Synaesthesia, mirror neurons and mirror-touch.

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Abstract

Mirror-touch synaesthesia describes a condition in which individuals experience the sensation of being touched on their own body when observing touch to another person. This chapter reviews studies examining the prevalence and characteristics of developmental and acquired cases of mirror-touch synaesthesia, the neurocognitive mechanisms that contribute to the tactile experiences evoked in mirror-touch, and how mirror-touch synaesthesia may be used to help inform us about mechanisms of social perception in non-synaesthetes.

Keywords: Mirror-touch; mirror system; somatosensory; empathy; emotion; synaesthesia; social perception

Introduction

As noted in previous chapters, synaesthesia is a condition where a stimulus in one attribute (the inducer) triggers a conscious experience of another attribute (the concurrent) not typically associated with the inducer. For example, in grapheme-colour synaesthesia the letter ‘A’ (or ‘B’ or ‘C’ and so on) may trigger synaesthetic experiences of colours (Rich and Mattingley 2002; Cohen Kadosh and Heink 2007). A large body of synaesthesia research has focussed on synaesthesia involving colour, which is often reported as being the most common concurrent of the condition (Baron-Cohen, et al. 1996; Rich, Bradshaw, and Mattingley 2005; Simner et al. 2006). More recently, however, a newly documented form of synaesthesia has been described in which individuals experience tactile sensations on their own body when simply observing touch to another’s body (Banissy and Ward 2007; Blakemoreet al. 2005; Holle et al. 2011). This variant of synaesthesia, known as mirror-touch synaesthesia, is the focus of the present chapter and here I will describe the prevalence and characteristics of developmental mirror-touch synaesthesia, the neurocognitive mechanisms that contribute to this variant, and the extent to which we can use this interpersonal variant of synaesthesia to inform us about mechanisms of social perception more generally. I shall also discuss cases in which mirror-touch synaesthesia has been reported to be acquired after injury, and I will consider them in relation to acquired synaesthesia more generally.

Developmental mirror-touch synaesthesia: Prevalence and Characteristics

Synaesthesia is has been considered by some as having three defining characteristics; 1) concurrents 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). This section describes evidence indicating how mirror-touch synaesthesia matches onto these three criteria and also considers wider characteristics of this variant of synaesthetic experience.

With regards to the automaticity of developmental mirror-touch synaesthesia, the question is whether mirror-touch synaesthetes experience their synaesthetic touch sensations immediately/automatically, or whether they require some type of conscious effort (of a kind not normally associated with 'synaesthesia' proper). Banissy and Ward (2007) reported a behavioural study of ten developmental mirror-touch synaesthetes in which they explored this aspect of mirror-touch synaesthesia by developing a "visuo-tactile synaesthetic stroop experiment[1]". In the task, synaesthetes and matched non-synaesthetic controls were asked to detect a site

[1] It is of note that in other forms of synaesthesia associative training in healthy subjects can induce this kind of Stroop interference effect (eg. Elias et al 2003; Hancock, 2006; Meier and Rothen, 2009)

touched on their own body (either the left, right or both facial cheeks; or no touch) while observing touch to another person's facial cheeks or to a corresponding object. Participants were asked to report the site of actual touch (left side of the body, right side of the body, or no touch at all) and to ignore observed touch (which was either on the left, right or both sides). For synaesthetes, but not controls, the synaesthetic experience evoked by observed touch could either be congruent or incongruent with the site of actual touch. For example, if observing touch to the left cheek evokes synaesthetic touch on the right cheek then actual touch to the right cheek would be congruent with their synaesthesia, but actual touch to the left cheek would be incongruent with their synaesthesia (Figure 1). Synaesthetes, but not control participants, were faster at detecting the location of actual touch during the congruent condition relative to the incongruent condition. Further, synaesthetes produced a higher percentage of errors consistent with their synaesthesia (e.g. reporting touch on trials involving no actual touch; hereafter referred to as "mirror-touch errors"). No significant differences were found when the observed stimuli (i.e. observing touch to another person's cheek) were replaced with a stimulus that did not evoke synaesthetic experiences of touch (e.g. a flash of light on the cheek rather than a touch; Banissy et al.2009a). In other words, synaesthetes had previously reported that observing a flash of light against another person's body did not cause touch sensations against their own body, and as a consequence, there were no "mirror-touch" errors found under these conditions. Our findings therefore provided evidence supporting the suggestion that mirror-touch synaesthetes experience touch on their own body when observing bodily touch and imply that the synaesthetic experience in mirror-touch synaesthesia is percept-like.

