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Little evidence for an effect of the rubber hand illusion on basic movement

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Abstract

Body ownership refers to the distinct sensation that our observed body belongs to us, which is believed to stem from multisensory integration. This is commonly shown through the rubber hand illusion (RHI), which induces a sense of ownership over a false limb. Whilst the RHI may interfere with object-directed action and alter motor cortical activity, it is not yet clear whether a sense of ownership over an artificial hand has functional consequences for movement production per se. As such, we performed two motion-tracking experiments ($n = 117$) to examine the effects of the RHI on the reaction time, acceleration, and velocity of rapid index finger abduction. We observed little convincing evidence that the induction of the RHI altered these kinematic variables. Moreover, the subjective sensations of rubber hand ownership, referral of touch, and agency did not convincingly correlate with kinematic variables, and nor did proprioceptive drift, suggesting that changes in body representation elicited by the RHI may not influence basic movement. Whilst experiment 1 suggested that individuals reporting a greater sensation of the real hand disappearing performed movements with smaller acceleration and velocity following illusion induction, we did not replicate this effect in a second experiment, suggesting that these effects may be small or not particularly robust. Overall, these results indicate that manipulating the conscious experience of body ownership has little impact on basic motor control, at least in the RHI with healthy participants.

KEYWORDS
body ownership, kinematics, motor control, multisensory integration

1 | INTRODUCTION

When we move, we normally feel that the body we see before us is our own. This sense of body ownership is believed to arise through multisensory integration (Blanke et al., 2015; Ehrsson, 2020; Ehrsson & Chancel, 2019; Fang et al., 2019; Guterstam et al., 2018; Kilteni et al., 2015) whereby a combination of sensory

Abbreviations: M1, primary motor cortex; PPC, posterior parietal cortex; RHI, rubber hand illusion; TMS, transcranial magnetic stimulation.

cues (e.g., visual, tactile, proprioceptive, and kinaesthetic) provides a coherent experience of an owned body that is distinct from the world around us. However, our sense of body ownership is surprisingly malleable. This is shown clearly by the classic rubber hand illusion (RHI), in which the synchronous stroking of a fake hand and the participant's real hidden hand can induce a sense of ownership over the false limb and cause the perceived position of the real hand to drift towards the fake one (Botvinick & Cohen, 1998). Asynchronous stroking considerably weakens the illusion, and this mode of incongruent visuotactile stimulation is often used as a control condition. The RHI occurs due to the brain combining visual information from the rubber hand with tactile and proprioceptive information from the hidden real hand, leading to the formation of a single coherent multisensory percept of the rubber hand as one's own (Ehrsson, 2020; Kilteni et al., 2015; Samad et al., 2015). When probed about the experience of their real hand during the RHI, some individuals report that it seems like their real hand has disappeared, that it is no longer part of their body, or that they can no longer tell where it is located (Lane et al., 2017; Longo et al., 2008, 2009; Preston, 2013). However, the functional consequences of the RHI for the ability to generate movement is unclear. Does the illusion of owning a false hand, or 'losing' the real one, affect the ability to move?

Body ownership illusions seem to change the way in which target-directed *actions* are performed (Burin et al., 2019; Heed et al., 2011; Kammers et al., 2010; Newport et al., 2010; Newport & Preston, 2011; Zopf et al., 2011; but see Kammers, de Vignemont, et al., 2009; Kammers, Longo, et al., 2009). However, it is still unclear whether our ability to actually generate or perform a *movement* is supported by a sense of ownership over our body. Even though movement may contribute to changes in the sense of body ownership (Bassolino et al., 2018; Burin et al., 2015; Burin et al., 2017; Dummer et al., 2009; Fiorio et al., 2011; Kalckert & Ehrsson, 2012, 2014; Longo & Haggard, 2009; Mangalam et al., 2019; Pyasik et al., 2019; Scandola et al., 2017; Shibuya et al., 2018; Tidoni et al., 2014; Tsakiris et al., 2006), how it does so is a matter of debate. One view holds that somatosensory feedback from movement contributes to body ownership (only) through multisensory integration with visual and other types of sensory feedback (Kalckert & Ehrsson, 2012, 2014), others that the feeling of being in voluntary control of the movement (sense of agency, Haggard, 2017) influences body ownership (Tsakiris et al., 2006), whilst others still have argued for a functional reciprocal relationship between body ownership and the motor system (Burin et al., 2015; Burin et al., 2017). However, it has

not yet been established whether body ownership determines movement production. Studies using target-directed action do not provide strong evidence for a role of body ownership in basic movement, since actions necessarily rely on accurately quantifying the spatial relationship between the body and the world. Indeed, actions are also influenced by altering the visual–spatial relationship between body and world, without necessarily inducing changes in body ownership (e.g., Ambron et al., 2017; Bernardi et al., 2013; Heed et al., 2011; Holmes et al., 2006; Karok & Newport, 2010; Marino et al., 2010).

Whilst behavioural evidence for an effect of body ownership on low level motor control is lacking, experiments using transcranial magnetic stimulation (TMS) to record changes in corticospinal excitability and parietal-motor cortical connectivity from muscles of the arm and hand suggest that basic physiological markers of motor system function are susceptible to multisensory conflict and body illusions (Dilena et al., 2019). For example, the illusion of missing a part of the lower arm and hand in virtual reality has been reported to reduce corticospinal excitability (Kilteni et al., 2016). Similarly, della Gatta et al. (2016) observed that the RHI can result in reduced corticospinal excitability, which they suggested is due to disownership of the real hand. Conversely, when using a moving version of the RHI (Kalckert & Ehrsson, 2012), Karabanov et al. (2017) did not observe reductions in corticospinal excitability as a result of the illusion. They did, however, observe that ownership and agency over a rubber hand was associated with a resting inhibitory pattern of connectivity between the anterior intraparietal sulcus and the primary motor cortex (M1) (Karabanov et al., 2017). Similarly, another study reported that the classic RHI might be associated with inhibitory connectivity between the posterior parietal cortex (PPC) and M1, such that those who had a greater sensation of ownership over the rubber hand showed a greater inhibitory PPC-M1 interaction (Isayama et al., 2019).

The behavioural implications of these previously reported effects of the RHI on corticospinal excitability and parietal-motor cortical connectivity are still unclear. Given that motor output for simple movements is closely tied to the excitability of the motor system (Chen et al., 1998; Davey et al., 1998; Duque et al., 2017; Hortobágyi et al., 2017; Leocani et al., 2000; MacKinnon & Rothwell, 2000; Rossini et al., 1988; Starr et al., 1988) and that the RHI might reduce corticospinal excitability (della Gatta et al., 2016), we might expect that such manipulations of body ownership would have functional consequences. Despite this, in a recent experiment, we found that

using multisensory disintegration to reduce the subjective sense of ownership over participants' real hand—caused by exposure to incongruent visual, tactile, and proprioceptive information from the hand using online digital manipulation of visual feedback—did not result in changes in rapid finger movement (Reader & Ehrsson, 2019). This seemed to suggest that a strong sense of ownership over the real hand is not essential for basic movement. However, one possibility is that the manipulation of body ownership in the RHI has implications for movement, whilst altering the sense of body ownership using multisensory disintegration does not. It is not yet clear why this should be the case, but there are a number of potential sensory and cognitive interactions that might feasibly play a role. For example, changes in limb position sense from the location of the real hand towards the rubber hand (proprioceptive drift; e.g., Abdulkarim & Ehrsson, 2016; Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005) might create a situation where the sensorimotor system has access to less accurate or conflicting proprioceptive information, leading to suboptimal planning for efferent motor commands. Alternatively, an incomplete or weak RHI in some participants could possibly create a conflict between visual and proprioceptive representations of the hand that is not resolved, and this conflict within the sensorimotor system could impair its effectiveness in controlling the hand. Finally, and admittedly speculatively, the fact that the rubber hand is rigid and immobile might influence the motor system when ownership is experienced for such a hand that one cannot move.

We decided to assess whether the rubber hand illusion would result in changes in simple rapid finger movement. If the manipulation of body ownership in the RHI is sufficient to influence movement alone, then the classic RHI should result in changes in reaction time, peak velocity, and peak acceleration for rapid finger movements after illusion induction. Based on the TMS study of della Gatta et al. (2016), such illusion-induced effects should correspond to slower reaction time, increased peak velocity, and reduced acceleration. In our first experiment, we also examined whether three components of the RHI would have this effect: proprioceptive drift, the sensation of ownership over the rubber hand, and the sensation that the real hand has disappeared (an experience that has been associated with feelings of hand disownership; Longo et al., 2008, 2009). In a second experiment, we aimed to replicate and extend the results from the first experiment and additionally explore possible relationships between movement generation and sense of agency and referral of touch on the rubber hand.

2 | EXPERIMENT 1

2.1 | Methods

2.1.1 | Power analysis

We used G*Power 3.1 (Faul et al., 2007) to perform an a priori power analysis for sample size based on an effect size of dz = 0.85. This effect size was reported by della Gatta et al. (2016) for a difference in corticospinal excitability between the synchronous and asynchronous conditions of the RHI. This study appeared to be the most directly relevant in the context of basic movement as there is typically a link between corticospinal excitability assessed with TMS for a given muscle (e.g., first dorsal interosseous) and the reaction time for a movement involving the same muscle (e.g., abduction of the right index finger) (Chen et al., 1998; Leocani et al., 2000; Rossini et al., 1988; Starr et al., 1988). For a two-tailed paired t test at 95% power, the suggested sample size was 21. Since the effect reported by della Gatta et al. was for those susceptible to the RHI, and they suggested that disownership of the real hand might reduce corticospinal excitability, we recruited participants until we tested at least 21 who experienced the RHI and at least 21 who reported a sense of disownership for their real hand, or until we recruited 60 participants in total.

Illusion susceptibility was assessed based on level of agreement with questionnaire statements S1.1 (ownership illusion) and S1.2 (disownership illusion) described in Section 2.1.3 (response greater than zero in the synchronous condition and response greater in the synchronous condition than the asynchronous condition). Susceptibility was assessed separately for ownership and disownership, such that participants could be categorised as susceptible to one, neither, or both phenomena. We did not exclude those participants who did not experience the RHI, or did not report a sensation of disownership, since we also planned to correlate illusion questionnaire responses with kinematic variables, along with examining illusion-susceptible subsets.

2.1.2 | Participants

We recruited a total of 60 participants, though two were excluded due to having less than 50% viable trials in at least one of the conditions (see Section 2.1.5). The final sample size used for statistical analysis was 58 participants, mean ± SD age = 26.3 ± 5.47 years, 29 female, 7 left-handed (self-report). Thirty-three participants were deemed to be susceptible to the sense of ownership and 15 to disownership. Twenty-three participants did not

report either ownership or disownership sensations as defined by the aforementioned criteria. Participants gave written informed consent, and the experiment was approved by the Swedish Ethical Review Authority (application number 2010/548-31/2 and 2018/2117).

