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Interpersonal representations of touch in somatosensory cortex are modulated by perspective

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Highlights

- We found that vicarious touch consists of two separable somatosensory components
- Anatomical mapping for touch in first person perspective occurs at P45
- Specular (mirror-like) mapping in third person perspective occurs at P100
- Vicarious representations predict own and others' bodily events at distinct stages

ABSTRACT

Observing others being touched activates similar brain areas as those activated when one experiences a touch oneself. Event-related potential (ERP) studies have revealed that modulation of somatosensory components by observed touch occurs within 100 ms after stimulus onset, and such vicarious effects have been taken as evidence for empathy for others' tactile experiences. In previous studies body parts have been presented from a first person perspective. This raises the question of the extent to which somatosensory activation by observed touch to body parts depends on the perspective from which the body part is observed. In this study (N=18), we examined the modulation of somatosensory ERPs by observed touch delivered to another person's hand when viewed as if from a first person versus a third person perspective. We found that vicarious touch effects primarily consist of two separable components in the early stages of somatosensory processing: an anatomical mapping for touch in first person perspective at P45, and a specular (mirror like) mapping for touch in third person perspective at P100. This is consistent with suggestions that vicarious representations exist to support predictions for one's own bodily events, but also to enable predictions of a social or interpersonal kind, at distinct temporal stages.

KEYWORDS: Somatosensory; vicarious touch; empathy; perspective; EEG; ERPs

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Introduction

Neural networks that enable us to vicariously experience states that we observe in others may be crucial to our understanding of the social world around us (e.g. Keysers, Kaas, & Gazzola, 2010; Keysers & Gazzola, 2009). A number of studies have now established that seeing other people experiencing touches activates similar brain areas as when we experience touches ourselves (for reviews see Keysers et al., 2010; Gillmeister, Bowling, Rigato, & Banissy, 2017). Furthermore, interpersonal representations of touch and pain have been associated with activations in neural regions that support the sensorimotor and affective experience of these states (e.g., Avenanti, Buetti, Galati, & Aglioti, 2005; Grice-Jackson, Critchley, Banissy, & Ward, 2017; Lamm, Decety, & Singer, 2011; Morrison, Lloyd, di Pellegrino, & Roberts, 2004).

The time course of somatosensory cortical modulations by vicariously observed sensory events was first demonstrated by Bufalari and colleagues (Bufalari, Aprile, Avenanti, Di Russo, & Aglioti, 2007). They found that observing a touch to another person's hand in first person perspective modulated early somatosensory component P45. The P45 is likely to reflect neural activity of the crown of the primary somatosensory cortex (S1) (Allison, McCarthy, Wood & Jones, 1991; Allison, McCarthy & Wood, 1992; Schubert, Ritter, Wüstenberg, Preuschhof, Curio et al., 2008), and has since been shown to be involved in vicarious touch in other ERP studies (e.g. Adler, Schabinger, Michal, Beutel, & Gillmeister, 2016; Deschrijver, Wiersema, & Brass, 2015, 2017; Martinez-Jauand, González-Roldán, Muñoz, Sitges, Cifre, & Montoya, 2012).

These effects of vicarious touch have often been interpreted as representing neural processes underlying empathy for pain or touch (e.g., Banissy & Ward, 2007; Avenanti et al., 2005). However, in previous studies investigating this phenomenon participants observed body parts from the observer's own (first person) perspective. Under these circumstances, the observed touches appear fairly similar to touches on the observer's own limb. This raises the possibility that vicarious touch effects may be easy to elicit, not because of an empathy for the observed body part, but because the

observed body part is perceived as one's own (Lloyd, 2007; Mahayana, Banissy, Chen, Walsh, Juan, & Muggleton, 2014). As such it is difficult to disentangle the extent to which neural correlates of vicarious touch reflect genuine empathic processes or more simply a perceptual process which identifies a touch as occurring on the observer's own body.

One way to disentangle the contribution of an observer's sense of body ownership to vicarious touch is by systematically varying the perspective in which it is presented (Rochat, 1998; Tsakiris & Haggard, 2005; Vandenbroucke, Crombez, Loeys, & Goubert, 2015). One functional magnetic resonance imaging (fMRI) study (Schaefer, Xu, Flor, & Cohen, 2009) reported that observing touch to another's hand from a first person perspective (1PP) evokes activity in anterior portions of S1, while observing touch from a third person perspective (3PP) evokes activity in posterior portions of S1. In a further study, Schaefer, Heinze, and Rotte (2012) showed that observing touch to a hand presented from a 1PP elicits stronger activation in the S1 compared to observing touch from a 3PP. This evidence suggests that the nature of visual influence on somatosensory cortical activation is dependent on the extent to which the viewed body part resembles the observer's own. Indeed, there is a similar influence of the viewed perspective of body parts on cortical activity associated with visual representations of the body (Bach, Fenton-Adams, & Tipper, 2014; Brady, Maguinness, & Choisdealbha, 2011; Conson, Aromino, & Trojano, 2010; Hoover & Harris, 2015; Saxe, Jamal, & Powell, 2005; but see Anquetil & Jeannerod, 2007).

The differentiation of somatosensory cortical responses to viewing touches occurring to one's own body as opposed to others' bodies in fMRI and TMS studies has led authors to argue that there is a processing hierarchy in which S1 processes only own body information, with later stages (posterior S1 and secondary somatosensory cortex, S2) additionally processing information concerning touches that are observed on other people (Keysers et al., 2010). A full test of this idea, however, still remains to be completed. Importantly, no studies have yet explored the temporal dynamics of the

effect of touches viewed from different perspectives on somatosensory processing. To date all ERP studies examining the temporal dynamics of vicarious touch effects have used stimuli in which body parts are shown in such a way as to be highly indicative of body ownership (e.g. hands viewed from a 1PP).

