A Touching Sight: SII/PV Activation during the Observation and Experience of Touch

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Summary

Watching the movie scene in which a tarantula crawls on James Bond's chest can make us literally shiver—as if the spider crawled on our own chest. What neural mechanisms are responsible for this "tactile empathy"? The observation of the actions of others activates the premotor cortex normally involved in the execution of the same actions. If a similar mechanism applies to the sight of touch, movies depicting touch should automatically activate the somatosensory cortex of the observer. Here we found using fMRI that the secondary but not the primary somatosensory cortex is activated both when the participants were touched and when they observed someone or something else getting touched by objects. The neural mechanisms enabling our own sensation of touch may therefore be a window also to our understanding of touch.

Introduction

The example of shivering while watching a movie scene of a tarantula crawling on James Bond epitomizes our capacity to effortlessly understand what another human being is feeling. Although we all take our capacity to perceive what other people feel for granted, little if anything is known about the neural mechanisms that underlie this capacity.

In principle, one could hypothesize two ways of understanding the fact that another person has been touched. According to the first (cognitive account), a visual processing of the stimulus is followed by a cognitive deduction of what this stimulus means. This then leads us to

understand what the other person might be feeling. In this scenario, the neural centers normally involved in our own experience of touch, especially our somatosensory cortices, are not directly involved. Alternatively, in accord with our introspective experience of "almost feeling the spider crawling on our own chest," a much less cognitively flavored explanation would propose that the vision of the other person being touched might automatically be associated with an activation of the cortical network of regions normally involved in our own experience of being touched. We would then understand that the other person is being touched through aspects of our own experience of touch, which have been automatically activated by the visual stimulus. A testable difference between these two accounts is that the somatosensory cortices should be systematically activated by the observation of touch in the latter but not in the former.

Touch, though, is not restricted to the social world: we often witness objects touching each other. How does our brain process the sight of two cars bumping into each other? It might be that such "inanimate touch" is processed by the brain in ways fundamentally different from those used to process the sight of touch occurring to another living being. In contrast, in the light of the classical experiments of Heider and Simmel (1944), in which the sight of circles and triangles touching each other is interpreted as two people punching each other, one might speculate that even inanimate touch might be processed through our own experience of touch. This latter hypothesis would predict that the sight of inanimate touch would activate parts of the observer's somatosensory cortices.

Evidence for the fact that the observation of other individuals can activate some of the neural circuitries normally involved when we do or feel similar things comes from two lines of investigation. First, in humans and monkeys, performing goal-directed actions activates a network of cortical areas including the premotor, motor, and posterior parietal areas. Observing or listening to another individual performing those same actions also activates the premotor and parietal cortex (Buccino et al., 2001; Iacoboni et al., 1999; Gallese et al., 1996, 2002; Kohler et al., 2002; Rizzolatti et al., 1996, 2001). It has therefore been hypothesized that we understand the actions of others by activating our own neural representation of these actions (Gallese et al., 1996; Gallese, 2003; Keysers et al., 2003; Rizzolatti et al., 2001).

Second, in a recent experiment, we have shown that a similar mechanism applies to the emotion of disgust. When we experience disgust, we activate our anterior insular cortex. The same area is also activated when we observe the disgusted facial expression of another individual (Wicker et al., 2003). Neuropsychological studies show that lesions of the insula cause a deficit in feeling disgust but also in perceiving disgust in the facial expression of others (Calder et al., 2000; Adolphs et al., 2003).

In the current experiments, we asked whether movies depicting various types of touch activate the somatosensory cortices of the observer. We designed three

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Table 1. Location, Size, and t Value of Functional Activation Clusters in MNI Space for the Three Examined Contrasts Separately Arranged in Order of Decreasing Peak t Value

Anatomical Description	MNI Location (x, y, z)	Size (Voxels[a])	Peak t Value
(A) Touch Left Leg − Rest, p < 0.001, k = 5			
Right SII/PV	56, −30, 22	1012	13.85
Left SII/PV	−46, −40, 20	553	7.94
Right SI	20, −44, 68	257	7.74
(B) Touch Right Leg − Rest, p < 0.001, k = 5			
Right SII/PV	54, −32, 22	501	9.40
Left SI	−16, −46, 74	220	8.22
Left SII/PV	−58, −34, 18	698	7.78
Left SII/PV	−30, −26, 14	121	6.81
(C) Vision-of-Touch − Visual Control, p < 0.001, k = 5			
Left SII/PV and the lateral inferior parietal lobule	−64, −24, 24	700	13.61
Left superior parietal lobule	−28, −44, 52	279	12.85
Left inferior occipital gyrus	−22, −90, −10	936	11.00
Right inferior occipital gyrus	36, −80, 0	628	8.91
Right posterior cingulated	10, −46, 20	134	6.33

[a] Only clusters of at least 100 voxels are reported here. A comprehensive table containing smaller clusters as well is in the Supplemental Data at http://www.neuron.org/cgi/content/full/42/2/335/DC1.

fMRI experiments in which participants were touched on their legs and viewed movies of other people or objects being touched. We found that the secondary somatosensory cortex is activated both when the participants were touched and when they observed someone or something else getting touched by objects. This response did not depend on the perspective from which the touched body parts are observed. The primary somatosensory cortex showed no significant activation during the observation of touch, although it showed a trend in that direction.

Results

In a first study, 14 healthy right-handed volunteers were subjected to a blocked design functional magnetic resonance imaging (fMRI) study. All subjects underwent two tactile and two visual stimulation sessions. The two tactile sessions served to functionally define the locations of the primary (SI) and secondary (SII/PV) (Disbrow et al., 2000) somatosensory cortices. The visual sessions were then used to localize areas activated by the vision of touch and to determine if these areas overlapped with the functionally defined somatosensory cortices. Eight subjects underwent the tactile before the visual runs and six the visual before the tactile ones.

Results of the Somatosensory Stimulation
The cortical location of the participant's lower leg representations in SI and SII/PV were defined by brushing the subjects' exposed lower legs back and forth for blocks of 24 s using a washing glove ("tactile" condition). These activations were contrasted with the BOLD signal obtained during a 24 s rest period using a random-effect analysis (p < 0.001, n = 14 subjects, k ≥ 5 voxels). Statistical maps reveal that touching the right leg (versus rest) activated mainly a contralateral dorsal aspect of the postcentral gyrus (likely corresponding to SI) and both the contra- and ipsilateral parietal operculum, ex-

tending onto the lateral surface of the parietal lobe (likely SII/PV; Disbrow et al., 2000). The same was true for touching the left leg. Results are shown in Tables 1A and 1B and in Figure 1. Given that our aim was to determine if observing touch activates somatosensory brain areas, we defined as somatosensory those voxels activated by the touch of either the right or left leg of the subjects (both p < 0.001 and k ≥ 5, uncorrected).

