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Research Report

Dissociable routes for personal and interpersonal visual enhancement of touch

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ABSTRACT

Seeing a hand can enhance tactile acuity on the hand, even when tactile stimulation is not visible. This visual enhancement of touch (VET) occurs both when participants see their own hand (personal VET), and when they see another person's hand (interpersonal VET). Interpersonal VET occurs irrespective of where the viewed hand appears, while personal VET is eliminated when visual and proprioceptive signals about the location of *one's own* hand are incongruent. This suggests that the neural mechanisms for VET may differ according to ownership of the seen hand. We used continuous theta-burst transcranial magnetic stimulation (TMS) to disrupt either the human ventral intraparietal area (hVIP), which integrates tactile, proprioceptive, and visual information about one's own body, or the extrastriate body area (EBA), which processes visual body information irrespective of ownership. Participants then judged the orientation of tactile gratings applied to their hand while viewing images of their own hand, another person's hand, or a non-body object on a screen placed over their actual hand. Disrupting the hVIP attenuated personal VET but did not affect interpersonal VET, suggesting the hVIP is only involved in VET when one's own hand is seen. Disrupting the EBA reduced both personal and interpersonal VET, suggesting it is common to both routes.

1. Introduction

Vision of the body enhances spatial tactile acuity on the seen body part, even if the tactile stimulation itself is invisible, or vision is non-informative about the stimulus (Cardini, Haggard, & Làdavas, 2013; Cardini, Longo, Driver, & Haggard, 2012; Cardini, Longo, & Haggard, 2011; Fiorio & Haggard, 2005; Haggard, 2006; Haggard, Christakou, & Serino, 2007;

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Harris, Arabzadeh, Moore, & Clifford, 2007; Kennett, Taylor-Clarke, & Haggard, 2001; Konen & Haggard, 2014; Press, Taylor-Clarke, Kennett, & Haggard, 2004; Serino, Farnè, Rinaldesi, Haggard, & Làdavas, 2007; Serino, Padiglioni, Haggard, & Làdavas, 2009; Taylor-Clarke, Kennett, & Haggard, 2002, 2004). This visual enhancement of touch (VET) is unlikely to be simply an effect of directing visuo-spatial attention because looking at a non-body object appearing in the same location as the body part does not improve tactile acuity relative to a control condition of complete darkness (Kennett et al., 2001; Serino et al., 2009). Rather, seeing a body part may activate a multisensory representation of the body that is able to modulate the activity of unimodal, somatotopically organized somatosensory cortex (Fiorio & Haggard, 2005; Konen & Haggard, 2014; Serino et al., 2009; Taylor-Clarke et al., 2002).

Prior research suggests that VET involves changes in the activity of the primary somatosensory cortex (SI) (Fiorio & Haggard, 2005; Serino et al., 2009; Taylor-Clarke et al., 2002). However, the sources of this modulation are not well understood. According to one view, posterior parietal cortex may receive inputs from body-specific areas in the occipito-temporal visual cortex and then send feedback to SI that influences the corresponding part of the somatotopic map (Fiorio & Haggard, 2005; Kennett et al., 2001; Taylor-Clarke et al., 2002). This view is consistent with primate studies that identified multisensory body-centered response patterns from single-cell recordings in the monkey ventral intraparietal area (VIP). Neurons in this posterior parietal area responded to visual, tactile, vestibular, and auditory information pertaining to self-motion (Avillac, Ben Hamed, & Duhamel, 2007; Bremmer, Klam, Duhamel, Ben Hamed, & Graf, 2002; Duhamel, Colby, & Goldberg, 1998; Schlack, Hoffmann, & Bremmer, 2002; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005). Functional magnetic resonance imaging (fMRI) studies support the existence of a similar multisensory body-centered representation in the human intraparietal sulcus (IPS) (Bremmer et al., 2001; Gentile, Petkova, & Ehrsson, 2011; Makin, Holmes, & Zohary, 2007). Importantly, Makin et al. (2007) found a hand-centered representation in the anterior IPS where visual, tactile, and proprioceptive inputs converge. Disrupting this area by delivering transcranial magnetic stimulation (TMS) during a brief interval between viewing one's own hand and receiving tactile stimulation eliminates VET (Konen & Haggard, 2014). The anatomical and temporal specificity of the disruptive effect suggests that the human ventral intraparietal area (hVIP) of the anterior IPS contributes to VET by providing a relay between visual and tactile cortices.

