

On the Perceptual Reality of Synesthetic Color

Randolph Blake

Thomas J. Palmeri

Rene Marois

Chai-Youn Kim

Department of Psychology

Vanderbilt University

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Address Correspondences to:

Randolph Blake

Department of Psychology

301 Wilson Hall

Vanderbilt University

Nashville, TN 37206

randolph.blake@vanderbilt.edu

tel: 615-343-7010

fax: 615-343-8449

Synesthesia – the mental mixture of real and illusory sensory experiences – is incredibly fascinating to read or hear about but frustratingly complex to study. Those of us who are not synesthetes are spellbound by the accounts of those who are, but at the same time we are mystified by why these mixtures would occur. As the chapters in this volume document, scientific investigation of synesthesia has rapidly developed into an area of great interest and debate within cognitive neuroscience, and our group at Vanderbilt is among those seeking to understand this fascinating phenomenon.

In our work, we have focused on color-graphemic synesthesia: the perception of color when viewing achromatic alphanumeric characters (in this chapter, we use the term “achromatic” to refer to figures printed in black ink against a white background). Judging from the existing literature on synesthesia, as well as from the tremendous volume of unsolicited, anecdotal accounts we have received from synesthetes, color-graphemic synesthesia appears to be the most common form of the condition. Certainly this variety of synesthesia provides for some of the most memorable and amusing accounts. Thus, for example, one individual who sees digits vividly colored volunteered to us that she performed arithmetic using her colors and was surprised upon first learning that others did not: “I thought everyone did math with colors – that yellow plus yellow was red for everyone.” Another individual complained that she often confused appointments scheduled for Tuesday or for Thursday, because both days are “red.” Still another confessed to an unfounded dislike of the city of Houston “just because the word was a ugly shade of brown” and another acknowledged that “my husband knows that I couldn't have married him if his name had been the ‘wrong’ color for me ... we are, color-wise, perfectly compatible.” These and the many other transcriptions we have compiled from synesthetic volunteers lead us to accept that their graphemic colors are vivid and, in some sense, real.

The great challenge in learning about synesthesia, of course, is to develop objective experimental strategies for going beyond these colorful verbal accounts. To be honest, our interest in synesthesia grew entirely out of the fortuitous identification of a few individuals within our academic community who experience color-graphemic synesthesia. While none in our research group was expert in color vision, we were all intrigued by the initial descriptions offered by these individuals, and we were gratified by their motivation to explore their synesthetic experiences in more detail. The overarching theme to our work with these two people – LR and WO – has been an exploration of the perceptual reality of their synesthetic colors.

In this chapter we address three important issues concerning synesthesia: 1) the extent to which synesthesia is genuinely perceptual in nature, 2) the degree to which attention and awareness are necessary to the synesthetic experience, and 3) possible neural substrates for this most unusual perceptual experience.

An Introduction to WO and LR

Both of our adult synesthetes (one male and one female) have perfectly normal vision, including excellent trichromatic color perception as assessed by the modified version of the Munsell 100-Hue test and the Ichihara color plates. WO describes seeing “colored” numbers and letters as far back as he can remember, but LR actually dates her color associations to a set of colored letters and numbers affixed to her refrigerator door (and, indeed, her color associations correspond exactly to the color sequence of those magnets). On multiple occasions we have asked these two individuals to match their synesthetic colors using one of the color palettes from Adobe Photoshop®, and their color matches are remarkably reliable (as illustrated in Figure 1). When performing their matches, WO and LR typically spend considerable time getting each color just right, implying that their experiences are subtle and not simply categorical in nature.

Incidentally, WO and LR both take great pleasure in their colors and refuse to perform any exercise that might eliminate or alter their colors. WO in particular relies on his colors for remembering technical terms (he's a neuroanatomist) as well as for recalling telephone numbers. We have not yet documented the extent to which WO's memory performance indeed benefits from his colors, but based on the results of others (Smilek et al., 2002) we have no reason to doubt his claims.

[FIGURE 1 ABOUT HERE]

Both synesthetes describe seeing their colors upon the achromatic letters themselves, not simply in their mind's eye; this description would place them in the category of "projective" synesthetes as opposed to "associative" synesthetes (e.g., see Dixon et al., 2002). When viewing alphanumeric characters printed in colored ink, WO and LR readily perceive the real colors of the characters but, at the same time, can perceive their synesthetic colors in the characters. This simultaneous existence of two colors in a single figure is one of the most baffling aspects of their descriptions. We have tried presenting a given letter against a background whose color exactly matches the individual's synesthetic color (e.g., a P, which is synesthetically yellow for WO, against a yellow background), but the letter remains synesthetically visible. We have employed a speeded reaction time task on which WO and LR must make a vowel/consonant judgment for achromatic characters presented against colored backgrounds (some matched to the synesthetic color of the character presented on a given trial). Here, too, we find no differences in speed or in accuracy regardless of the relation between the synesthetic color of the character and the real color of the background (but see Smilek et al., 2001).

LR and WO both consistently describe seeing synesthetic colors when shown characters defined solely by retinal disparity (random-dot stereograms) and in characters defined solely by

differential motion (random-dot cinematograms). These observations point to cortical processes in the induction of color-graphemic synesthesia, for the figural information specifying the character's identity must be extracted by neural mechanisms sensitive to binocular disparity and mechanisms sensitive to structured motion. This does not necessarily mean, however, that the synesthetic experience itself is expressed within these areas; we shall return to this issue of interactions between induction and expression of the actual synesthetic experience in a later section of this chapter.

Concerning the stimulus conditions eliciting synesthetic experiences, there is one enigmatic way in which WO and LR differ. We have induced afterimages of alphanumeric characters by having WO and LR stare for 1-minute at achromatic induction figures, after which they stare at a white background. Not surprisingly, both WO and LR experience a clear afterimage of the induction character. LR perceives the synesthetic color appropriate for that character (e.g., her afterimage of the letter A is perceived as red, her synesthetic color for A), but to his surprise and our's WO experiences no color whatsoever for his afterimages. Indeed, the first time we performed this test on him, WO spontaneously exclaimed that he had never seen letters without colors and he continues to puzzle over his missing colors for characters viewed as afterimages. We have convinced ourselves that the "problem" has nothing to do with the clarity of WO's afterimages, for he does see colors in real characters blurred and reduced in contrast to a degree mimicking his afterimages. Moreover, we have confirmed that the absence of colors in his afterimages is not attributable to the synesthetic color he invariably experiences during the induction period. And, finally, we have verified that WO experiences normal colored afterimages when exposed to colored inducing figures. To date, WO's failure to perceive synesthetic colors in achromatic afterimages remains a mystery.

For both WO and LR, semantic context can modulate the perceived color of an alphanumeric character. Looking at Figure 2a, you may experience the middle “character” either as the number 13 or as the capital letter B, depending on the context in which the character appears. WO and LR both describe the character as one color when it’s seen as a number and an entirely different color when it’s seen as a letter. Both individuals report that the color competes between these two alternatives when both contexts are present simultaneously, and they claim to be able to influence this competition by attending to one context or the other. In a similar vein, both WO and LR can see either of two colors when viewing Navon-type figures (Navon, 1977) such as the one shown in Figure 2b – the entire figure takes on one color when attending to the global form and another color when attending to the local elements comprising that form (see also Ramachandran & Hubbard, 2001b, and Rich & Mattingley, 2001). In a subsequent section, we return to this question of the possible role of attention in the perception of synesthetic colors.

[FIGURE 2 ABOUT HERE]

WO and LR’s verbal descriptions make it very tempting to conclude that color-graphemic synesthetes genuinely perceive colors when viewing achromatic characters, colors that are as perceptually real as those the rest of us experience when viewing characters printed in colored ink. Based on the observations described so far, however, we cannot rule out the possibility that these descriptions are conceptually based, arising from strongly over-learned associations between colors and alphanumeric characters. Most of us associate “green” with “envy” because we’ve heard or read this metaphor over and over, but we do not actually experience the color green when we see the word envy. Perhaps graphemic synesthetes have a richer catalog of these same kinds of conceptually grounded associations, so deeply ingrained that viewing a given character automatically brings to mind a given color. To rule out this conceptual account of

color-graphemic synesthesia requires going beyond verbal description and relying on more indirect techniques for assessing the perceptual reality of synesthetic colors. Toward that end, we have developed variants of several well-known visual tasks, our aim being to learn whether synesthetic colors behave like real colors.

Do Synesthetic Colors Behave Like Real Colors?

