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Vision of the body and the differentiation of perceived body side in touch

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Running head: TACTILE INTERACTIONS WITHIN AND BETWEEN HANDS

Abstract

Although tactile representations of the two body sides are initially segregated into opposite hemispheres of the brain, behavioural interactions between body sides exist and can be revealed under conditions of tactile double simultaneous stimulation (DSS) at the hands. Here we examined to what extent vision can affect body side segregation in touch. To this aim, we changed hand-related visual input while 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). Across experiments, the two hands were visible or occluded from view (Exp.1), images of the two hands were either merged using a morphing technique (Exp.2), or were shown in a compatible vs. incompatible position with respect to the actual posture (Exp.3). Overall, the results showed reliable interference effects of DSS, as compared to target-only stimulation. This interference varied as a function of which non-target finger was stimulated, and emerged both within and between hands. These results imply that the competition between tactile events is not clearly segregated across body sides. Crucially, non-informative vision of the hand affected overall tactile performance only when a visual/proprioceptive conflict was present, while neither congruent nor morphed hand vision affected tactile DSS interference. This suggests that DSS operates at a tactile processing stage in which interactions between body sides can occur regardless of the available visual input from the body.

Keywords: DOUBLE SIMULTANEOUS STIMULATION, TOUCH, BODY-SIDES, VISION, EXTINCTION

1. Introduction

Whenever we feel a tactile sensation we distinguish seemingly without effort on which side of our body it occurred (left or right). This experience is convergent with the textbook notion that the neural representations of the two body sides are initially segregated into opposite hemispheres of the brain in primary somatosensory areas (SI; e.g., Ruben et al., 2001). However, it has been known for several years that secondary somatosensory cortices (SII) actually hold bilateral representations of the body (e.g., Maldjian et al., 1999; Ruben et al., 2001). Moreover, neurophysiological studies in monkeys and neuroimaging work in humans has recently challenged the notion that neural representations of the body in SI are only contralateral (Iwamura et al., 2001; Iwamura et al., 2002; Hlushchuk and Hari, 2006). Behavioural studies in humans have corroborated these observations by showing that touch representations may not fully differentiate between body sides. For instance, people trained to discriminate punctate pressure or roughness stimuli on one finger of the right hand (e.g., the index) can transfer this training to the first neighbouring 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 et al., 2001; for related findings see also Schweizer et al., 2001; Braun et al., 2005).

Recently, by adopting a paradigm of tactile double simultaneous stimulation (DSS) at the hands we also documented clear interactions between touches delivered to opposite body sides (Tamè et al., 2011). We asked participants to make speeded detection responses to tactile stimuli at a pre-defined target finger, when this was stimulated alone or concurrently with another finger either on the same or the opposite hand. For instance, when the target finger was the right index, the concurrent stimulation could be presented

to the middle finger of the same hand, to the left index finger or to the left middle finger. Results showed that tactile DSS produces interference effects on RTs and percentage of errors both within and between hands, that are more dependent upon the identity of the stimulated body-part (i.e., which finger is touched) than body-side (i.e., which hemisoma is touched). This finding implies that some aspects of the processing of concurrent touches occur regardless of distinctions based on stimulation side. Importantly, a follow-up experiment showed that when a proprioceptive modulation was introduced (i.e., one hand was rotated palm-up), interactions between the hands became weaker or even disappeared. This suggests that although some stages of tactile processing emphasise body part identity more than side, proprioceptive modulations can contribute to emphasise laterality.

Owing to its higher spatial acuity, vision largely contributes and even dominates other senses in the spatial encoding of body parts (Ernst and Banks, 2002; Alais and Burr, 2004b). Goal-directed hand movements to visual or proprioceptive targets are performed more precisely when visual information about initial hand-position is available, in addition to proprioception (Prablanc et al., 1979; Rossetti et al., 1994). Static localisation of a body part is similarly more precise when based on integrated, compared to isolated inputs from vision and proprioception (van Beers et al., 1996). Vision also helps in segregating tactile inputs that originate from nearby locations. For instance, tactile two-point discrimination is improved by non-informative vision of the arm, as compared to a no-arm vision condition (Kennett et al., 2001). This result has been taken as evidence that even non-informative spatial vision can improve tactile acuity by reducing receptive field size (Kennett et al., 2001; see also Haggard and Serino, 2010).

