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With hand on heart: A cardiac Rubber Hand Illusion

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ABSTRACT

Body illusions such as the Rubber Hand Illusion (RHI) have highlighted how multisensory integration underpins the sense of one's own body. Much of this research has focused on senses arising from outside the body (e.g. vision and touch), but sensations from within the body may also play a role. In a pre-registered study, participants completed a cardiac variation of the RHI, where taps to the finger occurred in or out of time with the heartbeat. We replicated the RHI effect, showing that synchronous but not asynchronous taps to the real and rubber hand increased sensations of embodiment over the rubber hand and caused a shift in the perceived hand location. However, there were no significant influences of cardiac timing on embodiment, nor did it interact with visuo-tactile synchrony. An exploratory analysis found a three-way interaction between synchrony, cardiac timing and interoceptive accuracy as measured by a heartbeat counting task, such that greater interoceptive accuracy was associated with lower embodiment ratings in the systole condition compared to diastole, but only during synchronous stimulation. Although our novel methodology successfully replicated the RHI, our findings suggest that the cooccurence of vision and touch with cardiac signals may make little contribution to the sense of one's body.

1. Introduction

As I sit at my desk there is a clear sense that there is a dividing line between my fingers and the keyboard, and between my body and my chair. That feeling of ownership over the body, that each of my individual body parts belong uniquely and certainly to me, is known as the sense of body ownership, and is thought to be a critical component of the sense of self (Gallagher, 2000). Though normally intact, body ownership illusions refer to a set of experimental techniques for temporarily disrupting the sense of one's own body and have revealed much about what contributes to a stable sense of body ownership (Kilteni, Maselli, Kording, & Slater, 2015). The most widely studied of these techniques is the Rubber Hand Illusion (RHI, Botvinick & Cohen, 1998). In the classic RHI, brushstrokes delivered simultaneously to a hidden real hand and a visible rubber hand cause an extension of the sense of the body to incorporate the rubber hand. Participants report both self-reported feelings of ownership over the fake hand (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008) and a shift in the perceived location of the real hand towards the rubber hand, a phenomenon known as proprioceptive drift (Tsakiris & Haggard, 2005). Importantly, if the touch to the real and rubber hands are separated in time, the effect is weakened and usually disappears entirely. Therefore, the altered sense of the body in the RHI arises from the multisensory pairing of the touch to the real hand, and the sight of a simultaneous touch to the rubber hand, highlighting how multisensory integration contributes to the sense of the body (Costantini et al., 2016; Ehrsson, 2020; Finotti, Garofalo, Costantini, & Proffitt, 2023).

According to the predictive coding framework, the experience of ownership in the RHI arises because our sense of the body is a 'best guess' at making sense of incoming sensory signals and prior expectations about the body (Apps & Tsakiris, 2014), most likely through Bayesian computational principles (Chancel, Ehrsson, & Ma, 2022). During the RHI, one feels a touch on their own hidden hand, but sees a similar tactile event happening to a realistic rubber hand, resulting in a conflict (prediction error), which is resolved by updating the model of one's own body to include the rubber hand. Externally arising sensations, such as vision and touch, are one source of sensory information about the body, but the sense of the body is also likely to be driven by sensations arising from within the body itself (Seth, 2013; Seth & Tsakiris, 2018; Tsakiris, 2010).

Interoception is the term given to the sensing, integration and interpreting of sensory information generated from within the body

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(Khalsa et al., 2018). The study of interoception covers multiple modalities, including the sensing of the cardiac, respiratory and gastric systems, and multiple levels of measurement, from the neural representation of afferent signals from the body to individual ability in perceiving internally-arising sensations (Suksasilp & Garfinkel, 2022). Two main strands of empirical research have explored the influence of interoceptive sensations on the sense of body ownership, the majority of which has focused on cardioception. First, several studies have investigated how body ownership illusions are influenced by the natural internal rhythms of the body, such as the rhythm of the heart (Aspell et al., 2013; Suzuki, Garfinkel, Critchley, & Seth, 2013). Second, others have investigated how susceptibility to body ownership illusions relate to individual differences in ability to detect interoceptive sensations (e.g. Tsakiris, Jiménez, & Costantini, 2011).

The cardiac cycle can be divided into two phases. The systolic phase refers to the ventricular ejection period, when the heart contracts and stretch-sensitive arterial baroreceptors convey information about the heartbeat to the brainstem via afferent pathways, whereas the diastolic phase refers to the period between heartbeats when heart-brain signalling is quiescent. The steady rhythm of the heart allows researchers to time-lock stimuli to appear at systole or diastole, and such studies have revealed that the cardiac cycle can influence perception. For example, pain thresholds are higher in response to shocks delivered at systole compared to diastole (Wilkinson, McIntyre, & Edwards, 2013), and fearful faces are more quickly identified and rated as more intense when presented at systole (Garfinkel et al., 2014). Recent research has also demonstrated coupling of the heart and perception even when stimuli are not time-locked to the cardiac cycle. In a visual search task, eye movements occurred more frequently at systole, whereas fixations and saccades were more likely to occur at diastole or the later stages of the cardiac cycle (Galvez-Pol, McConnell, & Kilner, 2020). Furthermore, touches voluntarily initiated at systole were prolonged during a discriminative touch task (Galvez-Pol, Virdee, Villacampa, & Kilner, 2022).

The natural fluctuations of the cardiac cycle can also influence body ownership. One study used augmented reality to create a virtual projection of the participant's own hand, and found greater feelings of ownership over the virtual hand if it visually pulsed at systole compared to diastole (Suzuki et al., 2013). Another study found a similar effect with visual pulses applied to a visual overlay of the full body, with systolic pulses resulting in greater ownership over the virtual body (Aspell et al., 2013). Interestingly, this study found that visual pulses timed at systole led to greater errors on a cross-modal task requiring participants to judge the location of tactile sensations while ignoring distracting visual information – suggesting that cardio-visual integration can influence visuo-tactile processing. Similar effects have been found with non-cardiac interoceptive rhythms. Embodiment over a virtual mannequin viewed from a first-person perspective was enhanced when the mannequin's chest rose and fell in synchrony with the participant's breathing patterns (Monti, Porciello, Tieri, & Aglioti, 2020). Cardiac timing influences on body perception also extends beyond body ownership to other aspects of self-awareness. Morphed faces, made to be ambiguous by combining one's own face with other peoples faces, were more likely to be identified as oneself after viewing a face flashing at systole (Sel, Azevedo, & Tsakiris, 2017) and were more quickly identified as oneself when presented at systole compared to diastole (Ambrosini, Finotti, Azevedo, Tsakiris, & Ferri, 2019). By pairing cardiac and visual signals, these studies suggest that the sense of body ownership can be influenced by fluctuations in the rhythm of the heart, however studies to date have not assessed how cardiac, visual and tactile signals conjointly influence the sense of the body. It is therefore unclear whether timing visuo-tactile sensations to coincide with body-brain signalling would influence the sense of the body, though the current literature suggests that systolic timing would enhance embodiment.

A second strand of research has investigated how the RHI is influenced by individual differences in ability to detect interoceptive sensations, termed Interoceptive Accuracy (IAcc). The most common of these involve the Heartbeat Counting task, where participants count their heartbeats during set periods of time (Schandry, 1981), and the Heartbeat Discrimination task (Katkin, Blascovich, & Goldband, 1981; Whitehead, Drescher, Heiman, & Blackwell, 1977), where participants must decide whether sequences of tones are played in- or out-of-time with their heartbeat. An early study found that individuals with lower IAcc was associated with a larger proprioceptive drift and elevated feelings of ownership over the rubber hand in the RHI (Tsakiris et al., 2011). These findings suggest that interoception serves to stabilise the sense of the body, and can be protective against the classic RHI. Furthermore, Suzuki et al. (2013) found that heightened IAcc, assessed with the Heartbeat Discrimination task, was associated with an increased effect of cardio-visual pairing on body ownership over a virtual hand, suggesting that IAcc might facilitate Cardiac Timing effects in the RHI.

The evidence base concerning the relationship between IAcc and the RHI is mixed, with some studies reporting no association (Bekrater-Bodmann, Azevedo, Ainley, & Tsakiris, 2020; Crucianelli, Krahé, Jenkinson, & Fotopoulou, 2018; Horváth et al., 2020). In recent years, the assessment of IAcc has been the topic of some debate (see Ainley, Tsakiris, Pollatos, Schulz, & Herbert, 2020; Corneille, Desmedt, Zamariola, Luminet, & Maurage, 2020; Zamariola, Maurage, Luminet, & Corneille, 2018; Zimprich, Nusser, & Pollatos, 2020). For instance, the Heartbeat Counting task has been criticised for being influenced by non-perceptual processes such as prior knowledge of one's heart rate. Researchers advise either using adapted instructions to ensure participants do not make guesses about their number of heartbeats (Desmedt, Luminet, & Corneille, 2018) or using more robust psychophysical methods such as the Method of Constant Stimuli to infer IAcc (Brener & Ring, 2016). To date, no study has investigated how IAcc assessed with the Method of Constant Stimuli relates to susceptibility to the RHI.

