

Taking the pulse of social cognition: cardiac afferent activity and interoceptive accuracy modulate emotional egocentricity bias

Mariana von Mohr^{1*}, Gianluca Finotti¹, Valerio Villani¹, Manos Tsakiris^{1,2,3}

¹Lab of Action and Body, Department of Psychology, Royal Holloway, University of London

²The Warburg Institute, School of Advanced Study, University of London

³Department of Behavioural and Cognitive Sciences, Faculty of Humanities, Education and Social Sciences, University of Luxembourg, Luxembourg

*Corresponding Author : Mariana von Mohr, Department of Psychology, Royal Holloway University of London, Egham TW20 0EX, Email: mariana.vonmohr@rhul.ac.uk

Abstract

At the heart of social cognition is our ability to distinguish between self and other and correctly attribute mental and affective states to their origin. Emotional egocentricity bias (EEB) reflects the tendency to use one's own emotional state when relating to others. Although interoception underpins our emotional experience, little is known about its role on how we affectively relate to others. Here, we assessed how cardiac interoceptive impact, manipulated by presenting affective stimuli across different phases of the cardiac cycle coupled with trait-like levels of interoceptive accuracy, modulate the EEB. Individuals with higher interoceptive accuracy displayed an increased EEB when the other's emotional state was presented at the point of maximum interoceptive impact (i.e., at systole), whereas the reverse was observed for individuals with lower interoceptive accuracy. These findings show how interoceptive activity provides the physiological context within which we process other's emotional states in parallel to ours.

Key words: emotional egocentricity bias; self-other distinction; interoception; baroreceptor firing

Highlights

- EEB is the tendency to use one's own emotional state when relating to others
- Interoception underpins our emotional experience
- Trait-like and state-like cardiac interoceptive impact modulate EEB
- Increased EEB at systole in those with higher interoceptive accuracy
- Lower EEB at systole in those with lower interoceptive accuracy

Introduction

How can we distinguish between self and other at the very time that we are trying to relate to each other? From the mundane situation of emotion contagion to the affectively salient case of empathy for pain to the complex case of reconciliation, the brain must monitor whether sensations, mental and emotional states should be attributed to the self or others. Shared neural activations underpin our ability to represent our own internal state as well as that of others (Jenkins, Macrae, & Mitchell, 2008; Lamm, Porges, Cacioppo, & Decety, 2008; Singer et al., 2004). Consequently, social neuroscience models posit that first-person affective representations serve as a basis for understanding of others (Bastiaansen, Thioux, & Keysers, 2009; Mitchell, 2009; Singer & Lamm, 2009), and that attributing emotional and mental states to others seems to be influenced by egocentric tendencies (Greenwald, 1980; Nickerson, 1999; Royzman, Cassidy, & Baron, 2003). Nevertheless, this process can be inappropriate when the emotions experienced by self and other are incongruent, resulting in emotional egocentricity bias (EEB): the tendency to project one's own emotional state onto others. For example, when we feel sad, we may falsely assume that the other person is sad as well, which may lead to a biased representation of others' emotional state. Indeed, switching from a self to other perspective is an effortful process that to some extent requires the attenuation of self-representations (Bird & Viding, 2014), especially when there is an affective mismatch between self and other.

Recently, interoception has become central to our understanding of how internal bodily states underpin emotional experience. Often viewed as a trait, interoceptive accuracy (IAcc) and awareness have been linked to the intensity of an individual's own emotional experience (Barrett, Bliss-Moreau, Quigley, & Aronson, 2004; Pollatos, Kirsch, & Schandry, 2005) as well as emotional regulation (Dunn, Evans, Makarova, White, & Clark, 2012; Füstös, Gramann, Herbert, & Pollatos, 2013). Neuroimaging studies also indicate an overlap between the neural substrates of emotion and interoception (see Critchley & Garfinkel, 2017 for a review). More recently it has been shown that IAcc (as measured by the Heartbeat Counting Task; Schandry, 1981) correlates with emotional, but

not cognitive (Ainley, Maister, & Tsakiris, 2015), aspects of empathy (Grynberg & Pollatos, 2015; Shah, Catmur, & Bird, 2017). Thus, even though interoception is well known to underpin one's own emotional experience, its role in social cognition remains mainly correlational and largely unexplored. In fact, to date, only one study has examined whether interoception impacts perspective taking (Heydrich et al., 2021) yet, this study only focused on differences in spatial perspective taking.

Despite the scarce evidence, recent theoretical frameworks have proposed that interoception plays a key role in social cognition. Emotional contagion, mimicry, perspective-taking, theory of mind, empathy and egocentricity biases have been used to operationalize different facets of empathy and social relatedness. Palmer & Tsakiris (2018) proposed that interoception plays a critical role in enabling us to navigate the different degrees of social relatedness, by allowing us to attribute emotional states to the self or to others without blurring the self-other distinction. Thus, at the most basic levels of empathy that involve self-other overlap, such as emotional contagion, those with lower IAcc are hypothesized to more readily relate to other's emotional state. By contrast, at higher levels of empathy that require us to represent another's emotional state that may be incongruent with our own emotional state, higher IAcc may be important for maintaining self-other distinction (see Figure 1). Specifically, individuals with higher IAcc are suggested to better relate to the emotional state of others, given that they possess a more stable representation of their bodily self and consequently their emotional state (Palmer & Tsakiris, 2018). As such, in cases of affective mismatch, higher IAcc may be important to enable individuals to accurately "assign" affective states to the self or the other as the source. However, research is still needed to test this hypothesis, as well as to move beyond correlational designs. Indeed, studies have provided means of causally manipulating interoceptive impact by presenting stimuli at specific points of the cardiac cycle, which allows control over the autonomic context within which stimuli are perceived. At systole, during a heartbeat, arterial baroreceptors signal to the brain, but at diastole, between heartbeats, this pathway is silent. Recent studies have shown that presentation of stimuli at systole decreases memory for words (Garfinkel et al., 2013) amplifies threat processing to fearful faces (Garfinkel et al., 2014) increases the expression

of fear-related racial stereotyping (Azevedo, Garfinkel, Critchley, & Tsakiris, 2017) and speeds up self-face recognition (Ambrosini, Finotti, Azevedo, Tsakiris, & Ferri, 2019).

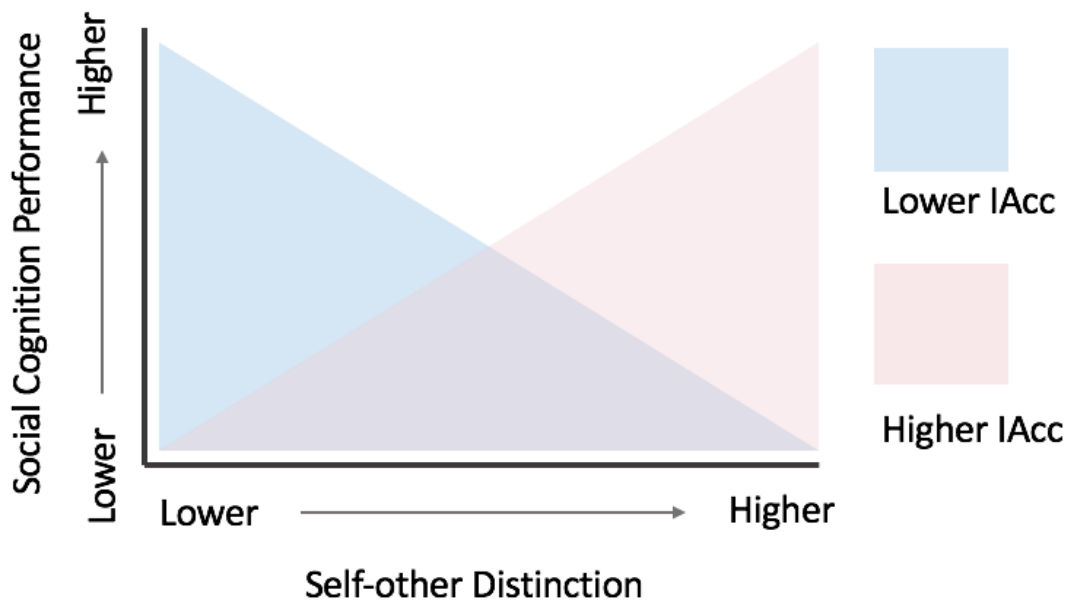


Figure 1. Illustration adapted from Palmer & Tsakiris (2018). This figure illustrates hypotheses on how IAcc may impact social cognition performance depending on the level of self-other overlap in the task. For tasks with a low level of self-other distinction, for example emotional contagion, it may be advantageous to have lower level of IAcc, such that individuals will display greater emotional contagion. By contrast, when a social task requires a high level of self-other distinction, such as EEB, individuals with higher IAcc may be better able to understand the emotional state of others because these individuals have a more stable representation of their own bodily self, which prevents the blurring of self and other resulting in improved performance.

