Network Activity Underlying the Illusory Self-Attribution of a Dummy Arm

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Abstract: Neuroimaging has demonstrated that the illusory self-attribution of body parts engages frontal and intraparietal brain areas, and recent evidence further suggests an involvement of visual body-selective regions in the occipitotemporal cortex. However, little is known about the principles of information exchange within this network. Here, using automated congruent versus incongruent visuotactile stimulation of distinct anatomical locations on the participant's right arm and a realistic dummy counterpart in an fMRI scanner, we induced an illusory self-attribution of the dummy arm. The illusion consistently activated a left-hemispheric network comprising ventral premotor cortex (PMv), intraparietal sulcus (IPS), and body-selective regions of the lateral occipitotemporal cortex (LOC). Importantly, during the illusion, the functional coupling of the PMv and the IPS with the LOC increased substantially, and dynamic causal modeling revealed a significant enhancement of connections from the LOC and the secondary somatosensory cortex to the IPS. These results comply with the idea that the brain's inference mechanisms rely on the hierarchical propagation of prediction error. During illusory self-attribution, unpredicted ambiguous sensory input about one's body configuration may result in the generation of such prediction errors in visual and somatosensory areas, which may be conveyed to parietal integrative areas. *Hum Brain Mapp* 36:2284–2304, 2015. © 2015 Wiley Periodicals, Inc.

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INTRODUCTION

The rubber hand illusion [RHI, Botvinick and Cohen, 1998] is an illusory self-attribution of a dummy hand induced via congruent touch on the dummy hand and

one's real hand. Its classical explanation emphasizes the integration of conflicting information from vision, touch, and proprioception about one's hand's position in space [Botvinick and Cohen, 1998; Ehrsson 2012; Makin et al., 2008]. The RHI arises because the touch seen on the dummy hand and the touch felt on one's real hand are (falsely) bound together and taken to convey concurrent information about one and the same external event [Driver and Spence, 2000; Hohwy, 2012]. Due to the dominance of the visual modality, this event—the “felt” touch—is then attributed to the dummy hand [Armell and Ramachandran, 2003; Botvinick and Cohen, 1998]. Thus, by resolving the intersensory conflict via multisensory integration, the brain updates an internal multimodal body model to incorporate the dummy hand [Graziano and Botvinick, 2002; Maravita et al., 2003; Tsakiris, 2010].

In line with this explanation, brain imaging has demonstrated that the self-attribution of body parts during

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the RHI activates parietal and frontal multimodal areas [Ehrsson et al., 2004; Petkova et al., 2011] and increases their functional coupling [Gentile et al., 2013; Guterstam et al., 2013]. These areas implement the processing of stimuli in the space surrounding the body [peripersonal space, (PPS); Graziano and Cooke, 2006; Graziano, 1999; Làdavas, 2002; Maravita et al., 2003; Rizzolatti et al., 1981, 1997], and it has been proposed that their increased (co)activation during the RHI reflects nonlinear responses to convergent multisensory information—indicative of multisensory integration—and a resulting recalibration of multimodal PPS coordinates onto the dummy hand and a coherent experience of body ownership [Brozzoli, Gentile et al. 2012; Ehrsson, 2012; Gentile et al., 2011; Makin et al., 2008]. Recent studies moreover suggest an important contribution of extrastriate visual areas in the lateral occipitotemporal cortex (LOC) to the RHI, most notably the body-selective extrastriate body area [EBA; Downing et al., 2001; Limanowski et al., 2014; Wold et al., 2014]. An involvement of visually body-selective areas in the RHI fits with previous reports of visuosomatosensory interactions in the EBA [Blanke, 2012; Costantini et al., 2011; Haggard et al., 2007], and with the fact that vision of body parts alone affects the processing of stimuli in the PPS [Graziano et al., 2000; Makin et al., 2007] and enhances the processing of tactile stimuli on the body itself [Haggard et al., 2007; Kennett et al., 2001; Taylor-Clarke et al., 2002]. In sum, frontoparietal and occipitotemporal brain areas seem to work in concert during the RHI to resolve intersensory conflicts by integrating multisensory information. However, which mechanisms within this network guide the brain's decision to self-attribute a body part or not is still largely based on speculations. Empirical evidence clarifying the nature of these mechanisms would substantially enrich existing models of body ownership and PPS processing [Brozzoli, Gentile et al., 2012; Graziano and Cooke, 2006; Makin et al., 2008; Tsakiris 2010].

A compelling speculation is that the interactions of the fronto-parietal network and body-selective occipitotemporal areas observed during the RHI may reflect reciprocal information exchange according to the principles of predictive coding [Friston and Kiebel, 2009; Friston and Stephan, 2007; Friston, 2005]. The predictive coding account of information processing within the brain is built upon the assumption that the brain constantly interprets its sensory information under a hierarchical generative model of the world. Thereby prediction errors are generated by a mismatch between predicted and actual sensory data at any given level and are passed on to the level above via bottom-up, feedforward connections. The guiding principle of the brain is to constantly minimize prediction error across all levels of the hierarchy to infer the causes of its current sensory state. This can be achieved by adjusting the model's predictions, which are conveyed to the level below via top-down, feedback connections to “explain away” the prediction error [Murray et al., 2002].

One important assumption derived from predictive coding is that stimulus-evoked neuronal activity increases reflect the computation and propagation of such prediction errors [Friston, 2005; Kok et al., 2012; Summerfield and Koechlin, 2008]. During the RHI, such prediction error-related activity increases should hence be observable in regions of the brain network subserving limb ownership that detect mismatches between the predictions of one's body model and the visuosomatosensory information provided [Apps and Tsakiris, 2014; Hohwy, 2012; Limanowski and Blankenburg, 2013].

Here, we used an automated setup to deliver tactile stimulation to the participant's hidden right palm, forearm, or both, and synchronously or asynchronously to their counterpart on a realistic dummy arm inside an fMRI scanner. We hypothesized that the RHI would depend on the congruence of visuotactile stimulation, with neuronal mechanisms implemented within the same, potentially visually body-selective, brain areas for all locations. We therefore identified common effects of visuotactile congruence versus incongruence across stimulation locations, and independently tested for the visual body-selectivity of these brain areas. Moreover, we compared these effects to results of spatially (in)congruent stimulation, obtained using the same setup [Limanowski et al., 2014]. As expected, we observed increases of ventral premotor, intraparietal, and occipitotemporal activity during the RHI. Psychophysiological interaction analyses moreover demonstrated an increased functional coupling among these areas during the illusion. We further examined these illusion-related interactions using dynamic causal modeling [DCM, Friston et al., 2003]. Bayesian model comparison identified as the most parsimonious model one in which the RHI modulated the connectivity from lower-level visual and somatosensory areas to higher-level intraparietal areas. We interpret these results as support for a predictive coding account of hierarchical inference in the brain, whereby the probabilistic self-attribution of body parts during the RHI rests on the propagation of forward-flowing multisensory prediction errors to higher-level integrative brain areas.

MATERIALS AND METHODS

Participants

Twenty healthy volunteers [14 females, age 23–36 years, 19 right-handed, 1 left-handed as measured with the Edinburgh Handedness Inventory, Oldfield, 1971] participated in the main experiment. All participants issued informed consent before the experiment, and were paid after the scanning session. Participants were treated in accordance with the Human Subject Guidelines of the Declaration of Helsinki, and the experiment was approved by the local Ethical Committee of the Charité University Hospital Berlin.

Figure 1.

Experimental setup and design. We used an automatic setup to deliver tactile stimulation to two locations on the participant's right arm and a realistic ipsilateral dummy arm. **A:** The participants lay inside the MR scanner with their right arm hidden from view, while looking at the dummy arm. Two pairs of sponge brushes, driven by computer-controlled stepping motors, were installed at the palm and the forearm of each arm. **B:** View of the dummy arm from the participant's perspective. Participants were instructed to fixate the black dot in the middle of the dummy arm throughout the experiment. Visuo-tactile stimulation was delivered by 180° back-and-forth rotations of the brushes (symbolized with white arrows) at approx. 1.3 Hz. **C:** The experimental design for the main experiment was a 3 by 2

factorial block design, in which we manipulated the stimulation location (palm, forearm, or both), and the congruence of visuo-tactile stimulation (congruent versus incongruent). Thereby incongruent stimulation consisted of asynchronous touch, which was achieved by delaying the rotation of the felt brush strokes by 50 % relative to the rotation of the seen brush strokes. **D:** Participants' mean verbal ratings of the experienced self-attribution of the dummy arm during each condition. Error bars are standard errors of the mean. The congruent versus incongruent stimulation conditions produced a strong illusory self-attribution of the dummy arm at each anatomical location (Wilcoxon signed-ranks, $n = 20$, all $Z_s > 3.5$, all $p_s < 0.001$, see Results for details).

Experimental Setup and Design

We used a custom automatic setup to deliver tactile stimulation to a realistic, life-size right dummy arm and the participant's real arm (Fig. 1A). The dummy arm was mounted on a transparent acrylic console in full view atop the participant's chest, while her (fixated) real arm was occluded from view, placed approx. 13 cm behind the dummy arm in a corresponding posture. The participant's head was tilted and foam padded to guarantee full vision of the dummy arm. The gap between the dummy arm and the participant's shoulder was covered with black cloth. Two pairs of brushes were installed at corresponding anatomical locations of the dummy arm and the real arm—one at each palm, and one at each forearm (Fig. 1B). The brushes were adjusted and tested before the start of the experiment, and the perceived synchrony of brush strokes in the RHI condition was validated in a brief practice run. Participants were instructed to fixate a small black dot in the middle of the dummy arm throughout the whole experiment. Each brush could deliver touch via back and forth 180° rotations at a

frequency of approx. 1.3 Hz with randomly varying inter-stimulus intervals (0 or 250 ms) to make stimulation less predictable. To eliminate any potential effects of human interaction or vision of another human's (the experimenter's) hands during the illusion induction, the experimental setup was completely automated. The brushes were driven by four identical stepping motors (1.8° stepping angle; RS Components GmbH, Mörfelden-Walldorf, Germany), which were controlled by a custom MATLAB (The Mathworks, Natick) script via a computer parallel port that also received the scanner-triggers to synchronize stimulation onsets with the fMRI acquisition. The motors' torque was transmitted from outside the scanner room to the brushes using nonmagnetic cables and gears.

