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Synaesthesia — A Window Into Perception, Thought and Language

Abstract: *We investigated grapheme–colour synaesthesia and found that: (1) The induced colours led to perceptual grouping and pop-out, (2) a grapheme rendered invisible through 'crowding' or lateral masking induced synaesthetic colours — a form of blindsight — and (3) peripherally presented graphemes did not induce colours even when they were clearly visible. Taken collectively, these and other experiments prove conclusively that synaesthesia is a genuine perceptual phenomenon, not an effect based on memory associations from childhood or on vague metaphorical speech. We identify different subtypes of number–colour synaesthesia and propose that they are caused by hyperconnectivity between colour and number areas at different stages in processing; lower synaesthetes may have cross-wiring (or cross-activation) within the fusiform gyrus, whereas higher synaesthetes may have cross-activation in the angular gyrus. This hyperconnectivity might be caused by a genetic mutation that causes defective pruning of connections between brain maps. The mutation may further be expressed selectively (due to transcription factors) in the fusiform or angular gyri, and this may explain the existence of different forms of synaesthesia. If expressed very diffusely, there may be extensive cross-wiring between brain regions that represent abstract concepts, which would explain the link between creativity, metaphor and synaesthesia (and the higher incidence of synaesthesia among artists and poets). Also, hyperconnectivity between the sensory cortex and amygdala would explain the heightened aversion synaesthetes experience when seeing numbers printed in the 'wrong' colour. Lastly, kindling (induced hyperconnectivity in the temporal lobes of temporal lobe epilepsy [TLE] patients) may explain the purported higher incidence of synaesthesia in these patients. We conclude with a synaesthesia-based theory of the evolution of language. Thus, our experiments on synaesthesia and our theoretical framework attempt to link several seemingly unrelated facts about the human mind. Far from being a mere curiosity, synaesthesia may provide a window into perception, thought and language.*

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Introduction

Synaesthesia is a curious condition in which an otherwise normal person experiences sensations in one modality when a second modality is stimulated. For example, a synaesthete may experience a specific colour whenever she encounters a particular tone (e.g., C-sharp may be blue) or may see any given number as always tinged a certain colour (e.g., '5' may be green and '6' may be red). The condition was first clearly documented by Galton (1880) who also noted that it tends to run in families. One problem that has plagued research in this field is that, until recently, it was not even clear that synaesthesia is a genuine sensory/ perceptual phenomenon (Baron-Cohen & Harrison, 1997; Cytowic, 1989; Harrison, 2001; Ramachandran & Hubbard, 2001a). Indeed, despite a century of research, the phenomenon is still sometimes dismissed as bogus. We have frequently encountered the following types of explanations in the literature as well as in conversations with professional colleagues:

1) They are just crazy. The phenomenon is simply the result of a hyperactive imagination. Or maybe they are trying to draw attention to themselves by claiming to be special or different in some way.
2) They are just remembering childhood memories such as seeing coloured numbers in books or playing with coloured refrigerator magnets.
3) They are just engaging in vague tangential speech or just being metaphorical just as you and I might say 'bitter cold' or 'sharp cheese'. Cheese is *soft* to touch, not sharp, so why do we say 'sharp'? Obviously, one means that the taste is sharp but why is a *tactile* adjective being applied to *taste*?
4) They are 'potheads' or 'acid junkies' who have been on drugs. This idea is not entirely without substance since LSD users often do report synaesthesia both during the high as well as long after.

Although common, none of these accounts provides a satisfactory explanation of synaesthesia. For example, the idea that synaesthetes are trying to draw attention to themselves would predict that synaesthetes should be telling everyone around them about how different they are. In our experience, it is usually quite the opposite. Synaesthetes often think that everyone else experiences the world the same way they do, or else they have been ridiculed as children and have not told anyone about their synaesthesia for years.

The memory hypothesis also fails as an explanation of synaesthesia because it cannot address the questions of why only some individuals have these memories intact, why only specific classes of stimuli are able to induce synaesthesia, and why there should be a genetic basis for synaesthesia (see below).

The problem with the metaphor explanation is that it commits one of the classical blunders in science, trying to explain one mystery (synaesthesia) in terms of another mystery (metaphor). Since we know very little about the neural basis of metaphor, saying that 'synaesthesia is just metaphor' helps to explain neither synaesthesia nor metaphor. Indeed, in this paper we will turn the problem on its head and suggest the very opposite: Synaesthesia is a concrete sensory phenomenon whose neural basis we are beginning to understand and it can therefore

provide an experimental lever for understanding more elusive phenomena such as metaphor (Ramachandran & Hubbard, 2001a).

Finally, the idea that synaesthesia is a result of drug use is only applicable to a few people, and seems to occur only during the 'trip'. One explanation of this is that certain drugs might pharmacologically mimic the same physiological mechanisms that underlie genetically based synaesthesia. However, it may also be that pharmacologically induced synaesthesia is not based on the same neural mechanisms as the congenital, lifelong experiences of *true* synaesthetes, in spite of the superficial similarities. Additionally, not everyone who uses psychedelics experiences synaesthesia; perhaps only those with a genetic predisposition will experience synaesthesia under the influence of psychoactive drugs.

In this paper we have four major goals. First, we will review some recent experiments we have done which establish clearly, for the first time, that synaesthesia is genuinely sensory (Hubbard & Ramachandran, 2001; Ramachandran & Hubbard, 2000; 2001a). Second, we will consider a number of seemingly unrelated facts about synaesthesia and certain other neurological disorders and link these into a coherent new theoretical perspective. Third, we will discuss the relevance of this scheme to certain enigmatic aspects of human nature such as metaphorical thinking, art and the origin of language. And fourth, we will use this theoretical framework to make several new experimental predictions about both synaesthesia and other, more elusive, aspects of the mind.

The facts we propose to link together are the following:[1]

1) Synaesthesia runs in families.
2) Synaesthetes often report 'odd' or weird colours they cannot see in the real world but see only in association with numbers. We even saw a colour-blind subject recently who saw certain colours *only* upon seeing numbers.
3) If a person has one type of synaesthesia, she is also more likely to have a second or third type.
4) There appears to be tremendous heterogeneity in synaesthesia. We have recently suggested that there may be distinct groups we call 'higher' and 'lower' synaesthetes that can be operationally defined and distinguished by our experiments.
5) Patients with damage to the left angular gyrus have dyscalculia — they cannot perform even elementary arithmetic. But they can still recognize number graphemes.
6) The angular gyrus is a seat of polymodal convergence of sensory information.
7) Angular gyrus lesions also lead to anomia and, intriguingly, loss of ability to understand metaphors.
8) Ordinary language use is rich with synaesthetic metaphors ('loud shirt' or 'hot babe'). This raises a fascinating question: What is the exact connection — if any — between metaphor and synaesthesia?
9) Synaesthesia appears to be more common among artists, poets, novelists and creative people in general. Why? What is the link? (Unfortunately, this

[1] See text below for references for these points.

higher prevalence among artists fuels the view that the phenomenon is just the result of 'craziness' or vague metaphorical speech because, as one student told us, 'artists are all crazy anyway'.)

10) Synaesthetes often report that if the number is printed in the wrong colour 'it looks ugly'. It seems disproportionately aversive. Why do they have such a violent emotional reaction to such a trifling discord?
11) There are hints that patients with TLE may have a higher incidence of synaesthesia. Why?
12) Most synaesthetes claim that even when they *visualize* the number, the corresponding colour is seen, and surprisingly, the colour is *more* vivid than when it is actually seen (presumably not being vetoed by actual sensory input). But in some synaesthetes, the colour associated with imagined numbers is actually less vivid.

While this collection of facts may seem at first to be rather arbitrary, we will show that they are indeed related, and that our research into synaesthesia has the potential to illuminate a number of more elusive aspects of the human mind. The ideas we will present are very speculative but have the advantage of being, for the most part, empirically testable.

Genetic Basis of Synaesthesia

Estimates of the prevalence of synaesthesia vary dramatically. Cytowic (1989; 1997) estimates that it occurs in 1 in 20,000 people, while Galton (1880) placed the prevalence at 1 in 20. More recent, systematic, studies have estimated that synaesthesia occurs in 1 in 2,000 people (Baron-Cohen *et al*., 1996). Our own results indicate that the prevalence may be even greater, perhaps as much as 1 in 200 (Ramachandran *et al*., unpublished observations). Some of this variability is probably due to differences in definitional criteria used by different researchers, but some of this might also be due to the different subtypes examined by different investigators. For example, Cytowic focussed on taste–shape synaesthesia, while we focus on grapheme–colour synaesthesia, which is the most common subtype (Day, 2001).

In spite of the variability in estimates of its prevalence, almost every study of synaesthesia has agreed that synaesthesia seems to run in families. Galton (1880) first noticed this; many of his subjects had relatives who were also synaesthetic. More recently, Baron-Cohen *et al*. (1996) conducted a more formal survey to determine the familiality of synaesthesia. They found that synaesthesia is more common in females than males (6:1) and that approximately one-third of their respondents had known family members who were also synaesthetic. Family studies show that the trait seems to be passed along the X-chromosome, and that it may be dominant (Bailey & Johnson, 1997).[2]

[2] The patterns of inheritance are likely to be complicated, given the existence of different types of synaesthesia (possibly with different genes being involved). The genetics might become clearer once the different phenotypes have been more clearly characterized using our psychophysical probes. Also, perhaps not all cases of grapheme–colour synaesthesia have a genetic basis; some may have an epigenetic cause.

Synaesthetic Associations are Stable over Time

Synaesthetically induced colours are consistent across months or even years of testing (Baron-Cohen *et al*., 1993). Baron-Cohen *et al*. asked nine synaesthetic subjects and nine controls to give colour associations for a list of 130 words. Control subjects were told that they would be tested one week later, while synaesthetic subjects were retested one year later and were not informed prior to testing that they would be retested. Synaesthetic subjects were 92.3% consistent, while control subjects were only 37.6% consistent.

