

Psychophysical investigations into the neural basis of synaesthesia

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We studied two otherwise normal, synaesthetic subjects who ‘saw’ a specific colour every time they saw a specific number or letter. We conducted four experiments in order to show that this was a genuine perceptual experience rather than merely a memory association. (i) The synaesthetically induced colours could lead to perceptual grouping, even though the inducing numerals or letters did not. (ii) Synaesthetically induced colours were not experienced if the graphemes were presented peripherally. (iii) Roman numerals were ineffective: the actual number grapheme was required. (iv) If two graphemes were alternated the induced colours were also seen in alternation. However, colours were no longer experienced if the graphemes were alternated at more than 4 Hz. We propose that grapheme colour synaesthesia arises from ‘cross-wiring’ between the ‘colour centre’ (area V4 or V8) and the ‘number area’, both of which lie in the fusiform gyrus. We also suggest a similar explanation for the representation of metaphors in the brain: hence, the higher incidence of synaesthesia among artists and poets.

Keywords: synaesthesia; multisensory; extrastriate visual areas; psychophysics

1. INTRODUCTION

The bizarre phenomenon of synaesthesia, e.g. ‘seeing sounds’ or seeing specific colours upon seeing specific numerals (Galton 1880, 1883; Cytowic 1989; Paulesu *et al.* 1995; Gray *et al.* 1997; Harrison & Baron-Cohen 1997), was first clearly documented by Galton (1880). Galton (1880) also noted that it tends to run in families. We now report on several new psychophysical experiments for exploring the effect and determining its neural locus. We studied two ‘grapheme-colour’ synaesthetes who were otherwise completely normal. They saw specific colours when looking at specific letters or numerals (subject J.C. experienced colours with both letters and numerals, while subject E.R. experienced colours for numerals only). Our first questions were as follows. Is synaesthesia a genuine sensory phenomenon? Or is the phenomenon just a memory association from early childhood (e.g. from books with coloured numbers)? When some synaesthetes speak of chicken tasting ‘pointy’ are they merely being metaphorical (as in when we say ‘cheddar cheese is sharp’ or that ‘he wears loud shirts’)?

Anecdotally, we were convinced that the effect in our two subjects was a sensory one. First, the subjects said they ‘saw’ the colours spatially in the same location as the grapheme and said ‘it is not just memory’. Second, when shown half-tone black and white photographs of fruits and vegetables (e.g. a cucumber, tomato, orange and banana) they readily identified the fruit, but said that no colours were evoked (e.g. when looking at the banana, ‘it reminds me of yellow, but I do not actually see yellow the way I see yellow when you show me an F’). This argues against the memory hypothesis or at least the simple version of it (although, as we shall see, the memory, metaphor and cross-wiring interpretations are not quite as incompatible with each other as they might at first seem). Furthermore, neither subject experienced colours with Roman numerals or when graphemes were traced on their palms, implying

that the visual number grapheme rather than the numerical concept is required for evoking colours. However, they both noted that if they ‘imaged’ the corresponding Arabic numeral then the corresponding colour was evoked, but more faintly than when looking at the actual numerals.

2. METHODS AND RESULTS

In order to show conclusively that the evoked colours were indeed perceptual rather than memories, we asked whether synaesthetically induced colours could influence perceptual grouping. Perceptual grouping is a convenient diagnostic test for determining whether a given feature is genuinely perceptual or not (Beck 1966; Treisman & Gelade 1980; Julesz 1981) (e.g. tilted lines will segregate and group separately from vertical lines but Ts will not segregate from Ls). In order to explore whether synaesthetically induced colours are able to affect grouping, we created a 7 × 5 matrix of 35 graphemes (see figure 1*a*). The probability of seeing vertical columns or horizontal rows in such a matrix is *ca.* 50%. However, by choosing the graphemes carefully we can bias normal subjects to group on the basis of similarity of shape. Taking advantage of the fact that the synaesthetic subjects often saw the same (or very similar) colour in two different graphemes, we chose graphemes for each synaesthetic subject such that grouping by colour, for example, would lead to vertical organization whereas grouping by similarity of shape would lead to a horizontally biased organization as in normals (compare figure 1*b*).

