

# The physiology of coloured hearing

## A PET activation study of colour–word synaesthesia

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### Summary

In a small proportion of the normal population, stimulation in one modality can lead to perceptual experience in another, a phenomenon known as synaesthesia. In the most common form of synaesthesia, hearing a word can result in the experience of colour. We have used the technique of PET, which detects brain activity as changes of regional cerebral blood flow (rCBF), to study the physiology of colour–word synaesthesia in a group of six synaesthete women. During rCBF measurements synaesthetes and six controls were blindfolded and were presented with spoken words or pure tones. Auditory word, but not tone, stimulation triggered synaesthesia in synaesthetes. In both groups word stimulation compared with tone stimulation activated the classical language areas of the perisylvian regions. In synaesthetes, a

number of additional visual associative areas, including the posterior inferior temporal cortex and the parieto-occipital junctions, were activated. The former has been implicated in the integration of colour with shape and in verbal tasks which require attention to visual features of objects to which words refer. Synaesthetes also showed activations in the right prefrontal cortex, insula and superior temporal gyrus. By contrast, no significant activity was detected in relatively lower visual areas, including areas V1, V2 and V4. These results suggest that colour–word synaesthesia may result from the activity of brain areas concerned with language and visual feature integration. In the case of colour–word synaesthesia, conscious visual experience appears to occur without activation of the primary visual cortex.

**Keywords:** conscious perception; visual physiology; multimodal integration

### Introduction

In this paper we seek to examine the neural basis of colour–word synaesthesia (from the Greek; ‘syn’ = union, ‘aisthesis’ = sensation), which has been described in the scientific literature for almost 300 years. John Locke (1690) described ‘a studious blind man who bragged one day that he now understood what scarlet was . . . like the sound of a trumpet’. A similar account was given by Thomas Woolhouse (1710), who described a blind subject who reported perceiving sound-induced coloured experiences. However, no systematic studies of synaesthesia were reported until the end of the last

century when Francis Galton (1883) described the experiences of synaesthetes. He noted that the most frequently occurring form appears to be that known as coloured hearing.

A number of composers have been described as having synaesthesia; for example, Marks (1975) suggested that Scriabin had synaesthesia and reported that the composer added a coloured dimension to live performances of his works. Other writers have pointed to the many synaesthetic statements made by Messiaen in describing his musical composition (Bernard, 1986). Since Galton’s studies,

compared with an appropriate baseline). We used the technique of PET which permits measurement of changes in relative rCBF as an index of altered synaptic activity across the entire brain volume simultaneously (Raichle, 1987). There are several types of synaesthesia; we have narrowed our study to those whose synaesthesia consists of seeing colours in response to the letters of a word, a phenomenon we call colour-word synaesthesia. We hypothesised that in synaesthetes, hearing words might elicit unusual levels of activity in extrastriate brain areas responsible, under normal circumstances, for colour perception (i.e. the fusiform gyrus) (Lueck *et al.*, 1989; Zeki *et al.*, 1991). Alternatively, synaesthesia could be due to the simultaneous activity of auditory verbal cortex with some associative visual area responsible for a conjoint representation of letter shapes and colours. A suitable candidate for such an area would be the inferior temporal region which is active when subjects have to detect objects on the basis of conjoint features such as shape and colour (Corbetta *et al.*, 1991a). Finally, we were also interested to see whether primary visual cortex (areas V1 and V2) is active during colour-word synaesthesia. There are feedback connections between associative and primary visual areas (Shipp and Zeki, 1989a, b). Activation of V1 and V2 during synaesthesia would provide strong evidence for a role for such modulatory feedback in visual experience since no direct visual stimulation would be occurring. On the other hand, a lack of activity in V1 and V2 would suggest that the brain is capable of generating conscious percepts without the contribution of primary sensory areas (Barbur *et al.*, 1993; Zeki *et al.*, 1993).