Consider first the Stroop task (Stroop, 1935), on which color names interfere with the speed and accuracy of naming the colors of ink in which those words are written (thus, for example, it takes longer to respond “red” when presented with the word BLUE printed in red ink than it does when presented with the word BOAT printed in red ink). Several research groups, ours included, have created variants of the classic Stroop task on which non-color-related words are printed in ink colors that are congruent and incongruent with the color associations of a synesthetic observer. For example, when WO is asked to name the colors of ink in which successively exposed words are printed, he is especially fast if those words are printed in colors that match his synesthetic colors for those words (e.g., BANK printed in pink). But when words are printed in ink colors that do not match his synesthetic colors (e.g., BANK printed in blue), WO takes longer to name the ink colors and stumbles over many words. His speed and accuracy at naming the colors of inks in which arbitrary characters are printed fall in between his congruent and incongruent performance levels. Comparable synesthetic Stroop effects have been reported by others (Dixon et al, 2000; Mills et al, 1999; Mattingly et al, 2001; Odgaard et al., 1999), pointing to an inability to ignore the synesthetic colors associated with words (in the same way that nonsynesthetic observers cannot ignore the real colors of the ink in which color names are printed). Still, these results do not definitively rule out conceptual processing as the basis of

the synesthetic Stroop effect. After all, normal observers can show Stroop interference when tested with geometric figures and color names that have been repeatedly associated to the point where the associations are highly automatized (MacLeod & Dunbar, 1988; see also MacLeod, 1991). If conceptual association leads to Stroop interference for normal observers, it could certainly do the same thing in the case of synesthesia. For this reason, we were motivated to try another task – visual search – where color plays a potent role that is generally believed to be genuinely perceptual in nature.

It is well known that a “target” of one color can easily be picked out from an array of background “distractors” differing in color from the target (Treisman & Gelade, 1980). Do synesthetically colored targets and distractors behave in a same fashion? In one of our first interviews with WO, we showed him an array of letters like that depicted in Figure 3a and simply asked him what he saw. Without hesitation, he exclaimed that the “2” stood out conspicuously from the “5”s because it was a different color. When shown different variants of these kinds of arrays, he continued to respond quickly and with confidence based on the color disparity between the oddball digit and the background of distractors. This “pop-out” effect encouraged us to perform a more systematic study of WO’s ability to find a target digit amongst a background of distractors digits, using the classic visual search paradigm.

[FIGURE 3 ABOUT HERE]

In this visual search task, the targets and distractors always appeared as white numerals against a black background, but, of course, WO always described these numerals with their characteristic colors. On half the presentations, the target digit was present among distractors and on the other half the target was absent; from trial to trial the number of elements in an array (set size) varied from 16 to 36. Observers (WO and seven non synesthetic control observers) were

instructed to press one of two keys as quickly as possible to indicate whether or not the target was present. We devised two categories of search arrays, “color-similar” trials in which target and background elements were highly similar in synesthetic color (e.g., a “8” amongst “6”s, which are both blue for WO) and “color-different” trials in which target and background elements differed in synesthetic color (e.g., a “2” amongst “5”s, which are orange and green for WO, respectively).

Results from this study are shown in Figures 3b. For non-synesthetic observers, response times (RT) on target-present trials increased with set size for both categories of search arrays. For WO, RTs on color-similar trials (i.e., 8 among 6’s) were comparable to those for non-synesthetes, increasing markedly with set size. But for color-different trials (2 among 5’s) WO showed considerably faster RTs, especially for the largest set size. Moreover, these extraordinarily fast RTs were not achieved at the expense of accuracy – WO’s error rate in the color-different condition was equivalent to that for the color-same condition, and both matched the error rates of non-synesthetic observers. These RT results substantiate WO’s subjective report that the oddball “colored” item “pops out” in much the same way that a real orange item would pop-out amongst an array of green distractor items. However, as can be seen in Figure 3b, it did take WO a little longer to find the target amongst a large set of distractors, implying that search was not performed in a strictly parallel fashion. We return to the implications of this finding in a subsequent section.

Our visual search results dovetail nicely with experiments by Ramachandran and Hubbard (2001a) showing that color-graphemic synesthetes are more accurate than non-synesthetic controls at judging the shape formed by a cluster of letters whose “color” differs from that of the background letters. Presumably the common color of the elements defining the

shape promotes perceptual grouping, which, in turn, causes the shape to emerge from amongst the background letters. Of course, the skeptic could develop an alternative account for this observation in which semantically related features (e.g., digits previously associated with a given color) automatically form salient groupings which readily segregate from groupings formed by other semantically related features. For that matter, this kind of explanation, which downplays the visual potency of synesthetic colors, could perhaps be extended to our visual search results as well.

To test definitively whether synesthetic colors are perceptually equivalent to real colors, we devised another, more foolproof test of the perceptual reality of synesthetic colors: we determined whether synesthetically experienced colors can produce an orientation contingent color aftereffect – the McCollough effect (McCollough, 1965). Ordinarily to induce such an aftereffect, observers alternately view, say, red vertical contours and green horizontal contours, with this alternating adaptation continuing for many minutes. Thereafter, an achromatic test figure composed of horizontal and vertical gratings appears faintly colored but in the reversed pairing of color and form, with the vertical bars appearing greenish and the horizontal bars appearing pinkish. In the pilot experiment of work soon to be reported (Kim et al, 2003), we devised tailor-made inducing figures for WO and for LR, figures in which vertical contours were defined by letters generating the experience of red and horizontal contours were defined by letters generating the experience of green (see Figure 4). It is important to keep in mind that the letters themselves were achromatic – it was the synesthetic experience that “colored” the horizontal and vertical gratings. The observer was exposed to one of these synesthetic gratings and then the other for 5 seconds at a time, for a total of 5 minutes of adaptation. Next, the

observer was shown a test figure composed of horizontal and vertical contours defined by non-alphabetic characters that elicited no synesthetic sensation on their own.

[FIGURE 4 ABOUT HERE]

Upon viewing this test figure, LR described the vertical contours as having a faint green appearance and the horizontal ones as being faint pink. It should be stressed that LR has never seen nor heard of the McCollough effect, and she expressed puzzlement at the color appearance of the forms in the test figure, forms that never before had appeared colored. WO's experience was somewhat different, but in a very intriguing way. He too saw the horizontal contours as pinkish but he experienced no color whatsoever on the vertical contours. While he had not heard of the McCollough effect, WO was aware of colored afterimages. We next tested WO using vertical and horizontal induction gratings that were really colored red and green, once again alternately adapting him for a total of 5 minutes. At the end of this period, he again experienced horizontal contours as pinkish and vertical contours as colorless. We have no idea why WO gets only half of the McCollough effect, but it is noteworthy that this pattern of results obtains for contours that are really colored as well as those that are synesthetically colored.

These remarkable aftereffects defy explanation in terms of overlearned associations between color names and alphanumeric characters. If WO and LR were merely "thinking" about their colors during adaptation, not actually seeing them, why would they subsequently report seeing complementary colors in portions of a test figure that ordinarily appear achromatic? We believe WO and LR were reporting what they saw in the achromatic test figure – genuine orientation-selective color aftereffects, not synesthetic associations – and those color experiences were generated by the colors of the inducing figures, not the names of the inducing colors. These results thus provide compelling evidence for the perceptual reality of synesthetic colors.

But if synesthetic colors are indeed comparable to “real” colors, we are once again confronted with the paradox mentioned earlier: WO and LR experience both real and synesthetic colors in the same figure at the same time. How can the letter A printed in blue ink look at once both “blue” and “red”? Does the synesthetic “redness” of the A alter its genuine blueness? What, in other words, is the nature of the interaction between synesthetic colors and real colors? The following section summarizes some of our efforts to answer this question.

Do Synesthetic Colors Interact with Real Colors?

We began by having WO carefully and repeatedly match the perceived synesthetic color of digits printed in different colored inks. WO reliably sets a point within the Adobe Photoshop© color palate map to essentially the same hue/brightness value upon repeated testing of a given character printed in a variety of different colored inks. His synesthetic color matches, in other words, are not affected by the actual color of the inducing figures. This conclusion stands up to forced-choice testing in which WO must select the best synesthetic match from among an array of eight color chips differing slightly from one another in hue and brightness. Despite random variations in the position and values of the chips, WO always selects the chip displaying the same color/brightness value.

Similarly, we have asked WO to match the color of a circular patch composed of one group of identical digits (e.g., a circular patch of 9s which, for WO, appear yellow) surrounded by a large annulus of many repetitions of a non-alphanumeric character printed in ink of a given color (e.g., an annular patch of &s printed in blue). We were careful to select synesthetic color and real color combinations that, under ordinary circumstances yield reliable color contrast effects (e.g., the central “yellow” patch would appear slightly brighter and more orangish

compared to its appearance in the absence of the surrounding blue annulus). Again, the real colored surround did not influence WO's matches, implying that his synesthetic colors are immune to an effect from real colors. This observation stands in contrast to the results described by Smilek et al (2001), who report that a digit-color synesthete made more errors locating a digit presented against a colored background when the synesthetic color of the digit matched the real color of the background (the statistically significant difference in percent-correct performance for congruent vs. incongruent trials was 8%). Smilek et al. employed a speeded decision task whereas we have allowed WO extended viewing when making color matches; conceivably, exposure duration is critical in determining the strength of the interaction between real and synesthetic colors, although our vowel/consonant RT experiments with WO and LR, described earlier, were designed to encourage speeded decisions, yet we did not find differences in RT between background congruent and background incongruent conditions. We have no ready explanation for this seeming discrepancy between our findings and those of Smilek et al.

