Heart Is Deceitful Above All Things: illusory perception of heartbeat is induced by pain expectation.

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Abstract

Our interoceptive states and their perception are thought to be heavily shaped by interactions between expectations and interoceptive information. Surprisingly, previous research mostly investigated the impact of expectations on interoceptive states themselves (i.e. cardiac activity), rather than the perception of these states (i.e. heartbeat perception).

This study investigated whether expectations of pain induce an illusory perception of heartbeat frequency, so that heartbeat perception reflects expectations about how the heartbeat will change, rather than only the actual change. Participants were instructed to report continuously their heartbeat, either tapping along to it (i.e., Experiment 1, heartbeat tapping task) or silently counting (i.e., Experiment 2, heartbeat counting task), while ECG was recorded. Crucially, while completing this task, subjects were presented with two types of cues, which provided valid predictive information about the intensity of an upcoming cutaneous stimulation, that is a high- or low- pain electrical stimulus. Results showed that, whenever participants were exposed to cues that signalled the upcoming high-painful stimulation, they reported a higher number of heartbeats compared to when they were anticipating a low-painful shock. Importantly, the perceived increase was not mirrored by the real cardiac frequency, which showed no difference when participants were anticipating a high- vs. low- pain stimulus. Moreover, such perceptual modulations were dramatically reduced when participants executed the same tapping task but with an exteroceptive visual stimulus (i.e., Experiment 3, exteroceptive tapping task). Together, the findings reveal, for the first time, a perceptual illusion of heartbeats associated to pain expectation. This study offers some important insights for understanding how inferential processes can actively generate interoceptive perception, emphasizing its pivotal role within the predictive aspects of the processing of bodily signals and of physiological regulation.

Introduction

The perception of signals from our heart forms the basis of 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 pathophysiologies (Carrol & Whellock, 1980; Carrol et al., 1977; Clark et al., 1997; Dunn et al., 2010).

Traditional views of interoception as a bottom-up, sensory-driven process that provides a veridical representation of the internal and external environment (for a full discussion, see Rauss & Pourtois, 2013) have recently been challenged by Embodied Predictive Coding (EPIC) approaches (for a full discussion see Barrett and Simmons, 2015). Under these views, interoception is not a mere mirror of reality but profoundly enriched by our prior knowledge, thoughts, and expectations. The brain is cast as an active generator of inferences that constantly creates and updates a model of the external (i.e., environmental conditions) and internal (i.e., body's physiological condition) world, and attempts to fit it with current inputs through an iterative process of Bayesian hypothesis testing and revision (Barrett and Simmons 2015; Pezzulo 2013; Pezzulo et al. 2015; Seth et al. 2012; Seth, 2013). The goal of interoception is to reduce the difference between one's internal models and the actual interoceptive input, thus converging towards a 'best brain's guess' that accurately represents the body's state.

An important feature of EPIC accounts is that this reduction can be achieved either by perceptual (i.e., changing the model to fit the world) or active (i.e., changing the world to fit the model) 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 speeding up a 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, or by *actually* accelerating one's heartbeat, thereby changing the actual bodily state to fit expectations.

So far, research has primarily focussed on the active inference component, demonstrating that predictive processes change internal states themselves. There is ample evidence for such influences across several interoceptive modalities, showing that prior expectations affect, among others, cardiac activity (Denson et al., 2011; Jamieson et al., 2012; Nasso et al., 2019) and pain experience (Wager et al., 2004; Zilcha-Mano et al., 2019; Jepma, et al, 2018;Benedetti, 2014; Benedetti et al., 2011). For example, there is evidence that prior pain expectations, and pain itself, modulate physiological responses, in line with the idea that unfulfilled predictions can be resolved by engaging autonomous responses. Expecting pain induces augmented activity in the sympathetic system (e.g. increases in blood pressure and skin conductance) to prepare for potential avoidance responses (Barlow et al., 1996; Oka et al., 2007; Tousignant-Laflamme, 2006; Yang et al., 2003), as well as the characteristic decrease in heart rate to promote orienting responses, attention and sensory processing (Lykken et al., 1972; Taggart et al., 1976; Bradley et al., 2005; Bradley et al., 2008; Colloca et al., 2012; Tracy et al.,2017).

Much less evidence exists for the hypothesis that predictive processes impact how we *perceive* our internal states, so 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). While ample research has demonstrated such influences in exteroceptive modalities (e.g., Bach et al., 2014; Bach & Schenke, 2017; Kilner et al., 2007ab, Rao & Ballard, 1999; Kerzel et al., 2001; Hubbard, 2005; Doherty et al., 2005; Thornton, Hayes, 2004; Kok et al., 2012), research on interoception has investigated only a few modalities, probably due to the intrinsic difficulty in measuring interoception (Allen, 2018), with the perception of pain being a major research focus. Decades of work on placebo

and nocebo effects (Benedetti et al., 2014; Benedetti et al., 2011; Colloca & Benedetti, 2005; Wager et al., 2015; Oken et al., 2008; Price et al., 2008; Enck et al., 2008; Tracey, 2010; Häuser et al., 2012), provide robust evidence that expectations about pain intensity lead people to adjust their pain ratings towards the expected levels (Colloca & Benedetti, 2005; Büchel et al., 2014; Wiech, 2016; Atlas et al., 2012; Lund et al., 2014; Schenk et al., 2014). Furthermore, neuroimaging studies showed that predictions modulated treatment-relevant neuronal processes even before treatment and that these changes, in turn, mediated pain treatment outcomes (Wager et al., 2004; Zilcha-Mano et al., 2019). The finding that the perception of pain heavily reflects prior expectations has led to the suggestion that pain is an expectation-based process, comparable to illusions in the exteroceptive domain (Tabor et al., 2017ab).