The studies described above examined the effect of seeing *one's own* body on tactile acuity. Seeing the body of another person can also enhance spatial tactile acuity on the corresponding body part of the observer (Cardini et al., 2013; Haggard, 2006). Nevertheless, the mechanisms mediating VET in these two situations may be different, because they are differentially sensitive to spatial incongruence. VET was abolished when one's own hand was seen in a location incongruent with the hand's true location, suggesting that proprioceptive signals regarding spatial location contribute to personal (own-body) VET. However, when the viewed hand clearly belonged to another person, VET was found irrespective of whether the hand appeared at the proprioceptively sensed location of the participant's own hand or elsewhere (Cardini et al., 2013). Thus, personal VET relies on congruent proprioceptive information, and is therefore *inherently* self-referential (O'Shaughnessy, 1995). In contrast, the integration of congruent proprioceptive information is not required for interpersonal VET, when the seen hand belongs to another person.

This behavioral dissociation raises the possibility of two dissociable routes linking visual and somatosensory areas to produce VET. A self-specific route would pass through multisensory regions that also process proprioceptive signals, while the second, interpersonal route would pass through a set of intermediate relays insensitive to proprioceptive processing. Importantly, both routes might originate in a common visual source area; indeed, extrastriate occipital cortex contains visual areas that are specific for viewing bodies and body parts irrespective of whether they belong to oneself or another person (Chan, Peelen, & Downing, 2004; Downing, Jiang, Shuman, & Kanwisher, 2001; Hodzic, Kaas, Muckli, Stirn, & Singer, 2009; Hodzic, Muckli, Singer, & Stirn, 2009; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Urgesi, Berlucchi, & Aglioti, 2004). Equally, both VET routes presumably converge on SI, which contains the key cortical circuitry underlying tactile acuity (Roland, 1987). Nevertheless, the neural mechanisms that *mediate* personal (own-body) and interpersonal (other-body) VET may be at least partially distinct, relying upon different sources of SI modulation.

We have tested the hypothesis of dissociated routes for personal and interpersonal VET by using TMS to disrupt the intermediate relay specific to the personal route, the hVIP (Konen & Haggard, 2014). Changes to personal but not interpersonal VET from such disruption would support the dual route hypothesis. We further sought to confirm that both routes have a common visual source in body-specific areas of the occipital cortex. We tested tactile acuity while participants viewed high-quality visual images of their own hand, another person's hand, and a non-body object. Prior to the tactile acuity task, participants underwent continuous theta-burst stimulation (cTBS) to modulate the left hVIP, a multisensory area implicated as a source of SI modulation in personal VET (Konen & Haggard, 2014) but untested as of yet in interpersonal VET. We hypothesized that temporarily disrupting the hVIP would reduce enhancement of tactile acuity at the sight of one's own hand but leave enhancement at the sight of another's hand intact. In a further session, cTBS was applied over the extrastriate body area (EBA), a region in the lateral occipito-temporal cortex involved in the visual processing of human bodies (Downing et al., 2001; Pitcher et al., 2009; Urgesi et al., 2004). The EBA appears either insensitive (Chan et al., 2004; Hodzic, Kaas, et al., 2009; Hodzic, Muckli, et al., 2009) or only minimally sensitive (Vocks et al., 2010) to whether one's own body or another's body is viewed. We predicted that disrupting the EBA would affect both personal and interpersonal VET because it provides a common visual source for VET, before the personal and interpersonal routes divide.

2. Materials and methods

2.1. Participants

Twenty-six volunteers (19 female, 21 to 30 years old) participated in the experiment after being screened for contraindications to TMS (Rossi, Hallett, Rossini, Pascual-Leone, & The Safety of TMS Consensus Group, 2009; Wassermann, 1998). They gave written informed consent to participate in the experiment and were tested in accordance with the ethical standards of the 1964 Declaration of Helsinki. The study was approved by the Ethics Committee for Psychological Research and the Bioethics Committee of the University of Bologna.

