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**THE COGNITIVE NEUROSCIENCE OF SYNAESTHESIA**

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## **Abstract**

This thesis expands on the knowledge of the cognitive neuroscience of synaesthesia. Three experiments examined aspects of cognition and neural activity in synaesthetes.

Experiment 1 examined how synaesthesia affects visual binding. Grapheme-colour synaesthetes were presented with sets of differently coloured letters, followed by a single coloured letter which made up a colour-letter combination that had either appeared in the preceding array, or not. Synaesthetes indicated whether or not they thought it had. In addition, the colour-letter combination was either synaesthetically congruent or not. No evidence was found that synaesthesia affected the pattern of binding errors, with congruent and incongruent letters equally subject to binding errors.

Experiment 2 used EEG to examine brain activation in synaesthetes when they view graphemes presented in the synaesthetically congruent colour versus graphemes presented in an incongruent colour. Matched nonsynaesthetes were also as yoked controls. For incongruent stimuli, synaesthetes had a more negative N200 component. The N200 indexes visual mismatch, indicating that synaesthetes responded to incongruently coloured letters as perceptually different from congruently coloured letters, and underscoring that synaesthesia is a perceptual phenomenon rather than simply memory associations.

Experiment 3 used EEG to explore how the brain activations of synaesthetes differ from that nonsynaesthetes when they are viewing stimuli that induce a synaesthetic experience. Grapheme-

colour synaesthetes and yoked controls viewed black graphemes. The synaesthetes differed significantly from nonsynaesthetes on three negativities, peaking at 230ms, 305ms, and 375ms poststimulus onset. These results are consistent with the theory that synaesthesia involves brain activity comparable to colour processing.

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## **Chapter 1: Introduction and Literature Review**

### **Why synaesthesia?**

Synaesthesia is a topic that has in recent years captured the public imagination, with television documentaries, popular articles, and more, devoted to the topic. Synaesthesia is a condition where different kinds of sensory stimuli induce an extra sensation. For example, one of the most common forms, known as grapheme-colour synaesthesia, is for letters of the alphabet to have colours associated with them: A could be red, B could be blue, C could be yellow. Someone with this form of synaesthesia would experience the colour red when seeing the letter A. The experience of the colour varies among synaesthetes, ranging from seeing the printed A on the page in red, to simply feeling that red is an inherent characteristic of the letter A.

When one first hears about synaesthesia, it is usually a surprise to discover it is not all that rare. Currently, it is estimated that 1 in 23 people (or just over 4%) have some form of synaesthesia (Simner et al., 2006), and it is common for synaesthetes to have multiple kinds (Novich et al., 2011). As we shall see, though, there is considerable variation, and indeed controversy, as to the precise nature of the synaesthetic experience. For instance, even when a synaesthete sees a letter, say, as being a certain colour, the colour does not respond in the same way as real colours do to variations in adaptation or contrast effects.

Not only is synaesthesia not all that uncommon, but it can affect those who have it in ways that are sometimes unexpected. For example, there are anecdotal reports of synaesthesia affecting

learning ability, both negatively and positively. Green and Goswami (2008), in a study of child grapheme-colour synaesthetes, report that they experience difficulties with numerical tasks if digits are presented in colours not congruent with their synaesthesia.

Synaesthesia has also been linked to creativity. Some synaesthetes, such as painter and sculptor Carol Steen, explicitly use their synaesthesia for artistic inspiration, and there may also be a higher proportion of synaesthetes among artists. For example, Rothan and Meier (2010) found a higher prevalence of synaesthesia among art students than the general university student population. In a test of creativity, synaesthetes on average performed better than control subjects matched for gender, major, verbal intelligence and year in school (Domino, 1989), while Sitton and Pierce (2004) found a correlation between synaesthesia and verbal creativity (though see Ward, Thompson-Lake, Ely & Kaminski, 2008).

Similarly, Thalbourne, Houran, Alias and Brugger (2001) found a moderate correlation (.57) of synaesthesia with transliminality, a construct including aspects of fantasy-proneness, absorption, creative personality, positive attitude toward dream interpretation, mystical experience, paranormal belief and experience, and magical thinking, though Rich et al. (2005) found they were not more prone to precognitive thinking.

Barnett and Newell (2008), found that synaesthetes on average experience more vivid mental imagery than nonsynaesthetes, while a number of studies Yaro and Ward (2007) found they have better memories. Depending on the kind of synaesthesia, they may also have enhanced visual acuity (Simner et al., 2006), and better visuo-spatial skills (Simner et al. 2009; Price, 2009; Rizza

and Price, 2012). Gross et al. (2011) compared grapheme-colour synaesthetes to controls on a number of memory-based tests, finding a general pattern of superior performance among the synaesthetes, attributing this primarily to superior encoding among the synaesthetes than controls.

Cohen Kadosh and Henik (2007) found that synaesthetes are no more likely to suffer mental illness or neurological defects than nonsynaesthetes, though Banissy et al. (2012) found in higher rates of positive and disorganized schizotypy among synaesthetes. Based on a single case study, Baron-Cohen et al. (2007) suggested that when synaesthesia is present in autistic spectrum individuals, they may have a greater tendency to savantism.

Synaesthesia then is a worthy subject of study, not just because it is fascinating, but because it is relevant to the everyday inner life of a non-trivial number of people. In addition, synaesthesia may be more relevant to all people than one would first suspect.

To a certain extent, it can be said that everyone makes synaesthesia-like connections. For instance, most people associate shapes with sounds: people presented with two shapes and given the choice of two names for them, consistently name the rounded shape *bouba* and the pointed shape *kiki* (Davis, 1961) - or similarly, *maluma* and *takete* (Kohler, 1929) - a finding that has been replicated in many countries ( Davis, 1961, Holland & Wertheimer, 1964, Lindauer, 1990). Similarly, people consistently associate high pitch sounds with brightness and low pitch sounds with darkness (Smith and Sera, 1992), and most people agree on the general mood that a given piece of music evokes. Synaesthesia then has a lot of similarities with the kind of cross-modal

connections all people make.

One intriguing example of this is the finding that even nonsynaesthetes appreciate the aesthetic appeal of synaesthetic associations. With the help of synaesthetes, Ward, Moore, Thomson-Lake, Salih and Beck (2008) produced animated audiovisual clips derived from the synaesthetic experiences of music evoking visual images. Nonsynaesthetes greatly preferred the clips that matched the synaesthetes' real experiences, compared to clips with random AV pairings, or those generated by nonsynaesthetes. This suggests that the cross-modal pairings these synaesthetes experience are not arbitrary, and are tapping into something deeper all people share.

Another example is the subconscious number line that about 65% of nonsynaesthete people seem to have (Wood, Nuerk & Willmes, 2006). On this number line, numbers are mapped into spatial representations, so that for example, 1 occupies a space on the left, 2 occupies a space to the right of 1, 3 is to the right of 2, and so on, although the shape of the number line differs between individuals (see for example Jarick et al, 2009). Having numbers arranged in a spatial pattern, at least subconsciously, is so common that researchers believe it may be a prerequisite to basic mathematical ability and understanding. For many synaesthetes, this same association of numbers to space is experienced explicitly, so that the number line is vividly seen in the mind's eye every time they deal with numbers. This gives rise to the intriguing possibility that the only difference between synaesthetes and nonsynaesthetes is the degree of conscious awareness associated with cross-modal connections (Cohen Kadosh & Henik, 2007), though the shape of synaesthetic number lines is often different from those of non-synaesthetic number lines.

Thus the study of synaesthesia has the potential to inform other areas of cognitive neuroscience, including numerical cognition, conscious awareness and cross-modal processes. At the same time, more thorough knowledge of synaesthesia in its own right is called for. The principal aim of this thesis is to add to the understanding of the cognitive neuroscience of synaesthesia – that is, the cognitive processes involved and the underlying biology associated with them. The following sections of this chapter are a review of the relevant literature, followed by a preview of the experimental studies of this thesis. Section 2 discusses the basic characteristics of synaesthesia, as well as introducing terms, while Section 3 serves to discuss some behavioural studies that establish some of the basic cognitive characteristics of synaesthesia. Section 4 discusses neurocognitive models, looking at the cognitive processes in synaesthesia including the role of attention, and also looking at the neurobiology of synaesthesia, including discussion of the anatomical location and physiological mechanisms involved in synaesthesia. Section 5 gives an overview of the imaging studies of synaesthesia in light of this discussion, looking in turn at studies that address anatomical correlates, connectivity and event-related activity associated with synaesthesia. Section 6 provides an overview and general discussion of this thesis.

### **Basic characteristics of synaesthesia**

Synaesthesia is a condition where information perceived in one sensory modality is also experienced as a perception within the same or another modality. The stimulus that invokes such a response is termed the *inducer*, and the resulting perceptual experience is known as the

*concurrent* (Grossanbacher and Lovelace, 2001).

The specific mapping of inducers to concurrents is idiosyncratic, though for a given individual appears to remain constant over their lifetime. Consistency in synaesthetic associations was demonstrated as early as 1917, in a study that tested a synaesthete's colour associations before and after a period of five years (Jordan, 1917), and a demonstration of consistency is the accepted way to verify synaesthesia for research purposes. The longest-spanning empirical study shows consistency over a period of 27 years (Simner and Logie, 2007). While synaesthetes typically report having had synesthesia for as long as they could remember, synesthesia has been induced following brain injury (e.g., Ro et al., 2007, Vike, Jabbari and Maitland, 1984), and temporarily with the use of LSD and mescaline (Hartman and Hollister, 1963), and during migraines, though it has not been established to what extent these temporary forms of synaesthesia resemble developmental synaesthesia.

Although synaesthetic mappings are idiosyncratic, a large-scale study on grapheme-colour synaesthesia found that some colours are more likely to be mapped onto certain letters than others. For instance, out of 192 synaesthetes in the study, 47% had brown for D, 36% had red for R, and 45% had yellow for Y (Rich, Bradshaw & Mattingley, 2005). Beeli, Esslen, and Jancke (2007) suggested that grapheme frequency was correlated with colour saturation, while Simner and Ward (2008) suggested the results were better explained by a correlation between grapheme frequency and colour frequency. An alternative explanation is that some frequent letter-colour mappings may be derived from innate cortical associations (Spector & Maurer, 2008).

There is a very wide range of stimuli that induce synaesthesia, from the purely sensory, such as sounds, temperatures, and tastes, to more conceptual inducers such as months of the year, emotions, and the differing timbres of musical instruments. In addition, the inducers can activate a range of different kinds of concurrents, including colours, personalities, tastes, and spatial patterns. It seems that virtually any combination of inducer to concurrent is possible, with at least 56 forms of synaesthesia having been reported so far, though some possible combinations (including temperature inducing taste, touch or smell concurrents) have not been reported (<http://home.comcast.net/~sean.day/html/types.htm>). Certain types of concurrents are more common than others: colour is by far the most common (a colour concurrent is known as a *photism*), followed by smell and then sound (Day, 2005). Typically the relationship between inducer and concurrent is unidirectional: for example, if B induces the colour blue, seeing blue in the real world will not be accompanied by an experience of B. There are however a minority of synaesthetes who do report bidirectional synaesthesia (Day, 2005).

A large-scale study found that the most common form of synaesthesia is coloured days, while grapheme-colour synaesthesia is less common than this and occurs in about 1% of the general population (Simner et al., 2006). Novich et al. (2011) in another large-scale study, noting that many synaesthetes have more than one type of synaesthesia, analysed which types of synaesthesia frequently co-occur. Five clusters of synaesthesia types were identified: colour induced by sequences such as months, days of the week, and the alphabet; colour induced by aspects of music such as pitch and timbre; spatial patterns induced by sequences; colour induced by sensation, such as touch or pain; and synaesthesias triggering non-visual concurrents such as smell or taste.

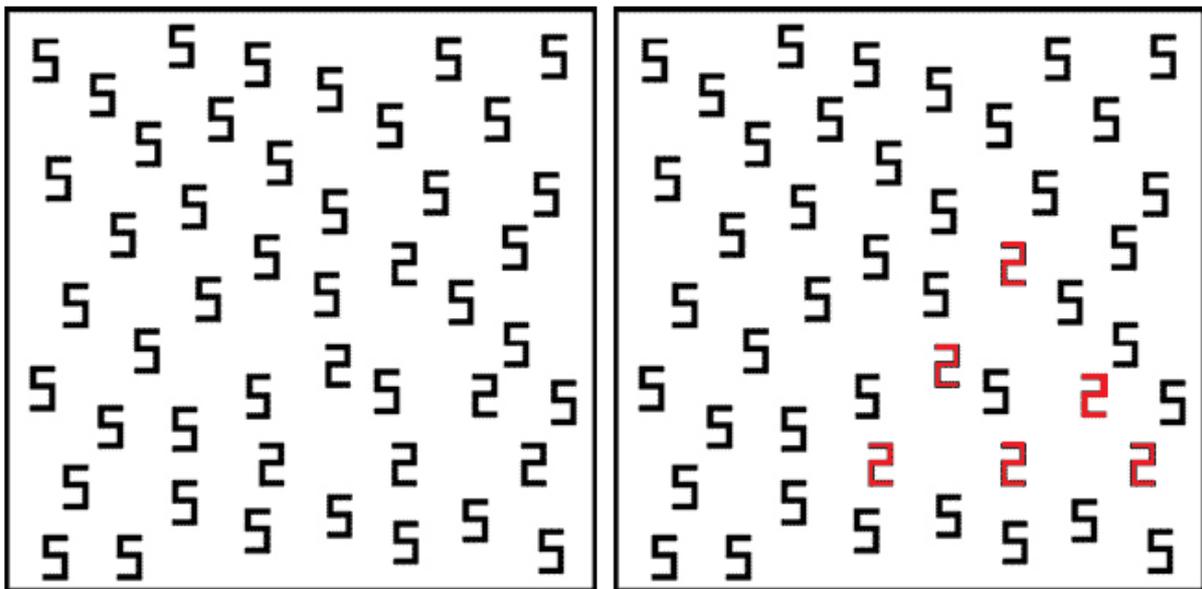
Synaesthesia often runs in families, though many synaesthetes report having no family members with the condition (for example, out of 192 synaesthetes in the Rich et al. study (2005), two-thirds report having no family members with the condition). An extensive study of families of synaesthetes showed that while individuals inherit a genetic predisposition to synaesthesia in general, the variant of synaesthesia an individual has is not inherited, so that synaesthetes within the same family often have different variants (Barnett et al., 2008). In addition, it appears that females inheriting the predisposition are more likely to have synaesthesia than males. Studies addressing the issue have found that female synaesthetes outnumber male synaesthetes, with researchers frequently finding ratios as high as 6:1 (Barnett et al., 2008, Baron-Cohen, Burt, Smith-Laitton, Harrison & Bolton, 1996, Rich et al., 2005), though lower ratios have also been found (Ward & Simner 2005, Simner et al., 2006).

### **Studying the cognitive mechanisms in synaesthesia**

Behavioural studies investigating the cognitive processes of synaesthesia have made valuable contributions to its understanding. Following is a review of some of the most important of such research. The vast majority of this research was done on synaesthesia with a colour concurrent.

