# Differential Involvement of Somatosensory and Interoceptive Cortices during the Observation of Affective Touch

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## Abstract

■ Previous studies suggested that the observation of other individuals' somatosensory experiences also activates brain circuits processing one's own somatosensory experiences. However, it is unclear whether cortical regions involved with the elementary stages of touch processing are also involved in the automatic coding of the affective consequences of observed touch and to which extent they show overlapping activation for somatosensory experiences of self and others. In order to investigate these issues, in the present functional magnetic resonance imaging study, healthy participants either experienced touch or watched videos depicting other individuals' inanimate and animate/social touch experiences. Essentially, a distinction can be made between exteroceptive and interoceptive components of touch processing, involved with physical stimulus characteristics and internal feeling states, respectively. Consistent with this distinction, a specific neg-

ative modulation was found in the posterior insula by the mere visual perception of other individuals' social or affective cutaneous experiences, compared to neutral inanimate touch. On the other hand, activation in secondary somatosensory and posterior superior temporal regions, strongest for the most intense stimuli, seemed more dependent on the observed physical stimulus characteristics. In contrast to the detected vicarious activation in somatosensory regions, opposite activation patterns for the experience (positive modulation) and observation (negative modulation) of touch suggest that the posterior insula does not reflect a shared representation of self and others' experiences. Embedded in a distributed network of brain regions underpinning a sense of the bodily self, the posterior insula rather appears to differentiate between self and other conditions when affective experiences are implicated. ■

## INTRODUCTION

Skin-to-skin contact between individuals has a pivotal role in social interactions subserving a nonverbal communication of intentions and affect. For example, a caress may express appreciation or an affiliative relationship between individuals and a hit may express anger or an aversive relationship. Besides being subject to direct skin-to-skin contact with other individuals in everyday life, we frequently observe skin-to-skin contact between other individuals as well. During the observation of touch experienced by others, there usually is no real tactile experience, unlike when directly experiencing touch. However, even in a touch observation situation, we are able to distinguish its intentions and are aware of the sensations or feelings a touch would provoke (Hertenstein, Keltner, App, Bulleit, & Jaskolka, 2006; Gibson, 1962). Although neuroscientific research started shedding light upon the neural mechanism

involved in the visual recognition of others' intentions and feelings, its exact functioning is not well understood.

The present functional magnetic resonance imaging (fMRI) study aimed at elucidating the neural processes during the observation of others' social somatosensory experiences and, more specifically, the role of basic somatosensory and interoceptive brain regions.

Numerous neuroimaging and neurophysiological studies suggest that shared brain circuits processing one's own somatosensory and affective experiences contribute to the recognition of other individuals' neutral (Pihko, Nangini, Jousmäki, & Hari, 2010; Schaefer, Xu, Flor, & Cohen, 2009; Ebisch et al., 2008; Blakemore, Bristow, Bird, Frith, & Ward, 2005; Keysers et al., 2004), painful (Costantini, Galati, Romani, & Aglioti, 2008; Jackson, Meltzoff, & Decety, 2005; Morrison, Lloyd, di Pellegrino, & Roberts, 2004; Singer et al., 2004; Hutchison, Davis, Lozano, Tasker, & Dostrovsky, 1999), or pleasant (McCabe, Rolls, Bilderbeck, & McGlone, 2008) somatosensory experiences. These data support neuroscientific models of embodied simulation, proposing that multimodal brain regions underlying first-person bodily experiences are also involved with

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an implicit, automatic, bottom–up understanding of the actions, sensations, and emotions of other individuals, hence, playing a role in intersubjectivity and empathic experiences (Gallese, 2003, 2005; Rizzolatti, Fogassi, & Gallese, 2001).

It is still a major issue to which extent brain regions involved with the basic processing stages of cutaneous information are also involved in the automatic coding of the affective consequences of observed touch (e.g., Avenanti, Bueti, Galati, & Aglioti, 2005; Singer & Frith, 2005; Singer et al., 2004). Importantly, two distinct neural systems can be identified regarding the processing of cutaneous information. An exteroceptive modality in the somatosensory cortices is mainly involved in the discrimination of the physical characteristics of tactile stimuli, whereas an interoceptive modality in posterior insular cortex is believed to process the internal affective feeling states evoked by experienced touch (Björnsdotter, Löken, Olausson, Vallbo, & Wessberg, 2009; Craig, 2002; Olausson et al., 2002; Servos, Lederman, Wilson, & Gati, 2001; Schnitzler & Ploner, 2000). A modulation of the activation of somatosensory cortices by the observation of others' affective tactile experiences is found, in particular, by studies that required explicit processing of the sensory-discriminative aspects of the visual stimuli, mostly depicting intense or painful tactile stimulation, or measured sensory-evoked potentials (e.g., Bufalari, Aprili, Avenanti, Di Russo, & Aglioti, 2007; Cheng et al., 2007; Lamm, Nusbaum, Meltzoff, & Decety, 2007), whereas no studies reported evidence for involvement of posterior insular cortices. Considering an exteroceptive–interoceptive distinction, however, it could be expected that the interoceptive modality would be specifically involved in an automatic coding of the affective consequences of observed touch.

On the other hand, although shared neural circuits are likely involved in the understanding of others' feelings (Keysers & Gazzola, 2009; Gallese, 2003, 2005), one could argue that it would be crucial to distinguish to whom these feelings belong (e.g., Banissy, Cohen Kadosh, Maus, Walsh, & Ward, 2009; Eisenberg et al., 1989; Batson, Fultz, & Schoenrade, 1987). It has been proposed that full-blown empathic abilities may rather emerge from a complex interplay between embodied simulation processes, and higher cognitive and self-regulation functions (Decety & Meyer, 2009; de Waal, 2008; Eisenberg, 2000). In other words, in functional empathic experiences, there possibly is no complete overlap between one's own and others' mental states. For example, personal emotional arousal during empathic experiences could be down-regulated by control mechanisms in frontal cortices (Cheng et al., 2007). Furthermore, Singer et al. (2004) reported overlapping activation for one's own and one's partner's painful experiences in brain regions underlying emotional processing, but not in somatosensory and posterior insular cortices, while using an experimental set up where the cutaneous stimulation of the other was not directly observable. However, it is still unclear what the role of exteroceptive and interoceptive sensory re-

gions during the observation of affective social touch in this context is; for example, whether they mirror others' social skin-to-skin experiences or whether they show distinct activation patterns.

To address these issues, 19 healthy participants underwent fMRI scanning while watching video clips depicting neutral inanimate touch, or neutral or affective skin-to-skin contact. Essentially, the experimental paradigm did not require an explicit processing of the sensory and affective characteristics of the touch depicted by the visual stimuli, while avoiding possible confounding effects of aversive visceromotor responses to the visual stimuli in the observer, and included a tactile localizer condition always run at the end of the scanning session.

