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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.*, 1991*a*). 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, 1989*a, 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 ±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±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 synaesthesias 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 synaesthesias 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 synaesthesias 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

a T_1-weighted MRI scan, in order to improve anatomical localization of significantly activated areas via PET/MRI co-registration.

PET data acquisition

Regional CBF was measured by recording the distribution of cerebral radioactivity following the intravenous injection of ^{15}O-labelled water ($H_2{}^{15}O$) with the CTI 953B PET scanner (CTI Inc., Knoxville, Tenn., USA). Data were acquired by scanning with inter-detector collimating septa retracted (3D mode) (Townsend *et al.*, 1991). Each rCBF scan was divided into two frames: (i) 30-s measure of the background radiation; (ii) 2.45-min rCBF measurement with concurrent psychological stimulation. A $H_2{}^{15}O$ infusion (10 ml/min; 55 MBq/ml) was started at the beginning of the background frame and lasted for 2 min, followed by a 30-s flush of non-radioactive saline. Radioactivity reached the head at about 40 s after the start of infusion. Scans were corrected for attenuation (measured by a transmission scan), and the scans were reconstructed in 31 axial planes by three-dimensional filtered back projection with a Hanning filter of cut-off frequency 0.5 cycles/pixel. The resolution of the resulting images was 8.5×8.5×4.3 mm at full width half-maximum (Spinks *et al.*, 1992). The integrated counts accumulated over the second PET frame, after correction for background activity, were used as rCBF equivalents (Mazziotta *et al.*, 1985).

MRI data acquisition

The MRI scans were obtained with a 1 tesla Picker HPQ Vista system (Picker International, Cleveland, USA) using a radiofrequency spoiled volume acquisition that is relatively spin-lattice relaxation time (T_1) weighted to give good grey–white contrast and anatomical resolution [repeat time (TR) 24 ms; echo-time (TE) 6 ms; non-selective excitation with a flip angle of 35°; field of view in plane 25×25 cm; 192×256 in plane matrix with 128 secondary phase-encoding steps oversampled to 256; resolution 1.3×1.3×1.5 mm; total imaging time 20 min]. After reconstruction, MRI images were aligned parallel with the intercommissural line and interpolated to obtain a cubic voxel size of 1 mm, which permitted co-registration with PET images. The MRI images were also used to exclude anatomical lesions in our volunteers.

Image analysis

Calculations and image manipulations of PET and MRI images were carried out on SPARC 2 workstations (SUN Microsystems Inc., Surrey, UK) using ANALYZE version 5 image display software (BRU, Mayo Foundation, Rochester, Minn., USA) (Robb, 1990). Calculations and PET image matrix manipulations were performed in PRO MATLAB version 3.5i (MathWorks Inc., Natick, Mass., USA) with Statistical Parametric Mapping software (SPM, MRC Cyclotron Unit, London, UK) (Frackowiak and Friston, 1994).

Stereotactic normalization and smoothing of PET images

The 31 original PET scan slices were interpolated into 43 planes in order to render the voxels approximately cubic. The MRI scans were also interpolated into 43 planes (voxel sizes were modified to be cubic). Head movement between PET scans was corrected by aligning each subject's scans with the first one recorded, using Automated Image Registration (AIR) software (Laboratory Brain Mapping, UCLA, Los Angeles, USA) (Woods *et al.*, 1992). The PET data were co-registered onto individual MRI data oriented along the intercommissural line (Watson *et al.*, 1993; Woods *et al.*, 1993). The PET axial plane corresponding to the intercommissural line was fixed and the height of the brain above and below the intercommissural plane was directly measured on individual MRI scans. This information was used during the stereotactic fitting of PET scans by the SPM software onto a standard stereotactic template (Talairach and Tournoux, 1988) of 26 planes of 2×2×4 mm voxels. In order to increase signal to noise ratio and accommodate normal variability in functional gyral anatomy each PET image was smoothed in three dimensions with a low-pass Gaussian filter (full width half-maximum 5×5×3 pixels, 10×10×6 mm) (Friston *et al.*, 1991*a*). Finally, individual MRI images were transformed into the same stereotactic space and an average stereotactic MRI template was generated from all the subjects' data by averaging (*see* Fig. 1).

Statistical analysis

The main effects of rCBF changes induced by our experiment (words minus tones and vice versa) were first computed in each group of subjects (synaesthesia and controls). Significant changes were identified by applying a statistical threshold of 0.05 corrected for multiple non-independent comparisons (Friston *et al.*, 1991*b*). In addition, because some of our hypotheses regarding brain activations during synaesthesia were constrained to a few locations (*see* Introduction), a less conservative analysis was also performed where the level of significance was thresholded at the omnibus significance level $P < 0.01$ (Z score threshold 2.4). This approach is justified in hypothesis-led experiments (Friston *et al.*, 1991*b*). Finally, differences in rCBF changes for subjects with synaesthesia compared with controls were assessed as interactions between treatments. As before, the omnibus significance threshold corresponding to $P < 0.01$ was chosen as the sites of interactions were predicted from the results obtained in the main effects analysis of the data from the synaesthetes.

