

Synesthesia and the Binding Problem

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For a synesthete, certain stimuli or the thought of certain concepts may be accompanied by perceptual qualities not normally experienced by most people (e.g., Cytowic, 1997). For some synesthetes, letter shapes may induce a color (e.g., A is red, B is blue); others may experience gustatory qualities when hearing words ("Jeremy" tastes like shellfish consommé), or see moving colored shapes when listening to music (e.g., Sibelius's "Valse Triste" may evoke the sight of slowly drifting pink dots). These correspondences are consistent across time and idiosyncratic, though some trends have been observed (e.g., Day, this volume; Shanon, 1982; Ward, Simner, & Auyeung, in press).

This may sound very odd to most people, and it is often hard to believe for those of us who have never had such experiences. Indeed, a central issue in synesthesia research has been the development of methods to test the perceptual reality of such reported phenomena. Such methods have been developed and have demonstrated that synesthesia is indeed a real perceptual phenomenon (Blake et al., this volume; Palmeri, Blake, Marois, Flanery & Whetsell, 2002; Ramachandran and Hubbard, 2001a, this volume; Smilek, Dixon, Cudahy & Merikle, 2001, this volume). Given the peculiarity of synesthetes' reports, it is not surprising that theories of synesthesia have begun to focus on the question of how synesthetes' brains may be different from the brains of nonsynesthetes, as evident in other chapters of this book. However, one simple question has been largely overlooked: What does synesthesia share in common with normal perception? In particular, what cognitive and neural mechanisms ordinarily used in perception are essential for synesthesia?

Odd as it may sound, synesthesia does share much in common with normal perception. First, although particular synesthetic colors, tastes, and so

on, may sometimes be hard to describe, they are still experienced as having one or more of the familiar sensory qualities. Synesthesia is not a sixth sense (see Tyler, this volume) as some are tempted to declare. Additionally, synesthetic qualities are consistent. Just as nonsynesthetes' experience of seeing one particular color induced by certain wavelengths is consistent across time, the same can be said about synesthetic aspects of stimuli. In fact, consistency of reported correspondences has been widely accepted as one diagnostic criterion for synesthesia. A color-graphemic synesthete who perceives the letter H as crimson always sees H this way. He or she will consistently choose the same crimson color patch among similar color patches across testing sessions that can be months or years apart. Moreover, crimson becomes a property of the letter H, just as redness is a property of strawberries. The color crimson is bound to the letter H, in the sense that it consistently co-occurs with it.

The idea that synesthetic correspondences are, in fact, prevalent in human cognition is not new (e.g., Marks, 1987; Merleau-Ponty, 1962; Ramachandran and Hubbard, 2001b). However, little is known about whether binding of synesthetic stimulus properties (in this example synesthetic color to shape) obeys the rules of normal binding of surface properties such as color and shape, and in particular whether attention plays a central role in synesthetic binding as it appears to do in normal perception.

We begin this chapter by briefly reviewing how binding is thought to occur for nonsynesthetes (sometimes referred to as normal perceivers). The visual system must solve several binding problems to make correct inferences about the world around us (e.g., Treisman, 1996). However, the problem of correctly combining color, shape, and other surface features into objects has been a hotly debated issue (for a review, see Wolfe & Cave, 1999). According to one popular theory, Feature Integration Theory (FIT), proposed by Treisman and Gelade (1980), this type of binding is achieved by engaging spatial attention. When binding fails (e.g., under conditions of divided attention), wrong combinations of features may be seen. For instance, if a blue A and green X are presented briefly and attention is focused elsewhere, a person might see a green A and blue X. These incorrect combinations of features are known as illusory conjunctions (e.g., Treisman & Schmidt, 1982) and reflect early independence of feature registration, which must then be bound into the colored shape we see.

Many deny that feature binding is a problem at all (e.g., Garson, 2001; Shadlen & Movshon, 1999), and there are ongoing debates about whether the brain works in a way that creates a binding problem in the first place. There is, however, ample behavioral evidence that binding is a problem, at least as operationally defined by paradigms requiring judgments about feature conjunctions. Other behavioral evidence has been derived from the study of neurological patients. Neuropsychological data have perhaps offered the most persuasive evidence that binding is more than a theoretical construct.

For some individuals with brain injury resulting in spatial deficits, binding can be a real problem that occurs in everyday life. As FIT would predict, illusory conjunctions happen more frequently when spatial attention is disrupted (for a review, see Robertson, 1999, 2004).

The case of R.M. is perhaps the most remarkable example. R.M. suffered from Balint's syndrome produced by bilateral parietal lesions. He nearly completely lost all spatial information outside that of his own body and consequently showed illusory conjunctions even in free viewing conditions (Bernstein & Robertson, 1998; Friedman-Hill, Robertson & Treisman, 1995; Robertson, Treisman, Friedman-Hill & Grabowecky, 1997; see Humphreys, Cinel, Wolfe, Olsen & Klempe, 2000, for confirming evidence). While neurophysiological data suggest that color and shape are initially processed in different areas of the cortex in ventral visual pathways (e.g., Felleman & Van Essen, 1991; Livingstone & Hubel, 1988), data from R.M. show that accurate integration of such features requires dorsal pathway input (e.g., spatial processing of the parietal lobe).