One important aim of initial research was to verify synaesthetic experiences as genuine phenomena, as opposed to, for instance, common memory-based associations. Visual search paradigms provide evidence for the perceptual reality of synaesthetic colour perception. A typical visual search task involves searching for a target grapheme among an array of distracter

graphemes. In this task, colour-grapheme synaesthetes show faster search times than controls, though slower than that of a real pop-out effect, where the target grapheme is a different colour from the distractors (Sagiv & Robertson, 2005). In the Embedded Figures Task (see Figure 1.1), synaesthetes are also more accurate than controls at identifying the shape that is formed by a number of one type of letter embedded in other types of letters of the same colour ink (Ramachandran & Hubbard, 2001) (see below for implications of attention in synaesthesia for the Embedded Figures Task). As only elementary features - colour, shape, and depth - can produce such an effect (Treisman, 1982), this finding emphasises that synaesthetically perceived colours are not memorised associations. Rather, the colour is experienced as perceived rather than remembered.



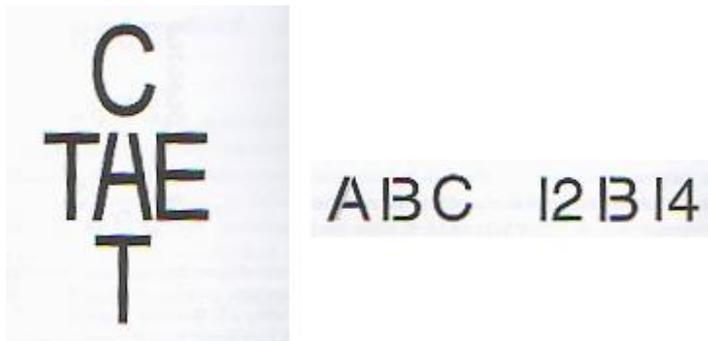
**Figure 1.1** '2's are embedded among '5's, forming the shape of a triangle. The triangle is hard to detect if the two digits are the same colour, but readily visible if they are seen as different colours. From Ramachandran and Hubbard (2001).

Nevertheless, certain perceptual effects that alter the perception of real colours do not apply to synaesthetic colours (Blake et al., 2005), and synaesthetic colours remain constant across differently coloured inducers, so that induced photisms are invariable. Synaesthetic colours interact with real colours to produce effects such as the bistable apparent motion illusion (Kim, Blake & Palmeri, 2006), and perceptual groupings (for example, a red letter is grouped with a black letter that induces a red photism) (Blake et al. 2005).

A phenomenon known as the SNARC effect demonstrates the perceptual reality of sequence-form synaesthesia. The SNARC effect refers to the way that behavioural responses to numerals are influenced by the hand which must make the response. SNARC stands for spatial-numerical association of response codes; the left hand responds more quickly to lower numbers, while the right hand responds more quickly to higher numbers. For synaesthetes who experienced the months of the year beginning on the left and ending on the right, the left hand responded more quickly to earlier months of the year, while the right hand responded fastest to later months of the year (Price & Mentzoni, 2008). For synaesthetes who experience the year beginning on the right and ending on the left, the opposite effect was seen, while nonsynaesthetes did not show these effects.

Other behavioural studies have gone some way towards establishing a cognitive model of synaesthesia. For instance Ramachandran and Hubbard (2001) observed that at times it is the semantic rather than sensory nature of inducer that is critical. In grapheme-colour synaesthetes, the colour of photisms is often context dependent and colours elicited by global/local letter stimuli are dependent on which attribute attention is paid to (see Figure 1.2). This demonstrates

that synaesthesia is subject to top-down cognitive processes.



**Figure 1.2** Ambiguous stimuli demonstrate the context-dependent nature of synaesthesia: the same shape can elicit different colours depending on its interpretation. (From Ramachandran and Hubbard, 2001)

Indeed, a large number of studies have demonstrated that in many cases, it is the conceptual nature of the inducer, rather than its sensory nature, that is relevant to the synaesthetic association. For example, Ward and Sagiv (2007) showed that a synaesthete experienced the same colours for numbers whether they were presented as digits, dice patterns or finger counting. Clearly, it is the semantic meaning of the stimulus, rather than any sensory aspect that causes the synaesthesia to be induced. Similarly, Jansari, Spiller and Redfern (2006) demonstrated a synaesthetic Stroop-like effect whether the task was presented aurally or visually (see page 16 for discussion of Stroop effects in synaesthesia).

In addition to these concise and simple studies, more elaborate techniques have been employed to demonstrate the conceptual nature of many synaesthetic inducers. For example Simner,

Glover, and Mowat (2006) showed that for grapheme-colour synaesthesia, the colour of a word is most often determined by the vowel of the stressed syllable. Hence, *'con-vict* and *con-'vict* would each generate different colours. This effect of stressed syllable is true even when the words are read (as opposed to heard), and so syllable stress is not perceived, but can only be conceptually determined, after lexical processing has taken place.

Cohen Kadosh and Henik (2006) also demonstrated the conceptual nature of the inducer by exploiting a size congruity paradigm on a single synaesthete. This paradigm is similar to the classic Stroop task, where subjects must name the colour that a colour word is presented in (for example, the word 'red' presented in the colour blue) (Stroop, 1935). Similarly, in the size congruity paradigm, subjects must compare two digits while ignoring the relative font size these digits are presented in. Adapting this to synaesthesia, the authors instead had a coloured-digit synaesthete compare digits of different colours. Digit pairs were presented in two conditions. When the stimuli were congruent, each digit in the pair appeared in its synaesthetic colour. When the stimuli were incongruent, each digit in the pair appeared in the other digit's colour. This manipulation of congruity affected response times. Crucially, in addition to this, the numerical distance of the digits modulated this effect of colour on her judgements. As in the original size congruity paradigm, when the digits were numerically far apart, the irrelevant aspect of the stimuli, their colour, did not have very much effect. When the digits were numerically closer, the colour of the digits had a larger influence on reaction times, with incongruent colours causing an increase in reaction time. This means that the synaesthete was not basing her comparisons on just the physical mismatch of colours; the concept of that colour (i.e. the digit associated with it) had an influence. So, the colours and digits were interacting at a conceptual level.

At the same time, for many synaesthetes, the inducer is indeed sensory. For instance, there are synaesthetes for whom every sound heard triggers a colour, pain triggers a taste, sound, or colour, and touch triggers colour (<http://home.comcast.net/~sean.day/html/types.htm>).

Hong & Blake (2008) performed a series of experiments designed to test whether synaesthetic colour processing occurred in the early stages of visual processing. They found that the experience of synaesthetic colours, unlike that of real colours, was not subject to changes of brightness contrast or chromatic adaptation. This shows that the neural events involved in synaesthetic colour experience occur later in the processing stream than those governed by the retina and primary visual cortex.

To summarise, behavioural studies of synaesthesia have provided a number of conclusions that go some way toward establishing a neurocognitive model of synaesthesia. These conclusions include that, firstly, the concurrent is a genuinely perceptual phenomenon; secondly, that the inducer is sometimes perceptual in nature, and at other times conceptual and semantic; and finally, that processing of the concurrent does not involve the mechanisms of early visual processing.

## **Neurocognitive models of synaesthesia**

### **Cognitive Processes**

#### **Higher/lower or conceptual/perceptual – the inducer.**

In 2001, Ramachandran and Hubbard made the distinction between what they termed higher or lower synaesthetes, as a means of reflecting the level of perceptual processing involved. Directly related to this was the idea that higher and lower synaesthetes would have different sites at which synaesthesia would occur in the brain. For instance, the angular gyrus mediates cognition of spatial sequences, and a patient with spatial locations for months, weeks and letters lost this synesthesia following injury to the right angular gyrus (Spalding and Zangwill, 1950). This is an example of higher synaesthesia, occurring in the angular gyrus. On the other hand, a patient with coloured hearing of musical notes lost this ability following brain injury that caused colour blindness (Sacks, Wasserman, Zeki and Siegel, 1988). This is an example of lower synaesthesia, mediated by the fusiform gyrus.

#### **Associative/projective – the concurrent.**

In addition to dividing the many forms of synaesthesia into two types based on the inducer, synaesthesia has also been divided into two types based on the nature of the concurrent. These types are projective synaesthesia and associative synaesthesia. Projective synaesthetes, or projectors, are those who experience their concurrent in the outside world, such as a grapheme-

colour synaesthete who experiences photisms projected onto a letter. Associative synaesthetes, or associators, experience the concurrent ‘in the mind’s eye’.

This distinction is contentious, as some forms of synaesthesia are not easily categorised into either group (for example, see Edquist, Rich, Brinkman and Mattingley, 2006). A large part of the difficulty is that categorisation is couched in the language used as synaesthetes struggle to describe their experiences to nonsynaesthetes. Imagine the following conversation between a researcher and a grapheme-colour synaesthete:

Researcher: “Do you see red when you see the letter A?”

Synaesthete: “Yes, A is red.”

Researcher: “But does it actually look red on the page, or is it in your head?”

Synaesthete: “It’s in my head”

Bearing in mind that synaesthetes do have normal visual perception – even a projective synaesthete can accurately report the colour a letter is presented in – if questioned closely enough they will be forced to reveal that the association is not the same as a real colour, but is “in their head.”

Dixon et al. (2004) suggested an objective measure for distinguishing between associators and projectors, by comparing a synaesthete’s performance on a modified Stroop task. In the classic Stroop task (Stroop, 1935), colour words, such as ‘red’ or ‘blue’ are presented in a colour either congruent or incongruent with the semantic meaning of the word. For example, the word ‘red’

could be presented in red (congruent), or in blue (incongruent). When participants are asked to name the colour the word has been presented in while ignoring the semantic meaning of the word itself, incongruent trials are subject to much longer reaction times and greater inaccuracy than congruent trials, due to interference from the automaticity of reading. This difference is known as the Stroop effect. A synaesthetic version of the Stroop test was first introduced by Wollen and Ruggiero (1983). Letters were presented in a colour either congruent or incongruent with the individual's concurrent photism, and the synaesthete's task was to name the colour as soon as the stimuli were presented. The synaesthete had lower reaction times and increased accuracy for congruent trials compared to incongruent trials, suggesting that synaesthetic colours are elicited voluntarily and can't be suppressed. Numerous variations of this synaesthetic Stroop effect have been done with equivalent results (e.g., Dixon, Smilek, Cudahy and Merikle (2000), Mattingley, Rich, Yellend & Bradshaw, 2001), though a similar Stroop effect has also been shown in nonsynaesthetes that have been explicitly taught colour-word associations, so it is not reliably diagnostic of synaesthesia (MacLeod and Dunbar, 1988).

In the Dixon et al. (2004) study, synaesthetes performed a variation of modified Stroop task in two different ways: naming the colour of their induced photism, and naming the colour the stimulus was presented in. For synaesthetes that self-reported as projectors, their photisms interfered in naming the presented colour, more than the presented colour interfered in naming their photism. In addition, the interference from photisms when naming the presented colour was greater among the projectors than among the associators.

Ward, Li, Salih and Sagiv (2007) argued that it is more productive to describe synaesthetic

experiences in terms of spatial reference frames than in terms of associators and projectors. In this way synaesthetes evoke either external or internal frames of reference. External reference frames normally support real visual perception, while internal reference frames normally support visual imagery. In addition to reference frames, it is important to distinguish the location of the concurrent within that frame of reference. Thus various grapheme-colour synaesthetes could be described as surface-projectors (colour experienced on surface of letter), near space-projectors (colour experienced as cloud with external physical location, but not on the page), see-associators (colour experienced akin to visual imagery), and know-associators (colour is known but perhaps not linked to any spatial reference frame at all) (Ward et al., 2007). Of course, it is also possible to use external reference frames to project colours to a location inside the head, or some other location that is not generally physically visible, such as behind the head.

It should also be noted that the perceptual/conceptual distinction can be applied to the concurrent as well, though this has never been addressed in published literature. Many concurrents are conceptual, such as gender for numbers, and personalities for objects.

### **Attention in synaesthesia.**

The two dichotomies of perceptual/conceptual synaesthesia, and projective/associative synaesthesia, lead to four possible combinations that reflect processing in synaesthesia. Starting from this point, the next step in establishing a cognitive model of synaesthesia is to address the level of processing required to induce the synaesthesia. In particular, is it necessary for the

inducer to be processed to the extent of conscious awareness before the concurrent is experienced? In other words, is attention required?

The role of attention in synaesthesia has been informed by the Embedded Figures Task as discussed above (see Figure 1.1). The pop-out effect found in synaesthetes by Ramachandran and Hubbard (2001) suggest the concurrent is induced pre-attentively, allowing it to act as a robust visual feature.

Subsequent studies however have failed to fully replicate the pop-out effect among synaesthetes. In visual search tasks, participants must identify a target grapheme among an array of distractor graphemes. When the target has visual features (colour, or elements of a shape) that are distinct from those of the distractors, the target is easily identified pre-attentively, giving the task a short search time regardless of the number of distractors, in what is known as a pop-out effect. In cases where the target and distractors share similar visual features (such as a black '2' among an array of black '5's), attention must be applied to the graphemes in order to identify the target. In these cases, the search time increases with the number of distractors, in a characteristic search slope. Because a difference in colour between the target and distractors elicit a pop-out effect (or absence of a search slope), the visual search paradigm can be exploited to examine the role of attention in grapheme-colour synaesthesia.

