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Note

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 (graphemecolor 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 crossactivation 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 semisynesthetic 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 susceptibility to this illusion, which would be indicative of increased automatic crossmodal integration.

2.1. Methods: Experiment 1

2.1.1. Participants

Seven synesthetes ranging in age from 19 to 22 [mean age = 20.1 years, standard deviation (SD) = 1.1, 5 women] and 25 control subjects ranging in age from 18 to 23 (mean age = 20.3 years, SD = 1.4, 16 women) were recruited. All were healthy fluent English speakers with normal color vision, and none reported any history of psychiatric or neurological disorder. Synesthetes reported the experience of colors in response to viewing letters and/or numbers, and claims were confirmed by means of consistency matching (on-line testing with the Synesthesia Battery; Eagleman et al., 2007), including reaction time testing for color congruency.

2.1.2. Materials and procedure

Subjects were seated in front of a PC screen (refresh rate 60 hz) with their eyes 57 cm from the center of the screen. During each trial, a combination of 0, 1, or 2 auditory beeps and 0, 1, or 2 visual flashes were shown to the subject. Each visual flash was a uniform white disk (2 cm subtending 2 degrees of visual angle) shown very briefly at eccentricity (9 degrees of visual angle below fixation) on a black background. Each auditory beep was a 3.5 khz tone and lasted 7 msec. Subjects were instructed to only report the number of flashes seen by pressing 0, 1, or 2 on the PC keyboard. On each trial a variable number of flashes and beeps were presented for a total of 7 experimental conditions. For the main analysis we are most interested in contrasting the 'illusion' condition, in which a single flash is surrounded by two beeps, with a wellmatched 'control' condition, in which a single flash follows two beeps by 300 msec. Both the illusion and control condition are composed of identical elements (1 flash, 2 beeps), but the temporal separation in the control condition fails to induce the illusion, allowing us to rule out a simple difference in response bias between our groups. The additional five conditions were included to prevent subjects from predicting the number of flashes or beeps and to ensure subjects were not incorrectly responding to the auditory cues (0 flashes 2 beeps), were accurately able to identify the visual cues presented in isolation (1 flash 0 beeps, 2 flashes 0 beeps), and that both groups had similar response patterns to other multisensory cue combinations (1 flash 1 beep and 2 flashes 1 beep). Each flash of the disk lasted 17 msec, with 50 msec interstimulus interval in the two-flash condition. Trials were initiated by the participant with a spacebar press followed by a 1 sec fixation cross and the onset of the trial. Subjects were acclimated to the task with an initial practice block. Participants completed 6 blocks of 77 trials (7 practice trials, one from each condition, and 10 of each trial type) for a total of 60 trials/condition.

None of the synesthetes experienced a synesthetic percept for any of the auditory or visual targets used. By utilizing stimuli that caused no synesthetic experiences, we can be confident that group differences reflect generalized processing, as opposed to differences driven by synesthetic percepts.

2.2. Results

Results from all seven conditions are presented in Fig. 1. As noted in the Methods section above, incidence of the illusion is quantified by the comparison between the two critical conditions with the additional five conditions preventing response biases and quantifying unisensory perception in both groups. Accuracy data from the critical illusion and control conditions were subjected to a 2 \times 2 repeated measures analysis of variance (ANOVA) with factors of Group (synesthetes/controls) and Condition (2 beep 1 flash illusions, 2 beep 1 flash control), yielding a main effect of Condition [F(1,30) = 74.5, p < .001] and a significant interaction of Group × Condition [F(1,30) = 7.76, p < .01]. Orthogonal planned contrasts were conducted to compare synesthetes' and controls' relative accuracy in the illusion and control conditions. In the 2 beep 1 flash illusion condition, synesthetes' average accuracy rate of 10.5% (range: 3.3-23.3%) was significantly lower than that of control subject's average accuracy rate of 37.4% [range: 3.3–98.3%; t(30) = 2.28, p < .05], indicating a higher incidence of the double-flash illusion in synesthetes. In the 2 beep 1 flash control condition, however, synesthete's average accuracy rate of 82.8% (range: 48.3-100%) did not significantly differ from control subject's average accuracy of 74.4% [range: 28.3–100%; t(30) = .89, p = .38].

