Robust neurophysiological correlates of the rubber hand illusion emerge at early latencies but are unrelated to changes in skin conductance accompanying the illusion

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Abstract

The neurophysiological processes reflecting the illusory ownership over an artificial limb remain debated. We used multivariate (cross-)classification of evoked EEG responses to probe for signatures of the illusion that robustly generalize across a number of confounding factors identified based on previous studies: the spatial arrangement of limbs, controls involving either a misaligned artificial object or participant's own hand, and which provide evidence of illusory ownership directly within an experimental trial. Our results show that sensory-evoked responses differ between illusion and non-illusion epochs from early latencies on. While these responses exhibit distinct sensitivity to the experimental factors at distinct times, around 140 ms the evoked activity reflects the illusory state robustly across experimental manipulations. This neurophysiological signature of illusory ownership was not correlated with increases in skin conductance accompanying the illusion, suggesting that neurophysiological and bodily signals reflect distinct processes related to the embodiment of an artificial limb.

1. Introduction

The bodily sense of ownership is often studied using illusions such as the rubber hand (Botvinick and Cohen, 1998), during which participants watch an artificial hand being touched in synchrony with their own but occluded hand. The synchronous sensory stimulation of, or near, their own and the rubber hands results in the illusory experience of the rubber hand becoming embodied (Tsakiris and Haggard, 2005; Blanke, 2012). Despite its widespread use to study bodily self-consciousness and multisensory body perception, the neurophysiological correlates of the rubber hand illusion (RHI) have remained controversial.

Using neurophysiological measurements with high temporal resolution, such as EEG or MEG, several studies investigated the sensory-evoked potentials produced by the repetitive visuo-tactile stimulation and asked when and how the cerebral encoding of the tactile stimulus is affected by the illusory body ownership (termed illusory state in the following). Some studies reported illusion-correlates at early (~50ms) latencies relative to the stimulation events (Zeller et al., 2015) and advocated for a low-level origin of the illusion-related processes. Other studies, in contrast, found correlates only at much longer latencies and implied high-level cognitive or attention-related processes as source of these neurophysiological correlates (Aspell et al., 2012; Faivre et al., 2017; Peled et al., 2003; Rao and Kayser, 2017). However, there is no agreement whether the observed effects emerge as consequence of the multisensory stimulation, attentional differences or reflect ownership of the rubber hand.

One reason for this may be differences in the experimental procedures used to induce the illusion. For example, the sensation of the illusory ownership over the rubber hand can be induced when the real hand is next to (Kammers et al., 2011; Lloyd, 2007; Rao and Kayser, 2017, Riemer et al., 2015) or under the rubber hand (Zeller et al., 2015; Rohde et al., 2011, Preston, 2013). However, vertical and horizontal distances are often judged differently (Loomis and Philbeck, 1999; Snijders et al., 2007), and the precise spatial arrangement of the real and artificial limbs affects the efficacy of the illusion (Bekrater-Bodmann et al., 2012). Another reason can be the stimulation procedure: the RHI has been induced by manual stroking or using computer-controlled stimulation devices (Rao and Kayser, 2017). Manual stimulation as well as the presence of the experimenter can give rise to “suggestibility effects” (Lush, 2020), and introduces variability in the timing of evoked brain activity, hence potentially exacerbating differences between studies (Rao and Kayser, 2017). A third reason could be that previous studies contrasting evoked activity between illusion and control conditions made the implicit assumption that neurophysiological correlates of the illusory state have the very same spatial configuration across participants. However, individual variability in brain morphology may render the spatial configuration of the illusion-related processes variable across participants, possibly obscuring the statistical significance of condition differences.

The aim of this study was to determine the neurophysiological correlates of the RHI using a refined experimental and statistical approach, and to test whether these are associated with a physiological marker of bodily arousal. Skin conductance as a proxy to autonomous body responses has been used previously to probe the embodiment of the rubber hand (Armel and Ramachandran, 2003, Ehrsson et al., 2007). However, these studies focused on an experimental manipulation imposing an external threat to the embodied artificial limb at the end of the visuo-tactile stimulation (Armel and Ramachandran, 2003) and did not probe whether changes in autonomous body signals emerge directly around the time of reported embodiment. Hence, we asked whether changes in skin conductance covary with the illusory

state and whether or how they relate to illusion-correlates in brain-derived signals, with the idea that any potential correlation between brain and skin-derived physiological changes could help to refine the interpretation of each individual effect.

To address these questions, we investigated the (neuro-)physiological correlates of the illusory ownership in EEG-derived evoked and in measurements of skin conductance. By using a computer-controlled setup to deliver the visual-tactile stimulation we were able to extract precisely time-locked patterns of evoked brain activity. In addition, by using a multivariate classifier to test for illusion-correlates in the evoked EEG activity we avoided the implicit assumption that illusion-related activations have an identical spatial topography across participants. To test which (neuro-)physiological signatures of the illusory state generalize across experimental conditions we relied on two illusion conditions, which differed in the spatial plane along which the real and rubber hands are displaced. We combined these with control conditions involving either a titled rubber hand or the absence of this. Importantly, to render the analyses of EEG and bodily signals as specific to the illusion as possible, we implemented two types of statistical comparisons in the EEG analysis: in one we contrasted separate illusion and control conditions and in another we directly contrasted the activity immediately before and during the illusory state within individual illusion trials. And last, to test whether the neurophysiological sources differentiating illusion and non-illusion epochs generalize across spatial configurations of the illusion setup, or across distinct types of non-illusion epochs, we exploited a cross-decoding approach, which can identify spatio-temporal configurations of brain activity that reliably differentiate multiple experimental conditions. In brief, our results show that during the illusory state evoked responses differ from those during different non-illusion conditions. Around 120 to 150 ms following stimulus onset this illusion-correlate generalizes across all non-illusion conditions, hence providing a robust marker of the illusory state. However, this neurophysiological signature was not correlated to changes in skin conductance, which preceded the onset of the illusion.

2. Materials and methods

2.1. Participants

A total of 54 right-handed volunteers participated in this study. Before the main experiment, we conducted a behavioural pre-test to screen whether participants are in principle able to feel the illusion. From this pre-test we selected 24 participants for the main study (both sexes). For the main study we included participants who in the pre-test indicated feeling the illusion in both Illusion conditions and who did not report feeling the illusion in any Control condition (see Experimental Set-Up and Conditions). To assess whether participants felt the illusion, they were asked to complete a standardized questionnaire (Table 1) (Botvinick and Cohen, 1998). From this we computed the average scores for the statements pertaining to the illusion and for the control questions. To be included in the main study, we required that participants report on average a positive mean for the three illusion statements and an average negative score for the control statements. None of the participants reported having participated in a study involving the rubber hand or similar body illusions previously. One participant was excluded from the main study as this participant reported feeling the illusion also during one control condition. All participants gave written informed consent before participation in accordance with the Declaration of Helsinki. All protocols conducted in this study were approved by the Ethics Committee of Bielefeld University.

