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

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SUMMARY

Self-consciousness has mostly been approached by philosophical enquiry and not by empirical neuroscientific study, 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

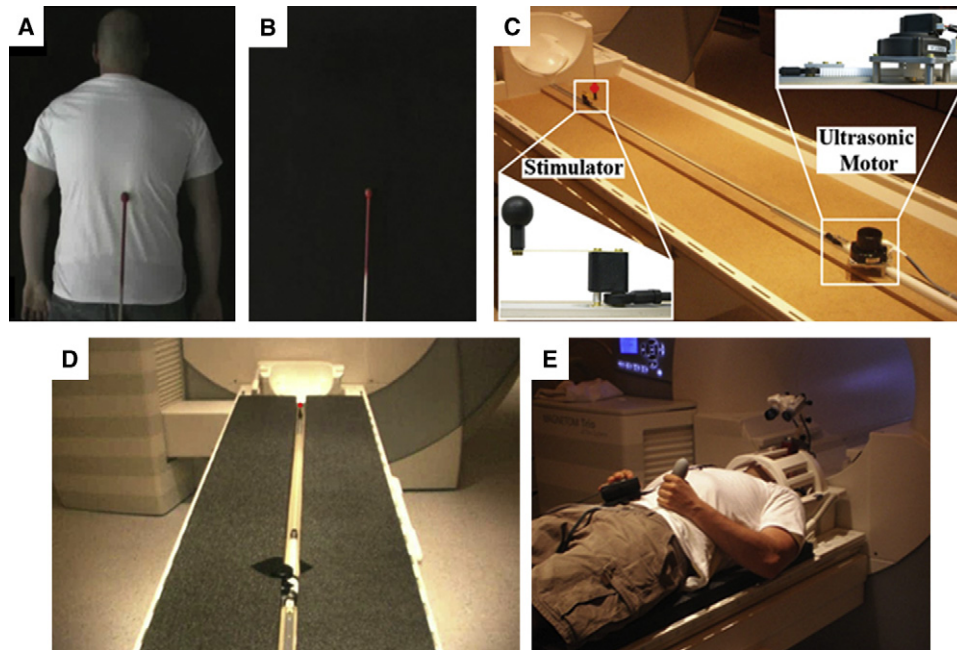


Figure 1. Visual and Tactile-Robotic Stimulation

(A and B) Visual stimuli. In the body conditions, participants were shown a video of a wooden rod with a stimulation sphere (in red) that moved vertically along the midline of the virtual person's back (A). During the control conditions, the video showed only the moving rod and the stimulator (B).

(C) Robotic stimulator installed on the scanner bed. The tactile stimulation of the participant's back was performed by a custom-made robotic device generating the same movement profile for the body and the control conditions. An ultrasonic motor placed at the level of the feet actuated the stimulation sphere over a rack-and-pinion mechanism. Motion was transmitted over a guided fiberglass rod, which held the stimulation sphere over a compliant blade in order to follow the participant's back with constant pressure.

(D) The robotic device (stroking sphere in red) was placed between the two custom-made mattresses (in gray; the standard mattress is removed from the sliding scanner bed).

(E) Participant (outside the scanner) placed on the two mattresses and the robotic device.

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

A		Condition	Up-Group
S3	S		"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."
	AS		"Always well relaxed but the fact that I could not feel the same thing that I was watching disturbed me."
S5	S		"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."
	AS		"It was clear that I was watching a movie unrelated to my experience."
S8	S		"I felt <i>rising</i> in a strange way towards the roof."
	AS		"I had the impression of watching a video in the rewind mode."
S12	S		"I did not have any particular sensation despite a general, but nevertheless mild, elevation."
	AS		"Not even elevation."
B		Condition	Down-Group
S4	S		"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."
	AS		"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."
S9	S		"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."
	AS		"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."
S11	S		"I asked myself: if the one that I see in the movie is me, how can they move the mattress up and down?"
	AS		"I felt as if I was floating high and I did not know where I was."
S17	S		"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."
	AS		"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."

