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Proprioceptive drift without illusions of ownership for rotated hands in the “rubber hand illusion” paradigm

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The rubber hand illusion is one reliable way to experimentally manipulate the experience of body ownership. However, debate continues about the necessary and sufficient conditions eliciting the illusion. We measured proprioceptive drift and the subjective experience (via questionnaire) while manipulating two variables that have been suggested to affect the intensity of the illusion. First, the rubber hand was positioned either in a posturally congruent position, or rotated by 180°. Second, either the anatomically same rubber hand was used, or an anatomically incongruent one. We found in two independent experiments that a rubber hand rotated by 180° leads to increased proprioceptive drift during synchronous visuo-tactile stroking, although it does not lead to feelings of ownership (as measured by questionnaire). This dissociation between drift and ownership suggests that proprioceptive drift is not necessarily a valid proxy for the illusion when using hands rotated by 180°.

Keywords: Body representation; Embodiment; Rotation; Touch; Visuo-tactile.

When we are being touched, the touch sensation has a specific quality which assures us that “my body belongs to me.” This feeling of body ownership is typically not experienced when we simply observe other people being touched but is confined to one’s own body (but see Holle, Banissy, Wright, Bowling, & Ward, 2011). One way to investigate and experimentally manipulate this experience of body ownership is by means of the rubber hand illusion (RHI) (cf. Tsakiris, Jimenez, & Costantini, 2010). The typical RHI paradigm consists of the following parts: (1) the real hand of the participant, which is concealed from view (e.g., placed in a box); (2) a rubber hand, which is placed before the participant; and (3) tactile stimulation of the real hand and the rubber hand. Under these circumstances, watching the rubber hand being touched in synchrony with one’s own unseen hand causes the rubber hand to be attributed to one’s own body, and it starts to “feel like it’s my hand” (Botvinick & Cohen, 1998). One recent questionnaire devised by Longo, Schuur, Kammers, Tsakiris, and Haggard (2008) identified three components of the RHI: ownership (e.g., “it seemed like the rubber hand was part of my body”), location (e.g., “it seemed like my hand was in the location where the rubber hand was”), and agency (e.g., “it seemed like I could have moved the rubber hand if I had wanted”). In addition to such questionnaire-based data, one can also measure the degree to which the RHI induces a proprioceptive drift by asking participants to report the position of their unseen hand before and after each block. Participants tend to mislocalize their unseen real hand toward the rubber hand while under the illusion (Botvinick & Cohen, 1998), and the amount of this proprioceptive drift is usually correlated with the intensity of the subjective experience (Longo et al., 2008).
To sum up, the RHI consists of illusory feelings of ownership, location change, and agency. The intensity of the illusion is often correlated with the amount of proprioceptive drift.

One contentious research question has been what the necessary and sufficient conditions to elicit the RHI are. It is rather uncontroversial that synchrony of touch with vision is a necessary condition. Participants tend to report the illusion for synchronous, but not for asynchronous touch. More controversial is the question about what the sufficient conditions are. Armel and Ramachandran (2003) argued for a strong bottom-up view of the RHI. According to their view, synchronous stimulation is both a necessary and sufficient condition to elicit the RHI. In other words, they would predict that synchronous touch is sufficient to incorporate any object into one’s own body representation. However, there is now ample evidence that the RHI is not purely bottom-up. For instance, rubber hands but not objects elicit the illusion (Tsakiris & Haggard, 2005). Objects that are closer to the real hand tend to elicit stronger illusions than more distant ones (Lloyd, 2007). Anatomically or posturally incongruent rubber hands tend not to elicit the RHI (Austen, Soto-Faraco, Enns, & Kingston, 2004; Costantini & Haggard, 2007; Ehrsson, Spence, & Passingham, 2004; Pavani, Spence, & Driver, 2000; Tsakiris & Haggard, 2005). In light of such top-down interactions, Tsakiris (2010) has modeled the RHI as an interaction between current multisensory input and internal models of the body. The extracorporeal object first undergoes a goodness-of-fit evaluation, and only extracorporeal objects with a sufficient fit (e.g., an anatomically and posturally matching rubber hand) then undergo an additional comparison, where the observed touch is compared with the felt touch. Tsakiris (2010) stresses that the body model underlying the initial goodness-of-fit evaluation is rather underspecified, and not all aspects of one’s own hand, such as skin color (Longo, Schuur, Kammers, Tsakiris, & Haggard, 2009), enter into this comparison.