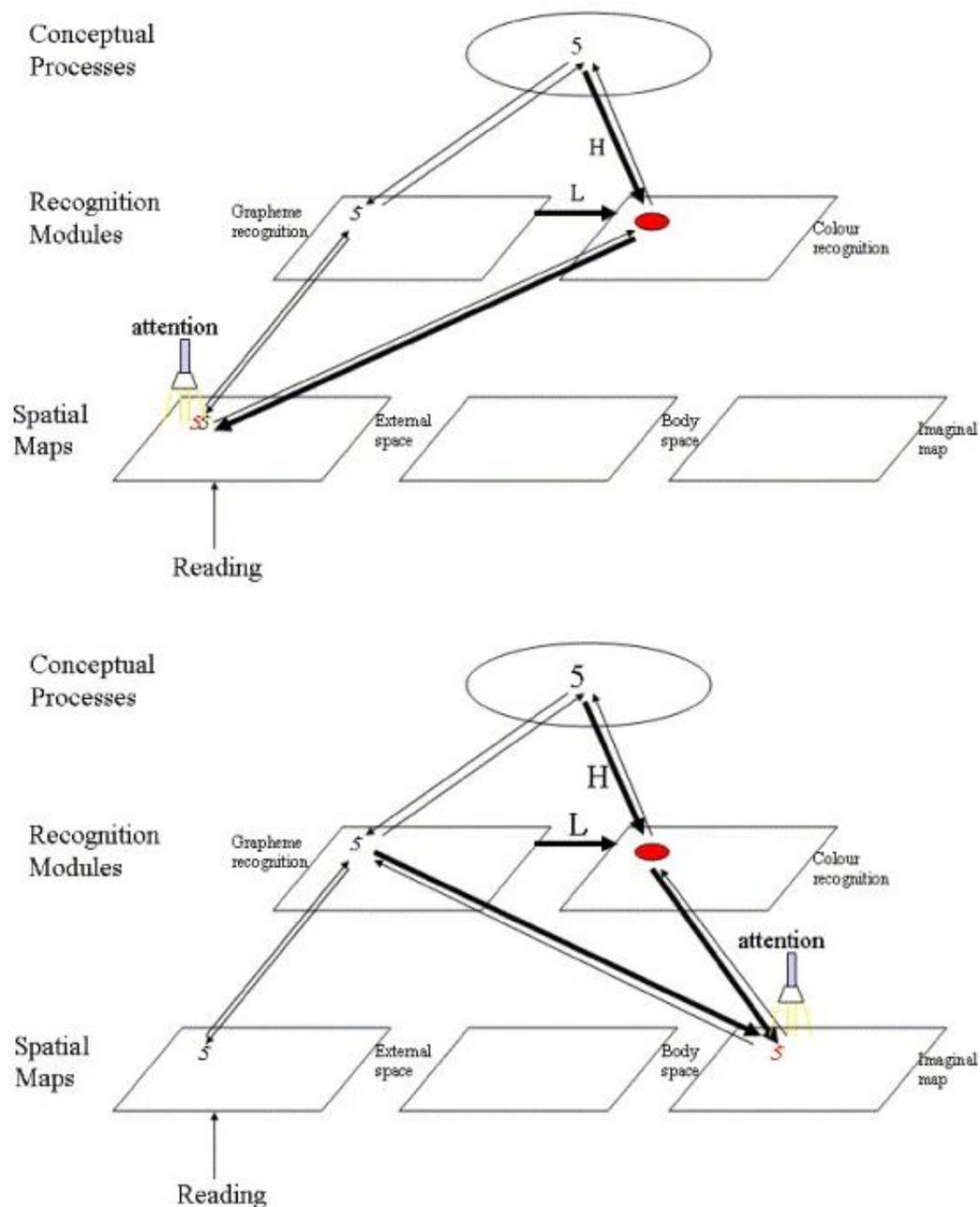
Palmeri et al. (2002) found that a synaesthete had a search time advantage over nonsynaesthete controls when the target and distractors induced different synaesthetic colours; though this advantage was not as strong as true pop-out. When the distractors did not induce synaesthesia but

the target did, the synaesthete showed no advantage over controls. Palmeri et al. suggested the synaesthete's advantage resulted from being able to more quickly reject distractors. This hypothesis was tested by a study by Laeng et al. (2004). A synaesthete showed advantage over nonsynaesthetes when the target was near the central fixation, but not when the target was further away, in line with idea that the synaesthetes' advantage is not from pre-attentive pop-out, but from quicker rejection of distractors. Edquist et al. (2006) and Sagiv et al. (2006) failed to show any advantage for synaesthetes in visual search tasks, while Ward et al. (2010) and Rich et al. (2013) did find an advantage for synaesthetes in the Embedded Figures Task, though again not to the level of a true pop-out effect, indicating that the synaesthesia does not occur pre-attentively.

Ward et al. (2007)'s own conclusion is that attention is necessary for all kinds of synaesthesia, though there is a difference in the amount of attention required for projective and associative synaesthetes, and this difference explains the previous differing results. Specifically, surface-projectors are not required to shift attention between reference frames, because both the grapheme and the photism appear in the same place, while other types of synaesthetes may have to divide attention between the two.

The schematic diagrams in Figure 1.3, below, encapsulate these ideas, showing the different cognitive processes that give rise to the heterogeneity of synaesthesia, even within a given variant (grapheme-colour synaesthesia). The first part of the diagram shows surface-projectors, and the second part shows see-associators. When a letter is perceived (in external space), this leads to recognition of the grapheme (in the 'recognition module'). In lower synaesthetes, or perceptual synaesthetes, recognition alone is enough to trigger activation of a hypothetical colour

module. In higher, or conceptual synaesthetes, the recognition of the grapheme must lead to conceptual processing of the grapheme before the colour module is activated. For a surface-projector, this colour is then projected onto the grapheme perceived in external space. For a see-associator, the colour activation and the activation of the grapheme recognition model act together to cause the synaesthete to ‘see’ the coloured grapheme in imaginal space.



**Figure 1.3** Models depicting the various cognitive processes involved in different types of grapheme-colour synaesthesia. The top diagram depicts surface projectors while the bottom depicts see associators. For each, there are also distinctions between higher and lower synaesthesia (indicated by H and L respectively). Figure from Ward et al. (2007).

An important aspect of the model is that each activation pathway acts bidirectionally. This is included in the model to account for the implicit, and in some synaesthetes explicit, bidirectional nature of synaesthesia. Cohen Kadosh and Henik (2007) note that the difference is that the processes occur at different levels of awareness, so that explicitly bidirectional synaesthetes have a greater level of awareness of the cognitive processes than synaesthetes that are only implicitly bidirectional. This then leads to the idea that synaesthesia is not an all-or-nothing phenomenon, but a graded one. This ties in very well with the idea that even nonsynaesthetes do in fact have an implicit synaesthesia (see Section 1).

## **Underlying Biology**

### **Anatomical location.**

Several different models of the neural architecture of synesthesia have been proposed. All share the common idea, as shown repeatedly in neuroimaging studies discussed below, that synesthesia occurs when the relevant area associated with the concurrent is activated. In terms of the cognitive model for grapheme-colour synesthesia discussed above, the brain area that processes the concurrent is the 'colour recognition module'. In the cognitive model, the grapheme is processed, either perceptually or semantically, and this leads to activation of the hypothetical colour recognition module. This section addresses the question of the anatomical areas involved in this activation.

The most prevalent model, known as direct cross-activation, posits that activity in the area

associated with the inducer directly causes activation in the concurrent area, via direct axon connections. In general, this presumes areas for the inducer and concurrent are cortically adjacent, and several examples of direct cross-activation have been hypothesised in this way for specific kinds of synesthesia. For example, it is hypothesised that lexical-gustatory synesthesia involves the anterior insula, related to speech production and perception, directly causing activation in the adjacent primary gustatory area (Jones et al, 2011). In the same way, auditory word-to-taste synaesthesia may involve the insula (taste processing) causing activation in the superior temporal or frontal cortex, which processes auditory word comprehension.

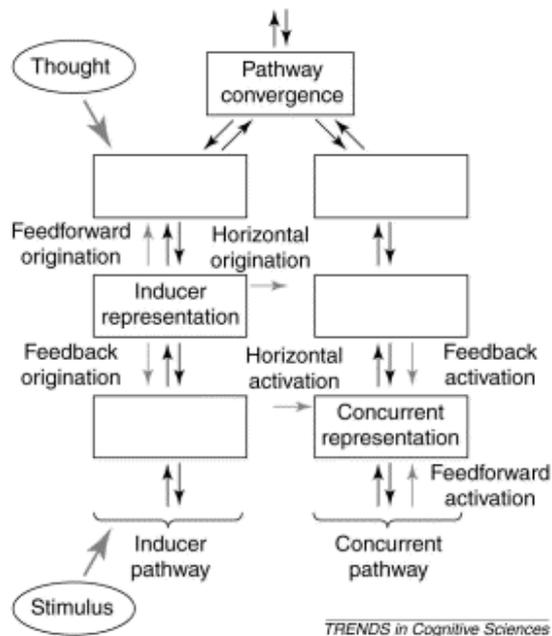
Ramachandran and Hubbard (2005) point out that that the area for recognising visual words is the fusiform gyrus (particularly the left) is adjacent to the area for processing colours, and so synaesthesia could be caused by cross-activation of these areas in a similar way that phantom limbs arise due to cross activation of face and hand representations.

For more unusual types of synaesthesia, it could be that the usual connections between distant functional modules (such as primary auditory cortex and V4) are enhanced (Ramachandran and Hubbard, 2005). Some synaesthetes have colour associations with higher numerical concepts, such as days of the week, or months of the year. The angular gyrus is probably responsible for the ability to work with sequences and ordinality, as patients with lesions to the angular gyrus often express problems with arithmetic (dyscalculia), and this area is involved in processing numerical quantities (e.g. Rickard et al., 2000) and abstract spatial maps (see Burgess, Jeffery & O'Keefe, 1999). The angular gyrus is located close to the colour areas that are higher in the colour processing hierarchy (areas that receive input from V4), so it may be that cross activation between these areas can cause this kind of synaesthesia. Also, many synaesthetes experience

numbers as forming 'curvy lines' or shapes in space, which may be due to cross activation between the angular gyrus (numerical sequence) and the posterior superior parietal lobe (representations of space) (Ramachandran and Hubbard, 2005).

An alternative to direct cross-activation is a re-entrant processing model, in which top-down feedback connections cause activation of the concurrent area (Smilek et al, 2001). This model only fits those kinds of synesthesia where the inducer and concurrent are part of the same sensory processing stream (such as the visual sight of letters causing an experience of colour).

Neither of these models account for kinds of synaesthesia where the inducer and the concurrent are part of different sensory processing streams. In addition, the direct cross-activation model is very parsimonious, but does not provide a universal explanation of synesthesia, as for many forms of synesthesia the hypothetical brain areas associated with processing the inducers and concurrents are simply not adjacent. A third model, proposed by Grossanbacher and Lovelace (2001) accommodates these limitations by positing that when the concurrent and inducer areas are in different processing streams, activation may be via a multisensory nexus, where these pathways converge (see Figure 1.4). This model however does not take into account differences between conceptual and perceptual inducers.



**Figure 1.4** A schematic model for the anatomical areas involved in synaesthesia. The area that processes the inducer may cause activation in the area that processes the concurrent via a point of pathway convergence, at the multisensory nexus. From Grossanbacher and Lovelace (2001).

Finally, there is a ‘hyperbinding’ model, which suggests that synaesthesia is caused from an over-activation of parietal binding activity; so that extra features (such as the photism in grapheme-colour synaesthesia) are bound to the inducing object. Many forms of synaesthesia are not experienced as binding (for example when a word has a taste; these are two qualities that do not act as possible features to be bound in classic binding), but for forms where binding could be said to take place, such as surface-projective grapheme-colour synaesthesia, hyperbinding could act in addition to other mechanisms to give rise to this perception.

These models are not mutually exclusive, and each has merit for different variants of

synaesthesia. Therefore all may be ultimately correct. However, the genetics of synaesthesia suggests a universal mechanism, as a predisposition for synaesthesia in general, rather than specific forms of synaesthesia. The lack of a single universal model of synaesthesia is an issue yet to be resolved.

### **Physiological mechanism.**

Separate from the question of which brain areas synaesthesia involves, is the question of the physical nature of the connections between the relevant areas. Broadly, there are two possible ways for the connections to be made. The first is that there is a hard-wired difference between synaesthetes' brains and nonsynaesthetes' brains, taking the form of extra anatomical projections. The second is that the differences are not anatomical, but functional, with synaesthetes having a disinhibition of activation.

The first option could occur due to inhibited early childhood pruning of cortical connections, or due to extra growth, or both. It has been suggested that all babies experience synaesthesia (Maurer and Mondloch, 2005), so that pruning of cross-modal cortical connections could cause the loss of synaesthesia. If pruning were inhibited, the synaesthesia would not be lost. The prenatal monkey brain has connections from the inferior temporal lobe to V4 that are later pruned (Kennedy, Batardiere, Dehay & Barone, 1997). In humans, this could be the basis of coloured-number synaesthesia. Of course, some mechanism would need to be in place so that once one number-to-colour link is learnt, the number does not become linked to another colour as well, and vice versa (Ramachandran, Hubbard and Butcher, 2004).

Synaesthesia could also occur if there is disinhibited feedback of top-down connections between functional modules (Grossanbacher and Lovelace, 2001; Cohen Kadosh and Walsh, 2006). Such a disinhibition could explain drug-induced synaesthesia, and also provides a connection with the disinhibition of schizophrenia, another condition in which perceptions not normally experienced by others occur.

Cohen Kadosh, Henik, Catena, Walsh and Fuentes (2009) utilised the fact that posthypnotic suggestion has been used to modulate cortical inhibition, and used post-hypnotic suggestion to successfully induce grapheme-colour synaesthesia in subjects that had no congenital synaesthesia. This research provides very strong evidence for the disinhibition hypothesis, as it is not possible that the subjects grew extra anatomical connections over the course of the study.

On a final note, it has been suggested that the amount of abnormal connection, however it comes about, could be directly correlated to the degree of awareness of the experience of synaesthesia, discussed above (Cohen Kadosh and Henik, 2007).

### **Neuroimaging studies**

Over the past decade, neuroimaging techniques have been employed more and more in the study of synaesthesia, affording considerable advances in the understanding of its neural substrates.

There are two main themes to these studies. The first major aim has been establishing the

anatomical location of the experience of synaesthesia. The second major aim has been looking at timing of neural events in synaesthesia.

### **Anatomical correlates of synaesthesia**

A focus of neuroimaging studies has been to test the hypothesis that the brain area activated during the processing of usual perception is also that activated during synaesthetic experiences of a similar perceptual nature. Specifically, since the research has focused on synaesthesia with colour concurrents, research has sought to confirm that the V4 area, thought to be responsible for colour processing, is also active during a synaesthete's experience of photisms. Several studies have produced results that appear to be consistent with this hypothesis.

The first imaging study of synaesthesia used positron emission tomography (PET) to study synaesthetes with colour concurrents for heard words. It was found that synaesthetes showed activation of the visual association cortex when hearing words, but not in the lower visual cortex, including V1, V2, and V4 (Paulesu et al., 1995).

Weiss, Shah, Toni, Zilles and Frink (2001) extended this further by directly comparing activation when viewing coloured images, and when experiencing colour synaesthetically. In the first functional magnetic resonance imaging (fMRI) study of synaesthesia, it was found that the synaesthetic subject had bilateral V4 activation when viewing coloured images (as did nonsynaesthete controls), while the experience of synaesthesia showed different activations. Synaesthetic experience was found to be mediated by secondary visual areas, interacting with the

retrosplenial cortex.

In 2002, Nunn et al. used fMRI to compare synaesthetes and nonsynaesthete controls as they listened to spoken words and tones. The synaesthetes had synaesthesia for the words, but not tones. Accordingly, the synaesthetes, but not controls, showed left V4 activation for the word stimuli. V4 is the area activated when processing colour. An important finding in this study was that synaesthetic colour experience is not associated with processing earlier in the visual stream, such as in area V1. This is significant as it is in contrast to all real visual processing, which always involves processing in these areas before colour is processed.

In 2003, Elias, Saucier, Hardie and Sarty used fMRI to compare the brain activation of a synaesthete, nonsynaesthete controls, and a semantic control without synaesthesia that had well-learned colour-number associations. The subjects performed various tasks that involved Stroop and cognitive priming effects. The synaesthete showed more activation in the left dorsal visual stream for some of the tasks, but did not show significantly different brain activation from controls during the Stroop task. In addition, the behavioural results showed that the synaesthete and the semantic control performed comparably on the tasks, showing that it is not possible to distinguish synaesthesia from well-learned associations based on behavioural results.

