Learning, Memory, and Synesthesia

Nathan Witthoft and Jonathan Winawer

Psychological Science published online 10 January 2013
DOI: 10.1177/0956797612452573

Psychological Science OnlineFirst, published on January 10, 2013 as doi:10.1177/0956797612452573

Research Article

ASSOCIATION FOR PSYCHOLOGICAL SCIENCE

Psychological Science
XX(X) 1–8

DOI: 10.1177/0956797612452573
http://pss.sagepub.com
SAGE

Learning, Memory, and Synesthesia

Nathan Witthoft and Jonathan Winawer
Stanford University

Abstract

People with color-grapheme synesthesia experience color when viewing written letters or numerals, usually with a particular color evoked by each grapheme. Here, we report on data from 11 color-grapheme synesthetes who had startlingly similar color-grapheme pairings traceable to childhood toys containing colored letters. These are the first and only data to show learned synesthesia of this kind in more than a single individual. Whereas some researchers have focused on genetic and perceptual aspects of synesthesia, our results indicate that a complete explanation of synesthesia must also incorporate a central role for learning and memory. We argue that these two positions can be reconciled by thinking of synesthesia as the automatic retrieval of highly specific mnemonic associations, in which perceptual contents are brought to mind in a manner akin to mental imagery or the perceptual-reinstatement effects found in memory studies.

Keywords

visual perception, memory, learning, consciousness

Received 1/24/12; Revision accepted 5/10/12

A person is said to have synesthesia when his or her perception of a physical stimulus, such as this black letter *A*, automatically produces an impression that is not directly derived from the stimulus—for example, if this *A* evokes the color red. Experiencing colors in response to reading achromatic printed letters and numbers (grapheme-color synesthesia) is among the most common and widely studied kinds of synesthesia (Simner et al., 2006). Other pairings within and between sensory modalities have also been reported, including colors evoked by musical pitches (Marks, 1975), spatial arrangements elicited by numbers (Calkins, 1893; Galton, 1881), and tastes in response to words (Ward & Simner, 2003).

More than a century ago, Galton (1881) prefaced his description of color-number synesthesia by cautioning readers that the contents of every sane person's mind are not the same. He was aware that, to some people, synesthesia appeared implausible or, at best, an anomaly with little relation to the study of ordinary cognition. Since then, many results in psychophysics and neuroimaging have attested to the perceptual and neural basis of synesthesia (Blake, Palmeri, Marois, & Kim, 2005; Hubbard & Ramachandran, 2005; Kim & Blake, 2005; Kim, Blake, & Palmeri, 2006; Ramachandran & Hubbard, 2001a; Witthoft & Winawer, 2006). Researchers have argued that synesthesia matters because relationships between ideas or modes of experience, such as those between pitch and brightness or space and number, that are implicit in the nonsynesthete are made explicit in the synesthete (Cohen Kadosh & Henik, 2007; Marks, 1975; Martino & Marks, 2001; Ramachandran & Hubbard, 2001b); making these relationships explicit provides an unobscured view of the representations underlying normal cognitive processes, such as cross-modal perception, abstraction, and metaphor.

The idea that grapheme-color synesthetes learn their colors from childhood toys was proposed more than 100 years ago (Calkins, 1893), but documented cases have been exceedingly rare. In one large-scale investigation, Rich, Bradshaw, and Mattingley (2005) compared colored letters and numbers found in 46 Australian children's books and toys with matched color-grapheme pairs generated from 150 synesthetes and found little evidence that color-grapheme correspondences were learned. Subsequently, there have been two reported cases (including one by the present authors) in which grapheme-color matches were learned from a childhood toy: The first case was one half of a pair of monozygotic twins (Hancock, 2006), and the second case was a single individual (Witthoft & Winawer, 2006). Blake et al. (2005) also noted that one of their well-studied synesthetes reported learning her colors from a set of refrigerator magnets. Given the limited number of cases and the failure to find additional examples in a large survey, these findings have failed to affect the general theoretical perspective on synesthesia (Ward & Mattingley, 2006). Rather, they are considered by some researchers to be an irrelevant "red herring" (Spector & Maurer, 2009, p. 179)

Corresponding Author:
Nathan Witthoft, Department of Psychology, Stanford University, 416 Jordan Hall, Stanford, CA 94305
E-mail: witthoft@stanford.edu

or instances of pseudosynesthesia (Baron-Cohen & Harrison, 2005), but others worry reasonably of an unfruitful case-study approach to synesthesia (Novich, Cheng, & Eagleman, 2011).

In this article, we present data from 11 grapheme-color synesthetes, all with highly similar letter-color pairings that were apparently learned from a very common letter toy in the United States. In 10 of 11 cases, the subjects recalled owning or still own the toy. In all cases, the correspondence between the letter-color matches and the toy is obvious; these correspondences demonstrate that the pairings in color-grapheme synesthesia can be learned from external letter-color pairings. We propose that this result, along with other recent findings showing more general influences of experience on synesthesia, indicate that learning has a central role in synesthesia. A coherent framework for organizing many results reported in the literature can be constructed by defining synesthesia as comprised by relatively fixed and unusually detailed memories and by positing that synesthesia points to a strong relationship between memory and perception.

