The *Sense* of Touch: Embodied Simulation in a Visuotactile Mirroring Mechanism for Observed Animate or Inanimate Touch

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Abstract

■ Previous studies have shown a shared neural circuitry in the somatosensory cortices for the experience of one's own body being touched and the sight of intentional touch. Using functional magnetic resonance imaging (fMRI), the present study aimed to elucidate whether the activation of a visuotactile mirroring mechanism during touch observation applies to the sight of *any* touch, that is, whether it is independent of the intentionality of observed touching agent. During fMRI scanning, healthy participants viewed video clips depicting a touch that was intentional or accidental, and occurring between animate or inanimate objects. Analyses showed equal overlapping activation for all the touch observation conditions and the experience of one's own body being touched in the bilateral secondary somatosensory cortex (SII), left inferior parietal lobule (IPL)/supramarginal gyrus, bilateral temporal–occipital junction, and left precentral gyrus. A significant difference between the sight of an intentional touch, compared to an accidental touch, was found in the left primary somatosensory cortex (SI/ Brodmann's area [BA] 2). Interestingly, activation in SI/BA 2 significantly correlated with the degree of intentionality of the observed touch stimuli as rated by participants. Our findings show that activation of a visuotactile mirroring mechanism for touch observation might underpin an abstract notion of touch, whereas activation in SI might reflect a human tendency to "resonate" more with a present or assumed intentional touching agent. ■

INTRODUCTION

The observation of touch is an ordinary and relevant occurrence in a variety of everyday situations, ranging from social interactions to natural events. For instance, we witness a person touching the hand of another person, or a tree branch moved by the wind touching a window. However, although an observed touch often has a meaningful content, the neural mechanism underlying the activation of the *meaning of touch* is poorly understood. The present study aims to elucidate how the human brain maps the occurrence of an observed touch, and more specifically, to which degree the observation of touch can be grounded in the activation of the brain areas underpinning our own tactile experiences.

Current neuroscientific models of embodied simulation propose that the same neural structures involved in our own body-related experiences also contribute to the conceptualization of what we observe in the world around us (Gallese, 2005, 2006; Gallese & Lakoff, 2005). Extensive empirical evidence for a shared neural circuitry in the sensory–motor system for first- and third-person experiences in humans and primates in the domains of actions (e.g., Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Ferrari, Rozzi, & Fogassi, 2005; Fogassi et al., 2005; Buccino et al., 2001, 2004; Kohler et al., 2002; Umilta et al., 2001; Iacoboni et al., 1999; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), emotion (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Wicker et al., 2003), and pain (Saarela et al., 2007; Avenanti, Paluello, Bufalari, & Aglioti, 2006; Avenanti, Bueti, Galati, & Aglioti, 2005; Botvinick et al., 2005; Jackson, Meltzoff, & Decety, 2005; Singer & Frith, 2005; Morrison, Lloyd, di Pellegrino, & Roberts, 2004; Singer et al., 2004) supports this idea of understanding in terms of the way we function with our bodies in the world (for recent reviews, see Iacoboni & Dapretto, 2006; Gallese, 2005; Gallese, Keysers, & Rizzolatti, 2004; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001; Rizzolatti & Luppino, 2001).

The tactile dimension (i.e., touch) plays a peculiar role in our interaction with the external world. As the German philosopher Edmund Husserl wrote, everything we see, we simultaneously also see it as a tactile object, as something which is directly related to the alive body (Husserl, 1989). Also, linguistic expressions, like "let's

keep in touch,'' figuratively expressing the wish of being related or in contact with someone, indicate a fundamental role of the tactile dimension for social cognition (Gallese, 2005, 2006). Interestingly, the same notion of touch is normally employed when we use language to describe contact between inanimate objects.

Recently, functional neuroimaging studies reported automatic activation of a shared neural circuitry in the somatosensory cortices, which is normally involved in our experience of touch, during the observation of another person being touched (Blakemore, Bristow, Bird, Frith, & Ward, 2005; Keysers et al., 2004). Moreover, Keysers et al. (2004) demonstrated that activation of this shared mechanism for touch also occurred for the sight of an object being touched. Thus, in order to activate a shared neural circuitry for touch by vision, it does not matter what is being touched (animate or inanimate) as long as touch occurs. Furthermore, such activation is independent of whether the touch is seen from a first-person or third-person perspective, that is, how easily it can be integrated in one's own body scheme. In addition to the domains of action, emotion, and pain, these findings suggest the existence of a visuotactile mirroring mechanism, and that the understanding of an observed touch, even of an object known to be devoid of any inner life, could be mediated by embodied simulation (Gallese, 2005, 2006).

However, the touch stimuli presented by Blakemore et al. (2005) and Keysers et al. (2004) were always intentional because, in both studies, participants saw human body parts or inanimate objects being touched either by a human hand or by an object intentionally moved by a human agent. Therefore, it is still an open issue whether activation of a mirroring mechanism for touch applies to the sight of *any* touch, or whether it is restricted to the domain of intentional touch. In contrast to actions and emotions, touch is not restricted to the social domain and to motor behavior. As already mentioned, we can also witness touch in nature—for instance, when two tree branches touch each other. What neural mechanism brings about the understanding in terms of ''touch'' of such an event without any human involvement? It might be that in similar events an abstract notion of touch is processed by the brain in a way fundamentally different from when processing a touch intended by another human being. For example, according to an abstract cognitive account, visual processing of a stimulus is followed by an amodal cognitive evaluation of what this stimulus means.

Alternatively, models of embodied simulation suggest that activation of a visuotactile mirroring mechanism could ground the perception of touch, including the perception of nonintentional contact, where the touching agent is accidentally moved by an external nonbiological force. In that case, the same mirroring/simulation principles would apply to the sight of any touch. Embodied simulation processes in a visuotactile mirroring mechanism could therefore support the activation of an ''abstract'' notion of touch, building on the neural mechanisms for interpreting actual touch even for inanimate contact, where abstraction is the prelinguistic outcome of a polymodal integration mechanism.

