Cognition

Heart Is Deceitful Above All Things: Threat Expectancy Induces the Illusory Perception of Increased Heartrate

--Manuscript Draft--

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Abstract

It has been suggested that our perception of the internal milieu, or the body's internal state, is shaped by our beliefs and previous knowledge about the body's expected state, rather than being solely based on actual interoceptive experiences. This study investigated whether heartbeat perception could be illusorily distorted towards prior subjective beliefs, such that threat expectations suffice to induce a misperception of heartbeat frequency. Participants were instructed to focus on their cardiac activity and report their heartbeat, either tapping along to it (Experiment 1) or silently counting (Experiment 2) while ECG was recorded. While completing this task, different cues provided valid predictive information about the intensity of an upcoming cutaneous stimulation (high- vs. low- pain). Results showed that participants expected a heart rate increase over the anticipation of high- vs. low-pain stimuli and that this belief was perceptually instantiated, as suggested by their interoceptive reports. Importantly, the perceived increase was not mirrored by the real heart rate. Perceptual modulations were absent when participants executed the same task but with an exteroceptive stimulus (Experiment 3). The findings reveal, for the first time, an interoceptive illusion of increased heartbeats elicited by threat expectancy and shed new light on interoceptive processes through the lenses of Bayesian predictive processes, providing tantalizing insights into how such illusory phenomena may intersect with the recognition and regulation of people’s internal states.

1. Introduction

The perception of our heartbeat contributes to feelings and emotional recognition, shaping our subjective experience of being relaxed, excited, stressed, or thrilled, as well as the perception of disease-specific symptoms. Uncovering the dynamics of how we perceive and interpret signals from our cardiovascular system, therefore, represents a key step toward a broader understanding of body and emotion regulation and associated pathophysiology (Carroll, 1977; Carroll & Whellock, 1980; Clark et al., 1997; Dunn et al., 2010).

Traditional approaches have cast interoception as a bottom-up and sensory-driven process, which faithfully represents our inner body states (for a full discussion, see Rauss & Pourtois, 2013). Recently, emerging Embodied Predictive Coding (EPIC) approaches challenge such views (for a full discussion see, Barrett & Simmons, 2015). They frame interoception not as a mere mirror of people's internal states, but see it as profoundly enriched by our prior knowledge, thoughts, and expectations. Accordingly, the brain is cast as an active generator of inferences that constantly compares a model of the expected external and internal world with current inputs through an iterative process of Bayesian hypothesis testing and revision (Barrett & Simmons, 2015; Pezzulo, 2014; Seth, 2013; Seth et al., 2011; Tschantz et al., 2022). The role of interoception is to reduce the difference between one's internal models and the actual interoceptive input, thus converging towards a 'best guess' that accurately represents the body's state.

An important feature of EPIC accounts is that the difference between the expected and actual state of the body can be achieved either by perceptual or active inference (i.e., free-energy minimization, for a full discussion, see Friston 2005, 2010). Put differently, prediction errors can either ascend the hierarchy to revise prior beliefs, manifesting as perceptual changes, or descend to the periphery to make those prior beliefs come true by engaging peripheral reflexes (Ainley et al., 2016). For instance, an expectation of a sped-up heartbeat

(for example, because one is anxious) could be realised either by making one's heart *appear* to beat more quickly than it really does, thereby illusorily distorting perception towards expectations. It could also be achieved by *actually* accelerating one's heartbeat, thereby changing the actual bodily state to fit expectations.

So far, research has primarily focussed on the latter active inference component, demonstrating that predictive processes shape internal states towards the expected target state (Benedetti, 2014; Benedetti et al., 2011; Denson et al., 2011; Jamieson et al., 2012; Jepma et al., 2018; Nasso et al., 2019; Wager et al., 2004; Zilcha-Mano et al., 2019). Much less evidence exists for the hypothesis that predictive processes impact how we *perceive* our internal states, in other words, that interoception reflects, in part, our expectations about the body's internal state, rather than only its objective physiological condition (i.e., perceptual inference, Friston 2005, 2010).

Here, we ask whether such an integration of expectations and sensory evidence occurs for the perception of one's heartbeat, that is, whether the perception of our cardiac state is illusorily distorted towards expectations. On the one hand, heartbeat sensations are assumed to reflect blood ejection from the heart into the aorta at ventricular systole, as well as physical changes within the vessels, chest and body (including the somatosensory, quasi-interoceptive, hitting of the inner chest wall by the heart, Betka et al. 2020). On the other hand, while people are sensitive to their actual heart rate changes (mean $d' > 1$, Fittipaldi et al. 2020), they tend to undercount their actual heart rates (Corneille et al., 2020; Zamariola et al., 2018), and their reports are biased by their prior beliefs about how quickly their heart would beat (Körmendi et al., 2021; Ring & Brener, 1996).

Together, these findings suggest that the reporting of one's heart rate relies, at least in part, on people's expectations of their cardiac state, instead of only their actual internal sensations. Individuals have valid knowledge about how their heart rate is affected by

different tasks and events, and they use this knowledge to improve their estimates of the otherwise highly ambiguous cardiac state. Importantly, so far, research focussed on whether such internal models help in deriving a *truthful* estimate of the cardiac state but did not test the crucial hypothesis that inaccurate expectations can induce *false* cardiac perception. Even if under normal conditions internal models support a faithful representation of internal states, our daily life is permeated by ambiguous circumstances which can lead to inaccurate predictions. It is, therefore, crucial to resolve whether (1) people may spontaneously generate false beliefs about their heartbeat and whether (2) these misleading expectations falsely distort their cardiac perception, potentially generating mis-perceptual phenomena or interoceptive illusions.

To test this idea, we exploited common beliefs about heart rates that most people have, but that are essentially fictitious. One of these beliefs is that when we are expecting a threatening event heart rates increase to prepare our body to react. Surprisingly, research showed that this is not always reflected by actual heart rates and that, in fact, the opposite is likely to occur. Decelerating cardiac frequency typically occurs when stimuli signal forthcoming threat (Bradley et al., 2005, 2008; Colloca et al., 2006; Lykken et al., 1972; Taggart et al., 1976; Tracy et al., 2017), or highly salient events more generally (Crone et al., 2003, 2005; Ullsperger et al., 2014). If cardioception is shaped by our beliefs and is only partially constrained by the actual state of our body, then any misconceptions about our heart rate should be incorporated into the Bayesian inference, leading to biased cardiac perception. As a result, when individuals anticipate an imminent threat, they may perceive their heart rate as accelerating, regardless of their actual heart rate.

We tested this hypothesis in three experiments. Participants were asked to monitor and report their heartbeat, by either tapping along to it (i.e., Experiment 1, the heartbeat tapping task, McFarland 1975) or silently counting (i.e., Experiment 2, the heartbeat counting

task, Schandry 1981), while their ECG was recorded. While completing this task, participants were presented with visual cues that provided valid predictive information about upcoming cutaneous stimulation, which would be delivered through a pair of electrodes attached to their wrist: either a threatening high-intensity (i.e., pain) or harmless low-intensity (i.e., safe) electrical noxious stimulus. We expected that cues threatening high pain would cause participants to mis-perceive their heart to accelerate – and report a higher number of heartbeats – compared to cues signalling a low-pain stimulus. Importantly, this difference in the number of *perceived* (i.e., reported) beats should not be reflected in the real state of the body and therefore absent in the real heart rate measured with ECG.

Experiment 3 tested whether this interoceptive illusion would be eliminated when participants reported the rate of an exteroceptive (visual) rhythmic stimulus that was not related to their cardiac state, and which they should not expect to respond to threat. Instead of tapping along with their heartbeat (as in Experiment 1), participants tapped along with an ambiguous visual stimulus pulsing on the screen, while being exposed to the same cue that indicate an upcoming painful (i.e., high-intensity) or harmless (i.e., low-intensity) stimulus. In contrast to Experiments 1 and 2, we predicted no discrepancy between the real and perceived number of pulses when anticipating threat or safe cutaneous stimulation.

If confirmed, these results would show for the first time that threat expectations can influence cardiac perception, generating an interoceptive illusion of increased heartrate. This evidence would provide important insights into how inferential processes influence the perception of our body state and raise intriguing questions about how these illusory interoceptive phenomena may shape the regulation of our internal states.

2. Experiment 1

In Experiment 1, participants were asked to tap along with their heartrate, to measure the perception of their heart rate (i.e., the heartbeat tapping task, Flynn e Clemens 1988;

McFarland 1975; Melloni et al. 2013), while we measured their actual cardiac frequency with ECG. In each trial, both perceived and real heartrate were measured, first in a neutral baseline phase and then in a predictive phase, wherein they expected to receive either a harmless (low-intensity) or threatening (high-intensity) pain stimulus (Fig. 1). This task allowed us to quantify whether recorded and reported beats changed differently as a function of the expectation of threatening vs. non-threatening stimulation.

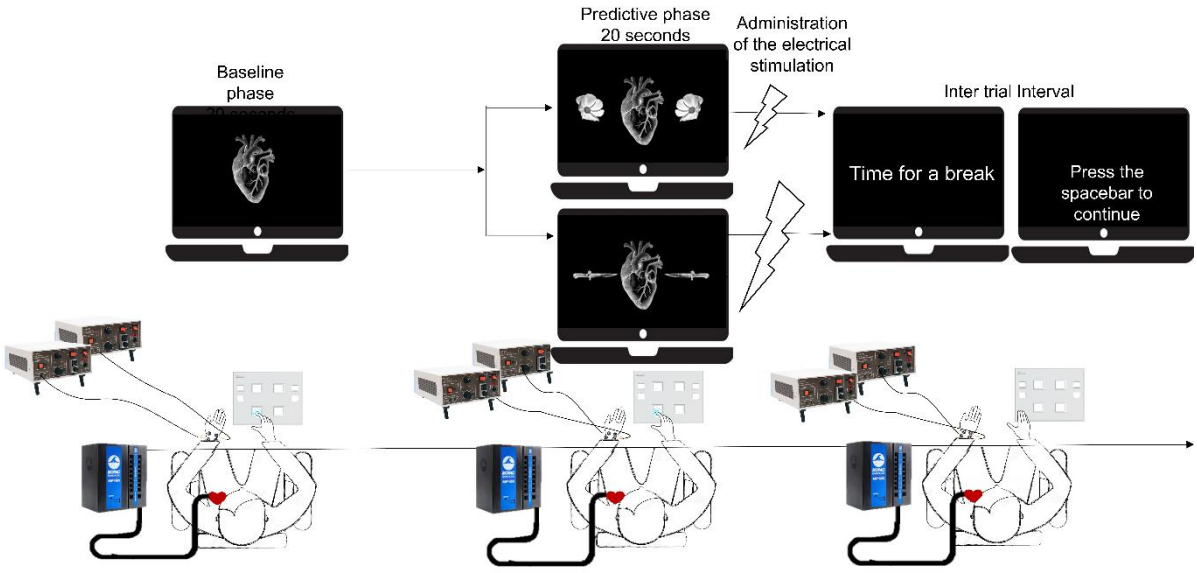

Figure 1. **Trial timeline of Experiment 1.**

2.1 Methods

2.1.1 Participants

The final sample size of the study comprised twenty-five healthy volunteers (mean age 25.7, *SD* = 4.1, 17 women), which were recruited from Gabriele d'Annunzio University and the wider community. Prior to the experiment, participants were asked to refrain from consuming coffee or smoking cigarettes within 60 minutes. Exclusion criteria for participation included chronic and acute pain, neurological disease, serious cardiovascular disease (i.e., any type of disease involving the heart or blood vessels that might result in life-

threatening medical emergencies, e.g., arrhythmias, infarct, stroke), and current self-reported drugs use. One participant was excluded due to an inability to reach the desired pain threshold, indicating an abnormal level of sensitivity to the electrical stimulation. Moreover, participants were considered outliers if the mean value of any of the four variables (reported beats in the predictive safe condition, reported beats in the predictive pain condition, recorded beats in the predictive safe condition, and recorded beats in the predictive pain condition) exceeded three standard deviations (*SD*) from the group mean. The outlier detection was performed using the 'isoutlier()' function in MATLAB (version R2022B, MathWorks Inc., Natick, MA, USA). However, this criterion did not result in the exclusion of any participants.

The experiment was conducted in accordance with the Declaration of Helsinki. Ethical approval from the local ethics board was obtained. Participants provided informed consent, and information about the study's purpose was provided only after the experimental tests were completed (see Supplementary Materials 1.5.2). The sensitivity analysis with G*Power 3.1 (Faul et al., 2007) revealed that a sample size of 25 provides .80 power to detect effects with Cohen's $d = .58$ (SESOI of $\delta = .40$). Previous studies with this type of experimental paradigm in the exteroceptive modality (e.g., Hudson et al., 2016) suggest that effect sizes are most likely larger ($.241 < \eta p^2 < .395$).

2.1.2 Apparatus and Stimuli

Visual stimuli were presented on a desktop computer screen, one metre away from the participant. The images were gathered from Google Images, scaled to black and white, and matched in dimension, orientation, and background colour using Adobe Photoshop software. The stimulus set included (1) a neutral cue, which was a heart located at the centre of the screen, which was shown during the baseline phase and (2) two different warning cues, appearing to the sides of the heart picture. These could be either two flowers or knives indicating that participants would receive a harmless (low-pain) stimulation or a threatening

(high-pain) stimulation, respectively. Stimulus presentation was controlled through E-Prime 3.0 (Psychology Software Tools, Pittsburgh, PA, USA) on a computer with an ASUS VH232 monitor (resolution: 1920 x 1080, refresh rate: 59 Hz)

Painful stimuli were electrical pulses delivered using a constant current electrical stimulator (model DS7A, Digitimer Ltd., Welwyn Garden City, UK) controlling a pair of electrodes attached to the inner wrist of the participant's left hand, which provide a precise constant current, isolated stimulus, controllable in pulse duration and amplitude. The intensity of the high- and low-intensity electrical stimuli was kept fixed over the experiment as established during a calibration phase before the experiment.

