

# ANOMALOUS PERCEPTION IN SYNAESTHESIA: A COGNITIVE NEUROSCIENCE PERSPECTIVE

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An enduring question in cognitive neuroscience is how the physical properties of the world are represented in the brain to yield conscious perception. In most people, a particular physical stimulus gives rise to a unitary, unimodal perceptual experience. So, light energy leads to the sensation of seeing, whereas sound waves produce the experience of hearing. However, for individuals with the rare phenomenon of synaesthesia, specific physical stimuli consistently induce more than one perceptual experience. For example, hearing particular sounds might induce vivid experiences of colour, taste or odour, as might the sight of visual symbols, such as letters or digits. Here we review the latest findings on synaesthesia, and consider its possible genetic, neural and cognitive bases. We also propose a neurocognitive framework for understanding such anomalous perceptual experiences.

Does the letter 'A' cause you to see red? Has the sound of a simple melody ever triggered a rainbow of colours before your eyes? Do you distinguish the taste of your favourite dessert by the feeling of cold, sharpened steel on your fingertips? If so, you might have a form of synaesthesia, an unusual 'mixing of the senses'<sup>1</sup>, in which physical stimuli that elicit perceptions in a single sensory modality in most people also trigger extraordinary synaesthetic experiences. For example, for most of us, a sound reaching the ears is solely an auditory experience, whereas for a synaesthete, the same stimulation might also be 'seen' as a vivid and consistent colour<sup>2</sup>. In some cases, synaesthesia can arise from the mere thought of a particular stimulus or concept<sup>3,4</sup>, indicating that external stimulation is not required for its occurrence.

Metaphorical language is commonly used to describe the quality of sensory experiences — we speak of 'bright sounds' and 'sharp tastes' — but for synaesthetes, the link between real and synaesthetic experiences reflects more than metaphorical language or thought. For these individuals, there is an enduring and idiosyncratic tendency for particular sensory experiences to arise in ways that are not characteristic of

most people. The experiences seem to be involuntary, in the sense that they occur without conscious effort; they are typically present from very early childhood; and they are highly consistent over time. The study of synaesthesia has the potential to advance our understanding of the way in which humans perceive and categorize sensory information. It might provide important clues to the neural mechanisms that underlie the integration of sensory information from within and between modalities<sup>5,6</sup>. Within the broad field of cognitive neuroscience, the study of synaesthesia might also contribute to our knowledge of brain–behaviour relationships in such areas as mental imagery<sup>7,8</sup>, associative learning (L. J. Elias *et al.*, unpublished observations) and emotion<sup>1,9–11</sup>.

Here we review the phenomenon of synaesthesia from a cognitive neuroscience perspective, integrating recent findings from psychology and functional brain imaging. We focus on the most common form of synaesthesia, in which digits, letters or words elicit specific colours when they are seen or heard (colour–graphemic and colour–phonemic synaesthesia, respectively), and propose a new theoretical framework for

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DOI: 10.1038/nrn702

Box 1 | **Forms of synaesthesia**

Synaesthesia is a heterogeneous phenomenon. In this article, we focus on the two most common forms, in which experiences of colour are elicited by digits, letters or words, in either their written form (colour–graphemic synaesthesia) or their spoken form (colour–phonemic synaesthesia)<sup>2,13,17,35</sup>. Although some individuals experience both of these types of synaesthesia, others experience just one. As, by definition, sensations involve personal experience, it is difficult for most of us to understand what synaesthesia is like. Below are some quotes from synaesthetes:

“When I’m reading I can see that what I’m looking at is in black and white, but I also see the ‘correct’ colours for the letters and symbols.”

“I may call someone ‘Debbie’ when she is really ‘Paula’, because D and P are more or less the same colour green.”

“Tuesday is yellow. I don’t ‘see’ it anywhere in particular; rather, I have a general awareness of yellowness in relation to the word.”

More rarely, colours can be elicited by musical tones, chords or styles<sup>28,30,34</sup>, by non-musical sounds, such as a dog barking or a car horn<sup>63</sup>; or by particular odours or tastes<sup>64</sup>. Synaesthetic concurrents not involving colour are far less common. They include odours and tastes arising from particular sounds, including musical notes<sup>65</sup>, as described by another synaesthete:

“I avoid middle C when I play the piano, because it has an earthy, musky smell I don’t like.”

In his classic account of the mnemonist known as S., Aleksandr Luria<sup>29</sup> described the complex synaesthetic experiences that arise in some rare cases:

“Presented with a tone pitched at 50 cycles per second and an amplitude of 100 decibels, S. saw a brown strip against a dark background that had red, tongue-like edges. The sense of taste he experienced was like that of sweet and sour borscht, a sensation that gripped his entire tongue.”

understanding synaesthesia. We also raise a number of theoretical questions for future research.

**What is synaesthesia?**

The term synaesthesia (from the Greek *syn* meaning ‘union’ and *aisthises* meaning ‘of the senses’) has been used to describe a range of unusual sensory experiences. The heterogeneous manifestations of synaesthesia have been documented extensively elsewhere<sup>1,4,12</sup> and so will not be dealt with at length here. Recent reports indicate the existence of many different types of inducer (the stimulus that triggers synaesthetic experience) and concurrent (the synaesthetic experience itself)<sup>4</sup>, resulting in many different manifestations of the phenomenon (BOX 1).

The available evidence indicates that the most common type of synaesthesia involves specific colours elicited by particular digits, letters or words, in their written (orthographic) and/or spoken (phonological) forms. Words are typically described as having an overall colour that is determined by the first letter, although individual letter colours also have an influence. Synaesthetic colours can also arise from the mere thought of a particular inducer, rather than through afferent processing of an external source<sup>3</sup>. This indicates that mental imagery might have an important role in the generation of synaesthetic colours. In virtually all cases, the roles of inducer and concurrent are fixed. So, whereas particular digits, letters or words can induce synaesthetic colours, the converse is not true: colours do not elicit digits, letters or words. This unidirectionality has important implications for physiological and cognitive models of synaesthesia<sup>4</sup>.

Given the subjective nature of perception, it has been difficult to determine precisely how or where synaesthetic colours are experienced. Some individuals report a transparent mist, floating patch or patterned overlay in their field of view<sup>3,13</sup>. Others experience colours ‘in the mind’s eye’ as a distinct form of mental imagery for colour<sup>4</sup>. Synaesthetes typically do not confuse induced colours with those of surfaces in the world<sup>14</sup>. To our knowledge, there have been no cases in which synaesthetic colours have been reported to interfere with colour vision. Colour perception, as assessed by the ISHIHARA COLOUR PLATES, is normal, as is colour naming<sup>14</sup>, but detailed psychophysical testing in these individuals has not yet been carried out.

