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Synaesthesia: The existing state of affairs

Matej Hochel and Emilio G. Milán
Departamento de Psicología Experimental, Universidad de Granada, Granada, Spain

In synaesthesia one type of stimulation evokes the sensation of another, such as when hearing a sound produces photisms—that is, mental percepts of colours. In the past, the idiosyncrasy of this phenomenon, as well as the natural mistrust of scientists towards the subjective, consigned synaesthesia to the periphery of scientific interest. However, the landscape has changed radically in the last two decades. The labour of many researchers, inside as well as outside of cognitive neuroscience, has transformed synaesthesia into a scientific reality whose existence can be demonstrated and studied empirically. The present paper summarizes and reflects on our current knowledge concerning synaesthesia in all its aspects (cognition, behaviour, neurology, genetics, and demographics).

Keywords: Synaesthesia; Cross-modal perception; Neurocognitive models of synaesthesia.

When R. listens to music, his mind generates colours that do not exist in the "real" world as perceived by "normal" people. He perceives classical music as "dark brown", electronic music as mostly "purple", and symphonic compositions as "red" (Milán et al., 2007). Undoubtedly, in a more distant past this kind of perception would have been considered witchcraft, and not so long ago R.'s extraordinary ability to "see music" could have led him to an imposed stay in a mental institution (Cytowic, 1993; Day, 2005). Even today many people with synaesthesia prefer not to talk about their condition, trying to act "normal" in order to avoid the common hostility towards the unusual and the unknown (Day, 2005). The term synaesthesia comes from Greek, meaning "joined perception" (aesthesis translates perception, and syn = joined, together). In synaesthetes one type of stimulation evokes the sensation of another, such as when hearing a sound produces photisms—that is, mental percepts of colours. Quite frequently this condition involves a "transduction" of a learnt semantic category (e.g., letters, numbers, human faces, or days of the week) into a sensory experience (e.g., perception of synaesthetic colour).

The first legitimate report on synaesthesia is attributed to Sachs in 1812 (cited in Krohn, 1982; also in Dann, 1998), who described the condition in himself and his sister as a part of a PhD dissertation on his albinism. In the nineteenth century there might have been a dozen of

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Correspondence should be addressed to Matej Hochel, Departamento de Psicología Experimental, Universidad de Granada, c/ Campus de Cartuja s/n, 18071, Granada, Spain (E-mail: mhochel@ugr.es).

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reported cases of possible synaesthetes but these early studies seem to have aroused very little interest. (For a review, see Wheeler, 1920.) Within the scientific community synaesthesia was "brought into existence" by Francis Galton (1880/1997), who observed that a small number of people had the peculiar capacity of experiencing the stimulation of one sense in a multimodal way—that is, in two or even more sensory modalities (Ramachandran & Hubbard, 2001b). Following Galton, a number of studies were published until the gradual onset of behaviourism in the 1930s. The idiosyncrasy of the phenomenon, as well as the natural mistrust of scientists towards the subjective, consigned synaesthesia to the periphery of scientific interest; many decades would have to pass for synaesthesia to be brought back into the realms of empirical science. Consequently, the lack of medical and psychological information led to numerous personal misfortunes when synaesthetes who "came out of the closet" were diagnosed as schizophrenics and drug addicts or even confined to mental hospitals (Day, 2005). In the most fortunate cases, medical professionals were sceptical, considering that the synaesthete who was speaking about a "yellow melody" or a food that "tastes pointy" (Cytowic, 1993), was just being excessively metaphorical.

Most of the first modern investigations into synaesthesia either passed unnoticed or were seen as mere curiosity. For instance, Luria (1968) described a case of eidetic memory in a multimodal synaesthete who showed peculiar interconnections between virtually all the senses. Ten years later, Lawrence Marks in his book *The Unity of the Senses* pointed out the scientific importance of synaesthesia, emphasizing its potential for studying the neurological bases of metaphor (Marks, 1978). However, due to the predominant influence of behaviourism and its absolute distrust in subjective experience, psychology did not find it important to study a phenomenon that was only revealed through first-person verbal reports. Apparently, "scientists in the 20th century[. . .] consistently strove to eliminate the subjective role of a human observer in gathering empirical data" (Cytowic, 2002).

However, the landscape has changed in the last two decades. A number of contemporary researchers have transformed synaesthesia into a scientific reality whose existence can be demonstrated and studied empirically. The application of psychometric methods to synaesthesia has provided an experimental "certificate of authenticity" that has finally convinced the scientific community. Since the turn of the century, a substantial number of papers have been published in top-tier scientific forums. In addition to abundant psychometric studies, scientists eagerly take advantage of modern neuroimaging techniques in order to study the brains of synaesthetes. (See the review by Hubbard & Ramachandran, 2005.) In summary, synaesthesia is fully recognized as a phenomenon that can open new doors in our understanding of scientific and philosophic enigmas, such as the nature of perceptual qualia or the neural bases of metaphor and language.

What is it like to be a synaesthete?

When N., a synaesthete, reads the Spanish first name "Noelia", each letter makes her see a specific colour. Coincidentally, the colours of "Noelia" make up a rainbow colour sequence. When it comes to colour-to-letter matching in grapheme-chromatic synaesthesia, no two people's synaesthetic associations are identical. If another grapheme–colour synaesthete saw the same letters, the pattern of colour–letter correspondence would change. In the same way, a synaesthete whose photisms are elicited by musical sounds presents unique tone-to-colour matching, different from that of any other musical synaesthete. However, even though cross-modal matches vary from synaesthete to synaesthete in all the known varieties of synaesthesia, a few trends have been observed such as almost two thirds of grapheme–colour synaesthetes perceiving the letter "O" as white (Day, 2005).

Besides the idiosyncratic nature of synaesthetic mappings, subjective reports also point to other kinds of discrepancies in synaesthetic experience. Some synaesthetes describe their photisms as spots of colour "floating in their mind's eye", in a way similar to normal mental imagery. Meanwhile, other synaesthetes speak about perceptions that are projected externally onto the eliciting stimulus, appearing as a coloured "aura" surrounding the synaesthetic inducer.

The idiosyncrasy and the subjective nature of the phenomenon make synaesthesia difficult to fit into common scientific taxonomy. Furthermore, confusion arises from the imprecise use of the term synaesthesia, which has been applied to a wide array of phenomena, ranging from idiopathic synaesthesia (a naturally occurring cross-modal perception), to altered states of consciousness caused by psychotropic substances, to metaphorical language, and even to visual arts and theatre performances (Cytowic, 1996, 2002).

Despite this phenomenological heterogeneity, Cytowic (1996, 2002) tried to establish a series of "diagnostic criteria" in order to distinguish idiopathic synaesthesia from different psychological conditions (e.g., hallucinations and drug-induced experiences) and artistic extravagancies. Following Cytowic (2002), synaesthetic perception is:

1. Involuntary and automatic.
2. Consistent and generic.
3. Spatially extended.
4. Memorable.
5. Affect-laden.

Before providing a more detailed description of these features, it should be noted that the first two (i.e., synaesthesia being involuntary and automatic, consistent, and generic) are probably the least problematic and the most agreed upon in the scientific community. The rest of Cytowic's criteria are more controversial, and, rather than being "diagnostic" in the strict sense of the word, they represent features that are likely (but not necessarily) to be observed, to a higher or lesser degree, in the majority of synaesthetes.

The involuntary character of synaesthesia refers to the impossibility to manipulate synaesthetic perception or to suppress it by will (e.g., Dixon, Smilek, Cudahy, & Merikle, 2000; Mattingley, Rich, Yelland, & Bradshow, 2001; Wollen & Ruggiero, 1983). When a grapheme–colour synaesthete sees a printed character (e.g., the letter "R"), simultaneously he will perceive a colour halo surrounding the grapheme. The feeling is much different from that of a memory brought to one's mind due to some kind of association with certain sensory aspects of the outer world. While usually we are able to stop thinking about unpleasant memories, it is not possible to stop seeing, hearing, or smelling external stimuli unless you eliminate sensory input. The same applies to synaesthesia in the sense that it is virtually immune to any voluntary control.

Synaesthetes' reports suggest that synaesthesia is acquired very early during development and it lasts for a lifetime.[1] Once established, synaesthetic associations remain unchanged; when a synaesthete is presented with a series of inducers across multiple time points, he or she will experience the same synaesthetic *concurrents* in response to the triggering stimuli. Studies report on consistency measures with test–retest periods of weeks, months, or even years. For instance, Baron-Cohen, Wyke, and Binnie (1987) studied a case of a synaesthete who experienced photisms in response to spoken language. In a preliminary interview they asked E.P. to describe in detail the colours she saw when listening to 103 different auditory stimuli (words, letters, and numbers). After 10 weeks they did a retest. The participant's answers were 100% consistent with respect to the previous experimental session. In contrast, a non-synaesthete participant who was asked to associate colours with the same inducers was far less accurate in her responses. (With a test–retest period of 2 weeks only, the measure of consistency was less than 17%.) In brief, the connection between inducing stimuli and synaesthetic responses is extremely stable over time, and, as is shown later, it cannot be explained by memory performance.

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[1] Typically synaesthetes claim they have been synaesthetic from as early as they can remember. No cases of spontaneous remission of synaesthesia have been reported so far even though synaesthetic capacity can sometimes be lost as a consequence of cerebral trauma. (See Sacks, Waserman, Zeki & Siegel, 1988; Spalding & Zangwill, 1950.)

In addition to its consistency and durability, there is another aspect of synaesthesia that makes it different from other phenomena such as hallucinations present in psychotic disorders. Synaesthetic responses are typically generic; they correspond to basic perceptual qualities such as colour, texture, and fundamental visual forms, tactile sensations, and so on. Moreover, quite often the synaesthetic percepts, through their association to the inducing stimulus, may enhance the synaesthete's memory by serving as additional memory cues. (For instance, number–colour synaesthesia may help to remember telephone numbers.) Even though Cytowic (2002) argues that synaesthetic experience is never pictorial or laden with semantic content, it should be noted that there have been cases of letter–colour synaesthetes who, when they hear a word (e.g., "table"), may actually see the letters (T-A-B-L-E) spelled out in colour.

When synaesthetes describe their subjective experience, they often speak about colours being projected onto a written character (grapheme–colour synaesthesia) or about visual entities on a "screen" situated a few inches in front of one's face (audio-visual synaesthesia). Cytowic (1993) reports the case of a synaesthete who experienced tactile sensations in response to gustatory stimulation. The participant used to alter the position of his hands in order to better "reach" for the feeling. All these aspects illustrate the "spatial quality" of synaesthetic sensations. However, this feature is less obvious if we consider those people whose synaesthesia is more similar to visual imagery. (See "associator synaesthetes" further on in this paper.) This variety of synaesthesia is also completely automatic but the ability to spatially localize is uncertain, given that percepts are not projected externally.

