



BIROn - Birkbeck Institutional Research Online

Tamè, Luigi and Carr, Alex and Longo, Matthew R. (2017) Vision of the body improves inter-hemispheric integration of tactile-motor responses. *Acta Psychologica* 175 , pp. 21-27. ISSN 0001-6918.

Downloaded from: <https://eprints.bbk.ac.uk/id/eprint/18238/>

Usage Guidelines:

Please refer to usage guidelines at <https://eprints.bbk.ac.uk/policies.html>
contact lib-eprints@bbk.ac.uk.

or alternatively

Vision of the body improves inter-hemispheric integration of tactile-motor responses

Luigi Tamè, Alex Carr, and Matthew R Longo

Department of Psychological Sciences, Birkbeck, University of London, London, United Kingdom

Address for correspondence:

Luigi Tamè

Department of Psychological Sciences

Birkbeck, University of London

WC1E 7HX, London, United Kingdom

E-Mail: luigi.tame@gmail.com

Pages: 26; Figures: 2; Abstract: 243; Words=4,570

Keywords: VISION, BODY, TACTILE, MOTOR, INTERHEMISPHERIC INTEGRATION, CUD

Running head: Vision affect inter-hemispheric integration

Abstract

Sensory input from and motor output to the two sides of the body needs to be continuously integrated between the two cerebral hemispheres. This integration can be measured through its cost in terms of processing speed. In simple detection tasks, reaction times (RTs) are faster when stimuli are presented to the side of the body ipsilateral to the body part used to respond. This advantage – the *contralateral-ipsilateral difference* (also known as the crossed-uncrossed difference: CUD) – is thought to reflect inter-hemispheric interactions needed for sensorimotor information to be integrated between the two hemispheres. Several studies have shown that non-informative vision of the body enhances performance in tactile tasks. However, it is unknown whether the CUD can be similarly affected by vision. Here, we investigated whether the CUD is modulated by vision of the body (i.e., the stimulated hand) by presenting tactile stimuli unpredictably on the middle fingers when one hand was visible (i.e., either the right or left hand). Participants detected the stimulus and responded as fast as possible using either their left or right foot. Consistent with previous results, a clear CUD (5.8 ms) was apparent on the unseen hand. Critically, however, no such effect was found on the hand that was visible (-2.2 ms). Thus, when touch is delivered to a seen hand, the usual cost in processing speed of responding with a contralateral effector is eliminated. This result suggests that vision of the body improves the interhemispheric integration of tactile-motor responses.

1. Introduction

Performing finely tuned movements and complex motor skills using the hands requires close coordination between the two sides of the body. However, sensory input and motor functions are lateralised to the contralateral cerebral hemisphere (Fritsch & Hitzig, 1870; Penfield & Boldrey, 1937), although recent studies have also revealed some level of ipsilateral processing (Tamè et al., 2012; Tamè, Pavani, Papadelis, Farnè, & Braun, 2015; for a review see Tamè, Braun, Holmes, Farnè, & Pavani, 2016). This raises the question of how this coordination between the sensory and motor systems happens. A century ago, Poffenberger developed a behavioural approach to quantify the sensorimotor transfer, which has proven useful in studying this process (Marzi, 1999; Poffenberger, 1912). He showed that people have faster reaction times (RTs) when visual stimuli are presented in the visual field ipsilateral to the hand used to respond, than when presented in the contralateral visual field. He proposed that this contralateral-ipsilateral difference (also known as crossed-uncrossed difference: CUD) reflects the time required for signals to transfer between the two cerebral hemispheres. The logic of the Poffenberger paradigm is that when the sensory stimulus and motor effector are on the same side of the body, sensorimotor information can be integrated and processed within the same hemisphere (uncrossed time). By contrast, if sensory input is presented contralateral to the effector used to respond, the information has to be integrated across hemispheres (crossed time). The most likely anatomical pathway to mediate this effect is considered to be the corpus callosum (CC) (Berlucchi, Aglioti, Marzi, & Tassinari, 1995; Marzi, Bisiacchi, & Nicoletti, 1991; Poffenberger, 1912).

Although most studies using this paradigm have investigated the CUD effect in the visual domain (Bashore, 1981; Chaumillon, Blouin, & Guillaume, 2014; Jeeves, 1969; Pellicano, Barna, Nicoletti, Rubichi, & Marzi, 2013), several studies have found that the same effect also holds for other sensory modalities such as audition (Böhr et al., 2007; Elias, Bulman-Fleming, & McManus, 2000) and touch (Kaluzny, Palmeri, & Wiesendanger, 1994; Moscovitch & Smith, 1979; Muram & Carmon, 1972; Schieppati, Musazzi, Nardone, & Seveso, 1984; Tamè & Longo, 2015; Tassinari &

Campara, 1996). Recently we used this paradigm to show that interhemispheric integration of the tactile and motor responses varies as a function of the specific body part stimulated (Tamè & Longo, 2015). Specifically, we found that sensorimotor interactions change along the proximal-distal axis with faster integration when tactile stimuli were delivered on the forearm than on the fingers.

The high spatial acuity of vision strongly contributes to the spatial encoding of body parts, affecting the processing of signals coming from other sensory modalities such as touch (Cardini, Longo, & Haggard, 2011; Pavani, Spence, & Driver, 2000). In this respect, vision of the body has been shown to affect perception of multisensory stimuli by modulating unisensory performance in several ways. For instance, seeing the body, even when vision is completely non-informative about the tactile stimulus, modulates tactile distance perception (Longo & Sadibolova, 2013), reduces pain (Longo, Betti, Aglioti, & Haggard, 2009; Romano & Maravita, 2014), and also produces limb-specific modulation in skin temperature (Sadibolova & Longo, 2014). Moreover, vision of the body has been shown to enhance tactile performance (Cardini et al., 2011; Kennett, Taylor-Clarke, & Haggard, 2001; Press, Taylor-Clarke, Kennett, & Haggard, 2004; Tamè, Farnè, & Pavani, 2013; Tipper et al., 1998, 2001). For instance, tactile two-point discrimination is improved by vision of the arm (Kennett et al., 2001). Press and colleagues (2004) investigated whether vision of the body enhances tactile performance generally or whether this effect instead depends on specific characteristics such as the spatial nature and the difficulty of the task. Their results showed that non-informative vision of the body enhances tactile performance only when the task is difficult (e.g., tactile discrimination) and requires a spatial computation. Therefore, the effect of vision on tactile processing seems to rely on quite specific multimodal interactions (Press et al., 2004).

