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Familial patterns and the origins of individual differences in synaesthesia

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Abstract

The term synaesthesia has been applied to a range of different sensory-perceptual and cognitive experiences, yet how these experiences are related to each other is not well understood. Not only are there disparate types of synaesthesia, but even within types there are vast individual differences in the way that stimuli induce synaesthesia and in the subjective synaesthetic experience. An investigation of the inheritance patterns of different types of synaesthesia is likely to elucidate whether a single underlying mechanism can explain all types. This study is the first to systematically survey all types of synaesthesia within a familial framework. We recruited 53 synaesthetes and 42% of these probands reported a first-degree relative with synaesthesia. We then directly contacted as many first-degree relatives as possible and collected complete data on synaesthetic status for all family members for 17 families. We found that different types of synaesthesia can occur within the same family and that the qualitative

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nature of the experience can differ between family members. Our findings strongly indicate that various types of synaesthesia are fundamentally related at the genetic level, but that the explicit associations and the individual differences between synaesthetes are influenced by other factors. Synaesthesia thus provides a good model to explore the interplay of all these factors in the development of cognitive traits in general.
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1. Introduction

Synaesthesia has been defined as the experience of involuntary sensory cross-activation whereby the presentation of a particular stimulus elicits a secondary sensory-perceptual experience (Baron-Cohen, Wyke, & Binnie, 1987; Cytowic, 1989, 1997). This definition has been extended to include a number of more cognitive categories, both for the inducing stimulus and the concurrent synaesthetic experience. The term ‘synaesthesia’ has been applied to a wide range of quite disparate phenomena (Baron-Cohen et al., 1987; Cytowic, 1989, 1997; Marks, 1975). These include forms acquired after optical injury of some sort (Armel & Ramachandran, 1999), patterns of information integration in multisensory perception (Gallace & Spence, 2006), temporary forms induced by hallucinogens such as mescaline or lysergic acid diethylamide (LSD) (Cytowic, 1989; Nichols, 2004) and an apparently hereditary form that has been called idiopathic or developmental synaesthesia (Ward & Mattingley, 2005). There are, in turn, many different forms of the latter, most of which are described within the sensory-perceptual domains but are not strictly restricted to these domains (Dixon, Smilek, Cudahy, & Merikle, 2000; Jansari, Spiller, & Redfern, 2005). The most common and best-studied forms of synaesthesia involve the association of colour with linguistic stimuli such as letters, numbers, or words (Baron-Cohen, Harrison, Goldstein, & Wyke, 1993). We use the term linguistic–colour synaesthesia to describe such phenomena. This can occur as ‘coloured hearing’, where sounds, including spoken phonemes or words induce a colour percept or ‘coloured reading’ where visually presented letters or numerals induce an associated colour. In fact, the concept of an inducer is often sufficient to elicit a concurrent experience (Dixon et al., 2000). There are many additional phenomena to which the term synaesthesia has been applied, including for example, the induction of tastes by words (Ward & Simner, 2003), the induction of touch by vision (Blakemore, Bristow, Bird, Frith, & Ward, 2005), the induction of shapes by tastes (Cytowic, 1993), the personification of numbers (Simner & Holstein, 2007; Smilek, Callejas, Dixon, & Merikle, 2007) and experiencing numbers or units of time in spatial arrangement (Dixon, Callejas, Smilek, & Merikle, 2006). To date, it is unknown how these different types of synaesthesia relate to each other (Sagiv, Simner, Collins, Butterworth, & Ward, 2005). Reports of individual synaesthetes with more than one type of synaesthesia (e.g., Simner & Hubbard, 2006) support the view that the different types are indeed related by a single mechanism. On the other hand, the mechanisms leading to multiple forms of synaesthesia in an individual may be distinct from those causing discrete unitary forms, just as the mechanisms underlying acquired, drug-induced and developmental synaesthesia may differ.

The heterogeneity of developmental synaesthesia extends beyond category type such as linguistic–colour synaesthesia or number-lines (Beeli, Esslen, & Jäncke, 2005; Hubbard, Arman, Ramachandran, & Boynton, 2005; Marks, 1975; Mills, Boteler, & Larcombe, 2003). For example, even within linguistic–colour synaesthesia there are many individual differences in various parameters including the number of stimuli that act as inducers, the presentation modality (e.g., visual versus auditory presentation of words), the reported complexity of the evoked percept (the 'concurrent') and whether it is reported as being perceived in external space (so-called 'projector' synaesthesia) or in the 'mind's eye' (so-called 'associator' synaesthesia) (Dixon, Smilek, & Merikle, 2004). Moreover, particular paired associations (e.g., green Wednesday or purple F) tend also to be highly idiosyncratic, although there are certain trends across populations (Rich, Bradshaw, & Mattingley, 2005; Simner et al., 2005). How individual differences in these various parameters arise is not known.

From an information processing point of view, the common link between these phenomena is that all involve a set of involuntary, arbitrary, stable and reproducible associations between inducing stimuli of one type (e.g., different words, tastes or musical notes) and the concurrent experience of another (e.g., different colours, shapes or spatial positions). This link suggests that these phenomena are related to each other, at least at the cognitive level, and possibly at the underlying neural level. Several researchers have already appealed to a common neural mechanism to describe how these phenomena are related. For example, Ramachandran and Hubbard (2001) proposed that an exuberance of cortical connections between adjacent cortical areas may account for all sub-types of synaesthesia. On the other hand, Grossenbacher and Lovelace (2001) argue that disinhibition of feedback mechanisms between cortical areas which are normally inhibited underlies different types of synaesthesia. For the moment, however, there is very little evidence that any of these models can adequately explain all types of synaesthesia and the differences in the subjective experience.