Despite attempts to formulate a unified theory of synaesthesia<sup>4</sup>, there is little evidence to suggest that the heterogeneity of synaesthetic experiences arises from a common underlying mechanism. We predict that, as for many other neurocognitive phenomena, synaesthesia will eventually be fractionated according to specific dissociations between cognitive and neural markers. In keeping with this prediction, in this review we shall not seek an overarching explanation for all manifestations of synaesthesia. Instead, our aim is to focus on the unique colour experiences that arise from orthographic and phonological processing of symbolic forms, such as digits and letters<sup>2,7,14–16</sup>. We believe that by working intensively on this most common form of synaesthetic experience, we might eventually reveal its crucial cognitive and neurophysiological underpinnings.

**Prevalence and familiarity**

The prevalence of synaesthesia in the adult population has been estimated variously at between 1 in 2,000 and 1 in 25,000 (REFS 1,17). The proportion might be even higher in children<sup>18</sup>, although there have been few empirical studies. Many synaesthetes report being previously unaware that their experiences were different from those of others, indicating that synaesthesia might be more common than is assumed at present. Until properly conducted epidemiological studies are undertaken, the prevalence of synaesthesia must remain speculative. By contrast, there is strong evidence for a sex bias, with around six times more females than males reporting the phenomenon<sup>17,19</sup>. Moreover, there is a high prevalence of synaesthesia among biological relatives of synaesthetes<sup>17</sup>. These findings support claims of a possible genetic predisposition transmitted by an X-linked autosomal dominant gene<sup>20</sup>.

Given the possible genetic and developmental bases of synaesthesia, it is perhaps not surprising that scientists have sought psychological and neurological correlates of the phenomenon. The literature is replete with assertions that synaesthetes tend to be creative, artistic and highly emotional individuals (see REF 21). In addition, there are claims that individuals with synaesthesia are more likely to be left-handed, and to suffer various neuropsychological impairments, including left–right confusion, poor arithmetical reasoning and deficient topographical cognition (for example, map-reading ability)<sup>1</sup>. To our knowledge, there have been no systematic investigations

ISHIHARA COLOUR PLATES  
A series of plates used for the diagnosis of colour blindness. They are designed so that individuals with normal colour vision can see shapes or characters, but colour-blind people cannot.

of these factors. In the only published study of the prevalence of self-reported synaesthesia, Baron-Cohen *et al.*<sup>17</sup> found the same incidence of left-handedness in their UK sample as in the general population (roughly 10%; REF. 22), but their small sample size ( $n = 26$ ) does not allow population inferences to be drawn. In our sample of 184 self-reported synaesthetes in Australia (Australian Synaesthesia Database, University of Melbourne), 10% are left-handed, confirming the findings of REF. 17.

In addition to the synaesthesia described here, various acquired conditions have been suggested to result in synaesthesia-like experiences. These include central nervous system pathologies, such as optic nerve damage<sup>23</sup>, and ingestion of specific psychoactive drugs, such as mescaline<sup>1,24</sup>. As yet, there is no evidence as to the relationship of these conditions to synaesthesia.

#### Explanations of synaesthesia

Many early investigations catalogued the anecdotal reports of synaesthetes, often focusing on the extent to which synaesthetic experiences were linked to particular emotions, cognitive styles or artistic abilities<sup>7,8,25</sup>. The few experimental investigations reported in the early literature tested the hypothesis that synaesthesia is a form of conditioned reflex<sup>26,27</sup>. These studies found that although non-synaesthetic individuals could be trained to associate arbitrary pairs of tones and colours, there was no evidence that colour experiences accompanied the newly learned associations.

It has also been suggested that synaesthetes might be particularly susceptible to forming new associations. Rizzo and Eslinger<sup>28</sup> tested a synaesthete for whom musical notes elicited colours. He was able to associate an additional, arbitrarily selected colour with each musical note in a single learning trial, an ability that far surpassed that of non-synaesthetic controls. Such enhanced abilities could explain the report of superior memory in synaesthesia<sup>29</sup>.

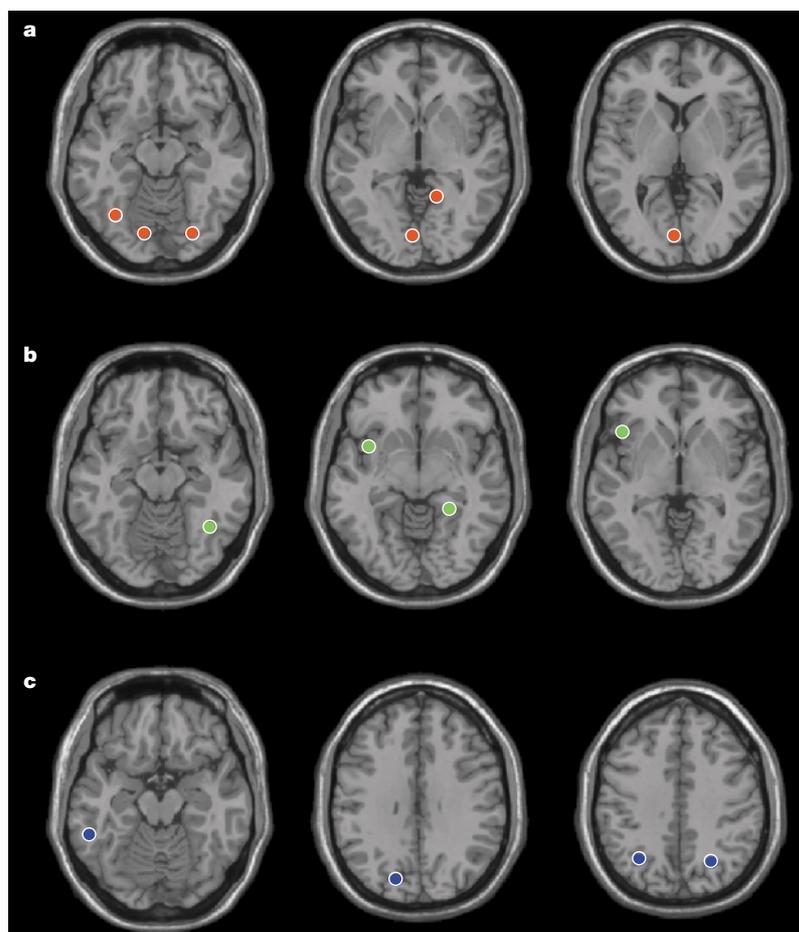
#### Box 2 | Anatomical and cognitive modularity