## Methods

### Subjects

Experimental subjects included five right-handed females and one left-handed female with colour-word synaesthesia (mean age  $45 \pm 7$  years). Subjects were selected on the basis of the presence of colour-word synaesthesia exclusively, with no similar experiences for any other auditory stimuli (e.g. music). Magnetic resonance imaging scans excluded macroscopic anatomical damage. The control group included five right-handed normal females and one left-handed normal female (mean age  $40 \pm 6$  years) who had never experienced synaesthesia. All subjects were neurologically normal, with no history of neurological or psychiatric disease, and none was taking psychoactive drugs. Handedness was tested with the Edinburgh Inventory (Oldfield, 1971). The studies were approved by the Hammersmith Hospital Medical Ethics Committee and permission to administer radioactivity was obtained from the Administration of Radioactive Substances Advisory Committee (ARSAC), UK. All subjects gave written informed consent. The total radiation dose in effective dose equivalents did not exceed 7.2 MSv per subject.

### Psychological assessment

All subjects were tested for general intelligence using the National Adult Reading Test (NART) (Nelson, 1982). In

addition, the test of genuineness for synaesthesia (Baron-Cohen *et al.*, 1987) was administered in order to verify that subjects did indeed have synaesthesia. This test requires subjects to describe colours triggered by more than 100 lexical items. At a later date (average span 6 months; range 1–10 months), and without prior warning, subjects are again tested on the same word list and the two sets of responses are compared to test for consistency.

In order to determine whether colour-word synaesthetics are triggered by the phonological characteristics of verbal stimuli or by their letters, we also administered a further test of words paired such that they shared homophonic first syllables (e.g. *photograph* and *fish*) or non-homophonic first syllables starting with the same letter (e.g. *apple* and *art*). If the synaesthetics were based on a phonological code, then paired items such as *photograph* and *fish* would elicit the same colour; if the same colours were triggered by pairs such as *apple* and *art* this would suggest that synaesthetics were based on letters. A full description of this test is given in the Appendix.

## PET activation experiment

### Psychological stimulation

Subjects underwent 12 consecutive relative rCBF measurements, six for each of the two following conditions.