The main experiment was conducted as a within-subject block design, comprising five experimental runs plus one separate run for visuotactile localizers, and a separate functional localizer for visually body part-selective brain areas (see below). During the experimental runs, tactile stimulation was applied to anatomically congruent locations of the real arm and the dummy arm, that is, to the palm, the forearm, or both locations

together (Fig. 1C) in two conditions: temporally congruent (synchronous touch at the same location) or incongruent (asynchronous touch at the same location, achieved by delaying the real arm brush strokes by 50%, i.e., approx. 400 ms). Each condition was presented twice per run and location in blocks of 20.16 s, followed by 12.6 s rest. The experiment also comprised two additional conditions where stimulation was synchronous at one location and asynchronous at the other, which we do not report here because of our explicit focus on clearly congruent versus incongruent multisensory information. Immediately after the functional runs, the verbal ratings of illusion intensity and its temporal onset were collected; for this purpose participants remained lying inside the scanner in the same way as during image acquisition, and the experimental conditions were presented again. Participants first indicated the strength of experienced illusory self-attribution of the dummy arm in the congruent and incongruent conditions ("During the stimulation, it felt as if the dummy arm was my own arm.", Botvinick and Cohen, 1998) on a 7-point Likert-scale ranging from -3 "completely disagree" to +3 "completely agree." Moreover, for the congruent condition only (as this was the condition in which we expected a RHI to occur), the elapsed time between the beginning of congruent stimulation and the participant's first verbal report of experienced illusory self-attribution of the dummy arm was measured with a stopwatch to represent the individual onset of the ownership illusion. Thus, in addition to the self-attribution ratings of each condition, we were able to calculate an illusion score that reflected both the strength and prevalence of the illusion: the ownership rating difference between the congruent and incongruent condition was multiplied by the difference between total stimulation duration minus the reported illusion onset [Ehrsson et al., 2004].

As part of our analysis, we compared our data to those reported in Limanowski et al. [2014; these data were obtained more than 6 months before the data acquired for the present experiment]. In that experiment ($N = 20$, two of which also took part in the present experiment), we have used the same experimental setup; in contrast to the present experiment, tactile stimulation was always synchronous, and applied either to congruent locations on the real arm and the dummy arm (palms or forearms) or to incongruent locations (one's palm together with the dummy forearm, or vice versa); only the former condition induced a RHI. By analyzing both datasets together, we were able to identify general effects of temporally (the present experiment) and spatially [Limanowski et al., 2014] congruent versus incongruent stimulation of the real arm and dummy arm underlying the illusion. Moreover, we were able to combine the functional localizer sessions for identification of visually body part-selective regions from the two samples, since the two protocols were identical.

Individual Localization of Visually Body Part-Selective Areas

The extrastriate body area (EBA) is a functionally defined area within the lateral occipital cortex, usually characterized by its preferential response to images of human body parts versus images of other objects [Downing et al., 2001; Downing and Peelen, 2011; Urgesi et al., 2007]. Therefore, for each participant, we implemented a standard functional localizer in a separate scanning session, in which we presented participants images of human hands and feet, and used images of motorcycle parts as control stimuli (following Urgesi et al., 2007, see Fig. 4 for sample stimuli). Images were color photographs presented on a blank white screen ($18.7^\circ \times 13.7^\circ$ visual angle) for 700 ms (150 ms interstimulus intervals) within blocks of 20 s duration and 20 s rest with a black fixation cross. Image categories were presented randomly, and the order of images within each category was randomized as well. Since the protocol for both datasets [present study and Limanowski et al., 2014] was identical, we were able to analyze all participants' data [$N = 36$ due to four dropouts in the dataset from Limanowski et al., 2014] in one group-level GLM, calculating the contrast Body parts vs Objects. The fMRI parameters, data preprocessing, and analyses used for the functional data obtained in this scanning session were identical as described in the following for the main experiment.

fMRI Data Acquisition, Preprocessing, and Analysis

The fMRI data were recorded using a 3 T scanner (Tim Trio, Siemens, Germany), equipped with a 32-channel head coil. T2*-weighted functional images were acquired using a customized high-resolution 3D-EPI sequence [Lutti et al., 2012]. Parallel imaging (GRAPPA image reconstruction) was used along the phase and partition directions with an acceleration factor of two, yielding a functional image resolution of $2.0 \times 2.0 \times 2.0 \text{ mm}^3$ at an acquisition time of 2520 ms per image volume (TR = 70 ms, matrix size [96, 96, 64], TE = 33 ms, flip angle = 20° , BW = 1408 Hz). A total of 1266 functional volumes were recorded for each participant (six runs à 211 volumes each), with an additional GRE field map (TE₁ = 10.00 ms, TE₂ = 12.46 ms) recorded after each scanning session. A high-resolution T1-weighted structural image was acquired for each participant (3D MPRAGE, voxel size = $1 \times 1 \times 1 \text{ mm}^3$, FOV = 256 mm $\times$ 256 mm, 176 slices, TR = 1900 ms, TE = 2.52 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/). First, possible artifacts (i.e., artifacts that may be induced by abrupt head motion or spikes) in individual

slices of the functional image volumes were corrected via interpolation using the SPM ArtRepair toolbox [Mazaika et al., 2009; `art_slice` procedure, applying default settings]. To account for both dynamic (head motion-related) and static distortions, the functional images were realigned to the first image of each run using a least squares approach and a six-parameter rigid body transformation, and unwarped. To achieve better intersubject alignment, the functional images were spatially normalized using the DARTEL procedure as implemented in SPM8 [Ashburner, 2007]: Each participant's functional images were coregistered to the respective T1-weighted structural image. The structural images were segmented into grey matter (GM), white matter (WM), and cerebrospinal fluid (CSF) components, and the GM and WM segments of all participants were aligned and warped together. The nonlinear deformation information from this step was then used to normalize each participant's functional images to MNI space. In the same way, we also normalized the individual structural images, and averaged them to obtain a sample-specific mean structural image onto which we projected our T-maps. Functional images were further spatially smoothed using a 6 mm full width at half maximum Gaussian kernel. To improve signal to noise ratio, global BOLD signal effects were removed from the functional images using a voxel-level linear model of the global signal [Macey et al., 2004], and subsequently the functional images were scanned for outlier volumes featuring excessive scan-to-scan movement, which were corrected via interpolation using the SPM ArtRepair toolbox (`art_global` procedure). Finally, to remove physiological noise from the BOLD signal of grey matter regions, we created participant-specific noise regressors using a component-based approach as described by Behzadi et al. [2007]: The WM and CSF structural segments were first smoothed with a 4 mm full width at half maximum Gaussian kernel. For each run, these segments were then multiplied with the first unwarped functional image (using the `ImCalc` function and thresholds of 80% for the CSF segment, and 90% for the WM segment). The resulting images were used as noise ROIs (regions in which the time signal is unlikely to reflect neural activity). From within these ROIs, we extracted the first five principal components that accounted for the most variance in the CSF or WM signal timecourse, respectively, for each functional run and participant. The ten extracted principal components were added to each run of the first-level general linear models (GLMs) as regressors of no interest. The fMRI data of Limanowski et al. [2014; acquired using the same scanner, head coil, and sequence, $2.0 \times 2.0 \times 2.0 \text{ mm}^3$ at an acquisition time of 2240 ms per image volume] were preprocessed in the same way as described above for the present experiment.

On the first level, we fitted a GLM to each participant's fMRI data (microtime onset set to the middle slice, 300 s high-pass filter); each condition was modeled as a regressor with a boxcar function and convoluted with the standard hemodynamic response function of SPM. Contrast images of the regressors modeling each condition versus baseline were entered into flexible factorial GLMs on the second level (random effects, group analysis), including a factor modeling the subject constants. Thus we first set up a three-by-two factorial GLM in which we manipulated the stimulation location (*Palm*, *Forearm*, *Both*) and the congruence (*Cong*, *Incong*) of visuotactile stimulation (see Fig. 1C). Although we did not necessarily expect the same voxels to be activated by the different stimulation contrasts, brain regions that are universally involved in multisensory integration should still consistently respond to congruent versus incongruent stimulation. Therefore, we used the global conjunction analyses [Friston et al., 2005] on the respective congruent versus incongruent contrasts of each location and experiment to identify voxels that showed consistent effects across locations and type of comparison. As a complementary analysis, we tested for brain areas in which activity differences between the congruent and incongruent stimulations would additionally change over time, i.e., during the blocks of stimulation. This analysis was motivated by our assumptions based on predictive coding, whereby prediction error should be generated dynamically throughout the illusion. To test for such effects, we added a parametric modulation to each condition on the first-level. The parametric modulator was modeled as linearly increasing, and centered on the scan within the stimulation block in which the onset of the illusion was reported by the participant (obtained from the verbal illusion onset ratings, see above). The resulting contrast images were entered into a group-level design analogous to that of the main GLM analysis. We looked for stronger parametric activity increases over stimulation blocks (i.e., significantly higher beta values for the parametric regression slope) during the congruent versus incongruent conditions. We performed the analogous conjunction analysis of the three respective congruent versus incongruent contrasts for the palm, forearm, and both locations. Finally, to compare our data to those of Limanowski et al. [2014, see above], we set up a group-level GLM comprising a group factor and an experimental factor featuring four stimulation types: one congruent and one incongruent condition per stimulation location (the palm or the forearm). Thereby, to account for the differences between experiments in our design, all relevant contrasts were calculated on the interaction terms of the experimental factor with the group factor, i.e., on the following eight regressors: *Palm*_{TEMP_CONG}, *Palm*_{TEMP_INCONG}, *Forearm*_{TEMP_CONG}, *Forearm*_{TEMP_INCONG} (present experiment, temporal (in)congruence), and *Palm*_{SPATIAL_CONG}, *Palm*_{SPATIAL_INCONG}, *Forearm*_{SPATIAL_CONG}, *Forearm*_{SPATIAL_INCONG} [Limanowski et al., 2014, spatial (in)congruence]. For the analysis of correlations between brain activity and

between-participant differences in the reported intensity of the ownership illusion, we calculated the relevant congruent versus incongruent contrasts on the first-level, and entered the resulting contrast images into a group-level one-sample *t*-test (for the main experiment) or two-sample *t*-test [for the comparison of the current dataset with the dataset of Limanowski et al., 2014] including the behavioral illusion scores as a covariate (following Ehrsson et al., 2004). For activations obtained from this analysis, we also report the correlations (Pearson's *r*, using two-tailed significance) between the parameter estimate at the respective peak voxel, and the behavioral illusion scores.

