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Brief communication

Similarly shaped letters evoke similar colors in grapheme–color synesthesia

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ABSTRACT

Grapheme–color synesthesia is a neurological condition in which viewing numbers or letters (graphemes) results in the concurrent sensation of color. While the anatomical substrates underlying this experience are well understood, little research to date has investigated factors influencing the particular colors associated with particular graphemes or how synesthesia occurs developmentally. A recent suggestion of such an interaction has been proposed in the cascaded cross-tuning (CCT) model of synesthesia, which posits that in synesthetes connections between grapheme regions and color area V4 participate in a competitive activation process, with synesthetic colors arising during the component-stage of grapheme processing. This model more directly suggests that graphemes sharing similar component features (lines, curves, etc.) should accordingly activate more similar synesthetic colors. To test this proposal, we created and regressed synesthetic color-similarity matrices for each of 52 synesthetes against a letter-confusability matrix, an unbiased measure of visual similarity among graphemes. Results of synesthetes' grapheme–color correspondences indeed revealed that more similarly shaped graphemes corresponded with more similar synesthetic colors, with stronger effects observed in individuals with more intense synesthetic experiences (projector synesthetes). These results support the CCT model of synesthesia, implicate early perceptual mechanisms as driving factors in the elicitation of synesthetic hues, and further highlight the relationship between conceptual and perceptual factors in this phenomenon.

1. Introduction

Grapheme–color synesthesia is a neurological condition in which viewing numbers or letters (graphemes) results in the concurrent sensation of color (Baron-Cohen, Burt, Smith-Laittan, Harrison, & Bolton, 1996; Cytowic & Eagleman, 2009). In a given synesthete, the associations between graphemes and colors are very specific, in that each grapheme corresponds to a particular hue that is largely consistent across the lifespan. However, the particular associations between individual graphemes and colors differ across individuals, and synesthetes further differ in the degree to which these associations are perceptual or conceptual (Ramachandran & Hubbard, 2001). The majority of synesthetes, known as *associators*, report that the concurrent color sensation is present in their "mind's eye", whereas *projectors* experience the concurrent color as an intrinsic feature of the grapheme (Dixon, Smilek, & Merikle, 2004). Here we address the factors that mediate associations between particular graphemes and colors in synesthesia, and how they differ as a function of the projector–associator continuum.

While it was previously believed that the associations in grapheme–color synesthesia were random pairings between graphemes and hues (e.g. Jordan, 1917), studies examining large groups of synesthetes have shown some commonality in associations between individuals (e.g. A is typically red across multiple synesthetes; Simner et al., 2005). Furthermore, careful analyses of synesthetic correspondences demonstrated that the frequency of the stimulus predicted the relative intensity of the concurrent synesthetic experience. That is, higher frequency letters often pair with higher frequency color names (Simner et al., 2005), vowels tend to elicit more luminant and 'intense' colors than consonants in grapheme–color synesthesia due to their relative frequency (Beeli, Esslen, & Jancke, 2007; Smilek, Carriere, Dixon, & Merikle, 2007), and common words elicit more intense flavors than infrequent words in lexical-gustatory synesthesia (Simner & Haywood, 2009; Ward, Simner, & Auyeung, 2005). Although these studies failed to explain the factors driving the particular grapheme–hue pairings within a single individual, the common report of a non-arbitrary relationship between objective properties of the inducing stimuli (such as the frequency of graphemes) and subjective aspects of the concurrent sensations is in keeping with the cross-activation model of synesthesia (Ramachandran & Hubbard, 2001), and a more recent version of the model known as the cascaded cross-tuning (CCT) model of grapheme–color synesthesia (Brang et al., 2010).

