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VARIANTS OF SYNESTHESIA INTERACT IN COGNITIVE TASKS: EVIDENCE FOR IMPLICIT ASSOCIATIONS AND LATE CONNECTIVITY IN CROSS-TALK THEORIES

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Abstract—This study examines the interaction between two types of synesthesia: ordinal linguistic personification (OLP; the involuntary association of animate qualities such as gender/personality to linguistic units such as letters/numbers/days) and grapheme-color synesthesia (the involuntary association of colors to letters and/or numbers). By examining both variants in the same individual we aim to: (a) show that features of different synesthetic variants interact in cognitive tasks, (b) provide a cognitive model of this interaction, and (c) constrain models of the underlying neurological roots of this connectivity. Studies have shown inhibition in Stroop-type tasks for naming font colors that clash with synesthetic colors (e.g. slower naming of green font for synesthetically red letters). We show that Stroop-type slow-down occurs only when incongruent colors come from other letters with matching (but not mis-matching) gender (experiment 2). We also measure the speed of OLP gender judgments (e.g. a=female; experiment 1) and show that response times are slowed by incongruent colors from other letters with mis-matching (but not matching) genders. Our studies suggest that synesthetic variants interact and that their concurrents can become implicitly connected without mediation from inducing stimuli. We interpret these findings in light of recent developmental data showing protracted heterochronous neuronal development in humans, which continues through adolescence in parietal, frontal and perisylvian areas. © 2006 IBRO. Published by Elsevier Ltd. All rights reserved.

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Synesthesia is a familial condition (e.g. Baron-Cohen et al. (1996; Ward and Simner, 2005) in which perceptual sensations (e.g. tastes) or concepts (e.g. words) trigger consistent and incongruous experiences. For example, smells may trigger the experience of shape (Cytowic, 1993) or spoken/written words give rise to the perceptual experience of taste (Ward and Simner, 2003; Ward et al., 2005). The condition is found in approximately 4% of the population (Simner et al., 2006b), implicating over 2.5 million people in the UK alone. The most common types of triggering stimuli (or *inducers*; Grossenbacher, 1997) are linguistic units such as letters, numerals and words (e.g. Simner et al., 2006b) and the most common *concurrents* (i.e. resultant synesthetic experiences) are in the visual domain (e.g. colors, patterns).

Behavioral studies have illustrated the consistency of synesthetes' reports over time (Baron-Cohen et al., 1996; Palmeri et al., 2002; Rich et al., 2005; Ward and Simner, 2003, 2005) as well as indicating their automaticity. For example, Stroop-type paradigms (Stroop, 1935) show inhibition for naming font colors that clash with synesthetic colors (e.g. slower naming of green font for letters that are synesthetically red) and this provides evidence that synesthetic associations cannot be easily inhibited (e.g. Mattingley et al., 2001; Mills et al., 1999; Odgaard et al., 1999). Imaging studies show that synesthetic colors (e.g. from grapheme-color synesthesia) produce functional magnetic resonance imaging (fMRI) activation in areas normally associated with the color perception of external stimuli (e.g. left V4). This provides evidence of genuineness, and of the condition's neurological basis (Hubbard et al., 2005a; Nunn et al., 2002).

Synesthesia is thought to stem from neuro-developmental differences in the brain maturation of synesthetes, and there are three classes of theories to account for these differences (for a review see Hubbard and Ramachandran, 2005). The "cross-activation" theory proposes that brain regions that are normally segregated in non-synesthetes remain connected in synesthetes due to a genetically mediated failure of pruning. This may cause one region to cross-activate another, in a manner similar to that observed in phantom limb patients. However, unlike phantom limbs, which result from cross-activation within the somatosensory modality, synesthetic experiences cross boundaries between processing streams that are normally segregated (Hubbard and Ramachandran, 2003; Ramachandran and Hubbard, 2001). The "disinhibited feedback" model suggests that synesthesia arises from disinhibition of the feedback that is present in all brains (Grossenbacher, 1997; Grossenbacher and Lovelace, 2001). It is known that information flows not only bottom-up from the sensory receptors to higher order areas, but also from the top-down to lower-level sensory areas (Felleman and Van Essen, 1991). This feedback, which is normally inhibited, may become disinhibited in synesthetes (perhaps due to differences in the balance of excitatory and inhibitory neurotransmitters) and lead to conscious synesthetic experiences. Finally, the "re-entrant processing" model (Smilek

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Abbreviations: CONG, congruent; fMRI, functional magnetic resonance imaging; INCON-MATCH, incongruent/gender-match; INCON-MIS, incongruent/gender-mismatch; IPL, inferior parietal lobule; OPL, ordinal linguistic personification; TPJ, temporal–parietal junction.

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et al., 2001) suggests that, as with normal visual processing, synesthetic experiences are mediated by a recursive, bidirectional flow of bottom-up and top-down information. Despite their differences, all three models suggest that synesthesia stems from a neuro-developmental tendency to preserve or develop atypical interactions between brain regions that normally do not (directly) communicate. By better understanding the developmental basis of synesthesia, we may shed light on these potential neural mechanisms, and show how different modalities become segregated during both synesthetic and normal development.

