Posterior Cingulate Cortex Integrates the Senses of Self-Location and Body Ownership

Highlights

- We used an out-of-body illusion to perceptually teleport participants during fMRI
- Self-location could be decoded from parieto-cingulate-hippocampal activity
- Ownership of a seen full body was associated with premotor-intraparietal activity
- The posterior cingulate plays a key role in merging self-location and body ownership

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In Brief

Guterstam et al. used an out-of-body illusion to perceptually teleport subjects during fMRI. Self-location could be decoded from parieto-cingulate-hippocampal activity; posterior cingulate activity reflected integration of self-location and body ownership, suggesting a key role in the coherent experience of the bodily self in space
Posterior Cingulate Cortex Integrates the Senses of Self-Location and Body Ownership

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http://dx.doi.org/10.1016/j.cub.2015.03.059

SUMMARY

The senses of owning a body and being localized somewhere in space are two key components of human self-consciousness. Despite a wealth of neurophysiological and neuroimaging research on the representations of the spatial environment in the parietal and medial temporal cortices, the relationship between body ownership and self-location remains unexplored. To investigate this relationship, we used a multisensory out-of-body illusion to manipulate healthy participants’ perceived self-location, head direction, and sense of body ownership during high-resolution fMRI. Activity patterns in the hippocampus and the posterior cingulate, retrosplenial, and intraparietal cortices reflected the sense of self-location, whereas the sense of body ownership was associated with premotor-intraparietal activity. The functional interplay between these two sets of areas was mediated by the posterior cingulate cortex. These results extend our understanding of the role of the posterior parietal and medial temporal cortices in spatial cognition by demonstrating that these areas not only are important for ecological behaviors, such as navigation and perspective taking, but also support the perceptual representation of the bodily self in space. Our results further suggest that the posterior cingulate cortex has a key role in integrating the neural representations of self-location and body ownership.

INTRODUCTION

We experience our body as a physical entity with a specific location in the external space. For instance, when sitting at your desk, you are aware of your body and its approximate position with respect to objects and the spatial boundaries of the room [1]. This sense is essential for our interactions with the outside world [2] and has long been regarded among philosophers and psychologists as a fundamental aspect of self-consciousness [3, 4]. Recently, neuroscientists have started to explore its neural correlates and have highlighted two factors, implemented in partially distinct neural substrates, as key to bodily self-consciousness: the feeling that the body is part of the self (body ownership) and the experience that the body is located somewhere in space (self-location) [5–7]. This view is supported by the existence of neurological impairments that specifically affect the sense of body ownership or the sense of self-location. For instance, patients suffering from asomatognosia fail to recognize their own limbs as part of the self [8], whereas focal epilepsy and electrical stimulation of the temporal and parietal cortices can sometimes induce out-of-body experiences (OBEs), in which the perceived self-location is temporarily detached from the patient’s physical body [9–11]. Although the existence of these conditions suggests that body ownership and self-location require intact neural processing in fronto-parietal and temporoparietal areas, respectively, their underlying mechanisms and their relationship remain poorly understood.

Recent studies using perceptual illusions in healthy participants have demonstrated that multisensory integration of signals from the body viewed from the first-person visual perspective (1PP) is a key mechanism for the emergence of body ownership [12, 13]. The illusory experience that an artificial hand [14] or an entire body [13] is one’s own is associated with increased activity in the premotor-intraparietal regions [13, 15]. These areas integrate visual, tactile, and proprioceptive information and contain neurons with visuo-tactile receptive fields anchored to a portion of the body surface and its surrounding (peripersonal) space [16, 17]. Neuronal populations in these areas construct multisensory representations of the boundaries of one’s body and are ideally suited to support the feeling of body ownership [7, 18, 19]. Conversely, theories regarding the neural mechanisms underlying the sense of self-location draw primarily from the study of spatial navigation in rodents and virtual navigation in humans. Abundant evidence from such studies indicates that the medial temporal and posterior parietal cortices are involved in the construction of internal representations of an individual’s spatial location [20–22] and head direction [23–27]. However, it remains unclear how these representations relate to the perceptual experience of self-location and the representation of one’s own body.

In light of the above, we set out to investigate the neural representations of self-location and body ownership and their functional interplay. We manipulated these factors by making use of a perceptual out-of-body illusion [12]. In the original experiment, the participants sit on a chair and wear a set of head-mounted displays (HMDs) through which they observe the real-time 3D video feed from a pair of cameras located 2 m behind them. The experimenter then synchronously touches the participant’s chest, which is hidden from view, and the space just below the cameras with two identical small objects. This mode of visuo-tactile stimulation leads to the illusory experience of
being physically located at the position of the cameras and that the observed real body is no longer part of the self [12, 28]. Crucially, the delivery of asynchronous touches significantly reduces the illusion and allows for the comparison of otherwise equivalent conditions [12, 28]. Here, we adapted the out-of-body illusion to a supine, head-tilted posture inside a MRI scanner. This experimental setup allowed us to manipulate the sense of body ownership and study self-location by perceptually "teleporting" the participants between locations within the real-world scanner environment while recording brain activity using high-resolution fMRI (see the Experimental Procedures).

Fifteen healthy participants were positioned inside an MRI scanner with their head tilted forward while wearing HMDs. Through the displays, they viewed the scanner room and themselves in stereoscopic vision from the perspective of a stranger lying on the floor in one of three positions: positions A, B, and C (Figures 1 and S1). Positions A and B corresponded to two different corners of the room with identical head directions, whereas positions B and C represented perpendicular head directions in the same corner. To elicit the illusion of owning the stranger’s body seen from the 1PP and being physically located in position A, B, or C, the experimenter applied synchronous touches to the participant’s body and the corresponding location on the stranger’s body (Figure 1 and Movie S1) [12, 13]. The touches delivered to the real body were hidden from the participants’ view in the HMDs (see the Supplemental Experimental Procedures for details). For each position, we also included a control condition in which the touches occurred asynchronously to reduce the illusion.

This experimental design allowed us to test for changes in brain activity that reflect alterations in the feelings of body ownership, self-location, and the functional interplay between ownership and self-location. We conducted three main analyses. First, we estimated the main effect of visuo-tactile synchrony across positions to examine the activity related to the feeling of ownership of the stranger’s body viewed from the 1PP [13, 15]. Second, to identify the neural substrates of the perceived self-location, we used multivoxel pattern analysis [29] to decode position A versus B (for perceived head direction, we decoded position B versus C) in the synchronous condition, using the asynchronous condition as a control for illusion non-specific effects. Finally, we investigated the neural interplay between the representations of body ownership and self-location by examining the illusion-induced changes in effective connectivity between the corresponding sets of brain regions.

RESULTS

Illusion Quantification—Behavioral and Psychophysiological Results

Before examining the fMRI results related to the illusion experience, we tested the efficacy of the experimental manipulation of body ownership and self-location [12, 28]. To this end, we conducted three behavioral experiments in parallel with, or immediately after, the brain-scanning sessions and quantified subjective and objective changes in the perceived self-location and body ownership. In a post-scan self-location task (see the Experimental Procedures and Figure S2A), we presented the participants with a map of the scanner room and asked them to rate how strongly they perceived themselves to be located in different candidate positions [28]. The results showed that the synchronous, as opposed to the asynchronous, condition...
A separate post-scan questionnaire experiment confirmed that the participants vividly experienced ownership of the stranger’s body in the out-of-body position (A, B, or C) during the synchronous, but not during the asynchronous condition. See also Figure S2B for the ratings of each individual statement.

 Concurrently with the brain scanning, we examined the skin conductance response (SCR) evoked by physical threats directed toward the stranger’s body and the real body (Figure 2C and Movie S1). Previous studies have shown that such SCRs can be used as an objective physiological proxy of body ownership [12, 28, 30]. In line with the subjective reports, we found that threatening the stranger’s body with a knife elicited a significantly greater SCR in the synchronous compared to the asynchronous condition. Importantly, this was not the case when the knife was substituted with a neutral object such as a spoon (p = 0.002, interaction effect; Figure 2D). Moreover, we examined the blood-oxygen-level-dependent (BOLD) responses evoked by these threats in brain regions involved in the experience of fear and pain anticipation, as well as the SCR and BOLD responses to threats directed toward the real body, providing further psycho- and neurophysiological support for successful induction of the illusion (Figure S3).

Taken together, these behavioral, psychophysiological, and threat-evoked BOLD results are consistent with the notion that the illusion experience is dependent on temporally congruent visuo-tactile stimulation and involves ownership of the stranger’s body in the out-of-body position and a weak sense of self-location inside the scanner (p = 0.010; Figure 2A). A separate post-scan questionnaire experiment confirmed that the participants vividly experienced ownership of the stranger’s body in the out-of-body position (A, B, or C) during the synchronous, but not during the asynchronous condition. See also Figure S2B for the ratings of each individual statement.