We used these insights to apply this framework in a new EEB design. Specifically, we employed the audio-visual EEB task (von Mohr, Finotti, Ambroziak, & Tsakiris, 2019): a recently validated paradigm that induces incongruent and congruent emotions between a participant and another person by means of unpleasant or pleasant audio-visual stimulation. Namely, the visual stimuli reflect the auditory stimuli (which can be positive or negative) that the other person is listening to, whereas simultaneously, the participant himself listens to positive or negative auditory stimuli. This paradigm allows the presentation of visual stimuli in discrete, short-term, physiological contexts

(i.e., at systole vs. diastole) in order to individuate the potential cardiac interoceptive impact on EEB, paving the way for a causal investigation of the role that interoceptive impact plays in social cognition. In particular, given that the visual stimuli depict what the other person is listening to, participants receive accentuated physiological information about the other's emotional state during the systolic vs. diastolic, baseline condition. Based on past results (Barrett et al., 2004; Dunn et al., 2012; Füstös et al., 2013; Pollatos et al., 2005) that highlight the critical role of IAcc in emotional processing, we also measured trait IAcc using the Heartbeat Counting Task (HCT; Schandry, 1981), an established measure of cardioception that reflects individual differences on a range of affective and cognitive processes (Manos Tsakiris & Critchley, 2016).

Consistent with recent studies (Grynberg & Pollatos, 2015; Shah et al., 2017) and theoretical postulations (Palmer & Tsakiris, 2018), we hypothesized lower EEB at higher levels of IAcc in the diastolic, baseline condition, indicating that people who are more accurate and aware of their own cardiac activity can better judge other's emotional state without overimposing their own. Specifically, if higher IAcc is indeed advantageous, EEB scores are expected to be lower in this scenario, consistent with past research (see von Mohr et al., 2019) where lower EEB values indicate that individuals are accurately attributing the emotional experience to self or the other. By contrast, at the systolic condition, when participant's receive information about the other's emotional state at a time when their own cardiac physiological is accentuated, we hypothesized enhanced EEB at higher but not lower levels of IAcc, given that individuals with higher IAcc experience increased emotional intensity (Barrett et al., 2004; Pollatos et al., 2005) and also possess a stronger sense of self, grounded in their interoceptive states (Sel, Azevedo, & Tsakiris, 2017; Suzuki, Garfinkel, Critchley, & Seth, 2013; M. Tsakiris, Jimenez, & Costantini, 2011). Thus, indicating the tendency to resist the overwhelming of the self by the other's emotional state.

Methods

Participants

Forty-six healthy participants (31 female, 15 male; $M_{\text{age}} = 21.80$, $SD_{\text{age}} = 4.39$) were recruited via the Departmental Subject Pool and were compensated for their participation with £10. The study was approved by Royal Holloway's Ethics Committee. The sample size was determined based on simulation-based power-analysis (ANOVApower R package; see 27) in accordance with weighted by sample means reported in prior experimental studies validating the AV-EEB task (von Mohr et al., 2019) in order to detect an EEB effect with 95% power. We opted for a conservative approach (95% power) given that only if we obtained an EEB effect, we could then examine the role of IAcc and cardiac cycle (continuous by categorical interaction) on EEB scores. Participants were recruited in same-gender pairs, unknown to each other. In cases when another participant was not recruited, a same-gendered confederate was used to complete the pair (this was the case only twice and their data were not analyzed or included in the reported N).

Design

We used a recently developed and validated audio-visual EEB task (von Mohr et al., 2019) to quantify the degree of EEB. In this task, people listen to sounds intended to elicit positive or negative affect, while at the same time they look at pictures on the screen which are intended to convey what the other member of the pair is listening to. On each trial they are asked to make a judgment about their emotional experience while listening to the sound (the "self judgement"), or to rate the experience that they thought the other person had while listening to the sound (the "other judgement") depicted by the picture on the screen.

Our key interoceptive manipulation was to control the timing of the presentation of the images by time-locking them to different phases of the cardiac cycle. As such, our within-subjects design comprised two main experimental conditions: pictures (200 ms duration) depicting what the 'other person is listening to' were presented at systole (200 ms after R peak detection); and at diastole (450 ms after R peak detection), accompanied by sounds that were congruent or incongruent in terms of

valence. Our outcome measure was the EEB score calculated for each of the two cardiac conditions systole and diastole. In the EEB paradigm, this is obtained by calculating the difference between other-related ratings for incongruent vs. congruent audio-visual trials. The self-condition in the EEB task acts as a control for unspecific effects such as incongruence detection or stimulus conflict. Therefore, the difference between the incongruent and the congruent audio-visual trials in the “self-judgement” is always subtracted from the corresponding measure in the “other-judgment” run.

The moderating role of IAcc was measured using the Heartbeat Counting Task (HCT; Schandry, 1981).

Materials and measures

Cardiac audio-visual EEB task. The stimuli consisted of eight previously validated pictures (von Mohr et al., 2019) that were matched with eight sounds (4 positive and 4 negative; see Table 1 for the stimuli). In each trial, participants were presented with a black and white picture that flashed approximately three times on the screen (picture size 16×28.5 cm, viewing distance ~ 40 cm, 200 ms duration) accompanied by a label at top of the picture that read “The OTHER person is listening to”. Visual presentation, for both participants, was accompanied simultaneously by a 3 sec audio recording. (The volume of the headphones was set at 25% of the computer’s speakers maximum output). Immediately after the 3 seconds of stimuli presentation, participants were asked to judge the experienced pleasantness or unpleasantness of the stimulation. Depending on the condition (self vs. other judgement), on the screen they saw either the question “How pleasant was the sound for you?” or “How pleasant was the sound for the other?” (see Figure S1 in Supplementary Materials for an example of an experimental trial and screen display). They responded using a visual analogue scale (VAS) centered around zero and ranging from -10 “not at all” to +10 “extremely”. Thus, in the self-judgment condition, participants had to judge their own emotions resulting from the trial, whereas in the other-judgment condition participants had to judge the emotion they thought the other participant had. As in previous EEB paradigms (e.g., Silani et al., 2013) the self-judgement condition is a control for perceptual and cognitive confounds, including visual and audio stimulus comparison and general

response conflict. In the congruent trials, both participants listened to stimuli of the same valence (negative or positive), whereas in the incongruent trials one participant listened to positive sounds while the other participant listened to negative sounds, as depicted by the picture on the screen, and vice versa (see Figure 2A).

Table 1. List of Stimuli

Sounds	Pictures	Valence
Applause	Applauding crowd	Pleasant
Party	People in a party	Pleasant
Seagulls	Seagull	Pleasant
Baby laugh	Baby laughing	Pleasant
Attack	Woman being attacked	Unpleasant
Dentist drill	Dentist with a drill	Unpleasant
Bees	Bees	Unpleasant
Baby cry	Baby crying	Unpleasant

Note. See Table S1 in Supplementary Materials for an example of trials and pairing of audio-visual stimuli per each condition

Critically, the flashing black and white pictures were presented for 200 ms, with the onset time set to coincide with the systolic phase of the participant's heartbeat (that is, 200 ms after the R-wave) or their diastolic period (that is, 450 ms after the R-wave; see Azevedo et al., 2017). Note that the flashing pictures were presented in every heart cycle throughout the duration of the auditory stimuli, which lasted 3 sec. These two conditions – i.e., the flashing of the picture stimulus at systole and diastole – were presented in both the other- and self- judgments, creating a total of four blocks: 'self-judgement at systole', 'other-judgement at systole', 'self-judgment at diastole', and 'other-judgment at diastole'. Each block consisted of 32 pseudorandomized trials with 16 pleasant (8 congruent/ 8 incongruent) and 16 unpleasant (8 congruent/8 incongruent) audio-visual stimuli. Thus, there were 128 experimental trials in total. The order of the blocks was randomized across participants. The experimental set up resulted in a three-factorial design (see Figure 2A) with the factors: target (self judgement, other judgement); valence (pleasant, unpleasant); and congruency (congruent, incongruent) for the systole and diastole conditions (see Figure 2B). First, a grand mean EEB score as a manipulation check was computed to make sure there was in fact the presence of EEB. Second, we computed the mean inter-beat interval (ms) during stimuli presentation for each condition as a manipulation check to discard the possibility that our main cardiac manipulation in the

EEB task was influenced by differences in heart rate (HR) associated to a specific condition. Next, to examine the effects of interoceptive impact, an EEB score was computed separately for the systole and diastole conditions. As done in past studies (Riva, Triscoli, Lamm, Carnaghi, & Silani, 2016; Silani et al., 2013; von Mohr et al., 2019), this score was extracted by calculating the difference between ‘other-judgment’ ratings for incongruent vs. congruent audio-visual trials (Δ_1 : *incongruent minus congruent*). Then, as explained above, as a control for unspecific aspects such as incongruence detection or stimulus conflict, the differences between incongruent and congruent audio-visual trials in the ‘self-judgement’ (Δ_2 : *incongruent minus congruent*) are always subtracted from this ‘other-judgment’. Specifically, we used the following equations for the systole and diastole conditions, respectively:

$$[-1*(Systole \Delta_1 \text{ pleasant} - Systole \Delta_2 \text{ pleasant}) + (Systole \Delta_1 \text{ unpleasant} - Systole \Delta_2 \text{ unpleasant})]/2$$

$$[-1*(Diastole \Delta_1 \text{ pleasant} - Diastole \Delta_2 \text{ pleasant}) + (Diastole \Delta_1 \text{ unpleasant} - Diastole \Delta_2 \text{ unpleasant})]/2$$

ECG recording. A Powerlab 8/35 box and two Bio Amps 132 were used in conjunction with the LabChart 8 software (<https://www.adinstruments.com>) in order to collect cardiac activity on a laptop. For this purpose, a modified lead I chest configuration was employed: for each participant, two disposable electrodes were placed under the left and right collarbones and one on the left lower back. The ECG signal was sampled at 1 kHz and an analogue band-pass filter between 3 and 1000 Hz was applied, as well as an adaptive filter to reduce electric hum. During the audio-visual EEB task, heartbeats were detected online with the fast response output add-on, a LabChart’s function that identifies the ECG’s R-peak each time the amplitude exceeds an individually-tailored threshold. The ECG trace was inspected online by the experimenter throughout the session to guarantee data quality for subsequent analyses. Importantly, a polarized plastic sheet was attached to the laptop’s screen to prevent participants from seeing their own physiological recordings.

