

Neural Signatures of Body Ownership: A Sensory Network for Bodily Self-Consciousness

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Body ownership refers to the special perceptual status of one's own body, which makes bodily sensations seem unique to oneself. We studied the neural correlates of body ownership by controlling whether an external object was accepted as part of the body or not. In the rubber hand illusion (RHI), correlated visuotactile stimulation causes a fake hand to be perceived as part of one's own body. In the present study, we distinguished between the causes (i.e., multisensory stimulation) and the effect (i.e., the feeling of ownership) of the RHI. Participants watched a right or a left rubber hand being touched either synchronously or asynchronously with respect to their own unseen right hand. A quantifiable correlate of the RHI is a shift in the perceived position of the subject's hand toward the rubber hand. We used positron emission tomography to identify brain areas whose activity correlated with this proprioceptive measure of body ownership. Body ownership was related to activity in the right posterior insula and the right frontal operculum. Conversely, when the rubber hand was not attributed to the self, activity was observed in the contralateral parietal cortex, particularly the somatosensory cortex. These structures form a network that plays a fundamental role in linking current sensory stimuli to one's own body and thus also in self-consciousness.

Keywords: agency, body ownership, insula, rubber hand illusion, self-consciousness, somatosensory cortex

Introduction

When I decide to write, I do not need to look for my hand in the same way that I have to look for a pen or a piece of paper, for the simple reason that my hand is “always there” (James 1890), present with me. This example illustrates the immediacy of experiences of one's own body. The feeling that “my body” belongs to me, and is ever present in my mental life, is called body ownership (Gallagher 2000). The sense of body ownership gives somatosensory signals a special phenomenal quality, and it is fundamental to self-consciousness: the relation between my body and “me” differs from both the relation between my body and other people's bodies and the relation between “me” and external objects. However, the scientific study of body ownership raises important methodological problems.

It is difficult to study experimentally the neural and functional signatures of body ownership, simply because the body is “always there” (James 1890). Classical experimental designs cannot isolate the sense of body ownership by direct manipulations that make the body present in one experimental condition but absent in another. Moreover, body ownership may be easily confounded with the sense of controlling one's body because

agency is a powerful cue to ownership: my body feels like “mine” because I can control it at will. For example, recent neuro-imaging studies on self-attribution of voluntary actions report activations in the insular lobe when subjects attribute an observed action to themselves (Farrer and Frith 2002; Farrer et al. 2003). However, it is not clear whether this activity reflects a sense of agency due to the match between motor intention and sensory feedback or whether it reflects body ownership due to intersensory match between proprioceptive and visual stimuli. Intersensory matching may be sufficient for body ownership, even in the absence of agency, because somatosensory signals clearly relate to the self even in the absence of voluntary movement (Tsakiris et al. 2005, 2006). In the present study, we used an experimental paradigm that allowed the manipulation of body ownership alone to investigate the neural causes and effects of sensory-driven body ownership. Body ownership may arise from unimodal sensory input (e.g., touch, see Ehrsson, Holmes, and Passingham 2005). However, the unique experience of seeing and at the same time feeling one's own hand relies on interactions between different sensory modalities (e.g., touch, proprioception, and vision) and may contribute to a better understanding of the body-related sensory processing.

The rubber hand illusion (RHI) is an experimental paradigm that isolates the pure sense of body ownership in the absence of movement and efferent information. Briefly, watching a rubber hand being stroked synchronously with one's own unseen hand causes the rubber hand to be attributed to one's own body, to “feel like it's my hand” (Botvinick and Cohen 1998). This illusion does not occur when the rubber hand is stroked asynchronously with respect to the participant's own hand. Thus, the RHI allows an external object to be treated as part of the body, or not, under experimental control. For that reason, it offers a useful experimental manipulation of body ownership. One behavioral correlate of the RHI is an induced change in the perceived location of the participant's own hand toward the rubber hand. Botvinick and Cohen (1998) showed that the prevalence of illusion over time is positively correlated with a drift in the felt location of the subject's own hand toward the rubber hand. In Tsakiris and Haggard (2005b), participants perceived their hand to be significantly closer to the rubber hand after synchronous visuotactile stimulation than after asynchronous visuotactile stimulation, suggesting integration between the visually perceived rubber hand and the tactile experience on the participant's own hand.

How does the rubber hand come to be experienced as part of one's own body? First, integration of correlated synchronous

visual and tactile stimulation is a necessary condition for the RHI to occur (Botvinick and Cohen 1998; Ehrsson et al. 2004; Tsakiris and Haggard 2005b). In addition, the inducement of the illusion entails the assimilation of correlated visuotactile percepts in a preexisting reference of one's own body. When, for example, participants were stimulated on their left hand, while they were looking at a right rubber hand being touched synchronously with their own hand, they did not experience the RHI (see Experiment 2 in Tsakiris and Haggard 2005b). Thus, correlation of visual and tactile percepts is necessary but perhaps not sufficient to elicit a sense of body ownership. Ownership requires the viewed object to fit with a general preexisting representation of the body scheme, suggesting that body ownership is also modulated by top-down influences based on prior visual, proprioceptive, and functional representations of the body.

These observations suggest that the primary sensory events that "cause" the rubber hand to be attributed to one's own body (e.g., multisensory correlation) may be different from the phenomenal "effects" of ownership. Put another way, seeing the rubber hand and feeling tactile stimulation may cause the rubber hand to "feel like it is mine." This feeling is clearly distinct from the tactile and visual sensations themselves. Integrating synchronized visual and tactile percepts, then, is a necessary condition for producing the RHI. The result of this process is a persistent, vivid phenomenological change in body representation, namely, the experience that the rubber hand is part of one's own body. The content of the changed body representation might be quite different from, and goes beyond, the perception of correlated visual and tactile stimulation.

In the present study, we investigated the neural basis of the sense of body ownership by separately analyzing the "causes" and also the "effects" of the RHI. Participants were always stimulated on their unseen right hand, while they viewed a right or a left rubber hand being stimulated either synchronously or asynchronously with respect to their own hand. Across all conditions, participants judged the felt position of their own hand before and after visuotactile stimulation. The proprioceptive judgment was used as a behavioral measure of body ownership during the RHI. We used PET to detect sustained neural activity that was specifically related to the stable state of ownership of the rubber hand and not the onset of the RHI per se.

