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RESEARCH ARTICLE

Prevalence, characteristics and a neurocognitive model of mirror-touch synaesthesia

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Abstract In so-called 'mirror-touch synaesthesia', observing touch to another person induces a subjective tactile sensation on the synaesthete's own body. It has been suggested that this type of synaesthesia depends on increased activity in neural systems activated when observing touch to others. Here we report the first study on the prevalence of this variant of synaesthesia. Our findings indicate that this type of synaesthesia is just as common, if not more common than some of the more frequently studied varieties of synaesthesia such as grapheme-colour synaesthesia. Additionally, we examine behavioural correlates associated with the condition. In a second experiment, we show that synaesthetic experiences are not related to somatotopic cueing—a flash of light on an observed body part does not elicit the behavioural or subjective characteristics of synaesthesia. Finally, we propose a neurocognitive model to account for these characteristics and discuss the implications of our findings for general theories of synaesthesia.

Keywords Synaesthesia · Crossmodal processing · Somatosensory processing · Self · Body representation

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Introduction

The term synaesthesia is used to describe a condition in which one property of a stimulus (the inducer) results in conscious experiences of an additional attribute (the concurrent). This inducer-concurrent relationship can occur either within or between modalities. For example, in grapheme-colour synaesthesia a visually presented grapheme can result in synaesthetic experiences of colour (Cohen Kadosh and Henik 2007; Rich and Mattingley 2002), whereas in lexical-gustatory synaesthesia written or heard words trigger a subjective sensation of taste (Ward and Simner 2003).

Early research on the prevalence of synaesthesia indicated that the condition may have a minimum prevalence rate of 1 in 2,000 with a female-to-male ratio of 6:1 (Baron-Cohen et al. 1996; Rich et al. 2005). These studies assessed the prevalence of the condition based upon the number of respondents to newspaper advertisements who pass an objective measure of synaesthesia (relative to newspaper circulation figures). This method of assessment does not permit inferences about non-responders and may also lead to an over inflated female to male ratio. More recent studies, which overcome these difficulties by screening a large population and supplementing this with the use of objective measures of different variants of synaesthesia suggest a higher prevalence rate of 4% and a female to male ratio of 1:1 (Simner et al. 2006; Ward and Simner 2005). A trend of all prevalence studies is to yield a higher proportion of grapheme-colour synaesthesia, estimated to have a prevalence of 1.4% (Simner et al. 2006), relative to other types of the condition (Baron-Cohen et al. 1996; Rich et al. 2005; Simner et al. 2006).

Since these studies, a new variant of synaesthesia has been documented in which observing touch to another person induces a tactile sensation on the synaesthete's own body (mirror-touch synaesthesia). A single case fMRI study suggests that this variant of synaesthesia is a consequence of increased neural activity in a network of brain regions which are also activated in non-synaesthetic control subjects when observing touch to another person (Blakemore et al. 2005). In that study, the authors contrasted brain activity in a single mirror-touch synaesthete with twelve non-synaesthetic control subjects while observing humans relative to objects being touched. This indicated that while all subjects activated similar brain regions as when they were touched (a mirror-touch system), the synaesthete showed increased activity within bilateral primary somatosensory cortex (SI), secondary somatosensory cortex (SII), left premotor cortex and additional activity in the anterior insula. In view of this, it was argued that mirror-touch synaesthesia reflects hyper-activation of normal (i.e. non-synaesthetic) visual–tactile interactions in the mirror-touch network (i.e. SI, SII, premotor cortex). Notably, the general role of SI activations in the mirror-touch system in non-synaesthetes remains to be clarified, with some authors reporting SI activity when non-synaesthetes observe touch to another's face (Blakemore et al. 2005) or arm (McCabe et al. 2008), others reporting SII, but not SI, activation following observed touch to the legs (Keyers et al. 2004), and others reporting SI activity when non-synaesthetes observe intentional but not unintentional touch (Ebisch et al. 2008).

Extending the single case report, a group study of ten mirror-touch synaesthetes showed that individuals with mirror-touch synaesthesia can be divided into two subtypes based upon the spatial mapping between observed and synaesthetically induced touch. Some synaesthetes report a spatial mapping as if looking in a mirror (i.e. observed touch to another person's left cheek induces synaesthetic touch on their right cheek—hereafter referred to as specular subtype), while others report a spatial mapping as if self and other share the same anatomical body space (i.e. experiencing synaesthetic touch on their left cheek when observing touch to another person's left cheek—hereafter referred to as anatomical subtype; Banissy and Ward 2007).

Authenticity and characteristics of synaesthesia

When considering the prevalence of mirror-touch synaesthesia it is important to note what constitutes synaesthesia in general and the methods used to confirm the authenticity of the condition. Synaesthesia is typically considered as having three defining features: (1) experiences are conscious perceptual or percept-like experiences; (2) experiences are induced by an attribute not typically associated with that conscious experience; (3) these experiences occur automatically (Ward and Mattingley 2006). In line with this, mirror-touch synaesthesia requires the conscious experience of a tactile stimulus which occurs automatically following the observation of touch to another person (or possibly an object).

