# Synaesthetic Photisms Influence Visual Perception

## Daniel Smilek, Mike J. Dixon, Cera Cudahy, and Philip M. Merikle

#### **Abstract**

■ When C, a digit—color synaesthete, views black digits, she reports that each digit elicits a highly specific color (a photism), which is experienced as though the color was externally projected onto the digit. We evaluated this claim by assessing whether C's photisms influenced her ability to perceive visually presented digits. C identified and localized target digits presented against backgrounds that were either congruent or incongruent with the color of her photism for

the digits. The results showed that C was poorer at identifying and localizing digits on congruent than incongruent trials. Such differences in performance between congruent and incongruent trials were not found with nonsynaesthete control participants. These results suggest that C's colored photisms influence her perception of black digits. We propose a model in which color information influences the perception of digits through reentrant pathways in the visual system.

#### INTRODUCTION

People who experience digit—color synaesthesia report that viewing a black digit elicits a photism—an accompanying experience of a highly specific color. Empirical investigations of digit—color synaesthesia generally corroborate these subjective reports. For digit—color synaesthetes, the available evidence suggests that (a) each digit elicits an experience of a highly specific color (Dixon, Smilek, Cudahy, & Merikle, 2000), (b) the digit—color pairings do not change over time (Dixon et al., 2000; Baron-Cohen, Harrison, Goldstein, & Wyke, 1993; Svartdal & Iversen, 1989), and (c) the photisms are elicited automatically (Dixon et al., 2000; Mills, Boteler, & Oliver, 1999; Odgaard, Flowers, & Bradman, 1999; Wollen & Ruggiero, 1983).

Some digit-color synaesthetes also report a curious subjective phenomenon. When shown a digit, the color of the photism is not experienced "in the mind's eye," but rather it is experienced as though the color was "externally projected" onto the digit—for example, when C, a digit-color synaesthete whom we have studied (Dixon et al., 2000), is shown a black 4, she describes the blue photism triggered by the 4 as being seen "out there, on the page, overlaid on top of the 4." C describes these synaesthetic overlays as shapes that conform to the contours of the presented digit, but which also completely cover the presented digit. This binding of the photism to the external digit suggests that under certain conditions the photism might influence how easily the black digit is perceived and identifiedfor example, if a 2 is presented against a red background (the same color as her photism for 2), the 2 may be

more difficult to perceive than if it was presented against a blue background.

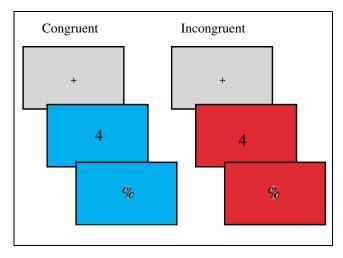
The purpose of the present investigation was to evaluate whether the color experiences elicited by digits influence how the digit-color synaesthete, C, perceives digits. C performed two different tasks. In one task, C identified digits that were briefly presented and followed by a pattern mask. In a second task, C localized one of two possible target digits (2 or 4) when presented among 6, 12, or 18 distractor digits (a group of 8s). Examples of the displays used for the two tasks are shown in Figures 1 and 2, respectively. Critically, as illustrated in the figures, for both tasks, the color of the background was either congruent with the color of C's photisms for the target digits (e.g., a 4 was presented against a blue background) or incongruent with the color of C's photisms for the target digits (e.g., a 4 was presented against a red background). We predicted that if the photisms elicited by digits influence the perception of the digits, then C should be less accurate in identifying, and slower at localizing, digits on congruent trials than on incongruent trials. This should occur because on congruent trials the digit and the background would be experienced as similar in color, whereas on incongruent trials, the background and the digit would be experienced as different in color. Thus, discriminating the digit from the background should be easier on incongruent than on congruent trials.

