A Sensorimotor Network for the Bodily Self

Francesca Ferri[1], Francesca Frassinetti[2,3], Martina Ardizzi[1], Marcello Costantini[4,5], and Vittorio Gallese[1,6]

Abstract

■ Neuroscientists and philosophers, among others, have long questioned the contribution of bodily experience to the constitution of self-consciousness. Contemporary research answers this question by focusing on the notions of sense of agency and/or sense of ownership. Recently, however, it has been proposed that the bodily self might also be rooted in bodily motor experience, that is, in the experience of oneself as instantiating a bodily structure that enables a specific range of actions. In the current fMRI study, we tested this hypothesis by making participants undergo a hand laterality judgment task, which is known to be solved by simulating a motor rotation of one's own hand. The stimulus to be judged was either the participant's own hand or the hand of a stranger. We used this task to investigate whether mental rotation of pictures depicting one's own hands leads to a different activation of the sensorimotor areas as compared with the mental rotation of pictures depicting another's hand. We revealed a neural network for the general representation of the bodily self encompassing the SMA and pre-SMA, the anterior insula, and the occipital cortex, bilaterally. Crucially, the representation of one's own dominant hand turned out to be primarily confined to the left premotor cortex. Our data seem to support the existence of a sense of bodily self encased within the sensorimotor system. We propose that such a sensorimotor representation of the bodily self might help us to differentiate our own body from that of others. ■

INTRODUCTION

In everyday life, we move, see, and feel our body and have no doubt that it is our own. Any experience of our body provides us with a variety of information related to it, such as our visual, tactile, and, more generally, physiological state. Besides the distinction between exteroceptive, interoceptive, and proprioceptive awareness, what is the basic experience of our body as a bodily self? What enables us to implicitly distinguish our body from other human bodies (Ferri, Frassinetti, Costantini, & Gallese, 2011; Frassinetti, Ferri, Maini, Benassi, & Gallese, 2011; Frassinetti et al., 2009, 2010; Frassinetti, Maini, Romualdi, Galante, & Avanzi, 2008)? Recently, it has been proposed that the bodily self can be conceived as motor in nature (Gallese & Sinigaglia, 2010; Legrand, 2006), that is, based on the experience of our own body parts according to their motor potentialities, as they are represented in a motor bodily format (see Gallese & Sinigaglia, 2011). Accordingly, Smith (2007) explained the concept of bodily self as follows: "The bodily self is a physical agent. Knowledge of oneself as bodily is fundamentally knowledge of oneself as agentive; such knowledge is grounded in both experience of oneself as instantiating a bodily structure that affords a limited range of actions, and experience of oneself as a physical agent that tries to perform a limited range of actions over time" (p. 4).

The existence of such motor-experience-based representation of the bodily self has been investigated at the behavioral level in a previous study from our group (Ferri et al., 2011). In that study, right-handed participants underwent a laterality judgment task using rotated hand stimuli, where the hand to be judged could either be the participant's own hand or another person's hand. The results showed faster RTs when judging one's right hand compared with all the other hand stimuli, regardless of the magnitude of the rotation. According to previous studies (Frassinetti et al., 2008, 2009, 2010), we named this effect "self-advantage." Moreover, Ferri and colleagues (2011) found that self-advantage does not emerge when participants are asked to explicitly recognize the owner of the observed hand. On the basis of these empirical data, we argued in favor of the assumption that an implicit motor representation of the bodily self exists and that it might help us in distinguishing one's own from others' body, thus leading to the effect of self-advantage.

In this fMRI study, we tested the hypothesis that the sensorimotor system plays a pivotal role in the implicit self/other distinction during the laterality judgment task and, more specifically, in the self-advantage for right hand in right-handed participants.

We adopted the laterality judgment task because it is now accepted that, to perform it, one simulates a motor

[1]University of Parma, [2]University of Bologna, [3]IRCCS - Istituto Scientifico di Castel Goffredo, Mantova, Italy, [4]University G. d'Annunzio, Chieti, Italy, [5]Foundation University G. d'Annunzio, Chieti, Italy, [6]Italian Institute of Technology

rotation of her own hand. Such simulation shares the same temporal and kinematic properties with actual body rotation in space (Parsons, 1994). The linear increases in both RTs (Cooper & Shepard, 1973) and BOLD signal (Milivojevic, Hamm, & Corballis, 2009), as a function of angular displacement of the stimulus, are "hallmarks" of this mental process. Furthermore, slope and intercept of the described linear regressions are thought to reflect the efficiency on the task (Christova, Lewis, Tagaris, Ugurbil, & Georgopoulos, 2008; Ionta, Fourkas, Fiorio, & Aglioti, 2007; Shepard & Cooper, 1982), depending on the actual mental rotation process (rotational factor) and more general processes (nonrotational factors) occurring before or after mental rotation proper (Shepard & Cooper, 1982), respectively.

If a motor-experience-based representation of the bodily self does exist, likely leading to the self-advantage, measures of the rotational factors in right-handed participants should reveal higher efficiency (i.e., slower slope) for the actual mental rotation of one's own right hand compared with all the other hand stimuli. Such modulation should be found within the sensorimotor nodes of the network recruited during the laterality judgment task.

Neuroimaging results associated with this task, using both corporeal and noncorporeal stimuli, showed activation in several dominant spatial–motor processing regions, including the posterior parietal (superior parietal and the intraparietal sulcus), premotor and primary motor cortices, the SMA, and the cerebellum (Podzebenko, Egan, & Watson, 2005; Seurinck, Vingerhoets, de Lange, & Achten, 2004; Vingerhoets, de Lange, Vandemaele, Deblaere, & Achten, 2002; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Alivisatos & Petrides, 1997; Cohen et al., 1996; Parsons et al., 1995).

As far as parietal activations are concerned, Bonda, Petrides, Frey, and Evans (1995) proposed that areas of the superior and inferior parietal cortex are components of a neural system underlying a constantly updated representation of the body in space. This interpretation is supported by evidence that parietal lesions are associated with disorders of body schema, personal space, and left/right orientation (DeRenzi, 1982).