1	During the last trial it seemed as I were feeling the touch in the location where I	Illusion
2	During the last trial it seemed as though the touch I felt was caused by the	Illusion
3	During the last trial I felt as if the rubber hand were my hand	Illusion
4	During the last trial it felt as my (real) hand was drifting towards the rubber	Control
5	During the last trial it seemed as I might have more than one left hand or arm	Control
6	During the last trial it seemed as if the touch I was feeling came from	Control
7	During the last trial I felt as my (real) hand was turning rubbery	Control
8	During the trial it appeared (visually) as if the rubber hand were	Control
9	During the trial the rubber hand began to resemble to my own hand in term of	Control

Table 1. *Questionnaire used to assess the feeling of the illusion (adapted from Botvinick and Cohen, 1998). The questionnaire included nine statements describing the underlined phenomena. Subjects indicated their response on a 7-scale ranging from "strongly agree" (-3) to "strongly disagree" (+3).*

2.2. Experimental Conditions

Experiments were performed in a darkened and electrically shielded room (Ebox, Desone, Germany). Participants sat on a comfortable chair in front of a one compartment, open-ended box placed on a two-storey wooden platform. Visual stimulation was delivered by white light-

emitting diodes (LED; Seeedstudio, 10 mm diameter). Tactile stimulation was delivered by a vibration motor (Grove: Vibration motor, Seeedstudio) placed close to the participants' skin below the left index finger. Visual and tactile stimulation were controlled via Matlab and two Arduino Uno prototyping platforms. To facilitate the alignment of stimulation events with the EEG data we routed a copy of the voltage controlling the DC motor to an Analog Input of the EEG system. Visuo-tactile stimuli lasted 100 ms and the interstimulus interval (ISI) was 900 ms, resulting in a visuo-tactile stimulation frequency of 1Hz. The choice of the stimulus duration was based on pilot tests (n=6), in which we varied the ISI between 300, 600 or 900 ms and based on our previous work (Rao and Kayser, 2007). During the pilot test the 900 ms ISI yielded the highest fraction of illusory states.

Five experimental conditions were used in this study. They were presented in a pseudo-randomized order for each participant. The conditions differed in the relative orientation of real and artificial hands (RH aligned to the body, or tilted by 90° degrees), the relative hand position (besides or below the real hand), and one condition did not involve a rubber hand (Real condition). In the 'Illusion hand next' condition, a lifelike rubber hand (for men: a silicon cosmetic glove, model 102LS, for women: model 102LS, ORTHO-REHA Neuhof GmbH) was positioned on top of the platform in front of the participants in an anatomically congruent orientation, as typically used to induce the illusion. The index finger of the rubber hand was placed on a dummy vibration motor, which did not vibrate. The participant's left hand was covered with a blanket, hidden to the participant view, and was positioned at a distance of 10 cm from the rubber hand in the horizontal or vertical planes. The tip of the participant's index finger was placed on the vibration motor, while the right hand was placed at the other end of the platform in reaching distance of a keyboard. The LED was positioned 5 mm above the dummy motor near the rubber hand. In the incongruent Control condition with the 'hand next', the rubber hand was placed in anatomically incongruent position at 90°-degree angle. Otherwise the setup was the same as for the respective Illusion condition. Placing the rubber hand in an anatomical implausible position (not bodily-aligned) is a common control condition in RHI studies (Ehrsson, 2004; Moseley et al., 2008, Rao and Kayser, 2017). In the 'Illusion hand under' condition, the rubber hand was placed in front of the participant, while the participant's real hand was covered with a blanket and placed in the lower panel of the platform 10 cm under the RH in the vertical plane. Otherwise the setup was the same as for the Illusion hand next condition. In the incongruent Control condition with 'hand under', the rubber hand was placed in anatomically incongruent position, at a 90°-degree angle below participants' hand. We also included a Control condition in which the rubber hand was absent. This 'Real condition' is useful as it allows comparing conditions with an embodied artificial and an embodied real hand, a dimension not probed by the misalignment of any real and artificial hands. In the Real condition no rubber hand was present, and the index finger of the left hand was placed in view on a vibration motor positioned 5 mm below the LED. The right hand was in the same position as in the Illusion and Incongruent conditions.

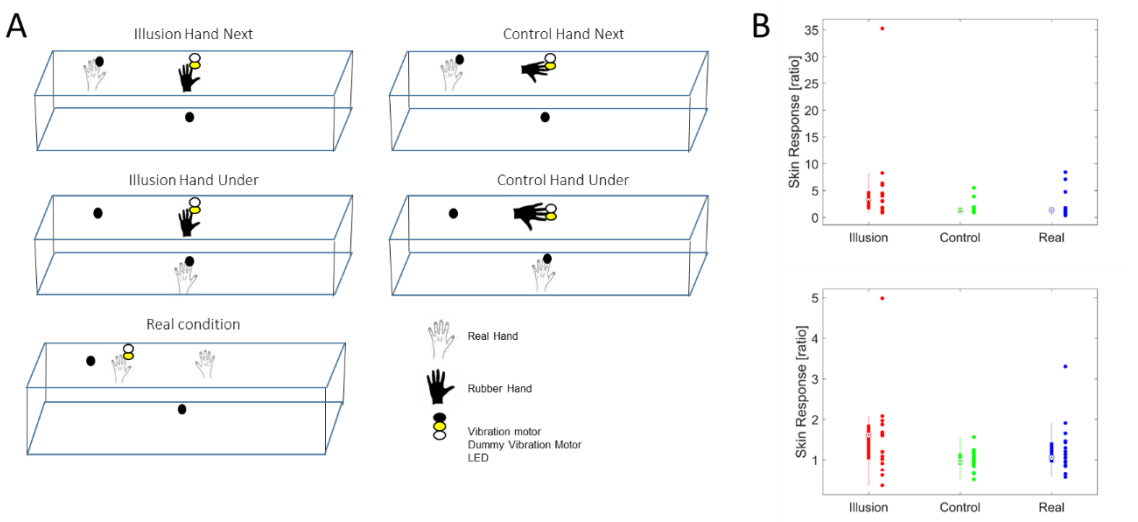

Figure 1. A. Schematic of the five experimental conditions. *The experiment involved two 'Illusion conditions' that differed in the spatial arrangement of the real and artificial limbs (horizontal or vertical displacement of 10cm), and the two respective 'Control conditions' obtained by rotating the rubber hand into an unphysiological position by 90 degrees. Finally, there was a 'Real condition' in which the rubber hand was absent and multisensory stimulation was delivered to the real hand.* ***B Changes in skin conductance associated with the illusion****. Boxplots show skin responses around the reported onset of illusion (upper panel) and in a 3s period prior to the reported onset of the illusion (lower panel). Skin responses were defined as the ratio of the conductance in a 3s window of interest, normalized to a preceding 3s baseline. Boxplots indicate the median (circle), 25th and 75th percentiles (thick line). Dots indicate individual participants.*

