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Having a body versus moving your body: neural signatures of agency and body-ownership

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Version: Accepted (Refereed)

Citation:

Tsakiris, M., Longo, M.R. and Haggard, P. (2010)
Having a body versus moving your body: neural signatures of agency
and body-ownership –
Neuropsychologia 48

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Journal Section : Behavioral/Systems/Cognitive

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Title: Having a body versus moving your body: neural signatures of agency and body-ownership

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Abbreviated title: Neural signatures of agency and body-ownership

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Number of figures: 4

Formatted: English (U.S.)

Number of tables : 3

Formatted: English (U.S.)

Contents of supplemental material (if applicable)

Formatted: English (U.S.)

Number of pages

Formatted: English (U.S.)

Number of words for Abstract (250), Introduction (497), and Discussion (1,487)

Formatted: English (U.S.)

Formatted: English (U.S.)

Keywords: agency, body-ownership, supplementary motor area, angular gyrus, parietal cortex, cortical midline structures

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Acknowledgments: This research was supported by Bial Foundation Research Grant 165/06 to MT, by Biotechnology and Biological Sciences Research Council (BBSRC) grant BB/D009529/1 to PH, and by a Leverhulme Trust Senior Research Fellowship to PH. We would like to thank Henrik Ehrsson, Peter Aston and David Bradbury.

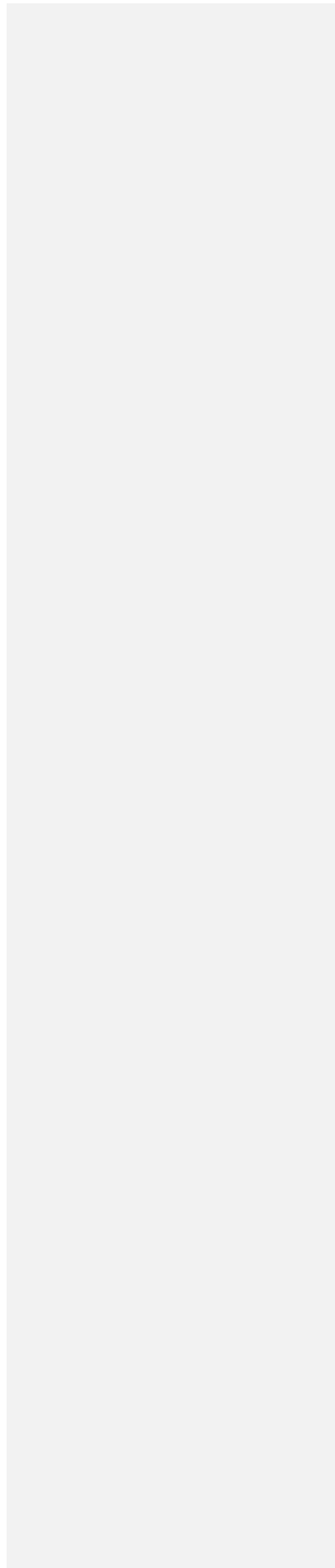
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Abstract

The exact relation between the sense that one's body is part of self (body-ownership) and the sense that one controls one's body (agency) remains unknown. According to an 'additive' model, agency and body-ownership are strongly related, because the ability to control actions is a powerful cue to body-ownership. This view implies a common component to the senses of body-ownership and agency, plus possible additional components unique to agency. An alternative view holds that agency and body-ownership are qualitatively different experiences, triggered by different inputs, and recruiting distinct brain networks. We tested these two specific models, by investigating the sensory and motor aspects of body representation in the brain using fMRI. Participants made self-generated finger-movements, or remained passive while similar movements were applied to their fingers. Participants saw a video image of their hand either in real-time or with a systematic delay that generated a conflict. Activations in midline cortical structures were associated with a purely sensory-driven sense of body-ownership, and were absent in agency conditions. In contrast, activity in the pre-SMA was linked to the sense of agency, but distinct from the sense of body-ownership. Importantly, no shared activations that would support the additive model were found. The results support an independence model of agency and body-ownership, and do not support the additive model. Body-ownership involves a psychophysiological baseline, linked to activation of the brain's default mode network. Agency over one's body is linked to premotor and parietal areas involved in the generation of motor intentions and subsequent action monitoring.

Introduction

The feeling that the body I inhabit is ‘my own’ (sense of body-ownership, SoB), is normally experienced not only during voluntary actions, but also during passive movement and at rest. In contrast, only voluntary actions should produce the feeling that I can move and control my body (sense of agency, SoA). On one view, the relation between SoB and SoA is additive, meaning that agency entails body-ownership, because one can control movements of one’s own body, but not other objects, at will. Thus, agency offers a strong cue to body ownership. Accordingly, the SoA should involve the SoB, plus a possible additional experience of voluntary control. An alternative view holds that SoA and SoB are qualitatively different experiences, without any common component.