## **RESULTS**

## **Identification of Masked Digits**

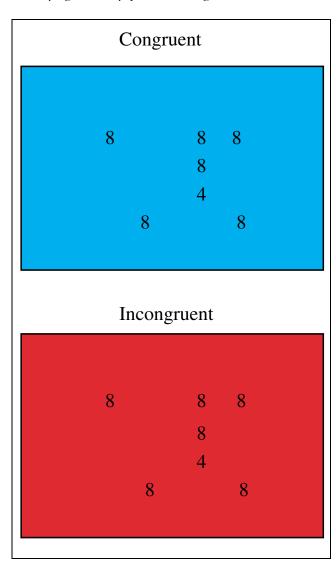
C's accuracy in identifying digits on congruent and incongruent trials is shown on the left side of Figure 3.

University of Waterloo, Waterloo, Ontario, Canada

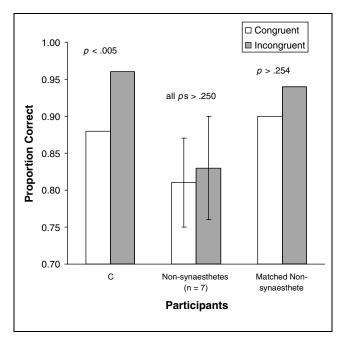


**Figure 1.** Examples of the stimulus displays used in the identification task.

As can be seen from the figure, C was less accurate at identifying a briefly presented digit when the color of



**Figure 2.** Examples of the stimulus displays used in the localization task.



**Figure 3.** Proportion correct identification of digits on congruent and incongruent trials for C, the group of seven nonsynaesthetes, and the nonsynaesthete most closely matched to C in overall accuracy.

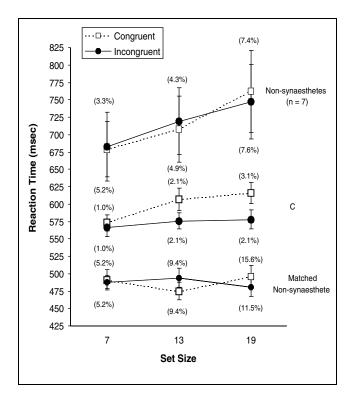
the background was congruent with her photism for the digit (M = 0.88), than when the color of the background was incongruent with her photism for the digit (M = 0.96),  $\chi^2$  (1) = 8.59, p < .005. This result strongly suggests that C's photisms influence her perception of digits.

In contrast to C's rather large mean difference (0.08) between digit identification on congruent and incongruent trials, seven nonsynaesthetes showed only a small mean difference in digit identification between congruent and incongruent trials (0.02). When the seven nonsynaesthetes were considered individually, the differences in accuracy between congruent and incongruent trials ranged from -0.01 to 0.04. Importantly, none of these differences were statistically significant (all  $\chi^2$ s < 1.20, ps > .250), including the nonsynaesthetes who were either similar to or better than C in overall accuracy. The middle and the right side of Figure 3 show the average results of seven nonsynaesthetes and the one nonsynasthete most similar to C in overall accuracy, respectively.

## **Localization of Digits**

#### RT Data<sup>1</sup>

The mean RTs for C to localize target digits are shown in the middle of Figure 4. The data were submitted to a 2 (congruent vs. incongruent)  $\times$  3 (6, 12, 18 distractors) independent sample analyses of variance (ANOVA). As can be seen from Figure 4, C was slower at localizing target digit when her photism for a target digit was congruent with the color of the background, than when



**Figure 4.** Mean reaction times and percentage errors (in parentheses) for localizing target digits on congruent and incongruent trials for C, the group of nonsynaesthetes, and the nonsynaesthete most closely matched to C in overall RT. Error bars depict one standard error of the mean

her photism for a target digit was incongruent with the color of the background, F(1,550) = 5.214, MSE = 17526.8, p < .025. These results suggest that the photisms elicited by the target digits influenced C's perception of the digits. The analyses revealed that search difficulty was equivalent across set size, F(2,550) = 2.281, MSE = 17526.8, p > .103, and that the small difference in slopes between congruent and incongruent trials shown in Figure 4 was not statistically significant, F(2,550) = 0.701, MSE = 12287.5, p > .496.

