How do we relate to our heart? Neurobehavioral differences across three types of engagement with cardiac interoception

Lilla Hodossy[1], Vivien Ainley[1] & Manos Tsakiris[1,2,3]

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

[2] Centre for the Politics of Feelings, School of Advanced Study, University of London

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

Accepted for publication in Biological Psychology for the Special Issue on Interoceptive Methods.

Acknowledgments

Manos Tsakiris was supported by the European Research Council Consolidator Grant (ERC-2016-CoG-724537) for the INtheSELF project under the FP7 and the NOMIS Foundation Distinguished Scientist Award for the 'Body & Image in Arts & Science' (BIAS) Project

Abstract

Standard measures of interoception are typically limited to the conscious perception of heartbeats. However, the fundamental purpose of interoceptive signaling, is to regulate the body. We present a novel biofeedback paradigm to explore the neurobehavioral consequences of three different types of engagement with cardiac interoception (Attend, Feel, Regulate) while participants perform a ‘cardiac recognition’ task. For both the Feel and Regulate conditions, participants displayed enhanced recognition of their own heartbeat, accompanied by larger heartbeat-evoked potentials (HEPs), suggesting that these approaches could be used interchangeably. Importantly, meta-cognitive interoceptive insight was highest in the Regulate condition, indicative of stronger engagement with interoceptive signals in addition to greater ecological validity. Only in the passive interoception condition (Feel) was a significant association found between accuracy in recognising one’s own heartbeat and the amplitude of HEPs. Overall, our results imply that active conditions have an important role to play in future investigation of interoception.

Keywords: interoception, metacognition, biofeedback, predictive coding, self-recognition

Introduction

Interoception has been defined as the ability to monitor (Khalsa et al, 2017) and predict (Pezzulo et al., 2015) changes in the internal body. In that sense, interoception plays an active control-oriented role in self-processing (Seth & Tsakiris, 2018). However, classic measures of cardiac interoception limit the ways in which participants are required to engage with their own bodily signals to passive monitoring of single heartbeats within short time windows. It is therefore noteworthy that many of the existing interoceptive measures that we have are rather passive and do not reflect how interoception is defined nor its important functional and regulatory role. Our study was designed to redress this imbalance, as it aimed to implement and test an active, control-based condition for cardiac recognition, and to contrast this with classic approaches to cardiac interoception.

It has been proposed that the subjectivity of experience is underpinned by interoception (internal signaling to the brain from within the body), that continuously maps internal homeostatic states of the body (Damasio, 2010). While most interoceptive signals support homeostasis without the need for awareness, we are also capable of consciously attending to certain interoceptive sensations. Research into the potential effects of individual differences in interoception has centered on some key distinct dimensions of interoception (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). First, 'interoceptive accuracy' is defined as the ability to perceive an internal signal in close correspondence with a physiological measurement of it. This dimension is usually measured in the cardiac domain, as heartbeats are discrete physiological events, conscious perception of which can be easily quantified. Second, interoceptive sensibility refers to the self-evaluation of interoceptive ability, as typically assessed through interviews or questionnaires. Third, interoceptive awareness or metacognitive awareness of interoceptive accuracy reflects how well a person’s beliefs (e.g., their confidence) about their interoceptive ability is matched by their actual performance on tests of interoceptive accuracy (Khalsa et al., 2017). As with interoceptive accuracy, metacognitive awareness is also usually assessed in the cardiac domain. However, it should be borne in mind that the heart is not the only organ that produces relevant (and discrete) internal signals and that, ideally, interoception should be explored across multiple organ systems.

In ‘Heartbeat Discrimination’ tasks (Whitehead, Drescher, Heiman, & Blackwell, 1977) individuals report (on multiple trials) whether they perceive synchrony between their own heartbeats and a series of external stimuli (usually auditory cues). By contrast, ‘Heartbeat Counting’ (Schandry, 1981) requires the individual to mentally track their hearts over short periods and report the number of heartbeats they perceive. However, these two standard tasks for measuring cardiac interoceptive accuracy have both been heavily criticised (for a summary see Paulus et al., 2019) and new approaches are required.

A recent study by Petzschner and colleagues (2019) illustrated how the amplitude of the heartbeat-evoked potential (HEP) - which is an electrophysiological brain response reflecting the cortical processing of individual heartbeats, is sensitive to differences in attention. When attention is directed exteroceptively (to white noise) the HEP amplitude is lower than when attention is directly interoceptively, to focus on one’s own heartbeats. Moreover, it has been suggested that interoceptive accuracy may reflect the ability of individuals to attend to their interoceptive signals (Petzschner et al, 2019). It has been shown that people with high interoceptive accuracy (measured by heartbeat counting) have greater amplitude of the heartbeat-evoked potential (Pollatos & Schandry, 2004). We accordingly used the amplitude of the heartbeat-evoked potential as a measure in this experiment. In the two types of interoceptive accuracy tasks outlined above it has been assumed that people can (i) consciously perceive individual heartbeats and (ii) use this single heartbeat-related sensory signal to make perceptual inferences (such as in the Heartbeat Discrimination task, where they make the perceptual inference that ‘the heartbeat I am hearing is mine, not that of another person’).

In our novel paradigm, we follow these assumptions but we also emphasize that, in the context of the aforementioned studies, the term ‘interoception’ seems to be restricted to simply sensing interoceptive signals. However, interoception also refers to interpreting and integrating information about the state of the inner body in order to regulate it (Khalsa et al., 2017). Previous studies have ignored this crucial regulatory function of interoception in sustaining optimal allostatic control (Khalsa et al., 2017, Pezzulo et al., 2015). The present study aimed to remedy this. We used a cardiac biofeedback paradigm, to test whether ‘cardiac recognition’, by which we mean the ability to correctly recognize whether the cardiac biofeedback that participants see is their own or another person’s, differs across three conditions. We used signal detection methods to quantify cardiac recognition using the metric d' (Macmillan & Creelman, 2004) which represents the distance between the signal (hit rate) and noise (false alarm rate), with larger values of d' represent greater sensitivity to the signal.

All three conditions involve a combination of interoceptive and exteroceptive elements but vary in the manner in which the participant engages with the feedback, by altering the feature of the cardiac biofeedback that it emphasizes. Specifically, we were interested in how different conditions might produce differences in participants’ ability to recognize cardiac biofeedback as their own. We implemented the cardiac feedback by showing participants, on a PC, a display rather like a thermometer, that reflected their (or another person’s) ongoing cardiac activity (see Figure 1).

We designed three conditions that reflect different types of engagement with interoceptive signals. The first, Condition (‘*Attend*’) acted as a control and was intended to make the participant consciously focus and attend solely to certain exteroceptive characteristics of the cardiac biofeedback signal, as described in the Methods section below. The second Condition (‘*Feel*’) relied on passive interoception, in the same manner as classic heartbeat perception tests. Participants were asked to attend to the biofeedback given and report whether they felt distinct heartbeats at certain time points. The third condition (‘*Regulate*’) took an active, control-oriented approach to interoception, whereby participants were asked to regulate their own interoceptive signals (i.e., to bring down their heart rate, HR) while looking at the cardiac biofeedback. The *Regulate* Condition was crucial in emphasising the true function of interoception (often overlooked in this type of research), which is to maintain the body within the bounds necessary for organism’s Darwinian success (Stephan et al., 2016a). Specifically, we propose that our *Regulate* Condition has the potential to track interoception in a manner that is relevant to anticipatory control (i.e., allostasis), as it requires not only attention to inner bodily states, (as represented here by our *Feel* Condition and classic heartbeat perception tasks), but also attention to the control of those internal bodily states. At the end of each trial, during which participants had to *Attend*, *Feel* or *Regulate*, participants were asked to indicate whether they thought that the biofeedback depicted their own HR or not. Thus, in addition to the three-level factor of Condition, we manipulated the Congruency of the biofeedback, as the thermometer-like display depicted either the participant’s own HR or someone else’s.

To summarise, using a novel paradigm, we investigated the effects of three different Conditions (i.e., *Attend*, *Feel*, *Regulate*), on the participant’s ability to recognize their own cardiac biofeedback (vs. someone’s else’s heartbeat). In addition to this, we employed a variety of further measures to capture cortical and metacognitive aspects of the task, comprising: the participant’s confidence in their decision on each trial; the individual’s meta-cognitive insight into their performance (as accuracy/confidence correspondence); and the amplitude of the heartbeat-evoked potential, in each Condition. We preregistered our hypotheses under the Preregistration Challenge by the Open Science Framework which can be viewed at https://osf.io/k3zsf.

Our hypotheses:

1. Given that the present study involves a novel paradigm, our predictions needed, firstly, to cover the sensitivity of the paradigm itself. We predicted that our cardiac recognition paradigm would be a sufficiently sensitive task, meaning that it would be able to detect individual differences in participants’ performance in cardiac recognition accuracy (i.e., there would be no ceiling or floor effects).
2. We predicted that accuracy on the cardiac recognition task (represented by higher d' values) would differ across Conditions in following the pattern *Attend* < *Feel* < *Regulate*.
3. We hypothesized that the amplitudes of the heartbeat-evoked potential would show an interaction between the three Conditions and the ‘Congruency’ of the biofeedback and would reflect the participant’s increasing levels of engagement with the biofeedback, across the three Conditions (i.e., *Attend* < *Feel* < *Regulate*).

In addition to the preregistered hypotheses, we ran exploratory analyses on:

(4) the differences in metacognition across the three Conditions (*Attend, Feel, Regulate*) (metacognition was measured as how well the participant’s confidence in their decision matched the accuracy of that decision);

and (5) potential links between the participant's cardiac recognition accuracy and modulation of the amplitude of the heartbeat-evoked potential.

Methods

Participants

We recruited a total of N = 34 healthy participants (14 females; $M_{AGE} = 28.71$, $SD_{AGE} = 8.71$), through the Psychology Participant Pool of Royal Holloway, University of London. Participants gave their written informed consent. The study was approved by the Ethics Committee, Department of Psychology, Royal Holloway University of London. During recruitment we checked that none of the participants had had head/brain surgery or any neurological condition or suffered from epilepsy. As our design involved a combination of behavioral and neural measures, we carefully considered our sample size and the number of trials, from several angles, in justifying our sample size and the number of trials.

In the case of our main behavioral measure (d') we followed the recommendations of Brysbaert and Stevens (2018) that suggests 1600 trials per condition across all participants, to reach good levels of power in a mixed effects analysis. Note that because calculation of d' depends on the number of Hits and False Alarms, 'Congruency/Incongruency' is inherently covered within the calculation, and therefore our estimated number of trials concerns the total number of trials needed for each Condition. Therefore, each participant received 52 trials per Condition (evenly split between Congruent and Incongruent trials), resulting in 1768 trials per Condition, across all 34 participants – which also meets the requirements of a signal detection task (Macmillan & Creelman, 2004).

In terms of the EEG data, the unit of the analysis are the *epochs* around individual heartbeats (in contrast to what we considered to be a trial in our behavioral analysis). Also, the neural analysis (unlike the behavioral analysis) requires Congruency to be treated as a separate factor alongside Condition. With an average of 60 BPM and 26 trials (i.e., the number of Congruent/Incongruent trials per Condition, per participant) of 10s we anticipated about 260 epochs, which meets the recommendations for ERP studies by Boudewyn, Luck, Farrens, and Kappenman (2018). While a normal HR can vary between 60 and 100 BPM, to be more conservative we assumed 60 BPM in our calculations, as a slower HR would result in a smaller number of epochs.