The experimental design allowed us to use the "interactions" between the bottom-up (i.e., synchronous vs. asynchronous visuotactile stimulation) and top-down (i.e., congruent vs. incongruent rubber hand identity) factors to investigate the causes of the RHI, that is, the sensory conditions that induce alterations in ownership. In an additional analysis, we correlated neural activity with the strength of the RHI as measured by the "proprioceptive drift" in the felt position of the participant's hand. This analysis would identify the neural correlates of the phenomenal "effect" of the RHI, namely, the feeling that the rubber hand is part of one's own body or, alternatively, the feeling that the rubber hand is not one's own hand.

Overall, the alterations in body ownership during the RHI involve several processes such as the monitoring of body-related sensory signals, the integration of these signals when there is no conflict, and finally the update of a body-related self-representation. We wanted to distinguish between causes and effects of the RHI for the reasons given above. As regards the factors causing the RHI, we hypothesized that areas associated with the integration of multisensory signals, such the premotor

and parietal cortices (see Ehrsson et al. 2004), will be active when visual and tactile events are congruent. In the case of a conflict between visual and tactile events, we hypothesized that frontal areas would be activated, especially in the right hemisphere (see Fink et al. 1999). We also made specific hypotheses about the neural correlates of the phenomenal effects of the RHI. We predicted that the subjective experience of body ownership would activate the brain's self-processing network. In particular, we predicted that the right posterior insula, an area linked to self-representations of sensorimotor events (Farrer et al. 2003), representations of egocentric reference frame and first-person perspective (Fink et al. 2003; Vogeley et al. 2004), would be correlated with the strength of ownership over the rubber hand.

Materials and Methods

Experimental Design

The experimental design was 2×2 factorial (see Fig. 1). The first factor was the identity of the rubber hand that was either congruent to the participant's stimulated hand or incongruent. Participants were always stimulated on their right hand, while looking at a right or a left rubber hand. The second factor was the mode of visuotactile stimulation. Participants saw the rubber hand being touched either synchronously with the touch delivered on their own hand or asynchronously. The experiment consisted of 4 blocked conditions, and each condition was repeated 3 times, resulting in 12 trials. Each participant performed the blocks in a different pseudorandom order.

Experimental Setup and Methods

The methods were based on a previous behavioral study (see Experiment 4 in Tsakiris and Haggard 2005b), with modifications appropriate for the PET scanning environment (see Fig. 2). Participants rested in a supine position on the bed in the PET scanner. Their right arm was extended and placed on a tilted support (-75°) inside a frame. Their right hand was placed by the experimenter at a fixed point inside the frame, whose topside was covered by a black screen. Participants did not have vision of their hand. The rubber hand was placed on the same frame and was presented in front of the participants, aligned with their midline and on the same plane as their hidden hand. A pair of life-size rubber prosthetic hands (Otto Bock HealthCare, Duderstadt, Germany) was used. The distance between the rubber hand and the participant's hand was 15 cm.

At the beginning of each trial, both the participant's right hand and the rubber hand were out of sight. A pretest baseline estimate of finger position was obtained prior to stimulation. A ruler was presented on a horizontal surface, 18 cm above the hands and aligned with the participant's frontoparallel plane. Participants were asked "Where is

		Mode of Visuo-Tactile Stimulation	
		Synchronous	Asynchronous
Rubber Hand Identity	Congruent	Congruent Synchronous (CS)	Congruent Asynchronous (CA)
	Incongruent	Incongruent Synchronous (IS)	Incongruent Asynchronous (IA)

Figure 1. The 2×2 factorial experimental design.

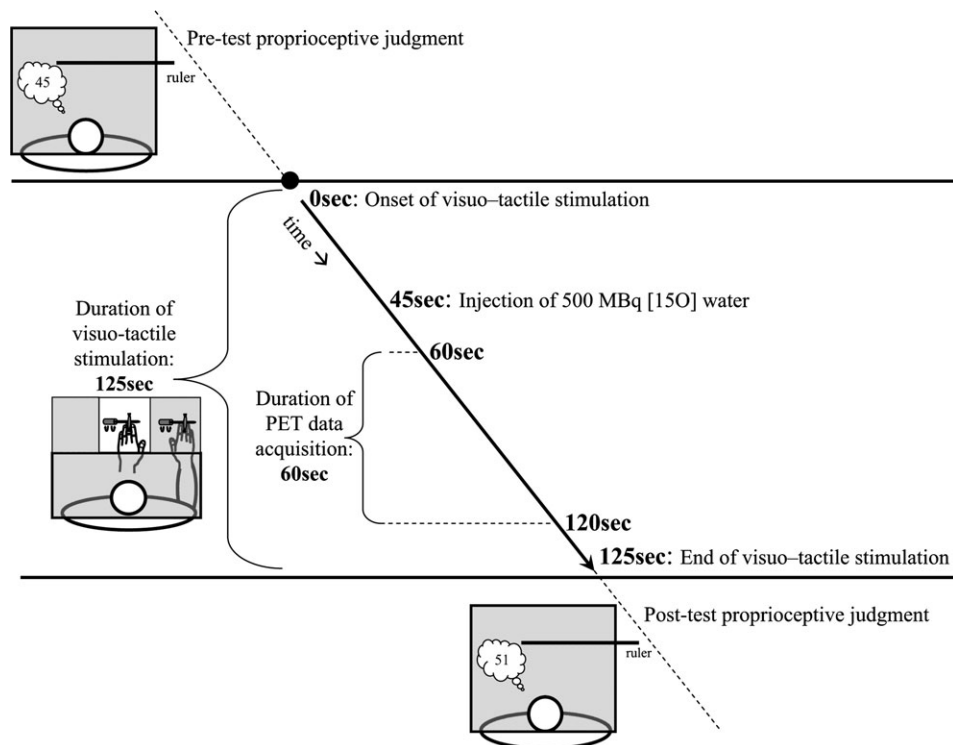


Figure 2. The experimental setup and temporal sequence of events. At the beginning of the trial, participants judged the felt location of their own middle finger. Then the rubber hand appeared and visuotactile stimulation was delivered for 125 s. Acquisition of the PET data began 60 s after the onset of visuotactile stimulation and lasted for 60 s. In the condition shown, the participant is looking at an incongruent rubber hand identity with respect to his/her own stimulated hand. At the end of trial, participants judged anew the felt location of their own middle finger.

your middle finger?" and verbally reported a number on the ruler in response. They were instructed to judge the position of their finger by projecting a parasagittal line from the center of their fingertip to the ruler. The judgment was recorded, and no feedback was given.

