That's not quite me: limb ownership encoding in the brain

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Abstract

With congruent stimulation of one's limb together with a fake counterpart, an illusory self-attribution of the fake limb can be induced. Such illusions have brought profound insights into the cognitive and neuronal mechanisms underlying temporary changes in body representation, but to put them in perspective, they need to be compared with ownership as experienced for one's real body. We used functional magnetic resonance imaging (fMRI) to compare the neuronal correlates of touch under different degrees of body ownership. Participants' left and right arms were stimulated either alone or together with a fake counterpart while this stimulation was synchronous, ambiguous or asynchronous. Synchronous stimulation induced illusory fake arm ownership, but the brain still differentiated between touch to one's real arm and to an illusory 'owned' arm: the degree of arm ownership was encoded positively by activity in the ventromedial prefrontal cortex and lateral occipitotemporal cortex and negatively in the temporoparietal cortex. Conversely, the ventral premotor cortex responded more strongly to synchronous stimulation compared with asynchronous stimulation and with real arm only stimulation. These results offer new insights into the differential representation of the real body *vs* a body that is temporarily self-attributed following the resolution of multisensory conflict.

Key words: body representation; ownership; rubber hand illusion; self-other distinction; touch

Introduction

The sense of having a body is one of the most basic conditions for self-awareness (Gallagher, 2000; Blanke and Metzinger, 2009; Tsakiris, 2010; Ehrsson, 2012). Although of such apparent importance, this sense of body 'ownership' can be easily manipulated in most individuals: synchronous touch applied to one's hidden hand together with a visible fake counterpart is a reliable way to induce a self-attribution or feeling of ownership of the fake hand, known as the rubber hand illusion (RHI, Botvinick and Cohen, 1998). Initially, this stimulation produces a crossmodal conflict by vision of the touch occurring on the fake hand and simultaneous somatosensation on the real hand (Makin *et al.*, 2008; Macaluso and Maravita, 2010). The RHI then results from the resolution of this conflict via integration ('binding together') of the simultaneously occurring seen and felt touches into one perceptual event—the touch 'felt' on the now self-attributed fake hand—which seems to involve a network comprising multisensory areas in the frontal, parietal and occipitotemporal cortex (Ehrsson *et al.*, 2004; Tsakiris and Haggard, 2005; Costantini and Haggard, 2007; Tsakiris *et al.*, 2007; Petkova *et al.*, 2011; Blanke, 2012; Gentile *et al.*, 2013; Limanowski and Blankenburg, 2015).

The interpretation of the RHI as a manipulation of body ownership implies that after induction, the body representation is updated so that the fake hand is represented as one's own. However, the change in body representation induced by the RHI is only a temporary solution to an unusual crossmodal conflict, which requires 'ignoring' some bodily information such as proprioceptive information about one's real hand's location (Botvinick and Cohen, 1998; Zeller *et al.*, 2014). Correspondingly, the behavioral effects of the RHI are typically only partial, e.g. participants mislocalize their real hand merely toward the fake hand instead of at the fake hand's location (Tsakiris and

Haggard, 2005). This may suggest that the RHI is not a completely 'convincing' recalibration of one's body representation. How then, if at all, does the brain's representation of such a temporary illusory body differ from the representation of one's lifelong owned body? Here, we addressed this question by comparing the neuronal correlates of touch to one's real arm (RA) with touch to a fake arm (FA) that is perceived as one's own due to an induced ownership illusion. We used an automated setup to stimulate our participants' left and right arms inside an fMRI scanner, either alone or together with a FA of corresponding laterality. We hypothesized that experienced arm ownership would be strongest during stimulation of one's RA. Further, we expected that synchronous, but not asynchronous, stimulation of RA and FA would induce illusory arm ownership (the RHI). We additionally introduced a mixed condition, in which touch to the RA and the FA was synchronous at one anatomical location and asynchronous at another one, speculating that this ambiguous input would be perceptually different from purely synchronous or asynchronous stimulation. In a first exploratory step, we looked for touch-related brain activity that would systematically co-vary with the degree of arm ownership, i.e. decrease or increase from stimulation of one's RA through synchronous, ambiguous and asynchronous FA stimulation. Second, we looked for brain activity specific to multisensory integration processes thought to underlie the updating of body representation in the RHI. During the RHI, the synchronously occurring seen and felt touches are integrated, whereas during asynchronous stimulation, the seen and felt touches are clearly attributable to two different hands based on their temporal discrepancy (Botvinick and Cohen, 1998; Ehrsson, 2012; Hohwy, 2012). During touch to one's real body, the seen and felt touch naturally correspond, and there is no need to resolve crossmodal conflicts. Therefore our second hypothesis was that brain areas involved in integrating multisensory body-related information during the RHI would show stronger responses during synchronous, compared with asynchronous FA stimulation and compared with RA stimulation alone. Finally, work in monkeys has demonstrated that the fronto-parietal brain areas implied in multisensory integration during the RHI contain neurons with body part-centered visuo-tactile receptive fields, which may help code the space around the body (Fogassi et al., 1996; Graziano, 1999; Graziano et al., 2000; Graziano and Cooke, 2006). Recent evidence from work in humans suggests that these areas may implement a general mechanism of updating one's body representation during the RHI and similar paradigms, which generalizes across stimulation of different body parts (Tsakiris, 2008; Petkova et al., 2011; Blanke, 2012; Apps et al., 2013). Therefore we tested for consistent effects across both arm sides.

Methods

Participants

Thirteen healthy volunteers (10 females, age 23–35 years, all but one right-handed as measured with the Edinburgh Handedness Inventory, Oldfield, 1971) participated in the study. All participants signed an informed consent before and were paid after each of the scanning sessions. The study was approved by the local Ethical Committee of the Charité University Hospital Berlin and participants were treated in accordance with the Human Subject Guidelines of the Declaration of Helsinki.

