Please cite this article in press as: Brozzoli et al., A Shared Representation of the Space Near Oneself and Others in the Human Premotor Cortex, Current Biology (2013), http://dx.doi.org/10.1016/j.cub.2013.07.004

Current Biology *23*, 1–5, September 23, 2013 ©2013 Elsevier Ltd All rights reserved http://dx.doi.org/10.1016/j.cub.2013.07.004

Report

A Shared Representation of the Space Near Oneself and Others in the Human Premotor Cortex

Claudio Brozzoli,[1],* Giovanni Gentile,[1]
Loretxu Bergouignan,[1] and H. Henrik Ehrsson[1]
[1]Brain, Body and Self Laboratory, Department of
Neuroscience, Karolinska Institutet,
17177 Stockholm, Sweden

Summary

Interactions between people require shared high-level cognitive representations of action goals, intentions [1], and mental states [2], but do people also share their representation of space? The human ventral premotor (PMv) and parietal cortices contain neuronal populations coding for the execution and observation of actions [1, 3–5], analogous to the mirror neurons identified in monkeys [1, 5]. This neuronal system is tuned to the location of the acting person relative to the observer and the target of the action [4, 5]. Therefore, it can be theorized that the observer's brain constructs a low-level, body-centered representation of the space around others similar to one's own peripersonal space representation [6–11]. Single-cell recordings have reported that parietal visuotactile neurons discharge for objects near specific parts of a monkey's own body and near the corresponding body parts of another individual [9]. In humans, no neuroimaging study has investigated this issue. Here, we identified neuronal populations in the human PMv that encode the space near both one's own hand and another person's hand. The shared peripersonal space representation could support social interactions by coding sensory events, actions, and cognitive processes in a common spatial reference frame.

Results and Discussion

We measured blood oxygen level-dependent (BOLD) adaptation [3, 10–12] in healthy individuals to test whether neuronal populations showing selectivity to an object near one's own hand [10, 11] also encode an object near another person's hand. Adaptation is a robust phenomenon in electrophysiology that has been extended to fMRI [3, 10–12]. This phenomenon is based on the premise that repeated presentation of identical stimuli leads to a reduction in the signal measured from neuronal populations that respond selectively to specific stimulus features. Because a voxel in fMRI acquisition represents a volumetric portion of the brain, a voxel signal typically represents the activity of thousands of neurons, which potentially comprise multiple subpopulations. Compared with traditional fMRI, BOLD adaptation provides the advantage of revealing subpopulations of neurons within single voxels that exhibit selectivity to specific stimulus features. Here, the specific feature under examination is the proximity of a physical visual stimulus to the hand, regardless of whether the hand is the participant's own or that of another person.

During the scans, the participant lies on the bed of the MRI scanner with their head tilted forward and their right hand placed on a table in direct view (Figure 1A). At a distance of 100 cm in front of their right hand, the participant sees another person's hand placed on a support with an orientation similar to the participant's hand (in experiment 1, a prosthetic hand is also presented as a control; see below). All other objects in the scanner room, including the two experimenters, were occluded from view of the participant by white curtains. To probe BOLD adaptation reflecting activity of peripersonal space neurons with mirror properties, we presented a moving spherical object—a small ball attached to a stick—close to the participant's own hand for 3 s and then, in direct succession, the same visual stimulus close to the other person's hand for another 3 s (Figure 1B).

In the first experiment ($n = 26$), we compared the BOLD adaptation response to the physical stimulus appearing near either the real right hand of another person or a real-looking prosthetic right hand following identical visual stimulation near the participant's own right hand (Figure 1C). The inclusion of the prosthetic hand as a control allowed us to rule out any nonspecific BOLD adaptation effects related to just viewing the small ball moving next to an external object. Importantly, the participants were informed about the nature of the prosthetic hand before the scanning commenced and could recognize and distinguish the prosthetic hand from the other person's hand. By swapping the relative locations of the prosthetic and other person's hand (in a two-by-two factorial design; Figure 1D), we could control for the nonspecific effects of seeing the spherical object moving in particular spatial positions in non-hand-centered coordinates or close to a hand-shaped object. Therefore, we could assess whether the spatial encoding of the visual stimulus was "anchored" to the other person's hand. Thus, we could directly test the existence of a shared neuronal representation of peripersonal space for self and other.

In support of our hypothesis, we found a cluster in the left ventral premotor (PMv) (peak in the inferior part of the precentral sulcus with the cluster encompassing the precentral gyrus; $T = 3.95$, $p_{\text{FWE-corrected}} = 0.015$; Figure 2A; Table 1) showing stronger BOLD adaptation to the moving object presented near the real rather than the artificial hand following stimulation near the participant's own hand. Thus, the left PMv contains neuronal populations that encode the space both around the participant's and another person's hand. Moreover, neuronal populations in the left PMv encode the physical stimulus near the participant's and the other person's hand irrespective of whether the other's hand was located in the left ($T = 3.25$, $p < 0.001$ uncorrected) or the right hemispace ($T = 3.63$, $p_{\text{FWE-corrected}} = 0.045$; Figure 2A).

In a second, independent fMRI experiment ($n = 20$), we tested for bidirectional adaptation [3], a conservative test for a shared perihand representation in PMv (Figure 3). If the first experiment genuinely detected the activation of peripersonal space neurons with mirror properties, neurons should display response suppression (1) when stimulation near one's own hand follows stimulation near the other person's hand and (2) when stimulation near the other person's hand follows

*Correspondence: claudio.brozzoli@ki.se

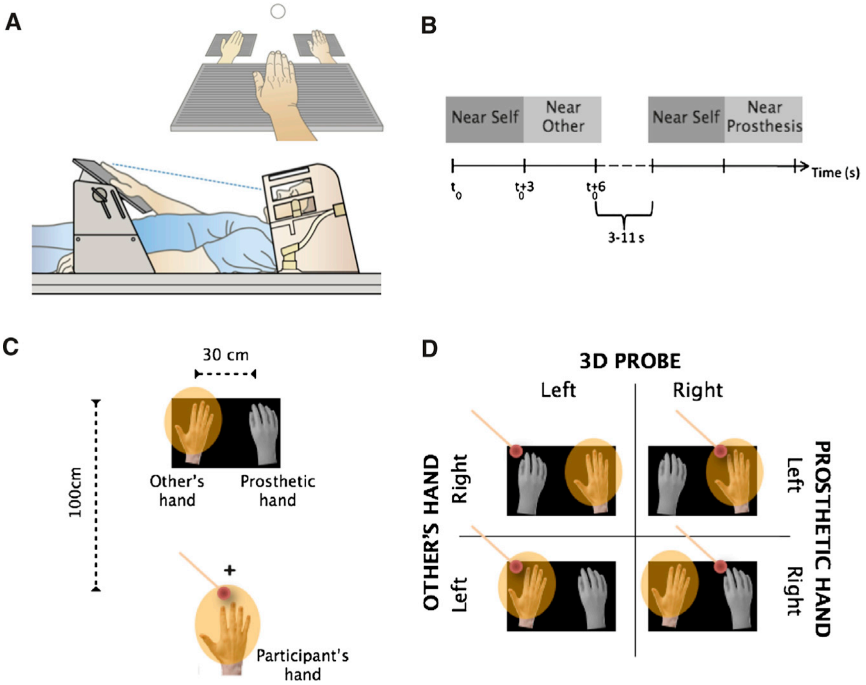

Figure 1. Methods, Experiment 1

(A) Bottom panel: participant's tilted head and hand. The participant's real right hand was placed in direct view centrally on the table. Top panel: illustration of what participants saw from within the scanner tunnel. The participant could see the prosthetic hand (furthest left of the three hands) and the other person's hand (furthest right), both at a distant location, and their own hand on the table (center). The white circle corresponds to the fixation point. The relative locations of the other's hand and the prosthetic hand were alternated across runs.

