Multisensory Mechanisms in Temporo-Parietal Cortex Support Self-Location and First-Person Perspective

Silvio Ionta,1,5 Lukas Heydrich,1,4,5 Bigna Lenggenhager,1 Michael Mouthon,1 Eleonora Fornari,3 Dominique Chapuis,2,6 Roger Gassert,2,6 and Olaf Blanke1,4,*

1Laboratory of Cognitive Neuroscience
2Robotic Systems Laboratory
Ecole Polytechnique Fédérale de Lausanne (EPFL), Lausanne, 1015, Switzerland
3Department of Radiology, CIBM-CHUV unit, Centre Hospitalier Universitaire Vaudois and University of Lausanne, Lausanne, 1011, Switzerland
4Department of Neurology, University Hospital, Geneva, 1211, Switzerland
5These authors contributed equally to this work
6Present address: Rehabilitation Engineering Laboratory, Eidgenössische Technische Hochschule Zürich (ETHZ), LEO B 9.1, Leonhardstrasse 27, 8092 Zurich, Switzerland
*Correspondence: olaf.blanke@epfl.ch
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SUMMARY

Self-consciousness has mostly been approached by philosophical enquiry and not by empirical neuroscience, leading to an overabundance of diverging theories and an absence of data-driven theories. Using robotic technology, we achieved specific bodily conflicts and induced predictable changes in a fundamental aspect of self-consciousness by altering where healthy subjects experienced themselves to be (self-location). Functional magnetic resonance imaging revealed that temporo-parietal junction (TPJ) activity reflected experimental changes in self-location that also depended on the first-person perspective due to visuo-tactile and visuo-vestibular conflicts. Moreover, in a large lesion analysis study of neurological patients with a well-defined state of abnormal self-location, brain damage was also localized at TPJ, providing causal evidence that TPJ encodes self-location. Our findings reveal that multisensory integration at the TPJ reflects one of the most fundamental subjective feelings of humans: the feeling of being an entity localized at a position in space and perceiving the world from this position and perspective.

INTRODUCTION

How can a human brain develop self-consciousness? What are the brain mechanisms involved in this process? Extending earlier data from neurological patients (Critchley, 1953; Hécaen and Ajuriaguerra, 1952; Schilder, 1935), recent neurological theories stress the importance of bodily processing for the self and self-consciousness. These theories highlight the importance of interoceptive, proprioceptive, and motor signals and their multisensory and sensorimotor integration with other bodily signals (Damasio, 1999; Frith, 2005; Gallagher, 2000; Jeannerod, 2003), but do not indicate how such integration induces key subjective states such as self-location (“Where am I in space?”) and the first-person perspective (“From where do I perceive the world?”) and which neural mechanisms are involved (Blanke and Metzinger, 2009). Data from neurological patients suffering from out-of-body experiences (OBEs) provide such evidence, showing that focal brain damage may lead to pathological changes of the first-person perspective and self-location (Blanke et al., 2002; De Ridder et al., 2007), due to interference with the integration of multisensory bodily information at the TPJ. It was argued that such changes in first-person perspective and self-location are due to a double disintegration of bodily signals, a disintegration between somatosensory (proprioceptive and tactile) and visual signals combined with an additional visuo-vestibular disintegration (Blanke et al., 2004; Lopez et al., 2008); yet this has not been tested experimentally. Moreover, there is a low number of investigated cases, and OBEs have been associated with many different brain structures: the right and left TPJ (Blanke et al., 2002, 2004; Brandt et al., 2005; Maillard et al., 2004) and several structures within the TPJ (Blanke et al., 2002, 2005; Heydrich et al., 2011; Brandt et al., 2005; De Ridder et al., 2007; Maillard et al., 2004), precuneus (De Ridder et al., 2007), and fronto-temporal cortex (Devinsky et al., 1989). Accordingly, it is not clear which of these structures are involved in abnormal conscious states of first-person perspective and self-location and the significance of these clinical findings for self-consciousness under normal conditions.

Recent behavioral and physiological work, using video-projection and various visuo-tactile conflicts, showed that self-location can also be manipulated experimentally in healthy participants (Ehrsson, 2007; Lenggenhager et al., 2007). Thus, synchronous stroking of the participant’s back and the back of a visually presented virtual body led to changes in self-location (toward a virtual body at a position outside the participant’s bodily borders) and self-identification with the virtual body (Lenggenhager et al., 2007). So far, these experimental findings and techniques have not been integrated with neuroimaging, such as fMRI, probably because the above-mentioned experimental setups require
participants to sit, stand, or move, and it is difficult to apply and film the visuo-tactile conflicts on the participant’s body in a well-controlled manner during standard fMRI acquisitions. The neural mechanisms of a fundamental aspect of self-consciousness, self-location, under normal and pathological conditions have therefore remained elusive and are addressed here.

In the present fMRI study, we adapted a previous research protocol to the MR-environment: the “Mental Ball Dropping” (MBD) task (Lenggenhager et al., 2009). We manipulated the synchrony between the stroking of the participant’s back and the back of a visually presented virtual human body to induce changes in self-location. In the MBD task, participants were asked to estimate the time that a ball they were holding in their hands would take to hit the ground if they were to release it, providing repeated quantifiable measurements of self-location (height above the ground) during scanning (see Supplemental Information available online). We expected longer response times (RTs) for higher self-location and shorter RTs for lower self-location (Lenggenhager et al., 2009). The visual stimuli in the experimental conditions (Supplemental Information), presented through video goggles, consisted of short movies showing a back view of the virtual body filmed from an elevated position (Lenggenhager et al., 2009) (body conditions) being stroked by a sphere positioned at the end of a rod and moving vertically along the midline of the virtual person’s back (Figure 1A). The video during the control conditions only showed the moving rod and stimulator without the person’s body (no-body conditions; Figure 1B). A custom-built robotic device (Figures 1C and 1D) allowed us to control the trajectory of tactile stimulation of the participant’s back in both body and control conditions (using the same movement profile). This trajectory either matched (synchronous) or did not match (asynchronous) the applied tactile stimuli to the visually displayed position of the virtual rod (Supplemental Information). Thus, we precisely controlled the spatial and temporal aspects of the stimulation sphere’s movement during scanning within and across participants (Supplemental Information). Participants performed the MBD task under four different conditions according to a 2 × 2 factorial design with Object (body; no-body) and Stroking (synchronous; asynchronous) as main factors. Immediately after the fMRI session (before the acquisition of the anatomical images), participants completed a six-items questionnaire (Supplemental Information) to measure the experienced direction of the first-person perspective and illusory self-identification with the virtual body (Lenggenhager et al., 2007) (Table S1).

To define the structures that are involved in abnormal states of first-person perspective and self-location, we also studied a large group of neurological patients suffering from OBEs...
Table 1. Free Reports during Robotic Visuo-Tactile Stroking

<table>
<thead>
<tr>
<th>A Condition</th>
<th>Up-Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>S3 S</td>
<td>&quot;This time the only thing that made me doubt that the filmed body was not me, is that I could not see the hands. Indeed I had the clear impression of floating even if I knew I was not moving.&quot;</td>
</tr>
<tr>
<td>AS</td>
<td>&quot;Always well relaxed but the fact that I could not feel the same thing that I was watching disturbed me.&quot;</td>
</tr>
<tr>
<td>S5 S</td>
<td>&quot;When I focused to estimate the timing, it was as if I did not feel anymore what was happening on my back, as if I was only watching the video in front of me.&quot;</td>
</tr>
<tr>
<td>AS</td>
<td>&quot;It was clear that I was watching a movie unrelated to my experience.&quot;</td>
</tr>
<tr>
<td>S8 S</td>
<td>&quot;I felt rising in a strange way towards the roof.&quot;</td>
</tr>
<tr>
<td>AS</td>
<td>&quot;I had the impression of watching a video in the rewind mode.&quot;</td>
</tr>
<tr>
<td>S12 S</td>
<td>&quot;I did not have any particular sensation despite a general, but nevertheless mild, elevation.&quot;</td>
</tr>
<tr>
<td>AS</td>
<td>&quot;Not even elevation.&quot;</td>
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<table>
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<tr>
<th>B Condition</th>
<th>Down-Group</th>
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<tr>
<td>S4 S</td>
<td>&quot;I was looking at my own body from above. The perception of being apart from my body was a bit weak but still there. I saw the stick moving onto my back and I perceived it to be somehow at odds with what I was looking at.&quot;</td>
</tr>
<tr>
<td>AS</td>
<td>&quot;This time what I felt on my back did not correspond at all to what I saw. I had the impression of being very far from the real me.&quot;</td>
</tr>
<tr>
<td>S9 S</td>
<td>&quot;I felt myself a bit floating but in a descendent direction. On the contrary of the reality I had the impression that my body was thicker as if front and back were not as close as before the stick touched my back.&quot;</td>
</tr>
<tr>
<td>AS</td>
<td>&quot;I felt like I was watching someone else’s body from above, while someone was rubbing my chest with a stick. I also felt as being above the body I was watching at. I felt I was physically located above the body I was watching.&quot;</td>
</tr>
<tr>
<td>S11 S</td>
<td>&quot;I asked myself: if the one that I see in the movie is me, how can they move the mattress up and down?&quot;</td>
</tr>
<tr>
<td>AS</td>
<td>&quot;I felt as if I was floating high and I did not know where I was.&quot;</td>
</tr>
<tr>
<td>S17 S</td>
<td>&quot;At the beginning I was expecting to feel the stick on my front side, but then I realized that it was touching my back. I felt as if I was laying on myself, face to face.&quot;</td>
</tr>
<tr>
<td>AS</td>
<td>&quot;I felt as if I was floating, very light, without weight. I had the impression of feeling the impact of a surface on my back as if I was touching the roof.&quot;</td>
</tr>
</tbody>
</table>

Participants were asked to write down what they experienced during synchronous (S) and asynchronous (AS) visuo-tactile stroking conditions. Selected responses are listed for participants from the Up-group (A) and the Down-group (B).

