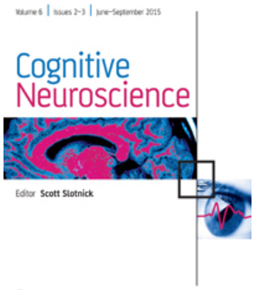

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A task control theory of mirror-touch synesthesia

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(includes Discussion Paper and Commentaries)

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Discussion Paper

Explaining mirror-touch synesthesia

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Mirror-touch synesthesia (MTS) is the conscious experience of tactile sensations induced by seeing someone else touched. This paper considers two different, although not mutually exclusive, theoretical explanations and, in the final section, considers the relation between MTS and other forms of synesthesia and also other kinds of vicarious perception (e.g., contagious yawning). The Threshold Theory explains MTS in terms of hyper-activity within a mirror system for touch and/or pain. This offers a good account for some of the evidence (e.g., from fMRI) but fails to explain the whole pattern (e.g., structural brain differences outside of this system; performance on some tests of social cognition). The Self-Other Theory explains MTS in terms of disturbances in the ability to distinguish the self from others. This can be construed in terms of over-extension of the bodily self in to others, or as difficulties in the control of body-based self-other representations. In this account, MTS is a symptom of a broader cognitive profile. We suggest this meets the criteria for synesthesia, despite the proximal causal mechanisms remaining largely unknown, and that the tendency to localize vicarious sensory experiences distinguishes it from other kinds of seemingly related phenomena (e.g., non-localized affective responses to observing pain).

Keywords: Mirror-touch; Synesthesia/synesthesia; Pain; Mirror systems; Social neuroscience; Phantom limb.

First reported in a single case functional brain imaging study (Blakemore, Bristow, Bird, Frith, & Ward, 2005), mirror-touch synesthesia (MTS) refers to an experience in which observing touch to another person evokes tactile experiences on the observer's own body (Banissy, 2013). The existence of MTS has prompted important theoretical questions within psychology and neuroscience and, indeed, in other disciplines such as the arts and humanities (Martin, in press). What mechanisms enable us to embody a purely visual event such as the sight of someone being touched? How do these mechanisms differ from individual to individual such that in some people it results in a consciously reportable state whereas in others it does not? How do differences in the way that the world is perceived affect other aspects of cognition (or, indeed, how might a different cognitive style result in a different way of perceiving)? What implications does MTS have for the wider construct of synesthesia and the causal processes that give rise to it (in both developmental and acquired forms)? In this Discussion Paper we provide initial answers to these questions, based on the evidence available, and provide a theoretical framework for explaining MTS that will serve as a roadmap for future research in this area.

In the original case study by Blakemore et al. (2005), a single individual was reported for whom

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observing touch to another human evoked tactile experiences under a mirrored frame of reference (i.e., observing touch to the left side of somebody else's face evoked touch on the right-hand side of the synesthetes' face). Building on this, Banissy and Ward (2007) conducted the first group study of MTS and showed that there are at least two spatial frames under which MTS experiences can be evoked: Mirrored (as per the original case) or anatomical (where observing touch to the left side of somebody else's face evoked touch on the left-hand side of the synesthetes' face). More recently, a further spatial mapping has been suggested by White and Davies (2012) who report two variants of experience within the mirrored frame of reference related to the direction of touch: One in which direction of experience is matched in a body-centered reference frame and another in a viewer-centered reference frame. The spatial mappings of anatomical or mirrored experience have been shown to be consistent across body parts (e.g., if someone has a mirrored experience for observed touch to the face they would also experience this for observed touch to the hands from a third person perspective; Banissy & Ward, 2007) and consistent across time (Holle, Banissy, Wright, Bowling, & Ward, 2011).

Current estimates of prevalence of developmental MTS suggest at least 1.6% of people meet objective criteria for the experience (Banissy, Kadosh, Maus, Walsh, & Ward, 2009), with self-report prevalence being considerably higher (Banissy et al., 2009; Chun & Hupe, 2013). The mirrored frame tends to be more common relative to the anatomical reference frame (Banissy et al., 2009a). The relative ratio of those whom experience sensations under body-centered or viewer-centered frames is untested. A minority of individuals also report experiencing tactile sensations when observing touch to objects, either on their hands or body, in addition to when observing touch to humans (Banissy & Ward, 2007; Banissy et al., 2009a). Observing touch to dummy body parts tend to elicit fewer, and less intense, self-reported sensations, thus making dummies more comparable to objects than the human body (Holle et al., 2011). However, observing touch to a rubber hand has been reported to be sufficient to elicit the Rubber Hand Illusion (the feeling that one's own hand is replaced by the dummy hand), even in the absence of physical touch, in two participants with MTS but not controls (Aimola Davies & White, 2013; see also Giummarra et al., 2010). The fact that observing touch to most inanimate objects does not trigger mirror-touch sensations, is reminiscent of the fact that the Rubber Hand Illusion (in non-synesthetes) is not elicited by touch to most inanimate objects unless they closely resemble a hand (Tsakiris & Haggard, 2005; Tsakiris et al., 2010).

There have been a number of studies examining perceptual and cognitive characteristics involved in developmental MTS. This includes studies examining the nature of the inducer in MTS (e.g., Banissy et al., 2009a; Holle et al., 2011) and broader traits that have been found to be different in individuals that have MTS including sensory sensitivity, empathy, and emotion processing (Banissy et al., 2011; Banissy, Walsh, & Ward, 2009; Banissy & Ward, 2007). The precise mechanisms that contribute to MTS and how they link with wider traits observed in MTS remain a topic of debate. Further, the extent to which MTS (and other mirrored sensory experiences) really do qualify as forms of synesthesia has been questioned (e.g., Rothen & Meier, 2013). Here, we seek to discuss these issues, beginning with a discussion of the mechanisms that contribute to MTS and related experiences (e.g., cases where individuals experience pain when observing pain to others, hereafter referred to as mirror-pain) in both developmental and acquired cases by focusing on two prominent theories of MTS: Threshold Theory and Self-Other Theory. Following this, we discuss the relationship between MTS and other forms of synesthesia. Finally, we consider how MTS relates to other forms of mirrored-sensory experiences (e.g., contagious itching; Holle, Warne, Seth, Critchley, & Ward, 2012), which we discuss in relation to the notion of mirrored-sensory synesthesia more widely (Fitzgibbon et al., 2012).

THE THRESHOLD THEORY OF MTS

The Threshold Theory of MTS states that this form of synesthesia is an extreme end-point of a normal neural mechanism (a mirror system for touch). Falling on this end-point gives rise to a qualitatively different experience to most other people (i.e., a conscious experience of touch) and this occurs because the level of activity in the somatosensory system is assumed to cross a threshold for awareness in mirror-touch synesthetes (leading to conscious feelings of being touched) but tends to remain below that level in others (leading to an implicit vicarious response). Thus, although there may be continuous variability in the underlying mechanism across individuals, the presence/absence of MTS is considered a categorical one (assuming their position above/below this threshold is relatively stable over time). This is the first explanation that was offered for MTS (Blakemore et al., 2005) and has subsequently been adopted by others as further evidence in the field has accumulated (e.g., Fitzgibbon et al., 2012; Serino, Pizzoferrato, & Ladavas, 2008). One of the main purposes of this Discussion Paper is to evaluate the evidence for and against the Threshold Theory and, subsequently, to discuss an alternative (but related) account for MTS that we term the Self-Other Theory.

Evidence that MTS reflects increased activity in a mirror system for touch

Blakemore et al. (2005) showed a series of movie clips depicting touch to a human (face/neck) and touch to an object in both a single case of MTS and a group of controls during fMRI. The experimental design was motivated by the first-person reports of the synesthete that only touch to humans elicited felt sensations. In the control group, observing touch to humans (relative to objects) activated regions involved in the physical perception of touch (including primary and secondary somatosensory cortex) in addition to other regions involved more generally in sensorimotor processing (premotor cortex, parietal cortex). This provides evidence for a mirror system for touch—i.e., a neural network that responds to touch applied both to the self and to others. This is conceptually related to the previously documented action-based mirror neuron system that responds to both self-generated and observed actions (Rizzolatti & Craighero, 2004). The synesthete was also noted to activate the same mirror system for touch but to a significantly greater extent than controls, which was assumed to be the neural correlate of her conscious tactile experiences (i.e., the activity crossed some threshold for awareness).

Further evidence has accumulated for a mirror system for touch. The most direct evidence comes from single cell recordings from the primate parietal cortex of so-called "body matching neurons" that respond to the same body part both when it is physically touched but also when the same body part is observed to be touched on another person (Ishida, Nakajima, Inase, & Murata, 2010). Single cell recordings from neurons in the anterior cingulate cortex of humans have been shown to respond to both physical pain and the sight of pain in others (Hutchison, Davis, Lozano, Tasker, & Dostrovsky, 1999). Other convergent evidence has come from human fMRI studies (for a review, see Keysers, Kaas, & Gazzola, 2010). There are, however, some inconsistencies with the Blakemore et al. (2005) findings. In particular, other studies have shown that observing touch to objects also activates the somatosensory system (Ebisch et al., 2008; Keysers et al., 2004). These studies, unlike the one of Blakemore et al. (2005), have tended to use no-touch baseline stimuli in which body parts or objects are approached but not touched. Activation of somatosensory system to observing touch to objects could either reflect some kind of anthropomorphism, or a general semantic concept of touch or, alternatively, the somatosensory activations may represent the tactile consequences of actions rather than the thing being touched (Keysers et al., 2010). However, the latter does not offer a complete account of the literature. For instance, one study using MEG revealed that observed touch to the right hand by the left hand activated *left* SI consistent with (given the known laterality of SI) representing the touched hand rather than touching hand (Pihko, Nangini, Jousmaki, & Hari, 2011).

Holle, Banissy, and Ward (2013) attempted to address some of these issues using fMRI by directly contrasting a group of MTS participants with controls and contrasting three types of stimuli (human faces, dummy faces, objects) in both observed touch and no-touch conditions. Both synesthetes and controls showed activity in somatosensory regions in the touch relative to the no-touch conditions. Moreover, some somatosensory regions (e.g., part of the *face* region in SI) did not differentiate between the stimulus that was touched (consistent with an anthropomorphic response to objects). Both groups also showed activity in the SI *hand* area suggesting that both the toucher and touched are simulated (and even though hands were not visible because touch was delivered by a paintbrush). In the crucial between-group comparison that contrasted stimuli that induce a conscious tactile experience (observed touch to human face) against the matched non-inducing stimuli (no-touch to human face), synesthetes show hyper-activity in both primary (SI) and secondary (SII) somatosensory cortex activity relative to controls—i.e., as predicted by the Threshold Theory. However, Holle et al. (2013) argued that SII, rather than SI, may be more closely tied to the conscious tactile experiences. This is because further analyses established that SII (but not this SI area) was activated by physical touch to the face, correlated with intensity ratings of synesthesia (acquired outside the scanner), and showed increased grey matter density in a VBM (voxel-based morphometry) analysis.

In general, perceptual stimuli that are consciously perceived (as opposed to subliminal) tend to be linked to greater activity in parts of the brain involved in the perception of that stimulus (e.g., Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). Thus, consciously perceived houses and faces are linked to greater activity in ventral stream regions specialized for perceiving those stimuli, relative to when the same stimuli are subliminally presented (Moutoussis & Zeki, 2002). In the domain of touch, the same applies within the somatosensory system and has been linked specifically with feedforward processing to SII (Auksztulewicz & Blankenburg, 2013; Auksztulewicz, Spitzer, & Blankenburg, 2012; see also Gallace & Spence, 2008). Conscious experiences of touch in a case of acquired auditory-tactile synesthesia, following thalamic lesion, were also linked to increased activity in SII and increased anatomical connectivity in that region (Beauchamp & Ro, 2008).

Osborn and Derbyshire (2010) examined conscious perceptions of pain in response to seeing others in pain (e.g., broken limbs). A group who reported conscious pain experiences (which we term mirror-pain) were compared with a group who did not (which we consider as controls). During fMRI, painful and non-painful/emotional images were contrasted. Both groups showed similar levels of activity to pain relative to no-pain stimuli in a mid-anterior cingulate region. Other research has linked this region to the affective aspects of pain and it is often activated in response to seeing others in pain (Lamm, Decety, & Singer, 2011). However, the mirror-pain group showed significantly higher levels of activity in SII (a region related to sensory aspects of pain) and the anterior insula. Damage to the insula results in impaired judgments of others' pain (Gu et al., 2012; Wang et al., 2014) and, moreover, high levels of anterior insula activity were found in the MTS participant reported by Blakemore et al. (2005; but not by Holle et al., 2013). Although Osborn and Derbyshire (2010) did not make any link to synesthesia, their findings are clearly in line with the Threshold Theory. The question of whether this should be considered a type of synesthesia in its own right (or, indeed, is another instance of MTS) is returned to later.

Aside from brain imaging, several recent studies have attempted to induce symptoms of MTS in non-synesthetes using brain stimulation (Bolognini, Miniussi, Gallo, & Vallar, 2013; Bolognini, Rossetti, Fusaro, Vallar, & Miniussi, 2014). Bolognini et al. (2013) applied tDCS (transcranial direct current stimulation) over SI to increase cortical excitability and, hence, to potentially raise activity above the threshold for perceptual awareness. They adapted the behavioral paradigm of Banissy and Ward (2007) showing that people with MTS show interference in detecting the location of physical touch when concurrently presented with observed touch (to humans not objects) that induces synesthetic touch to another location. tDCS targeted at SI also led to a similar behavioral profile in non-synesthetes (greater interference from observed touch to humans, not objects, when spatially incongruent), but control stimulation (sham, or tDCS to another site) did not. Moreover, the degree of behavioral interference in the key condition was correlated with self-reports of symptoms similar to MTS during the task.

Mirror touch/pain synesthesia in amputees

There is evidence that observing pain and touch to other humans can—in some acquired amputees (either upper or lower limb)—elicit felt sensations of pain and touch. However, there is one crucial difference between mirror touch/pain in amputees and normal-bodied individuals: Namely, in amputees the sensations are typically felt on the phantom or stump but in normal-bodied people (developmental MTS) there is a close correspondence between the observed bodily location and the felt one. This has been explained in terms of compensatory hyper-activity of a localized part of the somatosensory system (that corresponding to the missing limb) arising due to removal of inhibitory pathways into that region (Fitzgibbon et al., 2012; Ramachandran & Brang, 2009). That is, the Threshold Theory discussed previously has been extended to an acquired form of mirror touch/pain synesthesia.

Fitzgibbon et al. (2010) administered a questionnaire to a group of amputees that included an item about mirror pain ("phantom pain is triggered by observing or imagining pain in another person [yes/no]") plus various follow-up questions (e.g., concerning possible seen bodily locations, whether it has to be a loved one, etc.). Sixteen percent of their sample (12/74) of amputees responded affirmatively to the question. Almost all agreed that it was triggered by observing *any* pain (rather than pain to particular bodily locations or people). Most reported that the subjective experience was comparable to that experienced during spontaneous phantom pain. Goller, Richards, Nowak and Ward (2013) conducted a similar study to Fitzgibbon et al. (2010) but tried to experimentally induce (self-reported) pain/tactile sensations using movie clips rather than relying on retrospective reports of mirror pain from a questionnaire. Of their sample of 28 amputees, 9 participants (32%) reported mirror-pain sensations that tended to gravitate toward the phantom/stump (a small number of other individuals reported occasional trials that tended to be linked to correspondence between seen and felt locations). As with developmental MTS, felt touch/pain was more likely to be elicited following observed touch to a real body than a dummy or object.

Giummarra et al. (2010) used a version of the Rubber Hand Illusion on amputees and found that *leg* amputees report sensations of pain and movement in their phantom when a rubber *hand* is threatened. Further research has established that amputees with mirror-pain synesthesia have a different EEG response to observing painful images (Fitzgibbon et al., 2011) but, aside from this, very little is known about the neural basis in amputees.