After the judgment, the ruler and the black screen covering the rubber hand were removed to make the rubber hand appear, and tactile stimulation of the hands began. Stimulation was delivered mechanically by a custom-built stroking machine, consisting of 2 computer-controlled stepper motors at the end of which we attached 2 identical paintbrushes. Participants were always stimulated on the middle finger of their right hand. A left (i.e., incongruent) or a right (i.e., congruent) rubber hand was also stimulated on the middle finger. We stimulated the middle finger because the relative position of the middle finger is the same for both left and right hands. Stimulation was delivered along the finger, from the knuckle to the fingertip or vice versa. To simulate the unpredictable nature of manual stroking, the direction and speed of stroking were randomly varied within condition. The participant's hand and the rubber hand always received the same random direction and speed on each stroke. In the synchronous conditions, both hands were stroked simultaneously. In the asynchronous conditions, the participant's hand was stroked with a random delay of 500–1000 ms after the stimulation of the rubber hand. The total amount and spatial pattern of stimulation were the same across all conditions. Synchronous and asynchronous conditions differed only in the degree of temporal correlation of visual and tactile stimulation. Stimulation lasted for 125 s.

After the stimulation period, the rubber hand was covered with a black screen, and the ruler was presented in front of the participants. The ruler was always presented with a random offset to ensure that participants judged finger position anew on each trial and that they could not simply repeat previous responses. They were asked to make one more judgment regarding the felt position of their right middle finger. After their response, the ruler was removed, and the participants were asked to move their right hand and have a rest. Following the rest period (7 min), their right hand was again passively placed inside the

frame and out of sight. The same procedure was followed for each condition.

In each block, injection of 500 MBq [^{15}O] water occurred 45 s after the onset of visuotactile stimulation. PET data acquisition started 15 s after the injection to allow the contrast agent to reach the brain and lasted for 60 s, allowing another 5 s of visuotactile stimulation to ensure that stimulation did not stop before the completion of the scanning (see Fig. 2, and also PET Hardware and Procedures).

At the end of the experiment, participants completed a questionnaire based on a previous questionnaire devised by Botvinick and Cohen (1998). Subjects used a Likert scale (from -3 to 3) to rate 18 statements. Participants were asked to indicate their response on a 7-step visual analogue scale ranging from "agree strongly" (+++) to "disagree strongly" (—). The questions focused on comparing the sense of ownership for each rubber hand identity condition, but only for the conditions where the stimulation between the participant's hand and the rubber hand was synchronous (i.e., conditions CS and IS). Thus, the questionnaire included 18 questions. Half of these 18 questions referred to the synchronous congruent conditions (i.e., right rubber hand, condition CS), and the other half referred to the synchronous incongruent conditions (i.e., left rubber hand, condition IS). The order of presentation of congruent-related and incongruent-related questions was counterbalanced across subjects (see Appendix).

Participants

Fifteen naive, healthy, right-handed volunteers (9 females, 6 males, mean age 36.8 ± 7.2 years) with no history of neurological or psychiatric illness gave their informed written consent to participate in this study. The study was approved by the local ethics committee (Medical Faculty of the RWTH Aachen, Aachen, Germany). One participant was excluded because his/her head displacement during the experimental session was >6 mm. Unlike previous studies (e.g., Ehrsson et al. 2004), participants were not screened prior to the experiment to check whether they could experience the RHI or not. Because any prior knowledge or experience of the illusion could have confounded the

neuroimaging data, we decided to test unscreened volunteers. Therefore, all participants were naive as to the illusion and purposes of the experiment. Because we were specifically interested in the experience of the illusion, we included in the analysis only those subjects who experienced the illusion as measured by the proprioceptive drift. We therefore excluded 4 participants who did not show the predicted interaction between body scheme and sensory stimulation associated with the sense of ownership in the RHI (Tsakiris and Haggard 2005b). Specifically, subjects with smaller perceptual shifts, defined as the difference between proprioceptive drifts in the synchronous and asynchronous conditions, for the congruent rubber hand condition compared with the incongruent rubber hand condition were excluded ($(CS - CA) \leq (IS - IA)$). Thus, surviving data refer to the 10 participants who experienced the illusion as measured by proprioceptive drift (6 females, mean age 37.2 ± 7.2 years). Each of the 10 subjects included in the analysis satisfied this criterion of showing larger perceptual shifts for the congruent rubber hand condition compared with the incongruent rubber hand condition, that is $(CS - CA) > (IS - IA)$. In these subjects, the mean size of the critical interaction $[(CS - CA) - (IS - IA)]$ was 3 cm (standard error: 0.5, min: 1.3 cm, max: 7 cm).

PET Hardware and Procedures

Measurements of regional cerebral blood flow (rCBF) were taken using an ECAT EXACT 922/47 PET scanner (Siemens-CTI, Knoxville, TN) in a 3-dimensional (3D) acquisition mode using standard technology and procedures previously described in detail (see Weiss et al. 2000, 2003). Attenuation correction was performed by transmission scanning prior to emission scanning using 3 external [^{68}Ge]/[^{68}Ga] rod sources (transmission scan time, 15 min). Simultaneously with the intravenous bolus injection of 500 MBq [^{15}O] water, a dynamic emission scan protocol: $6 \times 5 \text{ s}, 5 \times 10 \text{ s} = 80 \text{ s}$ was started in 3D acquisition mode. The integrated counts over 60 s were used as an index of the rCBF. After Fourier rebinning of 3D data, 47 fully corrected transaxial planes of 3.38 mm slice thickness were reconstructed in a 128×128 matrix (pixel size, 1.72 mm) using 2D filtered back-projection (FBP) algorithm and a Hanning filter with a cutoff frequency of 0.5 Ny (ECAT 7.2 software). Participants laid comfortably in the PET scanner with the head positioned in a dedicated holder. An intravenous cannula was placed in their left cubital vein for injection of the radioactive tracer. Each subject underwent 12 PET scans in a single session, comprising 3 replications of each of the 4 conditions. Acquisition of the PET data began 60 s after the onset of visuotactile stimulation and lasted for 60 s. For each subject, anatomical magnetic resonance imaging scans were obtained with a T_1 -weighted 3D fast field-echo (FFE) sequence on a 1.5-T Philips Gyroscan NT (Philips Medical Systems, Best, The Netherlands) using a standard head coil.

