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Can synaesthesia research inform cognitive science?

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The renaissance of synaesthesia research has produced many insights regarding the aetiology and mechanisms that might underlie this intriguing phenomenon, which abnormally binds features between and within modalities. Synaesthesia is interesting in its own right, but whether it contributes to our knowledge of neurocognitive systems that underlie non-synaesthete experience is an open question. In this review, we show that results from the field of synaesthesia can constrain cognitive theories in numerical cognition, automaticity, crossmodal interaction and awareness. Therefore, research of synaesthesia provides a unique window into other domains of cognitive neuroscience. We conclude that the study of synaesthesia could advance our understanding of the normal and abnormal human brain and cognition.

Introduction

> 'Vermillion has a sound like a tuba and a parallel can be drawn with a loud drum beat.'
>
> Vassily Kandinsky (1866–1944)

As the quote by the famous artist and music–colour synaesthete Kandinsky [1] demonstrates, synaesthesia is a fascinating phenomenon in which sensory experiences (e.g. sound or taste) or concepts (e.g. word, number or time) automatically evoke additional precepts (e.g. colour) [2].

The majority of experimental work that deals with synaesthesia, as well as review articles [3–5], has focused on understanding the phenomenon in isolation. For example, research has attempted to reveal the mechanism(s) that underlies synaesthesia [5–7], or the stage(s) of processing on which the synaesthetic experience depends [8–11]. However, independent of this line of research, the study of synaesthesia might help improve our understanding of the non-synaesthetic mind. Understanding the phenomenon requires forays into fields such as perception, awareness, representation, development and neuroanatomy and, therefore, it provides a good testing ground for many ideas and theories about different areas of cognitive science. The rapid growth of the field of synaesthesia in recent years enables us to examine the possible contribution of synaesthesia outside the field of synaesthesia *per se*.

Strictly speaking, synaesthesia is not a normal phenomenon because it exists in ~4% of the population [12]. However, it should be noted that, aside from their exceptional crossmodal experience, synaesthetes have normal cognitive abilities and brain activation. For example, brain imaging of synaesthetes shows elevated activation in areas that correspond to the synaesthetic experience but not in other brain areas [13,14]. In addition, in a variety of cognitive tasks and domains, independent of the synaesthetic experience, synaesthetes show effects that are comparable with those of non-synaesthete participants [8,9,15,16], and the incidence of mental illnesses or neurological deficits among synaesthetes is the same as in the normal population [17].

Many studies have shown that the synaesthetic experience is triggered involuntarily (e.g. Refs [6,8,10,11, 15,17]). One particular aspect of synaesthetic experience, which involves numbers – whether digit–colour (Figure 1) or number–form synaesthesia (Figure 2) – has been widely investigated [9,18–23]. In what follows, we present several examples that are related to numerical cognition, automaticity and crossmodal interaction. We present themes that are of interest to each field of study, and we show how research into synaesthesia can advance our understanding of these subjects. Other topics that will be discussed are awareness (Box 1), synaesthetic-like experience such as hallucinations, and sensory deprivation (Box 2).

We hope that the current review will encourage researchers in the field of cognitive sciences to use synaesthesia as an additional tool for studying the human brain and cognition.

Synaesthesia and numerical cognition

The mental number line

Findings in the study of numerical cognition are frequently interpreted in terms of analogue operations in which the representation and comparison of numerical magnitude exploit a number line [24]. On this line, numbers that are numerically close are represented by points that are spatially close to each other and numbers that are numerically far apart are represented by points that are spatially far apart from each other [25] (see also Refs [26,27]). However, certain experimental effects, presumably indicative of the existence of the number line, are not as common

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Figure 1. A digit–colour pairing for synaesthete A.

as one might expect. One such example is the spatial–numerical association of response codes (SNARC) effect [28], where responding is faster to small numbers with a left key-press and to large numbers with a right key-press in western society. The SNARC effect indicates that the orientation of the mental number line, in western cultures, is from left to right. However, it has been shown recently that only ~65% of participants show the SNARC effect [29]. Debriefing non-synaesthete subjects might be useless because people have limited access to their mind's eye. However, this is not the case with synaesthetes; as early as 1880, Sir Francis Galton documented what is termed 'number–form synaesthesia', in which synaesthetes experience explicit spatial arrangement of numbers [18,22,23]. Therefore, whereas SNARC and other numerical effects might stem from an implicit representation of numbers in space, number–form synaesthesia is an explicit representation of numbers in space (Figure 2). The prevalence of a left-to-right representation of numbers in number–form synaesthetes is similar to the prevalence of the SNARC effect in non-synaesthetes (which also implies a left-to-right representation). Between 63% [23] and 66% [22]

