Review

Inter-Individual Differences in Vicarious Tactile Perception: A View across the Lifespan in Typical and Atypical Populations

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Abstract

Touch is our most interpersonal sense, and so it stands to reason that we represent not only our own bodily experiences, but also those felt by others. This review will summarise brain and behavioural research on vicarious tactile perception (mirror touch). Specifically, we will focus on vicarious touch across the lifespan in typical and atypical groups, and will identify the knowledge gaps that are in urgent need of filling by examining what is known about how individuals differ within and between typical and atypical groups.

Keywords

Vicarious touch, mirror touch, synaesthesia, individual differences, somatosensory

1. Introduction

The tactile sensory modality represents information in personal space (i.e., on the body surface) and has garnered accelerated interest within multisensory and body-related research communities. To illustrate, the abstract book of the annual meeting of the International Multisensory Research Forum in 2005 (Rovereto, Italy) contained 159 instances of the words touch, tactile and somatosensory. Ten years later in 2015 (Pisa, Italy), there were 418 such instances.

Touch as a sensory modality (and its interaction with other senses, particularly vision) is so important in these research arenas because it provides a fundamental experience of our own body that is critical for the development and experience of one's sense of self (e.g., Blanke *et al*., 2015; Gallese and Sinigaglia, 2010; Legrand, 2006; Rochat and Striano, 2000). Intertwined with the experience of ourselves as agentive bodies, touch is also important in our everyday social interactions from birth through to old age. Social touch can affect the way we feel about and behave toward others (see Gallace and Spence, 2010). Non-human and human animal studies indicate that bodily contact forges positive affiliative bonds between two or more individuals (e.g., Boccia, 1986; Coelho *et al.*, 1983; Light *et al.*, 2005).

Brain mechanisms involved in representing the first-hand experience of touch involve a number of subsystems depending on a) the type and location of tactile input and b) the function of tactile receptors. This input typically leads to neural activation within a set of brain regions: the somatosensory cortices. In recent decades a number of findings have suggested that the somatosensory cortices are not only involved in the first-hand experience of touch, but also the perception of touch to others (hereafter referred to as vicarious tactile perception or mirror touch; see Keysers *et al.*, 2010 for review). Vicarious tactile perception has been linked to brain activation in a network of brain regions involved in the first-hand experience of touch (e.g., primary and secondary somatosensory cortices), sensorimotor processing (e.g., premotor and parietal cortices), and self–other distinction (e.g., superior temporal sulcus). In this regard, vicarious tactile perception in the brain is often referred to as being a consequence of a mirroring system for touch (or mirror-touch system) — a neural network that responds to touch applied both to the self and to others. Brain activation in the mirror-touch system has been reported to have a somatotopic arrangement (i.e., seeing touch to another person's face activates representations of one's own face) (e.g,. Keysers *et al.*, 2004; Blakemore *et al.*, 2005). Patterns of brain activation in the mirror-touch system have also been shown to vary within and between groups (for reviews of how vicarious perception has been shown to differ according to the presence of a variety of clinical and subclinical conditions see Lockwood, 2016; Ward and Banissy, 2015).

In this review, we will provide an overview of the evidence for, and the underlying mechanisms proposed to explain, vicarious touch in neurotypical adults and what is known about their inter-individual differences. This will be followed by a similar section dedicated to mirror-touch synaesthesia, one subclinical condition that has been associated with altered vicarious tactile perception in which the visual observation of touch leads to the conscious feeling of touch on the body. The third section will give an account of vicarious tactile perceptions from a developmental perspective, examining the evidence for vicarious touch in infants and older adults.

The aim of this review is to identify gaps in our knowledge and understanding of the mechanisms of vicarious touch, how they develop and how they differ in certain subgroups (e.g., synaesthetes) and between individuals within a population. We believe that the study of inter-individual differences is instrumental in delineating the mechanisms of vicarious touch. This is because the aspects of personality, sensorimotor aptitude, or social mindedness, along which individuals may differ from one another, may form the basis of what makes atypical groups (e.g., mirror-touch synaesthetes, depersonalised individuals) vary from the typical population. These inter-individual differences may have early developmental origins. Therefore, understanding individual differences in vicarious touch across the entire lifespan will help to explain the similarities as well as the differences between typical and atypical populations.

2. Vicarious Touch in Neurotypical Adults

There is copious evidence for the representation of other's touch in brain and behaviour. In the following, we give a brief overview of vicarious touch research over the past decade and examine the evidence for inter-individual differences in mirror touch in neurotypical adults.

