Neuropsychologia 84 (2016) 213–221

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Congruency of body-related information induces somatosensory reorganization

Flavia Cardini[a,b,*], Matthew R. Longo[a]

[a] Department of Psychological Sciences, Birkbeck, University of London, Malet Street, London WC1E 7HX, United Kingdom
[b] Department of Psychology, Anglia Ruskin University, East Road, Cambridge CB1 1PT, United Kingdom

ARTICLE INFO

Article history:
Received 21 September 2015
Received in revised form
16 January 2016
Accepted 18 February 2016
Available online 19 February 2016

Keywords:
Body representation
Lateral inhibition
Multisensory integration
Somatosensory evoked potentials
Suppressive interaction

ABSTRACT

Chronic pain and impaired tactile sensitivity are frequently associated with "blurred" representations in the somatosensory cortex. The factors that produce such somatosensory blurring, however, remain poorly understood. We manipulated visuo-tactile congruence to investigate its role in promoting somatosensory reorganization. To this aim we used the mirror box illusion that produced in participants the subjective feeling of looking directly at their left hand, though they were seeing the reflection of their right hand. Simultaneous touches were applied to the middle or ring finger of each hand. In one session, the same fingers were touched (for example both middle fingers), producing a *congruent* percept; in the other session different fingers were touched, producing an *incongruent* percept. In the somatosensory system, suppressive interactions between adjacent stimuli are an index of intracortical inhibitory function. After each congruent and incongruent session, we recorded somatosensory evoked potential (SEPs) elicited by electrocutaneous stimulation of the left ring and middle fingers, either individually or simultaneously. A somatosensory suppression index (SSI) was calculated as the difference in amplitude between the sum of potentials evoked by the two individually stimulated fingers and the potentials evoked by simultaneous stimulation of both fingers. This SSI can be taken as an index of the strength of inhibitory interactions and consequently can provide a measure of how distinct the representations of the two fingers are. Results showed stronger SSI in the P100 component after congruent than incongruent stimulation, suggesting the key role of congruent sensory information about the body in inducing somatosensory reorganization.

1. Introduction

A large literature has linked somatosensation with cortical representations of the body. For example, chronic pain is commonly associated with reduced tactile sensitivity (Moriwaki and Yuge, 1999; Moseley, 2008; Pleger et al., 2006) and disorganization in the somatosensory cortex (Flor et al., 1995; Maihöfner et al., 2003; Tecchio et al., 2002). Moreover, tactile discrimination training, which should promote organized somatosensory maps, reduces chronic pain (Flor et al., 2001; Moseley et al., 2008). Similarly, chronic pain is also associated with distorted representations of the size and shape of the affected body part (Moseley, 2008, 2005). One influential hypothesis about this relation is that both pain and reduced tactile sensitivity result from a breakdown of functional borders between representations of body parts in the somatosensory cortex (Flor et al., 2006; Harris, 1999), a process of *somatosensory blurring* (Haggard et al., 2013).

Such blurring could result from reduced intracortical inhibition in somatosensory cortex (Lenz et al., 2011). Lateral inhibition consists of a local network of inhibitory interneurons that connect adjacent cortical neurons. Firing of one cortical neuron tends to lead to inhibition of its neighbours (Brown et al., 2004). This arrangement enhances responses to small, spatially detailed stimuli – that do not trigger the lateral inhibition from neighbouring receptive fields – increasing spatial acuity. On the other side, reduced strength in inhibitory connections promotes less distinct somatosensory maps, eventually facilitating pain to spread across adjacent, overlapping regions (Haggard et al., 2013).

Interestingly, vision of the body enhances the spatial acuity of touch (Kennett et al., 2001) and reduces the perceived intensity of acute pain (Longo et al., 2009). Longo et al. (2009) suggested that such effects could result from a visually-driven increase in somatosensory intracortical inhibition, producing a sharpening of

---

[*] Corresponding author at: Department of Psychological Sciences, Birkbeck, University of London, Malet Street, London WC1E 7HX, United Kingdom.

E-mail addresses: flavia.cardini@anglia.ac.uk (F. Cardini), m.longo@bbk.ac.uk (M.R. Longo).

http://dx.doi.org/10.1016/j.neuropsychologia.2016.02.013

somatosensory maps, opposite to that seen in chronic pain. Cardini et al. (2011) tested this hypothesis by measuring suppressive interactions between the representations of adjacent fingers in somatosensory cortex. The somatosensory evoked potential (SEP) elicited by two stimuli applied simultaneously to adjacent skin regions is reduced relative to the sum of responses evoked by stimulating each skin region independently (Gandevia et al., 1983). This suppression is known to reflect the activity of inhibitory interneuronal connections in somatosensory cortex (Hsieh et al., 1995; Ishibashi et al., 2000). Cardini et al. (2011) found that vision of the stimulated hand increased suppression of the P50 SEP component. Further, the magnitude of this modulation was correlated across participants with the magnitude of enhancement of tactile spatial acuity. These results show that seeing the body increases somatosensory intracortical inhibition, producing a sharpening of somatosensory maps.

Here, we investigated whether the opposite effect, somatosensory blurring analogous to that seen in chronic pain, can be induced by manipulating the coherence of visual and tactile signals about a body part. Recent research (Harris et al., 2007; Longo et al., 2012; Papeo et al., 2010) has used the mirror box to manipulate the coherence of visual and tactile signals about the body. Briefly, participants look into a mirror aligned with their body midline and facing rightwards, with their hands symmetrically arranged on either side. What they visually experience is direct vision of their left hand, while they actually see the mirror reflection of their right hand. The congruence of vision and touch can, thus, be manipulated by touching both hands simultaneously on either the same or on different fingers.

In the *Congruent* condition, the same finger (e.g., middle finger) was touched on both hands. The participant thus saw one finger on the left hand being touched, while simultaneously feeling touch on that same finger. In the *Incongruent* condition, different fingers were touched on each hand (e.g., left middle and right ring finger). Thus in the mirror reflection the participant saw one finger being touched (i.e. ring finger), while feeling touch on a *different* finger (i.e. middle finger). In this condition, participants often mislocalized touch on the hand behind the mirror to the wrong finger. In a recent study, Longo et al. (2012) found that such visuo-tactile incongruence was associated with altered activity over contralateral SI and posterior parietal cortex. These results seem to suggest that incongruent visual and tactile signals blurred somatosensory representation of the fingers, making them less distinct.

We therefore used the mirror box illusion to present congruent or incongruent visual and tactile cues about which finger had been touched (Longo et al., 2012; Papeo et al., 2010) and, in line with previous evidence, we predicted that congruent visuo-tactile stimulation would drive a coherent body representation able to enhance somatosensory inhibitory interactions, eventually sharpening somatotopic maps. Conversely, a reduction in the strength of somatosensory suppressive interactions will be measured after delivering incongruent bodily-related inputs.

2. Material and methods

2.1. Participants

Thirteen naïve, paid healthy volunteers (nine female) between the ages of 19 and 37 years participated after giving informed consent. Participants were generally right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971; M: 87.7, range: 11.1–100). They reported normal or corrected-to-normal vision and no abnormalities of touch. Procedures were approved by the local research ethics committee and were in accordance with the principles of the Declaration of Helsinki.

2.2. Apparatus and materials

Participants sat at a table and looked into a mirror aligned with their body midline. Their two hands were placed symmetrically on either side of the mirror. The tip of the middle finger of each hand was positioned ~20 cm from the mirror. The mirror was positioned facing rightward, so that a participant gazing leftward saw the reflection of the right hand, which appeared to be a direct view of the left hand (Fig. 1) (see Longo et al. (2012)).