The neuropsychological approach of studying patients with certain lesions and deficits to learn how the brain might work has taught us a great deal. But studying positive phenomena, in which something is added rather than missing, also has much to offer. Synesthesia is such a case and is another example of abnormal binding that is a type of "hyperbinding." In this case, a property such as color that is not part of the stimulus itself is nevertheless bound to it in perception.

In one sense this may be thought of as the converse to the binding problem observed in R.M. For R.M., colors and shapes appear to be independently registered (as they are for normal perceivers), but the features are not bound correctly, presumably due to an inadequate spatial signal from the parietal lobes. However, for some synesthetes this signal may not be necessary for binding, perhaps due to a more direct link between brain areas that encode separate features than is present for the rest of us (e.g., Ramachandran and Hubbard, 2001b). This may lead to preattentive binding (binding that occurs without the need for attention). It would seem that the strongest test of this proposal would be with color-graphemic synesthetes, especially those who see synesthetic colors bound tightly to shapes.

Even within the color-graphemic category of synesthesia, the percept varies widely across individuals. Some synesthetes report that the color is projected externally, while others do not (e.g., Smilek and Dixon, 2002). As reported throughout this volume, synesthetic colors do influence performance, and they are not a delusion. Another important distinction is whether the color is seen as a surface feature of the grapheme (either projected on the actual presented grapheme or a second visualized copy some synesthetes report seeing) or is seen in a different location. Our focus has been on the type that most resembles normal feature binding, where letters or digits

induce an externally projected color that appears as a surface feature of a grapheme (e.g., Smilek et al., 2001). For these synesthetes, the synesthetic color somehow coexists in the same space as the actual surface color but without mixing.

Our studies were designed to explore the role of attention, and in particular spatial attention, in this type of synesthesia. Is attention necessary for synesthetic binding, as it appears to be for normal feature binding? One popular account of synesthesia is that certain brain areas are abnormally and more directly connected than in nonsynesthetes (Baron-Cohen, Harrison, Goldstein & Wyke, 1993). Particularly, in the case of color-graphemic synesthesia, Ramachandran and Hubbard (2001b) propose that these would most likely connect two ventral cortical areas: the color area V4/V8 (e.g., Hadjikhani, Liu, Dale, Cavanagh & Tootell, 1998; Zeki & Marini, 1998) and the grapheme area (e.g., Nobre, Allison & McCarthy, 1994). To date, there is no direct evidence for the anatomical claims about hyperconnectivity giving rise to synesthesia. Nevertheless, if this theory is correct, it could be the case that cross-talk between ventral areas subserving synesthesia occur directly and without parietal input. Moreover, as synesthetic features are not actually present in the scene, perhaps there is no a priori reason to believe that attention should play a role. Alternatively, because in many cases, perceived synesthetic features do have a well-defined spatial location and extent, it may rely on parietal mechanisms that support spatial attention after all. Indeed, we found that synesthesia does require attention and appears to follow at least some of the rules of normal feature binding (Robertson, 2003; Robertson & Sagiv, 2002; Sagiv, 2001; Sagiv, Heer, & Robertson, in preparation). Here we review some of these findings, but first we introduce our participants.

A.D. and C.P. are both color-graphemic synesthetes. Both report that letters and digits evoke colors that are determined by the graphemic shape (e.g., 5 and S have similar colors; see plate 6.1). Both synesthetes are in their late 20s, and both report that they have always seen letters and digits this way, at least as far back as they can remember. They provided us with R,G,B values that best matched their synesthetic colors when presented with an achromatic number or digit, and on a consistency test given several months later they chose the same colors. Both reported that synesthetic colors were externally projected on the grapheme surface (i.e., experienced as a surface feature as illustrated in plate 6.2, and coexisting with the actual surface color.

Synesthesia Facilitates Visual Search: **Pop Out** or Guided Search?

One challenge in designing experiments to study synesthesia is selection of objective measures that can verify its presence. A common design used for

this purpose is a variant of Stroop-like methods (e.g., Bergfeld-Mills, Howell Boteler & Oliver, 1999; Dixon, Smilek, Cudahy & Merikle, 2000; Odgaard, Flowers & Bradman, 1999), in which effects of a task-irrelevant variable on color naming are evaluated. A typical finding with synesthetes is that reaction time (RT) to judge a color patch is influenced by a task-irrelevant synesthetic color evoked by an achromatic stimulus in the display. RT is faster when the color patch is consistent with the synesthetic color than when it is inconsistent. Others sought to document the perceptual reality of synesthesia by embedding a complex target in a multi-item achromatic display (e.g., Ramachandran and Hubbard, 2001a). The evidence using this method demonstrated that synesthetic colors could facilitate search in otherwise monochromatic grapheme displays. However, the nature of this facilitation at first was poorly understood: Ramachandran and Hubbard described it as pop out, implying that binding of synesthetic color to grapheme shape occurs preattentively. This is indeed a plausible outcome of cross-activation between grapheme and color areas in brain via direct connections between these areas. In the displays used by Ramachandran and Hubbard, both distractors and targets induced synesthetic colors. Under such conditions, it is hard to know whether the facilitation was due to a true pop out of the target's synesthetic color or to faster rejection of distractor items based on their synesthetic color (i.e., guided search rather than pop out of synesthetic color induced by a yet-to-be detected target).

