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Proprioception but not cardiac interoception is related to the rubber hand illusion

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ABSTRACT

The rubber hand illusion (RHI) is a widely used tool in the study of multisensory integration. It develops as the interaction of temporally consistent visual and tactile input, which can overwrite proprioceptive information. Theoretically, the accuracy of proprioception may influence the proneness to the RHI but this has received little research attention to date. Concerning the role of cardioceptive information, the available empirical evidence is equivocal. The current study aimed to test the impact of proprioceptive and cardioceptive input on the RHI.

60 undergraduate students (32 females) completed sensory tasks assessing proprioceptive accuracy with respect to the angle of the elbow joint, a heartbeat tracking task assessing cardioceptive accuracy (the Schandry-task) and the RHI.

We found that those with more consistent joint position judgements (i.e., less variable error) in the proprioceptive task were less prone to the illusion, particularly with respect to disembodiment ratings in the asynchronous condition. Systematic error, indicating a systematic distortion in position judgements influenced the illusion in the synchronous condition. Participants with more proprioceptive bias toward the direction of the rubber hand in the proprioceptive test reported a stronger felt embodiment. The results are in accordance with Bayesian causal inference models of multisensory integration. Cardioceptive accuracy, however, was not associated with the strength of the illusion.

We concluded that individual differences in proprioceptive processing impact the RHI, while cardioceptive accuracy is unrelated to it. Theoretical and practical relevance of the findings are discussed.

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1. Introduction

The fact that our self is embodied plays a fundamental role in the way we perceive the world (Allen & Tsakiris, 2018; Gallagher, 2005). The actual physiological state of our body forms the basis for emotions and decision making (Damasio, 1994; Dunn et al., 2010; Garfinkel & Critchley, 2013; Herbert et al., 2007; Quadt et al., 2018; Schachter & Singer, 1962; Schandry, 1981). Moreover, we interact with the world via bodily movements, and while doing so, we develop motor abilities that also influence our conscious experience (Gallagher, 2005). Also, bodily self-consciousness, i.e., the pre-reflexive awareness of the body and its functioning plays a vital role in the development of self-consciousness (Aspell et al., 2013; Gallagher, 2005; Lenggenhager et al., 2007; Tsakiris, 2010). It has two major aspects: agency and the feeling of body ownership (Tsakiris et al., 2006). Empirical investigation of these features has gained new momentum recently.

Concerning research on body ownership, one of the most widely used paradigms is the Rubber Hand Illusion (RHI). In this paradigm, one of the participants' hand is covered and visually replaced with a rubber hand. If the latter is synchronously stroked with the unseen real hand, participants will experience a feeling of body ownership (i.e., the feeling that the respective body part is their own hand) towards the fake hand, in addition, a feeling of disownership towards their own hand can also develop. On the behavioral level, when asked to indicate the felt position of their hand, a so-called proprioceptive drift can appear, i.e., the hand will be located between the actual and the rubber hand (Botvinick & Cohen, 1998).

The major factor behind the RHI is the congruency (temporal consistency) of visual and haptic information (Botvinick & Cohen, 1998). A third and incongruent source of information, i.e., the proprioceptive input, is adjusted to the former two by the brain in order to construct a unitary representation of the hand (Ehrsson et al., 2004; Ehrsson, 2011, 2020). As voluntary movements could completely block this process, participants are asked to avoid motor actions during the procedure (Hohwy, 2014). The brain, however, still receives proprioceptive information about the actual position of the hand: mechanoreceptors located in the joints, muscles, as well as in the skin around the joints continuously send input even in resting states (Proske & Gandevia, 2012). As proprioceptive information does not become completely overwritten, the illusion does not work in an all or nothing pattern. The impact of proprioceptive input is also indicated by the observation that increasing the distance between the real and the rubber hand makes the illusion less vivid (Kalckert & Ehrsson, 2014; Lloyd, 2007; Mirams et al., 2017; Preston, 2013).

Beyond exteroceptive and proprioceptive signals, visceroceptive information (i.e., afferent input from the internal organs) might also contribute to the feeling of body ownership. For example, it has been shown that seeing a virtual hand (Suzuki et al., 2013), body (Aspell et al., 2013; Park et al., 2016, 2018), or face (Sel et al., 2017) flashing up in synchrony with participants' heartbeat can increase the feeling of ownership towards it. It was concluded that interoceptive signals play an important role in the maintenance of the stability of bodily self-awareness (Allen & Tsakiris, 2018).

As interoceptive signals impact the feeling of body ownership, and people show individual differences in the perception of interoceptive information, it is reasonable to assume that individual differences in the proneness to the RHI will be associated with individual differences in the perception of interoceptive stimuli. In accordance with this idea, Tsakiris et al. (2011) reported a negative association between cardioceptive accuracy (i.e., the accuracy of the perception of heartbeats) and the strength of the RHI. In more detail, participants with high cardioceptive accuracy, as assessed by the mental heartbeat tracking task (Schandry, 1981), experienced a weaker RHI (as assessed by proprioceptive drift) than those with low cardioceptive accuracy when the rubber hand was stroked in synchrony with the real hand. However, this association was not replicated by Crucianelli et al. (2018) and there is one study that reports the opposite relationship, namely that higher cardioceptive accuracy is associated with a stronger illusion (Suzuki et al., 2013). Overall, the relationship between cardioceptive accuracy and the RHI is yet to be clarified.

Similar to cardioceptive accuracy, proprioceptive acuity (i.e., the accuracy of perception of the position of the joints), as assessed with joint reproduction tests (Goble, 2010), shows substantial individual differences (Han et al., 2016). For example, acuity with respect to the elbow joint is influenced by handedness (Goble et al., 2006, 2009), age (Goble, 2010), and sport experience (Niespodziński et al., 2018). Considering the role of proprioception in the sensation of body posture (Proske & Gandevia, 2012) and that proprioceptive input is assumed to play a fundamental role in the development and maintenance of the feeling of body ownership (Gallagher, 2005; Sacks, 1985, pp. 43–54), these individual differences could also impact the RHI. It is also important to note, that interoceptive accuracy can not be generalized across modalities, i.e., there is no significant association between proprioceptive and cardioceptive accuracy (Ferentzi et al., 2018; Horváth et al., n.d.), which indicates that results established with cardioception are not generalizable to the proprioceptive modality.