Imaging Processing and Statistical Analysis

Following standard image preprocessing (including image realignment, image normalization into standard stereotactic space, and smoothing using a 12-mm full width half maximum Gaussian smoothing kernel), statistical analyses were performed using SPM2 (<http://www.fil.ion.ucl.ac.uk/spm>). For each voxel, across all participants and all scans, the mean relative rCBF values were calculated separately for each of the main effects. Comparisons of the means were made using the t -statistic and thereafter transformed into normally distributed Z -statistics. The resulting set of Z values constituted a statistical parametric map (SPM $\{Z\}$ map), thresholded at $P < 0.0005$ uncorrected at the voxel level. For the contrasts of interest, the significance of these statistical parametric maps was assessed by comparing the expected and observed distribution of the t -statistic under the null hypothesis of no differential activation effect on rCBF. SPM2 was also used to identify brain areas where activity was associated with a phenomenal measure of the illusion, namely, the proprioceptive drift of the stimulated hand toward the rubber hand (Tsakiris and Haggard 2005b). The proprioceptive drift for each trial was used as a covariate, and regression with this covariate was calculated for every voxel in the whole brain. The significance of the regression was displayed in a SPM $[t]$ map, which was then transformed into a SPM $\{Z\}$ and thresholded at $P < 0.0005$ uncorrected at the voxel level. Brain activity localization was identified using the atlas of neuroanatomy by Duvernoy (1999) and the SPM anatomy toolbox (Eickhoff et al. 2005).

Results

Behavioral Data

A baseline pretest proprioceptive judgment was obtained prior to visuotactile stimulation and a posttest judgment after stimulation in each trial. The pretest judgment was subtracted from the posttest judgment. The term proprioceptive drift refers to this change in perceived hand position as a result of visuotactile stimulation. Figure 3 shows the change in the perceived position of the hand between the start and the end of the stimulation period in each condition of the factorial design, averaged over 10 participants.

The mean proprioceptive drifts across conditions (see Fig. 3) were submitted to a 2×2 repeated measures analysis of variance with 2 within-subjects factors. The first factor was the rubber hand identity (congruent vs. incongruent), and the second factor was the mode of visuotactile stimulation (synchronous vs. asynchronous). The main effect of the rubber hand identity was not significant ($F_{1,9} = 0.005, P > 0.05$). The mode of visuotactile stimulation showed a significant main effect ($F_{1,9} = 7.397, P < 0.05$). Importantly, the interaction of the 2 factors was highly significant ($F_{1,9} = 50.922, P < 0.05$). We then compared the mean drift in each condition against zero, adjusting for the number of conditions using a Bonferroni correction. This showed a significant drift only in the congruent synchronous condition ($t_9 = 5.4, P < 0.001$), confirming previous results (Tsakiris and Haggard 2005b).

After the scanning session, participants completed a questionnaire adjusted from Botvinick and Cohen (1998) regarding the illusory sense of body ownership during the RHI. Participants experienced the illusion only when they were looking at a congruent rubber hand identity. In particular, they affirmed that 1) they felt as if they were feeling the touch at the location where the congruent rubber hand was being touched ($t_8 = 1.9, P < 0.05$) and 2) they felt as if the congruent rubber hand was their own hand ($t_8 = 2.2, P < 0.05$). These introspective data replicate previous studies (Botvinick and Cohen 1998; Ehrsson et al. 2004) and corroborate the quantitative psychophysical data on the perceived position of the hand.

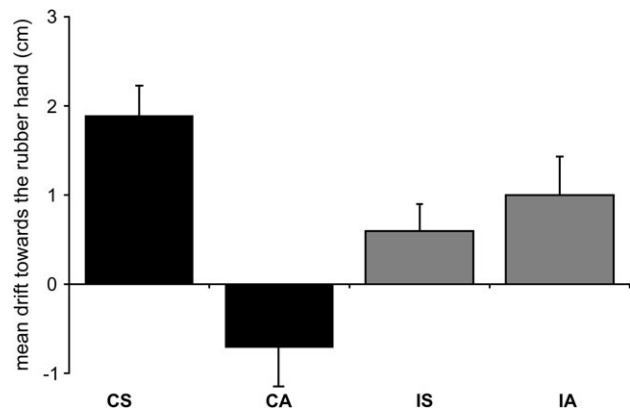


Figure 3. Mean proprioceptive drifts averaged over 10 participants across conditions. Error bars indicate standard errors. Point “zero” represents the felt position of the participant’s hand prior to stimulation. A positive proprioceptive drift represents a mislocalization toward the rubber hand. CS: congruent rubber hand/synchronous stimulation, CA: congruent rubber hand/asynchronous stimulation, IS: incongruent rubber hand/synchronous stimulation, IA: incongruent rubber hand/asynchronous stimulation.

PET Data

We analyzed the PET data in 2 ways. First, we used a 2×2 factorial design to investigate the conditions that caused the illusion (see Table 1). Second, we used a parametric design to investigate the neural correlates of the effects of the illusion, that is, the experience of ownership of the rubber hand or the failure to incorporate the rubber hand, by focusing on the correlation between neural activity and a quantitative proxy of the RHI, namely, the proprioceptive drift toward or away from the rubber hand (see Table 2).

The main effect of synchronous visuotactile stimulation corresponding to the contrast (CS + IS) - (CA + IA) showed activity in the left middle frontal gyrus and the right inferior lingual gyrus. The main effect of asynchronous stimulation corresponding to the contrast (CA + IA) - (CS + IS) showed activations in the thalamus, the right rolandic operculum, the left superior postcentral sulcus and postcentral gyrus, the left superior frontal sulcus, and the right circular insular sulcus. The main effect of looking at a congruent rubber hand being stimulated corresponding to the contrast (CS + CA) - (IS + IA) showed activity in the right precentral gyrus, the right putamen, and the left superior occipital gyrus. The main effect of looking at an incongruent identity corresponding to the contrast (IS + IA) - (CS + CA) showed bilateral activity in amygdala and the left parahippocampal gyrus.