In this study, we aimed to understand the contribution of cardioception to the sense of the body in the RHI. Firstly, we performed the RHI with a novel setup with tappers programmed to deliver touch to a real and rubber hand either in or out of synchrony, and at either the systolic or diastolic phase of the heartbeat. Secondly, participants completed two tasks assessing Interoceptive Accuracy: the Method of Constant Stimuli (Brener, Liu, & Ring, 1993) and the Heartbeat Counting task with adapted instructions (Desmedt et al., 2018) to assess relationships between susceptibility to the RHI and IAcc.

We pre-registered the following hypotheses, method and analysis plan on the Open Science Framework, prior to the onset of data collection (https://osf.io/mbgj6).

2. Hypotheses

Hypothesis 1. There will be higher proprioceptive drift and embodiment ratings when touch delivered to the real and the rubber hand is synchronous, rather than asynchronous.

Hypothesis 2. There will be higher proprioceptive drift and embodiment ratings when touch is delivered to the real hand at the systolic phase of the heart (in time with the heartbeat) compared to the diastolic phase of the heart (between heartbeats).

Hypothesis 3. There will be a significant interaction between Visuo-Tactile Synchrony and Cardiac Timing, such that synchronous-systolic touch will produce higher proprioceptive drift and embodiment ratings than all other conditions.

Hypothesis 4. Higher levels of interoceptive ability will be associated with a smaller effect of Visuo-Tactile Synchrony on the RHI.

Hypothesis 5. Higher levels of interoceptive ability will be associated with a larger effect of Cardiac Timing on the RHI.

3. Methods

3.1. Participants

Ethical approval for the research study was obtained from the University Research Ethics Committee at Royal Holloway, University of London. 42 participants were recruited to take part, and participants could only take part if they were right-handed and had not previously taken part in a rubber hand illusion experiment.

Sample size was determined following a power analysis. The study was powered to test our main effect of interest, specifically the effect of cardiac timing on proprioceptive drift in the rubber hand illusion. A previous study, (Suzuki et al., 2013), timed the visual flashing of a virtual hand with the heartbeat in 21 participants and found a significant difference in proprioceptive drift between systole and diastole conditions, $t(20) = 2.7, p = 0.014$, which suggests an effect size of $d = 0.59$ following the calculation $d = \frac{t}{\sqrt{N}}$ (Lakens, 2013). It should be noted the difference between the cited study and the present study is that cardiac timing will be linked to visuo-tactile stimuli rather than just visual stimuli, which may influence the size of the effect. Assuming a more conservative estimate of effect size of $d = 0.5$, an a priori difference between two dependent means power calculation in GPower software (Faul, Erdfelder, Lang, & Buchner, 2007), suggested a sample size of 36 to achieve 90% power.

3.2. Materials

The setup for the Rubber Hand Illusion used a custom-made rectangular box (Fig. 1). The participants rested their left hand inside the box at a fixed position 18 cm to the left of the rubber hand. A two-way mirror positioned above the hands enabled participants to view the rubber hand, but not their real hand, when a lamp inside the box was switched on at the start of each trial. The rest of the body was covered with a cape, and the right hand was placed on the lap. Two solenoid tappers with an attached brush within the box delivered touch to each hand. The tappers were driven by an Arduino Uno motherboard and the timing of each touch was controlled with custom scripts written in Arduino and MATLAB software (Mathworks, Natick, MA). The tappers were positioned to deliver touch to the index fingers of the real and fake hands between the knuckle and first joint of the index finger (Zbinden & Ortiz-Catalan, 2021). Noise-cancelling headphones played white noise throughout the task to ensure that sounds generated by the tappers could not be heard, as auditory cues can influence the RHI (Radziun & Ehrsson, 2018).

Heart rate was recorded throughout the experiment with Electrocardiography (ECG), using three disposable ECG electrodes. An electrode was positioned underneath each collarbone and a third on the left side of the lower back. The ECG signal was recorded with a Powerlab 8/35 (Powerlab, ADInstruments, http://www.adinstruments.com/) using Labchart 8 Pro software. The sampling rate was 1000 Hz and a hardware band-pass filter (Bio Amp 132) between 0.3 and 1000 Hz was applied. A hardware-based function (fast output response) identified each R-wave with a <1 ms delay to enable time-locking of stimuli to different phases of the cardiac cycle.

The instructions provided to participants for each task are provided in the Supplementary Materials, and the MATLAB scripts are provided in the Open Science Framework repository for this study (https://osf.io/mbgj6).

3.3. Design

3.3.1. Rubber Hand Illusion

In the rubber hand illusion, motorised tappers delivered a series of single taps with a brush to the index finger of a visible rubber hand and the hidden real hand (Fig. 1). The timing of the touches on each trial were manipulated according to a 2 (Visuo-Tactile Synchrony: synchronous, asynchronous) x 2 (Cardiac Timing: systole, diastole) repeated measures design. In the synchronous conditions, both the real hand and the rubber hand were tapped simultaneously. In the asynchronous conditions, the rubber hand was tapped at a randomly jittered timepoint between 400–500 ms after the offset of the tapping to the real hand. A delay of 400–500 ms was chosen because this level of delay reduces RHI embodiment effects, (e.g. Shimada, Fukuda, & Hiraki, 2009). For both systole and diastole conditions, a LabChart built-in function identified each R-wave based on an individually tailored threshold. Once a heartbeat was identified, a hardware-based function (Fast Response Output) generated a digital output trigger with a <1 ms delay, allowing

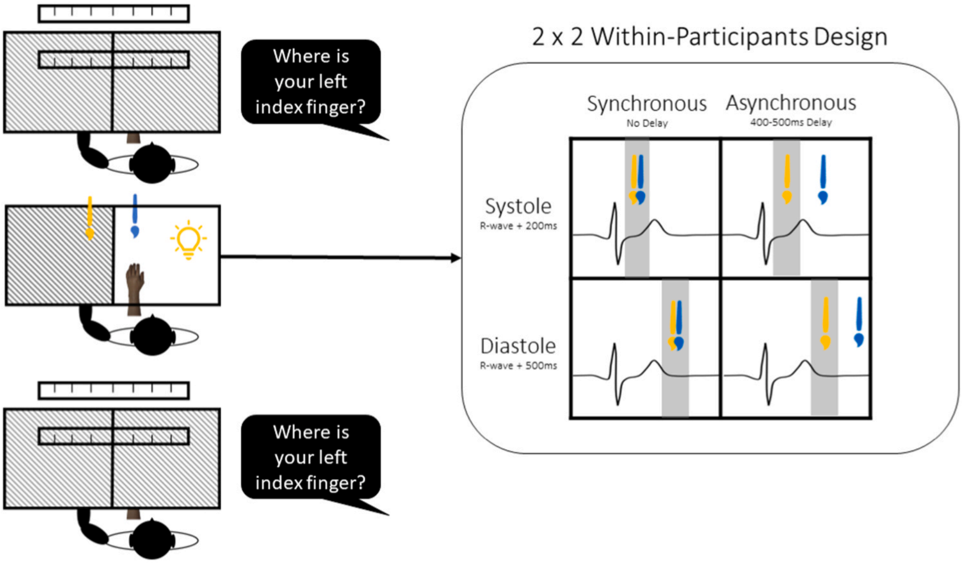

Fig. 1. Experimental method for the Cardiac Rubber Hand Illusion. For each trial, tapping occurred for 90 s and was delivered to the rubber and real hands according to a 2 (Cardiac Timing: systole, diastole) x 2 (Visuo-Tactile Synchrony: synchronous, asynchronous) within-participants design. Each tap was delivered relative to every second heartbeat. A light inside the box illuminated the rubber hand during the trial, but the real hand was hidden from view. Before and after each trial, participants indicated the location of their index finger on a ruler reflected on a two-way mirror and positioned at a random horizontal position.

for precise timing of the tactile stimulation. In systole conditions, each tap to the real hand was timed to coincide with the heartbeat (200 ms after the R-wave, during the cardiac ejection period). In diastole conditions, each tap to the real hand was timed to occur between heartbeats (500 ms after the R-wave). For each tap, tactile contact with the finger lasted for approximately 300 ms. A series of single taps were delivered over the course of 90 s on each trial. Rather than delivering a tap relative to every heartbeat, each tap was delivered relative to every second heartbeat (i.e. non-consecutive heartbeats) for both systole and diastole conditions, therefore frequency of tapping was tied to the participants heart rate. Taps were delivered relative to every second heartbeat to ensure taps were presented at a consistent rhythm. If they were delivered at every heartbeat, there was a possibility that the delay period could encompass a second heartbeat. This was particularly true of diastole trials which involved a delay of 500 ms between the R-wave and the tap. On these trials, a heart rate of 120BPM or greater (corresponding to an inter-beat interval of 500 ms), would result in a second heartbeat occurring during the delay period. This would cause a larger gap than intended between one tap and the next because the custom MATLAB script would 'miss' the heartbeat that happened during the delay period, and wait until another heartbeat occurred to deliver the next tap. To avoid this potential risk and to ensure taps were presented with a consistent rhythm, taps were presented relative to every second heartbeat. There were 8 trials, divided into two blocks where each combination of Visuo-Tactile Synchrony and Cardiac Timing was conducted in a random order.

