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Quantifying body ownership information processing and perceptual bias in the rubber hand illusion

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ABSTRACT

Bodily illusions have fascinated humankind for centuries, and researchers have studied them to learn about the perceptual and neural processes that underpin multisensory channels of bodily awareness. The influential rubber hand illusion (RHI) has been used to study changes in the sense of body ownership — that is, how a limb is perceived to belong to one's body, which is a fundamental building block in many theories of bodily awareness, self-consciousness, embodiment, and self-representation. However, the methods used to quantify perceptual changes in bodily illusions, including the RHI, have mainly relied on subjective questionnaires and rating scales, and the degree to which such illusory sensations depend on sensory information processing has been difficult to test directly. Here, we introduce a signal detection theory (SDT) framework to study the sense of body ownership in the RHI. We provide evidence that the illusion is associated with changes in body ownership sensitivity that depend on the information carried in the degree of asynchrony of correlated visual and tactile signals, as well as with perceptual bias and sensitivity that reflect the distance between the rubber hand and the participant's body. We found that the illusion's sensitivity to asynchrony is remarkably precise; even a 50 ms visuotactile delay significantly affected body ownership information processing. Our findings conclusively link changes in a complex bodily experience such as body ownership to basic sensory information processing and provide a proof of concept that SDT can be used to study bodily illusions.

1. Introduction

Optical illusions have fascinated humankind for thousands of years (Shapiro & Todorovic, 2017). Over two millennia ago, Aristotle described a tactile illusion occurring when touching a small pea between two crossed fingers—it feels like touching two different peas (Aristotle., 1984)—and bodily illusions have fascinated academics as well as school children in the West since the "Japanese" illusion became popular over a century ago (Van Riper, 1935). Perceptual illusions are "errors" in perception where perception deviates to a notable degree from the state of physical reality; these illusions reflect the fundamental constraints and processing principles of the perceptual system that play out under certain conditions (Morgan, Hole, & Glennerster, 1990; Shapiro & Todorovic, 2017). Since illusions have a subjective quality to them, studying them experimentally has posed a challenge. The classic approach to studying the relationship between physical stimulation and sensation is called psychophysics. In psychophysics, the aim is to determine how a change in a physical stimulus leads to a noticeable change in an observer's perceptual behaviour. However, the problem with illusions is that they typically do not arise from a single parameter of a sensory stimulus (such as luminance or tactile pressure) but through combinations of different sources of information. These combinations are sometimes not well understood, making it less straightforward to apply classic psychophysics to the relationship of sensory signals and illusory perception. Thus, in illusion research, there is a long tradition of relying on subjective reports, such as questionnaires, rating scales, or indirect behavioural measures, rather than psychophysics, and this has been particularly true for bodily illusion studies to date.

Over the last 40 years, the interest in studying bodily illusions has constantly increased, from the discovery of limb movement illusions triggered by muscle vibration in the 1970s and 1980s (Goodwin, McCloskey, & Matthews, 1972; Jones, 1988; Lackner & Taublieb, 1984; Landelle, Chancel, Blanchard, Guerraz, & Kavounoudias, 2021; Taylor, Taylor, & Seizova-Cajic, 2017) and the large number of studies on the

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Abbreviations: SDT, Signal detection theory; 2AFC, 2-alternative forced-choice; RHI, Rubber hand illusion.

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rubber hand illusion and its various versions following the original report in 1998 (Botvinick & Cohen, 1998; for a recent review, see Ehrsson, 2020) to various full-body illusion paradigms over the last decade (Ehrsson, 2007; Lenggenhager, Tadi, Metzinger, & Blanke, 2007; Petkova & Ehrsson, 2008; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010). In bodily illusions, people experience changes in their immediate bodily awareness that are inconsistent with the physical state of their body (Ehrsson, 2020). The increase in bodily illusion research can be attributed to the unique paradigm it offers, which allows for non-invasive experimental induction and manipulation of changes in bodily awareness in healthy participants that are not otherwise possible. This research has opened up the scientific study of various higher-order aspects of body representation, such as the perception of the size, shape, self-attribution and relative spatial configuration of body parts and whole bodies. The principles of bodily illusion (Collins et al., 2017; Ehrsson et al., 2008; Marasco et al., 2021; Marasco, Kim, Colgate, Peshkin, & Kuiken, 2011; Petrini et al., 2019; Zbinden, Lendaro, & Ortiz-Catalan, 2022) may have clinical and industrial applications for developing artificial limbs that feel more like real limbs and making avatars in virtual reality feel more like real bodies (Kilteni, Groten, & Slater, 2012; Maselli & Slater, 2013), thereby enhancing the overall realism and vividness of experiences in virtual worlds, games, and social media platforms (Kilteni et al., 2012; Maselli & Slater, 2013). However, one critical question has remained unanswered: how can we measure bodily illusions in a rigorous, objective, and unbiased fashion?

A particularly influential and popular bodily illusion is the rubber hand illusion (RHI), which involves stroking a participant's hand, hidden behind a screen, alongside a visible rubber hand placed in front of them that one strokes in the corresponding way. A period of repeated and synchronised stroking, typically on the order of 10–20 s in most cases (Botvinick & Cohen, 1998; Chancel & Ehrsson, 2020; Lloyd, 2007), elicits an illusion that one is sensing the touch directly on the rubber hand (where one sees it being stroked) together with a sense that the rubber hand is one's own and part of the rest of one's body ("sense of body ownership"; Botvinick & Cohen, 1998; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008; Reader, Trifonova, & Ehrsson, 2021). The illusion happens as a consequence of the perceptual systems resolving the conflict between visual and somatosensory information, which, initially segregated, become combined, leading to a coherent visual-somatosensory experience of the rubber hand as one's own (Botvinick & Cohen, 1998; Ehrsson, 2020; Ehrsson, Spence, & Passingham, 2004). There are temporal and spatial congruence rules that determine the success of the illusion, which correspond to the temporal and spatial principles of multisensory integration (Ehrsson et al., 2004; Fuchs, Riemer, Diers, Flor, & Trojan, 2016; Haans, IJsselsteijn, & de Kort, 2008; Kalckert & Ehrsson, 2014; Kalckert, Perera, Ganesan, & Tan, 2019; Romano, Caffa, Hernandez-Arieta, Brugger, & Maravita, 2015; Shimada, Fukuda, & Hiraki, 2009): simultaneously stroking the rubber hand and the real hand produces the strongest illusion (temporal rule), and asynchronies longer than 200–300 ms typically abolish the illusion (Chancel & Ehrsson, 2020; Shimada et al., 2009). In addition, the position and orientation of the rubber hand with respect to the real hand influence the illusion, and when placed in an anatomically implausible position or at a greater distance than 30–40 cm, the illusion starts to decay (spatial rule; Ehrsson et al., 2004; Fuchs et al., 2016; Haans et al., 2008; Kalckert et al., 2019; Kalckert & Ehrsson, 2014; Romano et al., 2015). Different models for the RHI have been proposed (Chancel & Ehrsson, 2020; Ehrsson, 2012, 2020; Makin, Holmes, & Ehrsson, 2008; Samad, Chung, & Shams, 2015; Tsakiris, 2010), but they all revolve around the ("erroneous") binding of visual information from the rubber hand and somatosensory information from the hidden real hand and emphasise the integration of sensory signals from different sensory modalities (multisensory integration). In Bayesian causal inference models, the automatic perceptual decision to integrate as opposed to segregate the visual and somatosensory signals to trigger the illusion depends on probabilistic principles that take into account the spatiotemporal correlations as well as prior knowledge (Chancel, Ehrsson, & Ma, 2022; Chancel, Hasenack, & Ehrsson, 2021; Fang, Zhang, Zhao, Wang, & Zhou, 2019; Kilteni, Maselli, Kording, & Slater, 2015; Samad et al., 2015).

The subjective experience of the RHI is typically assessed by using questionnaires where participants are asked to rate various sensations associated with the illusion using Likert and visual analogue rating scales (e.g., how much the rubber hand felt like their own and how vividly they felt somatosensory sensations originating from the rubber hand (Botvinick & Cohen, 1998; Longo et al., 2008; Reader et al., 2021). However, questionnaires have limited reliability as they depend on participants' introspective abilities and therefore are vulnerable to various cognitive biases, expectations, and the participant's individual interpretation of the scales used; this can be particularly problematic when one wants to quantify subtle differences in illusory perception as is necessary for computational modelling and to test precise quantitative predictions regarding the critical information that drives the sense of body ownership. The RHI is also often assessed using behavioural and physiological measures such as changes in perceived hand position toward the rubber hand ("proprioceptive drift"; Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005), increases in skin conductance responses (SCRs) triggered by physical threats directed to the rubber hand (Armel & Ramachandran, 2003; Guterstam, Petkova, & Ehrsson, 2011; Petkova & Ehrsson, 2009), spatial error in goal-directed reaching (Heed et al., 2011; Kammers, Kootker, Hogendoorn, & Dijkerman, 2010; Newport, Pearce, & Preston, 2010; Zopf, Truong, Finkbeiner, Friedman, & Williams, 2011), sensory attenuation of self-touch (Kilteni & Ehrsson, 2017), and reaction-time changes in cross-modal congruence tasks (Pavani, Spence, & Driver, 2000; Zopf, Savage, & Williams, 2010). In line with the behaviouralist tradition of experimental psychology, behavioural and physiological measures are often viewed as being more objective than questionnaire ratings. However, these measures are indirect, as they serve as proxy variables, allowing inferences to be made about the illusion, but they may not always capture the specific aspects of the subjective illusory experience. While changes in these indirect measures are known to correspond to changes in body representation during the illusion, the embodiment of the fake hand in the RHI may involve additional changes in motor, emotional, and proprioceptive processing that participants may not be consciously aware of. These changes may have more complex relationships with the subjective experience of the illusion. Moreover, the extent to which these indirect measures correlate with changes in subjective illusory perception is a matter of ongoing debate (Abdulkarim & Ehrsson, 2016; Preuss Mattsson, Coppi, Chancel, & Ehrsson, 2022; Roel Lesur, Weijs, Simon, Kannape, & Lenggenhager, 2020; Rohde, Luca, & Ernst, 2011; Tosi, Mentesana, & Romano, 2023); for example, proprioceptive drift is believed to reflect visuoproprioceptive interactions during the illusion, but the correlations with subjective reports of rubber hand ownership are modest (Tosi et al., 2023), and under certain conditions, proprioceptive drift can occur in the absence of subjective changes in the RHI (Abdulkarim & Ehrsson, 2016; Holmes, Snijders, & Spence, 2006; Rohde et al., 2011). The shortcomings of the questionnaire approach and the uncertainties surrounding the interpretations of the various indirect measures have slowed down conceptual advances in the field. Thus, a major limitation in body representation research is the lack of methods to directly and objectively register the perceptual effects occurring in illusions such as the RHI.