While this proves that the effect is not confabulatory in origin, it does not necessarily show that it is sensory rather than conceptual or based on early memories. After all, if each number triggers a highly specific memory, this might have been remembered by the subject with each occurrence of the number over a lifetime, providing plenty of opportunity for rehearsal, even without external reinforcement.

Is Synaesthesia Perceptual or Cognitive?

We conducted five experiments[3] with our first two synaesthetes (JC and ER), all of which suggest that grapheme–colour synaesthesia is a sensory effect rather than a cognitive one or based on memory associations (Ramachandran & Hubbard, 2000; 2001a).

1) Synaesthetically induced colours can lead to pop-out. We presented subjects with displays composed of graphemes (e.g., a matrix of randomly placed, computer-generated '2's). Within the display, we embedded a shape — such as a triangle — composed of other graphemes (e.g. computer-generated '5's; see fig. 1; back cover). Since '5's are mirror images of '2's and made up of identical features (horizontal and vertical line segments), non-synaesthetic subjects find it hard to detect the embedded shape composed of '5's. Our two synaesthetes, on the other hand, see the '2's as one colour and the '5's as a different colour, so they claim to see the display as (for example) a red triangle amidst a background of green '2's. We measured their performance and found that they were significantly better at detecting the embedded shape than non-synaesthetic control subjects (Ramachandran & Hubbard, 2001a), making it clear that they were not confabulating and could not have been 'faking it'. Perceptual grouping and pop-out are often used as diagnostic tests

[3] Common sense suggests that it would also be worth probing the introspective phenomenological reports of these subjects, even though this strategy is unpopular in conventional psychophysics. For instance, to the question 'Do you literally *see* the number "5" as red or does it merely remind you of red — the way a black-and-white half tone photo of a banana reminds you of yellow?', our first two subjects replied with remarks like, 'Well, that's hard to answer. It's not a memory thing. I do *see* the colour red. But I also *know* it's just black. But with the banana I can also imagine it to be a different colour. It's hard to do that with the 5', all of which further suggests that synaesthesia is a sensory phenomenon (Ramachandran & Hubbard, 2001a). Also, synaesthetes often report hybrid colours on the number, such as 'reddish blue — but not purple' or 'whitish green'; the colours are splotchy as in a Dalmatian dog. They don't blend (yet another bit of evidence against the memory hypothesis). Another intriguing observation is that some synaesthetes experience colours *only* for numbers but not letters. Many of these individuals also have a 'calendar line' or wheel with each month tinged a particular colour (the same for days of the week). Sometimes clusters of adjacent days or months will have very similar colours (e.g., April, May and June will all be green).

to determine whether a given feature is genuinely perceptual or not (Beck, 1966; Treisman, 1982). For example, tilted lines can be grouped and segregated from a background of vertical lines but printed words cannot be segregated from nonsense words or even mirror reversed words. The former is a perceptual difference in orientation signalled early in visual processing by cells in area V1; the latter is a high-level linguistic concept.

2) We have found that even 'invisible graphemes' can induce synaesthetic colours. Individual graphemes presented in the periphery are easily identified. However, when other letters flank the target, it is difficult to identify the target grapheme (fig. 2; back cover). This effect ('crowding') is not due to the low visual acuity in the periphery (Bouma, 1970; He *et al*., 1996). In fact, the target grapheme is large enough to be resolved clearly and can be readily identified if the flankers are not present. We have found that the crowded grapheme nevertheless evoked the appropriate colour; a curious new form of blindsight (Hubbard & Ramachandran, 2001; Ramachandran & Hubbard, 2001b). The subject said, 'I can't see that middle letter but it must be an "O" because it looks blue.' This observation implies, again, that the colour is evoked at an early sensory — indeed preconscious — level rather than at a higher cognitive level.
3) We have found that when a number was moved beyond 11 degrees into peripheral vision and scaled for eccentricity (Anstis, 1998), it lost its colour (Ramachandran & Hubbard, 2000; 2001a), even though it was still clearly visible (fig. 3; back cover).
4) We optically superposed two different graphemes and alternated them. Subjects experienced colours alternating up to 4 Hz. At higher speeds — up to 10 Hz — the numbers could still be seen alternating but our subjects said they no longer experienced colours (Ramachandran & Hubbard, 2000; 2001a). In a third subject the colours started alternating at a much slower rate of once every two or three seconds (as in binocular rivalry).
5) Roman numerals and subitizable clusters of dots were ineffective in eliciting synaesthetic colours, suggesting that it is the visual grapheme, not the numerical concept that is critical (but see below for exceptions). Tactile and auditory letters were also ineffective in evoking colours unless the subject visualized the grapheme (Ramachandran & Hubbard, 2000; 2001a). Thus, it is the visual grapheme, not the numerical concept, that triggers the perception of colour.

Taken collectively, these five sets of experiments prove conclusively that, at least in some synaesthetes, the induced colours are genuinely sensory in nature.[4] The question is, what causes the condition?

The Cross-Activation Hypothesis

The idea that synaesthesia may be the result of some form of cross-wiring has been around for at least 100 years (for lucid reviews, see Harrison & Baron-

[4] This conclusion also receives confirmation from a recent study which showed that a grapheme that evokes a synaesthetic colour is more difficult to detect against a background of identical colour (Smilek *et al*., 2001); i.e., the converse of the pop-out effect we have previously described.

Cohen, 1997; Marks, 1997). However, it is usually stated in very vague terms and anatomical localization has not been properly investigated. Our goal here will be to make some concrete testable proposals regarding the exact anatomical locus (or loci) and the extent of 'cross-wiring' and to link this idea with the long list of other seemingly unrelated facts listed above.

To date, there has been only one imaging study. Paulesu *et al*. (1995) report a PET study in which word–colour synaesthetes were presented with pure tones or single words. Regional cerebral blood flow (rCBF) measurements were taken during tone listening and word listening. Areas of the posterior inferior temporal cortex and parieto–occipital junction — but not early visual areas such as V1, V2 or V4 — were activated significantly more during word listening than during tone listening in synaesthetic subjects, but not in controls. However, no precise anatomical localization was possible given the limits of resolution of the technique. In addition, the failure to find activity in early visual areas (e.g., V4) may also have been due to the limited power of PET, as opposed to a true absence of activity (Gray, 1998).

The most common type of synaesthesia is grapheme–colour (i.e., number–colour or letter–colour) synaesthesia. We will therefore confine our speculations, in this paper, mainly to this particular form of synaesthesia, although we believe the argument may be valid for other kinds as well. The key insight comes from anatomical, physiological and imaging studies in both humans and monkeys, which show that colour areas in the brain (V4; Lueck *et al*., 1989; Zeki & Marini, 1998 and V8; Hadjikhani *et al*., 1998) are in the fusiform gyrus. We were struck by the fact that, remarkably, the visual grapheme area is *also* in the fusiform (Allison *et al*., 1994; Nobre *et al*., 1994; Pesenti *et al*., 2000), especially in the left hemisphere (Tarkiainen *et al*., 1999), adjacent to V4 (fig. 4; back cover). Can it be a coincidence that the most common form of synaesthesia involves graphemes and colours *and* the brain areas corresponding to these are right next to each other? We propose, therefore, that synaesthesia is caused by cross-wiring between these two areas, in a manner analogous to the cross-activation of the hand area by the face in amputees with phantom arms (Ramachandran *et al*., 1992; Ramachandran & Rogers-Ramachandran, 1995; Ramachandran & Hirstein, 1998).[5]

Since synaesthesia runs in families we suggest that a single gene mutation causes an excess of cross-connections or defective pruning of connections between different brain areas. Consequently, every time there is activation of neurons representing numbers, there may be a corresponding activation of colour neurons.[6]

One potential mechanism for this would be the observed prenatal connections between inferior temporal regions and area V4 (Kennedy *et al*., 1997; Rodman & Moore, 1997). In the immature brain, there are substantially more connections between (and within) areas than are present in the adult brain. Some of these

[5] A similar idea has more recently been proposed by Smilek *et al.* (2001).

[6] The fusiform gyrus also has cells specialized for recognizing faces. If so, why doesn't the cross-wiring also occur between face cells and colour? To be sure, we have encountered at least one synaesthete who saw faces tinged with colour that was modulated by facial expression (Ramachandran & Hubbard, 2001a) but we don't know how common this may be. One possibility is that 'face nodes' are represented in too complex a manner for a simple one-to-one cross-activation of colour to occur.

connections are removed through a process of pruning, and others remain. It has been shown that there is a much larger feedback input from inferior temporal areas to V4 in prenatal monkeys. In the foetal macaque, approximately 70–90% of the connections are from higher areas (especially TEO, the macaque homologue of human inferior temporal cortex), while in the adult, approximately 20–30% of retrograde-labelled connections to V4 come from higher areas (Kennedy *et al.*, 1997; Kennedy, personal communication). Hence, if a genetic mutation were to lead to a failure of pruning (or stabilization) of these prenatal pathways, connections between the number grapheme area and V4 would persist into adulthood, leading to the experience of colour when viewing numbers or letters.

An important point to be made here is how our model differs from Grossenbacher's (1997; Grossenbacher & Lovelace, 2001) model of synaesthesia as a result of disinhibited cortical feedback. Grossenbacher's model generally assumes that information is processed up through several levels of the sensory hierarchy to some multi-modal sensory nexus before being fed back to lower areas, such as V4. In our model (at least for grapheme–colour synaesthesia), we propose that the connections are much more local, and that information does not have to go all the way 'downtown' before being sent back to colour areas.

