

Heartfelt embodiment: changes in body-ownership and self-identification produce distinct changes in interoceptive accuracy

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Abstract

Interoceptive and exteroceptive information are both essential for the construction and update of self-awareness. Whereas several studies have shown how interoceptive accuracy or cardiac feedback influences body-awareness, no studies have looked at the reverse effect, namely how exteroceptively-driven changes in body-ownership and self-identification can influence individuals' ability to detect internal bodily signals. We exposed participants to the Rubber Hand Illusion (Experiment 1) and to the Enfacement Illusion (Experiment 2), and tested how this change in the sense of body-ownership and self-identification affected their interoceptive accuracy (IAcc). The heartbeat-counting task was used to measure IAcc before the bodily illusions, and then the same task was interleaved with periods of visuo-tactile stimulation, during which synchronous and asynchronous multisensory stimulation was applied. We found that a change in body-ownership significantly improved performance of participants with lower interoceptive accuracy. In contrast, a change in self-identification significantly decreased performance of participants with higher interoceptive accuracy. These results suggest that changes in different domains of self-awareness can differentially impact individuals' ability to accurately detect signals arising from within the body, highlighting the distinct role that interoceptive signals play for different facets of bodily self-consciousness.

Keywords: self-awareness, body-ownership, self-identification, interoceptive accuracy, rubber hand illusion, Enfacement Illusion.

1. Introduction

Bodily self-consciousness (BSC) results from the integration of two fundamental sources of body-related information, namely signals arising from the body as perceived from the *outside* and external environment (i.e. exteroception) and from *within* the body (i.e. interoception). The perception of the body from the *outside* has been shown to be essential in order to maintain and update BSC. For example, the integration of multisensory signals has been shown to play a fundamental role in body-ownership (Botvinick & Cohen, 1998; Tsakiris, 2010; Ehrsson, 2007; Lenggenhager et al., 2007) and self-identification (Tsakiris, 2008). Bodily illusions such as the Rubber Hand Illusion (RHI) can modulate the awareness of one's own body through the manipulation of visual and tactile synchrony (Botvinick and Cohen, 1998). In these experiments, seeing a rubber hand being stroked together with one's own hidden hand provokes a change in body-ownership, whereby the rubber hand is perceived as belonging to one's own body (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). The influence of multisensory integration in updating our sense of body awareness has been shown in several other contexts, such as full body illusions (e.g. Ehrsson, 2007, Lenggenhager, et al., 2007) and self-identification (i.e. see the Enfacement Illusion (EI), Tsakiris, 2008). In the Enfacement Illusion, synchronous interpersonal multisensory stimulation (IMS) between the participant's face and another person's face evokes a measurable change in self-recognition, whereby a certain percentage of the other person's face is identified as "self" (Tajadura-Jimenez et al., 2012a), indicative of altered self-other boundaries (Paladino et al., 2010; Cardini et al., 2013; Tajadura-Jimenez & Tsakiris, 2014). Together, these findings seem to suggest that similar exteroceptive sensory processes are involved at different levels of body-awareness, from the ability to define ownership towards a body-part, to the ability to identify with one's own face.

Exteroceptive signals however are not the only relevant sources of information about the self. Together with exteroception, internal signals arising from within the body are essential in order to maintain a sense of self (Tsakiris, Tajadura-Jimenez, & Costantini, 2011). Interoceptive awareness - that is often operationalized as Interoceptive Accuracy (IAcc) - is the ability to perceive internal bodily signals such as cardiac activity, hunger, and distension of bladder and other visceral organs (Craig, 2002; 2010). IAcc has been considered a rather stable trait, whereby some individuals seem to be better than others in detecting and becoming aware of internal bodily signals (Herbert & Pollatos, 2012). Nevertheless, a renewed interest

in the topic of interoception has provided preliminary evidence of the interactive relationship between interoceptive and exteroceptive bodily signals.

Direct behavioural evidence of the effects of interoception on body-ownership comes from three recent studies. The first study that tested the potential link between exteroceptive and interoceptive awareness of the body measured and quantified IAcc and compared this measure with the change in body-ownership caused by multisensory stimulation, using the RHI as a paradigmatic case of the exteroceptive self. Tsakiris et al (2011) observed a negative correlation between IAcc and RHI, such that people with lower IAcc showed a stronger RHI measured behaviourally and homeostatically (i.e. drop in skin temperature), suggesting that, in the absence of accurate interoceptive representations, one's model of self is predominantly exteroceptive. Following this finding, two studies used cardio-visual feedback synchronous with one's own heartbeat to induce changes in body-ownership (Aspell et al., 2013; Suzuki et al., 2013). Aspell and colleagues (2013) used cardio-visual illumination of a virtual body either in synchrony or asynchrony with respect to the participant's heartbeat to show changes in body-ownership, providing evidence of the integration between internal and external signals of the body. On a similar line of research, Suzuki et al. (2013) demonstrated the influence of interoceptive signals at the exteroceptive level by applying cardio-visual feedback to implement the RHI. In their study, participants were exposed to a virtual RHI set-up and experienced an increased illusion during synchronous cardio-visual feedback, compared to asynchronous feedback (Suzuki et al., 2013). More recently, studies have focused on the effect of pleasant affective touch, which is known to engage interoceptive processing, on body-ownership (Crucianelli et al., 2013; Lloyd et al., 2013; van Stralen et al., 2014), suggesting again the influence of interoceptive cues on external signals related to the body. Taken together, these findings suggest that the relation between the perception of the body from the outside (i.e. exteroception) and the perception of the body from the inside (i.e. interoception) is fundamental to the coherence of the bodily self: their integration enables the self to feel grounded in a coherent body that consists of both exteroceptive and interoceptive representations. However, while these studies focused on the role of interoceptive signaling or levels of IAcc in modulating the experience of the body as perceived from the outside, the question of whether exteroceptively-driven changes in body-awareness can in turn influence interoceptive awareness remains unanswered.

A recent unifying account of the self proposes that self-related information results from the integration between incoming sensory events with the existent mental representation of the self (Apps and Tsakiris, 2014; Limanowski and Blankenburg, 2013). According to this

predictive coding model of the self (Seth, Suzuki, and Critchley 2011), incoming sensory inputs are interpreted in light of prediction signals derived from existing priors about the self (Apps and Tsakiris, 2014). The system's ultimate goal is to reduce 'free energy', by minimising prediction errors through a process of matching between incoming information and its predictions (Apps and Tsakiris, 2014; Limanowski and Blankenburg, 2013; see also for Samad, Chung & Shams, 2015 for direct evidence). In the context of maintaining an integrated sense of self, any update of self-representations is dependent upon prior beliefs derived from past events, with the aim of minimising prediction errors in favour of the most likely 'self' (Apps and Tsakiris, 2014). Thus, body-related multisensory signals (such as those implemented during the RHI and EI) may explain away prediction errors by creating a new model of the self, that incorporates the fake rubber hand or the other face into the self-mental representation (Suzuki et al., 2013). This change in BSC will result in an update of posterior probabilities and a decrease in the probability that one's actual body or face is represented as 'self' (Apps and Tsakiris, 2014). As a result, one could expect an increase in top-down attention to the self, which in turn will produce an enhanced general precision of all self-relevant data, including interoceptive inputs. Previous studies have addressed the role of interoceptive signals in the multisensory predictive model of the self (Suzuki et al., 2013; Aspell et al., 2013). This investigation aimed to test the opposite effect, namely the influence of exteroceptive signalling in modulating the experience of the body from within.