In this study, we investigated whether vision of the body affects the interhemispheric integration of tactile and motor information between the two sides of the body, using the Poffenberger paradigm. We tested whether tactile stimuli delivered on the middle fingers of the two hands produced comparable CUDs when one hand was visible, while the other was occluded. As described above, previous reports have shown that vision modulates performance both in terms of

accuracy and RT in response to tactile stimuli under specific circumstances, namely when the task is both difficult and has a spatial component (Press et al., 2004). If vision affects the interhemispheric integration of tactile-motor responses, the magnitude of the CUD should be reduced or absent for the visible hand compared to the occluded hand. In contrast, if vision does not affect interhemispheric tactile-motor integration, the CUD should be similar for both hands (i.e., contralateral and ipsilateral with respect to the responding foot).

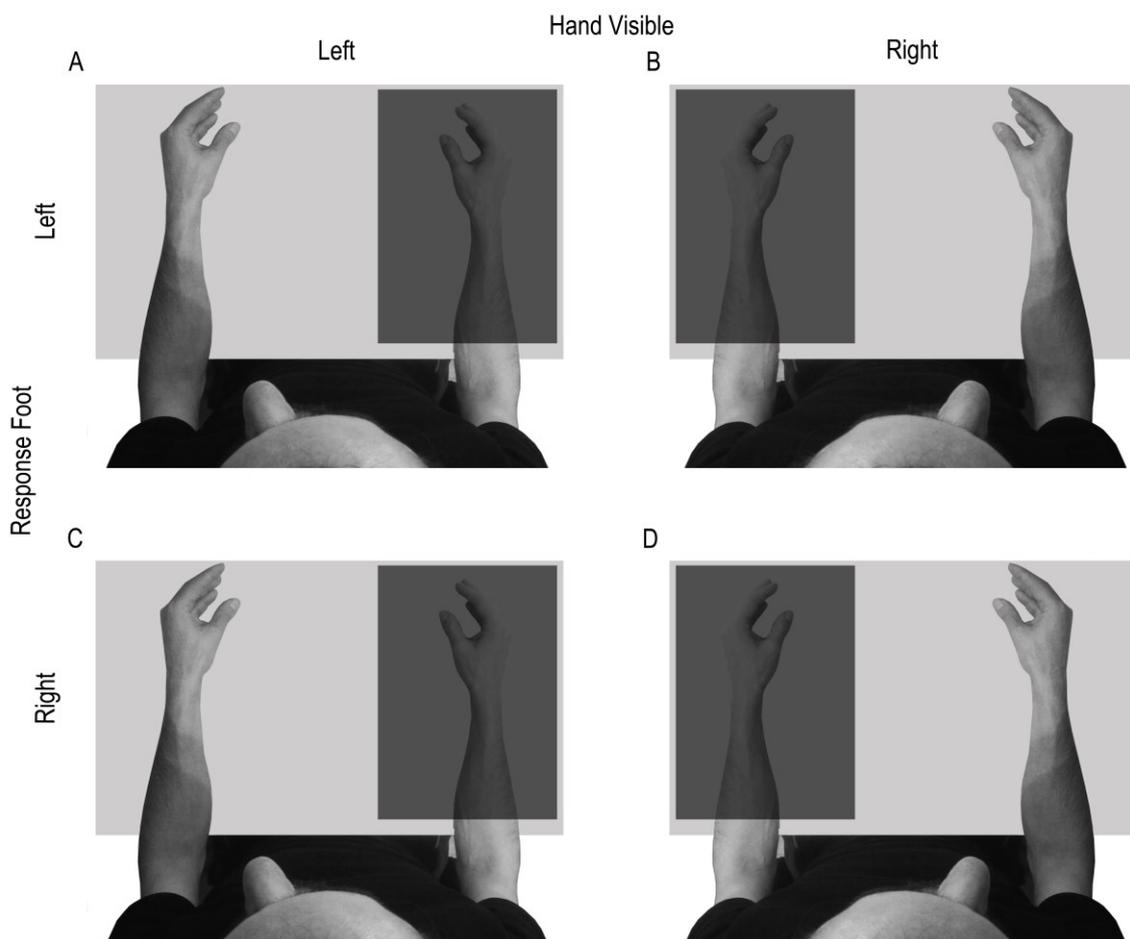


Figure 1. Schematic depiction of the four experimental conditions. Tactile stimuli were always delivered unpredictably on the left or right middle fingers. Across conditions, participants looked toward the left hand responding with the left (A) or right (C) foot or looked toward the right hand responding with the left (B) or right (D) foot. Vision of one hand was prevented by a sheet of black cardboard.

2. Material and methods

2.1 Participants

Twenty-nine participants (mean±SD=30±8.6 years; 12 females) took part in the study. Participants gave their informed consent prior to participation and reported normal or corrected to normal vision and normal touch. The study was approved by the local ethics panel. All participants were right-hand, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; M=79, range 11-100).

2.2 Apparatus and stimuli

Tactile stimuli were delivered on the middle fingers of both hands using two stimulators (Solenoid Tactile Tapper, M&E Solve, UK). The solenoid tappers (8 mm in diameter) producing the suprathreshold tactile stimuli were driven by a 9 V square wave. The apparatus was controlled by means of a National Instruments I/O Box (NI USB-6341) connected to a computer through a USB port. Tactile stimulation was delivered for 5 ms. Tappers assigned to the two sides of the body (left or right middle finger) were randomly changed for every participant, to control for undetectable intensity differences between the stimulator devices. To ensure that the stimulators produced an equal force to the skin, a piezoelectric pressure sensor (MLT1010, AD Instruments, Dunedin, New Zealand) was used to measure the intensity of each tapper before the start of testing.