A second important point is that, even though we postulate a genetic mutation that causes defective pruning or stabilization of connections between brain maps, the final expression must require learning — obviously one isn't born with number and letter graphemes hardwired in the brain (and, indeed, different synaesthetes have different colours evoked by the same numbers). The excess cross-activation merely *permits* the opportunity for a number to evoke a colour. There may be internal developmental or learning rules that dictate that once a connection has formed between a given 'number node' and a 'colour node', no further connections can form. This would explain why the connections are not haphazard. A given number only evokes a single colour.

The cross-activation hypothesis can explain our finding that in some synaesthetes the colours are evoked only in central vision. Since memories ordinarily show positional invariance our observations imply that synaesthesia is not just associative memory from childhood. On the other hand, since V4 mainly represents central vision (Gattass *et al.*, 1988; Rosa 1997), if the cross-wiring occurred disproportionately for central vision then one would expect the colours to be evoked selectively in this region.

The cross-wiring hypothesis is also consistent with the finding that synaesthetic colours were no longer experienced in two of our subjects when two spatially overlapping numbers were temporally alternated at rates exceeding 6 Hz, even though the alternating numbers could still be clearly seen. Recent evidence shows that the time course of central perceptual (i.e., cortical) phenomena all occur on relatively slow time scales (He & MacLeod, 1994; He *et al.*, 1995; Holcombe *et al.*, 2001). In a third subject (JC), at approximately 6 Hz, one colour dominated over the other for extended periods. For example, when presented with a '7' and a '3' (which elicit green and red, respectively), JC might see red dominate for a period of several seconds, then green, even though he could clearly see

the numbers alternating at a higher frequency. This 'rivalrous' phenomenon is difficult to explain on a memory or metaphor account of synaesthesia.

The idea also explains why, in JC and ER, only the actual Arabic numerals evoke colours — Roman numerals and subitizable clusters of dots do not. This observation suggests that it is the actual visual appearance of the grapheme, not the numerical *concept* that evokes colour. This is consistent with cross-activation in the fusiform because the latter structure represents the graphemes, not the concept.

Third, our hypothesis can also explain why a number rendered invisible through crowding can nevertheless evoke colours. Perhaps perceptual events do not reach consciousness in the fusiform — the place where we postulate the cross-activation to be occurring (i.e., neuronal activity in the fusiform is necessary, but not sufficient for conscious awareness; for example, see a recent fMRI study by Dehaene *et al*., 2001). Perhaps due to crowding, the processing of the graphemes does not extend beyond fusiform. However, this fusiform activity is sufficient to evoke colours in parallel (which are not affected by crowding), and therefore subsequent colour selective regions are also activated, leading to the conscious experience of the colours.

Fourth, our hypothesis may shed light on the neural basis of other forms of synaesthesia. Sacks and Wasserman (1987; Sacks *et al*., 1988) report a patient who became colour blind (cerebral achromatopsia) after his car was hit by a truck. Prior to the accident, the patient was an artist who also experienced colours when presented with musical tones. However, after the accident, he no longer experienced colours in response to musical tones. Interestingly, the subject also reported acute alexia, in which letters and numbers 'looked like Greek or Hebrew to him' (Sacks & Wasserman, 1987, p. 26). This would indicate that a single brain region might have been damaged in the accident, leading to both the loss of colour vision and the acute alexia, consistent with what is now known from the imaging literature. Perhaps this brain region was also critical for his synaesthesia (see below), and so when it was damaged he no longer experienced synaesthesia.

Finally, our model may explain why people who experience one kind of synaesthesia (e.g., grapheme–colour) are more likely to experience another (e.g., tone–colour). The failure of pruning might occur at multiple sites in some people. This leads to our next postulate: Even though a single gene might be involved, it may be expressed in a patchy manner to different extents and in different anatomical loci in different synaesthetes. This may depend on the expression of certain modulators or transcription factors.

One final piece of evidence for the 'hyperconnectivity' hypothesis comes from cases of acquired (as opposed to hereditary) synaesthesia. We recently examined a patient who had retinitis pigmentosa and became progressively blind starting from childhood until he became completely blind at 40. Remarkably, a few years later, he started to experience tactile sensations as visual phosphenes. The tactile thresholds for evoking the phosphenes ('synaesthesia threshold') were higher than the tactile thresholds themselves and the synaesthesia thresholds were constant across intervals separated by weeks — implying that the effect is genuine and not confabulatory in origin (Armel & Ramachandran, 1999). We suggested

that the visual deprivation causes tactile input to start activating visual areas; either the back-projections linking these areas become hyperactive or new pathways emerge. If such cross-activation (based on hyperconnectivity) is the basis of acquired synaesthesia, one could reasonably conclude that the hereditary condition might also have a similar neural basis, except that the cause is genetic rather than environmental.

Synaesthesia: Cross-Wiring or Disinhibition?

The cross-activation of brain maps that we postulate can come about by four different mechanisms: (1) cross-wiring between adjacent areas, either through an excess of anatomical connections or defective pruning, (2) disinhibition between adjacent areas, (3) increased feedback connections between successive stages of the sensory hierarchy and (4) excess activity between successive stages in the hierarchy as a result of disinhibition of feedback connections.

We use the expression 'cross-wiring' somewhat loosely; indeed the more neutral phrases 'cross-activation' or 'crosstalk' might be preferable. Bearing in mind the enormous number of reciprocal connections even between visual areas that are widely separated (e.g., Felleman & Van Essen, 1991; Van Essen & De Yoe, 1995), the strengthening (or failure of developmental pruning) of *any* of these connections could lead to cross-activation of brain maps that represent different features of the environment. However, since the length of neural connections tends to be conserved developmentally (Johnson & Vecera, 1996; Kaas, 1997), anatomically close maps are also often more likely to be cross-wired at birth, thereby providing greater opportunity for the enhanced cross-wiring that might underlie synaesthesia (Kennedy *et al*., 1997). Furthermore, instead of the creation of an actual excess of anatomical connections, there may be merely a failure of inhibition between adjacent regions causing leakage between areas that are normally insulated from each other (Baron-Cohen *et al*., 1993). Future imaging studies (Hubbard *et al*., preparation), augmented by ERPs should help to resolve the issue.

Top-Down Influences in Synaesthesia

Although we have so far focussed on cross-wiring and early sensory effects, it does not follow that synaesthesia cannot be affected by top-down influences. We have conducted several experiments to demonstrate such effects.

First, we have shown that, when presented with a hierarchical figure (say a '5' composed of '3's; see fig. 5), JC and ER can voluntarily switch back and forth between seeing the 'forest' and the 'trees', alternating between seeing (say) red and green (Ramachandran, 2000a). This shows that although the phenomenon is sensory, it can be modulated by top-down influences, such as attention.

Second, when we show our synaesthetic subjects a display like 'THE CAT' (see fig. 6) they report that they see the correct colour for the 'H' and the 'A' immediately, even though the two forms are identical. Hence, although the visual form is necessary for the perception of the colours, the way in which it is classified is important in determining which colour is actually evoked.

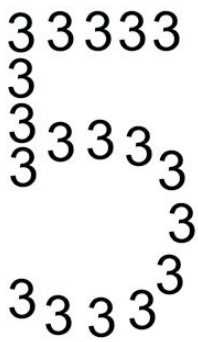

Figure 5.
Hierarchical figure demonstrating top-down influences in synaesthesia. When our synaesthetic subjects attend to the global 5, they report the colour appropriate for viewing a 5. However, when they shift their attention to the 3s that make up the 5, they report the colour switching to the one they see for a 3.

Third, when we presented another synaesthete with a display that could either be seen as the letters 'I' and 'V' or as the Roman numeral four (fig. 6), he reported seeing the colour appropriate to letters when the display was perceived as letters, but not when it was perceived as the numeral four.

Taken together, these experiments demonstrate that synaesthesia can also be strongly modulated by top-down influences. However, this should not be taken to imply that grapheme–colour synaesthesia is a conceptual phenomenon. Instead, it merely indicates that, like many other perceptual phenomena such as the famous Rubin face–vase or the Dalmatian, cognitive influences can also influence early sensory processing (Churchland *et al*., 1994).

Figure 6. Ambiguous stimuli demonstrating further top-down influences in synaesthesia. Left: When presented with the ambiguous H/A form in THE CAT, both of our synaesthetes reported that they experienced different colours for the H and the A, even though the physical stimulus was identical in both cases. Right: When presented with a display of this sort, that could be seen as either the Roman numeral 4 or the letters IV, our synaesthetes reported that they spontaneously saw the colours switch back and forth as the percept switched back and forth between the Roman numerals and letters.

Unitization Affects Synaesthesia

To further explore the idea that top-down influences affect synaesthesia, we presented the sentence 'Finished files are the result of years of scientific study combined with the experience of years' and other such examples of unitization (Goldstone, 2000; LaBerge & Samuels, 1974) to one of our higher synaesthetes (RT) and asked her to count the number of 'F's in it. Non-synaesthetes usually detect only three — they are 'blind' to 'F' in the three 'of's because words such as 'of' come to be treated as single lexical units. Likewise, our synaesthete said that she initially saw only three 'red graphemes' in the sentence, but on careful scrutiny saw all six 'F's tinged red, implying that the unitization constrains the emergence of the synaesthetic colour. Whether the result would be different for lower and higher synaesthetes (see below) remains to be seen.

Synaesthesia and Visual Imagery

We find that most synaesthetes report that when they *imagine* the numbers, the corresponding colours are evoked more strongly than by actual numbers, although we have seen occasional exceptions to this rule. This may be because engaging in mental imagery partially activates both category-specific regions involved in visual recognition (O'Craven & Kanwisher, 2000) and early visual pathways (Farah, 2000; Farah *et al*., 1992; Klein *et al*., 2000; Kosslyn *et al*., 1999; 1995). Depending on the locus of cross-wiring (whether they are higher, lower or mixed synaesthetes), the extent and locus of top-down partial activation, and the extent to which this is vetoed by *real* bottom-up activation from the retina, there may be varying degrees of synaesthesia induced by imagery in different subjects.