Method

Subjects

Our subjects were 11 color-grapheme synesthetes born in the United States between 1970 and 1985 (5 female, 6 male). The details of Subject 5's synesthesia, including the influence of lightness illusions on her color matches, can be found in Witthoft and Winawer (2006). Subject 7 was contacted prior to publication of that article in response to a post he made to a synesthesia mailing list stating that he had learned his colors from a childhood toy. Subjects 1, 2, 3, 8, 10, and 11 contacted us after they saw the 2006 article on the American Synesthesia Association Web site (http://www.synesthesia.info/). Subject 1 had already participated in several studies with the Vanderbilt Vision Research Center, and more details about the perceptual nature of her synesthesia, including mention that her color associations derived from a childhood toy, can be found in articles by Vanderbilt members (Blake et al., 2005; Kim & Blake, 2005; Kim et al., 2006). The connection between Subject 1 and Subject 5 did not become clear until we saw Subject 1's color-matching data, which have not been published before. Subject 9 is a synesthesia researcher and put us in touch with one of his subjects (Subject 4) who had similar letter-color pairings. Subject 6 is a vision scientist whom we encountered at a conference while presenting data from the first 10 subjects. Additional information about each person's synesthesia can be found in Table S1 in the Supplemental Material available online.

Procedure

Early researchers noted that the particular synesthetic experience a stimulus evokes in a synesthete is highly specific, automatically elicited, and remains relatively constant over time (Galton, 1881). This fixed relationship has been demonstrated many times and is a defining characteristic of synesthesia that usefully distinguishes it from the relative but consistent cross-modal matching behavior exhibited by most people (Marks, 1974; Martino & Marks, 2001; McDermott, Lehr, & Oxenham, 2008).

Grapheme-color matching data from 10 of our 11 subjects were collected using The Synesthesia Battery Web site (synesthete.org), which provides tests designed to identify synesthesia. These 10 subjects performed a letter-color matching task, in which they were presented with all 26 upper-case letters of the alphabet and 10 single digits (0–9) one at a time, three times each in random order. Subjects used a color picker that allowed them to adjust the red, green, and blue (RGB) values of each grapheme until its color matched their synesthetic color (D. E. Eagleman, Kagan, Nelson, Sagaram, & Sarma, 2007). Data from the remaining subject were collected using in-house software. Each subject participated in two matching sessions, and the consistency of matches was evaluated both within and between sessions.

Further evidence of genuine synesthesia for these 10 subjects was evaluated using a speeded congruency task on The Synesthesia Battery Web site (D. E. Eagleman et al., 2007). Subjects were presented with colored letters for 1 s each and required to rapidly determine whether the color was consistent with their synesthetic color. The selection of inconsistent colors was constrained so that they were not close to the consistent colors in the color space.

Results

Speeded congruency task

Previous work suggests that scoring at or above 85% on the speeded congruency task is typical for synesthetes (D. E. Eagleman et al., 2007), and all 10 subjects exceeded this threshold (lowest accuracy = 90%, mean accuracy = 93.5%, *SD* = 0.7%). Subjects performed this task rapidly (mean response time = 1.2 s, *SD* = 0.1 s; Fig. 1b). Stroop-test data showing automatic elicitation of synesthesia by graphemes in Subject 5 can be found in Witthoft and Winawer (2006).

Color matching within and between matching sessions

Within-session color-matching reliability was calculated by comparing the distances between the RGB image indices (ranging from 0 to 1) for each of the three matches for each grapheme. A distance metric was defined by summing the city-block distances for each of three pairwise matches and averaging over graphemes. A perfect reliability score of 0 was achieved by producing identical RGB matches for each presentation of a given grapheme. A mean reliability score of 3.0 (*SD* = 0.77) was obtained by randomly selecting RGB values for each match from a uniform distribution. This metric is computed for all users of The Synesthesia Battery Web site and so is useful for assessing reliability. A threshold of 1.0 has