Tactile stimulators were attached to the body using double-sided adhesive collars and kept in place during the entire experimental session. The hands rested on the table with the tips of the index fingers 60 cm apart. In this way, the stimulators exerted a similar pressure on all body parts. Tactile stimulators were positioned on the centre of the most distal phalanx of the middle fingers (for a similar arrangement see Tamè & Longo, 2015). Depending on the experimental condition, vision of either the left or right hand was prevented by a sheet of black cardboard, placed

horizontally on top of the hands without touching them (Figure 1). One foot-response pedal was positioned under the participant's feet aligned with their body midline. In order to prevent a potential confound of a compatibility effect due to sensorimotor interactions, we chose distant stimulation (i.e., hands) and response (i.e., feet) locations (Broadbent & Gregory, 1965; Fendrich, Hutsler, & Gazzaniga, 2004; Tamè & Longo, 2015). Stimulus presentation and response collection were controlled by a custom program written using MATLAB R2013b (Mathworks, Natick, MA) and the Psychtoolbox libraries (Brainard, 1997). Throughout the experiment, white noise was presented over closed-ear headphones (Sennheiser HD 439 Audio Headphones) to mask any sounds made by the tactile stimulators.

2.3 Design

The experiment followed a repeated-measures design with three factors. These were VISION (stimulated hand visible or unstimulated hand visible), response FOOT (left or right), and SIDE (contralateral or ipsilateral) representing the compatibility between side of stimulation and response. There were four types of block formed by the factorial combination of response foot (left, right) and hand viewed (left, right). Each condition was repeated twice in random sequence, resulting in eight blocks overall. Each block included 150 trials (half stimulation of the left hand and half of the right hand), resulting in a total of 1200 trials for each participant.

2.4 Procedure

Before the main experiment, the participant performed 40 practice trials to familiarize them with the task and to assure they could clearly perceive the stimuli equally on the two fingers and that tactile stimuli were clearly perceptible (i.e., suprathreshold) and not audible. Participants were asked to respond as quickly as possible with their foot as soon as they felt a tactile stimulus on one of the fingers. On each trial only one finger was stimulated. Participants were instructed to keep the foot-pedal pressed continuously and to respond by releasing their foot as soon as they felt the

touch. They were instructed to direct their gaze continuously towards the visible hand. At the beginning of each trial after a variable interval (ranging from 1000 to 2000 ms) a tactile stimulus was presented. Participants were allowed short breaks between blocks. The experimenter remained in the room throughout the session to ensure that participants complied with the instructions.

2.5 Data analysis

Responses shorter than 100 ms were considered anticipations and responses over 500 ms were considered attentional errors (Iacoboni & Zaidel, 2000; Tamè & Longo, 2015). Trials excluded were rerun at the end of each block to assure the same number of trials for each condition (Fendrich, Hutsler, & Gazzaniga, 2004). The overall number of rerun trials was $M \pm SE = 7.3\% \pm 1.2$. For each participant, we computed mean RT in the ipsilateral (i.e., stimulus and effector on the same side) and contralateral (i.e., stimulus and effector on different sides) conditions when the stimulated hand was visible or the unstimulated hand was visible and when participants used the left and right foot to respond. These values were entered into a three-way Analysis of Variance (ANOVA) with VISION (Stimulated hand visible, Unstimulated hand visible), SIDE (Ipsilateral, Contralateral) and FOOT (Left, Right) as within-participant factors. Two-tailed paired t-tests were used for all planned comparisons. Moreover, we computed the CUD by subtracting RT in the contralateral from RT in the ipsilateral stimulus-response combinations for the different visual conditions. A negative CUD indicates that participants were faster in responding when stimulation and response side were different, whereas a positive CUD indicates that participants were faster in responding when stimulation and response side were the same.

3. Results

An ANOVA on RTs revealed a significant interaction between VISION and SIDE, $F(1,28)=4.37$, $p=.046$, $MSE=210$, $\eta_p^2=.14$. As shown in Figure 2A, when the stimulus and effector used to respond

were on the same side of the body (ipsilateral), participants were equally fast to respond regardless of the fact that the stimulated hand was visible ($M \pm SE = 277 \pm 8.1$ ms) or the unstimulated hand was visible ($M \pm SE = 276 \pm 7.8$ ms; $t(28) = 0.72$, $p = .48$, $d_z = .13$). In contrast, when the stimulus and effector were on different sides of body (contralateral), participants were significantly faster in responding when the stimulated hand was visible ($M \pm SE = 275 \pm 7.9$ ms) compared to when the unstimulated hand was visible ($M \pm SE = 282 \pm 7.8$ ms; $t(28) = 3.04$, $p = .005$, $d_z = .56$). Moreover, there was a significant interaction between FOOT and SIDE, $F(1,28) = 7.61$, $p = .01$, $MSE = 263$, $\eta_p^2 = .21$. This was caused by the fact that when participants responded with the left foot they had a significant positive CUD effect (CUD = 7.7ms; $t(28) = 3.29$, $p = .003$, $d = .61$). In contrast, when participants responded with their right foot, there was a tendency towards a negative CUD (CUD = -4.1ms; $t(28) = -1.94$, $p = .06$, $d = .36$). This marked asymmetry in the CUD replicates the effect we previously reported (Tamè & Longo, 2015) using the feet as effectors and previous reports when hands were used as effectors (Fendrich et al., 2004; Kaluzny et al., 1994; Marzi et al., 1991; for a more detailed discussion of this effect see Tamè & Longo, 2015). There was also a significant main effect of SIDE, $F(1,28) = 8.67$, $p = .006$, $MSE = 22.11$, $\eta_p^2 = .24$, and a main effect of VISION, $F(1,28) = 8.20$, $p = .008$, $MSE = 43.91$, $\eta_p^2 = .23$, which were, however, subsidiary to the higher order interaction described above.