To address this question, the present functional magnetic resonance imaging (fMRI) study investigated whether the activation of a visuotactile mirroring mechanism during touch observation applies to the sight of any touch, that is, whether it is independent of the intentionality of the observed *touching* stimulus. During fMRI scanning, healthy participants viewed video clips depicting a touch that was intentional or accidental, and occurring between animate or inanimate objects. Additionally, the brain areas involved in one's own experience of touch were localized by means of tactile stimulation of the participants' hands. Our findings show that activation of a visuotactile mirroring mechanism in the secondary somatosensory cortex (SII) during touch observation applies to the sight of *any* touch, thus likely contributing to our capacity of entertaining an abstract notion of touch (Gallese, 2005; Gallese et al., 2005).

METHODS

Participants

Fifteen young adult participants were included in the present study, out of which eight were men and seven were women (range = 19–27 years of age). All participants were healthy, right-handed (Edinburgh Handedness Inventory score > 0.85) university students with normal vision capabilities (correction < 0.75). Written informed consent was obtained from all participants after full explanation of the procedure of the study, in line with the Declaration of Helsinki. The experimental protocol was approved by the local institutional ethics committee. The participants were given a recompense for participating in the fMRI experiment.

fMRI Data Acquisition

For each subject, blood oxygenation level-dependent (BOLD) contrast functional imaging was performed with a Siemens Magnetom Vision scanner at the Institute of Advanced Biomedical Technologies (Chieti) at 1.5 T by T2*-weighted echo-planar imaging (EPI) free induction decay (FID) sequences with the following parameters: TR = 2700 msec, TE = 60 msec, matrix size 64 × 64, FOV = 256 mm, in-plane voxel size = 4 × 4 mm, flip angle = 90°, slice thickness = 4 mm, and no gap. A standard head coil was used and the subject's head was fixed with foam pads to reduce involuntary movement. Functional volumes consisted of 23 transaxial slices. For each run, a mean number of 111 volumes was acquired.

A high-resolution structural volume was acquired at the end of the session via a 3-D MP-RAGE sequence with

the following features: sagittal, matrix 256 × 256, FoV 256 mm, slice thickness 1 mm, no gap, in-plane voxel size 1 × 1 mm, flip angle 12°, TR = 9.7 msec, TE = 4 msec.

Stimuli and Conditions

Twelve visual runs and one tactile run were acquired for each subject. Stimuli in the visual runs were 384 randomized video clips of 2700 msec each, representing a touch event according to one of four experimental conditions. In the intentional-animate (INT-ANI) condition, either a male hand touched the back of a female hand or a female hand touched the back of a male hand. In the intentional-inanimate (INT-INA) condition, either a male or a female hand touched the arm of a wooden garden chair. In the accidental-animate (ACC-ANI) condition, the back of either a male or female hand was touched by one of two different wind-moved palm tree branches. In the accidental-inanimate (ACC-INA) condition, the arm of a wooden garden chair was touched by one of two different wind-moved palm tree branches. The person and the chair were touched on their right side in half of the video clips and on their left side in the other half. The chair and the actors in the video clips were seen from a frontal point of view. To exclude effects of the perception of a face and facial expressions, the actors being touched in the video clips were visible only from the knees to the chest. The male and female actors wore a white T-shirt and beige trousers or skirt, respectively. Of the touching actor, only an uncovered arm and the hand were visible. In addition to the touch video clips, 48 nontouch video clips were randomly inserted in the visual runs, showing either a hand or palm tree branch moving near the other person or chair, but without touching them. The video clips were separated by a fixation cross at the center of the screen. The video clips were presented on a screen behind the scanner with a beamer. Participants could see the screen clearly through a mirror placed above their eyes. Examples of the visual stimuli are shown in Figure 1.

A tactile run was added to the experiment in order to determine overlap of neural activation between the sight and experience of touch. During the tactile run, the experimenter entered the scanning room and stimulated the back of either the right or the left hand by means of brushing with a soft brush. Brushing frequency was approximately 1 Hz.

Experimental Procedure

Prior to scanning, it was explained to the participants that they were randomly shown short video clips with a different content in 12 separated runs of approximately 5 min each. They were told that in the video clips they would see a hand touching another hand, a hand touching a chair, a wind-moved palm tree branch touching a hand, or a wind-moved palm tree branch touching a chair, and that in a few video clips with similar movements the touch would be absent. Participants were instructed to watch these video clips attentively, and to count the number of nontouch video clips in every run. They had to report the counted number verbally to the experimenter during the break between two runs (mean = 4/run). The nontouch trials were not included in the statistical analyses, but this task was added to direct the participants' attention implicitly to the touch during the experiment. In a recent study, Keysers et al. (2004) demonstrated thoroughly that SII activation is specific for the observation of touch stimuli and does not occur for visual stimuli with similar content and movements not leading to touch.

The experimental design of the visual runs was a rapid event-related fMRI design alternating a state of stimulation (video clips) of 2700 msec (one TR) with a baseline state (fixation cross) of 2700, 5400, or 8100 msec (corresponding to one to three TRs) (see Figure 1; Ollinger, Corbetta, & Shulman, 2001; Ollinger, Shulman, & Corbetta, 2001). The three baseline durations were presented randomly with a linear distribution (i.e., to each duration was assigned the same probability). All 12 visual runs consisted of 36 video clips and a mean intertrial interval of 5400 msec.

During the tactile run, participants were instructed to close their eyes and concentrate on the stimulation of their hands. The tactile run was a blocked-design fMRI study alternating a state of stimulation (brushing of the hands) of 15 sec with a baseline state (rest) of the same duration. In total, there were 20 randomized stimulation blocks: 10 blocks for the right hand and 10 blocks for the left hand.