Design

Our experiment followed a 3x2 repeated-measures design, with independent variables: (i) 'Condition', which refers to the instructions that the participant received, i.e., they should *Attend*, *Feel* or *Regulate*; and (ii) 'Congruency' i.e., whether the visual feedback was the participant's own heart (Congruent biofeedback) or another person's (Incongruent feedback).

Physiological Measurement: EEG and ECG Recording:

EEG was recorded with Ag-AgCl electrodes from 64 active scalp electrodes, according to the International 10/20 system, using ActiveTwo system (AD-box) and Actiview software (BioSemi; 512Hz sampling rate; band- pass filter 0.16-100Hz (down 3 dB); 24 bit resolution).

Electrodes were referenced to the Common Mode Sense (CMS) and Driven Right Leg (DRL) electrodes and re-referenced to the average offline. ECG signal was recorded with a standard 3-lead ECG attached to the participant's chest (Powerlab, ADInstrumens, www.adinstruments.com) which was used for sending triggers to MATLAB. Four external electrodes recorded eye movement artifacts. Another was attached to the participant's left sternum, to provide a clear ECG trace for cardiac artifact detection. Offline data analysis, including re-sampling rate, filters and independent compoments analysis (ICA) for artefacts are described in the 'EEG data analysis' section below.

Biofeedback Stimuli:

An analogue output of the participant's inter-beat-intervals (to calculate HR) was obtained online and recorded digitally on a PC into MATLAB (MathWorks, Sherborn, Mass., USA). Within MATLAB, a script was created to provide the cardiac visual display to the participant, as the biofeedback. On each trial, participants received 10s of continuous feedback of their own instantaneous cardiac activity (during 'Congruent' trials) or the pre-recorded activity from another person (on 'Incongruent' trials). This feedback was presented in the form of an outline vertical bar (approx. 5 mm by 100 mm when its full length was visible), presented as a thermometer-like display, within which a solid bar of colour rose and fell (i.e., pulsed). Two aspects of this bar were important. We discuss these, in turn.

Firstly, the height of the coloured bar represented the participant's HR, from moment to moment. As HR increased, the bar grew taller and as their HR dropped it became shorter. The height of the coloured bar (representing the HR) was set to the mid-point of the outline bar (approx. 50 mm) at the beginning of each trial. On Congruent trials, we took the average of the 10 heartbeats immediately prior to the beginning of the task and from this calculated a HR value for the mid-point for the first trial. Thereafter, for all other Congruent trials, the mid-point of the bar was updated at the beginning of each trial, based on the participants actual HR from the previous trial (whatever the condition). For Incongruent trials, by contrast, we based the mid-point of the bar on the HR from the previous Incongruent trial. In this way, we could ensure that the parameters of the biofeedback bar were continuously scaled. The minimum height of the coloured bar was set by subtracting a quarter of the baseline. This made the feedback more sensitive to the changes in the lower ranges of HR (and less sensitive to movement artifacts). The maximum height was set by adding half the baseline. The required change in HR for the bar to move one step up, or down, was standardized using the participant's baseline HR (for Congruent trials) or the other person's baseline HR (for Incongruent trials).

The second aspect of the thermometer display that was important was the depiction of the direct feedback of how HR changed from beat-to-beat. A short yellow pulse was superimposed on the whole bar on every heartbeat, occurring exactly 280ms after the R-wave. This coincides with the time window (i.e., 200–300ms post R-wave) of peak systolic pressure, which is thought to be the time window during which we have maximum perception of our heartbeats (Brener et al., 1993, Suzuki et al. 2013). This latency also ensured a sufficiently long, analyzable epoch of the heartbeat-evoked potential, that did not coincide with the visual-evoked potential induced by the pulses. On approximately 50% of all heartbeats (i.e., pulses of the bar), within each trial, the pulses changed from the default yellow to a different colour that corresponded to the experimental condition in the following way: *Attend* – green; *Feel* – blue; and *Regulate* – white.

With regard to the manipulation of congruency of the biofeedback, during the Congruent trials, feedback presentation was linked to the participant's cardiac systole. In the Incongruent trials, the biofeedback was linked to the systole of the series of ten heartbeats selected from another participant. The Incongruent feedback was tailored for each participant by matching it with the most similar heartbeat data from our database, based on the average HR at baseline (see Procedure, below, for when this baseline was measured). In the heartbeat perception literature, it is more common to create 'Incongruent' cardiac feedback by speeding up or slowing down the participant's own HR by about 30% (e.g., Suzuki et al., 2013). By contrast, our Incongruent feedback consisted of 72 recordings (with mean inter-beat interval = 779.9ms (HR of 77beats/min), standard deviation = 142.0), selected from a database of people who had completed the identical task on a different occasion. We also wished to minimize the risk of one participant's Incongruent feedback being more different from their own cardiac signal than that of any other participant. In other words, we wanted to avoid one participant having an easier cardiac recognition task than another. For this reason, on every trial, we adjusted for the percentage difference between the Incongruent signal and the participant's own HR at baseline. To introduce some extra noise across Incongruent trials, half of the Incongruent trials were adjusted to be 15% slower, than the series of ten heart beats that was selected for the Incongruent trial, while the other half were 15% faster (following a randomized order).

Procedure

Baseline HR and heart rate variability (HRV): On arrival, participants were seated on a comfortable chair 55 cm from a CRT monitor (19.6 x 19.7 inches, Sony CPD-E530) in a dimly lit, sound-attenuated room. Three disposable ECG electrodes were placed in a modified lead I chest configuration, as described above: two electrodes were positioned underneath the left and right collarbone and another on the participant's lower back on the left side. We measured their baseline HR and High Frequency Heart Rate Variability (HF-HRV), for 5 minutes, while they sat in silence with their eyes open, looking at a black screen. The participant practiced each of the three conditions once. After the practice session, participants were equipped with the EEG electrode cap as well as the external electrodes (see below).

Trial description and Instructions: The experiment consisted of 156 trials, presented in fully randomized order, each with a length of approx. 15-20 s (comprising 10 seconds of biofeedback presentation followed by an unlimited response time). The task took approximately 1 hour to complete, including a 10 min break half-way through.

On each trial, an outline bar, like an old analogue thermometer, (approx 5 mm by 100 mm) was shown on the PC, filled with a red colour which rose and fell in a pulsing movement (Figure 1). This bar followed, in real time, the HR of the participant (on Congruent trials) or that of another person (Incongruent trials) as explained above.

At the beginning of each trial, a colour-coded word appeared on the screen for one second, showing the Condition that participants were required to use (see Figure 1). The words were. "Count" – in green, "Feel" –in blue and "Regulate" – in red. The *Attend* condition was signaled by the green word "Count", and participants were instructed to attend to the digital thermometer and count how many times they saw the bar pulse green. These green pulses did not relate in any way to the participants' heartbeats. The *Feel* condition, which, as we explained above, is a passive condition, was signaled in blue font, and participants were instructed to track whether they felt a heartbeat of their own at the same time as any of the randomly presented blue pulse(s). The *Regulate* condition, as explained above, was intended to create active engagement with interoceptive signals, and was signaled in red font. Participants were instructed to focus only on the vertical movements of the bar and to try to reduce its height, by slowing their own HR while breathing normally.

After the Condition-prompting word, participants were presented with the heartbeat biofeedback for 10 seconds (as explained in the Stimuli section above).

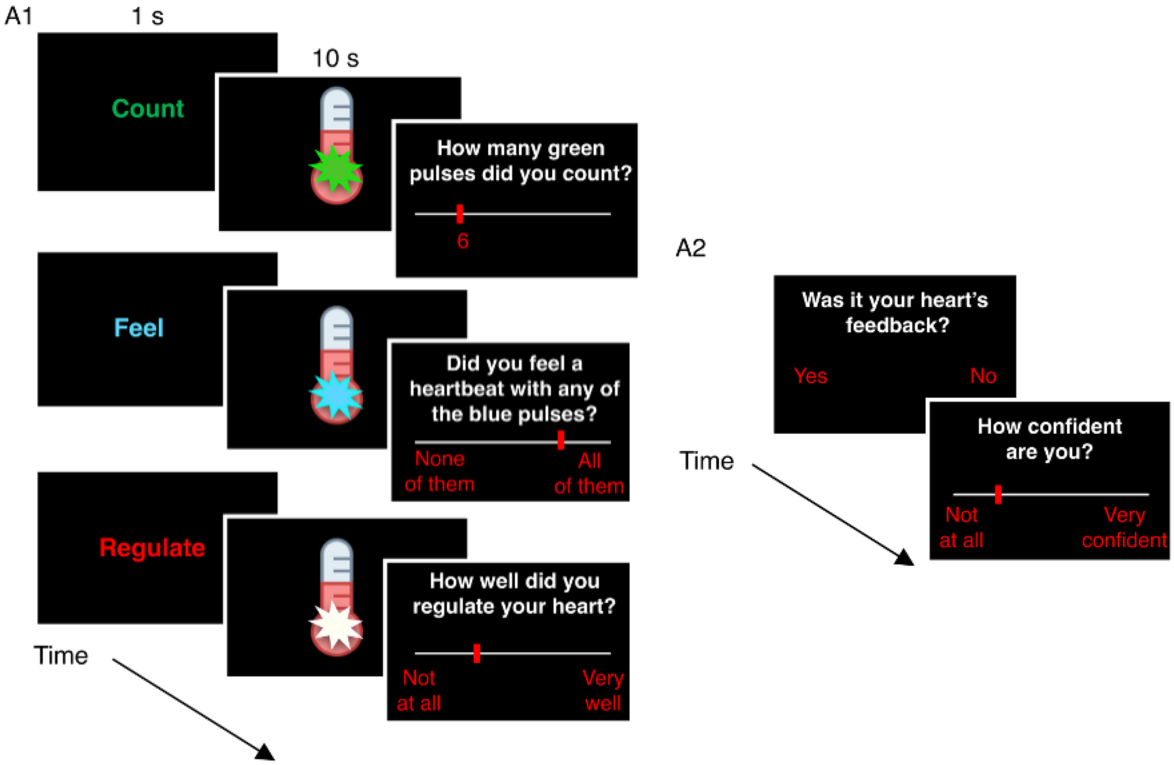

Figure 1. *Experimental procedure for the cardiac recognition task. (A1) Timeline of Condition-dependent stimulus presentation and Condition-specific questions. (A2) Questions on cardiac recognition and participants' confidence were presented after every trial in all three Conditions.*

Across all three Conditions, participants were instructed to avoid explicitly thinking about whether they were seeing their own or someone else's biofeedback during the time that the cardiac biofeedback was actually in progress. They were told to simply focus on applying the instruction (Attend, Feel or Regulate) that had been assigned to that trial. Once the biofeedback disappeared from the screen, participants answered a Condition-specific control question to ensure that they had followed the correct instructions on each trial. Accordingly, following an *Attend* trial, participants reported the number of green pulses they had counted, using a sliding scale; following a *Feel* trial, they indicated if they had felt any heartbeats at the times that the blue pulses appeared, by using a continuous sliding scale with the endpoints "None of them" and "All of them"; and following a *Regulate* trial, they reported how well they thought they had regulated their own heart (not how well they had moved the biofeedback bar, if at all), by using a sliding scale with endpoints: "Not at all" and "Very well" (Figure 1.A1). These variables, which we call 'task performance', were not the measures of interest but we included them in our linear effects model as covariates.