2.2. Materials

To produce images of participants' hands and the other-hand stimuli (which were the hands of 5 female and 5 male volunteers who did not participate in the experiment), a photograph of the right hand with the palm facing down was taken with a digital camera and placed on a black background in Adobe Photoshop CS3. A laptop computer running Presentation .60 was used to display the visual stimuli on a standard 4:3 ratio, 15-inch screen, to send auditory cues via earphones to the experimenter who delivered tactile stimulation, and to collect participants' responses.

TMS was delivered with a Magstim Rapid[2] figure-of-eight coil. A Biopac MP35 system was used to acquire electromyographic activity while each participant's resting motor threshold (RMT) was determined. Neuronavigation was conducted with an NDI Polaris Vicra system and SofTaxic Evolution 1.2 software.

The grating orientation task employed a set of plastic, circle-sectional square-wave gratings with alternating ridges and grooves of equal widths (Van Boven & Johnson, 1994). Ridge and groove widths varied between gratings from .50 mm to 2.00 mm in intervals of .25 mm. The smaller the width of the ridges and grooves, the more difficult it is to discriminate their orientation.

2.3. Procedure

Prior to the experiment, participants came to the laboratory for a preparatory session. During this session, each participant's grating orientation discrimination threshold was determined. Beginning with the largest ridge width (2.00 mm), the experimenter repeatedly applied the grating to the tip of the right middle finger in randomly selected orientations (horizontal/across the finger or vertical/along the finger) for approximately .5 sec per application. The participant's hand was hidden from view under a box with an opening at the back so the experimenter could apply the gratings. A computer screen placed face-up on top of the box showed a rectangle on a black background that the participant fixated while indicating whether the grating orientation was horizontal or vertical. This procedure continued with gratings of decreasing ridge width until the participant answered correctly on 55–65% of 40 trials for a given ridge width. This grating ($M_{\text{width}} = .74$ mm, $SD_{\text{width}} = \pm.18$ mm across participants) was then used in the subsequent experimental sessions. Next, each participant's RMT was determined using single pulses of TMS, with the coil handle pointed backwards and at 45° relative to the midline, to locate the hand area of the left primary motor cortex and determine the minimum stimulator output level required to elicit motor-evoked potentials of at least 50 μV from the right first dorsal interosseous hand muscle in 5 out of 10 trials ($M_{\text{RMT}} = 54.23\%$, $SD_{\text{RMT}} = \pm 8.86\%$). Then, neuronavigation software was used to create an estimated magnetic resonance imaging (MRI) volume for each participant for use in locating the left hVIP and EBA. Finally, participants had a photograph taken of their right hand with the palm facing down, and then rated the similarity of their own hand to the other-hand stimuli (gender-matched) on a scale from 1 (“looks nothing like my own hand”) to 6 (“looks very much like my own hand”). The lowest-rated hand was used as the other-hand stimulus in the experimental sessions. The rating for this hand was never higher than 2.

Participants underwent three experimental sessions on separate days. In one session, participants received cTBS over the left hVIP at Talaraich coordinates $x = -35$, $y = -51$, $z = 42$ (Konen & Kastner, 2008) with the coil handle pointing backwards and at 45° to the midline. In another session, cTBS was delivered over the left EBA with the handle pointing directly backwards and towards the midline. To locate the left EBA, we took the average Talaraich coordinates ($x = -47$, $y = -72$, and $z = 7$) from 22 studies using functional localizers (as reported by De Gelder et al., 2010). In the sham session, the coil was placed over the left hVIP but rotated 90° in a vertical plane. The sessions were otherwise identical, and session order was counterbalanced. At the beginning of each experimental session, neuronavigation data were used to locate the target site. Then the experimenter administered 20 grating discrimination trials using the ridge width selected in the preparatory session. If the participant answered correctly on more than 65% or less than 55% of trials, the procedure used in the preparatory session to determine the orientation discrimination threshold was repeated. Next, cTBS (3 pulses at 5 Hz, repeated at 50 Hz intervals) was delivered over the target site for 40 sec (600 pulses total), a procedure that has been shown to suppress neural activity in the underlying cortical area for 60 min (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005; but see Hamada, Murase, Hasan, Balaratnam, & Rothwell, 2013, for conflicting findings). Stimulator output level was set to 70% of the RMT found in the preparatory session.