2.3. Behavioural pre-test and main study

During the behavioural pre-test we included four conditions: the two Illusion conditions and their respective Controls. For each condition the visuo-tactile stimulation period lasted for 2 minutes. Each condition was repeated in a pseudo-random order. Participants were instructed to use their right hand to press a key on a computer keyboard when they felt the onset of the illusion (i.e. perceived the rubber hand as belonging to their body) and otherwise keep their gaze fixed on the LED. After each first illusion trial participants were asked to complete the standard RHI questionnaire (Table 1) (Botvinick and Cohen, 1998). To control for potential suggestion effects due to demand characteristics (Lush, 2020) immediately before starting with the visuo-tactile stimulation at the beginning of the first trial, participants were asked if they already felt the rubber hand to be the real hand (3rd statement of the questionnaire). Participants who reported to feel the illusion before the start of the stimulation were excluded from the main experiment and none of the participants included in the main study did report feeling the RH to be the real hand prior to the visuo-tactile stimulation. During the main study four repeats of each of the five conditions were administered in pseudo-random order for each participant. Each repeat (termed 'trial' in the following) lasted 3 minutes and consisted of 180 visuo-tactile stimulation events. For each illusion trial we determined the onset time at which participants started to feel the illusion as the time of the respective response (button press).

2.4. EEG recording and pre-processing

EEG signals were continuously recorded using a 128 channel BioSemi (BioSemi, B.V., Netherlands) system with Ag-AgCl electrodes mounted on an elastic cap (BioSemi). Four additional electrodes were placed at the outer canthi and below the eyes to obtain the electro-oculogram (EOG). Electrode offsets were kept below 25 mV. Data were acquired at a sampling rate of 1028 Hz. Data analysis was performed with MATLAB (The MathWorks Inc., Natick, MA, USA) using the FieldTrip toolbox (Oostenveld et al., 2011). Data were band-pass filtered between 0.4 Hz and 90 Hz, resampled to 200 Hz. Subsequently, the data were denoised with ICA. Components reflecting muscular artefacts, eye blinks, eye movements as well as poor electrode contacts were identified based on recommendations in the literature (O'Beirne and Patuzzi, 1999; Hipp and Siegel, 2013) were removed. Overall, we removed an average of 17.45 +/- 1.48 (mean and s.e.m.) components per participant.

For subsequent data analysis we epoched the data around each visuo-tactile stimulation event, with epochs lasting from 250 ms pre-stimulus to 400 ms post-stimulus onset This resulted in a total number of 180 epochs for each trial. Epochs were combined across trials of the same condition, were band-pass filtered between 2 Hz and 40 Hz, and epochs with signals exceeding a level of 250 mV were removed. Importantly, to render the analysis of the Illusion conditions specific to the actual illusory state, we only included epochs after the time point at which participants indicated the start of the illusory state. As a result, the effective number of data epochs used for each condition during data analysis differed. The average number of epochs for both Illusion conditions was 1347 +/-34 (mean +/- s.e.m.), for the Control conditions 1299 +/- 55, and for the Real condition 684 +/- 15. To avoid biasing analyses by these differences in epoch numbers we used sub-sampling of epochs to equalize the number of epochs per condition for each statistical contrast described below. Sub-sampling was based on randomly selecting (without replacement) 80% of the minimally available number of epochs for each contrasted condition, and repeating each calculation multiple times using random selections of epochs.

2.5. Analysis of evoked EEG responses using single-trial classification

To quantify whether and when EEG activity differed between experimental conditions, we used single-trial classification based on a regularized linear discriminant analysis (LDA) (Blankertz et al. 2011; Parra et al. 2005). The epoched data were binned into overlapping time bins of 60ms duration and the classifier was computed at 10 ms time steps. Results reported are aligned to the onset of the 60ms window. The regularization parameter was set to 0.1, as in previous work (Park and Kayser, 2019). For each contrast we combined the epochs from the respective trials of interest, using the sub-sampling procedure described above (e.g. all Illusion vs. all Control trials; or only the hand next illusion vs. only the hand next control trials). For each participant the classifier performance was characterized as the receiver operating characteristic area under curve (AUC), obtained from 6-fold cross-validation. We derived participant-wise scalp topographies for each classifier by estimating the corresponding forward model, defined as the normalized correlation between the discriminant component and the EEG activity (Parra et al. 2005). Importantly, by combining the signals from all electrodes for the classifier this analysis makes no assumption about a common spatial pattern in the neurophysiological signals between conditions.

To directly test whether the neurophysiological sources discriminating e.g. the Illusion and Control conditions are the same as those also differentiating the Illusion and Real conditions we used cross-classification. For this we trained the classifier on a half the Illusion and the Control trials and then applied classifier weights to differentiate the remaining half of the Illusion and the Real trials, repeating this procedure 10 times. Cross-classification was again quantified using the AUC and computed for both directions: training on Illusion vs. Control and testing on Illusion vs. Real, and training on Illusion vs. Real and testing on Illusion vs. Control. The respective AUC values for each participant and time point were averaged over both directions and repeats of the calculation. The same cross-classification analysis was used to test whether the neurophysiological sources discriminating Illusion and Control for the 'hand next' arrangement generalize to the 'hand under' arrangement, and vice versa, or to test whether activity differentiating the overall hand position (all 'hand next' vs. all 'hand under' epochs) also differentiates Illusion from Control epochs.

2.6. Recording of skin conductance signals

Skin conductance was continuously recorded using a Neulog GSR logger NUL-217 sensor in a sample of 17 participants. For technical reasons in some participants the recording of skin conductance was not possible, and hence the effective participant sample for EEG and skin responses differed. Ag/AgCl electrodes were placed on the palmar sites of the middle and ring finger of the participant's left hand. GSR measurements were recorded in micro-Siemens and at a sampling rate of 100 Hz. For offline analysis the data were resampled to 50 Hz, band-pass filtered between 0.5 Hz and 2 Hz (3rd-order Butterworth filter) and logarithmically scaled (Braithwaite et al., 2013). Trials were visually inspected and few trials with artefacts were manually removed. To determine whether the changes in skin conductance observed in the main experiment could be the result of simply pressing a button (vs. not pressing any button) we also recorded skin conductance data in a separate control session in which participants only had to press a button in response to a visual cue for eight times.

