

Perception: The seeing ear

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Some people perceive colours when they hear words – a phenomenon known as synaesthesia. Brain imaging techniques have revealed the areas of the cortex involved in this rare mingling of the senses.

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We have all been green with envy, purple with rage, and remembered golden years and dark times, and we all dislike being in the red. For some people such descriptions go beyond mere metaphor: the word ‘envy’ is green, ‘Monday’ really is blue and hearing the name of a bank may make them literally see red. This phenomenon of perceiving a colour when one hears words is the most common example of the phenomenon of synaesthesia. Synaesthesia is a rare but real phenomenon; it can be visual–tactile (perceiving visual stimuli when touching objects), visual–gustatory, tactile–visual or almost any combination of two senses, but reports are dominated by visually-related synaesthesias, and olfactory and gustatory synaesthesias are less common. Two possible reasons for this are the proximity in the cortex of the visual areas to the auditory and motor areas, the areas implicated in taste and olfaction being relatively distant, and the fact that, of all senses, vision dominates normal behaviour and is therefore more likely to form associations with the other senses.

The veracity of the experience of synaesthesia has been demonstrated beyond doubt [1] by presenting synaesthetes with lists of words, asking them to report which colour they perceive for any given word and retesting them, without warning, up to a year later. Remarkably the synaesthetes maintain over 90 % consistency, whereas non-synaesthetes who knew they would be retested maintained less than 40 % consistency after only one week. Clearly, the synaesthetes do not make random associations, but experience particular colours for particular words. The case histories of synaesthetic subjects also show a high degree of consistency: the onset is in childhood and the specific colour–word associations do not change over time.

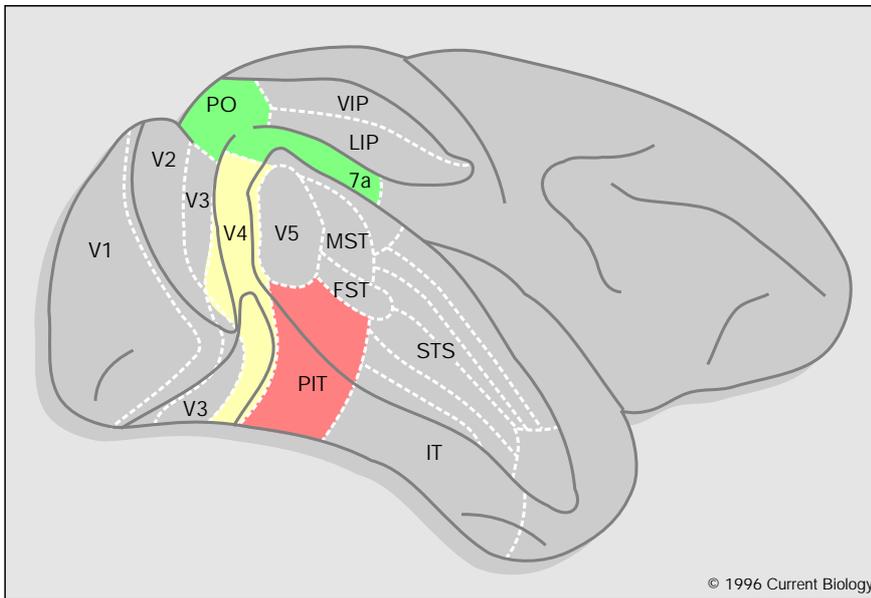
The nature of the colour–word associations made by synaesthetes is surprising. One might imagine that the colours perceived would be linked to some semantic aspect of the word or perhaps the sound of the word. This appears not to be the case. The link is not between

meaning and colour, or sound and colour, but between the visual appearance of the first letter of the word and colour [1–3]. Thus, a subject reporting the perception of red on hearing the word ‘photograph’ would also report perceiving red on hearing the word ‘palladium’, but a different colour on hearing the word ‘fish’. The experience is described more accurately, then, as a colour–grapheme association than as a colour–word association. This is not so far removed from normal experience, in which one makes a link between a spoken word and the letters in the word. For example, it takes longer to decide that ‘enough’ and ‘bough’ do not rhyme than ‘rough’ and ‘how’.