Experimental design and procedure

The study was conducted as a within-subject, repeated-measures design in four separate scanning sessions (Figure 1A). In two 'RA' sessions (conducted on the same day), participants viewed their RA being touched; in two 'FA' sessions (acquired at least 1 month from each other and from the RA sessions), participants viewed a FA being touched, while their RA was hidden from sight and also touched. In both RA and FA sessions, tactile stimulation occurred on the right arm in one session and on the left arm in the other session (using a mirrored version of the setup). In the FA sessions, a transparent console was set up atop the participants' chest, with a realistic right or left FA attached to it (palm facing). The participants' RA was placed 13 cm behind the FA in a congruent posture and was completely hidden from view, i.e. participants had direct vision on the FA with the corresponding brushes, but not of their RA. In the RA sessions, the participants' RA was mounted onto a similar console in a posture corresponding to that of the RA in the FA sessions; here, participants only saw their RA with corresponding brushes. Participants were instructed to fixate a black dot attached to the middle of the FA (FA sessions) or RA (RA sessions).

Stimulation was delivered at two possible locations (palm and/or forearm) of the FA and/or the RA with sponge brushes moving back and forth at ~1.3 Hz with random inter-stroking interval (0 or 250 ms) to intensify the illusion (Armel and Ramachandran, 2003). The brushes were driven by separate stepping motors controlled by a MATLAB (The Mathworks, Inc., Natick) script via parallel port output, which also received the scanner triggers to start and stop stimulation. The motors' torque was transmitted into the scanner room via non-magnetic cables and gears. We used the same motors, stroking parameters and brushes for the stimulation in the FA and RA sessions, and ensured comparable positions of the arms and brushes and somatotopical representation of the stimulation locations (see Supplementary material). In the FA sessions, stimulation of the corresponding locations on the RA and the FA could occur synchronously (RHI condition), asynchronously (control condition) or in a mixed condition (one location stimulated synchronously, the other one asynchronously). Immediately after the scanning session, participants remained inside the scanner to rate the degree of experienced arm ownership in each condition (briefly presented again) by answering the question 'During this stimulation, it felt as if the FA was my own arm' (cf. Botvinick and Cohen, 1998) on a 7-point Likert-scale ranging from −3 ('completely disagree') to +3 ('completely agree'). Subsequently, participants verbally indicated the onset of the illusion (any feeling of ownership of the FA as soon as first experienced, Ehrsson et al., 2004), which was measured by the experimenter with a stopwatch. Participants received stimulation in trials of 20.16 s duration and 12.6 s rest (10 trials total per condition) during five runs (two trials per run and condition) in each FA session (plus one visuo-tactile localizer run, see Supplementary material), and two runs (five trials per run and condition) in each RA session; the order of arms was randomized across participants and the order of stimulations was randomized for each run.

fMRI data acquisition, preprocessing and analysis

T2*-weighted functional images were acquired using a 3 Tesla Tim Trio scanner (Siemens, Germany, 32-channel head coil, high-resolution 3D-EPI sequence, Lutti et al., 2012). Parallel imaging (GRAPPA) was used along the phase and partition directions (acceleration factor 2), yielding a functional image resolution of $2.0 \times 2.0 \times 2.0$ mm^3 at an acquisition time of 2520 ms
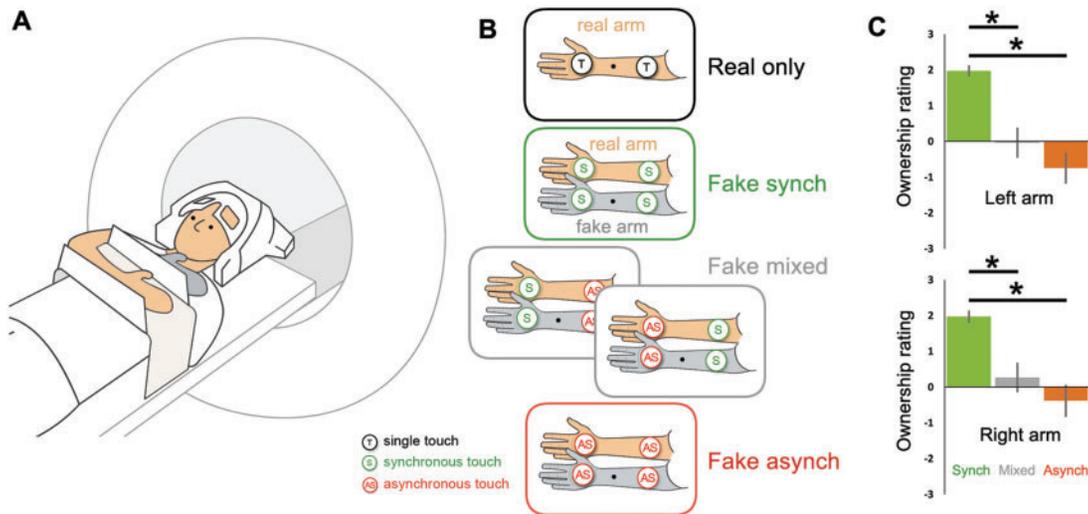
Fig. 1. Experimental setup and stimulation conditions (right arm sessions; a mirrored version of this setup was used for the left arm). A: Participants lay inside the scanner with direct vision of their real arm (RA) with the corresponding brushes ('RA' sessions), or with direct vision of an equilateral fake arm (FA) with corresponding brushes, while their RA was hidden from view behind the FA ('FA' sessions). B: Brush strokes were automatically delivered at two stimulation locations (palm, forearm) in various combinations that allowed us to implement gradual differences in limb ownership, operationalized in terms of congruence of visuo-tactile information. In the Fake arm sessions, visuo-tactile stimulation of the corresponding locations of the RA and FA could be either synchronous ('Fake synch'; RHI condition), mixed with respect to synchrony ('Fake mixed'; palm stimulated synchronously and forearm stimulated asynchronously, or vice versa) or asynchronous ('Fake asynch'; RHI control condition). C: Mean ratings of experienced ownership of the left and right FA during different types of visuo-tactile congruence. For both arm sides, synchronous stimulation produced greater illusory FA ownership than mixed or asynchronous stimulation. Asterisks denote significance at $P < 0.0056$ as obtained from Wilcoxon's signed-rank test, applying Bonferroni adjusted significance levels, error bars are SEM.