2.7. Analysis of skin conductance data

Because skin conductance tends to fluctuate over the scale of minutes for reasons such as drying of the skin (Boucsein et al., 2012), we opted for an analysis that directly contrasts the conductance in two adjacent time windows of 3 second duration. These were chosen around the key event of interest defined by the trial-specific onset of the illusion. The duration of the analysis window of 3 seconds was chosen as a compromise between the typical latency of changes in skin conductance which are on the order of 2-3 seconds (Sjouwerman and Lonsdorf, 2018) and the need to fit this window into the period prior to the illusion onset for most trials and participants (the shortest mean RT was 5.46 s). In one analysis we contrast the conductance in the 3 s immediately before the illusion onset ([-3 s, 0 s]) with the conductance in the immediately following window ([0 s, +3 s]), hence focusing on changes immediately occurring with the overt response indicating the feeling the illusion (button press). In a second analysis we focused on the skin conductance immediately before participants' overt response, and contrasted the data in the two time windows defined as [-6 s, -3 s] and [-3 s, 0 s]). To perform the same analysis on the data obtained during the Control and Real conditions, we used the reaction times obtained from the Illusion trials as surrogate time points to define the

corresponding time windows in the Control trials and Real trials. For this, Control / Real trials and Illusion trials were paired based on their respective trial number, and for Real trials we extracted two time windows per trial, one from the hand next and one from the respective hand under Illusion trial.

The effective number of time epochs trials included in the analyses were as follows: for the analysis centered on the response we included 6.25 +/- 0.43 (mean +- SEM) trials across both Illusion conditions, 6 +/-0.35 across Control conditions, and 6.1 +/- 0.46 for the Real condition. For the analysis centered prior to the response we included on average 5.5 +/- 0.42 (mean +- SEM) trials for the Illusion conditions, 5.45 +/-0.34 for the Control conditions, and 5.45 +/- 0.48 for the Real condition. For the button press session, we extracted the skin conductance date in TW's aligned on the button press time. To quantify the actual change in skin conductance induced by events of interest, termed 'skin response' in the following (e.g. illusion onsets, control time points), we computed the standard deviation of the signal in each time window (e.g. [-3 s, 0 s] and [-0 s, +3 s]) and then computed their ratio. For subsequent analysis these skin responses were averaged over trials and conditions.

2.8 Statistics

The statistical analyses focused on the following comparisons of interest: the effect of illusion obtained by comparing data (e.g. EEG LDA classification analysis or the oscillatory activity) combined across both Illusion conditions with the data combined across the two respective Control conditions, or with the Real condition; the effect of illusion (vs. control) separately for each hand position; and the main effect of hand position, obtained by comparing the response averaged across both hand next and both hand-under conditions. In addition, we implemented an analysis directly focusing on the effect of illusion within the same experimental Illusion trial: we directly contrasted the data (e.g. evoked EEG responses; skin responses) between epochs before participants indicated feeling the illusion (button press) and subsequent to this event. Statistical testing of the EEG data relied on randomization approach and cluster-based permutation procedures to exploit the smoothness of the data and to control for multiple comparisons (e.g. across time, electrodes) (Maris and Oostenveld, 2007; Nichols and Holmes, 2001). In general, we relied on 2000 randomizations for each test, applied spatial clustering based on a minimal cluster size of 3 and used the max-sum as cluster-statistics. Both classification and cross-classification performance (AUC values) was tested against chance at each time point by shuffling the sign of the true single-participant effects (the signs of the chance-level corrected AUC values) resulting in a distribution of group-level null effects (mean AUC). We thresholded the first-level effects based on the 99th percentile (i.e. $p < 0.01$) of the full distribution of randomized AUC values. To obtain a randomization distribution we randomly flipped the sign of participant-wise differences before computing the group-level t-value. To compare the median latencies of illusion onsets between conditions and to compare the skin responses between pairs of conditions we used Wilcoxon signed rank tests. Effect sizes for this test were obtained using the point-biserial correlation (Kerby, 2014).

3. Results

3.1. Illusion onset times

We compared the mean onset times of the illusory state between the two Illusion conditions to determine whether they were similarly effective in inducing the illusion. The onset of the illusory state in the 'hand next' condition occurred on average after 50 ± 36 s (n=22; mean ± SD; median: 42 s) and significantly later compared to the 'hand under' condition (31±20 s, mean ± SD; median: 32 ms; Wilcoxon signed rank test Zval=2,45, p=0.01, Effect size= 0.52). Hence, the hand-under arrangement was more efficient in inducing the illusion, despite the physical distance between the participant's and the rubber hand being the same in both configurations.

3.2 Skin conductance

We implemented two analyses on the skin conductance data geared to reveal changes in this signal emerging either in parallel with participant's overt behavioural response of feeling the illusion (button press), or prior to this. The latter was motivated by the observation that in many experimental settings anticipatory changes in skin conductance emerge prior to a conscious or overt behavioural response (Bechara et al., 1997). Hence autonomous physiological signals may reveal bodily changes already prior to participants' overt responses. To remove slow drifts in the recorded signals, the analysis was based on the ratio of the skin conductance in two subsequent 3 s windows (termed 'skin response'), either centered on the button press or an epoch preceding this. The analysis centered on the button press response revealed no significant differences in skin response between Illusion and Control conditions (n= 17, Wilcoxon sign-rank test, Z=2,58, pcorr = 0.054, r_{rb}=0.71; Figure 1B) or between Illusion and Real conditions (n=17, Z=1,59, pcorr=0.31, r_{rb}=0.43). We also did not find a significant difference between the Illusion condition and a separate control experiment in which participants simply pressed a response button (n=15, pcorr =0.77, r_{rb} = 0.25). However, the analysis focusing on the epochs prior to the overt response revealed significantly stronger skin responses during the Illusion compared to Control condition (n=18, Z=2,72, pcorr=0.019, r_{rb}=0.73), but not between the Illusion and Real condition (n=18, Z=1,02, pcorr= 0.46, r_{rb}=0.27). This suggests that bodily arousal is increased when watching an embodied hand (real or artificial) compared to watching a non-embodied object being stroked, such as in the Control conditions.