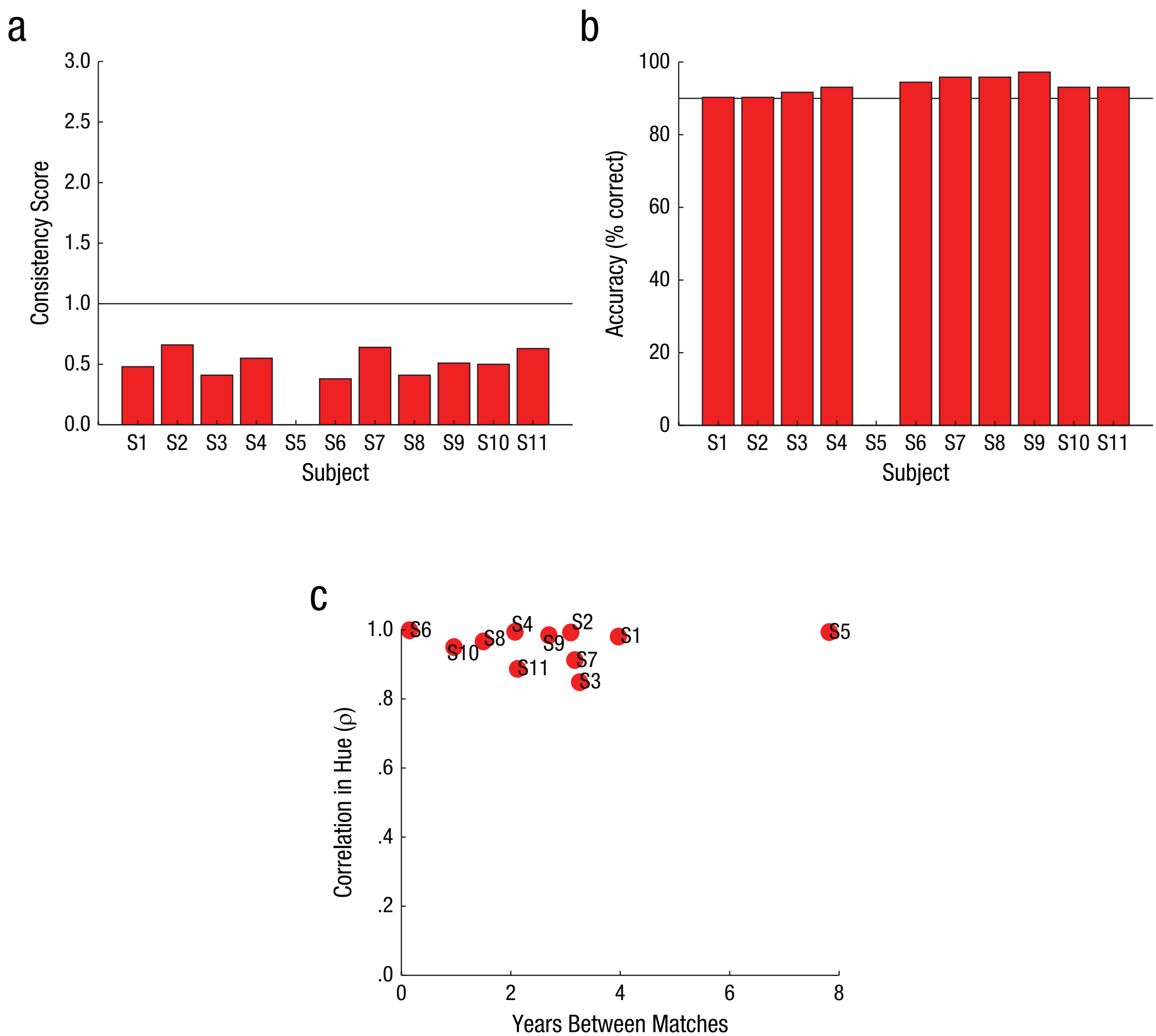

Fig. 1. Evidence for synesthesia among the subjects in the present study. Mean within-session consistency scores on a color-grapheme matching task are shown for 10 subjects in (a). Subjects must score less than 1 (indicated by the horizontal line) in order to be classified as a synesthete. Mean accuracy on a speeded congruency task is shown for 10 subjects in (b). The horizontal line indicates the minimum performance required in order to be classified as a synesthete. The average circular correlation between hues selected by subjects in the first session and in the second session is shown in (c) as a function of the number of years between sessions.

been observed to best discriminate synesthetes from control subjects attempting to produce consistent matches by association (D. E. Eagleman et al., 2007). All 10 of our subjects scored well below this threshold ($M = 0.517$, $SD = 0.03$, maximum = 0.66; Fig. 1a).

Matches across sessions proved to be nearly as reliable as matches within a single session. Subjects participated in a second color-matching session at least 54 days after the first session (10 of the 11 subjects had a delay greater than 1 year; maximum delay = 2,854 days). We quantified between-sessions reliability as the correlation between the selected hues for a given grapheme in the first matching session (average of three matches) and the selected hues for the same grapheme in the second matching session (average of three matches). Although the RGB metric used for the within-sessions performance was useful for comparison with nonsynesthetic performance reported in previous work (D. E. Eagleman et al., 2007), distances in RGB color space do not closely correspond to psychological distance. In contrast, hue correlations give a better, though not perfect, idea of the variability across matching sessions, and our previous research indicated that Subject 5 was especially precise about matching hues (Witthoft & Winawer, 2006). RGB color-matching data were converted to hue, saturation, and value (HSV) coordinates, and a circular correlation was generated between the average hue of each letter from Session 1 and Session 2 (Berens, 2009). Letters with achromatic color matches (total of 20 across all subjects) were excluded, as they have no hue.

Subjects' letter-color pairings proved to be highly reliable, with a mean circular correlation (ρ) of 0.96 and some correlations greater than 0.99 (Fig. 1c), even with 1 to 8 years intervening between testing sessions (see Color Calculations in the Supplemental Material for details). These numbers demonstrate the longevity and specificity of the synesthetic associations in these subjects.

Letter-color pairings learned from childhood toys

The degree of similarity across subjects' letter-color pairings along with the clearly visible regular repeating pattern in the colors found in each individual's set of matches (Fig. 2) is striking. Each subject, with the exception of Subject 9, reported having owned one of three toys widely sold by Fisher-Price between 1972 and 1989 (see Information About the Letter and Number Sets in the Supplemental Material and www.thisoldtoy.com/L_FP_Set/toy-pages/100-199/176-schooldaysplaydesk.html for information about one of the toys). Each of these toys contained a set of magnetic letters that always had the same color scheme. Subjects 2, 3, 4, and 5 still own their version of the toy, and photographs of these are shown in Figure 2 (a picture of Subject 5's toy was printed in Witthoft & Winawer, 2006). The color matches shown in Figure 2 are ordered from left to right based on how many of the subject's matches corresponded to the colors in the letter set. Subject 11 showed 14, which is the fewest matches among all subjects. We estimate the probability of observing 14 or more matches in 26 chances is less than 1 in 1 billion, and the probability of having 11 sequences meet this criterion is substantially less (see Estimating the Probability in the Supplemental Material for details of probability calculations).