An answer to whether different types are related to each other and to how individual differences in subjective experience emerge may come from an examination of the patterns of inheritance of synaesthesia. As first noted by Galton (1883), synaesthesia (specifically 'coloured hearing' in that case) tends to run in families. Two recent studies of synaesthesia reported that 36% (Rich et al., 2005) or 44% (Ward & Simner, 2005) of synaesthetes reported at least one other synaesthete family member although the nature of the synaesthesia in those other family members was not reported. An investigation of the familiality of other forms of synaesthesia is important in elucidating any links between different types. If separate families have, for example, taste–word synaesthesia versus linguistic–colour synaesthesia then perhaps the similarity between these forms is spurious and they do not share an underlying mechanism. On the other hand, if multiple forms exist within families then the most parsimonious interpretation would be that they are fundamentally related and any cognitive or neurological model must be able to explain the co-occurrence of all types. It is also not known whether variation in the other characteristics described above has a familial origin. If not then it leaves open the question of how these individual differences arise. For this reason we assessed not only synaesthetes but we also directly assessed their first-degree relatives.

As previous survey studies have focused predominantly on linguistic–colour synaesthesia (Rich et al., 2005; Ward & Simner, 2005), the familiality of different types of synaesthesia has not yet been fully investigated. To that end, we assessed a large number of families through direct contact with as many family members as possible. Our aim was to analyse, in this sample, the familiality of the overall type of synaesthesia and of various cognitive characteristics of the condition. Synaesthesia has been studied in relation to general aspects of cognition, including attentional processes (Mattingley, Rich, Yelland, & Bradshaw, 2001; Mattingley, Payne, & Rich, 2005), binding (Sagiv & Robertson, 2005; Treisman, 2005), associative learning and implicit associations (Ramachandran & Hubbard, 2005; Ward & Simner, 2005) and consciousness (Gray et al., 2002; Gray, 2005). An understanding of the underlying mechanisms causing synaesthesia should thus inform theories on these diverse topics as well as provide a model to understand normal development of connectivity between cortical areas or modules.

2. Methods

2.1. Participants

Participant recruitment was performed through a series of national and local newspaper articles, radio interviews, posters and a website (www.tcd.ie/Psychology/synres). Fifty-eight respondents were initially invited to participate in a familial study of synaesthesia and 53 of these individuals met our criteria for synaesthesia (see below). Probands (the first individuals within a family to contact us) were asked to state how many brothers, sisters, sons and daughters they had and whether any of their relatives has (or had) synaesthesia and if so what type. We were able to contact 11 reported synaesthete relatives and 51 non-synaesthete relatives and these were invited to participate in the study. In total, 22 families were assessed. Our protocol was approved by the School of Psychology Ethics Committee, Trinity College Dublin. All participants (or parents/guardians when appropriate) gave written informed consent to participate in this study and permission was sought from the probands before contacting family members.

2.2. Materials

Respondents were mailed a screening questionnaire regarding the characteristics and familiality of their synaesthesia (see Appendix A). We modified a questionnaire provided by Profs. Simon Baron-Cohen and Anthony Monaco. Individuals whose responses indicated possible synaesthesia received a more detailed questionnaire tailored to the type of synaesthesia they experienced. In order to provide a more objective measure of synaesthesia, we tested for consistency of inducer-concurrent associations using a test-retest procedure in all reported synaesthetes (see following section).

Responses to detailed questionnaires allowed us to determine the precise nature of the synaesthesia in each individual. Following Rich et al. (2005) we defined linguistic–colour synaesthetes as those who experience colour in response to either: letters, numbers, days of the week, months of the year, names, and/or place names. Non-linguistic inducers included music, taste, and pain. Finally, we collected information on other aspects of synaesthetic experience, such as whether a synaesthete was a 'projector' or an 'associator', based on self-report. In other words, synaesthetes were classified as projectors or associators based on whether they reported the locus of their experiences as being 'projected in external space' or 'in the mind's eye', respectively. Taken together, this information allowed us to determine common attributes of synaesthesia within and across families.

In order to avoid a reporting bias skewing of the sex ratio, we followed the model of Baron-Cohen, Burt, Smith-Laittan, Harrison, and Bolton (1996) and directly contacted as many family members as possible, including those reported as non-synaesthetes. Each family member was screened using a brief questionnaire, which was an abbreviated form of the original questionnaire (see Appendix B).

2.3. Response coding

In order to determine non-random trends towards certain linguistic–colour associations we categorized colour responses to graphemes (letters and digits) according to the 11 basic colour categories (red, yellow, green, blue, purple, pink, orange, brown, black, grey, white) outlined by Berlin and Kay (1969) and used by Rich et al. (2005) and Simner et al. (2005). Because of a tendency for synaesthetes to associate metallic colours (i.e. silver, gold, bronze, metallic) with the final letters of the alphabet (i.e. X, Y and Z), we added one extra category of 'metallic'. To analyze patterns across individuals for certain linguistic–colour associations, we compared the frequency at which a colour was chosen for a particular number or letter to the frequency at which that colour was chosen overall. This method takes into account the frequency at which different colours are reported overall (for example red is more commonly reported than purple).

2.4. Procedure

In our initial screening we used the defining criteria outlined by Baron-Cohen and Harrison (1997) and Cytowic (2002). In particular, synaesthetic percepts should be idiosyncratic, consistent over time and reported from early childhood. Inclusion criteria did not require that concurrents are experienced in external space as originally posited by Cytowic (2002). Five individuals did not meet these criteria and were not included in our sample. The remaining 53 respondents (i.e. probands) were sent a detailed questionnaire on the nature of their synaesthesia and were also asked for the names and contact details of family members (both reported synaesthetes and reported non-synaesthetes). These family members were screened for synaesthesia using our brief screening questionnaire and potential synaesthetes were subsequently sent detailed questionnaires.