We began to explore these issues by attempting to replicate the visual search findings under more restrictive conditions. We only used distractors that did not induce synesthetic colors and compared RTs to detect targets that were either synesthetic inducers or not. Sample displays are shown in figure 6.1. In one display the target was a 180°-rotated L, and the distractors were 90° rotated Ts. These were not referred to as Ls and Ts until after the experimental data were collected. The same displays were used in another condition, except now they were rotated 180°, making the L upright and an obvious letter, while the Ts remained rotated. As a result of this manipulation, all the physical features of the displays were equated between the two display conditions, and in neither case were the distractors synesthetic inducers. The critical difference was that in one case the target was a synesthetic inducer and in the other case it was not. We refer to the two conditions as "inverted" and "upright" in reference to the target. All stimuli were achromatic (gray) items on a white background.

Other than the change in the target's potential as a synesthetic inducer, the subjects engaged in a standard visual search experiment. They were asked to indicate whether the target was present or not, and response speed was emphasized. The target was present on half the trials, and set size was either 4, 9, or 16. Stimulus density was equated across set size.

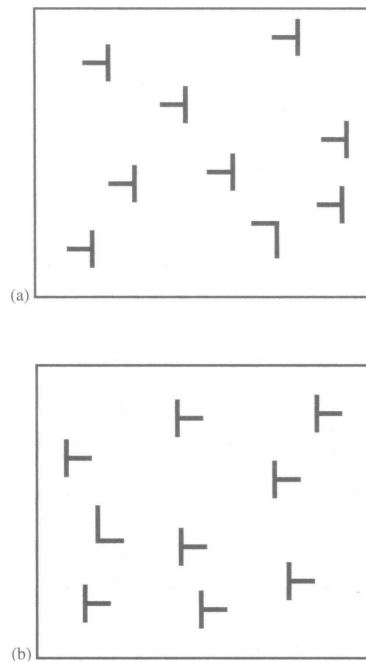


Figure 6.1. Sample search displays (with target present) used in experiment 1. (a) Initial inverted block, a nonletter target; (b) second upright block, a letter target.

As can be seen in plate 6.3, visual search was quite normal; RTs increased with set size, and slopes were steeper for target-absent than target-present conditions (in target-present conditions, search can be terminated as soon as the target is found). Critically, neither subject showed any evidence of (or even a trend toward) faster search rates for targets that induced a color (Ls) compared with targets that did not induce a color (inverted Ls); in other words, there was no interaction of set size and target orientation on those trials when the target was present. When distractors were not synesthetic inducers, synesthetic properties of the target did not make a difference, meaning that, at least for A.D. and C.P., synesthetic colors do not pop out. Rather, the synesthetic experience only began upon target detection when it became the focus of attention.

These findings are consistent with the subjective reports of both our participants who reported seeing the color associated with the letter L, but only upon detecting the target (and only when it was upright). Neither reported knowing the target was there as a consequence of seeing the corresponding synesthetic color before target detection.

Processing without awareness has been reported in a wide variety of tasks in different subject populations. However, our findings shed doubt on preattentive binding in synesthesia. Binding of the synesthetic color with the inducing shape required attention to the inducing stimulus. The data also suggest that the synesthetic properties of distractors can account for the improvement in visual search for other synesthetes tested in other laboratories.

Synesthetic color may help synesthetes group distractors into clusters of similar color, making them easier to reject, perhaps via a special form of guided search (Wolfe, 1994). Alternatively, the synesthetic color induced by distractors as the search proceeds may help synesthetes avoid returning to those distractors that have been rejected. The colors may group the distractors in ways they do not for normal perceivers, making the search more efficient. Palmeri et al. (2002; see also Blake et al, this volume) also provided confirming evidence that synesthetic color guides search but does not actually precede target detection. Like Ramachandran and Hubbard (2001a), they too found that synesthetes were faster than controls in finding a target grapheme among distractor graphemes. However, in a later experiment, they showed that this advantage disappeared when meaningless symbols (that do not induce color) were used as distractors. Their study also helps rule out other explanations of our findings based on factors such as the smaller set sizes or constant density we used, or that our findings are unique to the two synesthetes who participated in our study. In addition, A.D. and C.P. were tested by Hubbard and Ramachandran (2002) using their displays and procedures and showed an advantage over control subjects detecting the embedded target shape among letter distractors.

Other results reported by Ramachandran and Hubbard (2001a, 2001b) may also be explained along similar lines. In one experiment, grouping elements into rows or columns by synesthetes was determined by similarities of synesthetic colors induced by items in the display. However, given that stimuli were available for a prolonged time and speed was not a variable, these findings were probably not due to pop out. In another experiment, synesthetes were asked to identify a single achromatic target among four achromatic distractors (a crowding paradigm that normally produces performance decrements in naming the target for nonsynesthetes). The displays were placed in peripheral vision with a digit target in the center of these displays surrounded by digit distractors. In contrast to normal perceivers who are slower to name the target under such conditions, synesthetes were faster at naming the central target. However, here too, the distractors were synesthetic inducers, and it would be interesting to see whether this effect would be replicated with distractors that do not induce color surrounding a target that does.