The experience of body ownership was assessed behaviourally with a measure of proprioceptive drift. Before and after each trial, a ruler was positioned above the two-way mirror to appear at the same gaze depth as the rubber hand and at a random horizontal offset. Participants verbally stated the position of their real index finger on the ruler reflected in the mirror. Proprioceptive drift for each trial was calculated as the post-trial measure subtracted from the pre-trial measure, and expressed as a percentage of the true distance between the real and fake hands (18 cm, Riemer, Trojan, Beauchamp, & Fuchs, 2019).

Participants self-reported their experience of the illusion with questionnaire items adapted from statements loading on the "Embodiment" factor of a validated questionnaire commonly used with the Rubber Hand Illusion, (Longo et al., 2008). Two items representing "Ownership" ("It seemed like the rubber hand were my hand", "It seemed like I was looking directly at my own hand, rather than a rubber hand") and two items representing "Location" ("It seemed like the rubber hand was in the location where my hand was", "It seemed like my hand was in the location where the rubber hand was") were included, all of which loaded on an "Embodiment" factor. In addition, two control items were included, (Botvinick & Cohen, 1998, "It seemed like I had more than one left hand." "It seemed like my real hand were turning 'rubbery'"). The six statements were read in a random order by the experimenter after each trial, and participants verbally rated their agreement with each statement on a Likert scale from −3 (Strongly Disagree) to 3 (Strongly Agree). The embodiment score for each trial was calculated by averaging the rating for the embodiment items and subtracting the average rating on the control items. Internal reliability was good for the 4 embodiment items ($\alpha = 0.88$), and the two control items were significantly correlated, $r(314) = .45$, 95% CI $[35, .53]$, $t(312) = 8.82$, $p < .001$.

3.3.2. *Interoception tasks*

Prior to each interoception task, participants were warned not to feel for their pulse. Each task was implemented in Psychtoolbox-3 extension for MATLAB (Kleiner, Brainard, & Pelli, 2007).

3.3.2.1. Method of Constant Stimuli. The Method of Constant Stimuli procedure described by Brener et al. (1993) was adapted for use in this study. On each trial, participants were presented with a series of 5 auditory tones delivered at either 0 ms, 100 ms, 200 ms, 300 ms, 400 ms or 500 ms following the peak of the R wave, with 20 sequences at each level of delay. The 120 trials were divided into five blocks of 24 trials, with each delay time occurring 4 times in a random order within each block. After listening to each sequence of tones, participants judged if the tones were in or out of time with their heartbeat and rated their confidence in their judgement on a continuous scale from 0–100. The outcome measure of Interoceptive Accuracy represents precision in detecting heartbeats, and was calculated as the interquartile range (IQR) of the temporal distribution of "in-time" judgements (Brener et al., 1993). The cumulative proportions of "in-time" judgments were calculated for each level of delay (0 ms-500 ms) and data interpolated between these points (see Fig. 2A). The IQR of this distribution was calculated by subtracting the 1st percentile from the 3rd percentile. A smaller IQR is indicative of a steeper slope of this distribution, suggesting a more precise ability to detect heartbeats.

3.3.2.2. Heartbeat Counting. For the Heartbeat Counting task (Schandry, 1981), participants were asked to count their heartbeats during three randomly ordered time periods (25 s, 35 s, 45 s). After each time period, they stated how often they felt their heartbeat, and provided a confidence rating on a continuous scale from 0–100. Prior to the task, participants were given clear instructions to report how many heartbeats they explicitly felt during the time period, and to not guess their answer, in accordance with the adapted instructions of the Heartbeat Counting task suggested by Desmedt et al. (2018) to reduce the influence of non-interoceptive processes on the outcome measure. Interoceptive Accuracy was calculated by comparing reported and real heartbeats, with the following equation:

$$\frac{1}{3}\sum\left(1-\frac{|actualheartbeats-reportedheartbeats|}{actualheartbeats}\right)$$

3.3.2.3. Heart Rate Matching. A third measure of interoception, the Heart Rate Matching task (adapted from Palmer, Ainley, & Tsakiris, 2019) was also conducted, but will be analysed as part of a separate study. In the task, participants controlled the pace at which a visual cartoon heart was beating. Participant's were asked to match the pace of the beating heart on the screen with the pace of their own heartbeat.

3.4. *Procedure*

The study involved two sessions, no more than a week apart. The first session involved the rubber hand illusion and the second session involved the interoception tasks. In the second session, participants completed the Heartbeat Counting and the Heart Rate Matching tasks, the order of which was counterbalanced between-participants, with the Method of Constant Stimuli always completed last.

3.5. *Analysis*

All statistical analysis was conducted in R (R Core Team, 2022) and Rstudio (Rstudio Team, 2022), with the following packages: *lme4* (Bates, Mächler, Bolker, & Walker, 2015), *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2017), *papaja* (Aust & Barth, 2014/2022), *rbbt* (Dunnington, 2018/2023), *cowplot* (Wilke, 2020), *here* (Müller & Bryan, 2020), *flextable* (Gohel et al., 2023), *psych* (Revelle, 2023) and the *tidyverse* set of packages (Wickham et al., 2019).

Two linear mixed models were specified, with the outcome variables as proprioceptive drift and embodiment ratings. Each model included fixed effects of Visuo-Tactile Synchrony (synchronous, asynchronous) and Cardiac Timing (systole, diastole), as well as their two-way interaction. Additionally, IAcc scores derived from the Method of Constant Stimuli as the IQR of the cumulative proportion of 'in-time' judgements, were entered as an additional between-participants fixed effect, along with its interactions with Visuo-Tactile Synchrony and Cardiac Timing,