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

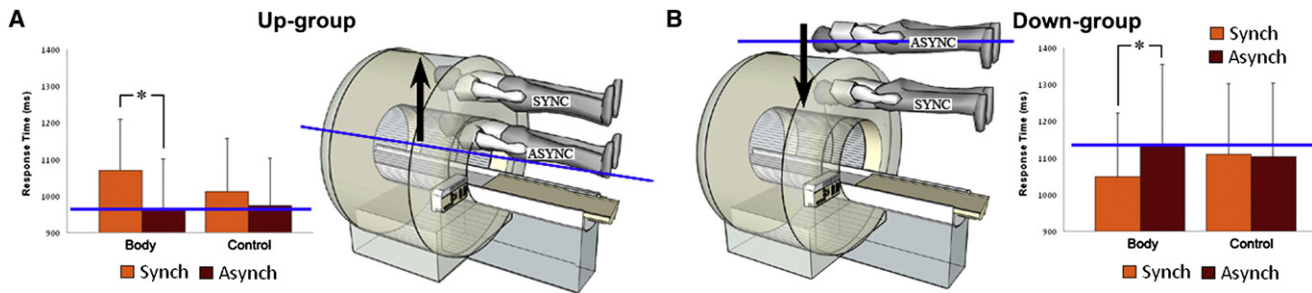


Figure 2. Self-Location Manipulation

Graphic representation of the experimentally induced changes in self-location and perspective in the Up- and Down-group. The position of the human bodies represents the experienced position as indicated by the self-location task (mental ball dropping). The labels on the trousers indicate the experimental conditions. The direction of the experienced first-person perspective (as measured through questionnaires) is represented by the direction of the feet and nose, as well as the black arrows (pointing upward or downward). In both perspective groups, the body/synchronous condition leads to a drift in self-location toward the virtual body, but in opposite directions depending on the experienced perspective.

(A) Thus, participants that had the impression of looking upward at the virtual body (Up-group) had increased response times (RTs) in the MBD task during the synchronous as compared to the asynchronous stroking condition (represented by a blue line), indicating an elevation of self-location.

(B) Participants that had the impression of looking downward at the virtual body from an elevated perspective (Down-group) had decreased RTs in the MBD task during the synchronous as compared to the asynchronous stroking condition (represented by a blue line) indicating a lowering of self-location. The drift in self-location occurred in the direction of the experienced perspective (black arrows). RTs for the MBD task are plotted for each group as a function of the factors Object and Stroking. Orange bars represent the synchronous stroking conditions and the red bars the asynchronous stroking conditions. Asterisks indicate significant differences. Error bars indicate standard error. Note the differences between synchronous and asynchronous stroking conditions only in the body conditions (not in the control conditions) and in opposite directions between Up- and Down-group. The MR-scanner is depicted only for illustration purposes (participants were not asked to estimate the position of the scanner bed).

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 $2 \times 2 \times 2$ 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.

Robotically-Induced 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 visually presented 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). Notably, RTs in the body conditions are modulated, within each group, as a function of stroking and the experienced direction of the first-person perspective. Thus, self-location changes for the Up-group were characterized by a generally lower self-location that was further modulated by stroking in the upward direction (toward the seen virtual body), whereas self-location changes for the Down-group were characterized by a generally higher self-location that was further modulated by stroking in the downward direction (toward the seen virtual body) (see Figure 2). For other effects see Supplemental Information.

Our questionnaire results showed that predictable changes in self-identification and illusory touch, depending on the factors Object and Stroking, can be induced using robotic stroking in the fMRI environment. As predicted, and in accordance with previous work (Ehrsson, 2007; Lenggenhager et al., 2007, 2009), statistical analysis of the questionnaires (Supplemental Information) showed that, regardless of Perspective, responses to Q3 (“How strong was the feeling that the body you saw was you?”) indicated stronger self-identification [$F(4,80) = 13.5$; $p < 0.01$] with the virtual body during synchronous (4.1) than asynchronous stroking (2.3), and that responses to Q5 (“How strong was the feeling that the touch you felt was located where you saw the stroking?”) indicated stronger illusory touch [$F(4,80) = 13.5$; $p < 0.001$] during the synchronous (8.1) than the asynchronous stroking (2.8; Figure 3; Supplemental Information).