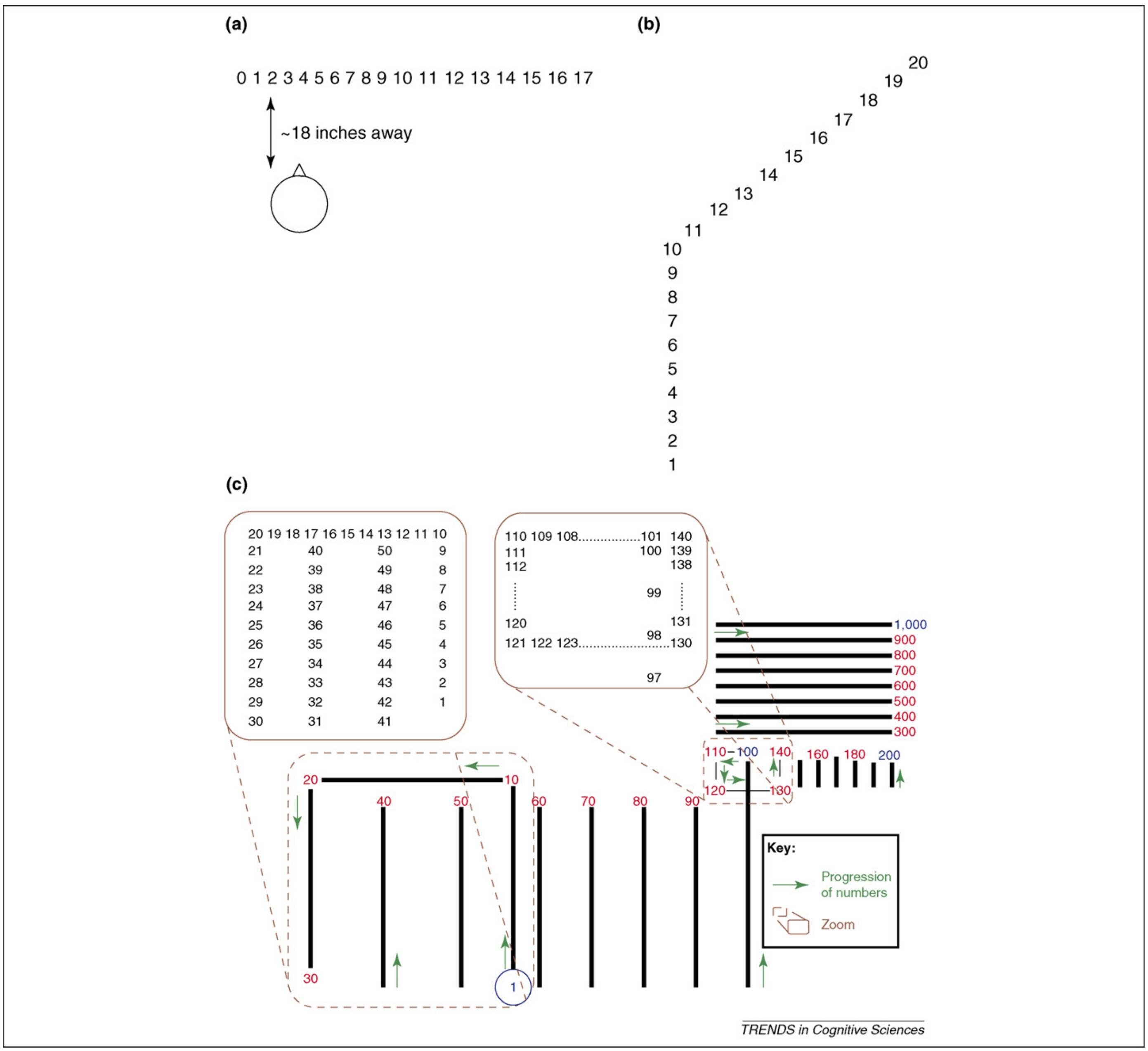

Figure 2. Examples of numerical representations of number–form synaesthesia. **(a)** A left-to-right straight-line representation in peripersonal space. **(b)** A vertical representation with a bend of 45 degrees at the digit 10. **(c)** A decade break in the form of a change of direction in synaesthete S.M. The beginning of the numerical sequence starts at the digit 1 (circled in blue). Progression of numbers is indicated by the green arrows. A change in the overall representation occurs at the numbers 100 and 200 (in blue). The representation continues to change after 1000 (in blue) but is not shown for simplicity. The zoom windows show a more detailed representation. (a) and (b) adapted from Ref. [23] with permission from Elsevier.