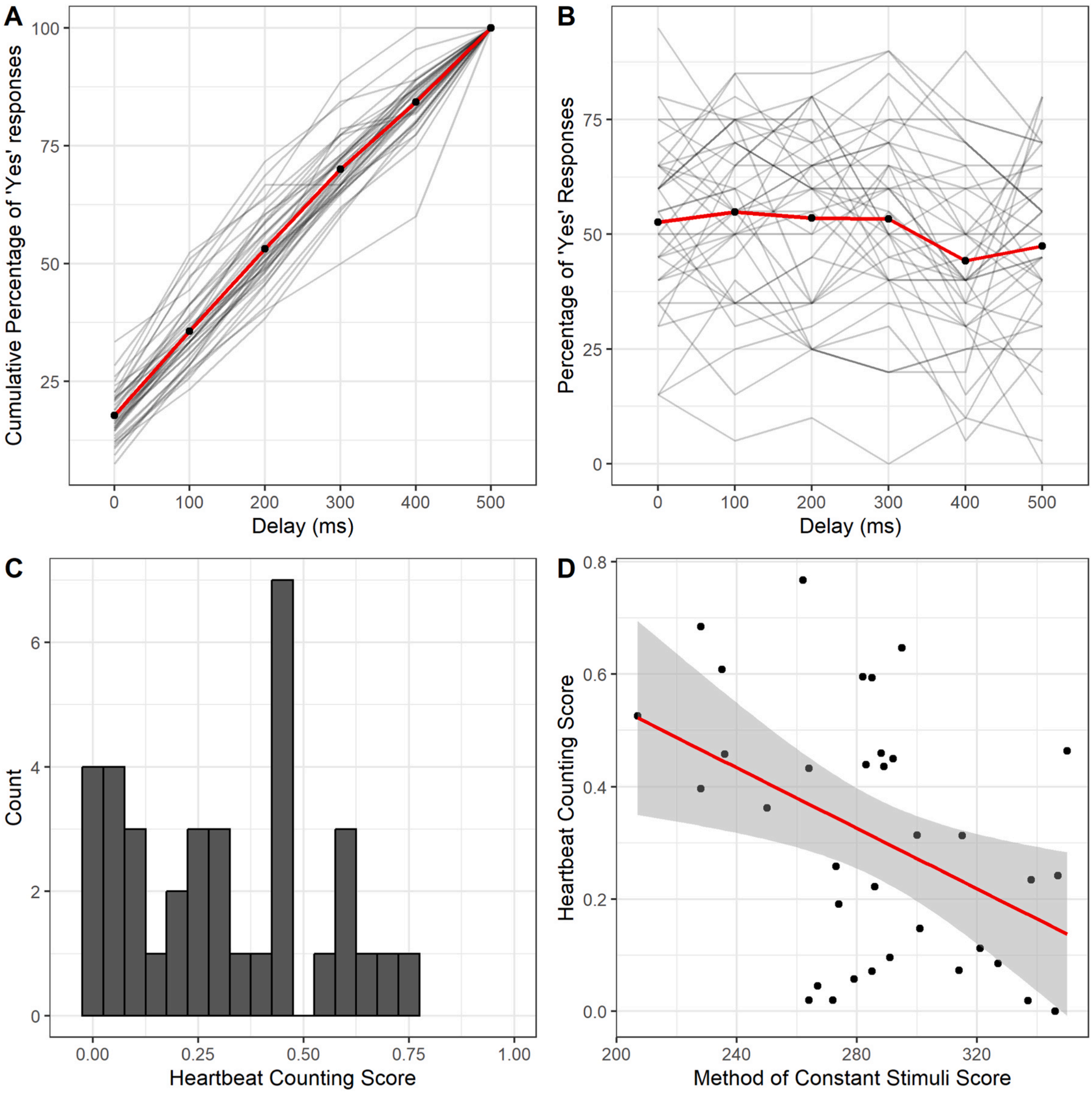

Fig. 2. Interoception Scores. A. Cumulative percentage distribution of simultaneous judgements at each level of delay on the Method of Constant Stimuli task. IQR of this distribution represents Interoceptive Accuracy, with a steeper slope (and therefore smaller IQR) indicating more precise ability to detect heartbeats. The red line indicates group means, grey lines indicate individual participant data. Data between points are interpolated. B. Average percentage of judgements that the light is simultaneous with the heartbeat on the Method of Constant Stimuli task, at each level of delay between the heartbeat and the auditory tone. The red line represents group average percentages, grey lines represent individual percentages. C. Histogram displaying distribution of scores on the Heartbeat Counting task, where higher scores indicate higher IAcc. D. Relationship between individual scores on the Method of Constant Stimuli task and the Heartbeat Counting task. The red line indicates the estimated regression line, and the shaded area indicates the standard error of this estimate. A significant negative correlation was observed, $r(35) = -.43$, 95% CI $[-.67, -.11]$, $t(33) = -2.75$, $p = .010$.

and the three-way interaction. IAcc scores were group mean-centred (i.e. the mean score was subtracted from each individual score) to improve interpretability of significant effects (Schielzeth, 2010) as recommended when adding between-participants predictors to linear mixed models (Brauer & Curtin, 2018). Significance of fixed-effects was determined with Satterthwaite's degrees of freedom method (Kuznetsova et al., 2017).

Each model included a by-subjects random intercept and random slopes for the effects of Visuo-Tactile Synchrony, Cardiac Timing and their interaction. The random effects structure was tested with a model selection procedure, taking a maximal approach (Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017). A maximal model was first specified, with all random intercepts and slopes included, which was then compared to progressively simpler models with a Likelihood Ratio Test. If the fit of the simpler model significantly differed from the more complex model according to a Likelihood Ratio Test, the more complex model was taken as the final model and the model selection procedure ended.

Exploratory analyses were conducted using the same models, but with the Interoceptive Accuracy score derived from the Heartbeat Counting task. Since heart rate determined how many taps an individual received in each trial, the potentially confounding influence of the number of taps on the RHI was also explored. Firstly, we specified a linear mixed model with number of taps as the outcome variable and Visuo-Tactile Synchrony and Cardiac timing as fixed effects, to ensure that the number of taps delivered was similar across conditions. Secondly, we conducted a linear mixed model with average number of taps as a mean-centred covariate to our primary models, to determine if the number of taps received could influence either embodiment ratings or proprioceptive drift.

4. Results

4.1. Sample

Of the 42 participants recruited, data from one participant was excluded due to equipment failure across all trials of the RHI, and one participant did not attend the second session involving the interoception tasks. Additionally, five participants had equipment failure in 1 or 2 of their trials of the RHI, and one participant experienced a coughing fit during their final trial. These trials are excluded, but the remaining data from these participants are included in the following analysis. The sample primarily consisted of young participants who identified as female, with an average age of 19.50 (SD = 2.32), and 92.50% identifying as female.

4.2. Interoceptive Accuracy

As Interoceptive Accuracy is included as a covariate in the linear mixed model analysis of the rubber hand illusion, we will first present descriptive statistics from the interoception tasks.

Average IAcc derived from the Method of Constant Stimuli, the IQR of the cumulative frequency distribution of synchronous judgements (Fig. 1A), was 286.57 ms (SD = 34.95 ms), with a range of 207–350 ms. Chi-squared tests of each individual's distribution of simultaneous judgements at each level of delay (Fig. 1B) revealed that only 4/40 participants (10%) demonstrated performance significantly different from random responding, indicating that the majority of participants were not able to detect their heartbeat..

Average IAcc derived from the Heartbeat Counting task (Fig. 1C) was 0.31 (SD = 0.22).

IAcc from both the Method of Constant Stimuli and the Heartbeat Counting tasks significantly negatively correlated, $r(35) = -.43$, 95% CI $[-.67, -.11]$, $t(33) = -2.75$, $p = .010$, such that a higher Heartbeat Counting score was associated with a smaller and more precise IQR on the Method of Constant Stimuli task (see Fig. 1D), suggesting that both tasks measured a similar construct.

4.3. Rubber Hand Illusion

4.3.1. Proprioceptive drift

The model selection procedure determined that the 'maximal model' had the most parsimonious random effects structure. As hypothesised, there was a significant effect of Visuo-Tactile Synchrony on proprioceptive drift, $\widehat{\beta} = 16.10$, 95% CI $[8.50, 23.70]$, $t(38) = 4.15$, $p < .001$, such that synchronous touch led to greater shift in the perceived location of the hand towards the rubber hand, compared to asynchronous touch (Fig. 2A).

In contrast to our hypotheses, there was no significant effect of Cardiac Timing on proprioceptive drift $\widehat{\beta} = 0.00$, 95% CI $[-6.31, 6.31]$, $t(37) = 0.00$, $p = .99$, nor was there a significant interaction between Visuo-Tactile Synchrony and Cardiac Timing, $\widehat{\beta} = -1.22$, 95% CI $[-14.61, 12.17]$, $t(46) = -0.18$, $p = .86$.

Additionally, there was no significant relationship between IAcc and proprioceptive drift, IAcc did not significantly interact with either Visuo-Tactile Synchrony, $\widehat{\beta} = 0.05$, 95% CI $[-0.17, 0.27]$, $t(38) = 0.47$, $p = .64$ or Cardiac Timing, $\widehat{\beta} = 0.00$, 95% CI $[-0.18, 0.18]$, $t(37) = 0.01$, $p = .99$, nor was there a significant 3-way interaction, $\widehat{\beta} = 0.04$, 95% CI $[-0.35, 0.43]$, $t(45) = 0.19$, $p = .85$.

4.3.2. Embodiment ratings

Model selection determined that the most parsimonious model included a random effects structure with only a by-subjects random intercept and a random slope for Visuo-Tactile Synchrony. Similarly to

