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MULTIPLE SPATIAL REPRESENTATIONS FOR HAPTIC PERCEPTION

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Estratto

Nella vita di tutti i giorni, il nostro corpo entra in contatto con stimolazioni tattili multiple provenienti dal mondo esterno. Come il nostro sistema somatosensoriale identifica e localizza questi stimoli multipli sulla nostra superficie corporea è il tema generale all'interno del quale si inquadrano le ricerche della presente tesi. Gli stimoli tattili sul nostro corpo, possono essere codificati e rappresentati spazialmente attraverso l'utilizzo di molteplici sistemi di riferimento. All'inizio il tocco è codificato in uno spazio sensoriale (sensory-space) basato sulla mappa somatotopica, successivamente livelli superiori di elaborazione si occupano di identificare spazialmente l'evento tattile in riferimento alla struttura complessiva del nostro corpo (body-space) ed al mondo esterno (external-space). Nel presente lavoro abbiamo svolto da una parte una serie di esperimenti comportamentali volti a verificare quali sistemi di rappresentazione spaziale siano utilizzati in un contesto di doppia stimolazione tattile simultanea (DSS). Dall'altra, attraverso l'utilizzo della risonanza magnetica funzionale (fMRI), abbiamo cercato di delineare quali siano le basi neurali dei processi cognitivi sottostanti l'elaborazione e la rappresentazione spaziale di stimoli tattili presentati alle dita in successione. In un primo studio comportamentale, utilizzando il paradigma di DSS, abbiamo definito il codice di codifica utilizzato in maniera preponderante, quando stimoli tattili sono presentati su dita differenti (i.e., intra- vs. inter-mano) con le mani poste in diverse posture (mani con palmo verso il basso vs. mano ruotata). Successivamente, in un secondo lavoro abbiamo testato l'influenza della visione (es., visione delle mani) e dei conflitti di natura visuo-propriocettiva sulla rappresentazione spaziale del tocco. Siamo passati poi ad indagare il ruolo giocato da un cambiamento a livello visivo della struttura morfologica della mano nella rappresentazione dello stimolo tattile. Infine, tramite l'utilizzo di un paradigma di fMRI adaptation con stimolazione tattile alle dita, abbiamo cercato di definire le basi neurali della percezione tattile durante un contesto di stimolazione ripetuta. In particolare, abbiamo verificato come interagiscono fra loro stimoli tattili localizzati su parti del corpo lontane in termini di struttura dello corpo (es., indice sinistro e destro), ma vicine in termini di rappresentazioni neurali (per effetto di alcuni aspetti bilaterali delle rappresentazioni somatotopiche).

Parole chiave: sensazione tattile, sistemi di riferimento, ricodifica spaziale, doppia stimolazione simultanea (DSS), estinzione tattile, Visual Enhancement of Touch (VET), propriocezione, morphing visivo del corpo, fMRI adaptation

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Abstract

In everyday life, our body gets in contact with multiple tactile stimuli from the outside world. How our somatosensory system identifies and localises these multiple stimuli entering in contact with our body surface, is the general framework to which the researches of the present thesis belong. Tactile stimuli on our body can be spatially coded and represented by using multiple reference frames. Touch is initially encoded into a sensory-space within primary somatosensory map and then further stages of processing can represent the location of tactile event with respect to the overall body structure (body-space) or to the outside world (external-space). In the present thesis we report first a series of behavioural experiments aimed at investigating which spatial reference frame is adopted in a special context of sensory stimulation, namely the double simultaneous stimulation (DSS). Then, we used functional magnetic resonance (fMRI) as a tool for delineating the neural bases of the cognitive processes sub-serving the elaboration and representation of concurrent stimuli for conscious tactile perception. In a first behavioural study using the tactile DSS paradigm, we defined the spatial coding used by observers when tactile stimuli are delivered with different fingers combinations (i.e., within vs. between hands) and hand postures (i.e., hands palm-down vs. palm-up). In a second behavioural work we tested the influence of different visual modulations (e.g., seeing body parts or objects) and visual-proprioceptive conflict (e.g., seeing body parts in a different position with respect to one adopted by the participant) on the spatial representation of touch. Furthermore, we investigated the effect of changes to the visual structural morphology of a body part on the spatial representation of touch. Finally, using a fMRI adaptation paradigm for touches at the fingers, we aimed to define the neural bases of tactile perception in a repeated stimulations context. In particular, we assessed the mutual interaction between tactile stimuli located at body parts that are clearly distinct in terms of the body-space (e.g., left and right index fingers), but proximal in terms of neural representations (due to some bilateral responses of the somatosensory cortices).

Keywords: touch, reference frames, spatial re-coding, double simultaneous stimulation (DSS), tactile extinction (TE), Visual Enhancement of Touch (VET), proprioception, visual body-morphing, fMRI adaptation

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1 Introduction

In the last decades an increasing amount of researches have investigated the multiple spatial representations in which sensory stimuli can be coded in the brain (e.g., Aglioti, Smania & Peru, 1999; Avillac, Denève, Olivier, Pouget & Duhamel, 2005; Colby, 1998; Kappers, 2004). We code sensory stimuli coming from the external world using multiple reference frames, based on egocentric coordinate systems that are eye-centered, head-centered, or arm-centered. In addition, allocentric reference frames can also be adopted in object- or external- space coordinates. These multiple coding endow our brain with remarkably flexible representations for acting in the environment (Colby & Duhamel, 1996). At the same time they pose constant computational challenges for our spatial perception. For instance, if we look towards our hand and we rotate it (e.g., palm-down vs. palm-up) our retinal coordinates remain constants, while the hand-centered coordinates are radically changed. In the same way, if we keep our hand in front of us but move the eyes to fixate a point to the left or to the right with respect to the hand, we change the eye-centered coordinates of the hand, while the body-centered coordinates are kept constants (i.e., hand is in the same position with respect to the body). When this issue is considered across sensory modalities it complicates even further. Different sensory modalities code stimuli in space according to different reference frames, in the respective primary sensory brain areas. However, in associative brain areas coherent representations of the stimuli in space are obtained (for a review see Gross & Graziano, 1995). The theoretical

framework for the present thesis is precisely this multiplicity of spatial representations in the specific context of tactile perception.

In the tactile modality stimuli can be represented using multiple spatial coding as a function of task demands (e.g., Serino & Haggard, 2009). These different coding likely occur at different stages of the information process. A low level representation is the well known somatotopic map in primary somatosensory cortex (SI) (Disbrow, Roberts & Krubitzer, 2000; Krubitzer, 2000; Kurth, Villringer, Mackert, Schwiemann, Braun, Curio, Villringer & Wolf, 1998; Penfield & Rasmussen, 1950), whereas higher representational stages are those based on body-parts coordinates, such as the head or the hands (e.g., Schicke & Röder, 2006), or on the overall structural representation of the body. Finally, the structural representation of the body has to be linked with coordinates in external space for us to determine where in the environment was the even that come into contact with our body (e.g., Azañón & Soto-Faraco, 2008; Maravita, 2006). Whenever we code a tactile stimulus on the skin one of these reference frames win likely dominate (i.e., it will receive higher relative weighting) when we detect, identify or localize tactile stimuli on our body surface and in the environment.

As we can easily observe from everyday life experience the different sensory modalities constantly work together to create a coherent representation of the external environment. Single sensory system functioning alone cannot represent the incredible richness of the outside world. In the contest of present work, it is thus important to emphasise that the

representation of tactile stimuli on our body surface can largely be influenced by information from the visual modality. For instance, looking at the body part where a tactile event occurs can modulate performance in the tactile task, likely affecting early representational stage of the elaboration process (Taylor-Clarke, Kennett & Haggard, 2002). This inter-modal interaction, between vision and touch has been named visual enhancement of touch (VET; Tipper, Lloyd, Shorland, Dancer, Howard & McGlone, 1998). The peculiarity of this effect is that it occurs even when the visual input is completely non-informative and therefore unnecessary for tactile stimulus coding (e.g., Kennett, Taylor-Clarke & Haggard, 2001). A number of other paradigms and effects have now documented interaction between tactile, visual and proprioceptive input in the spatial coding of touch (for reviews see Macaluso, 2006; Macaluso & Driver, 2005; Dijkerman & de Haan, 2007; Driver & Noesselt, 2008; Pears & Jackson, 2004; Spence, Pavani, Maravita & Holmes, 2004).

This introductory chapter of the thesis will contain a brief overview of the literature regarding the multiple spatial representation of touch, the multisensory nature of these representations with particular reference to the role of vision on coding of touch, and finally a brief account of the neuropsychological evidence supporting this fractionation of spatial representational stages in the human cognitive system.

1.1   Multiple spatial representation for touch

The most basic spatial representation of touch in our brain is the one available in primary somatosensory cortex, which contains a topographic representation of the skin surface (e.g., Blankenburg et al., 2003; Penfield & Rasmussen, 1950). At this primary level of spatial coding, however, the body is not categorically differentiated into parts (de Vignemont Tsakiris & Haggard, 2006) and the spatial relationships between body-parts differ with respect to the actual organisation of the body. For instance, hand and face are proximal in primary somatosensory cortex, but distant in terms of body space (e.g., Farnè, Roy, Giraux, Dubernard & Sirigu, 2002). Furthermore, the relative size of body parts is distorted in the somatotopic map. For instance, fingers and face are highly represented in the cortex when compared to other body parts like elbows or thighs (Penfield & Rasmussen, 1950). Because of this relative distortion in the cortical representation, fingers and face are magnificated and the extent of this sovra representation is termed "magnification factor" (Sur, Merzenich & Kaas, 1980). Therefore we have a somatotopic disproportion in the sensory homunculus for the hands, directly proportional to the receptors number on the skin. The cortex dimension for the different part of the body are directly proportional to afferent sensory projection density, and also to the importance of sensory input received from the specific body areas (Sur et al., 1980). Finally, at this representational stage even the distinction which body side is stimulated may be difficult. Although the primary somatosensory cortex is generally assumed to receive inputs only

from the controlateral body side, stimulations from ipsilateral body parts can also reach this sensory region. Interactions between body sides at this level of body representation have been documented by neurophysiological studies in Brodmann area 2 of the monkey (Iwamura, Taoka & Iriki, 2001; Iwamura, Tanaka, Iriki, Taoka & Toda, 2002), and they likely originate from direct projections from the thalamus as well as trans-callosal connections between homologous regions in the two hemispheres (Killackey, Gould, Cusick, Pons & Kaas, 1983). At the behavioural level, interaction between body sides have also been documented in a number of tactile tasks. For instance, errors in tactile localisation at the hands in humans is affected both by stimulation of adjacent fingers of the same hand (Schweizer, Braun, Fromm, Wilms & Birbaumer, 2001) and by concurrent stimulation on the opposite hand (Braun, Hess, Burkhardt, Wühle & Preissl, 2005).

Higher level of representation for touch are obtained when the spatial coding of touch takes into account the overall structure of the body (i.e., where was the tactile stimulation on the body). This higher-order spatial representation has been termed 'body space' (de Vignemont et al., 2006) or 'Mental Body Representation' (Serino & Haggard, 2009). Moreover, a intermediate representation between SI and the MBRs, representing different body parts and the relation between them, as been proposed (Rusconi, Gonzaga, Adriani, Braun & Haggard, 2009). This stage has been named Body Structural Representations (BSRs) and has some particular properties. For instance, it represents the body parts and the relationship between the

number and the order of the fingers on the hand. Moreover, BSRs seems to be stable along time, independent of the postural changes and present even when the body is not stimulated. Furthermore, spatial coding of touch can also occur with respect to the external environment (i.e., where the tactile event was in external space; for reviews see Holmes & Spence, 2004; and Maravita, 2006). During our dynamic interactions with the environment, the body assumes many different postures depending on the behavioural demands. To map tactile stimuli with respect to the external space our brain needs to take into account where the touch was on the body, and where the body was in space. The time course for this remapping has recently been documented by Azañón and Soto-Faraco (2008) who showed that an unconscious image of the tactile sensation in somatosensory space prevails until 60 ms after stimulus onset. By contrast, a representation of tactile sensation in external space is consolidated in the interval ranging from 180 to 360 ms after stimulus onset.

Recently, Serino & Haggard (2009), proposed a functional model suggesting the main nodes and pathways involved in the representation of tactile stimuli detected on the body surface (see Figure 1). The authors first describe the information flow from the external environment to the primary somatosensory cortex (SI), then hypothesise the existence of abstract mental body representations (MBRs). A final stage referred to the external object representations is also considered.
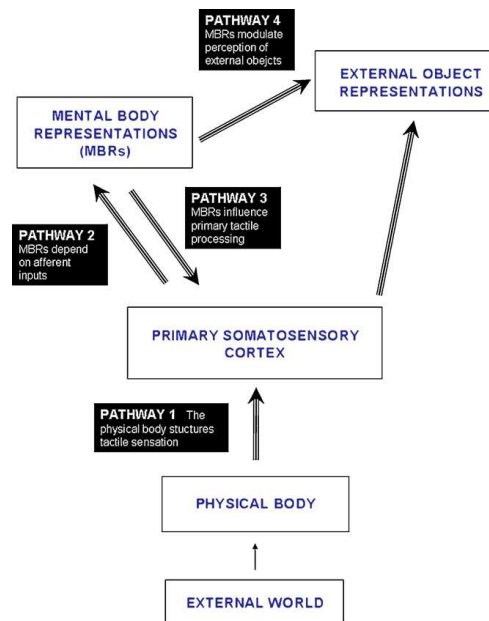
Figure 1: Analytic model of the relation between touch and the body proposed by Serino & Haggard (2009).

In their model the authors suggest that the different nodes are connected with one another through mainly unilateral information flow, even though feedback from MBRs to SI are also expected. As argued above, SI contains a spatial representation that follow the organization of the somatotopic map of the body surface. The mental body representations is defined as additional brain areas that contain an abstract representation of the body derived from sensory input, but it can be dissociated from it (body image and body schema are considered both part of this stage). In addition, this representation is considered a multimodal rather than a unimodal processing stage, in which the actual state with respect to the dynamic nature of the body is represented and feedback projections to the primary somatosensory representation are

possible. Finally, MBRs can also influence upper areas for perception of objects in the external space (external object representations).

1.2   Visuo/tactile interaction in the spatial coding of touch

Multisensory integration allows our brain to create a coherent and rich representation of the external environment (Calvert, Spence & Stein, 2004; Stein & Meredith, 1993). Different sensory modalities, such as vision and touch reciprocally, interact even when the task can in principle be solved using one sensory system in isolation. Recently, a great amount of studies have investigated the role played by vision on touch perception (e.g., Botvinick & Cohen, 1998; Ernst & Banks, 2002; Folegatti , de Vignemont, Pavani, Rossetti & Farnè, 2009; Honma, Koyama & Osada, 2009; Làdavas & Farnè, 2004; Macaluso & Driver, 2005; Macaluso & Maravita, 2009; Mancini, Bricolo & Vallar, 2009; Pavani, Spence & Driver, 2000; Serino & Haggard, 2009).

A classical phenomenon of this type of interaction is "visual enhancement of touch" (VET), in which non-informative vision of a body part results in responses to touch that are faster with respect to when the visual information is absent (e.g., Tipper, Lloyd, Shorland, Dancer, Howard & McGlone, 1998), and because even faster for familiar body parts (Tipper, Phillips, Dancer, Lloyd, Howard & McGlone, 2001). In addition, enhancement of tactile acuity have also been documented (Kennett, Taylor-Clarke & Haggard, 2001). In the

first work documenting this phenomenon Tipper and colleagues (1998) used a simple detection task and showed that mere vision of a body part (i.e., without proprioception) can influence tactile perception. In their work they asked three separate groups of observers to detect as fast as possible a predefined target vibration delivered to the thenar muscle (i.e., base of the thumbs) of each participant's hand under three different visual conditions. One group looked at a video in front of them where, depending of the experimental trial, their own right or left hand, was projected (vision without proprioception). The second participant's group were instructed to orient their head and eyes towards one of the two own hands occluded from view (proprioception without vision). Finally, the last participants' group did a task identical to the previous one with the only exception that they also viewed their hands (vision plus proprioception). The authors found that responses were faster when participants looked at their own hands and, more important, that vision alone was sufficient to produce there faster responses to the tactile stimulation (Tipper et al., 1998). Kennett and colleagues (2001) tested two-point tactile discrimination thresholds (2PDTs) on the forearm, while modulating visual input by presenting conditions in which the arm was visible or, instead, a neutral object (i.e., cylinder) was visible. Tactile spatial resolution was better when the arm was seen and even better when it was magnified in size. By contrast, performance was not improved when the neutral object was shown. The authors interpreted this result as direct demonstration that vision can improve tactile acuity (Kennett et al., 2001). A

possible explanation proposed by the authors is that feedback modulation to unimodal areas from multimodal areas (e.g., posterior parietal cortex, where there are neurons that respond both at visual an tactile stimuli, Graziano, Yap, & Gross, 1994), can pre-activate the somatosensory cortex, thus resulting in enhanced tactile discrimination. Taylor-Clarke and colleagues (2002) using the same paradigm (2PDTs) found a modulation of the somatosensory cortex activity by vision of the arm, as measured by event-related encephalography. When a visual input (i.e., participant's own arm) was presented, a modulation of the cortical activity in the somatosensory cortex was registered using somatosensory event-related potentials (ERPs) (Taylor-Clarke et al., 2002). In a further work Press, Taylor-Clarke, Kennett and Haggard (2004) tested VET while participants perform different tactile tasks: detection or discrimination, with or without spatial components. These experiments were done in order to verify whether the VET effect described in previous experiments was a generic effect on tactile perception or it occurred just under specific spatial conditions and task demand. What they found is that visual enhancement of touch was present only for difficult discrimination task that included spatial components. In the difficult discrimination task two tappers were applied on the left forearm in a spatial separation close to the 2PDT. Participants were instructed to discriminate the activated tapper (one was silent), far and near with respect to the elbow, as fast as possible. Response was given by pressing two keys with the right hand. Only task with those specific characteristics (i.e., difficult discrimination and spatial components) showed better

performance when participants saw their own arm with respect to when they saw an object. The authors attributed this effect to a feedback signal from multimodal to somatosensory areas that modify tactile receptive fields size (RFs), decreasing their dimension and improving spatial sensitivity. On the contrary, when participants performed an easy spatial discrimination task or a difficult non spatial discrimination task, there was a decrement in performance in viewing the arm with respect to viewing an object. No specific explanation about this last result was provided by the authors (Press et al., 2004). Interestingly, Serino and colleagues (2007) tested brain damage patients and found that visual enhancement of touch was present only in subjects with poor tactile acuity. This evidence has been interpreted as an intervention of visual input when the tactile domain is not sufficiently efficient in solving a specific spatial task (Serino, Farnè, Rinaldesi, Haggard & Làdavas, 2007). Furthermore, evidences for modulation of RFs size in primary somatosensory cortex by visual input has been recently documented, both behaviourally (Haggard, Christakou & Serino, 2007) and by using the transcranial magnetic stimulation (TMS) technique (Fiorio & Haggard, 2005). Haggard and colleagues (2007) used vibrotactile maskers presented with orthogonal arrangement with respect to the tactile target in a close or far spatial proximity on the participant's forearm. Participants were instructed to perform two-alternative forced choice (2AFC) spatial discriminations to localize the targets as proximal (i.e., closer to elbow) or distal (i.e., closer to hand). The rationale of the study was that maskers can influence the spatial

representation of the target only if they fall into their RFs. The authors found that viewing the body made far maskers less effective, while made near maskers more effective. This result has been taken as evidence that tactile receptive fields size was reduced when participants viewed the body (Haggard et al., 2007). A parallel line of research showed that application of a single-pulse TMS over SI, but not over SII, produced a suppression of the VET effect (Fiorio & Haggard, 2005). Additional evidences that VET may come at the SI level are provided by a recent work by Serino, Padiglioni, Haggard and Làdavas (2009), in which the authors tested whether VET can spread from body parts which are adjacent in terms of somatotopy. They verified that VET can indeed extend from one body part (i.e., hand) to another (i.e., cheek), but this spreading occurs only between parts that are close represented in the somatotopic map (i.e., cheek and hand, but not hand and foot).

In summary, studies on VET suggest a modulation of a non-informative visual input on the perception of a pure tactile stimulus. This modulation is unlikely to reflect an effect of spatial attention, because in the typical control condition of the VET studies participants see an object instead of a body part, but both kept in the same spatial position. Consequently attention is always overtly fixed to the same locus. In addition, the effect is not related to a particular visual information as all the studies refer to a non-informative visual input, therefore cross-modal integration of specific cues cannot explain the effect. As we described above, VET seems to derived from a top-down modulation coming from multimodal areas towards the primary

somatosensory cortex. These projections could affect touch by modulating the relative dimension of the tactile receptive fields of the stimulated body part (Serino & Haggard, 2009).

Some authors have recently proposed that VET could derive, at least in part, from a response bias boosting the propensity to respond when a body part, instead of an object, is seen (Johnson, Burton & Ro, 2006). Johnson and colleagues tested systematically this account in a series of experiments on the influence of a light on a finger on tactile perception at that same finger. Data were analysed by using Signal Detection Theory (SDT: Macmillan & Creelman, 1991) and showed an increase in the near-threshold tactile perception level. However, a shift in the response bias was also documented, when touch and visual stimuli were simultaneously presented. Participants were more prone to respond (i.e., less conservative) when tactile an visual stimuli were both presents. This bias has been interpreted as a possible consequence of multisensory experience that occur in the interaction with the external environment. Sensory information available from the external world, is synchronised in space and time the majority of the time when it originates from the same object (Johnson et al., 2006). Since the majority of work on VET did not used SDT procedure for analysing the data (e.g., Kennett et al., 2001) it is possible that some VET finding could reflect a shift in the response criterion. However, some study that reported VET used the two alternative forced-choice paradigm (e.g., Taylor-Clarke, Kennett & Haggard, 2004), which is intrinsically free of response bias (because a bias should make performance

close to chance level; Longo, Cardozo & Haggard, 2009). In summary, a shift in the criterion can partially explain the performance change in the visual enhancement of touch, but cannot completely account for this effect.

In the present section we described the VET in details as one of the effect resulting from visuo-tactile interaction. However, in literature there are many others phenomenon that documented multisensory effect on tactile perception (e.g., Calvert, Spence & Stein, 2004; Maravita & Iriki, 2004). For instance the rubber hand illusion (e.g, Folegatti et al., 2009), in which a visual proprioceptive conflict affects touch performance, or influence of auditory inputs on touch (e.g., Soto-Faraco & Deco, 2009). Conscious of the large amount of visual effects on touch, here, we primarily described VET effect because some of our studies mainly focused on the effects of visual inputs related to body parts on tactile spatial representation processing.

1.3   Spatial representation of touch in neuropsychological patients

A series of effects, derived particularly from neuropsychological conditions, revealed how different representational level can be used for spatial coding of touch on the body. These types of phenomenon includes, for instance, tactile extinction (patients that extinguish contralesional tactile stimulation during concurrent bilateral stimulation: e.g., Moscovitch and Behrmann, 1994), synchiria (patients with unilateral brain damaged that report to perceive bilateral sensation after unilateral stimulation: e.g., Medina

& Rapp, 2008) or finger agnosia (patients that make errors in identifying which finger is stimulated: e.g., Kinsbourne & Warrington, 1962).

Tactile extinction is a condition in which unilateral brain damaged patients fail to report a controlesional touch when this is presented together with an ipsilateral one (Bender, 1952). Moscovitch and Behrmann (1994) tested tactile extinction in 10 right brain-damaged patients, by delivering double simultaneous touches to the opposite side of the wrist of the right or left hand, when the hands were palm-down or palm-up. Regardless of hands posture the missed tactile stimulus was systematically the one that occupied the leftmost location in external space (see Figure 2A panel "c"). These results demonstrate that patients coded tactile stimuli using a representational stage at an high level of tactile information processing. Indeed, if patients would code stimuli using a reference frame based on a lower stage of spatial representation processing (e.g., somatotopic map), they should extinguish the stimulus on the same region of the skin regardless of the hands posture in external space. This finding is compatible with the results of a recent fMRI study showing that primary somatosensory cortex is always activated bilaterally in a right brain-damaged patient showing tactile extinction, suggesting that the competition leading to extinction occurs after the afferent tactile stimuli are processed by the primary somatosensory cortex (Beversdorf, Hughes & Heilman, 2008). Moreover, Valenza and colleagues (2004) found that patients with right parietal brain damage and visual neglect extinguished a tactile stimulus on the ipsilesional hand when the hand was

positioned in the contralesional (affected) hemispace, and a concurrent stimulation occurred on the elbow. On the contrary, extinction was not present when the same hand was positioned in the ipsilesional hemispace (see Figure 2B for the experimental set-up). The same test was repeated using functional magnetic resonance (fMRI), with the purpose of defining the neural bases of this spatial modulation of extinction. The authors found that when the right hand was positioned in the contralesional hemispace, there was a reduction in the blood-oxygenation level dependent (BOLD) responses to tactile stimuli in the primary somatosensory cortex of the intact hemisphere (Valenza, Seghier, Schwartz, Lazeyras & Vuilleumier, 2004). This finding was considered by the authors evidence that limb position affect elaboration process occurring at the level of the primary somatosensory cortex. Thus, considering these studies it seems not completely clear if the neural correlates of tactile extinction derive fully from higher stages of spatial representation processing or instead low stages can be partially responsible for the effect. Furthermore, a single-case electrophysiological study on a patient with right hemisphere brain damage showing tactile extinction revealed neuronal activity in the somatosensory cortex of the impaired hemisphere (Eimer, Maravita, Van Velzen, Husain & Driver, 2002). The authors suggested that this result is an evidence of residual unconscious processing of extinguished tactile stimulation. Moreover, the same activity has been registered in the injured hemisphere also with unilateral stimulation, even though attenuated with respect to the unimpaired hemisphere (Eimer et al., 2002). Thus, tactile

extinction can be related not to elimination of a sensory stimulus, but only to an attenuation of the brain response of it.
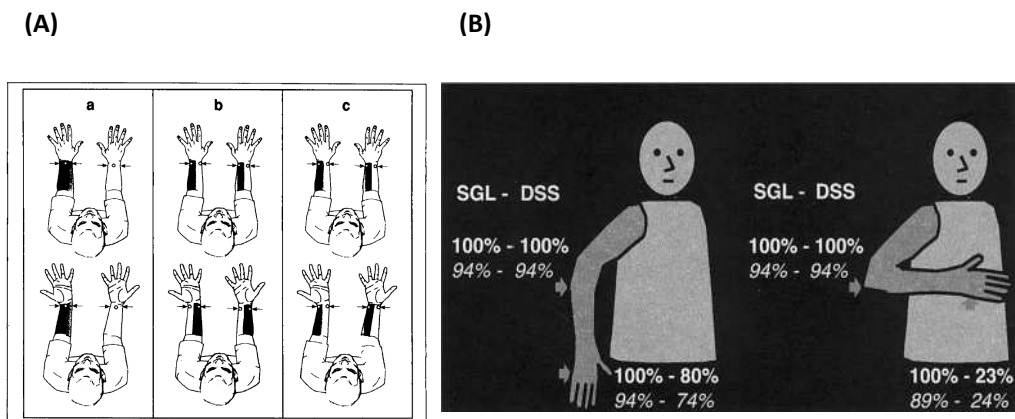
(A)   **(B)**

Figure 2. Experimental conditions with different postures assumed by the participants in Moscovitch and Behrmann (1994) (panel A) and Valenza and colleagues (2004) (panel B) studies.

Some patients with unilateral brain damaged report to perceive bilateral sensations after unilateral stimulation: a particular condition known as synchiria (Medina & Rapp, 2008). Medina and Rapp (2008) tested a patient with a left hemispheric brain damage and found that synchiria was affected by the position of the hand decreasing when the hand was moved from the contralesional to the ipsilasional hemispace in trunk- and head-centred coordinates. In addition, it was not present with crossed hands (Medina & Rapp, 2008). The authors suggested that these results imply the use of multiple stages in the spatial representation of the tactile stimuli. These two effects (i.e., extinction and synchiria), briefly described, gave opposite behavioural results (i.e., unprocessed or additional process of a tactile

stimulus at the level of awareness). However, both cases provide evidence about multiple representational stages involved in tactile stimuli perception. Indeed, both neurological conditions derived from a unilateral brain damage with patients that fail to report the correct perceptual experience. However, in extinction the deficit produce a suppression at the level of awareness of a stimulus that was physically present. Instead, in synchiria patients report to perceive two stimuli after single stimulation, experiencing an additional percept at the level of awareness, failing to represent at some stage of the information processing the correct perceptual sensory input.

Another deficit revealed in individuals with a selective brain damage is finger agnosia. In this neuropsychological condition patients with left parietal lobe damage are not able to clearly name which specific finger has been stimulated. This neurological impairment cannot permit patients to separate identity of the fingers (Kinsbourne & Warrington, 1962). Recently, Rusconi and colleagues (2009) suggested that finger agnosia should be referred to a deficit in the connection between SI and the BSRs. Body structural representation is defined as a stage, of the elaboration process, where the body parts order (e.g., number of fingers) and their relationship are represented. Therefore, this stage is clearly differentiated from the representation present in the somatotopic map in SI (for more details on the BSRs see Rusconi et al., 2009).

All these neuropsychological evidences, that we have briefly described, highlight the fact that the spatial coding of touch on our body surface occurs

by the mediation of multiple spatial representational stages. Moreover, individuals with brain damages clearly show selective impairments at one or more of these representation stages of the tactile information processing.

2 Results

Considering the actual state of the art about spatial representation of touch, we performed a series of behavioural experiments to investigate which spatial reference frame is adopted in a special context of sensory stimulation, namely double simultaneous stimulation (DSS). This was investigated in details in Study 1 through posture manipulations, and examined in relation to the role of vision in Study 2. Moreover, we used a neuroimaging technique (fMRI) in order to delineate the main neural pathways sub-serving these representational processes in Study 3. This section will briefly summaries the methods and the results of the behavioural experiments and the preliminary data of the imaging study. An extended description of each study is available in section 3 of this Thesis.

2.1 Overview of the behavioural studies

2.1.1 Study 1: Spatial coding in a Double Simultaneous tactile Stimulation (DSS)

In this first study we adapted the double simultaneous tactile stimulations paradigm (DSS) for stimuli delivered within as well as between hands to examine the role of multiple body representations in spatial coding of touch. In addition, we investigated the relative contribution of the different spatial representation for touch by manipulating hands posture. Unlike previous tactile DSS studies, which mainly modified temporal and frequency aspects of

the target and the masker (e.g., Craig & Evans, 1995; Craig, 1982), in Study 1 we modulated the relative position of the stimuli on the fingers. In the first experiment, we used tactile stimuli at threshold level, with the hands always resting in the same position (i.e., both hands palm-down). In the second experiment, we used supra-threshold stimulation with hands assuming different spatial positions across blocks (i.e., one hand palm-down and one palm-up).