INSERT FIGURE 1 HERE

Using the aforementioned "visuo-tactile congruity paradigm" as a measure for the authenticity of mirror-touch synaesthesia, my colleagues and I (Banissy et al. 2009a) examined the prevalence of developmental mirror-touch synaesthesia among university undergraduates at University College London and University of Sussex. Five hundred and sixty-seven participants were recruited for the study. All were undergraduate students recruited before/after classes being held at each university. Participants were given a description of synaesthesia (including examples of what did and did not constitute synaesthesia) and were then administered a questionnaire asking about different variants of synaesthesia. They were not told that the study was a prevalence study, nor were they did they receive specific details about mirror-touch synaesthesia (i.e. they received a general description of synaesthesia rather than specific details about individual sub-types). One question on the questionnaire related to mirror-touch synaesthesia, in which participants were asked to indicate 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?" All participants who gave positive responses to the above question (approximately 10.8% of all subjects) were contacted and interviewed about their experiences. These participants were presented with a series of videos that showed another person, object, or cartoon face being touched, and asked to indicate the location (if any) in which they experienced a tactile stimulus themselves and the type of experience. Typical responses of potential mirror-touch synaesthetes (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 (e.g. videos of a pin pricking a hand rather than observed touch to the hand). Of these fourteen subjects, nine showed a significantly different pattern of performance compared to matched non-synaesthetic subjects on the visuo-tactile synaesthetic stroop experiment developed by Banissy and Ward (2007), indicating 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 more common forms of synaesthesia, along with grapheme-colour synaesthesia (1.4% prevalence) and day-colour synaesthesia (2.8% prevalence; Simner et al. 2006).

A study examining the perceptual characteristics of the inducer in mirror-touch synaesthesia indicates a number of common factors that mediate the synaesthetic experience in mirror-touch (Holle et al. 2011). In that study, a group of fourteen previously verified mirror-touch synaesthetes were presented with a series of movie clips and asked to report the presence/absence of synaesthetic experience, the location of experience, and the intensity of the experience. Movies included painful stimulation (e.g. a person being prodded by a knife), thermal stimulation (e.g. a person being touched by a candle) and tactile stimulation (e.g. a person being touched by another person). The target of the stimulation (i.e. the person/thing touched) also differed insofar as whether we showed touch to another person, touch to an object, touch to a dummy body part, or touch shown only within a static photograph. The findings showed that observed touch to another person in a video evoked a significantly more intense synaesthetic experience than observing similar touch in static photographs, and was also more intense than observing touch to either dummy body parts or objects in videos. This implies that visual recognition of bodies alone (in the case of dummy body parts) is not driving mirror-touch synaesthesia. The intensity of synaesthetic sensations did not differ by the body part observed (face, hand, arm, leg etc) or by the spatial orientation of the body part when observing touch to a real person (e.g. whether the hands of another person appeared as crossed or uncrossed when touched). Painful stimuli to a real face (e.g. a sharp object prodding the face) did, however, evoke a stronger experience than a non-painful tactile stimulus to the face (e.g. a feather stroking the face).

In addition to commonalities, some important individual differences have also been found across mirror-touch synaesthetes (Banissy and Ward 2007; Banissy et al., 2009a). It appears that mirror-touch synaesthetes can be divided into at least two subgroups based upon the spatial mapping between observed and felt (synaesthetic) touch (Figure 2). Some synaesthetes report that an observed touch to the left cheek is felt on their right cheek (as if the observed person is a mirror reflection of oneself – and this type of experience is hereafter referred to as the 'specular' subtype), whereas others report synaesthetic touch on their left cheek when observing touch to another person's left cheek (as if self and other share the same anatomical body space – hereafter referred to as the 'anatomical' subtype). Our own studies indicate that the specular subtype is the more common, with approximately 80% of cases studied to date reporting a specular spatial mapping (see Banissy et al 2009a). This bias towards a specular mapping in synaesthetes is consistent with studies on imitation behaviour indicating that both adults and children tend to imitate in a specular mode (Schofield, 1976; Franz, Ford, and Werner 2007). The possibility that there may be at least two spatial frames of reference that could be adopted when observing another's tactile experiences is also consistent with neurophysiological findings in primates documenting anatomical and specular spatial frames of reference that mediate bimodal visual-tactile cells in the macaque parietal cortex. These cells respond when the monkey is touched and when the monkey observes touch to the same body part of someone else (Ishida et al.2009).

INSERT FIGURE 2 HERE

In addition to differences in the spatial frame of reference adopted by mirror-touch synaesthetes another intriguing characteristic shown by some but not all mirror-touch synaesthetes, is the extent to which observing touch to *objects* can elicit synaesthetic interactions. This type of experience has been reported as a consistent experience in approximately 18% of cases studied by our group (e.g. Banissy et al., 2009a). For some of these "object-touch" synaesthetes, this experience is reported to occur in the synaesthete's finger tip that corresponds to the finger observed touching the objects, but for others, synaesthetic touch is linked onto particular body locations that are thought to correspond to the object being touched (e.g. when looking directly at a monitor being touched by another, the synaesthetic touch experience maps onto the face, but when standing in front of the monitor the experience maps onto the trunk). The precise mechanisms of what drives this remains unknown, however functional magnetic resonance imaging (fMRI) studies suggest that non-synaesthetes recruit similar systems of the brain when observing touch to humans and objects under some circumstances (Ebisch et al. 2008; Keysers et al. 2004) and it is therefore likely that the same system mediates the synaesthetic experience when observing touch to another person or to an object. It is also likely that the degree to which observing touch to an object is able to elicit visual-tactile synaesthetic interactions may depend upon the extent to which the object is incorporated into visual-tactile representations of the body (Banissy et al. 2009a; also see section on neurocognitive mechanisms below).