To address this, we compared the effects of viewing a touch to a hand on somatosensory ERPs across conditions in which the touches occurred on a hand that was presented from either a 1PP or a 3PP. Somatosensory ERPs were evoked by presenting vibrotactile stimuli to one of the participant's hands simultaneously with the observed tactile event. An index of vicarious touch was attained within each of the perspective conditions by comparing somatosensory ERPs gathered whilst participants viewed a hand being touched ("hand" trials) against ERPs gathered whilst participants viewed the surface next to the hand being touched ("surface" trials) (see Adler et al., 2016; Rigato, Banissy, Romanska, Thomas, Van Velzen, & Bremner, 2017). Thus, by measuring the somatosensory ERPs to these stimuli, we operationalised the vicarious touch effect as the difference between somatosensory ERPs in hand and surface trials.

We expected to see ERP effects of vicarious touch primarily at the P45 because this component arises from activity in S1, which is commonly affected by vicarious touch perception and by observers' sense of self (Adler et al., 2016; Apps, Tajadura-Jiménez, Sereno, Blanke, & Tsakiris, 2013; Bufalari et al., 2007; Otsuru, Hashizume, Nakamura, Endo, Inui et al., 2014). To explore the subsequent time course of vicarious touch in posterior S1 and in S2, we also analysed the two somatosensory ERP components following P45: N80 and P100. For all of these, we expected there to be modulations by perspective. Although no previous research has looked into modulations of vicarious touch effects in ERPs by perspective, there is evidence that indicates stronger vicarious touch for more vs. less self-related stimuli (e.g. Serino, Pizzoferrato, & Làdavas, 2008; Serino, Giovagnoli, & Làdavas, 2009). Therefore, we anticipated larger vicarious touch effects for stimuli in 1PP than in 3PP, particularly at P45.

In order to obtain a more comprehensive picture of how perspective modulates vicarious touch, we also examined modulations of behaviour by vicarious touch. In a behavioural task previously used elsewhere (e.g., Banissy & Ward, 2007; Bowling & Banissy, 2017), participants were instructed to verbalise the location of a tactile stimulus delivered to their own hands while observing touch to another person's hands presented from a 1PP or 3PP. We expected to see effects of congruency, with better tactile localisation while observing touches in spatially matching than mismatching locations (see Bowling & Banissy, 2017). We also expected these effects of congruency to be larger for hands presented in 1PP than 3PP.

Further to this, we also explored whether there is a relationship between vicarious touch and individual levels of bodily self-awareness. This was because vicarious representations for touch on one's own body are reduced in individuals who frequently feel dissociated from their own bodily self (Adler et al., 2016). Feeling dissociated has in turn been linked to low interoceptive body awareness as measured by the Multidimensional Assessment of Interoceptive Awareness (MAIA) (Mehling, Price, Daubenmier, Acree, Bartmess, & Stewart, 2012). Therefore, we asked participants in the present study to complete the MAIA, and we used correlational analyses to explore whether individuals with lower scores show smaller effects of vicarious touch obtained through ERP and behavioural measures.

We report how we determined our sample size, all data exclusions, all manipulations, and all measures in the study.

Methods

Participants

Eighteen adults (7 males), aged between 18 and 25 years (mean age 20.9 years, $SD = 1.7$ years), volunteered in the experiment. Sample size was determined by a stopping rule and matched to that reported in previous ERP studies of mirror touch (Adler et al., 2016; Bufalari et al., 2007; Martinez-Jauand et al., 2012). All participants

were right-handed and had normal or corrected-to-normal vision by self-report. Informed written consent was obtained from participants. Ethical approval was gained from the Research Ethics Committee of University of Essex. The study conformed with The Code of Ethics of the World Medical Association (Declaration of Helsinki; British Medical Journal, 18 July 1964).

Stimuli

The participants sat at a table within a dimly lit, acoustically- and electrically-shielded room. ERPs were recorded while participants were presented with vibrotactile stimuli to their hands and with dynamic video displays projected onto a 21" screen at 90 cm distance. Vibrotactile stimulation was presented using two 12-volt solenoids, driving a metal rod with a blunt conical tip to the palm of the left and right hand, making contact with the palm whenever a current was passed through the solenoid. The solenoids were driven by a Heijo Tactile controller (Heijo research electronics, London, UK). In order to mask any noises emanating from the solenoids, white noise was played throughout the experiment. The dynamic video displays depicted a left hand in four different conditions (see Fig. 1B): 1) 1PP hand touched by a paintbrush ("first person hand"), 2) 1PP hand approached by a paintbrush ("first person surface") 3) 3PP hand touched by a paintbrush ("third person hand"), 4) 3PP hand approached by a paintbrush ("third person surface"). Because the video displays always presented a left hand (from both 1PP and 3PP), left hand tactile stimuli matched the visual presentation in anatomical coordinates for both 1PP and 3PP, whereas right hand stimuli did not. In the 3PP trials, right hand stimuli matched the visual presentation as from a specular anatomical reference frame.

--Insert Figure 1 about here--

Procedure

On arrival the participants completed the MAIA (Mehling et al., 2012) to glean a measure of their interoceptive awareness. The MAIA consists of a 32-item list of statements such as “I listen for information from my body about my emotional state”, scored on a 6-point Likert scale ranging from 0 (“This never applies to me on a daily basis”) to 5 (“This always applies to me on a daily basis”). The MAIA assesses interoceptive awareness across eight dimensions: noticing, not-distracting, not-worrying, attention regulation, emotion awareness, self-regulation, body listening, and trusting (see Mehling et al., 2012, Table 4).