While our simple color matching experiments do not hint at any systematic influences between synesthetic and real colors, more recent studies from our lab have revealed situations where these two forms of color perceptions interact (Kim et al, 2003). Although our results are still preliminary, we are confident reporting several interesting results. First, perception of bistable apparent motion (AM) sequences can be strongly influenced by the color relations among the AM tokens, even when one pair of tokens is colored in virtue of synesthesia and the other pair is actually colored. Looking at Figure 5, notice that frame 1 of this simple AM sequence consists of two achromatic letters and frame 2 consists of two colored figures. Non-synesthetic observers viewing these two frames shown in rapid succession can see the tokens moving in either of the two possible directions, clockwise or counterclockwise, and over trials

the likelihood of either motion path is approximately equal. Both WO and LR, however, consistently sees the path of motion for which their synesthetic colors in frame 1 correspond to the real colors in frame 2 (e.g., clockwise in the example shown in Figure 5). Now, it is well established that normal observers readily resolve ambiguous motion when real colors are available to solve the correspondence problem (Kolars & von Grünau, 1976). The behavior of WO and LR imply that motion correspondence also can be established between real colors and synesthetic colors. Incidentally, both WO and LR reliably perceive a given path of motion when real colored tokens are presented in frame 1 and synesthetically colored letters are presented in frame 2 and, for that matter, when different achromatic letters generating the same synesthetic color are presented in both frames of the AM sequence.

[FIGURE 5 ABOUT HERE]

In a second project, we are finding that a synesthetically colored letter readily groups with an actually colored, non-alphanumeric form during binocular rivalry, the result being an increased incidence of combined predominance of the achromatic letter and colored form. In fact, the magnitude of this “grouping” tendency is the same as that found in non-synesthetic observers viewing pairs of real colored figures. This tendency for synesthetically comparable digits to perceptually group is reminiscent of an observation reported by Hubbard and Ramachandran (2001a) – they found that strings of numerals tended to group into extended contours when their synesthetic colors were similar.

In summary, we do find conditions where synesthetic colors interact with real colors to influence performance on visual tasks. Given these reliable, robust interactions, it is all the more mysterious to us why real colors and synesthetic colors do not interact in the determination of color appearance. Resolution of this paradox awaits further work.

Are Attention and Awareness Necessary for Synesthesia?

Granting the perceptual reality of synesthesia, an independent issue concerns the role of attention to the achromatic figure that induces a color experience. In other words, must the synesthete attend to and be aware of the identity of the inducing stimulus before that stimulus can trigger a synesthetic experience? According to Mattingley et al. (2001) synesthetic interactions arise after overt recognition of inducing stimuli: “synaesthesia is elicited by selectively attended stimuli that are available for conscious report” (p. 582). In a similar vein, Rich and Mattingley (2002) conclude that “activation of the colour module might not occur before the letter or digit is fully processed and available for overt report” (p. 51). These two related conclusions imply the operation of a serial process, by which an alphanumeric form must first be explicitly recognized (“that figure is an A ...”), after which the synesthetic concurrent can be elicited (“... and it’s blue”).

Obviously, some recognition of the inducing stimulus must precede any elicitation of the concurrent synesthetic experience, but it is arguable whether inducer recognition and conscious awareness of its identity must both precede synesthetic experience. Maybe form recognition, and hence synesthetic elicitation, occurs in the absence of conscious awareness. In addition, it is not obvious why inducer recognition and synesthetic experience must proceed in a strictly serial fashion. Perhaps form recognition and synesthetic elicitation proceed in a cascaded fashion, with incremental evidence in favor of a particular form giving rise to incremental elicitation of synesthetic color. Although form processing would begin before synesthetic color was triggered,

the representations of form and color could emerge concurrently. In the following paragraphs we critique the one study that points to the need for attention and awareness of the inducer.

Mattingley et al. (2001) conducted a series of experiments to determine whether binding of synesthetic color to alphanumeric form can occur in the absence of conscious awareness of the inducer stimulus. Mattingley et al. essentially employed a modified version of the Stroop task by which the inducer letter was first presented for 500 ms followed by a colored target patch. As quickly as possible, the synesthetic observers named the color of the target patch, which could be congruent or incongruent with the synesthetic color of the prime. Just as in the standard synesthetic Stroop task, the synesthetic color of the inducer slowed the naming the color of the target patch when the colors were incongruent.

Having established a Stroop interference effect, Mattingley et al. next presented the inducer letter for a sufficiently brief duration and accompanied by a pattern mask so as to preclude visual awareness of that letter. Would “unconscious” identification of the inducer still lead to significant interference when its synesthetic color differed from the actual color of the target patch? In two different variants of this task, no significant Stroop interference was observed when the exposure duration of the inducer was 56 ms or 28 ms. At these brief durations, participants reported being unaware of the presence of the inducer.

Most critically, in order to demonstrate that some degree of processing of the prime did occur at these short presentation durations, Mattingley et al. conducted a control experiment involving letter naming. In this task, the primes were again letters, but the targets were now letters as well. The task was to name the identity of the target letter. The primes and the targets had different cases, with congruent trials having the same identity ($a \rightarrow A$) and incongruent trials having a different identity ($b \rightarrow A$). For prime durations of 56 ms and 28 ms the magnitudes of

the statistically significant “interference” effects on incongruent trials (relative to congruent trials) were 21ms and 7 ms, respectively (although that difference could just as well reflect a facilitation effect for congruent trials).

Although the results of Mattingly et al. could imply that conscious identification of the inducer stimulus is necessary for the elicitation of synesthetic color, there are some issues that must be considered before accepting this conclusion. Their critical finding was that at both 28 ms and 56 ms prime durations, a letter prime had significant influence on letter identification but the synesthetic color of a letter prime did not have significant influence on color naming. The influence of the prime on letter identification in the control task was rather small – 21 ms in the 56ms prime condition and only 7ms in the 28 ms prime condition – but that is not necessarily uncommon in priming experiments of this kind. Unfortunately, Mattingley et al. did not report absolute identification times in the letter identification control task, but we might expect letter identification to be somewhat faster and somewhat less variable than color naming. Statistically, with a relatively small number of observations (48 trials per observer per condition), a 21 ms or 7 ms interference effect can only be detected in a task with sufficiently low variability, such as letter identification. Even if a 21 ms or 7 ms interference effect were present in the color naming task, it would be difficult to detect such a small difference in a task with higher variability. Indeed, in the synesthetic color-priming version of the task, the 28 ms prime duration produced about a 5 ms interference effect and the 56 ms prime produced approximately a 29 ms interference effect (as estimated from their figures) – these differences, although statistically nonsignificant, are quite comparable to the 7 ms and 21 ms significant effects observed in the letter priming version of the task. Mattingley et al. (2001) did not report a power analysis on the sensitivity of their color naming task to reveal a priming effect of the magnitude observed in the

letter identification task. For these reasons, we are not entirely persuaded that these findings constitute evidence against unconscious realization of synesthetic colors.

Moreover, there are other recent results suggesting that concurrent synesthetic color can influence the detection and identification of the inducer, implying that induction of synesthetic color does not require the explicit conscious recognition of a form. The essential strategy of those studies was to assess identification of the inducer, not its real or synesthetic color. Thus if synesthetic color nonetheless influences identification, we can conclude that synesthetic color is available prior to the explicit identification of the inducer. If the inducer has already been consciously identified before the color emerges, how could synesthetic color further enhance with its identification?

One piece of evidence showing synesthetic color's influence on inducer identification is provided by our visual search study, the results from which appear in Figure 3b. Recall that search times for non-synesthetic observers increased linearly with set size regardless of target-distractor pairing, and this was true regardless whether nonsynesthetes were searching for a "2" among "5"s or an "8" among "6"s. WO too experienced difficulty searching for an "8" among "6"s, which both appear bluish to him. By contrast, WO was significantly faster searching for a "2" among "5"s. Also, WO described his search strategy as sometimes first seeing a patch of orange and then verifying that there was a "2" located at that position.