(B) Temporal schema of the stimulation trials. First, the stimulus was presented for 3 s near the participant's hand ("Near Self") and subsequently for 3 s in either of the two far locations to the right or to the left of the fixation point, which correspond to the other's hand ("Near Other") or the prosthetic hand ("Near Prosthesis"), depending on the condition in the factorial design. In each fMRI experiment, a baseline was collected without stimulation. The stimulus was presented for 6 s stimulation trials, with each trial separated by a jittered intertrial interval (7 ± 4 s). The order of the conditions was randomized.

(C) Schematic illustration of the spatial arrangement of the participant's hand, the other person's hand, and the prosthetic hand with respect to the fixation point (black cross). We employed the real hand of the participant and of another person in our setup. As a control, we used a realistic-looking 3D rubber hand ("prosthetic hand"). The visual stimulus consisted of a small red ball (3 cm in diameter) attached to a stick that was moved repeatedly up and down, 2 cm above the fingers, by a trained experimenter (out of view).

(D) Full-factorial design: independent manipulation of the positions of the prosthetic hand, other person's hand, and the location of the stimulus. The other's hand is indicated with the colored circle.

stimulation near one's own hand. The conjunction (logic AND) of these two conditions is strong evidence of the fact that the same neuronal population responds indifferently to an object near the participant's and the other person's hand. Thus, in this second paradigm, we presented the small moving ball for 3 s first near the participant's hand and then near the other person's hand or vice versa (Figure 3B). To probe for possible differences between self and other, we also included trials where we only presented the moving object near the participant's hand for 6 s or exclusively for 6 s near the other's hand.

Crucially, the results supported our main hypothesis: the left PMv adapted to the visual simulation near the participant's hand and the other person's hand independently of the order of presentation to the two hands (peak in the inferior part of the precentral sulcus; $T = 3.77$, $p_{FWE\text{-}corrected} = 0.016$; Figure 2B; Table 2; see also Figure S1 available online). This finding further strengthened the conclusion that the same neuronal populations in PMv encode perihand space both for self and other.

Finally, we looked for neuronal populations that preferentially represent the space around the participant's or the other person's hand. To this end, we contrasted the BOLD adaptation responses from trials where we only presented the moving ball near the participant's or the other's hand (Figure 3B). As we previously reported [10, 11], a parietopremotor network exhibited visual selectivity for the space near the participant's hand (Figure S2; Table S1). Interestingly, the right anterior cingulate cortex (ACC) showed greater selectivity for the space near another individual's hand compared to one's own hand ($T = 3.73$, $p_{FWE\text{-}corrected} = 0.047$; Figure S3; Table S2).

These findings show that the human PMv contains a low-level common representation of the space around one's own hand and another person's hand. We have previously shown that premotor and parietal areas encode objects in hand-centered coordinates [10, 11]. Here, we identify a subpopulation of peripersonal neurons in the left PMv with mirror properties; these neurons encode a physical stimulus in hand-centered coordinates regardless of whether the physical stimulus is near the participant's own hand or someone else's hand. Predictions about others' actions are accurately and automatically processed when the other's space is visible to the observer. In contrast, the cooperative performance of two individuals can be disrupted if the construction of the shared representation is hindered [13]. The shared premotor representation of the perihand space identified in this study could constitute a common reference frame allowing individuals to interactively deploy spatial attention ("joint attention") [14, 15] and anticipate the motor behavior of others [4, 5, 16–18].

One might argue that we interact more often with other people when their hands are visible from a third-person (allocentric) point of view, i.e., when the partners are facing each other. With respect to this concept, it has been shown that different populations of visuomotor mirror neurons in the macaque premotor cortex have visual selectivity for specific perspectives [19]. Similar results have also been reported in humans [20]. In these studies, PMv visuomotor mirror neurons appear to display a preference for actions performed by others observed from a first-person perspective. These earlier observations are consistent with the present results, where the participants observe the hands from a first-person point of view in all conditions (self, other, prosthesis).

Interestingly, our results show that the right ACC preferably adapts to the object near someone else's hand. This region

Please cite this article in press as: Brozzoli et al., A Shared Representation of the Space Near Oneself and Others in the Human Premotor Cortex, Current Biology (2013), http://dx.doi.org/10.1016/j.cub.2013.07.004

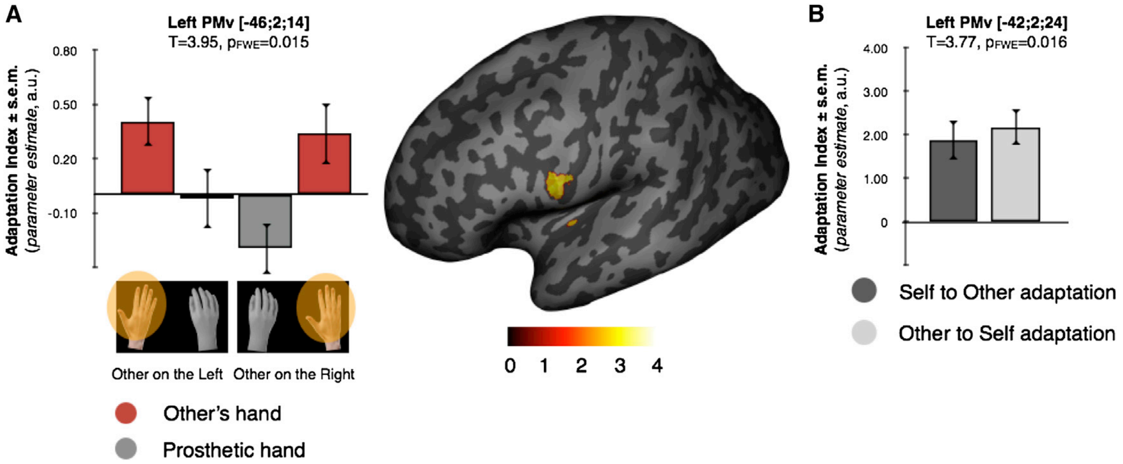

Figure 2. Results

(A) Experiment 1. A shared neuronal representation of the perihand space for self and other in the left PMv. The left PMv showed stronger BOLD adaptation to repeated perihand visual stimulation between self and other than between self and the prosthetic hand. Note that this finding holds true irrespective of whether the other's hand is placed in the right or left hemifield, as observed in the plots of the adaptation index (difference in contrast estimate when subtracting the second 3 s stimulation period from the first period). The significant cluster of adapting voxels (peak $p < 0.05$ corrected; voxels thresholded at $p < 0.005$ uncorrected for display purposes) from the random-effect group analysis is displayed on an inflated standard brain. The plots display the adaptation indices, and error bars represent the SEM.

(B) Experiment 2. There was significant bidirectional adaptation in the left PMv regardless of the order of stimulation (peak $p < 0.05$ corrected; see Figure S2 displaying the same amount of adaptation for the two orders of stimulation). The plots display the adaptation indices when first stimulating the participant's hand and then the other's hand (dark gray) or vice versa (light gray; see Figure 3 for details about the experimental design). The error bars represent the SEM. See also Figure S1.

has been consistently related to tasks in which the participant is required to "mentalize" the internal states of others [2]. Therefore, we speculate that the ACC might use the shared premotor peripersonal space to support higher-level representations of interacting individuals [21, 22]. A few behavioral studies have investigated the possibility that the representation of the peripersonal space might be modulated by the presence of another person, in either a static [22] or a social context [21]. Our results provide a possible neural basis for these behavioral modulations by showing the existence of a shared representation of peripersonal space for oneself and another person that is implemented by the same neuronal populations within the PMv.

Experimental Procedures

Subjects

Twenty-six participants (19–35 years old, mean ± SD age 28 ± 5 years; 18 males) took part in experiment 1, and 20 participants (22–42 years old, mean ± SD age = 29 ± 6; 12 males) took part in experiment 2 (five also participated in experiment 1). The study was approved by the Stockholm Regional Ethical Review Board (http://www.epn.se). Informed consent was obtained from all participants, none of whom had histories of neurological or sensory disorders.