Electrical stimulation was delivered via a pair of ring electrodes placed over the distal phalanxes of the left middle and ring fingers with a cathode 1 cm proximal to the anode, at a rate of 3 Hz. Two constant-current electrical stimulators (Digitimer DS7A, Welwyn, Hertfordshire, England) provided square-wave pulse current, for 0.2 ms, at an intensity 1.4 times higher than individual sensory detection threshold as measured by an initial staircase procedure (Cornsweet, 1962), as follows. Briefly, participants were asked to report the presence or absence of the electrical stimulus delivered to the finger by verbal 'yes' or 'no' responses. Shock intensity began at 0 mA increasing in steps of 10 mA until the participant reported the presence of the stimulus. If the participant responded 'yes' three times consecutively, the shock intensity was reduced by 5 mA. If they responded 'no', intensity was increased. Progressively smaller changes were made until the participant was able to detect between 55% and 60% of shocks delivered to the finger. The mean threshold for the middle finger was 44 mA (SD 14 mA) and for the ring finger was 50 mA (SD 13 mA).

In different trials the ring finger, the middle finger, or both fingers were stimulated, in random order. There were 600 stimuli delivered for each experimental condition.

2.3. Procedure

Participants performed two experimental sessions – Congruent visuo-tactile stimulation and Incongruent visuo-tactile stimulation – presented in counterbalanced order between subjects. Within each session, four blocks of visuo-tactile stimulation alternated with four blocks of electrical stimulation. During the visuo-tactile stimulation blocks, participants looked into the mirror aligned with their body midline, with their hands symmetrically arranged on either side. They thus visually experienced direct vision of their left hand, while actually seeing their reflected right hand.

The congruence of vision and touch was manipulated by touching both hands simultaneously. Touch was applied approximately every two seconds using identical paintbrushes. In the *Congruent* condition, in each trial the same finger (either the middle or the ring finger) was touched on both hands, producing a *congruent* visuo-tactile percept. In the *Incongruent* condition, in contrast, different fingers were touched on each hand (e.g., when the ring finger was touched on the left hand, the middle finger was touched on the right hand) producing an *incongruent* percept in which visual information showed one finger being touched whereas tactile information specified another, as in Longo et al. (2012).

In line with previous studies investigating plasticity of body representation by inducing bodily illusions (e.g., Botvinick and Cohen, 1998; Tsakiris, 2008; Sforza et al., 2010), we ensured that the first block lasted a sufficient amount of time to induce plastic changes in the cortical representation of the participant's left hand. For this reason the first block of visuo-tactile stimulation lasted 5 min, whereas the other three 'top up' blocks lasted 1 min each. All participants performed 2 sessions, counterbalanced between participants, while EEG activity was recorded. Within each session, four blocks of visuo-tactile stimulation alternated with four blocks of electrical stimulation. In the visuo-tactile stimulation blocks touch was applied approximately every two seconds to both hands (on the middle or the ring finger), using identical paintbrushes. In the Congruent condition, in each trial the same finger (either the middle or the ring finger) was touched on both hands, producing a congruent visuo-tactile percept. In the Incongruent condition, different fingers were touched on each hand (e.g., the ring finger on the left hand and the middle finger on the right hand) producing a mismatch between visual information-showing one finger being touched-and tactile information-specifying a different finger being touched. The first block of visuo-tactile stimulation lasted 5 minutes, whereas each of the remaining three "top-up" blocks lasted 1 minute. After each visuo-tactile stimulation block, participants' view of the hand was prevented and for 4min electrical stimuli were delivered to the left ring finger alone, the left middle finger alone or both left fingers simultaneously, in random order and in trains of either 10 or 20 shocks. Each of the four electrical stimulation blocks lasted approximately 4 minutes.

To force participants to attend to both tactile and visual stimuli along the entire block, 6% of the trials were designated as response trials after which participants were asked to make unspeeded verbal reports of which finger they saw touched in the mirror and which finger they felt touched behind the mirror.

After each visuo-tactile stimulation block, a box was moved over the right hand in order to prevent participants' view of the actual and the reflected hand (see Fig. 1). Then, for 4 min electrical stimuli were delivered to the left ring finger alone, the left middle finger alone or both left fingers simultaneously, in random order and in trains of either 10 or 20 shocks in order to make the timing of the tactile task unpredictable (see below). As for the visuo-tactile stimulation, to force participants to attend to tactile stimuli for the entire duration of the block, in 15% of the trains of

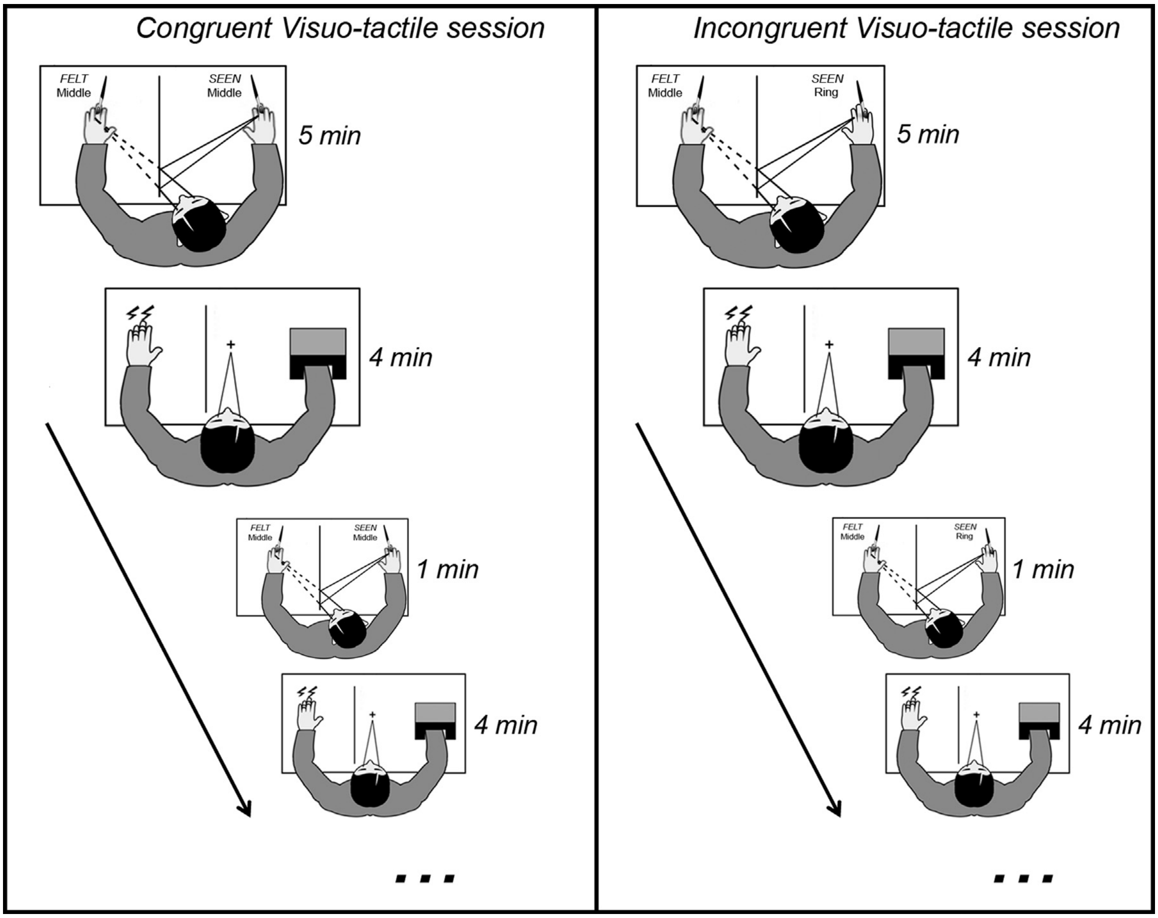

Fig. 1. Experimental paradigm. All participants performed 2 sessions, counterbalanced between participants, while EEG activity was recorded. Within each session, four blocks of visuo-tactile stimulation alternated with four blocks of electrical stimulation. In the visuo-tactile stimulation blocks touch was applied approximately every two seconds to both hands (on the middle or the ring finger), using identical paintbrushes. In the *Congruent* condition, in each trial the same finger (either the middle or the ring finger) was touched on both hands, producing a *congruent* visuo-tactile percept. In the *Incongruent* condition, different fingers were touched on each hand (e.g., the ring finger on the left hand and the middle finger on the right hand) producing a mismatch between visual information – showing one finger being touched – and tactile information – specifying a different finger being touched. The first block of visuo-tactile stimulation lasted 5 min, whereas each of the remaining three "top-up" blocks lasted 1 min. After each visuo-tactile stimulation block, participants' view of the hand was prevented and for 4 min electrical stimuli were delivered to the left ring finger alone, the left middle finger alone or both left fingers simultaneously, in random order and in trains of either 10 or 20 shocks. Each of the four electrical stimulation blocks lasted approximately 4 min.

shocks participants were asked to do a tactile task: as soon as the train finished, participants were asked to make unspeeded verbal reports of which was the last finger that had received the electrical shock (middle, ring, or both).

