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Dissociation of proprioceptive drift and feelings of ownership in the somatic rubber hand illusion

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ABSTRACT

The sense of self is a complex phenomenon, comprising various sensations of bodily self-consciousness. Interestingly, the experience of possessing a body – 'embodiment' – and locating the body within space may be modulated by the Rubber Hand Illusion (RHI). Measures of the RHI include proprioceptive drift (PD), the extent to which the hand is mis-localised towards the rubber hand, and subjective questionnaires. Although these measures often correlate, research from the visual RHI suggests that they reflect separate underlying processes. We investigated whether increasing the duration of tactile stimulation would affect PD and questionnaires differently during the somatic RHI. Participants experienced 30 s, 2 min, or 5 min of synchronous or asynchronous tactile stimulation. Increasing duration affected only PD, with increased drift following 5 min vs 30 s of stimulation. Our findings suggest that PD and questionnaires are not proxies for one another, but reflect separate underlying processes of the somatic RHI.

1. Introduction

Feeling as if my body belongs to me is a key aspect of the sense of self (Blanke & Metzinger, 2009; Carruthers, 2008; Gallagher, 2000; Serino et al., 2013). This sensation of body ownership has been frequently studied through a well-known and striking illusion: the rubber hand illusion (RHI) (Botvinick & Cohen, 1998). The visual RHI consists of placing a rubber hand near to the real hand of a participant. While the participant can see the rubber hand, their own hand is hidden from view. Touches are administered synchronously to both the real and rubber hands, resulting in a compelling sensation of ownership over the fake hand, and a mis-localisation of the participant's hand towards the rubber hand. The majority of RHI models suggest that multisensory integration of visual, tactile, and proprioceptive cues is key to producing the illusion (Ehrsson & Chancel, 2019; Makin et al., 2008; Samad et al., 2015). However, whether the RHI also requires the integration of "top-down" knowledge regarding the body is still debated (Carruthers, 2013; Tsakiris, 2010).

Various methods have been used to investigate the RHI, including questionnaires (Longo et al., 2008; Marotta et al., 2016), proprioceptive drift (the amount by which participants mis-localise their hand towards the location of the rubber hand; Costantini & Haggard, 2007; Fuchs et al., 2016; Rohde et al., 2011; Wold et al., 2014), onset time (Kalckert & Ehrsson, 2017) and potential physiological correlates (such as decreases in skin temperature and galvanic skin response; Llorens et al., 2017; Moseley et al., 2008, however see de Haan et al., 2017, for alternative findings). While these measures are complementary (Guterstam et al., 2013; Petkova & Ehrsson, 2009; Tsakiris, 2010), dissociations between them may suggest that they could reflect different underlying processes involved in the illusion (Abdulkarim & Ehrsson, 2016; Holle et al., 2011; Radziun & Ehrsson, 2018b; Riemer et al., 2015; Rohde et al., 2011).

Rohde et al. (2011) found that subjective ratings of embodiment were always higher following synchronous versus asynchronous tactile stimulation. However, only continuous asynchronous stimulation reduced proprioceptive drift; when tactile stimulation was frequently interrupted, similar drifts were seen in both synchronous and asynchronous conditions. These findings suggested that rather than synchronous stimulation *causing* proprioceptive drift, asynchronous stimulation *diminished* drift over time, implying a separate process for drift from subjective embodiment (Rohde et al., 2011). Moreover, Abdulkarim and Ehrsson (2016) found that proprioceptive drift was strongly affected by moving the participant's hand towards or away from the rubber hand during induction of the illusion, however this

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manipulation did not affect subjective questionnaire ratings. Finally, Holle et al. (2011) reported decreases in subjective feelings of ownership when the rubber hand was placed in an incongruent position to the real hand, however proprioceptive drift was unaffected.

Taken together, these findings suggest that proprioceptive drift and subjective questionnaires are not interchangeable, but rather reflect different underlying mechanisms. It has been suggested that questionnaires indicate ownership of the rubber hand, while proprioceptive drift instead reflects self-localisation (Carruthers, 2008, 2013; Dempsey-Jones & Kritikos, 2014; Serino et al., 2013). While both of these components make up key aspects of the sensation of embodiment (Serino et al., 2013), they are not necessarily always correlated, and can thus show differences in response to different manipulations, accounting for previous results (Holle et al., 2011; Radziun & Ehrsson, 2018a; Riemer et al., 2015; Rohde et al., 2011). Carruthers (2013) proposed that embodiment arises when stored offline representations of the body match online representations of the object to be embodied, for example when the real and rubber hands appear similar, in congruent postures, and when tactile sensations are spatiotemporally congruent. Proprioceptive drift by contrast can occur in the absence of embodiment, as visual and proprioceptive cues for hand location are integrated even when the object does not match stored offline representations of the body. Accordingly, reductions in subjective ownership were found when body posture was incongruent with the rubber hand position, while proprioceptive drift was unaffected by this cognitive manipulation (Dempsey-Jones & Kritikos, 2014). Recently, Bayesian multisensory integration mechanisms have been proposed to explain the RHI, omitting the need for explicit cognitive representations of the body (Ehrsson, 2020; Ehrsson & Chancel, 2019; Samad et al., 2015). According to these models, ownership of the rubber hand is induced when spatiotemporal sensory information is congruent, resulting in an inferred common cause, i.e., a unified percept of the body incorporating the rubber hand (Samad et al., 2015). It has been suggested that ownership arises from the integration of visual and somatosensory signals, while self-localisation instead results from the integration of visual and proprioceptive cues (Litwin, 2020). Thus, disruptions to either of these processes can therefore result in dissociations between proprioceptive drift and subjective questionnaires. Overall, however, further research is necessary to investigate the precise mechanisms underlying each measure of the RHI.