During debriefing, participants were asked to rate the degree of intentionality, judging the degree to which the tactile stimulus was caused by a human agent depicted by the video clips. The ratings were made on a 0 to 10 scale where 0 referred to completely accidental, and 10 to completely intentional.

Data Analyses

Raw data were analyzed with the Brain Voyager QX 1.7 software (Brain Innovation, Maastricht, The Netherlands). Due to T1 saturation effects, the first three scans of each run were discarded from the analysis. Preprocessing of functional data included slice scan time correction, motion correction, and removal of linear trends from voxel time series. No temporal smoothing was used in the current analyses. A three-dimensional motion correction was performed with a rigid-body transformation to match each functional volume to the reference volume (the fourth volume) estimating three translation and three rotation parameters. Preprocessed functional volumes of a participant were coregistered with the corresponding structural dataset. As the 2-D

Figure 1. Temporal course during the visual runs with examples of the video clips depicting touch (INT-ANI = intentional-animate; INT-INA = intentional-inanimate; ACC-ANI = accidental-animate; ACC-INA = accidental-inanimate), alternated by a resting state.

functional and 3-D structural measurements were acquired in the same session, the coregistration transformation was determined using the Siemens slice position parameters of the functional images and the position parameters of the structural volume.

Structural and functional volumes were transformed into the Talairach and Tournoux (1988) space using a piecewise affine and continuous transformation. Functional volumes were resampled at a voxel size of $3 \times 3 \times 3$ mm. In the single-subject analyses, no spatial smoothing was applied.

Because in a rapid event-related fMRI paradigm the hemodynamic responses to the closely spaced events will partially overlap, the visual runs were modeled by means of the deconvolution approach (e.g., Hinrichs et al., 2000). This approach is characterized by estimating the actual BOLD response to each condition without relying on the convolution of a canonical response function with a boxcar model of the stimulus presentation sequence.

For the block design tactile condition, a boxcar waveform representing the rest and task conditions was convolved with an empirically based hemodynamic response function to account for the hemodynamic delay (Boynton, Engel, Glover, & Heeger, 1996).

Prior to statistical analysis calculation, a percent signal change normalization of the time series from the different runs was performed.

Statistical maps were thresholded at $p < .001$ at the voxel level, and a cluster size of at least five voxels was required. This p value and an estimate of the spatial correlation of voxels were used as input in a Monte Carlo simulation to access the overall significance level (Cox, 1996; Forman et al., 1995). In this way, a significance level of $p < .05$ corrected for multiple comparisons was obtained.

Figure 2. Group statistical maps showing overlapping activation ($p < .001$, corrected) for the observation of touch conditions and the tactile condition.
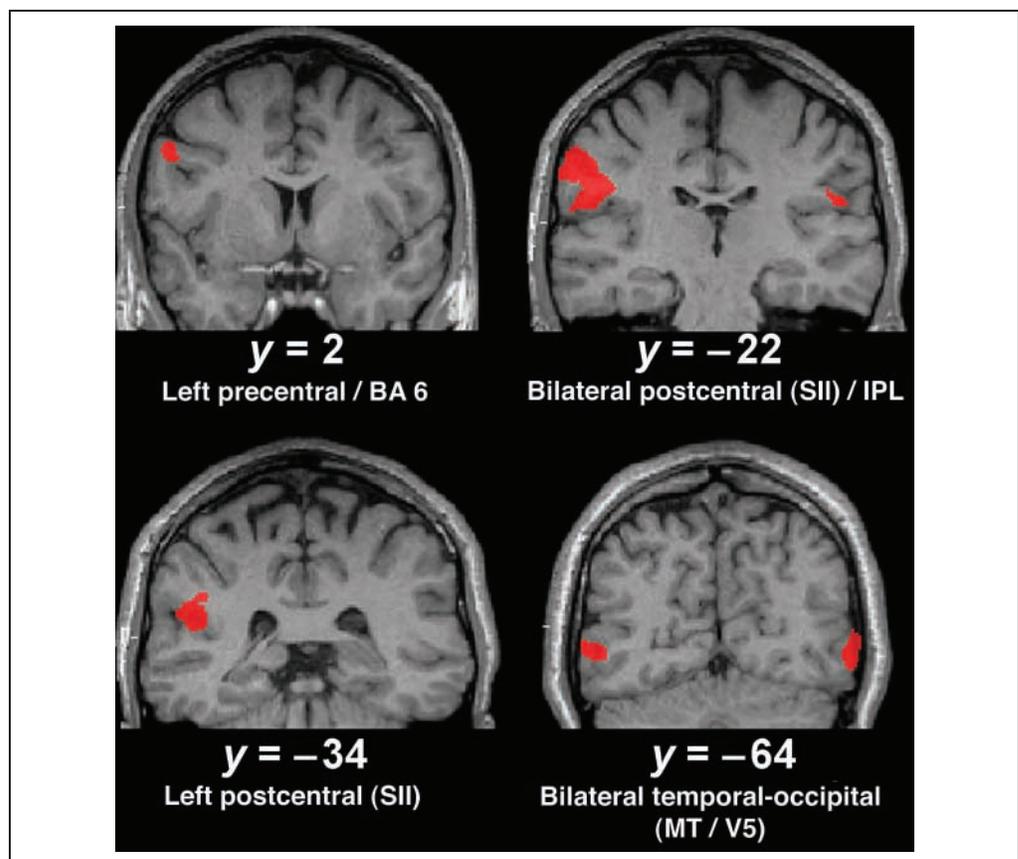
In order to determine overlap of activation between observation of touch conditions and the tactile stimulation condition, conjunction analysis was used, based on the minimum statistic compared to the conjunction null (Nichols, Brett, Andersson, Wager, & Poline, 2005). This method controls the false-positive error for conjunction inference and tests for common activations by creating the intersection of statistical maps thresholded at a specific alpha rate.