Table 1. Experiment 1: Shared Representation of Peripersonal Space

Anatomical Location	MNI Coordinates (x, y, z)	Peak t Value	Peak p Value
Left inferior precentral sulcus (PMv)	−46, 2, 14	3.95	0.015
Right putamen	20, −6, 14	3.15	0.042
Right anterior cingulate gyrus	8, 36, −2	3.66	0.001[a]

$\{[(\text{Near Self}_{\text{Before LEFT}} - \text{Near Other})_{\text{Other LEFT}} + (\text{Near Self}_{\text{Before RIGHT}} - \text{Near Other})_{\text{Other RIGHT}}]$ versus $[(\text{Near Self}_{\text{Before RIGHT}} - \text{Near Prosthesis})_{\text{Other LEFT}} + (\text{Near Self}_{\text{Before LEFT}} - \text{Near Prosthesis})_{\text{Other RIGHT}}]\}$

[a] $p < 0.001$, uncorrected.

General Experimental Setup, Procedure, and Analyses

During the brain scans, participants lay comfortably in a supine position on the MRI table with their head tilted approximately 30 degrees forward to allow a direct view of an MR-compatible table (42 × 35 cm, with an adjustable slope), which was mounted on the bed above the subject's waist (Figure 1). The required tilt of the head was obtained by slanting the head coil using a custom-made wooden wedge at an angle of approximately 11 degrees. The participants' heads were tilted another 20 degrees using pillows and foam pads.

The visual stimulus consisted of a red ball (3 cm diameter) on the tip of a wooden stick (50 cm long) that moved for 3 s [10, 11]. The experimenters wore earphones and received auditory cues regarding the onset and location of the stimuli. A metronome (80 beats per minute), audible only to the experimenters, ensured a regular pace for the stimulation. The ball was moved up and down four times every 3 s by the trained experimenter holding the stick. The ball was moved perpendicular to the hand, stopping 2 cm above the index finger but never touching it. Using white curtains, all other objects in the scanner room were occluded from view, except the participant's hand on the table, the other person's hand, the prosthetic hand (in experiment 1), and the fixation point. Therefore, given the reduced field of view from within the scanner tunnel and the use of white curtains, the participant could not see the experimenter's hand; only the ball and a part of the stick were visible. The other hand and the prosthetic hand were presented in a similar visual orientation relative to the participant (first-person point of view) in all conditions to match the low-level visual inputs as closely as possible.

To control the participant's gaze, a circular object (2 cm diameter) mounted centrally served as the fixation point (10 cm from the tip of the participant's hand). An MR-compatible camera (MRC Systems) monitored the participants to ensure that fixation was maintained throughout all scanning sessions. To monitor the participant's alertness, we presented catch trials randomly during each run. These trials involved the object stopping for 3 s in either the first or the second part of a trial. The participants were instructed to press a button with the left hand as soon as they noticed (96% and 97% accuracy for the first and the second experiments, respectively). Catch trials were modeled as a regressor of no interest.

Please cite this article in press as: Brozzoli et al., A Shared Representation of the Space Near Oneself and Others in the Human Premotor Cortex, Current Biology (2013), http://dx.doi.org/10.1016/j.cub.2013.07.004

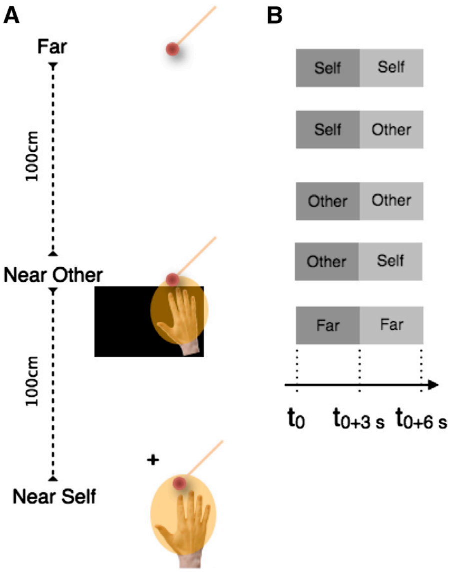

Figure 3. Methods, Experiment 2

(A) Schematic illustration of the spatial arrangement of the participant's hand and the other person's hand in the visual scene (the black cross represents the fixation point). In this experiment, the participant's right hand was always placed on the right side of the fixation point. Another person's hand was visible to the participant on a support located in the far position in the right visual hemifield (100 cm from the participant's hand).

(B) Temporal schema of the stimulation trials. The moving ball stimulus was presented near either the participant's or the other person's hand for 3 s each. The ball could appear near the participant's hand for 3 s and then near the other person's hand for 3 s, or vice versa. Trials with stimulation only near the participant's own hand (3 + 3 s) or exclusively near the other person's hand were also included. As a control condition for nonspecific effects, the physical stimulus could also appear for 3 + 3 s in a unique far position (100 cm from the other person's hand, i.e., 200 cm from the participant's hand). This design also allowed us to study the specific representation of perihand space for the participant and the other person separately (see Figures S2 and S3). In each of the three sessions, nine pairs of stimuli for each condition were presented in a fully randomized design.

fMRI Acquisition

fMRI acquisition was performed using a Siemens TIM Trio 3T scanner with a 12-channel head coil. Gradient echo T2*-weighted echo planar imagings with BOLD contrast were used as an index of brain activity. Each volume consisted of 40 continuous near-axial slices of 3 mm thickness (0.1 mm gap), encompassing the entire brain (field of view [FOV] = 58 × 76 matrix; 3 × 3 mm in-plane resolution; echo time [TE] = 40 ms; repetition time [TR] = 2,540 ms). Initial and final 15 s baseline recordings were included in each run. A high-resolution structural image was acquired for each participant at the end of the experiment (3D magnetization-prepared rapid gradient echo; voxel size = 1 × 1 × 1 mm; FOV = 250 × 250 mm; 176 slices; TR = 1,900 ms; TE = 2.27 ms; flip angle = 9°).

Table 2. Experiment 2: Shared Representation of Peripersonal Space: Bidirectional Adaptation

Anatomical Location	MNI Coordinates (x, y, z)	Peak t Value	Peak p Value
Left inferior precentral sulcus (PMv)	−42, 2, 24	3.77	0.016
Left inferior temporal gyrus	−36, −54, −10	5.13	0.036

[(Self$_{\text{before Other}}$ versus Other$_{\text{after Self}}$) ∩ (Other$_{\text{before Self}}$ versus Self$_{\text{after Other}}$)], exclusive mask by (Far$_{\text{before Far}}$ versus Far$_{\text{after Far}}$). $p < 0.01$, uncorrected.

Data Preprocessing and Analyses

fMRI data were analyzed with SPM8 (http://www.fil.ion.ucl.ac.uk/spm/). The first three volumes of each run were discarded because of non-steady-state magnetization. Functional images were realigned and coregistered with the high-resolution structural scan from each participant. The anatomical image was segmented into white matter, gray matter, and cerebrospinal fluid partitions and normalized to the Montreal Neurological Institute (MNI) standard brain. The same transformation was applied to all functional volumes, resampled to a 2 × 2 × 2 mm voxel size. The functional images were spatially smoothed (8 mm full width at half maximum isotropic Gaussian kernel).

In the first-level analyses, we defined regressors for the first and second parts of the visual stimulation (3 s each; see below for details regarding each experiment). The results of these analyses were used as contrast estimates for each condition and subject (contrast images) that were entered into a random-effects group analysis (second-level analysis) to accommodate intersubject variability. To account for the problem of multiple comparisons, we reported conclusions based on peaks of activation surviving a significance threshold of $p < 0.05$, corrected using the familywise error. For areas in which we have a priori hypotheses—the ventral premotor cortex, in particular—we corrected for the number of voxels in a small spherical search space using small-volume corrections centered at the peak coordinates from previous related studies [10, 11]. For each peak, the coordinates in MNI space and the t and p values were reported. The term "uncorrected" follows the p value in post hoc analyses that did not survive the correction for multiple comparisons, reported in a purely descriptive manner.