With relation to premotor regions, a dissociation has been found between mental rotation of body parts and mental rotation of noncorporeal objects (Arzy, Overney, Landis, & Blanke, 2006; Kosslyn et al., 1998). The selectivity of premotor regions for the mental rotation of corporeal stimuli has been shown by Arzy and colleagues (2006). They investigated the performance of a patient with a lesion centered on the right premotor cortex experiencing asomatognosia, a deficit of corporeal awareness, in two tasks requiring the mental rotation of hands and letters, respectively. They found an impairment in the mental rotation of body parts while the mental rotation of letters was preserved. These data suggest a pivotal role of the premotor cortex in corporeal awareness. Given the higher specificity of the premotor cortex for the

mental rotation of body-related stimuli and considering its role in body awareness (Arzy et al., 2006; Berti et al., 2005; Ehrsson, Spence, & Passingham, 2004), it is plausible to hypothesize that this brain area may represent one of the essential anatomical and functional basis for the motor aspect of bodily selfhood.

METHODS

Participants

Eighteen volunteers (9 women and 9 men; mean age = 24 years, range = 21–34 years) took part in this study after giving written informed consent. All were right-handed as defined by the Italian version of the Edinburgh Inventory (Oldfield, 1971). They had normal or corrected-to-normal visual acuity and were naive as to the purposes of the experiment. The experimental protocol was approved by the ethics committee of the University of Parma.

Apparatus

All images were collected with a 3T GE scanner operating at the University of Parma. Participants lay supine in the scanner with the response buttons (Resonance Technology, Inc., Northridge, CA) under their index fingers. Visual stimuli were presented by means of a head mounted display with a resolution of 800 horizontal pixels × 600 vertical pixels (Resonance Technology, Inc.). Sound-attenuating headphones were used to muffle scanner noise. The presentation of the stimuli and the recording of the participants' responses were controlled by E-Prime software (Psychology Software Tools, Inc., Sharpsburg, PA).

fMRI Data Acquisition

Functional images were collected with a gradient-echo EPI sequence. Each participant underwent four acquisition runs. Each run included 245 consecutive volumes comprising 40 consecutive 3-mm-thick slices oriented parallel to the anterior–posterior commissure and covering the whole brain (repetition time = 2.3 sec, echo time = 60 msec, image matrix = 64 × 64, in-plane resolution = 3 × 3 mm). T1-weighted anatomical images were collected using a multiplanar rapid acquisition gradient-echo sequence (156 sagittal slices, voxel size = 1 × 1 × 1 mm, repetition time = 8.08 msec, echo time = 3.7 msec).

Stimuli and Procedure

The experimental paradigm was modeled on a previous behavioral study (Ferri et al., 2011) with appropriate modification for fMRI scanning. The experimental stimuli consisted of grayscale pictures of the dorsal view of right and left hands. The hands of each participant were photographed with a digital camera in a session prior

to the experiment (1 week before). This session took place in a controlled environment with constant artificial light and a fixed distance between the camera lens and the hands (40 cm), which were always photographed in the same position. Subsequently, photographs were modified with Adobe Photoshop software: They were cut from the original picture, pasted on a white background, and reoriented into the different rotated positions. Other people's hands were selected from this database as the best match for size, skin color, age, and gender, in comparison with each participant's hands. Images of hands were presented one at a time at the center of the visual field in six different clockwise orientations (0°, 60°, 120°, 180°, 240°, 300°). The orientation at 0° (upright) was defined as fingers pointing upwards; 0° was also the angle identical to the orientation of participants' hands in the moment of responding while in the scanner. Indeed, before starting a scanning session, we always checked that participants held the button box at some comfortable angle centered around 0°. Thus, the design was a 2 × 2 × 6 factorial with owner (self, other), laterality (left, right), and orientation (0°, 60°, 120°, 180°, 240°, 300°) as main factors. Each trial lasted 2300 msec, starting with a central fixation cross for 500 msec followed by stimulus presentation for 1800 msec or timed out as soon as participants responded (see Figure 1). If a response was given before, the fixation cross was presented for the rest of the remaining trial time.

Participants were required to judge the laterality (left or right) of observed digital images of hands by pressing as accurately as possible and within the allowed time interval a left or a right response key. Responses were provided with their left and right index fingers, respectively. Each participant provided us with 40 trials per con-

Figure 1. A typical experimental trial. Participants were required to judge the laterality of the presented hand. The shown image is either the participant's own hand or another person's hand. Hands were presented in six different clockwise orientations (0°, 60°, 120°, 180°, 240°, 300°).

dition. The trial order was determined using the program optseq2 (Dale, 1999). Optseq2 arranges trials in an order that appears random to participants while trying to jitter the trial onset times so that the overlaps of the hemodynamic response course are removed from the image-processing estimate of the induced hemodynamic response. The overall result is a trial order where trials from every condition are intermixed along with variable fixation times. This method allows a maximum number of trials presented while eliminating possible behavioral effects of expectation of upcoming trials by participants. At the end of the fMRI session, we investigated, at the behavioral level, how well participants could discriminate between their own hands and those of others. We employed the same stimuli and the same experimental paradigm as in the laterality judgment task. However, in this case, participants were required to explicitly judge whether the displayed hand corresponded to their own hand by pressing, within the allowed time interval (1800 msec), the left or the right (previously assigned) response key, with their left and right index fingers, respectively. The response keys were counterbalanced across participants.