Here, we ask whether a similar integration of expectations and sensory evidence occurs for the perception of one's heartbeat (i.e., cardioception), in other words, whether the perception of our heartbeat is similarly illusorily distorted towards expectations. While this hypothesis has not been tested, the extant research suggests strong influences of prior beliefs on cardioception. For example, prior work suggests that participants' counts at the Heartbeat Counting tasks (Dale and Anderson, 1978, Schandry, 1981) reflect, in part, their prior beliefs about their heart rate (Ring & Brener, 1996; Körmendi et al., 2021). Moreover, false cardiac feedback biases participants' reports of their heart rate towards this false feedback, independent of actual changes (Phillips et al., 1999; Ring, Brener, Knapp, & Mailloux, 2015). Similarly, when participants are asked to estimate their heart rates across different tasks (e.g., meditation, reading, lifting), their estimates correlate with actual heart rate changes but are independent of participant's actual detection accuracy (Pennebaker & Hoover, 1984), suggesting a major influence of prior knowledge about how heart rate will change in these tasks.

Together, these findings suggest that the reporting of cardiac inputs 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 can use this knowledge to improve their estimates of their otherwise highly ambiguous cardiac state. Importantly, so far, research focussed on whether such internal models helped 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 pivotal to resolve whether (1) people may spontaneously generate false beliefs about their heartbeat and whether (2) these misleading expectations may 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 reflected by actual heart rates and that, in fact, the opposite is more likely to occur. Decelerating cardiac frequency typically occurs when stimuli signal a forthcoming threat (Lykken et al., 1972; Taggart et al., 1976; Bradley et al., 2005; Bradley et al., 2008; Colloca et al., 2006; Tracy et al., 2017), or, more generally, highly salient events (Crone et al., 2005; 2003; Ullsperger et al., 2014). According to the Embodied Predictive Coding account, interoceptive cardiac perception, as perception in general, is largely a construction of beliefs that are kept in check by the actual state of the body – rather than vice versa. People's (false) assumption about heart rate responseto the threat should then result in the consequence that when individuals generate an expectationof an imminent threatening event, they may feel and (falsely) perceive their heart to accelerate, independently of whether this cardiac pattern is mirrored by the real cardiac frequency.

We tested this hypothesis in three experiments. Participants were asked to monitor and report their heartbeat, 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, Shandry, 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, delivered through a pair of electrodes previously attached to their wrist: either a painful high-intensity (i.e. threatening) or harmless low-intensity (i.e. non-threatening) pain stimulus. We expected that cues threatening high-intensity 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* beats should not be reflected in the real state of the body, so that the real heart rate measured with ECG does not show such a specific increase to cues signalling pain. Additional exploratory investigations (See Supplementary materials) tested whether this distortion in cardiac perception was modulated by participants' (1) interoceptive accuracy, measured at rest before the experiment, and (2) their state- and trait- anxiety (STAI).

Finally, Experiment 3 tested whether this perceptual illusion would be eliminated when participants reported the rate of an exteroceptive rhythmic stimulus that was not related to their cardiac state. As participants would have no expectation that an external stimulus would be affected by a threat to their own body, perception of exteroceptive stimuli should be less affected by expectations of high or low pain. We, therefore, replicated Experiment 1 in an exteroceptive modality in which participants, instead of tapping along with their heartbeat, tapped along with an ambiguous visual stimulus pulsing on the screen, either in a resting condition or over the exposure to cues that signal either an upcoming threatening (i.e., high-intensity pain stimulus) or harmless (i.e., low- intensity pain stimulus) event. This allowed us to test whether the observed discrepancy between the real and perceived number of pulses when anticipating a threatening event (Experiment 1) was uniquely related to the interoceptive expectation of an increased heart rate over the anticipation of a harmful stimulus. Thus, in Experiment 3, we predict to observe no differences in the reported number of visual pulses when expecting high- vs. low-intensity pain.

If confirmed, these results will show for the first time that the expectation of a threatening stimulus can influence our interoceptive cardiac perception, generating an interoceptive

illusion. Such findings would suggest that other internal sensations permeating our daily life might not be only the result of our actual body's physiological changes, but would similarly prominently reflect our beliefs, knowledge, and anticipation of forthcoming events. This evidence may provide important insights on how inferential and predictive processes actively influence the perception of our state of the body, raising intriguing questions about how these illusory phenomena in interoception may intersect with the recognition and regulation of our internal states.

Results

Experiment 1

Participants' cardiac perception of their heart rate (i.e., the heartbeat tapping task, McFarland, 1967; Flynn & Clemens, 1988; Melloni et al., 2013) and their actual cardiac frequency (i.e., ECG), were measured in each trial first in a baseline neutral and then in a predictive phase, wherein they were expecting to receive either a harmless (low-intensity) or threatening (high-intensity) pain stimulus (see Figure 1). This task allowed us to quantify whether, relative to a baseline neutral phase, recorded and reported beats changed differently as a function of the expectation of threatening vs. non-threatening stimuli.

