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

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ABSTRACT

The exact relation between the sense that one's body is one's own (body-ownership) and the sense that one controls one's own bodily actions (agency) has been the focus of much speculation, but remains unclear. On an 'additive' model, agency and body-ownership are strongly related; the ability to control actions is a powerful cue to body-ownership. This view implies a component common to the senses of body-ownership and agency, plus possible additional components unique to agency. An alternative 'independence' model 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. Activations in midline cortical structures were associated with a sensory-driven sense of body-ownership, and were absent in agency conditions. Activity in the pre-SMA was linked to the sense of agency, but distinct from the sense of body-ownership. No shared activations that would support the additive model were found. The results support the independence model. Body-ownership involves a psychophysiological baseline, linked to activation of the brain's default mode network. Agency is linked to premotor and parietal areas involved in generating motor intentions and subsequent action monitoring.

1. Introduction

The basic embodied sense of self is a complex conscious state, with several dissociable components (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008). Among these are the sense of ownership of one's body (i.e., body-ownership), and also the sense of agency over one's own actions (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007; Tsakiris, Schütz-Bosbach, & Gallagher, 2007). The feeling that the body I inhabit is 'my own', and ever-present in my mental life, is called body-ownership (Tsakiris, 2010). My body is an integral part of 'me', in a way that other objects are not. Moreover, the relation between my body and 'me' is quite different from the relation between my body and other people (Descartes, 1637/2006). In contrast, the feeling that I can move and control my body is called the sense of agency. The sense of agency gives a special phenomenal quality to self-generated motor actions and external events caused by those actions. For example, the relationship between my actions and 'me' differs from the relation between observed actions carried out by other agents or without my voluntary control (de Vignemont & Fourneret, 2004).

The sense of body-ownership is normally continuous and omnipresent. Thus, we experience body-ownership not only during voluntary actions, but also during passive movement and at rest (van den Bos & Jeannerod, 2002). In contrast, only voluntary actions should produce a sense of agency. Several studies confirm that agency is closely linked to the generation of efferent motor signals and the monitoring of their effects (e.g., Blakemore, Wolpert, & Frith, 2002). In contrast, the sense of body-ownership can be induced by afferent sensory signals alone (Botvinick & Cohen, 1998). However, the exact relation between agency and body-ownership remains unknown. On one view, the relation between agency and body-ownership is additive, meaning that agency entails body-ownership. This view follows from the observation that one can control movements of one's own body, but not other objects, at will (Descartes, 1637/2006). Thus, agency offers a strong cue to body-ownership. On this view, the sense of agency should involve the sense of body-ownership, plus a possible additional experience of voluntary control. An alternative view holds that sense of agency and sense of body-ownership are qualitatively different experiences, without any common component.

Previous accounts based on introspective evidence favour the additive model, since they identified a common sense of body-ownership, plus an additional component unique to action control

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(Longo & Haggard, 2009). Recent behavioural and neuroimaging studies have also focused on the neurocognitive processes that underpin body-ownership and agency (Ehrsson, Spence, & Passingham 2004; Farrer & Frith, 2002; Farrer et al., 2003; Fink et al., 1999; Tsakiris, Hesse, et al., 2007), but the exact neural bases of these two aspects of self-consciousness remain unclear. For example, neuroimaging studies that investigated the sense of body-ownership using the Rubber Hand Illusion (RHI, see Botvinick & Cohen, 1998) report activations in the bilateral premotor cortex and the right posterior insula associated with the illusion of ownership of the rubber hand, and present only when visual and tactile stimulations are synchronized (Ehrsson et al., 2004; Tsakiris, Hesse, et al., 2007). Studies investigating the neural signatures of the sense of agency have used similar methods, such as the systematic manipulation of visual feedback to alter the experience of one's body in action. Activity in the right posterior insula was correlated with the degree of match between the performed and viewed movement, and thus with self-attribution (Farrer et al., 2003). Conversely, activity in the right dorsolateral prefrontal cortex (Fink et al., 1999; Leube, Knoblich, Erb, & Kircher, 2003), right inferior parietal lobe and temporoparietal junction (Farrer et al., 2003, 2008) was associated with degree of disparity between performed and viewed movement, and thus with actions not attributed to the self.

These studies were largely based on manipulating visual feedback to either match or mismatch the participant's manual action. However, such manipulations cannot separate the contributions of efferent and afferent signals that are both inevitably present in bodily action. These imaging data of these studies may therefore confound the neural correlates of agency and body-ownership. For example, with undistorted visual feedback of an action, there is a three-way match between efferent motor commands, afferent proprioceptive signals, and vision. Thus, any effects seen in such conditions could be due to congruence between (a) efferent and proprioceptive signals, (b) efferent signals and visual feedback, (c) proprioceptive signals and visual feedback, or (d) some complex interaction of all three signals. Conversely, when visual feedback is distorted (spatially or temporally), there is sensorimotor conflict between efferent signals and vision, but also intersensory conflict between proprioceptive and vision. As a result, any differences between match and mismatch conditions could reflect sensorimotor comparisons (relating to sense of agency) or proprioceptive–visual comparisons (relating to sense of body-ownership). As a result, such experimental designs cannot distinguish between the additive and the independence model of agency and body-ownership.

