INTRODUCTION

SYNAESTHESIA: AN OVERVIEW OF CONTEMPORARY FINDINGS AND CONTROVERSIES

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ABSTRACT

Research on synaesthesia is undergoing something of a renaissance, having initially been a hot topic in psychology and philosophy in the late 19th and early 20th centuries. One hundred years ago investigators failed to define an objective framework within which to characterise the phenomenon, and so interest in the topic waned. With the cognitive revolution and the rapid rise of new experimental techniques in human neuroscience, interest in synaesthesia as a legitimate topic for scientific investigation has been rekindled. Since the 1980s there has been rapid growth in scientific and media interest in synaesthesia, and there is now a sense that real progress is being made. This Special Issue of *Cortex* brings together the largest collection of empirical papers on the topic of synaesthesia to date. The 21 papers collected herein showcase the many significant advances that have been made in understanding the behavioural and neural bases of synaesthesia. The contributions reflect the work of more than 60 investigators from nine different countries. We are confident that the papers presented in this Special Issue will set the agenda for synaesthesia research for many years to come.

INTRODUCTION

Imagine a world in which the number "2" is pink, the word "computer" tastes of *jelly beans*, and F# has a conical shape. For people with synaesthesia, experiences such as these are an integral part of everyday life that goes beyond the realm of mere imagination. The aim of this paper is to briefly review the current theories and findings in synaesthesia research, with particular reference to the new set of empirical studies presented in this Special Issue of *Cortex.*

WHY SYNAESTHESIA?

Research into synaesthesia has grown, and is continuing to grow, at an unprecedented rate (for recent overviews see Ramachandran and Hubbard, 2001b; Rich and Mattingley, 2002; Robertson and Sagiv, 2005). Different researchers have their own reasons for being interested in the phenomenon. Undoubtedly, some have been drawn into the field because of its inherent quirkiness or disbelief that it could be a genuine trait. The ultimate worth of research into synaesthesia, however, will be measured by its ability to inform theories of "normal" or typical cognition. If synaesthesia turns out to be just "romantic neurology" (Humphreys, 1990) or little more than a "benign cognitive variant" (as described by one journal editor) then the decline of research in this field could be as rapid as its ascent.

Synaesthesia differs from most other neuropsychological conditions in that it is a positive symptom, i.e., it is defined by the presence of a trait not found in other members of the population, rather than by the absence of a function (as in neglect, amnesia, aphasia and so on). This, in itself, should not preclude it from informing theories of normal cognition. Other positive symptoms such as hallucinations (Frith, 1992), confabulations (Schnider and Ptak, 1999) and the anarchic hand syndrome (Della Sala et al., 1991) have been successfully explained by reference to models of normal cognitive function. However, unlike many other positive symptoms, it is not associated with obvious brain pathology or with general cognitive dysfunction. Most synaesthetes, including all those considered in this Special Issue, report synaesthesia of developmental origin. Developmental synaesthesia has no known onset, and persists throughout life. Many synaesthetes are surprised to find that others do not share their experiences. They typically do not seek the help of clinicians or other professionals, but there is a suggestion of an unusual balance of cognitive strengths and weaknesses (e.g., memory is often reported to be good, and numerical abilities bad; Cytowic, 1989; Rich et al., 2005). Although not pathological, it is probable that the brains of synaesthetes possess unique structural and/or functional properties. Functional imaging studies have demonstrated patterns of activation in synaesthetes that are clearly different from those of controls (Hubbard et al., 2005; Nunn et al., 2002), but no structural imaging data (e.g., voxel-based morphometry) have been published to date. Given that the aim of most neuropsychological research is to use atypical cognition to inform theories of normal cognition (rather than for rehabilitative

purposes), there is no reason why this framework should not be extended to the atypical experiences of synaesthetes. But to what aspect of normal cognition does research into synaesthesia speak? If amnesia is studied to inform theories of memory, or neglect is studied to inform theories of spatial attention, why study synaesthesia? One theme covered by many of the papers in the Special Issue is the question of how synaesthesia relates to theories of intra-modal and cross-modal perception. How different visual attributes such as form and colour are integrated in perception is an issue of interest to many cognitive neuroscientists (Treisman, 1999); synaesthesia may represent an instance of colour binding in the absence of external colour information (Robertson, 2003). A related reason why many are interested in synaesthesia is that it may shed light on the neural and cognitive substrates of perceptual awareness (e.g., Gray, 2003; Gray et al., 2006, in this issue, p. 309). By definition, synaesthesia is the elicitation of perceptual experiences in the absence of the normal sensory stimulation. As such, the study of synaesthesia offers a way of untangling conscious from preconscious processing. It is not surprising that synaesthesia has started to attract the attention of philosophers (e.g., Hurley and Noe, 2003). Although synaesthesia may be rare and atypical, the experiences themselves are combinations of common senses (colour, taste and so on) rather than some "sixth sense".