The exact neural bases of SoB and SoA remain unclear. Right posterior insula activation was associated with SoB (Tsakiris et al., 2007), and SoA (Farrer et al., 2003). Right inferior parietal activations were associated with breakdowns of SoA (Farrer et al., 2003, 2008) and SoB (Shimada, Hiraki & Oda, 2005). The agency studies manipulated the visual feedback to either match or mismatch proprioceptive and motor signals. However, such manipulations confound agency and body-ownership (Tsakiris, Schütz-Bosbach & Gallagher, 2007), because brain activations could reflect sensori-motor comparisons (relating to agency) or proprioceptive-visual comparisons (relating to body-ownership). Consequently, such experimental designs cannot distinguish between the additive and the independence model of agency and body-ownership.

The SoA and SoB can be disentangled experimentally, by comparing voluntary action with passive movement. Both involve physically comparable movement and proprioceptive feedback, but are physiologically and psychologically very different (Haggard, 2008). Comparing active with passive movements can test whether agency represents the addition of

action programming to the somatic experience of body movement or whether agency and body-ownership are qualitatively different. It also allows a clear operationalisation of body-ownership, without confounding by agency. We therefore manipulated the SoB by presenting real-time or delayed visual feedback of movements, and the SoA, by comparing voluntary and passive movements.

We tested two specific models on the relation between body-ownership and agency.. The first, additive model, holds that SoA entails body-ownership. Thus, active movements of the body should involve the SoB, plus an additional SoA. This produces three concrete predictions about brain activations in agency and body-ownership conditions: first there should be some activations common to agency and body-ownership conditions. Second, there should be an additional activation in agency, which is absent from body-ownership. Third, there should be no activation in the body-ownership condition that is not also present in the agency. A second model holds that the senses of agency and body-ownership are qualitatively different experiences, without any common component. Accordingly, the brain could contain distinct networks for body-ownership and agency. This produces three concrete predictions: first, there should be *no* common activations between agency and ownership. Second, there should be a specific activation in agency conditions that is absent from ownership. Third, there should be a specific activation in body-ownership that is absent from agency.

Materials and Methods

Experimental Design

A 2x2 factorial design was used (see Figure 1a). The first factor was the type of movement, active or passive, and the second factor was the visual feedback, real-time or delayed. Participants viewed a video image of their right hand that was covered with a woollen

glove. This image could be direct (synchronous) or delayed (asynchronous, 600 ms video delay). In a passive condition, an experimenter passively lifted and lowered the index finger up and down, at approximately 0.5 Hz, by pulling a thread attached to a ring around the participant's finger. In an active condition, the participant actively lifted and lowered their finger at a similar rate. Thus, there were four conditions: active synchronous (AS), active asynchronous (AA), passive synchronous (PS), and passive asynchronous (PA).

INSERT FIGURE 1 AROUND HERE

Experimental Set-up and Methods

The methods were based on a previous behavioural study (see Tsakiris, Prabhu & Haggard, 2007) with modifications appropriate for the fMRI scanning environment (see Figure 1B). Whilst the brain scans were being performed, the subjects rested comfortably in a supine position on the bed in the MRI scanner. All subjects wore headphones to reduce noise and to communicate with the experimenters between runs. The right arm was extended and placed on a support so that the right hand was positioned in a relaxed position. Within the cylindrical head coil the head was tilted approximately 20-30 degrees by placing foam wedges underneath. Thus the natural direction of the gaze was oblique so that the subjects could see a projection screen attached to the bore of the scanner through direct vision without any discomfort. The participant's arm was placed on a tilted (30-45°) plastic table that was positioned over the stomach of the subject. The table was covered with a soft black material. Finally, to reduce potential head movements, we fixed the position of the head using foam pads. Participants did not have direct vision of their hand.

A mirror was placed above the participant's hand at approximately a 45° angle and a colour MRI-compatible video camera recorded the mirror image of the hand. This video image was fed to a PC in the control room which projected the image of the hand onto a projection

screen either with minimal delay (synchronous condition) or with a systematic delay (asynchronous condition). The video presentation was controlled by a custom LabView (National Instruments, Austin, TX) script. In the synchronous condition, there was a irreducible delay of approximately 100 ms due to digitisation and projection of the image. In the asynchronous condition the delay was approximately 500 ms. Healthy adults perceive viewed actions as self-generated at delays up to 150 ms (Franck et al., 2001), suggesting that the 100 ms delay should not adversely affect illusion of body-ownership and agency (Blakemore et al., 1999). The script also flipped the image to undo the reversal created by filming the mirror image of the hand. The resulting image mimicked the perspective the participant would have had they directly viewed their hand. The distance of the camera from the hand was adjusted before the experiment so that the image of the hand on the projection screen was approximately life size.