3.3. EEG activity differs between Illusion and Control conditions at short latencies

We then asked whether and how brain activity differs between epochs in which participants feel the illusion and the different non-illusion conditions. Specifically, we focused on the electrophysiological response evoked by the repetitive visuo-tactile stimulus as a signature of the cerebral processing of the relevant distant signals. To quantify potential changes between conditions, we relied on a multivariate linear discriminant analysis. This avoids the assumption implicitly made in previous studies (Rao and Kayser, 2017; Zeller et al., 2015) that the illusion-related processes have the very same spatial topography across participants. Individual

variability in brain morphology may render the spatial location of the illusion-related processes variable across participants, but a traditional and electrode-wise difference analysis implicitly assumes that condition-effects have the same location across participants (Parra et al., 2005). Using a multivariate classifier based analysis avoids this assumption by allowing distinct spatial patterns of activity to contribute to condition-differences in individual participants, while assuming that any systematic group-level differences between conditions emerge around the same time in the data.

Group-level classification performance of Illusion versus Control conditions was significant from 0.02 s to 0.320 s after stimulus onset (n=22, Cluster-based permutation test correcting for multiple comparisons along time, $p<0.001$, AUC_sum = 3.68, max = 0.69 at 0.100s; Fig. 2A) suggesting that evoked activity differs between conditions early following the illusion-inducing sensory stimulus. In a subsequent analysis we confirmed that the difference between Illusion and Control conditions prevailed for both relative positions of the artificial and real hands: classification of each Illusion versus the respective Control condition was significant in similar time window (hand next: from 0.04 to 0.310 s, $p<0.001$, AUC_sum=3.67, max =0.71 at 0.100s; hand under: from 0.01 s to 0.310s, $p<0.001$, AUC_sum=3.20, max =0.67 at 0.100 s; Fig. 2B). Contrasting the illusion and Real conditions revealed a similar widespread difference (n=22, cluster from 0.04 s to 0.310 s, $p<0.001$, AUC_sum=2.64, max =0.65 at 0.100 s; Fig. 2A), suggesting that the illusory state affects evoked response compared to both types of non-Illusion conditions.

We then asked whether the differences seen between the Illusion and Control conditions and between Illusion and Real conditions arise from the same neurophysiological processes and hence have a similar spatial configuration. To address this question we relied on the concept of cross-decoding (Cichy and Pantazis, 2007). Using cross-decoding one can establish a signature of similarity between experimental conditions, here in the form of a spatio-temporal configuration of electrode-wise activity contributions, which are reflected by the electrode-specific classifier weights. Based on these, one can ask whether these configurations generalize across conditions. Practically, this is tested by training the classifier to discriminate between one pair of conditions (e.g. Illusion vs. Control) and testing this on another pair (e.g. Illusion vs. Real), using non-overlapping sets of trials.

The cross-decoding analysis was significant between 0.120 s to 0.150 s ($p<0.001$, AUC_sum=0.08, with a maximal performance of 0.53 at 0.130 s; Fig. 2C), suggesting that during these epoch illusion epochs are distinguished from both types of non-illusion epochs by a common pattern of evoked response. We then used the same cross-decoding approach to investigate whether the neurophysiological processes differentiating the Illusion and the Control for the ‘hand next’ conditions shared a similar spatial configuration compared to the ‘hand under’ conditions. Cross-decoding was significant for most time points (cluster 1: from 0.05 s to 0.130 s, $p<0.001$, AUC_sum=0.34; cluster 2: from 0.150 s to 0.200 s, $p<0.001$, AUC_sum=0.17; max= 0.55 at 0.100 s; Fig. 2D). These cross-decoding results suggest that the neurophysiological processes differentiating the Illusion from the two Control conditions fall into two types: one that generalizes across non-illusion conditions from 120 ms to 150 ms following the visuo-tactile stimulus, and others for which activity selectively differentiates the Illusion from either the Control conditions involving the rotated limb or a condition only involving participants real hand.