Finally, a series of authors (Cytowic, 2002; Milán et al., 2007; Ramachandran & Hubbard, 2001b; Ward, 2004) have emphasized the relationship of synaesthesia with emotion. Frequently synaesthetes claim experiencing pleasant sensations that accompany synaesthetic perception and are sometimes similar to a "Eureka!" feeling (Cytowic, 2002). Occasionally, synaesthesias can also be related to negative feelings, particularly when the synaesthetic perception is incongruent with the outer reality. (For example, when a grapheme–colour synaesthete sees a letter printed in a different colour from that of the associated photism.) Certain types of synaesthesia are directly related to the emotion. For instance, R., a synaesthete reported by Milán et al. (2007), experienced mental colours in response to faces, human figures, and visual scenes with emotional content. Normally the colours experienced were congruent with R.'s emotional assessment of the person or the visual stimulus in question. (R. often used the photisms to refine his opinions about people.) Very rarely, the synaesthetic "aura" experienced by R. was not congruent with respect to the personal relationship that R. maintained with a person—for example, when a good friend of his "had a very unpleasant green colour". This kind of incoherency was extremely uncomfortable to R. and was accompanied by negative emotions. A few similar cases have been reported in literature, one that is particularly interesting is a report by Ward (2004) about G.W., a synaesthete who experienced mental colours in response to human faces, known person's names, and affect-laden words.

Empirical demonstrations of synaesthesia

Initial scepticism around synaesthesia among psychologists, neurologists, and other professionals was, at least in part, due to the lack of experimental methods that would allow for an objective demonstration of the phenomenon. A few early experimental studies actually examined the hypothesis that synaesthesia was a consequence of a classical conditioning mechanism (Howells, 1944; Kelly, 1934). With the intent to corroborate this proposal, they trained nonsynaesthete participants to associate arbitrary pairs of tones and colours. Even though some participants were quite successful in this memory task, there was no evidence of any type of accompanying colour perception (Rich & Mattingley, 2002), such as that reported by synaesthetes. Behind these early attempts to empirically approach synaesthesia, it took decades for scientists to return to the subject matter and finally invite synaesthetes to participate in experimental studies that could confirm or refute the genuineness of their condition.

As we mentioned before, one of the indicators that strongly supports the reality of synaesthesia is its constancy over time. In order to assess the consistency of a synaesthete, the participant is normally shown a series of synaesthetic inducers (e.g., a grapheme for a grapheme–colour synaesthete). His or her task is to simply report on the elicited synaesthetic perception (for example, the colour of the photism). (In more sophisticated designs, a standardized colour set or a software colour palette can be used to match the colours of the photisms more precisely; e.g., Milán et al., 2007; Witthoft & Winawer, 2006.) The experimental session is replicated days, weeks, or even months later. Following this methodology, virtually all studies report consistency levels that are very close to 100% (e.g., Baron-Cohen et al., 1987; Dixon et al., 2000; Mattingley et al., 2001). The stability of synaesthetic associations is maintained over time, even when assessed after a time gap of several months (Baron-Cohen, Harrison, Goldstein, & Wyke, 1993).

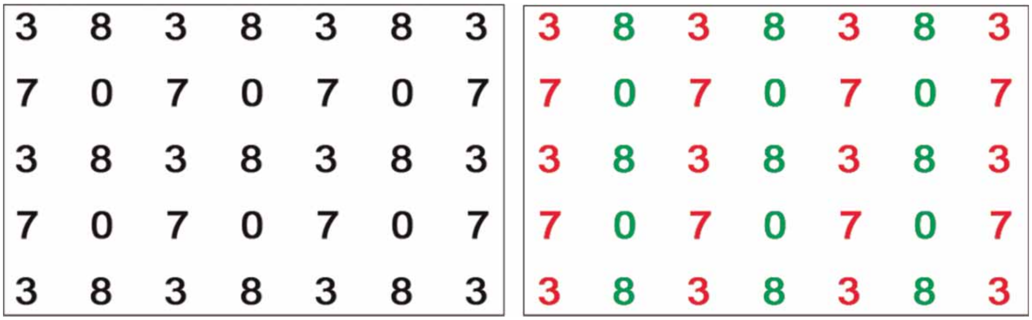
However, the high consistency by itself does not reveal the nature of the underlying neurocognitive mechanisms. Not so long ago, the most common explanation of synaesthesia was in terms of memory associations, possibly due to a learning experience in early childhood (Ramachandran & Hubbard, 2001b, 2003a). In theory, a lexical synaesthete could have played with refrigerator magnets with coloured letters and consequently could have developed powerful associations between printed characters and specific colour hues. A better understanding of the nature of synaesthesia required converging evidence from a number of sources: experiments designed to demonstrate that the experience of photisms is not under voluntary control; perceptual experiments to demonstrate that synaesthetes do indeed experience synaesthetic percepts when exposed to inducing stimuli; subjective reports to supplement and inform these objective inquiries.

In the 1980s, a series of studies sought to uncover whether synaesthesia was a perceptual or a memory phenomenon. Most of these studies (as well as much of the current research) worked with the most common grapheme–colour synaesthetes, employing modifications of the Stroop task (Stroop, 1935). Standard design consisted in presenting a printed character that was either of the same colour (congruent) or of a different colour from the synaesthete's photism (incongruent) and then asking the synaesthete to name the print colour (e.g., Mills, Boteler, & Oliver, 1999; Wollen & Ruggiero, 1983). Dixon, Smilek, Cudahy, and Merikle applied this same logic in a more recent study (Dixon et al., 2000) with C., a synaesthete who reacted synaesthetically to Arabic numerals. Stimuli consisted of a colour square (base line) or a coloured number whose hue was congruent or incongruent with respect to C.'s photism. The stimuli were presented on a computer screen in random order. C.'s task was to identify and say the colour of the stimulus as fast as possible. As expected, C. was significantly slower when responding to incongruent colours (797 ms, 2.8% error rate) than when responding to the congruent colours (525 ms, 1.4% errors) and the base line (545 ms, 0.0% errors).

This result has been replicated in several studies (e.g., a study with 15 synaesthetes by Mattingley et al., 2001), revealing clearly the automaticity of synaesthetic perception. However, this kind of result does not demonstrate whether synaesthesia is a genuinely perceptual process or not. MacLeod and Dunbar (1988) trained nonsynaesthete participants to associate black and white geometric shapes with the names of different colours. After thousands of trials, the participants were tested on a Stroop task where the original shapes were presented either in the same or in different colours with respect to the original matching. The results showed a clear interference pattern that could only be explained as an effect of the previous excess of learning. These data suggest that a simple associative mechanism, based on a memory performance, could be sufficient to explain the reaction times of synaesthetes. Nevertheless, subjective reports do not fit within this hypothesis. Synaesthetes normally do not speak in terms of "remembering or imagining a colour hue", when exposed to an inducer stimulus. In their verbal descriptions they typically mention a halo of specific colour tone (Smilek & Dixon, 2002), concrete tactile sensations (Cytowic, 1993), or tastes on the tongue (Ward & Simner, 2003). In other words, these reports suggest that synaesthesia is much better described as a sensory phenomenon, and it certainly cannot be seen as a high-level memory association (Ramachandran & Hubbard, 2001a, 2001b, 2003a).

In order to test this hypothesis it was necessary to explore to what degree the synaesthetic colours lead to sensory effects observed with real colours. Ramachandran and Hubbard (2001a) studied two synaesthetes (J.C. and E.R.) who experienced photisms upon observing letters and numbers. To see whether this was a sensory process or not, the authors set up number matrixes that, due to their visual characteristics, could be perceived as either a vertical arrangement (a series of columns) or a horizontal one (i.e., numbers grouped in rows). When a visual feature leads to formation of clusters that are perceived as wholes, it is assumed that such a feature is genuinely perceptual (Beck, 1966; Treisman & Gelade, 1980). For instance, if a series of neighbouring elements in a matrix is of a different colour from the rest, it will be recognized as a distinctive group, standing out in the background. This phenomenon, termed *perceptual grouping*, occurs in response to basic visual features such as colour, shape, and orientation. In Ramachandran and Hubbard's design, the matrix elements were numbers that due to the similarity in shape between the number elements (e.g., the 3s and 8s) could be perceived as organized in a specific manner (for example, as rows in Figure 1, left). However, the authors chose the matrix numbers for each synaesthetic participant in such a way that the grouping by synaesthetic colour would lead to a different visual organization than would the grouping by shape. In the stimulus represented in Figure 1, the elements in alternating columns (3s and 7s, 8s and 0s) induced the same synaesthetic colours for the synaesthete E.R. If the photisms behaved much like real colours, they should overcome the horizontal organization induced by the number shapes, leading to a perception of coloured vertical columns (Figure 1, right). This is what actually happened. While the control participants tended to group the elements solely on the basis of grapheme shape, the synaesthetes reported perceiving groupings based on their induced colours in 90.97% (J.C.) and 86.75% (E.R.) of the trials.

In another experiment with the same synaesthetes, Ramachandran and Hubbard (2001a) used arrangements of randomly scattered graphemes, containing an embedded shape (square, rectangle, parallelogram, or triangle) that consisted of a grouping of identical characters (Figure 2, left). The participant's task was to observe the figure for 1 second and then try to identify the "hidden" shape. Nonsynaesthete



3	8	3	8	3	8	3
7	0	7	0	7	0	7
3	8	3	8	3	8	3
7	0	7	0	7	0	7
3	8	3	8	3	8	3

3	8	3	8	3	8	3
7	0	7	0	7	0	7
3	8	3	8	3	8	3
7	0	7	0	7	0	7
3	8	3	8	3	8	3

Figure 1. *Normal participants usually perceive this number matrix as horizontally organized (left figure), due to the shape similarity between the numbers 3 and 8. Lexical synaesthetes studied by Ramachandran and Hubbard (2001a) observed a vertical set-up, induced by a chromatic pattern of the photisms (right). (Figure can be seen in colour online.)*

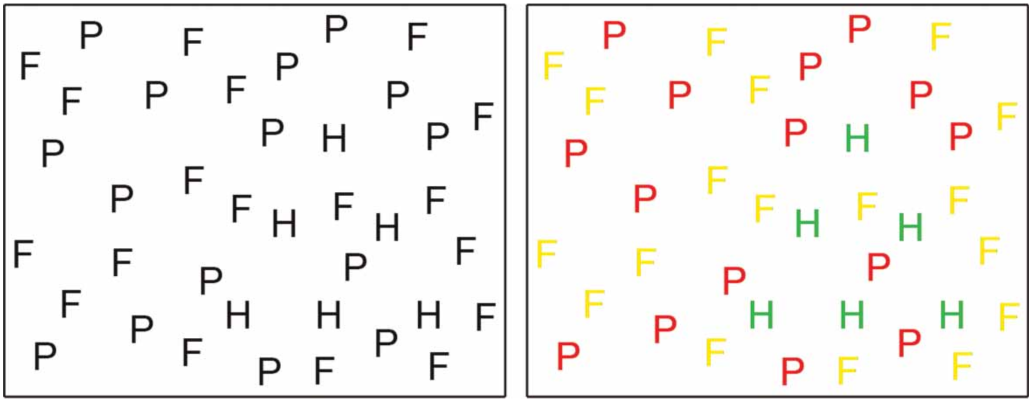


Figure 2. *The "letter soup" used in a visual search experiment by Ramachandran and Hubbard (2001b). Right figure represents the image as "seen" in synaesthetic colours. (Figure can be seen in colour online.)*

controls found the shape in 59.4% of trials. In contrast, synaesthetes got it right in 81.25% of trials. The most frugal explanation is that photisms induced by the graphemes led to a sensory segregation ("pop-out") of the embedded shapes. When this experiment was replicated later by Hubbard, Arman, Ramachandran, and Boynton (2005) with 6 synaesthetes, the results confirmed that the synaesthetes' performance was significantly better than that in the controls. However, the synaesthetes were inferior to a second group of control participants who were exposed to arrangements of actually coloured graphemes, such as in Figure 2, right. This suggests that photisms are not as effective as real colours in so far as reaction-time performance is concerned.

