do so, they used an arithmetic task, wherin the subject was displayed arithmetic symbols in succession, such as "5," "+," "2," and a yellow square. In this particular response, the subject would respond "yellow, seven." The square was manipulated such that it was either congruent for the subject's photism for the grapheme associated with the answer or it was not. Subjects were then tested on reaction time (RT) in giving the right answer; these RTs were compared with whether the photism was congruent with the displayed symbol.

RT's level of dependence on congruency is deemed the congruency effect (CE). The results were analyzed for each individual and compared with controls, utilizing the CE. In subject DF's visual system, a main effect of congruency was observed, yet not in the auditory condition. SB's visual test indicated a main-effect of neither congruency nor operator, but a significant effect of congruency in the auditory system. Finally, case KD revealed highly significant CE in the visual system and no other significant effects. One implication of this study was that Dixon's arithmetic paradigm extends to other forms of synesthesia beyond visual grapheme-color. Further, this study further strengthens the case for heterogeneity of synesthetes. Indeed, synesthesia may lie on a spectrum where there exist countless possibilities for expression. Or, it may be the case that there are 2 or more distinct types of synesthesia within which all cases can be categorized into. The researchers propose a mechanism for synesthesia involving a temporo-parieo-occipital (TPO) junction, which is said to be a location for convergence of sensory information from different modalities. This proposition is plausible given the evidence for a physical juxtaposition of the number recognition module and the color processing center, in V4 and V8 [11].

Study 3

The next study calls the Stroop test into question concerning its reliability of testing for synesthesia. They compare the results of synesthetic subjects with a "semantic control" group, who had arbitrary color-number associations that were learned. By doing this, Eliias et. al hoped to disentangle the perceptual aspect of synesthesia with the semantic one. Further, they compared neuroimaging data from these two groups in order to determine their differences and similarities [9].

Three types of participants were recruited for this study: a synesthete, a semantic-control, and four untrained controls with no digit-number associations. The semantic control had a learned association of colors to digits through 8 years of using cross stitch patterns, wherein 3 indicates red thread and 7 indicates yellow thread. These individuals were placed under three behavioral tests followed by fMRI analysis. The behavioral tests implemented were a color naming Stroop task, a mathematical Stroop task, and a priming task. In the color naming Stroop task, participants were recorded for reaction time in identifying the color of a numeral displayed in a color either congruent or incongruent with that number's associated color for the individual. Similarly in the mathematical Stroop task, participants were recorded for reaction time in verbally reporting the answer to a simple arithmetic problem, wherein a color was displayed that was either congruous or incongruous to the photism associated with the correct answer. The priming task was similar to the Stroop task, yet a priming alphaneumeric character was presented prior to a color patch. The prime was either congruent or incongruent and was presented for varying amounts of time between 48 ms and 500 ms, where to former was too quick for a conscious percept of the prime to be formed. Finally, they performed a color number Stroop task, a dice calculation task, and a closed-eye addition task under an fMRI to analyze brain activation areas. In the dice task, participants were asked the sum of two dice faces. In the closed-eye addition task, participants were presented auditory addition problems while their eyes were closed and asked to answer silently [9].

The behavioral results in all three tests showed that *both* the semantic control and the synesthete exhibited slower reaction times when an incongruent color was displayed. In the priming test, the effect disappeared when the prime was presented too quickly for conscious perception. This showed that the behavioral affects characterized to synesthetes are not, in fact, unique to synesthesia. Consequently, studies that use the Stroop task as an objective marker for synesthesia lose credibility because the same effects can be observed in individuals without the condition. The fMRI assessments during the color-number Stroop task displayed further similarities between the synesthete and semantic control – both individuals exhibited similar activations in both the congruent and incongruent conditions. However, their results under the dice arithmetic task and the eyes-closed addition task showed important differences between the two groups. Only the synesthetes – not the semantic control or the untrained control – exhibited significant activation along the left dorsal visual stream. This shows that photisms can be activated without physical presentation of the stimulus, while learned associations cannot [9].

The primary establishment of this study was that Stroop tests and priming tasks both do not distinguish between strong learned color associations and actual synesthetic responses. The fMRI results in both studies show that the cross-activation hypothesis may explain the semantic component of synesthesia but do not provide the whole picture. This is because though synesthetes and semantic-controls had similar behavior and fMRI results in a Stroop test, the qualitative, conscious aspects of their experience during this test could be argued to be very different. The photism for a synesthete is consciously perceived on the grapheme itself and its origin is unknown, whereas for semantic controls the origins of color associations are known and not directly included in the conscious experience of the grapheme. If it is true that conscious experience is generated through neurochemical activity, then there must be some difference between the neural activity of synesthetes and semantic controls that was not observed in the fMRI scans [9].