The illusion interaction term of the factorial design was assessed using the contrast (CS - CA) - (IS - IA). Activity reflecting this interaction was observed in the right middle cingulate cortex. We also investigated brain areas showing the inverse interaction pattern, (CA - CS) - (IA - IS). This interaction reveals brain activity when sensory evidence and preexisting body scheme representations give conflicting information about ownership. That is, a conflict between viewed and felt stimulation in the asynchronous condition suggests that the rubber hand does not correspond to the participant's own hand, but the visual appearance of the rubber hand suggests it does. Based on the study by Fink et al. (1999), we hypothesized that intersensory conflict would be related to right frontal activity. We therefore performed an additional small-volume correction (SVC) with $x = 40$, $y = 8$, $z = 22$ as coordinates (from the results from Fink et al. 1999) and a radius of 10 mm. This analysis showed a significant differential effect in the right rolandic operculum ($P < 0.05$; SVC). In addition to this predicted activation, conflict-related activity was detected in the left postcentral gyrus and the left precentral gyrus.

Correlation of Neuroimaging and Psychophysical Data

Our second analysis focused on identifying the neural correlates of the subjective experience of ownership rather than on the sensory conditions used to induce it. The effects of global changes in blood flow between conditions were modeled as a confound using a subject-specific analysis of covariance. SPM2 was used to identify brain areas where activity was predicted by the subjective experience of the illusion of owning the rubber hand. To this end, the proprioceptive drift was used as a covariate, and a linear regression was calculated for every voxel in the whole brain.

On the basis of previous studies on bodily self-awareness by Farrer et al. (2003) and Ehrsson et al. (2004), we hypothesized a priori that the insula (Farrer et al. 2003) and the frontal operculum (Ehrsson et al. 2004) should correlate positively with the felt proprioceptive drift. Using the respective coor-

Table 1

Local maxima of the areas of differentially increased neural activity associated with the main effects of the 2×2 factorial experimental design which are significant at $P < 0.0005$ uncorrected at the voxel level

Brain regions	MNI coordinates			K_E	Z-score
	x	y	z		
Main effect of synchronous stimulation (CS + IS) - (CA + IA)					
L middle frontal gyrus	-20	26	34	95	4.30
R inferior lingual gyrus (BA 18)	6	-64	-6	27	3.30
Main effect of asynchronous stimulation (CA + IA) - (CS + IS)					
Thalamus	-2	-2	0	262	5.58
R rolandic operculum	52	-20	22	468	5.19
L superior postcentral sulcus (BA 1)	-24	-50	72	148	3.90
L postcentral gyrus (BA 6)	-24	-42	74		3.79
L superior frontal sulcus	-30	0	68	41	3.78
R circular insular sulcus	42	0	-20	29	3.40
Main effect of congruent rubber hand identity (CS + CA) - (IS + IA)					
R precentral gyrus (BA 6)	66	4	26	49	3.82
R putamen	30	-6	6	64	3.67
L superior occipital gyrus	-26	-94	24	24	3.43
Main effect of incongruent rubber hand identity (IS + IA) - (CS + CA)					
L amygdala	-28	6	-28	49	3.59
L parahippocampal gyrus	-32	-40	-8	25	3.50
R amygdala	32	-2	-28	16	3.45
Illusion interaction effect (CS - CA) - (IS - IA)					
R middle cingulate cortex	8	20	36	35	3.46
Conflict interaction effect (CA - CS) - (IA - IS)					
L postcentral gyrus (BA 1)	-52	-26	62	28	3.70
L precentral gyrus (BA 6)	-28	-12	64	24	3.61
R rolandic operculum	44	0	14	42	3.47

Note: L, Left; R, Right; MNI, Montreal Neurological Institute.

Table 2

Local maxima of brain areas of increased neural activity (significant at $P < 0.0005$ uncorrected at the voxel level) that is positively or negatively correlated with the phenomenal proxy of the RHI, namely the proprioceptive drift toward or away from the rubber hand

Brain regions	MNI coordinates			K_E	Z-score
	x	y	z		
Positive correlation between rCBF and proprioceptive drift					
R posterior insula/R rolandic operculum	44	-10	14	53	3.63
L brainstem	-8	-34	-36	14	3.54
R frontal operculum (BA 44)	58	12	-4	36	3.54
L middle frontal gyrus	-30	54	26	15	3.36
Negative correlation between rCBF and proprioceptive drift					
L postcentral gyrus (BA 2/3b/3a)	-42	-24	40	443	5.11
L parietal operculum	-46	-22	26		3.69
L hippocampus	-28	-20	-22	103	3.92
R posterior cingulate cortex	4	-34	22	51	3.63

Note: L, Left; R, Right; MNI, Montreal Neurological Institute.

ordinates in the posterior insula ($x = 40$, $y = -10$, $z = 16$; Farrer et al. 2003) and frontal operculum ($x = 54$, $y = 18$, $z = 12$; Ehrsson et al. 2004) for SVC (10 mm radius), we observed significant activations ($P < 0.05$; SVC) in both these predicted areas. Regression analysis demonstrated a positive relation between rCBF and proprioceptive drift in the right posterior insula ($t = 3.41$, $P < 0.05$, see Fig. 4a) and the right frontal operculum ($t = 3.25$, $P < 0.05$). Extending the regression analysis to the whole brain without SVC revealed a positive correlation between rCBF and proprioceptive drift in the left brainstem and the left middle frontal gyrus in addition to the right posterior insula and the right frontal operculum.

