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Observing touch activates human primary somatosensory cortex

Elina Pihko,[1] Cathy Nangini,[1] Veikko Jousmäki[1] and Riitta Hari[1,2]

[1]Brain Research Unit, Low Temperature Laboratory, Aalto University School of Science and Technology, 00076 AALTO, Espoo, Finland

[2]Department of Clinical Neurophysiology, Helsinki University Central Hospital, 00290 Helsinki, Finland

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Abstract

We used magnetoencephalography to show that the human primary somatosensory (SI) cortex is activated by mere observation of touch. Somatosensory evoked fields were measured from adult human subjects in two conditions. First, the experimenter touched the subject's right hand with her index finger (Experienced touch). In the second condition, the experimenter touched her own hand in a similar manner (Observed touch). Minimum current estimates were computed across three consecutive 300-ms time windows (0–300, 300–600 and 600–900 ms) with respect to touch onset. During 'Experienced touch', as expected, the contralateral (left) SI cortex was strongly activated in the 0–300 ms time window. In the same time window, statistically significant activity also occurred in the ipsilateral SI, although it was only 2.5% of the strength of the contralateral activation; the ipsilateral activation continued in the 300–600 ms time window. During 'Observed touch', the left SI cortex was activated during the 300–600 ms interval; the activation strength was 7.5% of that during the significantly activated period (0–300 ms) of 'Experienced touch'. The results suggest that when people observe somebody else being touched, activation of their own somatosensory circuitry may contribute to understanding of the other person's somatosensory experience.

Introduction

When a person observes another person performing a goal-directed movement, overlapping brain areas are activated in both the actor and the observer (Rizzolatti & Craighero, 2004). In monkeys, a set of 'mirror neurons' in the ventral premotor cortex fires both when the monkey reaches for an object and when it sees another monkey or a human performing the same motor act (di Pellegrino *et al.*, 1992; Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996). In humans, a circuitry of motor-function-related cortical regions is active during both self-performed and observed motor acts (Fadiga *et al.*, 1995; Grafton *et al.*, 1996; Hari *et al.*, 1998; Iacoboni *et al.*, 1999; Buccino *et al.*, 2001; Perani *et al.*, 2001; Nishitani & Hari, 2002). This 'mirror-neuron system' may support understanding of other persons' actions and intentions (Gallese & Goldman, 1998; Iacoboni *et al.*, 2005).

During action observation, many brain areas beyond the mirror-neuron system are involved, such as the primary (SI) and secondary (SII) somatosensory cortices. For example, in a magnetoencephalography (MEG) study, somatosensory evoked fields (SEFs) from SI and SII cortices in response to electric median nerve stimulation were modulated while subjects observed an experimenter manipulating a small object (Avikainen *et al.*, 2002). Accordingly, SI-cortex SEFs to lip stimulation were modified when subjects observed articulatory movements (Möttönen *et al.*, 2005). Functional magnetic resonance imaging (fMRI) demonstrated activation of area 2 of the SI cortex when subjects were watching hand flexions (Oouchida *et al.*, 2004). Moreover, movie scenes involving object manipulation with the hands evoked fMRI activations in the mid-postcentral sulcus close to area 5, with highly correlated time courses across subjects (Hasson *et al.*, 2004).

If somatosensory areas are involved in the observation of movements, shouldn't they be activated by observation of a person being touched? Keysers *et al.* (2004) first showed with fMRI that watching another person being touched activates the SII cortex in the observer. Subsequent fMRI studies demonstrated that touch observation also activates the SI cortex (Blakemore *et al.*, 2005; Cheng *et al.*, 2007; Ebisch *et al.*, 2008; Schaefer *et al.*, 2009). To date, electrophysiological evidence of SI activation during observation of touch is indirect, obtained by monitoring modulation of somatosensory evoked responses to simultaneous external (probe) stimuli, such as electric pulses delivered to the median nerve (Avikainen *et al.*, 2002; Bufalari *et al.*, 2007) or touch applied to a finger (Schaefer *et al.*, 2005, 2006, 2008).

We tested whether the SI cortex can be directly activated by the observation of touch, in a manner similar to activation resulting from actual touch. Specifically, we compared the strength and temporal evolution of SI activation measured by MEG when subjects observed (i) their hand being touched by the experimenter (*Experienced touch*; EXP) and (ii) the hand of the experimenter being touched without the subjects receiving any other stimulation (*Observed touch*; OBS).