Interestingly, both proprioceptive drift and subjective feelings of embodiment have also been found for a non-visual variant of the RHI (occasionally termed the 'self-touch illusion' or somatic RHI; Ehrsson et al., 2005; Petkova et al., 2012; Radziun & Ehrsson, 2018a; White et al., 2011). In this variant, a blindfolded participant strokes a rubber hand with their right hand (the administering hand), while an experimenter strokes the left hand of the participant (the receptive hand). The participant therefore feels that they are touching their own hand, resulting in proprioceptive drift towards the rubber hand and a sensation of embodiment of the rubber hand, as in the visual RHI. The mechanisms underlying the somatic RHI are likely to be similar to those of the visual RHI. Specifically, in both visual and somatic variants the illusion is produced via the integration of multisensory cues (i.e., tactile and proprioceptive cues in the somatic RHI and visual, proprioceptive and tactile cues in the visual RHI), culminating in mis-localisation towards and ownership over the rubber hand (Ehrsson et al., 2005; Radziun & Ehrsson, 2018b; White et al., 2011). In addition, both somatic and visual RHI result in similar onset times (Ehrsson et al., 2005), and are subject to the same constraints, such as proximity of the real and rubber hands and temporal synchrony (Ehrsson, 2020). Moreover, fMRI results suggest that ownership over the rubber hand in both the visual and somatic RHI result in similar activations in bilateral ventral premotor cortex and fronto-parietal areas (Ehrsson et al., 2004; Ehrsson et al., 2005).

Despite these similarities, the visual and somatic RHI have been shown to differ in relation to different manipulations. Aimola Davies et al. (2013) compared the effect of increasing distance and misalignment between real and rubber hands on the somatic and visual RHI. While subjective ratings of the somatic RHI were significantly decreased with each level of increasing distance between the rubber and real hands, this decrease was only seen at much greater distances for the visual RHI. Curiously, proprioceptive drift was gradually decreased with increasing distance in the somatic RHI, while it was completely abolished with greater distances in the visual RHI. Furthermore, misalignment between the rubber and real hands led to decreased subjective illusion ratings in the somatic RHI, while there was no effect on the visual RHI (Aimola Davies et al., 2013). Finally, while incongruent auditory cues reduced subjective ownership of the rubber hand in the visual RHI, ownership in the somatic RHI was unaffected, suggesting potential differences in which cues are integrated to produce the two illusions (Radziun & Ehrsson, 2018a). Thus, these findings suggest that both subjective ratings and proprioceptive drift may show subtle differences in both visual and somatic RHI, however further research into these differences is necessary. Interestingly, previous research has suggested that visual and somatosensory regions are implicated at different levels of body representation, with somatosensory regions associated with more local representations (i.e., specific body parts, such as hands), while visual regions are associated with global representations (i.e., the whole body) (Perruchoud et al., 2016). As such, it is possible that differences in tactile versus visual processing may have different impacts on the visual versus somatic RHI.

Previous research has found that increasing the duration of tactile stimulation increases the level of proprioceptive drift towards the rubber hand during the visual RHI (Tsakiris & Haggard, 2005). However, it remains unclear whether increasing the duration of stimulation would also have subsequent effects on other aspects of RHI, such as subjective questionnaires. Moreover, little attention has been given to the time-course of the somatic RHI. Given previously reported differences between the somatic and visual RHI (Aimola Davies et al., 2013; Radziun & Ehrsson, 2018a, 2018b), it is important to consider whether increasing the duration of tactile stimulation would have similar effects on proprioceptive drift in the somatic RHI. Here we explored whether increasing the duration of tactile stimulation would modulate the strength of the somatic RHI in either or both proprioceptive drift and questionnaire measures. Participants underwent 30 s, 2 min, or 5 min of synchronous or asynchronous tactile stimulation, with the former inducing the RHI. Based on previous data from the visual RHI (Rohde et al., 2011), we predicted that longer durations of stimulation would increase the intensity of the illusion, however this would be reflected only in proprioceptive drift, while questionnaire measures would be unaffected by duration.