The top of Figure 4 shows the combined results for the seven nonsynaesthetes. A 2 (congruent vs. incongruent)  $\times$  3 (6, 12, 18 distractors) repeated measures ANOVA showed that the performance of the seven nonsynaesthetes as a group was considerably different from C. In contrast to C's results, the seven nonsynaesthetes showed no difference between congruent and incongruent trials, F < 0.001, p > .995. The results also showed that for the nonsynaesthetes search became more difficult as set size increased, F(2,12) = 10.118, MSE = 1870.70, p < .01, and the search slopes for localizing the target digits on congruent and incongruent trials were similar and did not statistically differ, F(2,12) = 1.258, MSE = 515.51, p > .30.

The RT data for each nonsynaesthete were also submitted to a 2 (congruent vs. incongruent)  $\times$  3 (6, 12, 18 distractors) independent sample ANOVA. When considered individually, five of the nonsynaesthetes showed no

difference between congruent and incongruent trials (Fs < 1.64, ps > .200), and two nonsynaesthetes were slower at localizing the targets on incongruent trials than congruent trials (Fs > 3.739, ps < .055)—a pattern of results opposite to the pattern shown by C. Importantly, none of the seven nonsynaesthetes, including the nonsynaesthetes who were either similar to or faster than C in overall RT, showed a pattern of results similar to C—a pattern characterized by slower localization of the target digits on congruent than incongruent trials.

The individual results of the nonsynaesthetes also showed that for five of the nonsynaesthetes search became more difficult with increases in set size (Fs > 4.350, ps < .02) and for two of the nonsynaesthetes the difficulty of search was equivalent across all set sizes (Fs < 1.687, ps > .186). Analysis of the error data suggests, however, that the RT results of the latter two nonsynaesthetes may have been due to speed–accuracy tradeoffs. That is, for both of these nonsynaesthetes, errors increased as set size increased (Fs > 3.021, ps < .051). Finally, the search slopes for congruent and incongruent trials did not differ for any of the seven nonsynaesthetes (Fs < 1.200, ps > .144). The bottom of Figure 4 shows the results for the nonsynasthete that was most similar in overall RT to C.

#### Error Data

The mean percentage errors are shown in parentheses in Figure 4. A 2 (congruent vs. incongruent)  $\times$  3 (6, 12, 18 distractors) independent sample ANOVA revealed that C's errors were comparable across conditions (Fs < 1, ps> .52). When the error data for the seven nonsynaesthetes were submitted to a 2 (congruent vs. incongruent) × 3 (6, 12, 18 distractors) repeated measures ANOVA, the analysis revealed that the nonsynaesthetes made a comparable number of errors on congruent and incongruent trials, F(1,6) = 4.273, MSE = 0.000664, p > .084. The analysis also revealed that errors increased as the number of distractors increased, F(2,12) = 5.529, MSE = 0.0008145, p < .021, and that there was no interaction between set size and trial congruency (F < 1, p > .50). These findings indicate that interpretation of the RT data is not compromised by speed-accuracy trade-offs. The error data for each nonsynaesthete were also submitted to a separate 2 (congruent vs. incongruent) × 3 (6, 12, 18 distractors) independent sample ANOVA. The results showed that the only significant differences in errors were observed in the two nonsynaesthetes who showed increased errors as set size increased (Fs > 3.021, ps < .051). There appeared to be no other speed-accuracy tradeoffs.

#### DISCUSSION

In two experiments, we evaluated whether the photisms elicited by digits in a digit-color synaesthete influenced

her perception of the digits. The experiments were based on the synaesthete C's subjective report that when she views a digit, her color experience is externally projected onto the digit. C either identified digits that were presented for a brief duration and followed by a pattern mask, or localized one of two possible target digits (2 or 4) presented among either 6, 12, or 18 distractor digits. In both experiments, the color of the background was varied such that it was either congruent with the color of C's photism for the target digit, or incongruent with the color of C's photism for the target digit. The results showed that for C, black digits were more difficult to identify and to localize on congruent trials than incongruent trials, whereas nonsynaesthetes performed equally on congruent and incongruent trials. Taken together, these findings provide converging evidence that the colors elicited by digits in digit-color synaesthesia can influence the perception of the digits.