The question of how different senses interact in the brain is also currently a hot topic in cognitive neuroscience (Calvert et al., 2004). Some go as far as to argue that cross-modal perception is the rule rather than the exception (Shimojo and Shams, 2001); certainly there is evidence that the senses are relatively undifferentiated in neonates (see Maurer, 1997; Maurer and Mondloch, 2005). Many forms of synaesthesia, such as those in which visual percepts arise from sound, are instances of cross-modal processing (albeit elicited by a unimodal stimulus). The question of whether this synaesthetic cross-modal processing resembles that observed in non-synaesthetes is an empirical one, but there is some evidence that it does (Ward et al., 2006, in this issue, p. 264). The study of acquired synaesthesia has received very little empirical research to date, but this condition may also prove to be invaluable for studying normal cross-modal perception. Some forms of synaesthesia (or synaesthesia-like phenomena) can be elicited pharmacologically (Hartman and Hollister, 1963), from sensory deprivation arising from damage to input pathways (e.g., Jacobs et al., 1981), or even from prolonged blindfolding (Merabet et al., 2004).

Not all research into synaesthesia speaks to issues directly related to perception. For example, some synaesthesia researchers are primarily interested in brain development and plasticity, and genetic influences upon it (Baron-Cohen, 1996;

Maurer, 1997; Maurer and Mondloch, 2005). Others are interested in synaesthesia because it provides a window onto how other types of information (e.g., words, memories) are represented in the brain. For example, the presence of coloured letters may be used to investigate the interaction of word-level and letter-level knowledge in models of reading. To what extent are visual words processed at a global level or as the sum of their parts? It may also be used to explore the overlap between perception, imagery and memory. Is it always the case that words perceived as coloured will also be imagined and remembered as coloured, or can perception be dissociated from imagery and memory? Additionally and perhaps relatedly, some believe that synaesthesia may be linked to certain types of mental ability (Ramachandran and Hubbard, 2001b). There is no shortage of candidates (e.g., memory, metaphor, musical aptitude, creativity) but there is presently a shortage of empirical data.

KEY CHARACTERISTICS OF SYNAESTHESIA AND VERIFICATION OF AUTHENTICITY

Given the rate of new discoveries in the field, we do not wish to be prescriptive in defining synaesthesia. Nevertheless, there would seem to be at least three important features that characterise the kinds of synaesthetic experience that have been described to date. First, the experiences are elicited by particular stimuli that would not evoke such experiences in most members of the population. We would add that these inducing "stimuli" might be perceptual or conceptual. Second, the experiences are automatic and are extremely difficult to suppress (although they may be modulated by attention; see Mattingley et al., 2006, in this issue, p. 213; Sagiv et al., 2006, in this issue, p. 232). Third, the nature of the synaesthetic experience itself is akin to that of a conscious perceptual event (though clearly the subjective nature of synaesthetic experiences is practically impossible to measure). To this list, a fourth feature potentially could be added: that synaesthetic experiences are consistent over time; if they were not, then again the phenomenon would be virtually untestable. Having said this, in our opinion reliability over time should be considered as an associated characteristic of synaesthesia rather than an *a priori* defining one. Would we not consider a person to be a synaesthete if the colours he or she experienced for particular musical notes changed over time?

Most contemporary studies of synaesthesia provide an objective test to discriminate between synaesthetes and non-synaesthetes based on one or more of the characteristics mentioned above. The "gold standard" has been to measure the internal consistency of synaesthetic experiences over time (the so-called 'test of genuineness'; Baron-Cohen et al., 1987). In this Special Issue, Asher et al.

(2006, p. 137) report a revised version of their "test of genuineness" using Pantone colour chips. They tested 26 synaesthetes who experience colours from spoken words and/or other auditory stimuli, and found greater internal consistency in these individuals than in a control group.

The question of whether synaesthetic experiences are automatic has typically been investigated using a synaesthetic variant of the Stroop task (Wollen and Ruggiero, 1983), in which participants are asked to name the actual colour of a visual stimulus (digit, letter or word) and ignore the synaesthetic colour it elicits. Given that the synaesthetic colour is irrelevant to the task, interference arising from it is attributed to automatic processing. In this Special Issue, Ward et al. (2006, p. 264) report the first *cross-modal* synaesthetic Stroop experiment in which, for example, a "red" sound interferes with naming a green target-patch. Also in this issue, Lupiáñez and Callejas (2006, p. 204) report a negative priming experiment with congruently and incongruently coloured digits and letters (see also Odgaard et al., 1999). Naming the synaesthetic colour and ignoring the text colour on trial N slows naming times when the ignored colour becomes the to-be-named colour on trial N + 1. Finally, Paulsen and Laeng (2006, in this issue, p. 290) report a novel measure of Stroop interference based upon a biological marker (pupil diameter) rather than a behavioural measure (reaction time). They found that pupil diameter increases with incongruently coloured graphemes relative to congruently coloured or black graphemes, thus revealing a direct physiological correlate of synaesthetic experience.

Perceptual Reality and Neural Substrates of Synaesthesia

Although measures of consistency and Stroop interference have diagnostic validity they do not unequivocally demonstrate that synaesthesia is perceptual in nature. It has long been recognised that Stroop-interference can arise at one or more of a number of processing stages, from early perception through to response selection (MacLeod, 1991). Recent studies have attempted to address the question of whether synaesthetic experiences really are akin to normal perceptual experiences. These can be broadly divided into two categories: (a) those that have used psychophysical approaches to show how synaesthetic colours behave comparably to "real" colours; and (b) those that have used functional neuroimaging to examine the extent of overlap between brain regions involved in synaesthetic perception and those involved in visual perception more broadly. Most of these studies are based on synaesthetic colours elicited by graphemes. It is to be noted that these studies refer to graphemes in the sense of graphic symbols (typically letters and digits), rather than orthographic equivalents of phonemes which often consist of letter clusters (for discussion see Henderson, 1985).