The parameters (beta values) estimated in individual subject analysis were entered in a second-level voxelwise random effect group analysis in order to search for activated areas that were consistent for the whole group of participants. Statistical significance was assessed by means of paired t tests. In this group analysis, a spatial smoothing with a Gaussian kernel of 6 mm full-width half-maximum was applied to functional images to account for intersubject variability.

RESULTS

Participants' intentionality ratings showed a significant difference ($F = 40.657, p < .001$) between the ratings for the video clips in the intentional condition (mean = 9.06, $SD = 1.12$) and the video clips in the accidental conditions (mean = 5.35, $SD = 1.88$).

Brain areas activated by the vision of touch conditions (vision of touch vs. baseline) comprise the bilateral superior parietal cortex/intraparietal sulcus, the precentral gyrus (Brodmann's area [BA] 6), extrastriate cortices, the medial and lateral occipital lobe, the posterior fusiform, the lateral temporal–occipital cortex (including MT/V5 [Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005; Orban et al., 1995] and extrastriate body area [Urgesi, Candidi, Ionta, & Aglioti, 2007; Downing, Jiang, Shuman, & Kanwisher, 2001]), the postcentral gyrus/SII, and the left hemisphere (LH) postcentral sulcus/inferior parietal lobule (IPL) and thalamus.

Stimulation of the participants' hands (tactile stimulation right hand vs. baseline, and left hand vs. baseline) activated the bilateral postcentral gyrus, including the primary somatosensory cortex (SI) and SII, the postcentral sulcus/IPL, the lateral precentral gyrus (BA 6), the posterior insula, the lateral temporal–occipital cortex (including MT/V5), the superior parietal/intraparietal cortex, and the left hemisphere thalamus. Activation was found for contralateral tactile stimulation, except in the temporal–occipital region, which responded mainly to ipsilateral stimulation.

Significant overlap for tactile stimulation and the vision of touch (conjunction between observation of touch vs. baseline, and tactile stimulation right/left hand vs. baseline) was found in the bilateral postcentral gyrus, including SII, the bilateral temporal–occipital junction, and the left hemisphere precentral gyrus (dorsal part of the left ventral premotor cortex; PMv/BA 6). The latter

was found only when all the different touch observation conditions were pooled together. Left hemisphere SII activation extended from $y = -18$ to $y = -40$, and dorsally onto the IPL/supramarginal gyrus. A relatively smaller cluster of overlapping activation was found in the right postcentral gyrus, corresponding to SII. Figure 2 shows group statistical maps of overlapping activation. Figure 3 shows the mean BOLD responses in the left SII cluster. Results were similar for the other hemisphere. Significant overlapping activation in the bilateral postcentral gyrus/SII was also found in most single subjects.

The reported overlapping activation was also found for all the touch observation conditions separated (INT-ANI, INT-INA, ACC-ANI, ACC-INA), except for the left precentral gyrus (see Table 1, Figure 4). No differences, or trends toward differences, were found in overlapping visuotactile areas for the contrasts between the sight of an animate and an inanimate touch [(INT-ANI vs. INT-INA) and (ACC-ANI vs. ACC-INA)], between the sight of an intentional touch to a human and the other conditions [(INT-ANI vs. INT-INA) > (ACC-ANI vs. ACC-INA)], or between the sight of a person's hand (animate) or object (chair; inanimate) being touched on the right or left side (see Table 1, Figure 3).

However, significantly increased activation for the observation of an intentional touch, compared to an accidental touch [conjunction between the observation of an intentional (INT) vs. accidental touch (ACC), and tactile stimulation right + left hand vs. baseline], was found in the left lateral posterior primary somatosensory cortex (SI), corresponding to BA 2 ($x = -58, y = -22, z = 43$; see Figure 5 and Table 2). Conjunction analysis confirmed that this region was also significantly activated for tactile stimulation of the participants' hands. Conjunction analyses with the
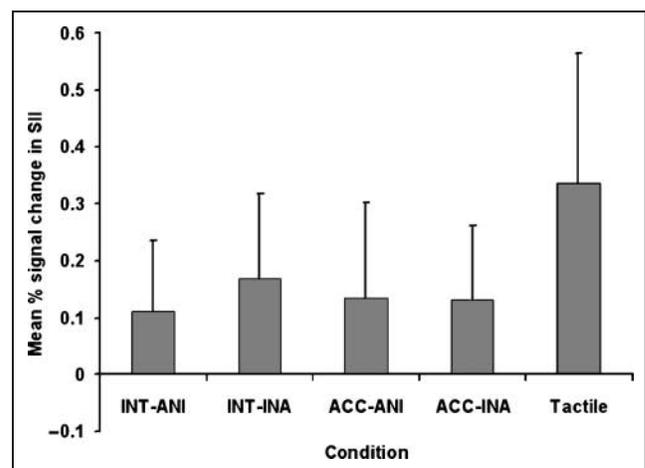
Figure 3. Mean % signal change (beta values) and SD in the left postcentral gyrus/SII (corresponding to Figure 2) for the intentional-animate (INT-ANI), intentional-inanimate (INT-INA), accidental-animate (ACC-ANI), accidental-inanimate (ACC-INA), and tactile condition, versus baseline. Results were similar for the other hemisphere.

