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Seeing and feeling the body

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Table of contents

Chapter 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

Abstract

Recognizing one's body as separate from the external world plays a crucial role in detecting external events, and thus in planning adequate reactions to them. In addition, recognizing one's body as distinct from others' bodies allows remapping the experiences of others onto one's sensory system, providing improved social understanding.

In line with these assumptions, two well-known multisensory mechanisms demonstrated modulations of somatosensation when viewing both one's own and someone else's body: the Visual Enhancement of Touch (VET) and the Visual Remapping of Touch (VRT) effects. Vision of the body, in the former, and vision of the body being touched, in the latter, enhance tactile processing.

The present dissertation investigated the multisensory nature of these mechanisms and their neural bases. Further experiments compared these effects for viewing one's own body or viewing another person's body. These experiments showed important differences in multisensory processing for one's own body, and for other bodies, and also highlighted interactions between VET and VRT effects.

The present experimental evidence demonstrated that a multisensory representation of one's body – underlie by a high order fronto-parietal network - sends rapid modulatory feedback to primary somatosensory cortex, thus functionally enhancing tactile processing. These effects were highly spatially-specific, and depended on current body position. In contrast, vision of another person's body can drive mental representations able to modulate tactile perception without any spatial constraint.

Finally, these modulatory effects seem sometimes to interact with high order information, such as emotional content of a face. This allows one's somatosensory system to adequately modulate perception of external events on the body surface, as a function of its interaction with the emotional state expressed by another individual.

Introduction

Information coming from different sensory systems interact each other providing a coherent view of the external world. The development of multiple sensory channels and the coexistence of different sensory modalities enhances individuals' likelihood of survival (Stein and Meredith, 1993). The ability of our brain to assemble these types of information and then to sinergically use them in combination is based on Multisensory Integration, whereby the final perceptual result is more than the sum of the unimodal components (Stein and Meredith, 1993). Such integration plays an important role in making sense of afferent inputs reaching the brain from different sensory modalities. Incoming information from different sensory modalities is initially processed in separate brain areas; then a subsequent integration of these signals occurs in specialized multisensory regions (Macaluso and Driver, 2005). This integrative mechanism is just one possible example of interaction between senses. Sensory inputs the brain receives are not only integrated with, but also continuously altered by one another (Stein and Meredith, 1993).

The present project will focus on the study of multisensory mechanisms involving mainly visual and tactile modalities. In order to justify the research questions of the experimental evidence discussed along this dissertation, the relevant multisensory literature will be reviewed, focusing on three specific concepts. First, the notion of the 'body as a multisensory object' will be discussed, thus outlining the topic of the present project. Second, as essential mechanisms involved in multisensory interaction in general, and in the representation of the body, in particular, bottom-up feedforward integrative processes and top-down feedback modulations will be described. Third, the role of the peripersonal space in multisensory interactions and its relation to self/other distinction will be addressed.

I. The body as a multisensory object

The body is a multisensory object par excellence. Our body is an effective means to explore the environment and to interact with objects and conspecifics. A stable representation of one's own body is essential for effective action, and for rapid processing of potentially threatening inputs approaching the body surface.

A crucial question might be: on which basis do I feel my body as my own? How can I assume that the hand I see is mine? Is it because its visual appearance is highly familiar to me? Or is it because as soon as I decide to move the hand, it actually moves? Or perhaps, because when I see it being touched I simultaneously feel a sensation? To answer these questions we should first consider that different body-related information can individually be processed by distinct brain areas. I can visually recognize my face and be able to distinguish it from another face; this process is thought to involve a distributed neural network encompassing the left fusiform gyrus, bilateral middle and inferior frontal gyri and the right precuneus (Platek, Wathne, Tierney, and Thomson, 2008). When I decide to move my arm, neural activity in the somatotopic representation of that arm is observed in the primary motor cortex. If an object touches my hand, tactile afferents are transmitted to the somatosensory cortices (SI and SII). These projections preserve the spatial organization of receptors in the skin, so that SI contains a spatial representation of the touched body part (Kandel, Schwartz, and Jessel, 2000).

Thus distinct representations of one's body seem to exist in our brain. However, we cannot consider the visual or motor or somatosensory representations of the body as working in isolation. Rather the idea that somehow these sensory representations interact to give rise to a complex, coherent sense of the bodily self is likely (Keenan, McCutcheon, Freund, Gallup, Sanders, and Pascual-Leone, 1999; Platek, Thomson, and Gallup, 2004). In fact some lines of evidence highlighted the involvement of crossmodal mechanisms in self-information processing (Driver and Spence, 2000; Spence and Driver, 2004). In particular, past and recent experimental results demonstrated that bodily experiences rely on multimodal mental representations of the body (MBRs), housed in brain areas other than unisensory cortices, such as high order associative regions (Berlucchi and Aglioti, 1997; Serino and Haggard, 2010).

Multisensory processing aims at the interaction between different sensory signals and in the resolution of potential conflicts to generate a coherent representation of the body, essential for a stable sense of bodily self (Tsakiris, 2010). Beyond early studies investigating the bodily ownership through explicit self-recognition tasks (Jeannerod, 2003), investigations of the *feeling* that 'this body really belongs to me' were possible thanks to an effective elegant experimental paradigm: the Rubber Hand Illusion (RHI). This illusion uses multisensory stimulation to manipulate the experience of the bodily self. In this illusion a fake hand is brushed synchronously with one's own unseen hand for a few minutes. Watching the rubber hand being stroked synchronously with one's own hand causes the rubber hand to be attributed to one's own body. After experiencing the illusion, subjects usually report 'to feel like the rubber hand is my hand' (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). This attribution can be measured quantitatively as a drift of the perceived position of one's own hand towards the rubber hand. Conversely, the illusion is not experienced when subjects' hand is stroked asynchronously with the fake hand. Thus, in one condition the sense of body ownership of an observed body part is present, whereas in another condition, it is absent (Botvinick and Cohen, 1998). This paradigm allows for an external object to be *felt*, rather than simply recognized, as part of one's own body.

Several studies took advantage of this paradigm, leading to conclusions that were sometimes controversial. In some cases it was suggested that the sense of body ownership arises in a bottom-up fashion, as an accumulative effect of frequent and recurring multisensory correlations during ontogeny (Armel and Ramachandran, 2003). Moreover it was assumed that, if the appropriate crossmodal matching is provided, any object might be felt as part of one's own body (2003). Thus the visuo-tactile correlation was thought to be both a necessary and a sufficient condition for a sense of ownership to arise.

Other results let to hypothesise that a different mechanism is responsible for the sense of body ownership: top-down modulations have been thought to play an essential role in that. In particular, stored non-primarily sensory representations of the body would be involved in the interpretation of peripheral inputs (Graziano and Botvinik, 2001; Tsakiris, 2010). In line with this assumption, recent works revisited the hypothesis that the sense of ownership might be developed for every object when the multisensory correlation is present. In fact, recent findings demonstrated that objects non-resembling the human hand, or a rubber hand placed in an incongruent anatomical position or of different laterality, with respect to one's stimulated hand could not induce the RHI (Tsakiris and Haggard, 2005; Costantini and Haggard, 2007; Tsakiris, Carpenter, James, and Fotopoulou, 2010). Thus, correlated multisensory inputs were considered a necessary but not anymore a sufficient condition to drive the sense of body ownership; rather the contribution of stored body representations, against which current multisensory inputs are integrated, seemed to play an important modulatory role in this mechanism.

This huge amount of controversial results has been recently taken into account to converge in a neurocognitive model of the sense of body ownership (Tsakiris, 2010). The brain mechanism underlying the sense of body ownership might consist in the interaction between current correlated multisensory inputs and modulations exerted by stored internal body models (Tsakiris, 2007; 2010). Inputs from different sensory modalities are processed and tested-for-fit against cognitive body representations that contain a multimodal description of one's body. Thus, the mental body model interprets current information preserving the coherence of bodily sensory experiences (Tsakiris and Haggard, 2005; Tsakiris, 2007). This conclusion allows assuming that self-representations are not stable, rather they are continuously updated by current inputs; as a consequence, modulations of the sense of ownership of a body part (Longo, Cardozo, and Haggard, 2008) or of the whole body (Ehrsson, 2007; Petkova and Ehrsson, 2008) and the sense of self as distinct from the other are observed.

Several neural structures have been demonstrated to play a crucial role in the process that produces the sense of body ownership: the right temporoparietal junction (rTPJ), the right insular lobe, the posterior parietal cortex (PPC) and the ventral premotor area (VPM) are differently involved. Neuropsychological studies showed that lesion in the rTPJ might result in the denial of ownership of the contralateral hand (Berti, Bottini, Gandola, Pia, Smania, Stracciari, Castiglioni, Vallar, and Paulesu, 2005), neglect of the left side of the body (Committeri, Pitzalis, Galati, Patria, Pelle, Sabatini, Castriota-Scanderbeg, Piccardi, Guariglia, and Pizzamiglio, 2007) and anosognosia for hemiplegia (Berlucchi and Aglioti, 1997). These data suggested the involvement of rTPJ in maintaining a coherent representation of one's body.

Recent neuroimaging studies with healthy volunteers and brain-damaged patients demonstrated a crucial role of the insular lobe in self-recognition (Devue, Collette, Balteau, Degueldre, Luxen, Maquet, and Bredart, 2007) and body ownership (Baier and Karnath, 2008). In their study, Baier and Karnath investigated patients with right brain damage showing anosognosia for hemiparesis/hemiplegia (AHP). Some of them showed in addition ‘disturbed sensation of limb ownership’ (DSO) for the paretic/plegic limb. Anatomical analysis showed that the right posterior insula was commonly damaged in patients showing both AHP and DSO, thus suggesting the involvement of this region in the sense of ownership for limb.

Neuroimaging studies using the RHI paradigm, demonstrated that both PPC and VPM were bilaterally activated in the conditions that induced the illusion (Ehrsson, Spence, and Passingham, 2004; Ehrsson, 2007). The PPC was suggested to contribute to the resolution of visuo-tactile conflicts, recalibrating visual and tactile reference frames (Makin, Holmes, and Ehrsson, 2008). In line with this assumption activation of PPC was found before the onset of the RHI. Conversely, VPM response was shown also when subjects experienced the illusion. This finding suggested that multisensory interaction in the premotor cortex underlies a mechanism for self-attribution (Ehrsson et al., 2004).

Beyond the huge amount of data provided by experiments using the RHI paradigm, a recently developed neuroimaging study (Gentile, Petkova, and Ehrsson, 2011) used natural stimuli to compare unisensory and visuo-tactile stimulations of participants’ hand, in order to identify the previously hypothesized multisensory regions responsible for the observed activations in humans, during the RHI (Ehrsson et al., 2004; 2007) and in animals, when a specific body part was stimulated across somatic and visual modalities (Hyvarinen, 1981; Colby, Duhamel, and Goldberg, 1993; Avillac, Deneve, Olivier, Pouget, and Duhamel, 2005). Gentile and colleagues tested which brain areas responded to visual an tactile stimulation of one’s hand, hypothesising selective activations of the multisensory regions previously identified in non-human primates, thus supporting the idea that visual and tactile signals are integrated to attain a coherent multisensory representation of the body (2011). In line with previous findings, Gentile and colleagues demonstrated specific premotor, parietal and subcortical activations, highlighting the neural networks previously described in non-human primates were neurons integrate visual and tactile signals. The importance of these findings relies on the fact that they provide robust evidence that these networks underlie multisensory perception of the hand in space. In conclusion, given the importance of integration of vision and touch for the sense of body ownership, as shown by RHI studies on self-attribution of limbs (Ehrsson et al., 2004; 2007; Makin et al., 2008), the finding that tactile stimulation of the *real* hand, being watched by its owner, activates specific premotor and parietal structures provides an important validation of the multisensory hypothesis of body ownership (Petkova and Ehrsson, 2008; Tsakiris, 2010).

II. Convergence vs Modulation: two directions of multisensory flow

A general remark from the previous section might be that the feeling that 'this body belongs to me' relies on a coherent multimodal representation of the body. The multisensory interactive processes, providing the sense of body ownership, seem to rely both on integrative/convergent and modulatory mechanisms. In a wider point of view, these different mechanisms provide not only a coherent representation of one's body but also of all the external events occurring around us.

Everyday situations require the different senses not working in isolation, but interacting each other. At the behavioural level, this interaction facilitates detection, and recognition of external events. Interactive mechanisms might occur in several ways. Most research on multisensory perception has focused on cases of *convergence* between inputs from different sensory modalities (Meredith and Stein, 1983). According to this mechanism, multimodal neurons receive information from different sensory modalities and synthesize these inputs in a harmonious percept (Stein and Meredith, 1993).

The mechanism of multisensory convergence follows three general rules (Stein and Meredith, 1993). First, in order to treat stimuli from different modalities as referring to the same external event, they should show spatial coincidence. Second, these stimuli should also arise at approximately the same time. Third, the activity of multisensory neurons shows a response gradient based on the efficacy of the modality-specific stimuli: whereas the pairing of weakly effective stimuli results in a vigorous enhancement of the multisensory neuronal activity, the combination of highly effective stimuli results in little increase in the neuron's response. This property reflects the 'inverse effectiveness rule'. The presence of an inverse relationship between stimulus effectiveness and multisensory enhancement has a great behavioural relevance, considering the survival value of the ability to detect minimal signals. In fact, minimal cues from different sensory modalities are easier to be detected in combination than they are individually. As a consequence, stimuli that are unlikely to produce either neural or behavioural responses when presented separately show the greater advantages from the multisensory combination. According to this property, the beneficial effects of combining different sensory modalities might be more evident at the behavioural level when at least one sensory processing is too weak to induce a behavioural response; thus, a concurrent stimulation of other senses might enhance the response of the weak sensory system. For example, it is well known that localization of an auditory stimulus is enhanced by the presence of a co-occurring spatially coincident near-threshold visual stimulus (Bolognini, Leo, Passamonti, Stein, and Ladavas, 2007; Passamonti, Frissen, and Ladavas, 2009).

Interaction between different modalities was found at the level of single neurons. Convergence at the single neuron level consists in the ability of the neuron to respond to inputs from multiple modalities. Concurrent stimulation in multiple modalities can lead both to enhanced and depressed responses, as compared to unimodal baselines. Response depression has been observed less frequently than enhancement. The reason why some neurons show reduced activity might depend on the presence of specific receptive fields (RFs) properties: whereas the majority of multisensory neurons' RFs is characterized by both excitatory and inhibitory regions, some of them do not have the spatial characteristics necessary for the multisensory inhibition, such as, for example, inhibitory surrounds (Stein and Meredith, 1993; Driver and Spence, 2000).

Meredith and Stein (1983) used standard single-cell recording techniques to investigate the response of superior colliculus neurons to visual, auditory and somatic stimuli. Initially stimuli for each modality were presented individually; then combinations of different sensory stimuli were presented simultaneously. When stimuli in one modality were presented, responses of cells in the deeper laminae of the superior colliculus consisted of few impulses, whereas in case of presentation of combined stimuli from different modalities, an enhancement of responses was observed. Thus convergence of input from different sensory modalities seems to involve enhancing superior colliculus responses above those evoked by individual modality-specific stimuli.

Further studies showed several other brain areas whose neurons might receive input from stimuli of different sensory modalities. For example, bimodal neurons were found in the macaque putamen (Graziano and Gross, 1993). The macaque putamen is somatotopically organized (Crutcher and DeLong, 1984) and it receives projections from the somatosensory and motor areas (Kemp and Powell, 1970). For these reasons the putamen has been largely considered a somatomotor structure (Alexander, DeLong, and Strick, 1986). However other areas project to the putamen, such as the parietal area 7b (Kunzle, 1975; Weber and Yin, 1984) and the ventral premotor area 6 (Kunzle, 1975). These areas contain some visually responsive neurons (Duhamel, Colby, and Goldberg, 1998; Rizzolatti, Fogassi, and Gallese, 2002). Recordings in the macaque putamen showed visual responses in the face and arm regions of the somatotopic map. Visual and tactile responses were combined in a single neuron and the visual RF matched the location of the tactile receptive field.

Bimodal neurons have been found also in the premotor cortex (Graziano, Yap, and Gross, 1994). Premotor neurons are active when the animal moves and they also respond to visual stimuli. Thus they play an import role in the visual guidance of movement. Moreover most of these visual neurons respond to tactile stimuli: their tactile RFs are on the face and on the arms and their visual RFs extend outwards into the space surrounding the tactile RF (Rizzolatti, Scandolara, Matelli, and Gentilucci, 1981). As in the putamen, in the premotor cortex tactile RFs of bimodal neurons are somatotopically organized (Gentilucci, Fogassi, Luppino, Matelli, Camarda, and Rizzolatti, 1988).

Convergence of input from different sensory modalities has been described also in parietal areas such as area 7b (Hyvarinen, 1981) and ventral intraparietal area (VIP; Duhamel et al., 1998; Avillac, Ben Hamed, and Duhamel, 2007). Recently, single-unit recordings in two alerted monkeys showed that the majority of ventral intraparietal neurons perform multisensory integration (Avillac et al., 2007). Despite the fact that activity of bimodal neurons is usually enhanced when multisensory integration mechanisms take place - as compared with activity evoked by single modality stimulation (Meredith and Stein, 1983; Perrault, Vaughan, Stein, and Wallace, 2003) - ventral intraparietal neurons are characterized by depression: activity elicited by convergent input is less than the sum of activities individually evoked by each sensory modality (Avillac et al., 2007).

Neuroimaging data provide evidence in support of this sensory-convergence hypothesis in humans. fMRI and PET studies showed brain activity during simultaneous presentation of stimuli from different modalities, demonstrating activation of both primary sensory areas and of multisensory regions, such as the intraparietal sulcus (IPS), the posterior part of the superior temporal sulcus (STS) and the ventral premotor cortex (Bremmer, Schlack, Shah, Zafiris, Kubischik, Hoffmann, Zilles, and Fink, 2001; Macaluso and Driver, 2001). Calvert and colleagues (Calvert, Campbell, and Brammer, 2000), for example, exposed ten human subjects to semantically congruent and incongruent audio-visual speech and to each individual modality. Brain activations during congruent and incongruent audio-visual inputs identified a multimodal area in the left superior temporal sulcus (STS) that showed supra-additive response enhancement for congruent audio-visual stimuli and sub-additive response for incongruent ones.

Multisensory convergence is thought to serve for sensitive detection of events (Stein and Meredith, 1993), on the basis of co-occurrence of minimal amounts of information from a common source. It might also allow sensory substitution when information is ambiguous, attenuated or not available at all. Several lines of evidence demonstrated that in cases of ambiguity or conflicts, auditory inputs strongly affect visual perception (Gebhard and Mowbray, 1959; Recanzone, 2003). One study demonstrated that sound can alter the visually perceived direction of motion, when the motion direction of the visual stimulus is ambiguous and could be interpreted in two different ways (Sekuler, Sekuler, and Lau, 1997). In their study Sekuler and colleagues presented two identical visual objects approaching and moving away from each other. However, when a brief sound was presented around the time of visual coincidence of the two objects, the probability of perceiving a bouncing motion increased compared to when no sound was provided.

Moreover, with the “the sound-induced flash illusion” Shams and colleagues demonstrated that the visual perception might be altered even when there is no ambiguity in the visual stimulus (Shams, Kamitani, and Shimojo, 2000; 2002). When a brief visual stimulus is accompanied by two brief sounds, it is often perceived as two flashes. The same kind of visual illusion is also induced by taps on the finger accompanying flashes (Shams and

Kim, 2010).

Our senses usually receive correlated information from the same objects or events (Driver and Spence, 2000). The ability of our nervous system to combine different sources of information providing a likely description of the external world, is thought to be highly adaptive (Ladavas and Farne, 2004). Convergence of input from different sources in multisensory areas also seems to play another important role in everyday life. Our senses are usually bombarded with simultaneous stimulation. In a world in which many different kinds of events occur at various times in various places, we must attend to some of them and ignore others if we aim to assess an environment comprehensively and adaptively: mechanisms of selective spatial attention are required to pick out relevant information, inhibiting the processing of irrelevant information and to determine which stimuli are related to one another and which are not (Driver and Spence, 1998). Since different sensory channels convey information to the brain based on the modality of its origin and not on the relatedness of stimulus combinations, stimuli from different modalities must be reassembled in order to relate them to one another. The convergence of information on the same, multisensory neurons is thought to be the mechanism with which this may be achieved in the brain.

A second, less investigated, form of multisensory interaction occurs when activity from one sensory modality *modulates* activity in another. Multisensory modulation is observed when processing of information in one sensory modality influences the effects of processing in another modality, thus involving horizontal interactions between different sensory pathways. Moreover, multisensory modulation might be the result of feedback influences from multimodal areas on predominantly unimodal functions. Whole brain neuroimaging techniques, such as fMRI, led to the discovery that regions that were classically considered purely sensory-specific could nevertheless show multisensory effects. For example, in a previous PET study Sathian and colleagues showed extrastriate visual areas activations during a tactile discrimination task (Sathian, Zangaladze, Hoffman, and Grafton, 1997). Participants were asked to judge the orientation (horizontal versus vertical) of tactile gratings applied on the participants' fingertip. Results showed parieto-occipital cortex activity during discrimination of grating's orientation. Similarly, unisensory visual input can modulate activity in unisensory-specific auditory areas, for example during silent lip-reading. Calvert and colleagues identified overlapping activations for heard speech and silent lip-reading within auditory areas in the temporal cortex (Calvert, Bullmore, Brammer, Campbell, Williams, McGuire, Woodruff, Iversen, and David, 1997). Another effective example of multisensory modulation is provided by the ventriloquist effect. Whereas co-occurring auditory and visual stimuli in spatial coincidence are known to enhance performance of auditory localization due to integration of stimuli from different sensory channels (*convergence*), presenting simultaneous but spatially discrepant auditory and visual stimuli is known to mostly induce a perceptual translocation of the sound towards the visual stimulus, i.e. a detrimental effect of visual event on auditory localization, the so-called ventriloquist effect (Howard and Templeton, 1966; Welch and Warren, 1980; Bertelson and Radeau, 1981; Vroomen, de Gelder, and Vroomen, 2004). More precisely this effect consists in a tendency to localize closer together simultaneous visual and auditory stimuli presented in slightly separate locations (Bertelson, 1999). The common finding is that visual stimulus attracts the sound, even if sometimes also the reverse is possible (Bertelson and Radeau, 1981; Vroomen, Bertelson, and de Gelder, 1998). Plasticity that underlies the ventriloquist effect might consist in alteration of the neural representation of auditory stimuli, by making them matching the visual representation of space in the map.

Two hypotheses have been developed in order to explain how information in one sensory modality might modulate the activity in brain regions dedicated to a different modality. Whereas the first hypothesis considers direct anatomical connections between sensory-specific areas, the second suggests the existence of top-down modulatory projections from multisensory areas to sensory-specific regions (Macaluso, 2006). This second hypothesis usually combines feed-forward hierarchical convergence of signals from primary areas into multisensory areas, with modulatory feedback projections from these associative higher-level regions towards sensory-specific cortices (Macaluso, Frith, and Driver, 2000; 2002; Macaluso and Driver, 2005; Driver and Noesselt, 2008).

It is worth noting that the feedback hypothesis has been often developed for audio-visual multisensory interactions (McDonald, Teder-Salejarvi, Di Russo, and Hillyard, 2003; 2005; Bizley, Nodal, Bajo, Nelken, and King, 2007), and its role in multisensory visuo-tactile body perception has been less studied, although the huge amount of data obtained with the RHI paradigm strongly suggests top-down contributions to body perception and to interpretation of incoming multisensory information (Botvinick and Cohen, 1998; Tsakiris, 2007; 2010).

The existence of these two different multisensory mechanisms (*convergence* versus *modulation*) is further confirmed by a recent study where the neural circuits underlying the audio-visual multisensory integration and the visual bias on auditory perception observed in the ventriloquist effect, were compared. Using repetitive transcranial magnetic stimulation (rTMS), Bertini and colleagues tested the role of right temporoparietal cortex (rTPC), right occipital cortex (rOC) and right posterior parietal cortex (rPPC) in an auditory localization task in which indices of multisensory convergence and ventriloquism were computed (Bertini, Leo, Avenanti, and Ladavas, 2011).

Results showed that the audio-visual multisensory enhancement in auditory localization when rTMS was delivered over the rTPC decreased, remaining unaffected when virtual lesions were induced in both rOC and rPPC. Conversely, the ventriloquist effect was affected only when rTMS was delivered over the rOC. The first result was in line with the functioning of *convergence*, confirming the crucial role of multimodal areas in facilitating the processing in one sensory modality, whereas the second result was in line with a *modulatory* activity of one sensory modality over another. Moreover, since virtually disrupting the functioning of the temporoparietal area – a well known multimodal area showing enhanced neural responses for audio-visual stimuli presented in spatial and temporal coincidence – reduced the facilitatory effect in auditory localization, further support was provided to the involvement of the rTPC in the multisensory audio-visual integration mechanism. Results on the ventriloquist effect, instead, provided support to the hypothesis that cortical activity in the occipital regions modulates the ventriloquist effect. In particular, neuroimaging studies (Pekkola, Ojanen, Autti, Jaaskelainen, Mottonen, Tarkiainen, and Sams, 2005; Meyer, Baumann, Marchina, and Jancke, 2007; Kayser, Petkov, and Logothetis, 2009) have already demonstrated that visual information might exert both excitatory and inhibitory effects on the activity of auditory cortex, supporting the hypothesis of the existence of direct modulatory projections from visual to auditory regions (Bonath, Noesselt, Martinez, Mishra, Schwiecker, Heinze, and Hillyard, 2007; Bertini et al., 2011). These projections might be responsible for the perceptual bias in auditory localization produced when audio-visual stimuli are spatially incongruent. Indeed, rTMS over rOC seemed to reduce the strength of projections from the visual areas to the auditory regions, thus reducing the bias in auditory localization (Bertini et al., 2011).

III. The role of Peripersonal Space in multisensory interaction and its relation to self/other distinctions

A stable representation of the space immediately around us - the peripersonal space - arises by integration of inputs from different sensory modalities. The peripersonal space is particularly relevant for behaviour (Rizzolatti, Fadiga, Fogassi, and Gallese, 1997). A sensory event occurring within the peripersonal space potentially requires fast and accurate motor responses. Indeed this event might represent potential threat for the body, triggering defence or object avoidance responses (Graziano and Cooke, 2006), or it could be interesting, thus eliciting a planned reaching movement towards the external object.

Early studies on brain-damaged patients confirmed the existence of a multimodal visuo-tactile representation of the peripersonal space. Patients who had suffered a right-hemisphere stroke showed a deficit in processing a tactile stimulus delivered on the contralesional hand when another stimulus was concurrently delivered on the other hand. This phenomenon has been called ‘extinction’ and it is interpreted as the result of an unbalanced competition between simultaneous targets for access to limited attentional resources (Desimone and Duncan, 1995; Di Pellegrino, Basso, and Frassinetti, 1997). It has been shown that extinction may occur both within (Ladavas, 1990; Di Pellegrino and De Renzi, 1995) and between different sensory modalities (Ladavas and Pavani, 1998; Ladavas, Zeloni, and Farne, 1998; Farne and Ladavas, 2002). More specifically, in the latter case, the competition between left and right space representations in one modality (for example the somatosensory representations activated by tactile stimuli), might be modulated by the activation of an intact spatial representation in a different modality (for example that activated by a visual stimulus). In patients with right-hemisphere lesion and tactile extinction on the left side of their body, a visual stimulus presented near the ipsilesional hand interfered with the processing of a tactile stimulus on the contralesional hand, to the same extent, as did an ipsilesional tactile stimulus. Moreover, under bilateral tactile stimulation, a visual stimulus presented close to the contralesional hand improved tactile processing on that hand. On the contrary, when the visual stimulus was presented far from the contralesional hand (i.e. in the extrapersonal space) no improvement in tactile processing was observed (Ladavas, Farne, Zeloni, and di Pellegrino, 2000). These results are an effective example of the existence of an integrated visuo-tactile system, coding stimuli located in the peripersonal space.

The presence of bimodal neurons in monkey parietal areas 7b and VIP, premotor area 6 and the putamen helps in understanding the nature of the mechanism underlying the crossmodal effects on representation of the body and the peripersonal space in humans. As already mentioned, neurons in these areas respond to tactile stimuli administered on a given part of the animal's body and to visual and/or auditory stimuli only if presented close to the same body part (Duhamel, Colby, and Goldberg, 1991; Graziano and Gross, 1995; Avillac et al., 2007). Importantly, proximity to the body is defined in body-part centered reference frames: if the body part anchoring the neuron's tactile RF moves, then the visual or auditory RF also coherently shifts (Graziano and Cooke, 2006).
Thus, going back to the previously described study, activation of these multimodal neurons by a visual stimulus near the contralesional hand resulted in an enhancement of the damaged somatosensory representation of the same hand, correcting the behavioural bias towards the ipsilesional hand and, as a consequence, reducing tactile extinction (Ladavas et al., 2000).

Multimodal sensory integration between visual signals close to *one's* body and tactile stimuli on its surface is of great importance to the bodily-self awareness (Beschin and Robertson, 1997; Murata and Ishida, 2007) and to allow an accurate recognition of events in the peripersonal space. Nevertheless it has recently been showed that even tactile stimulations seen on *someone* else's body and visual stimuli approaching that body, are somehow processed by the observer's brain (Keysers, Wicker, Gazzola, Anton, Fogassi, and Gallese, 2004; Ishida, Nakajima, Inase, and Murata, 2009). This suggests that mental representations of one's own body and the surrounding space are available for perception of others and the space around them.

A recent monkey study investigated responses of parietal structures, coding for one's body and the surrounding space, when visual stimuli were presented in the peripersonal space of an experimenter's body, sitting in front of the monkey. In particular, visuo-tactile bimodal neurons in the anterior part of the fundus of the Intraparietal Sulcus (IPS) and in the inferior parietal lobule of the monkey were tested. Interestingly, several neurons exhibited bimodal RFs on the monkey's body – thus being activated both by tactile stimuli on a certain body part and visual stimuli in a location congruent with the tactile RF - and visual RFs close to the experimenter's body. Thus, for example, a visual stimulus within 30 cm from the monkey's cheek evoked a strong discharge as much as a visual stimulus located at the same distance close to the experimenter's specular corresponding cheek. Moreover, when the visual stimulus was still present, and the experimenter was absent, these bimodal neurons showed a reduced or absent response. Given these findings, this kind of neurons was identified as 'body-matching bimodal neurons' (Ishida et al., 2009).

In conclusion, due to a strong spatial asymmetry between self and other, I can never be in the extrapersonal space, whereas the other bodies can be somehow 'projected' onto my bodily space; a mechanism whereby the bodily self and the space around it are used as references for perception of the other bodies and the surrounding space, seems to allow a link between the mental representation of my body with the mental representation of someone else's body. This is suggested by specific activations of those neural structures that respond both when a stimulus is on one's body or in close proximity to it and when a visual stimulus is close to another person's body (Ishida et al., 2009).

In a case of visuo-tactile synesthesia one subject experienced observation of another person being touched as tactile stimulation on the specular corresponding part of her own body (Blakemore, Bristow, Bird, Frith, and Ward, 2005; Banissy and Ward, 2007). In addition, in a case of anosognosia, the anosognosic patient denied another patient's paralysis (Ramachandran and Rogers-Ramachandran, 1996). These examples suggested the importance of one's own body representations for perceiving others' body. The mechanism representing the other's body and the surrounding space in the observer's brain might allow predicting other perceptual states based on mere observation of their bodies (Gallese, 2007). Finally, understanding other's states might facilitate the observer in adjusting adequate behavioural responses in face-to-face social interactions.

IV. Overview of the thesis

The topic of the research presented in this thesis is the effects on tactile processing of mental body representations, underlie by different kinds of crossmodal interactions between vision, proprioception and touch. In particular, with the present dissertation, several new issues related to the effect that viewing the body has on tactile perception – the so-called Visual Enhancement of Touch (VET) effect - will be addressed. A second crossmodal effect, strictly related to the VET, will be widely investigated. This mechanism, termed Visual Remapping of Touch (VRT), consists in a modulatory effect that vision of touch towards the body has on tactile perception.

The aims of the present thesis were to shed further light on a) the neuronal mechanisms underlying the VET effect, b) the mechanisms and the neural underpinnings of the VRT effect, c) the relationship between the VET and the VRT effects, d) the role high order mechanisms might play in modulating the VRT.

Common to all these aims was the attempt to clarify the multisensory nature of the VET and the VRT effects. Multisensory *convergence* and multisensory *modulation* co-occur in many perceptual situations. This fact makes it difficult to separate the processes of multisensory convergence from those of multisensory modulation. Unimodal signals converge in multimodal areas (multisensory convergence) that then feedback to influence unimodal areas (multisensory modulation). The present dissertation will be focused on the different contributions of these multisensory mechanisms in updating coherent body representations and on how these differently modulate tactile processing.

The first chapter (Chapter 1) describes data about the VET provided so far. In addition, some issues that have not hitherto been investigated are addressed. In particular two electrophysiological (EEG) studies are developed in order to investigate the neuronal mechanisms (Experiment 1) and the time-course (Experiment 2) of the VET. In the first study the hypothesis that the enhancement of tactile acuity when viewing the body might arise from a flexible modulation of cortical lateral inhibition – a widespread mechanism present in several sensory systems and responsible for enhancement of sensory acuity – is tested. Thanks to an indirect EEG measure of intracortical inhibition, the first experiment demonstrates that vision of the body enhances spatial sensitivity of touch by increasing inhibition in primary somatosensory cortex (SI). The second EEG experiment (Experiment 2) investigates the onset latency of this mechanism, showing an early and quick activation of the primary somatosensory cortex when viewing the body compared to when viewing an object. Results from Chapter 1 suggest that vision of the body immediately drives a body representation and that feedback modulatory projections from areas housing this representation are quickly sent to SI, sharpening the spatial tuning of tactile RFs, and finally increasing tactile acuity.

Vision of the body can exert different effects on tactile perception as a function of whose body it is. The second chapter (Chapter 2) discusses controversial results, present in literature, about the behavioral and neural effects of vision of *one's own* and of *someone else's* body. In this chapter it is hypothesized that these two visual contexts might drive mental body representations of a different nature, thus giving rise to different modulatory effects on tactile processing. Two behavioral studies (Experiments 3 and 4) shed light on the nature of these mental body representations, suggesting that vision of one's body might modulate tactile perception only once current multisensory inputs are integrated in a coherent representation of one's body, whereas simply vision of another person's body is sufficient to play its modulatory role to tactile processing. In addition, Experiment 4 demonstrates a crucial role of vision of touch towards one's body in updating a coherent bodily self-representation able to enhance somatosensation.

The third and the fourth chapters (Chapters 3 and 4) focus on the Visual Remapping of Touch effect. In particular, Chapter 3 provides a wide description of this effect addressing the issue related to its neural underpinnings. Since viewing touch towards a face enhances tactile perception on one's own face, with a maximum effect when the seen face is one's own, Chapter 3 present an fMRI study (Experiment 5), where a multisensory bodily self-representation is hypothesised as responsible for the self-specific VRT effect. As a confirmation of this hypothesis Experiment 5 demonstrates that a fronto-parietal network - usually involved in integrating multisensory information related to one's body – is specifically involved when viewing touch towards one's face.

The VRT has been thought as important in social interactions, since by implicitly referring what is seen expressed on the bodies of others to one's own body, one might better understand other people's feelings. Important information in face-to-face interaction is also the emotional content conveyed by a face. Chapter 4 describes two behavioural studies (Experiments 6 and 7) where the issue of a possible interaction between the VRT mechanism and the emotional expression processing is addressed. In particular, Experiment 6 tests the hypothesis of a different modulation of the VRT as a function of the valence of the emotion expressed by the observed face (positive versus negative). Results demonstrated a modulatory effect on the VRT only when the face shows a negative emotion. As a consequence, Experiment 7 investigates more in deep whether previous results are related to a general effect of all negative emotions on the VRT or rather if they reflect the effect of a specific negative emotional expression. Results show a fear-specific effect, suggesting that mechanisms underlying different emotions processing differently interact with the somatosensory system.

CHAPTER 1

Neuronal mechanisms and timing of the Visual Enhancement of Touch (VET)

As previously mentioned in the Introduction session the mental body representation is a synthetic result of multisensory interactive mechanisms. This multimodal representation might modulate unimodal processing. The present chapter focuses on one particular form of body-related multisensory modulation: the visual enhancement of touch (VET). The VET effect appears to be a contextual top-down effect, which might allow the study of multisensory modulation without the confounding co-occurrence of multisensory convergence.

It has previously been shown that simply viewing the body improves tactile perception, relative to viewing an object in the same location (Kennett, Taylor-Clarke, and Haggard, 2001). In their study Kennett and colleagues asked subjects to perform a two-point discrimination task (2PDT) on their forearm, while watching either at their touched body part or at an object presented in the same location. For the entire experiment no visual information pertaining to the tactile stimulation was provided. Results showed that spatial resolution of touch – i.e. the ability to discriminate spatially detailed stimuli - was improved when viewing the stimulated body site compared to viewing the object. This effect did not result simply from feedforward convergence of visual and tactile information, since it occurred when vision was entirely non-informative about touch. Explanations based on multisensory spatial attention are also insufficient, since the touched body part and the object were made to appear at the same spatial location using an arrangement of mirrors. Since vision provides no information about the tactile stimulus, but only a multisensory context in which tactile information occurs, such effects cannot simply be explained as integration of tactile and visual information. Rather, viewing the body seems to provide a visual context or ‘set’ that enhances tactile processing through a top-down modulatory mechanism (Serino and Haggard, 2010).