We tested two synaesthetes (J.C. and E.R.) and a total of 20 control subjects (ten for each synaesthete). Displays were constructed for each synaesthete so that each would evoke similar colours in our synaesthetes. We tested each synaesthete with displays that would induce red and green or yellow and blue percepts. If synaesthetically induced colours are truly perceptual and, therefore, are able to affect grouping, we would expect that synaesthetic subjects would be influenced by their evoked colours while controls would group solely on the basis of similarity of shape.

The displays were presented in pseudo-random order such that all possible combinations of horizontal and vertical

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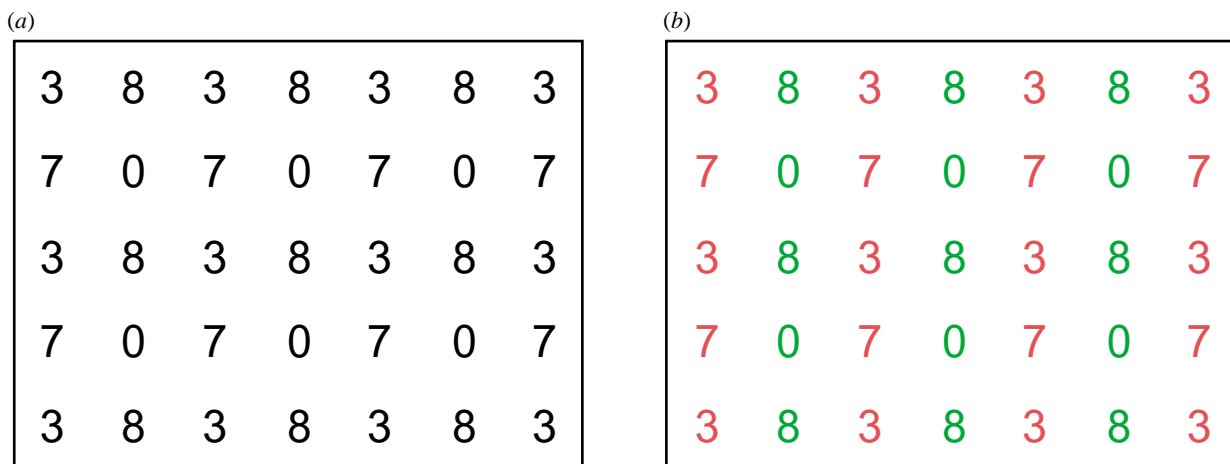


Figure 1. (a) Schematic of displays used to test whether synaesthetically induced colours are able to affect grouping. Black graphemes ($1.5^\circ \times 2.2^\circ$) on a white background were presented until the subject responded. The spacing between graphemes was 4.0° horizontally and 3.4° vertically. The total display was $34.7^\circ \times 25.5^\circ$. Control subjects consistently grouped this display horizontally (grouping the 3s with the 8s). (b) However, subject E.R. perceived 3s and 7s as red and 8s and 0s as green. She therefore grouped the display vertically, consistent with her synaesthetically induced colours.