To test for consistency, each synaesthete (i.e. proband and family member) was contacted by telephone (without warning) between 3 and 12 months (average interval = 7 months) after completing the detailed questionnaire and were asked to restate their synaesthetic concurrents associated with their inducers. In most cases these were colours associated with graphemes, numbers, days, months, names etc. A percent correct score was calculated based on the number of items assessed. We used a scale of 0–2 to score consistency of associations, following the criteria outlined by Rich et al. (2005) and a percent correct score was calculated based on the number of items assessed. A score of 0 was given if the item given at retest was a non-match. If the item given at retest differed by one hue (e.g., blue/grey vs. green/grey) a score of 1 was given. For identical descriptions involving one or more hues a score of 2 was given. Individuals with other forms of synesthesia were asked to match tastes, shapes, personalities for numbers etc., and a consistency score was calculated for each participant in the same way.

To ensure that synaesthetes were not simply better at memorizing inducer-concurrent associations, we compared consistency of linguistic–colour associations in synaesthetes with a non-synaesthete control group (10 males and 8 females with an average age of 36 years). This control group was first asked to associate a colour with a limited number of inducers (i.e. days of the week) and were retested on their associations, without warning, on average 2 months later.

The aims of our study were to determine individual differences and general characteristics of synaesthesia within our sample as a whole and within families in particular. To assess the prevalence of different types of synaesthesia within families we categorized the types of synaesthesia present in the families of probands who reported a synaesthete relative (22 families). Families classified as having the same type of synaesthesia included, for example, relatives with linguistic–colour synaesthesia, even if the proband had coloured numbers and another member had coloured letters. In families where more than one member had linguistic–colour synaesthesia, we counted the number of effective inducers across these individuals. For example, some individuals experience colour only for days and numbers (2 inducers), whereas others experience colour for letters, numbers, days of the week, months of the year, whole words, place names and inanimate sounds, such as rainfall (7 inducers).

Families were classified as having different types of synaesthesia if at least one family member experienced a different category of inducer-concurrent pairing from the proband (e.g., linguistic–colour synaesthesia and taste–shape synaesthesia). We also assessed the distribution of sub-types in families where more than one member had linguistic–colour synaesthesia by quantifying the distribution of projector and associator synaesthetes within each family.

3. Results

3.1. Characteristics of the sample

3.1.1. Recruitment

A total of 92 potential synaesthetes were recruited, of whom 64 were tested for consistency. Fifty-three of the potential synaesthetes were directly recruited probands (respondents to our recruitment advertisements); 35 were relatives referred by probands (10 children, 25 adults); and 4 were relatives initially reported as non-synaesthetes by probands. Sixty-four individuals (all probands and 11 referred relatives) met our criteria for synaesthesia and were confirmed as synaesthetes using a test of consistency (see procedure for details). Both quantitative and qualitative measures were used to evaluate reported synaesthetes (see Section 2). The average consistency score for a synaesthetic individual was 91% ($SD = 11.76$), which is comparable to other studies (Baron-Cohen et al., 1996; Rich et al., 2005). In contrast, the average consistency score for a non-synaesthete control participant was 33% ($SD = 17.08$), revealing a clear bimodal distribution with no overlap (even ±2 standard deviations from the mean).

In addition, we directly assessed synaesthesia in 51 reported non-synaesthete family members and confirmed the absence of synaesthesia in 47 individuals. This yielded 17 complete families where the status of all first-degree relatives as synaesthetes or non-synaesthetes was confirmed. Importantly, these families were not selected for the presence of multiple synaesthetes. Unfortunately, it was not possible to confirm the status of the remaining 263 living relatives. (See Table 1 for further details.) While our assessment confirmed that the majority of the relatives reported as non-synaesthetes were not synaesthetes, 4 of them did in fact report synaesthesia. We were, however, unable to conduct consistency tests on these 4 reported synaesthetes and they were not included in our final confirmed sample. Detailed data regarding the characteristics of their synaesthesia were obtained from the 64 confirmed synaesthetes. The age range was 8–77 years (Mean 44, $SD = 17$ years); 57 of the 64 were born in Ireland; and they worked across a range of occupations.

3.1.2. Sex bias

Our total sample of 92 confirmed and unconfirmed synaesthetes includes 78 females and 14 males, yielding a female to male ratio of 6:1 in the Irish population identical to that reported in two previous studies (Baron-Cohen et al., 1996; Rich et al., 2005). It has been previously been argued that the high ratio of female to male synaesthetes is influenced by a sex bias in responding to health related surveys (Simner et al., 2005). We find no difference, however, between the sex ratio for probands (46 females and 7 males) and that reported for the relatives who did not contact us directly (30 females and 5 males) (see Table 1). Furthermore, in the 17 families where we have data for all members, synaesthete parents are much more likely to pass the trait to their daughters (45/74; 61%) than to their sons (8/48; 17%); (a ratio of ~4:1, $\chi^2(1) = 13.7$, $P < .001$).

Table 1
Number and sex of individuals (synaesthetes and non-synaesthetes) in total sample

	Female	Male	Total
Probands[a]	46	7	53
Confirmed synaesthetes[b]	9	2	11
Non-confirmed synaesthetes[c]	4	0	4
Reported synaesthetes[d]	17	3	20
Synaesthetes reported as not[e]	2	2	4
Confirmed no[f]	26	21	47
Reported no[g]	14	26	40
Unknown[h]	90	133	223
Total	208	194	402

[a] First synaesthete to contact us, have complete data.
[b] Family member introduced by probands, have complete data.
[c] Have preliminary data but no consistency data.
[d] Have been reported as having synaesthesia by a family member, but who we have not been able to contact or have been reported as likely synaesthetes by a family member (includes reports of deceased individuals and young children).
[e] Synaesthetes who were originally reported as not having synaesthesia.
[f] Have filled out a screening questionnaire and have no synaesthesia.
[g] Have been asked by family members and report no synaesthesia.
[h] Includes deceased family members, overseas relatives, family members of adopted individuals and young children.