The contextual interpretation is further supported by the finding that VET persists for some seconds of darkness after viewing the hand (Taylor-Clarke, Kennett, and Haggard, 2004). In a first experiment participants judged orientations of tactile gratings applied to their right index fingertip. During the task participants viewed either their fingertip or an object. Tactile acuity was enhanced when viewing the fingertip compared to when viewing the object. In a second experiment participants saw either their fingertip or the object for a short time interval (in different trials, either two or ten seconds) and once in darkness, they were asked to judge the orientation of the grating applied to their fingertip. Results confirmed that viewing the body enhances tactile acuity, and demonstrated that this effect outlasts the visual input itself by several seconds. The temporal persistence of the effect of viewing one’s own body on tactile processing suggests that vision of the body is not merely altering simultaneously brain activity in unimodal somatosensory areas but is a ‘setting context’ for subsequent somatosensory processing. Other studies showed that tactile events might affect activity in unimodal visual areas when presented in the same spatial location and simultaneously to a visual target (Macaluso et al., 2000; Kennett, Eimer, Spence, and Driver, 2001). Taylor-Clarke and colleagues further showed that vision might affect tactile processing even when not temporally coincident with the tactile stimulus (2004).

Two previous studies investigated the possible locus of the VET effect. Taylor-Clarke and colleagues (Taylor-Clarke, Kennett, and Haggard, 2002) measured mechanical somatosensory evoked potentials (SEPs) in a two-point discrimination task while viewing the arm or an object. They found that the N80 component was enhanced while viewing the arm. This component has been identified with a second wave of recurrent processing within primary somatosensory cortex (Allison, McCarthy, and Wood, 1992). This result might be considered the first evidence that noninformative vision of the stimulated body part modulates somatosensory cortex activity, thus improving behavioral performance. A similar conclusion about the key role SI might play in VET was reached by Fiorio and Haggard (Fiorio and Haggard, 2005), who found that a single TMS pulse over primary somatosensory cortex, during a brief dark interval between vision and touch, abolished the visual enhancement of touch. TMS over another area in the somatosensory pathway, such as SII, was ineffective. Taken together behavioral, EEG and TMS results (Taylor-Clarke et al., 2002; Taylor-Clarke et al., 2004; Fiorio and Haggard, 2005) showed that vision of the body might play an important role in early stages of tactile processing, maybe pre-setting the neural circuits underling tactile acuity.

These neurophysiological results received further support from findings of Serino and colleagues (Serino, Padiglioni, Haggard, and Ladavas, 2009): viewing the hand improved tactile discrimination not only on the hand, but also on the cheek. Participants were tested in a 2PDT on the hand, face or foot, while watching their own hand or while being blindfolded. Viewing the hand improved tactile acuity both on the face and on the hand compared to when participants were blindfolded; on the contrary no difference between visual conditions was found in tactile acuity on the foot. Both the hand and the face are co-represented in a single lateral part of SI (Yang, Gallen, Schwartz, and Bloom, 1993; Sato, Nariai, Tanaka, Maehara, Miyakawa, Sasaki, Momose-Sato, and Ohno, 2005) and since this overlap of hand and face representations is a peculiarity of the somatotopic organisation of SI, but not of other cortical tactile maps (Huang and Sereno, 2007), this again suggests that the VET effect involves SI, and also that might follow SI specific somatotopic organization (Serino et al., 2009).

While these findings suggest that visual enhancement occurs within SI, the specific neuronal mechanism involved remains unclear. Several observations suggest that the mechanism is independent of the stimulated skin region: viewing the arm (Kennett et al., 2001) or the hand (Taylor-Clarke et al., 2004) all improve tactile discrimination on the viewed body part. Further, viewing the body modulates the spatial gradient of tactile masking, producing a more highly focused spatial pattern of interference from distractors, compared to viewing an object (Haggard, Christakou, and Serino, 2007). These effects suggest that viewing the body does not produce an undifferentiated modulation of somatosensory processing, but specifically sharpens the spatial tuning of tactile RFs. These changes are consistent with a reduction of RFs size of somatosensory cortical neurons.

The mechanism responsible for reduction of RFs size is the lateral inhibition that will be briefly described in the next paragraph.

1.1 Evidence for a lateral inhibition mechanism in the somatosensory system

Lateral inhibition is a neuronal mechanism that is widespread in sensory cortical areas, such as the visual and the somatosensory cortices (Kandel et al., 2000).

RFs of SI neurons have inhibitory regions adjacent to a central excitatory area (DiCarlo, Johnson, and Hsiao, 1998). For this reason inhibitory regions of the RFs are called *inhibitory surround.* This means that when a stimulus occurs only within the inhibitory region, there is no effect on neuron’s firing rate. On the contrary, whenever one or more stimuli occur within the excitatory area, the probability of firing is maximum. Finally, when stimuli fall in both inhibitory and excitatory areas of the RF, the probability of firing is reduced relative to that expected from the stimulation of the excitatory region alone (DiCarlo and Johnson, 2002). The inhibitory region in a RF serves to enhance the contrast between stimuli and thus enhancing spatial acuity (Kandel et al., 2000). Inhibition is thought to be produced by inhibitory interneurons located both in the thalamic relay nuclei and in the cortex. For this reason different possible mechanisms are responsible for RFs size of SI neurons. Whereas a first mechanism involves feed-forward circuits of thalamic inhibitory projections to the somatosensory cortex, a second mechanism involves activation of inhibitory interneurons located directly into the cortex. Briefly, a local network of inhibitory interneurons connects adjacent cortical neurons, so that firing of one cortical neuron tends to lead to inhibition of its neighbours. This arrangement enhances responses to small, spatially detailed stimuli, since these do not trigger the lateral inhibition from neighbouring receptive fields that are triggered by larger stimuli. As a result, increases in lateral inhibition tend to increase spatial acuity. This general principle has been confirmed by neurophysiological studies of RFs of SI neurons. RFs size is controlled by GABAergic inhibitory interneurons within SI. γ-aminobutyric acid (GABA) is an inhibitory transmitter in the cerebral cortex and administration of GABA antagonists such as bicuculline methiotide (BMI) or picrotoxin produces a dramatic enlargement of the RF (Batuev, Alexandrov, and Scheynikov, 1982; Dykes, Landry, Metherate, and Hicks, 1984). Thus, under normal circumstances, lateral inhibition reduces the RF to a small central subsection of the skin region that sends excitatory inputs to the neuron (Dykes et al., 1984). This modulation of the RF serves to improve detection of fine tactile details such as points and edges (Brown, Koerber, and Millecchia, 2004). Psychophysical measures of tactile spatial perception, such as two-point discrimination and grating orientation, thus depend strongly on intracortical inhibitory function. Therefore, the capacity to modulate the local interneuronal network that provides lateral inhibition may be an important means to flexibly enhance perception. However, direct evidence for such modulation is lacking.

1.2 Non-invasive measures of intracortical inhibitory mechanisms

In the somatosensory system, suppressive interactions between adjacent stimuli are thought to reflect intracortical inhibitory function. Several studies have shown that the somatosensory evoked response elicited by two stimuli applied simultaneously to adjacent skin regions, or to different nerves, is reduced relative to the sum of responses evoked by stimulating each skin region or nerve independently (Gandevia, Burke, and McKeon, 1983; Hsieh, Shima, Tobimatsu, Sun, and Kato, 1995; Ishibashi, Tobimatsu, Shigeto, Morioka, Yamamoto, and Fukui, 2000). In their physiological study, Gandevia and colleagues investigated the neural interaction between inputs from cutaneous afferents in the digital nerves in human subjects. They demonstrated that when strong stimuli were given to the digital nerves, by stimulating the right index and middle fingers, the cerebral potentials produced by stimulation of both fingers simultaneously was less than that expected by summation of the individual potentials (Gandevia et al., 1983). More recent researches compared somatosensory evoked potentials (SEPs) and somatosensory evoked magnetic fields (SEFs) arising from simultaneous stimulation of adjacent fingers with those evoked by simultaneous stimulation of distal fingers (Hsieh et al., 1995; Ishibashi et al., 2000).

This suppression phenomenon is thought to depend on the presence of inhibitory interneuronal connections between cortical neurons, for three reasons. First, suppression follows the somatotopic receptive field organization. Suppressive interactions are stronger when simultaneously stimulating the digital nerves of adjacent fingers (II and III), compared to when simultaneously stimulating distal fingers (II and V; Ishibashi et al., 2000). Second, analysis of somatosensory evoked field components showed suppressive interaction in several structures along the somatosensory pathway, such as the cuneate nucleus, thalamic sensory relay nucleus and sensory and motor cortices. Index of such suppressive interaction was the interaction ratio (IR), the ratio of amplitude attenuation when stimulating two fingers simultaneously compared with the amplitude of the arithmetic sum of two individually evoked potentials. Greater IRs were found in the cortex than in brainstem or thalamus (Hsieh et al., 1995). More precisely, SEPs recorded from the contralateral somatosensory cortex were initially characterized by a negative component (N20) and then by a positive component (P25). From the contralateral motor cortex an initial P22 was recorded, followed by a series of negative-positive waves. SEPs recorded from the thalamus were characterized by the positive $P17_{thal}$ and by a following negative deflection. Finger stimulation evoked a negative deflection ($N16_{cune}$) and then a positive slow wave ($P35_{cune}$) recorded from the ipsilateral cuneate nucleus. In both II and III fingers stimulation and II and V fingers stimulation the amplitude of simultaneously stimulated SEPs were always larger than those of the individually stimulated ones, but smaller than the amplitudes of the summed SEPs. P25 and P22 (recorded by the contralateral somatosensory and motor cortices respectively) showed the greatest IRs, suggesting the cortex as the level where convergence of sensory inputs and surrounding inhibition between RFs of different fingers are the greatest. Moreover N20 (recorded by the contralateral somatosensory cortex) showed stronger IR when evoked by simultaneous stimulation of the II and III fingers, than when evoked by stimulation of the II and V fingers in agreement with the somatotopic representation of fingers in area 3b, where N20 is generated (Allison, McCarthy, Wood, Darcey, Spencer, and Williamson, 1989). Third, somatosensory interactions can vary with the functional state of the sensorimotor system.

For example, in a recent study, before and after 20 min repetitive thumb abduction task, SEPs were recorded during individual and simultaneous stimulations of the median and ulnar nerves at the wrist. A SEP ratio was calculated dividing SEPs amplitudes, obtained from simultaneous nerves stimulation, by the arithmetic sum of SEPs amplitude obtained from individual nerves stimulation. Several cortical SEP components (N20, P25, P22, N30) showed a change in the ratios following the repetitive contractions. These changes persisted after the cessation of the contractions for several minutes. In particular a reduced inhibition of the dual input was observed at the level of the cortex, whereas no changes were observed in any of the subcortical SEP components (Haavik Taylor and Murphy, 2007). This reduction in cortical ability to suppress dual input after 20 min thumb abduction might help to elucidate the mechanism underlying use-dependent plastic changes in the sensory cortex. Enhancement of N20 evoked by simultaneous nerves stimulation after contractions, suggested that the cortical inhibition of the dual input was reduced in SI. This evidence might reflect the smearing of the SI maps after injury (Chen, Corwell, Yaseen, Hallett, and Cohen, 1998) or overuse (Byl, Merzenich, Cheung, Bedenbaugh, Nagarajan, and Jenkins, 1997). Some authors suggested that prolongation of afferent input might lead to abnormal plastic changes in susceptible individuals (Byl and Melnick, 1997; Byl et al., 1997; Byl, 2004). As a consequence abnormal motor control or co-contraction of antagonist muscles might be observed. Motor overuse can depress the inhibitory mechanisms that underlie somatosensory acuity. These studies might help in better understanding the role of the cortex in the initiation of overuse injuries.

Conclusive evidence linking suppressive interaction, interneuronal inhibitory networks and acuity would require intervention studies, for example using GABA antagonists, which have not yet been conducted. However, studies in rodents demonstrate the contribution of GABAergic interneurons to suppression. Recordings from neurons in the primary somatosensory forepaw representation in anesthetized raccoons showed that administration of a specific $GABA_B$ receptor antagonist, CGP 55845, produces significant enlargement of RFs (Chowdhury and Rasmusson, 2002). A similar effect was observed using administration of bicuculline methiodide (BMI), a $GABA_A$ receptor antagonist (Tremere, Hicks, and Rasmusson, 2001). Conversely, the $GABA_B$ receptor agonist baclofen reduced RFs size in most somatosensory neurons and enhanced the ON-centre/OFF-surround organization of somatosensory RFs (Kaneko and Hicks, 1990; Chowdhury and Rasmusson, 2002). Thus, both $GABA_A$ and $GABA_B$ play a major role in regulating RF boundaries by suppressing neuronal responses. These two types of receptor differ in the duration of inhibitory effects. Whereas $GABA_A$ receptors produce a short-lasting inhibition, $GABA_B$ receptors produce long-lasting postsynaptic hyperpolarization (Connors, Malenka, and Silva, 1988). Moreover $GABA_B$ receptors are located presynaptically, thus reducing GABA and glutamate release (Waldmeier, Wicki, Feldtrauer, Mickel, Bittiger, and Baumann, 1994).

An index of the state of intracortical inhibitory networks might be provided by measuring suppressive interactions in the cortex. However, it remains unclear how flexible this mechanism is, and in particular whether one sensory system - such as vision - can modulate the inhibitory mechanisms involved in another – such as touch.

Experiment 1. Neuronal mechanisms underlying the Visual Enhancement of Touch

Several findings suggest that the VET effect occurs within SI (Taylor-Clarke et al., 2002; Fiorio and Haggard, 2005). Moreover a psychophysical study confirmed the modulatory effect of vision of the body on tactile discrimination, suggesting a possible mechanism underling such effect: non-informative vision of the stimulated body part might modulate tactile RFs (Haggard et al., 2007). In this recent study participants were stimulated by a solenoid array and were asked to perform a two-alternative forced choice (2AFC) discrimination task on the forearm while viewing their stimulated body part or an object. One solenoid chosen at random was activated in each trial and participants had to localize the stimuli as proximal or distal. Vibrotactile maskers were placed at two different distances from the tactile target location (close and distant from the solenoid array). Results showed that viewing the body reduced the effect of distant markers and enhanced the effect of close markers as compared to viewing the object. Given that simply viewing the body enhanced tactile acuity (Kennett et al., 2001) and given that tactile acuity depends on cortical lateral inhibition (Kandel et al., 2000), a possible explanation of these results might be that vision of the body improved spatial discrimination by reducing tactile RFs size of SI neurons (Haggard et al., 2007). Thus, although several demonstrations of VET effects have been shown in the last years, these psychophysical findings are worth describing in some depth, because they provide important insights into a potential neuronal mechanism involved. In particular, the VET effect seems to respect the macroscopic receptive field organisation of SI and to modulate tactile discrimination by functional regulation of RFs size. Thus, one attractive hypothesis is that viewing the body shrinks tactile RFs in SI by increasing lateral inhibition.

Direct investigations of intracortical inhibition mechanisms in humans have not hitherto been conducted. Instead, indirect measures of the state of the intracortical inhibitory networks have been made in several studies. These showed that the magnitude of the SEPs elicited by simultaneous stimulation of adjacent skin regions is less than the sum of potentials evoked by stimulation of each region individually. It has been suggested that this suppression phenomenon between representations of adjacent skin regions might depend on lateral inhibitory interneurons in somatosensory cortex (Gandevia et al., 1983;

Hsieh et al., 1995; Ishibashi et al., 2000).

The present experiment tested the hypothesis that vision of the body exerts a top-down modulation of somatosensory intracortical inhibition, underlying flexible and adaptive enhancements of touch. This experiment therefore combined a tactile spatial discrimination task with an EEG measure of intracortical suppression, while participants looked directly either at their own hand or at an object, in different blocks. Suppression of SEPs elicited by simultaneous electrical stimulation of adjacent fingers was considered as an index of the state of cortical networks underlying lateral inhibition. It was predicted that viewing the body would lead to an increase in somatosensory intracortical inhibition, and hence, to an increase in the suppressive interaction between SEPs for adjacent skin regions. Thus, in case of simultaneous finger stimulation it might be expected to find smaller SEPs when viewing the hand compared to those evoked when viewing the object. Further, this increased inhibition should be associated with improved tactile acuity.

Materials and Methods

Participants

Fifteen naïve, paid healthy volunteers (age 20-35, mean 25.5, 8 females) participated in the experiment. All participants were right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971; M: 83.7, range: 11.1-100). They reported normal or corrected-to-normal vision and no abnormalities of touch. Procedures were approved by the UCL research ethics committee and were in accordance with the principles of the Declaration of Helsinki.

Stimuli and Procedure

Participants sat at a table with their right arm resting palm-up on a cushion, arranged so that they had a clear view of their hand. Electrical stimulation was delivered via a pair of ring electrodes place over the distal phalanxes of the right index and middle fingers with a cathode 1 cm proximal to the anode, at a rate of 2 Hz. Stimulation was delivered with a neurophysiological stimulator (a Digitimer stimulator was used for six participants and a custom Stanmore stimulator, Medical Physics Department, UCL, London, UK, for the others) as a square-wave pulse current, for 0.2 ms, at an intensity 1.4 times higher than individual sensory threshold (see later). A staircase procedure was used to identify the tactile threshold for each participant for each finger (Cornsweet, 1962). Participants were asked to report the occurrence of the electrical stimulus delivered to the finger. In half of the participants the threshold for the index finger was calibrated before that for the middle. The opposite order was followed with the other half. Shock intensity calibration started at 0 mA. The intensity was increased in steps of 10 mA until the participant reported the presence of the stimulus. Participants reported whether they felt the shock by responding 'yes' or 'no'. Every time the participant responded 'no', the shock intensity was increased. As soon as the participant responded 'yes' three times consecutively, the shock intensity was reduced by 5 mA. Progressively smaller changes in intensity were made until the participant was able to detect between 50% and 60% of shocks delivered to the finger. The intensities used to stimulate fingers were 1.4 times higher than individual sensory thresholds.

In different blocks the index finger, the middle finger, or both were stimulated. There were 450 stimuli delivered in each of the 12 experimental blocks.

The experiment took place under two visual conditions: viewing one's own hand or viewing an object. In the view hand condition participants were asked to focus their visual attention and gaze directly at the fingers of their stimulated right hand. In the view object condition, at the beginning of the block, a box was moved over the hand, and participants were asked to focus their visual attention and gaze on a wooden block (approximately hand-sized) fixed to the surface of the box. Blocks randomly alternated between view hand and view object conditions.

To measure effects of vision on tactile acuity, participants made judgments of the orientation of square-wave gratings (Van Boven and Johnson, 1994) applied to the tip of either the right index or middle finger. We selected the tactile grating for each subject by an initial staircase procedure. We applied increasingly finer gratings to identify the smallest ridge width for which accuracy was between 55% and 60% correct over 40 trials. The mean ridge width selected by this means was 1.16 mm (standard deviation = 0.45 mm). The finger touched varied between blocks, and was a factor of no interest. The gratings were applied periodically between the shocks. In each block, the experimenter applied manually the grating thirty times, with along and across orientations being random and equiprobable. The grating was held in readiness directly above the fingertip. As soon as the train of shocks stopped the tactile stimulation was delivered on the participant's fingertip. Thus, tactile stimulation and electric shocks always occurred at different, interleaved times. The number of electrical stimulations between touches was randomly varied (10 or 20) to make the timing of touch unpredictable, thereby forcing participants to maintain tactile attention continuously.

Care was taken to ensure that viewing the gratings did not provide any information about the tactile task. The outer, visible edge of the tactile grating stimuli was wrapped in plastic so that no visual information about grating orientation was available. Further, in the view object condition a second grating was held above the object and pressed down on the object at the same time as the to-be-judged grating was presented to the participant's finger. Thus the temporal and attentional cues provided by seeing the approach of the tactile grating were equivalent in the two visual conditions. Participants made unspeeded verbal judgements of grating orientation.

Participants completed 12 blocks, each representing a different combination of visual condition (view hand, view object), stimulated finger (index, middle, both), and touched finger (index, middle) (see Figure 1). Since the study was focused on visual modulation of SEPs and tactile acuity, regardless of which finger has been touched, data were averaged across all blocks in which the same finger was stimulated, regardless of which finger was touched.

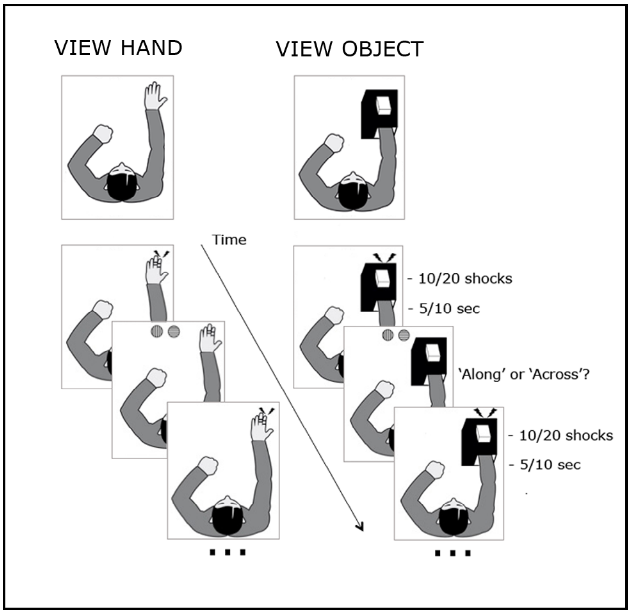


Figure 1. Experimental paradigm. All participants performed 12 blocks, lasting ~ 5 min each, while EEG activity was recorded. In different blocks the index finger, the middle finger or both were stimulated. In between electrical stimulations of fingers, participants were asked to judge the orientation of gratings applied to the tip of their right index or middle finger. Visual conditions, electrically stimulated fingers and touched fingers were blocked and counterbalanced.

Electrophysiological Recordings

A SynAmp amplifiers system and Scan 4.3 software (Neuroscan, El Paso, TX) were used to record electroencephalographic (EEG) data. Sixteen scalp electrodes were recorded (FP1, FP2, F3, F4, C5, C3, Cz, C4, C6, CP5, CP3, CPz, CP4, CP6, O1, O2), according to the 10-20 System. The reference electrode was AFz and the ground electrode was placed on the chin. Electrode impedances were kept below 5 KΩ. The left and right mastoids were also recorded. Horizontal electroculogram (EOG) was recorded from bipolar electrodes placed on the outer canthi of each eye, and vertical EOG was recorded from bipolar electrodes placed above and below the right eye. EEG signals were amplified and digitized at 1 KHz.

EEG data were analyzed with EEGLAB (Delorme and Makeig, 2004). Data were re-referenced to the average of the mastoids. Epochs of 250 ms were extracted from the raw EEG data from 50 ms before each shock to 200 ms after electric shock onset. For each epoch, signal between 2 ms and 13 ms after electric shock onset was linearly interpolated in order to remove electrical artifact. Data were then digitally low-pass filtered at 70 Hz. Trials with eyeblinks (any of FP1 and FP2, HEOG left and right, VEOG up and down exceeding +/- 80 μV) or with voltage exceeding +/- 120 μV at any channel between -50 and 200 ms relative to each shock were eliminated. The mean percentage of trials rejected was 9% (standard deviation 10%). Inspection of the grand averages was used to identify components of the evoked response. The peak values for each component were then calculated by identifying maxima/minima in individual subject averages in each condition in the time window appropriate for each component seen in the grand average.

Results

Behavioural Results

Judgments of grating orientation were significantly above chance both when viewing the hand (75% correct), [$t_{(14)} = 15.61$; $p < 0.0001$] and the object (70% correct), [$t_{(14)} = 11.22$; $p < 0.0001$]. More importantly, the difference between these conditions was significant, with performance being better when viewing the hand than when viewing the object [$t_{(14)} = 3.91$; $p < 0.01$, 2-tailed] (Figure 2). This result replicates the visual enhancement of touch reported previously (Kennett et al., 2001; Taylor-Clarke et al., 2002).

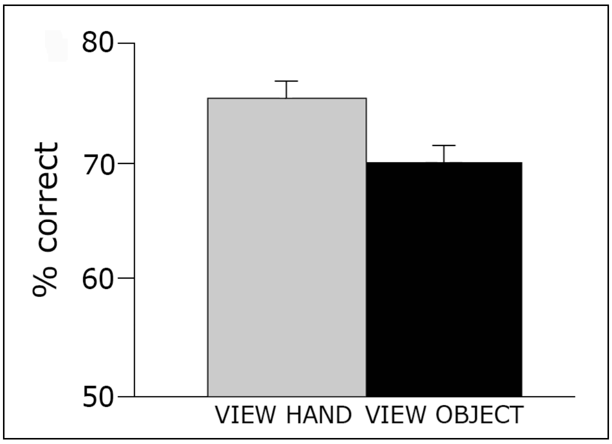


Figure 2. Behavioural results for the Grating Orientation Task. Participants made judgments of the orientation of square-wave gratings applied to the tip of either the right index or middle finger, in different blocks. Accuracy in discriminating the "Across" or "Along" orientation of gratings was higher when participants looked at their own hand than when they looked at an object. Error bars show standard error across participants.

Signal detection theory (SDT) was used to investigate separately any visual modulation of tactile sensitivity (*d'*) and response criterion (*c*) (Wickens, 2002). For this purpose, the 'across' response was arbitrarily designated as the to-be-detected target. *d'* was higher when viewing the hand (1.48) than when viewing the object (1.16), [$t_{(14)} = 4.16$; $p < 0.01$], indicating heightened sensitivity. In contrast, *c* scores did not show any significant difference between the two visual conditions (view hand = -0.14; view object = -0.01; p = N.S). These findings suggest that viewing the hand enhanced tactile sensitivity without affecting response biases.

Electrophysiological Results

Inspection of scalp topographic maps showed broadly consistent components across contralateral central and parietal leads (Figure 3A and 3B).

Figure 3A and 3B shows grand mean SEPs from C3, C5, CP3, CP5 channels.

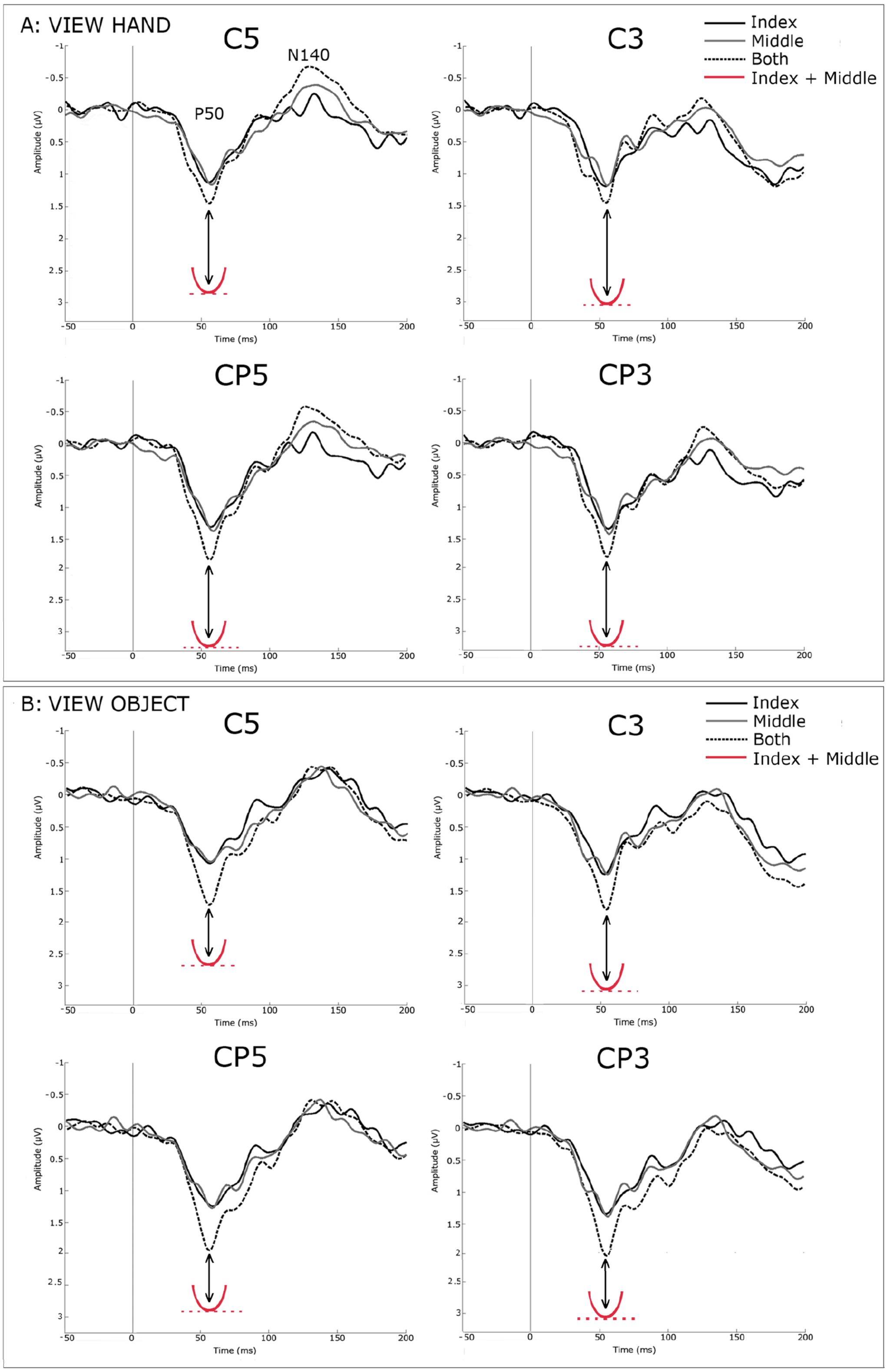


Figure 3. Visual modulation of somatosensory evoked potentials (SEPs).
A) Grand average SEPs, recorded from C3, C5, CP3, CP5 electrodes, in the view hand condition.
B) Grand average SEPs, recorded from C3, C5, CP3, CP5 electrodes, in the view object condition.

Black and gray lines show SEPs when stimulating the index and the middle finger respectively.
Dashed black line shows SEPs when stimulating both fingers simultaneously.
Red line represents the hypothetical sum of potentials evoked by stimulating the index and the middle finger individually in the P50 time window (40-70 ms).

Two clear somatosensory components are identifiable from the grand averages. These are a P50 in the 40-70 ms time window, and an N140 in the 120-150 ms time window. Consistent with other studies using comparable electrocutaneous stimuli (Schubert, Ritter, Wustenberg, Preuschhof, Curio, Sommer, and Villringer, 2008), components earlier than the P50 were not apparent in our grand averages. The absence of earlier components may reflect the relatively weak stimuli used.

Suppression is defined as the amplitude reduction for combined stimulation compared to the sum of the amplitudes for individual finger stimulation. To investigate suppression quantitatively, the amplitudes for individual index and middle finger stimulation were first summed. This effectively provides a prediction of the amplitude for combined stimulation under a hypothesis of no somatosensory suppression (i.e., perfect additivity). A 2-by-2 ANOVA was then performed with factors of view (hand vs object) and stimulation (both vs summed index and middle) (Figure 4).

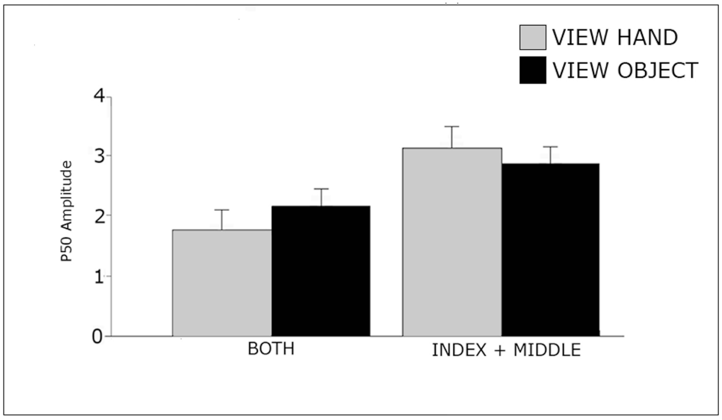


Figure 4. Results from a 2-by-2 ANOVA on the average of C3, C5, CP3 and CP5 P50 peak amplitudes, with factors of view (hand vs object) and stimulation (both vs summed index and middle). P50 peak amplitude when stimulating both fingers simultaneously was less than the sum of P50 peak amplitudes when stimulating each finger individually. Such suppression was found both when viewing the hand and the object. P50 peak amplitude for both fingers stimulation was smaller when viewing the hand than the object.

No visual modulation of P50 peak amplitude was found for summed individual fingers stimulation.

For P50 peak amplitudes, a main effect of stimulation [$F_{(1,14)} = 80.2$; $p < 0.001$] confirmed the suppression effect, since peak amplitudes following simultaneously stimulating two fingers were significantly smaller than the sum of activations from stimulation of each finger individually. Duncan post-hoc comparisons confirmed a suppression effect in both viewing conditions (both $p < 0.001$). There was no main effect of view [$F_{(1,14)} = 0.06$; $p = 0.79$]. However vision did significantly influence the magnitude of suppression [$F_{(1,14)} = 10.9$; $p < 0.01$], with greater suppression when viewing the hand compared to the object. The effects of vision for each form of stimulation were compared. This showed that vision of the hand reduced P50 peak amplitude compared to vision of the object ($p < 0.05$) for combined stimulation, while no effect was found for summed individual stimulations ($p > 0.05$).

An overview of this pattern of ANOVA interaction was provided by calculating a 'Somatosensory Suppression Index' (SSI), defined as the difference in amplitude between the arithmetic sum of potentials evoked by two individually stimulated fingers and the potentials evoked by simultaneous stimulation of two fingers. The SSI was calculated with the following equation:

$$SSI = Index\ alone + Middle\ alone - Combined$$

Higher values of SSI indicate stronger suppression within the somatosensory system. A 2-tailed t-test revealed greater SSI in the view hand condition than in the view object condition [$t_{(14)} = 3.31$; $p < 0.01$] (Figure 5), confirming the ANOVA interaction.

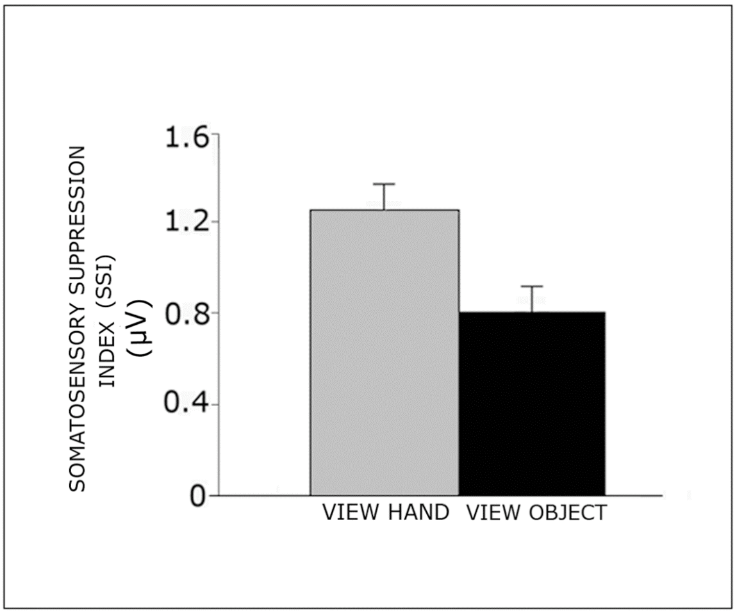


Figure 5. The Somatosensory Suppression Index (SSI) was defined as the difference between the arithmetic sum of potentials evoked by two individually stimulated fingers and the potential evoked by simultaneous stimulation of the two fingers. Higher values of SSI indicate stronger suppression when simultaneously stimulating fingers. SSI for the P50 component is higher when participants look at their own hand compared to when look at an object.

While previous studies expressed this difference as a proportion of the summed individual stimulations, by calculating an interaction ratio (Hsieh et al., 1995), in the present study this procedure produced unstable and non-normally distributed results, due to occasional small peak amplitudes in the denominator.

Similar analysis of N140 peak amplitude provided no evidence for suppressive interactions at this later stage of tactile processing. The 2-by-2 repeated measure ANOVA revealed a non-significant main effect of stimulation [$F_{(1,14)} = 2.12$; $p = 0.16$] and a non-significant main effect of view [$F_{(1,14)} = 1.76$; $p = 0.20$]. Although the interaction view x stimulation was significant [$F_{(1,14)} = 4.69$; $p < 0.05$], post-hoc comparisons showed that this was due to enhanced N140 peak amplitude for summed individual stimulations while viewing the object, compared to the other three conditions ($p < 0.05$ for all comparisons).

In particular, no significant difference was found between combined and summed individual stimulations, in the view hand condition ($p > 0.05$), suggesting inconsistent or no suppression. Visual modulation of suppression for the N140 component was therefore weak or absent. Indeed 2-tailed t-test revealed a greater SSI in the view object condition than in the view hand condition [$t_{(14)} = 2.16$; $p < 0.05$], due to the enhancement of N140 peak amplitude for summed individual stimulations when viewing the object, as previously shown by ANOVA.

Finally, to investigate the relation between psychophysical and electrophysiological measures, an association between visual enhancement of touch effect (expressed as the difference between accuracy in view hand condition and accuracy in view object condition) and visual modulation of P50 suppression (expressed as difference between SSI in view hand condition and in view object condition) was predicted. Correlating the psychophysical and electrophysiological effects across participants revealed that the visual enhancement of touch was reliably associated with the visual modulation of suppression for the P50 component [$r = 0.55$; $p < 0.05$] (Figure 6). In contrast, VET was not correlated with P50 amplitudes for stimulating either the index or middle finger alone, (respectively, $r = 0.18$ and $r = 0.38$; both $p > 0.16$), nor for stimulating both fingers together ($r = 0.005$; $p = 0.98$). To further investigate the specificity of the relation between perceptual and neurophysiological effects, a single multiple regression was performed by predicting each participant's visual enhancement of touch from either their SSI for P50, index P50, middle P50 and P50 for combined stimulation. SSI was a significant predictor of VET [$t_{(14)} = 2.27$; $p < 0.05$], while no other predictors reached significance (all $p > 0.05$).