For the ERP task, the solenoids were attached with elastic bands to the centre of the participant’s palms. The participants’ hands were closed and placed dorsum up on a table in front of them and the distance between the ring fingers of each hand was kept constant at 30 cm. They were also asked to watch the video displays, to avoid eye movements and also to blink as little as they could, but with no other instructions. Each display (Fig. 1A) lasted about 3.5 s and was followed by a 1-s screen with a central fixation (a small black and white pattern). The vibrotactile stimulus lasted 200 ms and was synchronised with the slide in which the object touched the palm of the hand (for the “hand” trials) or the surface next to the hand (for the “surface” trials). There were 150 trials in each of the observed four video conditions (see Fig. 1B), i.e. 600 stimuli in total, which were randomly presented.

Finally, the participants undertook a behavioural task adapted from prior studies (Banissy & Ward, 2007; Bowling & Banissy, 2017). During the task, the participants watched videos of a pair of hands either from a 1PP or a 3PP. The videos depicted these hands being touched by another person’s finger; either one hand, both hands, or neither hand was touched. At the same time as the touch in the video occurred, the

participants' hands were also stimulated; the location of the tactile stimulus could either match or not match the anatomical location of the touch in the video, resulting in randomly presented congruent and incongruent trials. Participants were told to watch the videos and indicate verbally, as quickly as they could, which of their own hands received a tactile stimulus whilst trying to ignore the visual stimulus. Each participant viewed a total of 480 trials, evenly split into 3 blocks of 1PP stimuli, and 3 blocks of 3PP stimuli. There were 4 different video conditions: right-hand touched, left-hand touched, both-hands touched and no-hands touched (for further details of the procedure see e.g. Bowling & Banissy, 2017). For the purpose of this study, only right-hand touched and left-hand touched conditions were analysed. The participants' vocal responses were recorded with a microphone.

EEG recording and analysis

Brain electrical activity was recorded continuously via a Hydrocel Geodesic Sensor Net, consisting of 128 Ag-AgCl electrodes evenly distributed across the scalp (Fig. 1C), referenced to the vertex. EEG was amplified with 0.1-100 Hz band-pass filter, and digitised at 500 Hz. The data were analysed using NetStation 4.5.7 analysis software (Electrical Geodesic Inc.). Continuous EEG was low-pass filtered at 30 Hz using digital elliptical filtering and segmented into epochs from 100 ms before until 400 ms after tactile stimulus onset (time zero thus corresponded to the onset of both tactile vibration and touch presented during the video). Segments with bad channels (voltages exceeding $\pm 200 \mu\text{V}$), eye blinks (voltages exceeding $\pm 140 \mu\text{V}$ in channels 127, 25 and 126, 8) and eye movements (voltages exceeding $\pm 55 \mu\text{V}$ in channels 128, 125) were rejected prior to further analysis. Artifact-free data were baseline-corrected to the average amplitude of the 100-ms pre-stimulus interval and re-referenced to the average potential over the scalp. Finally, individual and grand averages for the different combinations of video condition and stimulated hand were calculated.

Statistical analyses of the ERP data focused on sites close to somatosensory areas contralateral to the stimulated hand (see, e.g. Bufalari et al., 2007). The electrodes included were over the central and centroparietal sites, C3, C4, and CP3, CP4, respectively (electrodes 35, 36, 41, 42, 47, and 103, 104, 110, 93, 98; see Fig. 1C). The analyses focused on P45 and successive components N80 and P100. For all components, we focused on modulations of the peak amplitude values by the following factors: i) Condition (whether the participant viewed a “hand”, or “surface” trial, ii) Perspective (whether the observed hand was viewed as from a 1PP or a 3PP), and iii) Touched side (whether the participant’s right or left hand received a tactile stimulus). Greenhouse-Geisser corrected statistics are reported where assumptions of sphericity were not met. Following significant interactions between Condition and Perspective (or Condition, Perspective and Touched side) in an omnibus analysis of variance (ANOVA), pairwise comparisons were carried out for the effects of Condition in 1PP and 3PP, separately for each stimulated hand where appropriate using t-tests. The combination of the three ERP components and the four conditions of touch, perspective and hand meant that there were 12 implied t-tests at this stage, for which the Bonferroni-corrected alpha would be $p < .004$. Peak amplitude analyses were computed within time windows centred on the peak latency of the components identified by visual inspection of the grand averaged waveform over all conditions and confirmed for all individual average waveforms. The following time windows were identified: 30-50 ms (P45), 65-85 ms (N80), 85-115 ms (P100). The average number of artifact-free trials included in the analyses was 123.3 in the “first person hand” condition, 110.3 in the “first person surface” condition, 125.5 in the “third person hand” condition, and 121.9 in the “third person surface” condition.