It has previously been proposed that the sex ratio could be explained by X-linked male lethality (Baron-Cohen et al., 1996). To test this we identified the number of sons and daughters born to synaesthete mothers. Twenty-five confirmed synaesthete mothers gave birth to 32 sons and 35 daughters. Our results confirm previous findings that synaesthesia is not associated with significant male lethality across the overall sample (Cytowic, 2002; Ward & Simner, 2005).

3.1.3. Individual differences and types of synaesthesia

Ninety-five percent of the synaesthetes reported experiencing synaesthesia throughout their lifetime and the remaining 5% from very early childhood. Seventy-six percent reported no change in the range of stimuli inducing synaesthesia over time. We assessed the types of synaesthesia experienced and the content of specific inducer-concurrent pairings reported by the confirmed sample (see Table 2 for full details). The majority of our 64 confirmed synaesthetes experienced linguistic–colour synaesthesia only or experienced linguistic–colour synaesthesia plus one or more 'other' forms of synaesthesia, such as coloured music or spatial numbers or numbers with personalities (45% and 47%, respectively). The remaining 8% had other forms of synaesthesia such as coloured, textured, or shaped taste and smell.

Forty-two percent of the total sample reported that numbers, days, or months are spatially arranged, for example as ovals, circles, ellipses or other geometrical forms or patterns. For 95% of our synaesthetes the concept of the inducer was sufficient to elicit a concurrent (i.e., simply imagining an inducer elicits colour). Seventy-two percent of our synaesthetes can be classified by self-report as 'associators', who

Table 2
List of inducers and concurrent experiences reported by confirmed synaesthetes ($N = 64$)

Inducer	Concurrent experience	*N* (% of total sample)
Linguistic stimuli (letters, numbers, days, months)	Colour	*24 (37.5) 5 (7.81)*
Linguistic stimuli (letters, numbers, days, months)	Colour and spatial patterns	*11 (17.18) 2 (3.13)*
Other (music, pain, taste)	Colour and spatial patterns	11 (17.18)
Music	Colour	9 (14.06) *3 (4.69)*
Taste	Colour	5 (7.8)
Emotion	Colour	3 (4.7)
Taste	Shape[a]	3 (4.7)
Inanimate sounds	Colour	3 (4.7)
Music	Shape/texture/pattern[b]	2 (3)
Pain	Colour	2 (3)
Numbers	Personalities	1 (1.56) *1 (1.56)*
Pain	Colour & shape	1 (2)
Smell	Actions[c]	1 (2)
Words	Shape[d]	1 (2)
Colour	Emotion	1 (2)
Colour	Pain	1 (2)

Data in italics represent males. Of the total sample 8% of the total sample had synaesthesia in responses to non-linguistic inducers only.

[a] In both cases the shape is felt "in the mouth" (i.e. somatosensory).

[b] In both cases shapes, textures and patterns are projected externally.

[c] Smells elicited associated actions experienced in the minds' eye.

[d] Shape experienced in the 'mind's eye'.

experience concurrents in the 'mind's eye' and 12% can be classified as 'projectors', who experience their concurrents projected into external space. This percentage included individuals who have experiences, such as colour for music projected externally, or shapes for taste felt 'in the mouth'. While the validity of the associator–projector distinction, especially based on self-report, is open for debate, it should be noted that the ratio in our sample is similar to that previously reported (Dixon et al., 2004). The remaining 16% of our sample can be categorized as both associator and projector synaesthetes.

3.1.4. General trends in linguistic–colour associations

To analyze non-idiosyncratic trends in linguistic–colour associations, grapheme-colour data were obtained from 43 participants with number–colour associations and 48 participants with letter–colour associations. The colour responses were coded according to the Berlin and Kay (1969) typology (plus an extra category of metallic) (see Section 2 for additional detail). Some trends in particular associations stand out: '0' and 'O' are commonly white (80% and 76%, respectively) and '1' and 'I' are commonly white (44% and 52%, respectively) or black (28% and 22%, respectively). We observe a good deal of similarity between the trends found in our study and those reported by Rich et al. (2005); Simner et al. (2005) and Day (2005). For example all three studies concur that 'A' is statistically more likely to be red. However there are cases where there is no concordance between studies; for example 'J' is reported as more commonly blue (current study); orange (Rich et al., 2005) or red (Simner et al., 2005). Tables 3A and 3B list common digit- and letter–colour associations.

3.2. Familial patterns of synaesthesia

Forty-two percent of probands (22 of a total of 53) reported at least one other family member with synaesthesia, consistent with previous estimates of 36% and 48% (Rich et al., 2005; Baron-Cohen et al., 1996). Five probands reported two or more other family members with synaesthesia and five reported three or more other family members with synaesthesia. Of the remaining probands, 26% reported no family history and 24% were unsure (this includes individuals who are adopted or whose family members are deceased). Eight percent said it was possible that other members of their family had synaesthesia although it was difficult to assess. For example, this percentage includes young children who have spoken of experiences characteristic of synaesthesia (e.g., coloured days), but were too young to assess, or relatives who had mentioned such experiences but are now deceased.

If the population prevalence of synaesthesia is as high as some reports suggest (~1 in 20; Galton, 1883; Simner et al., 2006), it is possible that the apparent familiality of synaesthesia might be due to chance. We have a complete sample of 402 subjects; 64 are confirmed synaesthetes and another 30 are reported synaesthetes. That gives the

Table 3A
Common number–colour associations: Table compares significant associations reported in the current data ($N = 43$) and by Rich et al. (2005) ($N = 150$)

Number	Number–colour associations (% of total sample)	
	Barnett et al. (current)	Rich et al. (2005)
0	**White (80%)**	No data
1	White (44%)/black (28%)	**White (60%)/black (20%)**
3	**Yellow (40%)**	**Pink (10%)**
4	**Blue (40%)**	**Red (24%)**
9	**Brown (42%)**	Brown (25%)

Data in bold indicate cases in which the percentage is more than 2 standard deviations above the mean reported for that colour (95% confidence interval). Data in regular font indicate the most common number–colour association reported.