There are several ways to determine the validity of mirror touch synaesthetes (e.g. see Blakemore et al. 2005). With regards to automaticity, Banissy and Ward (2007) developed a visuo-tactile congruity experiment to explore this aspect of synaesthesia. Touch was applied to participants' cheeks or hands (either right, left, both or no touch) while observing touch to another person's cheek/hands or to a corresponding object (a lamp). Participants were required to report the location of actual touch while ignoring observed touch. Synaesthetes, but not controls, were faster when the observed/synaesthetic touch and actual touch were in the same spatial location relative to when they were in different locations. They also reported a higher proportion of errors in which they reported synaesthetic touch in place or in addition to actual touch. For example, if they experience actual touch on their left cheek and synaesthetic touch on their right cheek (due to an observed touch on the other person's right cheek, for the anatomical sub-type, or left cheek for the specular sub-type) then they tended to report touch to both cheeks—here after referred to as a "mirror-touch error" (Fig. 1). These behavioural correlates provide evidence for the authenticity of mirror-touch synaesthesia and suggest that synaesthetic touch is an automatic experience that can interact with actual tactile experiences.

Synaesthesia has a number of other important characteristics that also appear to be found in the mirror-touch variety. Synaesthetic experiences tend to be consistent over time (e.g. if 'A' is red at time 1 then it will be at time 2 several weeks or months later; Baron-Cohen et al. 1987). Mirror-touch synaesthetes report their experiences to be enduring and an individual's spatial sub-type (i.e. whether they belong to the specular or anatomical category) is consistent both across time and across different body parts. Further, whilst it was once believed that synaesthetic experiences reflect random but consistent associations this view is no longer widely held. For example, non-random associations have been found between pitch and lightness (Ward et al. 2006), number and lightness (Cohen Kadosh et al. 2007), grapheme frequencies and colour (Simner et al. 2005); and phonology and tastes (Ward and Simner 2003). More overt semantic links are also found: it is not uncommon for the word "sausage" to taste of sausage (and similarly for other food names; Ward et al. 2005) or for the

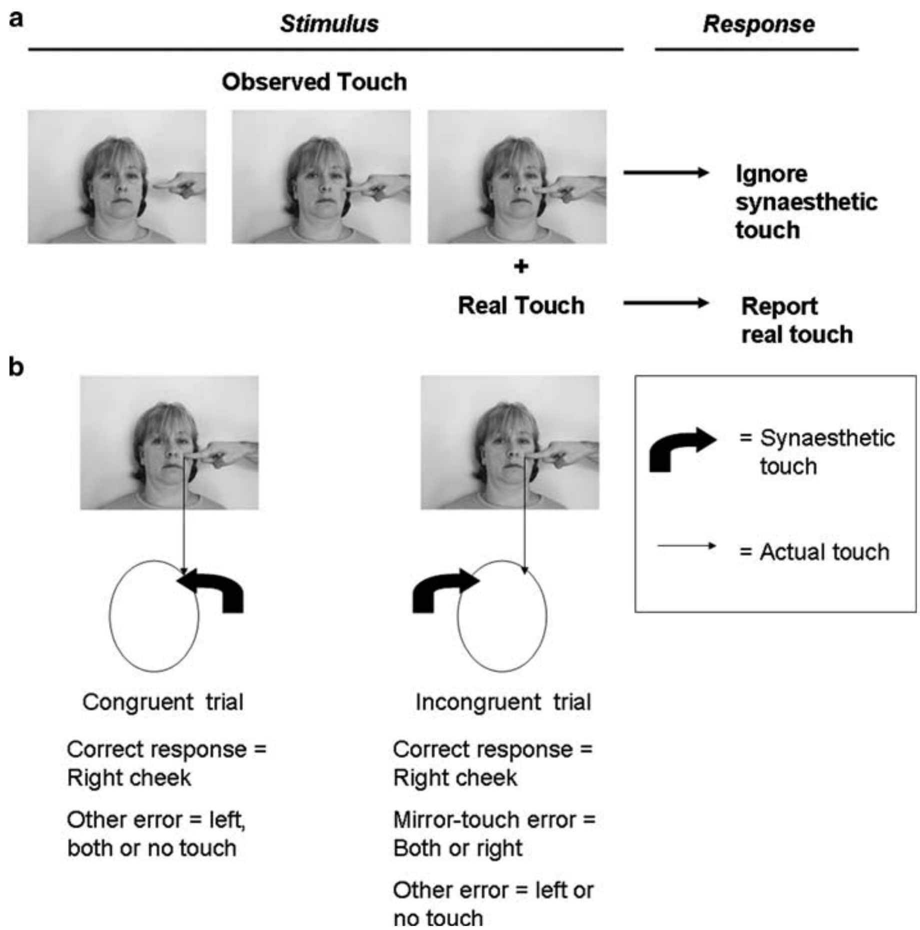

Fig. 1 **a** Summary of the task used to confirm potential cases of mirror-touch synaesthesia in Experiment 1. Participants were asked to detect the site of real touch while observing another person being touched. For mirror-touch synaesthetes observed touch elicited a tactile sensation which could either be in a congruent or incongruent location as the site real touch. **b** Example of congruent and incongruent trials including error types for a specular mirror-touch synaesthete (*dashed arrows* indicate site of synaesthetic touch, *complete arrows* indicate site of real touch). On a congruent trial, real touch was applied to the same side of the face as synaesthetic experience. On an incongruent trial real touch was applied to the side of the face which was opposite to synaesthetic experience. Participants were asked to report the location of real touch and to ignore synaesthetic touch. 'Mirror-touch' errors could be produced on incongruent trials if the subject was to report real touch to both cheeks (despite real touch being applied to one cheek only) or if the subject was to report synaesthetic rather than real touch. All other error types were classified as 'Other' error types

word "red" to be coloured red (and similarly for other colour names; Gray et al. 2002; Rich et al. 2005). The mappings in mirror-touch synaesthesia are non-arbitrary in that somatotopy is generally preserved between the observed and felt touch.