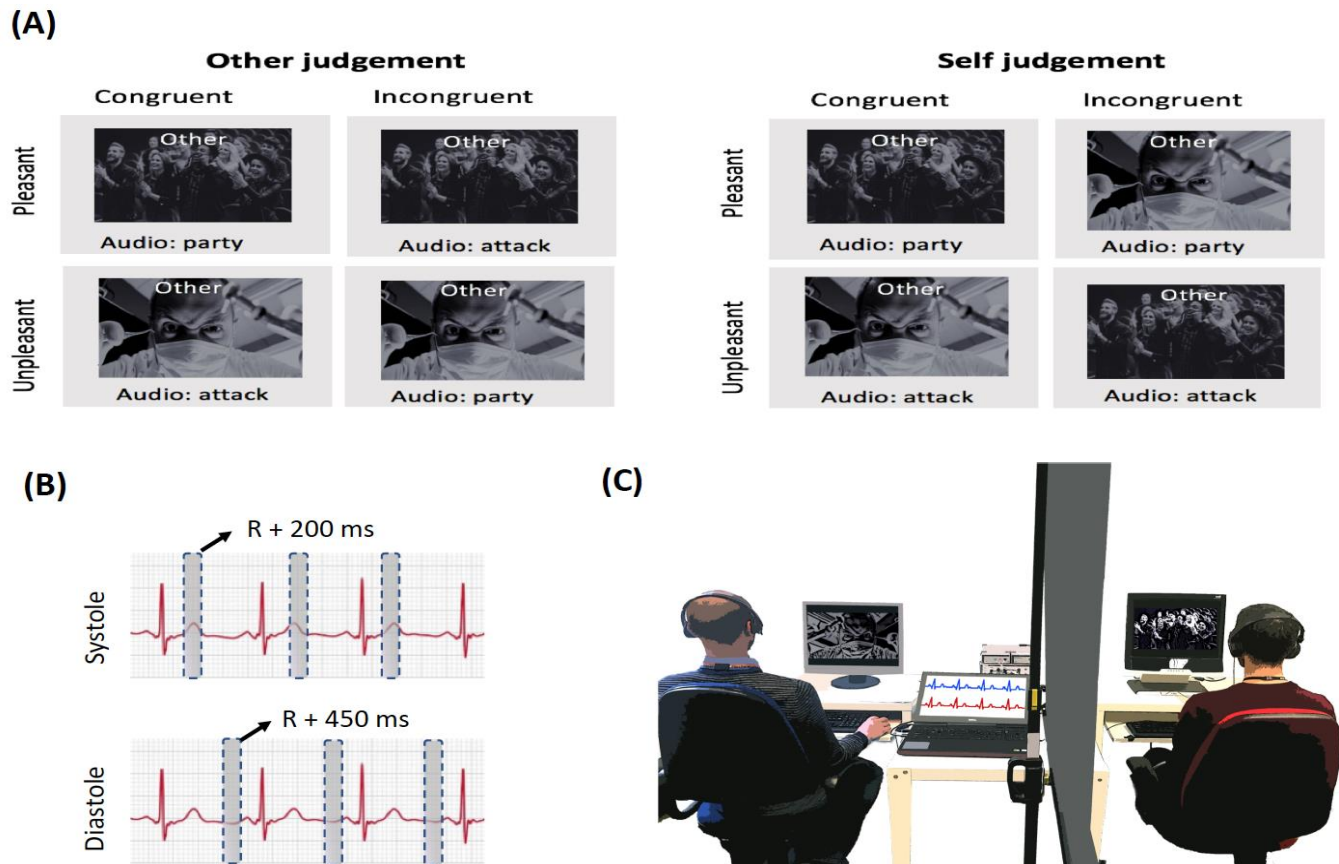


Figure 2. (A) Schematic overview of the EEB task with the factors target (other/self), congruency (congruent/incongruent) and valence (pleasant/unpleasant). The black and white picture in each box illustrates an example of the visual stimuli the participant saw on the screen, which were accompanied by the label ‘the other participant is listening to’. The caption for the auditory stimulus below the picture is presented here for illustrative purposes only and was not shown during the experiment. Please note that congruency refers to affective congruency (e.g., negative sound and negative image depicting what the other person is listening to, such as attack audio and dentist image) but not the same concept in two modalities (e.g., attack sound and attack image). (B) For the systole condition, the picture on the screen was presented in a train of approximately three flashes, each occurring 200 ms after the R peak detection; for the diastole condition, the picture on the screen was presented in three flashes each occurring 450 ms after the R peak detection. (C) Schematic representation of the experimental set up.

Heartbeat counting task. We used the HCT as an index of IAcc. Participants were instructed to silently count their heartbeats without taking their pulse during six time intervals (25s, 30s, 35s, 40s, 45s and 50s). A beep tone signaled the beginning of the trial and a second one signaled its end. Participants were then asked to input the number of counted heartbeats. The order of trials was randomized. In each trial, reported and actual heartbeats were compared to calculate an index of IAcc using the following equation: $1 - (|nbeats_{\text{Real}} - nbeats_{\text{Reported}}|) / ((nbeats_{\text{Real}} + nbeats_{\text{Reported}}) / 2)$. As in previous studies (e.g., Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015), the inclusion

of $n_{\text{beats}_{\text{reported}}}$ was included in the denominator to mitigate against overestimating performance in people showing high variance, particularly when more heartbeats were reported than occurred (please see Supplementary Materials Figure S2, for a strong correlation between this and the original HCT formula). Resulting accuracy scores were averaged across the six trials, yielding a mean score for each participant (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015; Hart, McGowan, Minati, & Critchley, 2012).

Time estimation task. In order to control for nonspecific factors that may influence the HCT performance such as motivation, fatigue, or even people's ability to estimate time or count (Ainley, Brass, & Tsakiris, 2014; Murphy, Geary, Millgate, Catmur, & Bird, 2018; Shah, Hall, Catmur, & Bird, 2016), the Time Estimation Task (TET) was also collected. In the TET, participants had to count seconds instead of heartbeats over four randomized time intervals (22s, 31s, 37s and 43s). Similar to the HCT, participants were then asked to input the number of counted seconds. In each trial, reported and actual seconds were compared to estimate an index of time estimation using the following equation: $1 - (|n_{\text{seconds}_{\text{real}}} - n_{\text{seconds}_{\text{reported}}}|) / (n_{\text{seconds}_{\text{real}}})$. Resulting accuracy scores were averaged across the four trials, yielding a mean score for each participant.

Procedure

After obtaining written informed consent, the instructions for the audio-visual EEB task were explained and participants were told that their cardiac activity would be measured throughout the experimental session (without disclosing the cardiac manipulation in the main task). Although participants were recruited in pairs, they were unknown to each other and did not speak to each other during the experimental session. They were also prevented from seeing each other by using a black curtain (see Figure 2C for a schematic representation of the experimental set up).

Participants were first presented with eight randomized trials wherein the matched audio-visual stimuli were simultaneously presented for 3 seconds (e.g., sound of bees with an image of bees), in order for them to know which picture matched each sound (i.e., the familiarization phase). After familiarization with the stimuli and a short practice trial, participants completed the cardiac

audio-visual EEB task. This task consisted of 4 blocks ('self-judgement systole', 'other-judgement systole', 'self-judgment diastole', and 'other-judgment diastole'), each with 32 trials, lasting approximately 25 minutes.

Upon completion of the main task, participants completed the HCT and the TET. Unknown to the participants, ECG recordings were only collected from the cardiac audio-visual EEB and HCT. At the end of the study visit (~60 min), participants were debriefed.