Overall, the results of both experiments by Ramachandran and Hubbard (2001a; see also Hubbard et al., 2005) suggest that the nature of the mechanism underlying synaesthesia is sensory and cannot be accounted for by simple memory associations or attributed to an excessive use of metaphoric language. In line with these data, Smilek, Dixon, Cudahy, and Merikle (2001) demonstrated that photisms could actually influence visual perception. The researchers presented an achromatic number character on a plain colour background, followed by a mask. When the number was presented on a background of the same hue (a congruent condition), the performance was significantly worse (88% correct) than that with the incongruent condition (96% correct). In other words, the discrimination seemed to be more difficult for the synaesthete when the photism projected on the grapheme stimulus was of the same colour as the background. The same result was obtained in a visual search task where the participant had to look for a specific grapheme among distractors (Figure 3). Again, her performance was impaired (longer reaction time) for colour congruent trials compared to the incongruent trials.

The amount of available evidence suggests that theories of synaesthesia in terms of childhood memories or metaphorical language are definitively out of place. Synaesthesia seems to be a sensory-like process that can be accounted for by an anomalous communication between specific brain regions, as we see later on. In the following sections we examine the evidence concerning the incidence of synaesthesia in the population and explore the different modalities of this peculiar neuropsychological condition.

Synaesthesia prevalence and subtypes

Synaesthesia is not a widespread condition. Even though estimations of prevalence have been changing widely across different studies, until recently

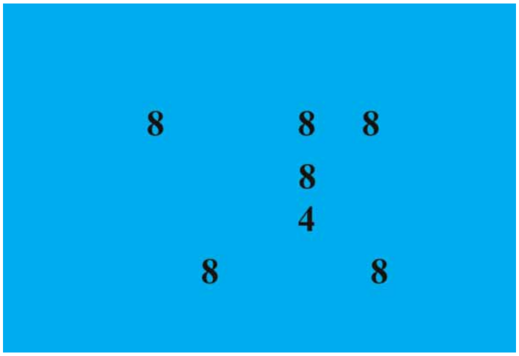


Figure 3. *The synaesthete C. was significantly slower when looking for a number grapheme that was presented on a background of the same colour as the associated photism (e.g., a "blue" 4 on a blue background). When the background was incongruent (i.e., of a different colour from the photism of the target), the number of distractors did not influence C.'s performance (Smilek et al., 2001). (Figure can be seen in colour online.)*

the consensus seemed to lie somewhere around 1 in 2,000 (0.05%), as proposed by Baron-Cohen, Burt, Smith-Laittan, Harrison, and Bolton (1996). The same study estimated a proportion of 6 female synaesthetes for every male with the condition. Even though the latter estimation is in accordance with quite a few other papers (e.g., Rich, Bradshaw, & Mattingley, 2005), it should be noted that the majority (if not all) of these studies probably suffered from a sampling bias caused by a higher willingness in women to inform about their synaesthesia (Simner et al., 2006; Ward & Simner, 2005). In a more recent study, using opportunistic samples (participants recruited from the communities of Glasgow and Edinburgh Universities), Simner et al. (2006) did not find any significant gender asymmetry. Besides challenging previous reports on this account, the result could possibly, but not necessarily, undermine purported X-linked inheritance of synaesthesia. (The subject of synaesthesia genetics is discussed later on in this paper.) Moreover, Simner et al.'s assessment of synaesthesia prevalence yielded a considerably higher value (4.4%) than previously assumed. Given the scope and the type of sampling employed, Simner et al.'s data are likely to be the best estimates to date.[2]

Besides the prevalence and the likely absence of sex bias, there are additional demographic aspects of synaesthesia that ought to be mentioned. A series of authors have reported high incidences of synaesthesia among people dedicated to artistic and/or creative professions and hobbies (Dailey, Martindale, & Borkum, 1997; Domino, 1989; Galton, 1880/1997; Ramachandran & Hubbard, 2001b). This idea has been confirmed in a large-scale study by Rich et al. (2005); 24% out of the 192 synaesthetes who participated in the research were professional artists or had a career linked to the arts. (In comparison, in the normal population of reference only 2% of people worked in the field of arts.) Interestingly, some authors believe that there are specific neurophysiological mechanisms that lead to above-average creative abilities in synaesthetes. As we discuss later, virtually all current neurocognitive models suggest an existence of some kind of neural hyperconnectivity between specific regions of a synaesthete's brain. Ramachandran and Hubbard (2001a) proposed that if such hyperconnectivity was more diffusely expressed, it could lead to "a greater propensity and opportunity for creatively mapping from one concept to another". However, up to date there have been only a few empirical studies focused on creativity in synaesthesia (e.g., Domino, 1989; Sitton & Pierce, 2004), and more research will be necessary in order to confirm (or refute) this proposal.

A large number of authors agree that synaesthesia is a familial condition (e.g., Baron-Cohen et al., 1996; Galton, 1880/1997; Rich et al., 2005). Rich et al. reported that 36% of synaesthetes participating in this large-scale study informed having at least one biological relative with synaesthesia. The authors also interviewed the participants about potential advantages and disadvantages of synaesthesia. The majority of synaesthetes (71%) perceived their condition

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[2] It must be noted that even in this study (Simner et al., 2006), testing of certain subtypes of synaesthesia was excluded for ethical and/or technical reasons: namely, the variants triggered by, or inducing, pain and emotional states.

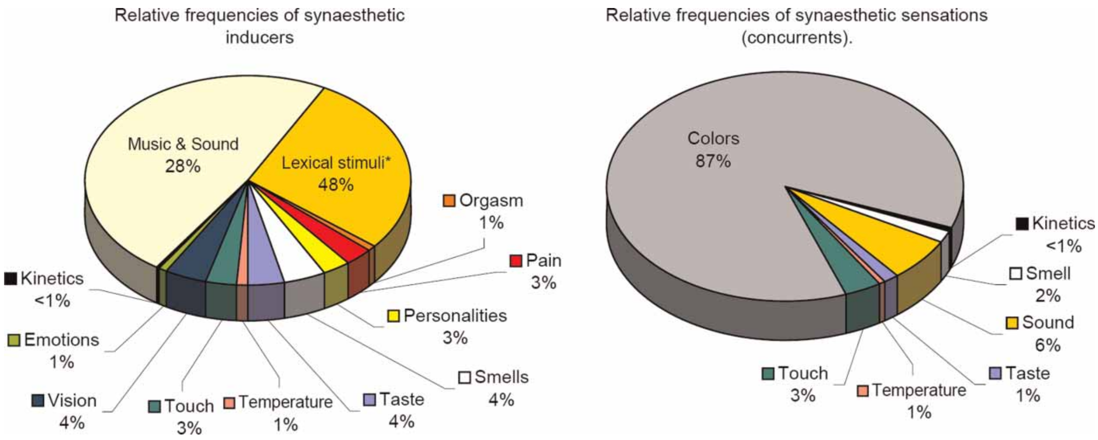
positively, claiming that synaesthesia enhances their memory skills, eases data organization, and provides a source of mental pleasure and creative inspiration. Approximately one third of those interviewed mentioned some negative aspects, mainly synaesthesia being a source of confusion due to incongruence between synaesthetic perception and physical reality (e.g., when the meaning of a word does not fit with the elicited photism). Lexical synaesthetes reported contradictory feelings caused by a negative disposition towards persons whose names were perceived in negative mental colours. A small number of synaesthetes complained about sensory overload and feelings of discomfort because of "being different".

On account of anecdotal reports it has often been assumed that synaesthetes tend to be bad in arithmetic, have a poor sense of direction, and frequently have "precognitive" experiences such as "déjà vu" or premonitory dreams (Cytowic, 1989). The data collected by Rich et al. (2005) support the suggestion concerning synaesthetes' poor sense of direction. Conversely, synaesthetes do not seem to be more likely to report precognitive phenomena than the general population.

As far as different subtypes of synaesthesia are concerned, all the authors agree that the most frequent modality of synaesthesia is the one induced by lexical stimuli, such as numbers, letters, and words (Baron-Cohen et al., 1996; Cytowic, 1993; Day, 2005; Rich et al., 2005; Rich & Mattingley, 2002; Simner et al., 2006). For instance, in the study by Rich et al. less than 2% of the interviewed synaesthetes did not experience synaesthesia in response to lexical stimuli (words, phonemes, or graphemes) and only presented other kinds of synaesthesia. If lexical stimuli are further subdivided into more specific categories, the days of the week turn out to be the most frequent synaesthetic inducers (Simner et al., 2006). On the other hand, nonlexical modalities of synaesthesia are much less frequent. Up to 50% of synaesthetes (estimate based on the data by Day, 2007) experience synaesthesia in more than one sensory modality. (For example, "lexical" synaesthete can "see colours" when seeing, hearing, or merely thinking of numbers and letters.) Even though for the majority of synaesthetes the synaesthetic sensation is colour (Day, 2005, 2007; Simner et al., 2006), there are reported cases of smell, tactile sensations, sound, taste, and proprioception as concurrent percepts. (See Figure 4.)

According to Day (2005), there are two major categories of synaesthesia:

1. *Cognitive synaesthesia*: Photisms or other synaesthetic perceptions are induced by


Relative frequencies of synaesthetic inducers

Relative frequencies of synaesthetic sensations (concurrents).

Figure 4. *Relative frequency of synaesthetic inducers and concurrents (Source of data: Day, 2007). (Figure can be seen in colour online.)*
Note: Lexical stimuli include graphemes, digits, time units and written and spoken words.

stimuli associated to symbolic meanings, transmitted within specific culture (graphemes, phonemes, people's names, week days, etc.).

2. *Synaesthesia "proper"*: Stimuli of one sensory modality are perceived simultaneously and involuntarily through an additional sensory channel (e.g., seeing music).

This classification partially overlaps with the distinction put forward by Marks and Odgaard (2005) who distinguish between an *intramodal synaesthesia* (the inducer and the synaesthetic response belong to the same sensory modality, e.g., when graphemes are perceived as coloured) and an *intermodal synaesthesia* (the stimulus induces a concurrent in a different modality, e.g., tactile sensations elicited by taste). However, the overlap is only partial given that there have been cases of both intramodal and intermodal cognitive synaesthesia.[3] There are also synaesthetes with intramodal nonlexical synaesthesia for whom when observing shapes and visual scenes photisms are induced. For instance, the synaesthete R., described by Milán et al. (2007), experienced the colour red when watching the sky with clouds. This kind of synaesthesia would be clearly intramodal. It does not seem to be related to any kind of culturally acquired semantics—that is, it is not the cognitive subtype—but neither is it a case of synaesthesia "proper", as defined by Day. Taking into account these nuances, we prefer to use Marks and Odgaard's taxonomy, along with additional clarification of the cognitive aspects that are sometimes difficult to determine. For instance, in the case of "coloured music" we might be dealing with a culturally conditioned synaesthesia, triggered by musical education, or it could be the result of a more straightforward "transduction" of auditory input into visual percepts of colour.