Cognition and its neural representations are organized into subsystems that are specialized for distinct aspects of perception, language, memory, motor actions and so on. The neuroscience literature is replete with examples from functional brain imaging of localized cortical areas that are selectively active during the presentation of words, colours, faces or places<sup>66</sup>. To what extent is this apparent anatomical and physiological parcellation of the brain consistent with its cognitive architecture? Some time ago, Fodor<sup>67</sup> proposed an influential hypothesis concerning the organization of human cognition, known as the '**modularity of mind**'. The basic idea, as initially proposed, is that the mind is constructed from several independently functioning, insulated subsystems, the inputs of which are restricted to a particular class of stimulus, and the operations of which cannot be influenced by activity in other modules or systems. Evidence for modularity has emerged from many disciplines in experimental psychology (for example, psycholinguistics). The principle of modularity has also been supported by evidence from neuropsychology. Patients with brain lesions can show profound impairments in a relatively restricted domain of cognitive processing (such as face recognition), but show intact cognition in all other domains<sup>68</sup>. The concept of modularity continues to influence theories in cognitive psychology<sup>69</sup>, and has proved to be a useful heuristic for conceptualizing the behaviour of synaesthetes in various contexts.

There is much evidence that non-synaesthetes show a spontaneous bias to associate specific stimulus dimensions across sensory modalities. So, when compelled to choose, most people will associate a high-frequency tone with a white visual target, and a low-frequency tone with a black target<sup>30–32</sup>. Other patterns of association exist between pitch and lightness, pitch and brightness, loudness and brightness, and pitch and shape<sup>33</sup>. This has been shown to be automatic, in the sense that one dimension (for example, pitch) can either interfere with or facilitate responses to another (for example, lightness). So, responses to dark and dim visual stimuli are faster and more accurate when accompanied by a low- rather than a high-pitched sound; similarly, light and bright visual stimuli are responded to faster when accompanied by a high- rather than a low-pitched sound<sup>33</sup>.

It has been proposed that synaesthetic correspondences are based on the same patterns as non-synaesthetic associations<sup>30</sup>. For instance, Karwoski *et al.*<sup>34</sup> found that synaesthetes' visual responses to sounds were similar to those of non-synaesthetes: high pitches evoked light colours and appeared angular in shape, whereas low pitches elicited dark colours and were more rounded. Marks<sup>30</sup> found similar patterns in a meta-analysis of the colours reported by synaesthetes for phonemes and musical notes. However, it should be noted that the cross-modal correspondences in non-synaesthetes have been examined using low-level stimulus dimensions, such as pitch and luminance, whereas the associations in colour-graphemic synaesthesia involve lexical stimuli that require higher-level processing. It is still unclear how the cross-modal associations made by non-synaesthetes might relate to the experiences of those with synaesthesia.

More recent accounts of synaesthesia have dealt with possible biological causes. One proposal is that synaesthesia arises from anomalous connectivity between brain areas that subservise the relevant sensory modalities<sup>35</sup>. For example, numerous investigators have suggested that colour-phonemic synaesthesia might result from additional synaptic connections between brain regions that are responsible for processing auditory inputs and those involved in colour perception<sup>15,35</sup>. The infants of several species have extensive functional connections between brain areas that subservise the different sensory modalities, many of which are lost during maturation through synaptic pruning<sup>36</sup>. Maurer<sup>37</sup> has suggested that all humans experience synaesthesia early in life, and that pruning of cross-modal connections results in a loss of these synaesthetic experiences. This hypothesis is consistent with research indicating that infants have less differentiation between the senses<sup>38</sup> than adults, and with reports that synaesthesia is present from early childhood in most cases. It would be informative for future studies to examine this proposal by testing infants and children for synaesthesia. It has also been proposed that synaesthesia might occur as a result of the sprouting of additional synaptic connections, rather than from a failure of synaptic pruning<sup>35</sup>. Baron-Cohen and colleagues<sup>35</sup> have suggested that extra connections between brain areas might lead to a breakdown of modularity between otherwise independent functional units (BOX 2).



**Figure 1 | Brain activation during colour vision, imagery and synaesthesia.** Axial slices through a standard magnetic resonance image of the human brain, with different colours indicating regions of significant activity derived from functional imaging studies of colour perception (**a**), colour imagery (**b**) and colour–phonemic synaesthesia (**c**). **a** | Areas in red show significant activity that is centred on the posterior fusiform gyrus (area V4) during the perception of coloured Mondrians<sup>41</sup>. **b** | Areas in green show significant activity in the anterior fusiform and parahippocampal gyri related to colour imagery (elicited by having participants answer a series of questions, such as “Is a canary darker yellow than a banana?”)<sup>41</sup>. Significant activity was also present in the left insula. **c** | Areas in blue show regions of significant activity during colour–phonemic synaesthesia<sup>15</sup>. These include the superior occipital and parietal cortices and posterior inferior temporal gyrus. Significant activity was also present in the right prefrontal and insular cortex (not shown).

Rather than postulating the existence of anomalous or additional connections between brain areas, Grossenbacher<sup>4,6</sup> has suggested that synaesthesia might result from disinhibited feedback in existing neural pathways. There is clear evidence in primates that processing of afferent signals within modality-specific areas is characterized by reciprocal FEEDFORWARD and FEEDBACK information flow. This reciprocity is particularly evident in the visual system, where feedback from such high-level regions as AREA MT/V5 can influence neural activity at the earliest stages of cortical processing, including the PRIMARY VISUAL CORTIX (area V1; REF. 39). According to the disinhibited feedback theory, neural activity associated with the processing of a particular inducing stimulus eventually converges with activity associated with stimulation from other intra- and interstimulus domains. In normal subjects, feedback from this convergence zone is

restricted to the pathway in which afferent (feedforward) information has arisen. However, in synaesthesia, activity associated with the inducer can ‘leak’ back along other pathways as well, perhaps owing to absent or attenuated inhibitory mechanisms. This leads to co-activation of otherwise independent perceptual pathways that in turn causes the concurrent anomalous sensory experiences that characterize synaesthesia.