After a 5-min pause, participants then underwent two blocks (60 trials each) of the grating orientation task (5 sec per trial, 5 min per block). The blocks were separated by a few

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[1] Note that this would not contradict our finding that the EBA is common to both personal and interpersonal VET, as the offline cTBS procedure we used would be expected to affect activity in neuronal sub-populations processing both own-body and other-body stimuli.

[2] Chan et al. (2004) did not find a differential BOLD response to self-body versus other-body images. However, this could be due to the lower sensitivity of the standard region-of-interest fMRI contrast they used compared to Myers and Sowden's (2008) adaptation approach, which allowed the latter to distinguish the response properties of distinct neuronal sub-populations within the EBA.

minutes of rest during which the orientation discrimination threshold was re-checked. As in the preparatory session, the participant's right hand was hidden under a box with a screen on top where visual fixation was maintained. Each trial began with a fixation cross on a black background and an auditory cue to the experimenter's headphones telling her which orientation to deliver at visual stimulus onset. After 2 sec, an image of the participant's own hand, another person's hand, or a wooden block appeared on the screen for 3 sec, along with another auditory cue to the experimenter signaling her to touch the grating to the participant's middle fingertip. The second auditory cue allowed the experimenter to be blind to the visual stimulus condition because she could time the tactile stimulation with the visual stimulus onset without looking at the screen. Each visual stimulus (own-hand, other-hand, and wooden block) was presented 20 times in each block in a random sequence. The two grating orientations were also presented randomly and equiprobably with each visual stimulus. Participants used a mouse with their left hand to indicate whether the grating orientation was horizontal (left button) or vertical (right button) on each trial. A schematic drawing of the experimental setup is shown in Fig. 1.

2.4. *Design and analysis*

This experiment used a 3 × 3 factorial repeated measures design with the independent variables visual stimulus type (own-hand, other-hand, or wooden block) and TMS condition (hVIP, EBA, or sham stimulation). The dependent measure was the number of correct grating orientation judgments in each condition.

3. Results

To use parametric analyses of variance (ANOVAs) with binomially distributed data expressed as percentages, one must first verify that assumptions of normality and equality of variances are not violated, and that the 95% confidence intervals are interpretable (i.e., between 0% and 100%; Jaeger, 2008). To this end, we performed Shapiro–Wilks normality tests on the percent correct scores from each condition. None of these tests were significant (all p-values $\geq .116$), indicating that our data did not violate the assumption of normal distribution. Mauchly's sphericity tests (reported with each ANOVA below) further indicate that the assumption of equal variances was not violated. Furthermore, all 95% confidence intervals fell between 0% and 100% (see Supplementary Table 1). Consequently, we used ANOVAs on the percent correct scores from the grating orientation task.

An alpha level of .05 (two-tailed) was used for all statistical tests. To examine the effects of TMS on VET, a 3 (TMS target: hVIP, EBA, or sham) × 3 (visual condition: own-hand, other-hand, or object) repeated measures ANOVA was conducted on tactile grating orientation discrimination accuracy. Mauchly's tests were not significant (TMS target: $p = .140$; visual condition: $p = .677$; TMS target × visual condition interaction: $p = .555$), so no sphericity corrections were applied. There was neither a main effect of TMS target, $F(2, 50) = 1.51$, $p = .232$, partial $\eta^2 = .057$, nor a main effect of visual condition, $F(2, 50) = 2.38$, $p = .103$, partial $\eta^2 = .087$. Crucially, there was a significant interaction between visual condition and TMS target, $F(4, 100) = 3.63$, $p = .008$, partial $\eta^2 = .127$.