2.4. EEG recording and analysis

A SynAmp amplifier system and Scan 4.3 software (Neuroscan, El Paso, TX) were used to record EEG data. Recordings were obtained from 26 scalp electrodes, 20 electrodes of the standard 10–20 system (Fp1, Fpz, Fp2, F7, F3, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, Oz, O2), plus an additional 6 electrodes centered over the parietal cortex (C5, C6, CP3, CP5, CP4, CP6), placed according to the 10–10 system. Horizontal electroculogram was recorded bipolarly from electrodes placed on the outer canthi of each eye, and vertical electroculogram from electrodes above and below the right eye. The reference electrode was Fz, and the ground was on the chin. Electrode impedances were kept below 5 kΩ. EEG signals were amplified and digitized at 1000 Hz.

EEG data were analysed using the EEGLAB toolbox (Delorme and Makeig, 2004) for MATLAB (Mathworks, Natick, MA). Data were digitally filtered with a low-pass filter at 45 Hz, re-referenced to the average of the left and right mastoid, and segmented into epoched from (−50 to 300 ms). The 50 ms before stimulation was used for baseline correction. Epochs with blinks or other artefacts (voltage at any electrode exceeding $\pm 120\ \mu V$) were eliminated (M=7%, SD=6%).

ERP components of interest were selected on the basis of visual inspection and on the basis of previous studies on tactile processing (Cardini et al., 2012, 2011; Gandevia et al., 1983; Gillmeister and Forster, 2012). Inspection of scalp topographic maps show broadly consistent components across ipsilateral and contralateral central and parietal leads. Four clear somatosensory components were identifiable from the grand averages: a P50 in the 40–60 ms time window, a N80 in the 70–90 ms time window, a P100 in the 80–120 ms time window, and a N140 in the 130–150 ms time window. The electrodes overlying the ipsilateral and contralateral somatosensory cortices (C3, C4, C5, C6, CP3, CP4, CP5, CP6) were selected to investigate modulations of somatosensory suppression across experimental conditions.

Suppression is defined as the amplitude reduction for combined stimulation compared with the sum of the amplitude for individual finger stimulation. To investigate suppression quantitatively, in line with our previous work (Cardini et al., 2011), first mean amplitudes for each component in each experimental condition were calculated. Then we summed the amplitudes for individual middle and ring finger stimulation. This effectively provides a prediction of the amplitude for combined stimulation under a hypothesis of no somatosensory suppression (i.e. perfect additivity). We then performed 4 separate $2 \times 4x2 \times 2$ ANOVAs for each component with within-subjects factors: Hemisphere (Ipsilateral vs Contralateral), Electrode (C3/4, C5/6, CP3/4, CP5/6), Finger (Both vs Summed Middle and Ring), and Congruence (Congruent vs Incongruent visuo-tactile stimulation). Finally we calculated the "Somatosensory Suppression Index" (SSI), defined as the difference in amplitude between the arithmetic sum of potentials evoked by the two individually stimulated fingers and the potentials evoked by simultaneous stimulation of the two fingers. The SSI was calculated with the following equation:

$$\text{SSI} = \text{Middle alone} + \text{Ring alone} - \text{Combined}$$

Higher values of SSI indicate stronger suppression within the somatosensory system.

3. Results

3.1. Behavioral results

3.1.1. Visuo-tactile stimulation

Accuracy in reporting the finger seen touched in the mirror and the finger felt touched behind the mirror was measured during both *Congruent* and *Incongruent* visuo-tactile sessions. A 2 × 2 ANOVA was conducted on the percentage of correct responses with as within-subjects factors Congruence (Congruent vs Incongruent visuo-tactile stimulation) and Finger (Seen vs Felt). Neither main effects nor interactions were significant: Congruence, $[F_{(1,12)}=1.25;\ p=0.29]$; Finger, $[F_{(1,12)}=1.15;\ p=0.31]$; Congruence × Finger, $[F_{(1,12)}=1.17;\ p=0.30]$. Given the high accuracy scores in each condition (for Congruent stimulation: Seen finger, M=97%, SE=3%; Felt finger, M=94%, SE=3%; for Incongruent stimulation: Seen finger, M=85%, SE=5%; Felt finger, M=82%, SE=5%) and the lack of significant differences between them, we can conclude that participants paid equal attention during both visuo-tactile stimulation sessions.

3.1.2. Electrical stimulation

Accuracy in reporting the finger that received the last electrical shock of a train was measured during the electrical stimulation blocks. Accuracy after the Congruent visuo-tactile session (M=53%, SE=5%) did not differ from accuracy after the Incongruent visuo-tactile session (M=55%, SE=4%) $[t_{(12)}=-0.59,\ p=0.57,\ d_z=0.16]$. More importantly, accuracy after both visuo-tactile conditions was significantly above chance level (i.e., 33%) (Accuracy after Congruent vs chance, $[t_{(12)}=4.33,\ p=0.001,\ d_z=1.20]$; Accuracy after Incongruent vs chance $[t_{(12)}=6.15,\ p=0.001,\ d_z=1.71]$). Chance level was set at 33% because participants could report one of the three possible options: middle finger alone, ring finger alone or both fingers. These results demonstrate that participants were paying attention to the electrical stimuli during the entire duration of the blocks.

3.2. Electrophysiological results

For each identified somatosensory component we performed a 2 × 4 × 2 × 2 ANOVA as described above.

For the P50 component a main effect of Hemisphere was found $[F_{(1,12)}=18.06;\ p=0.001;\ \eta_p^2=0.60]$, with larger amplitude in the Contralateral (M=1.51 μV, SE=0.23) than in the Ipsilateral hemisphere (M=0.65 μV, SE=0.51). Moreover, there was a significant interaction between Hemisphere and Finger $[F_{(1,12)}=13.48;\ p=0.003;\ \eta_p^2=0.53]$, showing a larger amplitude for Summed (M=1.84 μV, SE=0.30) than for Both fingers (M=1.16 μV, SE=0.17), $[t_{(12)}=3.86,\ p=0.002,\ d_z=1.07]$, but only in the Contralateral hemisphere (Summed vs Both fingers, in the Ipsilateral hemisphere: $[t_{(12)}=1.24,\ p=0.24,\ d_z=0.34]$). In line with our previous work (Cardini et al., 2011), further confirmation of a contralateral suppression effect was provided by comparing the SSIs computed for the two hemispheres. A one-tailed *t-test* showed a significantly higher SSI in the Contralateral (M=0.67 μV, SE=0.17) than in the Ipsilateral hemisphere (M=−0.41 μV, SE=0.33), $[t_{(12)}=3.67,\ p=0.003,\ d_z=1.02]$ (Fig. 2 A).

For the N80 component, only the Electrode × Finger interaction was significant $[F_{(3,36)}=5.61;\ p=0.003;\ \eta_p^2=0.32]$, but no somatosensory suppression was found at any of the four sites (all $p>0.56$).