Proprioceptive acuity with respect to the elbow joint might be especially worthy of investigation, as during the elicitation of RHI the position of the elbow is very probably differs for the real and the rubber hand, further enhancing the incongruency between them. Although this might be an important influencing factor, the position of the two hand is not always exactly specified. In the classical study, the rubber hand was placed “directly in front of the subject” (Botvinick & Cohen, 1998, p. 756), while the two hands were parallel in other studies (e.g., Tsakiris et al., 2011). In both cases, the actual angle of the respective elbow joint (and perhaps also that of the shoulder) is not the same for the real and the rubber hand which might impact the RHI. Although studies showed that a certain level of congruency is needed between the real and the rubber hand (Pavani et al., 2000; Tsakiris & Haggard, 2005), only one study investigated the role of the individual differences in proprioceptive acuity (Motyka & Litwin, 2019). Motyka and Litwin (2019) reported controversial results: they proposed that precision of proprioceptive information (proprioceptive accuracy) does not play a role in the RHI, and also did not replicate the well-established (Kalckert & Ehrsson, 2014; Lloyd, 2007; Mirams et al., 2017; Preston, 2013) effect of the distance between the real and the rubber hand on the strength of the illusion. The goal of the present study was to test whether individual differences in the processing of cardiac and proprioceptive signals are significantly associated with proneness to the RHI. Based on previous findings and the theoretical considerations presented above, we hypothesized that the accuracy of the perception of (1) the elbow joint position and (2) cardioceptive signals would show a negative association with the proneness to the RHI.

2. Method

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. *Participants*

A priori sample size calculation was conducted using the G*Power v3.1.9.4. software (Faul et al., 2007). Based on the effect size ($d = -.758$) derived from the data of Tsakiris and colleagues (Tsakiris et al., 2011) the minimum required sample size for a Student *t*-test was $n = 58$ ($\alpha = .05$, $1\text{-}\beta = .8$, two-tailed). Participants, who consumed alcohol and/or took psychoactive drugs within 8 h before the experiment, and those with severe injury/disability of the arm were excluded. Participants were undergraduate students of the Eötvös Loránd University ($N = 60$, age $= 20.4 \pm 1.54$ yrs, 53% females, 87% right-handed). The participants took part in the experiment for partial course credit; before the participation in the experiment, they completed a number of questionnaires that belong to another study. Questionnaire data belonging to asynchronous stimulation is missing for two cases due to technical issues. Everyone signed an informed consent at the beginning of the experiments. The research was approved by the Research Ethics Committee of the university.

2.2. *Measurements*

2.2.1. *Experimental setup*

Participants were asked to place their left arm in a box, which made them unable to see the distal part of their arm from the elbow joint to the fingers. Firstly, they were asked to indicate the assumed position of their unseen hand with blinded eyes (see below for details). This served as a baseline measurement for proprioceptive drift. After that, they put on a jacket, which had two left arms down from the elbow joint. The left arm of the participants was placed into the outer arm of the jacket. Next, participants placed their left hand back into the box, and we positioned the rubber hand 40 grades apart (i.e., toward the midline) from the real hand while participants' eyes were covered. When placing the rubber hand, we positioned it to match the length of the forearm and hand of the participants: the end of the middle finger of the rubber hand was placed in the same distance from the elbow joint than the end of the middle finger of the real hand (Fig. 1). The next step was the presentation of the synchronous and the asynchronous stimulation block in a random order.

In the synchronous condition, the rubber hand and the real hand were stroked in a synchronous and spatially matched manner by the experimenter with a brush. One stroking lasted approximately one half second. We stroked each knuckle on the hand multiple times in a random order. The rhythm of the stroking (one stroke per second) was kept with acoustic help via a head set. The stroking period lasted for 90 s. After it, participants were asked to indicate the assumed position of their left hand three times (in the same way as in the baseline measurement) and to fill out the rubber hand questionnaire.

Concerning the asynchronous condition, the rubber hand and the real hand were stroked in an asynchronous manner, i.e., the experimenter stroked the real and the rubber hand in a different place and time. The rhythm and duration of the stroking were comparable to those of the synchronous condition. Following the stimulation, measurement of the perceived position of the left hand was conducted. Finally, the rubber hand questionnaire was filled out.

2.2.2. *Proprioceptive drift*

To assess proprioceptive drift, participants had to indicate the spatial position of their left hand. The measurement was conducted before any stimulation (baseline measurement), after synchronous stimulation and after asynchronous stimulation. To establish the position, in the first step, the experimenter placed the right index finger of the participant on a rotatable lever, which could move on a circle line. The finger was placed on the lever to be able to reach the same

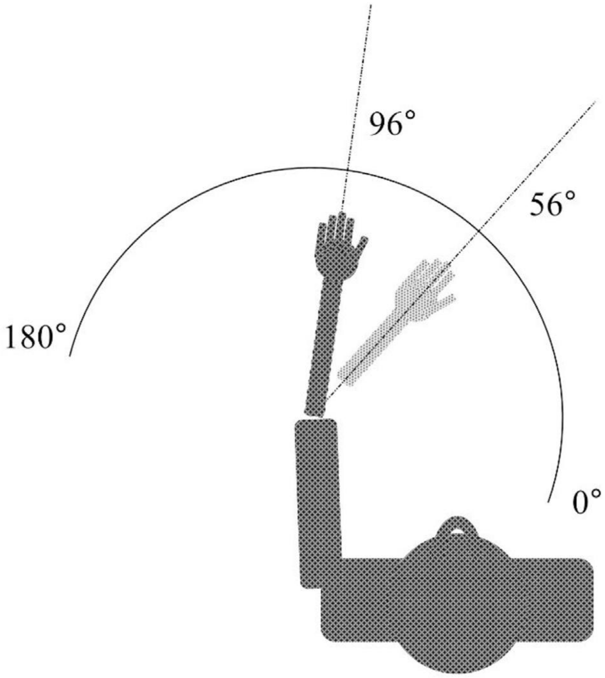

Fig. 1 – The concept of the experimental setup. The black arm is the real arm of the participant, hidden by a box. The grey arm indicates the rubber hand. The difference between the real and the rubber hand was 40°, and the rubber hand was in the same distance from the elbow joint than the real hand. Measurements on proprioceptive drift were made in grades, using the elbow joint as center.