To elucidate the nature of this interaction, separate ANOVAs with the factor 'visual condition' (own-hand, other-hand, or object) were conducted for each TMS session. Significant ANOVAs were then followed up with paired-samples t-tests (Fig. 2). In the sham condition, the effect of visual condition was significant, $F(2, 50) = 3.36$, $p = .043$, partial $\eta^2 = .119$ (Mauchly's test was non-significant, $p = .841$). Pairwise comparisons of means were used to explore the sources of this effect. Such comparisons between three conditions do not require correction for multiple comparisons when the overall ANOVA is significant (Cardinal & Aitken, 2006). Participants were better at discriminating grating orientations when viewing their own hand ($M = 70.03\%$, $SEM = \pm 2.36\%$) than when viewing the object ($M = 65.09\%$, $SEM = \pm 2.04\%$), $t(25) = 2.58$, $p = .016$, Cohen's $d_z = .506$. Thus the basic VET effect was replicated in the sham condition. Tactile acuity was also marginally better when viewing the other person's hand ($M = 69.07\%$, $SEM = \pm 2.03\%$) than when viewing the neutral

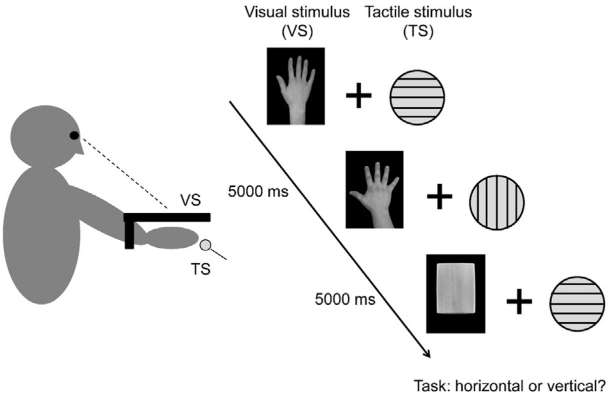

Fig. 1 – Diagram of the visual enhancement of touch (VET) paradigm showing delivery of the visual stimulus (VS) and the tactile stimulus (TS).

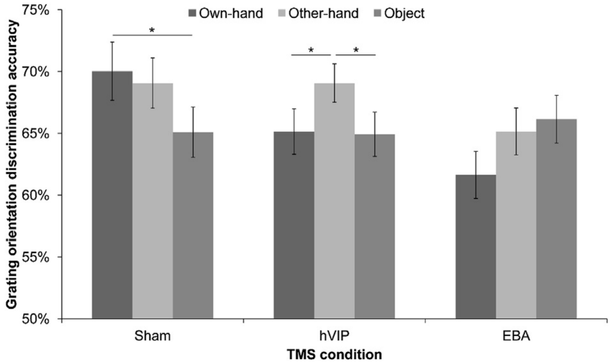

Fig. 2 – Mean (±SEM) tactile grating orientation discrimination accuracy in each visual condition (own-hand, other-hand, and object) and TMS condition (sham, hVIP, and EBA). * = $p < .05$.

object, $t(25) = 1.98$, $p = .059$, Cohen's $d_z = .388$. There was no significant difference in accuracy between the own-hand and other-hand conditions, $t(25) = .45$, $p = .654$, Cohen's $d_z = .088$. This pattern of results replicates previous studies that have found enhancement of spatial tactile acuity both when viewing one's own hand and when viewing another's hand (Cardini et al., 2013; Haggard, 2006).

Following TMS over the hVIP, the effect of visual condition was also significant, $F(2, 50) = 3.60$, $p = .035$, partial $\eta^2 = .126$ (Mauchly's test was non-significant, $p = .089$). Accuracy was higher in the other-hand condition ($M = 69.07\%$, $SEM = \pm1.56\%$) than in both the object condition ($M = 64.92\%$, $SEM = \pm1.80\%$), $t(25) = 2.08$, $p = .048$, Cohen's $d_z = .408$, and the own-hand condition ($M = 65.15\%$, $SEM = \pm1.84\%$), $t(25) = -2.15$, $p = .041$, Cohen's $d_z = .422$. There was no difference in accuracy between the own-hand and object conditions, $t(25) = .17$, $p = .869$, Cohen's $d_z = .033$. This corroborates the hypothesis that disrupting the hVIP would reduce personal VET but not interpersonal VET.