As an alternative to reduced inhibition, another contributing neural mechanism might be central sensitization of the pain system that occurs following injury resulting in hyper-sensitivity to mildly painful stimuli and pain responses to stimuli that are normally non-painful such as light touch (Woolf, 2011). Whether central sensitization makes people more susceptible to vicarious pain (measured neurophysiologically) or mirror pain (measured via self-report) is unclear (but see Lee et al., 2013). One characteristic of central sensitization is that the whole body becomes sensitized to pain, and not just the part of the body corresponding to the initial site of damage. This may possibly account for the fact that observed touch/pain to any body part can act as an inducer (i.e., observed pain in the arm triggering pain in a phantom foot).

Why do some amputees have these experiences whereas most others do not? Neither Fitzgibbon et al. (2010) or Goller et al. (2013) found an association between MTS and characteristics of the amputation (e.g., time since amputation, extent of loss). Fitzgibbon et al. (2010) noted that a high proportion (5/12) of the mirror-pain amputees reported other types of synesthesia (e.g., grapheme-color) although this was not verified with testing. Whereas, Goller et al. (2013) reported that these amputees had higher “emotional reactivity” on an empathy scale, similar to that documented in developmental cases of MTS (Banissy & Ward, 2007). Although these results are preliminary, they suggest a role for pre-existing characteristics of the individual that influence changes in the functioning or organization of the mirror system for touch following loss of somatosensory input. Some research suggests that even temporary and localized disruption of sensory inputs (from dental anesthetics or numbing cream) can result in reports of mirror-touch-like experiences in the desensitized part of the body (Case, Gosavi, & Ramachandran, 2013).

Problematic evidence for the threshold theory

Threshold Theory is not fundamentally wrong, but is incomplete as an explanation. Specifically, people with MTS differ in ways that go beyond what would be predicted by the simple form of this theory articulated thus far. For instance, people with MTS show structural differences in their brain, assessed by VBM, that are not limited to the somatosensory system (Holle et al., 2013). These include *reduced* grey matter density in a right temporo-parietal junction region (rTPJ) and the medial prefrontal cortex (mPFC), and *increased* grey and white matter density in the right temporal pole. These three brain regions have been consistently implicated in studies of so-called “mentalizing” or theory-of-mind, i.e., the attribution of mental states to others (Frith & Frith, 2003). However, the precise function of these regions remains contested. This particular region of the mPFC tends to be activated more when thinking about the self relative to others, but close others (e.g., family or people who are similar to oneself) activate the region too (Krueger, Barbey, & Grafman, 2009). The rTPJ region tends to be activated more when thinking about others than self (Ruby & Decety, 2004). It has been linked to bodily perspective taking (Arzy, Thut, Mohr, Michel, & Blanke, 2006), and the ability to appropriately control self and other representations (e.g., to inhibit oneself and boost representations of others or vice versa; Santiesteban, Banissy, Catmur, & Bird, 2012; Spengler, Von Cramon, & Brass, 2009).

People with MTS report various unusual bodily experiences that extend beyond touch and pain. Consider the following quotes from people with MTS:[1]

> “I loved to stand in front of the Giacometti [sculpture]. . . and it is a very good feeling. So I love to stand in front of them and feel I am getting longer”

> “As Nadia [Comaneci; the gymnast] moved through her routines my body would twitch and my muscles would move as she moved, and my friends just considered me a freak, and I couldn’t explain it, and I wasn’t trying to do it, and I just found the more I watched her the muscles in my legs would fire, and my legs would move. I remember being not able to explain what I was doing or why I was doing it, or even really realising that I was doing it, until my friends would point things out to me.”

[1]These quotes were obtained by Daria Martin and Eleanor Cleghorn.

> "if I were to attend to a lamp or a potted plant, I feel my body become many of their elements—the roundness of the lamp or the hollow round sensation of the lamp shade… I sense my body shaped with the pointed characteristics of the branches of the plant and smooth portions corresponding to its leaves".

Although anecdotal in nature, these descriptions have been noted in multiple case histories beyond those listed here. These quotes imply a general tendency for bodily sensations to be driven by visual input and they extend beyond somatosensation to include feelings of body shape and body movement. The Threshold Theory, by contrast, only offers an account of touch and pain. It is to be noted that the quotes do not describe out-of-body experiences (projection of the self externally) but rather the opposite scenario of incorporating others into the bodily self. In the subsequent section we interpret this evidence, and other evidence, in terms of disturbances in Self-Other processing in MTS.

THE SELF-OTHER THEORY OF MTS

The Self-Other Theory states that MTS is a result of disturbances in the ability to distinguish the self from others (Banissy & Ward, 2013; Banissy et al., 2009a). The account is not necessarily in opposition to Threshold Theory, but compliments it by suggesting that, for individuals with MTS, atypical self-other representation abilities amplify vicarious responses when observing touch to others. In this regard, self-other processing may act as a gating mechanism for neural activity within the mirror system for touch, akin to the role that mechanisms of self-other control (also referred to as self-other switching) have been suggested to play in empathy and other socio-cognitive abilities more generally (e.g., Bird & Viding, in press; Sowden & Shah, 2014). To date, accounts of self-other processing disturbances in MTS have commonly fallen under two related themes: (1) atypical representations of self-awareness, and (2) atypical abilities to control representations of the self and others. We consider each below.

Self-awareness in MTS ("who" mechanisms)

Original accounts of differences in self-other processing in MTS built upon work in non-synesthetes showing that levels of self-similarity modulate the extent to which we all vicariously represent the pain and touch of others (e.g., Avenanti, Sirigu, & Aglioti, 2010; Azevedo et al., 2013; Mahayana et al., 2014; Serino, Giovagnoli, & Ladavas, 2009; Serino et al., 2008). For example, Serino et al. (2008, 2009) show that observing another person being touched can modulate the perception of touch, but that this is mediated by the extent to which the other person is perceived as being similar to the self. Further, in-group/out-group membership has been shown to influence vicarious representations (e.g., Serino et al., 2009), suggesting that even contextual cues about the self can modulate the extent to which we all share the experiences of others. Extending this to MTS, it has been suggested that representations of the self might be more expansive in individuals who experience mirror-touch sensations leading to the incorporation of other's experiences into their own body representation (Banissy et al., 2009a; Aimola Davies & White, 2013). That is to say that one mechanism that might be atypical in MTS is the ability to determine "who" is the subject of touch (Banissy et al., 2009a).

In support of this, Maister, Banissy, and Tsakiris (2013) showed that, in MTS, simply observing touch to others could evoke a change in mental representations of the self. This was measured using the "enfacement illusion" in which observing touch to another person's face while simultaneously receiving synchronous tactile stimulation to one's own face leads to a tendency for individuals to incorporate more of the other into representations of themselves when making judgments about morphed stimuli of faces containing varying proportions of the self or other (Tsakiris, 2008). Individuals with MTS experienced the enfacement illusion when simply viewing touch to others (i.e., without physical tactile stimulation; Maister et al., 2013). Further, Aimola Davies and White (2013) report that individuals with MTS experience the Rubber Hand Illusion when simply observing touch to a prosthetic hand. In the typical rubber hand illusion observing touch to a prosthetic hand paired with synchronous tactile stimulation of one's own hand leads to the prosthetic hand being incorporated into one's sense of body ownership, but in MTS simply observing touch without any physical tactile stimulation is sufficient to evoke the illusion. In a similar context, during the rubber hand illusion, individuals that report mirror-pain sensations have been shown to experience a sense of ownership over the prosthetic hand during synchronous and asynchronous stroking (Derbyshire, Osborn, & Brown, 2013), whereas non-synesthete controls only experience the illusion during synchronous stroking. In this regard, sense of body ownership appears distorted in MTS and mirror-pain, which may contribute to self-other confusion in these individuals. We also speculate that people with MTS may experience these illusions in situations in which the illusion is normally attenuated or not found (e.g., when the rubber hand is an allocentric orientation).

The extent to which changes in sense of body ownership alone or broader changes in self-awareness are present in MTS (and mirror-pain) remains to be determined. Self-awareness is often discussed in the context of two related socio-cognitive processes: Sense of body ownership and sense of agency. While individuals with MTS and mirror pain have been shown to have more malleable self-representations in terms of sense of body ownership, little is known about how this relates to sense of agency. There are reasons, however, to predict changes in sense of agency in these experiences. For example, previous research in typical adults has shown that sense of agency can play a role in structuring bodily awareness (e.g., Tsakiris, Prabhu, & Haggard, 2006); and patients with impairments in self-other discrimination perform poorly on agency tasks (Daprati et al., 1997). Based on this, it has been suggested that agency-processing differences may exacerbate more basic disturbances in bodily awareness in MTS (Cioffi, Moore, & Banissy, 2014). The extent to which individuals that experience MTS and/or mirror pain show atypical sense of agency, and how this combines with previously reported differences in sense of body ownership (e.g., Aimola Davies & White, 2013; Derbyshire et al., 2013; Maister et al., 2013) requires further investigation. There are also preliminary findings suggesting that reduced self-awareness to one's own bodily pain may to some extent be associated with an increased tendency to experience mirror-pain sensations, implying some degree of broader altered self-awareness in mirror-pain responders (Vandenbroucke et al., 2013).

Self-other control mechanisms in MTS

In addition to representations of the self, more recently it has been suggested that self-other disturbances in MTS may be associated with a more specific impairment in the ability to *control* self-other representations (Banissy & Ward, 2013; Sowden & Shah, 2014; Ward, 2013). That is to say MTS may be related to difficulties in the ability to control the extent to which they can inhibit the experiences of others, while boosting representations of the self (or vice versa). For example, in order to take another's perspective we are required to boost representations of another while inhibiting representations of ourselves, while in order to suppress imitative behaviors we are required to inhibit representations of another and boost representations of ourselves. One hypothesis is that individuals with MTS will show impairment in mechanisms that mediate the ability to appropriately control self-other representations leading to a more general failure to inhibit the experiences of others (Banissy & Ward, 2013).

This proposal builds on neuroimaging data showing that individuals with MTS show less grey matter volume in the rTPJ relative to non-synesthetes (Holle et al., 2013). As noted above, in typical adults, the rTPJ has been shown to be important in the ability to control the extent to which representations of the self or other are enhanced or inhibited (e.g., Hogeveen et al., in press; Santiesteban et al., 2012; Spengler et al., 2009). For example, Santiesteban and colleagues (2012) used transcranial direct current stimulation (tDCS) to show that modulating cortical excitability in the rTPJ enhances the ability to control self-other representations. More specifically, in one task tDCS of rTPJ enhanced self representations and inhibited representation of the other, but in another it enhanced other representations and inhibited self representations, suggesting that rTPJ plays a role in the control of self and other representations rather than processing self-only or other-only representations. In other domains there is evidence to suggest that neural activity in the TPJ may play a role in mediating vicarious responses. For example, a recent fMRI study examined the phenomenon of "compassional hyperalgesia"—where seeing another person in pain (images of burns, wounds, etc.) increases the perceived intensity of a subsequent physical pain stimulus applied to the observer (Godinho et al., 2012). One might have expected the increased painfulness to be related to increased activity within the pain matrix itself (given that parts of this system function as a mirror system for pain) but, instead, the increased painfulness was related to the recruitment of a non-pain brain network that included the TPJ. Thus, compassional hyperalgesia may relate more to the engagement of self-other discrimination mechanisms (in addition to wider contextual appraisals; Martin, Tuttle & Mogil, 2014). We contend that a similar self-other process may contribute to MTS.

While there are currently no published studies on mechanisms of self-other control in MTS, difficulties in controlling self-other representations have been reported in individuals who experience mirror-pain sensations. For example, Derbyshire et al. (2013) report that individuals that report experiencing mirror-pain sensations show greater levels of self-other confusion than controls. In that study the authors compared performances of individuals that did or did not report mirror-pain sensations on a version of the Dot Perspective task (Samson, Apperly, Braithwaite, Andrews, & Bodley Scott, 2010), which is a commonly employed measure of self-other processing. In the task used by Derbyshire et al. (2013), participants viewed an avatar facing to the left or the right. Dots appeared on the wall in front of the avatar, behind the avatar, or both, with the number of dots varying from trial to trial. Prior to each trial participants were cued to adopt either their own perspective (self-trials) or the perspective of the avatar (other-trials). They were asked to report the number of dots seen from the cued perspective. There were two types of trial: Consistent and inconsistent. In consistent trials, the participant and the avatar saw the same number of dots. In inconsistent trials the participant and the avatar saw a different numbers of dots, thus information from one source (self or other) should have been inhibited while the other source (self or other) enhanced depending on the cued perspective. Typically, participants are slower to verify the number of dots they can see in a picture in inconsistent trials, even when explicitly instructed to adopt their own perspective (Samson et al., 2010)—i.e., they have difficulty inhibiting the other and enhancing the self. Derbyshire et al. (2013) found this interference effect to be greater in individuals that report experiencing mirror-pain relative to those that do not. They interpreted this as evidence of greater levels of self-other confusion in individuals that experience mirror-pain. While indicative of this, unfortunately, the Dot Perspective task has recently been criticized for not being a pure measure of self-other processing (Santiesteban, Catmur, Hopkins, Bird, & Heyes, 2014). Moreover, Santiesteban and colleagues (2014) report that replacing the avatar in the Dot Perspective task with an arrow produces a similar patterns of data, suggesting that domain-general differences in attention allocation rather than self-other confusion contribute to interference effects on this task. Delineating the extent to which self-other control versus domain general attention control are or are not atypical in MTS and other phenomena, such as mirror pain, remains an important future challenge.

Whatever the precise mechanism, differences in performance on self-other perspective tasks are suggestive of a wider profile of cognitive differences (including those unrelated to touch and pain) that are not predicted by simpler versions of the Threshold Theory. Similarly, potential differences in controlling self-other representations in MTS provide a clearer explanation for wider social processing differences that have been reported in MTS (e.g., empathy: Banissy & Ward, 2007; Goller et al., 2013; emotion recognition: Banissy et al., 2011) than Threshold Theory alone. Recent accounts suggest that the ability to control self-other representation may play a key role in a number of socio-cognitive processes including perspective-taking, theory of mind, and empathy (see, e.g., Bird & Viding, 2014; Sowden & Shah, 2014). For example, in the context of empathy, Bird and Viding (2014) suggest that the ability to switch between the processing of self and other representations may play a key role in biasing processing toward affective cues displayed by others in order to change one's own affective state to match another person's state (i.e., to experience empathy). If MTS is linked to general difficulties in the ability to suppress the representations of others, then it is not difficult to see how this could contribute to broader biases in social perception reported in this group. In fact, it may even lead to some problems (e.g., in interactions in which we need to inhibit imitative behaviors by inhibiting representations pertaining to the other and enhancing representations related to ourselves).

In this context Self-Other Theory provides a stronger rebuttal to a limitation that has been indirectly targeted at Threshold Theory—namely, the extent to which differences in vicarious responses to touch contribute to broader socio-cognitive abilities that differ in MTS. For example, De Vignemont (in press) states:

> Let us imagine that you see me being stroked by a paintbrush. You then understand that I feel touch. So what? What kind of prediction can you make on the basis of this newly acquired knowledge?… First, the role of vicarious touch for mindreading, and more generally for social cognition, is minimal. Secondly, it is not clear in what sense it is useful to empathize with someone's tactile experiences anyway. (De Vignemont, in press).

In the context of MTS, a simple response to this critique is that although labelled as "mirror-touch" the experience is not only about touch: It is a symptom related to disturbances in self-other representations, which can play a role in a number of socio-cognitive processes including perspective-taking, theory of mind, and empathy.

Limitations of self-other theory

It is important to discuss other features that may be considered limitations of Self-Other Theory of MTS. One feature is how well Self-Other Theory can account for cases in which MTS experiences are induced when observing touch to objects. Moreover, while the majority of individuals with MTS only experience sensations when observing humans being touched, a small subset do report experiences when observing touch to objects (Banissy et al., 2009a). At first sight it may seem difficult to reconcile this with self-other accounts, since by definition an object is not another person. One possibility is that, for individuals who experience MTS from objects, domain general difficulties with the ability to differentiate/control task-relevant from task-irrelevant representations is a fundamental disturbance, whereas for individuals who only experience MTS when observing touch to other people, a domain-specific disturbance in the ability to control self-other representations is at play. This feeds into broader debates about the role of the rTPJ in domain general attention control versus domain specific self-other control processes and evidence that sub-divisions within the rTPJ may play a function in each process (e.g., Cook, 2014; Nicolle et al., 2012).