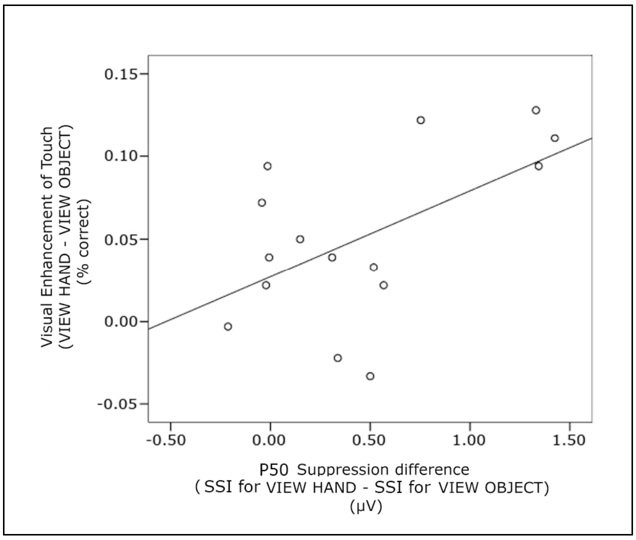


Figure 6. The visual enhancement of tactile performance (VET), expressed as the difference between accuracy in view hand condition and accuracy in view object condition, correlates across participants with the visual modulation of suppression, expressed as the difference between SSI in view hand condition and SSI in view object condition.

Discussion

The aim of the present study was to investigate the neural mechanisms underlying the VET effect. In particular, taking advantage of an indirect measure of intracortical lateral inhibition(Gandevia et al., 1983; Ishibashi et al., 2000; Severens, Farquhar, Desain, Duysens, and Gielen, 2010), the present study tested whether the enhancement of tactile acuity when viewing the body relative to when viewing an object (Haggard et al., 2007; Kennett et al., 2001) relied on a modulation of intracortical inhibitory interactions.

Viewing the body modulated somatosensory intracortical inhibition. The suppression of SEPs produced by simultaneous stimulation of the adjacent index and middle fingers was significantly increased when participants looked at their hand compared to an object. Consistent with previous results (Kennett et al., 2001), viewing the hand also enhanced tactile spatial acuity. Moreover, the visual enhancement of touch correlated across participants with the visual modulation of suppression, suggesting a functional relation between these effects. Results suggested that vision of the body, even when non-informative, enhances the spatial sensitivity of touch by increasing inhibition in SI. This increased inhibition produced both a shrinking of tactile RFs, implying improved acuity, and stronger suppressive interactions between SEPs for adjacent skin regions. Both results were consistent with the hypothesis that viewing the body increases activation in the system of GABAergic interneurons that gives rise to the RF organisation of the somatosensory cortex (Dykes et al., 1984).

Previous studies reported attenuated sensory responses when two stimuli either of different modalities (Cheron and Borenstein, 1987; Jones, Allison, McCarthy, and Wood, 1992) or within a single sensory modality (Gandevia et al., 1983) were applied simultaneously to adjacent skin regions. For example, suppressive interactions between simultaneous cutaneous afferent volleys were elicited by electrical stimulation of different fingers (Gandevia et al., 1983). More recently Okajima and colleagues (Okajima, Chino, Saitoh, and Kimura, 1991) demonstrated that suppressive interactions can also result from stimulation of non-adjacent skin regions, such as the left and right median nerves. Suppression of sensory inputs has been observed in several locations along the sensory afferent pathway, including the cuneate nucleus, the thalamus, and the somatosensory cortex, with the greatest interaction occurring in the cortex (Hsieh et al., 1995). This finding is consistent with the general observation that suppressive interactions may be relevant to the specific cortical mechanism of lateral inhibition that underlies tactile spatial perception.

In line with previous results, suppressive effects were shown at around 50 ms (Biermann, Schmitz, Witte, Konczak, Freund, and Schnitzler, 1998; Ishibashi et al., 2000), whereas suppression of later components was unaffected by inhibitory interactions. As previously suggested, P50 might be generated in the primary somatosensory cortex (Allison et al., 1989; Ishibashi et al., 2000), whereas the later component N140, might be generated bilaterally in regions of the frontal lobes (Allison et al., 1992). The present findings might reflect visual modulation of early activity in SI. The visual enhancement of touch was previously localised to SI on the basis both of amplitude modulations of N80 component evoked by touch itself (Taylor-Clarke et al., 2002) and also of abolition of VET by SI-TMS delivered just prior to touch (Fiorio and Haggard, 2005). In the present study, SEPs were recorded to task-irrelevant electrical stimuli, rather than to to-be-judged tactile stimuli. Nevertheless, inspection of different somatosensory components showed clear evidence that viewing the body modulates somatosensory processing in early cortical areas. Multisensory effects in early cortex have also been reported for interactions between other sensory modalities (Macaluso, 2006).

Previous neurophysiological findings suggested that suppressive somatosensory interactions depended on lateral inhibitory interneurons, and involved GABAergic intracortical circuits (Laskin and Spencer, 1979; 1979). Most of these studies assumed a fixed level of inhibitory connectivity. However, more recent studies showed plasticity of lateral inhibition mechanism, which would be required by any role in multisensory modulation. For example, cortical maps show high input-dependent plasticity, including profound and rapid reorganization in response to altered afferent inputs. In particular, surgical amputation of a digit lead to cortical neurons having RFs on that digit rapidly developing RFs on adjacent skin regions (Merzenich, Nelson, Stryker, Cynader, Schoppmann, and Zook, 1984; Calford and Tweedale, 1991). This was attributed to unmasking of latent afferent drive from the adjacent skin regions. Normally, the latent input would have been suppressed by lateral inhibitory connections from the amputated digit. Removal of the afferent input post-amputation effectively removed the normal effects of lateral inhibition.

The present data suggested that lateral inhibitory mechanisms are not solely driven by afferent input in a feedforward manner. Rather, the strength of lateral inhibition in somatosensory cortex appears to be modulated by visual context, specifically by vision of the body. Areas in occipital cortex, or in multisensory parietal or prefrontal cortex, might be involved in this mechanism: they house a representation of the body, driven in this case by viewing the hand. Results suggest that this representation can modulate the strength of somatosensory lateral inhibition by top-down projections.

The effects of multisensory interactions on unisensory cortical processing have already been shown for different sensory modalities (Sathian and Stilla, 2010). However, it remains unclear how such multisensory interactions can alter activations in primary sensory areas, and change the way that primary areas respond to unisensory inputs. Thus, the present results suggested, for the first time, that top-down regulation of lateral inhibition might be the mechanism underlying such multisensory modulation. The same mechanism might underlie other modulatory effects in perceptual systems, such as within-modality top-down attentional modulation of early perceptual processing (Noudoost, Chang, Steinmetz, and Moore, 2010).

Multisensory convergence involves bringing together information from distinct sensory streams. The most striking examples involve single neurons that respond to inputs from two or more modalities, for example in the superior colliculus (Meredith and Stein, 1983), putamen (Graziano and Gross, 1993), premotor cortex (Graziano et al., 1994), and posterior parietal cortex (Avillac et al., 2007).

Multisensory modulation, in contrast, involves activity from one sensory channel modulating activity in another sensory channel. Examples include intersensory substitutions, such as ventriloquism (Bertelson, Vroomen, de Gelder, and Driver, 2000; Shams et al., 2000), signals from one modality biasing perception in another modality (Shams et al., 2000), and synaesthetic cross-talk (Bargary, Barnett, Mitchell, and Newell, 2009). Importantly, whereas convergence can be considered as a purely feedforward process in which sensory information is increasingly pooled across several source modalities, modulation involves direct influences between primary sensory areas, or top-down projections from multimodal to unimodal areas.

In many cases, convergence and modulation will co-occur. For example, both cortical (Avillac et al., 2007) and subcortical (Stein, Meredith, and Wallace, 1993) areas contain multimodal cells that respond to inputs in two (or more) modalities. Moreover, the response to a stimulus in each modality also depends on the other modality. For example, the response to combined tactile and visual stimulation may exceed the sum of responses to either visual stimulation or tactile stimulation alone. In this case, the presence of a response to either modality is evidence of integration (*convergence*), while the nonlinearity of the bimodal response is evidence of intersensory *modulation*. The fact that both convergence and modulation co-occur in such cases makes it difficult to separate the processes of multisensory integration from those of multisensory modulation. Further, the widespread co-occurrence of convergence and modulation has made the modulation component hard to characterise. In the present study, vision of the body provided a continuous context, rather than a time-locked afferent signal describing a specific sensory event. Thus the experimental paradigm used in this study served to investigate the neural basis of a particular form of multisensory modulation, in a case where the contribution of feedforward convergence of multisensory inputs can be excluded. In other words, with the present study it has been possible to isolate the multisensory modulation component, as distinct from multisensory convergence.

To conclude, the present findings shed light on a possible mechanism for multisensory modulation. The new suggestion of this study was that multisensory interactions might involve top-down feedback projections from multisensory representations of the body to primary sensory cortex. These projections had the functional role of enhancing perception, in this case enhancing tactile acuity by boosting the gain of a network of inhibitory interneuronal connections within primary somatosensory cortex.

Previous studies suggested that the key function of multisensory convergence was sensitive detection, orienting and alerting (Stein and Meredith, 1993). A conclusion that might be reached with this study is that the key function of multisensory modulation is the enhancement of perceptual detail.

Given previous findings that suggested the primary somatosensory cortex as the specific brain area that is modulated as the effect develops, and given the present study that shed light on the neuronal mechanism underlying the VET, a further aspect of this effect still remains to be investigated: its time-course. A broader knowledge about the onset latency of the VET effect would be necessary to better understand how visual contexts modulate tactile information processing. For this reason the next experiment took advantage of the EEG technique that thanks to its high temporal resolution allowed shedding light on the timing of the modulatory effect of vision of the body on tactile processing.

Experiment 2. Time-course of the Visual Enhancement of Touch

Strong multisensory interactions exist between vision and touch. Studies in humans have emphasised perceptual (Ernst and Banks, 2002) or attentional (Driver and Grossenbacher, 1996) links which integrate visual and tactile information to improve multisensory representation of a common stimulus object. Studies in animals emphasised spatial overlap between visual and tactile receptive fields (RFs) of bimodal neurons in association areas of the brain (Graziano et al., 1994). These studies also suggest a multimodal mechanism for object detection and for monitoring peripersonal space (Graziano and Cooke, 2006). Importantly, these interactions are highly temporally specific: as already mentioned in the Introduction, information in two modalities must arrive within a narrow time-window in order for these multisensory neurons to quickly integrate their various inputs (Avillac et al., 2007) thereby creating a single percept (Di Luca, Machulla, and Ernst, 2009). Indeed, fast $GABA_A$ and AMPA receptor pathways are thought to be involved in this integration (Salin and Bullier, 1995). This suggests that temporal summation of action potentials from lower-level unisensory areas onto higher order neurons plays an important role in multisensory interactions at the millisecond timescale (Stein et al., 1993).

A different class of multisensory effects, that does not result by a "real-time" integration between different sensory inputs, but rather emerges over a slightly longer timescale, involves neuroplastic changes in representations within a sensory area either following deprivation of stimuli in another sensory modality (Shimojo and Shams, 2001) or after associations between multisensory stimuli (Zhou and Fuster, 2000). These crossmodal effects, beyond affecting the brain activity and its neural organization, disclose influences at the behavioural level as well. One striking example of neuroplastic changes that can occur between modalities was provided by a recent study with healthy volunteers. Facchini and Aglioti kept 14 participants for 90 minutes in complete darkness, and they found that after light-deprivation a reversible improvement of participants' tactile acuity was observed. These results suggested that absence of visual input might allow visual cortex to be activated for tactile processing by latent somatosensory inputs. Thus, a short-term visual deprivation may disclose dynamic plastic interactions between visual and tactile systems (Facchini and Aglioti, 2003). The potential access of tactile signals to visual cortex is further supported by functional imaging studies in healthy volunteers

(Zangaladze, Epstein, Grafton, and Sathian, 1999; Sathian and Zangaladze, 2002), and by the finding that visual cortex is recruited during tactile Braille reading in the blind (Sadato, Pascual-Leone, Grafman, Ibanez, Deiber, Dold, and Hallett, 1996), and in blindfolded volunteers (Merabet, Hamilton, Schlaug, Swisher, Kiriakopoulos, Pitskel, Kauffman, and Pascual-Leone, 2008). Moreover, neuroplastic changes in cortical processing may also result by Hebbian associative processes: repeated paired stimulation within a single modality (Hodzic, Veit, Karim, Erb, and Godde, 2004; Stavrinou, Della Penna, Pizzella, Torquati, Cianflone, Franciotti, Bezerianos, Romani, and Rossini, 2007), or crossmodal pairing between different modalities leads to changes in sensory cortical representations. Neurons in somatosensory cortex were found to respond to visual cues following cross-modal training involving association of visual and tactile events (Zhou and Fuster, 2000). In this case, extensive learning of visual-tactile associations is thought to underlie the multimodal activity. More interesting for the research question underlying the present study is a recent finding that even short-lasting crossmodal associations might induce cortical reorganizations. In particular it has been shown that associated visual and tactile stimulations – i.e. vision of a hand being touched on the first digit (D1) while receiving a tactile stimulus on the same digit of one's hidden hand – affected both the cortical representation of D1, that moved to a more inferior location, and a psychometric measure related to the feeling that the seen touch represented the touch on one's hand (Zhou and Fuster, 2000; Schaefer, Flor, Heinze, and Rotte, 2006). These changes were observed only when visual and tactile stimuli where temporally correlated; in fact, whereas in case of synchronous stimulation between the seen hand and the participant's hand a shift in D1 cortical representation was found, no effects on the somatosensory representations and on the subjective reports were observed when a small asynchrony was introduced between the touches delivered on the seen and the actual hand (Schaefer et al., 2006). Beyond previous findings demonstrating that neurons in monkey SI fire both in response to a tactile stimulus and to a visual stimulus previously associated with the tactile stimulus (Zhou and Fuster, 1996), Schaefer and colleagues showed rapid dynamic changes of the organization of somatosensory cortical maps even without preceding long-lasting crossmodal association training. Thus a possible mechanism explaining this neuroimaging data might rely on a short-term reversible modulation of SI when viewing one's hand being touched. However, given the prolonged duration of the experimental blocks in this study (about 15 minutes) it still remains unclear the exact onset latency of this modulatory effect. Finally the huge amount of data in literature widely demonstrates that neuroplastic changes need at least some minutes to develop (Calford and Tweedale, 1988; Rossini, Martino, Narici, Pasquarelli, Peresson, Pizzella, Tecchio, Torrioli, and Romani, 1994; Xu and Wall, 1999; Braun, Wilms, Schweizer, Godde, Preissl, and Birbaumer, 2000).

In summary, multisensory integration involves a fixed and almost instantaneous response to a simple combination of inputs from different modalities, whereas multisensory neuroplasticity would take place over different timescales from minutes up to the whole lifespan (Merabet and Pascual-Leone, 2010).

As previously suggested, VET effect does not involve standard feedforward convergence of visual and tactile information about a common object, since it occurs when vision is entirely non-informative about touch, for example when the tactile stimulation itself cannot be seen (Taylor-Clarke et al., 2004). Moreover, no visuo-tactile associations should underlie this effect since no visual event is paired with the tactile input. Instead, viewing the body seems to provide a visual context that modulates tactile processing. Electrophysiological and TMS studies suggest that the visual context of the body can influence processing in early somatosensory cortex (Taylor-Clarke et al., 2002; Fiorio and

Haggard, 2005; Longo, Pernigo, and Haggard, 2011). In particular, viewing the body appears to preset the tactile circuits involved in tactile discrimination, perhaps via top-down projections from visual or multisensory areas into somatosensory cortex.

The time-course of such modulatory effects has been little studied. It remains unclear if they resemble fast mechanisms of feedforward multisensory integration operating over milliseconds, or slower mechanisms of neuroplastic change operating over minutes or hours. One VET study showed that viewing the hand enhanced tactile acuity after a 2 s dark interval, and to a lesser, but still-significant degree after 10 s (Taylor-Clarke et al., 2004). This study shows that VET *persists* for at least some seconds. However, either multisensory integration, or a neuroplastic change could have effects over this timescale (Stein et al., 1993; Facchini and Aglioti, 2003). The critical distinction between the two mechanisms likes in the time taken for the VET effect to *develop* from the moment the body is viewed. Here, the two multisensory mechanisms outlined above make different predictions. If VET depends on integration of visual context of the body with incoming tactile information, it should be present very rapidly after viewing the body. On the other hand, if VET depends on plastic reorganisation of visuo-tactile links following co-occurrence of touch with vision of the body, then it should require at least some minutes. To date, the time course of VET has not been systematically investigated. In particular it is still unclear whether the VET effect is immediately observed as soon as the visual context is seen. In previous studies, vision of either the body or a neutral object was investigated in separate blocks, lasting several minutes (Kennett et al., 2001; Taylor-Clarke et al., 2002; Cardini, Longo, and Haggard, 2011). In blocked designs, vision might influence touch either through fast or slow mechanisms. Identifying the time taken for viewing one's own body to influence touch may be important in clarifying the relations between multisensory processing and self-representation. Fast activation of the representation of one's own body is crucial in quickly detecting external events in the peripersonal space looming towards the body surface. Given the highly salient information provided by viewing one's body, one might expect that even a brief glimpse of the body is sufficient to facilitate tactile processing on the seen skin location.

In order to clarify this issue, in the present study tactile acuity was measured on the right middle fingertip during a dark interval immediately after random and unpredictable vision of either the participant's hand, or an object appearing at the same location. Further, by continuously recording SEPs, elicited by electrical stimulation of the finger, it was tested whether this rapid, unpredictable switching of visual context could produce rapid modulation of somatosensory processing. If suddenly viewing one's own hand is immediately able to modulate somatosensory processing, differences between SEPs after viewing the hand and those after viewing an object, might be observed.

Materials and Methods

Participants

Thirty-three naïve, paid healthy volunteers (age 21-37, mean 24.2, 18 females) participated in the experiment. All were right-handed as assessed by the Edinburgh Inventory (M: 81.6, range: 12.3-100). Data acquired from two further participants were excluded due to technical difficulties with EEG recording. Procedures were approved by the UCL research ethics committee and were in accordance with the principles of the Declaration of Helsinki.

Stimuli and Procedure

Participants sat in complete darkness with their right arm resting palm-up on a table and looked into a semi-silvered mirror aligned with their parasagittal plane. Their right hand was positioned behind the mirror, while a hand-size wooden block was placed in front of the mirror (Figure 7A). Computer-controlled LED arrays were suspended above the hand and the object. When the LED array behind the mirror was illuminated, the mirror functioned as a window and participants saw their hand. When the LED array in front of the mirror was illuminated, participants saw the wooden block appearing at the hand's location. Participants were asked to focus visual attention and gaze directly towards the location of their hand.

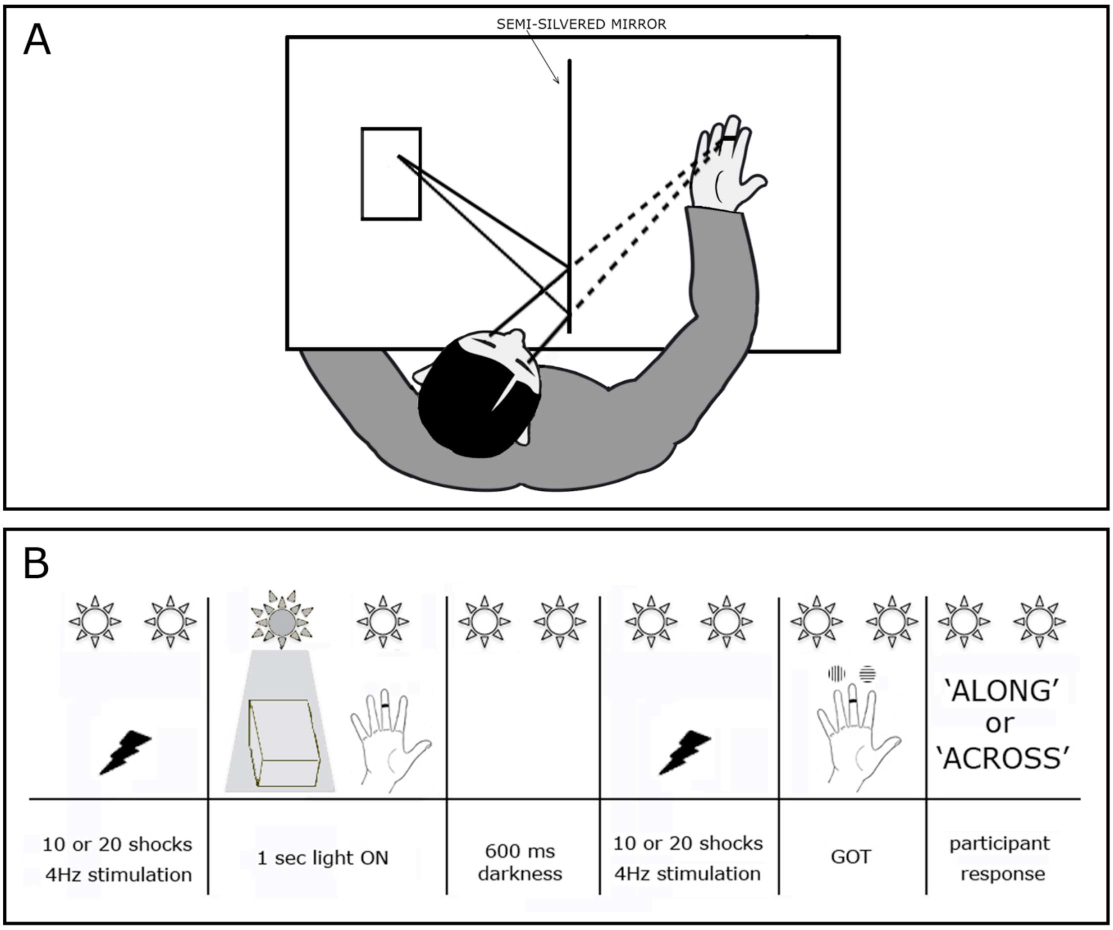


Figure 7 A. Schematic depiction of experimental setup. Depending on illumination, participants either saw their right hand through the semi-silvered mirror (dashed lines), or saw an object reflected in the mirror (solid lines).
B. Schematic depiction of an experimental trial. In complete darkness participants were electrically stimulated on the right middle finger. Then either the hand or object was illuminated for 1 s at random. After illumination a second train of shocks was presented. Finally, a robot applied an oriented tactile grating to the index finger, and participants verbally reported orientation.

Electrical stimulation was delivered at 4 Hz through ring electrodes placed over the distal phalanx of the right middle finger. A neurophysiological stimulator provided a square-wave pulse for 0.2 ms, at an intensity 1.4 times each participant's sensory detection threshold as measured by an initial staircase procedure (Cornsweet, 1962). Briefly, participants were asked to report the occurrence of the electrical stimulus delivered to the finger by verbal 'yes' or 'no' responses. Shock intensity began at 0 mA, increasing in steps of 10 mA until the participant reported the presence of the stimulus. If the participant responded 'yes' three times consecutively, the shock intensity was reduced by 5 mA. If they responded 'no', intensity was increased. Progressively smaller changes were made until the participant was able to detect between 55% and 60% of shocks delivered to the finger. The mean threshold was 54 mA (SD 18 mA).

On each experimental trial, participants first received a train of either 10 or 20 electrical suprathreshold stimuli in darkness. Then, one of the LED arrays selected at random illuminated hand or object for 1 s. After illumination ceased, a further train of either 10 or 20 shocks was presented in darkness. Finally, a tactile grating (Van Boven and Johnson, 1994) was applied by a robotic apparatus to the right middle fingertip. Participants made unspeeded verbal judgements regarding whether the grating ran along or across the finger (Figure 7B). We selected the tactile grating for each subject by an initial staircase procedure, using increasingly finer gratings to identify the smallest ridge width for which accuracy was between 55% and 60% correct over 40 trials. The mean of the ridge widths selected by this means was 1.01mm (standard deviation = 0.35mm).

Electrophysiological Recordings

A Neuroscan system (Neuroscan, El Paso, TX) was used to record EEG from electrodes placed at 17 standard scalp locations (FP1, FP2, F3, F4, C5, C3, Cz, C4, C6, CP5, CP3, CPz, CP4, CP6, O1, Oz, O2). The reference electrode was AFz and the ground electrode was placed on the chin. Electrode impedances were kept below 5 KΩ. The left and right mastoids were also recorded. Horizontal electroculogram (EOG) was recorded from bipolar electrodes placed on the outer canthi of each eye, and vertical EOG was recorded from bipolar electrodes placed above and below the right eye. EEG signals were amplified and digitized at 1 KHz.

EEG data were analyzed with EEGLAB (Delorme and Makeig, 2004). Data were re-referenced to the average of the mastoids. Epochs were extracted from 50 ms before each shock to 200 ms after the shock trigger. A stimulation artifact 1-11 ms after the shock trigger was removed by linear interpolation. Data were low-pass filtered at 45 Hz. Trials with eyeblinks (any of FP1 and FP2, HEOG left and right, VEOG up exceeding +/- 80 μV) or any channel exceeding +/- 120 μV were eliminated (mean 14% SD 11% of trials). Grand averages were visually inspected to identify somatosensory event-related potential components. The values of peak potentials for each component were then calculated by identifying maxima/minima in individual subject averages in each condition in the time window appropriate for each component seen in the grand average (40-70 ms for the P50 and 130-160 ms for the N140).

An improvement in tactile orientation discrimination from viewing the hand, relative to viewing the object, was predicted. As regards the ERPs, no differences between ERP components before visual exposure, but a significant enhancement of somatosensory processing after viewing the hand, relative to after viewing the object, were predicted.

Results

Behavioural Results

Judgments of grating orientation were significantly above chance both after viewing the hand (65% correct), [$t_{(32)} = 7.98$; $p < 0.0001$] and the object (62% correct), [$t_{(32)} = 5.39$; $p < 0.0001$]. More importantly, the difference between these conditions was significant, with enhanced performance after viewing the hand relative to viewing the object [$t_{(32)} = 2.46$; $p < 0.05$, 2-tailed] (Figure 8).

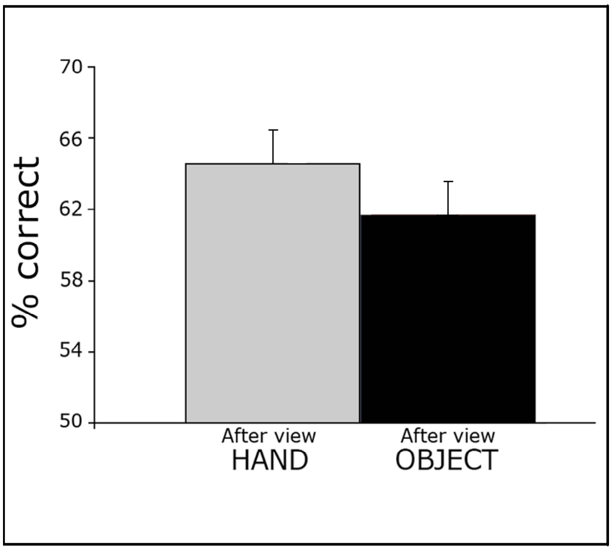


Figure 8. Behavioural results for the Grating Orientation Task. Participants made judgments of the orientation of square-wave gratings applied to the tip of the right middle finger. Accuracy in discriminating the "Across" or "Along" orientation of gratings was higher after participants viewed their own hand than after viewed an object. Error bars show standard error across participants.

Electrophysiological Results

Scalp topographic maps showed broadly consistent components across contralateral central and parietal leads, corresponding to classical somatosensory cortices.

Figure 9 shows grand average SEP traces of the contralateral centro-parietal cluster (C3, C5, CP3, CP5 electrodes), which overlies the somatosensory cortex. Two clear somatosensory components were identifiable from the grand averages: a P50 in the 40-70 ms time window, and an N140 in the 130-160 ms time window. Figure 9 shows the scalp distribution of these components. Note that the P50 is maximal over the left centro-parietal sites, while the N140 is more diffuse.

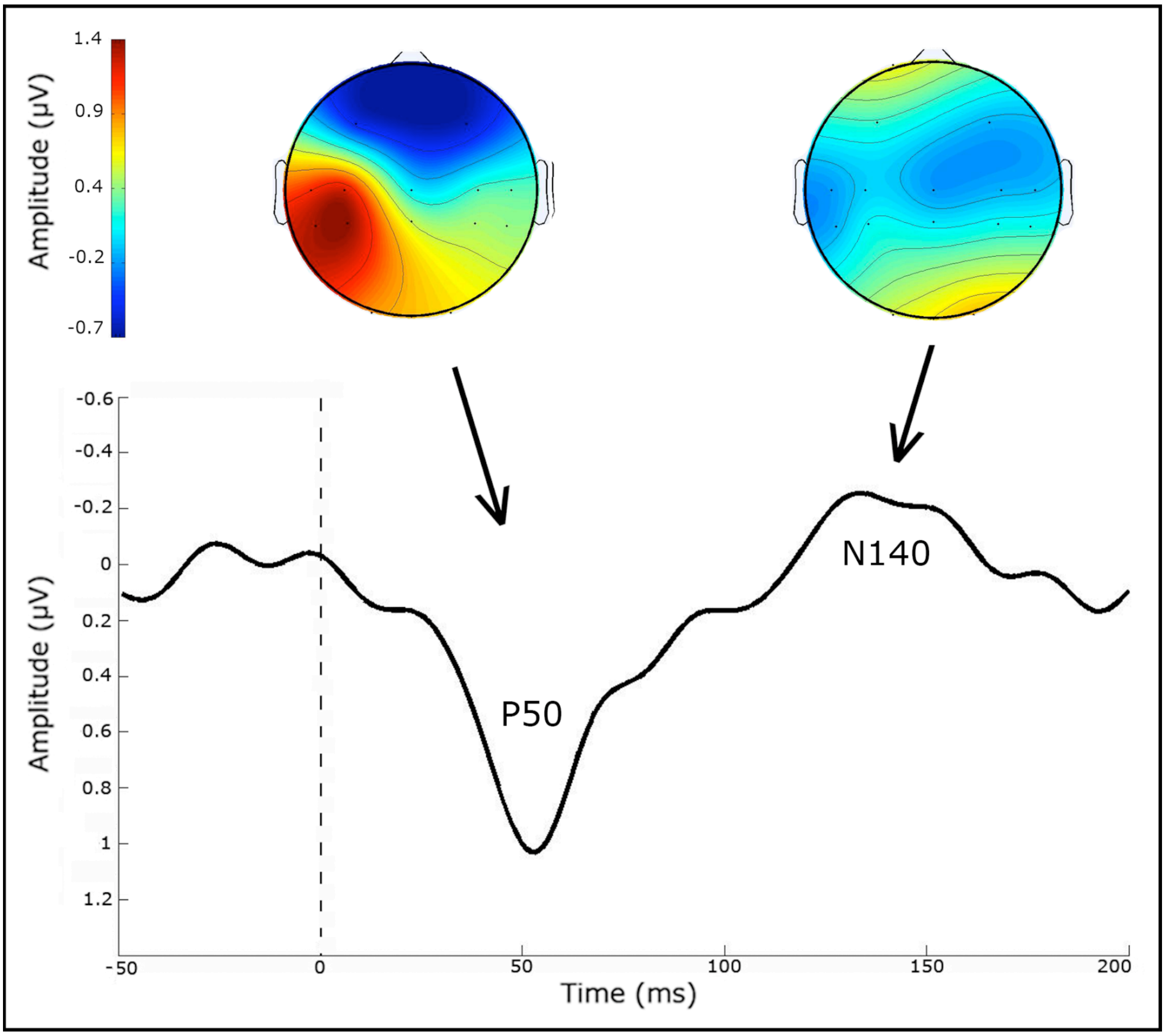
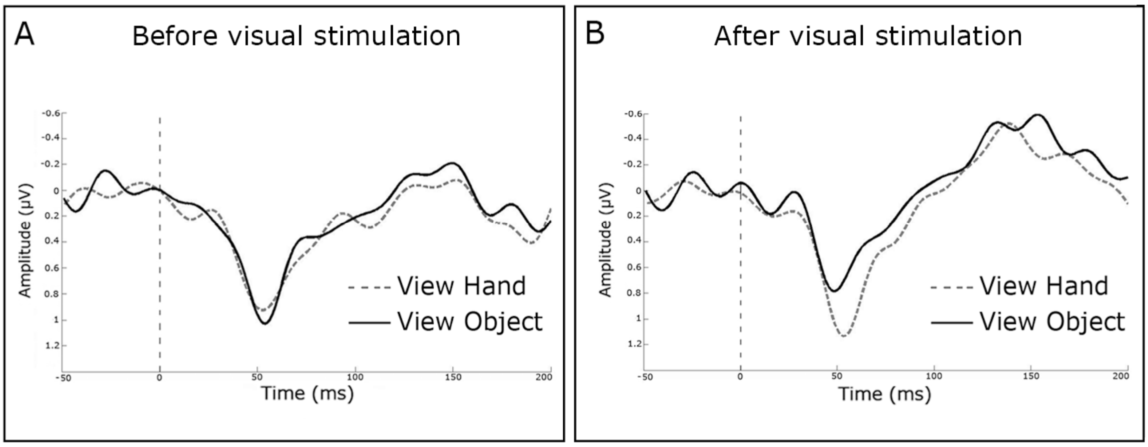


Figure 9. Grand average ERP waveforms across all conditions in the contralateral centro-parietal cluster (C3, C5, CP3, CP5). Scalp maps for the P50 and N140 ERP components are shown.

Peak amplitudes for each component were calculated, averaged across contralateral sensory cortex electrodes (C3, C5, CP3 and CP5), and analysed using 2-by-2 ANOVAs with factors of view (hand vs object) and time (pre-vision vs post-vision). For P50 peak amplitude this revealed a main effect of view [$F_{(1,32)} = 8.46$; $p < 0.01$], but no effect of time [$F_{(1,32)} = 0.82$; $p = 0.37$]. Importantly, the view x time interaction was also significant [$F_{(1,32)} = 4.34$; $p < 0.05$], suggesting a visual modulation of somatosensory processing. The interaction was explored by follow-up t-testing. This revealed a significant enhancement of P50 amplitude after viewing the hand [$t_{(32)}$ = -2.19; $p < 0.05$, 2-tailed] compared to before vision. No such enhancement, however, was found after viewing the object [$t_{(32)}$ = 0.92; p = 0.36, 2-tailed]. Finally, a larger P50 was found after viewing the hand compared to after viewing the object [$t_{(32)}$ = 3.01; $p < 0.01$, 2-tailed], while P50 amplitudes were comparable before visual exposure [$t_{(32)}$ = 0.13; p = 0.89, 2-tailed] (see Figure 10).

Similar analysis of N140 peak amplitude provided no evidence for visual modulation at this later stage of somatosensory processing. The 2-by-2 ANOVA revealed no effect of view [$F_{(1,32)}$ = 1.41; p = 0.24], a significant main effect of time [$F_{(1,32)}$ = 13.38; $p < 0.01$], and no significant interaction between these factors [$F_{(1,32)}$ = 1.41; p = 0.96]. In summary, N140 peak amplitude showed a general enhancement after visual exposure relative to before, but this was independent of the visual context of what was seen.



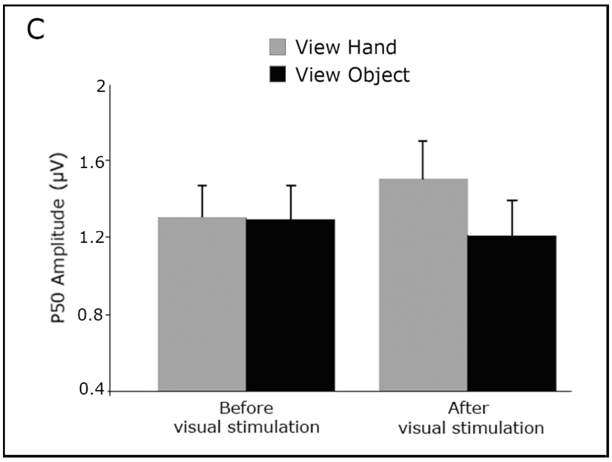


Figure 10. Grand average ERP waveforms in the contralateral centro-parietal cluster (C3, C5, CP3, CP5) before (A) and immediately after (B) visual presentation of the hand (dashed line), and object (solid line). C:mean of peak P50 amplitudes in each condition, +/- standard error.

Discussion

This study was designed to investigate whether visual modulation of touch occurs over the millisecond timescale of multisensory integration, or over the minute timescale of neuroplastic changes.

Brief, unpredictable, and non-informative vision of one's own body produced rapid enhancement of tactile discrimination ability and also facilitated early somatosensory processing of stimulation at the viewed skin location. The behavioural results showed enhancement of tactile acuity on the fingertip after viewing one's own hand, compared to the object. They thus extended previous reports of VET during continuous vision of the hand (Kennett et al., 2001; Cardini et al., 2011) or following short dark intervals (Taylor-Clarke et al., 2004). Here, brief 1 sec glimpses of hand or object were randomized, and this showed that viewing one's own body could influence tactile acuity within a few seconds. Moreover, somatosensory potentials showed that brief vision of the body also affects the early P50 components of tactile processing. This component is thought to arise from early somatosensory cortex (Desmedt and Tomberg, 1989), and has been specifically identified with a generator in area 1 (Allison et al., 1992). In contrast, no context-specific modulation of the later N140 component was found. This component is known to be sensitive to general attentional factors (Ohara, Lenz, and Zhou, 2006), and may reflect frontal responses driven by somatosensory inputs (Allison et al., 1992).