EXPERIMENT 1

A series of tactile stimuli at threshold level were delivered to the index and/or middle fingers by using four stimulators. We asked participants to detect whether a pre-specified target finger was tactually stimulated or not. Across blocks, the target finger was either the index or the middle finger of the right or left hand and it could be stimulated alone or together with a non-target finger. DSS stimulation was delivered within the same hand (e.g., Figure 2.1b) or between hands (e.g., Figure 2.1c). We expected that DSS would lead to slower and less sensitive detection of the target (i.e., tactile interference) with respect to the condition in which the target finger was stimulated alone. More critical for the issue of spatial coding of touch, our experimental set-up lead to substantially different predictions of interference pattern as a function of the adopted spatial code. If interference occurs in somatosensory space it should be maximal when target and non-target fingers belong to the same hand, because the non-target stimulation would activate

cortical territories in primary and secondary somatosensory cortices which can inhibit the adjacent territories activated by the target.
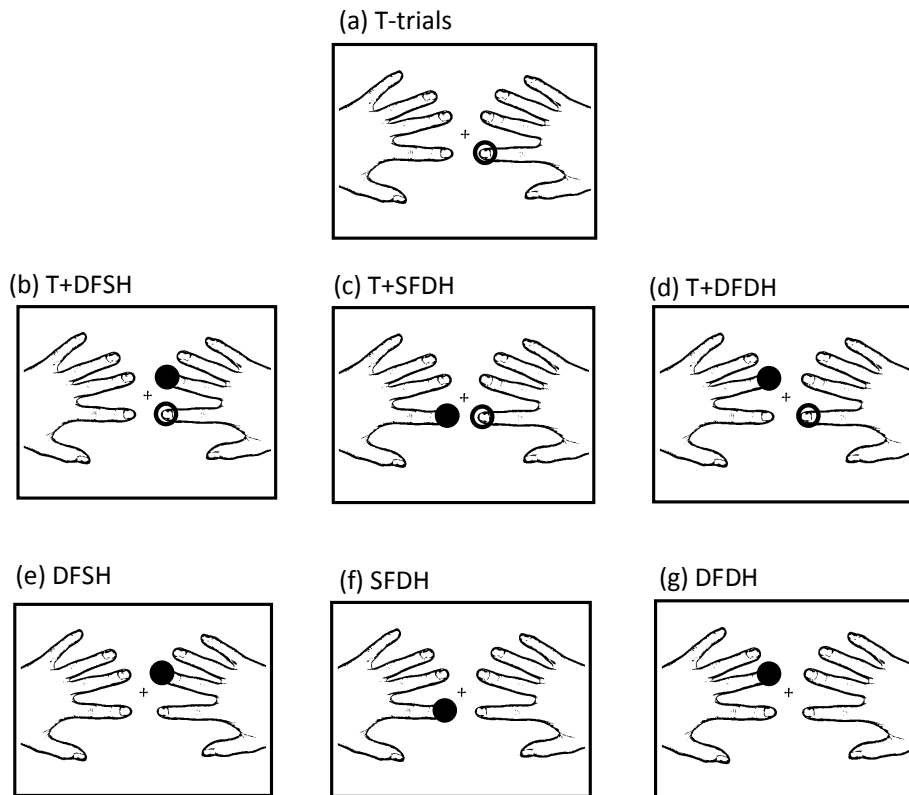

Figure 2.1. Schematic drawing of the experimental setup. Note that hands and tactile stimulators are shown here only for illustrative purposes, as they were in fact occluded under the horizontal computer display throughout the experiment.

In addition, because cortical territories neighbouring to the target can also be activated through inter-hemispheric transfer (Harris et al., 2001; Iwamura et al., 1994, 2001, 2002), substantial interference effects should also emerge when the non-target stimulation occurs at the finger of the other hand which is non-homologous with respect to the target. By contrast, a body space representation of touch should lead to strong tactile interference mainly within hands, with little or no tactile interference between hands. This

because filtering of irrelevant stimulation between hands should be easier whenever the target hand is clearly specified by a structural body representation.

Finally, if participants solve the task entirely based on the location of touches in external space, comparable interference should emerge when the non-target finger is on the same hand as the target or is the homologous finger of the other hand. This because distance in external space was identical in these two experimental conditions (see experimental set-up in Figure 2.2).
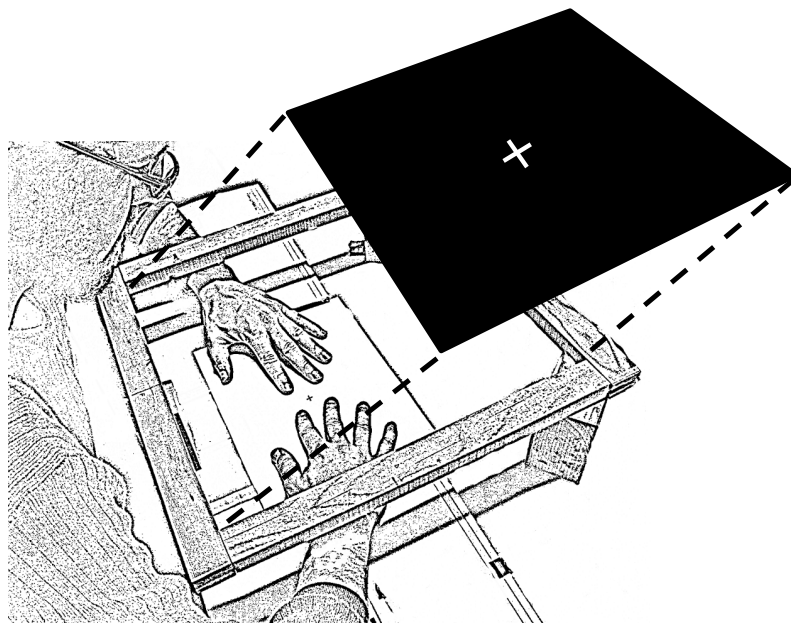

Figure 2.2. Schematic drawing of the experimental setup. Note that hands and tactile stimulators are shown here only for illustrative purposes, as they were in fact occluded under the horizontal computer display throughout the experiment.

Results and discussion

Results showed significant interference effects only in terms of reaction times and not for sensitivity. These were not affected by the specific pairings between target and non-target fingers, however, between-hands interference

effect in RTs were numerically smaller when the non-target finger was homologous to the target (T+SFDH) with respect to the other conditions. We speculated that one potential reason for the weak tactile interference documented in this first experiment was that tactile stimulators were not entirely reliable when driven at voltages closer to threshold levels. This could have produced an uncontrolled inter-finger variability and could have changed the stimulation ratio between the different target and non-target finger in DSS trials, making the between finger competition less effective. (This experiment was considered preliminary and is not reported in full in the extended manuscript of Study 1 that appears in Section 3).

EXPERIMENT 2

In this second experiment we made all tactile stimuli clearly supra-threshold. In addition, we examined the role of hands posture to assess the potential involvement of any spatial coding of touch beyond body representations. We asked participants to perform the same task of Experiment 1, adopting two different hand postures across blocks. In half of the blocks, both hands were palm down (as in Experiment 1). In the remaining blocks, one hand was palm down while the other hand was palm up (as shown in Figure 2.3, in which the hand rotated palm-up is shown as darker for illustrative purposes only).

The logic of this manipulation is the following: if any between-hand modulation of tactile interference would occur in somatosensory- or body-

space (rather than external-space), tactile interference should remain unchanged across hands posture. By contrast, if tactile interference operates on an external space reference frame it should change as a function of the adopted hands posture.
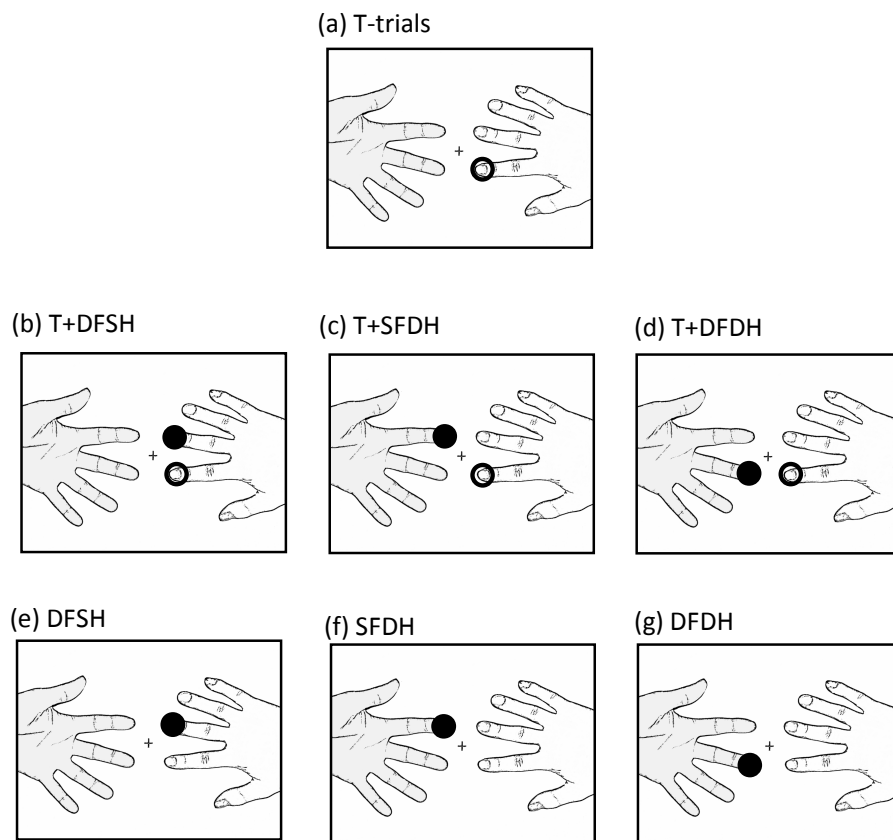

(a) T-trials

(b) T+DFSH (c) T+SFDH (d) T+DFDH

(e) DFSH (f) SFDH (g) DFDH

Figure 2.3. Example of the stimulation conditions with one hand palm-down and the other rotated palm-up, when the target finger is the right index finger. Unfilled circles indicate the stimulation at the target finger; filled black circles indicate stimulation at the non-target finger. a) target only trial; b-d) DSS trials; e-g) catch trials.

Results and discussion

The results of the present experiment revealed interference effects of DSS stimulation compared to target only trials. It emerged reliably with our clearly suprathreshold stimulation both in terms of sensitivity and RTs. This

predicted interference effect on sensitivity was manifest only within the same hand (see Figure 2.4). This pattern of results were confirmed by RTs that, in addition, showed interference also between hands, particularly for distractors delivered to fingers non-homologous with respect to the target (e.g., the left middle finger when the target was the right index). Importantly, these interference effects within and between hands were not modulated as a function of hand posture, supporting the notion that within and between interference effects may be solved at low stage of body representation. This interference is compatible with DSS competition occurring in somatotopic space, because at this low representational stage the differentiation between the two hands is less clearly defined and stimulation delivered to the non-homologous finger of the other hand can reach cortical territories ipsilateral to the target (Braun et al., 2005; Iwamura et al., 2001, 2002; Killackey et al., 1983).

The results of Experiment 2 also revealed an unexpected increase in tactile sensitivity that occurred between hands and was strictly dependant upon hand posture (see Figure 2.4). This effect emerged when the target finger was stimulated together with the homologous fingers of the other hand and both hands were palm down. Instead, it disappeared when either hand was rotated palm-up. This posture dependent modulation rules out the possibility that this increased tactile sensitivity emerged at a low representational stage. Instead, this phenomenon reveals the use of a spatial representation for touch which takes into account the overall structure of the body as well as its layout in space.
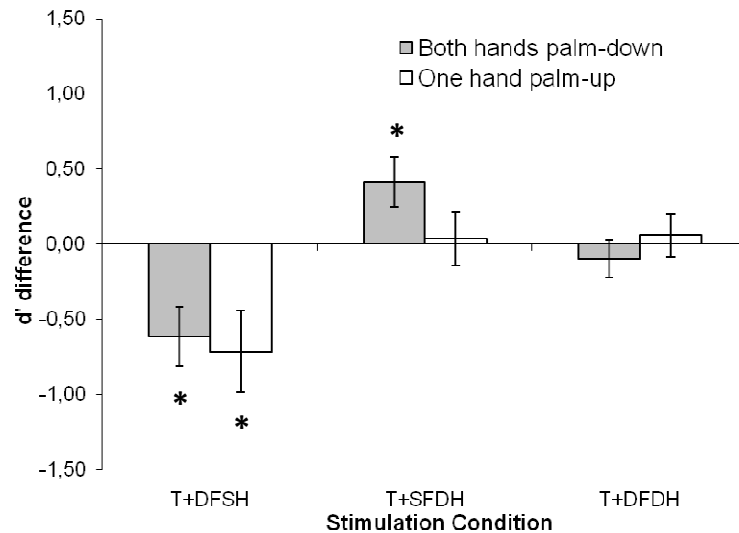
Figure 2.4. Sensitivity difference (d′ difference) computed by subtraction between single and DSS trials as a function of Stimulation Condition. Error bars represent the Standard Errors (SE). "T+DFSH" represent DSS trial in which target finger and the non-homologous finger of the same hand were stimulated, "T+SFDH" target finger and the homologous finger of the opposite hand with respect to the target were stimulated and "T+DFDH" represent the condition in which target finger and non-homologous finger of opposite hand were stimulated.

2.1.2   Study 2: Assessing the role of vision on tactile DSS

In this second study, we tested the sensitivity of tactile DSS paradigm with stimuli delivered within and between-hands to different levels of hand-related visual inputs (see Figure 2.5). In Experiment 1, we examined the role of seeing vs. not seeing the hands. In Experiment 2, we examined the role of a visual/proprioceptive conflict by showing images of participant's own hands that either matched or not matched their unseen hand posture. Finally, in Experiment 3 we introduced a novel manipulation of visual hand-morphing (i.e., merging of fingers), to determine whether different types of visual

structural distortions of the hands could affect the low level stage of the tactile
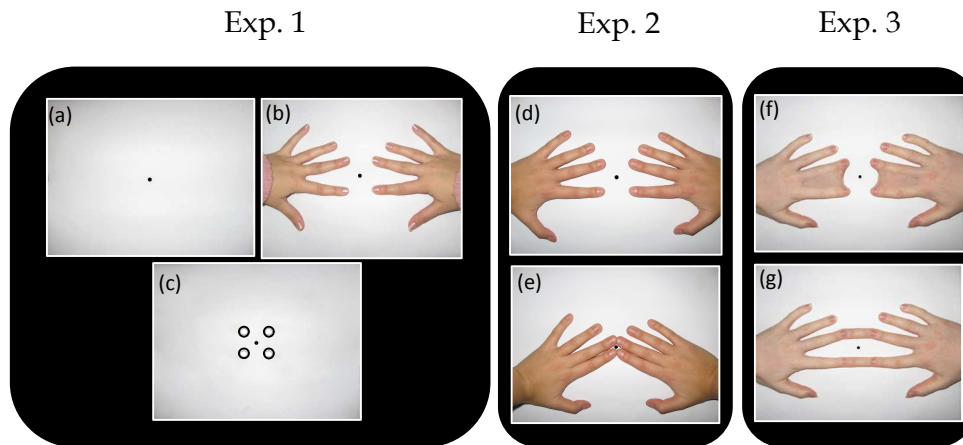
processing at which DSS interference occurs.

Figure 2.5. Illustrations of the possible Visual Conditions for Experiment 1, 2 and 3 are presented.

EXPERIMENT 1

The aim of the first experiment was to investigate whether vision of a body

part (i.e., participant's own hands) can modulates detection of a target tactile

stimulus presented with a concurrent non-target stimulation on another

finger (tactile DSS). Across blocks participants saw: 1) a fixation cross in the

middle of the screen; 2) an image of their <u>own</u> hands exactly reproducing the

fingers as positioned under the screen; 3) four empty circles, each vertically

aligned with the first phalanx of each fingers just below the screen. If vision of

a body part affect tactile perception under DSS type of interference, one

should expect better performance when the participant's own hands (see

Figure 2.5b), compared to circles (see Figure 2.5c), are displayed.

Participants performed a go/no-go task to detect whether a tactile stimulus was delivered to a pre-specified target finger (e.g., right index), which could be stimulated alone or simultaneously with a non-target finger, either on the same hand as the target (e.g., right middle finger), or on the other hand (at homologous or non-homologous finger with respect to the target finger; e.g., left index or left middle finger, respectively) (for the same type of methodology see Study 1 of the present thesis).

Results and discussion

The results showed reliable interference effect of DSS trials with respect to target only stimulations. Similar to our previous study (see Study 1 of the present thesis) significant tactile interference emerged for conditions in which the non-target finger stimulation was on the same hand as the target and also when it was on the non-homologous finger on the non-target hand. These findings imply, as we previously suggested, that DSS interference is driven by competition being solved at a relatively low stage of touch representation (Study 1). Also consistent with our previous work, we found that DSS interference was significantly reduced, if not absent, when homologous fingers across hands were stimulated (i.e., T and T+SFDH conditions did not differ).

Although interference effect in tactile domain was clear, vision of the hands did not affect tactile DSS performance. A significant enhancement of overall tactile sensitivity emerged when the circles, but not the subjects'

hands, were added to the visual scene. We suggest that this finding is compatible with the circles allowing for a better focusing of selective spatial attention on the spatial regions above which the tactile stimuli were delivered (Spence, Pavani & Driver, 2000). However, catch trials showed that mislocalisazation of single target within the same hand as the target was modulated by vision to some extent. Finally, examination of the criterion revealed a change in the participants responses tending to be more conservative in the tactile conditions that were more difficulties (i.e., when the distractor finger was the non-homologous finger of the same hand or the non-homologous finger of the opposite hand). In addition, we found a more liberal responses criterion when participants saw their own hands with respect to fixation only, possibly suggesting a tendency in favour of the 'go' response when a body part is seen (see Johnson et al., 2006).

Taken together these data suggest that, even though tactile DSS paradigm proved particularly sensible to low stage of tactile spatial representation processing, it seems not to be affected by VET.

EXPERIMENT 2

It is possible that the tactile interference reported under DSS in Experiment 1, although not sensitive to visual manipulation that would have improved performance, would still be worsened by conflicting visual-proprioceptive information. Indeed, while VET would have produced improvements in tactile behaviour, there are other ways through which vision

may affect touch perception, namely by hampering tactile performance (e.g., Folegatti et al, 2009). To test this possibility, in Experiment 2 we modulated the spatial congruency between the seen and felt hand posture. Participants were shown a visual scene in which their hands were positioned with fingers placed close to each others (see Figure 2.5e), thus creating a conflict between the visual and proprioceptive hand position (i.e., a visual-proprioceptive conflict). In another condition, participants' hands were visually displayed in a congruent position as the proprioceptive one (see Figure 2.5d). Note that the latter condition is identical to Experiment 1. If such a conflict between vision and proprioception is effective in modulating the tactile interference under DSS, one should expect better performance for intermodal congruent as compared to the incongruent and conflicting condition.

Methods were identical to Experiment 1, with the following exceptions. We changed the visual condition by adopting two different images of the participant's <u>own</u> hands with fingers placed at dissimilar positions (congruent vs. incongruent).

Results and discussion

Similar to Experiment 1 significant tactile interference emerged in terms of sensitivity, only for the conditions in which the non-target finger was stimulated on the same hand as the target and when it was the non-homologous finger of the other hand. Regarding of the RTs an interference effect was revealed, however, it was equally distributed across fingers.

We revealed also a general decrement of tactile sensitivity when we presented the incongruent hands image with respect to the congruent hands image. This visual effect can be referred to the spatial incompatibility between seen hands and the real ones, similarly to what has been reported recently by Folegatti and colleagues in a single detection task approach (Folegatti et al, 2009). However, similarly to Experiment 1, there was no significant modulation of the pattern of tactile interference effect (DSS trials conditions) by visual-proprioceptive incongruence. Finally, analysis on the criterion revealed a change in the participants responses, which tended to be more conservative in DSS trials with respect to Target only trials and more liberal when they saw their own hands in the congruent, as compared to the incongruent position.

EXPERIMENT 3

As we showed in Experiment 2, a visual/proprioceptive conflict can affect touch (see also Folegatti et al., 2009), but not DSS modulation. In this final experiment, we tried to alter visually the structural morphology of the body part from which proprioceptive information could be derived, to see if it can play a role in shaping the interference effects under DSS. To the best of our knowledge this is an entirely novel manipulation in literature on the influence of vision on touch perception. To this aim, in Experiment 3 we introduced visual changes in the structural morphology of the hands (i.e., intra- and inter-hands), by showing to the participants two conditions in

which their own hands seen were modified in their morphology (i.e., fingers webbed). A recent study provided evidence that real fingers webbing affect perception at a low stage of the information processing (e.g., Stavrinou, Della Penna, Pizzella, Torquati, Cianflone, Franciotti, Bezerianos, Romani & Rossini, 2006).

Methods were identical to Experiment 1 and 2, with the following exceptions. The first visual morphing condition was characterised by webbing index and middle finger of either hand (i.e., intra-hand morphing) (see Figure 6f). The second visual morphing condition was done exactly like the previous one except that in this case we merged the homologous fingers of either hands (left and right index fingers and left and right middle fingers) (i.e., inter-hands morphing) (see Figure 6g).

Results and discussion

Similar to the previous Experiments a cost for DSS trial with respect to single touch condition (interference effect) was revealed, confirming again the stability and constancy of our basic effect. Also the interference was strongly present at the intra-hand level and at the inter-hand level only for the non-homologous finger, following the exact same pattern described in the previous experiments. However, the visual structural morphing, did not affect tactile DSS or the grade of interference between fingers. Finally, data on the criterion revealed a change in the participants responses, who become more conservative in DSS trials with respect to single touch trials. However,

note that compared to the previous Experiments we did not find changes in the response criterion when participants saw their own hands with intra- or inter-hand morphing.

Overall conclusions from the behavioural studies

Taken together the behavioural experiments have shown that DSS stimulation can produce interference effects when stimuli are delivered both within and between hands. In addition, we documented an increase in target sensitivity during between-hand DSS at homologous fingers which may relate to a redundancy of spatial codes for the concurrent tactile events. Only the latter phenomenon was affected by changes in hand posture. In keeping with the notion that touch can be spatially coded in different frames of reference we suggested that tactile DSS interference is resolved at a low representational stage (somatotopic), whereas increased tactile sensitivity in this task relies on a higher representational stage which takes into account the layout of the body in space. This conclusion was further strengthened by our second behavioural study. Non-informative visual inputs about the stimulated body parts did not affect DSS tactile interference. Thus, the DSS paradigm seems to be largely immune to matching or conflicting vision from the stimulated body part, suggesting that DSS interference may occur within the somatosensory system, and possibly prior to any modulations of vision on touch perception.

2.2 Overview of imaging study

2.2.1 *Study 3: Neural correlates of tactile coding, an fMRI adaptation paradigm*

In the previous behavioural studies we examined how multiple spatial representation can serve tactile spatial coding of touch, in the special context of DSS. In the present work, we used an fMRI adaptation paradigm (for a review see Grill-Spector & Malach, 2001; Krekelberg, Boynton & van Wezel, 2005) to probe the possible neural basis of these multiple spatial coding. The adaptation effect is a typical physiological response of the neurons that results from the successive repetition of a feature to which neurons are selective. Following the logic of this physiological effect when two tactile events are repeated on exactly the same region of skin, all neurons that have a strictly somatotopic response should reduce their activity. These neurons should instead show no reduction of activity if the stimulation repeats over two distinct regions of skin. The crucial question, in relation to the issue of reference frames for touch, is whether some population of neurons in the brain can adapt to stimulation that repeats over distinct region of skin, when some other aspect of spatial coding is in fact identical. For instance when the repeated stimulation is delivered to homologous body parts (e.g., indexes of either hands). In that a case the region of the skin would differ, but the identity of the body part would stay the same. Our expectation is to find a different grade of fMRI adaptation to these finger pairing specifically in SI and SII. We expect that SI should mainly adapt when the stimulation repeats

over the same region of skin (i.e., same finger stimulated twice), because in this sensory area the dominant representation of touch should be primarily contralateral. By contrast, we predicted that SII could adapt to stimulation that repeats over the same finger (i.e., indexes of either hands), because in this sensory area bilateral representations of touch have been extensively documented (e.g., Blatow, Nennig, Durst, Sartor & Stippich, 2007).

We used the fMRI adaptation paradigm with two successive vibrotactile stimuli (see Figure 2.6) delivered to the first phalanx of the index and middle fingers of either hands. These produced four different finger pairs stimulation conditions: (1) Left index stimulated twice (Li – Li); (2) Left middle and index fingers (Lm – Li); (3) Right and left indexes (Ri – Li); Right middle and left index fingers (Rm – Li). The experiment consisted of 4 event-related fMRI adaptation scans. Participants were instructed to pay attention always to the left index finger throughout the experiment.
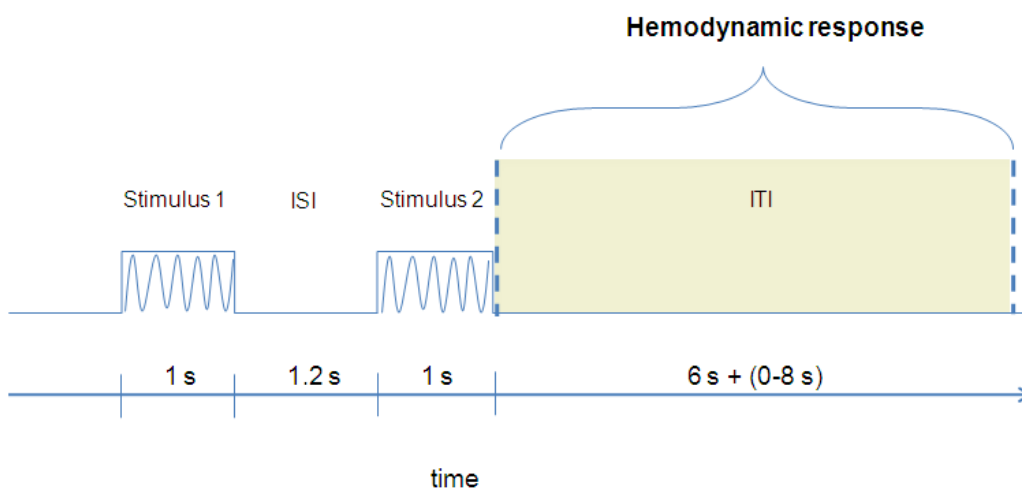

Figure 2.6. Schematic representation of the trial consisted of two vibrotactile stimulations lasting 1 s each with an inter-stimulus interval (ISI) of 1.2 s. After the double stimulation there was a variable interval between 6 and 14 s were we registered the hemodynamic response.

We calculated individual functional maps for each participant. Maps for the right and left hemisphere were functionally defined as all voxels that were significant in the omnibus test (fixed effects analysis; FFX) with four regressors corresponding to the experimental conditions (i.e., Li - Li, Lm - Li, Ri - Li, Rm - Li). On the resulting maps we identify four Patches of Interests (POIs), separately for each participant, consisting in the primary and secondary somatosensory cortex of both hemispheres on the basis of brain anatomy and functional response (see Figure 2.7).
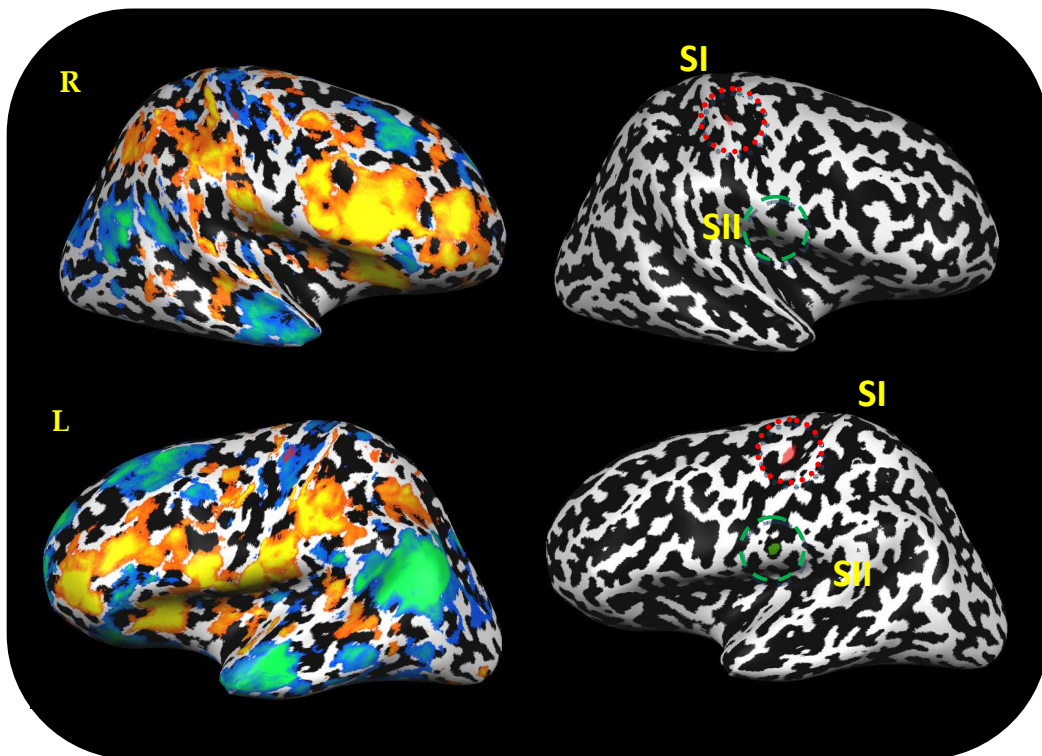

Figure 2.7. A paradigmatic example of the four Patches of Interests (POIs) of subject 2 defined from the fixed effect analysis with the four conditions as regressors.

For each POIs, we generated a correspondent Region of Interests (ROIs) in 3D space. On the ROIs we calculated the Beta values, on the

hemodynamic response. Within these ROIs we analysed the Beta values by executing a repeated measure Analysis of Variance (ANOVA) with Area (SI, SII), Hemisphere (Right, Left), Hand (within, between) and Finger (homologous, non-homologous) as within participants variables.

Results and discussion

The results revealed more adaptation effect when homologous as compared with non-homologous fingers were stimulated. Remarkably this occurred regardless of the hemisphere and of the somatosensory cortical area (i.e., SI, SII) (see Figure 2.8). Therefore, adaptation occurred for stimuli delivered on the same region of the skin (i.e., left index stimulated twice) and for stimuli delivered on homologous fingers of different hands (i.e., right and left indexes) regardless of the somatosensory area (i.e., SI and SII). The activity difference between homologous and non-homologous stimulations show that at low stage of spatial representation processing (SI) segregation of Finger identity (i.e., which finger was stimulated within the same hand, index or middle finger), is clearly establish. However, when homologous fingers of opposite hands are stimulated, side identification seems not to be entirely unambiguous, even in SI.

Finally, we revealed a main effect of area that indicates more activation in SII as compared with SI. This latter result can derived from a disproportion in the hand representation at the level of SII between hands (i.e., greater

represented) with respect to other body parts (see Maldjian, Gottschalk, Patel, Detre & Alsop, 1999).
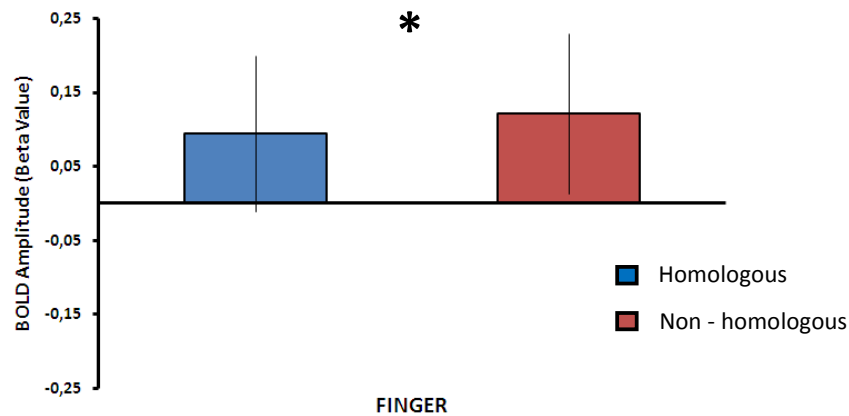

Figure 2.8. BOLD amplitude (Beta Values) for homologous and non-homologous fingers regardless of the body side (RH, LH) and areas (i.e., SI, SII). Error bars reflect the standard error of the mean (SE).