Here we present two studies investigating the prevalence and the characteristics of mirror-touch synaesthesia. In Experiment 1, we investigate the prevalence of mirror-touch synaesthesia by screening a large population and confirming self reports using a behavioural paradigm designed to test for the authenticity of the condition. We then address potential factors which may contribute to the behavioural correlates observed. In Experiment 2, we investigate the nature of the synaesthetic inducer and consider the role of somatotopic cueing on synaesthetic experience. Finally, we discuss the factors which may underpin synaesthetic experience and outline a neurocognitive model of mirror-touch synaesthesia

Experiment 1: prevalence of mirror-touch synaesthesia

This study investigates the prevalence of mirror-touch synaesthesia and compares new cases with previously reported cases of mirror-touch synaesthesia to ascertain the main cognitive characteristics of the condition.

Method

All participants ($n = 567$) were recruited from the University College London and University of Sussex undergraduate communities. Each participant was given a written and verbal description of synaesthesia including examples of what did and did not constitute synaesthesia. Participants were then administered a questionnaire asking about different variants of synaesthesia with one question specifically related to mirror-touch synaesthesia (see Supplementary Material). Namely, participants were asked to indicate on a five point scale the extent to which they agreed with the question “do you experience touch sensations on your own body when you see them on another person’s body?” Following initial screening, all participants who gave positive responses to the above question ($n = 61$; approximately 10.8% of all subjects) were contacted and interviewed about their experiences. This included them being shown a series of online videos showing another person, object, or cartoon face being touched. Participants were asked to indicate the location (if any) in which they experienced a tactile stimulus and the type of experience. Typical responses of potential mirror-touch synaesthetes ($n = 14$; approximately 2.5% of all subjects) included reports that observing touch elicits a tingling somatic sensation in the corresponding location on their own body, and that a more intense and qualitatively different sensation is felt for painful stimuli (i.e. videos of a pin pricking a hand rather than observed touch to the hand).

In an attempt to investigate reports of mirror-touch synaesthesia, we compared the performance of each potential synaesthete to ten age and gender matched non-synaesthetic control subjects on the paradigm developed by Banissy and Ward (2007). In the task, participants were required to detect a site touched on their own face (left, right, both or none) while observing touch to another person’s face or to a corresponding object (a lamp). For true synaesthetes, but not for controls, observed touch elicited a synaesthetic sensation in a congruent or incongruent location as actual touch (Fig. 1). The tactile stimuli were administered via two miniature solenoid tappers attached to the face with a Velcro strap. Each tapper was controlled using a Dual Solenoid Tapper Controller (MSTC3-2, M and E Solve; as in Banissy and Ward 2007). The visual stimuli were presented on a 17″ CRT monitor with a refresh rate of 100 Hz and consisted of two presentations of 100 ms each followed by a third stimulus which remained on the screen until the participant responded. The first two stimuli showed the approach of the hand towards the face and the third showed contact with the face. The tactile stimulus was applied concurrently with the onset of the third stimulus so that observed touch and felt touch were simultaneous. The location of the felt touch (left, right, both or none) was indicated with a button press and the need for both speed and accuracy was emphasised. Following this, there was a gap of 1,500 ms with a fixation cross before the start of the next trial. A pulse of white noise was presented via headphones for the duration of each trial in order to prevent participants from using auditory cues to determine the location of actual touch.

A total of 80 congruent trials, 80 incongruent trials and 80 trials involving no actual touch were completed. For each potential synaesthete, congruency was determined according to self reports when observing videos showing another person being touched. Within each condition, 60 trials involved observed touch to either a female or male actor, with the remaining 20 trials involving observed touch to a corresponding object. The order of trials was randomised over three blocks of 80 trials (preceded by 5 practice trials). Reaction times and error rates were measured. Based upon previous findings we expected true synaesthetes to be faster at identifying a site touched in the congruent compared to incongruent condition and/or to show a higher proportion of mirror-touch errors compared to non-synaesthetic controls. The control data were scored according to the reported sub-type of the corresponding mirror-touch synaesthete (i.e. anatomical vs. specular congruency).

Results and discussion

Behavioural performance of each potential synaesthete was compared to an age and gender matched non-synaesthetic control group using Crawford’s modified *t* test (Crawford and Garthwaite 2002). Reaction time performance (filtered prior to analysis, ±3 SD and all errors removed) and the percentage of error types on human and object trials were compared separately (Table 1). For reaction time performance, we used the size of congruency effect (incongruent minus congruent reaction time) as an index of synaesthetic experience. For errors, the percentage of mirror-touch errors (errors consistent with synaesthetic experience) and other error types were compared. Subjects who showed either significantly larger reaction time differences or significantly more mirror-touch errors relative to controls were counted as synaesthetes. Using this method we were able to confirm nine cases of mirror-touch synaesthesia on either reaction time performance, the percentage of mirror-touch errors produced, or both (Table 1). This indicates a prevalence rate of 1.6%. In comparison to previous prevalence estimates of other types of synaesthesia this places mirror-touch synaesthesia as one of the most common forms of synaesthesia along with grapheme-colour synaesthesia (1.4% prevalence) and day-colour synaesthesia (2.8% prevalence; Simner et al. 2006).