Following these condition-specific question, participants had to answer two more questions that were the same across all three conditions. Participants had first to report whether they thought that the feedback they had seen had represented their own heart or not ("Yes" or "No"). Participants could take as long as they wished when responding and they received no comment on their accuracy. They had been given specific instructions, in advance, on how to make this decision on cardiac recognition under the three different Conditions: on the *Attend* trials they should simply guess whose feedback they had seen (this was designed to remove the necessity for them to think about their own heartbeat during the trial and thus act as a control); for the *Feel* trials they should report the feedback as their own if they had felt at least one heartbeat in time with any of the blue pulse (this was designed to require the participants to compare their own cardiac sensations against the feedback, similar to the demands of common heartbeat perception tasks); during the novel *Regulate* Condition, participants were told that they should report the cardiac feedback was their own if they judged that the vertical movements of the feedback bar were responding to their attempts to regulate it. Finally, on each trial, participants reported their confidence in their cardiac recognition decision, by using a slider on a visual analogue scale with the endpoints “Not at all confident” and “Very confident” (Figure 1.A2).

Data analysis

EEG Data Analysis:

Offline EEG pre-processing was performed using BrainVision Analyzer (Brain Products, Munich, Germany). EEG data was filtered with a bandpass filter of 0.1–30 Hz (24 dB/oct) and a 50 Hz notch filter. Independent Component Analysis was applied on resampled data (250Hz) to remove ocular and cardiac-field artifacts (Terhaar, Viola, Bär, & Debener, 2012), based on their timing, topographical and physical characteristics (Park, Correia, Ducorps, and Tallon-Baudry, 2014; Terhaar et al., 2012; Luft & Bhattacharya, 2015). The EEG signal was segmented into 600ms epochs, starting 150ms before the R-wave (i.e., epochs of -200ms to 400ms around the R-wave). Segments were then baseline-corrected using an interval from −150 to −50ms before R-wave onset, in order to avoid the inclusion of artifacts related to the rising edge of the R-wave (Canales-Johnson et al., 2015) and late components of visual-evoked responses to the pulsing stimulus of the immediately preceding trial. Semiautomatic artifact rejection was followed by visual inspection. Epochs exceeding a voltage step of 200 μV/200ms, a maximal allowed difference of 250 μV/200ms, amplitudes exceeding ±250 μV, and low activity less than 0.5 μV /50ms were rejected from analyses. There were no significant differences in the numbers of included epochs between Conditions (p = .98). These segments then were referenced to the arithmetic average and a grand average was calculated for each Condition.

The heartbeat-evoked potential (HEP) has a distribution from frontal-to-parietal, with higher amplitudes over the right hemisphere (Dirlich, Vogl, Plaschke, & Strian, 1997; Kern, Aertsen, Schulze-Bonhage, & Ball, 2013; Pollatos & Schandry, 2004; Schulz et al., 2015). The polarity of the HEP varies with the task, region and latency analyzed (Canales-Johnson et al., 2015; Couto et al., 2013; Gray et al., 2007). In our analysis, for the HEP we followed the a-priori time window locations reported by Sel and colleagues (2017), to minimize the overlap of HEPs with Visual-Evoked Potentials (VEPs). Following Sel, Azevedo, and Tsakiris (2017), our analysis considered 6 regions of interests (see Figure 5), as previous studies have revealed a widespread frontal-to-parietal distribution of the HEP topography with higher amplitudes over the right hemisphere (Dirlich et al. 1997; Pollatos & Schandry 2004; Kern et al. 2013; Schulz et al. 2015). To estimate the group level effects of Condition and Congruency on mean HEP amplitudes, a Monte-Carlo random cluster-permutation method (see Supplementary information) was implemented in FieldTrip (Maris & Oostenveld, 2007) When making comparisons between Conditions at a neural level, we used the absolute measure of HEP amplitudes. To test the relationship between Condition, HEP amplitude and behavioral measures, we used the difference score of heartbeat-evoked potential amplitudes: Congruency (C) minus Incongruency (IC) in each of the three conditions (i.e.: *Attend* (C-IC); *Feel* (C-IC); and *Regulate* (C-IC)). These difference values for the HEP amplitudes, for each participant, were calculated by subtracting grand averages.

The Monte-Carlo cluster-based permutation test corrects for multiple comparisons in space and time, which is cardinal issue for a multidimensional data such as an EEG trace. Using this method, first all samples that showed a significant ($p < .05$) relationship with the independent variable were identified and clustered following spatiotemporal adjacencies. Following this, cluster-level statistics were produced based on the sum of all the test statistic values within each cluster. Then, through a high number of random shuffling and resampling repetitions (10000 in our case), Monte-Carlo permutation calculated the probability of achieving the cluster-level statistic by chance only. Spatiotemporal clusters that resulted in a Monte-Carlo corrected p-value of less than the critical alpha level of .025 (necessary when running two tailed tests expecting either positive/negative clusters) were interpreted as significant.

Heart Rate Variability

We analyzed the beat-to-beat interval variation of heartbeat traces using the HRV Add-On of LabChart8 Pro, which generates the Spectrum Plot (Frequency to Power) using the Lomb Periodgram Method (least-squares spectral analysis). Periodic components of heart rate variability aggregates in frequency bands. The respiratory frequency band is considered to range from 0.15 to 0.4 Hz in the high frequency band. We decided to used respiratory/high frequency heart rate variability as our main measure, because under appropriate recording and data processing conditions it reflects phasic vagal impact upon the heart (Berntson, Cacioppo, & Grossman, 2007) and it has been reliably used during shorter periods (i.e. 2–5 min) at psychophysiological studies (Camm et al., 1996). We have specifically chosen the high frequency range instead of low-frequency (LF) or the LF/HF measure as LF reflects an indistinguishable mixture of sympathetic a parasympathetic influences rather than changes in vagal control only (Billman, 2013; e.g. Eckberg, 1997; Goedhart, Willemsen, Houtveen, Boomsma, & De Geus, 2008; Heathers, 2012; Reyes del Paso, Langewitz, Mulder, van Roon, & Duschek, 2013).

Cardiac recognition data analysis (the ability to detect if the feedback was one's own heart)

We used signal detection methods to quantified 'sensitivity', using the metric d' (Macmillan & Creelman, 2004), as employed elsewhere in the interoception literature (e.g., Khalsa, Rudrauf and Tranel, 2009). d' represents the distance between the signal (hit rate) and noise (false alarm rate), where larger values of d' represent greater sensitivity. We calculated d' by using the difference between the participant's normalized hit rate (the proportion of trials on which the participant answered 'yes' on Congruent trials) and normalized false alarm rate (proportion of 'yes' responses on Incongruent trials).

As d' inherently involves Congruency (given that calculating this requires the number of Hits and False Alarms), our experiment had one predictor at this level of the analysis, which was Condition (1 = *Attend*; 2 = *Feel*, 3 = *Regulate*). We chose to model our d' data with a mixed effects linear model, as the d' values followed a Gaussian distribution (Shapiro-Wilks test p = .190). We excluded from analysis those Congruent trials (1.3 % of our data) where technical difficulties led to undetected heartbeats and disruption of Congruent feedback (see Supplementary Information for details of this analysis). We used R (Version 3.5.1; R Core Team, 2018) for our analyses. Specifically, we selected the optimal model by using the *buildmer* package (Version 1.0; Voeten, 2019) which can perform backward stepwise elimination, based on the change in the set criterion (AIC in our case). For linear mixed effects modeling we used the package *lme4* (Version 1.1.17; Bates, Mächler, Bolker, & Walker, 2015). Relevant test-statistic were gathered by using *sjPlot* (Version 2.5.0; Lüdecke, 2018b) and *sjmisc* (Version 2.7.4; Lüdecke, 2018a). Mixed effects modelling is particularly useful in within-participant designs, where each participant has several measurements resulting in correlated errors for those measurements (Baayen, Davidson, & Bates, 2008). The solution to this problem is to let each participant have their own personal intercept (and/or slope), randomly deviating from the mean intercept, as the errors around the personal regression lines will be uncorrelated when using this approach. Although our variable of interest on all three Conditions was cardiac recognition, participants were required to answer other questions on each trial, (which were unrelated to cardiac recognition) but were designed to focus participants' attention onto various aspects of the cardiac feedback. Thus, in *Attend* trials they counted random green pulses, in the *Feel* trials they counted blue pulses that they had felt as heartbeats and in the *Regulate* trials they attempted to bring their HRs down. With these 'measures of task performance' we aimed to quantify how accurately participants had applied the instruction required by the Condition. For the *Attend* trials we simply compared the reported number of green pulses to the number of green pulses actually presented on the trial, using the following equation:

$$'Attend'\ Performance \quad = 1 - \mid (target\ pulses - reported\ pulses) \mid /\ target\ pulses$$

In the *Feel* condition, participant had to report an estimate of the number of the blue pulse that they had experienced as if these had occurred simultaneously with their own heartbeat - using an analog scale with endpoints "None of them" and "All of them". The reason for asking for an estimate rather than a precise number of heartbeats was to allow participants to concentrate on the subjective experience of single heartbeats without the need to do another task simultaneously (e.g., counting or pressing buttons). A *Feel* trial would be 100% *accurate* if, when a blue pulse was present, the participant reported that they experienced *all* the heartbeats in the *Congruent* condition, or *no* heartbeats at all in the *Incongruent* condition. Given that we used an analog scale, we could quantify the difference from 100%. We calculated the scores for each *Feel* trial in the following way:

$$Feel\ Congruent\ Condition\ Performance$$
$$= value\ associated\ with\ the\ position\ on\ scale * 2\ /\ 100$$

$$Feel\ Incogruent\ Condition\ Performance$$
$$= 1 - (value\ associated\ with\ the\ position\ on\ scale * 2\ /\ 100)$$

Finally, for the *Regulate* trials we calculated the difference in inter-beat-intervals (IBIs), as a measure of HR, comparing the mean inter-beat-interval during the *Regulate* trial to the mean inter-beat-interval from the previous trial, in the following way:

$$Regulate\ Performance$$
$$= (mean\ IBI\ _{(TRIAL)} - mean\ IBI\ _{(PREV.TRIAL)}\ )/\ mean\ IBI\ _{(PREV.TRIAL)}$$

We tested for the effects of these ‘measures of task performance’; average HR; the average change in HR from baseline to task; and baseline HF-HRV. We included the HF-HRV index in our analysis as a covariate of interest because. As we state in the preregistration of this study, the HRV analysis was intended to be exploratory to assess the potential effect of baseline HF-HRV on cardiac recognition, or any interaction effect with the types of engagement people had with their cardiac signal. Specifically, given that HF-HRV is a selective index of phasic vagal cardiac control it could have been that individual differences affected participants' performance in the Regulate condition. Centered covariates were included in the final model only if they significantly improved the model fit. We defined the maximal model as:

$$d' \sim Condition\ +\ Condition\ performance\ +\ Baseline\ HF - HRV_{BASELINE}\ +\ HR_{CHANGE}$$
$$+\ HR\ +\ (1|ID)$$

In the model selection phase, the optimal model was identified by automatic stepwise elimination based on the AIC values. The optimal model that provided the best fit with our data was the following:

$$d' \sim Condition + (1|ID)$$

The expression outside the parentheses indicates fixed effects, while the expression inside reflects the random effects defined in the model (i.e., the intercept over participants).