Although WO described his experience as a pop-out of the synesthetic color of the "2", the slope of WO's search function for a "2" among "5"s was not completely flat, as would be expected of true pop-out produced by searching for a real orange "2" among real green "5"s. We conjectured that WO performs a serial-like search through the visual display, just like nonsynesthetic individuals, but that he was able to reject distractors more quickly using his

synesthetic color. To examine this further, we tested WO and nonsynesthetes on a visual search display in which the distractors had no synesthetic color. On each trial, observers searched for either a Ɔ (which is orange for WO) or a Ǝ (which has no synesthetic color) amongst a background of Ǝs (which also have no synesthetic color). Both WO and nonsynesthetes showed no difference in searching for the two types of targets amongst the nonsense distractors.

So according to our thinking, searching for a target that has a very different synesthetic color from that of the distractors is not entirely analogous to the true, preattentive pop-out that occurs when a target's real color differs from the real color of the distractors. Thus, attention may very well be involved in graphemic-color synesthesia, thereby allowing a synesthete to more rapidly reject a distractor and accept a target in a visual search task, but not in a manner requiring the inducer to achieve the level of conscious recognition before eliciting a synesthetic color, as suggested by Mattingley et al. (2002). After all, WO was over 500 ms faster than nonsynesthetes when searching for a target that differed from its distractors in synesthetic color. It is hard to reconcile this finding with the claim that synesthesia is elicited by stimuli that are already available for conscious report. Once a target is available for conscious report, the search task is finished. Why would a synesthete wait an additional 200-300 ms (see Grossenbacher & Lovelace, 2001) for the synesthetic color to appear? And how could that confer an advantage over searching among items with no synesthetic color to guide them?

Results from other groups also seem to suggest that synesthetic color can be available prior to conscious awareness of the identity of the inducer stimulus. For example, Wager et al. (2002) found that synesthetic color eliminated object-substitution masking (Enns & Di Lollo, 1997), and Ramachandran and Hubbard (2001b) outlined some results suggesting that synesthetic color can attenuate crowding effects (He et al., 1996). And as mentioned earlier, Ramachandran and

Hubbard (2001a) found that synesthetes were more accurate at locating geometric arrangements of letters embedded among distractor letters when the letters had different synesthetic color.

Although Ramachandran and Hubbard (2001b) attribute this improved accuracy to a true pop-out effect, their experimental design did not allow the determination of a pop-out effect in the classical visual search sense (Treisman & Gelade, 1980; see also Rich & Mattingley, 2001).

Finally, Smilek et al. (2001) had observers search for a target digit among a variable number of distractor digits. But rather than using targets and distractors that had similar or different synesthetic colors (like Palmeri et al., 2002, and Ramachandran & Hubbard, 2001a), they instead varied the color of the background to be congruent or incongruent with the synesthetic color of the target. Synesthetes were significantly faster at locating the target when the display background color was incongruent with the synesthetic color of the target. In order for the incongruence of real color and synesthetic color to influence target search, synesthetic color must be bound to alphanumeric form prior to the explicit conscious identification of the target.

So to sum up, we are led to take an intermediate position on the question of the degree to which an inducer must be processed before eliciting a synesthetic color. Requiring complete identification and conscious awareness of an inducer prior to the elicitation of the synesthetic color seems inconsistent with several sets of results, and the one finding pointing to this conclusion can be questioned on methodological grounds. At the same time, the evidence for preattentive pop-out of synesthetic color is primarily anecdotal, and the failure to find flat visual search functions undermines the analogy between genuine color pop-out and speeded visual search aided by synesthetic colors (but see Smilek et al., 2001).

What is the Neural Basis of Synesthesia?

Given the results summarized in the previous sections, it is impossible to believe that synesthesia is simply metaphorical speech or the product of bizarre minds. Synesthetic colors have a genuine perceptual reality that allows synesthetes to exploit their color experiences when performing visual tasks or when memorizing and recalling otherwise arbitrary material. The reality of synesthetic color, then, brings to center stage the following question: How does form recognition ultimately elicit a color experience in the brains of synesthetes?

Virtually all neural models of synesthesia propose that it arises from an atypical pattern of connectivity between form processing and color processing centers of the brain. Figure 6 displays a simple, schematic diagram of the putative pathways involved in form recognition and color recognition, as adapted from depictions presented in recent reviews by Grossenbacher and Lovelace (2001) and by Rich and Mattingley (2002). Visual processing is organized in parallel, roughly hierarchical systems with early areas processing primitive visual features that feed forward to areas processing more complex scenic elements that ultimately provide input to areas involved in form recognition or color recognition. According to traditional views, these concurrent systems ultimately converge upon multimodal areas supporting high-level cognitive processes. As shown in the diagram, feedforward connections are almost always accompanied by dense feedback connections. Horizontal connections between form and color processing areas may also be present.

[FIGURE 6 ABOUT HERE]

On this scheme, at least three possible routes emerge for eliciting a synesthetic color experience from an alphanumeric form (but see Cytowic, 1993, for an alternative conceptualization). One possibility is that synesthesia arises at a very late stage of processing

where outputs from form recognition and color recognition are associated. Interaction at this late stage would imply that synesthesia is largely conceptual in nature, with associations between colors and forms simply being stronger versions of the kinds of semantic associations non-synesthetes experience (e.g., “apple” and “red”). It is difficult, however, to reconcile this idea with the strong evidence, reviewed earlier, for the perceptual reality of synesthesia. It is nevertheless conceivable that the convergence of color and form information occurs at earlier, more perceptual stages of processing. However, although some visual cortex areas such as V4 are known to be sensitive to both color and form (Gallant et al., 2000), there is as yet no evidence that a given brain region responds both to alphanumeric characters and colors..

Another possibility is that synesthesia arises from disinhibited feedback from the convergence areas shown at the top of the flow diagram (Grossenbacher & Lovelace, 2001). The form pathway is used to recognize alphanumeric characters, ultimately leading to activity in high-level areas of convergence from multiple modalities. In nonsynesthetes, top-down feedback is sufficiently inhibited to prevent anomalous synesthetic experiences in nonstimulated modalities (except perhaps when under the influence of hallucinogenic drugs). By contrast, these feedback connections are disinhibited in synesthetes (for unspecified reasons), leading to representations of a concurrent synesthetic color experience when viewing an alphanumeric inducer stimulus. How far back into the color processing pathway a concurrent stimulus is represented may determine whether a synesthete is a projector, who sees the inducer itself as colored, or an associator, who experiences the color in the “mind’s eye”. For this model to work, disinhibition must be highly selective and idiosyncratic among lexical-chromatic synesthetes, for we know that color experiences are highly reliable and differ widely among these individuals. In terms of neural organization, the disinhibited-feedback theory implies that the brains of

synesthetes and nonsynesthetes are wired the same, but for some reason the modulation of specific feedback connections is attenuated in synesthetes.

A third possibility is that synesthetes have patterns of horizontal cross-wiring that are at least quantitatively, if not also qualitatively, different from that of nonsynesthetes (see Harrison & Baron-Cohen, 1997). As illustrated in the diagram, such cross-wiring could take place at different stages of form processing and color processing; once the form pathway makes contact with the color pathway via these horizontal connections, feedback to earlier stages in the color pathway could result as well (e.g., see Grossenbacher & Lovelace, 2001, and Rich & Mattingley, 2001). It is reasonable to presume that the likelihood of strong cross wiring is greater between physically adjacent neural areas (e.g., see Ramachandran & Hubbard, 2001b).

What could be the etiology of this putative cross wiring? Maurer (1993; see also this volume) has proposed that all infants are born with extensive cross wiring between modalities, which would mean, of course, that all infants routinely experience synesthesia. But, according to Maurer, this rich nexus between sensory areas is usually lost during the course of normal development. According to this hypothesis, synesthesia is retained into adulthood because cross wiring endures owing to a failure of the pruning process (perhaps because of an unusually high density of connections to begin with). The notion of cross wiring is broadly consistent with neurodevelopmental data documenting early diffuse projections followed later by massive pruning (e.g., see Huttenlocher & Dabholkar, 1997). Finally, there is some behavioral evidence implying that young infants may not segregate modalities properly (Maurer, 1997), as the cross-wiring hypothesis would predict.

Restricting our attention to color-graphemic synesthesia, what can be inferred about the putative underlying cross wiring? First, it seems clear that the inducing event must be the recognition of an alphanumeric character. Indeed, to our knowledge, there have been no demonstrations of synesthetic experience from simple visual features, such as oriented lines, gratings or simple geometric shapes. Moreover, the color experiences elicited by visually similar alphanumeric characters are often quite different – for example, LR sees B as orange but P as green. Conversely, color experiences for dissimilar characters are often identical – LR sees D and Y as the same shade of green. Finally, color experiences also depend on context, with identical ambiguous characters taking on different colors (recall Figure 2a). These various characteristics of color-graphemic synesthesia place serious constraints on the patterns of underlying cross wiring, and they certainly defy explanation in terms of cross-wiring at stages of early feature analysis.