vertical line as the left middle finger (Fig. 2). In this way, the end of the left middle finger of the rubber hand and the right index finger of the participant were on the same line, but in a different height (Fig. 2). In the next step, the participant was instructed to push the lever until the tip of the right index finger reached the felt position of the tip of the left middle finger (i.e., it was presumably above the left middle finger). The indicated position was registered in grades (°; see Fig. 1). Participants' eye was blinded during the measurements (Fig. 2.). Within every measurement (baseline, synchronous, asynchronous), this procedure was repeated three times with different random starting points, and the three judgements were averaged. Internal consistency (Cronbach's alpha coefficient) of the measures was excellent for the baseline (.860), synchronous (.970), and asynchronous (.976) conditions. Proprioceptive drift in the synchronous and asynchronous conditions was calculated by subtracting the baseline value from the respective post-intervention value. Negative values indicated a bias towards the rubber hand (i.e., towards the medial plane), while positive values showed a lateral bias (if the baseline judgment was bigger than 56° which was always the case).

2.2.3. *Self-reported aspects of the RHI*

To assess the subjective strength of the illusion, participants filled out The Rubber Hand Questionnaire (Hegedüs et al., 2014) after both interventions (synchronous and asynchronous). All but one statements were also included in the psychometric study of Longo et al. (2008) The questionnaire consists of 2 scales. One of them measures perceived embodiment towards the rubber hand with 4 items, whereas the other assesses the feeling of disembodiment towards the real hand with 3 items (see the items in Table 1.). Participants rated the statements on 11-point Likert scales (1 = strongly disagree ... 11 = strongly agree). Embodiment and disembodiment scores were calculated as the average of the respective items. Higher scores referred to higher levels of the RHI for both scales. Both scales in both conditions showed a high level of internal consistency (embodiment synchronous = .932, embodiment asynchronous = .909, disembodiment synchronous = .828, disembodiment asynchronous = .890).

Fig. 2 – Measurement of the perceived position of the participants' left hand. Participants had to move the lever until they felt that their right index finger (placed on the lever) was over their left middle finger (placed inside the box). A: rubber hand; B: participant's real hand; C: rotatable level, D: box hiding the real hand.

2.2.4. *Proprioceptive accuracy*

Proprioceptive accuracy was assessed via a passive version of the Joint Position Matching Test in the left elbow joint (Goble, 2010). We used a motorized proprioceptor, which was able to measure the position of the elbow joint with a precision of .1° and move the hand with a given speed. 180° referred to a fully extended elbow, and 10–15° to a fully flexed elbow. Participants were blindfolded and instructed to hold a stable posture (straight torso, upper arm parallel with the ground, and in a straight line with of the chest), set with the help of an adjustable chair during the measurements. The starting position of the elbow joint was 160° (i.e., a conveniently extended elbow). From there, the device moved the participants' arm to the target positions with a speed of 12°/sec. After staying for 4 s in the target position, the arm was moved back to the starting position and stayed there for 1 s. Then the machine started moving again, with a speed of 8°/sec, and participants had to push the button of the device when they felt that their arm reached back to the target position. After the button press the proprioceptor stopped and a new trial began. Participants executed overall 9 trials, with different target positions (30°, 45°, 60°, 75°, 90°, 105°, 120°, 135°, 150°) presented in a random order.

To evaluate performance, in the first step we calculated the error score for every trial, by taking the difference between the reproduced and the target position. Outliers above and below 2 standard deviations were removed because they may reflect the lack of attention in the given trial. This is especially relevant for this study, as participants' arm was moved by the device, thus they could not execute corrective movements. Missing values were imputed using the fully conditional specification (MCMC) and linear regression model options of SPSS v20 software. To evaluate performance, two scores were used. The systematic error score refers to the mean of the nine error scores; it showed a sufficient level of internal consistency (Cronbach α = .745). Variable error was calculated by taking the standard deviation of the error scores. Whereas systematic error score indicates participants' overall systematic bias, the variable error score reflects the consistency of their performance (Boisgontier et al., 2012; Goble et al., 2012; Iandolo et al., 2015; Stilson et al., 1980). Negative values of systematic error score refer to a bias towards the "inside" direction (toward the midline of the body), while positive values mean error towards the "outside" direction. Higher values of

Table 1 – Items and descriptive statistics of the Rubber Hand Questionnaire.

Scale	Question	synchronous M±SD	asynchronous M±SD
embodiment	It seemed like I was feeling the touch of the paintbrush in the location where I saw the rubber hand being touched	8.38 ± 3.157	2.448 ± 2.087
	It seemed like the touch I felt was caused by the paintbrush touching the rubber hand	6.77 ± 3.397	2.757 ± 1.759
	It seemed like the rubber hand was my hand	7.22 ± 3.435	2.76 ± 2.611
	It seemed like the rubber hand belonged to me	6.55 ± 3.301	2.83 ± 2.657
disembodiment	It seemed like I was unable to move my hand	5.017 ± 3.58	3.09 ± 2.952
	It seemed like my hand had disappeared	4.72 ± 3.44	3.24 ± 3.310
	It seemed like my hand was out of control	4.99 ± 3.71	3.48 ± 3.299

variable error score indicate a greater deviation around the systematic error, i.e., less consistency in elbow position judgements.