Box 1. Synaesthesia and awareness

Awareness is usually a prerequisite for synaesthesia [5]. Although it might be that we are all 'synaesthete-like' to some degree, in the sense that we tend to have a fuller experience in everyday life, in contrast to (conscious) synaesthetes, we are unaware of this experience. The evidence from number–form synaesthesia indicates that this might be the case. Behavioural studies suggest that synaesthetes as well as non-synaesthetes experience numbers [23,28] or months [58,59] in space. Similar correspondence between synaesthetes and non-synaesthetes can also be found in cross-modal interaction of pitch and lightness [48], or letter and colour [49]. Synaesthetes give a rich description of their synaesthetic experience, whereas non-synaesthetes do not. Accordingly, other types of synaesthesia-like experience might also exist in non-synaesthetes.

Synaesthetes also might not be aware of the full extent of the novel connections that are made by their brains. They commonly report that their synaesthetic experience is unidirectional: digits evoke colours, but colours do not evoke digits. Based on this phenomenology, researchers concluded that synaesthesia is unidirectional [60,61]. However, recent studies have shown that, in some synaesthetes, colours probably evoke digits or their magnitude implicitly [21,62,63], or explicitly [20]. The quote at the beginning of the current paper provides a nice demonstration of bidirectionality by the music–colour synaesthete Kandinsky (vermillion triggers the sound of a tuba). The bidirectionality suggests that the previous findings might be a result of implicit bidirectional synaesthesia [19]. For example, the performance of synaesthete C was attributed to synaesthetic experience due to the meaning of the digit [19]. When she was presented with a numerical equation followed by a coloured patch, naming the colour of the patch was faster when it matched the solution to the equation than when it did not match. This effect was attributed to synaesthetic experience at the conceptual level [19]. However, colour might actually have triggered the percept of the digit (i.e. bidirectionality), thus leading to the observed effect. The existence of both implicit and explicit bidirectionality demonstrates that synaesthesia could be a phenomenon that is graded as a function of awareness, rather than an all-or-nothing function [61] (Figure I in this box).

It has been suggested that the greater the abnormal neuronal connections, the greater the activity in the area that relates to the synaesthetic experience [13], thus enabling it to enter conscious awareness. However, if the pathways are heavily pruned, only a residual activation might remain, which might be insufficient to reach conscious awareness [4]. Accordingly, it can be suggested that awareness might be graded and be a function of the amount of abnormal connections. Such quantitative differences might lead to differences in conscious perception [20]. Alternatively, access to conscious awareness might vary according to the degree of disinhibition (i.e. unmasking) [64].

The various degrees of synaesthesia and awareness (Figure I) could help in studying the mechanism that underlies conscious awareness, by looking for parametric changes in neuronal connections (via diffusion tensor imaging), different degrees of inhibition, or both.

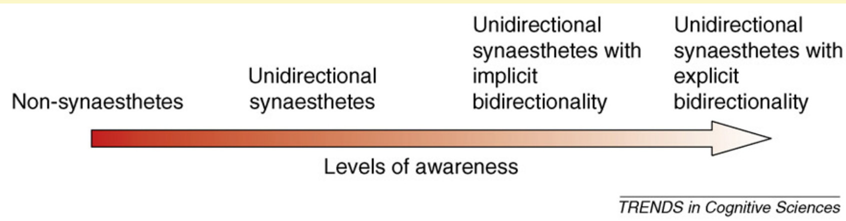

Figure I. Four types of synaesthesia that have different degrees of awareness. First on the left, non-synaesthetes, who might show synaesthesia-like performance but lack awareness of it, such as in the case of the implicit representation of a mental number line [29], which is similar to number–form synaesthesia [22]. Second from the left, synaesthetes who have only unidirectional synaesthesia. Third from the left, synaesthetes who have unidirectional synaesthesia in addition to implicit bidirectionality [20,55,56]. And on the right, synaesthetes who have conscious awareness of their bidirectionality [19]. The colour of the arrow indicates the estimated prevalence of each group in the entire population, with red indicating common prevalence and white indicating very rare phenomena.