See also Table S4.

(Blanke et al., 2002, 2004; Heydrich et al., 2011; Devinsky et al., 1989; Maillard et al., 2004). We performed quantitative lesion analysis (Rorden et al., 2007a) and compared the distribution of brain lesions in nine OBE-patients with those of eight other patients showing complex hallucinations involving people or faces, but without abnormal self-location, self-identification, or first-person perspective (control group; Table S3). This allowed us to determine the anatomical sub-regions of maximal lesion overlap and to perform statistical comparisons contrasting the lesions of OBE and control patients (voxel-based lesion symptom mapping; VLSM) (Bates et al., 2003a). Based on previous data in patients with OBEs, we predicted to find maximal involvement of the TPJ. Based on these clinical data, we also predicted that the BOLD response of this structure in healthy subjects would reflect changes in self-location that are dependent on the experimental factors Stroking and Object. Importantly, we further predicted that TPJ activity should also reflect changes in self-location that depend on the direction of the first-person perspective because (1) such changes are a key element of OBEs and because (2) we were able to manipulate the experienced direction of the first-person perspective and its influence on self-location with our robotic stroking setup (interaction between Stroking, Object, and Perspective; see next section).

RESULTS

Robotically-Induced Changes in the Direction of the First-Person Perspective

Earlier pilot questionnaire data revealed that, next to self-location and self-identification, we were also able to manipulate the experienced direction of the first-person perspective. In the pilot study, several participants mentioned spontaneously that they felt as if they were looking down at the virtual body (even though they were physically in a supine position and facing upward). Thus, for the present study, we added a related question (question 1; Q1) to the questionnaire (Table S1). To answer Q1, while being still within the MR-scanner, our participants were asked to indicate the direction of their experienced first-person perspective by placing a cursor on one out of three possible answers (up, not sure, down). After the fMRI session, all participants were, in addition, asked to write a free report about their experience during the stroking (Table 1; Table S4). With respect to Q1, participants who chose the “not sure” response were also interviewed after the experiment and asked to estimate which perspective they used most of the time. On the basis of both written free reports and interviews, the most frequent perspective across conditions was determined for these participants and allowed us to assign all participants to either the Up- or the Down-group. As in the pilot study, in the present study we found that many participants reported looking always upward (n = 10) or looking for most of the time upward (n = 1) at the virtual body located above them (i.e., congruent with their physical perspective: Up-group, n = 11). Selected experiences of the Up-group participants during the synchronous and asynchronous body conditions are listed in Table 1A. The remaining participants reported that they had the impression that they were always looking down (n = 6) or were for most of the time...
considering each group of participants. This led to a 2 × 2 × 2 factorial design with Perspective (up; down) as in-between factor, and Object (body; no-body) and Stroking (synchronous; asynchronous) as within factors that were applied to the analysis of self-location, self-identification, and the fMRI data.

RoboticInduced Changes in Self-Location and Self-Identification
Statistical analysis of RTs in the MBD task showed that self-location depended on Object, Stroking, and Perspective [significant three-way interaction; F(1,20) = 4.4; p < 0.05]. Post hoc comparisons showed that in the body conditions, the participants of the Up-group (participants experiencing themselves to be looking upward at the visually presented body) estimated self-location as higher (longer RTs) during the synchronous (1071 ms) compared with the asynchronous stroking (991 ms; p < 0.01; Figure 2A). The opposite pattern was found in the Down-group (participants experiencing that they were looking downward at the virtual body): lower self-location and shorter RTs during the synchronous stroking (1047 ms) with respect to the asynchronous stroking while viewing the body (1138 ms; p < 0.03; Figure 2B). No significant differences were found between synchronous and asynchronous stroking in the control conditions in both groups (all p > 0.2; see Figures 2A and 2B).

To summarize these findings, participants from the Up-group experienced themselves to be looking up at the body above looking down (n = 5) at the virtual body located below them (i.e., incongruent with their physical perspective: Down-group, n = 11). Selected experiences of the Down-group participants during the synchronous and asynchronous body conditions are listed in Table 1B. In summary, whereas several participants felt as if they were looking upward at the virtual body “above them” (Up-group), the remaining participants had the impression that they were looking down at the virtual body “below them” (Down-group). This was found despite somatosensory, motor, and cognitive cues from our participants about their body position (they were lying on their back, facing upward, and were head-constrained in the head coil; Figure 1E; Supplemental Information). Based on these findings, we carried out data analysis considering each group of participants. This led to a 2 × 2 × 2 factorial design with Perspective (up; down) as in-between factor, and Object (body; no-body) and Stroking (synchronous; asynchronous) as within factors that were applied to the analysis of self-location, self-identification, and the fMRI data.
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Temporo-Parietal Junction Encodes Self-Location

Figure 3. Questionnaire Scores
Self-identification with the virtual body (Q3) and mislocalization of touch toward the virtual body (Q6) are stronger during the synchronous stroking condition in both the Up-group and Down-group. Orange bars indicate ratings in the synchronous stroking condition. Red bars indicate ratings in the asynchronous stroking condition. Asterisks indicate significant differences. Error bars indicate standard error.

See also Table S1.

The cluster at the right TPJ was also centered on the pSTG. Mimicking behavioral changes in self-location and the reported first-person perspective, left TPJ activation in the Up- and Down-groups differed between synchronous and asynchronous stroking only during the body conditions (Figure 4A). In the Up-group, the BOLD response during the synchronous-body condition (~0.14%) was lower than in the asynchronous-body condition (0.73%; F(1,20) = 6.1; p < 0.02). The opposite effect was found in the Down-group, where the BOLD response during the synchronous-body condition (1.22%) was higher than in the asynchronous-body condition (0.42%; p < 0.03). The difference between synchronous and asynchronous stroking in the control conditions was not significant in both groups (all p > 0.15; Supplementary Information). We also found a significant Perspective by Stroking interaction (Supplementary Information). No other main effect or interaction was significant in this region (Supplemental Information).

The cluster at the right TPJ was also centered on the pSTG, and the BOLD response in this region also differed between synchronous and asynchronous stroking during the body conditions for both groups (Figure 4C). In the Up-group we found a lower BOLD response during synchronous (0.11%) than
asynchronous stroking \([1.14\%; \text{F}(1, 20) = 7; p < 0.016]\), whereas in the Down-group we found the opposite trend with a higher BOLD response during the synchronous \((1.03\%\); \(p = 0.09\)) than the asynchronous stroking condition \((0.34\%; p > 0.32)\). No other main effect or interaction was significant in this region \((\text{Supplemental Information})\).

Other fMRI Data
To target brain regions reflecting self-identification \((\text{as measured by the questionnaire; question Q3; Figure 3})\) we searched for activity that could not be accounted for by the summation of the effects of seeing the body and feeling synchronous stroking. To this aim, we searched for brain regions showing an interaction between Object and Stroking characterized by a difference between the two body conditions, but not the control conditions. Such activity was only found in the right EBA. The ANOVA performed on the BOLD signal change in right EBA \((\text{Supplemental Information})\) showed a significant two-way interaction between Object and Stroking \([\text{F}(1,20) = 6.56; p < 0.02]\), accounted for by the higher BOLD response in the body/asynchronous condition \((1.2\%)\) with respect to the body/synchronous \((0.47\%)\) and the no-body/asynchronous conditions \((0.72\%; p < 0.05)\).

Yet right EBA activity in the body/synchronous condition \((0.47\%)\) did not differ from any of the two no-body control conditions \((p > 0.14)\). No other brain region revealed BOLD signal changes that reflected changes in self-identification with the seen virtual body \((\text{Supplemental Information})\). Finally, only activity in the cluster centered at the right postcentral gyrus revealed a main effect of Stroking \([\text{F}(1,20) = 24.02; p < 0.001]\) revealing a lower BOLD in the synchronous \((-0.51\%)\) with respect to the asynchronous conditions \((0.13\%)\). For other fMRI data descriptions, see the \text{Supplemental Information}.

Lesion Analysis
We found that in eight out of nine OBE-patients, brain damage affected the right temporal and/or parietal cortex, most often at the TPJ \((\text{Table S3})\). Lesion analysis revealed maximal lesion overlap at the right angular gyrus, pSTG, and middle temporal gyrus in seven out of eight OBE-patients \((\text{Figure 5A})\). This was confirmed by VLSM showing maximal involvement of the right TPJ \((\text{MNI}: 54, -52, 26; \text{Z-score} = 3.53; p < 0.01, \text{FDR-corrected})\), centered at the angular gyrus and posterior STG \((32\% \text{ of the voxels were within the pSTG, } 27\% \text{ within the middle temporal gyrus, } 26\% \text{ within the angular gyrus, and } 6\% \text{ within the supramarginal gyrus; Figure 5B})\).