For the P100 component, a significant interaction Finger × Congruence was observed $[F_{(1,12)}=6.43;\ p=0.026;\ \eta_p^2=0.35]$. Two-tailed *t-tests* post hoc comparisons showed a larger amplitude for Summed (M=1.56 μV, SE=0.47) than for Both fingers (M=0.89 μV, SE=0.33) after the Congruent condition $[t_{(12)}=2.88,\ p=0.014,\ d_z=0.80]$ (Fig. 2). These findings showed that

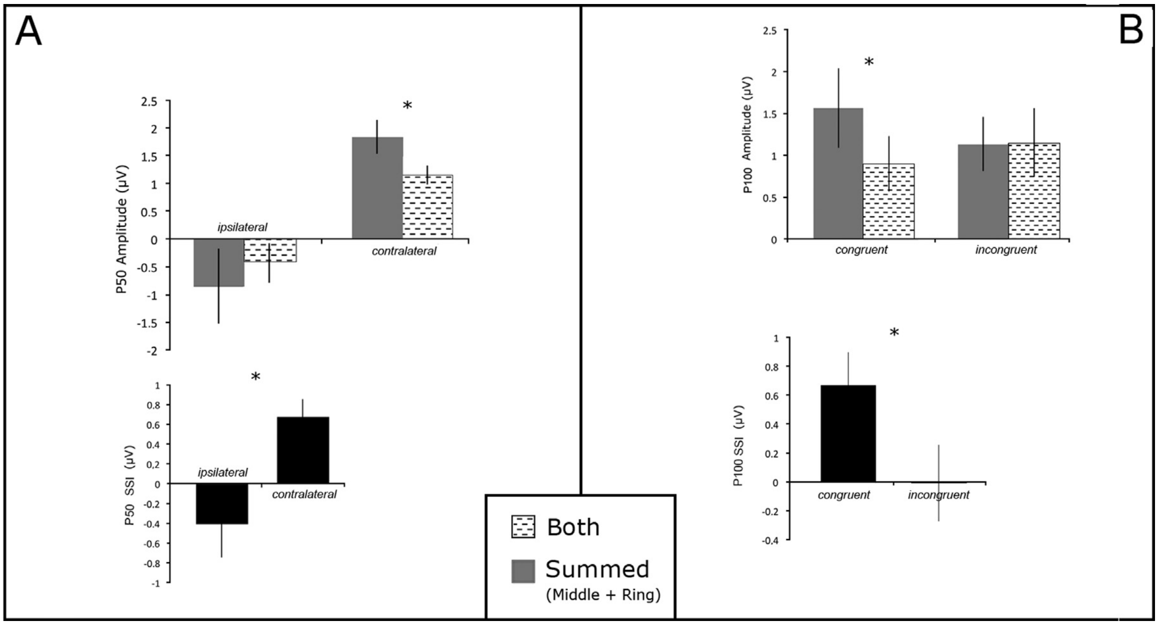

Fig. 2. Electrophysiological results. A) Top: Average of the ipsilateral (C3, C5, Cp3 and Cp5) and contrateral (C4, C6, Cp4 and Cp6) centro-parietal cluster P50 peak amplitudes in each condition, ± standard error. Grey bars represent the Sum of potentials' amplitude evoked by stimulation of individual middle and ring finger. Dashed bars represent potentials' amplitude evoked by simultaneous stimulation of Both middle and ring fingers. Bottom: The Somatosensory Suppression Index (SSI) for the P50 component. The SSI was defined as the difference between the arithmetic sum of potentials evoked by the two individually stimulated fingers and the potential evoked by simultaneous stimulation of the two fingers. SSI in the P50 component is stronger in the contralateral than in the ipsilateral hemisphere. B) Top: Average of bilateral centro-parietal clusters (C3, C4, C5, C6, Cp3, Cp4, Cp5 and Cp6) P100 mean amplitudes in each condition, ± standard error, after Congruent and Incongruent visuo-tactile stimulation sessions. Grey bars represent the Sum of potentials' amplitude evoked by stimulation of individual middle and ring finger. Dashed bars represent potentials' amplitude evoked by simultaneous stimulation of Both middle and ring fingers. Bottom: SSI in the P100 component. The SSI is larger after Congruent than Incongruent visuo-tactile session.

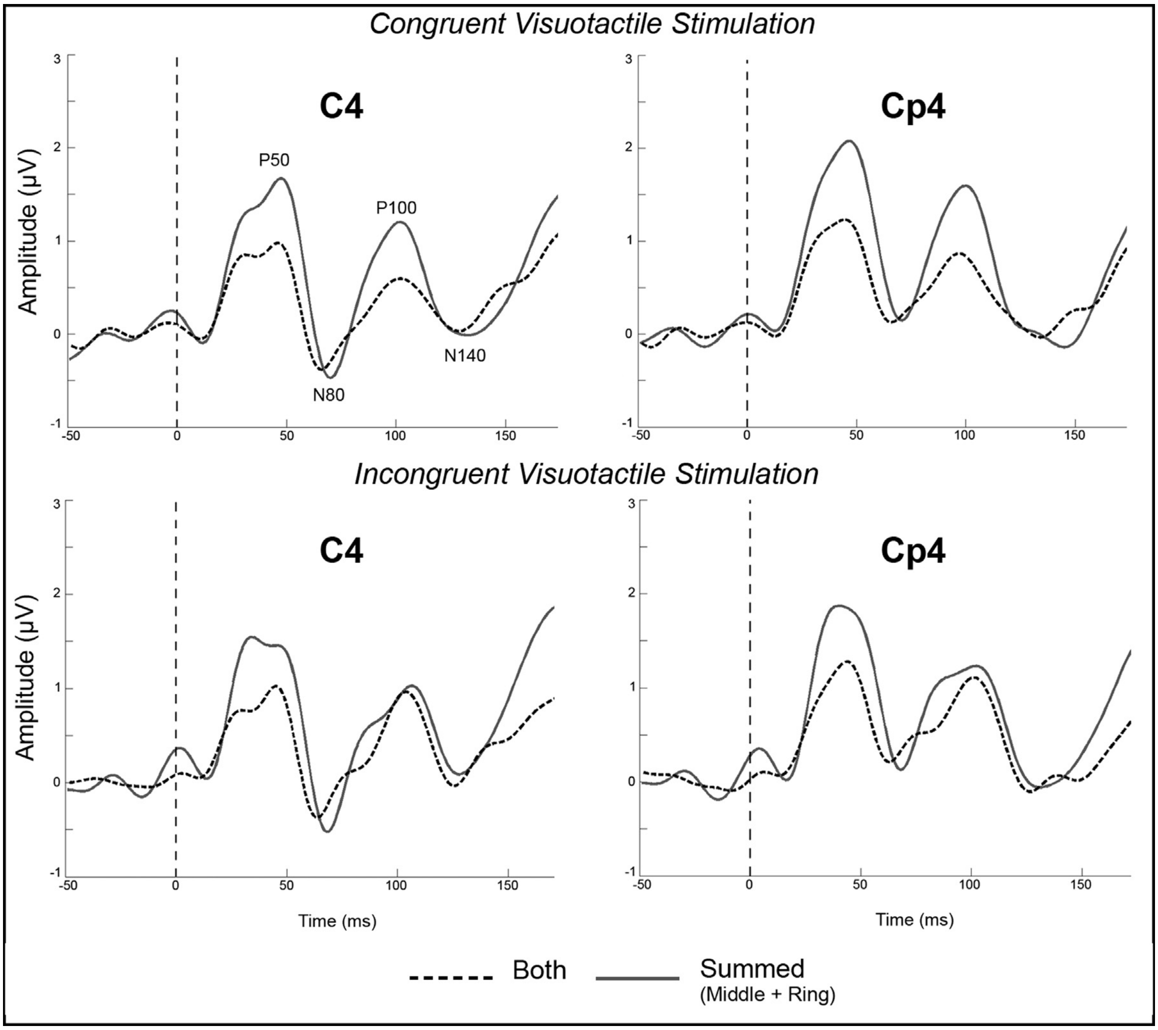

Fig. 3. Electrophysiological results. Grand average SEPs waveforms in the contralateral centro-parietal sites (C4 and Cp4) after the Congruent (top) and Incongruent (bottom) visuo-tactile stimulation sessions. Grey line represents the arithmetic sum of potentials evoked by the individually stimulated middle and ring fingers. Dashed black line represents the potentials evoked by stimulating both fingers simultaneously.

somatosensory suppression was induced only by congruent visuo-tactile stimulation, whereas no suppression was found after incongruent stimulation (Summed fingers M=1.13 µV, $SE=0.32$; Both fingers M=1.14 µV, $SE=0.41$) [$t_{(12)}=-0.03$, $p=0.97$, $d_z=0.01$]. An overview of this pattern of ANOVA interaction was provided by comparing the SSI for the Congruent with the SSI for the Incongruent visuo-tactile stimulation session. A two-tailed *t-test* revealed a larger SSI after the Congruent (M=0.67 µV, $SE=0.23$) than after the Incongruent session (M=−0.01 µV, $SE=0.26$) [$t_{(12)}=2.54$; $p=0.026$, $d_z=0.70$], confirming the ANOVA interaction (Fig. 2B).