Box 2. Synaesthetic-like experience in non-synaesthete patients

Synaesthetes have experiences over and above the normal. However, there are other populations that have synaesthetic-like experiences. That is, certain individuals have experiences that are absent in most of the population and/or activation in brain areas without the specific external stimuli that commonly activate these areas [65–68]. For example, people who have paranoid schizophrenia show activation in Heschl's gyrus during auditory hallucinations in the absence of external speech [65], and people who have Charles Bonnet syndrome show activation in visual areas due to visual hallucinations (e.g. activation of the fusiform face area during hallucinations of faces) [66]. This is similar to the experience of colour and the activation of visual area V4 in grapheme–colour synaesthetes, in the absence of colour presentation [6]. Other examples come from people who have sensory deprivation. For instance, blind people might have a somatosensory experience following stimulation of the visual cortex [69].

Similarities between some of these phenomena and synaesthesia [64] have been noted, and it is possible that these phenomena share a common mechanism – that is, they all stem from abnormal neuronal connections or a type of disinhibition (i.e. unmasking in the case of the deprived brain). Future studies should examine the relationship between these phenomena. Providing such knowledge will further our understanding of why some people perceive information consciously whereas others do not [64].

of number–form synaesthetes experience (explicit) left-to-right representation of the numbers 1 to 10, which is similar to the ~65% of non-synaesthetes who show the SNARC effect [29]. In our opinion, this similarity suggests that the existence of individual differences in the SNARC effect of non-synaesthetes is, at least partly, due to individual differences in implicit mental representation of numbers, which differs from left-to-right representation. In turn, this raises the possibility that the experience of synaesthesia can be graded in terms of awareness [30] (Box 1). Indeed, the fact that synaesthetes are aware of their experience enables one to study phenomena that are otherwise difficult to access empirically. For example, Sagiv and colleagues [23] contrasted the performance of a synaesthete who had an unusual right-to-left number–form representation with that of synaesthetes who had a more common left-to-right number–form representation. Responding to congruent trials (i.e. in contrast to SNARC, responding to the smaller number with a right key for the participant who had right-to-left number–form; and, in line with SNARC, responding to the larger number with a right key for the participants who had the left-to-right number–form) was faster than responding to incongruent trials in all participants. Accordingly, it is possible to conclude that (i) the left-to-right mental number line is not necessarily common to all, and (ii) access to such mental representation of numbers might be automatic. However, the assumption of a common implicit left-to-right mental number line might preclude the detection of uncommon representations (e.g. circular arrangement of numbers).

Numerical representation: compressed or linear?

Subjects are faster at comparing small numbers (e.g. 1–2) than large numbers (e.g. 7–8) in spite of the same numerical distance – this is called the size effect. This effect reflects the fact that the representations of numbers become less discriminable, owing to logarithmic scaling [25] or scalar variability [26], as numerical magnitude increases. Recently, it has been suggested that the size effect is task specific – that is, it appears in comparison tasks but not in other tasks that also require access to the mental number line, such as parity or naming tasks [27]. These results led to the suggestion that the observance of the size effect under magnitude comparison stems from mappings of the number line to the task-relevant output component and not from the number line *per se*. Cohen Kadosh *et al.* [31] used an explicit bidirectional synaesthesia (e.g. a case in which digits evoke colours, and vice versa; Box 1) to examine this suggestion. To avoid a comparison task, a digit–colour synaesthete was asked in one experiment to name a presented digit while ignoring its ink colour and in another experiment to name the digit that corresponded to the ink colour while ignoring the presented digit. The digits could be small (i.e. 1 or 2) or large (i.e. 7 or 8), coloured in a congruent (e.g. 1 coloured in the colour of 1) or in an incongruent manner (e.g. 1 coloured in the colour of 2). Because the colour activates the corresponding digits, the assumption that representations of numbers change with their size [25,26] predicted that the congruity effect would be modulated by the size of the number. By contrast, if the representation does not change with size (i.e. the size effect does not characterize the mental number line) [27], the congruity effect should be the same for small and large numbers. The results showed an interaction between numerical magnitude and congruity (Figure 3), thus challenging the idea of a linear number line [27].