We are currently investigating these issues using the 'Perky effect' (Perky, 1910; Craver-Lemley & Reeves, 1992), an effect that provides an elegant technique for probing the elusive interface between imagery and perception. In Perky's original experiment, subjects looked at a translucent white screen and were asked to imagine common objects. Using a slide projector, a real image of the object was back-projected on the screen and gradually made brighter. Remarkably, even though the projected object would have been clearly visible under normal circumstances (that is, it was clearly above threshold), subjects failed to report the presence of the image. More recent work has clearly shown that this is not a simple criterion shift, but rather, is a true reduction in perceptual sensitivity (Craver-Lemley & Reeves, 1992; Segal, 1971).

An analogous experiment can be performed on synaesthetic subjects. One could show them a red number on a white background at varying contrasts. If we then test synaesthetes and non-synaesthetes to determine the lowest contrast (or saturation) at which they can detect the number, would synaesthetes find it harder to detect this than non-synaesthetes? And would the outcome be different for higher and lower synaesthetes? As a control one could measure the threshold for detecting the 'wrong' colour, say green, introduced into the number.

Higher and Lower Synaesthetes

The findings we have discussed so far were true for the first two synaesthetes we tested: They both saw colours only in central vision and only with Arabic numbers. However, we have subsequently encountered other synaesthetes in whom even the Roman numeral or a cluster of dots elicited the colour. In them it is the *concept* of numerical magnitude that seemed to generate colours. Intriguingly, in some synaesthetes, even days of the week or months of the year were coloured. Could it be that there is a brain region that encodes the abstract numerical *sequence* or *cardinality* — in whatever form — and perhaps in these synaesthetes, it is this higher or more abstract number area that is cross-wired to the colour area?

A suitable candidate is the angular gyrus in the left hemisphere. It has been known from several decades of clinical neurology that this region is concerned with abstract numerical calculation; damage to it causes acalculia (Gerstmann, 1940; Grewel, 1952; Dehaene, 1997). The patient cannot do even simple

arithmetic such as multiplication or subtraction. Remarkably, the subsequent colour areas in the cortical colour-processing hierarchy lie in the superior temporal gyrus, adjacent to angular gyrus (Zeki & Marini, 1998). It is tempting to postulate that these two regions — the higher colour area and the abstract numerical computation area are cross-wired in some synaesthetes. Indeed, depending on the level at which the gene is expressed (fusiform or angular), the level of cross-wiring would be different so that one could loosely speak of 'higher' synaesthetes and 'lower' synaesthetes.[7]

Perhaps the angular gyrus represents the abstract concept of numerical sequence or cardinality and this would explain why in some higher synaesthetes even days of the week or months of the year elicit colours. Consistent with this hypothesis, Spalding & Zangwill (1950) report a patient with a gunshot wound, which entered near the right angular gyrus and lodged near the left temporal–parietal junction. Five years after injury he complained of spatial problems and showed difficulty in number tasks. In addition, the patient, who experienced synaesthesia prior to the injury, complained that his 'number plan', his forms for months, days of the week and letters of the alphabet, was no longer distinct. In view of this, it might be interesting to see if patients with angular gyrus lesions have difficulty with tasks involving sequence judgment (e.g., days of the week). Furthermore, it would be interesting to see if, in these higher synaesthetes, runs of colours corresponding to numerical sequences match up at least partially with runs corresponding to weeks or months.

One clear prediction is that the psychophysical properties of the colours evoked in higher synaesthetes might be different from those of lower synaesthetes, since different cortical colour areas are involved. For example, in higher synaesthetes the colours might not fall off with eccentricity and/or might not be produced if crowding masks the grapheme.[8] Another such difference is that

[7] Our distinction between higher and lower synaesthesia is orthogonal to Martino and Marks' distinction (2001) between 'strong' and 'weak' synaesthesia. We believe that both higher and lower synaesthesia represent a form of strong synaesthesia, but involve different hierarchical levels and have different neuroanatomical correlates. Our view also differs from Martino and Marks' in that they do not consider the anatomy, while ours is specifically based on possible neuroanatomical divisions.

[8] Several intriguing new questions are raised by these speculations: What if the grapheme is embedded in a word but is silent (e.g., as with the 'p' in 'psychology')? Is the 'p' tinged the same colour in psychology as in Pat? In JC, this was the case; the fact that it was silent didn't matter, whereas a second subject reported that the silent /p/ lost its colour when he was reading fast but not when he read slowly. If a synaesthete is bilingual (e.g., Japanese and English), would visually dissimilar graphemes that represent the same phoneme (in Japanese and English characters) evoke the same or different colours? We have encountered both types; the answer seems to depend on whether one is dealing with higher or lower synaesthetes. Until we know more about the neural underpinnings of synaesthesia we must be prepared for some surprises. For instance, we usually find that upper and lower case letters evoke the same colour, and the lower case letters were usually less saturated, 'shiny' or 'patchy' compared to the upper case letter. (However, we recently encountered an exception. In subject SP most letters followed the rule but one letter had completely different colours for upper and lower case: E was green, e was red.) Also, in JC, even the actual font seemed to matter; different fonts would evoke the same approximate colour but slightly different hue values. Subitizable dot clusters are usually seen as not coloured (although this might depend on whether the subject is a higher or lower synaesthete). For example, subject RT said 'When you roll the dice, I know it's a six or a four but I don't see colours. But, if I *say* "Hey I got a five" and I imagine five then the colour is seen'. It would be interesting to test Japanese-American synaesthetes to see if /r/ and /l/ evoke the same colour or not given that they sound the

higher synaesthetes may require more focussed attention in order to experience their colours. This would be consistent with data supporting the idea that attentional gating is more effective at higher levels of the visual hierarchy (Moran & Desimone, 1985).

Finally, consider the so-called 'number line' (Dehaene *et al.*, 1990) seen in normal subjects. If we ask subjects which of two numbers is bigger, '2 or 4?', or, '2 or 15?', remarkably, the reaction time (RT) is not the same; they take longer in the first case than in the second. It has been suggested that there is an analogue representation of numbers in the brains — a 'number line' which can be read off from to determine which number is bigger — and obviously it will be more difficult if the numbers are closer on this line (Dehaene, 1997).

Galton (1880) found that some otherwise normal people claimed that when they visualized numbers, each number always occupied a specific location in space. Numbers that were close (e.g., 2 and 4) were close spatially in this imaginary space, so that if all the number locations were mapped out they formed a continuous line with no breaks or jumps. However, even though the line was continuous, it was not straight. It was often highly convoluted, even curving back on itself. We have two subjects with this condition in our sample of synaesthetes.[9]

Unfortunately, other than the subjects' introspective reports, there has not been a single study that demonstrates objectively that these subjects really do have a complex convoluted number line. To demonstrate this we propose the following experiment. One could give them two numbers that are *numerically* far apart (e.g. 2 and 15) but *spatially* close together because of the convoluted number line. If so, would the reaction time for responding which number is bigger depend on proximity in abstract number space or would the subject take a 'short-cut' (e.g., if the convoluted line doubles back on itself, 2 and 15 may be closer to each other 'as the crow flies' but farther along the number line itself)? Such a result would provide objective evidence for the subjective reports of these synaesthetes in a manner analogous to the texture segregation and crowding experiments for grapheme–colour synaesthetes described above. This experiment may also provide an experimental method to differentiate higher and lower synaesthetes, since lower synaesthetes may not experience the convoluted number line, and therefore may not demonstrate the effect predicted above.

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same to them. Lastly, we have also noticed some intriguing spatial interaction effects between synaesthetically induced colours. In some synaesthetes, the colour of the first grapheme seems to dominate: It influences the perceived colour of the entire word (or even non-word). Also, if different graphemes in a word evoke similar colours, the colours tend to enhance each other, whereas if they evoke dissimilar colours the colours tend to weaken each other (especially when they are close together). Surely, observations such as these may eventually give us valuable insights into the manner in which neurons in the human brain represent knowledge (we have dubbed this new discipline 'neuro-epistemology').

[9] In one of our subjects, the number line is a series of segments going upwards and rightwards, with the distance decreasing between numbers as the numerical magnitude increases. The number line continues left of fixation to represent negative numbers and its shape is a mirror reflection — on both axes — of the number line for positive numbers. Additionally, the graphemes on the number line are are seen to be rotated so that they remain orthogonal to the line. In the other, the number line is curved, and does not extend into the negative numbers.

Finally, we should note that it is possible that the distribution of gene expression and level of cross-activation is not bimodal; hence the heterogeneity of the phenomenon. Indeed, one might expect to encounter 'mixed' types rather than just higher and lower. Ironically it is this heterogeneity that has often caused researchers to avoid studying synaesthesia altogether or led them to conclude that the whole phenomenon is bogus.

Artists, Poets and Synaesthesia

Synaesthesia is purported to be more common in artists, poets and novelists (Dailey *et al*., 1997; Domino, 1989; Root-Bernstein & Root-Bernstein, 1999). For example, Domino (1989) reports that, in a sample of 358 fine-arts students, 84 (23%) reported experiencing synaesthesia. This incidence is higher than any reported in the literature (see above), suggesting that synaesthesia may be more common among fine-arts students than the population at large. Domino then tested 61 of the self-reported synaesthetes and 61 control subjects (equated on gender, major, year in school and verbal intelligence) on four experimental measures of creativity. He found that, as a group, synaesthetes performed better than controls on all four experimental measures of creativity. While this study has the advantage of using an experimental method to assess creativity, it suffers a severe limitation in that no experimental tests were conducted to assess synaesthetic experiences. Further studies making use of our objective experimental measures of synaesthesia are clearly required to confirm this result.