Providing additional confirmation that these results are not the product of a few outliers, we examined synesthetes' accuracy as a function of z-scores relative to the distribution of performance by controls; individual synesthetes' z-scores ranged from -1.12 to -.48 SDs from the mean accuracy of controls (synesthete's average z-score: -.88). Fig. 2 presents subjects' individual score in the illusion condition and demonstrates noticible overlap between the groups, even though all seven synesthetes showed low performance (high incidence of the illusion); it is possible this overlap is due to task-specific variability, floor effects, or veridical overlap between the groups. Further confirming the specificity of this difference between synesthetes and controls in only the illusion condition, no significant group differences were found for any of the five additional control conditions using two-tailed ttests (uncorrected): 0 flashes 2 beeps t(30) = .29, p = .78; 1 flash 0 beeps t(30) = .84, p = .41; 2 flashes 0 beeps t(30) = .74, p = .47; 1 flash 1 beep t(30) = .83, p = .41; 2 flashes 1 beep t(30) = 1.48, p = .15. Lastly, in the critical illusion condition subjects on average incorrectly reported perceiving zero flashes on .55% of trials, confirming that these results are driven by the illusory perception of two-visual flashes and not reduced performance due to lack of attention or other reasons.

2.3. Discussion

The double-flash illusion was more pronounced in synesthetes compared to controls, reflected by their reduced accuracy in the critical illusion condition. This illusion represents an instance where subjects' visual perception is modulated by the incongruence of a sound pairing, in turn reducing veridical perceptual judgments. We suggest that synesthetes' increased susceptibility to the illusion represents increased crossmodal processing relative to controls. This notion is further supported by the specificity of the difference between





Fig. 1 – Accuracy in reporting the number of flashes in response to varying flash/beep conditions. Shaded region highlights the illusion condition (1 flash paired with 2 beeps, no delay) and the control condition (1 flash spaced 300 ms between 2 beeps). Error bars represent standard error of the mean. Asterisk reflects p < .05.

the groups; synesthetes showed reduced accuracy in only the critical illusion condition, and none of the control conditions. Interestingly, however, of the six control conditions, the only one to approach a marginally significant difference between the groups was the 2 flashes 1 beep condition, which some have argued is a multisensory illusion in itself (Mishra et al., 2008). It is important to note that while this illusion operates through audio and visual communication, none of our subjects experiences a form of synesthesia in which visual cues trigger auditory concurrents, or vice versa. Accordingly, as synesthesia was not engaged during this task, the increased crossmodal processing seen in synesthetes can be interpreted as a generalized increase in crossmodal interactions between auditory and visual centers.

3. Experiment 2 – intersensory facilitation of reaction time

As a test of crossmodal integration between congruent auditory and visual cues we quantified intersensory facilitation of reaction time for both our groups. Intersensory facilitation of reaction time is a well-documented behavioral effect first reported





by Hershenson (1962), in which reaction times to multimodal stimuli (e.g., auditory and visual presented simultaneously) are reduced compared to either unimodal stimulus alone. Multiple studies (e.g., Miller, 1982, 1986; Laurienti et al., 2006) have found that this speeding of reaction times in the multimodal condition is above and beyond what would be expected by statistical summation of the two targets, and is thought to reflect genuine facilitation between multiple sensory cues originating from the same source. Accordingly, multisensory stimuli that are spatially and temporally coincident typically result in behavioral and/or perceptual enhancements. Hershenson (1962) concluded that the two senses interact in a beneficial manner, reflecting crossmodal processes present in us all. This test of multisensory response utilizes reaction time measures to evaluate the degree of crossmodal integration within each individual by comparing response time on a target detection task between a multimodal condition (a paired visual and auditory stimulus) and the unimodal conditions (visual alone or auditory alone). While previous research has shown responses in the multimodal condition to be faster than those in the unimodal in the general population, we expected this facilitation to be even greater in synesthetes, owning to increased crossmodal processes.

3.1. Methods

3.1.1. Participants

The same group of synesthetes and controls from Experiment 1 participated in Experiment 2.

3.1.2. Stimuli

Participants were seated in front of a PC screen (refresh rate 60 hz) with their eyes 57 cm from the center of the screen. The experiment was programmed in E-Prime software (Psychology Software Tools, Inc.). Participants pressed the spacebar on a PC keyboard to start each trial. Trials began with a 1.5 sec fixation cross followed by a variable random delay (500–1500 msec) by either a visual stimulus – a red letter X printed in Times New Roman font, 12 pt, subtending

.7 degrees of visual angle, presented for 100 msec, an auditory stimulus – a brief, 100 msec tone presented binaurally via headphones, or both targets simultaneously in the multimodal condition. Blank trials were also included to discourage anticipatory responding. Participants were instructed to press the "K" key of a PC keyboard with the index finger of their preferred hand (right hand for all participants) as quickly as possible when they detected a visual and/or auditory cue. There were 4 blocks of 74 trials; each block began with 4 randomly selected trials that were treated as practice trials and excluded from analysis, followed by 20 trials in each condition (auditory, visual, and multimodal) plus 10 blank catch trials. As such, each participant generated 80 reaction times for each experimental condition.

