REVISITING THE PERCEPTUAL REALITY OF SYNESTHETIC COLOR

CHAI-YOUN KIM AND RANDOLPH BLAKE

INTRODUCTION

Emerging over the past decade is the view that synesthesia is not attributable to over-learned semantic associations, florid imagination, metaphorical thinking, or, for that matter, frank hallucination (see Box 15.1). Instead, some forms of synesthesia are thought to be mediated by at least some of the same neural processes engaged during ordinary perception. A growing number of papers report evidence that purportedly supports this view, and we see it endorsed in some of the most widely read publications in this field of study (e.g., Cytowic 2002; Ramachandran and Hubbard 2003). This chapter takes a critical look at the various lines of reasoning used to arrive at this conclusion concerning the perceptual nature of synesthesia.

Rather than comprehensively reviewing studies bearing on this question, this chapter focuses on: (1) distilling from this literature some of the general strategies that have been utilized to examine the perceptual reality of synesthesia, and (2) evaluating limitations to those strategies and, hence, the validity of results obtained from them. We will focus primarily, but not exclusively, on color-graphemic synesthesia because it represents a common, widely studied form of this beguiling condition and because it is the form of synesthesia we are most familiar with from our own work. Our chapter is motivated, in part, by a provocative paper questioning much of the evidence often cited in favor of the perceptual basis of color reports by people with color-graphemic synesthesia (Gheri et al. 2008). That paper challenges those of us interested in synesthesia to think carefully about the reasoning underlying the tests we use to assess whether or not color-graphemic synesthesia includes a genuine perceptual component. This chapter is our attempt to grapple with that challenge.

Box 15.1

Synesthetic experiences in the visual domain (e.g., a "colored" achromatic letter) are sometimes referred to as "photisms" (e.g., Witthoft and Winawer 2006). This is an interesting word choice, for Webster's unabridged dictionary defines photoism as "A luminous image or appearance of a hallucinatory character." Is visual synesthesia a form of hallucination? When, for example, LR (a synesthete tested by us on many tasks) describes seeing this character—A—as vivid red, is she hallucinating? In one sense of that term, she is: the visual stimulus ordinarily "appropriate" for this perceptual experience would be the character A printed in real colored ink, but that's not what LR is looking at when she reports seeing "A" as red. Yet, she insists that "A" looks as red as "A." In that sense, she seems to be hallucinating: she describes seeing something that is not really there (Collerton, Perry, and McKeith 2005). Yet in other ways, those "photisms" do not resemble hallucinations. For one thing, LR readily acknowledges that she knows that the letter "A" is really "A" and not "A." This is not always the case in other contexts where hallucinations occur. For example, some, but not all, schizophrenia patients describe hearing voices and believe that those voices are real to the extent that they act on those beliefs. In schizophrenia, these hallucinatory experiences are attributable to deficits in core speech perception (Hoffman et al. 1999). For another thing, there is a fundamental distinction between synesthesia and the hallucinatory experiences of, say, schizophrenic patients. In the former, there is an external stimulus triggering the unusual sensory experience whereas in the latter there is not. Moreover, hallucinations in schizophrenia are accompanied by decreased activity in sensory brain areas that would ordinarily respond to an external stimulus of the sort described by the patients (Aleman et al. 2001; Shergill et al. 2003), but, as summarized in our chapter, synesthetic experiences can be accompanied by increases in brain activations in at least some of the sensory areas appropriate for the experience being reported. Finally, hallucinations tend to have a narrative quality that incorporates recent events, prejudices, and even cultural symbols. Synesthesia, however, does not come with a story nor is it so attuned to the vagaries of daily events.

So, we are disinclined to characterize synesthetic experiences as hallucinations. If anything, synesthesia may have more in common with imagery, willfully generated forms of sensory experience (Tong 2003). Indeed, self-rated visual imagery tends to be stronger in people with synesthesia (Barnett and Newell 2008), and simply imagining an inducer can trigger a synesthetic experience (Dixon et al. 2000). Still, there is indirect evidence implying that synesthesia is not merely a form of extra vivid mental imagery (Rich et al. 2006; Steven and Blakemore 2004; Steven, Hansen, and Blakemore 2006; but also see Price, Chapter 37, this volume). Nonetheless, the correlation between imagery and synesthesia means investigators must be mindful of it and control for its influence in studies of synesthesia where salience, vividness, or intensity could be controlling factors (Barnett and Newell 2008).

To be clear, by "genuine perceptual component" we mean that at least some of the mechanisms mediating synesthetic experiences are the same mechanisms involved in non-synesthetically induced analogues of those experiences. In the case of color-graphemic synesthesia, for example, do the purported experiences of color influence

performance on tasks known to be sensitive to the presence of color? Does synesthetic color behave like real color on tests where color appearance depends on the spatial and temporal context in which colored stimuli are presented, including contexts that produce illusions of color or after-effects of color? Is the reported experience of synesthetic color accompanied by neural activation within sensory brain areas believed to be involved in color perception?

From the outset, we wish to stress that this question of the perceptual nature of synesthesia is different from the question of whether synesthesia can be experienced when stimuli inducing synesthesia fall outside of awareness (e.g., Ramachandran and Hubbard 2001) or outside the focus of attention (e.g., Mattingley et al. 2001; Sagiv, Heer, and Robertson 2006).[1] Answers to these two questions do not tell us whether or not synesthesia is perceptual in nature.

Strategies for Evaluating the Perceptual Reality of Synesthetic Experiences

Most investigators of synesthesia are themselves not synesthetes; for us, our first peek into the world of synesthesia comes from conversations with individuals who do have the condition. The verbal descriptions of their synesthetic experiences sound both familiar and incredible: familiar because we can easily understand what is meant when the person says, for example, that the letter A appears red, and incredible because the letter provoking that description is obviously black and not red. Of course, as psychologists we have been taught not to place too much stock in people's verbal reports of their mental experiences—those reports can be misleading, not because people lie but because they—we—are very good at fabricating plausible accounts that bear little relation to the actual causes of our mental experiences and our behaviors (Nisbett and Wilson 1977). Consequently, those of us interested in this mystery of the mental representations associated with synesthesia must resort to indirect techniques. So, what kinds of indirect measures allow us to evaluate the bases for the beguiling verbal descriptions offered by synesthetes? What, in other words, can we do to convince ourselves that the letter A indeed looks like A?

Fortunately when it comes to color, we have a variety of strategies to use in pursuit of an answer to this question. We divide these strategies into two broad groups, one comprising strategies based on behavioral performance measures obtained using perceptual and/or cognitive tasks and the other comprising strategies using indirect measures based on oculomotor responses, brain imaging, or electrophysiology.

---

[1] Readers interested in those questions will want to see the chapters by Rich and Mattingley (Chapter 14) and by Alvarez and Robertson (Chapter 16), in this volume.

Behavioral Measures

In the following sections we consider strategies that exploit: (1) well-established tasks where real colors exert robust effects on performance, and (2) visual phenomena where contextual factors influence color appearance. The best tasks are ones where participants do not know the expected outcome on the task, to preclude response bias or, in the worst case, blatant cheating to confirm an expected outcome. Moreover, as others have opined (Gheri, Chopping, and Morgan 2008), we must also be mindful of the possibility that experimenter bias could influence the outcomes of behavioral tests of synesthesia, for testing is rarely if ever done blind. While not a foolproof antidote to experimenter bias, computer-based, forced-choice testing together with written, not verbal, instructions can go some way toward minimizing this contaminating effect. It is imperative, of course, that participants in these studies be given no clues about the expected outcome or the hypothesis under test.

Performance enhancement

It is well known that appropriately created color differences among spatially distributed objects in the visual scene can promote robust segmentation of a figure from its background. One of the most widely studied versions of this phenomenon is visual search wherein observers judge as quickly as possible whether or not a specific target is present amongst an array of distractors (e.g., Treisman and Gelade 1980). When the target conspicuously differs in color from the distractors, observers can quickly spot it and respond, a phenomenon sometimes dubbed pop-out. In principle, these kind of visual search tasks lend themselves nicely to the study of color-graphemic synesthesia using digits and/or letters as targets and distractors, for the potential conspicuity of the target owing to its synesthetic color can be systematically varied relative to the synesthetic color(s) of the distractors. For example, a visual search task might use an achromatic display of distractor 5s with a single embedded target digit 2 (see Figure 14.7, in Rich and Mattingley, Chapter 14, this volume; the right-hand side of the figure shows how the achromatic display is "seen" by synesthete WO, who experiences green on the digit 5 and orange on the digit 2; Palmeri et al. 2002). If synesthetic color promotes figure/ground segmentation, it is not unreasonable to expect that visual search will be consistently faster (with no loss in accuracy) when targets differ in perceived color from distractors. When target and distractors comprise characters with identical color associations, however, this benefit should disappear. The same pattern of results would be predicted for accuracy (percentage correct) on tasks where shapes are defined by the configuration of alphabetic characters appearing within a larger array of other characters.

Versions of these kinds of tasks involving the use of achromatic inducers have been employed in a number of studies, including single-subject case studies and group

studies. Some of those studies report faster or more accurate search performance by synesthetes relative to normal controls (Hubbard et al. 2005; Kim and Blake 2005; Laeng, Svartdal, and Oelmann 2004; Palmeri et al. 2002; Ramachandran and Hubbard 2001; Smilek, Dixon, and Merikle 2003; Smilek et al. 2001), whereas other studies find that synesthetes enjoy no significant advantage over control subjects (Edquist et al. 2006; Gheri, Chopping, and Morgan 2008) and one recent study found a small performance advantage for some but not all of the 13 synesthetes tested (Rothen and Meier 2009). Two research groups have found that synesthesia does not produce speeded search when only the target, but not the distractors, has an associated color (Palmeri et al. 2002; Sagiv, Heer, and Robertson 2006). Laeng (2009) found that search efficiency can be enhanced when the synesthetic colors of a target and distractors are "nearly complementary" (p. 1461) resembling pop-out search. In reviewing this confusing literature, Rothen and Meier (2009) speculate that individual differences among synesthetes might underlie the conflicting patterns of results with, perhaps, so-called projector synesthetes (whose synesthetic colors are seen projected into space) being more likely than associators (whose colors appear in the mind's eye) to enjoy enhanced visual search owing to the vividness and external localization of their color experiences.[2] From this Rothen and Meier conclude that the diverse nature of synesthesia can be more appropriately understood from results of group studies, not single-case reports. To this we would add the recommendation that studies using visual search employ a full array of conditions that include mixtures of synesthetic and real colors in which the synesthetic colors are congruent with or incongruent with the real colors—with this array of conditions, investigators have the opportunity to look for performance improvement and performance impairment within the same set of trials. At the same time, it is also important to be mindful of the overall angular size of the array of target and distractors as well as the angular subtense of those individual items. Acuity falls off with eccentricity, and the loss of spatial resolution for alphanumeric characters located off fixation is bound to adversely affect their clarity. We cannot expect a small alphanumeric character imaged away from fixation to induce a synesthetic color if its features are unresolvable—the character may be visible but indistinguishable and, therefore, ineffective as an inducer. This constraint does not apply, of course, to real colored graphemes unless it is imaged far enough into the periphery where color vision itself is reduced. It would be informative to see results from a visual search task in which letters are rendered equally readable based on their sizes and retinal eccentricity (Anstis 1974), but this would require careful fixation and, hence, eye movement monitoring.

Another strategy for exploring whether color-graphemic synesthesia enhances performance capitalizes on visual crowding, the impairment in identification of a peripherally viewed target stimulus when that target is surrounded by flanking stimuli

---

[2] Using diffusion tensor imaging, Rouw and Scholte (2007) found stronger connectivity in projectors relative to associators within brain areas in close proximity to color areas and a region believed to be involved in visual word processing. For more on the distinction between projectors and associators, see van Leeuwen (Chapter 13, this volume).

