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Report

From Part- to Whole-Body Ownership in the Multisensory Brain

Valeria I. Petkova,[1,*] Malin Björnsdotter,[1,3] Giovanni Gentile,[1,3] Tomas Jonsson,[2] Tie-Qiang Li,[2] and H. Henrik Ehrsson[1]

[1]Brain, Body & Self Laboratory, Department of Neuroscience, Karolinska Institutet, Retzius väg 8, SE-171 77 Stockholm, Sweden

[2]Department of Medical Physics, Karolinska University Hospital Huddinge, SE-141 86 Stockholm, Sweden

Summary

The question of how we experience ownership of an entire body distinct from the external world is a fundamental problem in psychology and neuroscience [1–6]. Earlier studies suggest that integration of visual, tactile, and proprioceptive information in multisensory areas [7–11] mediates self-attribution of single limbs. However, it is still unknown how ownership of individual body parts translates into the unitary experience of owning a whole body. Here, we used a "body-swap" illusion [12], in which people experienced an artificial body to be their own, in combination with functional magnetic resonance imaging to reveal a coupling between the experience of full-body ownership and neural responses in bilateral ventral premotor and left intraparietal cortices, and left putamen. Importantly, activity in the ventral premotor cortex reflected the construction of ownership of a whole body from the parts, because it was stronger when the stimulated body part was attached to a body, was present irrespective of whether the illusion was triggered by stimulation of the hand or the abdomen, and displayed multivoxel patterns carrying information about full-body ownership. These findings suggest that the unitary experience of owning an entire body is produced by neuronal populations that integrate multisensory information across body segments.

Results and Discussion

When we look down at our body, we immediately experience that it belongs to us. We experience our body not as a set of fragmented parts, but rather as a single entity. How does this perception of owning an entire body arise? At the heart of this problem lies the necessity of binding together visual, tactile, and proprioceptive information from multiple body parts into a unitary multisensory percept of one's own whole body. Here, we addressed this question by measuring healthy participants' brain activity with functional magnetic resonance imaging (fMRI) as they experienced controlled changes in ownership of an entire body using the "body-swap" illusion paradigm [12]. This illusion is elicited when a participant observes tactile stimulation on the body of a mannequin from the point of view of the mannequin's head while feeling identical synchronous touches on his or her own body, which is out of sight.

We hypothesized that two basic processes would mediate ownership of an entire body. First, the self-attribution of individual body parts was expected to be mediated through integration of visual, tactile, and proprioceptive information in body-part-centered coordinates by neuronal populations in the ventral premotor and intraparietal cortices [3]. This prediction was based on neuroimaging studies investigating feelings of limb ownership [8, 9] and on neurophysiological studies in nonhuman primates revealing that these areas contain neurons that integrate visual, tactile, and proprioceptive information in reference frames centered on different parts of the body (e.g., the hand, arm, and head) [13–17].

Second, we hypothesized that the perceptual binding of owned body parts into a unified whole is supported by multisensory integration across body segments. This hypothesis was based on the observation that, during full-body illusion, the feeling of ownership spreads out from the stimulated body part to the rest of the (unstimulated) body [12]. We predicted that the underlying neural mechanism would be the visuosomatic integration across body segments, performed by special groups of multisensory neurons located in the premotor and intraparietal areas that have visuosomatic receptive fields extending across several body segments [14, 15, 18, 19], sometimes even encompassing the entire body [20].

To test the first hypothesis (above), we developed an fMRI-compatible setup to induce the body-swap illusion (see Supplemental Results and Supplemental Experimental Procedures available online) and performed two separate fMRI experiments. In the first experiment, involving 26 naive participants, we investigated the specific hypothesis that full-body ownership is associated with visuotactile integration in key multisensory regions, but only in the context of seeing a humanoid body [12]. To this end, we employed a two-by-two factorial design in which we systematically varied the type of object observed (humanoid body versus wooden object) and the timing of the visual and tactile stimuli (synchronous versus asynchronous) and computed the interaction term, which identified areas showing a greater effect of visuotactile synchrony in the context of seeing the humanoid body [8, 9, 12] (see Figure S1). In support of our hypothesis, we found significant activation in the right ventral premotor cortex (PMv) (54, 4, 34; $t = 3.41$; $p = 0.031$) (all coordinates reported are in MNI space), the left PMv (−60, 12, 28; $t = 3.76$; $p = 0.012$), and the left intraparietal sulcus (IPS) (−38, −48, 54; $t = 3.72$; $p = 0.014$) (Figure 1; Table S1). We also observed activation in the left putamen that did not reach significance after correction for multiple comparisons (−22, −8, 8; $t = 3.18$; $p < 0.001$, uncorrected). However, because this multisensory structure [21] was significantly activated in subsequent experiments, it is noteworthy to report here (Figure S2).