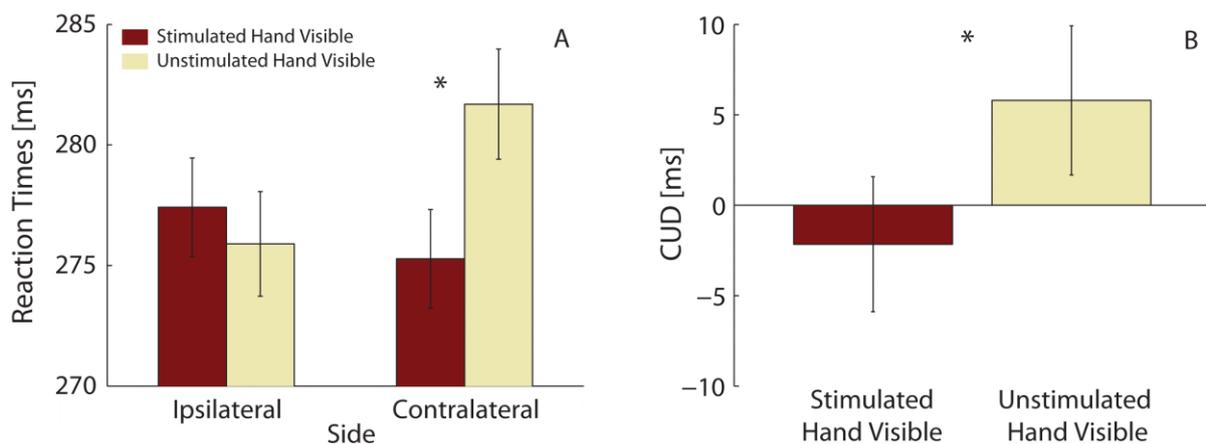


Figure 2. Reaction Times (RTs) as a function of whether the stimulated hand was visible or the unstimulated hand was visible in the ipsilateral (i.e., stimulus and effector on the same side of the body) and contralateral (i.e., stimulus and effector on different sides of the body) conditions (A). Contralateral-ipsilateral difference (CUD) as a function

of the hand's visibility (B). Error bars indicate 95% Confidence Interval of the within participants variability (95%CI). *denotes $P < 0.05$.

Moreover, we performed a one-sample t-test against zero when the stimulated hand was visible or the unstimulated hand was visible. When the unstimulated hand was visible, a significant CUD was found ($M \pm SE = 5.80 \pm 2.1$ ms; $t(28) = 2.76$, $p = .01$, $d = .51$), consistent with previous results using similar paradigms (Fendrich et al., 2004; Kaluzny et al., 1994; Muram & Carmon, 1972; Tamè & Longo, 2015). In contrast, when the stimulated hand was visible, no CUD was apparent at all ($M \pm SE = -2.16 \pm 1.9$ ms), $t(28) = -1.14$, $p = .26$, $d = .21$. Moreover, as shown in Figure 2B a direct comparison between the CUDs when the stimulated hand was visible compared to when the unstimulated hand was visible shows a significant difference ($t(28) = 2.09$, $p = .046$, $d_z = .40$). Note that this is formally equivalent to the previously reported interaction between VISION and SIDE.

Finally, an ANOVA on the number of re-entered trials for the different experimental conditions, as performed for the main data, showed a main effect of VISION ($F(1,28) = 5.05$, $p = .03$, $MSE = 13.35$, $\eta_p^2 = .15$) and an interaction between VISION and FOOT ($F(1,28) = 7.64$, $p = .01$, $MSE = 10.91$, $\eta_p^2 = .21$). This indicates that participants did more anticipations and/or attentional errors when the unstimulated hand was visible and in particular when they used the right foot to respond. This is compatible with the beneficial effect of vision we found in the RTs data and rule out the possibility of a speed-accuracy trade-off. Indeed, it may have been the case that participants were faster in responding when the contralateral stimulated hand was visible, compared to when the unstimulated hand was visible, just because they were making more mistakes in the form of anticipation and/or attentional errors, however, this was not the case.

4. Discussion

This study investigated whether the interhemispheric transfer of tactile stimuli is modulated by vision of the stimulated body part. We presented tactile stimuli unpredictably on the middle

fingers of the two hands, when vision of one hand was prevented. For the occluded hand, the usual CUD was found. In contrast, for the visible hand, the CUD was eliminated. This reduction of the CUD effect when the hand was visible suggests that vision of a body part can compensate for the cost of integration of the sensorimotor signals when stimulus and effector are on different sides of the body (i.e., crossed condition). These results are compatible with previous reports in showing that vision of the body does not have a general effect on the speed of tactile responses in a simple detection task (e.g., Press et al., 2004). Our results do, however, show a more subtle effect on detection, namely when information needs to be transferred between the cerebral hemispheres. We found that vision is effective only in the presence of a particular context, namely when the tactile stimulus and effector belong to different sides of the body and the two signals (i.e., sensory and motor) have to be integrated between the two hemispheres. Therefore, our data suggest that vision of the body does not generally improve tactile detection performance, but instead promotes the integration of the sensorimotor signals when these belong to different sides of the body. These results are also compatible with previous reports in showing a positive CUD when the unstimulated hand is visible (about 5.8 ms) and extend them by showing that the CUD is reduced when the stimulated hand is visible (about -2.2 ms).

The CUD effect we found here when the unstimulated hand was visible is consistent with previous studies on the interhemispheric transfer in touch (Fendrich et al., 2004; Moscovitch & Smith, 1979; Muram & Carmon, 1972; Tamè & Longo, 2015), corroborating the suitability of our approach. We also confirmed the presence of a CUD when the foot is used as effector with tactile stimulation, differently from vision (e.g., Aglioti, Dall'Agnola, Girelli, & Marzi, 1991). Although a direct comparison between the effectors used for visual and tactile stimuli was outside the scope of the study, this result suggest that interhemispheric sensorimotor transfer may involve different mechanisms for vision and touch. The critical finding of the present work is that vision of the body improves the interhemispheric integration of tactile and motor signals. As we have seen, the CUD reflects the time required for signals to transfer between the two cerebral hemispheres when the

sensory input is presented contralateral to the effector used to respond (crossed time), compared to when the sensory stimulus and motor effector are on the same side of the body (uncrossed time). When vision of the contralateral hand was present, the contralateral-ipsilateral difference vanished, dissolving the cost of interhemispheric sensorimotor integration.