In the present study, we examined whether non-informative vision can also contribute to the segregation of tactile stimuli on different body sides (left and right hand) and on different body parts (index and middle finger). To this aim, we varied hand-related visual input while participants performed a tactile DSS task. Specifically, we compared tactile DSS interference within and between hands, when the hands were hidden from view and when they were clearly visible as two distinct objects in the scene. If seeing the hands and the fingers helps to segregate touch in space, then interactions between concurrent tactile stimulations in DSS trials should decrease when the hands are visible, leading to reduced interference in speeded target detection. By contrast, if vision does not promote segregation of concurrent tactile inputs, no modulation of DSS interference should emerge as a function of the presence or absence of visual input about the hands. Note that in all cases no transient visual events occurred at the time of tactile stimulation, and the visual input was completely uninformative about the time or location of touch.

2. Experiment 1

2.1 Materials and Methods

2.1.1 Participants

Eighteen participants (mean age = 22 years, SD = 1 year; 11 females) were recruited among undergraduate students at the Faculty of Cognitive Science (University of Trento) to take part in the experiment. All reported normal or corrected to normal vision and normal somatosensation and were unaware of the purpose of the experiment. Sixteen were right-handed and two were left-handed by self-report. All 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.

2.1.2 Apparatus and stimuli

Tactile stimuli were delivered to the index or middle finger of each hand using one of four stimulators (Piezo System, Q220-A4-203YB model). The stimulators were connected to four independent custom built amplifiers 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 ms. Wave amplitude was fixed at 70 V. This resulted in a clear perceptible tap-like sensation.

Tactile stimulators were arranged on a semi-rigid foamed-plastic plane, with their unconnected ends forming an imaginary square of 4 cm.. During the experimental session, direct 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. The screen served two purposes: first, it prevented vision of the stimulation devices and the real hands; second, it allowed free manipulation of the visual input delivered to the participant. Fixation was a filled black circle (4.3° of visual angle) presented on the monitor, which was aligned with the midsagittal plane of the participant and fell at the center of the imaginary 4 cm square created by the fingertips. A foot-response pedal was positioned under the participant's right foot. 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.

2.1.3 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). Hand posture for the picture was identical to that adopted later during the experiment. To avoid any visual distortion caused by the digital picture presentation on the flat screen, the image was scaled in order to maintain the same proportions as the real participants' 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, as quickly as possible, to indicate if they felt a tactile stimulus at the target finger. The experiment comprised six separate blocks. Throughout the study, participants rested the index and middle fingers of each hand on the stimulators. The position of the stimulators (i.e., which tactile stimulator was applied to which finger) was swapped every 4 participants, to counterbalance for any possible difference among the stimulation devices. At the beginning of each block a sentence appeared on the computer screen to indicate the target finger for the upcoming block (e.g., "The target finger is the right index"). Understanding of this instruction was always double-checked by asking participants at the beginning of each block which was the designated target finger.

Each trial started with the fixation point appearing in the centre of the screen against a white background. Participants were instructed to keep fixation throughout the block. After a variable delay (200 to 400 ms), tactile stimulation was presented. The tactile stimulation consisted of 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 a non-target finger (double simultaneous stimulation trials); (3) a single touch delivered to one of the non-target fingers (catch trials).

<Please insert Figure 1 about here>

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. A solid black circle indicates the target finger, whereas an empty circle indicates the non-target finger. Double simultaneous trials are 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 a different *hand* with respect to the target, and it could be on the same or a different *finger* with respect to the target. As illustrated by Figures 1b-d, three DSS trials were possible: target finger plus a different finger of the same hand (Fig. 1b); target finger plus the same finger of the different hand (Fig. 1c); or target finger plus a different finger of the different hand (Fig. 1d). 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: a non-target occurring at a different finger of the same hand (Fig. 1e); a non-target occurring at the same finger of

the different hand (Fig. 1f); and a non-target occurring at the different finger of the different hand (Fig. 1g).