Another important aspect of synaesthesia has to do with the mode of experiencing synaesthetic sensations. According to Dixon et al. (2004), there are at least two qualitatively different varieties of visual synaesthesia. *Projector synaesthetes* perceive their photisms as located in external space, usually being projected onto the eliciting stimulus (e.g., a grapheme in lexical synaesthesia). On the contrary, *associator synaesthetes* observe synaesthetic colours in their mind's eye; there is no external projection of the photisms. Dixon and colleagues discovered that these two groups differed not only in their subjective reports but also in their performance on a modified Stroop task. The experiment included two tasks: to name the colour of a grapheme presented on a computer screen or to name the colour of the photism triggered by the grapheme. The colour of the grapheme could be congruent or incongruent with respect to the photism. The results show that "projector" synaesthetes are more sensitive to interference of the photisms when naming the grapheme colour than vice versa. That is, the photisms somehow disrupt the ability to name the grapheme colour, while the real colour interferes little or not at all with the ability to name the photism. On the other hand, the "associator" synaesthetes were faster at naming the grapheme colour, and they showed the same interference pattern in both tasks. This double dissociation in Stroop interference pattern has also been reported in a more recent study by Ward, Li, Salih, and Sagiv (2007).

Ramachandran and Hubbard (2001b, 2003b; Hubbard & Ramachandran, 2005) proposed an alternative higher versus lower distinction, motivated by differences in the level of representation of the inducing stimulus. In synaesthetes termed as *lower*, the photisms are elicited by specific perceptual features of the inducer (e.g., the form of a digit), and they most probably occur in early stages of perceptual processing. On the contrary, photisms of *higher* synaesthetes arise in response to more abstract, conceptual aspects of the inducer (e.g., the meaning of a number), which are processed by different brain areas. The matter of the level of representation of synaesthetic

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[3] For instance, when hearing phonemes leads to the perception of photisms, we are dealing with a cognitive intermodal subtype of synaesthesia.

triggers is indeed critical to the debate about the underlying neurocognitive mechanisms.[4] On the other hand, the distinction put forward by Ramachandran and Hubbard seems to be more problematic than Dixon et al.'s (2004), because it is founded on theoretical, yet-to-be-proved assumptions rather then phenomenological reports of synaesthetes (Ward et al., 2007). Some authors (Dixon & Smilek, 2005; Hubbard & Ramachandran, 2005) speculated that the projector–associator distinction actually mapped on to the lower–higher dimension. However, a recent study by Ward et al. (2007) demonstrates that the two distinctions are most probably orthogonal. According to previous accounts on this issue, certain behavioural characteristics are expected of higher/associator or lower/projector synaesthetes, respectively. For instance, the higher level synaesthesia may be particularly associated with ordinal sequences (a conceptual level property); digits, roman numerals, spelled out numbers, or dice patterns should elicit the same synaesthetic colours in higher synaesthetes (but not lower synaesthetes) because they represent the same number concept. On the other hand, in lower/projector synaesthetes the colours of words should be more frequently derived from graphemic constituents, provided that it is true that they are sensitive to the external stimulus per se (i.e., the graphemes) and not the underlying concept. First, Ward et al.'s findings indicate that the presence or absence of the lower or higher characteristics is independent of the projector/associator classification (assessed by first-person reports). Some of their associator participants presented "lower" features, as well as "higher" features being observed in many projector synaesthetes. Moreover, the only reliable difference (beyond phenomenological reports) between the associators and the projectors was found in their respective patterns of Stroop-type interference, first reported in the study by Dixon et al. (2004). (Remember that projector synaesthetes were faster in naming photism colours than real colours of graphemes; the opposite was observed in the associators.) According to Ward and colleagues, this behavioural discrepancy results from diverse spatial frames of reference evoked during synaesthesia. While the projectors employ an externalized frame of reference defined relative to the location of graphemic stimuli, the associators use an internalized frame ("their mind's eye") or perhaps do not have any specific frame of reference with respect to their photisms.[5] Following this proposition, the slower reaction times of the associators in a photism naming task actually reflect an attentional effect. They need to shift their attention from one spatial location to a new one; the projectors' attentional resources remain in the same location during the task.

In summary, the study by Ward et al. (2007) brings in important new data and a novel approach to the problem of phenomenological and behavioural differences, and it may have important implications for present neurocognitive models of synaesthesia. Even though the consensus regarding this issue is still to be sought, it is clear that interindividual variability could account for a number of inconsistencies observed across various experimental studies (Hubbard & Ramachandran, 2005; Ward et al., 2007). For example, Palmeri, Blake, Marois, Flanery, and Whetsell (2002) demonstrated a strong sensory segregation effect with a synaesthete W.O. in a visual search task (the participant's task was to detect a grapheme target among distractors). In a similar experiment with 14 synaesthetes (Edquist, Rich, Brinkman, & Mattingley, 2005), only 2 participants showed facilitation in visual searches in comparison to the control group of nonsynaesthetes, and they did not present a sensory "pop-out" pattern that had appeared in Palmeri's results. In theory, it is possible that the participant in the Palmeri et al. study was of a

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[4] It is not clear whether this classification reflects a dichotomic dimension, which corresponds to qualitative differences between the synaesthetes, or whether there is a continuum with cases laying "halfway" between the "lower" and the "higher" synaesthesia.

[5] Ward et al. (in press) suggest that the projector–associator dichotomy needs to be further subdivided, in order to include all types of frames of reference reported by synaesthetes. See the original paper for a full account on this topic.

"projector" or "lower" type, while there were no such synaesthetes in the latter experiment. Given the heterogeneity of the phenomenon of synaesthesia, particular caution is necessary when designing and analysing data. If individual data are averaged indiscriminately, the obtained results and their interpretation are likely to be distorted. Frequently, single-case designs and/or interindividual comparisons between synaesthetes are highly recommended research strategies (Smilek & Dixon, 2002).

Preconscious and sensory or conscious and conceptual?

If you fix your gaze at the central cross in Figure 5A, you can discern the number 5 located at your visual periphery. However, if the same number is surrounded by distractors (Figure 5B), it is virtually impossible to identify (Bouma, 1970). This effect, termed as "crowding", is a result of attention overload due to the distractors. Quite contrary to the data obtained with normal participants, two synaesthetes studied by Ramachandran and Hubbard (2001b), who were tested on the same perceptual "crowding" task, easily identified the "invisible" number. As reflected in their verbal reports, they were able to deduce the number identity through the photism colour, elicited by the grapheme. This result is analogous to that observed in nonsynaesthetic participants when the target is actually coloured (Kooi, Toet, Tripathy, & Levi, 1994) and suggests that the synaesthetic colour percept occurs on a preconscious level, before the crowding effect takes place.

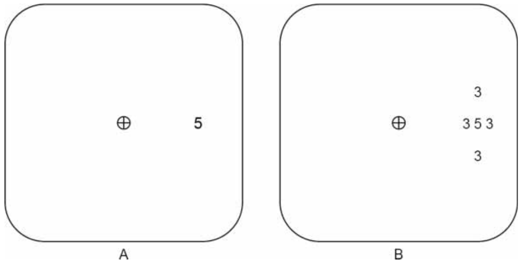

Figure 5. *The crowding task, applied to synaesthetes by Ramachandran and Hubbard (2001b), suggests that the induction of photisms precedes the conscious identification of graphemes.*

Evidence provided by Smilek et al. (2001) goes in the same direction. The synaesthete C. carried out a number identification task that consisted in naming a number briefly presented on a computer screen. When the graphemes were placed on a background of a different colour from the associated photism (i.e., incongruent condition), C.'s responses were significantly faster than in a colour-congruent condition. It is hard to think that the photism would influence the number identification in such a way, if it occurred after the conscious recognition of the grapheme.

However, not all the evidence is consistent with the preconscious hypothesis. Mattingley et al. (2001) subjected 15 lexical synaesthetes to two priming tasks. In the first one, they presented a grapheme during 28 or 56 ms and immediately followed by a mask, in order to eliminate conscious identification of the character. Participants' task was to name the colour of a square patch that appeared on the screen right after the masked stimulus (the prime). If photisms had occurred before conscious recognition of the masked character, they would have influenced the colour-naming task, facilitating colour identification when the grapheme photism and the colour patch were of the same hue. Nevertheless, none of the participants showed any synaesthetic priming effect, but they did present "classical" priming in a letter identification task. (In a second task they had to identify another grapheme presented after the masked character.) As expected, synaesthetes' reaction times were faster when the target grapheme and the prime were identical. This demonstrates that even though the grapheme presentation time of 28 or 56 ms was sufficient to produce unconscious "classical" priming, most likely it did not lead to photism induction. On the basis of these findings, the authors suggested that "synaesthetic colors typically arise only for inducers that are represented at conscious levels of visual processing" (Rich & Mattingley, 2002). Furthermore, in a more recent experimental series Mattingley, Payne, and Rich (2006) also demonstrated that when the primes are presented long enough so as to produce conscious percepts of colour, reducing the amount of attention available to process the synaesthetic inducer considerably reduces the priming effects. Again, this seems to indicate that conscious, selective attention to the stimulus might play an important role in synaesthesia.

The controversy of whether or not conscious identification of synaesthetic inducers is necessary for synaesthesia to occur is closely related to a debate concerning the perceptual versus conceptual nature of synaesthetic triggers. While some suggest that the recognition of the lexical stimulus as such is a necessary condition for photisms to occur, other studies seem to go in the opposite direction, defending that synaesthetic colours are a direct response to perceptual features of the inducer. At least in some synaesthetes, photisms produce effects typically observed with real colours: They can provide an input to apparent motion perception (Ramachandran & Azoulai, 2006; Ramachandran & Hubbard, 2002), produce McCollough colour aftereffect (Blake, Palmeri, Marois, & Chai-Youn, 2005), or be influenced by changes in physical attributes of the inducer, such as contrast, eccentricity (with respect to central vision), and frequency rate of alternately presented graphemes (Ramachandran & Hubbard, 2001a, 2001b). On the other hand, the fact that grapheme–colour synaesthetes experience photisms with rare typographic fonts or even with handwriting points to the importance of cognitive interpretation of the graphemes more than just their visual features per se.

So then are we dealing with a sensory phenomenon or not? First, we propose that it is necessary to make further progress in differentiating between lower and higher as well as projector and associator synaesthetes (Ward et al., in press). In order to overcome the inconsistencies it is essential to take into account and to control the presence of different varieties of synaesthesia in experimental designs. Available data suggest that the degree of dependence upon either perceptual or conceptual aspects is not the same for all synaesthetes, and it may also vary across different stimulus modes (e.g., spoken words vs. written words) in the same synaesthete. Secondly, it is necessary to take into consideration the different spatial frames of reference evoked by synaesthetes, as suggested by Ward et al. Finally, it should be noted that dichotomic categorizations of cognitive processes (as unconscious vs. conscious, perceptual vs. conceptual, or pre- vs. postattentional) are possibly too simplistic to account for synaesthetes' behavioural data (Ramachandran & Hubbard, 2005). Even in those rare cases of grapheme–colour synaesthetes who show typical sensory patterns in their behavioural performance, it is logical to expect at least some influence of conceptual processes. It is hard to believe that grapheme–colour synaesthesia, whose origin is intimately related to the acquisition of reading skills, is a purely sensory process, independent of lexical knowledge. In fact, the synaesthetic colour of ambiguous stimuli (e.g., the "O" in 9O89 and LOVE) typically changes in accordance with the surrounding lexical context (Dixon, Smilek, Duffy, Zanna, & Merikle, 2006; Ramachandran & Hubbard, 2003a). The matter to be solved is whether this and other similar effects are the consequence of a top-down modulation, as proposed by Ramachandran and Hubbard (2001b), or whether the photisms only arise once the grapheme has been identified, as put forward by Mattingley et al. (2001).