Experiment 1

Experimental Procedure

The positions of the moving ball stimulus are denoted as Stimulus near Self (Self), Stimulus Far Left (Far$_{\text{LEFT}}$), and Stimulus Far Right (Far$_{\text{RIGHT}}$); the sessions are denoted as Other person Left (Other$_{\text{LEFT}}$) or Other person Right (Other$_{\text{RIGHT}}$), depending on the location of the other person's right hand with respect to the fixation point (the rubber hand was in the contralateral location with respect to the other person's hand). For each of the two arrangements of the hands, 26 pairs of Self and then Far$_{\text{LEFT}}$ and Self and then Far$_{\text{RIGHT}}$ stimuli were presented in a fully randomized miniblock design. Thus, we had 26 trials with the stimulus first appearing near self and then other, and 26 trials with the self-stimulation followed by stimulation near the prosthetic hand (Figure 1D).

Data Analyses

In the first-level analyses, we defined four regressors: "Near Self$_{\text{Before LEFT}}$," "Near Self$_{\text{Before RIGHT}}$," "Far$_{\text{LEFT}}$," and "Far$_{\text{RIGHT}}$," containing the entire 3 s presentation of the corresponding stimulus in the same way as for the Other$_{\text{LEFT}}$ and Other$_{\text{RIGHT}}$ sessions. As a consequence, "Far$_{\text{LEFT}}$" during the Other$_{\text{LEFT}}$ session and "Far$_{\text{RIGHT}}$" during the Other$_{\text{RIGHT}}$ session both correspond to the moving ball stimulus appearing near the other person's hand ("Near Other"). By contrast, "Far$_{\text{LEFT}}$" during the Other$_{\text{RIGHT}}$ session and "Far$_{\text{RIGHT}}$" during the Other$_{\text{LEFT}}$ session both correspond to the stimulus appearing near the rubber hand ("Near Prosthesis").

The relevant contrast to test our hypothesis is the one-tailed interaction contrast, which is defined as {[(Near Self$_{\text{Before LEFT}}$ − Near Other)$_{\text{Other LEFT}}$ + (Near Self$_{\text{Before RIGHT}}$ − Near Other)$_{\text{Other RIGHT}}$] versus [(Near Self$_{\text{Before RIGHT}}$ − Near Prosthesis)$_{\text{Other LEFT}}$ + (Near Self$_{\text{Before LEFT}}$ − Near Prosthesis)$_{\text{Other RIGHT}}$]}.

We predicted a larger BOLD adaptation response when the moving ball was presented in the far position where the other person's hand was located (first term of the interaction: [(Near Self$_{\text{Before LEFT}}$ − Near Other)$_{\text{Other LEFT}}$ + (Near Self$_{\text{Before RIGHT}}$ − Near Other)$_{\text{Other RIGHT}}$]), as opposed to when the stimulus was subsequently presented in the far position near the prosthetic hand (second term of the interaction: [(Near Self$_{\text{Before RIGHT}}$ − Near Prosthesis)$_{\text{Other LEFT}}$ + (Near Self$_{\text{Before LEFT}}$ − Near Prosthesis)$_{\text{Other RIGHT}}$]). A one-tailed t test allowed us to highlight all the voxels showing stronger adaptation to the object presented near the two real hands compared to the response when the object was presented to a real and a fake hand. Importantly, this contrast allowed us to identify brain regions that displayed a significant interaction while rigorously controlling for all properties of the stimuli other than their proximity to or distance from the other person's and the prosthetic hands.

To assess whether the significant BOLD adaptation found in the left PMv was similarly present for the left and right locations of the other person's hand, we inspected the independent terms of the interaction. To this end, we studied the following contrasts, first separately and then in

Please cite this article in press as: Brozzoli et al., A Shared Representation of the Space Near Oneself and Others in the Human Premotor Cortex, Current Biology (2013), http://dx.doi.org/10.1016/j.cub.2013.07.004

conjunction, with both contrasts set at an uncorrected threshold of $p < 0.01$, as follows:

(1) Other person's hand to the left:

$$\begin{gathered}\big[(\text{Near Self}_{\text{Before LEFT}} - \text{Near Other})_{\text{Other LEFT}}\ \text{vs.}\\ (\text{Near Self}_{\text{Before RIGHT}} - \text{Near Prosthesis})_{\text{Other LEFT}}\big]\end{gathered}$$

(2) Other person's hand to the right:

$$\begin{gathered}\big[(\text{Near Self}_{\text{Before RIGHT}} - \text{Near Other})_{\text{Other RIGHT}}\ \text{vs.}\\ (\text{Near Self}_{\text{Before LEFT}} - \text{Near Prosthesis})_{\text{Other RIGHT}}\big]\end{gathered}$$

Experiment 2

Data Analyses

In the first-level analyses, we defined ten regressors (3 s each) named after the hand to which the stimulus was presented: "Self before Self" (SbS), "Self after Self" (SaS), "Other before Other" (ObO), "Other after Other" (OaO), "Self before Other" (SbO), "Other after Self" (OaS), "Other before Self" (ObS), "Self after Other" (SaO), "Far before Far" (FbF), and "Far after Far" (FaF) (Figure 3).

For studying the bidirectional adaptation between Self and Other, i.e., the adaptation that is independent of the order of stimulation, we first defined the contrasts (SbO versus OaS) and (ObS versus SaO) separately. These contrasts revealed voxels showing significant adaptation when stimulation near one's own hand follows or precedes stimulation near the other person's hand. We inspected the conjunction between the two contrasts to depict voxels that showed adaptation irrespective of the order of presentation. Because we were interested in voxels that showed significant adaptation for both the contrasts (SbO versus OaS) and (SbO versus OaS), we examined each of the two contrasts separately but used one as an inclusive mask for the other (at an uncorrected threshold of $p < 0.01$). It did not matter which contrast we used for the statistical inference and which we used as inclusive mask: both tests revealed significant ($p < 0.05$ corrected) activation in PMv (see Figures 2B and S1; SbO versus OaS: $p = 0.016$, $T = 3.77$ in [42, 2; 24]; ObS versus SaO: $p = 0.035$, $T = 3.56$ in [−40; 4; 24]). To exclude areas that displayed nonspecific adaptation effects to the presentation of a visual stimulus anywhere in space (such as early visual areas), we further applied an exclusive mask defined by the contrast (FbF versus FaF) with an uncorrected threshold of $p < 0.01$. This procedure revealed voxels that displayed significant and selective BOLD adaptation for the visual stimulus presented in the space near the hands; voxels showing adaptation for the far position were excluded.

Supplemental Information

Supplemental Information includes three figures, two tables, and Supplemental Results and Discussion and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.07.004.

Acknowledgments

This study was funded by the Swedish Foundation for Strategic Research, the European Research Council, the James S. McDonnell Foundation, the Swedish Research Council, and Söderberska Stiftelsen. C.B. was supported by Marie Curie Actions, and G.G. was supported by the Karolinska Institute's central doctoral program (KID). The fMRI scans were conducted at the MR Center at the Karolinska University Hospital in Huddinge, Stockholm, Sweden.