The question of the neural basis of synaesthesia could be addressed by carefully constructed neuroimaging experiments. So far, there has been only a handful of relevant studies, and the conclusions that can be drawn from these are limited. In a pioneering study, Paulesu and colleagues used **positron emission tomography** (PET) to examine patterns of brain activity in six women with colour–phonemic synaesthesia<sup>15</sup> and six non-synaesthetic controls. Participants either listened to pure tones (which did not induce any synaesthesia) or to words spoken over headphones. In the spoken word condition, but not the tone condition, the synaesthetes showed significantly greater activity than controls in several extrastriate visual areas, including the superior occipital and parietal cortices bilaterally, the posterior region of the inferior temporal gyrus bilaterally, and to a lesser extent, the left lingual gyrus (FIG. 1). Interestingly, there was no evidence for increased activity in early visual areas, or in the region of the fusiform gyrus corresponding to AREA V4, which has been associated with colour perception.

These PET results seem to indicate that in synaesthesia, auditory inducing stimuli (spoken words) result in co-activation of higher-order colour processing areas, but not early visual areas associated with the perceptual processing of colour. Unfortunately, the findings do not reveal which perceptual or cognitive processes might underlie differences between synaesthetes and controls. The experimenters did not attempt to measure or quantify their participants’ synaesthesia; nor did they have them engage in a relevant behavioural task during acquisition, a problem also evident in a recent functional **magnetic resonance imaging** (fMRI) study of an individual with colour–phonemic synaesthesia<sup>40</sup>. A further ambiguity of the Paulesu *et al.* study<sup>15</sup> is that the pattern of extrastriate activity observed in the synaesthetes closely matches that found in studies of colour imagery in non-synaesthetic individuals<sup>41</sup> (FIG. 1). As Paulesu and colleagues asked their synaesthetes (but not their controls) to “let the colour perception [for each word] occur automatically”, their results could reflect the neural correlates of colour imagery rather than synaesthesia. Alternatively, they might indicate that synaesthesia is itself closely akin to colour imagery.

Attempts have also been made to characterize the temporal relationship between brain activity associated with synaesthetic inducers and the concurrents that they elicit. Schiltz and colleagues<sup>42</sup> used scalp-recorded **EVENT-RELATED POTENTIALS** (ERPs) to examine neural responses associated with the detection of visually presented letter stimuli in a group of 17 colour–graphemic synaesthetes. They observed an enhancement in the amplitude of positive waveforms over frontal and prefrontal scalp

#### FEEDFORWARD INFORMATION FLOW

Information processing that proceeds in a single direction from sensory input, through perceptual analysis, to motor output, without involving feedback information flowing backwards from ‘higher’ centres to ‘lower’ centres.

#### FEEDBACK INFORMATION FLOW

The flow of information from ‘higher’ to ‘lower’ centres.

sites, relative to a group of non-synaesthetic controls, beginning around 200 ms after letter presentation. However, the task-related ERP activity was identical for the groups, as was performance on the task. These results indicate that synaesthetic concurrents (colours) are associated with activity evoked considerably later than that triggered by the inducing (letter) stimuli, and that any such concurrent activity might arise initially from frontal brain areas that lie well beyond the perceptual processing hierarchy.

Despite the limited scope of existing studies, we believe that functional neuroimaging will ultimately provide a powerful tool for determining the spatial and temporal correlates of neural activity during synaesthetic experience. As in other areas of cognitive neuroscience, the most significant new findings are likely to emerge from approaches that combine brain imaging with sensitive behavioural measures designed systematically to manipulate the perceptual environment of and cognitive demands on the individual. As we discuss below, significant progress has already been made in this direction, with the advent of a range of innovative techniques that have addressed the cognitive characteristics of synaesthesia.

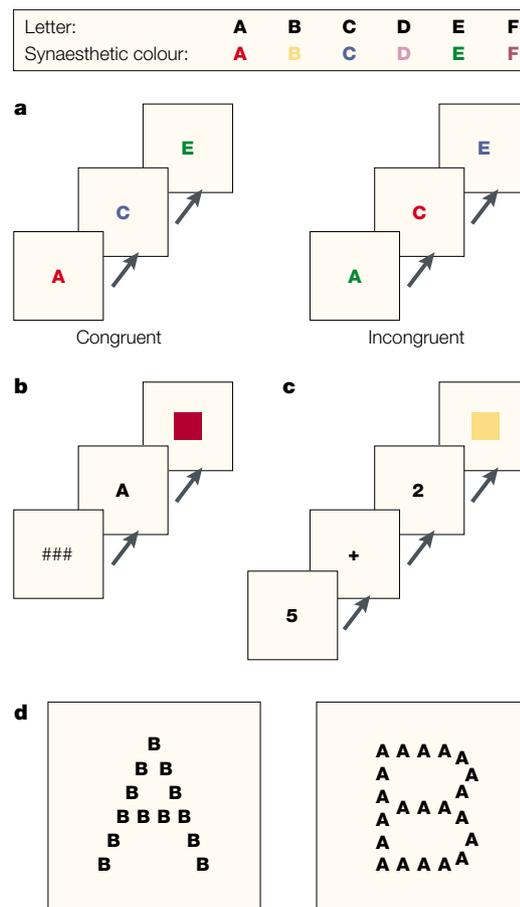
**Perceptual and cognitive measures**

Recent behavioural research on synaesthesia has focused on two main issues. The first concerns the extent to which induced synaesthetic experiences arise automatically, and whether they can be brought under voluntary control. The evidence bearing on this question has been reasonably clear and fairly uncontroversial. The second concerns the degree of processing that is required for a given inducer to trigger a synaesthetic experience. This issue has proved to be less tractable, and continues to be a focus for debate. In this section, we review recent findings relevant to the issues of automaticity and inducer processing, and consider their implications for a cognitive model of colour–graphemic synaesthesia.

In an attempt to avoid the subjectivity associated with anecdotal reports, several investigators have developed objective measures of synaesthesia. Most of these have been aimed at determining whether synaesthetic experiences arise automatically, as claimed by most synaesthetes, and whether they can be brought under voluntary control. The most widely adopted approach has been to examine the speed with which a synaesthete can identify and name the colour of a target letter or digit. Performance is then compared across two conditions: in one, the synaesthetic colour elicited by the target is congruent with its display colour (for example, if the letter ‘A’ elicits a synaesthetic colour of red, a congruent trial would involve the presentation of a red ‘A’); in the other, the synaesthetic colour elicited by the target is incongruent with its actual colour (in this example, the letter ‘A’ printed in green; see FIG. 2a). If synaesthetic colours are triggered automatically by their graphemic inducers, they might be expected to interfere with the identification and naming of target colours under incongruent conditions. This is a variant of the classic

Stroop colour–word task<sup>43</sup> (BOX 3), which produces robust cognitive interference in normal participants under a range of conditions<sup>44</sup>.