The experience of synaesthetic colour was again shown to be associated with activation of colour-processing areas, by Hubbard et al. (2005). Grapheme-colour synaesthetes showed larger activation in V4 than nonsynaesthete controls when viewing graphemes. Intriguingly, among the synaesthetes there was also a positive correlation between the extent of this activation, and the

‘strength’ of the synaesthesia, as assessed by behavioural responses to various visual perception-based tasks. An important outcome of this study was this demonstration of the heterogeneity of synaesthesia.

In 2006, Steven, Hansen and Blakemore in a fascinating study showed that even in an individual who was no longer able to see, the experience of synaesthetic colours was akin to a visual experience. The late-blind coloured-hearing synaesthete showed hV4 activation during synaesthetic colour experiences, while colour imagery activated a region anterior to this, as it does in nonsynaesthetes.

Rich et al. (2006) tested the hypothesis that synaesthetic colour experience is neurally equivalent to colour imagery. Using fMRI to compare grapheme-colour synaesthetes and matched nonsynaesthete controls, they found that for both groups, colour imagery activated the right V4 area. Synaesthetic colour experience on the other hand showed activation in the left medial lingual gyrus, an area known to be involved in colour-knowledge related tasks. This study demonstrated conclusively that colour imagery and synaesthetic colour experience are mediated by different neural areas.

Sperling, Prvulovic, Linden, Singer and Stirn (2006) compared the effect of graphemes that did and did not induce photisms in synaesthetes. The inducing letters produced higher activation in V4, in both hemispheres, than the non-inducing letters. In their discussion, Sperling et al. discussed the limitations of fMRI studies, noting that it reveals nothing about the chronological order of cortical activation, and stressing the need for imaging techniques with higher temporal

resolution: “a challenge for future studies of synaesthesia will be the identification of the pathways that mediate this activation of early visual areas and to determine whether this coactivation occurs before or after semantic decoding of the colour inducing stimuli” (Sperling et al., 2006, p301).

### **Connectivity**

Collectively, these imaging studies suggest that activation in the colour processing area, V4, is indeed associated with the synaesthetic colour experience. A study by Hupe et al. (2011) tested this hypothesis directly. In this paper, Hupe widely criticised previously published papers about the use of fMRI in synaesthesia research, arguing that there were major flaws in the analysis methodology, including incorrectly identifying participants’ colour processing centres and using statistical criteria that were too liberal. Hupe et al. used fMRI to individually evaluate each participant’s colour centre to more accurately compare synaesthetic colour and real colour experience. Colour areas for each individual were first defined via retinotopic mapping and as the cluster of fusiform gyrus that maximally responded to coloured Mondrians. The synaesthetes’ colour areas were not activated by synaesthetic colours, and in addition, voxel-based morphometry showed there were no white or grey matter differences in those areas between synaesthetes and controls. Synaesthetes did however show increased white matter in the bilateral retrosplenial cortex (RSC).

The RSC is implicated in emotion processing, and has both functional and anatomical links with the memory system (Maddock, 1999), as well as to the V4 area (Koboyashi and Amarel, 2007).

Hupe et al. (2011) suggested therefore that it is increased connectivity, rather than comparing colour areas, that is the key to understanding the neural correlates of synaesthesia. A few recent studies have investigated this further.

### **Structural connectivity.**

A number of studies have examined structural differences in the brains of synaesthetes. Using diffusion tensor imaging (DTI), Rouw and Scholte (2007) found that synaesthetes showed greater anisotropic fusion, implying increased connectivity (that is, greater amounts of white matter) than nonsynaesthete controls in the superior parietal, frontal, and inferior temporal cortex. A particularly interesting result from this study was that among the synaesthetes, those who experienced their synaesthetic colours as external colours, rather than in the mind's eye, showed greater connectivity. Jancke et al. (2009) did not find any connectivity difference between synaesthetes and controls, but did find increased grey matter in colour sensitive areas, consistent again with the hypothesis that these regions are responsible for synaesthesia. Weiss and Fink (2009) got the same result, but Rouw and Scholte (2010) and Hanggi et al. (2008) did not.

Banissy et al. (2012) used voxel-based morphometry (VBM) to examine whether grapheme-colour and tone-colour synaesthetes had differences in grey matter volume from nonsynaesthetes. They found that synaesthetes had greater grey matter volume in the left posterior fusiform gyrus, but also less such volume in the anterior fusiform gyrus and left medial temporal/V5 area. This demonstrates that synaesthesia is linked to neuroanatomical changes between adjacent regions of the visual system.

### **Functional connectivity.**

Transcranial magnetic stimulation (TMS) was used by Esterman, Verstynen, Ivry and Robertson (2006) to see if it could disrupt the synaesthetic Stroop in grapheme-colour synaesthetes. It was found that synaesthesia was disrupted when TMS was applied over the right parietal lobe. Muggleton, Tsakanikos, Walsh and Ward (2007) extended this by applying TMS over four parietal sites, posterior and anterior areas of the parietal lobe in both hemispheres. It was found the synaesthesia was disrupted when applied over the right posterior parietal lobe, but not over the more anterior position or on the left hemisphere. It was proposed that the right posterior parietal area is involved in synaesthetic binding.

Two studies have also explicitly analysed the functional connectivity of synaesthetes. Neufeld et al. (2011) used fMRI to perform a functional connectivity analysis in auditory-visual synaesthetes. No differences were found in the connectivity of the audio cortex and the visual areas among controls and synaesthetes. There was stronger connectivity of the left inferior parietal sulcus with the left primary auditory and the right primary visual cortex. Dovern et al. (2012) analysed the resting-state functional activity of synaesthetes and nonsynaesthetes and found increased intranetwork connectivity at a global level, as well as in the medial and lateral visual networks to the right parietal network, which was correlated with the strength of synaesthesia.

## **Event Focused Studies**

In addition to the types of studies mentioned above, there have been a number of studies focusing on the timing of neural events in synaesthesia. An early study was conducted by Schlitz, Trocha, Wieranga, Johannes and Munte (1999) using event-related potential (ERP) analysis. ERPs of a group of digit-colour synaesthetes were recorded while they responded to visually presented digits. Compared to matched controls, the synaesthetes showed a more positive P300 waveform over frontal and prefrontal regions. The P300 is a positive waveform that occurs approximately 300 ms after stimulus onset, and is a relatively late component, and reflects postperceptual processes such as evaluating and categorising the stimulus (Kok, 2001).

In 2003, another ERP study by Sagiv, Knight and Robertson (2003) compared the waveforms of a congruent letter to an incongruent letter. In contrast to the Schlitz et al. (1999) study, it was found that recorded ERPs for the two stimuli diverged very early, at 150ms (subject 1) and 200ms (subject 2) post stimulus onset at posterior scalp sites. This is consistent with the N170 (i.e. a negative waveform that occurs approximately 170ms post stimulus onset), a component associated with the processing of graphemes (Bentin, Mouchetant-Rostaing, Giard, Echallier & Pernier, 1999).

The conflicting results of these two studies are elegantly explained by Cohen Kadosh, Cohen Kadosh and Henik (2007), who used ERP recordings in conjunction with fMRI to examine the neural correlates of a bidirectional colour-digit synaesthesia. The synaesthete performed numerical tasks, comparing two numbers, and size comparison tasks, comparing two triangles.

For both tasks, the stimuli were coloured in a way that was either congruent or incongruent with the synaesthete's synaesthesia. In the incongruent condition, the synaesthete must inhibit the interference caused by the synaesthesia. Accordingly, it is expected that this would cause greater activation. It was found that different brain areas were recruited for each task. In the numerical task, the intraparietal sulcus and the left angular gyrus were modulated by the congruity effect, along with the amplitude of the P300. This indicates an inhibition of the irrelevant stimulus, colour. In comparison, for the triangle task, the N170 was modulated along with the fusiform gyrus, indicating some number-processing.

Beeli, Esslen and Jancke (2008) recorded ERPs of coloured-sound synaesthetes as they listened to verbal stimuli, and used electric brain tomography to estimate the intracerebral sources of the components. Synaesthetes had larger latencies and lower amplitudes for the N1 and P2 components. From 122ms after the onset of the stimulus, synaesthetes showed stronger activation in the left posterior inferior temporal regions, and orbitofrontal brain regions. This activation is line with previous studies showing V4 activation, and demonstrates the very early processing associated with synaesthesia.

Brang, Edwards, Ramachandran and Coulson (2008) compared the ERPs of grapheme-colour synaesthetes and nonsynaesthetes while they read sentences where a colour-word was replaced by a digit, such as "looking very clear, the lake was a most beautiful hue of 7". The aim of this study was to determine whether the synaesthetes would regard the colour associated with the digit as a meaningful stimulus. If so, these sentences would sometimes be congruous, with the colour of the digit making sense in the context of the sentence (e.g. if 7 is blue), or incongruous

if it doesn't fit (e.g. if the 7 is yellow). For congruous sentences, the synaesthetes showed a more negative N1 component, a less positive P2 component, and a less negative N400 component. The congruity of the synaesthetic digit colour effected brain response as early as 100ms after the stimulus was presented. This is very early in the visual processing stream, indicating that synaesthesia is highly automatic, and can affect the higher-order aspects of visual processing, such as meaning-integration processes.

Over all, the neuroimaging studies of synaesthesia have served to verify and extend conclusions drawn from behavioural studies. In addition, areas devoted to earlier visual processing are not associated with synaesthesia. Imaging studies have also demonstrated that synaesthesia is different from imagery, it is associated with hyperconnectivity, it is heterogeneous in nature, and is associated with very early cognitive processing.

### **Thesis outline**

Chapter 1 has been an introduction to the study, including a discussion of the significance of synaesthesia and a literature review. As stated above, the general goal of the thesis is to add to the understanding of the cognitive neuroscience of synaesthesia. This thesis involves three experimental studies, using different research methods. Chapter 2 is a behavioural study designed to investigate how the synaesthesia of grapheme-colour synaesthetes affects the colour to letter binding that normal vision entails. In Chapter 3, an EEG study is discussed, examining the brain activity of grapheme-colour synaesthetes when viewing congruent and incongruently coloured letters. In Chapter 4, a second EEG study, this time comparing brain activation of

grapheme-colour synaesthetes and nonsynaesthetes when viewing black-and-white letters, is discussed. Chapter 5 will conclude with an overall summary of the experiments, highlighting their main contributions, and include a discussion of their findings as a whole.

## **Chapter 2: Experiment 1: Visual Binding in Synaesthetes**

### **Introduction**

Information entering the visual system, such as color, shape, and motion, is processed in functionally independent channels of information (Bartels & Zeki, 1998; Livingstone & Hubel, 1988; Zeki & Bartels, 1998). For instance, in the V2 and V4 areas, some neurons selectively respond to object orientation independent of color, while others respond to color independently of shape (Livingstone & Hubel, 1988), and temporal asynchronies have been shown between the processing of different features, such as color and orientation (Moutoussis & Zeki, 1997a, 1997b; Viviani & Aymoz, 2001). Despite this functional segregation of feature processing, we perceive unified objects, with features of color, shape, and motion bound together. The question of how this binding of features is achieved has become known as the binding problem.

An early insight into the binding problem was that attention is necessary for binding to occur. According to Feature Integration Theory (FIT), in cases where insufficient attention is applied, features of objects may be bound incorrectly, producing binding errors, or illusory conjunctions (Treisman & Gelade, 1980). For example, Treisman and Schmidt (1982) presented participants with displays of three letters, each colored differently. Flanking the colored letters, were two black digits. The participants had to report the digits, and then describe the letters they had seen. The participants frequently reported illusory conjunctions, mismatching the shape and color of the letters.

Wheeler and Treisman (2002) described a model for visual feature binding in which visual

feature representations are different from representations that code for the *association* between visual features. However, working memory and visual perception recruit the same limited neural resources, i.e. attention, which may induce errors in these processes when the working memory has been loaded above capacity. During experiments that induce binding errors in visual perception, such as the one mentioned above, the illusory conjunctions occur because the working memory has been overloaded to the point that it is unable to maintain the representation of the association between the visual features. Under this model, synaesthetes can be thought of as having permanent association representations.

Much research on the cognitive processes of synaesthesia has focused on the extent to which a synaesthetic inducer (such as a grapheme) must be processed in order for the photism to be induced. The literature on this is conflicted, but there is a growing consensus that photisms are elicited only after attention is given to the inducer (e.g. Edquist, Rich, Brinkman, & Mattingley, 2006; Mattingley, Payne, & Rich, 2006; Sagiv, Simner, Collins, Butterworth, & Ward, 2006). Cases in the literature that suggest to the contrary have been explained by the heterogeneity of the synaesthetic experience, or by methodological issues (see Laeng, Svartdal, & Oelmann, 2004). Assuming, then, that attention is required for both the induction of photisms in synaesthesia, and for normal visual binding, the present study was designed to examine the role that synaesthesia might play in visual binding. Further, both binding and the induction of photisms are experienced as occurring instantaneously. The question is how they interact. I asked two specific questions. First, in cases where there is a binding error and an illusory conjunction occurs, does synaesthesia influence which combination of letter to color is incorrectly bound? The second question is whether synaesthesia influences binding itself. That

is, will letters presented in their synaesthetically congruent colors be less prone to binding errors?

To test this, I adapted Treisman and Schmidt's (1982) paradigm for inducing illusory conjunctions. I presented synaesthetes with displays of three letters, with each letter a different color. The colors assigned to the letters were drawn from the group of colors synaesthetically corresponding to the letters used in the experiment. Following each display, one of the letters was presented again, either in the same color or a different color. Participants had to report whether or not this single letter had appeared in the same color in the preceding three-letter display.

## **Methods**

### **Participants**

Eight grapheme-colour synaesthetes (7 female, mean age = 38.6 years, SD = 16.3 years, range: 23 - 68 years), and 8 non-synaesthete controls (7 female, mean age = 35.8 years, SD = 16.3 years, range: 23 - 61 years) participated in this study. All synaesthetes had previously demonstrated consistent letter to color associations, across a minimum test interval of 3 weeks. All synaesthetes, when questioned closely, described their synaesthesia as associative rather than projective. The controls were matched for sex and age. The mean ages of the groups were not significantly different,  $t(7) = -1.48, p > .05$ . All participants gave informed consent and had normal or corrected-to-normal vision.

## **Stimuli**

Five synaesthetes were tested at the University of Melbourne, with stimulus presentation and data recording controlled by E-Prime running through Windows XP Pro on a Pentium M Centrino 1.6 GHz computer. Stimuli were presented on a 17-inch Dell CRT monitor with a vertical refresh rate of 75 Hz. The remaining participants were tested at the University of Auckland, with a Pentium 4 3.4GHz running E-Prime and stimuli presented on 17-inch Dell LCD monitor with a vertical refresh rate of 75 Hz.