Synesthetic experiences can be categorized two different ways depending on whether one focuses on the inducer or the concurrent (see also Flournoy, 1893 for a taxonomy that includes both of the distinctions made below). Ramachandran and Hubbard (2001; Hubbard and Ramachandran, 2005) suggest that different types synesthesia be divided into "lower" and "higher" forms depending on whether the inducer of the synesthetic experience occurs at a lower, perceptual, level of processing (e.g. visual form recognition of numbers), or at a higher, conceptual, level of processing, such as assessing the numerical quantity or ordinal sequence (see also Grossenbacher and Lovelace, 2001). Regarding concurrents, it is clear that some are phenomenologically similar to the experiences of veridical perception, as for example, when colored photisms are seen projected into space (Ward et al., 2006). In other cases, however, the concurrent equates to a "mind's eye impression" or an overwhelming cognitive association (e.g. the *notion* of a color; Simner et al., 2006a) and these two variants have been labeled "projector" and "associator" synesthesias respectively (Dixon et al., 2004). An examination of synesthetic mechanisms can inform theories of neuronal connectivity, and here we examine two synesthetic variants that interact in ways to suggest connectivity that is relatively late-acquired, and which can give rise to implicit as well as explicit synesthetic associations.

The first of the synesthetic variants we examine in this paper is ordinal linguistic personification (OLP): the involuntary and automatic tendency in certain individuals to attribute animate-like qualities such as personality and gender to sequential linguistic units (e.g. letters, numerals, days, months; Calkins, 1893; Cytowic, 2002; Flournoy, 1893; Luria, 1968; Sagiv, 2005; Simner and Holenstein, in press). Flournoy (1893), for example, documents the case of Mme L. for whom "*4* is a good peaceful woman, absorbed by down-to-earth occupations and who takes pleasure in them. *5* is a young man, ordinary and common in his tastes and appearance, but extravagant and self-centered." (Flournoy, 1893, p. 219). Similar accounts have been given by Calkins (1893) who describes a case for whom whose "*T*'s are generally crabbed, ungenerous creatures. *U* is a soulless sort of thing. *4* is honest, but . . . *3* I cannot trust. . . *9* is dark, a gentleman, tall and graceful, but politic under his suavity" (Calkins, 1893, p. 454). Remarkably similar reports are apparent in a number of historical accounts (Patrick, 1893; Luria, 1968), and the OLP phenomenon has recently been revisited in the modern literature. Cytowic (2002) documents the case MT, for whom "*I* [is] a bit of a worrier at times, although easy-going; *J* [is] male; appearing jocular, but with strength of character; *K* [is] female; quiet, responsible. . ." (Cytowic, 2002; p. 298), and Simner and Holenstein (in press) introduced case AP, to be re-examined here, for whom letters, numbers and months all have personified genders and personalities (see Table 1 for her letter OLPs; and Simner and Holenstein, in press, for examples of numerals and months). In all cases reported here and in the literature, participants are unaware of the roots of their associations, which have occurred automatically for as long as they can remember. The term OLP reflects the fact that personifications are triggered, specifically, by the units of ordinal sequences (letters, numbers, days, months), and further evidence for the ordinal quality of the inducer comes from the fact that units close in a sequences are more likely to generate related personifications, compared with those that are more remote (e.g. p might be the son of q, but not of a distal unit like b; Simner and Holenstein, in press).

The second synesthetic variant under consideration is grapheme-color synesthesia, in which numerals and/or letters induce colored photisms. From recent prevalence estimates, grapheme-color synesthesia and OLP each occur in 1%-3% of the population, (depending on whether classifications include variants triggered by either, or all possible classes of linguistic inducers; Simner et al. (2006b; Simner and Holenstein, in press). Simner and Holenstein have shown that these two manifestations tend to co-occur and share characteristics in common with other variants of synesthesia. Hence, both variants are highly consistent over considerable time intervals, both generate concurrents automatically (even where this interferes in behavioral tasks) and both have the characteristic of letter-to-word transference: the tendency to spread a concurrent features from the initial letter throughout a word (but generally excluding days/months (e.g. Calkins, 1893; Simner et al., 2006a; Simner and Holenstein, in press; Tyler, 2005). In the current study, we aim to show that these variants also interact in cognitive tasks. We present behavioral evidence that synesthetic concurrents such as color and gender can come to be directly associated if they are triggered by the same inducer (e.g. letter-color, letter-gender). This finding allows us to suggest a model of the underlying neurological system, and the developmental time course of these effects, topics we return to in the General Discussion.

EXPERIMENTAL PROCEDURES

In this paper we examine synesthete AP, whose letters have both synesthetic personifications and colors. The participant will respond to letters presented in one of three types of font color: congruent (CONG i.e. in APs synesthetic color for that letter), incongruent/gender-match (INCON-MATCH i.e. in AP's color for a different letter, but one with the same gender) and incongruent/gender-mismatch (INCON-MIS i.e. in AP's color for a different letter, and one with a different gender). Experiment 1 elicits judgments about letters' OLP genders (e.g. *a*=female) and tests two hypotheses. First, we ask whether the synesthetic color of a letter and its OLP gender are features within the same broad cognitive system. If so, we predict that activation of the former could influ-

Table 1. Letter OLP inducer-concurrent associations for participant AP (f=female; m=male)