In this Special Issue, Kim et al. (2006, p. 195) report two experiments based on perceptual grouping of synaesthetic colours. In one experiment, two static arrays of graphemes were presented repeatedly in rapid succession to induce bistable apparent motion. For synaesthetes, the perceived direction of motion was biased by the presence of synaesthetic colours. For example, if achromatic letters that induced the same synaesthetic colour appeared at 0 degrees in frame 1 and at + 45 degrees in frame 2 (a situation that normally renders the direction of motion ambiguous), the display was reliably perceived as rotating in a clockwise direction by the synaesthetes, but not by controls. In a second experiment, Kim et al. (2005) examined the extent to which real and synaesthetically induced colours interact to facilitate grouping under conditions of binocular rivalry. Normally, if two stimuli are presented to different eyes then the perceived image alternates between them, rather than being a blend of the two. Kim et al. (2006) found that real colours and synaesthetic colours elicited by achromatic letters tended to group together, thus prolonging the periods of perceived global dominance. Also in this issue, Witthoft and Winawer (2006) report findings from a study in which they demonstrate that synaesthetic colours are susceptible to normal mechanisms of lightness constancy. They presented graphemes against physically identical grey backgrounds that were structured so that a square patch placed in one region appeared perceptually lighter than an identical patch in another region (the 'checkershadow illusion'). They found that the grey background also affected the perceived lightness of the synaesthetic colour induced by an achromatic grapheme, suggesting that synaesthetic colours are incorporated within the stream of normal visual processing. In a further psychophysical investigation, Hubbard et al. (2006, in this issue, p. 184) systematically varied the contrast between grapheme and background in an embedded-figures task and a crowding task, and found that contrast affected the extent to which synaesthetic colours biased performance. They conclude that synaesthetic colours may be elicited at contrast-dependent stages of visual processing.

The other approach that has been taken to verify the perceptual nature of synaesthesia involves functional brain imaging. In this Special Issue, Steven et al. (2006, p. 304) report activation of visual areas, including left V4 and bilateral V1, in a synaesthete who has been blind for 10 years. The regions were active when the synaesthete listened to colour-inducing words (days, months) but not during a control task that involved colour imagery. Most imaging studies to date have used spoken words as inducing stimuli (Aleman et al., 2001; Elias et al., 2003; Nunn et al., 2002; Paulesu et al., 1995). In the paper by Sperling et al. (2006, in this issue, p. 295),

visually presented graphemes were used rather than auditorily presented stimuli. The authors contrasted patterns of brain activity for achromatic graphemes that elicited either coloured or "colourless" synaesthetic experiences (i.e., greys, whites or blacks), and found bilateral activity in area V4. Another imaging study conducted by the late Gray et al. (2006, in this issue, p. 309) was based on Stroop conflict elicited by visually presented colour words (Gray et al., 2006, in this issue, p. 309). For some synaesthetes, colour names have a synaesthetic colour that does not match the meaning of the word (e.g., where the word 'blue' is experienced as red) – a phenomenon that Gray et al. (2006) call the "alien colour effect" (ACE). A comparison between synaesthetes who experience the ACE and those that experience the same colour as the word's meaning (e.g., 'blue' as blue) revealed significant hippocampal activation, which the authors interpret as reflecting conscious conflict resolution.

At What Stage in Processing does Synaesthesia Occur?

There are two main controversies in the literature concerning the stage of processing at which synaesthetic colours emerge. The first debate revolves around the role played by mechanisms of selective attention. To date this debate has focused exclusively on the most common form of synaesthesia, in which graphemes (letters or digits) elicit colours (so-called grapheme-colour synaesthesia; see Rich et al., 2005). Is attention to a grapheme necessary or can synaesthetic colours emerge in the absence of focused attention? The second debate concerns which aspect of an inducing stimulus is critical for eliciting the colour. Is it the shape of the grapheme, its abstract identity (independent of font or case), or some other property such as its pronunciation? Although these two questions could effectively collapse on to each other, it is helpful to consider them separately.

Attention or Pre-attentive "Pop-out"?

One of the most influential studies in the synaesthesia literature is the demonstration of "pop-out" based on grouping of synaesthetic colours. Ramachandran and Hubbard (2001a) presented arrays of target graphemes (e.g., black 2's) amongst distractors (e.g., black 5's) such that the targets were arranged to form shapes (e.g., triangles, rectangles). At viewing times of 1 second they found that their synaesthetes were significantly better than controls at identifying the shapes. Why might this be? The standard explanation is that the colours of stimuli are processed in parallel and prior to attention (e.g., Treisman, 1988). Synaesthetes, but not controls, perceive the stimuli as coloured and so benefit from this mechanism whereas controls must perform an

attention demanding serial search to find the embedded shapes.