Analysis of the N140 component showed a main effect of Hemisphere [$F_{(1,12)}=41.09$; $p=0.001$; $\eta_p^2=0.77$] with larger amplitude in the Ipsilateral (M=1.79 µV, $SE=0.53$) than in the Contralateral hemisphere (M=0.51 µV, $SE=0.63$). Moreover a significant interaction Hemisphere × Congruency was found [$F_{(1,12)}=5.20$; $p=.042$; $\eta_p^2=0.30$]. *t-Tests* post hoc comparisons showed larger amplitude after Congruent visuo-tactile stimulation in the Ipsilateral (M=1.72, $SE=0.48$) than in the Contralateral hemisphere (M=0.26 µV, $SE=0.54$), [$t_{(12)}=-7.64$, $p=0.001$, $d_z=2.12$]. A similar pattern was observed after Incongruent visuo-tactile stimulation, with larger amplitude in the Ipsilateral (M=1.86 µV, $SE=0.68$) than in the Contralateral hemisphere (M=0.77 µV, $SE=0.80$), [$t_{(12)}=-4.64$, $p=0.001$, $d_z=1.29$]. Finally, the significant interaction Hemisphere × Finger [$F_{(1,12)}=10.99$, $p=0.006$, $\eta_p^2=0.47$] showed larger amplitude for Summed fingers in the Ipsilateral hemisphere (M=2.04 µV, $SE=0.57$) than in the Contralateral hemisphere (M=0.52 µV, $SE=0.67$), [$t_{(12)}=-6.14$, $p=0.001$, $d_z=1.70$]. Similarly, larger amplitude for Both fingers was shown in the Ipsilateral hemisphere (M=1.53 µV, $SE=0.53$) than in the Contralateral hemisphere (M=0.51 µV, $SE=0.60$), [$t_{(12)}=-6.07$, $p=0.001$, $d_z=1.68$], but no somatosensory suppression was found in either hemisphere (all $p>0.08$) (Fig. 3).

Finally, given the well-known decrease in tactile acuity with age (Manning and Tremblay, 2006; Stevens and Choo, 1996) we predicted an association between participants' age and the strength of somatosensory reorganization (expressed as the difference between the P100 SSI after Congruent and Incongruent conditions). Correlating the participants' age with the difference between SSIs, no significant relationship was observed ($r=-0.16$; $p=0.60$). Furthermore we investigated whether age differently affects the somatosensory reorganization under the two experimental conditions (Congruent and Incongruent stimulation). By correlating the participants' age with each SSI we did not observe any significant association (all $p>0.67$).

4. Discussion

Incongruent information related to the hand reduces the strength of suppressive interactions within the somatosensory hand representation. In particular, the suppression of the P100 SEP component produced by simultaneous electrical stimulation of the left middle and ring fingers was eliminated after a period of conflicting signals about the left hand, compared to a period of congruent stimulation. We suggest that such incongruent cues had induced transient 'blurring' of the representations of the digits in SI.

Previous studies have shown that somatosensory evoked potentials elicited by simultaneous stimulation of adjacent fingers are reduced relative to the sum of responses evoked by stimulating each finger independently (Gandevia et al., 1983). This suppression of sensory inputs is known to reflect the activity of inhibitory connections in several locations along the sensory afferent pathway, with the greatest inhibitory interactions occurring in the somatosensory cortex (Hsieh et al., 1995; Ishibashi et al., 2000). Further, we recently showed that vision of the stimulated hand, compared to vision of a non-body object, increases somatosensory suppression, as well as enhancing tactile sensitivity on the observed location (Cardini et al., 2011). Moreover, the magnitude of this modulation was correlated across participants with the magnitude of enhancement of tactile acuity.

4.1. Intracortical inhibition and visual modulation of somatosensation

Flexibility of lateral inhibition has been recently hypothesised to underlie the widespread effects of vision of the body on somatosensory processing, for example on touch (Cardini et al., 2011; Haggard et al., 2007) and pain (Haggard et al., 2007; Longo et al., 2009). The results of Cardini et al. (2011) provided evidence supporting this interpretation (see Haggard et al. (2013) for review). Little research, however, has investigated the factors responsible for this modulation. One speculative interpretation of our results is that multisensory information about the body plays a key role in modulating the organization of somatosensory cortex. In particular, congruent multisensory signals arising from a body part might promote somatosensory suppression within its somatotopic representation, whereas conflicting information affects these suppressive interactions, increasing the overlap between adjacent somatotopic maps. We therefore suggest that only when coherent convergent sensory inputs are integrated into a multisensory representation of the body, this in turn projects top-down modulatory feedback to somatosensory areas, strengthening intracortical inhibitory connections and promoting somatosensory sharpening. Conversely, the failure in integrating discrepant sources of information might fragment or distort the body representation, promoting blurring of the boundaries between adjacent somatotopic maps (Haggard et al., 2013).

Results from a recent EEG study showed a modulation of late parietal activity during delivery of visuo-tactile stimulation on the hand (Longo et al., 2012). As in the present study, participants looked into a mirror aligned with their body midline and received congruent or incongruent touches on their left and right hands. Results showed a larger P300 component over parietal sites evoked by congruent as compared to incongruent visuo-tactile stimulation. Previous single-cell recording studies in monkeys (Avillac et al., 2007; Duhamel et al., 1998; Graziano et al., 2000; Grefkes and Fink, 2005; Iriki et al., 1996) and more recent neuroimaging studies in humans (Gentile et al., 2013, 2011; Sereno and Huang, 2006) highlighted the presence of multisensory neurons responding to both tactile stimuli and visual stimuli approaching the stimulated site. In particular, recent fMRI studies have identified a set of fronto-parietal regions involved in the integration of different bodily-related sensory inputs (Bremmer et al., 2001; Gentile et al., 2011; Makin et al., 2008) and in detecting the conflict between discrepant sources of information (Gentile et al., 2013; Leube et al., 2003). In line with these studies, Longo et al. (2012) suggested that the larger P300 component measured over the parietal sites during congruent visuo-tactile stimulation could reflect the classic pattern of neural tuning occurring during multisensory integration, i.e. when inputs from different sensory modalities, presented in temporal and spatial coincidence, converge in multimodal areas (Stein and Meredith, 1993). Importantly, this late parietal activation has been suggested to reflect integration of convergent sensory inputs into a multisensory representation of one's own body (Blanke et al., 2004; Gentile et al., 2011; Graziano et al., 1994; Leube et al., 2003; Papeo et al., 2010; Tsakiris et al., 2008).

Previous research has suggested an important link between somatosensory cortex organization, somatosensation, and body representation (see Haggard et al. (2013) for review). For example, studies on chronic pain have suggested an association between pain and disorganization of the somatosensory cortex (Knecht et al., 1995; Tecchio et al., 2002). In line with these findings, tactile discrimination training – that seems to promote organization within somatosensory areas – has been shown to reduce chronic pain (Flor et al., 2001; Moseley et al., 2008). Furthermore, a recent study by Pamment and Aspell (submitted) demonstrates that chronic pain symptoms were reduced after patients had experienced the full-body illusion, therefore after congruent visual and tactile inputs about the body were coherently integrated into a multisensory body representation.