Critically, three different visual conditions were provided across blocks. One consisted of just the fixation point (see Fig. 2b). Another condition additionally displayed an image of the participant's own hands, as taken just before the experiment (see Fig. 2c). Finally, to control for possible visual attention biases, a third condition consisted of four circles (9 mm diameter approximately, 6.5° visual angle), vertically aligned with the distal phalanx of each finger just below the screen (Fig. 2d). In this control condition, the spatial location of the tactile stimulation was clearly specified thorough vision, but the hands were not visible. Importantly, all images were presented at the beginning of each block and remained statically present for its entire duration. Thus, no transient visual events occurred at the time of tactile stimulation, and the visual input was completely uninformative about the time of touch.

<Please insert Figure 2 about here>

Fixation outlasted tactile stimulation for 100 ms then disappeared. The participants were instructed to respond as to whether the target finger had been stimulated or not as quickly and as accurately as possible and were informed of the time-out delay (2 s). 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. 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. 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 participant.

2.2 Results

For each condition comprising the target (i.e., target-only and DSS trials) we computed the percentage of errors (i.e., omissions) and the mean response times (RTs) for correct trials. For RTs, left and right hand data were pooled together to have a minimum of 8 correct responses per cell for each participant and condition (average trials per condition = 21, SD = 3). We also computed the percent errors in catch trials (i.e., responses when the target was in fact absent).

The percentages of errors in target only and DSS trials were entered into an analysis of variance (ANOVA) with Stimulation Condition (see Figure 1a-d) and Visual Condition (Fixation, Hands, Circles) as within-participant variables and Target Finger (index finger, middle finger) as a between-participant variable. The Tukey HSD test was used for all post-hoc comparisons. This analysis revealed a main effect of Stimulation Condition ($F_{(3,48)} = 17.06$, $p < .0001$). As shown in Figure 3a, participants made fewer errors when the target finger was stimulated alone (mean = 3%, SE = 1%) or together with the homologous finger of the other hand (mean = 6%, SE = 3%), compared to when the target finger was stimulated together with the non-homologous finger of the same or different hand (mean = 23%, SE = 6%; mean = 16%, SE = 5%, respectively; in all comparisons $p < .02$). No other main effects or interactions were significant (all $F_s < 1.5$).

A similar analysis on the RT data revealed a main effect of Stimulation Condition ($F_{(3,48)} = 26.09$, $p < .0001$), caused by faster responses in the target only condition (mean = 551 ms, SE = 23 ms) compared to all other DSS conditions (all $p < .0002$; see Fig. 3b). Notably, when stimulation was delivered to opposite hands, RTs were faster for homologous than non-homologous pairings (mean = 600 ms, SE = 28 ms; mean = 625 ms, SE = 44 ms, respectively; $p = .038$). No other main effect or interaction was significant (all $F_s < 1.4$).

Finally, the analysis on the percentage of errors in the catch trials (Fig. 3c) revealed a main effect of Stimulation Condition ($F_{(2, 32)} = 9.4$, $p = .001$), caused by more errors for catch trials at the target hand (mean = 4%, SE = .02) than at the non-target hand (homologous: mean = 1.5%, SE = .01; $p < .02$; non-homologous: mean = .3%, SE = .004; $p < .001$). There was also a main effect of Visual Condition ($F_{(2, 32)} = 11.6$, $p = .0002$), caused by participants making more errors when their own Hands were shown on screen (mean = 3%, SE = .01) compared to when the Circles (mean = 1%, SE = .004; $p < .03$) or just the Fixation point were displayed (mean = 2%, SE = .01; $p < .0002$). This pattern of results was however specific for catch trials at the target hand (Hands: mean = 6%, SE = .01; Fixation only: mean = 3%, SE = .01; Circles: mean = 1%, SE = .01), resulting in a significant interaction between Stimulation Condition and Visual Condition ($F_{(4,64)} = 5.2$, $p = .001$).

< Please insert Figure 3 about here >

2.3 Discussion

In Experiment 1 we assessed whether seeing the hands, compared to not seeing the hands, or seeing just four circles indicating all possible target locations, could modulate processing of tactile stimuli within and between hands in a tactile DSS paradigm.