Here, we introduce a novel approach to the RHI by using signal detection theory (SDT) and a discrimination psychophysics task. SDT metrics quantify the ability to discriminate between information-containing patterns (signal) and random patterns (noise). The RHI paradigm is attractive from this perspective, as the illusion critically depends on the temporal correlation between visual and tactile signals, which is under the experimenter's control and, therefore, can be compared to the participant's classifying behaviour on a trial-by-trial basis. Importantly, the RHI can be used in a 2-alternative forced-choice (2AFC) discrimination task (Chancel et al., 2021; Chancel & Ehrsson, 2020), which is a well-suited task for SDT (Stanislaw & Todorov, 1999; Wickens, 2001). In this task, two identical rubber hands are placed side-by-side, both are stroked with different degrees of synchrony with respect to the hidden real hand, and the participant has to judge which of the two rubber hands they feel the strongest illusion from (as a sidenote: if both are stroked in perfect synchrony, participants report experiencing the illusion equally strongly on both rubber hands as if they had two right hands; Ehrsson, 2009; Fan, Coppi, & Ehrsson, 2021; Guterstam et al., 2011; Newport et al., 2010). More specifically, in a study by Chancel and Ehrsson (2020), one of the rubber hands was synchronously tapped with the real hand, whereas the other rubber hand was tapped with a varying delay (at 0, 50, 100, or 200 ms). Participants had to respond which hand felt most like their own, i.e., making a discrimination of their feeling of illusory hand ownership. By fitting psychometric functions to participants' discrimination responses, the authors presented evidence that the degree of asynchrony (temporal rule) and the relative distance between the rubber hands and the real hand (spatial rule) determine the RHI at a finer scale and in a better-controlled manner than previous questionnaire studies. Here, we use this 2AFC paradigm and SDT metrics to examine whether illusory hand-ownership judgements reflect changes in the processing of visuotactile correlative signals (henceforth, "body ownership information").

SDT analysis allows quantifying perceptual sensitivity (i.e., how well participants can discriminate a signal from noise) along with decision criterion (i.e., participants' willingness or bias to report a signal when in doubt) in an independent manner. Past studies have established the usefulness of SDT analysis of visual and audio-visual illusions (Brosvic et al., 1994; Lown, 1988; Morgan et al., 1990; Witt, Taylor, Sugovic, & Wixted, 2015), such as the Müller-Lyer illusion, which occurs when inward- or outward-facing tails are added to the ends of a horizontal line, making it appear shorter or longer, respectively. Interestingly, these studies found that the tails do not affect sensitivity to the length of the horizontal lines, but rather, they induce perceptual biases that can be captured by the decision criterion index (Morgan et al., 1990; Witt et al., 2015; Witt, Taylor, Sugovic, & Wixted, 2016). This captures the common wisdom in vision science that "when perceptual biases are obvious and shared by most observers they are called illusions" (Morgan et al., 1990, p. 1794). Thus, while in standard perceptual discrimination paradigms, the decision criterion is often thought of as capturing decisional strategies or response bias, in perceptual illusion paradigms, the decision criterion captures response bias and perceptual bias effects together, with perceptual biases capturing key perceptual aspects of the illusion under investigation (Morgan et al., 1990; Witt et al., 2015). Importantly, while the decision criterion might also be affected by postperceptual factors such as expectations, perceptual sensitivity is independent of postperceptual factors and quantifies objective perceptual processing (Bang & Rahnev, 2017; Haddara & Rahnev, 2022). Therefore, SDT should allow us to disentangle sensitivity to body ownership information (i.e., the information bearing patterns of the visuotactile signals) and perceptual bias effects in the RHI. Furthermore, since 2AFC tasks are naturally well-protected against response bias effects (Macmillan & Creelman, 1990, 2004; Peters, Ro, & Lau, 2016; Stanislaw & Todorov, 1999), RHI effects on decision criterion should mainly reflect changes in perceptual bias, at least when these changes go in the anticipated direction of the perceptual rules of the illusion based on how most people experience it.

Here, we analyse the hand ownership discrimination datasets collected by Chancel and Ehrsson (2020) under an SDT framework. In the main experiment, the stimulation asynchrony is varied (temporal rule manipulation), as is the distance between the two rubber hands (spatial rule manipulation), and their effects on participants' sensitivity to body ownership information and perceptual bias are measured. In the control experiment, we ascertain that the effects attributed to body ownership sensitivity are valid and not due to visuotactile correlations unrelated to the RHI. Our overarching goal was to establish an unbiased and therefore objective body ownership sensitivity measure for the RHI based on perceptual discrimination rather than subjective ratings and to see what we could learn about multisensory bodily awareness by analysing a bodily illusion using SDT. We hypothesised that the RHI would be associated with both changes in body ownership sensitivity and perceptual bias toward the rubber hand for which the illusion is experienced.

2. Main experiment

We tested how visuotactile stimulation asynchronies applied to the two rubber hands (with one always synchronously tapped with the real hand) in the order of 50, 100, and 200 ms modulated body ownership sensitivity and perceptual bias in an RHI-based discrimination paradigm (Chancel & Ehrsson, 2020). If two rubber hands are placed in front of a participant and these rubber hands and the participant's hidden real hand are synchronously tapped, the participant will be able to experience both rubber hands as their own. However, how sensitive is their illusory feeling of body ownership to subtle variations in how these rubber hands are tapped in terms of asynchrony in visuotactile correlations? Do these variations in multisensory stimulation patterns involve changes in body ownership sensitivity and/or a shift in perceptual bias?

2.1. Method

2.1.1. Participants

Since the original study, upon which the current analyses were based, was the first of its kind and there was no prior information about effect sizes, Chancel and Ehrsson (2020) did not perform a power analysis; sample sizes were chosen to match prior studies' sample sizes (Brozzoli, Gentile, & Ehrsson, 2012; Guterstam et al., 2011; Preston, 2013; Rohde, Wold, Karnath, & Ernst, 2013). As suggested by the statistical results and the results of Bayesian analyses, our sample size is sufficient (see further below).

Thirty RHI-naïve participants were recruited. However, since the ability to experience the RHI was necessary to perform the task, and prior reports have shown that between 20% and 25% of participants deny experiencing the RHI in questionnaire ratings (Kalckert & Ehrsson, 2014), we included only the data of participants who could experience a vivid illusion — a common practice in the field if the primary interest is in the illusion itself (Ehrsson et al., 2004; Lloyd, 2007; Nitta, Tomita, Zhang, Zhou, & Yamada, 2018; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007; Wold, Limanowski, Walter, & Blankenburg, 2014). Therefore, each participant was first assessed through the classic RHI paradigm; five participants did not reach the minimum threshold for a sufficiently strong RHI, thus leaving 25 participants (12 female; $M_{age} = 30.04$, $SD_{age} = 7.16$) in the main experiment. For a detailed account of these inclusion tests, see Appendix A: Supplementary Material 1.

All experiments upon which the current study is based were approved by the Ethical Review Authority. All participants provided informed consent in accordance with the Declaration of Helsinki and were paid 300 SEK for participating in the two-hour experiment.

2.1.2. Experimental setup

Participants placed their right hand, palm down, in a natural resting position on a flat support surface beneath a wooden table (30 cm from the body midline). On this wooden table (15 cm above the real hand and tilted 30° upward on the front), two identical rubber hands were placed next to each other, both in anatomically plausible positions and within reaching space (peripersonal space), and each was at the same distance from the real hand (see Fig. 1A). This setup allows the RHI to be induced on each of the two rubber hands or even on both simultaneously (Ehrsson, 2009; Fan et al., 2021). A white circular fixation mark was positioned between the two rubber hands. Participants placed their left hand on their lap. A chin rest and an elbow rest (Ergorest Oy®, Finland) kept participants' heads steady and their right arm relaxed throughout