Statistical analysis was performed on a voxel by voxel basis as follows. Regional CBF equivalents were first normalized to

however, most of the reports of coloured hearing have distinguished between coloured sounds on the one hand, and coloured words and letters on the other.

Irrespective of the form of the synaesthesia, most cases show a similar historical pattern. Subjects report having mentioned their experiences to others at an early age, prompting ridicule or disbelief. As a consequence, many subjects say they said no more about their synaesthesia until hearing or reading about the condition as adults; but despite keeping their experiences private, they remained vivid and irrepressible. Other consistencies are apparent, especially regarding the quality and nature of synaesthetic percepts and the words or letters that elicit colours. Typically, the synaesthete reports that a colour percept, triggered by a specific sound, has remained the same, in many cases since the age of four or even earlier (Luria, 1968). Indeed, all subjects claim that they have experienced synaesthesia for as long as they can remember (Baron-Cohen *et al.*, 1993).

A problem with this condition is that the principal source of data is the subjective account of those who report the synaesthetic experiences, which understandably prompts scepticism, since such self-reported data do not allow a distinction between *metaphorical descriptions* and *genuine* synaesthesia. Metaphor is widespread in language and frequently includes reference to a kind of synaesthesia. For instance, an individual may say that the experience of listening to Dvorak's 'New World' symphony is one of 'greenness', or of reading Keats one of 'purpleness'. However, these uses of metaphor are very different to genuine synaesthesia, since only in the latter do people affirm that these stimuli result in actually seeing colours.

Genuine synaesthesia is characterized by a very high degree of consistency with which a colour experience is triggered by an auditory stimulus. The 'chromatic lexical' synaesthetic subject E.P. achieved 100% consistency between >100 words and colours across a period of 10 weeks, compared with only 17% consistency for a (non-synaesthetic) control subject who was asked to think of colour associations for each word (Baron-Cohen *et al.*, 1987). Baron-Cohen *et al.* (1993) have replicated this previous result in a group of eight individuals with chromatic–lexical synaesthesia tested twice, 18 months apart. Subjects with synaesthesia had a test–retest score of 92.7% which was more than twice as consistent as controls. An interesting difference emerged between this group of eight subjects and subject E.P. For E.P., each word had a detailed and unique associated colour, but the eight subjects experienced colours that were dictated by the colour of the dominant, usually first, letter of the word. For example, if 'penny' triggered blue, so too did 'pound', 'philosophy' and so forth. Thus, the experience depends upon orthography rather then on sound. Five out of seven of these subjects reported that the colour was not in a particular part of the visual field, whilst for two subjects it was just above the centre of gaze, and six out of seven said that the colour had the shape of the word, whilst one said it had no particular shape. In all of these subjects, coloured hearing is a one-way phenomenon, in the sense that perception of the visual world does not elicit auditory verbal perception. Taken together, these findings suggest that synaesthesia is a real perceptual phenomenon, which cannot be accounted for by either mnemonic or metaphorical associations.

Despite this phenomenological evidence, very little is known about the anatomical and physiological bases of colour–word synaesthesia or other forms of synaesthesia.

Cytowic and Wood (1982) have suggested that in all forms of synaesthesia, sensorial integration is likely to occur in the limbic system, in conjunction with neocortical inhibition. This hypothesis is partially based on a functional imaging experiment in a single subject with taste–shape synaesthesia (Cytowic and Wood, 1982; Cytowic, 1989). Measurements of cerebral blood flow (CBF) with the non-tomographic ^{133}Xenon inhalation technique showed widespread CBF decreases in the neocortex (Cytowic, 1989); however, the technical limitations of the ^{133}Xenon inhalation technique did not allow testing of the limbic system hypothesis.

On the other hand, a correlation between specific (neocortical) perceptual abilities and synaesthesia would be suggested by the description of a patient who, following a car accident, became colour-blind (Sacks and Wasserman, 1987; Sacks *et al.*, 1988). Before the car accident this patient was also a sound–colour synaesthete, a condition that vanished in conjunction with the loss of colour perception. It is unfortunate that no reliable anatomical information is available about this patient who died 3 years after the accident (S. Zeki, personal communication).

Aims

There are a number of reasons that make synaesthesia interesting to the neuro-physiologist. In the first place, it represents a variant of common human perceptual abilities, whose mechanisms are at present unexplained. Secondly, synaesthesia can be seen as a special case of integrated cross-modal perception, one of the least understood physiological properties of the brain. A typical (normal) example of such perception is the appreciation of our body in space, where visual, somaesthetic and vestibular signals, recorded by anatomically separated sensory systems, are combined into a unitary non-ambiguous representation (Ventre *et al.*, 1984). A similar integration must occur also within single systems; for example, in the visual system where the various attributes of the visual world (shapes, colours, movement, etc.) are processed in a segregated fashion and then recombined (Zeki and Shipp, 1988). Thirdly, synaesthesia is likely to tell us more about the physiology involved in the generation of visual perception without direct external input to the visual system.