As expected, tactile DSS led to significant tactile interference effects, both in percentage of errors and RTs. These effects were most pronounced when the two stimuli occurred within the same hand. However, they also emerged between hands, particularly when the non-target finger was the finger non-homologous to the target. For instance, if the right index was the target finger, we found more errors and longer RTs when the left middle finger was stimulated concurrently, compared to the left index finger. These findings replicate our previous work (Tamè et al., 2011) and imply that tactile DSS interference originates from a competition at a stage of somatosensory processing in which bilateral representations of the fingers are available. In others words, a somatosensory processing stage in which the differentiation between body sides is not clearly defined.

However, contrary to our predictions, seeing the two hands as clearly distinct visual objects in space did not facilitate body side segregation in the DSS task. Tactile DSS interference was not modulated by vision of the hands. The only modulation caused by the visual conditions emerged in the catch trials, which were misattributed more often to the target-finger when the stimulated non-target finger was on the same hand as the target, than on the other hand. This unexpected finding may reflect s broadening of visual attention to the entire (target) hand when this is visible, which in turn makes the participant's ability to focus on a specific target location harder. Note, however, that this

visually dependent misattribution occurred only within, but not between the hands, thus corroborating the main conclusion that vision of the separated hands does not help to disambiguate the side of a touch on the body.

3. Experiment 2

The visual manipulation adopted in Experiment 1 may have failed because it was not specific to the target finger. We manipulated the presence or absence of visual input about the entire hands, while tactile stimuli occurred only on one specified finger. One more direct way to address our central question (i.e., whether non-informative vision of hands can contribute to segregation of touches) is to manipulate vision precisely for the touched body parts. To this aim, in Experiment 2, we changed the visible structure of the participant's hands, by showing an image with webbed index and middle fingers either from one hand (i.e., within-hand visual morphing; see Fig. 4a), or an image with merged homologous fingers of the two hands (i.e., between-hands visual morphing; see Fig. 4b). Note that this manipulation reverses the logic of our approach with respect to Experiment 1, as here we aimed to 'visually decrease' the segregation between perceived touches.

Our predictions were straightforward. If the changed structural morphology of the seen hands reduces the segregation of touches at the hands and fingers we should observe a corresponding increase of tactile DSS interference within- and between-hand. In particular, 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).

< Please insert Figure 4 about here >

3.1 Materials and methods

3.1.1 *Participants*

Ten participants took part in Experiment 2 (mean age = 24 years, SD = 8; 8 females). Participants were recruited as in Experiment 1, 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.

3.1.2 *Apparatus, Stimuli, Procedure and Design*

These were identical to Experiment 1, with the following exceptions. Tactile stimulation consisted of 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). Images always matched the actual hand posture of the participant. However, by using photo editing commercial software (Adobe Photoshop CS3) we altered the visual image of the fingers. The first morphed digital image was characterised by a webbed index and middle finger, obtained by adding a portion the back of the hand (within-hand visual morphing, Fig. 4a). The second morphed digital image was characterised by a fusion of the distal phalanges of the index and middle finger of either hand (between-hand visual morphing, Fig. 4b), obtained by adding a portion of the medial phalanx from each finger. The experiment comprised eight separate blocks, four for each type of morphing (within- and between-hand). Participants first completed 4 blocks with a visual condition identical to the visible hands used in Experiment 1 (see Fig. 1c). This provided a baseline for interpreting the morphed-hands

conditions. All blocks comprised 70 trials (i.e., 7 stimulation conditions repeated 10 times), resulting in a total of 840 trials.

3.2 Results

Percentages of errors and RTs in target only and DSS trials are reported in Figure 5 as a function of the three visual conditions (not-morphed, between-hands morphing or within-hand morphing). Similarly to Experiment 1, RT data were pooled across hands (average trials per condition = 30, SD = 9). One participant was excluded from the RT analysis because they did not reach the minimum number of points per cell.