2.1.3 | Materials and stimuli

Participants sat at a round table opposite the experimenter and placed their right hand behind a narrow, L-shaped wooden screen (Figure 1a). The wooden screen was 60 cm long in total, 54 cm high (and 18 cm long) nearest the participant, and 31 cm high nearest the experimenter. A plaster-filled life-sized male cosmetic prosthetic right hand (Fillauer Europe AB, Sollentuna, Sweden) (hereby referred to as the rubber hand) was placed left of the screen, aligned as closely as possible to the participant's right shoulder in order to look anatomically plausible. The middle finger of the rubber hand and the middle finger of the real right hand were placed 20 cm apart, both 10 cm away from the screen. The participant's upper body and arms were covered with a black cloth to occlude the gap between the rubber hand and the participant's body. The rubber arm then appeared beneath the cloth visible to the participant in a forward-pointing orientation so that it looked like it could be the participant's own limb. Tactile stimulation was applied to the rubber hand and the participants hidden right hand by the experimenter using two small brushes with moderately soft bristles of 1 cm width (details below).

Subjective experience during the RHI was assessed using three questionnaire items that participants were requested to respond to on a 7-point Likert scale (−3: strongly disagree, +3: strongly agree) (Table 1). The statements were adapted from previous studies (Botvinick & Cohen, 1998; Longo et al., 2008) and aimed to assess the sense of ownership over the rubber hand, the experience of disownership of the real hand, and a control statement for susceptibility and demand characteristics.

Statement S1.2 was chosen to assess a sensation of disownership of the real hand since this is in keeping with some previous studies (della Gatta et al., 2016; Fossataro et al., 2018) and may correlate with other statements probing the perceptual loss of the real hand (e.g., 'It seemed like I could not really tell where my hand was') (Longo et al., 2008).

The proprioceptive drift towards the rubber hand was assessed by placing a custom card 'ruler' over the real hand, centred on the middle finger, from which participants reported the number that corresponded to their felt middle finger position. Twelve rulers were used—one for each measurement of proprioceptive drift during the experiment. Each was split into 21 rectangles of 1 cm width, with a number from 1 to 21 in each rectangle. The order of the numbers was randomised. With the central rectangle situated over the middle finger, 10 rectangles extended to the wooden screen (10 cm), and 10 rectangles extended laterally (10 cm). The experimenter placed an A4-sized cardboard screen above the rubber hand during the recording of proprioceptive drift, and during movements (for details, see further below).

During the movement task, the position of participants' right index finger was recorded using a wired Polhemus Fastrak motion tracking system (Polhemus Inc., Colchester, VT, USA) at 120 Hz with 6 degrees of freedom (x, y, z, azimuth, elevation, and roll). The tracker

TABLE 1 Experiment 1 questionnaire statements and purpose

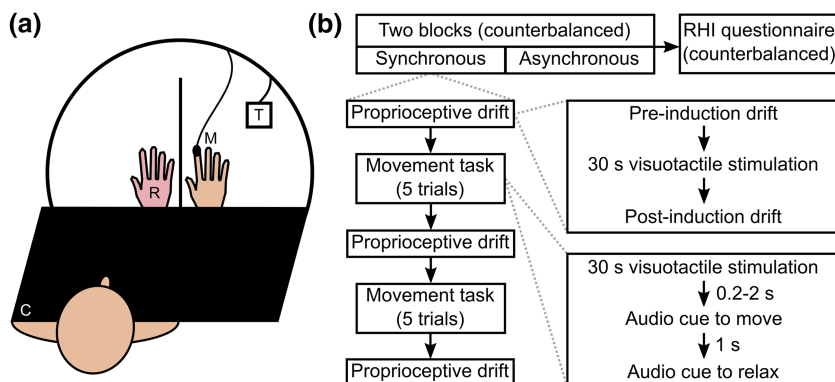| Item	Statement	Purpose
S1.1	'It seemed like the rubber hand was my hand'	Feeling of ownership over the rubber hand
S1.2	'It seemed like my real hand had disappeared'	Feeling of disownership over the real hand
S1.3	'It appeared as if the rubber hand were drifting towards my real hand'	Control statement

FIGURE 1 Experimental set-up and procedure. (a) Top-down schematic of experimental set-up (C, cloth; R, rubber hand; M, motion-tracker; T, motion-tracking transmitter); (b) simplified experimental procedure

was placed over the fingernail and attached using adhesive medical tape. Data were collected in MATLAB R2017b (MathWorks, Inc., Natick, MA, USA) for offline analysis using a custom script and functions from the HandLabToolBox (https://github.com/TheHandLab/HandLabToolBox). Participants wore headphones (Maxell, Tokyo, Japan) to provide them with audio triggers indicating when to move their index finger (see details in Section 2.1.4).

2.1.4 | Procedure

Participants took part in two blocks (synchronous and asynchronous tactile stimulation conditions), which were counterbalanced (Figure 1b). Each block consisted of 10 movement trials, each consisting of a 30-s period of repeated visuotactile stimulation delivered to the rubber hand and the hidden real hand followed by a finger movement, and three measurements of proprioceptive drift (which also included a 30-s period of repeated visuotactile stimulation). Proprioceptive drift was registered in trials (without movement) at the start and end of each block, as well as following the fifth trial (see below for details). The procedure was designed to maximise the number of movement trials that could be collected and minimise participant boredom (e.g., by breaking up movement trials with proprioceptive drift). We wanted to ensure that participants would remain focussed and alert throughout the experiment and ready to rapidly respond when needed. During the experiment, participants were instructed to place their right hand palm down on the table in a posture matched with the rubber hand (digits relaxed, slightly apart). They were asked to relax their right hand and arm during all periods of visuotactile stimulation and proprioceptive drift measurement as movement can disrupt the RHI and the drift. The experimenter was visible to the participant throughout the entire experiment.

During the movement task, participants observed the rubber hand whilst tactile stimulation was applied (prior to performing the movement). At the start of each trial, the experimenter pressed a key on a keyboard placed on their lap, which triggered a timer on the computer used for motion-tracking. The experimenter also initiated an audio file on a smartphone which, after 2 s, began playing a tone through the headphones worn by the experimenter. This tone was used by the experimenter to time the tactile stimulation, which was applied to the middle finger of the rubber hand, from the metacarpophalangeal to the distal interphalangeal joint, at a frequency of 0.5 Hz (1 s on, 1 s off), for 30 s. This relatively short duration was used to allow more

movement trials and is sufficient for illusion induction, which has previously been found to occur within less than 20 s (Chancel & Ehrsson, 2020; Ehrsson et al., 2004; Lloyd, 2007). In the synchronous condition, stimulation was also applied to the participant's own middle finger, matched as closely as possible to that performed on the rubber hand. In the asynchronous condition, stimulation of the participant's hand was applied in a medial to lateral direction over the top of the hand (just below the metacarpophalangeal joints), during the 'off' period of the rubber hand stimulation. Thus, the asynchronous condition included both temporal and spatial incongruence of the visual and tactile information from the hand, a combination that is known to strongly suppress the sensation of body ownership (e.g., Gentile et al., 2013).

For movement trials in both conditions, following tactile stimulation, the experimenter obscured the view of the rubber hand by holding the cardboard screen approximately 1 cm above it, and pressed a key on the keyboard. This stopped the timer (providing a record of trial duration, for preprocessing below) and triggered a randomised interval of 0.2–2 s, after which a tone played in the headphones provided to the participant. This signalled them to, as quickly as possible, abduct their index finger from a resting position to maximal abduction (moving the index fingertip approximately 4–6 cm to the left). They maintained the abduction until a second, lower pitched tone played 1 s later, signalling them to relax their finger again. Participants were then requested to observe their real hand and move their fingers to remove any illusory sense of ownership over the rubber hand and thus to avoid carry-over effects for the next trial. When the rubber hand was obscured prior to movement, participants were required to look at and keep their attention focussed towards the location of the rubber hand (behind the cardboard screen), and not to change the direction of their gaze (i.e., to avoid switching their attention). The experimenter checked that the participants complied with this instruction and they were reminded of this if necessary.

The rubber hand illusion is associated with a proprioceptive drift in the direction of the rubber hand (Abdulkarim & Ehrsson, 2016; Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). Proprioceptive drift is attained by subtracting the participant's felt position of their real hand after illusion induction from the perceived position of their real hand before illusion induction. For obtaining the initial pre-induction proprioceptive drift measurement, the experimenter always reset the participant's proprioceptive estimate of their right hand by lifting and moving it away from the wooden screen, in a lateral direction, then replacing it at the original position on the table 20 cm away from the rubber hand. The

experimenter obscured the rubber hand (with the cardboard screen, see above), placed the ruler above the participant's real hand, and then asked the participant to verbally state the number under which they felt the tip of their middle finger on their hidden right hand. Tactile stimulation was then performed for 30 s as described above, the rubber hand obscured again, and a new proprioceptive drift measurement (post-induction) of middle finger position recorded using a new randomised selection of numbers. The experimenter then moved the participant's right hand laterally once again to re-establish veridical proprioception and asked them to observe and move their fingers in order to fully eliminate any remaining RHI and avoid carry-over effects, before the right hand was placed back in the required position for the next trial.

Following both blocks, two more 30-s periods of visuotactile stimulation were applied, one for each condition (synchronous, asynchronous), in the counterbalanced order used for that participant. After tactile stimulation was applied, the experimenter obscured the rubber hand and verbally presented the participants with the three questionnaire statements (as described above) in a random order, storing their subsequent verbal responses on a computer for offline analysis. The participant was again asked to observe their real hand and move their fingers between the two periods of tactile stimulation in order to eliminate carry-over effects.

2.1.5 | Data analysis

A custom automated script written in Python 3 was used for extracting questionnaire and proprioceptive drift responses, as well as pre-processing and extraction of kinematic variables from motion-tracking position data. The first 10 samples of every movement trial (83 ms) were removed from position data due to a brief but consistent artefact occurring at the onset of sampling. Eighty-three milliseconds were subsequently added to reaction time for each trial to account for this. Single timepoint spikes (>3 SD from the mean) in each trial's double-differentiated time series were deemed electromagnetic artefacts and removed by replacing the value with the mean of two adjacent samples on either side; 4.60% of samples were interpolated in this fashion. Position data were then filtered with a second-order dual-pass Butterworth filter, with a 10-Hz low-pass cut-off. Reaction time was classed as the time between the tone indicating the participant to move and the tracker 3D velocity reaching an arbitrary value of 2.5 cm/s. Movement end time was considered the point

at which the tracker 3D velocity returned below 2.5 cm/s, and the 3D peak velocity was extracted from between the reaction time and this timepoint. Three-dimensional peak acceleration was extracted from between the reaction time and the time of peak velocity.