If the integrated percepts of synaesthesia are the result of unusual neural connectivity, which may become manifest as brain regional changes of energy consumption, we reasoned that it might be studied using functional imaging techniques, especially in comparison to normal subjects stimulated in the same fashion (i.e. during auditory presentation of words

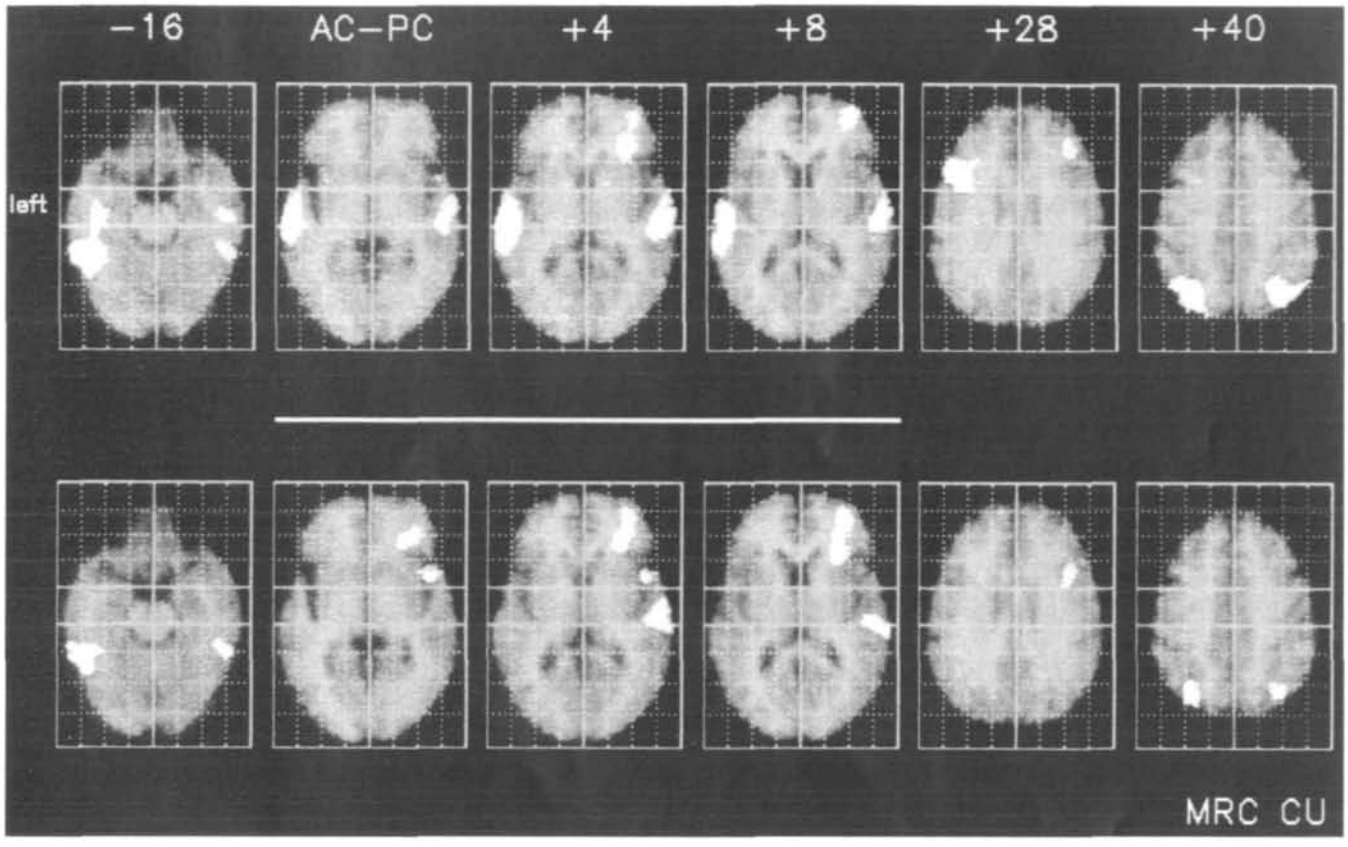

Fig. 1 Activations during colour–word synaesthesia. (**A**) The location of the rCBF increases induced by word perception in synaesthetes is illustrated. Areas of significant rCBF increase have been plotted on averaged MRI images transformed into the stereotactic space of Talairach and Tournoux (1988). 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, 1991*b*; Frackowiak and Friston, 1994) which were transformed to *Z* distribution maps.

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).

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 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

report synaesthesia also in conjunction with inner speech, whenever this is used explicitly, for instance when thinking. As during extrinsic stimulation, the perception is dominated by the first letter of each word. Our subjects do not have synaesthesias during reading, unless they subvocalize what they read. Localization of the percept in a particular part of the visual field was not possible except for subject A.C., who localized synaesthetic percepts in the centre of her visual field. In addition, in no subject was there interference between synaesthesia and perception of the visual world.

Synaesthetic experiences during the scanning procedure

All subjects in the experimental group reported synaesthetic experiences for words and none reported colour perception for tones. None of the normal controls interviewed at the end of scanning reported any colour perceptions during the experiment.