Behavioural results

Data from three participants were excluded from analyses due to technical error. We looked for outliers in errors and reaction times (RTs), and one further participant

was removed because their percentage of errors was three standard deviations above the group mean. Mean RTs were analysed with a 2x2 ANOVA with the within-participants factors Anatomical Congruency (whether the observed touches occurred on a hand that was congruent or incongruent with the tactile stimuli in anatomical space), and Perspective (whether the video hands were shown in 1PP or 3PP). Greenhouse-Geisser corrected statistics are reported where assumptions of sphericity were not met. The analysis revealed a significant effect of Perspective, $F_{1,13}=4.91$, $p=.045$, $\eta_p^2=.27$, as participants were quicker to localise the touch on their hands when the visual hand stimuli matched a 1PP ($M=714.2$ ms) than a 3PP ($M=745.2$ ms). While there was no overall significant effect of Anatomical Congruency, $F_{1,13}=.64$, $p=.437$, $\eta_p^2=.05$, we found an interaction between Anatomical Congruency and Perspective, $F_{1,13}=9.17$, $p=.010$, $\eta_p^2=.41$ (Figure 2). Pairwise comparisons of each of the levels of Perspective and Anatomical Congruency showed that participants were quicker to localise anatomically congruent vs. incongruent touches in the 1PP, $t(13)=3.05$, $p=.009$, $d_z=.82$, but not in the 3PP, $t(13)=1.87$, $p=.084$, $d_z=.50$. Furthermore, for anatomically congruent touches, these were localised more quickly while viewing touched hands in the 1PP than in the 3PP, $t(13)=3.933$, $p=.002$, $d_z=1.05$. No effect of perspective on RT was seen for anatomically incongruent touches, $t(13)=.16$, $p=.879$, $d_z=.04$. This demonstrates that the spatial congruency of an observed touch with a felt touch influenced the participants' somatosensory spatial localisation, but that this seems to have been specific to viewing a touch as if from a first person perspective.

--Insert Figure 2 about here--

ERP results

Figure 3 shows grand averaged somatosensory ERPs at contralateral sites during hand and surface video conditions for 1PP and 3PP. Significant statistical findings for all components and comparisons are displayed in Table 1¹.

For the P45 component, the overall analysis of peak amplitudes considering effects of Condition (hand, surface), Perspective (1PP, 3PP), and Touched side (right, left) showed a main effect of Condition, $F_{1,17}=25.76$, $p<.001$, $\eta_p^2=.60$, such that the P45 amplitude was larger in the surface ($M=1.51 \mu\text{V}$) than in the hand ($M=1.04 \mu\text{V}$) condition, and a main effect of Perspective, $F_{1,17}=5.45$, $p=.032$, $\eta_p^2=.24$, in which the P45 amplitude was larger for the 3PP ($M=1.38 \mu\text{V}$) than for the 1PP ($M=1.18 \mu\text{V}$) perspective. We also found two-way interactions between Condition and Perspective, $F_{1,17}=10.39$, $p=.005$, $\eta_p^2=.38$, and between Perspective and Touched side, $F_{1,17}=9.05$, $p=.008$, $\eta_p^2=.35$. In addition, a 3-way interaction was also found ($F_{1,17}=14.36$, $p<.001$, $\eta_p^2=.46$). Pairwise comparisons of the effects of Condition in each of the levels of Perspective and Touched side showed that, in the 1PP, the difference between hand and surface ($M=1.19 \mu\text{V}$) was significant for the left hand, which was anatomically and spatially congruent with the observed left hand, $t(17)=4.34$, $p<.001$, $d_z=1.02$, and for the right hand ($M=.90 \mu\text{V}$), which was spatially incongruent with the observed hand, $t(17)=2.31$, $p=.033$, $d_z=.55$. In the 3PP, the effect of Condition was only significant for touches presented to the right hand ($M=.63 \mu\text{V}$), which was a specular spatial match with the observed left hand in this perspective, $t(17)=3.19$, $p=.005$, $d_z=.75$ (see Fig. 4A).

For the N80 component, we observed significant main effects of Condition [$F_{1,17}=4.86$, $p=.04$, $\eta_p^2=.22$, in which the N80 amplitude was larger in the hand ($M=-.97 \mu\text{V}$) than in the surface ($M=-.78 \mu\text{V}$) condition], and Perspective [$F_{1,17}=14.09$, $p=.002$, $\eta_p^2=.45$, in which the N80 amplitude was larger for first person ($M=-1.07 \mu\text{V}$) than for third person ($M=-.69 \mu\text{V}$) perspective]. A Condition x Perspective interaction. $F_{1,17}=4.83$,

¹ See also Figure 3 legend for analysis of waveform differences around time zero.

$p=.04$, $\eta_p^2=.22$, and a 3-way interaction were also uncovered, $F_{1,17}=17.36$, $p<.001$, $\eta_p^2=.51$. In the 1PP, pairwise comparisons showed an effect of Condition for the left hand only ($M=.75 \mu\text{V}$), $t(17)=3.15$, $p=.006$, $d_z=.74$, while in the 3PP, Condition was significant for both the right hand ($M=.44 \mu\text{V}$), $t(17)=2.64$, $p=.017$, $d_z=.62$, and the left hand ($M=.63 \mu\text{V}$), $t(17)=-3.20$, $p=.005$, $d_z=.76$ (see Fig. 4A).

For the P100 component, the analyses yielded main effects of Condition, $F_{1,17}=9.52$, $p=.007$, $\eta_p^2=.36$ (hand: $M=.24 \mu\text{V}$, surface: $M=.48 \mu\text{V}$), and of Perspective, $F_{1,17}=20.73$, $p<.001$, $\eta_p^2=.55$ (first person: $M=.13 \mu\text{V}$, third person: $M=.58 \mu\text{V}$). There was an interaction between Condition and Touched side, $F_{1,17}=8.52$, $p=.01$, $\eta_p^2=.33$, and a 3-way interaction, $F_{1,17}=5.93$, $p=.026$, $\eta_p^2=.26$. Pairwise comparisons were only significant in the 3PP, and showed an effect of condition for both the left hand (hand: $M=.67 \mu\text{V}$, surface: $M=.22 \mu\text{V}$; $t(17)=-2.31$, $p=.034$, $d_z=.54$) and the right hand (hand: $M=.33 \mu\text{V}$, surface: $M=1.1 \mu\text{V}$; $t(17)=6.35$, $p<.001$, $d_z=1.50$).