4.1 Vision of the body in sensorimotor integration across body sides

Our visual effect is consistent with previous research showing that direct but non-informative (Kennett et al., 2001; Maravita, Spence, Clarke, Husain, & Driver, 2000; Press et al., 2004; Tipper et al., 1998) or indirect (Pavani & Galfano, 2007; Tipper et al., 2001) vision of the body facilitates tactile perception. Several paradigms and effects have documented interactions between tactile, visual, and proprioceptive input in the spatial coding of touch (for reviews see Dijkerman & de Haan, 2007; Macaluso & Driver, 2005; Spence, Pavani, Maravita, & Holmes, 2004). A classic phenomenon of this type of interaction is the “visual enhancement of touch” (VET), in which non-informative vision of a body part results in responses to touch that are faster with respect to when the visual information is absent (Tipper et al., 1998), and even faster for familiar body parts (Tipper et al., 2001).

Kennett and colleagues (2001) tested two-point tactile discrimination thresholds (2PDTs) on the forearm, while modulating visual input by presenting conditions in which the stimulated arm or a neutral object was visible. Tactile spatial resolution was better when the arm was seen, and better still when it was magnified in size. The authors interpreted this result as evidence that vision can improve tactile acuity. A possible explanation proposed by these authors is that feedback modulation to unimodal areas from multimodal areas (e.g., posterior parietal cortex, where there are neurons that respond both to visual and tactile stimuli, Graziano, Yap, & Gross, 1994), can pre-activate the somatosensory cortex, thus resulting in enhanced tactile discrimination. These interactions between different unimodal sensory brain areas could be useful for compensating for possible deficits present in one modality. For instance, Serino and colleagues (2007) showed that in

healthy participants the effectiveness of VET varies as a function of their tactile acuity, with the strongest effects found for participants for whom the stimuli were close to discrimination threshold. Moreover, they tested brain damaged patients and found that VET was present only in those patients with poor tactile acuity. This evidence has been interpreted as an intervention of visual input when the tactile domain is not sufficiently efficient in solving a specific spatial task (Serino et al., 2007).

In many studies of the VET, such as the ones just described, vision could affect touch through tonic pre-activation of the somatosensory cortex. Critically, however, such a mechanism cannot account for our results. This because, we found faster responses to tactile stimuli when viewing the stimulated hand compared to viewing the unstimulated hand in the contralateral, but not in the ipsilateral condition, which were randomly interleaved within experimental blocks. Pre-activation, or any other tonic modulation, of the somatosensory cortex should have reduced the response time both when the stimulus and effector were on the same and different sides of the body. Our paradigm shares some characteristics with previous studies showing VET. For instance, we used a detection task similar to Tipper and colleagues (2001). Unlike that study, however, we varied the side of stimulus and effector, adding a certain amount of complexity (i.e., tactile stimulus occurred unpredictably on the same or different side of the body with respect to the effector). However, unlike Press et al. we did not have an explicit spatial component in our task. Therefore, it is difficult to draw a parallel between the present study and previous reports showing VET, which primarily focused on the sensory (i.e., visuo-tactile) rather than the sensorimotor components of tactile processing, as in the present study. We suggest that our results cannot be explained by the VET effect as previously described, but instead represent a direct effect of vision of the body specifically on sensorimotor integration.

Tamè and colleagues (2013), investigating the role of vision in the differentiation of body side using a tactile double simultaneous stimulation (DSS) task, found no side specific effect of vision. As in a previous report using a similar paradigm (Tamè, Farnè, & Pavani, 2011), the authors

found an interference effect of DSS compared to the target-only stimulation varying as a function of the non-target finger stimulated both within and between the hands. However, non-informative vision of the hands, though it affected overall tactile performance when a visual/proprioceptive conflict was present, did not affect the DSS interference either within or – more critically – between the hands. In the present work we adopted a different approach, in which we directly tested the relationship between the sensory and motor components. It is possible that vision of the body affects tactile interhemispheric transfer only when triggered by a direct motor output, specifically contralateral to the stimulated side. In this respect, there is evidence that goal-directed hand movements to visual or proprioceptive targets are performed more precisely when visual information about initial hand-position is available, in addition to proprioception (Blanchard, Roll, Roll, & Kavounoudias, 2013; Prablanc, Echallier, Jeannerod, & Komilis, 1979; Rossetti, Stelmach, Desmurget, Prablanc, & Jeannerod, 1994). Indeed, vision of the one's own hand can prime manual motor responses (Longo & Haggard, 2009).

4.2 Gaze direction in sensorimotor integration across body sides

The experimental design of this study cannot differentiate the pure effect of vision of the body from the effect of orienting the head or directing gaze towards the hand. Previous reports have shown that vision can affect touch even in the absence of proprioceptive orienting of the eyes or head (Tipper et al., 1998, 2001). For instance, Tipper and colleagues (1998) asked participants to detect, as quickly as possible, a tactile stimulus delivered either on the right or left hand. Across blocks, vision of the hands was occluded and participants looked at a monitor in front of them on which a real-time image of their hand was presented (visual-only). In another condition participants oriented their gaze/head toward one hand while direct vision was prevented (proprioceptive-only). Finally, in another condition participants oriented their gaze/head toward one hand that was visible (vision-proprioceptive). They found that vision of the body facilitated detection of the tactile target in the absence of proprioceptive orienting (Tipper et al., 1998). This result demonstrates that vision

of a body part can affect somatosensation independent of proprioceptive orienting. Nevertheless, it is possible that our effect may be due partly to the allocation of attentive resources in the portion of the space where the stimulation occurs (Driver & Grossenbacher, 1988; Honoré, Bourdeaud'hui, & Sparrow, 1989), rather than vision of the body per se. However, there is reason to think that vision of the body, rather than gaze direction, is most likely to modulate the sensorimotor interaction we report. Forster and Eimer (2005) showed using EEG that vision of the body and gaze direction modulates touch at different stages of somatosensory processing. In particular, vision of the body modulated tactile processing in the primary somatosensory cortex, whereas the effect of gaze direction occurred in higher somatosensory areas (Forster & Eimer, 2005). Given that, integration between motor command and somatic perception is thought to occur early in the tactile representation processing (Gerloff & Andres, 2002; Nelson, 1996; Ruddy, Jaspers, Keller, & Wenderoth, 2016; Tamè, Pavani, Braun, et al., 2015), our results would be more compatible with a primarily effect of vision of the body rather than gaze direction on sensorimotor integration.