per volume (TR $= 70$ ms, matrix size [96, 96, 64], TE $= 33$ ms, nominal flip angle $= 20°$, BW $= 1408$ Hz). A total of 3596 functional volumes were recorded for each participant, plus GRE field maps (TE$_1 = 10.00$ ms, TE$_2 = 12.46$ ms) and a T1-weighted structural image (3D MPRAGE, voxel size $= 1 \times 1 \times 1$ mm, FOV $= 256 \times 256$ mm, 176 slices, TR $= 1900$ ms, TE $= 2.52$ ms, TI $= 900$ ms, flip angle $= 9°$).

fMRI data were preprocessed and analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London, UK: www.fil.ion.ucl.ac.uk/spm/). Physically based artifacts in individual slices were corrected via interpolation using the ArtRepair toolbox (Mazaika *et al.*, 2009; default settings). Functional images were realigned and unwarped, coregistered to the respective structural image, spatially normalized to MNI space using DARTEL and spatially smoothed with a 6-mm full width at half maximum Gaussian kernel. Global blood oxygen level dependent (BOLD) signal effects were removed (Macey *et al.*, 2004), and volumes with excessive head motion were interpolated using the ArtRepair toolbox ($<10\%$ of volumes corrected). To remove physiological noise from the gray matter BOLD signal, the first five principal components accounting for the most variance in the cerebrospinal fluid or white matter signal timecourse were added to the first-level general linear models (GLMs) as regressors of no interest (Behzadi *et al.*, 2007).

On the first level, we fitted a GLM to each participant (microtime onset set to the middle slice, 300-s high-pass filter, the individual runs were concatenated into one run per arm and session). Each stimulation condition was modeled as a regressor (boxcar) and convoluted with the standard hemodynamic response function of SPM8. On the second level, the contrast images of each regressor *vs* baseline were entered into flexible factorial within-subject GLMs including a between-subjects factor modeling the subject constants.

For the first analysis, investigating linear effects of arm ownership, we calculated four Ownership regressors (Real only, Fake synch, Fake mixed, Fake asynch) per arm side on the first level. These regressors were modeling only those stimulations in which both locations (palm and forearm) were stimulated together, since the mixed condition could not be implemented by stimulating only one of the two locations. On the second level, to identify brain areas whose activity was parametrically modulated by the degree of experienced ownership of the touched arm, we calculated a balanced linear contrast with the contrast weights $+1.5$ (Real only), $+0.5$ (Fake synch), -0.5 (Fake mixed) and -1.5 (Fake asynch) for each arm side (or the respective negative weights for the reverse contrast). Moreover, to assess the effects of between-participant differences in experienced ownership, we calculated a parametric contrast on the first level, in which the contrast weight of each condition regressor was determined by the respective participant's reported ownership ratings (values for Real only set to $+3$, the highest value of the rating scale, per default). These individually weighted contrast images were evaluated on the second level using a two-sample t-test.

For the second analysis, comparing the RHI condition with asynchronous and RA stimulation, we created separate first level GLMs, in which we randomly split each Fake synch condition into two separate regressors (Fake synch$_a$, Fake synch$_b$) to render the conjunction analyses across the Fake synch *vs* Real only and Fake synch *vs* Fake asynch contrasts independent. As this comparison did not involve the mixed condition, here we used regressors pooled across stimulation at the palm, forearm and both locations together in each condition. In addition, we compared the effects in the phase before and after the onset of the RHI by dividing each regressor into a pre-illusion onset and a post-illusion onset regressor on the first level, defined by each participant's verbal onset report (Ehrsson *et al.*, 2004). The second level GLMs used for this analysis thus comprised the regressors Real only, Fake synch$_a$, Fake synch$_b$ and Fake asynch for each arm side, where these regressors modeled the entire stimulation period, or only the pre-illusion onset or post-illusion onset period, respectively.

Statistic images were assessed for significant activations in the whole brain using an initial voxel-wise threshold of $P < 0.001$, and a threshold of $P < 0.05$, family-wise error (FWE) corrected for false positives on the cluster level. For brain areas that we hypothesized to be involved in the RHI based on previous literature, we used small volume correction within 10 mm radius spheres centered upon the peak coordinates reported in Petkova *et al.* (2011). Since we were interested in effects that generalize across body parts (see Introduction), we performed global conjunction analyses (a test for voxels that show consistent effects across multiple contrasts, Friston *et al.*, 2005) on the two respective contrasts of interest for each arm. Reported coordinates are in MNI space, neuroanatomical labels are derived from the SPM Anatomy toolbox (Eickhoff *et al.*, 2005). Statistical parametric maps are projected onto the mean normalized structural image at $P < 0.001$, uncorrected, with a cluster extent threshold of 5 voxels.

Results

Behavioral effects of visuo-tactile congruence

To verify that the RHI depended on visuo-tactile congruence, we analyzed the obtained ownership ratings, using the non-parametric Wilcoxon's signed-rank test since they did not pass the Jarque-Bera test for normality, and applying Bonferroni adjusted significance levels of $0.05/9 = 0.0056$ per test. For both arms, the synchronous condition produced significantly higher ownership ratings than the mixed and the asynchronous conditions (all $Ps < 0.001$, see Figure 1B). Mean ownership ratings showed a trend for being higher for the mixed than for the asynchronous conditions (left arm, $P = 0.014$; right arm, $P = 0.016$). No differences between arm sides were significant (all $Ps > 0.45$). The reported illusion onsets indicate an induction of the RHI early throughout stimulation (left arm: mean $= 6.05$ s, s.d. $= 3.13$; right arm: mean $= 4.80$ s, s.d. $= 2.41$; no significant differences between arm sides, two-tailed paired t-test, $P = 0.14$). A control experiment on a small independent sample similarly revealed significantly stronger mislocalization of the real hand following synchronous *vs* mixed or asynchronous stimulation and trends for mixed *vs* asynchronous stimulation (see Supplementary material).