Thus, visual modulation of touch occurred soon after viewing the body, and rapidly influenced early somatosensory processing. On the one hand, VET appeared to operate over shorter time-scales than neuroplastic changes involved in intersensory substitution (Merabet and Pascual-Leone, 2010), use-dependent somatosensory plasticity (Godde, Spengler, and Dinse, 1996), or learning of multisensory associations (Zhou and Fuster, 2000). In particular, the present randomized design prevented a continuous build-up of any multisensory associations due to prolonged training (Zhou and Fuster, 2000). On the other hand, VET could not be considered to result from a pure multisensory integration mechanism between different sensory inputs, because, as already mentioned, information in different modalities must arrive within a narrow time-window in order for multisensory neurons to integrate their various inputs. Previous studies of multisensory integration, for example, emphasised rapid feed-forward integration of visual and tactile information, both subcortically (Stein and Meredith, 1993) and cortically (Avillac et al., 2007). In human multisensory perception, visual and haptic information must be present simultaneously, and perceptually bound to the same object, for efficient feed-forward integration to occur (Helbig and Ernst, 2007). In contrast, the present hand and object visual stimuli were both non-informative about touch, ruling out explanations based on binding events in separate modalities to form a single perceptual object (Driver, 1996).

Thus, VET cannot simply reflect feed-forward integration of simultaneous visual and tactile input from the same multisensory source. Rather, it might be suggested that viewing the body rapidly activates a representation of the body. Human and primate studies confirm that such a multisensory, higher-order representation of the body exists in parietal and premotor association cortices (Gentile et al., 2011). Recurrent projections from these body representations would provide a top-down modulatory feedback to early somatosensory cortex. This circuit allows an ongoing context in association areas to influence touch even after the activating visual input is removed. Finally, given the speed of its occurrence, VET might be underlie by a special multisensory mechanism: sudden, unpredictable vision of the body provides a fast, short-term, reversible modulatory influence on the somatosensory system.

It is worth noting that the present contextual modulation differs in important ways from cross-modal effects in spatial attention. Spatial attention was carefully controlled by ensuring that both hand and object were viewed at the same location. An elegant study dissociating effects of viewing the hand from effects of gazing in the direction of the hand (Forster and Eimer, 2005) suggested that gaze acted as a modulator of spatial attention, and it was found that manipulation of gaze direction only affected the N140 component. In contrast, vision of the hand affected the earlier P45 and N80 components, whereas no modulatory effects of vision of the body were observed on the N140. The present findings agree with the latter result showing a significant enhancement of the N140 after viewing either hand or object, compared to before visual exposure. This could reflect either non-specific alerting effect of visual exposure on somatosensory processing, or a visual-tactile link in spatial attention. Specifically, visual stimulation could have enhanced tactile attention at the corresponding location. Finally, these results confirmed the susceptibility of the N140 to attention (Nakajima and Imamura, 2000). Moreover, the present findings add the important information that P50 enhancement when viewing the body emerges rapidly, after only a brief glimpse of the hand, and then persists during a subsequent dark interval. Therefore, the present results underline the distinction between effects of attention and effects of viewing the body.

Multisensory enhancement, and visual enhancement of touch in particular, have clear adaptive value. The VET effect facilitates processing of tactile events on one's own body. For this reason, as soon as the body is seen, an *early* and *quick* activation of the primary somatosensory cortex may be required for detecting objects.

The rapid onset of VET may be related to self-representation. The brain's ability to form and use multisensory representations of one's own body plays a crucial role in everyday interaction with the external world, and may constitute a basic form of self-consciousness (Bermudez, Marcel, and Eilan, 1995). Psychophysical studies with human volunteers show that even brief and minimal visual input is sufficient for self-recognition (Tsakiris, Haggard, Franck, Mainy, and Sirigu, 2005). However, explicit self-recognition judgement is rare in everyday life, so the cognitive capacity for self-recognition presumably also has other functions. Given the present results, it might be suggested that visual self-recognition could provide a contextual modulation that facilitates multisensory processing of stimuli on the body or in close proximity to it. This view clearly predicts that rapid-onset VET should not be found for viewing another person's hand. Previous studies showed that tactile acuity was increased when subjects viewed a rubber hand only when they experienced it as their own hand (Longo et al., 2008). Similarly, the analgesic effect of seeing one's own body does not generalise to seeing someone else's hand (Longo, Betti, Aglioti, and Haggard, 2009). Moreover, in a recent study participants were asked to look at a hand in a video being touched in synchrony or asynchrony with the felt touch on their hidden hand. At the end of the experiment participants reported to have felt the tactile sensation on the video hand during synchronous stimulation, whereas this feeling disappeared in the asynchronous condition (Schaefer et al., 2006). Findings demonstrated a positive correlation between neuroplastic changes in somatosensory representation of the stimulated digit (D1) and the amount of believing that the seen touch was related to the actual touch: the more the subjects related the seen touch to the felt touch, the more the cortical representation of D1 was moved to an inferior position. In conclusion, only when the seen touch was attributed to one's body, SI showed a modulation.

Conversely, one study did find a VET effect comparing vision of an experimenter's hand to a non-hand object (Haggard, 2006), but the blocked design used did not allow comparison of VET time courses when viewing one's own body and others' bodies. Future research could usefully compare self-specific and non-self-specific components of the rapid-onset VET established here.

CHAPTER 2

Different roles of self and other representations in the visual modulation of touch

Interaction between internal sensory information, such as touch and proprioception, and external sensory information, such as vision, provides a complex representation of one's own body. This complex sensory interaction allows perceiving one's body as one's own and as distinct from the others (Sathian et al., 1997; Haggard, Newman, Blundell, and Andrew, 2000). The cognitive capacity for self-recognition might be a crucial mechanism involved in processing events occurring on the body surface or in the space surrounding the body - the peripersonal space (Bermudez et al., 1995). Detection of events approaching one's own body, visuo-motor control and planning behavioural responses to external stimuli might be some important functions of self-recognition. For example, when a tactile stimulus approaches the hand, it draws attention to that body site and the surrounding space. Our brain's ability to respond to both tactile stimuli on the body surface and visual stimuli looming towards the body, facilitates a complete representation of the stimulated body part and of the peripersonal space, thus speeding up recognition of an event and allowing to adjust our behavioural reactions (Graziano and Cooke, 2006).

2.1 Evidence for shared interpersonal body representations in visual modulation of somatosensation

In some cases, crossmodal links, crucial for representing one's own body, might also be involved in representing the bodies of other people (Thomas, Press, and Haggard, 2006). A common experience of feeling vicariously the sensation of another person hurting the elbow on a table corner might be an example of how simply viewing another body activates the tactile representation of that feeling in the corresponding body part of one's own body. The relation between self and other body events, involving associating sensory experiences related to another person to one's own sensory systems, is based on the so-called Interpersonal Body Representation (IBR) (Haggard, 2006; Thomas et al., 2006). A possible role of these interpersonal representations might be to understand other's perceptual states, by registering them against the representations used to perceive our own body (Thomas et al., 2006). The tendency to understand events occurring to other people is a peculiarity of human beings. Thus, simple associations between sensory information from two different bodies might be considered basic precursor to empathy and theory of mind abilities.

The presence of Interpersonal representations in the domains of action and affect is well established. For example, Reed and Farah (1995) demonstrated that when participants observed a model, they were better at noticing changes in the model's body part position when they moved the corresponding body part of their own body. A possible explanation of this effect was that the body schema – a predominantly unconscious representation of the location of body parts in space, which is continuously updated as the body moves (Longo et al., 2008) - is used for encoding body position for both the self and others. Thus a common mechanism seems to underlie processing of actions associated both with one's own and other people's bodies.

Further, as far as the affective domain is concerned, high-level social cognition mechanisms, such as emotion recognition, might sometimes activate interpersonal representations as well. According to an influential model of emotion processing in the human brain, specific emotional expressions recognition might depend on the activation of representations within the somatosensory system (Adolphs, 2002). In particular, the somatosensory cortex is thought to play a role in recognizing negative facial emotions, because this area is involved in representing somatic information associated with such emotions. We recognize another individual's emotional state by internally generating representations within the somatosensory system that simulate how the other individual would feel when displaying a certain expression (Damasio, 1994; Adolphs, Damasio, Tranel, Cooper, and Damasio, 2000). This interpersonal representation of an emotion might allow the observer to match the seen emotional expression with bodily dependent traces associated with personal experiences of the same emotion (Carr, Iacoboni, Dubeau, Mazziotta, and Lenzi, 2003; Niedenthal, 2007). Results on interpersonal motor and affective representations showed that human minds make sensorimotor and emotional links between people and this has been suggested to be aimed at better understanding other people's experiences.

A few studies have investigated pure interpersonal sensory representations, i.e. the link between mental representation of one's own body and the body of other people. In previous studies on visuo-tactile interaction, for example, participants were usually asked to perform tactile discrimination tasks while looking directly at their own body or, as a control condition, at an object in the same location. An enhancement of tactile acuity when viewing one's stimulated body part was found compared to when viewing an object (Kennett et al., 2001; Taylor-Clarke et al., 2004; Cardini et al., 2011). These previous results suggested an important functional relationship between tactile perception and the mental representation of *one's own* body (Haggard, Taylor-Clarke, and Kennett, 2003). Nevertheless a possible issue might arise on the distinction between viewing *one's* body or *a* body. In fact recent studies investigated the modulation of somatosensation – the private sense of touch – by vision of a body, either one's own or another body (Gallagher, 2005; Haggard, 2006; Thomas et al., 2006; Tsakiris, Hesse, Boy, Haggard, and Fink, 2007).

In their recent study, Thomas and colleagues (2006) tested the role of interpersonal body representation during tactile detection tasks. Participants were asked to respond to tactile events on their body, after a visual cuing event was presented either in the same location, or in a different site on a model's body. In case of visuo-tactile register - thus when the visual cue on the model and the tactile target on the participant's body appeared in corresponding locations – reaction times were faster compared to when visual cue and tactile stimulation were presented in non-corresponding locations in the two bodies. In our everyday life we continuously interact with other people and try to understand their perpetual experiences. To this aim, Thomas and colleagues suggested that the percepts of others are somehow registered against the representations we used to perceive our own body (Thomas et al., 2006).

Further support to the involvement of interpersonal sensory representations in modulating one's sensory experiences was given by other recent findings (Haggard, 2006). In his study, Haggard asked participants to perform a tactile discrimination task on their index fingertip, while viewing either their own hand, another person's hand or an object presented approximately in the same location. Results showed an enhancement of tactile acuity on the fingertip when participants viewed both their own hand and the other hand, relative to when viewing the object. Thus the visual enhancement of touch effect was obtained both with one's own and someone else's hand. The fact that the VET was found regardless of the hand's identity is in line with the suggestion of the presence of interpersonal sharing of body representations.

The interpersonal equivalence in the visual modulation of somatosensation has been suggested to rely on the fact that visual body images are in principles ambiguous between self and other – thus being the visual experience of one's body often very similar to the experience of other bodies (Longo et al., 2008).

2.2 Evidence for self-specific body representation in visual modulation of somatosensation

In contradiction with previously discussed evidence, recent studies demonstrated a self-specific modulation of visuo-tactile interaction effects. Longo and colleagues (2008) investigated the VET effect using the Rubber Hand Illusion (RHI). In this illusion a fake hand is brushed synchronously with one's own unseen hand for a few minutes. Watching the rubber hand being stroked synchronously with one's own hand causes the rubber hand to be attributed to one's own body. After experiencing the illusion subjects usually report 'to feel like the rubber hand is my hand' (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). The illusion is not experienced when subjects' hand is stroked asynchronously with the fake hand (Botvinick and Cohen, 1998). In Longo et al.'s study (2008) a 90 sec induction period – during which, in different blocks, participants' hand was stroked either synchronously or asynchronously with the rubber hand, or not stroked at all – was followed by a tactile grating discrimination task on the fingertip. Results showed significant enhancement of tactile discrimination ability following synchronous stroking compared either to asynchronous stroking and no brushing (Longo et al., 2008). Thus VET was observed when viewing a rubber hand, but only when participants experienced it as their own hand. These results suggest that VET is not driven by a generic visual image of the hand, but rather by a specific representation of the hand as part of one's own body.

Similar self-specific effects on somatic senses were demonstrated also in a recent electroencephalographic (EEG) study. Longo and colleagues (2009) induced pain to participants using an infrared laser, during EEG recordings. In different sessions participants were asked to look into a mirror, aligned with their body midline, at either the reflection of their own hand, of the experimenter's hand or of an object. In a further session the mirror was removed and participants were asked to look directly at their own hand. Analgesic effects of seeing one's own body - both directly and as reflected in a mirror – were found on subjective reports of pain intensity and on laser-evoked potentials (LEPs), compared to vision both of another person's hand and an object. Thus, modulation of vision of the body exerted on somatic senses did not seem to generalise to seeing someone else's body (Longo et al., 2009).

Saxe and colleagues (2006) further demonstrated a non-interpersonal equivalence in visual modulation of somatosensory activity. They recently showed that viewing body parts in first-person perspective produced greater somatosensory activation than viewing the same body parts in third-person perspective (Saxe, Jamal, and Powell, 2006). In particular these results showed that the primary somatosensory cortex activity was suppressed when participants looked at images from a perspective incompatible with looking at their own body. Moreover, a region located in the right human visual cortex - the right extrastriate body area (EBA), usually activated by vision of human bodies and body parts, relative to other categories of visual stimuli (Downing, Jiang, Shuman, and Kanwisher, 2001) – showed greater activation when viewing body parts from an allocentric perspective, thus from a perspective inconsistent with looking at one's own body, compared to when viewing the body from an egocentric perspective (Saxe et al., 2006).

In order to shed light on the controversial results about the different effects of vision of one's own or another body on somatosensation, two main considerations should be done: first, about the different characteristics of the *sense of touch* and second, about the *functional* roles *body representation* plays on the sense of touch.

First, it is a common belief that tactile experience, differently from other sensory modalities, is totally limited to the subject who perceives touch. Indeed, while we can easily understand another person's visual percept by simply looking in the same direction, it is not possible to have direct experience of another person's sensation. Thus, touch has been commonly thought as a private sensory modality (Bermudez, 1998). However recent studies demonstrated that mere observation of another person being touched automatically induces activity in the neural circuitry that is normally recruited in our experience of touch, even in absence of any direct tactile stimulation of one's own body (Keysers et al., 2004; Blakemore et al., 2005). Thus touch is both an important *private* modality informing our brain about one's own physical body states and a *shared* modality that during interactions with the external world allows understanding others' sensory states.

Second, taken together the results on the enhancement of touch when viewing one's own body (Kennett et al., 2001; Taylor-Clarke et al., 2002) and another body (Haggard, 2006; Thomas et al., 2006) with those about self-specific modulation of somatosensation (Longo et al., 2009) one might suggest that the ability of a specific body image to activate a mental body representation depends on the functional contribution of the current visual context to touch. In other words, when viewing one's body, it is likely to expect that the representation of the seen body part exerts an *adaptive* influence on one's somatosensory system in order to get it ready to quickly detect external events approaching the observed body site. On the other hand, even vision of another person's body is sometimes able to modulate one's own bodily sensations. In this case, a mental body representation might play a different, but still important, role in modulating one's somatosensory experience. In particular, viewing someone else's body might activate a mental body representation that allows preparing one's own sensory system to simulate any others' sensory states, and, as a consequence this facilitates to better understand others' sensory experiences. Thus tactile modulation by vision of another person's body might reflect a *social* mechanism of re-experiencing what we observe on the other person by activating our own somatosensory system.

In summary, whereas vision of one's body seems to play an *adaptive* role pre-alerting the somatosensory system, thus functionally modulating one's *private* sense of touch, vision of someone else's body might play a *social* role by promoting a *sharing* of the observed sensory experience thus facilitating to understand others sensory states.

Given the different roles the two visual contexts might play in the visual modulation of touch mechanisms, an interesting issue might be to identify on one hand, the sensory inputs required to drive a mental body representation in case of vision of one's body and, on the other hand, the sensory inputs that are instead essential when viewing someone else's body. The following experiments are aimed at testing the interaction between different sensory information related to the body and their role in driving either a coherent bodily self-representation or a more general body representation able to functionally enhance touch under the two different visual contexts.

Experiment 3. The relevance of visual and proprioceptive information in mental body representations

The present experiment was aimed at shedding further light on the nature of the mental body representation driven by vision of either *one's own* or *someone else's* body. In particular the present experiment tested, for each visual context, which kind of sensory information was required to drive these body representations, whether they need a combination of correlated visuo-proprioceptive inputs to be activated, or rather if a unique sensory information - such as vision - is sufficient to this mechanism. In other words, one might wonder whether the VET when viewing one's hand is restricted to the peripersonal spatial locations defined by proprioceptive representations, whereas the proprioceptive description of one's peripersonal space does not mediate the VET in case of viewing someone else's hand.

In everyday life the ability of our system to build up an integrated representation of one's own body and the surrounding space is crucial to quickly detect external events close to the body, to interact with them and to plan adjusted behavioural responses (Graziano and Cooke, 2006). Viewing one's own body is thought to be able to drive mental representation of the body that, through top-down projections, sends modulatory feedbacks to the primary somatosensory areas (Serino and Haggard, 2010). Previous studies suggested that this mental representation of the body might preactivate the somatosensory system to get it ready to process external stimuli. As a consequence, facilitatory effects have been observed on tactile perception when viewing the body as compared to when viewing a non-body object, the well-known visual enhancement of touch (Kennett et al., 2001; Fiorio and Haggard, 2005; Longo et al., 2008; Cardini et al., 2011).

As previously mentioned, even vision of another person's body is sometimes able to activate a mental representation of the body and to modulate one's own bodily sensations (Haggard, 2006; Thomas et al., 2006). Unlike one's body, vision of someone else's body promotes in the observer a simulation mechanism whereby others' somatosensory states are registered against the representation used to perceive one's own body (Thomas et al., 2006). With this mechanism one can better understand the other person's sensory experiences.

An interesting issue might be whether vision of either one's own or someone else's body is actually sufficient for activating complete mental body representations or rather if a combination of multisensory inputs is required. In the majority of the studies investigating the VET effect, participants were usually asked to perform a tactile discrimination task while looking directly at their own stimulated body site or at an object in the same location (Kennett et al., 2001; Taylor-Clarke et al., 2002; Taylor-Clarke et al., 2004). In order to process a tactile stimulus on one's own body, both viewing the body part and localizing it in the space might play a crucial role. On one hand, looking at the stimulated body site allows to visually recognize it as belonging to one's own body; on the other hand, localizing a stimulated body part in the space, might help in identifying the source of the tactile stimulation (Honore, Bourdeaud'hui, and Sparrow, 1989). Thus visual and proprioceptive information related to the stimulated body site might be encoded and drive a coherent representation of one's body in the space. The well-established facilitatory effect of viewing one's body on tactile processing might rely on a top-down modulation projected by a complex mental body representation where visual and proprioceptive inputs are functionally integrated.

Conversely, in case of vision of another body the mechanism underlying the facilitatory effects on tactile processing seem to rely on a form of "somatosensory empathy". This basically consists in a simulation mechanism, by re-experiencing the observed sensory states with one's sensory systems, or just in preparing one's sensory system to simulate any other's sensory experience, not even occurred but possibly occurring soon. It seems unlikely that the mental representation driven in the observer by vision of the other body requires also special proprioceptive inputs in order to prime this simulation mechanism. The ability of my sensory system to simulate the observed sensory states should be independent from the position of my body in relation to the other body. For this reason, simply viewing someone else's body might be sufficient to drive a mental body representation where no proprioceptive inputs related to one's own body are required to be integrated.

These issues open automatically the question related to which areas might house these representations and, as a consequence, which are the neural sources of the top-down projections suggested to modulate the somatosensory activity. In fact, while the possible site of the VET has been localised to the primary somatosensory area (Taylor-Clarke et al., 2002; Fiorio and Haggard, 2005; Cardini et al., 2011), the source of the signal that modulates SI when viewing the body is still unknown. Which kind of mental representation is activated when viewing one's own or someone else's body part? Is it a visual representation, possibly housed in the occipital cortex (Downing et al., 2001; Astafiev, Stanley, Shulman, and Corbetta, 2004), or a multisensory representation present in the posterior parietal areas (Graziano et al., 1994) or in prefrontal regions (Graziano, Cooke, and Taylor, 2000)? Neural maps receiving convergent inputs from different sensory modalities have been suggested as essential for the analysis of spatial relations between body parts and peripersonal space and for building up a coherent, continuously updated representation of one's body in the space (Driver and Spence, 1998; Ursino, Zavaglia, Magosso, Serino, and di Pellegrino, 2007). This might support the multisensory nature of the mental representation driven by viewing one's body in the VET effect.

Conversely, as previously suggested, vision of someone else's body should not drive a multimodal representation of the body, rather a simply visual representation. A recent neuroimaging study showed greater activation the right extrastriate body area - a region located in the right human visual cortex (Downing et al., 2001)- when viewing body parts from an allocentric perspective, thus from a perspective consistent with looking at someone else's body, compared to when viewing the body from an egocentric perspective (Saxe et al., 2006).

Nevertheless, coincidence between the location where the body part is seen and the location where the body part is felt has been scarcely manipulated and no clear evidence about the different contribution of vision and proprioception to touch has hitherto been provided.

An interesting study by Tipper and colleagues (1998) tried to isolate the contribution of different sensory information in facilitating tactile processing. Authors investigated different roles vision of the stimulated body part and proprioceptive orienting to that body site – i.e. the orientation of the eyes and head towards the stimulated site - play in speeding up tactile reaction times. Previous results demonstrated that proprioceptive orienting to the body site facilitates tactile processing both in case of vision of the body (Pierson, Bradshaw, Meyer, Howard, and Bradshaw, 1991) and when subjects cannot see the stimulated body part (Driver and Grossenbacher, 1996). Tipper and colleagues investigated the role of vision alone in the case where the contribution of proprioceptive orienting might be excluded. Participants were asked to respond as quickly as possible to a tactile stimulus, in three different visual conditions. In different blocks participants were asked to look either at a monitor in front of them where a camera presented an upside down real-time image of the stimulated hand (vision alone), to look directly at the stimulated hand (proprioceptive orienting and vision) or to look towards the hand, occluded from direct view by a cardboard box (proprioceptive orienting alone). The experiments were undertaken on four consecutive days, the first one being a practice session where participants were trained in order to adjust to the unusual visual presentation of the hand in the vision alone condition. Results demonstrated an overall facilitatory effect of looking towards the stimulated body site – i.e. both when vision of the hand was provided and when it was prevented by a cardboard box - compared to looking away from it. From this result one might conclude that viewing the stimulated body part does not add facilitating inputs to tactile processing, rather that proprioceptive orienting plays a crucial role in this mechanism. Surprisingly, further analysis demonstrated that the enhancement of tactile processing persisted even when proprioceptive orienting was prevented: looking at a monitor showing the stimulated hand speeded tactile reaction times compared to when the monitor showed the non-stimulated hand (Tipper, Lloyd, Shorland, Dancer, Howard, and McGlone, 1998). Thus, even vision alone – without the contribution of proprioceptive orienting - seemed able to exert a facilitatory effect on somatosensation. However, a possible explanation might rely on the presence of the practice session, during which participants were trained to the unusual vision of one's body: while looking in the direction where there was not the actual stimulated body part, rather an upside down real-time image of it, they were encouraged to move the fingers of the stimulated hand, so that the simultaneous observed and felt fingers movement facilitated the link between the image of the hand and the actual hand. The visual image of the hand might be perceived to be disembodied since presented in a different location relative to the proprioceptive representation of the actual hand. The training session might abolish this effect providing the necessary integration between dissociated sensory inputs.

The facilitatory effect vision of one's body has on touch might be underlie by an adaptive neural network that preactivates the somatosensory circuit as soon as the body is seen, with the aim to quickly prepare the system to process tactile external events approaching the body. Thus a sudden unpredictable vision of one's body might be a more likely stimulus in order to properly test whether vision itself facilitates the sense of touch, even in case of visual and proprioceptive inputs arising from a different spatial location. Moreover, a randomized, unpredictable switching of visual context between one's and someone else's body might further help in disambiguating on one hand the individual contribution of vision and, on the other hand the role of visuo-proprioception integration in facilitating tactile processing under the two different visual contexts.

The present experiment tested whether the VET effect relies on a mental body representation that requires convergent visual and proprioceptive inputs related to *one's own* stimulated body part or whether visual input alone is sufficient. Moreover, the present study investigated whether this requirement changes when the observed body part belongs to someone else. In order to test these issues, in the present study tactile acuity was measured on the right middle fingertip while participants viewed, in different trials, either a picture of their own hand, of another hand or of an object, presented on a monitor that might be located, in different sessions, either in front of them (vision alone), or just above their actual hand (vision and proprioceptive information). In the latter case tactile processing might benefit from visual and proprioceptive alignment.

If spatial alignment between seen and felt body part is crucial in building up a coherent representation of one's body, an enhancement of tactile acuity when viewing one's hand compared to when viewing the object, should have been found only when the image of one's hand was presented exactly above the actual hand. Conversely, no VET effect should have been observed when the image of the hand and its proprioceptive representation did not spatially match. However, if the VET effect is not space-specific, simply viewing one's body, regardless of its location with respect to the actual hand, should be sufficient to drive a representation of the stimulated body site and then to modulate one's tactile acuity. Thus, an overall enhancement of tactile acuity might be found when viewing one's body compared to when viewing an object, regardless of where the images were presented.

Different results might be expected in case of viewing *another* person's body: in consideration of the fact that the other hand is not one's hand, there should not be a conflict between the proprioceptive information arising from my hand and the visual image of the other hand. Regardless of its spatial location, simply vision of someone else's hand was expected to be able to drive a mental body representation and then to exert its facilitatory effect on tactile processing. In line with this hypothesis, an enhancement of tactile acuity might be expected when viewing the other hand, compared to when viewing the object, regardless of where the images were presented.

Materials and Methods

Participants

Fifteen naïve, healthy volunteers (age 20-30, mean 23.5, 12 females) participated in the experiment. All participants were right-handed, had normal or corrected-to-normal vision, and reported normal touch. The study was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Stimuli and Procedure

Preprocessing. A digital photograph of the participant's right hand dorsum was taken in a session prior to the experiment. The participant's hand in the photograph was cut out and paste on a black background with Adobe Photoshop CS4. The image of another hand dorsum – matched for the participant's gender - was selected from a set of images of different hands, on the basis of physical dissimilarity: a hand very different relative to the participant's one was selected by the experimenter. As a confirmation of the correct selection of the hand, at the end of the experiment participants were asked to rate the similarity between their own hand and the other hand using a seven-point Likert scale from 1 (completely different) to 7 (completely the same). Participants who rated the other hand similar to their own more than 4 were rejected. The mean rate for similarity judgment was 1.53 (standard deviation = 0.51).

Procedure

The experimental design consisted of two sessions: 'Vision alone' session and 'Vision and proprioception' session. Participants underwent both sessions in a counterbalanced order: half of the participants underwent first the 'Vision alone' session and, in a different day, the 'Vision and proprioception' session. The other half of the participants underwent the two sessions in the opposite order.

In session 'Vision alone' participants sat at a table with their right hand resting palm-down on a cushion, arranged so that their fingers were kept outside the cushion, ~ 6 cm above the table. This allowed the experimenter to touch participant's fingertip with a grating (see below). The direct view of the hand was prevented by moving, at the beginning of the experiment, a cardboard box over the hand. An aperture at the back of the occluding box, allowed the experimenter to see and touch participant's hand (see below). In order to prevent the view of the left hand, participants were asked to keep it under the table for the entire duration of the experiment. A 17" computer monitor was placed in front of the participant at a distance of ~ 60 cm (Figure 11A). In different trials an image of either the participant's hand, the other hand or an object (a wooden block, approximately hand-sized) was presented on the monitor (Figure 12). Participants were asked to focus visual attention and gaze directly towards the monitor. A PC running C.I.R.O. (www.cnc.unibo.psice.unibo/ciro) software was used to control the presentation of the stimuli and record responses.

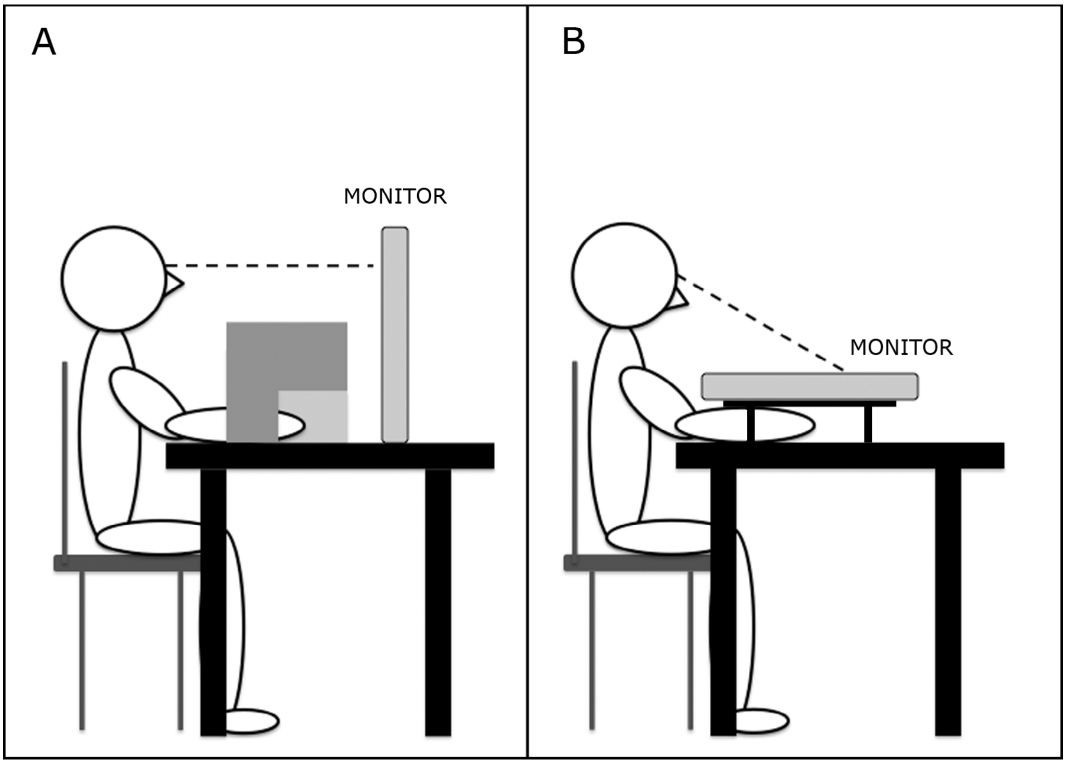


Figure 11. Schematic depiction of experimental setup.
A. In ‘Vision alone’ session participants were asked to look towards (dashed lines) a monitor where different images where projected, while keeping their right hand palm-down lying on the table and occluded by a cardboard box.
B. In ‘Vision and proprioception’ session a small table was placed over the participants’ hand and the monitor was laid on it. Participants were asked to look downward towards the monitor.

To measure effects of vision on tactile acuity, participants made unspeeded verbal judgments of the orientation of square-wave gratings (Van Boven and Johnson, 1994) applied by the experimenter to the tip of the right middle finger. The grating ran half along and half across the long axis of the finger. The tactile grating for each subject was selected by an initial staircase procedure, using increasingly finer gratings to identify the smallest ridge width for which accuracy was between 55% and 60% correct over 40 trials. The mean ridge width selected by this means was 1.10 mm (standard deviation = 0.45 mm). The experimenter held the grating in readiness close to the fingertip. As soon as the image showed up, the experimenter delivered the tactile stimulation. Participants completed two blocks of 60 trials each. A pause of a few minutes, during which participants could stretch their arm, was interspersed between blocks.

In session ‘Vision and proprioception’ participants sat at a low table with their right hand resting palm-down on a cushion, aligned with their parasagittal plane, arranged so that their fingers were kept outside the cushion, ~ 6 cm over the table. A little and low table was moved over the participant’s right hand and the 17’’ computer monitor was in turn laid on it (Figure 11B). In different trials an image of either the participant’s hand, the other hand or the object was presented on the computer screen (Figure 12). In this experimental set-up participant’s right hand and visual image were spatially aligned. The procedure for the tactile task was the same as in the previously described session.

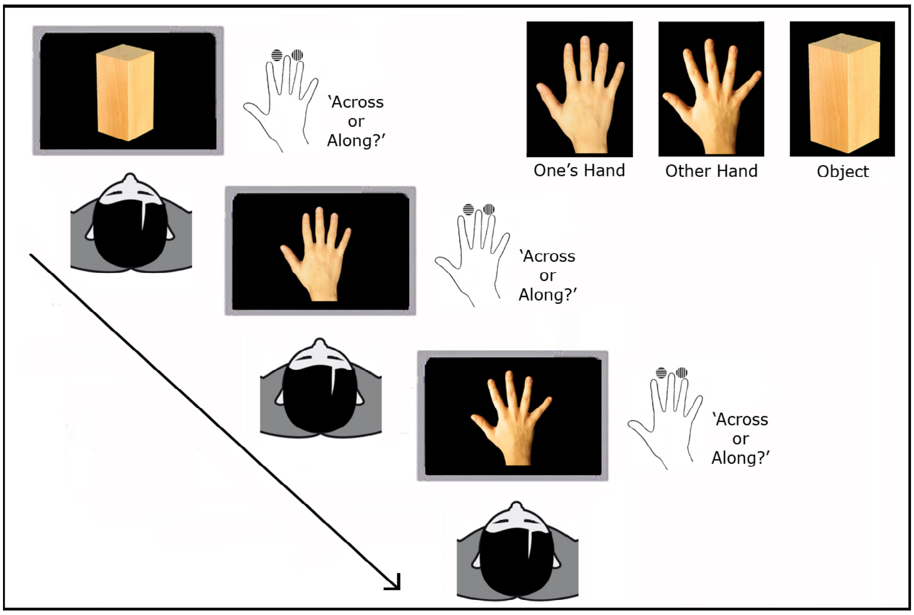


Figure 12. Schematic depiction of the experimental paradigm. Participants were asked to look at a monitor where in different trials either the image of one’s hand, of another hand or of an object was projected. As soon as the image showed up, the experimenter applied on the participant’s right middle fingertip a grating running, in different trials, half along and half across the long axes of the finger. Participants verbally reported the orientation of the grating.

Results

In order to study VET modulations in case of visual information alone and combined visuo-proprioceptive information related to one’s or to another body, participants’ accuracy in discriminating the orientation of square-wave gratings applied to the tip of the right fingertip was compared across conditions. In the ‘Vision alone’ session judgments of grating orientation were significantly above chance both when viewing one’s hand (64% correct), [$t_{(14)} = 6.44$; $p < 0.0001$], the other hand (70% correct), [$t_{(14)} = 7.94$; $p < 0.0001$] and the object (64% correct), [$t_{(14)} = 6.77$; $p < 0.0001$]. Also in the ‘Vision and proprioception’ session judgments of grating orientation were significantly above chance both when viewing one’s hand (72% correct), [$t_{(14)} = 14.79$; $p < 0.0001$], the other hand (70% correct), [$t_{(14)} = 6.77$; $p < 0.0001$] and the object (65% correct), [$t_{(14)} = 5.09$; $p < 0.0001$].

A 2-by-3 ANOVA was conducted on the percentage of correct responses to grating orientation with the within-participants factors of Session (‘Vision alone’ and ‘Vision and proprioception’’) and Image (One’s hand, Other hand, Object). Duncan post-hoc comparisons were performed, when necessary, to compare single effects. The main effect of Session was not significant [$F_{(1,14)} = 1.25$, $p = 0.28$], whereas the main effect of Image was significant [$F_{(2,28)} = 3.81$, $p < 0.05$]: accuracy was higher when viewing the Other hand (mean accuracy = 70%; s.e.m. = 2%) than when viewing the Object (64%; s.e.m. = 2%, $p < 0.05$). No difference was found between viewing the Other (mean accuracy = 70%; s.e.m. = 2%) and One’s own hand (67%; s.e.m. = 3%; $p = 0.26$). Moreover, the critical interaction Session x Image was significant [$F_{(2,28)} = 3.93$, $p < 0.05$]. In the ‘Vision alone’ session the VET effect was observed only when viewing the Other hand. Indeed, whereas vision of the Other hand enhanced tactile acuity on the fingertip (mean accuracy = 70%; s.e.m. = 2.5%) compared to viewing the Object (mean accuracy = 64%; s.e.m. = 2%; $p < 0.05$), no difference in tactile acuity was found between viewing the Object and viewing One’s hand (mean accuracy = 64% and 64%; s.e.m. = 2% and 2% respectively; $p = 0.98$).

A different pattern of results was observed in the ‘Vision and proprioception’ session – thus when the participant’s hand was aligned with the visual image presented on the screen. The enhancement of tactile acuity was observed both when viewing the Other hand (mean accuracy = 70%; s.e.m. = 3%) and One's own (mean accuracy = 72%; s.e.m. = 1%), relative to when viewing the Object (mean accuracy = 65%; s.e.m. = 3%; $p < 0.05$ in both cases). Moreover, whereas in the 'Vision alone' session vision of the Other hand (mean accuracy = 70%; s.e.m. = 2.5%) enhanced tactile acuity compared to vision of One's hand (mean accuracy = 64%; s.e.m. = 2%; $p < 0.05$), in the 'Vision and proprioception' session no difference in tactile acuity was observed between the two images (mean accuracy for Other hand = 70%; s.e.m. = 3%; mean accuracy for One's hand 72%; s.e.m. = 1%; $p = 0.43$).

An interesting way to look at the present data is to compare changes in tactile acuity when viewing an image in the two different Sessions. When viewing the Object, tactile acuity did not significantly change between Sessions ('Vision alone': mean accuracy = 64%; s.e.m. = 2%; 'Vision and proprioception': mean accuracy = 65%; s.e.m. = 3%; $p = 0.54$). The same non-significant pattern of results was found when viewing the Other hand ('Vision alone': mean accuracy = 70%; s.e.m. = 2.5%; 'Vision and proprioception': mean accuracy = 70%; s.e.m. = 3%; $p = 0.83$). Conversely, a significant difference was observed as a function of spatial location of the image of one's hand. A significant higher accuracy was found when the image of One's hand was aligned with the participant's actual hand, i.e. in the 'Vision and proprioception' session (mean accuracy = 72%; s.e.m. = 1%) than when the image was displaced in front of him, i.e. in the 'Vision alone' session (mean accuracy = 64%; s.e.m. = 2%; $p < 0.01$) (Figure 13).