The synaesthetes indicated on a RGB color palette their colors for each letter of the alphabet. They gave each selected color a rating on a scale of 1 (very poorly matched) to 5 (perfectly matched) of how closely matched the selected color was to their synaesthetic experience for that letter. For each synaesthete, 5 letters were selected with the criteria that the colors were easy to visually discriminate and had a rating of 4 or 5.

Forty display stimuli and 40 corresponding probes were constructed for each synaesthete. Each display stimulus consisted of 3 different letters, drawn from the set of 5 selected for that synaesthete. To construct 40 such displays, first 10 different 3-letter combinations were chosen. For each combination, 4 unique stimuli were constructed by varying the positions of the letters. Overall, each letter appeared an equal number of times, and the letters were equally likely to appear in each position. Each letter in the stimulus was colored differently, with colors drawn from the set of 5 colors corresponding to the 5 letters selected for that synaesthete. In each display stimulus, 1 letter was colored in the congruent synaesthetic color, 1 letter was colored

incongruently in a synaesthetic color for one of the other letters present, and the third letter was colored incongruently in any of the 3 remaining colors. The stimuli were balanced so that each letter appeared in its congruent color an equal number of times.

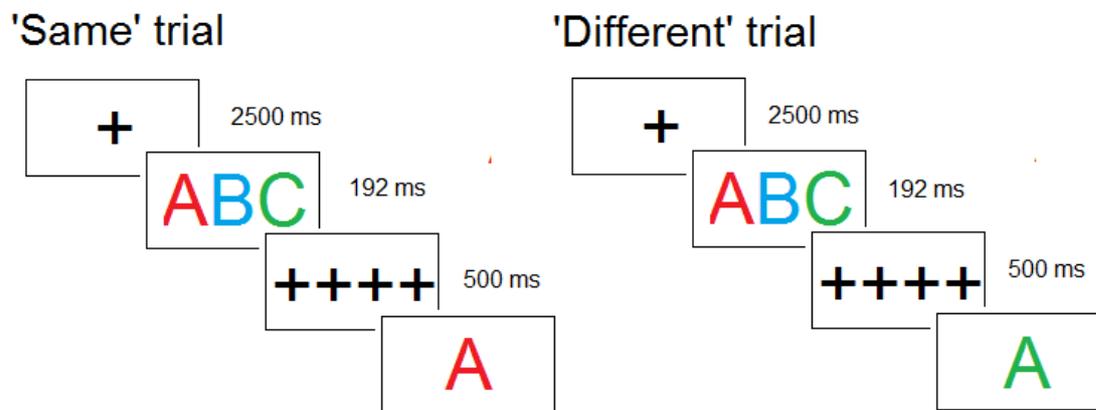
The probe consisted of a single letter that had appeared in the corresponding display, and was selected so that its synaesthetic color had been present in the display. The probe letter appeared as one of four possible conditions: it was either colored in a synaesthetically congruent color, or not; and it was either colored the same as it was presented in the 3-letter display, or not. This produces a 2X2 design with the crossed factors congruency and presence. In addition, the probe was always colored with one of the colors that had appeared in the 3-letter display.

Each synaesthete participated in the experiment with stimuli thus tailored to their own synaesthesia. Each control participated in an experiment with identical stimuli to the synaesthete they had been matched to, in a yoked design.

## **Procedure**

Each trial began with a fixation cross shown for 2500ms. This was replaced by the display stimulus, presented for 192ms. The display was replaced with a row of crosses, of the same visual angle as the display, for 500ms, followed by the probe. Subjects pressed '1' if it was colored the same as in the display and '2' if it was different (see Figure 2.1 for example trial).

Once this response was made the next trial commenced immediately. The trials were completed in 3 blocks of 160 trials each, with short breaks in between blocks. Overall, each of the 40 displays and corresponding probes were presented 12 times, for a total of 480 trials.



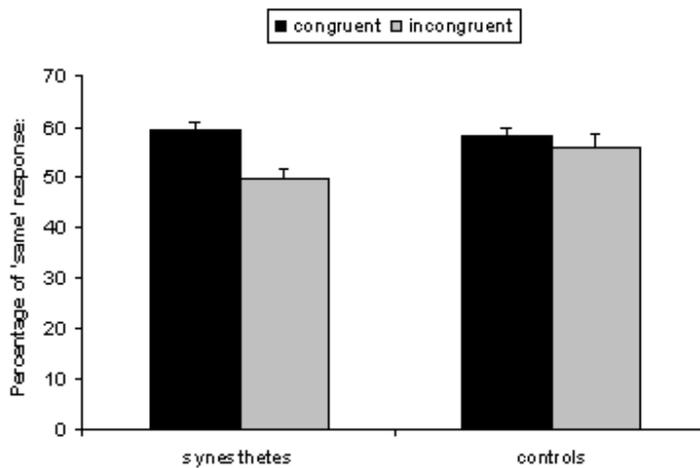
**Figure 2.1** Examples of trials with ‘same’ condition and ‘different’ condition.

## Results

The mean number of errors per participant was 71 of 480 trials (14.8%) (SD 40.18). There was no significant difference between the number of errors for synaesthetes (M 76, SD 44.12) and controls (M 66, SD 38.17),  $t(7) = .421, p > .05$ . Table 2.1 shows the mean accuracy percentage for each condition for each group.

A repeated-measures ANOVA was conducted on the number of “same” responses participants made, with congruence, presence and whether the participant had synaesthesia or not as factors. The main effect of presence was highly significant,  $F(1, 7)=399.26, p<.001$ , indicating that overall the participants scored well above chance. The triple interaction between presence, congruence, and synaesthesia did not approach significance,  $F(1, 7)=0.91, p=.371$ , indicating that congruence did not affect accuracy differentially in synaesthetes and nonsynaesthetes. Presence did not interact significantly with any of the other variables.

Although the independent variables had no significant influence on accuracy, there was a significant main effect of congruence on the frequency of “same” responses,  $F(1, 7)=22.97$ ,  $p=.002$ , indicating fewer “same” responses to incongruent than to congruent stimuli. However, congruence interacted significantly with synaesthesia,  $F(1, 7)= 5.72$  ,  $p= 0.048$ . To examine this interaction, post-hoc comparisons were conducted. Synaesthetes gave significantly more “same” responses to congruent probes than incongruent probes,  $F(1, 7)= 55.54$ ,  $p<.001$ , while nonsynaesthetes did not show significant differences between these conditions,  $F(1,7)=1.079$ ,  $p=.334$ . For congruent stimuli, there was no significant difference between synaesthetes and nonsynaesthetes  $F(1, 7) =1.123$ ,  $p=.736$ . For incongruent stimuli, the difference is closer to significance  $F(1,7)= 1.734$ ,  $p=.229$ . These comparisons lack statistical power, however, because they are between rather than within individuals. Note that these are not within group comparisons, and so are subject to larger error terms due to the large variation between individuals. Taken together, these results indicate that the key difference between synaesthetes and nonsynaesthetes is that the synaesthetes were less likely to respond “same”, or equivalently, more likely to respond “different”, to incongruent stimuli.



**Figure 2.2** Mean percentage of 'same' responses (+ 1 s.e.) to congruent and incongruent stimuli for synaesthetes and controls.

**Table 2.1**

**Mean Percentage of Accurate Responses for Synaesthetes and Nonsynaesthetes to Stimuli in Each**

**Condition**

	Same, Congruent	Same, Incongruent	Different, Congruent	Different, Incongruent
Synaesthetes	84.2	75	85.4	92
Nonsynaesthetes	86.5	80.9	89.5	88.1

**Discussion**

The principal aim of this study was to examine how synaesthesia may influence binding and binding errors. Synaesthetes and nonsynaesthetes differed in the patterns of their binding errors, although they did not differ in the number of errors made overall.

There are two important conclusions. First, synaesthetes show a response bias to incongruent stimuli, in that they are more likely to deny the presence of incongruent stimuli than of congruent stimuli. This bias is independent of any effect on accuracy. This result is consistent with the idea that visual working memory, and visual perception, use the same neural resources (attention), and thus can influence each other. Kang, Wook Hong, Blake and Woodman (2011) demonstrated an example of this employing the motion repulsion effect. In this study, participants had to estimate the direction a set of dots were travelling, while at the same time maintaining in working memory the direction of another set of dots. The working memory was overloaded to an extent that errors were made, and it was found that participants biased their estimates away from that maintained in working memory, in a repulsion effect. The current results are analogous to this. The synaesthetes' working memory held the synaesthetically congruent pairing of the probe, and they then made their decisions in opposition to this.

The second conclusion is that synaesthesia does not affect the accuracy of the identification stimuli. Synaesthetes are just as likely to make errors perceiving congruent stimuli as they are for incongruent stimuli. This is consistent with the idea that photisms are only induced after attention has been allocated and the letter has been identified; so synaesthesia can have no influence unless attention is applied, in which case a binding error is unlikely to occur anyway. This result also allows us to draw conclusions about the interaction of normal color vision and synaesthetic color experience. Clearly, synaesthesia does not influence the competition among color features to bind to a given letter, and so synaesthetic color does not act as a robust primary visual feature in the same way that actual color does.

The result also implies that real and synaesthetic color perception are mediated by different neural mechanisms. Much synaesthesia research has been geared towards demonstrating that synaesthetic color associations are perceptual rather than merely memory-based, and imaging studies have achieved this by finding equivalent neural activations for both kinds of color experience. Hubbard, Arman, Ramachandran, & Boynton (2005), Nunn et al. (2002), and Sperling, Pruvolic, Linden, Singer, & Stirn (2006) found that experience of synaesthetic color is associated with activation of the V4 area. However, the most recent imaging study of this kind finds that the two are not exactly alike, with synaesthesia color perception being associated with a more medial locus of the left lingual gyrus (Rich et al., 2006). The latter study used more participants, as well as different analysis methods, providing greater statistical power, but the discrepancy is yet to be fully explained. While this issue is unresolved, our finding is consistent with the idea that synaesthetic color experience is not as robust as true color vision.

Finally, it should be noted that all the synaesthetes that participated in this study were associators rather than projectors, and it is possible that the conclusions here do not apply to projectors. However, this is true of the majority of synaesthesia studies as projective synaesthesia is very rare (Simner et al., 2006). Specifically, because projective synaesthesia is an experience much more akin to normal color vision, we could expect that it requires more attentional resources, and thus means the visual working memory is more likely to fail, and so projector synaesthetes would make more binding errors than either controls or associator synaesthetes. It would be interesting to test self-declared projective synaesthetes in the current experiment as a gauge of the extent to which projector synaesthesia is like normal colour vision.

In this study I have shown that synaesthesia did not influence the accuracy perceptual binding. However, there was a response bias, with synaesthetes more likely to report the presence of incongruent stimuli. In addition, the short-term memory of the real colour of the grapheme persists in spite of the synaesthetic colour being induced. Experiment 2 will examine the neural event-related activity that occurs when graphemes are presented in their synaesthetic colour compared to incongruent colour.

## **Chapter 3: Experiment 2: ERP Correlates of Congruent and Incongruent Graphemes in Synaesthetes**

### **Introduction**

The study of synaesthesia has in recent years grown from clarifying the fundamentals of synaesthesia through behavioural studies, and research has now extended to the use of neuro-imaging methods including fMRI and DTI. While this latest step has proved fruitful, the vast majority of imaging studies have been focused on anatomical correlates of synaesthesia, using techniques that lack temporal resolution. What is needed in addition to anatomically focused studies is research into the timing of neural events associated with synaesthesia.

Thus far, there have been very few such studies, and they have often involved examining the event related potentials (ERPs) of synaesthesia-relevant cognitive tasks, or have compared the ERPs of synaesthetes experiencing synaesthesia to those of nonsynaesthetes. These comparisons can be problematic given evidence that synaesthetes and nonsynaesthetes may have different ERPs even for non-inducing stimuli (Barnett et al., 2008), and that task specificity can account for differing results (Cohen Kadosh, Cohen Kadosh & Henik, 2007).

In synaesthetic Stroop tasks, stimuli that are synaesthetically incongruent yield longer response times than congruent stimuli, mirroring the results of the classic Stroop task. Several studies have examined the neurophysiological correlates of the synaesthetic Stroop effect, but always within the context of a task. Two such studies, Bien et al. (2012) and Terhune et al. (2010) employed TMS and posthypnotic suggestion respectively to effectively ‘turn off’ the innate pairings held

by the participants. This served to eliminate the behavioural synaesthetic Stroop effect, and to change some of the ERP signatures of incongruence: the N400 effect was erased, but the earlier differences were not.

The aim of this study is to compare the ERPs that occur when grapheme-colour synaesthetes view congruent and incongruently coloured letters without the context of a related task, to test whether the differences occur earlier or later in the processing stream.

## **Method**

### **Participants**

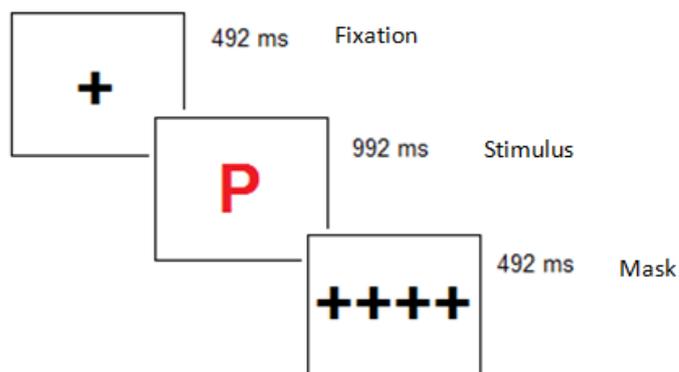
Six synaesthetes (5 female, 1 male) with associative grapheme-colour synaesthesia, and 12 yoked controls matched by age, sex, and handedness participated in this experiment. The mean age was 35 (sd 14.2), and all had normal or corrected-to-normal visual acuity. All were right-handed (self-declared). The experimental procedures were approved by the University of Auckland Human Subjects Ethics Committee, and all participants gave their informed consent to participate in the experiment.

### **Stimuli and procedure**

For each participant, the RGB colour coordinates of colours synaesthetically associated with each letter of the alphabet were obtained using Adobe Photoshop or Windows Paint. Each

participant was asked to pinpoint the correct colour to the best of their ability, and to give a rating out of 5 as to how well they felt the final colour represented their synaesthetic association. For each participant, a set of 5 letters were then selected from the range available such that each associated colour had a rating of 4 or 5, and each colour in the set was subjectively judged to be as visually different from the others as possible, based on the basic dominant colour. From each participant's set of letters, a range of stimuli were created, consisting of a single letter in upper case. Each of the five letters was shown in its corresponding colour 24 times and in each of the four non-corresponding colours six times, for a total of 120 congruent and 120 incongruent trials.

An experimental trial involved the presentation of a fixation cross for 492ms, followed immediately by the letter stimulus for 992 ms, followed by a masking stimulus for 492 ms (see Figure 1). Stimuli were presented in randomised order within a single block. Throughout the experiment, participants passively viewed the trials while seated comfortably.