Brain activity co-varying with subjective ownership of the touched arm

The conjunction across the linear ownership contrast (Real only > Fake synch > Fake mixed > Fake asynch) for the left and right arm revealed significant ($P < 0.05$, corrected) activity in the ventromedial prefrontal cortex (vmPFC), comprising bilateral rectal and mid orbital gyri and parts of the subgenual anterior cingulate cortex (sgACC), in the left (and a statistical trend for the right) lateral occipitotemporal cortex (LOC) and in the bilateral cerebellum and right parahippocampal gyrus (Figure 2A and Table 1). By weighting the subject-specific regressors with the individual ownership ratings, we found that between-participant differences related to arm ownership were also significantly ($P < 0.05$, corrected) reflected by activity in the vmPFC ($x = -14$, $y = 36$, $z = -16$, $T = 4.86$) and the bilateral LOC (L: $x = -38$, $y = -66$, $z = 4$, $T = 3.25$; R: $x = 56$, $y = -64$, $z = 2$, $T = 4.03$; $P < 0.05$, small volume corrected), and by a trend in the right cerebellum ($x = 18$, $y = -48$, $z = -30$, $T = 3.64$, $P = 0.097$, corrected). This analysis thus corroborated the results obtained using the linear ownership contrast, showing that the vmPFC,

LOC and also the cerebellum responded more strongly, the higher the experienced ownership of the touched limb. Interestingly, the bilateral LOC activations obtained from both comparisons also fell within the body-selective extrastriate body area (EBA; defined by activations obtained from a functional localizer using the same scanner and pulse sequence in Limanowski and Blankenburg, 2015).

The conjunction across the negative linear ownership contrasts (Real only < Fake synch < Fake mixed < Fake asynch) showed significant ($P < 0.05$, corrected) activity differences in large inferior parietal clusters, comprising the bilateral secondary somatosensory cortex (SII) and the right temporoparietal junction (TPJ), and further in the cuneus and left dorsal premotor cortex (Figure 2B and Table 1). When analyzing the individually weighted regressors, we found that between-participant differences related inversely to arm ownership were significantly ($P < 0.05$, corrected) reflected by activity in the bilateral TPJ and SII, cuneus, left PMd, right supplementary motor area (SMA) and right inferior frontal gyrus (IFG), at locations corresponding to those obtained from the linear contrast (Table 1). Notably, these individual differences were most strongly reflected by activity in the right TPJ ($x = 62$, $y = -48$, $z = 12$, $T = 6.43$, $P < 0.05$, corrected, cluster extent $= 530$ voxels).

Brain activity differences specific to the RHI

The conjunction across the Fake synch$_a$ *vs* Fake asynch and Fake synch$_b$ *vs* Real only contrasts for each arm side revealed significant ($P < 0.05$, small volume corrected) activity increases during synchronous stimulation in the bilateral ventral premotor cortex (PMv) and in the right putamen (Figure 3A and Table 2). Notably, activity differences at corresponding locations in the bilateral PMv ($P < 0.05$, small volume corrected) and a trend in the right putamen ($P = 0.063$, small volume corrected) emerged when only analyzing the post-illusion onset scans (no significant differences in the pre-illusion onset period); this comparison also revealed activity in the right posterior parietal cortex/intraparietal sulcus (IPS, $x = 42$, $y = -56$, $z = 56$, $P < 0.001$; at a lower threshold also in the left IPS: $x = -38$, $y = -58$, $z = 56$, $P = 0.002$).

The conjunction across the reverse contrasts (Real only *vs* Fake synch$_a$ and Fake asynch *vs* Fake synch$_b$) revealed significant activity differences within the bilateral primary somatosensory cortex (SI; $P < 0.05$, small volume corrected within masks created from the tactile localizer, see Table 2, Figure 3B and Supplementary material).

Discussion

In this study, brain activity during touch to one's real arm *vs* to a (self-attributed) fake arm was compared in two different ways: we first identified brain areas whose activity co-varied with the degree of ownership of the touched arm. Second, we looked for brain activity increases specific to the RHI, which may indicate an update of the body representation.