(Bouma 1970). When flankers and target differ in color, this crowding effect is weakened, i.e., target identification performance improves (Kooi et al. 1994). Hubbard et al. (2005) created crowding displays in which target and flankers were achromatic letters specially selected such that the associated synesthetic color of the target differed from that of its surrounding flankers. Three out of six color-graphemic synesthetes were more accurate than control observers when tested using these achromatic crowding displays; coincidentally or not, these three synesthetic participants also performed significantly better than controls on the embedded figures task described in the next paragraph. Hubbard et al. (2005) did not test the synesthetes on a condition where the associated synesthetic color of the target and crowding flankers was identical, an even more revealing comparison. They did note, however, that the improvement in performance associated with synesthetic color was still significantly weaker than the improvement produced by actual color differences.

While not explicitly assessing performance enhancement, some perceptual tasks ask whether color associations enable people with synesthesia to perceptually organize a visual display differently than do individuals without synesthesia and, thereby, react to that display in a qualitatively different way. To give an example, Ramachandran and Azoulai (2006) created an apparent motion (AM) display that would produce motion in a given direction only if synesthetic color contributed to solution of the "motion correspondence" problem. To understand this, let us consider the task used by Ramachandran and Azoulai, who created an AM animation of four frames. Each frame comprised achromatic numerals whose locations were spatially jittered from frame to frame. In addition, a small cluster of the numerals within each frame differed from the "background" numerals and formed a virtual shape (e.g., a vertical bar); this shape fell at neighboring locations in the successive frames of the animation. When a similar task is performed with real colors, the perceived experience is that of a bar moving laterally. In this version, people without color-graphemic synesthesia experienced no sense of coherent motion when viewing the AM display and, instead, saw individual letters jittering around idiosyncratically. The synesthetic individual tested by Ramachandran and Azoulai, however, did spontaneously report seeing a bar moving laterally, with its direction of motion perfectly correlated with the direction of the shift in the positions of the characters. These subjective reports were substantiated in a four-choice categorization task: observers were required to indicate the direction of motion—up, down, left, or right—where on each trial the correct answer was defined by the correspondence between the successive positions of the cluster of numerals forming the virtual bar. Control participants performed at chance level[3] but the synesthete performed the task without mistakes. It would have been good if Ramachandran and Azoulai had also tested their synesthetic observer using achromatic digits all of which have the same color association, to show that this benefit disappears under that condition. Still, this kind of display, together with an appropriately designed forced-choice task, offers a compelling way to test for the

---

[3]   Without color, the strong local motion signals produced by the positional jitter overwhelm motion associated with spatio-temporal displacement of the form-defined bar.

involvement of color in synesthesia: individuals with synesthesia who genuinely experience colors when viewing the digits comprising the AM animation should—and apparently do—benefit from a potent AM cue (Papathomas, Gorea, and Julesz 1991) that is unavailable to individuals without synesthesia. In this respect, the display created by Ramachandran and Azoulai in which there is, potentially, an objectively correct answer is superior to displays that use inherently ambiguous AM sequences to ask whether synesthetic color can induce judgment biases in perceived direction of motion (Kim, Blake, and Palmeri 2006)—the Ramachandran and Azoulai display is less susceptible to effects of response bias.

There are other examples of tasks where color influences spatial grouping, including perception of form based on figural grouping (e.g., Gorea and Papathomas 1993) and figural coherence in binocular rivalry (Kim and Blake 2007; Papathomas, Kovács, and Conway 2005). Guided by those findings, investigators have created synesthetic versions of displays used in these tasks to learn whether colors associated with letters and numbers behave comparably to real colors. The answer to that question appears to be "yes" both in the case of a figural grouping task (Hubbard, Manohar, and Ramachandran 2006; Hubbard et al. 2005) and global coherence on a binocular rivalry tracking task (Kim, Blake, and Palmeri 2006).[4] In both instances, however, synesthetic colors produced significantly weaker grouping than did real colors and, in the case of Hubbard et al. (2006) grouping based on synesthesia disappeared at low contrast levels of the inducers.

Finally, we should mention that another version of the enhancement strategy is simply to ask whether people with a given form of synesthesia perform better than non-synesthetic observers on conventional tasks that measure sensory acuity for the modality in which synesthesia is experienced. Do color-graphemic synesthetes, for example, exhibit better color vision than non-synesthetes or synesthetes whose experiences are confined to another modality? While not a widely employed strategy, those studies that have asked the question report an affirmative answer: individuals in whom color is a concurrent synesthetic experience tend to perform better on conventional tests of color discrimination (Yaro and Ward 2007) and individuals for whom touch is a concurrent experience tend to have better tactile acuity (Banissy, Walsh, and Ward 2009). This enhanced discrimination could result from more refined category boundaries within a given stimulus dimension owing to the enriched experiences that come with synesthesia or, alternatively, to inherent differences in brain connectivity between synesthetes and non-synesthetes and, for that matter, between different categories of synesthetes.

Performance impairment

Turning now to the opposite side of the coin, one can imagine tasks where synesthetic colors, if genuinely perceptual in nature, should impair performance under appropriate

---

[4] Paffen and colleagues have also found that the likelihood of binocular rivalry is increased when the two eyes receive inducers that generate different synesthetic colors (Paffen, van der Smagt, and Nijboer 2011).
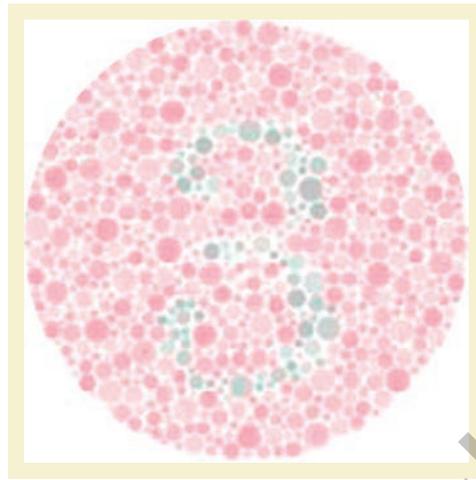
FIGURE 15.1 This stimulus, a variant of the classic Ishihara test plate, presents a numeral embedded within a background of texture elements whose colors ("pinkish") match the synesthetic color experienced by WO. When tested with this and other comparably designed test plates, he very quickly and accurately names the test figure even when, according to his self-report, the background perfectly matches his experience of the numeral's synesthetic color.

conditions. Is it possible, for example, to camouflage an ordinarily visible grapheme by embedding it in comparably shaped texture elements whose colors are matched to that induced by the grapheme? Using specially constructed test plates like the one shown in Figure 15.1 we tried but failed to render inducers invisible to color-graphemic synesthetes, even though our observers verified that the color matches were accurate. This negative result, however, may simply mean that synesthetes must first be aware of the identity of an inducer before that inducer can inherit its characteristic color (e.g., Rich and Mattingley 2005).

Using a variant of this masking strategy, Smilek et al. (2001) measured digit identification accuracy by briefly flashing a black digit against a uniformly colored background, with the background color either being congruent or incongruent with the synesthetic color of the digit experienced by their single synesthetic subject. This individual made significantly more errors on congruent versus incongruent trials; non-synesthetic control participants did not have significantly different error rates for the two categories of trials. Stronger interference on congruent trials was also observed on a second task that used reaction time (RT) in a visual search paradigm. On the other hand, Sagiv et al. (2006) found the opposite pattern of results in the single synesthete that they tested, i.e., RTs were actually faster on trials where the target's associated color was congruent with the background color. Adding to the confusion, Cohen Kadosh et al. (2009) reported that interference on congruent trials could be induced temporarily in non-synesthetic participants through the use of hypnotic suggestion associating particular colors and

digits. So while the logic underlying this particular interference task seems straightforward, the results certainly are not.

One well-known interference effect observed in color-graphemic synesthesia is the so-called synesthetic Stroop effect, wherein words are printed in colors either congruent or incongruent with a synesthete's associated colors for those words. It is repeatedly found that color naming is slower and more error-prone for the words portrayed in an incongruent color (e.g., Dixon et al. 2000; Myles et al. 2003).[5] Several groups have argued that this synesthetic Stroop effect could, in fact, stem from semantic interference and not the perceptual experience of color (e.g., Palmeri et al. 2002). An account based exclusively on semantic confusion, however, is difficult to reconcile with the findings of Nikolić, Lichti, and Singer(2007) that synesthetically induced Stroop interference is greatest when the real and synesthetic colors presented on a given trial constitute opponent pairs (e.g., red/green) rather than non-opponent pairs (e.g., blue/red). In a control experiment, these authors demonstrated that this effect of opponency was not related to color naming per se, as evidenced by results on a shape/color version of the Stroop task (yellow lemon versus red lemon). Nikolić and colleagues believe their results point to the involvement of color opponent mechanisms in the synesthetic Stroop task.

At this stage, the jury is still out on the verdict of whether the color associations implicated in the Stroop effect are genuinely perceptual. Still, it is safe to conclude that the Stroop effect can confirm whether someone purporting to experience colors when viewing achromatic characters is indeed a color-graphemic synesthete—a genuine synesthete should exhibit the synesthetic Stroop effect. The converse, however, is not necessarily true: with extensive practice associating specific colors and alphanumeric characters, someone who does not experience synesthesia can still exhibit a synesthetic Stroop effect (Elias et al. 2003). The Stroop task, incidentally, has the virtue of not requiring performance comparison between groups (synesthetic versus non-synesthetic), because response times are compared within an individual for congruent and incongruent test stimuli. It is also possible to use the pupillary reflex to assess the synesthetic Stroop effect, capitalizing on the fact that the appearance of an unexpected or incongruent stimulus can evoke a brief, measurable increase in pupil size (Paulsen and Laeng 2006).

Another interference strategy was developed by Gheri et al. (2008) capitalizing on the observation that identification of a unique item among an array of distractors is slowed when the item and distractors are drawn in different, random colors. Gheri et al. reasoned that color-graphemic synesthetes should be impaired on such a task when the array items were actually randomly colored and, if synesthetic colors are perceptual, also when the items were achromatic and generated different synesthetic experiences. Non-synesthetes, of course, would exhibit impairment only on the real color condition. Evidently this task was quite difficult because the search times averaged almost 6 seconds, unusually slow times for a task where one must find the unique numeral among

---

[5] See Beeli, Esslen, and Jä ncke (2005) for a clever adaptation of the Stroop task to a case of tone-evoked taste sensations.

an array of 16 numerals. In any event, synesthetes performed no worse than non-syn-esthetes on both versions of the task, leading Gheri et al. to conclude that synesthetic colors are not perceptual, at least in the individuals they tested. Note, however, that the logic underlying their interference condition predicts that synesthetes' responses should be slower than those made by control participants if synesthetic color has a perceptual component; as noted earlier, search times were quite slow for all observers, raising the possibility of ceiling effects. Would the same pattern of results be found if the number of distractors was varied or if a dependent variable other than reaction time were used (e.g., accuracy with brief presentation)? Moreover, the individuals tested by Gheri et al. were characterized as colored hearing synesthetes, not color-graphemic synesthetes, in an earlier study in which they participated (Nunn et al. 2002). It is true that Gheri and colleagues confirmed that these individuals exhibited stable associations between colors and achromatic numerals, but the authors did not specify whether these individuals "saw" the numerals in color or, instead, associated a given color when thinking about a given numeral. The participants studied by Gheri and colleagues thus may not have possessed the type of synesthesia that influences color appearance target and distractor items defining visual search arrays.[6]

Contextual effects

The vision literature is replete with examples of stimulus conditions where one's percep-tual experience of color depends on the context—spatial and temporal—in which the colored stimulus appears, and among these are conditions that produce vivid illusions in perceived color. These contextual phenomena offer a potentially revealing window onto the determinants of color-graphemic synesthesia, in part because we can make educated guesses about the neural mechanisms underlying at least some of those phe-nomena. The following paragraphs describe several examples where such phenomena have been employed in studies of color-graphemic synesthesia.