Given the close relationship between questionnaire measures and proprioceptive drift, one (normally tacit) assumption is that they arise from the same mechanism. Indeed, it is not uncommon for studies to use proprioceptive drift as a proxy of the illusion itself (e.g., Costantini & Haggard, 2007), and to use the degree of drift as an index for the strength of the illusion (Kammers et al., 2009). However, there may be special conditions under which they dissociate. Kammers et al. (2009) found that transcranial magnetic stimulation (TMS) applied over the left inferior parietal lobe disrupted proprioceptive drift measures of the RHI (for right hand stroking), but it did not affect the subjective illusion, as measured via questionnaire. In a rather different paradigm that used only a visual presentation of a rubber hand (presented in a parasagittal mirror), Holmes, Snijders, and Spence (2006) observed a disrupted proprioception of the unseen hand, but this was not accompanied by strong illusory feelings of ownership. The effect was greater for a rubber hand than a wooden block. Holmes and colleagues suggested that visual presentation alone of an appropriate body part (without any tactile stimulus) can result in proprioceptive recalibration.

The present study was motivated by an incidental finding that we subsequently went on to replicate twice (the latter two reported here). Previous studies have failed to demonstrate the RHI for rotations of 180° (Ehrsson et al., 2004), 90° (Tsakiris & Haggard, 2005), or even smaller deviations (Costantini & Haggard, 2007). In two studies, we show that (given a sufficient sample size) proprioceptive drift arising from synchronous visuo-tactile stimulation is present when the anatomically identical hand is rotated by 180° but not when the anatomically mismatching hand is presented at 180° (which can be construed as a mirrored version of the stimulated hand). However, the effect is limited to proprioceptive drift only, and it does not manifest itself in the self-reported illusion (measured via questionnaire).

**METHOD**

**Design**

Two separate experiments were conducted. However, the method and results of both studies are presented together because the second experiment was very similar to the first. In both studies, the participants’ right hand was always used for tactile stimulation. The first experiment consisted of a 3 × 2 factorial design contrasting rubber hand stimulus (right hand unrotated, right hand rotated, and left hand rotated: R, R180, and L180, respectively) and synchrony (synchronous, asynchronous). The second experiment contained an additional rubber hand stimulus (left hand unrotated), enabling a more sophisticated 2 × 2 × 2 factorial design contrasting hand (left, right), rotation (rotated, unrotated), and synchrony.

**Participants**

All participants were students at the University of Sussex, who participated either for course credits or
for a payment of £5 (corresponding to about 8 US$). They gave informed consent according to the ethics committee of the School of Psychology, University of Sussex. Thirty participants took part in the first experiment (mean age = 23.74; range = 18–50; 7 men), and 39 took part in the second experiment (mean age = 21.1; range = 18–30; 8 men). No participant took part in both. Two participants in Experiment 2 were excluded for having unusually large mean drift scores across all conditions (falling in the upper 5% of the normalized distribution of overall drift scores).

Procedure

Participants were seated at a table, facing the experimenter. On the table was a box, which was open to the sides. Participants were instructed to place their right hand at a marked position inside the box where it was concealed from their view. A rubber hand was also placed at a marked position inside the box, at a position approximately 20 cm to the right of the midline of the participant. The location of the rubber hand was identical in all conditions, differing only in handedness and orientation. The location of the participants’ real hand was at an additional 20 cm further to the right. This spatial arrangement of rubber hand and real hand is known to elicit a reliable illusion (Lloyd, 2007). The top cover of the box contained a hole, through which participants could see the rubber hand but not their real hand. Before each trial, the rubber hand was concealed by placing an additional cover on top of the box. A ruler was placed on top of the box, and participants were asked to indicate where they thought that their right index finger was located, by saying the corresponding number on the ruler (the prestimulus position). A different offset was used for the ruler in each trial to reduce memory effects. Next, the ruler and the top cover were removed, and the rubber hand and the real hand were stroked by the experimenter with two identical paintbrushes. Stroking occurred horizontally on the index finger, from knuckle to finger tip and lasted for 1 min. Each stroke lasted approximately 500–1000 ms. The experimenter immediately repositioned the paintbrushes at the knuckle and began the next stroke some 500–1000 ms after the end of the previous stroke. In the asynchronous conditions, asynchrony was randomly varied between 500 and 1000 ms (cf. Tsakiris & Haggard, 2005). For the rotated conditions, the rubber hand was rotated by 180° around the position of the rubber index finger. The direction of stroking in the rotated condition was congruent in hand-centered space (e.g., knuckle to fingertip) but not in external space (see also Tsakiris & Haggard, 2005). Participants were asked to look at the rubber hand throughout the stroking period, which lasted for 60 s. After the stroking had finished, the top cover and ruler were again placed onto the box, and participants were again asked to indicate the position of their right index finger (the poststimulus position). The amount of proprioceptive drift elicited by a trial was subsequently calculated by subtracting the prestimulus position from the poststimulus position.