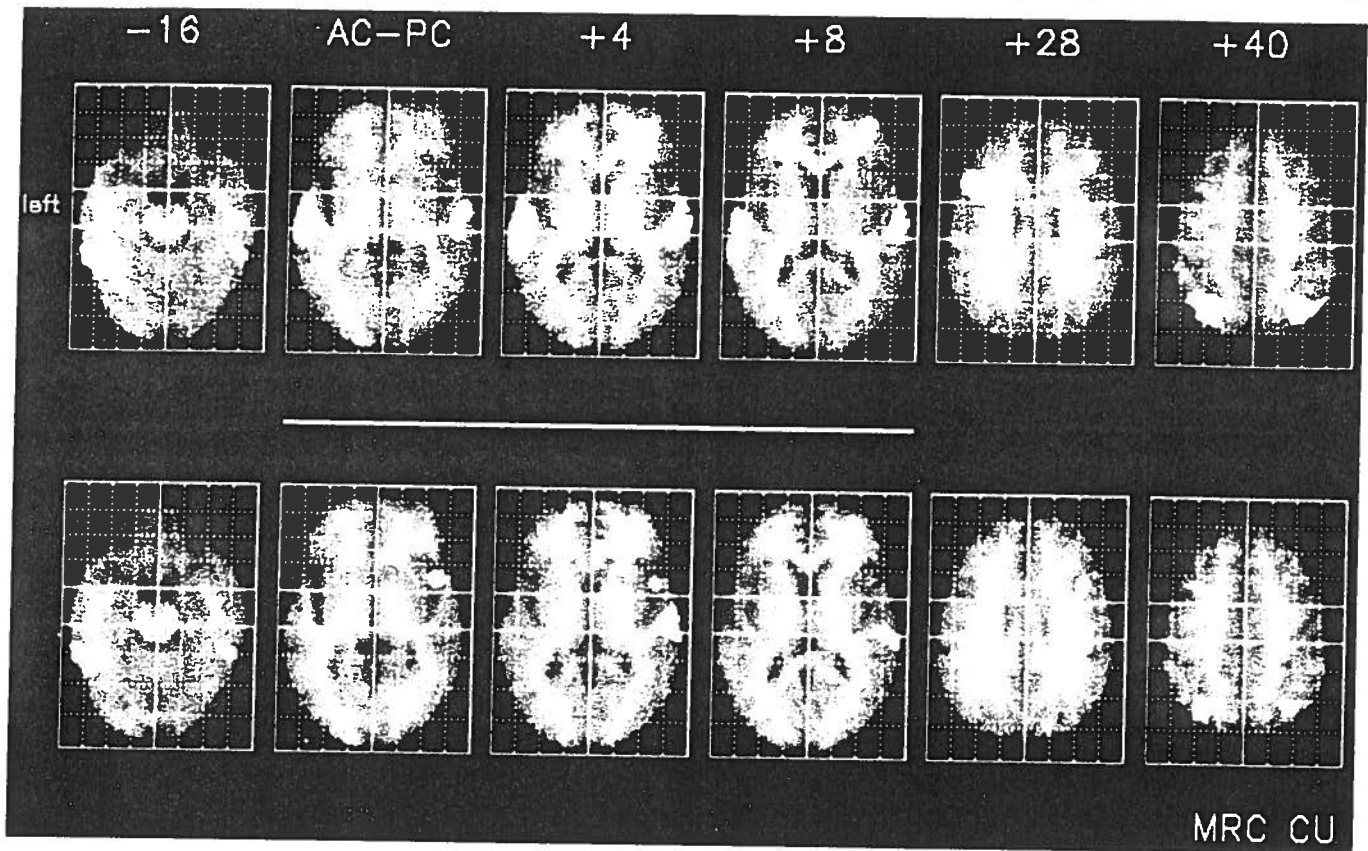
(i) Control task: single tone perception. Single pure tones were delivered through earphones. Tone frequencies ranged randomly from 262 to 523 Hz (within human voice frequencies). Subjects were blindfolded and instructed to listen to the tones and tap their left index finger for every tone heard. Stimulus duration was 0.5 s. To minimize automaticity in performance, interstimulus intervals were randomly varied from 0.5 to 1.5 s.

(ii) Experimental task: single word perception. Single words were delivered in the same fashion as tones and subjects tapped their left index finger for every word heard. Performance requirements were the same as for tones. All stimuli were highly imaginable concrete words derived from the Oxford Psycholinguistic data base (Quinlan, 1992).

The subjects with synaesthesia were invited to listen passively to the stimuli and to let the colour perception occur automatically. Normal controls were not informed in advance that they were acting as a control group for synaesthesia. They were also invited to perceive the words in a passive fashion.

### Experimental design

We used a fully factorial design for our experiment with one between-group factor (synaesthesia+ versus synaesthesia-) and two within-group factors (nature of stimuli: words versus tones; replications). Accordingly, we postulated that the functional anatomy of synaesthesia would be detected in those brain regions where differences in perfusion between the two groups were detectable. Each subject also underwent



**Fig. 1** Activations during colour-word synaesthesia. (A) The location of the rCBF increases induced by word perception in synaesthetes is illustrated. Areas of significant rCBF increase have been plotted on averaged MRI images transformed into the stereotactic space of Talairach and Tournoux (1988). The activated areas are displayed in white. Level of significance (expressed as Z scores) and stereotactic co-ordinates of activation foci are reported in Table 2A. (B) The locations where subjects with synaesthesia showed significantly greater activation than controls in response to the same word stimuli are illustrated. These areas include the left inferior temporal cortex, the right prefrontal, insular and superior temporal cortex, and the parieto-occipital junctions bilaterally (see also Table 2C). AC-PC = plane corresponding to the anterior commissure-posterior commissure (bicommissural) line. Distances (in millimetres) refer to the AC-PC plane.