Additional support for an increase in overlap as number magnitude increases comes from the phenomenology of number–form synaesthetes who report that, as numbers increase, the representation becomes fuzzier and no longer visible [22], although this experience relates to large numbers (e.g. above 100).

Representation of two-digit numbers

There are two opposing viewpoints on the mental representation of two-digit numbers. The holistic model [32] assumes that numbers are represented as wholes. For example, the number 54 is represented without the differentiation between decades and units, such as five tens and four units. By contrast, the parallel model [33] suggests that there are separate representations for decades and units. Number–form synaesthetes report that numbers are represented continuously in space from 1 to several hundreds or even thousands, which supports the holistic model [18,22,23].

However, those number–forms often have decade breaks (i.e. in the form of a change of direction) and a minority of number–form synaesthetes have a matrix-like representation with discontinuities (Figure 2c). Moreover, digit–colour synaesthesia provides evidence in favour of the parallel model. Digits that are experienced in colour are commonly 0 to 9. Most digit–colour synaesthetes do not have a special colour for the number 45 or 54, for example; rather, their colour experience corresponds with individual numbers [22]. For example, in A, a digit–colour synaesthete, '54'

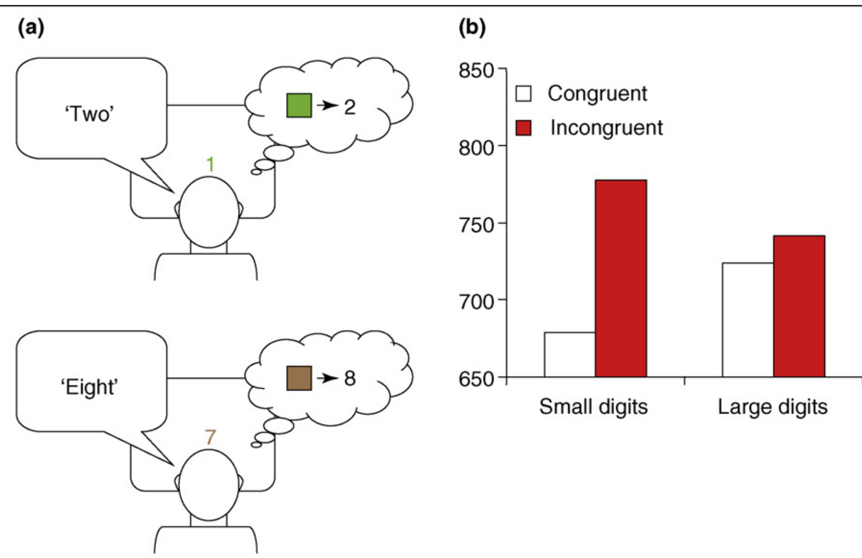

Figure 3. A synaesthetic walk on the mental number line. **(a)** An incongruent trial from a naming experiment. I.S., a digit–colour synaesthete, was asked to name the digit that was triggered by the coloured font. In the speech bubble is the correct verbal response (e.g. 'Two'); in the thought bubble is the association triggered by the colour, which, according to the synaesthete I.S., represents the number (e.g. 2). **(b)** The reaction-time data (in milliseconds) for small digits (i.e. 1 and 2) and large digits (i.e. 7 and 8) as a function of congruity. With small digits, the congruity effect was larger. This indicates that the size effect reflects a basic feature of the nonlinear mental number line, in which smaller numbers are more discriminable, thus leading to faster access of their numerical value and larger interference. Modified from Ref. [31] with permission from Elsevier.

would evoke the colour brown for the digit '5' and light green for the digit '4'. Importantly, in some digit–colour synaesthetes, synaesthesia has been shown to be due to a conceptual rather than a perceptual origin [9,19,34]. Thus, the base ten representation of digit–colour is not due to the limited perceptual representation of graphemes. Such limited pairing of digit–colour suggests that two-digit numbers are represented in different bins for tens and units [33,35]. Considering evidence from number–form synaesthesia and digit–colour synaesthesia together, it seems that there exists a bipartite mechanism of both holistic and parallel processing [33]. A recent imaging study has validated the existence of such a hybrid mechanism in non-synaesthete brains [36].

The examples provided in this section show that synaesthesia can serve as an important tool for examining cognitive theories. Moreover, it seems that the phenomenology of synaesthetes can guide research in normal participants and, by that, constrain cognitive theories. In the next section, we focus on the mechanism for automaticity, and how synaesthesia can contribute to this subject.