DISCUSSION
Self-Location Depends on the Direction of the First-Person Perspective and Stroking
Using robotic technology, the present data show that, in the noisy and physically constraining MR-environment, we were able to manipulate two key aspects of self-consciousness: self-location and the first-person perspective. We induced
changes in the experienced direction of the first-person perspective (Up- and Down-group) and also showed that within each group the drift of self-location is differently modulated by robotically controlled visuo-tactile stimulation. These data show that within each group, but only in the body conditions, self-location—the illusion where our participants experienced themselves to be localized in space—is significantly different between the synchronous and the asynchronous conditions. Importantly, the direction of this effect differs between the two groups: in the Up-group we found an increase of RTs (higher self-location) during the synchronous condition (as compared to the asynchronous condition), and in the Down-group we found a decrease of RTs (or lower self-location) during the synchronous condition (as compared to the asynchronous condition). This directional effect on RTs (or drift) corroborates the difference in the experienced direction of the first-person perspective that subjects from both groups reported (as measured by questionnaire scores; Q1). It suggests that synchronous stroking results in an illusory drift of self-location in the direction of the seen virtual body for both groups, but—due to the differences in the experienced direction of the first-person perspective—this drift occurs in opposite directions (in the upward direction for the Up-group; in the downward direction for the Down-group).

The robotically-induced drift in self-location confirms a classical finding of visual dominance (the “stroking” on the video) over somatosensory cues (the robotic stroking on the participant’s back) by inducing predicted changes in self-location (Lenggenhager et al., 2007, 2009; Aspell et al., 2009) that have also been observed in drift measures during the related rubber hand illusion (Ehrsson et al., 2004; Tsakiris and Haggard, 2005). We report that the direction of these drift-related changes in self-location is consistent with the experienced direction of the first-person perspective during robotic stimulation. We argue that this is due to a different visual versus bodily conflict that is related to the visual-vestibular gravitational conflict that we presented during stimulation. Thus, we used a visual image that

Figure 5. Brain Damage in Patients with Abnormal Self-Location Due to Out-of-Body Experience
(A) Brain damage and results of lesion overlap analysis in nine patients with OBEs due to focal brain damage is shown. Maximal lesion overlap centers at the right TPJ at the angular gyrus (red). Overlap color code ranges from violet (one patient) to red (seven patients). Note that only one patient suffered from damage to the left TPJ.
(B) Voxel-based lesion symptom mapping (VLSM) of focal brain damage leading to OBEs. The violet-to-red cluster shows the region that VLSM analysis associated statistically with OBEs as compared to control patients. The color-code indicates significant Z-Scores (p < 0.05; FDR-corrected) of the respective voxels showing maximal involvement of the right TPJ, including the right pSTG, angular gyrus, and middle temporal gyrus.
(C) Self-location and the TPJ. Comparison between the area reflecting experimentally induced changes in self-location in healthy participants at the right TPJ using fMRI (red) and the area reflecting pathologically induced changes in self-location in neurological patients with OBEs using VLSM (blue). See also Table S3.
contained a conflict between the visual gravitational cues of the seen body and the actual vestibular (and somatosensory) gravitational cues signaled from the physical body of the participants. Showing a visual body that was filmed from an elevated camera perspective (Figure 1A), these visual gravitational cues of the seen body are in conflict with the actual vestibular (and somatosensory) gravitational cues from the participants’ physical bodies signaling that they are actually lying on their backs and looking upward. Accordingly, we argue that in participants from the Up-group, there is stronger reliance on vestibular (and somatosensory) cues than on visual gravitational cues (from the seen virtual body), whereas participants from the Down-group show the opposite pattern. This is concordant with three related findings. First, comparable effects have been reported in patients with OBEs of neurological origin with abnormal self-location and first-person perspective (Blanke et al., 2002, 2004). Thus, the large majority of patients with OBEs experience themselves to be seeing from an elevated and down-looking, first-person perspective (Blanke and Arzy, 2005; Blanke and Mohr, 2005), and this perspective is inverted and rotated by 180° with respect to their supine and upward-oriented physical body position (Lopez and Blanke, 2011). OBEs have been previously linked with abnormal vestibular/gravitational signals and a deficit in visuo-vestibular integration (Lopez et al., 2008; Schwabe and Blanke, 2008). The importance of vestibular signals and visuo-vestibular integration was also suggested in a recent self-location study in healthy subjects using manual stroking, that reported an association of vestibular sensations with experimentally induced changes in self-location (Lenggenhager et al., 2009). Second, visuo-vestibular integration is characterized by strong individual differences, as also found in the present study. Thus, previous work on vestibular perception has shown individual differences in the strength of relying on visual versus vestibular cues (e.g., for subjective body orientation or postural control) (Lopez et al., 2006; Young et al., 1984). People also depend differently on visual as compared to vestibular (and somatosensory) signals when, for example, judging their orientation in space or performing postural control tasks—some rely more on visual and some more on the vestibular cues (Golomer et al., 1999, Lopez et al., 2006, Isableu et al., 1997). Our data suggest that these individual differences in the weighting of visual and vestibular cues during robotic visuo-tactile stimulation also contribute to the experience of the direction of the experienced perspective and self-location and that this differs for participants from both groups. Third, interactions between vestibular and visual gravitational cues have been reported in primate vestibular cortex that is in close proximity to both TPJ clusters reported in our study (also see below). Future work is needed to further distinguish between these different sensory mechanisms (and probably also cognitive mechanisms) with respect to experienced perspective and self-location. Based on these findings, we argue that in participants from the Down-group there is stronger reliance on visual gravitational cues (from the seen virtual body) than on vestibular (and somatosensory) cues from the participants’ physical bodies (in a supine position in the scanner) and that participants from the Up-group show the opposite pattern (stronger reliance on vestibular and somatosensory cues than visual cues).

Inspection of RT responses in the Down-group during the body and control conditions shows a generally elevated self-location (that was lowest in the body/synchronous condition) with respect to a generally lower self-location in the Up-group also for the body and control conditions (that was highest in the body/synchronous condition). Some of the free reports of participants from the Down-group (Table 1; Table S4) and, in particular, subjective reports by neurological patients with OBEs, are helpful and important to understand this difference in self-location that we refer to as a level of self-location. Thus, generally elevated self-location (mental ball dropping task) was associated with a down-looking perspective (Q1) and subjective reports about an elevated self-location and/or various feelings of flying, floating, rising, lightness, and being far from the body. This was found in 82% of participants from the Down-group (mostly in the body asynchronous condition), but only in 36% of participants from the Up-group. Importantly, neurological patients with OBEs due to brain damage experience similar subjective changes as participants from the down-group: they report being located at a position above their physical body; describe floating, flying, lightness, and elevation; and they experience themselves to be looking down (Perspective). Based on this consistency between the subjective and behavioral responses of participants from the Down-group and the subjective responses in patients with OBEs, we suggest that self-location in the present experimental setup was also modulated on its level. This would account for our observation that RTs in the body/synchronous conditions are not significantly different between the two groups, as drift and level of self-location (as measured by the mental ball dropping task that estimates elevation above the ground) were altered in opposite directions in the two groups. We note that, despite this consistency across analyzed participants (healthy subjects and patients) and measures (subjective and behavioral), the behavioral evidence for the level-related mechanism was not significant in the Down-group and not associated with a main effect between groups. We also note that not all free reports of our participants from the Down-group are consistent with RT-based self-location, yet free reports are often variable. Further work is needed to explore subjective and behavioral measures of self-location and their modulation by the experienced direction of the first-person perspective, ideally within subjects.

TPJ Activity Reflects Self-Location

These experimentally induced changes in self-location and the direction of the first-person perspective are also reflected in TPJ activity. The present fMRI data show that activity in both left and right TPJ differed between synchronous and asynchronous stroking, but only when a body was seen. These data suggest that in both groups, right and left TPJ activity reflects self-location. Our data show that in both groups, the magnitude of the BOLD response was lower in conditions with higher self-location as quantified by the MBD task (synchronous stroking in the Up-group; asynchronous stroking in the Down-group), as compared to conditions with lower self-location that were associated with a higher BOLD response (asynchronous stroking in the Up-group; synchronous stroking in the Down-group). We argue that TPJ activity reflects drift-related changes in self-location within each group that depend differently on the
experienced direction of the first-person perspective. This is compatible with prominent differences for the direction of the first-person perspective that were measured through questionnaire data, participants’ free reports, and drift-related RTs in both groups. These changes are also compatible with subjective data from OBE patients suffering from TPJ damage (see next section). Alternatively, TPJ activity may reflect stroking-related changes in self-location with respect to the participants’ physical body position in both groups, but based on the questionnaire, free report, and RT data in healthy participants and the subjective reports by OBE patients, this account is less likely. More work in healthy subjects is needed to describe TPJ activity with respect to self-location and the first-person perspective.