The majority of what is known about vicarious touch comes from fMRI studies. In 2004, Keysers *et al.* first reported that the observation of another person's legs (or of blocks of wood) being stroked with a brush caused activations in the secondary somatosensory cortex (SII) of the observer, similar to activations in response to being brushed on their own legs. At a similar time, Blakemore *et al.* (2005) presented the first published case study of mirror-touch synaesthesia (see Section 3 below). Their group of non-synaesthetic control participants showed somatotopically organised activity in response to observed touch in the primary somatosensory cortex (SI), in addition to activity in the premotor and parietal cortices (fronto-parietal action mirroring network) and superior temporal sulcus (self–other distinction network). Since then, several fMRI studies have been published showing vicarious activations of the somatosensory cortices, both SI and SII, as well as associated activity in frontoparietal mirroring networks, self–other distinction networks, and insula (Cardini *et al.*, 2011; Ebisch *et al.*, 2008, 2011; Holle *et al.*, 2013; Kuehn *et al.*, 2013, 2014; Meyer *et al.*, 2011; Nummenmaa *et al.*, 2014; Schaefer *et al.*, 2006, 2009, 2012, 2013; see Bufalari and Ionta, 2013; Keysers *et al.*, 2010 for reviews; see also Lamm *et al.*, 2015, for evidence of vicarious touch perception networks specific for pleasant touch and for unpleasant touch). Distinct neural indices of vicarious tactile perception have also been provided in EEG/ERP and MEG studies (e.g., Adler *et al.*, 2016; Bufalari *et al.*, 2007; Coll *et al.*, 2015; Deschrijver *et al.*, 2015; Lankinen *et al.*, 2016; Martinez-Jauand *et al.*, 2012; Pihko *et al.*, 2010; Streltsova and McCleery, 2014).

Interestingly, one of the most recently published fMRI studies (Chan and Baker, 2015) found consistent activations of posterior parietal cortices (PPC) but not of SI or SII during touch observation. This led the authors to question the role of somatosensory cortices in favour of PPC. PPC contains visual-tactile multisensory neural populations coding for body–object interactions (see Chan and Baker, 2015) and shared body maps (e.g., Bolognini and Maravita, 2007; Ishida *et al.*, 2010), and is the main source of visual inputs to the fronto-parietal mirroring system (e.g., Keysers *et al.*, 2010; Rizzolatti and Craighero, 2004).

More causal implications of both SI and PPC in vicarious touch have come from transcranial magnetic and direct-current stimulation (TMS/tDCS) studies (Bolognini *et al.*, 2011a, b, 2013, 2014; Wood *et al.*, 2010). For example, Bolognini *et al.* (2011) showed that rTMS over contralateral, but not ipsilateral, SI selectively impaired visual perceptions of a hand touching another hand, while rTMS over SII interfered with visual perception only in a non-touch-specific manner. After stimulating SI with paired-pulse TMS, Bolognini *et al.*'s (2014) participants misreported feeling touches on the hand contralateral to stimulation while viewing a similar hand being touched. This was found both when SI was primed intracortically and when it was primed via posterior parietal cortical stimulation. These TMS studies thus suggest that SI is causally involved in vicarious touch via links with posterior parietal cortex, which are activated by body-related visual inputs (Keysers *et al.*, 2010).

It is thought that there are functional dissociations within SI, where earlier processing stages (in BA3) are confined to signals that originate on our own body (remain 'private', Keysers *et al.*, 2010; but see Lankinen *et al.*, 2016 for claims that this may differ for haptic touch), while later processing stages (in BA2, SII, and probably BA1) may include representations of other people's somatic experiences (see also Schaefer *et al.*, 2012). This mirroring aspect of SI is considered to be part of a broader neural network responsible for mirroring (e.g., Avikainen *et al.*, 2002; Keysers and Gazzola, 2009; Molenberghs *et al.*, 2012; Molnar-Szakasc and Uddin, 2013; Pineda, 2005; Ruby and Decety, 2001) and emotion recognition (e.g., Adolphs *et al.*, 2000; Wood *et al.*, 2016).

Bufalari and Ionta (2013) suggested that the mirroring part of the SI has a twofold function in social interactions: it encodes the sensory qualities of one's own and others' bodily sensations via feedback from multisensory areas in the broader frontal-parietal network, and is further modulated by the attributed affective components of human tactile interactions on the basis of its links with insular cortex.

In line with this, the sensory qualities of observed touch do appear to affect the somatosensory response. In a behavioural study, the enhancement of felt tactile intensity during the visual observation of touch on another person's hand was found to be stronger for active than passive touch (Gillmeister, 2014). In another study, Meyer *et al.* (2011) showed that visual observation of touch can cause differential activity in SI depending on the object that was observed to be touched. SI activity has also been found to correlate with the rated intensity (Bufalari *et al.*, 2007) and with the rated unpleasantness (Martinez-Jauand *et al.*, 2012) of observed tactile sensations. In these studies, SI activity was measured electrophysiologically and indexed by early somatosensory evoked potentials (SEPs) induced by median nerve stimulation at around 50 ms post-stimulus onset. The SEP component around this time (variably called P50, P45 or P40) is thought to be generated in SI (e.g., Allison *et al.* 1989, 1992; Schubert *et al.*, 2008), and has also been implicated in touch mirroring in other ERP studies using mechanical rather than electrical tactile stimulation (Adler *et al.*, 2016; Deschrijver *et al.*, 2015).