In Experiment 1, each participant completed a total of 12 trials (two for each of the six conditions) and in Experiment 2, each completed 16 trials (two for each of the eight conditions). The order of the different conditions was randomized for each participant with the constraint that the first and second half of the experiment contained only one of each trial type. Questionnaire data were obtained for the first six trials and eight trials in Experiments 1 and 2, respectively, immediately after the drift measure was taken. We used the short version of the rubber hand questionnaire from Longo et al. (2008). The short version consists of a total of 10 items, referring to three different components of the experience of embodiment during the RHI paradigm: ownership (five items), location (three items), and agency (two items). Participants answered each question on a 7-point Likert scale ranging from −3 ("strongly disagree") to +3 ("strongly agree"), with 0 being “neither agree nor disagree.” Questions were randomized separately for each block. Questionnaire data from one participant were incomplete. At the end of each block, participants were asked to remove their hand from the box and wiggle it around to reduce carry-over effects from block to block.

Data analysis

Drift and questionnaire data were analyzed by repeated-measure ANOVAs. Greenhouse–Geisser correction was used where appropriate. In that case, we report the uncorrected degrees of freedom, the corrected $p$ values as well as the correction factor $\epsilon$. Post-hoc paired $t$-tests where used where appropriate to evaluate the pattern of significant interactions. We also provide Cohen’s $d$ as an effect size measure for these post-hoc tests. Cohen’s $d$ gives the standardized difference between two means, and values of 0.2, 0.5, and 0.8 have been suggested to reflect small, medium, and large effects, respectively (Cohen, 1992).
RESULTS

Proprioceptive drift

The results for both experiments are summarized in Figure 1. For Experiment 1, the corresponding 3 × 2 ANOVA for the drift data revealed a significant main effect of Synchrony, $F(1, 24) = 23.45, p < .0001$, as well as an interaction between Stimulus Type and Synchrony, $F(2, 48) = 6.21, p < .01, \varepsilon = .88$. Post-hoc paired $t$-tests (two-tailed) indicated that the simple main effect of Synchrony was significant for conditions R, $t(29) = 5.52, p < .0001$, Cohen’s $d = 1.29$, and R180, $t(29) = 2.76, p < .01$, Cohen’s $d = 0.72$, but not for condition L180, $t(29) = 0.61, p > .5$. For Experiment 2, the corresponding 2 × 2 × 2 ANOVA revealed main effects of Synchrony, $F(1, 36) = 7.68, p < .01$; Hand, $F(1, 36) = 7.24, p < .05$; and Rotation, $F(1, 36) = 10.17, p < .005$. The interaction between Hand and Rotation was of borderline significance, $F(1, 36) = 3.60, p = .066$, but no other interactions approached significance. Post-hoc tests indicated that the simple main effect of Synchrony was significant for conditions R, $t(36) = 2.18, p < .05$, Cohen’s $d = 1.09$, and R180, $t(36) = 2.04, p < .05$, Cohen’s $d = 0.44$, but not for conditions L, $t(36) = 1.82, p = .08$, and L180, $t(36) = 0.37, p > .5$. As such, the main novel finding from these experiments is that one measure of the RHI, proprioceptive drift, can be found for the anatomically congruent hand in at least one orientation other than the standard one (i.e., the anatomically and posturally congruent condition R). The effect is not driven solely by visuo-tactile synchrony because it is not found for the left hand when rotated. It involves the combination of an anatomically congruent, but rotated, body part combined with visuo-tactile synchrony.

One might wonder whether those participants who show the largest proprioceptive drift in the standard condition are the ones who show the greatest effect for the rotated right hand. This was found not to be the case. There was no significant correlation between drift scores between rotated and unrotated right hand (synchronous) across both experiments ($r = .05, n.s.$).