In summary, early somatosensory components (P45, N80, P100) were affected by Condition and Perspective, showing more positive amplitudes for surface than hand conditions, and for 3PP than 1PP². The P45 and N80 were affected by an interaction between Perspective and Condition, while the P100 was affected by an interaction between Condition and Touched side. Finally, all these components were qualified by a 3-way interaction. The nature of this interaction changed over time, such that vicarious touch was initially (i.e., at the P45) strongest for anatomically matching stimuli (left-hand touch while observing left-hand touch in 1PP), and later (i.e., at the P100) strongest for stimuli which matched in a specular frame of reference (i.e., right-hand touch while observing left-hand touch in 3PP) (see Figs. 4A and B). Only these two effects of vicarious touch survived a Bonferroni-corrected alpha ($p<.004$), which was applied given

² Analyses of later ERP components (N140, P200, N200, P300 / LPC) showed only independent main effects of Condition and / or Perspective, with greater positivities for surface than hand conditions, and for the 3PP than 1PP. There were no interactions between Condition and Perspective at these later components, which have origins outside of somatosensory cortices.

the twelve t-tests implied across the combination of the three ERP components and the four conditions of touch, perspective and hand (see Fig. 4A).

Relationships between interoception and vicarious touch effects

Pearson correlations were performed between the individual scores of each MAIA subscale (average of scores for statements pertaining to each of the eight MAIA dimension) and the significant ERP effects of vicarious touch and behavioural congruency effects that were sensitive to perspective. While some positive correlations were found, these did not pass correction for multiple correlations using the Benjamini & Hochberg (1995) method, which controls false discovery rates (corrected alpha of $p < .002$ for 24 correlations: 8 MAIA dimensions x 3 significant effects of vicarious touch, see Fig. 4A for the two significant ERP effects, and Fig. 2 for the significant behavioural effect). They are reported here only as exploratory analyses, which may be useful in informing future studies in this area. There was a positive correlation between the “not distracting” MAIA subscale and the vicarious touch effect found over P45 in the 1PP for the left hand ($r = .58$, $p = .011$). In other words, individuals who had lower tendencies to ignore or distract themselves from bodily sensations had larger effects of anatomically matched vicarious touch at P45. We also found a negative correlation between the “trusting” subscale and the behavioural vicarious touch effect ($r = -.60$, $p = .024$). That is, individuals who trust their bodily signals more had smaller effects of anatomically congruent touch in 1PP than 3PP.

--Insert Figures 3 and 4 about here--

Discussion

This study demonstrates the effects of perspective on vicarious touch in behaviour and electrophysiology. As seen in previous studies (e.g., Bufalari et al., 2007), ERP vicarious touch effects consisted of a modulation of somatosensory ERPs by the observation of touch to another person's hand as compared to a surface over early ERP components, starting 40 ms from the presentation of the tactile stimulus. Previous investigations of the time course of the effect of vicarious observation of touch on somatosensory processing have all presented touch events to participants in 1PP, i.e. in such a manner that the observed touches resemble closely touches occurring to the participant's own body. The study we report here compared vicarious touch effects when the touched hand was observed from 1PP and 3PP.

The vicarious touch effects reported here were systematically modulated by perspective. When participants observed a hand being touched from a 1PP, vicarious touch effects were strongest over the first somatosensory ERP component (P45) when the observed and felt touches both occurred on the same hand (i.e., they were in congruent anatomical space). When participants observed a hand being touched from a 3PP, vicarious touch effects were strongest over a later component (P100), when the observed and the felt touches were congruent not in anatomical space but according to a mirror image of the participant's own body (i.e., a specular match). This indicates that the matching of visual-tactile information in anatomical spatial coordinates is primarily supported at earlier somatosensory cortical processing stages, while the matching of visual-tactile information in specular spatial coordinates is primarily supported at later somatosensory cortical processing stages.

Our interpretation of the above findings is that vicarious mapping between viewed and felt touch primarily consists of two qualitatively different feedforward processing stages: an anatomical mapping stage that occurs at the earliest stages of somatosensory processing, followed by a somewhat later specular mapping stage at P100. The earlier effect at P45 is likely to reflect activity within contralateral S1 (e.g.

Allison et al., 1991, 1992; Schubert et al., 2008; see also Schaefer et al., 2009). P100 is considered to reflect a separate somatosensory processing stage (e.g. Cardini & Longo, 2016; Schubert, Blankenburg, Lemm, Villringer, & Curio, 2006), with assumed origins in bilateral secondary somatosensory cortex (S2; e.g. Allison et al., 1991, 1992; Hari et al., 1984; Mima, Nagamine, Nakamura, & Shibasaki, 1998; Zhu, Disbrow, Zumer, McGonigle, & Nagarajan, 2007). However, we cannot exclude the possibility that vicarious touch effects over P100 are solely or additionally the result of processing in posterior portions of S1, which have also been shown to be activated by the observation of touch from a 3PP (Schaefer et al., 2009).