The cardiac signal was continuously recorded with a BIOPAC MP160 System (BIOPAC System, Inc., Goleta, CA, USA) (low-pass filter: 35 Hz; high-pass filter: .05 Hz; notch filter: 50 Hz; sampling rate: 2000 Hz) using the AcqKnowledge software (version 5.0.5, BIOPAC System, Inc., Goleta, CA, USA). ECG was recorded continuously from two electrodes attached to the lower ribs and one over the right mid-clavicle bone (reference electrode). ECG signal was fully analysed in MATLAB (version R2022B, MathWorks Inc., Natick, MA, USA). To rely on precise timing for response registration over the tapping task (HBD), a Cedrus USB response pad was used for the recording of each participant's keypress (i.e., Cedrus RB-844 guarantees 1 ms resolution).

2.1.3 Procedure

Upon arrival at the lab, participants were briefed by the experimenter. After providing consent, they were placed in a comfortable chair, and the ECG electrodes were applied after cleaning the skin. In a first step, we assessed participants' cardiac interoception at rest, through a modified version of a validated HBD task (Couto et al., 2014; García-Cordero et al., 2017; Melloni et al., 2013; Sedeño et al., 2014; Yoris et al., 2015, 2018) (for more details, see Supplementary materials 1.3).

In a second step, participants were informed that they would undergo a psychophysical procedure to determine the subjective low- and high- intensity pain stimulus that would then be delivered over the experiment. This calibration was conducted using the method of limits psychophysical approach. Current (pulse duration 2 ms) intensity was set at an initial value below the threshold for pain perception in most people. Stimulus intensity increased in a ramping procedure up to a maximum of 0.5 mA. Participants were required to verbally rate the pain intensity for each stimulus, using a 0-100 Numerical Pain Scale (NPS). Following previous research (Atlas et al., 2014; Colloca et al., 2006), a pain intensity rating of NPS 20 denoted "just painful", NPS 50 denoted "medium pain", and NPS 80 marked the point at which the stimulus was "just tolerable". We repeated this procedure three times and computed the average stimulus intensities corresponding to NPSs 20 (i.e., the low intensity stimulation) and 80 (i.e., the high intensity stimulation), to be later used as experimental stimuli. Subsequently, participants were exposed to stimulus intensities corresponding to their pain intensity ratings NPS 20 and 80, which were delivered randomly four times each. Participants were instructed to identify the intensity of each pulse. If they correctly identified the stimulus intensities 75% of the time, they would proceed to the main experiment. If they did not achieve the 75%, the intensities were adjusted, and the test was repeated until participants correctly identified 75% of stimulus intensities.

Having established the level of intensity for low and high pain stimulation levels, participants were instructed about the experiment proper. They were informed that their task was to tap along with each heartbeat sensation through a key press. Crucially, they were informed that they had to do this while waiting for either a low-intensity or high-intensity pain stimulus to be delivered later, indicated by one of two visual cues (the heart flanked by flowers vs. knives). Participants were comfortably seated in front of the computer, with the ECG electrodes attached, their left hand placed on the table with the electrodes of the

cutaneous electrical stimulation fixed on their inner wrist, and their right hand placed on the keypad, ready to start the task (Fig. 1), while their ECG was recorded.

Each trial started with the presentation of a neutral cue appearing on the screen (i.e., 20 seconds, *baseline phase*). Participants were informed that when this neutral cue appeared, they had to focus on their heartbeat, and report it by pressing the keypad continuously throughout the whole trial. Then, the second "warning" cue appeared (i.e., 20 seconds, *predictive phase*). Depending on whether the cue depicted knives or flowers, participants could form a reliable expectation of the upcoming high or low electrical stimulation, respectively. They were asked to continue reporting their heart rate in this phase until the warning cue disappeared. Then, the electrical stimulation was administered, marking the end of the trial. Between trials, a pause screen was shown for 30 seconds, in order to avoid the subsequent trial to be contaminated by the heart rate response to the shock. Then, a new screen appeared with the instructions to press the spacebar to start the new trial.

The experiment consisted of 20 experimental trials interspersed with 4 catch trials. In these catch trials the interval of the predictive phase did not last twenty seconds but randomly varied between 8 and 12 seconds, after which the electric shock was administered. Catch trials were included with the purpose of creating uncertainty regarding the time interval of the predictive phase, and to avoid the equal length of the phases to influence participants' perceptual reports and to adjust the number of reported beats accordingly.

At the end of the experiment participants completed the State-Trait Anxiety Inventory (STAI) and subjective reports (see Supplementary materials 1.5)

2.1.4 Data Analysis

We ascertained how perceived (i.e., number of beats reported at the tapping task) and actual (i.e., number of beats recorded by the ECG) heart rate would change when expecting a

low- and high- painful stimuli. The final number of analysed trials was 20 (4 additional catch trials excluded, see 2.1.3), divided equally between painful and safe trials.

For each participant and trial, the number of reported and recorded beats, acquired in the baseline and in the prediction phase, was transformed into frequency, defined as the number of beats per minute (bpm), simply multiplying the number of beats in each 20 seconds phase by three to relate them to 60 (seconds), which is equivalent to one minute. The percentage signal change in %bpm for each trial was then calculated, by expressing the difference between the relative "predictive" and "baseline" values, for the reported and recorded beats separately (i.e, % signal change = ($BPM_{Predictive}$- $BPM_{Baseline}$)*100 / $BPM_{Baseline}$) (Loggia et al., 2011). This allowed us to extract, for each participant, the mean % change of bpm, averaged across trials, when a low-pain stimulus was expected or when a high-pain stimulus was predicted, for both reported and recorded beats. These values provided a directional measure of whether expecting a threat or a harmless event in the predictive phase elicited a bpm decrease or increase relative to the preceding neutral baseline phase, in either the reported or recorded beats.

Each participant's percentage change in bpm was entered into a 2 x 2 repeated measures analysis of variance (ANOVA), with Type of Beat (Reported vs. Recorded) and Type of Expectation (Pain vs. Safe) as within-participants factors. We expected perceptual judgments to reflect the expectation of an increased heart rate when anticipating threat. Participants should therefore report a higher number of beats when exposed to cues that signal a high-intensity pain stimulus compared to cues signalling a low-intensity pain stimulus. Moreover, we expect this difference to be reduced for the recorded beats, derived from the real cardiac state. Our predictions are tested by the main effect of Type of Beat, and its interaction with Type of Expectation. We used an alpha level of .05 for all statistical tests. For unpredicted effects we used Bonferroni-adjusted threshold (Cramer et al., 2016).

Moreover, planned paired sample t-tests were executed between variables of interest, namely, Reported Pain vs. Reported Safe and Recorded Pain vs. Recorded Safe, to determine whether anticipating a threatening (i.e., pain) vs. non-threatening (i.e., safe) stimulus elicited significant changes in the perceived and the real heart rate. In cases when one variable out of four was not normally distributed, the results were verified with non-parametric analyses (Supplementary materials 1.1). Effect sizes and p-values are reported for planned two-sided tests using JASP software (JASP Team, 2018).

Finally, planned Bayesian t-tests were executed to quantify relative evidence to support the models assuming an effect against the null effect model (or vice versa). Specifically, three Bayesian t-tests were executed. The first Bayesian t-test compared the difference between reported beats when anticipating threatening and non-threatening stimuli (i.e., Reported beats pain – Reported beats safe) with the difference between recorded beats when anticipating threatening and non-threatening stimuli (i.e., Recorded beats pain – Recorded beats safe), mathematically equivalent to the interaction of Pain Expectation and Type of Beat of the ANOVA. The second and third Bayesian planned t-tests compared whether anticipating pain vs. safe stimuli elicited different changes in reported (i.e., Reported Pain vs. Reported Safe) and recorded beats (Recorded Pain vs. Recorded Safe) separately.

Finally, we calculated interoceptive accuracy scores for baseline and predictive phases for each participant, estimated based on Heartbeat Tapping task outcomes via signal detection (Killeen, 2015; Macmillan & Creelman, 2004), as validated by previous studies (Fittipaldi et al., 2020; Gonzalez Campo et al., 2020) (Supplementary materials 1.2, 1.3, 1.4).

2.2 Results

Results showed, first, that participants' subjective reports about their heart rate response when anticipating threat were in line with our hypothesis. When asked, at the end of the experiment, "*What do you think happens to your heart rate when you are under a threat,*

for example when you are expecting to receive pain?", twenty-four out of twenty-five participants answered that they believed their heart rate to accelerate (see Supplementary materials 1.5.1).

Second, the analysis of real and reported beats showed that this expectation shaped participants' perception of their heart beat. The number of reported beats showed a larger increase when anticipating high- vs. low- noxious stimuli. Importantly, this perceived increase was not mirrored by the real heartrate (i.e., number of recorded beats with the ECG), as demonstrated by the two-way interaction of Type of Beat (recorded/reported) * Type of Expectation (pain/safe), F (1,24) = 6.527, p = .017, ηp^2 = .214, BF_{10} = 5.959, Fig. 2. Planned comparisons, using two-tailed paired t-tests, revealed that anticipating a pain vs. safe stimulus increased the number of reported beats (t(24) = 2.58, p = .016, BF_{10} = 6.282), but not actual heart rates (t(24) = .12, p = .907, BF_{10} = .231). This pattern of results was replicated when using non-parametric tests (see Supplementary materials 1.1).

In addition to these predicted effects, participants' perceived cardiac frequency increased in the predictive phase, while the real heart rate slightly decreased, irrespective of whether they were anticipating a high- or a low- pain stimulus, as indicated by the main effect of Type of Beat (F (1,24) = 19.1, p < .001, ηp^2 = .444).

Participants' performance on Heartbeat Tapping Task was further analyzed via signal detection as validated by previous studies (Fittipaldi et al., 2020; Gonzalez Campo et al., 2020) (see Supplementary materials 1.2). The results revealed two key findings.

First, consistent with previous studies (Fittipaldi et al., 2020; Gonzalez Campo et al., 2020), participants' sensitivity to heartbeats (d') was above chance on average (Predictive pain, M = 1.36, SD = .47, p < .001; Predictive safe, M = 1.30, SD = .37, p < .001). The findings indicated that participants were not merely guessing the presence of heartbeats, but reveal a genuine relationship between the real heartbeats and participants' responses (see

Supplementary materials 1.4). Importantly, this sensitivity to heartbeats also remained consistent across the experimental manipulations. A two-way ANOVA with Predictiveness (Baseline vs. Predictive) and Type of Expectation (Pain vs. Safe) as within-participants factors showed no significant differences between the experimental phases (all $p > .48$, See Supplementary materials 1.4). Thus, while threat expectation biased participants' reports of heartbeat perception upwards or downwards, it did not affect their ability to detect their heart rate more generally.

The same analysis was applied to the criterion (*c*), which indexes the amount of evidence required to detect a heartbeat. A liberal criterion indicates that relatively little evidence is needed to consider a stimulus as a target, while a conservative criterion means that relatively more evidence is necessary (Killeen, 2015; Macmillan & Creelman, 2004; Stanislaw & Todorov, 1999; Wylie et al., 2021) (See Supplementary materials 1.4). The results revealed that participants' required amount of evidence to detect a heartbeat (criterion) was modulated by two factors: whether they expected stimulation in the predictive compared to the neutral phase, and whether the stimulus was threatening or not, indicated by Main effects of Predictiveness ($F(1,24) = 16.23$, $p < .001$, $\eta p^2 = .403$) and Type of Expectation ($F(1,24) = 9.05$, $p = .006$, $\eta p^2 = .274$), respectively. Post-hoc t-tests with Bonferroni correction showed that relative to both the Baseline and Predictive safe phases, the mean value of the criterion in the Predictive Pain phase was generally lower (i.e., $p < .05$ for all). In other words, participants were more inclined to accept the presence of a heartbeat, regardless of its actual occurrence, when they expected a threat relative to a low-pain stimulus.

Finally, the likelihood of developing an illusory perception of heartbeats was not significantly related to participants' general level of their interoceptive accuracy as measured before the experiment, $r(23) = .21$, $p = .31$ (see Supplementary materials 1.3), nor with their

levels of state-anxiety, $r(23) = -.08$, $p = .70$ or trait- anxiety, $r(23) = -.10$, $p = .63$ (see Supplementary materials 1.5.3).

To inspect the distribution of both real and perceived cardiac frequencies over the experimental trial, Figure 3 shows, for illustrative purposes, the time course of reported and recorded beats over both the baseline and the predictive phases.