To start, consider chromatic adaptation wherein exposure to a given color alters the color appearance of a subsequently viewed patch of color. To give an example, exposure to a patch of green light causes subsequently viewed yellow light to appear slightly red-dish, and to eliminate that reddish appearance requires adding a given amount of green light to the mixture to restore it to equilibrium yellow. This technique, called hue cancel-lation, provides a precise quantitative measure of the magnitude of chromatic adapta-tion (Hurvich and Jameson 1957). The neural concomitants of these short-lasting shifts in color appearance are generally thought to arise very early within the visual path-ways, probably from gain changes in the cone receptors and in the opponent process

---

[6] As mentioned in an earlier section, Gheri et al. also measured search speed under a condition where synesthetic color should have facilitated performance, but they found no facilitation relative to performance by non-synesthetic controls. Again, the question of type of synesthesia may be pertinent here as well.

mechanism they innervate (Hurvich and Jameson 1957; Jameson and Hurvich 1972). What happens when the real colored adaptation field is replaced with a dense array of graphemes all of which have the same color association (Figure 15.2)? Does adaptation to this field of synesthetic color produce a temporary shift in the ratio of red to green necessary to achieve equilibrium yellow? Hong and Blake (2008) found that it did *not*, even though same dense array of graphemes did produce robust adaptation when those graphemes were presented in real colors. Moreover, it did not matter whether those real colors were congruent or not with the synesthetic color of the graphemes. In a related set of measurements, Hong and Blake found that the red/green ratio yielding equilibrium yellow did not shift when the nulling target itself was a grapheme whose associated
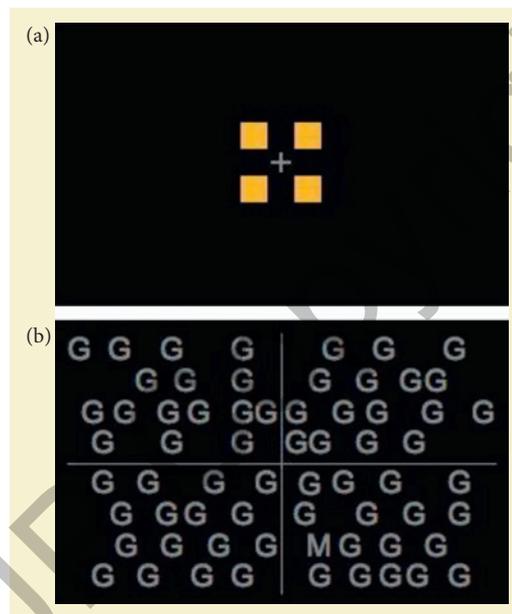

FIGURE 15.2 Displays used to induce and measure color adaptation using a nulling technique. (a) The test display comprised four small squares each composed of red and green light, and the observer could adjust the amount of green light necessary to make the mixture appear neither red nor green: equilibrium yellow. (b) The adaptation display consisted of 16 gray letters, 15 being distractors and one being the target; all 16 letters had the same associated synesthetic color for a given observer ("red"). During the 5-minute adaptation period, the observer maintained fixation on the central cross and reported for each display the quadrant containing the "target" letter; this response triggered presentation of another 16-character display with the target and distractors rearranged. Even though the adapting field appeared "red" to the observers, their equilibrium yellow settings were unaffected by the prolonged period of exposure to this adaptation display. Adaptation to real colored versions of these arrays produced a robust shift in equilibrium yellow. Reprinted from *Vision Research*, 48 (8), Hong, Sang Wook, and Randolph Blake, Early visual mechanisms do not contribute to synesthetic color experience, pp. 1018–1026, Copyright (2008), with permission from Elsevier.

color was either green or was red, implying that the synesthetic color did not enter into the equation when making these judgments. Evidently, then, color experiences associated with synesthesia have no impact on color judgments dependent on neural processes believed to arise within peripheral stages of the visual pathway. On the other hand, results from a related strategy that isolates cortical color adaptation reveals that color associated with graphemes can impact color/form adaptation, and it is to that strategy that we turn next.

The upper panel in Figure 15.3 shows the configuration used to induce (green and red bars) and observe (black/white bars) the well-known McCollough effect (McCollough 1965), a form of adaptation characterized by the long-lasting experience of desaturated, illusory color the hue of which depends on the orientation of the contours of the test pattern. In the original version of this test, participants inspect alternately the red horizontal and green vertical gratings; after a few minutes they switch to the black-and-white gratings, which now look greenish on the horizontal sections and pinkish on the vertical sections. This orientation-contingent color aftereffect provides a nifty means for testing the perceptual reality of synesthetic colors without tipping off participants about the expected outcome. The lower panel shows a synesthetic version of the induction and test stimuli for the McCollough effect (Blake et al. 2005). Here the oriented contours of the induction pattern are formed from closely spaced, achromatic letters that can be
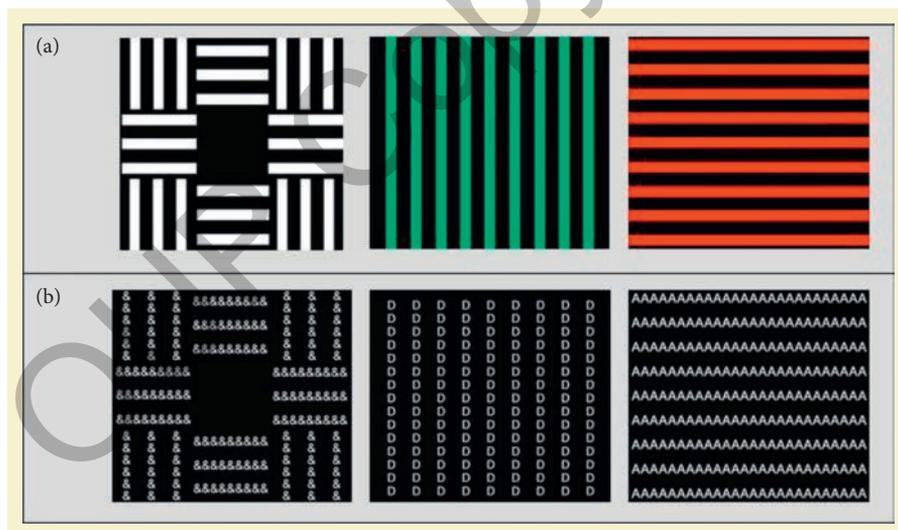

FIGURE 15.3 (a) The configuration used to induce and observe the conventional McCollough effect. After being adapted to the green/black vertical (middle) and red/black horizontal gratings (right-hand side), observers report faint pink on the horizontal, faint green on the vertical part of the white/black test pattern (left-hand side). (b) A synesthetic version of the induction and test stimuli for the McCollough effect. For LR, who "sees" green on the letter D and red on the letter A, those stimuli shown in the middle and on the right-hand side serve as adapting stimuli. The test pattern was made with "&" which doesn't induce any synesthetic color for LR.

appropriately selected for their associated colors (e.g., A = red and D = green); the test pattern comprises closely spaced characters that have no color association. Following prolonged inspection of the inducing "gratings" does the synesthetic observer experience faint pink and green colors on the appropriate parts of the test figure? For LR, a participant in our studies, the answer is "yes"—not only did she spontaneously report the appropriate hues without prompting, she also experienced this adaptation aftereffect only when the inducing patterns and test pattern were presented to the same eye, matching the absence of interocular transfer seen with the conventional McCollough effect. And like the conventional McCollough effect, her synesthetic version was restricted to the region of the visual field where the adapting stimuli were imaged, and the effect lasted several days. Unfortunately, the McCollough effect remains a conundrum in vision science: its boundary conditions have been studied in some detail, but there is still no uniformly accepted explanation for why it occurs or what brain regions might give rise to it. Still, we recommend this test as a foolproof means for assessing the nature of the color experiences of color-graphemic synesthetes, for expected responses are not obvious and the stimulus selectivity for eye and visual field are additional signatures of the reality of the effect. Moreover, it is possible to measure this aftereffect without relying on verbal descriptions, using a nulling technique modeled after the one developed by Vul and colleagues (Vul and MacLeod 2006; Vul, Krizay, and MacLeod 2008).

Another illusion that has been used to study color synesthesia is lightness constancy wherein the perceived variations in surface illumination influence the perceived lightness of objects located in that scene. A compelling example of this illusion is the checker-shadow display devised by Adelson (2000) and reproduced with permission in Figure 15.4. Witthoft and Winawer (2006) used this and related displays in conjunction with a color/brightness matching procedure to learn whether colors associated
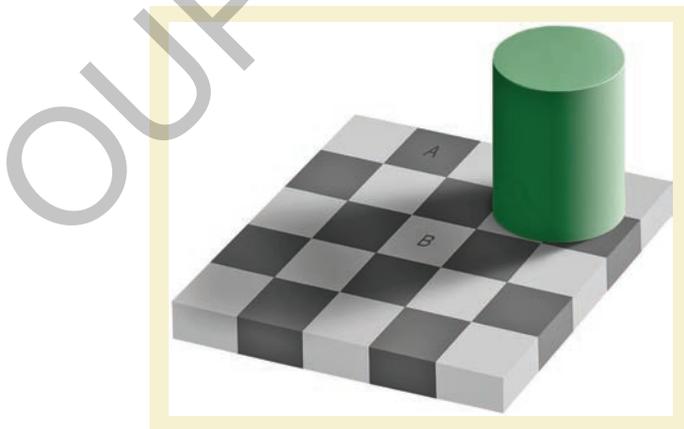

FIGURE 15.4 The squares marked A and B look very different in lightness but are indeed the same shade of gray. Withoft and Winawer (2006) asked a synesthete whether the induced synesthetic color was influenced by the brightness setting by presenting an inducing letter on the squares A and B. ©1995, Edward H. Adelson.

with synesthesia were susceptible to the illusion. Testing one color-graphemic synesthete categorized as a projector, they found that this person's color/brightness settings depended on whether the character appeared directly illuminated (e.g., the letter A in Figure 15.4) or appeared to fall within an apparent shadow (e.g., the letter B in Figure 15.4). This influence was not as great, however, as when the letters were actually colored, leading Witthoft and Winawer to conclude that, "it is likely that the synesthetic color is not available to some of the earliest constancy mechanisms" (182). That conclusion could explain why Hong and Blake (2008) failed to find evidence for synesthetically mediated brightness induction using a much simpler stimulus configuration devoid of three-dimensional cues that imply illumination and shading, a configuration more likely to engage very low-level constancy mechanisms only. And in a variant of this lightness constancy task, Nijboer and colleagues (Nijboer, Satris, and van der Stigchel 2011) asked whether the color appearance associated with a given grapheme was susceptible to the real color of the background against which that grapheme appeared, i.e., whether simultaneous color contrast could be induced in a synesthetic color. They attempted to answer this question by having observers adjust the color of an achromatic grapheme that appeared against a background matched to the grapheme's color and to one that was opposite in color to the grapheme's color; for purposes of comparison, non-synesthetic individuals performed identical matches in which the grapheme was actually colored to match the associated color of a given synesthete. Results from these measurements gave an affirmative answer to this question (i.e., matched color depended on the background color) but, oddly, the shift in perceived color of the grapheme was in the opposite direction to that experienced by the control observers viewing real colored graphemes placed on colored backgrounds. Nijboer and colleagues speculated that high-level visual memory associated with synesthesia might have something to do with this counter-intuitive result. This conundrum needs to be sorted out before we can place faith in simultaneous color contrast as a useful strategy for assessing the perceptual reality of synesthetic color.