Inducer	Concurrent personifications
a	f: Mother type; very busy; sensible; “the boss”
b	m: Related to *a*; either her husband or toddler son
c	m: A boy; perfectly nice; either son of *a*, or friend to *a*’s son
d	m: Older than *c*; single; “out on his own”; seeks advice from *e* and *f*
e	m: “Cheeky chappy” (i.e. light-hearted; flippant); “wheeler dealer” (i.e. entrepreneurial); talks when he does not know what he’s talking about
f	m: “A dodgy geezer” (i.e. untrustworthy); has connections; like *e* but less nice
g	f: Middle-aged; best-friends with *h*; gossips about *d*, *e*, and *f*; little bit posh
h	f: Busy; energetic; preoccupied; best friends with g; bit more old-fashioned; not as posh
i	m: Little guy; *h* and *g* are always fussing over him; independent; wants to get on
j	f: Busy; energetic; mother of *i*; preoccupied
k	f: Very energetic; bubbles along; not always approachable; mother of *l*
l	m: Shy/quiet; son of *k*; they do not spend much time together because she’s busy with other things
m	f: *m* And *n* are two old ladies; spend all their time together and natter a lot; always together
n	See *m*; *n* is slightly less dominant
o	m: Single; bit like *e* in personality; fat/short; gets a bit annoyed by *m* and *n*, who boss him about a little
p	m: Son of *q*; nice; quite young man; close to *q* in a pragmatic way; follows in *q*’s footsteps
q	f: Mother of *p*; preoccupied with teaching him all about life
r	m: Servant to *s* (and less directly, to *t*); very loyal; cute; short
s	f: Beautiful; difficult; demanding; posh; extremely snobbish
t	m: New husband to *s*; older than her; protective; always pandering to her
u	f: Quite tough; female “bouncer” (i.e., doorman); gatekeeper to a secret palace at the end of the alphabet
v	f: Beautiful “femme fatale”; lady-in-waiting to *z*; bit snobby
w	f: Beautiful; evil too; feels she’s not as beautiful as the others; chubby; slightly excluded by the others
x	f: Very tough; intelligent; beautiful and evil; right-hand woman to *y*; older/senior
y	f: Servant and right-hand woman to *z*; very loyal; the oldest of the ladies-in-waiting; advisor/confidante to *z*
z	f: The queen of all the alphabet

ence activation of the latter, and hence, we should find faster gender-responses for targets presented in colors from other letters with matching gender (INCON-MATCH) compared with mismatching gender (INCON-MIS). For example, responses to the female letter *a* would be faster when presented in the color of another female letter (e.g. gray; given that u=gray/female) compared with the color of a male letter (e.g. green; given that d=green/male). Assuming a network of nodes and connections, this finding might suggest that the colors of all like-gendered letters are linked via their gender node (as with the example in Fig. 1 below), since this would explain how responses about the gender of any given letter (e.g. *a*) could be influenced by the color of a different letter.

This model is further refined in the second aim of the study. In this, we test whether the links between color and gender are direct, (as in Fig. 2a below) or mediated by the letter node (as in Fig. 2b).

If colors are linked directly to the gender node (2a), then responses about the gender of any given letter (e.g. *a*=female) should be facilitated equally by its own color (red), as by the color of any other like-gendered letter (gray). This is because the latter color would feed directly to the gender node, without being mediated (i.e. muted) by its own intervening letter. Such an effect translates into gender-responses that are equivalently fast in the CONG and INCON-MATCH conditions. This can be seen by the elaboration of Fig. 2a (in Fig. 3 below) to provide an example illustrating how responses would be generated for the female letters *a*-red (CONG) and *a*-gray (INCON-MATCH) respectively.

The arrows in bold represent activation of the gender node from the features of the stimuli. If colors are linked directly to the gender node, as shown, this node would be equally activated by the colors red and gray, and hence would give equivalent response times to name the gender of the letter *a* across conditions. The latter model (Fig. 2b), however, predicts slower responses in the INCON-MATCH condition because the incongruent color could access the gender node only via its own letter node (i.e. gray→*u*→female).

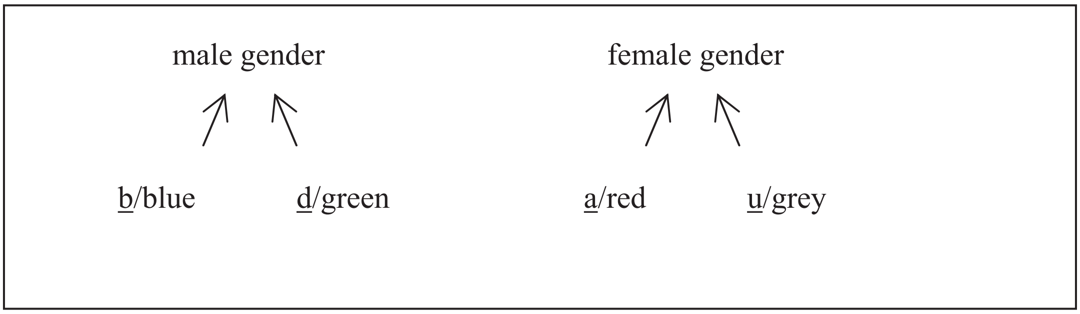

Fig. 1. Model showing the association of letters/colors to gender, for the letters *b* and *d* (male) and *a* and *u* (female). Arrows represent connections between nodes.