A further limitation of Self-Other Theory relates to the extent to which it can account for acquired cases of MTS—e.g., in amputees (e.g., Goller et al., 2013). One possibility is that inter-individual variability in self-other representations influences which amputees report MTS and which do not following amputation. That is, this theory predicts that it is more likely for individuals to acquire MTS if they have greater levels of self-other confusion to begin with. To date this has not been tested, but some of the paradigms described above could be extended to this group. An alternative possibility is that developmental cases of MTS and cases in amputees both reflect overactive mirroring (as Threshold Theory would predict), but the mechanisms through which this occurs differ. In developmental cases, disturbances in controlling self-other representations may lead to atypical cortical responses within neural systems involved in mirroring touch, whereas in acquired cases shifts in vicarious activation may be related to disturbances in bodily feedback directly influencing representations within the somatosensory system (e.g., the missing limb may lead to a failure to inhibit observed touch/pain; Ramachandran & Brang, 2009). These remain open questions for future studies, but highlight how it is likely that an integrative account combining both Self-Other Theory and Threshold Theory will be the most parsimonious means to explain MTS in developmental and acquired cases.

IS THIS SYNESTHESIA?

The debate around what does and does not constitute synesthesia is a long-standing one (e.g., Baron-Cohen & Harrison, 1997). More recently, some researchers have questioned whether mirror-touch is a form of synesthesia (e.g., De Vignemont, in press; Rothen & Meier, 2013). In addressing this question, we break the argument down into two sets of issues. Does it have the key characteristics of other types of synesthesia? Does it share the same mechanisms as other types of synesthesia? Finally, if one does accept mirror-touch as a form of synesthesia, then have the floodgates been opened to a host of other phenomena? This would include contagious yawning (Provine, 1996) and contagious itching (Holle et al., 2012)—that is, watching someone else yawning or itching elicits a comparable response in the observer. We will argue why these should *not* be considered types of synesthesia.

Does MTS share characteristics with other types of synesthesia?

Ward (2013), in broad agreement with others in the field, has argued that synesthesia has three defining features:

1. That the experiences are explicit and percept-like.
2. That the experiences are elicited (that is, they can be described as a concurrent experience triggered by an inducer).
3. That the experiences are automatic.

The percept-like nature of synesthesia is essentially based on first-person report that there is a homology between the synesthetic experience and that of physical seeing, feeling, tasting, etc. If given a list of qualitative descriptors that includes "touch" but also includes other plausible options such as "tingling," "itchiness," or "other" most mirror-touch synesthetes choose "touch" (with a minority consistently reporting "tingling"). Other lines of evidence, discussed above, corroborate the percept-like nature: Namely, fMRI studies show that perceptual regions of the brain are active during synesthesia. If anything, the evidence from mirror-touch more clearly supports the perceptual criterion than, say, grapheme-color in which visual cortex is less consistently implicated (Rouw, Scholte, & Colizoli, 2011).

Mirror-touch synesthesia meets the criteria of being elicited. However, the nature of that inducer is less straightforward to articulate than in other examples of synesthesia. Blakemore et al. (2005) referred to it as vision-touch synesthesia which is not accurate (vision of bodily sensations may be more accurate). Rothen and Meier (2013) argue that MTS differs from other kinds of synesthesia in that there is only one inducing stimulus compared to, say, grapheme-color synesthesia in which many letters and digits act as inducers. However, we suggest that there are an infinite number of inducing stimuli in MTS (infinitely varying locations on the body with differing intensities and qualities) making it more akin to auditory-visual synesthesia (in which the inducing stimuli vary infinitely according to pitch, loudness, timbre, etc.).

The third criteria, automaticity, is demonstrated by research showing that when asked to respond to physical touch (delivered from an electronic tapper attached to the face or hands), participants with MTS are unable to ignore their synesthetic touch (elicited by observing touch to another person presented on a computer screen; Banissy & Ward, 2007). The fact that synesthetic experiences are automatic can explain why synesthesia subjectively resembles perceiving rather than imagining. Imagining touch also activates the somatosensory system (e.g., Schmidt, Ostwald, & Blankenburg, 2014) but, in the case of imagery, there is a sense of self-causality ("I caused that experience") that is absent in both synesthetic and physical tactile perception ("that experience was caused by some external event").

Other candidate criteria, proposed by some, include consistency over time and an idiosyncratic relationship between the inducer and the concurrent. Mirror-touch synesthesia meets the former criteria (Holle et al., 2011) but not the latter. The non-arbitrary nature between inducer (seeing touch) and concurrent (feeling touch) was one consideration that led Rothen and Meier (2013) to question whether it should be considered synesthesia at all. We note that other forms of synesthesia are only *partially* idiosyncratic, with most types being influenced by correspondence rules (e.g., high pitch being lighter; Sagiv & Ward, 2006). These rules either derive from the statistical properties of the world or, else, are grounded by the innate multi-sensory architecture of the brain (Spence, 2011). However, the lack of idiosyncrasy in MTS does generate some difficult questions that we tackle later (e.g., why not mirror-yawn synesthesia?).

Does MTS share the same causal mechanisms as other types of synesthesia?

Simner (2012) has argued that the definition of synesthesia should ultimately depend on the underlying causal mechanisms. Do different types of synesthesia have the same causal mechanisms—genetic dispositions, effects on brain structure and function, and so on? Other forms of synesthesia are known to run in families and have a genetic contribution (e.g., Asher et al., 2009). It is unclear whether this applies in mirror-touch synesthesia. Some mirror-touch synesthetes report a familial history of grapheme-color synesthesia, but it is important to establish whether this occurs more than by chance and current evidence is equivocal (Chun & Hupé, 2013). Mirror-touch synesthesia typically has a developmental origin like other typical examples of synesthesia. If one were to find genes linked to, say, grapheme-color synesthesia, one could potentially test to see if the same held true for MTS. But what if it didn't hold true? Would we then be forced to conclude that this was not a form of synesthesia? Presumably not, but one would have to acknowledge instead different causal and developmental trajectories.

At this point it may be helpful to distinguish between distal causes and proximal causes. The distal causes refer to the precipitating event (e.g., a claim such as "MTS is caused by a set of genes that develop the brain in certain ways") and the proximal causes refer to a more mechanistic level of explanation (e.g., such as "MTS is caused by differences in a brain network that treats bodily self and other as similar but different"). It is theoretically possible to have different distal causes giving rise to similar proximal causes. Fitzgibbon et al. (2012) offer an account along these lines of both developmental and acquired (in amputees) MTS based on the assumption of different distal causes but a similar proximal cause (namely, hyper-activity within a mirror system for touch). Attempts to create MTS via brain stimulation (Bolognini et al., 2013) can also be construed as attempting to recreate the proximal, but not distal, causal mechanisms.

In order to understand whether MTS and other variants (e.g., grapheme-color synesthesia) share distal or proximal causal mechanisms it is important to study each using comparable tasks and methodologies. For instance, one body of research has shown that grapheme-color synesthetes appear to show increased sensitivity to color (Banissy et al., 2009), have a lower phosphene threshold to brain stimulation (Terhune, Tai, Cowey, Popescu, & Kadosh, 2011), and also have increased EEG visual-evoked potential to certain achromatic (non-inducing) stimuli (Barnett et al., 2008). That is, their visual system appears to function differently from the norm. It would be important to understand the mechanisms behind this (including whether such differences are a cause or consequence of having synesthesia) and also to explore whether parallel effects are found for somatosensory perception in MTS. One study has indeed shown better tactile acuity in MTS (Banissy et al., 2009b), suggesting that comparable functional differences exist in perceptual processing here too. Other research has shown atypical multi-sensory integration in grapheme-color synesthesia (Brang, Williams, & Ramachandran, 2012; Sinke et al., 2014) and it would be important to ascertain whether the same holds true in MTS.

Why not mirror-itch and mirror-yawn synesthesia? Why is mirror-pain so prevalent?

Contagious yawning and contagious itching, when observing other people yawning or scratching, are normative phenomenon in which it is more common to experience some contagion than not (Holle et al., 2012; Platek, Critton, Myers, & Gallup, 2003). Rarity aside, these phenomena bear close superficial resemblance to MTS. Few, if any, researchers would endorse rarity as a *defining* characteristic of synesthesia, but it is hard to imagine how a common set of mechanisms/principles can account for both a rare developmental trajectory (such as grapheme-color synesthesia) and a near-universal one (such as contagious itch). The danger is that the term “synesthesia” becomes meaningless as a theoretical construct if it is applied too widely. The converse problem is that it seems arbitrary to allow mirror-touch to be classed as synesthesia but not “mirror-itch” or “mirror-yawn.” Similar concerns can be raised about mirror-pain for which Osborn and Derbyshire (2010) reported a prevalence of 33% (but note that they did not interpret this in terms of synesthesia).

In order to unpack these issues it is important to consider the nature of the information that is being shared. In the case of yawning it is a motor response/urge to yawn that is shared (although it could be the concept of sleepiness too). In the case of observing scratching it could be a feeling/affective response (itchiness) and/or a motor response/urge to scratch. Lloyd, Hall, Hall, and McGlone (2013) found that images of bugs on the skin tended to be more potent visual inducers of itch than images of scratching actions themselves. This observation is of interest because it implies that contagious itchiness may be more to do with induction of the feeling state (itchiness/unpleasantness) rather than contagion of the motor act. (Previous speculations concerning contagious itching have centered on the action-based mirror system; Ikoma, Steinhoff, Ständer, Yosipovitch, & Schmelz, 2006.) Similarly, Ward, Burckhardt, and Holle (2013) found that when people scratch themselves as a result of watching others scratching, they do not mirror either the location of itch or the hand that does the scratching (e.g., observing someone scratching their chest with their left hand may elicit a scratch to their head using their right hand).

Pain, like itch, is also a multi-faceted construct consisting of affective, sensory, and evaluative components. When viewing or thinking of others in pain (in non-synesthetes), research with fMRI has shown consistent activity in regions specialized for processing the affective aspects of pain, with more variability across studies with respect to regions that process sensory aspects of pain (e.g., Lamm et al., 2011). This may relate to factors such as whether the source of the pain is known (e.g., seeing an injection) or not (e.g., seeing a pained facial grimace). What is largely unknown is whether *conscious* reports of feeling the pain of others (a candidate for being called “synesthesia”) are sensory or affective in nature. We predict that it is the sensory aspects of pain that are likely to show the greatest variability across individuals and also the closer links (mechanistically and superficially) to MTS. The prevalence of 33% reported by Osborn and Derbyshire (2010) is likely to reflect a mixture of both affective and sensory-based mirror-pain. They also used a liberal threshold of experiencing pain to one or more images/movies (as opposed to zero). It would be important for future research to characterize this further but we expect the prevalence to be considerably lower.

In a preliminary study, we explored how people with MTS respond to movies depicting pain or itch. An online test showed movie clips depicting neutral touch (N = 14 stimuli; a subset of those used by Holle et al., 2011), clips depicting painful touch (N = 6; all were injections), and clips depicting scratching (N = 4; a subset of those used by Holle et al., 2012). These were shown to a group of 12 individuals reporting mirror-touch synesthesia (two male, one left handed, age range = 19–71 years). To be classified as having MTS these individuals reported sensations on their own body on 40% or more trials depicting neutral touch, in addition to previously reporting such experiences in daily life. This cut-off results in an average of 67% of trials depicting touch to a human eliciting a tactile experience, which is consistent with previous research with these stimuli (Holle et al., 2011). A second group, classified as controls, reported very few or no sensations on their own body to these stimuli (N = 17 participants, four males, one left handed, age range = 19–36 years). As such, the assignment of MTS or control was based entirely on the neutral touch trials and we then sought to determine how the two groups would differ on the trials depicting pain and itch (orthogonal to our initial classification). For these stimuli, participants were asked to rate the intensity of any experience on their own body (0–10 scale). For ratings greater than 1, they were then given a list of qualitative descriptors from which they could choose only one (these were: Touch without pain, tingling, itchiness, feeling of being scratched, painful touch, pain (without touch), and other/specify) and a second set of descriptors that described the location of the experience and corresponded to at least one body part depicted in the clips (left hand, right hand, left face, right face, left arm, right arm, neck, back, chest, not localizable, other).

The results are summarized in Figure 1. For the videos depicting itch, the two groups did not differ in terms of the number of stimuli that elicited feelings of "itchiness" or "tingling" (collapsing these two related descriptors together). However, the MTS group were significantly more likely to report "touch" in response to seeing scratching (Mann Whitney, p = .011) and a non-significant tendency to report a "feeling of being scratched." The location felt on the body was categorized as anatomical, mirrored, or not localizable. The MTS group were significantly more likely to give mirrored locations (Mann Whitney, p = .038). As noted previously (Ward et al., 2013), controls show no preference for mirroring the laterality of these stimuli.

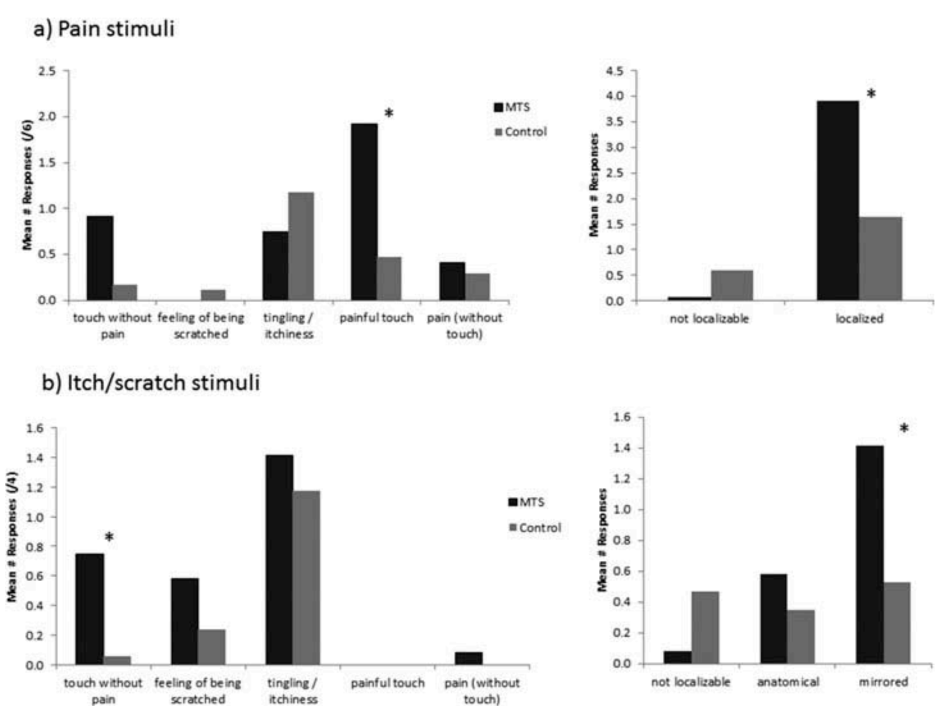

Figure 1. People with MTS and controls were shown movies depicting injections (pain stimuli) and movies depicting intense scratching (itch/scratch stimuli) and were asked to note the nature and location of any vicarious experience.
*p < .05.

For the videos depicting pain, the two groups again did not differ in terms of the number of stimuli that elicited feelings of "itchiness" or "tingling" (collapsing these two descriptors together). However, the MTS group showed a significantly greater tendency to report "painful touch" (Mann Whitney, p = .014) and a numerical trend toward reporting more non-painful touch. The pain stimuli tended to depict bodies from an egocentric rather than allocentric perspective and, hence, could not be classed as mirrored or anatomical. They could, however, be classified according to whether the experience was localized or not. The MTS group reported significantly more localized experiences (Mann Whitney, p = .025), whereas the controls showed a non-significant trend to report non-localized experiences.