2. Methods

2.1. Ethics

Written informed consent was collected from participants before commencing the experiment. The experimental protocol was approved by the School of Social Sciences Ethics Committee at Heriot-Watt University (Approval Number 2016-383). The experiment was conducted in line with the Declaration of Helsinki.

2.2. Participants

Thirty-eight participants (14 male, *M* age = 25.58 SD = 6.05) were recruited for the experiment. One was excluded as they did not show the expected proprioceptive drift (i.e. their drift was not towards the rubber hand – see below for details) and two were excluded as they did not attend the second session. Thus, 35 participants (14 male, *M* age = 25.97 SD = 6.12) completed the study and were included in the main analysis. All participants were right-handed according to the Edinburgh Handedness Inventory-Short Form results. Exclusion criteria were any history of severe head injury, neurological conditions, psychiatric conditions, and motor/tactile conditions. The sample size was chosen on the basis of previous similar experiments (Ehrsson et al., 2005; Rohde et al., 2011; Tsakiris & Haggard, 2005). Reported effect sizes for differences between synchronous and asynchronous stimulation for proprioceptive drift and questionnaire measures in the somatic RHI range between η_p^2 = 0.19–0.73 (Aimola Davies et al., 2013; White et al., 2010; White et al., 2011). Accordingly, we conducted a power analysis using G*Power 3 (Faul et al., 2007) assuming a $\eta_p^2 = 0.3$ (Cohen's f = 0.654), α = 0.05, power = 0.85, n groups = 3, and numerator df = 2. This yielded a total required sample size of 29 participants.

2.3. Somatic rubber hand illusion

Participants were seated, asked to wear a blindfold and to place their hands on a table in front of them. The left hand was placed 15 cm to the left of the rubber hand (Fig. 1). A ruler was placed on a wooden support above the hands. Tactile stimulation was administered by the experimenter moving the participant's. Right index finger onto the index finger of the rubber hand from knuckle to fingertip. The experimenter also stroked the left index finger of the participant, either synchronously or asynchronously to the rubber hand stimulation (Fig. 1A). Each stroke lasted on average 500 ms. The order of synchrony of the stimulation was counterbalanced across participants.

Participants first completed a baseline session consisting of 2 min each of synchronous/asynchronous stimulation. Prior to commencing stimulation, participants were asked to point at the felt location of the left index finger using their right index finger. This served as a baseline measure to calculate the amount of drift following inducement of the RHI. After stimulation, participants were again asked to indicate the felt position of their left index finger. The difference between the perceived position before and after stimulation was therefore used as the proprioceptive drift measure.

A second session was conducted on a different day, with participants receiving either 30 s (N = 12), 2 min (N = 12), or 5 min (N = 11) of stimulation in a between-subjects design. These durations were chosen on the basis of previous studies (Ehrsson et al., 2005; Rohde et al., 2011; Tsakiris & Haggard, 2005). Demographics were similar across all three groups (30s group mean age = 27.75, SD = 6.98, 7 male; 2 min group mean age = 26.08, SD = 6.64, 3 male; 5 min group mean age = 23.91, SD = 4.09, 4 male). Participants were invited to return for the second session if they showed any proprioceptive drift towards the rubber hand in the synchronous stimulation condition as compared to no stimulation during the first session. In other words, participants were included in the study if their proprioceptive drift towards the rubber hand in the synchronous condition was higher than in the no stimulation condition. One participant was excluded as they showed proprioceptive drift away from the rubber hand on the basis of this criterion. Proprioceptive drift was chosen as the critical measure over the questionnaire for several reasons. Firstly, this measure may be considered less susceptible to biases such as participant expectations, and is regarded as a more implicit illusion measure than the questionnaire. Secondly, a key aim of the study was to investigate whether increasing duration increases proprioceptive drift in the somatic RHI, similar to previous visual RHI findings (Tsakiris & Haggard, 2005). Accordingly, it was vital that the participants showed the expected proprioceptive drift in order for the duration manipulation to be meaningful. Finally, selecting only participants with high agreement to the questionnaire statements may have risked ceiling effects, masking any changes in illusion perception with increasing duration. Rohde et al. (2011) highlighted how repeatedly interrupting the RHI procedure could affect the proprioceptive drift experienced by participants. Thus, in order to avoid this confound, we used a between-subjects design, rather than repeatedly measuring proprioceptive drift across time. In addition, administering the RHI procedure to each participant in multiple sessions according to duration may have introduced carry-over effects, confounding results (Samad et al., 2015).

Participants also completed a questionnaire assessing the strength of the RHI (Lopez et al., 2012). This questionnaire measured aspects of the illusion such as ownership, deafference, movement, compliance, and affect (Table 1). Responses ranged through 'Totally Disagree', 'Disagree', 'Somewhat Disagree', 'Neutral', 'Somewhat Agree', 'Agree', 'Totally Agree', with responses scoring −3 to +3 respectively. Thus, negative scores corresponded to disagreement with the statements, while positive scores corresponded to agreement with the statements. Questionnaire items 1, 8, 9 and 10 assessed ownership, 2, 3, 4, and 5 assessed compliance; 7 assessed affect; 6 and 11 assessed movement; and 12 and 13 assessed deafference. Averages for these items therefore gave the scores for each of the RHI components.