The appeal of the cross-wiring model to account for synesthesia resides in its simplicity: activation of a grapheme-encoding area leads, via aberrant connectivity, to color perception. However, for cross-wiring to be considered a serious explanatory concept, it should account for several key characteristics of synesthesia; including its specificity (familiar names but not other names induce colors), its variety (it can occur not only between aspects of the same modality, such as visual form and color, but also between anatomically and functionally distant modalities, such as taste and touch) and its unidirectionality (e.g. form induces color, but not vice versa). Finally, it is also worth considering alternatives to cross-wiring models. In particular, there is no *a priori* reason to rule out the possibility that synesthetes possess a functionally novel brain area, absent in the rest of us, that both processes the inducing stimulus (e.g. a letter) and evokes the color experience.

In thinking about how to untangle these alternative accounts, we are skeptical whether behavioral results alone will allow us to draw firm conclusions about how the brains of synesthetes and nonsynesthetes are wired. We are more optimistic about the possibility of using recently developed brain imaging techniques to learn how cortical areas within the brains of synesthetes are interconnected. In particular, analytical procedures are now available for estimating the levels of functional connectivity between areas (Büchel et al 1998; Hampson et al, 2001; Biwal et al, 1995; Friston & Büchel, 2001). Assuming brain regions underlying processing of the inducer stimulus and the evoked color experience can be isolated, it should be possible to assess the strength of the correlation of activity between these areas. If there are unusually strong connections between these areas, then their activity should be more strongly correlated than in control observers. Another, complementary technique for assessing patterns of connectivity is diffusion tensor imaging, which can estimate the presence and density of anatomical connections between brain regions (Le Bihan et al., 2001).

What is the Neural Locus of the Synesthetic Experience?

The discussion above focused on the difficult issue of connectivity among brain areas putatively involved in synesthesia. A potentially more tractable question with neuro-imaging concerns the neural locus of the induced synesthetic quality: What brain areas are uniquely activated when an individual has a synesthetic experience? More specifically, which areas are associated with the induction of the synesthetic experience (e.g. form computation), and which are associated with its expression (e.g. color perception)? From the outset, it should be kept in mind what exactly we may hope to learn about synesthesia from functional brain imaging. To be

sure, neuroimaging is unlikely to reveal anything about the etiology of synesthesia, or anything about synesthesia's underlying genetic, molecular or cellular mechanisms. However, this technique has the potential to pinpoint brain areas activated during the synesthetic experience. In turn, these activation maps can reveal the extent to which the neural networks underlying synesthesia overlap with those underlying normal color processing, color perception, color imagery, or high-level cognitive processing. In addition, with functional brain imaging we should ultimately be able to determine whether common principles or mechanisms operate across different forms of synesthesia. In the following paragraphs, we summarize and discuss the handful of functional brain-imaging studies that have attempted to determine the neural locus of synesthesia.

Cytowic (1989) performed the first neuroimaging study of synesthesia, in this case an individual who experienced specific shapes associated with specific tastes. Using the non-tomographic Xenon-133 inhalation technique, Cytowic observed widespread decreased blood flow in the cerebral cortex during synesthetic experiences, but more accurate localization of specific brain activity was not possible using this imaging technique.

Using positron-emission tomography (PET), Paulesu and colleagues (1995) were able to provide a more specific neural locus for the synesthetic experience of six women with color-phonemic synesthesia (i.e., color experience triggered by hearing phonemic utterances). Synesthetic observers and nonsynesthetic controls listened to a series of individual spoken words or a series of individual pure tones. For synesthetes only, the contrast of words versus tones yielded significant activation in the right middle frontal gyrus and insula and in the left posterior inferior temporal cortex. The location of these activations, as well as the lack of activation in early visual cortex, led the authors to conclude that color-word synesthesia results from brain

areas involved in language and feature integration, but not from activity in areas of cortex involved in early visual processing.

Using functional magnetic resonance imaging (fMRI), Weiss et al. (2001) studied a single observer who experienced color-word synesthesia, but only for names of personally familiar people. In a blocked-trials design, the observer was shown familiar names or unfamiliar names presented in either colored letters or in achromatic letters. The observer's task was to indicate by pressing a button whether each name induced synesthesia or not. Of particular interest was the comparison of brain activity for familiar names versus unfamiliar names. Synesthesia-inducing familiar names activated retro-splenial cortex and extra-striate cortex bilaterally. The authors conclude that the observer's synesthesia is attributable to an interaction between the retro-splenial cortex, which has been implicated in emotional processing and judgments of personal familiarity (Maddock, 1999; Shah et al., 2001), and extra-striate regions of cortex involved in color processing (Beauchamp et al., 1999).

Aleman et al. (2001) used fMRI to test an individual who experienced color-phonemic synesthesia, focusing in particular on possible activation within primary visual cortex during performance of two contrasting tasks. In the first task, the observer passively listened to words. In the second task, the observer listened to single letters and was asked to covertly generate as many words as possible that began with that letter (a word generation task). The control condition for both tasks involved listening to the regular presentation of pure tones. Analysis of blood-oxygen level dependent signals in area V1, identified based on anatomical landmarks, revealed activation in both experimental tasks relative to the control task. In addition, whole brain analyses detected several other activation sites, including the posterior inferior temporal cortex and prefrontal cortex. The authors concluded that the activation of primary visual cortex

in their synesthete was consistent with the perceptual reality of synesthesia because it activates the same neural substrates critical for sensory perception. While we do not doubt their conclusion, we feel it is premature to conclude that synesthesia is associated with V1 activation. In our experience, it is difficult to delineate V1's borders based on anatomical landmarks (which is what Aleman et al did), whereas functional isolation of V1 is straightforward using the well-validated technique of retinotopic mapping (Engel et al., 1997). In addition, activated regions in Aleman et al's study were peppered throughout the brain, raising uncertainty about the specificity of the visual cortex activation.

Finally, Nunn et al. (2002) recently reported the most thorough imaging experiment on synesthesia to date, scanning 13 color-phonemic synesthetes and 28 control observers. Their first experiment consisted of a block design of passive listening to words and passive listening to pure tones. Not surprisingly, the words versus tones contrast revealed language-related areas activated for both synesthetes and controls. More importantly, for synesthetes this contrast also highlighted a left inferior temporal activation not observed in non-synesthetes. The locus of this activation was in the neighborhood of visual cortex areas V4/V8, which are purported color-processing regions of the human brain (Hajani & Tootel, 1998). In addition, no primary visual cortex activation was observed for either synesthetes or controls. These findings suggest that color-word synesthesia recruits a key locus of normal color processing. However, the second experiment of Nunn et al. showed that while this same left inferior temporal area was recruited by physically real color stimuli (compared to achromatic stimuli) in control observers, they were not in synesthetes. The authors argued that the left V4/V8 is involved in color-word synesthesia, and that the participation of this area in synesthetic color perception may reduce or prevent its availability for normal color processing. These results seem to imply that brain areas involved in

synesthetic and physical color perception may be segregated. Perhaps this could explain why synesthetes report so little confusion between real and synesthetic colors occupying the same part of the visual field.

The most striking characteristic of the functional imaging data summarized above is the almost complete absence of overlap of activations across the four PET and fMRI studies. Given the diversity of synesthetic experiences, it is not unreasonable to expect that the various types of synesthesia would have their own distinct neural substrates. Indeed, the imaging experiments discussed above focused on shape-taste synesthesia (Cytowic, 1989), color-phonemic synesthesia (Aleman et al., 2001; Nunn et al., 2002; Paulesu, 1995), and color-familiar-name synesthesia (Weiss et al., 2001). Still, it is baffling why there is no overlap in brain activations even among the subset of studies that have investigated the same form of (color-phonemic) synesthesia (Aleman et al., 2001; Nunn et al., 2002; Paulesu et al., 1995).

We suspect that these divergent findings are attributable, in part, to differences in the experimental designs used in these studies. First, most of the imaging experiments have not employed objective methods to determine whether observers were indeed experiencing synesthesia during scanning sessions. Second, some of the studies (Aleman et al., 2001; Cytowic, 1993; Weiss et al., 2001) did not scan nonsynesthetic individuals, so little can be concluded about the specificity of the reported brain activations for synesthesia. Third, most of the studies did not explicitly distinguish between the inducing and expressing substrates of synesthesia. Fourth, the control conditions and synesthesia-inducing conditions differed in ways other than just the mode of induction of synesthesia. For instance, three of the imaging studies compared spoken words to tones (Aleman et al., 2001; Nunn et al., 2002; Paulesu et al., 1995), even though there are potentially important differences between words and tones (e.g., semantic content)

besides their differential ability to induce color synesthesia. Ideally, one would like for the control task to be identical to the experimental task in all respects except for its ability to induce synesthesia. Admittedly, it is challenging to devise control conditions that closely match the stimulus qualities of the synesthetic inducers without inducing synesthesia. For this reason, it may be preferable to shy away from subtraction techniques altogether (Friston et al., 1996) and, instead, to capitalize on parametric approaches (Braver et al., 1997) or on fMRI adaptation techniques (Grill-Spector & Malach, 2001). The latter approach offers particularly great promise in isolating areas specifically involved in synesthesia without having to rely on the comparisons of synesthesia-inducing and non-synesthesia-inducing tasks.