Metacognition data analysis

Metacognitive aspects of interoception, also known as ‘interoceptive insight’, indicate how well a person’s beliefs (e.g., their confidence) about their interoceptive ability is matched by their actual performance on tests of interoceptive accuracy (Khalsa et al., 2017). Using the Area Under the type 2 Receiver Operating Curve (AUROC2) as a measure of metacognition, previous studies have found a significant association between interoceptive accuracy and confidence (Khalsa et al., 2008), in those individuals who have high interoceptive accuracy. However, the use of this measure has been criticized as biased, because changes in task performance can lead to changes in AUROC2, even when the participant’s metacognitive “efficiency” stays the same (Fleming & Lau, 2014; Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). Our study, therefore, employed ‘Confidence Accuracy Calibration’ (see Supplementary Information), which measures the relationship between categorical levels of confidence and the binary measure of accuracy, resulting in a statistic called the Normalised Resolution Index (NRI) (Mickes, 2015). By simply regressing accuracy on confidence, and plotting their relationship, one can gain interesting insights into metacognition. Moreover, it is possible to quantify such confidence – accuracy relationship by statistics commonly used in eyewitness research (for more see Brewer & Wells, 2006). Here we use the normalized resolution index (NRI) which provides a quantitative index of the ability to use levels of confidence to effectively distinguish when an event occurs (i.e., feedback of own heart) and when it does not (i.e., feedback of someone else's heart) (Petrusic & Baranski, 1997). The NRI is calculated as:

$$\left[\frac{1}{n}\sum_{j=1}^{J} n_j(a_j - a)^2\right] \Big/ a(1 - a)$$

Where: n is the number of trials; a_j denotes the proportion of correct responses at a given confidence level j; and a denotes overall mean accuracy. The NRI ranges from 0 ('no discrimination') to 1 ('perfect discrimination'). Given that the NRI can be interpreted as eta-square (Petrusic & Baranski, 1997) – which is directly related to Cohen's f. Cutoffs for NRI values can also be created (small: .010, medium: .059, large: .138) (Brewer & Wells, 2006). Confidence Accuracy Calibration requires a large number of trials, in general, but the separation of confidence judgments into more or fewer levels (bins) also affects the reliability of the analysis (i.e., the larger the number of confidence levels/bins the more trials that are needed in order to be reliable).

To understand the link between self-reported confidence and our measure of accuracy in recognising one's own HR, we ran an exploratory Confidence Accuracy Calibration analysis (see Supplementary Information for details). We used the beta R package legalPsych (Version 3; Van Boeijen & Saraiva, 2018). The main part of this analysis is simply plotting the proportion correct for cardiac recognition, for each level of confidence – classically ranging between 0% - 100% and separated into bins of 10% increases or collapsed within wider ranges (Figure 3A).

Results

Results revealed that, d' did not differ significantly between the *Feel* and *Regulate* Conditions (p = .35), but d' was significantly lower in the control *Attend* Condition, where participants were instructed to guess (M_{ATTEND} = 0.27, SD_{ATTEND} = 0.45) compared with both the *Feel* (M_{FEEL} = 0.49, SD_{FEEL} = 0.58) β = 0.22, [CI] = 0.04 – 0.40, p = .017) and the *Regulate* Conditions ($M_{REGULATE}$ = 0.58, $SD_{REGULATE}$ = 0.68); β = 0.31, [CI] = 0.13 – 0.49, p = .001; $R^2_{MARGINAL}$ = 0.05; $R^2_{CONDITIONAL}$ = 0.59. Results (see Figure 2) are depicted by raincloud plots (Allen, Poggiali, Whitaker, Marshall, & Kievit, 2018). These results remain significant after Bonferroni correction for three comparisons. A negative score for d' indicates a performance that is worse than chance (i.e., participants cannot discriminate Congruent feedback from Incongruent), which hampers the interpretation of results. For this reason, we ran the same analysis again, excluding participants who had negative d' in any of the three Conditions and we found a similar significant pattern. In this subsample of our data (n=20), both the *Feel* Condition (β = 0.29; [CI] = 0.06 – 0.53; p = .014) and *Regulate* Condition (β = 0.39; [CI] = 0.16 – 0.62; p = .001; $R^2_{MARGINAL}$ = 0.12; $R^2_{CONDITIONAL}$ = 0.38) were associated with higher d' than the *Attend* Condition - without differing significantly from each other (p = .42). It is important to note that mean HR remained the same across all three Conditions, meaning that the observed effects were driven by differences in the way that participants engaged with the biofeedback signal, rather than by changes in their physiological state.

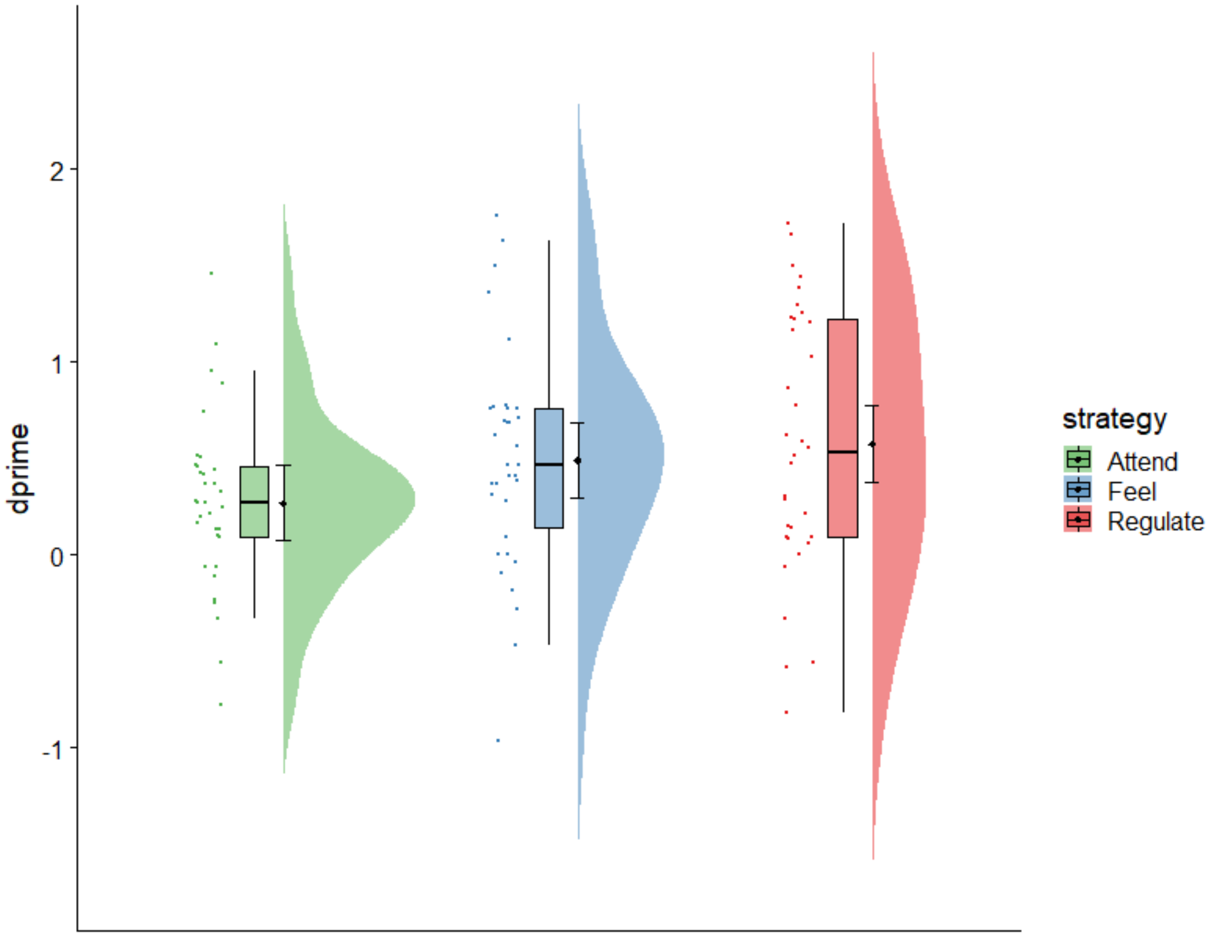

Figure 2. *Participants' cardiac recognition measured by d', shown by Condition. The raincloud plots of d' show: raw data; data distribution; and central tendency (by boxplots). Error bars indicate 95% confidence intervals around the estimates of the linear mixed effects model with a random intercept.*

<u>Metacognition (Confidence Accuracy Calibration)</u>

First, we ran a generalized linear mixed model, which is an extension of linear mixed models, allowing response variables to have different distributions. Given the binary nature of our trial level outcome variable (i.e., accuracy with levels 0 = Incorrect, 1 = Correct), we fitted a random intercept model with a binomial distribution and a logit link. We found a positive – but, in terms of effect size, rather small – link between Accuracy and Confidence: Odds Ratio = 1.08; [CI] = 1.05 – 1.10; p = < .001; R^2_{MARGINAL} = 0.01; $R^2_{\text{CONDITIONAL}}$ = 0.05. To reduce noise, we collapsed Confidence into two categories by median split (i.e., Low: 0% – 50% and High: 60% – 100%) and again plotted the proportion correct against confidence for each of the three Conditions (Figure 3B). The Normalized Resolution Index (NRI) was calculated for each individual. When contrasting the different Conditions in a linear mixed effects analysis, we found a significantly higher value of the NRI for the *Regulate* Condition (M_{REGULATE} = 0.13, SD_{REGULATE} = 0.18) compared to both the *Attend* Condition (M_{ATTEND} = 0.05; SD_{ATTEND} = 0.07; β = 0.08; [CI] = 0.02 – 0.14; p = .006) and *Feel* Condition (M_{FEEL} = 0.07; SD_{FEEL} = 0.12; β = -0.06; [CI] = -0.11 – 0.001; p = .046 (nonsignificant after Bonferroni correction); R^2_{MARGINAL} = 0.06; $R^2_{\text{CONDITIONAL}}$ = 0.21; while there was no difference between the *Attend* and *Feel* Conditions (p = .46). For descriptive statistics see Table 1.