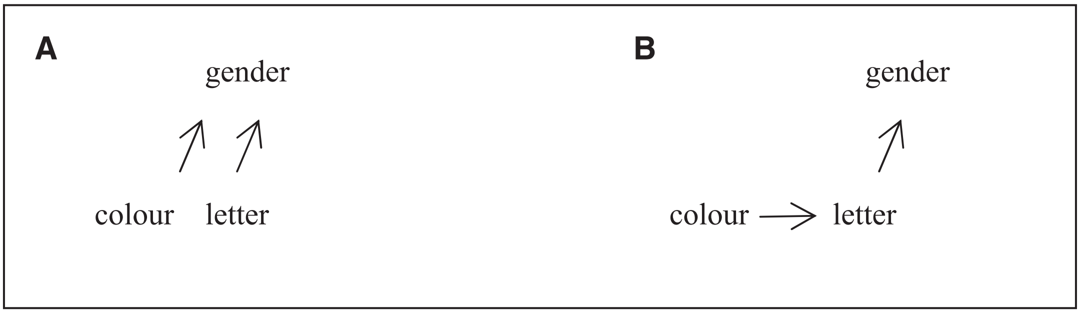

Fig. 2. (a, b) Model showing two possible types of association between letters, colors and gender. Arrows represent connections between nodes.

Experiment 2 elicits judgments about font color, and tests two hypotheses. First, we seek evidence of a standard synesthetic color Stroop effect (e.g. Mattingley et al., 2001; Mills et al., 1999; Odgaard et al., 1999) in which font-colors are named fastest when the font color matches the synesthetic color of the letter (CONG condition). Such a finding would suggest that letters automatically elicit their synesthetic colors (i.e. by a connection from the letter node to color node) and that these colors can compete (see also Mattingley et al., 2001; Mills et al., 1999; Odgaard et al., 1999). However, our second hypothesis modifies this claim, while at the same time seeking additional evidence for the assumption that colors are linked to each other through a single gender node.

One implication of the single gender-node hypothesis is that colors would be adjacent in a micro-network (i.e. daughters of a shared gender node) if their letters have the same gender, but not if they have different genders. For example, the colors red and gray would be adjacent (i.e. daughters) under the same female gender node because their respective letters—a and u—are both female (while red and green would be under different gender nodes because their respective letters—a and d—have different genders). In standard models of activation and inhibition, it is this adjacency that causes competition when two nodes are activated simultaneously. Given this, our color manipulation gives the following prediction: any detrimental competition between colors causing a Stroop effect should only occur (or especially occur) when those colors are within the same gender. This is because the implicit activation of a synesthetic color would only provide competition for naming the font color if the two colors are adjacent in the same network (i.e. daughters of the same gender node). When the colors are in different localities (i.e. beneath different gender nodes), this competition should be diminished or eliminated. In other words, the Stroop effect should be found only (or especially) when comparing the CONG condition with the INCON-MATCH condition, but not (or less so) with the INCON-MIS condition.

The predictions of experiments 1 and 2 are summarized as follows. If features of OLP gender and synesthetic color can influence each other, and if the colors of letters with the same gender are associated directly to a single gender node, experiment 1 should generate faster gender-responses in the INCON-MATCH versus INCON-MIS condition, and equivalent responses for the CONG condition and the INCON-MATCH condition. In experiment 2, if the single gender-node hypothesis is indeed correct, and if letters automatically activate their synesthetic colors, we predict faster font color naming in the CONG versus INCON-MATCH condition, but that this Stroop effect will be diminished, or absent in the INCON-MIS condition.

Case-history AP

AP is a 23-year-old right-handed female graduate, who experiences a range of synesthetic variants, including grapheme-color, day-color, OLP and taste-shape. The genuineness of her reports has been attested elsewhere with objective measures (Simner and Holenstein, in press; Simner et al., 2006b). Her OLP experiences are triggered by letters, numbers, and months, and her colors by letters, numbers and days. Her synesthetic concurrents are highly detailed, and she goes to considerable trouble to describe them. This characteristic has been seen in previous reports of OLPs, and been observed in other areas of synesthesia more generally (Ward and Simner, 2003). AP reports that she has had her OLP (and other synesthetic) associations for as long as she can remember, and is unaware of their origins.

Experiment 1

Method. Materials. The materials comprised eight letters, half with a male personification (*b*, *d*, *o*, *t*) and half with a female personification (*a*, *j*, *u*, *w*). Each letter was repeated eight times in each of the following three conditions: CONG (i.e. in APs synesthetic color for that letter), INCON-MATCH (i.e. in AP's color for a different letter, but one with the same gender) and INCON-MIS (i.e. in AP's color for a different letter that has the opposite gender). For example, the female letter *a* appeared eight times in its own color, red (CONG), eight times in the color of another