In the second fMRI experiment, we tested the hypothesis that the multisensory processes giving rise to the full-body illusion operate in body-centered reference frames [22, 23]. We compared conditions where the artificial body was presented in a similar location and orientation as the participant's real body (i.e., viewed from the first-person visual perspective

[3]These authors contributed equally to this work
*Correspondence: valeria.petkova@ki.se

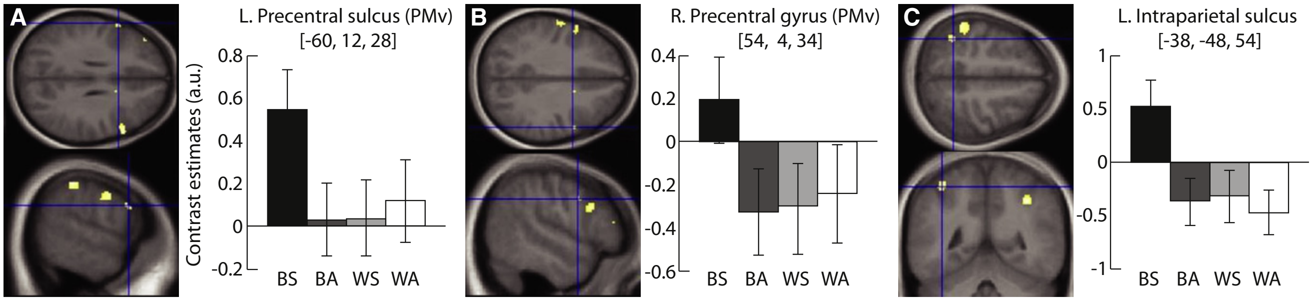

Figure 1. Activation during the Full-Body Illusion in Experiment 1: Stronger Effect of Visuotactile Synchrony When Observing the Mannequin

Activation maps corresponding to the interaction term in the factorial design (synchrony × human body), superimposed on a mean anatomical image for all 26 participants (threshold at $p < 0.001$, uncorrected for display purposes). The plots represent the contrast estimates (beta parameters of the general linear model) for the significant peaks ($p < 0.05$ after small volume correction) for the left and right ventral premotor area (A and B) and the left intraparietal sulcus (C). B and W stand for body and wood, respectively; S and A stand for synchronous and asynchronous visuotactile stimulation, respectively. Error bars represent the standard error. For further details, see Figure S1 and Table S1.

in near-personal space) or when the body was lying directly opposite the participant (i.e., viewed from the third-person visual perspective in far extrapersonal space) (Figure S1). Accordingly, in a new group of 20 naive participants, we manipulated the visual perspective (first-person versus third-person) and the timing of touches (synchronous versus asynchronous) in a two-by-two factorial design. We examined the interaction term, which in this analysis identifies enhanced responses to visuotactile synchronicity when the body is seen from the first-person perspective in near-personal space. In agreement with our hypothesis, we observed significant interaction in the right PMv (62, 2, 26; $t = 3.61$; $p = 0.032$) and the left IPS (−46, −48, 58; $t = 3.33$, $p = 0.041$) and a statistical trend in the left PMv (−54, 20, 34; $t = 3.07$; $p = 0.001$, uncorrected) (Figure 2; Table S1). In addition, we found significant activity in the left putamen matching that observed in the first experiment (−26, −8, 6; $t = 3.60$; $p = 0.021$) (Figure S2).