Overall conclusion of the imaging study

The imaging results revealed the usefulness of the fMRI adaptation paradigm to investigate the neural basis of touch, with particular regards to the same and to different body sides. We reported evidence in favour of the existence of bilateral representation of tactile stimuli delivered at the fingers in both primary and secondary somatosensory areas. Importantly, the present imaging data support the previous behavioural results on DSS interference within and between hands (Study 1; Study 2).

3 Papers

3.1 Double simultaneous tactile stimulation within and between hands: insights for spatial coding of touch at the fingers

(Under review in Experimental Brain Research)

Double simultaneous tactile stimulation within and between hands:
Insights for spatial coding of touch at the fingers

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Running head: DOUBLE SIMULTANEOUS TACTILE STIMULATION

Abstract

We studied the effect of double simultaneous tactile stimulation within and between hands to examine the role of multiple body representations in spatial coding of touch. Participants performed a go/no-go task to detect a tactile stimulus delivered to one target finger (e.g., right index), stimulated alone or with a concurrent non-target finger either on the same hand (e.g., right middle finger) or on the other hand (e.g., left index finger = homologous; left middle finger = non-homologous). We also examined the role of hand posture to assess the potential involvement of any spatial coding of touch beyond body representations. When the non-homologous finger served as non-target, interference effects emerged both within and between hands. These were not affected by changes in hand posture, suggesting that this competition was primarily solved within a somatotopic representation. By contrast, when the homologous contralateral finger served as non-target, we observed increased tactile sensitivity. This was clearly affected by changes in hand posture, suggesting the involvement of a spatial coding of touch beyond purely somatotopic representations. These findings provide behavioural evidence in humans for multiple spatial coding of touch during double simultaneous stimulation at the fingers.

Introduction

During everyday life, we localise somatosensory stimuli on our body surface almost without effort. However, this seemingly simple task hides the existence of multiple spatial representations of the tactile event in our brain (e.g., de Vignemont, Tsakiris & Haggard, 2006; Gallace & Spence, 2008; Haggard, Kitadono, Press & Taylor-Clarke, 2006). In a recently proposed flow-chart of sensory representations for touch (Serino & Haggard, 2009), touch is initially encoded into a sensory space within the <u>primary somatosensory</u> map (Blankenburg, Ruben, Meyer, Schwiemann & Villringer, 2003; Penfield & Rasmussen, 1950), but the location of the tactile event is coded also with respect to other frames of reference in further processing stages. Tactile sensation can be mapped in a <u>mental body representation</u>, to localise tactile events with respect to body-parts and body-side (e.g., Schicke & Röder, 2006), or in <u>egocentric/allocentric representations of external space</u>, to localise tactile events in the outside world (e.g., Azañón & Soto-Faraco, 2008; Brozzoli, Ishihara, Göbel, Salemme, Rossetti & Farnè, 2008). In the present work, we adapted a paradigm of double simultaneous tactile stimulation on the fingers to investigate at which representation level the competition between concurrent tactile stimuli is resolved, and infer which spatial representation of touch may be dominant while solving this task. In addition, we assessed to what extent manipulations of hand posture can change the preferred spatial representation of touch.

Multiple spatial representations of touch

The most basic spatial representation of touch in the cortex is the one available in primary somatosensory cortex, which contains a topographic representation of the skin surface (Blankenburg et al., 2003; Penfield & Rasmussen, 1950). At this primary level of spatial representation, however, the body is not categorically differentiated into parts (de Vignemont et al., 2006) and the spatial relationships between body-parts differ with respect to the actual organisation of the body. For instance, hand and face are adjacent in primary somatosensory cortex, but distant in terms of body space (e.g., Farnè, Roy, Giraux, Dubernard & Sirigu, 2002). Furthermore, even the distinction as to which body side is stimulated may be difficult at this stage. Although the primary somatosensory cortex is generally assumed to receive inputs only from the controlateral body side, stimulations from ipsilateral body parts can also reach this sensory region. Interaction between body sides at this level of body representation have been documented by neurophysiological studies in area 2 of the monkeys (Iwamura, Taoka & Iriki, 2001; Iwamura, Tanaka, Iriki, Taoka & Toda, 2002), and they likely originate from direct projections as well as trans-callosal connections between homologous regions in the two hemispheres (Killackey, Gould, Cusick, Pons & Kaas, 1983). Furthermore, magnetoencephalography in humans revealed modulations of somatosensory evoked potentials by stimulation of one hand, as a function of concurrent stimulation occurring on the other hand (Kakigi,

Koyama, Hoshiyama, Kitamura, Shimojo, Watanabe & Nakamura, 1996). At the behavioural level, interactions between body sides have also been documented in a number of tactile tasks. For instance, errors in tactile localisation at the hands are affected both by stimulation of adjacent fingers on the same (Schweizer, Braun, Fromm, Wilms & Birbaumer, 2001) and by stimulation of one finger on the opposite hand (Braun, Hess, Burkhardt, Wühle & Preissl, 2005). Similarly, if participants are trained to discriminate punctuate pressure or roughness on one finger of the right hand (e.g., the index), this training transfers to the first neighbour finger of the same hand (i.e., the right middle finger) as well as to the homologous finger of the opposite hand (i.e., the left index finger; Harris, Harris & Diamond, 2001).

Higher level representations for touch emerge when the overall structure of the body is taken into account (i.e., where was the tactile stimulation on the body). These higher-order spatial representations have been termed 'mental body representations' (Serino & Haggard, 2009; see also de Vignemont et al., 2006)[1]. Because the body can assume many different postures depending on behavioural demands, the brain often needs take into account where the touch was on the body and where the body was in space (Holmes & Spence, 2004; Maravita, 2006). A paradigmatic example of what happens when this combination of touch and posture fails is the 'Aristotle Illusion', in which participants report two distinct tactile sensations despite touching a single object, when tactile exploration occurs with the fingertips of

the index finger and middle finger crossed one over the other (McKeon, 1941; Benedetti, 1985). Recently, Azañón and Soto-Faraco (2008) elegantly tracked the time-course of this remapping of touch as a function of posture in space, showing that an unconscious image of the tactile sensation in somatosensory space prevails until 60 ms after stimulus onset. By contrast, an updated representation of tactile sensation that takes postural changes into account is consolidated in the interval ranging from 180 to 360 ms after stimulus onset.

A study by Haggard and colleagues (2006) illustrates well how tactile spatial processing can be updated into different representations as a function of task-demands. Haggard and colleagues asked participants to perform three different tactile tasks. In one task (simple detection), they were instructed to make a speeded vocal response to the onset of a tactile stimulus delivered to one of the fingertips, irrespective of stimulus location. In a second task (finger identification), participants had to name the finger that was touched. In a third task (hand identification), participants were instructed to name the hand that was touched (left or right), regardless of which specific finger had been stimulated. The three tasks were performed with two different hand postures: a 'vertical' posture, with the hands held at the midline, the right hand above the left one; and an 'interwoven' posture, with palms touching each others and fingers interwoven at the midline. The results showed that simple detection of touches and identification of which finger was stimulated were unaffected by hand posture. Instead, identification of which hand was stimulated was slower and less accurate for the interwoven than vertical

posture. Haggard and colleagues (2006) interpreted these results as evidence that detection of fingers occurs in a somatotopic reference frame, whereas hands identification occurs within a higher level reference frame which take postural information into account.

Double simultaneous tactile stimulation and the spatial representation of touch

The context of double simultaneous stimulation (DSS), in which two concurrent tactile events compete with one another, proved useful in the past to probe sensory processing of touch. In brain damaged patients, this competition typically leads to extinction effects (Bender, 1952). Tactile extinction is the phenomenon by which unilateral brain damaged patients fail to report a contralesional touch when this is presented together with an ipsilesional one. Furthermore, extinction-like effects have been recently documented in neurologically healthy participants, when the conscious report of both stimuli is required (e.g., Farnè, Brozzoli, Làdavas & Ro, 2007; Marcel et al., 2004; Meador, Ray, Day & Loring, 2001; Serino, Pizzoferrato & Làdavas, 2008). Finally, a number of studies have reported modulations of tactile performance in neurological healthy individuals even when a single predefined target has to be consciously reported under DSS (Gilson, 1969; Laskin & Spencer, 1979; Evans & Craig, 1991). This interference typically occurs when the two tactile stimuli are presented in close temporal and spatial proximity (e.g., Craig, 1995), and its exact nature is still debated, as it

can reflect a competition occurring at the sensory level (masking) as well as a competition at the response level (Craig & Evans, 1995; Craig, 2000; for further discussion of this issue see Johansen-Berg & Lloyd, 2000).

A consistent finding of this literature is that DSS leads to decreased performance particularly when the stimulation occurs <u>within</u> the same hand and to adjacent fingers (e.g., Craig, Green & Rhodes, 1985; Craig, 1985a; Craig & Qian, 1997; Evans, Craig & Rinker, 1992; Evans & Craig, 1991; Uttal, 1960). For instance, Craig (1985a) found that vibrotactile discrimination performance was strongly impaired when two vibrotactile patterns occurred simultaneously on the index and middle finger of left hand. By contrast, it remains controversial whether DSS can consistently lead to tactile interference when the stimulation occurs <u>between</u> hands (e.g., Craig, 1985a; Craig et al., 1985; Evans & Craig, 1991; Sherrick, 1964). Evans and colleagues (1992) documented a significant interference of contralateral distractors when participants discriminate pin-bars with different orientations at the left little finger during concurrent stimulation on the right ring finger (albeit this decrement of performance was smaller with respect to that observed when the non-target finger was ipsilateral to the target). However, an earlier report by Laskin and Spencer (1979) reported that double identical tactile stimuli delivered to the two hands produced little interference effects (see also Evans & Craig, 1991). Craig (1968) observed that contralateral vibrotactile stimuli can even lead to performance enhancement instead of interference. Finally, a facilitation effect under DSS stimulation has been documented also by Lappin

and Foulke (1973), which investigated the ability of blind and sighted participants in processing tactile inputs. Participants were asked to identify as rapidly as possible the number of one-dot patterns in successive sets of four patterns, which they explored using one, two or four fingers simultaneously (index and middle finger of either hands). For both blind and sighted participants, the fastest scanning performance emerged when the pattern was explored with the two index fingers together.

Interference effects occurring within the same hand are not informative of the body representational level, because adjacent fingers on the same hand are near in somatotopic space, mental body space and external space (unless finger posture is manipulated). By contrast, the presence or absence of interference effects between hands is more relevant for the understanding of which reference frame is adopted when processing the concurrent tactile targets. A dominance of the somatotopic representation predicts consistent interference effects between hands, because differentiation between body sides is less clearly defined at this representational stage. Instead, a dominance of mental body maps would predict little or no interference effects between hands, because in these representations the differentiation between the two hands should already be taken into account by the structural description of the body.

The present study

The present study adapted a DSS paradigm for stimuli delivered within and between hands to investigate the relative contribution of the different reference frames for touch. Unlike previous tactile competition studies, which modified temporal separation (e.g., Craig & Evans, 1995) and relative intensity (e.g., Craig, 1982) of target and non-target, here we changed the relative position of the stimuli on the fingers. We asked participants to detect whether a target finger was tactually stimulated or not. Across blocks, the target finger was either the index or the middle finger of the right or left hand. Stimulation was always restricted to the first phalanx of the finger, and the target finger could be stimulated alone or together with a non-target finger.

Figure 1 illustrates all possible stimulus combination for an example condition in which the target finger was the index finger of the right hand (Figure 1a). DSS stimulation was delivered within the same hand (Figure 1b) or between hands. In the latter case, the non-target finger was either homologous with respect to the target finger (e.g., right index finger as target and left index finger as non-target; see Figure 1c) or non-homologous with respect to the target finger (e.g., right index finger as target and left middle finger as non-target; see Figure 1d). Finally, during catch trials the non-target finger was stimulated alone (Figure 1e-g). Hands and fingers were arranged with the fingertips of the index and middle finger forming an imaginary square of 4 centimetres (cm). Note that in such a spatial arrangement, the

distance in external space between the stimulated skin regions of target and non-target fingers was comparable when the non-target finger was on the same hand as the target and when it was the homologous finger on the other hand (compare Figure 2b and 2c). Vision of the hands and fingers was prevented throughout.

To test whether changes in posture could affect DSS interactions, we asked participants to perform the task in two different hand postures across blocks. In half of the blocks, both hands were palm down (as shown in Figure 1). In the remaining blocks, one hand was palm down while the other hand was palm up (as shown in Figure 2, in which the hand rotated palm-up is shown as darker for illustrative purposes only).

< Please insert Figure 1 and 2 about here >

We expected worse performance on the target finger with DSS than single stimulation conditions. Moreover, If DSS interference occurs in somatotopic space, it should appear when target and non-target fingers belong to the same hand (e.g., Figure 1b), because DSS stimulation would activate competing adjacent cortical territories in primary and secondary somatosensory cortices, and when target and non-target fingers belong to different hands, because of inter-hemispheric interactions occurring at this representational level (e.g., Harris et al., 2001; Iwamura et al., 1994, 2001,

2002). By contrast, if DSS interference occurs at the level of mental body representation, tactile interference should be maximal within hands and minimal or absent between hands, because filtering of irrelevant stimulation between hands should be easier when the body structural representation has been activated and the hand side is clearly specified. Finally, if DSS interference occurs once tactile sensation has been coded in external space locations, tactile interference should change as a function of postural changes.

Methods

Participants

Sixteen participants (mean age = 28 years, SD = 5; 8 females, 8 males) took part to the study. All reported normal or corrected to normal vision and normal touch. Thirteen were right-handed by self-report, three were left-handed. All participants gave their informed consent prior to participation in the study that was carried out according to the principles of the Declaration of Helsinki.

Stimuli and apparatus

Tactile stimuli were delivered to the index and/or middle fingers of either hand by using four vibrators (Piezo System, Q220-A4-203YB model). Tactile stimulation consisted of a supra-threshold square impulse, resulting from fixed current of 40V fed into the vibrators for 8 ms (Current generator: Lafayette M10-DP-305E, Dual Output Adjustable DC Power Supply). To

maintain an homogeneous contact between fingers and vibrotactile stimulators across all posture changes, the distal and intermediate phalanges of each index and middle finger were inserted inside a plastic square parallelepiped (width 75 mm, height 40 mm, length 80 mm), padded inside with foamed-plastic. In addition, stimulators were secured to the fingers using medical tape. Vibrators' position (i.e., which vibrator stimulated which finger) was changed every 4 participants to control for possible intensity differences between the stimulation devices.

Figure 3 shows a schematic picture of the apparatus. Stimulated fingers were arranged to form an imaginary square of 4 cm (at the fingertips). During the experimental session, vision of the hands was prevented by means of a flat computer screen (SAMSUNG SyncMaster 171MP, 17"), placed horizontally on a wooden structure fixed to the table, on top of the vibrators (note that the computer screen is shown as lifted in Figure 3 for illustrative purpose only). The screen was also used to present instructions. In addition, during tactile stimulation trials it served for displaying a fixation cross. Fixation was aligned with the midsaggital plane of the participant and fell at the centre of the imaginary 4 cm square created by the fingertips. One foot-pedal positioned under the participant's right foot served for response collection, and was connected to the data-acquisition card. Stimulus presentation and response collection were controlled by custom program written using MATLAB R2006b programming software and Psychtoolbox libraries (Brainard, 1997).

Throughout the experiment, white noise was presented over a closed-ear headphone (Panasonic Portable CD Player SL-S220 XBS, Sennheiser HD 580 precision headphone) to mask any sounds made by the operation of the tactile stimulators.

< Please insert Figure 3 about here >

Procedure

At the beginning of each experimental block a drawing of the two hands with one single finger clearly marked (similar to the example shown in Figure 1a) was presented on the computer screen placed horizontal above the participant's hands. This drawing designated the target finger for an entire block of trials. Participants also reported verbally to the experimenter which was the designated target finger for that experimental block (e.g., "The target finger for this block is the right index finger"). Participants were informed that they had to perform a speeded go-no-go task to indicate whether the target finger had been stimulated or not. Specifically, they were instructed to keep the right foot-pedal pressed, unless they wanted to indicate the presence of a tactile stimulus at the target finger.

Each experimental trial started with a black cross appearing on white background in the center of screen. Participants were instructed to fixate the cross throughout the duration of the experimental block. After a variable interval ranging between 200 and 400 ms from fixation onset, tactile

stimulation was presented. The stimulation was either: (1) a single touch delivered to the designated target finger (target only trials); (2) two touches delivered simultaneously, one to the target finger and one to another finger (DSS trials); or (3) a single touch delivered to one of the non-target fingers (catch trials). As anticipated earlier, the diagram in Figure 1 illustrates all the possible stimulation conditions for an example block in which the target-finger is the right index finger. Target only trials (Figure 1a), will be identified from now on as 'T' trials, whereas DSS trials will be divided as a function of the relative position of the target and non-target fingers. Three DSS trials were possible: target finger plus the neighbouring finger of the same hand (Figure 1b; from now on 'T+DFSH trials', for Target + Different Finger Same Hand); target finger plus the homologous finger of the other hand (Figure 1c; from now on 'T+SFDH trials', for Target + Same Finger Different Hand); or target finger plus the non-homologous finger of the other hand (Figure 1d; from now on T+DFDH, for Target + Different Finger Different Hand). Finally, catch trials were also presented as a function of the position of the non-target finger with respect to the target finger designated for the entire block. Three types of catch trials were possible: 'DFSH trials', for Different Finger Same Hand non-target (Figure 1e); 'SFDH trials', for Same Finger Different Hand non-target (Figure 1f); and 'DFDH trials', for Different Finger Different Hand non-target (Figure 1g).

Fixation overstayed tactile stimulation for 100 ms then was replaced by a question-mark symbol that instructed participants to make their choice as to whether the target finger had been stimulated or not. Participants were instructed to react as fast and accurately as possible and were informed that they had a maximum of 2 seconds to respond before the beginning of the next trial. No accuracy feedback was provided, but a warning message was presented on screen if the foot-pedal was released before the tactile stimulation. Participants were invited to take short breaks between blocks. The experimenter remained in the room throughout the session to ensure that participants complied with the instructions.

Design and analyses

The experiment comprised eight separate blocks. In four blocks, both hands were palm down (one block for each of the four possible target locations; i.e., right index finger, right middle finger, left index finger and left middle finger). In the remaining blocks, one hand was palm down while the other was palm up (i.e., the hand rotated by 180 degrees around the wrist). Half of participants rotated the left hand and the other half rotated the right hand. Note that in the 4 rotated-posture blocks, the designated target occurred on the rotated hand in 2 of the blocks, and on the non-rotated hand in the remaining 2 blocks. Each block comprised 70 trials (i.e., 7 stimulation conditions repeated 10 times), resulting in a total 560 trials.

Sensitivity (d′), criterion (c) and response times (RTs) were considered as dependent variables. Sensitivity and criterion measures were computed according to standard signal detection theory (Macmillan & Creelman, 1991). For the three DSS conditions we used proportion correct in T+DFSH, T+SFDH and T+DFDH conditions as hits, and proportion of errors in DFSH, SFDH and DFDH conditions as false alarms. For the target only condition, false alarms were computed as the mean of the proportion of errors in the three catch trial conditions. Mean RTs were computed for each participant for correct trials only.

We expressed the effect of double vs. single touches as the difference in performance between DSS and target only trials, and focused our analyses on the three DSS Conditions (e.g., T+DFSH, T+SFDH or T+DFDH). In addition, we considered the identity of the Target Finger (index or middle finger) and Hand Posture (both hands palm-down or one hand palm-up) as within-participant variables. Instead, we pooled together the data when the target was at the left hand and when the target was at the right hand. This resulted in a 3x2x2 factorial design, and 20 trials for each cell of the design.

Results

Overall sensitivity when the target was presented alone was 2.93 (SE = 0.44), whereas sensitivity in DSS trials was 2.27 (SE = 0.23) for the T+DFSH condition, 3.15 (SE = 0.33) for the T+SFDH condition and 2.91

(SE = 0.29) for the T+DFDH condition. Overall RT when the target was presented alone was 553 ms (SE = 62 ms), whereas RTs in DSS trials was 644 ms (SE = 72 ms) for the T+DFSH condition, 596 ms (SE = 65 ms) for the T+SFDH condition and 637 ms (SE = 66 ms) for the T+DFDH condition.

Sensitivity (d') differences between DSS and target only trials were entered into a repeated measure Analysis of Variance (ANOVA) with Stimulation Condition (T+DFSH, T+SFDH, T+DFDH), Target Finger (forefinger or middle finger) and Hand Posture (both palm-down, one palm-up) as within participants variables. This analysis revealed no overall effect of the intercept (F = 1.3), indicating that interference was not present when all conditions were averaged together. However, there was a main effect of Stimulation Condition, ($F_{(2,30)}$ = 20.1, p < 0.0001), caused by larger costs for DSS trials when the non-target finger was on the same hand as the target (i.e., DFSH, mean = -0.67, SE = 0.44) than when it was on the other hand (SFDH, mean = 0.22, SE = 0.26; DFDH, mean = -0.02, SE = 0.20; p < 0.002 for both comparisons on Newman-Keuls test). The cost for DFSH was significantly greater than zero (t(15) = 3.0, p = 0.009). Finally, there was a significant interaction between Hand Posture and Stimulation Condition, ($F_{(2,30)}$ = 5.85, p = 0.007). No other main effect or interaction reached significance (all Fs < 2.4).

The two-way interaction between Hand Posture and Stimulation Condition is illustrated in Figure 4a. When the non-target finger was on the same hand as the target (i.e., T+DFSH condition) the effect of DSS trials did

not change as a function of hand posture. In this condition, DSS trials resulted is a substantial cost in terms of sensitivity (i.e., tactile interference, when performance was tested with t-tests against zero), both when the hands were palms-down (mean = -0.62, SE = 0.28; t(15) = 3.08, p = 0.008) and when one of the two hands was palm-up (mean = -0.71, SE = 0.39; t(15) = 2.59, p = 0.02). This DSS interference effect did not emerge when the non-target finger was the non-homologous finger of the other hand (i.e., T+DFDH condition) regardless of hand posture (hands palm-down: mean = -0.10, SE = 0.17; t(15) = 0.81, n.s.; one hand palm-up: mean = 0.06, SE = 0.20; t(15) = 0.41, n.s.). Interestingly, when the non-target finger was the homologous finger of the other hand (i.e., SFDH condition) a significant improvement during DSS trials was observed with hands palm-down (mean = 0.41, SE = 0.23; t(15) = 2.49, p = 0.02), which disappeared when one of the two hands rotated palm-up (mean = 0.03, SE = 0.26; t(15) = 0.19, n.s.).

A similar analysis on criterion revealed no significant change in criterion for the main effect of Stimulation Condition, the main effect of Posture, or the interaction between these two variables (all Fs < 2.1).

< Please insert Figure 4 about here >

To assess any DSS interference in terms of RTs, we calculated RT differences between DSS and target only trials and entered these data into an

ANOVA with Stimulation Condition (T+DFSH, T+SFDH, T+DFDH) and Hand Posture (both palm-down, one palm-up) as within-participant variables. To ensure sufficient power to this analysis, mean RTs we pooled regardless of target finger (note that this factor was included in the previous analysis on sensitivity, but proved not relevant), setting the criterion to a minimum of 10 correct responses in each design cell (i.e., 25% correct responses, given a total number of 40 trials in each cell). After removal of one participant who did not meeting this criterion, the analysis were run on an average of 29 trials per cell (SD = 7). This analysis revealed a significant effect of the intercept, ($F_{(1,14)}$ = 86.2, p < 0.0001), indicating an overall RT cost for DSS trials. There was also a main effect of Stimulation Condition, ($F_{(2,28)}$ = 4.3, p = 0.02), caused by worse performance when the non-target finger belonged to the same hand as the target (T+DFSH condition: mean = 67 ms, SE = 16 ms) or when it was the non-homologous finger of the other hand (T+DFDH condition: mean = 76 ms, SE = 15 ms), with respect to when the non-target finger was the homologous finger of the other hand (T+SFDH condition: mean = 40 ms, SE = 9 ms; p = 0.04 on both Newman-Keuls test). The lower RT costs in T+SFDH condition indicates relatively better performance precisely for the DSS pairing for which sensitivity improvement was previously observed. As illustrated in Figure 4b, this pattern of results was numerically stronger when both hands were palm-down than when one hand was palm-up. However, the interaction between Hand Posture and Stimulation Condition was not significant ($F_{(2,28)}$ = 1.45, p = 0.2).

Finally, we examined the percentage of errors made by participants in the catch trials conditions (see Figure 4c). The inter-participant errors percentage in catch trials was entered into a repeated measure ANOVA with Stimulation Condition (DFSH, SFDH and DFDH) and Hand Posture (both hands palm-down or one hand palm-up) as within-participants variables. This analysis revealed a main effect of Stimulation Condition, ($F_{(2, 30)}$ = 12.62, p = 0.0001), caused by more errors for DFSH (mean = 6%, SE = 0.02) than SFDH (mean = 1%, SE = 0.004) or DFDH (mean = 1%, SE = 0.01; p < 0.001 for both comparisons on Newman-Keuls test). No other main effect or interaction was significant (all Fs < 1).

Discussion

The aim of the present study was to investigate spatial coding of touch using a DSS paradigm for stimuli at the fingers of the two hands. Two main effects of DSS trials (compared to target only trials) emerged: first, a predicted interference effect, which was manifest both within and between hands and was independent of changes in hand posture; second, an unexpected increase in tactile sensitivity that occurred between hands and was strictly dependant upon hand posture. These two results will be discussed in turns, with emphasis on the presumed spatial coding of touch subtending each effect.

Interference effects emerged reliably with our clearly suprathreshold stimulation both in terms of sensitivity and RTs (note that a similar pattern of

results was also documented in a pilot work with near-threshold stimuli[2]). Interference effects on sensitivity were selective for DSS trials occurring within the same hand, at the net of any change in response criterion. Within hand interference was also confirmed by the RT results, which additionally showed a significant slow-down for between hand DSS stimulation. Notably, the latter was more pronounced when the target and non-target fingers were non-homologous between hands. For example, when target was the right index a comparable interference in RT emerged both during concurrent stimulation of the ipsilateral and contralateral middle-finger. This pattern of interference is compatible with DSS competition occurring in <u>somatotopic space</u>, because at this low representational stage the differentiation between the two hands is less clearly defined and stimulation delivered to the non-homologous finger of the other hand can reach cortical territories ipsilateral to the target (Braun et al., 2005; Iwamura et al., 2001, 2002; Killackey et al., 1983). Importantly, these interference effects within and between hands were <u>not</u> modulated as a function of hand posture, thus providing further support to the notion that within and between interference effects may be solved at a low stage of body representation.

The results of the present study also revealed that part of the behavioural response to DSS trials is solved at higher representational stages. We documented increased tactile sensitivity for concurrent stimulation between hands, which was strictly depend upon the relative posture of the fingers in space. Namely, it emerged when the target finger was stimulated

together with the homologous fingers of the other hand and both hands were palm down, but disappeared when either hand was rotated palm-up. This posture dependent modulation rules out the possibility that increased tactile sensitivity emerged at a low representational stage. Instead, it reveals the use of a spatial representation for touch which takes into account the overall structure of the body as well as its layout in space.

While the spatial coding underlying increased tactile sensitivity is clear, the interpretation of its nature remains speculative. This effect was present when index (or middle) fingers were aligned in space and when they were equally distant with respect to the trunk. We suggest that it may reflect a redundancy of spatial codes identifying the target finger (same finger stimulated between hands) and the region of external space (same location with respect to the trunk). This redundancy of spatial codes could have produced better target detection. In agreement with this interpretation, the condition in which the target was stimulated together with the homologous finger of the other hand was also the situation in which the least DSS interference was observed in RTs. Rotating one hand disrupted this double code redundancy, making better target detection disappear.

Performance improvements under DSS stimulation have occasionally been documented in previous work. In blind and sighted individuals, Lappin and Foulke (1973) observed that identification of actively explored tactile patterns was faster when the two index fingers were used together. Instead,

exploring the tactile patterns with two adjacent fingers of the same hand tended to decrease performance (somewhat similar to the within hand interference effect observed in the present study). More similar to the present study, Craig (1968) reported increased sensitivity at the index fingers following double compared to single tactile stimulation. Finally, one recent example of performance improvement during DSS tactile stimulation has been documented by Forster and colleagues (Forster, Cavina-Pratesi, Aglioti & Berlucchi, 2002) in a study on unisensory and multisensory redundant target effects (RTE). RTE consists in the RT advantage for DSS than single stimulation trials when participants are required to respond as fast as possible to the mere occurrence of any of the sensory events. When double simultaneous touches were delivered to homologous fingers (little fingers) of both hands, faster responses for DSS than single stimulations were observed, although the tactile RTE did not violate the race model (Miller, 1982) and thus could not be accounted in terms of neural summation. Although a direct comparison between these earlier findings and our own results is made difficult by the substantial diversity of paradigms, it is interesting to note that a redundancy of spatial codes was present also in these previous evidence of improved tactile performance under DSS stimulation.

The modulation of DSS performance as a function of changes in hand posture is reminiscent of the neuropsychological evidence that tactile extinction may occur in external rather than somatotopic space. Moscovitch and Behrmann (1994) tested tactile extinction in 10 right brain-damaged

patients, by delivering double simultaneous touches to the opposite side of the wrist of the right or left hand, when the hands were palm-down or palm-up. Regardless of hand posture the missed tactile stimulus was systematically the one that occupied the leftmost location in external space (see also Tinazzi, Ferrari, Zampini & Aglioti, 2000). This finding is compatible with the results of a recent fMRI study showing that primary somatosensory cortex is always activated bilaterally in a right brain-damaged patient showing tactile extinction, suggesting that the competition leading to extinction occurs after the afferent tactile stimuli are processed by the primary somatosensory cortex (Beversdorf, Hughes & Heilman, 2008), thus at a higher stage of tactile processing. It should be emphasised however that these findings do not imply allocentric coding of touch because egocentric coding was also possible, nonetheless they clearly show that changes of the body layout in space affect both behavioral and neuronal processing of DSS in touch (Valenza, Seghier, Schwartz, Lazeyras & Vuilleumier, 2004).

A final aspect worth discussing is the pattern of errors observed in the catch trials (i.e., when the non-target finger was stimulated without the target). As shown in Figure 4c, participants made significantly more errors when the non-target finger was stimulated alone (i.e., without the target) on the same hand designated to contain the target, than on the other hand. This finding is very unlikely to be the consequence of mechanical transfer of stimulation to the adjacent non-stimulated fingers, because fingers were well

spaced-apart and foam-isolated in our setup, plus we used short tactile pulses. One interpretation for this result is that increased within-hand mislocalisation reflects the partial overlapping of tactile receptive fields for adjacent fingers in somatosensory cortex (see also Schweizer et al., 2000; Braun et al., 2005). Evidence in support of this account comes from animal studies showing that receptive fields in primary somatosensory cortex can cover more than one digit (Iwamura, Tanaka & Hikosaka, 1980). Similarly, somatosensory evoked field potentials recorded in humans also suggest a functional overlap of finger representations within the same hand in primary somatosensory cortex (Simõe et al., 2001). Support to this interpretation of within hand mislocalisations of touch also comes from the present observation that errors in catch trials were totally unaffected by postural changes.