Our findings provide additional evidence of the important role of spatial frames of reference in mediating representations of one's own and others' bodies, and are commensurate with dual-route models for inferring body ownership and recognising ourselves from visual information (Fotopoulou, Jenkinson, Tsakiris, Haggard, Rudd, & Kopelman, 2011). For instance, the literature on mirror-touch synaesthesia (e.g. Banissy & Ward, 2007) and on bimodal visual-tactile neurons in monkey posterior parietal cortex (PPC, e.g. Ishida, Nakajima, Inase, & Murata, 2010) reports both anatomical and specular matching between felt touch and viewed touch on another person. PPC includes populations of visual-tactile multisensory neurons that code body-object interactions (see Chan & Baker, 2015) and shared body maps (e.g. Bolognini & Maravita, 2007; Ishida et al., 2010), and is also the main source of visual inputs to the frontoparietal mirroring system (e.g. Keysers et al., 2010; Rizzolatti & Craighero, 2004). In sum, it is thought that vicariously perceived touch is the result of the activation of PPC by body-related visual information (e.g. Keysers et al., 2010), which in turn activates S1 (Bolognini, Rossetti, Fusaro, Vallar, & Miniussi, 2014). It is of particular interest to note that PPC encodes multiple body maps, since it may support both the anatomical mapping between seen and felt touch, which we found to occur at P45, and the specular mapping that we found to occur at P100.

However, it is important to acknowledge that it seems unlikely that there is a straightforward mapping between tactile spatial reference frame and representations of self and other. Although first person viewing of limbs is likely to cue self perception, and third person viewing to cue other perception, some ability to empathise with sensory states may require a blurring of these distinctions (see de Guzman, Bird, Banissy, & Catmur, 2016, for a discussion of the importance of self-other control processes). There is certainly evidence that more than one spatial frame of reference concerning the body can be adopted. For instance, specular congruency appears to drive the enhanced identification with another person's face following repeated synchronous visual-tactile stimulation on the cheek (e.g. Tsakiris, 2008; Tajadura-Jiménez & Tsakiris, 2014). As such, our finding that touches observed as if from 1PP affect somatosensory processing earlier than those observed from 3PP is commensurate with current arguments that vicarious touch is enhanced when the visual tactile event could more reasonably be (mis)attributed to one's own body (Adler et al., 2016; Bach et al., 2014; Gillmeister et al., 2017; Mahayana et al., 2014; Ward & Banissy, 2015). Feelings of body ownership can be evoked when observing hands in an anatomically plausible (i.e., first person) posture (Lloyd, 2007; Mahayana et al., 2014).

Finally, we explored the associations between vicarious touch and aspects of interoceptive body awareness as measured by the MAIA (Mehling et al., 2012). We observed some non-significant trends indicating that greater interoceptive awareness may be associated with stronger integration of anatomically matching visual information at early somatosensory cortical processing stages (see also Adler et al., 2016), and with less integration of matching visual information at the behavioural level. Bodily and interoceptive self-awareness is a growing research field (e.g. Khalsa et al., 2018), and the investigation of potential relationships with vicarious representations is likely to be advanced through the development of more refined tools to measure both explicit (e.g. IAQ; Murphy et al., 2018) and implicit interoception (e.g. heartbeat evoked potentials; e.g. Schulz et al., 2015).

One aspect of our findings that needs addressing further is the direction of the P45 effect. Like Bufalari and colleagues (2007) we show that contralateral P45 amplitude is reduced by the observation of an object touching a hand as compared to an object approaching but not touching it. Other ERP studies reporting vicarious touch over P45 (e.g. Martinez-Jauand et al. 2012; Adler et al., 2016) have shown that observing touch on a body part leads to an increase rather than a decrease in P45 amplitude compared to observing the body part alone or observing touch next to the body part. These inconsistencies appear to occur independently of variations in study design³. One possible explanation for what drives the direction of P45 effects is the experiential similarity between felt and seen touch. S1, which gives rise to P45, is involved in the encoding of the sensory qualities of touch (Ploner, Schmitz, Freund, & Schnitzler, 2000), and those sensory qualities would have been similar in Martinez-Jauand et al. and Adler et al.'s studies (non-noxious indentations of a small, distinct part of the skin). Like Bufalari et al. (2007), the present study used stimuli that evoked sensations that were similar in their quality (both the viewed paintbrush and the felt vibration caused a pleasant tickle in our study), but probably less alike than those used by Martinez-Jauand et al. (2012) and Adler et al. (2016). The effects of the experiential quality of the sensation evoked by seen and felt touch, and perhaps even the congruency between seen and felt regions of stimulation, should be explored in future studies to confirm how they drive the direction of P45 vicarious touch effects.

In sum, our findings support the idea of a vicarious touch mechanism that exists both to support simulations of bodily events in first person as well as third person perspectives, with the former occurring at the earliest stage of cortical somatosensory processing (P45) and the latter at somewhat later stages (P100). We also show some

³ such as the touched body parts (hands, faces), the range of stimulation observed (touch only, touch and pain), the range of felt tactile stimulation (electrical, mechanical, pneumatic), and the task employed (attending to some aspect of the observed touch, passive observation)

evidence that the integration of anatomically matching visual and tactile information in brain and behaviour is associated with aspects of interoceptive awareness.