We end this section with another color illusion produced by spatial context, this one being color assimilation wherein an achromatic region of a surface appears colored because that region is bounded by a real colored border (Broerse, Vladusich, and O'Shea 1999; Pinna 2005). Nowadays called the watercolor illusion, this spread of illusory color is compelling, surprising and puzzling to naïve observers (and, for that matter, to some seasoned vision scientists). To experience the illusion for yourself, compare the interiors of the two figures shown in Figure 15.5a. As you will see, the interior region of the left-hand figure looks faintly yellow/gold and in the right-hand figure the interior looks white with a faint tint of purple. In fact, the two interior regions are identical, and it's the color of the inner border defining the figure that induces the illusory, spreading color. Shown in Figure 15.5b are two figures where the borders that ordinarily promote color induction are replaced by two adjacent rings of achromatic letters, with the letters forming a given ring all having a given color association. When first shown achromatic configurations like that illustrated in Figure 15.5b,
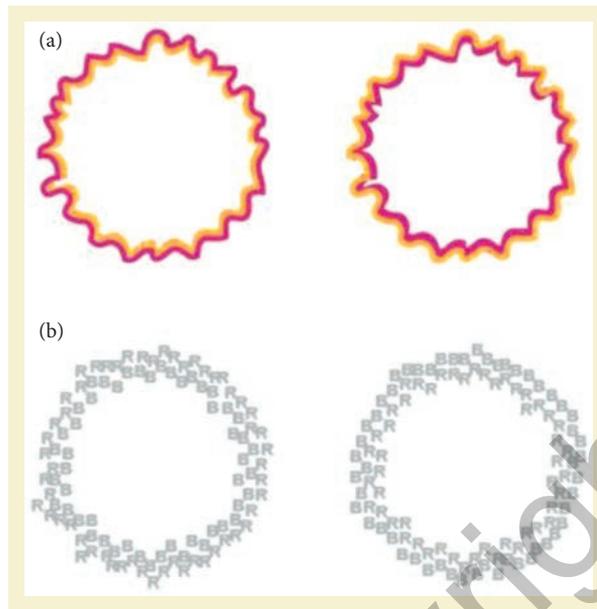
FIGURE 15.5 (a) The watercolor effect. When an orange contour is surrounded by a purple contour, the enclosed area looks yellowish (left-hand side). When a purple contour is surrounded by an orange contour, however, this illusory color spreading is not experienced (right-hand side). (b) An example display for a synesthetic version of the watercolor test. For a synesthete LR, the letter "B" appears orange and the letter "R" appears purple. LR sees the watercolor illusion induced within the left-hand circle but not within the right-hand circle. Reproduced from *Perception* 34(12), Watercolor illusion induced by synesthetic color, Kim, Chai-Youn, and Randolph Blake, pp. 1501–1507 © 2005, Pion, with permission Pion Ltd, London: www.pion.co.uk and www.envplan.com.

the projector synesthetes in our lab spontaneously described the interior regions as faintly colored, and their reports varied depending on the inducing characters forming the interior border (Kim and Blake 2005). It is noteworthy that these individuals had not seen real color versions of this display ever before, and they were puzzled by what they saw. When next shown real color versions of the displays, they described the same illusion with the interior color being less washed out than in the synesthetic version. These verbal reports were supplemented by an indirect task that capitalized on the propensity of illusory colored surfaces to stand out when presented among other forms that do not induce color spreading. Observers were required to indicate the location of an oddball target among four equally sized shapes whose borders were defined by characters that, for the synesthetes, had color associations. The task did not require judging color, only the one shape whose letter configuration differed from the other three. However, color spreading associated with the oddball shape on some trials tended to draw attention it and, thus, speed performance on the task. Again, this speeding was also found for synesthetes, but not for age-matched control observers,

using displays where the achromatic characters defining the oddball target had a different associated color than the achromatic characters defining the interior of the other three shapes. The synesthetes, in other words, were faster than normal observers spotting an oddball target whose interior region was described as different from the interiors of the other three shapes.

Precision of color matching

We close this section on behavioral strategies by describing a task that to date has not been utilized in published work on color-graphemic synesthesia but that would seem to have promise as a means for quantitatively assessing the preciseness of the color associations experienced in this condition. Specifically, we can ask whether the synesthetic colors associated with different inducers can be reproduced with the precision known to be achieved when people with normal color vision perform a color discrimination task. In one version of this kind of task, a person is given control of the hue, saturation, and brightness of a test patch displayed on a video monitor and is instructed to adjust those settings until the test patch appears identical to a comparison stimulus also displayed on the monitor. People are remarkably accurate (as evidenced by the near-equivalence of test and comparison values) and reliable (as evidenced by the variance among repeated test settings). Indeed, performance of this task appears to be limited primarily by an individual's wavelength discrimination ability, which is known to be quite good except at extremes of the wavelength spectrum (Wright and Pitt 1934).

Now suppose we ask a color-graphemic synesthete to use this matching procedure to reproduce the colors evoked by different achromatic inducers (i.e., letters or numbers). We would not be able to score the accuracy of those matches, of course, because we would have no objectively "correct" color against which to score the accuracy of the settings. But we could derive the variance from repeated color matches, and we could compare those variance estimates with the variance associated with matches using real colors. We have implemented this procedure in synesthete LR in our laboratory, and find that her synesthetic color matches are highly reliable with repeated measurement. An example of this consistency can be seen in Figure 15.6a, which shows, in CIE color space, color matches produced on three different occasions when tested using the alphabetic characters A, B, C, D, E, and F. For purposes of comparison, we also asked LR to produce color matches for five different real colors portrayed by a symbol with the same average contour length as the alphabetic letters we used to assess her synesthetic colors (the symbol had no synesthetic association whatsoever for LR). Those results are summarized in Figure 15.6b. Comparison of the two sets of results—synesthetic and real color matches—reveals remarkable consistency over time with the between-session variability of synesthetic settings rivaling the within-session variability for real color matches. If her judgments were based on categorical labeling, this level of matching consistency would be unimaginable (Chapanis and Overbey
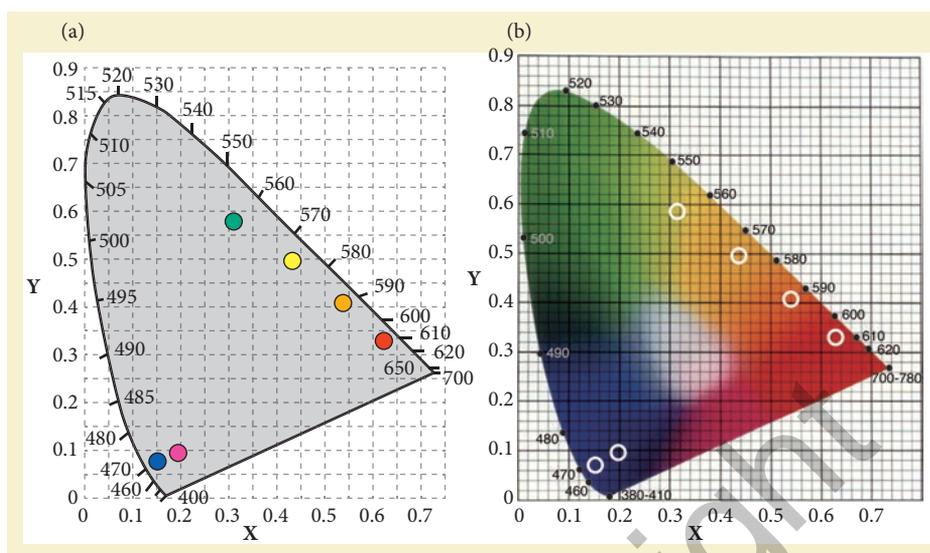
FIGURE 15.6 (a) Synesthetic color matching results from a synesthete LR for achromatic alphabetic characters A, B, C, D, E, and F. (b) Real color matching results from the same synesthete for non-inducing symbols in physical colors consistent with her reported synesthetic colors for A, B, C, D, E, and F. Note the remarkable similarity between the synesthetic and real color matching results. Each data point is the average of four settings obtained on each of three weekly test sessions; the error bars cannot be plotted because they are smaller than the plotting symbols. We are very grateful to Sang-Wook Hong for writing the MatLab code to implement this test and supervising the testing.

1971). Instead, her performance implies fine-grained color resolution for these synesthetic colors.[7]

So, measuring the reliability of color matches is one strategy for testing the claim that synesthetic colors are genuinely perceptual in character. In fact, however, no studies to date have gone the trouble of assessing reliability using refined color matching tasks like the one exemplified in the data of Figure 15.6; instead, most rely on categorical, subjective reports. There are several standardized, web-based tests that provide reasonable estimates of reliability (Asher et al. 2006; Eagleman et al. 2007), but neither of these

---

[7] A key concept in colorimetry, the science of quantifying and physically describing human color vision, is metamerism: two color samples differing in spectral power distributions that appear to be identical constitute a metameric match. Are we to conclude that a synesthetic color and its matched, real color counterpart are metameric? It is certainly true that, following careful color adjustments, the person achieves a setting where the colors are deemed to be equivalent and, yet, the stimuli differ in their spectral content. There is, however, a fundamental difference between synesthetic color matches and the metameric matches measured in colorimetry: people cannot tell the difference between true metameric matches (e.g., pure "yellow" light cannot be distinguished from the "yellow" produced by an appropriate mixture of red and green lights), but a synesthete never confuses a synesthetically colored inducer and a real colored character that matches the synesthetic color.

achieves the degree of accuracy afforded by a genuine color matching task of the sort described earlier. And none of these tests, including color matching, captures the surface appearance accompanying color experiences such as luster, sheen, or matte appearance described by some synesthetes (Eagleman and Goodale 2009).

Compelling evidence for high reliability still does not constitute unequivocal evidence for the perceptual reality of synesthetic colors. One could reasonably argue that the appropriate benchmark for gauging the basis of the reproducibility of synesthetic colors should be repeated matches from memory made by non-synesthetic individuals who have spent years associating particular colors with particular letters. This benchmark is all the more relevant when we take into account the tendency for synesthetes to exhibit superior performance on standardized tests of memory (e.g., Cytowic 1997).[8] Unfortunately it will be very difficult to identify people whose color associations have the richness and long history of associations reported by synesthetes, whose color experiences typically date back to early childhood. Nor have we been able to find non-synesthetic volunteers willing to spend the time embedding these associations in their memory. Unless that hurdle is cleared, the reliability of synesthetic color matches must remain suggestive but not definitive with respect to the perceptual nature of the condition.

Interim Conclusions

As the previous sections document, there are strategies for going beyond simple phenomenological reports to learn whether color associations reported by color-graphemic synesthetes behave as if they have a genuine perceptual component. Moreover, versions of some of these strategies can minimize the potential, contaminating influence of bias resulting from expectations on the part of the participant(s), owing to the technique itself (e.g., genuine forced-choice testing) or to the counterintuitive nature of the phenomenon being employed (e.g., the McCollough effect). Some strategies depend on comparison of test performance of synesthetes to non-synesthetic control participants, and in those instances it is important to ensure that non-synesthetic individuals forming the comparison group are equally motivated, equally attentive, and as well trained on the task as the synesthetes, for otherwise group differences cannot be interpreted definitively. It is also desirable to utilize tasks where it is possible to test synesthetes under conditions where their color associations could plausibly improve their performance and conditions where their color associations could interfere with performance.

---

[8] Synesthetes report that their novel sensory experiences enhance their memory abilities, but in reality the causal arrow could point in the opposite direction.

Indirect Measures

To circumvent potential problems inherent in behavioral measures (e.g., response bias), one can turn to indirect measures of physiological responses that accompany synesthesia. Here the general strategy is to ask whether those measurements are equivalent to physiological responses measured in response to real stimulation (e.g., color) that mimics the induced experiences (color-graphemic synesthesia). In the following sections, we consider several physiological responses that have been used to address this question; these include: (1) saccades and pupil reflex, (2) hemodynamic responses measured using magnetic resonance imaging (MRI), and (3) event-related brain potentials measured using scalp electrodes.[9]

Our purpose is not to review the extensive set of studies utilizing those kinds of indirect measures but, rather, to show specifically how those indirect measures are used to examine the perceptual reality of synesthetic experience. This is a narrower question than asking about the neural bases of synesthesia (Bargary and Mitchell 2008; Grossenbacher and Lovelace, 2001).[10]

Oculomotor responses

When it comes to presentation of real colored stimuli, the eyes themselves exhibit telltale signs of reactions to color. So, for example, saccadic eye movements are affected by the variety of colors among potential eye movement targets (Ludwig and Gilchrist 2003). Pupillary reflexes, too, can show sensitivity to stimulus color (Gamlin et al. 1998). There are a couple of studies that have asked whether synesthetic colors evoke comparable oculomotor responses.[11]

---

[9] These measures can produce suggestive correlations between synesthesia and neural activity, but not the causal relationship. One technique that potentially can point to causality is Transcranial Magnetic Stimulation (TMS), a non-invasive means for producing neural activity using magnetic induction to induce weak currents into targeted regions of the brain (Hallett 2000). However, TMS can hardly be used in the study bearing on the question of the perceptual reality of synesthetic color, since it cannot be applied selectively to the color-related brain regions along the ventral visual processing stream (e.g., hV4, V8). Thus existing studies of the effect of TMS on synesthesia have targeted posterior parietal areas in an attempt to learn whether those areas are involved in color-shape binding (Eastermann et al. 2006; Muggleton et al. 2007), which is not within the scope of the current chapter. One recent study targeted the primary visual cortex which can be accessed by TMS and found enhanced cortical excitability (threefold lower phosphene threshold in synesthetes than in non-synesthetes) In this study, another technique that can point to causality—transcranial direct current stimulation (TDCS)—was also exploited to demonstrate modulation of synesthetic experience (Terhune et al. 2011).