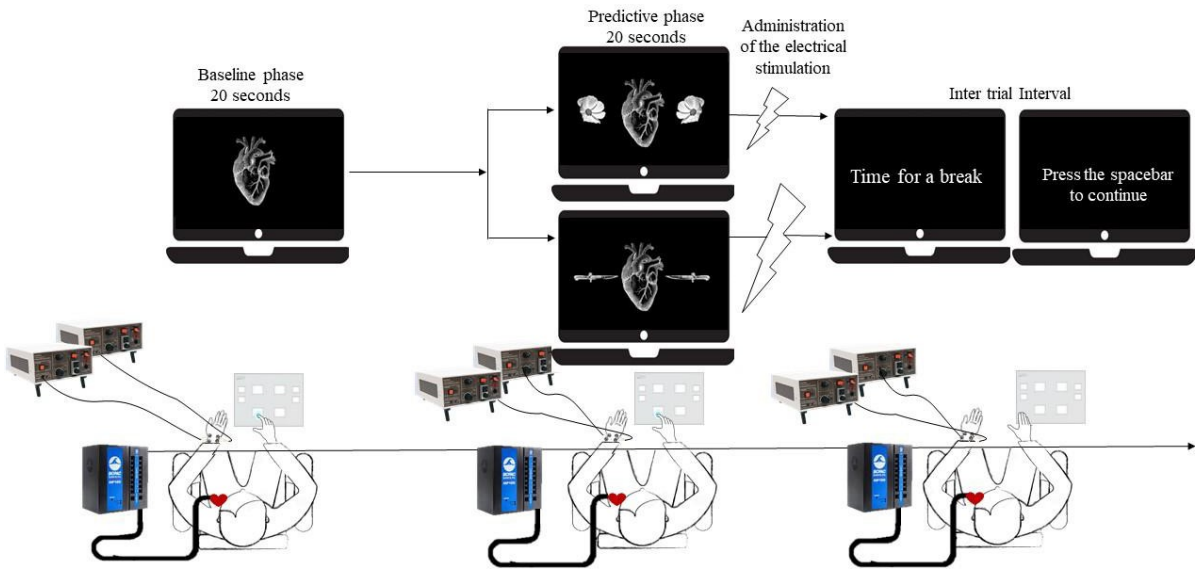

Figure 1. Trial timeline of Experiment 1. The trial starts with a baseline phase, in which a neutral visual cue instructed participants to start tapping along with each heartbeat sensation. After 20 seconds, the predictive phase started. One of the two warning cues appeared, flanking the neutral cue. Knives signalled upcoming high-intensity pain stimulus and flowers signalled the low-intensity harmless stimulation. After a further 20 seconds, the electrical cutaneous shock was delivered, marking the end of the trial and of the tapping task. After a 30- second pause, participants started the next trial by pressing the spacebar.

We predicted, first, that participants would expect their heart rate to accelerate when anticipating a threatening (high-pain) vs. harmless (low-pain) stimulus, which was assessed through subjective reports at the end of the experiment. Second, we predicted that participants' cardioception (i.e., number of reported beats at the heartbeat tapping task) was shaped by this expectation, thus showing a significantly larger increase in the perceived heartbeats when anticipating high- vs. low- pain stimuli, relative to baseline. Third, this difference in the perceived cardiac frequency should be not mirrored by the real heart rate (i.e., number of recorded beats with the ECG), which should show, if anything, a general decrease, in line with the observed cardiac deceleration after alerting stimuli (for a full discussion, see Skora et al., 2022).

The results confirmed these predictions. They showed, first, that participants' beliefs about their heart rate response in anticipation of a 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 spontaneously answered that they believed their heart rate to increase.

Second, the analysis of real and reported beats showed that this belief was mirrored by cardioception but not in the change of actual heart rates (Figure 2). Relative to the baseline phase, participants' perceived cardiac frequency generally increased over the predictive phase, while the real heart rate slightly decreased, no matter if they were anticipating a high- or a low-pain stimulus (Main effect of Type of beat, $F(1,24) = 19.1$, $p < 0.001$, $\eta p^2 = 0.444$). Moreover, expecting high-pain generally increased beat frequencies, both recorded and reported (Main Effect of Pain Expectation, $F(1,24) = 5.81$, $p = 0.024$, $\eta p^2 = 0.195$). Importantly, expecting a threatening relative to a harmless stimulus elicited different changes in the recorded compared to the perceived heart rate (Type of Beat * Pain Expectation, $F(1,24) = 6.527$, $p = 0.017$, $\eta p2 = 0.214$). Specifically, anticipating a high- vs. low-pain stimulus increased reported heart rates ($t(1,23) = 2.58$, $p = 0.016$), which was not mirrored by the actual heart rate ($t(1,23) = 0.12$, $p = 0.907$).

Finally, the likelihood of reporting such an increase in the perceived heart rate over the expectation of a threatening vs non-threatening event was not associated with participants' general level of their interoceptive accuracy, r (1,23) = 0.20, p = 0.34, nor with their levels of state-anxiety, r(1,24) = -0.23, p = 0.26) or trait- anxiety, r(1,24) = -0.08, p = 0.70 (see Supplementary materials for more details).

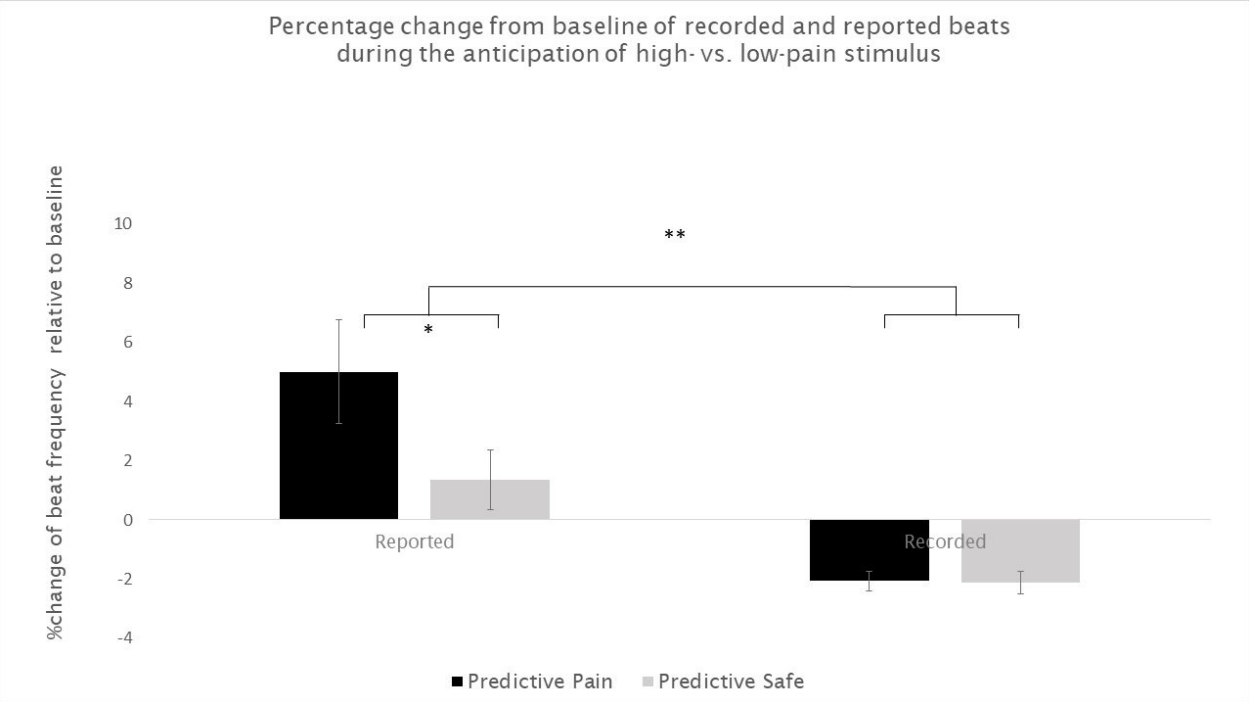

Figure 2. Experiment 1: Interoceptive Tapping Task. The %change in the frequency of reported (i.e., perceived) and recorded (i.e., real) beats relative to baseline, either when a threatening (i.e., high-intensity pain stimulus, Predictive Pain) or a harmless (i.e., low-intensity pain stimulus, Predictive Safe) stimulus was expected. Values represent the percentage change in the number of beats in the predictive phase compared to the neutral baseline phase. 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. Error bars represent SEM. Asterisks indicate significant differences: * p= 0.016; ** p = 0.017.