Data Analysis

fMRI data were analyzed using SPM8 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London) according to the following procedure. For each subject, functional images were first corrected for head movement using a least squares approach and a six-parameter rigid body spatial transformation (Friston et al., 1995) and for difference in acquisition timing between slices. The high-resolution anatomical image and the functional images were then stereotactically normalized to the Montreal Neurological Institute (MNI) brain template used in SPM8 (Mazziotta, Toga, Evans, Fox, & Lancaster, 1995). Functional images were resampled with a voxel size of 3 × 3 × 3 mm and spatially smoothed with a three-dimensional Gaussian filter of 6 mm FWHM to accommodate anatomical variations between participants (Friston et al., 1995). The time series of functional MR images obtained from each participant were analyzed on a voxel-by-voxel basis using the principles of the general linear model extended to allow the analysis of fMRI data as a time series (Worsley & Friston, 1995). The onset of each stimulus constituted a neural event that was modeled through a canonical hemodynamic response function, chosen to represent the relationship between neuronal activation and BOLD signal changes (Friston et al., 1998).

We analyzed the fMRI data in two ways. First, we used a 2 × 2 factorial design to investigate the neural correlates of the self-advantage for one's dominant hand (see Behavioral Results; Ferri et al., 2011) regardless of the different orientation. The neuronal correlates of the interaction term, namely, owner (self, other) by laterality (right, left) was assessed using the contrast [(self-right hand, SR > self-left hand, SL) − (other-right hand, OR > other-left
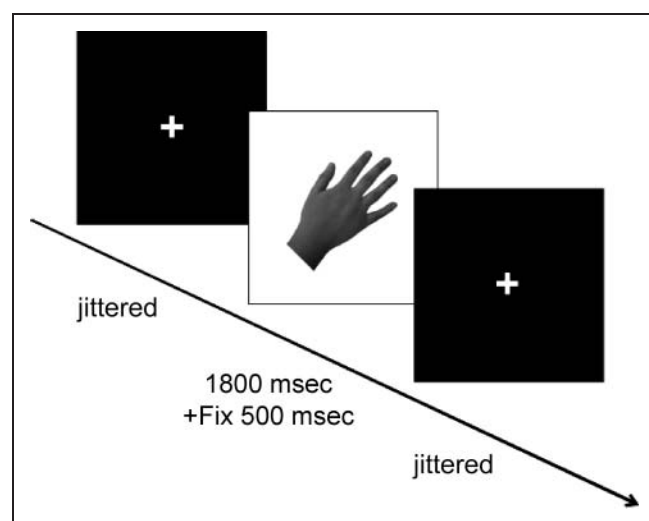
hand, OL)], at .05 false discovery rate corrected. To localize and visualize the activated clusters, we used the BrainShow software (Galati et al., 2008, 2011) implemented in Matlab (MathWorks, Inc., Natick, MA). The BrainShow software was also used to project group activations onto the standard cerebral cortex and to automatically assign anatomical labels (Tzourio-Mazoyer et al., 2002).

A second analysis was performed to tease apart different components of the mental rotation process and see how they are related to the self/other distinction and self-advantage. We used a $2 \times 2 \times 6$ factorial design to assess the neuronal correlates of the main effect of different orientation, at .01 family-wise error corrected (www.fil.ion.ucl.ac.uk/~wpenny/publications/rik_anova.pdf). Then for each brain region resulting from the above main effect and for each participant, we performed four linear regression analyses, one per stimulus category (SR, SL, OR, OL). BOLD response (beta values extracted by each cluster) and RTs at different orientations were included in the regression analyses as dependent and predictor variables, respectively (Richter et al., 2000; Richter, Ugurbil, Georgopoulos, & Kim, 1997). Then we computed slopes and intercepts. The slope would reflect the efficiency of the neural mechanism underlying the actual mental rotation process (BOLD signal per RT at each degree of rotated angle): The smaller the slope, the higher the efficiency of neural mental rotation (Christova et al., 2008). The intercept would reflect the efficiency of the neural mechanism underlying more general processes occurring before (e.g., stimulus encoding) or after (e.g., response preparation) mental rotation proper (Shepard & Cooper, 1982): The smaller the intercept, the higher the efficiency of processing hand stimuli unrelated to the actual mental rotation. Slopes and intercepts were compared by means of two separate two-way ANOVAs, each including owner (self, other) and laterality (right, left) as main factors. These analyses were carried out to assess whether any cortical regions among those involved in the motor task also (i) specifically contributed to the self-advantage for right hand and/or (ii) generally supported an implicit discrimination between one's own and other people hands, either for rotational or nonrotational processes, or both.

RESULTS

Behavioral Results

Trials in which participants did not respond (5.8%) or failed to respond correctly (6%) were discarded from the analysis. The mean RT of the correct responses was calculated for each condition; responses longer than 2 standard deviations from the individual mean were treated as outliers and were not considered (3.2% of the data set).