## METHODS

### Participants

Nineteen participants were included in the present study (10 women, age range = 22–34 years). All participants were healthy, right-handed (Edinburgh Handedness Inventory score > 0.85), and had 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 oxygen level dependent (BOLD) contrast functional imaging was performed with a Philips Achieva scanner at the Institute of Advanced Biomedical Technologies (Chieti) at 1.5 T by T2*-weighted gradient echo-planar sequences with the following parameters: TR = 2400 msec, TE = 50 msec, matrix size 64 × 64, field of view (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. Functional volumes consisted of 26 transaxial slices.

A high-resolution structural volume was acquired at the end of the session via a 3-D MP-RAGE sequence with the following features: 170 sagittal slices, voxel size = 1.25 × 1.25 × 1.20 mm, TR = 8.6 msec, TE = 4.0 msec, 192 × 192 image matrix, FOV = 240 mm.

### Stimuli and Conditions

Four visual runs (mean = 166 functional volumes) and one tactile run (200 functional volumes) were acquired for each subject. In visual runs, stimuli consisted of 208 randomized video clips of 2360 msec each, representing a touch event according to one of four experimental conditions. In the neutral inanimate condition (BRANCH), either a male or female hand was touched by a wind-moving palm tree

branch moved by an invisible fan. In the animate or social conditions, either a male hand touched the back of a female hand or a female hand touched the back of a male hand by means of a neutral social touch (NEUTRAL) or an affective social touch that could have a negative (HIT) or positive (CARESS) valence. The actors shown in the video clips were touched on their right hand in half of the video clips and on their left hand in the other half. The actors in the video clips were sitting on a chair and seen from a frontal point of view. To exclude effects due to the perception of a face and facial expressions, actors being touched in the video clips were visible only from the lower legs to the chest. The actors wore a white T-shirt. Only the uncovered arm and hand of the touching actor were visible. Examples of the visual stimuli are shown in Figure 1. In addition to the touch video clips, 31 nontouch video clips were randomly inserted in the visual runs, showing either a hand or palm tree branch moving near the hand of the other person, but without touching it. The video clips were separated by a fixation cross at the center of the screen. The video clips were presented by means of custom software (Galati et al., 2008) on a screen behind the scanner with a beamer. Participants could see the screen clearly through a mirror placed above their eyes.

A tactile localizer run was added to the experiment in order to determine an 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 soft stroking with a washing glove. Brushing frequency was approximately 1 Hz.

### Experimental Procedure

Prior to scanning, it was explained to participants that they would see randomly shown short video clips with a different content in four separated runs of approximately 6.7 min each. They were told that in the video clips they would see a hand touching another hand or a wind-moved palm tree branch touching a hand, 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 mentally 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 = 8/run). The nontouch trials were

not included in the statistical analyses, but this task was added to direct participants' attention to the touch during the experiment, without requiring an explicit processing of the sensory and affective characteristics of the depicted touch. Prior to scanning, participants practiced the task outside the scanner to ensure that they had understood the instructions.

The experimental design of the visual runs was a rapid event-related fMRI design alternating a state of stimulation (video clips) of 2400 msec (one TR) with a baseline state (fixation cross) of 2400, 4800, or 7200 msec (corresponding to one to three TRs) (see Figure 1). The three baseline durations were presented randomly with a linear distribution (i.e., to each duration was assigned the same probability). All four visual runs consisted of 48 touch video clips and a mean intertrial interval of 4800 msec. The time course of stimulus presentation during a visual run is illustrated in Figure 1.

During the tactile run, participants were instructed to close their eyes and think of nothing in particular. The tactile run was a blocked design fMRI study alternating a state of stimulation of 15 sec with a baseline state (rest) of the same duration. In total, there were 16 randomized stimulation blocks: 8 blocks for the right hand and 8 blocks for the left hand.

At debriefing, participants were asked to rate the pleasantness and intensity of the different types of touch depicted by the videos in random order. For this purpose, participants indicated the subjectively perceived pleasantness and intensity of the depicted touch with a pencil on a vertical line where the lowest point meant very unpleasant and the highest point meant very pleasant. Participants were not informed about the content of the rating prior to scanning in order to avoid eventual effects of attention directed to particular aspects of the visual stimuli.

### fMRI Data Preprocessing and Analysis

Raw data were analyzed with the Brain Voyager QX 1.9 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. A three-dimensional motion correction was performed with a rigid-body transformation to match each functional



**Figure 1.** Examples of the time course of stimulus presentation during the observation of touch conditions and examples of the visual stimuli (i.e., neutral inanimate touch "BRANCH," positive social affective touch "CARESS," negative social affective touch "HIT," neutral social touch "NEUTRAL").

volume to the reference 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 functional and 3-D structural measurements were acquired in the same session, the coregistration transformation was determined using the Philips 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 a rapid event-related fMRI paradigm, the hemodynamic responses to the closely spaced events will partially overlap, thus the visual runs were modeled by means of the deconvolution approach (e.g., Ollinger, Corbetta, & Shulman, 2001; Ollinger, Shulman, & Corbetta, 2001). 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. 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.

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 and to determine a cluster size threshold (Cox, 1996; Forman et al., 1995). In this way, a significance level of $p < .05$ cluster level corrected for multiple comparisons was obtained.

In order to determine overlap of activation between observation of touch conditions and the tactile stimulation condition, conjunction analysis was performed (contrast: *any* touch observation condition vs. baseline ∩ tactile stimulation vs. baseline), 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.

For the purpose of investigating whether there was a statistically significant modulation effect of observation condition in the brain regions showing overlapping or opposite activation patterns for the experience and observation of touch, ROI-based ANOVAs were performed with observation condition as within-subject variable and percentage signal changes extracted from the ROIs as dependent variable. Percentage signal change was calculated as the mean Beta value across all voxels within each ROI. The ROIs were determined by means of conjunction analysis described above.

A psychophysical interaction (PPI; Friston et al., 1997) analysis was applied to investigate the effective connectivity of brain ROIs. This method essentially identifies voxels whose time course correlated more strongly with the time course of activity in a seed ROI. In other words, voxels are identified that are functionally more connected to the seed ROI in the affective touch observation conditions, compared to the inanimate neutral touch observation conditions (Friston et al., 1997). For this analysis, the time courses of all individual participants were extracted from a seed ROI determined by the group statistical map. Subsequently, an interaction term was generated for each participant by multiplying point by point the (mean corrected) individual time course of activity in the seed ROI with the psychological (i.e., task) variable containing the value 1 for the affective touch observation condition, −1 for the inanimate neutral touch observation condition, and zero elsewhere. The interaction terms, together with both the time course of the seed ROI and the psychological/task variables, were then entered as regressors in a whole-brain random effect GLM group analysis.