Experiment 2

An open question is whether the observed cardiac frequency estimations in Experiment 1 only reflect the perceptual representations of participants' cardiac state in anticipation of a 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 (HBC) (Dale and Anderson, 1978, Schandry, 1981), which requires participants 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, both within the baseline and the predictive phases, specific time intervals in which participants were asked to silently count their heartbeats (as indicated by the appearance of a red cue on the screen) to then report the number out loud (as instructed by the disappearance of the red cue on the screen) (Figure 3).

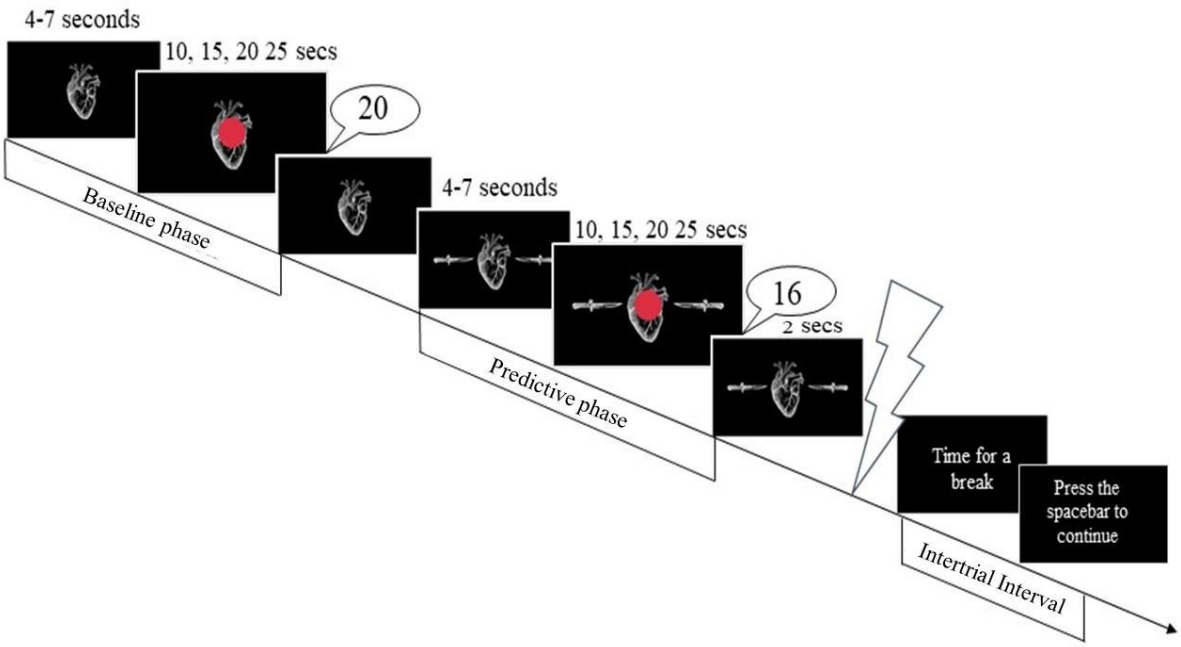

Figure 3. Trial timeline of Experiment 2. Participants are instructed to silently count their heartbeats for all intervals in which a red circle appeared at the centre of the screen. Once it disappeared, participants reported out loud the number of counted beats. In the baseline phase, they simply reported back the number of counted beats. In the predictive phase, two seconds after the disappearance of the red cue and participants had reported the number of counted beats, the cutaneous electrical stimulation was administered. After a 30-secs pause, participants were instructed to press the spacebar to proceed to the next trial.

The results fully replicated Experiment 1. First, the majority of participants (twenty-one out of twenty-four) spontaneously declared that they believed their heart rate to increase 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 (Figure 4). Relative to the baseline phase, in the predictive phase reported heartbeats increased more strongly than actually recorded ones, even though this difference failed to reach two-tailed significance (Main effect of Type of Beat, $F(1,23) = 4.227$, $p = 0.051$, $\eta p^2 = 0.155$). As in Experiment 1, expecting high-

pain vs. low-pain increased reports of both recorded and reported beats (Main Effect of Pain Expectation, $F(1,23) = 10.104$, $p = 0.004$, $\eta p^2 = 0.305$). Importantly, expecting a threatening relative to a harmless stimulus elicited different changes in the recorded compared to the perceived heart rate (Type of Beat * Pain Expectation $F(1, 23) = 6.55$, $p = 0.017$, $\eta p^2 = 0.222$, Figure 4). When participants anticipated a threat (high-pain) relative to a harmless (low-pain) event, the reported number of heartbeats increased ($t(1,22) = 3.09$, $p = 0.005$). However, this difference was not mirrored by the real cardiac state ($t(1,22) = 1.56$, $p = 0.132$).

Finally, as in Experiment 1, the likelihood of reporting such an increase in the perceived heart rate over the expectation of a threatening vs non-threatening event was not associated with participants' interoceptive accuracy, $r(1,23) = 0.16$, $p = 0.45$, nor with their levels of state-anxiety, $r(1,23) = -0.20$, $p = 0.34$), or trait-anxiety, $r(1,23) = -0.01$, $p = 0.96$) (See supplementary materials for more details).