Visual inspection of behavioral data suggested that, for each stimulus category (SR, SL, OR, OL), we obtained the classic RT function of a bell-shaped curve, constituting the behavioral signature of mental rotation (Figure 2A). Tests on trends indicated that the three-way linear interaction was not significant ($F(1, 17) = 1.01$, $p = .33$), whereas the three-way quadratic interaction (owner by laterality by orientation) was significant ($F(1, 17) = 18.6$, $p < .001$). Simple effect analyses on the three-way quadratic interaction revealed the following: as for the right hand, slopes (mean ± *SEM*; msec/degree) were lower (in absolute value) for self than other stimuli at 60° [1.73 ± 0.09 vs. 2.08 ± 0.14; $t(17) = -2.96$, $p < .01$], 120° [0.67 ± 0.05 vs. 0.82 ± 0.07; $t(17) = -2.53$, $p < .05$], and 300° [-2.53 ± 0.15 vs. -2.96 ± 0.20; $t(17) = 2.25$, $p < .05$]; regarding the left hand, slopes were lower (in absolute value) for other than self stimuli at 60° [1.73 ± 0.15 vs. 1.36 ± 0.16; $t(17) = 2.51$, $p < .05$], 180° [-0.32 ± 0.08 vs. -0.05 ± 0.10; $t(17) = -3.83$, $p < .001$], 240° [-1.35 ± 0.17 vs. -0.75 ± 0.20; $t(17) = -3.78$, $p < .005$], and 300° [-2.38 ± 0.27 vs. -1.46 ± 0.32; $t(17) = -3.64$, $p < .005$]. These comparisons suggest that, whereas for the right hand the mental rotation process is more efficient for self-related than other-related stimuli, the opposite is true for the left hand. As the aim of the present work was to investigate the role played by the sensorimotor system in the self/other distinction and the self-advantage, we limited the ANOVA to the factors Owner (self, other) and Laterality (left, right), and the levels of the factor orientation were collapsed. Mean RTs of the correct responses were calculated for each condition and entered in the above-described two-way ANOVA. The Tukey's test was used for all post hoc comparisons. Statistical analysis of RTs recorded from participants lying in the scanner showed significant main effects of Owner [$F(1, 17) = 5.2$, $p < .05$] and Laterality [$F(1, 17) = 14.1$, $p < .005$]. Also, the two-way interaction Owner × Laterality [$F(1, 17) = 4.4$, $p = .05$] was significant. The Owner main effect was accounted for by faster performance (mean ± *SEM*; msec) for self-related stimuli (783 ± 24) with respect to other-related stimuli (791 ± 25). The Laterality main effect was accounted for by faster performance for right stimuli (766 ± 24) with respect to left stimuli (808 ± 26). Finally, the interaction Owner × Laterality was accounted for by faster performance to self-right stimuli (758 ± 24) compared with all the other conditions (other-right: 774 ± 25, self-left: 809 ± 25, other-left: 808 ± 27; $p < .05$ in all cases; see Figure 2B). By contrast, RTs for self-left and other-left stimuli did not differ ($p = 1$) from each other. In conclusion, behavioral data confirmed the self-advantage for one's dominant hand we previously described (Ferri et al., 2011).

Strikingly, the self-advantage effect was not due to the fact that participants can better recognize their own right hand with respect to all the others' hand stimuli. Indeed, participants were quite accurate in categorizing all hand stimuli. The mean accuracy was 89.2% (SR = 88.2%; SL = 86.5%; OR = 91.5%; OL = 90.7%). ANOVA on these values did not reveal any significant difference. Importantly,

Figure 2. Mean RTs at the self-left, self-right, other-left, and other-right hand stimuli as a function of the angular orientation (A). Mean RTs at the self and other hand stimuli, regardless of the stimulus orientation (B). Error bars depict *SEM*s.
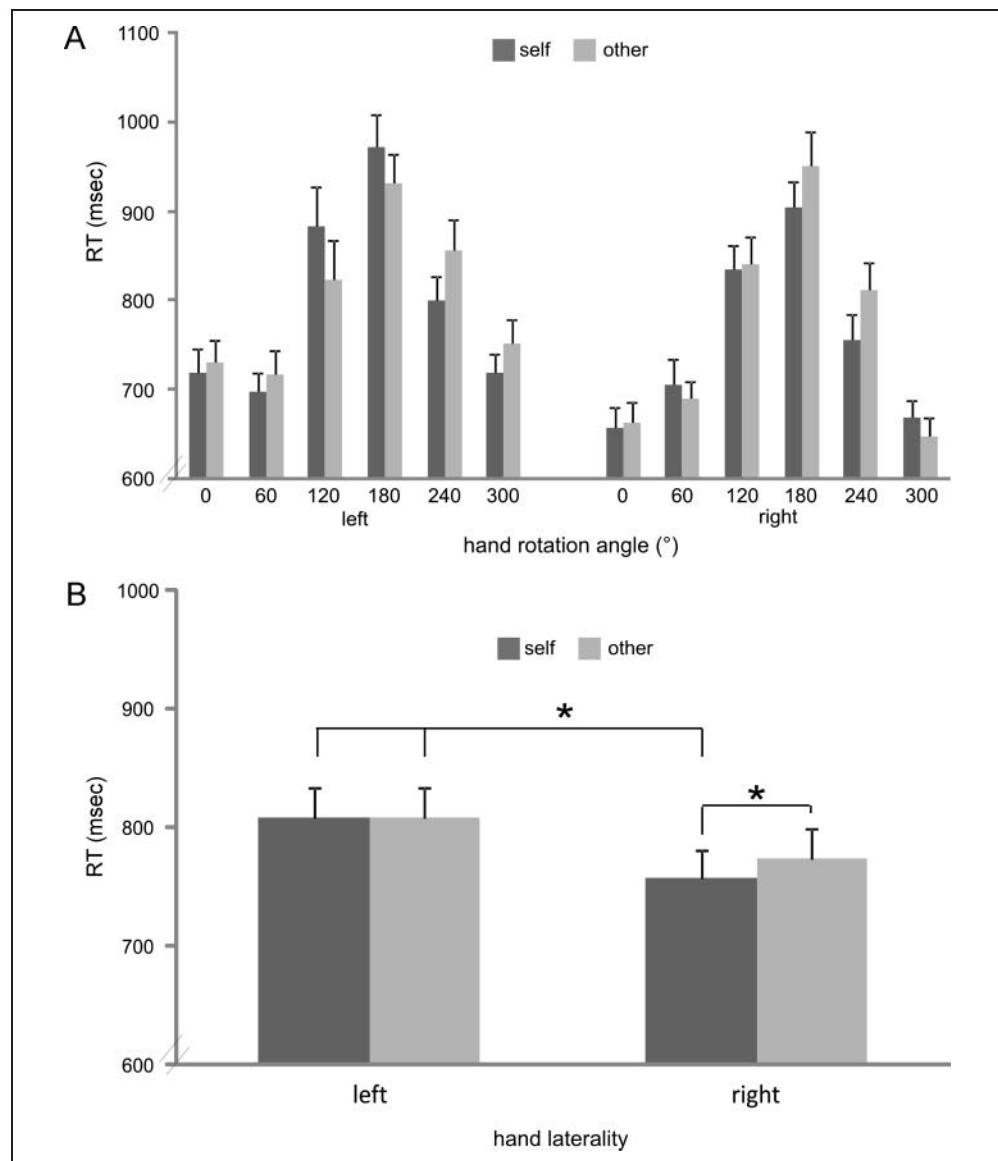
when comparing the sensitivity of our participants in making an explicit self/other discrimination between right ($d' = 2.59$) and left ($d' = 2.43$) hands, we found that d' scores did not differ from each other [$t(17) = 0.41, p = .69$].