However, the senses of agency and body-ownership 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. In particular, voluntary action depends on a cascade of preparatory cognitive-motor processes within the brain's frontal lobes (Haggard, 2008). These preparatory processes contribute to our sense of agency over the action and its subsequent external effects, but are absent during passive movement. Comparing active with passive movements experimentalises Wittgenstein's (1953/1958) question (p. 621): "what is left over if I subtract the fact that my arm goes up from the fact that I raise my arm?" This approach 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.

Here we sought to disentangle the neural basis of the relation between the sense of body-ownership and agency using fMRI. We manipulated body-ownership by presenting real-time or delayed visual feedback of movements, and agency, by comparing voluntary and passive movements. Synchronous visual feedback causes body-parts and bodily events to be attributed to one's own self (Longo & Haggard, 2009). This factorial design effectively operationalizes the senses of agency and body-ownership; the passive movement condition with synchronous visual feedback is a canonical condition producing body-ownership (Tsakiris, Prabhu, & Haggard, 2006), and the active movement condition with synchronous visual feedback is a canonical condition producing agency (Longo & Haggard, 2009). To investigate the relation between body-ownership and agency, we aimed to test two specific models. The first, additive model, holds that agency entails body-ownership. On this view, active movements of the body should produce both a sense of body-ownership and a sense of agency. The feeling of being in control of one's body should involve the sense of body-ownership, plus an additional sense of agency. This produces three concrete predictions about brain activations in agency and ownership conditions (see also Table 1): first there should be some activations common to conditions that produce agency and body-ownership. Second, there should be an additional activation in the condition that produces agency, which is absent from the condition that produces body-ownership. Third, there should be no activation in the condition that produces body-ownership that is not also present in the condition that produces agency. A second model, the independence model, holds that sense of agency and sense of body-ownership are qualitatively different experiences, without any common component. On this view, the brain could contain distinct networks for sense of body-ownership and sense of agency. The independence model produces three concrete predictions: first, there should be no common activations between conditions that produce agency and ownership. Second, there should be specific activations in conditions producing a sense of agency that are absent from other conditions. Third, there should be a specific activation in conditions that produce ownership without agency that are absent from condition inducing agency.

2. Materials and methods

2.1. Experimental design

A 2 × 2 factorial design was used. 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, 500 ms video delay). In the 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 the 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).

2.2. Experimental set-up and methods

The methods were based on a previous behavioural study (Tsakiris et al., 2006) with modifications appropriate for the fMRI scanning environment. Whilst the brain scans were being performed, the participant rested comfortably in a supine position on the bed in the MRI scanner. All participants wore headphones to reduce noise and to communicate with the experimenters between runs. Within the cylindrical head coil, the head was tilted approximately 20–30° by placing foam wedges underneath. To reduce potential head movements, we fixed the position of the head using foam pads. The natural direction of gaze was oblique so that the participants saw a projection screen attached to the bore of the scanner through direct vision without discomfort. The participant's right arm was placed on a tilted (30–45°) plastic table that was positioned over the stomach of the participant, in a relaxed position. The table was covered with a soft black material. Participants did not have direct vision of their hand.

A mirror was placed above the participant's hand at approximately 45° angle and a colour MRI-compatible video camera recorded the mirror image of the participant's right 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 an irreducible delay of approximately 100 ms due to digitisation and projection of the image. In the asyn-

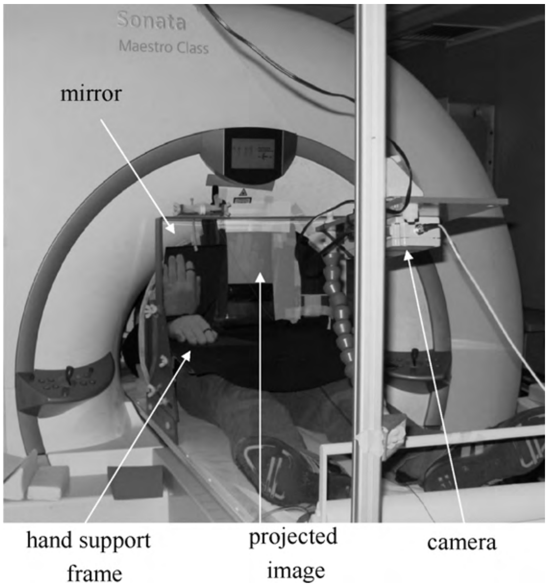

Fig. 1. The experimental set-up in the fMRI suite.

chronous 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, Frith, & Wolpert, 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 (Fig. 1).