Correspondence: Dr Elina Pihko, as above.
E-mail: pihko@neuro.hut.fi

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Materials and methods

Subjects and conditions

Fourteen healthy adult subjects (18–57 years, mean 32 years; four females) participated in the study. All subjects were right-handed by their own report. The study was in accordance with the Declaration of Helsinki, and approved by the local Ethics committee of the Hospital district of Helsinki and Uusimaa, and undertaken with the informed consent of the volunteers. Data from one subject were discarded because of sleepiness during the recordings.

Stimuli

The experimenter was sitting on the subject's right side throughout the recordings. In the EXP condition, the experimenter tapped with her right index finger the dorsal surface of the subject's right hand in the area between the index finger and thumb (Fig. 1). The subject was instructed to observe the touched hand. A black cross, drawn on the skin with a marker pen, guided the experimenter and allowed the subject to fixate on the same spot. About 200 stimuli were applied with an interstimulus interval of 2–3 s. The finger-to-hand contact lasted ~100–200 ms, as measured off-line from the raw-data trigger channel.

In the OBS condition, the experimenter touched her own left hand in a similar manner, and the subject's task was again to observe the touched hand (Fig. 1). To keep the stimulation parameters as stable as possible, the same experimenter was used throughout.

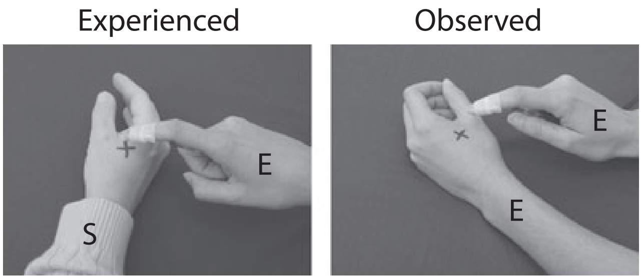

FIG. 1. Experimental setup: stimulation in the experienced (left panel) and in the observed (right) touch conditions. E, experimenter's hand; S, subject's hand.

A small triggering system, consisting of a flexible multifilament fibre-optic cable (size 1.5; Schott SpectraFlex, Mainz, Germany) connected to a photoelectric switch (E3X-N41; Omron, Osaka, Japan), was taped to the experimenter's index finger. A similar system was previously used by Jousmäki *et al.* (2007). Half of the filaments at the end of the cable emitted red light and the other half detected the reflectance from the skin. The reflectance threshold was adjusted so that, when the filaments made contact with the skin, a trigger signal was generated by the photoelectric switch and delivered to the MEG data-acquisition system. The threshold was adjusted for each subject prior to the measurements. The subject could not feel the filaments during the touch.

Measurements

MEG signals were measured in a magnetically shielded room (Euroshield Ltd., Eura, Finland) with a 306-channel helmet-shaped neuromagnetometer (Elekta Neuromag Oy, Helsinki, Finland) comprising 102 sensor units, each consisting of two orthogonal planar gradiometers and one magnetometer which together provide three independent measurements of the magnetic field at each location.

The head position relative to the MEG sensors was determined at the beginning of each recording block using the signals from four indicator coils. These coils were attached to the subject's head at locations known in an anatomical coordinate system, defined by the nasion and the preauricular points. MEG was recorded with a bandpass filter of 0.03–167 Hz and sampled at 1004 Hz. The electro-oculogram was measured from the upper left and lower right eye canthi.

Analysis

The raw data were offline-filtered with the temporal Signal Space Separation (tSSS) method (Taulu & Simola, 2006; Taulu & Hari, 2009) to remove artifacts originating outside the head (such as line frequency noise, stimulus artifacts). After tSSS, the data were offline-averaged (from −100 ms to +1500 ms with respect to stimulus onset), and epochs with signals exceeding ± 1500 fT/cm on gradiometer channels, ± 1200 fT on magnetometer channels, or ± 150 μV on the electro-oculogram channel were rejected.