Interestingly, Martinez-Jauand *et al.*'s (2012) study reported that P50 amplitudes during touch observation were positively correlated with self-reported perspective-taking abilities, a cognitive empathy trait. Similarly, individual differences in perspective-taking have been found to correlate with hemodynamic S1 responses to observed touch (Schaefer *et al.*, 2012) and action-related sounds (Gazzola *et al.*, 2006): individuals with greater perspective-taking abilities had greater SI activations. Bolognini *et al.* (2014) reported that the effects of SI transcranial magnetic stimulation on behaviour correlated with reports of feeling touch from viewing it, as well as with both perspective-taking and empathic concern. Specifically, individuals who misreported feeling touches on the hand contralateral to stimulation while viewing a similar hand being touched also felt better able to put themselves into others' shoes, and reported to have more sympathy and concern for others. Greater perspective-taking was further associated with greater impairments in encoding the affective valence of others' bodily states resulting from disruption of S1 activity (Bolognini *et al.*, 2013b).

Perspective-taking is one of the cognitive empathy subscales of the Interpersonal Reactivity Index (IRI, Davis, 1983). This subscale measures the extent to which respondents take other people's mental perspective through seven statements such as "I sometimes try to understand my friends better by imagining how things look from their perspective" and "If I'm sure I'm right about something, I don't waste much time listening to other people's arguments", which are scored on a Likert scale according to how well it describes the respondent. Empathic concern is an emotional or affective empathy IRI subscale probed through statement such as "I often have tender, concerned feelings for people less fortunate than me" and "Sometimes I don't feel sorry for other people when they are having problems". It is more typically linked to the individual variation in the degree of activation within brain networks involved in the observation of painful touch (e.g., Avenanti *et al*., 2005; Singer *et al*., 2004).

In addition to these inconsistencies, it is also noteworthy that no relationships have been reported between indices of vicarious touch and other cognitive IRI subscales (fantasy), other affective / emotional IRI subscales (personal distress), or between vicarious touch and other tools that measure trait empathy (e.g., Empathy Quotient, Baron-Cohen and Wheelwright, 2004; Emotional Contagion Scale, Doherty, 1997 — although fewer studies have tended to employ these specific measures). In this regard it is of interest that Lamm *et al*.'s (2011) meta-analysis of empathy for pain found that state empathy measures (e.g., trial by trial affective ratings) predict empathic cortical activations more sensitively than trait measures (e.g., questionnaires like IRI). This strongly indicates that the study of empathy-related inter-individual differences in mirror touch would benefit from employing experimental designs that probe state empathy.

The affective meaning conveyed by interactive bodily touch has been shown to increase S1, S2, and insular activity (Bjornsdotter and Olausson, 2011; Kress *et al*., 2011).

Observing human-based intentional touch causes stronger S1 activations (Ebisch *et al*., 2008; Kress *et al*., 2011) and engages tactile mirroring processes to a larger extent (Deschrijver *et al*., 2015; Holle *et al*., 2011; Streltsova and McCleery, 2014), compared to object-based non-intentional touch. These S1 activations are said to play a key role in understanding the affective consequences (Bolognini *et al*., 2013b) of tactile interactions between people (Rossetti *et al*., 2012). While the observation of facial touch on another person generally facilitates tactile detection on the face (Serino *et al*., 2008, 2009; Vandenbroucke *et al*., 2015), this facilitation is measurably increased when observing persons we feel a greater affiliation with (Serino *et al*., 2009; see also Fini *et al*., 2013). Interestingly, the strongest enhancement of tactile detection is in fact seen when observing one's own face (Cardini *et al*., 2011s, 2013; Serino *et al*., 2008). In a recent study, somatosensory cortical activity was also found to be positively related to one's own self-reported levels of engagement with the haptic contents of a movie showing dynamic bodily interactions with surfaces (water, sand, rocks; Lankinen *et al*., 2016). This suggests that these affective modulations of SI may be more than reflecting interpersonal somatic experiences; they may be driven by how well we can, and perhaps are willing to, resonate with the viewed touch. Resonance is likely to increase the more self-related a viewed bodily experience is.

It is thought that affective SI modulations are based on its links with insular cortex (e.g., Bufalari and Ionta, 2013), which is involved in various aspects of self-awareness (see e.g., Blanke *et al*., 2015) and also has mirroring properties (e.g., Keysers *et al*., 2010). In addition to somatosensory activation, pleasant touch on the arm elicits similar responses in the posterior insula during the personal experience and the observation of somebody else's arm being stroked (Bjornsdotter and Olausson, 2011; Ebisch *et al*., 2011; see also Schaefer *et al*., 2012, for evidence of mid-insular activity). The anterior insula specifically has been implicated in mirror-touch synaesthesia (Blakemore *et al*., 2005) and in empathy for pain (Lamm *et al*., 2011).