Synaesthesia and automaticity

Potential underlying mechanism for automaticity

Much discussion and research in cognitive psychology revolves around the concept of automaticity. Many researchers distinguish between two modes of human operation: one is automatic–reflexive and the other is controlled–voluntary. This distinction characterises various areas of cognitive functioning, such as language [37], memory [38] and visual-spatial orienting [39]. A given process might be automatic owing to a specialized neuronal mechanism(s) [40,41]. Such a dedicated operation works as a 'module' [42], which functions autonomously, is not influenced by other mechanisms and is obligatory [41]. Therefore, synaesthesia, which embodies interactions between modules, does not fit this simplified notion of modularity [43]. Yet, most synaesthetes report that their synaesthetic experience is involuntary [17], and a wide range of experimental manipulations show that this is indeed the case [6,8,10,11,15,17].

Understanding the neuronal mechanism behind synaesthesia might suggest a potential substrate for automaticity. A long-standing debate is whether synaesthesia is a result of (i) extra neuronal connections [6,43], probably due to failure of synaptic pruning at an early developmental stage [44], which leads to additional connections in synaesthetes' brains, or (ii) failure in inhibition [5]. In failure in inhibition, synaesthesia is mediated by the same amount of neuronal connections that exist in non-synaesthetes and is induced by disinhibition of feedback signals, probably from a 'multisensory nexus'. In our opinion, either way, through neuronal connections or changes in inhibition, a process can be switched from being voluntary in nature to being obligatory. What is essential for automaticity is not the lack of connections among systems or being encapsulated but rather the obligatory nature of the process [41,45]. Note that automaticity can emerge in a short time frame of even a few hours. For example, motor-skill automaticity can occur within 3 h [46]. However, this time frame cannot enable new neural connections to emerge [47]. We believe that, to automatize a given process, the two candidate mechanisms for synaesthesia might operate in concert, with an early disinhibition followed by the production of specialized neuronal connections. This suggestion can also explain why some tasks become automatized more quickly than others. According to this view, processes that have predefined strong neuronal connections, which enable the modulation of inhibition, are more likely to become automatic than processes that have fewer connections.

It seems that research efforts in automaticity and synaesthesia are pursuing a similar question regarding their underlying mechanism. In our view, finding an answer or confining options in one field would provide an important clue for the other field. Moreover, adding a developmental perspective might provide a powerful and important contribution to the field of cognitive science (Box 3).

Synaesthesia and crossmodal interaction

Several studies showed that the principle organization behind pitch–colour (hearing tone induces a colour) [48] and even letter–colour [49] connections in synaesthetes and non-synaesthetes might be, at least partly, shared. This evidence suggests that synaesthetes recruit the same mechanism as non-synaesthetes [48], but this use might be quantitatively different. However, it should be examined whether this holds true for all types of synaesthesia. As was suggested in the previous section, researchers suggested that the crossmodal interaction in synaesthetes is due to failure in pruning (i.e. the extra neuronal connections hypothesis) [6,43]. This idea was based on the findings that infants showed visual evoked potentials to auditory stimuli [44]. However, an alternative explanation is that the crossmodal interaction is due to the unmasking

Box 3. Questions for future research

- How early in life can synaesthesia be detected, and how can this inform theories of development? For example, might synaesthesia be due to failure in specialization of certain areas (e.g. the auditory cortex fails to specialize in audition), resulting in these areas responding also to other modalities (e.g. vision, in hearing–colour synaesthesia) and greater crossmodal interaction?
- How does brain damage affect synaesthesia? How does the location of damage alter the experience? Will it eliminate, elevate or even add an experience? Given the relatively high prevalence of synaesthesia, combining patient research with synaesthesia might elucidate the neural correlates of crossmodal experience.
- Can some general principles that are more explicit in synaesthesia than in non-synaesthetes, such as pitch–colour interaction, be used to understand aesthetic tendencies?
- Will synaesthetes learn to bind different modalities, which they do not bind in their everyday life, faster than non-synaesthetes? If so, this evidence would provide strong support for the unitary nature of synaesthesia.
- What is the connection between metaphors and synaesthesia? Finding out whether synaesthesia is a higher degree of quantitative metaphorical thinking [60] or qualitatively different [61] might give some insights into the understanding of metaphorical thinking.
- Is automaticity due to the accumulation of instances (i.e. the instance theory [70]) that, in the long run, can be retrieved from memory, or is it due to improved efficiency of algorithmic processes? At the moment, there is little evidence to suggest that synaesthesia, although automatic, is due to memory during childhood [60].