Results of the Visual Stimulation
We also measured changes of the BOLD signal in two visual sessions where participants viewed video clips of actors having their right or left lower leg being touched by an object ("vision-of-touch") or simply approached by the same object without being touched ("visual-control"). Participants were instructed to look carefully at these video clips. Examples of the stimuli are shown as Supplemental Movies S1 and S2 (see Supplemental Data at http://www.neuron.org/cgi/content/full/42/2/335/DC1), respectively.

Table 1C shows the results of the visual stimulation. When comparing the vision-of-touch with the visual-control conditions, the cluster showing the largest t value had its maximum within our functionally defined left SII/PV. We will refer to this visually activated cluster as the "vision-of-touch area," while SII/PV will always be used to refer to the area functionally defined from the tactile runs. No such activation was found in the functionally defined SI. In addition, we found that the observation of the vision-of-touch movies caused larger activations than the visual-control movies in a cluster in the superior parietal lobule and in visual areas of the occipital lobe (including V5).

Overlap between the Visual and Somatosensory Responses
Figure 2A shows the relative spatial locations of SII/PV (red) and the vision-of-touch area (blue), with their overlap shown in white. Our SII/PV starts in the depth
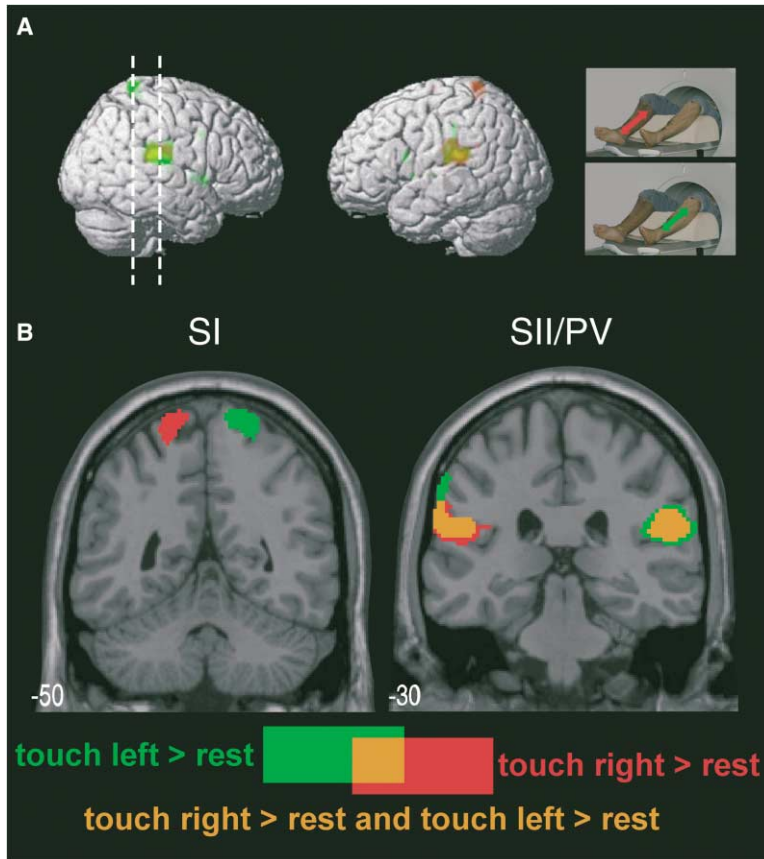
Figure 1. Somatosensory Activations

(A) Rendering on lateral views of the standard MNI single subject brain of the clusters activated by brushing the right leg (red) or left leg (green) determined using a random effect analysis of all 14 subjects of the first study (p < 0.001, uncorrected and k = 5). The intensity of the color reflects the distance from the cortical surface, with more superficial activations being brighter. The photographs to the right illustrate the respective locations on the subjects' legs stimulated by the experimenter.

(B) Coronal sections taken at y = −50 and y = −30 (as shown by the vertical bars in A) illustrating the location of SI and SII/PV, respectively. The term SII/PV is tentative and is used to refer to functionally defined area. Areas activated by the touch of both legs are shown in orange. SII/PV but not SI was therefore bilaterally activated.

of the lateral sulcus and extends laterally and dorsally toward the upper lip of the sulcus. The vision-of-touch area starts in the parietal convexity and extends ventrally into the lateral sulcus. The overlap region (white) therefore encompasses the upper lip of the lateral sulcus and extends ∼20 mm rostrocaudally (from y = −40 to y = −18; Figure 2B) totaling a volume of 2024 mm³ (=253 2 × 2 × 2 mm³ voxels) centered around x = −62,
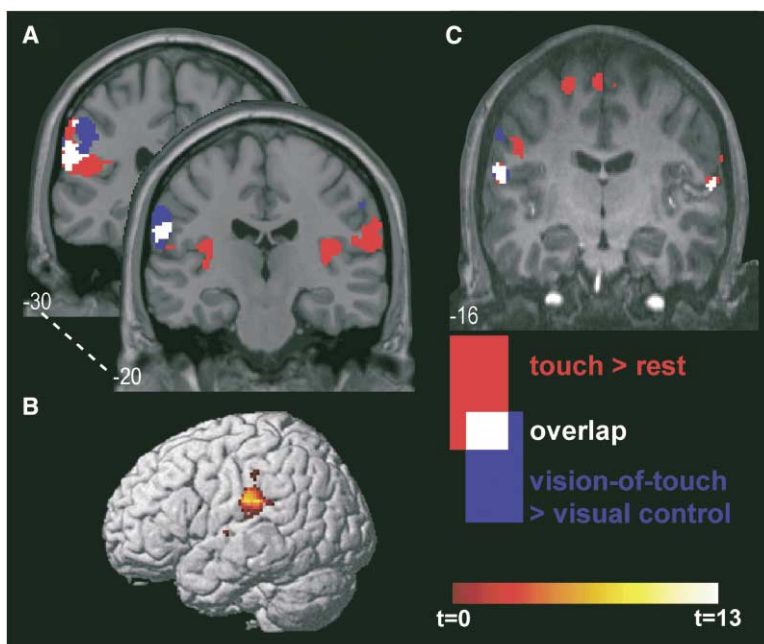

Figure 2. Overlap between Areas Activated by Touch and Areas Activated by the Vision-of-Touch

(A) Two coronal sections taken at y = −30 and y = −20 illustrate the extent of the overlap between visual and somatosensory activations. Areas activated only by the touch of the right or left leg are shown in red (touch-rest, p < 0.001, k = 5, random effect, n = 14 subjects); areas activated only by the vision-of-touch are shown in blue (vision-of-touch − visual control, p < 0.001, k = 5, random effect, n = 14 subjects); areas activated by both the touch and the vision-of-touch conditions are shown in white. Note that the overlap is lateralized to the left hemisphere.

(B) Rendering of the area of overlap on a lateral view of the brain. Only voxels significant in both the vision-of-touch − visual-control and the touch-rest contrasts are shown, with the color-coding reflecting the t values of the vision-of-touch − visual-control contrast.