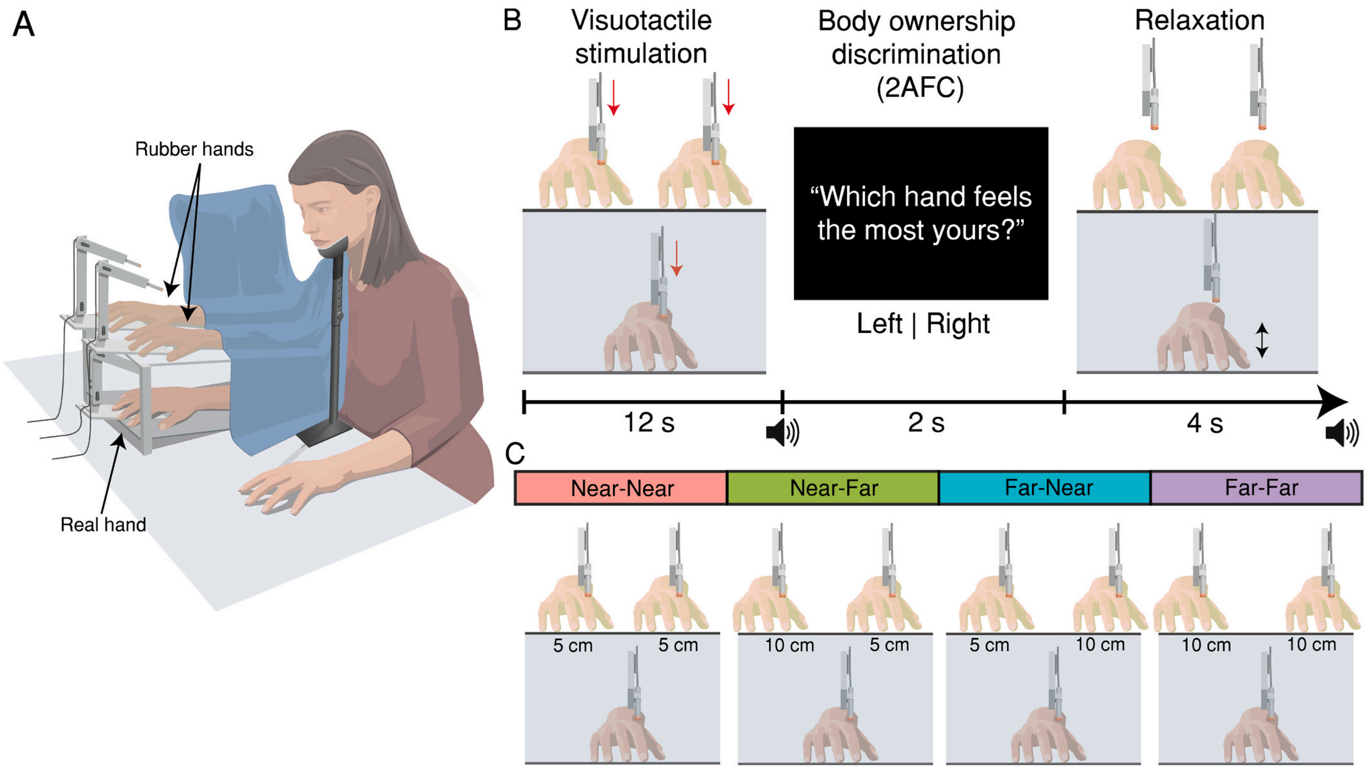

Fig. 1. (A) Experimental setting. Two robot arms apply touches to both rubber hands placed on top of the table, and one robot arm applies touches to the participant's real hand under the table. (B) Trial schematics. The robot arms tap the rubber hands and real hand with different degrees of asynchrony between the rubber hands; crucially, one rubber hand is always synchronously tapped with the real hand, which is the condition that we know produces the strongest RHI. Next, an auditory cue informs participants that they must verbally respond which rubber hand felt most like their own (left or right). An auditory cue informs them when the next trial is about to begin. (C) The relative distances between the rubber hands (skin colour) and the real hand (grey) in the horizontal plane across the four conditions. The distances are defined as the distance between each rubber hand's index finger and the real hand's index finger (hidden underneath). The white fixation dot is located halfway between the two rubber hands. Illustration by Mattias Karlén.

the experiments.

Tactile stimuli (taps) were applied to the two rubber hands and the real hand by three robot arms; the taps were applied on each hand's index finger. The robot arms have three parts: two 17-cm-long and 3-cm-wide metal pieces and a metal slab (10 × 20 cm). The joint between the two metal pieces and the piece between the proximal and support parts were powered by two HS-7950TH UltraTorque servos that contained 7.2 V optimised coreless engines (Hitec Multiplex®, USA). The distal metal piece had a ring on its end, which held the plastic tube (7 mm diameter) that touched the hands during the stimulation procedure, and E3X-HD41 fibre sensors (OMRON®, Netherlands) to register the exact timing of the taps by measuring how long it takes a red laser light to bounce back when the plastic tubes contact the hands. These lasers allowed us to ascertain that the theoretical and applied degrees of asynchrony did not differ substantially from each other. To prevent participants from becoming distracted by the noise produced by the robot arms, they wore earphones and listened to white noise throughout the whole experiment. White noise levels were adjusted for each participant so that the noise was at a comfortable volume but the participants could not hear the robot arms.

2.1.3. *Procedure*

Participants were instructed to focus their gaze on the fixation mark. In each trial, the robots repeatedly tapped the index fingers six times for a period of 12 s. Prior studies have shown that the RHI can be reliably induced in 10 s in the majority of participants susceptible to the illusion (Chancel & Ehrsson, 2020; Ehrsson et al., 2004; Lloyd, 2007), which was confirmed in pilot sessions. Five different locations were tapped (proximal to the nail on the distal phalanx, on the distal interphalangeal joint, on the middle phalanx, on the proximal interphalangeal joint, or on the proximal phalanx) in a randomised order but congruent across hands to avoid stimulation-induced skin irritation. Then, participants heard an auditory cue, after which they had to identify which rubber hand felt most like their own (left or right; 2AFC discrimination task). Next, they were asked to relax their gaze and wiggle their fingers briefly to break the illusion and avoid muscle numbness or any discomfort, thereby ensuring that their hand was relaxed before the next trial and reducing the risk of carry-over effects (see Fig. 1B). Finally, another auditory cue played 5 s later informed them that the next trial was about to begin.

The experiment consisted of 336 pseudorandomly ordered trials, which were evenly distributed over two crossed experimental factors: first, the degree of asynchrony between the taps applied to both rubber hands (one of which always obeyed the temporal rule of the RHI), and second, the distance between the rubber hands (spatial rule of the RHI). Seven degrees of asynchrony were applied, with either the left or the right hand touched with delay (0, 50, 100, or 200 ms; in the 0 ms condition, the three hands were synchronously tapped), and four distances between rubber hands were defined by placing the rubber hands' index fingers 5 or 10 cm to the left or right of the real hand's index finger (Near-Near, Near-Far, Far-Near, and Far-Far; these condition names correspond to the distances between the left-right rubber hands; see Fig. 1C).

2.1.4. *Analysis*

We used SDT analysis to assess how sensitivity to body ownership signals (i.e., the information carried by the visuotactile correlations) and perceptual bias changed across different conditions of stimulation asynchrony and distance between hands. All measures were calculated for each combination of these factors per participant. To determine bias-independent sensitivity to body ownership signals (henceforth also referred to as body ownership sensitivity or d'), hits were defined as trials in which the participant identified the right rubber hand as feeling most like their own when the right rubber hand was synchronously tapped with the real hand, whereas false alarms (FAs) were defined as trials in which the participant identified the right rubber hand as feeling most like their own when the left rubber hand was synchronously tapped with the real hand. For each measure, we calculated d' by using the 2AFC formula, $d'ownership = \left(\frac{1}{\sqrt{2}}\right)(Z(Hit) - Z(FA))$, where Z(Hit) stands for the Z score associated with the probability of a hit and Z(FA) stands for the Z score associated with the probability of an FA (Macmillan & Creelman, 2004; Wickens, 2001). To avoid zero counts, padding (edge correction) was applied by either adding or subtracting half a trial (Macmillan & Creelman, 2004). To estimate each participant's bias to the left or right (henceforth also referred to as perceptual bias), we used the 2AFC formula for decision criterion $Crubber\ hand = -\left(\frac{1}{2}\right)(Z(Hit) + Z(FA))$. Positive and negative values here indicate a bias toward claiming illusory ownership over the left and right rubber hand, respectively. We expected a bias toward the rubber hand placed closer to the real hand (Ehrsson, 2020; Lloyd, 2007), as well as a bias toward the left rubber hand that was placed closest to the body and the body midline, as described in earlier work (Chancel & Ehrsson, 2020; Fan et al., 2021; Preston, 2013). The zero-asynchrony condition was not included in this analysis since its trials cannot be classified as hits or FAs, making it unsuitable for SDT analysis (note that the zero-asynchrony condition was relevant in the original study by Chancel & Ehrsson, 2020).

We analysed body ownership sensitivity and perceptual bias using repeated-measures analysis of variance (ANOVA); wherever Mauchly's test indicated that the sphericity assumption was violated, Greenhouse–Geisser correction was applied to degrees of freedom. When interactions reached statistical significance ($p < .05$), we explored them using post hoc Holm–Bonferroni-corrected pairwise comparisons based on the pooled variance of the ANOVA model (using estimated marginal means, with error terms pooled by the ANOVA factors). Where null results were of theoretical interest, we calculated Bayes factors to assess the strength of the evidence for the null using a Cauchy prior distribution centred around zero with a width parameter of 0.707, which are widely accepted default parameters when no real prior information is available (Albert, 2009; Jeffreys, 1998; Marsman & Wagenmakers, 2017; Rouder & Morey, 2012; van de Schoot et al., 2018; van Doorn et al., 2020; Zondervan-Zwijnenburg, Peeters, Depaoli, & Van de Schoot, 2017). Statistical analyses were performed using MATLAB 2021a (MathWorks, Inc.) and JASP (JASP Team, 2021) and corroborated in R. Data are publicly available on the Open Science Framework (https://osf.io/n8drm/).

2.2. Results

2.2.1. Body ownership sensitivity

By-condition body ownership d' scores were entered into a 3 (degree of asynchrony: 50, 100, 200 ms) × 4 (space between rubber hands: Near-Near, Near-Far, Far-Near, and Far-Far) repeated-measures ANOVA. We found a significant main effect of the degree of asynchrony ($F(2,48) = 195.77, p < .001, \eta p2 = .891$), which shows that body ownership sensitivity increased as the degree of stimulation asynchrony increased (Fig. 2A): with 50 ($M = 0.612$ [$95\ \%\ CI: 0.428, 0.797$]), 100 ($M = 1.178$ [$0.965, 1.415$]), and 200 ms ($M = 2.232$ [$1.959, 2.455$]) of asynchrony. Post hoc comparisons between degrees of asynchrony revealed significant differences between all paired comparisons, that is, between 50 and 100 ms ($t(24) = 6.871, p < .001$, Cohen's $d = 1.374$), between 100 and 200 ms of asynchrony ($t(24) = 12.637, p < .001, d = 2.527$), and between 50 and 200 ms of asynchrony ($t(24) = 19.508, p < .001, d = 3.902$). We also found a significant main effect of space between hands ($F(3,72) = 5.28, p = .002, \eta p2 = .180$). Post hoc comparisons of different conditions of space between hands revealed significant differences between Near-Far and Near-Near ($t(24) = 3.135, p = .012, d = 0.44$), between Near-Far and Far-Near ($t(24) = 3.467, p = .005, d = 0.487$), and between Near-Far and Far-Far ($t(24) = 3.093, p = .012, d = 0.434$).