Received: April 15, 2013
Revised: June 17, 2013
Accepted: July 1, 2013
Published: September 5, 2013

References

1. Rizzolatti, G., and Craighero, L. (2004). The mirror-neuron system. Annu. Rev. Neurosci. *27*, 169–192.
2. Amodio, D.M., and Frith, C.D. (2006). Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. *7*, 268–277.
3. Kilner, J.M., Neal, A., Weiskopf, N., Friston, K.J., and Frith, C.D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. J. Neurosci. *29*, 10153–10159.
4. Newman-Norlund, R.D., van Schie, H.T., van Zuijlen, A.M.J., and Bekkering, H. (2007). The mirror neuron system is more active during complementary compared with imitative action. Nat. Neurosci. *10*, 817–818.
5. Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P., and Casile, A. (2009). Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. Science *324*, 403–406.
6. Rizzolatti, G., Scandolara, C., Matelli, M., and Gentilucci, M. (1981). Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. Behav. Brain Res. *2*, 147–163.
7. Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., and Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. Exp. Brain Res. *71*, 491–507.
8. Rizzolatti, G., Fadiga, L., Fogassi, L., and Gallese, V. (1997). The space around us. Science *277*, 190–191.
9. Ishida, H., Nakajima, K., Inase, M., and Murata, A. (2010). Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. J. Cogn. Neurosci. *22*, 83–96.
10. Brozzoli, C., Gentile, G., Petkova, V.I., and Ehrsson, H.H. (2011). FMRI adaptation reveals a cortical mechanism for the coding of space near the hand. J. Neurosci. *31*, 9023–9031.
11. Brozzoli, C., Gentile, G., and Ehrsson, H.H. (2012). That's near my hand! Parietal and premotor coding of hand-centered space contributes to localization and self-attribution of the hand. J. Neurosci. *32*, 14573–14582.
12. Grill-Spector, K., Henson, R., and Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. Trends Cogn. Sci. *10*, 14–23.
13. Clark, H.H., and Krych, M.A. (2004). Speaking while monitoring addressees for understanding. J. Mem. Lang. *50*, 62–81.
14. Sebanz, N., Bekkering, H., and Knoblich, G. (2006). Joint action: bodies and minds moving together. Trends Cogn. Sci. *10*, 70–76.
15. Williams, J.H., Waiter, G.D., Perra, O., Perrett, D.I., and Whiten, A. (2005). An fMRI study of joint attention experience. Neuroimage *25*, 133–140.
16. Flanagan, J.R., and Johansson, R.S. (2003). Action plans used in action observation. Nature *424*, 769–771.
17. Kilner, J.M., Vargas, C., Duval, S., Blakemore, S.J., and Sirigu, A. (2004). Motor activation prior to observation of a predicted movement. Nat. Neurosci. *7*, 1299–1301.
18. Ramnani, N., and Miall, R.C. (2004). A system in the human brain for predicting the actions of others. Nat. Neurosci. *7*, 85–90.
19. Caggiano, V., Fogassi, L., Rizzolatti, G., Pomper, J.K., Thier, P., Giese, M.A., and Casile, A. (2011). View-based encoding of actions in mirror neurons of area f5 in macaque premotor cortex. Curr. Biol. *21*, 144–148.
20. Oosterhof, N.N., Tipper, S.P., and Downing, P.E. (2012). Viewpoint (in) dependence of action representations: an MVPA study. J. Cogn. Neurosci. *24*, 975–989.
21. Teneggi, C., Canzoneri, E., di Pellegrino, G., and Serino, A. (2013). Social modulation of peripersonal space boundaries. Curr. Biol. *23*, 406–411.
22. Heed, T., Habets, B., Sebanz, N., and Knoblich, G. (2010). Others' actions reduce crossmodal integration in peripersonal space. Curr. Biol. *20*, 1345–1349.

Current Biology, Volume *23*

Supplemental Information

A Shared Representation
of the Space Near Oneself and Others
in the Human Premotor Cortex

Claudio Brozzoli, Giovanni Gentile, Loretxu Bergouignan, and H. Henrik Ehrsson

Supplemental Inventory

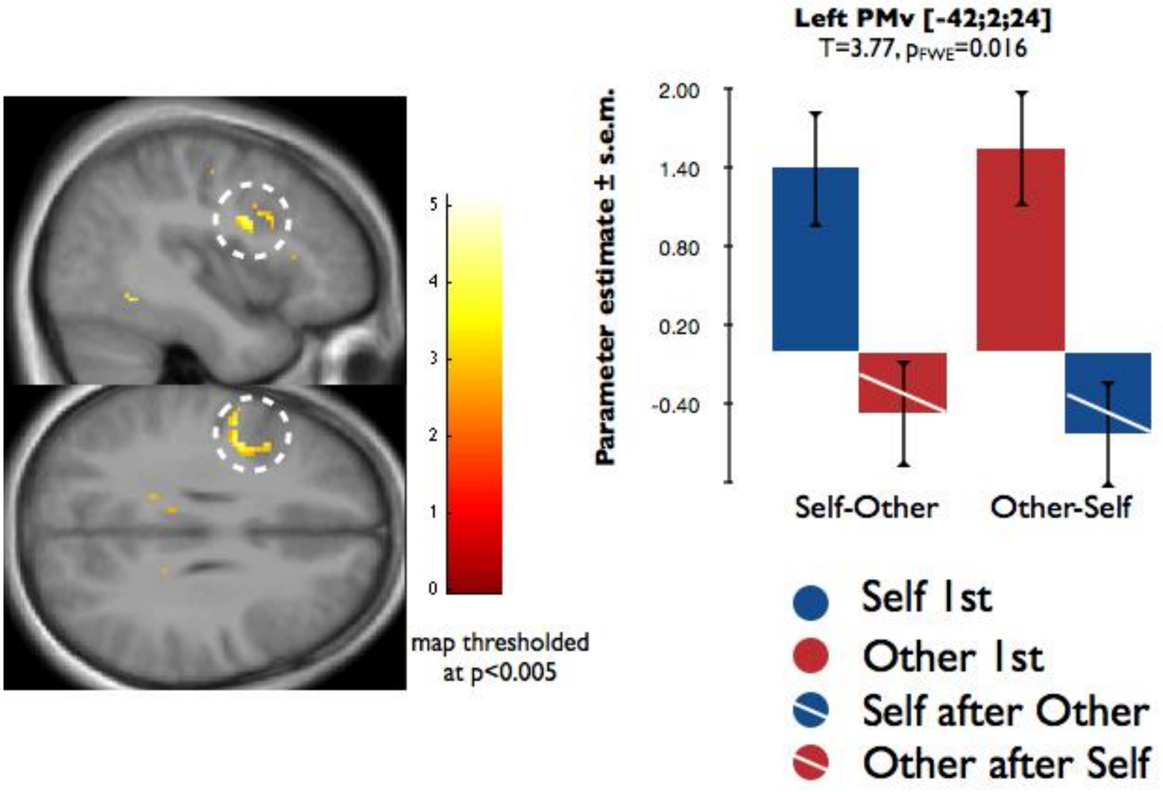

Figure S1. Experiment 2: Bidirectional Adaptation to the Object Near the Participant's and Another Person's Hand

To the left the white circle indicates the cluster of significantly bi-directionally adapting voxels in the left PMv (SbO vs OaS: $p=0.016$ corrected, $T=3.77$, in [-42, 2, 24]; voxels at $p<0.005$ uncorrected for display purposes; note that the corresponding contrast ObS vs. SaO was also significant: $p=0.035$ corrected, $T=3.56$ in [-40, 4, 24], data not shown in the figure) superimposed on the 20 participants average structural MRI. The crucial test for bidirectional adaptation shows that the left PMv adapts irrespective of the order of the presentation of the visual stimuli (plot in the figure). Bidirectional adaptation confirms that the left PMv contains a shared representation of the space near the hand of the participant and the space near the hand of the other person. To the left, the white circle indicates the cluster of voxels that show significant bi-directional adaptation in the left PMv (peak at $p< 0.05$ corrected; voxels at $p<0.005$ uncorrected for display purposes) superimposed on the average structural MRI of the 20 participants. The plot to the right shows the estimated effect size of the BOLD activation for the first and second part of each 6 s stimulation period. Taken together, the results of the first and second experiments support the conclusion that the perihand space of the participant and the other person is encoded within the same neuronal population in the left PMv.