PET results

Main effects: word stimulation compared with pure tone stimulation in synaesthetes and controls

As expected, hearing words compared with hearing tones revealed, in both groups, activation of a series of perisylvian brain areas implicated in language: these included the superior and middle temporal gyri bilaterally and also the inferior frontal gyrus on the left (*see* also Table 2A and B).

However, in the group with synaesthesia we saw additional activation foci which included the middle frontal gyrus and the insula on the right and, on the left, the posterior inferior temporal (PIT) cortex. All of these foci of activation survived a correction for multiple non-independent comparisons (Z score > 3.7).

The comparison of rCBF between tasks also showed a rich pattern of de-activation as shown in Table 3A and B and in Fig. 2A.

Hypothesis-led analysis in synaesthetes

In subjects with synaesthesia, the 'hypothesis-led' analysis showed rCBF increases close to the location of putative human area V4 described by Zeki *et al.* (1991); this area, however, did not reach our *a priori* criterion for significance set at $P < 0.01$ (stereotactic coordinates $x = -22$, $y = -72$, $z = -8$; Z score 2.1). On the other hand, at this lower threshold an additional activation focus was detected in the homologous right PIT cortex and there were also bilateral activation foci in the parieto/occipital junctions that were not seen in normal subjects. Activation foci in those with synaesthesia are also illustrated in Fig. 1A.

Interactions: differences in rCBF changes between groups

The differences of activation between synaesthete and normal groups were tested formally as interactions between treatments by using the appropriate linear contrasts. All of the areas described above that were not readily related to word perception were significantly more active in subjects with synaesthesia than in normals (*see* Table 2C and Fig. 1B). In addition, activation in the right superior temporal gyrus and insula was also significantly greater than in normal subjects.

The formal comparison of the rCBF decrease magnitudes between groups showed in synaesthetes significantly greater de-activation of the left insula and of the left lingual gyrus (Table 3C and Fig. 2B). In the statistical maps, the area of de-activation observed in the lingual gyrus spread into left primary visual cortex.

Single subject analyses

Similar patterns of activity were also detected in subject by subject analyses. An example of rCBF increases in a single subject with synaesthesia mapped onto her MRI scan is illustrated in Fig. 3.

Discussion

This study reports the first neurophysiological account of brain activity related to colour–word synaesthesia, which we regard as a centrally synthesized percept rather than as a form of mental imagery. We will first discuss the phenomenology of colour–word synaesthesia observed in our experimental group. The discussion of the neurophysiological findings will be in two stages. In the first, more analytical presentation, the various brain areas that have shown greater rCBF changes in synaesthetes will be discussed individually in the context of current knowledge about the anatomy, physiology and pathophysiology of colour perception. In the latter, the neurophysiological pattern of synaesthesia will be discussed in the light of existing theories of cortical integration and conscious visual perception.

Colour–word synaesthesia: phenomenology

All of our subjects were free from neurological or psychiatric disease, free from psychoactive medication and were living normal lives. All reported that their synaesthesia had lasted for as long as they could remember and all met the criteria for genuineness of synaesthesia. Indeed, in our group the average consistency of colour–word associations was 98%. Colour perceptions were mostly related to the letters of the words rather than to phonology or meaning (*see* the Appendix). According to our synaesthetes' reports (but *see* also Baron-Cohen *et al.*, 1993) the association between a letter and a colour has remained the same for decades, suggesting that the cerebral basis for such percepts is not

Table 2

Brain structure	Left				Right			
	x	*y*	*z*	*Z* score	*x*	*y*	*z*	*Z* score
(A) *Cerebral structures activated by word perception in normal controls*								
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
(B) *Cerebral structures activated by word perception in synaesthetes*								
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 –50	–42 –44	–12 –16	4.1 3.8	40	–46	–16	2.6
Superior occipital gyrus/superior parietal lobule (BA 19/7)	–26 –26	–78 –68	40 44	2.5 2.7	32	–68	40	2.5
(C) *Differences in activation in synaesthetes compared with controls*								
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 –30	–78 –62	32 40	2.9 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).

Table 3

Brain structure	Left				Right			
	x	*y*	*z*	*Z* score	*x*	*y*	*z*	*Z* score
(**A**) *Cerebral structures inhibited by word perception in normal controls*								
Insula	−36	−6	0	3.72	—	—	—	—
Temporoparietal junction (BA 42/22/40)	—	—	—	—	34	−32	20	3.7
Thalamus					16	−20	0	3.8
Cerebellum	−12	−52	−20	3.1	22	−54	−20	3.6
(**B**) *Cerebral structures inhibited by word perception in synaesthetes*								
Cingulate (BA 24/31)	—	—	—	—	2	−18	40	5.4
Insula	−34	−6	−4	4.9	—	—	—	—
Temporo-parietal junction (BA 42/22/40)	−54	−24	28	4.5	54	−24	24	3.8
Lingual gyrus (BA 18)	−10	−64	0	3.7	—	—	—	—
Cerebellum	−16	−58	−20	4.2	—	—	—	—
(**C**) *Differences in inhibitions in synaesthetes compared with controls*								
Insula	−28	−2	−4	3.1				
Lingual gyrus (BA 18)	−8	−66	0	3.1				

For details *see* footnotes to Table 2.