The percentages of errors were analysed using repeated measures ANOVA with Stimulation Condition (see Figure 1a-d) and Visual Posture (not-morphed, within-hand visual morphing, between-hands visual morphing) as within-participant variables. This analysis revealed a main effect of Stimulation Condition ($F_{(3,27)} = 21.91, p < .0001$). As shown in Figure 5b, this pattern of results fully replicated that of Experiment 1. No other main effect or interaction reached significance (all $F_s < .7$). A similar analysis on mean RT data revealed a main effect of Stimulation Condition ($F_{(3,24)} = 63.80, p < .0001$) also compatible with the results of Experiment 1. No other main effect or interaction reached significance (all $F_s < 1$).

< Please insert Figure 5 about here >

The analysis on catch trials, similar to the one conducted in Experiment 1, revealed a main effect of Stimulation Condition ($F_{(2,18)} = 12.0, p = .0005$), driven by more errors for the catch trials at the target hand (mean = 6%, SE = .03%) than at the non-

target hand (homologous: mean = 1%, SE = .07%; non-homologous: mean = 1%, SE = .06%; $p < .002$ for both comparisons). No other main effect or interaction was significant (all $F_s < 1$).

3.3 Discussion

Experiment 2 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. To our knowledge, the manipulation we introduced in this second experiment is the first attempt at changing some aspects of the hand morphology through vision (for a manipulations of hand size see Marino et al., 2010; Newport and Preston 2010; Kennett et al., 2001; Pavani and Zampini, 2007; Taylor-Clarke et al., 2004). If changing the visual separation between the hands or fingers affects somatosensory processing for DSS we should have observed a modulation of the interference as a function of the within- or between-hand morphing.

In accordance with Experiment 1, we found a cost for DSS trials with respect to target only trials, confirming once again the robustness of the DSS interference effect. Moreover, we corroborated further the finding that tactile DSS interference clearly emerges both within and between hands, and in the latter case it is more pronounced for the non-homologous finger than the homologous finger. Similarly to Experiment 1, however, we found that the visual image of the body, even when changed in its visual structural morphology, did not alter the interactions occurring between the hands or between the fingers. The amount of tactile DSS interference between the fingers was unaffected by the visual changes in the structural morphology of the hands. At first sight, this may be surprising given the very salient visual change of body structure. However, it

is in line with the idea that tactile DSS interference arises from a competition that is solved prior to any influence from body related visual input.

4. Experiment 3

As a further attempt to modulate the DSS effects by manipulating vision of the hands, we examined the effects of a change in the visual posture of the hands. Across blocks, participants saw an image of their hands holding a posture with the stimulated fingers spaced well apart (Fig. 6a), or with the fingers close to one another (Fig. 6b).

It is important to note that the visual conditions with fingers close together inevitably resulted in a visual-proprioceptive conflict. If such a conflict specifically influences finger segregation within the hand or between the hands, we should expect tactile interference to be modulated as a function of the specific configuration of DSS stimulation. Instead, if the visuo-proprioceptive conflict modulates tactile processing overall, we should observe a general decrease in performance, but no selective change of the DSS interference pattern as a function of finger or hand.

< Please insert Figure 6 about here >

4.1 Materials and methods

4.1.1 Participants

Fourteen participants (mean age = 23 years, SD = 7; 12 females) took part in the experiment. Ten of them took part also in Experiment 2. 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.

4.1.2 Apparatus, Stimuli and Procedure

These were identical to Experiment 2, with the following exceptions. 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 Fig. 6a). In the other condition, the fingers were much closer and centred around the fixation point, depicting a posture that was incongruent with the participant's actual posture (see Fig. 6b).

The experiment comprised eight separate blocks, four per image condition (congruent vs incongruent), with 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). Each block comprised 70 trials (i.e., 7 stimulation conditions repeated 10 times), resulting in a total of 560 trials.