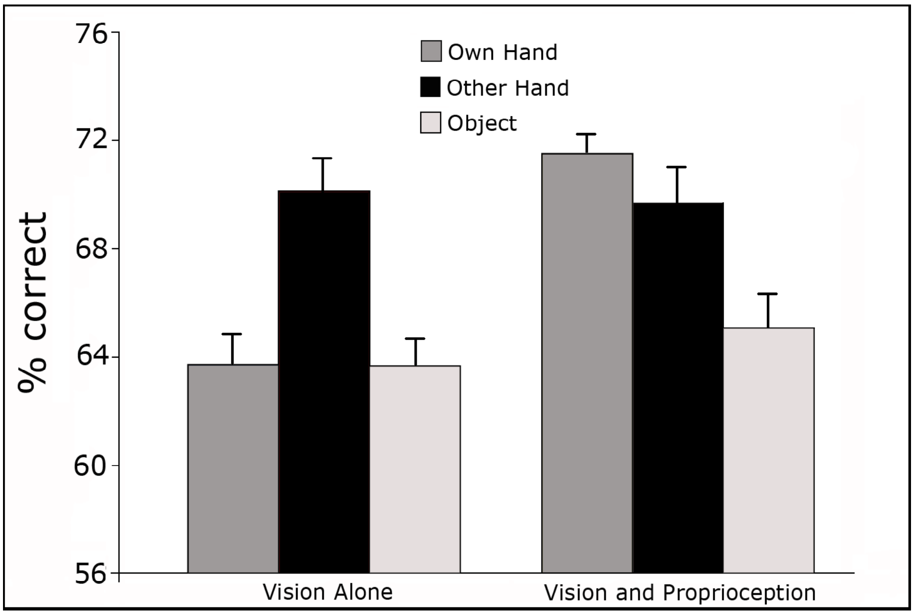


Figure 13. Behavioural results for the Grating Orientation Task. Participants made judgments of the orientation of square-wave gratings applied to the tip of the right middle finger.
In the 'Vision alone' session, accuracy in discriminating the "Across" or "Along" orientation of gratings was higher when participants viewed another hand than when they viewed both their own hand and an object.
In the 'Vision and proprioception' session accuracy in discriminating the "Across" or "Along" orientation of gratings was higher when participants viewed both their own hand and another hand than when they viewed an object.
Accuracy when viewing one's hand enhanced in the 'Vision and proprioception' session compared to accuracy in the 'Vision alone' session. No changes between the two sessions were observed both when viewing the other hand and the object. Error bars show standard error across participants.

Discussion

The present study investigated whether the VET effect when viewing one's body depends on convergent visuo-proprioceptive information related to the stimulated body part or rather on simply visual inputs. The same issue was tested in case of viewing someone else's body, hypothesizing a different involvement of visual and proprioceptive inputs related to the body in the two different visual contexts.

Viewing one's hand enhanced tactile acuity compared to viewing an object only when visual and proprioceptive information related to the stimulated body part matched, i.e. when the visual image of the stimulated hand was seen in the same location of the proprioceptive representation of the actual body part. In fact as a confirmation of this result, when viewing the image of one's hand in a location different from where the actual hand was, no significant change in tactile acuity was found as compared to when viewing the object. The present results suggested that the positional conflict between visual and proprioceptive information related to one's body might be considered costly: when the image of one's hand was seen elsewhere relative to where the actual hand was, a significant decrease in tactile acuity was found as compared to when the visual image was presented in the exact location of the actual hand. Interestingly, viewing someone else's hand always produced a VET effect regardless of its spatial location: when participants viewed an image of another person's hand both in front of them and exactly above their own hand, an enhancement of tactile acuity was observed compared to when viewing the object.

The present results suggested that vision of one's own body and of someone else's body modulate somatosensation in different ways. A possible mechanism underlying visual modulation of touch might consist in activation of a mental body representation driven by vision of the body. This representation is thought to send top-down modulatory projections to the primary somatosensory cortex, preactivating it and thus improving tactile processing (Fiorio and Haggard, 2005). While this mechanism might be activated both in case of viewing one's own body and of another body (Taylor-Clarke et al., 2002; Haggard, 2006; Thomas et al., 2006; Longo et al., 2009), the present results suggested that different sensory information are required to activate the mental body representation in the two different visual contexts. Indeed, when viewing one's body, congruent visual and proprioceptive information related to the stimulated body part seemed essential to drive a coherent mental representation of that site, able to functionally modulate one's tactile acuity. Conversely, simply vision of another body seemed to be sufficient to activate a mental body representation, even when it is not spatially congruent with the proprioceptive representation of one's own stimulated body part.

One possible explanation of these different sensory requirements might rely on different functional relationships between vision of one's body or vision of someone else's body and one's own somatosensory experience.

Viewing one's body might preactivate one's own somatosensory system, as soon as the body is seen, in order to get it ready to detect and process external events. This might be an adaptive mechanism aimed at facilitating our system in defending against external source of danger (Graziano and Cooke, 2006). Visual inputs facilitate the recognition of the stimulated body site. Proprioceptive inputs might help in localizing the body part in the space and, as a consequence, the source of the external stimulus (Honore, 1982; Honore et al., 1989). Thus, coherence between different sensory information might be crucial in building up a complete representation of one's own body and the surrounding space. The present study suggested that the occurrence of VET when viewing one's body, only when multisensory inputs are in spatial register, might reflect this adaptive mechanism: only when all necessary inputs related to a body site are integrated in a coherent representation of one's own body, the sense of ownership of that body-part is updated (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005; Tsakiris, 2008) and modulatory projections – from this multimodal representation - can preactivate the somatosensory system, thus facilitating processing of tactile events approaching the body surface, and, as shown in the present experiment, improving tactile discrimination abilities (Graziano and Cooke, 2006; Cardini et al., 2011).

In contrast, the functional role of viewing another body in modulating one's own somatosensation seems related to a simulation mechanism rather then to alert one's perceptual systems (Haggard, 2006; Thomas et al., 2006). Simulation is thought to consist in remapping the sensory experience observed on someone else's body, onto one's own somatosensory system. This simulation mechanism is decoupled from spatial location:

indeed, its general application across both peripersonal space and extrapersonal space may be the feature that allows equating perceptual processing for self and other. This might in turn produce a social form of “somatosensory empathy” that facilitates understanding of other people’s states. The relevance of others to our own sensory experience does not require them to be treated as equivalent to us. In fact we can show this “somatosensory empathy” while recognizing the spatial, perspectival and personal difference between self and other. Visual information is sufficient to recognize the seen body as belonging to another person, and then to drive a mental body representation used to perceive – and to understand – the other’s states. In conclusion, visual context seems to prepare one’s own primary somatosensory areas to re-experience the observed sensory state.

To summarize, in case of viewing one’s hand multisensory visuo-proprioceptive inputs are required to be in spatial register to drive a coherent multimodal representation of the body. Conversely, in case of vision of another hand, convergence between visual inputs related to the other and proprioceptive inputs related to one’s body should not occur. Thus, whereas when viewing one’s body, the mental body representation seems to exert its modulatory effect towards primary somatosensory areas only after receiving convergent multisensory inputs, a direct modulation from a visual representation of the body should occur as soon as someone else’s body is seen. As far as the assumption related to one’s body is concerned, it is important to remind that the mechanism of multisensory integration follows three general rules (Stein and Meredith, 1993). As one of these claims, in order to treat stimuli from different modalities as referring to the same external event, they should show spatial coincidence. Moreover, behavioural responses to spatially coincident multisensory inputs exhibit lower threshold and reduced reaction times than their unimodal counterpart (Hershenson, 1962; Calvert et al., 2000). Incongruent inputs have the opposite effect, slowing response times and producing perceptual anomalies (McGurk and MacDonald, 1976). In line with this rule, the present results demonstrated that only when visual and proprioceptive inputs were spatially aligned, they could be treated as belonging to the same source, i.e. one's own hand. These inputs thus drove a multimodal representation of the stimulated body part, essential in preparing the somatosensory system to process external events around the body.

Thus, to answer the question in the introduction – about which kind of mental representations are activated when viewing a body part - the representation that is driven by viewing *one's* own body and modulates somatosensory processing appears to be a truly multisensory representation, in the sense of requiring convergent sensory inputs to be integrated within a proprioceptively-defined peripersonal space, whereas that driven in case of viewing *someone else's* body seems to be purely visual.

In conclusion it might be suggested that whereas vision of one's own body has an important adaptive meaning, being a potent alerting input to many sensory systems (Fiorio and Haggard, 2005), viewing another body might trigger social tendencies in understanding others' sensory experiences. Thus two kinds of body representation do exist: a first-order body model that represents one's own body and that is specific to the perceiving body, highly susceptible to current afferent information, and a more general body model that represents the human body independently whose body it is (Gallagher, 2005).

Given that when multisensory inputs related to one's body are ambiguous multisensory integration mechanisms are affected – with following reduction in sensory processing - the next experiment was aimed at identifying crossmodal compensatory mechanisms able to improve sensory processing even in presence of multisensory conflicts.

Experiment 4. Vision of touch in the Visual Enhancement of Touch

Multisensory literature widely showed that under normal circumstances, multimodal events arise from common sources, are in spatial and temporal register, and probably share other similar features (such as a common motion direction) (Stein and Meredith, 1993). When the senses provide conflicting information, the perceptual resolution slows down processing and might give rise to a decrease of perceptual sensitivity, misperceptions and rather striking perceptual illusions (McGurk and MacDonald, 1976; Botvinick and Cohen, 1998). An often cited phenomenon, demonstrating how resolution of sensory conflicts might give rise to perceptual illusions, is the so-called ventriloquist effect (Howard and Templeton, 1966; Bertelson and Aschersleben, 1998). This phenomenon consists in a tendency to localize closer together visual and auditory stimuli, in temporal register, presented in slightly separate locations (Bertelson, 1999). More precisely, the perceived source of a static sound shifts towards the location of the visual source. In classical ventriloquism, speech is perceived at the puppet’s moving mouth, precisely because it is the puppet’s, not the ventriloquist’s mouth that moves.

Even the body as a multisensory object has provided examples of perceptual illusions following integration of ambiguous sensory inputs. In the Rubber Hand Illusion, for example, viewing touch on a fake hand and feeling synchronously touch on one’s own hidden hand result in an illusory percept of the fake hand as one’s own hand. No illusion is evoked when one’s own and the rubber hand are touched asynchronously (Botvinick and Cohen, 1998). The multisensory correlation between the seen and the felt touch adapts the proprioception by shifting the felt position of one’s hand towards the fake one and updates the sense of ownership of the rubber hand (Tsakiris and Haggard, 2005).

It is worth noting that senses probably evolved to work in concert to aid one another when one or the other sensory modality is not able to clearly inform our brain. For example, in the Visual Remapping of Touch (VRT) effect, the perception of near-threshold tactile stimuli on the face is enhanced when concurrently viewing a face being touched (Serino, Pizzoferrato, and Ladavas, 2008). According to the inverse effectiveness principle (Stein and Meredith, 1993; Stein, Jiang, and Stanford, 2004; Stanford, Quessy, and Stein, 2005) visual information pertaining to touch is used to boost tactile processing – thus facilitating tactile perception – only in case of ambiguous, week tactile afferent inputs that do not allow touch alone to solve detection task close to perceptual limits.

In the previously discussed experiment, vision of one's hand and proprioceptive information related to the stimulated body part provided conflicting but rather unambiguous sensory inputs that were neither in spatial nor in temporal register. For these reasons, crossmodal integration and mutual interaction could not take place. This reflected in an inability of our system to build up a multimodal representation of one's hand.

An interesting question might be whether a positional conflict definitively affected a coherent representation of one's body, or whether it might be somehow solved or, at least, reduced by developing new crossmodal strategies. One possible example might be the presence of new incoming information able to link the two separated reference frames of the conflicting signals.

Partially modifying the previous experiment, the present study hypothesized that by adding a third, new, meaningful information able to link the image of one's hand with one's own stimulated hand, the positional conflict might be reduced. In particular, it was hypothesized that viewing on the screen the image of one's hand being touched, as soon as the tactile stimulation - the to-be-judged grating - was presented to the actual hand might allow the seen touch to be remapped onto the felt touch. This might thus reduce the spatial gap between visual and proprioceptive representations of the hand and as a consequence to refer the seen hand to one's own body. RHI studies demonstrated that synchronous visuo-tactile stimulation caused a drift in the perceived position of one's hand towards the rubber hand (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). In line with previous findings the present study hypothesized that the new visuo-tactile correlation might cause a positional readjustment. If this new information is able to reduce the positional conflict, the image of one's hand might be expected to be treated as part of one's own body. Further, a multisensory representation of one's hand might be updated and finally might be able to send modulatory projections to the somatosensory system. In conclusion, as prerequisite of VET mechanism, improved tactile acuity was expected.

In order to test this hypothesis, in the present study tactile acuity was measured on the right middle fingertip while participants viewed a movie depicting, in different trials, either a picture of their own hand, of someone else's hand or of an object that could be touched or just approached by a cotton bud. Movies were presented on a monitor located in front of the participant. This induced a positional conflict between the image of one's hand and the actual hand. Visual and tactile stimuli were made as synchronous as possible so that as soon as the cotton bud reached the image, or a fixed location close to the image, the experimenter delivered the tactile stimulation on the participant's fingertip. If the multisensory correlation between vision and touch was able to link the visual image of the hand with one's own hand, thus reducing the positional conflict, first the VET when viewing one's hand might be expected to reappear. Second a difference in tactile acuity when viewing one's hand being touched compared to when viewing one's hand not being touched might be found.

No clear predictions can be made about effects of vision of touch towards someone else's hand. According to the previous experiment, VET when viewing another person's hand might be always expected, both when the hand is touched and when the cotton bud drifts away from it. In that study it was suggested that vision of the other exerts a genuine effect on one's somatosensory system, that seems to depend on a form of generalization across spaces and persons, rather than on substituting others for self or treating them as equivalent to ourselves. Thus, no difference between viewing touch and no-touch might be expected in case of viewing someone else's hand. Conversely, vision of touch might somehow be integrated in the mechanism underlying VET when viewing someone else's hand. In line with this hypothesis, in literature a huge amount of data has widely demonstrated that a fronto-parietal network, normally recruited during tactile perception, is activated also when viewing another body being touched (Keysers et al., 2004; Blakemore et al., 2005; Ebisch, Perrucci, Ferretti, Del Gratta, Romani, and Gallese, 2008). For these reasons from the present study it might be expected to find either no difference in tactile acuity when new sensory congruent information was added to the image of the other hand relative to the control condition (viewing touch versus no-touch) or an enhancement of tactile acuity when viewing the cotton bud touching the finger of the other hand compared to when it was seen not being touched.

Materials and Methods

Participants

Twenty naïve, healthy volunteers (age 22-31, mean 25.5, 15 females) participated in the experiment. All participants were right-handed, had normal or corrected-to-normal vision, and reported normal touch. The study was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Stimuli and Procedure

Preprocessing. A digital photograph of the participant's right hand dorsum was taken in a session prior to the experiment. The participant's hand in the photograph was cut out and paste on a black background with Adobe Photoshop CS4. The image of another hand dorsum – matched for the participant's gender - was selected from a set of images of different hands, on the basis of physical dissimilarity: a hand very different relative to the participant's one was selected by the experimenter. As a confirmation of the correct selection of the other hand, at the end of the experiment participants were asked to rate the similarity between their own hand and the other hand using a seven-point Likert scale from 1 (completely different) to 7 (completely the same). Participants who rated the other hand similar to their own more than 4 were rejected. The mean rate for similarity judgment was 1.55 (standard deviation = 0.62). Then, movies showing a cotton bud that could either touch or drift away from the participant's hand, the other hand or an object (a wooden block, approximately hand-sized) were built using PowerPoint, PPT-DVD (http://www.ppt-to-dvd.com) and Windows Movie Maker. In different trials, one of the three images was presented as a central, static image in the background of the movie. In the foreground, however, the cotton bud was presented, initially positioned on the upper central part of the screen. In different trials the cotton bud motion could follow one of two trajectories. In the Touch condition, along the movie, the cotton bud actually touched the fingertip of the right middle finger of the shown hand or the top of the object, moving towards the centrally presented image, and then backwards to its starting position. In the No-Touch condition, the cotton bud drifted away from the image and then backwards to its starting position. A PC running C.I.R.O. (www.cnc.unibo.psice.unibo/ciro) software was used to control the presentation of the stimuli and to record responses.

Procedure

Participants sat at a table with their right hand resting palm-down on a cushion, arranged so that their fingers were kept outside the cushion, ~ 6 cm over the table. This allowed the experimenter to touch participant's fingertip with a grating (see below). The direct view of the hand was prevented by moving, at the beginning of the experiment, a cardboard box over the hand. An aperture at the back of the occluding box allowed the experimenter to see and touch participant's fingertip (see below). In order to prevent the view of the left hand, participants were asked to keep it under the table for the entire duration of the experiment. A 17" computer monitor was placed in front of the participant at a distance of ~ 60 cm (Figure 14). In different trials, a movie depicting one of the three images (participant's hand, the other hand or the object) - that could be touched or just approached by the cotton bud - was presented on the monitor (Figure 15). Participants were asked to focus visual attention and gaze directly towards the monitor.

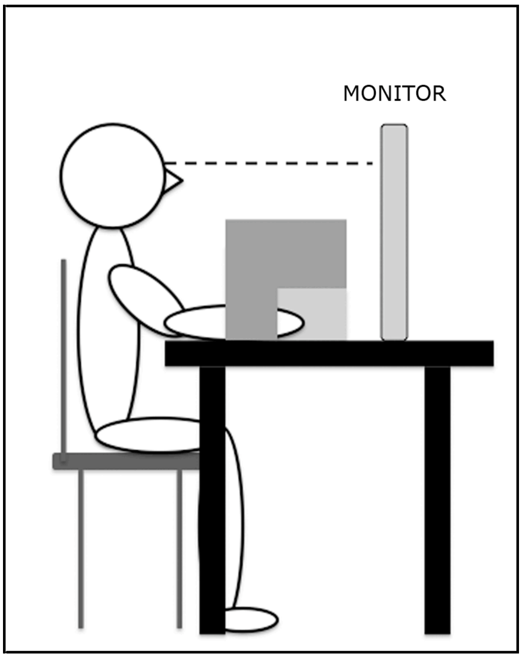


Figure 14. Schematic depiction of experimental setup. Participants were asked to look towards (dashed lines) a monitor where different images where projected, while keeping their right hand palm-down lying on the table and occluded by a cardboard box.

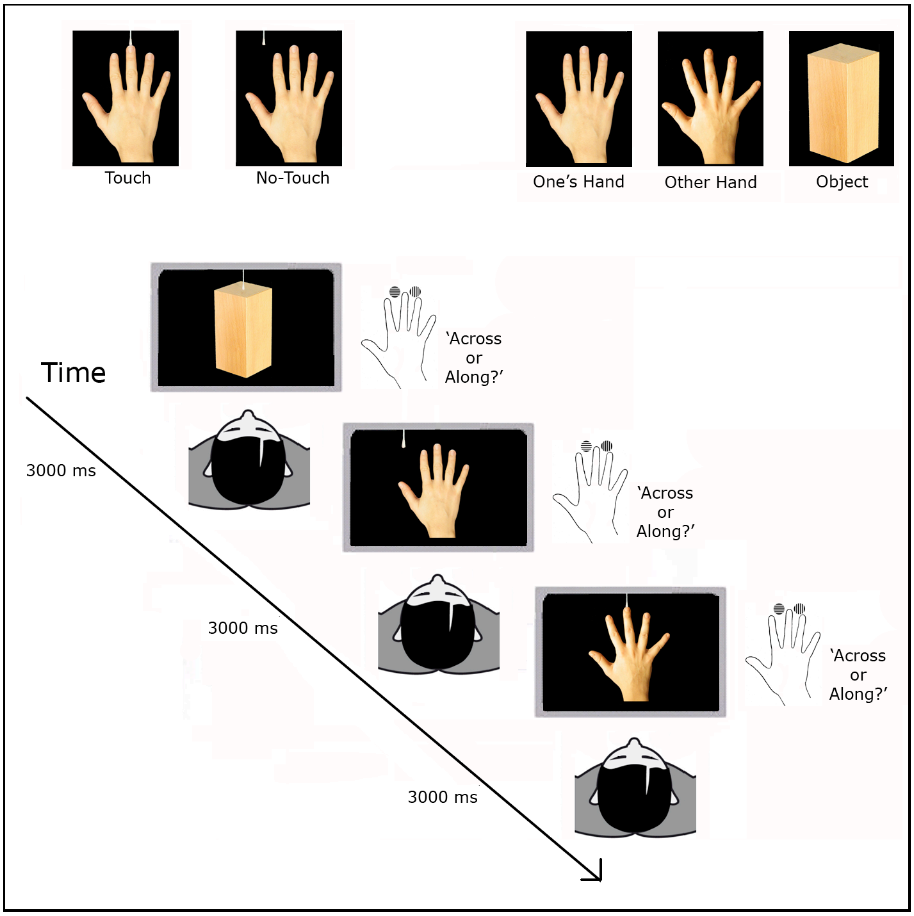


Figure 15. Schematic depiction of the experimental paradigm. Participants were asked to look at a monitor where in different trials either the image of one's hand, of another hand or of an object, that could be touched or just approached by a cotton bud, was projected. As soon as the cotton bud reached the final step of its forward trajectory, the experimenter applied on the participant's right middle fingertip a grating running, in different trials, half along and half across the long axes of the finger. Participants verbally reported the orientation of the grating.

To measure effects of vision on tactile acuity, participants made unspeeded verbal judgments of the orientation of square-wave gratings (Van Boven and Johnson, 1994) applied by the experimenter to the tip of the right middle finger. The grating ran half along and half across the long axis of the finger (Figure 15). The tactile grating for each subject was selected by an initial staircase procedure, using increasingly finer gratings to identify the smallest ridge width for which accuracy was between 55% and 60% correct over 40 trials. The mean ridge width selected by this means was 1.20 mm (standard deviation = 0.37 mm). The experimenter held the grating in readiness close to the fingertip. Visual and tactile stimuli were made as synchronous as possible so that as soon as the cotton bud reached the final step of its forward trajectory (thus when it reached the image, in the Touch condition, or the farthest position in the No-Touch condition) the experimenter delivered the tactile stimulation. Each movie lasted in total ~3000 ms, and tactile stimulation was delivered at ~1500 ms from the beginning of the movie.

Participants completed four blocks of 60 trials each. A pause of a few minutes, during which participants could stretch their arm, was interspersed between blocks.

Results

Participants' accuracy in discriminating the orientation of square-wave gratings applied to the tip of the right fingertip was compared across conditions. Judgments of grating orientation were significantly above chance both when viewing One's hand being touched (66% correct), [$t_{(19)} = 8.83$; $p < 0.0001$], One's hand not being touched (57% correct), [$t_{(19)} = 5.21$; $p < 0.0001$], the Other hand being touched (63% correct), [$t_{(19)} = 8.20$; $p < 0.0001$], the Other hand not being touched (61% correct), [$t_{(19)} = 8.49$; $p < 0.0001$], the Object being touched (58% correct), [$t_{(19)} = 5.99$; $p < 0.0001$] and the Object not being touched (58% correct), [$t_{(19)} = 4.89$; $p < 0.0001$].

A 3-by-2 ANOVA was conducted on the percentage of correct responses to grating orientation with the within-participants factors of Image (One's hand, Other hand, Object) and Tactile event (Touch vs No-Touch). Duncan post-hoc comparisons were performed, when necessary, to compare single effects.

The main effect of Image was significant [$F_{(2,38)} = 6.54$, $p < 0.01$]: accuracy was higher both when viewing One's hand (mean accuracy = 62%; s.e.m. = 1%) and the Other hand (mean accuracy = 62%; s.e.m. = 1%) than when viewing the Object (58%; s.e.m. = 1%; $p < 0.01$ in both cases). No difference was found between viewing One's hand and the Other hand ($p = 0.80$). Moreover, the main effect of Tactile event was significant [$F_{(1,19)} = 6.72$, $p < 0.05$], with enhanced tactile acuity when viewing the cotton bud touching the image (mean accuracy = 62%; s.e.m. = 1%) compared to when it did not touch the image (mean accuracy = 59%; s.e.m. = 1%). Finally, the critical interaction Image x Tactile event was significant [$F_{(2,38)} = 5.83$, $p < 0.01$]. Post-hoc comparisons showed that in the Touch condition, tactile acuity when viewing One's hand (mean accuracy = 66%; s.e.m. = 2%) was enhanced in comparison to that when viewing the Object (mean accuracy = 58%; s.e.m. = 1%; $p < 0.01$). Even vision of the Other hand (mean accuracy = 63%; s.e.m. = 1%) enhanced tactile acuity compared to vision of the Object ($p < 0.05$). Conversely, no difference was found between viewing One's hand and the Other hand ($p = 0.09$). In the No-Touch condition no difference in tactile acuity was observed between viewing One's hand (mean accuracy = 57%; s.e.m. = 1%) and the Object (mean accuracy = 58%; s.e.m. = 2%; $p = 0.83$) whereas nearly-significant enhancement when viewing the Other hand (mean accuracy = 61%; s.e.m. = 1%) was found compared to when viewing both the Object (mean accuracy = 58%; s.e.m. = 2%; $p = 0.07$) and One's hand (mean accuracy = 58%; s.e.m. = 1%; $p = 0.06$).

When tactile acuity between Touch and No-Touch condition was compared for the different images, a significant enhancement when viewing the cotton bud touching the image compared to when it did not touch the image, was found only for One's hand (mean accuracy = 66% and 57%; s.e.m. = 2% and 1% respectively; $p < 0.01$). Indeed no differences between Touch and No-Touch were observed both when viewing the Other hand (mean accuracy = 63% and 61%; s.e.m. = 1% and 1% respectively; $p = 0.54$) and the Object (mean accuracy = 58% and 58%; s.e.m. = 1% and 2% respectively; $p = 0.98$) (Figure 16).

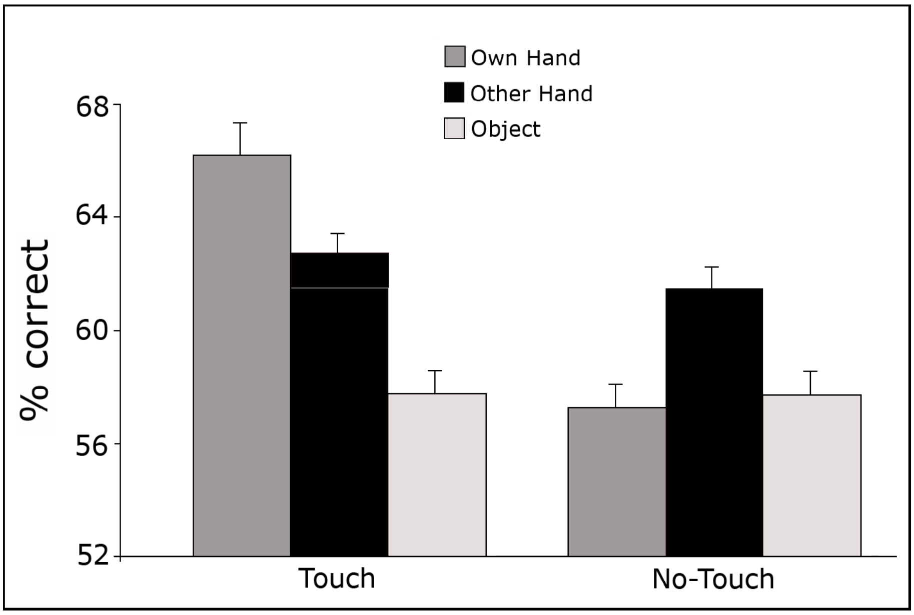


Figure 16. Behavioural results for the Grating Orientation Task. Participants made judgments of the orientation of square-wave gratings applied to the tip of the right middle finger.
In the Touch condition, accuracy in discriminating the “Across” or “Along” orientation of gratings was higher when participants viewed both one’s own and another hand than when they viewed an object.
In the No-Touch condition accuracy in discriminating the “Across” or “Along” orientation of gratings was slightly higher when participants viewed another hand than when they viewed both their own hand and an object.
Viewing one’s hand being touched enhanced accuracy compared to viewing one’s hand not being touched. No changes between viewing touch and no-touch were observed both when viewing the other hand and the object. Error bars show standard error across participants.

Discussion

Given results from the previous experiment, the present study was aimed at investigating whether by reducing the positional conflict between viewing the image of one’s hand and the proprioceptive representation of the actual hand, the VET effect reappeared. Moreover, the present experiment tested whether the costs in tactile processing when the seen hand was one’s own compared to when it belonged to someone else might be reduced as the perceptual conflict reduced.

The present study expected to replicate some of the findings in Experiment 3. In particular, the No-Touch condition was expected to show the same pattern of results obtained in Experiment 3 in the ‘Vision alone’ session, i.e. when a positional conflict was induced between vision of one’s hand and proprioceptive representation of the actual hand. Thus, VET was expected only when viewing someone else's hand and no in case of vision of one's hand. Moreover, the significant decrease in tactile processing when viewing one's hand compared to when viewing someone else's hand should have been replicated.

Results showed that viewing a cotton bud touching the image of one's hand when the to-be-judged grating was simultaneously presented to the actual hand enhanced tactile acuity compared to viewing an object being touched; conversely, in line with expected results based on the previous experiment (Experiment 3), in the No-Touch condition tactile acuity when viewing one's hand did not significantly differ from that when viewing an object. Thus, viewing the image of one's hand being touched let the VET effect reappear. Also viewing another hand being touched enhanced tactile acuity compared to viewing an object being touched, thus confirming the occurrence of VET effect also when viewing someone else's hand. In the No-Touch condition a slightly significant tactile improvement was observed when viewing the other hand compared to when viewing the object.

As expected by data described in the previous experiment (Experiment 3), in the No-Touch condition tactile acuity when viewing one's hand slightly decreased compared to when viewing the other hand. Conversely, when a tactile event was directed towards the images, tactile acuity when viewing one's hand improved so that no differences were observed between viewing one's and someone else's hand. Finally, while tactile acuity when viewing touch towards the image of one's hand significantly improved compared to when the cotton bud did not touch this image, no such a facilitatory effect of vision of touch, relative to vision of no touch, was shown when viewing the other hand and the object.

In line with the previous study (Experiment 3), the pattern of results shown in the No-Touch condition supported the idea that when two sensory inputs related to one's hand did not arise from the same spatial location, the positional conflict affected tactile processing on that site. The new finding of the present study was an enhancement of tactile acuity when the image of one's hand was seen being touched synchronously with a tactile stimulation delivered on the actual hand.

The present results suggested that the multisensory correlation between vision and touch seemed to adjust a conflicting visuo-proprioceptive relationship related to one's body. In line with the general rules multisensory integration mechanisms follow (Stein and Meredith, 1993), in the present study it was hypothesized that by introducing correlation between the visual input from the approaching cotton bud, and the tactile input from the GOT, these two events could be associated. The association between the events would in turn lead to an association between the viewed hand, and the participant's hand where touch was felt. As in the Rubber Hand Illusion, the participant might experience the viewed hand as one's own, despite the spatial disparity between the position of the viewed hand and the proprioceptively-sensed position of the participant's hand. The newly correlated sensory inputs were thus able to drive an updated multimodal representation of the stimulated body part. Finally, an enhancement in the sense of ownership of the seen hand (Ehrsson et al., 2004; Tsakiris and Haggard, 2005; Tsakiris, 2008) produced the VET effect.

Multisensory processing might be considered the main cue to selfhood (Jeannerod, 2003; Tsakiris, 2008). Several studies emphasized the importance of integration of current sensory inflows and also their interaction with efferent signals in bodily self-recognition (Jeannerod, 2003; Tsakiris and Haggard, 2005). I recognize my face in the mirror because the face I see moves when I move (Tsakiris, 2008). I am sure that this hand is my hand because when I see it being touched I concurrently feel a tactile sensation. Moreover, the recognition of one's body as belonging to us and as distinct from the other does not solely derived from a stable self-representation; rather this representation is susceptible to current multisensory inputs, and is always updated by continuous interactions between sensory information (Gallagher, 2005; Serino and Haggard, 2010). Further demonstration of the changeable feature of mental body representations was given by a recent study by de Vignemont and colleagues (de Vignemont, Ehrsson, and Haggard, 2005). They showed that qualities of a tactile object might be directly affected by the perceived size of the body part touching it. Thus perception of an external object is referenced to an implicit mental body representation and changes as the representation updates. This might be the reason why in the present study, in one experimental condition (the No-Touch condition), where discordant afferent signals did not allow updating the cognitive representation of the seen body part (Botvinick and Cohen, 1998; Ehrsson et al., 2004), correct processing of the external tactile stimulus did not occur and no VET effect was observed, whereas in the other condition (the Touch condition), where correlated afferent signals were able to drive a coherent mental representation of the stimulated body part, this was able to functionally modulate tactile perception.

In conclusion, taking together present with previous results, it might be suggested that the VET effect depends on a coherent multisensory representation of one's own body, where different sensory inputs must be in spatial register (Experiment 3) or at least share some temporal features that put them in correlation (present results).

If the VET effect when viewing one's stimulated body site seems functionally related to a multisensory bodily self-representation, the relevance of viewing another person's hand to one's own sensory experience, relies on a more social dimension.

In line with this idea, the present results did not show any difference in tactile acuity between viewing Touch and No-Touch towards another person's hand. In Experiment 3 also changing the spatial position of the visual image of the other hand – relative to one's own stimulated hand – did not affect the VET. Thus previous results suggested that vision of another person's hand might be sufficient to drive a mental bodily representation able to modulate one's own somatosensory system. It has been hypothesized that this mechanism might play a crucial role in understanding other's perceptual states, by registering them against the representations used to perceive our own body (Thomas et al., 2006). This form of "somatosensory empathy" clearly includes the idea that we do not need to treat others as equivalent to us, rather it is likely to suppose that we are able to distinguish other people's status in terms of multisensory correlation and peripersonal space from one's own.

The present results were in line with this hypothesis. Multisensory correlation between seen touch towards another person's hand and felt touch on one's hand seemed not to add essential information to evoke a visual modulation of tactile acuity.

Since viewing another person's hand was sufficient to functionally modulate tactile processing (see Experiment 3) and since viewing the other hand being touched did not significantly enhance tactile acuity compared to viewing the same hand not being touched (present experiment), the VET effect when viewing someone else's hand should have been expected both in the Touch and in the No-Touch condition. In line with this prediction, the present results demonstrated a clear VET effect when viewing the other hand being touched, and a nearly significant enhancement of tactile acuity when viewing the other hand compared to when viewing the object, in the No-Touch condition. Given this pattern of results, it might be suggested that vision of someone else's hand is sufficient to functionally modulate one's somatosensory system, and that vision of touch on that site does not add useful information to further improve behavioural performance, relative to viewing no touch; thus the occurrence of the VET effect was observed both when the hand was seen being touched and when it was seen not being touched.

In line with this conclusion it is likely to think that simply viewing another body boosts a form of “somatosensory empathy” whereby we prepare our own sensory system to simulate both an expected and an observed sensory state experienced by the others.

Multisensory literature widely demonstrated that vision of touch is able to activate brain regions normally recruited during tactile perception, even if the observer’s body is not directly tactilely stimulated (Keysers et al., 2004; Blakemore et al., 2005; Ebisch et al., 2008). Moreover, more recent studies demonstrated that vision of touch is also able to enhance tactile perception on the observer’s body (Serino et al., 2008; Serino, Giovagnoli, and Ladavas, 2009). This effect, termed Visual Remapping of Touch (VRT) has been observed both when viewing one’s body and another body, being maximum for the former. Observation of touch may be important for the recognition and understanding of tactile experience, to form an internal representation of an event and to estimate consequences for action preparation (Schaefer, Xu, Flor, and Cohen, 2009).

The fact that previous studies found a modulation of tactile perception when viewing touch compared to when viewing no touch towards someone else’s body, whereas in the present experiment tactile acuity in Touch and No-Touch condition did not differ, will be discussed in the following chapter were a more in deep description of the VRT mechanism will be provided.

CHAPTER 3

Neural underpinnings of the Visual Remapping of Touch (VRT)

3.1 Evidence for a shared circuit between felt and seen touch

Current neuroscientific models of embodied simulation propose that the same neural structures involved in our own body-related experiences also contribute to the conceptualization of what we observe around us (Gallese and Lakoff, 2005; Gallese, 2006; 2007). Extensive evidence for a shared neural circuitry between first- and third-person experiences has been demonstrated in the domain of action (Gallese, Fadiga, Fogassi, and Rizzolatti, 1996; Buccino, Vogt, Ritzl, Fink, Zilles, Freund, and Rizzolatti, 2004), emotion (Carr et al., 2003), pain (Avenanti, Bueti, Galati, and Aglioti, 2005; Avenanti, Minio-Paluello, Bufalari, and Aglioti, 2006) and touch (Blakemore et al., 2005; Schaefer et al., 2009).

The observation of touch is an ordinary and crucial experience in everyday life, both in social and natural events. Several studies demonstrated that our brain is not passively witness to external events occurring to other people or objects (Keysers et al., 2004; Blakemore et al., 2005; Schaefer et al., 2006; Ebisch et al., 2008). Viewing another person, or even an object, being touched activates brain regions normally recruited during tactile perception, even if the observer's body is not directly tactilely stimulated. Such visually-evoked somatosensory activity involves a network of fronto-parietal areas distributed along the postcentral gyrus, the supramarginal gyrus and the precentral gyrus (Keysers et al., 2004; Blakemore et al., 2005; Ebisch et al., 2008). This overlap of brain activity for perceiving and viewing touch has been taken as an evidence for the existence of a neural mechanism remapping tactile sensation seen on the body of others onto one's own somatosensory system.

