Opinion

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Why color synesthesia involves more than color

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Synesthesia is a perceptual phenomenon in which stimuli can trigger experiences in non-stimulated sensory dimensions. The literature has focused on forms of synesthesia in which stimuli (e.g. music, touch or numbers) trigger experiences of color. Generally missing, however, is the observation that synesthetic colors are often accompanied by the experience of other surface properties such as texture (e.g. a visual experience of linen, metal, marble, velvet, etc). Current frameworks for synesthesia focus only upon the involvement of brain regions such as the V4 color complex. Here, we propose an expanded framework that includes brain regions involved in the encoding of material properties – specifically, larger regions of the medial ventral stream. The overlap of visual texture and color processing within ventral regions might explain why many experiences of synesthesia extend beyond color to other material properties.

Introduction

In synesthesia, ordinary stimuli elicit anomalous perceptual experiences [1–4]. Although there are many types of synesthetic cross-sensory pairings, those involving color are the most common variety (accounting for somewhere between 80.6% [5] and 95% [6] of all synesthetic reports). For example, some synesthetes experience colors in response to sounds [7,8], overlearned sequences such as letters, digits, months and weekdays [9–13], music [14–18] and several other inducers [1,5]. Synesthetic experiences differ from imagery in their consistency and automaticity. Synesthesia is thought to reflect an increased degree of crosstalk between normally separated brain areas, such that activity in one area kindles activity in another (Box 1). Our aim here is to attend to the details of the subjective descriptions to elucidate which areas are involved in that crosstalk.

Measuring color synesthesia

Although synesthesia has been long noted in the scientific literature [19,20], a lack of tests to verify the phenomenon slowed its study until recently [9,21–24]. Synesthesia is now confidently phenotyped in the laboratory based on the finding that synesthetes are consistent in their letter–color matches or sound–color matches over periods of months or years [7,25]. By contrast, controls (encouraged to fake synesthesia) perform inconsistently. For example, when subjects are asked to describe the color experienced on hearing items from a list of words, phrases and letters, synesthetes show 92.3% consistency over a year later, whereas controls cluster around 32% consistency [26]. Additionally, synesthetes show Stroop-like interference when the elicited synesthetic color differs from the actual color of a stimulus [11,27], indicating that the binding of synesthetic colors to forms occurs automatically and cannot be suppressed, even when it interferes with performance.

To understand the neural basis of synesthesia, several research groups have turned to neuroimaging. In 2002, it was first reported that when a word–color synesthete hears a spoken word, there is measurably higher activity in the region specialized for color vision (V4) when contrasted with non-synesthetic controls [28]. This activation was not reproducible in controls who were asked to imagine colors or to memorize letter–color pairings. Other studies have reported similar activations of color areas using visual (instead of auditory) presentation of letters or words [10,29,30]. For example, when subjects were presented with achromatic letters on a gray background, there was more activity overlapping color areas in synesthetes than in non–synesthetic controls.

Collectively, these findings have demonstrated that synesthetic brains are characterized by increased neural crosstalk between neighboring areas involved in letter or word representation and those involved in color. These data have supported the hypothesis that color-selective areas are stimulated by brain areas involved in grapheme representation (such as the visual word form area [4,31]), higher conceptual representations (such as anterior inferior temporal cortex [32]) or newly discovered areas encoding overlearned sequences (right middle temporal gyrus; Pariyadath *et al.*, 2008, unpublished). Thus, the neural framework for understanding this type of synesthesia seems to be promising. But are there any clues from the brain anatomy or reported synesthetic phenomenology that should call our attention to an incompleteness in the story?

The spontaneous reporting of material properties with synesthesia

When participating in the tests of the Synesthesia Battery (http://synesthete.org [26]), some synesthetes report that the matte computer colors work well for them to capture their synesthetic experiences because their synesthetic colors are, in fact, matte. Other synesthetes, however, complain that a simple color-choosing interface is too limited to capture their full synesthetic experience of

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Box 1. The origin of crosstalk in synesthetic brains

How does abnormally increased crosstalk come about in synesthetic brains? The two main hypotheses are increased connectivity or decreased inhibition.

Hypothesis 1: increased connectivity

The fetus makes two million synapses each second, leaving newborns with an excess of working connections between brain areas. One hypothesis of synesthetic crosstalk stipulates that these excess connections are insufficiently pruned, causing extra connections to persist into adulthood [7,47,48]. A variant of this idea suggests increased outgrowth of neurons in a synesthete's brain. Both ideas (insufficient pruning and increased arborization) share the conjecture that a synesthetic brain harbors more than the normal amount of synaptic connections (Figure Ia).