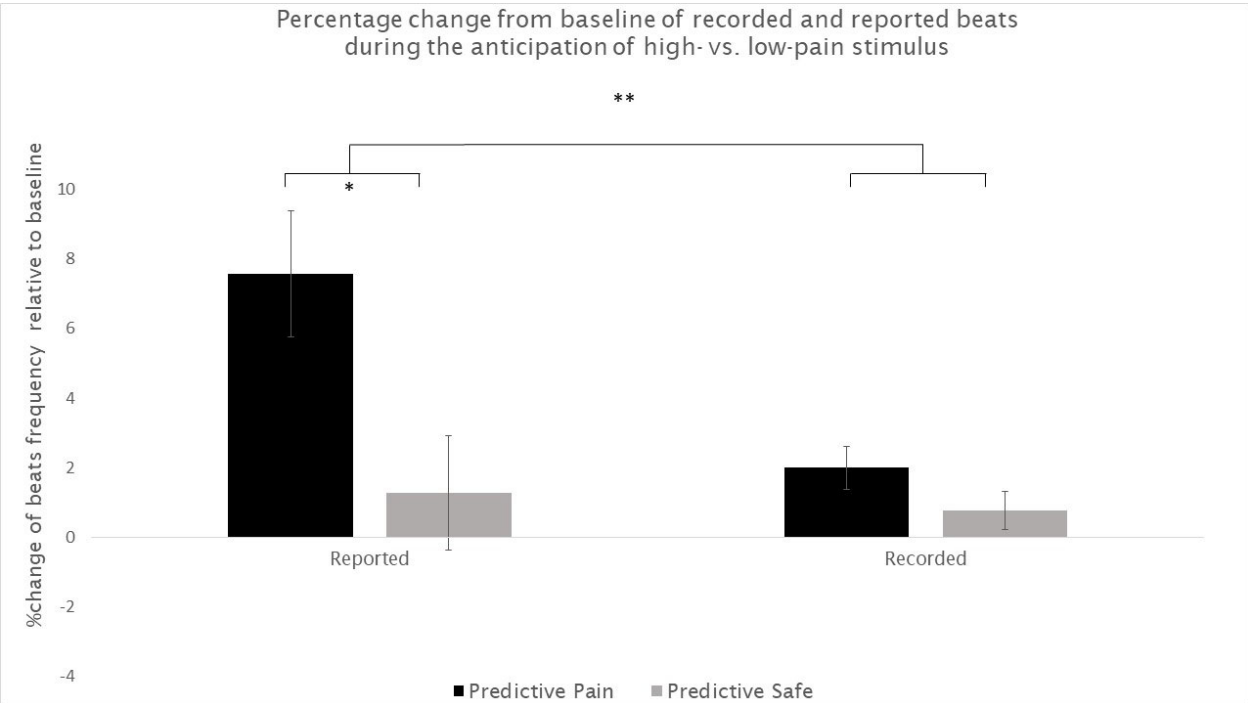

Figure 4. Experiment 2: Interoceptive Counting Task. The %change of reported (i.e., perceived) and recorded (i.e., real) beats relative to baseline, either when a threatening (i.e., high-intensity pain stimulus, Predictive Pain) or a harmless (i.e., low-intensity pain stimulus, Predictive Safe) is expected. Values

represent the percentage change in the number of beats in the predictive phase compared to the neutral baseline phase. 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. Error bars represent SEM. Asterisks indicate significant differences: * p= 0.005; ** p = 0.017.

Experiment 3

Having established that the threat of pain induced an illusory increase in perceived heart rate, Experiment 3 tested whether the same perceptual illusion would be observed if participants reported the perceived frequency of a highly similar non-interoceptive stimulus that participants would not expect to change in response to threat. Experiment 3 replicated Experiment 1 in a task in which people 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 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 specific interoceptive expectations about the response of the heart to the 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 pain stimulus) event.

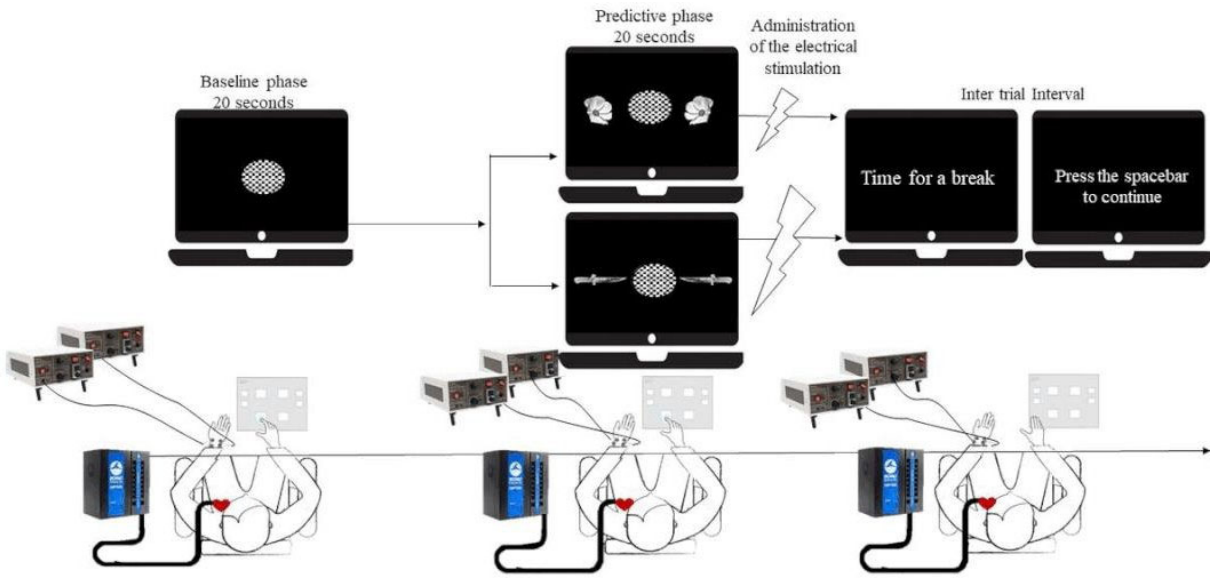

Figure 5. Trial timeline of Experiment 3. The circle appears, covered with a checkerboard. The circle pulses intermittently through the baseline and prediction phase. The prediction phase starts with the presentation of the warning cue, which signals the forthcoming threatening high- or the harmless low-intensity cutaneous stimulation (i.e., knives or flowers), while the circle keeps pulsing and participants report each pulse with a keypress.