One further feature where developmental mirror-touch synaesthesia shares characteristics with more commonly studied variants of synaesthesia is how consistent the sensations are over time. In grapheme-colour synaesthesia, for example, if 'A' is red at time 1 then it will be at time 2, several weeks, months, years or even decades later; Baron-Cohen, Wyke, and Binnie 1987; Simner and Logie 2007). The experiences of mirror-touch synaesthetes are also enduring, and an individual's spatial sub-type (i.e. whether they belong to the specular or anatomical category) is consistent both across time (Holle et al. 2011) and across different body parts (Banissy and Ward 2007). There are also additional characteristics that appear common to mirror-touch synaesthesia and other variants of the condition. Mirror-touch synaesthetes have been found to show an increased tactile sensitivity (Banissy, Walsh, and Ward 2009b), which is in line with evidence of heightened perceptual processing of the synaesthetic concurrent in other variants of synaesthesia (e.g. increased colour responsiveness in synaesthetes who experience colour [Yaro and Ward 2007] and increased colour and tactile responsiveness in synaesthetes who experience both touch and colour [Banissy et al. 2009b]). It is also common for mirror-touch synaesthetes to report an additional type of synaesthesia (e.g. Banissy et al. 2009a; Banissy et al. 2009b) and a similar trend is found in other types of the condition (Simner et al. 2006).

One aspect in which developmental mirror-touch may be considered to differ slightly from other more commonly studied variants of synaesthesia is that the mappings in mirror-touch synaesthesia appear to be non-arbitrary, insofar as somatotopy is typically preserved between observed and felt touch (e.g. observing touch to face will normally trigger an experience on the synaesthetes' face). Indeed, when mirror-touch synaesthesia was first documented there was some resistance (and arguably still is) to notion that it was a variant of synaesthesia because the experience was simply 'too literal' to be synaesthesia. On closer inspection this may not be such an apparent difference. While it was once believed that synaesthetic experiences were consistent arbitrary associations, this view is no longer widely held and there is growing evidence of non-random associations in other variants of synaesthesia: for example, between pitch and lightness in tone-colour synaesthesia (Ward, Huckstep, and Tsakanikos 2006); number and lightness in number-colour synaesthesia (Cohen Kadosh, Henik, and Walsh 2007); grapheme frequencies and colour in grapheme-colour synaesthesia (Simner et al. 2005); and phonology and tastes in lexical gustatory synaesthesia (Ward and Simner 2003). Direct links have also been reported: for example, in lexical-gustatory synaesthesia food-words often taste of the denoted food (e.g. the word "sausage" tends to taste of sausage; Ward, Simner and Auyeung 2005) and colour words sometimes map onto the same colours in linguistic-colour synaesthesia (e.g. for the word "red" to be coloured red; Gray et al. 2002; Rich et al. 2005). Thus, non-arbitrariness may in fact be a further commonality between mirror-touch synaesthesia and other variants of the condition. In this regard, there is a growing consensus to view mirror-touch synaesthesia being part of the 'synaesthesia family', as opposed to an unusual experience that is more common in and shares phenomenological similarities with synaesthesia (e.g. mitemfindung – Burrack, Knoch, and Brugger, 2006).

In sum, mirror-touch synaesthesia describes an automatic percept-like tactile experience when simply observing touch to another person (or possibly to an object). Despite only recently being systematically investigated, it appears to be surprisingly common and shares some similarities with other more commonly studied variants of synaesthesia (e.g. in terms of consistency over time and in relation to extended perceptual characteristics). There are, however, some important individual differences between mirror-touch synaesthetes, including the frame of reference adopted when perceiving touch to another person (specular/anatomical distinction). These will be considered below in relation to potential neurocognitive mechanisms that may mediate the synaesthetic experience in mirror-touch synaesthesia.