Considering both previous evidence (Cardini et al., 2013, 2011; Longo et al., 2009) and the present findings, we speculate that promoting stable representation of the body – by delivering coherent body-related inputs – might consequently induce sharpening in somatosensory maps, potentially improving tactile sensitivity and reducing pain. Conversely, distorted bodily representation, evoked by co-occurrence of discrepant signals, could be responsible for somatosensory blurring, eventually affecting tactile discrimination ability and causing or exacerbating pain.

4.2. Early and late suppression effects

In order to use our body to effectively interact with the external world, the brain constantly tries to maintain sensory coherence in the mental representation of the body. Previous studies suggested that integration of congruent body-related visual, tactile, and proprioceptive inputs promotes this coherence, eventually enhancing somatosensation (Cardini et al., 2011; 2013). Modulation of the strength of lateral inhibition in somatosensory cortex is thought to be the key mechanism responsible for these changes.

In our recent paper we suggested that lateral inhibitory mechanisms are not uniquely driven by afferent input in a feedforward manner. We speculated that the strength of lateral inhibition in the somatosensory cortex is also modulated by feedback projections (Cardini et al., 2011). In particular, we showed that somatosensory inhibition within the somatosensory representation of the hand was enhanced when directly viewing that body part as compared to viewing an object. Notably, this somatosensory modulation was observed at early latencies, with suppressive effects measured for the P50 component that is known to originate from the primary somatosensory cortex (SI; Mauguière et al., 1983; Allison et al., 1989a; Ishibashi et al., 2000). We therefore concluded that a coherent representation of the body, housed in occipital or multisensory parietal areas and driven by vision of the hand, might promote an *on-line* reorganization of somatotopic maps, enhancing intracortical inhibitory connections in SI. Moreover this visually-induced plastic reorganization of primary somatosensory region can be very rapid and phasic (Cardini et al., 2012).

The present results additionally show that this somatosensory reorganization can occur *off-line*, i.e. after the multisensory stimulation of the body has been delivered. Therefore, whereas in our previous study we observed somatosensory reorganization *while* coherence in the body representation was induced (i.e. when looking at the hand as compared to when looking at the object), the present results suggest that *after* coherence is established modulatory projections could still be sent to the somatosensory cortex inducing an off-line reorganization.

However, unlike previous results (Cardini et al., 2011; Schubert et al., 2008), the present findings show that this off-line modulation of suppressive effects occurs at later latencies, in particular for the P100 SEP component. Previous studies have identified the generators of this component in the upper wall of the Sylvian Sulcus in the secondary somatosensory area (SII; Allison et al., 1992, 1989b; Hämäläinen et al., 1990; Hari et al., 1990). Thus, one possibility is that whereas on-line modulation of SI organization seems to have a clear functional role in rapidly enhancing object perception on the body surface (Cardini et al., 2012, 2011), off-line projections – directed instead towards secondary somatosensory regions – might perhaps be aimed at modulating more complex functions, such as tactile learning and memory processes (Fitzgerald et al., 2006a, 2006b; Hari et al., 1990).

Alternatively, it is possible that off-line feedback projections are directed to both primary and secondary somatosensory cortices. However, given our experimental paradigm, the effects of these off-line projections on the inhibitory connections within SI might not be strong enough to induce any reorganization. As widely shown in animal and human research, extensive tactile stimulation of a body part induces both short- and long-term modification of receptive fields (RF) and reorganization of the respective SI cortical area (Jenkins et al., 1990; Weinberger, 1995). In our experimental paradigm, the initial sessions of tactile stimulation of the ring and middle fingers might have already induced an expansion of their somatotopic representations in SI, resistant to the following top-down modulation projected off-line. However it is worth stressing the highly speculative nature of our explanation and we hope that future investigations will be able to shed further light on the different effects that top-down projections have on the somatosensory cortices and on their role in relation with the different stages of tactile information processing.

4.3. *Visuo-tactile vs tactile-tactile effects*

Although the current interpretation is in line with the extensive evidence of modulation of unisensory processing by high-order multisensory areas (Driver and Noesselt, 2008), an alternative mechanism underlying the present results could also be suggested. The observed reduction in strength of somatosensory suppressive interactions, instead of being caused by incongruent *visuo-tactile* information, could result by a *tactile-tactile* conflict. According to this interpretation, touches delivered to either homologous or to non-homologous fingers may have contributed to the observed difference in the P100 SSI between Incongruent and Congruent conditions. In support to this alternative interpretation it is worth remembering that the area where the P100 component is assumed to be generated – i.e. the secondary somatosensory cortex (Frot and Mauguière, 1999; Hari et al., 1984) – has been suggested to receive and integrate information from both sides of the body (Desmedt and Robertson, 1977; Eickhoff et al., 2010) via transcallosal connections between homologous SII regions that allow inputs from a stimulated body part to reach the ipsilateral SII area (Schnitzler et al., 1995; Tamè et al., 2015b; Tommerdahl et al., 2006). Additionally, the P100 component has been shown to be the first SEP component integrating contralateral and ipsilateral tactile processing (Hämäläinen et al., 1990).

Therefore, an alternative explanation for the present results might be that when the two non-homologous fingers (for example, right middle and left ring) are simultaneously touched, their somatosensory representations are activated bilaterally: whereas direct afferent inputs reach the contralateral SII, transcallosal inputs are then projected from here to the ipsilateral homologous SII region. This results in the simultaneous activation of adjacent fingers representations, even if tactile inputs come from the two different sides of the body. Importantly, activation of adjacent maps might induce blurring of their boundaries, eventually reducing suppression of the P100 component when evoked by simultaneous fingers stimulation.

The two suggested alternative explanations are not mutually exclusive and we could speculate that reorganization of somatosensory areas can result by a combination of bottom-up and top-down projections. However, it is worth noticing that, despite bilateral integration of tactile information being generally accepted for structures beyond SI – in particular SII (Eickhoff et al., 2010) – growing evidence has demonstrated contribution of SI in the integration of somatosensory inputs from the two sides of the body (Tamè et al., 2012, 2011; Tommerdahl et al., 2006). Importantly, in a recent MEG study, Tamè et al. (2015a, 2015b) took advantage of a tactile repetition-suppression paradigm to investigate the role of SI in integrating tactile stimuli from the two sides of the body. The authors found tactile suppression when touches were presented on the same, but also on opposite body parts, occurring very early in time. This new result suggests that responses to bilateral touches could not be solely ascribed to higher stages of processing, such as those involving SII.

According to this recent evidence, if *tactile-tactile* interaction is the mechanism responsible for the present results, one should expect, together with the late modulation of the P100 component that we observed, a modulation of early SEPs – as a result of SI involvement in bilateral tactile processing. The observed lack of any change in the P50 component as a function of the experimental manipulation might suggest that the current results do not emerge – at least not uniquely – from a bottom-up integration of somatosensory information. Therefore, although only a third control condition – where pure tactile-tactile interactions can be tested – could completely disambiguate effects of multisensory vs unisensory integration, an off-line top-down modulation from higher-order areas to somatosensory regions seems to be a more plausible explanation of the current data.

4.4. *Conclusion*

To conclude, our study demonstrates an effect of congruent information related to the body on the plastic reorganization of somatosensory cortex. Conflicting sensory signals from a body part can disrupt the stability in the representation of the body and consequently causing a breakdown of functional boundaries between somatosensory representations. We speculate that promoting coherence in the mental representation of the body could facilitate reorganization of somatosensory cortex by inducing neuroplastic changes eventually resulting in improved tactile sensitivity on one side, and reduced pain on the other. Whereas we initially aimed at testing the multisensory nature of this coherence, the present results cannot rule out the possibility that mere unisensory stimulation might exert similar effects. Therefore this alternative interpretation remains open and we hope future investigations will help in disambiguating the role of multisensory versus unisensory body-related signals in promoting somatosensory reorganization.