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1.1. Cross-activation and the cascaded cross-tuning (CCT) model of synesthesia

In these models of grapheme–color synesthesia, the perceptual experience of colored graphemes reflects increased connectivity between brain regions underlying grapheme and color processing, respectively (Brang et al., 2010; Ramachandran & Hubbard, 2001). The proposal follows that greater structural connectivity between adjacent color and grapheme areas in the fusiform gyrus increases the probability that cells mediating grapheme processing will fire in synchrony with those representing color, thereby resulting in Hebbian connections between particular graphemes and particular hues. Among associator synesthetes, for whom grapheme–color associations are more conceptual, the increased connectivity (relative to non-synesthetes) is in frontal, parietal, and anterior temporal lobe structures, perhaps explaining the more associative and less perceptual experience of color. In projector synesthetes, who experience the concurrent color sensations as inherent perceptual properties of the graphemes, the increased connectivity extends to color processing area V4 and nearby posterior temporal lobe structures involved in the earliest stages of grapheme processing.

In an important test of this model, Rouw and Scholte (2007) compared structural connectivity in grapheme–color synesthetes and non-synesthetic controls using diffusion tensor imaging, and found greater connectivity in the frontal, parietal, and inferior temporal cortices of synesthetes than controls (but see Jancke, Beeli, Eulig, & Hanggi, 2009). Moreover, connectivity in the inferior temporal lobes was correlated with synesthetes' scores on the projector–associator continuum, as individuals with more characteristics of projector synesthetes show higher inferior temporal lobe connectivity. Besides studies assessing fractional anisotropy (Rouw & Scholte, 2007), voxel-based morphometry (VBM) has also been used to demonstrate that synesthetes have increased grey matter volume compared to non-synesthetes in regions in the inferior temporal lobe, implicated in both grapheme and color processing (Jancke et al., 2009; Weiss & Fink, 2009). Further, Rouw and Scholte (2010) also demonstrated strong differences in VBM between projector and associator synesthetes. Critically, projectors relative to associators showed large differences in grey matter volume in the sensory systems (visual cortex, auditory cortex, and motor cortex), consistent with the notion that they experience synesthetic colors as perceptual qualia. Associators, however, differed from projectors in grey matter volume within the hippocampus and parahippocampus, confirming subjective reports from synesthetes that the experience is associative in nature, more akin to memory recall than a sensory experience.

Consistent with the CCT model, studies have shown that reading or thinking about simple numbers or letters is associated with the activation of posterior temporal lobe grapheme areas (PTGA) in controls, but with engagement of both the PTGA and color processing area V4 in synesthetes (e.g. Hubbard, Ambrosio, Azoulai, & Ramachandran, 2005; Hubbard, Arman, Ramachandran, & Boynton, 2005; Sperling, Prvulovic, Linden, Singer, & Stirn, 2006, but see Rich et al., 2006; Weiss, Zilles, & Fink, 2005). This result was recently extended using magnetoencephalography (MEG), replicating the activation of PTGA in controls, and that of PTGA and color processing area V4 in projector synesthetes (Brang et al., 2010). Moreover, as MEG is able to capitalize on temporal aspects of neural processing, Brang et al. (2010) demonstrated near simultaneous activation of V4 and the PTGA in projector synesthetes, beginning as early as 110 ms after stimulus onset. Studies of synesthetes using event-related brain potentials (ERPs) from the electroencephalogram (EEG) also reveal the impact of synesthetic colors at a very early stage of grapheme processing, 100–150 ms post-stimulus (Brang, Edwards, Ramachandran, & Coulson, 2008; Brang, Kanai, Ramachandran, & Coulson, in press). Taken together, these data suggest the importance of cross-activation during the initial stages of letter processing.

The CCT model incorporates recent insights on the neural underpinnings of grapheme recognition in neurotypical individuals into cross-activation accounts of synesthesia. Recent accounts in neurotypical individuals describe grapheme recognition as a process of hierarchical feature analysis (see Dehaene, Cohen, Sigman, & Vinckier, 2005; Grainger, Rey, & Dufau, 2008 for reviews). In the initial stages of letter processing, visual input activates component features of the letter (line segments, curves, etc.), and results in the partial activation of letters containing some or all of the component features. Grapheme recognition occurs over time via a competitive activation process involving some combination of excitatory and inhibitory connections both within the grapheme level, and between the grapheme level and other representational levels, both bottom-up and top-down.