Statistic images were assessed for significant activations in the whole brain using an initial voxel-wise threshold of $P < 0.001$, and a cluster-wise threshold of $P < 0.05$, family-wise error (FWE) corrected, was used to correct for false positives due to multiple comparisons. Based on extensive work done by others [Ehrsson et al., 2004; Petkova et al., 2011], we had specific *a priori* hypotheses about the involvement of the left PMv and the left IPS in the RHI; we hence corrected for multiple comparisons in these regions of interest (ROIs) using peak-FWE small volume correction within 10 mm radius spheres centered on the peak coordinates reported in the most recent fMRI study using a classical RHI paradigm [Petkova et al., 2011; left PMv: $x = -48$, $y = 6$, $z = 32$; left IPS: $x = -46$, $y = -48$, $z = 56$]. Likewise, we used the activations in the EBA as obtained from the joint visual body-selectivity localizer, and the activation in left primary somatosensory cortex (SI) and left secondary somatosensory cortex (SII) as obtained from the tactile localizer (touch to the real arm only), all thresholded at $P < 0.001$, uncorrected, as ROI mask images for small volume correction in the RHI experiments. We only report activations that survived either cluster-wise FWE-correction or small volume correction based on the pre-defined ROIs, unless explicitly stating so (in a few cases where activity in regions of interest did not survive correction, we explicitly report the statistics and uncorrected *P*-value). For a better interpretation of the results of the conjunction analyses, we report the corresponding peak *T* and *Z* values. For visualization of the results, we projected the resulting statistical parametric maps (thresholded at $P < 0.001$, uncorrected) onto the mean normalized structural image. All reported coordinates are in MNI space, and neuroanatomical labels are derived from the SPM Anatomy toolbox [Eickhoff et al., 2005] where possible. Activations that fell within the corresponding masks of EBA or FBA obtained from the visual body-selectivity localizer (which corresponded to published literature, see Results) were labeled accordingly.

Connectivity Analysis

We analyzed the brain connectivity (i.e., changes in the statistical dependencies of BOLD signal time-series under the illusion context) of the key cortical regions revealed by our standard GLM analysis by means of psychophysiological interactions [PPIs, Friston et al., 1997], and the

effective connectivity within the corresponding network (i.e., how influences of certain nodes onto others change under the illusion context) by means of dynamic causal modeling [DCM, Friston et al., 2003]. Both analyses (PPI and DCM) were performed based on the same seed regions, and separately for each stimulation location (palm, forearm, or both together) and type of congruence versus incongruence (spatial and temporal). The nodes of our model were chosen based on the results of our univariate analysis and their correspondence with previous literature on illusory body ownership: Our group-level GLM analysis identified three main sources of cortical activity related to congruent versus incongruent stimulation of the dummy arm and the real arm, whose involvement in the RHI is well documented: LOC/EBA, IPS, and PMv [e.g., Brozzoli, Gentile et al., 2012; Ehrsson et al., 2004; Gentile et al., 2013; Petkova et al., 2011]. Notably, our GLM analysis revealed a much stronger and more consistent response to spatiotemporal congruence of touches to a right arm within the respective areas of the left hemisphere (see Results). This result is consistent with previous evidence for predominantly left-hemispheric activation of the IPS and PMv to tactile stimulation of the right hand across the body midline [Lloyd et al., 2002], as well as with the implied general importance of the left IPS and PMv during the RHI [Ehrsson et al., 2004; Gentile et al., 2013; Guterstam et al., 2013; Petkova et al., 2011]; there is also evidence for a left-lateralized response to vision of hands in the IPS and LOC/EBA [Astafiev et al., 2004; Bracci et al., 2010, 2012; Zopf and Williams, 2013]. We therefore based the connectivity analyses on a left-hemispheric network comprising seed regions in the LOC, IPS, and PMv, and, since the RHI depends on visual and somatosensory information integration, we further included the left SII as the input area for somatosensory information from the contralateral hand in the DCM analysis. We did not include the cerebellum (our standard GLM analysis revealed some activity differences in the cerebellum) in the network, as we were interested in the interaction of secondary visual and somatosensory cortices with multisensory integrative areas in the IPS [following models of the RHI by Makin et al., 2008; Tsakiris, 2010] and the PMv. For each participant, the experimental runs, with their extracted physiological noise regressors, were concatenated into a single data sequence [Friston, 2004]. Region-specific BOLD time-series were extracted as the first eigenvariate of all significant voxels within a 6 mm radius sphere centered on each participant's local maxima in left SII, LOC, IPS, and PMv, as obtained from the respective T-contrast congruent versus incongruent stimulation (congruent plus incongruent stimulation versus baseline for SII); mean MNI coordinates and standard deviations of the centers of these VOIs were: SII ($x = -55.7 \pm 7.2$, $y = -24.3 \pm 5.4$, $z = 16.9 \pm 2.8$), LOC ($x = -45.9 \pm 5.3$, $y = -70.5 \pm 5.3$, $z = -1.5 \pm 4.6$), IPS ($x = -44.3 \pm 5.1$, $y = -45.3 \pm 6.5$, $z = 53.8 \pm 4.9$), PMv ($x = -45.9 \pm 5.5$, $y = 9.7 \pm 6.2$, $z = 31.3 \pm 5.7$).

First, we used PPI to examine changes in connectivity of each seed region under the RHI context (congruent versus

incongruent stimulation of the real and dummy arm). Taking the extracted BOLD time-series, we calculated the psycho-physiological interaction term with the experimental vector “congruent versus incongruent stimulation,” and then performed a second GLM analysis including the seed region’s time-series, the experimental vector, and the interaction term. For each seed region, the first-level contrast images of each stimulation location’s PPI (palm, forearm, or both) were entered into a group-level within-subject GLM as three levels of one factor. Significant voxels were selected based on a global conjunction analysis of the three group-level T-contrasts, following the same logic as in our standard GLM analysis.

Next, we examined the mutual influences within this brain network involved in the RHI using DCM. The idea behind DCM is to construct a plausible model of interacting brain regions, whose parameters can be estimated from the data [Friston et al., 2003]. Thereby the connectivity targeted by DCM is the coupling of neuronal states among certain brain regions; more specifically, one typically tries to model how the influence of activity in one brain area on activity in other brain areas changes under a certain experimental factor. In DCM one distinguishes between the endogenous connectivity (the “architecture” of the model, i.e., the latent coupling of responses among brain areas that is independent of experimental manipulations, encoded in the DCM.A matrix) and the effective connectivity (changes in connectivity among brain areas due to experimental factors, DCM.B matrix). Experimental variables can affect the model in two ways, by directly changing activity in certain nodes (driving input), or by changing the coupling among two nodes (modulatory input). In a typical DCM analysis, one first constructs different plausible models varying in their connectivity among the nodes of the network, and then inverts these models (fits them to the data), to finally compare their evidence given the particular set of data using Bayesian inference. Classical statistical inference can then be performed on the different parameters of the “winning” model. Our DCM design matrices comprised a regressor modeling the sensory input (congruent and incongruent stimulation), and a regressor modeling the contextual effect of the RHI (congruent stimulation). After estimation, the individual models were compared using random-effects Bayesian model selection (RFX BMS) to determine the model with the overall highest evidence [Stephan et al., 2009]; we report each model’s exceedance probability, which reflects how likely a model is compared with the competing models. Multisensory (visuo-tactile) stimulation was modeled with a boxcar function and defined as the driving input entering left SII and left LOC. We modeled all connections bidirectionally, and included self-connections on all nodes. In a first step, we tested various endogenous connectivity patterns (i.e., independent of experimental context) against each other, assuming connections between SII-IPS, LOC-IPS, and IPS-PMv, and evaluating all other possible connectivity patterns among SII, LOC, and PMv. This assumption was based upon previous investigations of multisensory integration and crossmodal effects,

where information transmission occurs between “lower-level” sensory areas (SII and LOC) and “higher-level” multisensory convergence zones in the PPC/IPS [Beauchamp et al., 2007, 2010; Macaluso and Driver, 2001]; such a hierarchy—with a central role of the IPS—is also implied by the RHI literature [Blanke, 2012; Brozzoli, Gentile et al., 2012]. Moreover, many studies investigating the RHI have put emphasis on a fronto-parietal brain network comprising the PMv and the IPS [e.g., Gentile et al., 2013], whereby some have argued that the PMv may have more complex functions [Ehrsson et al., 2004]. The winning endogenous connectivity model served as the basis for our comparison of models with differential effective connectivity, as follows: We tested whether the RHI context would affect feedforward and/or feedback connections across the network’s hierarchy in a model space motivated by previous results on the RHI (see above). We defined a “bottom-up” model in which the RHI was allowed to modulate the connections from the SII and the LOC to the IPS, and a “top-down” model in which the RHI condition was allowed to modulate the respective reverse connections. Furthermore, for each model, modulations of the connectivity between the PMv and the IPS by the RHI were allowed (a) not at all, (b) from the IPS to the PMv (for the bottom-up model) or vice versa (for the top-down model), or (c) bidirectionally. We created two additional models: One in which the connections between all nodes were modulated by the RHI, and one in which bidirectional IPS-LOC/IPS-SII connections were modulated. Together with the null model (no modulatory effect of the RHI allowed) this resulted in a model space of nine models for each experiment and stimulation location (see Fig. 6A). Following RFX BMS to identify the most likely model given our data, we extracted all participants’ parameter estimates of the winning model, and assessed them for significance using two-tailed t-tests and Bonferroni-adjusted alpha levels to account for the number of comparisons in each case.

