Neurobehavioral Differences across Strategies Used in Cardiac Recognition

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Abstract

The maintenance of psycho-physiological stability requires the ability to infer the state of our body (interoception) and to predict its future evolution. Yet standard measures of interoception do not have this functional approach as they are typically limited to the conscious perception of single heartbeats. We here present a new biofeedback paradigm to explore the effect of three strategies (i.e. exteroceptive, active or passive interoceptive) on interoceptive inference – defined here as the ability to recognize one’s own heart. We observed an increase of cardiac recognition and a more pronounced cortical processing of heartbeats across both interoceptive strategies as compared to the exteroceptive one. We also observed the highest level of metacognition at the active, control-based interoceptive strategy. Strategy-specific cardiac recognition was linked to the modulation of cortical processing of heartbeats, exclusively in the passive interoceptive condition. We suggest that while both active and passive strategies increase the precision of the interoceptive channel, they exert distinct influences on different levels of the interoceptive hierarchy.

Keywords: interoception, strategies, metacognition, biofeedback, predictive coding

Word count: 8579

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Introduction

The same external world surrounds everyone, yet its experience will always be *unique* to the individual, because it is anchored to what one feels, thinks and does in the moment. It has been proposed that the subjectivity of this experience is underpinned by the continuous mapping of internal homeostatic states of the body (Damasio, 2010). In an ever-changing physical and social environment, the brain and body need to find ways to maintain psycho-physiological stability to preserve one's viability and self-continuity at a psychophysiological level. The maintenance of a stable internal environment is realized on various hierarchical levels (Seth & Tsakiris, 2018), via homeostatic (reactive) and allostatic (prospective) control (Khalsa et al., 2017). On a lower hierarchical level, the autonomic nervous system supplies homeostasis and adaptive response to stress or more generally perturbations. Its functioning is mainly non-conscious as it operates through reflex-like *autonomic responses* (Pezzulo, Rigoli & Friston, 2015). In contrast, allostasis is a proactive control process that is aimed at minimizing energy costs by adaptively anticipating future needs of the body – oftentimes manifesting in conscious regulatory *actions* (Paulus, Feinstein & Khalsa, 2019).

Both control mechanisms necessitate the ability to distinguish between exteroceptive (originating from the external world) and interoceptive (arising from our body) sources of sensations. Evidence from multisensory studies suggests that interoceptive and exteroceptive signals are not processed in isolation (e.g. Pfeiffer & De Lucia, 2017; Salomon et al., 2016; Suzuki, Garfinkel, Critchley & Seth, 2013), which aligns with current concepts from computational neuroscience on the “Bayesian brain” (e.g. Allen and Friston, 2018). Within this framework the brain is assumed to actively construct generative models by integrating different

sources of inputs. The appeal of predictive coding (PC) theories is that they offer an elegant description for the intertwined processes of inference, learning and prediction. The core principle in PC proposes that an organism is driven to minimize ‘free energy’, which is the sum of differences between the actual and predicted sensory input (Friston, 2009). The brain’s *prior* predictions about the causes of its sensations are updated by *prediction errors* (PE-s), which are that part of the sensory data that the prior cannot explain. In perceptual inference, the flow of information for probabilistic predictions is top-down through hierarchical brain pathways. In contrast, PE-s are passed upward to hierarchically higher cortical levels – encoding abstract, supramodal representations - until they are resolved.

Priors, predictions and PE-s are characterized by their respective precision (Friston, 2009) that represents the reliability of the information. Therefore precise PE-s will update less precise priors. In contrast, precise priors will be less likely to lead to an update. In other words, in any moment, context or modality, precision will determine if PE-s *or* priors will have bigger role in the resulting percept (Ainley, Apps, Fotopoulou & Tsakiris, 2016). Several studies within the PC framework support the view that the optimization of precision-weighting happens through attention-gating (Vossel et al., 2014). This means that attention directed at a certain exteroceptive or interoceptive channel will increase its relative precision and thus the impact of associated PE-s arising from that channel (Feldman & Friston, 2010).

While most interoceptive signals support homeostasis without the need for awareness, we are also capable of consciously attending to our interoceptive sensations. Research on interoceptive accuracy (IAcc) – the ability to precisely and correctly monitor changes in the internal body state – has been mainly studies in the context of cardioception. The reason behind this is practical as heartbeats represent discreet physiological events whose conscious perception can be easily quantified. It has recently been proposed that individual differences in IAcc depend on the

precision in interoceptive systems (Ainley et al., 2016). According to this argument, people with high IAcc are able, by attention, to prioritize interoception over other sensory channels and thus adjust the relative precision of their interoceptive priors and PE-s.

Of relevance, the heartbeat evoked potential (HEP) – an electrophysiological brain response reflecting the cortical processing of individual heartbeats – has been found to be more pronounced in people with high IAcc (Pollatos & Schandry, 2004). Focusing on the potential underlying mechanism, HEP is proposed to reflect the precision-weighted PE of every heartbeat (Ainley et al., 2016). A recent study by Petzschner and colleagues (2019) provides support for this interpretation. Their results revealed that the amplitude of HEP is indeed sensitive to attentional differences between exteroceptive (attention to white noise) and interoceptive conditions (focus on heartbeats).