There were three functional runs. Each run began with 15 s 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 4 s of written instructions (‘Passive’ or ‘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 s. Following each block, there was a rest period of 25 s 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, and once the participants were outside the MRI suite, they were asked to rate their agreement or disagreement with ten statements concerning their experience during the various conditions of the fMRI experiment (see Table 2). 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.

2.3. *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 to 100) as assessed by the Edinburgh Inventory (Oldfield, 1971). The study was approved by the local ethics committee. One participant was excluded because of large head-movement artefacts. The analyses reported refer to the 19 remaining participants.

2.4. *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 3 mm 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 participant 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 unwraped to correct for head movements. The voxel size of normalized images was 2 mm × 2 mm × 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 participant, we fitted a linear regression model (general linear model) to the data (first-level analysis). First-level analyses were conducted for each participant 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 (see Results section), 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 results of this analysis were contrast estimates for each condition from each of the 19 participants (contrast images). To accommodate inter-subject variability, the contrast images from all participants were entered into a random effect group analysis (second level analysis) using a 2 × 2 factorial (movement [active, passive], synchrony [synchronous, asynchronous]) analysis of variance (ANOVA). Brain activity localization was identified using the atlas of neuroanatomy by Duvernoy (1999) and the SPM anatomy toolbox (Eickhoff et al., 2005).

To analyse the main effects of our experimental manipulations, 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 similarly computed 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 (Farrer et al., 2008). 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. Exclusive masking procedures identify clusters that are active for one contrast but not for the other, while inclusive masking procedures allow for the identification of clusters that are active for both contrasts.

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, expressed as [(AS − PS) − (AA − PA)], does not specifically isolate such activations, 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, and absent from the PA condition, we instead 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.

The two models make one common prediction, that the AS condition should involve an activation unique to agency (see Table 1). More importantly, the models also make two divergent predictions. The independence model predicts some activation 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.

Table 1
The respective predictions of the additive and independence models, along with the masking contrasts used to test them.

	"Additive Model" Predictions	"Independence Model" Predictions	Contrasts used to test each hypothesis
1	There should be an additional activation in agency, which is absent from body-ownership.		(AS – PS) masked *exclusively* by (AA – PA)
2	There should be no activation in the body-ownership that is not also present in agency.	There should be a specific activation in body-ownership that is absent from agency.	(PS – AS) masked *exclusively* by (PA – AA)
3	There should be some activations common to agency and body-ownership.	There should be no common activations between agency and ownership.	(AS – AA) masked *inclusively* with (PS – PA)

3. Results

3.1. Subjective reports

The mean ratings for the body-ownership questions per condition were submitted to a 2 × 2 ANOVA with the two factors of movement (i.e., active vs. passive movement) and feedback (i.e., synchronous vs. asynchronous) (see Table 2 and Fig. 2). There were significant main effects of type of movement and feedback ($F(1,18) = 17.48$, $p < 0.05$) and $F(1,18) = 28.25$, $p < 0.05$, respectively). The interaction between the two factors, however, was not significant ($F(1,18) = 0.1$, $p > 0.05$). 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 (i.e., that the viewed image is linked to one's own body), uncontaminated by sense of agency. Active movement with synchronous feedback also elicited a significantly stronger sense of body-ownership than the equivalent passive movement condition ($t(18) = 4.4$, $p < 0.05$).

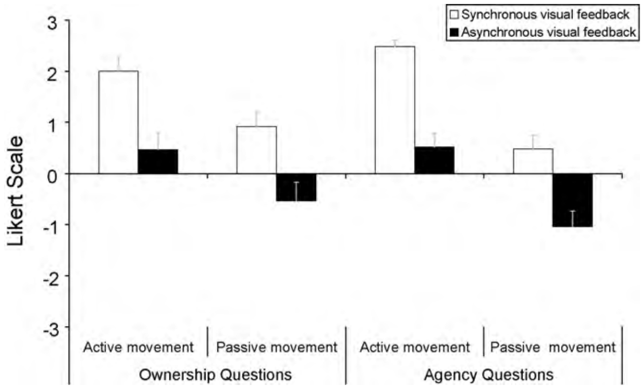

Fig. 2. Psychometric data. Error bars indicate standard errors.

The mean ratings for the agency questions were analysed with a 2 × 2 ANOVA with the two factors of movement (i.e., active vs. passive movement) and feedback (i.e., synchronous vs. asynchronous). There were significant main effects of type of movement and feedback ($F(1,18) = 40.85$, $p < 0.05$) and $F(1,18) = 64.61$, $p < 0.05$, respectively). The interaction between the two factors was also significant ($F(1,18) = 4.35$, $p = 0.05$). This interaction shows that the feeling that one can voluntarily control the body at will is selectively present in the AS condition. As predicted, active movement with synchronous feedback elicited a significantly stronger sense of agency than the equivalent passive movement condition ($t(18) = 7.1$, $p < 0.0001$).