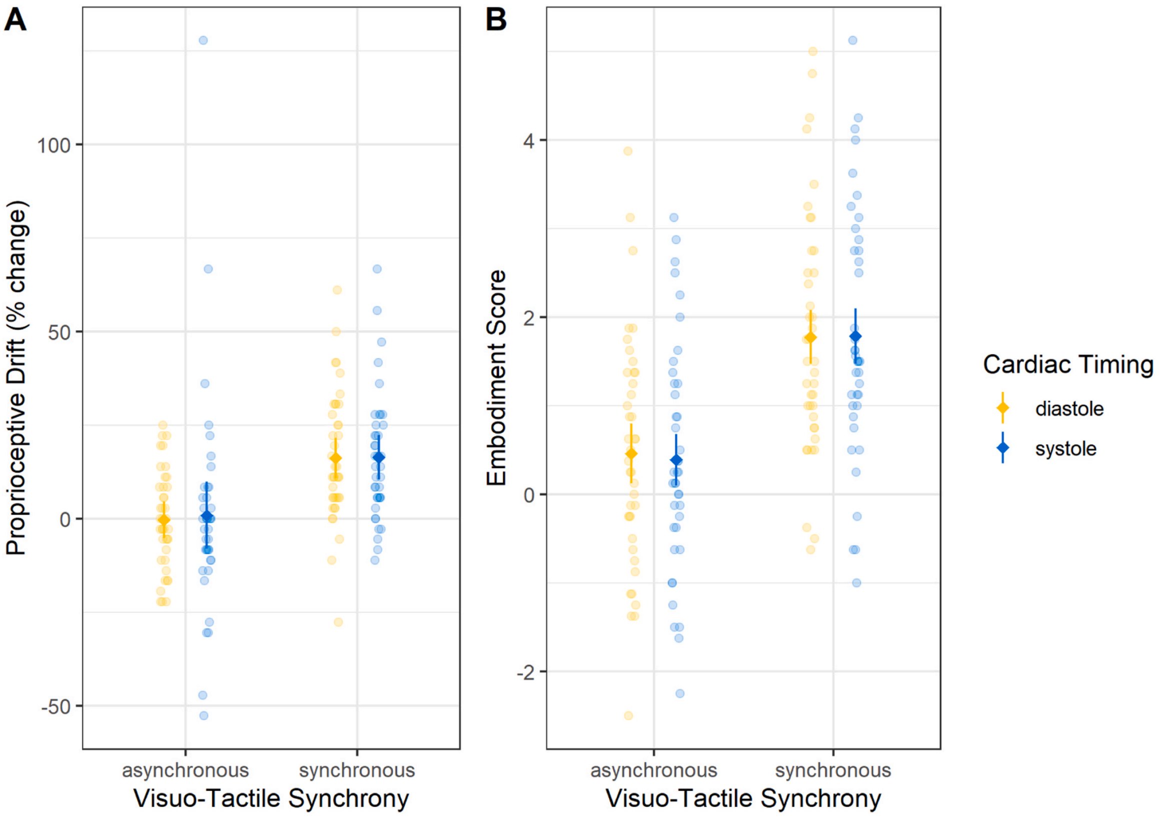

Fig. 3. A. Proprioceptive drift is calculated as the pre-trial subtracted from the post-trial perceived location of the real hand, and expressed as a % of the true distance between the real and rubber hands (18 cm). B. Embodiment score is calculated as the pooled average ratings from the 'Control' statements subtracted from the pooled average 'Embodiment' ratings. The diamond in each plot represents the mean score, with the ranges representing 95% Confidence Intervals.

proprioceptive drift, we found a significant effect of Visuo-Tactile Synchrony on embodiment ratings (see Fig. 2B), $\widehat{\beta} = 1.33$, 95% CI $[0.91, 1.75]$, $t(37) = 6.24, p < .001$, but there was no significant effect of Cardiac Timing, $\widehat{\beta} = -0.05$, 95% CI $[-0.29, 0.20]$, $t(218) = -0.37, p = .72$, nor was there a significant interaction between Synchrony and Cardiac Timing, $\widehat{\beta} = 0.17$, 95% CI $[-0.32, 0.65]$, $t(218) = 0.67, p = .50$.

Additionally, there was a non-significant relationship between IAcc and embodiment ratings, $\widehat{\beta} = 0.00$, 95% CI $[-0.01, 0.01]$, $t(37) = 0.53$, $p = .59$, nor were there significant two-way interactions between IAcc and Visuo-Tactile Synchrony, $\widehat{\beta} = -0.01$, 95% CI $[-0.02, 0.01]$, $t(37) = -1.10, p = .28$ or between IAcc and Cardiac Timing, $\widehat{\beta} = 0.00$, 95% CI $[0.00, 0.01]$, $t(218) = 1.24$, $p = .22$. There was also no significant three-way interaction, $\widehat{\beta} = 0.01$, 95% CI $[-0.01, 0.02]$, $t(218) = 0.99, p = .32$.

4.4. Exploratory analysis

4.4.1. Heartbeat Counting

We conducted the same analysis using the Heartbeat Counting score as the IAcc measure, instead of the IQR of the cumulative frequency distribution of the Method of Constant Stimuli.

All findings were similar, except for a significant three-way interaction between Heartbeat Counting score, Visuo-Tactile Synchrony and Cardiac Timing for embodiment ratings, $\widehat{\beta} = -2.45$, 95% CI $[-4.67, -0.23]$, $t(212) = -2.17, p = .031$.

To examine the three-way interaction, we correlated Heartbeat Counting score with the difference scores between the different conditions. In other words, we calculated the difference in embodiment ratings in response to a) synchronous touches at systole versus diastole conditions, b) asynchronous touches at systole versus diastole conditions, c) systole touches at synchronous versus asynchronous conditions and d) diastole touches at synchronous versus asynchronous conditions. The only significant correlation (Fig. 4) was a negative correlation between Heartbeat Counting score and the effect of Cardiac Timing in the synchronous condition (i.e. synchronous touches at systole versus diastole), $r(36) = -.39$, 95% CI $[-.64, -.07]$, $t(34) = -2.48$, $p = .018$. This negative correlation suggests that individuals with greater interoceptive ability, as measured by the Heartbeat Counting task, were more likely to provide greater embodiment ratings in response to diastolic presentation of touch vs systolic presentation of touch, but only when touch was synchronized between the real and rubber hands. .

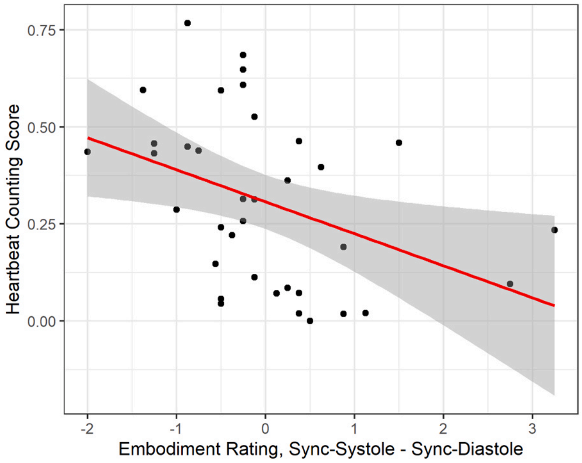

Fig. 4. The x-axis captures the effect of cardiac timing on embodiment ratings when touch was synchronized between the real and the rubber hand. Scores less than 0 indicate greater embodiment ratings during diastole trials, scores greater than 0 indicate greater embodiment ratings during systole trials. The red line indicates the regression line between the two variables, and the shaded area represents the standard error of this estimate. A significant negative correlation was observed between Heartbeat Counting score and the change in Embodiment ratings from synchronous-systole to synchronous-diastole conditions, $r(36) = -.39$, 95% CI $[-.64, -.07]$, $t(34) = -2.48$, $p = .018$.

4.4.2. Number of taps

Since the number of touches delivered in each condition is tied to heart rate, there is a potential for the number of touches delivered to vary between each condition for each individual and between participants. Typical RHI paradigms maintain consistent numbers of touches between conditions and participants, so we sought to clarify whether number of taps experienced influenced RHI outcomes.

First, we conducted a linear mixed model, with number of taps as the outcome variable, Visuo-Tactile Synchrony and Cardiac Timing as fixed effects, and a by-subjects random intercept. There was a significant effect of Cardiac Timing, $\widehat{\beta} = 0.83$, 95% CI $[0.19, 1.46]$, $t(273) = 2.56, p = .011$, but no significant effect of Visuo-Tactile Synchrony, $\widehat{\beta} = -0.30$, 95% CI $[-0.93, 0.34]$, $t(273) = -0.92, p = .36$, nor a significant two-way interaction, $\widehat{\beta} = 0.53$, 95% CI $[-0.74, 1.80]$, $t(273) = 0.82$, $p = .41$. This suggests that there were more taps in the systole condition compared to the diastole conditions. Though statistically significant, this amounted to a difference of 1 additional tap on average in the systole trials (see Fig. 4).

Second, we investigated whether the number of taps influenced the effect of Visuo-Tactile Synchrony or Cardiac Timing on the rubber hand illusion. We calculated the average number of taps in each condition for each individual. We carried out two linear mixed models, with proprioceptive drift and embodiment score as the outcome variables. In each model, the fixed effects were Visuo-Tactile Synchrony, Cardiac Timing and mean-centred Number of Taps, with the interactions between these effects. A by-subject random intercept was also included.

There was no significant fixed effect of number of taps for either proprioceptive drift, $\widehat{\beta} = 0.03$, 95% CI $[-0.41, 0.46]$, $t(47) = 0.12, p = .91$, or embodiment score, $\widehat{\beta} = 0.03$, 95% CI $[-0.01, 0.08]$, $t(40) = 1.53, p = .13$. Number of taps did not significantly interact with Visuo-Tactile Synchrony for proprioceptive drift, $\widehat{\beta} = -0.66$, 95% CI $[-1.66, 0.34]$, $t(42) = -1.29, p = .20$, or embodiment score, $\widehat{\beta} = 0.02$, 95% CI $[-0.04, 0.07]$, $t(41) = 0.51$, $p = .61$. Number of taps did not significantly interact with Cardiac Timing for proprioceptive drift, $\widehat{\beta} = 0.21$, 95% CI $[-0.63, 1.06]$, $t(53) = 0.49$, $p = .63$, or embodiment score, $\widehat{\beta} = 0.02$, 95% CI $[-0.02, 0.05]$, $t(196) = 0.88$, $p = .38$. There was also no significant three-way interaction for proprioceptive drift,

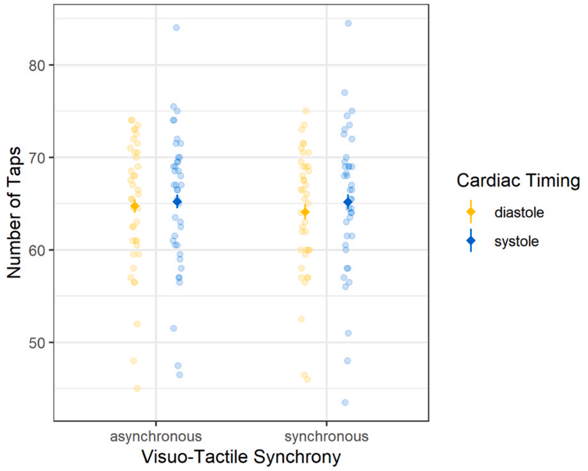

Fig. 5. Comparison of number of taps in each condition of the rubber hand illusion. The diamond represents mean number of taps in each condition, with the ranges representing the 95% Confidence Interval.