Trials in which the reaction time was shorter than 200 ms (suggesting a false start) or longer than 800 ms (suggesting a delayed start), or in which the peak velocity was smaller than 5 cm/s (suggesting non-rapid action) or greater than 100 cm/s (suggesting a remaining artefact), were excluded. Trials were also excluded if the time from reaction time to peak velocity was unusually short (<33 ms) or long (>200 ms). Since we were interested in the first, rapid digit abduction, trials were not excluded if the participant returned their finger prior to the tone indicating them to do this. However, trials were excluded if peak velocity was preceded by a local reduction in velocity (i.e., if participants slowed or stopped during their initial movement, or they returned their finger too early but more rapidly than their initial abduction). Trials were also excluded if tactile stimulation was not applied for the full 30 seconds before the tone to signal movement was triggered. The 3D velocity profiles for every trial were visually inspected for remaining artefacts. Participants with less than five trials in either block were excluded entirely (only 2 out of 60 participants). For the remaining participants, 90.5% of trials were maintained for statistical analysis. For every participant, mean values for each kinematic variable over each trial were calculated for each condition (synchronous, asynchronous).

All statistical analyses were performed in JASP (JASP Team, 2019). Questionnaire items were compared across conditions using Wilcoxon signed-rank tests, with the effect size r given as the rank-biserial correlation. The mean proprioceptive drift value for each participant for each condition was calculated by taking the mean value for each proprioceptive drift assessment (post-induction–pre-induction). Since a Shapiro–Wilk test indicated a deviation from normality, proprioceptive drift across conditions was also compared using a Wilcoxon signed-rank test. We planned to exclude any participants who provided a rating >0 to all questionnaire statements (including the control statement) in every condition, which would suggest high susceptibility to agreement, though none met this criterion.

Kinematic variables were checked for normality using a Shapiro–Wilk test and then compared across conditions using two-tailed paired t tests. Hedges' g_{rm} was used to assess effect sizes (Lakens, 2013). We also performed Bayesian paired samples t tests (Rouder et al., 2009) in JASP, using a default Cauchy prior with a scale of 0.707, zero-centred (where 50% of the density is located between effect sizes −0.707 and 0.707, for a two-sided hypothesis).

This prior distribution effectively specifies an alternative hypothesis in which one is 50% confident that the true effect size lies between -0.707 and 0.707. This analysis provided information regarding the level of support for the null hypothesis (synchronous = asynchronous) compared with the alternative hypothesis, or for the alternative hypothesis (synchronous $\neq$ asynchronous) compared with the null hypothesis, given the data. We used a typical heuristic for assessing evidence for either hypothesis, in which $BF_{10} > 3$ suggests better support for the alternative hypothesis, and $BF_{10} < 0.333$ better support for the null hypothesis (Jarosz & Wiley, 2014; Raftery, 1995). The hypothesis was that, should the RHI have a general effect on rapid movement, then in the synchronous condition reaction time should be greater and peak acceleration and peak velocity should be smaller.

To assess whether those who reported a greater sense of ownership over the rubber hand in the synchronous condition also had a greater reaction time and smaller peak velocity and peak acceleration, we correlated change in response to S1.1 across conditions with the change in kinematic variables. This was done with Kendall rank correlations (tau-b), along with Bayesian Kendall rank correlations (stretched beta prior width of 1, i.e., a non-informative prior) (van Doorn et al., 2018). To assess whether those who showed a greater sense of disownership for their real hand had a greater reaction time, and smaller peak velocity and peak acceleration, we performed an identical analysis for S1.2. To assess whether those who showed a stronger proprioceptive drift of their hand position sense towards the rubber hand had a greater reaction time, and smaller peak velocity and peak acceleration, we also performed this analysis for proprioceptive drift.

Finally, we compared kinematic variables (reaction time, peak acceleration, and peak velocity) between conditions on different illusion-susceptible subsets of individuals using a Bayesian approach, in order to ascertain how convincing any correlation (or absence of correlation) was under different prior distributions. Illusion-susceptible subsets were defined as those who had both a greater value for the illusion component (questionnaire items or proprioceptive drift) in the synchronous versus asynchronous condition and a value greater than zero in the synchronous condition. We used one-sided Bayesian t tests with the default Cauchy prior, as well as two normally distributed priors centred on two different effect sizes. The first effect size was based on dz = 0.85 reported by della Gatta et al. (2016). We reasoned that since externally induced motor-evoked potentials (i.e., through a magnetic pulse applied over M1) could result in a larger effect than might be observed in naturalistic movement, our second prior was centred on half this effect size

(0.43). The SD of the prior distributions was set at 0.22, such that the medians of the two alternate distributions were separated by approximately 2 SDs. For reaction time we assessed the alternative hypothesis that synchronous > asynchronous, whilst for peak acceleration and peak velocity we assessed the alternative hypothesis that asynchronous > synchronous. We also performed two-tailed paired t tests for reference.

In all Bayesian analyses, we also assessed the robustness of the Bayes factor. That is, we report the maximum possible Bayes factor and the associated scaling value of the default prior distribution (i.e., the Cauchy prior width or stretched beta prior width) (van Doorn et al., 2021).

2.2 | Results

2.2.1 | Questionnaire

There was a statistically significant difference between the level of agreement to statement S1.1 across the synchronous and asynchronous conditions ($W = 1156$, $p < 0.001$, $r = 0.351$), confirming that participants reported a greater sense of ownership over the rubber hand in the synchronous condition as expected (Figure 2). In addition, participants were less certain in rejecting the feeling that the real hand had disappeared—a marker of hand disownership—in the synchronous condition, as reflected in a statistically significant difference between the conditions in responses to S1.2 ($W = 483$, $p < 0.001$, $r = -0.436$). There was a statistically significant difference between the conditions in responses to control statement S1.3 (W = 255, $p = 0.0110$, $r = -0.702$), though a post hoc assessment of the magnitude of this difference (synchronous–asynchronous) indicated that it was less than was observed between the conditions in S1.1 ($W = 1122$, $p < 0.001$, $r = 0.311$) and S1.2 ($W = 472$, $p = 0.0265$, $r = -0.448$).

2.2.2 | Proprioceptive drift

There was a statistically significant difference in the extent of proprioceptive drift towards the rubber hand between the synchronous and asynchronous conditions ($W = 765$, $p = 0.0139$, $r = -0.106$), suggesting that proprioceptive drift towards the false hand was greater in the synchronous (mean $\pm$ SE = 0.305 $\pm$ 0.0682 cm) compared with the asynchronous (0.0402 $\pm$ 0.0774 cm) condition (Figure 2). Since the proprioceptive drift in the synchronous condition appeared to be relatively small compared with that observed in some previous studies
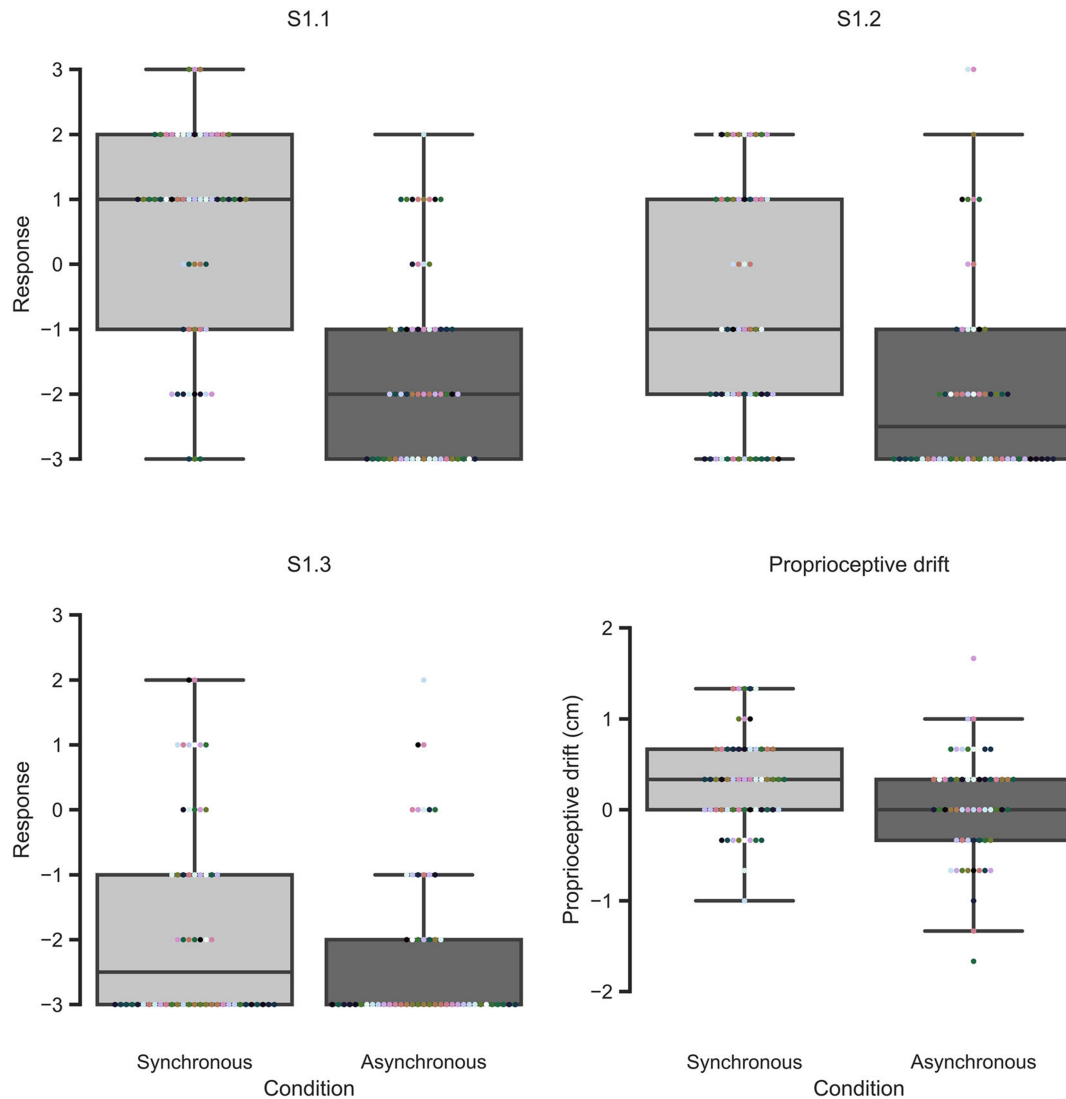
FIGURE 2 Experiment 1 questionnaire and proprioceptive drift results. Coloured circles indicate individual participant values

(e.g., (Abdulkarim & Ehrsson, 2016; Tsakiris et al., 2008; Tsakiris & Haggard, 2005), we decided post hoc to also perform a one-tailed Wilcoxon signed-rank test which confirmed that proprioceptive drift in this condition was greater than zero ($V = 827$, $p < 0.001$, $r = -0.0333$).