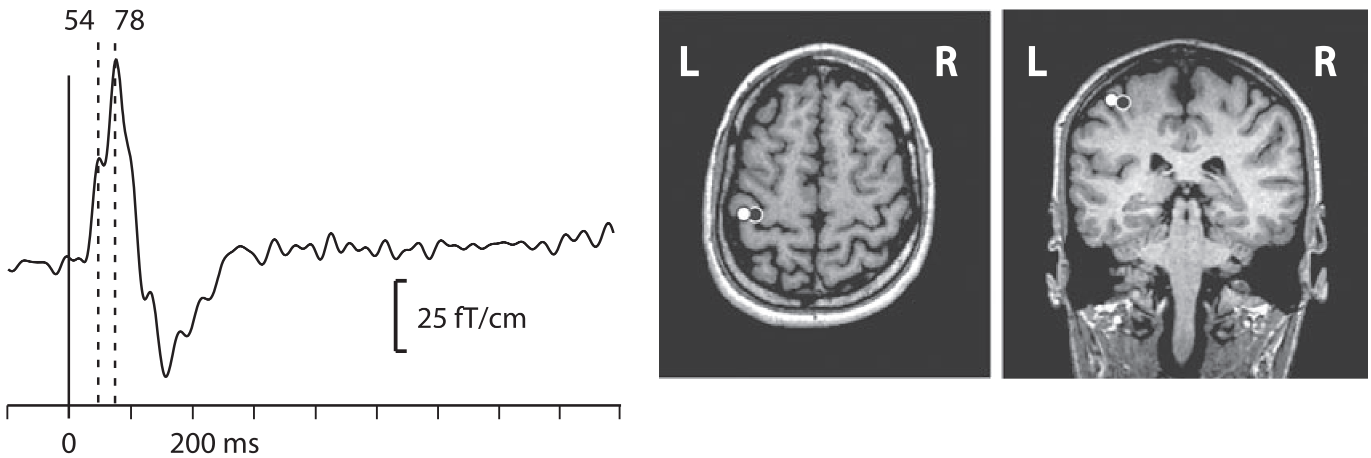

FIG. 2. (Left) One gradiometer channel showing the evoked response of Subject 1 to EXP. Zero indicates the onset of the touch. (Right) The sites of the current dipoles (white dot at 54 ms, black dot at 78 ms; see the dashed vertical lines on the left) overlaid onto the subject's own MR images. L, left; R, right.

Equivalent current dipoles (ECDs) were fitted to the SEFs of the left (contralateral) hemisphere during the first prominent deflection (35–80 ms) in the EXP condition. For dipole fitting, the baseline was defined 100 ms before the trigger, the low-pass filter was set at 90 Hz and a selection of ~100 channels over the contralateral somatosensory cortex was used. The averaged goodness of fit for all ECDs was 96% (range 88.7–99%; SD = 2.3%).

Further data analysis was carried out using minimum-current estimates (MCEs; Uutela *et al.*, 1999) with a standard boundary element model. The standard head model also enabled us to calculate group averages for initial data visualization. For the MCE analysis of both EXP and OBS conditions, a spherical region of interest (ROI) in the left hemisphere was selected with a center at each subject's SI source location (ROI_{SI}), defined in the EXP condition as the site of the ECD. Anatomical magnetic resonance images were available for eight out of the 13 subjects and were used to adjust the location of the origin of the sphere model for both ECD and MCE calculations. A mirror location in the right hemisphere was used to study activity in the ipsilateral SI cortex; such a procedure was adopted as the ECD locations between the hemispheres did not differ when electric stimulation was applied to the little finger, thumb and median nerve (Tecchio *et al.*, 1997). An additional region of interest (ROI_{MI}), 10 mm anterior, superior and medial to ROI_{SI}, was used to compare activations between SI and primary motor (MI) cortices. These two ROIs were slightly overlapping (by up to ~3.5 mm). All three regions of interest were 20 mm in diameter, and the strength of activity was calculated as the sum of values at grid points spaced 5 mm apart. For MCE analysis, the signals were lowpass-filtered at 40 Hz.

Signal amplitudes from 0 to 900 ms were computed with respect to the mean amplitude of a baseline defined from −100 to 0 ms. Next, the mean strength was calculated for three time windows (0–300, 300–600 and 600–900 ms), and the baseline value was subtracted. The time windows were selected after preliminary visual inspection of the averaged activity inside the ROIs (Fig. 3), showing strongest changes in the activation level at ~300 ms. Four factors, EXP_{LH} (LH, left hemisphere), EXP_{RH} (RH, right hemisphere), OBS_{LH} and OBS_{RH}, each comprising three levels (the three time windows), were used for repeated-measures analysis with a general lineal model (GLM) (SPSS 14.0; SPSS Inc.). Statistically significant main effects were further analyzed with a one-sample, two-tailed *t*-test. Activity from SI and MI cortices was compared during the first 300 ms after stimulation. Greenhouse–Geisser correction was used for factors with more than two levels.

Results

Dipole modelling

The EXP evoked a prominent response in the left, contralateral SI cortex. The main response consisted of two peaks: an earlier one peaking at 50 ± 7 ms (mean ± SD) and a later one peaking at 77 ± 7 ms. The ECD was located on average 5 mm more medial for the 50-ms than the 77-ms deflection (*x* coordinates −34.5 ± 4.5 mm vs. −39.4 ± 4.9 mm, respectively; $P = 0.0002$, two-tailed *t*-test), with no significant differences in the anterior–posterior (*y* coordinates 7.9 ± 7.8 vs. 8.4 ± 8.1 mm, respectively) or superior–inferior (*z* coordinates 95.8 ± 7.2 vs. 93.3 ± 5.9 mm) directions (Fig. 2). The source was statistically significantly weaker for the 50-ms than the 77-ms deflection [23.2 ± 10.0 vs. 33.7 ± 14.2 nA × m (nAm), respectively; $P = 0.0006$]. The ECD locations of the 77-ms deflection were used to define individual ROIs for the MCE analysis. Both dipoles were roughly oriented in the anterior–posterior direction.