## RESULTS

### fMRI Results: Tactile Stimulation

Tactile stimulation of the left and right hand of the participants [tactile stimulation left/right hand vs. baseline] significantly enhanced BOLD response in bilateral dorsal and ventral postcentral gyrus (dPostCG, vPostCG), including primary somatosensory cortex (SI) and parietal operculum (PO; secondary somatosensory cortex, SII; parietal ventral area, PV), inferior parietal lobe (IPL), anterior superior parietal cortex (aSPC), dorsal precentral gyrus (dPreCG), ventral precentral–inferior frontal gyrus (vPreCG–IFG), lateral occipito-temporal junction (OT), mid and posterior insular cortex (mIC, pIC), thalamus, ventral supramarginal gyrus (vSMG), mid-cingulate cortex (MCC), fusiform gyrus, and right hemisphere (RH) posterior superior temporal gyrus/sulcus (pST) ($p < .05$, corrected).

### fMRI Results: Observation of Touch Conditions

The observation of touch stimuli [any touch observation condition vs. baseline] elicited significant activation ($p < .05$

corrected) in bilateral occipital cortex, extrastriate cortices, OT, fusiform gyrus, thalamus, aSPC, intraparietal cortex (IPC), frontal and supplementary eye fields (FEF, SEF), vPreCG–IFG, left hemisphere (LH) PO (SII/PV); vPostCG, MCC, and RH pST and dorsolateral prefrontal cortex (DLPFC). Specifically for the observation of a social affective touch, activation was found also in LH anterior insular cortex (aIC; coordinates $x = -29, y = 23, z = 10$; HIT: $p < .05$, corrected; CARESS: $p < .001$, uncorrected). Significant deactivation during the observation of touch [any touch observation condition vs. baseline] could be detected in bilateral ventral medial prefrontal cortex (vMPFC), pIC, and LH lateral superior temporal gyrus.

## Overlapping and Differential BOLD Response for Touch Experience and Observation

With respect to overlapping activation for the experience and observation of touch (i.e., vicarious activation), group statistical maps of conjunction analysis [*any* observation of touch condition vs. baseline ∩ tactile stimulation right/left hand vs. baseline] showed overlapping activation ($p < .05$ corrected) in bilateral OT (Brodmann's area [BA] 19/37/21, Brodmann, 1909), vPreCG–IFG (BA 6), fusiform gyrus, LH anterior and posterior SII (a/pSII), vPostCG (BA 2), aSPC (BA 7/40), and RH pST (BA 22/42). Using an uncorrected statistical threshold of $p < .001$, overlapping activation also could be detected in RH pSII.

An opposite pattern of activation for the experience and observation of touch (i.e., distinguishing between self and other's sensory experiences) was found in LH as well as in RH pIC. Whereas pIC was significantly activated compared to baseline during the experience of touch, the same region was significantly deactivated compared to baseline during the observation of touch in another individual ($p < .05$, corrected).

Group statistical maps of overlapping and opposite activation for the experience and observation of touch conditions are shown in Figure 2. Detailed information about these activation clusters and different conditions is provided in Table 1.

## Modulation of BOLD Response by Observation Condition in Brain Regions Showing Overlapping or Opposite Activation for Touch Experience and Observation

In order to investigate whether BOLD response in the overlapping and differentiating brain regions was modulated by specific observation conditions, ROI-based ANOVAs were performed with observation condition as the within-subject variable and mean percent signal change in the ROIs displayed in Figure 2 as the within-subject variable. A significant modulation (main effect) was found in the LH PostIC cluster [$F(3, 54) = 5.502, p = .002$]. LH PostIC showed an increased deactivation for HIT [$F(1, 18) = 13.461, p = $

.002)] and CARESS [$F(1, 18) = 15.000, p = .001$], compared to BRANCH.

A significant main effect for condition was found also in RH pST [$F(3, 54) = 7.654, p = .001$], LH vPostCG $F(3, 54) = 7.650, p < .001$], LH pSII [$F(3, 54) = 3.541, p = .02$], and RH pSII clusters [$F(3, 54) = 3.764, p = .016$].

pST showed an increased activation for HIT, compared to BRANCH [$F(1, 18) = 13.833, p = .002$], CARESS [$F(1, 18) = 27.042, p < .001$], and NEUTRAL [$F(1, 18) = 12.575, p = .002$].

vPostCG showed an increased activation for BRANCH, compared to HIT [$F(1, 18) = 7.628, p = .01$] and NEUTRAL [$F(1, 18) = 22.385, p < .001$], and CARESS compared to NEUTRAL [$F(1, 18) = 10.005, p = .005$].

LH pSII showed an increased activation for HIT, compared to CARESS [$F(1, 18) = 6.297, p = .02$], NEUTRAL [$F(1, 18) = 7.439, p = .01$], and BRANCH [$F(1, 18) = 5.734, p = .02$].

Similar to LH pSII, RH pSII showed an increased activation for HIT, compared to CARESS [$F(1, 18) = 11.429, p = .003$], NEUTRAL [$F(1, 18) = 5.769, p = .02$], and BRANCH [$F(1, 18) = 6.657, p = .01$].

In addition, direct contrasts between the different touch observation conditions were performed to verify if these modulations are also reliable at a whole-brain level ($p < .05$, corrected). Whole-brain analysis showed an increased deactivation for both HIT and CARESS, compared to BRANCH in bilateral pIC [BRANCH vs. HIT ∩ BRANCH vs. CARESS ∩ tactile stimulation vs. baseline]. Increased activation was found for HIT, compared to BRANCH, CARESS, and NEUTRAL in RH pSII (and LH pSII at $p < .005$, uncorrected) and pST [HIT vs. BRANCH ∩ HIT vs. CARESS ∩ HIT vs. NEUTRAL ∩ tactile stimulation vs. baseline]. Increased activation for BRANCH, compared to HIT, CARESS, and NEUTRAL was detected in LH vPostCG [BRANCH vs. HIT ∩ BRANCH vs. CARESS ∩ BRANCH vs. NEUTRAL ∩ tactile stimulation vs. baseline].

Graphics representing percent signal change for the individual conditions in these modulating brain regions are shown in Figure 2.

## Functional Connectivity of LH pIC

PPI analysis was performed to provide more insight in the task-related functional interactions (i.e., effective connectivity) between LH pIC and other brain regions in relationship with the deactivation effect in LH pIC during the observation of affective touch. The time course of the seed ROI for the PPI analysis was composed by the mean values of all voxels within the LH pIC cluster (see Figure 2) at each time point during the touch observation fMRI runs.