Importantly, in both experiments, the levels of activity in key multisensory areas associated with body-centered visuosomatic integration correlated with the degree of subjectively experienced full-body ownership. In the first experiment, the blood oxygen level-dependent (BOLD) response in the left PMv was significantly related to the strength of the illusion as rated by the participants directly after the scans (regression analysis; see Supplemental Experimental Procedures) (−60, 16, 16; $t = 3.70$; $p = 0.05$) (Figure 3A). In the second experiment, we found such significant relationships in the right PMv (44, 18, 34; $t = 4.09$; $p = 0.036$) and the left dorsal premotor cortex (PMd) (−42, 6, 48; $t = 3.98$; $p = 0.042$) (Figures 3B and 3C). In summary, the results from the two first experiments provide compelling evidence that the illusion of owning an entire body relies on body-part-centered integration of visual and somatic signals in multisensory areas.

Next, we focused on the central issue of how the feeling of ownership spreads from the site of stimulation to encompass the whole body, as is known to occur during the body-swap illusion [12]. In a third fMRI experiment, with a new group of 20 naive participants, we employed two complementary experimental designs to directly test the hypothesis that multisensory integration across body segments mediates the perceptual binding of owned body parts.

In the first design, we stimulated the right hand either when it was visually perceived as part of the mannequin's body or when the same hand was presented in isolation, i.e., as a detached limb. On the basis of previous work on the rubber-hand illusion [24–26] and our own pilot experiments, we hypothesized that strong ownership of a limb would only be present when the limb was perceived to be part of a body and that, in this context, the self-attribution of the limb would spread to the rest of the body. Thus, in a two-by-two factorial design, we manipulated the integrity of the body and the right hand (attached versus detached) and the timing of the touches

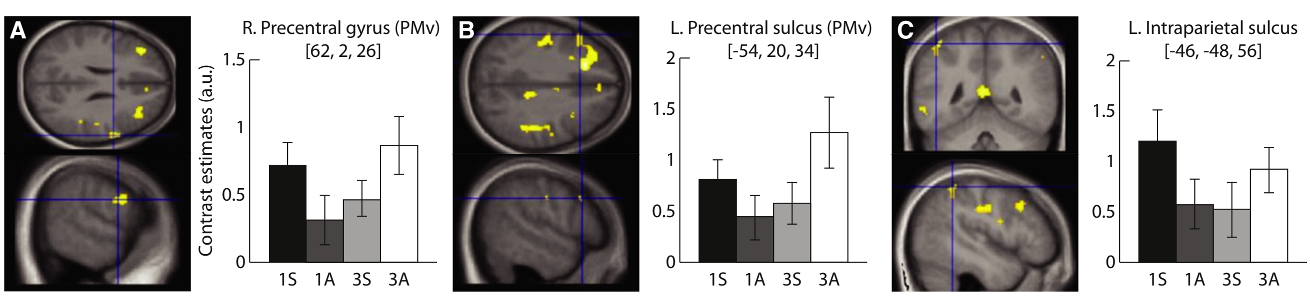

Figure 2. Activation during the Full-Body Illusion in Experiment 2: Stronger Effect of Visuotactile Synchrony When Viewing the Body from the First-Person Perspective

Activation maps corresponding to the interaction term in the factorial design (synchrony × first-person perspective), superimposed on a mean anatomical image for all 20 participants ($p < 0.001$, uncorrected for display purposes). The plots represent the contrast estimates (beta parameters of the general linear model) for the significant peaks of activation in the right PMv (A) and left IPS (C) ($p < 0.05$ after small volume correction) and activity in the left PMv (B) ($p < 0.001$, uncorrected), which did not reach significance after correction for multiple comparisons. 1 and 3 stand for first- and third-person perspective, respectively; S and A stand for synchronous and asynchronous visuotactile stimulation, respectively. Error bars represent the standard error. For activations in the putamen, see Figure S2.