(C) Illustration of the activations observed in a single subject at y = −16. Note that in this subject, the right hemisphere also shows overlapping somatosensory and visual activations (all conventions as in A, but based on the single-subject analysis).
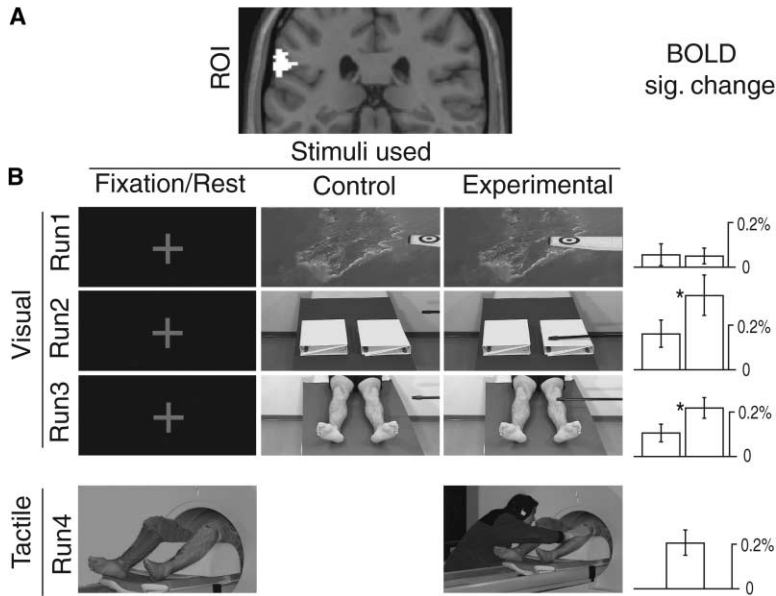
Figure 3. Results of the Second Experiment

(A) The location of the ROI is shown in white on a single coronal slice.

(B) Stimuli and results of the second study. The four rows correspond to the four functional runs of the second study. For the first three runs (top three rows), the stimulation conditions are illustrated by the fixation cross or a representative frame from the movies actually used in the experiment. For the tactile run (bottom row), no visual stimuli were used, and the conditions are illustrated by photographs taken in the actual scanner room showing either the position of the subject during the rest condition or the experimenter stimulating the legs in the experimental condition. The rightmost column shows bar graphs of the average BOLD signal changes (±SEM) relative to the fixation/rest condition (0 = fixation/rest). For the first three runs, this change is shown for the control and experimental conditions (as illustrated in the two preceding columns), while in the last run, results are shown as means of the touch-right and touch-left leg condition. All responses involving the vision of human legs or objects significantly differed from fixation (one-sided t test, all p < 0.02), but neither of the responses involving the wings did (p > 0.1). Asterisks indicate significantly larger BOLD signal changes for the experimental compared with the control condition (LSD planned comparison post hoc, p < 0.01).

y = −26, z = 24 in MNI space. Figure 2B shows a rendering of the region of overlap. This overlap in SII/PV was confirmed using a conjunction analysis (see Experimental Procedures). This analysis found one large cluster in the left SII/PV (k = 252, t_{max} = 13.61, x = −64, y = −24, z = 24) and one much smaller cluster (k = 7, t_{max} = 5.72, x = −46, y = −8, z = 4) in the posterior left insula.

While the group analysis reveals an overlap only in the left hemisphere, 7/14 participants showed voxels of overlap also in the right hemisphere when analyzed individually. Figure 2C illustrates an example of such a participant.

To check if SI or the right SII/PV show a trend toward being activated by the vision-of-touch, we lowered the threshold to p = 0.01 and k = 5 for the visual contrast, while leaving the threshold for the touch right/rest or touch left/rest contrasts unchanged. At this lenient threshold, we found 26 voxels in the left SI (t_{max} = 3.48, x = −18, y = −50, z = 68) and 85 voxels in the right SII/PV (t_{max} = 4.48, x = 68, y = −14, z = 28) to be significant. In the remainder of the manuscript, we will thus consider the left SII/PV as being the site of significant overlap between the vision-of-touch and the somatosensory conditions. The contralateral SII/PV and the left SI nevertheless show a trend in the same direction.

In order to confirm these findings using a different approach, for each subject we defined the right and left SI and SII/PV based on the results of the tactile runs. The mean activity of these regions of interest (ROI) was then analyzed during the visual runs. We found that in both hemispheres, the SII/PV ROIs showed significantly larger activity during the vision-of-touch compared to the visual-control conditions. The same was not true for the SI ROI. Since these results simply support the findings of the random-effect group analyses, we do not present the analysis further in this article.

Study II: Further Analysis of the Visual Responses in the Region of Overlap

After localizing the area of overlap, we designed a second study aimed at addressing two issues regarding our earlier findings. First, since we observed stronger activation in the visual areas of the occipital lobes during the vision-of-touch compared to the visual-control conditions, we needed to exclude that the stronger activation we found in SII/PV during the observation of the vision-of-touch compared to visual-control was not simply due to differences in the movement components of the movies. Second, to address the question of the specificity of the SII/PV activation for human legs, we needed to test whether SII/PV would also be activated if inanimate objects instead of human legs were being touched in the movies.

To address these questions, we monitored the mean BOLD signal in a region of interest (ROI) corresponding to the cluster of overlap defined in the first study (Figures 2 and 3A) while subjecting eight new participants to four new functional runs. Results are shown in Figure 3, as percentage BOLD signal change during the period of stimulation compared to a fixation or rest period. The last two functional runs (Figure 3B, bottom two rows) replicated the findings of the first study using identical stimuli in an independent population: the ROI was significantly activated by both the touch of the participants own legs and the observation of another individual's leg being touched. The remaining runs were designed to address the two abovementioned questions.

The Presence of Touch Is Necessary for the Activation of the Region of Overlap: Run 1

The vision-of-touch and visual-control movies used in the first study (Supplemental Movies S1 and S2 at http://www.neuron.org/cgi/content/full/42/2/335/DC1) differed in two ways: the presence and absence of touch

and the location in which the rod was moving (central for the vision-of-touch and peripheral for the visual-control). To exclude the possibility that the center-periphery difference in movement location was important, we modified these movies by replacing, frame by frame, the legs by islands and the rods by airplane wings (see Figure 3B, top row, and Supplemental Movies S3 and S4). This manipulation preserved the movement components of the original movies (eccentricity and velocity) but removed the "touch" component. Indeed, at debriefing, none of the subjects reported perceiving touch in those "wing-island" movies. The activation during the vision of these central and peripheral airplane wing movements did not differ from each other, nor did they differ from the activity during the fixation period. Our ROI therefore appeared only to be activated when subjects perceived touch—be it felt on their own body or seen to occur to someone else.

The Observation of Objects Being Touched Activates the Region of Overlap: Run 2

Here we measured the effect of replacing the legs of the actors in the movies by inanimate objects: rolls of paper towels and binders (Figure 3B, second row, and Supplemental Movies S5 and S6 at http://www.neuron.org/cgi/content/full/42/2/335/DC1). Results indicated that seeing even an object getting touched produced a significantly larger activation of the ROI compared to seeing the object being only approached. The critical stimulus for SII/PV activation therefore appears to be the perception of touch, be it the touch of an object, another human, or our own legs.