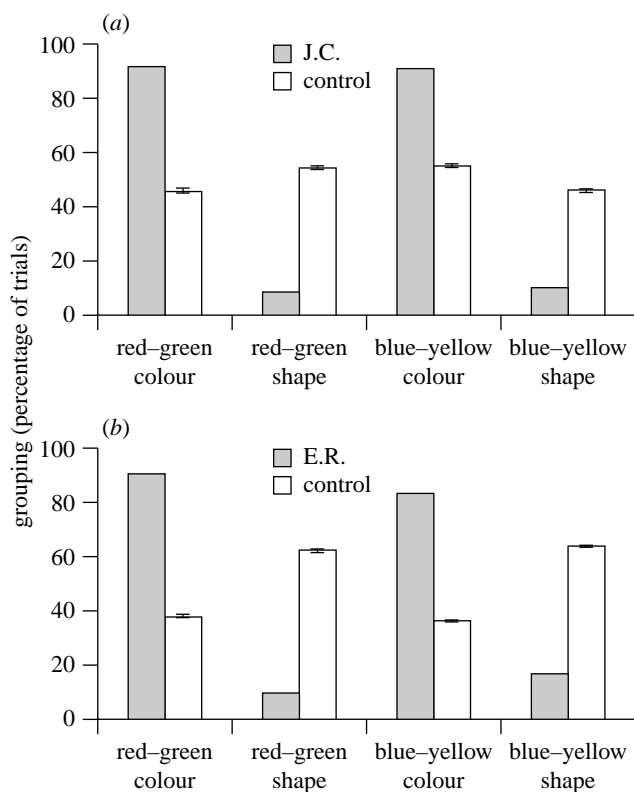


Figure 2. Individual comparisons for synaesthetes versus controls on the grouping task. The colours are those that were experienced by our two synaesthetes (J.C. and E.R.) when presented with our grouping displays. The scores are presented as the percentages of trials in which subjects grouped either on the basis of induced colours or on the basis of similarity of shape. White bars indicate control subject performance while shaded bars indicate synaesthete performance. The error bars indicate the standard error of the mean. No standard error is reported for the synaesthetes since they were unique observations. These comparisons were individually significant for J.C. (red-green, $t_9 = -4.25$ and $p < 0.01$ and blue-yellow, $t_9 = -2.52$ and $p < 0.05$) and for E.R. (red-green, $t_9 = -5.14$ and $p < 0.001$ and blue-yellow, $t_9 = -3.37$ and $p < 0.01$). See the text for pooled results.

grouping were presented once to each subject; this produced a total of 144 trials. The subjects were not informed of the purpose of the experiments. They were simply asked to indicate whether the display appeared to group horizontally or vertically. In order to be certain that the subjects understood the instructions, prior to testing they were initially presented with a simple dot display in which there was an unambiguous grouping into rows or columns on the basis of proximity.

Both synaesthetes grouped with their induced colours while control subjects generally grouped on the basis of shape. Subject J.C. consistently grouped the displays with his induced colours in 90.97% of trials, while control subjects showed a slight bias to grouping the displays on the basis of form for each of the two display types (red-green and blue-yellow) (see figure 2a). Because of differences in the graphemes selected, the difference between J.C.'s control population and E.R.'s was significant ($F_{3,39} = 4.71$ and $p < 0.01$), so we did not collapse over control populations. There were no significant differences between the conditions corresponding to the red-green and blue-yellow strategies among J.C.'s control population ($t_{19} = 1.8$ and $p > 0.05$). We therefore present the results for each subject pooled over the red-green and blue-yellow display types (see figure 2 for individual comparisons). The difference in grouping direction between J.C. and control subjects was significant ($t_{21} = 4.46$ and $p < 0.001$).

Subject E.R. consistently grouped the displays with her induced colours in 86.75% of trials, while control subjects were significantly biased to group in the opposite direction, grouping on the basis of similarity of shape in 62.4% ($t_9 = -3.29$ and $p < 0.01$) and 63.9% ($t_9 = -4.00$ and $p < 0.01$) of trials (see figure 2b). Again, there were no significant differences between the red-green and blue-yellow displays for E.R.'s control population ($t_{19} = 0.3$ and $p = 0.77$), so we collapsed over display type. The difference between E.R. and the controls was significant ($t_{21} = 6.09$ and $p < 0.001$). Our results therefore suggest that the synaesthetically induced colours are genuinely perceptual rather than being merely associative.

In our second experiment, we used stimuli analogous to the Ishihara (1997) pseudo-isochromatic tests for colour vision. As a preliminary demonstration, we had a matrix of small, black 5s scattered randomly on a white screen. Embedded among these