2.2.3 | Kinematics

There was no statistically significant difference for reaction time (Figure 3) between the synchronous (496 ± 8.07 ms) and asynchronous (502 ± 8.27 ms) conditions ($t(57) = -1.02$, $p = 0.312$, $g_{rm} = 0.100$, $BF_{10} = 0.235$, max $BF_{10} = 1.00$ at Cauchy prior width 0.0005). There was also no statistically significant difference for peak acceleration between the synchronous (351 ± 19.2 cm/s^2) and asynchronous (359 ± 22.9 cm/s^2) conditions ($t(57) = -0.625$, $p = 0.534$, $g_{rm} = 0.0423$, $BF_{10} = 0.172$, max $BF_{10} = 1.00$ at

Cauchy prior width 0.0005). There was no statistically significant difference for peak velocity between the synchronous (19.4 ± 0.879 cm/s) and asynchronous (19.8 ± 1.04 cm/s) conditions ($t(57) = -0.672$, $p = 0.504$, $g_{rm} = 0.0505$, $BF_{10} = 0.178$, max $BF_{10} = 1.00$ at Cauchy prior width 0.0005). The Bayes factor suggested greater support for the null than the alternative hypothesis in all cases. The robustness checks suggested that even exceedingly narrow priors with the majority of the density surrounding zero did not provide support for the alternative hypothesis. Example velocity plots are provided in Figures S1 and S2.

2.2.4 | Correlation

We observed statistically significant negative correlations between change in perceived hand disownership (S1.2)

FIGURE 3 Experiment 1 kinematic results. Coloured circles indicate individual participant values

across the synchronous and the asynchronous conditions and change in peak acceleration ($r_\tau = -0.285$, $p = 0.00420$) and peak velocity ($r_\tau = -0.270$, $p = 0.00681$, Table 2) between the same conditions. The Bayes factor suggested greater support for the alternative hypothesis than the null in both cases. This result suggested that the more that individuals tended to feel like their real hand had disappeared in the synchronous compared to asynchronous condition, the smaller their movement acceleration and velocity in the synchronous condition (Figure 4). To confirm that this result was not driven by participant suggestibility in the illusion, we decided post hoc to re-run these correlations after removing any individuals who reported a higher rating for control statement S1.3 in the synchronous condition than in

TABLE 2 Experiment 1 change in illusion measures correlated with change in kinematic variables (synchronous–asynchronous)

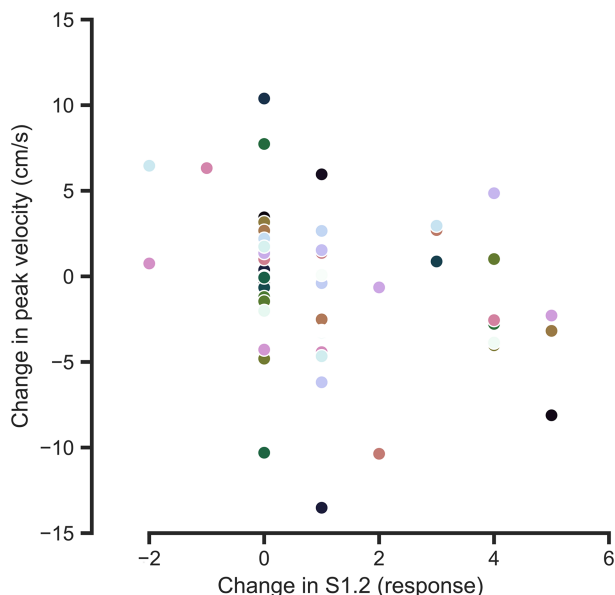| | Reaction time | | | Bayes factor robustness | | Peak acceleration | | | Bayes factor robustness | | Peak velocity | | | Bayes factor robustness | |
| | | | | Max BF$_{10}$ | Stretched beta prior width | | | | Max BF$_{10}$ | Stretched beta prior width | | | | Max BF$_{10}$ | Stretched beta prior width |
	r_τ	p	BF$_{10}$			r_τ	p	BF$_{10}$			r_τ	p	BF$_{10}$		
S1.1	−0.107	0.262	0.341	1.03	0.0164	−0.162	0.0905	0.827	1.70	0.0827	−0.196	0.0407	1.71	2.96	0.146
S1.2	−0.00852	0.932	0.171	1.00	0.0001	−0.285	0.00420	23.2	29.4	0.324	−0.270	0.00681	13.7	18.2	0.290
Proprioceptive drift	0.118	0.208	0.394	1.09	0.0256	−0.0723	0.441	0.234	1.00	0.0001	−0.125	0.181	0.441	1.15	0.0369

FIGURE 4 Scatterplot of change in disownership statement S1.2 ('It seemed like my real hand had disappeared') versus change in peak velocity (synchronous–asynchronous). Coloured circles indicate individual participant values

the asynchronous condition. The results held for both peak acceleration ($r_\tau = -0.472$, $p < 0.001$, $BF_{10} = 1201$) and peak velocity ($r_\tau = -0.397$, $p = 0.00134$, $BF_{10} = 96.1$).

We also observed a statistically significant negative correlation between change in rubber hand ownership (S1.1) for synchronous versus asynchronous and change in peak velocity for the same contrast ($p = 0.0407$, Table 2), possibly suggesting that the more that individuals felt like the rubber hand was their hand in the synchronous compared to asynchronous condition, the smaller their peak velocity in the synchronous condition. However, the Bayes factor, in this case, did not provide conclusive support for either the null or the alternative hypothesis, suggesting that this result be interpreted with caution. The same was true for most other correlations performed (Table 2), including the correlations between proprioceptive drift and reaction time/peak velocity.

2.2.5 | Assessment of illusion-susceptible subsets

Ownership

For those susceptible to the feeling of ownership over the rubber hand (S1.1, $n = 33$), 52% of the subset showed an increased reaction time in the synchronous condition compared with the asynchronous condition (493 ± 10.8 versus 497 ± 10.9 ms, $t(32) = -0.400$, $p = 0.692$,

$g_{rm} = 0.0500$), whilst 58% showed a reduced peak acceleration (348 ± 27.9 versus 359 ± 32.7 cm/s^2, $t(32) = -0.822$, $p = 0.417$, $g_{rm} = 0.0532$), and 48% showed a reduced peak velocity (19.3 ± 1.27 versus 19.9 ± 1.49 cm/s, $t(32) = -0.960$, $p = 0.344$, $g_{rm} = 0.0721$). The normally distributed prior centred on 0.85 suggested greater support for the null hypothesis for reaction time ($BF_{10} = 0.00306$), peak acceleration ($BF_{10} = 0.0373$), and peak velocity ($BF_{10} = 0.0524$). The normally distributed prior centred on 0.43 suggested greater support for the null hypothesis for reaction time ($BF_{10} = 0.115$), though we could not draw strong conclusions regarding either hypothesis for peak acceleration ($BF_{10} = 0.518$) and peak velocity ($BF_{10} = 0.642$). Analyses using the default Cauchy prior (width 0.707, zero-centred) suggested greater support for the null hypothesis for reaction time ($BF_{10} = 0.141$, max $BF_{10} = 0.993$ at Cauchy prior width 0.0005), but again we could not draw strong conclusions for either hypothesis for peak acceleration ($BF_{10} = 0.399$, max $BF_{10} = 1.10$ at Cauchy prior width 0.0343) and peak velocity ($BF_{10} = 0.466$, max $BF_{10} = 1.16$ at Cauchy prior width 0.0606).

These results suggested that even in individuals susceptible to the rubber hand illusion, an explicit sensation of ownership over the rubber hand was unlikely to interfere with reaction time, and unlikely to induce large changes in peak acceleration or peak velocity. However, we were not able to rule out the possibility of smaller effects on peak acceleration and peak velocity.

Disownership

For those susceptible to the feeling of the real hand disappearing (S1.2, $n = 15$), 46% of the subset showed an increased reaction time in the synchronous condition compared with the asynchronous condition (502 ± 18.3 versus 511 ± 19.6 ms, $t(14) = -0.682$, $p = 0.506$, $g_{rm} = 0.116$), whilst 73% showed a reduced peak acceleration (301 ± 37.9 versus 330 ± 45.9 cm/s^2, $t(14) = -1.78$, $p = 0.0961$, $g_{rm} = 0.145$), and 67% showed a reduced peak velocity (16.9 ± 1.66 versus 18.5 ± 1.98 cm/s, $t(14) = -2.06$, $p = 0.0586$, $g_{rm} = 0.211$).

The normally distributed prior centred on 0.85 suggested greater support for the null hypothesis for reaction time ($BF_{10} = 0.0101$), and we could not draw strong conclusions for either hypothesis when assessing peak acceleration ($BF_{10} = 1.89$). However, there was evidence in favour of the alternative hypothesis (asynchronous > synchronous) for peak velocity ($BF_{10} = 3.62$). The normally distributed prior centred on 0.43 suggested greater support for the null hypothesis for reaction time ($BF_{10} = 0.171$), but the Bayes factor suggested greater support for the alternative hypothesis for both peak acceleration ($BF_{10} = 3.48$) and peak

velocity ($BF_{10} = 5.17$), consistent with the correlation reported above. Analyses using the default Cauchy prior suggested greater support for the null hypothesis for reaction time ($BF_{10} = 0.171$, max $BF_{10} = 0.994$ at Cauchy prior width 0.0005), but we could not draw strong conclusions for either hypothesis for peak acceleration ($BF_{10} = 1.77$, max $BF_{10} = 2.19$ at Cauchy prior width 0.286) and peak velocity ($BF_{10} = 2.62$, max $BF_{10} = 2.99$ at Cauchy prior width 0.331).

These results generally supported the correlation between S1.2 and peak acceleration and peak velocity, suggesting that the experience of the real hand disappearing in the synchronous condition might have weakly interfered with the acceleration and velocity, but not the reaction time, of rapid finger movements. This indicated that the relationship with the feeling of disappearance extended to the performance, rather than the initiation, of movement.

Given the small size of the S1.2 subset, we decided post hoc to examine whether these were individuals who also had a greater feeling of ownership over the rubber hand or proprioceptive drift. Comparing this subset with the rest of the sample using a Mann–Whitney U test suggested that they had a greater level of agreement to statement S1.1 in the synchronous condition (median response = 2 versus 1, $W = 519$, $p < 0.001$), but there was no statistically significant difference between the groups in proprioceptive drift (median drift = 0.333 cm in both groups, $W = 351$, $p = 0.618$). This suggested that the S1.2 subset consisted of individuals who felt a greater degree of ownership over the rubber hand during the illusion.