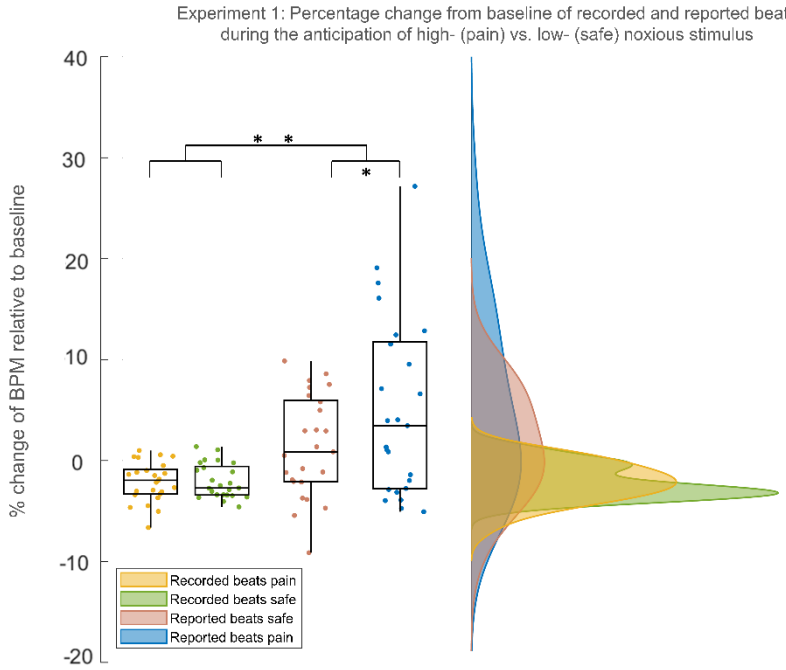

Figure 2. **Results of Experiment 1: Interoceptive Tapping Task.** Values represent percentage changes in the bpm of reported (i.e., perceived) and recorded (i.e., real) beats in the predictive phase relative to the baseline phase, either when a threatening (i.e., pain) or a harmless (i.e., safe) stimulus was expected. Values of zero on the vertical axis would represent no change in the predictive phase relative to baseline, positive and negative values would represent an increase and a decrease, respectively. The data were based on a sample size of 25 healthy volunteers and analysed with a 2 x 2 repeated measures analysis of variance (ANOVA), with Type of Beat (Reported vs. Recorded) and Pain Expectation (Pain vs. Safe) as within-participants factors. Results showed that expecting a threatening relative to a harmless stimulus elicited an increase in the perceived cardiac frequency, which was not mirrored by the real heartrate ($p = .017$, $\eta p^2 = .214$). The plot consists of a probability density plot, a box plot, and raw data points. In the boxplot, the line dividing the box represents the median of the data, the ends represent the upper/lower quartiles, and the extreme lines represent the highest and lowest values.

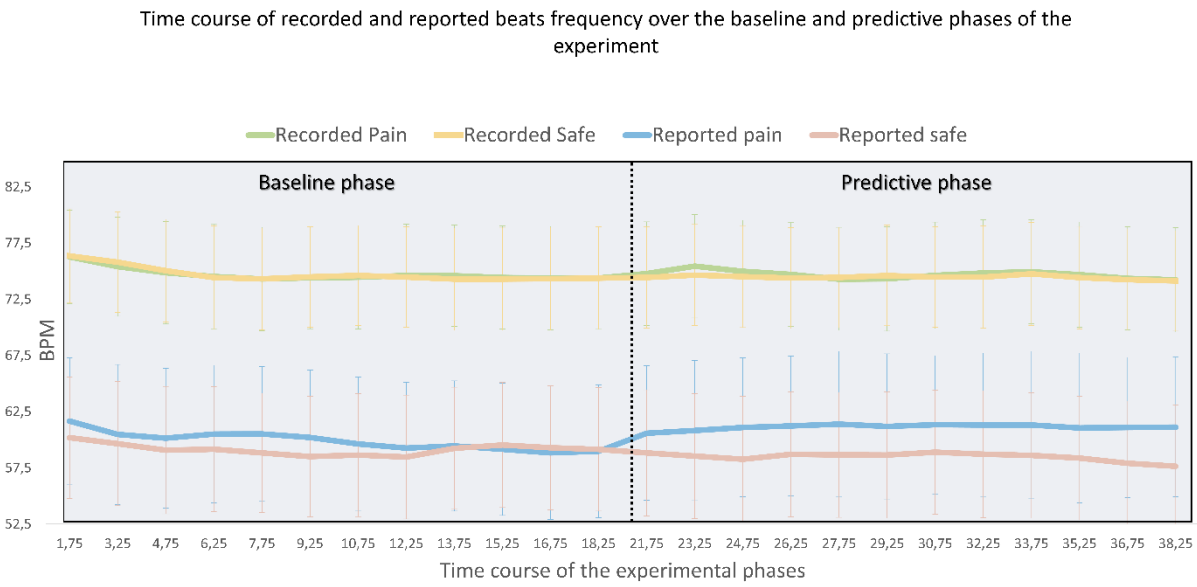

***Figure 3*.** **Time course of reported and recorded beats per minute (bpm) over the baseline and predictive phases**. Values represent the mean beats' frequency rate (bpm) of both recorded (real cardiac frequency) and reported (perceived cardiac frequency) beats, calculated for the whole trial, and obtained with a moving average that provides a dynamic and detailed analysis of both the ECG and tapped cardiac signal over time. Values on the vertical axis represent the beats' frequency rate while values on the horizontal axis indicate the median time point at which the frequency has been calculated. Real and reported bpm were calculated individually, for each participant and phase of the experiment. The calculation was executed with a moving average sliding window that determines the bpm within windows of 3.5 seconds each and that slides of 1.5 seconds. For example, the first data point (time 1.75) of the time series represents the bpm calculated from time 0 to 3.5 (median=1.75), the second data point shows the bpm calculated from time 1.5 to 5 (median=3.25), and so forth.

3. Experiment 2

An open question is whether the observed cardiac frequency estimations in Experiment 1 only reflect the perceptual representations of participants' cardiac state when anticipating threat, or whether they may also reflect effects on motor behaviour (Karos et al., 2017; Neige et al., 2018; Piedimonte et al., 2017). In essence, participants may simply tap more frequently when expecting pain, even if their perception of their heart rate does not change. To rule out this possibility, Experiment 2 replicated the findings of Experiment 1 with an adapted version of the Heartbeat Counting Task (Dale & Anderson, 1978; Schandry, 1981), in which participants are asked to count the number of times they perceive their heart beating during specified time periods, without requiring them to tap along with the heartbeat.

We adapted the procedure of Experiment 1 to the Heartbeat Counting Task, by introducing varying time intervals within both the baseline and the predictive phases, indicated by a red cue appearing on the image of the heart. During these intervals, participants were asked to silently count their heartbeats. They reported this number out loud as soon as the red cue disappeared (Fig. 4).

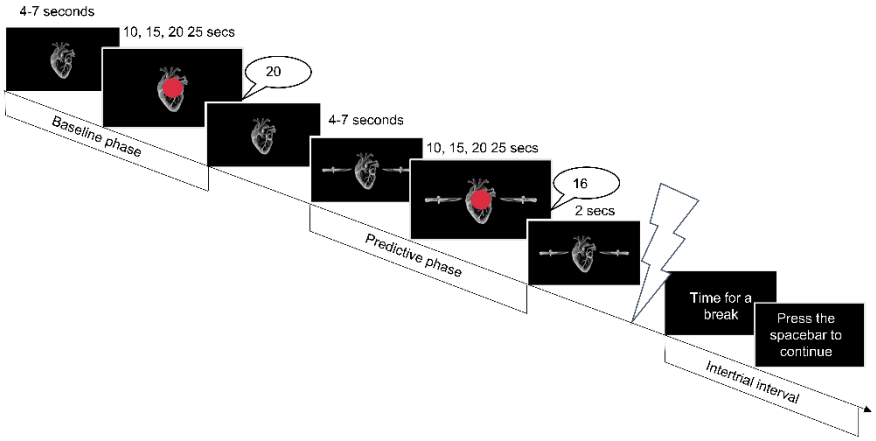

Figure 4. **Trial timeline of Experiment 2**.

3.1 Methods

3.1.1 Participants

The final sample size of the study comprised twenty-four healthy volunteers (mean age 25.41, SD = 4.31, 16 women) recruited from Gabriele d'Annunzio University and the wider community. Written informed consent was obtained from all participants. A sensitivity analysis using G*Power 3.1 (Faul et al., 2007) revealed that a sample size of 24 provides .80 power to detect effects with Cohen's d = .59 (SESOI of δ = .41). Exclusion criteria were identical to Experiment 1. One outlier was identified and subsequently excluded from the

analysis due to extreme values (± 3 SD relative to the mean) observed in one out of four variables of interest (for further details, see 2.1.1). One participant was removed from the analysis due to missing data. The experiment was conducted in accordance with the Declaration of Helsinki, and ethical approval was obtained from the local ethics board.

3.1.2 Apparatus and Stimuli

The apparatus and stimuli of Experiment 2 were the same as in Experiment 1.

3.1.3 Procedure

Participants were welcomed and briefed by the experimenter and provided their consent before proceeding to the ECG setup. As in Experiment 1, participants' cardiac interoception was assessed at rest using a modified version of the Heartbeat Counting Task (Dale & Anderson, 1978; Schandry, 1981). For more details, see Supplementary materials 2.2. Afterward, participants underwent the same psychophysical procedure as in Experiment 1 to determine the intensity of the noxious stimuli. Once the intensity of high- and low-stimulations was established, participants were instructed about the experiment proper.

Participants were instructed that their task involved silently counting their heartbeats and verbally reporting the count within different time windows, as indicated by the appearance and disappearance of a red circle presented at the centre of the screen. Importantly, this visual cue was presented both during the baseline phase, where a neutral image was presented on the screen, and the predictive phase. In the predictive phases, participants were presented with one of two warning visual cues (flowers vs. knives). These cues allowed them to anticipate the intensity of the upcoming electrical stimulation (Fig. 4).

When the experiment started, participants were seated in front of the computer, with their left hand placed on the table with the electrodes of the cutaneous electrical stimulation fixed on their inner wrist, while their ECG was recorded. We adapted the procedure of Experiment 1 to the Heartbeat Counting Task of Experiment 2. One necessary change was to

introduce variations in the duration of time intervals for participants to count. In Experiment 1, although we included 20% catch trials with different timings, the predictive and baseline phases in the majority of trials lasted 20 seconds. In contrast to the key presses in Experiment 1, this could potentially lead participants to memorize and repeat their reported counts from previous trials, rather than accurately counting their actual heartbeats. In Experiment 2, we therefore varied the timing by randomly varying not only the duration of the counting time window in both the predictive and baseline phases, but also the intervals preceding it.

In both the baseline and predictive phase of each trial, the neutral cue (i.e., heart) was presented first, instructing participants to focus on their heart beating (random duration of 4-7 seconds). A red circle appeared on top of the neutral cue, instructing participants to start counting their heartbeats until the red cue disappeared. Once the red cue disappeared, participants reported out loud the number of counted beats, and the experimenter noted it down. The duration of the red cue presentation varied randomly between intervals of 10 s, 15 s, 20 s, and 25 s for each trial and phase. Moreover, the randomization algorithm guaranteed that the counting time window for the baseline relative to the predictive phase was never of the same duration within a single trial, ensuring that participants could not re-use their count from the baseline in the predictive phase. A pause screen was shown for 30 seconds between trials. The experiment comprised 16 trials in total.

As in Experiment 1, at the end of Experiment 2, participants completed the State-Trait Anxiety Inventory (STAI) and subjective reports (see Supplementary materials 1.5).

3.1.4 Data Analysis

Data analysis was analogous to Experiment 1 but differed in how interoceptive accuracy was calculated. As the Heartbeat Counting task does not provide a timeline of participants' reported and recorded beats, it was impossible to apply signal detection

measures. Interoceptive accuracy was therefore calculated with the classical formula (Pollatos et al., 2008; Schandry, 1981).

3.2 Results

Despite the change in mode of report, the results of Experiment 2 fully replicated Experiment 1. First, the majority of participants (twenty-one out of twenty-four) declared that they believed their heart rate to accelerate when anticipating a threatening (i.e., painful) event. Second, the analysis of reported and real beats showed that this belief was mirrored by cardioception but not in the change of actual heart rates. Expecting a threatening relative to a harmless stimulus again elicited differential changes in the recorded compared to the perceived heart rate, as indicated by the two-way interaction of Type of Beat (recorded/reported) * Type of Expectation (pain/safe) (F (1, 23) = 6.55, p = .017, ηp^2 = .222, BF_{10} = 5.992, Fig. 5). Planned two-tailed paired t-tests confirmed that anticipating a threat (i.e., pain stimulus) relative to a harmless event (i.e., safe stimulus) increased the reported number of heartbeats (t (23) = 3.09, p = .005, BF_{10} = 16.783). However, this difference was not mirrored by the real cardiac state, which showed no differences between anticipating a threatening relative to a harmless event (t (23) = 1.56, p = .132, BF_{10} = 1.148). This pattern of results was replicated when using non-parametric tests (see Supplementary materials 2.1). In addition to these predicted effects, the results revealed that expecting high pain generally increased beat frequencies, both recorded and reported, as indicated by the main effect of Type of Expectation (F (1,23) = 10.104, p = .004, ηp^2 = .305).

Participants' performance was also evaluated in terms of their level of interoceptive accuracy, calculated here with the classical formula (Schandry, 1981). As in Experiment 1, participants' interoceptive accuracy was above chance (e.g., Predictive pain, IA: M = .71, SD = .20; IA: M = .70, SD = .21) and not affected by the different experimental phases, as revealed by the results of the two-way ANOVA with Predictiveness (Baseline vs. Predictive)

and Type of Expectation (Pain vs. Safe) as within-participants factors. There was no main effect no Main Effect of Type of Expectation (F=0.01, p = 0.92), nor Predictivness (F=0.01, p = .92). However, there was suggesting evidence of an interaction of Type of Expectation*Predictiveness (F = 3.25, p = .08) (See Supplementary materials 2.3).