There are two standard IAcc tasks currently in use. In the *Heartbeat Discrimination* task (Whitehead, Drescher, Heiman, & Blackwell, 1977) individuals report the perceived synchrony of their heartbeats with a series of external stimuli (usually auditory cues). In contrast, *Heartbeat Counting* (Schandry, 1981) requires the individual to mentally track their heart beating during short time windows and report the counted number of heartbeats. Although these tasks are not flawless (for a summary see Paulus et al., 2019) the research on conscious cardiac perception remains highly relevant, as it provides the means to explore how the brain-body communication is achieved through inference. Understanding how interoceptive inference takes place is crucial because for the attainment of optimal control, the brain requires a model of the external world and the ability to make inferences and then choose suitable (not necessarily motor) actions in advance of any potential instability (Sterling, 2014).

Unfortunately, the aim to sustain optimal control has not been an integral part of the IAcc tasks described above, due to their assumptions about the way people process their cardiac signal while interacting with the world. Specifically, such tasks assume that people can (i) consciously perceive individual heartbeats and (ii) use this single heartbeat-related sensory input for making inferences. These assumptions do not reflect the functional and ecological role that interoception plays, namely the ability to monitor changes of internal body state (Khalsa et al., 2017) and to predict their future (Pezzulo et al., 2015). The present study aimed at bridging the gap between measure and definition and sought to go beyond these limiting assumptions to explore a more functional aspect of interoception. Using a biofeedback paradigm, we tested if the accuracy of interoceptive inference (here the ability to correctly recognize biofeedback representing one's own cardiac activity) differs across different strategies used when engaging with one's ongoing cardiac activity. We choose three strategies that all involve a combination of interoceptive and exteroceptive elements but differ in the levels of engagement they require and the feature of the biofeedback they emphasize. Specifically, we were interested in how these different strategies could inform the process of inference - measured by explicit cardiac recognition. The first, neutral strategy *Attend* aims to bring participant's focus to exteroceptive characteristics of the cardiac biofeedback signal by asking participants to attend for randomly appearing pulses while looking at their cardiac biofeedback. The second strategy *Feel* relies on *passive* interoception, where participants attempt to feel random pulses while looking at their cardiac biofeedback. And lastly, the third strategy *Regulate* has an *active*, control-oriented approach to interoception as participants attempt to regulate their own interoceptive signal while looking at their cardiac biofeedback. The reason for including the *Regulate* condition was to emphasize the *function* of interoception, which is to maintain homeostatic/allostatic control (Stephan et al., 2016a). Specifically, we propose that a control-based inference (*Regulate*) has the potential to track

interoception in a manner that is more relevant to anticipatory control (i.e. allostasis), as it requires the attention *to* but also the control of bodily states and their development, rather than the simple perception of individual heartbeats (*Feel*).

Interoception has several facets related to sensing, interpreting, and integrating information about the state of inner body systems (Khalsa et al., 2017). As recent studies have highlighted the importance of visceral precision on metacognition (Allen et al., 2016; Hauser et al., 2017), we also decided to explore strategy-related changes of interoceptive insight (i.e. correspondence between subjective experience and behavior) with our cardiac recognition paradigm.

To summarize, here we investigate the consequences of three different strategies (i.e. *Attend*, *Feel*, *Regulate*) for inferences about the self, in relation to the external world, with an integrative approach. Our study uses a novel cardiac recognition paradigm and employs measures from several domains of interoception to capture behavioral, cortical and metacognitive aspects. Specifically, we contrast exteroception and the traditional passive interoceptive approach with an active regulation strategy, with which we aim to harness the functionality of interoception related to the monitoring and prediction of *changes* of broader internal states. We preregistered our hypotheses under the Preregistration Challenge by the Open Science Framework which can be viewed at <https://tinyurl.com/y33bgvcd>. Below we present the summary of our hypotheses about the expected neurobehavioral differences across strategies.

1. Participants' performance on the cardiac recognition task will not have a ceiling or floor effect, therefore will be able to detect individual differences.
2. Strategies will differ in their ability to inform accurate cardiac recognition on a behavioral level, leading to better performance in the cardiac recognition task (represented by higher

d' values) following the pattern of increasing levels of engagement across strategies (i.e. *Attend < Feel < Regulate*).

3. There will be an interaction between the three distinct strategies and lower-level biofeedback congruency (i.e. synchrony) which will affect HEP amplitudes, again in the direction of increasing levels of engagement (i.e. *Attend < Feel < Regulate*).

In addition, we also employed exploratory analyses on the differences in metacognitive abilities across the three distinct strategies (i.e. *Attend, Feel, Regulate*) and the link between behavioral measures of strategy-specific cardiac recognition performance and corresponding modulation of HEP amplitudes.

Methods

We report how we determined our sample size, all data exclusions, all manipulations and all measures in the study.

Participants

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 before running our experiment. When conducting mixed effects analysis Brysbaert and Stevens (2018) suggests 1600 trials across all participants to reach good levels of power. To avoid fatigue, we maximized the total number of trials for each participant at 156 trials, taking approximately 1 hour (i.e. 26 trials/condition; for more information see Figure 2B), which also fits 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. With an average of 60 BPM and 26 ten-second-long

trials we can expect around 260 epochs in every condition, which fits the recommendations for ERP studies by Boudewyn, Luck, Farrens, and Kappenman (2018). To be conservative, we recruited a total of $N = 34$ healthy participants (14 females; $M_{AGE} = 28.71$, $SD_{AGE} = 8.71$) through the Psychology Subject Pool of Royal Holloway, University of London. Participants gave their informed consent, with approval by the Ethics Committee, Department of Psychology, Royal Holloway University of London.

Procedure

Our experiment had a 2×3 repeated measures design (Figure 1) with 2 conditions of interest: Strategy (referring to the instructions participants received about the strategy they should use for cardiac recognition i.e. *Attend*, *Feel* or *Regulate*) and Biofeedback Congruency (the congruency between participants own cardiac activity and the visual signal i.e. *Congruent* and *Incongruent* biofeedback).