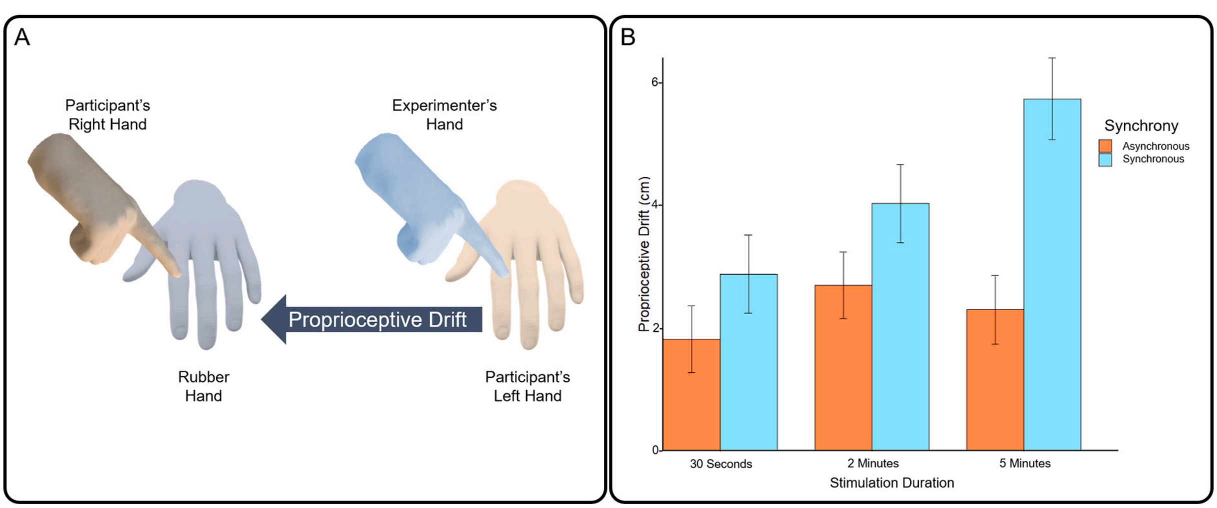

Fig. 1. A) Experimental Setup. The rubber hand was placed 15 cm to the left of the participant's left hand. The experimenter guided the participant's right index finger to stroke the index finger of the rubber hand, while the experimenter stroked the left index finger of the participant. When touches were administered synchronously, this resulted in a proprioceptive drift towards the rubber hand. B) Proprioceptive Drift results. Error bars represent standard error of the mean. The Asynchronous Stimulation condition is presented in orange, while the Synchronous Stimulation condition is presented in blue. Synchronous Stimulation elicited greater Proprioceptive Drift than Asynchronous Stimulation, while increasing durations of Synchronous Stimulation elicited greater Proprioceptive Drift than shorter durations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
RHI Questionnaire. Items 1, 8, 9 and 10 assessed ownership, 2, 3, 4, and 5 assessed compliance; 7 assessed affect; 6 and 11 assessed movement; and 12 and 13 assessed deafference.

1. I felt as if I was touching my left hand with my right index finger
2. It felt as if I had more than one left hand.
3. My left hand felt larger than normal
4. I experienced that my left hand was moving
5. I could not feel my own left hand.
6. It felt as if my left hand were drifting towards the right.
7. I enjoyed that experience.
8. It seemed like the rubber hand belonged to me.
9. It seemed like my left hand was in the location where the rubber hand.
10. It seemed like the rubber hand was in the location my left hand was.
11. I felt as if the rubber hand were drifting towards my real left hand.
12. I had the sensation that my left hand was numb.
13. It seemed like the experience of my left hand was less vivid than normal

2.4. Procedure

After completing informed consent procedures and filling out the Edinburgh Handedness Inventory, participants underwent a first session of stimulation to assess their susceptibility for the RHI. Synchronous and asynchronous tactile stimulation was administered for two minutes and measures of proprioceptive drift were completed. If participants experienced the RHI, they returned on a second day to repeat the procedure. Participants were randomly assigned to one of three groups, corresponding to the duration of stimulation (30 s, 2 min, or 5 min). Synchronous and asynchronous stimulation was administered in a counterbalanced order across participants. At the end of each stimulation session, participants indicated the location of their left index finger and completed the questionnaire.

2.5. Data analysis

For each dependent variable (proprioceptive drift and each of the six questionnaire measures), a 2 (Session: baseline vs experimental) × 2 (Synchrony: synchronous vs asynchronous stimulation) × 3 (Group: 30 s, 2 min, 5 min) mixed ANOVA was conducted. Session and Synchrony were within-subject variables, while Group was a between-subject variable. Bonferroni-corrected pairwise comparisons were conducted to follow-up significant interactions.