**Out-of-Body Experiences and TPJ**

The above-mentioned account of TPJ activity is also corroborated by classically reported changes in self-location and the direction of the first-person perspective in patients with OBEs suffering from TPJ damage: such patients report an elevated perspective that is distanced from the body and down-looking (i.e., comparable to participants from the Down-group in the asynchronous body condition). The present lesion data from a group of OBE-patients put previous anecdotal data about abnormal self-location and first-person perspective on solid grounds. They also show that the detailed analysis of such clinical neuroanatomical data on self-consciousness translate to functional neuroimaging data on self-consciousness in healthy participants, highlighting collectively the significance of the TPJ as an important brain structure for self-consciousness related to self-location and the first-person perspective (Figure 5C). There are only a few carefully analyzed case studies in neurological patients with OBEs due to focal brain damage or electrical brain stimulation. In addition, previous work has associated OBEs with many different brain structures, such as the right and left TPJ (Blanke et al., 2002, 2004; Brandt et al., 2005; Maillard et al., 2004), and several structures within the TPJ: posterior superior temporal gyrus (Blanke et al., 2004), angular gyrus (Blanke et al., 2002; Brandt et al., 2005; Heydrich et al., 2011), and supramarginal gyrus (De Ridder et al., 2007; Maillard et al., 2004), but also the precuneus (De Ridder et al., 2007) and fronto-temporal cortex (Devinsky et al., 1989). Here we lateralized and localized brain damage in OBE-patients to the right TPJ. The right TPJ is the classical lesion site and side associated with visuo-spatial neglect (Halligan et al., 2003; Karnath et al., 2001), a clinical condition shown to disturb the patient’s egocentric spatial relationship with extrapersonal space, visuo-spatial perspective taking (Farrell and Robertson, 2000), and own body perception such as somatoparaphrenia (Vallar and Ronchi, 2009). A bilateral, but right lateralized, implication of the TPJ has also been observed during egocentric visuo-spatial perspective taking (Maguire et al., 1998; Ruby and Decety, 2001), multisensory integration, as well as imagined changes in self-location (Arzy et al., 2006; Blanke et al., 2005; Schwabe et al., 2009) in healthy subjects. Despite the present strongly right-lateralized lesion data, our fMRI data reveal that self-location and first-person perspective likely depends on cortical processing in both TPJs. One of our patients suffered from OBEs due to left TPJ involvement. It may thus be that OBEs following interference with the left TPJ may be less reported by patients, potentially due to interference with the language cortex at the left TPJ. More data in larger patient samples in patients with OBEs will be necessary to clarify this.

**Self-Consciousness and Multisensory Integration at the TPJ**

The TPJ is an excellent candidate for self-consciousness. TPJ has been implicated in cognitive manipulations of the first-person perspective (Ruby and Decety, 2001; Vogeley and Fink, 2003; Vogeley et al., 2004) as well as self-other discriminations based on perceptual, cognitive, and motor cues (Farrer et al., 2003; Frith, 2005). Neurons in the primate TPJ (and functionally-related regions in the posterior parietal cortex) encode the seen and felt position of one’s body and such neurons discharge when the trunk or face is touched or when an approaching stimulus is seen close to the body (Bremmer et al., 2002; Grüsser et al., 1990). The receptive fields are most often large and bilateral, may encompass the face, trunk, hemibody, or entire body, and have bimodal visuo-tactile receptive fields that are anchored to the body (Bremmer et al., 2002; Duhamel et al., 1998; Grüsser et al., 1990). It may be argued that TPJ activity reflects a matching between visual and tactile signals from the participant’s body and the seen body through multisensory correlation and thus is compatible with related findings on hand ownership that have been reported for bimodal visuo-tactile neurons in the premotor and intraparietal sulcus region that are anchored to the hand (Graziano et al., 2000; Iriki et al., 1996; Maravita and Iriki, 2004). Yet, in the present study, TPJ activity was not only modulated by the visuo-tactile synchrony of stroking, but was also differently influenced by the modulation of self-location depending on the experienced direction of the first-person perspective. This excludes the possibility that mere multisensory correlations (a matching between visual and tactile signals from the participant’s body and the seen body; Graziano et al., 2000; Iriki et al., 1996; Maravita and Iriki, 2004) alone account for TPJ activity. The present data suggest that TPJ activity also reflects visuo-vestibular effects on self-location and first-person perspective. This is compatible with neurological data (Blanke et al., 2004; Kahane et al., 2003) that were based on a comparative analysis between OBEs and the related experiences of heautoscopy and autoscopic hallucinations (Brugger et al., 1994; Brugger, 2002). These clinical data suggest that remapping of self-location and first-person perspective from the physical body position to an elevated and distanced position and first-person perspective in extrapersonal space at the TPJ is based on a double disintegration of bodily signals, including disintegration between visual and vestibular signals. Our fMRI findings corroborate and extend these data and suggest that the magnitude of TPJ activity reflects drift- and perspective-related changes in self-location that depend on visuo-tactile and visuo-vestibular conflicts respectively. This is compatible with the tuning of TPJ neurons to vestibular stimuli (Grüsser et al., 1990; Guldin and Grüsser, 1998); the presence of trimodal neurons in this region integrating somatosensory, visual, and vestibular signals (Bremmer et al., 2002; Schlack et al., 2002); and the location of human vestibular cortex in close proximity to the TPJ (Brandt and Dieterich, 1999; Kahane et al., 2003;
et al., 1998). Although the exact location of the human vestibular cortex is still under debate (for review see Guldin and Grüsser, 1998; Lopez et al., 2008; Lopez and Blanke, 2011), fMRI work consistently identified the vestibular area in the parietal operculum (Eickhoff et al., 2006; Fasold et al., 2002) and the posterior insula (Bucher et al., 1998; Fasold et al., 2002; Vitte et al., 1996). Earlier lesion work also associated vestibular deficits with damage of the posterior insula (Brandt and Dieterich, 1999). Although none of these regions were significantly activated in our fMRI study, the proximity of the present fMRI and lesion TPJ locations to vestibular cortex suggests a potential involvement of vestibular cortex or adjacent multisensory cortex (integrating visual, vestibular, and somatosensory signals) in self-location and the first-person perspective.

**Extrastriate Body Area and Self-Identification**
Our questionnaire data (Q3) show that participants from both groups self-identified more strongly with the virtual body when the tactile stroking was applied synchronously with the visual stroking (Aspell et al., 2009; Lenggenhager et al., 2007). Our fMRI analysis detected an activation in the right middle-inferior temporal cortex that may partly reflect changes in self-identification with the seen virtual body. This activation was found to be partially overlapping with the stereotaxic location of the right extrastriate body area (EBA). Yet, although right EBA activity showed a body-specific difference between synchronous versus asynchronous stimulation in both groups (Supplemental Information) that are compatible with EBA’s involvement in self-identification, EBA activity in the body/synchronous conditions was not significantly different from those in the control conditions, where no self-identification occurs (Supplemental Information). Accordingly, we are cautious to interpret this activity as related to self-identification, also because related changes concerning self-attribution of a fake or virtual hand (during the rubber hand illusion) were associated with activity increases (not decreases as in our right EBA data) in lateral premotor and frontal opercular regions (Ehrsson et al., 2004). We note however, that this finding of a potential implication of right EBA in self-identification with a full body extends previous notions that the EBA is involved in the processing of human bodies (Downing et al., 2001; Grossman and Blake, 2002; Astafiev et al., 2004) and human body form recognition (Urgesi et al., 2007). The synchrony-related differences in the right EBA activity during the visual presentation of a human body are also of interest as they are concordant with higher consistency (Downing et al., 2001) and selectivity (Downing et al., 2006a, 2006b) of the right versus left EBA. Finally, other studies have revealed the role of the EBA in the perception (Downing et al., 2001; Grossman and Blake, 2002; Urgesi et al., 2007), mental imagery (Arzy et al., 2006; Blanke et al., 2010), and sensorimotor coding of human bodies (Astafiev et al., 2004) and EBA damage leads to deficits in body, but not face, recognition (Moro et al., 2008).

**Conclusion**
In conclusion, our results illustrate the power of merging technologies from engineering with those of MRI for the understanding of the nature of one of the greatest mysteries of the human mind: self-consciousness and its neural mechanisms. Using robotically-controlled multisensory conflicts, we induced changes in two fundamental aspects of self-consciousness—self-location and the first-person perspective—that selectively depended on the timing between the tactile stroking and the “visual” stroking of a seen virtual body and on the subjects’ spontaneously adopted first-person perspective that was manipulated through visuo-vestibular conflict. These subjective changes about the location and perspective of the self were reflected in TPJ activity and causally linked to TPJ damage in a group of neurological patients. Based on fMRI and lesion data, we argue that the magnitude of TPJ activity as manipulated through visuo-tactile and visuo-vestibular conflicts reflects the drift-related changes in self-location that depend on the experienced direction of the first-person perspective. TPJ activity thus reflects the conscious experience of being localized at a position with a perspective in space and was manipulated here through specific bodily conflicts highlighting the importance of multisensory bodily signals for self-consciousness (Blanke and Metzinger, 2009). We also show that the daily “inside-body-experience” of humans depends on bilateral TPJ. These findings on experimentally and pathologically induced altered states of self-consciousness present a powerful research technology and reveal that TPJ activity reflects one of the most fundamental subjective feelings of humans: the feeling that “I” am an entity that is localized at a position in space and that “I” perceive the world from here.

**EXPERIMENTAL PROCEDURES**

**MR-Compatible Robotics**
The device was built entirely from MR-compatible materials (wood, aluminum, and brass for the grounded parts; polymers and fiberglass for the moving parts) and was mounted on a flexible wooden board that could be placed on the scanner bed and adapted to its shape (Gassert et al., 2008). The motor actuated a stimulation sphere over a polymer rack and pinion mechanism. To ensure a constant pressure against the participant’s back, the sphere was attached to a compliant blade, which was translated over a guided fiber-glass rod (Figure 1C). To ensure MR-compatibility, a commercial MR-compatible traveling wave ultrasonic motor was used (USR 60; Shinsei Corp.; Japan) (Gassert et al., 2006). The actuator and rod were embedded within two custom-designed mattresses to provide a comfortable support for the participant (Figure 1D) and to define the distance between the participant’s back and the stroking rod (i.e., a paramedian position, 3 cm to the right of the participant’s spine, with a maximal vertical stroke of 20 cm for the application of the tactile stimulation during the experiment) (Supplemental Information).