The interaction between the degree of asynchrony and the space between rubber hands also reached significance ($F(6,144) = 3.27, p = .005, \eta p2 = .120$). Post hoc comparisons revealed an advantage for Near-Near over Near-Far distance conditions but only at 200 ms of stimulation asynchrony ($t(24) = 3.422, p = .049, d = 0.684$), indicating that when the stimulation asynchrony between rubber hands is sufficiently high, body ownership becomes more sensitive to the placement of the rubber

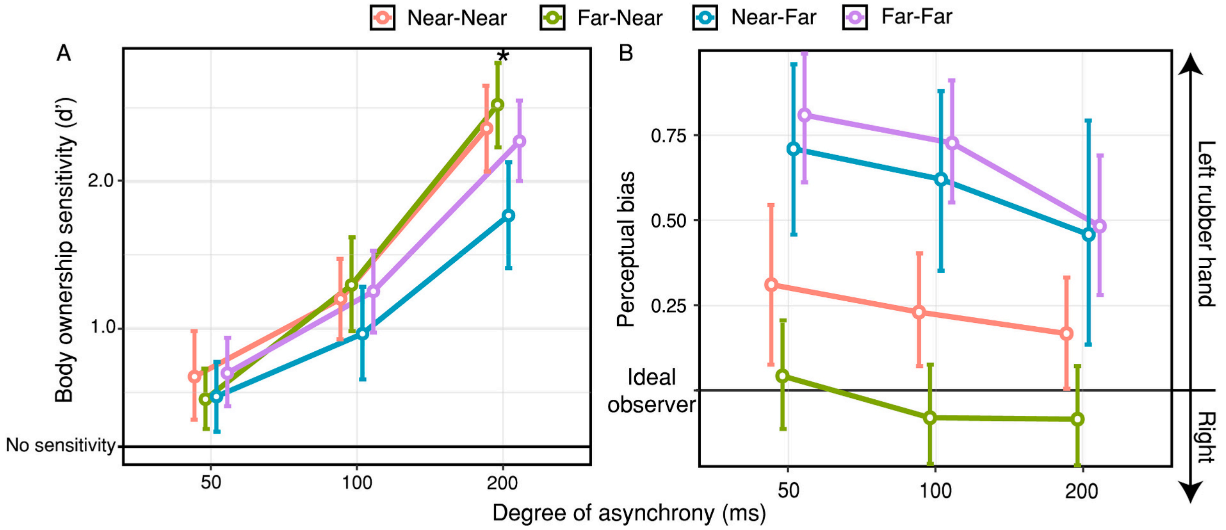

Fig. 2. Results of the main experiment. (A) Body ownership sensitivity (d'). Body ownership d' increased with increasing degrees of asynchrony. The Near-Near condition was associated with significantly higher body ownership d' than the Near-Far condition but only at a degree of asynchrony of 200 ms. The four spatial conditions each exhibited above-chance body ownership sensitivity for asynchrony as brief as 50 ms. (B) Perceptual bias. Participants exhibited a bias favouring the left rubber hand; however, this bias decreased as the degree of asynchrony increased. In other words, the better body ownership sensitivity they had, the less they relied on this perceptual bias. The asterisk denotes a significant difference between the Near-Near and Near-Far conditions; importantly, this is the only post hoc comparison that reached statistical significance, showing a significant interaction. In contrast, the interaction did not reach significance with perceptual bias. Data points have been jittered along the x-axis for clarity. Error bars represent 95% confidence intervals (CIs).

hands, favouring the rubber hand closer to the participant's body (i.e., Near-Near condition). Indeed, this was the only condition that had a significant advantage over the condition with the rubber hands being the furthest away (i.e., Near-Far condition). In summary, body ownership sensitivity is modulated by visuotactile asynchrony and the spatial distance between the rubber hands and the real hand. Furthermore, when the stimulation asynchrony is the highest, the distance between rubber hands has the largest impact on body ownership sensitivity, thus demonstrating that the two RHI rules (the temporal rule and the spatial rule) interact.

However, can participants reliably discriminate illusory body ownership signals with just 50 ms of stimulation asynchrony between the two rubber hands? Our results indicate that no confidence interval crossed zero sensitivity. However, to test this directly, we also ran a series of one-sample t-tests (one-tailed) against zero (i.e., no sensitivity) for body ownership d' scores obtained with 50 ms of stimulation asynchrony. As expected, all d' values were significantly above zero: Near-Near ($t(24) = 4.55, p < .001, d = 0.909$), Far-Near ($t(24) = 5.38, p < .001, d = 1.077$), Near-Far ($t(24) = 4.15, p < .001, d = 0.830$), and Far-Far conditions ($t(24) = 6.77, p < .001, d = 1.354$). Therefore, the temporal rule of the RHI strongly influences body ownership sensitivity, and even very brief asynchronies in visuotactile correlations reduce the influence of the multisensory information that drives the illusion.

2.2.2. *Perceptual bias*

Does the illusion induce a bias to feel ownership more strongly with either rubber hand? If so, does the spatial distance between the body and the rubber hand modulate this perceptual bias? Testing this, we found a significant main effect of the degree of asynchrony ($F(1.55, 37.23) = 6.892, p = .005, \eta p2 = .223$), showing that participants favoured the left rubber hand, especially with lower stimulation asynchronies. This bias decreased as stimulation asynchrony increased (Fig. 2B). Indeed, post hoc comparisons between degree of asynchrony conditions revealed a significant difference in perceptual bias between 50 and 200 *ms* ($t(24) = 3.705, p = .002, d = 0.741$) but not between 50 and 100 ms ($t(24) = 1.638, p = .108, d = 0.328$) or between 100 and 200 ms ($t(24) = 2.066, p = .088, d = 0.413$). Convergently, Bayes factor analysis provided moderate ($BF01 = 4.072$) and anecdotal support ($BF01 = 2.630$) for the null hypothesis between comparisons. These results show that participants favoured the rubber hand closer to their body and that this perceptual bias decreased as stimulation asynchrony increased.

However, did the distance between the rubber hands and the real hand also modulate this perceptual bias? Indeed, we found a significant main effect of distance between rubber hands ($F(1.69, 40.68) = 24.652$, $p < .001, \eta p2 = .507$), and post hoc comparisons revealed that only the paired comparisons between Near-Near and Near-Far ($t(24) = 38.16, p < .001, d = 0.763$) and between Near-Near and Far-Near ($t(24) = 29.32$, $p = .009, d = 0.586$) reached significance (Fig. 2B), arguably reflecting comparisons of the rubber hands closer to the body with the rubber hands furthest away from it. These results indicate that having the right rubber hand further away from the body had a stronger effect on perceptual bias than having the left rubber hand further away, thus suggesting a perceptual bias for hand ownership that favours the rubber hand closer to the body.

2.3. *Discussion*

Our main experiment showed that very small visuotactile stimulation asynchronies between the two rubber hands led to significant changes in body ownership sensitivity in the RHI. Notably, even 50-ms stimulation asynchronies produced sufficiently noticeable changes in illusory hand ownership for participants to reliably discriminate in accordance with the general notion that temporal incongruence reduces the RHI. However, prior studies have shown that the RHI is significantly diminished when the visuotactile delays are longer than 300 ms (Shimada et al., 2009) or 200 ms (Chancel & Ehrsson, 2020), in line with the temporal window of multisensory integration. Our findings contribute to this body of knowledge by showing that stimulation asynchronies as short as 50 ms –, i.e., within the classic temporal binding window – change how much information about body ownership is carried in the multisensory correlations driving the RHI.

Distance between the rubber hands and the real hand and the body also impacted body ownership sensitivity at the longest degree of asynchrony and exclusively between the Near-Near and Near-Far conditions, i.e., when the right rubber hand was either closer to or farther away from the body and the real hand. This finding shows that the spatial distance between the rubber hand and the real hand and the body modulates body ownership sensitivity, in line with the spatial rule (Ehrsson, 2020) and the spatial congruence principle of multisensory integration (Holmes & Spence, 2005; Stein & Stanford, 2008), and provides evidence supporting the empirical observation that this effect is most pronounced when the rubber hand is placed further away laterally from the real hand.

The distance between the body and the rubber hands also modulated perceptual bias, favouring the rubber hand closer to the body. However, this perceptual bias decreased as stimulation asynchrony increased. In other words, participants relied less on perceptual bias as body ownership sensitivity increased, which may suggest that the more visuotactile correlative evidence there is in favour of the illusion, the smaller the relative contribution of the spatial-perceptual bias. In the previous literature, two types of spatial effects have been discussed: a distance effect, in which the closer the rubber hand is to the real hand, the stronger the illusion is (Brozzoli et al., 2012; Kalckert & Ehrsson, 2014; Lloyd, 2007), and a "midline" or body proximity effect, in which the closer the rubber hand is to the body, and to the body midline in particular, the stronger the illusion is, with increased distance toward lateral space being associated with weaker illusions (Chancel & Ehrsson, 2020; Fan et al., 2021; Preston, 2013). In the present data, both effects appear to have been present, with the clearest evidence for the second type of spatial effect. There was a significant perceptual bias toward the left rubber hand (closest to body/body-midline) and significant differences in perceptual bias between the Near-Far and Near-Near conditions as well as between the Far-Near and Near-Near conditions, but the direct comparison of Near-Near vs. Far-Far was not significant. The fact that the Far-Near condition was the only condition in which perceptual bias did not favour either rubber hand is possibly because the left rubber hand closer to the body midline "cancelled out" the right rubber hand closer to the real hand (similar observation was made by Fan et al., 2021, based on their questionnaire data). Although future experiments are needed to disentangle different types of spatial effects in the RHI (e.g., by varying the placement of both rubber hands and the real hand, including orthogonally in the distance of the rubber hand to the real hand and the rubber hand to the body), our results provide evidence that spatial manipulation in the RHI is associated with both body ownership sensitivity changes and changes in perceptual bias.

To ascertain that participants did not perform the task using visuotactile asynchrony alone, i.e., judging illusory hand ownership by differences in timed tactile stimulations independent of the RHI and the task instruction, a control experiment was conducted.

3. Control experiment

Did participants' discrimination reflect their sensitivity to body ownership information? In other words, did they follow task instructions to judge the illusory feeling of body ownership, or could some have used a strategy to solve the task by judging only visuotactile simultaneity and ignoring the RHI? To rule out this latter possibility, we conducted a control experiment whereby participants were evaluated in two conditions: an RHI condition (corresponding to the Near-Near condition in the main experiment) and a rotated condition with the rubber hands rotated 90 degrees clockwise. Crucially, this second condition violated the spatial rule of the RHI since both rubber hands were in an anatomically implausible orientation — we know from previous studies that this manipulation effectively abolishes the RHI (Ehrsson et al., 2004; Ide, 2013; Tsakiris & Haggard, 2005). If participants exhibit above-chance body ownership sensitivity in the rotated hands condition, they may be using visuotactile simultaneity when making their discriminations rather than staying true to the instructions. In contrast, if they exhibit above-chance body ownership sensitivity in the RHI condition but not in the rotated condition, it will indicate that participants' reports are based on their feeling of body ownership, as we would expect.

