ANOMALOUS PERCEPTION IN SYNAXAESTHESIA: 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 colour, 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', 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. In some cases, synaesthesia can arise from the mere thought of a particular stimulus or concept, 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. 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, associative learning (L. J. Elias et al., unpublished observations), and emotion.

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
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). Although some individuals experience both of these types of synaesthesia, others experience just one. As, by definition, synaesthetic 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 what I'm looking at in black and white, but I also see the 'correct' colours for the letters and symbols."

"I may call someone 'Dubbie' when she is really 'Paulie' 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; by non-musical sounds, such as a dog barking or a car horn; or by physical objects or tastes. Synaesthetic concurrents not involving colour are far less common. They include odours and tastes arising from particular sounds, including musical notes, as described by another synaesthete:

"I avoid middle C when I play the piano, because it has an earthy, muddy smell I don't like."

In his classic account of the phenomena known as S. Aleksandr Luria 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."

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. Others experience colours 'in the mind's eye' as a distinct form of mental imagery for colour. Synaesthetes typically do not confuse induced colours with those of surfaces in the world. 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, but detailed psychophysical testing in these individuals has not yet been carried out.

Despite attempts to formulate a unified theory of synaesthesia, 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 both a cognitive and neurophysiological perspective.

Prevalence and family history

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, 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 (refs 19,20). Moreover, there is a high prevalence of synaesthesia among biological relatives of synaesthetes (refs 21-24). These findings support claims of a possible genetic predisposition transmitted by an X-linked autosomal dominant gene.

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 synaesthesia 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 arithmetic reasoning and deficient topographical cognition (for example, map-reading ability). To our knowledge, there have been no systematic investigations...
of these factors. In the only published study of the prevalence of self-reported synaesthesia, Baron-Cohen et al.\textsuperscript{17} found the same incidence of left-handedness in their UK sample as in the general population (roughly 10%; ref. 32), 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\textsuperscript{33}, and ingestion of specific psychoactive drugs, such as mescaline\textsuperscript{34,35}. 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\textsuperscript{36-38}. The few experimental investigations reported in the early literature tested the hypothesis that synaesthesia is a form of conditioned reflex\textsuperscript{39,40}. 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 Edinger\textsuperscript{41} 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\textsuperscript{42}.

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\textsuperscript{43-45}. Other patterns of association exist between pitch and lightness, pitch and brightness, loudness and brightness, and pitch and shape\textsuperscript{46}. 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\textsuperscript{47}.

It has been proposed that synaesthetic correspondences are based on the same patterns as non-synaesthetic associations\textsuperscript{48}. For instance, Karwowski et al.\textsuperscript{49} 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\textsuperscript{50} 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.

Recent accounts of synaesthesia have dealt with possible biological causes. One proposal is that synaesthesia arises from anomalous connectivity between brain areas that subserve the relevant sensory modalities\textsuperscript{51}. 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\textsuperscript{52,53}. The infants of several species have extensive functional connections between brain areas that subserve the different sensory modalities, many of which are lost during maturation through synaptic pruning\textsuperscript{54}. Maurer\textsuperscript{55} 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\textsuperscript{56} 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\textsuperscript{57}. Baron-Cohen and colleagues\textsuperscript{58} have suggested that extra connections between brain areas might lead to a breakdown of modularity between otherwise independent functional units (Box 2).

Box 2. Anatomical and cognitive modularity

Cognition and 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, sounds, faces or places\textsuperscript{59}. To what extent is this apparent anatomical and physiological partitioning of the brain consistent with a 'cognitive architecture'\textsuperscript{60}? Some time ago, Fodor\textsuperscript{61} 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, simulated subsystems, the inputs of which are restricted to a particular class of stimuli, 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 other domains\textsuperscript{62}. The concept of modularity continues to influence theories in cognitive psychology\textsuperscript{63}, and has proved to be a useful heuristic for conceptualizing the behaviour of synaesthetes in various contexts.
Rather than postulating the existence of anomalous or additional connections between brain areas, Groenendaal 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 a balance of feedback and feedforward information flows. This reciprocity is particularly evident in the visual system, where feedback from such high-level regions as area V1 can influence neural activity at the earliest stages of cortical processing, including the primary visual cortex (area V1; ref. 19). 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, Paulus and colleagues used positron emission tomography (PET) to examine patterns of brain activity in six women with colour–phonemic synaesthesia 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. A further ambiguity of the Paulus et al. study is that the pattern of extrastriate activity observed in the synaesthetes closely matches that found in studies of colour imagery in non-synaesthetes (fig. 1). As Paulus 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 used scalp-recorded evoked-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 areas.
sites, relative to a group of non-synesthetic 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 synesthetic 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 synesthetes, and whether they can be brought under voluntary control. The most widely adopted approach has been to examine the speed with which a synesthete 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 ’K’ elicits a synaesthetic colour of red, a congruent trial would involve the presentation of a red ’K’); in the other, the synaesthetic colour elicited by the target is incongruent with its actual colour (in this example, the letter ’K’ 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 (Box 1), which produces robust cognitive interference in normal participants under a range of conditions.

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](image_url)
**The Stroop effect**

The Stroop effect\(^1\) 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 in 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 trying the colour of each word in list A (below), and then doing the same for list B. The visual explanation for this effect is that reading is a highly automatic 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 words 'left' or 'right' above them are themselves pointing to the left or right\(^2\), and in identifying the number of elements in arrays of Arabic numerals\(^3\). Although there is still disagreement concerning the cognitive mechanisms that underlie Stroop effects\(^4,5\), the task has nevertheless served as a powerful tool in both cognitive psychology and neuropsychology\(^6,7\).