Comparison of the prevalence group with previously reported cases

In order to ensure that these cases were consistent with previously reported cases of mirror-touch synaesthesia, we

Table 1 Reaction time performance (incongruent condition reaction time − congruent condition reaction time) and percentage of mirror-touch and other error types for potential synaesthetes compared to non-synaesthetic controls when observing a human or corresponding object being touched

Synaesthete	Human trials			Object trials		
	Reaction time	% Mirror-touch	% Other	Reaction time	% Mirror-touch	% Other
D	431.24***	5.81**	0.58	11.26	0	0
I	38.97	10.29***	3.43**	−51.11	10.34***	5.17*
Z	−34.98	6.86**	0.57	−28.52	6.67**	1.67
E	79.45*	1.14	0	−18.2	0	0
K	84.84*	2.25	4.49***	−20.2	1.67	0
J	53.96	6.62***	0.60	7.77	0	1.75
R	532.13***	6.43***	0.58	54.38	0	0
H·S	214.25***	0.68	0.68	−7.05	0	0
H.G	136.38**	24.02***	0.56	52.67	10.17***	1.69

Three synaesthetes showed behavioural correlates of mirror-touch synaesthesia on reaction time only, three on mirror-touch errors only, and three on both reaction times and errors (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

considered these characteristics of synaesthetic experience further by contrasting synaesthetes recruited through the prevalence study ($n = 9$) with mirror-touch synaesthetes recruited via self referral including some previously reported cases ($n = 12$). Reaction time (Congruency × Group) and the percentage of error types (Error Type × Group) were compared separately using 2 × 2 ANOVA (Fig. 2a, b—for comparison non-synaesthetic control data, $n = 20$, is also shown, but not included in analysis). One participant from the self referral group was withdrawn from analysis of reaction times due to an insufficient number of correct responses (<25% correct responses in anyone condition).

Analysis of reaction time data revealed a significant main effect of congruency, with subjects performing faster overall on trials which were congruent with their synaesthesia compared to incongruent trials [$F(1, 18) = 13.98$, $p < 0.01$]. Analysis of error type data revealed a significant main effect of error type, which was due to a higher proportion of mirror-touch errors being produced relative to other error types [$F(1, 19) = 11.18$, $p < 0.01$]. No significant interaction or main effect of group was found for reaction time (Group: [$F(1, 18) = 0.048$, $p = 0.829$]; Group × Cong: [$F(1. 18) = 0.095$, $p = 0.761$]) or error type analysis (Group: [$F(1, 19) = 2.77$, $p = 0.113$]; Group × Cong: [$F(1. 19) = 2.75$, $p = 0.114$]). This indicates that performance of the prevalence group falls within the same population as self-referred mirror-touch synaesthetes. Therefore, we now combine both prevalence and self-referred cases to consider additional cognitive characteristics of mirror-touch synaesthesia.

For the majority of cases, the effects of spatial congruity are found for bodies but not objects and this corresponds well with their phenomenological reports. There are, however, a minority of synaesthetes who do report tactile experiences when watching objects being touched (4 out of 21). For some of these synaesthetes, this experience is reported in the finger tip that is touching the objects, but for others synaesthetic touch is mapped onto particular body locations which are thought to spatially correspond to the object being touched (e.g. when looking directly at a monitor the experience maps onto the face, but when standing in front of the monitor the experience maps onto the trunk). In addition, another minority of synaesthetes (6 out of 21, including I., Z. and H.G. in Table 1) show an effect of spatial congruity for both bodies and objects

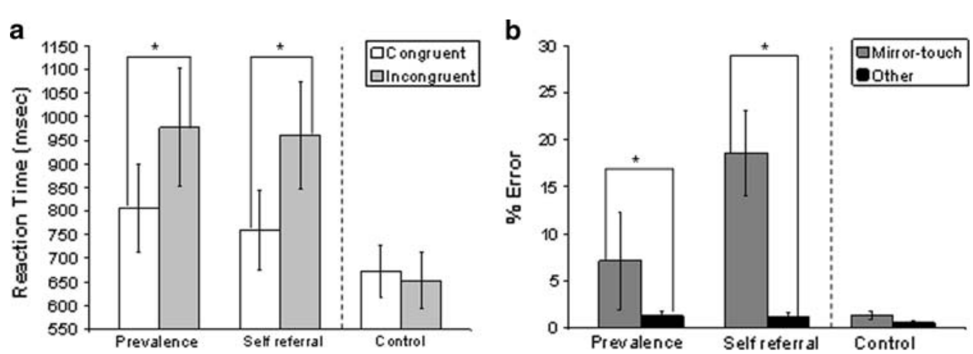

Fig. 2 Mean reaction time performance (**a**) and percentage of error types (**b**) on human trials for mirror-touch synaesthetes recruited within the prevalence study compared to synaesthetes recruited via self-referral (control group performance is shown for comparison). ±SEM (*$p < 0.05$)

despite initially claiming to experience synaesthesia for touched bodies alone. One possibility is that this reflects the fact that object trials are interleaved with the more frequent human trials and this leads to objects being treated more like human bodies than expected. In the normal population, fMRI studies suggest that the tactile mirror system does respond to objects under some circumstances (Ebisch et al. 2008; Keyers et al. 2004).