4.2 Results

Percentages of errors and RTs in target only and DSS trials are reported in Figure 7 as a function of the visual conditions. Percentage of errors data were analysed by a repeated measures ANOVA with Stimulation Condition (see Figure 1a-d) and Visual Condition (congruent vs. incongruent) as within-participant variables. This analysis revealed a main effect of Stimulation Condition ($F_{(3,39)} = 24.855$, $p < .0001$) caused by fewer errors for target only condition (mean = 8 %, SE = 3 %) than same (mean = 30 %, SE = 6 %), and different hand fingers stimulation (homologous: mean = 23 %, SE = 7 %; non-homologous: mean = 34 %, SE = 7 %). Between hands, the non-homologous finger

stimulation produced more errors than the homologous fingers: homologous condition (mean = 23 %, SE = 6 %) proved significantly better than non-homologous condition (mean = 34 %, SE = 7 %; $p = .006$). This analysis also revealed a main effect of Visual Condition, ($F_{(1, 13)} = 9.886$, $p = .008$), caused by fewer errors when the seen hands were congruent (mean = 21 %, SE = 8 %) than incongruent (mean = 26 %, SE = 8 %; $p < .008$) with the actual hands' posture. No other main effect or interaction proved significant (all $F_s < 1.0$).

A similar analysis on mean RT data revealed a main effect of Stimulation Condition ($F_{(3,36)} = 23.872$, $p < .0001$), compatibly with the RT pattern observed in Experiments 1 and 2. No other main effect or interaction reached significance (all $F_s < 1$).

Finally we examined the percentage of errors made by participants in the catch trials (see Fig. 7c). This analysis revealed a main effect of Stimulation Condition ($F_{(2, 26)} = 9.98$, $p = .001$), driven by more errors for catch trials at the target hand (mean = 7 %, SE = .001) than at the non-target hand (homologous: mean = 1 %, SE = .003; non-homologous: mean = 1 %, SE = .001; $p < .003$ for both comparisons). No other main effect or interaction was significant (all $F_s < 1$).

< Please insert Figure 7 about here >

4.3 Discussion

Experiment 3 examined a possible role of a visual-proprioceptive conflict on tactile DSS, by comparing conditions in which the image of the participant's own hands was congruent or incongruent with the real hand posture (see Fig. 6). A substantial

amount of tactile interference emerged in terms of percentage errors and RTs for all the DSS trials. Further, in replication of Experiment 1, clear between-hand interference emerged, particularly when the non-target finger was non-homologous to the target finger. Again, this pattern indicates that the competition occurs between tactile events that are not yet segregated as a function of body-side. When considering RTs, an interference effect was also revealed albeit more evenly distributed across fingers (see Fig. 7b).

Experiment 3 also revealed a significant overall reduction of tactile performance when incongruent hand images were presented with respect to congruent hands. This visual effect may be related? to the postural mismatch between visual and proprioceptive inputs, similarly to what was reported by Folegatti and colleagues in a simple detection approach (Folegatti et al., 2009). However, it should be emphasised that the pattern of tactile interference effect produced by the DSS trials was not modulated by visual-proprioceptive congruency. This finding suggests that conflicting information between vision and proprioception did not alter the specific pattern of within- and between-hand interference that was observed under tactile DSS conditions.

The findings of the Experiment 3, combined with evidence from Experiment 2, indicate that even minimal visuo-proprioceptive discrepancies (i.e., in Experiment 3) can affect tactile perception, remarkably more so than the salient but morphological changes applied to the visual body-structure in Experiment 2.

5. General Discussion

In the present study we examined the role of vision in segregating body side for touch. In Experiment 1, we showed the hands in their actual position, which appeared as

clearly distinct visual objects. In Experiment 2, we reduced visual segregation between hands or fingers by showing morphed hands. In Experiment 3, we introduced a visual-proprioceptive conflict. We will first discuss the pattern of DSS tactile interference within- and between-hands, as a function of homologous and non-homologous finger stimulation, which constituted our proxy for investigating the interactions between hands and between fingers in touch. Next, we will discuss the overall effect of the visual manipulations and why vision did not affect directly the DSS task and therefore, specifically, the segregation of body parts.