In conclusion, we have shown that between-hands DSS stimulation can produce interference effects both within and between hands. In addition, we documented an increase in target sensitivity during between-hand DSS, which may relate to a redundancy of spatial codes for the concurrent tactile events. Only the latter phenomenon was affected by changes in hand posture. In keeping with the notion that touch can be spatially coded in different frames of reference we showed that tactile interference is resolved at a low representational stage (somatotopic), whereas increased tactile sensitivity relies on a higher representational stage which takes into account the layout of the body in space.

Footnotes

1. Different fractionations of the concept of mental body representations have been proposed in the literature, starting from the classic distinction between postural schema and surface schema drawn by Head and Holmes (1911) on the basis of neuropsychological observations. A more detailed discussion of the multifaceted nature of these representations can be found in Dijkerman & De Haan (2007).

2. A pilot experiment adopting a similar DSS stimulation but no postural change was run on 12 participants (mean age = 29 years, SD = 3; 3 females) using near-threshold tactile stimulations. Results showed significant interference effects only in terms of reaction times and not for sensitivity. These were not affected by the specific pairings between target and non-target fingers. However, between-hands interference effect in RTs were numerically smaller when the non-target finger was homologous to the target (T+SFDH) with respect to the other conditions, in agreement with the RT pattern shown in Figure 4b.

Acknowledgements

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Figure captions

Figure 1. Example of the stimulation conditions with hands palm-down, when the target finger is the right index finger. Unfilled circles indicate the stimulation at the target finger; filled black circles indicate stimulation at the non-target finger. a) target only trial; b-d) DSS trials; e-g) catch trials.

Figure 2. Example of the stimulation conditions with one hand palm-down and the other rotated palm-up, when the target finger is the right index finger. Unfilled circles indicate the stimulation at the target finger; filled black circles indicate stimulation at the non-target finger. a) target only trial; b-d) DSS trials; e-g) catch trials.

Figure 3. Schematic drawing of the experimental setup. Note that hands are shown here only to illustrate the adopted posture when both hands were palm-down. They were occluded under the horizontal computer display throughout the experiment. Tactile stimulators are not shown in the figure.

Figure 4. Sensitivity (a) and mean reaction times (b) as a function of Stimulation Condition. Error percentages in the catch trial condition are indicated in (c). Error bars represent the Standard Errors (SE).
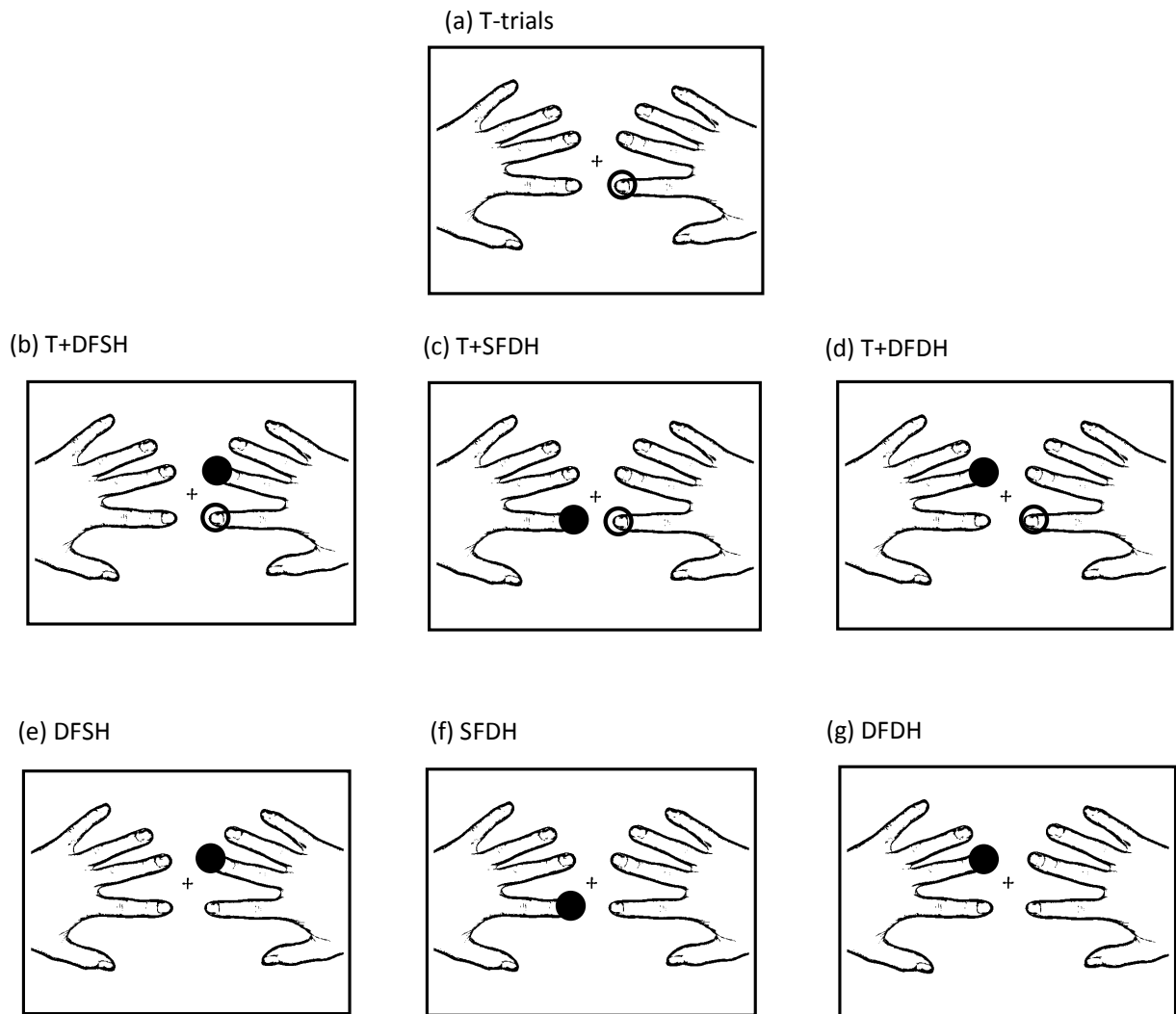
Figure 1

(a) T-trials
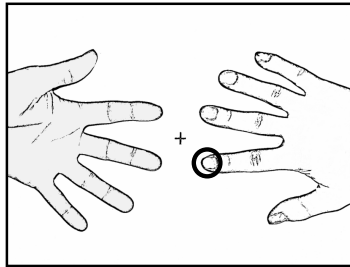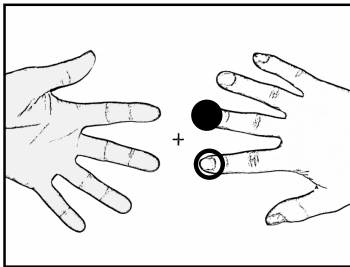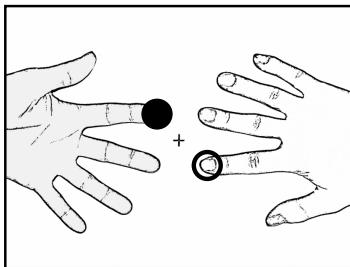

(b) T+DFSH

(c) T+SFDH

(d) T+DFDH

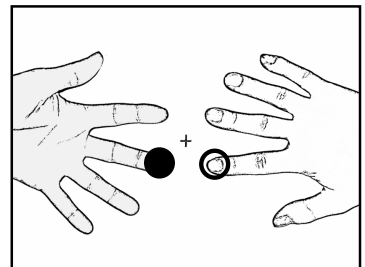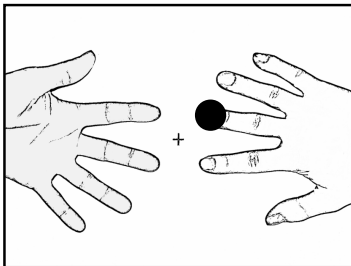(e) DFSH

(f) SFDH

(g) DFDH
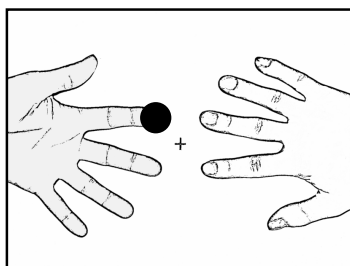
Figure 2

(a) T-trials

(b) T+DFSH

(c) T+SFDH

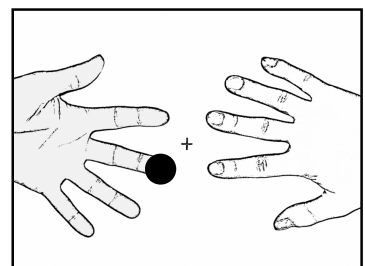
(d) T+DFDH

(e) DFSH

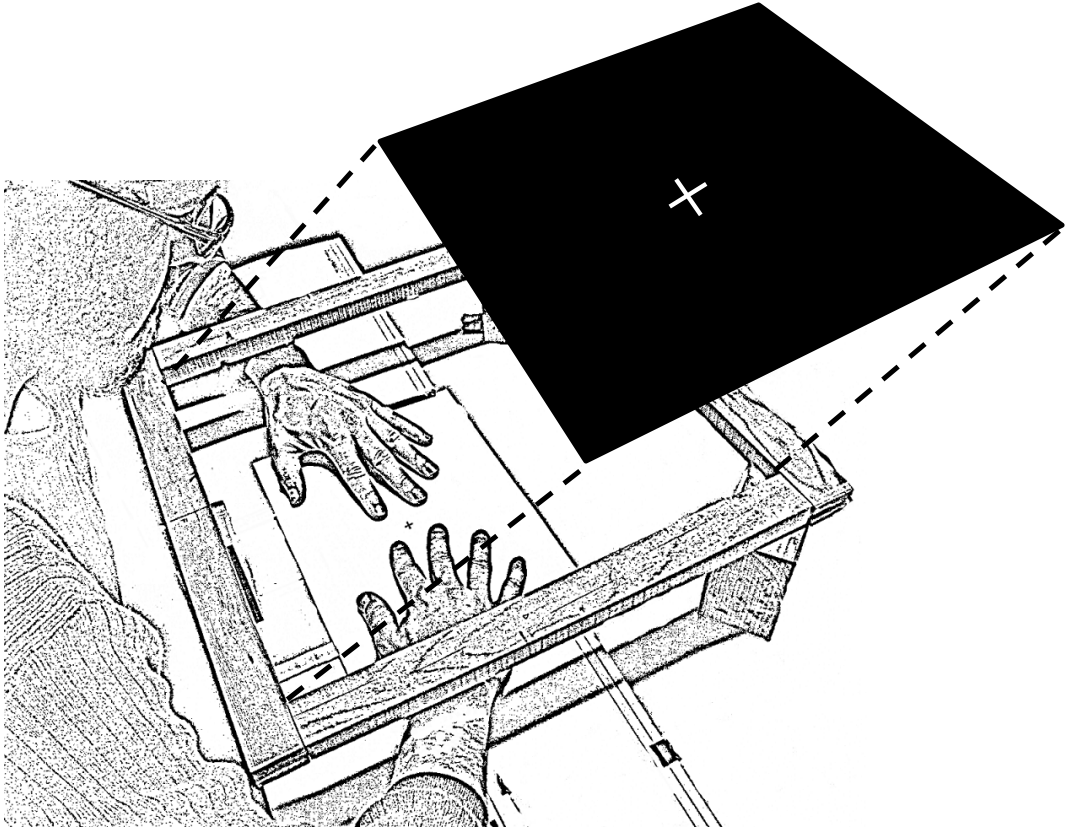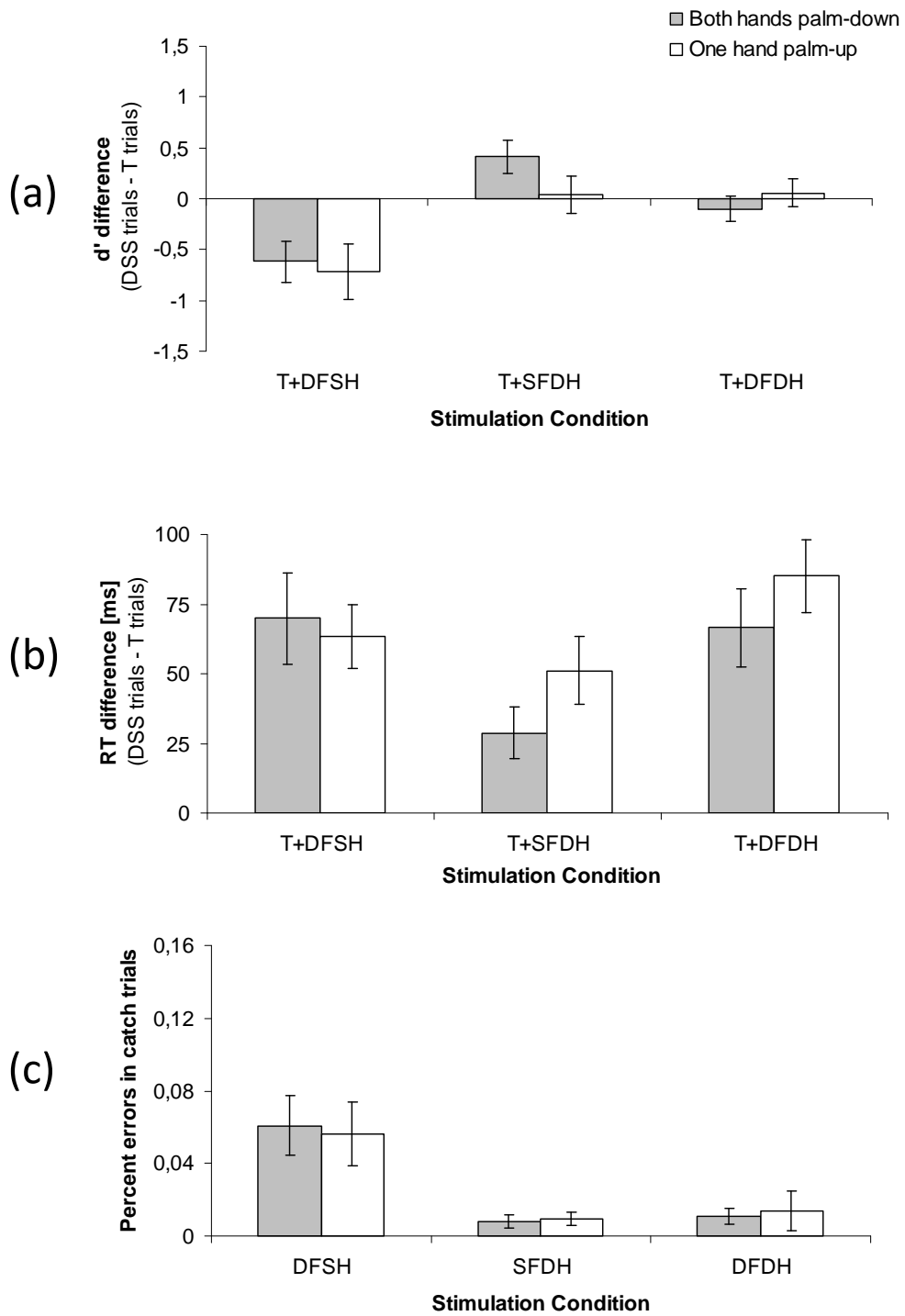(f) SFDH

(g) DFDH

Figure 3

Figure 4

3.2 When vision does not affect touch: A limited role for vision in tactile double simultaneous stimulation

**(Under review in the Journal of Experimental Psychology:
Human Perception and Performance)**

When vision does not affect touch: A limited role for vision in tactile double simultaneous stimulation

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Running head: WHEN VISION DOES NOT AFFECT TOUCH

Abstract

Double simultaneous stimulation (DSS) is known to hamper tactile perception compared to single stimulation, even when a single target has to be reported. Here we tested the sensitivity of tactile DSS interference to different levels of hand-related visual input. Participants decided whether a pre-specified target finger was touched or not (go/no-go task). The target finger could be stimulated alone or simultaneously with a non-target finger, either on the same or on the other hand (at homologous or non-homologous fingers). Exp.1 examined the role of seeing vs. not seeing the hands. Exp.2 examined the role of visual/proprioceptive conflict by showing images of participant's own hands that either matched or not matched their unseen finger posture. Exp.3 examined the role structural distortions of the fingers, that were visually morphed within and between hands. Both within and between hands, results showed highly consistent interference effects of DSS (compared to target-only stimulation) that systematically varied as a function of which non-target finger was stimulated. Moreover, this DSS interference pattern was highly resistant to hand-related visual information. Instead, hand vision affected overall tactile sensitivity and caused misattribution of single non-target touches to the adjacent target finger. Response criterion also shifted across conditions as a function of the presence and reliability of the hand-related visual input. These results show that tactile processing under DSS paradigms is largely immune to matching or conflicting vision from the stimulated body part, suggesting that tactile DSS interference may essentially depend from competition occurring within the somatosensory modality.

Introduction

Similar to vision, touch perception is regulated by limited capacities of selective attention so that multiple stimuli are less likely to be fully reported than single ones (for reviews see: Brozzoli, Demattè, Frassinetti, Pavani & Farnè, 2006; Farnè, Brozzoli, Làdavas & Ro, 2007). The context of double simultaneous stimulation (DSS), in which two concurrent events compete for awareness, proved useful in the past to probe sensory processing of touch. In brain damaged patients, DSS typically leads to extinction (Bender, 1952) and tactile extinction is the phenomenon by which patients fail to report a contralesional touch only when this is presented together with an ipsilesional one. Extinction-like effects in the somatosensory modality have been also documented in neurologically healthy participants, when the conscious report and spatial localisation of both stimuli is required (e.g., Farnè, Brozzoli, Làdavas & Ro, 2007; Marcel, Postma, Gillmeister, Cox, Rorden, Nimmo-Smith & Mackintosh, 2004; Meador, Ray, Day & Loring, 2001; Serino, Pizzoferrato & Làdavas, 2008). Furthermore, a number of studies have reported reduced tactile performance in neurological healthy individuals even when a single predefined target has to be consciously reported under DSS (Gilson, 1969; Laskin & Spencer, 1979; Evans & Craig, 1991). The exact nature of this competition phenomenon is still debated, as it could emerge at the sensory (masking) and/or the response level (Craig & Evans, 1995; Craig, 2000; Johansen-Berg & Lloyd, 2000). This interference typically occurs when the two

tactile stimuli are presented in close temporal and spatial proximity (e.g., Craig, 1995).

A consistent spatial feature in the tactile modality is that DSS leads to decreased performance particularly when both stimuli are applied to the same hand and to adjacent fingers (Craig, Green & Rhodes, 1985; Craig, 1985a; Craig & Qian, 1997; Evans, Craig & Rinker, 1992; Evans & Craig, 1991; Uttal, 1960). For instance, simultaneous stimulation of the index and middle fingers of the left hand produces the strongest impairment in tactile discrimination tasks. By contrast, whether DSS can consistently lead to tactile interference when the stimulation occurs between hands remains partially controversial (Craig, 1985a; Craig et al., 1985; Evans & Craig, 1991; Sherrick, 1964). Identical tactile stimuli delivered to the two hands have been reported to produce little interference effects (Evans & Craig, 1991; Laskin & Spencer 1979), or even performance enhancement (Craig, 1968). In contrast, Evans and colleagues (1992) have documented that a significant interference by contralateral distractors can occur when participants discriminate pin-bars with different orientations at the left little finger during concurrent stimulation on the right ring finger (but note that this interference is smaller with respect to that observed when the non-target finger was ipsilateral to the target).

More recently, we documented clear interference effects under DSS paradigm both within and between hands (Tamè, Farnè & Pavani, under review), especially in terms of modulations of response time (RT). Unlike previous tactile competition studies, which modified temporal (e.g., Craig &

Evans, 1995) and frequency (e.g., Craig, 1982) aspects of target and non-target, we introduced spatial changes in the relative position of the stimuli at the hands and additionally manipulated the participant's hands posture. Results revealed strong interference effects that were manifest both within and between hands when the non-target touch occurred at non-homologous fingers (e.g., the middle finger of either hand, when the target was the right finger). Notably, such interference was significantly reduced when target and non-target fingers where homologous between hands (e.g., both index fingers). This finding adds to the notion that DSS tactile interference occurs at a relatively low stage (i.e., somatotopic) of the representation of touch on the body (Tamè et al., under review).

While our previous work focused exclusively on touch, here we widen the investigation of DDS interference effects by taking into account the intimately multisensory nature of our perceptual systems. Stimuli in the outside world come from different sensory modalities and our perceptual experience is profoundly shaped by the merging of various senses (Calvert, Spence & Stein, 2004; Stein & Meredith, 1993). Various forms of tactile tasks have already been demonstrated to be highly sensitive to visual stimulation in the healthy and damaged brain (e.g., Làdavas & Farnè, 2004; Macaluso & Maravita, 2009; Serino & Haggard, 2009; Spence, Pavani, Maravita & Holmes, 2008). In accordance with this notion, in the present work we investigated whether the DSS interference is modulated by different degrees of non-informative visual inputs concerning the participant's own hands. In

particular, Experiment 1 manipulated the visibility of the participant's hands (present vs. absent). Experiment 2 varied their degree of spatial correspondence between the seen hands and the actual hand posture, as specified by proprioception (congruent vs. incongruent). Finally, Experiment 3 examined the role of violating the body structural mereology, by making the stimulated fingers to appear as fused within- or between-hands.

Participants' performance was measured by using psychophysical indices provided by the Signal Detection Theory (Green & Swets, 1966) to discern between modulations deriving from changes in tactile sensitivity (d-prime: d') and/or criterion shift (criterion: c). This issue is particularly relevant when considering that some visuo-tactile modulations may be partially accounted for by response biases, at least to some extent (Johnson, Burton & Ro, 2006).

Across all experiments, participants were required to detect whether a pre-defined target finger was tactually stimulated or not (i.e., a go/no-go task). Stimulation was always restricted to the distal phalanx of each finger, and the target finger could be stimulated alone or concurrently with a non-target finger. All possible stimulus combinations are illustrated in Figure 1, for an example condition in which the target finger was the index finger of the right hand. Tactile DSS were delivered within (Figure 1b) or between hands. In the latter case, the non-target finger was either homologous with respect to the target finger (e.g., right index finger as target and left index finger as non-target; see Figure 1c) or non-homologous with respect to the target finger

(e.g., right index finger as target and left middle finger as non-target; see Figure 1d). The stimulus combination included the occurrence of catch trials, in which one of the non-target fingers was stimulated alone (Figure 1e-g), and the participant had to refrain from responding.

< Please add Figure 1 about here >

EXPERIMENT 1

Our first visual manipulation concerned the presence or absence of task-irrelevant vision of the stimulated hands on DSS. In the last decade, several studies have examined the multisensory interaction that can result from this basic manipulation, and typically observed that non-informative vision of the stimulated body part can result in enhanced tactile performance in terms of faster responses to tactile targets (e.g., Tipper, Lloyd, Shorland, Dancer, Howard & McGlone, 1998), particularly when familiar body parts are seen (Tipper, Phillips, Dancer, Lloyd, Howard & McGlone, 2001), or tactile spatial acuity (e.g., Kennett, Taylor-Clarke & Haggard, 2001). This effect has been termed 'visual enhancement of touch' (VET; e.g., Taylor-Clarke, Kennett & Haggard, 2002; 2004; Serino, Farnè, Rinaldesi, Haggard & Làdavas, 2007). For instance, Kennett and colleagues (2001), tested participants in two-point tactile discrimination thresholds on the forearm, while modulating visual input by showing either the participant's arm or a wooden cylinder. Participants' accuracy increased when the arm, but not the object, was seen.

Furthermore, tactile performance increased even further when the visible arm was visually enlarged using a magnifying lens. This improvement of tactile acuity by non-informative vision was explained in terms of somatosensory cortex pre-activation, through feedback originating from multimodal areas (e.g., posterior parietal cortex, where neurons that respond both to visual and tactile stimuli have been reported, see Graziano, Yap, & Gross, 1994). Convergent support to this neural account of VET, derive from electrophysiology (Taylor-Clarke, Kennett & Haggard, 2002) and transcranial magnetic stimulation (TMS) approaches in healthy humans (Fiorio & Haggard, 2005). These works specifically suggest that the visual modulations resulting in VET occur at the level of primary somatosensory cortex (SI). Complementary evidence to this view come from the finding that VET can selectively spread to body parts that are adjacent in terms of somatotopy, so that seeing the hand can boost feeling on the cheek, but not the foot (Serino, Padiglioni, Haggard & Làdavas, 2009).

The aim of this first experiment was to investigate whether detection of a touch presented to a target-finger with concurrent stimulation of a non-target finger (i.e., tactile DSS) could be improved by non-informative vision of the stimulated body parts (i.e., the hands). In order to apply our visual modulation, we prevented direct vision of the hands and fingers throughout, by means of a flat computer screen placed horizontally above the participant's hands (see Figure 2). Across blocks, participants saw either: 1) a fixation cross in the middle of the screen; 2) an image of their own hands, exactly

reproducing the fingers posture and alignment under the screen; 3) four circles vertically aligned with the distal phalanx of each finger just below the screen. If non-informative vision of stimulated body parts affects tactile perception under DDS, one should expect better performance when the participant's own hands are displayed, compared to the fixation only or circles only conditions.

< Please add Figure 2 about here >

Methods

Participants

Eighteen participants (mean age = 22 years, SD = 1; 11 females) took part in the experiment. All reported normal or corrected to normal vision, normal somatosensation and were unaware of the purpose of the experiment. Sixteen were right-handed and two were left-handed by self-report. For this, as well as for the following experiments, participants gave their informed consent prior to participate in the study that was approved by the ethics review board of the University of Trento and was carried out according to the principles of the Declaration of Helsinki.

Apparatus and stimuli

Tactile stimuli could be delivered to the index or middle finger of each hand using four stimulators (Piezo System, Q220-A4-203YB model).

Stimulators were connected to four independent custom built amplifiers (High Voltage Linear Piezo Amplifier) controlled by a data-acquisition card (National Instruments, PCI-6229). All connections between stimulators and cables were covered with insulating tape to avoid current dispersion. Tactile stimulation consisted of a 200 Hz supra-threshold sinusoidal wave, fed into the stimulators for 5 milliseconds (ms). Wave amplitude was fixed at 70 volt (V), which resulted in a clear perceptible tap-like sensation. Stimulators' position (i.e., which tactile stimulator applied to which finger) was switched every 4 participants, to counterbalance for any possible difference among the stimulation devices.

Tactile stimulators were arranged on a semi-rigid foamed-plastic plane, with their unconnected ends forming an imaginary square of 4 cm. Throughout the study, participants rested the index and middle fingers of each hand on the stimulators. During the experimental session, vision of the hands was prevented by means of a flat computer screen (SAMSUNG SyncMaster 171MP, 17″) placed horizontally on a wooden structure fixed to the table, just above the stimulators (see Figure 2a). The screen was used to present instructions at the beginning of the block and the visual experimental manipulations during the block (see procedure for a complete description of the visual conditions). Fixation (a filled black circle; 4.3° of visual angle) was aligned with the midsaggital plane of the participant and fell at the center of the imaginary 4 cm square created by the fingertips. A foot-pedal was positioned under the participant's right foot for response collection, and was

connected to the data-acquisition card. Stimulus presentation and response collection were controlled by a custom program written using MATLAB R2006b programming software and Psychtoolbox libraries (Brainard, 1997). Throughout the experiment, white noise was presented over a closed-ear headphone (Sennheiser HD 580 precision headphone) connected to a portable CD player (Panasonic SL-S220 XBS), to mask any sounds made by the operation of the tactile stimulators.

Procedure

Before starting the experimental session, a digital picture of the participant's own hands was taken. This image served subsequently for one of the visual conditions (see below). Hands posture for the picture was identical to that adopted later during the experiment. To avoid any visual distortion caused by the digital picture transfer on the flat screen, the image was scaled for maintaining the same proportion of the real hands.

Participants were informed at the beginning of the experiment that they had to perform a go/no-go task to indicate whether the target finger had been stimulated (go) or not (no-go). Specifically, they were instructed to keep the right foot-pedal pressed and to release it to indicate they felt a tactile stimulus at the target finger. The experiment comprised six separate blocks. At the beginning of each block a sentence was presented on the computer screen above the participant's hands to indicate the target finger for the entire block of trials (e.g., "The target finger is the right index"). Understanding of

this instruction was always double checked by asking participants to report verbally to the experimenter which was the designated target finger for each given block.

Each trial started with the fixation point appearing on white background in the centre of the screen. Participants were instructed to keep fixation throughout the duration of the experimental block. After a variable interval ranging between 200 and 400 ms from fixation onset, tactile stimulation was presented. The tactile stimulation consisted of either: (1) a <u>single</u> touch delivered to designated target finger (target only trials); (2) <u>two</u> touches delivered simultaneously, one to the target finger and one to a non-target finger (double simultaneous stimulation trials); (3) a <u>single</u> touch delivered to one of the non-target fingers (catch trials).

The diagram in Figure 1 illustrates all of the possible stimulation conditions for an example block in which the target-finger is the right index finger. <u>Target only trials</u> (Figure 1a), will be identified hereinafter as 'T' trials. <u>Double simultaneous trials</u> will be divided as a function of position of the stimulated non-target finger with respect to the target-finger. Namely, the non-target finger could be on the same or different *hand* with respect to the target, and it could be on the same or different *finger* with respect to the target. As illustrated by Figures 1b-d, three DSS trials were possible: (1b) target plus the different finger of the same hand (i.e., 'T+DFSH' trials); (1c) target finger plus the same finger of the different hand (i.e., 'T+SFDH' trials); or (1d) target finger plus different finger of the different hand (i.e., 'T+DFDH'

trials). Finally, catch trials were also coded with respect to the position of the stimulated non-target finger relative to the target finger. As illustrated in Figures 1e-g, three types of catch trials were possible: (1e) 'DFSH' trials, for a non-target occurring at a different finger of the same hand; (1f) 'SFDH' trials, for a non-target occurring at the same finger of the different hand; and (1g) 'DFDH' trials, a non-target occurring at the different finger of the different hand.

Critically, three different visual conditions were provided across blocks. The first visual condition consisted of just the fixation point (Fixation only) (see Figure 2b). The second visual condition consisted of the fixation point with the addition of an image of the participant's own hands (see Figure 2c). The third visual condition consisted of the fixation point with the addition of four empty circles (diameter 9 mm, 6.5° of visual angle), arranged to match exactly the position of the stimulated fingertips of the hands under the screen (Circles) (see Figure 2d).

Fixation overstayed tactile stimulation for 100 ms then was replaced by a question-mark instructing participants to respond as to whether the target finger had been stimulated or not. Participants were instructed to react as fast and accurately as possible and were informed that they had a maximum of 2 seconds to respond before the beginning of the next trial. No accuracy feedback was provided, but a warning message was presented on the screen if the foot-pedal was released before the tactile stimulation. Participants were allowed short breaks between blocks. The experimenter remained in the room

throughout the session to ensure that participants complied with the instructions. The order of visual conditions and target hand (left or right) was pseudo-randomised across participants. By contrast, the designated target finger (index vs. middle) was changed between participants: half of the participants performed the task with the index as target finger and the other with the middle finger as target, for a total of 1008 trials. Stimulation conditions were equiprobable and randomised within each block of trials. Each block comprised 84 trials (i.e., 7 stimulation conditions repeated 12 times), resulting in a total 504 trials for each experimental group.