RESULTS

Illusory Self-Attribution of the Dummy Arm During Congruent Versus Incongruent Visuo-tactile Stimulation

In this study, we stimulated the palm, forearm, or both locations on the participant’s real hidden arm together with the corresponding location of a realistic ipsilateral dummy arm; To validate the induction of illusory self-attribution of the dummy arm by congruent (synchronous), but not incongruent (asynchronous) visuo-tactile stimulation of the two arms, we analyzed the behavioral self-attribution ratings obtained from our participants (using nonparametric tests since the ratings did not pass the Kolmogorov–Smirnov test for normality). As expected, the congruent versus incongruent visuo-tactile stimulation conditions produced a strong illusory self-attribution of the dummy arm, at the palm location (mean rating $\pm$ SD: congruent = 2.00 ± 0.73 , incongruent = -0.85 ± 1.79 , Wilcoxon signed-ranks, $n = 20$, $Z = 3.64$, $P = 0.00027$), the

TABLE I. Consistent effects of congruent versus incongruent visuo-tactile stimulation across touch locations, obtained from the conjunction of the contrasts $Palm_{CONG}$ vs $Palm_{INCONG}$, $Forearm_{CONG}$ vs $Forearm_{INCONG}$, and $Both_{CONG}$ vs $Both_{INCONG}$

Anatomical region	Peak MNI			Peak t	Peak z	P (corrected)
	x	y	z			
L middle occipital gyrus (LOC/EBA)	-40	-70	-2	2.59	5.11	$< 0.001^{a,b}$
R cerebellum	24	-64	-36	2.26	4.60	$< 0.001^a$
L middle frontal gyrus	-20	18	40	2.09	4.33	0.017^a
L precentral sulcus (PMv)	-38	10	28	2.09	4.32	$0.022^{a,c}$
L intraparietal sulcus	-42	-50	58	1.59	3.56	0.0497^c

Significance at $P < 0.05$ (FWE-corrected) based on

^aCluster-wise correction.

^bSmall volume correction using ROIs from the visual body-selectivity localizer.

^cSmall volume correction using pre-defined ROIs based on published literature.

forearm location (mean rating $\pm$ SD: congruent = 2.10 ± 0.72 , incongruent = -0.25 ± 1.86 , Wilcoxon signed-ranks, $n = 20$, $Z = 3.54$, $P = 0.00039$), and both locations (mean rating $\pm$ SD: congruent = 1.85 ± 0.93 , incongruent = -0.20 ± 1.51 , Wilcoxon signed-ranks, $n = 20$, $Z = 3.60$, $P = 0.00032$), see Figure 1D.

Brain Activity in Fronto-Parietal and Occipito-Temporal Areas Increases during Congruent Versus Incongruent Visuotactile Stimulation Across Anatomical Locations

We expected that congruent visuotactile touch information (i.e., synchronous touch on the real arm and the corresponding location on the dummy arm) would selectively engage fronto-parietal and occipito temporal brain areas [Ehrsson et al., 2004; Gentile et al., 2013; Limanowski et al., 2014; Petkova et al., 2011]. The main effect of congruent versus incongruent visuo-tactile stimulation of the two arms revealed significantly ($P < 0.05$, corrected for multiple comparisons) increased BOLD responses during congruent versus incongruent stimulation in the left LOC ($x = -40$, $y = -60$, $z = -2$, $T = 4.64$), the cerebellum ($x = -2$, $y = -60$, $z = -34$, $T = 4.39$), the left PMv ($x = -40$, $y = 12$, $z = 28$, $T = 4.00$), and a strong trend in the left IPS ($x = -40$, $y = -54$, $z = 58$, $T = 3.22$, $P = 0.078$). We expected that the responses to congruent versus incongruent visuo tactile stimulation in these brain areas would generalize across the different stimulation locations, and therefore calculated a conjunction analysis of the congruent versus incongruent stimulation contrasts for each location: $Palm_{CONG}$ vs $Palm_{INCONG}$, $Forearm_{CONG}$ vs $Forearm_{INCONG}$, and $Both_{CONG}$ vs $Both_{INCONG}$. This analysis revealed significantly ($P < 0.05$, corrected, see Fig. 2 and Table I) higher activity during visuo tactile congruence versus incongruence in the left LOC, left PMv, left IPS, and the cerebellum across the three comparisons, thus supporting the observed main effect. Further activations

obtained from this conjunction (thresholded at $P < 0.001$, uncorrected) that corresponded to regions previously reported in RHI experiments were observed in the bilateral anterior insulae (L: $x = -34$, $y = 18$, $z = -2$, $T = 1.42$, $Z = 3.30$; R: $x = 32$, $y = 22$, $z = -2$, $T = 1.43$, $Z = 3.31$). Notably, the activations we observed within the left LOC, the left IPS, and the left PMv were also contained within the activations obtained from the visual body-selectivity localizer (see Fig. 4 and Table II), as revealed by masking the results of the conjunction analysis with the visual body-selectivity contrast (mask image thresholded at $P < 0.001$).

We also sought to identify brain areas whose activity would reflect individual differences in the reported strength and prevalence of the experienced illusory self-attribution, which we quantified via compound illusion scores reflecting both the rating difference between congruent and incongruent conditions, and the prevalence of the ownership illusion in the congruent condition [see Materials and methods and Ehrsson et al., 2004]. This analysis yielded voxels within the left ($x = -26$, $y = -86$, $z = 30$, $T = 3.71$, $P < 0.001$, uncorrected) and right ($x = 36$, $y = -72$, $z = 32$, $T = 4.10$, $P < 0.05$, corrected) posterior IPS (pIPS), and, at a more liberal threshold also in the left ($x = -46$, $y = -84$, $z = 4$, $T = 2.94$, $P = 0.002$, uncorrected) and right LOC/EBA ($x = 56$, $y = -62$, $z = -10$, $T = 2.93$, $P = 0.002$, uncorrected), both contained within the EBA as localized independently, and both showing significant positive correlations with the behavioral illusion scores (Pearson's $r = 0.36$, $P < 0.01$, for each location). An additional regression analysis looking for activity correlated with only the ownership ratings of each condition revealed a cluster in the left EBA ($x = -42$, $y = -68$, $z = -6$, $T = 3.38$, $P = 0.095$, corrected; Pearson's $r = .30$, $P < 0.001$).

Finally, we tested for brain areas in which activity in the congruent relative to the incongruent stimulation conditions would be differently modulated over time (i.e., during the stimulation blocks). We compared individually centered, linearly increasing parametric modulations of the

Figure 2.

Brain areas showing consistently stronger responses to congruent versus incongruent visuo-tactile stimulation across the different stimulation locations on the real arm and the dummy arm. A conjunction analysis of the differential contrasts $Palm_{CONG}$ vs $Palm_{INCONG}$, $Forearm_{CONG}$ vs $Forearm_{INCONG}$, and $Both_{CONG}$ vs $Both_{INCONG}$ revealed significant ($P < 0.05$, corrected) voxels within the left lateral occipitotemporal cortex (LOC, largely overlapping with the extrastriate body area, EBA), the left ven-

tral premotor cortex (PMv), and the left intraparietal sulcus (IPS). The SPM{T} maps are displayed at a threshold of $P < 0.001$, uncorrected, and superimposed onto the mean normalized structural image. Bar plots depict the parameter estimates and associated standard errors at the given MNI coordinates. P: Palm locations, F: Forearm location, B: Both locations. See Table I for details.

same regressors as in the main GLM. The main effect of congruent versus incongruent stimulation revealed significantly ($P < 0.05$, corrected) stronger modulations of activity in the left SII (L: $x = -62$, $y = -18$, $z = 24$, $T = 4.44$), the left LOC ($x = -42$, $y = -68$, $z = 6$, $T = 5.15$), and in the bilateral PMv (L: $x = -52$, $y = 2$, $z = 40$, $T = 3.33$, $P = 0.055$; R: $x = 48$, $y = 2$, $z = 38$, $T = 3.75$); these activations all reached corrected significance in a conjunction across stimulation locations.

Generalizable Effects of Spatial and Temporal Congruence Versus Incongruence of Visuotactile Stimulation

As part of our analysis, we aimed to show that the effects of the main analysis (increased BOLD activations during temporal congruence versus incongruence of visuotactile stimulation) would also generalize to spatial congruence versus incongruence of visuotactile stimulation. Therefore, we compared the data obtained in the current experiment to a previously acquired dataset featuring spatially (in)congruent visuotactile stimulation (see Materials and methods). We observed a significant ($P < 0.05$, corrected) main effect of congruent versus incongruent stimulation in the left LOC

($x = -44$, $y = -72$, $z = 2$, $T = 4.72$), the cerebellum ($x = -10$, $y = -62$, $z = -40$, $T = 4.76$), the left IPS ($x = -42$, $y = -46$, $z = 56$, $T = 3.94$) and superior parietal lobule ($x = -24$, $y = -50$, $z = 50$, $T = 4.90$), as well as statistical trends in the left PMv ($x = -44$, $y = 14$, $z = 34$, $T = 3.17$, $P = 0.083$, corrected) and the left IPS ($x = -40$, $y = -48$, $z = 58$, $T = 3.14$, $P = 0.052$, corrected, at a more liberal voxel-wise threshold of $P < 0.005$). To test for the consistency of these results, we calculated a conjunction across the contrasts of the different experiments reflecting temporal or spatial (in)congruence at the palm or the forearm location, i.e., $Palm_{TEMP_CONG}$ vs $Palm_{TEMP_INCONG}$, $Forearm_{TEMP_CONG}$ vs $Forearm_{TEMP_INCONG}$, $Palm_{SPATIAL_CONG}$ vs $Palm_{SPATIAL_INCONG}$, and $Forearm_{SPATIAL_CONG}$ vs $Forearm_{SPATIAL_INCONG}$. This conjunction (Fig. 3 and Table II) revealed voxels showing consistently stronger activity ($P < 0.05$, corrected) to temporally and spatially congruent versus incongruent visuo-tactile stimulation across the locations in the left LOC/EBA and the left IPS and inferior parietal lobule (the activations in the LOC and the IPS thereby again fell within the corresponding body-selective clusters, see Table II), further in the bilateral fusiform gyri and the cerebellum. These results strongly support the involvement of the visual body-selective left LOC/EBA and IPS in the illusory self-attribution of the dummy arm.