3.1.3. Analysis

The multimodal condition presents participants with two redundant targets compared to the single target presented in either the auditory or visual conditions. Thus, some of the speeding of reaction time to multimodal targets is attributable to the advantage of having two independent stimuli contributing to response generation and execution. To calculate the extent of multisensory benefit in addition to that which is predicted by the redundant nature of the multimodal condition (e.g., two stimuli as opposed to one), the independent race-model was used as a comparison for multisensory benefits compared to the joint probability of responses from either sensory stimulus alone (Miller, 1982, 1986; Laurienti et al., 2006). The independent race-model utilizes cumulative distribution functions (CDFs) to compare relative probabilities for a response within grouped 1 msec time windows. A racemodel is constructed from the joint probabilities of the auditory alone and visual alone conditions [(Pr Auditory + Pr Visual) – (Pr Auditory \times Pr Visual)]. If the CDF for the multimodal condition exceeds that which would be predicted by the race-model, then the model is violated. These violations of the race-model are thought to reflect true multisensory integration at the neural level (Miller, 1982; Laurienti et al., 2006). Accordingly, each subjects' data was divided into 1 msec reaction time bins, used to create individual CDFs for each condition (auditory, visual, and multimodal). Next, the racemodel predictions at each time bin were computed for each subject based on the auditory and visual CDFs. Finally, average race-model predictions were calculated for each subject from the mean of the response times in the race-model CDFs for comparison against the raw multimodal response times.

3.2. Results

Results are presented in Table 1. Data were subjected to repeated measures ANOVA with factors of Group (synesthetes, controls) and Condition (multimodal, race-model). ANOVA revealed main effect of Condition [F(1,30) = 49.3, p < .001], suggesting that multimodal response times across groups exceeded those predicted by the race-model, confirming the benefit of multisensory information, and the presence of crossmodal enhancement. Follow-up paired t-tests comparing multimodal and race-modal conditions within each group confirmed the presence of this effect in both synesthetes [two-tailed t(6) = 6.29, p < .001] and controls [two-tailed t(24) = 5.18,

Table 1 – Intersensory facilitation of reaction time (Experiment 2) response times for synesthetes and controls. Race-model predictions calculated from joint probability of responses from auditory and visual conditions, and serve as the baseline for multimodal response times.

	Auditory response times	Visual response times	Race-model predictions	Multimodal response times
Synesthetes $(n = 7)$	440 msec	442 msec	380 msec	348 msec
Controls $(n = 25)$	409 msec	422 msec	358 msec	340 msec

p < .001]. Critically, repeated measures ANOVA revealed a marginal Group × Condition interaction [F(1,30) = 3.87, p = .058], such that synesthetes demonstrated more benefit from multimodal stimuli over race-model predictions compared to control subjects (Fig. 3). Even though each subjects' race-model prediction serves as a within subject baseline, numerical differences in this baseline could superficially be argued to drive group differences. However, synesthete's mean reactions times did not differ from control's on either visual alone trials [two-tailed t(30) = .85, p = .40] or auditory alone trials [two-tailed t(30) = .91, p = .37].

To test whether the enhanced cross-modal processing in synesthetes operates as a general group effect or reflects multisensory benefits differing between individuals, we tested the relationship of synesthetes' performance on these two tasks using a Pearson *r* correlation. While this is a small sample size and so the results must be considered with caution, a robust relationship was found for synesthetes' accuracy on the double-flash task and response time benefit to a multimodal response compared to race-model predictions [R = -.77, t(5) = -2.74, p < .05]. Notably, the negative correlation yielded here reflects an increase in multisensory processing in both tasks; i.e., reduced performance on the double-flash is associated with decreased response time (heightened benefit) in the detection task (Experiment 2).