Hierarchical feature analysis models are supported by a wealth of studies on letter recognition, indicating that the number of component features shared by a pair of letters predicts the likelihood of those letters being confused (Geyer & DeWald, 1973). Integrating these behavioral measures with the neuro-anatomical models of visual perception, careful examination of the brain response to pseudo-letters (non-letter shapes visually matched to the component features comprising real letters), as well as infrequent and frequent letters shows a cascading hierarchy of processing within the PTGA, proceeding from posterior to anterior regions (Vinckier et al., 2007). Further, ERP studies of letter processing (e.g., comparing the brain response to letters and pseudo-letters) suggest feature level processing occurs prior to 145 ms, and letter-level processes occur thereafter (Rey, Dufau, Massol, & Grainger, 2009).

In light of these findings, the CCT model suggested that in synesthetes, connections between PTGA and V4 play a computational role in the competitive activation process. In projector synesthetes, interactions between color and grapheme processing begin during component level activations, as visual input activates not only component features of the letter, but also associated regions in V4. Just as activation of components at the feature level results in partial activation of a number of compatible candidates at the letter level, in synesthetes such activations are hypothesized to result in the partial activation of a range of colors within area V4, and later tuned to the correct color only after the letter has been subjected to further processing.

1.2. The present study

A key prediction follows from the CCT model claim that cross-activation between V4 and PTGA begins during the component stage of processing: at least in projector synesthetes, letters that share component features are more likely to activate similar hues in color space than are letters that do not share features. That is, for an individual synesthete, 'b' and 'd' should be closer in color space than say 'b' and 'm' as the latter share very few visual features.

The present study was designed to test this prediction of the CCT model. Accordingly, we tested the import of visual similarity on synesthetic colors evoked by letters. To this end we calculated color similarity matrices for each synesthete's set of letter–color correspondences, and examined the extent to which they correlated with visual letter confusability. To assess whether letters with similar visual features evoke similar hues, we regressed each synesthete's color similarity matrix against a letter confusability matrix. For a given synesthete, a strong correlation with visual similarity would suggest the importance of brain areas mediating component level processing of graphemes, consistent with the CCT model.

Table 1
Information on projector and associator synesthetes' correlations between visual similarity and hue similarity. Positive scores reflect a stronger impact of shape on synesthetic hues.

	Projectors (n = 16)	Associators (n = 36)
Average Fisher's corrected r	.145	.054
Minimum Fisher's corrected r	−.044	−.119
Maximum Fisher's corrected r	.600	.300
Number of significant correlations at the individual level	9 (56.2%)	16 (44.4%)

2. Methods

2.1. Participants

Data were collected from 52 English-fluent grapheme–color synesthetes (all possessing letter–color associations; 16 projectors, 36 associators), recruited via fliers posted on the UCSD campus, as well as similar ads on the web, and through a database of synesthetes at the University of Amsterdam. Synesthesia was confirmed by means of consistency matching as well as reaction-time testing for color congruency, standardized by Eagleman, Kagan, Nelson, Sagaram, and Sarma (2007).

2.2. Procedure and analysis

Synesthetes were presented with black letters (A–Z) and numbers (0–9) randomly, and instructed to pick the corresponding color from a color-picker palette via synesthete.org (see Eagleman et al., 2007 for additional details on data acquisition). Colors were registered in RGB color-space for subsequent analysis. Synesthetes also provided answers to Rouw and Scholte's associator/projector questionnaire, shown to correlate with the amount of connectivity in the inferior temporal lobe.

Colors were converted from RGB to CIE Lab color space to calculate color distances in a perceptual color space. Individual subject matrices were computed by comparing the distance between synesthetic colors (Euclidean distance between L, a, and b channels of Lab color space) for each of the possible letter combinations (yielding up to 325 color–distance values per subject). Some subjects reported that synesthetic colors did not exist for all letters, so such letters were excluded where appropriate. Each individual's set of color–distances was subsequently correlated to Courrieu, Farioli, and Grainger (2004) measure of visual similarity. In order to assess visual similarity, data were extracted from Courrieu et al.'s study investing values in response to same-different judgments of visually presented letters (325 combinations; 2004), with positive correlations suggesting more similar colors pair with more visually similar letters.