3.2. Number of movements

The total number of movements performed in each condition by each subject was counted after the experiment by observation of the recorded videos. The mean number of movements

Table 2
Mean responses (plus SD) to subjective report questionnaire.

Questionnaire item:		Synchronous		Asynchronous	
	"During the block there were times when. . ."	Active	Passive	Active	Passive
1	". . .it felt like the hand I was looking at was my own hand." (Ownership)	2.42 (*1.17*)	1.58 (*1.22*)	1.11 (*1.66*)	−0.03 (*2.03*)
2	". . .it felt like the hand I was looking at wasn't mine." (Ownership)	−1.79 (*1.51*)	−0.47 (*1.58*)	0.16 (*1.71*)	1.05 (*1.75*)
3	". . .it felt like the hand I was looking at was somebody else's hand." (Ownership)	−1.74 (*1.63*)	−0.63 (*1.67*)	−0.42 (*1.77*)	0.61 (*1.89*)
4	". . .it felt like I was in control of the hand I was looking at." (Agency)	2.74 (*.56*)	0.42 (*1.92*)	0.63 (*1.57*)	−1.42 (*1.77*)
5	". . .it felt like I could move the hand I was looking at if I wanted." (Agency)	2.58 (*.61*)	1.16 (*1.83*)	0.84 (*1.54*)	−0.29 (*1.98*)
6	". . .it felt like the hand I was looking at was out of my control." (Agency)	−2.11 (*1.05*)	.21 (*1.69*)	−0.05 (*1.75*)	1.58 (*1.54*)
7	". . .it felt like my hand was somewhere between the table and the location where the video image was projected."	−0.42 (*1.98*)	−0.26 (*1.91*)	−0.63 (*1.77*)	−0.58 (*1.68*)
8	". . .it felt like I could not really tell where my hand was."	−1.47 (*1.81*)	−0.37 (*2.09*)	−0.74 (*2.00*)	0.26 (*2.13*)
9	". . .it felt like my hand was in the location where the video image was projected."	0.47 (*2.20*)	0.26 (*1.91*)	−0.42 (*1.80*)	−0.63 (*1.83*)
10	". . .it felt like I was looking directly at my hand, rather than at a video image."	0.37 (*2.17*)	−0.37 (*1.86*)	−1.42 (*1.54*)	−1.82 (*1.45*)

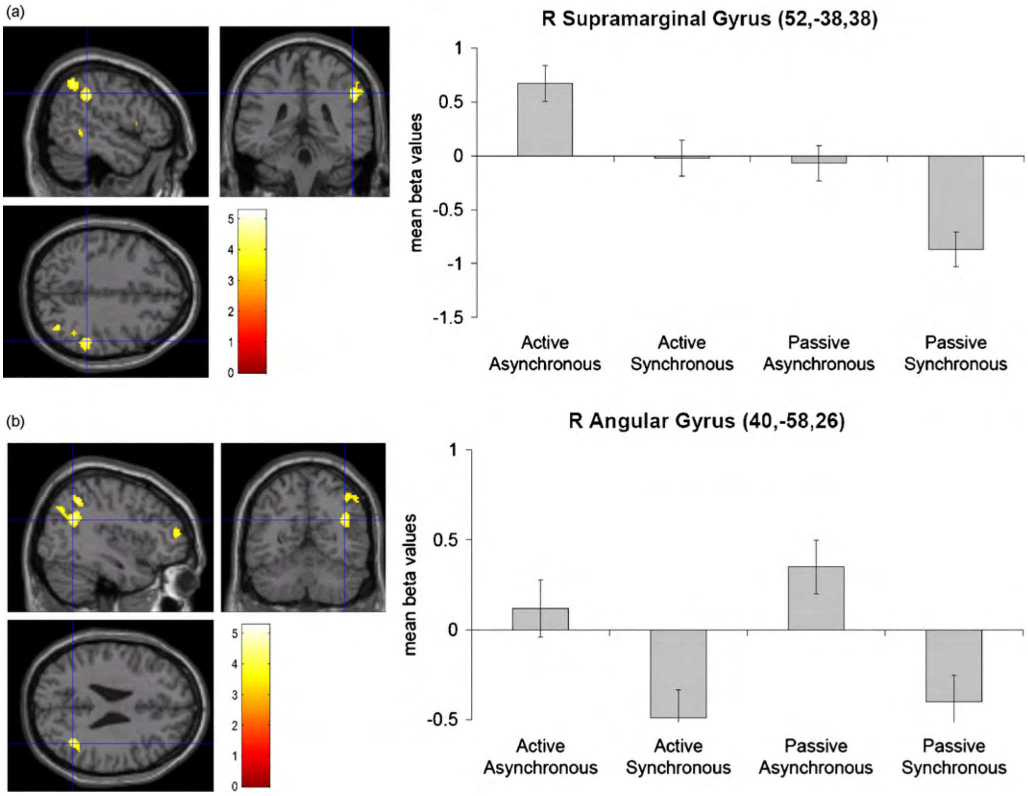

Fig. 3. Mean bold responses across conditions for the main effect of asynchronous visual feedback in the supramarginal (a) and angular gyri (b). Error bars indicate standard errors.