To summarize these findings, participants from the Up-group experienced themselves to be looking up at the body above

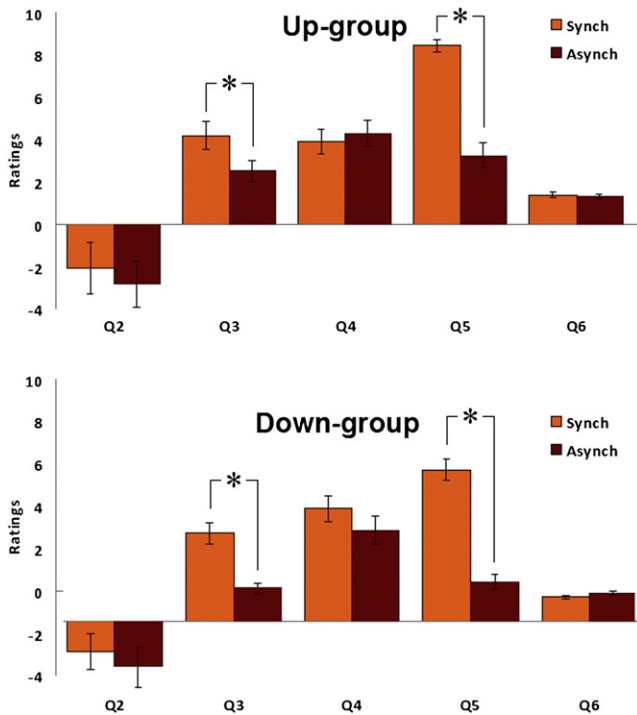


Figure 3. Questionnaire Scores

Self-identification with the virtual body (Q3) and mislocalization of touch toward the virtual body (Q5) 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.

them (Q1), self-identified with that body during synchronous stimulation (Q3), and experienced themselves to be spatially closer to the seen virtual body during synchronous stimulation (free reports). We argue that this was associated—at least partly—with compatible changes in self-location (mental ball dropping task): a low position or level of self-location (comparable to those indicated during the control conditions; see blue line in Figure 2A) and a drift in self-location characterized by an elevation during synchronous versus asynchronous stroking (difference between the two gray bodies in Figure 2A). This was different in participants from the Down-group. They felt themselves to be looking down at the body below them (different from participants from the Up-group), self-identified with that body during synchronous stimulation (as participants from the Up-group), and experienced themselves to be spatially closer with the virtual body during synchronous stimulation (as participants from the Up-group). We note that some free reports also suggested that they experienced themselves to be floating and to be elevated during asynchronous stroking. This was associated—at least partly—with compatible changes in self-location (mental ball dropping task): a high position or level of self-location during asynchronous stroking (comparable to those indicated during the control conditions; see blue lines in Figure 2B) and a drift in self-location characterized by a descent during

synchronous versus asynchronous stroking (difference between the two gray bodies in Figure 2B that is opposite in direction with respect to the drift-related change in self-location in the Up-group; black arrows in Figure 2).