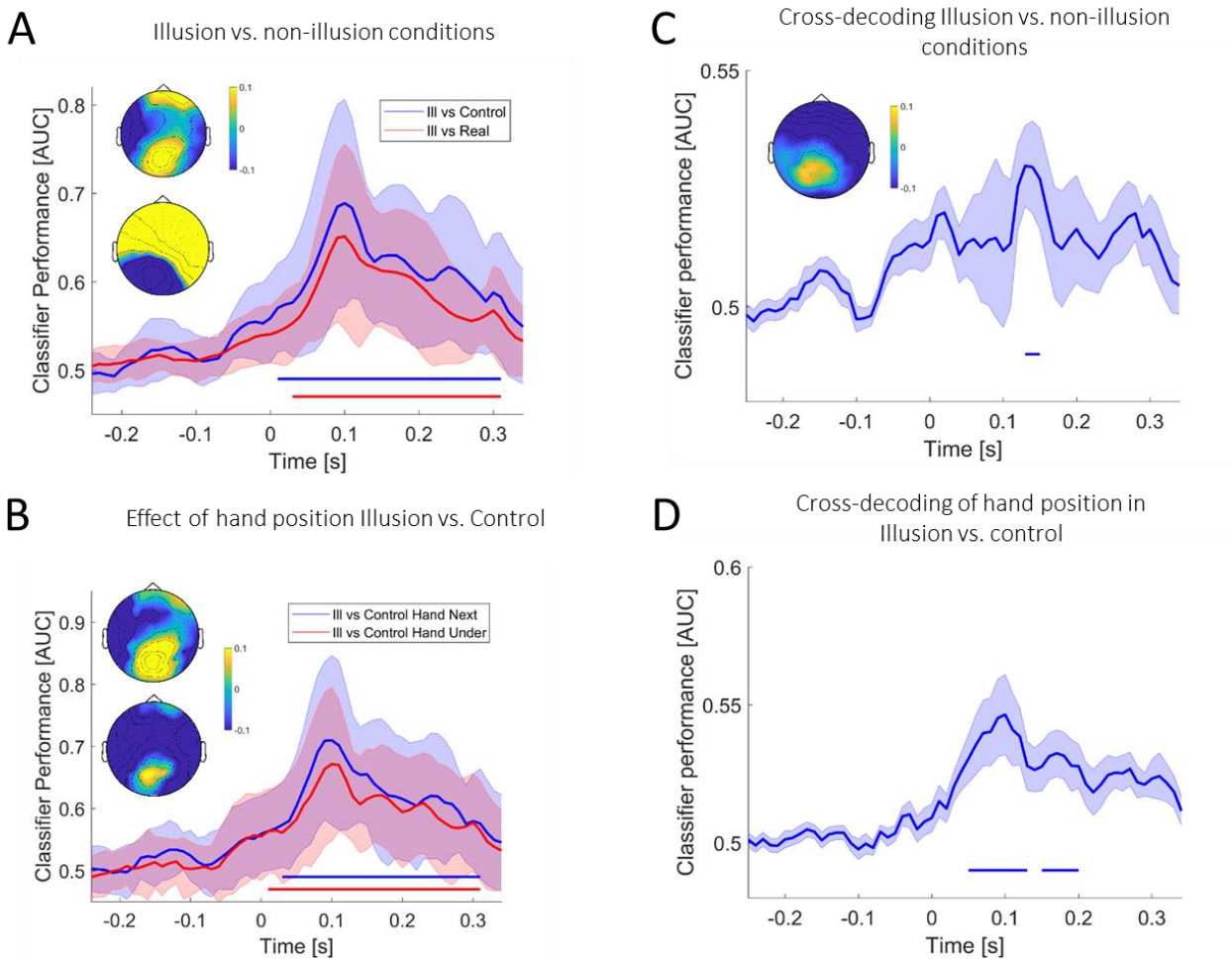

Figure 2. Differences in EEG evoked responses associated with the illusion. A) *Differences in EEG activity between Illusion and Control conditions and between Illusion and the Real condition quantified using linear multivariate classification. Classifier performance was computed as the area under the receiver-operator characteristic (AUC). Thick curves indicate the mean and shaded areas indicate the s.e.m. Straight lines at the bottom indicate periods of significant classification performance (cluster-based permutation test corrected for multiple comparisons along time, at p<0.01). Group-level forward models of the classifier weights at the time of the maximal classification performance. Upper right: Illusion vs Control. Lower right: Illusion vs Real.* ***B)*** *Same results for a classification between each individual Illusion condition and the respective Control condition. Group-level forward models of the classifier weights at the time of the maximal classification performance. Upper right: Illusion vs Control for hand next conditions. Lower right: Illusion vs Control for hand under conditions.* ***C)*** *Performance of a cross-decoding analysis between Illusion vs. Control and Illusion vs. Real conditions. The classifier was trained on one of these contrasts and tested on the other, with the result averaged over both directions. Group-level forward models of the classifier weights at the time of the maximal classification performance* ***D)*** *Performance of a cross-decoding analysis between each individual Illusion and its respective Control condition.*

3.4 EEG activity differs between pre and post illusion epochs

Statistical comparisons between Illusion and Control conditions are usually performed by comparing all epochs from the Illusion condition against all those from the Control conditions.

However, the experimental Illusion and Control conditions are provided at different times during the experiment and hence may differ not only in the subjective illusory state. To render the comparison of illusion and non-illusion related brain activity more specific, we directly contrasted evoked responses between illusion and non-illusion states within the same experimental Illusion trials while maintaining other factors constant. Based on participants' responses indicating the onset of the illusory state, we split the EEG recordings into epochs before the illusion onset and those during illusory state. Based on these groups of epochs it was also possible to significantly classify illusion vs. pre-illusion epochs, with a similar time course as obtained when contrasting the entire epochs and control epochs (n=22, cluster from 0.03 to 0.340s, $p<0.01$, AUC_sum=2.11, max=0.60 at 0.130s; Fig. 3A).

3.5 Effect of hand position

The use of two spatial arrangements to induce the illusion allowed us to separate an effect of the illusory state from a potential influence arising from the relative positioning of real and artificial hands. While our results show that the two Illusion conditions differed in their efficacy in inducing the illusory state (the 'hand under' condition led to a more rapid onset of the illusion) the cross-classification analysis confirmed neurophysiological processes that reflect the illusory state regardless of the spatial configuration. In an additional analysis we then asked whether brain activity also differs with the main effect of hand position, hence between the two conditions (Illusion and Control) featuring the participants real hand *next* to the rubber hand and the two conditions featuring the participants hand *under* the rubber hand. While we expect such processes to exist, the above results suggest that these should be independent of those characterizing the illusory state. We tested these questions using the following classification and cross-classification analyses. First, we probed classification performance between conditions featuring the 'hand next' and 'hand under' arrangements: this was significant from 0.02 s to 0.310 s (n=22, $p<0.01$, AUC_sum=3.02, max=0.65 at 0.120 s; Fig. 3B). Second, we used cross-decoding to test whether the spatial configuration of the EEG activity discriminating hand positions also discriminate the effect of illusion, defined by the contrast Illusion vs. Control conditions. Cross-classification between the effects of illusion and hand position was not significant (cluster-based permutation test, no significant clusters at $p<0.05$, max AUC = 0.51).

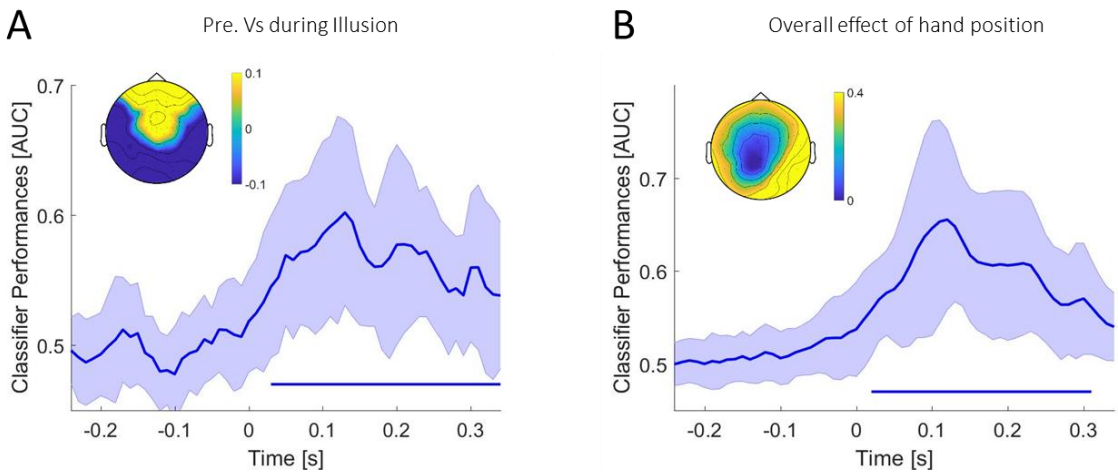

Figure 3. Differences in pre-illusion vs. during-illusion epochs within a trial, and effect of hand position. A) Classification of EEG activity between the epochs before the illusion onset and the epochs after the illusion onset within the Illusion trials. Classifier performance is shown as the area under the receiver-operator characteristic (AUC). Thick curves indicate the mean and shaded areas indicate the standard errors of the mean. Straight lines at the bottom indicate periods of significant classification performance (cluster-based permutation test correcting for multiple comparisons along time, at p<0.01). Scalp topographies show the classifier forward models at the time of the maximal classification performance. B) Main effect of hand position. Classification performance (AUC) for 'hand next' versus 'hand under' epochs regardless of illusory state. Thick curves indicate the mean and shaded areas indicate the standard errors of the mean. Straight lines at the bottom indicate periods of significant classification performance (cluster-based permutation test correcting for multiple comparisons along time, at p<0.01).