Neural Correlates of the Self-advantage for Right Hands

The Owner × Laterality interaction term (see Methods for the contrast definition), that is, the superior performance when judging the laterality of one's right hand (self-advantage), revealed activation in the precentral gyrus bilaterally, the SMA and pre-SMA extending to the middle cingulate cortex, the left postcentral gyrus, the right hippocampus, the right temporal cortex encompassing the extrastriate body area (EBA; Downing, Jiang, Shuman, & Kanwisher, 2001), the right fusiform gyrus,

the occipital cortex, and the cerebellum bilaterally (see Figure 3 and Table 1).

Correlation of Neuroimaging and Psychophysical Data

The standard BOLD analyses carried out so far clearly indicated a stronger involvement of sensorimotor regions while judging the laterality of one's own right hand as compared with others' right hand. Nevertheless, they do not reveal whether and to what extent regions specifically involved in our motor task also participate to the behavioral self-advantage effect. Indeed, the facilitation in judging the laterality of one's own right hand could be triggered by a higher efficiency of either the neural mental rotation process or by more general, nonrotational processes, or both. To tackle this issue, we first isolated all the brain regions involved in the task, irrespective of the

Figure 3. Regions showing higher activation during the mental rotation of one's own right hand as compared with the mental rotation of one's own left and other's hand. Group activation data are rendered on the cortical surface of a "canonical" brain (Mazziotta et al., 1995).
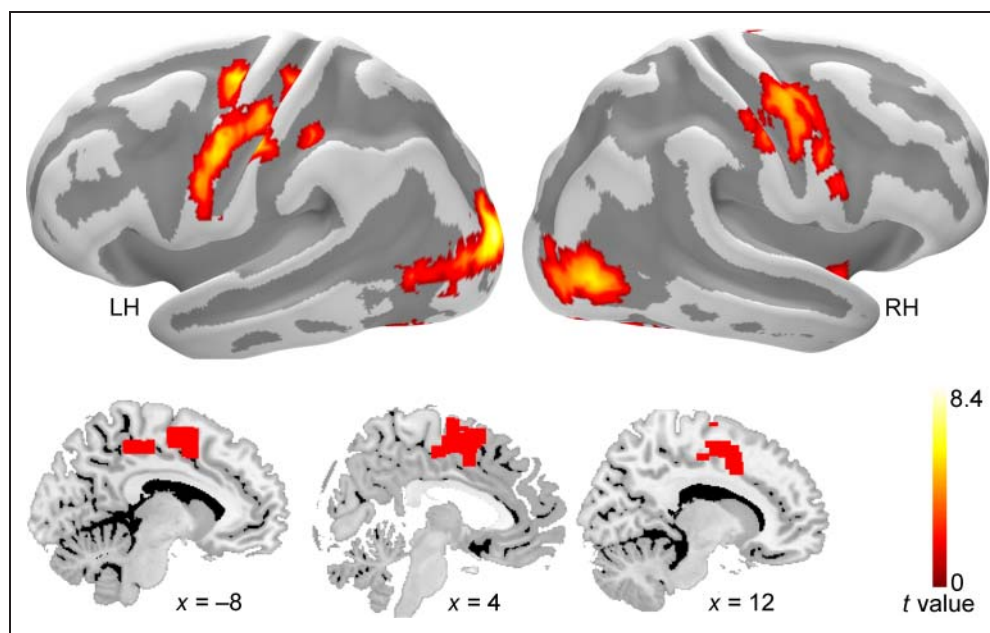
variables Owner and Laterality ($p < .01$, family-wise error corrected, see Methods). These regions were localized in the left insula, the right insula encompassing the pars orbitalis of the inferior frontal gyrus, the SMA and pre-SMA, the left premotor cortex, the right middle frontal gyrus, the superior frontal gyrus bilaterally, the left inferior parietal lobe, the left precuneus, the superior parietal lobule, and the calcarine cortex bilaterally (see Figure 4 and Table 2). Then we performed two ANOVAs for each cluster: one to assess reliable differences between slopes and the other to assess reliable differences between intercepts for the different stimulus categories (SR, SL, OR, OL). Such differences would be due to effects of Owner, Laterality, and their interaction on regression lines on BOLD response for RTs at different orientations. We can make the following predictions:

1. If sensorimotor resources involved in the laterality judgment task also contribute to self-advantage for right hand because of higher neural efficiency when rotating one's own compared with another's hand, then slopes should be lower (higher efficiency) for self- than for other-right hand. The same difference should not be found for left hands.
2. If sensorimotor resources involved in the task contribute to self-advantage for right hand because of more general, nonrotational processes, such as those occurring before or after actual mental rotation, then intercepts should be lower for self- than for other-right hand.

As far as slopes are concerned, a significant main effect of Owner was found in the left insula [$F(1, 17) = 11.8, p < .005$], the right insula [$F(1, 17) = 9.3, p < .01$], the SMA and pre-SMA [$F(1, 17) = 11.4, p < .005$], the left premotor cortex [$F(1, 17) = 13.8, p < .005$], and the calcarine cortex [$F(1, 17) = 10.3, p < .005$]. In all of