Figure 2. Behavioral Results
(A) The results of the post-scan self-location task revealed that the synchronous condition was associated with a strong sense of self-location in the out-of-body positions and a weak sense of self-location inside the scanner.
(B) Participants consistently rated statements reflecting the illusion experience, but not the control statements, as significantly higher for the synchronous, but not for the asynchronous, condition. See also Figure S2B for the ratings of each individual statement.
(C) Sample frames depicting the three different threat events.
(D) The SCR evoked by a knife, but not a spoon, threatening the stranger’s body was significantly higher in the synchronous compared to the asynchronous condition.

Error bars indicate the SEM. See also Movie S1.
body seen from the 1PP and a clear sense of self-location in the out-of-body positions. These findings support the feasibility of our approach of using this perceptual illusion to manipulate the senses of body ownership and self-location during fMRI.

**Body Ownership-Related Brain Responses**

Next, we characterized the BOLD responses associated with the feeling of ownership of the stranger’s body viewed from the 1PP by computing the main effect of visuo-tactile synchrony across positions (see the Supplemental Experimental Procedures). This analysis revealed activations in key multisensory areas in the left premotor (ventral, $t = 3.11$, $p = 0.037$; dorsal, $t = 4.17$, $p = 0.002$, corrected) and bilateral intraparietal cortices (left, $t = 4.40$, $p = 0.001$; right, $t = 3.37$, $p = 0.019$, corrected) that have previously been associated with the feeling of ownership of an entire artificial body viewed from the 1PP [13] (Figures 3A and 3B). In addition, we reproduced a significant positive relationship between the level of activity in the left ventral premotor cortex and the subjectively rated strength of ownership of the stranger’s body [13, 15] ($t = 4.33$, $p = 0.038$, corrected; Figure 3C), confirming that activity in this region reflects changes in the subjective feeling of body ownership. Finally, we found increased activity in the bilateral lateral occipital cortices (tentative “extrastriate body area”; see Figure 3A and Table S1), which are known to be involved in the visual processing of body parts [31] and have been consistently observed in previous fMRI studies of limb [15] and whole-body ownership [13] (see the Supplemental Discussion). Together, these findings support the hypothesis that activity in the multisensory premotor-intraparietal cortices is associated with the feeling of ownership of a body seen from the 1PP in a real-world environment.

**Decoding Self-Location and Head Direction**

To identify brain regions involved in the processing of perceived self-location and head direction, we employed multivoxel pattern analysis [29]. First, we sought evidence for patterns of neural activity that carry information concerning the perceived self-location (position A versus B) in the synchronous and asynchronous conditions. To control for effects that were unrelated to the illusion, such as differences in the 1PP visual input between the positions, we only looked for regions that decoded position A versus B significantly better in the synchronous compared to the asynchronous condition, as well as compared to the chance level (50%; using an inclusive mask thresholded at $p < 0.001$, uncorrected; see the Supplemental Experimental Procedures). We hypothesized that the hippocampus, posterior midline areas, such as the posterior cingulate (PCC) and retrosplenial cortices (RSC), and intraparietal cortex would be involved in representing the perceived self-location. The hippocampus features place cells that encode a rat’s allocentric spatial location [20, 32], and human fMRI studies have shown that goal locations in virtual environments can be decoded from this structure [22]. The intraparietal cortex contains egocentric maps of somatosensory and visual space [33–35].
and is activated during spatial navigation [21] and imagined changes in the 1PP [36], whereas the PCC and RSC have been implicated in the translation of egocentric-to-allocentric representations of space [33, 34, 37]. Thus, this set of areas is ideally suited to construct a multisensory representation of the spatial location of one’s bodily self.

In keeping with our hypotheses, the results revealed significant decoding of self-location in the left hippocampus (t = 7.46, p = 0.001, corrected), left posterior cingulate cortex (PCC; t = 3.65, p = 0.041, corrected), and right IPS (t = 4.84, p = 0.034, corrected) (see Figure 4A). The left hippocampal decoding peak was located on the border between the hippocampus and the parahippocampal gyrus (PHG). The corresponding cluster extended from the left posterior hippocampus into the PHG. In a post hoc analysis, we manually segmented the hippocampus to qualitatively isolate the voxels belonging to the self-location cluster that overlapped with the hippocampus proper. This analysis confirmed the presence of voxels in the left posterior hippocampus proper that significantly decoded self-location (Montreal Neurological Institute [MNI]: /C0 22, /C0 30, /C0 12; t = 4.96, p = 0.006, corrected; Figures S4A and S4B). In addition, we found decoding of self-location in the left supramarginal gyrus of the left inferior parietal cortex at a reduced significance threshold (SMG; t = 5.10, p < 0.001, uncorrected for multiple comparisons; Figure 4A). Interestingly, the decoding accuracy was positively correlated with the behavioral self-location score in the left PCC (t = 4.00, p = 0.028, corrected), right IPS (t = 4.32, p = 0.019, corrected), and left retrosplenial cortex (RSC; t = 6.21, p = 0.002, corrected) (Figure 4B). This result suggests that activity patterns in these areas are tightly linked to the subjective sense of self-location.

Second, we sought to identify brain regions involved in the processing of the perceived head direction (position B versus C). Single-cell recordings in navigating rats have revealed head direction cells in the retrosplenial [38, 39] and entorhinal cortices [40], and neuroimaging studies have shown that the posterior midline and intraparietal cortices are involved in representing imagined [41] and navigation-related [25, 26] directions in space. Thus, we expected to find significant decoding in this set of areas. In line with our hypotheses, the results showed that the
perceived head direction could be significantly decoded from the right IPS ($t = 3.56, p = 0.047$, corrected), left precuneus ($t = 3.74, p = 0.037$, corrected), left RSC ($t = 3.59, p = 0.045$, corrected), and right RSC ($t = 4.80, p = 0.008$, corrected) (Figure 4C).

Thus, fine-grained BOLD activity patterns in the intraparietal, retrosplenial, and posterior cingulate cortices contain information not only on the perceived self-location, but also on the perceived directional heading.

### The Neural Interplay between Body Ownership and Self-Location

Finally, we investigated the interplay between the neural representations of body ownership and self-location in terms of the illusion-induced changes in effective connectivity. In the process of localizing one’s own body in the environment, the brain must combine information concerning the representation of the body—processed by multisensory areas identified in the premotor-posterior-parietal cortices—with information concerning self-location—encoded in the parieto-hippocampal circuits. We hypothesized that the PCC and RSC play key roles in this integrative process because they have strong anatomical connections to both the intraparietal and medial temporal areas [42] and compute transformations between body-centered and allocentric spatial reference frames [33, 34, 37]. This notion is compatible with our findings showing that activity patterns in the left PCC contained information on self-location (Figure 4A) and that the level of self-location information in the left PCC was positively correlated with the subjectively rated self-location score (Figure 4B).

Based on these empirical and theoretical considerations, we chose the left PCC decoding peak as our seed region. We then searched for voxels that displayed ownership-related increases in connectivity to the PCC that were positively related to the PCC decoding accuracy of self-location. Specifically, we performed a psychophysiological interaction (PPI) analysis using the contrast synchronous versus asynchronous across positions as the psychological factor, and searched for voxels in which the PPI parameter estimate significantly co-varied with the PCC decoding accuracy across subjects (see the Supplemental Experimental Procedures for details). This analysis brings together the univariate general linear modeling (GLM) findings related to the feeling of ownership of the body seen from the 1PP (Figure 3) and the multivariate decoding results related to the representation of the perceived self-location. As such, this effective connectivity analysis allowed us to examine the interplay between the neural representations of the body and the perceived self-location. The results showed that participants with higher decoding accuracies of self-location (position A versus B) in the left PCC showed proportionally stronger effective connectivity to the left IPS ($t = 4.38, p = 0.023$, corrected), right RSC ($t = 4.46, p = 0.021$, corrected), and left hippocampus ($t = 5.93, p = 0.003$, corrected) (Figure 5). These findings suggest that ownership of the stranger’s body viewed from the 1PP is associated with an effective connectivity increase between the PCC and the intraparietal-retrostplenial-hippocampal cortices that is intimately linked to the representation of self-location in the PCC.