What Is Being Touched Does Not Matter as Long as Touch Occurs

The results of the three visual runs of the second experiment were analyzed quantitatively using a 2-way repeated measurement ANOVA with three targets (island, object, legs) × two conditions (touch versus nontouch, with central wing movements considered as "touch" and the peripheral ones as "nontouch"). A single mean BOLD signal change relative to fixation was entered for each condition and subject. This analysis revealed a main effect of target [$F_{(2,14)} = 4.1$, $p < 0.05$] and condition [$F_{(1,7)} = 6.8$, $p < 0.05$] and an interaction between target and condition [$F_{(2,14)} = 6.7$, $p < 0.01$]. An LSD post hoc test revealed no difference between the observation of central and peripheral wing movements ($p > 0.86$) but significantly larger activation to the observation of touch compared with nontouch ($p < 0.0003$ and $p < 0.007$ for the objects and legs, respectively). Repeating the ANOVA with only the objects and legs revealed only a main effect of condition ($p < 0.02$) but no interaction or main effect of object (both $p > 0.19$). For our ROI, there was no difference between observing human legs and objects getting touched. What mattered was the presence or absence of touch in the visual stimuli.

Study III: The Amplitude of Response Does Not Depend on the Perspective from which the Touch Is Observed

In a third experiment, we investigated how the perspective from which touch is observed affects the amplitude
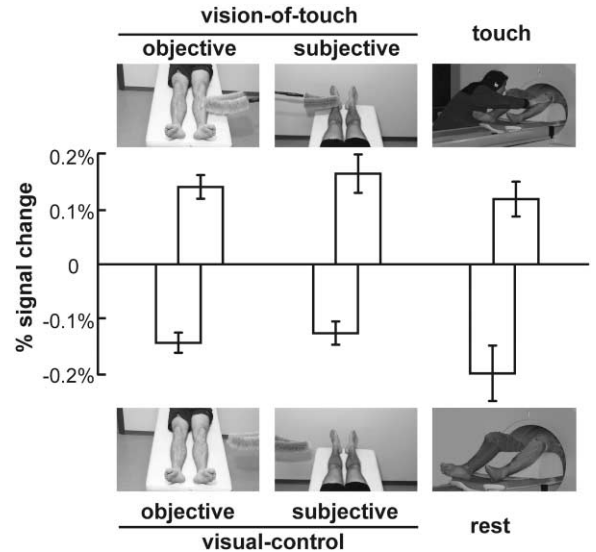

Figure 4. Results of the Third Experiment

Percent signal change relative to the mean BOLD activity for the visual (left two columns) and tactile (right column) runs. The leftmost column shows the results of the analysis of the blocks during which stimuli were presented from the objective perspective (i.e., as seen by another person). The vision-touch condition caused an increase (top) of the BOLD signal, and the visual control condition caused a decrease (bottom). The middle column shows not significantly differing results for the subjective perspective (i.e., as seen by the actor himself). The rightmost column indicates an augmentation of the BOLD signal when the left or right leg (averaged) of the participant is being touched, and a decrease during the rest period. Decreases should not be interpreted as inhibition, as the BOLD signal is expressed relative to the average of the run. A within-subject ANOVA considering all three columns with two conditions each revealed only a significant main effect of touch (top) versus nontouch [bottom, $F_{(1,6)} = 52$, $p < 0.001$] but no significant main effect of column (i.e., who is being touched and from where the event is seen, $p > 0.07$) and no significant interaction ($p > 0.87$).

of the visual activation in the region of overlap. Seven new subjects were scanned during two visual and two tactile runs. The tactile runs were identical to those of the first study. In the visual runs, subjects viewed the same vision-of-touch and visual-control movies of the first experiment intermixed with blocks in which the same events are filmed from a "subjective" perspective, seen from a camera positioned close to the face of the actor that is being touched (see Figure 4). The mean BOLD signal changes in the region of overlap are shown for all six conditions in Figure 4 relative to the mean BOLD signal of each run. As can be seen, the vision-of-touch condition produced larger BOLD signal changes than the visual-control condition independent of whether the movies are filmed from a subjective or an objective perspective. A 2 views (objective versus subjective) × 2 conditions (vision-of-touch versus visual-control) within subject ANOVA revealed a main effect of condition, with the vision-of-touch producing significantly larger BOLD signal changes [$F_{(1,6)} = 67$, $p < 0.001$] but no main effect of view [$F_{(1,6)} = 0.5$, $p > 0.49$] and no interaction between view and condition [$F_{(1,6)} = 0.04$, $p > 0.84$]. This clear-cut effect indicates that the BOLD signal change in the region of overlap does not depend on

how easily the observed touching event can be integrated into the body schema of the observer.

Discussion

In the first experiment, we mapped the primary and secondary somatosensory representations of the lower legs of our participants. The primary somatosensory representation was localized in the contralateral dorsal aspect of the postcentral gyrus. The secondary somatosensory representation was found in both the ipsi- and the contralateral frontoparietal operculum, extending laterally onto the convexity of the inferior parietal lobule. Most importantly, we found that the secondary somatosensory cortex was significantly more activated during the observation of movies of other people being touched compared to the observation of the same people not being touched. Indeed, activation of the secondary somatosensory cortex differentiated the two types of movies more consistently than any other brain area. In a second experiment, we showed that this region of overlap did not respond to the sight of objects (airplane wings) moving without causing the percept of touch. On the other hand, observing objects being touched activated the region of overlap in a way that was similar to the activation during the observation of legs being touched. In a third experiment, we finally show that this effect does not depend on the perspective from which the touch is seen.

The Human Secondary Somatosensory Cortex

A substantial number of imaging studies have localized the primary and secondary somatosensory areas in humans (Burton et al., 1993; Del Gratta et al., 2000; Disbrow et al., 2000; Gelnar et al., 1998). All of them agree that there is a secondary somatosensory representation in the fronto-parietal operculum, extending onto the lateral convexity of the inferior parietal lobule. The location of our secondary somatosensory activation is in agreement with that described by these investigations. In particular, the region of overlap we describe, lying on the upper lip of the lateral sulcus, is well within the SII or SII/PV locations found by Disbrow et al. (2000) and Del Gratta et al. (2000).