Of the 21 cases of mirror-touch synaesthesia reported to date, seventeen report a specular frame of reference and four report an anatomical frame of reference. This finding is consistent with studies on imitation behaviour which demonstrate that both adults and children tend to imitate in a specular mode (Schofield 1976; Franz et al. 2007). The relative bias in synaesthetes could be due to the fact that one's own head is only ever seen from a mirror-reflected perspective and this regularity may drive the choice of spatial frame. However, it is to be noted that those synaesthetes who adopt a specular frame for the head also do so with the hands (Banissy and Ward 2007) even though this part of one's own body is not normally viewed from a reflected perspective.

A general characteristic of synaesthesia is that different variants of synaesthesia tend to co-occur (Simner et al. 2006). Some preliminary evidence based upon self reports suggests that this may also be the case with mirror-touch synaesthetes. Nine of the 21 mirror-touch synaesthetes sampled also report genders or personalities for graphemes and/or certain other linguistic stimuli (e.g. 3 is a bossy male; Simner and Holenstein 2007; Smilek et al. 2007). Five of these cases have been confirmed using behavioural tests for this phenomenon (N. Sagiv, personal communication). Additionally, seven report synaesthetic experiences of colour for linguistic stimuli.

Experiment 2: behavioural correlates and somatotopic cueing

While results from Experiment 1 establish evidence for the authenticity of mirror-touch synaesthesia and suggest that behavioural correlates are related to 'observed bodily touch', it remains unclear if our behavioural data could also be consistent with 'observed bodily cueing'—whereby an observed visual event cues a particular location on the body. There is growing evidence from research investigating visual–tactile interactions that non-informative vision associated with one's own body can influence tactile processing (i.e. Johnson et al. 2006). In order to establish whether our findings could be related to somatotopic cueing, we compared the performance of mirror-touch synaesthetes and non-synaesthetic subjects on a condition in which a human face is observed but is accompanied by a flash of light on the cheek rather than a touch. As these stimuli did not induce synaesthesia we expected that the pattern of effects shown by synaesthetes on Experiment 1 would be related specifically to 'observed bodily touch' and that we would not observe differences between synaesthetes and non-synaesthete controls for 'observed bodily cueing'.

Method

Ten mirror-touch synaesthetes (7 females and 3 male, mean age ± SD. Error = 30.1 ± 11.17 years) and ten non-synaesthetic controls matched for age and gender (7 females and 3 males, mean age ± SD. Error = 31 ± 13.23 years) took part. Congruency was determined according to synaesthete's self reports when observing touch to another person. Controls were randomly allocated to either a specular or anatomical congruency group to match the synaesthetic group.

The experimental task and procedure was the same as Experiment 1, with the exception of the stimuli presented (Fig. 3). For the human trials, rather than observing touch to the cheek(s), a flash of light appeared on the observed person's cheek(s). As before, the visual stimuli consisted of 3 frames. The first stimulus, lasting 100 ms, depicted a male or female face. The second stimulus, also lasting 100 ms, was the same as the first except that a patch of white light appeared on the person's left/right/both cheek(s). The flash was then removed for the third stimulus which remained on the screen until the participant responded. The tactile stimulus was applied immediately after the flash, i.e. at the onset of the third stimulus. For the control trials, the picture of the person was replaced by a blank screen with a 100 ms flash of light on the left, right or both sides of space immediately before the tactile event. A total of 306 trials were completed, of which 180 involved human stimuli and 126 involved control stimuli.

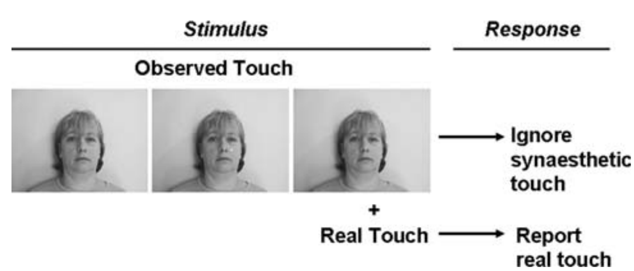

Fig. 3 Summary of the task used for somatotopic cueing experiment. Participants observed a flash of light on the left/right/or both cheek(s) of another person. Immediately following the light flash, subjects were touched on their own facial cheeks (either left, right or both cheeks). Participants were asked to report the site of real touch

Results and discussion

The results are summarised in Fig. 4. Reaction times and error rates were measured. Reaction time data were filtered prior to analysis (±3 SD and all errors removed). A 2 (Group) × 2 (Congruency) ANOVA conducted on reaction times revealed no significant main effects or interactions ($p > 0.05$ in all cases; Fig. 4a). Although the direction of the effect is the same as in Experiment 1 the effect is not significant. Analysis of the percentage of error types made by participants on human trials also revealed no significant main effects or interactions ($p > 0.05$ in all cases; Fig. 4b). Similarly, no significant differences were observed on control trials (Fig. 4c, d). These findings are unlikely to be due to the fact that the flash of light is less salient than the hand, because the synaesthetes also fail to show an effect in Experiment 1 when a hand is used on a non-human object.