There were three functional runs. Each ran began with 15 seconds of rest followed by four blocks of stimulation. Each block was comprised of four trials, one of each of the four conditions in random order. Trials began with four seconds of written instructions ('Passive' of 'Active') indicating to the participant whether the upcoming trial would involve active or passive movements. Following the instructions, the video image was displayed and finger movements began. The video image was displayed for 36 seconds. Following each block, there was a rest period of 25 seconds in which participants saw a black screen. Thus, there were a total of 16 trials (4 of each condition) in each run.

Following the experiment, participants were asked to rate their agreement or disagreement with ten statements concerning their experience during the various conditions (see Table 1). Responses were made using a 7-point Likert scale, where a score of +3 indicated strong agreement with the statement, -3 strong disagreement with the statement, and 0 neither

agreement nor disagreement. Judgments for each statement were made separately for each of the four conditions. The order of statements was randomised for each participant. This questionnaire has been used previously to measure subjective experiences of body-ownership and agency in a similar experimental situation (Longo & Haggard, 2009). An overall measure of body-ownership was computed by averaging across items (1) – (3), with items (2) and (3) being scored in reverse. An overall measure of agency was computed by averaging across items (4) – (6), with item 6 being scored negatively.

Participants

Twenty naïve healthy right-handed volunteers (eight female), between 18 and 36 years of age ($M = 24.8$, $SD = 5$), with no history of neurological or psychiatric illness participated with informed consent. All but one were right handed ($M = 77.2$, $SD = 43.6$, range: $-81.8 - 100$) as assessed by the Edinburgh Inventory (Oldfield, 1971). The study was approved by the local ethics committee. All participants were naïve as to the purposes of the experiment. One participant was excluded because of large head-movement artefacts. The analyses reported refer to the 19 remaining participants.

fMRI Methods: Image Acquisition and data analysis

The functional imaging was conducted in a Siemens Sonata 1.5T Scanner to acquire gradient echo T2*-weighted echo-planar images with blood oxygenation level dependent contrast (BOLD) as an index of local increases in synaptic activity. A functional image volume comprised 48 continuous slices of 3mm thickness which ensured that the whole brain was within the field of view. Volumes were acquired continuously with a TR of 4.32 s. A total of 175 scans were collected during each functional run (12.6 min), with the first four volumes subsequently discarded to allow for T1 equilibration effects. Thus during the three experimental runs performed for each subject a total 525 image volumes were collected.

Data analyses were conducted using Statistical Parametric Mapping (SPM5; Wellcome Trust Centre for Neuroimaging, London, UK, <http://www.fil.ion.ucl.ac.uk/spm>) using MATLAB 7.3 (Mathworks, Natick, MA). All volumes were realigned and unwarped to correct for head movements. The voxel size of normalized images was 2 x 2 x 2 mm. Resulting volumes were normalized to a standard EPI template based on the Montreal Neurological Institute (MNI) reference brain, and smoothed with an isotropic 8 mm full-width half-maximum Gaussian kernel. For each run, time series in each voxel were high-pass filtered at 1/128 Hz to remove low-frequency confounds.

For each individual subject, we fitted a linear regression model (general linear model) to the data (first level analysis). First-level analyses were conducted for each subject by modelling the four experimental conditions and instructions with box-car functions and convolving them with a canonical hemodynamic response function. To eliminate confounds associated with the total amount of movement in each condition, the number of finger movements in each block was included as a separate block-level regressor. We defined linear contrasts in the general linear model. The result from this analysis was contrast estimates for each condition from each of the 19 subjects (contrast images). To accommodate inter-subject variability, the contrast images from all subjects were entered into a random effect group analysis (second level analysis) using a 2x2 factorial (movement [active, passive], synchrony [synchronous, asynchronous]) analysis of variance (ANOVA).

We computed differential activation patterns associated with synchronous in contrast to asynchronous visual feedback [(AS+PS)-(AA+PA)] and vice versa [(AA+PA)-(AS+PS)]. We then report differential patterns of activations associated with active movement in contrast to passive movement [(AS+AA)-(PS+PA)] and vice versa [(PS+PA)-(AS+AA)]. Activations were identified using a corrected (with False Discovery Rate; Genovese, Lazar, & Nichols, 2002)

two-tailed height threshold of $p < 0.05$ and an extent threshold of $k > 10$ contiguous voxels throughout the brain. We also report areas predicted that survive $p < 0.05$ small volume correction using a 10 mm sphere over coordinates from previous studies. We additionally report regions surviving a two-tailed uncorrected threshold of $p < 0.001$.