Keysers and colleagues (2004) showed that vision of touch activates SII, but not SI, with comparable neural responses when viewing a human body part (i.e. a leg) as well as an object. These results suggested that SII does not distinguish between the identities of the touched stimuli and that SI does not respond to vision of touch without concurrent tactile stimulation of one's body.

The lack of activity in SI when viewing touch reported by Keysers and colleagues (2004) might simply be due to the fact that in this study participants, lying in the scanner, were asked to look at movies depicting a human leg being touched, whereas the majority of the studies investigating the neural activity underlying vision of touch used a human face or hand (Bolognini, Rossetti, Maravita, and Miniussi, 2011; Blakemore et al., 2005; Ebisch et al., 2008; Schaefer et al., 2009). Relevant to note that the cortical representation of the leg in SI is relatively smaller compared to the face or hand representations, and this might explain why when viewing a human leg being touched no activity was observed in SI. However, the lack of activity in SI was not confirmed by several other recent findings. Blakemore and colleagues (2005) demonstrated that some differentiation between viewing a body part being touched versus viewing an object being touched does emerge at the level of SI. Furthermore, Ebisch and colleagues demonstrated that also viewing a human body part touching versus viewing an object touching differentiates activity in SI and this activity correlates with the degree of perceived intentionality of the observed touch (Ebisch et al., 2008). In the light of social cognition theories (Gallese, Keysers, and Rizzolatti, 2004; Iacoboni and Dapretto, 2006) it can be suggested that the observer tends to more easily remap onto one's own somatosensory system an intentional touch performed by a human agent than an accidentally touching object. This might be underlie by a human empathic tendency to understand others' experiences through simulating the observed states with one's own somatosensory system.

On the other hand, the undifferentiated response of SII for viewing touch towards an object or a human body part (Keysers et al., 2004) might rely on a generalized activation of this region to the sight of *any* touch. In line with this finding, in a recent fMRI study, participants viewed movies depicting a touch that occurred between animate or inanimate objects and that might be intentional or accidental (Ebisch et al., 2008). Results demonstrated an overall SII activation when viewing touch, irrespective of the intentionality of the observed touch, the type of touching stimuli (animate vs inanimate) and the side where the stimulus was touched (right vs left side). Thus it seems plausible that the activation in SII for viewing touch reflects an automatic undifferentiated tendency to activate brain regions usually recruited during our own tactile experience.

Recent data have shown that SI codes for visuo-tactile associations. SI neurons in monkey were observed to fire both in response to a tactile stimulus as well as in response to a visual stimulus previously associated with touch (Zhou and Fuster, 1996; 2000). Moreover, SI is strictly interconnected with multimodal areas, such as PPC, which contain bimodal visuo-tactile neurons (Duhamel et al., 1998). Further, SII functions have been considered related to higher-level somatosensory processing, such as multimodal integration between information directly received from SI and information form other sensory modalities (Carlsson, Petrovic, Skare, Petersson, and Ingvar, 2000; Bremmer et al., 2001; Avikainen, Forss, and Hari, 2002). Finally, somatosensory areas are thought as part of a complex neural network coding the visual presented touch and encompassing several higher-order areas. Thus, beyond the well-established involvement of both SI and SII when viewing touches, it is still unknown whether these areas are essential for the visual processing of touch. Bolognini et al. (2011), investigated this issue by applying high frequency repetitive TMS (rTMS) over SI and SII during a visual discrimination task involving tactile stimuli. Participants were asked to look at movies depicting a hand that could be touched or just approached by a human finger, and were asked to press a key button to report whether the finger had touched the hand and refrain from responding whether it just approached the hand. Results demonstrated that SI-rTMS selectively interfered with the task. Moreover this interference was side-specific: rTMS applied over either the right or left SI affected only the perception of the contralateral touched stimuli. Conversely, SII-rTMS affected visual processing regardless of the tactile component, thus inducing a non-specific impairment in detecting visual stimuli depicting both kinds of hand movement (a finger touching the hand and a finger just approaching the hand). In conclusion SI, but not SII, was suggested to play an essential role in the visual processing of touch.

In line with this recent finding, previous studies highlighted an important characteristic of the neural mechanism underlying observation of touch towards a human body: somatosensory activations when viewing a body part being touched reflect the somatotopical organisation of SI. This organisation follows the sensory homunculus magnification in SI (Penfield and Boldrey, 1937). As a result, viewing a face being touched, for example, activates the corresponding ‘face’ area in the observer’s primary somatosensory cortex (Blakemore et al, 2005). Moreover, the lateralization in SI activity when viewing someone else being touched on one side of their body reflects the SI lateralized activation when being touched on one side of one’s body (Blakemore et al, 2005; Serino et al., 2009; Schaefer et al., 2009).

The well-established distinction in SI activity between viewing touch towards a human body and towards an object (Blakemore at al., 2005; Ebisch et al., 2008) suggested the likely human tendency to resonate with someone else's states, but not with the tactile experience of an object. Schaefer and colleagues addressed a new issue about the neural responses of somatosensory cortices when the observed touch relates to the observer's own body or to somebody else (Schaefer et al., 2009). Participants viewed movies depicting a hand that could be touched or not by a paintbrush. The hand was presented either in an egocentric perspective, so that it matched the orientation of the participants' own hand, or in an allocentric perspective. In the former case participants could attribute the observed touch to oneself. In line with previous results, data showed that the observation of touch relative to no touch activated both SI and SII (Blakemore et al., 2005; Ebisch et al., 2008). Interestingly, when contrasting the perspectives of viewing touch against each other, somatosensory activations appear to be roughly independent of how easily the observed touch events could be integrated into one's own body schema; however, slightly different patterns of responses in SI were associated with the two different viewpoints. Whereas viewing a hand from an egocentric point of view activated the anterior part of SI (BA 3a, 3b), the allocentric perspective involved the posterior part of SI (BA 2) (Schaefer et al., 2009).

From these results it might be simply hypothesised that slight differences in referring a seen touch to one's body or to someone else might rely on different mechanisms: whereas visual information pertaining to touch towards one's body might provide an adaptive advantage by anticipating the effects of tactile stimulation on our body, vision of touch towards someone else's body might simply further an empathic tendency to understand others' sensory experiences (Gallese, 2006; 2007; Grafton, 2009).

3.2 Evidence for a modulation of tactile perception by observation of touch

The previously described visually-dependent somatosensory activity does not normally result in an actual tactile percept, as most subjects do not report to feel touch when observing touch on the body of others. Visuo-tactile synaesthetes represent an interesting exception, in that they report feeling touch on their body when they view the body of others being touched (Banissy and Ward, 2007). Synaesthesia comes from the Greek roots ‘syn’ that means together, and ‘aisthesis’ that means sensation. This is a condition in which stimulation of one sensory pathway leads to automatic, involuntary experiences in a second sensory pathway (Cytowic, 2002; 2003; Cytowic and Eagelman, 2009). The most common form of synaesthesia is the color-graphemic, in which letters or numbers are perceived as inherently coloured (Rich and Mattingley, 2002; Hubbard and Ramachandran, 2005). A new form of synaesthesia was recently described between vision and touch. A neuroimaging study run on a single synaesthetic subject showed that the brain activity evoked by the observation of touch in the aforementioned fronto-parietal areas was stronger in this subject than in non-synaesthetic controls. Moreover these regions were activated more by the observation of a human body part being touched than by the observation of a similar shaped object being touched (Blakemore et al., 2005). Interestingly, unlike individuals in the control group, the synaesthetic subject experienced the observed touch towards the human body as an actual tactile stimulation on one’s own body (Blakemore et al., 2005). These findings suggested that a modulation of tactile processing due to the vision of touch occurs in all subjects, but only in synaesthetes this effect is sufficient to overcome the threshold of conscious experience.

In line with this view, it has recently been shown that, if perceptual thresholds are experimentally manipulated, an effect of viewing touch on tactile perception can be behaviourally unmasked also in non-synesthetes (Serino et al., 2008). In their recent work, Serino and colleagues demonstrated that the perception of near-threshold tactile stimuli on the face of non-synaesthetic subjects was modulated if they observed a face being touched by two fingers in comparison to when they observed the same face being just approached by the fingers. This effect, called Visual Remapping of Touch (VRT; Ladavas and Serino, 2010), was specific for viewing a bodily stimulus, because the effect of vision on touch disappeared if the subjects observed the picture of an object instead of a face. Moreover, the amount of enhancement depends on the similarity between the body of the observer and that of the observed: the effect is self-other specific, being stronger when the other is perceived as similar to the self, and the effect is maximum when observing touch on one's own face (Serino et al., 2008; Serino et al., 2009). In their first study Serino and colleagues (2008) demonstrated that the effect of vision on touch was stronger when participants observed their own face being touched instead of the face of another person, suggesting that the VRT effect increases as much as the observer's and the observed body match. To further investigate this assumption, Serino and colleagues (2009) performed a second study where the identity of the shown face was manipulated. Participants viewed, in different trials, a face belonging either to their own or to a different ethnic group that could be touched or just approached by human fingers. Results demonstrated that tactile perception on the face was enhanced when viewing touch towards a face belonging to one's own ethnic group compared to when it belonged to the different ethnic group. In conclusion the remapping mechanism increases as a function of the congruity between the observer's and the observed body (Serino et al., 2009). It might be suggested that, in order to re-map a sensation from one sensory modality to another - namely from vision to touch - the two modalities should share a common reference system, in this case the same body or at least, a similar body.

Going back to the experiment discussed in the present dissertation it is worth reminding that, in line with previous data found in literature, Experiment 4 showed a significant enhancement of tactile acuity when viewing one's hand being touched, compared to when viewing one's hand not being touched. Conversely, no difference was observed when the seen hand belonged to someone else. Thus, in contrast with literature, from the present results it might be concluded that the remapping of the seen touch onto the felt touch is boosted only when viewing one' body.

A possible explanation of these controversial findings might rely on the body part that was seen being touched in the different studies. In fact, whereas in the present Experiment 4 participants were looking at a *hand* being touched, previous studies on the VRT effect presented a *face.* A possible consideration might be the following: touch observed towards either a hand or a face might signal different sensory experiences of different relevance.

The hand is a special body part essential to manipulate objects and often in contact with the external environment. For this reason it is likely to frequently observe touches on other hands: we see hands touching each other, holding a cup, picking up shoes from the floor…and all these examples are related to very different tactile experiences: active and passive touch, manipulation, haptic exploration, grasping…Thus, simply viewing a hand seems to prepare one's sensory system for any possible impending tactile experience. Moreover the disparate tactile states a person daily experiences through his (or her) hands should not require an observer to process in details the seen touch. Just being prepared that any kind of touch is going to occur on that site, might be enough.

Conversely, the face is less frequently observed being touched in everyday life and, moreover, when this occurs, both detection and recognition of the touching stimulus - potential signal of something dangerous happening on the face – are crucial.

Thus, remapping onto one's sensory system every tactile state of a seen hand might require an ability to continuously regulate the preparatory state of the tactile somatosensory processing, maintaining readiness for frequent tactile events. Conversely, viewing someone experiencing a tactile stimulation towards the face might highlight an adverse situation the observer should understand - by remapping the seen touch onto one's own sensory system - to adjust an adequate behavioural reaction.

From a psychological point of view, it may be important to process observed touch to one's own body, regardless of which body part is touched. Viewing touch on one's own body might signal an adverse situation that should be detected as quickly as possible (Schaefer et al., 2009). Viewing touch towards someone else's body might simply encourage the observer to recognize and understand this sensory experience to adjust an adequate social reaction. This tendency seems to be boosted only when the observed bodily experience is worth to be understood, requiring an adequate reaction from the observer.

Given the important role vision of touch towards one's body seems to play in modulating one's sensory system, the following experiment was aimed at testing which brain areas underlie the self-specific effect in the visual remapping of touch mechanism.

Experiment 5. Neural underpinnings of the self-specific Visual Remapping of Touch effect

As previously mentioned, visual information about the Self may modulate the sense of touch. In fact, viewing one's face being touched enhances tactile perception on the face, compared to viewing one's face not being touched. Moreover, the same modulatory effect of vision of touch on tactile perception has been observed also when viewing another face. However, the effect of vision on tactile perception is stronger when the seen face is one's own compared to when it is someone else's (Serino et al., 2008).

These experimental findings open an intriguing issue. On the one hand, multisensory integration has typically been studied between low levels of sensory processing. On the other hand, the study of Self-representation usually concerns high levels of information processing. In the case of Serino et al.'s results (2008), high-order visual information concerning the representation of oneself, as different from others, modulates the perception of tactile stimuli. How does this effect occur? Which are the neural underpinnings of such complex form of multisensory interaction?

When viewing a face, high order visual areas in the extrastriate cortex, connected to portions of the middle and inferior frontal gyrus (Platek et al., 2008), signal whether that face belongs to oneself or to another individual. In particular, evidence recently reviewed indicated that the brain possesses an information-processing system for self-related facial stimuli, encompassing the left fusiform gyrus, bilateral middle and inferior frontal gyri and right precuneus.

Moreover, in the case of viewing one's own face, this complex visual processing might activate different representations of the Self. Cognitive neuroscience literature (Stamenov, 2005) individuates at least two levels of representations of the Self: a semantic, conceptual representation, the Narrative Self (Buckner and Carroll, 2006; D'Argembeau, Ruby, Collette, Degueldre, Balteau, Luxen, Maquet, and Salmon, 2007), and a sensory-motor representation of one's own body, the Embodied Self (Ehrsson, Holmes, and Passingham, 2005; Tsakiris et al., 2007; Blanke and Metzinger, 2009). A pool of brain structures in the ventro-medial prefrontal cortex are thought to support the representation of the Narrative Self, since those areas are engaged during a number of tasks requiring the processing of self-knowledge, self-referencing (Northoff and Bermpohl, 2004; Heatherton, Wyland, Macrae, Demos, Denny, and Kelley, 2006; D'Argembeau et al., 2007), mentalizing, or judgments about oneself relative to other people in general (Mitchell, Macrae, and Banaji, 2006; Jenkins, Macrae, and Mitchell, 2008). A recent fMRI study developed by D'Argembeau and colleagues demonstrated, in line with previous works, that reflecting on one's own psychological characteristics and on those of a close friend, recruited different cortical midline structures (CMS; Amodio and Frith, 2006; Lieberman, 2007). In particular the ventral and dorsal medial prefrontal cortex and the posterior cingulate cortex were more activated when reflecting on oneself than when reflecting on the other (D'Argembeau, Feyers, Majerus, Collette, Van der Linden, Maquet, and Salmon, 2008). More interestingly, the same dissociated patter of CMS recruitment were observed when participants reflected on oneself in the present time period and in a past time period. These findings suggested that CMS might contribute to differentiate between present and past conceptual self-representations.

On the other hand, a network of fronto-parietal areas is supposed to underlie the representation of the Embodied Self, since those areas are involved in integrating multisensory information pertaining to one's own body, and are engaged when people experience a sense of ownership of a body-like stimulus, such as in the so-called Rubber Hand Illusion (Botvinick and Cohen, 1998; Ehrsson et al., 2005; Tsakiris et al., 2007). In fact over the past few decades, an extensive body of evidence showed that neuronal populations in the parietal and ventral premotor cortices encode both the seen and the felt position of the arm (Graziano et al., 2000). In a recent monkey study neurons in parietal area 5 were found to encode the position of the monkey's arm while it was covered from view, and further, the same neurons responded to the position of a visible, realistic fake arm, placed just above the actual one (Graziano et al., 2000). Moreover the ventral premotor cortex contributes to the feeling of ownership of body parts (Ehrsson et al., 2005). This assumption is in line with the well-established role of this area in multisensory integration mechanisms. The ventral premotor cortex responds to both tactile stimuli delivered on the body surface and visual stimuli close to the body (Rizzolatti et al., 1981; Graziano et al., 1994). Finally, studies on the RHI revealed that touches perceived on an owned rubber hand were associated with activations of premotor and intraparietal areas (Ehrsson et al., 2004; Ehrsson, 2007). In the present study the issue related to which kind of Self-representation could modulate tactile perception was addressed; moreover it was investigated how such high-level representation could directly influence low-level perceptual processing.

To answer these questions, in the present work, participants took part in a tactile confrontation task, set as in Serino et al.'s studies (2008; 2009). The paradigm from Serino et al. was adapted for fMRI scanning. The tactile confrontation task is a classic experimental paradigm used in brain-damaged patients to investigate extinction: participants are touched on either one side of their body or the other, or on both sides and are required to report the side of stimulation. Patients with extinction usually fail to report the contralesional stimulus in conditions of double stimulation. This is due to attentional resource competition between the two hemispaces (Bender, 1952; Ladavas, 2002). This paradigm was applied to healthy participants in order to induce a level of uncertainty in their tactile percept: this allows the effect of viewing touch on the feeling of touch (i.e. VRT effect) to be unmasked (Serino et al., 2009; Ladavas and Serino, 2010).

In the present study participants received an electrical stimulation either on their right, left or both cheeks and were requested to discriminate between unilateral and bilateral stimulation. To manipulate perceptual thresholds, the stimulus on the left cheek was stronger than that on the right cheek. In this way, in condition of bilateral stimulation, the stronger stimulus would frequently extinguish the weaker one (Serino et al., 2008). During the task, participants were watching a movie showing, in different trials, either the image of their own face, of another person's face or of a non-body stimulus, namely a ball. The image could be touched or just approached bilaterally by two human fingers (one on its left and one on its right side) in different trials. Participants were instructed to respond only on the basis of tactile stimulation and not of visual stimulation. The neural activity evoked in different brain areas was studied as a function of the different experimental conditions and in relationship to subjects' perceptual reports.

The first question was whether the modulation of visual remapping of touch due to viewing one's own face relies on the activation of a conceptual or of a physical representation of Self. Given the presence of different neural substrates underlying these two levels of representation of the Self (Ehrsson et al., 2004; D'Argembeau et al., 2007; Jenkins et al., 2008; Tsakiris et al., 2010), if the Narrative Self is responsible for the effect, a specific modulation of brain activity in ventro-medial prefrontal areas (Amodio and Frith, 2006) should have been found when subjects viewed one's own face being touched in comparison to when viewing another person's face or an object. Conversely, if the Embodied Self is the origin of the effect, such modulation of brain activity should have been found in fronto-parietal multisensory areas (Tsakiris, 2007), and not in ventro-medial frontal areas.

Second, once either representation of the Self is activated, the issue related to how such representation could affect the perception of touch was addressed. A possible explanation was that visual information about the Self modulates tactile processing, because the activity in high-order Self-related areas projects to somatosensory cortices, where the tactile stimulus is processed. If this is the case, the same modulation of neural activity for the different experimental conditions found in the brain network underlying the Self-representation should have been found also in somatosensory cortices.

Materials and Methods

Participants

Fifteen healthy young adults were included in the present study (mean age 23.6; range: 19-30; 10 female). All participants were right-handed, had normal or corrected-to-normal vision, normal touch and were naive as to the purposes of the experiment. Participants gave their written informed consent to participate in the study and were paid (25 euros) for their participation. The study was approved by the Ethics Committee of the "G. d'Annunzio" University, Chieti, and was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki.

fMRI Data Acquisition

All images were collected with a 1.5 T Philips Achieva scanner operating at the Institute of Advanced Biomedical Technologies (I.T.A.B. Fondazione G. d'Annunzio, Chieti, Italy). T1-weighted anatomical images were collected using a multiplanar rapid acquisition gradient-echo sequence (230 sagittal slices, voxel size: 0.5 x 0.5 x 0.8 mm, TR = 8.08 ms, TE = 3.7 ms). Functional images were collected with a gradient echo EPI sequence. Each subject underwent four acquisition runs, each including 198 consecutive volumes comprising 25 consecutive 4-mm-thick slices oriented parallel to the anterior-posterior commissure and covering the whole brain (TR = 2.3 s, TE = 60 ms, 64 x 64 image matrix, 4 x 4 mm in-plane resolution).

Stimuli and Procedure

Preprocessing

A digital photograph of the participant's face was taken in a session prior to the experiment. The participant's face in the photograph was cut out and paste on a black background with Adobe Photoshop CS4. Then, two movies showing the participant's face that could be touched or just approached bilaterally, by two human fingers, were built using Adobe Flash Player.

Procedure

The experimental stimuli consisted of both tactile and visual stimuli.

Tactile stimuli were delivered via a pair of miniaturized screen electrodes placed on the participants' cheeks (stimulus duration: 5 ms). In different trials, a tactile stimulus was administered to the right, left or both cheeks. The tactile stimulus on the left cheek was calibrated to be more intense than that on the right cheek. Prior to the experiment, while the subject was lying in the fMRI scanner, the intensity of the electrical stimuli was titrated for each subject in the absence of visual information. Using a staircase procedure (Cornsweet, 1962), stimulus intensity was titrated at a threshold of 100% of detection for the stronger stimulus (mean threshold: 20 mA ± 3) and of 60% for the weaker stimulus (mean threshold: 13 mA ± 4). Thresholds were recalibrated before each experimental block.

Visual stimuli consisted of three sets of grey-scale movies, one depicting the participant's own face, the second depicting the face of another person (of the same age and sex as the participant), and the third depicting a ball. A ball has a perceptual configuration similar to a face, but is anatomically categorized as a non-bodily stimulus.

The movie also showed two fingers initially positioned on the lower part of the screen, one on the right and one on the left. During the movie, both fingers moved towards the centrally presented image and then backwards to their starting position. In different trials the motion followed one of two trajectories: in the Touch condition the fingers actually touched the central image; in the No-Touch condition the fingers stopped about 5 cm away from the image.

Visual and tactile stimuli were synchronized so that when the fingers reached the image, a tactile input (a bilateral or unilateral tactile stimulation) was delivered to the subject's face. Each movie lasted in total 1000 msec, and tactile stimulation was delivered at ~500 msec from the beginning of the movie. Each movie was preceded by a fixation stimulus lasting a variable, non-predicable interval of either 2000, 2500 or 3000 msec (Figure 17).

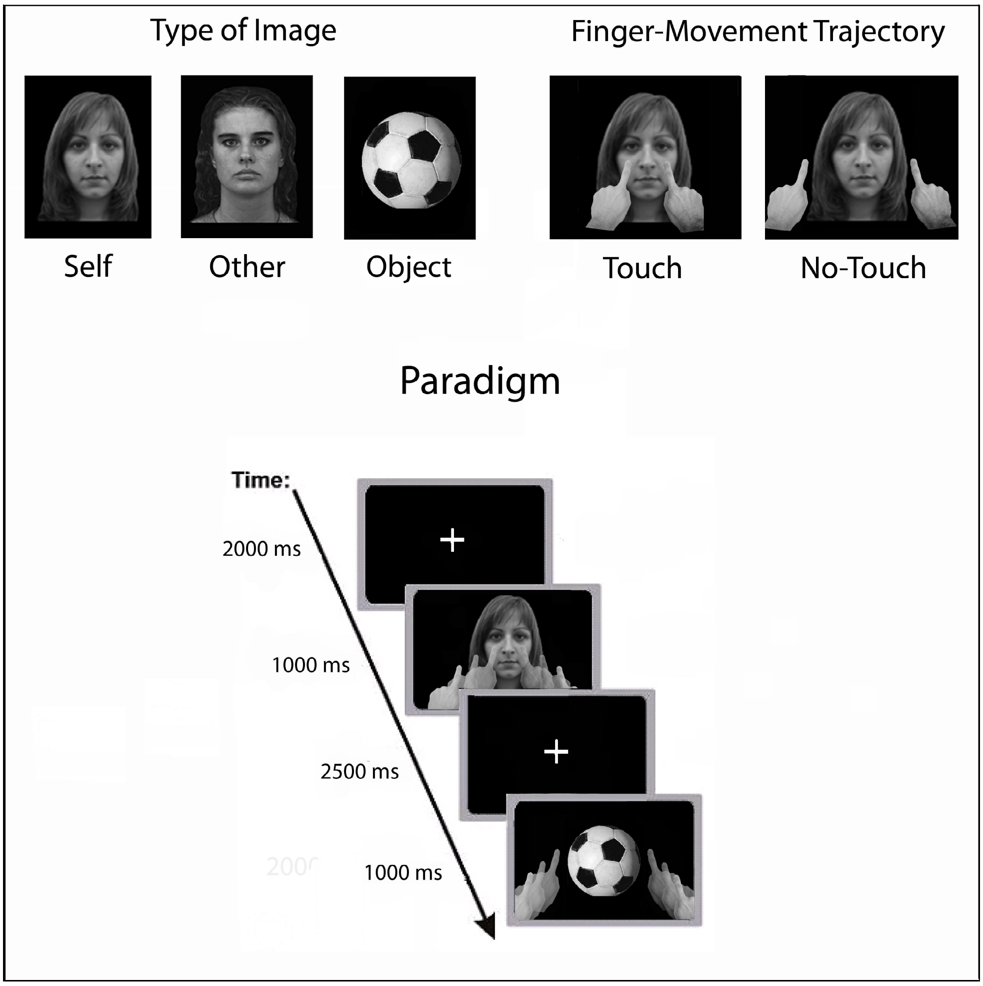


Figure 17. Upper panel: Visual stimuli used in the tactile confrontation task.
Lower panel: A typical experimental trial. In randomized blocks subjects receive either a unilateral or a bilateral tactile stimulation on their cheeks. Concurrently they are required to pay attention to the screen in front of them showing a movie where an image is touched, or only approached, by two human fingers. The shown image is either the subject's own face, another person's face or a ball, in different conditions.

Participants laid supine in the scanner with their arms outstretched beside their abdomen.

Visual stimuli were projected onto a back-projection screen situated behind the participant's head and were visible via a mirror (10x15 cm).

Sound-attenuating headphones were used to muffle scanner noise. The presentation of the stimuli and the recording of the participants' responses were controlled by a PC running Cogent 2000 (developed by the Cogent 2000 team at the FIL and the ICN, University College London, UK) and Cogent Graphics (developed by John Romaya at the LON at the Wellcome Department of Imaging Neuroscience, University College London, UK) under Matlab (The Mathworks Company, Natick, MA, USA) on the Microsoft Windows XP operating system.

The event-related paradigm consisted of four acquisition runs of the tactile confrontation task. Each run presented 6 unique stimuli representing all combinations of type of image (Own face, Other face and Object) and fingers movement trajectory (Touch, No-touch), synchronized with a bilateral tactile stimulation. Thus the experimental design was a three (Image: Own face, Other face and Object) by two (Trajectory: Touch, No-Touch) within-subjects factorial design. The 6 unique stimuli were repeated eighteen times, for a total of 108 trials per run, presented in pseudo-random order. Tactile stimulation was presented simultaneously with visual stimulation. In each run 22 unilateral tactile stimuli were also included. In total the experiment consisted of 520 trials.

Prior to scanning, participants were told that electrical stimuli would be delivered either to one or both cheeks and that concurrently they would be presented with short movies with a different content. They were instructed to press a button with the right hand when they would perceive a unilateral tactile stimulus and to refrain from responding when they would perceive a bilateral tactile stimulus. Participants were instructed to look at the visual movies and to answer on the basis only of tactile stimulation.

The fMRI design differed from the behavioural study by Serino et al. (2008) for two important aspects. First, in the present study, participants actively responded only to unilateral tactile stimuli, which were rare in the total number of trials, whereas in Serino et al.'s study (2008) participants were asked to differently respond to unilateral left, right and bilateral stimuli. Second, in the present study, visual information always signalled a bilateral stimulation, whereas in Serino et al. (2008) the side of tactile and visual stimulations was completely crossed. These modifications were necessary to study the neural basis of the VRT effect. The current paradigm, indeed, was designed in order to maximize the number of trials critical to show the modulation of the effect (i.e. bilateral tactile stimulation), to minimize the number of possible combinations of visuo-tactile stimuli (using only bilateral visual stimulation) and minimize possible brain activations not directly involved in the effect, such as those derived from motor responses. For these reasons participants received much less unilateral than bilateral tactile stimuli, viewed only bilateral stimuli, and were requested to actively respond only to trials with unilateral tactile stimulation (which were not included in fMRI analyses).

The experimental design was a rapid event-related fMRI design alternating a state of stimulation - i.e., 1000 msec movies plus electrical stimulation - with a baseline state consisting in the fixation interval lasting 2000, 2500 or 3000 msec; each of the three different baseline durations had the same probability of occurrence. Each run lasted about 7 minutes. A pause of 5 minutes, during which tactile stimuli were recalibrated, was interspersed between runs.

Data Analysis

fMRI data were analyzed using SPM5 (Wellcome Trust Centre for Neuroimaging, University College, London). Functional images were first corrected for head movement using a least-squares approach and six-parameters rigid body spatial transformation (Friston, Ashburner, Poline, Frith, Heather, and Frackowiak, 1995) and for difference in acquisition timing between slices. The high-resolution anatomical image and the functional images were coregistered and stereotactically normalized to the Montreal Neurological Institute (MNI) brain template used in SPM5 (Mazziotta, Toga, Evans, Fox, and Lancaster, 1995). Functional images were re-sampled with a voxel size of 4 x 4 x 4 mm and spatially smoothed with a three-dimensional Gaussian filter of 8 mm full-width-at-half-maximum (Friston et al., 1995).

The time series of functional MR images obtained from each participant was then analyzed on a voxel-by-voxel basis using the principles of the general linear model extended to allow the analysis of fMRI data as a time series (Worsley and Friston, 1995). The onset of each trial constituted a neural event, that was modelled through a canonical hemodynamic response function, chosen to represent the relationship between neuronal activation and BOLD signal changes (Friston, Fletcher, Josephs, Holmes, Rugg, and Turner, 1998). Unilateral catch trials (20%) and false alarm trials (i.e., when participants had pressed the button in the presence of a bilateral tactile stimulus; 18%) were modelled as separate conditions and then excluded from further analyses, which concentrated on correct responses (i.e., no-response to bilateral stimulation).

Group analysis was performed in two steps. First we used a conventional voxel-by-voxel group random-effects analysis, which allowed to test hypotheses relative to the whole population and to identify brain regions responding during the experimental trials relative to the baseline condition of the study, i.e. the inter-trial fixation interval. This was done through an omnibus F-test comparing each of the six conditions resulting from the combination of the Image and Trajectory factors with the inter-trial fixation. The resulting statistical parametric maps of the F statistics were thresholded at $p < 0.01$, corrected for multiple comparisons over the total amount of acquired brain volume using false discovery rate (Genovese, Lazar, and Nichols, 2002). The resulting regions are listed in Table 1 and rendered in Figure 18 and include all voxels showing a reliable BOLD response evoked by the onset of the experimental trials, irrespective of the somatosensory stimulus, visual image, and fingers movement trajectory delivered in any particular trial, and of the sign (positive or negative) of the evoked BOLD response.

The second step consisted in searching for modulation of BOLD responses in these voxels as a function of the type of image (Image factor: Self, Other, and Object) and finger-movement trajectory (Trajectory factor: Touch, No-Touch). To increase sensitivity of the analysis, this step was performed on regionally averaged data as follows: voxels resulting from the first step were grouped into regions, i.e. clusters of adjacent significant voxels. For each subject and region, we computed a regional estimate of the amplitude of the hemodynamic response in each experimental condition, by entering a spatial average (across all voxels in the region) of the pre-processed time series into the individual general linear models. Such regional hemodynamic response estimates, which are shown in the plots in Figure 18, were then analyzed through a 3-by-2, Image by Trajectory, repeated-measures ANOVA. For bilaterally activated regions, the Hemisphere factor was added to the ANOVA.

Results

Behavioural results

The behavioural effect of visual stimulation on tactile perception was studied by comparing participants' accuracy in responding to bilateral tactile stimuli when the fingers touched or did not touch the different images. In the light of the results from Serino et al. (2008), it was expected that the perception of bilateral tactile stimuli was higher when participants saw their own face being touched rather than approached. For each Image condition (Own face, Other face and Object), participants' accuracy was compared between the two fingers movement Trajectories (Touch and No-Touch), by means of t-tests (1 tail). In order to prevent the risk of inflating 1-type error, a Bonferroni correction was applied, thus only p values < 0.025 were considered significant. When viewing one's Own face, tactile perception was enhanced when fingers touched the face (accuracy = 84%; s.e.m = 4.1%) than when just approached the face (81%; s.e.m = 3.9%), [$t_{(14)} = 2.28$; $p < 0.019$]. A similar nearly-significant pattern [$t_{(14)} = 1.57$; $p = 0.06$] was found for viewing the Other face: the accuracy was 82% (s.e.m = 4.1%) in Touch condition and 79% (s.e.m = 4.1%) in the No-Touch condition. No modulation of tactile perception was found for the Object condition: the same accuracy was found for Touch (80%; s.e.m = 4.8%) and No-Touch (80%; s.e.m = 4.2%), [$t_{(14)} = 0.13$; $p = 0.44$] conditions.

fMRI results

From the group-level whole-brain analysis of functional MR images, we identified six different cortical regions where BOLD signal was significantly different during any of the six conditions resulting from the combination of type of image (Own face, Other face and Object) and finger-movement trajectory (Touch, No-touch), relative to the inter-trial fixation intervals. The six regions were located in the bilateral occipital cortex, ventral intraparietal area, somatosensory cortex, ventral premotor cortex, the right insula and the dorso-medial prefrontal cortex (see Table 1 and Figure 18). To study the modulation of neural activity within these areas as a function of the experimental conditions, for each area an ANOVA on the estimated percent BOLD signal change was run with the factors Image (Own face, Other face, Object) and Trajectory (Touch, No-Touch). A factor Hemisphere (Right and Left) was added when both left and right activation of homologue areas was found. Post-hoc comparisons were conducted, when necessary, by means of the Duncan post-hoc test.

Table 1. Montreal Neurological Institute (MNI) coordinates of peaks of relative activation in the cortical regions where BOLD signal was significantly different during observation of any of the six conditions compared with the inter-trial baseline. Table shows local maxima more than 4 mm apart.

Regions of activation				Main local maxima			
Anatomical location	Extent (voxels)	Side	Anatomical subdivisions	MNI coordinates			F value
				X	Y	Z	
Occipital cortex	849	L	Middle occipital gyrus	-12	-104	4	25.28
				-48	-76	4	20.62
				-20	-88	-20	14.78
			Inferior occipital gyrus	-24	-84	-4	6.83
		R	Cuneus	12	-96	12	17.35
			Calcarine cortex	16	-96	0	15.48
				4	-88	4	15.20
			Inferior occipital gyrus	32	-84	-4	7.36
Ventral intraparietal area (VIP)	21	L	Inferior parietal lobule	-40	-36	36	7.21
	48	R	Inferior parietal lobule	32	-52	44	6.62
				48	-36	48	4.85
Somatosensory cortices (SI/SII)	54	L	Postcentral gyrus (inferior)	-60	-20	20	12.24
			Superior temporal gyrus	-52	-36	20	5.86
	29	R	Postcentral gyrus (inferior)	60	-16	20	8.15
Ventral premotor cortex (VPM)	44	L	Precentral gyrus	-44	-4	60	8.77
				-36	-6	68	7.56
	25	R	Precentral gyrus	52	8	36	6.66
Insula	43	R	Insula	48	16	-4	7.93
			Inferior frontal gyrus	60	12	4	6.91
Dorso-Medial Prefrontal cortex (MPFCd)	25	L	Superior frontal gyrus	-6	58	24	7.88

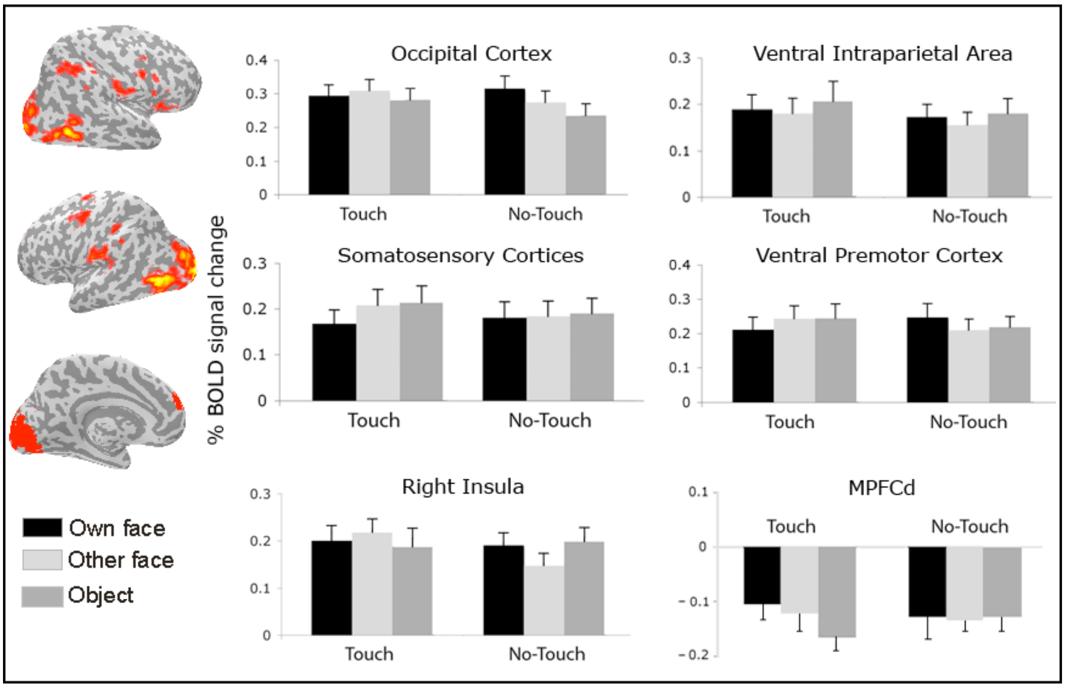


Figure 18. Regions showing different activation (and percentage signal change) during observation of any of the six conditions (Own face Touched, Own face No-Touched, Other face Touched, Other face No-Touched, Object Touched, Object No-Touched) compared to the inter-trial baseline. Group activation data are rendered on the cortical surface of a "canonical" brain (Mazziotta et al., 1995). MPFCd, dorso-medial Prefrontal Cortex.