How can the cross-wiring hypothesis explain these results? One thing these groups of people have in common is a remarkable facility linking two seemingly unrelated realms in order to highlight a hidden deep similarity (Root-Bernstein & Root-Bernstein, 1999). When Shakespeare writes 'It is the East and Juliet is the sun', our brains instantly understand this. You don't say, 'Juliet is the sun. Does that mean she is a glowing ball of fire?' (Schizophrenics might say this; they often interpret metaphors literally). Instead, your brain instantly forms the right links, 'She is warm like the sun, nurturing like the sun, radiant like the sun' and so on. How is this achieved?

It has often been suggested that concepts are represented in brain maps in the same way that percepts (like colours or faces) are. One such example is the concept of number, a fairly abstract concept, yet we know that specific brain regions (the fusiform and the angular) are involved. Perhaps many other concepts are also represented in non-topographic maps in the brain. If so, we can think of metaphors as involving cross-activation of conceptual maps in a manner analogous to cross-activation of perceptual maps in synaesthesia.

If this idea is correct then it might explain the higher incidence of synaesthesia in artists and poets. If mutation-induced cross-wiring selectively affects the fusiform or angular gyrus someone may experience synaesthesia. However, if this mutation is more diffusely expressed it may produce a more generally cross-wired brain creating a greater propensity and opportunity for creatively mapping from one concept to another (and if the hyperconnectivity also involves

sensory-to-limbic connections the reward value of such mappings would also be higher among synaesthetes).[10]

The Angular Gyrus and Synaesthetic Metaphors

In addition to its role in abstract numerical cognition, the angular gyrus has long been known to be concerned with cross-modal association (which would be consistent with its strategic location at the crossroads between the temporal, parietal and occipital lobes). Intriguingly, patients with lesions here tend to be literal minded (Gardner, 1975), which we would interpret as a difficulty with metaphor. However, no satisfactory explanation has yet been given for this deficit.

Based on what we have said so far, we would argue that the pivotal role of the angular gyrus in forming cross-modal associations is perfectly consistent with our suggestion that it is also involved in metaphors — especially cross-modal metaphors. (Indeed, we recently saw an anomic aphasic with left angular gyrus damage who, unlike normals, showed no propensity for the bouba/kiki effect described in the next section.) It is even possible that the angular gyrus was originally involved only in cross-modal metaphor but the same machinery was then co-opted during evolution for other kinds of metaphor as well. Our idea that excess cross-wiring might explain the penchant for metaphors among artists and poets is also consistent with data suggesting that there may be a larger number of cross connections in specific regions of the right hemisphere (Scheibel *et al.*, 1985), and the observed role of the right hemisphere in processing non-literal aspects of language (Anaki *et al.*, 1998; Brownell *et al.*, 1990).

We realize that this is an unashamedly phrenological view of metaphor and synaesthesia. The reason it may seem slightly implausible at first is because of the apparent *arbitrariness* of metaphorical associations (e.g., 'a rolling stone gathers no moss'). Yet, metaphors are *not* arbitrary. Lakoff and Johnson (1980) have systematically documented the non-arbitrary way in which metaphors are structured, and how they in turn structure thought. A large number of metaphors refer to the body and many more are inter-sensory (or synaesthetic). Furthermore, we have noticed that synaesthetic metaphors (e.g., 'loud shirt') also respect the directionality seen in synaesthesia (Day, 1996; Ullman, 1945; Williams, 1976). That is, they are more frequent one direction than the other (e.g., from the auditory to the visual modality). We suggest that these rules are a result of strong anatomical constraints that permit certain types of cross-activation, but not others.

Evolution of Language

One of the oldest puzzles in psychology is the question of how language evolved. The problem is that several interlocking pieces needed to co-evolve. But how could this have happened given that evolution has no foresight? Alfred Russell Wallace was so frustrated in trying to answer this that he felt compelled to invoke

[10] This argument does not address the important question of why almost anyone can *understand* a metaphor once it is spelled out, but only a gifted few (the ones with more cross-wired brains in our scheme) can be creative in generating them. Why is such excess cross-wiring needed only for producing metaphors but not for recognizing them?

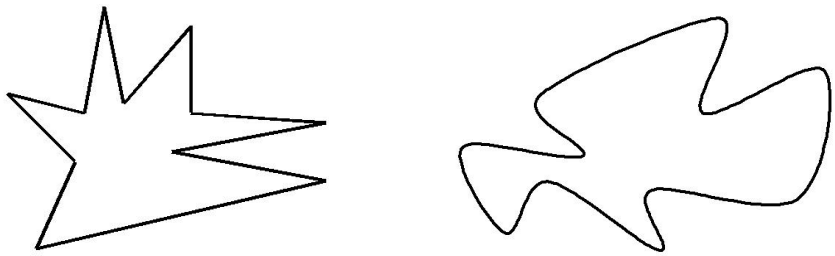

Figure 7. Demonstration of kiki and bouba. Because of the sharp inflection of the visual shape, subjects tend to map the name kiki onto the figure on the left, while the rounded contours of the figure on the right make it more like the rounded auditory inflection of bouba.

divine intervention. More recently, even Chomsky, the founding father of modern linguistics, has expressed the view that, given the complexity of language, it could not have possibly evolved through natural selection.

Our solution to the riddle of language origins comes from synaesthesia. To understand this argument, we need to put together several ideas.

First, consider stimuli like those shown in figure 7, originally developed by Köhler (1929; 1947) and further explored by Werner (1934; 1957; Werner & Wapner, 1952). If you show fig. 7 (left and right) to people and say 'In Martian language, one of these two figures is a "bouba" and the other is a "kiki", try to guess which is which', 95% of people pick the left as kiki and the right as bouba, even though they have never seen these stimuli before.[11] The reason is that the sharp changes in visual direction of the lines in the right-hand figure mimics the sharp phonemic inflections of the sound kiki, as well as the sharp inflection of the tongue on the palate. The bouba/kiki example provides our first vital clue for understanding the origins of proto-language, for it suggests that there may be natural constraints on the ways in which sounds are mapped on to objects.[12]

Second, we propose the existence of a kind of sensory-to-motor synaesthesia, which may have played a pivotal role in the evolution of language. A familiar example of this is dance, where the rhythm of movements synaesthetically mimics the auditory rhythm. This type of synaesthesia may be based on cross- activation not between two sensory maps but between a sensory (i.e., auditory) and a motor map (i.e., Broca's area). This means that there would be a natural bias towards mapping certain sound contours onto certain vocalizations.

This somewhat speculative proposal gains credibility from recent work on 'mirror neurons' by Rizzolatti and colleagues (di Pellegrino, *et al*., 1992; Fadiga *et al*., 2000; Rizzolatti *et al*., 2001). These are neurons found in the ventral premotor area in monkeys and (possibly) humans (Altschuler *et al*., 1997; 2000;

[11] In his original experiments, Köhler (1929) called the stimuli *takete* and *baluma*. He later renamed the *baluma* stimulus *maluma* (Köhler, 1947). However, the results were essentially unchanged and 'most people answer[ed] without hesitation' (p. 133). (For further discussion, see Lindauer, 1990; Marks, 1996.) Our results again confirm these findings with a different set of stimuli and different names.

[12] This idea reminded us of the onomatopoeic theory of language origins ('bow-wow' = dog) but is quite different in that the relationship between the visual appearance of a dog and the *sound* made by a dog is completely arbitrary (unlike the kiki/bouba example). The case of 'suck', which is the actual sound produced when you suck may be an interesting hybrid example.

Iacoboni *et al*., 1999). Most neurons in this area will fire when the monkey performs complex manual tasks (e.g., grasping a peanut, pulling something or pushing something). But a subset of them, mirror neurons, will fire even when the monkey watches another 'actor' monkey or human performing the same action. We can think of these neurons as doing an internal simulation of such actions.[13]

Another piece of circumstantial evidence for the notion of sensorimotor synaesthesia (and its possible link to mirror neurons) is the occurrence of a rare form of synaesthesia in which sounds evoke the automatic and uncontrollable adoption of certain, highly specific postures (Devereux, 1966).

Putting these ideas together, we conjecture that the representation of certain lip and tongue movements in motor brain maps may be mapped in non-arbitrary ways onto certain sound inflections and phonemic representations in auditory regions and the latter in turn may have non-arbitrary links to an external object's visual appearance (as in bouba and kiki).[14] The stage is then set for a sort of 'resonance' or bootstrapping in the co-evolution of these factors, thereby making the origin of proto-language seem much less mysterious than people have assumed (see figure 8).

We would also point out that lip and tongue movements and other vocalizations may be synaesthetically linked to objects and events they refer to in closer ways than we usually assume and this may have been especially true early in the evolution of the proto-language of ancestral hominids, e.g., words referring to something small often involve making a synaesthetic small /ɪ/ with the lips and a narrowing of the vocal tracts (e.g., words such as 'little', 'petite', 'teeny' and 'diminutive') whereas the opposite is true for words denoting large or enormous.[15]

A third, important factor that may have contributed to this bootstrapping is synaesthesia caused by cross-activation between two motor maps rather than between two sensory maps (a better phrase might be 'synkinaesia'). For example, Darwin (1872) noted that when cutting something with a pair of scissors we often unconsciously clench and unclench our jaws, as if to sympathetically mimic the hand movements; in our scheme this would be an example of synkinaesia between the motor maps for the mouth and hand, which are right next to each other in the Penfield motor homunculus of the pre-central gyrus. In the example cited above, mouth shape for 'petite', 'teeny' and 'diminutive' might be synkinetic

[13] With knowledge of these neurons, you have the basis for understanding a host of puzzling aspects of the human mind: 'mind reading', empathy, imitation learning (Iacoboni *et al*., 1999; Ramachandran, 2000b), and even the evolution of language (Rizzolatti & Arbib, 1998).