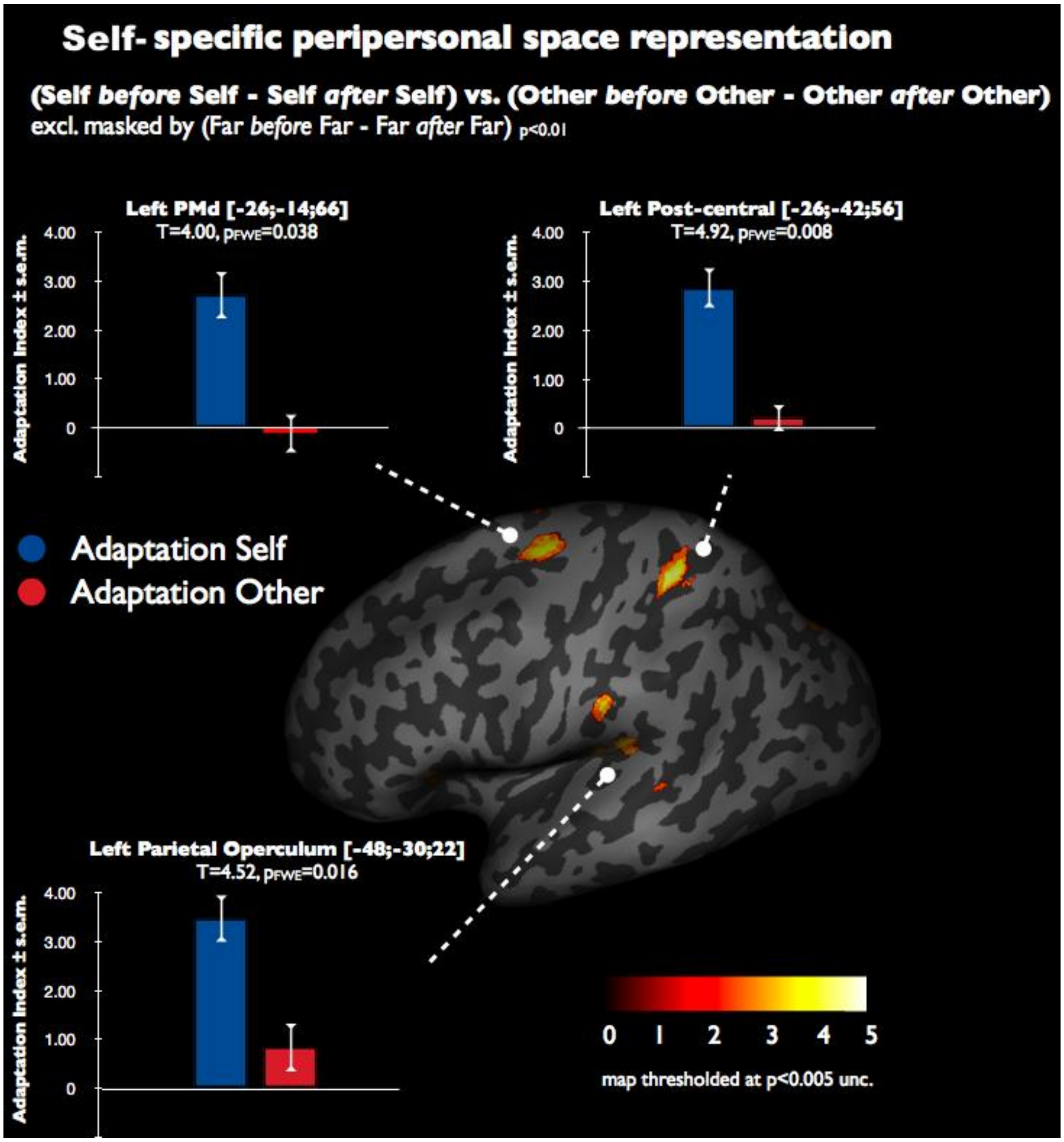

Figure S2. Experiment 2: Self-Specific Representation of Peripersonal Space in Parietal-Premotor Regions

The dorsal premotor (PMd) and parietal areas show selectivity for the space near the participant's hand. These areas show greater BOLD adaptation for the object presented near the participant's own hand compared to the object presented near the hand of the other individual. The clusters of voxels showing significant adaptation (peak $p<0.05$ corrected; voxels thresholded at $p<0.005$ uncorrected for display purposes) from the random effect group analysis are displayed on an inflated standard brain. The t-values and corrected p-values for each significant peak are indicated, together with the anatomical localization in standard space (x; y and z coordinates in MNI). The plots display the adaptation index, which are defined as the difference in contrast estimate when subtracting the second stimulation period from the first stimulation period (3 seconds each).

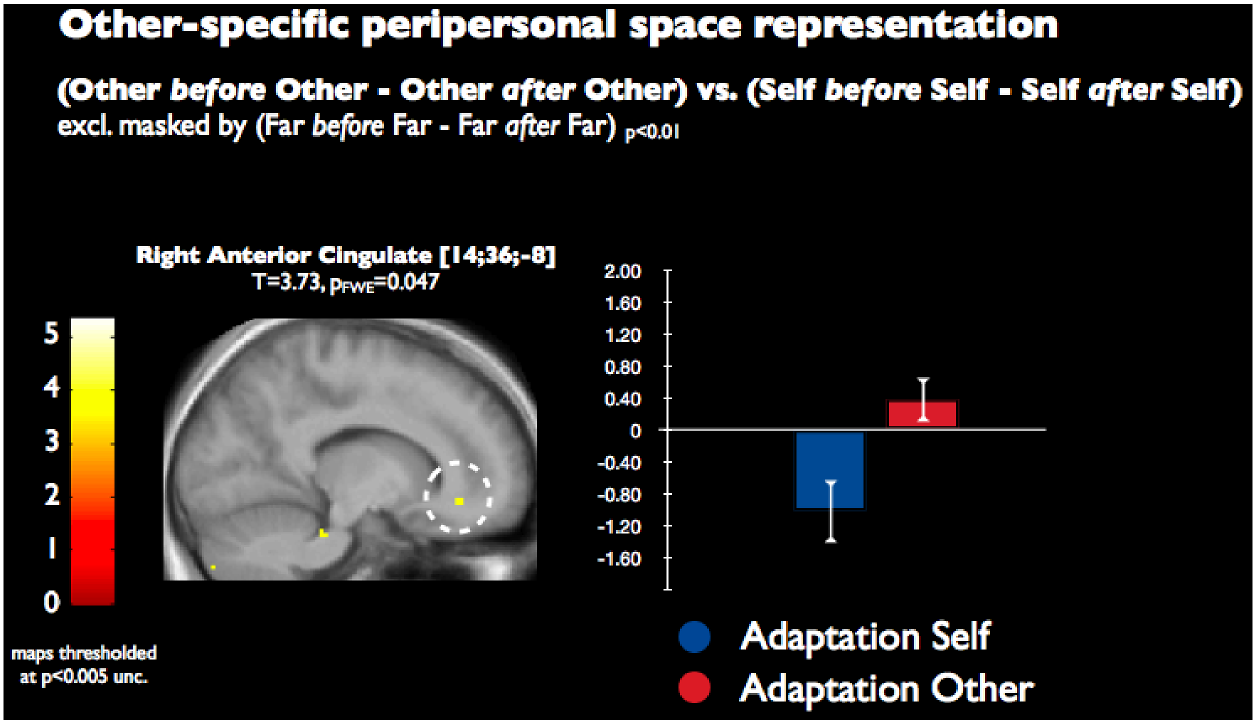

Figure S3. Experiment 2: Right Anterior Cingulate Cortex and Other's Hand-Centered Representation of Space

The right ACC shows greater BOLD adaptation for the moving object stimulus presented near the other's hand compared to near the participant's hand. The clusters of voxels showing significant adaptation (peak $p<0.05$ corrected; voxels thresholded at $p<0.005$ uncorrected for display purposes) from the random effect group analysis are displayed on the average structural MRI of the 20 participants (left). The plots to the right display the adaptation index, as defined above, for the six second periods of presenting the moving ball stimulus only near the participant's hand ("Adaptation Self") or only near the other's hand ("Adaption Other").