Developmental mirror-touch synaesthesia: Neurocognitive mechanisms

In addition to describing the perceptual characteristics of mirror-touch synaesthesia, another important question is what mechanisms evoke synaesthetic experiences of touch in this variant of synaesthesia. Several biasing principles have been suggested as mechanisms that mediate what forms of synaesthesia will or will not be developed (e.g. Bargary and Mitchell 2008; Cohen Kadosh and Walsh 2008; Eagleman, 2009; Hubbard and Ramachandran 2005; Smilek et al. 2001; Ramachandran and Hubbard 2001; Sagiv and Ward 2006; Cohen Kadosh, Henik, and Walsh 2009). One common biasing principle that has been associated with accounts of synaesthesia is the role of adjacency between neighbouring brain regions (e.g. between adjacent visual grapheme and colour processing areas in grapheme-colour synaesthesia; Ramachandran and Hubbard 2001). The principle of adjacency is less clear in developmental mirror-touch synaesthesia because there are no apparent neighbouring brain areas that may mediate visuo-tactile experiences. An alternative biasing principle that may be more relevant is the 'normal' architecture for multi-sensory interactions (Sagiv and Ward 2006). Moreover, there is now good evidence for a network of brain regions that are recruited by non-synaesthetes when observing touch to others (Blakemore et al. 2005; Ebisch et al. 2008; Keysers et al. 2004; McCabe et al. 2008) and mirror-touch synaesthesia may reflect hyper-activity within this network (Blakemore et al. 2005). Here, this possibility is discussed and additional neurocognitive mechanisms that may mediate individual differences between mirror-touch synaesthetes are described.

The observed touch network is comprised of the primary and secondary somatosensory cortices, premotor cortex, intraparietal sulcus, and the superior temporal sulcus (Keysers et al. 2004; Blakemore et al. 2005; Ebisch et al. 2008; McCabe et al. 2008). The overlap between brain areas that are involved in passively experiencing touch to oneself and observing touch to another person (i.e. primary somatosensory and secondary somatosensory cortices) has been interpreted as evidence of a mirror-touch system in which observed touch is matched to the observer's own sensorimotor representation of touch. This interpretation builds upon the findings of mirror neurons within the monkey premotor cortex and inferior parietal lobule (Gallese et al. 1996; Rizzolatti and Craighero 2004), which respond both when a monkey performs an action and when the monkey watches another person perform a similar action. In humans, indirect evidence of brain areas with similar mirroring properties has been found for action (Buccino et al. 2001), pain (Singer et al. 2004; Aventani et al. 2005), disgust (Wicker et al. 2003) and other emotions (Carr et al. 2003; Warren et al. 2006). Therefore, the overlap between the brain areas that become active when observing touch and experiencing touch are consistent with the notion of a mirror system for touch in the human brain.

Blakemore and colleagues (2005) examined the role of the mirror-touch system in non-synaesthetes and a single mirror-touch synaesthete named 'C'. C reports experiencing touch on her own body when observing another person being touched, but not when observing inanimate objects being touched. Her experiences mirror observed touch to another person, such that observing touch to another person's left facial cheek leads to a sensation of touch on her own right facial cheek (i.e. she adopts a specular frame of reference). Using fMRI Blakemore and colleagues investigated the neural systems underlying C's synaesthetic experience by contrasting brain activity when watching videos of humans relative to objects being touched (the latter did not elicit synaesthesia) in the synaesthete and in twelve non-synaesthetic control subjects. As expected, non-synaesthetes activated a network of brain regions during the observation of touch to a human relative to an object (including primary and secondary somatosensory cortex, premotor regions and the superior temporal sulcus). Similar brain regions were also activated during actual touch, indicating that observing touch to another person activates a similar neural circuit as actual tactile experience – the mirror touch system. A comparison between synaesthete C and non-synaesthetic subjects indicated that the synaesthete showed hyper activity within a number of regions within this network (including primary somatosensory cortex) and additional activity in the anterior insula. This suggests that mirror-touch synaesthesia is a consequence of increased neural activity in the same mirror-touch network that is evoked in non-synaesthetic controls when observing touch to another person (Blakemore et al. 2005) and therefore may be mediated by the 'normal' architecture for multi-sensory interactions.

The fact that additional bilateral anterior insula activation was observed in C, but not in non-synaesthetes when observing touch is also of interest. Neural activity in the anterior insula has been related to self-awareness (Critichley et al. 2004) and processing one's awareness of others (Craig 2004; Lamm and Singer 2010). It is therefore thought to be involved in self-other distinctions (Fink et al.1996; Kircher et al. 2001; Ruby and Decety 2001) and one possibility is that the additional activation of the insula in mirror-touch synaesthesia reflects an error in the neural systems distinguishing between self and other, leading to the source of another persons' tactile experience being mislocated onto the synaesthetes' own body (Banissy, Walsh, and Muggleton 2011a).

In addition to hyper-activity in the mirror-touch system, it is also likely that there are a number of factors mediating individual differences (e.g. specular/anatomical distinction) between mirror-touch synaesthetes. While this has not yet been studied systematically at a neural level, my colleagues and I provided a neurocognitive model to account for these differences and suggested three key mechanisms that are important to mirror-touch synaesthesia: i) identifying the type of visual stimulus touched ('What' mechanism), ii) discriminating between self and other ('Who' mechanism), and iii) locating where on the body and in space observed touch occurs ('Where' mechanism) (Banissy et al. 2009a).