Several other visual search studies have been conducted, but these have yielded somewhat different results and interpretations (Laeng et al., 2004; Palmeri et al., 2002). In a study reported in this Special Issue, Edquist et al. (2006, p. 222) presented a single target grapheme, rather than several targets making up a global shape, amongst distractor graphemes. The targets and distractors differed either in their actual colour, or in the synaesthetic colour they elicited when both the targets and distractors were entirely achromatic. For both synaesthetes and their matched controls, pop-out was found only for coloured displays; the achromatic displays required serial searches for both groups. In another search study presented in this issue, Sagiv et al. (2006, p. 232) also failed to find pop-out when target graphemes inducing synaesthesia were embedded amongst distractors that did not elicit synaesthetic experiences (rotated graphemes). The study of Mattingley et al. (2006, in this issue, p. 213) also investigated the influence of selective attention on synaesthesia but this time for graphemes presented briefly during a concurrent attentional task. They found that synaesthetic Stroop interference from incongruently coloured graphemes was diminished when synaesthetes had to perform a difficult visual discrimination at fixation (high attentional load) relative to an easier discrimination (low attentional load). They conclude that attention has an important modulatory influence on synaesthetic colour induction.

How can the results of these studies be reconciled with the earlier ones of Ramachandran and Hubbard (2001a)? There are methodological differences between the studies. Ramachandran and Hubbard (2001a) presented their stimuli for 1 second and measured the percentage of shapes detected. The two synaesthetes detected 81% correctly (controls = 59%). However, performance should have been at ceiling at these viewing times if they literally popped out (e.g., as demonstrated by the studies of Edquist et al., 2006; and Sagiv et al., 2006; which used real coloured stimuli as controls). By contrast, the studies of Edquist et al. (2006) and Sagiv et al. (2006) had unlimited viewing and measured response time to detect a target. It is possible that synaesthetic colours can facilitate visual search without the assumption of pre-attentive pop-out. Laeng et al. (2004) found that visual search could be facilitated when eye movements happened to land in the vicinity of the target. They argued that colours emerge when graphemes fall within an attentional "spotlight", but that the spotlight itself may encompass several graphemes. A somewhat different interpretation is that the presence of synaesthetic colours can be elicited when serially scanning stimuli, thus enabling more efficient rejection of distractors and facilitating visual search in the absence of pop-out (Sagiv et al., 2006). Indeed, two other recent studies have shown

facilitation during visual search although arguably not pop-out (Palmeri et al., 2002; Smilek et al., 2003).

Bottom-up versus Top-down Influences

What aspects of a grapheme determine the colour it will take – is it its appearance or a more abstract level of representation? Dixon et al. (2006, in this issue, p. 243) provide evidence in favour of the latter. They presented their synaesthete with ambiguous graphemes (e.g., a grapheme that could either be interpreted as 'S' or '5') in biasing contexts (e.g., 34_67 or MU_IC). The colour of the ambiguous grapheme was determined by the context, as demonstrated by Stroop interference. This suggests that it is the identity of a grapheme, and not just its physical appearance, that determines synaesthetic colour. However, this does not necessarily mean that the appearance of an inducing stimulus has no influence at all. The study by Witthoft and Winawer (2006, in this issue, p. 175) shows that the saturation of synaesthetic colours can depend on the font and case of letter stimuli, although the colour category itself is not strongly affected by these manipulations.

Numbers are particularly interesting because these stimuli also have semantic representations (single letters don't have semantics in the traditional sense except when they function as words as in 'I' and 'a'). Cohen-Kadosh and Henik (2006, in this issue, p. 259) asked their synaesthete to judge which of two numerals was physically larger; for example, presenting "3" in a large font and "5" in a small font. In this instance, physical size is incongruent with numerical size resulting in slower response times. This effect was biased by the display colour of the numerals. If the colours implied a larger numerical separation (e.g., '3' was presented in the colour of '1' and '5' in the colour of '7') then performance slowed. The authors suggest that it is the numerical concept that determines colour. A similar conclusion was reached by Jansari et al. (2006, in this issue, p. 253). They presented synaesthetes with arithmetical sums (e.g., 5 + 4) followed by a colour patch to name. Stroop interference was found if the colour was incongruent with the colour of the solution, even though the solution was never physically presented. This extends the previous research of Dixon et al. (2000) by showing conceptual effects for spoken and written presentations and for different operands.

Simner et al. (2006, in this issue, p. 281) also present evidence for both top-down and bottom-up influences in determining the synaesthetic colour of words. In their synaesthete the colour of words is determined by a salient grapheme within the word, as noted in other cases (Baron-Cohen et al., 1993). Simner et al. (2006, in this issue, p. 281) show that the stress of a word (e.g., **'con**-vict *versus* con-**'vict**) influences the naming time of the colour (although

not the synaesthetic colour itself). This is found for written as well as spoken words suggesting an effect of "conceptual stress" acting top-down. They also argue for bottom-up processes such that different graphemes compete for dominance over the word as a whole (e.g., it is faster to name the colour of *ether* relative to *ethos* because the critical vowel graphemes are the same in the former).

Finally, de Thornley Head (2006, in this issue, p. 164) investigated the role of top-down influences in synaesthetes who experience colour for pitch. His synaesthetes were required to choose colours corresponding to pitches in which the name of the note (e.g., 'C sharp') was also given. In some instances the name of the note was misleading. However, the choice of colour was not biased by this information suggesting a true effect of pitch (for both synaesthetes with and without perfect pitch).