3.6 Neurophysiological illusion signatures are not related to skin responses

Given that the illusory state was associated with changes in evoked response and with changes in skin conductance, we asked whether the respective effects in each physiological signal were correlated across participants. To test this, we computed the correlation between the LDA classifier performance in discriminating Illusion and Control trials as a measure of illusion effect in the EEG signal and the skin responses in the Illusion condition as a measure of autonomic body response (Fig. 4A). To assess the significance of these correlations we derived group-level bootstrap confidence intervals (at p<0.05, two-sided). Based on these the correlations were not significant at any time point. The same result applied to the correlation between the LDA classifier performance in discriminating illusion and real trials and the skin response (Fig. 4B).

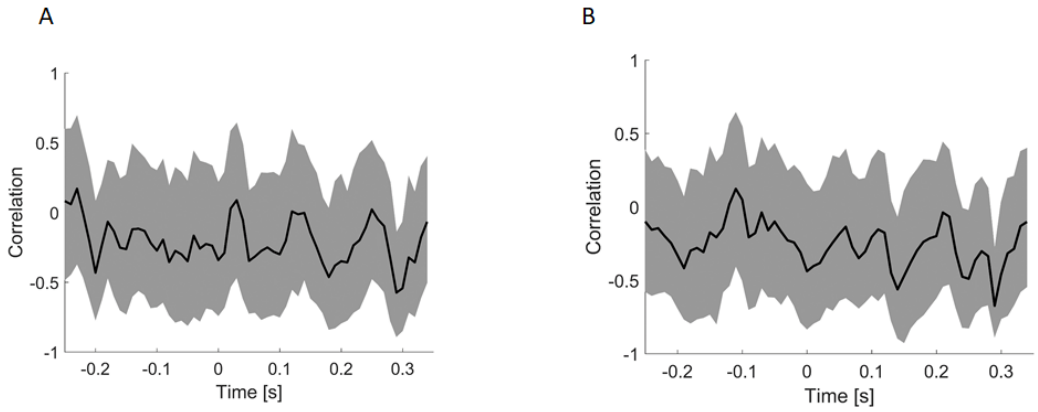

Figure 4. Correlation of condition effects in EEG evoked activity and skin responses. A) *Correlation across participants of the classifier performance in Illusion vs. Control comparison and the skin response in Illusion condition.* ***B)*** *Correlation across participants of the classifier performance in Illusion vs real comparison and the skin response in Illusion condition. Thick lines indicate the Pearson correlation, grey areas the (two-sided) 95% bootstrap confidence intervals.*

4. Discussion

The aim of this study was to investigate the physiological and neural correlates of the illusory ownership during the RHI that robustly characterize the illusory state. We combined a refined experimental and analytical setup and used multivariate (cross-)classification of evoked EEG responses to ask whether and when neurophysiological signals differentiate the illusory state reliably from non-illusory conditions that control for a number of potentially confounding factors, such as the relative position of both hands or the precise nature of the control condition. We found that evoked responses differed between illusion and non-illusion states already at short latencies following stimulation onset and over prolonged time. Importantly, between 120 ms and 150 ms following stimulus onset did the underlying neurophysiological processes allow differentiating the illusory state from multiple non-illusion conditions, pointing to a robust marker of the illusory state. However, this neurophysiological signature was not related to changes in skin conductance that accompanied the onset of the illusory state.

4.1 Correlates of the illusory state in evoked responses

A number of studies aimed to understand the neural correlates of the RHI by investigating the evoked-responses to the tactile stimulus on the participant's real hand. This approach rests on the idea that the cerebral representation of the inducing stimulus changes when the embodiment shifts from the real to the rubber hand. However, previous studies described conflicting results: while some reported suppression of evoked responses at early (55ms) latencies (Zeller et al, 2015) others reported effects only much later (Rao and Kayser, 2017; Peled et al., 2003). Importantly, many studies made the implicit assumption that the neurophysiological sources differentiating illusion and non-illusion conditions have the same spatial configuration across participants, which may not be valid. We here exploited a multivariate classification framework, which allowed us to relax this assumption. Importantly, the classification analysis allowed us to directly test, within each participant, which neurophysiological sources generalize between conditions, such as the Control and Real conditions as non-illusion states, or horizontal and vertical arrangements of real and artificial hands. Our results show that evoked responses differ reliably between illusion and non-illusion conditions over prolonged periods and at short latencies.

The earliest differences between illusion and non-illusion conditions emerged shortly after stimulus onset, and hence likely arise from early somatosensory cortices. These condition differences did not generalize between non-illusion conditions or between hand positions, in line with the underlying primary sensory regions encoding information in a highly specific manner. Subsequently, between 60-100 ms, the illusion-related processes generalized across hand positions in the Illusion vs. Control contrast, suggesting that respective processes are invariant to relative body arrangements. However, the effect did not generalize to the Real condition, possibly because the underlying cerebral processes in higher somatosensory regions are sensitive to the bodily nature of the seen hand. Potential correlates of the illusion at these latencies have been suggested previously (Aspell et al., 2012, Zeller et al., 2015) but

those studies did not directly test whether and which illusion correlates generalize between factors. Then, between 120 and 150 ms, the difference between illusion and non-illusion conditions generalized across all conditions and factors, making activity around this time a robust marker for the illusory state. Supporting this, Press et al., 2008 found an enhanced somatosensory N140 after synchronous versus asynchronous stimulation, irrespective of whether the participants were viewed a rubber hand or object. Together with the present data, this suggests that systematic and consistent differences between illusion and various potential control conditions arise at these latencies. Still, the precise origin of the underlying neurophysiological processes remains debated, and previous studies have implied parietal regions and premotor regions as reflecting the position of body parts, the integration of the visual-tactile sensory stimulation and the sensation of ownership (Ehrsson et al., 2004, 2005; Graziano 1994, Fang et al., 2019). Combined EEG-fMRI studies capitalizing on the present experimental and analytical protocols could be used to more precisely determine the brain regions giving rise to the illusion. In particular, such experiments could provide insights into what aspects of the illusory setting (e.g. spatial attention, seeing an artificial body, feeling ownership over an object) affect the neurophysiological representation of the sensory stimulation at distinct stages of somatosensory or interoceptive pathways.