the above listed regions, the Owner main effect was accounted for by lower slopes (higher efficiency of actual motor process) for self hands as compared with others' hands (see Table 2). Strikingly, the interaction of owner and laterality was significant only in the left premotor cortex [$F(1, 17) = 5.4, p < .05$]. Post hoc comparisons (Tukey's test) showed that slope was lower ($p < .001$) for self-right stimuli compared with other-right stimuli, whereas slopes of self-left and other-left stimuli did not differ from each other ($p = .33$). As far as intercepts are concerned, a significant main effect of Owner was found in the left insula [$F(1, 17) = 17.6, p < .001$], the right insula [$F(1, 17) = 15.3, p < .005$], the SMA and pre-SMA [$F(1, 17) = 17.3, p < .001$], the left premotor cortex [$F(1, 17) = 19.9, p < .001$], and the calcarine cortex [$F(1, 17) = 13.1, p < .005$]. In all of the above listed regions, the Owner main effect was accounted for by lower intercepts (higher efficiency of nonrotational processes) for others' hands as compared with self hands (see Table 2). Again, the interaction of Owner × Laterality was significant only in the left premotor cortex [$F(1, 17) = 6.3, p < .05$]. Post hoc comparisons (Tukey's test) showed that intercepts were lower ($p < .001$) for other-right stimuli compared with self-right stimuli, whereas intercepts of other-left and self-left stimuli did not differ from each other ($p = .32$). The main effect of Laterality was never significant. In summary, these results suggest that, among regions involved in the mental rotation task, the left premotor cortex' activity is likely to be related also to self-advantage for right hand. Such a relation between the local neural activity and the behavioral effect seems to be specifically explained by a higher neural efficiency during the actual mental rotation process and not by neural efficiency for more general, nonrotational processes. Also, our results indicate that (for similar reasons) bilateral

Table 1. MNI Coordinates of Peaks of Relative Activation in the Cortical Regions where BOLD Signal Was Higher during the Mental Rotation of One's Own Right Hand as Compared with the Mental Rotation of One's Own Left and Other's Hand

Brain Region	Side	Cluster Size (Voxels)	Local Maxima (MNI) x	y	z	Brodmann's area
Middle frontal gyrus	R	97	48	3	57	6
SMA	L	289	−3	3	57	6
	R		9	3	51	6
Precentral gyrus	L	175	−54	−3	48	6
	R	124	60	9	21	6
	R		51	−3	36	4
Middle cingulate cortex	L	75	−9	−36	48	na
	R	51	12	9	36	32
Postcentral gyrus	L	64	−27	−33	48	3
Hippocampus	R	184	30	−12	−18	20
Temporal cortex	R	161	48	−72	3	37
	R		42	−54	−15	37
Fusiform gyrus	R	152	27	−78	−15	19
Occipital cortex		1895				
	L		−12	−75	12	17
	R		15	−72	15	18
	L		−27	−93	12	18
	L		−21	−57	−9	19
	R		24	−51	−6	37
Cerebellum	L	431	−36	−66	−21	19
	R	437	27	−48	−30	37

The table shows local maxima of more than 4 mm apart.

insula, SMA and pre-SMA, and calcarine cortex are engaged in general self/other distinction.

DISCUSSION

The hand laterality judgment task requires participants to simulate a mental rotation of the observed stimulus. Specifically, when performing this task, participants imagine their own hand rotating into the stimulus position to confirm a judgment of handedness (Parsons, 1994). This means that the imagined hand is translated into its motor representation, engaging sensorimotor rather than visual processes (de Lange, Helmich, & Toni, 2006; Kosslyn et al., 1998; Parsons, Gabrieli, Phelps, & Gazzaniga, 1998; Parsons et al., 1995). This idea is further corroborated by imaging studies, showing an involvement of sensorimotor areas while performing the task (for a review, Zacks, 2008). In this study, we took advantage of this task to investigate whether mental rotation of pictures of participant's own hand leads to a different activation of sensorimotor areas as compared with the mental rotation of pictures of another's hand. If this holds, it would be evidence for the existence of a motor representation of the participant's hand that allows for the efficient differentiation between one's own hand and another person's hand.

Empirical data support the notion of a bodily self rooted in the sensorimotor system. For instance, Loula, Prasad, Harber, and Shiffrar (2005) asked participants to identify and discriminate actors during tasks in which the action could be performed either by the participant or by a stranger. They found the highest sensitivity to one's own motion in both tasks. These results have been interpreted in light of the fact that the neural mechanism responsible for identity perception is deeply entrenched within the action production system.

In the same vein, during a hand laterality judgment task, we recently found faster RTs in the implicit processing of one's own hand, compared with others' hands (Ferri et al., 2011). Such self-advantage, likely related to

Figure 4. Regions involved in the mental rotation process (main effect of angular orientation), irrespective of the variables' owner and laterality. Group activation data are rendered on the cortical surface of a "canonical" brain (Mazziotta et al., 1995). Red clusters indentify areas where the slopes and the intercepts were significantly different between self and other conditions, regardless of the laterality. The yellow cluster identifies the cortical region where slope and intercept were significantly different between self right and other right hand stimuli. White clusters indentify areas where both slopes and intercepts were not different between self and other conditions.
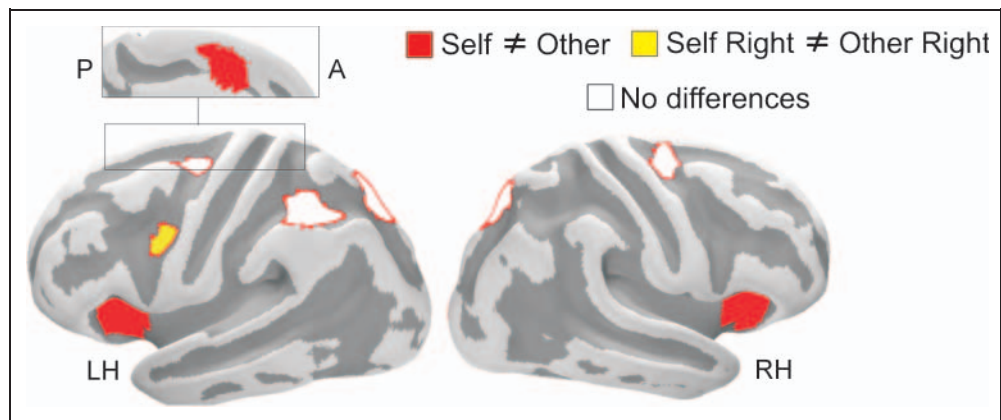
the motor-experience-based bodily self, was specific for the participant's right dominant hand. Furthermore, it was not observed during a self/other discrimination task, thus suggesting that an explicit recognition of one's

own body parts is not mandatory for the self-advantage to emerge.