Interestingly, both SI and posterior insula activity are sensitive to whether the touched body part is seen from a first- or third-person perspective (Ebisch *et al*., 2011; Schaefer *et al*., 2009). Behaviourally, visual-spatial perspective has typically been shown to affect tactile detection only when painful touch is observed (Bach *et al*., 2014; Vandenbroucke *et al*., 2015). However, Banissy and Ward (2007) have reported a greater impact of viewed touch from a first-person relative to third-person perspective on visual-tactile congruency effects (see Section 3 below) in mirror-touch synaesthetes and typical adult controls. These findings suggest that both SI and insula may encode the source of tactile sensation (self vs. other; or more broadly self vs. non-self, see also Section 3) and thus play a role in mediating body ownership. In line with this, posterior insula lesions are associated with heautoscopy (Heydrich and Blanke, 2013). In heautoscopy a second own body is perceived and strongly identified with, such that some patients can feel present in two locations at the same time.

SI is also thought to be a critical component in the sense of body ownership (Aspell, Palluel, and Blanke, 2012; Otsuru *et al*., 2014). These studies measured systematic changes in SI activations during the experience of body ownership of a fake hand or back using variations of the rubber hand illusion (RHI). The RHI is an illusion of body ownership in which seeing touch to an inanimate hand that occurs in synchrony with first-hand touch to the participants' own hand can lead to a greater sense of body ownership towards the inanimate hand (Botvinick and Cohen, 1998).

In line with this, a recent study from our lab has implicated SI in vicarious tactile representations during self-face observation in healthy adults (Adler *et al*., 2016; see also Cardini *et al*., 2011 for related findings). Importantly, we found that the P45 index of vicarious touch was not observable in individuals who feel less connected with their bodily self (high levels of depersonalisation). Depersonalisation is a psychological condition characterised by estrangement, detachment or disconnection from one’s own being (e.g., Simeon, 2004), and in its mild form it has a high life-time prevalence (up to 80%, e.g., Hunter, Sierra, and David, 2004). Interestingly, individuals with higher levels of depersonalisation are also reported to have higher levels of body ownership illusions (Kanayama *et al*., 2009; see also Sierra *et al*., 2002), in which SI has been implicated (e.g., Aspell *et al*., 2012; Otsuru *et al*., 2014). This further supports the suggestion that the (altered) sense of bodily self is associated with (atypical) SI activity.

The involvement of the insular pathway to SI may be of particular interest in these phenomena. This is because insula activation is classically associated with interoceptive awareness (anterior insula: Ernst *et al*., 2012; posterior insula: Kuehn *et al.*2016). Interoceptive awareness is the ability to perceive and regulate one’s attention to bodily signals (e.g., Mehling *et al*., 2012). Aspects of interoceptive awareness are in turn negatively correlated with feelings of dissociation from one’s bodily self (Mehling *et al*., 2012), which has been shown to reduce vicarious touch responses at SI stages of processing (Adler *et al*., 2016).

A stronger sense of bodily self also entails a stronger sense of the difference between self and non-self sources of stimulation. This may be because incoming tactile information can be better mapped to existing models of self-related bodily experiences (e.g., Tsakiris *et al*., 2011), processes in which the insula is critically involved (Critchley *et al*., 2004). Accordingly, the RHI, which relies on a blurring of self–other boundaries through synchronous visual-tactile stimulation, is stronger in individuals with a more malleable sense of self: within neurotypicals (Tsakiris *et al*., 2011), within anorexic individuals and between anorexic and healthy control groups (Eshkevari *et al*., 2012; see also Mussap and Salton, 2006), between neurotypical groups with low and high levels of depersonalisation

(Kanayama *et al.*, 2009), and between schizophrenic and healthy control groups (e.g., Thakkar *et al.*, 2011). More directly related to vicarious sensations, Adler *et al.* (2016) showed reduced differences between later-stage SEP indices of vicarious touch (P200) during self-face and other-face observation in individuals with high levels of depersonalisation. Also, Bird *et al.* (2010) found weaker vicarious pain responses in the anterior insula of autistic and control individuals with higher levels of alexithymia, which is also related to interoceptive deficits and low trait empathy.

Altogether, this suggests that the study of interoceptive awareness and its multiple dimensions, and the associated processes of distinguishing self and non-self sources of stimulation, may provide a rich ground for understanding inter-individual differences in vicarious touch perception.

3. Conscious Vicarious Tactile Experiences in Mirror-Touch Synaesthesia

While the majority of people do not experience a conscious sensation of touch on their own body from pure observation, for those with mirror-touch synaesthesia (MTS), a first-hand tactile sensation is experienced (Ward and Banissy, 2015). The prevalence of MTS is estimated at 1.6%; however, self-reported prevalence is much higher, at around 10.8% (Banissy *et al.*, 2009a). The 1.6% estimate comes from participants that objectively differ to control participants on behavioural tests designed to verify the presence of MTS, and therefore this conservative estimate and approach is considered best practice for studies on MTS. A prevalence of 1.6% also relates to the proportion of individuals that experience conscious response to observed touch to humans, but it is of note that some individuals also report vicarious touch in response to inanimate stimuli (such as objects or dummy body parts) (Banissy and Ward, 2007; Banissy *et al.*, 2009a; Holle *et al.*, 2011).