Proprioceptive drift
For the subset susceptible to proprioceptive drift ($n = 26$) 62% showed an increased reaction time in the synchronous condition compared with the asynchronous condition (505 ± 13.8 versus 502 ± 13.7 ms, $t(25) = 0.352$, $p = 0.728$, $g_{rm} = 0.0423$), whilst 50% showed a reduced peak acceleration (357 ± 26.7 versus 369 ± 33.1 cm/s^2, $t(25) = -0.604$, $p = 0.551$, $g_{rm} = 0.0689$), and 50% showed a reduced peak velocity (19.0 ± 1.25 versus 19.9 ± 1.51 cm/s, $t(25) = -0.913$, $p = 0.370$, $g_{rm} = 0.111$).

The normally distributed prior centred on 0.85 suggested greater support for the null hypothesis for reaction time ($BF_{10} = 0.0214$), peak acceleration ($BF_{10} = 0.0376$), and peak velocity ($BF_{10} = 0.0786$). The normally distributed prior centred on 0.43 suggested greater support for the null hypothesis for reaction time ($BF_{10} = 0.325$), though we could not draw strong conclusions for either hypothesis for peak acceleration ($BF_{10} = 0.455$) and peak velocity ($BF_{10} = 0.712$).

Analyses using the default Cauchy prior suggested greater support for the null hypothesis for reaction time ($BF_{10} = 0.277$, max $BF_{10} = 1.00$ at Cauchy prior width 0.00430), but we could not draw strong conclusions for either hypothesis for peak acceleration ($BF_{10} = 0.351$, max $BF_{10} = 1.03$ at Cauchy prior width 0.0230) and peak velocity ($BF_{10} = 0.487$, max $BF_{10} = 1.14$ at Cauchy prior width 0.0569).

These results suggested that proprioceptive drift towards the rubber hand was unlikely to interfere with reaction time, and unlikely to induce large changes in peak acceleration or peak velocity. However, we were not able to rule out the possibility of smaller effects on peak acceleration and peak velocity.

2.2.6 | Post hoc exploratory regression

Since Bayesian analyses did not always provide reasonable support for either the null or alternative hypotheses when correlating illusion measures with kinematics and examining small effects in illusion-susceptible subsets, we decided to perform exploratory multiple regression. The purpose of this analysis was to assess if changes in peak acceleration and peak velocity were predicted by change in illusion measures. In all analyses we checked the linearity of the relationship between the dependent variable and independent variables, and assessed multicollinearity between independent variables ($|r| < 0.500$ in all cases). Independence ($1 <$ Durbin-Watson < 3), homoscedasticity, and normal distribution of residuals were also checked. Standardised residuals greater than 3 were removed (never more than one participant in any analysis).

First, a multiple regression was performed to predict the difference in peak acceleration between conditions from the difference in S1.1, S1.2, and proprioceptive drift (forced entry method). The model appeared to provide a prediction for change in peak acceleration ($F(3, 56) = 3.22$, $p = 0.0299$, adj. $R^2 = 0.106$). Change in S1.1 or proprioceptive drift was not related to change in peak acceleration, but change in S1.2 negatively predicted change in peak acceleration (Table 3), in keeping with the aforementioned correlation. Removing S1.1 and proprioceptive drift from the model did not drastically change the predicted variance ($F(1, 56) = 7.53$, $p = 0.00818$, adj. $R^2 = 0.104$, $\beta = -0.347$).

A second multiple regression was performed to predict the change in peak velocity between conditions based on change in S1.1, S1.2, and proprioceptive drift. This resulted in a model that provided a prediction for change in peak velocity ($F(3, 57) = 4.20$, $p = 0.00964$, adj. $R^2 = 0.144$). Change in S1.2 or S1.1 were not related

TABLE 3 Experiment 1 initial exploratory multiple regression outputs

Variable	Peak acceleration			Peak velocity		
	β	t	p	β	t	p
Intercept		1.75	0.0854		1.82	0.0737
S1.1	−0.109	−0.766	0.447	−0.149	−1.08	0.283
S1.2	−0.319	−2.25	0.0286	−0.267	−1.95	0.0566
Proprioceptive drift	−0.168	−1.31	0.196	−0.306	−2.46	0.0172

to change in peak velocity, but change in proprioceptive drift negatively predicted change in peak velocity (Table 3). Removing S1.1 and S1.2 reduced the variance predicted by over half ($F(1, 57) = 3.75$, $p = 0.0579$, adj. $R^2 = 0.0460$, $\beta = −0.250$). Removing S1.1 and proprioceptive drift slightly reduced the predicted variance ($F(1, 56) = 6.61$, $p = 0.0130$, adj. $R^2 = 0.0910$, $\beta = −0.327$). These results suggested that change in S1.2 could possibly predict ~10% of the variance in the change in peak acceleration and peak velocity, following illusion induction.

2.3 | Discussion

We tested whether the RHI influences basic movement. We observed that reaction time and finger movement acceleration and velocity were virtually unaffected by the RHI when we compared the synchronous and asynchronous conditions (with Bayesian analyses indicating support in favour of the null hypothesis), suggesting that simply manipulating visuotactile and visuoproprioceptive information to interfere with body ownership may not influence motor performance (see also Reader & Ehrsson, 2019).

We also assessed the effects of different components of the illusion (sense of ownership over the rubber hand, feeling of real hand disownership, and proprioceptive drift) on movement. We did not observe convincing evidence for effects of proprioceptive drift on rapid finger movements, and an exploratory regression analysis suggested that change in proprioceptive drift predicted little change in kinematics. A feeling of ownership over the rubber hand did not show any reliable systematic relationship with any of the movement parameters, but we could not draw strong conclusions regarding a possible negative correlation between S1.1 ratings and peak velocity ($r_\tau = −0.196$, $p = 0.0407$, $BF_{10} = 1.71$). However, that clear effects of ownership over the rubber hand were not observed in the illusion-susceptible subset suggests treating this correlation with caution.

Our most notable finding was that those who felt more like their real hand had disappeared in the synchronous relative to asynchronous condition, or at least displayed uncertainty in denying this statement, also performed finger movements with a slower acceleration and velocity. The absence of similar effects on reaction time suggests that this relationship was specific to motor performance, rather than initiation. The effect was confirmed when examining only the individuals susceptible to the feeling of disappearance. Overall this result seemed to suggest that a feeling of the real hand disappearing during the RHI, which may reflect experiences related to real hand disownership more generally, might interfere with basic movement. However, an exploratory regression suggested that an increased sensation of the real hand disappearing might explain only ~10% of the variance in the change in acceleration and velocity. This may have been due to the fact that few participants explicitly reported a feeling of their real hand disappearing (only 15/58 participants gave an affirmative rating ≥1), or that this statement is ineffective at capturing different individuals' feelings of real hand disownership during the RHI. It is also possible that some reports of disappearance are only post-perceptual reflections or judgements (de Vignemont, 2011) that arise in a subgroup of individuals when they consider (at a cognitive level) what is going on (i.e., 'I really feel like the rubber hand is my hand, so what has happened to my real hand behind the screen?').

With the above in mind, we decided to perform a second experiment with a greater number of statements addressing the feeling of real hand disownership, in the hope that this would allow us to better capture different participant experiences and therefore any effects on movement. We also decided to add statements to capture other conscious experiences that might feasibly interfere with movement. For example, if changes in corticospinal excitability during the RHI result from an altered influence of somatosensory and parietal inputs to the motor cortex (Isayama et al., 2019), then the referral of touch from the real to the false hand might feasibly be related

to changes in movement. In addition, changes in the capacity to execute rapid finger movement could also result from a feeling of ownership over a rigid artificial hand that one cannot move, which speculatively could lead to a reduction in agency, or an incomplete multisensory percept of the hand (i.e., to some degree one somehow feels like they have more than one right hand during the illusion).

3 | EXPERIMENT 2

3.1 | Methods

Unless otherwise stated, all methods were identical to Experiment 1.

3.1.1 | Participants

We aimed to test at least 60 participants, in keeping with Experiment 1. We recruited 69 participants, though five were excluded due to an inadequate number of valid trials, and five were excluded due to technical difficulties during data collection. The final sample size used for statistical analysis was 59 participants, mean $\pm$ SD age = 26.4 $\pm$ 5.63 years, 30 female, 6 left-handed (self-report). Participants gave written informed consent, and the experiment was approved by the Swedish Ethical Review Authority (application number 2010/548-31/2 and 2018/2117).

3.1.2 | Materials and stimuli

Questionnaire items were adapted from previous studies (Longo et al., 2008; Newport & Preston, 2011; Preston, 2013), aside from the control statement. The statements aimed to assess the sense of ownership over the rubber hand, referral of touch, the potential for agency over the rubber hand, the perceptual experience of having more than one hand, a sense of disownership for the real hand, and a control statement for compliance and susceptibility (Table 4).

3.1.3 | Procedure

The experimental protocol was identical to Experiment 1, except that no measurement of proprioceptive drift was recorded, 12 movements were recorded per condition, and an extended questionnaire (Table 4) was used.

TABLE 4 Experiment 2 questionnaire statements and purpose

Item	Statement ('It seemed like ...')	Purpose
S2.1	... the rubber hand was my hand'	Feeling of ownership over the rubber hand
S2.2	... the touch I felt was caused by the brush touching the rubber hand'	Referral of touch
S2.3	... I could have moved the rubber hand if I had wanted'	Potential for agency over the rubber hand
S2.4	... I had two right hands'	Experience of having more than one hand[a]
S2.5	... my real hand had disappeared'	Feeling of disownership over the real hand
S2.6	... I could not really tell where my real hand was'	
S2.7	... I was unable to move my real hand'	
S2.8	... my real hand no longer belonged to me'	
S2.9	... my real hand was no longer part of my body'	
S2.10	... the rubber hand replaced my real hand'[b]	
S2.11	... the rubber hand was changing colour'	Control statement

[a]Note that although this statement typically is used as a control statement in RHI studies, we were here interested in exploring the possibility that weaker rejection of this statement could be related to changes in kinematics, perhaps due to a more incoherent visuoproprioceptive representation of the upper limb.

[b]Although some earlier studies have used this statement to probe real hand disownership, it could also very well describe illusory ownership over the rubber hand in participants that experience a vivid RHI where the only hand they experience as their own is the rubber hand.

3.1.4 | Data analysis

Questionnaire items were compared across conditions using Wilcoxon signed-rank tests, with the effect size r given as the rank-biserial correlation. An FDR-corrected alpha value was used for assessing statistical significance (Benjamini & Yekutieli, 2001).