A negative correlation between rCBF and proprioceptive drift was observed in the left postcentral gyrus (see Fig. 4b), the left parietal operculum, the left hippocampus, and the left posterior cingulate cortex. Note that activity in the left postcentral gyrus

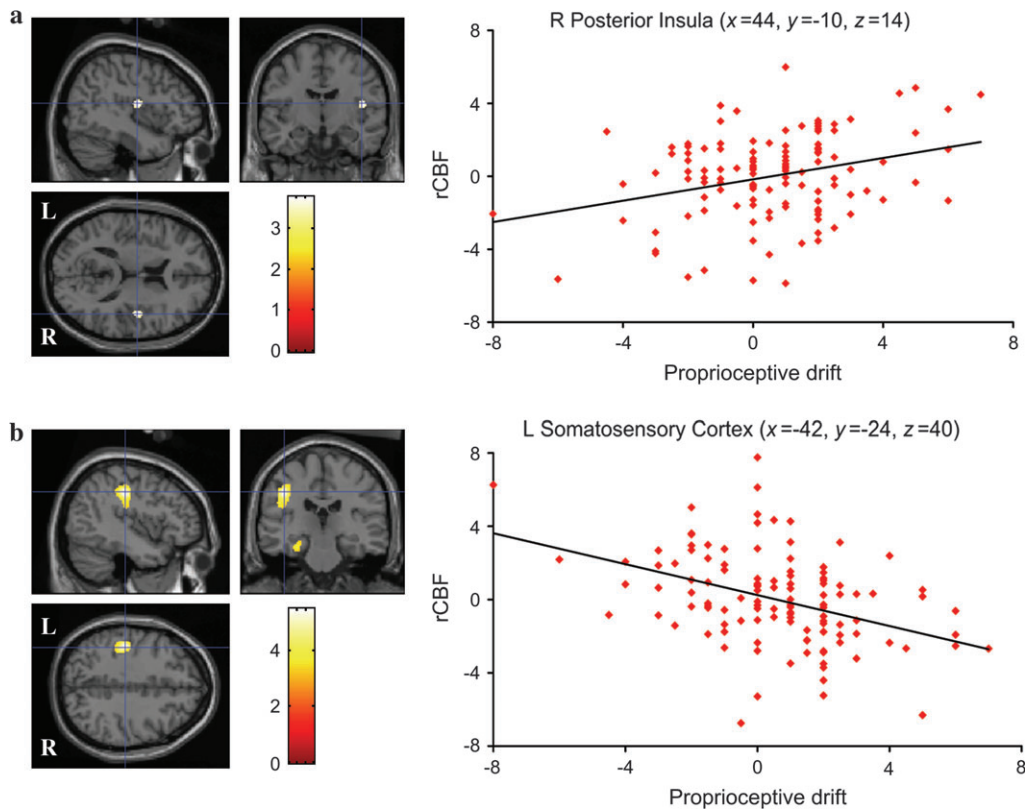


Figure 4. (a) Activity in the right posterior insula ($x = 44, y = -10, z = 14$) was positively correlated ($t = 3.41, P < 0.05$) with the proprioceptive drift toward the rubber hand. (b) Activity in the left somatosensory cortex ($x = -42, y = -24, z = 40$) was negatively correlated ($t = -4.84, P < 0.05$) with the proprioceptive drift toward the rubber hand. Positive drifts indicate a drift toward the rubber hand, and negative drifts indicate a drift away from the rubber hand. Activations show averaged data over 10 participants (L = Left, R = Right).

survived whole-brain volume correction for multiple comparisons ($P < 0.05$ using family-wise error rate).

Discussion

We investigated the neural signatures of body ownership using the RHI. The conditions that induce the illusion involve visual and tactile stimulation, but the perceptual experience that induces the illusion may be quite distinct from the sense of ownership itself. For this reason, we distinguished between the neural activations and perceptual conditions that lead to sense of ownership and the neural correlates corresponding to phenomenal experience of ownership. We particularly focused on the correlation between neural activity and a quantitative proxy of the RHI, namely, the proprioceptive drift toward or away from the rubber hand. The present results suggest that the phenomenal incorporation of a rubber hand is reflected by activity of the right posterior insula and the right frontal operculum. Conversely, the failure to experience ownership over the rubber hand is related to activity in the contralateral primary and secondary somatosensory cortices.

Few neuroimaging studies have studied body ownership (Ehrsson et al. 2004; Ehrsson, Holmes, and Passingham 2005). Ehrsson et al. (2004) showed bilateral neural activity in the ventral premotor cortex and the frontal operculum in the conditions that “induced” the RHI. That study focused on the causes (i.e., congruent visual and tactile stimulation) of the RHI, but the RHI was not quantified behaviorally. In addition, the

phenomenal effect of the illusion, namely, the sense of body ownership of the rubber hand, was not separated from the conditions that induced it. The present study replicated the activation in the right frontal operculum but failed to show activity in premotor cortex. This may perhaps be explained by differences in the methods and experimental designs of the 2 studies. The study by Ehrsson et al. emphasized the dynamic process of visuotactile integration that occurs around the onset of the illusion by using shorter blocks of visuotactile stimulation (42 s) than the present study (125 s). In fact, in that study the onset of the illusion, which subjects had to indicate by pressing a button with their left foot, was used as an event in their analysis model. To that end, the results of Ehrsson et al. reflect the onset of the incorporation process, whereas the present results reflect the steady state of being incorporated.

In our study, acquisition of the neuroimaging data began only after the first 45 s of visuotactile stimulation and lasted for 60 s. Data collected by Ehrsson et al. suggest that the RHI begins approximately after 11 (± 7) s of stimulation. Data collected by Tsakiris and Haggard (2005b) suggest that the main effect of correlated visuotactile stimulation on generating proprioceptive drifts toward the rubber hand is particularly strong during the first 60 s, after which the drift increases in a less exponential manner for up to 3 min. Based on these observations, it seems that by the onset of PET data acquisition in the present study (60 s after the onset of visuotactile stimulation), participants were already experiencing the illusion and that the recalibration of their hand position associated with the onset of the

illusion had already occurred. It is unclear whether sustained activity in the premotor cortex occurs during prolonged stimulation periods or whether premotor activity reflects only the onset of the dynamic processes involved in ownership changes. The dynamic changes associated with the illusion onset were not emphasized in the present study due to the low temporal resolution of PET. Typically, epoch-related neural responses are assessed in PET because of the relatively long half-life of the radiotracers used. Thus, the use of PET allowed us to detect sustained neural activity that was specifically related to the assimilation of visuotactile stimulation that leads to the feeling of ownership of the rubber hand and not to the onset of the RHI per se.