Other recent studies have been concerned with the question of whether attention is necessary for synesthetic binding. The largest group of synesthetes ($N = 15$) was studied by Mattingley, Rich, Yelland, and Bradshaw (2001; see also Rich & Mattingley, this volume). They found that under conditions sufficient to produce letter priming from below threshold achromatic letter primes, synesthetic color priming was not observed. The synesthetic color only primed when the inducer was perceived.

In sum, synesthesia acts rapidly enough to influence perception and performance. However, it appears that the majority of color-graphemic

synesthetes do not bind synesthetic color to graphemic shape preattentively and that awareness of the inducing grapheme is generally necessary for synesthetic colors to be experienced (an exception reported by Smilek et al. will be discussed later). But can attention modulate synesthesia at suprathreshold levels? If attention is required for synesthetic binding, then manipulations of spatial attention may modulate the strength of the experience as well.

Attention Modulates Synesthesia

In the previous section we reviewed results consistent with the conclusion that synesthetic colors do not pop out of a cluttered array, but rather are experienced when inducers become the focus of attention and the inducing shape reaches visual awareness. To directly assess the role of attention, particularly spatial attention, we conducted a second experiment. In this experiment we varied the size of the attentional window so that it either included or did not include task-irrelevant but clearly visible digit inducers placed on both sides of fixation. Sample displays are shown in plate 6.4. On each trial two identical achromatic digits (either 2 or 7) appeared 200 ms before presentation of a target. The target was four identically colored dots. Subjects were asked to report the color of the dots as rapidly as possible by pressing a key, and the dots were either a consistent or inconsistent color to that induced by the 2s or by the 7s. Target dots appeared either close to fixation, which was at the center of the screen, or more peripherally, closer to the color-inducing digits. The position of the target dots was blocked to encourage subjects to focus attention either narrowly or widely before a trial began. It is also important to note that the position of the inducer digits was the same in both blocks and never changed throughout each block of trials. By changing only target dot position, the inducer digits would be within a wide attentional window when dots were expected in more peripheral locations and outside the attentional window when dots were expected close to fixation. Note that to optimize the occurrence of synesthesia, the digits always appeared before the target dots.¹

We compared RTs to judge the color of the target dots that were either congruent or incongruent with the synesthetic color of the inducers. Congruency effects between synesthetic color and actual target color have been frequently used as an objective measure of synesthesia. RT to colored shapes congruent with the synesthetic color are typically faster than to incongruently colored shapes, and we have obtained a similar result with A.D. and C.P. in other experiments. Here we also manipulated attention to determine its effects on the inducers. If attention can modulate synesthesia, we predicted that a smaller congruency effect would be observed when attention was focused narrowly and the inducer digits were outside the focus of attention.

Indeed, this is what we found; the congruency effect was markedly reduced when inducers were outside the attentional window. This was demonstrated by a significant interaction between color congruency and attention for both A.D. and C.P. (plate 6.5). In A.D.'s case the difference in RT between the incongruent and congruent case dropped from 74 ms to 35 ms when the inducers were outside the window of attention (attention narrowly focused), and for C.P. the effect was even larger—from 256 ms to 69 ms.

In sum, inducers had a smaller effect when they were outside the focus of spatial attention, even though they were in the same retinal location as when attention was spread widely. Consistent with these findings, both subjects reported experiencing more vivid colors when the target dots were farther in the periphery.

Of course, with such simple displays, inattention would not be expected to be complete, and some residual effect would be expected even when inducers were not within a narrowly focused attentional window. This means that whether or not some processing of the synesthetic properties of graphemes took place without attention could not be addressed with this study alone. However, these results clearly demonstrate that attention substantially modulates the strength of synesthesia.

Several other studies (some by contributors to this volume) also support a central role for attention in synesthesia. These include modulation by attentional load (Rich and Mattingley, this volume) and synesthete's reports when viewing hierarchical stimulus (e.g., a large 5 made by the placement of smaller 2s). The reported color depends on whether synesthete's attend to the global or local stimulus levels (Mattingley et al, in press; Palmeri et al, 2002; Ramachandran and Hubbard, 2001b). Also, synesthetes' reports are generally consistent with the finding that paying attention makes a difference.

The literature as a whole also suggests that synesthesia is automatic, which is one of the attributes that on the surface suggests that it should not require attention. In fact, automaticity is typically one of the requirements for diagnosing synesthesia (Cytowic, 1997). However, the evidence as a whole suggests that once the inducer is attended, synesthesia appears automatically (Mattingley et al., 2001). It happens without effort, but awareness of the inducer shape or identity appears to be necessary, at least for the majority of synesthetes and clearly for those we tested.