TABLE II. Brain regions showing consistently stronger responses to both temporal and spatial congruence versus incongruence of visuo-tactile stimulation, obtained from the conjunction of the contrasts $Palm_{TEMP_CONG}$ vs $Palm_{TEMP_INCONG}$, $Forearm_{TEMP_CONG}$ vs $Forearm_{TEMP_INCONG}$, $Palm_{SPATIAL_CONG}$ vs $Palm_{SPATIAL_INCONG}$, and $Forearm_{SPATIAL_CONG}$ vs $Forearm_{SPATIAL_INCONG}$

Anatomical region	Peak MNI			Peak t	Peak z	P (corrected)
	x	y	z			
L middle occipital gyrus (EBA)	-42	-70	2	1.83	4.67	<0.001 ^{a,b}
L cerebellum	-10	-62	-42	1.81	4.63	<0.001 ^a
R fusiform gyrus (FBA)	42	-48	-20	1.71	4.45	0.007 ^b
L inferior parietal lobule	-26	-44	48	1.61	4.28	0.002 ^a
L fusiform gyrus (FBA)	-36	-48	-20	1.48	4.06	0.032 ^b
L intraparietal sulcus	-42	-48	58	1.34	3.81	0.021 ^{b,c}

Significance at $P < 0.05$ (FWE-corrected) based on

^aCluster-wise correction.

^bSmall volume correction using ROIs from the visual body-selectivity localizer.

^cSmall volume correction using pre-defined ROIs based on published literature.

Next, we compared the behavioral effects of the two experiments. There were no significant differences between the reported ownership ratings or the respective rating differences reported for temporal versus spatial (in)congruence (Wilcoxon signed-ranks, $n = 20$, all $Z_s < 1.71$, all $p_s > 0.2$): Participants reported significantly higher self-attribution of the dummy arm following temporally congruent (mean $\pm$ SD = 2.30 ± 0.66) versus incongruent (mean $\pm$ SD = 0.25 ± 1.29) and spatially congruent (mean $\pm$ SD = 1.98 ± 0.70) versus incongruent (mean $\pm$ SD = -0.43 ± 1.43) stimulation (Wilcoxon signed-ranks, $n = 20$, $Z = 3.83$, $P = 0.0001$) stimulation (Wilcoxon signed-ranks, $n = 20$, $Z = 3.99$, $P = 0.00006$). Hence temporal and spatial congruence versus incongruence of visuo-tactile stimulation of the dummy arm and the real arm both successfully induced an illusory self-attribution of the dummy arm. A conjunction analysis across the participants' behavioral illusion scores as separate covariates in a two-sample t -test revealed significant ($P < 0.05$, corrected) voxels within the left LOC/EBA ($x = -40$, $y = -74$, $z = -2$, $T = 2.81$, $Z = 4.27$), whose activity was consistently positively correlated with the behavioral illusion scores (Fig. 3D). Further significant correlations were observed in voxels in the left PPC ($x = -18$, $y = -66$, $z = 64$, $T = 3.21$, $Z = 4.76$), and in the left ($x = -14$, $y = -84$, $z = 40$, $T = 2.88$, $Z = 4.13$) and right ($x = 18$, $y = -78$, $z = 48$, $T = 2.84$, $Z = 4.30$) PPC, both spanning to the posterior IPS. Similar correlations were also observed in voxels in the left Thalamus ($x = -12$, $y = -16$, $z = 0$, $T = 2.25$, $Z = 3.56$), the right SMG ($x = 60$, $y = -18$, $z = 30$, $T = 2.33$, $Z = 3.66$), and the right LOC/EBA ($x = 50$, $y = -72$, $z = 8$, $T = 2.04$, $Z = 3.29$), but these activations did not survive correction for multiple comparisons. Correspondingly, an analogous regression analysis on the ownership ratings revealed a cluster in the left EBA ($x = -58$, $y = -66$, $z = 6$, $T = 2.16$, $Z = 3.47$, $P = 0.089$,

corrected), where activity was significantly positively correlated with the ownership ratings across experiments (Pearson's $r = .29$, $P < 0.01$ and $r = 0.23$, $P < 0.05$); further ($P < 0.001$, uncorrected) activations were observed in the right LOC/EBA ($x = 54$, $y = -60$, $z = -12$, $T = 1.89$, $Z = 3.11$) and the left pIPS ($x = -22$, $y = -74$, $z = 26$, $T = 2.44$, $Z = 3.84$). These results imply that the left EBA (and IPS) reflected individual differences in the experienced intensity of the illusory self-attribution of the dummy arm across both touch locations and types of (in)congruence.

Brain Regions Showing a Preferential Response to Vision of Human Body Parts

We hypothesized that brain areas involved in the visual processing of the body play an important role in the self-attribution of body parts. To identify such brain areas, we implemented an independent functional localizer run, in which we presented our participants pictures of human hands and feet versus motorcycle parts [following Urgesi et al., 2007]. The contrast *Body parts vs Objects* (Fig. 4 and Table III) revealed the strongest activity ($P < 0.05$, corrected for multiple comparisons) in bilateral LOC, matching coordinates previously reported for the body-selective extrastriate body area [EBA; e.g., Astafiev et al., 2004; Costantini et al., 2011; Downing et al., 2001]. These large clusters each spanned to more inferior parts of the temporal and fusiform gyri, thus including locations reported for the body-selective fusiform body area [FBA; e.g., Schwarzklose et al., 2005]. Interestingly, significant activations were also observable in frontal and parietal areas, namely, bilaterally in the SMG, anterior parts of the IPS and superior parietal cortex, the PMv, and in the right inferior frontal gyrus.

Figure 3.

Consistent Increases in Functional Coupling during Congruent Versus Incongruent Visuo-tactile Stimulation of each Anatomical Location

In the next step, we sought to illuminate the illusion-related connectivity changes in the network implied by our standard GLM analyses. To this end, we first examined changes in functional coupling of the key nodes of this network using psycho-physiological interaction analyses (PPIs) with seed regions in the left LOC, left IPS, and left PMv. To test for the consistency of these changes, we calculated a conjunction analysis of the congruent versus incongruent stimulation contrasts for each location, that is: $Palm_{CONG} vs Palm_{INCONG}$, $Forearm_{CONG} vs Forearm_{INCONG}$, and $Both_{CONG} vs Both_{INCONG}$. This (see Fig. 5A and Table IV) revealed consistent, significantly ($P < 0.05$, corrected) increased functional coupling during congruent versus incongruent stimulation of the left IPS with regions in the bilateral LOC/EBA, the left PMv, and the left SI. The left PMv and the left LOC each showed similar significant ($P < 0.05$, corrected) increases in functional coupling with the bilateral LOC/EBA, and the left SI and SII during congruent versus incongruent touch across all locations. We also compared the connectivity of each seed region across stimulation locations and type of (in)congruence [temporal, present experiment, and spatial, Limanowski et al., 2014] by calculating a group-level conjunction analysis of the PPIs corresponding to the contrasts $Palm_{TEMP_CONG} vs Palm_{TEMP_INCONG}$, $Forearm_{TEMP_CONG} vs Forearm_{TEMP_INCONG}$, $Palm_{SPATIAL_CONG} vs Palm_{SPATIAL_INCONG}$, and $Forearm_{SPATIAL_CONG} vs Forearm_{SPATIAL_INCONG}$, for each seed region. The results of this analysis (Fig. 5B, see Table IV for details) replicated the connectivity pattern observed for the main experiment: The left IPS also showed consistent,

The effects of congruent versus incongruent visuo-tactile stimulation generalized across touch locations for spatial and temporal (in)congruence. **A:** Schematic depiction of the four differential contrasts examined in the conjunction analysis: $Palm_{TEMP_CONG} vs Palm_{TEMP_INCONG}$, $Palm_{SPATIAL_CONG} vs Palm_{SPATIAL_INCONG}$, $Forearm_{TEMP_CONG} vs Forearm_{TEMP_INCONG}$, and $Forearm_{SPATIAL_CONG} vs Forearm_{SPATIAL_INCONG}$. **B:** SPM{T} maps of the significant activations obtained from the conjunction of all four contrasts located in the left IPS and the left LOC/EBA ($P < 0.05$, corrected, displayed at a threshold of $P < 0.001$, uncorrected, and superimposed onto the mean normalized structural image). Bar plots depict the parameter estimates and associated standard errors at the given MNI coordinates for each stimulation type and location (P: Palm, F: Forearm). See Table II for details. **C:** A conjunction analysis of the effects of the illusion scores as separate covariates for each type of (in)congruence revealed significant positive correlations with the reported illusory self-attribution within left LOC/EBA ($P < 0.05$, corrected). The plots show significant correlations of left LOC/EBA response differences between congruent and incongruent stimulation, and the respective illusion scores (Pearson's $r = .42$, $P < 0.01$, and $r = .41$, $P < 0.01$).

Figure 4.

Significant activations obtained from the joint visual body-selectivity localizer (contrast *Body parts* vs *Objects*, sample stimuli shown left). Voxels that showed a strong preferential response to vision of human body parts versus objects were located bilaterally in the extrastriate visual cortex, matching reported locations of the extrastriate body area (EBA). Further significant

activations were located bilaterally in anterior parts of the intraparietal sulcus (IPS), the supramarginal gyrus (SMG), and the ventral premotor cortex (PMv). The group-level surface render is displayed at a threshold of $P < 0.001$, uncorrected; labels mark significant activations ($P < 0.05$, corrected for multiple comparisons), see Table III for details. L/R: left/right hemisphere.

significantly increased functional coupling with the bilateral LOC/EBA, the left PMv, and the left SI and SII. The left PMv and the left LOC again showed significant ($P < 0.05$, corrected) increases in functional coupling with the bilateral LOC/EBA and the left SI and SII. Notably, in all analyses, the activations in LOC always fell within the visual body-selective EBA ($P < 0.05$, small volume corrected within mask images thresholded at $P < 0.001$).