The Causes of the RHI

The factorial analysis of the conditions causing ownership revealed a frontoparietal network for the perception of body-related multisensory signals. Activations in the left parietal cortex associated with asynchronous visuotactile stimulation were localized in the contralateral primary somatosensory cortex and the contralateral superior parietal lobule (SPL). In the asynchronous condition, subjects saw first the rubber hand being touched, and they then felt touch on their own hand. Activity in the contralateral somatosensory cortex during asynchronous stimulation may reflect neural processing related to the anticipation of the tactile stimulus on the participant's hand that always followed the visual stimulation of the rubber hand. This view is supported by a recent study showing that the contralateral somatosensory cortex is activated during anticipation of tactile stimulation (Carlsson et al. 2000).

The left SPL may play an important role in body-part localization. Felician et al. (2004) showed a selective activation of the left SPL at similar coordinates to the present study ($x = -18$, $y = -50$, $z = 72$) when subjects were asked to localize their body parts. In that study, subjects were asked to point with either their left or their right hand to an indicated body part or a spatial location inside the scanner. Pointing movements were performed by rotating their wrist along a vertical axis in the direction of the opposite side of the body or space. The contrast of body localization versus space localization showed strong activation in the left SPL, irrespective of the side of the part that had to be localized and of the hand used. In the present study, asynchronous stimulation did not elicit significant proprioceptive drifts toward the rubber hand. Put another way, subjects retained a strong sense of the actual body-part localization despite the appearance of the rubber hand in an adjacent location. The observed activation in the left SPL in the asynchronous condition may thus reflect this internal sense of body-part localization.

Our main interest in the factorial analysis focused on the interaction term. In particular, the conflict interaction (CA - CS) - (IA - IS) identified the specific activation for a visual appearance of the rubber hand which was congruent with the subject's own hand, but the timing of visual and tactile stimulation suggested the opposite. The right rolandic operculum was active when participants experienced this conflict between proprioception, touch, and vision. The functional role of this area would be to detect and resolve various conflicting signals between internal and external representations of body-related events. Fink et al. (1999) used a mirror to manipulate visual feedback, while subjects performed the Luria bimanual coordination task. In some conditions, the participant's intention and proprioceptive

feedback indicated out-of-phase hand movements, whereas the mirror showed in-phase hand movements. The mismatch between intention, proprioception, and vision activated the right dorsolateral prefrontal cortex, in particular, a dorsal area (Brodmann area [BA] 9/46) in right lateral prefrontal cortex. In a second experiment, using passive movements, a right ventral, lateral frontal region, anterior to the peak of activation in the present study, was again activated by intersensory conflict. Importantly, the observed right frontal activity in the study by Fink et al. associated with the detection of sensorimotor and also intersensory conflict during bimanual hand movements was independent of the hand attended. In the present study, tactile attention was always focused on the subject's right hand. The right hand was stimulated across all conditions, whereas visual attention was focused either on a left or on a right rubber hand. It seems possible that the sensitivity of the right (i.e., ipsilateral) frontal cortex to sensory conflict is independent to the stimulated or attended hand. Here, unlike in previous studies, this conflict is purely sensory and does not involve action. This area may thus be involved not only in conflicts of agency but also in conflicts of ownership.

The Failure of Incorporation of the Rubber Hand

A negative correlation between the proprioceptive measure of the illusion and rCBF was observed in the contralateral parietal cortex, in particular in the left primary and secondary somatosensory cortices. An important behavioral/phenomenal correlate of the attribution of the rubber hand to one's own body is a change in the perceived location of the subject's hand toward the rubber hand (Tsakiris and Haggard 2005b). That is, larger proprioceptive drifts toward the rubber hand correspond to more powerful illusions or ownership (Botvinick and Cohen 1998). A small or negative proprioceptive drift indicates that the rubber hand has not been attributed to one's own body, presumably because of a discrepancy between the proprioceptive and tactile experience of the subject's own hand and the visual perception of the rubber hand. In these situations, the internal proprioceptive representation of the body is not captured by visual input.

We found strong contralateral somatosensory activation to correlate with this internal representation of one's own body. This result is consistent with previous research on visual perspective taking and abstract forms of self-processing. Other studies have reported that the left parietal cortex is involved not only in distinguishing between self and other but also in maintaining a stored reference of the self. For example, Ruby and Decety (2001) showed that the left inferior parietal and the left somatosensory cortices were specifically involved in distinguishing assertions about the self versus others. In that study, the somatosensory cortex was activated only when the first-person perspective was compared with the third-person perspective, suggesting that this area is critically involved in distinguishing self from other. Other studies have also suggested that primary and secondary somatosensory cortices are associated with body awareness (Hari et al. 1998; Schwartz et al. 2005). A patient reported by Hari et al. (1998) occasionally perceived a "ghost" left hand, which copied the previous positions of his/her real left hand with approximately 1 min time lag. Neuromagnetic recordings revealed that activity of the left secondary somatosensory cortex was strongly suppressed during the experience of the left ghost arm. Activation in left secondary somatosensory cortex was also observed when

subjects watched someone else's leg being touched (Keyzers et al. 2004; see also Blakemore et al. 2005), independently of whether subjects saw a left or a right leg being touched. This finding seems compatible with the "not me" quality of the failure to experience ownership over the rubber hand in the present study.

It may be suggested that the somatosensory cortex, by maintaining a stored reference of the body, is particularly sensitive to handedness (i.e., left- vs. right-hand manipulation) and related anatomic constraints (see also Costantini et al. 2005), to the kinesthetic proprioceptive space (i.e., proprioceptive drift), and to both visual and tactile inputs (see also Schaefer et al. 2005; Schaefer, Flor, et al. 2006; Schaefer, Noennig, et al. 2006). Thus, the somatosensory cortex may be involved in the processing of an internal reference body representation. More specifically, as suggested in the relevant literature (Hari et al. 1998; Ruby and Decety 2001; Keyzers et al. 2004), self-other distinctions seem to involve specifically the "left" secondary somatosensory cortex. This would be in line with our results. However, given the fact that tactile stimulation in the present study was always delivered on the participant's right hand, it is difficult to interpret the left, contralateral somatosensory activation in terms of its laterality. To solve this question, further investigations including tactile stimulation of both hands would be necessary.