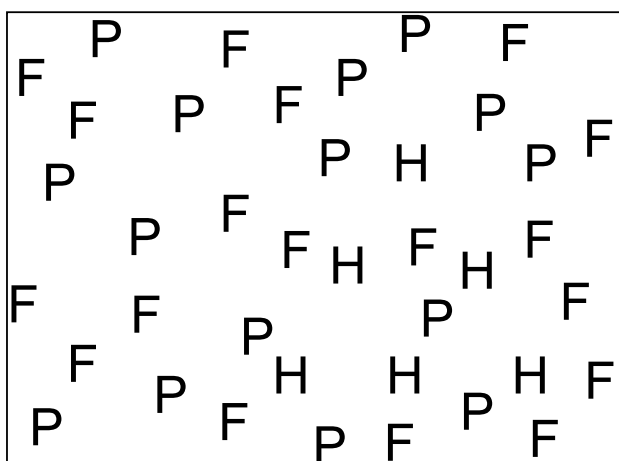


Figure 3. A matrix of Hs forming a triangle shape embedded in a background of distractors. Normals find it difficult to detect the triangle. Synaesthete J.C. did so easily (for him the Hs were seen as green, the background Fs were seen as yellow and the Ps were seen as red). Figures were presented in blocks of eight trials with the same grapheme used to create the embedded figure and two other graphemes used to create the remainder of the matrix throughout each block. The display, which consisted of 44–48 graphemes (each $0.6^\circ \times 0.8^\circ$), did not make use of the full screen, but instead used the central $13.2^\circ \times 10.0^\circ$ area, which is indicated by a black outline. The subjects were told which grapheme would compose the embedded form at the beginning of each block. Embedded forms, which were composed of six to eight graphemes, were presented in randomly selected locations near the centre of the screen and were *ca.* $6\text{--}7^\circ$ wide and $4\text{--}5^\circ$ high. Rectangles were clearly different from squares, with the width of each rectangle being twice its height. Each subject was given two practice trials prior to the first trial, one in which the display remained on screen until a keyboard press indicated that the subject was ready to continue and one timed presentation in order to familiarize the subjects with the procedure in each trial. The block presentation order was counterbalanced across subjects. Twenty normal controls were tested for each synaesthete in order to determine baseline performance and assess potential differences in task difficulty. Because the graphemes used to create the embedded figure were tailored separately for each synaesthete, two-tailed *t*-tests were used for determining whether group differences existed in the two tasks. The groups were not significantly different from each other ($t_{39} = 0.88$ and $p = 0.39$). We therefore pooled the results of the 40 control subjects.

was a set of black 2s (mirror images of 5s) forming a global shape such as a square or a triangle. Normal subjects cannot segregate the 2s from the 5s since they are too similar (Beck 1966; Treisman & Gelade 1980; Julesz 1981) but we found that the synaesthetic subjects could do so easily and discern the global shape.

We conducted a more formal experiment along these lines on our two synaesthetes (J.C. and E.R.) and 40 normal controls (20 for each synaesthete). One of four different shapes (a square, rectangle, triangle or diamond) composed of small graphemes was embedded in a matrix of other small graphemes (figure 3). The graphemes were again chosen so that each synaesthete would experience either red–green or blue–yellow pairs (e.g. the figure would appear red to each synaesthete while the background would appear green or vice versa). Each stimulus matrix was presented for 1s after which subjects would indicate which of the

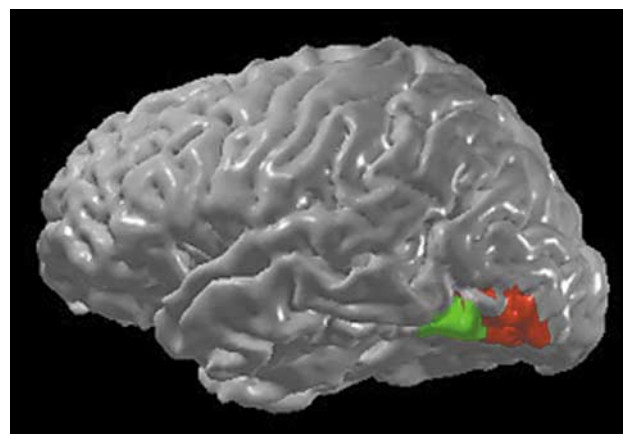


Figure 4. Schematic showing that cross-wiring between area V4 and the number-grapheme area in the fusiform gyrus might be the neural basis of grapheme-colour synaesthesia. Area V4 is shown in red and the number-grapheme area is shown in green (after Rickard *et al.* 2000). Area V4 was defined in one of the authors (E.M.H.) using standard functional magnetic resonance imaging methods for defining retinotopic visual areas (Engel *et al.* 1994, 1997); the location of the number area was estimated from the results of Rickard *et al.* (2000) (average coordinates for left hemisphere, -29.5 , -54.8 and -12.0).

four shapes they had seen via a keyboard button press (see the legend to figure 3 for details). The two synaesthetes were significantly better (mean per cent correct 81.25%) ($t_{40} = -2.07$ and $p < 0.05$) than the controls. Performance for the control subjects was better than chance (59.4%), indicating that they understood the task, but found it difficult to find the embedded shape. Since synaesthetes were better and significantly so than normals, we conclude that the phenomenon is genuinely perceptual and not confabulatory in origin, nor based on memory associations.