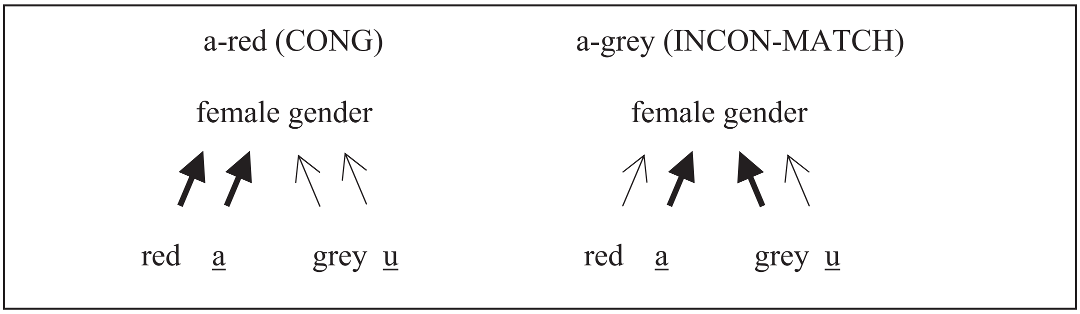

Fig. 3. Model showing the activation of the gender node in the CONG (a-red) condition and the INCONG-MATCH (*a*-gray) condition. Thin arrows represent unactivated connections between nodes, and arrows in bold represent activated connections.

female letter, gray (INCON-MATCH) and eight times in the color of a male letter, green (INCON-MIS). The specific shade of each color had been determined in advance by a pre-test in which participant AP indicated her synesthetic colors for each letter of the alphabet, by moving a cross-hair cursor over the standard "Windows API Choose Color" dialog box.

Procedure. The participant was seated at a pc computer running Eprime software (Psychological Software Tools, 2002) with a high-resolution color monitor. Each trial began with an on-screen fixation point ("+"). After 1500 ms, this was replaced by a letter, randomly selected without replacement from the materials list. Letters appeared in one of eight colors (blue, green, purple, brown, red, orange, gray, yellow) according to the experimental manipulation. Stimuli remained on-screen until the participant made a response from a button-box which had two buttons revealed, marked MALE and FEMALE. The button press indicated whether the letter's OLP gender was male or female, and the participant was instructed to respond as quickly and accurately as possible. The experiment lasted approximately 10 min.

Results

Errors comprised 1% of responses and were equally distributed throughout the data. These were removed, and the remaining gender-naming reaction times (RTs) were treated for outliers, by removing all data points beyond two standard deviations from the mean. Outliers represented 4.2% of the data and were equally distributed across conditions. The means from the remaining items were: CONG=545 ms, INCON-MATCH 534 ms, INCON-MIS 585 ms, and a repeated measures one-way ANOVA showed a significant main effect of the experimental manipulation ($F(2)=4.8$, $P<0.01$). As predicted, planned comparisons revealed that the INCON-MIS condition was significantly slower than the CONG condition ($t(63)=2.4$, $P<0.02$) and the INCON-MATCH condition ($t(63)=2.7$, $P<0.01$), but that there no difference between these latter two ($t(63)<1$).

Discussion, experiment 1

The results of experiment 1 suggest that features of OLP and grapheme-color synesthesia exist in the same broad cognitive domain, since the colors of letters influenced decisions about their gender. Hence, participant AP was significantly faster to indicate the gender of a female letter, for example, if it was presented in the color of another female letter, compared with a male letter (i.e. INCON-MATCH<INCON-MIS). The fact that the color of non-target letters can facilitate gender responses to the target (i.e. a different letter) suggests that all like-gendered letters may be associated under a single gender node. Furthermore, the fact that the color of non-target letters facilitates gender responses *to the same extent* as the color of the target itself (i.e. CONG=INCON-MATCH), suggests that all colors may be attached *directly* to this gender node, without an intervening letter node (which might otherwise temper the spread of activation). In the General Discussion we examine the extent to which these associations may exist at implicit versus explicit levels of consciousness, but for now turn to experiment 2, where we provide further evidence for the hypotheses generated here.

Experiment 2

Method. Materials. As in experiment 1, the materials systematically combined letters with font colors. Since responses in the current experiment were for font-color naming, our three-level manipulation was based around target font colors, of which four were selected (red, yellow, gray, green). Since this experiment elicits color responses, fewer colors were used than in experiment 1 to simplify the procedure, and to avoid letter-color pairings that might otherwise produce confounds of linguistic priming (e.g. orange). (Target colors correspond to both OLP male and OLP female letters, but not in equal proportions (red, yellow, gray=female; green=male). This was the coincidental outcome of creating materials by editing those of experiment 1 to remove the potential linguistic priming confound. However, Simner and Holenstein (in press) have illustrated that AP shows absolutely no differential effect of processing OLP male versus female letters, and hence, there should be no detrimental outcome of the balance in the current study.) Each color was repeated eight times, in each of the following three conditions: CONG (i.e. paired with APs synesthetic letter for that color), INCON-MATCH (i.e. paired with a different letter, but one that matched in gender to the synesthetically-associated letter) and INCON-MIS (i.e. paired with a different letter, and one that did not match in gender to the synesthetically-associated letter). For example, the color red appeared eight times with its own (female) letter *a* (CONG), eight times with another female letter *u* (INCON-MATCH) and eight times with a male letter *d* (INCON-MIS).

Procedure. The same apparatus from experiment 1 were used in the current study, except that the button-box was now attached to a microphone with a voice-activated relay. This measured ms response timings between the onset of the target on-screen, and the onset of the response utterance. AP was instructed to simply state the font color as quickly and accurately as possible, and the experiment lasted approximately seven minutes.