Reliably different between-subjects matches

Despite the strong similarity between the subject matches, each subject's letter-color pairings show some subtle but reliable specificity in the exact hue match to each letter. We noted qualitatively that when shown Figure 2, individual synesthetes could easily pick out which set of matches was their own. To quantify the individual differences in matches, we computed the circular correlation between every pair of subjects' matches (using HSV coordinates) and compared these with the circular correlation obtained for each subject over the two matching sessions, as described previously. We then ranked the correlations for each subject from 1 to 11, with 1 indicating that a subject's cross-session matches were better correlated than any of the between-subjects matches and 6 indicating that a subject's cross-session matches were no better correlated than

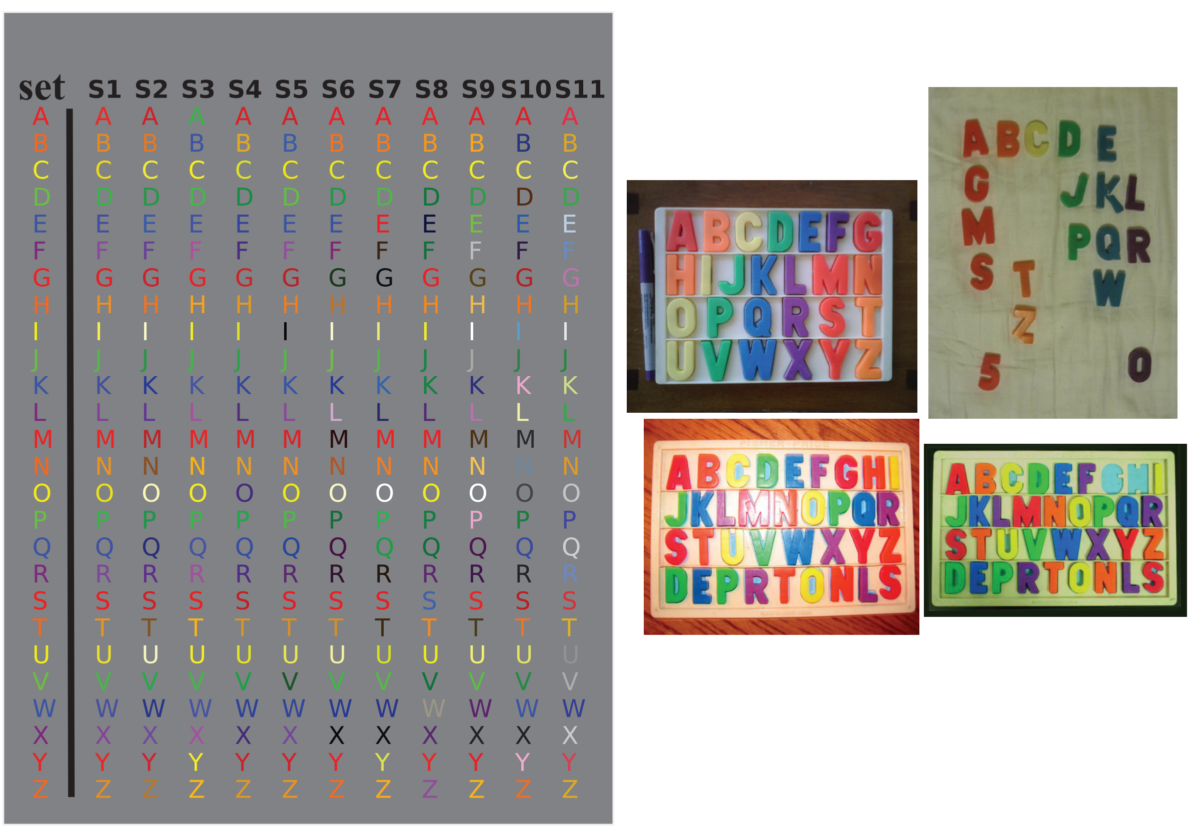

Fig. 2. Letter-color matching data from the 11 subjects. The diagram shows the color selected for each letter, averaged across three trials for each subject. The left-most column indicates the colors of the Fisher-Price refrigerator magnets used by all but 1 of the subjects as children. Subjects' photos of the magnets are shown on the right.

that subject's matches to another's. The inability to differentiate different subjects' matches is what might be expected if subjects simply picked colors corresponding to a verbal label, such as "red." The mean rank of the cross-session matching data was 1.5. The low mean rank demonstrates that the individual differences are specific and reliable.

Letter-color pairings that deviate from the group pattern

One possible explanation for the similarity between our subjects' data is that the pattern of color matches common to this group of 11 subjects is found in many synesthetes. Available published work demonstrates that the letter-color pairings corresponding to the toys do not reflect tendencies in all color-grapheme synesthetes. Surveys of large numbers of synesthetic and nonsynesthetic English speakers have shown significant agreement on color choices for some letters and numbers. Depending on the survey, 33% to 40% of synesthetes have reported that the letter *A* is red, and 40% to 50% have said that *Y* is yellow (Barnett et al., 2008; Rich et al., 2005; Simner, 2005), with above-chance agreement usually found for approximately 12 letters. With the exception of the frequent choice of red for *A*, none of synesthetes' modal color choices for letters matched the letters in the toy or in our group. Instead, when the synesthetes in our group did deviate from the letter set in their matches, their deviations matched the modal choice from the surveys more than 50% of the time (see Fig. S1 in the Supplemental Material). For example, approximately 45% of synesthetes in one survey by Rich et al. (2005) chose yellow for *Y*. Nine of the 11 synesthetes in our group made *Y* orange, as it is in the set, but the other 2 chose yellow.