fMRI Data and Self-Location

We next analyzed whether changes in illusory self-location—based on the experimental factors of Stroking, Object, and Perspective—were reflected in the fMRI data. Group-level whole-brain analysis indicated seven cortical regions where the BOLD signal was significantly different during any of the eight conditions compared to the baseline condition (Figure 4). These regions (Table S2) were located at the left and right temporo-parietal junction (TPJ), left and right postcentral gyrus (Figures 4A–4C), left and right temporo-occipital cortex (posterior middle and inferior temporal gyri, or extrastriate body area; EBA), and bilateral occipital lobe (Figure 4D). To target brain regions reflecting self-location (as measured by the MBD task; Figure 2) we searched for activity that could not be accounted for by the summation of the effects of seeing the body, feeling synchronous stroking, and the spontaneously reported perspective. Based on our subjective and behavioral data on self-location, we searched for BOLD responses that reflected changes in self-location (i.e., BOLD responses that depend on Stroking and Object), and that also differed for the two perspective groups. Only brain regions revealing a Stroking by Object by Perspective interaction may reflect the induced changes in self-location, whereas brain activity revealing a Stroking by Object interaction may reflect self-identification with the seen virtual body. Such activity was only found in the left and right TPJ. No other brain region revealed BOLD signal changes that reflected such illusory changes in self-location. Although activity in right and left EBA and occipital cortex also revealed a three-way interaction, activity in these regions did not reflect self-location (see the Supplemental Information).

The left TPJ activation was centered on the posterior part of the superior temporal gyrus (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 $p > 0.15$; Supplemental Information). We also found a significant Perspective by Stroking interaction (Supplemental 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

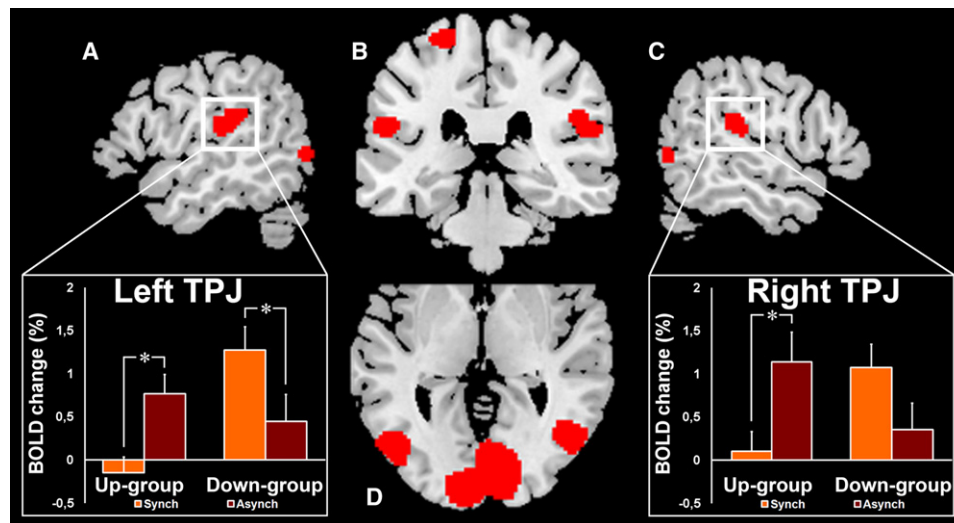


Figure 4. TPJ Activity and Self-Location

TPJ activity in the body conditions is shown for the Up- and the Down-group. In both groups, the magnitude of the BOLD response was lower in conditions with high 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 estimated self-location (asynchronous stroking in the Up-group; synchronous stroking in the Down-group).

(A) (higher panel) Left TPJ activation centered on pSTG. The lower panel shows the BOLD response at the left TPJ as a function of Perspective and Stroking during the body conditions.

(B) Activation in left and right TPJ and left superior postcentral gyrus.

(C) (higher panel) Right TPJ activation centered on pSTG. The lower panel shows the BOLD response at the right TPJ as a function of Perspective and Stroking during the body conditions. The pattern of the left TPJ BOLD response was the same as found at the right TPJ.

(D) Activation of left and right posterior middle and inferior temporal gyri.

See also Table S2. Asterisks indicate significant differences. Error bars indicate standard error.

asynchronous stroking [1.14%; $F(1, 20) = 7$; $p < 0.016$], whereas in the Down-group we found the opposite trend with a higher BOLD response during the synchronous (1.03%) than the asynchronous stroking condition (0.34%; $p = 0.09$). The BOLD response was not significantly different between synchronous and asynchronous stroking in the control conditions in both groups (all $p > 0.32$). No other main effect or interaction was significant in this region (Supplemental Information).