The finding of significant interference under incongruent conditions of the synaesthetic Stroop task is one of the more robust and ubiquitous in the field. Individuals with colour–graphemic synaesthesia



**Figure 2 | Example displays used in studies of the synaesthetic Stroop effect.** The row of letters at the top illustrates the colours experienced by a synaesthete. **a** | For congruent displays (left), the colour of each letter is consistent with the synaesthetic colour it induces. For incongruent displays (right), the colour of each letter is inconsistent with the synaesthetic colour it induces<sup>14</sup>. **b** | An example display sequence from a study of priming effects in synaesthesia. An initial pattern mask is followed by an alphanumeric prime (letter), which remains on the screen for 500 ms (the visible condition), or for 56 or 28 ms (the masked conditions). The task is to name the colour of the patterned target in the final display<sup>14</sup>, which can be synaesthetically congruent or incongruent with the prime. **c** | A display sequence used in a study of conceptual effects in synaesthesia<sup>3</sup>. A digit is presented in the first display, followed by an operator, and then a second digit. The task is to name the coloured target in the final display as rapidly as possible, and then to provide the solution to the arithmetical problem. Target colours can be synaesthetically congruent or incongruent with the solution. **d** | Navon-type local–global stimuli used to examine the effects of selective attention on synaesthesia<sup>50</sup>. Note that the letters are different at the local and global levels. This causes a bistable experience of colour that depends on the synaesthete’s current focus of attention.

**AREA MT/V5**  
A region of visual association cortex in the middle temporal extrastriate area that is important for the analysis of visual motion.

**PRIMARY VISUAL CORTEX**  
The cortical area that is the main recipient of visual information from the retinae (by way of the lateral geniculate nucleus); also known as V1 or striate cortex.

**AREA V4**  
A region of the posterior fusiform gyrus that has been implicated in colour perception.

**EVENT-RELATED POTENTIALS**  
Electrical potentials generated in the brain as a consequence of synchronized activation of neuronal networks by external stimuli. These evoked potentials are recorded at the scalp and consist of precisely timed sequences of waves or ‘components’.

Box 3 | **The Stroop effect**

The Stroop effect<sup>43</sup> describes the pattern of cognitive interference that arises when one dimension of a stimulus interferes with the processing of another. In the standard demonstration of the effect, participants are asked to name aloud the ink colours of printed words. When the words are incompatible colour names (such as the word ‘red’ printed in blue), participants are slower and more prone to error in their task of colour naming than when the words are unrelated to colour (such as ‘dog’ printed in blue). Readers can verify this effect for themselves by naming the colour of each word in list A (below), and then doing the same for list B. The usual explanation for this effect is that reading is a highly automated process in literate adults, whereas colour identification and naming are considerably more effortful and therefore slower. The difficulty associated with incongruent colour words is assumed to arise because the response associated with word reading must be suppressed so that the correct (print) colour can be named. Note that the incongruent colours do not interfere if the task is word reading. Analogous interference effects have been noted in other tasks, such as determining whether arrows with the words ‘left’ or ‘right’ above them are themselves pointing to the left or right<sup>70</sup>, and in identifying the number of elements in an array of Arabic numerals<sup>71</sup>. Although there is still disagreement concerning the cognitive mechanisms that underlie Stroop effects<sup>44</sup>, the task has nevertheless served as a powerful tool in both cognitive psychology and neuroscience<sup>44,72</sup>. Numerous variants of the conventional Stroop task have been developed to examine the issue of automaticity in colour–graphemic synaesthesia.

List A	List B
red	dog
blue	book
yellow	window
green	chair

are slower to name target colours under incongruent than congruent conditions<sup>3,14,45–47</sup>. This effect holds whether target items are presented in list form on a page or individually on a computer monitor, and whether the congruent and incongruent items are presented in separate conditions or randomly intermingled. The effect seems to be attributable to a reduction in the speed of processing for incongruent targets, although there might also be a subtle benefit for congruent targets relative to synaesthetically neutral ones (non-alphanumeric symbols, such as asterisks<sup>14</sup>). Crucially, the synaesthetic Stroop effect does not occur in reverse: the time required to identify and name the inducers is not affected by the colour in which they are shown<sup>45</sup>, confirming the unidirectionality of synaesthetic induction<sup>4,6</sup>.

Synaesthetic Stroop interference has also been observed under conditions in which the inducing letter or digit appears immediately before a target colour patch<sup>14</sup>, indicating that synaesthetic activation associated with the inducer persists over time (FIG. 2b). In an innovative variant of this synaesthetic priming paradigm, Dixon and colleagues<sup>3</sup> found that asking a synaesthete to calculate mentally the solution to a simple arithmetical problem affected naming times for coloured targets presented immediately thereafter (FIG. 2c). Taken together, the findings from these synaesthetic Stroop studies indicate that synaesthetic colours are elicited automatically by graphemic forms and are difficult to suppress, causing interference when pitted against the display colour of an inducer.

Although complete suppression of synaesthetic colours is difficult, as revealed by the synaesthetic Stroop tasks, inhibitory processes might nevertheless exert some influence on their occurrence. A recent study by

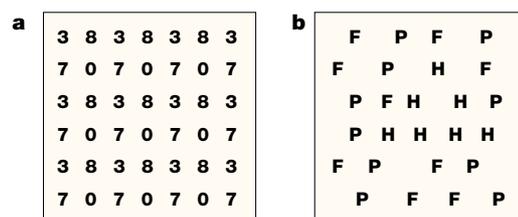
Odgaard and colleagues<sup>46</sup> suggests that there can be substantial inhibition of synaesthetic colours under certain conditions. In this study, a colour–graphemic synaesthete read aloud the print colours of digits, each of which was incongruent with the synaesthetic colour it induced. The time taken to identify and name the colour of each target increased significantly when it was necessary to retrieve a colour name that was the same as the synaesthetic colour induced by the preceding incongruently coloured item. This NEGATIVE PRIMING effect<sup>48</sup> implies that the representations of synaesthetic colours might be actively suppressed when they interfere with a task, and that this inhibitory effect might last for several seconds.

The second important issue that has arisen from behavioural studies of synaesthesia concerns the level to which relevant inducing stimuli must be processed to give rise to synaesthetic experiences. Some researchers have suggested that synaesthesia reflects a link between inducer and concurrent at a relatively early stage of perceptual analysis<sup>49</sup>. On the other hand, there is considerable evidence that substantial processing of the inducing stimulus is required before synaesthetic colour experiences are elicited<sup>14</sup>. For example, the colours experienced by synaesthetes are typically invariant across changes in the form of the symbols that induce them, such as their size and font. Indeed, the inducing stimuli do not even need to be physically present to generate synaesthetic colours<sup>3</sup>.