Synaesthetic brain

The first study of the synaesthetic brain, carried out by Cytowic and Wood (1982), supported the suspicion that neuronal functioning of synaesthetes was different from that of a normal person. Unfortunately, unexpected complications arouse due to the fact that the only subject of this investigation (M.W.) showed additional anomalous cerebral activity even when he did not experience synaesthesia. This fact made data interpretation quite problematic; the scientific community would have to wait more than a decade for new and finer neuroimaging data.

In 1995 Paulesu et al. seated 6 female with auditory lexical-chromatic synaesthesia in a positron emission tomography (PET) scanner. During the exposition of the synaesthetes to spoken words, neural activity was observed in visual areas (posterior-inferior temporal cortex and parieto-occipital junction). This was to be expected if, as hypothesized, synaesthesia was a perceptual phenomenon rather than a result of high-level associations. Surprisingly, activity in the area responsible for colour processing in humans (V4/V8) did not reach statistical significance. In any case, Paulesu et al.'s study provided a first clear-cut demonstration showing that the cerebral functioning of the synaesthete participants was different from that of normal, control participants. The nonsynaesthetes' visual areas gave no response to the same auditory stimulation.

Posterior studies used finer technology, which allowed making further progress in the understanding of functional neuroanatomy of synaesthesia possible. Weiss, Shah, Toni, Zilles, and Fink (2001) worked with R.S., a lexical-chromatic synaesthete who experienced photisms in response to the names of people he knew. When R.S. was being exposed to such stimuli, functional magnetic resonance imaging (fMRI) revealed a bilateral activity in the area V4, an activation of the extrastriate visual cortex, as well as the retro-splenial cortex (the region usually associated to person familiarity). Nunn et al. (2002) subjected lexical-chromatic synaesthetes to an experiment where they presented spoken words, pseudowords (i.e., nonsense syllables), and single pure tones. An fMRI scan showed increased activity in the left hemisphere colour area (V4/V8) when listening to words, but not when listening to pseudowords or tones. Nunn's design included a control group of nonsynaesthetes who received extensive training in associating specific words with colour hues. In contrast to the synaesthetes, these participants did not present any activity in colour regions when imagining colours in response to the words. The results agree with previous research, showing no activity in visual areas V1 or V2, and suggest that processing in earlier visual areas is not necessary to experience visual synaesthesia. The only study not in line with the aforementioned hypothesis was published by Aleman, Rutten, Sitskoorn, Dautzenberg, and Ramsey (2001), who detected activity in the V1 area of a lexical-chromatic synaesthete exposed to auditorily presented words. However, this seems to be an isolated result that only reached marginal levels of significance.

Virtually all research points to the importance of the colour processing area (V4/V8) for the generation and/or experiencing of photisms (Sperling, Prvulovic, Linden, Singer, & Stirn, 2006). In order to explore the degree of involvement of this as well as other brain regions, Hubbard et al. (2005) combined an fMRI scan with behavioural measures (a crowding task and a synaesthetic pop-out task, described earlier in this paper) in a study with 6 grapheme–colour synaesthetes and 6 control participants. When they compared the behavioural data and the fMRI data, they found a significant correlation between the degree of activation in visual areas (particularly the hV4) and the performance in the crowding task. The results were correlated between the two behavioural tasks, too. In other words, those synaesthetes who reached the best scores in the crowding and the pop-out tests also presented higher neuronal activity in the colour area (V4) when exposed to synaesthetic inducers (Figure 6). This result is in line with the idea that synaesthetes, including those who have the same kind of synaesthesia, are a heterogeneous group with important interindividual differences. It is possible that the activation of visual areas is stronger in those synaesthetes who perceive their photisms as externally projected. Interestingly, in a recent study Rouw and Scholte (2007) report on structural differences in neural connectivity between "associator" and "projector" synaesthetes. First, by means of diffusion tensor imaging (DTI) technology the authors have shown that synaesthesia is associated with increased (or more coherent) connectivity in white matter structure at various locations in the brain (inferior temporal cortex, parietal and frontal cortex). In addition, they observed that grapheme–colour synaesthetes with the strongest increased DTI signal in the inferior temporal cortex (adjacent to the fusiform gyrus) were "projectors" rather than "associator" synaesthetes.

In summary, the bulk of neuroimaging evidence indicates that at least in some synaesthetes, the

Figure 6. *The participants of this neuroimaging experiment were exposed to achromatic grapheme stimuli. An fMRI output shows ventral views of two inflated brains. The V4 area, responsible for colour processing, is indicated in purple, and the grapheme area is indicated in blue. In both participants there is activation in the grapheme area but only the synaesthete shows activity in the V4. From "Individual differences among grapheme-color synaesthetes: Brain-behavior correlations", by E. M. Hubbard, A. C. Arman, V. S. Ramachandran, and G. M. Boynton, 2005,* Neuron, 45, *975–985. Copyright 2005 by Elsevier. Reprinted with permission. (Figure can be seen in colour online.)*

experience of photisms resembles the perception of real colours, on both the subjective and the neurological levels. Yet, as more recent studies suggest (Hubbard et al., 2005; Rich et al., 2006; Rouw & Scholte, 2007), the implication of visual areas in synaesthesia is not equally strong across different individuals. Moreover, according to the aforementioned study by Rouw and Scholte (2007), white matter hyperconnectivity is present not only in inferior temporal visual areas but also in parietal and frontal cortices. More research would be needed to uncover the relationship between these structural abnormalities and the brain activation that leads to synaesthetic perception.

Origins of synaesthesia and current neurocognitive models

Before presenting the principal neurocognitive models, it is imperative to mention a series of data regarding the purported genetic background of synaesthesia. Despite the relative rarity of studies exploring the incidence and the heritability of synaesthesia, most researchers agree that idiopathic synaesthesia tends to run in families (e.g., Baron-Cohen et al., 1996; Galton, 1880/1997; Rich et al., 2005). This fact alone points to a possible genetic cause of the synaesthetic condition. Earlier investigations about incidence of synaesthesia suggested an X-chromosome-linked dominant trait (Bailey & Johnson, 1997), with a possible increase in male mortality that would explain the higher frequency of this condition in females (Baron-Cohen et al., 1996; Rich et al., 2005; Ward & Simner, 2005). However, the latter proposition, based on the skewed female-to-male ratio, has been called into question by a recent study by Simner et al. (2006), who report an almost perfectly equal proportion of female-to-male synaesthetes (1.1:1). (In fact, Ward & Simner's, 2005, study with 85 synaesthetic families did not find any evidence of the purported male mortality.) Yet, even if the absence of sex bias is confirmed, the higher incidence of synaesthesia among relatives provides a strong argument in favour of the genetic influence. The heritability of synaesthesia just might be more complex than previously thought. For instance, Smilek et al. (Smilek, Dixon, & Merikle, 2005; Smilek et al., 2002) have already reported two cases of monozygotic twins (two twin sisters and two twin brothers) who are discordant for synaesthesia.[6] These findings seriously question previous suggestions that synaesthesia is simply an X-linked dominant trait. If the genetic case for synaesthesia is correct, it means that the penetrance of the genotype for synaesthesia is probably incomplete (Smilek et al., 2005) and not sufficient by itself as a cause of the synaesthetic condition. (The discovery of male identical twins discordant for synaesthesia also contradicts a previous speculation in Smilek et al., 2002, based on a study of female monozygotic twins, that discordance of synaesthesia in identical twins is due to X-inactivation.)

In view of the evidence gathered thus far, the involvement of genetics in the development of synaesthesia still remains an open issue. First, what is the mechanism of genetic transmission of synaesthesia, and, second, how does the hypothesized gene (or genes) affect the neuroanatomy, giving rise to this sensory alteration. In relation to the second question, there are at least three modern theories regarding the neuronal mechanism through which a normal sensory stimulation leads to the experience of photisms. Because of the relatively higher prevalence (and availability) of grapheme-chromatic synaesthetes, all three models presented here have, in principle, been suggested to take account for this modality of the phenomenon.

Synaesthesia and "crossed wires"

The core idea of all current neurocognitive models of synaesthesia is a postulation of some kind of anomalous communication in the brain. If specific cortical areas, whose connectivity is limited in a normal brain, established active connections, this could produce "phantom" sensations typical for synaesthesia (Baron-Cohen et al., 1993). The underlying mechanism might be similar to the one present in amputee patients. The reorganization of the cortex following amputation frequently gives rise to tactile sensations on a nonexistent limb (Ramachandran, Rogers-Ramachandran, & Stewart, 1992). This phenomenon inspired Ramachandran and Hubbard, leading them to develop a *local cross-activation* model that accounts for the emergence of photisms in lexical-chromatic synaesthetes (Ramachandran & Hubbard, 2001b, 2003b; Hubbard & Ramachandran, 2005). When studying grapheme–colour synaesthesia, the authors realized that the colour area (V4) and the visual area responsible for grapheme identification were located in the same brain region—the fusiform gyrus. If neurons from these areas started to communicate, the expected subjective output would be an experience of colours upon seeing graphemes.[7] The question is: Why and how would these interconnections emerge between cortical areas that process completely different aspects of visual input?

In the course of cerebral maturation, the human brain goes through a phase of refinement in the formation of functional neural circuits, where a number of redundant and/or unnecessary pathways are eliminated through a process termed axonal pruning. If a genetic mutation caused a failure of pruning in specific cortical regions, these prenatal connections would persist in the adult brain, eventually leading to unusual sensory alterations—that is, synaesthesia. For instance, in the case of grapheme–colour synaesthesia the neuronal connections between the V4 and the grapheme area would be more numerous (less completely pruned) than in nonsynaesthetes. The fact that these two brain areas are close to each other increases the likelihood of reciprocal neuronal communication. In addition to the evidence demonstrating the implication of V4 in lexical-chromatic synaesthesia, the

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[6] It must be noted that in both studies the authors did not check for (or do not report on) the presence of subtypes of synaesthesia other than the grapheme–colour variety.

[7] In theory, the opposite result is also conceivable—that is, the participant could experience graphemes in response to colours. See the discussion by Hubbard and Ramachandran (2005), where they argue why such a possibility is much less plausible.

authors make reference to the discovery of the aforementioned connections in foetal monkeys. Kennedy, Batardiere, Dehay, and Barone (1997) found neuronal pathways between inferior temporal regions and the V4 area in the prenatal macaque brain. Thanks to the process of axonal pruning, in adult animals the proportion of neural afferences from higher areas to V4 is reduced radically. Ramachandran and Hubbard (2003b; Hubbard & Ramachandran, 2005) propose that in humans a genetic mutation could lead to defective axonal pruning in the fusiform gyrus and consequently to anomalous connectivity in the adult brain. Thus, synaesthetic photisms would be the result of the colour area being activated through connections originating in the area responsible for grapheme processing.