How do color photisms influence the perception of digits? Perhaps the best way to answer this question is to begin with what is currently known about color and form perception. Color from a visual display is thought to be processed by blob areas in primary visual cortex (human V1 and V2), and the resulting information is conveyed anteriorly to color-specific areas of the fusiform gyrus located along the bank of the collateral sulcus (human V4; McKeefrey & Zeki, 1997). Based on the initial processing of color and intensity, the form of the digit is segregated from the background. Information regarding form activates shape-processing areas of primary visual cortex (Hubel & Wiesel, 1977), as well as the extrastriate areas in the lingual and fusiform gyri (human V4). Form, comprised of the line segments in a digit, is then processed by anterior fusiform and PIT areas where the form activates the meaning of that digit (Allison et al., 1994). It is here, in anterior fusiform and PIT areas, that synaesthetes' processing of digits departs from normal color and form perception. We believe that for synaesthetes like C, PIT activation of the meaning of a digit influences color processing in V4 via feedback connections. It is this change in color processing at V4 that influences the perception of the externally presented digit.

Consider the pattern of activation that would accrue when a black digit was presented against a background that was incongruent to C's photism for that digit (e.g., a black 2 presented against a blue background). Whereas the feedforward connections from V1, through V2, to V4 would carry color and form information about the external display that was physically presented (i.e., a black 2 against a blue background), the feedback connections from anterior fusiform and PIT areas projecting back to V4 would carry information pertaining to the meaning of 2 (i.e., a red 2). We believe that the color information based on the meaning of the digit that is fed back from PIT influences digit—background segregation at V4. On incongruent trials such as this, the segregation

of the form of the digit from the background would be relatively easy because the color information associated with the digit is different than the color information associated with the background. In this case, for C, the percept that would accrue over successive iterations would be the dual perception of a red overlay sitting atop a black 2 against a blue background.

On the other hand, consider the pattern of activation that would accrue when a black digit was presented against a background that was congruent to C's photism for that digit (e.g., a black 2 presented against a red background). On trials such as these, the information feeding forward from V1, through V2, to V4 would include a black 2 against a red background, whereas the information feeding back from anterior fusiform and PIT areas back to V4 would carry information regarding a red 2. As before, the color information based on the meaning of the digit that is fed back from PIT would influence digit-background segregation at V4. On congruent trials such as this, however, the segregation of the form of the digit from the background would be relatively difficult because the color information associated with the digit would be similar to the color information associated with the background. In this case, for C, the percept that would accrue over successive iterations would be the dual perception of a red overlay sitting atop a black 2 against a red background. Critically, the digit-background discrimination on congruent trials would be much more difficult than the digit-background discrimination on incongruent trials. This increased difficulty on congruent trials would lead to more errors in identification and longer reaction times in visual search, compared to the errors and reaction times on incongruent trials where digitbackground segregation would be much easier.

Our reentrant model of synaesthesia is similar to that of Grossenbacher (1997) who proposed that synaesthetes have abnormal feedback from a high-level multimodel nexus to lower-level areas involved in the processing of the distinct perceptual attributes that converge onto that nexus. Grossenbacher did not attempt to link specific anatomical areas to either the nexi, or the low-level perceptual areas, since his goal was to present a general architecture for understanding soundcolor synaesthesia. Our model of digit-color synaesthesia, however, is consistent with Grossenbacher's general architecture—for digit-color synaesthetes like C, the high-level multimodal nexi are located in anterior fusiform/PIT, and the abnormal feedback travels along connections back to V4. Although it is possible that the feedback from anterior fusiform/PIT travels all the way to primary visual cortex (i.e., human V1 and V2), we believe that it is the feedback to the fusiform gyrus (i.e., human V4) that is most critical. The color feeding back from the meaning of a digit is likely to influence perception at V4 because it is at V4 that the activation of cells first correlates with perceived color rather than with wavelength composition (Zeki, 1983; see also McKeefry and Zeki, 1997). Also, while the relationship between color and form processing in V4 has not yet been determined (Zeki & Shipp, 1988), we believe that this area may also play a role in digit–background segregation because this is the area where color information is compared across the entire visual field and the topography of the visual is field is, at least coarsely, maintained (Zeki & Marini, 1998; McKeefry & Zeki, 1997). Although our model is speculative, at the present time we are using functional magnetic imaging to test the model.