Design and analysis

We used the proportion of hits and false alarms to compute sensitivity and criterion measures according to Signal Detection Theory (Macmillan & Creelman, 1991). For the three DSS trial conditions we used proportion correct in T+DFSH, T+SFDH and T+DFDH conditions as hits, and proportion of errors in DFSH, SFDH and DFDH conditions as false alarms. For the target only condition, false alarms were computed as the mean of the proportion of errors in the three catch trial conditions. Mean response times (RTs) were also computed for each participant for correct trials only. We pooled together the data when the target was at the left hand and when the target was at the right hand in order to have a minimum number of 8 points per cell.

Results

RTs, sensitivity, criterion and percentage of errors across conditions are reported in Table 1 and Figure 3 as a function of the visual conditions. As can be seen in Figure 3, a significant decrement of performance when the target finger was stimulated concurrently with a non-target finger was evident both in terms of RTs and sensitivity (compare T and DSS trial conditions). However, the impact of DSS differed as a function of the combination of target and non-target finger stimulation. Mean RT, sensitivity (d') and criterion data were entered separately into three analyses of variance (ANOVA) with Stimulation Condition (T, T+DFSH, T+SFDH, T+DFDH) and Visual Condition (Fixation, Hands, Circles) as within-participant variables and Target Finger (index finger, middle finger) as between-participant variable. The Tukey HSD test was used for all post-hoc comparisons.

The analysis on RT data revealed a main effect of Stimulation Condition ($F_{(3,48)}$ = 26.088, p < 0.0001) caused by faster responses in the T condition (mean = 551 ms, SE = 23 ms) than all DSS conditions (all p < 0.0002). Note that RTs were faster for the T+SFDH condition (mean = 600 ms, SE = 28 ms) than T+DFDH condition (mean = 630 ms, SE = 26 ms; p = 0.038) revealing less interference selectively for this between-hands condition. No other main effect or interaction was found (all Fs < 1.4).

The analysis on sensitivity also revealed a main effect of Stimulation Condition ($F_{(3, 48)}$ = 31.783, p = 0.0001) caused by better performance for T condition (mean = 4.11, SE = 0.1) than T+DFSH (mean = 2.89, SE = 0.15; p =

0.0002), and T+DFDH conditions (mean = 3.53, SE = 0.15; p = 0.001). Instead, no difference emerged between the T and T+SFDH conditions. In addition, T+SFDH (mean = 4.01, SE = 0.12) proved significantly better than T+DFSH (mean = 2.89, SE = 0.15; p = 0.0002) and T+DFDH condition (mean = 3.53, SE = 0.15; p = 0.007), similarly to the pattern described above for RTs. Moreover, the cost was more pronounced for DSS trials occurring within (T+DFSH) than between (T+DFDH) hands conditions (p < 0.0003).

This analysis also revealed a main effect of Visual Condition, ($F_{(2, 32)}$ = 7.345, p = 0.002), caused by better performance with Circles (mean = 3.80, SE = 0.11) compared to Fixation (mean = 3.55, SE = 0.13; p = 0.006) and Hands conditions (mean = 3.56, SE = 0.15; p = 0.007). No other main effect or interaction was found (all Fs < 1.7).

The analysis on criterion revealed a main effect of Stimulation Condition, ($F_{(3,48)}$ = 18.942, p = 0.0001), caused by a more conservative criterion adopted in T+DFSH condition (mean = 0.54, SE = 0.13) than the T (mean = -0.001, SE = 0.07; p = 0.0001) and the T+SFDH conditions (mean = 0.15, SE = 0.11; p = 0.0003). Moreover, a more conservative criterion was used in the T+DFDH condition (mean = 0.49, SE = 0.11) compared to the T (mean = -0.001, SE = 0.07; p = 0.0001) and the T+SFDH conditions (mean = 0.15, SE = 0.11; p = 0.001). The analysis also revealed a main effect of Visual Condition ($F_{(2, 32)}$ = 4.115, p = 0.03), caused by less conservative criterion when the participant's own hands were presented on the screen (mean = 0.21, SE = 0.1) as compared

to the Fixation only condition (mean = 0.35, SE = 0.1; p = 0.04). No other main effect or interactions were found (all Fs < 2.1).

Finally, we separately examined the percentage of errors made by the participants in the catch trials conditions (see Figure 4c). Inter-participant percentage of errors in catch trials was entered into a repeated measure ANOVA with Stimulation Condition (DFSH, SFDH and DFDH) and Visual Condition (Fixation, Circles and Hands) as within-participant variables. This analysis revealed a main effect of Stimulation Condition ($F_{(2, 32)} = 9.4$, p = 0.001), caused by more errors in the DFSH (mean = 4%, SE = 0.02) than SFDH (mean = 1.5%, SE = 0.01; p < 0.02) and DFDH conditions (mean = 0.3%, SE = 0.004; p < 0.001). There was also a main effect of Visual Condition ($F_{(2, 32)} = 11.6$, p = 0.0002), caused by participants making more errors when their own Hands were displayed (mean = 3%, SE = 0.01) as compared to when the Circles (mean = 1%, SE = 0.004; p < 0.03) or just the Fixation point were displayed (mean = 2%, SE = 0.01; p < 0.0002). This pattern of results emerged selectively in DFSH trials (Hands: mean = 6%, SE = 0.01; Fixation only: mean = 3%, SE = 0.01; Circles: mean = 1%, SE = 0.01), resulting in a significant interaction between Stimulation Condition and Visual Condition ($F_{(4,64)} = 5.2$, p = 0.001).

Discussion

Experiment 1 examined whether non-informative vision of the participants' own hands could improve target detection in a tactile DSS

paradigm, by comparing a condition in which a digital image of the participant's own hands was seen with a condition in which the hands were not visible. Furthermore, as a control for any spatial attention benefit related to the visible fingers acting like place-holders, a third condition was included in which no hands were visible, but circles were presented spatially aligned with the position of the stimulated fingertips to serve as non corporeal place-holders. Our working hypothesis was that if non-informative vision of the stimulated body parts can affect the tactile interference generated by DSS, then performance should be overall improved when the participant's own hands were visible with respect to the circles and the fixation only conditions.

Significant tactile interference effects emerged in terms of RTs and sensitivity, revealing substantial and replicable DSS costs both within and between hands. These findings confirm and extend our previous work (Tamè et al., under review), by showing that between hands DSS costs are not limited to RT interference, but also emerge as a drop in touch sensitivity (d'). These findings imply, as we previously suggested, that DSS interference is driven by a competition that is solved at a relatively low stage of tactile representation, in which bilateral representations of the fingers are available. Also consistent with our previous work, we found that DSS interference was significantly reduced, if not entirely abolished, when homologous fingers across hands were stimulated (i.e., T and T+SFDH conditions did not differ). We previously suggested (Tamè et al., under review) that this selective lack of interference may reflect a redundancy of spatial codes identifying the target

finger (same finger stimulated between hands) and the region of external space (same location with respect to the trunk). The redundancy of congruent spatial codes can, in turn, reduce the interference produced by DSS conditions. In sum, here we replicated and extended to sensitivity measure the DSS interference pattern we had previously observed. In particular, stronger interference was present when target and non-target combinations of stimuli were 1) delivered within as compared to between hands and, 2) delivered to non-homologous, as compared to homologous fingers.

The results of Experiment 1 also documented a significant modulation of the visual condition on tactile performance. However, a significant enhancement of sensitivity emerged when the circles, but not the participant's hands, were added to the visual scene. Moreover, seeing the circles changed only overall tactile performance, but not the pattern of DSS interference within or between fingers (i.e., the interaction between vision and stimulation condition was far from significance). We suggest that this finding is compatible with the circles allowing for a better focusing of selective spatial attention on the regions of visual space in which the tactile stimuli were delivered. In other words, the circles could efficiently serve the role of place-holders (for a discussion on the role of multisensory spatial attention in touch perception see Spence, 2002; see also Spence, Pavani & Driver, 2000). More relevant to our working hypothesis, however, vision of the participant's own hands did not improve overall sensitivity. One possible interpretation for this result in terms of spatial attention, also compared with the results of the

circles condition, is that seeing an image of the hands could lead to a more spread distribution of spatial attention over the hands, instead of being sharpened over the fingertips position (see Figure 2c). Whatever interpretation, the present findings reveal a context of tactile stimulation which appears to be largely insensitive to the benefits of non-informative vision of the stimulated body part (i.e., do not show VET effects).

As we mentioned in the Introduction, previous work on visuo/tactile interaction reported VET effects on a variety of tactile tasks (e.g., Fiorio & Haggard, 2005). Vision of a body part may result in faster responses to touch (Tipper et al., 1998) and enhancement of tactile acuity (Kennett et al., 2001). Recent evidence suggested that VET could be ascribed to top-down modulations on primary somatosensory cortex from multimodal areas. These projections could affect touch by modulating the relative dimension of the tactile receptive fields on the stimulated body part (Press et al., 2004; Serino & Haggard, 2009). Considering that tactile DSS interference is also proposed to occur at the relatively lower level of representation, vision of the hands should have in principle affected either the overall tactile performance, or the particular spatial pattern in which DSS interference manifests itself. Neither types of modulation occurred, despite the paradigm proved to be otherwise sensitive to visual modulations, as demonstrated by the overall improvement in performance when circles were added to the visual scene. One possible explanation could be that our task did not fully adhere to the requirements which have been proposed to be crucial for VET to emerge. In particular,

Press and colleagues (2004) have argued that VET would only be observed when the tactile task is difficult and spatial. While our task was surely difficult (see drop of d' values in Table 1 for several of the DSS conditions), it did not require an explicit spatial judgement on the stimuli. Nonetheless, it should be emphasised that good performance in the DSS task could only be achieved by correctly locating the touch in body space, because responses were requested only when the designated target finger was touched. Thus, an alternative explanation is that VET did not influence our task because DSS competition is resolved primarily within the somatosensory modality.

Interestingly, the analyses of catch trials (i.e., single stimulation of a non-target finger) did reveal a modulation of the visual conditions, with higher percentage of errors when the participant's own hands were presented visually. Notably, this visual modulation occurred within, but not between hands: catch trials were misattributed more often to the target-finger when stimulated non-target fingers were on the same hand as the target, but not on the other hand. This result cannot be ascribed to a proper form of VET (see Haggard, Christakou & Serino, 2007 for other evidence showing decrement of tactile performance when viewing the stimulated body part), and could reflect some broadening of visual attention to the entire (target) hand when this is visible. Alternatively, it could reflect a change in the response criterion which emerges selectively for this visual condition. Examination of the criterion did indeed reveal that participants changed their response bias as a function of the different conditions of the task. Responses were more conservative in the

most difficult tactile conditions (i.e., non-target stimulation at the non-homologous finger of the same hand or the non-homologous finger of the opposite hand). In addition, a change in the responses criterion was also found when participants saw their own hands with respect to fixation only. In the latter case, subjects adopted a more liberal criterion, possibly suggesting a tendency favouring 'go' responses when a body part was seen (see Johnson et al., 2006).

EXPERIMENT 2

In Experiment 1 we found a substantial amount of tactile interference under DSS that was stronger within, but consistently present also between hands, as well as an overall improvement in performance (i.e., a general reduction of such interference) when circles, but not hands, were visually added. While VET would have produced improvements in tactile behaviour, there are other ways through which vision may affect touch perception, namely by hampering tactile performance (e.g., Folegatti et al., 2009). Such interfering effects have been recently documented in the context of a paradigmatic example of visual dominance on touch and proprioception: the rubber hand illusion (RHI). In this famous multisensory illusion, vision of rubber hand stimulated in synchrony with the participant's own hand hidden from view produces a conflict between visual and tactile/proprioceptive inputs (Botvinick & Cohen, 1998). Following RHI, participants typically show shifts of the felt position of their own hand towards the fake one. In addition,

they report that synchronous touches were felt towards the location where they saw the rubber hand being touched. Recent works have investigated the implications of this visuo-proprioceptive conflict for tactile performance (Folegatti, de Vignemont, Pavani, Rossetti & Farnè, 2009; Longo, Schüür, Kammers, Tsakiris & Haggard, 2008; Moseley, Olthof, Venema, Don, Wijers, Gallace & Spence, 2008). In particular, Folegatti and colleagues (2009) aimed to disentangle whether any modulation of vision on touch in the RHI reflected some form of disownership of the participant's own hand, or instead the experienced visual-proprioceptive mismatch between the seen and felt hand position. In the first experiment they used the classical RHI paradigm, whereas in the second one they took advantage of optically deviating prismatic goggles to reproduce a visual-proprioceptive conflict between the seen and felt position of the actual participants' hand, without introducing any ambiguity about hand ownership. As a result of both manipulations they found a general lengthening of tactile reaction times. The finding that comparable interference effects were observed in absence of explicit feelings of disownership led the authors to suggest that tactile perception was hampered by the conflict between visual and proprioceptive information (Folegatti et al., 2009).

It is therefore possible that the tactile interference reported under DSS in Experiment 1, although not sensitive to visual manipulation that would improve performance, could still be worsened by conflicting visual-proprioceptive information. To test this possibility, in Experiment 2 we

modulated the spatial congruency between the seen and felt hand posture. Across blocks, participants saw an image of their hands with either a congruent or an incongruent posture with respect to that actually adopted (compare Figure 4a and 4b, respectively). If such a conflict between vision and proprioception is effective in modulating tactile interference under DSS, one should expect better performance for congruent compared to incongruent multisensory condition.

< Please insert Figure 4 about here >

Methods

Participants

Fourteen participants (mean age = 23 years, SD = 7; 12 females) took part in the experiment. All reported normal or corrected to normal vision, normal touch and were unaware of the purpose of the experiment. Thirteen were right-handed by self-report, one was left-handed.

Apparatus, Stimuli and Procedure

These were identical to Experiment 1, with the following exceptions. Tactile stimulation consisted of a supra-threshold square-wave pulses, resulting from fixed current (40V) fed into the stimulators for 8 ms (Current generator: Lafayette M10-DP-305E, Dual Output Adjustable DC Power Supply). The visual conditions displayed one of two different images of the

participant's own hands. In one visual condition, fingers formed an imaginary square of 4 cm as in Experiment 1, depicting a posture that was fully congruent with the actual one of the participant (see Figure 4a). In the other condition, the fingers were much closer and centred around the fixation point, depicting a posture that was incongruent with the actual one of the participant (see Figure 4b).

The experiment comprised eight separate blocks. In four blocks, the image of the participant's own hands was congruent with the actual hand position (one block for each of the four possible target locations; i.e., right index finger, right middle finger, left index finger and left middle finger). In the remaining blocks, the image was incongruent with the actual hand position. Each block comprised 70 trials (i.e., 7 stimulation conditions repeated 10 times), resulting in a total 560 trials.

Design and analysis

As for Experiment 1, RTs, sensitivity (d') and criterion (c) were considered and analysed. We ran an overall analysis comprising the Stimulation Conditions (e.g., T, T+DFSH, T+SFDH and T+DFDH), the identity of the Target Finger (index finger and middle finger) and Visual Condition (congruent and incongruent) as within-participant variables. To calculate the mean RTs on a minimum number of seven correct responses for each design cell, we pooled the data regardless of target finger and target hand. This resulted in a 4x2 factorial design. Mean response times (RTs) for

correct answers were also computed for each participant, for each cell of the experimental design.

Results

Response times, sensitivity and criterion across conditions are reported in Table 2 and Figure 5 as a function of the visual conditions (percent errors are also reported in Table 2 for completeness, though not analysed further because we chose to focus on sensitivity measure instead). Mean RT data were analysed by a repeated measure ANOVA with Stimulation Condition (T, T+DFSH, T+SFDH, T+DFDH) and Visual Condition (congruent vs. incongruent) as within-participant variables. This analysis revealed a main effect of Stimulation Condition ($F_{(3,39)}$ = 27.2, p < 0.0001), caused by better performance in target only trials (mean = 543 ms, SE = 30 ms) than in all DSS trials conditions (averaged DSS trials; mean = 626 ms, SE = 44 ms; p < 0.0003 for all DSS trials conditions). In addition, more interference emerged for T+DFDH (mean = 650 ms, SE = 44 ms) than T+DFSH condition (mean = 611 ms, SE = 43 ms; p < 0.01). No other main effect or interaction reached significance (all Fs < 1).

The analysis on sensitivity revealed a main effect of Stimulation Condition ($F_{(3,39)}$ = 24.3, p < 0.0001), caused by larger interference for DSS trials (averaged DSS trials; mean = 2.90, SE = 0.36) with respect to Target only trials (mean = 3.71, SE = 0.24; p < 0.02 for all comparisons). Moreover, less interference emerged for T+SFDH (mean = 3.26, SE = 0.35) than T+DFSH

(mean = 2.58, SE = 0.34; p < 0.0003), and T+DFDH conditions (mean = 2.85, SE = 0.40; p < 0.03). Moreover, the cost observed from non-target stimulation of non-homologous fingers (i.e., T+DFSH and T+DFDH conditions) was comparable within and between hands (p < 0.24), in accordance with the pattern described in Experiment 1.

In addition, there was a main effect of Visual Condition, ($F_{(1,13)}$ = 7.6, p < 0.02) caused by enhanced sensitivity when the seen hands were congruent (mean = 3.22, SE = 0.46) rather than incongruent (mean = 2.99, SE = 0.40; p < 0.02) with the actual hands posture. The analysis also revealed a main effect of Target Finger ($F_{(1,13)}$ = 12.1, p < 0.004), caused by a better sensitivity for the index (mean = 3.25, SE = 0.43) than middle fingers (mean = 2.96, SE = 0.43; p < 0.004). No other main effect or interaction proved significant (all Fs < 2.7).

The same analysis on criterion revealed a main effect of Stimulation Condition ($F_{(3,39)}$ = 27.323, p < 0.0001), caused by less conservative criterion when responding to Target only (mean = 0.13, SE = 0.14) than other DSS trials (all p < 0.001), and more conservative criterion when responding to the T+DFDH condition (mean = 0.84, SE = 0.21) than all others conditions (all p < 0.01). There was also a main effect of Visual Condition ($F_{(1,13)}$ = 11.127, p < 0.005), caused by less conservative criterion for the congruent (mean = 0.46, SE = 0.26) than the incongruent hand condition (mean = 0.59, SE = 0.26; p = 0.006). This was particularly evident for the index finger resulting in a

significant interaction between Visual Condition and Target Finger ($F_{(1,13)}$ = 13.434, p < 0.003).

< Please insert Figure 5 about here >

Finally, similar to Experiment 1, we examined the percentage of errors made by participants in the catch trials (see Figure 5c). The inter-participant errors percentage was entered into a repeated measure ANOVA with Stimulation Condition (DFSH, SFDH and DFDH) and Visual Condition (congruent vs. incongruent) as within-participant variables. This analysis revealed a main effect of Stimulation Condition ($F_{(2, 26)}$ = 9.98, p = 0.001), driven by more errors in the DFSH condition (mean = 7%, SE = 0.001) than in the SFDH (mean = 1%, SE = 0.003) and DFDH conditions (mean = 1%, SE = 0.001; p < 0.003 for both comparisons). No other main effect or interaction was significant (all Fs < 1).

Discussion

Experiment 2 examined the role of a visual proprioceptive conflict on tactile DSS, by comparing a condition in which an image of a participant's own hands was congruent with the real hand posture (see Figure 4a), with a condition in which the image was incongruent with the real hand posture (i.e., fingers close together; see Figure 4b). The rationale behind this manipulation was that if the conflict between vision and proprioception

affects tactile performance, as indexed by the DSS, one should expect a better performance for the visual congruent condition as compared to the incongruent condition.

A substantial amount of tactile interference emerged in terms of sensitivity for all the DSS trials. Further, the interference was more pronounced for the conditions in which the non-target finger was stimulated on the same hand as the target and when it was the non-homologous finger of the other hand. These data on sensitivity reflect the same trend showed by Experiment 1. When considering RTs, an interference effect was also revealed that, however, was more evenly distributed across fingers (see Figure 5a and b).

As predicted, Experiment 2 also revealed a significant overall reduction of sensitivity when incongruent hands images were presented with respect to congruent hands. This visual effect may indeed be referred to the postural mismatch between the visual and proprioceptive inputs, similarly to what reported by Folegatti and colleagues in a single detection task approach (Folegatti et al, 2009). However, similarly to Experiment 1, there was no significant modulation of the pattern of tactile interference effect produced by the DSS trials conditions as a function of visual-proprioceptive congruency. This finding clearly suggests that conflicting information between vision and proprioception is not able to alter the specific pattern of within- and between-hand interference that is observed under tactile DSS conditions. This finding is again compatible with the notion that any DSS interaction leading to

decreased performance in touch perception may be resolved trough primarily unisensory tactile processes.

The percentage of errors in the catch trials did not reveal differences between the two visual-proprioceptive conditions (congruent vs. incongruent), and the pattern of results was equal to that observed in Experiment 1, with more errors for catch trials occurring on the same hand as the target, than catch trials occurring on the other hand. Finally, the analysis of criterion revealed a change in the participants' responses tending to be more conservative in DSS trials with respect to Target only trials. A more liberal responses criterion was also found when participants saw their own hands in the congruent, as compared to the incongruent position, showing that not only sensitivity, but also response criterion may change as a function of whether congruent or incongruent visual and proprioceptive information are provided, thus concurring to the overall tactile performance.

EXPERIMENT 3

In Experiment 2 the influence of non-informative vision on touch emerged as an overall reduction of tactile sensitivity when the seen hands had an incongruent posture with respect to the participant's unseen hands. We interpret this finding as the result of impaired coding of touch caused by visual/proprioception mismatch. However, this mismatch did not affect tactile interference caused by DSS stimulation, nor the modulations of this interference as a function of the spatial relationship between target and non-

target fingers.

In this final experiment, we specifically aimed to alter (i.e., reduce) the visual separation between the fingers, both within and between hands, in the attempt to directly modulate the DSS across fingers and hands. To this aim we changed the visible structural morphology of the participant's own hands, by showing to the participants a visual image characterised by webbed index and middle fingers of either hand (i.e., within-hand visual morphing; see Figure 4c), or a visual image characterised by merging of the homologous fingers of the two hands (i.e., between-hands visual morphing; see Figure 4d). Evidence that actual binding of the fingers affects perception at a low stage of the information processing (SI) come from a recent work of Stavrinou and colleagues (2006). They bound together the fingers of the right hand (D2, D3, D4 and D5) using medical cloth and measured the changes in the hand representation in SI using magnetoencephalography (MEG), before, during and after this manipulation. The results showed decreased Euclidean distance between the activated cortical regions (D2, cortical area that represent the forefinger; D5, cortical areas that represent the small finger), indicating fast plastic changes after this transient modification of the hand structure (Stavrinou, Della Penna, Pizzella, Torquati, Cianflone, Franciotti, Bezerianos, Romani & Rossini, 2006). To our knowledge, the manipulation we introduced in this final experiment is the first attempt at changing some aspects of the hand morphology through vision.

Our predictions were straightforward. We expected to increase within-hand interference, when the index and middle fingers of the same hand appeared as webbed (within-hand visual morphing), and to increase between-hand interference when the homologous fingers of the two hands appeared as merged (between-hands visual morphing). To compare the performance in these two morphed conditions with a baseline in which 'normal' hands were visible, we recruited for this experiment 10 participants that also completed Experiment 2, for which data on the 'congruent' hand condition had already been acquired.

Methods

Participants

Ten participants from Experiment 2 (mean age = 24 years, SD = 8; 8 females) were recruited again to take part in this experiment. All reported normal or corrected to normal vision, normal touch and were unaware of the purpose of the experiment. Nine were right-handed and one was left-handed by self-report.

Apparatus, Stimuli, Procedure and Design

These were identical to Experiment 2, with the following exceptions. Images of the hands always matched the actual hands posture of the participant. However, by using an images modelling program (Adobe Photoshop CS3) we altered the visual morphology of the fingers. The first

morphed digital image was characterised by a webbed portion of a hand, that connected the index and middle fingers of the same hand (within-hand visual morphing, Figure 4c). The second morphed digital image was characterised by a webbed portion of the medial finger phalange that connected index and middle finger of either hand (between-hand visual morphing, Figure 4d).

The experiment comprised eight separate blocks. In four blocks, the within-hand morphed image was used. In the remaining blocks, the between-hand morphed image was adopted. Each block comprised 70 trials (i.e., 7 stimulation conditions repeated 10 times), resulting in a total 560 trials.

Results

RTs, sensitivity, criterion and percentage of errors across conditions are reported in Table 3 and Figure 6 as a function of the visual conditions (note that the 'normal hands' condition reports data from the congruent condition of Experiment 2, for the 10 participants who participated in both experiments).

Mean RT data were analysed using a repeated measure ANOVA with Stimulation Condition (T, T+DFSH, T+SFDH, T+DFDH) and Visual Posture (normal, within-hand visual morphing, between-hands visual morphing) as within-participant variables. This analysis revealed a main effect of Stimulation Condition ($F_{(3,27)}$ = 43.8, p < 0.0001), caused by better performance in target only trials (mean = 528 ms, SE = 24 ms) than in all DSS trials conditions (averaged DSS trials; mean = 600 ms, SE = 29 ms; p < 0.0002 for all

DSS trials conditions). No other main effect or interaction reached significance (all Fs < 1).

We ran another ANOVA on sensitivity with Stimulation Condition (T, T+DFSH, T+SFDH, T+DFDH), Target Finger (index finger or middle finger) and Visual Posture (normal, within-hand visual morphing, between-hand visual morphing) as within participants variables. This analysis revealed a main effect of Stimulation Condition, ($F_{(3,27)}$ = 24.3, p = 0.0001), caused by better performance for T (mean = 3.87, SE = 0.30) than all DSS conditions (T+DFSH: mean = 2.48, SE = 0.45; p < 0.0002; T+SFDH: mean = 3.37, SE = 0.49; p < 0.03; T+DFDH: mean = 2.99, SE = 0.46; p < 0.0002). This cost was more pronounced for DSS trials occurring within than between hands (both ps < 0.03). Unlike the previous experiments, in this smaller-sized group the difference between homologous and non-homologous fingers of the non-target hand failed to reach significance (p = 0.13), although the numerical trend corresponded exactly to the one previously observed (compared Figures 3b, 5b, and 6b). The analysis also revealed a main effect of Target Finger ($F_{(1,9)}$ = 9.27, p = 0.01) caused by a better performance for the index (mean = 3.31, SE = 0.42) than the middle finger (mean = 3.04, SE = 0.59; p < 0.01). No other main effect or interaction reached significance (All Fs < 1.6).

The same analysis on criterion revealed a main effect of Stimulation Condition ($F_{(3,27)}$ = 28.3, p < 0.0001), caused by less conservative criterion when responding to Target only (mean = 0.07, SE = 0.11) than other DSS trials (all p < 0.0002).

Finally, similar to previous Experiments, we examined the percentage of errors made by participants in the catch trials (see Figure 6c). The inter-participant errors percentage was entered into a repeated measure ANOVA with Stimulation Condition (DFSH, SFDH and DFDH) and Visual Posture (normal, within-hand visual morphing, between-hands visual morphing) as within-participant variables. This analysis revealed a main effect of Stimulation Condition ($F_{(2, 18)}$ = 12.0, p = 0.0005), driven by more errors in the DFSH condition (mean = 6%, SE = 0.03) than in the SFDH (mean = 1%, SE = 0.007) and DFDH conditions (mean = 1%, SE = 0.006; p < 0.002 for both comparisons). No other main effect or interaction was significant (all Fs < 1).

Discussion

Experiment 3 examined the role of visual changes in the structural morphology of the hands on tactile interference, using within- and between-hand visual morphing of the participant's own hands. Our working hypothesis was that if a change in the visual structural morphology affects the low stages of tactile representation, we should see a modulation of the interference as a function of the within- or between-hand morphing.

In accordance to the previous Experiments a cost for DSS trials with respect to the target only trials was observed, confirming once again the stability of the DSS interference effect. Moreover, and again in full agreement with the previous experiments, interference was stronger within- than between-hands. However, the structural visual morphing did not affect tactile

perception, nor the DSS interference within and between hands. At first sight, this may be surprising given the very salient visual change of body structure in this final experiment. However, it should be noted that the visual position of the fingers, although morphed, exactly matched the unseen hand and fingers posture. This finding, when combined with the evidence from Experiment 2 showing that even minimal visuo-proprioceptive discrepancies can affect tactile perception, clearly indicates that seemingly salient changes of the visual body-structure are actually less effective than intersensory mismatches in affecting touch perception.

The percentage of errors for the catch trial conditions were not modulated by the type of morphing, however data were consistent with Experiment 2 in showing that the highest percentage of errors emerged with catch trials within- than between-hands. Finally, the analysis on criterion revealed more conservative responses for DSS that target only trials, without any difference between DSS conditions. No difference in criterion emerged as a function of the visual form of the hands, again indicating that morphing is less effective than visuo-proprioceptive mismatch in changing the participant's response to touch.

General Discussion

The aim of the present study was to test whether and to what extent the DSS paradigm for tactile stimuli presented at the fingers of the two hands could be affected by different levels of manipulations of hand-related visual

inputs. We start by considering the pattern of DSS tactile interference within- and between-hands, as a function of homologous and non-homologous finger stimulation. We then discuss the role played by the different visual manipulations we have tested. Finally, we discuss the implication of criterion changes for studies measuring the effect of vision on touch perception.

DSS tactile interference extends across body sides

Across all experiments, DSS interference effects emerged reliably both in terms of RTs and sensitivity. Performance for target only trials was systematically better compared to DSS trials. While the cost for DSS trials within and between hands was comparable in RTs, a clear difference between the two conditions consistently emerged when considering the sensitivity measure (d′). First, interference was always larger within than between hands, in accord with previous reports on competing touch at the fingers (e.g., Craig, Green & Rhodes, 1985; Craig, 1985a; Evans, Craig & Rinker, 1992; Evans & Craig, 1991). Moreover, we documented a difference in sensitivity as a function of whether the non-target finger was homologous and non-homologous to the target finger. Stimulating the non-homologous finger invariably produced worse performance than stimulating the homologous finger, to the extent that in Experiment 1 the latter condition did not result in any interference with respect to the target presented alone. This finding replicates and extend previous work from our group (Tamè et al., under review), which documented reduced interference or even increased sensitivity

for the homologous finger of the non-target hand with respect to the target alone (see also Laskin & Spencer, 1979).

The higher DSS interference for non-homologous fingers is compatible with competition occurring in somatotopically organised brain regions (e.g., SI and SII). Furthermore, the fact that DSS interference extends across body sides also provides further support to this notion. Neurophysiological studies in animals (Iwamura et al., 2001, 2002; Killackey et al., 1983) and neuroimaging studies in humans (Hlushchuk & Hari, 2006; Staines, Graham, Black & McIlroy, 2002; see also Chapter 3.3 of the present thesis) have documented responses to ipsilateral tactile stimulations both in SI and SII (for behavioural evidence see also Braun et al., 2005; Harris, Harris & Diamond, 2001). Finally, the attribution of DSS interference to early stages of representation is supported by our previous work (Tamè et al., under review), which showed that the interference at non-homologous fingers was entirely unaffected by changes in the actual hand posture (i.e., whether the stimulated hands were palm-up or palm-down).

DSS tactile interference escapes modulations from hand related visual inputs

The second main finding of the present work is that competition between concurrent touches at the fingers giving rise to DSS interference is <u>not</u> affected by adding and/or modifying the appearance of the hands as visual recipients of the tactile stimuli. The presence or absence of the participant's own hand in the scene (Experiment 1), the congruency of seen

and felt hand posture (Experiment 2), or the modifications of the seen hand structure (Experiment 3) did not alter the grade of DSS interference or the way it manifested across hands and fingers. This is not say, however, that vision had no impact on tactile perception, because effects of non-informative vision did emerge in both Experiment 1 and 2.