### DISCUSSION

In summary, we have used a multisensory full-body illusion involving advanced 3D virtual reality technology in combination with fMRI brain-decoding methods to investigate the relationship between two fundamental components of self-consciousness [5–7]: self-location and body ownership. Our results revealed two novel main findings. First, we found that activity patterns in the IPS, RSC, PCC, and hippocampus reflected the sense of self-location. The illusion of self-location was contingent on the feeling of ownership of the stranger’s body from whose
perspective the participants observed the environment. This sense of owning a body viewed from the 1PP was associated with activity in the multisensory premotor-intraparietal cortices. Second, our results suggest that the PCC orchestrates the flow of information concerning bodily self-location between the IPS and the hippocampus. These findings extend beyond previous neuroimaging studies that used full-body illusions [13, 43] but did not investigate the interplay between body ownership and self-location. Similarly, studies based on visual [24] or imagined changes in the 1PP [25, 36] and spatial navigation [22] did not examine whether the spatial representations under investigation contribute to the perceptual experience of self-location or interact with central representations of the body. The present results thus extend our understanding of the role of the posterior parietal and medial temporal cortices in spatial cognition by demonstrating that these areas are not only important for ecological behaviors, such as navigation and perspective-taking, but also support the perceptual representation of the bodily self in space.

Consistent with earlier fMRI studies [13, 15, 44], we found that the sense of owning the stranger’s body was associated with activations in the left PMv, bilateral IPS, and LOC (for an in-depth discussion, see the Supplemental Discussion). The intraparietal and premotor cortices are convergence zones for visual, tactile, and proprioceptive information from the body [17], and neuronal populations in these regions continuously integrate multisensory signals to maintain an accurate central representation of one’s body in space [7, 44]. We assert that the premotor-intraparietal activations observed in this study reflect the dynamic integration of spatio-temporally congruent visual information from the stranger’s body being touched and tactile and proprioceptive signals, resulting in the coherent multisensory percept of the stranger’s body being part of the self. This multisensory integrative process could be accompanied by the remapping of peripersonal space from the “disowned” real body to center on the stranger’s body viewed from the 1PP, in line with our threat-evoked SCR results (Figures 2 and S3) and a previous study demonstrating such remapping during a single-limb ownership illusion [18]. Finally, we emphasize that our findings go beyond earlier work on body illusions because they reveal a dynamic interaction between fronto-parietal representations of body ownership and parieto-cingulate-hippocampal representations of self-location in the environment (see detailed discussion below).

Our decoding analyses revealed that patterns of BOLD activity in the posterior parietal cortex, PCC, and hippocampus reflect the perceived spatial location of the bodily self. In the posterior parietal cortex, information about self-location could be deciphered from activity patterns in the cortices lining the IPS (p < 0.05, corrected) and SMG (p < 0.001, uncorrected). The right IPS is particularly interesting because its decoding accuracy was positively related to the reported vividness of the place illusion, suggesting that neural activity in this region reflects the consciously perceived self-location. In the right IPS we also found multivoxel patterns that carried information concerning perceived head direction, and in the IPS bilaterally we observed univariate activations reflecting the feeling of ownership of the stranger’s body (see Figure S4E for a post hoc cluster overlap analysis). Previous studies have shown that the IPS contains neuronal populations that encode multimodal signals in various body-centered spatial reference frames [17], including head-centered coordinates [45], as well as retinotopic representations of the visual field [33, 35]. Thus, the IPS is involved in the construction of multisensory representations of the body and its spatial context. These properties and the current results point to the IPS as a good candidate to support an egocentric representation of self-location. We propose that the place- and head-direction-specific patterns detected in the right IPS reflect the dynamic updating of an egocentric spatial reference frame that is anchored to the perceived location and orientation of one’s own body in space.

The decoding accuracy in the PCC and RSC also mirrored the subjectively reported self-location score, indicating that these regions may play key roles in supporting the sense of self-location. Although relatively little is known about the cognitive functions of the PCC, this region is a central node in the “default mode network” and activity in this structure has been associated with decision-making, attention, memory, face perception, and spatial navigation [46–48]. The RSC (Brodmann areas 29 and 30), which together with the PCC (areas 23 and 31) constitutes the “retrosplenial complex” [37], has also been implicated in memory processing and navigation [38]. Interestingly, RSC lesions in humans impair the ability to represent one’s directional heading with respect to environmental landmarks [49]. This is compatible with our observation that the PCC and RSC elaborate information on the perceived head direction. As previously mentioned, the PCC and the RSC are anatomically interconnected with the intraparietal cortex and medial temporal regions [42] and are thought to mediate the translation between egocentric and allocentric spatial representations [84, 38]. Our effective connectivity analysis revealed illusion-specific changes in the functional coupling between the PCC and nodes in the IPS, RSC, and hippocampus that were positively correlated with the information content concerning self-location in the PCC (also see Figures S4C and S4D for effective connectivity results with respect to head direction). This observation suggests that the interplay between these brain areas reflects the coordinated processing of information encompassing both the body and the perceived self-location. Thus, these findings are compatible with the notion that the PCC and the RSC work in concert with the IPS and the hippocampus to represent the perceived spatial location of the bodily self. We propose that the role of the PCC and the RSC in this process may consist of translating egocentric intraparietal into allocentric hippocampal multisensory representations of self-location.

Studies on spatial memory have shown that the human brain uses both egocentric and allocentric representations of space and that regions in the medial temporal lobe contribute primarily to the latter [34]. We found that BOLD activity patterns in the hippocampus contained information concerning the perceived spatial location of one’s bodily self. However, we found no evidence of head direction decoding in this structure. In light of this, we propose that the hippocampus supports an allocentric representation of the perceived self-location and that—in line with our effective connectivity results—this representation is intimately linked to the egocentric representation of self-location in the IPS via intermediate processing in the PCC. Population activity of hippocampal place cells form the likely neuronal
underpinning for the multivoxel patterns that we observed in this region. These cells have been shown to represent the animal’s position in allocentric spatial reference frames, at the level of both neuronal spikes [20] and spatially distributed local field potentials [56]. The proposed role of the hippocampus in constructing an allocentric representation of self-location fits well with earlier studies on spatial navigation and path integration, in which the locations of the participants’ targets in virtual navigation tasks can be decoded from hippocampal activity patterns [22]. Our results extend the understanding of the role of the hippocampus in spatial cognition by demonstrating that hippocampal activity patterns reflect the currently perceived self-location and that multisensory integrative mechanisms related to body ownership can update this representation even in the absence of active navigation and path integration.

Our experimentally induced out-of-body illusion shares some key characteristics with OBEs elicited by focal epilepsy and electrical brain stimulation [9–11]. In both cases, the spatial location of the self is perceived at an extracorporeal position with respect to the real body viewed from a visual 3PP. In contrast to the illusion, clinical OBEs are often related to changes in the perceived location of the self with respect to the gravitational field and various vestibular sensations such as floating and rotation [11]. A previous neuroimaging study investigated the interaction between self-location and the perceived direction of the 1PP in healthy participants and presented evidence for the involvement of the bilateral posterior superior temporal gyrus (pSTG) [43]. In addition, direct electrical stimulation of the right angular gyrus in one patient elicited a complex body illusion featuring vestibular sensations and changes in body posture [11]. We speculate that the absence of significant decoding of self-location in the pSTG and angular gyrus in our study could be explained by the fact that our paradigm did not involve manipulations of self-orientation with respect to the gravitational field. We further speculate that the representations of self-location and body ownership characterized in the present study might interact with vestibular representations of self-orientation in the pSTG and angular gyrus to represent the full range of possible positions of one’s body in 3D space with six degrees of freedom.

In conclusion, this study has shed light on the mechanisms by which the senses of self-location and body ownership are combined in the human brain to build the coherent experience of being a body somewhere in space. Our results suggest that an interconnected set of regions in the hippocampus and the posterior cingulate, retrosplenial, and intraparietal cortices plays an important role in the construction of this fundamental subjective feeling of self. The characterization of these neural processes lies at the heart of neuroscience and psychology because the experience of one’s own body and its location in the environment defines the origin of the egocentric reference frame that is necessary for human self-consciousness [5, 51] and our behavioral interactions with the external environment [2].

EXPERIMENTAL PROCEDURES

Participants
Fifteen naive healthy volunteers (ages 21–33, mean age ± SD = 27 ± 3 years; six females) participated in the study. Informed consent was obtained prior to the experimental sessions. The Regional Ethical Review Board of Stockholm approved the study.

Illusion Induction
For induction of the illusory feeling of ownership of the stranger’s body seen from the 1PP, a white spherical object (6.5 cm in diameter) attached to a 1-m-long wooden stick (Figure 1) repetitively touched the abdomen, right upper leg, and left foot of the stranger’s body in the HMDs while the participant received temporally congruent tactile stimulation on the corresponding body parts. In the asynchronous control condition, the tactile stimulation was delayed by 1 s with respect to the touches of the stranger’s body in the HMDs. The stereoscopic visual stimuli were presented in a set of MR-compatible HMDs (Nordic NeuroLab). See the Supplemental Experimental Procedures for details on the experimental setup and the visuotactile stimulation protocols and Movie S1 for a sample clip from position A.