As the sampling distribution of Pearson's r is not normally distributed, Fisher's z' transformations must be applied when testing for group correlations or significant differences between correlations (Fisher, 1915). In instances where this transform has been applied, we refer to the values as Fisher corrected.

3. Results

Table 1 shows projector and associator synesthetes' average correlations for shape similarity; as a group, synesthetes showed an average correlation of r = .082 (Fisher corrected). While this correlation is small at the group level, the impact of shape similarity on synesthetic color, as assessed by Fisher corrected correlations, was highly significant for both projectors [one-sample t-test $t(15) = 3.64$, $p < .01$] and associators [one-sample t-test $t(35) = 3.73$, $p < .001$]. Furthermore, as predicted by the CCT model grapheme–color synesthesia, the effect of shape on color similarity was greater in projector synesthetes compared to associators, $t(50) = 2.63$, $p < .05$.

As the intensity of synesthetic experiences exist along a continuum, it is possible to quantify where along the projector–associator gradient each subject lies using a simple survey (Rouw & Scholte, 2007). Scores from the projector/associator survey ranged from −4 (associator classification) to +4 (projector classification). Results of this survey were compared to each synesthete's correlation between color similarity and visual similarity. Consistent with the group-level analysis, projector/associator scores showed a moderate positive correlation with color/shape correlations (r = .300, $t(50) = 2.214$, $p < .05$; Fig. 1), suggesting that the greater number of projector characteristics a synesthete showed, the greater their correlation between the relevant grapheme and color similarity metrics.

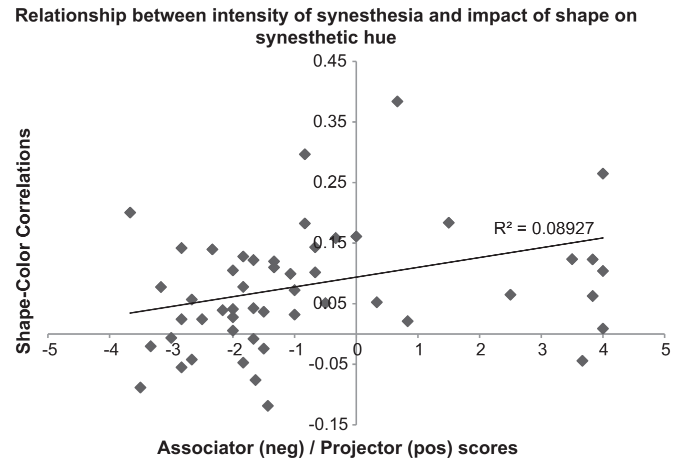

Fig. 1. Associator/projector scores for each synesthete reflecting the intensity of each synesthetes' experiences, compared against shape–color correlations (Fisher corrected). The positive correlation suggests that similarly shaped letters pair with similar synesthetic colors, with particularly strong an impact in projector synesthetes.

4. Discussion

The cascaded cross-tuning (CCT) model of grapheme–color synesthesia suggests that the concurrent sensation of color is evoked by graphemes due to cross-activation of grapheme and color processing areas in the posterior temporal lobes. In projector synesthetes, cross-activation begins during the initial feed-forward processing sweep involving feature component level processing of the graphemes. The present study was designed to test the prediction of the CCT model that letters sharing component features will be more likely to evoke similar synesthetic colors compared to letters that do not.

In keeping with this prediction, we have shown that in synesthetes, visually similar letter-forms were indeed associated with similar synesthetic colors. Moreover, this relationship was expressed more strongly in projectors than associators, consistent with the CCT model's claim that increased connectivity between V4 and PTGA is more likely to be present in the former group of synesthetes. Our findings are consistent with preliminary work by Hubbard, Ambrosio, et al. (2005) and Hubbard, Arman, et al. (2005), who demonstrated greater synesthetic color similarity within the letter-groups "KVWXY" or "CUDOQ" than when compared across the letter-groups, reflecting the pairing of visually similar letters with similar synesthetic colors. Furthermore, the present study is also consistent with preliminary results from multi-dimensional cluster analyses showing similar synesthetic colors tend to cluster around graphemes with similar low-level visual features (Eagleman, 2010), as well as basic feature analyses (round vs. angular, open vs. closed; Jürgens, Mausfeld, & Nikolić, 2010).