Table 1. Overlapping Activation for the Different Sight of Touch Conditions and Tactile Stimulation (Corresponding to Figure 4)

	Left/Right	Coordinates of Max. t Value Conjunction Analysis[a]	Max. t Value Conjunction Analysis	Size Cluster Overlap
Overlap INT-ANI and Tactile				
Postcentral gyrus/IPL (incl. SII)	L	−54 −22 34	5.49	1269
Temporal–occipital	R	48 −73 −2	7.216	3254
Postcentral gyrus/SII[d]	R	51 −31 25	4.63	82
Temporal–occipital	L	−51 −61 1	6.393	416
Overlap INT-INA and Tactile				
Postcentral gyrus/IPL (incl. SII)	L	−51 −28 34	6.044	4076
Temporal–occipital	R	48 −73 −2	8.191	4468
Postcentral gyrus/SII	R	48 −28 22	4.88	416
Postcentral gyrus/IPL	R	51 −22 31	5.71	267
Temporal–occipital	L	−51 −61 1	6.315	166
Overlap ACC-ANI and Tactile				
Postcentral gyrus/IPL (incl. SII)	L	−54 −19 28	5.73	1732
Temporal–occipital	R	45 −76 1	7.373	3247
Postcentral gyrus/SII	R	48 −28 25	4.998	143
Temporal–occipital	L	−51 −64 1	5.581	467
Overlap ACC-INA and Tactile				
Postcentral gyrus/IPL (incl. SII)	L	−51 −28 34	6.044	1477
Parietal/IPS	L	−36 −40 46	5.009	518
Temporal–occipital	R	48 −73 −2	5.702	1165
Postcentral gyrus/SII	R	51 −28 25	4.767	148
Temporal–occipital	L	−48 −64 1	5.016	224

[a]Talairach coordinates.

[b]Mean (±standard deviation).

[c]p Value from random effect analysis.

[d]Without cluster threshold correction for multiple comparisons.

*$p < .05$.

**$p < .001$.

***$p < .0001$.

****$p < .00001$.

touch observation conditions separated or pooled together did not show overlapping activation in this region between the experience and sight of touch. However, conjunction analysis between the observation of an intentional touch (INT-ANI + INT-INA) and tactile stimulation demonstrated overlapping activation in this region.

Activation in the left SI, but not in the other areas, correlated significantly with the degree of intentionality of the different video clips as rated by the participants ($r = .28$, $p < .004$). This correlation was also present within the accidental conditions ($r = .35$, $p < .011$; see Figure 5).

DISCUSSION

A Shared Neural Circuitry for Touch in SII

Using fMRI, the present study aimed at elucidating whether the activation of a visuotactile mirroring mechanism

Table 1. *(continued)*

Mean % Signal Change in Cluster (Contrast: <u>Touch Observation</u> vs. Baseline)[b,c]	Mean % Signal Change in Cluster (Contrast: <u>Tactile</u> vs. Baseline)[c]	Max. t Value in Cluster (Contrast: <u>Touch Observation</u> vs. Baseline)	Max. t Value in Cluster (Contrast: <u>Tactile</u> vs. Baseline)
0.15 (±0.11)**	0.41 (±0.21)****	5.259**	10.002****
0.67 (±0.27)****	0.57 (±0.26)***	10.479****	8.046****
0.16 (±0.11)**	0.38 (±0.34)**	4.721**	5.096**
0.71 (±0.49)***	0.40 (±0.31)**	7.037****	5.475***
0.13 (±0.09)**	0.38 (±0.18)****	5.532**	10.893****
0.61 (±0.27)****	0.55 (±0.28)****	9.795****	8.046****
0.14 (±0.15)**	0.44 (±0.21)****	5.313**	8.975****
0.08 (±0.09)***	0.31 (±0.31)*	6.233***	4.792**
0.64 (±0.47)**	0.33 (±0.26)**	6.121***	5.124**
0.12 (±0.13)**	0.41 (±0.20)***	5.034**	10.167****
0.68 (±0.26)****	0.55 (±0.28)****	10.631****	8.046****
0.14 (±0.11)**	0.42 (±0.28)***	4.419**	8.445****
0.59 (±0.39)***	0.41 (±0.30)**	7.317****	5.748***
0.14 (±0.12)**	0.37 (±0.21)***	6.589***	10.893****
0.12 (±0.11)***	0.34 (±0.20)***	6.338***	7.847****
0.65 (±0.34)****	0.57 (±0.29)****	8.165****	8.046****
0.10 (±0.12)*	0.43 (±0.26)***	4.741**	8.588****
0.54 (±0.42)**	0.39 (±0.30)**	6.487***	4.748**

applies to the sight of *any* touch, that is, whether activation in the somatosensory cortices is independent of the intentionality of observed touch stimuli. Results showed equal overlapping activation for touch experience and the different touch observation conditions in the bilateral postcentral gyrus (including SII and extending to the left IPL). This overlapping activation was independent of the intentionality of the observed touch stimuli, whether the touch was animate or inanimate, and whether an observed person or object was touched on the right or left side.

The overlapping activation in the bilateral postcentral gyrus for tactile hand stimulation and observation of a human hand/arm of a chair being touched corresponds well to the location of SII (e.g., Polonara, Fabri, Manzoni, & Salvolini, 1999; Burton, Videen, & Raichle, 1993; Penfield & Rasmussen, 1950; Woolsey, 1943, 1944), and matches the approximate location of the hand region of