A topic of debate, on the other hand, is the presence or absence of a somatotopical organization within the human SII/PV. In a recent study, Disbrow et al. (2000) touched different body parts of their participants while measuring brain activity using fMRI. They found large overlaps between the representations of the different body parts, and they comment that unlike SI, SII/PV probably has the purpose of integrating information across body parts. Employing a subject-by-subject analysis on the center of mass of their activations, they were able to determine not one but two reliable somatosensory representations in the frontoparietal operculum: one anterior (PV) and one posterior (SII). The two representations are mirror symmetrical, forming a single cluster for the more distal body parts where they are directly adjacent, but two distinguishable clusters for the more proximal body parts. Both representations were roughly somatotopically organized, with the head being represented lateral to the foot, but the overlaps between different body parts were substantial. Simultaneously, Del Gratta et al. (2000) also used single-subject analyses and also found a rough somatotopical organization of SII/PV, although one subject actually showed a reversed somatotopy, with the hand being medial and the foot lateral. This latter study only found a single SII representation, probably because they only stimulated distal body parts. As we also stimulate a distal body part, we will use the term SII in our Discussion to describe our opercular somatosensory representation, although we are aware of the fact that our activation probably includes both SII and PV. Inspection of the data shown by those two experiments suggests, however, that a conventional random effect group analysis might not have evidenced a somatotopical organization of SII because of the differences between subjects. Indeed, Burton et al. (1993) using group analyses did not observe a somatotopical organization of SII. As a result, in the present paper we did not attempt to determine the somatotopy of the experience and observation of touch, but concentrated on establishing the presence of an overlap between the observation and the experience of touch per se. It will remain for future investigations to establish if there are differences between the localizations of the activations during the observation of different body parts being touched.

Anatomy and Connectivity of SII

Little if anything is known about the connections of area SII in humans. Based on comparing single-cell recordings in macaque monkeys (Krubitzer et al., 1995) and fMRI experiments in humans, Disbrow et al. (2000) concluded that the human SII/PV is probably the functional homolog of the monkey's SII/PV. Independently, Brodmann (1909), using cytoarchitectonic criteria, came to the same conclusion. He described a subcentral zone (BA43) in humans and commented that "monkeys also possess a specific structural field on the Rolandic operculum corresponding to the subcentral area of man" (p. 130). Von Economo and Koskinas (1925) and Vogt (1911) came to similar anatomical conclusions. Accordingly, findings regarding the connectivity of the primate SII might be directly relevant for our interpretation of the human SII.

Cipolloni and Pandya (1999) investigated the cytoarchitecture and connectivity of the frontoparietal operculum of macaque monkeys. Their injection of retrograde tracers into the caudal sector of the parietal operculum, an area probably corresponding to the functionally defined SII/PV complex, indicated that it receives somatosensory, visual, and polysensory informations, coming from the primary somatosensory cortices, from extrastriate visual areas (TPO and MST), and from polysensory areas of the posterior parietal lobe (PF and the cortices lining the intraparietal sulcus), respectively. Cipolloni and Pandya (1999), therefore, conclude that "the caudal opercular cortex may integrate somatosensory information with other sensory modalities" (p. 450). In addition, the putative SII/PV is known to entertain strong reciprocal connections with the ventral premotor areas F4 and F5 (Cipolloni and Pandya, 1999; Matelli et al., 1986) and the prefrontal cortex (BA 46; Cipolloni and Pandya, 1999). Interestingly, two of the cortical areas

with which SII is reciprocally connected, PF and F5, are known to contain mirror neurons, i.e., neurons responding during both the execution and observation of goal-directed actions (Gallese et al., 1996, 2002; Rizzolatti et al., 1996). These connections, together with the connections with MST and TPO, could provide neurons in SII with the information necessary for responding to both the experience of touch and the observation of someone or something else being touched.

Most recently, a cytoarchitectonic parcellation of the human SII challenged the idea of a single region. Eickhoff et al. (2002) analyzed the cytoarchitectonic organization of the human parietal operculum using quantitative cytoarchitectonic parameters. He determined four subareas, labeled OP1–4: two medial areas (a caudal OP2 and a rostral OP3) and two lateral areas extending onto the convexity of the parietal lobe (a caudal OP1 and a rostral OP4). Our region of overlap appears to fall within OP1. We will discuss the functional relevance of this parcellation below.

Polymodal Integration in the Secondary Somatosensory Cortex

The function of SII is still poorly understood. In the past, SII was considered to be a higher-order, but purely somatosensory, area (Robinson and Burton, 1980). It was thought to play an important role in the learning of tactile discriminations and the recognition of shape from tactile information (Garcha and Ettlinger, 1980; Servos et al., 2001). Indeed, the most prominent symptom after lesions of SII in humans is tactile agnosia (e.g., Caselli, 1993), an incapacity to recognize objects by touch. More recently, investigations of the anatomical connections (see above) identify SII as a site of integration between somatosensory information and information stemming from other senses. This hypothesis was confirmed in a recent fMRI study (Bremmer et al., 2001) in which participants were exposed to moving stimuli using three different modalities. They received either a puff of air on their face, viewed random dots moving in the tangential plane, or heard a sound moving sideways. The authors identified three clusters in the brain that seemed to process all three modalities: the ventral premotor cortex, the intraparietal sulcus, and the upper lip of the lateral sulcus. The latter of these clusters was in a location very similar to our zone of overlap (his $x = -64$, $y = -18$, $z = 30$). The functional significance of this integration is evident in our everyday experience: whenever a bus passes in front of us, we feel the draft of air it causes, hear its sound passing from left to right, and see it moving in a tangential plane. The joint responses of this cluster to the tactile, visual, and auditory modality may thus reflect the fact that these three types of information often occur simultaneously in the natural world, when something is moving in our immediate vicinity.

Evidence for nontactile input to SII comes also from studies of the expectation of touch. Carlsson et al. (2000) instructed their participants to look at a screen. A green square meant that nothing was going to happen, whereas a red square meant that they were soon going to be tickled on their right foot. They observed an activation of SII in response to the red square even in the absence of the tickling stimulus, demonstrating that SII

can respond to the mere expectation of a somatosensory stimulus indicated by a visual stimulus. It should be noted, however, that the visual stimuli that caused responses in SII in this latter study predicted touch to occur to the participants themselves.

SII and the Sight of Touch

In the current experiment, we show that the sight of human legs being touched, or that of objects touching each other, both activate a section of SII that is also activated when the participant's leg is being touched. The same area is not activated by the sight of similar movements not leading to touch, as was the case for the airplane wings. In our hands, the main difference between the stimuli not activating SII and those successful at activating it was the absence or presence of touch, respectively. The complexity of all the stimuli was similar. In particular, the movement components between the central airplane wings and the vision-of-touch stimuli were deliberately matched, yet the SII response clearly differed. The anatomical and functional investigations discussed above indicate that SII receives visual input. The peculiarity of our present finding is the fact that SII was not activated by stimuli that predict touch soon to occur to the participants (as in Carlsson et al., 2000), nor by stimuli such as random dots moving close to the subject that might often be accompanied by drafts of air (Bremmer et al., 2001). Instead, the zone of overlap we observed was activated by touch occurring to *another* individual or to an object.

Evidence for the fact that observing touch can activate the secondary somatosensory cortex also comes from a recent fMRI study investigating the cortical areas activated during the observation of a human arm grasping an object (Grezes et al., 2003). These authors observed that while participants looked at a human arm grasping (and hence touching) an object, SII was activated. In the light of the present findings, their activation of SII might reflect the detection of the touch between the hand and the object.

It is intriguing to note that both Bremmer et al. (2001) and we found only the lateral aspect of SII to be activated by visual stimuli. The mediolateral differences observed by Eickhoff et al. (2002) in the cytoarchitecture of SII might therefore reflect functional differences: the medial SII might be purely somatosensory while the more lateral SII appears to be multimodal. How such functional differences can be reconciled with the more traditional idea of a single somatotopical representation in SII remains a topic for future investigations.