These observations, although based on self-report, suggest that people with MTS are not simply exaggerated versions of normality. Although they do produce more subjective reports of bodily sensations when viewing pain and itch, it is not simply "more of the same": They have a greater tendency to localize (particularly within a mirrored frame of reference) and are more inclined to report touch-based sensory experiences when watching pain and itch (but show similar levels of contagious itch and similar levels of non-localized pain). We conclude from these initial observations that the mechanisms that support phenomena such as contagious itching, wincing/nausea when seeing someone in pain, and (most probably) contagious yawning are not the same mechanisms that drive mirror-touch synesthesia. We suggest that MTS involves shared self-other body representations (in which different parts of the body are delineated), whereas the other phenomena involve shared motor programs (for yawning), or shared affect/feeling (for itch and affective aspects of pain) that is either independent of the body or taps a more general body map. Mirror touch/pain in amputees also shows the key characteristic of being localized and sensory-like (rather than affective) even though the location itself is fixed to the phantom/stump rather than reflecting what is seen.

De Vignemont and Jacob (2012, p. 304) also make a distinction between different kinds of information that support vicarious perception: "vicarious sensory pain is self-centered and constitutes what we call an experience of contagious pain, whereas vicarious affective pain is other-directed and constitutes what we call an experience of empathetic pain." In terms of underlying representations, they assume that vicarious sensory pain is supported by representations that are capable of distinguishing between and localizing on different parts of the body, whereas vicarious affective pain may be supported by a non-localized or global representation of the body. To extend this to our account, we would say that MTS have differences specifically in the sensory component.

CONCLUSIONS

MTS is linked to differences in the functioning of a mirror system for touch and pain. However, we suggest that this is driven by neurocognitive differences that lie outside of the somatosensory system that are involved in bodily awareness (ownership and, possibly, agency) and/or in the control of self-other representations (e.g., bodily perspective-taking). Phenomenologically it resembles other forms of synesthesia, but also a range of other experiences not normally linked to synesthesia (contagious itch and yawn, certain types of empathy for pain). We suggest that MTS can be distinguished from the latter by its localized, sensory-based characteristics.

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REFERENCES

Arzy, S., Thut, G., Mohr, C., Michel, C. M., & Blanke, O. (2006). Neural basis of embodiment: Distinct contributions of temporoparietal junction and extrastriate body area. *Journal of Neuroscience*, *26*, 8074–8081. doi:10.1523/JNEUROSCI.0745-06.2006

Asher, J. E., Lamb, J. A., Brocklebank, D., Cazier, J. B., Maestrini, E., Addis, L., & Monaco, A. P. (2009). A whole-genome scan and fine-mapping linkage study of auditory-visual synesthesia reveals evidence of linkage to chromosomes 2q24, 5q33, 6p12, and 12p12. *American Journal of Human Genetics*, *84*(2), 279–285. doi:10.1016/j.ajhg.2009.01.012

Auksztulewicz, R., & Blankenburg, F. (2013). Subjective rating of weak tactile stimuli is parametrically encoded in event-related potentials. *Journal of Neuroscience*, *33* (29), 11878–11887. doi:10.1523/jneurosci.4243-12.2013

Auksztulewicz, R., Spitzer, B., & Blankenburg, F. (2012). Recurrent neural processing and somatosensory awareness. *Journal of Neuroscience*, *32*(3), 799–805. doi:10.1523/jneurosci.3974-11.2012

Avenanti, A., Sirigu, A., & Aglioti, S. M. (2010). Racial bias reduces empathic sensorimotor resonance with other-race pain. *Current Biology*, *20*(11), 1018–1022. doi:10.1016/j.cub.2010.03.071

Azevedo, R. T., Macaluso, E., Avenanti, A., Santangelo, V., Cazzato, V., & Aglioti, S. M. (2013). Their pain is not our pain: Brain and autonomic correlates of empathic resonance with the pain of same and different race individuals. *Human Brain Mapping*, *34*(12), 3168–3181. doi:10.1002/hbm.v34.12

Banissy, M. J. (2013). Synaesthesia, mirror neurons and mirror-touch. In E., Hubbard, & J., Simner (Eds.), *The oxford handbook of synaesthesia* (pp. 584–605). Oxford: Oxford University Press.

Banissy, M. J., Garrido, L., Kusnir, F., Duchaine, B., Walsh, V., & Ward, J. (2011). Superior facial expression, but not identity recognition, in mirror-touch synesthesia. *Journal of Neuroscience*, *31*, 1820–1824. doi:10.1523/JNEUROSCI.5759-09.2011

Banissy, M. J., Kadosh, R. C., Maus, G. W., Walsh, V., & Ward, J. (2009a). Prevalence, characteristics and a neurocognitive model of mirror-touch synaesthesia. *Experimental Brain Research*, *198*(2–3), 261–272. doi:10.1007/s00221-009-1810-9

Banissy, M. J., Walsh, V., & Ward, J. (2009b). Enhanced sensory perception in synaesthesia. *Experimental Brain Research*, *196*(4), 565–571. doi:10.1007/s00221-009-1888-0

Banissy, M. J., & Ward, J. (2007). Mirror-touch synesthesia is linked with empathy. *Nature Neuroscience*, *10*, 815–816. doi:10.1038/nn1926

Banissy, M. J., & Ward, J. (2013). Mechanisms of Self-other representations and vicarious experiences of touch in mirror-touch synesthesia. *Frontiers in Human Neuroscience*, *7*. doi:10.3389/fnhum.2013.00112

Barnett, K. J., Finucane, C., Asher, J. E., Bargary, G., Corvin, A. P., Newell, F. N., & Mitchell, K. J. (2008). Familial patterns and the origins of individual differences in synaesthesia. *Cognition*, *106*, 871–893. doi:10.1016/j.cognition.2007.05.003

Baron-Cohen, S., & Harrison, J. E. (1997). *Synaesthesia: Classic and contemporary readings*. Oxford: Blackwell.

Beauchamp, M. S., & Ro, T. (2008). Neural substrates of sound-touch synesthesia after a thalamic lesion. *Journal of Neuroscience*, *28*, 13696–13702. doi:10.1523/JNEUROSCI.3872-08.2008

Bird, G., & Viding, E. (2014). The self to other model of empathy: Providing a new framework for understanding empathy impairments in psychopathy, autism, and alexithymia. *Neuroscience and Biobehavioral Review*, *47*, 520–532. doi:10.1016/j.neubiorev.2014.09.021

Blakemore, S.-J., Bristow, D., Bird, G., Frith, C., & Ward, J. (2005). Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain*, *128*, 1571–1583. doi:10.1093/brain/awh500

Bolognini, N., Miniussi, C., Gallo, S., & Vallar, G. (2013). Induction of mirror-touch synaesthesia by increasing somatosensory cortical excitability. *Current Biology*, *23* (10), R436–R437. doi:10.1016/j.cub.2013.03.036

Bolognini, N., Rossetti, A., Fusaro, M., Vallar, G., & Miniussi, C. (2014). Sharing social touch in the primary somatosensory cortex. *Current Biology*, *24* (13), 1513–1517. doi:10.1016/j.cub.2014.05.025

Brang, D., Williams, L. E., & Ramachandran, V. S. (2012). Grapheme-color synesthetes show enhanced crossmodal processing between auditory and visual modalities. *Cortex*, *48*(5), 630–637. doi:10.1016/j.cortex.2011.06.008

Case, L. K., Gosavi, R., & Ramachandran, V. S. (2013). Heightened motor and sensory (Mirror-touch) referral induced by nerve block or topical anesthetic. *Neuropsychologia*, *51*(10), 1823–1828. doi:10.1016/j.neuropsychologia.2013.06.010

Chun, C. A., & Hupé, J.-M. (2013). Mirror-touch and ticker tape experiences in synesthesia. *Frontiers in Psychology*, *4*. doi:10.3389/fpsyg.2013.00776

Cioffi, M. C., Moore, J. W., & Banissy, M. J. (2014). What can mirror-touch synaesthesia tell us about the sense of agency? *Frontiers in Human Neuroscience*, *8*. doi:10.3389/fnhum.2014.00256

Cook, J. L. (2014). Task-relevance dependent gradients in medial prefrontal and temporoparietal cortices suggest solutions to paradoxes concerning self/other control. *Neuroscience and Biobehavioral Reviews*, *42*, 298–302. doi:10.1016/j.neubiorev.2014.02.007

Daprati, E., Franck, N., Georgieff, N., Proust, J., Pacherie, E., Dalery, J., & Jeannerod, M. (1997). Looking for the agent: An investigation into consciousness of action and self-consciousness in schizophrenic patients. *Cognition*, *65*(1), 71–86. doi:10.1016/s0010-0277(97)00039-5

Davies, A. M. A., & White, R. C. (2013). A sensational illusion: Vision-touch synaesthesia and the rubber hand paradigm. *Cortex*, *49*(3), 806–818. doi:10.1016/j.cortex.2012.01.007

De Vignemont, F. (in press). Mirror touch synaesthesia: Intersubjective or intermodal fusion? In Deroy, O. (Ed.), *Sensory blending: New essays on synaesthesia*. Oxford: OUP.

De Vignemont, F., & Jacob, P. (2012). What is it like to feel another's pain? *Philosophy of Science*, *79*(2), 295–316. doi:10.1086/664742

Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends in Cognitive Sciences*, *10*(5), 204–211.

Derbyshire, S. W. G., Osborn, J., & Brown, S. (2013). Feeling the pain of others is associated with self-other confusion and prior pain experience. *Frontiers in Human Neuroscience*, *7*. doi:10.3389/fnhum.2013.00470

Ebisch, S. J. H., Perrucci, M. G., Ferretti, A., Del Gratta, C., Romani, G. L., & Gallese, V. (2008). The sense of touch: Embodied simulation in a visuotactile mirroring mechanisms for observed animate or inanimate touch. *Journal of Cognitive Neuroscience*, *20*, 1611–1623. doi:10.1162/jocn.2008.20111

Fitzgibbon, B. M., Enticott, P. G., Giummarra, M. J., Thomson, R. H., Georgiou-Karistianis, N., & Bradshaw, J. L. (2012). Atypical electrphysiological activity during pain observation in amputees who experience synaesthetic pain. *Social, Cognitive and Affective Neuroscience*, *7*(3), 357–368. doi:10.1093/scan/nsr016

Fitzgibbon, B. M., Enticott, P. G., Rich, A. N., Giummarra, M. J., Georgiou-Karistianis, N., & Bradshaw, J. L. (2012). Mirror-sensory synaesthesia: Exploring 'shared' sensory experiences as synaesthesia. *Neuroscience and Biobehavioral Reviews*, *36*(1), 645–657. doi:10.1016/j.neubiorev.2011.09.006

Fitzgibbon, B. M., Enticott, P. G., Rich, A. N., Giummarra, M. J., Georgiou-Karistianis, N., Tsao, J. W., & Bradshaw, J. L. (2010). High incidence of 'synaesthesia for pain' in amputees. *Neuropsychologia*, *48*(12), 3675–3678. doi:10.1016/j.neuropsychologia.2010.07.029

Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society of London B*, *358*, 459–472. doi:10.1098/rstb.2002.1218

Gallace, A., & Spence, C. (2008). The cognitive and neural correlates of "tactile consciousness": A multisensory perspective. *Consciousness and Cognition*, *17*(1), 370–407. doi:10.1016/j.concog.2007.01.005

Giummarra, M. J., Fitzgibbon, B. M., Georgiou-Karistianis, N., Nicholls, M. E. R., Gibson, S. J., & Bradshaw, J. L. (2010). Ouch! My phantom leg jumps/hurts when you stab "my" virtual hand. *Perception*, *39*(10), 1396–1407. doi:10.1068/p6582

Godinho, F., Faillenot, I., Perchet, C., Frot, M., Magnin, M., & Garcia-Larrea, L. (2012). How the pain of others enhances our pain: Searching the cerebral correlates of 'compassional hyperalgesia'. *European Journal of Pain*, *16*(5), 748–759. doi:10.1002/j.1532-2149.2011.00039.x

Goller, A. I., Richards, K., Novak, S., & Ward, J. (2013). Mirror-touch synaesthesia in the phantom limbs of amputees. *Cortex*, *49*(1), 243–251. doi:10.1016/j.cortex.2011.05.002

Gu, X., Gao, Z., Wang, X., Liu, X., Knight, R. T., Hof, P. R., & Fan, J. (2012). Anterior insular cortex is necessary for empathetic pain perception. *Brain*, *135*, 2726–2735. doi:10.1093/brain/aws199

Hogeveen, J., Obhi, S. S., Banissy, M. J., Santiesteban, I., Press, C., Catmur, C., & Bird, G. (in press). Task-Dependent and Distinct Roles of the Temporoparietal Junction and Inferior Frontal Cortex in the Control of Imitation. *Social Cognitive and Affective Neuroscience*.

Holle, H., Banissy, M., Wright, T. D., Bowling, N., & Ward, J. (2011). "That's not a real body": Identifying stimulus qualities that modulate synaesthetic experiences of touch. *Consciousness and Cognition*, *20*, 720–726. doi:10.1016/j.concog.2010.12.002

Holle, H., Banissy, M. J., & Ward, J. (2013). Functional and structural brain differences associated with mirror-touch synaesthesia. *NeuroImage*, *83*, 1041–1050. doi:10.1016/j.neuroimage.2013.07.073

Holle, H., Warne, K., Seth, A. K., Critchley, H. D., & Ward, J. (2012). The neural basis of contagious itch and why some people are more prone to it. *Proceedings of the National Academy of Science, USA*, *109*, 19816–19821. doi:10.1073/pnas.1216160109

Hutchison, W. D., Davis, K. D., Lozano, A. M., Tasker, R. R., & Dostrovsky, J. O. (1999). Pain-related neurons in the human cingulate cortex. *Nature Neuroscience*, *2*(5), 403–405. doi:10.1038/8065

Ikoma, A., Steinhoff, M., Ständer, S., Yosipovitch, G., & Schmelz, M. (2006). The neurobiology of itch. *Nature Reviews Neuroscience*, *7*(7), 535–547. doi:10.1038/nrn1950

Ishida, H., Nakajima, K., Inase, M., & Murata, A. (2010). Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. *Journal of Cognitive Neuroscience*, *22*(1), 83–96. doi:10.1162/jocn.2009.21185

Keysers, C., Kaas, J. H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience*, *11*, 417–428. doi:10.1038/nrn2833

Keysers, C., Wicker, B., Gazzola, V., Anton, J. L., Fogassi, L., & Gallese, V. (2004). A touching sight: SII/PV activation during the observation and experience of touch. *Neuron*, *42*, 335–346. doi:10.1016/S0896-6273(04)00156-4

Krueger, F., Barbey, A. K., & Grafman, J. (2009). The medial prefrontal cortex mediates social event knowledge. *Trends in Cognitive Sciences*, *13*(3), 103–109. doi:10.1016/j.tics.2008.12.005

Lamm, C., Decety, J., & Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *NeuroImage*, *54*, 2492–2502. doi:10.1016/j.neuroimage.2010.10.014

Lee, S. J., Song, H. J., Decety, J., Seo, J., Kim, S. H., Kim, S. H. … Chang, Y. (2013). Do patients with fibromyalgia show abnormal neural responses to the observation of pain in others? *Neuroscience Research*, *75*(4), 305–315. doi:10.1016/j.neures.2013.01.013

Lloyd, D. M., Hall, E., Hall, S., & McGlone, F. P. (2013). Can itch-related visual stimuli alone provoke a scratch response in healthy individuals? *British Journal of Dermatology*, *168*(1), 106–111. doi:10.1111/bjd.2012.168.issue-1

Mahayana, I. T., Banissy, M. J., Chen, C.-Y., Walsh, V., Juan, C.-H., & Muggleton, N. G. (2014). Motor empathy is a consequence of misattribution of sensory information in observers. *Frontiers in Human Neuroscience*, *8*. doi:10.3389/fnhum.2014.00047

Maister, L., Banissy, M. J., & Tsakiris, M. (2013). Mirror-touch synaesthesia changes representations of self-identity. *Neuropsychologia*, *51*(5), 802–808. doi:10.1016/j.neuropsychologia.2013.01.020