To further validate that performance of mirror-touch synaesthetes significantly differed between Experiment 1 and 2 we also conducted a within-group comparison on the size of congruency effect (incongruent − congruent trial reaction time) shown by synaesthetes across each task. This revealed that synaesthetes showed a significantly greater effect of congruency on trials involving observed touch to a human face in Experiment 1 (mean ± SEM = 208.24 ± 52.32 ms) compared to a flash of light shown on a human face in Experiment 2 (mean ± SEM = 51.49 ± 34.18 ms), $t(9) = 2.98$, $p < 0.02$. Thus the findings from Experiment 1 are related specifically to 'observed bodily touch' and cannot be attributed to somatotopic cueing.

General discussion

Taken together, our measures detail the prevalence and characteristics of mirror-touch synaesthesia. In relation to prevalence, our findings suggest that:

- mirror-touch synaesthesia is one of the more common forms of synaesthesia
- there are two sub-types (specular and anatomical) depending on the visuo-tactile spatial transformation used
- the specular (mirror-reflected) sub-type is the more common
- the effects are quite specific to observed touch to a human body.

In many respects, mirror-touch synaesthesia shares common ground with other types of synaesthesia; for instance, with regards to phenomenology, automaticity, consistency (of the spatial mapping), reliability over time, and possibly with regards to associated traits (e.g. attributing personalities and genders to graphemes). However, when one turns to consider its neural basis the similarities are less apparent. A current area of debate in the synaesthesia literature is whether synaesthetic experience is due to cross-activation between brain regions or cortical disinhibition (Bargary and Mitchell 2008; Cohen Kadosh et al. 2009; Cohen Kadosh and Walsh 2008; Grossenbacher and Lovelace 2001; Hubbard and Ramachandran 2005; Rouw and Scholte 2007). Thus far, accounts of synaesthesia in terms of cross-activation have mainly focussed on

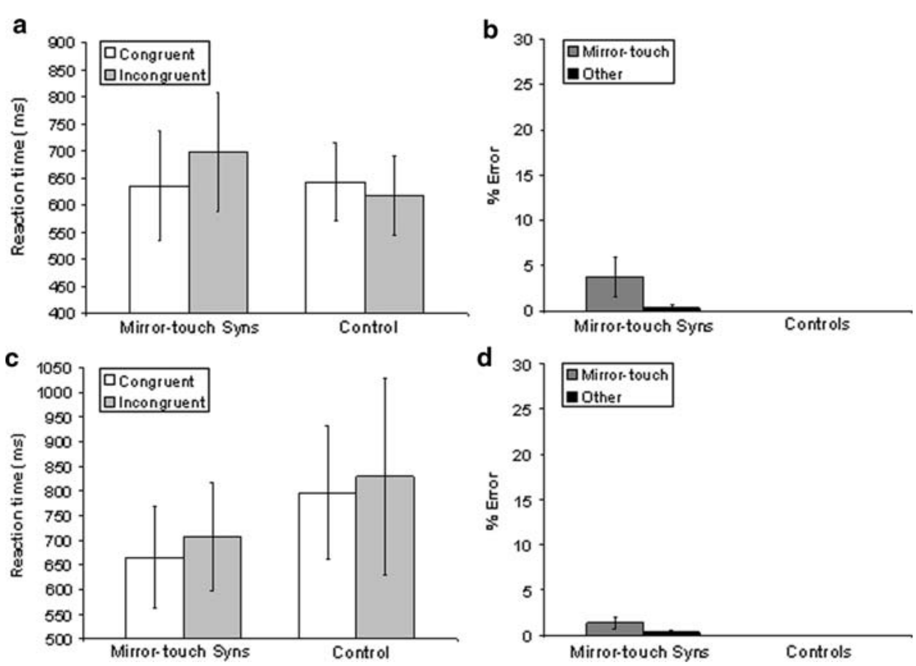

Fig. 4 Mean reaction time performance and percentage of error types for mirror-touch synaesthetes and non-synaesthetic control subjects observing a light flash on another person's face (**a**, **b**) or a light flash only (**c**, **d**). ±SEM