There are other phenomenological characteristics of our synaesthetes which are of interest and may guide the interpretation of the neurophysiological results. Coloured hearing does not interfere with vision, nor with colour perception due to stimulation of the conventional visual channel. Synaesthesias are also different from the colour perceptions (chromatophenes) induced in man by magnetic stimulation of area V4. According to Zeki (1993, from a personal communication from K. and G. Beckers), the spatial localization of chromatophenes within the optic field is reminiscent of the topographic organization of V4 in the monkey. On the contrary, the colour percepts of synaesthesia cannot be localized to any part of the visual field. The ambiguous spatial distribution of synaesthesias would point to the engagement of visual areas where neurons have a much looser representation of the visual field than in primary visual cortex or even then in area V4.

Visual areas and the neurophysiology of synaesthesia

One of the aims of our study was to test the hypothesis that synaesthesia occurs in conjunction with activity in specific visual areas. In the following discussion, we will refer to the literature on primates as well, although homologies between primates and humans brains should be treated with caution. This caution also involves the use of acronyms derived from the literature on primates especially for exstrastiate visual areas (e.g. V3, V4 and so forth). A considerable amount of empirical evidence derived from lesional data and functional imaging suggests that it is possible to identify human homologues of primate visual areas. However, given that a complete assessment of such correspondence (e.g. based on histochemistry, connectivity, etc.) is not in our hands, the use of such acronyms should be regarded as an operational short-hand. As we shall see for the case of colour perception, this short-hand retains considerable explanatory value.

In studying colour–word synaesthesia, central to our assumptions is the supposition that the associative visual cortex is organized into functionally specialized areas. This is now a prevalent notion. A number of specialized visual areas have been identified in the macaque: area V3 for dynamic form perception, area V5 for motion perception and area V4 for colour and colour with form perception (for review *see* Zeki, 1978; Van Essen, 1985; Livingstone and Hubel, 1988). Functional imaging studies have given information on the localization of putative human homologues of some of the monkey's extrastriate visual areas: it has been proposed that V4 lies in the fusiform gyrus (Lueck *et al.*, 1989; Zeki *et al.*, 1991), whereas V5 would be located ventrally on the lateral surface of the occipito-temporal junction (Zeki *et al.*, 1991; Watson *et al.*, 1993; Zeki *et al.*, 1993). These notions are complemented by neuropathological data; for example, cerebral colour blindness (central achromatopsia) is usually associated with lingual-fusiform gyri lesions (Verrey, 1888; Meadows, 1974; Damasio *et al.*, 1980; Rizzo *et al.*, 1993; for review, *see* also Zeki, 1990). Further evidence is provided by the fact that no cases of central colour blindness have been reported for lesions that do not involve the lingual-fusiform gyri. However, other