While the CCT may well explain the pattern of similar synesthetic colors between graphemes for projector synesthetes, this explanation may be incomplete for the associator form of grapheme–color synesthesia, which has been argued to rely less on low-level visual features, and tend to operate through conceptual processes (Ramachandran & Hubbard, 2001). Indeed, it is likely that some of the remaining variance in grapheme–color associations, that is, variance that is not accounted for by visual letter similarity, is due to linguistic (Simner et al., 2005) and cultural factors (Witthoft & Winawer, 2006). Moreover, it remains possible that some pairings are, as originally postulated, truly arbitrary.

Finally, these results, in conjunction with the CCT model, are in keeping with a developmental account of synesthesia in which the condition emerges before children begin to read. One tentative prediction made by the CCT model suggests that synesthesia might pre-date literacy, with colors initially elicited by basic shapes; it is then during development that synesthetic colors are redefined and tuned to individual graphemes. However, the notion of when during development synesthesia emerges remains a matter for future research.

In conclusion, grapheme–color synesthetes demonstrated a significant correlation between the visual similarity of graphemes and that of their associated synesthetic colors. This correlation was largest in projector synesthetes, implicating a stronger impact of early perceptual mechanisms. Further, the relationship between visual similarity and color similarity was a graded one, highlighting the intertwined relationship between conceptual and perceptual factors in synesthesia. Overall, these data support the CCT model of grapheme–color synesthesia, in which concurrent color experiences arise from cross-activation between brain areas important for processing graphemes (PTGA) and color (V4), as well as the notion that grapheme–color synesthesia emerges in development prior to the onset of literacy.

References

Baron-Cohen, S., Burt, L., Smith-Laittan, F., Harrison, J., & Bolton, P. (1996). Synaesthesia: Prevalence and familiarity. *Perception*, *25*, 1073–1079.

Beeli, G., Esslen, M., & Jancke, L. (2007). Frequency correlates in grapheme–color synaesthesia. *Psychological Science*, *18*(9), 788.

Brang, D., Edwards, L., Ramachandran, V. S., & Coulson, S. (2008). Is the sky 2? Contextual priming in grapheme–color synaesthesia. *Psychological Science*, *19*, 421–428.

Brang, D., Hubbard, E. M., Coulson, S., Huang, M. X., Song, T., & Ramachandran, V. S. (2010). Magnetoencephalography reveals early activation of V4 in grapheme color synesthesia. *NeuroImage*, *53*(1), 268–274.

Brang, D., Kanai, S., Ramachandran, V. S., & Coulson, S. (in press). Contextual priming in grapheme–color synesthetes and yoked controls: 400 ms in the life of a synesthete. *Journal of Cognitive Neuroscience*, doi:10.1162/jocn.2010.21486.

Courrieu, P., Farioli, F., & Grainger, J. (2004). Inverse discrimination time as a perceptual distance for alphabetic characters. *Visual Cognition*, *11*(7), 601–919.

Cytowic, R. E., & Eagleman, D. M. (2009). *Wednesday is indigo blue: Discovering the brain of synesthesia*. Cambridge, MA: MIT Press.

Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences*, *9*(7), 335–341.

Dixon, M. J., Smilek, D., & Merikle, P. M. (2004). Not all synaesthetes are created equal: Projector vs. associator synaesthetes. *Cognitive, Affective, and Behavioral Neuroscience*, *4*, 335–343.

Eagleman, D. M. (2010). What has large-scale analysis taught us? In *UK Synesthesia Association conference abstract* March, 2010,

Eagleman, D. M., Kagan, A. D., Nelson, S. S., Sagaram, S., & Sarma, A. K. (2007). A standardized test battery for the study of synesthesia. *Journal of Neuroscience Methods*, *159*(1), 139–145.

Fisher, R. A. (1915). Frequency distribution of the values of the correlation coefficient in samples of an indefinitely large population. *Biometrika (Biometrika Trust)*, *10*(4), 507–521.