The finding that the association is graphemic in colour–word synaesthesia greatly constrains the possible explanations of the experience. Grapheme perception is not present at birth and only begins to develop when a child is learning to write. This opens up the possibility that colour–grapheme synaesthesia emerges at a time of increased plasticity in the visual system, when it is involved in learning to link letters with sounds and strings of letters with objects. Evidence from neuropsychological studies also points to the visual system. In 1893, Phillipe (see [4]) reported that 30 out of 150 blind subjects reported coloured-hearing after they had lost the sense of sight, which is consistent with the remedial plasticity that occurs following cortical damage [5]. Another patient who was synaesthetic lost the experience after he suffered brain damage resulting in cortical colour blindness [6]. These findings suggest that colour–grapheme synaesthesia is dependent to some extent on activity within visually-related cortical areas in which cells have response properties consistent with a role in the integration of features such as colour and shape.

A different view [7] suggests that limbic areas are more important for synaesthesia. A crucial part of the reasoning behind this claim, however, lies in the argument that only humans can make cross-modal associations, and that the substrate for these is subcortical and unconscious. This is mistaken on both counts. It is widely known that monkeys [8], and of course apes [9], can make cross-modal associations, and it is by no means clear that the cortex is not involved. For example, Haenny *et al.* [10] recorded from neurons in cortical visual area V4 while monkeys were performing orientation discrimination tasks, and found that many neurons responded to the visual orientation of the stimuli, as one might expect from this visual area [11], but that many were also sensitive to the tactile orientation of a grooved plate if this was relevant to the task. Further evidence implicating visual

Figure 1



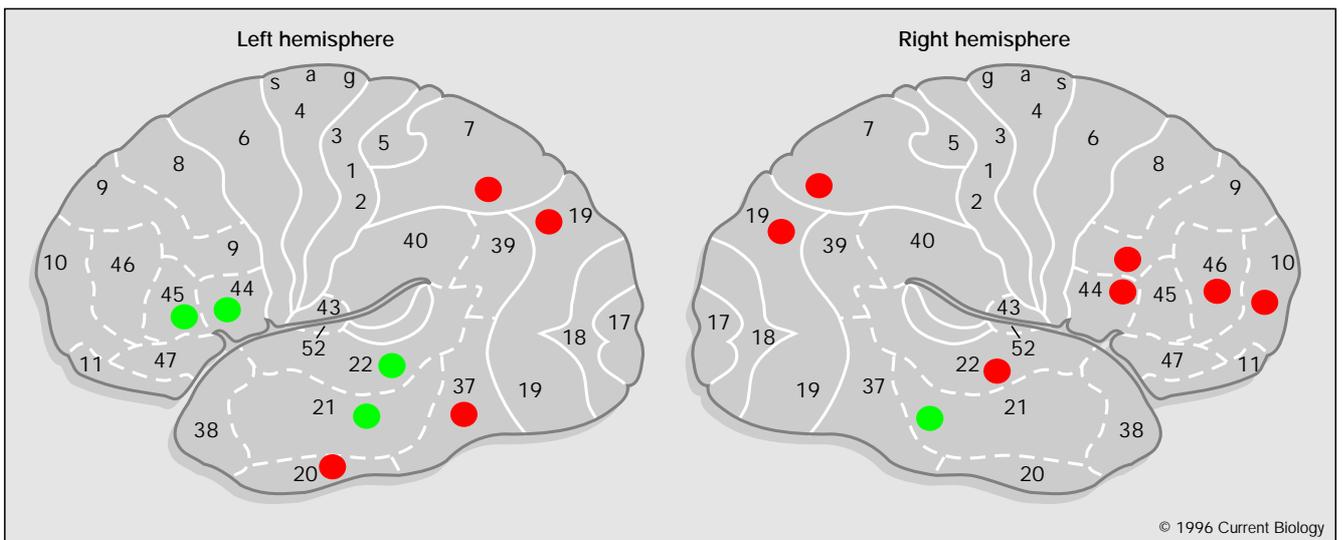
The cortex of a macaque monkey, with visual areas implicated in tactile–visual cross-modal matching highlighted in colour: red, posterior inferior temporal cortex (PIT); green, parieto-occipital cortex (PO) and area 7a; yellow, V4. PIT lies at the junction of the secondary visual areas (V2, V3, V4 and V5), which are usually associated with visual perception, and the classical inferotemporal cortex, which may be important for visual memory. PO and 7a receive information from areas associated with form and colour perception (V3 and V4) and motion perception (V5).