VARIETIES OF SYNAESTHESIA AND INDIVIDUAL DIFFERENCES

It is clear to all researchers in the field that not all synaesthetes are alike. What remains controversial is how such differences should be characterised, and what they might mean in terms of underlying perceptual and neural mechanisms. At the most superficial level, synaesthetes differ in the range of stimuli that trigger the sensations (inducers) and the modality in which the sensation is experienced (the concurrent) (following the terminology of Grossenbacher and Lovelace, 2001). In the present volume, all of the studies have colour as the concurrent, and most have letters, numbers or words as the inducer (with three studies reporting colours elicited by nonverbal sounds). Although other types of synaesthesia undoubtedly exist (e.g., Cytowic, 1989) it is unclear why some types predominate. It is also the case that whilst some people appear to have synaesthesia involving many inducers and/or many concurrents others have a more restricted involvement (e.g., coloured days of the week). Again, it is presently unclear why this might be, although Asher et al. (2006, in this issue, p. 137) speculate on genetic influences.

It is also possible for individual differences to exist within the same inducer-concurrent pairing. These may reflect different stages of cognitive processing and/or different phenomenological reports. As already noted, stimuli such as words and numbers are represented at multiple levels within the cognitive system. Ramachandran and Hubbard (2001b) have proposed a distinction between "higher" and "lower" synaesthesia to capture putative individual differences between conceptual and perceptual processing of the inducer respectively. The fact that some synaesthetes show a strong "alien colour effect" whilst others do not (Gray et al., 2006, in this issue, p. 309) could be accounted for by differences in the extent to which

semantics can dominate the colour. There may also be interactions between semantic processing and input modality. Jansari et al. (2006, in this issue, p. 253) report a double dissociation between spoken *versus* written input in two synaesthetes in an arithmetical Stroop task, which as outlined earlier is regarded as a measure of conceptual synaesthesia.

Perhaps the thorniest individual differences to study concern phenomenology. Quite apart from the obvious difficulty of objectively measuring personal experiences (for discussion see Smilek and Dixon, 2002), different people also tend to use very different language to describe their perceptual experiences. Notwithstanding such difficulties, it is the reported experiences of synaesthetes that provides the *raison d'etre* for most research in this area, and issues of phenomenology are hard to sidestep[1]. One proposal currently in the literature is that grapheme-colour synaesthetes can be classified as being either "projectors" or "associators" (Dixon et al., 2004). Projectors describe their colours as existing in external space such that, when reading, the colours appear to be in or around the text (in most cases, the synaesthetic colours apparently do not completely obscure the text colour but are reported as co-existing with it). Associators, by contrast, describe their colours as existing in some internalised space or in their "mind's eye". Dixon et al. (2004) have reported differences in the performance of Stroop tasks that correspond with the distinction. They suggest that synaesthetic colours in projectors are triggered during early stages of grapheme analysis, whereas in associators they arise at a later stage of processing (possibly co-extensive with the 'lower' *versus* 'higher' distinction of Ramachandran and Hubbard 2001b). A number of the studies in this volume have classified their synaesthetes according to this distinction. However, Edquist et al. (2006, in this issue, p. 222) explicitly tested for differences between associators and projectors in visual search and claim there is none. One might have expected projectors with hypothetically earlier colour induction to show efficient visual search in achromatic displays (perhaps even pop-out in extreme cases). Moreover, they found that the classification of synaesthetes according to the projector *versus* associator distinction was rather unreliable, so that individuals who initially described their synaesthetic experiences as being projected in space later described them as if they were like mental images, and vice versa. It is possible that synaesthetes use terms such as "mind's eye" and even "in space" in different ways. For example, one lay notion of space is that it is the empty gap that exists between objects, rather than the more scientific notion of the medium in which objects exist. This does not necessarily discount the projector-associator distinction or dismiss the importance of phenomenological differences, but it does underscore the need for an adequate system for accounting for synaesthetic experiences that is reproducible within and between individuals.

THE ORIGINS OF SYNAESTHESIA: INFLUENCES OF NATURE *VERSUS* NURTURE

Following on from the observations of Galton (1880), it is generally believed that synaesthesia has a genetic component. The high proportion of female to male synaesthetes (~ 5 : 1) and the patterns of inheritance have lead some researchers to argue for an X-linked dominant mode of inheritance with possible lethality in males (Baron-Cohen et al., 1996). However, not all studies have shown such a large female: male bias or found evidence for male lethality (Ward and Simner, 2005). As such, the nature of the genetic mechanism remains largely unknown. Nevertheless, the way in which gene expression affects brain development and, ultimately, cognition is one of the biggest growth areas in cognitive neuroscience, and synaesthesia may yet prove to be a model system.

Two of the papers in this Special Issue note that their participants were identical twins. In the study by Simner et al. (2006, p. 281) only one of the female twins was noted to have synaesthesia (see also Smilek et al., 2002b). Discordant patterns could either be explained by non-genetic factors, post-conception genetic events, or skewed patterns of gene expression (e.g., one of the X-chromosomes may be preferentially 'inactivated' in women, who possess two X-chromosomes). The study by Hancock (2006, p. 147) documents two male synaesthetic twins who both demonstrate synaesthesia to different degrees. What is exceptional about these cases is that the colours for numbers and letters are similar for each twin. Moreover, the origin of most colour associations can be traced back to a childhood toy. Whilst it would be easy to dismiss this as a form of "pseudo-synaesthesia" there is evidence of familial transmission in this particular case (their mother is noted to have it too). The case study of Witthoft and Winawer (2006, p. 175) also describes a "refrigerator magnet synaesthete" in whom the origin of the colour associations is known. Accounts based solely on associative learning are tempting but fail on a number of grounds. They do not explain why only some individuals develop synaesthesia, and why the experience is typically perceptual in nature (according to both self-report and objective measures, as discussed above). An alternative account is that although a disposition to synaesthesia might be genetically determined,

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[1]There are interesting parallels to be made with other neuropsychological conditions here. For example, it is the subjective reports of absence of vision or denial of impairment that provide the main motivation for research into blindsight and anosognosia, respectively. Use of subjective reports thus should not in principle preclude studies in these domains from being scientific.

environmental influences shape the nature of the associations formed. It is hard to determine the extent to which these cases are exceptional. One large survey comparing Australian childhood alphabet books published over many years with the associations of grapheme-colour synaesthetes failed to find close correspondences (Rich et al., 2005). However, weaker environmental biases may certainly exist. Graphemes themselves are culturally acquired, and no synaesthete is on record as experiencing colours for false fonts.