In addition, to evaluate the different models of agency discussed in the introduction, we performed a structured series of contrasts using the masking procedure of SPM5. Both the additive and independence models predict that there should be agency-related activations specific to the AS condition, that do not appear in the PS condition. The interaction term of the classic ANOVA does not specifically isolate such activations; expressed as $[(AS - PS) - (AA - PA)]$, since it identifies voxels active in *both* the AS and PA conditions, relative to the PS and AA conditions. Because our a priori hypothesis was that activations related to the sense of agency should be specific to the AS condition, we used a more specific contrast based on, an *exclusive* masking procedure: $[(AS-PS)$ at $p < 0.0005$ masked exclusively by $(AA-PA)$ at $p < 0.0005$, and $k > 10$]. This contrast identifies voxels selective for active movements with synchronous visual feedback that were not due to making active movements alone.

Second, the additive model predicts that the ownership-related activations in the PS condition should also appear in the AS condition. Thus, activations in the PS condition should be a subset of those in the AS condition and there should be no activations specific to PS. The independence hypothesis, in contrast, predicts that agency-related activations in the AS condition and ownership-related activations in the PS conditions should differ qualitatively. Thus, the independence model predicts that there should be activations found uniquely in the PS condition, while the additive model predicts that there should not. To identify any such activations, we used an exclusive masking procedure $[(PS-AS)$ at $p < 0.0005$ masked exclusively

by (PA-AA) at $p < 0.0005$, and $k > 10$], to identify voxels that were selective for synchronous visual feedback following passive, but not active, movements.

Third, the additive model predicts that ownership-related activations should be common to the PS and the AS conditions. The independence model, in contrast, predicts that there should not be activations common to the PS and AS conditions, that are not also shared by the asynchronous conditions. To identify such regions, we used an inclusive masking procedure [(AS-AA) at $p < 0.0005$ masked *inclusively* with (PS-PA) at $p < 0.0005$, and $k > 10$] to identify voxels that were *commonly* activated during synchronous video feedback, independent of movement type.

Thus, the two models make one common prediction, that activations unique to agency should be found in the AS condition, but more importantly make two divergent predictions. The independence model predicts activations unique to the PS condition, whereas the additive model predicts no such activations. Second, the additive model predicts activations common to the PS and AS conditions, while the independence model predicts no such activations. The set of masked contrasts described above, therefore, allow the two models to be directly tested.

Results

Subjective Reports

The mean ratings for the body-ownership questions per condition were submitted in a 2x2 ANOVA. The main effects of type of movement and feedback were significant ($F(1,18)=17.48$, $p<0.05$) and $F(1,18)=28.25$, $p<0.05$, respectively). The interaction between the two factors was not significant ($F(1,18)=.1$, $p>0.05$). Participants reported a stronger sense that the viewed image was their own hand for synchronous than for asynchronous views, in both passive and active conditions. The passive condition corresponds to a pure sense of body-ownership, uncontaminated by sense of agency: i.e., that the viewed image is linked to one's own body. Active movement with synchronous feedback also elicited a significantly stronger sense of body-ownership than the equivalent passive movement condition ($t(18)=4.4$, $p<0.05$).

The mean ratings for the agency questions per condition were analysed with a 2x2 ANOVA. The main effects of type of movement and feedback were significant ($F(1,18)=40.85$, $p<0.05$) and $F(1,18)=64.61$, $p<0.05$, respectively). The interaction between the two factors was also significant ($F(1,18)=4.35$, $p=.05$). This interaction suggests that the active condition induces both a sense of body-ownership, but also a sense of agency, or additional feeling that one can voluntarily control the body at will. Participants reported a stronger sense of agency for the active movement synchronous condition. As predicted, active movement with synchronous feedback elicited a significantly stronger sense of agency than the equivalent passive movement condition ($t(18)=7.1$, $p<0.05$).

INSERT FIGURE 2 AROUND HERE

Number of Movements

The mean number of movements performed in each condition were analysed using a 2x2 ANOVA. The main effect of type of movement (i.e. active vs passive) was not significant ($F(1,18)=2.62$, $p>0.05$). Significantly more finger movements occurred in synchronous than asynchronous blocks (15.5 vs. 14.5) ($F(1,18)=124.62$, $p<0.0001$). This effect was modulated by movement type, ($F(1,18)=11.34$, $p<0.05$); the difference between synchronous and asynchronous conditions was larger for active (15.9 vs. 14.4) than for passive (15.1 vs. 14.5) movement blocks. To eliminate confounds associated with total amount of movement, the number finger movements in each block was included as a separate block-level regressor in analyses of fMRI data.

fMRI Data

Main effects

We analyzed the fMRI data in two ways. First, we used a 2x2 factorial design to investigate the main effects of type of movement and visual feedback. Table 1 shows the local maxima of brain areas with increased neural activity assessed for the main effects of the 2x2 factorial design.

The main effect of active movement [(AA+AS)-(PA+PS)] was associated with bilateral activity in the cerebellum, primary motor cortex, the postcentral gyri, and the inferior parietal lobule. The main effect of passive movement [(PA+PS) - (AA+AS)] was associated with bilateral activations in the postcentral gyri and the medial frontal gyri, the right precuneus, and the anterior cingulate.