Table S1. Experiment 2: Self-Specific Peripersonal Space

Anatomical location	*MNI coordinates* *X Y Z*	*Peak* *t-value*	*Peak* *p-value*
Left post-central sulcus	-26 -42 56	4.92	0.008
Left superior precentral sulcus (PMd)	-26 -14 66	4.00	0.038
Left parietal operculum	-48 -30 22	4.52	0.016

[(Self *before* Self - Self *after* Self) vs. (Other *before* Other - Other *after* Other)]
exclusive mask by (Far *before* Far - Far *after* Far) $_{\text{p<0.01 unc.}}$

Table S2. Experiment 2: Other-Specific Peripersonal Space

Anatomical location	*MNI coordinates* *X Y Z*	*Peak* *t-value*	*Peak* *p-value*
Right anterior cingulate gyrus	14 36 -8	3.73	0.047
Right precentral sulcus/middle frontal gyrus (PMd)	34 8 52	4.24	0.026
Left anterior section of IPS/post-central sulcus	-42 -28 48	5.35	0.001†

[(Other *before* Other - Other *after* Other) vs. (Self *before* Self - Self *after* Self)]
exclusive mask by (Far *before* Far - Far *after* Far) $_{\text{p<0.01 unc.}}$

† p<0.001, uncorrected

Supplemental Results and Discussion

Experiment 1: Lateralized Responses

The first experiment revealed a significant 2x2 interaction of BOLD adaptation in a PMv cluster encompassing the left inferior part of the precentral sulcus and the precentral gyrus, as reported in the main text.

In **Table 1**, we list all the clusters of active adapting voxels that showed a similarly significant interaction. In addition to the significant effect in the left PMv as reported in the main text, we also noted clusters in the right putamen and, at a lower threshold ($p<0.001$ unc.), in the right ACC. These finding indicate that the activity of neuronal populations within the reported clusters adapts differentially for the real and the prosthetic hand after an identical presentation near the participant's own hand. However, it is still possible that such an effect might be specific to the right or left location of the other person's hand. To assess whether the significant interaction of BOLD adaptation found in the right putamen and the right ACC was present for both locations of the other person's hand, we inspected the independent terms of the interaction. To this end, we studied the following contrasts, first separately and then in conjunction: [(Near Self $_{\text{Before LEFT}}$ - Near Other) $_{\text{Other LEFT}}$ vs. (Near Self $_{\text{Before RIGHT}}$ - Near Prosthesis) $_{\text{Other LEFT}}$] or [(Near Self $_{\text{Before RIGHT}}$ - Near Other) $_{\text{Other RIGHT}}$ vs. (Near Self $_{\text{Before LEFT}}$ - Near Prosthesis) $_{\text{Other RIGHT}}$]. Both contrasts were set at an uncorrected threshold of $p<0.01$.

The right rostral ACC showed significantly larger BOLD adaptation to the object presented first near the self and then near the other's hand compared to the artificial hand. The adaptation was similar for both locations of the other person's hand (conjunction: $T=2.79$, $p<0.001$ unc.). However, neither the single contrasts nor the conjunction contrast reached statistical significance; therefore, the ACC responses remain a purely descriptive observation. Finally, the right putamen showed stronger adaptation between self and other hand than between self and the prosthetic hand *only* when the other person's hand was in the left hemispace ($T=3.86$, $p_{\text{FWE-corrected}}=0.007$).

The post-hoc analyses described herein are not perfectly counterbalanced in terms of the lateralization of the visual information regarding the probe and the hands in the visual scene. One should, therefore, be cautious in drawing conclusions based only on the results of these contrasts. The post-hoc analysis, nevertheless, indicates a possible involvement of the right ACC in the representation of the space around one's own hand and the space around another person's hand. This possibility was further investigated in the second experiment. In contrast, the right putamen seems to show a preference for the condition in which the other person's hand is presented in the left visual hemispace. This finding, together with the fact that we did not find bidirectional adaption in the putamen in our second experiment (see below), brings into question the existence of perihand space neurons with mirror properties in the putamen and indicates that further studies are warranted.

Experiment 2: Bidirectional Adaptation in Inferior Temporal Cortex

As reported in **Table 2** and discussed in the main text, the results of the conjunction contrast confirmed that the left PMv showed significant adaptation to the object presented in proximity to the participant's hand as well as to the object presented in proximity to the other person's hand. The analysis further revealed adapting activity in the posterior temporal cortex. Activation in this area has been previously reported in tasks involving the visual perception of body parts and biological movements of the hand [1-2] as well as in tasks involving predictions about the goal of an action performed by someone else [3]. On the basis of this ensemble of results, some authors have suggested that inferior and posterior temporal areas might be part of a wider "action understanding" network [4-6] that extends beyond the fronto-parietal mirror neuron system [7]. Although these studies are intriguing, the adaptation found in the posterior temporal cortex in the present study is more plausibly linked to the appearance of the hand in the visual scene rather than to a shared representation of the perihand space for the self and another *real* person. In our first experiment, the presence of a realistic prosthetic hand allowed us to control for low-level visual effects linked to the proximity of the moving stimulus to the hand-shaped object; under these conditions, we did not detect BOLD adaptation in the posterior temporal area. Nonetheless, we tested this possible interpretation of the inferior temporal adaptation. We used the coordinates of the significant peaks of activation in the inferior temporal cluster of the second experiment to conduct two post-hoc small-volume correction analyses with the data from the first experiment. One correction analysis tested the adaptation when the moving ball was presented first near the participant's hand and subsequently near the prosthetic hand. The other analysis tested the interaction contrast, that is, greater adaptation when the stimulus is presented near the other person's hand compared to the prosthetic hand. Logically, if the adaptation in the inferior temporal areas reflects the encoding of the physical stimulus with respect to an external (hand-shaped) object, one would expect the adaptation to be present regardless of the real or rubber nature of the other hand. Conversely, such an adaptation should not be present in the interaction contrast that examines differences between the other's hand and prosthetic hand (in which the visual information regarding the hand shaped objects is counterbalanced). As predicted, these analyses revealed a significant adaptation in the inferior temporal area (MNI coordinates $x=-34$, $y=-62$, $z=-14$; $T=7.00$, $p_{\text{FWE-corrected}}<0.001$) in response to the stimulus presented near the self and then near the prosthetic hand. Moreover, the interaction contrast that controlled for the low-level visual aspects of seeing hand-shaped objects did not show any significant activation within the inferior temporal area, even at a lower threshold ($p<0.01$ unc.). These two observations argue against the possibility that the inferior temporal cortex contains a shared peripersonal space representation for self and other.

Experiment 2: Self-Specific Representation of Peripersonal Space in Parietal-Premotor Areas

The setup and design of Experiment 2 allowed us to identify the brain regions involved in representing an independent perihand space for one's own hand and for another person's hand. The moving ball was presented either near the participant's or the other person's hand for 3+3 s and, as a control condition, in a far position for 3+3 s (100 cm from the other person's hand and 200 cm from the participant's hand). We then measured the adaptation to the repeated presentation of the physical stimulus near the participant's hand compared to the other person's hand, while excluding the adaptation to the stimulus presented in a far position. In particular, for the Self-specific representation of peripersonal space, we defined and inspected the following contrast:

Self-specific peripersonal space:

> [(Self *before* Self - Self *after* Self) vs. (Other *before* Other - Other *after* Other)]
> exclusive mask by (Far *before* Far - Far *after* Far) $_{p<0.01\ \text{unc.}}$

We confirmed that brain regions within the parieto-prefrontal network (**Figure S2**) selectively encode an object near the participant's hand [8-9]. The superior section of the precentral gyrus (dorsal premotor cortex, PMd), a cluster encompassing the post-central gyrus at the junction with the intraparietal sulcus and the inferior parietal lobe (parietal operculum) of the left hemisphere, showed significantly more adaptation to the object presented close to the participant's hand than to the object presented close to the other person's hand (**Table S1**).

These results are consistent with our previous findings and with information available from electrophysiological recordings in monkeys. Single-cell recordings in the posterior parietal and premotor cortices of macaques identified peripersonal space neurons that possess both tactile and visual receptive fields. The visual receptive fields are restricted to the space extending 30–40 cm from the location of the tactile receptive field [10-14]. The spatial alignment of visual and somatosensory receptive fields allows for the construction of a body part-centered representation of the peripersonal space [15-16]. The responses of perihand neurons to an object approaching the limb are "anchored" to the hand itself, such that when the arm moves, the visual receptive fields are updated accordingly [17]. Importantly, estimates of the proportion of such peripersonal space neurons that have mirror properties suggest that mirror neurons constitute a relatively low overall percentage (57 of 541 visuo-tactile neurons recorded in Ishida and colleagues' study presented mirror responses). Thus, the finding of stronger adaptation responses to repeated stimulation near one's own hand compared to another person's hand in frontal and parietal areas is consistent with the presence of a relatively low number of mirror neurons in the fronto-parietal circuits representing peripersonal space.