In Experiment 1, we observed a significant enhancement in sensitivity only when the circles were visually added to the scene. We suggested that this enhancement may derive from better focusing of selective spatial attention in the regions of space in which tactile stimuli occurred (see Spence, 2002; Spence et al., 2000). Contrary to our predictions based on the VET effect, no beneficial effect of seeing the own hands emerged. In fact, seeing the own hands (which were always in a congruent posture with respect to the unseen hands) resulted in higher percentage of errors in the catch trials, when the non-target was delivered on the same hand as the target. In Experiment 2, we observed a significant overall reduction of sensitivity when participants saw an image of their own hands in a posture that was incongruent with the actual posture they adopted, compared to when the seen and felt postures matched. We suggested that this visual effect may derive from the postural mismatch between the visual and proprioceptive inputs, similarly to what has been recently reported by Folegatti and colleagues in a single detection task approach (Folegatti et al, 2009). Notably, the spatial mismatch between vision and touch in Experiment 2 was considerably smaller than the one adopted by

Folegatti and colleagues (which was of 15 degrees), but nonetheless it proved sufficient to affect tactile perception.

Taken together these findings indicate that the competition between concurrent targets at the fingers may be resolved within the somatosensory modality.

Criterion

A final aspect worth discussing is the shift in criterion observed across experiments as a function of difficulty and the reliability of the own hands image. When stimulation conditions were more difficult (i.e., when the distractor finger was the non-homologous finger within or between hands) response criterion was more conservative compared to when the stimulation condition was easier (i.e., single touch or DSS stimulation on the homologous fingers of the non-target hand). This finding suggests that participants regulated their response criterion depending of task difficulty. More relevant to the purpose of the present work, a change in the responses criterion was also found when the participants saw their own hands in a congruent posture with respect to their unseen hands. In this visual condition, they were more prone to respond that the stimulus was present. Taken together the results on criterion suggest that participants were more prone to give a positive response, in an uncertain condition, when a plausible own body part was seen with respect to no visual input or not reliable image of their own body.

Our finding therefore adds to one recent observation that suggested a role of criterion shift in some of the studies that reported visual enhancement of touch (Johnson et al., 2006). The authors have argued that studies on VET that did not used SDT in their data analysis (e.g., Kennett et al., 2001) are open to an interpretation of performance enhancement in terms of a shift in criterion. While criterion shift cannot explain the VET effects reported in studies using two alternative forced-choice paradigm (e.g., Taylor-Clarke, Kennett & Haggard, 2004), in which a bias should makes performance close to chance level (Longo, Cardozo & Haggard, 2008), the precise role played by criterion shifts on tactile tasks performed under non-informative visual inputs remains to be qualified. Our results add to this debate by showing that criterion shifts should not be ignored, because non-informative hand vision does indeed modulate criterion independently of sensitivity.

Conclusions

Taken together the results of the present work suggest that the DSS interference effect is a reliable and constant phenomenon that occurs at low stage of tactile representation processes. In addition, at between-hand level this interference seems to be primarily modulated by the somatotopic relationships between fingers. Moreover, DSS interference is not affected by visual factors, in particular related to a seen body part. Thus, the DSS paradigm seems to be largely immune to matching or conflicting vision of the stimulated body part, suggesting the DSS interference may occur at a purely

somatosensory level, possibly prior to modulations of vision on touch perception. Finally, the similarly consistent criterion shifts, found when vision of the tactually stimulated body-parts is additionally provided, also proved to be inefficient in modulating the specific pattern of DSS interference. The latter finding, while strengthening the notion of the DSS interference as a unisensory phenomenon, definitively emphasises the usefulness of considering the SDT approach when assessing intersensory modulation of perception.

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Figure captions

Figure 1. Schematic drawing of the stimulation conditions. Stimulated target finger is indicated by the white circles, while the filled black circles represent the distractor finger. In this example the target finger is the right index finger (see panel a). Double simultaneous trials are illustrated in panels b, c, and d. Catch trials for this example block are illustrated in panels e, f, and g. See text for details.

Figure 2. Schematic drawing of the experimental setup as seen from the participants' perspective. Note that hands and tactile stimulators are shown here only for illustrative purposes, as they were in fact occluded under the horizontal computer display and not visible to the participant throughout the experiment (panel a). Tactile stimulation are not shown in the figure. Illustrations of the three possible visual conditions are showed in panels b, c, and d. The white screen with a black circle at the center (fixation point) is illustrated in panel b. The picture of the participant's own hands positioned vertically parallel to the real hands under the flat screen are illustrated in panel b. The four empty circles on the screen positioned forming an imaginary square of 4 cm corresponding to the fingertip position of the real hands were illustrated in panel d.

Figure 3. Mean reaction times (a), sensitivity (b) and criterion (d) as a function of Stimulation Condition and error percentages in the catch trial

condition (c) for Experiment 1. Error bars represent the Standard Errors (SE).

Figure 4. Illustrations of the possible Visual Condition for Experiment 2 and 3 are presented. For Experiment 2 the fingers congruent condition is illustrated in panel a and the fingers incongruent condition is illustrated in panel b. For Experiment 3 the within hand morphing (i.e., index and middle finger of either hand morphed together) is illustrated in panel c, while the between hands morphing (i.e., homologous fingers morphed together) is illustrated in panel d.

Figure 5. Mean reaction times (a), sensitivity (b) and criterion (d) as a function of Stimulation Condition and error percentages in the catch trial condition (c) for Experiment 2. Error bars represent the Standard Errors (SE).

Figure 6. Mean reaction times (a), sensitivity (b) and criterion (d) as a function of Stimulation Condition and error percentages in the catch trial condition (c) for Experiment 3. Note that the 'normal hands' condition reports data are from the congruent condition of Experiment 2, for the 10 participants who participated in both experiments. Error bars represent the Standard Errors (SE).
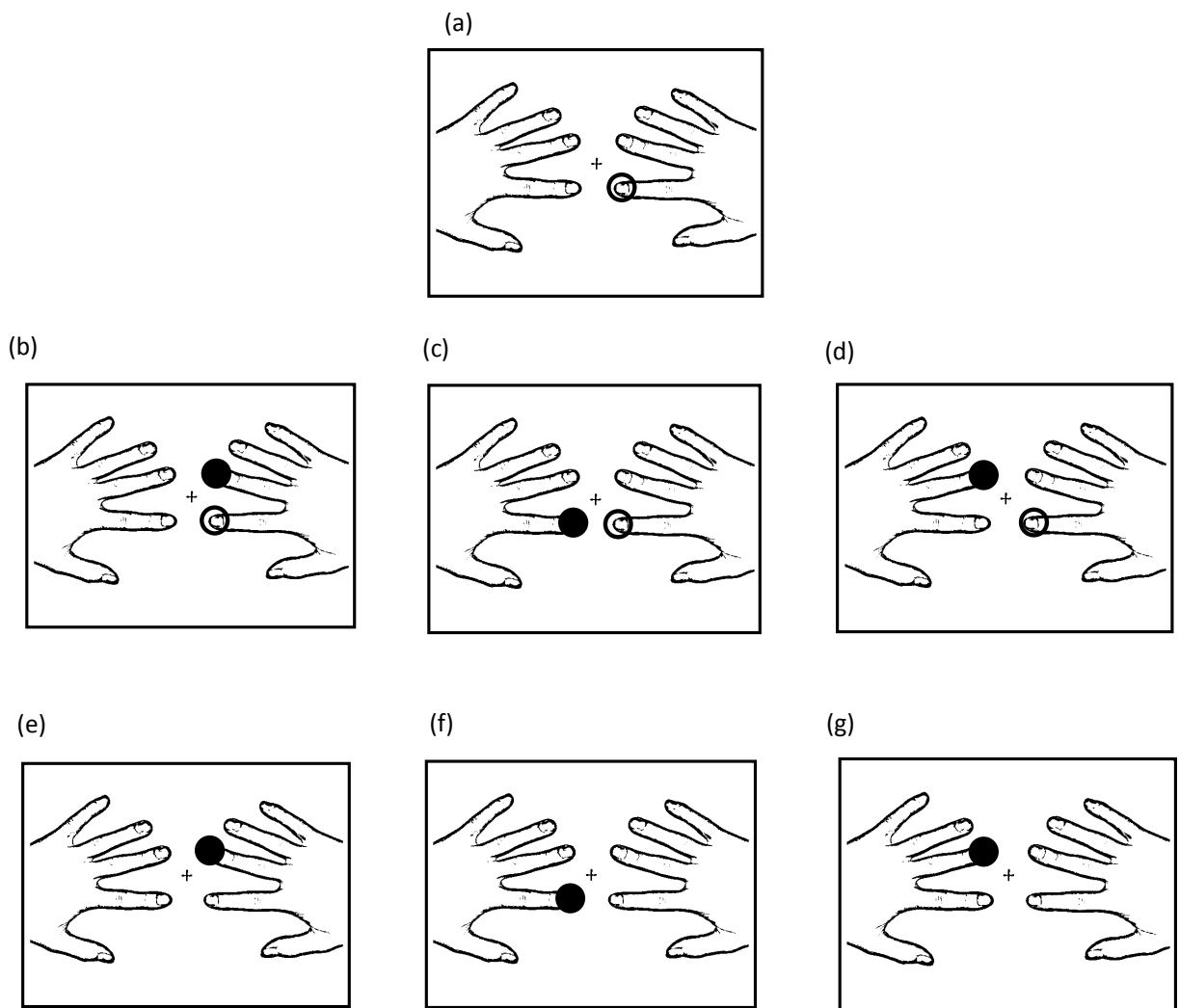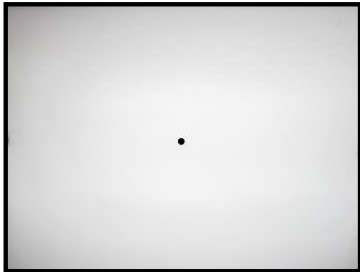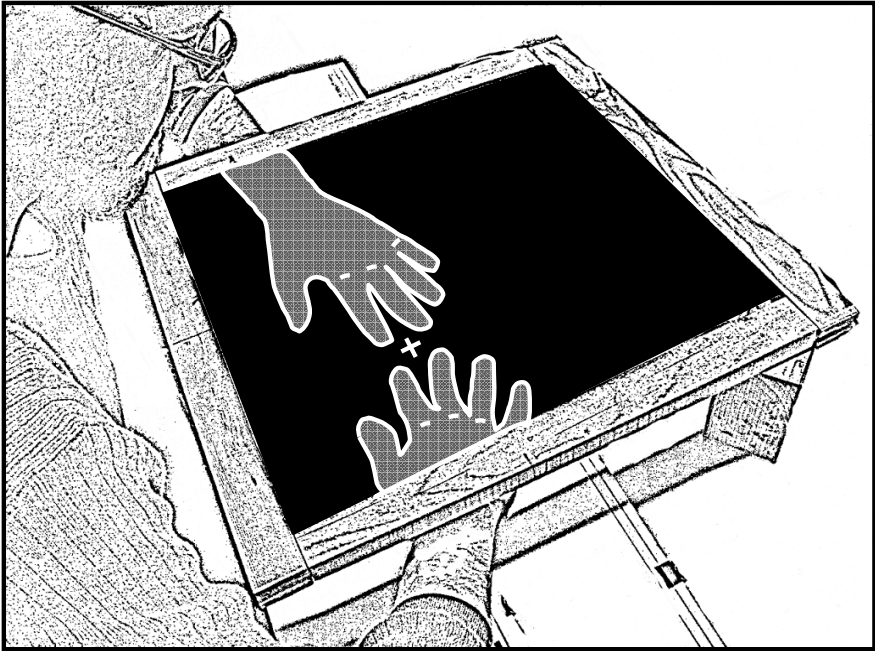
Figure 1

(a)

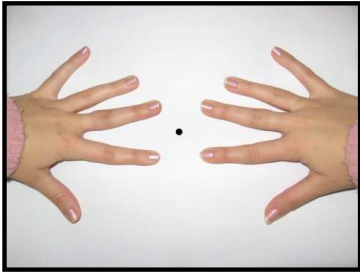
(b)

(c)

(d)

(e)

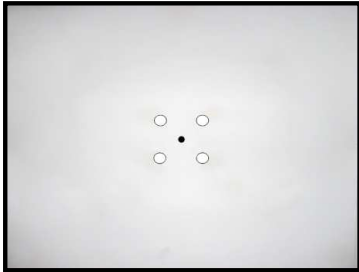(f)

(g)

Figure 2

(a)

(b)   Fixation only

(c)   Participant's own hands

(d)   Circles

Table 1. Mean reaction time, percentage corrects scores and d-prime for Experiment 1 in the Stimulation Conditions T (only target), T + DFSH (target finger and the same hand finger), T + SFDH (target finger and different hand same finger), and T + DFDH (target finger and different hand different finger) and in the Catch Trial conditions SH, DHSF and DHDF.

Experiment 1	Stimulation Condition				Catch Trials		
	T	T + DFSH	T + SFDH	T+ DFDH	SH	SFDH	DFDH
Fixation only							
d' (SE)	3.95 (0.10)	2.78 (0.16)	3.98 (0.09)	3.50 (0.18)	-	-	-
criterion (SE)	0.07 (0.05)	0.60 (0.11)	0.15 (0.05)	0.55 (0.10)	-	-	-
RT (SE)	543 (19)	620 (28)	610 (26)	628 (22)	-	-	-
% Errors (SE)	4.0 (1.0)	25 (4.0)	7.0 (2.0)	18 (4.0)	3.0 (1.0)	2.0 (0.0)	0.0 (0.0)
Circles							
d' (SE)	4.37 (0.07)	3.11 (0.13)	4.16 (0.12)	3.56 (0.16)	-	-	-
criterion (SE)	0.01 (0.05)	0.66 (0.10)	0.14 (0.07)	0.52 (0.07)	-	-	-
RT (SE)	543 (23)	620 (25)	585 (33)	628 (30)	-	-	-
% Errors (SE)	2.0 (1.0)	25 (4.0)	5.0 (2.0)	16 (3.0)	1.0 (1.0)	1.0 (0.0)	0.0 (0.0)
Hands							
d' (SE)	4.02 (0.13)	2.78 (0.18)	3.90 (0.14)	3.53 (0.15)	-	-	-
criterion (SE)	-0.08(0.05)	0.36 (0.09)	0.17 (0.09)	0.41 (0.07)	-	-	-
RT (SE)	567 (29)	624 (29)	603 (29)	619 (28)	-	-	-
% Errors (SE)	2.0 (1.0)	20 (3.0)	7.0 (2.0)	15 (3.0)	6.0 (1.0)	2.0 (1.0)	1.0 (0.0)

Standard errors are indicated in parenthesis

Table 2. Mean reaction time, percentage corrects scores and d-prime for Experiment 2 in the Stimulation Conditions and in the Catch Trials.

Experiment 2	Stimulation Condition				Catch Trials		
	T	T + DFSH	T + SFDH	T+ DFDH	SH	DHSF	DHDF
Congruent fingers							
d' (SE)	3.74 (0.20)	2.76 (0.30)	3.41 (0.32)	2.95 (0.29)	-	-	-
criterion (SE)	0.09 (0.09)	0.45 (0.19)	0.52 (0.16)	0.76 (0.16)	-	-	-
RT (SE)	543(23)	610 (33)	620 (36)	656 (38)	-	-	-
% Errors (SE)	7.1 (1.6)	26 (5.1)	20 (5.5)	31 (5.2)	7.1 (2.1)	1.0 (0.4)	1.0 (0.7)
Incongruent fingers							
d' (SE)	3.67 (0.25)	2.41 (0.20)	3.11 (0.23)	2.75 (0.31)	-	-	-
criterion (SE)	0.16 (0.13)	0.65 (0.19)	0.63 (0.14)	0.91 (0.16)	-	-	-
RT (SE)	543 (23)	612 (32)	615 (32)	645 (32)	-	-	-
% Errors (SE)	9.6 (3.0)	34 (4.4)	25 (4.2)	37 (5.8)	7.3 (2.9)	1.7 (1.0)	0.3 (0.2)

Standard errors are indicated in parenthesis

Table 3. Mean reaction time, percentage corrects scores and d-prime for Experiment 3 and congruent condition of Experiment 2 "Normal Hand" (n = 10) in the Stimulation Conditions and in the Catch Trials.

Experiment 3	Stimulation Condition				Catch Trials		
	T	T + DFSH	T + SFDH	T+ DFDH	SH	DHSF	DHDF
Normal hand (from Experiment 2, N = 10)							
d' (SE)	3.80 (0.22)	2.74 (0.40)	3.43 (0.42)	2.90 (0.40)	-	-	-
criterion (SE)	0.14 (0.11)	0.59 (0.23)	0.52 (0.21)	0.77 (0.22)	-	-	-
RT (SE)	536 (24)	611 (37)	609 (41)	643 (45)	-	-	-
% Errors (SE)	7.5 (2.2)	29.3 (6.8)	20.8 (7.2)	32 (7.3)	5.0 (2.0)	1.0 (1.0)	1.0 (1.0)
Hand Morphed							
d' (SE)	3.97 (0.19)	2.38 (0.22)	3.42 (0.24)	3.07 (0.27)	-	-	-
criterion (SE)	0.14 (0.18)	0.63 (0.39)	0.55 (0.27)	0.71 (0.31)	-	-	-
RT (SE)	533 (28)	611 (38)	586 (41)	624 (43)	-	-	-
% Errors (SE)	5.2 (3.1)	37 (7.3)	22 (6.1)	29 (7.2)	7.0 (2.4)	0.7 (0.5)	0.7 (0.3)
Finger Morphed							
d' (SE)	3.85 (0.16)	2.32 (0.15)	3.26 (0.28)	2.98 (0.28)	-	-	-
criterion (SE)	0.05 (0.22)	0.64 (0.34)	0.58 (0.31)	0.80 (0.29)	-	-	-
RT (SE)	519 (27)	591 (36)	579 (37)	601 (32)	-	-	-
% Errors (SE)	7.0 (2.8)	38 (5.2)	24 (6.3)	31 (7.1)	7.2 (2.5)	1.2 (0.5)	0.5 (0.5)

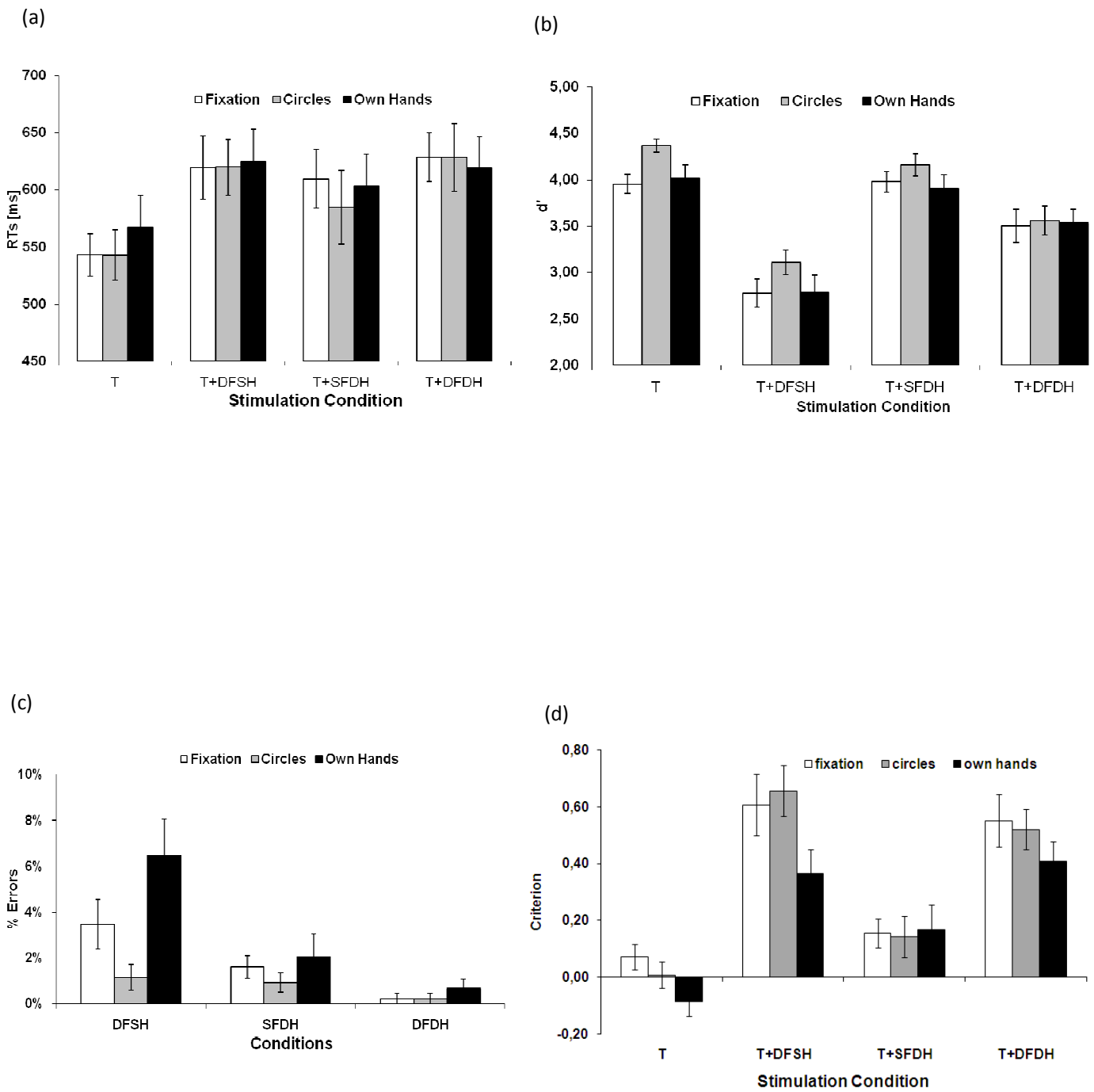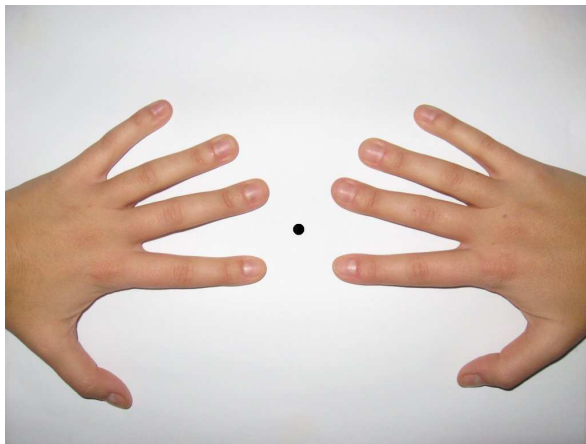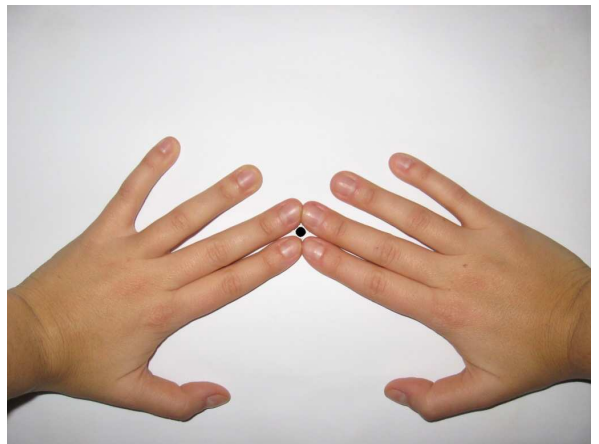Standard errors are indicated in parenthesis

Figure 3

(a)

(b)

(c)

(d)

Figure 4

Experiment 2

(a)

(b)

Experiment 3

(c)

(d)

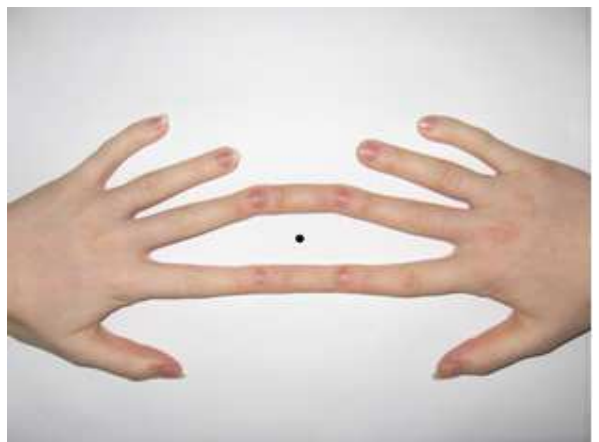Figure 5

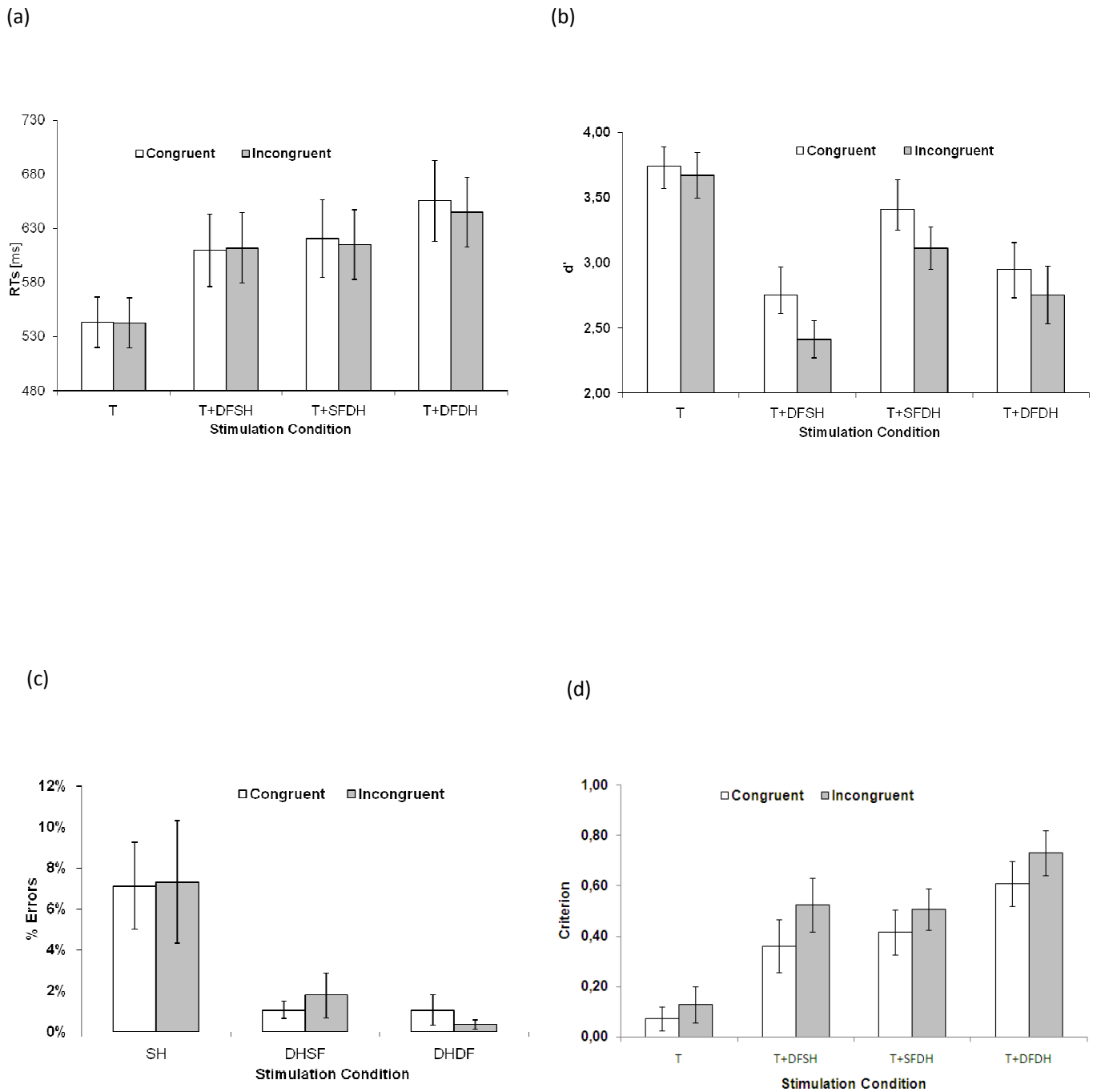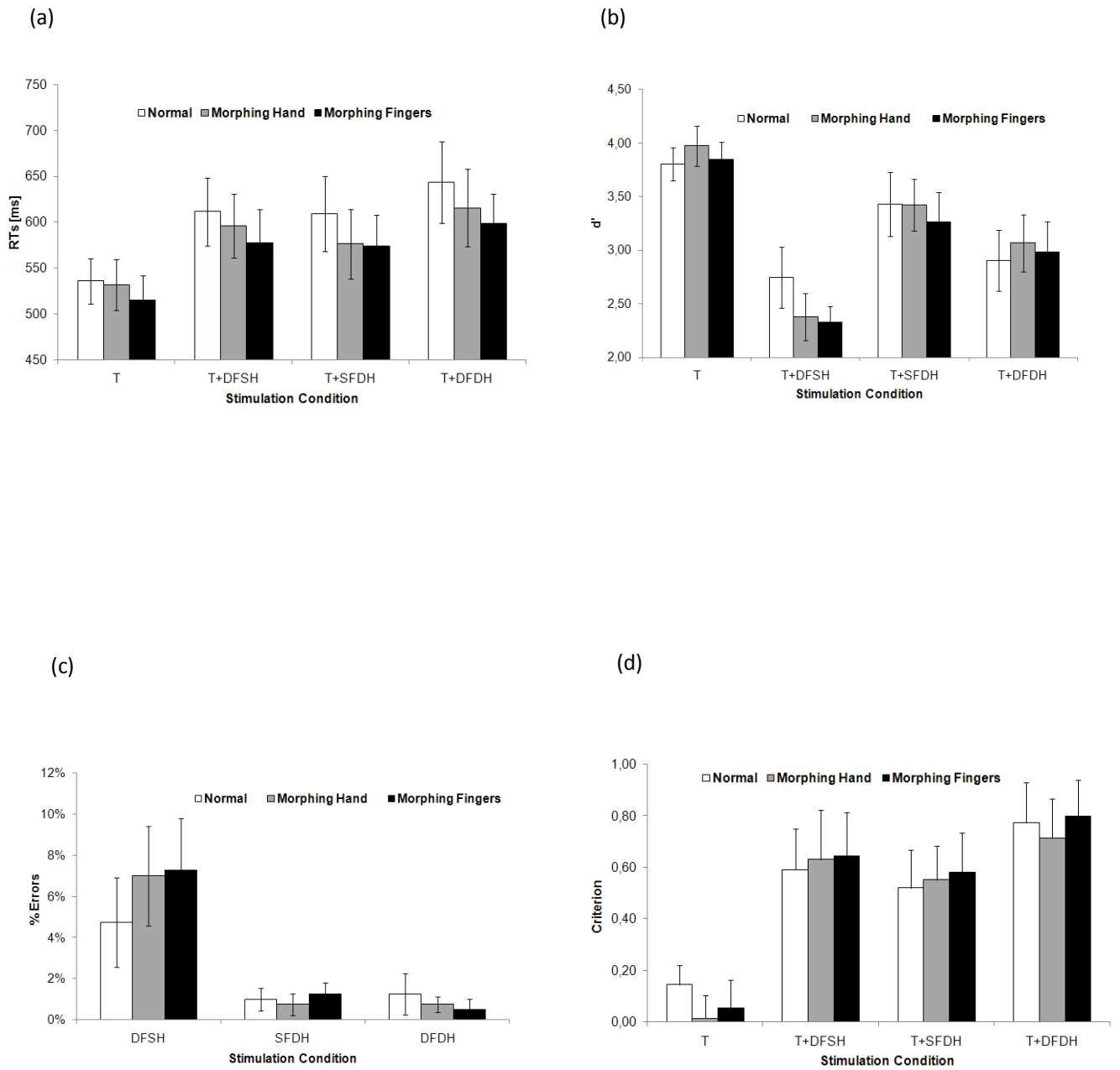(a)

(b)

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(d)

Figure 6

(a)

(b)

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(d)
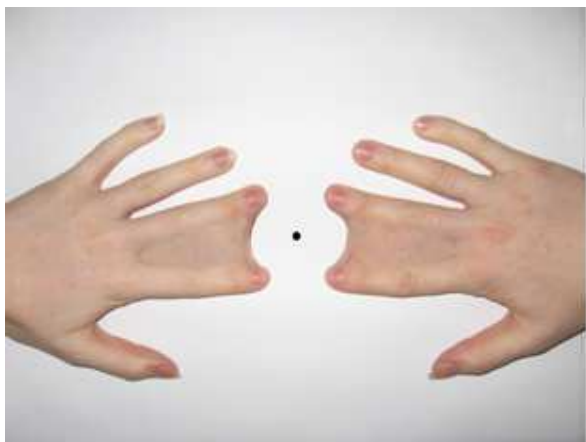
3.3 Multiple spatial representation of touch: an fMRI adaptation paradigm

(In preparation)

Multiple spatial representation of touch: an fMRI adaptation approach

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Running head: fMRI ADAPTATION FINGERS

Abstract

When two repeating stimuli activate the same neural population, a decreased overall neural response is observed. This neurophysiological response is detectable by functional magnetic resonance imaging, and has been termed fMRI adaptation. In the present study, we examined fMRI adaptation to touches delivered in sequence within or between hands, to homologous or non-homologous fingers. Participants received a test stimulus at the index or middle finger of either the left or right hand, followed by an adaptation stimulus delivered always to the left index finger. The results documented a significant adaptation when stimulation repeated over same than different fingers within the same hand. This adaptation pattern also emerged when stimulation occurred between hands, revealing the existence of bilateral representation for touch. Most strikingly, this bilateral response emerged both at the level of SI and SII, contrary to the general assumption that SI should primarily respond to controlateral tactile stimulation, but in agreement with behavioural and neurophysiological evidence documenting substantial interactions between the two sides of the body in somatotopically organised regions.