Lastly, after about 160ms, differences between the illusion and non-illusion conditions generalized across hand positions, but remained specific to the Control or Real condition. One possibility is that these effects reflect higher parietal and frontal processes sensitivity to multiple factors, such as body ownership, spatial attention (Press et al., 2008, Rao and Kayser, 2017) or reflect high-level processes pertaining to multisensory causal inference (Rohe and Noppeney, 2015; Cao et al., 2019). More work is required to understand the precise neurophysiological origins and what precise aspect of the experimental paradigm of subjective state these are selective to.

4.2 Changes in skin conductance associated with the onset of the illusion

Previous studies have reported correlates of the bodily state and arousal during the rubber hand illusion in measures of skin conductance (Armel and Ramachandran, 2003; Ehrsson et al., 2007). Many studies exploited an aversive stimulus imposing a threat to the embodied limb, and found differences in skin conductance between illusion and control conditions. However, such between-condition effects can be influenced by a number of factors not directly related to the immediate illusory state, such as changes in bodily state over the longer periods that separate distinct experimental conditions. Furthermore, a threat can induce hand movements which bias skin conductance (Kilteni et al., 2012) and increased skin conductance after a threat has also been found independently of embodiment, suggesting that threatening the rubber hand can engage defensive reflexes independent of the illusory state (Riemer et al., 2015). Other studies focused on changes in skin conductance during the entire experimental trial and reported changes in signal fluctuation between illusion and control conditions over the scale of many tens of seconds (D'Alonzo et al., 2020). While this has been interpreted as an enhanced arousal during the illusion, another study directly recording skin sympathetic nerve activity did not confirm such results (Critchley et al., 2020). Hence, whether and how correlates of the illusory state reflect in bodily signals remains unclear.

We here focused on the moment in the illusion trials at which the illusory state emerged and asked whether this emergence is characterized by changes in skin conductance. Our data support that a change in bodily state emerges prior to participants' actual and overt response of reporting the illusion, possibly because changes in autonomous function or arousal precede the subjective sensation of ownership. The increase in skin response was significant in comparison to the Control but not when compared to the Real condition. We take this to suggest that these autonomous responses are most strongly modulated by seeing a not-embodied object rather than by the nature of the embodied object, be it a real rubber or a real hand.

4.3 Changes in skin conductance are not correlated with differences in evoked activity

The role of bodily signals for understanding the RHI and their suitability as markers of the illusory state remains debated (Suzuki et al., 2013, Crucianelli et al., 2018, Horvath et al.,2020). In particular, it remains unclear whether and to what degree bodily and neurophysiological markers of the illusion reflect the same underlying process, as some studies also reported dissociations between various signatures of the illusion such as proprioceptive drift and questionnaires (Holle et al., 2011; Holmes et al., 2006, Horvath et al.,2020. Kammers et, al, 2011, Riemer et al., 2015). Here, we did not find a significant correlation between skin responses and the degree to which the evoked activity differed between illusion and non-Illusion conditions across participants. Hence, our data rather support the notion that both types of changes in physiological state are driven independently and characterize independent processes contributing to the subjective feeling of the illusion or arising as a cause of this.

For example, the increase in skin conductance following an explicit threat to the rubber hand may be mediated by insular and anterior cingulate regions linking interoception with body perception and hence reflect the basic arousal following an aversive event (Berntson and Khalsa, 2021; Ehrsson et al., 2007). In contrast, changes in the subjective perceived embodiment at the onset of the illusory state may originate from somatosensory and parieto-frontal cortices interfacing the multisensory environment with bodily self-perception and ownership (Ehrsson et al., 2004; 2005). These two systems may be sufficiently segregated such that the respective physiological effects appear independent.

Still, an alternative explanation could be the present analysis was not sufficiently sensitive to reveal such a correlation. The change in skin conductance was observed in a time period just prior to participants' response of feeling the illusion, while the neurophysiological correlates of the illusory state were quantified using longer data segments obtained during the entire stimulation period. Future work should try to relate both measures more closely, for example by relying on a larger number of shorter illusion trials than used here.

4.4 The impact of methodological details on outcomes in studies on the RHI

We employed two spatial configurations of the real and rubber hands to induce the illusion. Both hands were displaced either in the horizontal or vertical planes, while keeping the physical distance the same. The behavioural data show that the vertical configuration required less time to induce the illusion, confirming previous studies suggesting that the spatial configuration

affects the efficacy of the illusion (Bekrater-Bodmann et al., 2012). However, the cross-decoding analysis revealed that most neurophysiological signals differentiating Illusion and Control conditions generalized across hand positions. Hence, the neurophysiological correlates of the illusory state itself are independent of the spatial plane in which the illusion is induced. We also employed multiple control conditions as contrasts for the illusion. Following previous work, we manipulated the alignment between the participant's and the rubber hand by rotating the latter into an unrealistic position. This usually abolishes the illusion (Ehrsson et al., 2004; Rao and Kayser, 2017; Riemer, 2019), and we ensured that no participant reported feeling the illusion in any of the non-illusion trials. Such a rotated control seems preferable over the asynchronous stimulation of the participant's and rubber hand, which may not completely abolish the perceived ownership over the rubber hand (Costantini et al., 2016; Fuchs et al., 2016; Valenzuela et al., 2013). Still, the use of a single control condition may miss potential confounds, as illusion and control conditions can differ along a number of dimensions. Hence, we involved two additional controls: first, we included the Real condition, in which the RH was absent and the visuo-tactile stimulation directly occurred on the participant's hand. In comparison to the control condition involving the rubber hand, in the Real condition the stimulated hand is a natural hand, it belongs to the participant and it is embodied. Second, we involved a direct within-trial comparison of the activity within the Illusion trials, which compares data epochs that differ only by the participant's illusion report. The use of multiple non-illusion conditions can make it difficult to determine which pairwise differences generalize across different non-Illusion conditions. To overcome this problem, we relied on the concept of cross-decoding, which directly allowed us to establish whether and when the illusion differs from multiple control conditions. Previous work suggested that the presence of an experimenter during the illusion induction, and participants' tendency to meet requirements imposed by experimenter's instructions, can bias participants to report feeling the illusion (Lush, 2020). We aimed to minimize such effects. First, we used a computer controlled set-up not necessitating the presence of the experimenter. Second, we prompted participants to report whether they felt the illusion already before the stimulation onset: no participant indicated feeling the illusion before stimulation began. Third, we capitalized on a button press response to identify illusion epochs as the questionnaire can be susceptible to order effects (Lush, 2020) and illusion-related measures such as the proprioceptive drift tend to be unreliable (Abdulkarim and Ehrsson, 2016; Rohde et al., 2011). The skin conductance data provide evidence validating this measure, as participant's overt response indicating the onset of the illusion was preceded by changes in bodily arousal, which have previously been linked to the sensation of ownership (Armel and Ramachandran, 2003; Ehrsson et al., 2007).

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