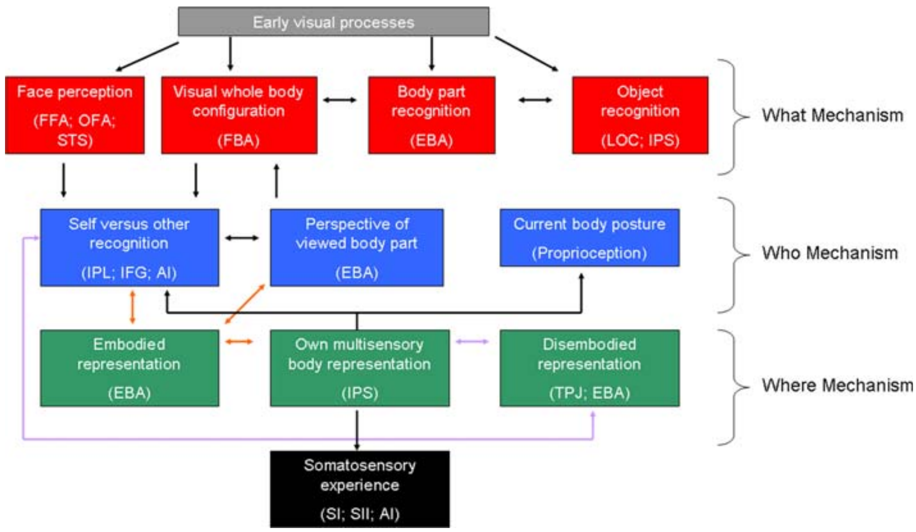

Fig. 5 The 'What, Who, Where Model of Mirror-Touch Synaesthesia'. 'What' mechanisms are shown in red boxes and are involved in defining the stimulus touched. 'Who' mechanisms implement discriminations between self and other, and are shown in *blue boxes*. 'Where' mechanisms are shown in *green boxes* and are involved in locating where on the body and in space observed touch occurs. Processes necessary for all subjects are shown with *black arrows*, necessary for specular mirror-touch synaesthetes with *orange arrows*, and for anatomical mirrortouch synaesthetes with *purple arrows*. Brain regions represented are considered with regard to importance for mirror-touch synaesthesia. *AI* Anterior insula, *EBA* extrastriate body area, *FBA* fusiform body area, *FFA* fusiform face area, *IFG* inferior frontal gyrus, *IPL* inferior parietal lobule, *IPS* intraparietal sulcus, *LOC* lateral occipital complex, *OFA* occipital face area, *SI* primary somatosensory cortex, *SII* secondary somatosensory cortex, *STS* superior temporal sulcus, *TPJ* temporoparietal junction

grapheme-colour synaesthesia and highlight the role of adjacency between visual grapheme and colour processing areas in the fusiform gyrus (Ramachandran and Hubbard 2001). It is possible that adjacency is one of several biasing principles that influence which forms of synaesthesia will, and will not, be found. Another biasing principle may be the 'normal' architecture for multi-sensory interactions. As noted before, there is now good evidence for a visuo-tactile mirror system in humans (Blakemore et al. 2005; Ebisch et al. 2008; Keyers et al. 2004) and mirror-touch synaesthesia could be construed as hyper-activity within this network (either as a result of cortical disinhibition or cross-activation).

Below we propose a model of this type of synaesthesia.

A neurocognitive model of mirror-touch synaesthesia: what, who, where

In this model, mechanisms thought to underpin synaesthetic experience are divided into processes involved in identifying the visual stimulus touched ("what" mechanism—shown in red boxes), discriminating between self and other ("who" mechanism—shown in blue boxes), and locating where on the body and in space observed touch occurs ("where" mechanism—shown in green boxes). Connections between processes common to all subjects are shown in black. Connections between processes necessary for an anatomical reference frame in purple. Connections between processes contributing to a specular reference frame are shown in orange (Fig. 5).

Visual encoding: "what" mechanisms

With regards to the tactile mirror system, the putative "what" mechanisms are needed to implement several discriminations. Is this a human or object? Is this a face or body? One potential brain region which may be crucial to human body perception in mirror-touch synaesthesia is the extrastriate body area (EBA; Downing et al. 2001). The EBA is a body-selective visual region which responds more to bodies and body parts, than faces, objects and object parts (Downing et al. 2001). This is in contrast to the fusiform body area (FBA; Peelen and Downing 2005), a further body selective visual region, which appears more important for processing body parts into wholes (Taylor et al. 2007).

In addition to the EBA, object selective visual regions and their interactions along higher-order visual systems may then be crucial for distinguishing between those synaesthetes for whom observing touch to objects elicit synaesthetic interactions and for those in which no synaesthetic interaction is experienced. In these cases, the processing of object information via the dorsal stream to areas along the medial bank of the intraparietal sulcus (IPS; Konen and Kaster 2008) may be particularly important. The IPS forms part of the tactile mirror system (Blakemore et al. 2005) and is known to contain visual–tactile body maps which are important for dynamic multisensory body representations (Bremmer et al. 2001; Duhamel et al. 1998; Iriki et al. 1996; Macaluso and Driver 2003; also see Colby 1998; Maravita and Iriki 2002 for review). We therefore suggest that the degree to which observing touch to an object is able to elicit visual–tactile synaesthetic interactions depends upon the extent to which the object is incorporated into visual–tactile representations of the body, potentially within the IPS.

Visual encoding: "who" mechanisms

The most crucial distinction to be made by the putative "who" mechanism is that between self and other. Is it my body/face that is seen?

One can consider mirror-touch synaesthesia as a breakdown in the mechanisms that normally distinguish self from other. We do not propose a dedicated module to distinguish between self and other; rather, this discrimination will emerge out of other processes involved in linking visual representations with internal representations of bodies. Namely, there may be a tendency to over-incorporate viewed bodies within the observer's current body schema (Coslett 1998; Gallagher 1995; Head and Holmes 1911–1912; Sirigu et al. 1991). This process is likely to depend on a variety of factors: the perspective of the viewed body part; the current posture of the mirror-touch synaesthete; and the similarity (facial or otherwise) between the perceiver and perceived.