Introduction

In the last decades many studies have examined the multiple reference frames involved in representing the spatial location of tactile stimuli that come in contact with our body surface (e.g., Azañón & Soto-Faraco, 2008; Brozzoli, Ishihara, Göbel, Salemme, Rossetti & Farnè, 2008; Haggard, Kitadono, Press & Taylor-Clarke, 2006; for reviews see Gallace & Spence, 2008; Serino & Haggard, 2009). At lower stages of information processing, touch is encoded in a reference frame that reflects the organisation in primary somatosensory cortex (SI; Blankenburg, Ruben, Meyer, Schwiemann & Villringer, 2003; Penfield & Rasmussen, 1950). At higher processing stages, however, tactile stimuli can be mapped in body-space, that defines their location with respect to a body structural representation (e.g., Rusconi, Gonzaga, Adriani, Braun & Haggard, 2009; de Vignemont, Tsakiris & Haggard, 2006) or in external space, that defines stimuli on the basis of egocentric or allocentric reference frames (e.g., Azañón & Soto-Faraco, 2008; Maravita, 2006).

The neural bases of the multiple representations used for coding tactile stimuli on the body are still not clearly defined and have only started being investigated with neuroimaging techniques in healthy humans (e.g., Blatow, Nennig, Durst, Sartor & Stippich, 2007; Francis, Kelly, Bowtell, Dunseath, Folger, McGlone, 2000; Hegner, Saur, Veit, Butts, Leiberg, Grodd & Braun, 2007; Maldjian, Gottschalk, Patel, Pincus, Detre & Alsop, 1999). These studies suggest that touch representations are more segregated at lower than higher

stages of cortical processing. For instance, tactile stimuli delivered to distal body parts such as the fingertips are represented in a quite segregated manner in controlateral SI (e.g., Francis, Kelly, Bowtell, Dunseath, Folger & McGlone, 2000; Overduin & Servos, 2004), but have bilaterally and less segregated representation in SII (e.g., Ruben, Schwiemmann, Deuchert, Meyer, Krause, Curio, Villringer, Kurth & Villringer, 2001). However, even the textbook assumption that the representation in SI should be primarily contralateral is partially controversial (Sutherland, 2006). Neural activity in SI in response to tactile stimulation on the ipsilateral side of the body have been documented by several investigators (e.g., Hlushchuk & Hari, 2006; Kanno, Nakasato, Hatanaka, Yoshimoto, 2003; Kanno, Nakasato, Nagamine, Tominaga, 2004; Staines, Graham, Black & McIlroy, 2002; Tommerdahl, Simons, Chiu, Favorov & Whitsel, 2006). More generally, it remains to be ascertained how and where the multiple reference frames for tactile perception take place in the brain.

In the present work, we used an fMRI adaptation paradigm to probe the possible neural basis of these multiple coding. The adaptation effect is a typical physiological response of the neurons that results from the successive repetition of a feature to which the neurons are selective. For instance, a population of neurons selective to upward motion, would decrease its overall neuronal activity when the sequence of repeated stimuli contain the same feature (i.e., upward motion). This physiological response was initially described in single cell recordings (e.g., Gross, Rocha-Miranda & Bender,

1972; Tanaka, Saito, Fukada & Moriya, 1991), but has now been largely documented also using fMRI (Grill-Spector & Malach, 2001; Kourtzi & Grill-Spector, 2004; Grill-Spector, Henson & Martin, 2006; Krekelberg, Boynton & van Wezel, 2006). This phenomenon has been termed fMRI adaptation and have been documented for unisensory (Hegner et al., 2007; Vuilleumier, Henson, Driver & Dolan, 2002; Wall, Lingnau, Ashida & Smith, 2008) and multisensory stimulus pairings (e.g., vision and touch: Tal & Amedi, 2009).

The rationale for the present study is the following: when two tactile events repeat on exactly the same region of skin, all neurons that have a strictly somatotopic response will reduce their activity. These neurons should instead show no reduction of activity if the stimulation repeats over two distinct regions of skin. The crucial question, in relation to the issue of reference frames for touch, is whether some population of neurons in the brain can adapt to stimulation that repeats over distinct region of skin, when some other aspect of spatial coding is in fact identical. This can occur for instance when the repeated stimulation is delivered to homologous body parts (e.g., the fingertips of the right and left index), because the finger is identical although the stimulated region of skin differs.

In accordance with the exposed logic, in our work two successive vibrotactile stimuli were delivered to the first phalange of the index or middle fingers of either hands. We used four different finger stimulation conditions (see Figure 1): (1) Repeated stimulation of the left index (Li) finger (Li - Li); (2) Repeated stimulation of non-homologous fingers of the same hand (left

middle and index finger: Lm - Li); (3) Repeated stimulation of homologous fingers of either hands (i.e., right index and left index fingers: Ri - Li); (4) Repeated stimulation of non-homologous fingers of either hands (i.e., right middle and left index fingers: Rm - Li). All these fingers combinations are characterised by different properties in terms of spatial representation that served to differentiate the multiple stages of tactile spatial representation processing. For instance, in the "Li-Li" condition the same region of the <u>skin</u> is stimulated. In the "Lm-Li", stimulation occurs in different regions of skin, but on the same <u>body side</u>. In the "Ri-Li" stimulation occurs in different regions of skin and different body sides, but on homologous <u>fingers</u>. Finally, in the "Rm-Li" condition none of the previous features was present (i.e., region of skin, body side and finger identity were all different).

We expected to find fMRI adaptation to these pairing in SI and SII in particular. More specifically, we expected that SI should mainly adapt when the stimulation repeats over the same region of skin (i.e., the Li – Li condition only), because in this sensory area the dominant representation of touch should be primarily contralateral. By contrast, we predicted that SII could adapt to stimulation that repeats over the same finger regardless of the body side (i.e., the Ri – Li condition, plus the Li – Li condition), because in this sensory area bilateral representations of touch have been extensively documented. Note that throughout the manuscript we mainly used the terms right and left hemispheres instead of controlateral and ipsilateral to refers at the localization of the activation in the brain. This was done because whole

experimental stimulation conditions involved at least one finger of the right hand. Consequently for instance, ipsilateral activation of the left hemisphere cannot be considered purely ipsilateral, because stimulation of the right hand was always follows by a stimulation of the left hand. Contrary, activation of the right hemisphere, in some condition (i.e., Li - Li and Lm - Li) can be considered fully lateralised.

Materials and Methods

Participants

Ten participants (mean age = 31, SD = 4, 5 females) took part in the experiment. All reported normal or correct to normal vision, normal touch and were unaware of the purpose of the experiment. All were right-handed by self-report. Participants gave their informed written consent prior to participate in the study, that was carried out according to the principles of the Declaration of Helsinki and was approved by the ethical committee at the University of Trento.

Apparatus, Stimuli and Materials

Tactile stimuli were delivered to the index and middle fingers of either hands using four MR compatibles vibrators (Piezo System TeleSensory, CA; casing and electrical connectivity board: metec AG, Stuttgart, Germany) driven by a custom-made amplifier. To avoid possible distortions caused by the cables and vibrators in the MR environment, a digital filter was applied on

the signals entering the MR room. The stimulator consisted of a single rod (1 mm in diameter), poking from a flat surface of 4 x 8 mm². The rod ascended and descended with a 20Hz rate for 1000 milliseconds (ms), producing clearly perceivable skin indentations. Wave signal intensity was set to the maximum level available, except for a 8% of the trials which served as fillers for the behavioural task that were delivered at halved intensity. Vibrotactile stimulators were attached to the finger pads of the middle and index finger of either hand using Velcro tape, to ensure constant contact between the fingers and the stimulation devices throughout the experiment. The hands rested in a comfortable posture, one on each side of the stomach, palm down and unseen.

During the experimental session, a fixation cross was visualised at the centre of the screen. The cross was green during the vibrotactile stimulation period, and grey during the rest period. Occasionally, a written question appeared on screen for 3000 ms probing the participants on whether they had just perceived a weaker stimulation at the target finger (see later). All visual stimuli were delivered using a liquid-crystal projector (refresh: 60 Hz; resolution: 1280 x 1024 pixels) and were visible to the participants through a mirror positioned above the head coil. Visual and vibrotactile stimulations were programmed using the in-house software "ASF" (available from jens.schwarzbach@unitn.it), based on the MATLAB Psychotoolbox-3 (Brainard, 1997) for Windows. A response box (Lumina LP-400 system by Cedrus) was placed in touch with the participant's right thumb for response collection. Closed-ear headphone (Serena Sound digital –system: Resonance

Technology Inc. California, U.S.A) was used for reducing noise caused by the operation of the scanner. Sounds made by the operation of vibrotactile stimulators were not audible.

fMRI Adaptation paradigm in our study

The experiment consisted of 4 event-related fMRI adaptation scans, consisting of 52 trials each. In each scan the 4 experimental conditions were repeated 12 times and responses were probed in 4 trials. Response conditions were excluded from the analyses.

At the beginning of each trial the green fixation cross appeared at the middle of the screen, to remained visible for the entire duration of the trial. After 1000 ms from fixation onset, two consecutively vibrotactile stimulations were delivered to the participants fingers, each for a duration of 1000 ms (S1, adaptation stimulus; S2, test stimulus) and separated by an inter-stimulus interval (ISI) of 1200 ms. After vibrotactile stimulation there was a fixed minimum inter-trial interval (ITI) of 6000 ms and then another ITI that was jittered randomly in a range between 0 and 8000 ms. After 3000 ms from the end of the second stimulation the green fixation cross turned to grey.

Participants were instructed to pay attention to the left index finger throughout the experiment. To force this, in a few trials (i.e., a total of 16 trials) a written question appeared on the screen "Hai sentito la stimolazione debole sull'indice sinistro?". They needed to press a button (response box

under the right thumb) if the response was "yes", and to press no button if the answer was "no".

The four experimental conditions were counterbalanced creating sequences in which each condition preceded the same number of times the others and itself. Conditions that included the written question were integrated into the counterbalanced sequence in a random fashion. At the start and at the end of each scan a black-screen was presented for 16 and 20 seconds, respectively.

Data Acquisition

MR scans were acquired using a 4 T Bruker MedSpec Biospin MR scanner and an 8-channel birdcage head coil. Functional images with blood oxygenation level-dependent (BOLD) were acquired using T2*-weighted gradient-recalled echo-planar imaging (EPI) sequence. An additional scan was performed to measure the point-spread function (PSF) of the acquired sequence, which served for correction of the distortions expected with high-field imaging (see Data analysis). We used 31 slices, acquired in ascending interleaved order providing almost full-brain coverage, with a TR (repetition time) of 2200 ms (voxel resolution: 3 x 3 x 3 mm; TE (echo time), 33 ms; flip angle (FA), 75°; field of view (FOV), 192 x 192; gap size, 0.45 mm). In addition, Fat Saturation pulse (FS) was used. For the main experiment, each participant performed 4 scans, with a variable numbers of volumes that varied between 360 and 391. These variations derived from the partial randomised duration of

the inter-trial interval (ITI) in the trials generation, creating a small variation in the number of volumes acquired across scans and participants.

In order to perform the coregistration between low-resolution functional and high-resolution anatomical images, we acquired a T1 weight anatomical scan (MP-RAGE; 1 x 1 x 1 mm; FOV, 256 x 224; 176 slices; GRAPPA acquisition with an acceleration factor of 2; TR, 2700 ms; TE, 4.18 ms; inversion time (IT), 1020 ms; 7° flip angle).

Data Analysis, ROIs definition and design

Data analysis was performed using BrainVoyager QX 2.0 (Brain Innovation B. V., The Netherlands). One participant was discarded from the analysis because of several rapid head movements (> 5 mm). Prior to the analysis, the first two volumes of the functional data of each scan were discarded. Distortion correction was applied on the basis of the PSF, executed before each EPI, to correct distortion derived from the EPI images (Zeng & Constable, 2002). Functional data preprocessing was performed applying a three-dimensional (3D) motion correction referred to the first volume in the run and a temporal high-pass filter with a cut-off of 3 cycles/scan. Next, functional data were co-registered with a high-resolution desculled anatomy for each participant in native space. For each participant, echo-planar and anatomical volumes were transformed into standardised (Talairach and Tournoux, 1988) space.

The whole functional data were analysed using general linear model (GLM) in BrainVoyager. Experimental events (mean duration = ~14.2 s) were convolved with a standard dual gamma hemodynamic response function. There were four regressors or interest (corresponding to the four experimental conditions) and six regressors of no interest, corresponding to the motion correction parameters obtained during preprocessing.

We calculated individual functional maps for each participant. Statistical maps where threshold using a false discovery rate (FDR) (Genovese, Lazar & Nichols, 2002) of 0.01 and a cluster threshold of 4 voxels. Maps for the right and left hemisphere were functionally defined as all voxels that were significant in the omnibus test (fixed effects analysis; FFX) in the four experimental conditions (i.e., Li-Li, Lm-Li, Ri-Li, Rm-Li). Functional maps and defined Patch of Interests (POIs) on the surface for each participant are shown in Figure 3. On the resulting maps, we identified four POIs separately for each participant consisting in the primary and secondary somatosensory cortex of both hemispheres. POIs were defined on the basis of brain anatomy and functional response in each smooth and inflated hemisphere (2D space) in a selected area included between 151 and 545 voxels depending on the single participant activation map (Euclidean coordinates for each participant are shown in Table 1). The hemispheres inflation was done by 500 interactions updated every 10 and a step size of 0.1. For the primary somatosensory cortex (SI) when more than one plausible area was activated we chose Brodmann area 3 otherwise 2. For secondary somatosensory cortex

(SII) when more than one plausible area was activated we chose Brodmann area 43 otherwise 13, parietal operculum or insula respectively. Finally, if multiple areas were closely activated we took the one that showed the higher BOLD response. Areas were identified by using Talairach Client software (Lancaster, Rainey, Summerlin, Freitas, Fox, Evans, Toga & Mazziotta, 1997; Lancaster, Woldorff, Parsons, Liotti, Freitas, Rainey, Kochunov, Nickerson, Mikiten & Fox, 2000).

For each individual POIs, we generated the corresponding region of interest (ROIs) in 3D space. Within these individual ROIs we extracted the Beta values on the hemodynamic response (see Figure 2). Each participant executed 4 separate runs with 52 trials each for a total of 208 trials with 48 repetitions for each condition. The BOLD amplitude for each ROIs was considered as a dependent variable. We ran an overall analysis comprising the Area (SI, SII), Hemisphere (Right, Left), Hand (within, between) and Finger (homologous, non-homologous) as within participants variables. This resulted in a 2x2x2x2 factorial design.

Results

We analysed the Beta values derived from the ROIs by executing a repeated measure Analysis of Variance (ANOVA) with Area (SI, SII), Hemisphere (Right, Left), Hand (within, between) and Finger (homologous, non-homologous) as within participants variables. This analysis revealed a main effect of Finger, $(F_{(1,9)} = 9.1$, $p < 0.014)$, caused by smaller BOLD

responses for homologous than non-homologous fingers (see Figure 4A). This main effect suggests that adaptation occurred whenever finger identity was kept constant (i.e., during homologous fingers stimulations, more than during non-homologous fingers stimulation). However, it should be mentioned that the interaction between Finger, Area and Hemisphere fell just short of significance $(F(1,9) = 4.15, p < 0.07)$. This marginally significant interaction indicates that the BOLD response was always smaller when the stimulation repeated over homologous than non-homologous fingers of either hands, but this was particularly true in SI contralateral to the target finger (i.e., the right hemisphere; see Figure 5).

The analysis also showed an interaction between Hemisphere*Hand, $(F(1,9) = 13.05, p < 0.006)$, caused by comparable activation in the right hemisphere (i.e., controlateral hemisphere to the adaptation stimulus) for within and between hand stimulations, but smaller activation for within hand than between hand stimulation in the left hemisphere (i.e., ipsilateral to the adaptation stimulus; $p < 0.01$ with Tukey HSD test; see Figure 4B). Finally, there was a main effect of Area, $(F(1,9) = 8.26, p < 0.02)$, caused by less activation in SI as compared with SII. No other main effects nor interactions were found, except one marginally significant interaction between Hand*Finger $(F(1,9) = 3.82, p < 0.08)$. This two-way interaction is probably caused by more adaptation when the same finger was stimulated twice compared to when stimulation occurred on the homologous finger of the other hand.

Discussion

In the present study we investigated the neural bases of spatial coding for touch at the fingers of either hands using an fMRI adaptation paradigm. The main rationale for the study was to examine what would constitute 'same stimulation', and thus lead to neural adaptation, in areas SI and SII. We predicted that SI would show signal reduction (i.e., adaptation) specifically when the same region of skin was stimulated twice, whereas SII would show adaptation also when the same finger was stimulated twice (even though this implies stimulating different regions of skin across the two hands).

We found that adaptation <u>within</u> the same hand was higher when tactile stimulation repeated on the same finger (Li – Li condition) compared to when it repeated over the two adjacent fingers (Lm – Li condition). This findings speaks for a clear segregation in the neural populations representing the index and middle fingers. Notably, this pattern of results emerged both in SI and SII, suggesting similar segregation of the digits representation at both these stages of tactile information processing. This is somewhat incongruent with the notion of higher segregation in SI than SII proposed in humans on the basis of standard functional MRI paradigms (Francis et al., 2000; Overduin & Servos, 2004; Ruben et al., 2001).

Our findings also showed that adaptation was larger when touch repeated across homologous than non-homologous fingers also <u>between</u> hands (i.e., regardless of which hand was stimulated, left or right). In other

words, adaptation emerged not just when the same region of the skin was stimulated (i.e., exactly the same tactile receptors), but also when the same finger was stimulated between hands (i.e., different tactile receptors, but same finger identity). Remarkably, this pattern of results emerged both for SI and SII, implying that both these somatosensory cortices contribute a spatial representation of the tactile stimuli that is not completely segregated with respect to the body side. In sum, the index and middle fingers appear to be well segregated within the same hand, despite the proximity (or even partial overlap) of their cortical territories within each hemisphere. By contrast, the right and left index fingers appear to be less segregated between the two hands, despite their clear separation in terms of body sides.

In addition, to the above mentioned effects we also documented more activation for SII than SI overall. This finding parallels a previous report showing higher activation volume in SII compared to SI (Maldjian et al., 1999). The authors suggested that this increase in volume activation could reflect disproportion in the fingers representation at the level of SII compared to SI. In accordance with this evidence in humans, studies on single cell recording in monkeys revealed greater representation of the hands with respect to other body parts at the level of SII (Friedman, Jones & Burton, 1980; Pons, Garraghty & Mishkin,1988).

On the segregation between body sides

Interactions between body sides have been documented in behavioural studies using a number of tactile tasks. For instance, errors in localisation of near-threshold tactile stimuli at the hands is affected both by stimulation of adjacent fingers of the same hand (Schweizer, Braun, Fromm, Wilms & Birbaumer, 2001) and by stimulation of finger on the opposite hand (Braun, Hess, Burkhardt, Wühle & Preissl, 2005). Similarly, if participants are trained to discriminate punctuate pressure or roughness on one finger of the right hand (e.g., the index), this training transfers to the first neighbour finger of the same hand (i.e., the right middle finger) as well as to the homologous finger of the opposite hand (i.e., the left index finger; Harris, Harris & Diamond, 2001). Finally, Haggard and colleagues (2006) have shown that when adopting a finger interwoven posture, with palms touching each others and fingers interwoven at the midline, identification of which hand was stimulated was slower and less accurate.

Moreover in a recent work, using double simultaneous tactile stimulation (DSS) paradigm for tactile stimuli delivered within and between hands, we documented (Tamè et al., under review; Tamè et al., submitted) that reporting of a target tactile event at the left index finger was interfered by concurrent stimulation of the middle finger, both adjacent (same hand) and contralateral (opposite hand). Notably, this DSS interference pattern was unaffected by hands posture (Tamè et al., under review) nor by visual inputs concerning the stimulated hands (Tamè et al., submitted). This supports the

notion that within and between hand interference effects may be solved at a low stages of tactile processing, and in this respect is compatible with the current observation that both SI and SII hold bilateral representations of the body.

The origin of bilateral representations in SI

While the existence of bilateral representations in SII is widely acknowledged (e.g., Blatow et al., 2002), in recent years the notion that even SI can contribute to bilateral representation of the body has emerged. Bilateral receptive fields in somatosensory area 2 have been documented by neurophysiological studies in monkeys (Iwamura, Taoka & Iriki, 2001; Iwamura, Tanaka, Iriki, Taoka & Toda, 2002). In addition, modulation of ipsilateral SI in humans have been shown using functional imaging. For instance, Hlushchuk and Hari (2006) observed controlateral activation and an ipsilateral deactivation of SI in response to tactile pulses delivered concurrently to three right hand fingers. While the authors suggested that this ipsilateral deactivation could result from transcallosal inhibition, the physiology regarding which neural pathways are responsible for the tactile information flow towards the ipsilateral hemisphere is still a matter of debate (Sutherland, 2006). Some researcher proposed that the input could come trans-callosally from controlateral SI (e.g., Allison, McCarthy, Wood, Williamson & Spencer, 1989). Others have suggested direct projections from the receptor surface to ipsilateral SI (e.g., Kanno et al., 2003; Kanno et al.,

2004). Finally, cortico-cortical SII-SI modulations could emerge after trans-callosal connections between homotopic SII regions (Schnitzler, Salmelin, Salenius, Jousmäk, Hari, 1995; Tommerdahl et al., 2006). In this respect it is worth mentioning that Kanno and colleagues (2004) have reported two cases with severe left hemisphere damage that showed only ipsilateral activation of the right SI after right medial nerve stimulation. This result has been interpreted as potentially dismissing the need of trans-callosal pathways for ipsilateral response of SI.

Although the present findings clearly speak in favour of the existence of bilateral representation of touch in SI, they cannot contribute to disambiguate which source of input is more like to produce this activation profile. In addition, it should be emphasised that the low temporal resolution of fMRI does not allow to determine the time course of the ipsilateral response in SI. In future studies it would be very interesting to define the time course of this neural response by using methodologies that can provide higher temporal resolution than fMRI. In this sense, ongoing work in our lab is adapting the exact same paradigm described in the present study for magnetoencephalography.

Conclusions

The present results demonstrate the usefulness of adopting tactile fMRI adaptation for investigating the neural basis of tactile processing. In particular, we provided evidence in favour of bilateral representations of the

tactile stimuli delivered at the fingers, both in primary and secondary somatosensory cortices. This result from neuroimaging provide a useful complement for the growing amount of behavioural data concerning the interactions between body sides in tactile perception, including data from our own lab on the effects of concurrent double stimulation between and within hands (see Tamè et al., under review; Tamè et al., submitted).

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Figure captions

Figure 1. Schematic drawing of the stimulation conditions in the fMRI adaptation paradigm. Specific finger that received the adaptation stimulus is indicated by the red triangles, while the blue triangles represent the test stimulus fingers. There are 4 possible conditions, stimulation on the same finger (Li-Li, panel a) and stimulation of different fingers (Li - Lm, panel b; Li - Ri, panel c and Li - Rm, panel d). Position of the hands in the drawing does not represent the actual participant's hands posture in the experiment, but serve exclusively to show the distribution of the vibration for different stimulation conditions.

Figure 2. Experimental design. The complete trial consist of two vibrotactile stimuli lasting 1 s each with an interstimulus interval (ISI) of 1.2 s. Participants were asked to pay attention to the left index finger (always the second stimulated finger) and report if they perceived a low vibratory intensity on the left index only when requested by the visual instruction on screen,.

Figure 3. Left panel represents the functional maps separately of each subject for the right and left hemisphere functionally defined as all voxels that were significant in the omnibus test (FFX) in the four tactile stimulation conditions. Right panel represents the Patches of Interests (POIs) that included the primary somatosensory cortex (red empty circle) and the secondary somatosensory cortex (green empty circle). Note that an
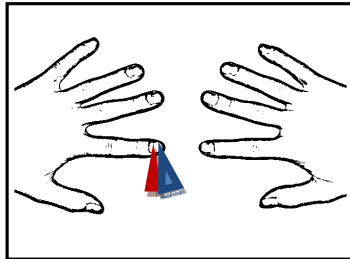
activation within the circled region was identified for each participant (even when non visible in the figure).