Brain areas encoding the degree of ownership of the touched arm

Activity in the vmPFC and the bilateral LOC, and also in the cerebellum co-varied with the degree of ownership of the touched arm, gradually decreasing from stimulation of one's RA alone, through synchronous, ambiguous and asynchronous
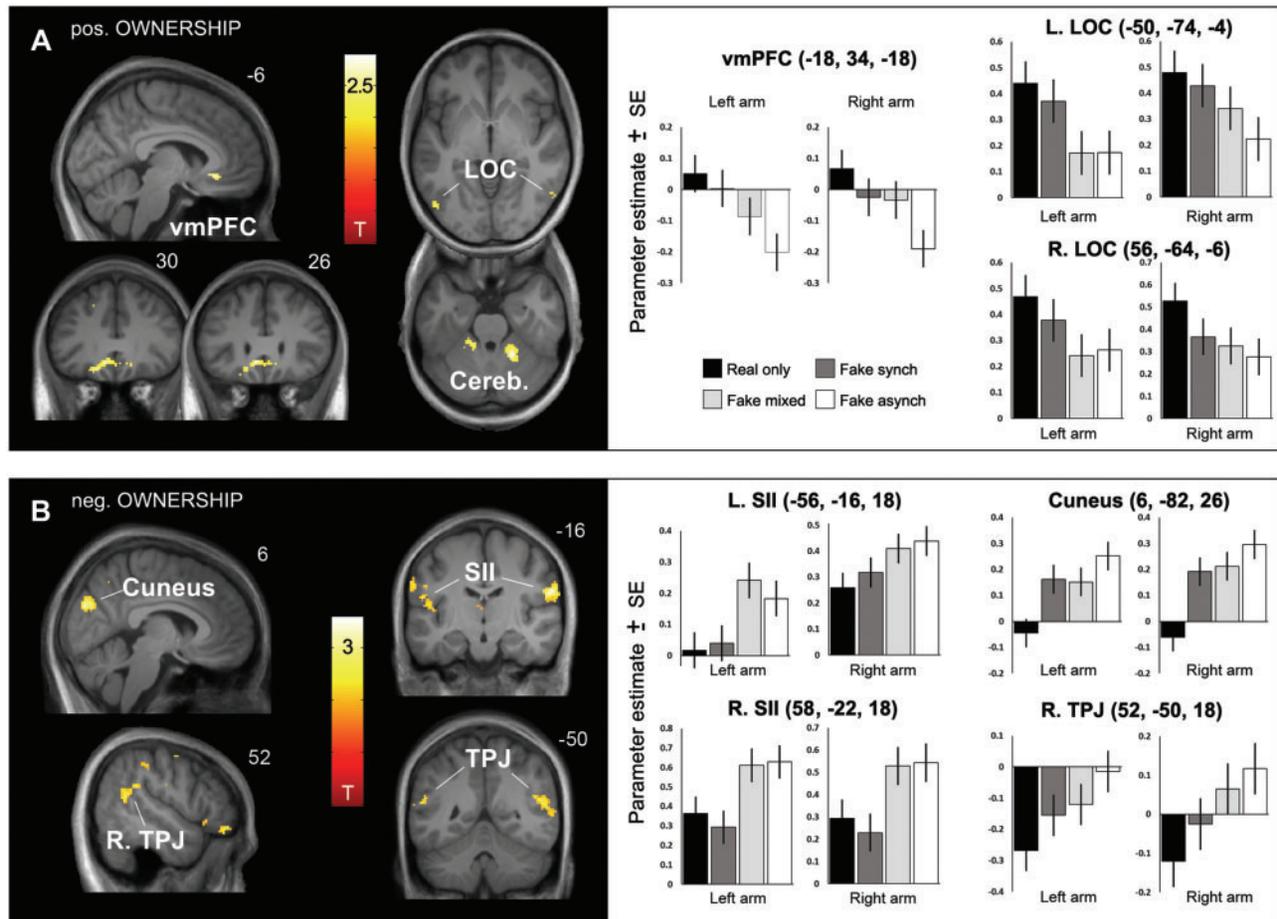
Fig. 2. Activity differences related to the degree of arm ownership. A: Statistical parametric maps showing significant ($P < 0.05$, corrected) activity differences related positively to the degree of arm ownership in the vmPFC (comprising bilateral mOFC and sgACC), in the bilateral LOC (left, $P < 0.05$/right, $P = 0.076$, small volume corrected), and in the cerebellum (left, $P = 0.05$/right, $P < 0.05$), obtained from the conjunction across the positive linear ownership contrasts (Real only > Fake synch > Fake mixed > Fake asynch) for the left and right arm. See Table 1 for details. SPMs are thresholded at $P < 0.001$, bar plots depict the parameter estimates at the given coordinates for each arm side and condition with associated standard errors. B: Activity differences related inversely to the degree of arm ownership. SPMs show significant ($P < 0.05$, corrected) activity differences in the cuneus and in the SII (as defined by significant activations obtained from the tactile localizer runs for the respective contralateral arm side, see Supplementary material) and regions corresponding to the right TPJ (see Table 1 for details) obtained from the conjunction across the negative linear ownership contrasts (Real only < Fake synch < Fake mixed < Fake asynch) for each arm side.

stimulation of a FA together with one's RA. These activation patterns were consistent for the left and right arm.

The vmPFC cluster encompassed bilateral medial orbitofrontal cortex (mOFC) and parts of the sgACC. The vmPFC/mOFC (often used synonymously, Zald and Rauch, 2006) receives information from all sensory modalities (Gusnard *et al.*, 2001; Kringelbach, 2005) and hence may qualify as a 'hub' region (Northoff *et al.*, 2006). VmPFC activity increases are generally observed during self-referential reflective tasks (Kjaer *et al.*, 2002; D'Argembeau *et al.*, 2005; Northoff *et al.*, 2006; Sui *et al.*, 2013) and during rest (in the absence of attention-demanding tasks, Raichle *et al.*, 2001; Gusnard *et al.*, 2001; D'Argembeau *et al.*, 2005). It has hence been argued that the vmPFC might instantiate basic self-referential processes that could modulate other cognitive and sensory processes (Northoff and Bermpohl, 2004; Schmitz and Johnson, 2007; Liao *et al.*, 2010; Bai *et al.*, 2012; however, perhaps the observed vmPFC activations may also be explained by general inferential or memory processes that are not exclusively self-specific, cf. Gillihan and Farah, 2005; Legrand and Ruby, 2009). Along similar lines, the vmPFC/mOFC contributes to stimulus valuation and stimulus-reinforcement learning (Rolls, 2004; Kringelbach, 2005; Nicolle *et al.*, 2012), in

particular to the evaluation of self-associated *vs* other-associated objects (Kim and Johnson, 2015) and to forming novel associations between neutral stimuli and oneself *vs* others (Sui *et al.*, 2013). The vmPFC is also involved in social cognition, for example, in adjusting social interactions to knowledge about the other (Stolk *et al.*, 2015) or processing others' predictions (Apps *et al.*, 2015) and value representations (Garvert *et al.*, 2015). Interestingly, in some cases this leads to updating one's own beliefs and preferences (Garvert *et al.*, 2015). Correspondingly, Murray *et al.* (2014) have proposed that the vmPFC could contribute to self-updating via the integration of self-relevant social information with one's self-representation.

Taken together, the increased activation of the vmPFC by conditions with higher arm ownership could reflect a response to the self-relevance of the seen touches, determined by the subjective ownership of the touched arm. Perhaps the (arguably) pleasant touch of the sponge brushes could have increased this effect further, as the vmPFC/mOFC reliably responds to pleasant touch to the hand (Rolls *et al.*, 2003), and this response may be subject to cognitive modulations (McCabe *et al.*, 2008). Likewise, the vmPFC could have contributed to 'higher-level' (cognitive) self-*vs*-other processing and

Table 1. Group-level activations obtained from the conjunction across the positive and negative linear ownership contrasts for the left and the right arm