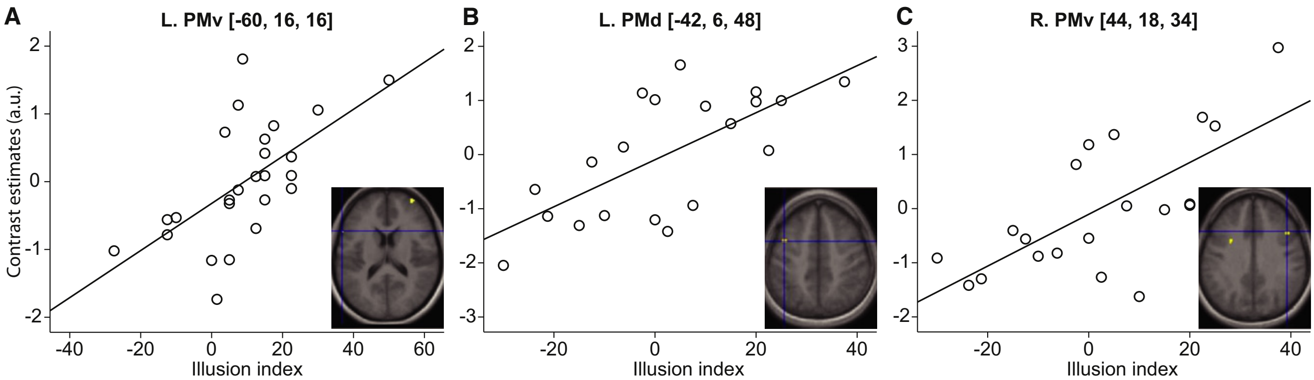

Figure 3. The Strength of the Illusion Is Linearly Related to the Amplitude of the BOLD Signal in the Premotor Cortex in Experiments 1 and 2

Participants who reported stronger self-attribution of the mannequin in the postscan questionnaires also exhibited greater illusion-related BOLD signal response (interaction term in the factorial designs) in the premotor cortex in study 1 (A) and study 2 (B and C) ($p < 0.05$ after small volume correction; activation maps have a threshold of $p < 0.001$, uncorrected for display purposes).

(synchronous versus asynchronous). Critically, we observed significant activations in the left PMv (−48, 6, 32; $t = 3.60$; $p = 0.020$) and the left IPS (−42, −38, 46; $t = 4.00$; $p = 0.006$) that reflected a greater effect of visuotactile synchrony when the arm was attached to the body (interaction term in the factorial design) (Figure 4A; Table S1). Again, weaker responses were noted in the left putamen (−26, 4, −8; $t = 3.97$; $p = 0.001$, uncorrected) (Figure S2). These results show that the perceived limb-body integrity augments the premotor-intraparietal activation, supporting our hypothesis that neural computations in these areas reflect the spread of ownership across connected body parts (see above).

In the second design, we compared conditions in which we elicited the illusion by stimulating either the hand or the abdomen (compared against the corresponding asynchronous controls). We hypothesized that the neuronal populations that mediate full-body ownership by integrating multisensory information across body parts should be active irrespective of the body part stimulated (i.e., body part independent). Consistent with this hypothesis, we found a significant cluster of voxels in the left PMv that was active when the body-swap illusion was triggered by stimulation in both the abdomen and the hand (−50, 0, 30; $t = 3.39$; $p = 0.030$; conjunction analysis; Figure 4B).

This premotor activation could, however, reflect either a genuine full-body ownership representation (i.e., one that could be implemented by multisensory neurons with receptive fields extending to multiple body segments) or activation of distinct groups of neurons with receptive fields restricted to individual body segments intermingled within the same voxels. To examine this effect, we applied multivoxel pattern analysis, a technique sensitive to fine-grained spatial patterns and subvoxel information [27, 28]. We used local multivariate brain mapping [29] to search for multivoxel patterns in the left ventral premotor cortex where classifiers trained to decode the illusion induced by stimulating the abdomen (i.e., distinguish synchronous from asynchronous visuotactile stimulation of the abdomen) could successfully generalize to decode patterns of activity reflecting the illusion when the hand was stimulated (i.e., distinguish synchronous from asynchronous visuotactile stimulation of the hand). We found such voxels in all 20 subjects (Figure 4C; $p < 0.05$, uncorrected, permutation test with 999 iterations; see Supplemental Experimental Procedures for details), and the decoding accuracy at the group level was significantly above chance, as was the reverse generalization from hand to abdomen ($p < 0.05$, permutation test, 999 iterations; Figure S3). Crucially, these multivoxel patterns were specific to the full-body illusion, because the classifiers failed to generalize when the hand was not attached to the mannequin's body (Figure 4C). Importantly, no body-part-specific patterns were identified within this body-part-independent section of the premotor cortex, because the classifiers failed to distinguish between synchronous visuotactile stimulation of the hand and abdomen. Taken together, these results suggest that activity in the left ventral premotor cortex reflects ownership generalized to the whole body.