Bonferroni correction was applied to questionnaire variables, with critical $\alpha = 0.01$. Thus, only results under this value were considered significant.

3. Results

3.1. Proprioceptive drift

The 2 × 2 × 3 ANOVA revealed a significant main effect of Synchrony, with a higher proprioceptive drift for synchronous ($M = 4.22$ cm, $SE = 0.38$ cm) versus asynchronous ($M = 2.27$ cm, $SE = 0.31$ cm) stimulation ($F(1,32) = 23.73$, $p < .001$, $\eta_p^2 = 0.426$). No main effects of Group ($F(2,32) = 2.92$, $p = .07$, $\eta_p^2 = 0.15$) or Session ($F(1, 32) = 0.38$, $p = .54$, $\eta_p^2 = 0.01$) were found.

An interaction between Synchrony and Group was found ($F(2, 32) = 3.43$, $p = .045$, $\eta_p^2 = 0.18$) (Fig. 1B). Specifically, 5 min of synchronous stimulation elicited greater proprioceptive drift ($M = 5.74$ cm, $SE = 0.67$) than 5 min of asynchronous stimulation ($M = 2.30$ cm, $SE = 0.56$) ($p < .001$). In addition, 5 min of synchronous stimulation also elicited greater proprioceptive drift than 30 s of synchronous stimulation ($M = 1.82$ cm, $SE = 0.64$) ($p = .013$) (Fig. 1B). No other interactions were significant ($p > .05$).

3.2. Ownership

Results for all questionnaire statements can be seen in Fig. 2. The 2 × 2 × 3 ANOVA revealed a significant main effect of Synchrony, with greater ownership for synchronous ($M = 0.18$, $SE = 0.35$) versus asynchronous ($M = -1.68$, $SE = 0.22$) stimulation ($F(1, 32) = 31.94$, $p < .001$, $\eta_p^2 = 0.50$). No other main effects or interactions were found ($p > .01$).

3.3. Deafference

No significant main effects or interactions were found ($p > .01$).

3.4. Movement

The 2 × 2 × 3 ANOVA revealed a significant main effect of Synchrony, with greater Movement for synchronous ($M = -0.62$, $SE = 0.27$) versus asynchronous ($M = -1.32$, $SE = 0.24$) stimulation ($F(1, 32) = 11.00$, $p = .002$, $\eta_p^2 = 0.26$. No other main effects or interactions were found ($p > .01$).

3.5. Affect

No significant main effects or interactions were found ($p > .01$).

3.6. Compliance

No significant main effects or interactions were found ($p > .01$).

4. Discussion

The RHI is a well-known body illusion, frequently used to investigate the sense of body ownership. Previous research has suggested that proprioceptive drift and subjective questionnaire measures may tap into different underlying processes of the RHI. However, these findings have been based on the visual RHI. Here we investigated whether increasing the duration of tactile stimulation would modulate the strength of the somatic RHI, assessed through proprioceptive drift and questionnaires. We found that proprioceptive drift increased following five minutes versus 30 seconds of synchronous tactile stimulation, in accordance with previous literature on the visual RHI (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). By contrast, questionnaire measures of ownership, deafference, movement, affect, and compliance were unaffected by duration. Therefore, our results add to the growing body of literature suggesting that proprioceptive drift and subjective questionnaires may not be interchangeable, but rather may reflect different processes (Abdulkarim & Ehrsson, 2016; Dempsey-Jones & Kritikos, 2014; Rohde et al., 2011; Serino et al., 2013). Crucially, these findings also extend results from the visual RHI to the somatic RHI, highlighting that increasing stimulation duration increases proprioceptive drift in both versions of the illusion (Tsakiris & Haggard, 2005).

Several models of the RHI suggested that a complex integration of both online multisensory information and higher-level cognitive representations of the body is necessary for experiencing the visual RHI (Carruthers, 2013; Tsakiris, 2010). For instance, Tsakiris (2010) proposed that comparisons are made between a ‘body model’, comprising of visual, anatomical and structural information about the body, and the visual form of the rubber hand; between the current state of the body and the structural and postural features of the rubber hand; and between online sensory information and visual and tactile reference frames. A sensation of referred touch ensues, leading to ownership over the rubber hand and a subsequent updating of the body model, establishing a loop which strengthens the RHI. Similarly, Carruthers (2013) suggested that embodiment over a rubber hand occurs only when online and offline representations of the body match. By contrast, self-localisation results from an overlapping, but distinct process, with vision ‘capturing’