[10] For more on the neural theories of synesthesia, see Part V in this volume.

[11] For more detailed discussions on this topic, see Nijboer and Laeng (Chapter 17, this volume).

Using a visual saccade paradigm, Nijboer and van der Stigchel (2009) revised the paradigm of Ludwig and Gilchrist to ask whether similarity between real and synesthetic color can affect oculomotor responses during visual search. In their study, color-graphemic synesthetes were instructed to make eye-movements to a real colored target. When that target was accompanied by a single distractor whose physical hue was identical to that of the target, many erroneous eye movements were made towards the distractor. In contrast, presentation of a synesthetically colored distractor did not trigger erroneous eye movements; it, instead, behaved like an achromatic, non-inducing symbol. In a second study, however, Carriere and colleagues showed that the interaction between real and synesthetic color can indeed influence oculomotor responses during visual search (Carriere et al. 2009). These researchers exploited the well-established synesthetic color congruity effect and showed that synesthetes rapidly fixated and identified the congruently colored target letters, but showed difficulty in identifying incongruently colored letters.

These seemingly contradictory results may be due to methodological differences. In Nijboer and van der Stigchel's study, synesthetes had to hold their fixation very carefully on a central fixation point and were asked to make only one eye movement to the target, whereas in Carriere et al.'s study synesthetes visually explored the search array freely until they detect the target. In line with different viewing conditions, the two studies employed different independent variables: Nijboer and van der Stigchel focused on percentage of capture by the distractor whereas Carriere et al. used probability of target fixation within the first two saccades. Regardless of the methodological differences, do those two studies tell us anything definitive about the perceptual reality of synesthetic color? Both groups discussed their findings in relation to the role of attention in synesthetic color experience, an issue distinguishable from the question of the perceptual reality of synesthesia as mentioned earlier in this chapter. Nijboer and van der Stigchel showed that unattended inducing stimulus failed to induce synesthetic color, and Carriere et al. showed that attentional bias favoring the congruently colored inducing grapheme can modulate synesthetes' performance during visual search task. Of course, an alternative, more sceptical interpretation of Nijboer and van der Stigchel's finding is that synesthetic color is not perceptually equivalent to real color.

For the past 15 years or so, investigation into the neural mechanisms has been a centre of attention in the field of synesthesia research. Regarding the perceptual reality, the question becomes whether neural mechanisms engaged during genuine color perception are also engaged during synesthetic color experience. To answer this question, several different techniques with relative advantages and disadvantages have been utilized, and it is those techniques that we turn to in the next several sections.

Brain imaging using MRI

The most frequently used technique for studying neural responses associated with synesthetic experience is functional MRI (fMRI), and most of those fMRI studies—but not all

(see, e.g., Beauchamp and Ro 2008; Blakemore et al. 2005; Tang, Ward, and Butterworth 2008) have focused on color synesthesia induced by viewing graphemes or listening to sounds. The general strategy has been to compare areas of activation associated with color synesthesia with activations in cortical areas believed to be involved in genuine color perception.[12] There is general agreement that this complex of areas includes primary visual cortex (V1) and extrastriate areas comprising the ventral occipital cortex (Wandell and Winawer 2011), with additional, higher-level processing spilling into the inferotemporal cortex (Shapley and Hawken, 2011). Are these same areas active when a synesthete experiences color induced by achromatic inducers or by sound? As the next several paragraphs indicate, the answer to this question is not unequivocal.

In a study targeting primary visual cortex, Aleman and colleagues observed increased activation in V1 when their colored hearing synesthete listened to color-inducing words relative to activations measured when she listened to non-inducing tones (Aleman et al. 2001). From this result, however, we cannot be certain that the V1 activations were causally related to the experience of color. After all, synesthetes can experience vivid color imagery when an associated color is retrieved from memory, and it is quite likely that visual imagery is associated with activation in early visual brain regions (Kosslyn et al. 1999). So perhaps the activations in the synesthete studied by Aleman and colleagues were arising from the conceptual association between inducing stimulus and color. This hypothesis cannot explain, however, why a blind synesthete who does not show V1 activations during visual imagery does show V1 activations when listening to color inducing words but not when listening to frequency matched, non-inducing words (Steven, Hansen, and Blakemore 2006). Further complicating the story, a study of 13 auditory word-color synesthetes (described later) failed to find significant V1 activations but did find reliable activations in extrastriate areas (Nunn et al. 2002).

More frequently pinpointed in fMRI studies of synesthesia are color-responsive regions in the ventral extrastriate cortex including hV4 and V8. Some of those studies find selective activation of these areas when synesthetes experience color (Hubbard et al. 2005; Nunn et al. 2002; Rouw and Scholte 2007; Sperling et al. 2006; Weiss et al. 2001). Studies showing hV4/V8 involvement in synesthetic color experience vary in terms of the number of synesthetes tested (ranging from 1 (Weiss et al. 2001) to 18 (Rouw and Scholte, 2007)), the type of synesthesia (colored hearing or color-graphemic), and the way color-responsive areas are identified (whole brain analysis (Nunn et al. 2002), anatomically defined, or functionally defined (Hubbard et al. 2005)). However, they all conclude that at least some of the brain regions involved in genuine color perception are also associated with synesthetic color perception (see, e.g., Figure 15.7). To quote Nunn

---

[12] Neural events involved in genuine color vision, of course, are inaugurated in the retina and then conveyed to the lateral geniculate nucleus (LGN), so the cortex is certainly not the first stage of visual processing associated with color perception. It is highly unlikely, however, that retinal mechanisms are involved in generating color experiences during synesthesia (aside from signaling features of the inducer). Whether the LGN is involved has not yet been studied, although the ability to image this structure (e.g., O'Connor et al. 2002) makes such a study possible.
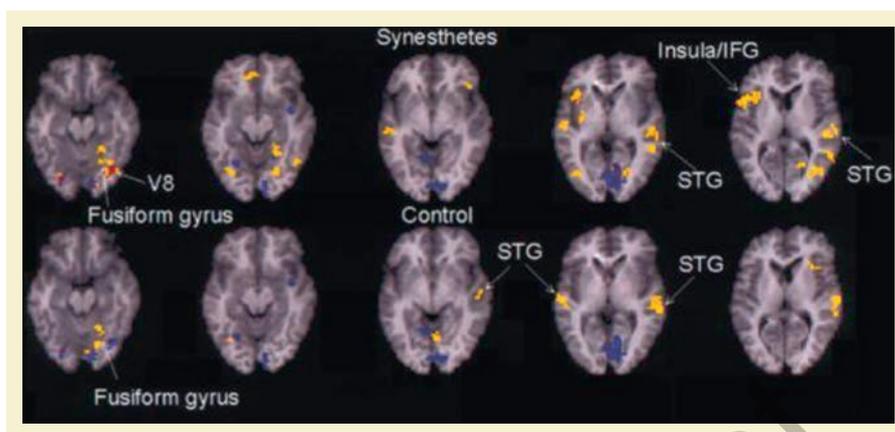
FIGURE 15.7 BOLD responses to real color stimuli and synesthesia inducing stimuli. Areas showing greater activation for synesthesia-inducing words than for non-inducing tones are presented in yellow. Areas showing greater activation for physically colored stimuli than for achromatic stimuli are presented in blue. For colored-hearing synesthetes, areas associated with induced synesthetic color (yellow) and real color (blue) showed intersection (red; *upper panel*). For non-synesthetes who don't experience any color when hearing words, however, such intersection was not observed (*lower panel*). Reprinted by permission from Macmillan Publishers Ltd: *Nature Neuroscience*, 5 (4), Nunn, J. A., L. J. Gregory, M. Brammer, S. C. R. Williams, D. M. Parslow, Michael J. Morgan, R. G. Morris, E. T. Bullmore, S. Baron-Cohen, and J. A. Gray, Functional magnetic resonance imaging of synesthesia: activation of V4/V8 by spoken words, pp. 371–375, copyright (2002).

et al. (2002), "differences between synesthetes and controls in activation of a color-selective region by spoken words, lend such phenomena an authenticity beyond reasonable doubt" (373). For that matter, there is also evidence for correlation between the blood oxygen level-dependent (BOLD) signal intensities in these color-selective visual areas and perceptual characteristics of synesthetic color experiences. Specifically, Hubbard et al. (2005) found a positive correlation between performance in synesthetic color tasks—spatial crowding and segregation of figure from background—and BOLD signal intensity in hV4. In other words, synesthetes whose color experience exerts a stronger influence on color-related visual tasks showed greater activation in hV4 when viewing color-inducing stimuli.

Complicating this tidy story however are a handful of studies that fail to find activations related to synesthesia in color-responsive areas in early visual cortex. For example, Weiss and colleagues tested color-graphemic synesthetes and found increased activation in the left intraparietal cortex associated with synesthesia, but not in the ventral visual processing areas (Weiss, Zilles, and Fink 2005). However, their results need to be interpreted with caution. Weiss and colleagues designed their fMRI experiments "to depict where in the human brain the hypothesized *binding* of alphanumeric form and synesthetic color occurs" (860). To do that, they manipulated both physical color

(presence or absence) and synesthetic color (induced or not-induced). Thus the lack of early visual area activation was based on the contrast between inducing stimuli with or without physical color and non-inducing stimuli with or without physical color. In all the studies successfully showing early visual area involvement in synesthetic color, only the contrast between inducing stimuli and non-inducing stimuli without physical color was considered.

But even if activations are observed in color-selective visual cortical areas of synesthetes experiencing color, this does not necessarily mean that the activated neurons are also those activated when those individuals view genuinely colored stimuli. For one thing, a voxel may contain anywhere from tens of thousands to more than a million neurons depending on the voxel's volume. Moreover, a typically localized color area includes multiple voxels. In the extreme case scenario, what if a subset of neurons within a color area subserves real color processing while another subset of neurons within the same area subserves synesthetic color processing, with little or no overlap between the subsets? To examine whether synesthetic and real color arise from activation of the same neurons, a technique called repetition suppression (aka repetition attenuation or fMR-adaptation) can be exploited: BOLD responses are generally reduced in amplitude following repeated presentation of the same stimulus (Grill-Spector, Henson, and Martin 2006). Using this technique, van Leeuwen and colleagues (van Leeuwen, Petersson, and Hagoort 2010) measured brain activations in carefully localized regions in the brains of color-graphemic synesthetes and matched control observers. In both groups of observers, as expected, two real colored targets presented one after the other produced weakened BOLD signals in color-responsive areas when and only when the two targets were the same color—this repetition suppression effect merely validates the technique. When the first target was an achromatic letter that induced a color identical to a second, real colored letter, repetition suppression was not observed in color-selective areas but was seen in the superior parietal lobule, an area uniquely activated using a synesthesia localizer. These authors concluded that, "synesthetic color experiences are mediated by higher-order visual pathways that lie beyond the scope of classical, ventral-occipital visual areas" (1). This potentially important conclusion would be stronger if the experiment had included conditions to rule out the possibility that activations in color-selective areas are generally weak for synesthetically induced colors. One such condition could involve presentation of two successive synesthetic colors, sometimes identical and sometimes different. Also in the critical condition of this study, the first letter of a pair was always an achromatic inducing grapheme, followed by a real color letter. Reversing the order of the two—real color followed by synesthetic color—might reveal the existence of a significant but weak repetition suppression effect.