Occipital cortex. The activation cluster in the occipital cortex included a wide portion of the occipital lobe encompassing Brodmann areas (BA) 17, 18 and 19. To functionally characterize this cluster three different anatomical masks encompassing BA 17, 18 and 19, respectively were created, and the BOLD percent signal change was computed in each area and in each condition. Anatomical masks were created by means of AAL toolbox available with SPM (Tzourio-Mazoyer, Landeau, Papathanassiou, Crivello, Etard, Delcroix, Mazoyer, and Joliot, 2002). Results showed no functional difference between the three areas, so the results will be discussed for the whole cluster.

The ANOVA showed that BOLD response in this cluster was modulated only by the type of image viewed by the participant, since only the effect of Image was significant [$F_{(2,28)} = 4.00$; $p < 0.05$]. Post-hoc comparisons showed that BOLD signal was higher when participants viewed both their Own face (0.30% increase relative to the inter-trial fixation baseline) and the Other face (0.29%) than an Object (0.25%; $p < 0.05$ in both cases; see Figure 18). Thus, BOLD signal in this area discriminated between bodily and non-bodily visual stimuli.

Ventral intraparietal area (VIP). An activation cluster was bilaterally found at the confluence of the postcentral and intraparietal sulci, compatibly with the location of the human ventral intraparietal area (Sereno and Huang, 2006). In both hemispheres VIP activation was mainly centered within BA 40. Neither the main effect of Hemisphere, nor any interaction between Hemisphere and the other factors were significant, thus the results for both hemispheres will be presented together (see Figure 18). Only the main effect of Trajectory was significant [$F_{(1,14)} = 4.56$; $p < 0.05$], showing a higher activation during observation of Touch (0.19%) than No-Touch (0.16%) trajectory (see Figure 18). Therefore neural activity in this area discriminates visual information specifically related to touch from that related to non-touch stimulation.

Ventral premotor cortex (VPM). An activation cluster was found bilaterally in the precentral gyrus. Although the cluster on the right hemisphere was more ventral than that on the left hemisphere, both clusters were located in the ventral half of the precentral gyrus and fell within BA 6, accordingly to the cyto-architectonic atlas (Eickhoff, Stephan, Mohlberg, Grefkes, Fink, Amunts, and Zilles, 2005). Nor the main effect of Hemisphere, neither any interaction between Hemisphere and the other factors were significant, thus the results were present for both hemispheres together (see Figure 18). The critical interaction Image x Trajectory was significant [$F_{(2,28)} = 7.04$; $p < 0.01$]. Post-hoc comparisons showed that in the Touch condition, BOLD response for the observation of one's Own face (0.21%) was reduced in comparison to that for the observation of the

Other's face (0.24%) and of the Object (0.24%; $p < 0.05$ in both cases). Conversely, in the No-Touch condition, BOLD response was enhanced for the observation of one's Own face (0.25%) in comparison to that for the observation of the Other's face (0.21%; $p < 0.03$) and of the Object (0.22%; $p < 0.05$). When neural response between Touch and No-Touch condition was compared for the different images, an opposite pattern of activity for viewing one's Own and the Other's face was found: for the Own face condition, neural activity was lower in the Touch (0.21%) than in the No-Touch condition (0.25%; $p < 0.05$), whereas for the Other condition, BOLD response was higher in the Touch (0.24%) than in the No-Touch condition (0.21%; $p < 0.05$) (see Figure 18). For the Object condition, the pattern of results showed a trend similar to that for the Other condition ($p = 0.09$). Thus, BOLD response in the left and right precentral gyrus seemed able to discriminate between the effect of viewing touch on one's own face as compared to viewing touch on another person's face or on an object. The self-specific effect consisted in a reduction of metabolic activity when viewing one's own face being touched.

Somatosensory cortices (SI/SII). An activation cluster was bilaterally found in the ventral postcentral gyrus. For both hemispheres, this activation site includes the face area in the primary somatosensory cortex (SI; Eickhoff, Grefkes, Fink, and Zilles, 2008) and the secondary somatosensory cortex (SII; Eickhoff et al., 2008). Face representations in the primary and secondary somatosensory cortices are very close to each other, both encompassing the ventral aspect of the postcentral gyrus (Sereno and Huang, 2006; Eickhoff et al., 2008). Although the present cluster clearly fell within this region, the present results did not discriminate any neural activity selectively related to either SI or SII. Thus, this activation cluster was named with the comprehensive term "somatosensory cortices".

The main effect of Image was significant [$F_{(2,28)} = 8.05$; $p < 0.01$], with a weaker activation for one's Own face (0.17%) than for the Other's face (0.20%; $p < 0.01$) and for the Object (0.20%; $p < 0.01$). These results should be interpreted in the light of the significant two-way interaction Image x Trajectory [$F_{(2,28)} = 4.03$; $p < 0.05$]. In the Touch condition, viewing one's Own face (0.17%) resulted in weaker activity than viewing both the Other face (0.21%; $p < 0.01$) and an Object (0.21%; $p < 0.01$). In contrast, in the No-Touch condition, no difference was found between one's Own face (0.18%), the Other face (0.18%), and the Object (0.18%; $p > 0.45$ in both cases) (see Figure 18). Such modulation resulted also in a different pattern of results when the effect of Touch and No-Touch was compared across the three images: while for the Object and for the Other face, neural activity in the Touch condition was higher than in the No-Touch condition ($p < 0.05$ in both comparisons), this difference was not found for one's Own face ($p = 0.22$), where rather a non-significant opposite trend was found. Thus, in summary, viewing one's own face being touched resulted in a reduction of the activity in right and left somatosensory cortices within the postcentral gyrus.

Right Insula. The activation cluster in the right insula was centred on BA 47. The ANOVA performed on the percent BOLD signal change in this cluster (see Figure 18) showed a significant interaction Image x Touch [$F_{(2,28)} = 10.53$; $p < 0.01$]. Post-hoc comparisons showed that in the Touch condition, the BOLD response for the Other face (0.22%) was higher than that for the Object (0.19%; $p < 0.05$). In the No-Touch condition, the BOLD response for the Other face (0.15%) was weaker than that for one's Own face (0.19%; $p < 0.05$) and for the Object (0.20%; $p < 0.01$). Finally, for the Other face condition the effect of Touch (0.22%) was higher than that of No-Touch (0.15%; $p < 0.01$) (see Figure 18).

Dorso-Medial Prefrontal Cortex (MPFCd). A deactivated cluster was found in the dorso-medial prefrontal cortex. The cluster was mainly centred within BA 10. The ANOVA performed on the percent BOLD signal change in this cluster showed no main effects, nor interaction (see Figure 18).

Discussion

Viewing one's own face being touched affects tactile perception on the face more than viewing another person's face or a non body stimulus (Serino et al., 2008). With the present experiment the brain areas underlying this effect were studied. In particular, the issue related to how high-level representations of the Self, conveyed by visual stimulation, may interact with the processing of tactile sensation, was addressed.

To this aim, fMRI technique was used to measure brain activity in subjects involved in a tactile sensory discrimination task on their face (discriminating between a unilateral and a bilateral electrical stimulation) while they viewed three different images, namely their own face, another person's face or an object, being touched bilaterally, or just approached, by fingers. The experimental paradigm was designed to maximize brain activity specifically related to the effect of interest (i.e. the modulation of touch due to visual information about the self) rather than to study the cognitive mechanism underlying the visual remapping of touch effect in general (see Serino et al., 2008; 2009). Nevertheless behavioural data basically replicate the main important finding of visual remapping of touch: participants more frequently reported to feel a bilateral stimulation on their face when they viewed a picture of their own face being touched bilaterally in comparison to when they viewed their own face being only approached. These behavioural findings were then related to neural activity recorded by fMRI.

Neural activity related to viewing a face

In a wide area of the Occipital cortex, involving BA areas 17, 18 and 19, BOLD signal was modulated as a function of the shown image: neural activity was higher when participants viewed a face, both their own and another person's face, than when they viewed a picture of a ball. Thus, this neural modulation may reflect the processing of complex visual information, such as that pertaining to a face, as compared to the processing of a simpler visual stimulus, such as a ball. These findings were in keeping with several previous data showing that the human body and its parts are specially relevant visual stimuli, processed by dedicated high-order visual areas, for example the so-called Extrastriate Body Area (EBA; Downing et al., 2001) for the body and the Occipital Face Area (Gauthier, Tarr, Moylan, Skudlarski, Gore, and Anderson, 2000; Haxby, Hoffman, and Gobbini, 2000; Pitcher, Walsh, Yovel, and Duchaine, 2007) and the so-called Fusiform Face Area (Kanwisher and Yovel, 2006) for the face.

Neural activity related to viewing touch

Neural activity in visual cortex did not discriminate visual information specifically related to touch from that not related to touch, since the modulation of BOLD signal due to viewing different images was independent from whether the image was touched or just approached by the fingers. Conversely, such information pertaining to finger movement trajectories affected neural activity in a portion of the parietal cortex, probably corresponding to the ventral intraparietal area (Sereno and Huang, 2006). VIP activity was enhanced when participants received a tactile stimulation on their face and viewed two fingers touching an image rather than pointing beside that image.

Neurons in the monkey VIP respond to both visual and somatosensory information directed towards the animal’s face (Colby et al., 1993; Duhamel et al., 1998; Avillac et al., 2005; Grefkes and Fink, 2005). Analogously, in humans, VIP contains a visuo-tactile somatotopic map of the face (Sereno and Huang, 2006). However, differently from the above-cited studies, in the present experiment, visual stimulation was not directed towards the participant’s real face but towards an image facing the subject. Thus, information derived from viewing touch was remapped such as touch was directed towards one’s own face and integrated with an actual tactile stimulation received on the face. It was suggested that the modulation of VIP activity found in the present study actually reflected such integrative and remapping process. This suggestion was supported by recent neurophysiological data on monkeys showing that some VIP neurons respond not only to visual and tactile stimulation administered on, or close to, a part of the animal’s body, but also when a stimulus is directed towards a part of the body of an experimenter facing the animal (Ishida et al., 2009). This response property of VIP cells allows linking the representation of an individual’s body with that of the body of others. A similar mechanism might underlie the VRT effect in humans, as shown by the present fMRI results.

Neural activity related to viewing touch on one’s own face

Therefore, neural activity in occipital and ventral intraparietal areas minght discriminate between viewing a face from viewing an object, and between viewing touch from viewing no-touch, respectively. However, the critical information strongly modulating subject’s perception, i.e. viewing touch on one’s own face, was processed elsewhere. A significant interaction between the viewed image and the fingers movement trajectory was found bilaterally in the ventral premotor cortex (VPM). In the VPM, BOLD signal when viewing one’s own face being touched was significantly different from that when viewing one’s own face not being touched and when viewing another person's face and an object being touched. In particular, a reduction of VPM activation was found for one's own face in the touch condition. Thus, neural activity in VPM might specifically represent information about touch on one's own face.

VPM is a well-known multisensory area, integrating visual, somatosensory and proprioceptive information about the body and the peripersonal space. In the monkey, the homologous VPM area (PZ) contains motor neurons with sensory proprieties, in that they respond also to visual, tactile and sometimes acoustic stimulation administered on the monkey's body or within monkey's peripersonal space (Rizzolatti et al., 2002; Graziano and Cooke, 2006). In humans, it has been demonstrated that VPM is activated when processing both tactile information on the face and visual, or acoustic, information approaching the face (Bremmer et al., 2001; Huang and Sereno, 2007). VPM receive important projections from both visual and somatosensory cortices (Godschalk, Lemon, Kuypers, and Ronday, 1984; Matelli, Camarda, Glickstein, and Rizzolatti, 1986) and is largely interconnected with VIP (Luppino, Murata, Govoni, and Matelli, 1999). Thus, VPM, together with VIP, represents an ideal candidate for integrating visual and tactile information related to face stimulation. The new finding from the present study was that, differently from VIP, VPM activity discriminated when the observed touch was administered to the observer's face rather than to another person's face or an object. In other words, VPM processed and integrated visuo-tactile information specifically pertaining to the Self.

Previous fMRI findings have shown that VPM is directly involved in the feeling of body ownership (Ehrsson et al., 2004; Ehrsson et al., 2005). In the rubber hand illusion, viewing touch on a fake hand and feeling synchronously touch on one's own hidden hand result in an illusory percept of the fake hand as one's own hand (Botvinick and Cohen, 1998).

During synchronous visuo-tactile stimulation causing the RHI, VPM is active. Moreover, brain lesions involving VPM are related to disorders of body ownership, such as anosognosia for hemiplegia (Pia, Neppi-Modona, Ricci, and Berti, 2004) and asomatognosia (Arzy, Overney, Landis, and Blanke, 2006). Thus VPM, together with other regions in the inferior parietal cortex (Berlucchi and Aglioti, 1997; 2010), is thought to be a key area in subserving the feeling of ownership of one's own body that is the Embodied Self. It is worth noting that no activation specifically related to the present experimental manipulations was found in medial prefrontal cortex, in areas processing more abstract and semantic representations of oneself, i.e. the Narrative Self (Mitchell et al., 2006; Jenkins et al., 2008). The cluster of activation change recorded in the MPFCd, indeed, did not vary as a function of the kind of visuo-tactile stimulation the participant was processing. Thus, coming back to the first questions of the present study, namely which brain areas and which representation of the Self underlie the self-related enhancement of visual remapping of touch effect, it might be concluded that VPM and the Embodied Self are the respective answers.

It remains to explain why such self-related VPM modulation was characterised by a reduction of neural activity, instead of by an enhancement, as one might more simply expect. Neural activity in VPM during the RHI positively correlates with the subjective feeling of body ownership. It has been proposed that the strength of VPM activation does reflect the effort of integrating different modalities into a unique body representation; accordingly to this view, VPM plays a specific role in embodying a non-body object (Tsakiris et al., 2007). Thus, the higher activation of this area, in the case of viewing another person's face and an object being touched, might reflect the effort in the embodying process, whereas viewing one's own face being touched facilitated embodiment and, as a consequence, less VPM activity was recorded.

Neural activity related to the modulation of touch perception when viewing one's own face

Finally, how did visuo-tactile integration related to oneself modulate tactile perception? The pattern of neural response shown in the premotor cortex was also reflected to the somatosensory areas. In particular, a reduced activity in the somatosensory cluster including the face area of SI and SII was found for viewing one's own face being touched in comparison to all other conditions. It is already known that visual information modulates tactile processing within somatosensory cortices (Macaluso, Frith, and Driver, 2005), probably via feed-back projections from multimodal fronto-parietal areas (Bremmer et al., 2001; Macaluso and Driver, 2005). In line with this view, in the present study it was suggested that VPM exerted a modulation on the somatosensory cortex (Macaluso, 2006). Thus, the most likely interpretation was that VPM integrates information about viewing touch on oneself with tactile information and then differently modulates the somatosensory areas where tactile information is processed.

To support this model, it remains to explain how a reduction in the activity of somatosensory areas resulted in an increase of reported bilateral tactile percept when viewing one's own face being touched. It might be suggested that when viewing oneself, visuo-tactile integration is favoured, and therefore visual information might be taken into account in perceiving tactile stimulation. In other words, perception of touch while viewing oneself being touched might rely more strongly on what is seen and less on what is felt. As a consequence, a weaker bilateral activation in the somatosensory cortices might be sufficient to evoke a bilateral tactile percept, since this percept is supported by bilateral visual information. In contrast, when the fingers just approached one's own face or when participants viewed another person or an object, visuo-tactile integration was less effective, and therefore tactile perception more strongly depended on unisensory tactile signals: as a consequence, a stronger bilateral activity in the somatosensory areas was necessary to elicit a bilateral tactile percept.

To sum up, Visual Remapping of Touch is defined as a modulation of tactile perception felt on one's own body when viewing touch on an external stimulus, this effect being maximum when viewing touch on one's own body. The present results showed that the neuronal counterpart of this effect relies on an extended network of fronto-parietal structures representing multisensory information pertaining to the bodily self.

CHAPTER 4

Emotional modulation of the Visual Remapping of Touch

4.1 Evidence for the involvement of emotional expressions in face-to-face interactions

During everyday social interactions we automatically try to understand the other we are currently interacting with. This human empathic tendency provides us with capacity of identifying thoughts, opinions, and feelings of our interlocutor. Recognition of someone else's emotional, mental and physical states allows us to adjust our own behavior towards that specific person.

As already mentioned, physical experiences observed on another person might further a simulation mechanism in the observer who usually first resonates with the seen sensory experience, then tries to understand its perceptual effects (Thomas et al., 2006; Haggard, 2006). In our every-day social interactions, understanding another person's current physical states might help in planning an adjusted behavioral attitude towards that person. Also the emotional experience of another individual is an important social cue an observer usually tries to recognize in order to adjust an adequate reaction.

Emotional expressions are a means of communication that are more rapid than language, with which people can quickly and accurately infer states of mind of their conspecifics (Batty and Taylor, 2003; Blakemore, Winston, and Frith, 2004). Thus, understanding others' emotional states is thought as a key tool in social cognition. How do we judge the emotion that another person is feeling? One key information in face-to-face interactions is the emotional content conveyed by facial expressions (Schulte-Ruther, Markowitsch, Fink, and Piefke, 2007). Six basic facial expressions were identified: anger, happiness, fear, surprise, disgust and sadness. These expressions are thought to be universal, since it was demonstrated that they are readily recognizable across very different cultures (Ekman and Friesen, 1971).

Visual information about faces is first processed in the early visual areas and then sent to the inferior and lateral temporal lobes and much of the frontal cortex . This system is functionally segregated, in that representational space for facial identity is stored predominantly in the fusiform face area (FFA), whereas the representational space for facial emotional expressions is stored in the superior temporal sulcus (STS). In line with this distinction, it has been demonstrated that in humans, STS responds more to facial expressions than to neutral faces (Engell and Haxby, 2007). In addition to the STS, an extended network underlying perception of facial emotional expressions encompasses the frontal operculum (FO), the premotor cortex and the somatosensory cortices (Haxby et al., 2000). Moreover, recognition of facial expressions of emotion has been shown to involve also subcortical structures such as the amygdala (Adolphs, Tranel, Damasio, and Damasio, 1994; Adolphs, Tranel, Damasio, and Damasio, 1995; Morris, Frith, Perrett, Rowland, Young, Calder, and Dolan, 1996). It is worth noting that the involvement of these several neural structures in emotion recognition has been demonstrated to change as a function of the emotion itself (Adolphs et al., 1994; Adolphs et al., 1995; Adolphs, 2008). For instance, ventral regions of the prefrontal cortex are activated in neuroimaging studies for fear and anger. Sectors of right parieto-temporal cortex seem important for fear recognition as well. Conversely, the insula appears to play an essential role in recognition of disgust. Lesions of the amygdala, as already well known, impair recognition of fear from facial expressions. More recent findings showed that amygdala lesions could also impair recognition of emotions other than fear (Phillips, Young, Senior, Brammer, Andrew, Calder, Bullmore, Perrett, Rowland, Williams, Gray, and David, 1997; Fitzgerald, Angstadt, Jelsone, Nathan, and Phan, 2006; Graham, Devinsky, and Labar, 2007; Adolphs, 2008).

Facial expressions can convey negative or positive emotions. Negative emotions signal the presence of a potential threat in the environment, hence fast and accurate recognition of these emotions is important for survival (Batty and Taylor, 2003). For example, the facial expression of fear serves as an adaptive social signal, simultaneously warning others of nearby threat in the environment and soliciting their help (Darwin, 1872; Ekman and Friesen, 1971; Chiao, Iidaka, Gordon, Nogawa, Bar, Aminoff, Sadato, and Ambady, 2008). This capacity confers an adaptive advantage allowing organisms to commit attentional resources during goal-directed behavior, while retaining an ability to quickly respond to potential harm (De Martino, Kalisch, Rees, and Dolan, 2009). Positive emotions, on the other hand, provide the observer with positive feedback and may act as a social reward signal, facilitating social relationships (Tsukiura and Cabeza, 2008). For example, happy expression might signal a willingness to engage in reciprocal altruism (Schmidt and Cohn, 2001). Moreover, a smiling face makes people appear more trustworthy (Winston, Strange, O'Doherty, and Dolan, 2002) and familiar (Baudouin, Gilibert, Sansone, and Tiberghien, 2000), as well as seeming more attractive and kind (Otta, Folladore Abrosio, and Hoshino, 1996). In keeping with the different value of facial expressions, different emotional expressions tend to elicit different behavioural responses: for example, fearful faces might activate defensive and avoidance responses (Zebrowitz, Kikuchi, and Fellous, 2007), whereas happy faces might activate positive, approaching behaviours (Knudson, 1996; Hess, Blairy, and Kleck, 2000).

The following experiment was aimed at investigating whether positive and negative emotional expressions might differently modulate the VRT as a function of their valence.

Experiment 6. Different roles of positive and negative emotional expressions in the Visual Remapping of Touch

Viewing a face being touched enhances tactile perception on one' s own face. This effect, termed Visual Remapping of Touch (VRT) might be important for social interactions: in order to understand other peoples' feelings, observers might implicitly refer what they see expressed on the bodies of others to their own body. Face-to-face interactions are critical in social relationships. Moreover the emotional content conveyed by a face is essential information in social contexts (Schulte-Ruther et al., 2007). In the present study it was investigated whether emotional content of facial expressions interacts with the VRT mechanism, thus modulating its perceptual effects.

Fast and accurate processing of the facial emotional expression of an observed individual might help in understanding his thoughts, feelings and emotional states and this in turn, might facilitate the observer in adjusting a coherent reaction to such an effective communicative sign. If emotional content of facial expressions interacts with the VRT mechanism, a differential modulation of tactile perception on the face might be hypothesised as a function of the type of expression shown by the other face. In other words, positive and negative emotional expressions, given the specific behavioural valence of these two different classes of emotions, might modulate the VRT effect in different ways. Two possible predictions could be tested. On the one hand, it might be hypothesised an enhancement of tactile perception on the face when viewing touch towards a face with a fearful expression as compared to viewing touch towards a happy face. Since recognition of negative emotions has a highly adaptive value, it was suggested that participants could more readily remap onto their own somatosensory system the fear specific information as perceived in the face of another individual. Indeed, understanding what is happening to a frightened person might be useful in allowing to quickly plan defensive and avoidance reactions. This attitude may have been selected through evolution as an adaptive behaviour (Adaptive Hypothesis). On the other hand, an opposite pattern of results might also be hypothesised, i.e. an enhancement of tactile perception on the face when viewing touch towards a happy face as compared to when viewing touch towards a fearful face. Since happiness has a high social value, facilitating social relationships (Tsukiura and Cabeza, 2008), viewing a happy face might make participants more prone to share tactile experience with that face (Pro-Social Hypothesis).

To test these two alternative hypotheses, participants took part in a tactile confrontation task, set as in Serino et al.'s studies (2008; 2009). Participants were electrically stimulated on the right, the left, or both cheeks and were asked to respond by pressing a button with the hand corresponding to the side where they felt the tactile stimulus. To simulate extinction, stimulus intensity on one cheek was stronger than that on the other cheek. In line with previous results, it was predicted that in trials of bilateral stimulation the stronger stimulus would frequently extinguish the weaker one (Serino et al., 2008; 2009). While performing the tactile confrontation task, participants watched different movie blocks: a human face with a fearful expression, a happy expression, or a neutral expression (Ekman and Friesen, 1976). The images on screen were seen to be touched or just approached unilaterally or bilaterally, by one or two human fingers (one on the left and one on the right side) in different trials. When the fingers reached the image the electrical stimulation was delivered to the participants' face. Participants were instructed to respond only to the tactile stimulus and not to the visual stimulus.

If emotional expressions modulate the VRT mechanism, then a differentiated modulation of tactile perception was predicted as a function of the shown facial expression. If the Adaptive Hypothesis is correct, observing a fearful expression should have enhanced the

VRT mechanism and therefore participants' ability to detect double tactile stimulations on their own face; thus, maximum effect should have been apparent when they viewed a frightened face being touched. On the other hand, if the Pro-Social Hypothesis is correct and viewing a face depicting a positive emotion promotes a tendency to share experiences with others, tactile detection on one's own face should have been highest when participants viewed a happy face being touched.

Materials and Methods

Participants

Twenty-two healthy young women were included in the present study (mean age 25 years; range: 23-28 years). All participants were right-handed, had normal or corrected-to-normal vision, reported normal touch and were naive as to the purposes of the experiment. The study was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Stimuli and Procedure

The experimental stimuli consisted of both tactile and visual stimuli.

Tactile stimuli were delivered by 2 constant current electrical stimulators (DS7A, Digitimer), via 2 couples of neurological electrodes (Neuroline, AMBU) placed on the participant's right and left cheeks. For half of the participants, the tactile stimulus on the left cheek was set to be more intense than that on the right cheek and vice-versa for the other half. Prior to the experiment, in absence of visual information, the intensity of the electrical stimuli for each participant was titrated with a staircase procedure (Cornsweet, 1962) to a threshold detection rate of 100% for the stronger stimulus and 60% for the weaker.

As a confirmation of the correct titration of the stimuli, the mean accuracy for unilateral strong and unilateral weak stimuli was 88% (s.e.m. = 4%) and 65% (s.e.m. = 8%), respectively ($p < 0.001$). This stimulus arrangement resulted in a tendency for participants to fail to report the weaker stimulus during trials with double stimulation. Mean accuracy for bilateral tactile detection was 58% (s.e.m. = 6%). Errors consisted mostly of reporting the side of the stronger stimulus: mean probability of reporting the side of the stronger stimulus in case of errors during bilateral stimulation was 90% (s.e.m. = 5%; $p < 0.001$).

Visual stimuli consisted of a movie presented on a 17” computer screen placed in front of the participant at a distance of ~ 60 cm. The movie depicted the image of a face covering about 10x20 cm of the screen area. In different blocks, a face with a neutral facial expression, with a fearful facial expression or with a happy facial expression was presented. The faces were static black and white pictures selected from the Pictures of Facial Affect (PFA) database (P. Ekman and W. V. Friesen, Consulting Psychologists Press, Palo Alto, CA, 1976) which is a set of highly recognizable and prototypic facial expressions. Overall, for each expression 3 different female faces were used.

The picture of the face was presented as a central, static image in the background of the movie. In the foreground, however, two fingers were presented, initially positioned on the lower part of the screen, one on the right and one on the left side. During the movie the fingers moved towards the centrally presented face and then returned back to their initial position. In different trials the finger-motion followed one of two trajectories; In the Touch condition, the fingers actually touched the cheeks of the shown face, approximately in the same position where tactile stimulation on the participants’ cheeks was administered. In the No-Touch condition, the fingers stopped about 5 cm from alongside the face (Figure 19). In different trials, either the finger on the right, on the left, or both fingers moved. Visual and tactile stimuli were synchronized so that when the fingers reached the image a tactile input (a unilateral or bilateral tactile stimulation) was delivered to the participant's face. Each movie lasted a total of 2000 ms, and tactile stimulation was delivered at ~1000 ms from movie onset.

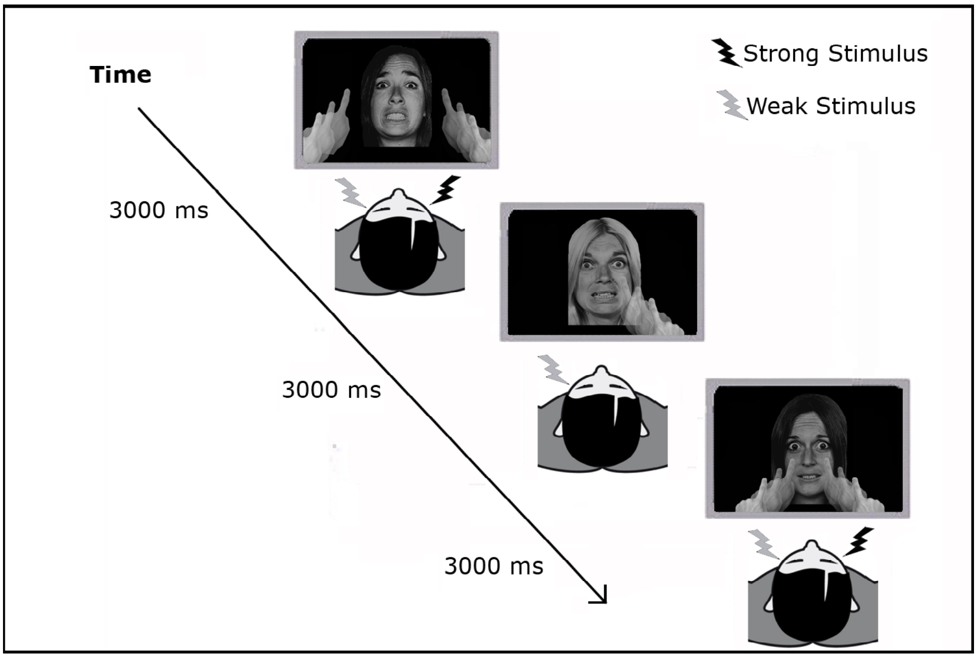


Figure 19. Schematic depiction of the experimental paradigm. Experiment 6. All participants performed 3 randomized blocks of tactile confrontation task, lasting ~ 5 min each. In each block, a different image (fearful face, happy face, neutral face) was presented in the movie. In different trials fingers moved towards the image and then backwards to their starting position. Fingers either touched the cheeks of the shown face or stopped about 5 cm alongside the face. In different trials, either the finger on the right, on the left or both fingers moved. As soon as the fingers reached the image, a tactile input (either the weak, the strong or both stimuli) was delivered on the participant's cheeks.

Experiment 7. All participants performed 4 blocks of tactile confrontation task, lasting ~ 3 min each. In different trials, a different image (fearful face, angry face) was presented in the movie. Movies' structure was the same as that of movies in Experiment 6.

A PC running C.I.R.O. (www.cnc.unibo.psice.unibo/ciro) software was used to control the presentation of the stimuli and record the responses. Each experiment consisted of 3 counterbalanced experimental blocks of the tactile confrontation task. In each block, a different image (fearful face, happy face, neutral face) was presented in the movie. Stimuli comprised a combination of the two types of tactile stimulation (Unilateral left or right, and Bilateral), the two sides of visual stimulation (Unilateral left or right, and Bilateral), the two fingers movement trajectories (Touch and No-Touch). Each combination was repeated 10 times, for a total of 80 trials per block, presented in random order. Each trial lasted about 3 seconds. A pause of 5 minutes, during which tactile thresholds were recalibrated, was interspersed between blocks.

Results

In order to study the effect of emotional content of the viewed face on the VRT effect, participants' accuracy in responding to bilateral tactile stimuli was compared to when both fingers (bilateral condition) did or did not touch the three different image types. Unilateral tactile and unilateral visual stimulations were used as catch trials and hence they were not included in the analysis. A two-way ANOVA was conducted on the percentage of correct responses to bilateral tactile stimulation with the within-participants factors of Face emotion (Fearful face, Happy face, Neutral face) and Finger movement trajectories (Touch and No-Touch). Duncan post-hoc comparisons were performed, when necessary, to compare single effects.

The main effect of Fingers movement trajectories was significant [$F_{(1,21)} = 11.20$, $p < 0.01$]: accuracy was higher when the fingers touched the face (mean accuracy = 70%; s.e.m. = 3%) than when the fingers did not touch the face (62%; s.e.m. = 3%). Moreover, the critical interaction Face emotion X Fingers movement trajectories was significant [$F_{(2,42)} = 3.93$, $p < 0.05$]. The strongest modulation of tactile perception due to visual information was found when participants saw a Fearful face being touched: accuracy in this condition was significantly higher (75%; s.e.m. = 4%) than that when viewing a Happy face (67%; s.e.m. = 3%; $p < 0.05$) or a Neutral face (68%, s.e.m. = 4%; $p = 0.05$) being touched. Interestingly, the boosting effect for the fearful facial expression was specific for viewing touch on the face because in the No-Touch condition accuracy was not significantly different when participants viewed a Fearful (61%; s.e.m. = 4%), a Happy (67%; s.e.m. = 4%) or a Neutral face (59%; s.e.m. = 4%; $p > 0.08$ for all conditions) (Figure 20). The lack of a significant difference found in the No-Touch condition is important as it rules out the possibility that the results were due to an increased attention to a fearful face.

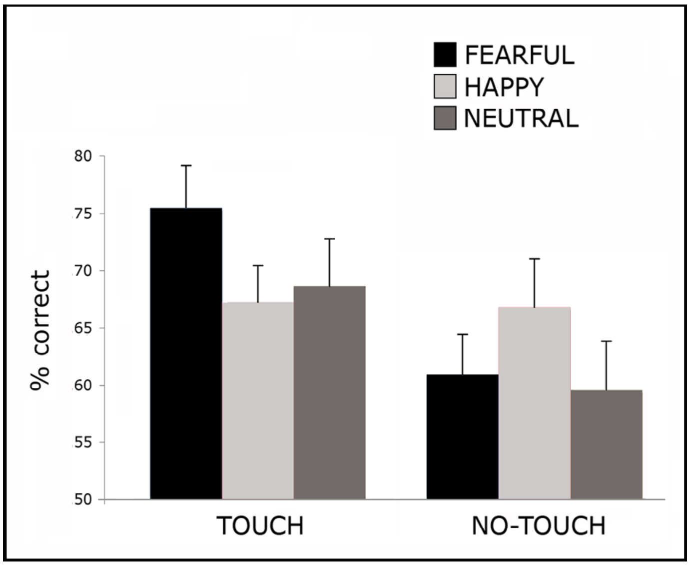


Figure 20. Results for the tactile confrontation task. Accuracy in detecting bilateral tactile stimulation while viewing movies showing either a fearful face, a happy face or a neutral face that could be touched or just approached by two human fingers. Error bars show standard error across participants.

Discussion

In keeping with previous results (Serino et al., 2008; 2009; see also Banissy & Ward, 2007), the present findings confirmed that viewing a face being touched enhances tactile perception on one's own face, compared to viewing the same face being just approached. The new finding of the present study was that emotional expression of the observed face modulates the VRT effect.

Two possible emotional effects on the VRT were compared: according to the Adaptive Hypothesis, viewing touch towards a face showing a fearful expression could enhance tactile perception on the observer's face. The remapping mechanism is automatically evoked in order to understand what is happening to a frightened individual.

Understanding what is happening to a frightened person might be useful for planning effective defensive and avoidance reactions, and, as already suggested, this attitude may have been selected through evolution as an adaptive behaviour. On the other hand, according to the Pro-Social Hypothesis, we should have expected an enhancement of tactile perception when viewing a happy face being touched because happiness makes the observer more prone to share tactile experiences with the other.

The present results were in line with the Adaptive rather than with the Pro-Social Hypothesis because the effect of viewing touch on the feeling of touch was stronger when the observed face showed a fearful expression, as compared to when the face showed a neutral expression or a happy expression. Importantly this effect could not be explained in terms of a generic arousal effect induced by fearful expressions. This is because when participants observed a face not being touched by fingers their tactile perception was not modulated by the emotional content of the face. Therefore, the present results showed that fearful emotion strengths the mechanism of remapping a tactile sensation into one's own somatosensory system. In other words, the fear we perceive in the face of others is remapped onto our own somatosensory system providing us with critical social information necessary for our survival and wellbeing. This follows the Adaptive Hypothesis as previously discussed in the introduction.

Given that fear enhanced the VRT effect whereas happiness did not seem to play any modulatory role on the VRT mechanism, one might wonder whether such a result could be generalized to other negative emotional expressions – such as anger – or if it is just specific for fear. The next second experiment was designed in order to answer this question.

Experiment 7. Fear-specific modulation of the Visual Remapping of Touch

The present study was aimed at investigating whether the fear-related modulatory effect on the VRT mechanism found in Experiment 6 could generalise to other negative emotions or if it was just specific for fear.

In order to answer this question, a second experiment, identical to the previous one, was run with the exception that new participants were involved in the tactile confrontation task, while they were watching a movie showing, in different trials, a human face with either a fearful expression or an angry expression (Ekman and Friesen, 1976). If the enhancement effect due to viewing fear generalises to other negative emotional expressions, it might be expected the same modulatory effect on the VRT both when viewing an angry and a fearful face. This result would suggest that different kinds of negative emotions have a similar adaptive value, such as warning signals for potential threat in the environment. On the contrary, if fear plays a selective role in modulating the remapping of seen touch onto felt touch, it might be expected a specific modulation of the VRT when viewing touch towards a fearful face in comparison to when viewing touch towards an angry face. Indeed, although both fear and anger convey negative feelings (Darwin, 1872; Ftijda, 1986), recognition of emotional signals associated with fear or anger is quite different and elicits different responses (Pichon, de Gelder, and Grezes, 2009). Facing a fearful situation usually requires a fast automatic recognition and a simple behavioural response, whereas coping with someone else’s anger requires more contextual information to be understood and more complex, socially determined behaviours (Pichon et al., 2009).

Materials and Methods

Participants

Seventeen healthy young women were included in the second experiment (mean age 25 years; range: 22-28 years). All participants were right-handed, had normal or corrected-to-normal vision, reported normal touch and were naive as to the purposes of the experiment. The study was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Stimuli and Procedure

The procedure was the same as in the previous experiment. As a confirmation of the correct titration of the stimuli, the mean accuracy for unilateral strong and unilateral weak stimuli was 95% (s.e.m. = 2%) and 82% (s.e.m. = 5%), respectively ($p < 0.001$). This stimulus arrangement results in a tendency for subjects to fail to report the weaker stimulus during trials with double stimulation. Mean accuracy for bilateral tactile detection was 64% (s.e.m. = 3%). Errors consisted mostly of reporting the side of the stronger stimulus (88% of times; s.e.m. = 4%; $p < 0.001$).