PPI analysis revealed a significant interaction between LH pIC, RH temporo-parietal junction (TPJ), LH PreCG, and RH posterior parietal cortex (PPC) during the observation of affective touch, compared to the observation of inanimate neutral touch ($p < .001$, corrected, $k > 5, t > 4$). The PPI group statistical map is shown in Figure 3.
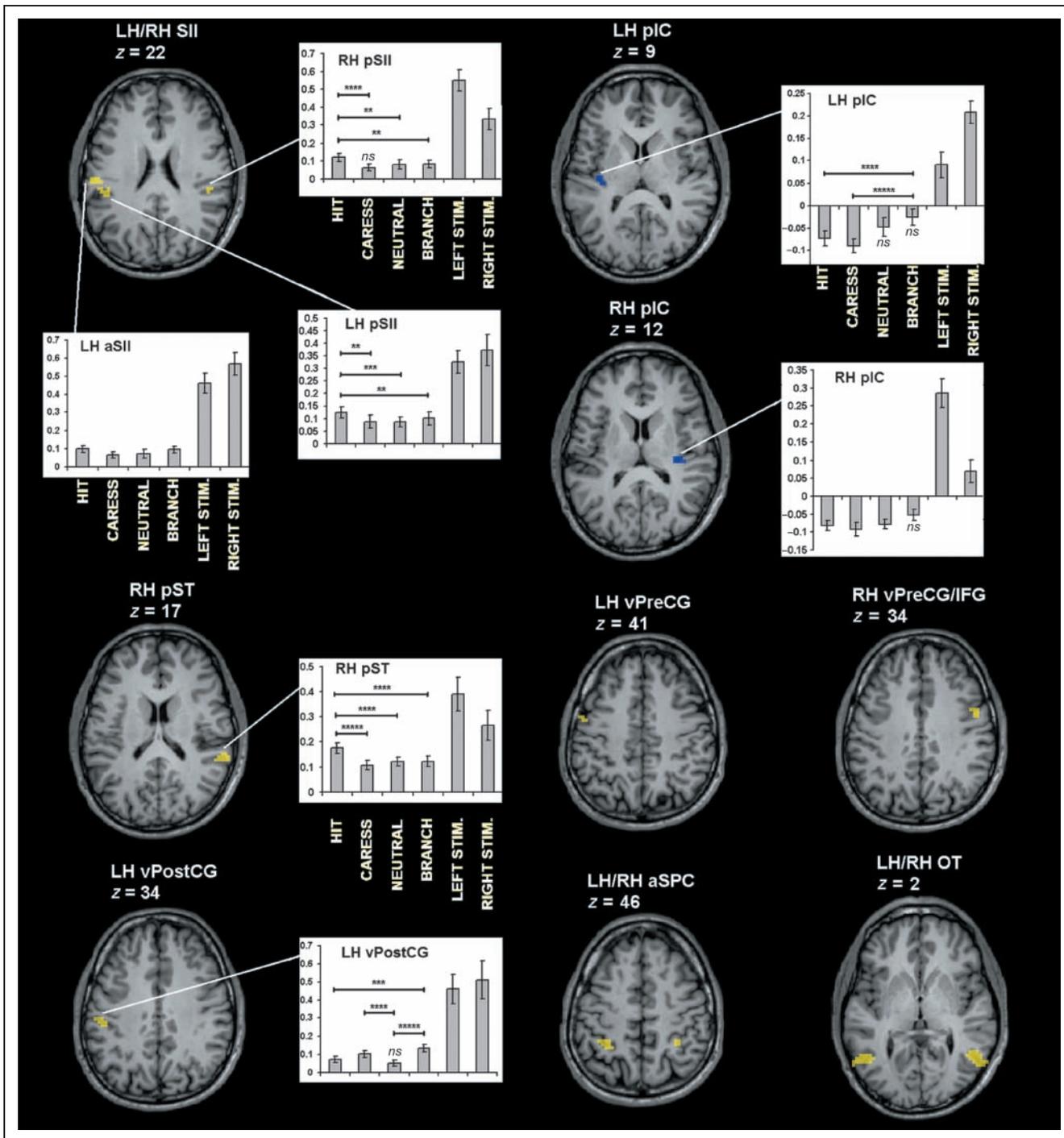
**Figure 2.** Group statistical maps with brain regions showing overlapping (yellow) or opposite (blue) activation patterns for the experience and observation of touch, and graphics showing % signal change for the different observation (HIT, CARESS, NEUTRAL, BRANCH) and experience of touch conditions (left-/right-hand stimulation) in modulating brain regions (**$p < .05$; ***$p < .01$; ****$p < .005$; *****$p < .001$).

### Visual Stimuli Ratings

As expected, pleasantness ratings of the different types of touch depicted by the videos showed that the participants attributed a clear unambiguous affective valence to the HIT and CARESS videos, compared to the NEUTRAL and BRANCH videos. The HIT videos were rated as strongly unpleasant (negative), whereas the CARESS videos were rated as strongly pleasant (positive). The BRANCH touch ratings were moderately pleasant, on average, and varied between neutral and pleasant. The NEUTRAL touch depicted by the videos was rated as neutral, on average, but

**Table 1.** Brain Regions Showing Opposite or Overlapping Activation for the Experience and Observation of Touch Conditions, Corresponding to Figure 2, and Statistical Information about the BOLD Responses for the Separate Touch Observation/Experience Conditions in These Clusters