Other fMRI Data

To target brain regions reflecting self-identification (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 (Supplemental Information) showed a significant two-way interaction between Object and Stroking [$F(1,20) = 6.56$; $p < 0.02$], 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%; all $p < 0.05$). Yet right EBA activity in the body/synchronous condition (strong self-identification) did not differ from any of the two no-body control conditions (all $p > 0.14$). No other brain region revealed BOLD signal changes that reflected changes in self-identification

with the seen virtual body (Supplemental Information). Finally, only activity in the cluster centered at the right postcentral gyrus revealed a main effect of Stroking [$F(1,20) = 24.02$; $p < 0.001$] revealing a lower BOLD in the synchronous (−0.51%) with respect to the asynchronous conditions (0.13%). For other fMRI data descriptions, see the 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 (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 (Figure 5A). This was confirmed by VLSM showing maximal involvement of the right TPJ (MNI: 54, −52, 26; Z-score = 3.53; $p < 0.01$, FDR-corrected), centered at the angular gyrus and posterior STG (32% of the voxels were within the pSTG, 27% within the middle temporal gyrus, 26% within the angular gyrus, and 6% within the supra-marginal 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

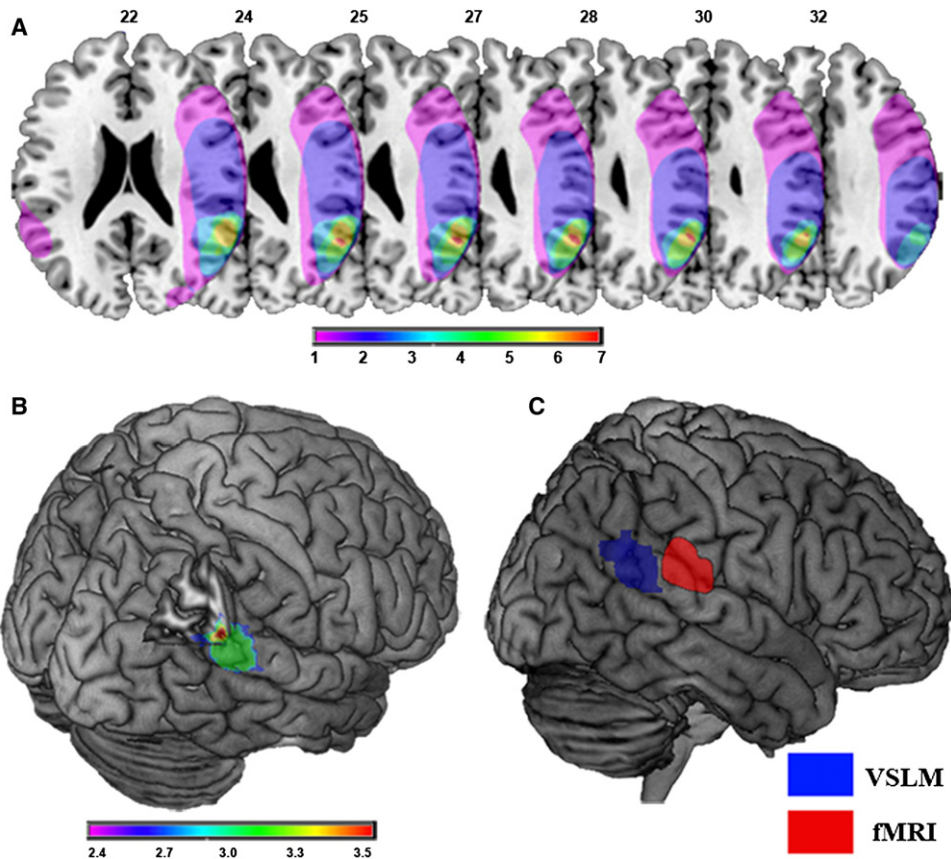


Figure 5. Brain Damage in Patients with Abnormal Self-Location Due to Out-of-Body Experience

(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.

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

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;

Label 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 cortex 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 fiberglass 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

ANOVA 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 (Tzourio-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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