Here we investigated the neural activity underlying this effect. Behavioral data collected inside the scanner basically

Table 2. MNI Coordinates of Peaks of Relative Activation in the Cortical Regions Involved in the Mental Rotation Process (Main Effect of Angular Orientation), Irrespective of the Variables Owner and Laterality

Brain Region	Side	Cluster Size (Voxels)	Local Maxima (MNI)			Slopes				Intercepts			
			x	y	z	SR	SL	OR	OL	SR	SL	OR	OL
Self ≠ Other													
Insula	LH	148	−27	24	−3	**3.8**	**2.4**	3.9	5.9	**−2.4**	**−1.3**	−2.7	−4.2
Insula/inferior frontal gyrus (*pars.orb*)	RH	277	42	21	−3	**3.8**	**3.9**	3.9	5.9	**−2.4**	**−1.3**	−2.7	−4.2
SMA/middle cingulated cortex	LH/RH	325	−3	12	48	**4.0**	**3.5**	5.7	7.1	**−1.7**	**−1.2**	−3.4	−4.1
Calcarine cortex	LH/RH	189	−9	−93	−6	**4.5**	**2.4**	6.9	6.3	**1.8**	**3.1**	−0.5	0.3
Self-Right ≠ Other-Right													
Premotor cortex	LH	25	−42	0	33	**3.4**	3.9	8.2	7.9	**−0.5**	−0.7	−4.6	−4.0
No Differences													
Middle/superior frontal gyrus	RH	48	30	−3	54	3.3	3.5	5.4	4.7	−1.0	−1.0	−2.8	−1.9
Superior frontal gyrus	LH	27	−24	−6	54	3.7	4.0	5.7	5.3	−1.1	−1.4	−2.9	−2.4
Inferior parietal lobe	LH	144	−36	−48	39	5.1	4.5	6.4	5.8	−2.1	−1.8	−3.2	−2.9
Precuneus/superior parietal lobe	LH	63	−12	−69	60	5.6	7.2	7.3	5.0	−2.2	−3.4	−3.3	−1.7
Superior parietal lobe	RH	65	18	−72	57	4.9	6.5	5.4	3.5	−1.4	−2.6	−1.8	−0.4

Rightmost columns report slopes and intercepts for each region calculated for self-right, other-right, self-left, and other-left conditions. In **bold** are slopes and intercepts of self hands significantly different from those of other hands, for both right and left stimuli. LH = left hand; RH = right hand; SR = self-right; OR = other-right; SL = self-left; OL = other-left.

replicate our previous findings (Ferri et al., 2011). We will now relate this behavior to neural activity recorded by fMRI. We found higher activation in bilateral premotor cortex, extending to the postcentral gyrus and the SMA and pre-SMA while rotating one's right hand as compared with others' hand stimuli. Strikingly, the analyses on slopes and intercepts revealed that only in the left premotor cortex a selective higher efficiency for self-right hand was present. Indeed, slope was lower for self-right as compared with other-right hand. This did not hold for the left hand. Conversely, in the same area, intercept was lower for other- than for self-right hand. This suggests that nonrotational factors, different from factors related to actual mental rotation, are not tuned to self stimuli. Possibly, one may argue that nonrotational processes in premotor cortex are better tuned to other right hands than to one's own right hand. According to us, it is more likely that this area houses a motor-experience-based representation of the bodily self. Hence, nonrotational processes are less effective to solve the task when self stimuli should be rotated. It should be noted that the notion of bodily self as motor in nature is not entirely new. For example, Legrand (2006) proposed to conceive the bodily self as an integrated system characterized by matching of sensorimotor information. Here we argue that such motor representation of our own body parts is likely and mostly based on our own motor experience of the same body parts. In other words, the more we have a motor experience of a body part, the better its "representation" will be in terms of neural efficiency at the level of the motor cortices. It follows that the motor representation of the right hand is better than the motor representation of the left hand in right-handers.

Current neuroimaging data (Ehrsson et al., 2004) suggest that the premotor cortex is an ideal candidate for the multisensory representation of one's own body. Indeed, it is anatomically connected to visual and somatosensory areas in the posterior parietal cortex and to frontal motor areas (Rizzolatti, Luppino, & Matelli, 1998). For this reason, it is plausible to assume that the premotor cortex activity reflects the detection of congruent multisensory signals from one's own body and that this could be the mechanism responsible for the feeling of body ownership (Ehrsson, Holmes, & Passingham, 2005). However, different studies on rubber hand illusion, (Botvinick & Cohen, 1998) showed that the multisensory integration leading to the experience of our body as our own is conditioned by the possibility—or not—to perform actions with a given body part (Tsakiris, Schutz-Bosbach, & Gallagher, 2007; Tsakiris, Prabhu, & Haggard, 2006; Tsakiris & Haggard, 2005). Neuropsychological evidence further corroborates the link between motor abilities and self-body recognition. For instance, the patient described by Arzy and colleagues (2006), who experienced asomatognosia, following a lesion in the right motor and premotor cortices, besides being unable to move her contralesional arm, was also unable to recognize it.

Interestingly, the second analysis of the fMRI data not only confirmed a pivotal role of the premotor cortex in the behavioral self-advantage for right hand but also allowed us to indentify another distinct pattern of self-processing neural activity, more generally discriminating between one's own and others' hands (general self/other distinction). Indeed, for both the right and left stimuli, self-hand slopes were lower than other-hand slopes in the SMA/pre-SMA, anterior insula bilaterally, and calcarine cortex. This shows that the actual mental rotation process was more efficient for both one's own hands as compared with others' hands, regardless of the laterality of the stimuli. In the same areas, self-hand intercepts were higher than other-hand intercepts for both the right and left stimuli, thus suggesting that nonrotational factors did not play any role in self-advantage. All in all these data show that the motor-experience-based bodily self recruited by our motor task is purely linked to the motor skills of our participants, rather than to nonrotational processes such as those occurring before (e.g., stimulus encoding and visual familiarity) or after (e.g., response preparation) mental rotation proper.