Martin, D. (2015, May 4). *Mirror touch, empathy, spectatorship and synaesthesia*. Retrieved from http://mirror-touch.co.uk/

Martin, L. J., Tuttle, A. H., & Mogil, J. S. (2014). The interaction between pain and social behavior in humans and rodents. *Current Topics in Behavioral Neurosciences*, *20*, 233–250. doi:10.1007/7854_2014_287

Moutoussis, K., & Zeki, S. (2002). The relationship between cortical activation and perception investigated with invisible stimuli. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(14), 9527–9532. doi:10.1073/pnas.142305699

Nicolle, A., Klein-Fluegge, M. C., Hunt, L. T., Vlaev, I., Dolan, R. J., & Behrens, T. E. J. (2012). An agent independent axis for executed and modeled choice in medial prefrontal cortex. *Neuron*, *75*(6), 1114–1121. doi:10.1016/j.neuron.2012.07.023

Osborn, J., & Derbyshire, S. W. G. (2010). Pain sensation evoked by observing injury in others. *Pain*, *148*, 268–274. doi:10.1016/j.pain.2009.11.007

Pihko, E., Nangini, C., Jousmaki, V., & Hari, R. (2011). Observing touch activates human primary somatosensory cortex. *European Journal of Neuroscience*, *31*(10), 1836–1843. doi:10.1111/j.1460-9568.2010.07192.x

Platek, S. M., Critton, S. R., Myers, T. E., & Gallup, G. G. (2003). Contagious yawning: The role of self-awareness and mental state attribution. *Cognitive Brain Research*, *17*(2), 223–227. doi:10.1016/s0926-6410(03)00109-5

Provine, R. R. (1996). Contagious yawning and laughter: Significance for sensory feature detection, motor pattern generation, imitation, and the evolution of social behavior. In Heyes, C. M., & Galef, B. G. (Eds.),

Social learning in animals: The roots of culture. San Diego: Academic Press.
Ramachandran, V. S., & Brang, D. (2009). Sensations evoked in patients with amputation from watching an individual whose corresponding intact limb is being touched. *Archives of Neurology*, *66*(10), 1281–1284. doi:10.1001/archneurol.2009.206
Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192. doi:10.1146/annurev.neuro.27.070203.144230
Rothen, N., & Meier, B. (2013). Why vicarious experience is not an instance of synesthesia. *Frontiers in Human Neuroscience*, *7*. doi:10.3389/fnhum.2013.00128
Rouw, R., Scholte, H. S., & Colizoli, O. (2011). Brain areas involved in synaesthesia: A review. *Journal of Neuropsychology*, *5*, 214–242. doi:10.1111/jnp.2011.5.issue-2
Ruby, P., & Decety, J. (2004). How would you feel versus how do you think she would feel? A neuroimaging study of perspective-taking with social emotions. *Journal of Cognitive Neuroscience*, *16*(6), 988–999. doi:10.1162/0898929041502661
Sagiv, N., & Ward, J. (2006). Cross-modal interactions: Lessons from synesthesia. *Progress in Brain Research*, *155*, 259–271.
Samson, D., Apperly, I. A., Braithwaite, J. J., Andrews, B. J., & Bodley Scott, S. E. (2010). Seeing it their way: Evidence for rapid and involuntary computation of what other people see. *Journal of Experimental Psychology: Human Perception and Performance*, *36*(5), 1255–1266.
Santiesteban, I., Banissy, M. J., Catmur, C., & Bird, G. (2012). Enhancing social ability by stimulating right temporoparietal junction. *Current Biology*, *22*(23), 2274–2277. doi:10.1016/j.cub.2012.10.018
Santiesteban, I., Catmur, C., Hopkins, S. C., Bird, G., & Heyes, C. (2014). Avatars and arrows: Implicit mentalizing or domain-general processing? *Journal of Experimental Psychology: Human Perception and Performance*, *40*(3), 929–937. doi:10.1037/a0035175
Schmidt, T. T., Ostwald, D., & Blankenburg, F. (2014). Imaging tactile imagery: Changes in brain connectivity support perceptual grounding of mental images in primary sensory cortices. *NeuroImage*, *98*, 216–224. doi:10.1016/j.neuroimage2014.05.014
Serino, A., Giovagnoli, G., & Ladavas, E. (2009). I feel what you feel if you are similar to me. *PLoS One*, *4*(3), 7. doi:10.1371/journal.pone.0004930
Serino, A., Pizzoferrato, F., & Làdavas, E. (2008). Viewing a face (especially one's own face) being touched enhances tactile perception on the face. *Psychological Science*, *19*, 434–438. doi:10.1111/j.1467-9280.2008.02105.x
Simner, J. (2012). Defining synaesthesia. *British Journal of Psychology*, *103*, 1–15. doi:10.1348/000712610X528305
Sinke, C., Neufeld, J., Zedler, M., Emrich, H. M., Bleich, S., Münte, T. F., & Szycik, G. R. (2014). Reduced audiovisual integration in synesthesia evidence from bimodal speech perception. *Journal of Neuropsychology*, *8*(1), 94–106. doi:10.1111/jnp.12006
Sowden, S., & Shah, P. (2014). Self-other control: A candidate mechanism for social cognitive function. *Frontiers in Human Neuroscience*, *8*. doi:10.3389/fnhum.2014.00789
Spence, C. (2011). Crossmodal correspondences: A tutorial review. *Attention Perception & Psychophysics*, *73*(4), 971–995. doi:10.3758/s13414-010-0073-7
Spengler, S., Von Cramon, D. Y., & Brass, M. (2009). Control of shared representations relies on key processes involved in mental state attribution. *Human Brain Mapping*, *30*(11), 3704–3718. doi:10.1002/hbm.20800
Terhune, D. B., Tai, S., Cowey, A., Popescu, T., & Kadosh, R. C. (2011). Enhanced cortical excitability in grapheme-color synesthesia and its modulation. *Current Biology*, *21*(23), 2006–2009. doi:10.1016/j.cub.2011.10.032
Tsakiris, M. (2008). Looking for myself: Current multisensory input alters self-face recognition. *PLoS One*, *3*, 12. doi:10.1371/journal.pone.0004040
Tsakiris, M., Carpenter, L., James, D., & Fotopoulou, A. (2010). Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Experimental Brain Research*, *204*(3), 343–352. doi:10.1007/s00221-009-2039-3
Tsakiris, M., & Haggard, P. (2005). The Rubber Hand Illusion revisited: Visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 80–91.
Tsakiris, M., Prabhu, G., & Haggard, P. (2006). Having a body versus moving your body: How agency structures body-ownership. *Consciousness and Cognition*, *15*(2), 423–432. doi:10.1016/j.concog.2005.09.004
Vandenbroucke, S., Crombez, G., Van Ryckeghem, D. M. L., Brass, M., Van Damme, S., & Goubert, L. (2013). Vicarious pain while observing another in pain: An experimental approach. *Frontiers in Human Neuroscience*, *7*, 265. doi:10.3389/fnhum.2013.00265
Wang, X., Gu, X., Fan, J., Wang, S., Zhao, F., Hof, P. R., & Gao, Z. (2014). Recovery of empathetic function following resection of insular gliomas. *Journal of Neuro-Oncology*, *117*(2), 269–277. doi:10.1007/s11060-014-1380-y
Ward, J. (2013). Synesthesia. *Annual Review of Psychology*, *64*, 49–75. doi:10.1146/annurev-psych-113011-143840
Ward, J., Burckhardt, V., & Holle, H. (2013). Contagious scratching: Shared feelings but not shared body locations. *Frontiers in Human Neuroscience*, *7*. doi:10.3389/fnhum.2013.00122
White, R. C., & Davies, A. M. A. (2012). Specular vision-touch synaesthesia: Two reference frames. *Perception*, *41*(7), 871–874. doi:10.1068/p7182
Woolf, C. J. (2011). Central sensitization: Implications for the diagnosis and treatment of pain. *Pain*, *152*, S2–S15. doi:10.1016/j.pain.2010.09.030

Commentaries

Are mirror-sensations really synesthetic?

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Abstract: Mirror-sensations, including touch and pain, are often referred to as synesthetic. The term can be challenged, however, because mirror-sensations lack the incongruency and saliency of synesthesia, may involve problems of perspective rather than entangled sensations, and may be easier to generate with suggestion. If mirror-sensations are truly sensations then they might be expected to act like the true sensation and mirror-pain, for example, might inhibit pain at a distance or itch in the same location. These predictions are highly testable.

Ward and Banissy have written a provocative review of mirror-touch synesthesia (MTS) that asks important and pertinent questions about MTS, including whether the term *synesthesia* is appropriate. One reason for thinking the term is not appropriate is that synesthesia involves a sensory experience clearly removed from what might be expected given the sensory input (Rothen & Meier, 2013). Synesthesia, for example, involves tasting words or hearing colors. MTS, in contrast, involves feeling an observed touch, which is perhaps more explicable than tasting or hearing an observed touch. Feeling an observed touch might involve a direct mirroring of the observed somatosensory event, whereas tasting a word is unlikely to involve mirroring. Thus, MTS might be a threshold phenomenon, where sensory neural mirroring from observation sometimes tips over into sensory experience.

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A second possible reason to reject the term “synesthesia” is that it can introduce too much precision and saliency to the MTS experience. People with synesthesia report incongruent and striking sensory experiences. The taste of words is clear and salient. The participants we have studied, who report what Ward and Banissy call mirror-pain, certainly report something that is akin to pain experience when observing others in pain or observing others being injured (Derbyshire, Osborn, & Brown, 2013; Osborn & Derbyshire, 2010), but the clarity and salience of a typical pain is missing. None of our participants, for example, have ever screamed or fallen to the floor holding a limb. They report something somatic, and neuroimaging data demonstrates something beyond just an emotional reaction, but the missing elements make it more ‘pain-lite’ than the real thing.

A third possible reason to reject the term “synesthesia” is that the mechanism of MTS and mirror-pain involve areas of the brain associated with social cognition. Crudely put, synesthesia involves a direct neural entanglement of primary sensory regions whereas MTS and mirror-pain may involve an entanglement of first-person perspectives. Those reporting mirror-pain might readily place themselves into the position of others such that their own feelings become entangled with the feelings of a person they observe. For most of us, that entanglement is sufficient that we report sharing some misery when the person observed is injured but not so sufficient that we report sharing pain (Singer et al., 2004). For those who report mirror-pain, in contrast, their entanglement is more complete and they feel something that approaches pain (Derbyshire et al., 2013). Ward and Banissy suggest that for those experiencing MTS, their entanglement might be such that the person shares a tactile sensation.

There is some work to be done to decide if a threshold or entanglement understanding is more likely, and to decide to what extent MTS and mirror-pain might be similar. Ward and Banissy note that mirror-pain, mirror-itch, and mirror-yawns are much more common than MTS. Consequently, the mechanisms might be wholly different. Images of bugs on the skin induces itch, better than watching someone scratch (Lloyd, Hall, Hall, & McGlone, 2013), seeing others yawn induces yawns (Platek, Critton, Myers, & Gallup, 2003), and verbal suggestion that a lamp or probe is becoming hot induces sensations of heat and pain (Derbyshire, Whalley, Stenger, & Oakley, 2004; Whalley & Oakley, 2003). These findings imply a role of suggestion or anxiety that may not play a role in MTS and may take mirror-pain, mirror-itch, and mirror-yawns further from synesthesia.

Finally, if mirror-pain, mirror-itch, and MTS are explicitly tactile sensations, similar to the synesthete tasting words, then some readily testable hypotheses can be generated. Mirror-pain, for example, might inhibit pain at a distance (Le Bars, Dickenson, & Besson, 1979) and might inhibit itch in the same location (Shim & Oh, 2008). MTS might also inhibit pain in the same location due to the soothing effect of rubbing. That is, if mirror-pain, mirror-itch, and MTS really are pain, itch, and touch, then they should do the things that real pain, itch, and touch do.

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REFERENCES

Derbyshire, S. W. G., Osborn, J., & Brown, S. (2013). Feeling the pain of others is associated with self-other confusion and prior pain experience. *Frontiers in Human Neuroscience*, *7*. doi:10.3389/fnhum.2013.00470.

Derbyshire, S. W. G., Whalley, M. G., Stenger, V. A., & Oakley, D. A. (2004). Cerebral activation during hypnotically induced and imagined pain. *Neuroimage*, *23*, 392–401. doi:10.1016/j.neuroimage.2004.04.033

Le Bars, D., Dickenson, A. H., & Besson, J. M. (1979). Diffuse noxious inhibitory controls (DNIC). I. Effects on dorsal horn convergent neurons in the rat. *Pain*, *6*, 283–304. doi:10.1016/0304-3959(79)90049-6

Lloyd, D. M., Hall, E., Hall, S., & McGlone, F. P. (2013). Can itch-related visual stimuli alone provoke a scratch response in healthy individuals? *British Journal of Dermatology*, *168*(1), 106–111. doi:10.1111/bjd.2012.168.issue-1

Osborn, J., & Derbyshire, S. W. G. (2010). Pain sensation evoked by observing injury in others. *Pain*, *148*, 268–274. doi:10.1016/j.pain.2009.11.007

Platek, S. M., Critton, S. R., Myers, T. E., & Gallup, G. G. (2003). Contagious yawning: The role of self-awareness and mental state attribution. *Cognitive Brain Research*, *17*(2), 223–227. doi:10.1016/s0926-6410(03)00109-5

Rothen, N., & Meier, B. (2013). Why vicarious experience is not an instance of synesthesia. *Frontiers in Human Neuroscience*, *7*. doi:10.3389/fnhum.2013.00128

Shim, W. S., & Oh, U. (2008). Histamine-induced itch and its relationship with pain. *Molecular Pain*, *4*, 29. doi:10.1186/1744-8069-4-29

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science*, *303*, 1157–1162. doi:10.1126/science.1093535

Whalley, M. G., & Oakley, D. A. (2003). Psychogenic pain: A study using multidimensional scaling. *Contemporary Hypnosis*, *20*, 16–24. doi:10.1002/(ISSN)1557-0711

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Into the looking glass: Broadening models to explain the spectrum of sensory and affective vicarious experiences

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Abstract: Ward and Bannisy's proposed conceptual framework—Threshold Theory and Self-Other Theory—for mirror touch synesthesia are welcomed as an explanation of mechanisms giving rise to innocuous vicarious phenomena. Herein we propose that these vicarious, or synesthetic, experiences should be considered along a spectrum of experiences, from innocuous through to noxious or threatening sensations. In particular, we would like to see these theories considered within a broader framework to explain the multitude of vicarious experiences that seem to share fundamental neurophysiological and trait characteristics.

Keywords: Vicarious; pain; touch; mechanism.

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The experience of vicarious sensations and emotions has captured our curiosity for centuries, particularly in the context of pain (Bourke, 2014); however, we have only recently made significant advances in understanding common patterns in neurophysiological and social mechanisms driving these responses. In their Discussion Paper in this issue, Ward and Banissy propose the Threshold Theory and Self-Other theory to explain mirror touch synesthesia (MTS). We support these theories, and welcome them as an explanation of some of the mechanisms that elicit vicarious reactivity. However, we would like to see these models take shape under a broader theoretical framework of mechanisms driving the multitude of vicarious sensory experiences (see Figure 1), from innocuous and pleasant sensations to noxious and threatening sensations, and the context in which they arise. This is particularly warranted given the considerable high co-occurrence of different types of vicarious states (e.g., taste, touch, pain), and the similarities in neural circuitry across vicarious phenomena.