2.2.5. *Cardioceptive accuracy*

Cardioceptive accuracy was assessed with the mental heartbeat tracking task (Schandry, 1981). Participants were in a seated position with both feet on the ground and hands on their legs. To avoid estimation that might bias their performance (Desmedt et al., 2018; Ehlers & Breuer, 1996), they were instructed to silently count if they had the slightest heartbeat sensation on any part of their body, but otherwise not to count (i.e., estimation of heartbeats was prohibited). Participants indicated if they were ready to begin the task. Subsequently, the trials started with the experimenter saying “START” and ended with “STOP” instruction. Overall, three test intervals of different length (25,35,50 sec) were presented in a random order after a 15 s practice trial. We measured actual heartbeats (ECG) with the NeXus recording system (NeXus Wireless Physiological Monitoring and Feedback: NeXus-10 Mark II, Version 1.02; BioTrace + Software for NeXus-10 Version: V201581; Mind Media BV, Herten, the Netherlands). For every interval, heartbeat perception scores were calculated as: $1 - |(HB_{recorded} - HB_{counted})/HB_{recorded}|$. Scores were averaged to determine individual cardioceptive accuracy. Internal consistency of the Schandry task was very high (Cronbach $\alpha = .950$).

2.3. *Procedure*

The three assessments - the RHI, proprioceptive accuracy, and cardioceptive accuracy - were presented in a randomized order in one testing session. The entire procedure took approximately 60 min.

2.4. *Statistical analysis*

No part of the study procedures and data analyses were preregistered. Raw data is available as supplementary materials. Data was analyzed with the JASP software v0.11 (JASP Team, 2019). Both frequentist and Bayesian statistical analyses were conducted. In the frequentist approach, six repeated-measures analyses of variance (ANOVA) for the two conditions (synchronous *vs* asynchronous stimulation) with proprioceptive (systematic error or error variability) and cardioceptive accuracy as covariates were carried out for the three outcome measures of the RHI (drift, embodiment, disembodiment). The centered version of both variables were used (Schneider et al., 2015). IAc was transformed to better fit normality (demeaned values were divided by the Gaussian membership values of the same demeaned values, and the effect of the demeaning was reset by adding the mean of the original data).

In the Bayesian ANOVA, first strength of the RHI was compared to a null model including subject, then cardioceptive accuracy was compared to a null model including subject and condition (synchronous and asynchronous), finally the measure of proprioceptive accuracy (systematic error or error variability) was compared to a null model including subject, condition and cardioceptive accuracy. Similar to the frequentist analysis, this pattern was repeated for the three RHI related outcome measures, resulting in six analyses overall. Results are uniformly presented as BF_{10} coefficients, i.e., the ratio of the likelihood of the data fitting under the alternative hypothesis to the likelihood of fitting under the null hypothesis. BF_{10} between .33 and 1 indicates weak or anecdotal evidence in favor of the null hypothesis; whereas values between 1 and 3 indicate weak or anecdotal evidence in favor of the alternative hypothesis; values above 100 are considered decisive (Jarosz & Wiley, 2014).

3. Results

Descriptive statistics of the assessed variables are presented in Table 2. Associations between indicators of the RHI and measures of interoceptive accuracy are summarized in Table 3. We found significant correlations in two cases: variable error was associated with embodiment score in the asynchronous condition ($r_s = .326$; $p = .012$) and disembodiment score in the asynchronous condition ($r_s = .302$; $p = .021$*) (Fig. 3).

Results of frequentist ANOVAs for the two measures of proprioceptive accuracy are presented in Tables 4 and 5, respectively. In summary, no significant effect for proprioceptive drift was found; however, main effects for embodiment and disembodiment were consistently significant. The systematic error measure of proprioceptive accuracy did not significantly impact the outcome of the stimulations, whereas the variable error measure was marginally significant for both embodiment and disembodiment In these cases, higher levels of embodiment and disembodiment indicating higher levels of the RHI, were positively associated with higher variable

Table 2 – Descriptive statistics.

	N	M±SD	min–max
Proprioceptive accuracy: Systematic error (°)	60	6.373 ± 4.892	−11.341–15.724
Proprioceptive accuracy: Variable error (°)	60	6.696 ± 2.398	2.344–11.612
Cardioceptive accuracy	60	.474 ± .302	.000–.939
Drift (synchronous) (°)	60	−.650 ± 6.341	−13.667–23.000
Drift (asynchronous) (°)	60	.117 ± 5.181	−9.333–21.333
Embodiment (synchronous)	60	7.229 ± 3.031	1.000–11.000
Embodiment (asynchronous)	58	2.621 ± 1.874	1.000–8.000
Disembodiment (synchronous)	60	4.906 ± 3.290	1.000–11.000
Disembodiment (asynchronous)	58	3.270 ± 2.890	1.000–11.000

Table 3 – Associations (Spearman rho coefficients; *p*-values) between measures of the RHI and cardioceptive accuracy.

	Cardioceptive accuracy	Proprioceptive accuracy: Systematic error	Proprioceptive accuracy: Variable error
Drift (synchronous)	−.009; .947	.031; .812	.053; .686
Drift (asynchronous)	−.003; .985	.076; .562	−.063; .633
Embodiment (synchronous)	.010; .939	−.137; .298	.141; .283
Embodiment (asynchronous)	−.074; .582	−.031; .815	.326; .012*
Disembodiment (synchronous)	−.102; .437	.056; .671	.050; .704
Disembodiment (asynchronous)	.084; .532	.054; .685	.302; .021*

*$p < 0,05$.

error. Moreover, the interaction between systematic error and embodiment, and between error variability and disembodiment were also significant. To better understand the origins of these interactions, measures of proprioceptive accuracy were transformed into binary form by median split and visualized (Figs. 4 and 5).

In the first case (Fig. 4), those with lower systematic error score (i.e., more prone to bias the position of the elbow-joint towards the body in Joint Position Matching test) reported higher embodiment scores in the synchronous condition than those with higher systematic error.

Concerning the second interaction (Fig. 5), lower variable error (i.e., higher consistency) was associated with less felt disembodiment (weaker illusion) in the asynchronous condition.