performed in each condition was analysed using a 2 × 2 ANOVA with the two factors of movement (i.e., active vs. passive movement) and feedback (i.e., synchronous vs. asynchronous). 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.

3.3. *fMRI data*

3.3.1. *Main effects*

First, we investigate the main effects of movement type and visual feedback. Table 3 shows the local maxima of brain areas with increased neural activity assessed for the main effects of the experimental design.

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

The main effect of synchronous 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 Fig. 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 (Fig. 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 (Fig. 3b). Therefore, the supramarginal gyrus may code for sensorimotor conflicts, while the angular gyrus may code for intersensory conflicts.

3.4. *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 4 shows the local maxima of brain areas that were active for this contrast, including the right superior parietal cortex, the pre-supplementary motor area (see Fig. 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 by 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.

In addition to this core, several other areas are listed in Table 4. Not all of these are discussed here, because of the risk of overinterpretation. However, some of these additional activations, such

Table 3
Transformed *Z* scores from an SPM{F} for the main effects.

Brain regions	MNI coordinates			*Z* score	K_E	
	x	*y*	*z*			
Main effect of synchronous stimulation $(AS + PS) - (AA + PA)$						
L Cerebellum VI	−22	−54	−24	4.44	77	†
R Postcentral Gyrus (BA 2)	24	−40	54	4.15	71	†
R Postcentral Gyrus (BA2)	38	−42	58	3.72	35	†
R Cerebellum, Culmen	12	−48	−20	3.69	20	†
L Posterior Insula/Rolandic Operculum (BA13)	−44	−18	18	3.56	33	†
R Precuneus (BA31)	24	−72	36	3.46	12	†
Main effect of asynchronous stimulation $(AA + PA) - (AS + PS)$						
R Angular Gyrus (BA39)	40	−58	26	4.82	634	b
R Supramarginal Gyrus (BA 40)	52	−38	38	4.53	156	b
L Insula (BA 13)	−38	20	2	4.01	43	†
L Cerebellum, Uvula	−16	−84	−26	3.88	32	†
L Cerebellum, Cerebellar Tonsil	−12	−62	−38	3.85	70	†
R Middle Frontal Gyrus (BA 10)	40	52	14	3.8	51	†
R Middle Orbital Gyrus	24	48	−14	3.56	22	†
R Middle Temporal Gyrus	50	−46	−2	3.51	14	†
R Inferior Frontal Gyrus (BA44)	60	20	6	3.5	54	†
Main effect of active movement $(AS + AA) - (PS + PA)$						
R Cerebellum III	20	−58	−26	6.03	4330	a
L Cerebellum Crus 1	−40	−64	−28	5.43		a
R Superior Parietal Lobule	32	−54	56	5.8	1995	a
R Inferior Parietal Lobule (BA 40)	40	−38	46	4.97		a
R Precentral Gyrus (BA 6)	54	4	42	5.43	2952	a
R Middle Occipital Gyrus	52	−72	0	5.31	789	a
L Inferior Parietal Lobule (BA 40)	−34	−38	46	5	836	a
L Postcentral Gyrus (BA 3)	−38	−26	52	4.96		a
L Middle Occipital Gyrus	−42	−86	4	4.3	316	a
L Insula (BA 13)	−46	0	−2	4.2	114	a
L Cingulate Gyrus (BA 24)	−22	−16	46	3.7	12	a
L Putamen	−14	2	8	3.69	20	a
L Precentral Gyrus (BA 6)	−54	−2	40	3.66	106	a
R Cerebellum VIII	16	−62	−48	3.57	23	a
R Middle Frontal Gyrus	44	36	36	3.54	165	a
R Superior Frontal Gyrus (BA 8)	42	26	46	3.51	12	a
R Inferior Frontal Gyrus	36	6	32	3.5	15	a
Main effect of passive movement $(PS + PA) - (AS + AA)$						
R Precuneus	0	−58	22	4.72	760	a
R Medial Frontal Gyrus (BA 10)	4	64	8	4.67	490	a
L Anterior Cingulate (BA 32)	−4	50	−2	4.09		a
L Medial Frontal Gyrus (BA 10)	−6	66	14	3.73		†
R Superior Temporal Gyrus (BA 39)	60	−58	22	4.36	112	a
R Middle Temporal Gyrus (BA 39)	54	−72	24	3.46		†
L Precuneus	−4	−50	52	4.15	57	†
R Medial Frontal Gyrus	2	52	34	3.96	143	†
R Superior Frontal Gyrus (BA 9)	8	62	24	3.8		†
L Superior Frontal Gyrus (BA 8)	−12	62	34	3.5		†
L Postcentral Gyrus	−26	−40	72	3.71	42	†
R Postcentral Gyrus	22	−48	76	3.39	13	†

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.