Illusion Quantification
To quantify the illusion experience, we used three separate psychometric or psychophysiological measurements. Concurrently with the brain scanning, we examined SCR evoked by threats directed toward the stranger’s body or the real body using a MR-compatible SCR-recording module (Brain Products) [58]. Immediately after the brain scanning, the participants were presented with additional repetitions of each experimental condition and asked to complete a self-location task and a questionnaire (in two separate sessions) to quantify the subjective feeling of self-location and body ownership, respectively. For details, see the Supplemental Experimental Procedures.

fMRI
Functional imaging data (voxel size 2 × 2 × 2 mm3) were collected using a Siemens TIM Trio 3T scanner. For the decoding analyses, the image volumes were analyzed in native space after standard preprocessing. Within each participant, we used locally multivariate mapping with support vector machine classifiers to identify multivoxel patterns [29]. The resulting decoding maps were spatially normalized to the standard MNI space and entered into a second-level analysis, using the Statistical Parametric Mapping software (SPM8) (for details, see the Supplemental Experimental Procedures). For the univariate GLM analysis, the image volumes were preprocessed, spatially normalized, and analyzed with standard procedures using SPM8 (see the Supplemental Experimental Procedures). In all of the fMRI analyses (multivariate and univariate), we employed a voxel-wise whole-brain approach. First, the whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average whole-brain activation maps were thresholded at p < 0.005 (uncorrected for multiple comparisons) and overlaid onto orthogonal sections.
can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.03.059.

AUTHOR CONTRIBUTIONS

A.G. and H.H.E. developed the study concept. All authors contributed to the study design. Testing and data collection were performed by A.G. and G.G. M.B. performed the multivoxel pattern analysis. A.G. and G.G. performed the rest of the data analyses. A.G. drafted the manuscript and wrote it together with H.H.E.; M.B. and G.G. provided important revisions. All authors approved the final version of the manuscript for submission.

ACKNOWLEDGMENTS

This research was made possible by funding from the Swedish Research Council, the James McDonnell Foundation, Söderbergska Stiftelsen, and the European Research Council. M.B. was further supported by the European Union Seventh Framework Programme (FP7/2007-2013) under grant agreement PIOF-GA-2012-302896.

Received: October 30, 2014
Revised: March 9, 2015
Accepted: March 30, 2015
Published: April 30, 2015

REFERENCES


Posterior Cingulate Cortex Integrates the Senses of Self-Location and Body Ownership

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Supplemental Figures and Legends

Figure S1, Individualized Visual Stimuli, Related to Figure 1. The stereoscopic visual stimuli were tailored for each individual participant such that they viewed their own body protruding the magnet from a third-person perspective (3PP). The results of the video editing process are shown for each participant (P1-P15) for Position A.
Figure S2, Behavioral Methods and Results, Related to Figure 2. (A) The map of the scanner room used in the self-location task. The participants were shown this map in the HMDs and asked to rate how strongly they perceived themselves to be located in positions A, B, and C. This procedure was repeated for each of the six experimental conditions (see figure 2A). (B) Results of the post-scan questionnaire experiment. The average rating of each individual statement for each of the six experimental conditions. The error bars represent the SEM.
Figure S3. Threat-evoked Brain Responses and Real Body Disownership, Related to Figure 3. (A) Sample frames depicting the three different threat events (see also figure 2C). (B) An interaction between threat type (Knife vs. Spoon) and ownership (Synchronous vs. Asynchronous) revealed stronger threat-evoked BOLD responses in brain regions involved in the anticipation of pain (the anterior insular cortex, AIC: \( r=3.72, P=0.055 \), corrected, trend toward significance) and the experience of fear (amygdala: \( t=4.22, P=0.028 \), corrected) when the participants experienced the stranger’s body as their own. (C) When the real body was threatened, the SCR was lower in the synchronous than in the asynchronous condition (\( P=0.056 \), trend towards significance). This result is compatible with a previous behavioral study [S1] and the interpretation that the real body is disowned during the illusion. (D) The BOLD responses evoked by threats directed towards the real body were significantly weaker in the AIC (\( t=3.58, P=0.012 \), corrected) and the anterior cingulate cortex (ACC: \( t=3.04, P=0.048 \), corrected) for the Synchronous, as opposed to the Asynchronous, condition. (E) Furthermore, the levels of threat-evoked BOLD activity in these areas were negatively related to the subjectively rated strength of the illusion (ACC: \( r=4.64, P=0.018 \), corrected; AIC: \( r=4.13, P<0.001 \), uncorrected). (A-E) Together, these results corroborate the notion that illusory ownership of the stranger’s body was associated with disownership of the real body in view. However, it should be noted that some of the effects did not reach statistical significance (\( P<0.05 \)), which is probably due to the relatively low number of participants in the present experiment compared to previous studies investigating ownership-related cortical anxiety responses [S2] and disownership-related threat-evoked SCRs [S1]. In addition, the disownership threat event (i.e., the hammer threat) took place further away from the participant’s 1PP in the background of image. This could explain the weaker threat-evoked SCR effect compared to the knife threat to the stranger’s body, which occurred closer to the 1PP in the foreground of the image. Nevertheless, the main results (figure 2) provided consistent and significant behavioral evidence (i.e., the questionnaire, SCR, and self-location task results) that the synchronous condition was associated with the illusory experience of owning the stranger’s body and being located in the out-of-body position. The error bars represent the SEM. For display purposes, the statistical threshold for the activation maps was set to \( P<0.005 \), uncorrected. A white circle indicates a cluster containing a significant peak (\( P<0.05 \), corrected).
Figure S4, Additional Analyses, Related to Figure 4 and 5. (A) To determine whether there were voxels within the hippocampus proper that significantly decoded self-location, we manually segmented the hippocampus from an average anatomical scan (according to the protocol of [S3]). We then inclusively masked the whole-brain decoding map with the hippocampus mask. This analysis confirmed that part of the self-location decoding cluster was within the hippocampus proper and that voxels overlapping with this anatomical structure significantly decoded self-location (peak MNI: -22, -30, -12; r=4.96, cluster size=6 voxels, P=0.006, corrected). All of the voxels that constituted the cluster were located in the left posterior hippocampus. A post hoc interaction contrast ([Synchronous_{A,B} - Asynchronous_{A,B}] - [Synchronous_{B,C} - Asynchronous_{B,C}]) showed that this cluster of voxels decoded self-location (A vs. B) significantly better than head direction (B vs. C) (r=2.66, P=0.023, corrected), which is compatible with the notion that the hippocampus supports an allocentric representation of perceived self-location. (B) For comparison, the unmasked whole-brain analysis is displayed in panel B. The peak voxel in the whole-brain analysis was located in the white matter between the left hippocampus and the parahippocampal gyrus (MNI: -24, -32, -16; r=7.46, P=0.001, corrected; see also figure 4). (C) In addition to effective connectivity changes related to self-location decoding (see figure 5 of the main text), we examined effective connectivity changes related to the decoding accuracy of head direction in the PCC. In rats, the PCC contains head direction cells [S4, S5], and the PCC is commonly activated in human fMRI experiments involving manipulation of facing direction [S6–8]. In this analysis, the PCC seed was defined based on the group peak coordinates in the head direction decoding analysis (figure 4C). Those results showed that the higher the decoding accuracy of head direction (B vs. C) in the PCC, the stronger its effective connectivity to the left hippocampus (r=4.03, P=0.039, corrected) and posterior parahippocampal cortex (PHC) (r=5.28, P=0.008, corrected). Intriguingly, neither the hippocampus nor the PHC significantly decoded head direction. However, both regions were implicated in the self-location decoding analysis (see panel B). In addition, the hippocampus cluster in the present analysis showed a significant overlap with the hippocampus cluster identified in the self-location decoding analysis (panel D; green=self-location decoding; red=head direction effective connectivity; yellow=overlap). We speculate that information concerning head direction is processed in the PCC and used in the construction of the representation of self-location in the medial temporal lobe. (E) Overlap between representations of self-location and body ownership in the right IPS. In a post hoc analysis, we created a binary image of the right IPS self-location decoding cluster (P<0.005 uncorrected) and used this image as an inclusive mask in the body ownership contrast (synchronous vs. asynchronous across positions; P<0.005 uncorrected). The result showed partial overlap in the right IPS, which supports the notion that this region is involved in the processing of both body ownership and self-location. (A)-(E). For display purposes, the statistical threshold for the decoding/activation maps was set to P<0.005, uncorrected.
Figure S5, Eye Tracking Results, Related to Experimental Procedures. The results of the eye tracking are displayed for each participant, position, and for the synchronous (red circles) and asynchronous conditions (black circles). The data were down-sampled to 1 Hz to minimize noise – thus, one data point here represents the average gaze coordinates within a 1-second interval. The tilted-head posture and the use of the HMDs resulted in inter-individual differences in the angle between the camera and the participant’s eye, which in turn led to variable accuracies in the calibration of the eye-tracking recording. In light of this, the gaze coordinates with respect to the visual stimuli presented here should be interpreted with caution. Nevertheless, the present data allowed us to compare the average gaze coordinates across the different experimental conditions and rule out any potential systematic differences that might confound the main analyses. We found that the gaze coordinates did not significantly differ between the Synchronous and Asynchronous conditions for any of the positions (all $P>0.05$), illustrated by the substantial overlap of the clouds of red and black data points.
### Supplemental Tables

<table>
<thead>
<tr>
<th>Anatomical region</th>
<th>MNI x, y, z {mm}</th>
<th>Peak T</th>
<th>P value</th>
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<td><strong>SUBCORTICAL STRUCTURES</strong></td>
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<td>R. thalamus</td>
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L = Left. R = Right. PMv/d = ventral/dorsal premotor cortex.