5.1 DSS tactile interference extends across body sides

In all experiments, DSS interference effects emerged reliably both in terms of percentage of errors and RTs. Considering that also the response time is used as a dependent variable we checked for possible speed-accuracy trade-off. However, as shown in Figures 3, 5 and 7, it was not the case. Performance was systematically better for target only trials compared to DSS trials. Most notably, it emerged both within and between hands and was somatotopically modulated. Previous reports on competing touch at the fingers (e.g., Craig et al., 1985; Craig, 1985a; Evans et al., 1992; Evans and Craig, 1991) typically found stronger interference for the within-hand compared to between-hands stimulations, albeit using different paradigm than the go-no go task. Our results showed instead comparable amount of interference when the stimulation was on the non-homologous finger of the same or the opposite hand with respect to the target. Interestingly, when the finger of the opposite hand was the homologous one, the amount of interference was considerably reduced. Previous studies have shown that the amount of interference within the same hand is quite strong, whereas between hands it is present,

but lower (e.g., Evans and Craig, 1991). In this respect, Laskin and Spencer (1979) showed that tactile stimuli delivered to identical sites of the two hands produce little interference effect, a result in accordance with our findings. This means that the amount of interference is modulated by finger identity (same or different finger stimulated) more than finger side (right or left hand).

Higher DSS interference for non-homologous fingers is compatible with competition occurring in somatotopically organised brain regions (e.g., SI and to a lesser extent SII). Furthermore, the fact that DSS interference extends across body sides also provides further support to the notion that disambiguation of body side is not completely resolved in somatosensory cortices. In a recent neuropsychological study Medina and Rapp (2008) described a patient with unilateral brain damaged that report to perceive bilateral sensations after unilateral stimulation: a particular condition known as synchiria (Medina and Rapp, 2008). The Authors attributed this phantom sensation to a normal interhemispheric interaction combined with a defeat of the inhibitory mechanisms to impede the bilateral percept. Neurophysiological studies in animals (Iwamura et al., 2001, 2002; Killackey et al., 1983) and neuroimaging studies in humans (Hlushchuk and Hari, 2006; Staines et al., 2002) have documented responses to ipsilateral tactile stimulations both in SI and SII (for behavioural evidence see also Braun et al., 2005; Harris et al., 2001). In a recent imaging study from our group (Tamè et al., under review), using an fMRI adaptation paradigm (see Grill-Spector et al., 2006; Hegner et al., 2007), we examined the fMRI adaptation to touches delivered in sequence within or between hands, to homologous or non-homologous fingers. The results documented a significant adaptation effect 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 at the level of SI, contrary to the general assumption that, because it primarily responds to contralateral tactile stimulation, it should not distinguish between body sides.

5.2 Hand related visual input and body side segregation

A surprising finding of the present work is that competition between concurrent touches at the fingers and the hands was neither enhanced nor reduced by manipulating vision of the hands. The presence or absence of the participant's own hand in the scene (Experiment 1), the modifications of the seen hand structural morphology (Experiment 2) and the congruency of seen and felt hand posture (Experiment 3) did not alter the amount of DSS interference, nor the way it manifested across hands and fingers. In sum, the DSS evoked pattern of tactile interference seems rather immune to non-informative vision of the body parts, leaving the segregation of tactile processing at the hands unaffected, at least in our behavioural task. It is important to note, however, that vision did produce a general impact on tactile perception, because the effects of non-informative vision did emerge where a visual/proprioceptive conflict was created (Experiment 3).

The absence of a modulatory effect of non-informative vision on touch processing in our study is most surprising, given the wealth of studies that provided examples of the contribution of vision on somatosensation in several tasks (e.g., Tipper et al., 1998; Taylor-Clarke et al., 2004; Serino et al., 2007; Folegatti et al., 2009; Moseley et al., 2008a; Moseley et al., 2008b). However, none of the previous reports tested the contribution of hand-related visual input in relation to the segregation of body sides (i.e.,

the two hands) for touch. In the present study, we show that, at least in the tactile DSS paradigm, hand-related visual inputs did not affect the tactile body side segregation. Thus, the DSS paradigm seems to represent a (rare) instance of a sensory encapsulated paradigm, occurring at a purely somatosensory level, possibly prior to modulations of vision on touch perception.