The fact that data from the synesthetes in the present study match the data from synesthetes at large only when they deviate from the letter set leads to two important conclusions. First, the matches that correspond to the letter set were likely learned from the letter set, rather than from general influences. Second, deviations from the letter set appear to be subject to more general influences, a finding that confirms prior results and argues against a distinction between the synesthetes in our study and other color-grapheme synesthetes (though see Tomson et al., 2011, for evidence of multiple subtypes of grapheme-color synesthesia). The latter finding reinforces the view that these subjects had some tendency toward synesthesia and that the presence of the toy shaped rather than created it.

Number-color matches

All of the synesthetes in the present study also reported number-color associations. The colors evoked by each number showed strong consistency over time, with 9 out of 11 of the subjects showing a circular correlation in hue across matching sessions of greater than 0.97 (see Fig. S2 in the Supplemental Material). The one exception was Subject 3, who transposed the colors of *2, 3, 7*, and *9*, showing a reliable pattern during a particular matching session but not between sessions (though other number-color associations remained the same between sessions). Subject 1 did not generate number-color matches in the second session.

Of the 11 subjects, only Subjects 2, 3, 4, and 6 explicitly recalled having colored number sets in childhood. Two of the toys that Fisher-Price manufactured contained colored number magnets as well as letters, both with the same color scheme for the numbers (Fig. 3). Subjects 2, 4, and 6 showed 10, 8, and 6 matches, respectively, with the letters from these toys (Fig. 3). Fisher-Price also made a third toy (Fig. 3), which consisted of a tray containing number magnets and arithmetic symbols. Subject 3 supplied a photo of this toy, and her data showed 5 out of 10 matches with its number-color pairings (6 out of 10 if the yellow *O* is the source for the yellow *0*). We estimate that the probability of finding 5 or more matches given 10 trials is less than 1 in 50,000 (see Estimating the Probability in the Supplemental Material). Most of the other subjects show 0 to 2 matches with either number set, $p(\text{matches} \geq 2) = .22$, and Subject 7 showed 4 matches to one of the sets. Given Subject 7's date of birth, it seems plausible that he owned one of the toys that came with the numbers, but he cannot recall this. As with most grapheme-color synesthetes, the origin of the particular pairings for the remaining subjects is unknown. In some cases (e.g., Subject 1), it seems that the colors found in the numbers

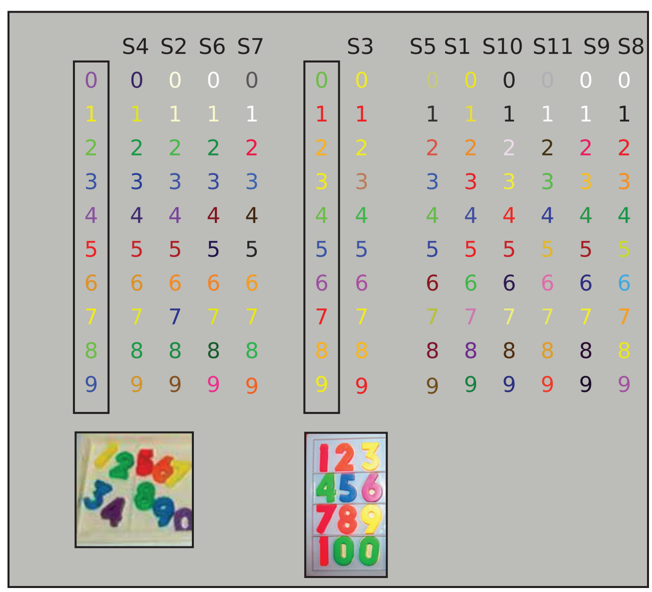

Fig. 3. Number-color matching data from the 11 subjects. Results are grouped according to the magnetic number sets that subjects may have had. On the left are results for subjects who had either of two versions of the toy, with the color scheme illustrated by the photograph below. In the middle, results are shown for 1 subject who owned a set with a different color scheme (also illustrated by the photograph below). The color of the numbers in each of the two sets is indicated in the black boxes. Results for the remaining subjects, who did not recall ever owning one of these toys, are displayed on the right. Color values for each letter were averaged across three trials for each subject.

were chosen from the available colors in the letters, but we do not see any obvious overall pattern, though there are intriguing similarities (e.g., associating *7* with yellow).

Discussion

Researchers in the late 19th and early 20th centuries often proposed learning as a cause of synesthesia (e.g., Calkins, 1893), though examples were nonexistent. By contrast, for many modern researchers, the questionable theoretical relevance of the few recently discovered instances of learned synesthesia, and the fact that synesthesia itself is uncommon, means that these case studies are viewed as anomalies among the anomalous (Baron-Cohen & Harrison, 2005; Marks & Odgaard, 2005; Ramachandran & Hubbard, 2001b; Ward & Mattingley, 2006). The data presented here provide clear evidence that synesthetic grapheme-color correspondences can be learned from external correspondences, which should be accounted for in any theory of synesthesia.