Anatomical description	Cluster size (voxels)	Peak T	Peak Z	P (corrected)	Peak (MNI)		
					x	y	z
Positive ownership contrast: Real only > Fake synch > Fake mixed > Fake asynch							
L./R. Middle orbital gyrus and	180	2.98	4.48	0.005	−18	32	−18
rect al gyrus (vmPFC)*					14	34	−14
R. Cerebellum (Lobule VI)	155	2.96	4.46	0.011	20	−50	−26
R. Parahippocampal gyrus	111	2.74	4.18	0.048	30	−32	−16
L. Cerebellum (Lobule V)	110	2.69	4.12	0.050	−20	−40	−24
L. Inferior occipital gyrus (LOC)	21	2.32	3.66	0.035[a]	−50	−74	−4
R. Inferior temporal gyrus (LOC)	7	1.99	3.23	0.076[a]	56	−64	−6
L. Fusiform gyrus	12	2.63	4.05		−40	−80	−14
L. Superior frontal gyrus	7	2.12	3.39		−20	32	42
L. Middle frontal gyrus	6	2.05	3.31		−26	14	50
Negative ownership contrast: Real only < Fake synch < Fake mixed < Fake asynch							
R. Supramarginal gyrus,	666	3.58	5.23	<0.001	62	−16	24
parietal operculum (SII), and		2.79	4.26	0.002[b]	58	−22	18
middle temporal gyrus (TPJ)		2.62	4.04	0.006[c]	52	−50	18
R./L. Cuneus	465	3.44	5.06	<0.001	6	−82	26
L. Postcentral gyrus/parietal operculum (SII)	54	2.50	3.88	0.016[b]	−56	−16	18
L. Precentral gyrus (PMd)	117	2.90	4.30	0.039	−54	−6	50
L. Postcentral gyrus/parietal operculum (SII)	110	2.74	4.19	0.047[b]	−66	−18	32
L. Superior temporal gyrus	58	2.59	4.00		−40	−30	0
L. Precentral gyrus	41	2.58	3.99		−60	6	30
L. Inferior frontal gyrus	12	2.55	3.94		−62	6	16
L. Precuneus	15	2.49	3.88		2	−62	46
L. Middle temporal gyrus (TPJ)	69	2.44	3.81		−56	−52	16
R. Inferior frontal gyrus	41	2.44	3.80		52	42	−12
R. Middle frontal gyrus	20	2.42	3.78		50	−6	54
L. Thalamus	26	2.36	3.70		−8	−10	12
R. Supramarginal gyrus	20	2.27	3.60		50	−30	44
R. Inferior frontal gyrus	30	2.27	3.59		44	26	22
R. Inferior frontal gyrus	21	2.27	3.59		60	18	32
L. SMA	10	2.13	3.42		0	−4	64
R. Inferior frontal gyrus	16	2.07	3.33		50	22	−6
L. Rolandic operculum	5	2.05	3.30		−44	−28	22

All significant activations at $P < 0.001$ (uncorrected, $k > 5$ voxels) are listed. vmPFC, ventromedial prefrontal cortex; LOC, lateral occipitotemporal cortex; PMd, dorsal premotor cortex; SII, secondary somatosensory cortex; SMA, supplementary motor area; TPJ, temporoparietal junction. FWE-corrected P values are based on cluster-wise correction or small volume correction as follows

[a,b]FWE-corrected peak P values based on small volume correction: [a]within the left or right LOC as defined by the significant activations obtained from the visual localizer run for the left or right arm or [b]within the SII as defined by the significant activations obtained from the tactile localizer run for the contralateral arm side (see Supplementary material for details).

[c]FWE-corrected peak P values based on small volume correction using coordinates from Ionta *et al.* (2011).

*As this large cluster spanned to bilateral mid orbital gyrus, the peak coordinates of its local maximum in the right hemisphere are also listed.

self-updating. However, this part of our analysis was exploratory and the existing literature at present does not suggest a role of the vmPFC in body ownership. Future work should therefore try to follow up on this finding, and clarify the potential function of the vmPFC in body ownership as related to self-*vs*-other representation and/or self-referential information processing (e.g. as rather an affective one, a cognitive one or both, Spangler and Allen, 2012).

The linear ownership contrast also revealed activity in the bilateral LOC. These activations fell within regions activated by the moving brushes in the visual localizer (touch to the FA only), but did not respond to tactile stimulation *per se* (no activation by the tactile localizer, see Supplementary material). Activity increases in the LOC are reliably evoked by spatially and temporally congruent *vs* incongruent stimulation of the real and fake body part during the RHI, and the extent of these activity increases correlates positively with the reported intensity of the illusion (Gentile *et al.*, 2013; Limanowski and