A critical assumption underlying our proposed reentrant model is that the color that is synaesthetically associated with the digit is part of, or dependent upon, the activation of the "meaning" of a digit. There are at least three lines of evidence that suggest that for C, her photisms are a consequence of the activation of meaning. First, we have shown that for C color photisms can be activated simply by thinking of a digit, in the absence of an externally presented stimulus (Dixon et al., 2000). Second, according to C's subjective reports, even though the perceptual qualities (e.g., size and font) of a digit may vary radically, the digit elicits the same photism. In order for this to occur, a digit must be categorized concurrently with, or just prior to the activation of the color. Finally, C also reports that an ambiguous stimulus that could be either a 5 or an S elicits different photisms depending on whether the stimulus is perceived as part of a letter string or a digit string. If the ambiguous stimulus is embedded in a letter string, C experiences the photism associated with an S (i.e., metallic bluish purple), whereas if the stimulus is embedded in a digit string, C experiences the photism associated with the number 5 (i.e., dark green). This evidence, taken together with the findings reported in this paper, suggests that the activation of colors in C's digit-color synaesthesia is part of, or dependent upon, the activation of the meaning of digits, and that activated color information influences the perception of digits through reentrant pathways in the visual system.

To date, few studies have used brain imaging to look at the neural correlates of color photisms. For example, Paulesu et al. (1995) used positron emission tomography to compare regional blood flow differences between six sound-color synaesthetes and six nonsynaesthetes when participants listened to words. Unlike C, who experiences photisms to both auditory and visual stimuli, these synaesthetes experienced photisms only to auditory stimuli. Upon hearing words, the synaesthetes showed significantly greater activity than the nonsynaesthetes in prefrontal cortex, insula, and superior temporal gyrus. More importantly, for synaesthetes the auditory stimuli elicited significant activation in visual association areas (PIT and parieto/occipital junctions). Increased activation was also seen in V4, but the level of activation did not reach the author's a priori criterion for significance. Although Paulesu et al. (1995) did not find

significant V4 activation, according to our model this area is crucial to C's synaesthetic experience when photisms are induced by visual stimuli. We propose that C's auditorially induced photisms are associated with PIT activation, while her visually induced photisms are associated with V4 activation.

#### **METHODS**

#### **Masking Task**

#### **Participants**

The participants were C, a 21-year-old undergraduate student who has digit-color synaesthesia, and seven nonsynaesthete undergraduates at the University of Waterloo. All nonsynaesthetes were questioned about whether they had ever experienced colors when viewing digits or letters. None reported any synaesthesia-like experiences. Both C and the nonsynaesthetes had normal or corrected-to-normal vision and were paid \$8.00 on completion of the 40-min experimental session.

#### Stimulus Displays

Examples of the stimulus displays are shown in Figure 1. The figure shows that three stimulus displays were presented on each trial. The first display contained a fixation cross (+), the second display contained one of nine possible digits (0 to 9 excluding 8), and the third display contained a pattern mask consisting of the superimposed characters % and \$. The characters measured 1.5 cm  $(1.43^\circ)^2$  in height and 1.0 cm  $(0.96^\circ)$  in width. All characters were presented in dark grey.