OTHER TRAITS ASSOCIATED WITH SYNAESTHESIA

By definition, synaesthetes differ from other members of the population because of their anomalous perceptual experiences. But do they differ in any other significant ways? There are a number of reasons why synaesthesia might affect cognitive function more generally. The presence of anomalous perceptual experiences in and of themselves could have knock-on effects on cognition; for example, by rendering verbal material more memorable (Mills et al., 2006 in this issue, p. 155). Alternatively, whatever it is that causes synaesthesia (e.g., a genetic variant, neural hyper-connectivity) may have more widespread influences on brain development and, hence, cognition. The claim that synaesthetes are more creative is related to the latter type of explanation (Ramachandran and Hubbard, 2001b). However, it is important to rule out that the co-occurrence of two seemingly unusual traits is more than just coincidence. For instance, it has been claimed that synaesthetes are more likely to be left-handed and more prone to magical ideation (e.g., feelings of clairvoyance) (Cytowic, 1989). Recent large-scale studies have failed to support such claims (Rich et al., 2005).

A number of studies in the Special Issue relate to unusual traits or skills possessed by synaesthetes. The study of Mills et al. (2006) documents superior memory in a synaesthete. Interestingly, the superior memory was found just for verbal material that elicits synaesthetic experiences and not for non-verbal material. This suggests that memory enhancement in this case is circumscribed rather than truly "photographic". The authors argue that synaesthetes code verbal memories in both a visual and a verbal format, giving them an advantage over pure verbal coding (as in the theory of Paivio, 1969). However, it remains unclear to what extent superior memory is a characteristic of all synaesthetes, given that all three of the published studies relevant to this issue are single cases, and two of these individuals initially came to the attention of researchers because of their superior memory rather than because of their synaesthesia (Luria, 1968; Smilek et al., 2002a).

The study by Burrack et al. (2006, in this issue, p. 151) argues that synaesthetes may be more prone to other types of atypical perceptual experiences, in particular, a phenomenon called *mitempfindung* in which tactile sensations are referred to a bodily location that is distant from the stimulation site. Technically this is not a type of synaesthesia because the inducer (a tactile stimulus) and experience (a touch sensation) are of the same kind, though of course the two phenomena may share some important underlying mechanisms. Burrack et al. (2006) report a higher prevalence of *mitempfindung* in grapheme-colour synaesthetes than in a non-synaesthetic control group.

CONCLUDING COMMENTS

Although the modern era of synaesthesia research is still in its infancy, there are a number of ways in which it can be used to inform theories of normal cognitive processing. The study of synaesthesia is likely to yield important insights into intra-modal and cross-modal perception; perceptual awareness; brain development and plasticity; the way that perception interacts with language and memory; and individual differences in cognition more generally. We hope that the contributions in this Special Issue of *Cortex* convey the excitement and progress that is being made in the field.

REFERENCES

ALEMAN A, RUTTEN GJM, SITSKOORN MM, DAUTZENBERG G and RAMSEY NF. Activation of striate cortex in the absence of visual stimulation: An fMRI study of synaesthesia. *NeuroReport, 12:* 2827-2830, 2001.

ASHER J, AITKEN MRF, FAROOQI N, KURMANI S and BARON-COHEN S. Diagnosing and phenotyping visual synaesthesia: A preliminary evaluation of the revised Test of Genuineness (TOG-R). *Cortex, 42:* 137-146, 2006.

BARON-COHEN S. Is there a normal phase of synaesthesia in development? *Psyche, 2,* 1996.

BARON-COHEN S, BURT L, SMITH-LAITTAN F, HARRISON J and BOLTON P. Synaesthesia: Prevalence and familiality. *Perception, 25:* 1073-1079, 1996.

BARON-COHEN S, HARRISON J, GOLDSTEIN LH and WYKE M. Coloured speech perception: Is synaesthesia what happens when modularity breaks down? *Perception, 22:* 419-426, 1993.

BARON-COHEN S, WYKE MA and BINNIE C. Hearing words and seeing colours: An experimental investigation of a case of synaesthesia. *Perception, 16:* 761-767, 1987.

BURRACK A, KNOCH D and BRUGGER P. Mitempfindung in synaesthetes: Co-incidence or meaningful association? *Cortex, 42:* 151-154, 2006.

CALVERT G, SPENCE C and STEIN BE. *The Handbook of Multisensory Processes.* Cambridge, MA: MIT Press, 2004.

COHEN-KADOSH R and HENIK A. Color congruity effect: Where do colors and numbers interact in synesthesia? *Cortex, 42:* 259-263, 2006.