How might the observation of touch be associated with the activation of SII? This matching of seen and experienced touch might be inborn. Alternatively, it might result from Hebbian learning. When we observe ourselves being touched, the activation of somatosensory neurons will overlap in time with the activation of visual neurons that represent the visual stimulus of the touching event. Hebbian learning rules predict that this correlation in time should lead to a strengthening of the synapses between these neurons. After repeated experience, the sight of a touch might be enough to trigger activity in the secondary somatosensory neurons—a mechanism similar to the one we have described for mirror neurons

(Keysers et al., 2003). As remarked above, visual information about touch could reach SII either through the inferior parietal lobule, the intraparietal sulcus, MST, or TPO, all of which have visual responses and are known to be connected with the monkey's functional SII.

Attention and Mental Imagery—a Critical Discussion of Our Results

We tested the observation of different types of touch, including touch of a body part and of different objects, and confronted these conditions against a similar visual stimulus not producing the percept of touch. We found SII activation only for the stimuli correlated with a percept of touch. Indeed, the statistically strongest difference between the observation of touch and the observation of nontouch was found to be in SII. While one might argue that stimuli containing touch are more salient and attract more attention than otherwise similar stimuli, it is hard to explain why SII should be selectively affected by this attentional bias.

Our participants were not explicitly instructed to imagine what the object or individual in the movies was feeling. Indeed, at debriefing, we asked our participants if they voluntarily imagined the sensations that the actors or objects may have felt while being touched. All participants reported that they did not. Nevertheless, our SII activation was systematic enough to reach a very high significance level (peak t > 13) in a random effect analysis. Given that random effect analyses are explicitly designed to exclude effects that are not systematic over the sample, it is therefore unreasonable to interpret the present activations as reflecting occasional *voluntary* mental imagery. Therefore, it appears more reasonable to submit that our activation reflects a systematic tendency of our brain to transform the visual stimulus of touch into an activation of brain areas involved in the processing of our own experience of touch. This "automatic" activation is similar to the one observed in premotor and posterior parietal cortex during the observation of actions (Buccino et al., 2001; Iacoboni et al., 1999; Rizzolatti et al., 2001). It should be noted, though, that the automatic activation we observe may share some mechanisms with the mental imagery of touch, in that both involve a "simulation" of touch (i.e., SII activation "as if" the person was being touched) in the absence of a *real* tactile stimulus (Gallese, 2003).

The Shared Circuitry

The present experiment demonstrates that the secondary somatosensory cortex activated when the participant is being touched (first person experience) is also activated when the participants view someone or something else being touched (third person experience). SII therefore appears to be part of a circuitry that is shared between the first and third person experience.

This finding should be viewed in the context of examples stemming from other domains where the first and third person experience share a common circuitry (see Gallese, 2003, for a review). As mentioned above, when we execute a goal-directed action, we activate specific parietal and premotor areas. Some of these areas are also activated during the observation of someone else performing similar actions (Buccino et al., 2001; Iacoboni

et al., 1999; Rizzolatti et al., 2001). When we feel disgust, for instance because we are exposed to a disgusting smell, we activate a number of cortical areas including the insula. Some of these areas, in particular the insula, are also activated when we observe the disgusted facial expressions of others (Phillips et al., 1999; Krolak-Salmon et al., 2003; Wicker et al., 2003). Lesions in the insula indeed make it difficult for us to recognize disgust in others (Calder et al., 2000; Adolphs et al., 2003). Finally, the experience of a needle pricking our finger activates neurons in the cingulate cortex. Some of these neurons are also active when we observe someone else pricking his finger (Hutchison et al., 1999).

The current finding suggests that the lateral aspects of SII might provide yet another shared circuitry between experience and observation, between first and third person experience. But this shared circuitry is not limited to the social world. Indeed, in everyday language, we can say, "The tree's branch is touching the window." We instinctively employ the same word as we would use to say, "She touched my leg" or "She touched his leg." We demonstrate that the sight of objects touching each other evokes activation in the same brain area responding when we are touched and when we see someone else being touched. This finding might suggest that the experience of *any* kind of touch might be associated in the brain with the activation of a part of the neural networks involved in our own subjective experience of touch. What remains to be investigated is how similar the result of the activation of SII is to our actual experience of touch. Whether the automatic SII activation we observe reflects an abstract activation of the idea of touch or something closer to the somatosensory sensation of touch remains to be determined. An interesting finding, though, is that electrostimulations in SII elicit sensations of "tingling" (Penfield and Jasper, 1954, p. 82), "shiver," or "pricking" (p. 79). Two of our subjects reported that they could almost feel a sensation of touch while looking at the movies, but all subjects clearly knew that they were not actually being touched during the observation of touch. It might be that SII activation in the context of weak SI activation only evokes a concept of touch that is relatively detached from our own immediate bodily experience, much like our imagination of the face of a loved person is not confused with the actual vision of the same person. Interestingly, there is an anecdotal case report regarding a patient that indeed mistook painful events that he saw with pain occurring to himself. Postmortem, his wife reported, "If I slightly knocked my finger, spontaneously showing him, he would immediately grasp his own finger and say "don't do that" (meaning not to show him); he actually felt it. If I merely commented (that I had knocked my finger), there was no such reaction" (Bradshaw and Mattingley, 2001). Unfortunately, there are no indications of the locations of the cortical lesions for this patient. It remains to be determined to which extent SII activations contribute to our understanding of the notion of touch in general. In particular, a testable prediction from our findings is that bilateral SII lesions should result in some changes of the way we would perceive touch in others, much like insula lesions result in an impairment of the detection of disgust in the facial expressions of others (Calder et al., 2000; Adolphs et al., 2003).

The current results therefore support the notion that both animate and inanimate touch activates our inner representation of touch. It is important at this point to clarify the fact that we do not believe that the activation we observe evolved in order to empathize with other objects or human beings. We do not know how or why this system evolved. It might be an overgeneralization of a system initially evolved to integrate the sensation of touch with the vision of our own body being touched, allowing the organism to visually anticipate the sensation of touch.

An alternative account is that our activation reflects an integration of other human beings or objects into our own body schema. In this case, the discrepancy between the visual input and the lack of somatosensory consequence may be an important factor for the activation. We tested three visual stimuli in which touch occurred: an objective and a subjective perspective of another human being and the objective perspective of an object being touched. All three cases determined activations in the region of overlap that did not differ significantly. This finding is hard to reconcile with the notion of integration in the body schema, as one would assume that there is a parametric variation in our conditions regarding how easily the visual stimulus could be integrated in the body schema, with the subjective view of legs being easiest and the objective view of objects such as binders being hardest to integrate. The activation we observed, though, was not affected by this manipulation, suggesting that no matter how or why the visual stimuli activate SII, they do so in a way that appears unaffected by what is being touched and how easily it can be integrated into our body schema.