Synesthesia and Visual Awareness

In our studies reported in the last two sections the stimuli were presented above threshold, so no direct test of an attentional role in binding was performed. However, other studies have examined synesthesia at or near perceptual threshold and have reported conflicting results in terms of whether

synesthetic binding occurs preattentively. In the largest study of synesthetes yet reported, Mattingley et al. (2001) presented evidence suggesting that synesthesia without awareness is unlikely, at least for a mixed group of 15 color-graphemic and color-phonemic synesthetes. However, some findings reported by Smilek and colleagues appear to provide at least one counter example. In a study reported in the *Journal of Cognitive Neuroscience*, Smilek et al. (2001) described a color-graphemic synesthete, C, who, like A.D. and C.P., projects synesthetic colors externally (a "projector" as categorized by Smilek & Dixon, 2002), onto the surface of the inducing shape. C. was less likely to detect an achromatic (black) digit presented on a colored background that was congruent with the synesthetic color of that digit than a background color that was incongruent. This pattern was replicated using different methods with C, including visual search, and suggests that the synesthetic color was bound to the digit preattentively (see Smilek et al., this volume).

Since C, A.D., and C.P. all bind colors within the boundaries of the shape, we attempted to replicate Smilek et al.'s (2001) findings with our subject A.D. (C.P. was unavailable for this experiment). Unlike C, A.D. was able to detect the letters equally well whether the background color was congruent or incongruent. In addition to the original design, we also ran a simpler, modified version of this experiment with only two possible graphemes and two possible background colors (rather than nine as used by Smilek et al.). We reasoned that RT measures would be less susceptible to strategic biases that might be introduced when errors were the dependent measure (e.g., using the background color as a default guess or, conversely, avoiding it when uncertain). Thus, we asked A.D. to determine as rapidly as possible which of two black letters was presented on each trial. In 50% of the trials letters were presented on a background congruent with the synesthetic color of the presented letter and in 50% letters were presented on a background that was incongruent (the color normally induced by the other possible letter in the stimulus set).

For the original design, we found no differences in error rates between background colors. In the reaction time version, RT to correctly identified letters was significantly shorter in the congruent condition (641 ms) than in the incongruent condition (711 ms). It appears that for A.D. synesthesia does not occur preattentively. Performance was affected by the background, perhaps at some later stage of processing or decision-making.

Coexistence of Stimulus and Synesthetic Color

The above differences between C. and A.D. may simply be yet another piece of evidence that synesthesia has wide individual differences. However, a

spontaneous comment by A.D. piqued our interest. She told us that the digit she saw was both black and the induced color at the same time. When probed about the locations of the two colors, A.D. reported that she didn't know how to explain it, but that both appeared on the shape in the same location at the same time. Her comments are consistent with several synesthetes we and others have interviewed in that they claim to see both the real color and the induced color at the same time (although not always as tightly coupled as for A.D.).

When two colors exist in the same place, they mix, but this does not appear to be the case with synesthetic colors and colors carried by wavelengths in the stimulus. When one color (we are including black) is generated by wavelengths from the stimulus and another by its shape, the two colors appear to coexist. How might this be explained? Suppose a red A is presented in the middle of a computer screen to a synesthete who sees green whenever an A is present. In such a case the brain should activate three feature maps (location, shape, color) registering one location signal (central), one shape signal (A), and two color signals (red and green). The question is how the visual system handles the extra color.

There are several possible solutions: to inhibit the stimulus color completely; to see two colors, one bound to the shape's location and one off to the side; to replicate the shape in another location and bind the color to it; or, as A.D. reports, to somehow see both colors in the same location in the same shape (see Robertson, 2003, for a detailed way in which the brain might manage this). Other synesthetes seem to solve the problem differently, reporting that the color is anywhere from slightly off the shape to hovering elsewhere or as an aura. Still others claim they see the color as real but in their mind (not projected into the world), which may represent a qualitatively different type of synesthesia (Smilek & Dixon, 2002) or a point on a continuum with one end represented by tightly bound sensations and the other by normal metaphors, a position that Ramachandran and Hubbard (2001b) favor.

To our knowledge no one has yet attempted to quantify the report that two colors can coexist at the same location at the same time, but several questions immediately arise that may be relevant for understanding individual differences in color-graphemic synesthetes such as C. and A.D. To what extent, if any, does either a synesthetic or stimulus color dominate, and do they compete for awareness? Do they alternate in perception so quickly for some synesthetes that they appear to be present in the same place at the same time but are actually not? At least some synesthetes report that synesthetic percepts are more easily accessed in the dark (Tyler, this volume), bringing forth the possibility that the stimulus color dominates under stronger lighting conditions and the synesthetic color under weaker lighting conditions. To what extent can controlled attention modulate the dominance of one color over the other?