Some researchers will still feel that despite such cases as the ones described here, learning cannot serve as an explanation for synesthesia. There are three main objections to learning accounts of synesthesia. The first objection is that synesthesia is perception rather than memory (Ramachandran & Hubbard, 2001b). The second is that learning alone cannot explain why only some people become synesthetes (Marks & Odgaard, 2005; Spector & Maurer, 2009). Finally, it can be objected that most synesthetic pairings are not learned. Nonetheless, the data here, the growing number of findings showing cultural influences on synesthetic matches (Barnett et al., 2008; Beeli, Esslen, & Jancke, 2007; Rich et al., 2005; Simner, 2005), and the fact that a large majority of synesthesias ($\geq$ 88%) are induced by learned linguistic sequences such as phonemes, graphemes, and numbers (Eagleman, 2009; Simner, 2005) show that learning and memory must play some role (Marks & Odgaard, 2005).

In recent years, there has been growing evidence that synesthesia can be a genuine perceptual phenomenon and not the explicit recall of a previously observed correspondence. Ramachandran and Hubbard (2001b), for example, argue that synesthesia is not just a memory of a childhood magnet set that the synesthete played with but rather a genuine perceptual experience. Although many grapheme-color synesthetes do not experience their synesthesia as part of the visual scene, this insistence on the perceptual nature of synesthesia in at least some cases (including two of those reported here) has been invaluable in demonstrating that the color associated with a grapheme can have a great deal more specific content than just associating a letter with a color name and may in some cases interact with the visual scene (Blake et al., 2005; Kim & Blake, 2005; Kim et al., 2006; Witthoft & Winawer, 2006).

We do not wish to argue against a perceptual component of synesthesia, but rather for a role of learning and memory. Associative learning and the perceptual experiences of synesthetes are not only compatible, but also lie on a continuum with ordinary experience. Suppose the introduction to this article had been written as follows, "A person may be said to have synesthesia when a stimulus, such as this letter *A*, automatically produces an additional idea—for example, that it has the sound /a/." Given this description, some readers would recognize themselves as synesthetes because many people report that reading is accompanied by auditory imagery (hearing words while reading; Alexander & Nygaard, 2008). It seems safe to state that the arbitrary, consistent, and automatic pairing some readers experience between visual symbols and the associated "sounds" is the product of learning. That people judge that their internal speech has perceptual qualities is no guarantee that their experience is supported by any of the same mechanisms as perception (Pylyshyn, 2002), but a large body of evidence supports a strong overlap between memory, imagery, and perception (Harrison & Tong, 2009; Paivio, 1969; Wheeler, Petersen, & Buckner, 2000; Winawer, Huk, & Boroditsky, 2010).

So what makes synesthetes different from nonsynesthetes if it is not the difference between seeing and remembering? Like readers who experience auditory imagery, synesthetes can separate their synesthesia from the external world (Blake et al., 2005; Marks, 1975). However, synesthetes differ from most people in that their "imagery" is fixed and automatic. For example, when asked to match pitches to patches of varying brightness, most people will match brighter patches to higher pitches, but this matching is relative, and they will simply distribute the range of available brightnesses (Marks, 1975). Pitch-color synesthetes also tend to have brighter colors for higher pitches, but for each pitch, there is a particular color, and changing the range of available matches will not change their choices. This distinction has been most fully developed by Martino and Marks (2001), who referred to the two types of matching behavior as "weak" and "strong" synesthesia, respectively (see Cohen Kadosh & Henik, 2007, for a related point about synesthesia making cross-modal relationships explicit).

For the average person to be a synesthete, then, it would be as if every time they read the letter *A*, they automatically heard it whispered into their left ear by a particular person from 6 in. away (Galton, 1881; Tyler, 2005). We hypothesize that it is just the reliability and specificity (what in imagery studies is loosely called *vividness*) of the content of the memory that causes subjects to experience it as part of (or to attribute it to) some external stimulus (Martino & Marks, 2001). Synesthesia is not "just" remembering, but it is remembering nonetheless.

Although learning is compatible with synesthesia as a perceptual phenomenon, most synesthetes probably do not learn their synesthetic correspondences from some external object present in childhood. This fact could reasonably be taken to suggest that this type of learning is irrelevant to understanding synesthesia. However, considered from a different perspective, learning is the defining characteristic of synesthesia. As noted, synesthetes experience a fixed and automatic synesthetic response to some stimuli. These responses across many types of synesthesia do not appear to be entirely random, but alignable with choices made by nonsynesthetes. Thus, an important way in which synesthesia informs normal cognition is that both synesthetes and nonsynesthetes are influenced by similar factors when matching two domains, say space and number (Cohen Kadosh & Henik, 2007). Studying synesthesia makes it easier to uncover these implicit correspondences in nonsynesthetes. However, when answering the question, "what is synesthesia?" we would point again to the fixed nature of the synesthetic association and say it is the learning of that association that makes someone a synesthete. The information guiding the association may be relatively innate, as suggested for brightness and size, or due to environmental statistics, such as the proposed relationship between frequency and grapheme brightness (Beeli et al., 2007), or come from some specific stimulus, as with the subjects in the present study.