In line with recent accounts, we assume that the self is a multilevel, multimodal construct, continually updated in the brain from all available interacting cues including interoception (Apps and Tsakiris, 2013; Seth, 2013). Precision necessarily varies along this hierarchy (Edwards et al., 2012). Self-focus can therefore enhance the precision of all self-relevant and self-specifying signals, including interoceptive prediction errors, thus enabling updating of priors in interoceptive systems and consequent perception of heartbeats. If self-focus enhances the precision of a high-level (conscious) prior for the multimodal self, this will affect the precision of priors and prediction errors at lower levels of the self-hierarchy (including those for the heartbeat itself). How such self-focus affects interoception under conditions that induce a change in self-representations induced by bodily illusions remains unknown. In the present study, we tackle two issues. First, we explore whether changes in body-awareness after exposure to the RHI and EI can affect individuals' accuracy in detecting their internal bodily signals, quantified by the heartbeat-counting task (Schandry, 1981). To answer this question, we conducted two experiments using two different bodily illusions in two independent samples of participants. In Experiment 1, we manipulated the experience of body-

ownership through the use of the RHI to measure changes in IAcc, whereas in Experiment 2 we used the Enfacement Illusion to test whether changes in self-identification will lead to changes IAcc. Second, we were interested to test whether the hypothesized modulations of IAcc would be comparable across the two illusions. Even though recent findings on the relationship between changes in body-ownership and IAcc and changes in self-identification and IAcc (Tsakiris et al., 2011; Tajadura-Jimenez et al., 2012a; 2012b) have shown consistent results, namely that lower levels of IAcc were correlated with stronger illusions, the question of how changes in body- versus self-face representations elicited by the RHI and EI respectively can affect processing in the interoceptive domain remains unanswered. This question is important because of the distinctive role that one's face plays not only for body-awareness but also for the representation of one's identity in relation to others. Nothing provides such a strong sense of self as looking at one's own face, and the enfacement illusion, as an experimental model of self-identification has been shown to alter self-other boundaries (Paladino et al., 2010; Cardini et al., 2013; Tajadura-Jimenez & Tsakiris, 2014). We therefore hypothesised that the experience of the RHI and EI would modulate performance in the heartbeat task differently. In particular, we hypothesised that individuals with lower-IAcc at baseline would show a significant increase in their IAcc after exposure to the RHI, where body-ownership is manipulated, consistent with past findings on the effects of self-processing on IAcc (Ainley et al, 2012). Specifically, we hypothesised that in these individuals exposure to the bodily illusion would increase attention to the body, which in turn will result in increased precision of all body-specifying information. However, in the case of the Enfacement Illusion where the affected body-part is closely linked to self-identity, for which interoceptive predictions may play an important role (Sedeño et al. 2014), we hypothesized a reduction in performance, especially for individuals with higher-IAcc. In particular individuals with higher IAcc would be more affected by exteroceptive stimulation on the face, because a change in self-identification may conflict with the interoceptive prediction of how identifying one's face feels like, resulting in disrupted IAcc in individuals who have more precise interoceptive predictions. To account for potential confounds of the heartbeat counting task (e.g. Ring et al., 2015), we have included in our analysis variables that reflect the participants' beliefs about heart rate, their time perception ability, and we did not provide any feedback on the participants' performance during the experiment.

2. Experiment 1

2.1 Materials and Methods

2.1.1 Participants

Participants were 42 students at Royal Holloway University of London. Twelve were excluded for artefacts in the heart rate data, which made it impossible to compute the number of recorded beats (7), for no experience of the RHI – mean score RHI questionnaire data < 0 (4) (see Ehrsson et al., 2004; Ehrsson, Holmes, & Passingham, 2005; Apps et al., 2015 for a similar screening criterion), and for a baseline IAcc score $< .20$, which questioned the participant's following of the instructions (1). Of the remaining 30 participants (2 male), the mean age was = 22.37yr (SD = 4.64). The study was approved by the Department of Psychology Ethics Committee, Royal Holloway, University of London.

2.1.2 Experimental setup

Heart rate was monitored with a piezo-electric pulse transducer attached to the participant's right index finger (PowerLab 26T, AD Instruments, UK). To assess interoceptive accuracy, we used the Mental Tracking Method (MTM) (Schandry, 1981). Participants were asked to silently count their own heartbeats on an audio start cue until they received a stop cue. They were provided with standard instructions to count their heartbeats simply by 'listening' to their body without taking their pulse. No feedback was given at the end of each trial. Whilst they counted, they were asked to focus on a rubber hand positioned in front of them and to avoid performing any movement with their hands. The four trials (25 s, 35 s, 45 s, and 100 s) were presented in random order and constituted a block. To control for guessing of the number of heartbeat (Ainley et al., 2013), at the end of the experiment participants were asked to estimate the length of four, randomly presented, intervals – Time Modulus (19 s, 37 s, 49 s, and 96 s) and to provide an estimate of their resting heart rate (question: "How many heartbeats do you think you have a rest, in a minute?") – EstimatedHBM (Dunn et al., 2010).

For the Rubber Hand Illusion task, a realistic rubber hand was situated 15 cm to the right of the participant's own hand. The participant's hand and the rubber hand were positioned in a box frame, which hid the participant's own hand from view but allowed the rubber hand to be viewed. The experimenter sat in front of the participant and manually delivered stimulation to the visible rubber hand and the participant's unseen hand using two identical paintbrushes. Both the participant's own hand and the rubber hand were stimulated in the same

manner, with each stroke lasting approximately 500 to 1500 ms. Participants were stimulated on their second finger from the proximal interphalangeal joint to the tip of the finger, either in synchrony (RHI) or asynchrony (RHA) with the rubber hand. In the synchronous condition, the participant's hand and the rubber hand were stroked simultaneously in the same anatomical location. In the asynchronous condition, the stimulation of the participant's hand and the rubber hand were offset. In both conditions, participants were instructed to keep their own hand still and carefully observe the rubber hand. To provide a measure of ownership over the rubber hand, participants were asked to complete a 7-item questionnaire, which investigated their subjective experiences of illusory ownership during multisensory stimulation (Table 1). Questions were derived from Longo, Schuur, Kammers, Tsakiris, and Haggard (2008). Participants were asked to indicate the extent of their agreement or disagreement with the statements, using a 7-point Likert scale (from -3, "strongly disagree", to +3, "strongly agree"). As the focus of the study was on changes in body-ownership rather than self-location, and given that recent studies have questioned the validity of proprioceptive drift as a measure of body-ownership in the RHI (e.g. Rohde, Di Luca, & Ernst, 2011; Holle et al., 2011), we decided to focus on established introspective measures of the experience of body-ownership (Longo et al., 2008).

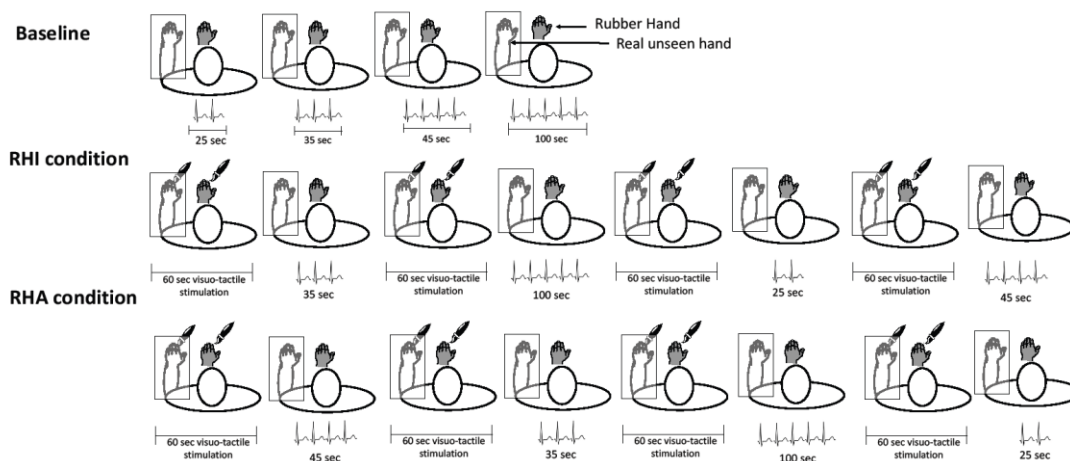


Figure 1 Illustration of the experimental paradigm, showing the procedure during baseline, visuo-tactile synchronous (RHI) and visuo-tactile asynchronous (RHA) conditions. In each condition, participants were instructed to watch a rubber hand positioned in front of them whilst keeping their left hand inside a box frame. Within each block of experimental condition, there were 4 MTM trials during which participants were asked to focus and count the number of heartbeats while they were looking at the rubber hand. Before each MTM trial participants received 60 s of visuo-tactile stimulation – synchronous to the rubber hand in the RHI condition and asynchronous in the RHA condition. The order of presentation of RHI and RHA conditions were counterbalanced across participants, while the order of presentation of the MTM trials within each block was randomized.