Finally, another significant challenge for brain imaging studies of synesthesia is to distinguish activations attributable to learned associations between words and colors from those attributable to genuine sensory events. It is entirely possible that one could observe synesthesia-like patterns of activation in nonsynesthetes who were instructed to imagine colors when they were presented words, or in nonsynesthetes who were trained to associate particular colors and words. One study (Nunn et al., 2002) attempted to address this possibility by scanning control observers who had been moderately trained to associate colors with words. While in the scanner, words were heard over headphones and nonsynesthetic observers alternated in blocked fashion between imagining the color of the words or thinking of the name of the color associated with the word. Contrasting the imaging versus thinking blocks, no significant activation was observed in left V4/V8, the area activated in synesthetes in the main experiment. However, one important limitation of this control study is that the contrast was not between words and tones, as in the main experiment contrasting synesthetes and nonsynesthetes, but between imagining a color versus thinking of the name of a color. Arguably, it may be difficult to think of the name of a

color without imagining that color as well, especially given that the original training consisted in auditory word presentation and visual presentation of the color. Thus, it is not too surprising that V4/V8 failed to show significant activity modulation in these trained control observers, given that the critical contrast was far more stringent than that applied to synesthetes.

To sum up, the small number of extant imaging studies on synesthesia and the inconsistency of their findings preclude any overarching conclusions about the neural basis of this condition.. Moreover, these studies have aimed at localizing specific areas activated during the synesthetic experience, yet extant theories of synesthesia focus more on how brain areas are (anomalously) interconnected. Clearly, greater progress will be achieved when theories and experiments converge on the same well-formulated questions. As mentioned earlier, potentially powerful fMRI and MRI techniques for assessing interconnectivity may help promote this convergence. Even then, however, a complete account of the neural basis of synesthesia faces the daunting challenge of the diversity of synesthetic experiences. This alone makes it unlikely that synesthesia will be distilled to a common neurobiological substrate. Nevertheless, it is possible that all forms of synesthesia arise from the same general neurobiological process, such as anomalous cross wiring between brain regions. To be sure, the successful approach to understanding synesthesia must deploy carefully crafted perceptual tasks carried out hand in hand with brain imaging studies assessing functional activations and anatomical connections techniques. Only then do we stand a chance of distinguishing fact from fiction about the exotic experiences characteristic of synesthesia.

Closing Remarks

We close by considering a question that was raised by a student in one of our classes after hearing a lecture on like: given all the challenging problems in the area of perception, why spend so much time and energy studying a condition that most of us can barely imagine let alone ever experience? No doubt most of the authors of chapters in this volume would offer an answer that goes something like this: by studying exceptional individuals we learn something about ourselves. After all, there is a long tradition in psychology of studying people with deficits in cognitive ability: visual neglect, amnesia, aphasia – the list goes on and on. The rationale is simple: we can learn about normal function by examining deviations from normal and, where possible, by relating those deviations to underlying neural abnormalities. To give just one example, the existence of brain areas specialized for color vision was first realized upon discovering rare cases of individuals suffering achromatopsia, acquired colorblindness consequent to neural damage specifically localized to occipito-temporal regions of the brain (Zeki, 1990). Clinical case studies provide revealing glimpses of normal neural mechanisms gone awry.

Likewise, studies of individuals with exceptional ability offer the tantalizing opportunity to learn about the potentials of the human brain and, moreover, how those potentials were realized developmentally. Thus, for example, students of music perception rely heavily on case studies of musical geniuses to glean insight into the bases of creativity and skill acquisition (e.g., Jourdain, 1997). The same can be argued for the study of synesthesia: for reasons yet to be learned, some people have brains organized in ways that promote highly organized, idiosyncratic associations between sensory qualities. No longer can we dismiss this remarkable propensity as the creation of a crazed mind: synesthesia is grounded in perceptual reality. Having affirmed this

characteristic of synesthesia, researchers are now poised to tackle the difficult questions surrounding this fascinating condition. Moreover, we have at our disposal an array of revealing behavioral tests that can be refined for use in neuro-imaging experiments that go beyond simply asking what areas of the brain “light up” when someone is having a synesthetic experience. And who knows – in the course of this work, we may stumble upon a means for evoking synesthetic-like experiences in the rest of us.

In the final analysis, though, we study these unusual, gifted individuals because they are utterly fascinating. The authors of this chapter will never forget the first opportunity we had to interview WO – here was an individual whose descriptions of his perceptual world challenged our conceptualizations of what it means to perceive. We still cannot imagine how the letter C can be seen as blue even though it is printed in black ink, but we are convinced that C is blue for WO (and is yellow for LR). And we are thankful that WO, LR and others like them are sufficiently patient with our burning curiosity to allow us the opportunity to probe deeper into their colorful visual worlds.

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REFERENCES

- Aleman, A., Rutten, G.-J.M., Sitskoorn, M.M., Dautzenberg, G. & Ramsey, N.F. (2001) Neuroreport 12, 2827-2830.
- Beauchamp MS, Haxby JV, Jennings JE, DeYoe EA. (1999) An fMRI version of the Farnsworth-Munsell 100-Hue test reveals multiple color-selective areas in human ventral occipitotemporal cortex. *Cereb Cortex*. 9,257-63.
- Biswal B, Yetkin FZ, Haughton VM, Hyde JS. (1995) Functional connectivity in the motor cortex of resting human brain using echo-planar MRI. *Magn Reson Med*. 34, 537-41.
- Braver TS, Cohen JD, Nystrom LE, Jonides J, Smith EE, Noll DC. (1997). A parametric study of prefrontal cortex involvement in human working memory. *Neuroimage*. 1, 49-62.
- Büchel, C, Coull, JT & Friston, KJ (1998) The functional anatomy of attention to visual motion: a functional MRI study. *Science*, 283, 1538-1544.
- Cytowic, R.E. (1989). *Synesthesia: A union of the senses*. Springer-Verlag: New York.
- Cytowic, R.E. (1993) *The man who tasted shapes: A bizarre medical mystery offers revolutionary insights into emotions, reasoning, and consciousness*. G.P. Putnam's Sons: New York.
- Dixon, M.J., Myles, KM., Smilek, D., & Merikle, P.M. (2002, April). Not all synaesthetes are created equal: Distinguishing between projector and associator synaesthetes. Paper presented at the 2nd Annual Meeting of the American Synesthesia Association. San Diego, California.
- Dixon, M.J., Smilek, D., Cudahy, C., & Merikle, P. M. (2000). Five plus two equals yellow: Mental arithmetic in people with synaesthesia is not coloured by visual experience. *Nature*, 406, 365.

- Engel, S.A., Glover, G.H. & Wandell, B.A. (1997) Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cerebral Cortex*, 7, 181-192.
- Enns, J.T. & DeLollo, V. (1997) Object substitution: a form of masking in unattended visual locations, *Psychological Science*, 4, 135-139.
- Felleman, D.J. & Van Essen, D.C. Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1, 1-47.
- Friston KJ, Holmes A, Poline JB, Price CJ, Frith CD. (1996) Detecting activations in PET and fMRI: levels of inference and power. *Neuroimage*. 4, 223-35.
- Friston, K.J. & Büchel, C. (2001) Attentional modulation of effective connectivity from V2 to V5/MT in humans. *Proceedings of the National Academy of Sciences, USA*, 97, 7591-7596.
- Gallant JL, Shoup RE, Mazer JA. (2000). A human extrastriate area functionally homologous to macaque V4. *Neuron*. 27(2):227-35
- Grill-Spector, K., Kushnir, T., Edelman, S., Itzhak, Y. & Malach, R. (1998) Neuron, Cue-invariant activation in object-related areas of the human occipital lobe. 21, 191-202.
- Grossenbacher, P.G., & Lovelace, C.T. (2001). Mechanisms of synaesthesia: Cognitive and physiological constraints. *Trends in Cognitive Sciences*, 5, 36-41.
- Hadjikhani, N, Liu, Ak, Dale, AM, Cavanagh, P, Tootell, RBH (1998) Retinotopy and color sensitivity in human visual cortical area V8. *Nature Neuroscience*, 1, 235-241.
- Hampson, M., Peterson, B.S., Skudlarski, P., Gatenby, J.C. & Gore, J.C. (2002) Detection of functional connectivity using temporal correlations in MR images. *Human Brain Mapping*, 15, 247-262.