Although not a repetition suppression study, Rich and colleagues (Rich et al. 2006) have also reported fMRI results that call into question the involvement of color-selective cortical areas in synesthesia. They compared brain regions activated during synesthetic color experience, during real color perception, during color imagery, and during color naming. From those comparisons, it appears that the brain regions involved in synesthetic color experience are adjacent to, but not identical with, the real color

responsive areas which, themselves, are associated with color imagery. Synesthetic color experiences were uniquely associated with activations in the lingual gyrus, an occipito-temporal region thought to be importantly involved in color naming. In general, the results of Rich et al. suggest that internally generated color experience in synesthesia is mediated by differential neural mechanisms than those involved in visual imagery of color.

In a recent study, Hupé and colleagues (Hupé, Bordier, and Dojat 2012) questioned the involvement of hV4 in synesthetic color experience. By contrasting brain responses to multicolored mondrians with those to achromatic mondrians, they localized color-sensitive brain regions including hV4. Next, they contrasted responses within those localized areas produced by synesthetic color-inducing graphemes and by pseudo fonts that did not induce synesthesia, and they failed to find significant differences between the two categories of stimuli. Hupé and colleagues reckoned that previous studies showing hV4 activation associated with synesthetic color managed to achieve statistical significance only by relaxing their statistical threshold. While not quarrelling with their statistical reasoning, we do question whether their design was optimal for maximizing BOLD responses associated with synesthetic color experiences. In Hupé and colleagues' study, mondrian stimuli were large (8× 6 degrees in visual angle) and multicolored, whereas the individual graphemes inducing synesthesia and the pseudo fonts were much smaller (approximately 1 degree), and only a single color experience was induced at a time during the stimulus sequence. It is possible, therefore, that the synesthesia-inducing stimuli were too weak to produce robust BOLD signal changes in the localized color area. In fact, one sees some hints of greater activation of hV4 in response to inducers compared to non-inducers, although this difference did not achieve their strict criterion for statistical significance. It is doubtful whether this negative result will overturn the current view that neural correlates of color-graphemic synesthesia include activity within visual cortex, but the study does raise important issues about statistical power and corrections for multiple comparisons.

Before leaving this section, we want to mention a study that uses MRI brain imaging to identify anatomical differences between synesthetes and normal controls and, intriguingly, among different synesthetic individuals.[13] Rouw and Scholte (2010) used voxel-based morphometry (VBM) to study the brains of 42 non-synesthetes and 42 synesthetes, some being projectors who see colors on object surfaces in the world and others being associators who see colors in the mind's eye. The investigators found increased gray matter volume at the posterior superior parietal cortex in synesthetes compared to non-synesthetes. Moreover, the projector-type synesthetes were different from non-synesthetes within gray matter volumes at the early visual processing streams including V1, whereas the associator-type synesthetes were different from non-synesthetes in

---

[13]   Several more studies utilizing structural brain imaging methods have showed differences between synesthetic brains from non-synesthetic brains, which suggest the neural bases of synesthesia (Hänggi, Wotruba, and Jäncke 2011; Jäncke et al. 2009; Weiss and Fink 2009). Readers interested in those questions will want to see Rouw, Chapter 25, in this volume.

gray-matter volume in the hippocampus, a brain region associated with memory. These findings, together with the results of Rouw and Scholte (2007) mentioned in footnote 2, provide an intriguing picture of the possible neural bases for these two types of synesthesia, with stronger connectivity between areas within early visual areas of individuals who see their colors localized on surfaces in the world. The extent to which synesthesia engages the same neural mechanisms as real color vision, in other words, may depend on the type of synesthesia.

Event-related potentials

The spatial resolution of modern fMRI makes it well suited for identifying brain areas involved in synesthesia, but the sluggishness of the BOLD signal means the technique is not so good for revealing the fine-grained temporal evolution of synesthetic experiences. But why would high temporal resolution matter when it comes to addressing the question of the perceptual reality of synesthesia? Because, in principle, neural signals arising within the first few hundred milliseconds following stimulus presentation are likely to reflect initial sensory/perceptual processing. For this reason, some investigations of synesthesia have turned to event-related potentials (ERPs), i.e., stimulus triggered, task dependent waveforms seen in the scalp-recorded electroencephalogram (EEG) signal reflecting neural activity measurable on the millisecond scale (Luck 2005). Woodman (2010) provides an excellent overview of ERPs, including the origins of the signal, the limitations in its measurement and the dissection of the various components of the ERP. For our purposes, it is useful to keep in mind that the early components of the ERP appearing within 200 ms of the onset of a stimulus are generally attributed to sensory/perceptual processing; later components, which can arise up to several seconds later, are attributed to deployment of attention, stimulus recognition and evaluation, reaction to unexpected or incongruent stimuli, and complex cognitive activity such as mental arithmetic and memory rehearsal. It is also worth noting that to obtain reliable ERP measurements of these components requires many trial repetitions and, then, signal averaging to pull out those components from the noise inherent in EEG recordings. With those aspects of ERP in mind, we turn to the handful of studies that have used ERP to evaluate the unfolding time course of neural responses associated with synesthesia.

To our knowledge, the first ERP study on synesthesia was performed by Schiltz and colleagues (Schiltz et al. 1999). They reported unusually large amplitude late components of the ERP (300–600 ms) in color-graphemic synesthetes following very brief presentation of an achromatic letter or number. These large signals were observed at electrode sites associated with frontal and central brain sites but not occipital sites, suggesting to the authors some form of inhibitory control possibly in response to the distracting quality of synesthetic color. These ERP measurements were obtained within the context of an oddball task based on memory for alphanumeric characters, so it is doubtful whether the results provide evidence for unique perceptual processing associated with synesthesia.

In a more elaborate study using ERP, Beeli et al. (2008) measured auditory evoked potentials in 16 colored-hearing synesthetes (which they defined for the purposes of their study as those who experience colors when hearing tones or spoken utterances) and 16 non-synesthetic control participants. Results revealed that the P1, N1, and P2 components, while clearly present in both groups, were longer in latency and smaller in amplitude in synesthetes relative to controls. Using a source localization technique, the researchers estimated the sources of these differences to be increased activation in the inferior temporal region including hV4 of the synesthetes. In fact, the N1 difference was measurable just 122 ms following onset of the auditory stimulus, implying to Beeli and colleagues that, "synesthetic perceptions are automatic and fast" (382). The involvement of early auditory-evoked components in synesthetic color experience was again reported in a subsequent study using a refined oddball paradigm (Goller, Otten, and Ward 2008).

It is noteworthy that the two ERP studies showing an association between synesthetic color experience and early ERP components tested individuals exhibiting "colored-hearing synesthesia," not color-graphemic synesthesia (or perhaps at least not color-graphemic synesthesia in isolation; see Simner 2007 for a discussion of how color-graphemic synesthetes are sometimes classified as "colored hearing" synesthetes). There might be methodological advantages to testing this type of synesthesia, because the inducer (sound) and the concurrent (color) are in different modalities and, therefore, are less likely to involve neural interference of the sort that could occur when an achromatic character evokes a concurrent experience of color (Hubbard 2007).

Later components of the ERP can reflect an influence of synesthesia, too. Brang et al. (2008) measured ERPs while synesthetes and control subjects read sentences (e.g., "Is the sky __?") ending in a color word (e.g., "blue"), a color patch (e.g., o) or a grapheme that evoked a color association for the synesthetes only; the colors of these sentence-ending stimuli were either congruent or incongruent with the first part of the sentence (e.g., in the sentence "Is the sky 2?" the digit would be contextually congruent for a synesthete if it induced "blue" but would be incongruent if it induced "brown"). ERPs were time-locked to the onset of the final item in the sentence. Besides finding an effect of synesthetic congruence on early, perception-related ERP components including N1 (in synesthetes, not controls), Brang et al. also found that the achromatic digits viewed by the synesthetes, but not controls, produced a significant reduction in the negativity of the N400 component that is known to be sensitive to contextual priming. From this pattern of results the authors concluded "the color-induction process in grapheme-color synesthesia is automatic and suggests that the concurrent color sensation is treated by the brain as a meaningful stimulus subject to con-textual integration processes" (Brang et al. 2008, 424). In a follow-up study by the same group of researchers, the modulation of N1 component observed when synesthetes viewed an achromatic inducing grapheme was extended to the condition where non-synesthetic controls viewed physically colored graphemes either congruent or incongruent with the semantic context in a sentence (Brang et al. 2011). Importantly, such modulation of N1 component was not found when non-synesthetes viewed a colored patch or colored words. These results point to

the similarity of synesthetes' experiences when viewing achromatic graphemes with non-synesthetes' experiences when viewing real-color graphemes, supporting the perceptual reality of synesthetic color experience.

Another tactic for studying synesthesia using ERPs is to assess whether signal components in synesthetes differ from those in non-synesthetes in response to basic sensory stimulation that itself does not evoke synesthetic experiences. So, for example, Barnett and colleagues (2008) used simple gratings and geometric forms tailored to bias ERP responses in favor of magnocellular pathway or parvocellular pathway activation. They found differences in early sensory-generated ERP components between linguistic-color synesthetes and normal controls, even though none of the visual stimuli evoked synesthetic experiences. The most pronounced difference was in a very early component arising less than 100 ms after onset of a high spatial frequency grating that, according to Barnett et al., activated parvocellular mechanisms only. The parvocellular pathway, of course, is the one associated with color vision. This represents an interesting, complimentary approach to the study of synesthesia, although the creation of stimuli that selectively isolate subpathways within a given modality can be tricky (e.g., Callaway 2005). Still, the approach reminds us of a suggestion discussed earlier in this chapter that people with a given form of synesthesia perform better than non-synesthetic observers on conventional tasks that measure sensory acuity for the modality in which synesthesia in experienced. This enhanced discrimination ability might result from inherent differences in brain connectivity between synesthetes and non-synesthetes (recall footnote 2).

Closing Comments

A paper we published several years ago (Kim, Blake, and Palmeri 2006) concluded, "Based on recent work in a number of laboratories it is now impossible to dispute that at least some forms of synesthesia entail mental experiences that have a genuine perceptual reality" (195). We acknowledge that this is a very strong claim, as others subsequently reminded us (Gheri et al. 2008), but we remain comfortable standing behind it. That said, the purpose of this chapter was not simply to weigh the evidence for—and against—this position but, instead, to identify and critique strategies deployed to test the claim. Hopefully readers are now convinced that some strategies for assessing the perceptual nature of synesthesia rest on firmer ground than do others: preferred strategies are ones that are relatively immune to response bias and expectations, and ideally ones that rest on foundational findings in perception science. We have also tried to emphasize that the question of the perceptual reality of synesthesia is distinct from the question of whether or not attention and/or awareness are essential to the phenomena. Research on synesthesia has matured considerably over the last dozen or so years, with less emphasis on case studies of one or two people and more emphasis on large subject samples that are constructed with possible subtypes of synesthesia in mind. Informal testing and clever demonstrations are giving way to more rigorous, subtle tests based on strategies that

disguise the purpose and expected outcomes of the tests from those being tested. There remains, however, one bias that will be difficult to overcome: positive results are more likely to be published than negative results, and this bias can unwittingly tip the balance of evidence in favor of the "perceptual reality" hypothesis. But this sword has two edges: many existing studies, especially in the field of brain imaging, are "statistically under-powered" to use Hubbard's phrase (Hubbard 2007). To overcome this, studies using fMRI should include independent functional localizers and, when dealing with vision, retinotopic mapping; these allow investigators to focus their analyses of BOLD signal to identified brain regions. But even when armed with valid strategies, experience teaches us that not all synesthetes yield the same pattern of results, even when tested in the same laboratory under identical conditions. Individual differences in the type of synesthesia could plausibly contribute to the seemingly contradictory results currently plaguing the literature (e.g., Smilek et al. 2001 versus Sagiv, Heer, and Robertson 2006) Case studies of single individuals have played a useful role in bringing this fascinating condition into the laboratory. Now it is time to tackle the subtleties of synesthesia using group studies that employ multiple tasks (e.g., Hubbard et al. 2005) that can potentially shed light on individual differences, their possible relation to the categories of synesthesia and, per-haps, to the genetic bases of the condition (e.g., Asher et al. 2009; Tomson et al. 2011).