2.1.3 Experimental procedure

After giving informed consent, participants' sex and age were recorded. Participants were instructed to sit in front of a table and position their left hand inside the box frame so that the tip of their left index finger would touch a small Velcro tape attached to the box. They were prompted to keep this position at the start of each block, avoiding any movement with their hand and fingers. After one brief training trial (15 s) during which participants familiarised with the MTM, there were 12 trials in total, consisting of 4 MTM trials per condition – baseline, RHI, and RHA. In the RHI and RHA conditions, before each MTM trial participants received 60 s of visuo-tactile stimulation – synchronous to the rubber hand in the RHI condition and asynchronous to the rubber hand in the RHA condition. Each MTM trial was performed after the 60 s of visuo-tactile stimulation was completed. After each MTM trial, participants were instructed to verbally indicate the number of heartbeats they had counted (see Figure 1).

At the end of both the RHI and RHA conditions, participants were given to complete the 7-item questionnaire on their experiences of illusory ownership during multisensory stimulation (Table 1). Participants were required to evaluate their agreement in relation to each statement, using a 7-point Likert scale (from -3, “strongly disagree”, to +3, “strongly agree”).

2.1.4 Data analysis

Heartbeat traces were analysed using LabChart8. We identified and counted the number of R-wave peaks on the heart trace recorded for each participant in each trial, as well as the average heart rates for each trial (Jennings et al., 1981). Artefacts were visually inspected and, if necessary, R-wave peaks were re-counted manually. Participants were excluded where artefacts created uncertainty about the number of recorded beats. Interoceptive accuracy was calculated as $(1/4 \sum (1 - (|\text{recorded heartbeats} - \text{counted heartbeats}| / \text{recorded heartbeats})))$ (Schandry, 1981; Ainley et al., 2014). Higher scores indicate higher interoceptive accuracy. As in Dunn et al. (2010) and Ainley et al. (2014) we used the Time Modulus and EstimatedHBM as additional measure to control on participants' guessing of heartbeats. The Time Modulus was calculated as $(1/4 \sum (1 - (|\text{estimated elapsed time} - \text{actual elapsed time}| / \text{actual elapsed time})))$.

As in previous studies that investigated IAcc (Ainley et al., 2012; 2014; Maister and Tsakiris, 2014), a median split of IAcc scores was performed in the baseline condition (median = 0.66) to divide the sample into higher-IAcc (above median) and lower-IAcc (below median) participants. In both groups, participants were 14 female and 1 male. We then subtracted the Baseline IAcc score from the RHI IAcc score and RHA IAcc score to generate two IAcc-change scores, one for each of the two experimental conditions. These scores reflected how IAcc changed from baseline after being exposed to the synchronous (RHI) or asynchronous (RHA) stroking, with positive scores indicating an improvement from baseline (Maister and Tsakiris, 2014). Data were analysed using an ANCOVA with Experimental Condition as a within-subjects variable and Order of Presentation (to control for carryover effect) and IAcc level as between-subject variables. The Time Modulus, the EstimatedHBM, and the Ownership scores (average scores in RHI and RHA) were used as covariates, to account for potential confounds of the heartbeat counting task (Ring et al., 2015), and for the possible modulation of the experienced body illusions in IAcc. Greenhouse–Geisser correction was applied when sphericity could not be assumed (Mauchly’s test for sphericity, $p = .05$). Comparisons were assessed for significance using planned two-tailed t-tests.

Questionnaire responses (Shapiro-Wilk test of normality: RHI, $p = 0.26$, RHA, $p = 0.31$) on the subjective experience of ownership were analysed by averaging together ratings across all 7 statements, which provided an estimate of ownership experienced for each participant in each condition.

3. Results

We first examined whether the RHI was successfully elicited using a mixed ANOVA. Ownership scores were entered into a 2 (Conditions: RHI vs RHA) x 2 (IAcc level: lower-IAcc vs higher-IAcc) ANOVA. We found that the RHI was successfully elicited in the synchronous but not the asynchronous condition, $F(1,28) = 58.15$ $p < .05$, and the strength of the illusion did not depend on baseline levels of IAcc, $F(1,28) = 2.08$, $p > .05$.

We used the two IAcc-change scores, one for each of the two experimental conditions, to investigate if and how IAcc was modulated by the experience of owning the rubber hand after being exposed to the RHI, using a mixed ANCOVA. We found no significant main effect of condition on IAcc, $F(1,22) = 0.82$, $p = 0.38$, after controlling for Time Modulus,

EstimatedHBM, and Ownership Scores (average scores in RHI and RHA). However, the interaction Condition X IAcc level was significant, $F(1,22) = 4.90$, $p = 0.037$, $\eta^2 = 0.18$ (Figure 2), indicating that the feeling of owning a rubber hand elicited by synchronous stroking significantly improved interoceptive accuracy for the lower-IAcc group, $t(14) = 2.57$, $p = 0.02$, $d = 0.46$, but not for the higher-IAcc group, $t(14) = -1.02$, $p = 0.33$. As expected, we observed a significant main effect of IAcc level, $F(1,22) = 5.03$, $p = 0.035$, $\eta^2 = 0.19$. All other interactions and main effects were not significant; interactions: Condition X Time Modulus, $F(1,22) = 0.88$, $p > 0.05$; Condition X EstimatedHBM, $F(1,22) = 0.11$, $p > 0.05$; Condition X Ownership Score RHI, $F(1,22) = 0.007$, $p > 0.05$; Condition X Ownership Score RHA, $F(1,22) = 0.12$, $p > 0.05$; Condition X Order of Condition, $F(1,22) = 2.17$, $p > 0.05$; main effects: Time Modulus, $F(1,22) = 0.21$, $p > 0.05$; EstimatedHBM, $F(1,22) = 0.37$, $p > 0.05$, Ownership Score RHI, $F(1,22) = 0.92$, $p > 0.05$; Ownership Score RHA, $F(1,22) = 0.42$, $p > 0.05$, Order of Condition, $F(1,22) = 0.14$, $p > 0.05$.

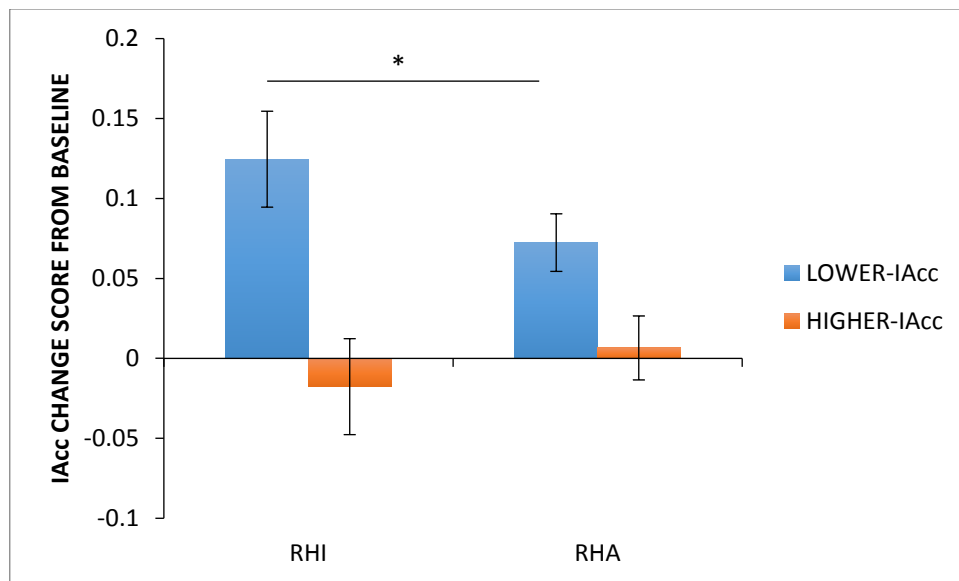


Figure 2 Mean IAcc-change scores of the lower-IAcc and higher-IAcc groups in the rubber hand illusion (RHI) and rubber hand asynchronous (RHA) conditions. Error bars show standard error (SE).