This discussion brings us back to the question of how C. might solve the binding problem presented by two color signals, one shape signal and one location signal. Assuming that she, like other synesthetes, sees the stimulus color and her synesthetic color together, the question then becomes why dark gray (the digit color used by Smilek et al. [2001] in the camouflage experiments) was not sufficient to detect the target on a colored background. Why would background color congruency with the synesthetic color have any effect? Perhaps C.'s visual system inhibits stimulus color, leaving only the synesthetic color and the background color. Under such circumstances a dark gray digit (or any other colored digit) would be replaced with its synesthetic color. If this is the explanation for why dark gray was not sufficient for C. to detect the digit in a colored background, this still means the induced color replaced the dark gray before C. became aware of the presented digit (preattentive inhibition and preattentive binding). It seems that under normal viewing conditions C does detect letters and their actual color, but whether the dynamics of her perception under more restricted conditions generalizes to other synesthetes remains an open question. This then would be consistent with hyperconnectivity between feature maps and the hypothesis that we originally tested but found no support for; namely, that binding under such conditions would be preattentive in synesthetes with tightly bound color-graphemic synesthesia.

Neural Contributions to Color Synesthesia

It is possible that C. represents an extreme case of quick, automatic, and vivid synesthesia, while the majority of other synesthetes, including other projector synesthetes, depend on attention at least to some extent. If such individual differences exist, we should be able to trace their neurophysiological origins. Candidates for neural bases of such differences include:

1. Quantitative differences of abnormal cortico-cortical hyperconnectivity as might be directly tested with diffusion-weighted imaging measures.
2. Qualitative differences in connectivity (e.g., the level of visual processing hierarchy at which abnormal connections are present). Such differences may be evident in the time course of electrophysiological correlates of synesthesia (Sagiv et al., 2003).
3. Quantitative differences in functional organization of the visual cortex: What proportion of color-sensitive tissue is dedicated to processing of synesthetic color? This may correlate with the likelihood that synesthesia will influence detection of certain stimuli. Further differences may

manifest in varying degrees of inhibition between putative stimulus and synesthetic color-responsive areas.

4. Qualitative differences in functional organization of the visual cortex: Do some synesthetes have shared circuits for stimulus and synesthetic color while others split the color area into two functionally segregated modules? One would expect that in the latter case, more accurate perception of actual stimulus properties may be permitted in parallel with the synesthetic experience. Imaging techniques such as functional magnetic resonance adaptation (Grill-Spector & Malach, 2001) would be valuable for assessing such differences. As noted above, both A.D. and C.P. reported that the synesthetic color does not replace the actual color, but rather they coexist.

Neuroimaging data have not been reported for most the synesthetes who have been tested in behavioral studies. From the handful of studies that have reported imaging data, a particularly interesting result is that areas of the brain that are active during colored-hearing synesthesia include those that normally correlate with perceived color (even though no color is presented; Nunn et al., 2002). Interestingly, for the subjects in the Nunn et al. study, there was a division of labor between hemispheres in regions that respond to externally presented color. One was more responsive to the color of the stimulus and the other to the synesthetic color. We hope that future studies will tell whether this pattern generalizes and will provide more quantitative information on the dynamics of activity correlated with normal and synthetic color perception or, alternatively, whether the degree of overlap in activity correlates with the ability to report both colors.

Another intriguing finding in the Nunn et al. (2002) data was that the angular gyrus and inferior parietal lobes were just as active as V4/V8 when synesthesia was induced. In fact, parietal activity has been present in all studies of synesthesia reported to date, but these findings have been downplayed or ignored for some reason. For instance, using PET, Paulesu et al. (1995) found strong activation bilaterally in the occipital/parietal junction which the authors considered puzzling.

Parietal activation in the functional imaging study of Nunn et al. (2002) was within areas of damage in R.M. and other Balint's syndrome patients. Recall that RM had severe binding deficits between color and shape as a result of spatial deficits (Robertson et al., 1997). In light of these findings and the parietal activation observed with synesthetes, we suggest that the spatial attentional signal generated by the parietal lobes also plays a major role in color-graphemic synesthesia. The hyperconnectivity suggested by others seems to require consideration of both dorsal and ventral visual pathways, although it would be interesting to know whether the synesthetes who do show evidence of preattentive binding (Smilek et al., 2001, this volume) activate only ventral areas during synesthesia.

Discussion

Although we expected to find evidence for preattentive binding with synesthetes, especially those demonstrating a strong spatial coupling between inducer shape and evoked color, this hypothesis was not supported. We had reasoned that if hyperconnectivity between ventral cortical visual areas that process shape and color was the underlying neural cause of the most common forms of synesthesia (color-graphemic and color-phonemic), evidence for preattentive binding would be present, and this would reduce the reliance on attentional mechanisms. Instead, our results demonstrated that attention of the inducer was needed before synesthesia arose and that spatial attention modulated the strength of synesthesia. These findings are in need of explanation considering other evidence that synesthetic binding can occur before awareness (Smilek et al., 2001) and results demonstrating that synesthesia can increase visual search efficiency (Palmeri et al., 2002; Ramachandran and Hubbard, 2001a).

The evidence demonstrating that search is more efficient is relatively easy to explain. In fact, our data are in accord with the results of Palmeri et al.'s (2002) last experiment, which has not received the attention it deserves. When Palmeri et al. used distractors that did not evoke a unique color, they observed that search for a synesthesia-evoking target was no longer more efficient than search for a target that has no synesthetic properties.