It should be noted that there are alternative theoretical models that fall within the "cross-wiring scheme" as well. Rich and Mattingley (2002) proposed that in grapheme–colour synaesthetes unique functional connections were present at later levels of the processing hierarchy: concretely between the module of letter recognition and the modules of colour categorization and colour imagery. Even though the lack of anatomical specificity makes this hypothesis difficult to test using neuroimaging techniques, recent data by Rich et al. (2006) give some support to the latter proposal. In their experimental series involving colour imagery tasks as well as exposition to synaesthetic inducers, the authors observed that synaesthetic colours were associated with fMRI activity of the left medial lingual gyrus in grapheme–colour synaesthetes. This area is known to be involved in tasks requiring the retrieval of colour knowledge, such as naming the colour of an object (e.g., Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). On the other hand, no significant activity in the V4 area was registered during photism experiences. Apparently the results contradict earlier neuroimaging investigations (Hubbard et al., 2005; Nunn et al., 2002; Sperling et al., 2006) that emphasized the role of the V4/V8 area for the generation of synaesthetic colours. On the other hand, it is likely that inter-individual differences observed in synaesthetes on behavioural and phenomenological levels may also account for the differences in brain–behaviour correlates (Hubbard et al., 2005). Indeed, it would have been interesting if Rich et al. (2006) had reported on whether their experimental participants were projector or associator synaesthetes. It is possible that for the associators the cross-activation involves higher visual areas related to more abstract attributes of colours, while the projectors' synaesthetic experience relies on areas activated earlier during visual processing.

Disinhibition of top-down connections

Not all of the authors agree with the necessity of assuming anomalous neural pathways in synaesthesia. Grossenbacher and Lovelace (2001) affirm that to account for synaesthetic perception it is sufficient to consider the functioning of a (structurally) normal brain. As the authors correctly point out, synaesthetic experiences have been reported by otherwise nonsynaesthetic individuals who were under the influence of hallucinogens. The processing of sensory input progresses through a series of hierarchically organized modules. After going through various processing stages along dedicated pathways, the signals progressively converge until reaching a multimodal area. According to the authors, in synaesthesia neural signals of the synaesthetic inducer (e.g., a sound) travel along a separate processing pathway before reaching a multimodal "crossroad" where they "meet" signals of other sensory modalities. However, in addition to these afferent (feedforward) connections, the human brain also presents connections where information can travel backwards in the "processing chain". Normally the feedback from the multimodal convergence zone is "restricted to the pathway in which afferent (feedforward) information has arisen" (Rich & Mattingley, 2002). For instance, top-down visual signals should only influence processing in the corresponding (lower level) visual areas, while other directions of information flow are inhibited in order to avoid neuronal "noise" and processing anomalies. What Grossenbacher and Lovelace propose is that a failure of such inhibition could lead to the activation of an otherwise independent

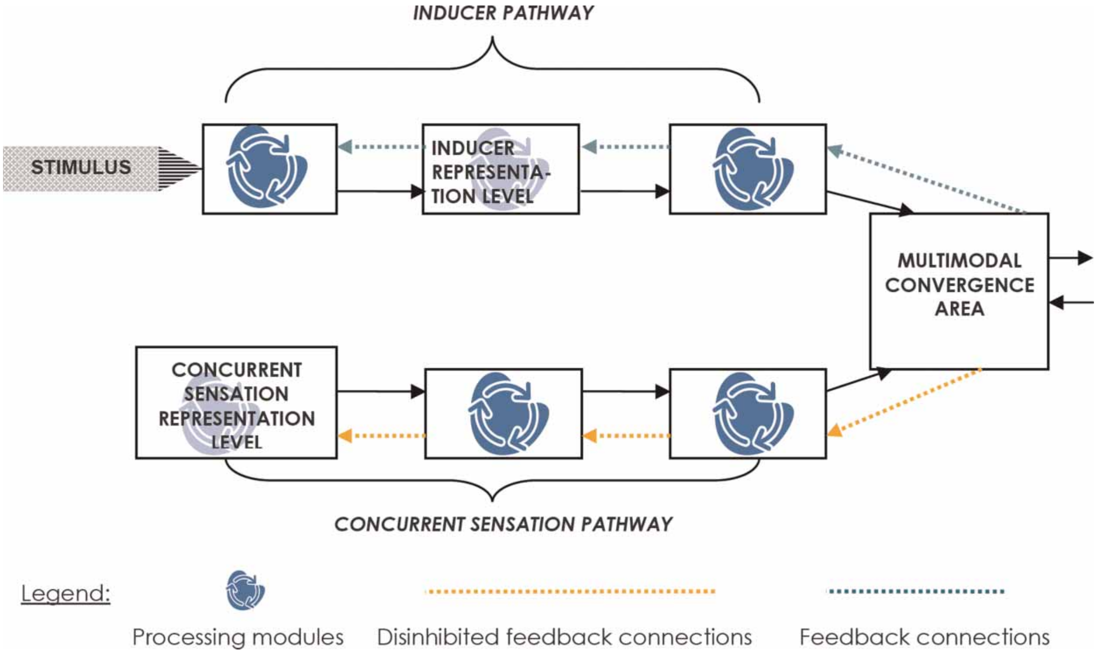

Figure 7. *Scheme of Grossenbacher's and Lovelace's model. Adapted from Grossenbacher & Lovelace (2001). (Figure can be seen in colour online.)*

neural pathway, generating synaesthetic perception.[8] More specifically, when the signal of a synaesthetic inducer reaches the zone of multimodal convergence (after going through all of the unimodal processing modules), it can travel backwards along the pathway of the synaesthetic modality and arrive at the level where the concurrent percept is generated. (See Figure 7.) In summary, Grossenbacher's model defends the view that synaesthesia is the result of a disinhibited feedback originating in a multimodal cortical area such as the superior temporal sulcus. (The aforementioned structure shows connections with unimodal areas, and, at the same time, it is responsive to specific perceptual features of several sensory modalities.)

The idea that synaesthesia occurs in a relatively late stage of sensory processing has received some empiric support from event-related potentials research. The authors emphasize the fact that differences in brain activity in synaesthetes and nonsynaesthetes are not observed until 200 milliseconds after the inducing stimulus onset (Schiltz et al., 1999). Moreover, synaesthetic perception is sometimes experienced during psychotropic "highs" in normal participants (Cytowic, 1993; Ramachandran & Hubbard, 2001b), and it can also be induced by posthypnotic suggestions in highly susceptible nonsynaesthetes (Fuentes, Cohen-Kadosh, & Catena, 2007). While it is true that these facts seem to show that the existence of anomalous anatomical connections is not a necessary condition for synaesthesia to occur,[9] it should also be pointed out that the recent study by Rouw and Scholte (2007) actually reports on increased white matter

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[8] A similar mechanism was proposed earlier by Armel and Ramachandran (1999) to explain acquired synaesthesia, observed in a patient who became blind as a consequence of suffering retinitis pigmentosa.

[9] Nonetheless, Ramachandran and Hubbard (2005) argue that the phenomenon of congenital synaesthesia can differ from the drug-induced experiences. Superficial similarity of the phenomena should not be straightforwardly interpreted in terms of identical neuronal mechanisms.

connectivity in grapheme–colour synaesthetes, favouring the hyperconnectivity accounts of synaesthesia.

Reentrant processing model

The reentrant processing model (Myles, Dixon, Smilek, & Merikle, 2003; Smilek et al., 2001) is, in some ways, a hybrid scheme that combines certain aspects of the aforementioned proposals. The authors base their model on the fact that visual information flows both forwards (bottom-up) and backwards (top-down) along the visual processing pathways. When a lexical–colour synaesthete observes an achromatic grapheme, the corresponding neural signals from the retina first arrive at lower visual areas. Subsequently they are processed by a shape-processing area (the posterior fusiform gyrus) before finally reaching the area in charge of the analysis of the meaning (the anterior fusiform gyrus). According to Smilek et al., the activation of photisms in "projector" synaesthetes is a result of cyclic feedback communication from the shape and the meaning processing areas to the colour region V4. As an illustration, let us consider a case of red photism induced by an achromatic letter "B". When the curves and the lines making up the letter are being processed by the striate cortex and the posterior fusiform gyrus, simultaneously signals originating from these areas travel to the anterior fusiform gyrus, where the meaning of the grapheme is analysed. In the beginning, before completion of the shape analysis, these signals are not sufficient to give way to conscious recognition of the letter. However, the authors propose that even a partial activation of the meaning can activate a red percept in the colour area (V4). More specifically, prior to the conclusion of the form and the meaning analyses, the anterior region of the fusiform gyrus will communicate with the colour area through top-down connections, activating the representation of the colour red. At the same time, this activation of red in the V4 will strengthen the activation of the meaning of "B" in the anterior fusiform, through bottom-up connections. (See the scheme of the model depicted in Figure 8.)

In this way, the neural signals will travel in a cyclical manner until they give rise to a complete conscious perception of a red "B". This mechanism also accounts for the fact that the context affecting the interpretation of a grapheme (e.g., the O in 9O89 and SOUL), also determines the synaesthetic colour of the stimulus (Dixon et al., 2006).

Given the fact that the top-down modulation is a general feature of human brain functioning, at the moment it is not possible to experimentally dissociate the processes proposed by the local cross-activation model (Hubbard & Ramachandran, 2005) and the reentrant processing model. In order to account for the contextual effects in photisms, Ramachandran and Hubbard (2001b) suggest that the same top-down mechanisms that are present in

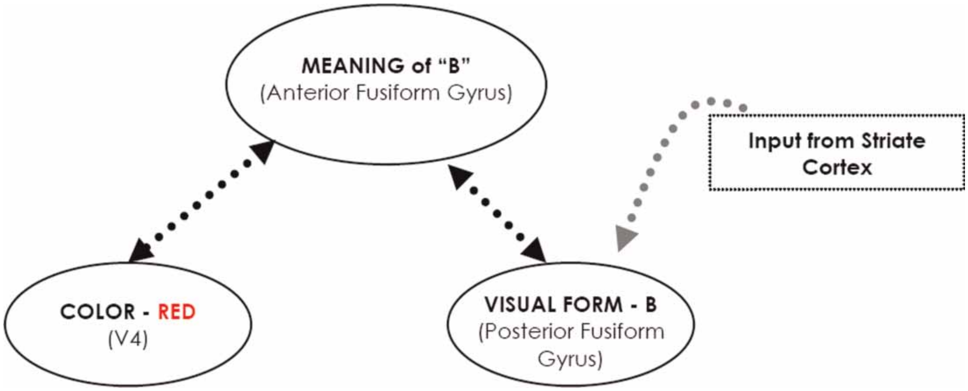

Figure 8. *Schematic depiction of a photism activation mechanism, following the model by Smilek et al. (2001). The "meaning of B" denotes a more abstract representation of the letter that is independent of font or case. (Figure can be seen in colour online.)*

normal people can explain the influence of semantic context on the photism colour. Specifically, if the context is able to skew the perception of the grapheme shape by a top-down influence from higher regions to the grapheme area, it makes sense to assume that, in synaesthetes, the latter region will consequently alter the activation of synaesthetic colours in the V4. In principle, the reentrant processing mechanism proposed by Smilek et al. (2001) would lead to the same behavioural output. In the future it will be necessary to reach a deeper level of specificity in both models, so that it will be possible to either corroborate or refute the respective proposals. At the same time, as Hubbard and Ramachandran (2005) have pointed out, the two models may not be mutually exclusive. It is perfectly plausible that a combination of both mechanisms (the local cross-activation and the disinhibited feedback from the meaning analysis areas) is present in some synaesthetes. In addition, we should also consider the possibility that different ways of experiencing synaesthesia in "projector" and "associator" synaesthetes imply diverse neurocognitive mechanisms. In fact, the aforementioned study by Rouw and Shoulte (2007) demonstrates that "projectors" showed stronger structural connectivity in the inferior temporal cortex than do "associators".