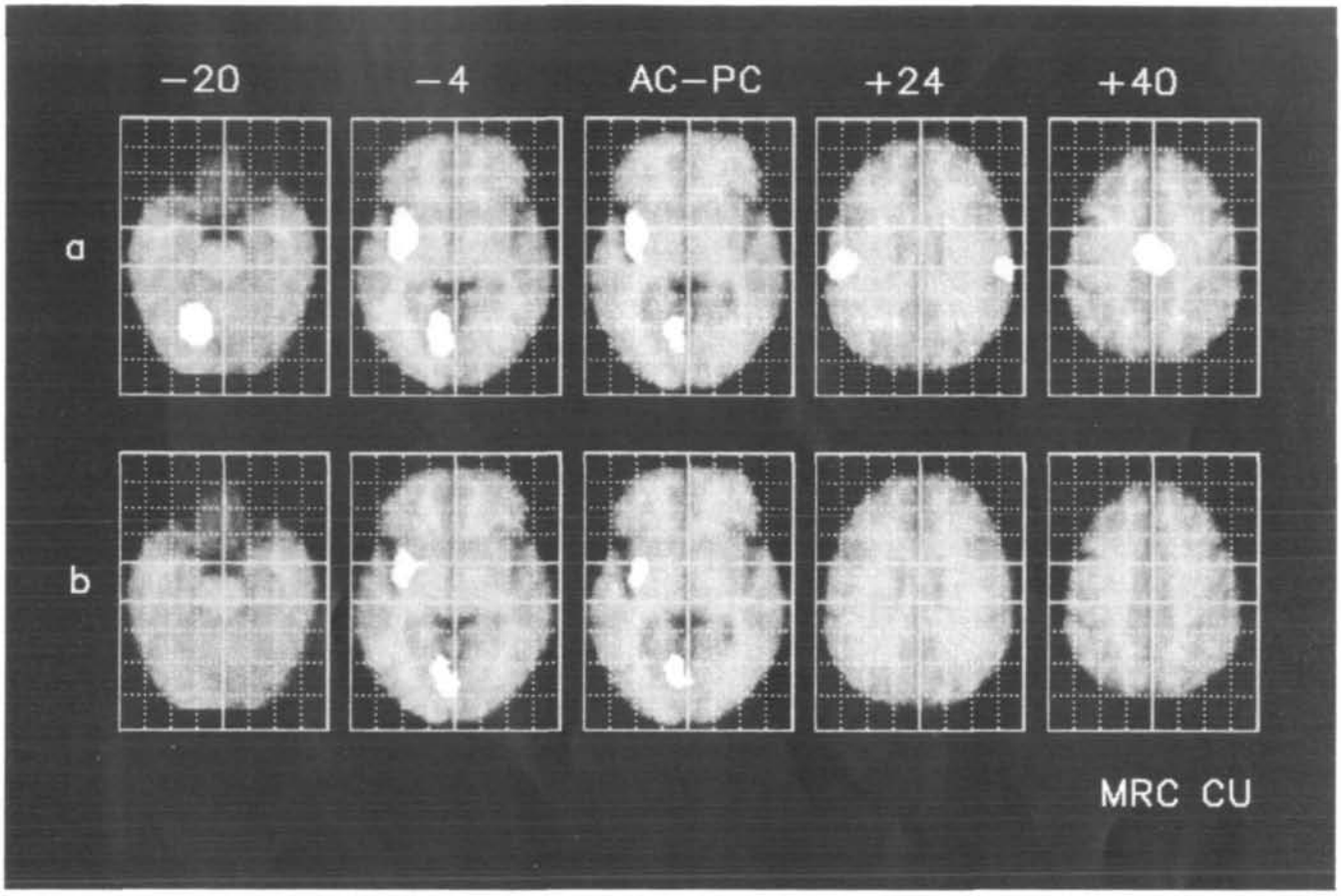

Fig. 2 Deactivations during colour–word synaesthesia. (**A**) Regional CBF decreases during word perception in synaesthetes are illustrated. Areas of significant rCBF decrease are displayed in the same fashion as in Fig. 1. Level of significance (expressed as *Z* scores) and stereotactic co-ordinates 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.*, 1991*a, 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.* (1991*a*) found activation of PIT