Blankenburg, 2015). Here, we observed a similar pattern, however, with even stronger responses to touch seen on one's RA. Makin *et al.* (2007) have shown that the LOC preferentially responds to moving stimuli in perihand space, which aligns nicely with previous findings that vision of body parts alone is sufficient to influence the processing of stimuli in peripersonal space (Graziano *et al.*, 2000; Làdavas, 2002; Graziano and Cooke, 2006). A similar importance of vision of the body is implied by crossmodal interactions between vision and somatosensation. For example, touch applied to the same location as a visual stimulus enhances visual cortex activity (Macaluso *et al.*, 2000). Similarly, non-informative vision of a body part improves tactile acuity on that body part (Kennett *et al.*, 2001; Haggard *et al.*, 2007). There is evidence that these effects are further enhanced when viewing a body part that is self-attributed (Haggard *et al.*, 2007; Longo *et al.*, 2008). It has therefore been proposed that these crossmodal effects may depend on body ownership processes and the attribution of these stimuli to one's body (rather
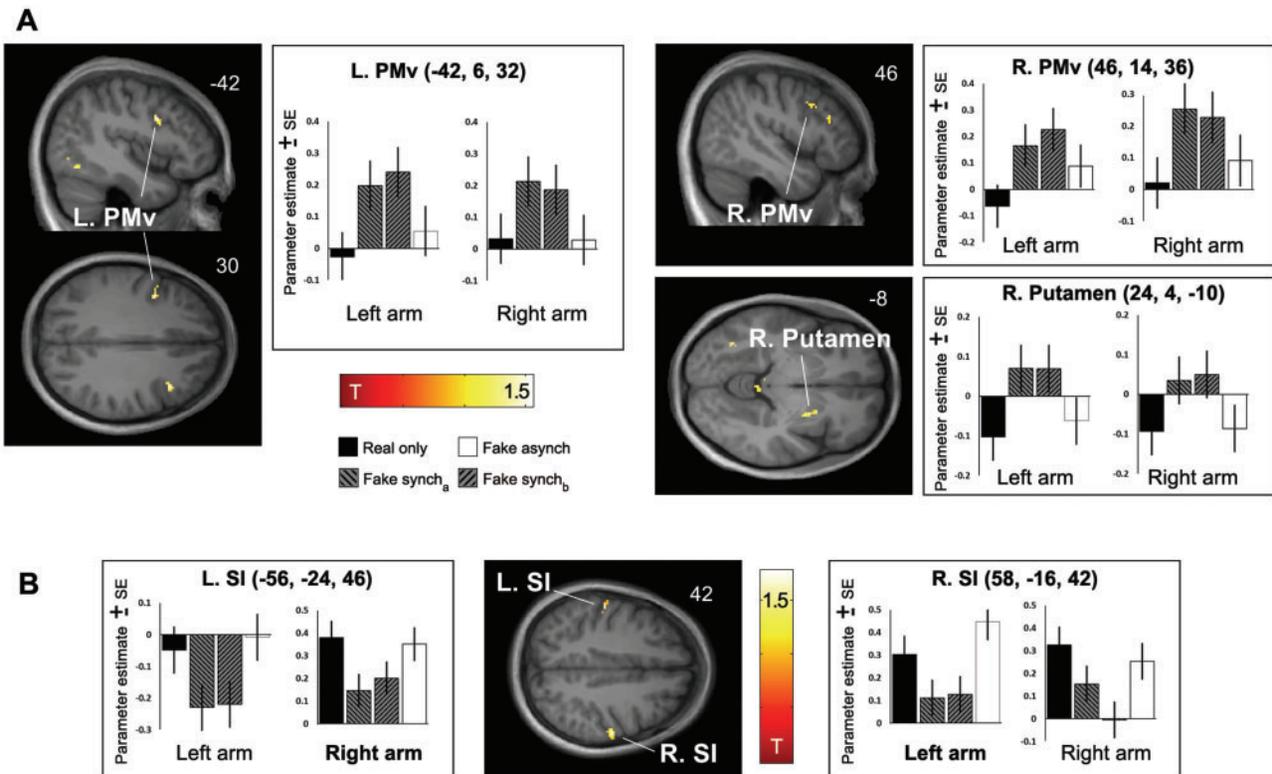
Fig. 3. Activity differences specific to the RHI. A: Results of the conjunction across the Fake synch$_a$ vs Fake asynch and Fake synch$_b$ vs Real only contrasts for each arm side (for this analysis, the Fake synch conditions were randomly split into Fake synch$_a$, Fake synch$_b$ to obtain independent regressors for the conjunction analysis, see Methods). Significant (P < 0.05, small volume corrected) activity increases during synchronous FA stimulation compared with asynchronous FA stimulation and compared with RA stimulation were observed in the bilateral PMv and in the right putamen. See Table 2 for details. SPMs are thresholded at P < 0.001, bar plots depict the parameter estimates at the given coordinates for each arm side and condition with associated standard errors. B: The conjunction across the reverse contrasts (Real only vs Fake synch$_a$ and Fake asynch vs Fake synch$_b$) revealed significant activity differences in the SI (P < 0.05, small volume corrected with significant activations obtained from the tactile localizer runs, see Table 2 and Supplementary material for details), which showed higher activity during stimulation of the RA and during asynchronous FA stimulation compared with synchronous FA stimulation (plots of the effects in the SI contralateral to the stimulated arm side are labeled in bold font).

than mere attentional effects, Whiteley *et al.*, 2004; Macaluso and Maravita, 2010). Notably, the LOC activations we observed also fell within body part-selective regions of the extrastriate visual cortex known as the EBA (Downing *et al.*, 2001; Limanowski and Blankenburg, 2015). Interestingly, there is evidence that the EBA also processes non-visual (e.g. proprioceptive) body-related information (Astafiev *et al.*, 2004), and several authors have proposed that the EBA may implement self-other distinction mechanisms (Jeannerod, 2004; Arzy *et al.*, 2006; David *et al.*, 2007; Haggard *et al.*, 2007). Taken together, a compelling interpretation of our results is that the LOC/EBA represents the body and the space around it differently than it does for a fake body (even if currently self-attributed) and may thus contribute to self-other distinction.

We also observed some activity modulations by arm ownership in the cerebellum, which has also been consistently reported in RHI studies (Ehrsson *et al.*, 2004; Petkova *et al.*, 2011; Gentile *et al.*, 2013). The cerebellum plays a role in the estimation of the sensory state of the body (Herzfeld and Shadmehr, 2013), in the prediction of sensory events (Roth *et al.*, 2013), and in the detection of intersensory congruence (Miall *et al.*, 1993), which could explain its activation by the increased predictability of touch sensation from the visual stimulus (highest for RA stimulation, lowest for asynchronous stimulation).

Strong activity increases with decreasing arm ownership were observed in the right (and to a lesser degree also in the left) TPJ. The right TPJ has been associated with abnormal bodily states like out-of-body experiences (Blanke *et al.*, 2005; De Ridder *et al.*, 2007) and disembodied self-location (Arzy *et al.*, 2006). In a recent fMRI study, TPJ activity reflected changes in perceived self-location induced by multisensory conflicts (Ionta *et al.*, 2011). Farrer *et al.* (2003, 2004) have shown that right inferior parietal/TPJ activity increases were related to decreasing feeling of control of a virtual fake hand. Tsakiris *et al.* (2008) found that interfering with right TPJ activity increased the RHI induced with a non-hand object, and speculated that the TPJ may 'test for fit' of a fake object with one's body representation. Interpreted with some caution, the increasing activation of the TPJ by conditions with increasing visuo-tactile incongruence (i.e. decreasing arm ownership) we observed could similarly imply a response to violations of bodily predictions. We observed further activity differences in neighboring inferior parietal regions including bilateral SII, which could reflect sensory mirroring (Keysers *et al.*, 2010) or the anticipation of a tactile stimulus on one's real limb (Carlsson *et al.*, 2000; Tsakiris *et al.*, 2007), since in the mixed and asynchronous conditions the FA was always touched before the RA.