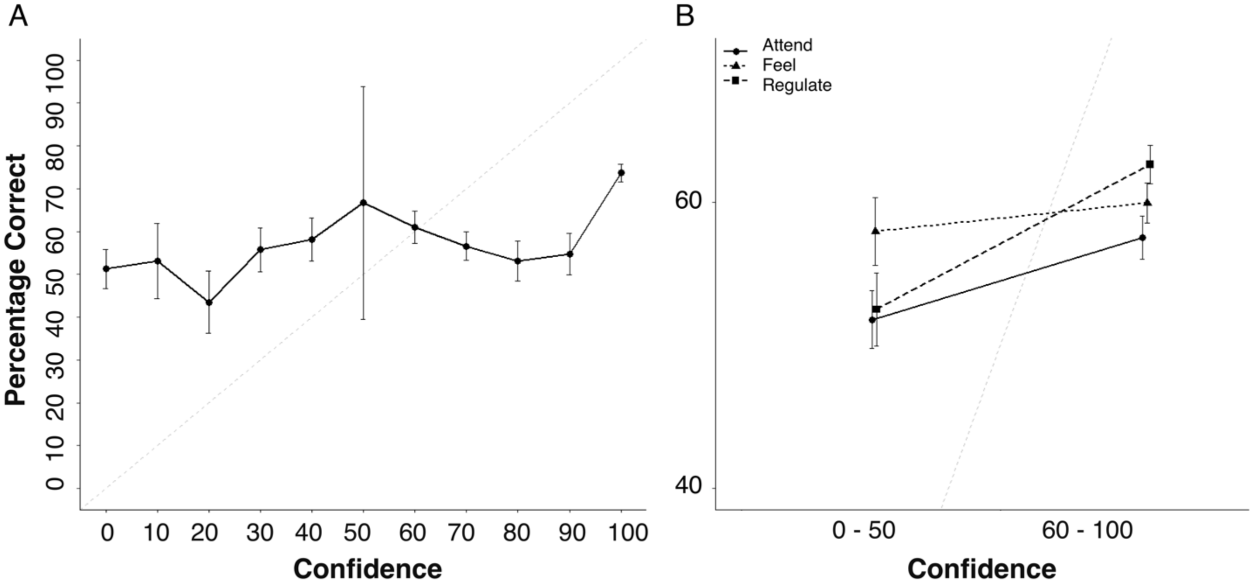

Figure 3. *Results of the confidence vs. accuracy analysis, depicting: (A) an overall positive*

linear relationship between confidence (shown in bins of 10%, 20% etc.) and accuracy in recognising one's own heart; and (B) divided by Condition, with confidence by median split. For reference, the diagonal line represents what would be perfect calibration between confidence and accuracy. Error bars indicate 95% confidence intervals.

To summarize the behavioral results, participants' performance on the cardiac recognition task did not have a ceiling or floor effect (hypothesis 1). With respect to hypothesis 2, cardiac recognition measured by d' was higher for both the *Feel* and *Regulate* conditions compared to the *Attend* Condition but there was no difference between *Feel* and *Regulate*. With regard to metacognition (accuracy and confidence association), the accuracy in cardiac recognition, (measured by the proportion of trials in which the feedback was correctly identified) was positively linked to self-reported confidence across all three Conditions. In particular, participants' metacognition (measured by Confidence Accuracy Calibration) was significantly better during *Regulate* trials, compared to the other two Conditions.

Table 1: Descriptive Statistics of Correct and Incorrect Response for Low and High Levels of Confidence

Condition	Levels %	Mean Confidence	Incorrect	Correct	Total	Proportion Correct
Regulate	0-50	26.14	179	198	377	0.53
Regulate	60-100	79.02	475	797	1272	0.63
Attend	0-50	25.26	292	314	606	0.52
Attend	60-100	77.51	447	606	1053	0.58
Feel	0-50	25.88	182	251	433	0.58
Feel	60-100	78.44	490	734	1224	0.60

Note: The total number of trials differs slightly across conditions because approx. 1% of trials of trials were excluded where the recording equipment occasionally missed heartbeats.

EEG: Cluster-based permutation analysis on the amplitudes of heartbeat-evoked potentials (HEPs)

The average number of heartbeat-evoked potential (HEP) epochs in Congruent conditions after artefact rejections were: $M_{ATTEND} = 317.26$ $SD_{ATTEND} = 50.27$; $M_{FEEL} = 313.94$, $SD_{FEEL} = 49.81$; $M_{REGULATE} = 314.29$, $SD_{REGULATE} = 50.20$. In the Incongruent conditions the average numbers were: $M_{ATTEND} = 310.65$, $SD_{ATTEND} = 53.94$; $M_{FEEL} = 309.65$, $SD_{FEEL} = 53.37$; $M_{REGULATE} = 306.50$, $SD_{REGULATE} = 53.10$. Importantly, there were no significant differences in the number of heartbeats between conditions $F(2,198) = 0.02$, $p = .98$.

At noted above under 'Participants', prior to the main analysis of heartbeat-evoked potentials, we inspected the distribution of EEG amplitudes within the time window of interest (i.e., 200 - 300ms after the R-wave onset), to identify outliers (see Supplementary information). We used the multivariate model approach for outlier identification because declaring an observation as an outlier based on a just one feature could lead to misleading inferences. Four influential outliers were identified, based on the amount of impact their data points had on the predicted outcome - represented by Cook's distance (Cook, 1977). We decided to remove these participants as they had more than one datapoint where Cook's distance was four times greater than the mean, leaving us with a sample of $N = 30$.

Given that our main interest at this level of the analysis was the potential interaction between Condition (1 = *Attend*, 2 = *Feel*, 3 = *Regulate*) and Congruency (1 = Congruent, 2 = Incongruent), we first determined whether there were differences in the amplitudes of HEP between Conditions. For this, we calculated a dependent samples F-statistic, for each sample, in each random reshuffling of the data. We used MATLAB (Version R2019a; MathWorks) with the toolbox FieldTrip (Version fieldtrip-lite-20190403; Maris and Oostenveld, 2007) for our analyses, applying cluster-based permutation and the external functions cbrewer and boundedline for plotting results. This analysis revealed a significant modulation of the HEP amplitude by Condition, as indicated by a significant positive cluster ($F_{SUM} = 400.48$, $p = .024$) between 232-280ms within the right-frontal ROI (specifically electrodes AF4, F4). To investigate the simple effects of the variables Condition and Congruency in this interaction, we ran six pair-wise comparisons (now specified with dependent samples T-statistics) at the right-frontal ROI. In the latency range from 200 - 300ms post R-peak, the cluster-based permutation test revealed a significant positive difference between the *Attend* and *Feel* Conditions during Incongruent biofeedback ($T_{SUM} = 141.13$, $p = .003$). In this latency range, the difference was globally pronounced over all sensors of this ROI, within the whole preset latency range. Similarly, the amplitude of the HEP in the *Regulate* Condition was significantly higher than in the *Attend* Condition, within the Incongruent feedback ($T_{SUM} = 69.24$, $p = .002$). This effect was most pronounced at the latency 204-268ms, at electrodes AF4, F4. All reported statistics survived Bonferroni correction for 6 comparisons (Figure 4 A and C).

In addition, to ensure that the observed HEP differences between Conditions cannot be explained by differences in the ECG signal, we analyzed the ECG trace, following the same protocol as in the HEP analysis reported above. The results of the cluster-based permutation test on the ECG did not reveal any clusters of significant interactions at $p < .05$ (Figure 4 B).

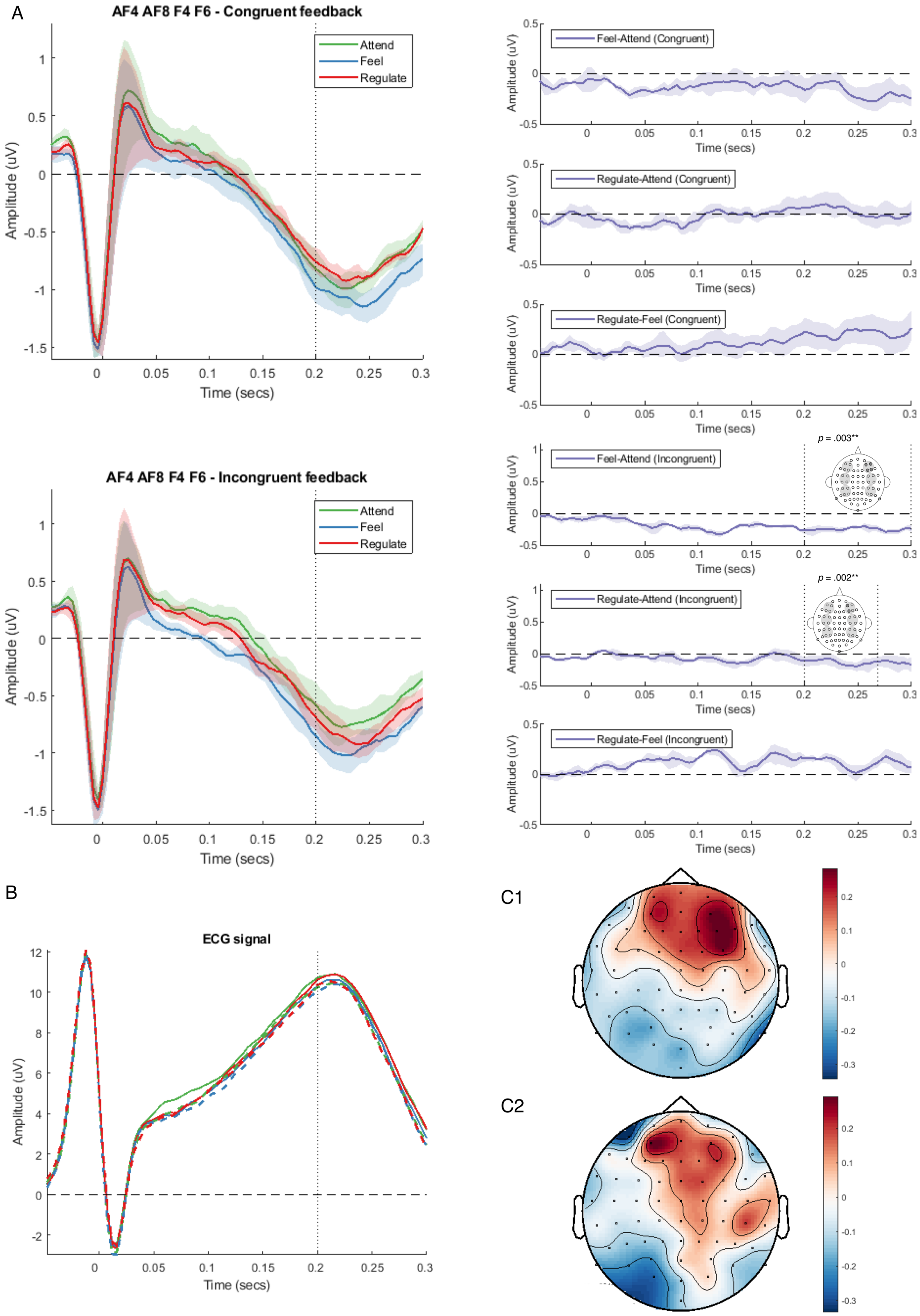

Figure 4. (A) Heartbeat evoked potentials (HEPs) by Condition, over the right frontal ROI, within the a priori latency of 200-300ms, during the presentation of cardiac biofeedback (N = 30, Monte-Carlo cluster analysis, $F_{SUM} = 400.48$, p = .024). For the two significant pairwise

comparisons we also note the electrodes and latencies where the effect was the most pronounced. (B) Average ECG signal across all three Conditions (the solid line refers to the Congruent biofeedback and dashed lines to Incongruent feedback). Shaded areas around mean amplitudes indicate 95% confidence intervals. (C) Topographical representation of positive right frontal clusters during Incongruent feedback when comparing the Attend condition to (C1) Feel and (C2) Regulate conditions. For the topographical plots, amplitudes were averaged within the time window (which is noted by the range between the dotted lines in Figure 4A) where the effect on the cluster was most the pronounced. Colour bars show Monte-Carlo cluster statistic (t).