In sum, the results of the PPI analyses suggest an overall increased connectivity between left-hemispheric fronto-parietal areas—the IPS and the PMv—with the LOC/EBA during the illusory self-attribution of a dummy arm induced by congruent visuotactile stimulation. Crucially, this connectivity pattern generalized across stimulation locations and type of visuotactile (in)congruence, thus supporting the results of our standard GLM analysis.

Dynamic Causal Modeling

Our standard GLM and PPI connectivity analyses together suggest that the self-attribution of the right dummy arm depended on interactions of left-hemispheric fronto-parietal areas with occipitotemporal areas. However, from correlation analyses like the PPI, one cannot clearly infer any directionality of the mutual influences among the nodes of a network. Therefore, we next constructed a dynamic causal model, comprising the left LOC, IPS, and PMv, and, as an input area for somatosensory information, the left SII. To ensure the generalizability of our results, we performed the same DCM analysis for each location, i.e., for the contrasts *Palm*_{CONG} vs *Palm*_{INCONG}, *Forearm*_{CONG} vs *Forearm*_{INCONG}, and *Both*_{CONG} vs *Both*_{INCONG}. In a first step, we examined a model space of all possible combinations of endogenous connectivity

TABLE III. Brain regions preferentially responding to vision of human body parts: Significant activations obtained from the visual body-selectivity localizer (contrast *Body parts* vs *Objects*)

Anatomical region	Peak MNI			Peak t	Peak z	P (corrected)
	x	y	z			
R middle temporal gyrus (EBA)	54	−68	2	10.22	Inf.	<0.001
L middle temporal gyrus (EBA)	−50	−74	6	10.11	Inf.	<0.001
L inferior temporal gyrus (FBA)	−42	−48	−18	6.88	6.57	0.003
R precentral gyrus (PMv)	52	10	32	5.47	5.31	<0.001
R postcentral gyrus / superior parietal lobule	30	−38	52	5.08	4.95	<0.001
R supramarginal gyrus and intraparietal sulcus	50	−24	38	5.03	4.90	<0.001
L supramarginal gyrus and intraparietal sulcus	−56	−24	36	4.98	4.86	<0.001
L precentral gyrus (PMv)	−52	8	28	4.76	4.65	0.002
R inferior frontal gyrus	50	28	22	4.22	4.14	0.043

Significance at $P < 0.05$ based on cluster-wise FWE-correction.

Figure 5.

Enhanced functional coupling of frontal and parietal regions with occipitotemporal regions during the rubber hand illusion. Psycho-physiological interaction analyses (PPIs) revealed consistently increased connectivity of the left IPS and the left PMv with the LOC/EBA during congruent versus incongruent visuo-tactile stimulation across stimulation locations and type of (in)congruence, as revealed by conjunction analyses across the individual PPI analyses. **A:** Results of the conjunction across the three PPIs for temporally congruent versus incongruent visuo-

tactile stimulation at the palm, forearm, and both locations (main experiment). **B:** Results of the conjunction across the corresponding PPIs from each seed region during spatially and temporally congruent versus incongruent visuo-tactile stimulation at the palm and forearm location. SPM{T} maps displayed at a threshold of $P < 0.001$, uncorrected, superimposed onto the mean normalized structural image. White circles mark significant ($P < 0.05$, corrected) activations. See Table IV for details.

among these nodes (i.e., connectivity independent of the illusion context, but related to visuotactile stimulation *per se*), thereby assuming connections of the IPS to all other nodes. Random-effects Bayesian model selection (RFX BMS) yielded the same winning model in each case, featuring bidirectional connections between SII-IPS, LOC-IPS, and IPS-PMv (model exceedance probabilities: 96.6% at the palm location, 99.8% at the forearm location, and 78.6% at both locations). This model therefore served as the architectural basis for the examination of RHI-evoked modulations of connectivity within this network (the resulting effective connectivity model space is described in Figure 6A, see Materials and methods for details).

In each of these comparisons, the model with the highest model exceedance probability (Model 4: 49.2% at the palm location, 64.2% at the forearm location, 44.9% at both locations) was the model featuring a modulation of the connections from the SII to the IPS and from the LOC to the IPS under congruent versus incongruent stimulation. The analysis of the parameter estimates of the winning model's DCM.B matrix revealed that in each case (palm, forearm, or both locations stimulated) the connectivity from the SII and LOC to the IPS was signifi-

cantly enhanced by congruent as compared with incongruent stimulation (two-tailed t -tests, all $ps < 0.025$, using Bonferroni-adjusted alpha levels to account for the number of comparisons). Additionally, we tested whether this model would also best fit our previous dataset (spatially congruent versus incongruent stimulation), with which we had compared the present data in the standard GLM analyses (see above). Therefore, we created and compared the same model space for spatially congruent versus incongruent stimulation at the palm and the forearm location. Notably, RFX BMS identified the same winning endogenous connectivity (model exceedance probabilities 82.2% and 55.0%), and more importantly, also the same winning effective connectivity (Model 4; model exceedance probabilities 52.6% at the palm location and 53.2% at the forearm location), as for the current experiment. Thus the RHI context also modulated the bottom-up connections from the SII and LOC to IPS; the DCM.B parameter estimates of these modulations reached significance for the SII to IPS connection (palm location: $+0.76$, $P = 0.0030$; forearm location: $+0.62$, $P = 0.0019$) but not for the LOC to IPS connection (palm location: -0.09 , $P = 0.68$; forearm location: $+0.12$, $P = 0.29$). In sum, our

Figure 6.

Dynamic causal modeling results. **A:** The effective connectivity model space for Bayesian model selection was defined based on our GLM results and according to hypotheses about the mechanisms underlying the RHI (see Materials and methods), and consisted of nine models; top row: a “null model” without any allowed modulations (model 1, this model was identified as the most likely endogenous connectivity pattern of the nodes in a previous step), a model with bidirectional modulations between SII-IPS and LOC-IPS, and a model with additional bidirectional modulations of IPS-PMv connectivity; middle row: “bottom-up” models allowing modulations of connections from SII to IPS and LOC to IPS, and additional modulation of bottom-up or bidirectional IPS-PMv connections; bottom row: “top-down” models allowing the modulation of the respective reverse connections.

DCM results strongly suggest that the processing of visuo tactile stimuli in peripersonal space depends on information exchange within a hierarchical network involving the SII and LOC at lower levels, and the IPS and PMv at higher levels, whereby visuo tactile temporal and spatial congruence modulates the bottom-up connections from the SII and LOC to the IPS.

DISCUSSION

This study demonstrated the involvement of a predominantly left-lateralized network comprising PMv, IPS, and visually body-selective LOC in the self-attribution of a right dummy arm. Our analyses revealed consistent increases in the functional coupling of the PMv and the IPS with the LOC, and consistent modulations of

Driving input entered SII and LOC. **B:** RFX BMS identified the same winning model (Model 4) in each case (congruent vs incongruent stimulation at the palm, forearm, or both locations). Shown are the model exceedance probabilities, the endogenous connectivity of the winning model with averaged coefficients extracted from the DCM.A matrix (connectivity regardless of context), and the significant modulations of this model’s connectivity from the SII to the IPS and from the LOC to the IPS, with averaged coefficients extracted from the DCM.B matrix. Bold arrows mark significant connections or modulations; the significance of all coefficients was assessed using two-tailed t-tests and Bonferroni-adjusted alpha levels ($0.05/10 = 0.005$ for the endogenous connections and $0.05/2 = 0.025$ for the modulated connections).

pathways from earlier sensory areas in the LOC and SII to higher-level integrative brain areas in the IPS during illusory self-attribution. These results offer important new insights into the nature of the interactions within the brain network underlying body ownership [Blanke, 2012; Ehrsson, 2012; Gallagher, 2000; Graziano and Botvinick, 2002; Makin et al., 2008; Tsakiris, 2010], as discussed in the following.

Processing of Congruent Visuotactile Information in Body-Selective Brain Areas Enables the Rubber Hand Illusion across Different Anatomical Locations

Congruent (synchronous) versus incongruent (asynchronous) visuo-tactile stimulation of the palm, forearm, or

both locations together on a realistic dummy arm and the real counterpart successfully induced an illusory self-attribution of the dummy arm, as demonstrated by the behavioral ratings. Conjunction analyses of the corresponding BOLD contrasts revealed consistently stronger responses to congruent versus incongruent stimulations in the left LOC, left IPS, and in the left PMv, as well as in the cerebellum. Temporal congruence of stimuli from multiple sensory modalities [as typically used in RHI experiments, e.g., Botvinick and Cohen, 1998; Ehrsson et al., 2004; Tsakiris and Haggard, 2005] is one crucial rule that the brain uses to decide whether to integrate these stimuli into a coherent percept—another such rule is the spatial co-occurrence of stimuli [Driver and Spence, 2000; Meredith and Stein, 1986]. Importantly, we replicated the involvement of the left LOC and the left IPS in the illusory self-attribution of the dummy arm by comparing the data of the current experiment with a dataset acquired using the same setup and fMRI scanner, in which the spatial, but not temporal, congruence of stimulation was manipulated [Limanowski et al., 2014]. Moreover, left LOC/EBA activity was consistently positively correlated with the behavioral illusion scores across locations and type of (in)congruence, although due to the post-hoc assessment of the behavioral ratings these correlations have to be considered with some caution. In sum, our results generalized across anatomical locations according to the spatio-temporal principles of multisensory integration [Ehrsson, 2012; Meredith and Stein, 1986].

The observed frontal, parietal, and occipitotemporal activations fit well with previous findings: The IPS and PMv are involved in processing stimuli in the PPS surrounding the upper limb [Bremmer et al., 2001; Graziano and Cooke, 2006; Grefkes and Fink, 2005; Lloyd et al., 2002; Rizzolatti et al., 1997]. Activations of the IPS and PMv by the RHI have hence been interpreted as reflecting the remapping of the PPS onto the dummy hand and the production of a coherent body ownership experience by multisensory integration [Brozzoli et al., 2012; Ehrsson et al., 2004; Gentile et al., 2013; Petkova et al., 2011]. Makin et al. [2007] reported a preferential response to visual stimuli in the space around real or dummy hands in the IPS, and notably, also in the LOC. Correspondingly, a body-selective area in the LOC has been shown to play a role during the RHI [Limanowski et al., 2014; Wold et al., 2014].