Figure 1. Schematic representation of the cardiac recognition paradigm. The 2×3 repeated measures design consisted of the factors of Strategy to use for cardiac recognition (exteroceptive: *Attend*; interoceptive: *Feel*, *Regulate*) and Biofeedback Congruency (*Congruent*, *Incongruent*). During the Congruent trials feedback presentation was linked to participants' cardiac systole. The

style of the arrow represents the passive/active (full/dashed line) stages of the participant's engagement with the cardiac/feedback signal when using a particular Strategy.

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. First a standard 3-lead electrocardiogram (ECG) was attached to participants' chest, then we measured their baseline high frequency heart rate variability (HF-HRV) for 5 minutes, while sitting in silence with their eyes open, looking at a black screen. This was followed by the practice version of the experiment, where the experimenter answered the participants' questions, made sure that all instructions were clear, and the participant had the chance to practice each of the three strategies *once* – all these steps taking approximately 15min in total. After the practice session, participants were equipped with the EEG electrode cap as well as the external electrodes. The experimenter explained to the participants the reason why artifacts are an issue for EEG analysis (i.e. blinks, saccades, and clench of jaw) and the ways they could contribute clean data, by asking participants to demonstrate such artifacts and showing them the resulting EEG signal. Participants were encouraged to time their blinking for the response phase only and to avoid any movements during the 10-second-long biofeedback presentation.

The experiment contained 156 randomly presented trials with a length of approx. 15-20 s (i.e. 10 seconds of biofeedback presentation and an unlimited response phase). At the beginning of every trial, a colour-coded word appeared on the screen for one second, representing the strategy participants should use to interact with their cardiac signals and/or the subsequent biofeedback (for details of the biofeedback see the Stimuli section). The words were colour-coded (i.e. "Count" – green, "Feel" – blue and "Regulate" – red) to guide participants attention to the feature of the biofeedback signal that was crucial for the upcoming strategy. In the *exteroceptive* trials

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(i.e. the *Attend* condition which was signaled by the *green* word “Count”) participants were asked to count randomly presented *green* pulse(s). During the *interoceptive* trials participants were required to engage with the biofeedback through the context of their own cardiac signals. Specifically, when presented with the *blue* word “Feel”, participants had to track whether they felt a heartbeat in time with the randomly presented *blue* pulse(s). When presented with the word “Regulate” written in *red*, participants were instructed to focus only on the up-and-down movements of the *red* bar – although to ensure compatibility with other conditions the pulsing was still present. In this trial their task was to attempt to lower the biofeedback bar, by reducing their own heartrate while breathing normally. After the strategy-prompting word participants were presented with the biofeedback for 10 seconds (for more on the stimulus itself please refer to the *Stimuli* section). Across all three strategies, participants were instructed to avoid explicitly thinking if they are seeing their own or someone else’s biofeedback and simply focus on applying the strategy that was assigned to the current trial. Once the biofeedback disappeared from the screen, participants answered a strategy-specific control question to ensure that the right strategy was used in that trial. In the *Attend* condition, participants input the exact counted number of counted green pulses using a sliding scale once feedback had concluded. For the *Feel* trials, individuals indicated if they felt *any* of the blue pulses, by using a continuous sliding scale with the endpoints “None of them” and “All of them”. In the *Regulate* condition, participants reported how well they thought they regulated their *own* heart (not the biofeedback bar), by using a sliding scale with endpoints: “Not at all” and “Very well” (Figure 2.A1).

The remaining two questions were the same for all three conditions. Participants first had to report if they thought the feedback represented their own heart (i.e. “Yes” or “No”). Participants could take as long as they wished when responding and received no feedback on their accuracy.

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As learned in practice phase, participants would use their strategy-specific experience to make their decision on cardiac-recognition. For the *Feel* trials they would report the feedback as their own if they felt at least one heartbeat in time with any of the blue pulses. In contrast, during the Regulate condition participants would indicate the feedback as their own if they felt that the movements of the feedback bar were responding to them. Lastly, for the *Attend* trials participants were instructed to simply *guess* whose feedback they have seen. Finally, 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 2.A2). Unbeknown to the participants, the positions of this scale corresponded to values ranging between 1 and 50. The task took approximately 1 hour to complete, including a 10 min break half-way through.

Figure 2. Experimental procedure of the cardiac recognition task. (A1) Timeline of Strategy dependent stimuli presentation and strategy-specific questions. (A2) Questions on cardiac

recognition and participants' subjective confidence were presented after every trial for all conditions. (B) Summary table of the number of behavioral trials within each condition and across the whole sample.

Stimuli

Analogue output of inter beat intervals (IBI-s) was obtained online and recorded digitally on a PC into MATLAB (MathWorks, Sherborn, Mass., USA). Within MATLAB, a script was created to provide the visual display to the subject during biofeedback exercises. During the 10-second-long biofeedback phase of each trial, participants received an instantaneous and continuous feedback of cardiac activity across two dimensions simultaneously. In general, as one's heart rate increased the bar became taller, and as the heart rate dropped the bar followed it by becoming shorter. To provide a more direct feedback of beat to beat changes, a short yellow pulse also appeared on the bar 280 ms after the R-wave peak, which coincides with the time window (200–300 ms post R-wave) of peak systolic pressure, which is the period of maximum subjective perception of heartbeats (Brener et al., 1993, Suzuki et al. 2013). This latency was chosen to ensure a sufficiently long, analyzable epoch of the HEP that did not coincide with the visual evoked potential induced by the pulse. At approximately 50% of all pulses within each trial, the pulses changed from the default yellow to a different colour following a randomized pattern in their order. The alternative colour corresponded to the Strategy condition in the following way: *Attend* – green, *Feel* – blue and *Regulate* – white.