Questionnaire items:	RHI		RHA	
	Mean	SD	Mean	SD
ITEM 1: During the block it seemed like I was looking directly at my own hand, rather than at a rubber hand.	1.47	1.28	-0.5	1.78
ITEM 2: During the block it seemed like the rubber hand	1.93	0.74	0.1	1.67

began to resemble my real hand.				
ITEM 3: During the block it seemed like the rubber hand belonged to me	1.87	1.04	-0.43	1.92
ITEM 4: During the block it seemed like the rubber hand was my hand.	1.8	1.03	-0.57	1.87
ITEM 5: During the block it seemed like the rubber hand was part of my body.	1.8	0.96	-0.4	1.99
ITEM 6: During the block it seemed like my hand was in the location where the rubber hand was.	1.83	1.29	-0.53	2.08
ITEM 7: During the block it seemed like the rubber hand was in the location where my hand was.	0.83	1.76	-0.77	1.99

Table 1 Questionnaire items presented after the body illusion, in both the synchronous and asynchronous stimulations, with mean and standard deviation of scores for each question. Participants were required to evaluate their agreement in relation to each statement, using a 7-point Likert scale (from -3, “strongly disagree”, to +3, “strongly agree”).

4. Discussion of Experiment 1

With Experiment 1 we investigated whether changes in body-ownership change interoceptive accuracy. We demonstrate that, after being exposed to a bodily illusion that changes body-ownership, individuals with initially lower levels of interoceptive accuracy improve their ability to accurately detect internal bodily signals. However, the experienced change in body-ownership did not benefit individuals with higher levels of accuracy. While these results provide evidence of exteroceptively-driven changes in interoceptive accuracy, the extent to which specific domains of self-awareness can differentially interact with our ability to focus on internal bodily signals remains unknown. With Experiment 2, we investigated whether the manipulation of self-identification can affect interoceptive accuracy, measured through heartbeat detection task (Schandry, 1991). To quantify the role of changes in self-identification in interoceptive accuracy, we exposed participants to the Enfacement Illusion (Tsakiris, 2008; Tajadura-Jimenez et al., 2012a; 2012b). In line with Experiment 1, we hypothesised that individual differences in interoceptive accuracy would account for the influence of the change in self-identification experienced during synchronous IMS. However, in contrast with Experiment 1, we expected that changes in the representation of one’s identity would have a different effect on interoceptive accuracy. Specifically, in line with a previous study that has shown the presence of a link between feeling of depersonalization and impairments of interoceptive awareness (Sedeno et al. 2014), we hypothesised that self-other

blurring would cause a reduced distinctness of the self, which would affect people with higher-IAcc in their ability to accurately detect any self-relevant information, including their internal bodily signals, such as heartbeat information (Apps and Tsakiris, 2013).

Experiment 2

3.1 Materials and Methods

3.1.1 Participants

Participants were 32 female students at Royal Holloway University of London. Three were excluded for artefacts at the heart rate data (2) and participant's inability to detect the heartbeat during the MTM task (1), leading to a final sample of 29 participants (Mean age = 20.31yr, SD =2.33). The study was approved by the Department of Psychology Ethics Committee, Royal Holloway, University of London.

3.1.2 Experimental setup

Heart rate was monitored using an identical procedure as in Experiment 1. We measured interoceptive accuracy using the Mental Tracking Method (MTM) (Schandry, 1981), and followed the same procedural guidelines as previously explained.

For the IMS task, two 120 s "induction movies" were produced to display the face of an unfamiliar female individual being touched on the right cheek with a cotton bud. Each stroke lasted about 1 s and covered a distance of approximately 2 cm from the zygomatic bone downwards (Tajadura-Jimenez et al., 2012a). The two videos only differed in the female unknown individual face displayed on the video, whose order was counterbalanced between participants. The individuals displayed were 24 and 25 years old. A digital photograph of the participant's face with a neutral facial expression was taken prior to the experimental session. The picture was converted to grayscale and mirror transposed and a black template was used to remove non-facial attributes (Tajadura-Jimenez, Grehl, and Tsakiris, 2012b). A keyboard and Presentation© software were used to control stimuli and collect participant's responses.

3.1.3 Procedure

After one brief training trial (15 s) during which participants familiarised with the MTM, the experimental session started with a Baseline measure of the MTM task. Participants were asked to silently count their heartbeat while focusing on the face appearing on the screen. The individual's face displayed could either be the own participant's face (Self) or the unfamiliar face shown during the IMS phase (Other). For each Face Identity block (Self/Other), participants repeated the MTM task three times. The three trials (25 s, 35 s, and 45s) were presented in random order and constituted a block. Upon completion of this Baseline task, participants were exposed to the IMS phase. While the participant was looking at the other's face being touched in one of the pre-recorded 120 s "induction movies", the experimenter touched the participant's face with an identical cotton bud on the specularly congruent location (i.e., left side on the participant's face, and right side on the other's face) either in synchrony, or asynchrony of 1 s, in different blocks. Next, to behaviourally quantify the effect of IMS on IAcc, participants performed the same MTM task as the one they had completed at Baseline. Participants completed two experimental blocks, one synchronous and one asynchronous, their order counterbalanced across participants. In each experimental block, a 40 s "top-up" IMS phase interleaved the two Face Identity blocks of MTM task (Self/Other). Throughout the experiment, the Other face would always match the face presented to participants during the Baseline MTM task. Participants completed 6 MTM task trials in the synchronous block (3 per each Face Identity – Self/Other) and 6 MTM tasks in the asynchronous block (3 per each Face Identity – Self/Other). The MTM trials were always performed after the visuo-tactile stimulation was completed.

At the end of each experimental block, participants were given to complete a 9-item questionnaire on the experience of illusory identification with the other face during multisensory stimulation (Table 2). Participants were required to evaluate their agreement in relation to each statement, using a 7-point Likert scale (from -3, "strongly disagree", to +3, "strongly agree").

To control for guessing of the number of heartbeat during the MTM task (Ainley et al., 2013), at the end of the experiment participants were asked to estimate the length of three, randomly presented, intervals – Time Modulus (19 s, 37 s, and 49 s) (Dunn et al., 2010).

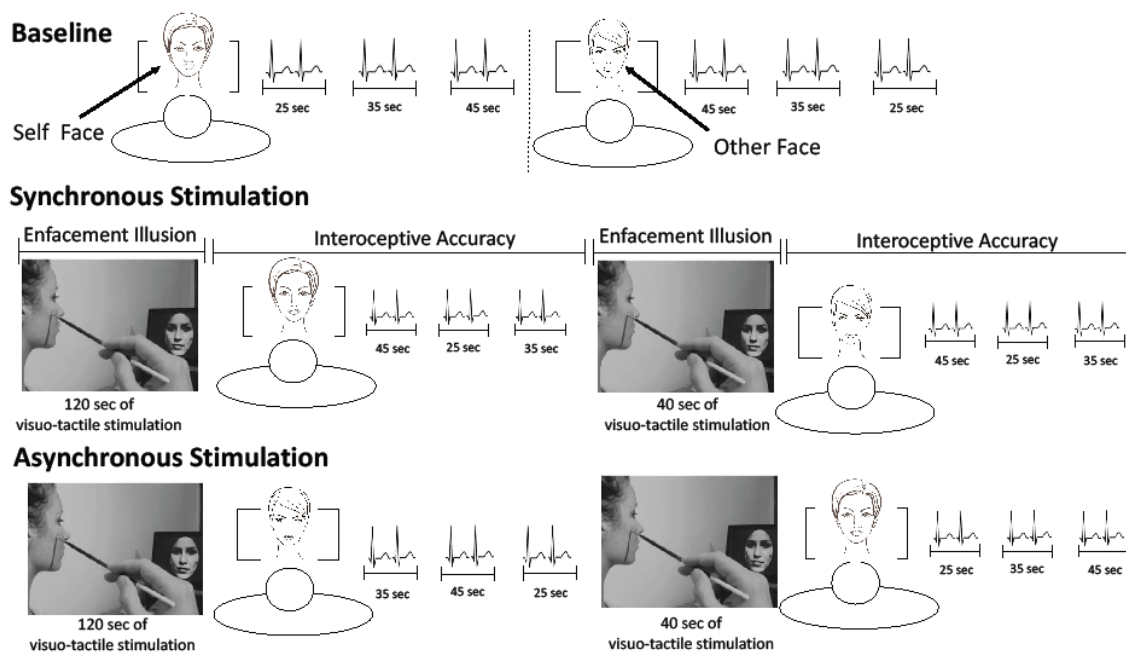


Figure 3 Illustration of the experimental paradigm used. Participants performed the MTM task for each Face Identity at Baseline. Upon completion of this task, participants were exposed to the IMS phase and then performed the MTM task again, with a 40 s “top-up” IMS phase in between MTM blocks (Self/Other). They completed one synchronous and one asynchronous block.