Using an independent functional localizer, we were able to show that across all comparisons, the areas within the left LOC and the left IPS (and partly also the PMv) that responded more strongly to congruent versus incongruent stimulation fell within areas that also preferentially respond to mere vision of the body: The visual presentation of human body parts versus objects produced strong bilateral BOLD responses in the LOC, corresponding to reported locations of the EBA, and frontoparietal areas including the IPS, the SMG, and the PMv. These results suggest that the visual body-selectivity of RHI-related

regions is indeed no coincidence, in line with previous speculations: The processing of visual stimuli on a hand is enhanced compared with on an object, which may be caused by the “attribution of these stimuli to the body” [Whiteley et al., 2004]. PPS processing in frontoparietal areas may also be modulated by mere vision of body parts [Graziano et al., 2000; Làdavas, 2002], and correspondingly, a visual body-selectivity of the IPS has been suggested [Konen and Haggard, 2014; Zopf and Williams, 2013]. A particularly promising candidate where modulatory effects of vision of the body on processing of visuo-somatosensory body-related information could be implemented is the EBA [Costantini et al., 2011; Haggard et al., 2007], which has traditionally been considered to process unimodal visual features of the human body [Downing et al., 2001]. However, recent studies have demonstrated a modulation of EBA activity in congenitally blind people during haptic exploration of body-shaped objects [Kitada et al., 2014, 2009], even when such haptic information was transmitted via an auditory sensory-substitution algorithm [Striem-Amit and Amedi, 2014], thus arguing against a purely unimodal visual function of the EBA. Crucially, the EBA is activated during planning and producing actions with one’s hand even in the absence of vision [Astafiev et al., 2004], suggesting that it also processes somatosensory (proprioceptive) information. Correspondingly, the EBA has been implied in processing action knowledge [Bracci et al., 2010], in predicting actions from visual action cues [van Elk, 2014], and in action imitation versus observation [Jackson et al., 2006]. These findings extend on previous proposals of cross-modal interactions in LOC [Beauchamp et al., 2007] in that they suggest a role of the EBA in a perception-action system that differentiates between oneself and others [Astafiev et al., 2004; Jeannerod, 2004]. Specifically, it has been speculated that the EBA might contribute to self-other differentiation via the detection of “violations of internal, possibly multimodal, body or action representations and incoming visual signals” [David et al., 2007, 2009]. Notably, David et al. [2007] reported increased functional coupling between the EBA and PPC when participants correctly identified mismatches between their movements and manipulated visual feedback, and Möhring et al. [2014] have speculated that the EBA may contribute to sensory-motor integration in the inferior parietal lobule. The fact that disrupting EBA activity using rTMS increased the proprioceptive mislocalization of one’s hand during the RHI [Wold et al., 2014] could be due to the interference with the EBA’s detecting multisensory mismatches (and signaling them to the IPS). In conjunction with these reports, our results show that body-selective regions in the IPS and LOC are essentially involved in the self-attribution of a dummy arm during the RHI, and also suggest a similar involvement of the PMv. Building up on this, our connectivity analysis sheds new light on the interplay of the frontoparietal circuit with the LOC/EBA during the RHI.

TABLE IV. Results of the PPI analysis

Anatomical region	Peak MNI			Peak <i>t</i>	Peak <i>z</i>	<i>P</i> (corrected)
	<i>x</i>	<i>y</i>	<i>z</i>			
Brain regions showing consistently increased functional connectivity with left LOC, left IPS, or left PMv during temporal visuo-tactile congruence versus incongruence across stimulation locations (main experiment)						
<i>Seed region: L IPS</i>						
L middle occipital gyrus (EBA)	−42	−72	14	3.06	5.64	< 0.001 ^{a,b}
L precentral gyrus (PMv)	−56	4	38	3.02	5.59	0.012 ^{a,c}
R middle temporal gyrus (EBA)	58	−66	−2	2.84	5.34	< 0.001 ^{a,b}
L postcentral gyrus (SI)	−60	−20	36	2.59	4.98	0.012 ^{a,d}
L precentral gyrus (PMd)	−34	−4	50	2.39	4.70	< 0.001 ^a
<i>Seed region: L PMv</i>						
R middle temporal gyrus (EBA)	54	−68	10	3.67	6.47	< 0.001 ^{a,b}
R inferior frontal gyrus	52	38	−6	2.82	5.31	0.001 ^a
L middle occipital gyrus (EBA)	−46	−76	8	2.36	4.66	0.006 ^{a,b}
L superior temporal gyrus (SII)	−62	−30	16	2.24	4.48	0.003 ^d
L postcentral gyrus (SI)	−60	−18	32	1.80	3.83	0.034 ^d
<i>Seed region: L LOC</i>						
L middle occipital gyrus (EBA)	−38	−76	2	2.47	4.82	< 0.001 ^{a,b}
R middle temporal gyrus (EBA)	50	−66	4	1.93	4.02	0.038 ^{a,b}
L supramarginal/postcentral gyrus (SI)	−62	−20	40	1.89	3.96	0.022 ^d
L supramarginal gyrus (SII)	−52	−24	18	1.68	3.66	(0.060) ^d
Brain regions showing consistently increased functional connectivity with left LOC, left IPS, or left PMv during temporal and spatial congruence versus incongruence of visuo-tactile stimulation across stimulation locations						
<i>Seed region: L IPS</i>						
R middle temporal gyrus (EBA)	50	−68	0	4.51	Inf.	<0.001 ^{a,b}
L middle occipital gyrus (EBA)	−52	−74	2	3.33	7.06	<0.001 ^{a,b}
L precentral gyrus (PMv/d)	−54	2	38	2.64	5.96	0.026 ^{a,c}
L supramarginal gyrus (SI/SII)	−60	−20	38	2.47	5.67	<0.001 ^{a,d}
L precentral grus	−40	−8	58	2.25	5.32	<0.001 ^a
R superior parietal lobule	28	−66	62	1.92	4.77	<0.001 ^a
R postcentral gyrus (SI)	64	−16	34	1.82	4.60	0.008 ^a
R superior temporal gyrus (SII)	62	−30	14	1.81	4.58	<0.001 ^a
R precentral gyrus	44	2	34	1.43	3.94	0.018 ^a
L inferior frontal gyrus (PMv)	−44	8	22	1.34	3.78	0.038 ^c
<i>Seed region: L PMv</i>						
R middle temporal gyrus (EBA)	56	−68	8	4.01	Inf.	<0.001 ^{a,b}
L middle frontal gyrus	−44	14	50	2.34	5.46	0.008 ^a
L superior temporal gyrus (SII)	−60	−32	16	2.28	5.37	0.003 ^a
L precentral gyrus	−42	−8	48	2.17	5.19	<0.001 ^a
L inferior frontal gyrus	−46	44	−8	2.02	4.94	<0.001 ^a
L middle occipital gyrus (EBA)	−50	−78	8	1.97	4.85	<0.001 ^{a,b}
R postcentral gyrus	36	−40	58	1.91	4.76	<0.001 ^a
R middle frontal gyrus	38	−6	54	1.76	4.50	0.022 ^a
L intraparietal sulcus	−38	−54	58	1.70	4.39	0.032 ^{a,c}
R postcentral gyrus	62	−12	36	1.69	4.37	0.0021 ^a
<i>Seed region: L LOC</i>						
L inferior occipital gyrus (EBA)	−48	−78	−8	2.11	5.08	<0.001 ^{a,b}
R inferior occipital gyrus (EBA)	54	−72	−14	2.01	4.92	<0.001 ^{a,b}
L supramarginal/postcentral gyrus (SI)	−62	−20	40	1.80	4.56	0.009 ^d
L postcentral gyrus (SII)	−56	−20	22	1.64	4.30	(0.051) ^d

Significance at $P < 0.05$ (FWE-corrected) based on^aCluster-wise correction.^bSmall volume correction using ROIs from the visual body-selectivity localizer.^cSmall volume correction using predefined ROIs based on published literature.^dSmall volume correction using ROIs from the tactile localizer.

The Rubber Hand Illusion Consistently Modulates Bottom-Up Connectivity within a Hierarchical Cortical Network

Our PPI analyses revealed a significantly increased functional coupling of the left IPS and the left PMv with the LOC/EBA under congruent versus incongruent visuotactile stimulation, consistent across all stimulation locations and type of (in)congruence. These results demonstrate an increased communication within a network comprising frontoparietal and occipitotemporal regions during the RHI, replicating previous reports of increased functional coupling of the left IPS with the PMv and the LOC during paradigms inspired by the RHI [Gentile et al., 2013; Guterstam et al., 2013]. Furthermore, our results show that the left PMv also increases its communication with the IPS and the LOC during the RHI.

Crucially, our DCM analysis extends these findings by demonstrating an information exchange between hierarchically lower areas in the SII and the LOC with the IPS, and between the IPS and the PMv. Our most important finding is that in this model, the connections from both the SII and the LOC to the IPS were significantly enhanced under the RHI, meaning that activity within the IPS was more strongly causally influenced by modulations of the bottom-up connections from the SII and the LOC. Notably, RFX BMS yielded the same winning models (featuring the same endogenous and effective connectivity) for stimulation at the palm, forearm, or both locations, and even when this analysis was repeated on the dataset implementing spatial (in)congruence. Although the model exceedance probabilities may perhaps not be considered very high, no other model lent itself as an alternative; this consistency across all comparisons suggests that the identified modulations of bottom-up connectivity might reflect a general process underlying the RHI.