A total of 4.54% of samples were interpolated in place of electromagnetic artefacts; 84.6% of movements were maintained following pre-processing. We decided to focus our analysis on reaction time and peak velocity, since peak velocity and peak acceleration were very strongly

positively correlated in Experiment 1 (synchronous condition: $r = 0.960$, asynchronous: $r = 0.978$). However, we report complementary analyses for peak acceleration in supplementary material. Peak velocity and reaction time were compared across conditions using paired t tests (after checking for normality using the Shapiro–Wilk test). We also performed Bayesian paired samples t tests, using a default Cauchy prior with a scale of 0.707, zero-centred. However, we did not expect any difference in peak velocity or reaction time between conditions, given that our previous experiment suggested that effects were only convincingly observed in relation to the subjective experience of the real hand disappearing.

The difference in questionnaire statements S2.1–S2.10 response between synchronous and asynchronous conditions was correlated with the difference between conditions in reaction time and peak velocity. Correlation was performed using Kendall rank correlations (tau-b) using an FDR-corrected alpha threshold, as well as Bayesian Kendall rank correlations (stretched beta prior width of 1). We predicted that change in statement S2.5 (S1.2 in experiment 1) should correlate with change in peak velocity, as observed in our previous experiment. We also expected that other statements assessing the subjective experience of disownership should correlate with peak velocity.

Finally, we aimed to perform two hierarchical multiple regression analyses. In the first analysis, we planned to examine how well changes in disownership statements (S2.5–S2.10) across conditions predicted changes in peak velocity across conditions, using statements that convincingly correlated with peak velocity. In a second regression, we planned to add any other statements that convincingly correlated with peak velocity. However, no questionnaire statements convincingly correlated with peak velocity (see Section 3.2), and so we did not perform either of these analyses.

3.2 | Results

3.2.1 | Questionnaire

Statistically significant Wilcoxon signed-rank tests (Figure 5) confirmed that in the synchronous condition participants felt more like the rubber hand was their hand (S2.1: $W = 991$, $p < 0.001$, $r = 0.119$), and more like the touch they felt was caused by the brush touching the rubber hand (S2.2: $W = 1356$, $p < 0.001$, $r = 0.532$), compared with the asynchronous condition, in line with successful induction of the RHI. Participants also showed a statistically significantly reduced disagreement with statement S2.3 in the synchronous condition, addressing

the potential for agency over the rubber hand ($W = 681$, $p = 0.00112$, $r = -0.231$).

Participants showed a reduced tendency to disagree with disownership statements S2.5 ($W = 708$, $p < 0.001$, $r = -0.200$), S2.6 ($W = 606$, $p < 0.001$, $r = -0.315$), S2.8 ($W = 574$, $p < 0.001$, $r = -0.352$), and S2.9 ($W = 655$, $p < 0.001$, $r = -0.260$) in the synchronous condition compared to the asynchronous condition. This was in keeping with what we had observed in our disownership statement in Experiment 1 (S2.5 here, S1.2 in Experiment 1). Furthermore, participants also more strongly agreed with statement S2.10 ('it seemed as if the rubber hand replaced my real hand') in the synchronous condition ($W = 881$, $p < 0.001$, $r = -0.00508$). Though this statement has been considered to capture feelings of disownership in previous studies (Lane et al., 2017; Preston, 2013), the wording could also capture the experience of illusory ownership of the rubber hand in individuals who experience a strong RHI. This latter view is supported by the similarity in rating scores to ownership statements S2.1 and referral of touch (S2.2).

There was no statistically significant difference between the synchronous and asynchronous conditions regarding the level of agreement to S2.4, addressing the feeling of having more than one right hand ($W = 191$, $p = 0.248$, $r = -0.785$). Both the synchronous and asynchronous conditions led to similar denial of this statement, which is in line with statements of this kind being occasionally used as control statements in the RHI (e.g., Abdulkarim & Ehrsson, 2016; Preston, 2013). There was also no statistically significant difference for disownership statement S2.7, regarding an inability to move the hand ($W = 403$, $p = 0.0661$, $r = -0.545$), or control statement S2.11 ($W = 45$, $p = 0.303$, $r = -0.949$).

3.2.2 | Kinematics

The Shapiro–Wilk test indicated a deviation from normality for the reaction time data, so a Wilcoxon signed-rank test was used to compare conditions. There was no significant difference between the synchronous (mean $\pm$ SE $= 520 \pm 8.42$ ms) and asynchronous (521 ± 7.61 ms) conditions ($W = 906$, $p = 0.880$, $r = 0.0232$, $BF_{10} = 0.143$, max $BF_{10} = 0.997$ at Cauchy prior width 0.0005), in keeping with Experiment 1. There was no statistically significant difference in peak velocity between the synchronous (16.0 ± 0.737 cm/s) and asynchronous (16.8 ± 0.728 cm/s) conditions ($t(58) = -1.60$, $p = 0.116$, $g_{rm} = 0.140$, $BF_{10} = 0.471$, max $BF_{10} = 1.10$ at Cauchy prior width 0.0681), but we were not able to draw strong conclusions in favour of the null or alternative hypothesis from the Bayesian analysis for peak velocity
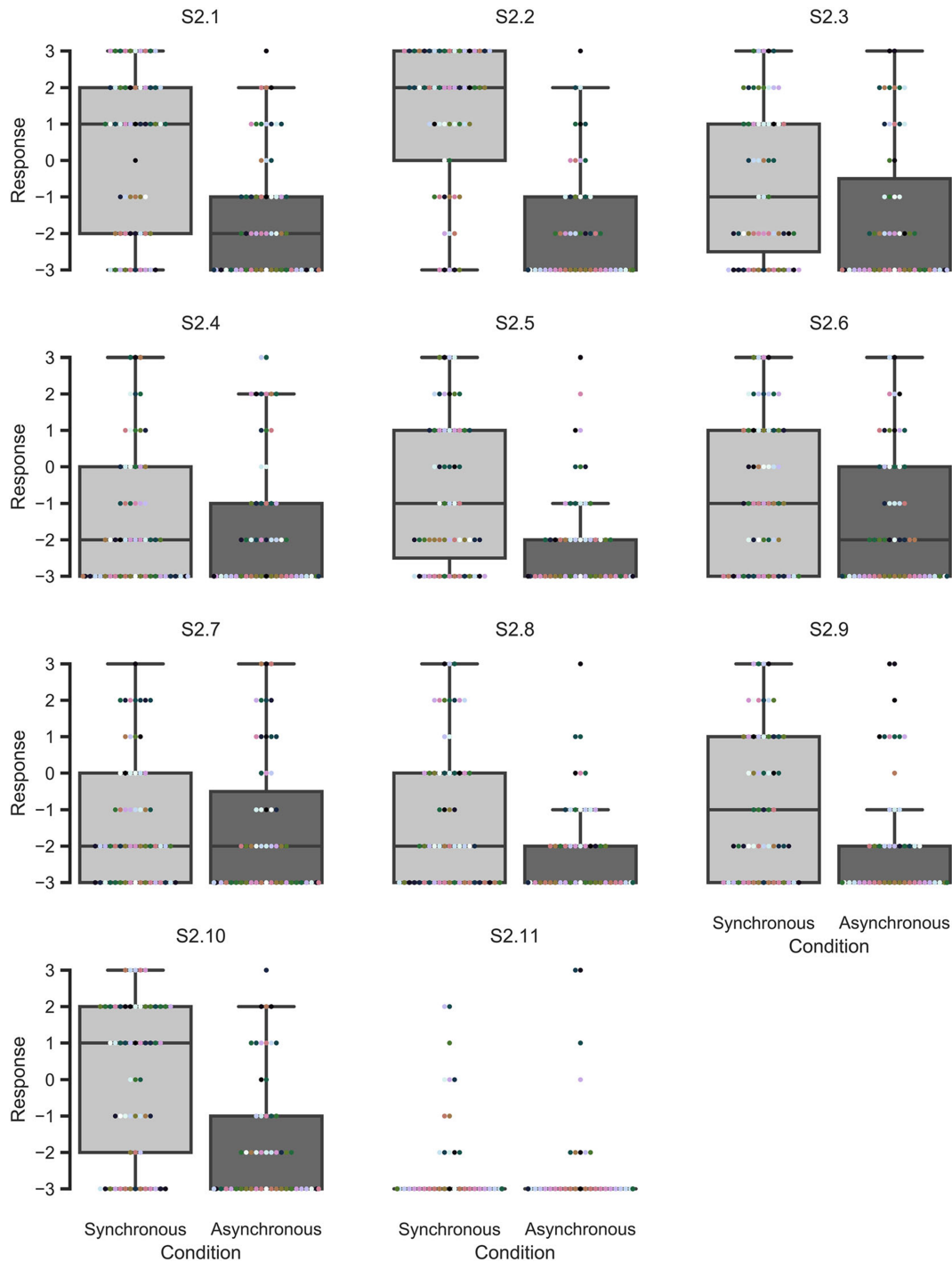
FIGURE 5 Experiment 2 questionnaire results. Coloured circles indicate individual participant values

(though $BF_{10} < 0.333$ for peak acceleration, see supporting information).

3.2.3 | Correlation

There were no statistically significant correlations between change in questionnaire responses across the synchronous and asynchronous conditions and change in reaction time or peak velocity across the same conditions ($0.00585 \leq |r_\tau| \leq 0.163$, $0.0915 \leq p \leq 0.952$, $0.170 \leq BF_{10} \leq 0.864$) (Table 5). We did not observe a statistically significant negative correlation between ownership statement S2.1 and peak velocity as observed in Experiment 1. This was true also for peak acceleration ($r_\tau = 0.123$, $p = 0.198$, $BF_{10} = 0.426$, see Table S1).