Results

The data were treated to remove errors and outliers in the way described in experiment 1. Errors comprised 1% of responses and were equally distributed throughout the data, as were outliers, which again represented 4.2% of the data. The color-naming means from the remaining items were: CONG=586 ms, INCON-MATCH 638 ms, INCON-MIS 569 ms, and a repeated measures ANOVA showed a significant main effect of the experimental manipulation ($F(2)=5.3$, $P<0.01$). As predicted, planned comparisons revealed that INCON-MATCH condition was significantly slower than the CONG condition ($t(31)=2.3$, $P<0.05$) as well as the INCON-MIS condition ($t(31)=3.0$, $P<0.01$), but that there no similar Stroop-type slow-down in the INCON-MIS condition (i.e. no difference between CONG and INCON-MIS: $t(31)<1$).

Discussion, experiment 2

The results from experiment 2 suggest that letters automatically activate their synesthetic colors because the data reveal a Stroop-type color-naming effect, with faster responses when the target color and letter are synesthetically CONG. Within a cognitive network model, this might suggest the presence of a connection between the letter node and color node (see Fig. 4 below). However, the fact that this Stroop effect is found for letters sharing the same gender (i.e. CONG<INCON-MATCH) but not different genders (i.e. CONG=INCON-MIS) suggests that colors compete only in the former circumstances. This provides support for a network model in which colors from like-gendered letters are represented as daughters under a shared gender node (Fig. 1). This is compatible with the finding that any detrimental competition between colors would only occur when those colors are adjacent in the same micro-network (i.e. under the same gender node).

DISCUSSION

The conclusions from experiments 1 and 2 are united in Fig. 4 below, which shows the network model of the relationship between AP's colors, letters and genders, and which are associated in such a way that the concurrent features of gender and color can influence each other in

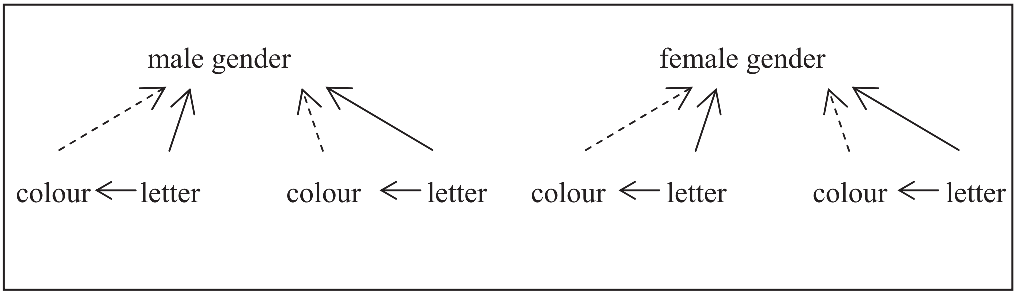

Fig. 4. Model uniting the findings from experiments 1 and 2, showing the associations between letters, colors and gender. Arrows represent connections between nodes; unbroken and broken lines show explicit and implicit connections, respectively.

cognitive tasks. In constructing our model, we flag the following aspects. We have coded connections with either unbroken or broken lines, and the former indicate pathways that are subject to explicit conscious report. For example, AP states that letters trigger colors and that letters trigger gender. Broken lines, in contrast, indicate connections that exist implicitly, in that they are found in our behavioral tasks but are not part of AP's conscious awareness (e.g. AP shows behavioral evidence of direct connections between gender and color, but does not report that colors have gender or vice versa at a conscious level). In this way, we add our findings of implicit connectivity to those from previous studies, which have shown a disparity between the explicit reports of synesthetes and the implicit connectivity of underlying systems. For example, Cohen Kadosh et al. (2005; see also Brugger et al., 2004; Cohen Kadosh and Henik, 2006; Knoch et al., 2005) show that although the explicit reports of synesthetes tend to have a fixed directionality, their underlying systems may be implicitly bi-directional. Their studies showed that synesthetic colors implicitly evoked number magnitude even though the number-color synesthetes had no experiential awareness of this (i.e. they report colors from numbers, but not vice versa). Given these findings of implicit bi-directionality, our model, also should be interpreted as compatible with the possibility of implicit bi-directional links, should these be found in future studies of letter-color synesthesia. Until then, our connections are shown with arrows to reflect the explicit directionality of AP's reports (e.g. letters generate colors, not vice versa) and the directionality of the findings in our study (e.g. experiment 1 shows that colors are activated from letter stimuli, but does not address the question vice versa).

Our paper also provides methodological information about the synesthetic Stroop task. This paradigm has been used extensively in the synesthesia literature (e.g. Dixon et al., 2000; Mattingley et al., 2001; Mills et al., 1999; Odgaard et al., 1999) although our data suggest that it might successfully be applied only under certain circumstances. Specifically, we have shown that incongruency effects depend not only on the nature of the task, but also on the presence of other variants of synesthesia. We have seen that letters presented in colors that are synesthetically incongruent can inhibit processing in color-naming (but not OLP gender identification), only if that color comes from like-gendered letters. Hence we suggest that the Stroop phenomenon should be interpreted with care in any synesthesia study where participants possess more than one variant.