[14] Brent Berlin provides an especially relevant example (Berlin, 1994). He presented English speakers with fish and bird names from a language completely unrelated to English (Huambisa, a language of the Jivoran language family in north central Peru). He found that English speakers were able to correctly discriminate bird names from fish names significantly more often than chance, even though they had never heard Huambisa, and it bears no family resemblance to English. After further analyses to rule out onomatopoeia, Berlin concludes that this is evidence for universal sound symbolism of the sort we describe here.

[15] This currently quite contentious issue is being studied within linguistics under the banner of 'phonesthemes' or sound symbolism (see, for example, Hinton *et al*., 1994). Recent research has supported the concept of phonesthemes in English (Hutchins, 1999) and cross-linguistically (Berlin, 1994). Our new studies on synaesthesia and our speculations on language origins obviously have considerable relevance to this issue of universal sound symbolism.

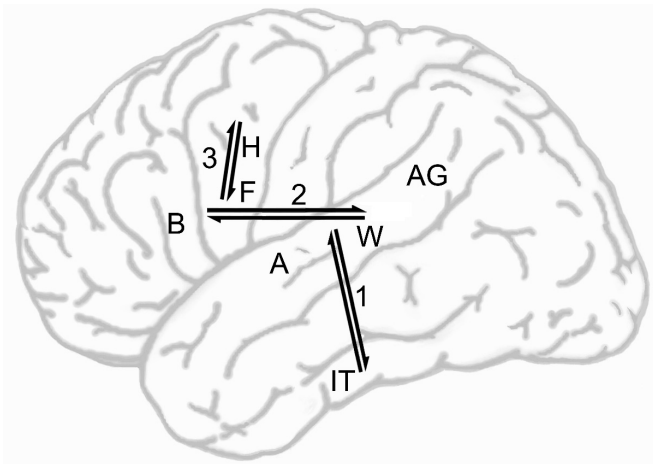

Figure 8. A new synaesthetic bootstrapping theory of language origins.

Arrows depict cross-domain remapping of the kind we postulate for synaesthesia in the fusiform gyrus. (1) A non- arbitrary synaesthetic correspondence between visual object shape (as represented in IT and other visual centers) and sound contours represented in the auditory cortex (as in our bouba/kiki example). Such synesthetic correspondence could be based on either direct cross-activation or mediated by the angular gyrus – long known to be involved in inter-sensory transformations. (2) Cross domain mapping (perhaps involving the arcuate fasiculus) between sound contours and motor maps in or close to Broca's area (mediated, perhaps, by mirror neurons). (3) Motor to motor mappings (synkinesia) caused by links between hand gestures and tongue, lip and mouth movements in the Penfield motor homunculus (e.g., the oral gestures for 'little' or 'diminutive' or 'teeny weeny' synkinetically mimic the small pincer gesture made by opposing thumb and index finger (as opposed to 'large' or 'enormous'). The cross-wiring would necessarily require transforming a map of two dimensional hand gestures into one-dimensional tongue and lip movements (e.g., the flexion of the fingers and palmar crease in 'come hither' is mimicked by the manner in which the tongue goes back progressively on the palate). And you pout your lips to say 'you', 'vous' or 'thoo' as if to mimic pointing outward whereas 'me', 'mois' and 'I' mimic pointing inwards towards yourself. If such oral echoes of hand gestures are accompanied by emotional guttural utterances it would lead to the creation of early proto-words. Notice that each of these effects might be quite small but through progressive mutual bootstrapping they could have evolved into the shared vocabulary of early hominids. Add to this additional bootstrapping provided by co-opting the circuits originally used for symbol manipulation, semantics and tool manipulation, and you have fully modern language (e.g., the use of tools requires sub-assemblies such as attaching a head to a handle before hammering a nail – and this has the same formal logical structure as hierarchical syntactic tree of language). We are currently testing these ideas by studying aphasics.

mimicry of the pincer-like opposition of thumb and forefinger to denote small size. Also, when pointing I use my index finger to point outward to you. I also produce a partial outward pout with my lips (as in English 'you', French 'tu' or 'vous' and Tamil 'thoo'), whereas when I point inward to myself, my lips and tongue move inwards (as in English 'me', French 'moi' and Tamil 'naan') In this manner a primitive vocabulary of gesture and pantomime could evolve through synkinaesia into a corresponding vocabulary of tongue/palate/lip movements (causing vocalizations, especially if accompanied by guttural utterances).

We are suggesting that these factors provided the initial impetus for language evolution, not that all modern language is synaesthetic in origin. The subsequent elaboration and refinement of the deep structure of language may have relied on other environmental selection pressures and biological constraints unrelated to

synaesthetic metaphor (and, indeed, was probably guided by offline, hierarchic, symbol manipulation as well as *semantic* constraints, mediated by influences from the Wernicke's area). It is, however, the *initial* emergence of a complex multi-component trait that usually poses a challenge for evolution through natural selection, and that is what we are trying to explain here. That is, our theory really pertains to the origin of *proto-language* rather than Chomskyan universal grammar, but we believe that given the pre-adaptation provided by proto-language, Chomskyan UG could have evolved more readily. Additionally, numerous thinkers (Bickerton, 1995; Devlin, 2000; Lieberman, 1992) have pointed out that syntactic structure may have arisen from the pre-adaptation provided by syllabic structure.

The key idea here is that each of these different effects (synaesthesia between object appearance and sound contour, between sound contour and vocalizations, and synkinaesia) in *isolation* may have been too small to have exerted adequate selection pressure for the emergence of proto-language, but a bootstrapping between all of them acting together may have indeed been sufficient. (And then add to this an additional bootstrapping between the syllabic structure, symbol manipulation and the syntactic/hierarchical structure, and you have fully evolved language.)

Another example of a 'synaesthetic metaphor' found in everyone is the use of the word 'disgusting'. We say this in response to unpleasant smells and tastes while at the same time raising our hands up and scrunching up our noses (Darwin showed that even a newborn infant would do this — suggesting that it is 'hard-wired'). The olfactory bulb projects to the orbito-frontal cortex, and olfactory and gustatory 'disgust' is almost certainly mediated by this part of the frontal lobes. But why do we use the same word, 'disgusting', and make the same face in response to someone whose behaviour is *morally* disgusting (e.g. , a drunk making an unwelcome sexual pass at a woman)? This is unlikely to be coincidence since it is cross-cultural: The Tamil phrase for moral disgust means 'he smells bad' and the French word 'dégoûtant(e)' (used for social situations) literally means, 'bad tasting'. We would argue that this usage emerged because moral and social disgust is also mediated by the orbito-frontal cortex; i.e., it is yet another example of cross-wiring or even of the same brain map being used for two seemingly unrelated functions (given evolution's tendency to be opportunistic in using pre-existing hardware). Early mammals may have used the orbito-frontal cortex exclusively for olfactory and gustatory disgust, but as mammals became more social it came to communicate or signal olfactory disgust to others (stay away from that rotten food) and then eventually to communicate moral and social disgust (stay away from that rotten man). This is how evolution works, given that there is no master design ('God is a hacker', as Francis Crick has said).

Even the great apes may have some such synaesthetic scatological propensities. When Washoe wanted to 'sign' her disgust at someone's behaviour she used the same word as for faeces (and indeed apes throw faeces at humans whom they are disgusted with).

One wonders, also, whether there exists a genetically based synaesthetic link between sex and aggression (and if so could this have anything to do with the proximity of nuclei concerned with sex with those concerned with aggression in

the hypothalamus)? Again, the use of sexually loaded words as aggressive swear words ('F*** you') appears to be cross-cultural. In French, the equivalent phrase is 'Va t'en faire f**tre', which translates to something like 'Go F*** yourself'. If there is no genetic basis related to anatomical/neural constraints, why do all (or most) languages say 'F*** you' and one never hears 'Bite you', which would be the more logical choice given the obvious *semantic* associations between biting and aggression?

Hyperconnectivity and Emotions

Synaesthetes often report strong emotions in response to multi-sensory stimuli (both positive and negative depending on whether the associations are the 'right' or 'wrong' ones). Additionally, patients with temporal lobe epilepsy seem to have a propensity towards synaesthetic experiences. Why?

Despite these subjective reports, there is no clear experimental validation of the claim that synaesthetes have strong responses to 'discordant' sensory inputs, leading one to wonder, is their aversion to such stimuli any different from what a non-synaesthete experiences when confronted with, say, a blue carrot or green rose? Anecdotally this seems to be true; one of our synaesthetes claimed that incorrectly coloured numbers were 'ugly' and felt like 'nails scratching on the blackboard'. Conversely, when numbers were the correct colour it 'felt right, like the "aha" when the solution to a problem finally emerges'. Assuming that the claim is true, can we explain it in terms of our cross-wiring or cross-activation hypothesis of synaesthesia?

Visual information that is 'recognized' by the cortex of the temporal lobe (e.g. the fusiform) ordinarily gets relayed to the amygdala, nucleus accumbens and other parts of the limbic system (Amaral *et al*., 1992; LeDoux, 1992). These structures evaluate the significance of the object, so that we may speak of the amygdala and nucleus accumbens as developing an 'emotional salience map' of objects and events in the world. If the object is emotionally significant or salient such as a predator, prey or mate, the message gets relayed to the hypothalamic nuclei to prepare the body for fighting, fleeing or mating. Neural signals cascade from the limbic structures down the autonomic nervous system to decrease gastric motility and increase heart rate and sweating (e.g., Lang *et al*., 1964; Mangina & Beuzeron-Mangina, 1996). This autonomic arousal can be measured by monitoring changes in skin conductance caused by sweat — the skin conductance response (SCR) — which provides a direct measure of emotional arousal and limbic activation. Typically, if you look at neutral objects such as a table or chair there is no arousal or change in SCR, but if you look at prey, mate or predator, there is.