In contrast to proprioceptive accuracy, cardioceptive accuracy had no impact on the results whatsoever (i.e., neither significant interactions nor significant main effects were found, see Tables 3 and 4).

Bayesian analysis supported these conclusions (see Table 6). Evidence on the main effect for embodiment and disembodiment was decisive, whereas weak evidence for the impact of the variable error measure of proprioceptive accuracy was revealed. No BF_{10} was higher than 1 for proprioceptive drift, cardioceptive accuracy, and the systematic error measure of proprioceptive accuracy.

3.1. *Post-hoc analysis*

In a post-hoc correlation approach, we extended our analysis with another three measures that indicate the strength of the illusion: proprioceptive shift, embodiment index and disembodiment index. These indices were calculated as the differences between the synchronous and asynchronous stimulation (see Supplementary material 1); positive values consistently indicate higher values in the synchronous stimulation. Systematic error was associated negatively with the embodiment index ($r_s = -.247$, $p = .037$), indicating that systematic distortion in hand position judgements towards the rubber hand predicts stronger illusion. Variable error was negatively associated with disembodiment index ($r_s = -.289$, $p = .028$), i.e., less reliable joint position sense predicts a stronger illusion. No other significant relationships were revealed (for details, see Supplementary material 1).

Further, to shed more light on the factors behind the associations, we subdivided the two self-report scales used in this study: the embodiment scale was subdivided into “referral of touch” and “ownership” subscales. The disembodiment scale was subdivided into “loss of agency” and “loss of hand position” subscales. The ownership subscale in the asynchronous condition correlated with variable error ($r_s = .287$, $p = .029$), and loss of agency subscale in the asynchronous condition also correlated with variable error ($r_s = .276$, $p = .036$). No other significant relationships were observed. For calculation and results, see Supplementary material 2.

Moreover, we replicated previous findings (Ferentzi et al., 2018; Horváth et al., n.d.) on the independence of cardioceptive and proprioceptive accuracy (Supplementary material 3).

4. Discussion

Somatosensory illusions such as the RHI represent intriguing phenomena and scientifically useful opportunities to better understand how the brain constructs the conscious representation of our body in terms of bodily self-consciousness.

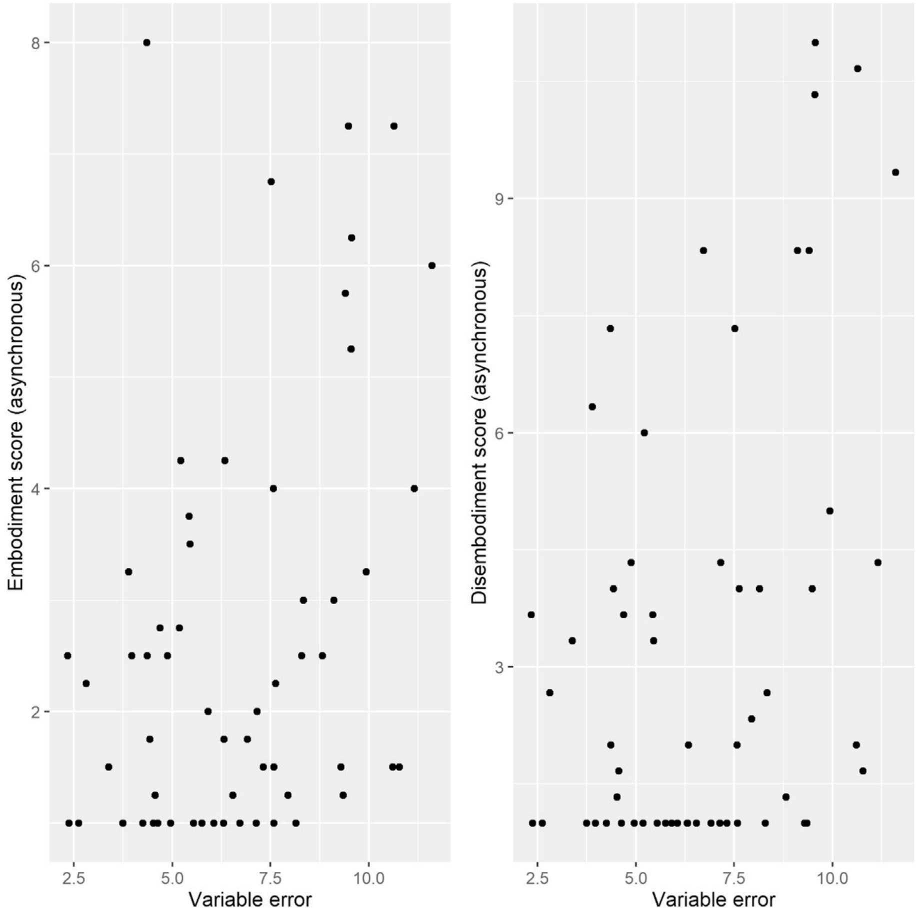

Fig. 3 – Associations of variable error in proprioceptive judgements and embodiment score and disembodiment score in the asynchronous condition.

The primary aim of this study was to test whether cardioceptive and proprioceptive accuracy are significantly associated with the strength of the RHI. In an experiment with the participation of 60 young individuals, no difference between synchronous and asynchronous skin stimulation with respect to proprioceptive drift was measured, whereas changes in felt embodiment of the rubber hand and disembodiment of the real hand were observed. Individual differences in the variance of position judgements (proprioceptive variable error) with respect to the elbow joint showed a weak positive association with felt embodiment and disembodiment, whereas no association for the systematic error measure of proprioceptive accuracy was revealed. Moreover, those with lower proprioceptive systematic error score reported higher embodiment scores in the synchronous condition than those with higher systematic error. Lower variance of the proprioceptive error score was associated with less felt disembodiment in the asynchronous condition. After subdividing the embodiment and disembodiment scales to referral of touch, ownership, loss of agency and loss of hand subscales, we found that only ownership and loss of agency subscales in the asynchronous condition correlated with variable error. These results suggest that probably these are the two key aspects of the RHI that are influenced by the reliability of proprioceptive signals. In a post-hoc analysis, we also found that embodiment index (the difference between embodiment scores the synchronous and the asynchronous stimulation) was associated with systematic error, while disembodiment index (the difference between disembodiment scores the synchronous and asynchronous stimulation) was associated with variable error. These results show that the conclusion of our study (i.e., proprioceptive accuracy is associated with the RHI) still holds true if the RHI is conceptualized differently. Finally, cardioceptive accuracy, as assessed by the mental heartbeat tracking paradigm by Schandry (1981), was not associated with any indicator of the strength of the illusion (embodiment, disembodiment or proprioceptive drift).