Figure 4. Group statistical maps showing overlapping activation ($p < .001$, corrected) for the different touch observation conditions (INT-ANI = intentional-animate; INT-INA = intentional-inanimate; ACC-ANI = accidental-animate; ACC-INA = accidental-inanimate) and the tactile condition.
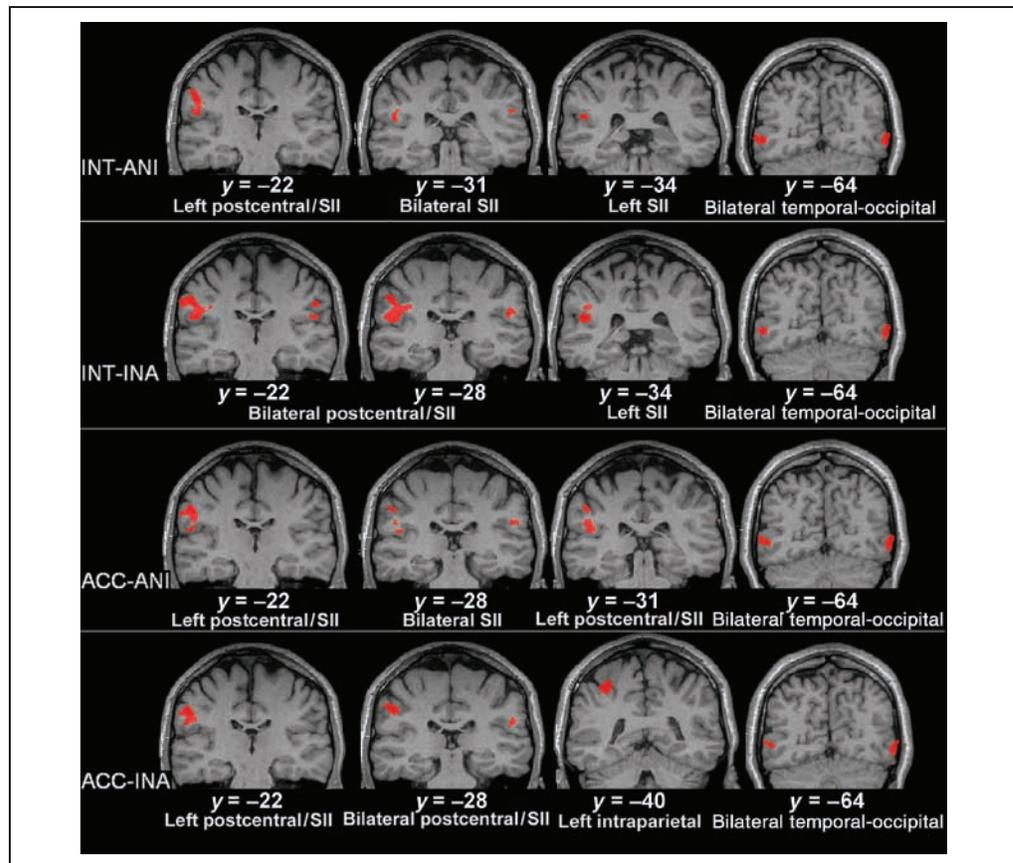
Figure 5. Group statistical map showing increased activation ($p < .001$, corrected) in SI/BA 2 for the intentional touch observation conditions (INT-ANI + INT-INA), compared to the accidental touch observation conditions (ACC-ANI + ACC-INA).
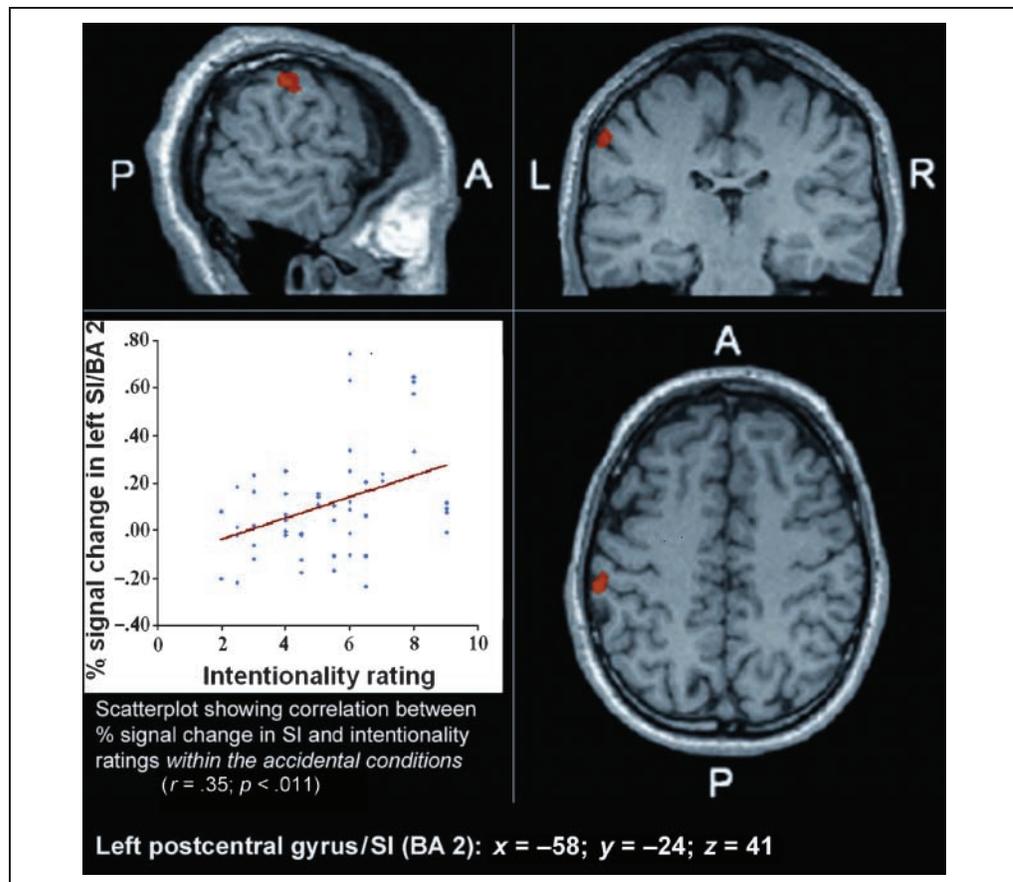
Table 2. Activation in Intentionality Specific Cluster in the Left Postcentral Gyrus/SI, and Related Statistical Values

Condition	Mean % Signal Change (Beta)[a]	Max. t Value
INT-ANI	0.17 (±0.07)	5.005
INT-INA	0.25 (±0.13)	4.261
ACC-ANI	0.14 (±0.14)	3.140
ACC-INA	0.10 (±0.10)	4.514
Tactile	0.47 (±0.15)	7.456

[a]Mean ± standard deviation.