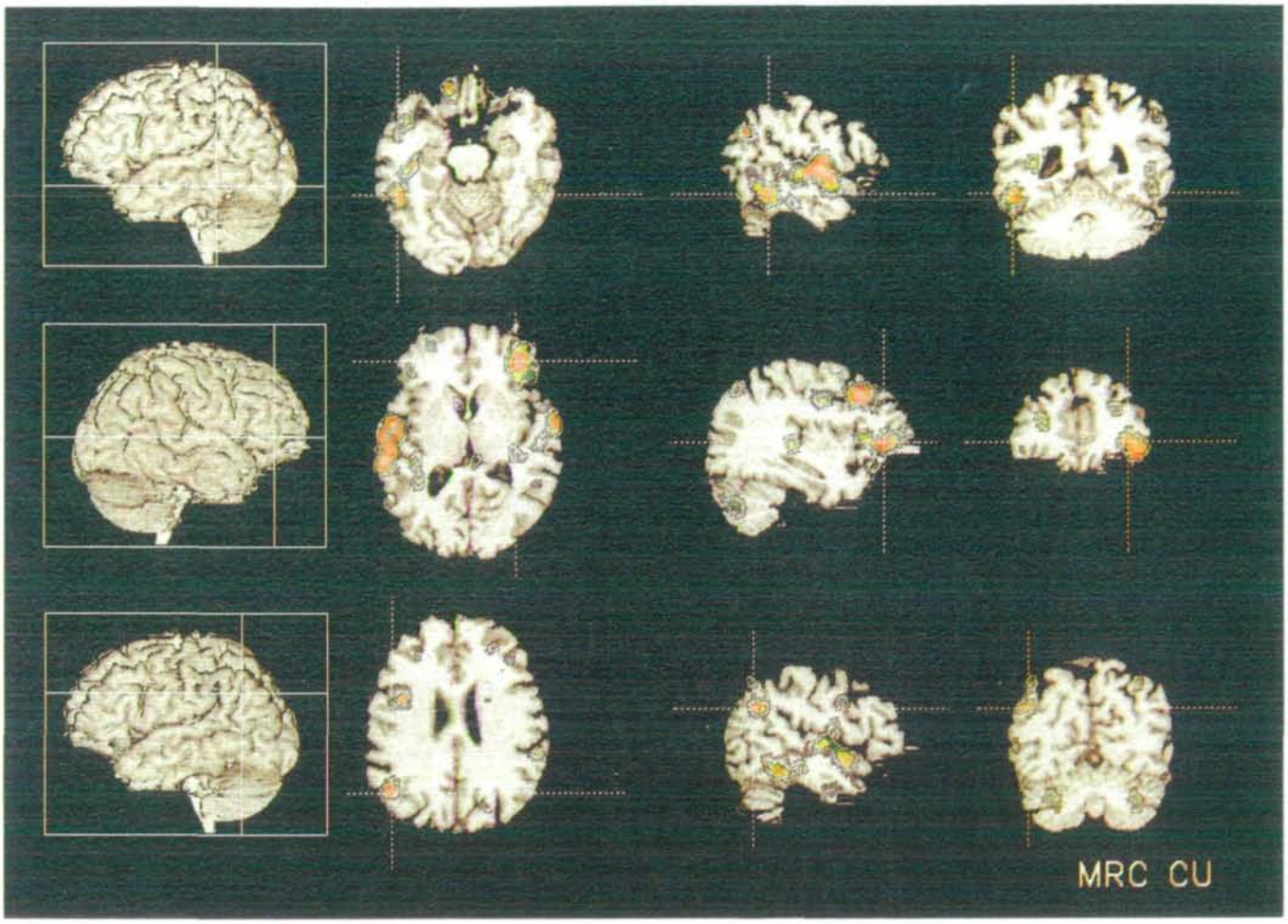

Fig. 3 Cerebral regions activated during synaesthesia in subject B.J. The details of subject B.J. are reported in Table 1. Regional CBF increases induced by word perception in each subject were co-registered onto the individual MRIs. In this figure, we provide an explicit description of those activation foci that we can attribute to synaesthesia on the basis of the group analysis (*see* also Table 1B and Fig. 1B: activation differences between subjects with synaesthesia and controls). From the left side of the figure: a three-dimensional MRI rendering of the surface of the cerebral hemisphere of the subject (from the top: left, right and left hemisphere); transaxial, sagittal and coronal images show the locations of principal activation foci. White intersecting lines on the three-dimensional MRI rendering indicate the level of the transaxial and coronal images. The level of the sagittal section is evident from the intersecting lines on the coronal sections. The top row shows the location of activation in the left inferior temporal cortex (the transaxial level is 16 mm below the bicommissural plane); the middle row (8 mm above the bicommissural plane) shows the location of maximal right prefrontal activation for this subject; the third row (36 mm above the bicommissural plane) shows an activation of the left inferior parietal gyrus (just above the superior temporal gyrus) as well as an activation of the right parieto-occipital junction (coronal section). Co-registration of SPM{t} maps and MRIs from individuals was performed using Automated Image Registration software (Woods *et al.*, 1993). Subsequent superimposition of SPM{t} maps allowed the detection of individual locations of rCBF changes (in colour; $P < 0.01$) induced by word stimulation. A comprehensive description of the PET to MRI co-registration methods has been given elsewhere (Watson *et al.*, 1993; Woods *et al.*, 1993).

cortex in a task where subjects were asked to discriminate visual stimuli on the basis of their colour (e.g. a red square was a target and distractors were squares of other colours). In a further experiment, Corbetta *et al.* (1991*a*) found activation of PIT in a task where subjects attended targets defined by the colour and by the spatial orientation of a geometric object (a red vertical rectangle was a target; distractors varied for orientation, for colour or for both features). Taken together, these results suggest that human PIT cortex may be involved in complex aspects of colour perception and in linking colour to shape.

In the macaque, this structure has a further interesting property, namely that it has a much more eroded topography than that of area V4 (Van Essen, 1985; Komatsu *et al.*, 1992), which is itself far less precise than that of area V1 (Van Essen and Zeki, 1978). The involvement of a visual area such as area PIT in colour–word synaesthesia is therefore also consistent with the degraded topographic organization of the synaesthesias in most cases of coloured hearing.

Posterior inferior temporal cortex lesions in the monkey can also produce defects of complex visual pattern recognition (Mishkin, 1972; Gross, 1973) and orientation selective

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 quadrantanopia 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. Leviant) 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

stimulation. The area de-activated in the lingual gyrus may represent the ventral portion of area V2 (Clarke and Miklossy, 1990) or part of area V3 (Horton and Hoyt, 1991). The location of lingual gyrus de-activation is very close to the area activated in the study of Corbetta *et al.* (1991*a*) when subjects passively viewed a set of coloured stimuli appearing on a display. Both the left lingual gyrus and insula have recently been implicated in brain imaging experiments in which normal volunteers had to convert visually presented letters into sounds (Paulesu *et al.*, 1993). This result complements the observation that patients with lesions in the left lingual gyrus are often unable to read while other language abilities remain intact (Damasio and Damasio, 1983; De Renzi *et al.*, 1987). The functional relevance of our finding is, however, uncertain; indeed, the interpretation of rCBF decreases is one of the most controversial issues in functional imaging. Jenkins *et al.* (1994) found large decreases of rCBF in associative visual areas during a motor learning task and interpreted these as a manifestation of a decrease in attentional resources allocated to brain structures irrelevant to their task. A similar interpretation of rCBF decreases was proposed by Kawashima *et al.* (1993). Regional CBF decreases in these structures may therefore correspond to the 'switching off' of a part of the reading system in the absence of direct visual stimulation.