**fMRI Data Analysis**
All MR images were collected using a Siemens Trio 3T scanner with a standard head birdcage-coil operating at the CHUV (Centre Hospitalier Universitaire Vaudois, Lausanne, Switzerland) in collaboration with the “Centre d’Imagerie BioMédicale” (CIBM) (Supplemental Information). Functional images were preprocessed with SPM8 (Wellcome Department of Cognitive Neurology, Institute of Neurology, UCL, London, UK), and subsequently analyzed at a single subject level using a first-level fixed effects analysis (Supplemental Information). According to a 2 × 2 design with Object (body; no-body) and Stroking (synchronous; asynchronous) as main factors, four contrast images representing the estimated amplitude of the hemodynamic response in the “synchronous” and “asynchronous” stroking for the “body” and “no-body” conditions relative to the “baseline” condition, were computed for each participant. Contrast images were then entered into a second-level random-effect analysis with nonsphericity correction as implemented in SPM8 (Worsley and Friston, 1995), in order to identify regions where the effect of any of these contrasts was significant (p < 0.05; FDR corrected). For each identified cluster, the BOLD percent signal change in each condition (relative to baseline) was computed for each participant and analyzed by means of a three-way
ANOVAS with the in-between factor Perspective (up; down), and the two within factors Object (body; no-body) and Stroking (synchronous; asynchronous) (Supplemental Information). Post hoc comparison for significant main effects and interactions were carried out using a Fisher Least Significant Difference (LSD), thresholded at p < 0.05. To localize and visualize the activated clusters we used the BrainShow software (Galati et al., 2008) implemented in Matlab (MathWorks Inc., MA). The BrainShow software was also used to project group activations onto the cortical surface of the PALS atlas, to superimpose them to the standard cerebral cortex, and to automatically assign anatomical labels (Tzourie-Mazoyer et al., 2002).

Lesion Analysis
The group of neurological patients with OBEs due to focal brain damage consisted of nine patients (Table S3). The control group comprised eight patients (Supplemental Information). Normalization of each patient’s lesion into the common MNI (Montreal Neurological Institute) reference space permitted voxel-wise algebraic comparisons within and between patient groups (Supplemental Information). Statistical lesion overlap comparison was carried out, contrasting the lesions of the OBEs-patients with those from the control group using voxel-based lesion symptom mapping (VLSM; Bates et al., 2003a). For VLSM we only included patients suffering from lesions on the right hemisphere (predominantly affected, as confirmed by the binomial test we applied; Supplemental Information).

SUPPLEMENTAL INFORMATION
Supplemental Information includes four tables and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.neuron.2011.03.009.

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REFERENCES


Note Added in Proof

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Supplemental Information

Multisensory Mechanisms in Temporo-Parietal Cortex

Support Self-Location and First-Person Perspective

Silvio Ionta, Lukas Heydrich, Bigna Lenggenhager, Michael Mouthon, Eleonora Fornari, Dominique Chapuis, Roger Gassert, and Olaf Blanke

Inventory of Supplemental Information

1. Supplemental Figures and Tables
   - Table S1, related to Figure 3
   - Table S2, related to Figure 4
   - Table S3, related to Figure 5
   - Table S4, related to Table 1

2. Supplemental Experimental Procedures

3. Supplemental References
### Table S1.

<table>
<thead>
<tr>
<th>Q1</th>
<th>Have you had the impression to look Up/Down at the image of a body Above/Below you?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q2</td>
<td>How strong was the feeling that you were located at some distance above/below the body that you saw?</td>
</tr>
<tr>
<td>Q3</td>
<td>How strong was the feeling that the body you saw was you?</td>
</tr>
<tr>
<td>Q4</td>
<td>Have you ever forgotten that you were located in the scanner?</td>
</tr>
<tr>
<td>Q5</td>
<td>How strong was the feeling that the touch you felt was located where you saw the stroking?</td>
</tr>
<tr>
<td>Q6</td>
<td>I felt my body as usual, nothing changed.</td>
</tr>
</tbody>
</table>

**Table S1.** Questions administrated to participant during the experimental session, related to Figure 3.
Table S2

![Table S2](image)

Table S2. Active Clusters. Anatomical region and statistical values for all active clusters resulting from the interaction between Object, Synchrony, and Perspective. The abbreviations (in brackets) refer to the different regions as used in the SI, related to Figure 4.
Table S3.

<table>
<thead>
<tr>
<th>Patient</th>
<th>Group</th>
<th>Diagnosis</th>
<th>Lesion site (lobe)</th>
<th>Side</th>
<th>Lesion analysis</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 A.B.</td>
<td>OBE</td>
<td>Ischemic lesion</td>
<td>Temporo-parietal</td>
<td>Right</td>
<td>MRI, PET</td>
</tr>
<tr>
<td>2 F.M. (Maillard et al., 2004)</td>
<td>OBE</td>
<td>Epilepsy (focal dysplasia)</td>
<td>Parietal</td>
<td>Right</td>
<td>MRI, EEG</td>
</tr>
<tr>
<td>3 B. (Brandt et al., 2005)</td>
<td>OBE</td>
<td>Epilepsy (focal dysplasia)</td>
<td>Parietal</td>
<td>Right</td>
<td>MRI</td>
</tr>
<tr>
<td>4 A.G.</td>
<td>OBE</td>
<td>Traumatic brain injury</td>
<td>Temporo-parietal</td>
<td>Right</td>
<td>MRI, EEG</td>
</tr>
<tr>
<td>5 C.R. (Blank, 2004)</td>
<td>OBE</td>
<td>Epilepsy (focal dysplasia)</td>
<td>Temporo-parietal</td>
<td>Left</td>
<td>MRI, SEEG</td>
</tr>
<tr>
<td>6 D.R. (De Ridder et al., 2007)</td>
<td>OBE</td>
<td>Tinnitus (no structural lesion)</td>
<td>Temporo-parietal</td>
<td>Right</td>
<td>Intracranial stimulation, MRI, PET</td>
</tr>
<tr>
<td>7 V.M.</td>
<td>OBE</td>
<td>Subarachnoid bleeding (post operative lesion)</td>
<td>Temporo-parietal</td>
<td>Right</td>
<td>MRI</td>
</tr>
<tr>
<td>8 H.B. (Blank, 2004)</td>
<td>OBE</td>
<td>Epilepsy (dysembryoblastic neuroepithelial tumor)</td>
<td>Parieto-occipital</td>
<td>Right</td>
<td>MRI, EEG, SPECT</td>
</tr>
<tr>
<td>9 F.M. (Blank, 2004)</td>
<td>OBE</td>
<td>Epilepsy (no structural lesion)</td>
<td>Temporo-parietal</td>
<td>Right</td>
<td>Intracranial stimulation, MRI</td>
</tr>
<tr>
<td>10 B.F. (Zamboini et al., 2005)</td>
<td>Control</td>
<td>Ischemic lesion (Eclampsia)</td>
<td>Occipital</td>
<td>Right</td>
<td>MRI</td>
</tr>
<tr>
<td>11 C.P. (Maillard et al., 2004)</td>
<td>Control</td>
<td>Epilepsy (hematoma)</td>
<td>Parieto-occipital</td>
<td>Right</td>
<td>MRI, EEG*</td>
</tr>
<tr>
<td>12 M (Maillard et al., 2004)</td>
<td>Control</td>
<td>Epilepsy (oligodendroglioma)</td>
<td>Occipital</td>
<td>Right</td>
<td>MRI, EEG*</td>
</tr>
<tr>
<td>13 A.T.</td>
<td>Control</td>
<td>Epilepsy (parasitosis)</td>
<td>Occipital</td>
<td>Right</td>
<td>MRI, EEG</td>
</tr>
<tr>
<td>14 S.M.</td>
<td>Control</td>
<td>Subarachnoid bleeding and ischemic insult</td>
<td>Temporal</td>
<td>Right</td>
<td>MRI*</td>
</tr>
<tr>
<td>15 F.M.</td>
<td>Control</td>
<td>Epilepsy (no structural lesion)</td>
<td>Temporo-occipital</td>
<td>Right</td>
<td>Intracranial stimulation, MRI</td>
</tr>
<tr>
<td>16 V.K.</td>
<td>Control</td>
<td>Epilepsy (Ischemic lesion)</td>
<td>Parieto-occipital</td>
<td>Right</td>
<td>MRI, EEG, PET, SPECT</td>
</tr>
<tr>
<td>17 A.M.</td>
<td>Control</td>
<td>Ischemic lesion</td>
<td>Occipital</td>
<td>Right</td>
<td>MRI, CT</td>
</tr>
</tbody>
</table>

* Enough imaging data were available for accurate tracing onto a normalized standard template brain. No normalization of the original data was possible in these cases.