3.1.4 Data analysis

Heartbeat traces were analysed using LabChart8, as detailed in Experiment 1. As in Experiment 1, a median split of IAcc scores was performed in the baseline to divide the sample into higher-IAcc (above median) and lower-IAcc (below median) participants. However, because this experiment comprised two Baseline measures of IAcc, one for the Self Face and one for the Other Face, the median split was computed by averaging together Baseline Self and Baseline Other (median = 0.698). There were no differences between baseline-Self and baseline-Other, $t(28) = 1.62$, $p = 0.12$. In the higher-IAcc group participants were 14 female, whereas in the lower-IAcc group there were 15 female. As in Experiment 1, we computed IAcc-change scores from the baseline; we subtracted the baseline IA score from the Self Synchronous-Face IAcc score, the Self Asynchronous-Face IAcc score, the Other-Synchronous Face IAcc score, and the Other-Asynchronous Face IAcc score to generate four IAcc-change scores. Positive scores reflected an improvement from baseline. Data were analysed using an ANCOVA with Experimental Condition as a within-subjects variable and Order of Presentation and IAcc level as between-subject variables. The Time Modulus and the

Enfacement scores (average scores in the Synchronous and Asynchronous conditions) were entered as covariates, to account for potential confounds of the heartbeat counting task (Ring et al., 2015), and for the possible modulation of the experienced body illusions in IAcc. Greenhouse–Geisser correction was applied when sphericity could not be assumed (Mauchly’s test for sphericity, $p = 0.05$). Comparisons were assessed for significance using planned paired two-tailed t-tests.

Questionnaire responses on the subjective experience of enfacement (Shapiro-Wilk test of normality: EI synchronous, $p = 0.26$, EI asynchronous, $p = 0.84$) were analysed by averaging together ratings across all 9 statements, which provided an estimate of enfacement experienced for each participant in each condition.

Questionnaire items:	Synchronous		Asynchronous	
	Mean	SD	Mean	SD
ITEM 1: I felt like the other's face was my face	0.14	1.88	-1.76	1.50
ITEM 2: It seemed like the other's face belonged to me	-0.18	1.81	-1.83	1.28
ITEM 3: It seemed like I was looking at my own mirror reflection	0.17	1.97	-1.14	1.75
ITEM 4: It seemed like the other's face began to resemble my own face	0.38	1.78	-1.69	1.56
ITEM 5: It seemed like my own face began to resemble the other person's face	-0.07	1.83	-1.38	1.86
ITEM 6: It seemed like my own face was out of my control	-0.04	1.62	-0.24	1.94
ITEM 7: It seemed like the experience of my face was less vivid than normal	0.48	1.38	0	1.94
ITEM 8: I felt that I was imitating the other person	0.65	1.63	-0.24	2.03
ITEM 9: I felt touch on my face when I saw the other person's face being touched	2.76	0.95	-1.24	2.05

Table 2 Questionnaire items presented after the IMS, in both the synchronous and asynchronous stimulations, with mean and standard deviation of scores for each question. Participants were required to evaluate their agreement in relation to each statement, using a 7-point Likert scale (from -3, “strongly disagree”, to +3, “strongly agree”).

3.2 Results

We first examined whether the Enfacement Illusion was successfully elicited using a mixed ANOVA. Enfacement scores were entered into a 2 (Conditions: Synchronous vs Asynchronous) x 2 (averaged IAcc level: lower-IAcc vs higher-IAcc) ANOVA. We found that the Enfacement Illusion was successfully elicited in the synchronous but not the asynchronous condition, $F(1,27) = 68.69$, $p < 0.05$, and the strength of the illusion did not depend on averaged baseline levels of IAcc, $F(1,29) = 0.52$, $p > 0.05$, high-IA group $M = 0.59$, $SD = 1.06$; low-IA group $M = 0.30$, $SD = 0.95$.

To investigate if and how IAcc was modulated by the experience of the Enfacement Illusion, we used a mixed ANCOVA with Condition (Synchronous vs Asynchronous) and Identity (Self Face vs Other Face) as within-subject variables, and averaged IAcc level (lower-IAcc vs higher-IAcc) and Order of Condition as between-subject factors. We found no significant main effect of condition on IAcc, $F(1,22) = 0.11$, $p = 0.74$, after controlling for Time Modulus, and Enfacement Scores (average scores in the Synchronous and Asynchronous conditions). Crucially, the three-way interaction Condition X Identity X IAcc level was significant, $F(1,22) = 5.33$, $p = 0.031$, $\eta^2 = 0.20$. To further investigate this interaction, we run two separate mixed ANOVAs for each Face Identity (Self and Other), using the averaged IAcc level as between-subject factor. With regard to the Self Identity we found that, while there was no main effect of condition on IAcc, $F(1,27) = 2.25$, $p = 0.16$, the interaction Condition X IAcc level was significant, $F(1,27) = 6.78$, $p = 0.015$, $\eta^2 = 0.20$, indicating that the feeling of enfacing another person's face through synchronous stroking significantly disrupted interoceptive accuracy when watching the Self face for the higher-IAcc group, $t(13) = 3.12$, $p = 0.008$, $d = 0.69$, but had no effect on the lower-IAcc group, $t(13) = -0.71$, $p = 0.49$ (Figure 4). We found no significant main effect of IAcc level, $F(1,27) = 2.84$, $p = 0.10$. In contrast with these results, the mixed ANOVA on Other Identity didn't reveal any significant main effect or interaction (main effect Condition, $F(1,27) = 1.10$, $p = 0.31$; main effect IAcc level, $F(1,27) = 1.49$, $p = 0.23$; interaction Condition X IAcc level, $F(1,27) = 0.08$, $p = 0.78$ – Figure 4), suggesting that our enfacement manipulation didn't affect individuals' ability to perform the MTM task when watching the other person's face.