[a] FDR

[b] SVC.

[†] $p < 0.001$ uncorrected.

as the left inferior temporal gyrus, have previously been found in other studies of self-consciousness. For example, Vogeley et al. (2004) found activation in this area for events viewed in first-person compared to third-person perspective. Similarly, we found an agency-specific activation in the right Anterior Insula. Activations in this area were found when participants judged visual feedback as congruent with their own action (Farrer & Frith, 2002). Interestingly, anterior insula activation is also associated with the marking of subjective time (for a review see Craig, 2009), distortions of which are an established feature of agency (Haggard, Clark, & Kalogers, 2002). The role of this area in self-consciousness is also confirmed by its activation for visual recognition of one's own face (Devue et al., 2007), while lesion in the mid-posterior insula has been linked to anosognosia for hemiplegia (Karnath, Baier & Nagele, 2005), and somatoparaphrenic delusions (Baier & Karnath, 2008; see also Tsakiris, Hesse, et al., 2007).

3.5. *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.

Table 4
Transformed Z scores from an SPM$\{F\}$ for the planned comparisons for the independence models of agency and body-ownership.

Brain regions	MNI coordinates			Z score	K_E
	x	y	z		
Additional activations for agency not present for body-ownership (AS – PS) exclusively masked by (AA – PA)					
R Cerebellum (VI)	24	60	24	5.97	1972
L Cerebellum (Crus 1)	−34	−68	30	5.70	1016
R Precentral Gyrus (BA6)	54	4	38	5.14	1072
R Anterior Insula	40	10	−2	4.95	352
R Precentral Gyrus (BA6)	38	−10	58	4.84	614
R Superior Parietal Lobule (BA7)	32	−58	58	4.68	
L Postcentral Gyrus (BA3)	−36	−26	54	4.76	337
L Precentral Gyrus (BA6)	−38	−14	54	4.75	
R Inferior Occipital Gyrus (BA19)	42	−82	0	4.69	263
L SMA (BA6)	−12	6	48	4.55	620
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	123
L Superior Temporal Gyrus	−48	0	−2	4.31	69
L Inferior Parietal Lobule (BA40)	−36	−42	52	4.26	169
L Middle Occipital Gyrus (BA19)	−52	−78	6	3.70	56
L Middle Frontal Gyrus (BA44)	−34	14	38	4.06	34
R Superior Frontal Gyrus (BA8)	42	26	46	3.95	18
L precentral Gyrus (BA6)	−28	−10	62	3.90	28
L Thalamus	−22	−18	−4	3.87	
L Precentral Gyrus (BA6)	−58	2	32	3.86	51
L Cerebellum	−16	−52	−50	3.74	14
R Middle Frontal Gyrus	36	50	30	3.62	15
Specific activations for body-ownership not present for agency (PS – AS) exclusively masked by (PA – AA)					
L Inferior Temporal Gyrus (BA20)	−58	−20	−34	4.69	138
L Fusiform gyrus (BA20)	−52	−12	−30	4.15	
L Fusiform gyrus (BA20)	−64	−8	−28	3.74	
R Superior Medial Gyrus (BA9)	8	62	24	4.40	536
L Superior Medial Gyrus (BA9)	−8	66	16	4.40	
L Superior Medial Gyrus (BA9)	−4	62	24	4.32	
L Posterior Cingulate (BA23)	−2	−56	18	4.40	195
L Precunues (BA19)	−46	−68	48	4.05	12
R Middle Temporal Gyrus (BA41)	48	−38	0	3.96	11
R Fusiform Gyrus (BA20)	56	−14	−30	3.90	22
L Postcentral Gyrus (BA5)	−28	−38	74	3.78	16
L Cuneus (BA18)	−2	−86	28	3.77	11
L Precuneus (BA7)	−4	−50	52	3.66	10
L Cuneus (BA7)	2	−72	30	3.64	23

Each contrast and its mask were thresholded at $p < 0.0005$ and $k > 10$ voxels. L/R: left and right hemispheres.

3.6. *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 underlying 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 4). Brain areas that were uniquely activated in the PS condition included medial anterior and posterior brain areas such as the superior medial gyrus (see Fig. 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.