*corrected P-value.

**Table S1. Body Ownership-related Activations.** All brain regions (peaks) that revealed significant activation at $P<0.001$ (uncorrected) are listed. FWE-corrected $P$-values are reported for regions that survived the correction for multiple comparisons in anatomically predefined regions (small volume corrections). Please note that activity in the cerebellum could not be examined due to the lack of coverage of this structure in several participants (see Supplemental Experimental Procedures).
<table>
<thead>
<tr>
<th>Anatomical region</th>
<th>MNI x, y, z {mm}</th>
<th>Peak T</th>
<th>P-value</th>
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<tbody>
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<td>-24, -32, -16</td>
<td>7.46</td>
<td>0.001*</td>
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L = Left. R = Right. PMd = dorsal premotor cortex.
*corrected P-value.
** see figure S4A-B for details.

**Table S2. Decoding of Self-location.** All brain regions (peaks) that revealed significant decoding at $P<0.001$ (uncorrected) are listed. FWE-corrected $P$-values are reported for regions that survived the correction for multiple comparisons in anatomically predefined regions (small volume corrections).
### Table S3. Decoding of Head Direction

<table>
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<th>Anatomical region</th>
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<td>R. middle frontal gyrus</td>
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<td><strong>PARIETAL LOBE</strong></td>
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<td>0.045*</td>
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<td>4.16</td>
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L = Left. R = Right.
*corrected P-value.

Table S3. Decoding of Head Direction. All brain regions (peaks) that revealed significant decoding at \( P < 0.001 \) (uncorrected) are listed. FWE-corrected \( P \)-values are reported for regions that survived the correction for multiple comparisons in anatomically predefined regions (small volume corrections). Notably, we did not observe significant decoding of head direction in the hypothesized entorhinal/subicular region.
Supplemental Discussion

Cortical Representations of Body Ownership

In the present study, we found that the feeling of owning a stranger’s body viewed from the 1PP was associated with increased activity in the premotor, intraparietal, and lateral occipital cortices (figure 3A-B) and that the subjectively rated strength of ownership was significantly correlated with the magnitude of the BOLD response in the left PMv (figure 3C). These results are consistent with those of previous studies on single limb [S9–12] and full-body ownership [S13, S14]. The premotor and intraparietal cortices contain neuronal populations with visuo-tactile receptive fields covering the skin surface and the space surrounding the body (peripersonal space) [S15–18], collectively representing a multisensory buffer zone between the body and the external environment. Neurons in these areas also have the capacity to integrate spatially and temporally congruent visual, tactile, and proprioceptive signals from the body [S12, S15, S19, S20]. These properties makes the IPS and PMv ideal candidates for mediating the feeling of body ownership [S9, S21, S22]. In line with these notions, a recent study revealed BOLD-adaptation responses in the IPS and PMv that were specific to visual stimulation close to a rubber hand experienced as one’s own, suggesting that activity in these regions in the human brain reflects the remapping of peripersonal space onto a body part perceived as part of the self [S9]. In addition, previous fMRI studies have shown that activity in the IPS and PMv reflects the integration of spatially and temporally congruent visual, tactile, and proprioceptive information from the seen upper limb [S12, S20] and that this multisensory integrative activity is intimately related to the sense of limb ownership [S10–12]. Moreover, the coherent percept of owning an entire body, as opposed to a single limb, has been associated with the integration of visual and somatosensory information across multiple segments of the body in the PMv and IPS [S13, S14]. Thus, we here propose that the self-attribution of the stranger’s body is reflected in two closely related processes implemented by neuronal populations in the IPS and PMv: first, the remapping of peripersonal space from being centered on the real body to being centered on the stranger’s body; second, the integration of visual, tactile, and proprioceptive information in body- and body part-centered spatial reference frames. This idea is consistent with the observed illusion-related decreases in SCRs and cortical (BOLD) anxiety responses evoked by threats toward the real body (figure S3), indicating that ownership of the stranger’s body is coupled with disownership of the real body (and vice versa). The multisensory peripersonal space mechanisms in the IPS and PMv may, in turn, be integrated with representations of self-location in the PCC, which is compatible with our effective connectivity results (figure 5) and the observed overlap between the self-location decoding cluster and the body ownership activation cluster in the right IPS (figure S4E). We further speculate that the bilateral LOC activity observed in the present study represents a modulation of the processing of visual information from the stranger’s body that is specific to the context of body ownership. Such a cross-modal interaction [S23, S24] may arise from top-down modulatory effects from the multisensory body representation in the IPS, in line with previous studies on single-limb ownership that found illusion-induced increases in connectivity between the LOC and the intraparietal cortices [S11, S12, S25]. This interpretation is compatible with previous evidence suggesting that tactile, proprioceptive, and motor signals from a limb modulate the
processing of visual information from the same body part in the LOC [S26–28]. Finally, based on earlier studies that have associated cerebellar activity with the experience of body ownership illusions [S10, S11, S13], we speculate that the cerebellum, in concert with the IPS, is involved in the recalibration of proprioceptive representations of the body that are important for the planning and execution of reaching movements from the spatial location of the owned stranger’s body. Unfortunately, we were not able to examine cerebellar activity in this study due to the lack of coverage of this structure in several participants (see Supplemental Experimental Procedures). In summary, the evidence reviewed above points to the right IPS as a key node in the fronto-parieto-occipital circuits involved in the construction of multisensory body representations and the emergence of the sense of body ownership.”

Perceptual Illusions and Attention
The approach of using perceptual illusions to investigate the processes that underlie normal perception has a long history in psychology [S29]. In this study, we used an out-of-body illusion to study the neural correlates of the senses of self-location and body ownership. Because humans have a continuous, ‘cognitively impenetrable’ feeling of having a body with a specific location in the external space [S30], it is arguably difficult, if not impossible, to study these senses by means other than perceptual illusions. A general limitation of this approach, however, is that brain activations observed during an illusion may potentially reflect unspecific effects related to arousal or the experience of an unusual percept. Specifically, in this experiment, it is theoretically possible that the synchronous visuo-tactile stimulation led to greater deployment of attention to the visual features in the images, which in turn resulted in better decoding of Position A vs. Position B in the synchronous compared to the asynchronous condition. However, there are several strong reasons arguing against this interpretation of our findings. First, the participants did not engage in any explicit cognitive, memory, or motor task during the experiment - they were simply instructed to lie still and look into the HMDs. This design feature ensured that any task-selective or task-preparatory activity could not confound the decoding results. Second, the participants were naïve to the purpose of the experiment. Thus, they did not have any expectations with regard to what they would experience in the different conditions. Third, if synchronous stimulation were associated with enhanced visual attention, one would expect stronger activity in visual areas in the synchronous compared to the asynchronous conditions [S31–33]. However, in a control analysis (see the final paragraph of Multivoxel Pattern Analysis below), we found no significant voxels in the primary visual areas even at the very liberal statistical threshold of $P<0.01$ (uncorrected). Fourth, we observed a significant correlation between decoding accuracy (neural measure) and self-location score (behavioral measure) in the intraparietal, posterior cingulate, and retrosplenial cortices. These findings support the notion that the decoding results in these regions are related to changes in the sense of self-location rather than to changes in visual attention brought about by the synchrony of the visual and tactile stimuli. Fifth, the eye-tracking results showed that the participants did not systematically differ in their average patterns of fixations between the synchronous and asynchronous conditions for each of the positions, which one would expect if synchronous stimulation led to increased attention to the certain visual features in the images (figure S5). Finally,
in a recent study, we employed an explicit visual attention task in the context of experiencing a ‘virtual hand illusion’ [S12]. Those results showed that the participants’ level of performance ($P=0.59$) and the reaction time ($P=0.48$) did not significantly differ between the synchronous and asynchronous conditions. Although the setup of that experiment differed substantially from the current study, the results suggest that experiencing body ownership illusions in general does not lead to impaired visual attention to portions of the visual field that are not subject to the visuo-tactile stimulation. Taken together, these arguments suggest that the illusion-related decoding effects reflect changes in the processing of perceived self-location rather than unspecific attentional effects.
Supplemental Experimental Procedures