The main effect of synchronous online visual feedback [(AS+PS)-(AA+PA)] elicited activations in the right (ipsilateral) postcentral gyrus, the left posterior insula, and the cerebellum bilaterally. The main effect of asynchronous delayed visual feedback [(AA+PA)-(AS+PS)] elicited activations in the right inferior parietal lobule, and more precisely in the supramarginal

gyrus and the angular gyrus. As shown in Figure 3, the patterns of activations in the supramarginal (BA40) and the angular gyri (BA39) are different. Mean beta values calculated in the supramarginal gyrus show that activity in this cluster was mainly driven by the AA condition (Figure 3a), while the mean beta values in the angular gyrus show that activity in this area was elicited both in the AA and PA conditions (Figure 3b). Therefore, the supramarginal gyrus may code for sensorimotor conflicts, while the angular gyrus may code for intersensory conflicts.

Specific activations related to agency

As described above, both models predict activations related to the sense of agency to be observed specifically in the AS condition. Thus, we performed an exclusive masking procedure [(AS-PS) at $p < 0.0005$ masked exclusively by (AA-PA) at $p < 0.0005$, and $k > 10$] to determine activations that were unique to the difference between active and passive movements with synchronous visual feedback, but that cannot be accounted by a general confound of the presence of intentional movement. Table 2 shows the local maxima of brain areas that were active for this contrast, including the right superior parietal cortex, the supplementary motor area (see Figure 4a), the dorsal premotor cortex (BA6) bilaterally, and the cerebellum bilaterally. A distributed neural network of sensorimotor brain areas in frontal and parietal areas was more active in the AS than the PS condition. These differences cannot be explained simply by the presence of movement alone or the synchronous visual feedback alone. The observed pattern suggests that the sense of agency is underpinned by different brain areas from those related to the sense of body-ownership. Importantly no activations in the primary motor cortex were observed.

Activations common to AS and PS conditions

The additive model predicts that body-ownership is common to conditions with synchronous video feedback, regardless of whether active or passive movements are made. We implemented an inclusive masking procedure [(AS-AA) at $p < 0.0005$ masked inclusively with (PS-PA) at $p < 0.0005$, and $k > 10$] to determine voxels that were commonly activated in the two contrasts. No suprathreshold activations were observed. This absence of activation is predicted by the independence model, but is inconsistent with the additive model.

Activations specific to the PS condition

To examine whether the sense of body-ownership in the absence of movement is underpinned by a distinct set of brain areas independent from those for the sense of agency we performed an additional analysis. We implemented an exclusive masking procedure [(PS-AS) at $p < 0.0005$ masked exclusively by (PA-AA) at $p < 0.0005$, and $k > 10$] to determine activations that were unique to a purely sensory sense of body-ownership (PS), that cannot be accounted for by the experiences present in AS condition (see Table 2). Brain areas that were uniquely activated in the PS condition included medial anterior and posterior brain areas such as the superior medial gyrus (see Figure 4b), the precuneus, and the posterior cingulate gyrus. In sharp contrast to the activations observed uniquely in the AS condition, the present contrast revealed activations in midline cortical structures. These activations suggest that the sense of body-ownership generated during sensory stimulation is underpinned by a different neural network from the one engaged during active movement and experienced agency. This finding provides direct support for the independence model, and is inconsistent with the additive model.

Discussion

We investigated the neural signatures of the SoA and SoB. We manipulated whether finger movements were actively generated by participants or passively generated by an experimenter, while presenting either real-time or systematically delayed visual feedback. Manipulating the timing of visual feedback caused the observed hand to be either attributed to the participant or not. Previous studies showed that temporal congruency can cause a sense of body-ownership in purely sensory situations such as the RHI (Botvinick & Cohen, 1998; Longo et al., 2008; Tsakiris & Haggard, 2005) and a sense of agency during voluntary movement (Longo & Haggard, 2009; Tsakiris et al., 2006). Analysis of the subjective reports collected after the fMRI session supported this view. The main effect of feedback was significant suggesting that synchronous video feedback produced the feeling that participants were seeing their own body, while asynchronous video feedback did not. In contrast, a sense of agency over the perceived hand appeared only following actively generated movements combined with synchronous video feedback.

The fMRI data shows that the main effect of synchronous visual feedback resulted in activations in the ipsilateral (right) somatosensory cortex. The ipsilateral rather than contralateral location suggests that this activation did not primarily reflect afferent input. Other studies suggested a role for the right somatosensory cortex in self-other distinction (Agnew & Wise, 2008; Ruby & Decety, 2001, 2003) and in body-awareness (Hari et al., 1998; Schwartz et al., 2005). In contrast, the main effects of asynchronous visual feedback resulted in activations in the right inferior parietal lobule, in the angular and supramarginal gyri. Interestingly, the profile of mean beta values in these clusters was not homogeneous (see Figure 3). Activation of the supramarginal gyrus was most prominent in the AA condition, while the angular gyrus was activated in both the AA and PA conditions. This pattern extends previous findings (Balslev,

Nielsen, Paulson, & Law, 2005; Farrer et al., 2008), suggesting that the angular gyrus codes for an intersensory conflict between vision and sensory information, that affects body-ownership and agency. In contrast, the supramarginal gyrus may code for sensorimotor conflicts that are critical only for the SoA.