Hypothesis 2: decreased inhibition

An alternative model implicates faulty inhibition as the cause of synesthesia [1,49]. This hypothesis states that excitation is balanced by inhibition in normal brains, whereas in synesthetic brains the excitation can overcome the weakened inhibition. In this framework, the same rich connectivity is present in all brains – the only difference between normals and synesthetes is the functioning of the inhibitory networks [50] (Figure Ib). Although the figure depicts inhibitory long range connections for simplicity, note that the abnormality might instead be in local networks of inhibitory interneurons. Such local networks are known to shape cortical responses to normal thalamic input, and one theory of multisensory binding pivots on such neurotransmitter-mediated inhibition [51]. Specifically, the idea is that local inhibitory networks keep high-frequency cortical activity confined to one region instead of letting it spread; when the inhibitory network is blocked with bicuculline, activity in one cortical area can spread more broadly [51].

One finding favoring the disinhibition hypothesis is that non–synesthetes sometimes have synesthetic experiences during meditation, drugs, deep absorption or while falling asleep. This suggests that the state of the brain in these conditions allows existing connections to change their functional relationships. Therefore, the connectivity might be present anatomically in all brains, but not necessarily functional because of counterbalancing by excitation and inhibition.

It could be difficult to disambiguate these two hypotheses, because a change in either connectivity or neurotransmission could engender a change in the other. For example, although a recent diffusion tensor imaging (DTI) study might lend support to the increased-connectivity hypothesis [29], it is also possible that the denser connections are secondary to neurotransmitter imbalances. To elucidate the root cause, researchers are currently performing family linkage analyses to pull the gene(s) for synesthesia [52] (D. Eagleman *et al.*, unpublished).

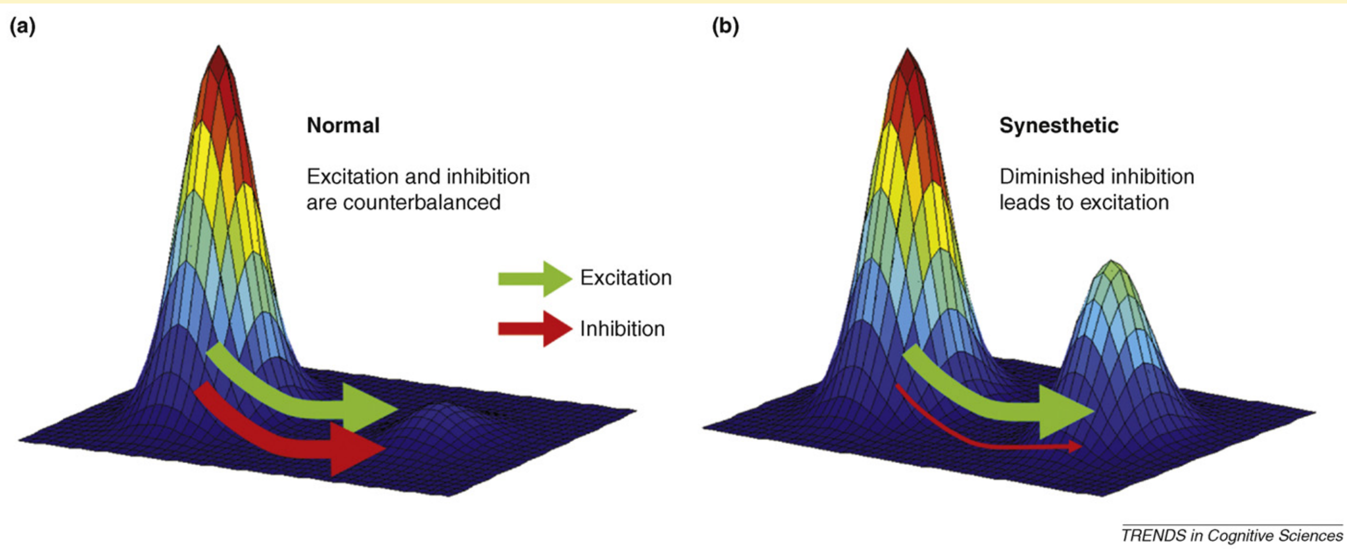

Figure I. Diminished inhibition leading to spreading activity. In this schematic, green represents excitatory connections and red represents inhibitory connections. **(a)** When inhibition functions normally, activity in one area remains sequestered because excitation and inhibition are counterbalanced. **(b)** When inhibition is diminished, activity in one area spreads to the other.

textures and other material properties. For example, synesthetic visual artist Carol Steen describes her letter ***i*** as possessing a 'hard metallic texture.' Her ***Z*** is 'the color of ale with a bubbly texture,' and her number ***1*** has 'the soft texture of a flannel blanket.' (Figure 1).