3.1. Method

3.1.1. Participants

Eleven naïve participants were recruited. However, one participant did not reach the minimum threshold for experiencing the RHI (we used the same exclusion criteria as Chancel and Ehrsson (2020), thus leaving 10 participants (5 female; $M_{age} = 28.8$, $SD_{age} = 3.33$) in this control experiment. Note that a power analysis determined that this sample size is sufficient to capture the effect of the degree of asynchrony found in the main experiment (see Appendix A: Supplementary Material 2).

3.1.2. Experimental setup, procedure, and analysis

The setup, procedure, and analysis were the same as in the main experiment, except that in the two conditions, the same distance between rubber hands was uniformly used (same as the Near-Near condition in the main experiment), and in the rotated condition, both rubber hands were rotated 90 degrees clockwise. Therefore, in the rotated condition, participants had to verbally respond up or down rather than left or right. The order of the conditions was counterbalanced across participants.

3.2. Results

3.2.1. Body ownership sensitivity

By-condition body ownership d' scores were entered into a 3 (degree of asynchrony: 50, 100, 200 ms) × 2 (condition: illusion, rotated) repeated-measures ANOVA. We found a significant effect of the degree of asynchrony ($F(1.30, 11.74) = 17.8, p < .001, \eta p2 = .665$) and a significant condition effect ($F(1,9) = 56, p < .001, \eta p2 = .862$). Notably, the interaction of asynchrony and condition was significant ($F(2,18) = 10.4, p < .001, \eta p2 = .537$). These results were expected and reflect that the body ownership discrimination in the Illusion condition is in line with the previous experiment. More importantly, the fact that the confidence interval bars for the three degrees of asynchrony crossed zero sensitivity in the rotated hands condition suggests that body ownership sensitivity was not related to the different levels of asynchrony in this condition. To test this directly, we ran a series of one-sample *t*-tests (one-tailed) against zero on the rotated hand data (Fig. 3A). Crucially, neither the d' scores obtained with 50 ($t(9) = 2.025, p = .963, d = 0.640, BF_{0+} = 7.722$), 100 ($t(9) = 2.047, p = .965, d = 0.647, BF_{0+} = 7.758$), or 200 ms of asynchrony ($t(9) = 0.904, p = .805, d = 0.287, BF_{0+} = 5.429$) differed significantly from zero. Furthermore, the Bayes factor analysis provided moderate support for the null hypothesis models for each level of asynchrony — approximately 5 to 8 times more likely than the alternative hypothesis. Since the RHI was abolished during the rotated condition, these results indicate that participants did not use visuotactile simultaneity information as an alternative strategy to perform the task and that they honestly followed the instructions to judge the perception of bodily illusion and not visuotactile synchrony or asynchrony as such, supporting the validity of the results obtained in the main experiment.

3.2.2. Perceptual bias

We did not find a significant effect of the degree of asynchrony ($F(2,18) = 0.865, p = .438, \eta p2 = .088$) or condition ($F(1,9) = 0.004, p = .954, \eta p2 = 0$) on the perceptual bias measure. Their interaction also did not reach significance ($F(2,18) = 3.37, p = .057, \eta p2 = 0.273$) (Fig. 3B). Note, however, that all mean scores were positive, which suggests the possibility of a small bias in favour of the rubber hand closer to the body (Fig. 3B). Indeed, this interpretation was supported by the results of a series of exploratory one-tailed one-sample *t*-tests against zero by showing a trend with 100 ms ($t(9) = 1.56, p = .076, d = 0.494, BF_{+0} = 1.422$) and a significant difference with 200 ms ($t(9) = 1.87, p = .048, d = 0.590, BF_{+0} = 2.056$) in the Illusion condition. Bayes factor analysis results provided anecdotal support for the alternative hypothesis model (i.e., a bias in favour of the left rubber hand). Conversely, the equivalent analyses of the rotated condition did not differ from zero with any degree of asynchrony (all $p > .133$; all $BF_{+0} > 0.918$), which suggests that the rotated condition was not associated with a bias toward one of the rubber hands (even though the left rubber hand was further from the participant due to the clockwise rotation). This is in line with our view

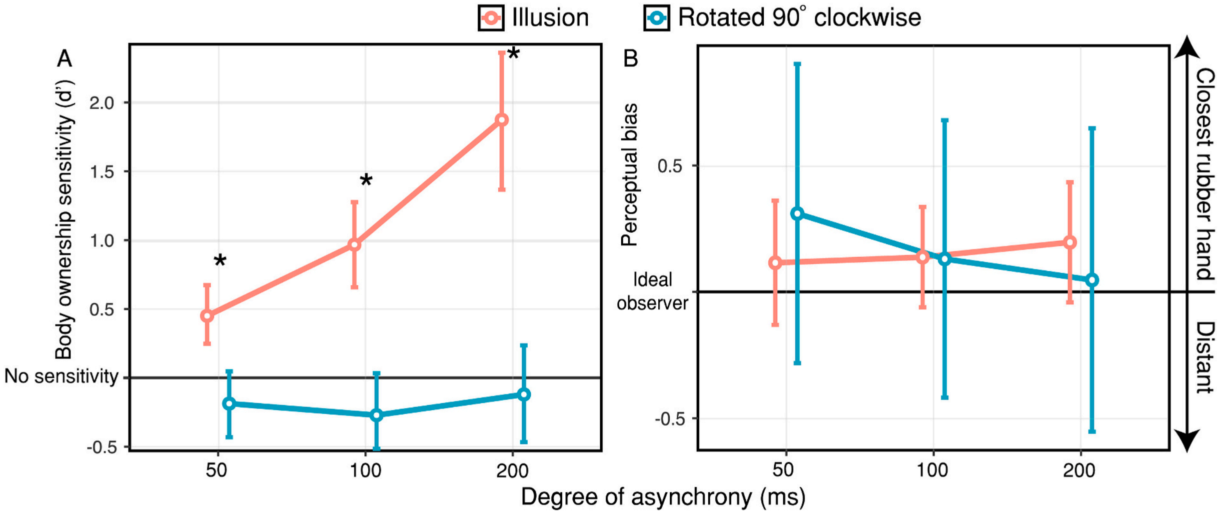

Fig. 3. Results of the control experiment. (A) Body ownership sensitivity. The Illusion condition replicated the results of the Near-Near condition in the main experiment. Crucially, none of the different levels of asynchrony during the rotated hands condition – a control condition that eliminates the rubber hand illusion – yielded above-chance d' scores, indicating that the participants did not use visuotactile simultaneity judgements as an alternative strategy to perform the task. (B) Perceptual bias. We did not find any effects of condition or the degree of asynchrony on perceptual bias. Nevertheless, all mean values were positive, which suggests the possibility of a very mild bias in favour of the rubber hand at the bottom, i.e., the hand closer to the participant's body. Asterisks denote significant differences between conditions. Data points have been jittered along the x-axis for clarity. Error bars represent 95% CI.

that the bias effects observed for the left rubber hand in the Illusion condition are perceptual in nature and related to the spatial rule of the RHI.

3.3. Discussion

The control experiment findings replicated the body ownership sensitivity findings of the main experiment in the Illusion condition by showing that body ownership d' scores increased with increasing stimulation asynchrony. Crucially, participants did not exhibit above-chance body ownership sensitivity in the rotated hands condition. Since rotating the rubber hands 90 degrees clockwise prevents the RHI from arising, these results indicate that body ownership sensitivity scores in the main experiment (and in the control experiment Illusion condition) cannot be attributed to visuotactile asynchrony *per se* but to the relevance of this information in the RHI when all other necessary conditions to elicit the illusion are met, including the spatial congruence of seen and felt arm position and orientation. Thus, the results of our control experiment suggest that participants did not employ an alternative strategy to solve the task — such as measuring the simultaneity of the taps — instead of following instructions and basing judgements on the experience of the illusion.

We also estimated perceptual bias. Since the rotated hands condition prevented the RHI from arising, we expected participants not to exhibit any particular perceptual bias. Indeed, participants did not favour either rubber hand during the rotated hands condition. In the Illusion condition, we found a tendency for participants to favour the left rubber hand in their hand-ownership judgement, in line with the findings from the main experiment and the notion of a spatial perceptual bias toward the rubber hand that is closest to the participants' body.

In conclusion, the control experiment findings support the validity of our task in measuring body ownership sensitivity and perceptual bias.

4. Pooled analysis of 83 participants: Body ownership sensitivity and perceptual bias

4.1. Method

4.1.1. Participants and rationale

The main experiment showed that 50, 100, and 200 ms of stimulation asynchrony are sufficient to induce noticeable changes in illusory hand ownership. These asynchronies between the visual and tactile stimuli that influence the RHI are much shorter than those previously reported. Therefore, it is reasonable to ask the following question: How robust is the evidence? To test this, we pooled the data of other experiments that have been carried out in our laboratory using the same setup and paradigm. In addition to the main experiment Near-Near Illusion condition ($n = 24$) and the control experiment Illusion condition ($n = 10$), we included the data of two other experiments. First, an experiment was included that tested whether the tactile congruence between the seen and felt robot taps modulates body ownership ($n = 21$; see Chancel & Ehrsson, 2020, in which the congruent condition is equivalent to our main experiment Near-Near condition). Second, an experiment was included that tested the effects of reducing the amount of visual information available to make tactile predictions by visually occluding the robot arms or the touch events, including a "no visual occlusion" condition that is equivalent to our main experiment Near-Near condition ($n = 28$; see Chancel et al., 2021). In total, that gave us data from eighty-four participants; however, one outlier was identified and therefore not included in the analysis (for normality and nonparametric tests, see Appendix A: Supplementary Material 3). All experiments upon which the pooled analysis was based were approved by the Ethical Review Authority, and the participants provided informed consent.