However, it's noteworthy that, unlike the signal detection measures observed in Experiment 1, accuracy scores in Experiment 2 are not independent of the predicted increase in perceived heart rates under threat. As heartbeat counting scores are driven by undercounting (Ainley et al., 2020; Corneille et al., 2020; Zamariola et al., 2018; Zimprich et al., 2020), any rise in heart rates due to expectations of pain could artificially inflate accuracy, as observed in the present results. The suggestive evidence for an interaction between Predictiveness and Type of Expectation thus replicates the main analysis result and signifies a reduced underestimation of heart rates when anticipating a threat.

Finally, as in Experiment 1, the likelihood of developing the interoceptive cardiac illusion was not associated with participants' general level of interoceptive accuracy assessed either before the experiment proper $r(22) = -.17$, $p = .43$ (see Supplementary materials 2.2), nor with their levels of state- anxiety, $r(22) = .10$, $p = .64$), or trait- anxiety, $r(22) = -.09$, $p = .67$ (see Supplementary materials 1.5.3)

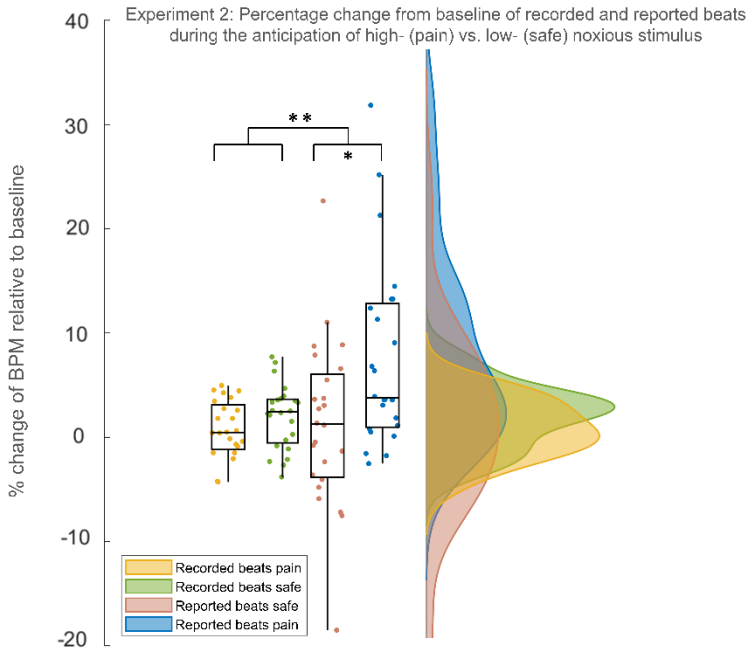

Figure 5. **Results of Experiment 2: Counting Task**. Values represent the percentage change in the bpm of reported (i.e. perceived) and recorded (i.e. real) beats in the predictive phase relative to the baseline phase, either when a threatening (i.e., high- intensity noxious stimulus, pain) or a harmless (i.e., low-intensity noxious stimulus, safe) stimulus was expected. Values of zero on the vertical axis would represent no change in the predictive phase relative to baseline, positive and negative values would represent an increase and a decrease, respectively. The data were based on a sample size of 24 healthy volunteers and analysed with a 2 x 2 repeated measures analysis of variance (ANOVA), with Type of Beat (Reported vs. Recorded) and Pain Expectation (Pain vs. Safe) as within-participants factors. Results showed that expecting a threatening relative to a harmless stimulus elicited an increase in the perceived cardiac frequency, which was not mirrored by the real heartrate ($p = .017$, $\eta p^2 = .222$). The plot consists of a probability density plot, a box plot, and raw data points. In the boxplot, the line dividing the box represents the median of the data, the ends represent the upper/lower quartiles, and the extreme lines represent the highest and lowest values. The code for raincloud plot visualization has been adapted from (Allen et al., 2019).

4. Experiment 3

Having established that the threat of pain induces an illusory increase in heart rate, Experiment 3 tested whether the same perceptual illusion would be observed if participants reported the perceived frequency of a similar non-interoceptive stimulus that would not be expected to change in response to threat. Experiment 3 replicated Experiment 1 in a task in which participants did not tap along with their heart rate, but with a diffuse visual stimulus (i.e., a light circle) pulsing intermittently on the screen. The visual stimulus was chosen to be unrelated to a heartbeat, while maintaining, as far as possible, its relevant characteristics. Therefore, for each participant in Experiment 3, the visual stimulus pulse rate was derived

from the cardiac frequency rate of one of the randomly chosen individuals who took part in Experiment 1. Furthermore, a preceding calibration phase was introduced to match the interoceptive and exteroceptive tapping tasks' difficulty to roughly the same level.

The aim of Experiment 3 was to establish that the perceptual illusion was uniquely associated to changes in cardiac perception, based on participants' interoceptive expectations about the heart's response to threat. Thus, we expect to find no differences in the number of real vs. perceived/reported beats during the anticipation of a threatening, high-intensity (pain stimulus) vs. harmless, low-intensity event (safe stimulus).

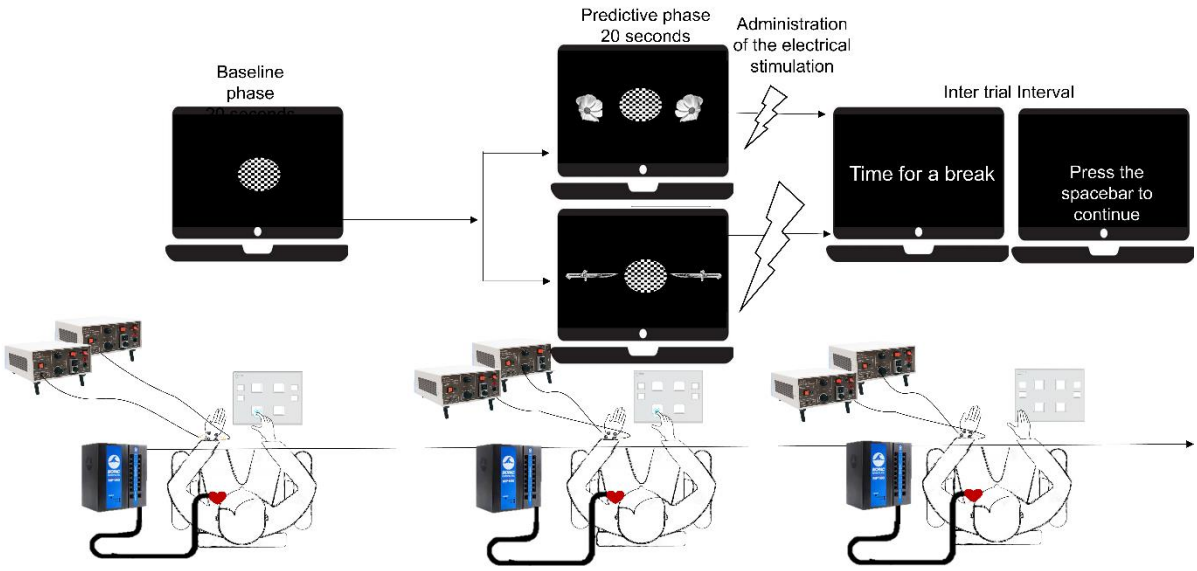

Figure 6. **Trial timeline of Experiment 3.**

4.1 Methods

4.1.1. Participants

The final sample size of the study comprised twenty-four healthy volunteers (mean age 25.9, SD = 3.6, 16 women) recruited from Gabriele d'Annunzio University and the wider community. All participants provided written informed consent. Exclusion criteria were

identical to Experiments 1 and 2. Additionally, participants were excluded if their level of visual accuracy could not be matched to that of their counterparts in Experiment 1 after 20 trials of the behavioural procedure. Two participants were excluded from the experiment based on this criterion. A sensitivity analysis using G*Power 3.1 (Faul et al., 2007) revealed that a sample size of 24 provides 0.80 power to detect effects with Cohen's d = .59 (SESOI of δ = .41). Information about the study's purpose was provided only after the experimental tests were completed. The experiment was conducted in accordance with the Declaration of Helsinki and ethical approval was obtained from a local ethics board.

4.1.2 Apparatus and Stimuli

Each participant was seated centrally in front of the computer's display, at a distance of 60 cm. The experiment was run on a computer with an ASUS VH232 monitor (resolution: 1920 x 1080, refresh rate: 59 Hz), programmed, and presented in Inquisit [6]. The apparatus and stimulus set used for Experiment 3 was essentially the same as in Experiment 1, except for some details (explained below). The visual stimulus was a circle drawn with Adobe Photoshop (3.30 cm) that pulsed intermittently at the centre of the screen and was overlapped by a black-and-white squared checkerboard (6 cm x 6 cm) gathered from Google Images. In order to create different difficulty levels, the brightness of the circle varied from 255,255,255 RGB code to 200,200,200 RGB code in steps of 5 RGB points. As a result, twelve stimulus images were created, that differed only in the brightness of the circle, ranging from the easiest (i.e., more visible) and farthest (i.e., white, RGB code 255,255,255) to the hardest (i.e., less visible) and closest (i.e., grey, RGB code 200,200,200) relative to the colour of the background (i.e., light grey, RGB code 195,195,195) (Fig. 7).

4.1.3 Procedure – Calibration phase

To ensure that performance in the visual task here and in the interoceptive task of Experiment 1 could be compared, we implemented a matching procedure before the

experiment proper, in which we attempted to match the visual accuracy of every participant in the exteroceptive tapping experiment one-to-one to the interoceptive accuracy of a participant in the interoceptive tapping experiment (Experiment 1). Therefore, the individual level of visual accuracy varied between participants of the exteroceptive task but should be equal to the interoceptive accuracy of the previous group, measured at rest, before the experiment proper.

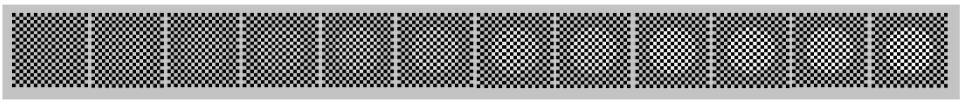

Figure 7. **Set of stimuli used in the behavioural phase**. Each level of difficulty, associated with a different RGB code of the stimulus, is illustrated. From the left, the circle with the lowest RGB code values is shown (200,200,200), until the right, where the highest RGB code of the stimulus (255,255,255) is shown.

Each trial of the calibration phase lasted for 20 seconds. It began with a checkerboard presented on the centre of the screen for a random interval between 500 and 1000 ms. Then, the target white circle appeared (45 ms) and disappeared intermittently behind the checkerboard. Participants were instructed to tap along so that their finger presses were synchronized with the appearance of the circle as accurately as possible. The frequency at which the visual stimulus appeared on the screen was different for each participant but matched to the individual heart rate of a random participant of the interoceptive task with whom the current participant should be matched in terms of accuracy. To do so, we extracted, in steps of 20 seconds, the timing of each heartbeat of this target interoceptive participant during the evaluation of each participant's interoceptive accuracy at the start of Experiment 1. We then synchronized the appearance of the circle to these timings.

The matching procedure always started with the highest brightness (RGB code 255,255,255). After each trial, accuracy was calculated exactly as for the interoceptive

accuracy in Experiment 1, by comparing the timing at which the response was given to the timing of each beat, either the appearance of the circle or the single heartbeat. We then checked whether this accuracy matched the accuracy of the target participant in Experiment 1, and if not, the brightness was automatically adjusted accordingly (i.e., decreased or increased) in the next trial. To do so, we measured the participants' interoceptive accuracy using a 20-second sliding window with an overlapping of 5 seconds over the whole ECG trace of the analogous accuracy at rest phase in Experiment 1 (2.30 min). The range of tolerance within which the visual accuracy had to fall was set to be equal to each participant's interoceptive accuracy ± 1*SD* (i.e., if the interoceptive accuracy over the entire interval was *d'* = 1.32 and the SD was .078, then the value of the visual accuracy that the next participant should display had to be comprised between *d'* = 1.24 and *d'* = 1.40). The procedure was repeated until the desired level of accuracy was stable (i.e., having 2 consecutive close accuracy values with the same RGB code). The final RGB values displayed at the end of the behavioural phase were then used in the script for the experiment, during which the RGB code of the circle was kept constant.

Once the RGB level was established, each participant went through the phase of calibration of nociceptive stimuli, in order to establish the individual level of intensity of the cutaneous stimulation for every participant. The calibration procedure was identical to the one used in Experiment 1. After the calibration phase, participants started the experiment.

4.1.4 Procedure - Main Experiment

As in Experiment 1, participants were informed that they would receive different electrical stimulations, either low- or high-intensity pain, and that, in each trial, they could predict the intensity of the upcoming shock by different warning visual cues presented on the screen. Crucially, while being exposed to these stimuli, here they were asked to accurately tap along with a visual stimulus pulsing on the centre of the screen.