While negative results should always be treated with greater caution, it should be noted that a recent study also failed to show improvement of tactile detection (Mirams et al., 2010). Moreover, Roberts and Humphreys (2010) found that visual effects on tactile selection occurred only when the hands were placed far apart (i.e., 100 cm). In a future investigation it would be very interesting to extend our manipulation to similar paradigms that showed between-hands interaction in the tactile domain (e.g., Braun et al., 2005; Harris et al., 2001) to verify whether our findings are peculiar to tactile DSS or instead reflect a more general effect. It would also be interesting to assess to what extent direct vision of the hands, rather than vision of a picture of the hands, plays a role in tactile detection. Note, however, that previous studies clearly showed that also indirect vision of the body parts can modulate tactile perception (e.g., Tipper et al., 2001).

Significant overall reduction of performance emerged when participants saw an image of their own hands in a posture that was incongruent with the actual posture they adopted, as compared to when the seen and felt postures matched. This result of Experiment 3 suggests 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 simple detection task approach (Folegatti et al., 2009). Notably, the spatial mismatch between vision and touch in Experiment 3 was considerably smaller (i.e., 5 degrees) than the one adopted by Folegatti and colleagues

(which was of 15 degrees), but nonetheless it proved sufficient to affect tactile perception. Moreover, using MEG it has recently been shown that proprioceptive changes of the body (i.e., changes in hand posture) can affect early (i.e., between 20 and 40 ms) the neural processing of touch in somatosensory cortex (Hamada and Suzuki, 2003; 2005).

5.3 Conclusions

The results of the present work suggest that the DSS interference effect is a reliable phenomenon that occurs at a stage of tactile processing in which: (1) tactile events are segregated between body parts (here, the fingers); (2) tactile events are not clearly segregated between body sides (here, the hands); (3) the contribution coming from body vision, although present, seems not be specific neither for body parts nor for body sides segregation. This evidence makes of the DSS paradigm a rare instance of sensory encapsulated paradigm, occurring at a purely somatosensory level, possibly even prior to an egocentric lateral segregation of the homuncular representation.

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Figure captions

Figure 1. Schematic drawing of the stimulation conditions. The stimulated target finger is indicated by open circles, while the filled black circles represent the non-target finger. In this example the target finger is the right index finger. Double simultaneous trials are illustrated by panels (b) when target finger plus a different finger of the same hand were stimulated; (c) when target finger plus the same finger of the different hand were stimulated; or (d) when target finger plus a different finger of the different hand were stimulated. Catch trials for this example block are illustrated in panels (e) when a non-target occurring at a different finger of the same hand; (f) when a non-target occurring at the same finger of the different hand; and (g) when a non-target occurring at the different finger of the different hand.

Figure 2. A schematic drawing of the experimental setup. Note that hands and tactile stimulators are outlined 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. Tactile stimulators are not shown in the figure. Illustrations of the three possible visual conditions: (b) white screen with central fixation (fixation point); (c) picture of the participant's own hands, vertically aligned with the real hands under the flat screen; (d) four open circles on the screen arranged to form an imaginary square of 4 cm and corresponding to the fingertip position of the real hands.

Figure 3. Percentage of errors in Target only and DSS trials (a), mean reaction times (b) and percentages of errors in the catch trial condition (c) in Experiment 1, as a function of Stimulation Condition and Visual Conditions. Error bars represent the Standard Error of the mean (SE).

Figure 4. Morphed visual Conditions for Experiment 2. (a) within hand visual morphing (i.e., index and middle finger of either hand morphed together); (b) between hands visual morphing (i.e., homologous fingers morphed together). Note that a non-morphed condition, identical to the one shown in Fig. 1e, was also included.

Figure 5. Percentage of errors in Target only and DSS trials (a), mean reaction times (b) and percentages of errors in the catch trial condition (c) in Experiment 2 as a function of Stimulation Conditions and Visual Conditions. Error bars represent the Standard Error of the mean (SE).

Figure 6. Visual Conditions for Experiment 3. (a) congruent visual posture; (b) incongruent visual posture.

Figure 7. Percentage of errors in Target only and DSS trials (a), mean reaction times (b) and percentages of errors in the catch trial condition (d) for Experiment 3. Error bars represent the Standard Errors (SE).