of unimodal neurons (e.g. vision) that exist in another unimodal area (e.g. the primary auditory cortex) [50]. This idea, which is similar to the disinhibition hypothesis [5] (albeit without assuming leaking from a 'multisensory nexus'), can explain the findings of synaesthetic-like crossmodal interaction in infants [44], without assuming extra neuronal connections. According to this view, the extra crossmodal interaction in synaesthetes might be due to failure of masking (i.e. inhibition) the irrelevant unimodal neurons that exist in us all. Alternatively, it might be that this failure is due to a larger proportion of such neurons, relative to the non-synaesthete brain.

Related to the crossmodal interaction is the binding problem – how independently processed features are reunited to produce a unified experience of objects [51]. Compared with non-synaesthetes, synaesthetes bind two features, one of which is not actually presented. By contrast, patients who have damage to the parietal lobe might show a problem in binding. It has been suggested that an integrative study of over-binding in synaesthesia and deficient binding in patients can contribute to our understanding of the binding problem [51].

Transcranial magnetic stimulation (TMS) is a non-invasive technique that induces a current that depolarizes the cell membrane in the cortex and can lead to temporary neuronal disruption. This enables the examination of how crucial the stimulated brain structure is to a given cognitive function. In contrast to patient studies, TMS enables causal relationships between malfunctions in a specific brain area and overt behaviour [52] to be addressed. Recently, two TMS studies on grapheme–colour synaesthetes (Figure 4) showed that the synaesthetic experience becomes less automatic after stimulation to the right parieto-occipital area [53,54], a region that has been shown to participate in binding in non-synaesthetes [55]. Esterman *et al.* [53] and Muggleton *et al.* [54] presented a coloured letter on a screen and asked synaesthetes to press the button that corresponded to the presented colour. The presented colour could have been congruent or incongruent with the colour that the letter induced in the synaesthetes. Following TMS to the right parieto-occipital area, the induced colour tended to interfere less. By contrast, TMS over V1 and the left posterior parietal area [53], or even to the left parieto-occipital, left parietal and right parietal areas [54], had no effect on interference. An open question for future research is whether the right parieto-occipital area is crucial for other types of synaesthesia, such as pitch–colour, taste–shape or number–form. The answer to this question should provide insights for several topics of interest:

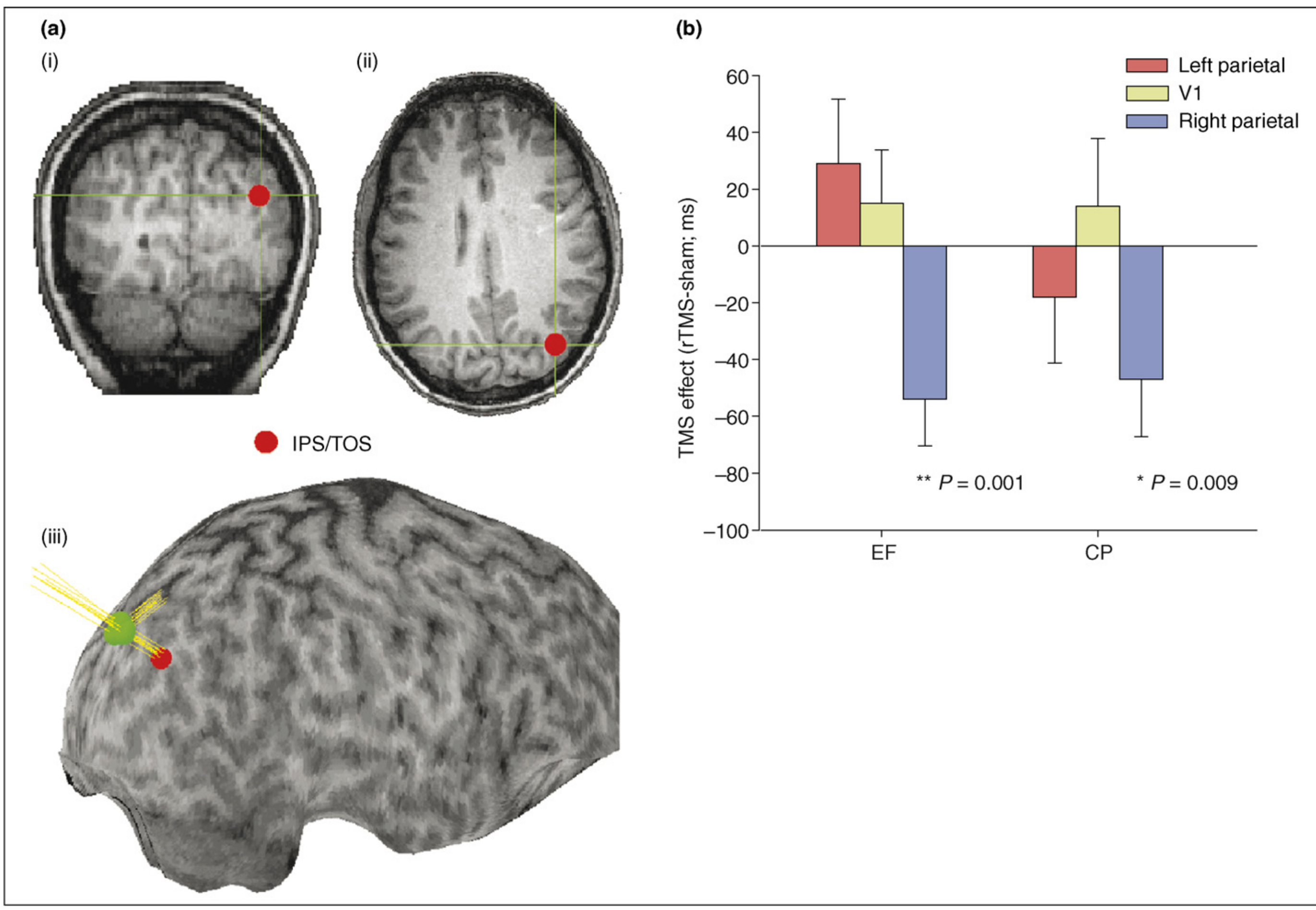

Figure 4. The effect of transcranial magnetic stimulation (TMS) on grapheme–colour experience in synaesthetes [53]. **(a)** Following TMS to the right parieto-occipital area (i,ii), the induced colour tends to interfere less. Target location (IPS/TOS; intraparietal sulcus/transverse occipital sulcus) is shown in red. (iii) The centre of the magnetic coil is shown in green and estimated pulse and orthogonal trajectories are shown as yellow lines. **(b)** Stroop-like interference following TMS to synaesthetes E.F. and C.P. In contrast to stimulation of the right parieto-occipital area (right parietal), Stroop-like interference was not affected after stimulation to V1 and the left posterior parietal area (left parietal). Adapted, with permission, from Ref. [53].

(i) Is synaesthesia a unitary phenomenon?
(ii) Assuming that stimulation of a single brain area affects the synaesthetic experience, this could serve as evidence that synaesthesia is due to failure in inhibition [5]. Such failure could be induced by disinhibition of feedback signals, probably from a 'multisensory nexus' at the parietal lobe, rather than due to extra neuronal connections [6,43].
(iii) Are different brain areas involved in the synthesis of different features of crossmodal interaction in synaesthetes as well as non-synaesthetes [56]?

As in other topics that we have discussed in this review, the use of synaesthesia research to study cross-modal interactions enables unique insights into cognitive architectures of non-synaesthetes and their neuronal correlate. The topics that we have provided here are wide and diffuse. Thus, this demonstrates that research in the field of synaesthesia can contribute to a wide context, in high-level cognition (e.g. numerical cognition), perception (e.g. crossmodal interaction and binding) and automaticity. Using synaesthesia as a tool to study normal cognition can provide better insights into non-synaesthetes' cognition, as well as the phenomena of synaesthesia.

Concluding remarks

It is clear that the knowledge gained from research on synaesthesia is not confined to the understanding of synaesthesia *per se*; rather, it can be used to constrain psychological theories in other areas. Moreover, we believe that the study of synaesthesia can contribute to additional areas that are not covered in the current article, such as language [57], emotion, imagery and attention. An integrative approach to perception and cognition requires an understanding that, by studying subjects using experiments over and above the usual, we can advance our understanding of normal brain mechanisms as well as of abnormal experiences (Box 2).

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