To discover whether the heartbeat-evoked potential (HEP) amplitudes reflected behavioural differences, we investigated potential links between cardiac recognition and the modulation of HEP amplitudes in each Condition (Figure 5). To match HEPs against d' - which inherently captures the Congruency to Incongruency relation - we first calculated 'Congruency Difference' amplitude measures for HEPs in each of the three Conditions, by subtracting the mean amplitudes on Incongruent trials from those on the Congruent trials. Then, to fully separate Condition-related effects from attentional processes, we treated the *Attend* Condition as a baseline control (as it captured all the exteroceptive aspects of the task) and therefore subtracted the Congruency Difference amplitudes in the *Attend* condition from the *Feel* and *Regulate* Conditions (Figure 5B). To mirror this on a behavioural level, we subtracted d' scores in the *Attend* Condition from d' in the other two interoceptive Conditions respectively (i.e., *Feel* and *Regulate*). We then performed a regression analysis, in the *Feel* and *Regulate* Conditions, on the d' differences and the HEP differences, using the same cluster-based permutation technique as before. Based on the results of our previous interaction analysis, we selected the a priori latency where HEP differences were the strongest (i.e., 232-280ms), with the right-frontal area as our ROI. The analysis revealed a significant positive relationship between Condition-specific HEP difference and d' difference in the *Feel* Condition (T_{SUM} = 24.64, p = .019), but not in the *Regulate* Condition. This effect was the most pronounced over electrodes AF8, F4, F6 within the time window of 272-284 ms after the R peak and survives Bonferroni correction for 2 comparisons.

To summarize the EEG findings, the two interoceptive Conditions (*Feel* and *Regulate*) compared to the exteroceptive Condition (*Attend*) were associated with greater amplitude of the heartbeat-evoked potential, over the right-frontal area within the latency of 200-300ms. In addition, in the *Feel* Condition only, we identified a link between cardiac recognition accuracy and the modulation of HEP amplitudes.

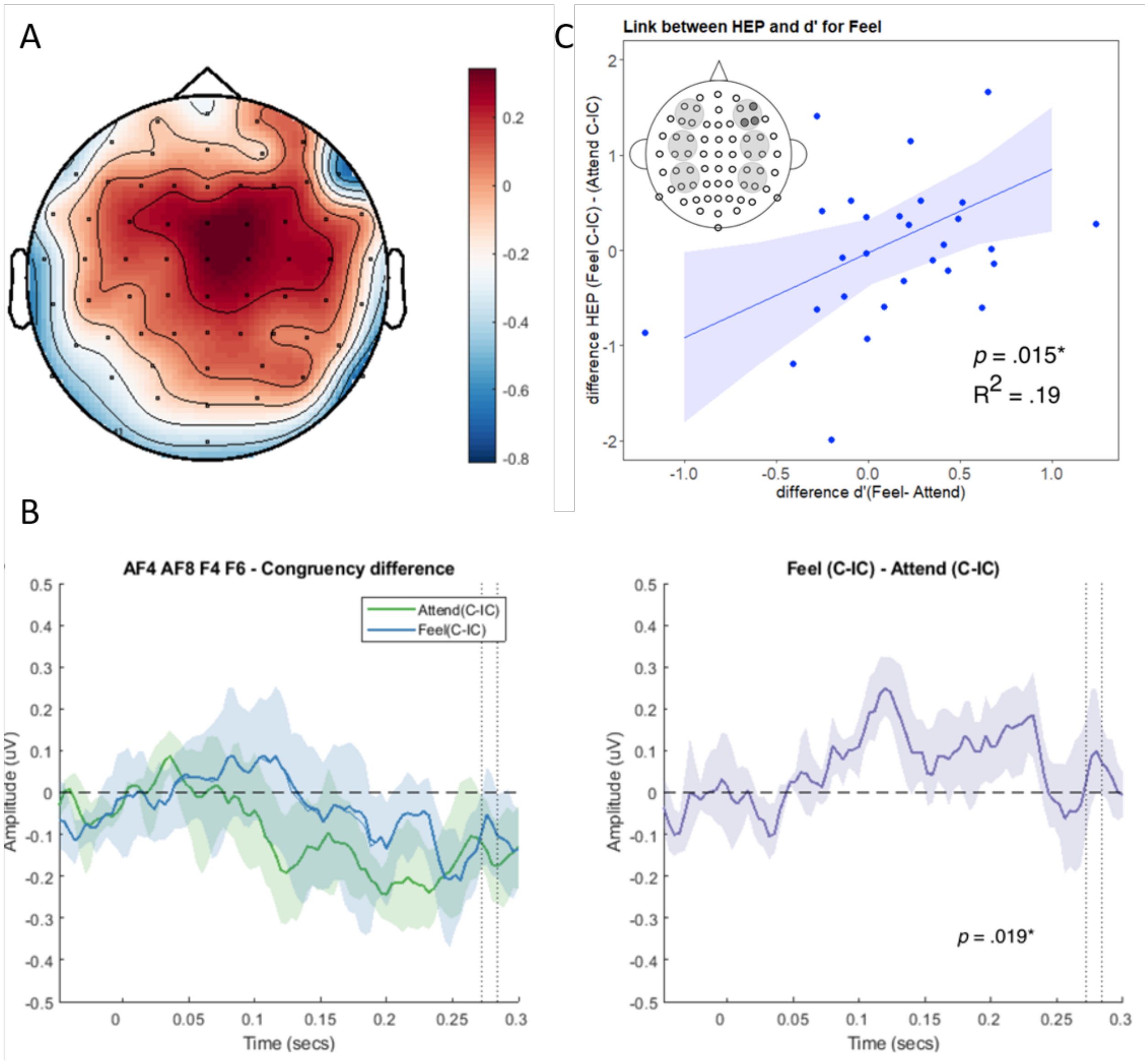

***Figure 5**. The amplitude of Heartbeat Evoked Potential (HEP) difference measure was related to the difference in d' in the Feel compared with the Attend Condition. (A) Topographical plots depict the HEP amplitude differences that were used in the regression (not the spatial effects associated with the regression itself) within the time window where the effect on the cluster was most the pronounced (which is noted by the range between the dotted lines in Figure 5B). (B) 'Congruency Difference' amplitudes in the two Conditions. Shaded areas represent the 95% confidence interval for the fitted regression line. (C) For illustrative purposes, parametric linear*

regression lines were plotted using participant-wise average signal over the three relevant frontal electrodes (dark shaded circles on the layout map) and within the latency (dashed lines on amplitude plots) where the relationship was the strongest (identified by the Monte-Carlo cluster-based permutation).

Discussion

The function of interoception is to maintain physiological stability (Khalsa et al., 2017) and to regulate the body (Pezzulo et al., 2015). However, standard measures of cardiac interoception used in research (Schandry, 1981; Whitehead et al., 1977) are distant from this functional definition, as they simply test the ability to perceive (e.g., heartbeats) – leaving the interpretation of participants' performance in these tasks limited to low, sensory levels. In order to get closer to the functional role of interoception and to contrast different ways of engaging with one's physiological state, we compared: (i) participants' 'cardiac recognition' (i.e., their ability to recognize feedback of their own heart as their own or another person's) across three different Conditions; (ii) the associated neural responses (the amplitude of heartbeat-evoked potentials); and (iii) the participants' metacognitive interoceptive insight. All three Conditions involved the same exteroceptive elements, but participants attended to different features of the biofeedback, which required increasing levels of interoceptive engagement, in the order of: (i) exteroceptive (*Attend)* where they counted random coloured pulses with no requirement to engage with their interoceptive signals; (ii) passive-interoceptive (*Feel*) where they attended to their own heartbeat and to the biofeedback, in order to report whether they felt a heartbeat at the time that a particular coloured pulse was presented (which has demands similar to those of standard heartbeat perception tasks); and (iii) active-interoceptive (*Regulate*) where the task was to control the cardiac biofeedback by reducing their HR.

There were no floor or ceiling effects in cardiac recognition (supporting our hypothesis 1), proving that the paradigm itself is sufficiently sensitive to detect individual differences in the accuracy of cardiac recognition. The expected improvement in cardiac recognition across Conditions (i.e., *Attend* < *Feel* < *Regulate*) was partly confirmed (hypothesis 2). Both *Regulate* and *Feel* Conditions resulted in significantly more accurate cardiac recognition, compared to *Attend* (where people were instructed simply to guess). However, no significant differences were observed between *Regulate* and *Feel*. Importantly, although only the task in the *Feel* Condition was specifically designed for participants to perceive their own heartbeats, people were equally accurate in recognising their own cardiac feedback in the *Regulate* Condition, where control not perception was the goal. Our results show that that when participants attempt to control their biofeedback this also enhances their perception of it.

The amplitude of heartbeat-evoked potentials, reflected and reinforced these behavioural results, showing that the two interoceptive Conditions (*Feel* and *Regulate*) compared to the exteroceptive Condition (*Attend*) were associated with greater amplitude of the heartbeat-evoked potential, over the right-frontal area within the latency of 200-300ms. This partly supported hypothesis 3, where we had expected that HEP amplitudes would follow the cardiac accuracy results in the pattern (*Attend* < *Feel* < *Regulate*). It is well-established that HEPs are modulated by attention (Coll, Hobson, Bird, Murphy, & Holloway, 2020). However, HEPs in the *Regulate* Condition, where participants were not explicitly required to attend to individual heartbeats, but simply to try to control their HR, showed similar modulation of the HEPs (Petzschner et al., 2019).

Importantly, the highest interoceptive metacognition/insight (Khalsa et al., 2017) was observed in the *Regulate* Condition. Considering that metacognition in the *Regulate* Condition proved to be superior than in the *Attend* and *Feel* Conditions, our results support the potential relevance of metacognition for allostatic control (Stephan et al. 2016b). Stephan and colleagues (2016b) postulate that the performance of the interoceptive cortical circuit is monitored by a higher metacognitive layer, potentially in the anterior prefrontal cortex. This metacognitive layer encodes and updates beliefs about the brain's capacity to regulate bodily states, with the resulting representation of one's own self-efficacy. Taken together, these results imply that future work could use the two types of approach (*Feel* i.e., Perceive and *Regulate* i.e., Control), interchangeably, with the *Regulate* Condition being more ecologically valid and associated with superior metacognitive insight. What we try to convey here in terms of ecological validity is the idea that in several occasions in daily life people feel compelled to regulate their heart rate when they find themselves in a high arousal condition, such as attending a job interview, giving a talk in front of an audience or going to meet someone they are romantically interested in , to give a few examples. Therefore the Regulate condition may reflect a more ecological approach to the study of the function of interoception , rather than simply the sensing of heartbeats as most research on interoceptive accuracy/awareness seems to be focused on.