| Brain Region | Talairach Coordinates (x, y, z) | Cluster Size | Condition | Mean % Signal Change | Standard Error | t |
|---|---|---|---|---|---|---|
| LH pIC | −37, −18, 9 | 216 | HIT | −0.073 | 0.017 | −4.22* |
| | | | CARESS | −0.090 | 0.015 | −5.82** |
| | | | NEUTRAL | −0.048 | 0.021 | ns |
| | | | BRANCH | −0.026 | 0.018 | ns |
| | | | LEFT STIM. | 0.090 | 0.028 | ns |
| | | | RIGHT STIM. | 0.208 | 0.025 | 8.08** |
| RH pIC | 38, −19, 10 | 635 | HIT | −0.067 | 0.014 | −4.87** |
| | | | CARESS | −0.081 | 0.018 | −4.79** |
| | | | NEUTRAL | −0.071 | 0.017 | −3.94* |
| | | | BRANCH | −0.052 | 0.016 | ns |
| | | | LEFT STIM. | 0.265 | 0.037 | 7.14** |
| | | | RIGHT STIM. | 0.066 | 0.028 | ns |
| LH pSII | −50, −27, 19 | 212 | HIT | 0.103 | 0.019 | 5.20** |
| | | | CARESS | 0.088 | 0.026 | 3.31*** |
| | | | NEUTRAL | 0.140 | 0.023 | 5.85** |
| | | | BRANCH | 0.101 | 0.021 | 4.78** |
| | | | LEFT STIM. | 0.304 | 0.052 | 5.77** |
| | | | RIGHT STIM. | 0.342 | 0.068 | 5.02** |
| LH aSII | −53, −22, 19 | 467 | HIT | 0.099 | 0.019 | 5.12** |
| | | | CARESS | 0.066 | 0.016 | 3.90* |
| | | | NEUTRAL | 0.073 | 0.023 | 3.13**** |
| | | | BRANCH | 0.096 | 0.019 | 4.91* |
| | | | LEFT STIM. | 0.461 | 0.054 | 8.40** |
| | | | RIGHT STIM. | 0.567 | 0.062 | 9.05** |
| LH vPostCG | −55, −25, 36 | 334 | HIT | 0.073 | 0.017 | 4.30* |
| | | | CARESS | 0.103 | 0.019 | 5.31** |
| | | | NEUTRAL | 0.052 | 0.018 | ns |
| | | | BRANCH | 0.135 | 0.022 | 6.05** |
| | | | LEFT STIM. | 0.460 | 0.081 | 5.66** |
| | | | RIGHT STIM. | 0.510 | 0.106 | 4.81* |
| RH pSII | −51, −28, 18 | 104 | HIT | 0.110 | 0.018 | 6.14** |
| | | | CARESS | 0.050 | 0.017 | ns |
| | | | NEUTRAL | 0.073 | 0.019 | 3.74* |
| | | | BRANCH | 0.066 | 0.014 | 4.59** |
| | | | LEFT STIM. | 0.548 | 0.059 | 9.23** |
| | | | RIGHT STIM. | 0.332 | 0.060 | 5.51** |

**Table 1.** (*continued*)

| Brain Region | Talairach Coordinates (x, y, z) | Cluster Size | Condition | Mean % Signal Change | Standard Error | t |
|---|---|---|---|---|---|---|
| RH pST | 57, −37, 17 | 582 | HIT | 0.176 | 0.020 | 8.55** |
| | | | CARESS | 0.108 | 0.019 | 5.47** |
| | | | NEUTRAL | 0.123 | 0.018 | 6.51** |
| | | | BRANCH | 0.123 | 0.021 | 5.81** |
| | | | LEFT STIM. | 0.390 | 0.067 | 5.75** |
| | | | RIGHT STIM. | 0.264 | 0.060 | 4.34* |
| LH aSPC | −36, −47, 52 | 1453 | HIT | 0.123 | 0.019 | 6.48** |
| | | | CARESS | 0.154 | 0.026 | 5.80** |
| | | | NEUTRAL | 0.094 | 0.022 | 4.21* |
| | | | BRANCH | 0.160 | 0.027 | 5.87** |
| | | | LEFT STIM. | 0.281 | 0.070 | 4.00* |
| | | | RIGHT STIM. | 0.591 | 0.102 | 5.75** |
| RH aSPC | 31, −45, 45 | 159 | HIT | 0.056 | 0.021 | *ns* |
| | | | CARESS | 0.094 | 0.020 | 4.63* |
| | | | NEUTRAL | 0.056 | 0.018 | *ns* |
| | | | BRANCH | 0.085 | 0.023 | 3.56*** |
| | | | LEFT STIM. | 0.332 | 0.067 | 4.95** |
| | | | RIGHT STIM. | 0.117 | 0.046 | *ns* |
| LH vPreCG–IFG | −54, −2, 40 | 149 | HIT | 0.160 | 0.034 | 4.61* |
| | | | CARESS | 0.181 | 0.030 | 5.84** |
| | | | NEUTRAL | 0.158 | 0.039 | 3.99* |
| | | | BRANCH | 0.201 | 0.045 | 4.41* |
| | | | LEFT STIM. | 0.275 | 0.057 | 4.76* |
| | | | RIGHT STIM. | 0.287 | 0.070 | 4.10* |
| RH vPreCG–IFG | 49, 2, 33 | 273 | HIT | 0.137 | 0.017 | 7.78** |
| | | | CARESS | 0.186 | 0.018 | 10.01** |
| | | | NEUTRAL | 0.124 | 0.024 | 5.16** |
| | | | BRANCH | 0.120 | 0.020 | 6.04** |
| | | | LEFT STIM. | 0.258 | 0.050 | 5.09** |
| | | | RIGHT STIM. | 0.137 | 0.045 | *ns* |
| LH OT | −50, −59, −2 | 1259 | HIT | 0.289 | 0.036 | 7.94** |
| | | | CARESS | 0.291 | 0.034 | 8.36** |
| | | | NEUTRAL | 0.261 | 0.038 | 6.87** |
| | | | BRANCH | 0.280 | 0.039 | 7.10** |
| | | | LEFT STIM. | 0.231 | 0.048 | 4.73* |
| | | | RIGHT STIM. | 0.251 | 0.042 | 5.90** |
| RH OT | 50, −58,2 | 1385 | HIT | 0.291 | 0.049 | 5.84** |
| | | | CARESS | 0.300 | 0.050 | 5.93** |
| | | | NEUTRAL | 0.261 | 0.048 | 5.43** |

**Table 1.** (continued)

| Brain Region | Talairach Coordinates (x, y, z) | Cluster Size | Condition | Mean % Signal Change | Standard Error | t |
|---|---|---|---|---|---|---|
| | | | BRANCH | 0.265 | 0.039 | 6.76** |
| | | | LEFT STIM. | 0.316 | 0.052 | 6.06** |
| | | | RIGHT STIM. | 0.208 | 0.049 | 4.22* |

LH = left hemisphere; RH = right hemisphere; pIC = posterior insular cortex; a/pSII = anterior/posterior secondary somatosensory cortex; vPostCG = ventral postcentral gyrus; pST = posterior superior temporal gyrus–sulcus; aSPC = anterior superior parietal cortex; vPreCG–IFG = ventral precentral gyrus–inferior frontal gyrus; OT = occipito-temporal cortex; left/right stim. = tactile stimulation left/right hand.

*$p < .001$.

**$p < .0001$.

***$p < .005$.

****$p < .01$.

appeared ambiguous in its valence, given that its ratings varied across the participants between unpleasant and pleasant.

With respect to their valence, independent of its positive or negative load, both the HIT and the CARESS videos were characterized by a strong affective valence, whereas NEUTRAL and BRANCH were characterized by a moderate affective valence. Intensity ratings of the touch depicted by the videos confirmed that HIT was consistently perceived as a very intense touch, whereas CARESS, NEUTRAL, and BRANCH obtained equally mild intensity ratings.