In an attempt to address the issue of inducer processing, we developed the synaesthetic priming task mentioned above<sup>14</sup>. We presented individual inducers (letters) as primes, before a target colour patch that had to be identified and named as rapidly as possible (FIG. 2b). When the prime was presented briefly but for long enough to be clearly visible (500 ms), synaesthetes showed a significant interference effect for incongruent versus congruent trials. We then reduced the prime duration to 28 or 56 ms, so that perceptual processing of the inducer was restricted. Participants had difficulty in identifying primes at these durations, even when they devoted their full attention to them. Under these masked conditions, the synaesthetic Stroop effect was eliminated entirely. Crucially, the absence of interference was not due to a general failure to process the prime under masked conditions: a control experiment revealed significant interference by the same primes in a letter-naming task<sup>14</sup>. On the basis of these findings, we suggested that synaesthetic colours typically arise only for inducers that are represented at conscious levels of visual processing<sup>14</sup>. We also speculated that selective attention has a crucial modulatory role in synaesthesia, both in terms of the potential for symbolic stimuli to induce concurrent colours, and in terms of individuals’ conscious perception of their synaesthetic experiences.

We have recently studied the effects of attention on synaesthesia using various paradigms<sup>50</sup>, one of which involved the use of Navon-type hierarchical stimuli<sup>51</sup> (FIG. 2d). When viewing such stimuli, most normal individuals perceive either the global or the local letters, but can alternate voluntarily between them. Such changes in the spatial scale of selective attention are necessary for

**NEGATIVE PRIMING**  
The increased time taken to respond to a target item that was an ignored distractor in a preceding trial. The effect is thought to occur because inhibition associated with the ignored distractor carries over to processing of the target.



**Figure 3 | Displays used to show perceptual grouping effects in colour-graphemic synaesthesia. a** | A matrix of achromatic digits, which were consistently grouped according to form by a sample of non-synaesthetic individuals. In this example, most non-synaesthetes grouped the display elements into rows. One synaesthete experienced '3's and '7's as red, and '8's and '0's as green. She tended to group the display elements on the basis of their synaesthetic colours, in this example into columns. **b** | A field of black letters, in which the targets ('H's) can be grouped to form a geometric shape (a triangle in this example). The black distractor letters ('P's and 'F's) make the task of finding the geometric shape difficult for non-synaesthetic participants. A synaesthete, on the other hand, was able to capitalize on the unique colours associated with the different letters to help her locate the target shape. Reproduced with permission from REF. 49 © 2001 The Royal Society.

many aspects of normal perception<sup>51</sup>. When colour-graphemic synaesthetes viewed these hierarchical stimuli, they reported seeing the colour of the letter to which they were attending rather than a mixture of the two colours elicited by the different letters<sup>50</sup>. The perceived colour changed as attention was switched from the local to the global form and vice versa, in a manner reminiscent of the stochastic changes in perception that occur when viewing ambiguous displays, such as Rubin's face-vase figure<sup>52</sup>. We have also examined the effect of attentional load during presentation of an inducing prime on colour naming in the synaesthetic priming task. Reducing the amount of attention available to process a letter prime reduced the extent to which synaesthetically induced colours affect naming times for a subsequently presented target colour<sup>50</sup>.

These findings indicate that synaesthetic induction might arise at a relatively late stage of perceptual processing, after the allocation of selective attention. However, not all evidence is consistent with this view. In a series of innovative experiments, Ramachandran and Hubbard<sup>49</sup> concluded that colour-graphemic synaesthesia is a 'sensory' phenomenon that arises from "cross-wiring between adjacent brain maps" that are responsible for the perception of colour and form. In one experiment, their two synaesthetes tended to group matrices of achromatic digits according to the synaesthetic colours they elicited, whereas non-synaesthetic controls tended to group them by shape (FIG. 3a). However, it is not clear that their data allow a distinction between grouping on the basis of sensory properties of the elements and grouping on the basis of their conceptual characteristics. For instance, even non-synaesthetes would be more likely to group digits one way or another if they formed part of a familiar sequence (for example, one's telephone number or postal code), than if they

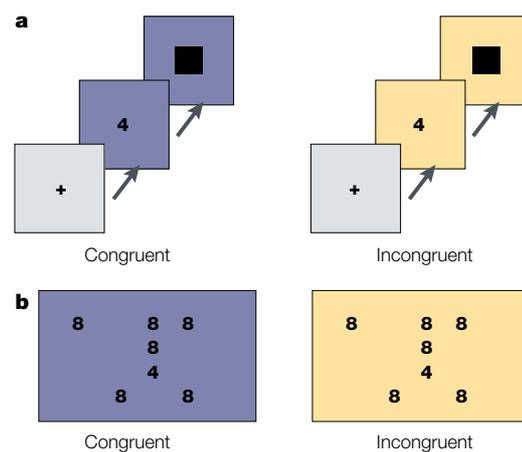
were simply a random list. The fact that for synaesthetes the matrices of digits carry additional conceptual information that is not available to non-synaesthetes could account for their pattern of grouping, but have no basis in low-level ('sensory') mechanisms.

In a second experiment, Ramachandran and Hubbard<sup>49</sup> found that synaesthetes were more accurate than controls in discriminating a geometric shape, such as a triangle or square, defined by a group of letters (for example, black 'H's) embedded in a random array of 'distractor' letters (such as black 'P's and 'F's of the same size; FIG. 3b). The implication is that the target letters were grouped by common colour for the synaesthetes alone, analogous to the POP-OUT effects observed for non-synaesthetes in visual search tasks involving displays containing uniquely coloured targets<sup>53</sup>. Such pop-out effects in non-synaesthetes typically arise rapidly (within a few hundred milliseconds) and are claimed to occur without the need for focused attention<sup>53</sup>, whereas the displays used by Ramachandran and Hubbard<sup>49</sup> were visible for a full second, allowing attentive processing. A more convincing demonstration of early perceptual grouping on the basis of synaesthetic colour would require speeded responses, and a demonstration that target detection times do not significantly increase with the number of distractors in the display<sup>54</sup>.