4. Discussion

We investigated the neural signatures of the sense of agency and sense of body-ownership. 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. Previous studies showed that temporal congruency between different sensory modalities can cause a sense of body-ownership in purely sensory situations such as the RHI (e.g., Botvinick & Cohen, 1998; Longo et al., 2008; Tsakiris & Haggard, 2005). Temporal congruency between sensory and motor signals can produce a sense of agency during voluntary movement (Longo & Haggard, 2009; Tsakiris et al., 2006). Analysis of 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 the 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 angular and supra-

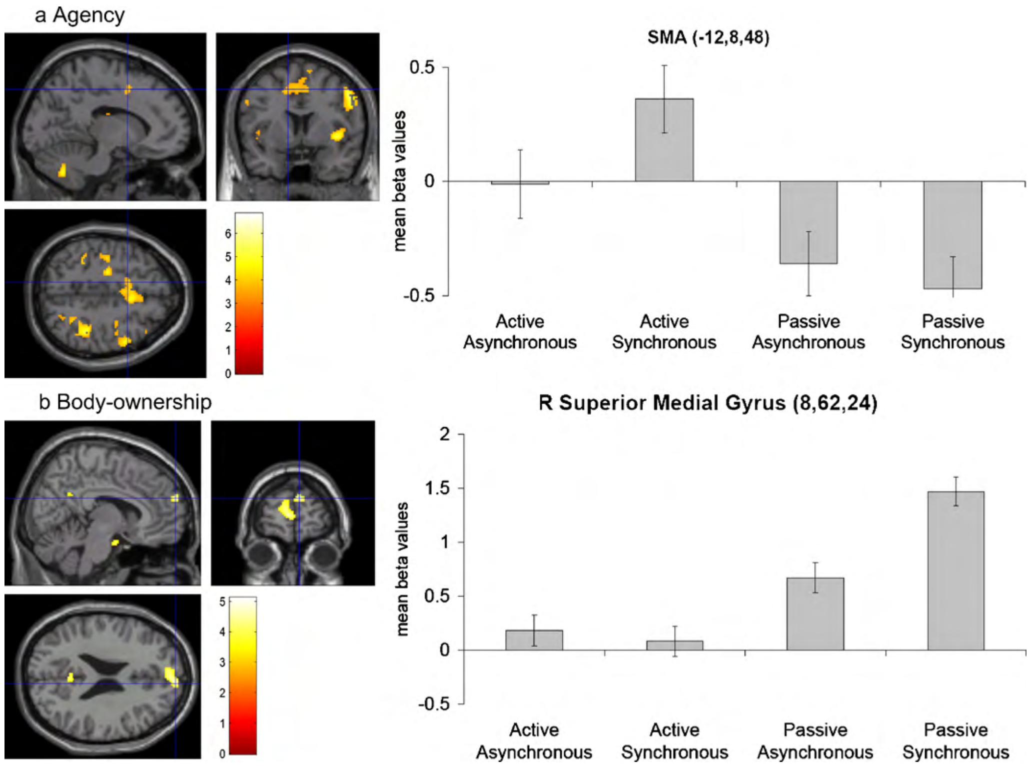

Fig. 4. Mean bold responses across conditions for the independence model of agency (a) and body-ownership (b). Error bars indicate standard errors.

marginal gyri. Interestingly, the profile of mean beta values in these clusters was not homogeneous (see Fig. 3). Activation of the supramarginal gyrus was most prominent when active movements were presented in asynchronous display (i.e., AA condition), while the angular gyrus was activated when both active and passive movements were presented in asynchronous display (i.e., for both the AA and PA conditions). This pattern extends previous findings (Balslev et al., 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 sense of agency, because of the selective response of this area to discrepancy between *active* movement and visual feedback. It is unlikely that is activation was caused simply by a conflict between proprioceptive and visual signals as this was also present in the passive movement condition. A recent study (Farrer et al., 2008) showed a key role of the right angular gyrus in action awareness. 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 the angular gyrus showed comparable activity for both the AA and PA conditions, 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 sensorimotor conflicts that may result in the experience of non-agency, while the angular gyrus is activated during intersensory conflicts that may result in a loss of body-ownership (see also Shimada, Hiraki, & Oda, 2005).

Timing information alone cannot distinguish the sense of body-ownership from the sense of agency, or identify the relation between them. According to the additive model, a similar sense of body-ownership would be present both for active and passive movement conditions with synchronous visual feedback, but the sense of agency would additionally be present following voluntary movements. Interestingly, the *introspective* evidence broadly supported the additive view: participants reported significantly more agreement with questionnaire items reflecting agency in the AS condition compared to the other three conditions. In particular, 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). 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.