$\widehat{\beta} = -1.65$, 95% CI $[-3.39, 0.08]$, $t(54) = -1.87$, $p = .067$ or embodiment score, $\widehat{\beta} = 0.00$, 95% CI $[-0.06, 0.07]$, $t(209) = 0.11$, $p = .91$.

5. Discussion

In the present study, we implemented the Rubber Hand Illusion (RHI, Botvinick & Cohen, 1998) with a novel manipulation of the timing of touch to coincide with the different phases of the cardiac cycle. Firstly, in a youthful sample consisting of mainly female participants, we replicated the classic RHI finding that synchronous touches to a real and fake hand can engender a greater sense of embodiment over the fake hand, and can cause a shift in the perceived location of the rubber hand. Of interest is that we were able to induce an extension to the sense of the body with tapping touches rather than brushstrokes, which are the most frequently used type of touch in RHI research (Riemer et al., 2019). This confirms that tapping stimuli can successfully induce the RHI (e.g. Zbinden & Ortiz-Catalan, 2021). Secondly, we synchronised the tapping sensations delivered to the real hand with either the systolic phase or the diastolic phase of the cardiac cycle. Systolic tapping was expected to increase feelings of ownership over the rubber hand (Aspell et al., 2013; Suzuki et al., 2013), particularly when tapping was delivered simultaneously to the real and rubber hands. However, we found no significant influence of cardiac timing on either proprioceptive drift or feelings of embodiment, nor did cardiac timing interact with visuo-tactile synchrony. Finally, we expected Interoceptive Accuracy (IAcc), measured with the Method of Constant Stimuli task (Brener et al., 1993; Ring & Brener, 2018) and the Heartbeat Counting task (Schandry, 1981) to predict susceptibility to RHI. The only significant relationship was a three-way interaction between Visuo-Tactile Synchrony, Cardiac Timing and Heartbeat Counting score. Post-hoc correlations revealed that higher IAcc in the Heartbeat Counting task was associated with elevated ratings of embodiment in the synchronous-diastole condition, compared to the synchronous-systole condition. Therefore, better detection of heartbeats was related with a boost in felt embodiment over the rubber hand when touch was delivered between heartbeats, rather than during the cardiac ejection period.

The lack of a cardiac timing effect on the RHI contrasts with previous research. In previous studies exploring the effect of cardiac timing on feelings of ownership over a fake body (Aspell et al., 2013; Suzuki et al., 2013), embodiment over a virtual body was enhanced when visual flashes overlaid on the virtual body occurred at systolic compared to the diastolic phase of the heart. A key difference in the present study was that we timed tactile stimuli to occur at different phases of the cardiac cycle, as opposed to visual stimuli. It may be the case that the cardiac timing has a greater effect when there is no tactile information provided to drive embodiment decisions. Visuo-Tactile Synchrony provides a powerful perceptual cue to determine if the hand belongs to one's own body and the timing of the sensations may therefore have minimal additional influence on the sense of ownership over the rubber hand.

We did observe a significant three-way interaction between IAcc measured by the Heartbeat Counting task, cardiac timing and visuo-tactile synchrony. Post-hoc analyses revealed this was driven by scores in the synchronous touch condition, where greater IAcc scores were associated with greater embodiment ratings in the diastole condition compared to the systole condition. A possible explanation for this result comes from the literature on how touch perception varies across the cardiac cycle. Several studies have demonstrated that touch detection (Al et al., 2020; Grund et al., 2022; Motyka et al., 2019) and discrimination (Al et al., 2020; Galvez-Pol et al., 2020) are enhanced at diastole compared to systole. These findings are explained by the need of the brain to suppress perception of internal bodily signals of the heart during normal functioning, due to them being predictable and unmeaningful. As a consequence, weak tactile signals are attenuated at systole. If participants in the cardiac RHI were more sensitive to the tactile sensations presented at diastole, there may have been more of an opportunity to associate the felt touch and viewed touch together – thus driving a stronger feeling of embodiment at diastole. However, the tactile sensations in our study were suprathreshold, meaning they were intended to be detectable, whereas past research has demonstrated that it is sensitivity to weaker or threshold tactile sensations is enhanced at diastole. Furthermore, the three-way interaction should be interpreted with caution because it was exploratory (i.e. not part of the pre-registered analysis), was not replicated with IAcc derived from the Method of Constant Stimuli task, and was based on the Heartbeat Counting task which has limitations in its ability to accurately measure IAcc. Future research could explore how threshold-level tactile sensations within the RHI paradigm are influenced by cardiac timing, to determine how the cardiac cycle's influence on tactile perception extends towards the sense of embodiment.IAcc was also relatively low in the current sample, which may have influenced the RHI results. IAcc derived from the Method of Constant Stimuli, the interquartile range of the cumulative percentage of simultaneous judgements, was on average higher and therefore less precise than previous research using this task (Ring & Brener, 2018). Moreover, according to chi-squared tests assessing if responding to the Method of Constant Stimuli task was different from random responding, only 10% of the sample could be classified as 'heartbeat detectors', which is again lower than previous research (e.g. 54% reported by Brener *et al.* 1993). The Method of Constant Stimuli used in the present study used sequences of 5 tones rather than 10 tones, which has previously been shown to preserve performance while minimizing task duration (Brener, Ring, & Liu, 1994). However, this change may have inadvertently made it more difficult for participants to judge if the tones were synchronized with their heartbeat. However, IAcc derived from Heartbeat Counting task was similar to other studies that have used the same instructions (Desmedt et al., 2018), and was significantly correlated with the accuracy score derived from the Method of Constant Stimuli task. In previous RHI research, lower IAcc has been related to a stronger influence of synchronous touches on the feeling of ownership over the rubber hand (Tsakiris et al., 2011). It may be that the low IAcc in the present sample led individuals to be particularly influenced by the exteroceptive manipulation of visuo-tactile synchrony, allowing less of an influence of cardiac timing.

The present study found little evidence that IAcc influenced either feelings of embodiment or proprioceptive drift on the RHI. We first expected IAcc to modulate the cardiac timing effect, given past research that greater cardiac awareness was associated with a more pronounced difference in proprioceptive drift between touches accompanied by systolic and diastolic-timed visual pulses (Suzuki et al., 2013). In the present study, IAcc assessed with Heartbeat Counting was associated with greater embodiment ratings in response to touch presented at diastole compared to systole, which is opposite to the direction found by Suzuki et al. (2013). However, IAcc assessed with the Method of Constant Stimuli showed no significant relationship with the effect of cardiac timing on the RHI.

Turning to the relationship between IAcc and visuo-tactile synchrony, we expected elevated IAcc scores to be associated with a weaker effect of visuo-tactile synchrony (Tsakiris et al., 2011), but found no significant association. Previous research is mixed regarding the relationship between IAcc and the RHI. Some research has found that greater IAcc is related to a smaller effect of visuo-tactile synchrony on embodiment over a fake hand (Tsakiris et al., 2011), some has found that IAcc is related to a larger effect of visuo-tactile synchrony(Suzuki et al., 2013) and other research has found no evidence of a significant association between IAcc and visuo-tactile synchrony on the RHI (Crucianelli et al., 2018; Horváth et al., 2020). In addition to accuracy at detecting heartbeats, performance on heartbeat detection tasks can also be assessed with confidence ratings and metacognitive awareness, the extent to which accuracy and confidence correspond (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). A recent study found that interoceptive metacognitive awareness, but not accuracy or confidence ratings alone, negatively correlated with the change in self-location on a body ownership illusion (Bekrater-Bodmann et al., 2020). It remains to be seen whether higher order interoceptive abilities associate with performance on the rubber hand illusion.