Table 3B
Common letter–colour associations: table compares significant associations reported in the current data ($N = 48$) and by Rich et al. (2005) ($N = 150$) and Simner et al. (2005) ($N = 70$)

Letter	Letter–colour associations (% of total sample)
	Barnett et al. Rich et al. (2005) Simner et al. (2005) (current)
A*	**Red (32%) Red (36%) Red (42%)**
B	Brown (28%) Blue (32%) **Blue (37%)**
C*	Yellow (33%) Yellow (33%) **Yellow (27%)**
D*	**Brown (33%) Brown (47%) Brown (34%)**
E*	**Green (39%)**Green (25%) **Green (28%)**
F*	Green (25%) Green (20%) **Green (27%)**
G	Brown (22%) Green (25%) **Green (29%) Brown (33%)**
H	**Grey (20%)**Brown (17%) **Green (26%)**
I*	**White (52%)**Black (22%) **White (48%)**Black (20%) **White (34%) Black (24%)**
J	Blue (15%) **Orange (16%) Red (15%)**
K	Blue (20%) Blue/green (ea. 13%)
L	Yellow (23%) Yellow (26%) **Grey (17%)**
M	Blue (26%) Red (25%) **Brown (28%)**
N	Blue (27%) Green (25%) **Brown (28%)**
O*	**White (76%) White (56%) White (52%)**
P	Green (20%) **Pink (13%) Blue (25%)**
Q	**Purple (26%)** Yellow (13%) **Purple (25%)**
R*	**Red (30%) Red (36%) Red (38%)**
S*	**Pink (15%)**Yellow (28%) Yellow (30%) **Yellow (37%)**
T	Green (24%) Green/blue (ea.15%) **Black (18%)**
U	Brown (30%) Brown (22%) **Grey (24%)**
V	Red/orange/yellow (ea. 14%) Purple (18%) **Purple (19%)**
W	Blue (18%) Brown (15%) **Blue (15%)**
X*	**Black (24%) Metallic (21%) Black (30%) Black (20%) Grey (18%)**
Y*	**Yellow (50%) Yellow (45%) Yellow (42%)**
Z	**Metallic (25%) Black (30%) Black (24%)**

Data in bold indicate significant cases (note Simner et al. used a slightly different statistical method). Data in regular font indicate the most common number–colour association reported. *Indicates concordance where all three studies report the same letter–colour association.

most conservative frequency within our sample of at least 64/402 or 16% and a more likely frequency of at least 94/402 or 23%. This sample includes 223 relatives of unknown status, some of whom are presumably also synaesthetes, which would raise the frequency higher still. Even the most conservative estimate differs significantly from the clustering that would be expected by chance with a general population prevalence of 5% ($\chi^2(1) = 43.4$, $P < .001$). Furthermore, within the 17 families where we have data on all members, the percentage of children of synaesthete parents who also have synaesthesia was 43% (53/123). This is far greater than expected by chance, even if prevalence were as high as 1 in 20 ($\chi^2(1) = 49.25$, $P < .001$).

We examined the distribution of different types of synaesthesia within the families of the 22 probands who reported synaesthetic relatives. In the majority of these families (73%) only one type of synaesthesia was present (in all cases linguistic–colour synaesthesia). On further analysis, however, differences in the precise nature of this synaesthesia became apparent in these families. For example, we found that the particular colour associations reported for linguistic inducers were not consistent within families and that the number of inducers that trigger synaesthesia differed from one family member to the next. Furthermore, associator and projector synaesthetes co-occurred in 5 of the 10 families containing multiple linguistic–colour synaesthetes.

The remaining 27% of families had members with different types of synaesthesia (for example linguistic–colour and taste–shape synaesthesia). Fig. 1 shows some examples of pedigrees where multiple members within the same family had synaes-

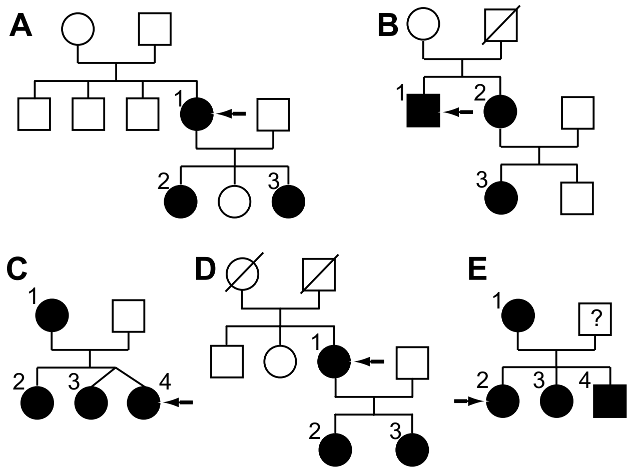

Fig. 1. Five example pedigrees. Probands are marked with arrows. Circles indicate females and squares indicate males. Non-synaesthetes are shown in white and synaesthetes are shown in black and coded below as projectors (P) or associators (A), where known. Question mark: unknown phenotypic status. LCS refers to linguistic–colour synaesthesia with a wide range of inducers, typically including letters, words, numbers and days of the week. Family A, 1: Taste to shape (P); 2: LCS, music to colour and emotion to colour (A); 3: Numbers and days of the week to colour (P). Family B, 1: Days of the week to colour and spatial arrangement, numbers to personalities (A); 2: LCS, music to colour and shapes (A); 3: Reported LCS. Family C, 1: LCS; 2: LCS (P); 3: LCS (A,P); 4: Taste, music, words to colour, numbers to personalities (reported non-synaesthete). Family D, 1: Words, days, months to colour (A); 2: LCS (P); 3: LCS (A). In Family D the number of inducers decreases over a generation. Here the mother experiences colour to words, days and months (3 inducers) and both daughters experience colour to letters, numbers, days, months, words and names (6 inducers). Family E, 1: LCS (A); 2: LCS (A); 3: Reported LCS; 4: LCS (A).