Next, we had our two synaesthetes (J.C. and E.R.) look at a fixation spot in the centre of the screen while we moved the target grapheme (e.g. a 5 or an E) gradually outwards. To our surprise, the subjects no longer saw the numbers as coloured at a critical distance! We repeated the experiment for both subjects after having enlarged the numbers in order to scale for eccentricity (Anstis 1998). Graphemes that elicited red, green, blue or yellow were presented for 1s while subjects fixated a central fixation cross. This presentation time was chosen in order to minimize the possibility of eye movements while allowing the synaesthetic subjects enough time to experience their colours (see below). The subjects indicated which number was presented and then indicated what, if any, colour they experienced. One of four graphemes was presented at one of three eccentricities: 5.5 , 10.9 and 12.1° . The graphemes were scaled for eccentricity and were $3.1^\circ \times 2.1^\circ$ (height \times width) when presented near fixation, while at the periphery they were $4.7^\circ \times 3.0^\circ$ (height \times width). Both subjects identified all graphemes perfectly, even at 12.1° eccentricity. Subject E.R. experienced no colours when numerals were presented beyond 11° eccentricity in either visual field while subject J.C. experienced no colours when graphemes were presented beyond 11° , but only for graphemes presented in his left visual field. This observation also argues strongly against metaphor or memory. Why would the grapheme fail to evoke a memory of a colour when it is still clearly visible? Memories ordinarily show positional invariance.

We propose instead that synaesthesia arises from cross-wiring between adjacent brain maps in a manner analogous to the

'remapping' of face to hand that occurs in area S1 following arm amputation (Ramachandran *et al.* 1992; Ramachandran & Rogers-Ramachandran 1995; Ramachandran & Hirstein 1998). Such cross-wiring could occur between colour areas V4 (Lueck *et al.* 1989; Zeki & Marini 1998) or V8 (Hadjikhani *et al.* 1998), which are located in the fusiform gyrus and the 'visual number grapheme' area, which is directly adjacent to it in the same gyrus (Pesenti *et al.* 2000; Rickard *et al.* 2000) (see figure 4). We are currently exploring this possibility using functional magnetic resonance imaging. Given that area V4 emphasizes central vision (Gattass *et al.* 1988), the cross-wiring might also be expected to affect central vision predominantly, even though the representation of area V4 extends over 35–40° of the contralateral visual field (Gattass *et al.* 1988). Consistent with this hypothesis, we found that, when presented with real colours in the periphery, both synaesthetes were able to identify the colours correctly in 100% of trials.

We then explored the temporal dynamics of the evoked colours. We presented J.C. and E.R. with a black grapheme (visual angle 2.5°×1.8°) at fixation and alternated it with a second grapheme at speeds varying from 1 to 20 Hz. At low speeds (less than 4 Hz), the subjects experienced their colours alternating with the graphemes. The number form could still be seen alternating at speeds higher than 5 Hz (up to *ca.* 10 Hz), but the colours were no longer experienced.

3. DISCUSSION

Taken collectively, these results strongly imply that synaesthesia is a genuine perceptual effect, which is possibly caused by cross-wiring in specific brain areas. Since the phenomenon runs in families, it is tempting to speculate that a mutation (perhaps X-linked; see Bailey & Johnson 1997) causes excessive proliferation (or defective pruning) of neural connections between adjacent brain maps, e.g. between area V4 and the number area in the fusiform gyrus (our two synaesthetic subjects both had parents who were synaesthetic). If so, one can go from a single gene to a specific brain area to detailed psychophysics all in a single 'preparation'—a strategy that has been tried with modest success in *Drosophila* (e.g. Cutforth & Gaul 1997) but not in humans. It is common knowledge that there is a great amount of heterogeneity among synaesthetes (which is perhaps caused by cross-wiring at different stages) and it remains to be seen how general the results reported here are. Regions concerned with more abstract numerical concepts and more sophisticated colour processing both lie near the angular gyrus. If cross-wiring occurred at this later stage, then the numerical concept itself might be expected to evoke specific colours.