In terms of authenticity, MTS has most commonly been authenticated behaviourally using a visual-tactile congruity task developed by Banissy and Ward (2007), in which participants report the location of a tactile stimulus, while observing another person (or object) being touched. Observed touch can either be spatially congruent or incongruent with the self-reported location of synaesthetic induced touch (i.e., the location where an individual reporting MTS claims to experience a sensation when observing touch). Compared with controls, MTS participants typically make more errors and show a greater congruency effect in their responses. This indicates that the observed touch generates a tactile sensation on the synaesthete's body that feels similar to first-hand tactile experience, leading to greater interference. This pattern of behaviour (i.e., greater interference on the visual-tactile congruity task) is also seen in a manner that is consistent with intra-individual differences within the MTS group.For instance, Banissy and Ward (2007) identify two contrasting spatial reference frames for vicarious tactile sensations in MTS: a) anatomical (e.g., when observing another person being touched on the left cheek, the synaesthete reports a sensation of touch on their own left cheek) and b) mirrored (e.g., when observing another person being touched on the left cheek, touch is reported on the right cheek, mapping to the same side of the body as if looking in a mirror). That is to say that an individual with a mirrored MTS shows congruency effects under a mirrored frame of reference, whereas an individual with an anatomical MTS shows congruency effects under an anatomical frame of reference (see also White & Davies, 2012).

Complementing behavioural differences, functional MRI studies have shown that, compared with controls, MTS participants display greater activation of both primary (SI) and secondary (SII) somatosensory cortex during the observation of touch (Blakemore *et al.*, 2005; Holle *et al.*, 2013) and that this can match a pattern that would be expected given their self-reported frame of reference (e.g., mirrored frame of reference; Holle *et al.*, 2013). In this regard, individuals with MTS show greater activation in the same regions involved in mirroring touch in typical adults. In addition, MTS participants show increased grey matter density in SII than controls (Holle *et al*., 2013). These observations have contributed to the development of Threshold Theory, which assumes that hyperactivity of tactile mirror systems underlies conscious vicarious experience in MTS (Blakemore *et al*., 2005; see Ward and Banissy, 2015 for review). In support of Threshold Theory, congruency effects akin to those found in MTS on the visual-tactile congruity task described above have been induced in controls by increasing excitability in somatosensory cortex with transcranial direct-current stimulation (tDCS; Bolognini *et al*., 2013a).

While evidence from fMRI and tDCS studies points to a hyperactive mirror system for touch in MTS (Blakemore *et al*., 2005; Bolognini *et al*., 2013a; Holle *et al*., 2013), the cause of this increased activity remains unclear. Furthermore, a somatosensory hyperactivity account cannot explain additional structural brain differences observed in MTS, such as reduced grey matter density in medial prefrontal cortex (mPFC) and the right temporoparietal junction (rTPJ; Holle *et al*., 2013). The more recent Self–Other Theory (Banissy and Ward, 2013; Ward and Banissy, 2015) has been proposed to account for some of these factors. Broadly, Self–Other Theory suggests that vicarious experiences in MTS are related to atypical abilities in distinguishing the self from others (or more broadly in distinguishing ‘me from not me’ in the case of objects). One mechanism by which this is thought to occur is through an extension of bodily self-awareness, with MTS being linked to a more expansive plasticity of the bodily self (Banissy *et al*., 2009a; Banissy and Ward, 2013; see also Tamir & Mitchell, 2010). In line with this, individuals with MTS experience the rubber hand illusion (RHI; see Section 2) and enfacement illusion (Tsakiris, 2008) without any tactile stimulation (Aimola Davies and White, 2013; Maister *et al*., 2013). Importantly, for non-synaesthetes, the RHI requires visual and tactile congruency (i.e., tactile stimulation of the participants’ own hand, while viewing synchronous touch on the dummy), but for MTS participants simply seeing touch to the dummy hand can lead to an atypical sense of ownership (Aimola Davies and White, 2013).

In addition to body-ownership, Cioffi *et al*. (2016) have demonstrated that MTS is associated with a greater sense of vicarious agency. In that study, participants were tested on a vicarious agency task in which they saw hand actions performed in a mirror placed in front of them while listening to action instructions that matched or mismatched with the actions performed. While the actions in the mirror appeared to the participant in a congruent location with where they would expect to see actions performed by their own body, the seen actions were actually performed by an experimenter (i.e., another person) while the participants were at rest (thereby inducing blurred boundaries between the self and other). Participants with MTS showed higher judgments of agency (relative to typical adult controls) over the experimenter's movements in the match condition. MTS participants also showed a stronger sense of ownership towards the experimenter's hand compared to controls, but importantly this was in both the match and mismatch conditions; suggesting that merely seeing another's body making an action in a location that corresponds to where one expects to see one's own body was sufficient for mirror-touch synaesthetes to treat other people's bodies as their own. Together with the findings on sense of ownership in MTS described above (also see Maister *et al*., 2013), this evidence indicates a greater susceptibility to self–other merging in MTS, which may contribute to altered patterns of vicarious response seen in this group.