- Harrison, J.E., & Baron-Cohen, S. (1997). Synaesthesia: A review of psychological theories, In S. Baron-Cohen & J.E. Harrison (Eds.), *Synaesthesia: Classic and contemporary readings*, Blackwell Publishers Inc: Malden, MA.
- He, S., Cavanagh, P., & Intriligator, J. (1997). Attentional resolution and the locus of visual awareness, *Nature*, 383, 334-337.
- Huttenlocher PR, Dabholkar AS. (1997) Regional differences in synaptogenesis in human cerebral cortex. *J Comp Neurol* 387:167-78
- Jourdain, R. *Music, the brain and ecstasy*. Quill/HarperCollins, New York (1997).
- Kim, C-Y., Blake, R., Palmeri, T., Marois, R. & Whetsell, W. (2003) Synesthetic colors act like real colors and interact with real colors. *Meetings of the Visual Sciences Society*, Sarasota FL.
- Kolers, P.A. & von Grünau, M. (1976) Shape and color in apparent motion. *Vision Research*, 16, 329-336.
- Le Bihan D, Mangin JF, Poupon C, Clark CA, Pappata S, Molko N, Chabriat H. (2001) Diffusion tensor imaging: concepts and applications. *Journal of Magnetic Resonance Imaging* 13, 534-46.
- MacLeod, C.M. (1991). Half a century or research on the Stroop effect: An integrative review. *Psychological Bulletin*, 109, 163-203.
- MacLeod, C.M. & Dunbar, K. (1988) Training and Stroop-like interference: evidence for a continuum of automaticity. *Journal of Experimental psychology: Learning, Memory & Cognition*, 10, 304-315.
- Maddock, R.H. (1999) The retrosplenial cortex and emotion: new insights from functional neuroimaging of the human brain. *Trends in Neuroscience*, 22, 310-316.

- Mattingley, J.B., Rich, A.N., Yelland, G., & Bradshaw, J.L. (2001). Unconscious priming eliminates automatic binding of colour and alphanumeric form in synaesthesia. *Nature*, 410, 580-582.
- Maurer, D. (1993) Neonatal synesthesia: Implications for the processing of speech and faces. In de Boysson-Bardies, B., Jusczyk, P., MacNeilage, P., Morton, J., & deSchonen, S. (Eds.), *Developmental Neurocognition: Speech and Face Processing in the First Year of Life*. Dordrecht: Kluwer, Pp. 109-124.
- McCollough, C. (1965) Color adaptation of edge-detectors in the human visual system. *Science*, 149, 1115-1116.
- Mills, C.B., Boteler, E.H. & Oliver, G.K. (1999) Digit synaesthesia: a case study using a Stroop-like test. *Cognitive Neuropsychology* 16, 181-191.
- Navon, D. (1977) Forest before trees: the precedence of global features in visual perception. *Cognitive Psychology*, 9, 353-383.
- Nunn, J.A., Gregory, L.J., Brammer, M., Williams, S.C.R., Parslow, D.M., Morgan, M.J., Morris, R.G., Bullmore, E.T., Baron-Cohen, S. & Gray, J.A. (2001) Functional magnetic resonance imaging of synesthesia: activation of V4/V8 by spoken words. *Nature Neuroscience*, 5, 371-375.
- Odgaard, E.C., Flowers, J.H., & Mradman, H.L. (1999). An investigation of the cognitive and perceptual dynamics of a colour-digit synaesthete. *Perception*, 28, 651-664.
- Palmeri, T.J., Blake, R., Marois, R., Flanery, M.A., & Whetsell, W. (2002). The perceptual reality of synesthetic colors. *Proceedings of the National Academy of Science*, 99, 4127-4131.

- Paulesu, E., Harrison, J. Baron-Cohen, S., Watson, J.D.G., Goldstein, L., Heather, J., Frackowial, R.S.J., & Frith, C.D. (1995). The physiology of coloured hearing: A PET activation study of colour-word synaesthesia, *Brain*, 118, 661-676.
- Ramachandran, V.S., & Hubbard, E.M. (2001a). Psychophysical investigations into the neural basis of synaesthesia. *Proceedings of the Royal Society of London B*, 268, 979-83.
- 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., & Mattingley, J.B. (2002). Anomalous perception in synaesthesia: A cognitive neuroscience perspective. *Nature Reviews Neuroscience*, 3, 43-52.
- Shah, N.J., Marshall, J.C., Zafiris, O., Schwab, A, Zilles, K., Markowitsch, H.J. & Fink, G.R. (2001) The neural correlates of person familiarity: a functional magnetic resonance imaging study with clinical applications. *Brain*, 124, 804-815.
- Smilek, D., Dixon, M.J., Cudahy, C., & Merikle, P. M. (2001), Synaesthetic photisms influence visual perception. *Journal of Cognitive Neuroscience*, 13, 930-936.
- Smilek, D., Dixon, M.J., Cudahy, C., & Merikle, P.M. (2002). Synesthetic color experiences influence memory. *Psychological Science*, 13, 548-552.
- Stroop, J.R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, 18, 643-662.
- Treisman, A.M. & Gelade, G. A feature-integration theory of attention. *Cognit Psychol* 12, 97-136 (1980).
- Wagar, B.M., Dixon, M.J., Smilek, D. & Cudahy, C. (2002). Coloured photisms prevent object-substitution masking in digit colour synaesthesia. *Brain and Cognition*, 48, 606-611.

Weiss, P.H., Shah, N.J., Toni, I., Zilles, K. & Fink, G.R. (2001) Associating colours with people: a case of chromatic-lexical synaesthesia. *Cortex*, 37, 750-753.

Zeki, S. A century of cerebral achromatopsia. *Brain*, 113, 1721-1777 (1990).

FIGURE CAPTIONS

FIGURE 1. Letter/color associations for synesthetic observers WO and LR.

FIGURE 2. Two examples of ambiguous “characters”. A) The middle character may be seen as the number 13 or the letter B. B) A Navon-type figure in which a global digit is comprised of many local digits.

FIGURE 3. Visual search for synesthetically colored digits. A) Schematic of target “present” display. B) Visual search results for non-synesthetic observers (left-hand panel) and synesthetic observer WO (right-hand panel). Reproduced with permission from #####.

FIGURE 4. “Gratings” used to induce a synesthetic McCollough effect. For LR the “horizontal” grating appears green and the “vertical” grating appears red.

FIGURE 5. The two frames comprising an apparent motion sequence in which the directions of motion are ambiguous. In frame 1, LR sees one of the achromatic characters as red and the other as green. In frame 2, the forms (non-alphabetic) are actually colored.

FIGURE 6. Schematic of possible pathways by which form evokes the synesthetic experience of color. Adapted from Grossenbacher and Lovelace (2001) and by Rich and Mattingley (2002).