thesia (families A–E). The members of families A, B, and C have different types of synaesthesia. In Family A the proband has taste–shape synaesthesia and reported that shapes are felt instantly in her mouth. Her parents and three brothers do not have synaesthesia, but two daughters have linguistic–colour synaesthesia. In family B the proband experiences colour for all linguistic stimuli, while her brother experiences colour only for numbers and days of the week. In family C the proband, her monozygotic (MZ) twin sister and her mother all experience linguistic–colour synaesthesia to a large range of inducers, while another sister (initially reported as a 'non-synaesthete') has coloured words and taste. Families A and D contain both projector and associator synaesthetes.

We assessed whether there was any similarity of associations of colour and digits, letters and days between paired family members (e.g., two sisters). The average consistency over a range of 26–55 inducers within the 9 related pairs was 20%. This score is comparable to the average consistency within 38 unrelated pairs of synaesthetes, which was 16%, suggesting that members within a family are no more likely to share colour associations than unrelated synaesthetes ($\chi^2(1) = 2.48$, $P = .114$).

4. Discussion

While often defined as a sensory or perceptual phenomenon, synaesthesia commonly involves non-sensory, learned categories as inducers, such as letters or days of the week, and can also include cognitive concurrents, such as numbers having personalities (e.g., "4 is demure") (Simner & Holstein, 2007; Smilek et al., 2007). In order to address individual differences in synaesthesia and the familiality of various types of synaesthesia we profiled 92 synaesthetes within 53 families and obtained detailed information from 64 of these individuals. The current study is the first to assess how different variants of synaesthesia are related and the current data enable us to address two important questions: firstly, are different types of synaesthesia related? Secondly, what determines the specific type of synaesthesia that emerges and the marked individual differences in the qualitative nature of the experience?

4.1. How are different types of synaesthesia related within families?

We found that 42% of synaesthetes have a family member with synaesthesia. Even if synaesthesia were as common as 1 in 20 (Galton, 1883; Simner et al., 2006), it is extremely unlikely that chance occurrence could account for this percentage. Our data and those from several other studies (Baron-Cohen et al., 1996; Rich et al., 2005; Ward & Simner, 2005) provide compelling evidence that synaesthesia is inherited. More precisely, what is most likely inherited is a predisposition to synaesthesia. As with many traits, such as handedness or many psychiatric disorders (Annett, 1985; Bouchard & McGue, 2003), not all people who inherit a predisposition will develop the trait. For example, while female MZ twins in our sample are concordant for synaesthesia, cases of MZ female (Smilek, Dixon, Cudahy, & Merikle, 2001) and male (Smilek, Dixon, & Merikle, 2005) twins discordant for synaesthesia have also been reported. Conversely, synaesthesia may occur in people without a genetic predisposition, but far less frequently. These factors may explain the cases where no synaesthete relative is reported.

Previous familial studies have focused on the most common form of synaesthesia, linguistic–colour synaesthesia (Baron-Cohen et al., 1996; Cytowic, 2002; Ward & Simner, 2005) although Ward, Simner, and Auyeung (2005) mention a case of a word-taste synaesthete who reports a relative with linguistic–colour synaesthesia. The current study extends previous work by providing evidence that very different types of synaesthesia, such as linguistic–colour and taste–shape synaesthesia can co-occur within the same family. These findings strongly suggest that the underlying predisposition to synaesthesia (regardless of type) is genetic. The fact that many variants of synaesthesia exist in the same family suggests that all forms of synaesthesia fit within a spectrum and share a single underlying genetic mechanism. These data allow a more definitive conclusion of a single underlying mechanism than the reported observation of multiple types within some individuals. The latter observation left open the possibility that "multiple synaesthesia" could be caused by quite a distinct mechanism from more discrete unitary forms. A familial framework, on the other hand, allows one to make the most parsimonious interpretation that inheritance of a single genetic variant can result in, for example, linguistic–colour synaesthesia in one individual and taste–shape synaesthesia in another. Possible factors affecting the type that emerge in an individual are discussed below.

The very different types of synaesthesia within families, along with the lack of concordance in specific letter–colour associations between family members (see below) also argue strongly against theories of cultural transmission of synaesthesia. Such theories would have to posit the transmission of a tendency to associate things in general without the transmission of specific associations and would also not explain transmission to some children and not others.

4.2. Sex differences in synaesthesia

An important and controversial question is the relative prevalence of synaesthesia in males and females. We find a marked sex bias in the number of females to males reporting synaesthesia. The sex ratio in our Irish sample (6 females: 1 male) is the same as ratios reported in UK and Australian studies (Baron-Cohen et al., 1996; Rich et al., 2005). However, it is discrepant with recent studies from the UK that report substantially lower female to male ratios of 4:1 in self-referred synaesthetes (this dropped to 2:1 in the ratio reported by relatives) (Ward & Simner, 2005) and 1:1 in an opportunistic sample (Simner et al., 2006; see also Sagiv et al., 2005 for spatial forms) although the total number of synaesthetes in these latter studies was small.