Figure 4. BOLD amplitude (Beta Values) for homologous and non-homologous fingers (A), as a function of the Hemisphere (RH vs. LH) and first stimulus Hand (B) and as a function of Somatosensory Area (Si or SII) (C). Error bars reflect the standard error of the mean (SE).
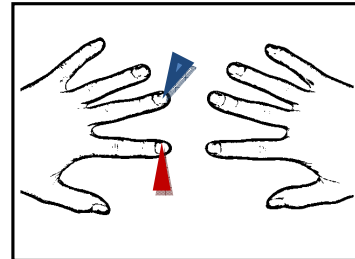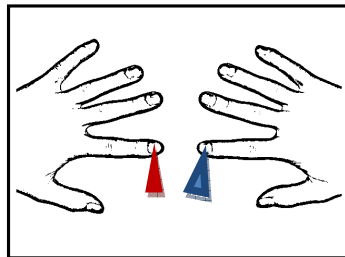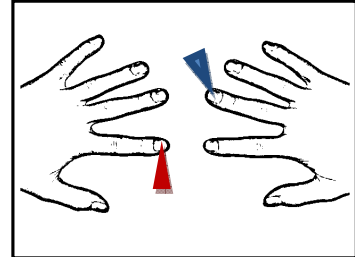
Figure 1

Adaptation stimulus

Test stimulus
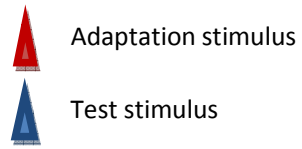
(a)

(b)

(c)

(d)
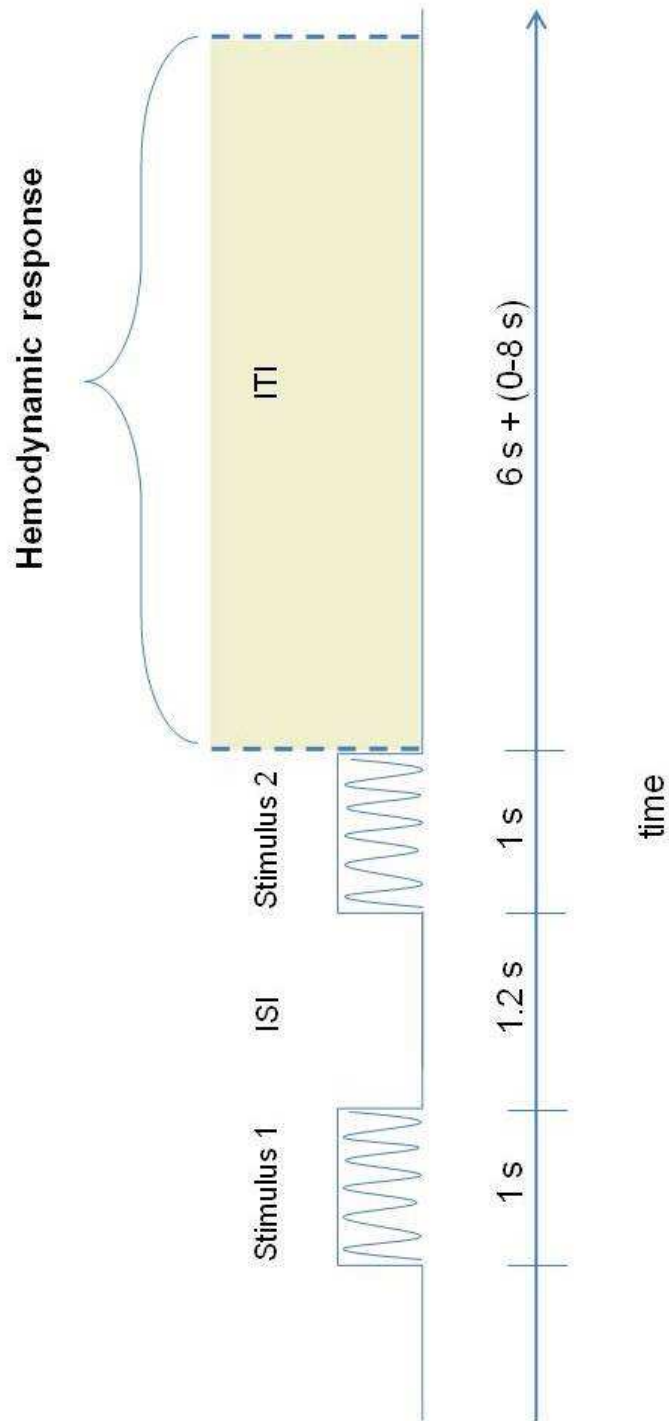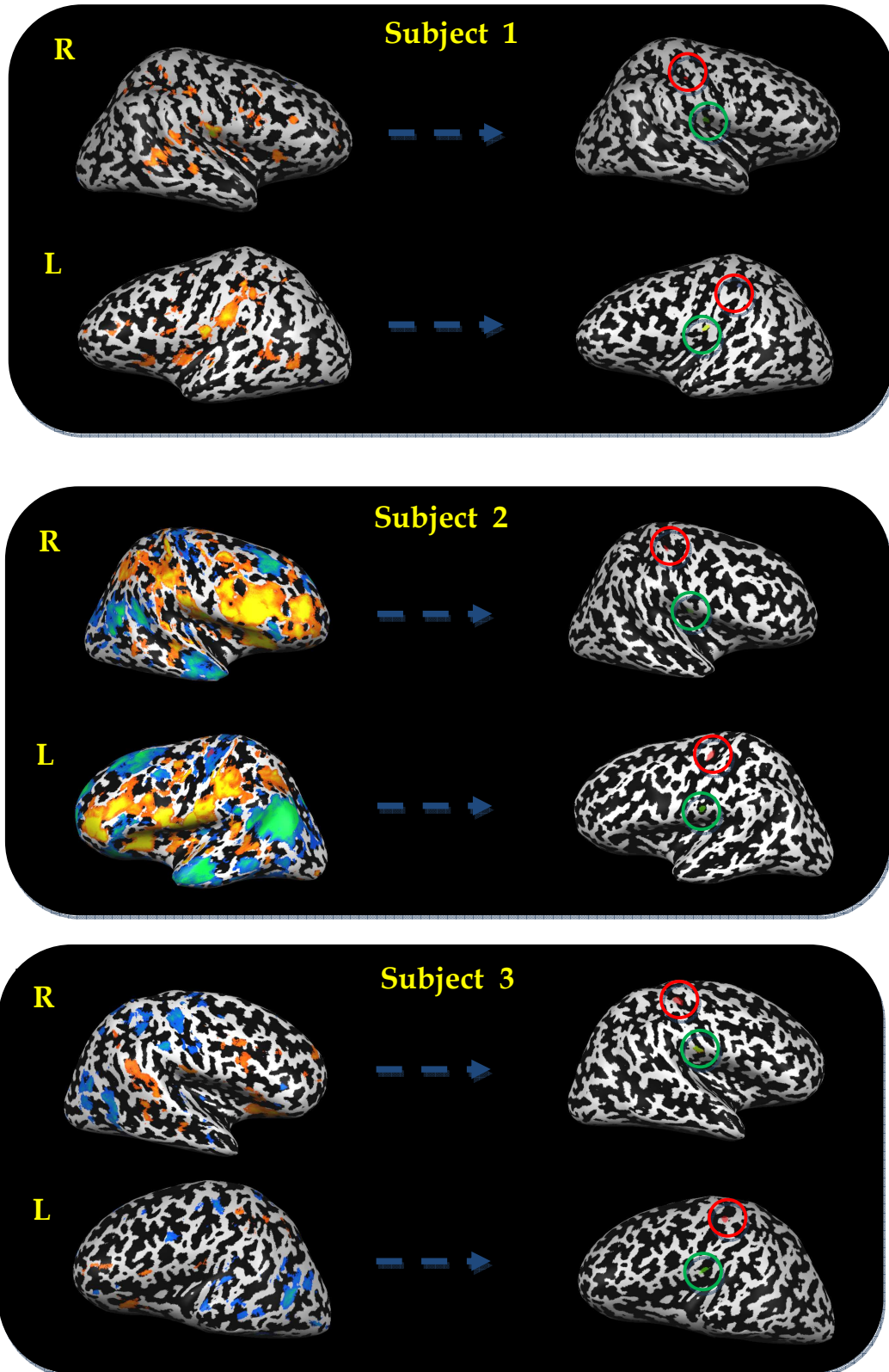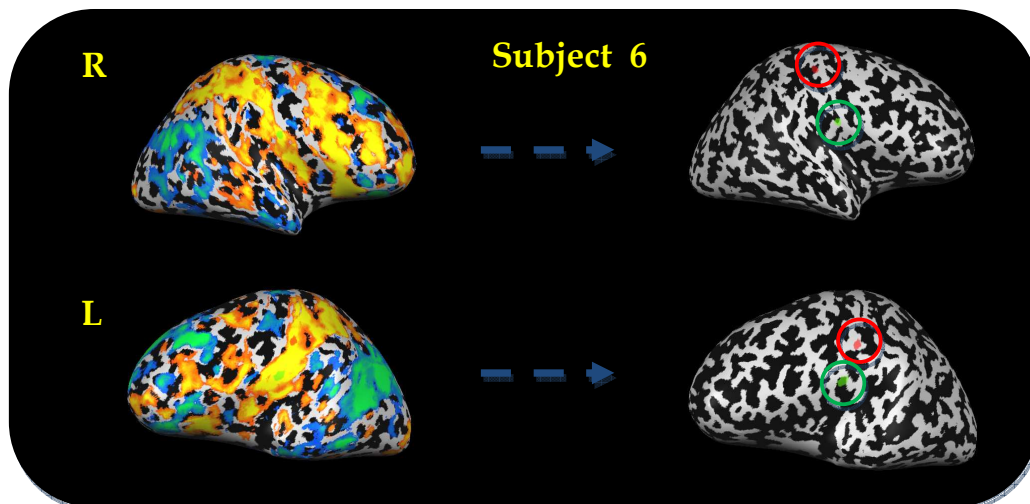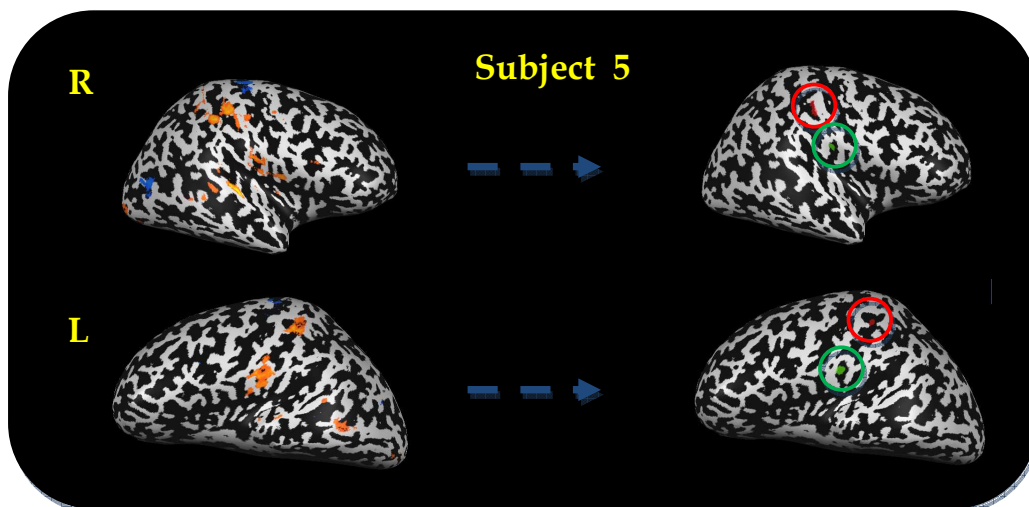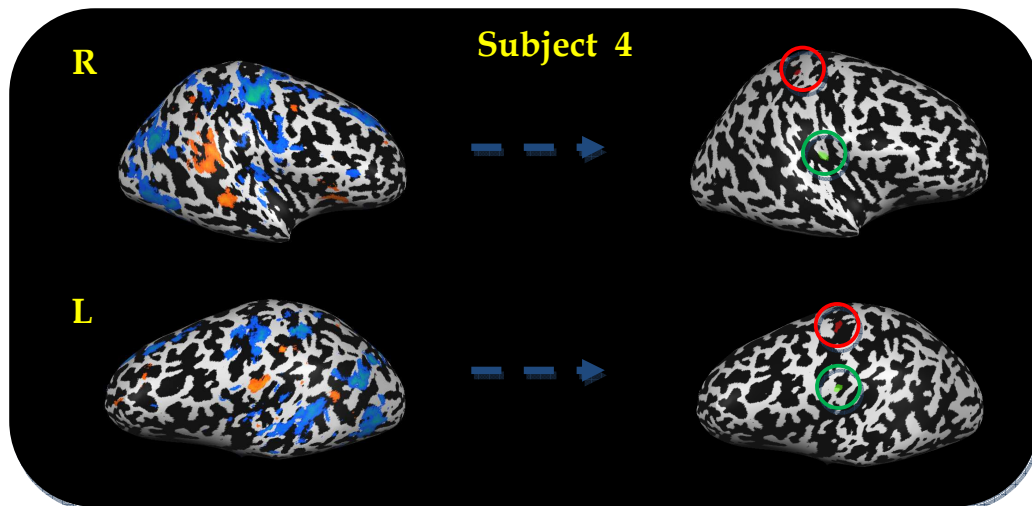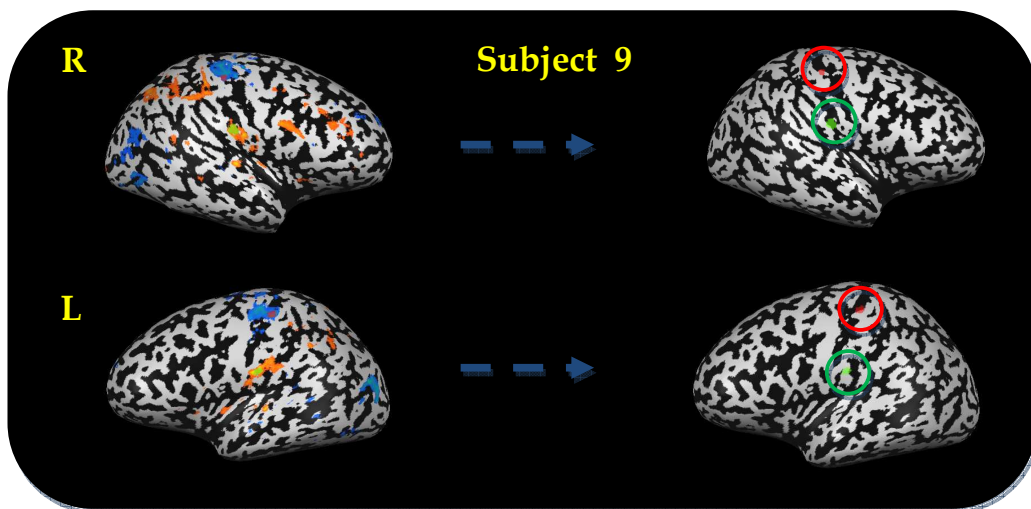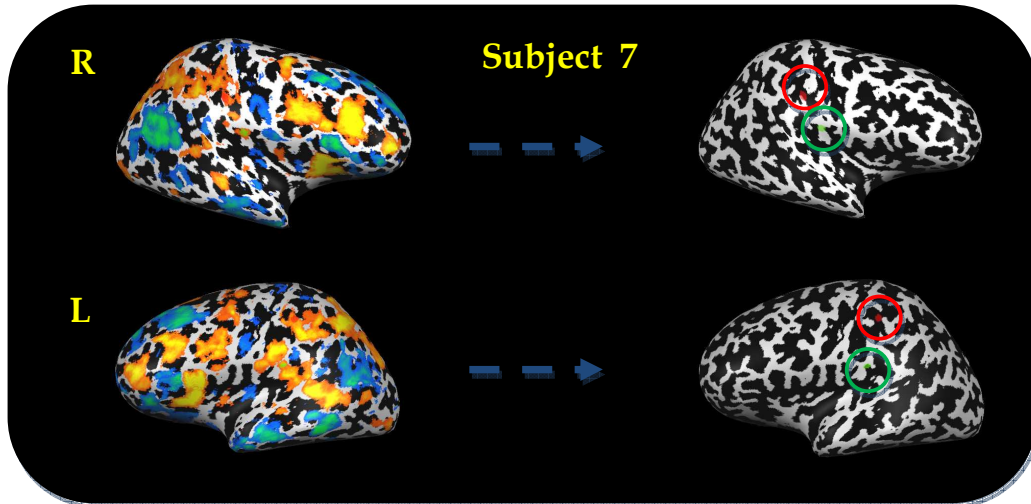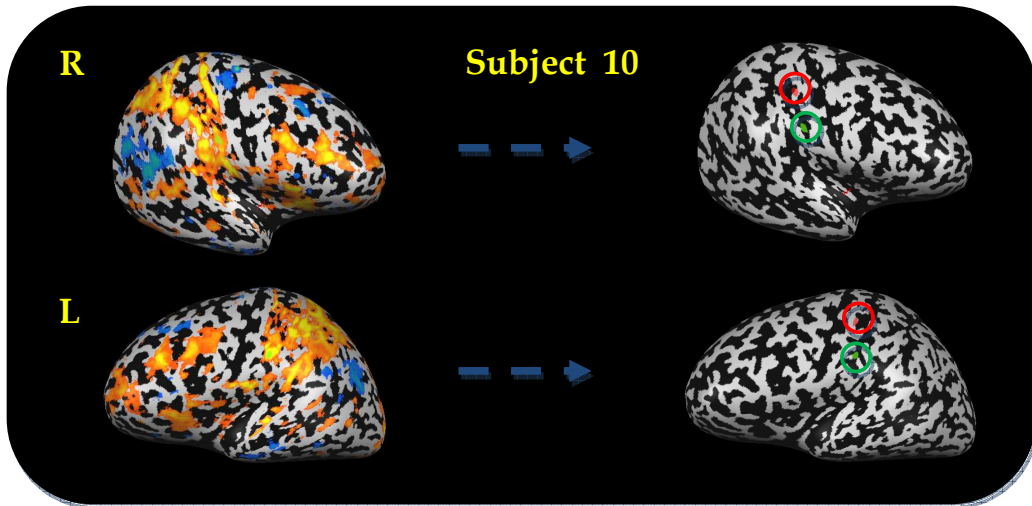
Figure 2

Figure 3

Figure 4
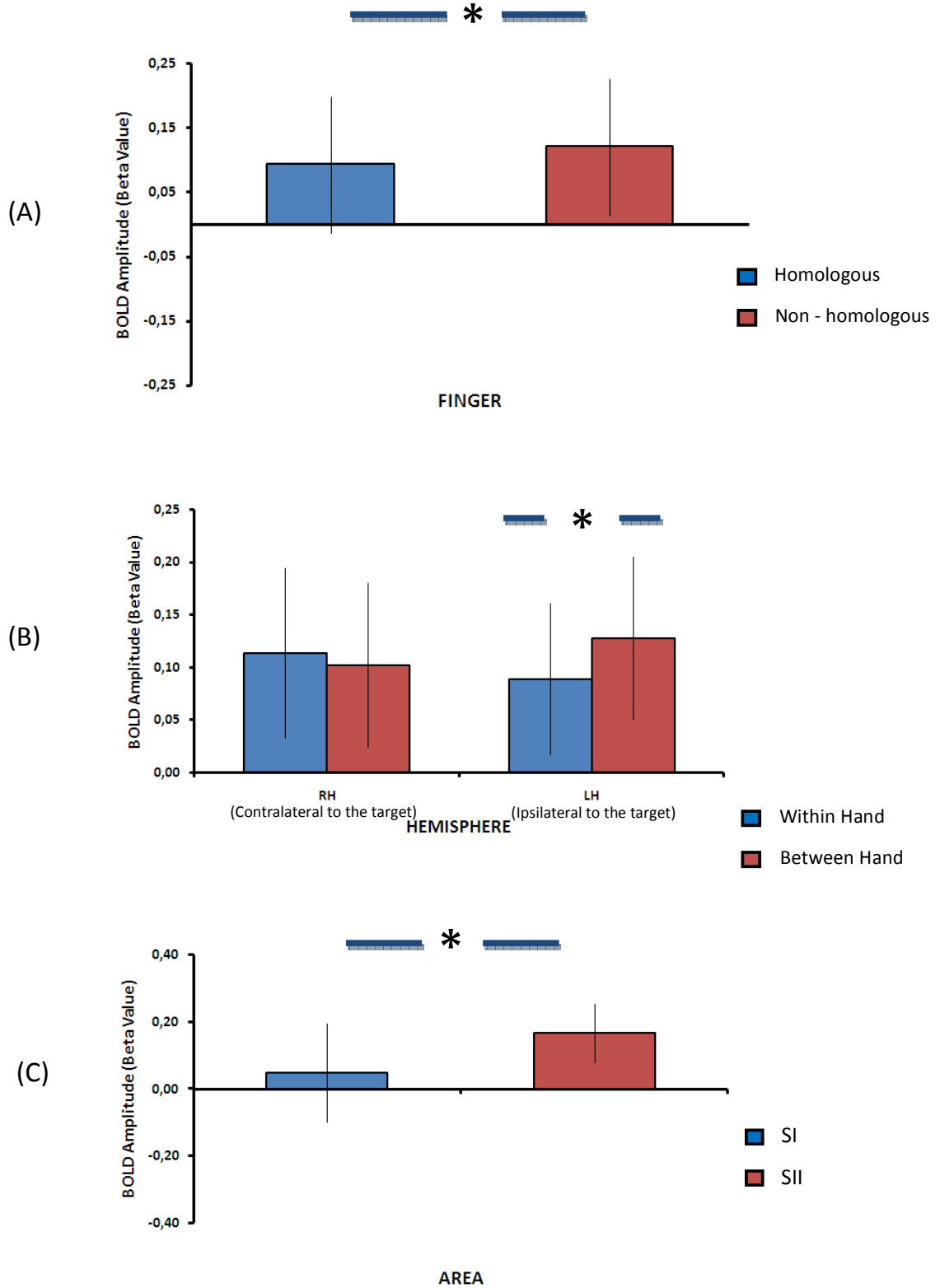
Table 1

Table 1
Euclidean coordinates of SI and SII activations

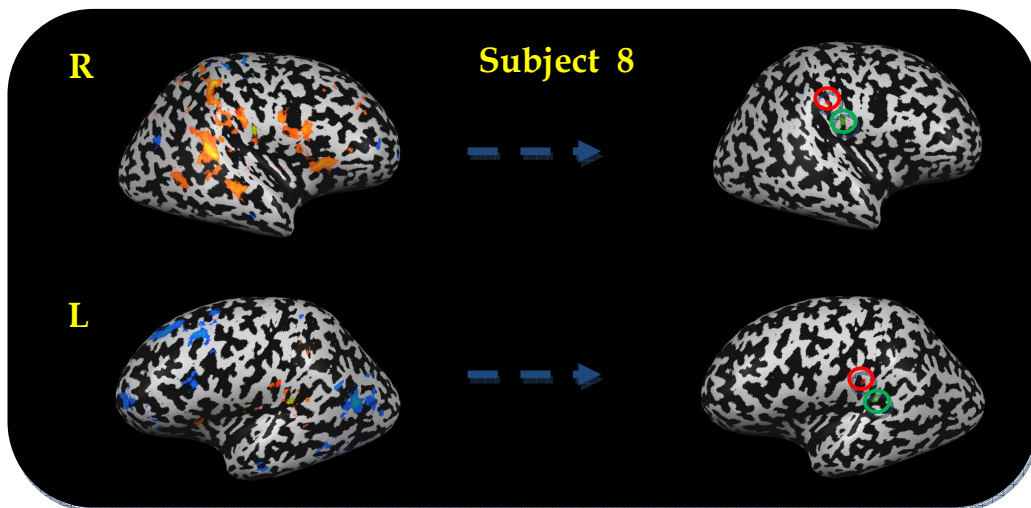| Subjects	RH SI x	RH SI y	RH SI z	RH SII x	RH SII y	RH SII z	LH SI x	LH SI y	LH SI z	LH SII x	LH SII y	LH SII z	N.° Voxels RH SI	N.° Voxels RH SII	N.° Voxels LH SI	N.° Voxels LH SII
1	48±1.9	-21±1.6	32±1.4	45±1.7	-16±1.8	17±1.6	-42±1.8	-23±1.8	34±1.5	-55±1.4	-14±1.8	14±1.5	182	201	193	158
2	38±1.8	-25±2	53±1.9	53±2.2	-12±1.6	12±2.3	-34±2.6	-29±1.5	52±2.1	-51±1.7	-18±1.5	21±2.3	267	323	327	256
3	33±2.5	-30±2	51±2.8	53±1.9	-19±1.5	23±1.8	-37±1.8	-24±2.1	44±1.9	-44±1.9	-19±1.6	20±2.1	545	210	290	195
4	36±2.1	-33±1.7	46±2	37±1.8	-20±2.8	14±1.7	-32±2.5	-22±1.5	42±1.5	-55±2	-17±2.2	21±1.7	257	341	202	322
5	50±2.6	-20±2.3	43±2.8	54±2.3	-14±1.7	21±1.5	-37±1.6	-33±1.9	44±1.8	-51±2.3	-16±1.6	20±1.8	381	247	221	252
6	40±1.7	-20±1.6	50±2.1	58±2	-14±2	17±1.8	-55±1.8	-22±1.9	36±2.2	-55±2	-18±1.8	17±1.5	229	271	298	219
7	44±1.9	-21±2.1	30±1.7	53±2.3	-24±2.2	16±2	-34±1.9	-30±1.6	33±1.8	-52±1.8	-36±1.6	17±2.4	267	359	229	278
8	58±2.2	-16±1.4	25±2	56±2.5	-15±1.5	14±1.8	-57±1.6	-19±1.5	29±1.6	-45±2.2	-36±1.9	21±1.6	258	241	151	284
9	39±1.5	-21±2.3	50±2.1	56±2.1	-17±1.6	19±2	-38±1.7	-25±2.3	49±2.1	-57±2.2	-20±1.9	16±2.2	311	266	302	325
10	45±2.5	-27±1.5	41±2.1	55±2.2	-13±1.5	21±2	-49±2.2	-26±1.7	46±2.3	-53±2	-18±1.5	20±1.5	326	264	344	198

4 General Discussion

In the present thesis we adapted a paradigm of double simultaneous tactile stimulation on the fingers to investigate at which representation level the competition between concurrent tactile stimuli is resolved, and infer which spatial representation of touch may be dominant while solving this task. Furthermore, we widen the investigation of this DSS effects by taking into account the intimately multisensory nature of our perceptual systems (Stein & Meredith, 1993). In particular, we investigated whether tactile DSS interference is modulated by different degrees of additional visual inputs concerning the participant's own hands. Finally, using a neuroimaging technique, we took advantage of the fMRI adaptation paradigm to investigate the neural basis of these interactions between multiple tactile stimuli at the fingertips of the two hands. An overview of these theoretical implications for these findings researches and the insights they provided for the field of spatial representation of touch are outlined in the present section.

4.1 Discussion of the behavioural results

In the first behavioural study, we changed the relative position of the stimuli on the fingers and the hands posture in external space while using the tactile DSS paradigm. In the second study we examined the susceptibility of tactile DSS paradigm to different levels of hand-related visual inputs.

4.1.1   Interference and facilitation effects in a DSS tactile task

In Study 1 we showed that between-hands DSS stimulation can produce reliable interference effects both within and between hands. This pattern of interference is compatible with DSS competition occurring in somatotopic space, because at this low representational stage the differentiation between the two hands is less clearly defined and stimulation delivered to the non-homologous finger of the other hand can reach cortical territories ipsilateral to the target (Braun et al., 2005; Iwamura et al., 2001, 2002; Killackey et al., 1983). Importantly, these interference effects within and between hands were not modulated as a function of hand posture, thus providing further support to the notion that within and between interference effects may be solved at a low stage of body representation. In addition, we documented an increase in target sensitivity during between-hand DSS which emerged selectivity for DSS involving homologous fingers and was affected by changes in hand posture. This unexpected effect may relate to a redundancy of spatial codes for the concurrent tactile events. Similar to our study, Craig (1968) reported increased sensitivity at the index fingers following double compared to single tactile stimulation. Although a direct comparison between this earlier findings and our own results is made difficult by the substantial diversity of paradigms, it is interesting to note that a redundancy of spatial codes was present also in this previous evidence of improved tactile performance under DSS stimulation. In sum, with respect to the notion that touch can be spatially coded in different frames of reference,

the first study showed that tactile DSS interference is resolved at a low representational stage (somatotopic), whereas increased tactile DSS sensitivity relies on a higher representational stage which takes into account the layout of the body in space.

4.1.2 Influence of visual inputs on tactile DSS

In Study 2 we aimed to test the susceptibility of the tactile DSS paradigm to different levels of hand-related visual inputs. Similar to Study 1 significant tactile DSS interference emerged in all the experiments, mainly for the conditions in which the non-target finger was on the same hand as the target and when it was the non-homologous finger on the non-target hand. These findings imply, as we previously suggested, that DSS interference is driven by competition being solved in a somatotopically organised representation of touch. Also consistent with Study 1, we found that DSS interference was significantly reduced, if not absent, when homologous fingers across hands were stimulated. This selective reduction of interference may thus reflect a redundancy of spatial codes identifying the target finger (same finger stimulated between hands) and the region of external space (same location with respect to the trunk). These results corroborate the notion that DSS stimulation between fingers can produce reliable interference effects at the within- and between-hand level.

In addition to confirming our previous findings on DSS interference, we also documented no effect of vision of the hands on tactile DSS regardless of

the adapted visual manipulation. Instead we found significant enhancement of sensitivity with circles indicating the stimulation locations (Study 2, Experiment 1), and a significant overall reduction of sensitivity when incongruent hands images were presented with respect to congruent hands (Study 2, Experiment 1). The latter visual modulation of touch may be referred to the detrimental effects of postural mis-matches between the visual and proprioceptive inputs, similarly to what has been recently reported in a single detection task approach (Folegatti et al, 2009). Finally, the structural morphing that we applied in the visual domain, did not affect tactile DSS nor overall tactile performance. The fact that DSS was not affected by the two morphed digital images could be referred to previous top-down knowledge about body mereology proved to limit the extent to which tactile sensations can be affected by illusory visual appearance (de Vignemont et al., 2006; Tsakiris & Haggard, 2005).

Taken together the results of Study 2 suggest that DSS interference effect is a reliable an constant phenomenon that occurs at low stage of the spatial representation process. However, DSS interference was not modulated by non-informative visual input related to the stimulated body part. We suggest that DSS competition is resolved within the somatosensory modality, and possibly prior to any modulatory influence of vision in SI and SII.

4.2 Brain mechanisms sub-serving tactile stimuli representation at the fingers

The aim of Study 3 was to investigate the neural bases of spatial representation of touch, by using an fMRI adaptation paradigm, for stimuli delivered at the fingers of either hands. The idea was to examine which fingers pairs would present common neural substrates and show an adaptation effect in the neural response in primary and secondary somatosensory cortices. We hypothesised that adaption should primarily emerge when the same finger was stimulated twice (i.e., same region of the skin) at the level of SI. Instead, we expected to find adaptation at the level of SII even when the stimulation repeated on homologous finger of different hands. These predictions derived from the common notion that at primary stages of sensory processing (i.e., SI) tactile stimuli are still separated between hands and only at subsequent stages (e.g., SII) they are merged between opposite body parts.

The results showed that adaptation was overall more pronounced when stimulation occurred at homologous with respect to non-homologous fingers. This support the notion that fingers were well segregated in the somatosensory cortices (e.g., Overduin & Servos, 2004). Remarkably, however, this modulation occurred regardless of which hand received the stimulation, both for SI and SII. These results imply that both primary and secondary somatosensory cortices contributed to a spatial representation of

the tactile stimuli that was not completely segregated with respect to the body side.

In the behavioural studies of the present thesis we documented that a target tactile event at the left index finger was interfered by a concurrent stimulation of the middle finger, both when it was adjacent (same hand) and when it was contralateral (opposite hand). This DSS interference pattern was unaffected by hands posture (Study 1) nor by visual inputs concerning the stimulated hands (Study 2). This suggested that within and between hand interference effects were solved at a low stages of tactile processing, and in this respect they are fully compatible with the current observation that both SI and SII hold bilateral representations of the body that are somatotopically organised.

Additional behavioural data supporting this notion came from a recent work of Haggard and colleagues (2006) in which they showed that identification of which hand was stimulated was affected by hand posture, but identification of which finger was stimulated was not. They interpreted these results as evidence that detection of fingers occurs in a somatotopic reference frame, whereas hands identification occurs within a higher level reference frame which take postural information into account (Haggard et al., 2006).

Taken together our imaging data provided evidence in favour of a bilateral representations of the tactile stimuli delivered at the fingers, both in primary and secondary somatosensory cortices. These results are in

accordance with neurophysiological studies on monkeys that documented bilateral receptive fields in somatosensory area 2 in monkeys (Iwamura, Taoka & Iriki, 2001; Iwamura, Tanaka, Iriki, Taoka & Toda, 2002) and behavioural data in humans (Braun et al., 2005; Harris et al., 2001).

4.3 Conclusions

The experimental works included in the present thesis aimed at delineating how our brain use multiple spatial coding for identify and represent tactile stimuli at the fingers. Altogether the behavioural studies revealed selective interactions between concurrent tactile stimuli as a function of the fingers stimulated (homologous vs. non-homologous), the relative position of body in space, the input coming from other senses (e.g., vision) and the specific task demand. However, they also clearly showed that the DSS task primarily relies on low level somatotopic representations. Our neuroimaging data provided ground for the interpretation of the behavioural results by showing that both primary and secondary somatosensory cortices can contribute somatotopically organised representations of touch which can encompass the two body sides.

With this in mind, the central advance of the present work is twofold. First, from a methodological prospective we validated a double simultaneous tactile stimulation paradigm, relative to previous work that modulate temporal and frequency aspects, changing the relative position of the

stimulated fingers and the body posture. In addition, we tested it even with related-hand visual inputs. Moreover, in the imaging study we adapted an fMRI adaptation paradigm with stimuli delivered at the fingers of either hands, varying the fingers pairs stimulated. This approach have the advantage to investigate possible common neural substrates between body areas that can be considered closer in terms of somatotopy, but quite far in terms of spatial distance (e.g., right and left indexes).

Second, from a theoretical prospective we showed that multiple spatial representations are used depending of the specific body parts stimulated, the relative posture adopted and in relation to the specific task demand. Moreover, we described a tactile paradigm which proved nearly immune from vision of body parts. Finally, the imaging study provided evidence in favour of a bilateral representations of the tactile stimuli delivered at the fingers, both in primary and secondary somatosensory cortices.

Further perspectives

With respect to future perspective we envisage at least three lines of research. First, considering that our tactile DSS interference proved to occur predominantly within the somatosensory system and was immune to changes in the visual structural morphology of the hands, it would be interesting to test whether the DSS paradigm can be influenced by tactile manipulations that could inform the participant of a different structural morphology of the hand (e.g., linking of the fingers through rings or webbing).

A second line or research, could consider expanding our DSS paradigm to visuo-tactile stimulation, to examine to what extent the rules of competition within and between hands we have outlined in the present thesis would manifest also in a multisensory context.

Finally, with regards to neural basis of tactile representation, it would be important to extend the paradigm to different fingers as a control for the present experiment. Indeed, even though remote, there is a possibility that part of the adaptation revealed for the homologous fingers could derive from the different grade of activation for the index as compared with middle fingers. For instance, it could be argued that the index finger is more sensitive to adaptation because of different functionality.

In addition, although our imaging findings clearly speak in favour of the existence of bilateral representation of touch in SI, they cannot contribute to disambiguate which source of input is more like to produce this activation profile. This because, the low temporal resolution of fMRI does not allow to determine the time course of the ipsilateral response in SI. In future studies it would be very interesting to define the time course of this neural response by using methodologies that can provide higher temporal resolution than fMRI. For instance, we plan to adapt the exact same paradigm described in the present thesis for magnetoencephalography

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