4.3 Possible attentional components

Vision of the body may induces adaptive changes in tactile sensitivity (Harris, Arabzadeh, Moore, & Clifford, 2007), that in turn makes the sensory signal available earlier for the transferring. As shown by several studies, vision of the body can modulate tactile spatial selective attention (Gillmeister & Forster, 2010; Làdavas, Farnè, Zeloni, & di Pellegrino, 2000; Macaluso & Maravita, 2010; Sambo, Gillmeister, & Forster, 2009).

Moreover, attentional factors can affect the functional organization of the primary somatosensory cortex (Braun et al., 2002). Neuropsychological research on split-brain patients has shown that callosal connectivity is required in order to process visuotactile spatial information (Spence, Kingstone, Shore, & Gazzaniga, 2001; Spence, Shore, Gazzaniga, Soto-Faraco, & Kingstone, 2001). Vaishnavi and colleagues (Vaishnavi, Calhoun, & Chatterjee, 1999) studied three patients suffering from a stroke involving the right temporal-parietal cortex following which they experienced

tactile extinction. These authors investigated somatosensory functions when vision of the body was or was not present. Across conditions they delivered tactile stimuli only on the left hand, only on the right hand, or bilaterally. Localisation was accurate with single stimulation (i.e., left or right hand), however, under bilateral stimulation the patients were impaired, detecting on average only 4.7% of the contralesional stimuli when presented simultaneously. Critically, when vision was allowed and patients were looking towards their left hand (i.e., contralesional) 2 out of 3 were significantly more likely to detect the tactile stimulus. The authors interpreted these results as evidence of a modulation of tactile awareness on the contralesional tactile stimuli. They proposed that patients' tactile extinction derived from a disorder of spatial attention to a specific spatial location (Vaishnavi et al., 1999). Similarly, in our study, vision of the hand could have facilitated the task by enhancing the processing of spatial tactile information on the body or by reducing the response coding conflict which occurs when stimulus and effectors belong to different side of the body (Pierson, Bradshaw, Meyer, Howard, & Bradshaw, 1991), through a visuo-tactile attentional mechanism.

4.4 Conclusion

The present results show that the tactile CUD is modulated by non-informative vision of the body. In agreement with previous reports, a positive CUD effect was present when vision of the hand was prevented. Critically, however, when the hand was visible, the CUD was significantly reduced, and indeed vanished. Therefore, non-informative vision of a body part (i.e., the hand) improves integration between tactile and motor signals when they belong to different sides of the body. This suggests that vision does not have a general enhancing effect on tactile processing, but instead acts only under particular circumstances, namely in our case when the sensorimotor information processing is more demanding, such as when the sensory and motor signals have to be integrated between the two sides of the body. We propose that this effect might result from the beneficial influence of vision of the body and maybe to some extent gaze direction on tactile perception possibly through a combination of modulatory effect of visuo-tactile interactions and

attentional mechanisms. These mechanisms may be important for mediating appropriate motor responses that regulate the synchronization between the sensory and motor signals when different types of actions (e.g., coordinated or not coordinated) change or have to be executed by the two body sides.

Acknowledgments

We would like to thank Mara Fabri and an anonymous reviewer for their constructive comments on an earlier version of the manuscript. This research was supported by a grant from the European Research Council (ERC-2013-StG-336050) under the FP7 to MRL.

References

- Aglioti, S., Dall'Agnola, R., Girelli, M., & Marzi, C. A. (1991). Bilateral hemispheric control of foot distal movements: evidence from normal subjects. *Cortex*, *27*(4), 571–581.
- Bashore, T. R. (1981). Vocal and manual reaction time estimates of interhemispheric transmission time. *Psychological Bulletin*, *89*(2), 352–368.
- Berlucchi, G., Aglioti, S., Marzi, C. A., & Tassinari, G. (1995). Corpus callosum and simple visuomotor integration. *Neuropsychologia*, *33*(8), 923–936.
- Blanchard, C., Roll, R., Roll, J.-P., & Kavounoudias, A. (2013). Differential contributions of vision, touch and muscle proprioception to the coding of hand movements. *PLoS One*, *8*(4), e62475. <http://doi.org/10.1371/journal.pone.0062475>
- Böhr, S., Güllmar, D., Knab, R., Reichenbach, J. R., Witte, O. W., & Haueisen, J. (2007). Fractional anisotropy correlates with auditory simple reaction time performance. *Brain Research*, *1186*, 194–202.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- Braun, C., Haug, M., Wiech, K., Birbaumer, N., Elbert, T., & Roberts, L. E. (2002). Functional organization of primary somatosensory cortex depends on the focus of attention. *NeuroImage*, *17*(3), 1451–1458.
- Broadbent, D. E., & Gregory, M. (1965). On the interaction of S-R compatibility with other variables affecting reaction time. *British Journal of Psychology (London, England: 1953)*, *56*, 61–67.
- Cardini, F., Longo, M. R., & Haggard, P. (2011). Vision of the body modulates somatosensory intracortical inhibition. *Cerebral Cortex (New York, N.Y.: 1991)*, *21*(9), 2014–2022. <http://doi.org/10.1093/cercor/bhq267>
- Chaumillon, R., Blouin, J., & Guillaume, A. (2014). Eye dominance influences triggering action: The Poffenberger paradigm revisited. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *58*, 86–98.