The methodological concerns outlined above were overcome by Smilek and colleagues<sup>16</sup>, who sought to pinpoint the representational level at which processing of an inducing form results in the experience of synaesthetic colour. In one experiment, they asked their colour-graphemic synaesthete to attempt to identify masked (black) digits presented briefly against a coloured background (FIG. 4a). They reasoned that if induced colours affect early stages of perceptual processing, then their synaesthete should find it more difficult to identify a target digit that was presented against a background coloured congruently with the synaesthetic colour it elicits, than one presented against a background coloured incongruently. In a second experiment, the task was to locate a black target digit within an array of black distractor digits, again with a uniform coloured background that was either congruent or incongruent with the colour induced by the target (FIG. 4b). The results of both experiments indicated that the synaesthete was significantly worse at identifying and locating digits presented against a congruently coloured background than against an incongruently coloured background, as predicted. A group of non-synaesthetic controls showed no such difference. Note, however, that even in the congruent condition, in which her performance was poor, the synaesthete was still more accurate than the non-synaesthetic controls in the same condition. This result seems to be inconsistent with the prediction that identification in the congruent condition should be particularly difficult for the synaesthete. The authors suggest that synaesthetic colours influence perception of inducing stimuli, probably through feedback from early colour areas, such as V4. Such an explanation requires that synaesthetic colours arise before explicit identification of the stimuli that induce them.

#### POP OUT

In displays composed of identical distractor stimuli (for example, red 'X's), a stimulus with a unique feature (for example, a blue 'X') can be detected rapidly and effortlessly, with little or no increase in reaction time as the number of distractor stimuli increases.



**Figure 4 | Tasks used to examine the influence of synaesthetic colour on perception of digit inducers.** The synaesthete was C., who experiences blue for the digit 4. **a** | After an initial fixation display, a black digit was presented briefly (32 ms) in the centre of a coloured background. This was followed immediately by a pattern mask, and C. was required to identify the target digit. In congruent trials (left), the colour of the background was the same as that elicited by the masked digit (blue in this example). In incongruent trials (right), the colour of the background was different from that elicited by the masked digit (yellow in this example). **b** | Example displays from a visual search task. C. was required to locate one of two black target digits ('2' or '4') in a display consisting of 6, 12 or 18 distractor digits ('8's). Congruent (left) and incongruent (right) trials were constructed by changing the background colour to be consistent or inconsistent, respectively, with that elicited synaesthetically by the target digit. Reproduced with permission from REF. 16 © 2001 Massachusetts Institute of Technology.

#### A model for colour–graphemic synaesthesia

Significant progress has been made in teasing apart the perceptual and cognitive factors that underlie the synaesthetic induction of colours by alphanumeric symbols. In this section, we present a neurocognitive model of colour–graphemic synaesthesia that positions these findings within an architecture that is consistent with the known properties of systems responsible for language and colour processing. In addition to providing a framework for generating testable predictions, this model provides a basis for future theories about other forms of synaesthetic experience.

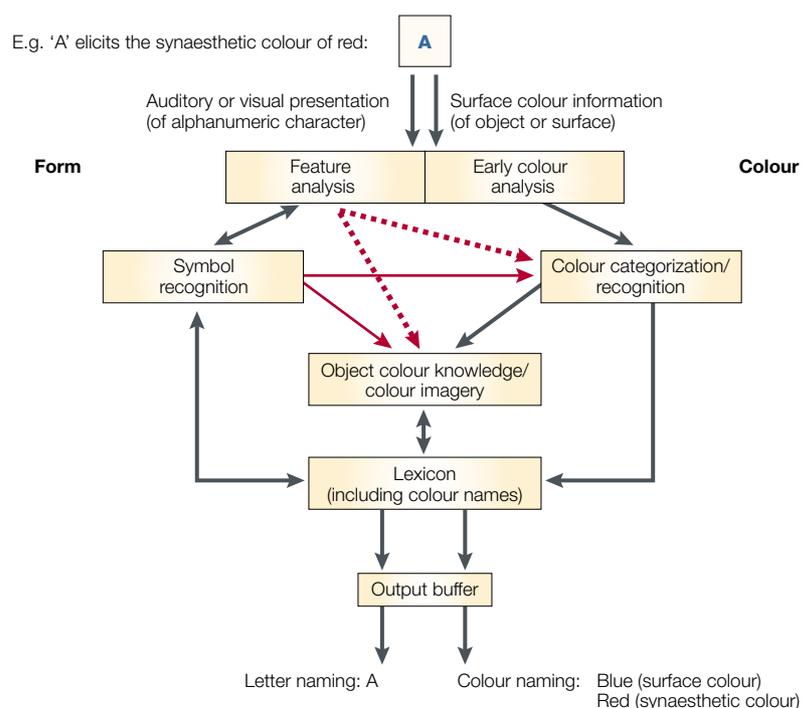
Our model is based on the assumption that there are multiple routes for processing symbolic form and colour in the human brain (FIG. 5). Inducing stimuli, such as digits, letters and words, must be processed initially by language mechanisms within the visual and auditory domains. The model embodies two separate aspects of synaesthetic phenomena: the level of inducer processing necessary to trigger synaesthesia, and the colour representations that give rise to the synaesthetic experience. We have reviewed data indicating that synaesthesia might occur either relatively early in processing<sup>16</sup>, before conscious identification of the inducing stimulus, or at a later stage that depends on explicit identification of the inducer<sup>14</sup>. Similarly, synaesthetic experiences could arise from activity at one of several stages of colour processing, from early wavelength

analysis to the later stages of colour recognition, imagery or knowledge (that is, knowledge of the canonical colours of objects).

There are already comprehensive models of language<sup>55–57</sup> and colour processing<sup>58</sup> in humans. We have incorporated the essential components of these approaches to illustrate how interactions between the different pathways might lead to the phenomena of colour–graphemic synaesthesia. As illustrated in FIG. 5, the model accounts for the various stages of processing between the initial perception of colour and form (top), and the final stage before production of an overt response (bottom). One pathway in the model shows the mechanism by which encoded digits, letters and words might access their appropriate stored representations, which in turn feed through to an output buffer in preparation for reading aloud. Note that this is a highly simplified illustration of the normal reading process. The other pathway in the model shows some of the stages involved in colour processing, from the earliest analysis of wavelength (areas V1 and V2), through colour-specific areas in the fusiform gyrus (V4), into a widely distributed network occupying anterior regions of the inferior temporal cortex that subserves colour categorization, colour knowledge and colour imagery.