Other methods of assessing the RHI may be more susceptible to cardiac timing. An alternative approach to assessing ownership over the rubber hand involves threatening the rubber hand with pain, and assessing physiological responses to the threat. Skin conductance, a physiological measure of arousal, tends to be heightened following threat delivered after synchronous touches compared to threat delivered after asynchronous touches (Armel & Ramachandran, 2003). In addition, other studies have found that the real hand displays physiological responses consistent with a 'rejection' of the real body after synchronous touch compared to asynchronous touch. A cooling of the real hand has been observed during synchronous touch (Moseley et al., 2008), as well as reduced local immune response to the application of histamine on the real hand (Barnsley et al., 2011). It is an open question for future research to determine if cardiac timing influences these aspects of the RHI. Moreover, it may be prudent to determine if the pairing of cardiac, tactile and visual signals influences embodiment over different body parts or the full body (e.g. Aspell et al., 2013), given that heartbeats are felt at various bodily locations, most commonly the chest (Betka et al., 2020). Our cardiac timing manipulation set out to address the pre-conscious impact of the cardiac cycle on body awareness, but was not designed to determine whether temporal and spatial synchronicity of felt heartbeats also influences bodily awareness. Finally, it should be noted that the recruited participants were primarily young participants, with almost all identifying as female. This limits the generalizability of the findings to other age and gender groups, and future research should look to clarify if similar results are observed in populations with different demographic profiles.

In conclusion, we carried out an adapted version of the rubber hand illusion, with touches delivered at different phases of the cardiac cycle corresponding to active and quiescent body-brain signalling. Though we were successful in inducing the classic effect that simultaneous touch delivered to a real and rubber hand results in an extension of the body to incorporate the rubber hand, we found no evidence for an influence of cardiac timing. Moreover, individual differences in the ability to detect internal sensations, measured with heartbeat detection tasks, did not influence the sense of body ownership on the RHI. It therefore appears that cardiac timing has little influence on the sense of body ownership over and above that of the multisensory integration of exteroceptive signals, such as touch and vision.

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CRediT authorship contribution statement

Finotti Gianluca: Writing – review & editing, Software, Resources, Methodology, Formal analysis, Conceptualization. **Moffatt Jamie:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tsakiris Manos:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

The author(s) did not use generative AI technologies for preparation of this work.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Anonymised data is available at the following link: https://osf.io/4vxze/.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.biopsycho.2024.108756.

References

Ainley, V., Tsakiris, M., Pollatos, O., Schulz, A., & Herbert, B. M. (2020). Comment on "Zamariola et al. (2018), Interoceptive Accuracy Scores are Problematic: Evidence from Simple Bivariate Correlations"—The empirical data base, the conceptual reasoning and the analysis behind this statement are misconceived and do not support the authors' conclusions. *Biological Psychology, 152*, Article 107870. https://doi.org/10.1016/j.biopsycho.2020.107870

Al, E., Iliopoulos, F., Forschack, N., Nierhaus, T., Grund, M., Motyka, P., & Villringer, A. (2020). Heart–brain interactions shape somatosensory perception and evoked potentials. *Proceedings of the National Academy of Sciences, 117*(19), 10575–10584. https://doi.org/10.1073/pnas.191562911

Ambrosini, E., Finotti, G., Azevedo, R. T., Tsakiris, M., & Ferri, F. (2019). Seeing myself through my heart: Cortical processing of a single heartbeat speeds up self-face recognition. *Biological Psychology, 144*, 64–73. https://doi.org/10.1016/j.biopsycho.2019.03.006

Apps, M. A. J., & Tsakiris, M. (2014). The free-energy self: A predictive coding account of self-recognition. *Neuroscience & Biobehavioral Reviews, 41*, 85–97. https://doi.org/10.1016/j.neubiorev.2013.01.029

Armel, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: evidence from skin conductance response. *Proceedings of the Royal Society of London Series B: Biological Sciences, 270*(1523), 1499–1506. https://doi.org/10.1098/rspb.2003.2364

Aspell, J. E., Heydrich, L., Marillier, G., Lavanchy, T., Herbelin, B., & Blanke, O. (2013). Turning body and self inside out: Visualized heartbeats alter bodily self-consciousness and tactile perception. *Psychological Science, 24*(12), 2445–2453. https://doi.org/10.1177/0956797613498395

Aust, F., & Barth, M. (2022). *papaja: Prepare reproducible APA journal articles with R Markdown* (Original work published 2014) https://github.com/crsh/papaja.

Barnsley, N., McAuley, J. H., Mohan, R., Dey, A., Thomas, P., & Moseley, G. L. (2011). The rubber hand illusion increases histamine reactivity in the real arm. *Current Biology, 21*(23), R945–R946. https://doi.org/10.1016/j.cub.2011.10.039

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 48. https://doi.org/10.18637/jss.v067.i01

Bekrater-Bodmann, R., Azevedo, R. T., Ainley, V., & Tsakiris, M. (2020). Interoceptive awareness is negatively related to the exteroceptive manipulation of bodily self-location. *Frontiers in Psychology, 0*. https://doi.org/10.3389/fpsyg.2020.562016

Betka, S., Łukowska, M., Silva, M., King, J., Garfinkel, S., & Critchley, H. (2020). Feeling the beat: Temporal and spatial perception of heartbeat sensations. *BioRxiv*. https://doi.org/10.1101/2020.07.27.222810

Botvinick, M., & Cohen, J. (1998). Rubber hands "feel" touch that eyes see, 756–756 *Nature, 391*(6669). https://doi.org/10.1038/35784.

Brauer, M., & Curtin, J. J. (2018). Linear mixed-effects models and the analysis of nonindependent data: A unified framework to analyze categorical and continuous independent variables that vary within-subjects and/or within-items. *Psychological Methods, 23*(3), 389. https://doi.org/10.1037/met0000159

Brener, J., Liu, X., & Ring, C. (1993). A method of constant stimuli for examining heartbeat detection: Comparison with the Brener-Kluvitse and Whitehead methods. *Psychophysiology, 30*(6), 657–665. https://doi.org/10.1111/j.1469-8986.1993.tb02091.x

Brener, J., Ring, C., & Liu, X. (1994). Effects of data limitations on heartbeat detection in the method of constant stimuli. *Psychophysiology, 31*(3), 309–312. https://doi.org/10.1111/j.1469-8986.1994.tb02219.x

Brener, J., & Ring, C. (2016). Towards a psychophysics of interoceptive processes: The measurement of heartbeat detection. *Philosophical Transactions of the Royal Society B:*

Biological Sciences, 371(1708), Article 20160015. https://doi.org/10.1098/rstb.2016.0015

Chancel, M., Ehrsson, H. H., & Ma, W. J. (2022). Uncertainty-based inference of a common cause for body ownership. *eLife, 11*, Article e77221. https://doi.org/10.7554/eLife.77221

Corneille, O., Desmedt, O., Zamariola, G., Luminet, O., & Maurage, P. (2020). A heartfelt response to Zimprich et al. (2020), and Ainley et al. (2020)'s commentaries: Acknowledging issues with the HCT would benefit interoception research. *Biological Psychology, 152*, Article 107869. https://doi.org/10.1016/j.biopsycho.2020.107869

Costantini, M., Robinson, J., Migliorati, D., Donno, B., Ferri, F., & Northoff, G. (2016). Temporal limits on rubber hand illusion reflect individuals' temporal resolution in multisensory perception. *Cognition, 157*, 39–48. https://doi.org/10.1016/j.cognition.2016.08.010

Crucianelli, L., Krahé, C., Jenkinson, P. M., & Fotopoulou, A. (Katerina (2018). Interoceptive ingredients of body ownership: Affective touch and cardiac awareness in the rubber hand illusion. *Cortex, 104*, 180–192. https://doi.org/10.1016/j.cortex.2017.04.018

Desmedt, O., Luminet, O., & Corneille, O. (2018). The heartbeat counting task largely involves non-interoceptive processes: Evidence from both the original and an adapted counting task. *Biological Psychology, 138*, 185–188. https://doi.org/10.1016/j.biopsycho.2018.09.004

Dunnington, D. (2023). *rbbt* [R]. Retrieved from https://github.com/paleolimbot/rbbt (Original work published 2018).

Ehrsson, H. H. (2020). Chapter 8 - Multisensory processes in body ownership. In K. Sathian, & V. S. Ramachandran (Eds.), *Multisensory perception* (pp. 179–200). Academic Press. https://doi.org/10.1016/B978-0-12-812492-5.00008-5.

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods, 39*(2), 175–191. https://doi.org/10.3758/BF03193146

Finotti, G., Garofalo, S., Costantini, M., & Proffitt, D. R. (2023). Temporal dynamics of the rubber hand illusion. *Scientific Reports, 13*(1), Article 7526. https://doi.org/10.1038/s41598-023-33747-2

Gallagher, S. (2000). Philosophical conceptions of the self: implications for cognitive science. *Trends in Cognitive Sciences, 4*(1), 14–21. https://doi.org/10.1016/S1364-6613(99)01417-5

Galvez-Pol, A., McConnell, R., & Kilner, J. M. (2020). Active sampling in visual search is coupled to the cardiac cycle. *Cognition, 196*, Article 104149. https://doi.org/10.1016/j.cognition.2019.104149

Galvez-Pol, A., Virdee, P., Villacampa, J., & Kilner, J. (2022). Active tactile discrimination is coupled with and modulated by the cardiac cycle. *Elife, 11*, Article e78126. https://doi.org/10.7554/eLife.78126

Garfinkel, S. N., Minati, L., Gray, M. A., Seth, A. K., Dolan, R. J., & Critchley, H. D. (2014). Fear from the heart: Sensitivity to fear stimuli depends on individual heartbeats. *Journal of Neuroscience, 34*(19), 6573–6582. https://doi.org/10.1523/JNEUROSCI.3507-13.2014

Garfinkel, S. N., Seth, A. K., Barrett, A. B., Suzuki, K., & Critchley, H. D. (2015). Knowing your own heart: Distinguishing interoceptive accuracy from interoceptive awareness. *Biological Psychology, 104*, 65–74. https://doi.org/10.1016/j.biopsycho.2014.11.004

Gohel, D., ArData, Jager, C., Skintzos, P., Fazilleau, Q., output), M. N. (rmarkdown. for docx, … pagination), S. J. (work. on (2023). *flextable: Functions for Tabular Reporting*. Retrieved from https://cran.r-project.org/web/packages/flextable/.