Plan of statistical analyses

Statistical analyses were conducted in SPSS (version 23) and STATA (version 15) for repeated-measures ANOVAs and generalized linear mixed modelling (GLMM), respectively. Averaging across cardiac conditions, we first conducted a repeated measures ANOVA specifying *Target* (self-judgement, other judgement), *Congruency* (congruent, incongruent) and *Valence* (pleasant, unpleasant) on the rating data. This is to examine the presence of EEB, which appears as a specific interaction of Congruency by Target (as in Silani et al., 2013; von Mohr et al., 2019). Specifically, we assessed whether the difference between incongruent vs. congruent judgements was higher for judgements about the other vs. the self. Individual EEB scores for each subject and for each condition (systole, diastole) were also extracted from this data (see above for the explicit computation of EEB scores) and used as the dependent variable to investigate our main hypothesis. Regarding our main analyses, inspection of the data revealed that our outcome variable (EEB scores) was not normally distributed (Shapiro-Wilks $p < 0.05$). Thus, we employed GLMMs for our statistical analyses – GLMM is an extension of linear mixed models (or 'mixed effects models') allowing response variables to have different distributions (Lo & Andrews, 2015). A gamma distribution (adding a constant of +10 in all EEB scores) with a log link function was chosen for further analyses, as it provided the best fit for our data. For our outcome variable, we specified the multi-level model, in which repeated measures (cardiac condition: systole, diastole) was nested within individuals, as follows. Cardiac condition was entered as a dummy-coded categorical predictor, and IAcc as a continuous predictor, and we included all interaction terms. The time estimation score was added to

our model as a covariate to control for potential confounds associated with the HCT. Continuous variables were mean-centered in order to avoid multicollinearity issues (Tabachnick & Fidell, 2007). Significant interactions were followed up by plotting values at low (-1 SD), moderate (mean) and high ($+1$ SD) continuous IAcc scores and then examining differences between systole and diastole conditions at those values (see Aiken & West, 1991 for testing and interpreting interactions on continuous variables). Using this method, we are not splitting participants into three bins or groups, but merely looking at differences between cardiac conditions plotted at specific points of the continuous (estimated marginal means, followed up in the same model).

Data Availability

Materials and data-sets are available at the Open Science Framework: <https://osf.io/7kqad>

Results

Descriptive statistics and manipulation checks

Interoceptive accuracy and time estimation. Mean IAcc and time estimation scores were respectively 0.61 (SD = 0.31) and 0.71 (SD = 0.21). The mean IAcc score is in line with previous studies using this paradigm (e.g., 30). Data inspection was assessed for cases with scores 3 SD above/below the mean and one participant scored 3 SD below the mean IAcc score (see Figure 3C). Results showed the exact same pattern of result when excluding this participant from our main analyses (see Supplementary Materials Figure S3 for details). Thus, we report below the results without any data exclusions. IAcc and time estimation were not correlated with each other, $r = 0.02$, $p = 0.889$, suggesting that participants' HCT performance was not related to their ability to estimate time or count.

EEB effect. As expected, the Target (self/other) \times Congruency (congruent/incongruent) interaction, $F(1,45) = 4.27$, $p = 0.045$, $\eta^2_{\text{partial}} = 0.09$, was statistically significant. In addition, the absence of a three-way interaction between the factors Congruency \times Valence \times Target, $F(1,45) = 1.25$, $p = 0.270$, $\eta^2_{\text{partial}} = 0.03$, indicates that the EEB was of similar size for pleasant and unpleasant emotions (we did not anticipate a three-way interaction of Congruency by Valence by Target, as the

sign of emotion judgements related to unpleasant stimulation were inverted for these analyses). Inspection of the pattern of results indicated that the Target \times Congruency interaction was driven by significantly larger differences between incongruent and congruent stimuli for ‘other-judgements’ [target other: congruent – incongruent (mean/SE) = 1.58/2.29, planned comparison difference, $F(1, 45) = 27.85$, $p = 0.001$] than for ‘self-judgements’ [target self: congruent – incongruent (mean/SE) = 0.94/.18, planned comparison difference, $F(1, 45) = 27.39$, $p = 0.001$], $F(1, 45) = 4.27$, $p = 0.045$. Thus, these results show that the difference between incongruent vs. congruent stimuli is higher for judgements about the other, relative to judgments about the self, in other words that there is an EEB (see Figure 3A).

The explicit computation of EEB (grand mean) yielded a score of $M = 0.64$ ($SD = 2.11$), as shown in Figure 3B. Descriptive statistics for EEB scores for the systole and diastole conditions were $M = 0.62$ ($SD = 2.44$) and $M = 0.66$ ($SD = 2.82$), respectively.

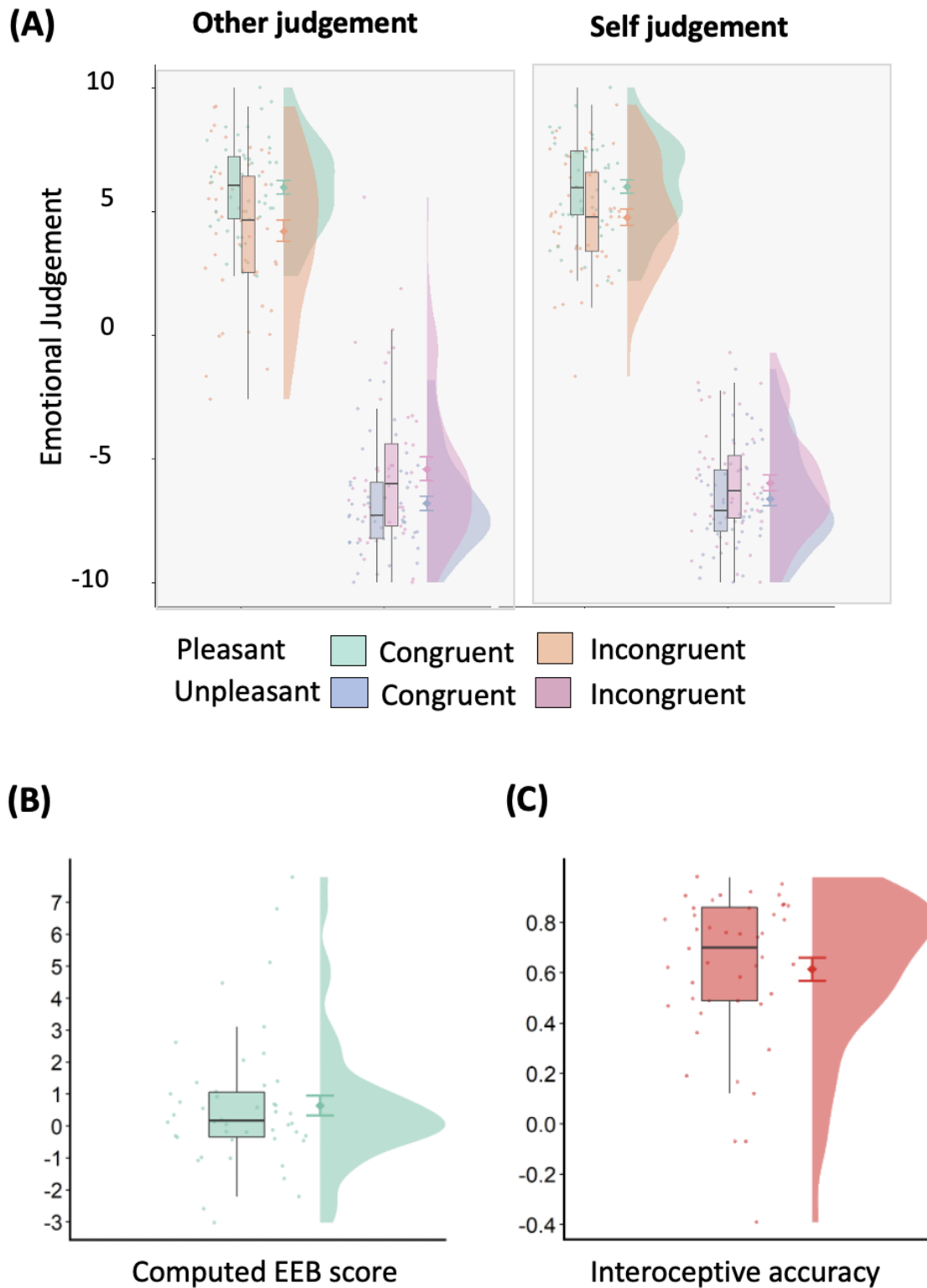


Figure 3. (A) Ratings for EEB task averaged across cardiac conditions. The raincloud plots provide data distribution, the central tendency by boxplots and the jittered presentation of our raw data. Error bars denote SEM for each condition. Pleasant incongruent consisted of negative for the self and positive for the other, and unpleasant incongruent of positive for the self and negative for the other, for the “other-judgment” condition; whereas pleasant incongruent consisted of positive for the self and negative for the other, and unpleasant incongruent of negative for the self and positive for the other, for the “self-judgement” condition. Ratings for ‘other-judgment’ are plotted on the left and for ‘self-judgement’ on the right. (B) Computed EEB scores averaging across cardiac conditions. Higher scores reflect more EEB. The raincloud plot provides data distribution and the jittered presentation

of our raw data. Error bars denote SEM. (C) Interoceptive accuracy scores. The raincloud plot provides data distribution, the central tendency by boxplot and the jittered presentation of our raw data. Error bars denote SEM.

Heart rate during the EEB task. Descriptive statistics for the inter-beat interval (IBI) during the EEB task for the systole and diastole conditions were $M = 744.22$ ms ($SD = 125.49$) and $M = 743.76$ ($SD = 127.80$), respectively. This is equivalent to a mean estimated HR of 81bpm in both systole and diastole conditions. Inspection of the data revealed no main effect of cardiac condition, $F(1,45) = 0.04$, $p = 0.846$, $\eta^2_{\text{partial}} = 0.00$, valence, $F(1,45) = 2.67$, $p = 0.109$, $\eta^2_{\text{partial}} = 0.06$, congruency, $F(1,45) = 0.120$, $p = 0.731$, $\eta^2_{\text{partial}} = 0.00$, target, $F(1,45) = 0.60$, $p = 0.443$, $\eta^2_{\text{partial}} = 0.01$, or their combination, F 's < 3.41 , p 's $> .071$, on the IBIs (see Figure 4). Thus, we can discard the possibility that our main cardiac manipulation in the EEB task was influenced by differences in heart rate associated to a specific condition.