The analysis of recorded and reported beats (Figure 6) showed that, relative to the baseline phase, the generation of the expectation did not differently modulate reported and real frequency of the exteroceptive stimulus, independently of whether participants were anticipating a high- or a low- pain stimulus (i.e. Main effect of Type of Beat $F(1,23) = 0.85$, $p = 0.35$, $\eta p^2 = 0.04$). Moreover, expecting high-pain or low-pain did not differently influence beat frequencies, neither when real nor reported (Main Effect of Pain Expectation, $F(1,23) = 0.43$, $p = 0.51$, $\eta p^2 = 0.02$). More importantly, unlike the previous experiments, the expectation of a threatening vs. harmless stimulus did not differentially affect the frequency with which the visual exteroceptive stimulus was reported compared to when it was really presented (F (1, 23) = 1.102, $p = 0.305$, $\eta p^2 = 0.046$). Anticipating a threat (high-pain) relative to a harmless (low-

pain) event, did not differently modulated the reported number of beat frequency ($t(1,22) = 0.89$, $p = 0.38$) nor the real number of visual pulses ($t(1,22) = -0.22$, $p = 0.83$)

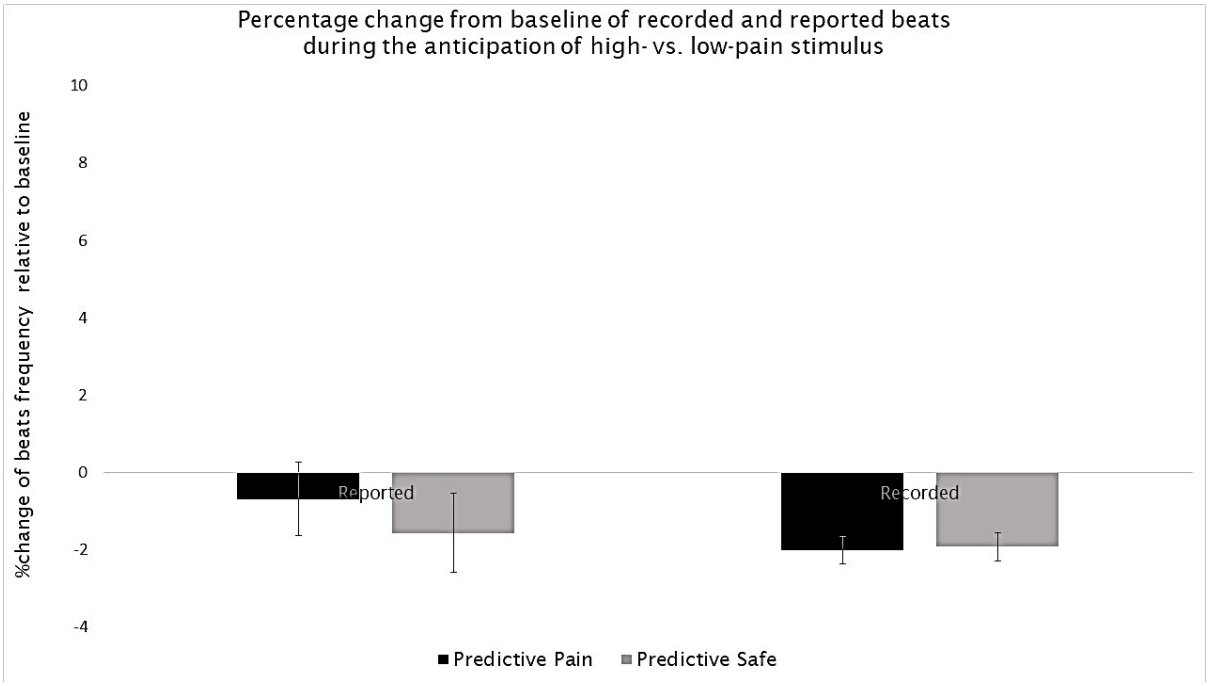

Figure 6. Experiment 3: Exteroceptive Tapping Task. The %change of reported and recorded beats (i.e., the occurrence of the visual stimulus) relative to baseline, either when a threatening (i.e., high-intensity pain stimulus, Predictive Pain) or a harmless (i.e., low-intensity pain stimulus, Predictive Safe) is expected. Values represent the percentage change in the number of beats in the predictive phase compared to the neutral baseline phase. 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. Error bars represent SEM.

It should be noted that the behavioural procedure implemented before the experiment failed at equalizing the difficulty of the interoceptive (Experiment 1) and exteroceptive (Experiment 3) tapping tasks, as shown by the significant difference in the mean accuracy between the exteroceptive tapping task in Experiment 3 ($d' = 3.10$, $SD = 0.70$) and interoceptive tapping

task in Experiment 1 (d' = 1.33, SD = 0.35) indicating that the accuracy was generally higher in the exteroceptive tapping task than the interoceptive tapping task ($t(47) = 10.979$, $p < 0.001$, $d = 3.16$). Importantly, however, there was no correlation between the individuals' magnitude of the exteroceptive illusion and their level of accuracy at the task in the baseline phase, $r(1,23) = 0.05$, $p = 0.81$, as also shown for Experiment 1, $r(1,23) = 0.20$, $p = 0.34$, and 2, $r(1,23) = 0.16$, $p = 0.45$, indicating that the uncertainty in perception did not underlie the likelihood of developing an interoceptive (Experiments 1) or exteroceptive (Experiment 3) illusion (see Supplementary materials for more details).

General Discussion

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 and Simmons, 2015; Pezzulo, 2013). Although such an internal model generally promotes an accurate estimate of bodily states, our expectations are not always correct, and should therefore sometimes lead to mis-perceptual phenomena. The present study tested whether a common false belief about the cardiac response to threats gives rise to an interoceptive cardiac illusion that is not mirrored by real heart rates.