Let us now take a deeper look at how the above-mentioned areas, recruited by the task, might contribute to the general self/other distinction.

As regards the SMA and pre-SMA, recordings of single neurons from monkeys revealed neurons in the medial frontal cortex, including the pre-SMA, which selectively encode others' action (Yoshida, Saito, Iriki, & Isoda, 2011). The authors suggested that these neural structures might be involved in self/other differentiation in the domain of action. Accordingly, evidence for the supplementary motor cortex playing such a role was provided by Mukamel, Ekstrom, Kaplan, Iacoboni, and Fried (2010). They recorded extracellular activity from cells in human medial frontal and temporal cortices while patients executed or observed hand-grasping actions. A subset of these neurons showed excitation during action execution and inhibition during action observation, thus suggesting a different recruitment of this area while processing self and others' motor acts. Concerning the possible role of anterior insular cortices in self/other distinction, previous studies showed that this area is involved in bodily self-awareness, sense of agency, and sense of body ownership (Craig, 2002, 2009; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007). This area is thought to be a convergence zone where interoceptive and exteroceptive self-related information is integrated (Craig, 2010). Reduced neural activity during rest periods, particularly in the bilateral anterior insula, was found in patients with major depressive disorder, together with abnormal body perception (Wiebking et al., 2010). Bilateral activation of the anterior insula was observed in a PET study where participants were requested to attribute an action to themselves compared with a condition where they attributed it to another person (Farrer & Frith, 2002). Insular lesions, prominently in the right hemisphere, have been reported to be responsible for

anosognosia for hemiparesis, asomatognosia, or somato-paraphrenia (Karnath & Baier, 2010; Baier & Karnath, 2008).

Given that the insular cortex deals with both interoceptive (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004) and sensorimotor information (Karnath & Baier, 2010), one may question whether the self/other distinction arises from the former or the latter. In particular, the question is whether interoceptive information feeds sensorimotor processes providing them with the sense of self or vice versa. At this stage, we are not able to answer this question. According to our data, we can only speculate that sensorimotor processes play a nontrivial role in self/other distinction (see also Jeannerod, 2007).

One may argue that the engagement of sensorimotor regions is strictly related to the task employed in this study, that is, a motor simulation task. However, evidence coming from literature on visuotactile integration goes in the same direction. Recently, Cardini and colleagues (2010) showed that observing one's own face being touched, while experiencing touch on the same anatomical location, resulted in a better behavioral performance in a tactile detection task. On the neural side, this behavioral advantage was associated to a reduction of BOLD signal in somatosensory and ventral premotor cortices. These data confirm that the sensorimotor system is involved during implicit self-processing, regardless of the motor nature of the task.

Besides sensorimotor regions, we also found stronger activation in the occipito-temporal cortices for self-related with respect to other-related stimuli. This finding expands previous knowledge showing that these cortices not only house a shared topographic representation of seen and moved body parts (Orlov, Makin, & Zohary, 2010) but would also be involved in the self/other distinction during a motor simulation task. Accordingly, sensorimotor influences on a region in the lateral occipito-temporal cortex, which is selectively activated by nonfacial body parts and named extrastriate body area (EBA; Downing et al., 2001), have already been shown by an earlier fMRI study by Astafiev, Stanley, Shulman, and Corbetta (2004). In that study, the authors showed that EBA is strongly modulated by limb movements even in the absence of visual feedback from the movement. The evidence that EBA responds to one's own goal-directed body movements suggests that, at least a portion of this region, plays a role in the self/other distinction.

The literature on body representation ascribes a crucial role to the parietal cortices in the assignment of body identity (Hodzic, Muckli, Singer, & Stirn, 2009; Sugiura et al., 2006; Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni, 2005) and in the representation of the position of body parts in space, that is, body schema (Creem-Regehr, Neil, & Yeh, 2007; Bonda et al., 1995). Also, right parietal lesions often give rise to a deficit of body identity such as personal neglect (Committeri et al., 2007; Guariglia & Antonucci, 1992; Bisiach, Vallar, Perani, Papagno, & Berti, 1986), whereas left parietal lesions lead to a deficit in localizing body parts in relation to one's own or others' body such as autotopagnosia and heterotopagnosia, respectively (Cleret de Langavant, Trinkler, Cesaro, & Bachoud-Levi, 2009; Sirigu, Grafman, Bressler, & Sunderland, 1991; Semenza, 1988; Ogden, 1985). At first glance, our results seem at odds with this literature; indeed, we did not find any involvement of parietal regions in the self/other distinctions, either in the first or in the second analysis on fMRI data. A possible explanation for the difference between the present and previous findings is that the involvement of the parietal areas in the recognition of body identity has been described in studies in which body identity was explicitly accessed. In contrast, in the current study, only implicit access to the self was required, suggesting that partially segregated neural networks may underpin implicit and explicit access to bodily self-representation. The lack of parietal involvement while implicitly processing self and others suggests that the body known in bodily self-knowledge is not necessarily the body conceived as a spatial organization of its parts, as the notion of a body schema might suggest (Medina & Coslett, 2010; Peelen & Downing, 2007; Maravita, Spence, & Driver, 2003; Berlucchi & Aglioti, 1997).

To sum up, by using a laterality judgment task with self and other hand stimuli, we highlighted, first, the neural correlates of the self-advantage, second, a neural network for the more general representation of the bodily self. The former seems to be confined within the left premotor cortex, whereas the latter encompasses pre-SMA/SMA, the anterior insula, and the occipital cortex. We believe the present data enrich the theoretical definition of the bodily self as motor in nature by grounding it in empirical evidence.

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