Table S3. Clinical Characteristics of Patients with OBEs and the Control Group. The lesion analysis was performed using a multimodal imaging approach including data from MRI, PET, SPECT, intracranial stimulation, and subdural EEG (SEEG), related to Figure 5.
<table>
<thead>
<tr>
<th>S.</th>
<th>COND</th>
<th>FREE REPORTS</th>
<th>GROUP</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Sync</td>
<td>&quot;I had the impression of watching a photo of myself, as if I was higher than before and I was looking at the back of another person in front of me.&quot;</td>
<td>Up</td>
</tr>
<tr>
<td>2</td>
<td>Async</td>
<td>&quot;I had the impression of having two bodies. I arrived to the point of asking myself whether my perceptions were correct.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>3</td>
<td>Sync</td>
<td>&quot;This time the only thing that made me doubt that the filmed body is not me, is that I could not see the hands. Indeed I had the clear impression of floating even if I knew I was not moving.&quot;</td>
<td>Up</td>
</tr>
<tr>
<td>4</td>
<td>Async</td>
<td>&quot;Always well relaxed but the fact that I did not feel the same thing that I was watching determined in me some disturbances.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>5</td>
<td>Sync</td>
<td>&quot;When I was concentrated to estimate the timing, it was as if I did not feel anymore what was happening on my back, as if I was only watching the video in front of me.&quot;</td>
<td>Up</td>
</tr>
<tr>
<td>6</td>
<td>Async</td>
<td>&quot;It was clear that I was watching a movie, unrelated to my experience.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>7</td>
<td>Sync</td>
<td>&quot;I felt as if I were “rising” in a strange way towards the roof.&quot;</td>
<td>Up</td>
</tr>
<tr>
<td>8</td>
<td>Async</td>
<td>&quot;I had the impression of watching a video in the rewind mode.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>9</td>
<td>Sync</td>
<td>&quot;I did not have any particular sensation despite a general, but nevertheless mild, elevation.&quot;</td>
<td>Up</td>
</tr>
<tr>
<td>10</td>
<td>Async</td>
<td>&quot;Not even elevation.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>11</td>
<td>Sync</td>
<td>&quot;The delay between the image and the reality increased the impression of watching somebody. For the duration of the stimulation I had the impression that my arms were always in the same place and my trunk moved up and down.&quot;</td>
<td>Up</td>
</tr>
<tr>
<td>12</td>
<td>Async</td>
<td>&quot;I felt the stimuli as if they were linked together. In spite of the absence from my real body, the sensation of being inside my virtual body was even stronger.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>13</td>
<td>Sync</td>
<td>&quot;This time the impression was less strong. I recognized the delay between what I saw and what I felt on my back. The impression of being touched as in the movie decreased.&quot;</td>
<td>Up</td>
</tr>
<tr>
<td>14</td>
<td>Async</td>
<td>&quot;I had the impression of being touched by the stick as if I was between two mirrors and I could see my back.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>15</td>
<td>Sync</td>
<td>&quot;There was simply no connection between the two stimulations.&quot;</td>
<td>Up</td>
</tr>
<tr>
<td>16</td>
<td>Async</td>
<td>&quot;It was kind of weird because I had the impression that I was watching myself in front of me but I knew I could not be here and there at the same time.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>17</td>
<td>Sync</td>
<td>&quot;I detected the stimulation on my back and it was quite &quot;pleasant&quot;. I felt as if I was not linked anymore with my body.&quot;</td>
<td>Up</td>
</tr>
<tr>
<td>18</td>
<td>Async</td>
<td>&quot;I did not feel as if I was flying. On the contrary the non-correspondence between the video and the touch made me come back to reality.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>19</td>
<td>Sync</td>
<td>&quot;I was looking at my own body from above. The perception of being apart from my body was a bit weak but was still there. I saw the stick moving on my back and I perceived it to be somehow at odds with what I was looking at.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>20</td>
<td>Async</td>
<td>&quot;With the &quot;stroking&quot; of the stick I lost my landmarks. I had bizarre sensations. The touch of the ball and the button press were completely different. The whole sense of touch was perturbed and the perception of the stick’s movement relied more on the camera below me than on the touch behind my back.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>21</td>
<td>Sync</td>
<td>&quot;I felt myself a bit floating but in a descendent direction. On the contrary of the reality I had the impression that my body was thicker as if front and back were not as close as before the stick touched my back.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>22</td>
<td>Async</td>
<td>&quot;The video was so realistic that I thought somebody was above me. My sensations and what I saw were concordant.&quot;</td>
<td>Up</td>
</tr>
<tr>
<td>23</td>
<td>Sync</td>
<td>&quot;I had the impression of being in two different places at the same time as if I had two bodies.&quot;</td>
<td>Up</td>
</tr>
<tr>
<td>24</td>
<td>Async</td>
<td>&quot;I felt like I was watching someone else’s body from above, while someone was rubbing my chest with a stick. I also felt as staying above the body I was watching. I felt I was physically located at the point I was looking from.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>25</td>
<td>Sync</td>
<td>&quot;At the beginning I was expecting to feel the stick on my front side, but after I realized that it was touching my back. I felt as if I was lying on myself, face to face.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>26</td>
<td>Async</td>
<td>&quot;I felt as if I was floating, very light, without weight. I had the impression of feeling the impact of a surface on my back as if I was touching the roof.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>27</td>
<td>Sync</td>
<td>&quot;I had the impression of forgetting my body as if my eyes were leaving my body and were going upwards. I was “watching” myself, “my real me”, from above.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>28</td>
<td>Async</td>
<td>&quot;What I saw did not correspond at all to what I was watching. It is interesting to see yourself from behind, but no sensations of displacement.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>29</td>
<td>Sync</td>
<td>&quot;With the virtual reality goggles the vision from above was very bizarre because I was looking downwards at my own body.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>30</td>
<td>Async</td>
<td>&quot;The delay in time makes it more difficult to believe that what you see is happening where you feel it.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>31</td>
<td>Sync</td>
<td>&quot;I had the impression of being two people at the same time. One myself was flying, and was watching the other (real) myself being touched by the stick.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>32</td>
<td>Async</td>
<td>&quot;This time what I felt on my back did not correspond at all to what I saw. I had the impression of being further away from the real me.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>33</td>
<td>Sync</td>
<td>&quot;I had the impression of being touched sometimes above and sometimes below the image.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>34</td>
<td>Async</td>
<td>&quot;What I saw in the goggles did not correspond to the reality that I felt on my back.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>35</td>
<td>Sync</td>
<td>&quot;It was strange to see the stick in a place different to where I felt it. This generated a doubt in me and I was a bit puzzled because I felt closer to the camera.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>36</td>
<td>Async</td>
<td>&quot;When I imagined releasing the ball, sometimes I had the impression of being lower sometimes the feeling was to be higher, so most of the times the ball was falling in front of me but sometimes it was falling behind my back.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>37</td>
<td>Sync</td>
<td>&quot;I asked myself: if the one that I see in the movie is me, how can they move the mattress up and down?&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>38</td>
<td>Async</td>
<td>&quot;I felt as if I was floating high and I did not know where I was.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>39</td>
<td>Sync</td>
<td>&quot;I identified a little more with what I saw but I felt quite uncomfortable with this vision.&quot;</td>
<td>Down</td>
</tr>
<tr>
<td>40</td>
<td>Async</td>
<td>&quot;I really did not feel that I was looking at myself since I could not really recognize any part of my body. The touch underneath me and my arms feel different because gravity is pushing on my body in the opposite direction.&quot;</td>
<td>Down</td>
</tr>
</tbody>
</table>

Table S4. Free Reports by participants from both groups (see main text), related to Table 1.
SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Study 1
fMRI

Procedure

Participants. Twenty-two right-handed healthy male volunteers (mean age=25.4 years; SD=5.7 years) took part in the experiment. All participants had normal vision and were naive to the purpose of the experiment. All participants gave their written informed consent before the inclusion in the study. The study was approved by the Ethics Committee of the University of Lausanne (Switzerland) and was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Stimuli. We showed a visual body that was filmed from an elevated camera perspective, lying on the chest facing a table, and with the shoulders bending somewhat downwards (Figure 1A). We note, that these visual gravitational cues are also in conflict with the cognitive and memory-related cues (participants know and remember that they are in a scanner looking upwards on an HMD) that are compatible with looking at a body that is above. The software E-Prime 2 (Psychology Software Tools Inc., Pittsburgh, PA, USA) was used to present the visual stimuli and to record participants’ responses. LabVIEW (Version 8.5, National Instruments Inc., Austin, TX, USA) was used to control the robotic device. Visual stimuli were projected onto MR compatible goggles (VisualSystem, NordicNeurolab. Resolution 800x600, refresh rate 85 Hz, horizontal field of view 30°, vertical field of view 23°). The goggles were placed in front of the participants’ eyes and the focus was adjusted to achieve a clear image. The distance from the eyes varied within a range of 3 to 5 cm, according to each participant’s face anatomy. The image projected comprised a dual view and covered the whole visual field. During the “body” conditions, a virtual human body wearing a white t-shirt was shown. The back view of the virtual body was previously filmed from an elevated position.

Training session. Prior to the training session participants were asked to wear a white t-shirt and were shown the set up. At the beginning they were explained the self-location task (see below) and that they were going to see a movie through goggles while also receiving tactile stimulation. During the training session they were asked to wear a pneumatic headphone device that occluded the scanner noise and was used to present acoustic cues used to trigger the self-location task (see
They were then installed comfortably on the robotic device holding the MR-emergency squeeze-ball in one hand and the response box in the other hand (counterbalanced across subjects). All the participants reported that they could feel the movement of the stroking sphere over the midline of their back, between the shoulder-blades. To prevent head movements, participants were installed with a neck cushion providing neck support and two compact square cushions inserted into the space between the headphones and the head coil. The training session consisted in performing exactly the same self-location task that was going to be performed during the fMRI session.

**Self-location task (Mental Ball Dropping task).** To evaluate our participants’ self-location during the training session and the experiment participants were asked to perform the mental ball dropping (MBD) task as described in (Lenggenhager et al., 2009). Participants held a small “ball” (MR-emergency squeeze-ball) in one hand counterbalanced across subjects and, according to the MBD procedure, were asked to imagine dropping the ball and to estimate the time the ball would need to “hit” the ground. The MBD task was cued by an auditory cue delivered through the headphones (white noise was constantly played in the background). Participants were asked to indicate the imagined onset of ball dropping by pressing a button on a response box, to keep it pressed, and to indicate the imagined impact of the ball on the ground by releasing the same button. Response times (RTs) were recorded and the time difference between pressing and releasing the button was calculated in milliseconds. Participants were instructed to press and release the button of the response box with the index finger of either the left or right hand, contralateral to the hand holding the squeeze-ball (counterbalanced across participants). They were also instructed to never physically release the ball (which no participant did).