An Implicit Understanding of Actions, Emotions, and Sensations—a Tentative Account

Together, these findings support the idea that we possess a shared circuitry in our brain dealing both with our personal experience of touch and with the corresponding event occurring to other living beings and inanimate objects. An intriguing finding of the present investigation is the fact that this shared circuit appears also to be activated while we observe objects being touched. We would therefore like to propose that the activation of such a shared circuit while we observe the events occurring in the world around us might form an intuitive and automatic key to an implicit understanding of touch. Equipped with such a shared circuit for touch, when we witness touch, we do not just *see* touch but also *understand* touch through an automatic link with our own experience of touch. The brain implicitly transforms the sight of touch into the inner representation of touch. This automatic system, of course, does not exist in isolation: it functions in the context of a complex cognitive system that can integrate these activations with cognitions. This integration is very different when we observe an object being touched, of which we know that it has no inner life, and when we see another human being. But the shared circuitry appears to be similar in these two cases.

In the context of the existing results on actions and emotions, one might speculate that the brain is parsimonious: it uses the same mechanism of shared circuitry

for actions, emotions, and sensations (see the Shared Manifold Hypothesis, Gallese, 2003).

Experimental Procedures

Subjects
Fourteen healthy right-handed volunteers (22–28 years of age, 6 females and 8 males), screened for neurological and psychiatric antecedents, participated in the first experiment; 8 participated in the second experiment and 7 in the third. Handedness was assessed by means of the Edinburgh questionnaire. All subjects had normal or corrected-to-normal vision. The subjects participating in the study provided informed written consent, and the experiment was approved by the local ethic committee and conducted according to French regulations on biomedical experiments on healthy volunteers. Subjects were informed about the aim of the study only after the study.

fMRI Data Acquisition
Images were acquired using a 3T whole-body imager MEDSPEC 30/80 AVANCE (Brucker, Ettlingen, Germany) equipped with a circular polarized head coil. For each participant, we first acquired a high-resolution structural T1-weighted anatomical image (inversion-recovery sequence, $1 \times 0.75 \times 1.22$ mm) parallel to the AC-PC plane, covering the whole brain.

For functional imaging, we used a T2*-weighted echo-planar sequence at 30 interleaved 3.5 mm thick axial slices with 1 mm gap (TR = 3000 ms, TE = 35 ms, flip angle = 80°, FOV = 19.2×19.2 cm, 64×64 matrix of 3×3 mm voxels).

Stimuli and Conditions for the First Study
Four functional runs (two tactile and two visual) were acquired for each subject in randomized order. 8/14 subjects were tested with two tactile runs followed by two visual runs, and 6/14 were tested with two visual runs followed by two tactile runs. In tactile runs, subjects were instructed to close their eyes, and an experimenter entered the scanner room and stimulated with a washing glove the anterior lower legs of the subject. Tactile runs consisted of three types of blocks: 24 s blocks of up and down brushing of the left leg (left tactile), 24 s brushing of the right leg (right tactile), or a 24 s rest block (rest). Brushing frequency was approximately 0.3 Hz.

In visual runs, the subject was instructed to look at a projection screen seen through a mirror. Visual runs consisted of four types of visual stimulation blocks separated by rest periods of blank screen. Visual blocks of 24 s were built as a succession of 6 films of 3 s, separated by 1 s of black screen, each showing in half of the cases a male and in half of the cases a female wearing short trousers lying on a medical examination bed. In right vision-of-touch blocks (Supplemental Movie S1 at http://www.neuron.org/cgi/content/full/42/2/335/DC1), a wooden rod, a metal rod, or a brush was slid up and down along the anterior lower right leg of the actors. In left vision-of-touch blocks, the left leg was stimulated. In right and left visual-control blocks (Supplemental Movie S2), the objects performed a similar trajectory but without touching the legs of the actors. All four blocks were repeated twice in each run using a randomized sequence. For analysis, the left and right vision-of-touch blocks were pooled together, i.e., treated as variants of a single, vision-of-touch condition. The same was true for the visual-control condition. This was done after analyzing the variants separately without finding any systematic difference. Considering the two runs, eight repetitions of each condition were therefore collected for each subject.

Stimuli and Conditions for the Second Study
The second study was composed of four functional runs (see Figure 3). These runs were arranged in order of increasing "touch," i.e., their order went from stimuli not related to touch to the touching of the subject's own leg. The first three runs were visual, and the last was tactile.

The three visual runs lasted for 648 s each and only differed by the movies used (see Figure 3). All three used a 24 s on, 3 s off block design with three conditions in pseudorandom order. The 3 s off period consisted of a black screen. Each run contained eight

repetitions of each condition. One of the conditions was always a fixation condition in which subject had to fixate a red cross for the entire 24 s. The two additional conditions depended on the run.

Run 1: Airplane Wings

Here the two additional conditions depicted airplane wings moving up and down over an island. The aim of the stimuli was to be similar to the movies of the first study in terms of movement, but without giving the impression of touch. The movies were obtained by substituting the rods of the original movies by airplane wings and the legs by an island. To that end, we analyzed the trajectory of the rod and the position of the legs in the original movies. We then reconstructed a similar trajectory for the island and the airplane wing using a commercial photo-editing program. These frames were then transformed into a movie. In analogy to the two types of legs and three types of rods used in the first study, three airplane wings and two different islands were used. The results were movies of airplane wings moving up and down in the periphery of the screen ("peripheral wings," corresponding to the visual-control movies of the first study) or moving near the center of the screen ("central wings"). As in the first study, in four blocks the wings moved in the right half of the screen, and in four blocks they moved in the left half of the screen, arranged in pseudorandom order.

Run 2: Objects

Here the two additional conditions depicted objects being touched. These movies had been filmed at the same time as the movies of the first study, using the same setting, but replacing the female legs with rolls of paper towels and the male legs with piles of office binders. The same three objects were used to touch these leg-substituting objects. The two additional conditions of this run are therefore labeled vision-of-object-touch and visual-object-control. Again, in half the blocks, the rods moved in the right side of the screen, and in half from the left side.

Run 3: Human Legs

Here the movies of the first study were used. The additional conditions were therefore vision-of-touch and visual-control.

Run 4: Tactile

Due to the strong tactile signal obtained in the first study, we reduced the length of the tactile stimulation blocks to 12 s. Again, an experimenter entered the scanner room and used a washing glove to brush up and down along the anterior lower leg of the subject. The three conditions were 12 s of brushing up and down on the subject's left leg ("touch left"), 12 s of up and down on the right leg ("touch right"), and 12 s without any event ("rest"). There was a 3 s pause between blocks, and blocks were arranged in pseudorandom order. 12 repetitions of each condition were acquired in a single run lasting 683 s.

Runs 3 and 4 were therefore replications of the first study. All subjects were tested using the same order of runs to avoid the fact that runs 3 and 4, which involve the touching of a leg, could bias the interpretation of the stimuli used in runs 1 and 2.