50 ml/100/ml/min and differences in global activity were removed following an analysis of covariance with global counts as covariate and activation condition as treatment (Friston *et al.*, 1990). This analysis generated 12 mean values across subjects for each treatment (condition) and the associated error variance estimates for every voxel. Appropriately weighted comparisons of means were made for all voxels by using the *t* statistic, thus generating images of *t* values that constituted statistical parametric maps (SPM{*t*}) (Friston *et al.*, 1990, 1991b; Frackowiak and Friston, 1994) which were transformed to Z distribution maps.

**Results**

**Psychological profile**

The IQ estimates were in the superior range for all subjects with synaesthesia who also achieved at least 90% consistency on the test of genuineness of synaesthesia (see Table 1). In addition, the Basis of Colour-Word Synaesthesia Test showed that in all subjects the chromatic quality of coloured hearing

**Table 1** Details of synaesthetes

Subject	Age	NART*	TOG† (% correct)	Handed‡
C.C.	45	124	100	90R
A.C.	61	124	95	100R
C.D.	64	128	100	80R
R.Y.	46	120	100	80L
E.H.	47	115	100	100R
B.J.	58	127	90	100R

\*National Adult Reading Test; †Test of Genuineness; ‡Edinburgh Inventory of Handedness (Oldfield, 1971).

was by far based on letters. An example of one subject's performance is reported in the Appendix.

For all the synaesthetic perception consisted of seeing the words themselves in a colour which was dominated by the colour of the first letter in five cases, or by the first vowel in one case. In five out of six of our subjects, numbers (from 1 to 9) have their own colour which is different from that of the first letter of the number names. Interestingly, our subjects