4.2. Results

4.2.1. Body ownership sensitivity

To address our question, we first ran a series of one-tailed one-sample *t*-tests against zero for each degree of asynchrony condition separately ($n = 83$). We found that body ownership sensitivity was significantly above zero with 50 ($t(82) = 12.989, p < .001, d = 1.426$), 100 ($t(82) = 18.142, p < .001, d = 1.991$), and 200 ms of stimulation asynchrony ($t(82) = 32.724, p < .001, d = 3.592$). Indeed, most participants obtained body ownership d' scores above zero with each stimulation asynchrony (Fig. 4A). In addition, we ran a one-way ANOVA to compare the effect of the degree of asynchrony on body ownership sensitivity, and as expected, we found a significant increase ($F(2,164) = 255.16, p < .001, \eta$ p2 = $.757, BF_{10} > 100$). Post hoc comparisons between degrees of asynchrony revealed significant differences between all delays: 50 ms and 100 ms ($t(82) = 7.821, p < .001, d = 0.831$), 100 ms and 200 ms ($t(82) = 14.444, p < .001, d = 1.535$), and 50 ms and 200 ms ($t(82) = 22.264, p < .001, d = 2.366$). Next, to further assess the extent to which the data support this alternative hypothesis model (i.e., body ownership d' > 0, i.e., one tailed), we ran a series of Bayesian one-sample t-tests against zero for each degree of asynchrony. Bayes factors provided overwhelming evidence in favour of the alternative hypothesis model (all $BF_{+0} > 100$; all $BF_{0+} < 0.01$). The posterior distribution of the effect size had a median of 1.402, with a 95% central credible interval between 1.097 and 1.712 with 50 ms of asynchrony; a median of 1.964, with a 95% central credible interval between 1.595 and 2.342 with 100 ms of asynchrony; and a median of 3.595, with a 95% central credible interval between 3.254 and 4.017 with 200 ms of asynchrony (Fig. 4B). Very similar results were obtained with wider prior distributions (Fig. 4C), which suggests that these results are robust. Both frequentist and Bayesian analyses yielded qualitatively convergent results, strongly indicating that body ownership sensitivity is above chance for the three degrees of stimulation asynchrony.

4.2.2. Perceptual bias

The main experiment also showed a perceptual bias favouring the left rubber hand, and this bias was more pronounced with smaller visuotactile stimulation asynchronies, i.e., when participants' body ownership was less sensitive to the temporal rule of the RHI. However, how robust is the evidence of this perceptual bias? To address this question, we ran a series of two-tailed one-sample *t*-tests against zero, including all the participants and conditions included in the body ownership sensitivity analysis described above. Similarly, we excluded the outlier previously identified, thus leaving the same 83 participants (for normality and nonparametric tests, see Appendix A: Supplementary Material 4).

We found that perceptual bias was significantly above zero with 50 ($t(82) = 4.748, p < .001, d = 0.521$), *100* ($t(82) = 5.582, p < .001, d = 0.613$), and 200 ms of stimulation asynchrony ($t(82) = 5.293, p < .001, d = 0.581$), i.e., a bias consistently favouring the left rubber hand (Fig. 4D). In addition, we ran a one-way ANOVA to compare the effect of the degree of asynchrony on perceptual bias, and as expected, we found a significant effect ($F(1.26, 103.15) = 7.024, p = .006, \eta$p2 $= .079, BF_{10} > 100$). Post hoc comparisons between degrees of asynchrony revealed significant differences between 50 ms and 200 ms ($t(82) = 3.715, p < .001, d = 0.45$) and between 100 ms and 200 ms ($t(82) = 2.286, p = .047, d = 0.28$). Next, to assess the support of the evidence for this alternative hypothesis model (i.e., rubber hand bias > 0), we ran a series of Bayesian one-sample t-tests against zero for each degree of asynchrony. Bayes factors provided overwhelming evidence in favour of this alternative hypothesis model (all $BF_{+0} > 100$; all $BF_{0+} < 0.01$). The posterior distribution of the effect size had a median of 0.505, with a 95% central credible interval of 0.278 and 0.734 with 50 ms of asynchrony; a median of 0.595, with a 95% central credible interval of 0.362 and 0.829 with 100 ms of asynchrony; and a median of 0.564, with a 95% central credible interval of 0.333 and 0.796 with 200 ms of

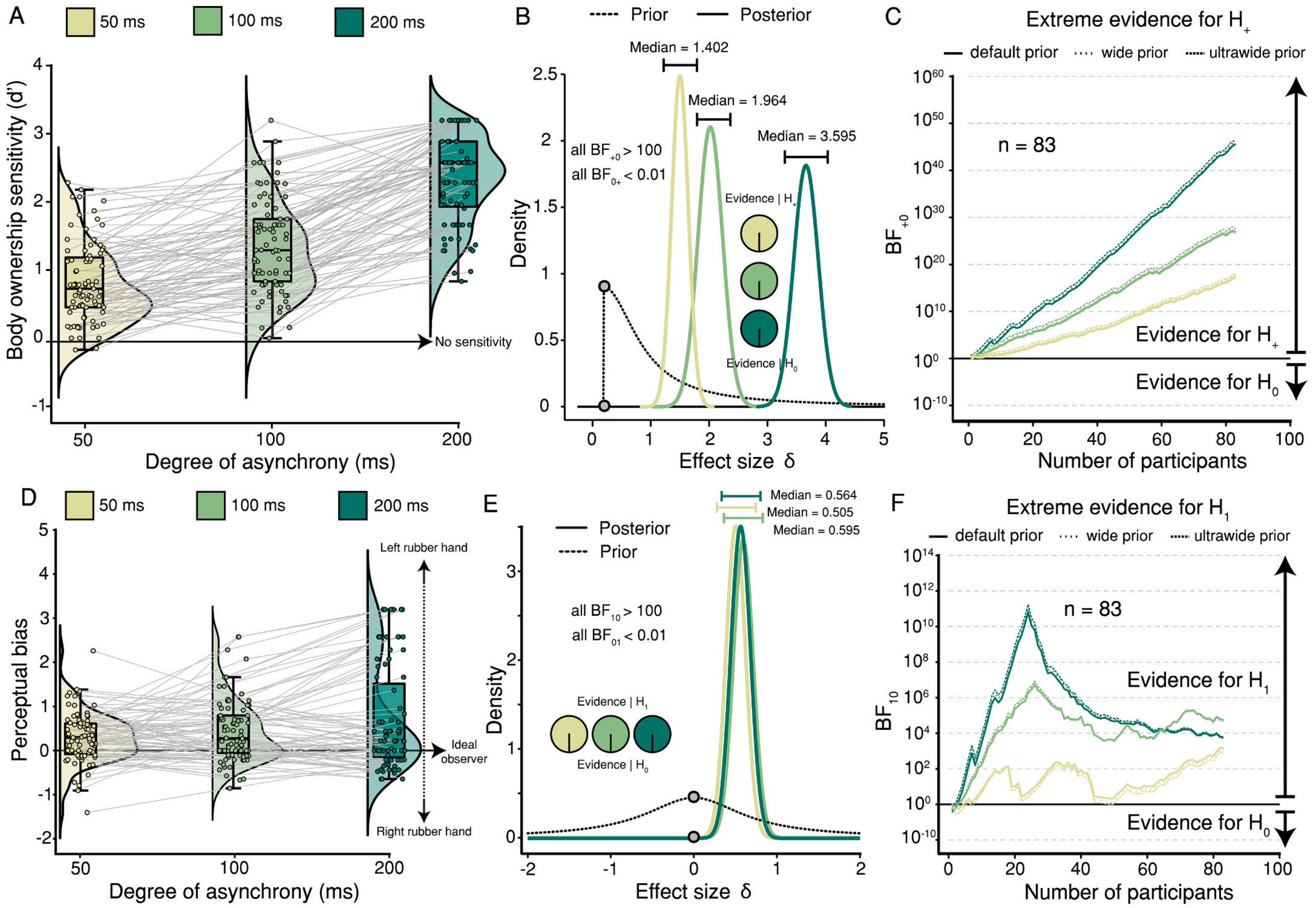

Fig. 4. (A – C) Pooled analysis of body ownership sensitivity ($n = 83$). (A) Individual one-sample *t*-tests against zero. Body ownership d' was significantly above zero with 50, 100, and 200 ms of stimulation asynchrony. Bayesian one-sample t-tests against zero (one-tailed): (B) Prior and posterior distributions. Bayes factors provided extreme evidence in favour of the alternative hypothesis model (i.e., body ownership d' > 0 per degree of asynchrony), which is clearly depicted by the estimated population effect size, with a median of 1.402 and a 95% central credible interval of 1.097 and 1.712 for 50 ms of asynchrony; a median of 1.964 and a 95% central credible interval of 1.595 and 2.342 for 100 ms of asynchrony; and a median of 3.595 and a 95% central credible interval of 3.254 and 4.017 for 200 ms of asynchrony. (C) Sequential analysis with robustness assessment. The evidence for the alternative hypothesis model increased as the sample size increased for each stimulation asynchrony. The evidence for the alternative hypothesis model is extremely stable across different prior distributions, ranging from 6.911×10^{18} to 8.565×10^{18} ($r = 1.406$) for 50 ms of asynchrony, ranging from 4.849×10^{27} to 3.21×10^{27} ($r = 1.5$) for 100 ms of asynchrony, and ranging from 4.09×10^{45} to 7.648×10^{45} (r = 1.5) for 200 ms of asynchrony. (D – F) Pooled analysis of perceptual bias ($n = 83$). (D) Individual one-sample *t*-tests against zero. Perceptual bias significantly favoured the left rubber hand with 50, 100, and 200 ms of stimulation asynchrony. Bayesian one-sample t-tests against zero (two-tailed). (E) Prior and posterior distributions. Bayes factors provided extreme evidence in favour of the alternative hypothesis model (i.e., perceptual bias for the left rubber hand), which is clearly depicted by the estimated population effect size, with a median of 0.505 and a 95% central credible interval of 0.278 and 0.734 for 50 ms of asynchrony; a median of 0.595 and a 95% central credible interval of 0.362 and 0.829 for 100 ms of asynchrony; and a median of 0.564 and a 95% central credible interval of 0.333 and 0.796 for 200 ms of asynchrony. (F) Sequential analysis with robustness assessment. The evidence for the alternative hypothesis model increased as the sample size increased. The evidence for the alternative hypothesis model is extremely stable across different prior distributions, ranging from 1297 to 2052 ($r = 0.482$) for 50 ms of asynchrony, ranging from 45,548 to 46,390 ($r = 0.5793$) for 100 ms of asynchrony, and ranging from 14,783 to 15,240 ($r = 0.545$) for 200 ms of asynchrony.

asynchrony (Fig. 4E). Very similar results were obtained with wider prior distributions (Fig. 4F), which suggests that these results are robust. Both frequentist and Bayesian analyses yielded qualitatively convergent results, strongly indicating that perceptual bias favoured the left rubber hand when 50, 100, and 200 ms of stimulation asynchrony were applied.