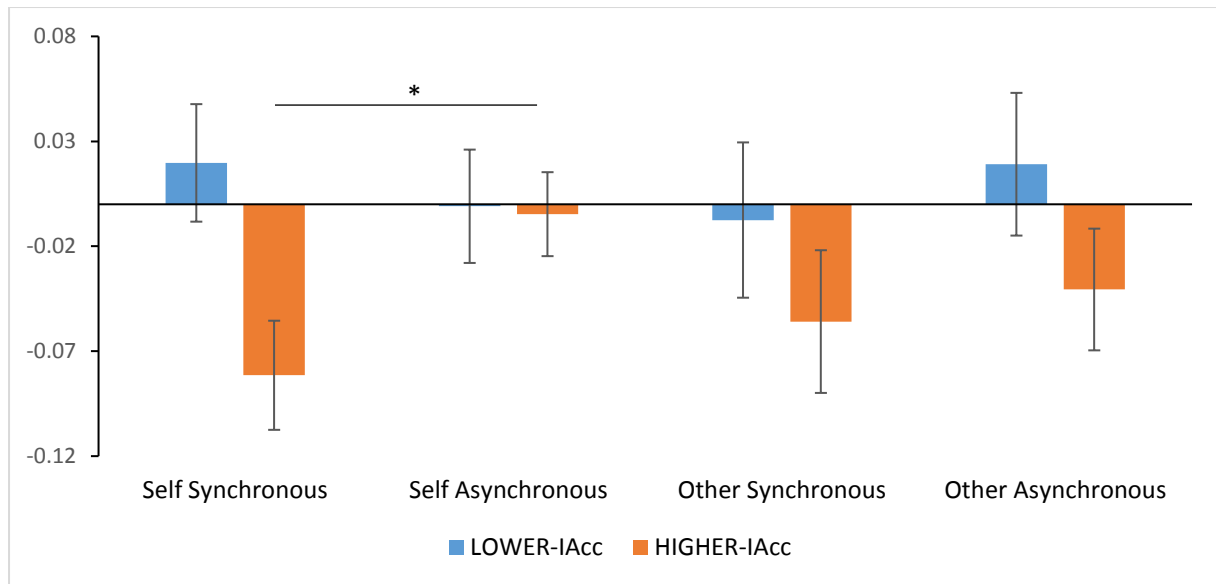


Figure 4 Mean IAcc-change scores of the lower-IAcc and higher-IAcc groups in Enfacement Illusion (Synchronous) and asynchronous (Asynchronous) conditions, under the Self Face Identity and Other-Face Identity manipulations. Error bars show standard error (SE).

4. Discussion

Across two experiments, we investigated whether changes in BSC change interoceptive accuracy. In Experiment 1 we manipulated participants' sense of body-ownership by applying the RHI. The induction of an illusory sense of body-ownership significantly improved the performance at a standard heartbeat-counting task in individuals with lower interoceptive accuracy at baseline, but did not benefit individuals with higher interoceptive accuracy. These results suggest that, in the process of re-instating a sense of body-ownership, individuals with initially lower accuracy in detecting internal bodily sensations benefit from exteroceptive bodily signals in order to acquire information about their internal state and improve their interoceptive accuracy.

Experiment 2 investigated whether the exteroceptively-driven change in interoceptive accuracy found in Experiment 1 could be extended to components of self-awareness other than body-ownership. Here we measured whether changes in self-identification through the use of the EI could affect individuals' ability to detect their internal bodily signals. We found that participants with initially higher-IAcc did not benefit from the illusion; instead, their IAcc performance while looking at their own face significantly decreased after experiencing the Enfacement Illusion with another face.

In both experiments, the effect was independent of the order in which the conditions were presented, the participants' own estimations of time intervals and heart rate. The presence of a

significant interaction between synchronous and asynchronous conditions excludes the possibility of a general practice effect. Importantly, participants showed a significant change after synchronous stroking, over and above the mere presence of multisensory stimulation (i.e. asynchronous condition), which exclude any possible effect due to regression to the mean. In our experiments, participants performed the MTM task after the visuo-tactile stimulation was completed. This setting allowed us to distinguish the exteroceptive and interoceptive tasks and minimize any possible interference between them. Additionally, across all trials participants were looking at the rubber hand (Experiment 1) and at the Self- or Other-face (Experiment 2) in the absence of any stimulation, to ensure that participants' attention was comparable across conditions.

In our sample the reported experiences of body-ownership and self-identification did not correlate with the performance in the heartbeat counting task. While previous studies found evidence of a negative correlation between measures of body-ownership and interoceptive accuracy (Tsakiris et al., 2011; see also Schauder et al., 2015 for a replication) and self-identification and interoceptive accuracy (Tajadura-Jimenez et al., 2014), research that implemented the cardio-visual feedback (Suzuki et al., 2013) reported a positive correlation between strength of the illusion and interoceptive accuracy. Importantly, in the present study, unlike the studies by Tsakiris et al (2011) and Schauder et al (2015) were participants performed the heartbeat counting task only at baseline, while looking at blank screen, participants performed the heartbeat counting task while they were looking at a body-part or face even at baseline. Overall, these results suggest that perhaps the relationship between interoceptive and exteroceptive bodily cues is more complex and largely context-dependent. In both experiments we found that participants reported a stronger illusion in the synchronous compared to the asynchronous condition, however the strength of subjective experience in the EI is lower compared to the RHI, consistent with previous studies. We believe this difference could be due to the different components of bodily self-consciousness underlying the two illusions. While the RHI involves the vivid experience of changes in ownership of body-parts, the EI tackles into a fundamental component of selfhood, that is one's face, where self-other blurring usually appears in a less vivid manner. In this sense, a self-recognition task would have perhaps helped in capturing changes in self-identification across conditions. Future investigations of the topic should introduce the self-recognition measure as an additional and probably subtler measure of the enfacement.

Previous research on the physiological mechanisms that underlie the experience of body-awareness has shown how changes in the experience of body-ownership in the RHI

results in changes in internal autonomic processes, such as a drop in skin temperature of the hand (Moseley et al., 2008; but see Rohde et al., 2013). Other studies have shown how accuracy in detection of interoceptive states such as heartbeats (Tsakiris et al., 2011; Tajadura-Jimenez & Tsakiris, 2014) and controlled changes in interoceptive input (Kammers, Rose, & Haggard, 2011, Crucianelli et al., 2013; Lloyd et al., 2013) modulate the experience of body-ownership. However, the present study is the first to provide direct evidence of the reverse effect, by showing how exteroceptively-driven changes in BSC can in turn alter interoceptive accuracy.

In Experiment 1, we show that after reporting a change in body-ownership, only individuals with lower-IAcc benefit from it. Recent studies have shown that attention to exteroceptive bodily signals facilitates processing of self-related information, like interoception (Ainley et al., 2012; Maister and Tsakiris, 2014; Maister et al., 2014). With the present study we corroborate this hypothesis and further demonstrate that the specific experiences of body-ownership seem to be crucial for interoceptive accuracy. In Experiment 2, however, we show a different effect, namely that after experiencing a change in self-identification, individuals with higher-IAcc decrease their ability to accurately detect their heartbeat. In these individuals, the change in self-identification may conflict with their interoceptive predictions of how looking at or identifying with one's face feels like (Aspell et al., 2013). Crucially, this was especially true after synchronous interpersonal multisensory stimulation, where self-other blurring presumably caused a decrease in vividness of the self, which in turn resulted in the reduced ability to accurately detect self-relevant information in another domain, namely interoception (Apps and Tsakiris, 2014). Taken together, the previous and current findings seem to support recent predictive coding models of self-awareness (Apps & Tsakiris, 2014; Sel, Harding & Tsakiris, 2016; Seth, 2013) according to which one's body is processed in a probabilistic manner as the most likely to be 'me'. Such probabilistic representations are created through the integration of top-down 'predictions' about the body and of bottom-up 'prediction errors' from unimodal sensory systems that are then accounted for. Bidirectional interactions between exteroceptive and interoceptive systems are essential for an integrated awareness of one's body. Our results can thus be explained in light of a predictive coding account. The observed results support the view that the self is a multimodal and hierarchical construct that is critically dependent on multisensory input. Furthermore, the effects of the multisensory-induced changes along this hierarchy depend on both the exact bodily representation affected (e.g. body-ownership or self-identification) and the precision of the prior.