Consistent with the notion that altered malleability of the self may contribute to mirror-touch synaesthesia, non-synaesthetes show greater levels of vicarious response to others that are perceived similar to themselves. For example, Adler *et al*. (2016) argued that vicarious touch as indexed by SEPs like P45 is stronger for touch that can be more easily (mis)attributed to the self. Indeed it may be suggested that SI activations in experimental studies of vicarious touch discussed in Section 2 reflect an amount of (mis)identification with a viewed body part (see Bach *et al*., 2014; Mahayana *et al*., 2014; Schaefer *et al*., 2006 for related arguments). This may be because these studies typically manipulate the viewed body part's location, orientation and/or felt experience of touch relative to the observer's own, hidden body part. Since the typically used body parts (e.g., hand, arm, leg or back) are less obviously one's own than the face, an identification with the viewed body part may occur at SI stages of sensory processing, not only when viewing one's own body, but also when the touched body part is a another person's (see Bufalari *et al*., 2007; Deschrijver *et al*., 2015; Martinez-Jauand *et al*., 2012; Schaefer *et al*., 2012).

Another important process that we tend to implement during vicarious perception is the ability to control the degree to which we privilege representations of the self or representations of other people. For example, in order to experience appropriate levels of vicarious response we must enhance the representations of others and inhibit the representation of one's own affective or sensory state; however in order to prevent excessive personal distress from another's negative state, it can be adaptive to inhibit the representation of the other's affective state and enhance the representations of the self. Interestingly, and consistent with Self–Other Theory, individuals with MTS have also been shown to have a difficulty with self–other control in situations that require inhibiting representations of others while boosting representations of the self. In the study by Santiesteban *et al.* (2015a), MTS participants showed impaired performance on an imitation-inhibition task requiring representations of the self to be enhanced, but representations of others to be inhibited; but comparable performance with controls on visual perspective-taking and theory of mind tasks which require enhancing representations of others while inhibiting the self (Santiesteban *et al.,* 2015a). In this regard, it seems that even in the absence of conscious vicarious tactile experiences (i.e., no synaesthetic inducer), individuals with MTS show difficulties inhibiting others. This difference is not well accounted for by Threshold Theory, but is in line with predictions of Self–Other Theory that promote the hypothesis that atypical self–other abilities lead to altered vicarious response. Importantly, it also appears that in non-synaesthetes self–other control mechanisms play a key role in vicarious perception. For instance, De Guzman and colleagues (2016) show that training the ability to control self–other representations can modulate the degree of vicarious pain experienced towards to other people. Mechanisms of self-other control have also been implicated in modulating imitative responses driven by motor mirror systems (Brass, Ruby and Spengler, 2009; Hogeveen et al., 2015). With this collected evidence in mind, interactions between mechanisms involved in mirroring others' experience (as per Threshold Theory) and self–other distinction (as per Self–Other Theory) may manifest themselves as individual differences in vicarious perception.

4. Vicarious Touch across the Lifespan

Like most psychological and neuroscientific research, all of the previously discussed studies have involved young adults. We know little about vicarious touch in infants, young children, and older people. In this section we provide an overview of developmental studies of (vicarious) touch and related multi-sensory-motor processes to date.

The tactile sense is the first to develop in the womb and matures earlier than other sensory modalities (e.g., Atkinson and Braddick, 1982; Bernhardt, 1987). Developmental studies have shown that SEPs can be reliably detected in preterm infants from the 25th week of gestation (Hrbek *et al*., 1973; Taylor *et al*., 1996) when their hand is stimulated. Reliable SEPs in response to vibrotactile stimuli in infants in the second half of their first year of life have also recently been shown (Rigato *et al*., 2014). In this study the strongest responses were recorded over somatosensory regions in the hemisphere contralateral to the stimulated hand, in line with another recent infant study (Saby *et al*., 2015).

It is likely that vicarious tactile experiences develop alongside the representation of one's own tactile sensations. Developmental psychologists surmised that experiences like seeing and feeling your own body move provide the multi-sensory-motor contingencies that are instrumental in giving rise to bodily self-consciousness (e.g., Rochat and Striano, 2000; Zmyj *et al*., 2011).

Consistent with this assumption, recent studies have shown that sensitivity to the synchrony between seen and felt body-related stimuli may be present from birth (Filippetti *et al*., 2013, 2015; see also Addabbo *et al*., 2015). Filippetti *et al.* (2013) demonstrated that newborns prefer to look at an infant face being touched by a brush when a synchronous tactile stimulation is applied to their own face. Such effects are specific to upright faces only (vs. inverted; Filippetti *et al*., 2013), present for hand-to-hand touch but not object-to-hand touch (Addabbo *et al*., 2015), and stronger when touch is applied to a spatially congruent (vs. incongruent; Filippetti *et al*., 2015) location on the face. This suggests that newborns' preference for synchronous (vs. asynchronous) visual-tactile stimulation is relatively specific to stimuli that are more clearly related to their own bodies.