Finally, why do only some people become synesthetes (Marks & Odgaard, 2005; Ramachandran & Hubbard, 2001b; Ward & Mattingley, 2006)? We do not argue that the presence of the magnet set was sufficient to induce synesthesia (though it possibly increased the chances), and we have met many nonsynesthetes who owned the same toy. Furthermore, most attempts to induce synesthesia via repeated association in adults have failed (Kelly, 1934; Marks, 1975; Marks & Odgaard, 2005). There is little to address why only some people become synesthetes beyond data suggesting that synesthesia is heritable (Barnett et al., 2008), and one could propose that something about learning mechanisms is inherited (Marks & Odgaard, 2005). Many researchers before us have noted that the prevalence of culturally learned sequences as inducers of synesthesia is overwhelming, and it seems that synesthesia arises around the age at which children are learning the alphabet and counting (Simner, Harrold, Creed, Monro, & Foulkes, 2009). In the search for mechanisms that are likely genetically specified, the field might be well served by considering or expanding the existing developmental and memory literature on how children learn and use these sequences (Marks & Odgaard, 2005; Rich et al., 2005).

Our proposals that synesthesia is best described as highly detailed and automatically retrieved memories and that particular mappings can be derived from external contingencies, when present, are intended to apply to synesthesia generally. However, it is possible that they apply only to some types of synesthesia (in particular, those involving learning sequences) or even some subtypes of color-grapheme synesthesia. Novich et al. (2011) argue that synesthesia encompasses several distinct groupings. They examined data from a large group of synesthetes (more than 1,200) and found that individuals who experienced any one kind of colored-sequence synesthesia (colors paired with either letters, numbers, days of the week, or months) were likely to also experience the other kinds of colored-sequence synesthesia. In contrast, having a colored-sequence synesthesia was roughly independent of other types of synesthesia, such as colors evoked by pitches. It has also been suggested on the basis of genetic evidence that grapheme-color synesthesia can be divided into at least two groups (Tomson et al., 2011). Given this evidence, it may be that the kind of learning found in our data is possible only because of the type of mechanisms associated with a particular subgroup of synesthesia, though whether that line should be drawn at sequences, colored sequences, or a subtype of color-grapheme synesthesia is unknown.

In summary, pairings in color-grapheme synesthesia can be learned from experience in childhood, and this learning produces color-grapheme mappings that are highly precise and stable over many years. The synesthetic responses retain many of the details of the original stimulus but also take on some specific idiosyncratic features. These results demonstrate an important role for learning and memory in synesthesia but are consistent with a role for perception in synesthetic experience. The two ideas are made compatible by positing that the learned associations between stimulus and response are highly detailed and automatically triggered, two important characteristics for giving a representation a perceptual quality. These associations may be determined by internal or external contingencies, though we emphasize that external contingencies are not sufficient to produce synesthesia, which is likely dependent on genetic factors.

Acknowledgments

The authors would like to thank Bart Anderson, Nicolas Davidenko, Josh McDermott, Anthony Wagner, and David Eagleman for their comments on previous drafts of this manuscript.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Funding

Nathan Witthoft was supported by National Institutes of Health (NIH) Grant RO1EY019279-01A1, and Jonathan Winawer received support from NIH Grant EY019244.

Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

References

Alexander, J. D., & Nygaard, L. C. (2008). Reading voices and hearing text: Talker-specific auditory imagery in reading. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 446–459. doi:10.1037/0096-1523.34.2.446

Barnett, K. J., Finucane, C., Asher, J. E., Bargary, G., Corvin, A. P., Newell, F. N., & Mitchell, K. J. (2008). Familial patterns and the origins of individual differences in synaesthesia. *Cognition*, *106*, 871–893. doi:10.1016/j.cognition.2007.05.003

Baron-Cohen, S., & Harrison, J. (2005). Synaesthesia. In L. Nadel (Ed.), *Encyclopedia of cognitive science*. Retrieved from http://onlinelibrary.wiley.com/doi/10.1002/0470018860.s00295/full. doi: 10.1002/0470018860.s00295

Beeli, G., Esslen, M., & Jäncke, L. (2007). Frequency correlates in grapheme-color synaesthesia. *Psychological Science*, *18*, 788–792. doi:10.1111/j.1467-9280.2007.01980.x

Berens, B. (2009). CircStat: A MATLAB toolbox for circular statistics. *Journal of Statistical Software*, *31*(10). Retrieved from http://www.jstatsoft.org/v31/i10/paper

Blake, R., Palmeri, T. J., Marois, R., & Kim, C.-Y. (2005). On the perceptual reality of synesthetic color. In L. C. Robertson & N. Sagiv (Eds.), *Synesthesia: Perspectives from cognitive neuroscience* (pp. 47–73). New York, NY: Oxford University Press.

Calkins, M. W. (1893). A statistical study of pseudo-chromesthesia and of mental forms. *American Journal of Psychology*, *5*, 439–464.

Cohen Kadosh, R., & Henik, A. (2007). Can synaesthesia research inform cognitive science? *Trends in Cognitive Sciences*, *11*, 177–184. doi:10.1016/j.tics.2007.01.00310.1016/j.cognition.2006.12.007

Eagleman, D. E., Kagan, A. D., Nelson, S. S., Sagaram, D., & Sarma, S. K. (2007). A standardized test battery for the study of synesthesia. *Journal of Neuroscience Methods*, *159*, 139–145. doi:10.1016/j.jneumeth.2006.07.012

Eagleman, D. M. (2009). The objectification of overlearned sequences: A new view of spatial sequence synesthesia. *Cortex*, *45*, 1266–1277. doi:10.1016/j.cortex.2009.06.012

Galton, F. (1881). Visualized numerals. *Journal of the Royal Anthropological Institute*, *10*, 85–102.