A recent study (Farrer et al. 2008) showed a key role of angular gyrus in action awareness. Activity in the right angular gyrus (conjunction analysis inferior parietal lobule BA39 angular gyrus: 46, -50, 48) was associated with both the awareness of discrepancy between intended and movement consequences (study 1) and the awareness of action authorship (study 2). Another study (Shimada et al., 2005) that used only passive movements reported activity in the right inferior parietal cortex that was observed during detection of a conflict between proprioception and visual feedback. This activation would contribute to body-ownership but not agency. In our study, one cluster (centred at 52, -38, 38) showed highest mean beta values for the AA condition, corresponding to the activation reported by Farrer et al (2008), while another, more inferior, cluster (40, -58, 26) in angular gyrus showed comparable activity for both the AA and PA, suggesting that it reflects neural responses to intersensory conflict between proprioception and vision. Overall, these results suggest that the right supramarginal gyrus is activated during sensori-motor conflicts (relevant to agency and action awareness), while the right inferior parietal cortex is activated during intersensory conflicts (relevant to body-ownership).

Timing information alone cannot distinguish the SoB from the SoA, or identify the relation between them. According to the additive model, a similar SoB would be present both for active and passive movement conditions with synchronous visual feedback, but the SoA would additionally be present following voluntary movements. The introspective evidence broadly supported this view: participants reported significantly more agreement with questionnaire items

reflecting agency in the AS condition compared to the other three conditions. Interestingly, body-ownership questions were also more highly rated in the AS condition as compared to the PS condition, suggesting that agency strengthens the experience of body-ownership. If the addition of agency to body-ownership enhances the same kind of experience, then we would expect to find at least some shared activations between agency and body-ownership. Another hypothesis suggests that agency is not simply an addition to body-ownership, but a qualitatively different process. This independence model would predict different patterns of brain activity in the two cases.

To distinguish between these possibilities, we first used an inclusive masking analysis to look for brain areas that are commonly activated by agency (induced via active movement) and a sensory-driven body-ownership (induced via passive movement) [(AS-AA) masked inclusively with (PS-PA)]. This analysis revealed no suprathreshold activations common to the two conditions, inconsistent with the additive model. A second analysis based on exclusive masking was used to evaluate the model of independence between agency and body-ownership. Both body-ownership and agency were associated with distinct and exclusive patterns of activation, providing direct evidence that their neural substrates differ. This may seem surprising given the similar responses in our questionnaire. The finding of activity present in the PS, but not the AS, condition, and vice versa, directly contradicts the additive model, in which activations related to body-ownership should be a subset of those related to agency.

The specific brain areas associated with agency and with ownership shed further light on these two components of self-consciousness. Suprathreshold activations unique to the experience of agency [(AS-PS) masked exclusively by (AA-PA)] were observed in the pre-supplementary motor area, the superior parietal lobe, the extrastriate body area and the dorsal premotor cortex bilaterally (BA6). The pre-SMA is strongly involved in the voluntary control of

action (Goldberg, 1985). Neurosurgical stimulation studies further suggest that it contributes to the experience of volition itself: stimulation here can produce an ‘urge’ to move, at stimulation levels below threshold for evoking physical movement (Fried et al., 1991). In our study, voluntary action was present in both the AS and AA conditions: these differed only in timing of visual feedback, and the resulting sense of agency.. However, the pre-SMA activation was greater in the AS condition, where visual feedback confirms that the observed movement is temporally related to the voluntary motor command. Our findings therefore suggest that the pre-SMA plays an important role not only in conscious intention (Lau et al., 2004), but also in the SoA. Interestingly, lesions to the supplementary motor area and/or the anterior corpus callosum may result in Anarchic Hand Syndrome (Della Sala, Marchetti & Spinnler, 1994; Goldberg, Mayer, & Togli, 1981), in which the contralateral hand performs goal-directed actions which are not intended by the patient. Despite the autonomous behaviour of the affected hand, these patients retain a SoB of the moving hand, but they report an inability to control it (see also Marcel, 2003). These results are consistent with our findings of a pre-SMA activation related specifically to agency.

The observed premotor activation (BA6) is also of relevance to a different type of action-awareness deficit. Anosognosia for hemiplegia involves denial of motor deficits after right hemisphere stroke. It arises, in part, by a failure to monitor the signals related to one’s own movement, and is associated with lesions in right BA44 and BA6 (Berti et al. 2005), Interestingly, anosognosic patients seem to ‘ignore’ the conflict between their own intention to move, and the manifest lack of movement of the left hand. They appear to perceive their intention, but not the failure of their intention to trigger appropriate proprioceptive and visual feedback (Fotopoulou et al., 2008). Our findings are consistent, therefore, with an involvement of this area in SoA, based on conflicts between sensory and motor signals.