Stimuli and Conditions for the Third Study

Seven new subjects were tested in two tactile and two visual runs. Tactile runs were identical to those of experiment 1. In the visual runs, the subject was instructed to look at a projection screen seen through a mirror. Visual runs consisted of four types of visual stimulation blocks separated by 3 s rest periods of blank screen. Each visual block lasted 24 s and was built as a succession of 6 films of 3 s, separated by 1 s of black screen. Within each block, the films showed a male (in half of the cases) and a female (in half of the cases) wearing short trousers lying on a medical examination bed. Two of the visual conditions were identical to those of the first study, showing the actor being touched (objective vision-of-touch) or only approached (objective visual-control) by the different objects. In the two remaining conditions (subjective vision-of-touch and subjective visual-control), the same events were shown from a "subjective" perspective, with the camera placed close to the head of the actor being touched. When seen through the mirror inside the scanner, this subjective view created a perspective that was similar to the participant seeing his/her own legs being touched. As in the first study, each condition was repeated four times within each run, with half of the repetitions showing objects approaching or touching the left leg of the actor and half the right leg. The right and left variants of each condition were analyzed together.

Group Data Analysis of the First Study

The first study was analyzed using standard SPM99 (http://www.fil.ion.ucl.ac.uk) procedures. Briefly, every subject's functions volumes were adjusted for differences in slice timing, spatially realigned to the first volume of this subject, and then transformed to match the MNI EPI template using a $2 \times 2 \times 2$ mm voxel resolution. The images were then smoothed using a $6 \times 6 \times 6$ mm filter and analyzed using rest, touch-left, and touch-right as effects of interest for the tactile runs, and vision-of-touch and visual-control for the visual runs using boxcar functions convolved with the hemodynamic response function after 120 s high-pass filtering. A standard random effect analysis was then performed. The touch-right minus rest, touch-left minus rest, and vision-of-touch minus visual-control t contrast images were created for each subject. Using all 14 subjects, a voxel-by-voxel t map was computed for each of these three contrasts using the student t distribution with df = 13 to determine voxels with contrasts significantly differing from zero. Clusters of less than 5 voxels were ignored. To look for overlaps between tactile and visually activated brain areas, a voxel was considered to be part of the overlap if it was both somatosensory and visual. In this analysis a voxel was called "somatosensory" if it was considered significantly activated in the touch-right minus rest or in the touch-left minus rest contrast, and "visual" if it was significantly activated in the vision-of-touch minus visual-control condition. Unfortunately, there is at present no established statistical method to estimate the likelihood of finding such voxels of overlap based on random effect analysis.

Conjunction Analysis

We used the same modified conjunction analysis developed in Wicker et al. (2003). Using SPM99, we calculated two t maps, one for the visual conditions and one for the somatosensory conditions, and we performed a conjunction analysis between those two t maps. The visual t map was obtained using standard random effect analysis: for each voxel, the mean vision-of-touch − visual-control contrast value across subjects was compared against 0. The somatosensory t map needed to reflect areas activated by touch to the right or left leg. We therefore calculated one random-effect t map for the touch-right − rest and one for the touch-left − rest contrast, and then calculated voxel-by-voxel the maximum of the two t values to operate a logical "or." We then calculated the conjunction analysis between the visual and somatosensory contrast at 0.001 and k = 5 (uncorrected) at the third level. As described in Wicker et al. 2003, we then masked this conjunction map with both the visual and somatosensory contrast, each at 0.001 and k = 5 to ensure that only voxels common to both maps are accepted in the analysis.

Single-Subject Analysis of the First Study

The random effect group analysis revealed a cluster of overlap with peak t value at −62, −26, 24 in the left hemisphere. To test if single subjects showed voxels of overlap also in their right hemisphere, we analyzed each subject of the first study separately. We used the same thresholds and criteria used for the group analysis but applied it to each single-subject analysis using the standard SPM t test, with p < 0.001 and k = 5. A subject was considered to show overlap in the right hemisphere if he/she had voxels common to the vision-of-touch minus visual-control t contrast and the touch-right minus rest or touch-left minus rest t contrast within 10 mm of the MNI coordinates 62, −26, 24. These coordinates were chosen as the right hemisphere counterpart of the region of overlap in the left hemisphere (i.e., by changing the fore sign of the x coordinate of the peak t value of the overlap in the left hemisphere). This spatial restriction was imposed to reduce the probability of including chance occurrences of overlap.

Data Analysis for the Second Study

The second study was not aimed at a whole brain approach; instead, it was designed to determine parameters important for the activation of the region of overlap defined in the first study. Accordingly, the preprocessing of the functional images was identical to that of the first study, but the statistical analysis was different. Every subject's functional volumes were adjusted for differences in slice timing and then transformed to match the MNI EPI template using a $2 \times 2 \times$

2 mm voxel resolution. The images were then smoothed using a $6 \times 6 \times 6$ mm filter. From there on, the analysis differed from the first study. We used the region of overlap of the first study as a region-of-interest (ROI, volume = 2024 mm³). Using the toolbox MarsBar (http://marsbar.sourceforge.net; Brett et al., 2002), we extracted the mean raw BOLD signal in this ROI for each functional volume of the second study. A temporal high-pass filtering with t = 120 s for each of the four functional runs was applied.

For the three visual runs, the resulting univariate time series were analyzed using methods introduced by Kanwisher and collaborators (e.g., Downing et al., 2001). Briefly, for each run and subject, the mean activity in each of the three conditions was measured as the mean BOLD signal in the volumes 2 to 8 following the beginning of each condition. The TR being 3 s, we ignored the first volume to allow for the hemodynamic response lag, while all other volumes are treated equally. The mean signal in the two conditions of interest (peripheral and central wings for run 1, vision-of-object-touch and visual-object-control for run 2, and vision-of-touch and visual-control for run 3) were expressed as percent signal change relative to the mean BOLD signal in the fixation period. This analysis results in a single grand mean percent signal change value for each of the conditions of interest for each subject. These values were then analyzed using a two-way repeated measurement ANOVA, with three targets (islands, objects, human legs) $\times$ 2 conditions (touch versus nontouch, with the central and peripheral wings considered as touch and nontouch, respectively; the labels touch and nontouch are therefore arbitrary, as touch never really occurred for the island overflown by the wings). Pair-wise planned contrasts between the two conditions of each target were then calculated using the LSD test to check if central wings > peripheral wings, vision-of-object-touch > visual-object-control, and vision-of-touch > visual-control. Using another post hoc (e.g., Newman-Keuls) yielded similar results. Finally, we tested if conditions deviated from baseline by performing a one-tailed t test testing the null hypothesis that the mean signal change compared to baseline is equal or smaller than 0.

Data Analysis for the Third Study

The analysis of the visual and tactile runs was done using methods very similar to the second study, except for the following changes. First, given that the tactile blocks lasted 24 s, just like the visual runs, all conditions were averaged from the 2nd to the 8th TR. Second, as we used no fixation condition in the third study, % signal changes are expressed relative to the mean BOLD activity of the entire run from which they were taken. Finally, the data were analyzed using two ANOVAs, as described in the text and Figure 4.

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