After TMS over the EBA, there was no effect of visual condition, $F(2, 50) = 2.63$, $p = .082$, partial $\eta^2 = .095$ (Mauchly's test was non-significant, $p = .238$). Thus, no follow-up comparisons were made. This supports the hypothesis that disrupting the EBA would reduce both personal and interpersonal VET (Own-hand: $M = 61.63\%$, $SEM = \pm1.90\%$; Other-hand: $M = 65.15\%$, $SEM = \pm1.89\%$; Object: $M = 66.14\%$, $SEM = \pm1.94\%$).

To further explore the nature of the interaction between TMS target and visual condition, we calculated personal and interpersonal VET indices by subtracting each participant's percent correct score in the object visual condition from the percent correct score in the own-hand and other-hand conditions, respectively. This was done separately for each TMS condition. We then used paired samples t-tests to compare each VET index from the sham TMS condition to the corresponding VET index from each of the active TMS conditions. Compared to sham TMS, TMS over the hVIP reduced the personal VET index, $t(25) = 2.11$, $p = .045$, but not the interpersonal VET index, $t(25) = .06$, $p = .954$. TMS over the EBA, relative to sham TMS, significantly reduced the personal VET index, $t(25) = 3.99$, $p = .001$, and showed a marginal trend toward reducing the interpersonal VET index, as well, $t(25) = 1.92$, $p = .066$.

4. Discussion

In our sham stimulation condition, we replicated previous findings that viewing either one's own hand or another person's hand could enhance tactile acuity (Cardini et al., 2013, 2012, 2011; Fiorio & Haggard, 2005; Haggard, 2006; Haggard et al., 2007; Harris et al., 2007; Kennett et al., 2001; Konen & Haggard, 2014; Press et al., 2004; Serino et al., 2007, 2009; Taylor-Clarke et al., 2002, 2004). Disrupting the hVIP within the anterior IPS reduced the enhancement of tactile acuity found when participants viewed their own hand, but not when they viewed another person's hand. This suggests that the neural pathways underlying personal and interpersonal VET are at least partially separate. Viewing one's own hand and another's hand might activate distinct body representations in the brain that enhance tactile perception by independent converging influences on somatosensory areas. One important difference between the effects of viewing one's own body or another person's body could lie in the contribution of proprioceptive information. A previous study showed that personal VET, but not interpersonal VET, involved integration of congruent visual and proprioceptive inputs (Cardini et al., 2013). Our results suggest that this integration of proprioceptive and visual information occurs in a cortical pathway that includes the hVIP. This is consistent with a previous fMRI study that found evidence for converging visual, tactile, and proprioceptive signals in a hand-centered representation of space in the anterior IPS (Gentile et al., 2011; Makin et al., 2007).

A previous study (Konen & Haggard, 2014) showed that single-pulse TMS over the hVIP reduced personal VET. Our results in the own-hand condition replicate and extend that finding in some important ways. We used an offline theta-burst TMS protocol, while they used event-locked single-pulse TMS. While the single-pulse TMS study confirmed that neural activity in the hVIP is causally relevant to personal VET, the present study confirms that the hVIP is a potential site of *enduring modulation* in the multisensory circuit underlying VET. Crucially, as discussed above, our study also showed that the hVIP is involved in personal but not interpersonal VET, suggesting that the mechanism behind this multisensory interaction depends on the identity of the viewed hand.

Theta-burst stimulation is thought to recruit long-term potentiation and long-term depression-like mechanisms in the stimulated cortical area and thus induce plastic changes in cortical circuits (Huang et al., 2005). A recent study identified important individual differences in susceptibility to the effects of motor cortical cTBS (Hamada et al., 2013), with no overall group effects. Nevertheless, this is not a concern for the interpretation of the present study, which found group-level effects of both hVIP and EBA stimulation.