Final notes

Along this review of current scientific knowledge relating to the phenomenon termed synaesthesia, we have tried to analyse a few central points that have marked the development of synaesthesia research. First, we have seen that this peculiar condition is not the result of childhood memories, and its origin is probably due to a genetic alteration. Second, we have observed that the synaesthetic sensations can lead to sensory effects where photisms can increase the efficiency with which graphemes can be detected in perceptual crowding tasks, visual search, and perceptual grouping tasks. Third, we have analysed behavioural and neuroimaging evidence, concluding that synaesthesia shares many aspects with normal perception on both behavioural and neurological levels. And finally, after revising the most influential neurocognitive models, we may conjecture that the root of synaesthesia is in some sort of anomalous communication between specific brain areas, which could be caused by abnormal "cross-wiring" in the sensory cortex, by top-down pathways disinhibition, or both. What then are the limitations of our present knowledge, and where is synaesthesia research heading? First of all, it is worth saying that the stage of verifying the reality of synaesthesia seems to be finally over. In our opinion, the scientists involved in the study of synaesthesia successfully demonstrated beyond any reasonable doubt that synaesthesia is authentic and that the subjective reports of synaesthetes are to be taken seriously. Even so, the investigation into the neurophysiological background of this condition is still in its beginnings. In order to make further progress in our understanding of synaesthesia, it will be necessary to expand the limits of existing research in several directions.

To begin with, it should be pointed out that a greater part of the hypotheses and models are built upon the basis of data proceeding from studies with lexical synaesthetes (Grossenbacher & Lovelace, 2001; Hubbard & Ramachandran, 2005). Even though this is understandable given the relatively high frequency of this subtype of synaesthesia, it would be imperative to broaden current experimental paradigms with the aim of exploring to what degree other varieties of this condition are similar to the lexical-chromatic synaesthesia on behavioural as well as neurological levels.

Furthermore, as we emphasized before in this text, it is vital to take into account individual discrepancies in the intensity and the phenomenological quality of the synaesthetic experience. If the theoretical division of synaesthetes into "lower/higher" and "projector/associator" subtypes is further confirmed, it will have important implications for the experimental designs, for the interpretation of the data, and, possibly, for the refinement of the neurocognitive models.

On the other hand, the term synaesthesia has been applied to a broad range of phenomena: idiopathic synaesthesia, drug-induced anomalous perception, artistic expositions involving the coupling of sound and light, and so on. Perhaps the imprecision with which the word synaesthesia is used actually reflects certain aspects of the truth. It is not an accident that various authors defend that synaesthesia research can bring new insights into our understanding of the neurological bases of metaphor and language (Cytowic, 2002; Marks, 1978; Maurer, Pathman, & Mondloch, 2006; Ramachandran & Hubbard, 2001b). Subjective reports reveal striking parallels between the synaesthesia and cross-modal associations reported by nonsynaesthetes. For instance, Ward, Huckstep, and Tsakanikos (2006) demonstrated that the associations of sounds to colours in synaesthesia showed the same pattern of correspondence between luminosity and tone pitch as in cross-modal associations of normal persons. Ramachandran and Hubbard (2003b) note that people frequently tend to form the same synaesthetic associations—for example, in the case of associating particular visual shapes to sounds (Köhler, 1929). (See Figure 9.) The authors believe that specific regions of the human brain have an innate capacity to extract common, abstract properties from otherwise unrelated domains (Ramachandran & Hubbard, 2005), such as the concept of "jaggedness" present in both the "kiki" sound and the shape depicted in Figure 9 on the left. If an elementary aptitude for cross-modal abstraction was in fact hardwired in our nervous systems, the synaesthetic phenomenon could be understood as a more enhanced (and "more perceptual") version of this natural property of the human mind. In any case, hypotheses concerning the relationship between synaesthesia and the cross-modal language and metaphor still remain on highly speculative grounds. Does the similarity of these phenomena to the congenital synaesthesia extend beyond superficial aspects? In theory, synaesthesia, in a broader sense, could encompass a great variety of conditions ranging from "lower" synaesthesia to more "associative" synaesthesias, to conceptually triggered synaesthesias, to emotional synaesthesias, eventually up to the level of multimodal artistic expression and, possibly, cross-modal metaphor. Future research should respond to the question of where the frontiers lie between these phenomena as well as to whether we are dealing with qualitatively different conditions or if it is only a matter of degree. Part of the answer may arise from the neuroanatomical research, which should elucidate whether the synaesthetes (and what types of synaesthetes) really present unusual neuronal connectivity or, on the opposite side, whether the "phantoms" in their brains show up due to the disinhibition of normal cerebral machinery.

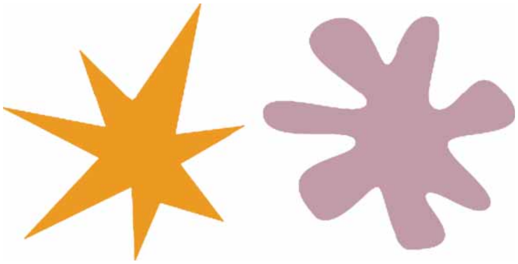

Figure 9. *Who is Kiki and who is Bouba? These figures demonstrate that humans do not associate shapes to images in an arbitrary manner. Almost 100% of the interviewed participants related "kiki" sound with the left figure and the "bouba" sound with the right figure (Köhler, 1929). (Figure can be seen in colour online.)*

As a final point of reflection, we believe it is worth mentioning the importance of synaesthesia for the progress of our understanding of subjective experience. The synaesthetic phenomenon constitutes a peculiar puzzle for cognitive science for one simple reason—it is a phenomenological experience that has a very low occurrence. Unlike disorders caused by brain injuries, it is a heritable and highly stable, life-long "condition". Moreover, synaesthesia is unlike schizophrenia (which is as likely as heritable as synaesthesia) in that it is not bothersome to the person who experiences it; it occurs in otherwise normal individuals. What attracts the attention of both the general public and the experts is the fact that the synaesthetes claim to see things that "normal" people cannot perceive. If, upon waiting for a pedestrian crossing you declare "observing a red light on a semaphore", there will be no cognitive scientist running to subject you to a Stroop task in order to corroborate that you really see what you claim to see. Oddly enough, from the synaesthetes' point of view the beginning of synaesthesia research was identical to the aforementioned situation. Numerous professionals tried to answer questions like: Is it true what you state, and do you actually perceive an achromatic "B" in red? In other words, cognitive science invested time and efforts in confirming the genuineness of subjective experience, achieving the same data that the synaesthetes had already provided through their own words. If we were to completely believe synaesthetes' verbal reports, then apparently science has done much work in vain. However, in our opinion, this effort in addition to empirically demonstrating the veracity of the introspection comprises a lesson for psychology in relation to the scientific understanding of subjective experience. Possibly for the first time empiric research has had to cope directly with the matter of qualia, trying to answer a question analogous to the renowned riddle proposed by Nagel (1974): "What is it like to be a bat?" (What is it like to be a synaesthete?) The development of our understanding of synaesthesia, accompanied by significant improvements in methodology, also amounts to an important advancement in the study of the "first-person experience" per se. In order to make further progress in this direction, it will be essential to combine behavioural and neurological evidence with subjective reports (Smilek & Dixon, 2002) and to convert the first-person viewpoint into an integral part of neuropsychological research.

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REFERENCES

Aleman, A., Rutten, G.-J. M., Sitskoorn, M. M., Dautzenberg, G., & Ramsey, N. F. (2001). Activation of striate cortex in the absence of visual stimulation: An fMRI study of synesthesia. *NeuroReport*, *12*, 2827–2830.

Armel, K. C., & Ramachandran, V. S. (1999). Acquired synesthesia in retinitis pigmentosa. *Neurocase*, *5*, 293–296.

Bailey, M. E. S., & Johnson, K. J. (1997). Synaesthesia: Is a genetic analysis feasible? In S. Baron-Cohen & J. E. Harrison (Eds.), *Synaesthesia: Classic and contemporary readings*. Oxford, UK: Blackwell.

Baron-Cohen, S., Burt, L., Smith-Laittan, F., Harrison, J., & Bolton, P. (1996). Synaesthesia: Prevalence and familiality. *Perception*, *25*, 1073–1079.

Baron-Cohen, S., Harrison, J., Goldstein, L. H., & Wyke, M. (1993). Coloured speech perception: Is synaesthesia what happens when modularity breaks down? *Perception*, *22*, 419–426.

Baron-Cohen, S., Wyke, M. A., & Binnie, C. (1987). Hearing words and seeing colours: An experimental investigation of a case of synaesthesia. *Perception*, *16*, 761–767.

Beck, J. (1966). Effect of orientation and shape similarity on perceptual grouping. *Perception & Psychophysics*, *1*, 300–302.

Blake, R., Palmeri, T. J., Marois, R., & Chai-Youn, K. (2005). On the perceptual reality of synesthetic color. In L. C. Robertson & N. Sagiv (Eds.), *Synesthesia: Perspectives from cognitive neuroscience* (pp. 47–73). New York: Oxford University Press.

Bouma, H. (1970). Interaction effects in parafoveal letter recognition. *Nature*, *226*, 177–178.

Cytowic, R. E. (1989). *Synesthesia: a union of the senses.* New York: Springer.

Cytowic, R. E. (1993). *The man who tasted shapes.* New York: Putnam.

Cytowic, R. E. (1996). Synesthesia: Phenomenology and neuropsychology. *Psyche*, *2*. Retrieved 10 January, 2007, from http://psyche.cs.monash.edu.au/v2/psyche-2-10-cytowic.html

Cytowic, R. E. (2002). Touching tastes, seeing smells—and shaking up brain science. *Cerebrum*, *4*, 7–26.

Cytowic, R. E., & Wood, F. B. (1982). Synesthesia I: A review of theories and their brain basis. *Brain and Cognition*, *1*, 23–35.

Dailey, A., Martindale, C., & Borkum, J. (1997). Creativity, synaesthesia and physiognomic perception. *Creativity Research Journal*, *10*, 1–8.

Dann, K. T. (1998). *Bright colors falsely seen: Synaesthesia and the search for transcendental knowledge*. New Haven, CT: Yale University Press.

Day, S. (2005). Some demographic and socio-cultural aspects of synesthesia. In L. C. Robertson & N. Sagiv (Eds.), *SYNESTHESIA: Perspectives from cognitive neuroscience* (pp. 11–33). New York: Oxford University Press.

Day, S. (2007). *Types of synaesthesia*. Retrieved January 20, 2007, from http://home.comcast.net/%7Esean.day/Types.htm

Dixon, M. J., & Smilek, D. (2005). The importance of individual differences in grapheme-color synesthesia. *Neuron*, *45*, 821–823.

Dixon, M. J., Smilek, D., Cudahy, C., & Merikle, P. M. (2000). Five plus two equals yellow. *Nature*, *406*, 365.

Dixon, M. J., Smilek, D., Duffy, P. L., Zanna, M. P., & Merikle, P. M. (2006). The role of meaning in grapheme-colour synaesthesia. *Cortex*, *42*, 243–252.

Dixon, M. J., Smilek, D., & Merikle, P. M. (2004). Not all synaesthetes are created equal: Projector versus associator synaesthetes. *Cognitive, Affective, & Behavioral Neuroscience*, *4*, 335–343.

Domino, G. (1989). Synaesthesia and creativity in fine arts students: An empirical look. *Creativity Research Journal*, *2*, 17–29.