In each trial, the checkerboard pattern appeared on the screen (Fig. 6), informing participants to get ready to start the visual tapping task. After a random interval between 500 and 1000 ms, the circle started to pulse intermittently behind the checkerboard pattern. The circle was presented with the previously established brightness (i.e., RGB code) while participants tapped along with each appearance of the visual stimulus that they were able to detect (i.e., baseline phase). After 20 seconds, the warning cue was shown left and right to the circle, which could be either an image of knives or flowers (Fig. 8), as in Experiment 1. Participants were informed that knives signalled a painful shock at the end of the trial, while flowers signalled harmless stimulation.

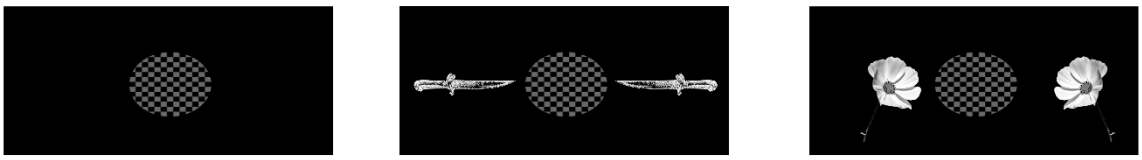

***Figure 8*. Set of stimuli used in Experiment 3.** From the left, 1) The neutral cue that indicates to participants to get ready to start the visual tapping task (i.e., baseline phase) 2) The predictive pain warning cue, that indicates to participants that they will receive the high-intensity cutaneous stimulation at the end of the trial (i.e., Predictive Pain phase) 3) The predictive safe warning cue, that indicates to participants that they will receive the low-intensity cutaneous stimulation at the end of the trial (i.e., Predictive Safe phase)

The warning cue remained on the screen for 20 seconds (i.e., predictive phase), and participants were required to keep tapping along with the pulsing circle, until a black screen appeared, marking the end of the trial and the delivery of the cutaneous stimulation. A pause screen was then shown for 30 seconds, to enable participants to recover from the cutaneous stimulation and avoid the subsequent trial to be contaminated by the heart rate response to the stimulation. They were then shown a screen with the instruction to press the spacebar, whenever they were ready to start the next trial.

As in the prior matching procedure, the frequency at which the circle pulsed on the screen was different for each participant and corresponded to the individual heart rate of the

participant of the interoceptive task with whom the current participant was matched. As before, this was achieved by extracting, for each participant of the interoceptive tapping task, the timing of all the peaks recorded during each trial and condition and by synchronizing the appearance of each circle with the timing of each recorded heartbeat. As a result, each participant in the exteroceptive task was matched with every participant in the interoceptive task, both in terms of the accuracy with which the stimulus was detected and the frequency at which the stimulus was presented during the experiment. As in the interoceptive tapping experiment, we inserted 20% of catch trials, which were needed to prevent participants from getting used to the length of the time window preceding the delivery of the cutaneous stimulation. In these catch trials, the electrical stimulation was delivered after 8 or 12 seconds from the onset of the warning cue. These trials were not analysed.

4.1.5 Data Analysis

As for Experiment 1, we extracted, for each participant and each trial, the number of reported and recorded beats and transformed them into frequencies, separately for the baseline and the predictive phases of each trial. The frequency of recorded beats reflected the frequency rate of the pulsing circle, which itself corresponded to the real cardiac frequency of participants who took part in Experiment 1. The frequency of reported beats reflected each participant's keypresses in each trial. The % change of bpm was then calculated for each individual trial and each phase (baseline, predictive) separately (% signal change = $(BPM_{Predictive} - BPM_{Baseline})*100 / BPM_{Baseline}$). Each participant's average percentage change was then entered into a 2 x 2 mixed measures analysis of variance (ANOVA), with Type of Beat (Reported vs. Recorded) and Type of Expectation (Pain vs. Safe) as within-participants factors. In contrast to Experiment 1, we predict that the expectation of a threatening vs. harmless stimulus should not affect the frequency with which participants report an exteroceptive stimulus, as there is no expectation that a visual stimulus would be

affected by threat to participants' own body. There should therefore be no interaction between Type of Beat and Type of Expectation. Finally, planned paired sample t-tests will be executed between variables of interest (i.e., Reported Pain vs. Reported Safe and Recorded Pain vs. Recorded Safe) to further investigate????whether anticipating a threatening (i.e., pain) vs. non-threatening (i.e., safe) stimulus elicited significant changes both in the perceived and the actual visual pulses. As in Experiment 1, accuracy (*d'*) and criterion scores were estimated for each participant based on Heartbeat Detection Task outcomes via signal detection, as validated by previous studies (Fittipaldi et al., 2020; Gonzalez Campo et al., 2020). Moreover, to test whether the difficulty of the exteroceptive (Experiment 3) and the interoceptive (Experiment 1) tapping task was balanced, an independent samples t-test was run between participants' mean accuracy displayed in both tasks only over the experimental baseline phases.

4.2 Results

First and foremost, analyses revealed that anticipating a threatening electrical stimulus compared to harmless one did not result in a differential effect on the frequency of reporting the visual exteroceptive stimulus when it was really presented. This finding was supported by the non-significant interaction of Type of Expectation*Type of Beat (F (1,23) = 1.102, p = .305, ηp^2 = .046, BF_{10} = .115, Fig. 9). Planned paired sample t-tests comparisons further demonstrated that the expectation of pain vs. safe stimuli did not differentially modulate the reported beat frequency of the pulsing visual stimulus (t (23) = .89, p = .38, $BF10$ = .490).

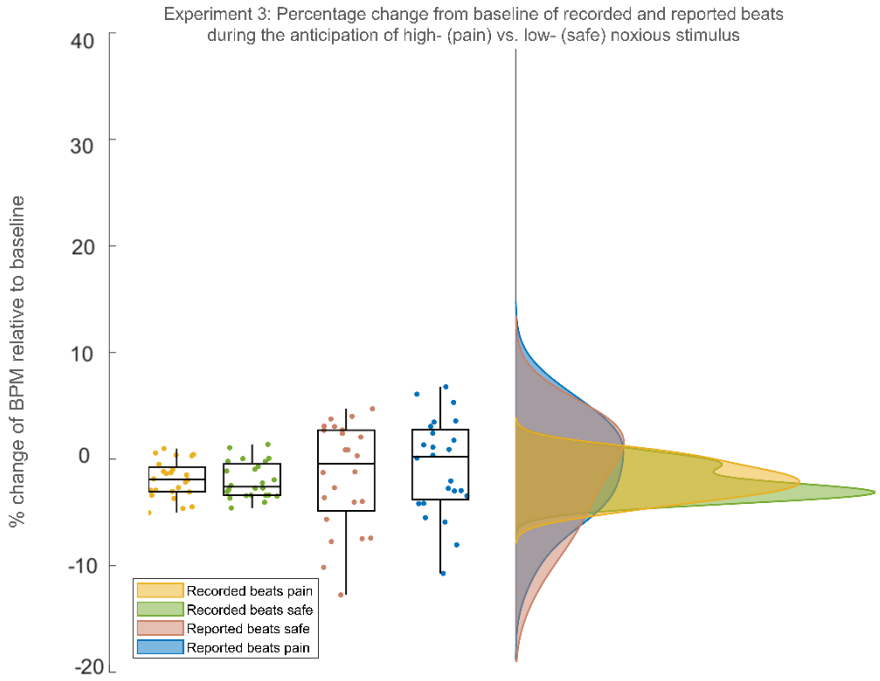

Figure 9. **Results of Experiment 3: Exteroceptive Tapping Task**. Values represent of the percentage change in the frequency of reported (i.e. perceived) and recorded (i.e. real) beats in the predictive phase relative to the baseline phase, either when a threatening (i.e., high- intensity noxious stimulus, pain) or a harmless (i.e., low-intensity noxious stimulus, safe) stimulus was expected. Values of zero on the vertical axis would represent no change in the predictive phase relative to baseline, positive and negative values would represent an increase and a decrease, respectively. The data were based on a sample size of 24 healthy volunteers and analysed with a 2 x 2 repeated measures analysis of variance (ANOVA), with Type of Beat (Reported vs. Recorded) and Pain Expectation (Pain vs. Safe) as within-participants factors. Results showed that expecting a threatening relative to a harmless stimulus did not elicit different changes in the perceived relative to the real beat frequency (p = .38). The plot consists of a probability density plot, a boxplot, and raw data points. In the box plot, the line dividing the box represents the median of the data, the ends represent the upper/lower quartiles, and the extreme lines represent the highest and lowest values. The code for raincloud plot visualization has been adapted from (Allen et al., 2019).

It should be noted that the calibration before the experiment (see Procedure – calibration phase) failed at equalizing the difficulty of the interoceptive (Experiment 1) and exteroceptive (Experiment 3) tapping tasks. Direct comparison of the mean baseline accuracy values revealed a higher accuracy in the exteroceptive tapping task in Experiment 3 (d' = 3.10, SD = .70) compared to the interoceptive tapping task in Experiment 1 (d' = 1.33, SD = .35), as confirmed by Welch's unequal variances t-test, $t(34.1) = -10.8$, $p < .001$, $d = -3.1$. Importantly, however, there was no correlation between the individuals' magnitude of the exteroceptive illusion and their level of accuracy during the task at baseline, r (22) = -.05, p = .81, as also shown for Experiment 1, r (23) = -.022, p = .91, Experiment 2, r (22) = -.08, p = .71, or even when the data was pooled across both experiments to increase statistical power,

$r(47) = -.05$, $p = .73$. This suggests that differences in uncertainty in perception did not underlie the likelihood of developing an interoceptive (Experiment 1) or exteroceptive (Experiment 3) illusion (see Supplementary materials 3.1 for further details).

Furthermore, participants' accuracy (d') in reporting visual pulses was modulated by experimental phases, with lower values observed when expecting stimulation in the predictive phase than during baseline (Main Effect of Predictiveness, $F(1,24) = 43.227$, $p < .001$, $\eta p2 = .65$). Post hoc comparisons showed that regardless of the intensity (low or high), participants' accuracy was consistently lower in the predictive than the baseline phase (Baseline Safe vs. Predictive Safe, $p = .001$, Baseline Pain vs. Predictive Pain, $p = .002$). In addition, accuracy values were lower when anticipating pain than when anticipating harmless stimulation (Main Effect of Type of Expectation, $F(1,24) = 5.902$, $p = .023$, $\eta p2 = .204$).

As in Experiment 1, we conducted the same analysis for the criterion. Participants adopted a more liberal criterion in the predictive than the baseline phase (Main effect of Predictiveness $F(1,23) = 19.007$, $p < .001$, $\eta p2 = .45$), but this occurred both when expecting high-pain (Predictive Pain vs. Baseline Pain $p = .04$) and low-pain stimulation (Predictive Safe vs. Baseline Safe, $p = .01$).

Thus, in contrast to Experiment 1, the exteroceptive tasks did not reveal the same illusory increase of reported pulses of the visual stimulus.

5. General Discussion

5.1 Overview of the results

Recent Embodied Predictive Coding (EPIC) approaches argue that interoception largely reflects our *internal model* of our body**,** based on our conceptions of its physiological condition, instead of only its veridical state (Barrett & Simmons, 2015; Pezzulo, 2014). Although such an internal model generally promotes an accurate estimate of bodily states, our

expectations are not always correct, and could sometimes lead to mis-perceptual phenomena. The present study tested whether a common false belief about the cardiac response to threats gives rise to such an interoceptive cardiac illusion. In two experiments, we asked participants to monitor and report their heartbeat, either by tapping along with it (Experiment 1) or by silently counting it (Experiment 2) while their ECG was recorded. Participants performed these tasks while visual cues reliably predicted a forthcoming harmless (low-intensity) vs. threatening (high-intensity) cutaneous electrical stimulus, delivered through a pair of electrodes attached to their wrist. We predicted that anticipating a painful vs. harmless stimulus would cause participants to report an increased cardiac frequency, which does not reflect their real cardiac response, but the common (false) belief that heart rates would accelerate under threat.

The two experiments confirmed, first, that most participants believed that their heart rate would accelerate when expecting a threatening painful stimulus. Second, they showed that these expectations were reflected in interoceptive changes when participants reported their heart rates. Participants reported a higher number of heartbeats whenever they expected a high-intensity pain stimulus, compared to a harmless low-intensity stimulus, but this pattern was not mirrored by the real heart rate, which was not modulated by threat expectation. This perceived increase in heart rate was found both in the Heartbeat Tapping task (Experiment 1) and replicated in the Heartbeat Counting task (Experiment 2) without motor components, ruling out that such a modulation reflects only motor changes associated with the anticipation of pain (Karos et al., 2017; Neige et al., 2018; Piedimonte et al., 2017).

When we investigated the changes in perceived heartrate with signal detection analyses, the results revealed that these effects reflected a change in criterion, that is, the sensory evidence participants needed to accept that they felt a heartbeat, while perceptual sensitivity (interoceptive accuracy, *d'*) was unaffected. This change in criterion is exactly

what would be predicted for an illusory increase in heartrates and is similar to several other perceptual illusions (Bach et al., 2014; Morrison et al., 2013; Peters et al., 2016; Witt et al., 2015), because such a change in criterion implies that participants' expectations of an accelerated heartbeat did not only make it more likely that actually occurring heartbeats were detected, but that participants were also more ready to perceive illusory heartbeats when there were none. However, it should be noted that this change in criterion was not accompanied by a decrease in sensitivity, that is, in participants' ability to distinguish the occurrence of a heartbeat from the absence of one. The additionally detected heartbeats under threat were therefore not randomly distributed across the tapping interval but they were more likely to coincide with actual heartbeats, and the lowered criterion threshold made it more likely that they were indeed detected relative to intervals were there was no heartbeats. In other words, the overall increase in responses was primarily due to a heightened number of hits rather than false alarms, underscoring the amplified detection of actual stimuli (see Supplementary Table 1).