The functional independence of the different colour-processing stages has been verified by neuropsychological studies of the effects of discrete brain lesions. Patients with achromatopsia after damage to area V4 show preserved form vision despite an inability to perceive colour<sup>59–61</sup>. They also retain the ability to indicate the canonical colours of objects (such as knowing that carrots are orange), and they report normal imagery for colour<sup>60,61</sup>. Conversely, patients with colour agnosia (loss of object colour knowledge) might have preserved colour perception and naming but can no longer use colour in semantic judgements<sup>62</sup> (pink elephants and blue tigers might seem acceptable). So, we separate the earliest stages of perceptual analysis from later stages concerned with semantic knowledge of object colour. Davidoff<sup>58</sup> has also suggested the existence of an 'internal colour space' between these stages, in which colour information is categorized without reference to information concerning visual form. In the model, the connections between the colour categorization/recognition stage and the stored representations of words reflect our ability to recognize and name surface colours. The ability to retrieve colour information about an object from its name is accounted for by the link between these stored representations and knowledge of object colours.

According to the model, the experience of colour in synaesthesia might be induced by different forms of symbolic input (visual or auditory), and might arise at different levels in the processing hierarchy. The level at which an inducer activates a representation in the colour pathway will have important consequences for the objective manifestations of synaesthesia and for its subjective quality. Whereas in non-synaesthetic individuals, there is minimal connectivity between the modules for letter recognition and colour processing (recognition, categorization, knowledge and imagery),



**Figure 5 | A cognitive model of colour-graphemic and colour-phonemic synaesthesia.** In the non-synaesthetic system (black arrows), a letter, digit or word is analysed in terms of its basic features (feature analysis). This leads to recognition of the identity of the symbol (symbol recognition), which in turn allows access to stored representations of alphanumeric characters and words. The analysis of surface colours of objects (colour perception) is accomplished through early colour analysis (such as wavelength discrimination) followed by colour categorization/recognition. Recognition of a colour can activate object colour knowledge (semantics) and allow colour imagery. Colour recognition can also activate stored representations of colour names. Synaesthesia occurs by spreading activation from one of two alternative modules (feature analysis or symbol recognition), depending on whether awareness of the identity of the inducing stimulus is required for synaesthetic experience. Two further functional connections arise from these modules (feature analysis, before awareness: dotted red arrows; symbol recognition, after awareness: thin red arrows). Synaesthetic colours can result from activity at one of two stages: either colour categorization/recognition (most closely related to colour perception) or object colour knowledge/imagery (a type of vivid colour imagery).

in synaesthetes, unique functional connections are present between them. Given the consistent finding of interference in synaesthetic Stroop tasks, the spread of activation from letter recognition to colour processing is likely to proceed automatically. It is possible, however, that a degree of top-down modulation is exerted through mechanisms of selective attention, as supported by findings on the effects of attentional load on synaesthesia<sup>50</sup>.

Visual masking of the inducer effectively eliminates any concurrent synaesthetic colours<sup>14</sup>, indicating that activation of the colour modules might not occur before the letter or digit is fully processed and available for overt report. So, we propose that activation of the symbol recognition module might spread to either the internal colour space (categorization and recognition) or the colour imagery module. Other evidence indicates that synaesthetic colours can be elicited before awareness of digit identity<sup>16,49</sup>, which would require activation of one of the colour modules directly from the feature analysis stage. Although theoretically this could include the early

colour analysis module, there is no evidence to support this link. Also note that links from symbol recognition to the internal colour space and colour imagery modules are unidirectional, as surface colours in the world do not induce synaesthetic symbols.

The challenge for future investigations of colour-graphemic synaesthesia is to test the adequacy of the model, which will undoubtedly need to be modified as new findings emerge. Further research will also be necessary to determine whether different subgroups can be distinguished, based on the level of inducer processing required to elicit synaesthesia, and on the stage of colour representation that gives rise to synaesthetic experiences.

### Conclusions

We have proposed a neurocognitive framework for understanding colour-graphemic synaesthesia, based on our current understanding of the processes that are normally involved in language and colour processing. However, many questions remain to be addressed. We do not yet understand why colour in particular should be so prominent in the various manifestations of synaesthesia. One possibility is that it is due to the uniqueness of colour as a visual experience. Whereas most objects can be represented across multiple perceptual domains (for example, a tennis ball can be perceived by sight, by the sound it makes when hit with a racquet, or by its weight and texture when held), surface colours have no perceptual correlate in any other modality.

Colour names must be learned, as must the visual symbols that constitute written and spoken language. To what extent might these facts provide a clue to the prevalence of colour-graphemic synaesthesia? Perhaps synaesthetes inherit a predisposition for co-activation of categorical information within the language and colour domains.

We are still a long way from having a model of synaesthesia that explains both its cognitive and biological causes. The most significant advances will probably emerge by combining psychophysical and cognitive markers of various aspects of the phenomenon with functional imaging measures, such as fMRI and ERPs. Several laboratories, including our own, are already making significant progress in this direction. Which brain areas are selectively active during the experience of synaesthetic colours, and what is the time course of this activity? To what extent do changes in the physical properties of inducing stimuli (their size, location, colour, modality of input and so on) affect the locus and timing of brain activity? We have suggested that mechanisms of selective attention have a crucial modulatory role in synaesthesia: to what extent are changes in attention reflected in the behavioural and neural correlates of synaesthetic experience? Finally, it might be possible to distinguish regions of brain activity that are necessary for synaesthesia, rather than merely correlated with it, by transient inactivation of focal cortical regions using TRANSCRANIAL MAGNETIC STIMULATION. As we have outlined here, synaesthesia research has already highlighted some fundamental questions for cognitive neuroscience.

#### TRANSCRANIAL MAGNETIC STIMULATION

A technique used to induce a transient interruption of normal activity in a relatively restricted area of the brain. It is based on the generation of a strong magnetic field near the area of interest, which, if changed rapidly enough, will induce an electric field sufficient to stimulate neurons.

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**Acknowledgements**  
We thank J. L. Bradshaw, M. Howard, M. O'Boyle and M. A. Williams for their helpful comments on the manuscript. A.N.R. is supported by an Australian Postgraduate Award. J.B.M. is supported by grants from the Australian Research Council, the National Health and Medical Research Council and Unilever (UK).

 **Online links**

**FURTHER INFORMATION**  
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**The International Synaesthesia Association:** <http://www.psychiatry.cam.ac.uk/isa/>  
**MIT Encyclopedia of Cognitive Sciences:** <http://cognet.mit.edu/MITECS/>  
electrophysiology, electric and magnetic evoked fields | positron emission tomography | magnetic resonance imaging | modularity of mind  
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