5. General discussion

The RHI is a bodily illusion that involves changes in body representation and the subjective experience of a fake limb as being part of one's own body. This illusion has been extensively studied over the past 20 years because it provides a way for scientists to manipulate the complex experience of body ownership that is otherwise difficult to study experimentally. However, the methods used to quantify the illusion have limitations that have hindered conceptual advances in the field and even led to discussions about the very nature of the processes involved (somatosensory, motoric, emotional, multisensory, cognitive, imaginative, conceptual, etc.). Here, we introduced an SDT approach to the RHI by using an RHI-adapted discrimination task (Chancel and Ehrsson, 2020). Critically, the SDT framework allowed us to examine how controlled changes in sensory information related to the subjective illusion, i.e., how the degree of asynchrony and spatial correspondence of the correlated visuotactile signals relate to body ownership sensitivity and RHI-induced perceptual bias. The fundamental strength of this approach compared to questionnaire rating scales is that it allows objective assessment of illusory perception; in addition, it does not rely on proxy measures of the illusion, such as drift in hand position sensation or changes in threat-evoked SCR, but instead probes the subjective experience of the illusion directly. Our analysis revealed three main novel findings. First, the degree of the temporal congruence of the visual and tactile stimuli, i.e., the level of visuotactile asynchrony, determines body ownership sensitivity. Second, the spatial distance between the rubber hand and the participant's body modulates both body ownership sensitivity and perceptual bias. These findings conclusively demonstrate that the spatiotemporal information carried in visuotactile correlations drives the emergence of illusory ownership perceptions and rules out explanations based on cognitive bias, suggestibility, or cognitive reasoning. Third, illusory rubber hand ownership is surprisingly sensitive to stimulation asynchronies between rubber hands, which was demonstrated by the fact that stimulation asynchronies of only 50 ms induced significant changes in body ownership sensitivity. This finding challenges the widely held assumption of a "fixed" temporal rule governing body ownership, where delays within a time window of 200 to 300 ms are tolerated, and instead suggests that information relevant to body ownership is extracted in a much more sensitive and continuous fashion from the patterns of sensory signals; this has important theoretical implications for cognitive and computational models of body ownership.

Collectively, these findings are conceptually important because they show that illusory changes in body ownership in the RHI are related to visuotactile information processing and spatial-perceptual bias toward the fake hand. They provide a validation of a critical assumption in multisensory theories of body ownership (Chancel, Ehrsson, & Ma, 2022; Ehrsson, 2012; Graziano & Botvinick, 2002; Kilteni et al., 2015; Samad et al., 2015; Tsakiris, 2010), bodily self-consciousness (Blanke, Slater, & Serino, 2015; de Vignemont, 2017; Gallagher, 2000; Noel, Blanke, & Serino, 2018; Tsakiris, 2010), prosthetic embodiment (Zbinden et al., 2022), embodiment in virtual reality (Kilteni et al., 2012), teleoperated humanoid robots (Ishiguro & Libera, 2018), self-recognition (Jeannerod, 2003), and certain theories of embodied cognition (Alsmith & de Vignemont, 2012) and the sense of self (Blanke & Metzinger, 2009; Merleau-Ponty, 1945; Rochat & Striano, 2000) by providing bias-free evidence (the sensitivity measure) that links subjective changes in body ownership to sensory signal processing. In addition, our study provides a proof of concept that SDT and psychophysics can be used to investigate bodily illusions and adds to the relatively few studies that have tried to analyse multisensory and visual perceptual illusions using this approach. Our results underscore that perceptual illusions not only are systematic biases or changes in the criterion that go in the direction of how most people experience illusions, as previously emphasised; but also correspond to objective changes in sensory information processing.

As mentioned, prior RHI studies have suggested that the temporal binding window for integrating visual and tactile information plays a crucial role in body ownership (Costantini et al., 2016; Maselli, Kilteni, López-Moliner, & Slater, 2016), where asynchronies up to approximately 200 (Chancel & Ehrsson, 2020) or 300 ms (Shimada et al., 2009) have been tolerated to allow the illusion to arise. In Chancel and Ehrsson (2020), the threshold used in the model fit of the data showed that participants need at least 200 ms to distinguish between illusory ownership of the two rubber hands in a reliable manner, but this does not necessarily mean that shorter asynchronies do not allow illusory-ownership discrimination, as this issue was not directly investigated. In the study by Shimada et al. (2009), the illusion was quantified with questionnaires and proprioceptive drift, which may be less sensitive than psychophysics approaches (as one may reasonably assume, although this needs to be formally investigated), and their work did not focus on the question of a possible effect for very short asynchronies. Thus, our current study advances the understanding of how temporal asynchrony influences the RHI by showing that even very brief visuotactile asynchronies contain information that modulates the illusion, i.e., that drives the segregation versus the combination of the visual and somatosensory signals in the multisensory binding process that underlies this illusion. Of note, asynchronies of 100 ms had a greater impact on body ownership sensitivity, and 200 ms asynchronies had an even greater impact, suggesting that the degree of asynchrony within the classic temporal window of integration influences the emergence of the illusion in a seemingly gradual function. This finding is important because it reconceptualises how we think about the temporal rule in the RHI; instead of a "fixed" rule that determines the illusion in a "binary", "all-or-nothing" manner, it suggests a more gradual and continuous perceptual decision process where sensory information speaking for, or against, multisensory binding is inferred from how well temporally correlated visual and tactile signals are.

In classic models of the temporal binding window, the stimuli in the two sensory modalities are thought to occur either within or outside the binding window (Wallace & Stevenson, 2014; Wallace, Woynaroski, & Stevenson, 2020), which then determines whether two signals are perceptually bound or segregated (Diederich & Colonius, 2004; Vroomen & Keetels, 2010; Wallace & Stevenson, 2014). Although the temporal binding window can be recalibrated based on task requirements, attention, and other variables (Diederich & Colonius, 2015), its basic shape is believed to be constrained by the basic temporal integration properties of multisensory neurons (Avillac, Hamed, & Duhamel, 2007; Meredith, Nemitz, & Stein, 1987; Wallace, Wilkinson, & Stein, 1996). However, in more recent Bayesian computational models of multisensory integration of the RHI (Chancel et al., 2021; Fang, Zhang, et al., 2019; Kilteni et al., 2015; Samad et al., 2015), all available sensory evidence is taken into account in a flexible manner that uses information about sensory uncertainty and prior knowledge. In such frameworks, even very small variations in temporal and spatial incongruence contribute to the final automatic perceptual decision to combine or segregate the signals. The present findings fit well within such probabilistic conceptualisations of multisensory integration and the RHI by showing that even very small variations in asynchrony do indeed influence the strength of the RHI, as shown by the d' index.

Our findings provide valuable insights for theories of body ownership and multisensory integration based on predictive coding (R. P. N. Rao & Ballard, 1999) and free energy frameworks, which emphasise the role of top-down processes in perception. According to these theories, cortical systems possess generative models, the prior probability of which is updated by sensory evidence (Friston, 2005; Picard & Friston, 2014). The RHI induces a multisensory conflict that increases the prediction error between the top-down predictions of the generative model and the bottom-up afferent sensory information. The prediction error serves as a learning signal to update the generative model, reducing future prediction errors in the system. As synchronous visuotactile stimulation continues in the RHI, and thereby multisensory evidence favouring the rubber hand accumulates, the prior probability distribution representing the rubber hand as one's own becomes increasingly more likely; hence, feeling the rubber hand as one's own may be associated with a minimisation of prediction error (Apps & Tsakiris, 2014; Limanowski & Blankenburg, 2013). Our findings suggest that the temporal precision with which such generative models generate top-down predictions and the precision by which prediction errors are detected may be very high. This is because the sensitivity of the feeling of body ownership in the current RHI experiments could distinguish between visuotactile stimulation asynchronies of 50 ms after a relatively short period of only six repeated visuotactile stimulations, which according to this theory, implies that prediction errors driving the emergence of the RHI must have arisen even for such very short asynchronies.

Our SDT results also revealed new findings regarding spatial congruence effects in the RHI. We found that varying the distance between the rubber hands and the participant's real hand and body modulated both body ownership sensitivity and perceptual bias in a way that agrees with the notion that the degree of spatial disparity between the visual and somatosensory signals is another source of information that drives the illusion (Brozzoli et al., 2012; Chancel & Ehrsson, 2020; Fan et al., 2021; Fang et al., 2019; Guterstam, Zeberg, Özçiftci, & Ehrsson, 2016; Lloyd, 2007; Makin et al., 2008; Mirams, Poliakoff, &

Lloyd, 2017; Newport et al., 2010; Van der Biest, Legrain, Paepe, & Crombez, 2016). Of note, our spatial manipulation was relatively small (5-cm changes laterally or medially in the horizontal plane), and the rubber hands were always placed within peripersonal space, i.e., within the portion of space and distance from the real hand where the RHI can effectively be elicited; the spatial rule of the RHI often refers to this portion of space (Brozzoli et al., 2012; Ehrsson, 2020; Lloyd, 2007; Makin et al., 2008). Thus, the present results demonstrate that even small spatial changes within peripersonal space influence the strength of the illusion both in terms of sensitivity and bias. Again, this fits with a more continuous and probabilistic understanding of how spatial congruence influences the RHI, as opposed to a "fixed rule" with a distinct boundary, similar to the temporal rule as discussed above (Chancel et al., 2021; Chancel & Ehrsson, 2020; Chancel, Iriye, & Ehrsson, 2022).