Interestingly, while in Experiment 1 the real heart rate showed a general slight decrease both when participants expected painful or harmless stimulation, in line with previous research (for a full discussion see Skora et al., 2022), in Experiment 2 a general increase was observed. Note that this pattern of results does not undermine our hypotheses, as the heart rate increment was not specific to the expectation of pain and did not mirror the change in perception. Potential interpretations might involve the different degrees of cognitive load of the two interoceptive tasks. Increased heart rate responses are usually linked to higher cognitive workload and task difficulty (Hankins & Wilson, 1998; Mulder, 1988; Schnall et al., 1990, 1994; Veltman & Gaillard, 1996; Wilson, 1992, 1993; Wilson & O'Donnell, 1988). As highlighted by previous research, the Heartbeat Counting Task requires higher cognitive load and working memory due to counting and keeping in mind the numbers (Matthias et al.,

2009; Richards et al., 1996; for a review see Körmendi & Ferentzi, 2023) than the keypress task in Experiment 1. This explanation blends well with the observed general increase in the counting task when predictive cues were shown, if one assumes that this additional information increased the cognitive load of an already demanding task, irrespective of whether the cues signalled forthcoming low or high pain.

To further demonstrate that the subjectively increased heartrates under threat were driven by interoceptive expectations, Experiment 3 confirmed that changing the interoceptive stimulus to an exteroceptive visual stimulus would induce no such changes. Thus, instead of monitoring and reporting each felt heartbeat, participants tapped along with a visual stimulus pulsing on the screen. As predicted, participants' perceptual judgments were not influenced by the different pain expectations. Participants reported a similar number of visual pulses when expecting a threatening vs. innocuous event. Moreover, in contrast to Experiment 1, signal detection analysis showed that the anticipation of low or high noxious stimulation had a detrimental impact on participants' accuracy in detecting and reporting visual pulses, in line with the idea that anticipating threat acts as a distractor that undermines accurate reporting of the visual stimulus, but not of the interoceptive heartbeat stimulus. These findings, therefore, suggest that predicting an imminent threat induces specific changes to interoception, in line with participants' prior beliefs that their heartrate would increase when anticipating threat.

However, it is important to outline that, despite attempts to equalize accuracy in both tasks, participants' visual accuracy in Experiment 3 increased unexpectedly from the initial matching procedure, probably due to the habituation to the visual stimulus over the course of the study. This led to overall higher accuracy in Experiment 3 than Experiment 1. In contrast to the substantial uncertainty in cardiac perception (Khalsa et al., 2018; Petersen et al., 2014), the visual stimulus may therefore not have been ambiguous enough to elicit a similar perceptual illusion as during interoception. Nevertheless, it is noteworthy that our findings

consistently demonstrated the absence of connections between accuracy and perceptual illusion, a pattern observed not only in both Experiment 1 and Experiment 2 when analyzed independently but also when the data from both experiments were pooled together. Similarly, no correlation was observed with the visual task in Experiment 3. In line with divergent outcomes of the signal detection analyses of Experiment 1 and 3, this might indicate that the absence of the illusion in Experiment 3 is not predominantly due to the ease with which the stimulus is detectable, but it is more likely to be influenced by other factors, such as the interoceptive or exteroceptive source of the stimulus. However, this remains an aspect of the study that requires further investigation in experiments that use alternative methods to equalize the accuracy between the two tasks.

Collectively, the findings of the current study suggest that people's expectations about their cardiac response are projected into their interoceptive cardiac perception, such that predicting an imminent threatening vs. innocuous event caused them to believe, and then report, an illusory increase in their cardiac frequency. However, several open questions and limitations remain that will need to be considered for the interpretation of our findings.

5.2 Disentangling perceptual from cognitive contributions.

One potential issue is that tasks used can be influenced by processes outside cardioception (e.g., Corneille et al., 2020; Desmedt et al., 2018). A particular concern is that perceptual reports in our tasks may not only reflect changed cardiac sensation per se, but participants' higher-order *beliefs* of heart rate increase during anxiety-eliciting situations. In the counting task of Experiment 2, for example, participants could have reported a higher number of beats not because they felt these additional heartbeats but because they believed there should have been a higher number. Similarly, in the tapping task in Experiment 1, participants could have pressed the button more often because they believed their heartrate to be higher under threat, not because they felt it increase.

Robustly distinguishing between perceptual and cognitive/decisional contributions is a common challenge across fields that has been mostly unresolved, even in fields like psychophysics where stimuli and responses are under much tighter experimental control (e.g., Ball et al., 2020; Storrs, 2015; for a full discussion, see Firestone & Scholl, 2016). Nevertheless, a growing body of evidence suggests that top-down influences in the tasks used here do not just reflect heartbeat beliefs themselves, but their integration into cardiac perception (Körmendi et al., 2021, 2022; Ring & Brener, 2018), as proposed by the predictive coding frameworks our work is based on (Barrett & Simmons, 2015; Costantini, 2014; Costantini et al., 2018; Critchley & Garfinkel, 2017; Ferri et al., 2013). Here, several aspects of the present data similarly point to the predicted integration of higher-order beliefs with the cardiac perception itself, rather than an influence of the heartrate beliefs themselves.

First, note that our experiments replicated the illusory increase of heartrate in two interoceptive tasks with almost identical effect sizes. This replication is important because, while both tasks can be influenced by factors beyond pure cardioception (Brener & Ring, 2016; Zamariola et al., 2018), they differ in which influence is most prominent. The counting task poses high demands on working memory and cognitive control, to keep current counts in mind (Couto et al., 2015; Richards et al., 1996). Moreover, high accuracies could in principle be achieved without sensing one's heartbeats at all, by just correctly estimating (guessing) one's likely heartbeat rate based on the available evidence and knowledge of one's body state (e.g., Ainley et al., 2020; Desmedt et al., 2018; Ring et al., 2015). Performance in the tapping task, in contrast, depends strongly on perceptual influences, such as the ability to discount tactile feedback from one's own button presses (Körmendi & Ferentzi, 2023). Moreover, it offers the advantage of recording each individually detected heartbeat, enabling us to distinguish between those detections that are synchronized with heartbeats and those that are not. Indeed, when accuracy is measured with signal detection techniques like we did here,

above-chance performance is impossible without actual perception of one's heartbeat. High accuracy can only be achieved if participants' key presses are in synchrony with their heartbeat and therefore more likely fall into the interval just after the R wave compared to the interval before it (Fittipaldi et al., 2020). These task differences therefore imply that any higher-order cognitive influences should be more prominent in the heartbeat counting task than the tapping task. However, effect sizes in both tasks were virtually identical. While this comparison relies on interpreting a null effect, it nevertheless argues against a major influence of cognitive, extra-perceptual factors that would affect the counting task more than the tapping task.

Another important consideration is that influences of prior beliefs that reflect decisional, non-perceptual processes should have varied with uncertainty. Higher-order belief information should become ever more prominent the more uncertain the sensory input becomes, because participants would increasingly need to "fill in" the absence of real perceptual information with higher-order information (Gallagher et al., 2019). In contrast, more precisely felt real heartbeats would constrain how much these accurately felt sensations can be shifted by prior beliefs. However, when we correlated participants' accuracy with the size of the induced illusion, we could not find a relationship in either task. This was the case both when tasks were analysed separately and when their data was pooled to increase power, and both when the heartrate increase was correlated with interoceptive accuracy during rest (i.e., before the experiment proper started), and during the task itself (i.e., in the baseline and predictive phases). Please note that even during the task any such correlation could be meaningfully interpreted because both variables – accuracy and interoceptive illusion – are measured by statistically independent scores, one reflecting the average accuracy *across* conditions, and the other differently induced heartbeat counts *between* conditions. While it has to be confirmed by replications with larger samples, the lack of correlation therefore

argues against the idea that subjective perception of increased heartrates merely reflects one's belief about the heartrate, rather than its integration with cardioception.

The last piece of evidence that argues against a major influence of non-perceptual belief information comes from the signal detection analysis (see Supplementary Materials 1.2). The analysis shows that the illusory acceleration of the heartbeat when anticipating pain could effectively be modelled through a decrease of participants' detection threshold (i.e., criterion *c*), without an accompanying decrease in their perceptual sensitivity (*d'*), which showed, if anything, a numerical increase (and was also larger than when compared with the *d'* measured at rest). This confirms that our threat manipulation induced no qualitative change to how heartbeats were detected: participants distinguished their heartbeats against noise just as well when expecting pain and when not, implying that even the additional "hallucinated" heartbeats under threat were as closely synchronized with the real heartrates as those under no threat. Thus, both when expecting threat and when not, participants were equally engaged in perceptual discrimination, instead of just adding expected heartbeats to their taps. This shift in the criterion can be conceptualised either as a lowering of participants' threshold for evidence they needed to accept that they felt a heartbeat, or a consistent addition of (illusory) cardiac evidence during the tapping interval (Fittipaldi et al., 2020; Gonzalez Campo et al., 2020; Huang & Ferreira, 2020; Stanislaw & Todorov, 1999). Both would conspire to make detected heartbeats more likely, but – with a generally liberal criterion such as found here – would especially affect detections close to the real heartbeats, as such a lowering of the threshold would make it even more likely that these sensations are detected, compared to situations where there was no existing evidence from perceptual processing.

A final consideration is the influence of demand characteristics and suggestibility in our tasks. Experiments are social situations. A common concern in perceptual judgment tasks is that participants might have just adjusted their responses to align with their understanding

of what the experiments tests, instead of reflecting their real perception (e.g., Firestone & Scholl, 2016; Corneille & Lush, 2023). To be able to estimate such a possible influence, we asked each participant to reveal what they thought was tested in the experiments, and the match of these guesses was rated blindly and independently by three raters. While we acknowledge that expecting participants to formulate scientific hypotheses about the interplay of manipulated variables is unrealistic, it is crucial to note that our study did not ask them to precisely pinpoint the experimental goal; rather, we solicited their best guesses. Moreover, high scores in hypothesis guessing ratings were attainable even when participants provided somewhat imprecise descriptions of the experiment's purpose. For instance, hypotheses such as "The experiment aimed to investigate the alteration in my accuracy in counting beats concerning pain expectation" and "The study sought to demonstrate that anticipation of pain leads to a diminished perception of heartbeats due to attentional diversion" received average ratings of 1.3 and 1, respectively.

The average score of successful hypotheses guesses was low (M = .10), indicating that our participants had little or no verbalizable insight of the purpose of the study (for more details, see Supplementary materials 1.5.2). Moreover, in correlations analyses, participants' hypothesis guessing scores were unrelated to the induced cardioceptive illusion, providing no evidence that the results were due to demand effects (for a similar result in the exteroceptive domain, see Parrotta et al., 2023). Of course, the absence of such a relationship could reflect, in part, a power problem in correlation analyses and difficulties of participants to verbalize the understanding they had. Nevertheless, if there were such an influence, one would still expect any induced illusory increase to be more prominent in those participants whose guesses more captured the predicted relationship between anticipating threat and subjectively increased heartrates.

Taken together, in our sample we find little evidence for purely non-perceptual explanations for the threat-induced illusory increase in heartrate. However, it should be noted that several (but not all) of the conclusion rest on the interpretation of null effects, which depend strongly on sample sizes and the power of the statistical test. It is therefore crucial that our findings are confirmed in larger samples and different experimental methodologies. For example, investigating to what extent the induced expectations affect the neural components of the illusion in terms of the cortical processing of the heartbeat (i.e., Heartbeat Evoked Potential, Park & Blanke, 2019; Zaccaro et al., 2022) could shed light on the distinct contribution of cognitive and perceptual processes. Future directions might also involve specific suggestibility measures to explore how these correlate with the illusion or employing different suggestion instructions that influence expectations and, consequently, the interoceptive illusion (e.g., Ehrsson et al., 2022). These approaches could provide valuable insights and offer promising paths for further understanding the intricate interplay between perception and cognition in the context of interoceptive illusions.

5.3 The Role of Illusions in Shaping Our Internal World: Aberrant Predictions and Dysfunctional Interoception

Our findings raise intriguing questions about how illusorily interoceptive phenomena may intersect with the recognition and regulation of our internal states and be causal in dysfunctional conditions. The idea that psychopathology may be explained in terms of *aberrant* predictions is not new and is based on the conception of atypical, evidence-resistant predictions, which may lead the brain to sometimes operate like a ‘stubborn’ scientist despite evidence to the contrary, explaining for example hallucinations or delusions in schizophrenia and related conditions (Corlett et al., 2019; Fletcher & Frith, 2009; Gagne et al., 2018; Lissek & van Meurs, 2015; Powers et al., 2017; Seriès, 2019).

Such stubborn predictions could have been acquired either through *genetic* 'priors', representing information about the kind of world we live in (e.g., that the body remains at the predicted temperature of ~37°C), or through statistical learning (Allen & Friston, 2018; Fotopoulou & Tsakiris, 2017; for a full discussion, see Yon et al., 2019). Embodied Predictive Coding approaches (Barrett & Simmons, 2015; Pezzulo, 2014; Seth, 2013; Seth et al., 2011) offer another alternative. They assume that our body is regulated through "*embodied simulations*" that anticipate imminent events and our bodily response to them, enabling allostatic regulation of our bodily states (Barrett, 2017). Indeed, here, the relationship between the increase in cardiac activity and the anticipation of a threat may have emerged from participants' first-hand experience of increased heart rates to actual, not anticipated, pain. Similar mis-perceptual interoceptive phenomena may occur for everyday events that are perceived as stressors and allow their anticipatory regulation, even in cases when the stressor is only perceived as a stressor or is unlikely to occur. The role of beliefs in generating such maladaptive perceptual and bodily changes should be investigated by future studies.