The 'What' mechanism is considered to be involved in several discriminations related to the nature of the inducer (e.g.'is this a human or object?'). As noted above, one intriguing characteristic shown by some mirror-touch synaesthetes is that observing touch to objects can elicit synaesthetic interactions (e.g. Banissy and Ward 2007). One brain region of the observed-touch network (Blakemore et al. 2005) that may be central to this is the intraparietal sulcus (IPS). Recent findings indicate that visual object information is processed along the dorsal stream to areas along the medial bank of the intraparietal sulcus (IPS; including IPS1 and IPS2, Konen and Kaster 2008). For mirror-touch synaesthetes, this pathway may be particularly important when considered in relationship to visual-tactile body maps within the intraparietal cortex. Single-cell recording in primates has identified bimodal neurons in the intraparietal cortex which fire in response to not only passive somatosensory stimulation, but also to a visual stimulus presented in close proximity to the touched body part (Duhamel, Colby and Goldberg 1998). Intriguingly, the visual spatial reference frames of such bimodal neurons are dynamic and if the monkey is trained to use a tool the visual receptive field extends to incorporate the tool into the representation of the body (Iriki, Tanaka and Iwamura. 1996). Similar evidence of dynamic multisensory body representations in the parietal cortex has been reported in human subjects (Bremmer et al. 2001; Colby 1998; Maravita and Iriki 2002; Berlucchi and Aglioti 1997). Therefore, one possibility is 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 intraparietal cortex.

The key process instigated by the ‘Who’ mechanism is to distinguish between the self and other. It has been suggested that mirror-touch synaesthesia may reflect a breakdown in the mechanisms that normally distinguish between self and other, leading to altered boundaries of perceived body space and misrepresentations of another’s body onto the synaesthete’s own body schema (e.g. Banissy et al. 2009a; Banissy et al. 2011a; Davies and White, in press). Some factors mediating this may include the perspective of the viewed body part and the similarity between the observers and observed. In relation to the later, if similarity is important in mediating activity within the mirror-touch system then one may predict that non-synaesthetes should show some level of modulation when observing touch to themselves versus other people. In accordance with this, Serino and colleagues (2008) report that, for non-synaesthetes, there is an enhancement in tactile sensitivity when observing touch, which is maximised when observing touch to one's own face rather than another's face (Serino, Pizzoferrato, and Làdavas 2008).

The final class of mechanism that also seems important in mediating individual differences between mirror-touch synaesthetes involves linking visual representations of body with tactile representations based on spatial frames of reference (Banissy et al. 2009a). One way to consider the differences in the spatial frame adopted by mirror-touch synaesthetes is through the notion of embodied and disembodied representations of perspective taking (see Giummarra et al.2007; Brugger 2002). Specular mirror-touch synaesthetes appear to process the visual representation of the other body as if looking at their own reflection (i.e. in an embodied manner to oneself), while for the anatomical subtype the spatial mapping between self and other could be considered to be disembodied because the synaesthete's own body appears to share the same bodily template as the others person (i.e. the synaesthete is rotating their body into the perspective of the other person). This distinction may then be borne out at the neural level. For example, disembodied experiences have been suggested to arise from functional disintegration of low-level multisensory processing mechanisms (Bünning and Blanke 2005; Blanke and Mohr 2005) and abnormal activity at the temporal parietal junction (TPJ; Arzy et al.2006; Blanke et al.2004; Blanke et al.2002), therefore one may suggest the anatomical, but not specular, sub-type will be associated with these neurocognitive mechanisms.

Acquired mirror-touch synaesthesia

So far the focus of this chapter has been on developmental cases of mirror-touch synaesthesia. Recently, however, a number of studies have begun to describe cases of mirror-touch synaesthesia that have been acquired following sensory loss or brain injury. In this section, these studies are reviewed and considered in relationship to other acquired variants of synaesthesia.

The first reported case of an acquired interpersonal synaesthesia was related to observed pain rather than observed touch. This anecdotal report, given to clinicians posthumously by the patient's wife, describes a man who experienced observed pain to others as actual pain on his own body (Bradshaw and Mattingley 2001). The patient was known to have suffered widespread cancer, but as this case was reported post-mortem no information about the functional neural circuitry involved was available. As alluded to above, more recently, evidence for the interpersonal sharing of observed pain has been provided (Singer et al. 2004; Morrison et al.2004; Avenanti et al. 2005). For example, observing pain to another person results in neural activity in similar brain regions as when we experience pain ourselves (Singer et al. 2004; Morrison et al. 2004) and leads to modulation of corticospinal motor representations in a somatotopic manner (e.g. observing pain to the first dorsal interosseous (FDI) muscle modulates the observers' own FDI muscle activity; Avenanti et al. 2005). These findings provide evidence for a mirror-pain resonance system in all people, in which observed pain is matched to the observer's own sensorimotor representation of pain, and may be important in both acquired and developmental cases of mirror-pain synaesthesia (Fitzgibbon et al.2010a).

In addition to the case above, other cases of acquired mirror-pain and/or mirror-touch synaesthesia have been reported. These cases tend to be related to sensory loss following limb amputation. For example, Ramachandran and Brang (2009) report cases of acquired mirror-touch synaesthesia following arm amputation. In that study, four patients with upper limb amputations who reported phantom limb sensations, and healthy controls, were shown videos of another person's hand being touched. Patients reported a consistent tactile experience in their phantom hand when simply observing touch to the intact hand of another person.