We have recently begun testing a third synaesthete (S.S.) who experiences colours evoked by faces (both photographs and cartoon faces), the saturation and hue of which vary monotonically with facial expression (e.g. happy evokes red while sad evokes green). This would be consistent with our speculations on cross-wiring in the fusiform gyrus, which is also known to contain cells that respond to faces (Rolls & Tovee 1995; Kanwisher *et al.* 1997). Intriguingly, this subject is colour anomalous (s-cone weakness), but he sees 'weird' number-evoked colours that are 'extra-spectral' for him (i.e. he cannot see them in the real world, but experiences them in response to graphemes or faces).

This observation again supports the cross-wiring hypothesis rather than the memory association hypothesis (you cannot 'remember' a colour you have never seen!). Further study of this subject may throw light on the old philosophical conundrum raised by Moyleux (see Locke 1690) as to whether someone can experience completely novel 'qualia' never before experienced.

Synaesthesia has too often in the past been dismissed as childhood memories or 'mere metaphor', which is an example of the classic fallacy of trying to explain an enigma (synaesthesia) with a mystery (metaphor). Since our understanding of the neural representation of metaphor is still in its infancy, explaining synaesthesia as mere metaphor is unlikely to be a fruitful strategy. Indeed, our results suggest that we can turn the problem on its head and argue that understanding synaesthesia (a concrete perceptual effect the anatomical locus of which can be potentially pinned down) can provide an experimental lever for understanding the neural basis of metaphors. Metaphor involves linking one conceptual map (e.g. taste of cheese) with another seemingly unrelated one (e.g. tactile; 'sharp' or 'flat'), perhaps as a way of economizing on computational burden (Lakoff 1987). In addition, it has been shown (Ullman 1945; Williams 1976) that sensory adjectives undergo systematic shifts from one sensory domain to another (e.g. loud colours or bitter cold).

Perhaps a genetically based excess of connections in some individuals leads to both synaesthesia and a propensity for metaphor and, hence, the higher incidence of synaesthesia among artists, poets and novelists (Root-Bernstein & Root-Bernstein 1999). It has not escaped our notice that this hypothesis may also explain why we find certain tastes and smells 'disgusting' and scrunch up our noses (Darwin 1872) but also speak of someone being morally 'disgusting' and make the same face (e.g. if a drunk makes an unwanted sexual pass at a woman). Is it entirely a coincidence that smell and taste 'maps' are in the orbitofrontal frontal lobes, the same place where 'maps' for moral disgust might lie (Lane *et al.* 1997; Northoff *et al.* 2000)?

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REFERENCES

- Anstis, S. 1998 Picturing peripheral acuity. *Perception* **27**, 817–825.
- Bailey, M. E. S. & Johnson, K. S. 1997 Synaesthesia: is a genetic analysis feasible? In *Synaesthesia: classic and contemporary readings* (ed. S. Baron-Cohen & J. E. Harrison), pp. 182–207. Oxford, UK: Blackwell Publishers, Inc.
- Beck, J. 1966 Effect of orientation and of shape similarity on perceptual grouping. *Percept. Psychophys.* **1**, 300–302.
- Cutforth, T. & Gaul, U. 1997 The genetics of visual system development in *Drosophila*: specification, connectivity and asymmetry. *Curr. Opin. Neurobiol.* **7**, 48–54.
- Cytowic, R. E. 1989 *Synaesthesia: a union of the senses*. New York: Springer.
- Darwin, C. 1872 *The expression of the emotions in man and animals*. London: John Murray.