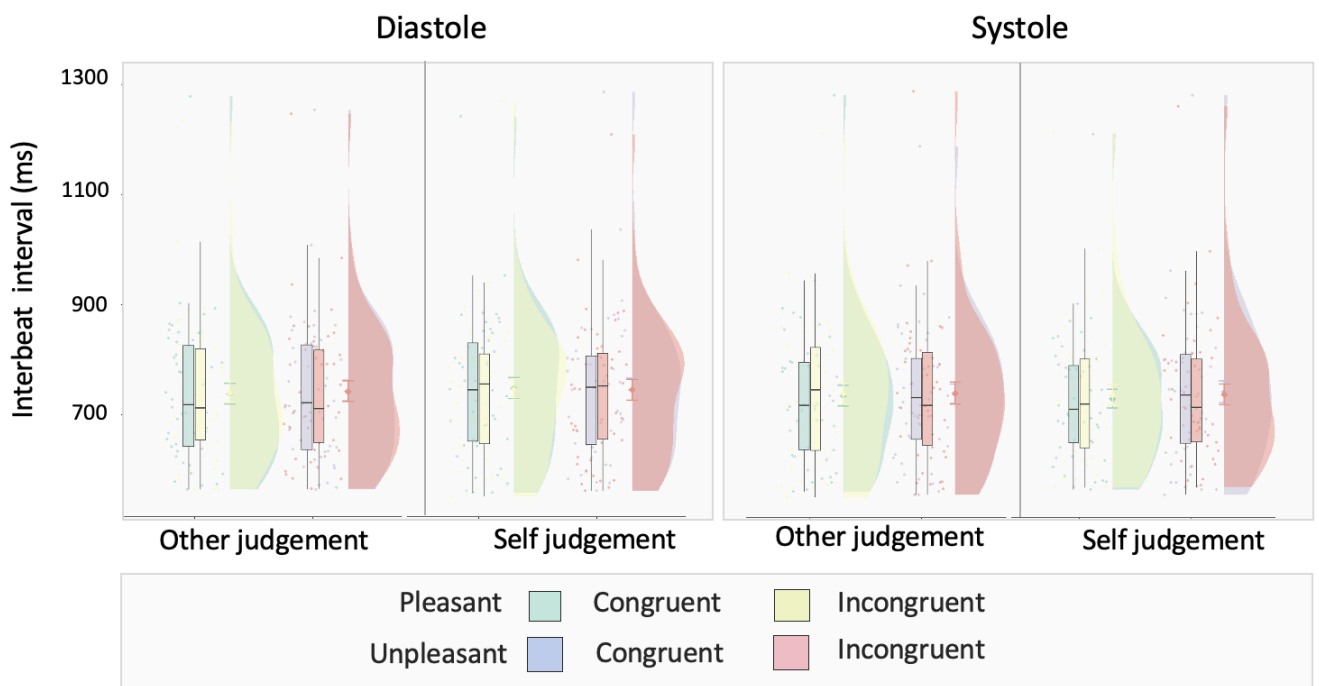


Figure 4. Inter-beat intervals (IBIs) for the heart, target, congruency and valence conditions involved in the EEB task. The raincloud plots provide data distribution, the central tendency by boxplots and the jittered presentation of our raw data. Error bars denote SEM for each condition.

Main results

Does the cardiac cycle and interoceptive accuracy modulate EEB?

Full multi-level model results are presented in Table 2. The main effect of cardiac condition was not statistically significant, $p = 0.710$: systole ($M = 10.56$, $SE = 0.34$); vs. diastole ($M = 10.67$, $SE = 0.34$), suggesting that there is no evidence to suggest difference in EEB between the systole and diastole conditions. Similarly, there was no main effect of IAcc, $p = 0.127$, indicating that there is evidence to suggest an association between trait IAcc and EEB scores. However, in support of our hypothesis, we found a significant cardiac condition by IAcc interaction, $b = .43$, $SE = .11$, $p < .001$. We estimated the (fixed) effect size for coefficient b, f_b^2 , in a mixed model using the following equation: $f_b^2 = \frac{R_{ab}^2 - R_a^2}{1 - R_{ab}^2}$ (Selya, Rose, Dierker, Hedeker, & Mermelstein, 2012). The estimated Cohen's f^2 effect size was 0.193 for the cardiac condition by IAcc interaction, indicating a medium effect size (Cohen, 1988). Follow-up tests were conducted by plotting values at low (-1 SD), moderate (mean) and high ($+1$ SD) continuous IAcc scores and then examining differences between systole and diastole conditions at those values. These showed that the difference between systole and diastole cardiac conditions was significant for high ($b = -1.29$, $SE = 0.52$, $p = 0.013$) and low ($b = 1.51$, $SE = 0.50$, $p = 0.003$), but not for moderate ($b = 0.13$, $SE = 0.36$, $p = 0.710$), IAcc; see Figure 5. Thus, the higher the IAcc, the higher the EEB score in the systole vs. diastole condition. By contrast, the lower the IAcc, the lower the EEB score in the systole vs. diastole condition.

Table 2. Generalised linear mixed model results for EEB computed scores

Fixed Effect	b	SE	p-value	Confidence intervals	
				Lower	Upper
Cardiac condition	-.01	.03	.710	-.08	.05
Interoceptive accuracy	-.16	.10	.127	-.36	.04
Cardiac condition Interoceptive accuracy	* .43	.11	<.001	.21	.65
Intercept	2.36	.03	.001	2.29	2.42

Random Effect

Participants	.02	.01	.01	.04
--------------	-----	-----	-----	-----

*Note. Number of observations = 90. Number of groups = 45, 2 observations per group. Wald $\chi^2(3)=15.43$. Given the log-linked Gamma GLMM the estimated coefficients are exponentiated. Including Time estimation as a covariate in our model yielded the same pattern of results with respect to our main variables of interest, and was not statistically significant, $p = 0.408$.

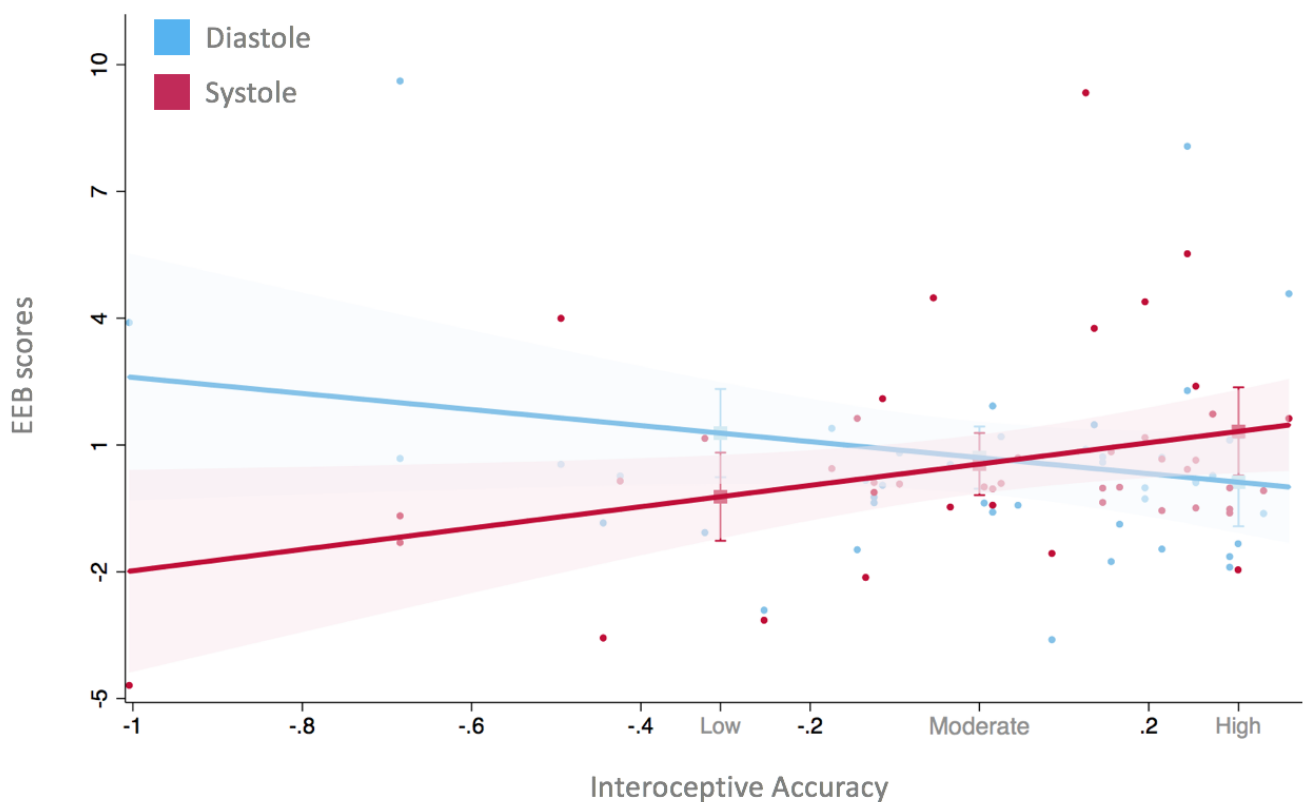


Figure 5. Effects on EEB scores of cardiac condition x interoceptive accuracy. The y-axis reflects the computed EEB scores, such that higher scores reflect more EEB. The EEB scores reflect the actual computed EEB scores, i.e., without the constant of +10 added in all EEB scores for the gamma family in the GLMM. The x-axis reflects interoceptive accuracy (IAcc) mean-centred with error bars depicting CI plotted at low (-1SD), moderate (mean) and high (+1SD) continuous scores for illustrative purposes. Differences between systole and diastole conditions were examined at those plotted values (estimated marginal means) of the continuous variable. Diastole and systole conditions are depicted by the blue and pink line, respectively, with shaded confidence intervals. Data points for each participant on both conditions are depicted by circle markers on their respective colors.