Frith *et al.* (1991) and Friston *et al.* (1991*c*, 1993) have provided an alternative explanation for the de-activation that they detected in superior temporal gyri during a verbal fluency task. They suggest that the superior temporal gyri are activated or de-activated depending on whether access to word representations is by external stimulation (e.g. hearing words) or due to intrinsic generation (e.g. generating words). Accordingly and by analogy, the de-activation of the left lingual gyrus could be explained by anomalous (without specific visual input) access to colour and letter representations. The differences between these experiments and our paradigm are such, however, that it is premature to accept these explanations other than as hypotheses.

It is interesting to note that rCBF decreases occurred in the absence of any direct stimulation of the visual system and that the only previous direct investigation of brain areas associated with another form of synaesthesia (taste–shape synaesthesia) was associated exclusively with widespread decreases of perfusion in the neocortex (Cytowic, 1989). However, we feel that more experimental evidence on the biological meaning of deactivations is needed before we can interpret their relevance in synaesthesia.

The neurophysiology of synaesthesia and mechanisms of integration

We turn now to a discussion of our results in the light of current concepts on cortical integration during complex perception and in the light of current theories of conscious visual perception.

Synaesthesia and mechanisms of integration

We define integration in broad terms as the sensory combinations that underlie complex perception. Integration may depend on anatomical connectivity and/or on temporal synchronicity. Few aspects of the latter can be readily studied with PET, and therefore they will not be considered further here (for ways in which temporal aspects can be examined with PET; *see* Frackowiak and Friston, 1994). Anatomical substrates for integration may include anatomical convergence in the form of forward (i.e. from primary to associative areas) and lateral connections, intrinsic connections within primary or associative areas, and feedback connections from associative areas to primary areas (Zeki and Shipp, 1988). Forward connectivity implies convergence of inputs from multiple simple neurons onto more complex ones, whereas feedback connectivity is thought to be a basis for modulation of primary areas by associative areas (Zeki and Shipp, 1988). The available anatomical evidence, however, is insufficient to provide unequivocal explanations as to how multimodal integration occurs, as in associative areas (e.g. the parietal cortex or the prefrontal cortex) the projections coming from different specialized areas remain segregated and their spatial overlap is limited (Goldman-Rakic, 1984; Zeki and Shipp, 1988).

To demonstrate any of these mechanisms using functional imaging with activation (cognitive subtraction) techniques has proved to be no easy task. Let us take as an example modulatory feedback from associative to primary areas, when stimuli are delivered via the usual sensory channel. Since brain activations are monitored as changes of rCBF, it remains ambiguous whether some of the activations observed in primary areas are simply due to more potent stimulation or to modulatory effects from associative areas (for a discussion of this issue, *see* Friston *et al.*, 1991*c*; Watson *et al.*, 1993; Zeki, 1993, pp. 333–4). In our experiment we circumvent this problem in a somewhat paradoxical way: we have studied a visual percept in the absence of direct visual stimulation. In this case we can legitimately speculate that changes in neural activity within the visual system must be due to some form of connectivity with the system directly stimulated (the auditory language system). Indeed, we observed in the synaesthetes a considerable perturbation of the visual cortex in the absence of any direct stimulation. This altered activity involved highly specialized visual areas (e.g. PIT cortex) which in both the macaque and in man may contribute to aspects of colour perception and integration between shape and colour. The activation of PIT cortex may well represent a form of forward convergence from basic perceptual language areas (e.g. the superior temporal cortex), as PIT is implicated in both colour perception and in lexical–semantic tasks (Corbetta *et al.*, 1991*b*; Démonet *et al.*, 1992). In addition, because coloured hearing is a one-way process (in our subjects synaesthesia occurs from language to colour but not vice versa) and because no direct visual stimulation occurred, we propose that the activity observed in at least some of the

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 geniculo-striate 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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Appendix

Performance of subject B.J. on a colour–word association test designed to establish whether synaesthesias are due to phonology or alphabetic qualities of words

Pair	Word	Colour	Word	Colour
(1)	Nice	Chocolate brown	Knock	Biscuit
(2)	Writer	Silver grey	Rice	Oxford blue
(3)	Geoffrey	Ginger brown	Judge	Pink
(4)	Fish	Grey	Photograph	Blue
(5)	Kind	Biscuit	Cut	Green
(6)	Aeon	Mid red	Eat	Green
(7)	Apple	Red	Art	Red
(8)	Knock	Biscuit	Kind	Biscuit
(9)	Pharmacy	Blue	Pill	Blue
(10)	Water	Silver grey	Writer	Silver grey
(11)	Geoffrey	Ginger brown	Goggle	Mid brown
(12)	Police	Blue	Photograph	Blue

In order to determine whether colour–word synaesthesias were 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 (examples 1–6; e.g. *photograph* and *fish*) or non-homophonic first syllables starting with the same letter (examples 7–12; e.g. *apple* and *art*). If colour–word synaesthesias are based on phonemes then we would expect the colour descriptions to be the same for pairs as *photograph* and *fish* but not for pairs as *apple* and *art*. As the list shows, for subject B.J., the prevalent trigger to determine the colour of synaesthesias is the first letter of a word rather than its first sound. The same rule applied to other synaesthetes for the large majority of words. This again indicates that in the synaesthetes reported in this paper, colour percepts are predominantly linked to letters rather than phonemes.