The feedback bar was set to the middle at the beginning of every trial. To establish the center of the feedback bar for the first congruent trial, 10 inter-beat-intervals (IBI-s) were averaged prior to the beginning of the task. Afterwards, for the congruent trials, the value representing the middle reference point of the bar was extracted and updated, based on the participants *real* IBI-s from the

previous trial (in any condition). In contrast, for the reference point of the Incongruent trials we used IBI-s from the previous Incongruent trial. In this way, we could ensure that the parameters of the biofeedback bar were continuously scaled. To make the feedback more sensitive to the changes in the lower ranges of heart rate (and less sensitive to movement artifacts) we set the minimum of the bar by subtracting a quarter of the baseline while we created the maximum value by adding half the baseline. The required change for every step was also relative to the participants' baseline (or the baseline of the incongruent IBI series).

Most previous studies created asynchronous feedback by changing the frequency of the participant's own estimated heartrate to be either 30% slower or faster (e.g. Suzuki et al., 2013). Unlike these studies, we used a database of incongruent IBI series ($N = 72$, $M_{IC_IBI} = 779.89$, $SD_{IC_IBI} = 142.03$) from a database of people who completed the same task on a different occasion. We decided to use this database instead of participants' own altered cardiac activity from previous trials, based on our pilot data because in the piloting stage of this experiment we found that participants performed consistently below chance when trying to differentiate between congruent and incongruent feedback (without using any strategies) when presented with their own altered heartbeats. In other words, participants were more likely to respond incorrectly than correctly when identifying the source of the feedback. By contrast, participants had a higher chance of being accurate when the incongruent feedback was based on the cardiac data of other individuals rather than their own. A potential explanation for this is that the difference between signal (congruent) and noise (incongruent trials) increased when using other people's cardiac signal, resulting in a paradigm that was accomplishable yet still challenging. The incongruent feedback was tailored for every participant by matching it with the most similar IBI series from our database, based on their average baseline IBI. We intended to keep the level of incongruency

between conditions (and across participants) as constant as possible. We addressed this by adjusting, in every trial, for the percentage difference between the incongruent signal and the participant's own baseline. To introduce some noise, half of the incongruent trials were presented 15% slower, while the other half were 15% faster than the original – the order of which was randomly generated.

EEG and ECG Recording

EEG was recorded with Ag-AgCl electrodes from 64 active scalp electrodes mounted on an elastic electrode cap, 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 reference offline. ECG signal was recorded with a standard 3-lead ECG attached to participants' chest (Powerlab, ADInstruments, www.adinstruments.com) which we used for sending out triggers for MATLAB in the cardiac recognition task and through MATLAB to the Actiview. The onset of the R-waves coming from the 6 conditions were marked in the EEG recording using 6 different triggers. In addition to four external electrodes recording eye movement artifacts, another external electrode was attached to the participants left sternum to provide a clear ECG trace for cardiac artifact detection. The average number HEP epochs in Congruent conditions were $M_{\text{ATTEND}} = 317.26$, $SD_{\text{ATTEND}} = 50.27$, $M_{\text{FEEL}} = 313.94$, $SD_{\text{FEEL}} = 49.81$, $M_{\text{REGULATE}} = 314.29$, $SD_{\text{REGULATE}} = 50.20$, while in the Incongruent conditions were $M_{\text{ATTEND}} = 310.65$, $SD_{\text{ATTEND}} = 53.94$, $M_{\text{FEEL}} = 309.65$, $SD_{\text{FEEL}} = 53.37$, $M_{\text{REGULATE}} = 306.50$, $SD_{\text{REGULATE}} = 53.10$. Importantly, there were no significant differences in the number of heartbeats between conditions $F(2,198) = 0.02$, $p = .980$.

308 **EEG Data Analysis**

309 Offline EEG pre-processing was performed using the BrainVision Analyzer software
 310 (Brain Products, Munich, Germany). The continuous EEG data was filtered with a bandpass filter
 311 of 0.1–30 Hz (24 dB/oct) and a 50 Hz notch filter. Then we applied Independent Component
 312 Analysis (ICA) on resampled data (250Hz) to remove ocular and cardiac-field artifacts (CFA-s)
 313 (Terhaar, Viola, Bär, & Debener, 2012) based on their timing, topographical and physical
 314 characteristics. The ICA method is of high efficiency in the removal of CFA-s from the EEG
 315 signal (e.g. Park, Correia, Ducorps, and Tallon-Baudry, 2014; Terhaar et al., 2012; Luft &
 316 Bhattacharya, 2015). After the ICA, the EEG signal was segmented into 600 ms epochs, starting
 317 150 ms before the R-wave onset using the R-wave onset related triggers sent by MATLAB (i.e. -
 318 200 ms to 400 ms epochs around the R-wave). Segments were then baseline corrected using an
 319 interval from –150 to –50 ms before the R-wave onset to avoid the inclusion of artifacts related
 320 to R-wave rising edge (Canales-Johnson et al., 2015) and late components of visual evoked
 321 responses to the pulsing stimulus of the immediately preceding trial. Semiautomatic artifact
 322 rejection was combined with visual inspection for all participants. Epochs exceeding a voltage
 323 step of 200 μ V/200 ms, a maximal allowed difference of 250 μ V/200 ms, amplitudes exceeding
 324 ± 250 μ V, and low activity less than 0.5 μ V /50 ms were rejected from analyses. There were no
 325 significant differences in included epochs between conditions ($p = .980$). These segments then
 326 were referenced to the arithmetic average and then grand averaged within every condition.