Disrupting the EBA attenuated both personal and interpersonal VET, consistent with the idea that this area processes visual input from both one's own body and the bodies of others (Chan et al., 2004; Hodzic, Kaas, et al., 2009; Hodzic, Muckli, et al., 2009; Vocks et al., 2010). Importantly, this also shows that appropriately targeted cTBS is able to modulate interpersonal VET. While the EBA is considered a visual area, the possibility that it contributes to non-visual functions has been suggested before (Astafiev, Stanley, Shulman, & Corbetta, 2004; Costantini, Urgesi, Galati, Romani, & Aglioti, 2011; Ishizu, Noguchi, Ito, Ayabe, & Kojima, 2009; Kitada, Johnsrude, Kochiyama, & Lederman, 2009; Orlov, Makin, & Zohary, 2010). Our result suggests that visual representations of the body in the EBA make an important contribution to multisensory processing, in this case visual modulation of touch. The EBA result also helps to exclude some alternative interpretations of hVIP TMS. In particular, the selective inhibition of personal but not interpersonal VET by theta-burst stimulation of the hVIP is thus unlikely to reflect an inability to modulate interpersonal VET because of any general factor associated with cTBS, such as participant expectation, or because of a general resilience of processing associated with the self.

Sirigu, Grafman, Bressler, and Sunderland (1991) proposed four independent levels of body knowledge in the brain based on a review of several neuropsychological conditions: the semantic/lexical level, the visuo-spatial level, the dynamic level, and the motor level. Two of these levels are particularly relevant in interpreting our result: the visuo-spatial level, a structural representation of bodies in general, and the dynamic level, an online representation of one's own body that updates with body posture and movement. Sirigu and colleagues argued for the independence of these two body representations based on a double dissociation between pure autotopagnosia—an inability to point to one's own body parts without an accompanying deficit in pointing to the body parts of others—and an inverse pattern of impaired and intact abilities in heterotopagnosia (Degos, Bachoud-Levi, Ergis, Petrissans, & Cesaro, 1997; Felician, Ceccaldi, Didic, Thinus-Blanc, & Poncet, 2003; Felician & Romaiguère, 2008). Our VET results can be accommodated within the same framework. Viewing hands may activate a visuo-spatial body representation regardless of the body to which the hands are attributed. Our results suggest that this representation is housed in the EBA, or in another structure receiving input from the EBA. However, only the sight of one's own hand, not that of another person, should activate a body representation dynamically updated with posture and movement (Cardini et al., 2013). Our results suggest that the hVIP may house this representation. Importantly, we make this dissociation in the context of a somatosensory perceptual task. Therefore, our results may also shed light on the functions of these different body representations. We suggest they may represent distinct but converging influences that participate in top-down modulation of perception (cf. Konen & Haggard, 2014). We further propose that the hVIP is an area where somatosensory and visual inputs converge to bind visuo-spatial representations of bodies with dynamic proprioceptive and tactile descriptions of one's own body.

The present study has yielded a single dissociation between the personal and interpersonal VET routes by demonstrating that the hVIP participates in the enhancement of tactile acuity when viewing one's own hand but not when viewing another's hand. However, the modulatory source responsible for interpersonal VET remains to be determined. One possibility could be another posterior parietal area that represents human bodies in terms of visuo-spatial configuration but without reference to exclusively self-originating sensory inputs such as proprioception. Lesion studies (Degos et al., 1997; Felician et al., 2003) and fMRI studies (Felician et al., 2009) suggest that the left angular gyrus (AG) of the inferior parietal lobule may be involved in a purely visuo-spatial representation of the body. Damage to this area can, in rare cases, produce heterotopagnosia, a deficit in pointing to the body parts of others without accompanying impairments in naming them or in pointing to or naming one's own body parts (Degos et al., 1997; Felician et al., 2003). This indicates preserved semantic knowledge of human body parts, but an inability to place them within an extrapersonal visuo-spatial context. However, lesions of the left AG frequently lead to autotopagnosia, a deficit in pointing to one's own body parts, as well (for a review, see Vallar & Papagno, 2003). Some neuroimaging (Spitoni, Galati, Antonucci, Haggard, & Pizzamiglio, 2010) and brain stimulation studies (Spitoni et al., 2013) also suggest that the AG in the right hemisphere may be involved in representing one's own body. Future research is thus needed to determine which neural structure might be the source of SI modulation in interpersonal VET.