CYTOWIC RE. *Synaesthesia: A Union of the Senses.* New York: Springer, 1989.

DELLA SALA S, MARCHETTI C and SPINNLER H. Right-sided anarchic (alien) hand: A longtitudinal study. *Neuropsychologia, 29:* 1113-1127, 1991.

DE THORNLEY HEAD P. Synaesthesia: Pitch-colour isomorphism in RGB-space? *Cortex, 42:* 164-174, 2006.

DIXON MJ, SMILEK D, CUDAHY C and MERIKLE PM. Five plus two equals yellow. *Nature, 406:* 365, 2000.

DIXON MJ, SMILEK D, DUFFY PL and MERIKLE PM. The role of meaning in grapheme-colour synaesthesia. *Cortex, 42:* 243-252, 2006.

DIXON MJ, SMILEK D and MERIKLE PM. Not all synaesthetes are created equal: Projector *versus* associator synaesthetes. *Cognitive, Affective and Behavioral Neuroscience, 4:* 335-343, 2004.

EDQUIST J, RICH AN, BRINKMAN C and MATTINGLEY JB. Do synaesthetic colours act as unique features in visual search? *Cortex, 42:* 222-231, 2006.

ELIAS LJ, SAUCIER DM, HARDIE C and SART GE. Dissociating semantic and perceptual components of synaesthesia: Behavioural and functional neuroanatomical investigations. *Cognitive Brain Research, 16:* 232-237, 2003.

FRITH CD. *The Cognitive Neuropsychology of Schizophrenia.* Hove: Psychology Press, 1992.

GALTON F. Visualised numerals. *Nature, 21:* 252-256, 1880.

GRAY JA. How are qualia coupled to functions? *Trends in Cognitive Sciences, 7:* 192-194, 2003.

GRAY JA, PARSLOW DM, BRAMMER MJ, CHOPPING S, VYTHELINGUM GN and FFYTCHE DH. Evidence against functionalism from neuroimaging of the alien colour effect in synaesthesia. *Cortex, 42:* 309-318, 2006.

GROSSENBACHER PG and LOVELACE CT. Mechanisms of synaesthesia: Cognitive and physiological constraints. *Trends in Cognitive Sciences, 5:* 36-41, 2001.

HANCOCK P. Monozygotic twins colour-number association: A case study. *Cortex, 42:* 147-150, 2006.

HARTMAN AM and HOLLISTER LE. Effect of mescaline, lysergic acid diethylamide and psilocybin on color perception. *Psychopharmacolgia, 4:* 441-451, 1963.

HENDERSON L. On the use of the term "grapheme". *Language and Cognitive Processes, 1:* 135-148, 1985.

HUBBARD EM, ARMAN AC, RAMACHANDRAN VS and BOYNTON GM. Individual differences among grapheme-color synesthetes: Brain-behavior correlations. *Neuron, 45:* 975-985, 2005.

HUBBARD EM, MANOHAR S and RAMACHANDRAN VS. Contrast affects the strength of synesthetic colors. *Cortex, 42:* 184-194, 2006.

HUMPHREYS G. Higher sight. *Nature, 343:* 30, 1990.

HURLEY S and NOE A. Neural plasticity and consciousness. *Biology and Philosophy, 18:* 131-168, 2003.

JACOBS L, KARPIK A, BOZIAN D and GOTHGEN S. Auditory-visual synesthesia: Sound-induced photisms. *Archives of Neurology, 38:* 211-216, 1981.

JANSARI AS, SPILLER MJ and REDFERN S. Number Synaesthesia: When hearing "four plus five" looks like gold. *Cortex, 42:* 253-258, 2006.

KIM C-Y, BLAKE R and PALMERI TJ. Perceptual interaction between real and synesthetic colors. *Cortex, 42:* 195-203, 2006.

LAENG B, SVARTDAL F and OELMANN H. Does colour synesthesia pose a paradox for early-selection theories of attention? *Psychological Science, 15:* 277-281, 2004.

LUPIÁÑEZ J and CALLEJAS A. Automatic perception and synaesthesia: Evidence from colour and photism naming in a stroop negative priming task. *Cortex, 42:* 204-212, 2006.

LURIA A. *The Mind of a Mnemonist.* New York: Basic Books, 1968.

MACLEOD CM. Half a century of research on the Stroop effect: An integrative review. *Psychological Bulletin, 109:* 163-203, 1991.

MATTINGLEY JB, PAYNE J and RICH AN. Attentional load attenuates synaesthetic priming effects in grapheme-colour synaesthesia. *Cortex, 42:* 213-221, 2006.

MAURER D. Neonatal synaesthesia: Implications for the processing of speech and faces. In Baron-Cohen S and Harrison JE (Eds), *Synaesthesia: Classic and Contemporary Readings.* Oxford: Blackwell, 1997.

MAURER D and MONDLOCH CJ. Neonatal synaesthesia: A re-evaluation. In Robertson LC and Sagiv N (Eds), *Synaesthesia: Perspectives from Cognitive Neuroscience.* Oxford: Oxford University Press, 2005.

MERABET LB, MAGUIRE D, WARDE A, ALTERESCU K, STICKGOLD R and PASCUAL-LEONE A. Visual hallucinations during prolonged blindfolding in sighted subjects. *Journal of Neuro-opthalmology, 24:* 109-113, 2004.