The Experience of Body Ownership

The experience of ownership of the rubber hand as measured by the proprioceptive behavioral data was positively correlated with activity in the right posterior insula and right frontal operculum. The insula and the frontal operculum are reciprocally connected through efferent and afferent projections (for a review, see Augustine 1996). Bilateral frontal operculum activity was found by Ehrsson et al. (2004) when subjects experienced the RHI. Activity in the insula has been found in numerous studies involving the self. Right insular activity is consistently implicated in self-attribution (Farrer and Frith 2002; Farrer et al. 2003), self-processing (Fink et al. 1996; Vogeley et al. 2004), and the representation of an egocentric reference frame (Fink et al. 2003). It should be kept in mind, however, that the activation observed in the insula extended into the right operculum. The right rolandic operculum was active during the detection of conflict between visuotactile stimulation and hand identity as shown in our factorial analysis. However, the 2 activations were distinct and did not overlap. Clearly, the separation of activations spreading across sulci or fissures always imposes problems in activation studies. Nevertheless, PET designs enable the separation of activation peaks even in the millimeter range (Shipp et al. 1995; Fink et al. 1997).

The role of right posterior insula in integrating body signals related to egocentric representation, agency, and possibly body ownership is supported by a series of recent studies. For example, Fink et al. (2003) showed that activation of right posterior insula was related to a distortion of the egocentric reference frame using galvanic vestibular stimulation. Farrer and Frith (2002) proposed that the sense of agency results from the integration of multiple body- and action-related signals. This integrating process was thought to involve the right insular cortex. For example, Farrer et al. (2003) showed that activation in the right posterior insula decreased when subjects experienced a discordance between what they did and what they saw, suggesting that activity in the posterior insula correlates with

the degree of congruence between different signals used for attribution of actions to oneself. The present study extends these findings by showing a correlation between activity in the insula and sense of body ownership. Body ownership might be considered a form of self-attribution specifically for body parts, and in parallel to the self-attribution of actions. Previous studies focused on posterior insula activation during self-attribution of actions. In contrast, we show that posterior insula is active even in the absence of efferent information, when a nonacting subject must integrate multisensory information to decide on the attribution of body parts to oneself. Thus, insular activity may reflect body ownership rather than agency. Because agency typically involves both efferent and afferent signals (Tsakiris and Haggard 2005a; Tsakiris et al. 2005), previous studies have been unable to distinguish between these alternatives. Attribution of body ownership may be more fundamental than action attribution because the latter involves an additional efferent component that the former lacks.

Interestingly, a recent lesion mapping study suggests that the right posterior insula is commonly damaged in patients with anosognosia for hemiparesis but is significantly less involved in hemiparetic patients without anosognosia (Karnath et al. 2005; see also Cereda et al. 2002). The present findings support the hypothesis that the insular cortex is integral to bodily self-awareness. Anosognosia for hemiplegia is also associated with lesions in right BA44 and right BA6 (Berti et al. 2005), suggesting that the denial of motor deficits arises, in part, by a failure to monitor the signals related to one's own movement. One consequence of that failure would be to "ignore" the conflict between signals related to the intended and the actual states of the limbs, resulting in anosognosia. Thus, the patient might not register that their limb fails to move on command. Our work, however, suggests that the normal construction of bodily awareness can be based on purely sensory signals processed in the right frontal and parietal cortices. This is in line with converging neuropsychological and neuroimaging evidence which suggests that the neural substrates of sensorimotor bodily awareness are functionally lateralized to the right hemisphere, whereas the left hemisphere seems to underpin mostly linguistic and semantic body representations (for a review, see Berlucchi and Aglioti 1997).

Conclusions

We used the RHI to study the neural correlates of body ownership. We suggested that the causes and the effect of the RHI are associated with distinct neural processes. Correlation between synchronous visual and tactile percepts is a necessary condition for the inducement of the RHI. A conflict between visual and tactile percepts does not induce the illusion. The present study showed that right frontal cortex monitors the perception of body-related sensory signals when a conflict arises, blocking the attribution of the rubber hand to one's own body. The effect of this failure to incorporate the rubber hand, namely, the feeling that the rubber hand is not part of one's own body, is associated with somatosensory activity contralateral to the stimulated right hand. Conversely, when visual and tactile percepts are congruent, the premotor cortex in both hemispheres seems to underpin the processes of multisensory integration that cause the RHI (Ehrsson et al. 2004; Ehrsson, Holmes, and Passingham 2005). Finally, the effect of multisensory integration and recalibration of hand position, namely, the

experience of body ownership of the rubber hand, is correlated with activity in the right posterior insula.

Importantly, we found activations in the right posterior insula and right frontal cortex related to a basic process of self-consciousness, namely, body ownership, in the absence of motor action. Previously, these areas have been associated with a sense of agency resulting from motor command prediction. Body ownership is a standard consequence of agency, but agency involves additional elements that do not occur in body ownership. Previous studies may have misidentified as signatures of motor agency neural activations, which in fact correspond to the body ownership that agency generally entails. This confusion can occur when experimental designs do not adequately disentangle afferent and efferent information. We suggest that a basic form of bodily self-consciousness is generated in the brain by sensory stimulation and assimilation to a preexisting body scheme. Agency would represent a special but important addition to this essentially sensory circuit for self-consciousness.

Notes

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Appendix: Questionnaire Administered after the Experiment

The questions for the congruent rubber hand identity were the following:

1. When I was looking at a right rubber hand, it seemed as if I were feeling the touch of the paintbrush in the location where I saw the fake hand being touched.
2. When I was looking at a right rubber hand, it seemed as though the touch I felt was caused by the paintbrush touching the rubber hand.
3. When I was looking at a right rubber hand, I felt as if the rubber hand were my hand.
4. When I was looking at a right rubber hand, it felt as if my (real) hand were drifting towards the rubber hand.
5. When I was looking at a right rubber hand, it seemed as if I might have more than one right hand or arm.
6. When I was looking at a right rubber hand, it seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand.
7. When I was looking at a right rubber hand, it felt as if my (real) hand were turning 'rubbery'.
8. When I was looking at a right rubber hand, it appeared (visually) as if the rubber hand were drifting towards my hand.
9. When I was looking at a right rubber hand, the rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.

The same questions were presented for the incongruent rubber hand identity, but now the "right rubber hand" was replaced by "left rubber hand."

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