In these regards, further investigations could delve into the role of interoceptive awareness (Garfinkel et al., 2015) in shaping these (mis-)perceptual interoceptive experiences. This is not only relevant for understanding how individuals interpret their own interoceptive states but also for understanding how such false interoceptive beliefs impact the ability to accurately infer others' interoceptive states (Arslanova et al., 2022; Galvez-Pol et al., 2022). If such beliefs shape people's own interoceptive experiences, they likely operate at even higher interpersonal levels, leading to potential misinterpretations of others' visceral sensations and derived emotional states.

5.4 Conclusions

The current work reveals for the first time how the expectation of a threatening stimulus can influence cardiac perception and induce an interoceptive illusion. Our results are in line with the recent proposal that the brain maintains an *interoceptive schema*, that is, a central representation of interoceptive variables (e.g., body temperature, cardiac activity, etc.) along with prior beliefs or "set points" for these variables (Tschantz et al., 2022). This internal model would support homeostatic and allostatic regulation by optimally weighting multiple (i.e., interoceptive and exteroceptive) streams of information to predict interoceptive signals (Iodice et al., 2019). Our evidence represents a first step toward a broader understanding of these processes, suggesting that when estimating cardiac activity, it might devote special attention to pain and anticipated threat. Future studies should therefore focus on whether this relationship is mutual, that is whether the brain also uses information about the cardiac activity to estimate pain. More generally, further research could be directed towards a deeper understanding of which homeostatic and physiological variables the brain relies on to build interoceptive inferences, which ones are integrated in the prediction of specific interoceptive parameters, and how these are combined to promote adaptive outcomes. Our results would suggest that also other interoceptive sensations in our daily life may be equally far from the real state of the body and reflect our (potentially false) interoceptive expectations and beliefs. More broadly, future research is needed to determine how such predictive mechanisms shape other interoceptive sensations and our bodily response to them, producing important insights for a deeper understanding of how illusory perception of our body state might underpin psychological conditions (i.e., anxiety, depression), as recently suggested (Barrett & Simmons, 2015).

References

Ainley, V., Apps, M. A., Fotopoulou, A., & Tsakiris, M. (2016). 'Bodily precision': A predictive coding account of individual differences in interoceptive accuracy. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1708), 20160003.

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

Allen, M., & Friston, K. J. (2018). From cognitivism to autopoiesis: Towards a computational framework for the embodied mind. *Synthese*, *195*(6), 2459–2482.

Allen, M., Poggiali, D., Whitaker, K., Marshall, T. R., & Kievit, R. A. (2019). Raincloud plots: A multi-platform tool for robust data visualization. *Wellcome open research*, *4*.

Arslanova, I., Galvez-Pol, A., Kilner, J., Finotti, G., & Tsakiris, M. (2022). Seeing through each other's hearts: Inferring others' heart rate as a function of own heart rate perception and perceived social intelligence. *Affective Science*, *3*(4), 862–877.

Atlas, L. Y., Wielgosz, J., Whittington, R. A., & Wager, T. D. (2014). Specifying the non-specific factors underlying opioid analgesia: Expectancy, attention, and affect. *Psychopharmacology*, *231*(5), 813–823.

Bach, P., Fenton-Adams, W., & Tipper, S. P. (2014). Can't touch this: The first-person perspective provides privileged access to predictions of sensory action outcomes. *Journal of Experimental Psychology: Human Perception and Performance*, *40*(2), 457.

Ball, F., Groth, R.-M., Agostino, C. S., Porcu, E., & Noesselt, T. (2020). Explicitly versus implicitly driven temporal expectations: No evidence for altered perceptual processing due to top-down modulations. *Attention, Perception, & Psychophysics*, *82*(4), 1793–1807. https://doi.org/10.3758/s13414-019-01879-1

Barrett, L. F. (2017). The theory of constructed emotion: An active inference account of interoception and categorization. *Social cognitive and affective neuroscience*, *12*(1), 1–23.

Barrett, L. F., & Simmons, W. K. (2015). Interoceptive predictions in the brain. *Nature reviews neuroscience*, *16*(7), 419–429.

Benedetti, F. (2014). Placebo effects: From the neurobiological paradigm to translational implications. *Neuron*, *84*(3), 623–637.

Benedetti, F., Carlino, E., & Pollo, A. (2011). How placebos change the patient's brain. *Neuropsychopharmacology*, *36*(1), 339–354.

Betka, S., \Lukowska, M., Silva, M., King, J., Garfinkel, S., & Critchley, H. (2020). Feeling the beat: Temporal and spatial perception of heartbeat sensations. *BioRxiv*.

Bradley, M. M., Moulder, B., & Lang, P. J. (2005). When good things go bad: The reflex physiology of defense. *Psychological science*, *16*(6), 468–473.

Bradley, M. M., Silakowski, T., & Lang, P. J. (2008). Fear of pain and defensive activation. *PAIN®*, *137*(1), 156–163.

Brener, J., & Ring, C. (2016). Towards a psychophysics of interoceptive processes: The measurement of heartbeat detection. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1708), 20160015.

Carroll, D. (1977). Cardiac perception and cardiac control. *Biofeedback and Self-regulation*, *2*(4), 349–369.

Carroll, D., & Whellock, J. (1980). Heart rate perception and the voluntary control of heart rate. *Biological Psychology*, *11*(3–4), 169–180.

Clark, D. M., Salkovskis, P. M., Öst, L.-G., Breitholtz, E., Koehler, K. A., Westling, B. E., Jeavons, A., & Gelder, M. (1997). Misinterpretation of body sensations in panic disorder. *Journal of consulting and clinical psychology*, *65*(2), 203.

Colloca, L., Benedetti, F., & Pollo, A. (2006). Repeatability of autonomic responses to pain anticipation and pain stimulation. *European Journal of Pain*, *10*(7), 659–665.

Corlett, P. R., Horga, G., Fletcher, P. C., Alderson-Day, B., Schmack, K., & Powers III, A. R. (2019). Hallucinations and strong priors. *Trends in cognitive sciences*, *23*(2), 114–127.

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

Costantini, M. (2014). Body perception, awareness, and illusions. *Wiley Interdisciplinary Reviews: Cognitive Science*, *5*(5), 551–560.

Costantini, M., Migliorati, D., Donno, B., Sirota, M., & Ferri, F. (2018). Expected but omitted stimuli affect crossmodal interaction. *Cognition*, *171*, 52–64.

Couto, B., Adolfi, F., Sedeño, L., Salles, A., Canales-Johnson, A., Alvarez-Abut, P., Garcia-Cordero, I., Pietto, M., Bekinschtein, T., & Sigman, M. (2015). Disentangling interoception: Insights from focal strokes affecting the perception of external and internal milieus. *Frontiers in psychology*, *6*, 503.

Couto, B., Salles, A., Sedeño, L., Peradejordi, M., Barttfeld, P., Canales-Johnson, A., Dos Santos, Y. V., Huepe, D., Bekinschtein, T., & Sigman, M. (2014). The man who feels

two hearts: The different pathways of interoception. *Social cognitive and affective neuroscience*, *9*(9), 1253–1260.

Cramer, A. O., van Ravenzwaaij, D., Matzke, D., Steingroever, H., Wetzels, R., Grasman, R. P., Waldorp, L. J., & Wagenmakers, E.-J. (2016). Hidden multiplicity in exploratory multiway ANOVA: Prevalence and remedies. *Psychonomic bulletin & review*, *23*(2), 640–647.

Critchley, H. D., & Garfinkel, S. N. (2017). Interoception and emotion. *Current Opinion in Psychology*, *17*, 7–14. https://doi.org/10.1016/j.copsyc.2017.04.020

Crone, E. A., Bunge, S. A., de Klerk, P., & van der Molen, M. W. (2005). Cardiac concomitants of performance monitoring: Context dependence and individual differences. *Cognitive Brain Research*, *23*(1), 93–106.

Crone, E. A., van der Veen, F. M., van der Molen, M. W., Somsen, R. J., van Beek, B., & Jennings, J. R. (2003). Cardiac concomitants of feedback processing. *Biological psychology*, *64*(1–2), 143–156.

Dale, A., & Anderson, D. (1978). Information variables in voluntary control and classical conditioning of heart rate: Field dependence and heart-rate perception. *Perceptual and Motor Skills*, *47*(1), 79–85.

Denson, T. F., Grisham, J. R., & Moulds, M. L. (2011). Cognitive reappraisal increases heart rate variability in response to an anger provocation. *Motivation and Emotion*, *35*(1), 14–22.

Desmedt, O., Luminet, O., & Corneille, O. (2018). The heartbeat counting task largely involves non-interoceptive processes: Evidence from both the original and an adapted counting task. *Biological psychology*, *138*, 185–188.

Dunn, B. D., Galton, H. C., Morgan, R., Evans, D., Oliver, C., Meyer, M., Cusack, R., Lawrence, A. D., & Dalgleish, T. (2010). Listening to your heart: How interoception

shapes emotion experience and intuitive decision making. *Psychological science*, *21*(12), 1835–1844.

Ehrsson, H. H., Fotopoulou, A., Radziun, D., Longo, M. R., & Tsakiris, M. (2022). No specific relationship between hypnotic suggestibility and the rubber hand illusion. *Nature Communications*, *13*(1), 564.

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G* Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior research methods*, *39*(2), 175–191.

Ferri, F., Chiarelli, A. M., Merla, A., Gallese, V., & Costantini, M. (2013). The body beyond the body: Expectation of a sensory event is enough to induce ownership over a fake hand. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1765), 20131140. https://doi.org/10.1098/rspb.2013.1140

Firestone, C., & Scholl, B. J. (2016). Cognition does not affect perception: Evaluating the evidence for "top-down" effects. *Behavioral and brain sciences*, *39*.

Fittipaldi, S., Abrevaya, S., de la Fuente, A., Pascariello, G. O., Hesse, E., Birba, A., Salamone, P., Hildebrandt, M., Martí, S. A., & Pautassi, R. M. (2020). A multidimensional and multi-feature framework for cardiac interoception. *Neuroimage*, *212*, 116677.

Fletcher, P. C., & Frith, C. D. (2009). Perceiving is believing: A Bayesian approach to explaining the positive symptoms of schizophrenia. *Nature Reviews Neuroscience*, *10*(1), 48–58.

Flynn, D. M., & Clemens, W. J. (1988). On the validity of heartbeat tracking tasks. *Psychophysiology*, *25*(1), 92–96.

Fotopoulou, A., & Tsakiris, M. (2017). Mentalizing homeostasis: The social origins of interoceptive inference – replies to Commentaries. *Neuropsychoanalysis*, *19*(1), 71–76. https://doi.org/10.1080/15294145.2017.1307667

Friston, K. (2005). A theory of cortical responses. *Philosophical transactions of the Royal Society B: Biological sciences*, *360*(1456), 815–836.

Friston, K. (2010). The free-energy principle: A unified brain theory? *Nature reviews neuroscience*, *11*(2), 127–138.

Gagne, C., Dayan, P., & Bishop, S. J. (2018). When planning to survive goes wrong: Predicting the future and replaying the past in anxiety and PTSD. *Current Opinion in Behavioral Sciences*, *24*, 89–95.

Galvez-Pol, A., Antoine, S., Li, C., & Kilner, J. M. (2022). People can identify the likely owner of heartbeats by looking at individuals' faces. *cortex*, *151*, 176–187.

García-Cordero, I., Esteves, S., Mikulan, E. P., Hesse, E., Baglivo, F. H., Silva, W., García, M. del C., Vaucheret, E., Ciraolo, C., & García, H. S. (2017). Attention, in and out: Scalp-level and intracranial EEG correlates of interoception and exteroception. *Frontiers in neuroscience*, *11*, 411.

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.

Gonzalez Campo, C., Salamone, P. C., Rodríguez-Arriagada, N., Richter, F., Herrera, E., Bruno, D., Pagani Cassara, F., Sinay, V., García, A. M., & Ibáñez, A. (2020). Fatigue in multiple sclerosis is associated with multimodal interoceptive abnormalities. *Multiple Sclerosis Journal*, *26*(14), 1845–1853.

Hankins, T. C., & Wilson, G. F. (1998). A comparison of heart rate, eye activity, EEG and subjective measures of pilot mental workload during flight. *Aviation, space, and environmental medicine*, *69*(4), 360–367.

Huang, Y., & Ferreira, F. (2020). The application of signal detection theory to acceptability judgments. *Frontiers in Psychology*, *11*, 73.

Hudson, M., Nicholson, T., Ellis, R., & Bach, P. (2016). I see what you say: Prior knowledge of other's goals automatically biases the perception of their actions. *Cognition*, *146*, 245–250.

Iodice, P., Porciello, G., Bufalari, I., Barca, L., & Pezzulo, G. (2019). An interoceptive illusion of effort induced by false heart-rate feedback. *Proceedings of the National Academy of Sciences*, *116*(28), 13897–13902.