In relation to a purely sensory-driven body-ownership [(PS-AS) masked exclusively by (PA-AA)], we observed suprathreshold activations in a network of midline cortical structures including the precuneus, the superior frontal gyrus and the posterior cingulate. These midline cortical activations recall recent suggestions of a dedicated self-referential processing network (Northoff & Bermpohl, 2004). Meta-analyses of imaging studies revealed activations in medial regions of the brain during processing of self-related stimuli (Northoff et al., 2006; Wicker et al., 2003). In particular, ventral and posterior cortical midline structures seem to underpin distinct self-related processes, with more anterior structures related to the processing of extero- and interoceptive stimuli for their relation to the self (Northoff & Bermpohl, 2004), and the more posterior areas with higher-order self-representations such as self-identity and perspective taking (Vogeley et al, 2001). These midline activations are also similar to regions of the so-called ‘default mode network’, activated in the absence of any goal-directed task (Raichle et al., 2001). Intriguingly, several lines of evidence suggest that this default network is involved in self-referential processes (Gusnard et al., 2001; Schneider et al., 2008). Northoff and Bermpohl (2004) ask ‘is there a ‘psychological baseline’?’ corresponding to this apparent physiological baseline. We suggest that the feeling of ownership over one’s body, ‘the feeling of the same old body always there’ in James’ (1890) terms, comprises an important (and perhaps dominant) part of this psychological baseline. Importantly, this baseline bodily self appears, from our results, quite unrelated to volition.

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Table Captions

Table 1. The table shows transformed Z scores from an SPM{F} for the main effects and interactions of the factorial design. We show areas predicted that survive $p < 0.05$ small volume correction using a 10 mm sphere over coordinates from previous studies ($x=44, y=-54, z=38$, see Farrer et al., 2008), areas that were not predicted, but that survive correction for multiple comparisons across whole brain (FDR) at $p < 0.05$, areas for which no prediction was made, which are significant at $p < 0.001$ uncorrected for clusters of more than 10 voxels. L/R: left and right hemispheres. [\dagger $p < 0.001$ uncorrected, \ddagger FDR, * SVC]

Table 2. The table shows transformed Z scores from an SPM{F} for the planned comparisons for the independence models of agency and bdy-ownership. Each contrast and its mask were thresholded at $p < 0.0005$ and $k > 10$ voxels. L/R: left and right hemispheres.

Figure Captions

Figure 1: The 2x2 factorial experimental design (1A), and the experimental set-up (1B).

Figure 2: Psychometric Data. Error bars indicate standard errors.

Figure 3: Mean bold responses across conditions for the main effect of asynchronous visual feedback in the supramarginal (see 3a) and angular gyri (see 3b). Error bars indicate standard errors.

Figure 4: Mean bold responses across conditions for the independence model of agency (see 4a) and body-ownership (see 4b). Error bars indicate standard errors.

Table 1

Brain Regions	MNI Coordinates			Z-score	
	x	Y	z		
<i>Main Effect of Synchronous Stimulation (AS+PS)-(AA+PA)</i>					
L Cerebellum VI	-22	-54	-24	4.44	†
R Postcentral Gyrus (BA 5)	24	-40	54	4.15	†
R Postcentral Gyrus (BA7)	38	-42	58	3.72	†
R Cerebellum, Culmen	12	-48	-20	3.69	†
L Posterior Insula / Rolandic Operculum (BA13)	-44	-18	18	3.56	†
R Precuneus (BA31)	24	-72	36	3.46	†
<i>Main Effect of Asynchronous Stimulation (AA+PA)-(AS+PS)</i>					
R Inferior Parietal Lobule (BA 39)	42	-52	46	4.82	*
R Supramarginal Gyrus (BA 40)	52	-38	38	4.53	*
R Inferior Parietal Lobule (BA39) (Ag)	40	-58	26	4.44	*
L Insula (BA 13)	-38	20	2	4.01	†
L Cerebellum,Uvula	-16	-84	-26	3.88	†
L Cerebellum, Cerebellar Tonsil	-12	-62	-38	3.85	†
R Middle Frontal Gyrus (BA 10)	40	52	14	3.8	†
R Middle Orbital Gyrus	24	48	-14	3.56	†
R Middle Temporal Gyrus	50	-46	-2	3.51	†
R Inferior Frontal Gyrus (BA44)	60	20	6	3.5	†
<i>Main Effect of Active Movement (AS+AA)-(PS+PA)</i>					
R Cerebellum III	20	-58	-26	6.03	‡
L Cerebellum Crus 1	-40	-64	-28	5.43	‡