According to predictive coding, changes in body-ownership after the RHI should result in increased IAcc for participants with lower IAcc at baseline, because synchronous multisensory stimulation raises the precision of higher-level priors for the self, and this in turn increases the precision of all self-relevant data, including interoceptive information (Apps & Tsakiris, 2014). In contrast, in the Enfacement Illusion, that uses multisensory stimulation as the RHI but in a more social context, the increased precision of high-level priors may have a different effect, as a result of self-other blurring. For faces, that are central to one's identity as well as inherently social stimuli, interoceptive priors and prediction errors of how it feels like to look at one's face (or at other people) may be more precise. It has been shown that prediction errors related to the processing of one's face identity as opposed to one's body-identity result in larger mismatch responses, indicative of larger prediction errors (see Experiment 2 in Sel, Harding, and Tsakiris, 2016). In explaining away such larger prediction errors, precision in the interoceptive domain may be reduced, affecting performance in participants with higher IAcc. By increasing the probability that the other face is represented as part of the self (and decreasing the probability that one's actual face is represented as 'self'), the ability to distinguish between self and other is reduced. In people with lower-IAcc, whose priors about the self are already imprecise, this is unlikely to have any added effect on heartbeat perception. However, in people with initially higher-IAcc this increase in 'surprise' as a result of the illusion may (erroneously) update the high-level prior, causing self-other blurring, which would explain why they become less accurate in heartbeat counting. Electrophysiological studies that quantify the Heartbeat Evoked Potential under such bodily illusions may elucidate the underlying neurophysiological mechanism.

We hypothesize that the observed changes in IAcc in both experiments could be attributed to modulations of neural processing in the right anterior insula, a candidate area for hierarchically organized multimodal predictive models of self-representations (Allen et al, 2015; Gu et al, 2013), where multisensory information from interoceptive and exteroceptive signals is processed to establish the predictive model of an integrated bodily self (Seth, 2013; Apps & Tsakiris, 2014). In fact, right anterior insula activity correlates with performance in interoceptive accuracy tasks (Critchley et al, 2004). Ronchi et al (2015) report a single-case study showing that heartbeat awareness decreased after insular resection. Salomon and colleagues (2016) showed that this region is sensitive to synchronicity of visual and cardiac signals, both in the case of visible and invisible visual cues. Right mid-posterior insula activity correlates with the body-ownership experienced during the RHI (Tsakiris et al, 2007), and the same area seems to be the critical lesion site for somatoparaphrenia, a striking loss of body-

ownership (Baier & Karnath, 2010). These findings suggest that the interoceptive and the exteroceptive body are integrated from the posterior to anterior subregions *across* the insular cortex (Simmons et al, 2013), that seems to underpin the experience of this body as *mine*, an experience that is the hallmark of the bodily self. Importantly, beyond the representation of the body, the insular cortex is also linked to the processing of representations of self and others, in terms of their facial identity (Devue & Brédart, 2011) and a wide range of social cognition processes such as empathy (Bernhardt & Singer, 2012), highlighting its importance beyond the self itself. However, future research and advances in methods are needed to understand for what are the precise neural computations that within the same neural network process information about the self or about the self in relation to others.

In summary, our data show that changes in exteroceptive self-awareness can influence interoceptive accuracy. We further show that changes on body-ownership and self-identification have contrasting effects on interoceptive accuracy. The specificity of this effect could be attributed to the component of bodily self-consciousness being manipulated across the two different bodily illusions (self-identification vs body-ownership). The evidence that lower interoceptive accuracy can be enhanced by attending to external body-related information corroborates previous work (Ainley et al., 2012; 2013; Maister et al., 2014) and further shows that changes in the specific experience of body-ownership can significantly modulate the detection of internal body signals. These findings have potential important implication for our understanding of intact as well as impaired body awareness, such as neuropsychological syndromes (Jenkinson et al., 2013; Fotopoulou et al., 2011) and psychiatric disorders such as eating and body-image disorders (Eshkevari et al., 2012; Pollatos et al., 2008; Keizer et al., 2014). Similarly, the findings that interoceptive accuracy may be affected under conditions that blur self-other boundaries may have important theoretical implications for our understanding of the social function that interoceptive states and their awareness may play in social interactions (Bird & Viding, 2014) and their disorders (Schilbach, 2016).

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References:

- Ainley, V., Brass, M., & Tsakiris, M. (2014). Heartfelt imitation: High interoceptive awareness is linked to greater automatic imitation. *Neuropsychologia*, 60, 21–28.
- Ainley, V., Maister, L., Brokfeld, J., Farmer, H., & Tsakiris, M. (2013). More of myself: Manipulating interoceptive awareness by heightened attention to bodily and narrative aspects of the self. *Consciousness and Cognition*, 22(4), 1231–1238.
- Ainley, V., Tajadura-Jiménez, A., Fotopoulou, A., & Tsakiris, M. (2012). Looking into myself: Changes in interoceptive sensitivity during mirror self-observation. *Psychophysiology*, 49(11), 1672–1676.
- Allen, M., Fardo, F., Dietz, M. J., Hillebrandt, H., Friston, K., Rees, G., & Roepstorff, A. (2015). Anterior insula coordinates hierarchical processing of tactile mismatch responses. *NeuroImage*.
- Apps, M. A., Tajadura-Jiménez, A., Sereno, M., Blanke, O., & Tsakiris, M. (2015). Plasticity in unimodal and multimodal brain areas reflects multisensory changes in self-face identification. *Cerebral Cortex (New York, NY: 1991)*, 25(1), 46–55.
- Apps, M. A., & Tsakiris, M. (2013). Predictive codes of familiarity and context during the perceptual learning of facial identities. *Nature communications*, 4.
- Apps, M. A., & Tsakiris, M. (2014). The free-energy self: A predictive coding account of self-recognition. *Neuroscience & Biobehavioral Reviews*, 41, 85–97.
- Aspell, J. E., Heydrich, L., Marillier, G., Lavanchy, T., Herbelin, B., & Blanke, O. (2013). Turning body and self inside out visualized heartbeats alter bodily selfconsciousness and tactile perception. *Psychological Science*. 0956797613498395.
- Baier, B., & Karnath, H. O. (2008). Tight link between our sense of limb ownership and self-awareness of actions. *Stroke*, 39(2), 486–488.
- Bernhardt, B. C., & Singer, T. (2012). The neural basis of empathy. *Neuroscience*, 35 (1), 1.
- Bird, G., & Viding, E. (2014). The self to other model of empathy: Providing a new framework for understanding empathy impairments in psychopathy, autism, and alexithymia. *Neuroscience and Biobehavioral Reviews*, 47, 520–532.
- Botvinick, M., & Cohen, J. (1998). Rubber hands ‘feel’ touch that eyes see. *Nature*, 391 (6669), 756.
- Cardini, F., Tajadura-Jiménez, A., Serino, A., & Tsakiris, M. (2013). It feels like it’s me: Interpersonal multisensory stimulation enhances visual remapping of touch from other to self. *Journal of Experimental Psychology: Human Perception and Performance*, 39(3), 630.
- Craig, A. D. (2002). How do you feel? Interoception: The sense of the physiological condition of the body. *Nature Reviews Neuroscience*, 3(8), 655–666.
- Craig, A. D. (2010). The sentient self. *Brain Structure and Function*, 1–15.
- Critchley, H. D., Wiens, S., Rotshtein, P., Öhman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, 7(2), 189–195.