327 With a distribution of frontal-to-parietal, heartbeat evoked potential (HEP) has higher amplitudes
 328 over the right hemisphere (Dirlich, Vogl, Plaschke, & Strian, 1997; Kern, Aertsen, Schulze-
 329 Bonhage, & Ball, 2013; Pollatos & Schandry, 2004; Schulz et al., 2015). The polarity of the HEP
 330 varies with the task, region and latency analyzed (Canales-Johnson et al., 2015; Couto et al.,

2013; Gray et al., 2007). Following Sel, Azevedo, and Tsakiris (2017), our analysis had 6 regions of interests (for ROI-s see Figure 6). To estimate the group level effects of Strategy and feedback Congruency on mean HEP voltages, Monte-Carlo random cluster-permutation method was implemented in FieldTrip (Maris & Oostenveld, 2007). When testing the relationship between interoceptive Strategy and specific HEP amplitudes and behavioral measures, we used the difference score of Congruency amplitudes (i.e. *Feel* (C-IC) – *Attend* (C-IC) and *Regulate* (C-IC) – *Attend* (C-IC)). To produce these difference values, subtraction was performed on the time-locked grand averages, keeping individuals distinct. When comparing different conditions at a neural level we used the absolute measure of HEP amplitudes.

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 show 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 (10000 repetitions 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’.

Data analysis

Cardiac recognition

One of the most commonly studied features of interoception interoceptive sensitivity reflects the ability to precisely and accurately monitor changes of internal body state (Khalsa et al., 2017). We quantified sensitivity in our cardiac recognition task by a signal detection metric: d' (“d-prime”, see Macmillan & Creelman, 2004), which is commonly used in heartbeat detection tasks (e.g. Khalsa, Rudrauf and Tranel, 2009). The benefit of signal detection measures is that they can differentiate response bias from one’s true ability to discriminate between signal (i.e. congruent feedback) and noise (i.e. incongruent feedback) – which simpler measures of accuracy (e.g. proportion correct) cannot. Our study calculated d' by using the difference between participants’ normalized hit rate (proportion of correct trials when the biofeedback represented one’s own heart) and normalized false alarm rate (proportion of correct responses when the biofeedback represented someone else’s heart):

$$d' = z(\text{hit rate}) - z(\text{false alarm rate})$$

To summarize, d' represents the distance between the signal (hit rate) and noise (false alarm rate), where larger distance (i.e. larger d') represents better sensitivity.

Metacognition

The correspondence between objective interoceptive abilities and the self-reported *evaluation* of this performance (e.g. confidence) – also known as interoceptive insight – has attracted interest over recent years, as it provides the potential to tap into metacognitive aspects of interoception (Khalsa et al., 2017). Previous studies have found an association between IAcc and reports of self-evaluation (Khalsa et al., 2008) and confidence measured by type 2 AUROC for those individuals who had high IAcc (for issues with this method see Fleming & Lau, 2014; Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). Our study employed a different, focused

approach to explore the link between confidence and accuracy. In our analysis, we used Confidence Accuracy (CA) calibration, which measures the relationship between categorical levels of confidence and the binary measure of accuracy (Mickes, 2015). By simply regressing accuracy on confidence and plotting their relationship one can already gain interesting insights on 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 confidence categories 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:

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

where a_j denotes the proportion of correct responses at confidence level j and a denotes overall mean accuracy. NRI ranges from 0 (no discrimination) to 1 (perfect discrimination). Given that 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). Note that CAC requires a high number of trials in general but that the separation of confidence judgments into more/fewer levels will also affect the reliability of the analysis (i.e. higher number of confidence bins will need more trials in order to be reliable).

Results

Behavioral analysis: d'

Our main behavioral outcome variable was the strategy-related cardiac recognition measured by d' . As d' already inherently captures the congruency to incongruency relation, our experiment only had one predictor on this level of the analysis: Strategy (i.e. engagement with the biofeedback signal: 1 = *Attend*; 2 = *Feel*, 3 = *Regulate*). We chose to model our d' data with a linear model as the d' values followed a Gaussian distribution (Shapiro-Wilks test $p = .190$). Descriptive statistics and confidence intervals are noted in text. We excluded from analysis those Congruent trials (1.3 % of our data) where technical difficulties lead to undetected heartbeats and disruption of congruent feedback.

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; Lüdtke, 2018b) and *sjmisc* (Version 2.7.4; Lüdtke, 2018a). Mixed effects modelling is particularly useful in within-subject designs where each subject has several measurements resulting in correlated errors for those measurements (Baayen, Davidson, & Bates, 2008). The solution to this problem is to let each subject 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 using this approach. Reported p-values were computed via Wald-statistics approximation (treating t as Wald z). We tested for the effects of task performance (unrelated to cardiac recognition), average heart rate, the average change in heart rate from baseline to task and baseline HF-HRV. Task performance measures were quantified as the following:

$$\text{Task Performance}_{(ATTEND)} = 1 - |(target\ pulses - reported\ pulses)| / target\ pulses$$

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417 $Task\ Performance_{(FEEL\ CORRECT)} = value\ associated\ with\ the\ position\ on\ scale * 2 / 100$

418 $Task\ Performance_{(FEEL\ INCORRECT)} = 1 - (value\ associated\ with\ the\ position\ on\ scale * 2 / 100)$