Multiple mechanisms in eliciting vicarious sensory and emotional states have been implicated, especially in vicarious pain, depending on the trait characteristics of the vicarious responder. In some of our latest work, for instance, approximately a quarter of vicarious pain responders have been found to be "anxious responders," having high trait anxiety, anxiety sensitivity, and personal distress toward others misfortune (Nazarewicz, Verdejo-Garcia, & Giummarra, in press). These persons show heightened anxious reactivity in laboratory experiments, with evidence of poor autonomic regulation under stress, particularly in the parasympathetic nervous system, which is responsible for inhibiting arousal (Nazarewicz, Verdejo-Garcia, & Giummarra, in press). In addition to anxiety, but not necessarily separate, we have also shown symptoms of post-traumatic stress disorder may be related to vicarious reactivity in groups such as amputees (Giummarra, Fitzgibbon, et al., in press). In a general community cohort, however, prior salient experiences of the observed pain seem to play a role (Derbyshire, Osborn, & Brown, 2013). These findings could reflect both bottom-up (e.g., central sensitization) and top-down (e.g., attentional vigilance, memory) mechanisms, which are implicated in cross-modal synesthesia (Chong & Mattingley, 2009). Moreover, crossing the threshold may elicit subjective vicarious states by reactivating higher-order bioregulatory and cognitive states linked to the observed situation as per the "as if" mechanisms described in the somatic marker model (Damasio, 1994).

Mechanisms driving non-anxious vicarious states, however, are not so clear. We suggest that they may reflect heightened sensorimotor resonance (as per the *Threshold Theory*), shared representations (Preston & de Waal, 2002), and/or diminished inhibition of the experiences of others (as per *Self-Other Theory*). The end result, regardless of underlying mechanism, must nonetheless arise through reactivation of prior

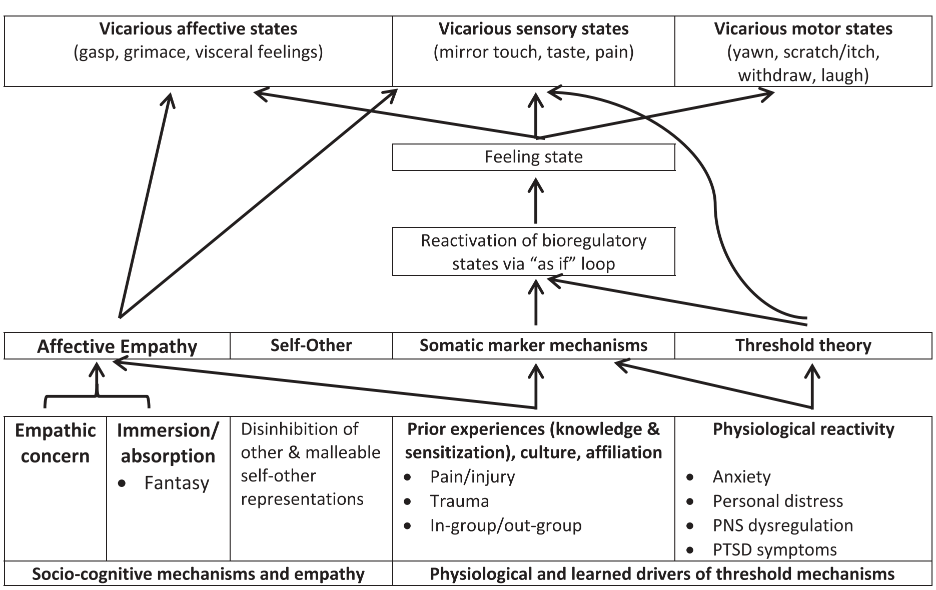

Figure 1. Schematic of the hypothesized and supported mechanisms driving different vicarious responses (affective, sensory, motor), as an extension of Ward & Banissy's (2015) model. *Note*: PNS = parasympathetic nervous system.

or innately represented states to qualify as a "vicarious" state.

Future research should continue to examine not only the existence of "threshold" mechanisms, but what it is that drives these mechanisms across vicarious states—i.e., sensory, motor, and affective—particularly focusing on whether these states are a reflection of intrinsic cognitive (e.g., attention, memory), affective and trait characteristics, or whether they're fundamentally driven by socio-cognitive processes of empathy and self-other perception. Or more likely, a little bit of both.

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REFERENCES

Bourke, J. (2014). *The story of pain*. New York, NY: Oxford University Press.

Chong, T. T., & Mattingley, J. B. (2009). *Automatic and controlled processing within the mirror neuron system Mirror neuron systems: The role of mirroring processes in social cognition* (pp. 213–233). Totowa, NJ: Humana Press.

Damasio, A. R. (1994). *Descartes' error: Emotion, reason and the human brain*. New York, NY: Grosset / Putnam.

Derbyshire, S. W. G., Osborn, J., & Brown, S. (2013). Feeling the pain of others is associated with self-other confusion and prior pain experience. *Frontiers in Human Neuroscience*, *7*, 1–8. doi:10.3389/fnhum.2013.00470

Giummarra, M. J., Fitzgibbon, B. M., Tsao, J. W., Gibson, S., Rich, A. N., Georgiou-Karistianis, N., … Enticott, P. G. (in press). Symptoms of post-traumatic stress disorder associated with painful and non-painful vicarious reactivity following amputation. *Journal of Traumatic Stress*.

Nazarewicz, J. A., Verdejo-Garcia, A., & Giummarra, M. J. (in press). Sympathetic pain? A role of poor parasympathetic nervous system engagement in vicarious pain states. *Psychophysiology*.

Preston, S. D., & de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*, *25*(01), 1–20. doi:10.1017/S0140525X02000018

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Causal mechanisms of mirror-touch synesthesia: Clues from neuropsychology

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Abstract: Ward and Banissy offer a critical discussion of Mirror-Touch Synesthesia (MTS), with reference to Threshold and Self-Other theories. The authors argue that developmental MTS is linked to differences in the functioning of a mirror system for touch (and pain), which are driven by neurocognitive alterations that lie outside of the somatosensory system and concern bodily awareness and/or the control of self-other representations. This commentary briefly presents some neuropsychological evidence in line with Ward and Banissy's argument, questioning the potential similarities between MTS and some post-stroke disorders of body representation.

The insightful Discussion Paper of Ward and Banissy considers strengths and limitations of two prominent accounts of developmental[1] MTS, Threshold Theory and Self-Other Theory. The authors advise that these two theories are not mutually exclusive: Disturbances in the ability to distinguish the self from others or in the control of body-based self-other representations put forward by the Self-Other Theory, may act as a gating process for the hyper-activity of the mirroring process for touch, the main cause of MTS for the Threshold Theory. This proposal is reminiscent of the Predictive Coding framework, which emphasizes the interaction between self-specific and shared body systems in MTS and emphasizing their influences on the somatosensory state in MTS (Ishida, Suzuki, & Grandi, 2015). So far, the causal association between dysfunctional self-other processing and over-activation of the mirror system for touch (or increased top-down influences from a shared body system) in MTS still needs empirical support.

The line of reasoning of Ward and Banissy brought to mind a set of thoughts about the neuropsychological literature. Halligan and co-workers (1997) described two stroke patients with somatosensory loss who could reliably report

[1]Acquired MST following limb amputation likely involves different exarcebating mechanisms, with a main role of disturbances in bodily feedback due to plastic cortical reorganization and/or central sensitization of the pain system (see Banissy and Ward in this issue).

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feelings of touch when viewing their affected limb being touched. Nevertheless, lesions affecting the post-central gyrus may impair both sense of touch and mirroring touch (Bolognini et al., 2011). This evidence suggests that the mirroring mechanism for touch, if spared by brain injury, can boost sub-threshold tactile stimulation into conscious awareness (Bolognini, Convento, Rossetti, & Mearbet, 2013). Yet, these crossmodal effects cannot be quoted as pure MTS, because those patients were not consciously aware that they experienced feeling with seeing. Consequently, some other mechanism beyond tactile mirroring should be recruited for inducing MTS, as Self-Other Theory would predict. Clues in this regard come from somatoparaphrenia.

Somatoparaphrenia is a body delusion usually brought about by right-hemisphere lesions, which manifests as a defective sense of ownership of contralesional (left) body parts. Although somatopaphrenia is frequently accompanied by tactile impairments in the disowned body part, seeing touch may affect both the body delusion and somatosensation. Indeed, in some cases, the disownership belief emerges only when the body part is visible to the patient or it is explored by touch (Vallar & Ronchi, 2009). In a case of somatoparaphrenia, tactile imperception in the left (disowned) hand improved when the patient was instructed to report touches delivered to her niece's hand, rather than to her own hand (Bottini, Bisiach, Sterzi, & Vallar, 2002). Patients with somatoparaphrenia also experience a reliable Rubber Hand illusion (i.e., ownership of the rubber hand, projection of touch from the rubber hand onto oneself), and synchronous touches applied to their visible (disowned) left hand and to their right invisible hand can induce an immediate self-attribution of the left hand, notwithstanding the presence of left-sided hemianesthesia (Bolognini, Ronchi, Casati, Fortis, & Vallar, 2014). Garbarini and collegueas (2014) described another intriguing neuropsychological condition in which right-brain-damaged patients misattribute another person's arm to themselves. The body part of another person can be so deeply embedded in the patient's own somatosensory representation to cause a feeling of pain when painful stimuli are applied to the other's (embodied) hand, an effect functionally akin to mirror pain synesthesia.

As for MTS induced by observing touch to objects, ownership of objects may also occur in somatoparaphenia (Aglioti, Smania, Manfredi, & Berlucchi, 1996). The closer association between somatoparaphrenia and extrapersonal neglect is further suggestive of a blurred distinction between corporeal and extra-corporeal objects, supporting the notion of an *extended* body schema, which may include (at least some) objects (Vallar & Ronchi, 2009).

These examples point to a tight link between feeling of body ownership and sense of own and other's touch in somatoparaphenia, as also supposed for MTS. The dominant role of the right hemisphere (particularly, the right temporo-parietal junction) is noteworthy in both somatoparaphrenia and MTS (Holle, Banissy, & Ward, 2013; Vallar & Ronchi, 2009). In contrast, there is no definitive evidence for hemispheric asymmetries in mirroring touch (Bolognini, Miniussi, Gallo, & Vallar, 2013; Holle et al., 2013).

We can speculate that some post-stroke disorders of body representation, in particular somatoparaphenia, and MTS share similar proximal causes. In both cases, signals from higher-order representations (right-hemisphere based) concerned with bodily ownership and self-other discrimination might project down to somatosensory areas, thus creating a common network that is responsible for tactile awareness (Gallace & Spence, 2008), body ownership, and the ability to discriminate self-specific touch from others' touch (Ishida et al., 2015). The integration of Self-Other and Threshold theories into a unitary framework fits both development MTS and possible MTS-like phenomena acquirable following stroke.

REFERENCES

Aglioti, S., Smania, N., Manfredi, M., & Berlucchi, G. (1996). Disownership of left hand and objects related to it in a patient with right brain damage. *Neuroreport*, *8*, 293–296. doi:10.1097/00001756-199612200-00058

Bolognini, N., Convento, S., Rossetti, A., & Merabet, L. B. (2013). Multisensory processing after a brain damage: Clues on post-injury crossmodal plasticity from neuropsychology. *Neuroscience & Biobehavioral Reviews*, *37*(3), 269–278. doi:10.1016/j.neubiorev.2012.12.006

Bolognini, N., Miniussi, C., Gallo, S., & Vallar, G. (2013). Induction of mirror-touch synaesthesia by increasing somatosensory cortical excitability. *Current Biology*, *23* (10), R436–R437. doi:10.1016/j.cub.2013.03.036

Bolognini, N., Olgiati, E., Xaiz, A., Posteraro, L., Ferraro, F., & Maravita, A. (2011). Touch to see: Neuropsychological evidence of a sensory mirror system for touch. *Cerebral Cortex*, *22*(9), 2055–2064. doi:10.1093/cercor/bhr283

Bolognini, N., Ronchi, R., Casati, C., Fortis, P., & Vallar, G. (2014). My hand is back! Multisensory remission of somatoparaphrenic delusion. *Neurology: Clinical & Practice*, *4*(3), 216–225.

Bottini, G., Bisiach, E., Sterzi, R., & Vallar, G. (2002). Feeling touches in someone else's hand. *Neuroreport*, *13*(2), 249–252. doi:10.1097/00001756-200202110-00015

Gallace, A., & Spence, C. (2008). The cognitive and neural correlates of "tactile consciousness": A multisensory perspective. *Consciousness & Cognition*, *17*(1), 370–407. doi:10.1016/j.concog.2007.01.005

Garbarini, F., Fornia, L., Fossataro, C., Pia, L., Gindri, P., & Berti, A. (2014). Embodiment of others' hands elicits arousal responses similar to one's own hands. *Current Biology*, *24*(16), R738–R739. doi:10.1016/j.cub.2014.07.023

Halligan, P. W., Marshall, J. C., Hunt, M., & Wade, D. T. (1997). Somatosensory assessment: Can seeing produce feeling? *Journal of Neurology*, *244*(3), 199–203. doi:10.1007/s004150050073

Holle, H., Banissy, M. J., & Ward, J. (2013). Functional and structural brain differences associated with mirror-touch synaesthesia. *NeuroImage*, *83*, 1041–1050. doi:10.1016/j.neuroimage.2013.07.073

Ishida, H., Suzuki, K., & Grandi, L. C. (2015). Predictive coding accounts of shared representations in parieto-insular networks. *Neuropsychologia*, *70*, 442–454. doi:10.1016/j.neuropsychologia.2014.10.020

Vallar, G., & Ronchi, R. (2009). Somatoparaphrenia: A body delusion. A review of the neuropsychological literature. *Experimental Brain Research*, *192*(3), 533–551. doi:10.1007/s00221-008-1562-y

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"Atypical touch perception in MTS may derive from an abnormally plastic self-representation"

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Abstract: Mirror Touch Synesthetes (MTSs) feel touch while they observe others being touched. According to the authors, two complementary theoretical frameworks, the Threshold Theory and the Self-Other Theory, explain Mirror Touch Synesthesia (MTS). Based on the behavioral evidence that in MTSs the mere observation of touch is sufficient to elicit *self-other merging* (i.e., self-representation changes), a condition that in non-MTSs just elicits *self-other sharing* (i.e., mirroring activity without self-other blurring), and on the rTPJ anatomical alterations in MTS, we argue that MTS may derive from an abnormally plastic self-representation and atypical multisensory integrative mechanisms.

COMMENTARY

Ward and Banissy (2015) provided a comprehensive review of recent literature concerning Mirror Touch Synesthesia (MTS), i.e., the feeling of touch on one's own body while observing others being touched (Banissy & Ward, 2007).

The authors explain MTS according to two complementary theoretical frameworks: (1) Threshold Theory, which posits that a specific hyperactivation of the mirror system for touch leads MT synesthetes (MTSs) to the conscious feeling of being touched; (2) Self-Other Theory, which posits that MTS relies on alterations in the ability to distinguish the self from others. More specifically, Ward and Banissy suggest that self-other distinction might act as a gating mechanism for neural activity within the mirror system for touch, and an atypical self-other representation in synesthetes may amplify their vicarious responses to observed touch.

Interestingly, the authors' interpretation may explain the range of atypical behavioral (extending to domains other than touch perception, such as empathic and emotion recognition abilities) and neural phenomena occurring in MTS. However, based on the evidence that MTSs experience self-other merging in conditions where non-MTSs experience just self-other sharing, we argue that abnormally plastic self-representation may underlie MTS.

As a matter of fact, mere observation of touch elicits in non-MTSs *self-other sharing*, i.e., resonant activity in neural structures (e.g., somatosensory and insular cortices) involved in the first person experience of sensory and affective qualities of touch (Bufalari & Ionta, 2013; Keysers et al., 2010), which might sub-serve the understanding of others' sensory and emotional states (Preston & De Waal, 2002). Also, observation of a facial tactile stimulus spatio-temporally congruent with the felt touch (Interpersonal Multisensory Stimulation; IMS) induces in non-synesthetes *self-other merging*, i.e., alters the ability to discriminate self from other face (Sforza, Bufalari, Haggard, & Aglioti, 2010; Tsakiris, 2008). Multisensory temporal congruency makes it possible to build and maintain a coherent representation of one's own body (a person's mirror reflection, for example, moves/is touched at the exact time when he/she moves/feels touch; Rochat, 2003). During synchronous IMS the felt touch is surprisingly mirrored in compatible visual events on another's face presented in front. Since participants cannot move and thus prove themselves the observed face is not their own, the brain attempts to minimize surprise by including facial features of others into the self-face representation (Apps & Tsakiris, 2014; Tajadura-Jiménez, Grehl, & Tsakiris, 2012).