Our results suggest that individual differences in proprioceptive information processing do impact the subjective strength of the illusion. This result is in contrast with that of Motyka and Litwin (2019), who found that proprioceptive accuracy is not associated with the strength of the RHI. One possible explanation for the inconsistency may be the difference in the measurement of proprioceptive accuracy: Motyka and Litwin (2019) used an active version of the Joint Position Matching task (i.e., participants had to move their arm), while we used a passive version (i.e., the arm was moved by the device). Accuracy measured with passive and active versions may underlie different aspects of proprioception (Elangovan

Table 4 – Results of repeated measures ANOVAs with systematic error as the measure of proprioceptive accuracy.

Measure of the RHI	Within-subject main effect (synchronous *vs* asynchronous condition)	Cardioceptive accuracy	Proprioceptive accuracy	Condition x cardioceptive accuracy interaction	Condition x proprioceptive accuracy interaction
Proprioceptive drift	F(1,57) = 1.980; *p* = .165; η^2 = .004	F(1,57) = 6.478e −4; *p* = .980; η^2 < .001	F(1,57) = .083; *p* = .775; η^2 < .001	F(1,57) = .005; *p* = .944; η^2 < .001	F(1,57) = .002; *p* = .967; η^2 < .001
Embodiment	F(1,55) = 149,587; *p* < .001; η^2 = .448*	F(1,55) = .115; *p* = .736; η^2 = .002	F(1,55) = .486; *p* = .488; η^2 = .009	F(1,55) = .009; *p* = .927; η^2 = 3.667e −5	F(1,55) = 5.421; *p* = .024; η2 = .016*
Disembodiment	F(1,55) = 17.051; *p* < .001; η^2 = .0071*	F(1,55) = .127; *p* = .722; η^2 = .002	F(1,55) = 1.335; *p* = .253; η^2 = .024	F(1,55) = 1.848; *p* = .180; η^2 = .008	F(1,55) = .061; *p* = .806; η^2 < .001

+*p* < .10, **p* < .05.

Table 5 – Results of repeated measures ANOVAs with error variability as the measure of proprioceptive accuracy.

Measure of the RHI	Within-subject main effect (synchronous *vs* asynchronous condition)	Cardioceptive accuracy	Proprioceptive accuracy	Condition x cardioceptive accuracy interaction	Condition x proprioceptive accuracy interaction
Proprioceptive drift	F(1,57) = 17.634; *p* = .165; η^2 = .004	F(1,57) = 2.365e −7; *p* = 1.000; η^2 < .001	F(1,57) = .178; *p* = .674; η^2 = .003	F(1,57) = .002; *p* = .969; η^2 < .001	F(1,57) = 1.277; *p* = .263; η^2 = .003
Embodiment	F(1,55) = 137.770; *p* < .001; η2 = .448*	F(1,55) = .002; *p* = .961; η2 <.001	F(1,55) = 3.374; *p* = .072; η2 = .058^{+}	F(1,55) = .116; *p* = .735; η2 <.001	F(1,55) = .737; *p* = .394; η2 = .002
Disembodiment	F(1,55) = 18.189; *p* < .001; η2 = .070*	F(1,55) = .069; *p* = .795; η2 = .001	F(1,55) = 3.674; *p* = .060; η2 = .063^{+}	F(1,55) = 2.429; *p* = .125; η2 = .009	F(1,55) = 4.608; *p* = .036; η2 = .018*

+*p* < .10, **p* < .05.

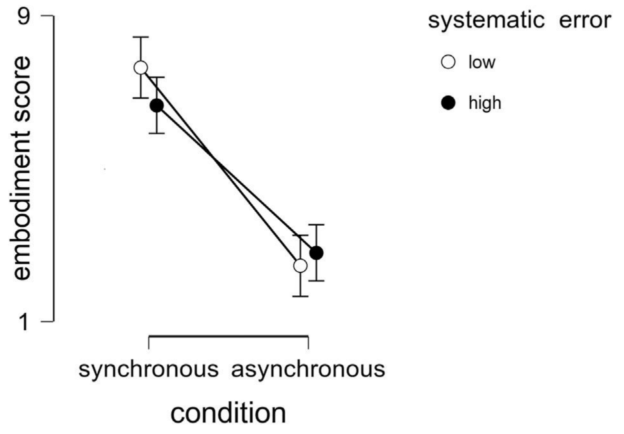

Fig. 4 – Visualization of the interaction between systematic error (using a binary form) and felt embodiment (error bars indicate 95% confidence intervals).

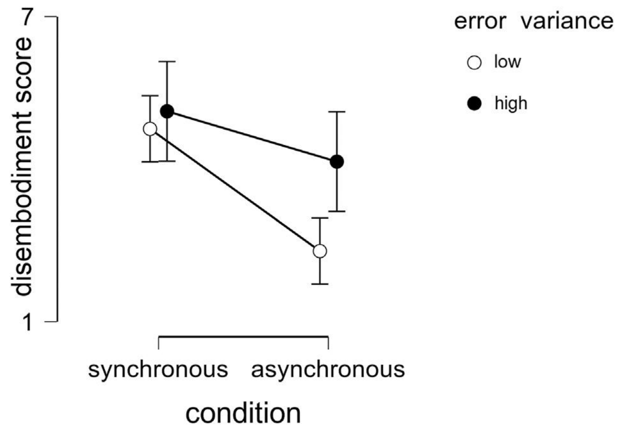

Fig. 5 – Visualization of the interaction between error variability (using a binary form) and felt disownership (error bars indicate 95% confidence intervals).

et al., 2014), and it is likely that the passive version is the more relevant in this case, as participants can not conduct movements during the induction of the RHI. Another possible explanation is that their setting to measure RHI was also different from ours, as they applied a subliminal and displacement procedure.