The fact that synesthetes are able to find a conjunction target faster than normal perceivers is consistent with guided search models of visual search (Wolfe, 1994), but with a twist. For a synesthete who begins searching a display of shapes in an area that does not contain the target, all the distractors within the window of attention will turn the synesthetic color. As spatial attention moves across the display, other items will turn colored, and items already scanned will remain colored, producing general areas of color that act also as a cue that those areas have already been searched. This process would increase search efficiency and reduce rescanning of distractor regions or overlapping regions of attention, and this explanation is consistent with the visual search literature and synesthesia. Increased search efficiency does not occur when the target and distractors produce the same color or when the distractors are not themselves inducers.

The evidence for preattentive binding presented by Smilek et al. (2001) is more difficult to explain, and the synesthete they reported (C.) may in fact reflect a form of synesthesia that produces preattentive binding of synthetic color with a shape. If true, this finding would also reflect the variability of synesthesia, even for those in the same category (e.g., projector color-graphemic). It would also suggest that the brain might solve the binding problem in different ways when confronted with two colors but only one shape, and it would predict different interactions between cortical areas for

different synesthetes that may vary in time or in neural connectivity between areas that are normally separate. Synesthesia may arise as a function of many constellations, with some synesthetic phenomena appearing more rapidly, more vividly, and more projective than others depending on the underlying neural machinery. The level at which binding occurs will also vary as a result.

In sum, although simple explanations of binding are not adequate to explain color-graphemic synesthesia, the role of attention in its occurrence has been supported across laboratories and with the majority of synesthetes who have been tested. Spatial attention changes the emergence and the strength of color-shape binding for synesthetes. Visual search studies demonstrate that attention must be directed to a target (or distractor inducer) location in a cluttered array before synesthesia appears, and methods that change the size of an attentional window influence the intensity or probability of synesthetic perception. Consistently, parietal and posterior temporal cortical activity correlates with color synesthesia, as observed when nonsynesthetes search for a conjunction of color and another feature. These similarities may indicate common mechanisms for feature binding even when one of the features does not exist in the external stimulus.

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Note

1. The choice of a 200-ms interval between inducers and targets was not arbitrary. Event-related potentials (ERPs) to orthographic versus nonorthographic material first diverge about 150 ms after stimulus presentation (Bentin, Mouchetant-Rostaing, Giard, Echallier & Pernier, 1999). We reasoned that minimally we should allow sufficient time for digits to be categorized to induce color. Indeed, preliminary ERP data from A.D. and C.P. show electrophysiological markers of synesthesia beginning between 150-200 ms (Sagiv, Knight & Robertson, 2003). Thus, we chose a stimulus onset asynchrony (SOA) of 200 ms. Furthermore, a control study using a similar design in control subjects showed that this SOA is sufficient to avoid confounding of the results by the different target-distractor distance (a concern for flanker paradigms in which the target and the distractors are presented synchronously).

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Plate 6*1 • A.D.'s (top) and C.P.'s (bottom) letter-color and digit-color mapping.

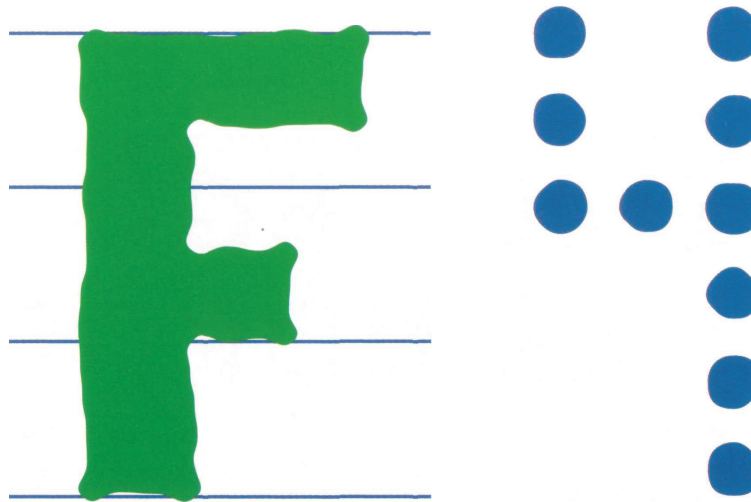


Plate 6*2* When A.D. was asked to color in an outline of an F and the circles making up a 4 to illustrate her color perception, she colored them as represented, reporting that the colors were "a property" of the letters.