The background color of the displays was varied across trials. For each digit and mask display, the background color was either congruent or incongruent with the color of C's photism for the digit presented on that trial. For C, the digit–color pairings were the following: 0—grey, 1—white, 2—red, 3—purple, 4—blue, 5—green, 6—pink, 7—yellow, and 9—orange. The precise colors of C's photisms were assessed prior to the experiment by having her adjust the color of a square to match the color of her photism for each digit. The digit 8 was excluded from the experiment because the color of C's photism associated with 8 was black.

The two types of trials (congruent vs. incongruent) and the nine possible digits (0 to 9 excluding 8) were varied within subjects. On each trial, a digit was randomly chosen from the nine possible digits and randomly assigned to either the congruent or incongruent condition with the constraint that there were 480 incongruent trials and 60 congruent trials in the experiment. This was done in order to ensure that each digit had an equal chance of being paired with each background color. When the background color was congruent, the color was predetermined to be the color that C associated with the digit presented on the trial. When the

background color was incongruent, the color was randomly chosen from the colors that C associated with one of the digits not presented on the trial. The stimulus displays were presented on a ViewSonic 17PS monitor, which was driven by a 200-MHz Pentium processor running the Micro Experimental Laboratory software (Schneider, 1990).

#### **Procedures**

C and the seven nonsynaesthetes were each tested in a single session consisting of one block of nine practice trials and three blocks of 180 experimental trials. Each trial began with the presentation of the fixation cross (+) for 800 msec. Following the offset of the fixation cross, a randomly chosen digit (0 to 9 excluding 8) was presented for 32 msec. At the onset of the digit, the background color changed to one of the nine possible colors and remained unchanged until the presentation of the digit on the next trial. Immediately following the offset of the digit, the pattern mask was presented in the center of the screen. The pattern mask remained on the computer screen until the participant pressed a key on the number pad of the keyboard indicating which digit they thought was presented. Following 1000 msec after the key was pressed, the fixation cross signaling the beginning of the next trial was presented.

#### Visual Search Task

#### **Participants**

The participants were C and seven nonsynaesthete undergraduates at the University of Waterloo. All nonsynaesthetes were questioned about whether they had ever experienced colors when viewing digits or letters. None reported any synaesthesia-like experiences. The nonsynaesthetes had normal or corrected-to-normal vision and had not participated in the masking task. C and the seven nonsynaethetes were paid \$8.00 on completion of the 40-min experimental session.

## Stimulus Displays

Example of the stimulus displays are shown in Figure 2. The stimulus displays consisted of one of two possible target digits (either a 2 or a 4) and 6, 12, or 18 distractor digits (a group of 8s). The target and distractor digits occupied random locations of an unseen  $6 \times 6$  matrix positioned at the center of the computer monitor. The  $6 \times 6$  matrix measured 10.6 cm  $(10.1^{\circ})$  vertically and horizontally, and the digits measured 0.5 cm  $(0.47^{\circ})$  vertically and 0.4 cm  $(0.38^{\circ})$  horizontally. The digits were always presented in dark grey and the background color of the displays was either red or blue, the color of C's photisms for the target digits, 2 and 4 respectively. On half of the trials, the color of the background was

congruent with C's photism for the target digit and on the other half of the trials, the color of the background was incongruent with C's photism for the target digit.

The two color correspondences (congruent vs. incongruent), the two targets (2 vs. 4), and the three set sizes (7, 13, or 19 digits) were varied within participants. Each of the 12 possible conditions occurred randomly throughout the experimental trials with the constraint that each condition was presented equally often across the 488 experimental trials. The stimulus displays were presented on a ViewSonic 17PS monitor that was driven by a 200-MHz Pentium processor running the Micro Experimental Laboratory software (Schneider, 1990).