SII (e.g., Ferretti et al., 2003; Ruben et al., 2001; Del Gratta et al., 2000; Disbrow, Roberts, & Krubitzer, 2000).

The function of SII is associated with higher order somatosensory functions (Servos, Lederman, Wilson, & Gati, 2001; Caselli, 1993; Garcha & Ettlinger, 1980). Subsequent studies suggested that SII is also involved in the polymodal integration of somatosensory information with associated information from the other senses (Avikainen, Forss, & Hari, 2002; Bremmer et al., 2001; Carlsson, Petrovic, Skare, Petersson, & Ingvar, 2000).

Finally, recent functional neuroimaging studies demonstrated activation of a region of SII when participants observed another person or an object being touched, as well as when they were touched themselves (Blakemore et al., 2005; Keysers et al., 2004). This overlapping activation was specific for the observation of touch, and was not found for the sight of similar stimuli with movements not leading to touch (Keysers et al., 2004). The current results are in line with these findings by showing overlapping activation in SII for tactile experiences and the sight of touch, and with the study of Keysers et al. (2004) by showing similar activation of a mirroring mechanism for touch during the sight of an animate and inanimate touch. With respect to the location of overlap, this is largely in agreement with the overlapping activation found by previous studies. The novelty of the present results consists in the demonstration that the activation of a visuotactile mirroring mechanism is independent of the intentionality of the observed touch, and thus, applies to the sight of *any* touch.

Let us now examine the differences with these previous studies. First, whereas group analyses here showed overlapping activation in bilateral SII, Keysers et al. (2004) found, by means of group analyses, overlapping activation for tactile stimulation of the legs, and observation of legs and objects being touched only in the left SII. Single-subject analyses showed overlapping activation in the right SII in half of the subjects.

Second, Blakemore et al. (2005) found overlapping activation for tactile stimulation of the face and the sight of a face being touched (compared to a touch of the neck) in the right SI, and activation in the right SII and SI during the observation of the touch of a human, compared to the observation of an object being touched. In the current study, a trend was observed for overlapping

activation in left SI/BA 2; significant overlapping activation in SI, though, was only found when the *intentional* touch observation conditions, animate and inanimate, were pooled together. Accordingly, the observed touch in the study of Blakemore et al. was always intentional. With respect to the increased activation in SI for an animate touch (the face) in their study, Blakemore et al. proposed that the presence of a human face in their videos might have evoked stronger somatosensory activation than the sight of other body parts, like the neck (Blakemore et al., 2005), or legs (Keysers et al., 2004). A similar explanation might apply to the observed touched hands of the present study. Furthermore, the use of the contrast between a face and a neck being touched might have excluded an effect in SII, but not in SI, given that SI contains a clearer somatotopic differentiation than SII (e.g., Ruben et al., 2001). Hence, although the current results suggest that intentionality is the key determinant for activating SI, it might be that SI activation during the sight of an intentional touch can be modulated by multiple factors. Future research should investigate possible modulating factors such as body part sensitivity, social relevance, and the somatotopic organization in SI.

Third, whereas in the study of Keysers et al. (2004) participants passively watched touch stimuli, and in the study of Blakemore et al. (2005) they rated the intensity of the observed touch, in the present study participants were instructed to count the nontouch stimuli. Therefore, their attention was directed specifically, but implicitly, to the touch. However, it is unlikely that SII would be selectively activated by a task/attentional effect for two reasons. The activation of a shared neural circuitry in the somatosensory cortices in the current study is consistent with the results of previous studies (Blakemore et al., 2005; Keysers et al., 2004), and the task to count the nontouch trials would suggest that the nontouch trials were the relevant stimuli for the participants.

One might argue that, given the event-related design, and the visual similarities between the stimuli from the different conditions, the current activation in SII during the observation of an inanimate touch might be driven by a carryover effect from the observation of an animate touch seen at some other point in the run. However, this is unlikely, because, in a previous article (Keysers et al., 2004), participants watched legs and objects touched by an object (a rod) in separate blocks. Nevertheless, both touch observation conditions were effective in activating SII, despite the use of a block design. One may still argue that the SII activation in Keysers et al. (2004) could be due to the anthropomorphizing of an intentionally moved object because the inanimate touch in that study was carried out by an object that was clearly moved by an intentional agent. Indeed, this alternative interpretation motivated the present experiment. The results, however, fail to support this hypothesis.

Overlapping activation in SII during the sight of two objects touching each other might reflect a multisensory,

spatio-temporal representation of contact, rather than touch. However, this interpretation seems implausible, given that this very same area is essentially involved in somatosensory perception. Moreover, the participants were not able to see their hand being contacted in the tactile run, excluding the possibility that overlapping activation in this area merely reflects visual processing. Therefore, overlapping activation occurring within a tactile area is likely to correspond to a representation beyond a visual mapping of contact. Rather, the results suggest the activation of a somatosensory representation very similar to that of our own body being touched, even when the contact is accidental and inanimate.

Finally, it could be argued that activation in SII during the observation of touch may reflect an effect of volitional mental imagery. However, the participants were not explicitly instructed to imagine the impact of the observed touch, neither on the observed person or object nor on their own body. Indeed, none of the participants declared at debriefing to have explicitly imagined the observed touch, and the high significance of SII activation in a random effect analysis suggests that the activation was systematic enough over the sample to exclude a possible effect of occasional voluntary mental imagery.

For these reasons, in line with previous studies (Blakemore et al., 2005; Keysers et al., 2004), it seems plausible that the activation in SII during the sight of any touch reported here reflects an automatic tendency to activate brain areas involved in the processing of our own experience of touch. This automatic activation is similar to the activation of the Mirror Neuron System (MNS) during the observation of actions and emotions, and might indicate involvement of implicit embodied simulation processes (e.g., Iacoboni & Dapretto, 2006; Gallese, 2005; Rizzolatti & Craighero, 2004; Gallese et al., 1996; Rizzolatti et al., 1996).