Brain responses specific to touch to a temporarily self-attributed arm

We expected to observe activity increases during the RHI in brain areas related to multisensory integration, i.e. the binding

Table 2. Group-level activations obtained from the conjunction across the contrasts Fake synch$_a$ *vs* Fake asynch and Fake synch$_b$ *vs* Real only (and the conjunction across the respective reverse contrasts) for the left and right arm

Anatomical description	Cluster size (voxels)	Peak T	Peak Z	P (corrected)	Peak (MNI)		
					x	y	z
Fake synch$_a$ vs Fake asynch and Fake synch$_b$ vs Real only							
L. Precentral gyrus (PMv)	38	1.55	4.18	0.006[a]	−42	6	32
R. Inferior frontal gyrus (PMv)	26	1.38	3.87	0.016[a]	38	20	30
R. Putamen	51	1.45	3.99	0.028[a]	24	4	−10
L./R. Superior medial gyrus	59	1.54	4.15		2	36	36
L. Inferior occipital gyrus	28	1.49	4.06		−38	−64	−10
R. Inferior frontal gyrus	45	1.45	4.00		54	30	16
Cerebellar vermis	32	1.39	3.89		0	−36	−6
L. Inferior occipital gyrus (LOC)	7	1.22	3.59		−46	−70	−4
L. Anterior insula	6	1.18	3.52		−30	18	−4
R. Anterior insula	11	1.11	3.40		28	26	0
L. Superior medial gyrus	8	1.10	3.39		−6	36	36
Real only vs Fake synch$_a$ and Fake asynch vs Fake synch$_b$							
R. Postcentral gyrus (SI)	45	1.60	4.25	0.006[b]	58	−16	42
L. Postcentral gyrus/inferior parietal lobule (SI)	31	1.55	4.17	0.008[c]	−56	−24	46
L. Precentral gyrus	60	1.77	4.56		−38	−14	66
L. Postcentral gyrus/superior parietal lobule	34	1.61	4.27		−20	−42	68
L. Superior temporal gyrus	24	1.28	3.70		−62	−2	0
R. SMA	16	1.24	3.63		4	−12	70
R. SMA	7	1.20	3.56		14	−4	68
R. Precentral gyrus	5	1.15	3.47		42	−14	58
R. Superior temporal gyrus	7	1.00	3.22		66	−10	10

All significant activations at $P < 0.001$ (uncorrected, $k > 5$ voxels) are listed. PMv, ventral premotor cortex; LOC, lateral occipitotemporal cortex; SI, primary somatosensory cortex, SMA = supplementary motor area.
[a]FWE-corrected peak P values based on small volume correction using coordinates from Petkova *et al.* (2011).
[b,c]FWE-corrected peak P values based on small volume correction within SI as defined by the significant activations obtained from the tactile localizer run for the left arm[b] or right arm[c] (see Supplementary material for details).

of seen touches on the 'owned' FA and felt touches on the RA, which is not occurring during asynchronous or RA stimulation. We identified such responses in the bilateral PMv and the right putamen. This corroborates the results of previous RHI studies implying the PMv (Ehrsson *et al.*, 2004; Brozzoli *et al.*, 2012; Gentile *et al.*, 2013; Zeller *et al.*, 2014) and also the putamen (Petkova *et al.*, 2011) in the integration of multisensory input and the updating of one's body representation during the RHI. Correspondingly, the response differences in the PMv were particularly pronounced in the period after onset of the RHI (at a lower threshold, this analysis revealed similar responses in the bilateral IPS, which has been implied in similar multisensory processes, Ehrsson *et al.*, 2004; Gentile *et al.*, 2013).

The reverse comparison revealed that touch-related activity in the SI contralateral to the stimulated arm was lower during the RHI than during both RA stimulation and asynchronous stimulation (similar patterns emerged in the ipsilateral SI). This result replicates a recent electroencephalography study reporting reduced early touch-evoked potentials in SI during the RHI (Zeller *et al.*, 2014), which the authors interpret as a suppression of somatosensory signals from the real hand that could be required to enable a recalibration of hand representation from one's real hand onto the fake hand.

Conclusion

In sum, our results suggest that whereas integrating visuo-tactile information and updating the body representation under crossmodal conflict involves known multisensory integration areas, the self-relevance of touch to the body may be encoded in brain areas thought to implement self-referential processes and self-other distinction. These areas could perhaps in this way differentiate between oneself, i.e. one's real body parts and those temporarily self-attributed as a result of an illusion. Both processes—updating the body representation and self-other distinction—may be considered crucial for a basic self-representation. Recently, it has been proposed that hierarchical prediction error minimization in the brain could underlie the sense of body ownership and even the experience of selfhood (Friston, 2011; Seth *et al.*, 2011; Hohwy, 2012; Limanowski and Blankenburg, 2013; Apps and Tsakiris, 2014). These accounts are based on the assumption that the brain implements a hierarchical generative model of the world to predict its sensory input, and that this predictive model also instantiates the representation of one's body and self. Some anatomical candidate regions for the underlying architecture are the PMv, LOC/EBA, IPS and also the TPJ, which have been proposed repeatedly as parts of a network implementing one's body representation (Tsakiris *et al.*, 2007; Makin *et al.*, 2008; Tsakiris, 2010; Blanke, 2012; Ehrsson, 2012; Gentile *et al.*, 2013; Apps and Tsakiris, 2014; Limanowski and Blankenburg, 2015). To identify the specific contribution of individual brain areas and larger networks in predictive body- and self-modeling is an important and promising task for future research. An understanding of such a predictive model's processing hierarchy could shed more light onto the mechanisms underlying a flexible self-representation and self-other distinction; specifically, it could help clarify which parts of one's body representation can in principle be changed or updated 'completely', and whether a fake body (and touch to it) can ever be represented just like the real body.

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Supplementary data

Supplementary data are available at *SCAN* online.

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