Numerous variants of the conventional Stroop task have been developed to examine the issue of automatization in colour-graphemic synaesthesia.

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**Box 2: The Stroop effect**

List A
- red
- blue
- yellow

List B
- dog
- back
- window

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are slower to name target colours under incongruent than congruent conditions\(^4,5,6,7\). 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\(^8\)). 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\(^9\), confirming the unidirectionality of synaesthetically induced\(^9\).

Synaesthetic Stroop interference has also been observed under conditions in which the inducing letter or digit appears immediately before a target colour patch\(^10\), indicating that synaesthetic activation associated with the inducer persists over time (Fig. 2a). In an innovative variant of this synaesthetic priming paradigm, Dixon and colleagues\(^11\) 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. 2e). Taken together, the findings from these synaesthetic Stroop studies indicate that synaesthetically colore d 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 synaesthetically colore d 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\(^12\) suggests that there can be substantial inhibition of synaesthetically colore d under certain conditions. In this study, a colour-graphemic synaesthete read aloud the print colours of digits, each of which was incongruent with the synaesthetically colore d. 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 synaesthetically colore d induced by the preceding incongruent colour item. This result showed that the representations of synaesthetically colore d 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 behaviour 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\(^13\). On the other hand, there is considerable evidence that substantial processing of the inducing stimulus is required before synaesthetic colour experiences are elicited\(^14\). 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 stimulus does not even need to be physically present to generate synaesthetically colore d.

In an attempt to address the issue of inducer processing, we developed the synaesthetic priming task mentioned above\(^15\). We presented individual inducers (letters) as primes, before a target colour patch that had to be identified and named as rapidly as possible (Fig. 2a). 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 26 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\(^17\). On the basis of these findings, we suggested that synaesthetically colore d typically arise only for inducers that are represented at conscious levels of visual processing\(^14\). 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\(^18,19\), one of which involved the use of Navon-type hierarchical stimuli (Fig. 2e). 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
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-synaesthetes. In this example, most non-synaesthetes grouped the display elements into rows. One synaesthete experienced ‘7’s and ‘1’s as red, and ‘9’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 target (‘H’) was 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-synaesthetes. 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 SRT 49 © 2001 The Royal Society.

many aspects of normal perception. 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. 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. We have also examined the effect of attentional load during presentation of an inducing prime on colour naming in the synaesthetes’ 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.

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 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, they provided a synaesthetestened to group matrices of achromatic digits according to the synaesthetesthe colours they elicited, whereas non-synaesthetes 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 synaesthetic 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 comprised 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 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. 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, whereas the displays used by Ramachandran and Hubbard were visible for a full second, allowing attentive processing. A more convincing demonstration of early perceptual grouping on the basis of synaesthetes’ colour would require speeded responses, and a demonstration that target detection times do not significantly increase with the number of distractors in the display.

The methodological concerns outlined above were overcome by Similecko and colleagues, 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 synaesthetes 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 the synaesthetes should find it more difficult to identify a target digit that was presented against a background coloured congruently with the synaesthetes’ colour than if the digit was 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 synaesthetes were 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-synaesthetes 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-synaesthetes 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 synaesthetes’ colours influence perception of inducing stimuli, probably through feedback from early colour areas, such as V4. Such an explanation requires that synaesthetes’ colours arise before explicit identification of the stimuli that induce them.
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, before conscious identification of the inducing stimulus, or at a later stage that depends on explicit identification of the inducer. 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 and colour processing 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 subserve 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. 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. 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 (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 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 colour recognition and colour processing (recognition, categorization, knowledge and imagery),

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**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 (25 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 (3) in a congruent trial (left); the colour of the background was the same as that elicited by the masked digit (blue in this example). In an incongruent trial (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 (3 or 4) in a display consisting of 12 or 18 distractor digits (1, 2, 4, 8). 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 Kadioglu et al. 2001 Massachusetts Institute of Technology.
E.g. 'A' elicits the synaesthetic colour of red:

![Diagram](image)

**Form**
- Auditory or visual presentation (of alphanumeric character)
- Surface colour information of object or surface

**Feature analysis**
- Early analysis

**Colour**
- Colour categorization/recognition
- Object colour knowledge (colour imagery)
- Lexicon (including colour names)

**Output buffer**
- Colour naming: Blue (surface colour)
- Lexicon naming: Red (synaesthetic colour)

**Conclusions**
We have proposed a neurocognitive framework for understanding the language-graphemic and colour-graphemic synaesthesia. Based on our current understanding of the processes that are normally involved in language and language processing, further research will also be necessary to determine whether different subgroups can be distinguished based on the level of induced processing required to elicit synaesthesia, and on the stage of colour representation that gives rise to synaesthetic experiences.

**Colour analysis**
In synaesthetes, unique functional connections are present between them. The consistent finding of interference in synaesthetic Stroop tasks, similar to 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 the effects of attentional load on synaesthesia.

**Visual masking**
Visual masking of the inducer effectively eliminates any concurrent synaesthetic colours, 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, 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 induced processing required to elicit synaesthesia, and on the stage of colour representation that gives rise to synaesthetic experiences.

**References**
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