Measured MEG waveforms over the ipsilateral SI cortex in EXP, and over both left and right SI cortices in OBS, were generally broad and/or low in amplitude and did not allow for successful source modelling.

MCE analysis

Figure 3 shows, for both EXP and OBS, grand-averaged amplitude curves of MCE activation inside three different ROIs: left and right somatosensory and occipital regions. In EXP, the strong activation in the contralateral SI cortex (upper left image) was followed by activation of the occipital areas (bottom left, MCE shown at 148 ms), and by weak activation of the ipsilateral side (middle, MCE shown at 583 ms). During OBS, the main activation appeared first in the occipital areas (bottom right, MCE shown at 168 ms) and was followed by weak activation of the left somatosensory region (upper right, MCE shown at 467 ms). In the OBS condition, no significant activity was found in the ipsilateral SI cortex (middle, right column). As the activity level of the somatosensory areas changed at ~300 ms in conditions EXP_{LH}, EXP_{RH} and OBS_{LH}, we used three time windows (0–300, 300–600 and 600–900 ms) for further analysis. Activation in the occipital parts of the brain was not analyzed further.

Figure 4 shows individual MCE results for Subjects 2–6 during EXP and OBS conditions. In all subjects, the EXP was associated with strong activation of the left (contralateral) SI cortex during the first 100 ms whereas in the OBS condition the same area was activated later and more weakly, with variation across the subjects. The SI cortex was mainly activated during the 400–700 ms time window in Subject 2 and from 300 ms onwards in Subject 3. Subject 4 showed activation starting from 200 ms, with a shift in locus and stronger amplitude after 500 ms. The SI cortex was weakly activated during the 100–400 and 500–600 ms time windows in Subject 5 and during 400–600 ms and 700–900 ms time windows in Subject 6.

Activation inside ROI_{SI}, quantified in 300-ms steps from 0 to 900 ms, differed statistically significantly from zero in three out of the four datasets: EXP_{LH}, EXP_{RH} and OBS_{LH} (EXP_{LH}: $F_{1,12} = 21.6$, $P = 0.001$; EXP_{RH}: $F_{1,12} = 8.8$, $P = 0.012$; OBS_{LH}: $F_{1,12} = 5.0$, $P = 0.045$; Fig. 3, gray horizontal bars). Activation in OBS_{RH} was not statistically significantly above the baseline ($F_{1,12} = 3.8$, $P = 0.075$).

In the left hemisphere, the overall activity within the 900-ms time window was stronger during EXP (mean ± SEM: 1.62 ± 0.35 nAm) than during OBS (0.25 ± 0.11 nAm). The analysis used a GLM with two factors: condition with two levels (EXP_{LH} and OBS_{LH}) and time-window with three levels (0–300, 300–600 and 600–900 ms). Significant main effects were found for condition ($F_{1,12} = 21.5$, $P = 0.001$), time-window ($F_{1,12.4} = 52.7$, $P < 0.001$) and their interaction ($F_{1,12.3} = 49$, $P < 0.001$).

Figure 5 illustrates differences in the temporal evolution of the MCEs, averaged across subjects in 300-ms steps, in the EXP and OBS conditions. In EXP_{LH}, the strength of activity during the 0–300 ms time window differed statistically significantly from the baseline (4.1 ± 0.7 nAm, $t = 6.3$, $P < 0.0001$), whereas during the 300–600 and 600–900 ms time windows, the difference did not reach significance (0.4 ± 0.2 nAm, $P = 0.13$ and 0.4 ± 0.2 nAm, $P = 0.1$, respectively). In EXP_{RH}, the strength of activity during the 0–300 and 300–600 ms time windows differed significantly from the baseline (0.1 ± 0.05 nAm, $t = 2.2$, $P = 0.045$, and 0.2 ± 0.06 nAm, $t = 2.3$, $P = 0.037$, respectively). During the 0–300 ms time window, the strength of the ipsilateral activity in the EXP_{RH} was only 2.5% of that in the contralateral $EXP_{LH.}$ In OBS_{LH}, during the first (0–300 ms) and last (600–900 ms) time windows, the activation was not statistically