Edquist, J., Rich, A. N., Brinkman, C., & Mattingley, J. B. (2005). Do synaesthetic colours act as unique features in visual search? *Cortex*, *42*, 222–231.

Fuentes, L., Cohen-Kadosh, R., Catena, A., & Henik, A. (2007, April). *Synesthesia experience under post-hypnotic suggestion: Evidence in favour of the disinhibition hypothesis*. Paper presented at the Synaesthesia, Science & Art: Second International Congress, Granada, Spain.

Galton, F. (1997). Colour associations. In S. Baron-Cohen & J. E. Harrison (Eds.), *Synesthesia: Classic and contemporary readings* (pp. 43–48). Oxford, UK: Blackwell. (Original work published 1880)

Grossenbacher, P. G., & Lovelace, C. T. (2001). Mechanisms of synesthesia: Cognitive and physiological constraints. *Trends In Cognitive Science*, *5*, 36–41.

Howells, T. H. (1944). The experimental development of color–tone synesthesia. *Journal of Experimental Psychology*, *34*, 87–103.

Hubbard, E. M., Arman, A. C., Ramachandran, V. S., & Boynton, G. M. (2005). Individual differences among grapheme-color synaesthetes: Brain-behavior correlations. *Neuron*, *45*, 975–985.

Hubbard, E. M., & Ramachandran, V. S. (2005). Neurocognitive mechanisms of synesthesia. *Neuron*, *48*, 509–520.

Kelly, E. L. (1934). An experimental attempt to produce artificial chromaesthesia by the technique of the conditioned response. *Journal of Experimental Psychology*, *17*, 315–341.

Kennedy, H., Batardiere, A., Dehay, C., & Barone, P. (1997). Synaesthesia: Implications for developmental neurobiology. In S. Baron-Cohen & J. E. Harrison (Eds.), *Synaesthesia: classic and contemporary readings* (pp. 243–256). Malden, MA: Blackwell Publishers.

Köhler, W. (1929). *Gestalt psychology*, New York: Liveright.

Kooi, F. L., Toet, A., Tripathy, S. P., & Levi, D. M. (1994). The effect of similarity and duration on spatial interaction in peripheral vision. *Spatial Vision*, *8*, 255–279.

Krohn, W. O. (1892). Pseudo-chromaesthesia, or the association of color with words, letters, and sounds. *American Journal of Psychology*, *5*, 20–41.

Luria, A. R. (1968). *The mind of a mnemonist.* New York: Basic Books.

MacLeod, C. M., & Dunbar, K. (1988). Training and Stroop-like interference: Evidence for a continuum of automaticity. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *14*, 126–135.

Marks, L. E. (1978). *The unity of the senses: Interrelations among the modalities.* New York: Academic Press.

Marks, L. E., & Odgaard, E. C. (2005). Developmental constraints on theories of synesthesia. In L. C. Robertson & N. Sagiv (Eds.), *SYNESTHESIA: Perspectives from cognitive neuroscience* (pp. 214–236). New York: Oxford University Press.

Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, *270*, 102–105.

Mattingley, J. B., Payne, J. M., & Rich, A. N. (2006). Attentional load attenuates synaesthetic priming effects in grapheme-colour synaesthesia. *Cortex*, *42*, 213–221.

Mattingley, J. B., Rich, A. N., Yelland, G., & Bradshaw, J. L. (2001). Unconscious priming eliminates automatic binding of colour and alphanumeric form in synaesthesia. *Nature*, *410*, 580–582.

Maurer, D., Pathman, T., & Mondloch, C. J. (2006). The shape of boubas: Sound–shape correspondences in toddlers and adults. *Developmental Science*, *9*, 316–322.

Milán, E. G., Hochel, M., González, A., Tornay, F., McKenney, K., Díaz Caviedes, R., et al. (2007). Experimental study of phantom colors in a color blind synaesthete. *Journal of Consciousness Studies*, *14*, 75–95.

Mills, C. B., Boteler, E. H., & Oliver, G. K. (1999). Digit synaesthesia: An ease using a Strooplike test. *Cognitive Neuropsychology*, *16*, 181–191.

Myles, K. M., Dixon, M. J., Smilek, D., & Merikle, P. M. (2003). Seeing double: The role of meaning in alphanumeric-colour synaesthesia. *Brain and Cognition*, *53*, 342–345.

Nagel, T. (1974). What is it like to be a bat? *Philosophical Review*, *83*, 435–450.

Nunn, J. A., Gregory, L. J., Brammer, M., Wiliams, S. C. R., Parslow, D. M., Morgan, M. J., et al. (2002). Functional magnetic resonance imaging of synesthesia: Activation of V4/V8 by spoken words. *Nature Neuroscience*, *5*, 371–375.

Palmeri, T. J., Blake, R., Marois, R., Flanery, M. A., & Whetsell, W., Jr. (2002). The perceptual reality of synesthetic colors. *Proceedings of the National Academy of Sciences*, *99*, 4127–4131.

Paulesu, E., Harrison, J., Baron-Cohen, S., Watson, J. D. G., Goldstein, L., Heather, J., et al. (1995). The physiology of coloured hearing: A PET activation study of colour word synaesthesia, *Brain*, *118*, 661–676.

Ramachandran, V. S., & Azoulai, S. (2006). Synesthetically induced colors evoke apparent motion. *Perception*, *35*, 1557–1560.

Ramachandran, V. S., & Hubbard, E. M. (2001a). Psychophysical investigations into the neural basis of synaesthesia. *Proceedings of the Royal Society of London, B*, *268*, 979–983.

Ramachandran, V. S., & Hubbard, E. M. (2001b). Synaesthesia: A window into perception, thought and language. *Journal of Consciousness Studies*, *8*, 3–34.

Ramachandran, V. S., & Hubbard, E. M. (2002). Synesthetic colors support symmetry perception, apparent motion and ambiguous crowding. *Abstracts of the Psychonomic Society*, *7*, 79.

Ramachandran, V. S., & Hubbard, E. M. (2003a). The phenomenology of synaesthesia. *Journal of Consciousness Studies*, *10*, 49–57.

Ramachandran, V., & Hubbard, E. M. (2003b). Hearing colors, tasting shapes. *Scientific American*, *288*, 52–59.

Ramachandran, V. S., & Hubbard, E. M. (2005). The emergence of the human mind: Some clues from synesthesia. In L. C. Robertson & N. Sagiv (Eds.), *Synesthesia: Perspectives from cognitive neuroscience* (pp. 147–190). New York: Oxford University Press.

Ramachandran, V. S., Rogers-Ramachandran, D., & Stewart, M. (1992). Perceptual correlates of massive cortical reorganization. *Science*, *258*, 1159–1160.

Rich, A. N., Bradshaw, J. L., & Mattingley, J. B. (2005). A systematic, large-scale study of synaesthesia: Implications for the role of early experience in lexical-colour associations. *Cognition*, *98*, 53–84.

Rich, A. N., & Mattingley, J. B. (2002). Anomalous perception in synaesthesia: A cognitive neuroscience perspective. *Nature Reviews Neuroscience*, *3*, 43–52.

Rich, A. N., Williams, M. A., Puce, A., Syngeniotis, A., Howard, M. A., McGlone, F., et al. (2006). Neural correlates of imagined and synaesthetic colours. *Neuropsychologia*, *44*, 2918–2925.

Rouw, R., & Scholte, S. (2007). Increased structural connectivity in grapheme-color synesthesia. *Nature Neuroscience*, *10*, 792–797.

Sacks, O., Wasserman, R. L., Zeki, S., & Siegel, R. M. (1988). Sudden color blindness of cerebral origin. *Society for Neuroscience Abstracts*, *14*, 1251.

Schiltz, K., Trocha, K., Wieringa, B. M., Emrich, H. M., Johannes, S, & Münte, T. F. (1999). Neurophysiological aspects of synesthetic experience. *The Journal of Neuropsychiatry and Clinical Neurosciences*, *11*, 58–65.

Simner, J., Mulvenna, C., Sagiv, N., Tsakanikos, E., Witherby, S. A., Fraser, C., et al. (2006). Synaesthesia: The prevalence of atypical cross-modal experiences. *Perception*, *35*, 1024–1033.

Sitton, S. C., & Pierce, E. R. (2004). Synesthesia, creativity and puns. *Psychological Reports*, *95*, 577–580.

Smilek, D., & Dixon, M. J. (2002). Towards a synergetic understanding of synaesthesia: Combining current experimental findings with synaesthetes' subjective description. *PSYCHE*, *8*(1). Retrieved December 12, 2006, from http://psyche.cs.monash.edu.au/v8/psyche-8–01-smilek.html

Smilek, D., Dixon, M. J., Cudahy, C., & Merikle, P. M. (2001). Synaesthetic photisms influence visual perception. *Journal of Cognitive Neuroscience*, *13*, 930–936.

Smilek, D., Dixon, M. J., & Merikle, P. M. (2005). Synaesthesia: Discordant male monozygotic twins. *Neurocase*, *11*, 363–370.

Smilek, D., Moffatt, B. A., Pasternak, J., White, B. N., Dixon, M. J., & Merikle, P. M. (2002). Synaesthesia: A case study of discordant monozygotic twins. *Neurocase*, *8*, 338–342.

Spalding, J. M. K., & Zangwill, O. (1950). Disturbance of number-form in a case of brain injury. *Journal of Neurology, Neurosurgery, and Psychiatry*, *12*, 24–29.

Sperling, J. M., Prvulovic, D., Linden, D. E. J., Singer, W., & Stirn, A. (2006). Neuronal correlates of color-graphemic synaesthesia: A fMRI study. *Cortex*, *42*, 295–303.

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*, 643–662.

Treisman, A. M., & Gelade, G. A. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*, 97–136.

Walker, P., & Smith, S. (1984). Stroop interference based on the synaesthetic qualities of auditory pitch. *Perception*, *13*, 75–81.

Ward, J. (2004). Emotionally mediated synaesthesia. *Cognitive Neuropsychology*, *21*, 761–772.

Ward, J., Huckstep, B., & Tsakanikos, E. (2006). Sound-colour synaesthesia: To what extent does it use cross-modal mechanisms common to us all? *Cortex*, *42*, 264–280.

Ward, J., Li, R., Salih, S., & Sagiv, N. (2007). Varieties of grapheme-colour synaesthesia: A new theory of phenomenological and behavioral differences. *Consciousness and Cognition*, *16*, 913–931.

Ward, J., & Simner, J. (2003). Lexical-gustatory synaesthesia: Linguistic and conceptual factors. *Cognition*, *89*, 237–261.

Ward, J., & Simner, J. (2005). Is synaesthesia an X-linked dominant trait with lethality in males? *Perception*, *34*, 611–623.

Weiss, P. H., Shah, N. J., Toni, I., Zilles, K., & Fink, G. R. (2001). Associating colours with people: A case of chromatic-lexical synaesthesia. *Cortex*, *37*, 750–753.

Wheeler, R. H. (1920). The synaesthesia of a blind subject. *University of Oregon Publications*, *5*, 1–61.

Witthoft, N., & Winawer, J. (2006). Synesthetic colors determined by having colored refrigerator magnets in childhood. *Cortex*, *42*, 175–183.

Wollen, K. A., & Ruggiero, F. T. (1983). Coloured-letter synaesthesia. *Journal of Mental Imagery*, *7*, 83–86.