419 $Task\ Performance_{(REGULATE)} = mean\ IBI_{(TRIAL)} - mean\ IBI_{(PREV.TRIAL)} / mean\ IBI_{(PREV.TRIAL)}$

420 Centered covariates were included in the final model only if they significantly improved the
421 model fit. We defined the maximal model as:

422 $d \sim Strategy + Task\ performance + Baseline\ HF - HRV_{BASELINE} + HR_{CHANGE} + HR + (1|ID)$

423 Based on the AIC values, the final model which provided the best fit with our data was the
424 following:

425 $d' = Strategy + (1|ID)$

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

428 Results revealed a significant increase of d' in comparison to the *Attend* condition ($M_{ATTEND} =$
429 $0.27, SD_{ATTEND} = 0.45$) in both the *Feel* ($M_{FEEL} = 0.49, SD_{FEEL} = 0.58$) $\beta = 0.22, [CI] = 0.04 -$
430 $0.40, p = .017$ and the *Regulate* conditions ($M_{REGULATE} = 0.58, SD_{REGULATE} = 0.68$) $\beta = 0.31, [CI]$
431 $= 0.13 - 0.49, p = .001, R^2_{MARGINAL} = 0.05, R^2_{CONDITIONAL} = 0.59$ without being significantly
432 different from each other ($p = .350$) (Figure 3). Results are depicted by raincloud plots (Allen,
433 Poggiali, Whitaker, Marshall, & Kievit, 2018). These results remain significant after Bonferroni
434 correction for three comparisons. A negative score of d' indicates a performance that is worse
435 than chance (i.e. participants cannot discriminate congruent feedback from incongruent), which
436 might hamper the interpretation of results at those participants. For this reason, we ran the same
437 analysis excluding participants with negative d' in any of the three conditions (N=20) but found

the same - even stronger - results. In this subsample, both the *Feel* $\beta = 0.29$, [CI] = 0.06 – 0.53, $p = .014$ and *Regulate* $\beta = 0.39$, [CI] = 0.16 – 0.62, $p = .001$, $R^2_{\text{MARGINAL}} = 0.12$, $R^2_{\text{CONDITIONAL}} = 0.38$ conditions were associated with higher d' than the *Attend* condition - without differing from each other ($p = .416$). It is important to note that heart rate remained the same across conditions (even in the Regulate condition), meaning that the observed effects were driven by differences in the type of engagement with the biofeedback signal rather than changes in physiological states.

Figure 3. Strategy related effects on participants' cardiac recognition measured by d' . The raincloud plots of d' provide information showing data distribution, the central tendency (by

boxplots) and the jittered presentation of our raw data. Error bars indicate 95% confidence intervals around the estimates of the linear mixed effects model with a random intercept.

Confidence accuracy calibration

To gather further understanding of the link between self-reported confidence and cardiac recognition accuracy, we ran an exploratory Confidence Accuracy (CA) calibration analysis for which 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 of 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 4A). 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 reported levels of Confidence, Odds Ratio (OR) = 1.08, [CI] = 1.05 – 1.10, $p = < .001$, $R^2_{\text{MARGINAL}} = 0.01$, $R^2_{\text{CONDITIONAL}} = 0.05$. To reduce noise, we collapsed Confidence into two categories (i.e. Low: 0% – 50% and High: 60% – 100%) and plotted proportion correct against confidence for every Strategy (Figure 4B). To quantify the differences in confidence-accuracy relationship across strategies, NRI was calculated for every individual. When contrasting different levels of Strategy in a linear mixed effects analysis, we found a significant increase in NRI for the *Regulate* ($M_{\text{REGULATE}} = 0.13$, $SD_{\text{REGULATE}} = 0.18$) condition when compared to the *Attend* ($M_{\text{ATTEND}} = 0.05$, $SD_{\text{ATTEND}} = 0.07$) $\beta = 0.08$, [CI] = 0.02 – 0.14, $p = .006$ and *Feel* ($M_{\text{FEEL}} = 0.07$, $SD_{\text{FEEL}} = 0.12$) conditions $\beta = -0.06$, [CI] = -0.11 – 0.001, $p = .046$ (n.s. after Bonferroni correction), $R^2_{\text{MARGINAL}} = 0.06$, $R^2_{\text{CONDITIONAL}} = 0.21$, while there was no

difference between the *Attend* and *Feel* conditions ($p = .459$). For descriptive statistics see Table 1.

Figure 4. Results of confidence accuracy calibration analysis depicting a (A) positive linear relationship between the binned values of confidence and accuracy in general and (B) within certain Strategies. The diagonal line represents perfect calibration between 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. Specifically, cardiac recognition measured by d' revealed a significant difference between interoceptive strategies (both *Feel* and *Regulate*) and exteroception (*Attend*) but not between the different types of interoceptive strategies (i.e. *Feel* vs *Regulate*). Accuracy measured by proportion correct positively mapped onto self-reported confidence across all conditions. In comparison to the other two strategies (both *Attend* and *Feel*), participants' metacognition (i.e. accuracy and confidence association) was higher during *Regulate* trials where the instruction was to use control-based inference for cardiac recognition.

Table 1

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

Strategy	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 might differ slightly across conditions as some trials were excluded as the recording equipment occasionally missed heartbeats (approx. 1% of trials).