Discussion

We combined a causal manipulation of interoceptive impact with trait-like levels of IAcc to study how interoception affects the parallel processing of self- and other-related emotional states using a new version of the established EEB task. We observed an interaction between cardiac interoceptive impact and IAcc on EEB. Specifically, we found that the higher the IAcc, the higher the EEB at the systolic vs. the diastolic condition, indicating that in these individuals there is a tendency to enhance one's own emotional experience when receiving information about the other's emotional state and their own physiological information is accentuated – possibly to resist the overpowering of the self by the other's emotional state. By contrast, the lower the IAcc, the lower the EEB at the systolic vs. diastolic, condition. Thus, for these individuals, the parallel processing of accentuated physiological information about the other's emotional state, in turn, leads to an overwhelming of the self by the emotional state of the other.

This pattern suggests that the effects of state-like interoceptive impact on EEB are moderated by trait-like interoceptive levels. On the one hand, when arterial baroreceptors are actively sending afferent signals to the brain (i.e., systole) there is an accentuation of EEB, relative to when this pathway is silent (i.e., diastole), although only in those with high trait-like interoceptive levels. Past research suggests that cardiac afferent signaling can modulate the processing of, and subsequent neurophysiological responses to, emotional stimuli (Azevedo et al., 2017; Garfinkel et al., 2014; Gray et al., 2012). We extend these findings by showing how these short-term fluctuations in baroreceptor activity also provide a physiological context that influences how we process other's emotional states, and negotiate self-other boundaries. Indeed, even though such body-brain effects are primarily preconscious (Garfinkel & Critchley, 2016), this type of cardiac interoceptive afferent signaling are thought to set the foundations for a sense of self as the basis for subjective emotional experience (Craig, 2009; Park & Tallon-Baudry, 2014; Seth & Tsakiris, 2018).

Regarding our first hypothesis about the role of IAcc on the diastolic, baseline condition, we show that the higher the IAcc, the lower the EEB is. At first glance, such findings seem to be

consistent with previous studies on empathy (Grynberg & Pollatos, 2015; Shah et al., 2017) indicating that people who are more accurate and aware of their own cardiac activity can better judge other's emotional state. However, it is worth noticing that the EEB scores for higher IAcc are very close to zero in this condition (i.e., $M = 0.12$ $SD = 0.53$) indicating that higher IAcc may not only be advantageous for judging other's emotional state but also their own, and thus speaks about correctly "assigning" emotional states either to the self or to others. Note that EEB scores above zero indicate a tendency to overimpose one's own emotional state, whereas below zero a tendency to overimpose the other's emotional state on the self and finally, and scores around zero reflect perfect accuracy for self and other. As such, these findings are in line with past suggestions (Palmer & Tsakiris, 2018) that IAcc plays a critical role in enabling us to navigate the different degrees of social relatedness, by allowing us to attribute emotional states to the self or to others without blurring the self-other distinction.

Turning now to our main findings at the systolic condition, past research suggests that individuals with higher IAcc do not only experience increased emotional intensity (Barrett et al., 2004; Pollatos et al., 2005) but also possess a less malleable sense of self, grounded in their interoceptive states (Sel et al., 2017; Suzuki et al., 2013; M. Tsakiris et al., 2011). By testing the role of IAcc and the processing of interoceptive impact we show that individuals with higher IAcc display a tendency to resist the overwhelming of the self by the other's emotional state when receiving accentuated physiological information about the other's emotional state, i.e., at systolic trials. For example, consider a couple arguing: the spouse is angry, her blood pressure and HR increase as she quarrels with her husband who suddenly gets angry as well. In this context of high physiological arousal, being aware of her own physiological reactions may help the spouse maintain her own self-emotional experience in the face of her partner's emotional state. Indeed, additional analyses conducted on the emotional ratings also indicate that at higher levels of IAcc, the lower the emotional ratings when judging the emotional experience of the 'other' at systolic, but not diastolic, conditions. Given that this effect is observed only during incongruent conditions and thus seems to be specific to

shifts in emotional experience between self and other, this suggests a tendency to over-impose self-experience in this particular context (see Supplementary Materials; Figure S4). Given that higher interoceptive accuracy is associated with emotional regulation (Dunn et al., 2012; Füstös et al., 2013), future research should examine whether this increase in EEB for higher interoceptive accuracy reflects an attempt for emotion regulation.

The reverse pattern observed in those individuals with lower IAcc, namely an attenuation of EEB at systole, suggests that in the absence of accurate representation of one's own interoceptive and, by extension, affective state, one's own emotional experience is greatly influenced by the emotional experience of others. In other terms, individuals with lower IAcc may be confusing the other's state for their own state. This interpretation is consistent with recent theoretical postulations (Palmer & Tsakiris, 2018) that have put forward that people with lower IAcc are more likely to readily switch to another person's emotional perspective given their tendency to blur self-other boundaries. Here we show that this is particularly the case when individuals receive information about the emotional state of the other in a heightened autonomic state.

To the best of our knowledge, our study was the first to investigate the coupling of trait- and state-like interoceptive impact on social cognition. This is important as we show a distinct pattern of effects when including a causal manipulation of state-like cardiac interoceptive impact. Specifically, while the pattern of effects observed at diastole/baseline are consistent with past research on empathy (Grynberg & Pollatos, 2015; Shah et al., 2017), in that the higher the IAcc the lower the EEB, our effects seem to follow an opposite pattern in a context of heightened autonomic state. Thus here we show, that the role of interoception on social cognition may be context-specific and that these short-term physiological fluctuations may provide the necessary context to optimally negotiate self-other boundaries. Furthermore, our study is one of the few studies reporting an interaction between trait- and state-like interoceptive impact. While some studies have examined the role of IAcc on baroreceptor firing (Azevedo et al., 2017), only one study (Garfinkel et al., 2013) has found a moderating role of IAcc on state-like interoceptive signals. Of interest, we here show that in the social

domain, and beyond purely cognitive processes, the interaction between interoceptive impact and overall interoceptive abilities may pave the way for a more nuanced understanding of how visceral states and their awareness are fundamentally social.

Despite these insights, our findings should be considered in light of our study's limitations. First, while we employed a recently validated EEB-task (von Mohr et al., 2019) and our manipulation checks corroborate the presence of EEB, our cardiac manipulation could only be time-locked to the visual stimuli, given the nature of this paradigm. Future studies should therefore examine whether the same pattern of effects are found when the cardiac manipulation is time-locked to the emotional experience of the "self", although second-person neuroscience perspectives suggest that rather than considering self and other-related affective states in isolation (Schilbach et al., 2013), we should focus on the relationality between self and other as we tried to do in present study. Relatedly, the visual stimulus presentation at systole/diastole had a duration of 200 ms on every cardiac cycle for the duration of the sound (3 sec), and is possible that identifying with the auditory stimulus depicting what the other person was experiencing would extend beyond this time window. Even though these short-term fluctuations in baroreceptor activity provided a physiological context that led to differences in EEB, future research should explore the timing required for the brain to process visual and auditory affect-related stimuli at different phases of the cardiac cycle.

Second, the validity of IAcc measures, such as the HCT, have been a center of debate in recent years (Ainley, Tsakiris, Pollatos, Schulz, & Herbert, 2020; Ring & Brener, 2018; Zamariola, Maurage, Luminet, & Corneille, 2018). Indeed, even though we controlled for counting seconds by using the time estimation task in this study, there are other confounds that could have played a role (e.g., acquired knowledge of cardiac performance). More generally however, although the HCT is among the most common measure employed in interoceptive research, emotional processing and empathy studies and has shown predictive validity for emotional and alexithymia parameters (Pollatos et al., 2005; Shah et al., 2017), we encourage the development and use of additional IAcc measures in the field. Similarly, unlike IAcc where there is a tendency to under count heartbeats

(Ainley et al., 2020), recent postulations suggest that people both over and under count seconds in the time estimation task, making this task possibly confounded by confusing those two different types of error (Ainley, Tsakiris, Pollatos, & Herbert, 2019; Ehlers & Breuer, 1992; Ehlers, Breuer, Dohn, & Fiegenbaum, 1995). In fact, this could explain why we found no association between IAcc and time estimation scores (note that this lack of association does not depend on differences between the equations, see Supplementary Materials Figure S5 for details).