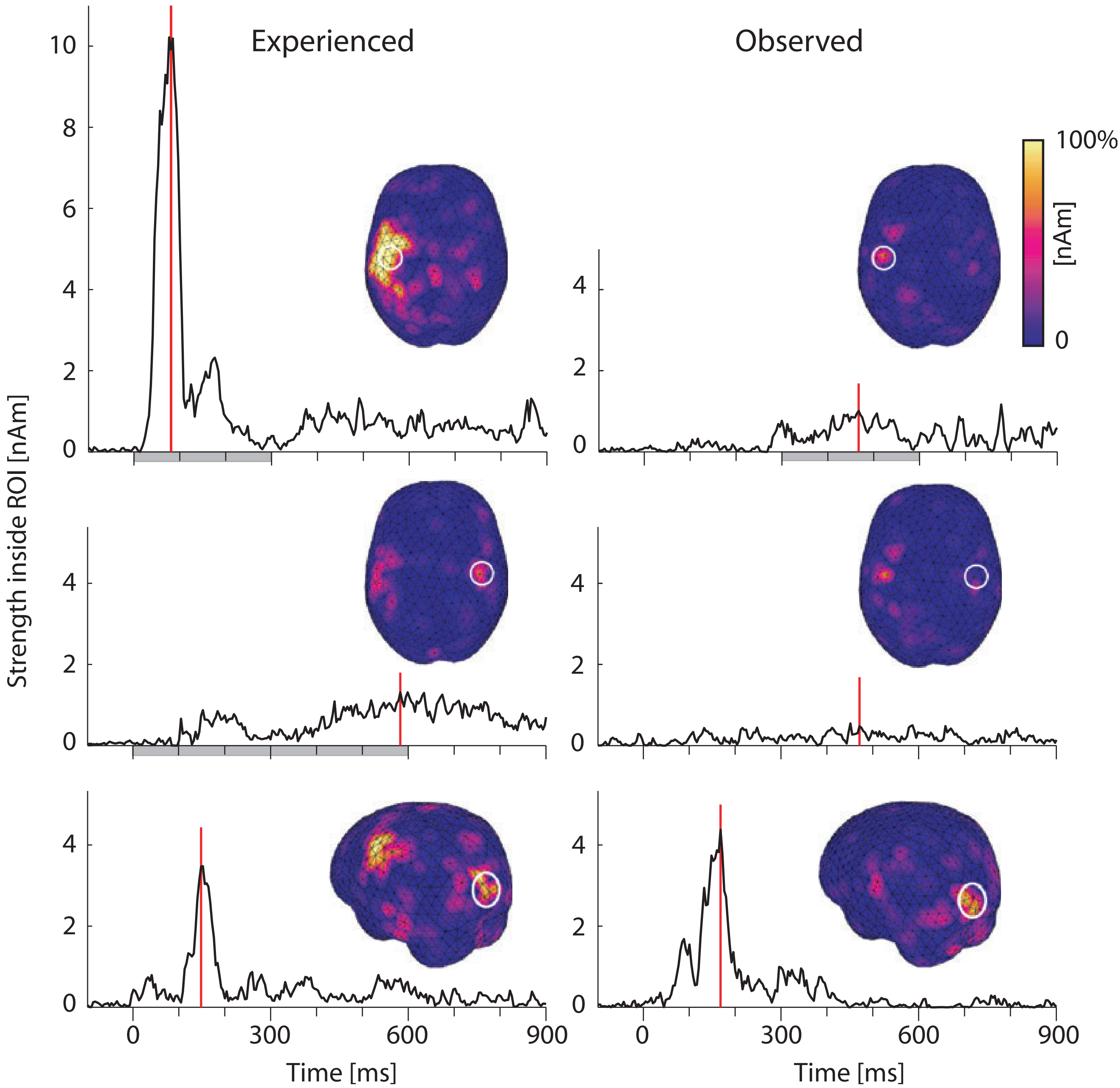

FIG. 3. Grand-averaged source strengths, measured inside three ROIs (white circles on the schematic brains), as a function of time. Minimum current estimates, displayed over the brains, show the mean activity across subjects at times indicated by the red vertical lines. The left panel shows activation in the experienced touch conditions and the right panel in the observed touch conditions. The brain is viewed from the top (anterior direction upwards, two upper rows) and back left (lower row). Gray horizontal bars indicate time windows with statistically significant activation in somatosensory areas. Scale bar represents normalized source strength relative to the peak activity of contralateral SI cortex during EXP condition.

significant (0.07 ± 0.04 nAm, $P = 0.09$ and 0.4 ± 0.2 nAm, $P = 0.07$, respectively), whereas during the 300–600 ms time window, activity significantly exceeded the baseline level (0.3 ± 0.1 nAm, $P < 0.05$). The strength of the activity in OBS_{LH} (300–600 ms) was 7.5% of that in the EXP_{LH} (0–300 ms).