We suggest a basic distinction between *self-other sharing* and *self-other merging* mechanisms. More specifically, while the former may allow one to understand the "other" without the risk of self-other misattribution, the latter blurs the distinction between self and others and changes the representation of the self.

This fundamental difference may possibly explain why affective and sensorimotor sharing mechanisms are modulated by both positive and negative interpersonal perception of the observed other (for a review, see Bufalari & Ionta, 2013; Van Baaren, Janssen, Chartrand, & Dijksterhuis, 2009), whereas self-other merging heavily depends on positive (but not on negative) interpersonal perception of the synchronously stimulated other (Bufalari, Lenggenhager, Porciello, Serra-Holmes, & Aglioti, 2014; Sforza et al., 2010). We posit that the absence of the self-other merging with undesirable others may index a strategy for defending the self from the risk of losing individuality derived from merging processes.

Interestingly, in MTS mere observation of touch is sufficient to elicit self-representation changes similar to those induced in non-synesthetes by synchronous IMS (Maister, Banissy, & Tsakiris, 2013). At a neural level, in non-MTSs the right Temporo Parietal Junction (rTPJ) responds as a "function of the extent to which, self or other, perspectives are being processed" during facial IMS (Apps, Tajadura-Jiménez, Sereno, Blanke, & Tsakiris, 2015), possibly by detecting the conflict between tactile afferents and visual signals that, although temporally and spatially congruent with self-percept, instead originate from another person's face (Bufalari, Porciello, Sperduti, & Minio-Paluello, 2014). Intriguingly, rTPJ show less gray volume in MTS population relative to non-synesthetes (Holle, Banissy, & Ward, 2013), a difference that may cause defective self-other control mechanisms (i.e., inability to determine "who" is the subject of touch), and consequent atypical somatosensory activations to touch observation. Thus, developmental MTSs may experience much more frequently than non-MTSs self-other merging and consequent changes in self-representation in conditions that in non-MTSs simply elicit self-other sharing.

All in all, we suggest that atypical touch perception in MTS may derive from an abnormally plastic self-representation (as revealed by self-other merging phenomena). Such suggestion brings us to several testable hypotheses. For example, if MTSs show aberrant multisensory integrative mechanisms relevant for building self-representations, self-other merging in MTSs may not only be elicited by observing touch but also by different types of interpersonal visuo-sensorimotor congruency (without touch being involved). Moreover, it would be interesting to test the "abnormal" malleability of self-representation in MTS people by investigating whether they show the same self-defensive strategies that controls use to prevent self-other merging with undesirable others.

REFERENCES

Apps, M., Tajadura-Jiménez, A., Sereno, M., Blanke, O., & Tsakiris, M. (2015). Plasticity in unimodal and multimodal brain areas reflects multisensory changes in self-face identification. *Cerebral Cortex*, *25*(1), 46–55. doi:10.1093/cercor/bht199

Apps, M., & Tsakiris, M. (2014). The free-energy self: A predictive coding account of self-recognition. *Neuroscience & Biobehavioral Reviews*, *41*, 85–97. doi:10.1016/j.neubiorev.2013.01.029

Banissy, M. J., & Ward, J. (2007). Mirror-touch synesthesia is linked with empathy. *Nature Neuroscience*, *10*(7), 815–816. doi:10.1038/nn1926

Bufalari, I., & Ionta, S. (2013). The social and personality neuroscience of empathy for pain and touch. *Frontiers in Human Neuroscience*, *7*(393). doi:10.3389/fnhum.2013.00393

Bufalari, I., Lenggenhager, B., Porciello, G., Serra-Holmes, B., & Aglioti, S. M. (2014). Enfacing others but only if they are nice to you. *Frontiers in Behavioral Neuroscience*, *8*(102). doi:10.3389/fnbeh.2014.00102

Bufalari, I., Porciello, G., Sperduti, M., & Minio-Paluello, I. (2014). Self-identification with another person's face: The time relevant role of multimodal brain areas in the enfacement illusion. *Journal of Neurophysiology*, *113*(7): 1959–1962. doi:10.1152/jn.00872.2013.

Holle, H., Banissy, M. J., & Ward, J. (2013). Functional and structural brain differences associated with mirror-touch synaesthesia. *NeuroImage*, *83*, 1041–1050. doi:10.1016/j.neuroimage.2013.07.073

Keysers, C., Kaas, J. H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience*, *11*(6), 417–428. doi:10.1038/nrn2833

Maister, L., Banissy, M., & Tsakiris, M. (2013). Mirror-touch synaesthesia changes representations of self-identity. *Neuropsychologia*, *51*(5), 802–808. doi:10.1016/j.neuropsychologia.2013.01.020

Preston, S. D., & De Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *The Behavioral and Brain Sciences*, *25*(1), 1–20. discussion 20–71.

Rochat, P. (2003). Five levels of self-awareness as they unfold early in life. *Consciousness and Cognition*, *12* (4), 717–731. doi:10.1016/S1053-8100(03)00081-3

Sforza, A., Bufalari, I., Haggard, P., & Aglioti, S. M. (2010). My face in yours: Visuo-tactile facial stimulation influences sense of identity. *Social Neuroscience*, *5*(2), 148–162. doi:10.1080/17470910903205503

Tajadura-Jiménez, A., Grehl, S., & Tsakiris, M. (2012). The other in me: Interpersonal multisensory stimulation changes the mental representation of the self. *PloS One*, *7*(7), e40682. doi:10.1371/journal.pone.0040682

Tsakiris, M. (2008). Looking for myself: Current multisensory input alters self-face recognition. *PloS One*, *3*(12), e4040. doi:10.1371/journal.pone.0004040

Van Baaren, R., Janssen, L., Chartrand, T. L., & Dijksterhuis, A. (2009). Where is the love? The social aspects of mimicry. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*(1528), 2381–2389. doi:10.1098/rstb.2009.0057

Ward, J., & Banissy, M. J. (2015). Explaining mirror-touch synaesthesia. *Cognitive Neuroscience*, *13*, 1–16.

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A task control theory of mirror-touch synesthesia

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Abstract: Ward and Banissy's illuminating discussion of mirror-touch synesthesia (MTS) encourages research testing *two* alternatives to Threshold Theory: Their own Self-Other Theory, and "Task Control Theory". MTS may be due to abnormal mirror activity plus a domain-general, rather than a specifically social, impairment in the ability to privilege processing of task-relevant over task-irrelevant information.

Ward and Banissy (this issue) argue convincingly that mirror-touch synesthesia (MTS) is not due solely to atypically strong activation of the somatosensory system by visual observation of touching—to "abnormal mirror activity"—and thereby make a compelling case for expansion of Threshold Theory. However, we propose that future research should encompass two alternatives: Self-Other Theory, the hypothesis that MTS is due to abnormal mirror activity plus an impairment in self-other processing; and what we will call Task Control Theory, the hypothesis that MTS is due to abnormal mirror activity plus a domain-general, rather than a specifically social, impairment in the ability to privilege processing of task-relevant over task-irrelevant information.

Task Control Theory is compatible with the two sets of findings that Ward and Banissy identify as troublesome for Threshold Theory: (1) *MTS does not only affect touch and pain perception*. Because it suggests that people with MTS have an impairment in a domain-general process, Task Control Theory predicts that they will have abnormal experiences, and show atypical patterns of behavior, well outside the domains of touch and pain. (2) *Structural differences beyond the somatosensory system*. Some areas of rTPJ/mPFC contribute more than others to self-other control. These areas may implement distinctive computations on social stimuli (strong specialization), or receive more input from social stimuli, but process these in the same way as other areas of rTPJ/mPFC (weak specialization; Sowden & Catmur, 2015). In either case, and in contrast with Self-Other Theory, Task Control Theory predicts that the gray matter density reduction observed in MTS will not be confined to socially specialized areas of rTPJ/mPFC, but rather will involve areas related to task-relevance (Cook, 2014).

Task Control Theory can also accommodate the evidence that Ward and Banissy cite as favoring Self-Other Theory over Threshold Theory: (1) *Self-awareness in MTS*. Individuals with MTS show the enfacement illusion and the rubber hand illusion without receiving, as part of the experimental procedure, the kind of experience that is normally necessary to induce these illusions, i.e., correlated experience of seeing touch and being touched themselves. These can be described as illusions of "self-perception"—the participant has abnormal experiences relating to their own body—but it does not follow from this description that dedicated self-other processing is involved in generating the enfacement and rubber hand illusions, in people with MTS or in controls. In both populations these illusions could be due to abnormal mirror activity induced by associative learning prior to (MTS) or in (controls) the experimental context (Cook, Bird, Catmur, Press, & Heyes, 2014; Press, Heyes, Haggard, & Eimer, 2008). In that case, the illusion data are compatible with all three theories of MTS because all three postulate abnormal mirror activity. (2) *Self-other control mechanisms in MTS*. In the dot perspective task, people who report mirror-pain show a larger interference effect—e.g., slower responding when a central stimulus points to a smaller number of dots than the number the participant can see—than people who do not report mirror-pain (Derbyshire, Osborn, & Brown, 2013). Self-Other Theory assumes that this interference is due to self-other processing, and therefore that its magnification in mirror-pain is due to an abnormality in self-other processing. In contrast, supported by evidence that controls show this interference effect when the central stimulus is inanimate, as well as when it is a human figure (Santiesteban et al., 2014), Task Control Theory suggests that the effect is larger in people with mirror-pain because they have an impairment in domain-general mechanisms of task control.

In sum, we agree with Ward and Banissy that Threshold Theory requires extension, but propose that a domain-general extension would be consistent with existing data. Thus, future research on MTS should test both Self-Other Theory and Task Control Theory against Threshold Theory.

REFERENCES

Cook, J. L. (2014). Task-relevance dependent gradients in medial prefrontal and temporoparietal cortices suggest solutions to paradoxes concerning self/other control. *Neuroscience and Biobehavioral Reviews*, *42*, 298–302. doi:10.1016/j.neubiorev.2014.02.007

Cook, R., Bird, G., Catmur, C., Press, C., & Heyes, C. M. (2014). Mirror neurons: From origin to function. *Behavioral and Brain Sciences*, *37*, 177–192. doi:10.1017/S0140525X13000903

Derbyshire, S. W. G., Osborn, J., & Brown, S. (2013). Feeling the pain of others is associated with self-other confusion and prior pain experience. *Frontiers in Human Neuroscience*, *7*, 470. doi:10.3389/fnhum.2013.00470

Press, C., Heyes, C. M., Haggard, P., & Eimer, M. (2008). Visuotactile learning and body representation: An ERP study with rubber hands and rubber objects. *Journal of Cognitive Neuroscience*, *20*, 312–323. doi:10.1162/jocn.2008.20022

Santiesteban, I., Catmur, C., Hopkins, S., Bird, G., & Heyes, C. M. (2014). Avatars and arrows: Implicit mentalizing or domain general processing? *Journal of Experimental Psychology: Human Perception and Performance*, *40*, 929–937.

Sowden, S., & Catmur, C. (2015). The role of rTPJ in the control of imitation. *Cerebral Cortex*, *25*(4), 1107–1113. doi:10.1093/cercor/bht306

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How mirror-touch informs theories of synesthesia

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Abstract: Ward and Banissy provide an excellent overview of the state of mirror-touch research in order to advance this field. They present a comparison of two prominent theoretical approaches for understanding mirror-touch phenomena. According to the threshold theory, the phenomena arise as a result of a hyperactive mirror neuron system. According to the Self-Other Theory, they are due to disturbances in the ability to distinguish the self from others. Here, we explore how these two theories can inform theories of synesthesia more generally. We conclude that both theories are not suited as general models of synesthesia.

The threshold theory of mirror-touch is based on the idea that the level of activity in the somatosensory mirror system crosses a threshold of awareness for some persons but not others. As typical forms of synesthesia are related to connections between distinct brain systems rather than relying on a single underlying subsystem (as the mirror system), an immediate generalization is not warranted. However, threshold theories have been proposed to account for crossmodal associations that can be found both in synesthetes and non-synesthetes (i.e., higher sounds pair with lighter colors) with the conscious awareness as the threshold. Moreover, within grapheme-color synesthesia a continuum exists between projectors

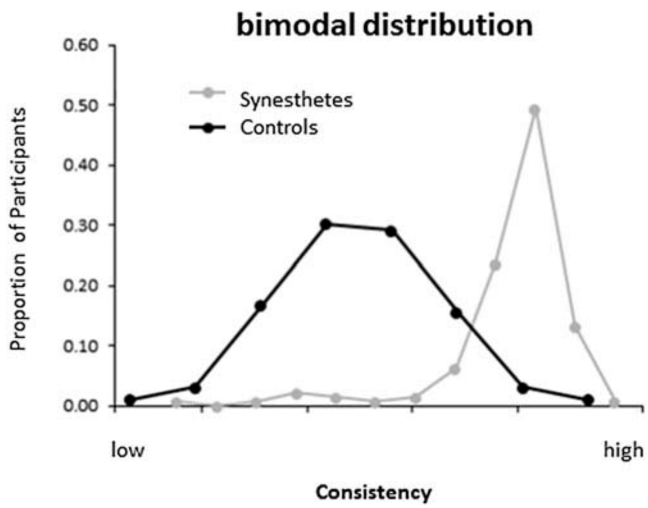

Figure 1. Bimodal distribution resulting from consistency scores of synesthetes and non-synesthetes (adopted from Rothen et al., 2013).

who experience colors in the outer space and associators who experience colors in the mind's eye. An implicit assumption of any threshold model is that the characteristic underlies a unimodal distribution (e.g., a standard normal distribution). Independent of awareness, the criterion for the diagnosis of synesthesia can be empirically defined by maximizing specificity and sensitivity in a common test of consistency, which is the gold-standard for verifying synesthesia. Notably, as illustrated in Figure 1 the resulting distribution is bimodal, thus conflicting with the explanatory power of a threshold model as a general theory of synesthesia (Rothen, Seth, Witzel, & Ward, 2013).

The Self-Other Theory is based on the assumption that aberrant self-other representations produce mirror-touch. Specifically, difficulties in distinguishing the self from another person as the source of agency form the basis of the experiences. In terms of synesthesia, the latter would refer to difficulties in distinguishing between the physical and synesthetic experience (i.e., of touch). However, one of the hallmarks of synesthesia is that despite the vivid experience of synesthetic concurrents, there is no confusion between physical and synesthetic experience (cf., Meier, Rey-Mermet, & Rothen, in press). Indeed, the fact that synesthetes do not get confused by their additional sensations has been denoted as the "most intriguing question in synesthesia research" (Rouw & Ridderinkhof, 2014; cf. Seth, 2014). Thus, the Self-Other Theory is not suited as a general theory of synesthesia.

In a previous paper, we have argued that mirror-touch phenomena differ from synesthesia in several important points (e.g., neural basis, bandwidth, consistency, idiosyncrasy; Rothen & Meier, 2013). Here, we do not want to re-iterate these points. Rather, we would like to emphasize that typically synesthesia is a unidirectional phenomenon in which the inducer elicits a conscious experience, but not the concurrent. For instance, graphemes trigger color experiences in grapheme-color synesthesia but colors do not trigger grapheme experiences. Only very rarely the concurrent can also elicit a conscious experience of the inducer (Cohen Kadosh, Cohen Kadosh, & Henik, 2007), although the concurrent typically triggers the representation of the inducer on an implicit level (Brang, Edwards, Ramachandran, & Coulson, 2008; Meier & Rothen, 2007; Rothen, Nyffeler, Von Wartburg, Müri, & Meier, 2010). In contrast, for mirror-touch phenomena explicit bidirectionality is the common case. Specifically, observed touch (i.e., the inducer) triggers a touch experience (i.e., the concurrent) and, as a matter of principle, being touched physically (i.e., the concurrent) can always be observed (i.e., the inducer).