Neural mechanisms

We now address the underlying neuro-developmental roots of the connections found in our studies. The fact that OLP and grapheme-color synesthesia are variants of the same condition (Sagiv, 2005; Simner and Holenstein, in press) suggests both are caused by the same pre-disposition for cross-activation. Given that the common factor across a range of synesthesia studies (e.g. Flournoy, 1893; Sagiv et al., 2006; Simner and Holenstein, in press) appears to be the ordinal sequence (e.g. letters, numbers, days, months) we suggest (following Hubbard et al., 2005b; Ramachandran and Hubbard, 2001) that its roots may lie in parietal circuits that have been implicated in ordinal processing, in particular in the region of the left inferior parietal lobule (IPL) and temporal–parietal junction (TPJ).

To further explore this possibility, we first distinguish between ordinal information (relating to sequence) and cardinal information (about the quantity or numerosity of items). Here we concentrate on neuroimaging data and patient studies that have examined the neural substrates of ordinal sequence processing, but it should be stressed that a partially overlapping network of parietal and frontal regions is implicated in both processes (for reviews, see Dehaene et al., 2003; Nieder, 2005). Studies of patients with semantic dementia show that ordinal sequences, as a group (days of the week, months of the year, letters and numbers) can be preserved together, despite severe deficits in semantic knowledge for many other categories of stimuli, suggesting shared substrate for different ordinal sequences (Cappelletti et al., 2001). Because the degeneration differentially affected temporal lobe structures while sparing the IPL, these data point toward the IPL as a possible neural substrate of ordinal sequence information. Similarly, fMRI studies of order information in working memory (Marshuetz et al., 2006; Marshuetz et al., 2000) demonstrate activation of the IPL and the intraparietal sulcus (IPS). Additionally, lesions to the parietal cortex sometimes lead to selective impairments in ordinal sequence representation, demonstrating that this region is critical for these processes (Dehaene and Cohen, 1997;

Turconi and Seron, 2002). We therefore predict that the IPL (in particular the angular gyrus) is critical for evoking these experiences.

For OLP concurrents (personality etc.), we might turn to a network of brain regions, including the amygdala, somatosensory cortex (especially on the right), inferior parietal and frontal regions, which have been shown to be critical for social cognition (for a review see Adolphs, 2003). Particularly relevant for our purposes are studies that demonstrate that the left IPL and TPJ, are critical for determining personality characteristics (Heberlein et al., 2004; Heberlein and Saxe, 2005) and inferring another's mental state, respectively (Saxe and Kanwisher, 2003; Samson et al., 2004). Examination of lesion overlap in patients suggests that inferring personality, but not emotion, from point-light walkers depends on left IPL regions (Heberlein et al., 2004). A follow-up fMRI also showed that the IPL was more active when participants were asked to judge personality traits from point-light walkers compared with when they were asked to judge emotions (Heberlein and Saxe, 2005). Similarly, when subjects are asked to read stories about a character's mental states, regions of the TPJ show increased activation (Saxe and Kanwisher, 2003). Samson et al. (2004) showed that this region was critical for such tasks by demonstrating that three patients were impaired at both a story-based and a video-based false belief task, but not on various control tasks. In sum, evidence from a range of techniques suggests that both ordinal sequence processing and personality attribution depend on a network of regions including the left inferior parietal lobe (especially in the region of the angular gyrus). We therefore propose that cross-activation between these regions might be crucial for the OLP phenomenon observed here.

The presence of color associations, and the direct connection between colors and personalities, further suggests the parietal lobe as a likely candidate. Although color processing is often a ventral stream function, a number of underappreciated pieces of evidence suggest a role for the parietal cortex in certain higher-order aspects of color processing. For example, color anomia is sometimes reported in patients with Gerstmann's syndrome due to lesions of the angular gyrus (Geschwind, 1965a,b) and direct cortical stimulation in patients undergoing neurosurgery demonstrated anomia with stimulation of the angular gyrus, or close to it, in the posterior part of the supramarginal gyrus (Roux et al., 2003). Functional imaging studies have also shown that regions of the parietal cortex are involved when subjects are asked to compare colored objects with their canonical color (Zeki and Marini, 1998) or when asked to make within linguistic-category color comparisons (Claeys et al., 2004). Taken together, these data suggest that connections between ordinal sequences and color may be mediated by structures in the IPL, such as the angular gyrus (giving a sort of "higher" synesthesia; Ramachandran and Hubbard, 2001). Combining these independent sources of information, we would predict that the link between ordinal sequences, personalities and colors is mediated through cross-activation in the region of the left angular gyrus.

Developmental considerations

We now turn to the question of developmental stages in the acquisition of the inducers and concurrents studied here. Developmental studies of ordinal sequence acquisition for numbers are extensive (for book length treatments, see Fuson, 1988; Geary, 1994). Some research has suggested that even non-human primates have the ability to compare ordinal sequences (Brannon and Terrace, 1998, 2000; see also Hauser et al., 2000) and these pre-linguistic abilities are probably mediated by the same mechanisms described above in relation to working memory for order (Marshuetz et al., 2000; Nieder, 2005). In children, acquisition of the verbal counting sequence probably builds on these more basic mechanisms, and begins very early. Brannon (2002) has shown that 11-month-old infants successfully discriminated sequences of numerosities that decreased in numerical value from those that increased. Later, children as young as 2 years make numerical discriminations and can represent ordinal relations between numerosities up to 6. They start to acquire number words around age 2–3, and most are able to recite the sequence up to 10 by the age of 3–4. Although acquisition beyond 10 is language-specific, depending on lexical irregularities (e.g. slower in English than Chinese) children in most cultures can count to 100 by age 7–8.