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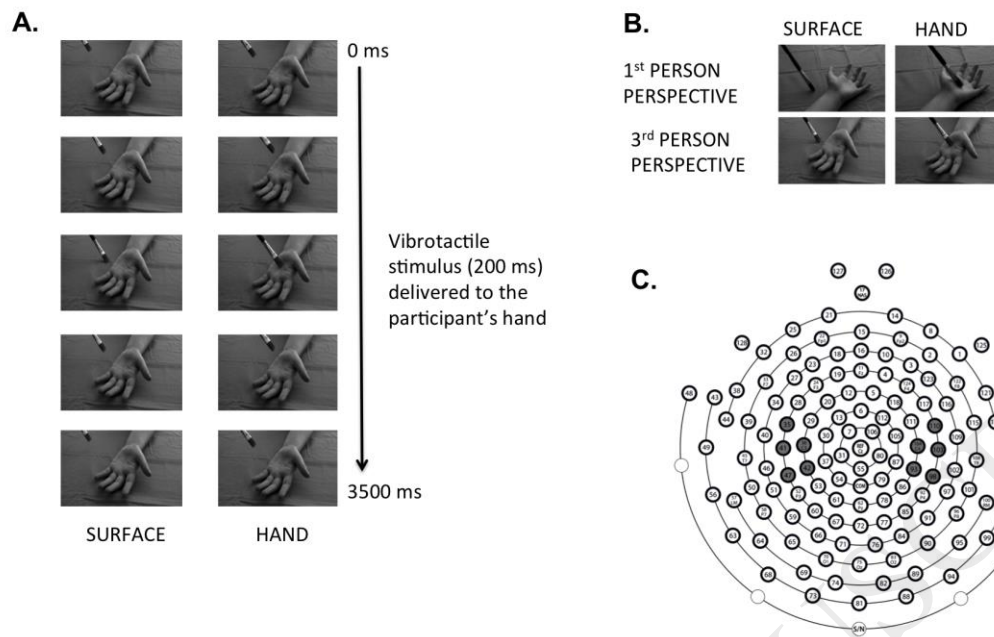


Figure 1. (A) A schematic representation of a typical sequence of visual stimuli. Touch to the participant's hand was presented simultaneously with the touch to the hand or surface shown in the video. (B) Representation of the four video conditions: first person hand touched by a moving object ("first person hand"), first person hand approached by a moving object ("first person surface"), third person hand touched by a moving object ("third person hand"), third person hand approached by a moving object ("third person surface"). (C) The Hydrocel Geodesic Sensor Net. The centroparietal electrodes around CP3/CP4 that were included in the analyses are highlighted.

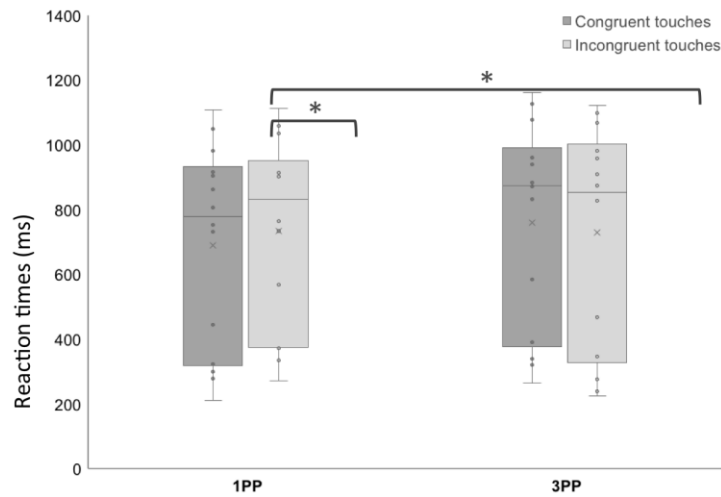


Figure 2. Box and whisker plots of reaction times (ms) to congruent (dark grey) and incongruent trials (light grey) in first person and third person visual perspectives. The boxes represent the 25th and 75th percentiles of responses, with whiskers showing local minima and maxima. The circles represent individual participant means, the crosses denote the grand means, and inner lines denote medians for each condition.

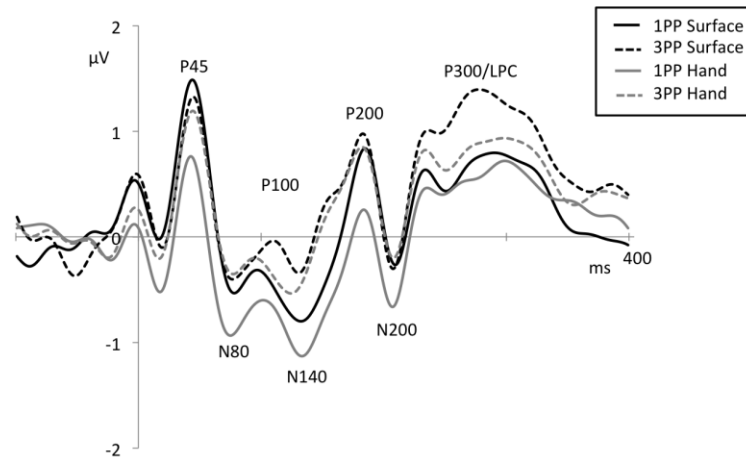


Figure 3. Grand averaged somatosensory ERPs at contralateral sites in surface (black lines) and hand (grey lines) conditions for first person (solid lines) and third person (dashed lines) visual perspectives. Time zero corresponds to the onset of the tactile stimulus (and viewed touch). Note that the ERP waveform appear to synchronise shortly (about 20ms) before tactile onset. Analysis of the peak amplitudes in the time window around zero (-10ms-10ms) showed a significant main effect of Condition (hand vs. surface, $p=.001$), but no interaction of Condition with Perspective ($p=.104$). This suggests that the differential synchronisation of the ERP waveforms may be due to anticipation of the visual-tactile stimulation as a result of repetitive viewing of hand vs. surface videos; but also that these cannot account for the interactions between Condition and Perspective from P45 onwards.