A possible contributor to a skewed sex ratio in some studies, including ours, would be a self-selection bias as females are thought to be more likely to respond to heath-related surveys, although this effect is usually small (i.e. 10%, see Dindia & Allen, 1992). Two pieces of evidence argue against self-report bias as the sole explanator of the sex bias we observe in our sample. First, we find the same ratio of females to males in the synaesthete relatives reported by probands, as in the probands themselves, although it remains possible that males are also less likely to discuss synaesthesia even within their families. Second, in the set of 17 families where we directly surveyed all members, we observe the same excess of female synaesthetes (45 of 53, or 6:1). Another possible explanation of a sex bias would be the model of X-linkage with male lethality in utero (Baron-Cohen et al., 1996). Data from our study and others (Cytowic, 2002; Ward & Simner, 2005), showing equal numbers of sons and daughters born to synaesthete mothers, excludes this possibility.

The current findings suggest instead that sex may be an independent factor that affects the likelihood of an individual developing synaesthesia. Sex influences a vast number of cognitive traits (Cahill, 2006), for example, mental rotation abilities (Parsons et al., 2004), visual-word learning (Chen et al., 2007) and verbal abilities (Medland, Geffen, & McFarland, 2002). Likewise, sex limitation is apparent in a wide variety of traits (for review see Cahill, 2006), including susceptibility to psychiatric disorders such as depression (Daradkeh, Ghubash, & Abou-Saleh, 2002) and schizophrenia (Salem & Kring, 1998).

4.3. Individual differences in synaesthesia

While genetics may determine general predisposition, it does not determine the marked individual differences in the subjective experience of synaesthesia. First of all, very different types of synaesthesia can occur in the same family. We also found that both associator and projector sub-types are reported in the same family, and even in the same individual. It should be noted that there is considerable variability in the way that people describe internal experiences and that the self-report 'associator/projector' dichotomy may be unreliable over time (Edquist, Rich, Brinkman, & Mattingley, 2005). The current data also show that in families who report the same type of synaesthesia, the number of inducers is not consistent. A recent study had argued that synaesthetes can be categorized based on whether they experience concurrents to a narrow (e.g., days and numbers) or wide (e.g., all linguistic stimuli) range of inducers and provided preliminary evidence to suggest that membership in these categories runs in multiplex families (i.e. >3 synaesthetes) (Asher, Aitken, Farooqi, Kurmani, & Baron-Cohen, 2005). In contrast, our data provide evidence that families can contain individuals who experience concurrents to either a large or small range of stimuli and that the number can increase or decrease from one generation to the next.

The individual differences between synaesthetes, even within families suggests that developmental variation or early experience play a major role in determining the characteristics that emerge. It is possible that synaesthetes inherit a general tendency to cross-activate or disinhibit normally functionally separate cortical areas, through any of a variety of proposed mechanisms (Grossenbacher, 1997; Grossenbacher & Lovelace, 2001; Ramachandran & Hubbard, 2001; Smilek, Dixon, & Merikle, 2001). In the case of grapheme-colour synaesthesia these areas are adjacent to each other (Ramachandran & Hubbard, 2001); whether this is true for other types of synaesthesia is an open question. The location of many functional areas shows a high level of interindividual variability in the general population (e.g., Spiridon, Fischl, & Kanwisher, 2006). Some examples include: the marked individual differences in the lateralization of the planum temporale for language (Sequeira et al., 2006), individual differences in the layout of cortical regions involved in reading in bilinguals (Roux et al., 2004), and individual variability in the cortical regions activated during colour-naming tasks (Roux, Lubrano, Lauwers-Cances, Mascott, & Demonet, 2006). If adjacency or proximity influences the probability of cross-activation or disinhibition, then potential individual differences in the relative layout of cortical areas may contribute to the heterogeneity of synaesthesia. Synaesthesia may thus be an overt reflection of 'random cerebral variation' that may also influence other cognitive traits (McManus, 2002).

In support of the idea that the cross-activation or disinhibition in synaesthetes may be more broad than the apparently discrete nature of the synaesthetic experience would suggest is the observation that 40% of synesthetes (versus 10% of controls) experience the phenomenon known as 'mitempfindung', where tactile stimulation in one part of the body simultaneously produces sensation at a different location (Burrack, Knoch, & Brugger, 2005). This finding also fits with reports from synesthetes who find upon introspection that they do have other associations of which they were not previously aware (e.g., Tyler, 2005).

4.4. What determines particular associations?

While the particular associations that a synaesthete experiences tend to be idiosyncratic, previous studies have found some non-random trends in letter- or number–colour pairings across populations of synaesthetes (Marks, 1975; Rich et al., 2005; Simner et al., 2005). To assess whether these trends show any familiality, we assessed paired associations across all synaesthetes and also between pairs of related synaesthetes.. We observe some similarity in the pattern of non-arbitrary associations to those reported in UK and Australian surveys (Rich et al., 2005; Simner et al., 2005), although we also note some differences. For example, there is no concordance between the three studies for the colour of the letter 'J'. Most letters and numbers, with the exception of '0' and '1', did not have a single dominating association and for those that did it was usually not overwhelming ('R' is statistically red more often than letters are red on average, but for only 32% of our linguistic–colour synaesthetes). Nevertheless, while the idiosyncratic nature of associations is more overwhelming than any shared mechanism, the trends observed do require an explanation.

There are two major models to explain such trends. One is that they arise from explicit learning, from cultural artifacts, for example, and the other is that they are influenced by implicit top–down processes. It has been proposed that learned associations at an early age, from say toys or refrigerator magnets of coloured letters, could contribute to a bias in associations, and there are a few rare cases where such associations seem to have occurred (Hancock, 2005; Witthoft & Winawer, 2005). There is little evidence, however, to suggest that this is a widespread mechanism (Rich et al., 2005). As an indirect test of this possibility and to assess whether particular associations could be consistent within families, we examined the concordance in the patterns of colour associations between relatives (including MZ twins and siblings) and compared this to the degree of concordance across synaesthetes from different families. We found no difference in concordance between these groups, suggesting that explicit learning of associations from an early age is unlikely to have had a large effect. The fact that parent-offspring pairs or sibling pairs, including MZ twins, are no more likely to agree on their particular letter–colour associations than unrelated synaesthetes is also a strong indicator that particular associations are not culturally transmitted.