In the EXP condition, the left-hemisphere SI responses were on average 4.1 ± 0.7 nAm in strength (0–300 ms window), which was significantly more than the mean strength in ROI_{MI} (0.7 ± 0.2 nAm, $t = 5.4$, $P < 0.0001$), located anterior, superior and medial to it. This finding supports the assumption that the signals within ROI_{SI} mainly reflected activity in the SI rather than MI cortex.

Discussion

We measured MEG responses from the SI cortices of subjects who first perceived and observed their own hand being touched and then observed the experimenter's hand being touched. In both conditions, the left SI cortex was activated but the activation was ten times stronger to EXP than to OBS. Furthermore, the time patterns of the left SI activation differed, with significant activity occurring during the first 0–300 ms to EXP, and during the 300–600 ms time-window to OBS. In addition, the ipsilateral (right) SI was weakly, but significantly, activated during EXP.

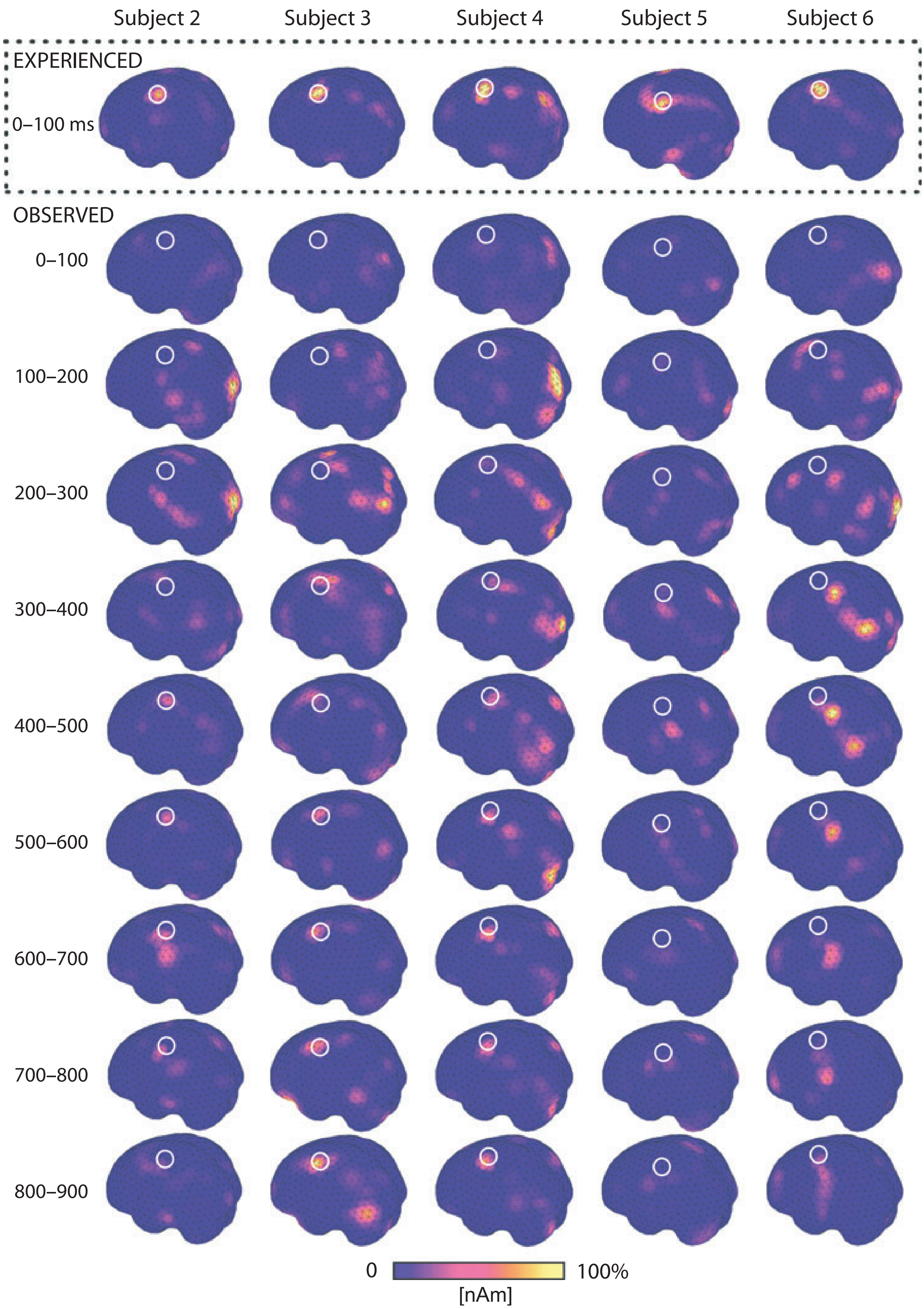

FIG. 4. MCE results of Subjects 2–6 in the experienced (top row) and in the observed touch conditions. Each row shows mean MCE activity in 100-ms windows. The brain is viewed from back left. White circles show the individual ROIs based on activation of the contralateral (left) SI cortex during EXP (upper row). Scale bar represents normalized source strength relative to the peak activity of contralateral SI cortex during EXP conditions.

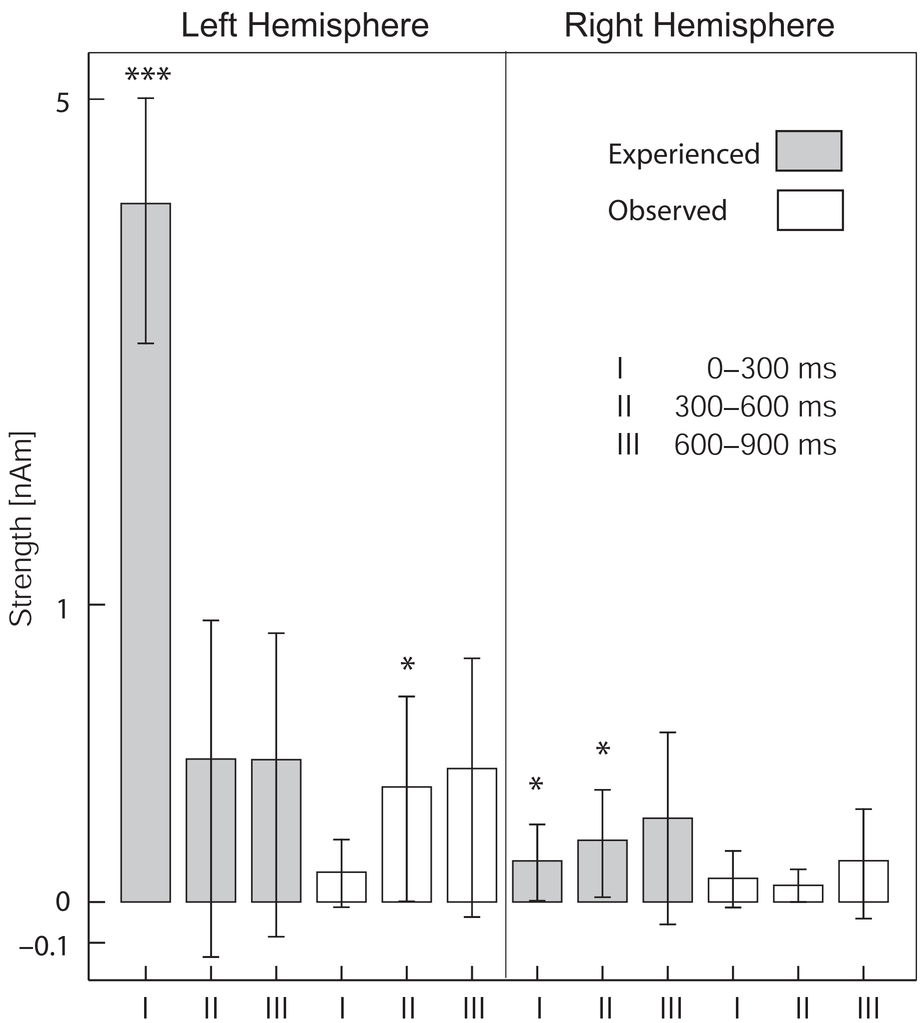

FIG. 5. Mean strengths (with ± 95% confidence intervals) of activation during the 300-ms time windows in the the experienced/EXP and the observed/OBS conditions within the regions of interest in the left and right hemispheres. The baseline activation (from −100 to 0 ms) has been subtracted. ***$P < 0.001$ and *$P < 0.05$ vs. baseline. Note the logarithmic amplitude scale.