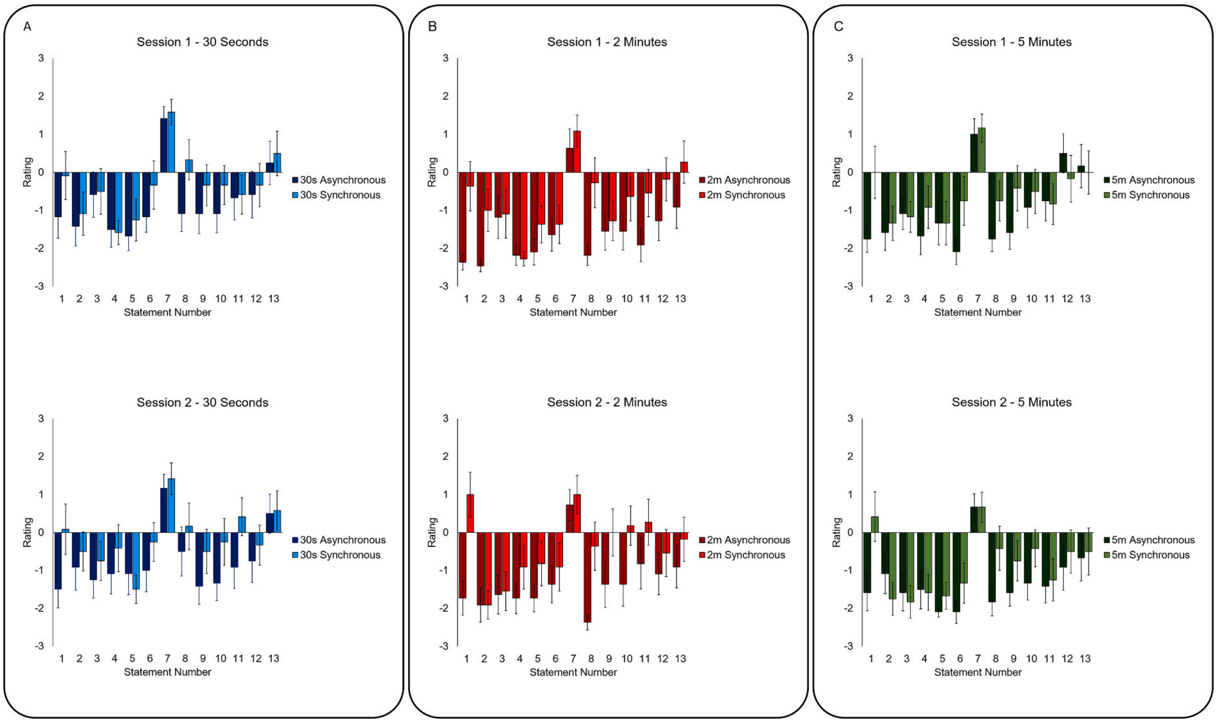

Fig. 2. Results for each questionnaire statement in the 30 s (A), 2 min (B), and 5 min (C) groups. Results for Session 1 are presented at the top of each panel and Session 2 in the bottom of each panel. Overall, synchronous stimulation resulted in greater agreement with the majority of statements. Error bars represent standard error of the mean.

proprioception, resulting in proprioceptive drift.

Crucially, dissociations between proprioceptive drift and subjective ownership may result from different aspects of these models. In particular, proprioceptive drift may reflect the multisensory integration of online sensory cues, while questionnaire measures of ownership may instead reflect cognitive aspects, such as the overall body model. Accordingly, while cumulating sensory evidence over time builds up an optimal multisensory representation of hand location, the offline representation of the body is unaffected. In support of this, previous findings suggested that when cognitive factors (such as perceived threat to the hand, Riemer et al., 2015) were modulated, changes in subjective questionnaire responses were found in the absence of changes in proprioceptive drift. By contrast, when changes in online sensory information were applied (such as prolonged stimulation, Rohde et al., 2011), proprioceptive drift was affected in the absence of changes in questionnaire responses. These findings could therefore suggest that proprioceptive drift reflects the integration of multisensory cues, while subjective questionnaires reflect cognitive aspects, however further research is necessary.

Recently, Bayesian multisensory integration models of the RHI have been proposed, which omit the need for cognitive, "higher-level" body representations for producing the illusion of embodiment (Ehrsson, 2020; Ehrsson & Chancel, 2019; Fang et al., 2019; Kilteni et al., 2015; Litwin, 2020; Makin et al., 2008; Samad et al., 2015). Rather than an interplay between online multisensory signals and offline body representations, the RHI is believed to occur as a result of Bayesian casual inference and optimal multisensory integration (Ehrsson & Chancel, 2019; Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Kilteni et al., 2015; Litwin, 2020). Specifically, experiencing the RHI may depend on ascribing seen and felt touches to the rubber and real hands to a single cause (Ehrsson & Chancel, 2019; Kilteni et al., 2015). The likelihood of this causal inference depends on factors such as the distance between real and rubber hands, spatiotemporal discrepancies, and semantic convergence, while prior influences may also include previous experience of the illusion (Ehrsson & Chancel, 2019; Kilteni et al., 2015). This causal inference may drive the integration of multisensory cues for limb ownership. Interestingly, Fang et al., 2019 reported that inference of a common cause during the visual RHI correlated with activity of multisensory neurons in the lateral premotor cortex, suggesting a neural mechanism for this model.