The point at which the pathways for personal and interpersonal VET diverge also remains to be determined. We have found that the EBA is common to both personal and interpersonal routes. Whether the bifurcation point occurs within the EBA or further along the information processing pathway is unknown. There is some evidence that sub-populations of neurons in the right EBA are sensitive to either one's own body parts or the body parts of others, consistent with a role for the EBA in sorting visual body stimuli according to identity (Myers & Sowden, 2008).[1] The right EBA also responds differentially to body parts presented in egocentric and allocentric viewpoints (Chan et al., 2004; Saxe, Jamal, & Powell, 2006), which could be an indicator of ownership.[2] One study even found differential responses to one's own body and the bodies of others in the right EBA (Vocks et al., 2010; but for contradictory findings see Chan et al., 2004; Hodzic, Kaas, et al., 2009; Hodzic, Muckli, et al., 2009). Thus, the EBA might visually discriminate the bodies of oneself and others, marking the bifurcation point of the two routes. However, this speculation must be tempered by the consideration that the above studies found evidence for own-body and other-body selectivity in the right EBA, not the left EBA. The present results suggest that the left EBA houses a *common* visual representation of the human body without regard to ownership or identity. In that case, the personal and interpersonal routes would bifurcate later in the processing stream. For example, one model (Hodzic, Kaas, et al., 2009; Hodzic, Muckli, et al., 2009) proposes that body identity is discriminated in the fusiform body area, a body-responsive region located ventrally to the EBA.

Though viewing both one's own body and another's body enhances spatial tactile acuity, this enhancement is accomplished via distinct neural mechanisms (Fig. 3). This suggests that common behavioral effects of viewing one's own and others' bodies need not indicate a shared *neural* representation. Reviewing the evidence for shared body representations, De Vignemont (2014) proposed that the appearance of common own-body and other-body activations may result from the two representations time-sharing some basic body information processing components (e.g., body part configuration) without entailing a complete self-other overlap. Our results suggest that the visual body information processed in EBA

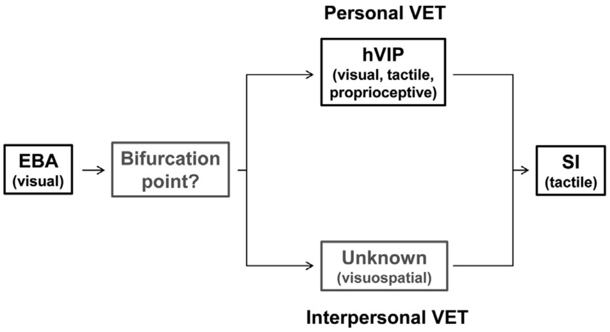

Fig. 3 – Model of the personal and interpersonal VET routes, based on evidence from previous studies (Fiorio & Haggard, 2005; Konen & Haggard, 2014) and the present study. Areas shown in gray have yet to be confirmed.

may be one shared component (but see Myers & Sowden, 2008 for contrary evidence), whereas hVIP is specific to a representation of one's own body, perhaps because of its integration of proprioceptive input.

One limitation of our study is that we did not have access to structural MRI scans for our participants. We instead used neuronavigation software to estimate a MRI volume for each participant by fitting a standard MRI template to the shape of each participant's skull. Moreover, because we did not have access to functional MRI, we used coordinates derived from previous fMRI research to localize hVIP (Konen & Kastner, 2008) and EBA (De Gelder et al., 2010). These hindrances to precise localization may have added noise to our data, and increased the risk of making a type II error. Despite these limitations, we were able to detect effects of TMS over the posterior parietal and occipito-temporal cortices on VET. Further, it is unlikely that imprecise localization could explain the finding that TMS over hVIP did not reduce interpersonal VET, as TMS over the same location was effective at reducing personal VET.

5. Conclusions

The present study suggests that personal VET, but not interpersonal VET, depends upon modulation from the multisensory hVIP. VET, a seemingly low-level crossmodal interaction, is in fact sensitive to the identity of the viewed body part. This sensitivity may reflect the strong tactile and proprioceptive inputs to the key VIP node of the personal VET circuit. This form of multisensory interaction therefore does not involve a ‘mirror system’ that maps both one's own body and the bodies of others onto the same neural circuitry (cf. Decety & Sommerville, 2003; Gallese, 2001). Personal and interpersonal VET effects appear to rely upon distinct crossmodal mechanisms rather than completely overlapping representations of the body in the brain.

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Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2015.09.008.

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