In fact, it appears that there might be a particularly high prevalence of mirror-touch/mirror-pain synaesthesia in individuals that experience phantom limb sensations following amputation. For example, Fitzgibbon and colleagues (2010b) report that 16.2% of self-referred amputees (n = 12 out of 74 amputees) experience sensations of phantom pain (i.e. pain in their phantom limb) when observing pain to others. Furthermore, Goller and colleagues (in press) report that almost a third of amputees (n = 8 out of 28 amputees) report tactile sensations on their phantom limb or stump when observing touch to another person. While these findings are based only on self-reports, and therefore may reflect some false positives, they are high levels when compared to the 10.8% of healthy adults who self-report developmental mirror-touch synaesthesia (Banissy et al. 2009a).

These acquired cases are in line with reports of developmental mirror-touch synaesthesia, but there are some differences. In the case of amputees who report acquired mirror-touch/mirror-pain, the most notable difference is the location of synaesthetic experience. In developmental mirror-touch synaesthesia, somatotopy is typically preserved such that observing touch to another person's face will evoke a synaesthetic sensation on the synaesthete's own face. In phantom limb amputees, synaesthetic sensations tend to be evoked on the phantom limb or stump, irrespective of the body part seen (i.e. synaesthetic experiences gravitate towards the stump; Goller et al., in press; Figure 3). This difference is consistent with other variants of acquired synaesthesia insofar as it is quite common for synaesthesia following sensory loss to occur close to the location where stimulation is removed (e.g. Ro et al.

2007). The difference may also be informative about the neural mechanisms that are contributing to mirror-touch/pain in amputees. One possibility is that these experiences reflect a removal of neural signals from the amputated limb that would normally inhibit activity within the mirror-touch system in order to prevent observed touch/pain being experienced when viewing touch to others (Ramachandran and Brang 2009).

INSERT FIGURE 3 HERE

Beyond mirror-touch synaesthesia: Sensorimotor simulation and social perception

A further reason why mirror-touch synaesthesia is of interest is in relation to what this variant of synaesthesia can tell us about mechanisms of social perception and cognition in non-synaesthetes. As noted above, functional brain imaging has linked mirror-touch synaesthesia to heightened neural activity in a network of brain regions which are also activated in non-synaesthetic control subjects when observing touch to others (the mirror-touch system; Blakemore et al. 2005). Therefore, it is reasonable to consider mirror-touch synaesthesia as a consequence of over-activity within the typical system that is activated by us all when observing touch to others and to ask what secondary impact this has on other aspects of perception that the mirror-touch system is thought to be involved in.

One component of perception that the mirror-touch system has been associated with is as a candidate neural mechanism to aid social perception through sensorimotor simulation (Gallese and Goldman 1998; Keysers and Gazzola 2006; Oberman and Ramachandran 2007). Accounts of social perception involving sensorimotor simulation contend that in order to understand another's emotions and physical states, the perceiver must map the bodily state of the observer onto the same representations involved in experiencing the perceived state oneself (Adolphs 2002; Adolphs 2003; Gallese, Keysers, and Rizzolatti2004; Gallese and Goldman 1998; Goldman, and Sripada 2005; Keysers and Gazzola 2006; Oberman and Ramachandran 2007). This view is supported by evidence from electrophysiological, functional brain imaging and psychophysical studies indicating an involvement of sensorimotor resources in aspects of social perception abilities. For example, responses in expression-relevant facial muscles are increased during subliminal exposure to emotional expressions (Dimberg, et al. 2000). Furthermore, preventing the activation of expression relevant muscles impairs expression recognition (Oberman, et al. 2007) and perceiving another's expressions and producing one's own recruits similar sensorimotor regions (e.g. Carr, et al. 2003; van der Gaag et al. 2007; Warren et al. 2006; Winston, O'Doherty, and Dolan 2003). In addition, neuropsychological findings indicate that damage to right somatosensory cortices is associated with expression recognition deficits (Adolphs et al.2000), and that transcranial magnetic stimulation of the sensorimotor cortices can disrupt expression recognition, but not identity recognition, in healthy adults (Banissy et al.2010; Pitcher et al.2008). Additionally, lesions to sensorimotor cortices result in impaired emotional empathy (Shamay-Tsoory, Aharon-Peretz, and Perry 2009) and gray matter volume in the neural regions linked to senorimotor resonance correlates with individual differences in emotional empathic abilities for healthy adults (Banissy et al., in press).