Spatial Environment
The scanner room was $7 \times 5 \text{ m}^2$ with a height of 3 m. One of the short walls featured a large window and a door leading into the control room. The MRI scanner was located close to the opposite wall. During the scanning sessions, the participants observed the room from the perspective of an unknown person lying on the floor in one out of three positions - Positions A, B, and C (see figure 1 for a schematic overview). Positions A and B represented different corners of the room with the same head direction, whereas Positions B and C represented the same corner of the room but with a 90° angular difference in head direction. Prior to the scanning sessions, the participants were given the opportunity to familiarize themselves with the spatial environment. During the experiment, the participants were placed comfortably on the MRI scanner bed in a supine position, with the head tilted forward by approximately 25 degrees. The participants had no task and were instructed to lie still and look into the HMDs.

Participant-specific Stereoscopic Visual Stimuli
The visual stimuli were presented in the form of stereoscopic (three-dimensional; 3D) videos recorded in the scanner room in a separate session. To record the videos, we used two identical cameras (CamOne Infinity HD, resolution 1920×1080, Touratech AG, Niedereschach, Germany) mounted 8 cm from each other on a custom-made tripod. The cameras were positioned to capture the visual perspective of an unknown person lying on the floor in Positions A, B, and C with the head tilted forward by approximately 25 degrees. The field-of-view of the videos included landmark objects such as the MRI scanner itself, a cupboard to the right of the scanner, a chair placed to the left of the scanner, one door leading to the corridor, one door leading to the control room, and a large window between the scanner and the control rooms, as well as the participant’s real body lying inside the scanner (see below for details). The spatial environment was maintained identical across the video recording sessions and fMRI experiments. In the lower part of the field-of-view, a stranger’s body (belonging to author GG) was observed from the 1PP. The stranger’s body was placed in a position that approximately matched the participant’s posture while lying on the scanner bed. To induce the illusory feeling of ownership of the body seen from the 1PP [S34, S35], a white spherical object (6.5 cm in diameter) attached to a 1-m-long wooden stick (figure 1) repetitively touched the abdomen, right upper leg, and left foot of the stranger’s body in the videos, while the participant received temporally congruent tactile stimulation on the corresponding body parts (see Tactile stimuli below). The touches were delivered in a predetermined 18-second-long sequence. The duration of each individual touch was 700 ms and the time interval between the offset of one touch and the onset of the next touch was 1300 ms. We created three 18-s video clips, one for each of the positions (A, B, and C), featuring identical sequences of touches (namely, “A-L-F-L-F-A-A-F-L”; A=abdomen; L=right upper leg; F=left foot). The synchronization of the left and right video streams was achieved with a frame-by-frame technique implemented in Final Cut Pro 7 (Apple Inc., California, USA). The recordings from the left and right cameras, which corresponded to the left and right eye in the HMDs, respectively, were arranged side-by-side in a single frame with a size of...
1600×600 pixels. A sound track was added to the video for each experimental condition to provide the experimenter with the appropriate audio cues for the delivery of the tactile stimuli.

To tailor the visual stimuli to each individual participant, we invited the participants to the MRI scanner room a couple of days before the scanning sessions and instructed them to wear the same clothes that they would wear during the upcoming experiment. We asked the participants to lie on the scanner bed and placed them in a position that matched the position that they would later take during the fMRI acquisition. We then captured 3D still images featuring the lower part of the participant’s body protruding from the bore of the MRI scanner, as seen from Positions A, B, and C. For each participant and position, a hand-drawn matte was used to segment the 3D image of the participant’s body protruding from the bore of magnet (for the left and right eye images), using Final Cut Pro 7. The image of the real body was then seamlessly pasted into each of the position-specific video clips described in the previous paragraph. This video editing process resulted in one 3D video for each position, in which the foreground featured the stranger’s body (identical across participants) and the background consisted of the scanner room, including the participant’s real body visible on the scanner bed (unique for each individual participant; see figure S1).

Using a frame-sequential technique implemented with custom-made hardware and software, the three-dimensional visual stimuli were transmitted to a pair of MR-compatible HMDs (Nordic Neurolab, Bergen, Norway) during the scanning sessions. Movie S1 features sample video clips from Position A for Participant 13.

Tactile Stimuli
During the scanning sessions, the experimenter stood to the left of the participant’s body and applied touches to the abdomen, right upper leg, and left foot using the same object used in the videos. The experimenter wore MRI-compatible headphones and listened to audio cues regarding the sequence of touches to ensure the appropriate timing and duration of the stimuli. In the Synchronous illusion condition, the audio cues were temporally synchronized with the touches delivered to the virtual body in the videos. In the Asynchronous control condition, the audio cues were delayed by 1000 ms with respect to the touches in the videos, resulting in a temporal incongruence between the visual and tactile stimuli. Importantly, the design of the audio cues ensured that the experimenter was blind with respect to the nature and the sequence of the experimental conditions of interest.

Experimental Conditions and Design
We employed a 2×3 factorial design with the factors visuo-tactile stimulation mode (Synchronous, Asynchronous) and visual 1PP (Position A, Position B, Position C). Eighteen-second blocks of all six conditions were presented in a fully randomized order with a random intertrial interval of 5-9 seconds. Each condition was repeated four times per run, for a total of ten runs per participant (except for Participant 6, who aborted the experiment after nine runs due to neck discomfort). The intertrial interval served as the baseline condition and consisted of a black screen with a fixation
cross. To test the alertness of the participants, catch trials were presented at rare (7.7% of the trials), random occasions during each run. These trials involved one single touch event in which the stroking direction of either the seen or the felt touch was distal-to-proximal instead of the normal proximal-to-distal direction. Participants were instructed to press a button using their left hand as soon as they noticed such an event (100% accuracy in all subjects).

**Post-scan Self-location Task**
Following the fMRI acquisition sessions, the participants were presented with one additional repetition of the six experimental conditions in a counterbalanced order. At the end of each repetition, the participants were shown a schematic map of the scanner room with letters indicating the following three locations: the lower left corner (corresponding to Position A), the upper left corner (corresponding to Positions B and C), and the scanner bed on which the subject’s real body was positioned (figure S2A). The participants were asked to rate how strongly they perceived themselves to be located in each of the three locations on a scale ranging from 0 (“I did not experience being located here at all”) to 100 (“I had a very strong experience of being located here”). Based on the results of a previous behavioral study that introduced the self-location task, [S1], we predicted that participants would report a stronger sense of self-location in the out-of-body position and a weaker sense of self-location in the veridical position inside the scanner in the *Synchronous* compared to the *Asynchronous* condition. In addition, we hypothesized that the participants would perceive an equally strong sense of self-location in the upper left corner for the two different heading directions, corresponding to *Positions B* and *C*. For visualization purposes, we mapped the average ratings for the three locations for each of the six experimental conditions onto a color-coded scale, and displayed the results as color-coded bodies placed in the respective locations (figure 2A). Statistically, the analysis-of-interest was the interaction effect between visuo-tactile stimulation mode (*Synchronous*, *Asynchronous*) x location (out-of-body position, veridical position). We used separate repeated measures ANOVAs for each of the three visual perspectives (*Positions A, B, and C*).