R Superior Parietal Lobule	32	-54	56	5.8	‡
R Inferior Parietal Lobule (BA 40)	40	-38	46	4.97	‡
R Precentral Gyrus (BA 6)	54	4	42	5.43	‡
R Middle Occipital Gyrus	52	-72	0	5.31	‡
L Inferior Parietal Lobule (BA 40)	-34	-38	46	5	‡
L Postcentral Gyrus (BA 3)	-38	-26	52	4.96	‡
L Middle Occipital Gyrus	-42	-86	4	4.3	‡
L Insula (BA 13)	-46	0	-2	4.2	‡
L Cingulate Gyrus (BA 24)	-22	-16	46	3.7	‡
L Putamen	-14	2	8	3.69	‡
L Precentral Gyrus (BA 6)	-54	-2	40	3.66	‡
R Cerebellum VIII	16	-62	-48	3.57	‡
R Middle Frontal Gyrus	44	36	36	3.54	‡
R Superior Frontal Gyrus (BA 8)	42	26	46	3.51	‡
R Inferior Frontal Gyrus	36	6	32	3.5	‡

Main Effect of Passive Movement (PS+PA) -(AS+AA)

R Precuneus	0	-58	22	4.72	‡
R Medial Frontal Gyrus (BA 10)	4	64	8	4.67	‡
L Anterior Cingulate (BA 32)	-4	50	-2	4.09	‡
R Superior Temporal Gyrus (BA 39)	60	-58	22	4.36	‡
L Medial Frontal Gyrus (BA 10)	-6	66	14	3.73	†
R Middle Temporal Gyrus (BA 39)	54	-72	24	3.46	†
L Precuneus	-4	-50	52	4.15	†
R Medial Frontal Gyrus	2	52	34	3.96	†
R Superior Frontal Gyrus (BA 9)	8	62	24	3.8	†

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L Superior Frontal Gyrus (BA 8)	-12	62	34	3.5	†
L Postcentral Gyrus	-26	-40	72	3.71	†
R Postcentral Gyrus	22	-48	76	3.39	†
L Middle Temporal Gyrus	-52	-64	24	3.37	†

Table 2

Brain Regions	MNI Coordinates			Z-score
	x	y	z	
<i>(AS-PS) exclusively masked by (AA-PA)</i>				
R Cerebellum (VI)	24	60	24	5.97
L Cerebellum (Crus 1)	-34	-68	30	5.70
R Precentral Gyrus (BA6)	54	4	38	5.14
R Anterior Insula	40	10	-2	4.95
R Precentral Gyrus (BA6)	38	-10	58	4.84
R Superior Parietal Lobule (BA2)	32	-58	58	4.68
L Postcentral Gyrus (BA3)	-36	-26	54	4.76
L Precentral Gyrus (BA6)	-38	-14	54	4.75
R Inferior Occipital Gyrus (BA19)	42	-82	0	4.69
L SMA (BA6)	-12	6	48	4.55
R SMA (BA6)	6	10	48	4.46
R SMA (BA6)	10	0	68	4.20
R Middle Frontal Gyrus (BA45)	52	44	14	4.44
L Superior Temporal Gyrus	-48	0	-2	4.31
L Inferior Parietal Lobule (BA40)	-36	-42	52	4.26
L Middle Occipital Gyrus (BA19)	-52	-78	6	3.70
L Middle Frontal Gyrus (BA44)	-34	14	38	4.06
R Superior Frontal Gyrus (BA8)	42	26	46	3.95
L precentral Gyrus (BA6)	-28	-10	62	3.90
L Thalamus	-22	-18	-4	3.87
L Precentral Gyrus (BA6)	-58	2	32	3.86
L Cerebellum	-16	-52	-50	3.74
R Middle Frontal Gyrus	36	50	30	3.62
<i>(PS-AS) exclusively masked by (PA-AA)</i>				
L Inferior Temporal Gyrus (BA20)	-58	-20	-34	4.69
L Fusiform gyrus (BA20)	-52	-12	-30	4.15
L Fusiform gyrus (BA20)	-64	-8	-28	3.74
L Superior Medial Gyrus (BA9)	-8	66	16	4.40

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R Superior Medial Gyrus (BA9)	8	62	24	4.40
L Superior Medial Gyrus (BA9)	-4	62	24	4.32
L Posterior Cingulate (BA23)	-2	-56	18	4.40
L Precunues (BA19)	-46	-68	48	4.05
R Middle Temporal Gyrus (BA41)	48	-38	0	3.96
R Fusiform Gyrus (BA20)	56	-14	-30	3.90
L Postcentral Gyrus (BA5)	-28	-38	74	3.78
L Cuneus (BA18)	-2	-86	28	3.77
L Precuneus (BA7)	-4	-50	52	3.66
L Cuneus (BA7)	2	-72	30	3.64