Table 2

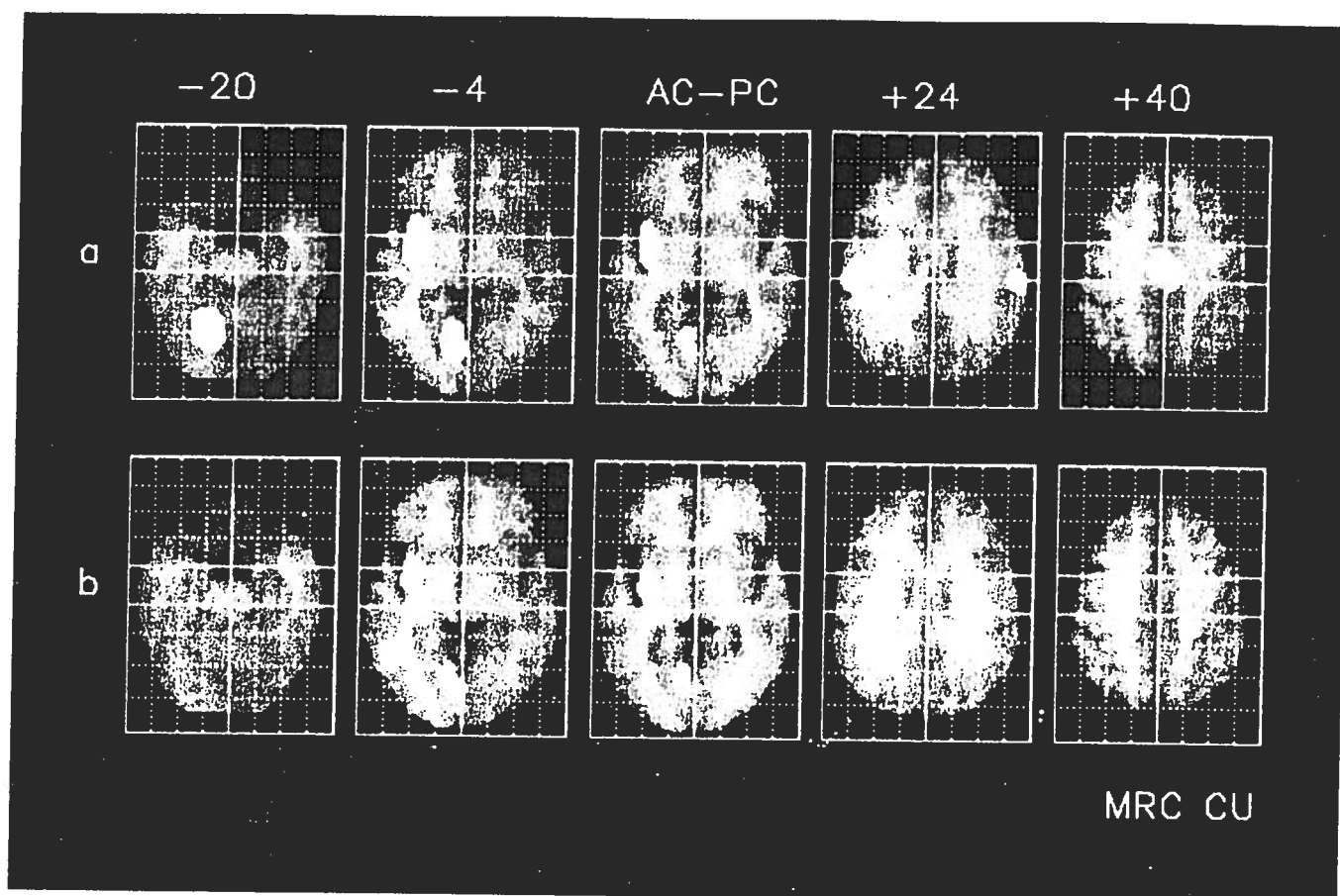
Brain structure	Left				Right			
	x	y	z	Z score	x	y	z	Z score
<i>(A) Cerebral structures activated by word perception in normal controls</i>								
Inferior frontal gyrus (BA 44/45)	-48	16	16	4.4	—	—	—	—
Superior temporal gyrus (BA 21/ 22)	-52	-14	0	6.1	52	-12	0	3.6
Middle temporal gyrus (BA 21)	-54	-42	4	4.0	46	-26	0	4.4
<i>(B) Cerebral structures activated by word perception in synaesthetes</i>								
Middle frontal gyrus (BA 46/10)	—	—	—	—	30	48	8	3.7
Inferior frontal gyrus (BA 44/9)	-42	12	28	4.3	—	—	—	—
Insula	—	—	—	—	44	8	0	4.5
Superior temporal gyrus (BA 22)	-52	-10	0	7.6	56	-10	4	6.8
Middle temporal gyrus (BA 21)	-54	-30	4	5.2	—	—	—	—
Posterior inferior temporal cortex (BA 20/37)	-50	-42	-12	4.1	40	-46	-16	2.6
Superior occipital gyrus/superior parietal lobule (BA 19/7)	-26	-78	40	2.5	32	-68	40	2.5
	-26	-68	44	2.7				
<i>(C) Differences in activation in synaesthetes compared with controls</i>								
Middle frontal gyrus (BA 46/10)	—	—	—	—	30	50	8	2.9
Inferior frontal gyrus (BA 44/9)	—	—	—	—	36	8	28	3.1
Insula	—	—	—	—	40	8	0	3.5
Superior temporal gyrus (BA 22)	—	—	—	—	54	-10	4	3.1
Posterior inferior temporal cortex (BA 20/37)	-54	-42	-16	2.4	—	—	—	—
Superior occipital gyrus/superior parietal lobule junction (BA 19/7)	-16	-78	32	2.9	—	—	—	—
	-30	-62	40	3.0	26	-64	40	3.0

PET results are reported with reference to anatomical structures/landmarks and to Brodmann's areas as tentatively defined in the stereotactic space by Talairach and Tournoux (1988). It should be remembered that Brodmann's areas topography can not be precisely defined in life and may be insufficient to identify an activated area. A complete identification of an activated area is provided by combining all the information given in the tables. *x*, *y* and *z* refer to the stereotactic co-ordinates in the three orthogonal dimensions of the atlas of Talairach and Tournoux (1988). The reference point is the junction of the vertical anterior commissural line and the intercommissural line. The reference plane is the bicommissural plane. *x* refers to millimetres left (-) and right of the reference point. *y* to millimetres anterior and posterior (-) to the reference point and *z* to planes above and below (-) the reference plane. The Z score indicates the significance of cerebral blood flow change for each comparison, at the relevant location. BA = Brodmann area.

generated *de novo* every time. It remains to be explained why coloured hearing is a one-way phenomenon: in our subjects, synaesthesia occurs with auditory stimulation but not with visual stimulation when reading, unless sub-vocalization occurs.