Understanding personality trait concepts appears to begin later in development. However, by the age of 5–6 (or perhaps as young as 3–4; Heyman and Gelman, 2000; Shimizu, 2000) children are already able to assign personality traits along two of the "big five" personality dimensions (Measelle et al., 2005) although these may stem from inferences based on general characteristics of "goodness" (Hayashi, 2004) and be restricted to inferences about temporary rather than permanent features (Rholes and Ruble, 1984). However, Gnepp and Chilamkurti (1988) have suggested that children as young as six *can* infer permanent, long-term personality traits if they are given sufficient information that a particular behavior represents a persistent attribute (e.g. viewing evidence of, say, generous behavior in more than one scenario). Older children (8+) appear to have no difficulty making spontaneous trait-based predictions about future actions based on even limited evidence of particular behaviors (e.g. Rholes and Ruble, 1984). In summary, the ability to make explicit personality-trait attributions appears to be developing by age 5, and develops from a general sense of temporary "goodness/badness" to more complex notions of enduring personality by the age of around 8.

Such developmental information about the acquisition of personality and ordinal sequence information is crucial for theories of synesthetic connectivity. Given the time course of these acquisitions, we can infer that the synesthetic associations in OLP (and between OLP and grapheme-color synesthesia) must necessarily emerge some time *after* the age of 5–8 years, i.e. only once personality and ordinal information is itself in place. At first glance, this protracted time course might seem at odds with developmental theories of synesthesia that suggest retention of early neural connectivity (Maurer, 1997; Ramachandran and Hubbard, 2001). However, this apparent discrepancy arises from the mistaken assumption that neural pruning occurs only during neonatal development (see e.g. Hunt, 2005; Marks and Odgaard, 2005). In the past 10 years, a variety of data has emerged which suggests that human brain development, unlike that of non-human primates, is heterochronous (occurring at different times in different brain regions) and protracted (compare data from Huttenlocher and Dabholkar, 1997 in the human with data from Rakic et al., 1986, 1994 in the monkey). Huttenlocher and Dabholkar (1997) found that while synaptic density in the visual cortex falls off approximately 500 days after conception, density in the primary auditory cortex starts to decrease only after age 3.5 years, while density in the frontal cortex decreases more slowly from 3.5 until at least 11 years.

Such data demonstrate that human brain development is a complex, staggered process, with different time courses for different brain regions. This has been supported by *in vivo* studies showing human brain development proceeding heterochronously into adolescence and beyond (e.g. using anatomical MRI and cortical gray/white matter segmentation techniques, Paus, 2005; Toga et al., 2006 for recent reviews). For example, Giedd et al. (1999) found that although white matter volume increased linearly with age in participants aged 4–22, gray matter volume showed non-linear changes (e.g. peaking at 11–12 years in frontal and parietal lobes, at 16 in the temporal lobe, and continuing to increase with age in occipital areas). Cortical thickness, too, shows developmental variations from region to region and across age groups (Sowell et al., 2001, 2004). For example, while cortical thickness increases at age 5–11 in the superior temporal cortex and left inferior frontal gyrus (regions classically associated with linguistic processing), it *decreases* in right frontal, dorsal parietal and occipital regions (e.g. Sowell et al., 2004), and such decreases in frontal regions accelerate in adolescence (age 12–16) and early adulthood (age 23–30). In the region of the angular gyrus, development is characterized by increased growth (as measured by the distance from the center of the brain) between childhood and adolescence, followed by cortical thinning between adolescence and adulthood (Sowell et al., 2004). It is tempting to speculate that these decreases in gray matter thickness might correlate with the synaptic pruning reported by Huttenlocher and Dabholkar (1997); however, MRI measures cannot distinguish between regressive events like pruning and progressive events like increased myelination.

Despite such caveats, it is clear from these studies that brain development continues well into adolescence in many brain regions, and that the exact pattern of growth and pruning depends on the region in question. Hence, although our studies suggest a relatively late connectivity between regions (i.e. after the acquisition of personality and ordinal sequence information) the late and varied changes in connectivity evidenced by the research reviewed here suggest we cannot distinguish between models of synesthetic connectivity based on pruning or neural growth. However, as basic neuroscience research continues to expand our knowledge of cortical development, we will achieve a closer understanding of the relationship between the development of synesthesia and changes in brain structure.

CONCLUSION

In summary, our study represents the first empirical comparison of two variants of synesthesia within, rather than across participants. We have used our findings to generate a cognitive model of the phenomena, and have provided evidence that OLP and grapheme-color synesthesia interact in cognitive tasks. We have shown that synesthetic concurrents with the same inducer can become directly associated at an implicit level, even where these associations are not open to conscious report, and we have provided a neuro-developmental overview of the underlying systems that are likely to be implicated in the generation of synesthetic colors and personalities.

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