![Figure 1. Mean proprioceptive drift for Experiment 1 (top panel) and Experiment 2 (lower panel). Error bars show SEM. *p < .05.](image)
Questionnaire measures of ownership, location, and agency

For Experiment 1, there were main effects of both Synchrony and Stimulus Type for the ownership subscale: Synchrony, $F(1, 29) = 22.96, p < .0001$; Stimulus Type, $F(2, 58) = 12.31, p < .001, \varepsilon = .87$; the location subscale: Synchrony, $F(1, 29) = 28.90, p < .0001$; Stimulus Type, $F(2, 58) = 11.49, p < .001, \varepsilon = .99$; and the agency subscale: Synchrony, $F(1, 29) = 14.41, p < .005$; Stimulus Type, $F(2, 58) = 16.71, p < .0005, \varepsilon = .70$. In no cases was the interaction significant.\(^1\)

Experiment 2 contained more participants and also enabled the Stimulus Type variable to be broken down into separate Hand and Rotation factors. In this analysis, there were significant Hand $\times$ Rotation interactions for all three subscales and these are summarized in Figure 2. For the ownership subscale, there were significant main effects of Synchrony, $F(1, 36) = 62.35, p < .001$; Hand, $F(1, 36) = 9.41, p < .005$; and Rotation, $F(1, 36) = 50.51, p < .001$, together with a significant Hand $\times$ Rotation interaction, $F(1, 36) = 17.08, p < .001$. No other interactions were significant.

As can be seen in Figure 2, the Hand $\times$ Rotation interaction seems to be driven by a stronger effect of Rotation for the right hand. A post-hoc paired $t$-test comparing the difference of (right unrotated – right rotated) with (left unrotated – left rotated) confirmed this impression, $t(36) = 4.13, p < .001$, Cohen’s $d = 0.98$. The same pattern was repeated for the other two subscales. For the location subscale, there were significant main effects of Synchrony, $F(1, 36) = 122.20, p < .001$; Hand, $F(1, 36) = 12.46, p < .001$; and Rotation, $F(1, 36) = 76.87, p < .001$, together with a significant Hand $\times$ Rotation interaction, $F(1, 36) = 14.08, p < .001$. No other interactions were significant. The Hand $\times$ Rotation interaction was again found to be driven by a larger Rotation effect for the right hand, $t(36) = 4.97, p < .001$, Cohen’s $d = 0.94$. No other interactions were significant.

Finally, we compared the relationship between questionnaire measures and the proprioceptive drift scores. When we correlated the differences scores (synchronous vs. asynchronous) of the drift data (collapsed across both experiments, $n = 67$) with the respective difference scores of the three questionnaire subscales, we found that drift and questionnaire measures were only correlated in the R condition (ownership: $r = .33, p < .01$; location: $r = .29, p < .05$; agency: $r = .36, p < .01$) but not in the R180 condition (ownership: $r = -.12, p > .31$; location: $r = -.18, p > .14$; agency: $r = -.07, p > .58$). Thus, although there is evidence for the RHI (in terms of proprioceptive drift) in both the R and the R180 condition, only in the former was there a reliable association between drift and subjective measures of the illusion.

DISCUSSION

We conducted two experiments investigating the degree to which the RHI is sensitive to rotations of 180° of either an anatomically congruent or an incongruent hand. Previous research has found that only posturally and anatomically congruent hands are sufficient to elicit the RHI. We found in two independent experiments that a rubber hand rotated by 180° can nonetheless elicit proprioceptive drift (which is often taken as a proxy measure of the illusion) with synchronized visuo-tactile stroking, although this condition does not necessarily lead to an illusory sense of ownership, location, or agency.

Previous studies have sometimes used proprioceptive drift as a proxy for the RHI illusion (Costantini & Haggard, 2007) or used the amount of drift as an index for the strength of the illusion (Kammers et al., 2009). Our data show that this assumption is not always justified. We observed significant drift effects for rotated hands, while at the same time participants denied illusory feelings of ownership. Furthermore, drift and questionnaire scores were found to be correlated only for unrotated, but not for rotated hands, suggesting that the RHI questionnaire and proprioceptive drift are not measuring the same construct, at least when rotated hands are used.