A complimentary approach to the studies described above is to consider whether facilitation of sensorimotor mechanisms in mirror-touch synaesthesia promotes social perception abilities. For example, Banissy and Ward (2007) examined empathy in developmental mirror-touch synaesthesia in an attempt to determine the relationship between heightened activity in the mirror-touch system and this aspect of social perception. They compared the empathic abilities of mirror-touch synaesthetes to non-synaesthetic and synaesthetic control subjects (i.e. individuals who experience synaesthesia but not mirror-touch synaesthesia) using the Empathy Quotient (a standardized self-report scale designed to empirically measure empathy; Baron-Cohen and Wheelwright 2004). Mirror-touch synaesthetes were found to show significantly higher levels of emotionally reactive empathy compared to controls (e.g. affective components of empathy and instinctive empathic responses to others), but did not differ in their levels of cognitive empathy (e.g. mentalizing and cognitive perspective taking) or in their social skills level. Importantly, synaesthetes without mirror-touch synaesthesia did not differ from non-synaesthetes in their levels of empathy, implying that heightened emotional empathy relates specifically to mirror-touch synaesthesia (and the neural system which underpins this condition). In accordance with this, fMRI findings indicate that, in healthy adults, emotional empathy (i.e. experiencing an appropriate emotional response as a consequence of another's state) engages the cortical sensorimotor network (including the premotor cortex, primary somatosensory cortex and motor cortex) more than cognitive empathy (i.e. predicting and understanding another's mental state by using cognitive processes; Nummenmaa et al.2008). Further, neuropsychological findings have demonstrated a functional and anatomical double dissociation between deficits in cognitive empathy and emotional empathy, with emotional empathy being linked to lesions to the human mirror system and cognitive empathy being associated to lesions to the ventromedial prefrontal cortices (Shamay-Tsoory et al. 2009). This functional coupling between emotional and cognitive empathy suggests that emotional empathy may be linked more closely to sensorimotor simulation of another's state and the evidence that mirror-touch synaesthetes only significantly differ from controls on levels of emotional reactivity is consistent with this.

It is not just developmental mirror-touch synaesthetes who have been shown to differ in their levels of emotional reactive empathy. A recent study by Goller and colleagues (in press) indicates that acquired cases of mirror-touch synaesthesia are also associated with increases in this aspect of social perception. In their study, the empathic abilities of amputees that reported mirror-touch synaesthesia were compared to amputees who do not report mirror-touch synaesthesia. As per Banissy and Ward (2007), the authors use the Empathy Quotient to examine empathic abilities and found that amputees who report mirror-touch synaesthesia showed higher levels of emotional reactive empathy, but not cognitive empathy or social skills (Goller et al. in press). Therefore, both developmental and acquired cases of mirror-touch synaesthesia appear to be related to increased emotional empathy, but not other aspects of this construct.

Developmental mirror-touch synaesthetes have also been shown to differ in another aspect of social perception that is thought to utilize sensorimotor systems, namely expression processing. My colleagues and I compared mirror-touch synaesthetes and non-synaesthetic controls on facial expression recognition, identity recognition and identity perception tasks (Banissy et al. 2011b). Based on the hypothesis that mirror-touch synaesthetes have heightened sensorimotor simulation mechanisms we predicted that synaesthetes would show superior performance on expression recognition tasks but not on the facial identity control tasks that are less dependent on simulation. Consistent with these predictions, mirror-touch synaesthetes were superior when recognizing the facial expressions, but not facial identities of others (Banissy et al.2011b). These findings are in accordance with transcranial magnetic stimulation, neuropsychological and functional brain imaging findings indicating the involvement of sensorimotor systems in expression processing but not identity processing (e.g. Banissy et al. 2010; Pitcher et al. 2008). They are therefore consistent with simulation accounts of expression recognition contending that one mechanism involved in expression, but not identity recognition, is an internal sensorimotor re-enactment of the perceived expression (Adolphs 2002; Gallese et al. 2004; Goldman, and Sripada 2005; Keysers and Gazzola 2006). When combined with the evidence of heightened affective empathy in developmental and acquired mirror-touch synaesthesia, they also help to demonstrate an interesting avenue in which mirror-touch synaesthesia may be able to inform us about mechanisms of social perception in non-synaesthetes.

Conclusions

In sum, this chapter has described the prevalence and characteristics of mirror-touch synaesthesia; the neurocognitive mechanisms that contribute to this experience; and discussed the extent to which mirror-touch synaesthesia can be used to inform us about mechanisms of social perception. While much has been learnt already, a number of key questions remain, including the mechanisms that mediate individual differences in mirror-touch synaesthesia and the extent to which mirror-touch synaesthesia shares similar neural differences as other variants of synaesthesia (e.g. with regards to structural connectivity/cortical excitability). These and other questions will provide interesting avenues for future studies into this variant of synaesthetic experience.

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Figure Legends

Figure 1. Summary of task used in Banissy and Ward (2007). Participants were required to report the site upon which they were actually touched (i.e. left cheek, right cheek, both cheeks or no touch) while ignoring observed touch (and the synaesthetic touch induced from it). Note that although the example given is for a specular mirror-touch synaesthete, both subtypes were tested and congruency was determined according to each synaesthetes' self-reports.