Optimal multisensory integration reduces uncertainty regarding the source percept, such that integrated estimates are more precise than estimates from a single modality (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Knill & Pouget, 2004). Cues about the same source property which are spatiotemporally co-occurring are likely to be integrated (Parise et al., 2012; Parise & Ernst, 2015). Importantly, noisier (i.e., less precise) sensory modalities are given lower weightings in favour of more reliable ones (Ernst & Banks, 2002; Ernst & Bülthoff, 2004). Accordingly, in the visual RHI, both vision and proprioception give spatial cues for hand location, while viewing tactile stimulation to the rubber hand while feeling touch on the real hand provide temporal cues (Fuchs et al., 2016; Samad et al., 2015). The co-occurrence of these spatiotemporal cues may result in an inference that the sensations are arising from a common cause, and that therefore the rubber hand is embodied by the participant (Samad et al., 2015). Importantly, when discrepancies arise, such as asynchronous stimulation or increasing distance between real and rubber hands, the strength of the illusion decreases as the sensory cues are no longer inferred to be the result of a common cause (Samad et al., 2015). Furthermore, proprioceptive drift increases when proprioceptive signals become less precise, due to greater reliance on the visual cue for hand location (Samad et al., 2015). In the case of the somatic RHI, cues for location come predominantly from proprioceptive cues from both of the participant's hands, while temporal congruency is ascertained from tactile signals (White et al., 2011), however the mechanisms of the somatic RHI have not been extensively studied.

Interestingly, neural correlates of the RHI may reflect the dichotomy between localisation and ownership. For example, Tsakiris et al. (2007) found that proprioceptive drift in the visual RHI correlated with activity in the right posterior insula and frontal operculum, as well as left brainstem and middle frontal gyrus (however, it is important to note that these results should be considered descriptive as they did not survive corrections for multiple comparisons). Similarly, Brozzoli et al. (2012) found modulations of activity in the right superior supramarginal gyrus and anterior intraparietal cortex correlated with increased proprioceptive drift in the visual RHI, while increases in ownership of the rubber hand correlated with modulations of activity in the left ventral premotor cortex. By contrast, activity in the ventral premotor cortex was associated with feelings of ownership and embodiment, and correlated with subjective questionnaire measures of both the visual and somatic RHI (Ehrsson et al., 2005, 2004). Moreover, dissociations between proprioceptive drift and subjective questionnaire measures have been found in the visual RHI when modulating activity in different brain regions during repeated Transcranial Magnetic Stimulation (rTMS). For example, 1 Hz rTMS over the left Extrastriate Body Area (EBA) increased proprioceptive drift during synchronous stimulation (Wold et al., 2014), while decreased proprioceptive drift was observed during rTMS over the Inferior Parietal Lobule (IPL) (Kammers et al., 2009). In both of these studies, no changes were found among questionnaire measures, suggesting that these multisensory regions primarily affected body localisation, rather than embodiment per se. Overall therefore, it is possible that changing duration would be reflected by different activity levels in regions implicated in body localisation, while regions associated with subjective feelings of embodiment would show similar activation irrespective of duration. Future research could consider this possibility, particularly with respect to the somatic RHI given that most of the available knowledge is on the visual version of this illusion.

A direct parallel between visual and somatic versions of the RHI with regards to increasing duration was not conducted in the present study, however remains an important avenue for future research. Interestingly, Aimola Davies et al. (2013) compared the effects of increasing distance and misalignment between the real and rubber hands on the visual and somatic RHI. While the visual RHI appeared robust against the manipulations, the somatic RHI was significantly diminished. Importantly, both subjective ratings and proprioceptive drift measures showed slight differences between the two illusions, in line with recent findings suggesting that proprioceptive drift and subjective ratings may reflect different underlying constructs (Holle et al., 2011; Riemer et al., 2015; Rohde et al., 2011). Here we found that proprioceptive drift increased with greater durations of tactile stimulation, although this was only reflected in proprioceptive drift. These findings are similar to previous studies on the visual RHI (Rohde et al., 2011; Tsakiris & Haggard, 2005), although future research could consider direct comparisons between the two illusions.