Notably, we also failed to replicate the negative correlation between change in disappearance statement

TABLE 5 Experiment 2 change in illusion measures correlated with change in reaction time and peak velocity (synchronous–asynchronous)

	Reaction time					Peak velocity				
				Bayes factor robustness					Bayes factor robustness	
	r_τ	p	BF_{10}	Max BF_{10}	Stretched beta prior width	r_τ	p	BF_{10}	Max BF_{10}	Stretched beta prior width
S2.1	−0.0387	0.684	0.186	1.00	0.0001	0.103	0.277	0.327	1.02	0.0164
S2.2	0.0296	0.755	0.179	1.00	0.0001	0.0170	0.857	0.172	1.00	0.0001
S2.3	−0.0679	0.478	0.225	1.00	0.0001	0.0589	0.538	0.209	1.00	0.0001
S2.4	−0.101	0.309	0.318	1.02	0.0092	0.142	0.152	0.590	1.36	0.0654
S2.5	−0.0439	0.653	0.191	1.00	0.0001	0.0918	0.347	0.284	1.00	0.0041
S2.6	−0.0436	0.651	0.190	1.00	0.0001	0.00585	0.952	0.170	1.00	0.0001
S2.7	0.0984	0.322	0.307	1.01	00092	−0.0337	0.734	0.182	1.00	0.0001
S2.8	0.0588	0.544	0.209	1.00	0.0001	0.0284	0.769	0.178	1.00	0.0001
S2.9	0.0104	0.914	0.170	1.00	0.0001	0.163	0.0915	0.864	1.76	0.0827
S2.10	0.0513	0.592	0.199	1.00	0.0001	0.00641	0.947	0.170	1.00	0.0001

S2.5 and peak velocity (Figure 6). In addition, most Bayesian analyses provided greater support for the null hypothesis rather than the alternative hypothesis. The only exceptions to this were statements S2.4 and S2.9, which were positively correlated with change in peak velocity, though these effects were not statistically significant and were in the opposite direction to what we would expect given the results of Experiment 1. We were not able to draw strong conclusions for either hypothesis in these instances, though the robustness tests suggested that there was little convincing support for the alternative hypothesis even with very narrow zero-centred prior widths. Similar results were observed when correlating peak acceleration with S2.4 ($r_\tau = 0.173$, $p = 0.0816$, $BF_{10} = 1.07$) and S2.9 ($r_\tau = 0.172$, $p = 0.0748$, $BF_{10} = 1.04$, see Table S1).

3.2.4 | Combined sample

Kinematics

Given that we did not replicate correlations between peak velocity and peak acceleration and statements S2.1 and S2.5, we decided post hoc to combine the datasets from experiments 1 and 2 for greater statistical power to detect true effects. There was no statistically significant difference in peak velocity between the synchronous (17.7 ± 0.591 cm/s) and asynchronous (18.3 ± 0.644 cm/s) conditions ($t(116) = -1.57$, $p = 0.120$, $g_{rm} = 0.0870$, $BF_{10} = 0.336$, max $BF_{10} = 1.09$ at Cauchy prior width 0.0456). To further develop our understanding of non-significant results, we decided to make the most of an
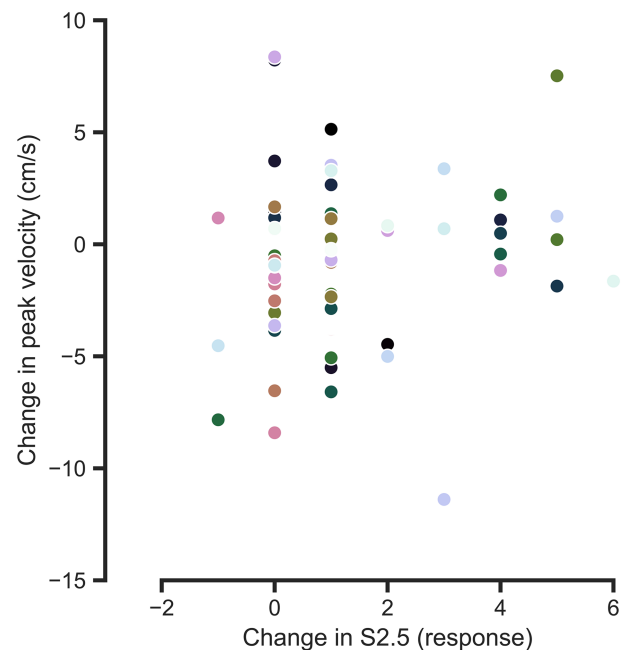

FIGURE 6 Scatterplot of change in disownership statement S2.5 ('It seemed like my real hand had disappeared') versus change in peak velocity (synchronous–asynchronous). Coloured circles indicate individual participant values

increased sample size by using equivalence testing (Lakens, 2017; Lakens et al., 2018). This was done using the TOST procedure (Lakens, 2017). Equivalence testing is a frequentist statistical procedure that allows one to reject the presence of effects as large or larger than a 'smallest effect size of interest', ascertaining whether

they are near enough to zero to be effectively equivalent (a different theoretical framework for assessing 'null' results compared to Bayesian analysis). We reasoned that $dz = 0.43$ could be a feasible smallest effect size of interest, given that this is half of the effect size observed between synchronous and asynchronous stroking of the rubber hand in motor-evoked potential amplitude reported by della Gatta et al. (2016). In the combined sample this was equivalent to a raw effect size of 1.77 cm/s. We were able to reject the presence of an effect greater than our smallest effect size of interest ($t(116) = -3.09$, $p = 0.00127$). Similar results were observed for peak acceleration (and $BF_{10} < 0.333$, see supporting information).

Correlation

We correlated the change in peak velocity/acceleration between conditions with the change in ownership statement S2.1 (S1.1 in Experiment 1) and disownership statement S2.5 (S1.2 in Experiment 1). For peak velocity, there was no statistically significant correlation for the ownership statement, and the Bayes factor suggested that there was evidence in favour of the null hypothesis ($r_\tau = -0.0335$, $p = 0.616$, $BF_{10} = 0.139$, max $BF_{10} = 1.00$ at stretched beta prior width 0.0001). Similar results were observed for peak acceleration (see supporting information). There was also no statistically significant correlation with the disownership statement, but we could not draw strong conclusions from the Bayesian analysis ($r_\tau = -0.0955$, $p = 0.167$, $BF_{10} = 0.383$, max $BF_{10} = 1.28$ at stretched beta prior width 0.0256). $BF_{10} < 0.333$ for the correlation with peak acceleration, however (see supporting information).

Illusion-susceptible subsets

We also performed one-sided Bayesian paired samples t tests on the subsets who positively responded to ownership statement S1.1/S2.1 ($n = 64$) and the disappearance statement S1.2/S2.5 ($n = 32$). As before, we used a default uninformed Cauchy prior as well as informed normally distributed priors. We also performed equivalence testing. For the ownership statement 47% of the subset showed a reduced peak velocity in the synchronous condition compared with the asynchronous condition (17.9 ± 0.833 versus 18.3 ± 0.925 cm/s, $g_{rm} = 0.0439$). We observed better evidence in favour of the null hypothesis than the alternative hypothesis for the Cauchy prior ($BF_{10} = 0.267$, max $BF_{10} = 1.06$ at Cauchy prior width 0.0230), as well as the normal priors situated on effect size 0.43 ($BF_{10} = 0.254$) and 0.85 (0.00712). The equivalence test also indicated that we could reject the presence of an effect greater than our smallest effect size of interest ($t(63) = -2.72$, $p = 0.00425$). Similar results were

observed for peak acceleration (see supporting information).

For the disappearance statement, 53% of the subset showed a reduced peak velocity in the synchronous condition compared with the asynchronous condition (16.5 ± 1.09 versus 17.3 ± 1.14 cm/s, $g_{rm} = 0.121$). The equivalence test indicated that we could not reject the presence of an effect size that we consider meaningful ($t(32) = -1.24$, $p = 0.112$). In addition, there was inconclusive support for either hypothesis using the Cauchy prior ($BF_{10} = 0.626$, max $BF_{10} = 1.32$ at Cauchy prior width 0.0832) and the normally distributed prior situated on 0.43 ($BF_{10} = 0.957$). However, there was evidence in favour of the null hypothesis for the effect size situated on 0.85 ($BF_{10} = 0.101$). Similar results were observed for peak acceleration (see supporting information).

3.3 | General discussion

We examined whether the induction of the RHI has an influence on rapid index finger abduction. There was little evidence that the RHI experimental paradigm interfered with movement. Although both questionnaire data and proprioceptive drift confirmed the induction of the RHI in the synchronous condition compared to the asynchronous control, Bayesian analysis generally supported the absence of an effect on kinematic parameters. There was little convincing evidence for a correlation between kinematic parameters and the ratings of sense of ownership over the false hand or proprioceptive drift. Notably, in Experiment 1, we observed that the degree to which participants felt as if their real hand had disappeared correlated with the acceleration and velocity of their movements. However, we did not replicate this effect in Experiment 2, and examining a combined dataset did not allow us to draw any strong conclusions in favour of the presence or absence of an effect. Overall, these results suggest the RHI is unlikely to negatively influence the basic ability to execute simple movements, implying that motor mechanisms involved in basic movement production are unrelated to the changes in multisensory body representation induced by this illusion.

Regarding the sense of ownership over the rubber hand, we observed mixed evidence in favour of a correlation between the sense of ownership and movement velocity and acceleration in Experiment 1, but this was not replicated in Experiment 2 or when combining the two experimental datasets. A Bayesian analysis of a large sample of illusion-susceptible individuals in the combined dataset ($n = 64$) suggested better support for the null hypothesis than an effect of the rubber hand illusion on movement. Across all experiments there was little

evidence for an effect of rubber hand ownership on reaction time. These results might suggest that the integration of a false limb into the central body representation also results in an integration into the motor system, with little negative impact on movement initiation or performance. This would be in keeping with research suggesting that false limbs might be integrated into action planning (Heed et al., 2011; Kammers et al., 2010; Newport & Preston, 2011). However, it is not possible to verify from which hand the movement was planned in our paradigm: Index finger abduction can be planned entirely in somatotopic space (i.e., in terms of muscle groups without any reference to the space surrounding the body), and the relative digit positions of the two hands (in somatotopic space) overlap when the movement must be performed. This is in contrast to the target-directed actions studied in previous experiments (Heed et al., 2011; Kammers et al., 2010; Newport et al., 2010; Newport & Preston, 2011; Zopf et al., 2011), where one can draw inferences about which hand an action was planned for (i.e., by examining reach trajectories). However, even in these previous experiments, effects on action tended to be small, suggesting that the motor system might not be as susceptible to body ownership illusions as conscious perception (see also Matsumiya, 2021). In addition, our results are at odds with the reduction in corticospinal excitability reported in illusion-susceptible individuals by della Gatta et al. (2016), particularly given that movement force or velocity is related to the discharge of neurons in M1 (Ashe & Georgopoulos, 1994; Cheney, 1985; Evarts, 1981; Graziano et al., 2002; Jäncke et al., 2004). It is possible that the change in corticospinal excitability reported by della Gatta et al. (2016) has little import to motor behaviour. For example, a disturbance in motor cortical processing (if it occurs) could be subject to top-down control when movement is necessary. Whilst there are inconsistent findings regarding the exact effects of illusory ownership on the motor system, at the very least our results suggest that manipulating the sense of ownership to encompass a new limb does not seem to have a negative impact on the generation of simple motor commands.