Different indicators of proprioceptive accuracy (systematic error and error variability) showed different relationship with the RHI. Error variability, indicating the unreliability of elbow joint position judgements (Boisgontier et al., 2012; Goble et al., 2012), had a weak main effect on felt embodiment and disembodiment. Thus, those who process proprioceptive

Table 6 – Results of Bayesian repeated measures ANOVAs.

Measure of the RHI	Within-subject main effect (synchronous/asynchronous condition) *vs* null model	Cardioceptive accuracy versus null model including condition	Proprioceptive accuracy (systematic error) *vs* null model including condition and cardioceptive accuracy	Proprioceptive accuracy (variable error) *vs* null model including condition and cardioceptive accuracy
Proprioceptive drift	$BF_{10} = .474$	$BF_{10} = .416$	$BF_{10} = .531$	$BF_{10} = .610$
Embodiment	$BF_{10} = 4.216e+16$	$BF_{10} = .290$	$BF_{10} = .458$	$BF_{10} = 1.385$
Disembodiment	$BF_{10} = 182.147$	$BF_{10} = .294$	$BF_{10} = .689$	$BF_{10} = 1.709$

Note: BF_{10}:Probability of the alternative hypothesis compared to the null hypothesis.

information in a less reliable way appear more likely to experience a more vivid RHI, independently of the stimulation (synchronous or asynchronous). One possible explanation for this finding is based on the nature of multisensory integration. Probabilistic models of multisensory integration propose that when information from different sources becomes integrated, various modalities are considered with different weight in the calculation. For optimal integration, the weight the given modality gets is based on its relative reliability (Ernst & Banks, 2002). When judging hand-position, the central nervous system can combine visual and proprioceptive information very efficiently by taking their direction-dependent precision into account (van Beers et al., 1999, 2002). Feeling of body ownership relies on multisensory integration and Bayesian causal inference (Kilteni et al., 2015). In relation to the RHI, Samad et al. (2015) presented a computational account for the RHI, and proposed that it is based on two factors: the spatial consistency of proprioceptive and visual information, and the temporal consistency of visual and haptic information. Fang et al. (2019) showed electrophysiological evidence in macaques, while Chancel and Ehrsson (2020) showed behavioral data in human participants, which supports the Bayesian causal interference model of body ownership. With respect to proprioceptive information, there are two important predictions of the aforementioned models: the less precise proprioceptive signals are, and the closer the rubber hand to the real hand is, the higher the probability of the occurrence of the illusion or its strength should be (Motyka & Litwin, 2019). Assuming that variable error in the Joint Position Matching test signals the precision of proprioceptive information, the prediction is in accordance with our findings: for those individuals, who process proprioceptive information in a less reliable way (i.e., show a higher level of variable error), proprioceptive information (indicating that the real hand belongs to the person) gets relatively less weight compared to other stimuli (suggesting that the rubber hand belongs to them). In consequence, the illusion will be stronger. Assuming that the direction and magnitude of the systematic error in position judgements are signaling the central nervous system's tendency to make a distortion in a similar magnitude and direction while encoding hand position, this prediction is also in accordance with our findings: for those individuals, whose central nervous system encodes the position of their hand closer to the rubber hand will experience a stronger illusion.

The above discussed multisensory explanation for the main effect of error variance is further supported by the significant interaction between proprioceptive error variance and the disembodiment scores. The analysis of the interaction revealed that lower levels of variability in proprioceptive accuracy was found to be associated with lower levels of disembodiment of own hand during asynchronous stimulation, whereas no such association was observed in the synchronous stroking condition (Fig. 5.). This finding is consistent with the Bayesian causal inference (BCI) model of body representation (Fang et al., 2019; Samad et al., 2015), which takes into account that multisensory integration is beneficial only if the different sensory cues have a common origin, therefore it assumes that the statistical-computational features of cue combination depends on the inferred probability of that the sensory stimuli originate from the same source. Evidence of how neural processes implement causal inference during the RHI was recently shown by Fang et al. (2019) who collected both behavioral and electrophysiological data from experiments in monkeys. As their analysis suggests, the probability that visual and proprioceptive stimuli share a common source influences two characteristic features of cue combination: (1) the extent to which sensory signals are fused corresponding to the computational rules of optimal integration, and (2) the extent to which sensory signals are segregated resulting in the separate unisensory processing of stimuli (see also: Ehrsson & Chancel, 2019). It follows that when the likelihood of the common cause is low, the segregation of visual and proprioceptive information dominates the statistical characteristics of cue combination, and not optimal integration (or forced fusion, as it was termed by Fang et al., 2019) - consequently, the representation of own hand is determined dominantly by proprioceptive information. The BCI model elaborated by Fang and colleague predicts that sensory uncertainty modulates the dynamics between the fusion and the segregation of signals (see also: Ehrsson & Chancel, 2019). Another important prediction of the model is that when the estimated probability of the common source is low, proprioception gets more weight in the dynamics mentioned above than vison, in contrast to when the integration of proprioceptive and visual information dominates the neural processes underlying the sense of hand ownership. The interaction between proprioceptive error variance and disembodiment confirms these predictions by showing that proprioceptive uncertainty had a greater impact on the RHI in the asynchronous condition (when the inferred likelihood of common cause is lower) than during synchronous stroking. Even though the interaction was significant only with respect to disembodiment ratings, it is important to emphasize that the correlational analysis of our data revealed the very same pattern of associations between embodiment and proprioceptive error variability scores as was discussed above in relation to disembodiment scores, when comparing synchronous and asynchronous conditions (see Table 2 and Fig. 4.).