It is interesting that, in most cases, numbers also have their own colour which is independent from the letters that constitute the name of the number. This observation would point further to a link between colours and specific language symbols. These peculiar associations are reminiscent of those links between some objects and a particular colour (e.g. blood-red, carrot-orange, etc.). If we accept that letters and numbers are special instances of coloured objects for synaesthetes, it is possible that these representations are evoked via auditory stimulation. Indeed, there is some evidence that points to such a possibility

in normals. For a skilled reader, there is an automatic connection between the sound of a word and its visual appearance. For example, orthography can interfere with rhyme judgements even when words are presented aurally, so that it takes longer than expected to decide that *cough* and *bough* do not rhyme (Seidenberg and Tanenhaus, 1979). Accordingly, the special feature of our synaesthetes is not that auditory verbal stimulation elicits a visual representation of words, rather it is the link between word sounds, orthography and specific colours. The *auditory* component of verbal stimulation is therefore a prerequisite to elicit synaesthesia as in our subjects silent reading does not provoke synaesthesia. This is surprising as visual presentation of words automatically activates the visual orthographic lexicon (Patterson and Morton, 1985).



**Fig. 2** Deactivations during colour-word synaesthesia. (A) Regional CBF decreases during word perception in synaesthetes are illustrated. Areas of significant rCBF decrease are displayed in the same fashion as in Fig. 1. Level of significance (expressed as Z scores) and stereotactic co-ordinates of de-activated regions are presented in Table 3B. (B) The locations where subjects with synaesthesia showed significantly greater de-activation than controls with the same stimuli are illustrated. These areas include the left lingual gyrus and insula (Table 3C). For conventions, see Fig. 1 caption.

functional imaging studies have shown activation of additional areas (temporal and dorsal occipital cortex, Corbetta *et al.*, 1991a, b; parietal cortex, Gulyas and Roland, 1991), during tasks that involve colour discrimination. A possible reconciliation of pathological and functional imaging data from normal subjects is to assume that within the brain areas of the 'colour stream' there must be a hierarchy, where the lingual-fusiform gyri represent the minimum and indispensable neuronal substrate to permit colour perception, whereas additional areas (dorsal occipital, temporal and parietal cortex) may represent higher stages of visual information processing which make use of colour.

The most striking observation of our study is that, unlike what happens with frank visual stimulation, there was no activity in classical visual areas. Among these we include area V1 and the surrounding V2 and V4. We have discounted the rCBF increase detected in left area V4 because of its small statistical magnitude and because no significant difference was detectable in comparison with the control group, though it is possible that area V4 contributes to synaesthesia in some of our subjects. At any rate, there were far more significant changes in other areas, which would

therefore seem to be more prominently involved in the particular phenomenon that we are investigating. Among these are (i) the left (and, to a lesser extent, right) PIT cortex, (ii) the parieto/occipital junctions, and (iii) the left lingual gyrus where rCBF decreases were observed. This pattern and the absence of consistent area V4 involvement raises the possibility that colour percepts triggered by a non-visual stimulus can be evoked by cortical areas other than area V4 in certain circumstances, even though they be aberrant or unusual, and that language stimulation can evoke such percepts. The potential relevance of these visual areas for synaesthesia is discussed below.