Cluster-based permutation analysis on HEP amplitudes

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

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. Given that our main interest on this level of the analysis was the potential interaction effect between Strategy

(1 = *Attend*, 2 = *Feel*, 3 = *Regulate*) and Biofeedback Congruency (1 = *Congruent*, 2 = *Incongruent*), first we needed to determine whether there are *any* differences between conditions on the amplitudes of HEP. For this reason, we specified a dependent samples F-statistic to be calculated for each sample, in each random reshuffling of the data. This analysis revealed a significant modulation of the HEP amplitude, as indicated by a significant positive cluster ($F_{\text{SUM}} = 400.48$, $p = .024$) between 232-280 ms within the right-frontal ROI (specifically electrodes AF4, F4). To investigate the simple effects of Strategy and Biofeedback Congruency in this interaction, we ran nine pair-wise comparisons (now specified with dependent samples T-statistic) at the right-frontal ROI. In the latency range from 200 to 300 ms post R-peak, the cluster-based permutation test revealed a significant positive difference between the *Attend* and *Feel* conditions during Incongruent biofeedback ($T_{\text{SUM}} = 141.13$, $p = .003$). In this latency range, the difference was globally pronounced over all sensors of this ROI within the whole preset latency range. Similarly, the *Regulate* condition was significantly different from the *Attend* strategy within the Incongruent feedback condition in a positive direction ($T_{\text{SUM}} = 69.24$, $p = .002$), which effect was most pronounced at the latency between 204-268 ms at the AF4, F4 electrodes. All statistic reported survived Bonferroni correction for 9 comparisons (Figure 5 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 significant cluster of significant interactions at $p < .050$ (Figure 5 B).

Figure 5. (A) Presentation of heartbeat evoked potentials (HEP-s) and their difference waves depicting the effect of condition over the right frontal ROI within the a-priori set latency of 200-300 ms during the presentation of biofeedback stimuli ($N = 30$, Monte-Carlo cluster analysis, $F_{\text{SUM}} = 400.48$, $p = .024$). For the two significant pairwise comparisons we also denoted the electrodes and latencies where the effect was the most pronounced. (B) Average ECG signal across all conditions (dashed lines represent the Incongruent while full line indicate the Congruent biofeedback condition). The 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 where the effect on the cluster was most the pronounced. Colour bars show Monte-Carlo cluster statistic (t).

To see the psychological relevance of neural responses we also tested a potential link between Strategy-specific cardiac recognition and strategy-specific modulation of HEP amplitudes (Figure 6). To match HEP with d' - which inherently captures the congruency to incongruency relation - first we calculated *Congruency difference* amplitudes for every Strategy condition, by subtracting the Incongruent condition from the Congruent condition. Then to fully separate Strategy related effects from attentional processes, we subtracted the Congruency difference amplitudes in the *Attend* condition from the *Feel* and *Regulate* conditions (Figure 6B). To mirror this on a behavioral level, we subtracted d' scores in the *Attend* condition respectively from the other two interoceptive Strategy conditions (i.e. *Feel* and *Regulate*). After this, we performed a regression analysis between the two types of interoceptive d' -s 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. 232-280 ms), with the right-frontal area as our ROI. The analysis revealed a significant positive relationship between strategy specific HEP difference and d' difference in the *Feel* condition ($T_{\text{SUM}} = 24.64$, $p = .019$), 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 neural findings, the use of interoceptive strategies compared to exteroception for cardiac recognition was associated with differences in HEP amplitude over the right-frontal area within the latency of 200-300 ms. The cortical processing of cardiac signals during incongruent feedback was more pronounced during interoception – regardless of the strategy they were instructed to use to interact with their cardiac signals. We also found that strategy-specific difference HEP reflected individuals' strategy-specific cardiac recognition performance when participants focused on individual heartbeats (*Feel*) but not during regulation (*Regulate*). Specifically, larger *Feel* strategy related HEP difference amplitudes were positively linked to the ability to differentiate feedback representing one's own heart from someone else's.

Figure 6. The amplitude of strategy-specific Heartbeat Evoked Potential (HEP) difference is related to interoceptive strategy-specific sensitivity. (A) Topographical plots depict the amplitude differences that were used in the regression (*not* the spatial effects associated with the regression itself). (B) Congruency difference amplitudes and their difference wave across certain strategies. Shaded area represents 95% confidence interval of fitted regression line. (C) For illustration purposes parametric linear regression lines were plotted using subject-wise average signal over the electrodes (dark shaded circles on 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 psycho-physiological stability (Khalsa et al., 2017) which requires the ability to infer the state of our body and to predict its future (Pezzulo et al., 2015). However, the standard measures of interoception are distant from this functional definition as they simply test the perception of single heartbeats – leaving the interpretation of participants' performance in these tasks limited to a lower, sensory level (Schandry, 1981; e.g. Whitehead et al., 1977). With the intention to get closer to the functional role of interoception and to contrast different ways of engaging with changes in one's physiological state, we measured participants' cardiac recognition, metacognitive abilities and associated neural responses across three different strategies. These strategies all involved a combination of interoceptive and exteroceptive elements, but they emphasized different features of the biofeedback and required different levels of engagement in an increasing order of (i) *neutral-exteroceptive (Attend)*, (ii) *passive-interoceptive (Feel)* and (iii) *active-interoceptive (Regulate)*.

We observed an increase in cardiac recognition for both the *Feel* and *Regulate* strategies when compared *Attend*, but there were no differences between the *Feel* and *Regulate* strategies. A similar pattern of results was revealed at the neural level, as we found that the cortical processing of cardiac signals (measured by the modulation of HEP amplitudes) during incongruent feedback was more pronounced at both interoceptive strategies (*Feel* or *Regulate*) when compared to exteroceptive *Attend*. According to these findings, our hypothesis about the gradual increase of cardiac recognition across strategies (i.e. *Attend* < *Feel* < *Regulate*) was

partly confirmed. Insofar both *Regulate* and *Feel* resulted in significantly more accurate cardiac recognition compared to *Attend*, whereas no significant differences were observed between *Regulation* and *Feel* (i.e. $Attend < Feel$, $Attend < Regulate$, $Feel = Regulate$). This pattern suggests that there are alternative ways of engaging with interoceptive signals and that these may be equally beneficial for inferences about the self in relation to the external world.