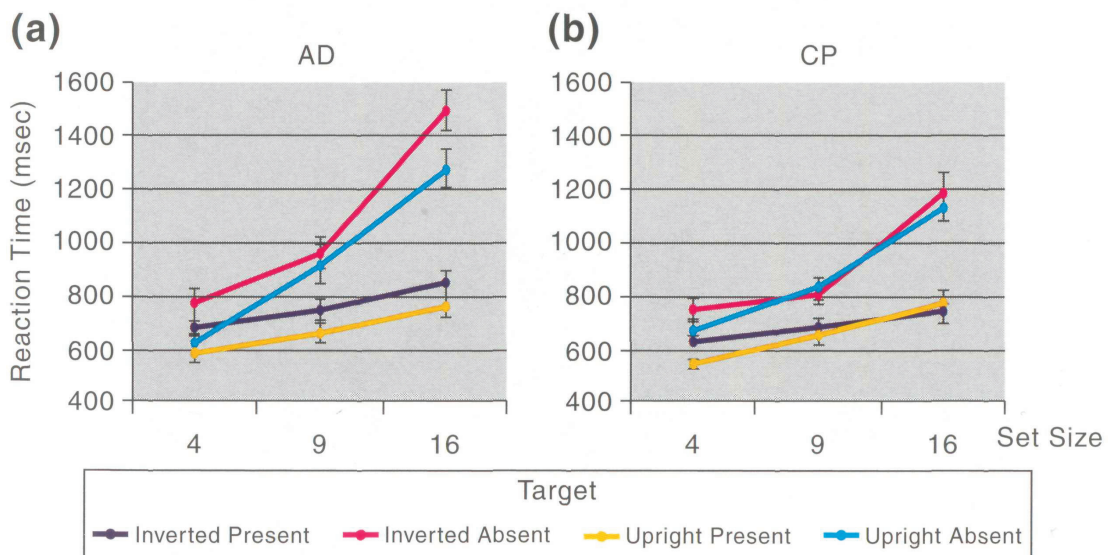


Plate 63, Mean reaction times (in milliseconds) as a function of set size for (a) A.D. and (b) C.P.

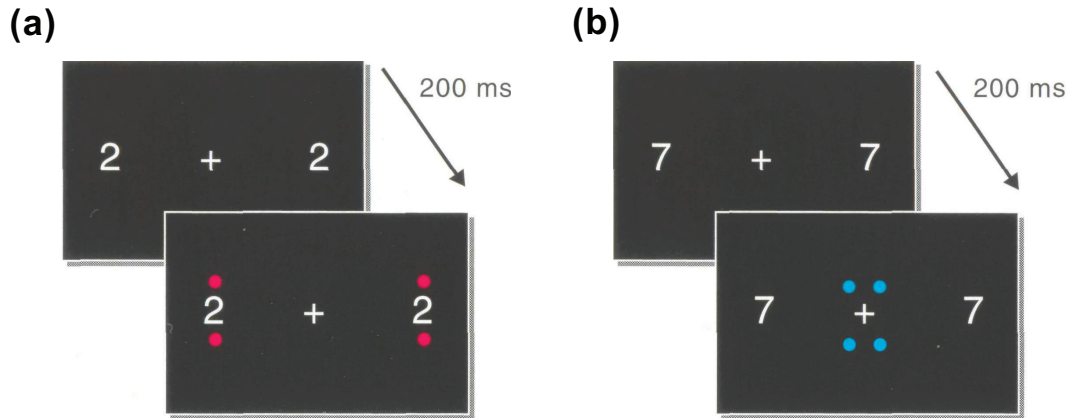


Plate 6*4* Sample displays used in experiment 2. Throughout each block, target colored dots appeared in positions that require motivated diffuse or focused attention, putting the previously presented digits either inside (a) or outside (b) the attentional window.

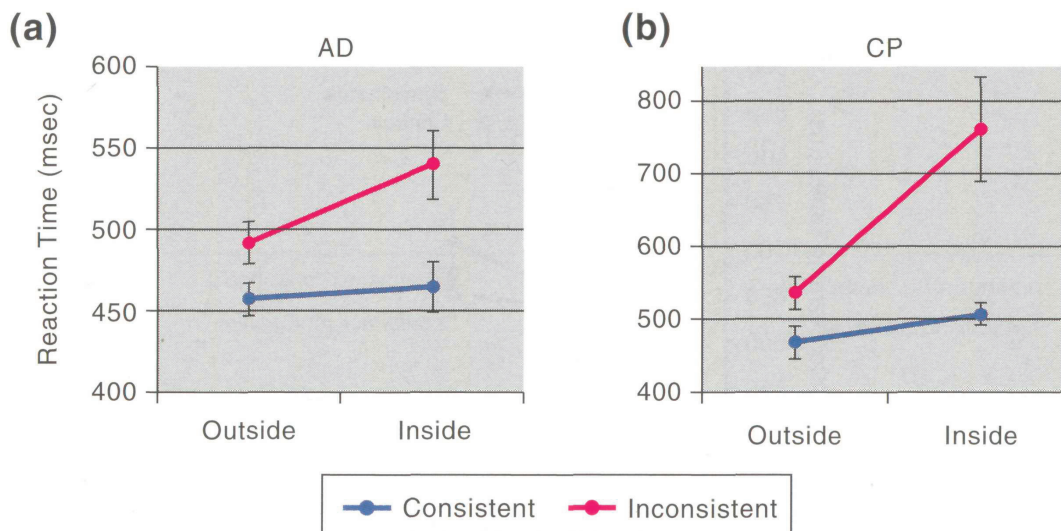


Plate 6,5, Mean reaction times (in milliseconds) for (a) A.D. and (b) C.P. in the inside and outside conditions for achromatic digits inducing either congruent or incongruent synesthetic colors.