**Figure 3.1.** Example of a single trial.

Stimuli were displayed on a SVGA computer monitor (1024 x 768 pixel resolution; 60Hz refresh rate) at a distance of 57cm. Stimulus presentation was controlled using E-Prime v1.1 (Psychology Software Tools). TTL pulses generated through the parallel port of the display computer provided synchronisation of stimulus events with EEG acquisition. Millisecond timing routines for the visual displays and pulse generation were conducted as outlined in the E-Prime User Guide (Psychology Software Tools).

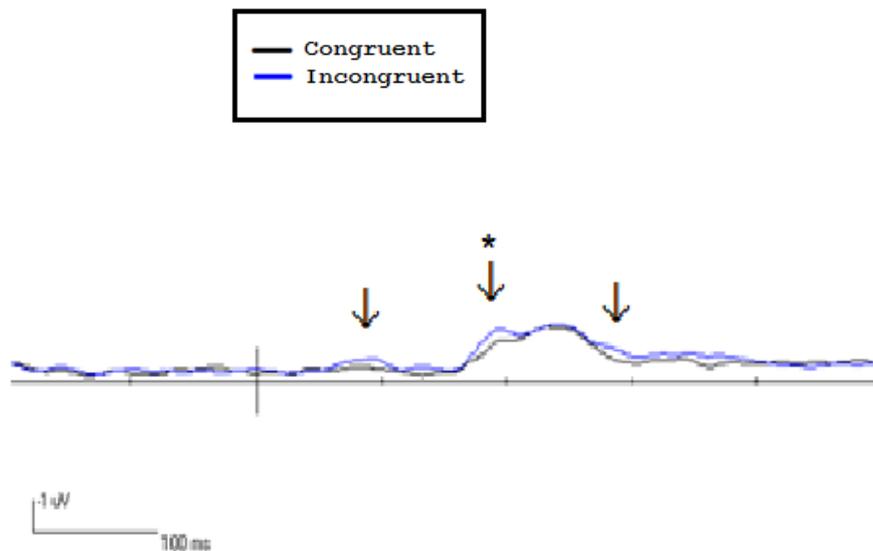
### **Electrophysiological recording**

EEG was recorded continuously (1000 Hz sampling rate; 400Hz Hz analogue band-pass filter using 128-channel Ag/AgCl electrode nets (Electrical Geodesics Inc., Eugene, OR, USA). All electrode impedances were below 50 k $\Omega$  (range 30 to 50 k $\Omega$ ), an acceptable level for this system (Ferree et al., 2001). The recordings took place in an electrically-shielded room. EEG was acquired using a common vertex (Cz) reference and later re-referenced to the average reference off-line.

### **Analysis**

EEG was segmented into epochs consisting of a 200ms pre-stimulus baseline and a 500ms period post-stimulus onset. DC offsets were calculated from the pre-stimulus baseline and removed from all waveforms. The data within each subject were then averaged according to condition (i.e. congruent and incongruent).

In an exploratory analysis time windows were selected by visually examining the global field power (GFP; Skandries, 1995) to identify peaks. Average amplitude across the time windows for each participant at each condition, for each electrode was obtained. For each electrode, t-tests were then conducted on the difference between conditions. Because of the large number of t-test involved, it was necessary to adjust the criterion level of alpha. Following the method of Hamm, Johnson and Kirk (2002), the correction to alpha was determined by conducting a principal components analysis (PCA) on the data. For each set of t-tests, the relevant data was subjected to a PCA, with the number of components revealed (i.e. those with eigenvalues greater than 1) then forming the correction factor for that set of t-tests. For example, if 10 principal components were revealed, the alpha level for that set of t-tests was adjusted to .005. After this correction factor is applied, it is still expected that on average 6.45 electrodes (ie.0.05 of 129) will produce significant results. To account for this an additional criterion was included, that the number of significant electrodes for a set of t-tests must significantly exceed 6.45 (at  $p < .05$ ), as tested by Chi-square tests.



**Figure 3.2.** Global field power for the two conditions for synaesthetes. Arrows indicates centre of the time windows. Vertical line indicates stimulus onset.

\* Marks significant difference between conditions.

## Results

For the GFP-determined time windows, 9 sets of t-tests were conducted in total. These were made up of 1) comparison of synaesthete-difference and control-difference, for all 3 time windows, 2) comparison among controls between the two conditions, for all 3 time windows, and 3) comparison among synaesthetes between the two conditions, for all 3 time windows. The results of the analysis of each set are given in Table 1.

Two sets of t-tests yielded significant electrodes above the critical number. These were the comparison between condition 1 and 2 among synaesthetes for the 180-190ms time window ( $\chi^2$

(1) = 412,  $p < .001$ ), and the comparison between condition differences for synaesthetes and controls, for 180-190ms time window ( $\chi^2$  (1) = 444.59,  $p < .001$ ).

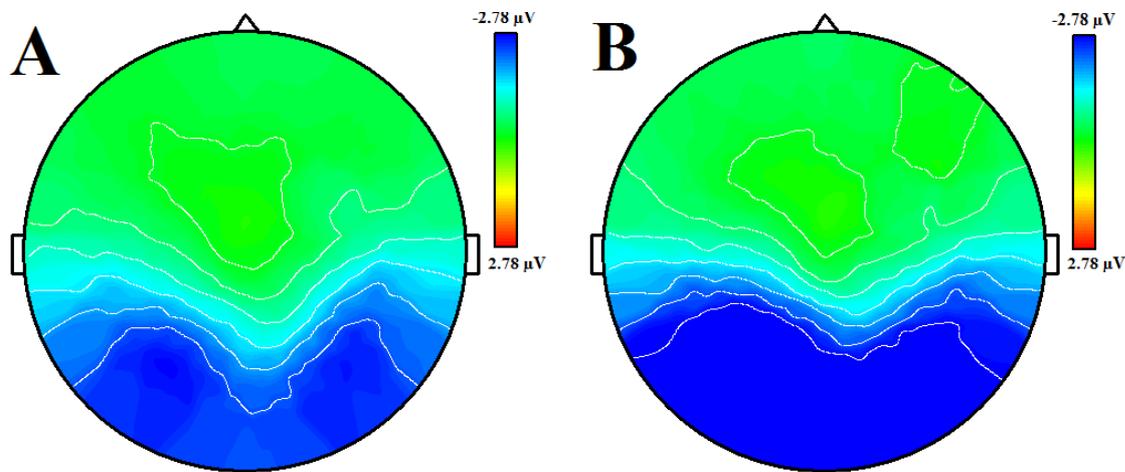
**Table 3.1**

**Correction Factors, Number of Significant Electrodes, Chi-Square Values ( $\chi^2$ ), and  $p$**

**Values, For Each Set of  $t$ -Tests**

	Time Window	Correction Factor	Significant Electrodes	$\chi^2$	$p$
Synaesthete	65-105ms	15	5	0.326	.568
difference vs. control	180-190ms*	14	60	444.59	<.001
difference	215-265ms	17	5	0.326	.568
Controls,	65-105ms	14	1	4.605	.032
congruent vs incongruent	180-190ms	13	0	6.45	.011
	215-265ms	11	2	3.07	.08
Synaesthetes,	65-105ms	10	2	3.07	.08
congruent vs incongruent	180-190ms*	8	58	412	<.001
	215-265ms	9	11	3.12	.073

\* denotes number of significant electrodes significantly exceeds 6.45



**Figure 3.3.** Topographic plots of the grand-averaged potential among synaesthetes for congruent stimuli (A) and incongruent stimuli (B) for the 180-190ms poststimulus onset time window.

### Discussion

The aim of the current study was to investigate the difference between the visual ERPs of associator synaesthetes, when presented with letters in their congruent and incongruent colours, in order to test whether differences occur earlier or later in the visual processing stream.

Nonsynaesthetes were also tested as controls. Among synaesthetes, the incongruent stimuli elicited a significantly more negative ERP than congruent stimuli in the 180-190ms poststimulus onset time window. This difference was also significantly different from the equivalent among controls. However, there were no significant differences found for later points in the processing stream.

The N200 component is linked to stimulus identification and distinction (Hoffman, 1990), and has various subcomponents, including a posterior N200 which has been found to index visual

mismatch (Czigler, Balazs & Winkler, 2002). Incongruent stimuli had a more negative N200 component than congruent stimuli. This result is consistent with a visual mismatch, indicating that synaesthetes responded to incongruently coloured letters as perceptually different from congruently coloured letters.

Bien et al. (2012) found a difference in parietal N1 amplitude between congruent and incongruent stimuli, with incongruent stimuli eliciting increased amplitudes. The Bien study was performed on nonsynaesthetes, and stimuli consisted of a tone and a visual stimulus of a grey circle, which together could make up a congruent trial (small circle with high pitch tone; large circle with low pitch tone) or an incongruent trial (small circle with low pitch tone; large circle with high pitch tone). Interestingly, TMS applied over the right parietal area did not affect this component, but did affect task performance and the P2 and N3 components. A similar result was achieved by Terhune et al. (2010), who recorded the ERPs of a face-colour synaesthete during a colour-naming task that involved congruent and incongruently coloured faces. Incongruent trials had greater P1 and N400 amplitudes. After posthypnotic suggestion to terminate the synaesthesia, the congruence variable no longer affected the behavioural results or the N400, but the difference in P1 between the two conditions remained. ERP components generated by the classic Stroop task also show a divergence of congruent and incongruent stimuli at a later point, at 300-450 ms (Markela-Lerence et al., 2004; Badzakova-Trajkov et al., 2009) and 450-550 ms poststimulus onset (Liotti et al., 2000), thought to reflect the detection or resolution of a conflict. Thus the result in the current study, and the earlier components difference found in the Bien study, reflect processes earlier than and unaffected by those involving task performance. This is again consistent with the suggestion that the current results reflect a perceptual mismatch.

My result is also similar to that of Brang et al. (2008), who found a negativity difference among grapheme-colour synaesthetes as early as 122ms poststimulus onset between congruent and incongruent graphemes. In their study, graphemes were presented at the ends of sentences, such that the colour induced by the grapheme could make semantic sense in the context of the preceding sentence (e.g. “The sky was 2”). Brang et al. suggested that the N1 difference they found reflected enhanced visual processing of contextually appropriate graphemes, i.e., the sentences served to prime the synaesthetes for certain numbers. However, the similar results between the current study and the Brang et al. study are probably unrelated; the context-related explanation does not apply to the current study, and the visual mismatch explanation does not apply to the Brang et al. study. One possibility is that both the current study and the Brang et al. study results reflect mismatch, even though the specific nature of the mismatch is different. This explanation does not hold up, because error detection effects are characterised by negativity occurring 80-100ms poststimulus onset, earlier than the effect found in the study.

Although the congruent and incongruent stimuli were each presented the same number of times, the instances of specific colour-letter pairings were unequal: congruent combinations appeared 24 times each, while incongruent combinations appeared 6 times each. This led to concern that the relative novelty of the incongruent stimuli, as opposed to their incongruency, could influence the results. For this reason, yoked controls were tested, to check for any effects independent of synaesthesia. The yoked controls showed no differences between the conditions, ruling out the possibility that the synaesthetes’ results were due to factors other than synaesthesia.

The visual processing of graphemes begins with the processing of visual features, such as shape

and colour, which is then followed by the increasingly higher order functions of binding, object identification, and deeper semantic processing. In Experiment 1, the results showed that the photisms of grapheme-colour synaesthesia in associator synaesthetes lack the saliency of basic visual features perceived by normal visual perception. This indicates that synaesthesia does not occur as early in the visual processing stream as the processing of visual features does; however the results of the current experiment indicate that synaesthetic processing occurs early enough in the processing stream that incongruencies are equivalent to perceptual, rather than semantic, mismatches. Thus we can conceive of synaesthetic processing beginning at a time point within the two soft boundaries of visual feature processing and semantic processing. In addition, grapheme-colour synaesthesia requires object identification of the graphemes to occur before it can take place.

In this study I have provided neurophysiological confirmation of the conclusion drawn from behavioural studies, that synaesthesia is a perceptual phenomenon, as opposed to a long term memory association. The following study, Experiment 3, will examine in more detail when the processing associated with the everyday experience of associative grapheme-colour synaesthesia takes place.

## **Chapter 4: Experiment 3: ERP Correlates of Inducing Graphemes in Synaesthesia**

### **Introduction**

As discussed in previous chapters, while the cognitive basis of synaesthesia has been studied by numerous behavioural studies, there has been a relative lack of studies investigating the neurophysiological correlates of synaesthesia, particularly with regard to the timing of neural events. In the effort to begin examining this aspect of synaesthesia, a first and obvious research question is “When viewing synaesthesia-inducing stimuli, what does a synaesthete brain do differently from a nonsynaesthete brain, if there is no task involved?” This basic question has been addressed using fMRI (for example Nunn et al. 2002; Elias et al., 2003; Hubbard et al., 2005; Rich et al., 2006; Tang et al., 2008), but only once by techniques with high temporal resolution. Schlitz et al. (1999) used EEG to compare the ERPs of digit-colour synaesthetes and matched controls as they viewed digits. The synaesthetes had more positive P300 waveforms, suggesting additional effort evaluating the stimuli.

In the current experiment, this research is extended by applying the same concept to grapheme-colour synaesthesia. Grapheme-colour synaesthetes and matched nonsynaesthete controls were presented with achromatic letters that elicit colour associations for the synaesthetes. To more thoroughly examine possible differences in processing between synaesthetes and nonsynaesthetes, stimuli were presented in either the upper or lower visual fields. Visual ERPs to upper and lower visual hemifield stimuli have typical differences, with the latter stimuli producing smaller P1 and larger N1 amplitudes (Qu et al., 2006). The aim was to examine

whether the differences between the two are the same for synaesthetes as for the controls. The following analysis was exploratory in nature and there were no a priori expectations of the results.

## **Methods**

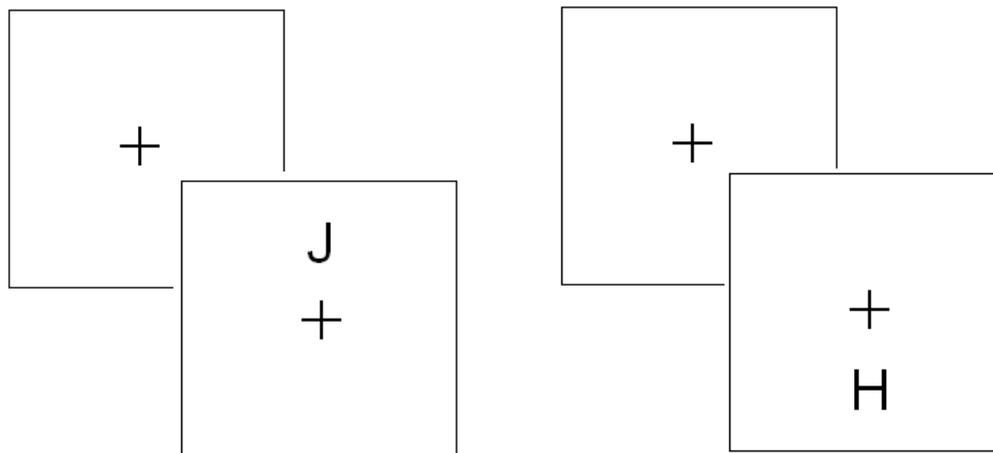
### **Participants**

The same participants as for the previous chapter took part. Six synaesthetes (5 female, 1 male) with associative grapheme-colour synaesthesia, and 12 yoked controls matched by age, sex, and handedness participated in this experiment. The mean age was 35 (sd 14.2), and all had normal or corrected-to-normal visual acuity. All participants were right-handed. The experimental procedures were approved by the University of Auckland Human Subjects Ethics Committee, and all subjects gave their informed consent to participate in the experiment.