Geyer, L. H., & DeWald, C. G. (1973). Feature lists and confusion matrices. *Perception & Psychophysics*, *14*, 471–482.

Grainger, J., Rey, A., & Dufau, S. (2008). Letter perception: From pixels to pandemonium. *Trends in Cognitive Sciences*, *12*(10), 381–387.

Hubbard, E. M., Ambrosio, P., Azoulai, S., & Ramachandran, V. S. (2005). Grapheme and letter name based patterns in synesthetic colors. *Cognitive Neuroscience Society Abstracts*.

Hubbard, E. M., Arman, A. C., Ramachandran, V. S., & Boynton, G. M. (2005). Individual differences among grapheme–color synesthetes: Brain–behavior correlations. *Neuron*, *45*, 975–985.

Jancke, L., Beeli, G., Eulig, C., & Hanggi, J. (2009). The neuroanatomy of grapheme–color synesthesia. *European Journal of Neuroscience*, *29*, 1287–1293.

Jordan, D. S. (1917). The colors of letters. *Science*, *46*, 311–312.

Jürgens, U. T., Mausfeld, R., & Nikolić, D. (2010). Grapheme–colour synaesthesia: Similar shapes take similar colours. In *UK Synesthesia Association conference abstract* March, 2010.

Ramachandran, V. S., & Hubbard, E. M. (2001). Synaesthesia: A window into perception, thought and language. *Journal of Consciousness Studies*, *8*, 3–34.

Rey, A, Dufau, S., Massol, S., & Grainger, J. (2009). Testing computational models of letter perception with item-level event-related potentials. *Cognitive Neuropsychology*, *26*(1), 7–22.

Rich, A. N., Williams, M. A., Puce, A., Syngeniotis, A., Howard, M. A., McGlone, F., et al. (2006). Neural correlates of imagined and synaesthetic colours. *Neuropsychologia*, *44*, 2918–2925.

Rouw, R., & Scholte, H. S. (2007). Increased structural connectivity in grapheme–color synesthesia. *Nature Neuroscience*, *10*, 792–797.

Rouw, R., & Scholte, H. S. (2010). Neural basis of individual differences in synesthetic experiences. *Journal of Neuroscience*, *30*(18), 6205–6213.

Simner, J., & Haywood, S. L. (2009). Tasty non-words and neighbours: The cognitive roots of lexical-gustatory synaesthesia. *Cognition*, *110*(2), 171–181.

Simner, J., Ward, J., Lanz, M., Jansari, A., Noonan, K., Glover, L., et al. (2005). Non-random associations of graphemes to colours in synaesthetic and non-synaesthetic populations. *Cognitive Neuropsychology*, *22*(8), 1069.

Smilek, D., Carriere, J. S., Dixon, M. J., & Merikle, P. M. (2007). Grapheme frequency and color luminance in grapheme–color synaesthesia. *Psychological Science*, *18*(9), 793.

Sperling, J. M., Prvulovic, D., Linden, D. E. J., Singer, W., & Stirn, A. (2006). Neuronal correlates of graphemic colour synaesthesia: A fMRI study. *Cortex*, *42*, 295–303.

Vinckier, F., Dehaene, S., Jobert, A., Dubus, J. P., Sigman, M., & Cohen, L. (2007). Hierarchical coding of letter strings in the ventral stream: Dissecting the inner organization of the visual word-form system. *Neuron*, *55*(1), 143–156.

Ward, J., Simner, J., & Auyeung, V. (2005). A comparison of lexical-gustatory and grapheme–colour synaesthesia. *Cognitive Neuropsychology*, *22*(1), 28–41.

Weiss, P. H., & Fink, G. R. (2009). Grapheme–colour synaesthetes show increased grey matter volumes of parietal and fusiform cortex. *Brain*, *132*, 65–70.

Weiss, P. H., Zilles, K., & Fink, G. R. (2005). When visual perception causes feeling: Enhanced cross-modal processing in grapheme–color synesthesia. *NeuroImage*, *28*, 859–868.

Witthoft, N., & Winawer, J. (2006). Synesthetic colors determined by having colored refrigerator magnets in childhood. *Cortex*, *42*, 175–183.