**Post-scan Questionnaire**
Immediately following the self-location task described above, the participants were again presented with one repetition of each experimental condition. At the end of each repetition, the participants were asked to rate seven statements on a scale that ranged from 0 (“I completely disagree with the statement”) to 10 (“I fully agree with the statement”). The statements were presented in a randomized order via the HMDs, and the experimenters logged the verbally reported subjective ratings. Four of the statements were designed to probe the illusion experience (S1-S4 in figure S2B), and three statements served as controls for the task demands and suggestibility (S5-S7 in figure S2B). In our statistical analyses, we defined the dependent variables as the mean subjective rating of the illusion statements (S1-S4) and of the control statements (S5-S7). For each of the three visual perspectives (Positions A, B, and C), we used a repeated measures ANOVA to test for a positive interaction effect between visuo-tactile stimulation mode (*Synchronous*, *Asynchronous*) x statement type (illusion, control).
Recording of Skin Conductance Responses during fMRI
We concurrently recorded BOLD and SCR responses to threats directed towards the virtual body viewed from the 1PP and the participant’s real body (viewed from the 3PP) following periods of exposure to synchronous or asynchronous visuo-tactile stimuli to provide an objective physiological measure of changes in body ownership [S1, S2, S12, S34–38]. A randomly selected 25% of the trials in the Synchronous and Asynchronous conditions (regardless of position) were followed by one of the following 2-second-long visual stimuli: i) a kitchen knife appearing and sliding swiftly just above the abdomen of the stranger’s body; ii) a kitchen spoon made out of wood performing the same motion as the knife; or iii) the experimenter entering the field of view and wielding a rubber sledgehammer towards the lower legs of participant’s real body lying on the scanner bed (figure 2C and movie S1). The knife threat was designed to probe the feeling of ownership of the virtual body, whereas the spoon trials served as a control for the presence of any moving object within the space close to the stranger’s body during the illusion [S35]. The hammer threat was designed to examine the feeling of disownership of the real body [S1]. We used a sledgehammer because the knife would be barely visible in the background through the HMDs, unlike the objects presented in the foreground close to the stranger’s body.

To record the threat-evoked SCR, we used an MR-compatible SCR-recording module (Brain Products GmbH, Gilching, Germany). Prior to the onset of the acquisition sessions, two electrodes were attached to the index and middle fingers of the participant’s left hand using electrode gel. The electrodes were connected to an MR-compatible amplifier (BrainAmp ExG MR, Brain Products), and continuous recordings for each session were collected using a computer running BrainVision Recorder (acquisition sampling rate 5000 Hz). All recordings were stored and imported into Matlab for further offline analysis. For each threat event, we identified the maximal and minimal values of the SCR within a five-second temporal window that was aligned to the event onset. For all trials, the event-specific SCR amplitude was then calculated as the difference between the maximal and minimal values, and an average value was computed for each participant and condition [S1, S34, S35, S39]. We analyzed the interaction effect between threat type (Knife, Spoon) x visuo-tactile stimulation mode (Synchronous, Asynchronous) in a 2×2 repeated measures ANOVA to probe the feeling of ownership of the stranger’s body. To quantify real body disownership, we analyzed the data from the hammer threat events using a paired t-test comparing the Synchronous and Asynchronous conditions. A one-tailed t-test was used because we had a strong a priori hypothesis regarding the direction of the results [S1].

Acquisition of Functional Imaging Data
We acquired T2*-weighted echo-planar images (voxel size 2×2×2 mm³) with blood oxygen level-dependent (BOLD)-contrast [S40] using a Siemens TIM Trio 3T scanner equipped with a 12-channel phased-array head coil. Each functional volume comprised 55 continuous near-axial slices (96×94 matrix, TE=30 ms). This size ensured that the whole brain, except the cerebellum, was within the field of view for all subjects. One complete volume was collected every 3.5 seconds (TR=3500 ms). For each participant, a total of 1870 functional volumes were collected (187 per run
for a total of 10 runs per experiment) and a high-resolution structural image was acquired at the end of the experiment (3D MPRAGE sequence, voxel size $1 \times 1 \times 1 \text{mm}^3$, FOV 250 mm $\times$ 250 mm, 176 slices, TR=1900 ms, TE=2.27 ms, flip angle=9 degrees).

**Eye Tracking**

An MRI-compatible video camera (acquisition frequency 60 Hz; MRC Systems, Heidelberg, Germany) mounted behind a mirror inside the left HMD was used to track the movements of the participant’s left eye. We used the ViewPoint EyeTracker software (Arrington Research, Arizona, USA) for calibration and recording of eye-videos as well as fixation coordinates throughout the experimental sessions. The recordings were monitored online by an experimenter in the MRI control room, and examined offline to evaluate the participant’s overall alertness. Furthermore, the registration of the gaze coordinates allowed us to test for systematic differences in condition-specific patterns of eye movements, which could contribute to the BOLD responses in the vicinity of the brain regions of interest [S41] and potentially confound our results. To rule out this possibility, we plotted the fixation coordinates for all of the experimental conditions for each participant (see figure S5; Participant 2 was excluded due to a technical issue with the recording). None of the participants showed significant differences in the average gaze location between the Synchronous and Asynchronous conditions for the different positions (all $P>0.05$; pair-wise $t$-tests for the X and Y coordinates, respectively, Bonferroni-corrected for multiple comparisons).

**Preprocessing**

The fMRI data were analyzed with SPM8 (Wellcome Department of Cognitive Neurology, London, UK). The first three volumes of each run were discarded from further analysis due to non-steady-state magnetization. Following slice timing correction, the functional images were realigned to correct for head movements and co-registered with the high-resolution structural scan of each participant. The anatomical image was subsequently segmented into white matter, gray matter and cerebrospinal fluid partitions, and it was normalized to the Montreal Neurological Institute (MNI) standard brain.

**Univariate GLM Analysis**

Following the preprocessing steps described above, the functional images were normalized to the MNI standard brain and spatially smoothed with an 8-mm full-width-at-half-maximum (FWHM) isotropic Gaussian kernel. In the first-level analysis we defined separate regressors for each of the six experimental conditions, modeling the 18-s epochs of visuo-tactile stimulation (Synchronous and Asynchronous) in the three spatial locations (Positions A, B and C). Three regressors were defined to model the threat events (Stranger’s body knife threat, Stranger’s body spoon control threat, Real body hammer threat), and one regressor of no interest was created to model the catch trials. Each condition was modeled with a boxcar function and convolved with the standard SPM8 hemodynamic response function. We defined linear contrasts in the GLM (see below) to test our hypotheses, and the contrast images from all subjects were entered into a random effects group analysis (second-level analysis). To account for the problem of multiple comparisons in the
statistical analysis of the whole-brain data, we report the peaks of activation that achieved a significance threshold of $P<0.05$ after correction using the topological family-wise error rate (FWE) implemented in SPM8. In areas in which we had an a priori defined hypothesis (premotor and intraparietal cortices for the body ownership-related activations; the ACC, AIC and the amygdala for the threat-related activations), we used a small volume correction (spheres with a radius of 6 mm) around the peaks from previously studies on body ownership [S11, S13] and pain anticipation [S42–44].

To identify the brain regions whose BOLD responses were associated with the experience of ownership of the stranger’s body, we contrasted the Synchronous and Asynchronous conditions across locations. The contrast weights were $+1/3$ for Position $A_{\text{Synchronous}}$, Position $B_{\text{Synchronous}}$ and Position $C_{\text{Synchronous}}$, and $-1/3$ for Position $A_{\text{Asynchronous}}$, Position $B_{\text{Asynchronous}}$ and Position $C_{\text{Asynchronous}}$. For visualization purposes, an activation map featuring all voxels that passed a significance threshold of $P<0.005$ (uncorrected) was overlaid onto a canonical inflated surface of both hemispheres using NeuroLens (Massachusetts General Hospital, Boston, USA; see figure 3A). The contrast estimates relative to a common baseline (the inter-trial rest intervals) were extracted for all of the significant peaks of activation and displayed as histogram plots (figure 3B).

To further corroborate our description of the neural basis of the feeling of ownership of the stranger’s body, we ran a multiple regression analysis with the aim of identifying areas with activity that was significantly correlated with the participants’ subjective reports in the post-scan behavioral experiment. Specifically, we computed an “ownership index” using the mean difference between the ratings of the illusion statements (S1-S4) and control statements (S5-S7) as a dependent variable, according to the following equation: $(Position\ A_{\text{Synchronous}} + Position\ B_{\text{Synchronous}} + Position\ C_{\text{Synchronous}})/3 \ - \ (Position\ A_{\text{Asynchronous}} + Position\ B_{\text{Asynchronous}} + Position\ C_{\text{Asynchronous}})/3$. We then entered the ownership indices (one per participant) as covariates in a separate second-level multiple regression analysis and evaluated positive correlations with the contrast estimates in a whole-brain voxel-wise fashion (figure 3C).

We subsequently examined the threat-evoked BOLD responses that were specifically related to the illusion. We expected that experiencing the illusion would lead to stronger threat-evoked BOLD responses in areas associated with pain anticipation and fear when the threat was directed towards the stranger’s body (i.e., the Knife threat). We used the spoon “threats” to control for the effect of viewing any object moving close to a body perceived as one’s own. Thus, we analyzed the following interaction: $(\text{Knife threat}_{\text{Synchronous}} - \text{Knife threat}_{\text{Asynchronous}}) - (\text{Spoon control}_{\text{Synchronous}} - \text{Spoon control}_{\text{Asynchronous}})$. Conversely, we predicted that the illusion would lead to weaker threat-evoked BOLD responses in the same areas when the threat was directed towards the participant’s real body (i.e., the Hammer threat), reflecting real body disownership [S1]. To this end, we analyzed the contrast $\text{Hammer threat}_{\text{Asynchronous}} - \text{Hammer threat}_{\text{Synchronous}}$. To corroborate this analysis, we ran a separate second-level multiple regression analysis and searched for positive correlations between the contrast estimates and the ownership index. In other words, this analysis
revealed voxels that displayed a negative correlation between the threat-evoked BOLD responses and the subjective illusion ratings (see figure S3E).