### **Stimuli and procedure**

Each trial began with the presentation of a fixation cross for 500ms, followed by the addition of a single upper case letter either above or below the fixation cross, for 1000ms. Between each trial, there was an interval of 500ms during which a blank screen was presented. A total of 240 trials were conducted, with the letter appearing above and below the fixation an equal number of times. In an effort to present letters to either the upper or lower visual hemifield, participants were instructed to maintain fixation on the cross and endeavour not to saccade to the letter as it

appeared. Trials were presented in randomised order in two blocks of 120 each. Throughout the experiment, participants passively viewed the stimuli while seated comfortably.



**Figure 4.1** Examples of trials with an upper visual field stimulus (left) and a lower visual field stimulus (right).

The letters used consisted of a set of 5 letters individual to each synaesthete, as used in Experiment 3 in Chapter 4. Nonsynaesthetes were yoked controls, giving 2 controls for each synaesthete, presented with the same set of stimuli that their matched synaesthete counterparts used.

Stimuli were displayed on a SVGA computer monitor (1024 x 768 pixel resolution; 60Hz refresh rate) at a distance of 57cm. Stimulus presentation was controlled using E-Prime v1.1 (Psychology Software Tools). TTL pulses generated through the parallel port of the display computer provided synchronisation of stimulus events with EEG acquisition. Millisecond timing routines for the visual displays and pulse generation were conducted as outlined in the E-Prime User Guide (Psychology Software Tools).

## **Electrophysiological recording**

EEG was recorded continuously (1000 Hz sampling rate; 0.1 – 100 Hz analogue band-pass filter) using 128-channel Ag/AgCl electrode nets (Electrical Geodesics Inc., Eugene, OR, USA). All electrode impedances were below 50 k $\Omega$  (range 30 to 50 k $\Omega$ ), an acceptable level for this system (Ferree et al., 2001). The recordings took place in an electrically-shielded room. EEG was acquired using a common vertex (Cz) reference and later re-referenced to the average reference off-line.

## **Analysis**

EEG was segmented into epochs consisting of a 200ms pre-stimulus baseline and a 500ms period post-stimulus onset. DC offsets were calculated from the pre-stimulus baseline and removed from all waveforms. The data within each participant were then averaged according to condition (i.e. upper and lower visual hemifields).

Grand averaged waveforms were calculated for each condition for each group (i.e., 4 in total). The global field power (GFP; Skandries 1995) of these was then calculated in order to determine which time windows to examine. Based on visual inspection of the GFP, 6 time windows were selected, consisting of 3 earlier time windows that appeared to demonstrate differences between groups as well as conditions, and 3 later time windows where there appeared to be differences between groups, but not the conditions within them. Following this observation, the analysis of the 3 earlier and the 3 later time windows was conducted differently.

The 6 time windows identified were 35-65, 70-100, 160-200, 215-245, 270-340 and 350-400ms poststimulus onset. Average amplitude for each participant at each condition, for each electrode was obtained. To determine if there were any significant differences between conditions or groups, the following t-tests were conducted on each electrode: the difference between conditions among synaesthetes; the difference between conditions among controls; the differences between the synaesthete-difference and the control-difference.

For the three later time windows, additional analysis was conducted. Within each participant, condition 1 and 2 were averaged together. From these data, the average amplitude within each time window was obtained, and the difference between each synaesthete and their yoked control was calculated, for each electrode. This generated a dataset of 12 numbers for each electrode in each time window analysed. T-tests were then conducted on each of these, to assess if the between group difference was different from zero.

Because of the large number of t-test involved, it was necessary to adjust the criterion level of alpha. Following the method of Hamm, Johnson and Kirk (2002), the correction to alpha was determined by conducting a principal components analysis (PCA) on the data. For each set of t-tests, the relevant data was subjected to a PCA, with the number of components revealed (i.e. those with eigenvalues greater than 1) then forming the correction factor for that set of t-tests. For example, if 10 principal components were revealed, the alpha level for that set of t-tests was adjusted to .005. After this correction factor is applied, it is still expected that on average 6.45 electrodes (ie.0.05 of 129) will produce significant results. To account for this an additional

criterion was included, that the number of significant electrodes for a set of t-tests must significantly exceed 6.45, as tested by Chi-square tests.

## **Results**

Twenty one sets of t-tests were conducted in total. These were made up of 1) comparison of synaesthetes averaged across conditions versus controls averaged across conditions, for the final 3 time windows, 2) comparison among synaesthetes between the two conditions, for all 6 time windows, 3) comparison among controls between the two conditions, for all 6 time windows , and 4) comparison of synaesthete-difference and control-difference, for all 6 time windows. The results of the analysis of each set are given in Table 1.

**Table 4.1****Correction Factors, Number of Significant Electrodes, Chi-Square Values ( $\chi^2$ ), and *p*****Values, For Each Set of *t*-Tests**

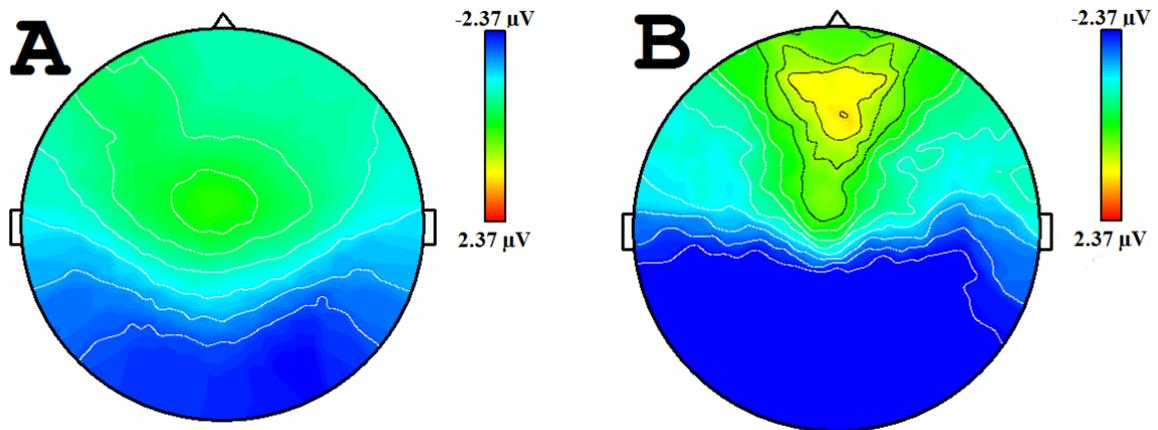
	Time Window	Correction Factor	Significant Electrodes	$\chi^2$	<i>p</i>
Synaesthete	215-245ms*	10	53	335.954	<.001
average vs.	270-340ms*	8	64	513.489	<.001
control	350-400ms*	10	25	53.349	<.001
average					
Synaesthete	35-65ms	17	0	6.45	0.011
difference vs.	70-100ms	16	11	3.21	0.073
control	160-200ms	14	1	4.605	0.032
difference	215-245ms	15	11	3.21	0.073
	270-340ms*	15	14	8.838	0.003
	350-400ms	17	5	0.326	0.568
Synaesthetes,	35-65ms	11	0	6.45	0.011
upper visual	70-100ms	10	2	3.07	0.08
field vs lower	160-200ms	9	2	3.07	0.08
visual field	215-245ms	9	0	6.45	0.011
	270-340ms	10	4	0.931	0.335
	350-400ms	10	0	6.45	0.011
Controls,	35-65ms	14	0	6.45	0.011
upper visual	70-100ms	14	0	6.45	0.011

field vs.	160-200ms*	12	38	154.326	<.001
lower visual	215-245ms	13	1	4.605	0.032
field	270-340ms	12	1	4.605	0.032
	350-400ms	16	6	0.003	0.859

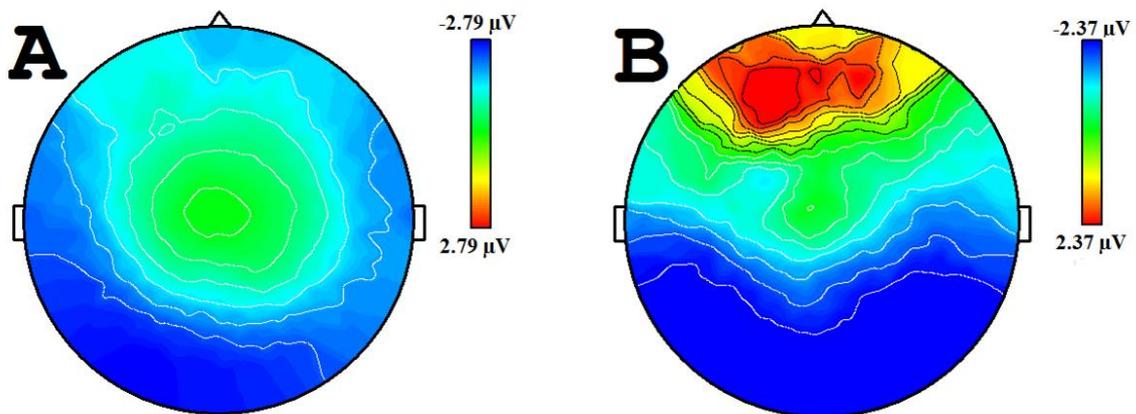
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\* denotes number of significant electrodes significantly exceeds 6.45

Five sets of t-tests yielded significant electrodes above the critical number. Firstly, the differences between the synaesthete average and the control average, akin to a main effect of synaesthesia in ANOVA, yielded significant as all three time windows: 215-245ms ( $\chi^2(1) = 335.954, p < .001$ ), 270-340ms ( $\chi^2(1) = 513.489, p < .001$ ), and 350-400ms ( $\chi^2(1) = 53.349, p < .001$ ). Secondly, the comparison between condition differences for synaesthetes and controls, akin to an interaction effect between synaesthesia and visual hemisphere, was significant for the 270-340ms time window ( $\chi^2(1) = 4.605, p = .032$ ). Finally, among controls, the comparison between upper and lower visual field among controls was significant for the 160-200ms time window ( $\chi^2(1) = 154.326, p < .001$ ).



**Figure 4.1.** Topographic plots of the grand-averaged potential among synaesthetes (A) and controls (B) at 230ms poststimulus onset time.



**Figure 4.2.** Topographic plots of the grand-averaged potential among synaesthetes (A) and controls (B) at 305ms poststimulus onset time.

## **Discussion**

This study compared the ERPs elicited by grapheme-colour synaesthetes to those of nonsynaesthetes when viewing achromatic letters presented in upper and lower visual hemifield. When viewing the letters, the synaesthetes experience a concurrent colour association that the nonsynaesthetes do not, so a comparison between the two should indicate what neurophysiological activity is directly associated with synaesthesia. The synaesthetes differed significantly from the nonsynaesthetes on three components: a negativity peaking at 230ms and centred over occipital areas, a negativity peaking at 305ms occipitally, and a negativity peaking at 375ms.

### **Lower and Upper Visual Hemifields**

Among controls there was a significant difference at the 160-200ms time window, with lower visual hemifield stimuli eliciting a less negative amplitude in central occipital areas, as well as a more negative amplitude in bilateral temporal areas. Stimuli presented to upper and lower visual hemifields produce diverging electrophysiological signatures, with lower hemifield producing smaller P1 and greater N1 amplitudes (Qu et al, 2006). The current results among the controls were consistent with this, however no such effect was present among the synaesthetes. Crucially, there was no statistical disparity found between the synaesthete-difference and the control-difference for this time window, ruling out the idea that the within-group findings reflect different early sensory processing in synaesthetes.

## **N200**

The presented stimuli used are everyday inducers for the synaesthetes, and were not presented in the context of a task. In addition both the synaesthetes and nonsynaesthetes were shown the same stimuli. Accordingly, the difference in brain activity between the two groups should indicate either the direct activity of synaesthesia, or fundamental differences between synaesthetes and nonsynaesthetes that is not related directly to the experience of synaesthesia. The increased frontal and left parietal negativity in synaesthetes, centred at 230ms, is possibly a reflection of the former. DiRusso et al. (2003), in a study employing source localisation of EEG signals, identified a negativity that peaked at 160ms over parietal areas, with neural generators in the V4/V8 colour area. It is possible that the increased negativity is comparable to this, and that it reflects colour processing. Similarly, Korshunova (1999) found increased negativity peaking at 180ms in response to illusory visual outlines (in the Kanizsa's square illusion), centred at occipital sites. Again, this appears to be a comparable example of the effect of visual processing out of context of usual vision.

Intriguingly, Barnett et al. (2008) also found a very similar result. However in their study, synaesthetes and controls were presented with a range of stimuli that expressly did not induce synaesthesia. They found that synaesthetes showed increased negativity centred at 190ms for coloured stimuli (red and green gratings), which the authors had difficulty interpreting. There are differences between the current study and the Barnett study, in which the stimuli were coloured and consisted of semantically meaningless shape. Crucially, their stimuli were not synaesthetic inducers. At this stage in synaesthesia research, it is difficult to know whether the results are

similar by coincidence or because there is something in common. It does leave the possibility that the explanation given above is not reflective of synaesthesia occurring but of general perception in synaesthetes. It would be interesting to compare ERPs to inducing and non-inducing stimuli that are more comparable. In fact, this has been done with fMRI by comparing inducing and non-inducing letters of the alphabet (Sperling et al., 2006), but not with any other neuroimaging methods. Sperling et al. found that for the inducing letters, but not the non-inducing ones, there was bilateral V4 activation.

### **N300**

The N300 component is associated with processing of emotional valency. The N300 has greater amplitude when viewing emotional faces than neutral faces, and is thought to reflect evaluation of affective valence; Wenbo et al., 2009). Synaesthetes often report an emotional reaction to their synaesthetic concurrents, such as a sense of appreciation of the colour of their favourite letters, and a sense of dislike of their least favourites (personal communications; Cytowic, 1997). The increased negativity in synaesthetes peaking at 305ms, chiefly in the left temporal area, could thus be a reflection of their greater emotional processing of the stimuli than the controls. It is interesting that for this time window, in addition to the significant difference between synaesthetes and controls when the upper and lower visual field conditions were averaged, there was also a significant difference between the magnitude of controls' within-group comparison and the synaesthetes' within-group comparison, with the synaesthetes showing greater differences between the conditions. It is difficult to interpret this result in terms of the emotional

processing explanation above, especially given that within both groups, differences between the conditions were not found for this time window.