In two experiments, we asked participants to monitor and report their heartbeat, either by tapping along to it (Experiment 1, the Heartbeat tapping task; McFarland, 1967; Flynn & Clemens, 1988; Melloni et al., 2013) or by silently counting it (Experiment 2, The Heartbeat Counting Task; Dale and Anderson, 1978, Schandry, 1981) while their ECG was recorded. Participants performed this task 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 their common (false) belief that heart rates would accelerate under threat.

Both experiments confirmed, first, that the vast majority of participants believed that their heart rate would accelerate whenever they were expecting a threatening painful stimulus. Second, they showed that these expectations were reflected in interoceptive changes when participants reported their heart rates. They reported a higher number of heartbeats – that is, they perceived a higher cardiac frequency – whenever they expected a high-intensity pain stimulus, compared to a low-intensity stimulus. This reported pattern of cardiac responses was not mirrored by the real heart rate, which was not modulated by the expectation of a threatening stimulus. Importantly, this perceived change 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). These findings 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 perceive, an illusory increase in their cardiac frequency. The likelihood of developing such an interoceptive illusion was unrelated to participants' interoceptive accuracy, nor to their degree of anxiety.

To further demonstrate that such cardiac perceptual changes were driven by interoceptive expectations, Experiment 3 tested whether changing the interoceptive stimulus to an unrelated exteroceptive stimulus would induce no such expectation-related changes. Thus, instead of monitoring and reporting each felt heartbeat, participants in Experiment 3 tapped along with a visual stimulus pulsing on the screen. We aimed at balancing the properties and difficulties of both tasks, by (1) synchronizing the frequency of the two stimuli, so that participants of

Experiment 3 watched a visual stimulus pulsing on the screen at the same frequency as the heart rate recorded from a matched participant of Experiment 1, and (2) through a preliminary matching procedure aimed at equalizing the visual accuracy of each participant in Experiment 3 to the cardiac accuracy of the matched participant in Experiment 1. As predicted, participants' perceptual judgments were not influenced by the different pain expectations in Experiment 3. They reported a similar number of visual pulses both when expecting a forthcoming threatening (i.e., high-intensity pain) vs. innocuous (i.e., low-intensity pain) event. These findings, therefore, suggest that predicting an imminent threat does not elicit specific distortions in exteroception, tying the effect to people's prior beliefs about how their heart changes in anticipation of a threat.

A potential limitation is 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, leading to higher accuracy in Experiment 3 than Experiment 1. In contrast to the substantial uncertainty in cardiac perception (Petersen et al., 2014; Khalsa et al., 2018), the visual stimulus may therefore not have been ambiguous enough to elicit a perceptual illusion. Nevertheless, it is noteworthy that participants' levels of visual accuracy did not show any correlation with the size of the perceptual illusion in either the interoceptive tasks of Experiment 1 or 2 or the visual task in Experiment 3, suggesting that the ability with which participants could detect and report either the exteroceptive or the interoceptive input was not linked to the likelihood of developing perceptual illusions.

Together, 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, 2019). This evidence represents the first step toward a broader understanding of how the brain integrates multimodal variables to infer interoceptive parameters, 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, new avenues 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 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; Powers et al., 2017; Powers III, 2016; Fletcher & Frith, 2009; Gagne, Dayan & Bishop, 2018; Series, 2019; Lissek & van Meurs, 2015).

Such stubborn predictions have been argued to be acquired either through *genetic* 'priors', representing information about the kind of world we live in (e.g., such that the body remains at the predicted temperature of ~37°C, Seth & Friston, 2016), or through a process of statistical learning of the environment (for a full discussion, see Yon et al., 2019). Embodied Predictive Coding models (Seth, 2013; Seth et al., 2012; Barrett & Simmons, 2015; Pezzulo, 2013) 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 people's first-hand experience of increased heart rates to actual, not anticipated, pain that would indeed be delivered later. If this is correct, similar mis-perceptual phenomena may occur in anticipation of everyday events that are *treated* as stressors, based on peoples' subjective estimations, 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.

To conclude, the current work highlighted for the first time how the expectation of a threatening stimulus can influence our interoceptive cardiac perception, generating an interoceptive illusion. The identification of this perceptual bias provides a fruitful area and an experimental paradigm that can serve as a platform for further work which explores neural signatures associated with predictive processes in interoception. Our results would suggest that, generally, also other interoceptive sensations that we experience in our daily life are far from being derived from the real state of the body, but they would rather reflect our interoceptive expectations and beliefs. More broadly, future research is needed to determine how such predictive mechanisms might shape other interoceptive sensations and our bodily response to them. Research in this field could produce important insights for a deeper understanding of how illusory perception of our body state might also underpin some psychological conditions (i.e., anxiety, depression), which might be understood in light of such aberrant predictions, as recently suggested by tantalizing lines of research (for a full discussion see Barrett and Simmons, 2015).

Methods

Experiment 1

Participants

Twenty-five healthy volunteers (mean age 25.7, *SD* = 4.1, 17 women) recruited from Gabriele D'Annunzio University and the wider community, participated in the study. Exclusion criteria for taking part were 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 use of drugs, as self-reported. Participants were asked to either not drink coffee or smoke cigarettes in the 60 minutes preceding the experiment. The experiment was conducted in accordance with the Declaration of Helsinki. Ethical approval from the local ethics board was obtained. Participants gave informed consent. Information about the purpose of the study was provided only after the experimental tests were completed. One additional participant was excluded from the experiment as she could not feel any unpleasant or painful sensation irrespective of the intensity of the stimulation (see Exclusion Criteria). Sensitivity analysis with G*Power 3.1 (Faul, Erdfelder, Lang, & Buchner, 2007) revealed that a sample size of 25 provides 0.80 power to detect effects with Cohen's $d = 0.58$ (SESOI of $\delta = 0.40$). Previous studies with this type of experimental paradigm in the exteroceptive modality (Hudson et al., 2016) suggest that effect sizes are most likely larger ($0.241 < \eta p^2 < 0.395$).