In the EXP condition, the well-known strong and early activation of the contralateral SI cortex was caused by direct thalamocortical input as a result of tactile stimulation of the periphery. The strongest response in the contralateral SI cortex peaked on average at 77 ms, but contained another peak, a 'shoulder' at ∼50 ms. The source for this earlier peak was more medial than the later deflection. In many previous SEF studies, tactile stimuli (applied, for example, to finger tips with balloon diaphragms driven by air pulses) elicited the main SI response at ∼50 ms (Mertens & Lütkenhöner, 2000; Simões *et al.*, 2001; Lauronen *et al.*, 2006; Zhu *et al.*, 2007; Pihko *et al.*, 2009). That 50-ms response is most probably generated in area 3b. Similarly, our first deflection at 50 ms appears to be generated around the hand-knob area in 3b. Notably, our stimulation included a clear indentation of the hairy skin, thus stimulating a wider set of mechanoreceptors than a tap to the glabrous skin of a finger tip (Vallbo *et al.*, 1995). Consequently, this kind of stimulus might activate slightly different SI subareas. The source of the 77-ms response could reflect either activation of 3b due to another set of afferents, and/or subsequent activation of more posterior parts of SI (areas 1 and 2) following area 3b activation, or possibly combined activation from different SI sources.

In the OBS condition, cortical information flow starts from occipital visual areas when the subject sees the experimenter's finger move, and it reaches SI later and in a less synchronized volley than during the EXP condition. When subjects of an earlier MEG study observed the experimenter's hand reach a manipulandum, cortical activation progressed from the occipital cortex to the inferior frontal cortex, and later to motor cortices; the whole sequence took ∼400 ms (Nishitani & Hari, 2000). In our OBS condition, the SI activation took place 300–600 ms after occipital activation.

Recent fMRI studies suggest an effect of viewer's perspective on the specific SI subarea activated during observation of another person being touched. For example, when subjects viewed video clips of a hand presented in first-person perspective, the anterior parts of the SI cortex (areas 3a and 3b) were activated, whereas observing the touch from the third-person perspective activated the posterior SI cortex (area 2; Schaefer *et al.*, 2009). Area 2 was also activated when subjects viewed a video of a person whose hand was touched by another person (Ebisch *et al.*, 2008). Because our subjects in the OBS condition viewed the experimenter's and not their own hand being touched, the main activation might well have occurred in area 2, although the low signal-to-noise ratio in most of the subjects did not allow the exact source location to be determined.

EXP also activated the ipsilateral SI cortex during the first 600 ms, although very weakly compared with the contralateral SI cortex. Ipsilateral SI activation by unilateral hand stimuli is still much debated.

In a minority of subjects, MEG responses have been observed in the ipsilateral SI cortex, with latencies varying between 50 and 100 ms after unilateral electrical stimulation of the median nerve (Korvenoja *et al.*, 1995; Kanno *et al.*, 2003), or at 60 ms after tactile stimulation of the index finger (Zhu *et al.*, 2007). However, some of these ipsilateral MEG responses may have been contaminated by slight movements of the table or chair used by the subject (Hari & Imada, 1999). Unlike the contralateral SEFs, known to arise predominantly from area 3b, the origin of the ipsilateral SI activation is unknown. Intracranial recordings of ipsilateral responses to median nerve stimulation in humans (Allison *et al.*, 1989; Noachtar *et al.*, 1997) and to tactile finger stimulation in monkeys (Iwamura *et al.*, 2002) suggest origin in ipsilateral SI subregions posterior to area 3b. Functional MRI combined with current-source density analysis in monkeys revealed inhibition of the ipsilateral area 3b after tactile and electric stimulation of the hand (Lipton *et al.*, 2006). In humans, as well, fMRI recordings indicate inhibition of the ipsilateral area 3b after tactile hand stimulation, whereas the ipsilateral area 2 is activated, especially in the right hemisphere (Hlushchuk & Hari, 2006; Eickhoff *et al.*, 2008). In MEG recordings, similar effects have not been convincingly demonstrated.

In conclusion, we have shown that when subjects observe someone else being touched, their own SI cortex is activated within 300–600 ms following the visual activation, i.e. considerably later than when the subject herself is touched. Analogous to ideas about mental simulation of motor acts based on the human mirror-neuron system (Rizzolatti & Craighero, 2004), we assume that people can comprehend another person's tactile experience because a part of their own touch-processing system, including the primary somatosensory cortex, is activated when they see another person being touched.

Acknowledgements

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Abbreviations

ECD, equivalent current dipole; EXP, Experienced touch; fMRI, functional magnetic resonance imaging; GLM, general linear model; LH, left hemisphere; MCE, minimum current estimate; MEG, magnetoencephalography; MI, primary motor; nAm, nA × m; OBS, Observed touch; RH, Right hemisphere; ROI, Region of interest; SEF, somatosensory evoked field; SI, primary somatosensory; SII, secondary somatosensory.

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