Thus, neuroimaging data supported an independence model, while questionnaire data supported an additive model. This somewhat surprising inconsistency may be explained in at least two distinct ways. First, the questionnaire data may reflect a limitation of the folk psychological concepts used to describe our embodied experience during sensation and movement. Folk psychology suggests that agency is a very strong cue for ownership, so that I experience ownership over more or less any events or object that I control. However, the experience of ownership of action during agency may represent a distinctive type of ownership that should not be necessarily conflated with ownership of sensations or body-parts. For example, Marcel distinguished between attributing an action to one's self, and attributing the intentional source of the action to one's self. Patients with anarchic hand have a clear sense that their involuntary movements are their own, but they strongly deny intending them (Marcel, 2003). Since the patients often themselves report this dissociation as surprising, folk psychology may not adequately capture the difference between ownership of intentional action and ownership of bodily sensation. Second, the apparent dissociation between neural activity and introspective reports may suggest that there is not a one-to-one mapping between brain activity and conscious experience. In our data, qualitatively similar subjective experiences of ownership appear to be generated by quite different brain processes in the PS and AS condition. In particular, our finding of activations 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. Models involving a single neural correlate of each specific consciousness experience have been highly successful in the study of individual sensory percepts, particularly in vision (Haynes & Rees, 2006). However, the aspects of self-consciousness which we call sense of body-ownership and sense of agency are not unique elemental percepts or qualia in the same way. Rather, they may be a cluster of subjective experiences, feelings and attitudes (Synofzik, Vosgerau, & Newen, 2008). Our data suggest identifying neural correlates of these kinds of experience may be more problematic than identifying neural correlates of single percepts.

The specific brain areas associated with agency and with ownership shed further light on these two components of self-consciousness. The pre-SMA is strongly involved in the voluntary control of action (Goldberg, 1985), and contributes to the experience of volition itself (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 sense of agency. The role of pre-SMA in the present experiment could either reflect an advance intention-based prediction of the sensory feedback of action, or a delayed postdictive attribution of sensory feedback to the self. Our fMRI data lack the temporal resolution to decide between these two alternatives. 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, & Toglia 1981). Despite the autonomous behaviour of the affected hand, these patients retain a sense of body-ownership 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.

In relation to a purely sensory-driven body-ownership, 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 for the bodily self appears to have a neural basis quite distinct from that for volition.

To conclude, the present experiment contrasted two alternative models of the relation between body-ownership and agency. While the analysis of the introspective reports lends support to the additive model, the analysis of the fMRI data show support for the independence model. Activity in premotor areas (pre-SMA and BA6) was associated with the sense of agency, while activity in midline cortical structures was associated with a purely sensory-driven sense of body-ownership. In addition, the analysis showed no shared activations between the two. This apparent dissociation between agency and body-ownership is further supported by the literature on the anarchic hand syndrome (Della Sala, Marchetti, & Spinnler, 1994; Marcel, 2003). Such patients report a lack of sense of agency over the anarchic hand, while they do retain a sense of body-ownership. Interestingly, the reverse dissociation, whereby people would experience agency, but not body-ownership, is harder to envisage. However, cases of patients with anosognosia with hemiplegia who also display somatoparaphrenic delusions may represent one such case. When the examiner asks the patient to look at her arm and report whose hand is this, the patient would say that this arm belongs to someone else (Vallar & Ronchi, 2009) However, if the patient is asked whether she can move her left arm, she would deny paralysis and report her ability to move voluntarily, displaying a non-veridical awareness of her agency (Fotopoulou et al., 2008). Note, however that anosognosia for hemiplegia can also dissociate from somatoparaphrenia (Cutting, 1978). Interestingly, recent lesion mapping studies show that the critical lesion site for anosognosia for hemiplegia is the right premotor cortex (BA6 and BA44, see Berti et al., 2005), while the critical lesion sites for somatoparaphrenia symptoms may involve the temporoparietal cortex and the posterior insula (Baier & Karnath, 2008; Vallar & Ronchi, 2009). Studies of deafferentation also support the dissociation between agency and body-ownership. IW's performance in agency tasks (Haggard & Cole, 2007) suggests that his sense of agency is normal, while his sense of his own body is clearly dramatically affected, as illustrated both by his subjective reports (Cole, 1995) and by his difficulty in using his own somatosensory experiences as a reference to understand others (Bosbach, Cole, Prinz, & Knoblich, 2005). Taken together, the results of the present study suggest a qualitative distinction between the brain bases of sense of agency and sense of body-ownership, consistent with the neuropsychological literature. Different neural networks appear to underlie our experience of embodiment in sensation and in action, even though the experiences themselves have common elements. There are many cases in psychology where quite different mechanisms can be enlisted for a common behavioural or perceptual goal: reading by words and reading by letters are the best known example. Our findings suggest that the unified experience of one's own body may similarly depend on two quite different neural mechanisms. How the various networks reported in the literature interact to produce the unity of bodily self-consciousness that characterises everyday life, and that appeared in our participants' subjective reports, remains a key topic for future research.

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