Acknowledgments

FC was supported by an InEurope short stay fellowship from the International Brain Research Organization (IBRO) (IBRO-CEERC-WERC InEurope Grant 2011) and by a short-term scientific mission under European Science Foundation COST action BM0605. MRL was supported by European Research Council Grant ERC-2013-StG-336050 under the FP7.

References

Allison, T., McCarthy, G., Wood, C.C., 1992. The relationship between human long-latency somatosensory evoked potentials recorded from the cortical surface and from the scalp. Electroencephalogr. Clin. Neurophysiol. 84, 301–314.

Allison, T., McCarthy, G., Wood, C.C., Williamson, P.D., Spencer, D.D., 1989b. Human cortical potentials evoked by stimulation of the median nerve. II. Cytoarchitectonic areas generating long-latency activity. J. Neurophysiol. 62, 711–722.

Allison, T., McCarthy, G., Wood, C.C., Darcey, T.M., Spencer, D.D., Williamson, P.D., 1989a. Human cortical potentials evoked by stimulation of the median nerve. I. Cytoarchitectonic areas generating short-latency activity. J. Neurophysiol. 62, 694–710.

Avillac, M., Ben Hamed, S., Duhamel, J.-R., 2007. Multisensory integration in the ventral intraparietal area of the macaque monkey. J. Neurosci. 27, 1922–1932.

Blanke, O., Landis, T., Spinelli, L., Seeck, M., 2004. Out-of-body experience and autoscopy of neurological origin. Brain 127, 243–258.

Botvinick, M., Cohen, J., 1998. Rubber hands "feel" touch that eyes see. Nature 391, 756. http://dx.doi.org/10.1038/35784.

Bremmer, F., Schlack, A., Shah, N.J., Zafiris, O., Kubischik, M., Hoffmann, K., Zilles, K., Fink, G.R., 2001. Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. Neuron 29, 287–296.

Brown, P.B., Koerber, H.R., Millecchia, R., 2004. From innervation density to tactile acuity: 1. Spatial representation. Brain Res. 1011, 14–32. http://dx.doi.org/10.1016/j.brainres.2004.03.009.

Cardini, F., Longo, M.R., Haggard, P., 2011. Vision of the body modulates somatosensory intracortical inhibition. Cereb. Cortex 21, 2014–2022.

Cardini, F., Haggard, P., Ladavas, E., 2013. Seeing and feeling for self and other: proprioceptive spatial location determines multisensory enhancement of touch. Cognition 127, 84–92.

Cardini, F., Longo, M.R., Driver, J., Haggard, P., 2012. Rapid enhancement of touch from non-informative vision of the hand. Neuropsychologia 50, 1954–1960.

Cornsweet, T.N., 1962. The staircrase-method in psychophysics. Am. J. Psychol. 75, 485–491.

Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Methods 134, 9–21.

Desmedt, J.E., Robertson, D., 1977. Differential enhancement of early and late components of the cerebral somatosensory evoked potentials during forced-paced cognitive tasks in man. J. Physiol. 271, 761–782.

Driver, J., Noesselt, T., 2008. Multisensory interplay reveals crossmodal influences on "sensory-specific" brain regions, neural responses, and judgments. Neuron 57, 11–23. http://dx.doi.org/10.1016/j.neuron.2007.12.013.

Duhamel, J.R., Colby, C.L., Goldberg, M.E., 1998. Ventral intraparietal area of the macaque: congruent visual and somatic response properties. J. Neurophysiol. 79, 126–136.

Eickhoff, S.B., Jbabdi, S., Caspers, S., Laird, A.R., Fox, P.T., Zilles, K., Behrens, T.E.J., 2010. Anatomical and functional connectivity of cytoarchitectonic areas within the human parietal operculum. J. Neurosci. 30, 6409–6421. http://dx.doi.org/10.1523/JNEUROSCI.5664-09.2010.

Fitzgerald, P.J., Lane, J.W., Thakur, P.H., Hsiao, S.S., 2006a. Receptive field properties of the macaque second somatosensory cortex: representation of orientation on different finger pads. J. Neurosci. 26, 6473–6484.

Fitzgerald, P.J., Lane, J.W., Thakur, P.H., Hsiao, S.S., 2006b. Receptive field (RF) properties of the macaque second somatosensory cortex: RF size, shape, and somatotopic organization. J. Neurosci. 26, 6485–6495.

Flor, H., Nikolajsen, L., Staehelin Jensen, T., 2006. Phantom limb pain: a case of maladaptive CNS plasticity? Nat. Rev. Neurosci. 7, 873–881.

Flor, H., Denke, C., Schaefer, M., Grüsser, S., 2001. Effect of sensory discrimination training on cortical reorganisation and phantom limb pain. Lancet 357, 1763–1764.

Flor, H., Elbert, T., Knecht, S., Wienbruch, C., Pantev, C., Birbaumer, N., Larbig, W., Taub, E., 1995. Phantom-limb pain as a perceptual correlate of cortical reorganization following arm amputation. Nature 375, 482–484.

Frot, M., Mauguière, F., 1999. Timing and spatial distribution of somatosensory responses recorded in the upper bank of the sylvian fissure (SII area) in humans. Cereb. Cortex 9, 854–863.

Gandevia, S.C., Burke, D., McKeon, B.B., 1983. Convergence in the somatosensory pathway between cutaneous afferents from the index and middle fingers in man. Exp. Brain Res. 50, 415–425.

Gentile, G., Petkova, V.I., Ehrsson, H.H., 2011. Integration of visual and tactile signals from the hand in the human brain: an FMRI study. J. Neurophysiol. 105, 910–922.

Gentile, G., Guterstam, A., Brozzoli, C., Ehrsson, H.H., 2013. Disintegration of multisensory signals from the real hand reduces default limb self-attribution: an fMRI study. J. Neurosci. 33, 13350–13366.

Gillmeister, H., Forster, B., 2012. Adverse effects of viewing the hand on tactile-spatial selection between fingers depend on finger posture. Exp. Brain Res. 221, 269–278.

Graziano, M.S., Yap, G.S., Gross, C.G., 1994. Coding of visual space by premotor neurons. Science 266, 1054–1057.

Graziano, M.S., Cooke, D.F., Taylor, C.S., 2000. Coding the location of the arm by sight. Science 290, 1782–1786.

Grefkes, C., Fink, G.R., 2005. The functional organization of the intraparietal sulcus in humans and monkeys. J. Anat. 207, 3–17.

Hämäläinen, H., Kekoni, J., Sams, M., Reinikainen, K., Näätänen, R., 1990. Human somatosensory evoked potentials to mechanical pulses and vibration: contributions of SI and SII somatosensory cortices to P50 and P100 components. Electroencephalogr. Clin. Neurophysiol. 75, 13–21.

Haggard, P., Christakou, A., Serino, A., 2007. Viewing the body modulates tactile receptive fields. Exp. Brain Res. 180, 187–193.

Haggard, P., Iannetti, G.D., Longo, M.R., 2013. Spatial sensory organization and body representation in pain perception. Curr. Biol. 23, R164–R176.

Hari, R., Hämäläinen, H., Hämäläinen, M., Kekoni, J., Sams, M., Tiihonen, J., 1990. Separate finger representations at the human second somatosensory cortex. Neuroscience 37, 245–249.

Hari, R., Reinikainen, K., Kaukoranta, E., Hämäläinen, M., Ilmoniemi, R., Penttinen, A., Salminen, J., Teszner, D., 1984. Somatosensory evoked cerebral magnetic fields from SI and SII in man. Electroencephalogr. Clin. Neurophysiol. 57, 254–263.

Harris, A.J., 1999. Cortical origin of pathological pain. Lancet 354, 1464–1466.

Harris, J.A., Arabzadeh, E., Moore, C.A., Clifford, C.W.G., 2007. Noninformative vision causes adaptive changes in tactile sensitivity. J. Neurosci. 27, 7136–7140. http://dx.doi.org/10.1523/JNEUROSCI.2102-07.2007.