**Questionnaire ratings.** At the end of the experiment participants were asked to complete a questionnaire (Botvinick and Cohen, 1998; Lenggenhager et al., 2009; Lenggenhager et al., 2007) (Table S1). Participants completed the questionnaire answering the questions with respect to the two conditions during which they saw the human body (the synchronous and the asynchronous stroking conditions, in counterbalanced order). Still within the MR-scanner, participants were asked to indicate their rating for each question referring to the body conditions only by using the buttons of the response box (see main text). For Q2 to Q6 participants were asked to move the cursor along a horizontal several-points visual analogue scale (VAS). By pressing the index (ring finger) button with the right (left) hand the cursor moved to the right. By pressing the ring finger (index) button with the left (right) hand, the cursor moved to the left. Reference questions and conditions were
randomly ordered. After the end of the experimental session, outside the scanner participants were asked to freely report their experience in writing (Table 1)

**Analysis of Questionnaires, Self-Location Evaluation, and fMRI Data**

**Questionnaires.** Question 1 was not answered on a continuous scale and therefore was not included in the analysis of variance. Accordingly, we analyzed the questionnaire ratings (VAS data for questions Q2 to Q6) by means of a 3-way analysis of variance (ANOVA) with Perspective (up, down) as in-between factor and Stroking (synchronous, asynchronous) and Question (Q2, Q3, Q4, Q5, Q6) as with-in factors. Post-hoc analyses were carried out using the Newman-Keuls test thresholded at p<0.05.

**Evaluation of self-location (Mental Ball Dropping).**
Trials in which RTs were below 200 ms were excluded from the data analyses (total loss, 3% of trials). RTs for the MBD were then analyzed by means of a 3-way repeated measures analysis of variance (ANOVA), with the in-between factor Perspective (up, down) and the with-in factors Object (body, no-body) and Stroking (synchronous, asynchronous). Post-hoc analyses were carried out using a Fisher Least Significant Difference (LSD) thresholded at p<0.05.

**fMRI Acquisition and Analysis**
T1-weighted anatomical images were collected using Siemens multiplanar rapid acquisition gradient echo sequence (1 mm isotropic voxels, 160 sagittal slices, TR = 9.7 ms, TE = 4 ms). Functional images were collected with a gradient echo EPI sequence. The experiment comprised two runs of 8 blocks. Twenty-seven volumes were recorded during each block, 216 consecutive volumes comprising 28 consecutive 3.5 mm thick slices oriented parallel to the anterior-posterior commissure and covering the whole brain (TR = 3 s, TE = 60 ms, 64 x 64 image matrix, 3.5 x 3.5 mm in-plane resolution) were recorded during each fMRI session. 108 volumes were recorded for each condition, a total of 432 volumes were recorded during the experiment and each run lasted 10 min 54s.

According to a block design, the four conditions (body synchronous/asynchronous, nobody synchronous/asynchronous) were presented in blocks lasting 78s each. Each block consisted of three elements presented in the following order: exposure to visual and tactile stroking (39s); three executions of the MBD task triggered by the auditory cue (15s); observation of a white cross on a black screen without stroking as a “baseline” (24s). The four experimental conditions were
presented four times during the experiment in a pseudo-randomized order. The anatomical images (mprage) were collected at the end of the experiment (after the questionnaires were completed). fMRI data were analyzed using SPM8 (Wellcome Department of Cognitive Neurology, Institute of Neurology, UCL, London, UK). For each subject, functional images were first corrected for head movements using a least-squares approach and six-parameter rigid body spatial transformations (Friston et al., 1995). 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 et al., 1995). Functional images were re-sampled with a voxel size of 2x2x2 mm and spatially smoothed with a three-dimensional isotropic Gaussian filter of 6 mm full width at half maximum to increase signal-to-noise ratio (Friston et al., 1994). Images were subsequently analyzed at a single subject level using a first-level fixed effects analysis. The effects of the experimental paradigm were estimated on a voxel-by-voxel basis using the principles of the general linear model extended to allow the analysis of fMRI data as time series (Worsley and Friston, 1995). Each experimental block was modeled using a boxcar, convolved with a canonical hemodynamic response function chosen to represent the relationship between neuronal activation and blood flow changes. These single-subject models were used to compute four contrast images per subject, each representing the estimated amplitude of the hemodynamic response in the “synchronous” and “asynchronous” stroking for the “body” and “no-body” conditions, relative to the “baseline” condition. Contrast images representing each of the mentioned conditions for all subject were entered into a second-level random-effect analysis with non-sphericity correction, as implemented in SPM8 (Worsley and Friston, 1995). In order to identify regions where the effect of any of these contrasts was significant in both Up- and Down-group (Perspective in-between factor), i.e. regions discriminating any of the eight conditions (resulting from the 2x2x2 factorial design with Perspective, Object, and Stroking as main factors) from the inter-trial baseline, we used a statistical threshold of p<0.05 FDR-corrected for multiple comparisons over the total amount of analyzed brain volume (cluster threshold of 10 voxels). Then, for each identified cluster, the BOLD percent signal change in each condition (relative to baseline) was computed for each subject, by extracting the mean beta value from the contrast across all voxels in the cluster. The estimates of averaged regional responses for each condition were analyzed by means of a 3-way ANOVA with the in-between factor Perspective (up, down), and the two with-in factors Object (body, no-body) and Stroking (synchronous, asynchronous). Post-hoc comparison for significant main effects and interactions were carried out using a Fisher Least Significant Difference (LSD), thresholded at p<0.05. To localize and visualize the activated clusters we used the BrainShow software (Galati et al., 2008) implemented in Matlab (The MathWorks Inc., Natick, MA, USA). Brainshow software
was also used to project group activations onto the cortical surface of the PALS atlas, to superimpose them to the standard cerebral cortex, and to automatically assign anatomical labels (Tzourio-Mazoyer et al., 2002).

**STUDY 2**

**Lesion analysis**

**Included Patients**

We included 5 patients from the Geneva University Hospital suffering from out-of-body experiences (OBEs) due to circumscribed structural brain lesions and/or transient functional neural dysfunction. The brain pathology was confirmed by magnetic resonance imaging (MRI), computer tomography (CT), ictal and interictal scalp electroencephalography (EEG), intracranial EEG using subdural electrodes, positron emission tomography (PET), ictal and interictal single photon emission computed tomography (SPECT) and intracranial electric stimulation (Table S3). From other clinical research groups, we were able to include 4 additional patients whose data have previously been published and in whom the original neuroradiological data were available for normalization and analysis (Brandt et al., 2005; De Ridder et al., 2007; Maillard et al., 2004). As a control group, 5 patients with complex visual hallucinations of people and/or faces without disturbance of self-location and first person perspective and circumscribed brain lesions affecting the right posterior cortex were recruited were recruited during the same time period at Geneva University Hospital, 2 patients were contributed by Maillard and colleagues (Maillard et al., 2004) and one patient by Zamboni and colleagues (Zamboni et al., 2005) (Table S3).

**Lesion Mapping and Analysis**

The group of neurological patients with OBEs due to focal brain damage consisted of 9 patients (Table S3). The control group comprised 8 patients (SI).

Normalization of each patient’s lesion into the common MNI (Montreal Neurological Institute) reference space permitted voxel-wise algebraic comparisons within and between patient groups. Structural lesions were confirmed by MRI or CT. The functional relevance of these lesions was confirmed by a multimodality imaging approach (Knowlton, 2004; Kurian et al., 2007), which combines structural with co-registered functional imaging. This multimodal approach is classically used to improve the ability to detect and define the extent of temporal and extra-temporal epileptogenic tissue (Blanke et al., 2004; Kurian et al., 2007). MRI brain scans were normalized to the smoothed T1 template using SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/spm5)
(Ashburner and Friston, 2005). As unified segmentation models give the most precise registration of lesioned structural images (Crinion et al., 2007), no cost-function masking was necessary. Functional imaging (PET, SPECT) was normalized using SPM5 and co-registered to the normalized MRI scans. Intracranial EEG was co-registered to the normalized MRI scans for each patient using the Cartool software developed by Denis Brunet (http://brainmapping.unige.ch/Cartool.htm). Lesions were subsequently traced manually slice by slice either on the individual normalized brain scans or on the T1 weighted images (control group case 2, 3 and 5) using MRICron (http://www.sph.sc.edu/comd/rorden/mricron) (Rorden et al., 2007). The later manual tracing on the template brain was only done when confidence could be achieved for matching corresponding slices between the lesioned brain and the template brain. If functional imaging highlighted brain areas adjacent to the structural lesions, these were included into the lesion analysis as well.

As to intracranial stimulation and intracranial recording of the seizure onset (OBE group case 3 and 9, control group case 6), the site of the electrode located on the standard T1 template and tissue with a radius of 10 mm around the electrode was declared dysfunctional). No patients with unclear lesion boundaries or metallic artifacts were included into the analysis. Lesion volumes (volume of interest, VOI) were determined as the sum of all voxels compromising the traced lesion in all slices and were spatially smoothed using a 5mm full width at half maximum (FWHM) Gaussian Kernel and a threshold of 0.5.