The perspective of the seen body part provides one way of discriminating between self and other. The importance of discriminations between first-person and third-person perspectives also varies between synaesthetic subtypes when observing touch to body parts (excluding the face) and this may require more computations for specular compared to anatomical synaesthetes. For specular synaesthetes, touch to the hands from a first-person perspective induces synaesthetic touch to the anatomically corresponding hand (i.e. right hand to right hand), but from a third-person perspective induces synaesthetic touch to the mirrored hand (i.e. right hand to left hand). In contrast, for anatomical synaesthetes, observed touch from either perspective elicits synaesthetic touch to the anatomically corresponding hand. The response of the right EBA is greater for body parts in the third-person than first-person perspective (Saxe et al. 2006) and this brain region may contribute to this distinction.

With regards to faces, viewing one's own face activates a different network of brain regions from other faces including famous or personally familiar ones (Uddin et al. 2007). FMRI research has highlighted the role of a right-fronto-parietal network in this process, including the right inferior parietal lobule (IPL) and right inferior frontal gyrus (IFG; Sugiura et al. 2005; Uddin et al. 2005). These two regions form part of the classical mirror neuron system in humans (Rizzolatti and Craighero 2004) and it has been suggested that they may be necessary to not only establish shared representations, but also to implement mechanisms to distinguish between self and other (Uddin et al. 2006). We suggest that this same sensory-motor network is over-active in mirror-touch synaesthetes when viewing faces other than their own, causing the body part to be incorporated into their own body representations. One prediction is that mirror-touch synaesthetes (at least the specular sub-type) will show little behavioural or phenomenological differences on the spatial congruity task used here if the unfamiliar faces were replaced with images of their own faces.[1] However, controls may begin to show similar behavioural performance to the synaesthetes if images of their own face are displayed. In accordance with this, Serino et al. (2008) report that, for non-synaesthetes, observing touch to one's own or another's face increases tactile sensitivity on the observers own face (also see Haggard 2006 for similar evidence of interpersonal enhancements of touch). This visual–tactile enhancement was maximised when observing touch to one's own face rather than another's face, indicating that self-similarity can modulate the extent of visuo-tactile resonance (Serino et al. 2008).

Perspective taking: "where" mechanisms

The third class of mechanism that we consider to be relevant involves linking visual representations of body with tactile representations based on proprioception and somatosensation. One distinction that has been made in the literature is between "embodied" and "disembodied" representations of body (Giummarra et al. 2008; also see Brugger 2002 for a discussion of similar spatial aspects of autoscopic phenomena). Evoked potential mapping indicates that the right temporoparietal junction (TPJ) is related to disembodied perspective taking (judging left/right from someone else's perspective), while left EBA activation is linked with embodied perspective taking (judging left/right from own perspective; Arzy et al. 2006). Moreover, stimulation of the TPJ has been shown to lead to disembodied experiences in neurological patients (Blanke et al. 2004; Blanke et al. 2002).

[1] The predictions for synaesthetes with the anatomical sub-type are unclear because their usual synaesthetic phenomenology would contradict their own prior experiences of observing their own face in a mirror (e.g. when shaving or putting on make-up).

This distinction is similar to the specular-anatomical division between mirror-touch synaesthetes. For the specular sub-type, the visual representation of the other body is spatially processed as if it is a mirror-image of one's own (embodied) body. For the anatomical sub-type, the spatial mapping is more disembodied in that one's own body is placed in the perspective of the other person (or one's own body and that of the other person are copied into some other shared bodily template). If this is the case, it makes a specific and testable prediction—namely, that the anatomical sub-type will be associated with greater activity in the TPJ than the specular sub-type.

Somatosensory processes

A final component within the model is the role of somatosensation in mirror-touch synaesthesia. Previous fMRI findings indicate that the condition is linked with increased activations in SI, SII and additional activations in bilateral anterior insula (Blakemore et al. 2005). The specific role of these regions in the experience of synaesthetic touch remains unclear. For example, the anterior insula has connectivity with both somesthetic cortex and visual association areas (Mesulam and Mufson 1982a, b) which may make this brain region a potential candidate for accounts of mirror-touch synaesthesia in terms of mechanisms of disinhibition or hyper-connectivity. This brain region also contains tactile receptive fields in the absence of activations of primary somatosensory cortices (Olausson et al. 2002) and is important in processing the affective consequences of touch (Craig 2002). In this sense, anterior insula activations observed in mirror-touch synaesthesia may reflect processing of tactile and affective consequences of synaesthetic experience; self reports indicate that the synaesthetic tactile sensation varies with the type of touch observed (i.e. pain vs. touch) and has differing affective consequences accordingly. Alternatively, the anterior insula is also important in distinguishing between self and other (Fink et al. 1996; Kircher et al. 2001; Ruby and Decety 2001) and this region could be involved in misattributing observed touch to oneself through mechanisms of self-other discrimination (Blakemore et al. 2005). The use of brain imaging to investigate more closely the interactions between activations in the anterior insula and primary somatosensory cortices observed in mirror-touch synaesthesia may shed light on these issues.

Summary

In summary, by investigating the prevalence and characteristics of mirror-touch synaesthesia we show that this variant of the condition may be one of the most common forms of synaesthesia. Furthermore, we highlight a number of important characteristics which indicate that the condition goes beyond a simple one to one mapping between observed and synaesthetic touch. We propose a neurocognitive model (Fig. 5) which distinguishes between subtypes of mirror-touch synaesthesia and suggest potential neural mechanisms to account for how differences in the interpersonal body maps adopted may lead to different cognitive processes related to synaesthetic experience.

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