- Crucianelli, L., Metcalf, N. K., Fotopoulou, A. K., & Jenkinson, P. M. (2013). Bodily pleasure matters: Velocity of touch modulates body ownership during the rubber hand illusion. *Frontiers in Psychology*, 4.
- Devue, C., & Brédart, S. (2011). The neural correlates of visual self-recognition. *Consciousness and Cognition*, 20(1), 40–51.
- Dunn, B. D., Galton, H. C., Morgan, R., Evans, D., Oliver, C., Meyer, M., ... Dalgleish, T. (2010). Listening to your heart how interoception shapes emotion experience and intuitive decision making. *Psychological Science*, 21(12), 1835–1844.
- Edwards, M. J., Adams, R. A., Brown, H., Pareés, I., & Friston, K. J. (2012). A Bayesian account of “hysteria”. *Brain*, 135(11), 3495–3512.
- Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science*, 317(5841), 1048.
- Ehrsson, H. H., Holmes, N. P., & Passingham, R. E. (2005). Touching a rubber hand: Feeling of body ownership is associated with activity in multisensory brain areas. *The Journal of Neuroscience*, 25(45), 10564–10573.
- Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That’s my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science*, 305(5685), 875–877.
- Eshkevari, E., Rieger, E., Longo, M. R., Haggard, P., & Treasure, J. (2012). Increased plasticity of the bodily self in eating disorders. *Psychological Medicine*, 42(04), 819–828.
- Fotopoulou, A., Jenkinson, P. M., Tsakiris, M., Haggard, P., Rudd, A., & Kopelman, M. D. (2011). Mirror-view reverses somatoparaphrenia: Dissociation between first-hand third-person perspectives on body ownership. *Neuropsychologia*, 49(14), 3946–3955.
- Gu, X., Hof, P. R., Friston, K. J., & Fan, J. (2013). Anterior insular cortex and emotional awareness. *Journal of Comparative Neurology*, 521(15), 3371–3388.
- Herbert, B. M., & Pollatos, O. (2012). The body in the mind: On the relationship between interoception and embodiment. *Topics in Cognitive Science*, 4(4), 692–704.
- Holle, H., McLatchie, N., Maurer, S., & Ward, J. (2011). Proprioceptive drift without illusions of ownership for rotated hands in the “rubber hand illusion” paradigm. *Cognitive Neuroscience*, 2(3–4), 171–178.
- Jenkinson, P. M., Haggard, P., Ferreira, N. C., & Fotopoulou, A. (2013). Body ownership and attention in the mirror: Insights from somatoparaphrenia and the rubber hand illusion. *Neuropsychologia*, 51(8), 1453–1462.
- Jennings, R., Berg, K., Hutcheson, J., Obrist, P., Porges, S., & Turpin, G. (1981). Publication guidelines for heart rate studies in man. *Psychophysiology*, 18(3), 227–231.
- Kammers, M. P., Rose, K., & Haggard, P. (2011). Feeling numb: Temperature, but not thermal pain, modulates feeling of body ownership. *Neuropsychologia*, 49(5), 1316–1321.

- Keizer, A., Smeets, M. A., Postma, A., van Elburg, A., & Dijkerman, H. C. (2014). Does the experience of ownership over a rubber hand change body size perception in anorexia nervosa patients? *Neuropsychologia*, *62*, 26–37.
- Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: Manipulating bodily self-consciousness. *Science*, *317*(5841), 1096–1099.
- Limanowski, J., & Blankenburg, F. (2013). Minimal self-models and the free energy principle. *Frontiers in Human Neuroscience*, *7*, 547. <http://dx.doi.org/10.3389/fnhum.2013.00547>.
- Lloyd, D. M., Gillis, V., Lewis, E., & Farrell, M. J. (2013). Pleasant touch moderates the subjective but not objective aspects of body perception. *Frontiers in Behavioral Neuroscience*, *7*.
- Longo, M. R., Schüür, F., Kammers, M. P., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition*, *107*(3), 978–998.
- Maister, L., & Tsakiris, M. (2014). My face, my heart: Cultural differences in integrated bodily self-awareness. *Cognitive Neuroscience*, *5*(1), 10–16.
- 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.
- Paladino, M. P., Mazzurega, M., Pavani, F., & Schubert, T. W. (2010). Synchronous multisensory stimulation blurs self-other boundaries. *Psychological Science*, *21* (9), 1202–1207.
- Pollatos, O., Kurz, A. L., Albrecht, J., Schreder, T., Kleemann, A. M., Schöpf, V., ... Schandry, R. (2008). Reduced perception of bodily signals in anorexia nervosa. *Eating Behaviors*, *9*(4), 381–388.
- Ring, C., Brener, J., Knapp, K., & Mailloux, J. (2015). Effects of heartbeat feedback on beliefs about heart rate and heartbeat counting: A cautionary tale about interoceptive awareness. *Biological psychology*, *104*, 193–198.
- Rohde, M., Di Luca, M., & Ernst, M. O. (2011). The rubber hand illusion: Feeling of ownership and proprioceptive drift do not go hand in hand. *PLoS ONE*, *6*(6), e21659.
- Rohde, M., Wold, A., Karnath, H. O., & Ernst, M. O. (2013). The human touch: Skin temperature during the rubber hand illusion in manual and automated stroking procedures. *PLoS ONE*, *8*(11).
- Ronchi, R., Bello-Ruiz, J., Lukowska, M., Herbelin, B., Cabrilo, I., Schaller, K., & Blanke, O. (2015). Right insular damage decreases heartbeat awareness and alters cardio-visual effects on bodily self-consciousness. *Neuropsychologia*, *70*, 11–20.
- Salomon, R., Ronchi, R., Dönz, J., Bello-Ruiz, J., Herbelin, B., Martet, R., ... Blanke, O. (2016). The insula mediates access to awareness of visual stimuli presented synchronously to the heartbeat. *The Journal of Neuroscience*, *36*(18), 5115–5127.

- Samad, M., Chung, A. J., & Shams, L. (2015). Perception of body ownership is driven by bayesian sensory inference. *PLoS ONE*, 10(2), e0117178.
- Schandry, R. (1981). Heart beat perception and emotional experience. *Psychophysiology*, 18(4), 483–488.
- Schauder, K. B., Mash, L. E., Bryant, L. K., & Cascio, C. J. (2015). Interoceptive ability and body awareness in autism spectrum disorder. *Journal of Experimental Child Psychology*, 131, 193–200.
- Schilbach, L. (2016). Towards a second-person neuropsychiatry. *Philosophical Transactions of the Royal Society of London B*, 371(1686), 20150081.
- Sedeño, L., Couto, B., Melloni, M., Canales-Johnson, A., Yoris, A., Baez, S., ... Kichic, R. (2014). How do you feel when you can't feel your body? Interoception, functional connectivity and emotional processing in depersonalization derealization disorder. *PLoS ONE*, 9(6), e98769.
- Sel, A., Harding, R., & Tsakiris, M. (2016). Electrophysiological correlates of self-specific prediction errors in the human brain. *NeuroImage*, 125, 13–24.
- Seth, A. K. (2013). Interoceptive inference, emotion, and the embodied self. *Trends in Cognitive Sciences*, 17(11), 565–573.
- Seth, A. K., Suzuki, K., & Critchley, H. D. (2011). An interoceptive predictive coding model of conscious presence. *Frontiers in psychology*, 2.
- Simmons, W. K., Avery, J. A., Barcalow, J. C., Bodurka, J., Drevets, W. C., & Bellgowan, P. (2013). Keeping the body in mind: Insula functional organization and functional connectivity integrate interoceptive, exteroceptive, and emotional awareness. *Human brain mapping*, 34(11), 2944–2958.
- 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.
- Tajadura-Jiménez, A., Grehl, S., & Tsakiris, M. (2012). The other in me: Interpersonal multisensory stimulation changes the mental representation of the self. *PLoS ONE*, 7(7), e40682.
- Tajadura-Jiménez, A., Longo, M. R., Coleman, R., & Tsakiris, M. (2012). The person in the mirror: Using the enfacement illusion to investigate the experiential structure of self-identification. *Consciousness and Cognition*, 21(4), 1725–1738.
- Tajadura-Jiménez, A., & Tsakiris, M. (2014). Balancing the “inner” and the “outer” self: Interoceptive sensitivity modulates self-other boundaries. *Journal of Experimental Psychology: General*, 143(2), 736.
- Tsakiris, M. (2008). Looking for myself: Current multisensory input alters self-face recognition. *PLoS ONE*, 3(12), e4040.

- Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body ownership. *Neuropsychologia*, 48(3), 703–712.
- 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.
- Tsakiris, M., Hesse, M. D., Boy, C., Haggard, P., & Fink, G. R. (2007). Neural signatures of body ownership: A sensory network for bodily self-consciousness. *Cerebral Cortex*, 17(10), 2235–2244.
- Tsakiris, M., Schütz-Bosbach, S., & Gallagher, S. (2007). On agency and body ownership: Phenomenological and neurocognitive reflections. *Consciousness and Cognition*, 16(3), 645–660.
- Tsakiris, M., Tajadura-Jiménez, A., & 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*. rspb20102547.
- van Stralen, H. E., van Zandvoort, M. J., Hoppenbrouwers, S. S., Vissers, L. M., Kappelle, L. J., & Dijkerman, H. C. (2014). Affective touch modulates the rubber hand illusion. *Cognition*, 131(1), 147–158.