In a subsequent functional near-infrared spectroscopy (fNIRS) study, Filippetti *et al.* (2014) demonstrated that five-month-old infants also process visual-motor information related to the body. Using delayed vs. real-time video feedback of infants' own facial and upper body movement, they showed a significantly reduced cortical response when visual-motor stimuli were not presented in synchrony.

Further related to the study of shared bodily experiences is prior work examining infants' brain responses during action production and observation of another person performing an action with her hand, or her foot (Marshall *et al*., 2013; Saby *et al*., 2013). Those studies found that at 14 months of age, a somatotopic pattern of mu rhythm desynchronization — indicating an increase in sensorimotor cortical activity — was present during both action production and action observation. Moreover, mu desynchronisation was somatotopically organised, that is, larger over the somatosensory areas specific to hands or feet respectively (see also Marshall and Meltzoff, 2014). This was also true for the somatotopic response pattern recorded at 7 months of age as shown by the somatosensory evoked potential elicited by brief tactile stimulation of infants' hands and feet (Saby *et al.*, 2015). These findings indicate that relatively sophisticated interconnections between the representations of the self and others' bodies are present shortly after the first year of life.

Magnetoencephalographical (MEG) techniques have also lent support for the notion of shared multi-sensory-motor body maps in early childhood. In a study by Remijn *et al.* (2014), three- to four-year-old children received touch stimulation to their index finger and at the same time watched a video of someone else being touched either at the index finger (congruent visuotactile information) or on the toe (incongruent visuotactile information). Over the contralateral somatosensory cortex, a middle-latency equivalent current dipole (ECD), occurring around 100 ms after stimulus onset, was modulated by the visual information so that it was higher for the congruent visuotactile information than for the incongruent visuotactile information or a tactile-only condition. This provides evidence that somatotopically organised interactions between visual and tactile information, which may originate very early in life (Filippetti *et al.*, 2015), are clearly present in children.

During development in childhood and younger adulthood, functional enlargements of the topographically organised maps in somatosensory cortex are associated with learning and enhanced tactile performance as a result of strengthened connectivity (e.g., Elbert *et al.*, 1995; Godde *et al.*, 2000; Pascual-Leone and Torres, 1993; Ragert *et al.*, 2004). Toward older adulthood, however, enlargements of the somatotopic maps are thought to reflect greater functional overlap between maps due to reduced intracortical inhibition (e.g., Kalisch *et al.*, 2009). In line with this, old-age-related cortical reorganisation has been shown to be associated with decline in tactile acuity and sensorimotor coordination (e.g., Kalisch *et al.*, 2009; Spengler *et al.*, 1995).

It would stand to reason that the decline in tactile performance related to cortical reorganisations in late adulthood also entails a decline in vicarious tactile representations. We are not aware of any studies actually demonstrating this, however. There are no studies that show, for example, that the increasing functional overlap of somatotopic maps in SI extends to representing touch on another's body, or that tactile perceptual performance decreases both for self-related and for non-self-related stimuli.

A further question is whether the presumed decline in vicarious touch precedes or co-occurs with the decline of self-related tactile representations. Individual differences in age-related decline of vicarious touch are also not known, but it may be speculated that those with relatively higher levels of intracortical inhibition would (have higher levels of vicarious touch and) be resistant for longer toward the decline in tactile acuity, sensorimotor coordination, as well as the accurate representation of another's somatosensory experiences.

Several other findings would also suggest a decline in vicarious tactile perceptions in older adulthood. For instance, reductions in vicarious perception have been associated with higher levels of alexithymia (e.g., Bird *et al.*, 2010); alexithymia is associated with a difficulty identifying and labelling emotions from bodily cues (Bagby *et al.*, 1994). Alexithymia has also been identified as a predictor of depersonalisation disorder (Simeon *et al.*, 2009); which, as noted above, has been linked with modulations of vicarious tactile perception in younger adults (Adler *et al.*, 2016). Interestingly, older adults tend to show greater self-reported alexithymia than younger adults (Lane *et al.*1998; Mattila *et al.*, 2006; Paradiso *et al.*, 2008). In this regard, one might predict that aging would be associated with declines in vicarious tactile perception (at least in those older adults that show greater self-reported alexithymia). This is an avenue that we are currently exploring.