#### Procedures

C and seven nonsynaesthetes completed one block of 12 practice trials and two blocks of 244 experimental trials in a single session. On each trial, as soon as the "b" key on the keyboard was pressed, a search display appeared on the computer screen. Both C and the seven nonsynaesthetes were instructed to search for one of two possible targets (i.e., 2 or 4) as fast as possible and press the "b" key again when they found the target digit. When the "b" key was pressed to end the trial, the digits were replaced by grey rectangles. Column and row numbers appeared above and to the left of the unseen  $6 \times 6$  matrix and the location of the target in the preceding display was indicated by having the participant enter the appropriate column and row numbers. Each entry was presented at the bottom of the computer screen, and following a 500-msec interval, the accuracy of the entry was displayed together with the prompt to initiate the next trial.

## Acknowledgments

This research was made possible by operating grants from the Natural Sciences and Engineering Research Council of Canada awarded to MJD and PMM, as well as postgraduate scholarship from the Natural Science and Engineering Research Council of Canada awarded to DS.

Reprint requests should be sent to Daniel Smilek, Department of Psychology, University of Waterloo, Waterloo, Ontario, Canada N2L 3G1, or via e-mail: dsmilek@watarts.uwaterloo.ca.

## **Notes**

- 1. Before the RT data for correct responses were analyzed, a recursive procedure was used to remove outliers (Van Selst & Jolicoeur, 1994).
- 2. Numbers in parentheses indicate degrees of visual angle subtended at the viewing distance of 60 cm.

## **REFERENCES**

Baron-Cohen, S., Harrison, J., Goldstein, L. H., & Wyke, M. (1993). Colored speech perception: Is synaesthesia what

- happens when modularity breaks down? *Perception*, 22, 419–426.
- Dixon, M. J., Smilek, D., Cudahy, C., & Merikle, P. M. (2000). Five plus two equals yellow. *Nature*, 406, 365.
- Grossenbacher, P. G. (1997). Perception and sensory information in synaesthetic experience. In J. E. Baron-Cohen, S., & Harrison (Eds.), *Synaesthesia: Classic and contemporary readings*. (pp. 148–172). Cambridge, MA: Blackwell.
- Hubel, D. H., & Wiesel, T. N. (1977). Functional architecture of macaque monkey visual cortex. *Proceedings of the Royal Society of London*, 198, 1–59.
- McKeefry, D. J., & Zeki, S. (1997). The position and topography of the human color centre as revealed by functional magnetic resonance imaging. *Brain*, *120*, 2229–2242.
- Mills, C. B., Boteler, E. H., & Oliver, G. K. (1999). Digit synaesthesia: A case study using a Stroop-type test. *Cognitive Neuropsychology*, *16*, 181–191.
- Odgaard, E. C., Flowers, J. H., & Bradman, H. L. (1999). An investigation of the cognitive and perceptual dynamics of a color–digit synaesthete. *Perception*, *28*, 651–664.
- Paulesu, E., Harrion, J., Baron-Cohen, S., Watson, J. D. G.,

- Goldstein, L., Heather, J., Frackowiak, R. S. J., & Frith, C. D. (1995). The physiology of colored hearing: A PET activation study of color–word synaesthesia. *Brain*, *118*, 661–676.
- Schneider, W. (1990) Mel user's guide: Computer techniques for real-time experimentation. Pittsburgh, PA: Psychology Software Tools.
- Svartdal, F., & Iversen, T. (1989). Consistency in synesthetic experience to vowels and consonants: Five case studies. *Scandinavian Journal of Psychology*, *30*, 220–227.
- Van Selst, M., & Jolicoeur, P. (1994). A solution to the effects of sample size on outlier elimination. *Quarterly Journal of Experimental Psychology A*, 47, 631–650.
- Wollen, K. A., & Ruggiero, F. T. (1983). Colored-letter synaesthesia. *Journal of Mental Imagery*, 7, 83–86.
- Zeki, S. (1983). Color coding in the cerebral cortex: The reaction of cells in monkey visual cortex to wavelengths and colors. *Neuroscience*, *9*, 741–765.
- Zeki, S., & Marini, L. (1998). Three cortical stages of color processing in the human brain. *Brain*, 121, 1669–1685.
- Zeki, S., & Shipp, S. (1988). The functional logic of cortical connections. *Nature*, *335*, 311–317.