- Dijkerman, H. C., & de Haan, E. H. F. (2007). Somatosensory processes subserving perception and action. *The Behavioral and Brain Sciences*, *30*(2), 189-201-239.
<http://doi.org/10.1017/S0140525X07001392>
- Driver, J., & Grossenbacher, P. (1988). Multimodal spatial constraints on tactile selective attention. In T. Inui & J. McClelland, *Information INtegration in Perception and Communication* (pp. 208–235). Attention and Performance XVI.
- Elias, L. J., Bulman-Fleming, M. B., & McManus, I. C. (2000). Linguistic lateralization and asymmetries in interhemispheric transmission time. *Brain and Cognition*, *43*(1–3), 181–185.
- Fendrich, R., Hutsler, J. J., & Gazzaniga, M. S. (2004). Visual and tactile interhemispheric transfer compared with the method of Poffenberger. *Experimental Brain Research*, *158*(1), 67–74.
- Forster, B., & Eimer, M. (2005). Vision and gaze direction modulate tactile processing in somatosensory cortex: evidence from event-related brain potentials. *Experimental Brain Research*, *165*(1), 8–18. <http://doi.org/10.1007/s00221-005-2274-1>
- Fritsch, G., & Hitzig, D. (1870). On the electrical excitability of the cerebrum. In *Some papers on the cerebral cortex*. Springfield, IL: Charles C. Thomas.
- Gerloff, C., & Andres, F. G. (2002). Bimanual coordination and interhemispheric interaction. *Acta Psychologica*, *110*(2–3), 161–186.
- Gillmeister, H., & Forster, B. (2010). Vision enhances selective attention to body-related information. *Neuroscience Letters*, *483*(3), 184–188. <http://doi.org/10.1016/j.neulet.2010.08.004>
- Graziano, M. S., Yap, G. S., & Gross, C. G. (1994). Coding of visual space by premotor neurons. *Science (New York, N.Y.)*, *266*(5187), 1054–1057.
- Harris, J. A., Arabzadeh, E., Moore, C. A., & Clifford, C. W. G. (2007). Noninformative vision causes adaptive changes in tactile sensitivity. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *27*(27), 7136–7140. <http://doi.org/10.1523/JNEUROSCI.2102-07.2007>

- Honoré, J., Bourdeaud'hui, M., & Sparrow, L. (1989). Reduction of cutaneous reaction time by directing eyes towards the source of stimulation. *Neuropsychologia*, *27*(3), 367–371.
- Iacoboni, M., & Zaidel, E. (2000). Crossed-uncrossed difference in simple reaction times to lateralized flashes: between- and within-subjects variability. *Neuropsychologia*, *38*(5), 535–541.
- Jeeves, M. A. (1969). A comparison of interhemispheric transmission times in acallosals and normals. *Psychonomic Science*, *16*(5), 245–246.
- Kaluzny, P., Palmeri, A., & Wiesendanger, M. (1994). The problem of bimanual coupling: a reaction time study of simple unimanual and bimanual finger responses. *Electroencephalography and Clinical Neurophysiology*, *93*(6), 450–458.
- Kennett, S., Taylor-Clarke, M., & Haggard, P. (2001). Noninformative vision improves the spatial resolution of touch in humans. *Current Biology: CB*, *11*(15), 1188–1191.
- Làdavas, E., Farnè, A., Zeloni, G., & di Pellegrino, G. (2000). Seeing or not seeing where your hands are. *Experimental Brain Research*, *131*(4), 458–467.
- Longo, M. R., Betti, V., Aglioti, S. M., & Haggard, P. (2009). Visually induced analgesia: seeing the body reduces pain. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *29*(39), 12125–12130. <http://doi.org/10.1523/JNEUROSCI.3072-09.2009>
- Longo, M. R., & Haggard, P. (2009). Sense of agency primes manual motor responses. *Perception*, *38*(1), 69–78.
- Longo, M. R., & Sadibolova, R. (2013). Seeing the body distorts tactile size perception. *Cognition*, *126*(3), 475–481. <http://doi.org/10.1016/j.cognition.2012.11.013>
- Macaluso, E., & Driver, J. (2005). Multisensory spatial interactions: a window onto functional integration in the human brain. *Trends in Neurosciences*, *28*(5), 264–271. <http://doi.org/10.1016/j.tins.2005.03.008>
- Macaluso, E., & Maravita, A. (2010). The representation of space near the body through touch and vision. *Neuropsychologia*, *48*(3), 782–795. <http://doi.org/10.1016/j.neuropsychologia.2009.10.010>

- Maravita, A., Spence, C., Clarke, K., Husain, M., & Driver, J. (2000). Vision and touch through the looking glass in a case of crossmodal extinction. *Neuroreport*, *11*(16), 3521–3526.
- Marzi, C. A. (1999). The Poffenberger paradigm: a first, simple, behavioural tool to study interhemispheric transmission in humans. *Brain Research Bulletin*, *50*(5–6), 421–422.
- Marzi, C. A., Bisiacchi, P., & Nicoletti, R. (1991). Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. *Neuropsychologia*, *29*(12), 1163–1177.
- Moscovitch, M., & Smith, L. C. (1979). Differences in neural organization between individuals with inverted and noninverted handwriting postures. *Science*, *205*(4407), 710–713.
- Muram, D., & Carmon, A. (1972). Behavioral properties of somatosensory-motor interhemispheric transfer. *Journal of Experimental Psychology*, *94*(2), 225–230.
- Nelson, R. J. (1996). Interactions between motor commands and somatic perception in sensorimotor cortex. *Current Opinion in Neurobiology*, *6*(6), 801–810.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113.
- Pavani, F., & Galfano, G. (2007). Self-attributed body-shadows modulate tactile attention. *Cognition*, *104*(1), 73–88. <http://doi.org/10.1016/j.cognition.2006.05.007>
- Pavani, F., Spence, C., & Driver, J. (2000). Visual capture of touch: out-of-the-body experiences with rubber gloves. *Psychological Science*, *11*(5), 353–359.
- Pellicano, A., Barna, V., Nicoletti, R., Rubichi, S., & Marzi, C. A. (2013). Interhemispheric vs. stimulus-response spatial compatibility effects in bimanual reaction times to lateralized visual stimuli. *Frontiers in Psychology*, *4*, 362.
- Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation, *60*(4), 389–443.
- Pierson, J. M., Bradshaw, J. L., Meyer, T. F., Howard, M. J., & Bradshaw, J. A. (1991). Direction of gaze during vibrotactile choice reaction time tasks. *Neuropsychologia*, *29*(9), 925–928.