Concerning proprioceptive drift, we were not able to draw strong conclusions for the presence or absence of a systematic relationship with movement. Proprioceptive drift was only registered in the first experiment, and although no statistically significant correlation with kinematic parameters was observed, the Bayesian analyses were inconclusive. One possibility is that our use of a visual reporting task, taken from a vertical distance 30 cm away from the real hand, rather than manual pointing reduced the size of the recorded drift in the synchronous condition, thus making it more difficult to rule

out or detect effects on movement related to this phenomenon. Indeed, manual proprioceptive drift tasks can result in values exceeding 6 cm (e.g., Abdulkarim & Ehrsson, 2016), considerably larger than the values reported here. Alternatively, it is possible that we might have observed movement effects linked to proprioceptive drift had we induced the illusion by stroking the index finger and using that digit to record perceived hand position, because the index finger was the one that was moved and there is some evidence to suggest that proprioceptive drift may be greater in magnitude when recorded from the stimulated finger (Tsakiris & Haggard, 2005). However, the middle finger was stroked to avoid interfering with the motion-tracker and this was the finger from which the drift measure was recorded, given the results of Tsakiris and Haggard (2005). Further work will be necessary to clarify whether proprioceptive updating and basic movement interact in the RHI.

In Experiment 1, we also observed that the difference in acceleration and velocity between the synchronous and asynchronous conditions was correlated with the difference in the feeling of real hand disappearance between the conditions. However, we did not replicate this effect in Experiment 2, nor observe similar correlations with other statements purported to capture a feeling of disownership for the real hand. Examining the combined datasets indicated that we could not draw strong conclusions for or against an influence of a feeling of real hand disappearance on basic movement. As such, these results might be in line with the convincing negative findings we have described regarding the lack of a basic RHI effect on movement, as well as in terms of rubber hand ownership ratings. Nevertheless, we will consider two possible interpretations of the mixed findings regarding the correlation between disownership ratings and movement parameters.

First, we might consider the effect observed in Experiment 1 to be true, but the small size of the population effect (and/or low level of population susceptibility to disownership-related experience) meant we were unable to detect it in a second sample (i.e., a false negative), as well as when combining disownership-susceptible subsets from the two experiments. If a true population effect exists, it may be smaller than that observed in experiment 1 (e.g., for peak velocity $r_\tau = -0.270$, 95% CIs = [-0.429, -0.111]). Therefore, we must consider that even our combined sample of over 100 participants (32 susceptible to the feeling of disappearance) was too small to reliably detect an effect.

The existence of such an effect might be in keeping with the claims of della Gatta et al. (2016), who suggested that the reduction in corticospinal excitability they observed during the RHI was due to disownership of the

real hand during the experiment: 'body ownership and the motor system are mutually interactive … an experimental manipulation of the sense of body ownership is accompanied by a coherent modulation of the motor system', and '[if] I believe that the hand is mine, then I must be ready to use it; if not, then the activity of the motor system is accordingly down-regulated' (p. 8). They could not provide direct evidence in favour of this proposal, since the subjective experience of disownership was not assessed for the group of participants in which reduced motor-evoked potentials were observed. However, given that our results suggest that affirmative feelings of disownership are only reported by ∼30% of participants, we think it unlikely that this would be a strong explanation for the effects reported by della Gatta et al. (2016) and therefore unlikely to be directly related to the findings reported here. A more reasonable account for the observed correlations in Experiment 1 could be related to top-down control of movement under uncertainty, which would not be specific to the feeling of body disownership. For example, some individuals who experience the feeling of the real hand 'disappearing' (or judge this to be the case) may move more slowly when the current state of their real hand appears more uncertain. Why this would not influence reaction time, however, is unclear. Given the specific nature of the RHI (an induction of ownership over a false limb), and that real hand disownership sensation is often expressed as a reduction in negative ratings rather than strong positive phenomenology, it seems like more work is necessary to confirm the robustness of the effect observed in experiment 1, and what it really tells us about natural movement.

The second possible explanation for the discrepancy between Experiments 1 and 2 is that the results of Experiment 1 were a false positive, and in fact, there is no population correlation between disownership sensation and basic movement in the RHI. Any uncertainty specified in the combined sample analysis could be the result of bias arising from the (erroneous) Experiment 1 results. This would be in keeping with some previous findings. For example, Osumi et al. (2018) asked participants to perform repetitive wrist flexion and extension movements whilst they observed their hand under different levels of visual delay. They found that participants reported a reduction in the feeling of ownership over their hand as visual delay increased, and also showed reduced muscle activity and movement speed. However, changes in motor output were not correlated with subjective perception, leading the authors to suggest that different mechanisms may underlie movement execution and body ownership. The fact that Osumi et al. (2018) did observe changes in motor output, unlike in our

study, is likely related to the fact that they used a repetitive rather than single movement. In their case, altered motor output may arise from the distortion of spatial feedback that occurs as a result of delaying visual feedback from a continuous movement (see also Botzer & Karniel, 2013; Fujisaki, 2012). That is, the required muscle flexion or extension at any one point is uncertain, since proprioceptive feedback that informs the veridical position of the limb is in conflict with vision, meaning that caution may have to be applied to avoid hyperflexion or hyperextension. In such a scenario, it is perhaps unsurprising to observe a reduction in motor output.

In addition, our own previous work using passive visuoproprioceptive and visuotactile disintegration to weaken the sense of ownership over the real hand provided null results (Reader & Ehrsson, 2019). That is, a reduction in the subjective sensation of ownership over participants' real hand did not interfere with rapid index finger abduction, further supporting a distinction between body ownership and basic movement. However, we should also note that the feeling of disownership in the RHI may be qualitatively different to that which occurs during multisensory disintegration. Feelings of disownership during multisensory disintegration paradigms occur due to the incongruence of multisensory information arising from the real hand (Gentile et al., 2013; Graham et al., 2014; Kannape et al., 2019; Lesur et al., 2019; Longo & Haggard, 2009; Newport & Gilpin, 2011; Newport & Preston, 2011; Osumi et al., 2018). The visual impression of the (real) hand in view is perceptually 'unbound' from tactile and proprioceptive sensation, and this unbinding induces a feeling that the hand is no longer one's own. In the RHI, however, a feeling of real hand disownership may occur as a consequence of the integration of a false limb into the central body representation. In a multisensory integration framework, this means that when proprioceptive and tactile information from the hidden real hand is perceptually combined with the visual information from the rubber hand, the participant experiences only the rubber hand as part of the own body without proprioceptive awareness of the real hand behind the screen. Notably, we observed that participants who positively reported the feeling that their real hand had disappeared tended to have a stronger feeling of ownership over the rubber hand than other participants. This suggests that they may have experienced one coherent multisensory representation of a hand (the rubber hand) and therefore concluded that the real hand had been replaced or was no longer a part of their body, possibly leading to a feeling or judgement of real hand disownership. It may be possible that such cognitive effects can induce changes in movement

in some individuals, whereas the more explicitly perceptual effects of multisensory disintegration do not. This would not be in keeping with a generalised role of body ownership in motor control, however.

Whilst our mixed results regarding the sensation of real hand disownership may be due to either a small or non-existent population effect, there are limitations of our experimental paradigm that must also be considered. Firstly, it is possible that we observe inconsistent effects due to the relatively low level of susceptibility to disownership feelings reported by participants. This may be due to the statements presented in the questionnaire, though these were drawn from previous studies and the magnitude of positive response to these subjective feelings seems to be in keeping with previous research (Lane et al., 2017; Preston, 2013). It appears that a vivid experience of real hand disownership, as measured by these commonly used statements, is quite uncommon during the RHI. To confirm the presence of a movement effect related to real hand disownership during the RHI is likely to require a more robust method of inducing such sensations, or a considerably larger sample size than presented here. Alternatively, the statements used to address feelings of disownership may fail to adequately capture the proposed phenomenon, or may be misunderstood by some individuals. Certainly there has been some discussion regarding whether agreement with disownership-related statements in the RHI truly reflects the experience of the participant, or rather what they 'judge' to be the case, that is, post-perceptual processes such as conscious reflection (de Vignemont, 2011; Lane et al., 2017). Different interpretations of the illusion statements could result in a smaller likelihood of capturing any true effect, or alternatively increasing the chance of observing effects related to some unknown variable.

Another possible limitation of our experimental paradigm and a possible explanation for our null results is that participants may have had too much time to prepare for movement following the illusion (between 0.2 and 2 s), potentially reducing the influence of any illusory sensation (and also resulting in a general lack of reaction time effects). However, the after-effects of limb ownership illusions and full-body ownership illusions tend to be long-lasting, and can influence behaviour for an extended period once multisensory stimulation has finished and the artificial body is obscured (Bergouignan et al., 2014; Guterstam et al., 2015; Perepelkina et al., 2018; Van der Hoort & Ehrsson, 2016). The RHI may be maintained for at least 20 s after brushstrokes are applied to the real and the rubber hands (Abdulkarim et al., 2021), and activity in areas related to the multisensory representation of the hand such as the ventral premotor cortex show sustained activity for at least 1300 ms following tactile stimulation (Guterstam et al., 2019).

To conclude, the induction of the RHI may not interfere with rapid index finger abduction, suggesting that passive manipulations of multisensory congruence or manipulations of body ownership do not necessarily induce changes in basic motor behaviour. However, more research is needed to conclusively determine whether real hand 'disownership' during the RHI may reduce the speed with which simple finger movements are performed, as our results were inconclusive in this regard. In general, our results speak against a strong functional effect of body ownership in basic movement (i.e., simply changing the position of the body, without reference to external objects or agents), at least for very simple tasks. Given that body ownership might support interaction with the environment through the segregation of self and world, there appears to be little a priori justification for a role of body ownership in purely self-relevant motor processing. Simple movements like an index finger abduction are unlikely to require spatial coordinate transformations, a multisensory representation of the muscle in question, or information about the location of the limb in external space. Activation of a single muscle is likely to be performed independently of the sense of body ownership, in our case effectively induced through the supplementary motor area signalling the cortical territory of M1 that innervates the first dorsal interosseous, a process sufficiently supported by sensory information signalling the current postural state of the body (e.g., from muscle spindles) (Naito et al., 2016; Proske & Gandevia, 2012). This would be consistent with theoretical models of body ownership that consider the phenomenon as a multisensory perception of the body separate from action planning, motor control, or the neural state of the primary motor cortex (Chancel & Ehrsson, 2020; Ehrsson, 2020; Kilteni et al., 2015; Samad et al., 2015). Finally, from an applied perspective, these results are encouraging as they suggest that the embodiment of technology and artificial limbs (Collins et al., 2017; Makin et al., 2017; Niedernhuber et al., 2018; Pazzaglia & Molinari, 2016) through multisensory mechanisms may not impair the users' ability to generate rapid movements, which supports the potential development of efficient motor control with embodied technology.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

A.T.R. and H.H.E. designed the experiments. A.T.R. and V.S.T. collected and analysed the data. All authors contributed to writing the manuscript.

PEER REVIEW

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