#### *The PIT cortex*

In the macaque, the PIT cortex has a large proportion of colour-selective neurons (46 out of 65 neurons sampled = 71%; Komatsu *et al.*, 1992); this area is massively connected to area V4 (Desimone *et al.*, 1980; Fries and Zeki, 1983) and it is currently considered primarily a visual cortical area rather than 'polyfunctional' in nature (Van Essen, 1985).

In man, Corbetta *et al.* (1991a) found activation of PIT

neurons have also been demonstrated in it with neurophysiological recordings (Komatsu and Ideura, 1993). This evidence is paralleled by a recent PET activation study in humans.

Bottini *et al.* (1994) have studied with PET the functional anatomy of retrieving prototypical object shapes. Subjects were invited to trace in the air with their right first finger the contour of a square, a circle, a triangle or the infinitive symbol, choosing the shapes at will. This task was associated with a robust activation of left PIT cortex.

It is of crucial importance that no activation has been found in PIT cortex in studies of single word perception (Petersen *et al.*, 1988; Wise *et al.*, 1991), nor was this area significantly activated in our controls during auditory verbal stimulation. However, semantic judgements based, in part, on visual associations of words do engage this area. In the experiment by Démonet *et al.* (1992) subjects were invited to monitor pairs of words (an animal name and an adjective); target pairs were a positive adjective followed by the name of a small animal (e.g. kind mouse = target; kind elephant = distractor). Judging whether the animal is large or small involves visual imagery elicited by words, which may induce activation of PIT cortex.

To summarize, in both primates and humans the PIT region may contribute to both complex forms of colour perception or to higher level cognitive processes involving colour such as, for example, multimodal visual integration concerned with object recognition. The engagement of the PIT in synaesthesia may therefore have a great explanatory value as it is involved in both visual and language feature integration. This is precisely the level of integration necessary for synaesthesia (colour, shape, language).

### *The parieto-occipital junctions*

The interpretation of the activations of these structures in synaesthesia is not simple as there is no agreement between the literature on primates, the neurophysiological literature on brain damaged patients and functional imaging data from normal subjects. In the macaque, the parietal cortex is consistently connected to visual areas concerned with colour processing (Zeki, 1977; Seltzer and Pandya, 1980) but single cell recordings indicate no colour sensitivity in parietal neurons (Mountcastle *et al.*, 1984) nor do lesions here cause colour imperception (Ecott and Gaffan, 1991).

No cases of central achromatopsia due to parietal lesion have ever been reported in the human literature, although there are occasional reports of central dyschromatopsia (a milder form of central colour imperception) following parietal lesions (Capitani *et al.*, 1978; Pirozzolo *et al.*, 1981). In addition, a lesion of the left parietal cortex (documented by CT scan) has been associated to colour amnesia, a syndrome where affected patients have 'forgotten' previously learned associations between familiar objects and their colour (Varney and Digre, 1983). This same patient, however, also showed upper right quadrantopia that could not be explained by

the parietal lesion, suggesting additional undetected lesions in the left hemisphere.

Early PET experiments on passive colour perception or on attention to colour (Lueck *et al.*, 1989; Corbetta *et al.*, 1991*b*) did not show activation of the parietal cortex. On the other hand, other PET experiments concerned with active colour discrimination or with perception of form-from-colour have shown activation of the parietal cortex (Gulyas and Roland, 1991; Gulyas *et al.*, 1994*a, b*).

Given the disagreement between the different studies, we do not wish to over-interpret the functional relevance of the parieto-occipital cortex in synaesthesia. However, our findings seen corroborated by increasing evidence of a colour-sensitive cortical field in the human posterior parietal cortex.