Study 4

The next study examines further the mechanisms for synesthesia and how they utilize cross-modal mechanisms that are not unique to synesthetes. This study was done specifically on sound-color synesthetics. The researchers wanted to compare synesthetic mechanisms with normal color mechanisms to see how similar they really are. The researchers took note of the fact that even non synesthetic individuals compare some perceptions cross-modally. Take, for example, the idea that darker colors seem related to deeper tones. It is also common to refer to a color as “warm” or “cold,” and many metaphorical explanations utilize cross-modal comparisons. Another way in which we all utilize cross-modal mechanisms is in the formation of a unified experience. It is not the case that humans have separate phenomenal experiences for each sensory modality; the information seems to be integrated into a single conscious experience. If this is mediated by integration pathways, it could be the case that synesthetes utilize the same integration pathways to integrate information cross modally [10].

The researchers first selected 10 sound color synesthetes and 10 non-synesthete controls. They then performed an auditory-color association test to measure internal consistency in assignment of colors to tones. They found that consistency was significantly higher among synesthetes and that both groups followed a trending pattern of assigning lower-pitched tones to darker colors. For synesthetes, dyads with multiple harmonics often produced an experience of more than one color. They then wanted to establish the automaticity of the response in synesthetes vs. controls. They did this by concurrently playing a congruent or incongruent tone through headphones and also displaying a color on a computer screen, either at the same time as the tone or 150 ms later. Participants were asked to ignore the sound and name the color as quickly as possible. The results showed a significantly greater effect of sound-color congruency in synesthetic participants vs. controls. Their next experiment was under similar conditions except there were two colored squares on either side of the screen and one contained an asterisk, and a tone played at the same time as the squares appeared. The participants were asked to attend to a fixation cross in the center of the screen and to identify the target square as quickly as possible. The results indicate a significant interaction between congruency and group, suggesting that synesthetic congruency between sound and color can result in spatial orienting of attention. If the target square was incongruous with the colored photism, synesthetes showed slowed response while controls showed no effect [10].

The researchers take these results to provide further evidence for the thesis that synesthesia is automatically elicited. They note that their study is the first to do this type of study on color-sound synesthesia, but that the results obtained were highly consistent with anecdotal reports. They theorize that both synesthetes and control individuals use the same cognitive mechanism to map the auditory and visual domain. However, their obtained results do not provide evidence for or against specific hypotheses regarding neural mechanisms [10].

Conclusion

These 4 studies all contain important information about synesthesia. It is rational to conclude that the population of synesthetes is highly heterogeneous. This finding was reiterated in almost every study and is important to keep in mind moving forward. This is because if a mechanism for a specific individual's synesthesia were elucidated, one would not be able to generalize this mechanism to all synesthetes. Because of this, all studies on synesthetes should focus not only on group effects of synesthetes as a whole, but also on individual effects and differences between participants. Further, these studies show that the cross-activation model may play an important role in the semantic component of synesthesia, but that there is much more to the story. This is because cross-activation alone does not necessarily dictate the presence of synesthetic qualities [9]. Another important thing to note is the role of attention and automaticity. The results from study four indicate an automaticity of synesthesia, which is consistent with study one's finding that synesthesia is mediated by preattentive mechanisms [10,5]. This further shows that the cross-activation model is insufficient. One model that may be able to synthesize with the cross-activation model to explain these results is the integration model, in which synesthetic mechanisms utilize integration pathways common to us all [11,10]. Since synesthesia can occur without physical presentation of a stimulus, conceptually driven mechanisms for synesthesia are supported [11]. However, preattentive, perceptual mechanisms of synesthesia need to also be examined in more detail as they play an important role in the difference between synesthetes and semantic controls [9].

Further studies should also further examine these differences between semantic controls and synesthetes in order to determine where synesthetic phenomenological qualities are produced. If the cross-activation model were the end of the story, it seems that semantic controls would report color experiences with presentation of graphemes. However, semantic controls report only rigid color *associations*, not conscious experience of color. Therefore, determining the difference between the utilized pathways for semantic controls and synesthetes could be the key to determining the specific neural hardware responsible for conscious experience and its integration.

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