Systematic error, indicating systematic distortion (towards the center of the body) in elbow joint position judgements (Boisgontier et al., 2012; Goble et al., 2012) had no main effect on embodiment and disembodiment ratings. However, based on the interaction between condition and systematic error, we can conclude that those whose perception of the hand is more biased towards their body experienced a comparatively stronger embodiment in the synchronous condition (Fig. 4.). Since the rubber hand was positioned toward the center of the body relative to the real hand in our experimental setting, systematic distortion towards the body in fact meant a bias towards the rubber hand. In this sense, this result is in accordance with studies showing that the closer the real and the rubber hands are, the stronger the illusion is (Kalckert & Ehrsson, 2014; Lloyd, 2007; Mirams et al., 2017; Preston, 2013). In our case not the real, but the felt position was closer to the rubber hand. However, we detected this effect only for the embodiment score in synchronous condition.

In this study, contrary to our hypothesis, we did not find a significant association between cardioceptive accuracy and the strength of the RHI. In fact, Bayesian analysis revealed positive evidence in favor of the null hypothesis (i.e., the lack of association). There is no agreement in the literature about the role of cardioceptive accuracy in the development of the RHI. Our results do not support the conclusions of previous studies that reported positive (Suzuki et al., 2013) or negative (Tsakiris et al., 2011) relationships between cardioceptive accuracy and the strength of the illusion. Our finding is rather in accordance with that of Crucianelli et al. (2018) namely, that cardioceptive accuracy is not associated with the vividness of the RHI. Cardioceptive accuracy is often considered generalizable to other interoceptive modalities and used as a measure of general interoceptive ability, however empirical findings do not support this approach (Ferentzi et al., 2018, 2017; Garfinkel et al., 2017). Thus, it seems more plausible that more localized interoceptive modalities, such as thermosensation and proprioception with respect to the hand, are primarily involved in the RHI. The present findings support this idea. It is also important to note that whereas the Crucianelli et al. (2018) study and the present study used the mental heartbeat tracking task, a forced-choice task was applied by Suzuki et al. (2013).

4.1. Limitations

One limitation of our study is that we did not find significant difference in proprioceptive drift between asynchronous and synchronous position. Other studies are quite consistent that participants feel the position of their stimulated hand more closely to the rubber hand in the synchronous condition than in the asynchronous (e.g., Botvinick & Cohen, 1998; Tsakiris et al., 2011). One possible explanation for the lack of proprioceptive drift is that we used a rather unusual experimental setting. In most of the studies, the rubber hand is parallel with the real hand which was not the case in our setting (e.g., Botvinick & Cohen, 1998; Tsakiris et al., 2011). The sharp difference in the subjective judgements between the two conditions showed that the illusion was evoked. Abdulkarim and Ehrsson (2016) also showed that proprioceptive drift is not a necessary factor in the development of the subjective changes in body ownership in the RHI.

In our experimental arrangement, the only difference in the position of the real and the rubber hand was in the angle of the elbow joint. This means that every other joint angle (most importantly the position of the shoulder), was consistent with the position of both the real and the rubber hand. Since proprioceptive accuracy scores measured in different joints are not necessarily related (Han et al., 2013), our findings are limited to the elbow joint only. Another notable point should be made concerning the measurement of cardioceptive accuracy. There are scholars who use the Whitehead-paradigm (Whitehead et al., 1977) along with the RHI, arguing that it involves the comparison of interoceptive and exteroceptive information, so it requires multisensory integration (Suzuki et al., 2013). Processes of multisensory integration, however, occur at a non-conscious level in the case of RHI, while the Whitehead-paradigm requires conscious multitasking. The Schandry task does not have this limitation. On the other hand, the validity of the Schandry task was questioned recently based on the argument that it is influenced by factors that are not inherent part of interoception (Corneille et al., 2020; Desmedt et al., 2018; Ring & Brener, 2018; Zamariola et al., 2018; Zimprich et al., 2020).

4.2. Future directions

These findings are of relevance not only for basic research on the phenomenon of the RHI but also for better understanding clinical phenomena that have been associated with disturbances in interoception and body representation such as chronic somatic symptom distress which has been found to be associated with alterations in the RHI (Miles et al., 2011). In this regard, a lower strength of the RHI as found in people with higher levels of chronic somatic symptoms and somatoform dissociation (Miles et al., 2011) may suggest an overreliance on proprioceptive information processing as part of chronic symptom perceptions. In accordance with the aforementioned study, a clinical group of somatoform patients also reported a less strong illusion than healthy control (Perepelkina et al., 2019). The cause of the lower level illusion is attributed to a decreased reliance on the current sensory input in these studies (Miles et al., 2011; Perepelkina et al., 2019). But our study's conclusion, namely that better proprioceptive accuracy is associated with a less strong illusion, and the results of Scholz et al. (2001), who found that somatoform patients showed better proprioceptive acuity, together may suggest an overreliance on proprioceptive information processing as part of chronic symptom perceptions. Further studies preferably in patients suffering from relevant clinical conditions are needed to directly test this hypothesis.

4.3. Conclusion

In this empirical study, we investigated the association between the RHI and cardioceptive accuracy and proprioceptive accuracy, respectively. We revealed that less consistent judgement and the degree of distortion towards the rubber hand in proprioception increased subjective aspects of the illusion. However, cardioceptive accuracy was not associated with it. These findings have important theoretical relevance for different models of multisensory integration and body ownership, and may have important consequences for clinical practice too.

Author contributions

Áron Horváth: Conceptualization, Methodology, Project administration, Writing: original draft; **Eszter Ferentzi**: Conceptualization, Methodology, Writing - original draft; **Tamás Bogdány**: Data curation, Investigation; **Tibor Szolcsányi**: Methodology, Writing - review & editing; **Michael Witthöft**: Conceptualization, Writing - review & editing; **Ferenc Köteles**: Conceptualization, Methodology, Supervision, Writing: original draft.

Open practices

The study in this article earned an Open Data badge for transparent practices.

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Supplementary data

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