FIGURE 2a

A B C | 2 B 14

FIGURE 2b

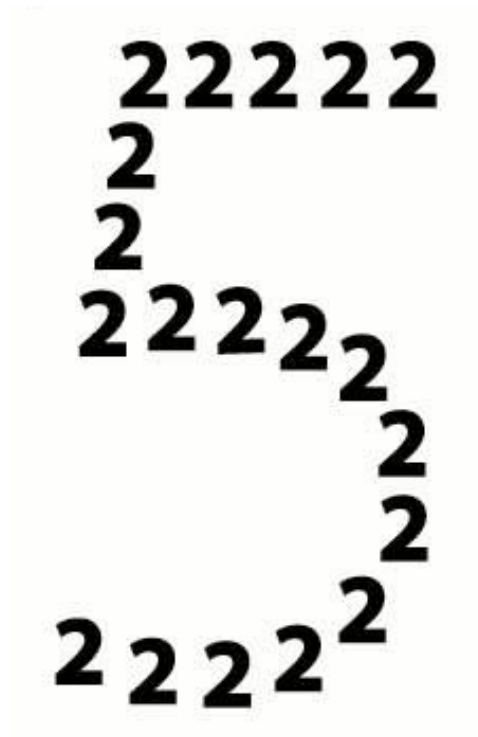


FIGURE 3

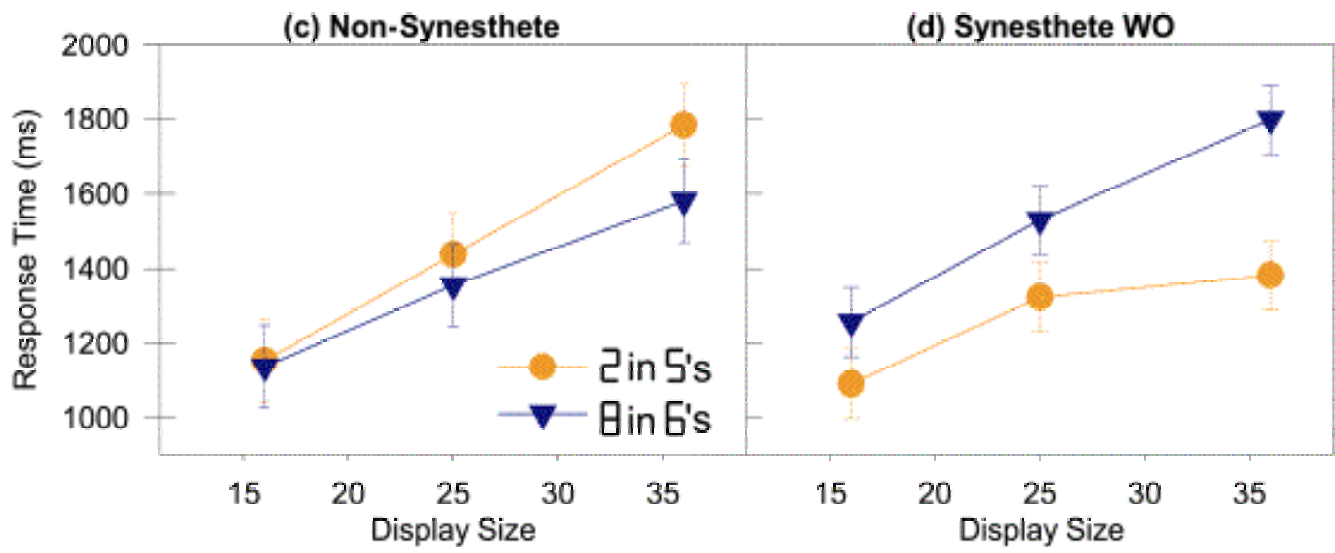
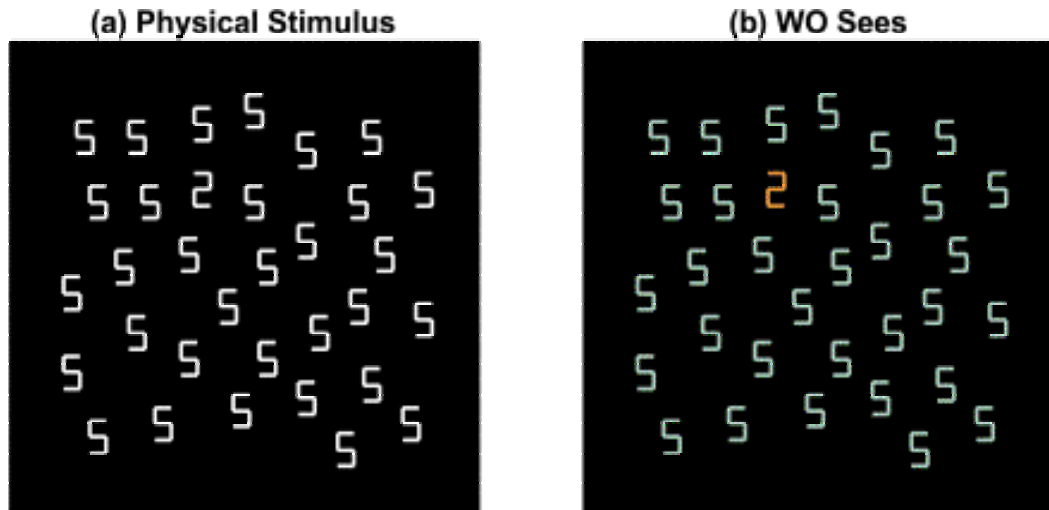
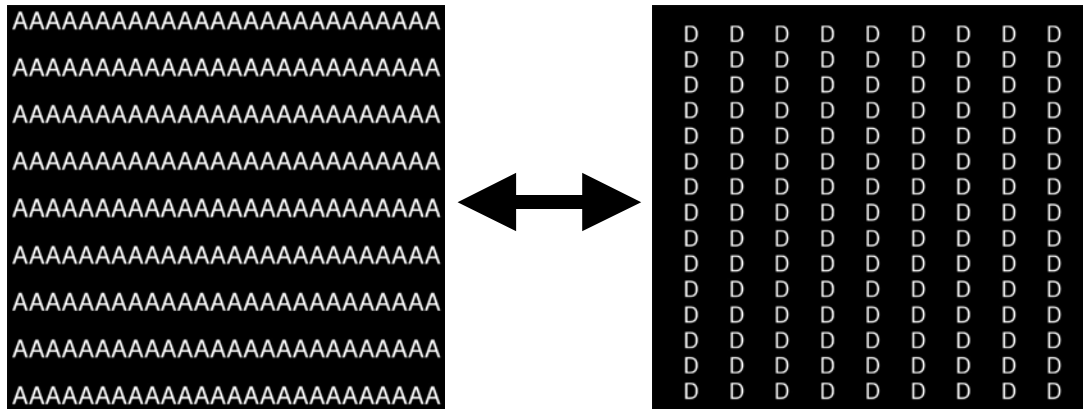


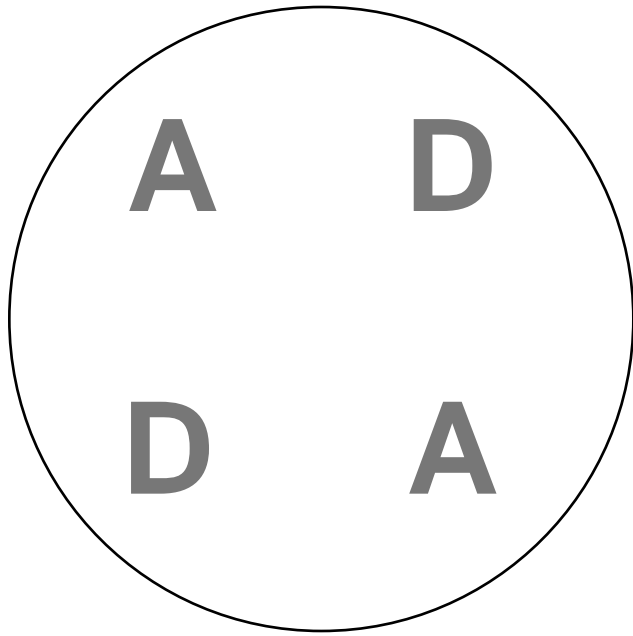
FIGURE 4

Inducing Figures

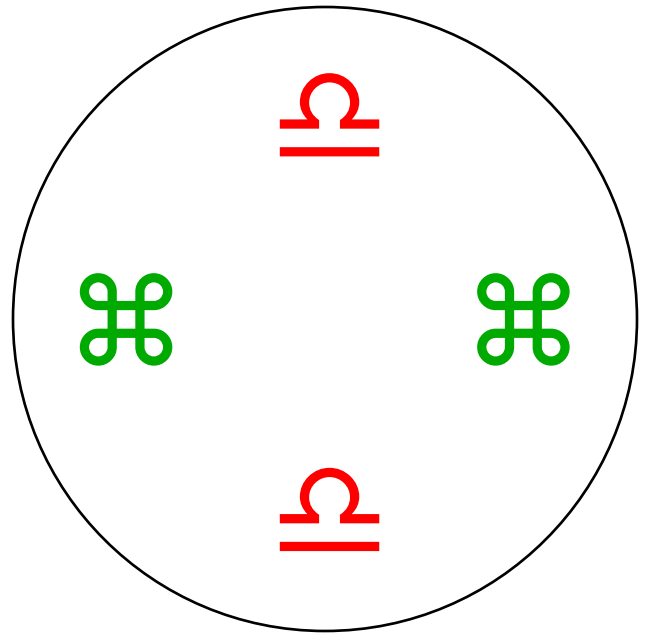


Test Figure





Frame 1



Frame 2

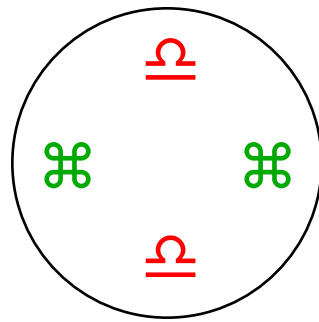
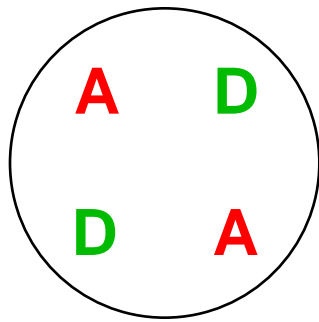


FIGURE 6