- Poffenberger, A. (1912). Reaction time to retinal stimulation with special reference to the time lost in conduction through nerve centers. *Arch Psychol*, pp. 1–73.
- Prablanc, C., Echallier, J. E., Jeannerod, M., & Komilis, E. (1979). Optimal response of eye and hand motor systems in pointing at a visual target. II. Static and dynamic visual cues in the control of hand movement. *Biological Cybernetics*, 35(3), 183–187.
- Press, C., Taylor-Clarke, M., Kennett, S., & Haggard, P. (2004). Visual enhancement of touch in spatial body representation. *Experimental Brain Research*, 154(2), 238–245.
<http://doi.org/10.1007/s00221-003-1651-x>
- Romano, D., & Maravita, A. (2014). The visual size of one's own hand modulates pain anticipation and perception. *Neuropsychologia*, 57, 93–100.
<http://doi.org/10.1016/j.neuropsychologia.2014.03.002>
- Rossetti, Y., Stelmach, G., Desmurget, M., Prablanc, C., & Jeannerod, M. (1994). The effect of viewing the static hand prior to movement onset on pointing kinematics and variability. *Experimental Brain Research*, 101(2), 323–330.
- Ruddy, K. L., Jaspers, E., Keller, M., & Wenderoth, N. (2016). Interhemispheric sensorimotor integration; an upper limb phenomenon? *Neuroscience*.
<http://doi.org/10.1016/j.neuroscience.2016.07.014>
- Sadibolova, R., & Longo, M. R. (2014). Seeing the body produces limb-specific modulation of skin temperature. *Biology Letters*, 10(4), 20140157. <http://doi.org/10.1098/rsbl.2014.0157>
- Sambo, C. F., Gillmeister, H., & Forster, B. (2009). Viewing the body modulates neural mechanisms underlying sustained spatial attention in touch. *The European Journal of Neuroscience*, 30(1), 143–150. <http://doi.org/10.1111/j.1460-9568.2009.06791.x>
- Schieppati, M., Musazzi, M., Nardone, A., & Seveso, G. (1984). Interhemispheric transfer of voluntary motor commands in man. *Electroencephalography and Clinical Neurophysiology*, 57(5), 441–447.

- Serino, A., Farnè, A., Rinaldesi, M. L., Haggard, P., & Làdavas, E. (2007). Can vision of the body ameliorate impaired somatosensory function? *Neuropsychologia*, *45*(5), 1101–1107.
<http://doi.org/10.1016/j.neuropsychologia.2006.09.013>
- Spence, C., Kingstone, A., Shore, D. I., & Gazzaniga, M. S. (2001). Representation of visuotactile space in the split brain. *Psychological Science*, *12*(1), 90–93.
- Spence, C., Pavani, F., Maravita, A., & Holmes, N. (2004). Multisensory contributions to the 3-D representation of visuotactile peripersonal space in humans: evidence from the crossmodal congruency task. *Journal of Physiology, Paris*, *98*(1–3), 171–189.
<http://doi.org/10.1016/j.jphysparis.2004.03.008>
- Spence, C., Shore, D. I., Gazzaniga, M. S., Soto-Faraco, S., & Kingstone, A. (2001). Failure to remap visuotactile space across the midline in the split-brain. *Canadian Journal of Experimental Psychology = Revue Canadienne De Psychologie Expérimentale*, *55*(2), 133–140.
- Tamè, L., Braun, C., Holmes, N. P., Farnè, A., & Pavani, F. (2016). Bilateral representations of touch in the primary somatosensory cortex. *Cognitive Neuropsychology*, 1–19.
<http://doi.org/10.1080/02643294.2016.1159547>
- Tamè, L., Braun, C., Lingnau, A., Schwarzbach, J., Demarchi, G., Li Hegner, Y., ... Pavani, F. (2012). The contribution of primary and secondary somatosensory cortices to the representation of body parts and body sides: an fMRI adaptation study. *Journal of Cognitive Neuroscience*, *24*(12), 2306–2320.
- Tamè, L., Farnè, A., & Pavani, F. (2011). Spatial coding of touch at the fingers: Insights from double simultaneous stimulation within and between hands. *Neuroscience Letters*, *487*(1), 78–82.
- Tamè, L., Farnè, A., & Pavani, F. (2013). Vision of the body and the differentiation of perceived body side in touch. *Cortex*, *49*(5), 1340–1351.
- Tamè, L., & Longo, M. R. (2015). Inter-hemispheric integration of tactile-motor responses across body parts. *Frontiers in Human Neuroscience*, *9*, 345.
<http://doi.org/10.3389/fnhum.2015.00345>

- Tamè, L., Pavani, F., Braun, C., Salemme, R., Farnè, A., & Reilly, K. T. (2015). Somatotopy and temporal dynamics of sensorimotor interactions: evidence from double afferent inhibition. *The European Journal of Neuroscience*, *41*(11), 1459–1465.
<http://doi.org/10.1111/ejn.12890>
- Tamè, L., Pavani, F., Papadelis, C., Farnè, A., & Braun, C. (2015). Early integration of bilateral touch in the primary somatosensory cortex. *Human Brain Mapping*, *36*(4), 1506–1523.
- Tassinari, G., & Campara, D. (1996). Consequences of covert orienting to non-informative stimuli of different modalities: a unitary mechanism? *Neuropsychologia*, *34*(3), 235–245.
- Tipper, S. P., Lloyd, D., Shorland, B., Dancer, C., Howard, L. A., & McGlone, F. (1998). Vision influences tactile perception without proprioceptive orienting. *Neuroreport*, *9*(8), 1741–1744.
- Tipper, S. P., Phillips, N., Dancer, C., Lloyd, D., Howard, L. A., & McGlone, F. (2001). Vision influences tactile perception at body sites that cannot be viewed directly. *Experimental Brain Research*, *139*(2), 160–167.
- Vaishnavi, S., Calhoun, J., & Chatterjee, A. (1999). Crossmodal and sensorimotor integration in tactile awareness. *Neurology*, *53*(7), 1596–1598.

Figure caption

Figure 1. Schematic depictions of the setup of the four experimental conditions. Tactile stimuli were always delivered unpredictably on the left or right middle fingers. Across conditions, participants looked toward the left hand responding with the left (A) or right (C) foot or looked toward the right hand responding with the left (B) or right (D) foot. Vision of one hand was prevented by a sheet of black cardboard.

Figure 2. Bar plots show the Reaction Times (RTs) when the stimulated hand was visible or when the unstimulated hand was visible in the ipsilateral (i.e., stimulus and effector on the same side of the body) and contralateral (i.e., stimulus and effector on different sides of the body) conditions (A). Contralateral-ipsilateral difference (CUD) as a function of the hand's visibility (B). Error bars indicate 95% Confidence Interval of the within participants variability (95%CI). *denotes $P < 0.05$.