Hancock, P. (2006). Monozygotic twins' colour-number association: A case study. *Cortex*, *42*, 147–150. doi:10.1016/S0010-9452(08)70338-1

Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*, 632–635. doi:10.1038/nature07832

Hubbard, E. M., & Ramachandran, V. S. (2005). Neurocognitive mechanisms of synesthesia. *Neuron*, *48*, 509–520. doi:10.1016/j.neuron.2005.10.012

Kelly, E. L. (1934). An experimental attempt to produce artificial chromaesthesia by the technique of conditioned response. *Journal of Experimental Psychology*, *17*, 315–341. doi:10.1037/h0074963

Kim, C.-Y., & Blake, R. (2005). Watercolor illusion induced by synesthetic colors. *Perception*, *34*, 1501–1507. doi:10.1068/p5422

Kim, C.-Y., Blake, R., & Palmeri, T. J. (2006). Perceptual interaction between real and synesthetic colors. *Cortex*, *42*, 195–203. doi:10.1016/S0010-9452(08)70344-7

Marks, L. E. (1974). On associations of light and sound: The mediation of brightness, pitch, and loudness. *American Journal of Psychology*, *87*, 173–188.

Marks, L. E. (1975). On colored-hearing synesthesia: Cross-modal translations of sensory dimensions. *Psychological Bulletin*, *82*, 303–331. doi:10.1037/0033-2909.82.3.303

Marks, L. E., & Odgaard, E. C. (2005). Developmental constraints on theories of synesthesia. In L. C. Robertson & N. Sagiv (Eds.), *Synesthesia: Perspectives from cognitive neuroscience* (pp. 214–236). New York, NY: Oxford University Press.

Martino, G., & Marks, L. E. (2001). Synesthesia: Strong and weak. *Current Directions in Psychological Science*, *10*, 62–65. doi:10.1111/1467-8721.00116

McDermott, J. H., Lehr, A. J., & Oxenham, A. J. (2008). Is relative pitch specific to pitch? *Psychological Science*, *19*, 1263–1271. doi:10.1111/j.1467-9280.2008.02235.x

Novich, S., Cheng, S., & Eagleman, D. M. (2011). Is synaesthesia one condition or many? A large-scale analysis reveals subgroups. *Journal of Neuropsychology*, *5*, 353–371. doi:10.1111/j.1748-6653.2011.02015.x

Paivio, A. (1969). Mental imagery in associative learning and memory. *Psychological Review*, *76*, 241–263. doi:10.1037/h0027272

Pylyshyn, Z. W. (2002). Mental imagery: In search of a theory. *Behavioral Brain Sciences*, *25*, 157–182.

Ramachandran, V. S., & Hubbard, E. M. (2001a). Psychophysical investigations into the neural basis of synaesthesia. *Proceedings of the Royal Society B: Biological Sciences*, *268*, 979–983. doi:10.1098/rspb.2001.1576

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

Rich, A. N., Bradshaw, J. L., & Mattingley, J. B. (2005). A systematic, large-scale study of synaesthesia: Implications for the role of early experience in lexical-colour associations. *Cognition*, *98*, 53–84. doi:10.1016/j.cognition.2004.11.003

Simner, J. (2005). Non-random associations of graphemes to colours in synaesthetic and non-synaesthetic populations. *Cognitive Neuropsychology*, *22*, 1–17. doi:10.1080/02643290500200122

Simner, J., Harrold, J., Creed, H., Monro, L., & Foulkes, L. (2009). Early detection of markers for synaesthesia in childhood populations. *Brain*, *132*, 57–64. doi:10.1093/brain/awn292

Simner, J., Mulvenna, C., Sagiv, N., Tsakanikos, E., Witherby, S. A., Fraser, C., . . . Ward, J. (2006). Synaesthesia: The prevalence of atypical cross-modal experiences. *Perception*, *35*, 1024–1033. doi:10.1068/p5469

Spector, F., & Maurer, D. (2009). Synesthesia: A new approach to understanding the development of perception. *Developmental Psychology*, *45*, 175–189. doi:10.1037/a0014171

Tomson, S. N., Avidan, N., Lee, K., Sarma, A. K., Tushe, R., Milewicz, D. M., . . . Eagleman, D. M. (2011). The genetics of colored sequence synesthesia: Suggestive evidence of linkage to 16q and genetic heterogeneity for the condition. *Behavioral Brain Research*, *223*, 48–52. doi:10.1016/j.bbr.2011.03.071

Tyler, C. (2005). Varieties of synesthetic experience. In L. C. Robertson & N. Sagiv (Eds.), *Synesthesia: Perspectives from cognitive neuroscience* (pp. 34–44). New York, NY: Oxford University Press.

Ward, J., & Mattingley, J. B. (2006). Synaesthesia: An overview of contemporary findings and controversies. *Cortex*, *42*, 129–136. doi:10.1016/S0010-9452(08)70336-8

Ward, J., & Simner, J. (2003). Lexical-gustatory synaesthesia: Linguistic and conceptual factors. *Cognition*, *89*, 237–261. doi:10.1016/S0010-0277(03)00122-7

Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: Vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences, USA*, *97*, 11125–11129. doi:10.1073/pnas.97.20.11125

Winawer, J., Huk, A. C., & Boroditsky, L. (2010). A motion aftereffect from visual imagery of motion. *Cognition*, *114*, 276–284.

Witthoft, N., & Winawer, J. (2006). Synesthetic colors determined by having colored refrigerator magnets in childhood. *Cortex*, *42*, 175–183. doi:10.1016/S0010-9452(08)70342-3