Finally, it is noteworthy that the activations related to stimulation of the hand or the abdomen overlapped only partly (Figure 4B), allowing us to identify sections in the premotor and intraparietal cortices that selectively responded to visuotactile stimulation to one body part only (body part specific). This result suggests the existence of groups of multisensory cells in the human brain with receptive fields restricted to individual body parts, in analogy to the brains of nonhuman primates [13–19, 30, 31]. Given our results, we questioned whether we could detect ownership-related modulation in the BOLD signal in these body-part-specific regions, in line with the psychological observation that ownership spreads from the stimulated body part to the rest of the body [12]. Interestingly, we observed augmentation of the BOLD signal in abdomen-specific cortical sections of both the ventral premotor and intraparietal cortices, especially when the stimulation was applied to the hand attached to the mannequin's body (interaction contrast; $p < 0.001$, uncorrected) (Figure 4D). We speculate that this effect is a sign of the facilitation of the integration of visual and proprioceptive information in abdomen-specific neuronal populations during the full-body illusion, driven by the integration of visual, tactile, and proprioceptive signals from the stimulated hand. Although the present experiment was not designed to test specific hypotheses about the mechanism producing this modulatory effect, we speculate that corticocortical connections within the premotor-intraparietal system [30] or horizontal connections within the ventral premotor cortex may mediate it.

In summary, two major findings have been revealed in the present study. First, we found activation in the premotor