Finally, we need to continue placing some stock in what people with synesthesia tell us they are experiencing. A grapheme-color synesthete who describes seeing the letter A as A—and who can repeatedly match that color with high reliability—is in a unique position to know what she's experiencing and to know what it's like to have a comparable experi-ence when viewing a real-colored letter. We are not recanting our introductory comment about the limitations of verbal reports, for it is indeed imperative to buttress those claims with carefully designed tests of performance that are sensitive to the concurrent report-edly experienced by the person. But it would be near-sighted indeed to limit our imagina-tion of what might be possible for the human brain to conjure up in the way of perceptual experiences just because we ourselves do not have first-hand access to those experiences.

Acknowledgments

References

Adelson, Edward H. 2000. Lightness perception and lightness illusions. In *The new cognitive neuroscience,* ed. Michael S. Gazzaniga, 339–351. Cambridge, MA: MIT Press.

Aleman, André, Geert-Jan M. Rutten, Margriet M. Sitskoorn, Geraud Dautzenberg, and Nick F. Ramsay. 2001. Activation of striate cortex in the absence of visual stimulation: An fMRI study of synesthesia. *Neuroreport* 12 (13):2827–2830.

Anstis, Stuart M. 1974. A chart demonstrating variations in acuity with retinal position. *Vision Research* 14:589–592.

Asher, Julian E., Michael R. F. Aitken, Nasr Farooqi, Sameer Kurmani, and Simon Baron-Cohen. 2006. Diagnosing and phenotyping visual synaesthesia: a preliminary evaluation of the revised test of genuineness (TOG-R). *Cortex* 42 (2):137–146.

Asher, Julian E., Janine Lamb, Denise Brocklebank, Jean-Baptiste Cazier, Elena Maestrini, Laura Addis, Mallika Sen, Simon Baron-Cohen, and Anthony P. Monaco. 2009. A whole-genome scan and fine-mapping linkage study of auditory-visual synesthesia reveals evidence of linkage to chromosomes 2q24, 5q33, 6p12, and 12p12. *The American Journal of Human Genetics* 84(2):279–285.

Banissy, Michael J., Vincent Walsh, and Jamie Ward. 2009. Enhanced sensory perception in synaesthesia. *Experimental Brain Research* 4: 565–571.

Bargary, Gary, and Kevin J. Mitchell. 2008. Synaesthesia and cortical connectivity. *Trends in Neuroscience* 31(7):335–342.

Barnett, Kylie J., John J. Foxe, Sophie Molholm, Simon P. Kelly, Shani Shalgi, Kevin J. Mitchell, and Fiona N. Newell. 2008. Differences in early sensory-perceptual processing in synesthesia: A visual evoked potential study. *NeuroImage* 43:605–613.

Barnett, Kylie J., and Fiona N. Newell. 2008. Synaesthesia is associated with enhanced, self-rated visual imagery. *Consciousness and Cognition* 17 (3):1032–1039.

Beauchamp, Michael S., and Tony Ro. 2008. Neural substrates of sound–touch synesthesia after a thalamic lesion. *Journal of Neuroscience* 28 (50):13696–13702.

Beeli, Gian, Michaela Esslen, and Lutz Jäncke. 2008. Time course of neural activity correlated with colored-hearing synesthesia. *Cerebral Cortex* 18:379–385.

Blake, Randolph, René Marois, Thomas J. Palmeri, and Chai-Youn Kim. 2005. On the perceptual reality of synesthetic color. In *Synesthesia: Perspectives from Cognitive Neuroscience*, ed. Lynn C. Robertson and Noam Sagiv, 47–73. New York: Oxford University Press.

Blakemore, Sarah-Jane, Davina Bristow, Geoffrey Bird, Christopher Frith, and Jamie Ward. 2005. Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain* 128(7):1571–1583.

Bouma, Herman. 1970. Interaction effects in parafoveal letter recognition. *Nature* 226 (5241):177–178.

Brang, David, L. Edwards, Vilayanur S. Ramachandran, and Seana Coulson. 2008. Is the sky 2? Contextual priming in grapheme-color synaesthesia. *Psychological Science* 19:421–428.

Brang, David, Stanley Kanai, Vilayanur S. Ramachandran, and Seana Coulson. 2011. Contextual priming in grapheme-color synesthetes and yoked controls: 400 msec in the life of a synesthete. *Journal of Cognitive Neuroscience* 23 (7):1681–1696.

Broerse, Jack, Tony Vladusich, and Robert P. O'Shea. 1999. Colour at edges and colour spreading in McCollough effect. *Vision Research* 39:1305–1320.

Callaway, Edward M. 2005. Neural substrates within primary visual cortex for in- teractions between parallel visual pathways. *Progress in Brain Research* 149:59–64.

Carriere, Jonathan S. A., Daniel Eaton, Michael G. Reynolds, Michael J. Dixon, and Daniel Smilek. 2009. Grapheme-color synesthesia influences overt visual attention. *Journal of Cognitive Neuroscience,* 21 (2):246–258.

Chapanis, Alphonse, and Charles M. Overbey. 1971. Absolute judgments of colors using natural color names. *Perception and Psychophysics* 9:356–360.

Cohen Kadosh, Roi, Avishai Henik, Andres Catena, Vincent Walsh, and Luis J. Fuentes. 2009. Induced cross-modal synaesthetic experience without abnormal neuronal connections. *Psychological Science* 20 (2): 258–265.

Collerton, Daniel, Elaine Perry, and Ian McKeith. 2005. Why people see things that are not there: A novel perception and attention deficit model for recurrent complex visual hallucinations. *Behavioral and Brain Sciences* 28 (6):737–757.

Cytowic, Richard E. 1997. Synesthesia: phenomenology and neuropsychology. In *Synesthesia: Classic and Contemporary Readings,* ed. Simon Baron-Cohen and John E. Harrison, 17–39. Oxford: Blackwell.

——. 2002. *Synesthesia: A Union of the Senses*. Cambridge: MA, MIT Press.

Cytowic, Richard E., and David M. Eagleman. 2009. *Wednesday is Indigo Blue: Discovering the Brain of Synesthesia*. Cambridge, MA: MIT Press.

Dixon, Mike J., Daniel Smilek, Cera Cudahy, and Philip M. Merikle. 2000. Five plus two equals yellow. *Nature* 406:365.

Eagleman, David M., Arielle D. Kagan, Stephanie S. Nelson, Deepak Sagaram, and Anand K. Sarma. 2007. A standardized test battery for the study of synesthesia. *Journal of Neuroscience Methods* 159:139–1345.

Eagleman, David M., and Melvin A. Goodale. 2009. Why color synesthesia involves more than color. *Trends in Cognitive Sciences* 13 (7):288–292.

Easterman, Michael, Timothy Verstynen, Richard B. Ivry, and Lynn C. Robertson. 2006. Coming unbound: Disrupting automatic integration of synesthetic color and graphemes by TMS of the right parietal lobe. *Journal of Cognitive Neuroscience* 18:1570–1576.

Edquist, Jessica, Anina N. Rich, Cobie Brinkman, and Jason B. Mattingley. 2006. Do synesthetic colors act as unique features in visual search? *Cortex* 42:222–231.

Elias, Lorin J., Deborah M. Saucier, Colleen Hardie, and Gordon E. Sarty. 2003. Dissociating semantic and perceptual components of synaesthesia: Behavioural and functional neuro-anatomical investigations. *Cognitive Brain Research* 16:232–237.

Gamlin, Paul D. R., Hongyu Zhang, Alistair Harlow, and John L. Barbur. (1998). Pupil responses to stimulus color, structure and light flux increments in the rhesus monkey. *Vision Research* 38 (21):3353–3358.

Gheri, Carolina, Susan Chopping, and Michael J. Morgan. 2008. Synaesthetic colors do not camouflage form in visual search. *Proceedings of the Royal Society of London B: Biological Sciences* 275:841–846.

Goller, Aviva I., Leun J. Otten, and Jamie Ward. 2008. Seeing sounds and hearing colors: An event-related potential study of auditory-visual synesthesia. *Journal of Cognitive Neuroscience* 21:1869–1881.

Gorea, Andrei, and Thomas V. Papathomas. 1993. Double-opponency as a generalized concept in texture segregation illustrated with color, luminance and orientation defined stimuli. *Journal of the Optical Society of America A* 10:1451–1462.

Grill-Spector, Kalanit, Richard Henson, and Alex Martin. 2006. Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences* 10:15–23.

Grossenbacher, Peter G., and Chrostopher T. Lovelace. 2001. Mechanisms of synesthesia: Cognitive and physiological constraints. *Trends in Cognitive Sciences* 5:36–41

Hallett, Mark. 2000. Transcranial magnetic stimulation and the human brain. *Nature* 406:147–150.

Hänggi, Jürgen, Diana Wotruba, and Lutz Jäncke. 2011. Globally altered structural brain net-
    work topology in grapheme-color synesthesia. *Journal of Neuroscience* 31 (15):5816–5828.

Hong, Sang Wook, and Randolph Blake. 2008. Early visual mechanisms do not contribute to
    synesthetic color experience. *Vision Research* 48 (8): 1018–1026.

Hoffman, Ralph E., Jill Rapaport, Carolyn M. Mazure, and Donald M. Quinlan. 1999. Selective
    speech perception alterations in schizophrenic patients reporting hallucinated "voices."
    American Journal of Psychiatry 156:393–399.

Hubbard, Edward M. 2007. Neurophysiology of synesthesia. *Current Psychiatry Reports* 9
    (3):193–199.

Hubbard, Edward M., A. Cyrus Arman, Vilayanur S. Ramachandran, and Geoffrey M. Boynton.
    2005. Individual differences among grapheme-color synesthetes: Brain-behavior correla-
    tions. *Neuron* 45 (6):975–985.

Hubbard, Edward M., Sanjay Manohar, and Vilayanur S. Ramachandran. 2006. Contrast affects
    the strength of synesthetic colors. *Cortex* 42 (2):183–194.

Hupé, Jean-Michael, Cécile Bordier, and Michel Dojat. 2012. The neural bases of graph-
    eme-color synesthesia are not localized in real-color sensitive areas. *Cerebral Cortex*
    22:1622–1633.

Hurvich, Leo M., and Dorothea Jameson.1957. An opponent-process theory of color vision.
    Psychological Review 64:384–404.

Jameson, Dorothea, and Leo M. Hurvich. 1972. Color adaptation: Sensitivity, contrast, after-
    images. In *Handbook of Sensory Physiology Vol. VII/4,* ed. Dorothea Jameson and Leo M.
    Hurvich, 568–581. New York: Springer.

Jäncke, Lutz, Gian Beeli, Cornelia Eulig, and Jürgen Hänggi. 2009. The neuroanatomy of graph-
    eme-color synesthesia. *European Journal of Neuroscience* 29:1287–1293.

Kim, Chai-Youn, and Randolph Blake. 2005. Watercolor illusion induced by synesthetic color.
    Perception 34 (12):1501–1507.

———. 2007. Illusory colors promote interocular grouping during binocular rivalry. *Psychonomic
    Bulletin & Review* 14 (2):356–362.

Kim, Chai-Youn, Randolph Blake, and Thomas J. Palmeri. 2006. Perceptual interaction between
    real and synesthetic colors. *Cortex* 42 (2):195–203.

Kooi, Frank L., Alex Toet, Srimant P. Tripathy, and Dennis M. Levi. 1994. The effect of similarity
    and duration on spatial interaction in peripheral vision. *Spatial Vision* 8:255–279.