By contrast, Condition-specific cardiac recognition sensitivity (d') was linked to the modulation of Condition-specific HEP amplitude differences exclusively in the *Feel* condition (which relates to perceiving heartbeats) and not when using the *Regulate* Condition. This observed dissociation between *Feel* and *Regulate* Conditions might reflect the fact that in the *Feel* condition participants were instructed to use single heartbeat-based experience for cardiac recognition. Tentatively, while both the *Feel* and *Regulate* Conditions can facilitate sensitivity on a behavioral level, control-based inference (*Regulate*) may rely on a different process than the cortical processing of single heartbeats. To test this suggestion, future work is required to identify a cortical response that maps onto performance in cardiac recognition under the *Regulate* Condition. P300 is a promising candidate to track such links to cardiac recognition, because it is thought to reflect higher-order perceptual processing of motivationally relevant input (e.g., Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Schupp et al., 2004). Given that the highest level of metacognition was observed in the *Regulate* Condition, there might be a link between the motivationally relevant processing of a stimulus (heartbeat feedback) and cardiac recognition performance in the *Regulate* Condition. The presence of such correspondence would further support the argument that the *Regulate* Condition captures a more functional aspect of interoception than the perception of single heartbeats (*Feel*).

While the core idea behind our experimental manipulation was to influence the participant's engagement with the cardiac signal, rather than to measure their actual physiological states, it is important to address the fact that participants failed to decrease their HR (as instructed) in the *Regulate* Condition. This might account for the lack of difference in cardiac recognition and HEP amplitude between *Feel* and *Regulate* Conditions. It may be that longer periods than a 10s trial are needed for self-induced HR regulation to take effect. Alternatively, perhaps voluntary regulation of HR simply cannot be achieved in this form. *As previously noted, heartbeat perception tests grew out of early biofeedback literature and the (now disproved) assumption that to regulate an ANS signal one must be aware of it* (Brener, 1974, 1977). *Within that literature, the results of attempts to regulate HR have produced inconclusive results. For example,* a well-powered study of N = 180 by White, Holmes and Bennett (1977) found that participants' attempts to regulate their HRs were no more effective than a condition where participants simply attended to biofeedback. Conversely, De Pascalis and colleagues reported that participants were able to increase and decrease their HRs, with or without feedback and that this ability was unrelated to their heartbeat perception but was enhanced by highly motivating vs. neutral instructions (De Pascalis, Palumbo, & Ronchitelli, 1991). Furthermore, asymmetry in the direction of control has frequently been noted, leading to the proposal that increasing and decreasing HR are potentially separate skills, (Carroll & Whellock, 1980; Clemens & MacDonald, 1976; McFarland, 1975), with success dependent on a variety of parameters (Twentyman & Lang, 1980). For our purposes, as we had a novel paradigm, we chose our 'Regulate' condition as an unambiguous way to ensure that participants engaged with the biofeedback in a control-oriented manner. Asking participants to regulate their HR communicates this aim most clearly. However, it is possible that simply asking participants to focus on the changes, and to try to match their physiological state to the changes of the biofeedback, would lead to similar effects as our instruction to regulate HR. Alternatively, other cardiac measures could be considered to trace participant's cardiac regulation abilities within such short time-windows, such as the pre-ejection period (PEP), that reflects changes in cardiac sympathetic activity (Sherwood et al., 1990)

Most of the time, healthy people do not consciously perceive their heartbeats (Ádám, 1998). Heartbeat perception tests thus lack ecological validity. However, people are more likely to become aware of perturbations in their physiological states. For instance, a physiological state characterized by a vagal withdrawal (i.e., imbalanced state) supports mobilization responses (i.e., fight and flight), while increased vagal control (i.e., balanced state) is associated with the appearance of spontaneous social engagement behaviors (Porges, 2007). Our *Regulate* Condition refers to this functional aspect of interoception. Specifically, it can provide a more direct access to the estimates of bodily states –which is essential information for maintaining homeostatic/allostatic control (Stephan et al., 2016b).

Our findings, therefore, have important implications for future research. First, we need to critically evaluate the underlying assumptions that certain tasks and measures make about interoception. To achieve this, we must gain better insight into the different ways in which people engage with their internal states in real life. In other words, it is important that we study interoception during the modelling of realistic contexts such as social interactions and associated perturbations, where interoception has true experiential significance for the individual. This includes, but is not limited to, the modeling of real-life stressful scenarios (e.g., job interviews), health-related behaviors (e.g., attending to one's own body with the aim of deciding if one is feeling ill), and social interactions that require the understanding and communication of one's subjective experience to others. This requires the application of a more functional approach to interoception, necessitating the study of the ability to monitor and control our internal bodily states by individuals who are embedded in the social and physical world surrounding them. The *Regulate* Condition that we employed in this study indicates that such approaches can be at least as good as tests of interoceptive perception (such as our *Feel* Condition) and are metacognitively superior.

To conclude, we adopted a novel approach to cardiac interoception by exploring a functional/control aspect of a participant's engagement with their interoceptive signals (by asking them to regulate their HR). We compared this to a *Feel* Condition, which mirrored the classic tests of whether participants can perceive their heartbeats. Across behavioral, neural and metacognitive domains, we found that our active control-oriented Condition (*Regulate*) resulted in an ability to recognize one's own cardiac biofeedback that was equally as good as a Condition where the focus was on the classic task of perceiving individual heartbeats (*Feel*). Importantly, metacognition was superior when using our control-oriented approach to cardiac recognition, indicating that while the two conditions (*Feel* and *Regulate*) might be used interchangeably, the *Regulate* Condition is not only more ecologically valid but also involves better interoceptive insight. We hope that this new approach will both motivate new methodological approaches and accelerate research into understanding the functional aspects of interoception - specifically, a person's vital ability to monitor and predict internal bodily states in relation to the ever-changing social and physical world.

References

Allen, M., Frank, D., Schwarzkopf, D. S., Fardo, F., Winston, J. S., Hauser, T. U., & Rees, G. (2016). Unexpected arousal modulates the influence of sensory noise on confidence. Elife, 5, e18103. https://doi.org/10.7554/eLife.18103.001

Allen, M., & Tsakiris, M. (2018). The body as first prior: Interoceptive predictive processing and the primacy of self-models. The Interoceptive Mind from Homeostasis to Awareness, 27–45.

Allen, M., Poggiali, D., Whitaker, K., Marshall, T. R., & Kievit, R. (2018). Raincloud plots: a multi-platform tool for robust data visualization. PeerJ Preprints. https://doi.org/10.7287/peerj.preprints.27137v1

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. Journal of Memory and Language, 59(4), 390–412. https://doi.org/10.1016/j.jml.2007.12.005

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

Berntson, G. G., Cacioppo, J. T., & Grossman, P. (2007). Whither vagal tone. *Biological Psychology*, *74*(2), 295–300. https://doi.org/10.1016/j.biopsycho.2006.08.006

Billman, G. E. (2013). The LF/HF ratio does not accurately measure cardiac sympatho-vagal balance. *Frontiers in Physiology*, *4*, 26. https://doi.org/10.3389/fphys.2013.00026

Boudewyn, M. A., Luck, S. J., Farrens, J. L., & Kappenman, E. S. (2018). How many trials does it take to get a significant ERP effect? It depends. Psychophysiology, 55(6). https://doi.org/10.1111/psyp.13049

Brener, J. (1974). A general model of voluntary control applied to the phenomenon of learned cardiovascualr change. In P. Obrist, A. Black, J. Brener, & L. V DiCara (Eds.), *Cardiovascualr Physiology* (pp. 365–391). Chicago: Aldine.

Brener, J. (1977). Factors influencing the specificty of voluntary cardiovascualr control. In L. V DiCara (Ed.), Limbic and autonomic nervous system research (pp. 335–368). New York: Plenum Press.

Brenner, S. L., & Beauchaine, T. P. (2011). Pre-ejection period reactivity and psychiatric comorbidity prospectively predict substance use initiation among middle-schoolers: A pilot study. Psychophysiology, 48(11), 1587–1595. https://doi.org/10.1111/j.1469-8986.2011.01230.x

Brewer, N., & Wells, G. L. (2006). The confidence-accuracy relationship in eyewitness identification: Effects of lineup instructions, foil similarity, and target-absent base rates. Journal of Experimental Psychology: Applied, 12(1), 11–30. https://doi.org/10.1037/1076-898X.12.1.11

Brown, H., Adams, R. A., Parees, I., Edwards, M., & Friston, K. (2013). Active inference, sensory attenuation and illusions. Cognitive Processing, 14(4), 411–427. https://doi.org/10.1007/s10339-013-0571-3

Brysbaert, M., & Stevens, M. (2018). Power Analysis and Effect Size in Mixed Effects Models: A Tutorial. Journal of Cognition, 1(1), 1–20. https://doi.org/10.5334/joc.10

Camm, A. J., Malik, M., Bigger, J. T., Breithardt, G., Cerutti, S., Cohen, R. J., & Lombardi, F. (1996). Heart rate variability: standards of measurement, physiological interpretation and clinical use.Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology. *Circulation*, *93*(5), 1043–1065. https://doi.org/10.1161/01.CIR.93.5.1043

Canales-Johnson, A., Silva, C., Huepe, D., Rivera-Rei, Á., Noreika, V., Del Carmen Garcia, M., … Bekinschtein, T. A. (2015). Auditory feedback differentially modulates behavioral and neural markers of objective and subjective performance when tapping to your heartbeat. Cerebral Cortex, 25(11), 4490–4503. https://doi.org/10.1093/cercor/bhv076

Carroll, D., & Whellock, J. (1980). Heart rate perception and the voluntary control of herat rate. Biological Psychology, 11, 169–180.

Clemens, W. J., & MacDonald, D. (1976). Relationship between Heart Rate Discrimination and Heart Rate Control. Psychophysiology, 13(2), 176.

Coll, M.-P., Hobson, H., Bird, G., Murphy, J., & Holloway, R. (2021). Systematic review and meta-analysis of the relationship between the heartbeat-evoked potential and interoception. Neurosci Biobehav Rev ;122:190-200.

Cook, R. D. (1977). Detection of Influential Observation in Linear Regression. Technometrics, 19(1), 15. https://doi.org/10.2307/1268249

Couto, B., Salles, A., Sedeño, L., Peradejordi, M., Barttfeld, P., Canales-Johnson, A., … Ibanez, A. (2013). The man who feels two hearts: The different pathways of interoception. Social Cognitive and Affective Neuroscience, 9(9), 1253–1260. https://doi.org/10.1093/scan/nst108

Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N., & Lang, P. J. (2000). Brain potentials in affective picture processing: Covariation with autonomic arousal and affective report. Biological Psychology, 52(2), 95–111. https://doi.org/10.1016/S0301-0511(99)00044-7

Damasio, A. (2010). Self comes to mind: Constructing the conscious brain. London: William Heinemann.