An alternative is that implicit lexical or semantic associations may explain some of these general trends, such as why a particular colour (e.g., red) is generally associated with a letter (e.g., 'A' is for 'apple' etc., see Rich et al., 2005) or a particular taste associated with a word (e.g., blue tastes inky, see Ward & Simner, 2003). There is data to suggest that particular biases arise from mechanisms that are also present in non-synaesthetes (Marks, 1975; Rich et al., 2005; **?**). For example, both synaesthetes and non-synaesthetes are somewhat more likely to say that 'A' is red (Rich et al., 2005). However, in most cases where a common association exists there is no appealing semantic explanation. For example, it is not clear why 'Q' should be purple or '9' should be brown. In contrast, these data are in agreement with previous research showing that low frequency letters (e.g., 'Q') tend to pair with low frequency colour terms (e.g., purple) (Simner et al., 2005), while higher numbers (e.g., '9') have a tendency to pair with colours that appear late in the Berlin and Kay typology (e.g., brown) (Shanon, 1982). Thus, the particular associations that arise in an individual are largely idiosyncratic and arbitrary but may be biased by top–down implicit or explicit associations common to both synaesthetes and non-synaesthetes (see also Simner et al., 2005).

In summary, our findings strongly indicate that various types of synaesthesia are fundamentally related at the genetic level, but that the explicit associations and the individual differences between synaesthetes are influenced by other factors. Synaesthesia thus provides a good model to explore the interplay of all these factors in the development of cognitive traits in general (Mitchell, 2007). Any cognitive or neural model to explain synaesthesia must be able to accommodate the diverse forms of the phenomenon while also explaining the differences in frequency of different types.

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Appendix A. Relevant questionnaire items

A.1. Demographic information

- Sex
- Date of birth
- Ethnicity
- Occupation
- Final level of education

A.2. Synaesthetic characteristics

- Which forms of synaesthesia do you have?
- How long have you experienced synaesthesia?
- If you have 2 or more forms of synaesthesia, how do you experience them?
- Has the overall strength of your synaesthesia changed over time?
- Has the range of stimuli (sounds, smells, etc.) which trigger your synaesthesia changed over time?
- Do you experience numbers, days of the week, or months of the year in a spatial arrangement (i.e. a circle, ellipse, oval)?
- Do you see colours when you HEAR spoken words?
- Do you see colours when you READ written words?
- Do you see colours when you HEAR individual letters of the alphabet?
- Do you see colours when you READ individual letters?
- Do you see colours when you HEAR individual numbers?
- Do you see colours when you READ individual numbers?
- What has the LARGEST influence on the OVERALL COLOUR of a word?
- What has the LARGEST influence on the OVERALL COLOUR of a multi-digit number, such as 1234?
- Please list the colours you experience for letters of the alphabet, numbers (0-9), days of the week, months of the year and names.
- Do the colours have a texture/pattern? If yes, please describe.
- Where do you see the colour? On the digit? Projected externally (in front of you)? Internally ('in the minds eyes)? Other, please explain.
- Is the concept of the stimulus enough to induce your synaesthetic experience of colour or do you have physically see the stimulus in front of you?
- Do you see colours when you HEAR music?
- Do you see colours when you READ music?
- Does the instrument being played affect your colours?
- What has the LARGEST influence on the COLOUR of a musical NOTE?

- What has the LARGEST influence on the OVERALL COLOUR of a SERIES of notes?
- Do you see colours when you hear animals, such as a dog barking?
- Do you see colours when you hear inanimate natural sounds, such as rain?
- Have you found that your synaesthesia has been an advantage or disadvantage in any area of your life?

A.3. Medical history

- Handedness
- Have you ever had a medical condition affecting the eyes, such as colour-blindness? (Do not include near- or far-sightedness.)
- Have you ever had a medical condition affecting the brain, such as migraines, head injury, epilepsy, brain tumour, or stroke?
- Have you ever had a mental health condition?
- What do you think caused your synaesthesia?

A.4. Family history

- Please state how many brothers, sisters, sons, daughters, grandsons, and granddaughters you have (please provide contact details).
- Are you a twin or other multiple?
- Does anyone else in your family have synaesthesia? If yes, how many? Who? What type?

Appendix B. Relevant screening questionnaire items

B.1. Demographic information

- Sex
- Date of birth
- Ethnicity
- Occupation
- Final level of education

B.2. Synaesthetic screening questions

- Do you see colours when you HEAR spoken words?
- Do you see colours when you READ written words?
- Do you see colours when you HEAR individual letters of the alphabet?
- Do you see colours when you READ individual letters?
- Do you see colours when you HEAR individual numbers?
- Do you see colours when you READ individual numbers?
- Do you see colours when you HEAR music?

- Do you see colours when you READ music?
- Do you experience colours for days of the week?
- Do you experience colours for taste? pain? smell?
- Do you taste shapes?
- Do you smell words?
- Do you experience personalities for numbers?
- Do you experience numbers, days of the week, or months of the year in a spatial arrangement (i.e. a circle, ellipse, oval)?

B.3. Medical history

- Have you ever had a medical condition affecting the eyes, such as colour-blindness? (Do not include near- or far-sightedness.)
- Have you ever had a medical condition affecting the brain, such as migraines, head injury, epilepsy, brain tumour or stroke?
- Have you ever had a mental health condition?

B.4. Family history

- Does anyone else in your family have synaesthesia? If yes, how many? Who? What type?

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