Third, given the dual nature of the task – namely that participants are focused simultaneously on their own as well as the others experience, which may be congruent or incongruent– it is reasonable to expect attention and conflict monitoring confounds. However, the current paradigm (like other versions such as the classic EEB task) aims to minimize such confounds in the EEB computations. In fact, even though we observe an expected effect of congruency vs incongruency (as in Silani et al., 2013; Hoffman et al., 2015; von Mohr et al., 2019), including a “self-judgement” condition as a control helps to minimize such effects, as it is then subtracted from the “other-judgement” condition. Nevertheless, it is still possible that it is easier for individuals to divert one's attention away from the visual stimulus to identify the auditory stimulus, rather than the other way around and as such, the EEB effect found here could be explained by potential confounders due to the stimulus modality. Thus, even though we have previously shown that about 91.54% of participants pay attention to both sensory modalities at least to a certain degree throughout the task (von Mohr et al., 2019), research is still needed to examine whether having the self-directed emotional stimulus as visual and the other-directed emotional stimulus as auditory gives rise to a different pattern of results.

Finally, even though there was no check, other than the instructions to participants, to make sure that participants were in fact judging the self-experience in relation to the auditory stimulus, we think it is unlikely that the self-emotional experience we observed was created by the visual stimulus instead, with our data supporting this notion. In fact, we observe that for the self-judgement condition, when both are congruently pleasant, there is on average an emotional judgement of 6.01. However, when it is pleasant for the self but unpleasant for the other (pleasant incongruent condition), there is

a slightly lower score of 4.76 (see Figure 3A right panel). If the visual (reflecting the other) and not the auditory stimuli were in fact creating the self-emotional experience, then in this pleasant incongruent condition for the self (where the visual stimuli are unpleasantly valenced), we would be expecting a negative score for emotional judgement. However, this is not the case. Instead, we observe a score that is very close to the congruent condition, yet slightly lower, which is likely due to conflict monitoring effects (Silani et al., 2013). Notably, we see the same yet reversed pattern for unpleasant conditions.

In sum, we found that the extent to which cardiac interoceptive impact influences EEB depends on the individual's trait-like levels of IAcc. Specifically, in those with lower IAcc, receiving physiological accentuated information about the other's emotional state leads to an overwhelming of the self by the emotional state of the other. By contrast, in those with higher IAcc, there is a tendency to resist the overwhelming of the self by the other's emotional state when receiving physiological accentuated information about the other's emotional state. These findings suggest that fluctuations in interoceptive activity may provide the physiological context within which we negotiate self-other boundaries.

References

- Aiken, L. S., & West, S. G. (1991). *Multiple regression: Testing and interpreting interactions*.
Multiple regression: Testing and interpreting interactions.
- Ainley, V., Brass, M., & Tsakiris, M. (2014). Heartfelt imitation: High interoceptive awareness is linked to greater automatic imitation. *Neuropsychologia*, *60*(1), 21–28.
<http://doi.org/10.1016/j.neuropsychologia.2014.05.010>
- Ainley, V., Maister, L., & Tsakiris, M. (2015). Heartfelt empathy? No association between interoceptive awareness, questionnaire measures of empathy, reading the mind in the eyes task or the director task. *Frontiers in Psychology*, *6*(MAY).
<http://doi.org/10.3389/fpsyg.2015.00554>
- Ainley, V., Tsakiris, M., Pollatos, O., & Herbert, B. (2019). 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. *PsyArXiv*.
- Ainley, V., Tsakiris, M., Pollatos, O., Schulz, A., & Herbert, B. M. (2020, April). 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*. Elsevier B.V. <http://doi.org/10.1016/j.biopsycho.2020.107870>
- 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. <http://doi.org/10.1016/j.biopsycho.2019.03.006>
- Azevedo, R. T., Garfinkel, S. N., Critchley, H. D., & Tsakiris, M. (2017). Cardiac afferent activity modulates the expression of racial stereotypes. *Nature Communications*, *8*.
<http://doi.org/10.1038/ncomms13854>
- Barrett, L. F., Bliss-Moreau, E., Quigley, K. S., & Aronson, K. R. (2004). Interoceptive sensitivity

and self-reports of emotional experience. *Journal of Personality and Social Psychology*, 87(5), 684–697. <http://doi.org/10.1037/0022-3514.87.5.684>

Bastiaansen, J. A. C. J., Thioux, M., & Keysers, C. (2009). Evidence for mirror systems in emotions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2391–2404. <http://doi.org/10.1098/rstb.2009.0058>

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*. <http://doi.org/10.1016/j.neubiorev.2014.09.021>

Cohen, J. (1988). Statistical power for the social sciences. *Hillsdale, NJ: Laurence Erlbaum and Associates*.

Craig, A. D. (2009). How do you feel - now? The anterior insula and human awareness. *Nature Reviews Neuroscience*. <http://doi.org/10.1038/nrn2555>

Critchley, H. D., & Garfinkel, S. N. (2017). Interoception and emotion. *Current Opinion in Psychology*. <http://doi.org/10.1016/j.copsyc.2017.04.020>

Dunn, B. D., Evans, D., Makarova, D., White, J., & Clark, L. (2012). Gut feelings and the reaction to perceived inequity: The interplay between bodily responses, regulation, and perception shapes the rejection of unfair offers on the ultimatum game. *Cognitive, Affective and Behavioral Neuroscience*, 12(3), 419–429. <http://doi.org/10.3758/s13415-012-0092-z>

Ehlers, A., & Breuer, P. (1992). Increased Cardiac Awareness in Panic Disorder. *Journal of Abnormal Psychology*, 101(3), 371–382. <http://doi.org/10.1037/0021-843X.101.3.371>

Ehlers, A., Breuer, P., Dohn, D., & Fiegenbaum, W. (1995). Heartbeat perception and panic disorder: possible explanations for discrepant findings. *Behaviour Research and Therapy*, 33(1), 69–76. [http://doi.org/10.1016/0005-7967\(94\)E0002-Z](http://doi.org/10.1016/0005-7967(94)E0002-Z)

Füstös, J., Gramann, K., Herbert, B. M., & Pollatos, O. (2013). On the embodiment of emotion regulation: Interoceptive awareness facilitates reappraisal. *Social Cognitive and Affective Neuroscience*, 8(8), 911–917. <http://doi.org/10.1093/scan/nss089>

- Garfinkel, S. N., Barrett, A. B., Minati, L., Dolan, R. J., Seth, A. K., & Critchley, H. D. (2013). What the heart forgets: Cardiac timing influences memory for words and is modulated by metacognition and interoceptive sensitivity. *Psychophysiology*, *50*(6), 505–512. <http://doi.org/10.1111/psyp.12039>
- Garfinkel, S. N., & Critchley, H. D. (2016). Threat and the Body: How the Heart Supports Fear Processing. *Trends in Cognitive Sciences*. <http://doi.org/10.1016/j.tics.2015.10.005>
- 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. <http://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. <http://doi.org/10.1016/j.biopsycho.2014.11.004>
- Gray, M. A., Beacher, F. D., Minati, L., Nagai, Y., Kemp, A. H., Harrison, N. A., & Critchley, H. D. (2012). Emotional appraisal is influenced by cardiac afferent information. *Emotion*, *12*(1), 180–191. <http://doi.org/10.1037/a0025083>
- Greenwald, A. (1980). Fabrication and Revision of Personal History. *American Psychologist*, *35*(7), 603–618. Retrieved from <http://psycnet.apa.org/journals/amp/35/7/603/>
- Grynberg, D., & Pollatos, O. (2015). Perceiving one's body shapes empathy. *Physiology and Behavior*, *140*, 54–60. <http://doi.org/10.1016/j.physbeh.2014.12.026>
- Hart, N., McGowan, J., Minati, L., & Critchley, H. D. (2012). Emotional Regulation and Bodily Sensation: Interoceptive Awareness Is Intact in Borderline Personality Disorder. *Journal of Personality Disorders*, *27*(4), 506–518. http://doi.org/10.1521/pedi_2012_26_049
- Heydrich, L., Walker, F., Blättler, L., Herbelin, B., Blanke, O., & Aspell, J. E. (2021). Interoception and Empathy Impact Perspective Taking. *Frontiers in Psychology*, *11*. <http://doi.org/10.3389/fpsyg.2020.599429>
- Jenkins, A. C., Macrae, C. N., & Mitchell, J. P. (2008). Repetition suppression of ventromedial

prefrontal activity during judgments of self and others. *Proceedings of the National Academy of Sciences*, 105(11), 4507–4512. <http://doi.org/10.1073/pnas.0708785105>

Lakens, D., & Caldwell, A. R. (2019). Simulation-Based Power-Analysis for Factorial ANOVA Designs. <http://doi.org/10.31234/osf.io/baxsff>

Lamm, C., Porges, E. C., Cacioppo, J. T., & Decety, J. (2008). Perspective taking is associated with specific facial responses during empathy for pain. *Brain Research*, 1227, 153–161. <http://doi.org/10.1016/j.brainres.2008.06.066>