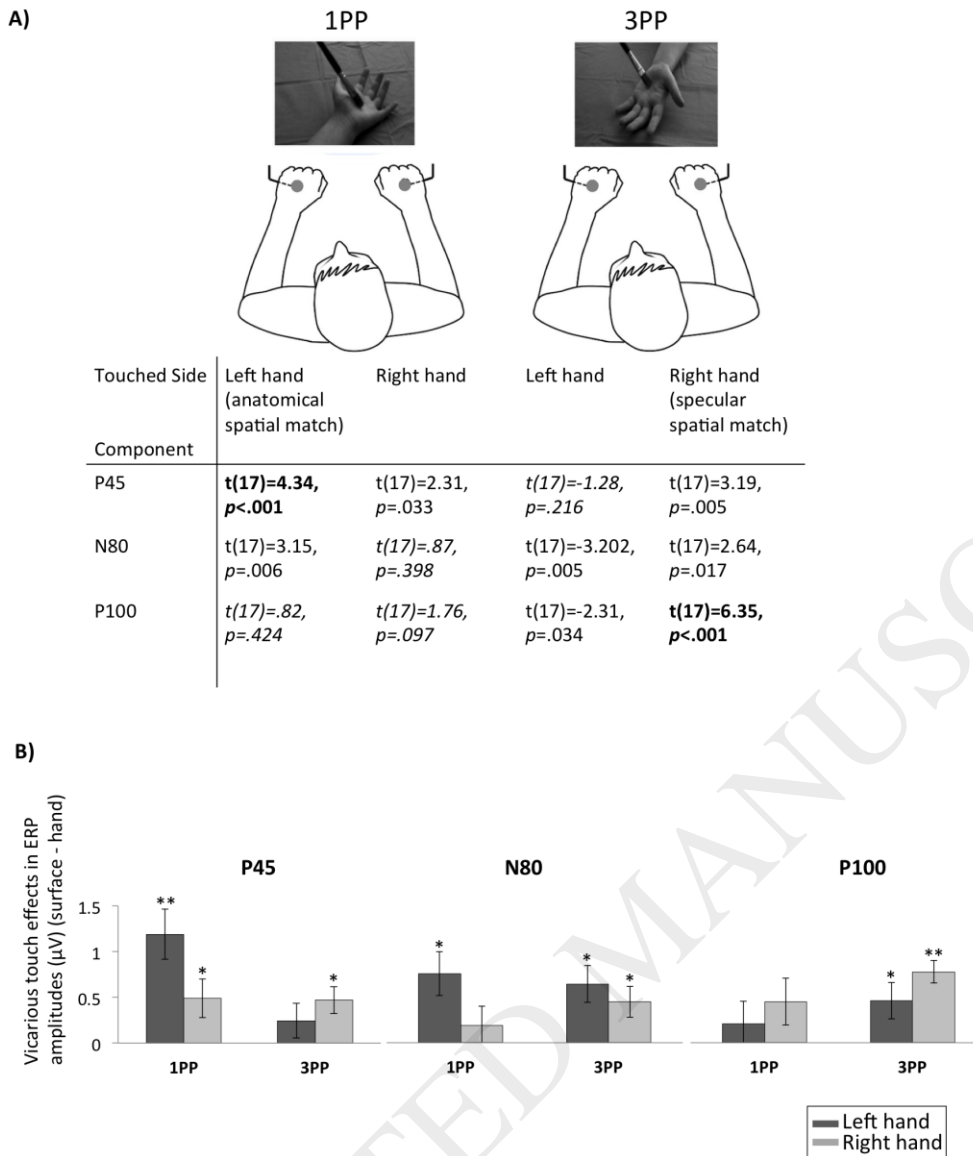


Figure 4. (A) Planned comparisons between surface and hand conditions for each level of Perspective and Touched side (Left hand, Right hand) over components P45, N80 and P100, with most significant effects ($p < .001$) highlighted. (B) Graphic representation of vicarious touch effects (surface minus hand conditions) over P45, N80 and P100 components in first person (1PP) and third person (3PP) perspectives for left hand (dark grey) and right hand (light grey). Error bars depict standard error of the means. ** indicates significant differences between surface and hand conditions at $p < .001$. * indicates significant differences between surface and hand conditions at $p < .05$.

TABLE CAPTION

Table 1. Significant statistical effects found for each somatosensory ERP component.

Of particular interest for the aim of this study were effects of vicarious touch (Condition) and their interactions with perspective (Condition X Perspective; Condition X Perspective X Touched side).

Table 1

Component	Condition (Surface, Hand)	Perspective (1st, 3rd)	Condition X Perspective	Condition X Touched side	Perspective X Touched side	Condition X Perspective X Touched side
P45	$F_{1,17}=25.76$ $p<.001$ $\eta^2=.60$	$F_{1,17}=5.45$ $p=.032$ $\eta^2=.24$	$F_{1,17}=10.39$ $p=.005$ $\eta^2=.38$	$F_{1,17}=.00$ $p=.98$ $\eta^2<.01$	$F_{1,17}=9.05$ $p=.008$ $\eta^2=.35$	$F_{1,17}=14.36$ $p<.001$ $\eta^2=.46$
N80	$F_{1,17}=4.86$ $p=.04$ $\eta^2=.22$	$F_{1,17}=14.09$ $p=.002$ $\eta^2=.45$	$F_{1,17}=4.83$ $p=.04$ $\eta^2=.22$	$F_{1,17}=1.79$ $p=.20$ $\eta^2=.09$	$F_{1,17}=.36$ $p=.56$ $\eta^2=.02$	$F_{1,17}=17.36$ $p<.001$ $\eta^2=.51$
P100	$F_{1,17}=9.52$ $p=.007$ $\eta^2=.36$	$F_{1,17}=20.73$ $p<.001$ $\eta^2=.55$	$F_{1,17}=.54$ $p=.47$ $\eta^2=.03$	$F_{1,17}=8.52$ $p=.01$ $\eta^2=.33$	$F_{1,17}=1.87$ $p=.19$ $\eta^2=.10$	$F_{1,17}=5.93$ $p=.026$ $\eta^2=.26$