To conclude, the discussion of mirror-touch in relation to synesthesia is thought-provoking as it sharpens the definitional criteria. The co-occurrence of mirror-touch experiences with other forms of synesthesia is striking and may indicate that mirror-touch synesthesia is a special case of synesthesia (Banissy, Cohen Kadosh, Maus, Walsh, & Ward, 2009; Chun & Hupé, 2013). However, we suggest that it co-occurs with other forms of synesthesia as a by-product, similar to enhanced memory abilities, a distinct cognitive style, or a certain personality profile (Banissy et al., 2012, 2013; Meier, 2013; Meier &

Rothen, 2013; Rothen, Meier, & Ward, 2012). This conclusion is in line with the fact that mirror-touch theories are restricted to these specific phenomena and are not suited as general models for synesthesia.

REFERENCES

Banissy, M. J., Cassell, J. E., Fitzpatrick, S., Ward, J., Walsh, V. X., & Muggleton, N. G. (2012). Increased positive and disorganised schizotypy in synaesthetes who experience colour from letters and tones. *Cortex*, *48*, 1085–1087. doi:10.1016/j.cortex.2011.06.009

Banissy, M. J., Cohen Kadosh, R., Maus, G., Walsh, V., & Ward, J. (2009). Prevalence, characteristics and a neurocognitive model of mirror-touch synaesthesia. *Experimental Brain Research*, *198*(2–3), 261–272. doi:10.1007/s00221-009-1810-9

Banissy, M. J., Holle, H., Cassell, J., Annett, L., Tsakanikos, E., Walsh, V., & Ward, J. (2013). Personality traits in people with synaesthesia: Do synaesthetes have an atypical personality profile? *Personality and Individual Differences*, *54*(7), 828–831. doi:10.1016/j.paid.2012.12.018

Brang, D., Edwards, L., Ramachandran, V. S., & Coulson, S. (2008). Is the sky 2? Contextual priming in grapheme-color synaesthesia. *Psychological Science*, *19*(5), 421–428. doi:10.1111/j.1467-9280.2008.02103.x

Chun, C. A., & Hupé, J.-M. (2013). Mirror-touch and tickertape experiences in synesthesia. *Frontiers in Psychology*, *4*, 776. doi:10.3389/fpsyg.2013.00776

Cohen Kadosh, R., Cohen Kadosh, K., & Henik, A. (2007). The neuronal correlate of bidirectional synesthesia: A combined event-related potential and functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, *19*(12), 2050–2059. doi:10.1162/jocn.2007.19.12.2050

Meier, B. (2013). Semantic representation of synaesthesia. *Theoria et Historia Scientiarum*, *10*, 125–134. doi:10.2478/ths-2013-0006

Meier, B., Rey-Mermet, A., & Rothen, N. (in press). Turning univalent stimuli bivalent: Synaesthesia can cause cognitive conflict in task switching. *Cognitive Neuroscience*. doi:10.1080/17588928.2015.1017449

Meier, B., & Rothen, N. (2007). When conditioned responses 'fire back': Bidirectional cross-activation creates learning opportunities in synesthesia. *Neuroscience*, *147*(3), 569–572. doi:10.1016/j.neuroscience.2007.04.008

Meier, B., & Rothen, N. (2013). Grapheme-color synaesthesia is associated with a distinct cognitive style. *Frontiers in Psychology*, *4*, 632. doi:10.3389/fpsyg.2013.00632

Rothen, N., & Meier, B. (2013) Why vicarious experience is not an instance of synesthesia. *Frontiers in Human Neuroscience*, *128*, doi:10.3389/fnhum.2013.00128

Rothen, N., Meier, B., & Ward, J. (2012). Enhanced memory ability: Insights from synaesthesia. *Neuroscience & Biobehavioral Reviews*, *36*(8), 1952–1963. doi:10.1016/j.neubiorev.2012.05.004

Rothen, N., Nyffeler, T., Von Wartburg, R., Müri, R., & Meier, B. (2010). Parieto-occipital suppression eliminates implicit bidirectionality in grapheme-colour synaesthesia. *Neuropsychologia*, *48*(12), 3482–3487. doi:10.1016/j.neuropsychologia.2010.07.032

Rothen, N., Seth, A. K., Witzel, C., & Ward, J. (2013). Diagnosing synaesthesia with online colour pickers: Maximising sensitivity and specificity. *Journal of Neuroscience Methods*, *215*(1), 156–160. doi:10.1016/j.jneumeth.2013.02.009

Rouw, R., & Ridderinkhof, K. R. (2014). The most intriguing question in synesthesia research. *Cognitive Neuroscience*, *5*(2), 128–130. doi:10.1080/17588928.2014.906400

Seth, A. K. (2014). A predictive processing theory of sensorimotor contingencies: Explaining the puzzle of perceptual presence and its absence in synesthesia. *Cognitive Neuroscience*, *5*(2), 97–118. doi:10.1080/17588928.2013.877880

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Use of hierarchical Bayesian framework in MTS studies to model different causes and novel possible forms of acquired MTS

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Abstract: An integrative account of MTS could be cast in terms of hierarchical Bayesian inference. It may help to highlight a central role of sensory (tactile) precision could play in MTS. We suggest that anosognosic patients, with anesthetic hemisoma, can also be interpreted as a form of acquired MTS, providing additional data for the model.

Ward and Banissy offer a comprehensive treatment of MTS, exploring two hypotheses for this interesting

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phenomenon. We agree that "an integrative account combining both Self-Other Theory and Threshold Theory will be the most parsimonious means to explain MTS in developmental and acquired cases" and suggest that an integrative account can be cast in terms of hierarchical Bayesian inference. We propose that sensory (tactile) precision could play a core role in MTS. We further suggest that anosognosic patients, with anesthetic hemisoma, can also be interpreted as a form of acquired MTS.

Bayesian modeling (Friston et al., 2015) could provide an interesting integrative formulation that connects distal and proximal causes of MTS. According to the Bayesian brain hypothesis, impaired sensation leads to abnormal sensory integration and perceptual inference. When integrating incongruent sensory signals from two modalities with precise (reliable) and imprecise information, Bayesian integration (*with a correct sensory model*) will favor the high precision modality. This can easily explain acquired MTS in amputees, and would point to a tactile (sensory precision) abnormality in developmental MTS. According to this hypothesis, developmental MTS will have impaired tactile processing (in some way similar to amputees) or an impaired generative model of tactile sensations. The latter should result in efficient perception in the absence of integration; otherwise, both cases will result in a false perception.

In hierarchical Bayesian inference, this false perception hypothesis rests on an aberrant bottom-up contribution to perception. Abnormalities in self-other representations and control reflect impaired top-down predictions. These two (ascending and descending) pathways are likely to be affected by different factors, such as habituation to tactile stimulation or the similarity between the observer and subject. Perspective and posture of the observer or occlusions and the temporal dynamics of the observed action (Ognibene & Demiris, 2013) can also profoundly affect the precision of visual input.

Brain damaged patients with hemianesthesia can report tactile sensations following observed touch (Halligan et al., 1996). Moreover, patients affected by hemianesthesia and anosognosia, (even if unable to detect tactile stimuli in the affected side with closed eyes) perceive touch when they can see the touched body part. Behavioral and neurophysiology data show that this can be considered as a real perception—and not a mere verbal confabulation (Pia et al., 2013; Romano et al., 2014). This phenomenon can be modeled under the Bayesian model above (in line with the ideas of Pia et al., 2015), even if it results from a different kind of failure and related brain adaptation. Related MTS data are also relevant to understand why a different frame (anatomical vs. Mirror) can be selected in developmental MTS subjects and why required MTS exhibits a reduced spatial selectivity. In this regard, one hypothesis is that impairments in the top-down or bottom-up pathway differentially affect the selection of the frame of reference, while an acquired MTS, such as amputation, results in a loss of precise (ascending) sensory information. In the same way, the findings of Bolognini, Miniussi, Gallo, and Vallar (2013) fit well with this hypothesis, as cortical excitation by tDCS can mimic the condition.

REFERENCES

Bolognini, N., Miniussi, C., Gallo, S., & Vallar, G. (2013). Induction of mirror-touch synaesthesia by increasing somatosensory cortical excitability. *Current Biology: CB*, *23*, R436–7. doi:10.1016/j.cub.2013.03.036

Friston, K., Rigoli, F., Ognibene, D., Mathys, C., Fitzgerald, T., & Pezzulo, G. (2015). Active inference and epistemic value. *Cognitive Neuroscience*, *13*, 1–28. doi:10.1080/17588928.2015.1020053

Halligan, P. W., Hunt, M., Marshall, J. C., & Wade, D. T. (1996). When seeing is feeling: Acquired synaesthesia or phantom touch? *NeuroCase*, *2*, 21–29. doi: 10.1080/13554799608402385

Ognibene, D., & Demiris, Y. (2013). Towards active event recognition.*The 23rd International Joint Conference of Artificial Intelligence (IJCAI13)*

Pia, L., Garbarini, F., Fossataro, C., Fornia, L., & Berti, A. (2013). Pain and body awareness: Evidence from brain-damaged patients with delusional body ownership. *Frontiers in Human Neuroscience*, *7*, 298. doi:10.3389/fnhum.2013.00298

Pia, L., Garbarini, F., Burin, D., Fossataro, C., & Berti, A. (2015). A predictive nature for tactile awareness? Insights from damaged and intact central-nervous-system functioning. *Frontiers in Human Neuroscience*, *9*, 287. doi:10.3389/fnhum.2015.00287

Romano, D., Gandola, M., Bottini, G., & Maravita, A. (2014). Arousal responses to noxious stimuli in somatoparaphrenia and anosognosia: Clues to body awareness. *Brain: A Journal of Neurology*, *137*, 1213–1223. doi:10.1093/brain/awu009

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The *no*-touch rubber hand paradigm and mirror-touch sensation: Support for the self-other theory of mirror-touch synesthesia

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Abstract: We thoroughly enjoyed Ward and Banissy's Discussion Paper on mirror-touch synesthesia. The authors contrast two theories for explaining this phenomenon—the Threshold Theory and their Self-Other Theory. Ward and Banissy note that the Self-Other Theory garners support from studies that have tested individuals with mirror-touch synesthesia using the rubber hand paradigm. In this Commentary, we provide further support for the Self-Other Theory by drawing on findings from control participants *without* mirror-touch synesthesia tested with two different no-touch rubber hand paradigms—one paradigm makes it easier while the other makes it more difficult to make the self-other distinction.

When an individual with mirror-touch synesthesia (MTS) observes touch administered to another person's body, she experiences synesthetic sensation on her own body. Ward and Banissy's Self-Other Theory provides a convincing explanation for this phenomenon. Their claim is that "one of the mechanisms that might be atypical in MTS is the ability to determine 'who' is the subject of touch." Furthermore, they report that their theory is supported by results from studies (see Aimola Davies & White, 2013; White & Aimola Davies, 2012) that have used the *no*-touch rubber hand paradigm (RHP) to assess MTS. We provide further support for Ward and Banissy's Self-Other Theory by comparing findings from *control* participants tested with two different no-touch RHPs—our own no-touch RHP and that of Giummarra, Georgiou-Karistianis, Nicholls, Gibson, and Bradshaw (2010).

The no-touch RHP is a variation of the traditional RHP. In the traditional RHP (Botvinick & Cohen, 1998), the participant views a prosthetic hand being touched by the Examiner while the participant's own hand (hidden from view) receives synchronous touch from the Examiner. Because of the tight correspondence between what the participant sees and what the participant feels, most participants experience a compelling rubber hand illusion. It may seem to the participant that the prosthetic hand is her own hand (illusion of ownership) and that she is feeling touch at the location of the viewed prosthetic hand (visual capture of touch).

In the no-touch RHP, there is *no touch* administered to the participant's hand. Aimola Davies and White (2013) used their no-touch RHP to test participants with MTS and control participants without MTS. The participant viewed a prosthetic left hand being touched by the Examiner but no touch was administered to the participant's own left hand, which was positioned 15 cm to the left of the prosthetic hand and hidden from view by a wooden vertical divider. One would predict that a participant without MTS would not experience the rubber hand illusion if her hidden hand and the prosthetic hand were not touched synchronously by the Examiner. In contrast, an individual with MTS would not need to be touched by the Examiner to experience the illusion because she should experience synesthetic sensation on her own hand when she sees the Examiner touch the prosthetic hand. This is precisely what Aimola Davies and White (2013) demonstrated with their no-touch RHP. When only the prosthetic hand was touched by the Examiner, control participants without MTS did *not* report any feeling of sensation on their own hidden hand, and they did *not* experience the rubber hand illusion; that is, control participants did not report ownership of the viewed prosthetic hand or the subjective impression of feeling touch at the location of the viewed prosthetic hand. In striking contrast, participants with MTS did report feeling sensation on their own hidden hand and they did experience the rubber hand illusion.

Giummarra et al.'s (2010) no-touch RHP was adapted from the elegant mirror-box apparatus devised by Ramachandran, Rogers-Ramachandran, and Cobb (1995). The researchers used their no-touch RHP to test participants with an amputated upper limb and control participants (who either had an amputated lower limb or no amputation). The study made use of a right prosthetic hand and a left prosthetic hand. For the sake of simplicity, we describe the experimental setup as it applies to the right prosthetic hand, and we focus on how the paradigm was used with control participants. A prosthetic right hand was positioned on the reflective right side of a mirror, and the participant's left hand was hidden on the other non-reflective side of the mirror. The participant was instructed to look into the mirror rather than directly at the prosthetic hand. The reflection of the right prosthetic hand in the mirror was that of a left hand and it would have seemed to the participant that it was occupying the position of the participant's own hidden left hand. Although only the prosthetic hand was touched by the Examiner, and no touch was administered to the participant's own left hand, the reported experience of Giummarra et al.'s control participants' matched that of Aimola Davies and White's (2013) participants with MTS. Thus, with a simple manipulation to the experimental setup (a mirror instead of a wooden vertical divider between the prosthetic hand and the real hand), Giummarra et al.'s control participants reported *feeling* sensation on their own hidden hand and they experienced the rubber hand illusion—ownership of the viewed mirror-reflected prosthetic hand and the subjective impression of feeling touch at the location of the viewed prosthetic hand.

Taken together, the results from the control participants in these two studies using the no-touch RHP fit beautifully with Ward and Banissy's Self-Other Theory of MTS. In the study by Aimola Davies and White (2013), it was easy for participants to make the self-other distinction, and control participants tested with this no-touch RHP did not experience the rubber hand illusion. In contrast, in the study by Giummarra et al. (2010), the experimental setup made it difficult for participants to make the self-other distinction and control participants tested with this no-touch RHP did experience the rubber hand illusion. Perhaps this is not surprising given that in the Giummarra et al. study it would have seemed to the participant that she was looking at her own left hand through a sheet of glass. What is surprising is that such a simple manipulation to the no-touch RHP resulted in control participants reporting the subjective impression of being touched on their own left hand. Ward and Banissy have argued that individuals with MTS experience synesthetic sensation because they find it difficult to make the self-other distinction in everyday life. It is exciting to consider that with some experimental setups, in which the boundary between self and other is not clearly demarcated, an individual may not need to have MTS to experience illusory sensation.

REFERENCES

Aimola Davies, A. M., & White, R. C. (2013). A sensational illusion: Vision-touch synaesthesia and the rubber hand paradigm. *Cortex*, *49*, 806–818. doi:10.1016/j.cortex.2012.01.007

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature*, *391*, 756. doi:10.1038/35784

Giummarra, M. J., Georgiou-Karistianis, N., Nicholls, M. E. R., Gibson, S. J., & Bradshaw, J. L. (2010). The phantom in the mirror: A modified rubber-hand illusion in amputees and normals. *Perception*, *39*, 103–118. doi:10.1068/p6519

Ramachandran, V. S., Rogers-Ramachandran, D., & Cobb, S. (1995). Touching the phantom limb. *Nature*, *377*, 489–490. doi:10.1038/377489a0

White, R. C., & Aimola Davies, A. M. (2012). Specular vision-touch synaesthesia: Two reference frames. *Perception*, *41*, 871–874. doi:10.1068/p7182