Grund, M., Al, E., Pabst, M., Dabbagh, A., Stephani, T., Nierhaus, T., … Villringer, A. (2022). Respiration, heartbeat, and conscious tactile perception. *Journal of Neuroscience, 42*(4), 643–656. https://doi.org/10.1523/JNEUROSCI.0592-21.2021

Horváth, Á., Ferentzi, E., Bogdány, T., Szolcsányi, T., Witthöft, M., & Köteles, F. (2020). Proprioception but not cardiac interoception is related to the rubber hand illusion. *Cortex, 132*, 361–373. https://doi.org/10.1016/j.cortex.2020.08.026

Katkin, E. S., Blascovich, J., & Goldband, S. (1981). Empirical assessment of visceral self-perception: Individual and sex differences in the acquisition of heartbeat discrimination. *Journal of Personality and Social Psychology, 40*(6), 1095–1101. https://doi.org/10.1037/0022-3514.40.6.1095

Khalsa, S. S., Adolphs, R., Cameron, O. G., Critchley, H. D., Davenport, P. W., Feinstein, J. S., … Zucker, N. (2018). Interoception and mental health: A roadmap. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging, 3*(6), 501–513. https://doi.org/10.1016/j.bpsc.2017.12.004

Kilteni, K., Maselli, A., Kording, K. P., & Slater, M. (2015). Over my fake body: body ownership illusions for studying the multisensory basis of own-body perception. *Frontiers in Human Neuroscience, 9*. Retrieved from https://www.frontiersin.org/articles/10.3389/fnhum.2015.00141.

Kleiner, M., Brainard, D., & Pelli, D. (2007). *What's New in Psychtoolbox-3?*, 89.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software, 82*, 1–26. https://doi.org/10.18637/jss.v082.i13

Lakens, D. (2013). Calculating and reporting effect sizes to facilitate cumulative science: A practical primer for t-tests and ANOVAs. *Frontiers in Psychology, 4*. https://doi.org/10.3389/fpsyg.2013.00863

Longo, M. R., Schüür, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition, 107*(3), 978–998. https://doi.org/10.1016/j.cognition.2007.12.004

Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., & Bates, D. (2017). Balancing type I error and power in linear mixed models. *Journal of Memory and Language, 94*, 305–315. https://doi.org/10.1016/j.jml.2017.01.001

Monti, A., Porciello, G., Tieri, G., & Aglioti, S. M. (2020). The "embreathment" illusion highlights the role of breathing in corporeal awareness. *Journal of Neurophysiology, 123*(1), 420–427. https://doi.org/10.1152/jn.00617.2019

Moseley, G. L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., & Spence, C. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proceedings of the National Academy of Sciences, 105*(35), 13169–13173. https://doi.org/10.1073/pnas.0803768105

Motyka, P., Grund, M., Forschack, N., Al, E., Villringer, A., & Gaebler, M. (2019). Interactions between cardiac activity and conscious somatosensory perception. *Psychophysiology, 56*(10), Article e13424. https://doi.org/10.1111/psyp.13424

Müller, K., & Bryan, J. (2020). *here: A Simpler Way to Find Your Files*. Retrieved from https://cran.r-project.org/web/packages/here/.

Palmer, C., Ainley, V., & Tsakiris, M. (2019). Fine tuning your heart: A novel method for measuring interoceptive accuracy. *PsyArXiv*. https://doi.org/10.31234/osf.io/qz7r9

Radziun, D., & Ehrsson, H. H. (2018). Auditory cues influence the rubber-hand illusion. *Journal of Experimental Psychology: Human Perception and Performance, 44*(7), 1012–1021. https://doi.org/10.1037/xhp0000508

Revelle, W. (2023). *psych: Procedures for Psychological, Psychometric, and Personality Research* . Retrieved from https://cran.r-project.org/web/packages/psych/.

Riemer, M., Trojan, J., Beauchamp, M., & Fuchs, X. (2019). The rubber hand universe: On the impact of methodological differences in the rubber hand illusion. *Neuroscience & Biobehavioral Reviews, 104*, 268–280. https://doi.org/10.1016/j.neubiorev.2019.07.008

Ring, C., & Brener, J. (2018). Heartbeat counting is unrelated to heartbeat detection: A comparison of methods to quantify interoception. *Psychophysiology, 55*(9), Article e13084. https://doi.org/10.1111/psyp.13084

Schandry, R. (1981). Heart beat perception and emotional experience. *Psychophysiology, 18*(4), 483–488. https://doi.org/10.1111/j.1469-8986.1981.tb02486.x

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution, 1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Sel, A., Azevedo, R. T., & Tsakiris, M. (2017). Heartfelt self: Cardio-visual integration affects self-face recognition and interoceptive cortical processing. *Cerebral Cortex, 27*(11), 5144–5155. https://doi.org/10.1093/cercor/bhw296

Seth, A. K. (2013). Interoceptive inference, emotion, and the embodied self. *Trends in Cognitive Sciences, 17*(11), 565–573. https://doi.org/10.1016/j.tics.2013.09.007

Seth, A. K., & Tsakiris, M. (2018). Being a beast machine: The somatic basis of selfhood. *Trends in Cognitive Sciences, 22*(11), 969–981. https://doi.org/10.1016/j.tics.2018.08.008

Shimada, S., Fukuda, K., & Hiraki, K. (2009). Rubber hand illusion under delayed visual feedback. *PLoS One, 4*(7), Article e6185. https://doi.org/10.1371/journal.pone.0006185

Suksasilp, C., & Garfinkel, S. N. (2022). Towards a comprehensive assessment of interoception in a multi-dimensional framework. *Biological Psychology, 168*, Article 108262. https://doi.org/10.1016/j.biopsycho.2022.108262

Suzuki, K., Garfinkel, S. N., Critchley, H. D., & Seth, A. K. (2013). Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion. *Neuropsychologia, 51*(13), 2909–2917. https://doi.org/10.1016/j.neuropsychologia.2013.08.014

Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia, 48*(3), 703–712. https://doi.org/10.1016/j.neuropsychologia.2009.09.034

Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: Visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance, 31*(1), 80–91. https://doi.org/10.1037/0096-1523.31.1.80

Tsakiris, M., Jiménez, A. T.-, & Costantini, M. (2011). Just a heartbeat away from one's body: Interoceptive sensitivity predicts malleability of body-representations. *Proceedings of the Royal Society B: Biological Sciences, 278*(1717), 2470–2476. https://doi.org/10.1098/rspb.2010.2547

Whitehead, W. E., Drescher, V. M., Heiman, P., & Blackwell, B. (1977). Relation of heart rate control to heartbeat perception. *Biofeedback and Self-Regulation, 2*(4), 371–392. https://doi.org/10.1007/BF00998623

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., … Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software, 4*(43), 1686. https://doi.org/10.21105/joss.01686

Wilke, C.O. (2020). *cowplot: Streamlined Plot Theme and Plot Annotations for "ggplot2"*. Retrieved from https://cran.r-project.org/web/packages/cowplot/index.html.

Wilkinson, M., McIntyre, D., & Edwards, L. (2013). Electrocutaneous pain thresholds are higher during systole than diastole. *Biological Psychology, 94*(1), 71–73. https://doi.org/10.1016/j.biopsycho.2013.05.002

Zamariola, G., Maurage, P., Luminet, O., & Corneille, O. (2018). Interoceptive accuracy scores from the heartbeat counting task are problematic: Evidence from simple bivariate correlations. *Biological Psychology, 137*, 12–17. https://doi.org/10.1016/j.biopsycho.2018.06.006

Zbinden, J., & Ortiz-Catalan, M. (2021). The rubber hand illusion is a fallible method to study ownership of prosthetic limbs. *Scientific Reports, 11*(1), Article 4423. https://doi.org/10.1038/s41598-021-83789-7

Zimprich, D., Nusser, L., & Pollatos, O. (2020). Are interoceptive accuracy scores from the heartbeat counting task problematic? A comment on Zamariola et al. (2018). *Biological Psychology, 152*, Article 107868. https://doi.org/10.1016/j.biopsycho.2020.107868