3.3. Discussion

Individuals with grapheme-color synesthesia were shown to benefit more from a multimodal stimulus, a sound and a simple visual cue presented simultaneously, than normal controls. As no subjects included in this study experienced synesthetic concurrents between visual and auditory modalities, we suggest that synesthesia is associated with enhanced crossmodal processing in modalities outside those related to their conscious synesthetic experiences. Crucially, as each subject serves as his or her own baseline, it is unlikely that these results are due to response biases, as that bias would be uniform throughout the conditions.

4. General discussion

To our knowledge, these studies provide the first evidence of enhanced crossmodal interactions in synesthesia beyond



Fig. 3 – CDFs for synesthetes' and control subjects' response times to auditory, visual, and multisensory stimuli. The independent race-model represents summed probability for auditory and visual responses. Shaded area between the curves represents multisensory benefit over race-model distributions. Note the increased shaded area in synesthetes compared to controls.

modalities involved in the synesthetic experience, suggesting that synesthesia may build upon the same mechanisms underlying typical crossmodal processes. These two studies used very different tasks and each point toward synesthetes possessing increased communication between auditory and visual areas compared to controls. Synesthetes showed reduced performance in Experiment 1 (higher incidence of illusion trials) and increased performance in Experiment 2 (more reaction time benefit) suggesting these effects are not merely driven by performance biases in the synesthetes. Furthermore, synesthetes did not statistically differ from controls in their unisensory response times in Experiment 2 (auditory alone and visual alone trials); indeed, numerically they were slower in these conditions compared to controls. However, it remains possible to test whether these effects are specific to crossmodal tasks or reflect some general speeding in synesthetes to increasingly complex or additive stimuli. One experiment well suited to rule out this alternative explanation would be the redundant target effect (Miniussi et al., 1998) in which subjects are faster to indiscriminatingly respond to two-visual cues as opposed to one, which is thought to be mediated by early visual areas as opposed to crossmodal processes. In such a task we would expect no difference between synesthetes and controls.

While preliminary, the correlation of synesthetes' performance between the two crossmodal tasks employed in this study suggests that not only do synesthetes show increased crossmodal processing compared to controls at the group level, but also that crossmodal enhancement is a generalizable and reliable aspect of the individual differences between synesthetes. One speculative possibility is that the strength of synesthesia or perceptual reality of the each synesthetes' experiences relates to the degree of crossmodal enhancement. Indeed, research suggests that synesthetes with more perceptually 'real' experiences display improved performance on tasks that utilize synesthetic experiences (Hubbard et al., 2005). However, as the current group of synesthetes were not classified according to their strength of synesthetic perceptions, this question will remain a matter for future research.

As the results presented here address only the behavioral output of crossmodal processing, further research is required to clarify the relationship between synesthesia, crossmodal mechanisms, and connectivity and activation patterns both between the individual sensory systems and within parietal areas. Indeed, this study fills one of the putative links in this matrix, such that synesthetes have been shown to possess increased connectivity between the senses and in the parietal lobes (Rouw and Scholte, 2007), and these results demonstrate increased crossmodal processing in synesthetes in tasks that are expected to engage similar networks. The missing critical value to aid in our understanding of multisensory processing in the general population is to examine how crossmodal performance on behavioral tasks relates to connectivity both between the senses and to the parietal lobes.

This study also adds to accumulating evidence of generalized processing benefits in synesthesia, providing a provocative evolutionary hypothesis (assuming of course synesthesia is not merely epiphenomenal). Contrary to notions that synesthesia serves no benefit, recent work suggests synesthesia may alter primary sensory processes. Barnett et al. (2008) show differences in early visual perception and there are studies showing increased (unimodal) perceptual sensitivity in synesthetes (Banissy et al., 2009; Yaro and Ward, 2007). Furthermore, research from our own laboratory suggests that grapheme-color synesthetes have lower color detection thresholds in a psychophysically low-level visual task (Wagner et al., in prep.). Taken collectively, these data suggest that synesthesia is associated with enhanced primary sensory processing as well as the integration between the senses. However, as these sensory enhancements could also be due to synesthetes' increased experience with sensory percepts due to synesthetic concurrent experiences, the causality of this relationship will remain a matter for future studies.

In conclusion, while the mechanisms supporting this enhanced crossmodal processing still require careful examination, the current study provides the first direct link between synesthesia and crossmodal processes in the general population. Further, while this initial result is based off of auditory and visual crossmodal tasks tested in only one form of the condition, subsequent studies are encouraged to examine additional types of synesthesia, crossmodal tasks across additional modalities, as well as the relationship between connectivity and crossmodal processing in all individuals.

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