The average pleasantness and intensity ratings of the videos by the participants are shown in Figure 4.

## DISCUSSION

The present study aimed at investigating to which degree brain regions involved with the basic processing stages of cutaneous information contribute to the understanding of the affective consequences of observed social skin-to-skin contact by means of fMRI scanning. Taking into account a distinction between exteroceptive and interoceptive aspects of tactile experiences, a specific modulation of the latter modality was hypothesized in the observation of affective skin-to-skin contact, whereas the former may be involved in the processing of the physical characteristics of

observed touch. Main methodological issues were the use of an experimental paradigm that implied an attentional processing of visual touch stimuli, but without requiring an explicit processing of the sensory and affective characteristics of the depicted touch, and the use of visual stimuli depicting affective touch experiences of other individuals that may not induce aversive visceromotor responses in the observer. Essentially, a tactile localizer task was included in the study, but always after the visual runs.

### Overlapping and Differential Activation for the Experience and Observation of Touch

The fMRI results showed overlapping activation for the experience and observation of touch in general in a distributed network of somatosensory and multimodal integration regions that is largely consistent with previous touch observation studies (see Ebisch et al., 2008 for a more detailed interpretation of these activations during the observation of touch). In few somatosensory regions, a modulation was also found between the different touch observation conditions. A BOLD response in LH pSII, RH pSII, and RH pST was significantly increased for the observation of the HIT videos, and in LH vPostCG for the CARESS and BRANCH videos, compared to the other touch observation conditions.

**Figure 3.** Group statistical maps of PPI analysis showing brain regions functionally interacting with pIC during the observation of affective social touch ($p < .05$, corrected).
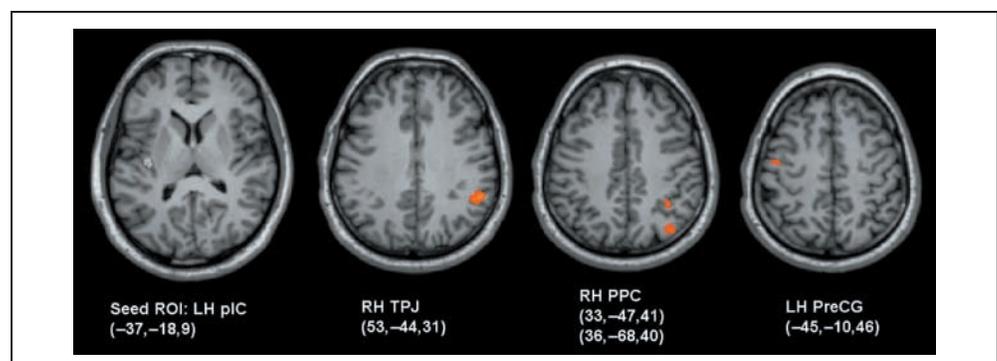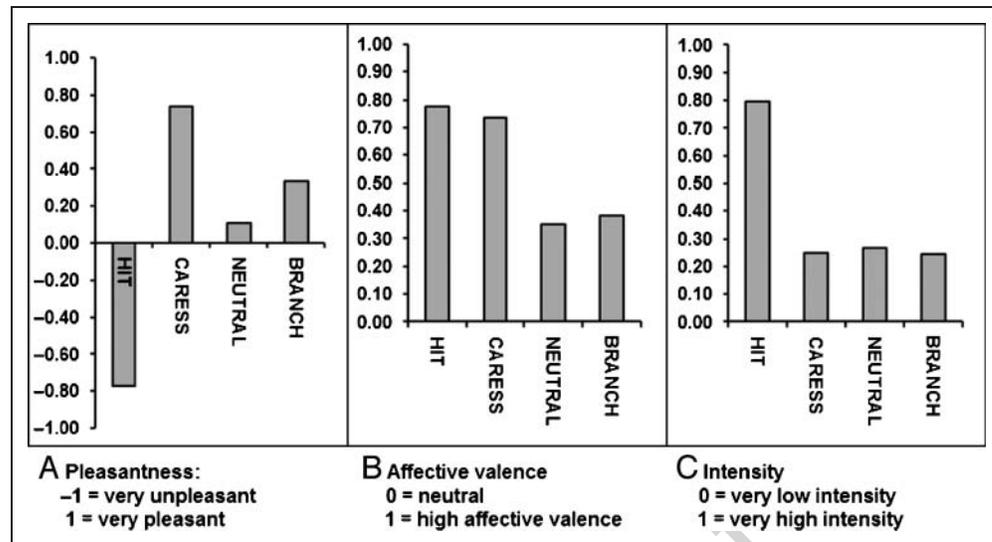


Seed ROI: LH pIC
(−37,−18,9)

RH TPJ
(53,−44,31)

RH PPC
(33,−47,41)
(36,−68,40)

LH PreCG
(−45,−10,46)

**Figure 4.** Ratings by the participants regarding the (A) pleasantness, (B) valence, and (C) intensity of the different types of touch depicted by the videos.



A Pleasantness:
−1 = very unpleasant
1 = very pleasant

B Affective valence
0 = neutral
1 = high affective valence

C Intensity
0 = very low intensity
1 = very high intensity

Interestingly, in addition to these overlapping activations, an opposite activation pattern was found in pIC, suggesting that pIC is part of a neural system that differentiates between affective bodily feelings of self and other. Compared to baseline, the posterior aspect of left as well as right insular cortex was activated by the experience of a touch on the back of participants' hand, but the same region was deactivated specifically during the observation of a social touch on the back of the hand of another individual. ROI analysis showed that signal decrease in LH pIC was significantly stronger for the observation of an affective social touch (CARESS, HIT), compared to a neutral inanimate touch (BRANCH).

## Deactivation of pIC during Touch Observation

The insula is considered a central brain region in sensorimotor, visceral, interoceptive processing, homeostatic/allostatic functions, and emotional awareness of self and others, interacting with limbic, somatosensory, and motor regions (Craig, 2009; Seminowicz & Davis, 2007; Critchley, 2005; Augustine, 1996). According to Craig (2002), thalamocortical pathways provide a direct representation of homeostatic afferent information to pIC, also labeled as primary interoceptive cortex, that engenders distinct bodily or interoceptive feelings by projections onto the anterior insula for an emotional evaluation (see also Saper, 2002). More specifically, regarding the cutaneous senses, pIC could constitute the primary cortical locus of an interoceptive system regulating affective feeling states from the skin such as pain, warmth, itch, and sensual touch. For example, specific afferent pathways have been identified as projecting threatening (e.g., painful stimulation; Craig, 2002) or comforting (e.g., pleasant stroking; Löken, Wessberg, Morrison, McGlone, & Olausson, 2009; Olausson et al., 2002) cutaneous information to thalamic nuclei and from thalamus to pIC.