areas in cross-modal transfer (Fig. 1) has come from a study in which monkeys were impaired in the learning of tactile–visual associations following lesions of the posterior inferior temporal cortex [12].

Using positron-emission tomography (PET), Paulesu *et al.* [3] have recently carried out a direct test of the hypothesis

that synaesthesia is based on sensory–sensory associations in cortical circuits. PET detects changes in regional cerebral blood flow (thought to reflect neural activity) that are associated with the performance of some task by human subjects. The brain activities of six female synaesthetes and six control subjects were compared on two tasks. Subjects were blindfolded and presented with spoken

Figure 2



Cortical areas that showed activation during synaesthesia in the study of Paulesu *et al.* [3]. Two lateral views of the human brain are shown; numbers refer to Brodmann's areas, which divide up the neocortex according to differences in cellular structure. Areas activated in both

synaesthetes and control subjects during the presentation of words, relative to the presentation of pure tones, are coloured green. Areas activated in the brains of synaesthetes relative to controls during the presentation of words are coloured red.

words in one condition, and pure tones in a control condition. All the synaesthetes and none of the control subjects experienced colour-grapheme synaesthesia during the presentation of words. Three patterns of results were observed (Fig. 2), as described below.

During the presentation of words, both groups of subjects showed activation in brain areas involved in language — Broca's area (around Brodmann's area 44 of the left hemisphere), the superior temporal gyrus (Brodmann's areas 21/22 of both hemispheres) and the middle temporal gyrus area (Brodmann's area 21 of both hemispheres). During synaesthetic perception, the synaesthetes showed increased activation relative to the controls in the parieto-occipital junction (around the junction of areas 19 and 7) of both hemispheres, the posterior inferior temporal cortex of the left hemisphere (areas 20 and 37), the insula of the right hemisphere, and the mid-frontal (areas 46 and 10), inferior frontal (areas 44 and 9) and superior temporal (area 22) gyri of the right hemisphere. Deactivation was also observed during coloured-hearing in some areas of the synaesthetes' brains — the insula of the left hemisphere and the lingual gyrus (area 18) of the same hemisphere. Interestingly, there was no significant increase in cerebral blood flow in areas V1, V2 and V4, areas usually associated with visual perception and in the case of V4 specifically with colour [13].

Taken together, these observations suggest that the experience of synaesthesia is mediated by a link between the sound of the word, the appearance of the first letter of the word and colour. Paulesu *et al.* [3] note that the posterior inferior temporal cortex, where activation was observed specifically during synaesthetic perception, is an area in which form and colour are integrated, but this leaves little room in their scheme for the contribution of the parieto-occipital junction. They speculate on the possibility that parietal cortex may have some, unclear, role in colour-related tasks, but a long history of investigations into parietal damage in humans and monkeys suggests another role. Damage to the parietal visual areas in humans can produce an inability to discriminate whether letters are presented in the correct orientation, and lesions to the parietal visual areas in monkeys also cause an inability to discriminate the correct orientation of forms [14]. The increased blood flow observed in parietal visual areas during synaesthesia may thus be related to the form component of synaesthesia rather than the colour component.

Whatever the origin of coloured-hearing it is certainly more than a mere "confusion between the senses" [15], and further studies may offer insights into aspects of plasticity and cross-modal perception that may otherwise be difficult to probe. Presumably we will hear more about this if the visual imaging studies continue.

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