The anatomical localization of the activations was related to the major sulci and gyri [S45], distinguishable on the average structural scan that was generated from the standardized anatomical MRIs from the 15 subjects.

**Multivoxel Pattern Analysis**

In this analysis, the functional data were analyzed in native space and were spatially smoothed using a 3-mm FWHM isotropic Gaussian kernel in SPM8. We defined separate regressors for each block of synchronous or asynchronous visuo-tactile stimulation in Positions A, B, or C, resulting in a total of 240 individual regressors (two visuo-tactile stimulation modes × three positions × four repetitions × ten runs = 240 trials). The resulting maps of parameter (beta) estimates were used as the MVPA input. The threat events and catch trials were modeled as regressors of no interest.

Within each participant, we used locally multivariate mapping to identify multivoxel patterns [S46]. The brain was partitioned into overlapping voxel clusters (each of which was approximately spherical in shape with a radius of 3 mm); in each of these clusters, we used linear support vector machines (SVMs; in the LIBSVM implementation, http://www.csie.ntu.edu.tw/wcjlin/libsvm/, with the fixed regularization parameter of C = 1) to compute decoding accuracies for the “self-location decoding analysis” (Position A versus B) and the “head direction decoding analysis” (Position B versus C) in the Synchronous and Asynchronous conditions separately. The experimental design was optimized for a SVM decoding analysis, in contrast to alternative MVPA approaches such as representational similarity analyses [S8], because the SVM decoding approach allows for more explorative whole-brain analyses [S46] and the direct use of the asynchronous condition as a rigorous control for visual input. We used a ten-fold leave-one-run-out cross-validation approach to ensure independent training and testing data. This process resulted in four decoding accuracy maps (Synchronous<sub>AvsB</sub>, Asynchronous<sub>AvsB</sub>, Synchronous<sub>BvsC</sub>, Asynchronous<sub>BvsC</sub>) for each subject, in which the value of each voxel represents the run-average percentage of trials that were correctly classified as Position A or B (self-location decoding analysis) or Position B or C (head direction decoding analysis).

For the group-level analysis, the chance decoding accuracies (50%) were subtracted and the maps were normalized and spatially smoothed (6-mm FWHM) to accommodate the parametric assumptions of SPM. We then entered the resulting decoding accuracy maps from all subjects into a random effects group analysis (second-level analysis) in SPM8 and defined linear contrasts to test our hypotheses.

To identify brain regions whose activity patterns carry illusion-specific information concerning the perceived self-location/head direction, we searched for voxels associated with significantly higher decoding accuracies in the Synchronous than in the Asynchronous condition, as well as values
significantly greater than chance (50%). In the self-location decoding analysis, we therefore contrasted \( \text{Synchronous}_{\text{AvsB}} \) and \( \text{Asynchronous}_{\text{AvsB}} \), using \( \text{Synchronous}_{\text{AvsB}} \) versus chance level as an inclusive mask (thresholded at \( P<0.001 \) uncorrected). In the head direction decoding analysis, we contrasted the \( \text{Synchronous}_{\text{BvsC}} \) and \( \text{Asynchronous}_{\text{BvsC}} \), using \( \text{Synchronous}_{\text{BvsC}} \) versus chance level as an inclusive mask (thresholded at \( P<0.001 \) uncorrected). This approach ensured the identification of voxels decoding self-location/head direction significantly higher in the \textit{Synchronous} compared to the \textit{Asynchronous} condition and significantly higher than chance.

To further investigate activity patterns reflecting perceived self-location, we ran a multiple regression analysis with the aim of identifying voxels with a decoding accuracy that were positively correlated with the participants’ ratings in the post-scan self-location task (i.e., the self-location score). We defined a “self-location index” by computing the difference in self-location scores between the \textit{Synchronous} and \textit{Asynchronous} conditions for Positions A and B. We then entered the self-location indices (one per participant) as covariates in a second-level analysis and evaluated significant positive correlations with a contrast image representing the decoding accuracy difference between \( \text{Synchronous}_{\text{AvsB}} \) and \( \text{Asynchronous}_{\text{AvsB}} \).

To control for potential univariate effects that could drive classifier performance in the self-location and head direction decoding analyses, we examined the bi-directional interaction position \( \times \) visuo-tactile synchrony. For the decoding of self-location (\textit{Position A vs B}), this univariate analysis corresponded to the two interaction contrasts (\textit{Position A – Position B})_{\textit{SYNCHRONOUS}} – (\textit{Position A – Position B})_{\textit{ASYNCHRONOUS}} (referred to as “Contrast A>B”) and (\textit{Position B – Position A})_{\textit{SYNCHRONOUS}} – (\textit{Position B – Position A})_{\textit{ASYNCHRONOUS}} (referred to as “Contrast B>A”). For the decoding of head direction (\textit{Position B vs C}), this analysis corresponded to the two interaction contrasts “Contrast B>C” and “Contrast C>B”. The results showed that there were no whole-brain significant activations (\( P<0.05 \), FWE-corrected) in any of the four contrasts (\textit{Contrast A>B}, \textit{Contrast B>A}, \textit{Contrast B>C}, and \textit{Contrast C>B}). Furthermore, we found no voxels anywhere in the brain at the statistical threshold of \( P<0.001 \) (uncorrected) for these four contrasts, except for one cluster in the middle frontal gyrus for the \textit{Contrast B>A}. This activation was located at a distance from the locations of our hypothesized regions (IPS, PCC, RSC, and the hippocampus) and did not overlap with the decoding results. These findings are compatible with previous studies (e.g., [S48]) that have demonstrated the superiority of pattern-sensitive multivariate analyses compared with conventional univariate approaches for detecting differences in activity between conditions with highly similar macroscopic characteristics.

\textbf{Effective Connectivity Analysis}

Finally, we sought to investigate the neural interplay between the representation of one’s own body and the perceived self-location. Based on the results from the multivoxel pattern analysis, as well as previous studies on anatomical connections and spatial cognition [S5, S49, S50], we first identified the left PCC as a key node in the set of regions associated with the representation of the perceived self-location. We then examined the illusion-induced connectivity changes between this region and
the rest of the brain using psychophysiological interaction (PPI) analyses [S51] and searched for connectivity increases that were positively correlated with the accuracy with which self-location could be decoded.

The PPI measures context-induced changes in the strength of connectivity between two brain regions, as measured by a change in the magnitude of the linear regression slope that relates their underlying activities. A significant PPI indicates that the contribution of one area to another changes significantly with the experimental or psychological context [S51]. We assessed connectivity changes between the left PCC and the rest of the brain. Specifically, the seed was defined for each subject and consisted of the peak voxel within a 10-mm radius from the group peak (the mean distance±SD was 8.35±1.95 mm from the group peak coordinate [-9 -54 44]) for the decoding contrast SynchronousAvsB versus AsynchronousAvsB. Having identified the subject-specific seed coordinates, we extracted the time series (first eigenvariate) of activity from the univariate GLM analysis and adjusted for effects of no interest (head motion parameters, threat events, and catch trials). We then performed a PPI analysis using the contrast of Synchronous versus Asynchronous (across positions) as the psychological factor. At the individual level, three regressors were created in a GLM that represented the time course of activity in the seed region (the physiological factor), the psychological factor and their product (the PPI). The parameter estimates for the PPI regressor from each participant were entered into a second-level analysis using the decoding accuracy in the seed region (one per participant) as a covariate. We then analyzed the contrast estimates for the covariate by using a one-sample t-test. Notably, by estimating the covariate (which is derived from the MVPA analysis) and not the PPI regressor itself, any voxel revealed by this analysis reflects illusion-related connectivity increases that significantly scale with the accuracy with which self-location can be predicted from the BOLD activity patterns in the PCC.

To account for the problem of multiple comparisons in the statistical analysis of the whole-brain MVPA and effective connectivity data, we report the peaks that achieved a significance threshold of $P<0.05$ after correction using the topological FWE implemented in SPM8. In areas in which we had an a priori defined hypothesis (the IPS, precuneus, RSC, PCC, entorhinal/subicular region, and the hippocampus), we used a small volume correction (spheres with a radius of 6 mm) around the peaks from a study in preparation [S52] and previously published studies [S53–59].
**Supplemental References**