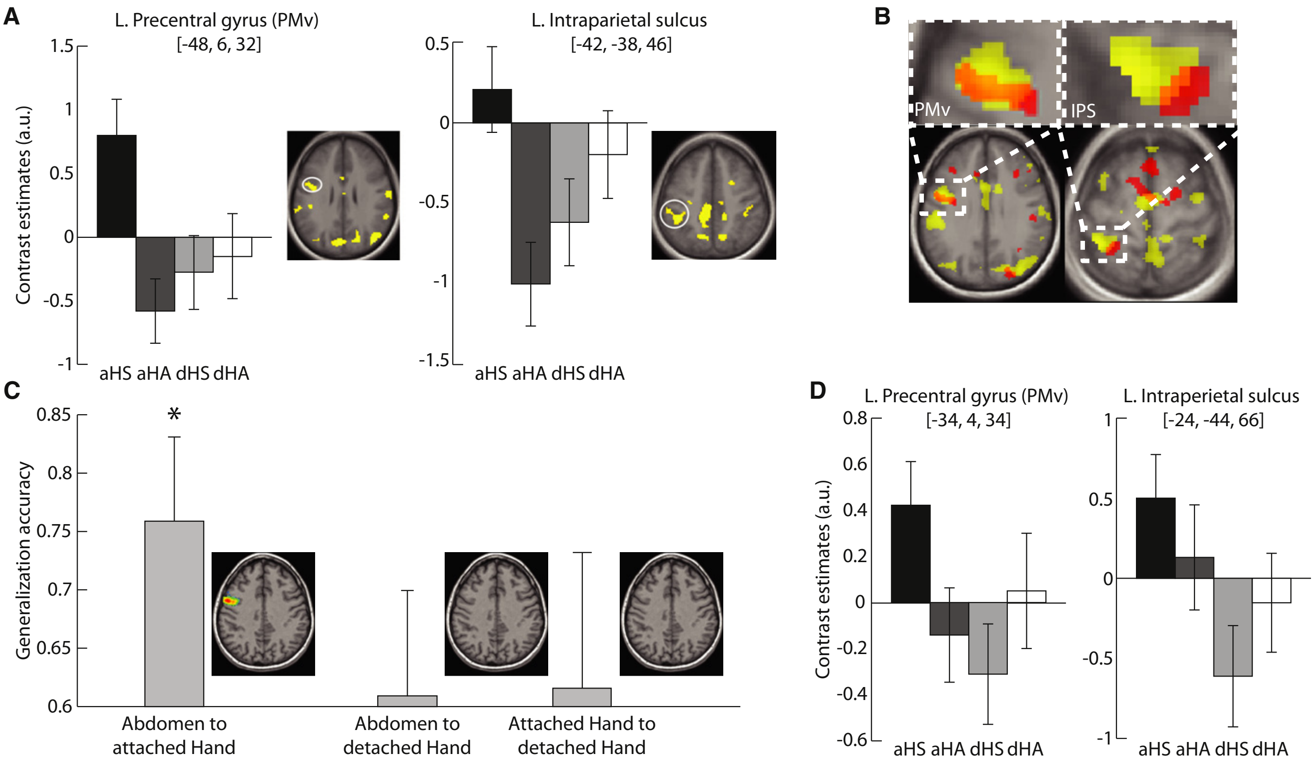

Figure 4. Activation Specific to Full-Body Ownership in Experiment 3

(A) The activation in the left ventral premotor cortex (PMv) and left intraparietal sulcus (IPS) related to the full-body illusion was significantly augmented when the hand was perceived as part of the body ($p < 0.05$, corrected). aH and dH indicate whether the hand was attached or detached, respectively; S and A stand for synchronous and asynchronous visuotactile stimulation, respectively. Error bars in (A) and (D) represent the standard error. Activation maps in (A) and (B) are at a threshold of $p < 0.001$, uncorrected for display purposes.

(B) Active voxels in the left PMv and IPS can be classified as body part specific (hand in yellow, abdomen in red) or body part independent (orange, conjunction of hand and abdomen).

(C) Multivoxel patterns in the left PMv reflect ownership generalized across body parts; classifiers trained to decode the illusion (synchronous versus asynchronous visuotactile stimulation) induced on the abdomen could successfully decode the illusion evoked when touching the hand. This generalization failed when the hand was perceived as a detached limb, both when the classifiers were trained on the abdomen and on the attached hand. The brain map shows voxels with a decoding accuracy significantly above chance in one representative subject ($p < 0.05$, permutation test, 999 iterations, uncorrected). The bar charts and error bars represent group average peak decoding accuracies (n = 20) and standard deviations, respectively. *$p < 0.05$ for group decoding accuracy, permutation test, 999 iterations. The reversed generalization was also confirmed (Figure S3).

(D) Abdomen-specific sections of the left PMv and IPS display an increase in the BOLD signal when the full-body illusion is driven by visuotactile stimulation on the hand, but only when it is attached to the mannequin's body ($p < 0.001$, uncorrected).

cortex, intraparietal cortex, and putamen that mirrored the perceptual rules of the full-body ownership illusion [12, 22, 23]. The anatomical locations of these activations were in regions that are well-known multisensory processing nodes in the primate brain (see Supplemental Discussion). Consistent activations across the three experiments were found only in these multisensory regions, and not in other parts of the brain, even when we lowered the statistical threshold ($p < 0.001$, uncorrected; see Supplemental Discussion). Our results thus suggest that the integration of visual, tactile, and proprioceptive information in body-part-centered reference frames represents a basic neural mechanism underlying the feeling of ownership of entire bodies. This finding generalizes existing models of limb ownership to the case of the entire body [3, 7, 10, 32]. Second, our results show that, in addition to body-part-specific multisensory integration, a process exists that mediates the perceptual binding of the parts into a unified percept of a whole owned body. Activation in the key multisensory areas (ventral premotor cortex, intraparietal cortex, and putamen) increased when the stimulated body part was attached to a body, as compared to when it was detached, showing that the context of integrity between body segments facilitates ownership of these parts. Furthermore, in the left ventral premotor cortex, we found an active area and multivoxel patterns of activity that reflected full-body ownership irrespectively of which body part was simulated. The latter two findings can best be explained by a parsimonious model in which the unitary experience of owning a whole body is produced by neuronal populations in the ventral premotor cortex, and possibly in other multisensory areas, that integrate multisensory information across body parts. This type of multisensory integration could be ideally implemented by neurons with large visual, tactile, and proprioceptive receptive fields extending over multiple body segments [15, 19, 33, 34].

Supplemental Information

Supplemental Information includes three figures, one table, Supplemental Results, Supplemental Discussion, and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2011.05.022.

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