Lo, S., & Andrews, S. (2015). To transform or not to transform: using generalized linear mixed models to analyse reaction time data. *Frontiers in Psychology*, 6. <http://doi.org/10.3389/fpsyg.2015.01171>

Mitchell, J. P. (2009). Inferences about mental states. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1521), 1309–1316. <http://doi.org/10.1098/rstb.2008.0318>

Murphy, J., Geary, H., Millgate, E., Catmur, C., & Bird, G. (2018). Direct and indirect effects of age on interoceptive accuracy and awareness across the adult lifespan. *Psychonomic Bulletin and Review*, 25(3), 1193–1202. <http://doi.org/10.3758/s13423-017-1339-z>

Nickerson, R. S. (1999). How we know - And sometimes misjudge - What others know: Imputing one's own knowledge to others. *Psychological Bulletin*, 125(6), 737–759. <http://doi.org/10.1037/0033-2909.125.6.737>

Palmer, C. E., & Tsakiris, M. (2018). Going at the heart of social cognition: is there a role for interoception in self-other distinction? *Current Opinion in Psychology*. <http://doi.org/10.1016/j.copsyc.2018.04.008>

Park, H. D., & Tallon-Baudry, C. (2014). The neural subjective frame: From bodily signals to perceptual consciousness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1641). <http://doi.org/10.1098/rstb.2013.0208>

Pollatos, O., Kirsch, W., & Schandry, R. (2005). On the relationship between interoceptive awareness, emotional experience, and brain processes. *Cognitive Brain Research*, 25(3), 948–

962. <http://doi.org/10.1016/j.cogbrainres.2005.09.019>

Ring, C., & Brener, J. (2018). Heartbeat counting is unrelated to heartbeat detection: A comparison of methods to quantify interoception. *Psychophysiology*, *55*(9).

<http://doi.org/10.1111/psyp.13084>

Riva, F., Triscoli, C., Lamm, C., Carnaghi, A., & Silani, G. (2016). Emotional egocentricity bias across the life-span. *Frontiers in Aging Neuroscience*, *8*(APR).

<http://doi.org/10.3389/fnagi.2016.00074>

Royzman, E. B., Cassidy, K. W., & Baron, J. (2003). “I Know, You Know”: Epistemic Egocentrism in Children and Adults. *Review of General Psychology*. [http://doi.org/10.1037/1089-](http://doi.org/10.1037/1089-2680.7.1.38)

2680.7.1.38

Schandry, R. (1981). Heart Beat Perception and Emotional Experience. *Psychophysiology*, *18*(4), 483–488. <http://doi.org/10.1111/j.1469-8986.1981.tb02486.x>

Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T., & Vogeley, K.

(2013). Toward a second-person neuroscience. *Behavioral and Brain Sciences*, *36*(4), 393–414. <http://doi.org/10.1017/S0140525X12000660>

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. <http://doi.org/10.1093/cercor/bhw296>

Selya, A. S., Rose, J. S., Dierker, L. C., Hedeker, D., & Mermelstein, R. J. (2012). A practical guide to calculating Cohen’s f^2 , a measure of local effect size, from PROC MIXED. *Frontiers in*

Psychology, *3*(APR). <http://doi.org/10.3389/fpsyg.2012.00111>

Seth, A. K., & Tsakiris, M. (2018). Being a Beast Machine: The Somatic Basis of Selfhood. *Trends in Cognitive Sciences*. <http://doi.org/10.1016/j.tics.2018.08.008>

Shah, P., Catmur, C., & Bird, G. (2017). From heart to mind: Linking interoception, emotion, and theory of mind. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*,

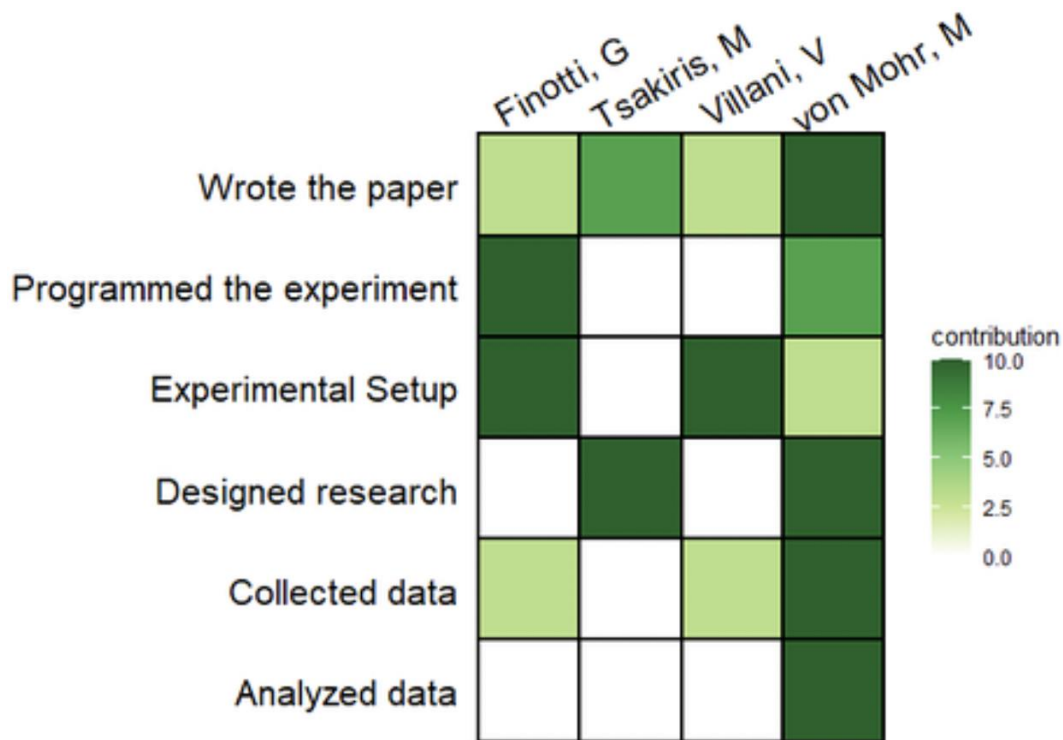
93, 220–223. <http://doi.org/10.1016/j.cortex.2017.02.010>

- Shah, P., Hall, R., Catmur, C., & Bird, G. (2016). Alexithymia, not autism, is associated with impaired interoception. *Cortex*, *81*, 215–220. <http://doi.org/10.1016/j.cortex.2016.03.021>
- Silani, G., Lamm, C., Ruff, C. C., & Singer, T. (2013). Right Supramarginal Gyrus Is Crucial to Overcome Emotional Egocentricity Bias in Social Judgments. *Journal of Neuroscience*, *33*(39), 15466–15476. <http://doi.org/10.1523/JNEUROSCI.1488-13.2013>
- Singer, T., & Lamm, C. (2009). The social neuroscience of empathy. *Annals of the New York Academy of Sciences*, *1156*, 81–96. <http://doi.org/10.1111/j.1749-6632.2009.04418.x>
- Singer, T., Seymour, B., O’Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for Pain Involves the Affective but not Sensory Components of Pain. *Science*, *303*(5661), 1157–1162. <http://doi.org/10.1126/science.1093535>
- 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. <http://doi.org/10.1016/j.neuropsychologia.2013.08.014>
- Tabachnick, B. G., & Fidell, L. S. (2007). *Using Multivariate Statistics*. Pearson Education, Inc. (Vol. 28). <http://doi.org/10.1037/022267>
- Tsakiris, M., & Critchley, H. (2016). Interoception beyond homeostasis: Affect, cognition and mental health. *Philosophical Transactions of the Royal Society B: Biological Sciences*. <http://doi.org/10.1098/rstb.2016.0002>
- Tsakiris, M., Jimenez, 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. <http://doi.org/10.1098/rspb.2010.2547>
- von Mohr, M., Finotti, G., Ambroziak, K., & Tsakiris, M. (2019). Do you hear what I see? An audio-visual paradigm to assess emotional egocentricity bias. *Cognition and Emotion*.
- Zamariola, G., Maurage, P., Luminet, O., & Corneille, O. (2018). Interoceptive Accuracy Scores are Problematic: Evidence from Simple Bivariate Correlations. *Biological Psychology*. <http://>

Author Notes

Author Contributions

Mariana Von Mohr: Conceptualization, Methodology, Formal analysis, Investigation, Writing-original draft preparation, Project administration. **Gianluca Finotti:** Software, Methodology, Visualization. **Valerio Villani:** Software **Manos Tsakiris:** Conceptualization, Methodology, Resources, Writing – review and editing, Supervision, Funding acquisition.



Author contribution: colour code shows the degree of contribution, from high (dark green) to low (light green). White cells are indicative of no contribution in that area.

Sample Size and Data Exclusion Statement

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

Pre-registration Statement

No part of the study procedures or analyses was pre-registered prior to the research being conducted

Declaration of Conflicting Interests

The authors report no conflicts of interest related to their authorship or the publication of this article.

Acknowledgements

M.T. is supported by the European Research Council Consolidator Grant (ERC-2016-CoG-724537) to M.T. under the FP7 for the INtheSELF project, and the NOMIS foundation Distinguished Scientist Award.