Experiment 2: Right Anterior Cingulate Cortex and Other's Specific Representation

As for the Self-specific representation of the perihand space, we defined and inspected the following contrast to study the possible hand-centered encoding of an object in the space near someone else's hand:

Other-specific peripersonal space:

> [(Other *before* Other - Other *after* Other) vs. (Self *before* Self - Self *after* Self)]
> exclusive mask by (Far *before* Far - Far *after* Far) $_{p<0.01\ \text{unc.}}$

The contrast revealed significant activations (**Table S2**) in a cluster covering part of the dorsal section of the right pre-central sulcus and middle frontal gyrus (PMd) and the right anterior cingulate cortex. At a lower threshold, a region within the left post-central sulcus and intra-parietal sulcus reached significance (p<0.001 unc.; see **Table S2**).

Summarizing the results of the two experiments, it appears that the right ACC shows stronger BOLD adaptation when the object is presented close to the real hand of another person rather than close to an artificial rubber hand following presentation near the participant's own hand (experiment 1, interaction contrast at lower threshold). Further, the ACC shows stronger adaptation to an object presented near someone else's hand rather than one's own hand (experiment 2; **Figure S3**). This pattern of results suggests that the right ACC is involved in the encoding of an object close to a real hand belonging to another person. This conclusion is supported by the fact that even with a very low threshold (p<0.01 unc.), the ACC does not exhibit significant adaptation for the moving object presented near the participant's own hand (self-specific peripersonal space contrast, see previous section). Interestingly, a meta-analysis of medial frontal cortex (MFC) activations [18] suggests that social cognition tasks that involve self-knowledge [19], person perception [20-24] and mentalizing [25-30] activate areas in the anterior rostral MFC. These findings are in accordance with the cluster of activation we found in the right perigenual ACC in the present study. Our finding is therefore in good accordance with the information available in literature, attributing a role to the medial frontal cortex (MFC) in social cognition [28] for the representation of self and other [29] and in joint attention [30]. This finding opens the possibility of a link between the low-level perceptual representation of space shared between self and others and the high-level representations of others available for social interactions.

Supplemental References

S1. Pelphrey, K.A., Morris, J.P., and McCarthy, G. (2004). Grasping the intentions of others: the perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. J. Cogn Neurosci. *16*, 1706-1716.

S2. Pelphrey, K.A., Morris, J.P., Michelich, C.R., Allison, T., and McCarthy, G. (2005). Functional anatomy of biological motion perception in posterior temporal cortex: an FMRI study of eye, mouth and hand movements. Cereb. Cortex. *15*, 1866-1876.

S3. Ramsey, R., and Hamilton, A.F. (2010). Understanding actors and object-goals in the human brain. Neuroimage. *50*, 1142-1147.

S4. Grafton, S.T., and Hamilton, A.F. (2007). Evidence for a distributed hierarchy of action representation in the brain. Hum. Mov. Sci. *26*, 590-616.

S5. Decety, J., and Grèzes, J. (1999). Neural mechanisms subserving the perception of human actions. Trends Cogn Sci. *3*, 172-178.

S6. Grèzes, J., and Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. Hum. Brain Mapp. *12*, 1-19.

S7. Rizzolatti, G., and Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. Nat. Rev. Neurosci. *11*, 264-74.

S8. Brozzoli, C., Gentile, G., Petkova, V.I., and Ehrsson H.H. (2011). fMRI-adaptation reveals a cortical mechanism for the coding of space near the hand. J. Neurosci. *31*, 9023-9031.

S9. Brozzoli, C., Gentile, G., and Ehrsson, H.H. (2012). That's near my hand! Parietal and premotor coding of hand-centered space contributes to localization and self-attribution of the hand. J. Neurosci. *32*, 14573-14582.

S10. Hyvärinen, J., and Poranen, A. (1974). Function of the parietal associative area 7 as revealed from cellular discharges in alert monkeys. Brain *97*, 673-692.

S11. Rizzolatti, G., Scandolara, C., Matelli, M., and Gentilucci, M. (1981a). Afferent properties of periarcuate neurons in macaque monkeys. I. Somatosensory responses. Behav. Brain Res. *2*, 125-146.

S12. Rizzolatti, G., Scandolara, C., Matelli, M., and Gentilucci, M. (1981b). Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. Behav. Brain Res. *2*, 147-163.

S13. Graziano, M.S., Yap, G.S., and Gross, C.G. (1994). Coding of visual space by premotor neurons. Science *266*, 1054-1057.

S14. Duhamel, J.R., Colby, C.L., and Goldberg, M.E. (1998). Ventral intraparietal area of the macaque: congruent visual and somatic response properties. J. Neurophysiol. *79*, 126-136.

S15. Graziano, M.S., and Gross, C.G. (1993). A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. Exp. Brain Res. *97***,** 96-109.

S16. Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M., and Rizzolatti, G. (1996). Coding of peripersonal space in inferior premotor cortex (area F4). J. Neurophysiol. *76*, 141-157 .

S17. Graziano, M.S., Hu, X.T., and Gross, C.G. (1997). Visuospatial properties of ventral premotor cortex. J. Neurophysiol. *77***,** 2268-2292.

S18. Amodio, D.M., and Frith, C.D. (2006). Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. *7*, 268-277.

S19. Johnson, S.C. et al. Neural correlates of self reflection. Brain *125*, 1808-1814 (2002).

S20. Mitchell, J.P., Heatherton, T.F., and Macrae, C.N. (2002). Distinct neural systems subserve person and object knowledge. Proc. Natl Acad. Sci. USA *99*, 15238-15243.

S21. Mason, M.F., Banfield, J.F., and Macrae, C.N. Thinking about actions: the neural substrates of person knowledge. Cereb. Cortex *14*, 209-214 (2004).

S22. Mitchell, J., Macrae, C., and Banaji, M. (2005). Forming impressions of people versus inanimate objects: social cognitive processing in the medial prefrontal cortex. Neuroimage *26*, 251-257.

S23. Iacoboni, M., Lieberman, M.D., Knowlton, B.J., Molnar-Szakacs, I., Moritz, M., Throop, C.J., and Fiske, A.P. (2004). Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD-fMRI signal increases compared to a resting baseline. Neuroimage *21*, 1167-1173.

S24. Harris, L.T., Todorov, A., and Fiske, S.T. (2005). Attributions on the brain: neuro-imaging dispositional inferences, beyond theory of mind. Neuroimage *28*, 763-769.

S25. Walter, H., Adenzato, M., Ciaramidaro, A., Enrici, I., Pia, L., and Bara, B.G. (2004). Understanding intentions in social interaction: the role of the anterior paracingulate cortex. J. Cogn. Neurosci. *16*, 1854-1863.

S26. Grezes, J., Frith, C., and Passingham, R.E. (2004). Brain mechanisms for inferring deceit in the actions of others. J. Neurosci. *24*, 5500-5505.

S27. Gallagher, H.L., Jack, A.I., Roepstorff, A., and Frith, C.D. (2002). Imaging the intentional stance in a competitive game. Neuroimage *16*, 814-821.

S28. Schilbach, L., Wohlschlaeger, A.M., Kraemer, N.C., Newen, A., Shah, N.J., Fink, G.R., and Vogeley, K. (2006). Being with virtual others: neural correlates of social interaction. Neuropsychologia *44*, 718-730.

S29. Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happé, F., Falkai, P., Maier, W., Shah, N.J., Fink, G.R., and Zilles, K. (2001). Mind reading: neural mechanisms of theory of mind and self-perspective. Neuroimage *14*, 170-181.

S30. Williams, J.H., Waiter, G.D., Perra, O., Perrett, D.I., and Whiten, A. (2005). An fMRI study of joint attention experience. Neuroimage *25*, 133-140