The specific modulation reported here in LH pIC by the mere observation of an affective social touch, either with a positive or with a negative valence, and not by an inanimate touch, would be in full accordance with these functions. Pleasantness ratings indeed confirmed that participants attributed a clear valence to the affective social touch events (i.e., HIT, CARESS) that was significantly higher compared to the neutral touch events depicted by the videos.

As already noted above, the activation pattern in pIC was opposite for the experience and observation of affective touch (for discussions about task-related deactivations, see Fransson, Krüger, Merboldt, & Frahm, 1999; Hutchinson et al., 1999). In this case, one could argue that this might be due to an expectancy-based incongruence between visual (i.e., touch) and tactile input (i.e., no touch). However, given the specificity of the effect for the observation of touch with social connotation for pIC, but not for PostCG–PO, we would go further by proposing that the observed deactivation in pIC could reflect a suppression of self-oriented arousal at the basis of a differentiation between self and other conditions, rather than being part of a shared neural circuit.

From a developmental perspective, it has been proposed that self-oriented emotional arousal observed in infants witnessing others' emotional experiences and involving a direct affective sharing gradually evolves in other-oriented empathic behavior with increasing cognition, self-awareness, and self-regulation (Decety & Meyer, 2008; de Waal, 2008; Eisenberg, 2000). Full-blown empathy emerges as a rather multifaceted function that relies on a dynamic interaction between automatic bottom–up simulation processes grounding an implicit, pre-reflexive understanding of others' feelings (Gallese, Keysers, & Rizzolatti, 2004; Gallese, 2003), and top–down control processes allowing to suppress self-oriented arousal and maintain a sense of self (de Waal, 2008; Cheng et al., 2007; Lamm et al., 2007; Batson et al., 1987). Moreover, a PET study

showed increased activation in the right posterior insula when an observed prosthetic rubber hand was stroked in synchrony with one's own unseen hand, causing the illusion (i.e., "rubber hand illusion"; RHI) that the stroked rubber hand belonged to one's own body (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007). Also relevant to note in relation to the described pIC functions is that a study using a similar experimental protocol to induce the RHI demonstrated a close link between awareness of the physical and the physiological self (Moseley et al., 2008).

Keeping in mind this framework, and the idea of pIC as a central cortical node in a system constituting a neural representation of "the material me" (Craig, 2002), it can be speculated that an inhibitory mechanism at the level of a primary interoceptive cortex (i.e., pIC) may facilitate the observer to distinguish at the phenomenal level to whom the observed feelings belong. Participants indeed did not report any experience of bodily feelings induced by the visual stimuli. BOLD response suppression in pIC might suggest that something could establish this actively in empathic situations. This interpretation, although being speculative at the present stage of research, offers an intriguing hypothesis for further investigations. These should address directly the relationship between posterior insula functioning and the subjective attribution of bodily feelings to the self or the other, also by extricating self conditions from actual experience. For example, the current findings do not exclude the possibility that deactivation in pIC reflects a self–other distinction based on a stored, nonactual, representation of an acquired internal model of the bodily self, rather than actual interoceptive representations. The opposite activation pattern here reported for the experience and observation of touch extends previous reports that pIC, although being at the basis of body-related feelings, is not activated in common for self and others' affective experiences (e.g., Singer et al., 2004). It rather seems to differentiate between self and other conditions.

Some other issues should be mentioned. No significant difference in BOLD response was found between an affective and neutral social touch in LH pIC. Furthermore, the observation of a neutral social touch (but not a neutral inanimate touch) elicited significant deactivation in RH pIC (see Table 1). A possible explanation for this could be that a neutral social touch is a rather ambiguous stimulus, as skin-to-skin contact has an intrinsic affective value at the basis of intersubjective representations (e.g., Morrison, Löken, & Olausson, 2009). Moreover, the videos depicted a cross-gender touch that could have influenced the perceived valence of the stimuli. Indeed, stimuli ratings showed that participants attributed a moderate degree of affective valence in terms of pleasantness to the neutral social touch videos as well, and that it was highly subjective whether they judged them as pleasant or unpleasant. The present results suggest that BOLD response in pIC is specifically modulated (i.e., deactivated) by the observation of social or intentional touch, independent of whether it has a positive or negative affective valence, but not by the observation of inanimate touch.

## Functional Connectivity of pIC

The next question, then, concerns the functional interactions between pIC and other brain regions that together may constitute a neural network explaining such a deactivation effect distinguishing between self and other in pIC. PPI analysis showed increased functional connectivity during the affective touch observation conditions, compared to the observation of a neutral inanimate touch, between LH pIC, RH TPJ, LH PreCG, and RH PPC.

Neuropsychological and neurophysiological studies suggest that RH TPJ contributes to multisensory integration of bodily information underlying a conscious and coherent experience of the bodily self (e.g., Committeri et al., 2007; Blanke et al., 2005; Berlucchi & Aglioti, 1997). Transcranial magnetic stimulation studies investigating the RHI showed that disruption of RH TPJ reduced the extent to which an observed prosthetic rubber hand stroked in synchrony with one's own, unseen, hand was incorporated into the mental representation of one's own body as measured by proprioceptive drift, whereas it did not affect subjective feelings of ownership, the latter likely mediated by pIC (Kammers et al., 2009; Tsakiris, Costantini, & Haggard, 2008). This suggests that a coherent sense of the bodily self in RH TPJ might be used to distinguish between self-related events and other events perceived in the outside world during multisensory processing. Accordingly, a meta-analysis of functional neuroimaging studies suggested that RH TPJ is engaged in a lower-level computational mechanism for generating, testing, and correcting internal predictions about external sensory events, functions that are also crucial for higher-level social interactions (Decety & Lamm, 2007).

PreCG is anatomically connected to visual and somatosensory areas in posterior parietal cortex and to frontal motor areas (Rizzolatti, Luppino, & Matelli, 1998), and contains a multisensory representation of the body involved in the matching of visual, proprioceptive, and somatic signals, as well as a representation of the space near specific body parts in a body-centered reference frame (Bremmer et al., 2001; Graziano, 1999; Graziano & Gross, 1998; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981a, 1981b). PPC is connected to visual, somatosensory, and premotor areas (Rizzolatti et al., 1998; Jones, Coulter, & Hendry, 1978) and neurons in this region integrate visual, tactile, and proprioceptive information from the hand (Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008; Graziano, Cooke, & Taylor, 2000; Sakata, Takaoka, Kawarasaki, & Shibutani, 1973). Similar to pIC and RH TPJ, brain regions in PreCG and PPC corresponding to the PPI clusters of the present study also have been associated with body-ownership experiences in RHI experiments, possibly by integrating multisensory information and calibrating one's own body part coordinates (Ehrsson, Spence, & Passingham, 2004).