Consider several more synesthetes' descriptions from Sean Day's Synesthesia List (an email forum for synesthetes). Catherine Y. describes her letters of the alphabet like this: '*A*: a buttery yellow with a linen texture, *E*: a deep velvety blue, *I*: white and slick, *O*: clear, like lucite, and 3-dimensional, *U*: grey.' Another synesthete, Emily B., describes O, X and Y as 'clear and shiny like glass.'

Several synesthetes were recently asked to describe their experiences in response to the name 'Mia.' Although texture descriptions were not specifically asked for, note their appearance in the following descriptions. One synesthete writes that the word Mia 'is soft brown in the texture of corduroy.' Another synesthete describes it as 'a deep red, just a shade darker than a true red, and a rich, almost velvety texture which is also/at the same time soft and mushy – like something to sink into (think a beanbag chair).' Another reports that 'the 'M' is solid with a velvety texture.' Mia herself describes the word as 'a pink that glimmers, a slimy texture, my name is apple green and yellow lemon in a checkerboard pattern and texture.' Typical descriptions for other letters, numbers or words include 'a deep burgundy red that is almost like a liquid', 'a baby blue and has a plaid yet silky texture', and so on.

Music, well-known to evoke colors in synesthetes [1,14–18], often evokes texture as well. Consider some of the following descriptions: 'the entire instrument is a defined

Figure 1. Graphemes with texture. Artist Carol Steen's representation of the material properties induced by individual letters for her. Figure courtesy of Carol Steen.

color and texture', 'when music plays...the air around me has become more 3-dimensional and filled with swirling colors and textures,' or 'I have strong reactions to music but rarely do I see pronounced color....What I get is depth and shapes and movement which creates what I call a 'musical landscape' effect.' Even the mellifluousness of voices can evoke texture experiences, as in these reports: 'my best friend's voice is the most gorgeous chocolate brown, which then ranges down to black and up into gold, and has a texture like the feel of velvet,' and 'different voices also cause a strong sense of movement and shape and each voice has its own 3D form and texture to me.'

Given previous hypotheses about the role of color areas such as V4, what explains the prevalence of these highly specific reports of synesthetic texture?

Texture in the brain

Recent neuroimaging studies might provide the answer. In the ventral visual stream, lateral areas seem to encode objects based on shape [33,34]. However, recent work shows that more medial aspects of the ventral pathway are involved in coding visual cues associated with an object's material properties (Figure 2) [35–37]. When participants view pictures of 3D objects that vary in shape, visual texture, or color, attention to visual texture (which is closely correlated with the material properties of the object) elicits relatively greater hemodynamic activity along the right collateral sulcus and inferior occipital gyrus, in addition to the left lingual sulcus and inferior temporal sulcus [35]. This, in context with other findings showing that damage to the lateral occipital complex (LOC) affects the ability to identify objects on the basis of their shape but does not affect the ability to recognize their material properties from color, texture and other surface cues [33,38], supports the claim that the medial part of the ventral pathway is specialized for processing surface cues related to the material properties of objects.

As for texture and color processing, they seem to be separable from one another both anatomically [35,39] and behaviorally [40], even though both are clearly related to the material properties of objects. Regions that process color, but not texture, are found in early visual areas, such as primary visual cortex and areas in the cuneus [35,39]. Texture processing, perhaps because it is more complex, arises later in the ventral stream. Note that there is a good

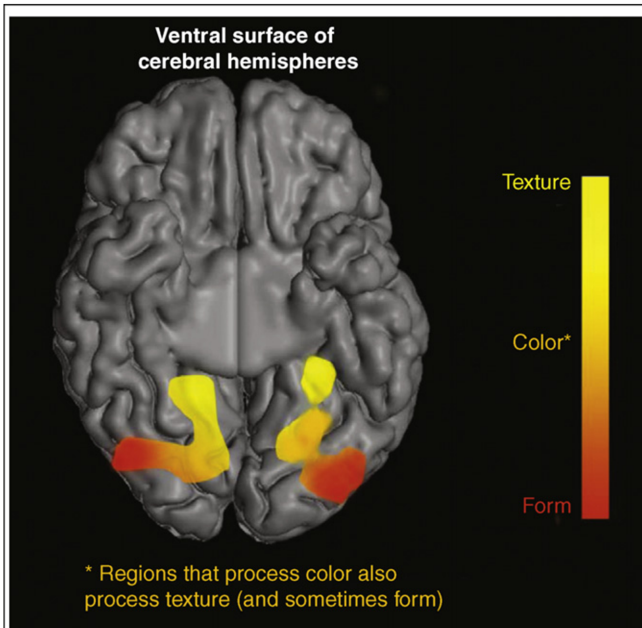

Figure 2. Towards a broader inclusion of ventral visual areas involved in synesthesia. Summary diagram of overlapping areas activated in fMRI when volunteers attend to the form, color or texture of objects [35,39]. Form is preferentially processed in more lateral regions of the ventral stream, whereas surface properties (such as color and texture) are processed in more anteromedial regions. Note that none of the areas depicted here show exclusive color-processing. Regions that respond to color but not texture are found much earlier in the cortical visual pathways (not shown).

deal of overlap as well: some of the texture-processing regions seem to deal with color, and there is evidence that V4 itself, long regarded as a 'color center', also processes texture [41,42].

Although previous frameworks of synesthesia have proposed only the involvement of the color processing networks in V4 [10,28–30,32,43], we suggest that a more complete framework must include the full coding capacities of the ventral visual stream (Figure 2).

The future of texture synesthesia

Why did earlier neuroimaging studies on synesthetic experience [28–31] not report activation of texture-sensitive areas (such as collateral sulcus and inferior occipital gyrus), but instead only color areas? First, note that there was indeed a spread of ventral stream activation reported in most of these studies, but only the previously-localized color areas were selected for discussion. Second, it is possible that particular choices of significance thresholds excluded a more widespread activation pattern in favor of a single cluster. Finally, for studies in which texture activity was not apparent (e.g. Ref. [28]), it is possible that the large diversity among synesthetes meant there was a spectrum of synesthetes in these studies, from those who experience textures to those who do not. There has been no attempt to characterize these differences in any of the studies thus far (Box 2).

We do not suggest that all synesthetes with color experience also have texture experiences. Similarly, we do not know if future investigations will unmask a new type of synesthesia involving only texture without color. If it turns out that textures are triggered more rarely than colors, this could, in theory, shed more light on preferred pathways of connectivity. Specifically, it has been speculated that proximity of brain areas will be key to allowing more cross-talk [43–45]; if grapheme areas tend to lie closer to color areas than to texture areas, then an increased prevalence of color synesthesia might be theorized on the basis of neural proximities. In contrast, if there is enough anatomical overlap between color and texture areas, then the two types of experience might turn out to be equally prevalent among synesthetes; this remains to be examined.

Now that texture experiences have been emphasized, and a broader inclusion of the medial aspects of the ventral stream has been proposed, this aspect of synesthesia calls to be studied with new, specifically targeted methods. Quantitatively testing these prevalences will be a challenge: it is straightforward to develop a user-friendly color chooser [9,25,46], but not so with the multidimensional varieties of texture. Perhaps Stroop tasks, which have been successfully used with the color aspects of synesthesia [11,27], can be leveraged for the same purposes with texture. Additionally, it might be possible to employ neuroimaging to measure functional connectivity patterns that correlate with texture synesthesia, as has been previously shown with other forms of synesthesia [29,31].

Box 2. Questions for future research

- What is the population prevalence of synesthetic texture experience compared to color experience?
- Texture can be experienced visually (metallic-looking), haptically (a rough surface) and sometimes auditorily (the crinkling of paper). To what extent do synesthetic texture experiences include these other modalities, and how will that be tied into the underlying anatomy?

Conclusions

Despite the singular role of area V4 in previous models of synesthesia, it must be emphasized that V4 is not the only neural region involved in the phenomenon. Color processing in this region, it seems, might account for only part of the overall synesthetic experience. Certainly more brain regions will be involved, if not least because synesthesia is often a multifaceted experience [1]. In the case of the widely studied 'color' synesthesias, it has previously seemed sufficient to propose crosstalk between two areas (e.g. those involved in graphemes and color). But there seems to be more to the experience than color, including texture, specularity, form and so on. More broadly, synesthetic experience includes an awareness of the percept, some level of affect towards it, and remembering it afterwards – accordingly, components for attention, affect and memory must be part of the circuit that underlies the experience. The minimally necessary circuit is even more elaborate in the case of synesthetic experiences in which, for example, sound triggers the simultaneous experiences of color, texture, location and movement [1].

The variability among synesthetes should be taken to facilitate research, not hinder it, because it allows mappings of the different elements of the network involved in the crosstalk. In this way, we will come to see which brain areas are most likely to be interlinked, and which ones are rarely or never paired. We hope that this process of cartography will allow us to leverage individual differences rather than sweeping them under the rug – and in this manner come to a better understanding of the neurobiological basis of synesthesia in all its forms.

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