In addition to changes in alexithymia in later life, it has been widely reported that older adults also show impairments in other aspects of social perception that might point to declined vicarious perception. For example, older adults tend to show reductions in emotion perception (Ruffman *et al.*, 2008), which can act as an important precursor to empathy (also see Yang and Banissy, 2016 for review). Indeed, self-reported trait cognitive empathy (as assessed by the Empathy Quotient; Baron-Cohen and Wheelwright, 2004) appears reduced for older compared with younger adults (Bailey *et al.*, 2008). As described in Section 2, in young adult participants decreased self-reported cognitive empathy has repeatedly been linked with reduced brain activation in somatosensory areas during vicarious tactile perception (Bolognini *et al.*, 2013a, 2014; Martinez-Jauand *et al.*, 2012; Schaefer *et al.*, 2012). With this in mind, if older adults recruit similar brain mechanisms, one might predict that vicarious somatosensory representations could decrease in later life.

5. Summary and Conclusions

In over a decade of research on vicarious touch, very few studies have looked explicitly at inter-individual differences. Overall, the evidence suggests that embodiment and self–other processes are important in determining the extent of vicarious tactile perception. The extent to which observed touch is embodied by the observer appears to depend on several factors: our prerequisite sense of bodily self (e.g., Adler *et al.*, 2016) and how much we engage with the viewed touch (e.g., Lankinen *et al.*, 2016). Our sense of self, as measured by our interoceptive awareness, our sense of body ownership, and our sense of agency, for example, is subject to large inter-individual differences (e.g., Tsakiris *et al.*, 2011), and this looks to be a promising avenue for vicarious touch research. Indeed the sense of self has been shown to be altered in individuals that experience mirror-touch synaesthesia (e.g., Maister *et al.*, 2013;

Aimola-Davies and White, 2013; Cioffi *et al*., 2016), and this variability in the malleability of the self is considered to play a key role in contributing to the degree to which we experience conscious versus unconscious vicarious sensations (Ward and Banissy, 2015). The sense of self is also altered in a variety of atypical populations (e.g., alexithymic, depersonalised, eating disordered and schizophrenic individuals), in whom the vicarious representation of touch is understudied.

Vicarious somatosensory activity may also be modulated by inter-individual differences in cognitive and affective empathy (e.g., Bolognini *et al.* 2013a, 2014, Schaefer *et al*., 2012). While findings are not entirely consistent across studies, the most frequently reported relationship is between vicarious touch and the ability to cognitively represent the mental contents of another person's mind ('perspective-taking'). It is important to note that the perspective-taking skills measured with the IRI are more similar to mentalising skills (e.g., Rutherford, 2004) than to visual-spatial perspective taking, which has been used to elucidate self-other-related processing (e.g., Santiesteban *et al*., 2012, 2015a; see also Heyes, 2014; Santiesteban *et al*., 2015b). Future studies should clarify how these sets of skills are linked to one another and to vicarious tactile perception. Further, measuring empathy (and other personality aspects) in a situational manner (e.g., on a trial-by-trial basis) during touch observation may serve to uncover the relationships between personality and vicarious touch perception better than measuring self-reported traits.

Future studies should also investigate how vicarious touch relates to the five-factor model of personality (see Bufalari and Ionta, 2013, for a similar call). Individual five-factor traits are known to be associated both with individual empathic traits (e.g., Mooradian *et al.*, 2011) and with SI activity in response to first-hand touch (Schaefer *et al*., 2012, 2013). While this would suggest that tactile mirroring mechanisms might be modulated by personality traits, to date, these two strands of research have not been combined.

The evidence also strongly points to the necessity to test groups other than healthy young adults to elucidate the aforementioned embodiment / interoception and self–other distinction mechanisms that contribute to individual differences, such as individuals suffering from depersonalisation, alexithymia, eating disorders, and schizophrenia. Mirror touch synaesthetes present one atypical group that has been studied extensively. Here, there is growing evidence linking conscious vicarious perception with altered self–other processing. For instance, alterations in self–other perception (e.g., sense of agency and body ownership — Aimola-Davies and White, 2013; Cioffi *et al*., 2016; Maister *et al*., 2013) and the ability to control self–other representations (specifically, difficulties in controlling self–other representation in conditions that require the ability to inhibit other people; Santiesteban *et al*., 2015b). These findings are consistent with work suggesting that interactions between mechanisms involved in mirroring other people's experiences and self–other representation (e.g., self–other control) play a key role in vicarious perception (e.g., Bird and Viding, 2014; De Guzman *et al*., 2016; Lamm *et al*., 2016). Collectively they point to the notion that the interplay between self–other and mirroring processes may manifest themselves as individual differences in vicarious touch.

While a number of important steps have been made in understanding normative mechanisms of vicarious tactile perception, less work has focussed on individual variation and development. Altogether, developmental studies suggest that common neural mechanisms support both infant and adult processing of body-related multisensory and sensorimotor stimuli, and that these mechanisms deteriorate in older age, but very little work has directly investigated vicarious tactile representations. Future research on tactile mirroring needs to include infants, children and older adults, and examination of a range of vicarious experiences (e.g., conscious vicarious response; unconscious vicarious response; reduced vicarious response). This will permit the ability to map out developmental trajectories, and garner a more holistic understanding of mechanisms contributing to vicarious perception as well as of factors contributing to individual variations in these.

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