Statistical lesion overlap comparison was carried out contrasting the lesions of the OBEs-patients with those from the control group using voxel-based lesion symptom mapping (VLSM; Bates et al., 2003). For VLSM we only included patients suffering from lesions on the right hemisphere (predominantly affected, as confirmed by the binomial test we applied). For lesion overlap and statistical analysis we used MRICron and Non Parametric Mapping (NPM), which is part of the MRICron software package (Rorden et al., 2007). In a first step simple voxel-based lesion overlap analysis establishing the anatomical sub regions of maximal lesion overlap for OBE was performed (see Figure 4A). In a second step nonparametric voxel based lesion symptom mapping (VLSM) analysis (Bates et al., 2003), contrasting OBE against the control group was computed on the hemisphere, which was significantly more often affected (as confirmed by the binomial test, see below). This resulted in 8 patients with OBEs suffering from a lesion in the right hemisphere (the remaining patient suffered from left temporo-parietal damage). The right hemispheric predominance was significant as confirmed by the binomial test with an expected frequency of 0.5 (p=0.039). Eight patients suffering from complex visual hallucinations due to a right posterior lesion were chosen as the control group (Table S3). We used the Liebermeister test and corrected the results for multiple comparisons using a 5% false discovery rate (FDR). The Liebermeister is a
nonparametric implementation of a two-group comparison on a binary variable. It is more appropriate than the chi square test (Rorden et al., 2007). We only included voxels affected in at least 30% of all subsequent analyses. Right vs. left hemispheric involvement was tested with a binomial distribution with an expected frequency of 0.5.

RESULTS

Questionnaires. Statistical analysis of the questionnaire data showed the main effect of Stroking \( [F(1,20)=33.2; p<0.01] \) and Question \( [F(4,80)=30.7; p<0.01] \) as well as the interaction between Stroking and Question \( [F(4,80)=13.5; p<0.01] \). The main effect of Stroking was accounted for by the higher responses during the synchronous (3.2) compared to the asynchronous stroking (1.7; \( p<0.01 \)). The main effect of Question was accounted for by the lowest responses given to questions Q2 (-2.2) and Q6 (1.3) as compared to questions Q3 (3.2), Q4 (4.3), Q5 (5.4) (all \( p<0.01 \)). The significant interaction between Stroking and Question showed that the difference between the responses given with respect to the synchronous and asynchronous stroking was significant for questions Q3 (\( p<0.006 \)) and Q5 (\( p<0.0001 \)) but not for questions Q2, Q4 and Q6 (all \( p>0.2 \)). Post-hoc analysis showed that responses to questions Q3 and Q5 were higher during the synchronous (4.1 and 8.1, respectively) than the asynchronous stroking (2.3 and 2.8, respectively).

Self-location. In addition to the significant 3-way interaction (see main text), RT analysis also showed a significant 2-way interaction between Perspective and Stroking \( [F(1,20)=6.2; p<0.02] \). Post-hoc comparisons of the 3-way interaction showed (in addition to the comparisons reported in the main text) that in the Up-group RTs for the body/synchronous condition (1071ms) were longer (higher self-location) with respect to the no-body/asynchronous (974ms; \( p<0.02 \)). Post-hoc comparisons of the 2-way interaction showed higher RTs (\( p<0.04 \)) in the Up-group during the synchronous (1042ms) as compared to the asynchronous stroking (968ms). This difference was not significant in the Down-group (\( p=0.2 \)).

fMRI results

The cluster at the left temporo-parietal junction (left TPJ) was centered on the posterior superior temporal gyrus (57% of voxels), including also supramarginal gyrus (36%), and anterior STG (2%). The ANOVA performed on the BOLD signal change in the left TPJ showed a significant 3-way interaction between Perspective, Object and Stroking \( [F(1,20)=6.08; p<0.02] \) (see main text) and a significant 2-way interaction between Perspective and Stroking \( [F(1,20)=8.17; p<0.01] \). The 2-way interaction was accounted for by the lowest BOLD response in the Up-group during the
synchronous stroking conditions (body and no-body together; 0.14%) with respect to the asynchronous stroking in the Up-group (0.82%) and both synchronous (0.88%) and asynchronous stroking (0.73%) in the Down-group (all p<0.01). The main effect of perspective was not significant, suggesting that activity of the left TPJ is not influenced by the experienced direction of the first person perspective per se No other main effect or interaction was significant in this region (all p>0.06).

The cluster at the right temporo-parietal junction (right TPJ) was also centered on the posterior superior temporal gyrus (63% of voxels), including also supramarginal gyrus (26%), and anterior STG (6%). The ANOVA performed on the BOLD signal change in right TPJ showed a significant 3-way interaction between Perspective, Object and Stroking [F(1,20)=7.01; p<0.01] (see main text). No other main effect or interaction was significant in this region (all p>0.32).

The cluster at the right extrastriate body area (rEBA) was centred on the posterior part of the right middle-temporal gyrus (72% of the voxels within the middle-temporal gyrus and 21% within the inferior-temporal gyrus). The ANOVA performed on the BOLD signal change in rEBA showed a 3-way interaction between Perspective, Object and Stroking [F(1,20)=20.54; p<0.001]. In the Up-group the percentage of BOLD signal change in the body conditions was lower during the synchronous (0.09%) compared to the asynchronous stroking (1.68%; p<0.001). In contrast to the BOLD response in right and left TPJ, the difference between synchronous and asynchronous stroking was also significant in the control conditions (in the Up-group) with higher BOLD response (1.2%) in the no-body/synchronous condition with respect to the no-body/asynchronous condition (0.4%; p<0.03). The significant 2-way interaction between Object and Stroking was accounted for by the higher BOLD response in the body/asynchronous condition (1.2%) with respect to the body/synchronous (0.47%) and the no-body/asynchronous conditions (0.72%; all p<0.05). No other main effect or interactions were significant (all p>0.11). To summarize, the signal in rEBA did not reflect self-location as the differences in BOLD response between synchronous and asynchronous stroking were not selective for the body condition. For a discussion of a potential role of right EBA in self-identification see main text.

The cluster at the left extrastriate body area (lEBA) was centred on the left middle-occipital gyrus, (70% of the voxels within the middle-occipital gyrus, 16% within the inferior-occipital gyrus, and 12% within the middle-temporal gyrus). The ANOVA performed on the BOLD signal change in lEBA showed a 3-way interaction between Perspective, Object and Stroking [F(1,20)=10.05; p<0.005]. Yet, in contrast to TPJ activity (and changes in self-location), in both the Up- and the Down-group, changes in BOLD response were not selective for the body conditions and stroking. Thus, in the Up-group the BOLD response in the body/asynchronous condition was higher (1.3%)
with respect to the body/synchronous (0.39%; p<0.02), but also with respect to the control/asynchronous (0.49%; p<0.03) condition. Similarly, in the Down-group, the BOLD response in the body/asynchronous condition was lower (0.23%) with respect to the body/synchronous (1.05%; p<0.04), but also with respect to the control/asynchronous (1.1%; p<0.03) condition. No other main effect or interactions were significant (all p>0.11). To summarize, the BOLD response in IEEA did not show the body-selective modulation due to synchrony as found in right and left TPJ and RTs in the mental ball dropping task (although it shared several aspects with TPJ activity).

The cluster at the right postcentral gyrus (rPtC) was centered on the postcentral gyrus, with 59% of the voxels within the superior postcentral gyrus, 32% within the inferior precentral gyrus, and 12% within the superior precentral gyrus. The ANOVA performed on the BOLD response showed a significant main effect of Stroking \( [F(1,20)=24.02; p<0.001] \) and a significant 2-way interaction between Perspective and Stroking \( [F(1,20)=16.65; p<0.001] \). The main effect of Stroking was accounted for by the smaller BOLD decrease for the asynchronous (-0.13%) with respect to the synchronous stroking (-0.51%). The interaction between Perspective and Stroking was accounted for by the greatest BOLD decrease for the synchronous stroking in the Up-group (-0.71%; all p<0.02).

The cluster at the right postcentral gyrus (rPtC) was centered on the superior part of postcentral gyrus with 91% of the voxels within the postcentral gyrus and 9% within the paracentral lobule. The ANOVA performed on the BOLD response showed a significant 2-way interaction between Perspective and Object \( [F(1,20)=7.05; p<0.02] \) as well as a significant interaction between Object and Stroking \( [F(1,20)=7.4; p<0.01] \). The former interaction was accounted for by the greater BOLD decrease for the body conditions in the Down-group (-0.63%) with respect to the body conditions in the Up-group (-0.22%; p<0.02). The latter interaction was accounted for by the synchrony-related difference in the BOLD response, but only between the control conditions, i.e. greater BOLD decrease in the no-body/synchronous (-0.66%) with respect to the no-body/asynchronous (-0.21%; p<0.02) condition, showing no involvement in self-identification or self-location.

In the cluster at the left and right occipital gyri (Occ) the activations were found in the right (45%) and the left (21%) medial occipital lobes, and the right (11%) and left (18%) lateral occipital lobes. The ANOVA performed on the BOLD response showed a significant 3-way interaction between Perspective, Object, and Stroking \( [F(1,20)=9.48; p<0.006] \). However, and in contrast to TPJ, the post-hoc comparison for the 3-way interaction showed that in the Up-group the BOLD response in the body/asynchronous condition (2.01%) was higher with respect to the body/synchronous and the control conditions (all p<0.04). Yet, in contrast to TPJ, no such differences in the BOLD response
due to Object or Stroking were found in the Down-group (all \( p>0.1 \)), suggesting activity in the occipital lobe does not reflect self-location or self-identification.

This fMRI analysis showed that the only two brain regions where the BOLD response reflected changes in self-location as manipulated by the factors Synchrony, Body, and Perspective were the left and right TPJ. Whereas, the BOLD response in left EBA and right EBA reflected some aspects of our experimental manipulations of self-location, both BOLD signals did not reflect self-location as the differences in BOLD response between synchronous and asynchronous stroking were not selective for the body condition.
SUPPLEMENTAL REFERENCES