We have suggested that a mutation that causes hyperconnectivity (either by defective pruning or reduced inhibition) may cause varying degrees and types of synaesthesia, depending on how extensively and where in the brain it is expressed (in turn modulated by transcription factors). Now imagine what would happen if there were hyperconnectivity between the fusiform gyrus (and other sensory cortices) and the limbic system (especially the amygdala and nucleus accumbens). If we assume that one's aesthetic and emotional responses to sensory inputs depend

on these connections, then presenting a discordant input, such as a grapheme in the wrong colour, would produce a disproportionately large emotional aversion (like 'nails scratching on a blackboard') and, conversely, harmonious blends of colour and grapheme will be especially pleasant to look at (which may involve the nucleus accumbens rather than the amygdala). The net result of this will also be a progressive 'bootstrapping' of pleasurable or aversive associations through limbic reinforcement of concordant and discordant inputs. This, by the way, allows us to also invoke a form of learning in the genesis of synaesthesia.

In order to test this idea, one could measure the SCR in synaesthetes in response to an incorrectly coloured number and compare this response to one produced in a non-synaesthetic subject who is looking at blue carrots. A non-synaesthete might be a bit amused or puzzled by the blue carrot but she is unlikely to say it feels like nails scratching on a blackboard. We would therefore predict a bigger SCR in the synaesthete looking at the incorrectly coloured grapheme than in control subjects.

The hyperconnectivity explanation for synaesthesia is also consistent with the claim that the phenomenon is more common among patients with temporal lobe epilepsy (TLE). The repeated seizure activity is likely to produce 'kindling' (causing hyperconnectivity between different brain regions) which would explain reports of synaesthesia in TLE (see e.g., Jacome, 1999). Furthermore, if the seizures (and kindling) were to strengthen the sensory–amygdala connections, then TLE patients might also be expected to have heightened emotional reactions to specific sensory inputs. There are strong hints that this is the case (Ramachandran *et al*., 1997).[16]

Something along these lines may also explain why some famous artists have had TLE, Van Gogh being the most famous example (e.g., Kivalo, 1990; Meissner, 1994). If our scheme is correct his heightened emotions in response to colours and visual attributes (resulting from kindling) might have indeed fuelled his artistic creativity.

Synaesthesia and the Philosophical Riddle of Qualia

Finally, the study of the unusual sensory experiences of synaesthetes may also shed light on the philosophical problem of qualia. There is now a growing consensus that the best way to solve this ancient philosophical riddle is to narrow down the neural circuitry (Crick & Koch, 1995; 1998; Metzinger, 2000) and, especially, the functional logic (Ramachandran & Blakeslee, 1998; Ramachandran & Hirstein, 1997) of those brain processes that are qualia laden as opposed to those that are not (e.g., the reflexive contraction of the pupil in response to light can occur in coma; however, there is no qualia as when you are awake and see a red

[16] There are also anecdotal reports that synaesthesia might be more common among individuals with perfect pitch. Given that people with perfect pitch have an enlarged auditory representation in the superior temporal gyrus (planum temporale) (Schlaug *et al*., 1995), we would predict that this enlargement may allow hyperconnectivity to occur more readily between auditory and colour maps, producing a higher incidence of sound–colour synaesthesia. This explanation reverses the traditional causal arrow that perfect pitch may be more common in people with synaesthesia because the colours allow people to uniquely identify the tones.

rose). One strategy used to explore the neural basis of qualia is to hold the physical stimulus constant, while tracking brain changes that co-vary with changes in the conscious percept (e.g., Sheinberg & Logothetis, 1997; Tong & Engel, 2001). In the case of synaesthesia, we are making use of the same strategy, but using pre-existing, stable differences in the conscious experiences of people who experience synaesthesia compared with those who do not.

Ramachandran and Hirstein (1997) have suggested three 'laws' of qualia; functional criteria that need to be fulfilled in order for certain neural events to be associated with qualia (a fourth has recently been added; see Ramachandran & Blakeslee, 1998). Of course, this still doesn't explain *why* these particular events are qualia laden and others are not (Chalmer's 'hard problem') but at least it narrows the scope of the problem.

The four laws are:

1) Qualia are irrevocable and indubitable. You don't say 'maybe it is red but I can visualize it as green if I want to'. An explicit neural representation of red is created that invariably and automatically 'reports' this to higher brain centres.
2) Once the representation is created, what can be *done* with it is open-ended. You have the luxury of choice, e.g., if you have the percept of an apple you can use it to tempt Adam, to keep the doctor away, bake a pie, or even just to eat. Even though the representation at the *input* level is immutable and automatic, the *output* is potentially infinite. This isn't true for, say, a spinal reflex arc where the output is also inevitable and automatic. Indeed, a paraplegic can even have an erection and ejaculate without an orgasm.
3) Short-term memory. The input invariably creates a representation that persists in short-term memory — long enough to allow time for choice of output. Without this component, again, you get just a reflex arc.
4) Attention. Qualia and attention are closely linked. You need attention to fulfil criterion number two; to *choose*. A study of circuits involved in attention, therefore, will shed much light on the riddle of qualia.

Based on these laws, and the study of brain-damaged patients, we have suggested that the critical brain circuits involved in qualia are the ones that lead from sensory input to amygdala to cingulate gyrus (Ramachandran & Hirstein, 1997).

Synaesthesia — the 'blending' of different sensory qualia — obviously has relevance to the qualia problem, as first pointed out by Jeffrey Gray (Gray *et al.*, 1997; Gray, 1998). In particular, we would argue that the lower synaesthetes have the qualia of red evoked when they see a '5' or hear C-sharp. But when you and I experience red while looking at a black-and-white picture of an apple, the red does not fulfil all four criteria specified above, so there is very little qualia (leaving aside the question of whether you can have partial qualia if some criteria alone are fulfilled). And lastly, the higher synaesthetes may be a borderline case. As such, they can be used to shed light on the nature of qualia as well as metaphor (such borderline cases can be valuable in science; consider the manner in which viruses helped us understand the chemistry of life).

To understand the importance of synaesthesia in illuminating the qualia problem consider the following thought experiment performed on your own brain. When you are asleep an evil East-coast genius, who we'll call DD, swaps or cross-wires the nerves coming into your brain from your ears and eyes. You then wake up. Consider the following places where the wiring could have been swapped.

1) If the swapping is done sufficiently early in sensory processing, the outcome is obvious: say the pathways from the auditory nucleus of the brain stem are diverted to the visual cortex and the optic radiations to the auditory cortex. Then you would 'hear' sights and 'see' sounds.
2) If the swapping were done at or close to the output stage (e.g., in Broca's area) where you generate the word 'red' or 'C-sharp', again, the answer would be obvious. You might say, 'When you play me that tone I know it's a tone and experience it as such but I feel an irresistible urge to *say* red' (like a patient with Tourette's Syndrome).

But now we come to the key question: What if the swapping or cross-wiring is done at some stage in between these two extremes? Is there a critical boundary between these two extremes, so if you cross wires after the boundary you merely experience an urge whereas if you cross wires before that boundary you literally see red? Is it a fuzzy boundary or a sharp one? We would argue that this boundary corresponds exactly to the point where the transition is made from the four laws of qualia being fulfilled (before the boundary) to where they are not fulfilled (after the boundary).

Of considerable relevance to this philosophical conundrum is a new observation that we made on a grapheme–colour synaesthete (Ramachandran and Hubbard, 2001a). This subject was colour anomalous (s-cone deficiency leading to a difficulty discriminating purples and blues) but intriguingly, he claimed to see numbers in colours that he could never see in the real world ('Martian colours'). This is yet another piece of evidence against the memory hypothesis — for how can you remember something you have never seen? On the other hand, the cross-wiring hypothesis explains it neatly. If we assume that the colour processing machinery in V4 in the fusiform is largely innate, then the genetically based cross-activation of cells in this area would evoke colour phosphenes even though the colours cannot be seen in the real world because of retinal cone deficiencies.

Indeed, even synaesthetes who are not colour blind sometimes say that the synaesthetically induced colours are somehow 'weird' or 'alien' and don't look quite the same as normal 'real world' colours. Previously, no satisfactory account has been proposed for this. The cross-wiring hypothesis explains this as well. For two reasons, the activation of cells in the visual centres caused by real world input is, in all likelihood, going to be somewhat different from the spurious or abnormal activation caused indirectly through numbers. First, given that it is abnormal, the cross-wiring is unlikely to be very precise. It might be slightly messy and this 'noise' may be experienced as weird Martian colours. This may be analogous to

phantom limb pain (also caused by abnormal cross-wiring, Ramachandran & Hirstein, 1998).

Second, the cross-activation obviously skips the earlier levels of the colour-processing hierarchy which may ordinarily contribute to the final qualia — and this unnatural stimulation might cause the subject to see Martian colours. The implication of this is that the experience of qualia may depend on the activation of the *whole* visual hierarchy (or a large part of it), not just the pontifical cells at the end of the chain.[17]

Summary and Conclusions

Synaesthesia has always been regarded as somewhat spooky. Even though it has been known for over 100 years, it has often been thought of as a curiosity — just a quirk based on early childhood memory associations or a mere metaphorical association between different sensory terms. Indeed, it has been largely ignored by mainstream neuroscience and psychology despite the fact that both Cytowic (1989; 1997) and Marks (e.g., 1975; 1982; 2000) have repeatedly emphasized its potential importance for understanding normal sensory function. More recently, interest in this phenomenon has been revived by the intriguing experimental work and theoretical speculations of Baron-Cohen, Harrison, Gray and colleagues (see above).