Jamieson, J. P., Nock, M. K., & Mendes, W. B. (2012). Mind over matter: Reappraising arousal improves cardiovascular and cognitive responses to stress. *Journal of experimental psychology: General*, *141*(3), 417.

Jepma, M., Koban, L., van Doorn, J., Jones, M., & Wager, T. D. (2018). Behavioural and neural evidence for self-reinforcing expectancy effects on pain. *Nature Human Behaviour*, *2*(11), 838–855.

Karos, K., Meulders, A., Gatzounis, R., Seelen, H. A., Geers, R. P., & Vlaeyen, J. W. (2017). Fear of pain changes movement: Motor behaviour following the acquisition of pain- related fear. *European journal of pain*, *21*(8), 1432–1442.

Khalsa, S. S., Adolphs, R., Cameron, O. G., Critchley, H. D., Davenport, P. W., Feinstein, J. S., Feusner, J. D., Garfinkel, S. N., Lane, R. D., & Mehling, W. E. (2018). Interoception and mental health: A roadmap. *Biological psychiatry: cognitive neuroscience and neuroimaging*, *3*(6), 501–513.

Killeen, P. R. (2015). Signal detection theory. *Encyclopedia of theory in psychology*, *2*, 855–859.

Körmendi, J., & Ferentzi, E. (2023). Heart activity perception: Narrative review on the measures of the cardiac perceptual ability. *Biologia Futura*. https://doi.org/10.1007/s42977-023-00181-4

Körmendi, J., Ferentzi, E., & Köteles, F. (2021). Expectation predicts performance in the mental heartbeat tracking task. *Biological Psychology*, *164*, 108170. https://doi.org/10.1016/j.biopsycho.2021.108170

Körmendi, J., Ferentzi, E., & Köteles, F. (2022). A heartbeat away from a valid tracking task. An empirical comparison of the mental and the motor tracking task. *Biological Psychology*, *171*, 108328.

Lissek, S., & van Meurs, B. (2015). Learning models of PTSD: Theoretical accounts and psychobiological evidence. *International journal of psychophysiology*, *98*(3), 594–605.

Loggia, M. L., Juneau, M., & Bushnell, C. M. (2011). Autonomic responses to heat pain: Heart rate, skin conductance, and their relation to verbal ratings and stimulus intensity. *Pain*, *152*(3), 592–598. https://doi.org/10.1016/j.pain.2010.11.032

Lykken, D., Macindoe, I., & Tellegen, A. (1972). Preception: Autonomic response to shock as a function of predictability in time and locus. *Psychophysiology*, *9*(3), 318–333.

Macmillan, N. A., & Creelman, C. D. (2004). *Detection theory: A user's guide*. Psychology press.

Matthias, E., Schandry, R., Duschek, S., & Pollatos, O. (2009). On the relationship between interoceptive awareness and the attentional processing of visual stimuli. *International Journal of Psychophysiology*, *72*(2), 154–159.

McFarland, R. A. (1975). Heart rate perception and heart rate control. *Psychophysiology*, *12*(4), 402–405.

Melloni, M., Sedeño, L., Couto, B., Reynoso, M., Gelormini, C., Favaloro, R., Canales-Johnson, A., Sigman, M., Manes, F., & Ibanez, A. (2013). Preliminary evidence about the effects of meditation on interoceptive sensitivity and social cognition. *Behavioral and Brain Functions*, *9*(1), 1–6.

Morrison, I., Tipper, S. P., Fenton- Adams, W. L., & Bach, P. (2013). "Feeling" others' painful actions: The sensorimotor integration of pain and action information. *Human Brain Mapping*, *34*(8), 1982–1998. https://doi.org/10.1002/hbm.22040

Mulder, L. J. M. (1988). *Assessment of cardiovascular reactivity by means of spectral analysis*.

Nasso, S., Vanderhasselt, M.-A., Demeyer, I., & De Raedt, R. (2019). Autonomic regulation in response to stress: The influence of anticipatory emotion regulation strategies and trait rumination. *Emotion*, *19*(3), 443.

Neige, C., Mavromatis, N., Gagné, M., Bouyer, L. J., & Mercier, C. (2018). Effect of movement- related pain on behaviour and corticospinal excitability changes associated with arm movement preparation. *The Journal of Physiology*, *596*(14), 2917–2929.

Park, H.-D., & Blanke, O. (2019). Heartbeat-evoked cortical responses: Underlying mechanisms, functional roles, and methodological considerations. *Neuroimage*, *197*, 502–511.

Parrotta, E., McDonough, K., & Bach, P. (2023). Imagination as predictive perception: Mental imagery predictively biases perceptual judgments of observed action kinematics. *bioRxiv*, 2023–06.

Peters, M. A., Ro, T., & Lau, H. (2016). Who's afraid of response bias? *Neuroscience of Consciousness*, *2016*(1), niw001.

Petersen, S., Schroijen, M., Mölders, C., Zenker, S., & Van den Bergh, O. (2014). Categorical interoception: Perceptual organization of sensations from inside. *Psychological science*, *25*(5), 1059–1066.

Pezzulo, G. (2014). Why do you fear the bogeyman? An embodied predictive coding model of perceptual inference. *Cognitive, Affective & Behavioral Neuroscience*, *14*(3), 902–911. https://doi.org/10.3758/s13415-013-0227-x

Piedimonte, A., Guerra, G., Vighetti, S., & Carlino, E. (2017). Measuring expectation of pain: Contingent negative variation in placebo and nocebo effects. *European Journal of Pain*, *21*(5), 874–885.

Pollatos, O., Kurz, A.-L., Albrecht, J., Schreder, T., Kleemann, A. M., Schöpf, V., Kopietz, R., Wiesmann, M., & Schandry, R. (2008). Reduced perception of bodily signals in anorexia nervosa. *Eating behaviors*, *9*(4), 381–388.

Powers, A. R., Mathys, C., & Corlett, P. R. (2017). Pavlovian conditioning–induced hallucinations result from overweighting of perceptual priors. *Science*, *357*(6351), 596–600.

Rauss, K., & Pourtois, G. (2013). What is bottom-up and what is top-down in predictive coding? *Frontiers in psychology*, *4*, 276.

Richards, J. C., Edgar, L. V., & Gibbon, P. (1996). Cardiac acuity in panic disorder. *Cognitive therapy and research*, *20*, 361–376.

Ring, C., & Brener, J. (1996). Influence of beliefs about heart rate and actual heart rate on heartbeat counting. *Psychophysiology*, *33*(5), 541–546.

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

Ring, C., Brener, J., Knapp, K., & Mailloux, J. (2015). Effects of heartbeat feedback on beliefs about heart rate and heartbeat counting: A cautionary tale about interoceptive awareness. *Biological psychology*, *104*, 193–198.

Schandry, R. (1981). Heart beat perception and emotional experience. *Psychophysiology*, *18*(4), 483–488.

Schnall, P. L., Landsbergis, P. A., & Baker, D. (1994). Job strain and cardiovascular disease. *Annual review of public health*, *15*(1), 381–411.

Schnall, P. L., Pieper, C., Schwartz, J. E., Karasek, R. A., Schlussel, Y., Devereux, R. B., Ganau, A., Alderman, M., Warren, K., & Pickering, T. G. (1990). The relationship between'job strain,'workplace diastolic blood pressure, and left ventricular mass index: Results of a case-control study. *Jama*, *263*(14), 1929–1935.

Sedeño, L., Couto, B., Melloni, M., Canales-Johnson, A., Yoris, A., Baez, S., Esteves, S., Velásquez, M., Barttfeld, P., & Sigman, M. (2014). How do you feel when you can't feel your body? Interoception, functional connectivity and emotional processing in depersonalization-derealization disorder. *PloS one*, *9*(6), e98769.

Seriès, P. (2019). Post-traumatic stress disorder as a disorder of prediction. *Nature Neuroscience*, *22*(3), 334–336. https://doi.org/10.1038/s41593-019-0345-z

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

Seth, A. K., Suzuki, K., & Critchley, H. D. (2011). An interoceptive predictive coding model of conscious presence. *Frontiers in Psychology*, *2*, 395. https://doi.org/10.3389/fpsyg.2011.00395

Skora, L. I., Livermore, J. J. A., & Roelofs, K. (2022). The functional role of cardiac activity in perception and action. *Neuroscience & Biobehavioral Reviews*, 104655.

Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior research methods, instruments, & computers*, *31*(1), 137–149.

Storrs, K. R. (2015). Are high-level aftereffects perceptual? In *Frontiers in psychology* (Vol. 6, p. 157). Frontiers Media SA. https://www.frontiersin.org/articles/10.3389/fpsyg.2015.00157/full

Taggart, P., Hedworth-Whitty, R., Carruthers, M., & Gordon, P. D. (1976). Observations on electrocardiogram and plasma catecholamines during dental procedures: The forgotten vagus. *British Medical Journal*, *2*(6039), 787–789. https://doi.org/10.1136/bmj.2.6039.787

Tracy, L. M., Gibson, S. J., Georgiou-Karistianis, N., & Giummarra, M. J. (2017). Effects of explicit cueing and ambiguity on the anticipation and experience of a painful thermal stimulus. *PloS One*, *12*(8), e0183650. https://doi.org/10.1371/journal.pone.0183650

Tschantz, A., Barca, L., Maisto, D., Buckley, C. L., Seth, A. K., & Pezzulo, G. (2022). Simulating homeostatic, allostatic and goal-directed forms of interoceptive control using active inference. *Biological Psychology*, *169*, 108266. https://doi.org/10.1016/j.biopsycho.2022.108266

Ullsperger, M., Danielmeier, C., & Jocham, G. (2014). Neurophysiology of performance monitoring and adaptive behavior. *Physiological Reviews*, *94*(1), 35–79. https://doi.org/10.1152/physrev.00041.2012

Veltman, J. A., & Gaillard, A. W. (1996). Physiological indices of workload in a simulated flight task. *Biological Psychology*, *42*(3), 323–342. https://doi.org/10.1016/0301-0511(95)05165-1

Wager, T. D., Rilling, J. K., Smith, E. E., Sokolik, A., Casey, K. L., Davidson, R. J., Kosslyn, S. M., Rose, R. M., & Cohen, J. D. (2004). Placebo-induced changes in FMRI in the anticipation and experience of pain. *Science (New York, N.Y.)*, *303*(5661), 1162–1167. https://doi.org/10.1126/science.1093065

Wilson, G. F. (1992). Applied use of cardiac and respiration measures: Practical considerations and precautions. *Biological Psychology*, *34*(2–3), 163–178. https://doi.org/10.1016/0301-0511(92)90014-l

Wilson, G. F. (1993). Air-to-ground training missions: A psychophysiological workload analysis. *Ergonomics*, *36*(9), 1071–1087. https://doi.org/10.1080/00140139308967979

Wilson, G. F., & O'Donnell, R. D. (1988). Measurement of operator workload with the neuropsychological workload test battery. In *Advances in Psychology* (Vol. 52, pp. 63–100). Elsevier.

Witt, J. K., Taylor, J. E. T., Sugovic, M., & Wixted, J. T. (2015). Signal Detection Measures Cannot Distinguish Perceptual Biases from Response Biases. *Perception*, *44*(3), 289–300. https://doi.org/10.1068/p7908

Wylie, G. R., Yao, B., Sandry, J., & DeLuca, J. (2021). Using Signal Detection Theory to Better Understand Cognitive Fatigue. *Frontiers in Psychology*, *11*. https://www.frontiersin.org/articles/10.3389/fpsyg.2020.579188

Yon, D., de Lange, F. P., & Press, C. (2019). The predictive brain as a stubborn scientist. *Trends in cognitive sciences*, *23*(1), 6–8.

Yoris, A., Abrevaya, S., Esteves, S., Salamone, P., Lori, N., Martorell, M., Legaz, A., Alifano, F., Petroni, A., Sánchez, R., Sedeño, L., García, A. M., & Ibáñez, A. (2018). Multilevel convergence of interoceptive impairments in hypertension: New evidence

of disrupted body-brain interactions. *Human Brain Mapping*, *39*(4), 1563–1581. https://doi.org/10.1002/hbm.23933

Yoris, A., Esteves, S., Couto, B., Melloni, M., Kichic, R., Cetkovich, M., Favaloro, R., Moser, J., Manes, F., & Ibanez, A. (2015). The roles of interoceptive sensitivity and metacognitive interoception in panic. *Behavioral and Brain Functions*, *11*(1), 1–6.

Zaccaro, A., Perrucci, M. G., Parrotta, E., Costantini, M., & Ferri, F. (2022). Brain-heart interactions are modulated across the respiratory cycle via interoceptive attention. *Neuroimage*, *262*, 119548.

Zamariola, G., Maurage, P., Luminet, O., & Corneille, O. (2018). Interoceptive accuracy scores from the heartbeat counting task are problematic: Evidence from simple bivariate correlations. *Biological psychology*, *137*, 12–17.

Zilcha-Mano, S., Wang, Z., Peterson, B. S., Wall, M. M., Chen, Y., Wager, T. D., Brown, P. J., Roose, S. P., & Rutherford, B. R. (2019). Neural mechanisms of expectancy-based placebo effects in antidepressant clinical trials. *Journal of Psychiatric Research*, *116*, 19–25. https://doi.org/10.1016/j.jpsychires.2019.05.023

Zimprich, D., Nusser, L., & Pollatos, O. (2020). Are interoceptive accuracy scores from the heartbeat counting task problematic? A comment on Zamariola et al.(2018). *Biological Psychology*, *152*, 107868.