### *Extravisual areas and synaesthesia*

Activations in extravisual areas in synaesthetes were lateralized to the right hemisphere: in the frontal lobe, in the superior temporal gyrus and in the insula. Such results would be consistent with the notion of right hemisphere dominance for the attentional demands required by visuo-perceptive tasks including those concerned with colour (De Renzi and Spinnler, 1967; Capitani *et al.*, 1978). Some recent PET studies support this suggestion. Corbetta *et al.* (1991*a*) found that the right dorsolateral prefrontal cortex is active when subjects are challenged with divided attention tasks for visual features (e.g. concurrent attention for colour and shape). A similar finding has been described by Zeki *et al.* (1993) for subjects engaged in observing a complex static drawing (the picture *Enigma* by I. Leviat) which generates an illusory visual motion perception. Prefrontal activity in this case may be explained by the attentional demands generated by the perceptual conflict inherent in the optical illusion. In line with these findings, we speculate that right prefrontal activity in subjects with synaesthesia may be due to the attentional demands of hearing words, which in this case convey double and sometimes conflicting information (verbal and chromatic: e.g. the word grass that elicits a blue percept). Interestingly, the patients with right frontal damage described by Capitani *et al.* (1978) were particularly impaired in the Farnsworth–Munsell 100 hue test, even when compared with patients with left-sided frontal lobe lesions. This observation rules out simple interpretations based on the malfunction of a general supervisory system and rather suggests a correlation between right frontal lobe activity and the visuo-perceptive attentional demands of the Farnsworth–Munsell task. Subjects with synaesthesia also showed greater activity in the right insula and in the right superior temporal gyrus than normal subjects which we cannot readily explain at this stage.

### *Cerebral deactivations: the left lingual gyrus and the insula*

In synaesthetes the left lingual gyrus, with the left insula, showed highly significant rCBF decreases during word

visual cortices (e.g. the lingual gyrus) might result from a form of modulatory (inhibitory) feedback.

### *Synaesthesia and conscious visual perception*

Implicit in a functional imaging experiment on perception is the desire to associate the brain activity detected and the perceptual events experienced by subjects. Accordingly, we propose that the brain activity detected in synaesthetes are the neurophysiological counterpart of synaesthetic perception. This statement has at least one important implication, namely that a *conscious visual perception* can occur in the absence of activation in the primary visual area, V1. Such a possibility has been denied for a long time on the basis of evidence from *blindsight*, a syndrome associated with area V1 lesions (for review, see Cowey and Stoerig, 1992; Zeki, 1993). However, a recent experiment by Barbur *et al.* (1993) shows that associative visual areas, possibly stimulated via alternative pathways to the geniculostriate connection, can promote a crude but *conscious* visual perception of motion even when area V1 is completely damaged. Indeed, Barbur *et al.* (1993) have been able to show that residual conscious motion perception in a 'blind' visual field was paralleled by activation of visual prestriate areas including the motion area V5. A further example of conscious visual perception in the absence of an explicit (additional) contribution of primary visual cortex is provided by the experiment on illusory visual motion perception in normal volunteers (Zeki *et al.*, 1993) which, in the visual cortex, was associated with the activation of visual area V5 without additional activity in V1. Conscious visual perception without the engagement of area V1 has a cost of poor topographical definition. In synaesthesia this may turn into an advantage since synaesthetic percepts are not confused with events in the outside visual world, while, in contrast, visual hallucinations are confused with reality by psychotic patients.

In conclusion, our thinking on colour-word synaesthesia and its neurophysiological implications can be summarized as follows. Colour-word synaesthesias are generated by an interaction between brain areas for language and higher vision. A key role in synaesthetic perception is played by associative areas, located at the boundary between the language and the visual systems. In man, some of these areas have been implicated in both attention for colour and complex language tasks based in part on imagery. Activation of some of these areas (e.g. PIT) may reflect a feed-forward convergence mechanism for integration.

Activity in the visual areas occurred in the absence of any direct visual stimulation, suggesting unusual anatomical connectivity between language and visual areas in synaesthesia.

We generalize our findings on colour-word synaesthesia and propose that the integration concerned with specific forms of synaesthesia is likely to occur where the two sensory dimensions implicated have a greater anatomical opportunity to be integrated, namely at their boundaries. Finally, the

neurophysiology of synaesthesia supports recent evidence that a conscious visual perception can occur in the absence of activation of primary visual cortex, implying that high level associative visual areas can contribute on their own to conscious visual perception.

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