Curiously, overall agreement with the subjective questionnaire statements was low in the present study, compared to previous studies of the RHI (Lopez et al., 2012, however see Holle et al., 2011; Riemer et al., 2015, for similar low questionnaire ratings). This suggested that participants on average did not feel a sense of ownership over the rubber hand. While synchronous stimulation did increase ownership relative to asynchronous stimulation, this did not further increase with greater durations of stimulation. The reason for the low ownership ratings are not entirely clear. For instance, phrasing of the questions may have influenced participant judgements. Tamè et al. (2018) reported that phrasing questionnaire statements based on *feeling* as if the rubber hand belonged to the participant resulted in higher agreement versus statements which asked if the participants *believed* that the rubber hand belonged to them. The questionnaire used in the present study included several statements which asked if various sensations *seemed* as if they were happening to the participants, which may be interpreted more ambiguously. When visually inspecting raw questionnaire data in Fig. 2, it appears that agreement was indeed higher for the ownership statement asking participants *"I felt as if I was touching my left hand with my right index finger"*, versus statements 8, 9, and 10, which asked if various sensations *seemed* to happen (however, see Rohde et al., 2011, for high agreement with similarly-phrased statements). Thus, we cannot rule out that use of an alternative questionnaire may yield different results. Importantly, non-responders may be classified as those whose questionnaire responses do not change between synchronous and asynchronous stimulation (Riemer et al., 2019). However, we note that crucially the effect of synchrony was significant for ownership-related questionnaire statements, with higher ratings for synchronous vs asynchronous stimulation, and that proprioceptive drift was comparable with previous RHI studies (Ehrsson et al., 2005; Lopez et al., 2012; Rohde et al., 2011). Thus, we believe that our participants did experience the illusion, despite low agreement with questionnaire statements. Importantly, the disparity between low agreement with the questionnaire statements despite typical levels of proprioceptive drift may further reflect the dichotomy between subjective questionnaires and proprioceptive drift in the somatic RHI, and the question remains open as to which component best reflects the illusion itself. However, further research into the effects of increasing duration with participants who show higher levels of agreement to the questionnaire statements is an important step. Specifically, while we suggest that questionnaires and proprioceptive drift reflect different illusion components and are therefore not interchangeable (Rohde et al., 2011; Holle et al., 2011; Abdulkarim & Ehrsson, 2016), we cannot rule out that the low ratings overall masked any potential findings, and therefore additional exploration is necessary.

Moreover, we note that the movement cluster was significantly affected by synchrony, despite these statements usually being considered as control statements. While this has been reported previously (Lopez et al., 2012), it is possible that this cluster is affected by synchrony in the somatic RHI, but not in the visual RHI, due to differences in the procedure involved in producing the illusion. Specifically, the somatic RHI involves the movement of the participant's administering hand which could result in an additional drift of this hand which is not experienced in the visual RHI (White et al., 2011). Accordingly, these additional components may increase agreement with the movement statements, suggesting that they may not necessarily equate to a control in this version of the illusion. More broadly, the use of control items in questionnaires has recently been debated, as empirical evidence for their non-specificity is currently limited (Longo et al., 2008; Riemer et al., 2019). As our study was not designed to directly compare visual and somatic RHI, and given the overall limited literature on the somatic RHI, further studies are necessary to replicate and explore these movement findings. Importantly, no impacts of synchrony were found on compliance statements, suggesting that the results were not simply a result of the suggestibility of the participants.

Finally, we found that five minutes of synchronous stimulation significantly increased drift relative to 30 seconds of stimulation. However, no significant increases were seen between two minutes and 30 secondss or five minutes and two minutes of stimulation. This may suggest that the change in drift is slow and incremental, rather than a simple linear increase. Specifically, our results do not suggest that doubling the amount of tactile stimulation will result in double the amount of proprioceptive drift. Rather, it is more likely that the increase in proprioceptive drift with increasing duration reflects a more complex multisensory integration process (Ehrsson & Chancel, 2019; Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Kilteni et al., 2015). Accordingly, increasing duration may result in strengthened proprioceptive drift as there is more opportunity to establish temporal congruence between the tactile stimulation to real and rubber hands, although as this process also incorporates priors and is the result of noisy sensory signals, a simple linear increase between more stimulation and greater drift is not likely. Further research is necessary to explore these mechanisms in greater depth.

In sum, we found that increasing the duration of synchronous tactile stimulation increased proprioceptive drift in the RHI, with greater drift with five minutes versus thirty seconds of stimulation. By contrast, duration had no impact on subjective questionnaire measures of the RHI. While previous findings suggested that both questionnaire and proprioceptive drift measures correlate (Botvinick & Cohen, 1998;

Tsakiris & Haggard, 2005), our results add to the growing literature highlighting that these measures assess different underlying processes of the RHI (Riemer et al., 2015; Rohde et al., 2011). Furthermore, although previous studies have investigated the effect of increased tactile stimulation on the visual RHI (Tsakiris & Haggard, 2005), the present study shows that similar effects are present during the somatic RHI. Overall, our findings suggest that distinctions between proprioceptive drift and subjective questionnaire measures of the RHI are present, and further work is necessary to uncover the underlying processes of both.

CRediT authorship contribution statement

Maria Gallagher: Formal analysis, Data curation, Writing – Original Draft, Writing – Review & Editing, Visualization; **Cristian Colzi:** Conceptualization, Methodology, Formal analysis, Investigation, Resources; **Anna Sedda:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – Original Draft, Writing – Review & Editing, Supervision, Project administration.

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Data accessibility

Data are available online at https://osf.io/qdm8s

Declaration of competing interest

None.

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