There is one intriguing interpretation of these results, which fits nicely with our knowledge about the RHI and with the assumptions about cortical information flow made by predictive coding [Friston, 2005; Friston and Stephan, 2007], namely, that the brain tries to infer the most likely causes of its sensory input via the inversion and optimization of the current hierarchical generative model of the world. The latent architecture of the DCM selected by our formal Bayesian model comparison is compatible with a predictive coding scheme, in which hierarchically lower areas in the secondary somatosensory and extrastriate visual cortex communicate with higher-level multimodal convergence zones in the IPS, from where information is potentially exchanged with the PMv. According to the principles of predictive coding, cortical activity at each processing stage of a hierarchical network is determined by bottom-up, forward-flowing information and its comparison with the feedback provided by the predictions of the next-highest level about the current state, conveyed via top-down connections. Importantly, the informative quantity passed from lower to higher levels is the *error* that

arises from unpredicted data. It has been speculated that such information exchange may account for the RHI [Apps and Tsakiris, 2014; Hohwy, 2013; Limanowski and Blankenburg, 2013]. During the RHI, there is conflicting information about one's limb's position in space: Whereas vision of touch seems to recalibrate and represent the reference frame of the PPS in dummy arm-centered coordinates, somatosensation represents touch information still in PPS coordinates centered on the real arm [Makin et al., 2008; Macaluso and Maravita, 2010]. This unpredicted incompatibility of information about the location of the touched arm is likely to elicit corresponding errors—in contrast to the incongruent (control) conditions, where seen and felt touch are clearly dissociable and attributable to different arms based on their spatiotemporal incongruence, and therefore no such intersensory conflict and related prediction error should arise. The results of our DCM analysis may offer an explanation for how such illusion-evoked prediction errors are generated and propagated within the brain network involved in establishing body ownership and the peripersonal space.

We propose that first, the LOC/EBA associates the touch seen on the dummy arm and the touch felt on one's real arm due to their spatio-temporal congruence on a body part within the peripersonal space—by this cross-modal interaction, the seen touch becomes self-relevant [Macaluso and Maravita, 2010]. The observed significant positive correlation of LOC/EBA activity and the behavioral illusion scores supports this interpretation, since the stronger the interaction of vision and touch (the interplay of seen and felt touches), the higher the chances of the RHI actually emerging. However, following this cross-modal interaction, there is a mismatch between the coordinates in which the seen touch is now represented (i.e., centered onto the dummy arm), and the predictions about one's arm's location made by the higher-level IPS. The increases in the BOLD signal within the LOC/EBA revealed by our standard GLM analysis may reflect the generation of such a prediction error, and the correspondingly significantly enhanced connections from LOC/EBA to IPS under the RHI may reflect the feedforward communication of this prediction error to the hierarchically higher IPS. Given the knowledge we have about the RHI [Ehrsson, 2012; Makin et al., 2008; Tsakiris, 2010] and the functions of the IPS [Avillac et al., 2007; Beauchamp et al., 2010; Bremmer et al., 2001; Graziano and Cooke, 2006], we propose that the IPS tries to counter this error by integrating the multisensory touch information and recalibrating the coordinates of the somatosensory reference frame onto the visual reference frame. This could suppress (some) prediction error in the lower-level LOC/EBA. However, the IPS would also signal these “adjusted” predictions to the SII, where they do not match the incoming somatosensory information (i.e., the proprioceptive information about the position of one's real arm and the skin-based information about touches on it), and hence generate

another (somatosensory) prediction error. In line with this speculation, our winning model also shows an enhancement of the connections from the SII to the IPS, which could indicate the forward-propagation of such a prediction error.

In all models, the endogenous connectivity pattern revealed enhanced connections from the IPS to the LOC. This could reflect enhanced top-down attention to the visual modality during the processing of stimuli in the PPS. According to predictive coding, attention interacts with predictions via top-down connections by enhancing the precision of the prediction errors in a relevant modality [Feldman and Friston, 2010; Kok et al., 2012]. Vision is more informative than somatosensation for spatial and temporal judgments [Ernst and Bühlhoff, 2004], thus it seems reasonable that the brain should try to put more weight on the incoming information from the visual cortex during processing visuo-tactile information in PPS [Ernst and Banks, 2002; Ma and Pouget, 2008; Pavani et al., 2000]. Using a paradigm similar to the RHI, Beauchamp et al. [2010] indeed showed that the connectivity between the IPS and the secondary somatosensory or extrastriate visual cortex strengthened depending on which modality was more reliable.

Similarly, we observed enhanced endogenous connections from the IPS to the PMv, which could indicate a potential information transfer about the PPS from parietal to frontal areas, in accordance with previous speculations [Graziano and Cooke, 2006; Makin et al., 2008]. Predictive coding states that representations at higher levels are encoded more abstractly, and at longer timescales, and some authors have argued for a more complex role of the PMv than the IPS in the RHI [Ehrsson et al., 2004]. The information transmitted from the IPS to the PMv could thus perhaps be a higher-level prediction error about current PPS representations that change depending on the type of (co)stimulation. The fact that our winning model did not feature modulations of PMv connectivity could perhaps be due to the duration of illusion induction being not intensive enough, or simply not long enough to fully engage the PMv [e.g., Petkova et al., 2011 used 30 s blocks]. Interestingly, in the left SII, left LOC, and in the bilateral PMv, activity in the congruent versus incongruent stimulation blocks was also differently modulated over time. This could hint toward a possible formation of prediction errors over time in brain areas that cannot (fully) adjust to the incorporation of the dummy arm. For example, the stronger PMv activity modulations could point towards a relatively slow formation of a high-level prediction error, whereas the stronger modulations in the SII and the LOC could mean that the prediction errors from vision and touch indeed mutually influence each other via the IPS.

Although in conjunction, our results comply with the idea that the information flow within the brain network underlying body ownership follows a predictive coding scheme (i.e., the forward-propagation of multisensory

prediction errors), predictive coding is only one candidate explanation for the mechanisms underlying the brain's hierarchical inference about the world and the body. For example, the activation of the IPS and the PMv may also be interpreted as reflecting processes of multisensory integration that produce the coherent ownership experience [Ehrsson, 2012], since there is evidence for neuronal populations in these areas showing non-linear responses (i.e., enhanced or depressed relative to the sum of unimodal input) to spatially or temporally congruent multisensory stimuli, which may indicate such integrative processes (Ehrsson, 2012; Gentile et al., 2011; Maravita et al., 2003). An alternative interpretation of the enhanced connectivity to the IPS could be that activity in the SII and the LOC is evoking multisensory integration processes in the IPS when visual and tactile information is congruent, but not when it is incongruent. Note that this interpretation does not necessarily contradict a predictive coding scheme—the resolution of intersensory conflict via multisensory integration could also be seen as an updating of higher-level representations in these areas to suppress prediction errors at lower levels. Next, it should also be pointed out that the parameter estimates of the DCMs calculated on the Limanowski et al. [2014] dataset showed some differences to those of the main experiment. This may be attributable to differences of the spatially-incongruent experimental design: Unlike the temporally incongruent design, this design involved touching different body parts (i.e., different parts of the real arm) during the control condition than the RHI condition, which might be differently “surprising” for the brain or involve more spatial attention than the RHI condition, and could explain the difference in LOC-IPS modulations in these models. However, both datasets were best fit by the same model, featuring the same endogenous coupling and modulation of bottom-up connectivity from the SII and the LOC to the IPS under the illusion context.

Our findings could be extended by future studies implementing online behavioral measures, which would allow assessing illusory body ownership before, during, and after stimulation. Such designs could be used to clarify the specific role of the PMv during illusory body ownership and thus perhaps shed light on why our DCM analysis did not imply a strong modulation of the IPS-PMv pathway by the RHI, somewhat in contrast to previous assumptions about the importance of fronto-parietal interplay during the illusion [Gentile et al., 2013; Guterstam et al., 2013]. Likewise, although the most parsimonious endogenous connectivity model identified by all of our RFX BMS comparisons did not suggest PMv-SII connections, possible interactions between these areas due to their anatomical connections (Cipolloni and Pandya, 1999) might still be worth investigating in future experiments. Further, we observed increased cerebellar activity during congruent visuo-tactile stimulation, although none of the seed regions of our PPI analysis increased its functional coupling with the cerebellum. Although most models of

body ownership do not include subcortical structures [e.g., Makin et al., 2008; Tsakiris, 2010], there is some evidence for a role of the cerebellum [Gentile et al., 2013; Guterstam et al., 2013] or the putamen [Petkova et al., 2011] in multisensory processes underlying body ownership, and this role should be addressed by future research. Finally, our results emphasize areas in the left hemisphere during the self-attribution of a right dummy arm, consistent with the results of other right-hand RHI paradigms [Ehrsson et al., 2004; Gentile et al., 2013; Petkova et al., 2011], BOLD responses touch to the right hand across the body midline [Lloyd et al., 2002], and with evidence for a left-lateralized hand-preference within the LOC [Astafiev et al., 2004; Bracci et al., 2010, 2012; Zopf and Williams, 2013]. Future research should investigate whether such a lateralization is due to stimulation of the contralateral hand, or whether it generalizes to the ipsilateral hand.

CONCLUSION

This study demonstrated that visually body-selective areas in the frontal, parietal, and occipito temporal cortex work in concert during the illusory self-attribution of a dummy arm. The information flow revealed by the DCM analysis supports the importance of visuomotor interaction and integration during the illusory self-attribution of body parts, and the hypothesis that the underlying multisensory integration mechanisms are implemented in the IPS and its connections. Crucially, our results suggest that the processing of touch information within the PPS during the RHI is not restricted to frontoparietal areas, but involves information exchange with the occipitotemporal cortex, most likely with the EBA. The hierarchical inference underlying illusory self-attribution during the RHI could be implemented within this brain network according to the principles of predictive coding: Thus congruent visuotactile information on a body part interacts in hierarchically lower areas in the LOC, which may then detect violations of multisensory predictions about one's arm's position in space and pass the corresponding prediction error on to the higher-level IPS. Adjusting these predictions by the IPS may explain away this error, while eliciting another (somatosensory) prediction error about the touched arm's location in the SII. Importantly, the interpretation of our results in terms of predictive coding rests on the assumption of a pre-existing hierarchical model that constantly generates predictions about the self and evaluates the incoming data in the light of these predictions, thus acknowledging the necessary interaction between current sensory input and the constraints of an internal body model proposed by traditional accounts of the RHI. In sum, our findings lend support to the multisensory hypothesis of body ownership and propose predictive coding as a plausible implementation of the underlying cortical information exchange and integration.

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