Visual stimuli were the same as for the first experiment with the exception that two image types were used: in different trials, a face with a fearful expression (the same as in the previous experiment) or with an angry expression, was shown to the subject. The faces were static black and white pictures selected from the Pictures of Facial Affect (PFA) database (P. Ekman and W. V. Friesen, Consulting Psychologists Press, Palo Alto, CA, 1976). For each expression 3 different female faces were used.

The experimental paradigm consisted of 4 counterbalanced experimental blocks of the tactile confrontation task. In each block, stimuli comprised a combination of the two different images (Fearful face and Angry face), the two types of tactile stimulation

(Unilateral left or right, and Bilateral), the two sides of visual stimulation (Unilateral left or right, and Bilateral), the two fingers movement trajectories (Touch and No-Touch). Each combination was repeated 8 times, for a total of 32 trials per block, presented in random order. Each trial lasted about 3 seconds. A pause of 5 minutes, during which tactile thresholds were recalibrated, was interspersed between blocks.

Results

In order to test whether the two types of negative emotions differentially modulated the VRT effect, subjects' accuracy in responding to bilateral tactile stimuli was compared to when the fingers bilaterally did, or did not, touch the two different types of image (fearful faces vs angry faces). As in the previous experiment unilateral tactile and unilateral visual stimulations were used as catch trials and hence they were not included in the analysis. A two-way ANOVA was conducted on the percentage of correct responses to bilateral tactile stimulation with the within-subjects factors of Face emotion (Fear and Anger) and Finger movement trajectories (Touch and No-Touch). Duncan post-hoc comparisons were performed when necessary, to compare single effects.

The critical interaction Face emotion X Fingers movement trajectories was significant [$F_{(1,16)} = 7.38$, $p < 0.05$]. Viewing a fearful face being touched enhanced tactile perception on the face (79%; s.e.m. = 4%) compared to viewing an angry face being touched (67%; s.e.m. = 5%; $p < 0.05$). Moreover accuracy was higher when the fingers touched the fearful face than when they did not touch the face (62%; s.e.m. = 4%; $p < 0.01$). On the contrary, when viewing an angry face, no difference between Touch (67%; s.e.m. = 5%) and No-Touch (67%; s.e.m. = 4%; $p = 0.94$) was found (Figure 21). Finally, accuracy was not significantly different when participants viewed a fearful (62%; s.e.m. = 4%) or an angry face (67%; s.e.m. = 4%; $p = 0.28$) not being touched by the fingers (see Figure 21). The lack of a difference in the No-Touch condition is important as it rules out the possibility that participants simply paid more attention to a fearful face for a generic arousal effect.

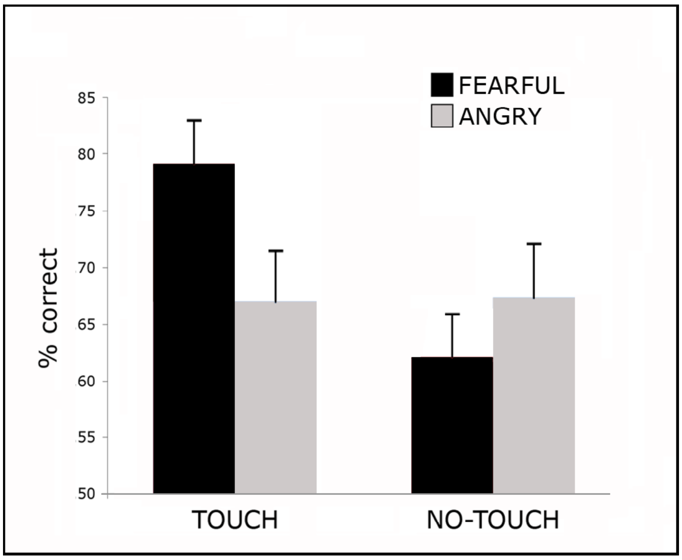


Figure 21. Results for the tactile confrontation task. Accuracy in detecting bilateral tactile stimulation while viewing movies showing either a fearful face or an angry face that could be touched or just approached by two human fingers. Error bars show standard error across participants.

Discussion

Whereas the previous experiment (experiment 6) shed light on the different roles of positive versus negative facial emotional expressions in modulating the VRT mechanism, showing a significant effect of fear rather than happiness, the present study investigated whether the emotional modulation of the VRT might generalise to other negative emotions or whether it is actually fear-specific.

Results from the present experiment showed that tactile perception on the face was enhanced when viewing touch towards a fearful face as compared to viewing no-touch. When viewing an angry face, no modulation of tactile perception was observed as a function of the finger movement trajectories. Thus, the emotional modulation of the VRT effect seemed to be specific for a fearful expression, and did not generalise to other negative emotions, such as anger.

Faces convey multiple types of information that are essential for interindividual interactions and for inferring the observed person's state of mind and feelings: our facial expressions signal to others our intentions and, in turn, others' facial expressions communicate their mental states (Adolphs, 2002).

Several findings suggest that the elaborate aspect of face perception activates different brain areas (Bruce and Young, 1986; Calder and Young, 2005) and involves different neural networks (de Gelder, Vroomen, Pourtois, and Weiskrantz, 1999; Morris, Ohman, and Dolan, 1999; Haxby et al., 2000). While the fusiform face area (FFA) is involved in processing the structural, static properties of faces, regions more anterior and dorsal in the temporal lobe process information about the changeable configurations of faces, such as those conveyed by facial expressions (Haxby et al., 2000). Thus, the FFA, the superior temporal gyrus, and other less well-specified regions of occipito-temporal cortex are thought to be an interconnected network underpinning a perceptual representation of different aspects of the face (Adolphs, 2002).

According to an influential model of emotion processing in the human brain, beyond the visual analysis of facial features by the occipito-temporal pathway (Bruce and Young, 1986; Haxby et al., 2000), emotional expression recognition might also depend on the activation of representations within the somatosensory system (Adolphs, 2002). In particular, primary and secondary somatosensory cortices are thought to play a role in recognizing negative facial emotions, because these areas are involved in representing somatic information associated with such emotions. We recognize another individual's emotional state by generating internal representations within the somatosensory cortices that simulate how the other individual would feel when displaying a certain facial expression (Damasio, 1994; Adolphs, 2002), in this way the observed emotion is "embodied". The embodiment of an emotion might allow the observer to match the seen emotional expression with bodily dependent traces associated with personal experiences of the same emotion (Carr et al., 2003; Niedenthal, 2007).

In line with this hypothesis, data from brain-damaged patients (Adolphs, Damasio, Tranel, and Damasio, 1996; Adolphs et al., 2000) have shown that lesions of the right somatosensory cortex are associated with impairment in facial emotional expressions recognition, in particular for negative emotions. Thirty-seven brain-damaged patients with circumscribed lesions in left or right sensory cortices were shown black-and-white slides of faces displaying the six basic emotional expressions. Patients were asked to judge each expression with respect to several verbal labels. Impairment in the processing of emotional facial expressions was found only in patients with lesions restricted to the right hemisphere. Further, the impairment in facial expression recognition correlated with damage to two regions: the right inferior parietal cortex and the right anterior infracalcarine cortex. Finally, none of patients was impaired in recognizing happy expressions, whereas several of them had difficulty in recognizing some negative emotions. In particular, a significant difference in recognizing fear compared to the other expressions was found. These results suggested that lesions in the right sensory cortices, encompassing discrete visual and somatosensory cortical systems, specifically impaired recognition of fearful facial expressions (Adolphs et al., 1996).

In addition, Pourtois and colleagues showed that single pulse TMS delivered to the face area of the right somatosensory cortex selectively interfered with perception of fearful, but not with happy, facial expressions (Pourtois, Sander, Andres, Grandjean, Reveret, Olivier, and Vuilleumier, 2004). Thus it seems that different emotions vary in the level of internal somatic representation required for their recognition (Hussey and Safford, 2009): fear processing strongly taps into the somatosensory system, whereas happiness, being more easily identified through a single visual feature (e.g., the spatial configuration of a smile), is less dependent on on-line somatosensory representation by internal simulation (Rizzolatti, Fadiga, Gallese, and Fogassi, 1996; Gallese and Goldman, 1998). Moreover, fearful faces constitute biologically relevant and salient signals of a potential threat in the environment, presumably leading to a more massive somatic behavioral preparation as compared with happy faces (Pourtois et al., 2004).

The results of Experiment 6 were in line with this interpretation. During the initial exposure to a fearful face, a stronger activation in the somatosensory cortices might occur, whereas less activation might be evoked in the case of viewing a happy or a neutral face. Therefore the somatosensory cortices might be precociously activated when viewing a fearful face and, as a consequence, processing of tactile information delivered on the participant's face was facilitated. This preparatory effect might enhance tactile perception on one's own face while viewing touch towards a fearful face. It is worth noting that the somatosensory cortices are responsible for processing tactile information and their activity is modulated during the VRT effect (Cardini, Costantini, Galati, Romani, Ladavas, and Serino, 2011).

Recognition of a fearful face has a higher salience and biological value as compared to recognition of neutral or happy faces. Viewing a fearful face might alert the observer by signalling the presence of a potential threat in the environment that needs to be identified in order to prepare a defensive response. A rapid and accurate recognition of such emotion is therefore critical for one's own survival. Precocious somatosensory activations might help this rapid recognition.

Results of the present experiment showed that this emotional modulation of the VRT effect was specific for fear, and did not generalise to just any negative emotion, since no VRT effect was observed when subjects viewed an angry face. Anger coveys more complex social signals in comparison to fear and requires additional contextual and social information to be understood and to cope with. Moreover, negative emotional expressions tend to elicit in the observer different behavioural responses: for example, a person showing an angry face is perceived to have traits associated with low affiliation, a highly dominant attitude, and tends to elicit defensive responses from the others (Marsh, Ambady, and Kleck, 2005). The emotional expression of fear has been frequently presumed to index the presence of threat in the environment (Adolphs, Russell, and Tranel, 1999) and therefore has been often though as an aversive stimulus. Any stimulus signalling potential threat is expected to activate avoidant mechanisms such as withdrawal (Cacioppo and Berntson, 1994; Lang, Bradley, and Cuthbert, 1997). Nevertheless, some data suggested that fearful expression might also promote approach from the observer. Animal models provide evidence that fear might constitute an appetitive stimulus. In fact, social species such as canines, display subordination or fear to keep them from becoming targets of conspecifics' aggression (Schenkel, 1967; Preuschoft, 1999). Thus, if fearful expression is perceived as affiliative and appeasing, it may elicit approaching reactions. A recent study compared motor responses elicited by vision of angry expressions with those elicited by vision of fearful expressions (Marsh et al., 2005). Results demonstrated that anger and fear facilitated opposite behaviours. Whereas angry expressions elicited avoidance-related responses, fear facilitated approaching movements. It is unsurprising that anger elicits avoidance behaviours. However, why does fear elicit approaching reactions? It was suggested that, beyond indexing threatening stimuli in the environment, fear expression might serve as an appeasement signal, aimed at ameliorating conflicts and promoting affiliative tendencies (Marsh et al., 2005).

In line with these behavioral results, recent neuroimaging findings show different neural activations when observing the two emotional expressions. Observation of actions of other people expressing anger elicits specific activity in a wide set of regions comprising the anterior temporal lobe, the premotor cortex and the ventromedial prefrontal cortex (Pichon et al., 2009). Activation of this network suggests that anger recognition involves theory of mind abilities by recruiting the temporal pole (Brunet, Sarfati, Hardy-Bayle, and Decety, 2000; Castelli, Happe, Frith, and Frith, 2000; Gallagher, Happe, Brunswick, Fletcher, Frith, and Frith, 2000), preparation of an adapted motor response by activating the premotor cortex (Hoshi and Tanji, 2004), and selection of specific behavioral strategies by prefrontal regions (de Waal, 2000). Thus, anger recognition depends on the activity of neural networks that are usually involved in processing high-order social cues, allowing to infer mental states of others (i.e. theory of mind) or to adapt one's own behavior to social relationships. On the other hand, and more importantly for the present study, viewing an angry face, as opposed to viewing a fearful face, does not automatically activate the somatosensory cortices (Pichon et al., 2009). It is for this reason, that no enhancement of the VRT effect was observed when participants were viewing an angry face.

In conclusion, the VRT effect interacts differentially with the emotional content of an observed face, readily activating the somatosensory system in response to fear: when facing a fearful face, potential harm arising from the immediate environment could be anticipated by "sharing" the observed somatosensory experience with the other – i.e. remapping the seen touch onto the felt touch - helping to understand the source of the potential common threat. In contrast, other emotional expressions, such as anger and happiness, communicate to the observer high-order negative or positive social signals. In fact, recognition of these expressions does not require activation of the somatosensory system, but rather the activation of neural networks involved in social signals processing (Brunet et al., 2000).

General Discussion

Multisensory mechanisms are essential means to correctly represent and perceive the external world. We are continuously bombarded by inputs from different sensory modalities, and our brain continuously synthesizes them in coherent percepts (Stein and Meredith, 1993). Moreover, multisensory mechanisms play a crucial role in building up a coherent mental representation of the body and the surrounding space – the peripersonal space (Rizzolatti et al., 1997). These mechanisms allow recognition of one's body as separate from the external events and distinct from the other bodies. Bodily self-recognition is important to identify external stimuli, either potential source of danger or of interest, and in turn, to plan adequate behavioural responses to them (Graziano et al., 2006). In addition, self-recognition allows using one's body representation as reference system for perceiving others' bodily experiences, by simulating on one's sensory system the observed states (Thomas et al., 2006). This, in turn, provides us useful information to develop adjusted social relationships.

The present dissertation discussed two multisensory mechanisms whereby body representations are thought to modulate sensory processing of stimuli on the body surface. In particular, the focus of the present project was directed on special forms of visuo-tactile interaction and on possible modulatory effects that high order variables might play on these bodily-related multisensory mechanisms.

The two visuo-tactile mechanisms discussed in the present dissertation are the Visual Enhancement of Touch (VET) and the Visual Remapping of Touch (VRT) effects, whereby vision of the body, in the former, and vision of the body being touched, in the latter, enhance tactile processing. Some aspects of these mechanisms have been extensively investigated in the last decades, whereas few crucial issues related to them need to be addressed.

It is worth mentioning that multisensory mechanisms might involve feedforward projections from unisensory areas to multimodal areas, as well as feedback modulations from either unisensory or multisensory regions to unisensory systems (Driver and Noesselt, 2008). Indeed, for example, the enhancement of auditory localization due to integration of co-occurring auditory and visual stimuli in spatial coincidence is a case of feedforward convergence (Bolognini et al., 2007; Passamonti et al., 2009), whereas the ventriloquism effect is a clear example of a feedback mechanism, since presenting simultaneous but spatially discrepant auditory and visual stimuli induces a perceptual translocation of the sound towards the visual stimulus, i.e. a detrimental effect of visual event on auditory localization (Howard and Templeton, 1966; Bertelson and Radeau, 1981).

Conversely, the debate on the multimodal nature of “the body as a multisensory object” is still open. Recently, it has been suggested that mental body representations are continuously updated by convergent multisensory signals (by feedforward projections) and that in turn, these updated body models send modulatory feedbacks to unisensory areas, contributing to the interpretation of current sensory inputs (Tsakiris, 2010). However, the multisensory nature of several visuo-tactile effects related to the body is still unclear.

Thus, the present dissertation, beyond providing an extensive literature review of these visuo-tactile mechanisms (VET and VRT), was aimed at disambiguating their multisensory dynamics.

I. Visual Enhancement of Touch

As mentioned before viewing the body enhances tactile discrimination ability. Several lines of evidence suggested that this mechanism seems to involve a modulation from high order mental body representations, driven by vision of a body part, towards the primary somatosensory area, enhancing tactile acuity on the seen location (Taylor-Clarke et al., 2002; Fiorio and Haggard, 2005; Longo et al., 2011). In particular, viewing the body appears to preset the tactile circuits involved in tactile discrimination, perhaps via feedbacks from visual or multisensory areas into somatosensory cortex. What has hitherto not been investigated is the neuronal mechanism underlying the VET effect.

As it is known, tactile acuity depends on cortical lateral inhibition, a widespread mechanism in sensory cortical areas, such as the visual and the somatosensory cortices (Kandel et al., 2000). Inhibition is thought to be produced by inhibitory interneurons located both in the thalamic relay nuclei and in the cortex. Briefly, a local network of inhibitory interneurons connects adjacent cortical neurons, so that firing of one cortical neuron tends to lead to inhibition of its neighbours. This arrangement enhances responses to small, spatially detailed stimuli, since these do not trigger the lateral inhibition from neighbouring receptive fields that are triggered by larger stimuli. As a result, increases in lateral inhibition tend to increase spatial acuity (Dykes et al., 1984). As a consequence, a possible mechanism underlying the VET might be a modulation exerted by vision of the body towards the intracortical inhibitory network in the somatosensory regions.

Experiment 1 was aimed to test this hypothesis. Participants performed a tactile spatial discrimination task (Grating Orientation Task, GOT; Van Boven & Johnson, 1994) while viewing their own hand or an object. In addition an indirect EEG measure of intracortical inhibition was computed by recording somatosensory evoked potentials (SEPs) while either the index finger alone, the middle finger alone or both fingers were stimulated, under the two different visual contexts (viewing the hand or viewing the object). As already demonstrated in literature, the difference in amplitude between the arithmetic sum of potentials evoked by two individually stimulated fingers and the potentials evoked by simultaneous stimulation of two fingers is an index of the inhibitory interactions boosted when two adjacent skin regions (in this case, two adjacent fingers) are simultaneously stimulated (Gandevia et al., 1983; Ishibashi et al., 2000; Severens et al., 2010). Combination of the GOT with the indirect EEG measure of intracortical inhibition demonstrated that viewing the body modulates the somatosensory inhibitory network, enhancing tactile acuity. In fact, behavioral results showed an enhancement of tactile acuity when viewing the hand, compared to when viewing the object. As far as the electrophysiological results are concerned, early SEPs components (at 50 msec post-stimulus) showed an increase of intracortical inhibitory interactions produced by simultaneous stimulation of adjacent fingers when participants looked at their hand compared to an object. These results finally suggested a multisensory modulatory nature of the VET, where vision of the body seems to enhance the spatial sensitivity of touch by modulating the strength of inhibitory interactions in early somatosensory cortex.

A second less investigated aspect of the VET effect is its time-course. Multisensory interactions are highly temporally specific: feedforward convergent mechanisms require sensory information in different modalities to arrive within a narrow time-window in order for multisensory neurons to quickly integrate their various inputs (Stein et al., 1993; Avillac et al., 2007). A different class of multisensory effects, that does not result by a "real-time" integration between different sensory inputs, but rather emerges over a slightly longer timescale, involves multisensory contextual modulations (Bar, 2003; Gilbert and

Sigman, 2007) and neuroplastic changes (Zhou and Fuster, 1996; Shimojo and Shams, 2001).

In consideration of these two possible mechanisms it is worth to wonder whether the VET effect resembles fast mechanisms of feedforward multisensory integration operating over milliseconds, or slower mechanisms of modulatory and neuroplastic changes operating over minutes or hours. Experiment 2 was aimed at investigating the *timing* of the VET effect, by recording the EEG activity before and after brief (1 sec) views of one's hand or an object, in random order. Moreover, in order to have a behavioral measure of the VET, soon after vision of the hand or the object, participants were asked to perform a Grating Orientation Task as in the previous experiment. Results demonstrated that viewing the stimulated body part produced a rapid enhancement of tactile discrimination ability and also facilitated early somatosensory processing (P50 component) of stimulation at the viewed skin location, relative to viewing an object. In particular an early and quick enhancement of the P50 component was observed as soon as the body was seen.

Thus, the present results would suggest that VET might simply reflect feed-forward integration of simultaneous visual and tactile inputs from the same multisensory source. However, given previous data suggesting the VET as a long-lasting modulatory feedback exerted by vision of the body to SI (Taylor-Clarke et al., 2004; Serino and Haggard, 2010), this effect might consist in a *fast*, *short-term*, reversible modulatory influence of vision of the body, on the somatosensory system.

To summarize, these findings shed further light on the mechanisms underlying the VET effect, suggesting a fast, short-term reversible modulation of the intracortical inhibitory network as responsible for the enhancement of tactile acuity when viewing the stimulated body part.

Given the assumption that the VET involves a body representation, driven by vision of the stimulated body part, modulating tactile processing, a further investigation of the present dissertation was focused on the nature of such a mental body representation. Moreover, since the VET has been sometimes observed also when the seen body part belongs to someone else (Haggard, 2006; Thomas et al., 2006; Longo et al., 2008; Longo et al., 2009), one might ask how others' bodies are processed in relation to one's own. In other words, it might be interesting to clarify whether perception of the others depends on the same bodily representation driven when viewing one's body. By investigating the nature of the mental body representations when viewing one's own or someone else's body, one might study how these two visual contexts might modulate somatosensory processing, and what role such modulation might potentially play in social cognition.

Experiment 3 aimed to test this hypothesis. In particular, it tested which kinds of sensory information are required to drive a body representation able to modulate tactile processing, under the two different visual contexts. The recognition of one's body reflects the combination of simultaneous visual images, sensations arising from the skin, positional changes of the different body parts. Thus a possible suggestion is that the mental representation of one's body requires current sensory information to be integrated in order to build a coherent complex sense of the bodily self. In line with multisensory integration rules (Stein and Merdith, 1993), different sensory inputs must arise form the same spatial source in order to be treated as belonging to the same event and thus, to be integrated. Thus, in Experiment 3, it was hypothesised that only spatially aligned sensory information related to one's body might drive a bodily self-representation able to modulate tactile processing. Conversely, vision of someone else's body might be sufficient to drive a mental body representation allowing the occurrence of the VET. In fact, vision of someone else's body might signal the observer that a possible tactile state is going to be experienced by the seen body, promoting a simulation mechanism in the observer (Thomas et al., 2006). It is likely to think that the other body might be everywhere with respect to one's own body, in order to foster this simulation. In this respect, no spatial constraints in the position of the seen body, in relation to our stimulated body part, should be expected to affect the visual modulation of touch.

The role of congruent visuo-proprioceptive signals in driving a multisensory mental body representation, able to functionally modulate tactile processing, was addressed in Experiment 3. With this aim, participants were asked to perform a GOT on the finger - as in previous experiments - under vision of the image of one's own or of someone else's hand (or of an object, in the control condition), either spatially aligned or misaligned with one's own stimulated hand.

Results suggested that whereas in case of viewing one's body a VET effect was observed only when spatially aligned current visuo-proprioceptive inputs were provided, simply viewing another hand was sufficient to enhance tactile acuity, regardless of the position of that image with respect to one's own stimulated body part. In line with these findings, when visuo-proprioceptive inputs related to one's body were in spatial conflict, no facilitation of tactile processing when viewing one's hand was observed, relative to viewing an object.

Viewing the body seems to differently modulate tactile processing as a function of the identity of the seen body part. This might be related with the involvement of different mental body representations when viewing one's own or someone else's body. In particular, whereas vision of one's body seems to drive a multisensory bodily self-representation, viewing another person's body might activate a simply visual representation.

In line with these results, the importance of a clear distinction between the bodily self and the other bodies can be highlighted. *My* body and *your* body cannot be treated in the same way. Recognizing one's body as one's own plays a crucial adaptive role. Being aware of the bodily self provides information related to how the different body parts are currently in relation to each other, whether tactile stimuli are in contact with the body surface, whether any change in the visual appearance of my body is occurring. To be aware of one's body, thus of its physical changes and of its capabilities, plays a crucial role in using the body to adequately interact with the external world.

Recognizing a body, as belonging to someone else is important in a social perspective, since it might prepare the observer to perceive and understand any sensory state the other is going to experience. This would provide the observer important information to adequately interact with his interlocutor, by continuously adjusting one's own social behaviour.

The self/other distinction is relevant also in another multisensory mechanism that will be presented in the next paragraph: the Visual Remapping of Touch (VRT).

II. Visual Remapping of Touch

Tactile perception on a body part is enhanced when concurrently viewing the same body part being touched, compared to when it was seen not being touched (Serino et al., 2008; 2009). This effect has been recently investigated by showing a face being touched by human fingers and by manipulating the perceptual thresholds for an electrical stimulation on the participants' face. In the original study, participants were more accurate in detecting near-threshold electrical stimulations on the face, when concurrently viewing a face being touched compared to when the face was only approached by the fingers, i.e. the control condition (Serino et al., 2008). It has been shown that the effect is self-other specific, because it disappears if participants observe the picture of an object instead of a face. Moreover the effect is stronger when the other is perceived as similar to the self, and is maximum when observing touch on one's own face (Serino et al., 2008; 2009). Thus, although the mechanism is present both when viewing one's own and someone else's face, the behavioural effect is stronger for the self than for the other.

This effect, very well known at the behavioural level, has not hitherto been investigated at the neural level. In addition, given the similarity between the VET and the VRT mechanisms, comparing the activations when viewing the body being touched with those when viewing the body not being touched, might help in highlighting neural commonalities and neural differences between the two multisensory phenomena.

Experiment 5 presented an fMRI study investigating the neural underpinnings of the self-specific effect in the VRT. In this study it was hypothesised that viewing one's face being touched might drive either a multisensory or a semantic representation of the self as responsible for the self-specific modulation of tactile perception. In literature, several studies highlighted a network of fronto-parietal structures underlying a multisensory representation of one's own body (Ehrsson et al., 2005; Ehrsson, 2007; Tsakiris et al., 2007; Blanke and Metzinger, 2009), whereas different lines of evidence showed structures in the ventro-medial prefrontal cortex responsible for a semantic, conceptual representation of the self.

In Experiment 5, participants were scanned while receiving near-threshold electrical stimulations on the face and concurrently looking at videos showing, either their own face, another face or an object that could be touched or just approached bilaterally by two human fingers. Results demonstrated a specific modulation of the fronto-parietal network – encompassing both the ventro premotor (VPM) and the somatosensory cortices (SI/SII) - when viewing one's face being touched. Given that this network has extensively been thought as involved in integrating multisensory information pertaining to one's own body (Ehrsson et al., 2005; Gentile et al., 2011), these results suggested that viewing one's face being touched, while simultaneously receiving a tactile stimulation on the face, drives a multisensory bodily self-representation that projects to primary somatosensory regions, modulating tactile perception.

An interesting and unexpected result was that viewing one's face being touched evoked a *reduced* activity both in VPM and in the somatosensory areas relative to viewing one's own face not being touched and viewing another person's face and an object being touched. The strength of VPM activity might reflect the effort of integrating different modalities into a unique body representation; according to this view, VPM plays a specific role in embodying a non-body object, such as a rubber hand (Tsakiris et al., 2007). Thus, the higher activation of this area, in the case of viewing another person's face and an object being touched might reflect the effort in the embodying process, whereas viewing one's own face being touched facilitated embodiment and, as a consequence, less VPM activity was required. The reduced activity in VPM was also reflected to SI and SII.

In conclusion, it might be suggested that, in case of viewing one's face being touched, congruent current sensory signals from different modalities drive a coherent multisensory representation of one's own body, reducing the activity in the regions housing such representation, and enhancing tactile perception on the face. The importance of a multisensory bodily self representation, where congruent inputs converge, is perfectly in line with previously discussed data on the VET, where a facilitation of tactile acuity seemed to be present only when visuo-proprioceptive inputs related to one's hand were spatially coincident (Experiment 3).

The special role a multisensory bodily self-representation plays in modulating tactile processing has been further demonstrated in the present dissertation with Experiment 4. This experiment was aimed at testing whether the decreased tactile acuity due to a positional conflict related to one's hand – i.e. when the image of one's hand was misaligned with respect to the position of the actual stimulated hand (Experiment 3) - could be improved as the spatial gap between the two spatial reference frames is reduced. In other words, the experiment tested whether adding a third, new, meaningful information able to link the image of one's hand with one's own stimulated hand, the positional conflict might disappear. A possible solution was hypothesised to rely on the presence of a tactile event on the visual image of one's hand synchronous with the tactile stimulus delivered on the actual hand.

As previously showed, viewing touch towards one's body enhances tactile perception (Serino et al., 2008; 2009). This mechanism is thought to be underlie by a process whereby the seen touch is remapped onto the felt touch. In order to remap a sensation from one sensory modality to another - namely from vision to touch - the two modalities should share a common reference system. If the two reference systems are spatially separate, it is likely to suppose that the visuo-tactile remapping process might first link them and then treat the seen touch as if it would arise from the source of the felt touch.

Thus, participants in Experiment 4 were asked to look at a monitor located in front of them showing a moving depicting, in different trials, either their own hand, another hand or an object that could be touched or just approached by a cotton bud. As soon as the cotton bud reached the final step of its forward trajectory (thus as soon as it touched the finger of either one's or someone else's hand or the top of the object) a grating was applied on the participants' fingertip, running half along and half across the long axis of the finger. The results showed that discrimination of the grating orientation was enhanced both when viewing one's hand and the other hand being touched, compared to when viewing the object being touched. Conversely, when the cotton bud did not touch the images, the visual enhancement of tactile acuity occurred only when viewing the other hand.

The results suggested that vision of touch was able to reduce the positional conflict between the image of one's hand and the proprioceptive representation of the actual hand. As a consequence an improvement of tactile acuity when viewing one's hand was observed. In line with the suggested hypothesis, vision of touch towards one's hand seems able to link the separate reference frames - for the seen and the felt hand - thus allowing the image of the hand to be treated as the actual one. Thus, multisensory inputs related to one's hand (the visual, the proprioceptive and the tactile inputs) can be considered as arising from the same spatial source, allowing these signals to converge in a coherent multisensory representation of one's hand, finally able to modulate tactile processing. In contrast, when the cotton bud did not touch the image of one's hand no VET occurred.

This experimental evidence confirmed the multisensory nature of the bodily self-representation able to modulate tactile processing, as previously suggested in Experiment 3 and further confirmed by fMRI data.

III. Interaction between VET and VRT

Considering all the findings of the present studies it might be concluded that viewing one's own body quickly facilitates tactile perception on the seen body part, only when current multisensory signals related to that site arise from the same spatial source. In this case, different signals converge in a coherent representation of the stimulate body part, update this representation, that in turn, modulates tactile processing on the body. Conversely, when different inputs related to the same body part are in conflict, arising from different spatial sources, they are not able to drive a multisensory representation of the body, and no facilitatory modulation of tactile perception is observed.

An essential role in linking body-related information arising from different locations is the visual information pertaining to touch. Viewing a body part being touched and, simultaneously feeling a tactile stimulation on the corresponding site of one's own body, seems to link the reference frames of the different sensory modalities, thus allowing our brain to treat the multisensory inputs as all arising from the same location, i.e. one's own body. This remapping mechanism might be considered crucial to induce coherence in the representation of one's body when intersensory conflicts occur.

The multisensory bodily self-representation seems to be housed in the ventral premotor area, a well-known multisensory region recruited during interactions between different sensory information related to the body. This region, together with parietal areas, seems responsible for the self-related enhancement of tactile perception.

Thus VET and VRT do not seem to be unrelated visuo-tactile mechanisms, rather they seem to share a multisensory nature with different contributions of each sensory modality. Viewing one's own stimulated body part is able to drive a mental body representation modulating tactile perception, only when current signals related to that site are in spatial alignment. When they are in spatial conflict, visual information related to the tactile event seems to be required for updating the bodily representation, so that it can provide a correct interpretation of the tactile stimulus.

Different considerations apply to the relation between VET and VRT when viewing someone else's body is concerned. Viewing someone else's hand enhances tactile perception, regardless of the spatial location of their hand in relation to the participant's stimulated hand. This result suggests that no spatial constraints seem to affect the VET when viewing someone else's body. For this reason, in the present dissertation it was suggested that viewing another person's body might simply drive a visual bodily representation, sufficient to activate a simulation mechanism whereby one's sensory system is prepared to re-experience any tactile state on the other body. In line with this suggestion, Experiment 4 showed that both viewing touch and no touch towards someone else's hand did not differently modulate tactile processing, suggesting that multisensory correlation between seen touch towards another person's hand and felt touch on one's hand seemed not to add essential information to evoke a visual modulation of tactile acuity.

Viewing one's body allows the VET effect only when all current multisensory inputs are spatially aligned. When intersensory conflict prevents this condition, providing visual information about the tactile stimulus might allow a visuo-tactile remapping that facilitates an improvement of tactile perception on the seen stimulated body part.

Conversely, spatial constraints seem not to be involved in the occurrence of the VET when viewing someone else's body. In fact vision of another body part always boosts the VET effect.

IV. High order information modulates VRT mechanisms

Finally VRT cannot be considered a purely body-related visuo-tactile mechanism. Rather, it is involved in social interactions, since it might be a means to understand other peoples' feelings, by implicitly referring what is seen expressed on the bodies of others to one's own body. Experiments 6 and 7 addressed the issue of a possible interaction between the VRT and a key factor in face-to-face social relationships, the emotional content conveyed by a face, was addressed. If, as previously suggested, understanding a tactile state on the face of an observed person is important to modulate one's own social behavior towards that person, further social cues conveyed by the face might facilitate the visuo-tactile remapping. First of all, given the highly different social meanings expressed by positive and negative emotions, it was tested the hypothesis that viewing touch towards a face expressing either a positive or a negative emotion might differently affect the way we remap the seen touch onto the felt touch. The high social value of a positive emotion, such as happiness, seems to facilitate social relationships (Tsukiura and Cabeza, 2008) and thus, viewing a happy face might make the observer more prone to share the sensory experiences. Conversely, negative emotions, such as fear, signal potential threats in the environment, thus understanding what is happening to a frightened person might be useful in allowing to quickly plan defensive and avoidance reactions (Darwin, 1972; Ekman and Friesen, 1971; Chiao et al., 2008). Thus, the remapping of the seen touch towards a fearful face might be facilitated.

The results showed that the VRT interacted with negative emotions, in that viewing a fearful face being touched enhanced tactile perception on one's face relative to viewing a neutral or a happy face being touched. As a consequence it was further investigated whether, within negative emotions, fear plays a specific VRT modulatory effect or rather if this modulation might generalize to other negative emotions, such as anger. Since results showed a modulation of the VRT only when viewing a fearful face, it was suggested that recognition of different emotions differently interacts with one's own somatosensory system. This might have been selected through evolution as an adaptive behaviour, allowing to quickly recognize external potential sources of danger, by precociously activating one's sensory systems, in order to adjust adequate reactions.

Thus, when a mental representation of the body receives current low-level body-related sensory signals, it is able to exert modulatory effects on somatosensory areas, thus enhancing tactile perception. Sometimes, however, these modulatory effects seem to interact with high order information, such as emotional content of a face. This allows one's somatosensory system to adequately interact with emotion recognition mechanism allowing an adjusted behavioural response as a function of the social context we are currently interacting with.

Concluding Remarks

In conclusion, in the present dissertation the importance of a coherent multisensory representation of the body for accurate, rapid somatosensory processing has been discussed. The results presented, overall, demonstrated the existence of sophisticated multisensory mechanisms updating a coherent representation of the body in the space, and then modulating processing of current sensory signals arising from the skin. Thus spatially aligned signals from different modalities seem to converge in a multimodal representation of the body; further, feedback projections, from this representation, modulate the way we process tactile stimuli.

The body is also a good means to share experiences with the other people and to understand their states. Thus a conscious experience of one's body as belonging to oneself and as distinct from others plays an important role also in a social perspective: understanding other's feelings and emotional experiences might help in planning adequate behaviours in face-to-face interactions.

In this respect, recognition of a body part as one's own reflects the combination of multisensory spatially aligned signals from that site. Only when a coherent representation of one's body in the space is updated, a functional enhancement of tactile processing is observed. In contrast, recognition of a sensory experience as occurring on someone else's body reflects a simulation mechanism, whereby a modulation of tactile perception when viewing another person's body results from the remapping of the seen sensory state onto one's sensory system, in order to understand what the other is feeling.

Given results discussed in the present project, a final consideration might be done. The body is a complex multimodal ensemble but its constituent parts might be used for different aims. Hands, and arms are usually used to explore the environment thus enriching our knowledge about the external world. In contrast, the face is a key means to non-verbally express one’s own thoughts, feelings, and emotional states, and thus seems to play a crucial role in social interactions.

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Glossary

2AFC: Two-Alternative Forced Choice.
AHP: Anosognosia for Hemiparesis/Hemiplegia
BA: Brodmann Area
BMI: Bicuculline Methiotide
CMS: Cortical Midline Structures
D1: First Digit
DSO: Disturbed Sensation of limb Ownership
EBA: Extrastriate Body Area
EEG: Electroencephalography
EOG: Electroculogram
FFA: Fusiform Face Area
fMRI: Functional Magnetic Resonance Imaging
FO: Frontal Operculum
GABA: γ-Aminobutyric Acid
GOT: Grating Orientation Task
HEOG: Horizontal Electroculogram
IBR: Interpersonal Body Representation
IPS: Intraparietal Sulcus
IR: Interaction Ratio
LED: Light-Emitting Diode
LEPs: Laser-Evoked Potentials
MBR: Mental Body Representation
MNI: Montreal Neurological Institute
MPFCd: Dorso-Medial Prefrontal Cortex
2PDT: Two-Points Discrimination Task
PET: Positron Emission Tomography
PFA: Pictures of Facial Affect
PPC: Posterior Parietal Cortex
RF: Receptive Field
RHI: Rubber Hand Illusion
rOC: Right Occipital Cortex
rPPC: Right Posterior Parietal Cortex
rTMS: Repetitive Transcranial Magnetic Stimulation
rTPC: Right Temporoparietal Cortex
rTPJ: Right Temporoparietal Junction
SDT: Signal Detection Theory
SEFs: Somatosensory Evoked magnetic Fields
SEPs: Somatosensory Evoked Potentials
SI: Primary Somatosensory Cortex
SII: Secondary Somatosensory Cortex
SSI: Somatosensory Suppression Index
STS: Superior Temporal Sulcus
TMS: Transcranial Magnetic Stimulation
VEOG: Vertical Electroculogram
VET: Visual Enhancement of Touch
VIP: Ventral Intraparietal area
VRT: Visual Remapping of Touch
VPM: Ventral Premotor area