When applying the PC framework (e.g. Allen & Friston, 2018) to our results, we suggest that the passive (*Feel*) and the active (*Regulate*) interoceptive strategies both increased sensitivity via the optimization of precision-weighting. Specifically, attention directed to the interoceptive channel (here to one's own heart) would increase the relative precision (i.e. the impact of associated PE-s) arising from that channel (Feldman & Friston, 2010), leading to more accurate inferences about the sources of the biofeedback signal. The brain evaluates the relative precision of PE-s on multiple hierarchical levels (Brown, Adams, Parees, Edwards, & Friston, 2013; Hohwy, 2012). While both the *Feel* and *Regulate* interoceptive strategies appeared to increase the precision of the interoceptive channel, it is possible that they exert their influence at different levels of the hierarchy. The experience of single heartbeats (*Feel*) is likely to affect precision on a lower level, as it is a more strictly sensory strategy that operates on a narrower temporal scale. In contrast, the control-oriented, active strategy (*Regulate*) may increase precision higher up the hierarchy, as it requires a more abstract representation of internal states over a wider temporal window than a single heartbeat. The finding that healthy people do not perceive their heartbeats *consciously* most of the time (Ádám, 1998) supports this argument. In comparison, people are more likely to become aware of perturbations in their physiological states as the optimal behavior differs between balanced and imbalanced 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). Considering the above arguments and noting that PC unifies action, interoception and homeostatic/allostatic control, we suggest that while both *Feel* and *Regulate* strategies may increase the precision of the interoceptive channel, the *Regulate* strategy relates to a more *functional* aspect of interoception. Specifically, it can provide a more direct access to the estimates of bodily states –an essential information for maintaining homeostatic/allostatic control (Stephan et al., 2016b).

This argument is further supported by our findings on metacognition (i.e. the association between accuracy and confidence). Interestingly, across conditions we found the highest interoceptive metacognition/insight (Khalsa et al., 2017) during the *Regulate* strategy. Stephan and colleagues (2016b) postulate that the performance of the interoceptive 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. Considering that *Regulate* proved to be distinctly different from *Attend* and *Feel* strategies in terms of metacognition, the results seem to support its higher relevance for allostatic control. In addition, strategy-specific cardiac recognition sensitivity (d') was linked to the modulation of strategy-specific HEP differences exclusively in the *Feel* condition and not when using the *Regulate* strategy. The observed dissociation between *Feel* and *Regulate* strategies is understandable, as only in the *Feel* condition were participants instructed to use single heartbeat-based experience for cardiac recognition. Remaining careful when interpreting a null-result, we suggest that while both the *Feel* and *Regulate* strategies 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, ideally, one would need to identify a cortical response that maps onto the performance in cardiac recognition under the *Regulate* condition. P300 is a promising candidate to track such link to cardiac recognition, given 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 when using the *Regulate* strategy for cardiac recognition, there could be a link between the motivationally relevant processing of a stimulus (here heartbeat feedback) and cardiac recognition performance in the *Regulate* condition. The presence of such correspondence would further support the argument about the *Regulate* strategy capturing a more *functional* aspect of interoception than the perception of single heartbeats (*Feel*).

While the core idea behind our strategy manipulation was to influence the engagement with the cardiac signal rather than actual physiological states, it is important to address the fact that participants failed to decrease their heartrate in the *Regulate* condition. It is possible that longer periods are needed for self-induced heartrate regulation to take an effect, but it also might be that voluntary regulation of heartrate simply cannot be achieved in this form. Supporting the latter, a well-powered study of N = 180 by White, Holmes and Bennett (1977) found that participants' regulation attempts were not more efficient in the reduction of heartrate than a condition where participants simply attended to the biofeedback. As we had a novel paradigm, we looked for an unambiguous way to ensure that control-oriented engagement was achieved in the *Regulate* condition. Asking participants to regulate communicates this aim more clearly than the instruction to just attend to the changes in the biofeedback bar. However, it is possible that simply asking participants to focus on the changes and try to match their physiological state to the changes of the biofeedback would lead to similar effects as our instruction to *Regulate*.

Our findings 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 a better insight about the way 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 perturbations, where interoception has true meaning and significance for the individual. This includes but is not limited to modeling real-life stressful scenarios (e.g. job interview), health-related behaviors (e.g. attending one's own body with the aim to decide if they are feeling ill) and social interactions that require the understanding and communication of one's subjective experience with others. In general, future research would greatly benefit from the application of a more *functional* approach to interoception. This necessitates studying the ability to monitor and control internal bodily states and their changes in individuals who are *embedded* in the social and physical world surrounding them.

To conclude, we adopted a novel approach on cardiac recognition by exploring a more functional aspect of interoceptive engagement through inferences about the self in relation to the external world. Across behavioral, neural and metacognitive domains we found evidence that an active control-oriented strategy increases cardiac recognition sensitivity to the same extent as the focus on individual heartbeats. Based on our results showing that metacognition was highest when using a control-oriented approach for cardiac recognition, we suggest that both the passive and active strategies increase precision within the interoceptive channel, but they exert their influence on different levels of the hierarchy.

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