## **N400**

Finally, the synaesthetes also showed increased negativity centred at 375ms over central frontal and right superior parietal sites. At this amount of time post stimulus onset, the activity will reflect post-sensory processing. The possible cognitive function of this activity is difficult to speculate on, without similar results in previous literature that can be compared in a way that makes sense in this context.

This study has shown that synaesthetes have different cortical activity to nonsynaesthetes in response to viewing inducing graphemes, and this difference is likely to reflect differences in both perceptual and emotional processing. Synaesthetes showed greater negativities than nonsynaesthetes in response to viewing graphemes at around 200ms-, 300ms- and 400ms poststimulus onset. The N200 difference is likely to reflect differences in perceptual processing, while N300 could be reflective of an emotional component to synaesthetic processing. Lastly, the N400 difference shows that synaesthetes have some difference from nonsynaesthetes in post-sensory processing of graphemes in ways not yet understood.

## **Chapter 5: Discussion**

### **Summary**

The aim of this thesis was to expand on the knowledge of how synaesthesia operates at a cognitive and neural level. Three different studies were done to examine different aspects of cognition and neural activity in associator grapheme-colour synaesthetes.

Experiment 1, reported in Chapter 2, asked the question, “How does synaesthesia affect normal visual binding, and binding errors?” To answer this question, grapheme-colour synaesthetes were briefly presented with sets of differently coloured letters, followed by a single coloured letter. The single coloured letter made up a colour-letter combination that had either appeared in the preceding array, or not, and the synaesthetes indicated whether or not they thought it had. In addition, the colour-letter combination was either congruent with the synaesthetes’ association, or not. Yoked controls were also tested for comparison.

This experiment enabled me to investigate the binding errors made by the synaesthetes. I found no evidence that synaesthesia affected the pattern of binding errors, and congruent letters were just as subject to binding errors as incongruent letters. The second finding of this study was that even when a colour-letter combination had not appeared in the preceding display, the synaesthetes were more likely to report that it had if it was a congruent combination. This experiment demonstrated that synaesthetic photisms do not act as robust visual features.

The second experiment employed EEG to examine brain activation in synaesthetes when they view graphemes presented in their synaesthetically congruent colour versus graphemes presented in an incongruent colour. Matched nonsynaesthetes were also tested as a yoked control. This experiment is reported in Chapter 3. Analysis of the visual ERPs revealed that for the incongruent stimuli, synaesthetes had a more negative N200 component. The N200 is an index of visual mismatch, indicating that synaesthetes responded to incongruently coloured letters as perceptually different from congruently coloured letters. This underscores the fundamentally perceptual nature of synaesthesia, and that synaesthetic perceptions are akin to usual visual experiences.

The final experiment, reported in Chapter 4 used EEG to explore how the brain activations of synaesthetes differ from that of nonsynaesthetes when they are viewing stimuli that induce a synaesthetic experience. Grapheme-colour synaesthetes and yoked matched controls viewed black graphemes. The visual ERPs were analysed, showing that the synaesthetes differed significantly from nonsynaesthetes on two components: a negativity peaking at 230ms and centred over occipital areas, a negativity peaking at 305ms occipitally, and a negativity peaking at 75ms over fronto-central and right superior parietal areas. These results were in agreement with the theory that synaesthesia involves brain activity comparable to that of colour processing and the processing of emotional stimuli.

In summary, this thesis advances our knowledge of letter-colour synaesthesia in several ways. First, synaesthesia did not influence perceptual binding. When asked whether a coloured letter was in the same colour as in a previous display, they were no more accurate when the colour

matched the colour induced synaesthetically than when it did not. Since binding involves attention, this suggests that attention can sustain binding in defiance of synaesthetic induction. Nevertheless, the induced colour did influence false positives: Synaesthetes were more likely to wrongly report the probe was in the same colour as in the display when it matched the synaesthetically induced colour than when it did not match. Short-term visual memory therefore sustains the actual colour of a memory despite the induction of a synaesthetic colour.

Second, electrophysiological recording showed that synaesthetes responded differently to coloured letters that were incongruent with the synaesthetically induced colour than when it was congruent. This difference was evident early in visual processing, suggesting that synaesthesia is perceptual, rather than being dependent on attention or higher-order associations. Synaesthetes also differed from yoked controls in cortical responses to black-and-white letters, presumably as a consequence of the coloured photisms induced by the letters. This study suggested that the differential response may include emotional as well as perceptual components.

### **Attention in synaesthesia**

The process by which synaesthesia occurs begins first with the perception of the inducing stimulus. In Experiment 1, we saw that congruently coloured graphemes were equally subject to binding errors as incongruently coloured ones. Binding only occurs when attention is applied; in cases where insufficient attention is applied, binding fails. The current results provide no evidence that synaesthesia had an influence on whether a particular letter-colour combination of presented features was bound or not; accordingly we find no evidence that synaesthesia has an

influence at pre-attentive levels, which suggests that attention to the inducing stimulus is necessary for synaesthesia to occur.

The idea that attention is necessary for synaesthesia is asserted by previous literature, such as Mattingley et al., (2001), Edquist et al., (2006), Sagiv, Heer & Robertson, (2006) and Ward et al. (2007). . On the other hand, several studies have claimed that attention is not necessary, including Palmeri, Blake, Marois, Flanery & Whetsell, 2002, Smilek et al., 2001, Smilek, Dixon & Merikle, 2003; also Wagar, Dixon, Smilek & Cudahy., 2002; also Johnson, Jepma & de Jong, 2007). Ward et al. (2010) asserts that there are two possible explanations for the conflicting findings. One is that projectors are more likely to become aware of their synaesthetic sensations, because the locus of the photism is in the same position as the letter, hence less attentional resources are needed to perceive the photism than an associator would require. The second explanation is that in visual search paradigms, the synaesthetic colours do not pop out, but may appear serially as the serial search of letters progresses, giving an advantage over nonsynesthetes. The current results lend additional support to Ward et al.'s (2010) conclusion that synaesthesia is not induced pre-attentively.

Ramachandran and Seckel (2011) published a case study showing the experience of photisms in a projector synaesthete before graphemes were consciously recognised in a series of images with camouflaged letters, such as 'Bregman's Bs'. In this case, attention was paid to the inducing images, however, they were not consciously recognised as graphemes, so it cannot be said that attention was given to the graphemes themselves. There are two possible explanations of the discrepancy between their results and mine. Firstly, it could be the case that projectors, unlike

associators, don't need to pay attention to the grapheme in order to induce a photism. Secondly, it is possible that in the Ramachandran and Seckel experiment there was sufficient latent, but not conscious, identification of the grapheme for synaesthesia to be induced. The second explanation is consistent with the idea that associative synaesthesia involves top-down processing, as in my experiment, whereas projective synaesthesia involves bottom-up processing with sensory cross-over occurring at a point before information reaches consciousness, as in the experiment by Ramachandran and Seckel.

### **Is synaesthetic perception the same as normal perception?**

A question of interest is how much the experience of synaesthesia is like the experience of normal sensation and perception, both at a phenomenological level and at a neural level. However, it is important to remember that synaesthesia is heterogeneous in nature, with anecdotal evidence ranging from reports of visual synaesthesia vivid enough to occlude usual vision (personal communication), to the more vague description of 'just knowing' that A is red, for example. It is also important to bear in mind that, barring unrelated visual deficits, synaesthetes experience veridical vision the same way nonsynaesthetes do. In particular, for the majority of synaesthetes, their synaesthesia does not interfere with their ability to accurately perceive colours. Therefore it is expected that there will always be a phenomenological difference between the two, with the exception of projective synaesthesia of such a nature as to occlude vision.

The results from Experiment 1 showed that the synaesthetic colour percepts did not act as visual

features in the same way that the real presented colours did: if they had, then in cases of binding errors, the synaesthetic colours would have been (incorrectly) bound to letters with higher frequency.

At a neural level, the current results suggest that synaesthesia is akin to normal perception. In Experiment 2, the increased N200 synaesthetes showed for incongruently coloured graphemes over congruently coloured graphemes suggests that the synaesthetic percepts induce a visual mismatch, indicating that the percept is at least partially like colour perception. Finally, Experiment 3 is also in accordance with idea that synaesthesia is the same as colour perception. While a host of neuroimaging research has engaged with the idea that synaesthetic colour perception is mediated by the V4 colour processing area (see discussion in Chapter 1), two studies have explicitly tested the hypothesis by comparing the neural activity associated with veridical colour perception and synaesthetic colour perception using fMRI. The first of these, by Van Leeuwen et al. (2011), found that V4 activation is implicated in both, but that synaesthetic perception is also mediated by higher-order visual areas that are outside of the standard ventro-occipital visual pathways. The van Leeuwen study also compared activation patterns in projector synaesthetes and associator synaesthetes. Their results suggested that in projector synaesthetes, the V4 area was activated via modulation of bottom-up sensory pathways, while in associators, activation occurred via top-down processes modulated by the superior parietal lobe.

The second study was by Hupe et al. (2011) which, in addition to widely lambasting the methodology of previous fMRI studies in synaesthesia, failed to find any synaesthesia-related activity in the individually defined colour processing areas of the synaesthetes. On top of this,

voxel-based morphometry failed to reveal any white or grey matter structural differences in these areas. Synaesthetes did however show greater white matter volume in the retrosplenial cortex (RSC).

Taken together, the sum of evidence suggests that at both an experiential and neural level, associative synaesthesia is like colour imagery in that it is mediated through top-down processes and is visually experienced in a similar way, while projective synaesthesia resembles usual colour vision, by occurring via bottom-up processing streams and experienced as a colour located on a visual object. This idea then predicts that among projectors, the more the phenomenology resembles usual vision, such as when synaesthetic colours visually occlude real objects, the more the neural substrates will also match those of usual colour vision.

### **What is the cause of synaesthetic processing?**

Separate from the question of which areas give rise to synaesthesia is the question of what causes the activation. The options include extra anatomical projections not present in synaesthetes, and functional differences, either by way of activation of functional pathways or by disinhibition of pathways already present in the general population. Interestingly, these may not be either/or propositions, as there is now evidence of both increased structural connectivity in synaesthetes, as well as a strong argument for a purely functional type of synaesthesia:

An intriguing study by Cohen-Kadosh et al. (2009) successfully used posthypnotic suggestion to induce synaesthesia in nonsynaesthetes that was behaviourally indistinguishable from that of

associator synaesthetes. As it is not possible for structural differences to occur over the short time of the study, this study provides very strong evidence that synaesthesia is modulated via disinhibited feedback processes. The hypnotic disinhibition is thought to only affect frontal activity, so that the hypnosis-induced synaesthesia must necessarily be modulated via top-down processes, and not bottom-up pathways.

On the other hand, there are now studies indicating increased structural connectivity among synaesthetes compared to nonsynaesthetes. In addition to the Hupe study mentioned above which found increased RSC white matter, Banissy et al. (2012) found synaesthetes had greater grey matter volume in the left posterior fusiform gyrus, with a concomitant decrease in the anterior fusiform gyrus and left medial temporal/V5 area.

Whether naturally arising synaesthesia (as opposed to associations deliberately trained into participants for research purposes) is necessarily predicated by increased structural connectivity is at this point unclear; perhaps there are cases of synaesthetes where no structural difference exists. Regardless, there is now strong evidence of increased functional activity among synaesthetes. Apart from studies that indirectly inferred a role for functional connectivity in synaesthesia by disrupting using TMS (Esterman et al., 2006; Muggleton et al., 2007), a study by Doern et al. (2012) examined resting-state fMRI among grapheme-colour synaesthetes and controls to directly show increased functional connectivity.

## **Limitations**

There are several limitations to the experiments conducted, chiefly due to the difficulty of recruiting suitable participants. For the behavioural experiment in Chapter 2, and the EEG experiments in Chapters 3 and 4, the relatively small sample of participants able to take part served to reduce the statistical power for analysis, and for the EEG experiments this problem was further compounded through equipment malfunctions, causing the discovery, after data collection, that a sizeable portion of the data was unusable. Of 9 synaesthetes tested for these experiments, only 6 produced data fit for analysis. It is possible that these same experiments, conducted with larger sample sizes and hence more statistical power, would reveal significant effects that were not discoverable with this data set. Nevertheless, it can be expected that the significant results that were obtained would remain significant in an expanded data set, and so the current results remain relevant.

In addition, the necessary reliance on a self-selected sample of synaesthetes raises concern about how well the sample tested represents the wider population of synaesthetes. Specifically, this would cause a problem if those with the tendency to volunteer for studies also have a systematic difference in the nature of their synaesthesia from those who do not volunteer for studies. While it is not possible to categorically negate the hypothesis that there is no such difference, pragmatically, it can be assumed that there is no correlation between the nature of synaesthesia and the tendency to self-nominate, and so the data is likely to be safe from this source of bias.

Finally, the interpretation of neuroimaging studies in synaesthesia is limited by the amount of neuroimaging research in general. Particularly in the case of EEG, the ability to interpret results on the topic of synaesthesia in terms of a neuro-cognitive model, relies in the existence of previous research to make comparisons to. An EEG effect which shows a difference between synaesthetes and nonsynaesthetes is interesting in its own right; however if there is no research with which to compare my results, it is difficult to discern what it means in terms of the larger picture.

### **Suggestions for Future Research**

The recent discoveries about differences in neural activation between projector and associator synaesthetes, as well as the relatively long-established knowledge about phenomenological differences between the two, naturally imply that it would be interesting to repeat the same experiments with projector synaesthetes. In particular, it would be interesting to test if in Experiment 1, synaesthetic colours do in fact act as visual features for projectors.

In addition to the associator-projector distinction, among projectors there are experiential differences that appear so fundamental that it's likely that there are neural differences as well – specifically, between those projectors who retain normal visual perception, and those for whom synaesthesia occludes normal visual perception. Of course, it is necessary to experimentally verify through cognitive behavioural studies what the extent of the visual occlusion is – currently one synaesthete has explained to me that this is his experience (and I expect that others with this experience also exist), but this claim has not been verified with behavioural experiments.

At the same time, the phenomenon of latent synaesthesia, in which synaesthetic associations are made on a pre-conscious level, is also a topic worthy of being studied. In Chapter 1, I wrote that part of the reason why it is interesting to study synaesthesia is that it is not that uncommon, and thus informs us about perceptual mechanisms that may be present in a large portion of the population. As a starting point, I think it would be very interesting to establish what the prevalence of latent synaesthesia within the general population is. It would also be interesting to confirm via neuroimaging studies the prediction that this form, being the least like normal vision, recruits less lower visual areas than the others, and involves mostly, if not exclusively, higher-order areas and frontal activity.

In the project of establishing a universal model of synaesthesia, it will also be necessary to see if the latest models of synaesthesia are applicable to forms that do not involve vision. At present count, there are tens of different forms of synaesthesia that have been recorded, and this number has increased during the course of producing this thesis. By focusing on primarily on visual-related synaesthesia, only a very narrow subset of synaesthesia is being studied.

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