Although synaesthesia has been studied for over 100 years, our psychophysical experiments were the first to prove conclusively that synaesthesia is a genuine *sensory* phenomenon. Four lines of evidence support this: (1) Synaesthetically induced colours can lead to perceptual grouping, segregation and pop-out. (2) Synaesthetic colours are not seen with eccentric viewing even if the numbers are scaled in size to make them clearly visible. (3) A crowded grapheme that is not consciously perceived can nevertheless evoke the corresponding colour. (4) A colour-blind synaesthete sees colours in numbers that he cannot otherwise see in real-life visual scenes.

The results of Stroop-like interference tasks are sometimes cited as evidence for the view that synaesthesia is sensory (Mills *et al*., 1999) and sometimes for the conflicting view that synaesthesia is conceptual (Dixon *et al*., 2000; Mattingley *et al*., 2001) but neither inference is justified. Stroop interference merely shows that the association between the grapheme and the colour is *automatic*. Since Stroop-like interference can occur at *any* stage in the system — from perception all the way up to motor output (MacLeod, 1991) — it is completely uninformative in determining whether synaesthesia is perceptual or conceptual. The main strength of our psychophysical approach to synaesthesia is that we make systematic predictions instead of relying solely on the subjects' introspective reports. This is even more important for synaesthesia than for ordinary psychophysics since the subject is often trying to express the ineffable.

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[17] This point is consistent with current ideas of distributed processing. The six synaptic levels do not form a static hierarchy wherein neural transformations of one level are passed on to the next level in a conveyor-like fashion. Rather, three or four levels are co-active at any one time as expected in a distributed system (we are indebted to an anonymous reviewer for bringing this point to our attention; see also Churchland *et al*., 1994).

Having established the sensory nature of synaesthesia in our first two subjects, we propose a specific testable hypothesis: That grapheme–colour synaesthesia is caused by a mutation causing defective pruning and cross-activation between V4 (or V8) and the number area, which lie right next to each other in the fusiform gyrus. Although the cross-talk idea has been around for some time, no specific brain areas have been suggested and the idea is usually couched in vague terms that do not take advantage of known patterns of localization.

In addition to the lower synaesthetes (JC and ER) there also appear to be other types of number–colour synaesthetes in whom the effect may be more concept driven; i.e., the effect is conceptual rather than sensory. We suggest that in them the cross-activation occurs at a higher level — perhaps between the angular gyrus (known to be involved in abstract number representation) and a higher colour area in the vicinity that receives input from V4.

We suggest, further, that synaesthesia is caused by a mutation that causes defective pruning between areas that are ordinarily connected only sparsely. Various transcription factors may then influence the exact locus and extent to which the gene is expressed. If it is expressed only in the fusiform someone may be a lower synaesthete. If expressed in the angular gyrus someone may be a higher synaesthete. And, if expressed between primary gustatory cortex and adjoining hand and face regions of primary somatosensory cortex, the result might be a person who 'tastes shapes'. The distribution may not be bimodal, however, so there may be mixed types who combine features of several different types of synaesthesia.

One prediction would be that higher synaesthetes should experience colours even with tactile numbers or subitizable clusters of dots. Furthermore, if the higher colour area has different psychophysical properties then the induced colours will also have different psychophysical properties in higher synaesthetes. For example, in higher synaesthetes, the colours may not fall off with eccentric viewing of numbers and the induced colours may not give rise to grouping or pop-out, nor would numbers rendered invisible by crowding evoke colours in these higher synaesthetes. These predictions are all easy to test, but we must bear in mind that if the gene is expressed in a patchy manner in multiple locations, there might be mixed synaesthetes who complicate the picture. It remains to be seen whether days of the week and months of the year — embodying the abstract rule of cardinality or sequence — would evoke colours only in higher synaesthetes, lower synaesthetes, or both.

We suggest, also, that the study of synaesthesia can help us understand the neural basis of metaphor and creativity. Perhaps the same mutation that causes cross-wiring in the fusiform, if expressed very diffusely, can lead to more extensive cross-wiring in their brains. If concepts are represented in brain maps just as percepts are, then cross-activation of brain maps may be the basis for metaphor and this would explain the higher incidence of synaesthesia in artists, poets and novelists (whose brains may be more cross-wired, giving them greater opportunity for metaphors).

Our speculations on the neural basis of metaphor also lead us to propose a novel synaesthetic theory of the origin of language. We postulate that at least four

earlier brain mechanisms were already in place before language evolved; a non-arbitrary synaesthetic link between object shapes and sound contours (e.g., bouba and kiki), a synaesthetic mapping between sound contour and motor lip and tongue movements (mediated, perhaps, by the recently discovered mirror neurons system in the ventral premotor area that must represent the movements of others, including vocal movements), a synaesthetic correspondence between visual appearance and vocalizations (e.g., 'petite', 'teeny' and 'little' for diminutive objects mimed synaesthetically by a small /ɪ/ formed by the lips and a small vocal tract), and cross-activation between motor maps concerned with gesticulation and vocalizations. This would have allowed an autocatalytic bootstrapping culminating in the emergence of a vocal proto-language. Once this was in place other selection pressures could kick in to refine it (through the combined effects of symbol manipulation/semantics and of the exaptation provided by the syllabic structure for syntactic deep structure).[18]

This idea is different from the two more traditional theories of language origins (Pinker, 1994): First, that language simply involves the specific implementation of a more general-purpose mechanism (such as thinking and symbol manipulation) or second, that it evolved exclusively as a specific adaptation for communication. On our scheme, neither of these extreme views is correct. Instead, we postulate that language evolved through co-opting and finding novel uses for multiple mechanisms evolved originally for very different functions and by a fortuitous synergistic bootstrapping between these functions. This sort of co-opting of pre-existing machinery for novel uses is the rule, rather than the exception, in evolution, but this seems to have escaped the notice of even sophisticated psycholinguists.

The mutation-based hyperconnectivity hypothesis may also explain why many synaesthetes exhibit such strong emotional reactions to even trivial sensory discord or harmony. We suggest that this occurs because of hyperactivation of the amygdala, nucleus accumbens and other limbic structures by sensory inputs. A similar hyperconnectivity (based on kindling rather than mutation) could explain the purported higher incidence of synaesthesia as well as heightened emotions in response to sensory stimuli seen in TLE. Such hyperconnectivity (whether caused by genes or by TLE-induced kindling) would also increase the *value* of a reward or aversion, thereby strengthening pre-existing associative links (this would allow learning to play a role in synaesthesia).

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[18] This raises the fascinating question of the relationship between language and thought — more specifically between the hierarchical/syntactic Chomskyan tree structure and abstract, offline symbol manipulation (including logic). Did the latter accelerate the evolution of the former, or was it the other way around? Or, did they co-evolve through mutual bootstrapping, as we suggest in this essay? Our neurological approach to this problem will be to give non-linguistic logic puzzles to patients with Broca's aphasia, who have lost syntax. For example, we know that they cannot use 'if', 'then', 'but' and 'unless', but can they play chess (which requires the tacit use of such relational concepts)? Can they still use a computer language or algebra (assuming that they could before the stroke)? And what about patients with Wernicke's aphasia — can they engage in symbol manipulation and logic, given that their syntax is intact? Another intriguing question is whether the hierarchical structure of tool use in early hominids provided an exaptation for the hierarchical structure of syntax (Greenfield, 1991). This seems very plausible to us: e.g., hammering a nail or stone core could give rise to distinctions such as 'active' and 'passive' or 'subject' and 'object'. Indeed, one wonders whether tool use may have even provided an exaptation for thought itself.

Our scheme invokes limbic structures for explaining the emotional overtones of synaesthesia but it is very different from Cytowic's (1989; 1997) view that it *all* happens in the limbic system because the limbic system is phylogenetically ancient and everything must eventually converge on it. In our hyperconnectivity model, the gene is expressed at multiple sites along the sensory processing hierarchy (in a patchy or diffuse manner) *including* the sensory-to-amygdala connections in some individuals — the limbic system is not the only player, nor even the most important one. But if one had to choose any single neuroanatomical locus for synaesthesia, better candidates would be the insula (where there is pre-existing convergence of information from many sensory modalities, including visceral sensations and pain) or the angular gyrus (as discussed above). 'Anatomy is destiny' was one of Freud's few insightful remarks and finds resonance with the main ideas expressed in this paper (e.g., the rare form of pain–colour synaesthesia may be due to cross-wiring in the insular cortex, and perhaps the same might be true for a woman that we recently encountered who reports orgasm–colour synaesthesia).

Finally, we discuss the relevance of this scheme for more subjective aspects of consciousness such as mental imagery and qualia. While both mental imagery and synaesthesia are paradigmatic examples of internal mental states, we have shown how the relation between the two might be fruitfully explored. In addition, we have shown how the cross-wiring hypothesis can explain synaesthetes' introspective reports. Because neural activation in the fusiform gyrus bypasses normal stages of processing at the retina, synaesthetes can experience qualia that are unavailable to non-synaesthetes. In addition, these results suggest that the *entire* perceptual pathway (or large portion) is essential for the experience of qualia, not merely the final stages.

The ideas we have presented in this essay are highly speculative but we hope they will provide a springboard for future speculations and experimental work on synaesthesia. Whether all of our ideas turn out to be correct or not, one thing is clear. Far from being an oddity, synaesthesia allows us to proceed (perhaps) from a single gene to a specific brain area (e.g. fusiform or angular) to phenotype — systematic psychophysics (e.g., pop-out fall off with eccentricity, masking, flicker and so on) — and perhaps even to metaphor, Shakespeare, and the evolution of language, all in a single experimental subject.

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