Hence, in the present context, the detected interactions of pIC suggest that pIC is functionally embedded in a neural mechanism underpinning a multisensory representation of the bodily self used to maintain a sense of self during social interactions.

## Vicarious Activation in Somatosensory Cortices

In contrast to pIC, and consistent with previous studies (Keysers, Kaas, & Gazzola, 2010), overlapping activation for the experience and observation of touch was found in somatosensory regions, in particular, vPostCG–PO. PostCG, including SI and SII, is considered to process mainly exteroceptive cutaneous information, such as texture and intensity, rather than the affective aspects of cutaneous stimulation (Servos et al., 2001; Schnitzler & Ploner, 2000; Kaas, 1983). SII is associated with higher-order somatosensory functions (Burton, Videen, & Raichle, 1993; Caselli, 1993; Garcha & Ettlinger, 1980; Woolsey, 1943), polymodal integration of somatosensory input with information from the other senses (Cardini et al., 2010; Bufalari et al., 2007; Avikainen, Forss, & Hari, 2002; Bremmer et al., 2001; Carlsson, Petrovic, Skare, Petersson, & Ingvar, 2000), and may ground an abstract notion of touch (Ebisch et al., 2008).

In the present study, three activation clusters could be distinguished in LH vPostCG–PO with distinct activation patterns: aSII, pSII, and the adjacent vPostCG (BA2). BOLD response in vPostCG (BA2) was enhanced for the observation of inanimate touch and, to a lesser degree, also for CARESS, compared to neutral social touch and HIT. Both the BRANCH touch and the CARESS depicted by the videos were consistently judged as pleasant experiences and might be characterized by a smoother motion in the videos. A similar region was reported by previous studies for the observation of animate as well as inanimate touch (Ebisch et al., 2008; Keysers et al., 2004) and is different from the specific social involvement of the SI/BA 2 cluster reported by Ebisch et al. (2008) located more dorsally on LH SI.

The present finding of two distinct activation clusters in LH SII for the observation of touch is consistent with SII topographical maps for hand stimulation reported by previous fMRI studies (e.g., Eickhoff, Amunts, Mohlberg, & Zilles, 2006; Ferretti et al., 2003). Whereas ROI analysis showed no differential activation for the various observation of touch conditions in aSII, increased activation could be detected in pSII for HIT, that is, the observation of an intense and unpleasant touch. At uncorrected statistical threshold, overlapping activation was also found in RH pSII and, similar to LH pSII, enhanced BOLD response was found for HIT, too. Interestingly, these distinct activation patterns during the observation of different types of touch correspond to the distinct activation patterns for neutral and more intense painful/unpleasant tactile experiences in aSII and pSII reported by Ferretti et al. (2003).

In their fMRI study, increased activation was detected in pSII for the experience of an intense unpleasant tactile stimulus, compared to neutral tactile stimuli, whereas BOLD response in aSII did not distinguish between different types of tactile stimuli. Therefore, the present results confirm the existence of shared representations for the experience and observation of touch in human SII and vPostCG, independent of whether the observed touch is social or inanimate. Moreover, although it was not studied directly how the BOLD response pattern during touch observation relates to the experience of different types of touch, they extend previous studies by suggesting that distinct anterior and posterior SII regions are characterized by corresponding activation patterns for the experience and observation of different types of cutaneous stimulation.

## Other Brain Regions

Except for brain regions primarily involved in the processing of cutaneous information, differential BOLD responses were detected also in some other multimodal regions. The pST region was more strongly activated for the observation of HIT, compared to other touch observation conditions. In accordance with monkey STP (Padberg, Seltzer, & Cusick, 2003; Bruce, Desimone, & Gross, 1981), pST, its putative human homolog, is believed to facilitate multisensory integration, containing a region that responds to auditory, visual, and somatosensory stimuli (Beauchamp, Yasar, Frye, & Ro, 2008). The same multisensory integration area also showed enhanced activation with increasing stimulus intensity (Beauchamp et al., 2008). The coordinates of the ST cluster activated by both tactile and visual stimuli in the present study ($x = 57$, $y = -37$, $z = 17$) correspond to the multimodal region reported by Beauchamp et al. (2008) ($x = 56$, $y = -41$, $z = 14$). Moreover, also in the present study, this cluster showed significantly stronger activation for the most intense stimulus, that is, the observation of a slap of another person's hand (HIT). Therefore, like for SII, the present results may extend previous studies by showing indirectly that pST also shows a similar pattern of activation for the experience and observation of different types of touch.

Finally, it should be noted that significant activation in LH aIC could be detected during the observation of touch. Although no significant modulation was found between the different observations of touch conditions in this region, this activation was found selectively for the observation of an actor's experience of affective social touch, such as a caress or a hit. This is relevant in the present context, because aIC is considered a key region for awareness of the physiological state of the body and emotional experiences (Craig, 2009; Critchley, 2005), and vicarious activation in aIC has been consistently reported during the perception of other individuals' emotions (Keysers & Gazzola, 2009). The activation in aIC, especially in LH (see Craig, 2005), found in the present study during the observation of

others' affective touch experiences, is in accordance with previous studies and might allow the understanding of the affective feeling states of other individuals depicted by the videos (Gallese et al., 2004; Gallese, 2003).

## Conclusion

In conclusion, the present results support the hypothesis that BOLD response in the interoceptive sensory system (i.e., pIC) is specifically modulated by the visual perception of other individuals' social or affective cutaneous experiences. However, given the opposite activation pattern, that is, a BOLD response increase during the experience of touch and a decrease during the observation of touch, in particular of social or affective touch, we propose that pIC does not reflect a shared representation of self and others' affective experiences. It rather seems to differentiate between self and other conditions when affective experiences are implicated. Such a differentiation between self and other in pIC seems to be embedded in a distributed network of brain regions underpinning a sense of the bodily self, comprising RH TPJ, LH PreCG, and RH PPC. On the other hand, shared neural representations for the experience and observation of touch are found in brain regions underlying exteroceptive somatosensory and multimodal integration processes, including vPostCG–SII and pST. Activation patterns in these regions during the observation of different types of touch seem consistent with their functions during first-person somatosensory experiences, suggesting an exact simulation of different observed somatosensory experiences based on specific bodily experiences. Whereas activation in pSII and pST seems more dependent on the physical stimulus characteristics, either observed or experienced, LH aSII possibly contains a more abstract representation of touch.

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