MILLS CB, INNIS J, WESTENDORF T, OWSIANIECKI L and MCDONALD A. Influence of a synesthete's photisms on name recall. *Cortex, 42:* 155-163, 2006.

NUNN JA, GREGORY LJ, BRAMMER M, WILLIAMS SCR, PARSLOW DM, MORGAN MJ, MORRIS RG, BULLMORE ET, BARON-COHEN S and GRAY JA. Functional magnetic resonance inaging of synesthesia: Activation of V4/V8 by spoken words. *Nature Neuroscience, 5:* 371-375, 2002.

ODGAARD EC, FLOWERS JH and BRADMAN HL. An investigation of the cognitive and perceptual dynamics of a colour-digit synaesthete. *Perception, 28:* 651-664, 1999.

PAIVIO A. Mental imagery in associative learning and memory. *Psychological Review, 76:* 241-263, 1969.

PALMERI TJ, BLAKE R, MAROIS R, FLANERY MA and WHETSELL W. The perceptual reality of synesthetic colors. *Proceedings of the National Academy of Science of the USA, 99:* 4127-4131, 2002.

PAULESU E, HARRISON J, BARON-COHEN S, WATSON JDG, GOLDSTEIN L, HEATHER J, FRACKOWIAK RSJ and FRITH CD. The physiology of coloured hearing: A PET activation study of colour-word synaesthesia. *Brain, 118:* 661-676, 1995.

PAULSEN HG and LAENG B. Pupillometry of grapheme-color synaesthesia. *Cortex, 42:* 290-294, 2006.

RAMACHANDRAN VS and HUBBARD EM. Psychophysical investigations into the neural basis of synaesthesia. *Proceedings of the Royal Society of London B, 268:* 979-983, 2001a.

RAMACHANDRAN VS and HUBBARD EM. Synaesthesia: A window into perception, thought and language. *Journal of Consciousness Studies, 8:* 3-34, 2001b.

RICH AN, BRADSHAW JL and MATTINGLEY JB. A systematic, large-scale study of synaesthesia: Implications for the role of early experience in lexical-colour associations. *Cognition, 98:* 53-84, 2005.

RICH AN and MATTINGLEY JB. Anomalous perception in synaesthesia: A cognitive neuroscience perspective. *Nature Reviews Neuroscience, 3:* 43-52, 2002.

ROBERTSON LC. Binding, spatial attention and perceptual awareness. *Nature Reviews Neuroscience, 4:* 93-102, 2003.

ROBERTSON LC and SAGIV N. *Synaesthesia: Perspectives from Cognitive Neuroscience.* Oxford: Oxford University Press, 2005.

SAGIV N, HEER J and ROBERTSON L. Does binding of synesthetic color to the evoking grapheme require attention? *Cortex, 42:* 232-242, 2006.

SCHNIDER A and PTAK R. Spontaneous confabulators fail to suppress currently irrelevant memory traces. *Nature Neuroscience, 2:* 677-681, 1999.

SHIMOJO S and SHAMS L. Sensory modalities are not separate modalities: Plasticity and interactions. *Current Opinion in Neurobiology, 11:* 505-509, 2001.

SIMNER J, GLOVER J and MOWAT A. Linguistic determinants of word colouring in grapheme-colour synaesthesia. *Cortex, 42:* 281-289, 2006.

SMILEK D and DIXON MJ. Towards a synergistic understanding of synaesthesia: Combining current experimental findings with synaesthetes' subjective descriptions. *Psyche, 8,* 2002.

SMILEK D, DIXON MJ, CUDAHY C and MERIKLE PM. Synaesthetic color experiences influence memory. *Psychological Science, 13:* 548-552, 2002a.

SMILEK D, DIXON MJ and MERIKLE PM. Synaesthetic photisms guide attention. *Brain and Cognition, 53:* 364-367, 2003.

SMILEK D, MOFFATT BA, PASTERNAK J, WHITE BN, DIXON MJ and MERIKLE PM. Synaesthesia: A case study of discordant monozygotic twins. *Neurocase, 8:* 338-342, 2002b.

SPERLING JM, PRVULOVIC D, LINDEN DEJ, SINGER W and STIRN A. Neuronal correlates of graphemic colour synaesthesia: A fMRI study. *Cortex, 42:* 295-303, 2006.

STEVEN MS, HANSEN PC and BLAKEMORE C. Activation of color-selective areas of visual cortex in a blind synesthete. *Cortex, 42:* 304-308, 2006.

TREISMAN A. Features and objects: The fourteenth Bartlett memorial lecture. *Quarterly Journal of Experimental Psychology, 40A:* 201-237, 1988.

TREISMAN A. Solutions to the binding problem: Progress through controversy and convergence. *Neuron, 24:* 105-110, 1999.

WARD J, HUCKSTEP B and TSAKANIKOS E. Sound-colour synaesthesia: To what extent does it use cross-modal mechanisms common to us all? *Cortex, 42:* 264-280, 2006.

WARD J and SIMNER J. Is synaesthesia an X-linked dominant trait with lethality in males? *Perception, 34:* 611-623, 2005.

WITTHOFT N and WINAWER J. Synesthetic colors determined by having colored refrigerator magnets in childhood. *Cortex, 42:* 175-183, 2006.

WOLLEN KA and RUGGIERO FT. Coloured-letter synaesthesia. *Journal of Mental Imagery, 7:* 83-86, 1983.

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