Hsieh, C.L., Shima, F., Tobimatsu, S., Sun, S.J., Kato, M., 1995. The interaction of the somatosensory evoked potentials to simultaneous finger stimuli in the human central nervous system. A study using direct recordings. Electroencephalogr. Clin. Neurophysiol. 96, 135–142.

Iriki, A., Tanaka, M., Iwamura, Y., 1996. Coding of modified body schema during tool use by macaque postcentral neurones. Neuroreport 7, 2325–2330.

Ishibashi, H., Tobimatsu, S., Shigeto, H., Morioka, T., Yamamoto, T., Fukui, M., 2000. Differential interaction of somatosensory inputs in the human primary sensory cortex: a magnetoencephalographic study. Clin. Neurophysiol. 111, 1095–1102.

Jenkins, W.M., Merzenich, M.M., Ochs, M.T., Allard, T., Guíc-Robles, E., 1990. Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. J. Neurophysiol. 63, 82–104.

Kennett, S., Taylor-Clarke, M., Haggard, P., 2001. Noninformative vision improves the spatial resolution of touch in humans. Curr. Biol. 11, 1188–1191.

Knecht, S., Henningsen, H., Elbert, T., Flor, H., Höhling, C., Pantev, C., Birbaumer, N., Taub, E., 1995. Cortical reorganization in human amputees and mislocalization of painful stimuli to the phantom limb. Neurosci. Lett. 201, 262–264.

Lenz, M., Höffken, O., Stude, P., Lissek, S., Schwenkreis, P., Reinersmann, A., Frettlöh, J., Richter, H., Tegenthoff, M., Maier, C., 2011. Bilateral somatosensory cortex disinhibition in complex regional pain syndrome type I. Neurology 77, 1096–1101.

Leube, D.T., Knoblich, G., Erb, M., Grodd, W., Bartels, M., Kircher, T.T.J., 2003. The neural correlates of perceiving one's own movements. Neuroimage 20, 2084–2090.

Longo, M.R., Musil, J.J., Haggard, P., 2012. Visuo-tactile integration in personal space. J. Cogn. Neurosci. 24, 543–552.

Longo, M.R., Betti, V., Aglioti, S.M., Haggard, P., 2009. Visually induced analgesia: seeing the body reduces pain. J. Neurosci. 29, 12125–12130.

Maihöfner, C., Handwerker, H.O., Neundörfer, B., Birklein, F., 2003. Patterns of cortical reorganization in complex regional pain syndrome. Neurology 61, 1707–1715.

Makin, T.R., Holmes, N.P., Ehrsson, H.H., 2008. On the other hand: dummy hands and peripersonal space. Behav. Brain Res. 191, 1–10. http://dx.doi.org/10.1016/j.bbr.2008.02.041.

Manning, H., Tremblay, F., 2006. Age differences in tactile pattern recognition at the fingertip. Somatosens. Mot. Res. 23, 147–155.

Mauguière, F., Desmedt, J.E., Courjon, J., 1983. Astereognosis and dissociated loss of frontal or parietal components of somatosensory evoked potentials in hemispheric lesions. Detailed correlations with clinical signs and computerized tomographic scanning. Brain 106 (Pt 2), 271–311.

Moriwaki, K., Yuge, O., 1999. Topographical features of cutaneous tactile hypoesthetic and hyperesthetic abnormalities in chronic pain. Pain 81, 1–6.

Moseley, G.L., 2005. Distorted body image in complex regional pain syndrome. Neurology 65, 773.

Moseley, G.L., 2008. I can't find it! Distorted body image and tactile dysfunction in patients with chronic back pain. Pain 140, 239–243.

Moseley, G.L., Zalucki, N.M., Wiech, K., 2008. Tactile discrimination, but not tactile stimulation alone, reduces chronic limb pain. Pain 137, 600–608.

Papeo, L., Longo, M.R., Feurra, M., Haggard, P., 2010. The role of the right temporoparietal junction in intersensory conflict: detection or resolution? Exp. Brain Res. 206, 129–139.

Pleger, B., Ragert, P., Schwenkreis, P., Förster, A.-F., Wilimzig, C., Dinse, H., Nicolas, V., Maier, C., Tegenthoff, M., 2006. Patterns of cortical reorganization parallel impaired tactile discrimination and pain intensity in complex regional pain syndrome. Neuroimage 32, 503–510.

Schnitzler, A., Salmelin, R., Salenius, S., Jousmäki, V., Hari, R., 1995. Tactile information from the human hand reaches the ipsilateral primary somatosensory cortex. Neurosci. Lett. 200, 25–28.

Schubert, R., Ritter, P., Wüstenberg, T., Preuschhof, C., Curio, G., Sommer, W., Villringer, A., 2008. Spatial attention related SEP amplitude modulations covary with BOLD signal in S1—a simultaneous EEG—fMRI study. Cereb. Cortex 18, 2686–2700.

Sereno, M.I., Huang, R.-S., 2006. A human parietal face area contains aligned head-centered visual and tactile maps. Nat. Neurosci. 9, 1337–1343.

Sforza, A., Bufalari, I., Haggard, P., Aglioti, S.M., 2010. My face in yours: visuo-tactile facial stimulation influences sense of identity. Soc. Neurosci. 5, 148–162.

Stein, B.E., Meredith, M.A., 1993. The Merging of the Senses. MIT Press, Cambridge, MA, USA.

Stevens, J.C., Choo, K.K., 1996. Spatial acuity of the body surface over the life span. Somatosens. Mot. Res. 13, 153–166.

Tamè, L., Farnè, A., Pavani, F., 2011. Spatial coding of touch at the fingers: insights from double simultaneous stimulation within and between hands. Neurosci. Lett. 487, 78–82. http://dx.doi.org/10.1016/j.neulet.2010.09.078.

Tamè, L., Pavani, F., Papadelis, C., Farnè, A., Braun, C., 2015b. Early integration of bilateral touch in the primary somatosensory cortex. Hum. Brain Mapp. 36, 1506–1523. http://dx.doi.org/10.1002/hbm.22719.

Tamè, L., Pavani, F., Braun, C., Salemme, R., Farn, A., Reilly, K.T., 2015a. Somatotopy and temporal dynamics of sensorimotor interactions: evidence from double afferent inhibition. Eur. J. Neurosci. 41, 1459–1465. http://dx.doi.org/10.1111/ejn.12890.

Tamè, L., Braun, C., Lingnau, A., Schwarzbach, J., Demarchi, G., Li Hegner, Y., Farnè, A., Pavani, F., 2012. The contribution of primary and secondary somatosensory cortices to the representation of body parts and body sides: an fMRI adaptation study. J. Cogn. Neurosci. 24, 2306–2320. http://dx.doi.org/10.1162/jocn_a_00272.

Tecchio, F., Padua, L., Aprile, I., Rossini, P.M., 2002. Carpal tunnel syndrome modifies sensory hand cortical somatotopy: a MEG study. Hum. Brain Mapp. 17, 28–36.

Tommerdahl, M., Simons, S.B., Chiu, J.S., Favorov, O., Whitsel, B.L., 2006. Ipsilateral input modifies the primary somatosensory cortex response to contralateral skin flutter. J. Neurosci. 26, 5970–5977. http://dx.doi.org/10.1523/JNEUROSCI.5270-05.2006.

Tsakiris, M., 2008. Looking for myself: current multisensory input alters self-face recognition. PLoS One 3, e4040.

Tsakiris, M., Costantini, M., Haggard, P., 2008. The role of the right temporo-parietal junction in maintaining a coherent sense of one's body. Neuropsychologia 46, 3014–3018.

Weinberger, N.M., 1995. Dynamic regulation of receptive fields and maps in the adult sensory cortex. Annu. Rev. Neurosci. 18, 129–158. http://dx.doi.org/10.1146/annurev.ne.18.030195.001021.