One question our data raise is why previous studies found that rotating the rubber hand abolishes the proprioceptive drift associated with the RHI (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005) whereas we observed that rotations by 180° do not abolish proprioceptive drift. Our results indicate that the drift effect for

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\(^1\)Although we found effects of Synchrony on subjective experiences of the illusion, the mean ratings in Experiment 1 tended to be negative (i.e., people tended to choose “disagree” rather than “agree”). If we compare just those people who reported a positive score on the synchronous ownership questions ($n = 11$) then we still get significant proprioceptive drift effects for the R, $t(10) = 2.88, p < .05$, and R180, $t(10) = 2.70, p < .05$, conditions but not for the L180 condition, $t(10) = 0.05$, n.s.
rotated hands is smaller than the effect for unrotated hands and therefore requires larger sample sizes to detect than have been typically used in previous research. We confirmed this impression in a post-hoc power analysis using G-Power (Faul, Erdfelder, Lang, & Buchner 2007), where we found that the two previous studies that measured drift while manipulating postural congruency were indeed underpowered in this respect (Tsakiris & Haggard, 2005: \( n = 8 \), probability of 42\% to detect an effect of Cohen’s \( d = 0.72 \) or greater, 19\% when using the smaller effect size obtained in our Experiment 2; Costantini & Haggard, 2007: \( n = 11 \) in the relevant group, probability of 58\% to detect an effect of Cohen’s \( d = 0.72 \) or greater, 26\% when using the smaller effect size).

Furthermore, our study underlines the importance of measuring both the subjective experience of the RHI and proprioceptive drift. For example, there were no interactions involving the crucial factor of Synchrony in the questionnaire data (i.e., Synchrony increased feelings of ownership, location, and agency to a similar degree, regardless of what rubber hand was being placed in front of the participant). In contrast, we found interactions involving Synchrony for some presentations of the rubber hand in the drift data (compare Figures 1 and 2). Similarly, the presence of the anatomically and posturally correct right hand had an effect in the asynchronous condition as well, not just in the synchronous condition (i.e., Synchrony did not interact with Hand or Rotation in the questionnaire data).

Figure 2. Questionnaire ratings. The Likert scale ranged from −3 (“strongly disagree”) to +3 (“strongly agree”), with 0 being “neither agree nor disagree.” The left panel shows the data from Experiment 1, and the right panel the data from Experiment 2.
This is consistent with the model of Tsakiris (2010), in which visuo-tactile synchrony and the illusory experience of body ownership are separate processes. However, this model requires refinement to incorporate the data presented in this study. Proprioceptive drift was greater for the anatomically correct hand in the incorrect posture (R180) than an anatomically incorrect hand in the same incorrect posture (L180). This suggests that visuo-tactile synchrony mapped to a hand-centered reference frame in near space may be sufficient to induce reliable proprioceptive drift. However, this does not mean that postural information is unimportant. We only observed a significant correlation between subjective and drift data in the anatomically and posturally correct condition (R). For the posturally incorrect hand (R180), we did observe a significant mislocalization; however, the degree of mislocalization was not associated with increased subjective sensations of ownership, location, and agency. Thus, illusory feelings of ownership may further depend on whether the rubber hand is posturally plausible.

Our finding that 180° rotated body parts can elicit proprioceptive drift in a RHI paradigm fits well with recent neuroimaging studies on observed touch. One emerging theme of this field is that observing a touch event activates the same brain regions that are also active during actual touch, including primary and secondary somatosensory cortex (SI and SII, respectively; for review, see Keysers, Kaas, & Gazzola, 2010). A recent study by Schaefer, Xu, Flor, and Cohen (2009) suggests that although SI and SII are activated during observed touch, they are relatively insensitive to the perspective of observed touch. In that study, similar levels of activity were observed for touch events filmed from an egocentric perspective (as if looking at one’s own hands) than for touch events filmed from an allocentric perspective (as if looking at the hands of someone else). This relative insensitivity to the spatial orientation at the initial cortical processing stages may explain why there is a certain tendency to incorporate rubber hands rotated by 180° into one’s body representation.

Finally, we also explored in Experiment 2 whether an anatomically incongruent, but posturally congruent rubber hand (condition L) elicits proprioceptive drift or illusory ownership. Unfortunately, the statistical test for the drift effect was not significant ($p = .08$), so we are unable to draw any strong conclusions about this condition. Generally, we observed a great degree of interindividual variation in this condition, with some participants showing strong mislocalizations, whereas others showed no such effect. Further research, especially into what distinguishes participants who report the illusion from those who do not in a rubber hand experiment (interoceptive awareness apparently being one factor; see Tsakiris et al., 2011), may shed further light on this issue.

In conclusion, we report a novel finding that rubber hands rotated by 180° can elicit proprioceptive drift, provided the rubber hand is anatomically congruent to the stimulated real hand. The results suggest that mapping onto a hand-centered space may drive proprioceptive drift toward the rubber hand but that postural alignment is additionally needed for the illusory experience of ownership as measured by questionnaire measures.

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