Shared Activation in Other Areas

Additional overlapping activation for the sight and experience of touch was found in three other regions. First, overlapping activation was found in the left IPL/supramarginal gyrus. This region is the supposed homologue of the monkey area 7b (e.g., Ruben et al., 2001), containing neurons that respond to somatosensory stimulation (Hyvarinen, 1982; Robinson & Burton, 1980). The current activation in this region during tactile stimulation of the hands is therefore consistent with these studies, and extends them by demonstrating that this area also responds to visual stimuli depicting touch.

Second, overlapping activation was found at the temporal–occipital junction (area MT/V5). This region is known to respond to visual perception of (biological) motion stimuli (Pelphrey et al., 2005; Orban et al., 1995), suggesting that this activation is not specific to the sight

of touch but could be related to the perception of motion in the stimuli. Consistent with previous findings (Hagen et al., 2002), the current overlapping of activation suggest that MT/V5 activation is not restricted to visual input, but can be elicited by tactile motion perception, too.

Third, overlapping activation was found in the left precentral gyrus (dorsal PMv/BA 6), when all the touch observation conditions were pooled together. In accordance with previous studies reporting a polysensory function in monkey and human dorsal PMv (Bremmer et al., 2001; Graziano & Gandhi, 2000; Fogassi et al., 1996), this activation during visual as well as tactile perception of touch might reflect polymodal motion processing.

SI and Intentionality

Interestingly, a significant difference between the sight of intentional touch (by a human hand), compared to accidental touch (by a tree branch), was found in the left SI/BA 2. Activation in this area significantly correlated with the degree of intentionality of the observed touch stimuli as rated by the participants.

Human SI is located in the postcentral gyrus and has classically been considered as purely involved in the personal perception of somatic sensations (e.g., Kaas, 1983; Vogt & Vogt, 1919; Brodmann, 1909). With respect to BA 2 in the posterior section of SI, it is known that in the monkey this area has reciprocal connections with somatosensory area 3b and the motor cortex, and receives proprioceptive information from deep receptors in muscles and joints (Gardner & Kandel, 2000; Yumiya & Ghez, 1984). BA 2 contains a bilateral hand representation to a greater extent than other SI areas (Hlushchuk & Hari, 2006; Iwamura, Iriki, & Tanaka, 1994).

Zhou and Fuster (2000) found that monkeys' SI neurons responded also to visual stimuli, if these were previously associated with tactile experiences. In humans, neurophysiological studies found also that SI activity can be modulated by task-relevant visual input (Taylor-Clarke, Kennett, & Haggard, 2002), and the observation of a painful as well as nonpainful touch (Bufalari, Aprili, Avenanti, Di Russo, & Aglioti, 2007; Caetano, Jousmaki, & Hari, 2007; Schaefer, Flor, Heinze, & Rotte, 2006; Blakemore et al., 2005; Avikainen et al., 2002). The current activation in SI/BA 2 corresponds approximately to the SI activations reported by Schaefer et al. (2006) when the observer tended to attribute an observed touch to the self, and by Blakemore et al. (2005), in a case of vision–touch synesthesia during the observation of a hand touching a face. Also relevant to note is that activation of the observer's hand section of BA 2 has been reported during passive observation of flexion–extension movements of an experimenter's hand, indicating an associative function between vision and kinesthesia (Oouchida et al., 2004).

Considering these results, it can be argued that the current activation in BA 2 would reflect an associative

visuo-kinesthetic function, evoked by the perception of human hand movements in the video clips. However, the significant correlation between activation in BA 2 and the degree of perceived intentionality, even within the accidental condition, suggests that this increased activation cannot be explained by visual differences in the stimulus characteristics per se. Rather, the activation in SI/BA 2 might reflect automatic simulation of proprioceptive aspects related to observed touch when intentionality is assumed by the observer. In the light of studies regarding the MNS, and its involvement in the understanding of others' intentions (Fogassi et al., 2005; Iacoboni et al., 2005), it can be speculated that observers tend to ''resonate'' more with an intentional agent, also when only assumed, than with a touched passive subject or an accidentally touching object. This would be consistent with theories regarding the MNS and its role in social cognition (e.g., Iacoboni et al., 2006; Gallese et al., 2004).

Conclusions

In the current experiment, overlapping activation was found in SII between the sight of either another person's hand or an object being touched, either by a hand or by a tree branch, and tactile stimulation of the participants' own hands.

The novelty of the present study is that the activation of such a visuotactile mirroring mechanism for touch in SII is independent of the intentionality of the observed touch stimuli. The same mirroring/simulation principles seem to apply to the observation of any touch. This mechanism might underpin the activation of an abstract notion of touch. It does not matter to which degree an observed touch is intentional or accidental, whether an observed touched object is animate or inanimate, or whether an observed person or object is touched on the right or left side; the sight of any touch evokes activation in a shared neural circuitry in the bilateral SII. Indeed, differently from other domains where a shared circuitry between first- and third-person experience has been demonstrated, like in the case of actions and emotions, the domain of touch appears not to be limited to the social world. Space around us is full of objects accidentally touching each other, that is, without any animate involvement. One could observe a pine cone falling on the garden bench in the park, or drips splashing on the leafs of a plant during a downpour. Models of embodied simulation posit that the same neural structures involved in our own body-related experiences contribute to the conceptualization of what we observe in the world around us (Gallese, 2005; Gallese & Lakoff, 2005). Extended to current results, simulation processes in a visuotactile mirroring mechanism may ground *any* perception of touch, and as such, contribute to the representation of an abstract, but prelinguistic, notion of touch.

Increased activation in SI/BA 2 when an observed touch is perceived as more intentional by the observer might reflect simulation of the proprioceptive aspects related to an intentional touch, based on a human tendency to ''resonate'' more with an (assumed) intentional agent than an accidentally moving object.

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