Figure 2. Specular and anatomical spatial mappings reported by mirror-touch synaesthetes. Under a specular frame of reference, mirror-touch synaesthetes report synaesthetic touch as if looking in a mirror. Under an anatomical frame of reference synaesthetic experience is as if self and other share the same anatomical body space.

Figure 3. The location of synaesthetic experience in developmental mirror-touch synaesthesia and acquired mirror-touch synaesthesia in amputees. For developmental mirror-touch synaesthetes, synaethetic touch is evoked in the corresponding body part (e.g. touch to face evokes synaesthetic touch on the face). For amputees, synaesthetic touch gravitates towards the phantom limb or stump irrespective of where touch is observed. Grey dots indicate the location of synaesthetic experience.

Fig 1:

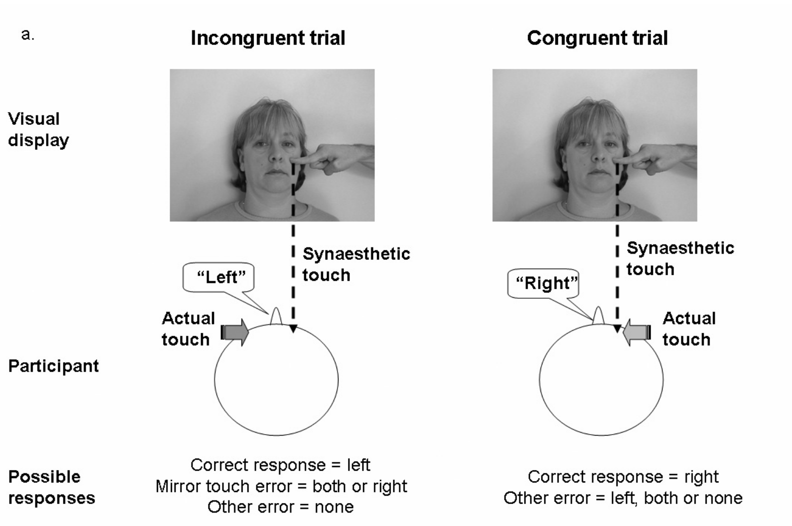

Fig 2:

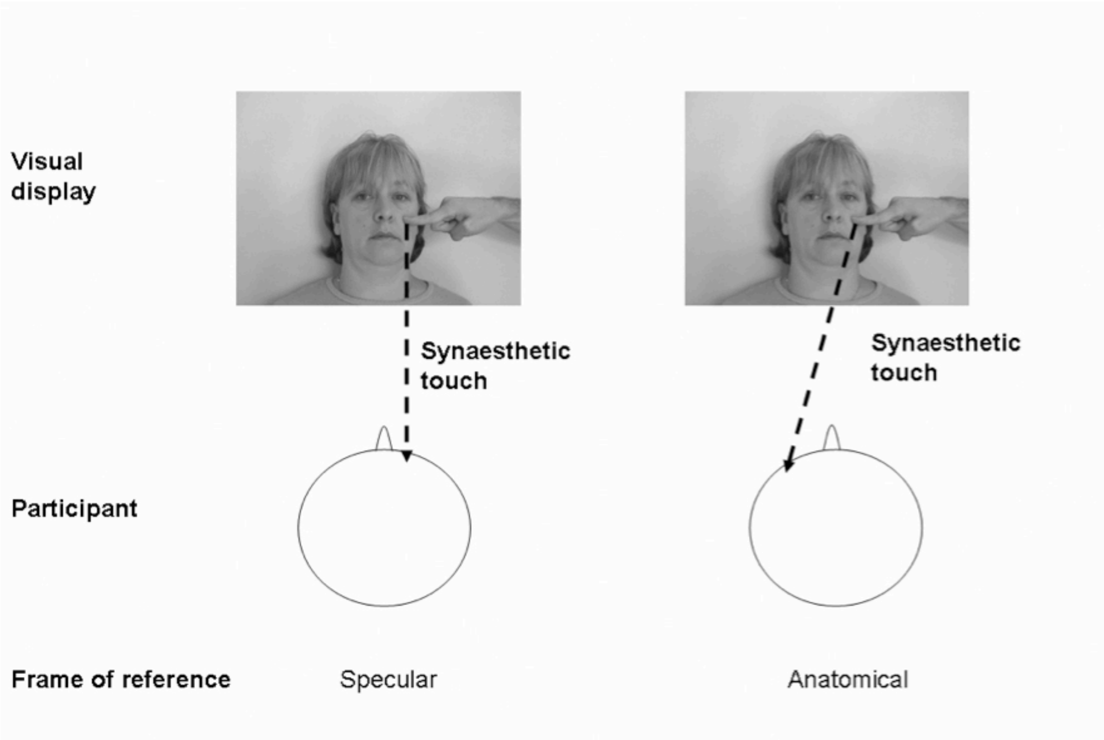
Visual display
Synaesthetic touch
Synaesthetic touch
Participant
Frame of reference
Specular
Anatomical

Fig 3: