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Grapheme-color synesthetes show enhanced crossmodal processing between auditory and visual modalities

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ABSTRACT

Synesthesia is an involuntary experience in which stimulation of one sensory modality triggers additional, atypical sensory experiences. Strong multisensory processes are present in the general population, but the relationship between these ‘normal’ sensory interactions and synesthesia is currently unknown. Neuroimaging research suggests that some forms of synesthesia are caused by enhanced cross-activation between brain areas specialized for the processing of different sensory attributes, and finds evidence of increased white matter connections among regions known to be involved in typical crossmodal processes. Using two classic crossmodal integration tasks we show that grapheme-color synesthetes exhibit enhanced crossmodal interactions between auditory and visual modalities, suggesting that the experience of synesthesia in one modality generalizes to enhanced crossmodal processes with other modalities. This finding supports our conjecture that the atypical sensory experiences of synesthetes represent a selective expression of a more diffuse propensity toward ‘typical’ crossmodality interactions.

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1. Introduction

Synesthesia is an involuntary experience in which stimulation of one sensory modality produces additional, atypical sensory experiences in either the same or a separate modality. In one of the most common forms, viewing numbers or letters (graphemes) elicits the percept of a specific color (grapheme-color synesthesia; Cytowic and Eagleman, 2009; Baron-Cohen et al., 1996). For example, to one of our synesthetes the number 2 always appears bright red, irrespective of its actual color. Synesthetic experiences typically begin early in childhood and remain extremely consistent over the lifespan. Further, synesthesia runs in families (Baron-Cohen et al.,

1996; Ward and Simner, 2005; Asher et al., 2009), suggesting it is a heritable trait. Although researchers have studied this phenomenon for well over a century (Galton, 1880), it has long been considered a curiosity and only recently has there been a resurgence of interest in synesthesia, along with attempts to discover the underlying mechanisms.

The neural substrates of synesthesia have been thoroughly studied using both psychophysical tests and neuroimaging techniques (e.g., Palmeri et al., 2002; Nunn et al., 2002; Hubbard et al., 2005; Goller et al., 2009; Brang et al., 2008, 2011; Beeli et al., 2008). When viewing achromatic numbers or letters, grapheme-color synesthetes show co-activation of grapheme regions in the posterior temporal lobe and color

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area V4, giving rise to the concurrent sensation of color (Hubbard et al., 2005; Sperling et al., 2006; Brang et al., 2010). Ramachandran and Hubbard (2001) proposed that this cross-activation is driven by an excess of neural connections in synesthetes, possibly due to decreases in neural pruning between typically interconnected areas. Confirming this suggestion, a number of studies have demonstrated anatomical differences in the inferior temporal lobes of synesthetes, near regions related to grapheme and color processing, including increased fractional anisotropy as assessed by diffusion tensor imaging (DTI; Rouw and Scholte, 2007), and increased gray matter volume, as assessed by voxel-based morphometry (VBM; Jancke et al., 2009; Weiss and Fink, 2009).

Extending the cross-activation theory of synesthesia, Hubbard (2007) proposed a two-stage model to explain how synesthesia is bound into a sensory experience. In this model, synesthetic sensations are initially activated by direct connections between the senses, then are subsequently bound together into a conscious percept via ‘hyperbinding’ mechanisms in the parietal lobes (Robertson, 2003). This model is consistent with studies showing enhanced parietal lobe activity associated with synesthetic concurrents (e.g., Weiss et al., 2005), as well as studies using transcranial magnetic stimulation (TMS) demonstrating that parietal lobe inhibition weakens the synesthetic experience (Esterman et al., 2006; Muggleton et al., 2007). Moreover, DTI and VBM studies on grapheme-color synesthetes show altered morphology of parietal regions compared to controls, with increased fractional anisotropy in the superior parietal lobe (Rouw and Scholte, 2007) and increased gray matter volume in the left superior parietal lobe (Rouw and Scholte, 2010) and left intraparietal sulcus (Weiss and Fink, 2009). Taken collectively, these studies suggest that synesthesia operates through both direct communications between the senses as well as integration of information at multisensory nexuses in parietal areas.

By definition, synesthesia is a process that activates additional sensory information (e.g., color) that was not present in the original sensory signal (e.g., the sound of C-sharp). The existence of connections between the senses is indeed not unique to synesthetes, and has been empirically studied in non-synesthetic participants within the field of multisensory processing (Spence et al., 2009). In typical multisensory processes, stimulation of any particular sensory modality can affect how information is processed by the other senses. One well-popularized example of how visual cues can affect auditory processing is the Ventriloquist illusion, in which individuals perceive a Ventriloquist’s voice as originating from the location of his puppet’s mouth due to visual cues ‘capturing’ the auditory information (Pick et al., 1969). A striking demonstration that auditory stimulation affects visual perception is the double-flash illusion (Shams et al., 2000), wherein two auditory beeps paired with a single visual flash is actually perceived as two distinct visual flashes. This percept of an additional “flash” is correlated with specific neural activity (Bhattacharya et al., 2002) and could be viewed as a semi-synesthetic experience observed in non-synesthetes. These visual illusions exemplify the processing costs and perceptual errors that can result from the presentation of incongruent multisensory stimulation. Conversely, researchers have

shown that being presented with congruent information from multiple modalities confers an advantage for speed and accuracy of processing (for review see Loveless et al., 1970). For example, in a target detection task reaction times are faster when auditory and visual cues are presented simultaneously compared to a cue in a single modality (Hershenson, 1962). Along similar lines, Frens et al. (1995) showed participants have faster saccades to a visual target when an irrelevant auditory cue is spatially and temporally aligned with the target. Interestingly, research into crossmodal integration in the normal population yields surprisingly consistent results with those of synesthesia studies: activation in parietal regions as well as direct co-activation of early sensory areas (e.g., Kayser and Logothetis, 2007; Driver and Spence, 2000; Foxe and Schroeder, 2005; Watkins et al., 2006, 2007).

The shared characteristics of synesthesia and multisensory processing paired with the established finding that feature binding in typical individuals relies on parietal lobe activity (e.g., Friedman-Hill et al., 1995; Critchley, 1953) have led several groups to suggest that synesthesia is an exaggeration of the crossmodal processes present in typical individuals (Robertson, 2003; Mulvenna and Walsh, 2005; Hubbard, 2007; Cohen Kadosh and Henik, 2007; Ward et al., 2006; for a review see Sagiv and Robertson 2005). Indeed, inhibitory parietal lobe TMS disrupts the binding of form and color similarly for non-synesthetes (Esterman et al., 2007) and synesthetes (Esterman et al., 2006; Muggleton et al., 2007) alike. If synesthesia is an exaggeration of typical multisensory processes, we would predict that synesthetes as a group will show an enhanced ability to integrate information from different sensory modalities, resulting in enhanced effects of crossmodal processing. While many studies have highlighted this possibility and the need for research in the area, no study to date has directly examined whether synesthetes show increased crossmodal processing between sensory modalities unrelated to the synesthetic experience. This increased, automatic binding should be observed regardless of whether it increases perceptual errors in the form of visual illusions in response to incongruent multimodal cues, or promotes enhanced processing of congruent multisensory stimuli. To this end, we compared the performance of 7 synesthetes to that of 25 controls on two psychophysical tasks that quantify an individuals’ integration of crossmodal information: the double-flash illusion (Shams et al., 2000) and intersensory facilitation of reaction time (Hershenson, 1962).

2. Experiment 1: double-flash

The double-flash illusion is a striking example of crossmodal interactions in which a single white disk presented very briefly, yet unambiguously, is actually perceived as two flashes when accompanied by two auditory beeps (Shams et al., 2000). This illusion critically demonstrates that an auditory stimulus is capable of altering a visual experience, operating via crossmodal links, with quantifiable differences between illusion and non-illusion trials at the neural level (Bhattacharya et al., 2002). Consistent with our view that synesthesia is an enhanced variant of normal crossmodal processes, we expect synesthetes to show increased

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