One further interesting observation is that positioning the rubber hand farthest from the participant's body (in the current paradigm, the right rubber hand) was associated with lower body ownership sensitivity and a lower probability of this hand being chosen as the hand with the strongest feeling of ownership. This observation helps resolve a discussion in the literature on whether the distance between the rubber hand and the body, in addition to the distance between the rubber hand and the real hand, influences the illusion. The results from both body ownership sensitivity and perceptual bias analyses were clear on this point, especially in the pooled analysis with 83 participants, which underscored the robustness of this finding. Despite the fact that such a spatial bias effect has been noted before in questionnaire studies (e.g., Fan et al., 2021), as well as in Chancel and Ehrsson's (2020) analyses (sometimes suggested to reflect a genuine spatial bias effect in the RHI; see Preston, 2013), this finding has remained somewhat unclear. Future studies could explore the mechanisms and precise sources of sensory information behind this effect, along with the spatial coordinate system involved (e.g., hand, trunk, or head-centred space). One hypothesis is that we have more prior experience of our hands in the medial space in front of the body as opposed to farther away more laterally (i.e., different priors). Another hypothesis is that small differences in the degree of postural incongruence between proprioceptive information from the real arm and shoulder and the visual information from the two rubber hands contribute to the effect (Ide, 2013).

Past studies have shown that when SDT analysis is applied to perceptual visual illusions, the decision criterion index (here equivalent to perceptual bias) indistinctly captures both response bias and perceptual bias effects (Morgan et al., 1990; Witt et al., 2015). However, since 2AFC paradigms such as ours are less prone to response bias (Macmillan & Creelman, 1990, 2004; Peters et al., 2016; Stanislaw & Todorov, 1999), we argue that our perceptual bias findings are predominantly driven by perceptual biases related to the RHI as a bodily illusion, especially because the direction of the biases is in line with the spatial rules of the illusion and consistent with that in a wealth of previous RHI studies. However, it should be noted that a limitation of the SDT approach is that it cannot unambiguously distinguish between perceptual bias and cognitive biases, so it is also possible that our perceptual bias findings are confounded by cognitive bias; for example, participants might infer that one rubber hand looks more plausibly positioned than the other, which might influence their RHI discrimination at a postperceptual cognitive level when making their judgements. Evidence against this includes the fact that our spatial manipulation was subtle, and most participants did not even spontaneously notice it, as revealed in postexperiment interviews; moreover, bias was not seen in the control experiment when one rubber hand was closer to the body than the other. Note that our body ownership sensitivity findings are completely protected from cognitive bias, and significant changes in body ownership sensitivity were observed through the manipulation of spatial distance for longer asynchronies (200 ms), which provides further support for the spatial congruence effect in the current study. Nevertheless, with this limitation of the bias measure in mind, the current findings suggest that bias systematically follows the multisensory rules of the RHI in line with the perceptual basis of this effect.

An assumption in the SDT approach to perceptual illusions is that we can classify the discrimination responses as correct or incorrect. This assumption deserves a brief discussion, as it is common wisdom that illusions are "subjective", and one cannot know what the participants feel during any given trial. However, this is based on a misunderstanding of what perceptual illusions actually are and how SDT works. Perceptual illusions are not fundamentally different from "normal" perception, which itself is never a totally accurate description of physical reality but our subjective experience of reality that is being generated by information processing in our perceptual systems. SDT in perception studies is about understanding the systematic relationship between subjective perception and signals (i.e., information patterns versus random noise patterns). Just as the sensory signals are precisely controlled by the experimenter in classic SDT studies on visual or discriminative touch perception, we controlled the visual and tactile signals in the current study, focusing especially on the precise temporal relationship. SDT thus allowed us to characterise the systematic relationship between the subjective judgement about illusory hand ownership and its sensory information patterns. The RHI might be particularly suitable for SDT analysis because extensive previous literature has established the critical role of visuotactile synchrony and asynchrony in the emergence of the illusion (for a recent review, see Ehrsson, 2020), and we have a good theoretical understanding of why this is so within the theoretical framework of multisensory perception, at the level of both computational processes (Chancel, Iriye, & Ehrsson, 2022; Fang, Zhang, et al., 2019; Kilteni et al., 2015; Samad et al., 2015) and neural mechanisms (Ehrsson et al., 2004; Fang, Li, et al., 2019; Gentile, Petkova, & Ehrsson, 2011; Graziano, Cooke, & Taylor, 2000; Guterstam et al., 2019; Limanowski & Blankenburg, 2016; I. S. Rao & Kayser, 2017). The current paradigm could be extended to other bodily illusions, for example, illusory limb movements (Goodwin et al., 1972) triggered by vibrations applied to muscles at specific frequencies (under experimental control; Naito, Ehrsson, Geyer, Zilles, & Roland, 1999; Roll, Vedel, & Ribot, 1989; Roll & Vedel, 1982; for a review, see Proske & Gandevia, 2018), or full-body illusions that are based on similar principles as the RHI (Petkova et al., 2011; Petkova & Ehrsson, 2008). However, the current approach may be unsuitable for certain illusions when little is known about the perceptual rules and specific types of sensory information that drive the illusion or in cases when it is difficult to precisely control the signals in the critical sensory channels (e.g., certain interoceptive submodalities).

Our method presents a promising opportunity for investigating individual differences in body ownership, especially those related to psychopathological traits and psychiatric and neurodevelopmental disorders. Prior studies have reported that individuals with schizophrenia (Ferri et al., 2014; Graham, Martin-Iverson, Holmes, Jablensky, & Waters, 2014; Peled, Pressman, Geva, & Modai, 2003; Peled, Ritsner, Hirschmann, Geva, & Modai, 2000; Thakkar, Nichols, McIntosh, & Park, 2011), eating disorders (Eshkevari, Rieger, Longo, Haggard, & Treasure, 2012; Keizer, Smeets, Postma, van Elburg, & Dijkerman, 2014), borderline personality disorder (Möller, Braun, Thöne, Herrmann, & Philipsen, 2020; Neustadter, Fineberg, Leavitt, Carr, & Corlett, 2019), and autism-spectrum disorders (Cascio, Foss-Feig, Burnette, Heacock, & Cosby, 2012; Palmer, Paton, Hohwy, & Enticott, 2013; Paton, Hohwy, & Enticott, 2012), or psychopathological traits in healthy individuals associated with these disorders, often exhibit an abnormal sense of ownership in the RHI as probed with questionnaires and behavioural tests such as the proprioceptive drift task. However, the methods utilised in these studies are unable to objectively quantify the sensitivity of body ownership and perceptual bias, let alone differentiate between them. This is a particular challenge in psychiatric disorders that are associated with disturbances in cognition, emotion, and thought (e.g., schizophrenia) and psychopathological traits (e.g., schizotypy) associated with differences in cognition, emotion, suggestibility, and attention, which can influence subjective ratings in questionnaires independent from genuine changes in bodily illusory perception (Asai, Mao, Sugimori, & Tanno, 2011; Torregrossa & Park, 2022). For example, individuals with disorganised thoughts and delusions may believe that the rubber hand is their own hand and claim so without actually perceiving the RHI. An important question for computational psychiatric research is whether individuals with schizophrenia are "immune" to certain perceptual illusions, such as the hollow mask illusion (Dima et al., 2009; Schmeider, Leweke, Sternemann, Emrich, & Weber, 1996). This could be due to impairments in using information from previous experiences and statistical regularities (priors) as top-down constraints in perceptual inference. Alternatively, individuals with schizophrenia may show an increased RHI, which could be caused by less reliable sensory information processing or an "overreliance" on bottom-up sensory correlations. To resolve this question, the current psychophysics approach and d' measures could be helpful. Thus, future studies could employ our approach to investigate whether the altered sense of ownership in these psychiatric conditions and psychopathological traits in neurotypical individuals is due to an altered sensitivity to body ownership signals, perceptual bias, or a combination of both.

Finally, what could be the neural mechanisms of the current behavioural findings? Previous fMRI and ECoG studies that have compared synchronous and asynchronous visuotactile conditions have associated the RHI with increases in neuronal population activity in regions of the brain associated with multisensory integration of bodily signals such as the posterior parietal cortex and the premotor cortex (Brozzoli et al., 2012; Ehrsson et al., 2004; Guterstam et al., 2019; Limanowski & Blankenburg, 2016). These regions also show activity changes that are sensitive to visuotactile stimuli on one's real hand (Gentile et al., 2011; Lloyd, 2007). As shown in electrophysiological recordings in nonhuman primates, the premotor cortex (Graziano, 1999; Graziano, Hu, & Gross, 1997) and the posterior parietal cortex (Avillac et al., 2007; Graziano et al., 2000) contain neurons that integrate visual, tactile, and proprioceptive signals (Avillac et al., 2007; Graziano, 1999; Graziano et al., 2000), and neural activity in the premotor cortex follows Bayesian principles of multisensory integration in RHI experiments (Fang, Li, et al., 2019). We recently scanned the RHI under a psychophysics detection task and found that activity in the premotor and posterior parietal cortices was related to illusion elicitation at the level of individual participants and trials. Moreover, activity in the posterior parietal cortex followed the predicted probability of illusion emergence of a Bayesian causal inference model (Chancel, Iriye, & Ehrsson, 2022). Thus, multisensory combination versus segregation performed by multisensory neuronal populations within frontoparietal circuits may implement the critical neuronal computations underlying the current findings of body ownership sensitivity and perceptual biases.

In conclusion, our results suggest that the temporal and spatial principles of body ownership can be assessed using SDT analysis and a 2AFC discrimination task. Our findings demonstrate that the temporal and spatial congruence effects of the RHI impact both body ownership information processing and perceptual bias. Notably, body ownership information processing is extremely temporally accurate, responding to changes in visuotactile delays on the order of 50 ms, which advances our understanding of how sensory signals relate to the subjective experience of body ownership. Our study suggests that the SDT psychophysics approach can be a valuable method for investigating bodily illusions as well as other types of multisensory perceptual illusions.

CRediT authorship contribution statement

Renzo C. Lanfranco: Conceptualization, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Marie Chancel:** Conceptualization, Methodology, Investigation, Writing – review & editing. **H. Henrik Ehrsson:** Conceptualization, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare no competing interests.

Data availability

Research data have been uploaded to the Open Science Framework. There is a link to this repository in the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2023.105491.

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