De Pascalis, V., Palumbo, G., & Ronchitelli, V. (1991). Heartbeat perception, instructions, and biofeedback in the control of heart rate. International Journal of Psychophysiology, 11(2), 179–193. https://doi.org/10.1016/0167-8760(91)90010-U

Dirlich, G., Vogl, L., Plaschke, M., & Strian, F. (1997). Cardiac field effects on the EEG. Electroencephalography and Clinical Neurophysiology, 102(4), 307–315. https://doi.org/10.1016/S0013-4694(96)96506-2

Eckberg, D. L. (1997). Sympathovagal balance: A critical appraisal. *Circulation*, *96*(9), 3224–3232. https://doi.org/10.1161/01.CIR.96.9.3224

Feldman, H., & Friston, K. J. (2010). Attention, Uncertainty, and Free-Energy. Frontiers in Human Neuroscience, 4, 215. https://doi.org/10.3389/fnhum.2010.00215

Fleming, S. M., & Lau, H. C. (2014). How to measure metacognition. Frontiers in Human Neuroscience, 8, 443. https://doi.org/10.3389/fnhum.2014.00443

Friston, K. (2009). The free-energy principle: a rough guide to the brain? Trends in Cognitive Sciences, 13(7), 293–301. https://doi.org/10.1016/J.TICS.2009.04.005

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

Goedhart, A. D., Willemsen, G., Houtveen, J. H., Boomsma, D. I., & De Geus, E. J. (2008). Comparing low frequency heart rate variability and preejection period: Two sides of a different coin. *Psychophysiology*, *45*(6), 1086–1090. https://doi.org/10.1111/j.1469-8986.2008.00710.x

Gray, M. A., Taggart, P., Sutton, P. M., Groves, D., Holdright, D. R., Bradbury, D., … Critchley, H. D. (2007). A cortical potential reflecting cardiac function. Proceedings of the National Academy of Sciences of the United States of America, 104(16), 6818–6823. https://doi.org/10.1073/pnas.0609509104

Hauser, T. U., Allen, M., Purg, N., Moutoussis, M., Rees, G., & Dolan, R. J. (2017). Noradrenaline blockade specifically enhances metacognitive performance. eLife, 6, e24901. https://doi.org/10.7554/elife.24901

Heathers, J. A. J. (2012). Sympathovagal balance from heart rate variability: an obituary. *Experimental Physiology*, *97*(4), 556–556. https://doi.org/10.1113/expphysiol.2011.063867

Hohwy, J. (2012). Attention and conscious perception in the hypothesis testing brain. Frontiers in Psychology, 3(APR), 96. https://doi.org/10.3389/fpsyg.2012.00096

Kern, M., Aertsen, A., Schulze-Bonhage, A., & Ball, T. (2013). Heart cycle-related effects on event-related potentials, spectral power changes, and connectivity patterns in the human ECoG. NeuroImage, 81, 178–190. https://doi.org/10.1016/j.neuroimage.2013.05.042

Khalsa, S. S., Adolphs, R., Cameron, O. G., Critchley, H. D., Davenport, P. W., Feinstein, J. S., … Paulus, M. P. (2017). Interoception and Mental Health: a Roadmap. Biological Psychiatry: Cognitive Neuroscience and Neuroimaging, 0(0). https://doi.org/10.1016/j.bpsc.2017.12.004

Khalsa, S. S., Rudrauf, D., Damasio, A. R., Davidson, R. J., Lutz, A., & Tranel, D. (2008). Interoceptive awareness in experienced meditators. Psychophysiology, 45(4), 671–677. https://doi.org/10.1111/j.1469-8986.2008.00666.x

Luft, C. D. B., & Bhattacharya, J. (2015). Aroused with heart: Modulation of heartbeat evoked potential by arousal induction and its oscillatory correlates. Scientific Reports, 5(1), 15717. https://doi.org/10.1038/srep15717

Lüdecke, D. (2018a). sjmisc: Data and Variable Transformation Functions. Journal of Open Source Software, 3(26), 754. https://doi.org/10.21105/joss.00754

Lüdecke, D. (2018b). sjPlot: Data Visualization for Statistics in Social Science. https://doi.org/10.5281/zenodo.1308157

Macmillan, N. A., & Creelman, C. D. (2004). Detection Theory: A User's Guide: 2nd edition (pp. 1–445). Psychology Press. https://doi.org/10.4324/9781410611147

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. Journal of Neuroscience Methods, 164(1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024

Mason J.W., Ramseth D.J., Chanter D.O., Moon T.E., Goodman D.B., Mendzelevski B. (2007). Electrocardiographic reference ranges derived from 79,743 ambulatory subjects. Journal of Electrocardiology, 40(3), 228-34. https://doi.org/10.1016/j.jelectrocard.2006.09.003

McFarland, R. A. (1975). Heart Rate Perception and Heart Rate Control. Psychophysiology, 12(4), 402–405. https://doi.org/10.1111/j.1469-8986.1975.tb00011.x

Mickes, L. (2015). Receiver operating characteristic analysis and confidence-accuracy characteristic analysis in investigations of system variables and estimator variables that affect eyewitness memory. Journal of Applied Research in Memory and Cognition, 4(2), 93–102. https://doi.org/10.1016/j.jarmac.2015.01.003

Park, H. D., Correia, S., Ducorps, A., & Tallon-Baudry, C. (2014). Spontaneous fluctuations in neural responses to heartbeats predict visual detection. Nature Neuroscience, 17(4), 612–618. https://doi.org/10.1038/nn.3671

Paulus, M. P., Feinstein, J. S., & Khalsa, S. S. (2019). An Active Inference Approach to Interoceptive Psychopathology. Annual Review of Clinical Psychology, 15, 97–122. https://doi.org/https://doi/10.1146/annurev-clinpsy-050718-095617

Petrusic, W. M., & Baranski, J. V. (1997). Context, feedback, and the calibration and resolution of confidence in perceptual judgments. American Journal of Psychology, 110(4), 543–572. https://doi.org/10.2307/1423410

Petzschner, F. H., Weber, L. A., Wellstein, K. V., Paolini, G., Do, C. T., & Stephan, K. E. (2019). Focus of attention modulates the heartbeat evoked potential. NeuroImage, 186, 595–606. https://doi.org/10.1016/j.neuroimage.2018.11.037

Pezzulo, G., Rigoli, F., & Friston, K. (2015). Active Inference, homeostatic regulation and adaptive behavioural control. Progress in Neurobiology, 134, 17–35. https://doi.org/10.1016/j.pneurobio.2015.09.001

Pfeiffer, C., & De Lucia, M. (2017). Cardio-audio synchronization drives neural surprise response. Scientific Reports, 7(1), 14842. https://doi.org/10.1038/s41598-017-13861-8

Pollatos, O., & Schandry, R. (2004a). Accuracy of heartbeat perception is reflected in the amplitude of the heartbeat-evoked brain potential. Psychophysiology, 41(3), 476–482. https://doi.org/10.1111/1469-8986.2004.00170.x

Pollatos, O., & Schandry, R. (2004b). Accuracy of heartbeat perception is reflected in the amplitude of the heartbeat-evoked brain potential. Psychophysiology, 41(3), 476–482. https://doi.org/10.1111/1469-8986.2004.00170.x

Porges, S. W. (2007). A phylogenetic journey through the vague and ambiguous Xth cranial nerve: A commentary on contemporary heart rate variability research. Biological Psychology, 74(2), 301–307. https://doi.org/10.1016/j.biopsycho.2006.08.007

R Core Team. (2018). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/

Reyes del Paso, G. A., Langewitz, W., Mulder, L. J., Roon, A. van, & Duschek, S. (2013). The utility of low frequency heart rate variability as an index of sympathetic cardiac tone: A review with emphasis on a reanalysis of previous studies. *Psychophysiology*, *50*(5), 477–487. https://doi.org/10.1111/psyp.12027

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. https://doi.org/10.1523/JNEUROSCI.4262-15.2016

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

Schulz, A., Ferreira de Sá, D. S., Dierolf, A. M., Lutz, A., Dyck, Z. van, Vögele, C., & Schächinger, H. (2015). Short-term food deprivation increases amplitudes of heartbeat-evoked potentials. Psychophysiology, 52(5), 695–703. https://doi.org/10.1111/psyp.12388

Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Hillman, C. H., Hamm, A. O., & Lang, P. J. (2004). Brain processes in emotional perception: Motivated attention. Cognition and Emotion, 18(5), 593–611. https://doi.org/10.1080/02699930341000239

Sel, A., Azevedo, R. T., & Tsakiris, M. (2017). Heartfelt Self: Cardio-Visual Integration Affects Self-Face Recognition and Interoceptive Cortical Processing. Cerebral Cortex, 27(11), 5144–5155. https://doi.org/10.1093/cercor/bhw296

Seth, A. K., & Tsakiris, M. (2018). Being a Beast Machine: The Somatic Basis of Selfhood. Trends in Cognitive Sciences, 1–30. https://doi.org/10.1016/j.tics.2018.08.008

Sherwood, A., Allen, M. T., Fahrenberg, J., Kelsey, R. M., Lovallo, W. R., & van Doornen, L. J. P. (1990). Methodological Guidelines for Impedance Cardiography. In Psychophysiology (Vol. 27, pp. 1–23). John Wiley & Sons, Ltd. https://doi.org/10.1111/j.1469-8986.1990.tb02171.x

Stephan, K. E., Binder, E. B., Breakspear, M., Dayan, P., Johnstone, E. C., Meyer-Lindenberg, A., … Friston, K. J. (2016a). Charting the landscape of priority problems in psychiatry, part 2: Pathogenesis and aetiology. The Lancet Psychiatry, 3(1), 84–90. https://doi.org/10.1016/S2215-0366(15)00360-0

Stephan, K. E., Manjaly, Z. M., Mathys, C. D., Weber, L. A. E., Paliwal, S., Gard, T., … Petzschner, F. H. (2016b). Allostatic Self-efficacy: A Metacognitive Theory of Dyshomeostasis-Induced Fatigue and Depression. Frontiers in Human Neuroscience, 10, 550. https://doi.org/10.3389/fnhum.2016.00550

Sterling, P. (2014). Homeostasis vs allostasis implications for brain function and mental disorders. JAMA Psychiatry, 71(10), 1192–1193. https://doi.org/10.1001/jamapsychiatry.2014.1043

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

Terhaar, J., Viola, F. C., Bär, K. J., & Debener, S. (2012). Heartbeat evoked potentials mirror altered body perception in depressed patients. Clinical Neurophysiology, 123(10), 1950–1957. https://doi.org/10.1016/j.clinph.2012.02.086

Twentyman, C. T., & Lang, P. J. (1980). Instructed heart rate control - Effects of varying feedback frequency and timing. Biofeedback and Self-Regulation, 5(4), 417–426. https://doi.org/10.1007/BF01001357

Van Boeijen, I., & Saraiva, R. (2018). egalPsych: A tool for calculating calibration statistics in eyewitness research. Retrieved from https://github.com/IngerMathilde/legalPsych

Voeten, C. (2019). buildmer: Stepwise Elimination and Term Reordering for Mixed-Effects Regression. Retrieved from https://github.com/cvoeten/buildmer/issues

Vossel, S., Mathys, C., Daunizeau, J., Bauer, M., Driver, J., Friston, K. J., & Stephan, K. E. (2014). Spatial Attention, Precision, and Bayesian Inference: A Study of Saccadic Response Speed. Cerebral Cortex, 24(6), 1436–1450. https://doi.org/10.1093/cercor/bhs418

White, T. W., Holmes, D. S., & Bennett, D. H. (1977). Effects of instructions, biofeedback, and cognitive activities on heart rate control. Journal of Experimental Psychology: Human Learning and Memory, 3(4), 477–484. https://doi.org/10.1037/0278-7393.3.4.477

Whitehead, W. E., Drescher, V. M., Heiman, P., & Blackwell, B. (1977). Relation of Heart Rate Control to Heartbeat Perception. Biofeedback and Self-Regulation, 2(4). Retrieved from https://link.springer.com/content/pdf/10.1007{\%}2FBF00998623.pdf