Kosslyn, Stephen M., Alvaro Pascual-Leone, Olivier Felician, Susana Camposano, Julian P.
    Keenan, William L. Thompson, Giorgio Ganis, Katherine E. Sukel, and Nathaniel M. Alpert.
    1999. The role of area 17 in visual imagery: Convergent evidence from PET and rTMS. *Science*
    284:167–170.

Laeng, Bruno. 2009. Searching through synaesthetic colors. *Attention, Perception, &
    Psychophysics* 71 (7):1461–1467.

Laeng, Bruno, Frode Svartdal, and Hella Oelmann. 2004. Does color synesthesia pose a para-
    dox for early-selection theories of attention? *Psychological Science* 15 (4):277–281.

Luck, Steven J. 2005. *An introduction to the event-related potential technique*. Cambridge, MA:
    MIT Press.

Ludwig, Casimir J. H., and Iain D. Gilchrist. 2003. Target similarity affects saccade curvature
    away from irrelevant onsets. *Experimental Brain Research* 152:60–69.

Mattingley, Jason B., Anina N. Rich, Greg Yelland, and John L. Bradshaw. 2001. Unconscious
    priming eliminates automatic binding of colour and alphanumeric form in synaesthesia.
    Nature 410:580–582.

McCollough, Celeste. 1965. Color adaptation of edge-detectors in the human visual system. *Science* 149 (3688):1115–1116.

Muggleton, Neil, Elias Tsakanikos, Vincent Walsh, and Jamie Ward. 2007. Disruption of synaesthesia following TMS of the right posterior parietal cortex. *Neuropsychologia* 45:1582–1585.

Myles, Kathleen M., Mike J. Dixon, Daniel Smilek, and Philip M. Merikle. 2003. Seeing double: The role of meaning in alphanumeric-colour synaesthesia. *Brain and Cognition* 53 (2):342–345.

Nikolić, Danko, Philipp Lichti, and Wolf Singer. 2007. Color opponency in synaesthetic experiences. *Psychological Science* 18 (6):481–486.

Nijboer, Tanja C. W., and Bruno Laeng. 2013. Synaesthesia, eye-movements, and pupillometry. In *Oxford Handbook of Synaesthesia*, ed. Julia Simner and Edward M. Hubbard, 334–346. Oxford: Oxford University Press.

Nijboer, Tanja. C. W., Gabriela Satris, and Stefan van der Stigchel. 2011. The influence of synesthesia on eye movements: No synesthetic pop-out in an oculomotor target selection task. *Consciousness and Cognition* 20 (4):1193–1200.

Nijboer, Tanja C. W., and Stefan van der Stigchel. 2009. Is attention essential for inducing synesthetic colors? Evidence from oculomotor distractors. *Journal of Vision* 9 (6):1–9.

Nisbett, Richard E., and Timothy D. Wilson. 1977. Telling more than we can know: Verbal reports on mental processes. *Psychological Review* 84 (3):231–259.

Nunn, Julia A., Lloyd J. Gregory, Michael Brammer, Steven C. R. Williams, David M. Parslow, Michael J. Morgan, Robin G. Morris, Edward T. Bullmore, Simon Baron-Cohen, and Jeffrey A. Gray. 2002. Functional magnetic resonance imaging of synesthesia: activation of V4/V8 by spoken words. *Nature Neuroscience* 5:371–375.

O'Connor, Daniel H., Miki M. Fukui, Mark A. Pinsk, and Sabine Kastner. 2002. Attention modulates responses in the human lateral geniculate nucleus. *Nature Neuroscience* 5 (11):1203–1209.

Paffen, Chris L. E., Maarten J. van der Smagt, and Tanja C. W. Nijboer. 2011. Colour-grapheme synaesthesia affects binocular vision. *Frontiers in Psychology* 2 (314):1–6.

Palmeri, Thomas J., Randolph Blake, René Marois, Marci A. Flanery, and William Whetsell Jr. 2002. The perceptual reality of synesthetic colors. *Proceedings of the National Academy of Sciences of the United States of America* 99 (6):4127–4131.

Papathomas, Thomas V., Andrei Gorea, and Bela Julesz. 1991. Two carriers for motion perception: Color and luminance. *Vision Research* 31 (11):1883–1892.

Papathomas, Thomas V., Illona Kovács, and Tiffany Conway. 2005. Interocular grouping in binocular rivalry: Basic attributes and combinations. In *Binocular Rivalry,* ed. David Alais and Randolph Blake, 155–168. Cambridge, MA: MIT Press.

Paulsen, Helle G., and Bruno Laeng. 2006. Pupillometry of grapheme-color synaesthesia. *Cortex* 42:290–294.

Pinna, Baingio, 2005. The role of Gestalt principle of similarity in the watercolour illusion. *Spatial Vision* 21:1–8.

Ramachandran, Vilayanur S., and Shai Azoulai. 2006. Synesthetically induced colors evoke apparent-motion perception. *Perception* 35 (11):1557–1560.

Ramachandran, Vilayanur S., and Edward M. Hubbard. 2001. Psychophysical investigations into the neural basis of synaesthesia. *Proceedings of the Royal Society of London B: Biological Sciences* 268 (1470):979–983.

——. 2003. Hearing colors, tasting shapes. *Scientific American* 288 (5):53–59.

Rich, Anina N., and Jason B. Mattingley. 2005. Can attention modulate color-graphemic syn-esthesia? In *Synesthesia: Perspectives from Cognitive Neuroscience*, ed. Lynn C. Robertson, and Noam Sagiv, 108–123. New York: Oxford University Press.

———. 2013. The role of attention in synaesthesia. In *Oxford Handbook of Synaesthesia,* ed. Julia Simner and Edward M. Hubbard, 265–282. Oxford: Oxford University Press.

Rich, Anina N., Mark A. Williams, Aina Puce, Ari Syngeniotis, Matthew A. Howard, Rancis McGlone, and Jason B. Mattingley. 2006. Neural correlates of imagined and synaesthetic colours. *Neuropsychologia* 44 (14):2918–2925.

Rothen, Nicolas, and Beat Meier. 2009. Do synesthetes have a general advantage in visual search and episodic memory? A case for group studies. *PLoS ONE* 4 (4): e5037. doi:10.1371/journal.pone.0005037.

Rouw, Romke. 2013. Synaesthesia, hyper-connectivity and diffusion tensor imaging. In *Oxford Handbook of Synaesthesia,* ed. Julia Simner and Edward M. Hubbard, 500–518. Oxford: Oxford University Press.

Rouw, Romke, and H. Steven Scholte. 2007. Increased structural connectivity in grapheme-color synesthesia. *Nature Neuroscience* 10:792–797.

———. 2010. Neural basis of individual differences in synesthetic experiences. *Journal of Neuroscience* 30 (18):6205–6213.

Sagiv, Noam, Jeffrey Heer, and Lynn C. Robertson. 2006. Does binding of synesthetic color to the evoking grapheme require attention? *Cortex* 42 (2):232–242.

Schiltz, Kolja, Karen Trocha, Bernardina M. Wieringa, Hinderk M. Emrich, Sönke Johannes, and Thomas F. Münte. 1999. Neurophysiological aspects of synesthetic experience. *Journal of Neuropsychiatry and Clinical Neurosciences* 11:58–65.

Shapley, Robert, and Michael J. Hawken. 2011. Color in the cortex: single- and double opponent cells. *Vision Research* 51:701–717.

Shergill, Sukhwinder S., Michael J. Brammer, Rimmei Fukuda, Steven C. R. Williams, Robin, M. Murray, and Philip K. McGuire. 2003. Engagement of brain areas implicated in process-ing inner speech in people with auditory hallucinations. *The British Journal of Psychiatry* 183:525–531.

Simner, Julia. 2007. Beyond perception: Synaesthesia as a psycholinguistic phenomenon. *Trends in Cognitive Sciences* 11:23–29.

Smilek, Daniel, Mike J. Dixon, Cera Cudahy, and Philip M. Merikle. 2001. Synaesthetic pho-tisms influence visual perception. *Journal of Cognitive Neuroscience* 13 (7):930–996.

Smilek, Daniel, Mike J. Dixon, and Philip M. Merikle. 2003. Synaesthetic photisms guide atten-tion. *Brain and Cognition* 53 (2):364–367.

Sperling, Julia M., David Prvulovic, David E. J. Linden, Wolf Singer, and Aglaja Stirn. 2006. Neuronal correlates of graphemic colour synaesthesia: A fMRI study. *Cortex* 42: 295–303.

Steven, Megan S., and Colin Blakemore. 2004. Visual synaesthesia in the blind. *Perception* 33 (7):855–868.

Steven, Megan S., Peter C. Hansen, and Colin Blakemore. 2006. Activation of color-selective areas of the visual cortex in a blind synesthete. *Cortex* 42 (2): 304–308.

Tang, Joey, Jamie Ward, and Brian Butterworth. 2008. Number forms in the brain. *Journal of Cognitive Neuroscience* 20 (9):1547–1556.

Terhune, Devin B., Sarah Tai, Alan Cowey, Tudor Popescu, and Roi Cohen Kadosh. 2011. Enhanced cortical excitability in grapheme-color synesthesia and its modulation. *Current Biology* 21: 2006–2009.

Tomson, Steffie N., Nili Avidan, Kwanghyuk Lee, Anand K. Sarma, Rejnal Tushe, Dianna M. Milewicz, Molly Bray, Suzanne M. Leal, and David M. Eagleman. 2011. The genetics of colored sequence synesthesia: Suggestive evidence of linkage to 16q and genetic heterogeneity for the condition. *Behavioral Brain Research* 223:48–52.

Tong, Frank. 2003. Primary visual cortex and visual awareness. *Nature Reviews Neuroscience* 4:219–229.

Treisman, Anne M., and Garry Gelade. 1980. A feature-integration theory of attention. *Cognitive Psychology* 12 (1):97–136.

van Leeuwen, Tessa M., Karl M. Petersson, and Peter Hagoort. 2010. Synaesthetic colour in the brain: Beyond color areas. A functional magnetic resonance imaging study of synaesthetes and matched controls. *PLoS ONE* 5 (8): e12074. doi:10.1371/journal.pone.0012074

Vul, Edward, Erin Krizay, and Donald I. A. MacLeod. 2008. The McCollough effect reflects permanent and transient adaptation in early visual cortex. *Journal of Vision* 8 (12):4.1–12. <http://journalofvision.org/8/12/4/> doi:10.1167/8.12.4.

Vul, Edward, and Donald I. A. MacLeod. 2006. Contingent aftereffects distinguish conscious and preconscious color processing. *Nature Neuroscience* 9:873–874.

Wandell, Brian A., and Jonathan Winawer. 2011. Imaging retinoptic maps in the human brain. *Vision Research* 51:718–737.

Weiss, Peter H., and Gerone R. Fink. 2009. Grapheme-colour synaesthetes show increased grey matter volumes of parietal and fusiform cortex. *Brain* 132:65–70.

Weiss, Peter H., N. Jon Shah, Ivan Toni, Karl Zilles, and Gerone R. Fink. 2001. Associating colours with people: a case of chromatic-lexical synaesthesia. *Cortex* 37:750–753.

Weiss, Peter H., Karl Zilles, and Gereon R. Fink. 2005. When visual perception causes feeling: enhanced cross-modal processing in grapheme-color synesthesia. *NeuroImage* 28:859–868.

Witthoft, Nathan, and Jonathan Winawer. 2006. Synesthetic colors determined by having colored refrigerator magnets in childhood. *Cortex* 42 (2):175–183.

Woodman, Geoffrey F. 2010. A brief introduction to the use of event-related potentials in studies of perception and attention. *Attention, Perception, & Psychophysics* 72:2031–2046.

Wright, William D., and Frederick. H. G. Pitt. 1934. Hue-discrimination in normal colour-vision. *Proceedings of the Physical Society* 46:459–473.

Yaro, Caroline, and Jamie Ward. 2007. Searching for Shereshevskii: What is superior about the memory of synaesthetes? *The Quarterly Journal of Experimental Psychology* 60 (5):681–695.