- Engel, S. A., Rumelhart, D. E., Wandell, B. A. & Lee, A. T. 1994 fMRI of human visual cortex. *Nature* **369**, 525.
- Engel, S. A., Zhang, X. & Wandell, B. A. 1997 Colour tuning in human visual cortex measured with functional magnetic resonance imaging. *Nature* **388**, 68–71.
- Galton, F. 1880 Visualised numerals. *Nature* **21**, 494–495.
- Galton, F. 1883 *Inquiries into human faculty and its development*. London: Dent & Sons.
- Gattass, R., Sousa, A. P. B. & Gross, C. G. 1988 Visuotopic organization and extent of V3 and V4 of the macaque. *J. Neurosci.* **8**, 1831–1845.
- Gray, J. A., Williams, S. C. R., Nunn, J. & Baron-Cohen, S. 1997 Possible implications of synaesthesia for the hard question of consciousness. In *Synaesthesia: classic and contemporary readings* (ed. S. Baron-Cohen & J. E. Harrison), pp. 173–181. Oxford, UK: Blackwell Publishers, Inc.
- Hadjikhani, N., Liu, A. K., Dale, A. M., Cavanagh, P. & Tootell, R. B. H. 1998 Retinotopy and colour sensitivity in human visual cortical area V8. *Nature Neurosci.* **1**, 235–241.
- Harrison, J. E. & Baron-Cohen, S. 1997 Synaesthesia: a review of psychological theories. In *Synaesthesia: classic and contemporary readings* (ed. S. Baron-Cohen & J. E. Harrison), pp. 109–122. Oxford, UK: Blackwell Publishers, Inc.
- Ishihara, S. 1997 *Ishihara's tests for colour deficiency*. Tokyo: Kanehara & Co., Ltd.
- Julesz, B. 1981 Textons, the elements of texture perception, and their interactions. *Nature* **290**, 91–97.
- Kanwisher, N., McDermott, J. & Chun, M. M. 1997 The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* **17**, 4302–4311.
- Lakoff, G. 1987 *Women, fire and dangerous things*. University of Chicago Press.
- Lane, R. D., Reiman, E. M., Ahern, G. L. & Schwartz, G. E. 1997 Neuroanatomical correlates of happiness, sadness, and disgust. *Am. J. Psychiatr.* **154**, 926–933.
- Locke, J. 1690 *Essay concerning human understanding*, ch. 8. London: E. Mory.
- Lueck, C. J., Zeki, S., Friston, K. J., Deiber, M. P., Cope, P., Cunningham, V. J., Lammertsma, A. A., Kennard, C. & Frackowiak, R. S. 1989 The colour centre in the cerebral cortex of man. *Nature* **340**, 386–389.
- Northoff, G. (and 16 others) 2000 Functional dissociation between medial and lateral prefrontal cortical spatiotemporal activation in negative and positive emotions: a combined fMRI/MEG study. *Cerebr. Cortex* **10**, 93–107.
- Paulesu, E., Harrison, J., Baron-Cohen, S., Watson, J. D. G., Goldstein, L., Heather, J., Frackowiak, R. S. J. & Frith, C. D. 1995 The physiology of coloured hearing: a PET activation study of colour-word synaesthesia. *Brain* **118**, 661–676.
- Pesenti, M., Thioux, M., Seron, X. & De Volder, A. 2000 Neuroanatomical substrates of Arabic number processing, numerical comparison, and simple addition: a PET study. *J. Cogn. Neurosci.* **12**, 461–479.
- Ramachandran, V. S. & Hirstein, W. 1998 The perception of phantom limbs: the D. O. Hebb lecture. *Brain* **121**, 1603–1630.
- Ramachandran, V. S. & Rogers-Ramachandran, D. 1995 Touching the phantom. *Nature* **377**, 489–490.
- Ramachandran, V. S., Rogers-Ramachandran, D. & Stewart, M. 1992 Perceptual correlates of massive cortical reorganization. *Science* **258**, 1159–1160.
- Rickard, T. C., Romero, S. G., Basso, G., Wharton, C., Flitman, S. & Grafman, J. 2000 The calculating brain: an fMRI study. *Neuropsychologia* **38**, 325–335.
- Rolls, E. T. & Tovee, M. J. 1995 Sparseness of the neuronal representation of stimuli in the primate temporal visual cortex. *J. Neurophysiol.* **73**, 713–726.
- Root-Bernstein, R. & Root-Bernstein, M. 1999 *Sparks of genius: the thirteen thinking tools of the world's most creative people*. Boston: Houghton Mifflin Co.
- Treisman, A. M. & Gelade, G. A. 1980 A feature-integration theory of attention. *Cogn. Psychol.* **12**, 97–136.
- Ullman, S. 1945 Romanticism and synaesthesia: a comparative study of sense transfer in Byron and Keats. *Publ. Mod. Lang. Assoc. Am.* **60**, 811–827.
- Williams, J. M. 1976 Synesthetic adjectives: a possible law of semantic change. *Language* **52**, 461–478.
- Zeki, S. & Marini, L. 1998 Three cortical stages of colour processing in the human brain. *Brain* **121**, 1669–1685.