Exclusion criteria

Participants were excluded if their individual average of either reported or recorded beats in either condition (i.e., predictive safe vs. predictive pain) exceeded 3 SD relative to the mean of

the group in any of the four conditions. No participants were excluded based on this criterion. Moreover, participants were excluded (*n*=1) if they could not reach the desired pain threshold, demonstrating an abnormal level of sensitivity relative to the electrical stimulation.

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 (https://google.co.uk), scaled to black and white, and matched in dimension, orientation, and background color using Adobe Photoshop software. All images were set to 5906x3322 pixels at a resolution of 300 dpi. The stimulus set included (1) a neutral cue, which was a heart located at the centre of the screen, which was shown over the baseline phase, signalling to participants to start tapping, and (2) the two warning cues, appearing to the sides of the heart picture. These could be either two flowers indicating participants that they would receive a harmless - low-pain - stimulation within the trial, or two knives signalling an upcoming threatening - high-pain - stimulation.

Painful stimuli were electrical pulses delivered using a constant current electrical stimulator (Digitimer DS7A) 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 two (high- and low-intensity pain) electrical stimuli was kept fixed over the experiment and it was established during a calibration phase before the experiment.

The recording of the cardiac signal (ECG) was performed by a Biopac MP 150 system (Biopac Systems Inc., USA). ECG was recorded continuously from two electrodes attached to the lower ribs and one over the right mid-clavicle bone (reference electrode). The ECG signal was

sampled at 2 kHz with the Biopac Acqknowledge 3.7.1 software (Biopac Systems Inc., USA) according to the manufacturer's guidelines. ECG signal was then fully analysed in MATLAB. 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).

Stimulus presentation was controlled through E-Prime 3.0 (Psychology Software Tools Inc., Pittsburgh, USA) on a computer with an ASUS VH232 monitor (resolution: 1920 x 1080, refresh rate: 59 Hz), connected with the electrical stimulators and the Biopac system via a parallel port.

Questionnaires

Anxiety measures. The STAI (Spielberger et al., 1987) was developed to measure state (STAI-X) and trait (STAI-Y) anxiety. The STAI consists of two self-report subscales consisting of 20 statements each. State anxiety items include: "*I am tense; I am worried" and "I feel calm; I feel secure*". Trait anxiety items include: "*I worry too much over something that really doesn't matter*" and "*I am content; I am a steady person*". All items are rated on a 4-point scale (e.g., from "Almost Never" to "Almost Always"). Each item is scored from one to four. Total scores for each subscale range from 20 – 80. Acceptable validity and reliability have been reported for each scale in various populations (Spielberger et al., 1983, 1987).

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 through a modified version of a

validated HBD task (Couto et al., 2013; García-Cordero et al., 2016; Melloni et al., 2013; Sedeno et al., 2014; Yoris et al., 2015, 2017). Participants were given a Cedrus RB-844 response pad and were asked to tap along with either an auditory presented heartbeat (exteroceptive) or their own heartbeat (interoceptive). Participants were instructed to respond with their dominant hand, to keep their eyes on the screen, and to avoid excessive movements.The exteroceptive task provides a (control) measure of external monitoring skills. Participants were instructed to tap a keypad to follow binaurally presented heartbeat sounds, for two blocks of 2.5-min, one featuring regularly timed heartbeats and the other irregularly timed heartbeats derived from a real recording (Yoris et al., 2017). The interoceptive task provides a measure of interoceptive accuracy, namely, the subjects' performance in following their own heartbeats (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). Participants were then asked to press a key along with their own heartbeats without any external cues, again in two 2.5-min blocks.

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. Participants were comfortably seated with their left hand placed on a table. Before the electrodes were placed, the skin was cleaned with a skin prep to reduce impedance. The calibration of pain stimuli was conducted using the method of limits psychophysical approach. Current (pulse duration 2 ms) intensity was set at an initial value that is below the threshold for pain perception in most people. The 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 could 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 each stimulation (high- and low- pain stimuli), participants were instructed about the experiment proper. Participants were informed that over the experiment, their task would be similar to what they just did, namely, 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 or by 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. 2). The ECG was recorded while participants kept tracking their heartbeats and reporting them through the keypad press.

Each trial started with the presentation of a neutral cue appearing on the screen for 20 seconds, providing a *baseline phase* for each trial. 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. Depending on whether the image 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 heartrate in this phase. After 20 seconds of this *predictive phase*, the warning cue disappeared and 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 comprised 20 trials, with four additional catch trials. In these catch trials, the electrical stimulation was delivered either after 8 or 12 seconds from the onset of the warning cue, that is, before the typical end of the tapping task. These trials were not analysed and mainly served to create uncertainty over the time interval when the shock would be administered.

At the end of the experiment, we collected subjective reports of each participant, where we asked them how they believed their heartbeat to vary in relation to the expectation of a threat, as well as in response to a painful stimulus. Participants also completed the State-Trait Anxiety Inventory (STAI) and filled out a brief questionnaire aimed at collecting their beliefs about the hypotheses of the study.

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 changes when expecting a forthcoming low- and high- painful stimuli. 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 in order to obtain a "baseline frequency value" and a "prediction frequency value". We then calculated, for each trial, the percent change in beat frequency from the 20s baseline phase to the 20s prediction phase, for the reported and recorded beats separately (i.e, % change of frequency = (frequencyPREDICTION - frequencyBASELINE)*100 / frequencyBASELINE). This allowed us to extract, for each participant, the mean % change of frequency, averaged across trials, when a low-pain stimulus was expected or when a high-pain stimulus was predicted, for both reported and recorded beats. Analysis was conducted on these values, which provided a directional measure of whether the generation of the expectation of a threat or a harmless event, relative to a neutral phase, elicited a decrease or increase in the frequency of either reported or recorded beats. No change in the predictive phase relative to baseline would produce a value of 0. Positive and negative values denote an increase or a

decrease in the beats' frequency, respectively.

Each participant's percentage change in beat frequency relative to baseline was entered into 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. The main effect of Type of Beat will reveal to what extent real and reported heartbeats to diverge in the prediction phase (relative to the baseline phase). The main effect of Pain Expectation will reveal whether expecting a threatening or a harmless event modulates heartbeats. Finally, interactions of Pain Expectation and Type of Beat will reveal whether expecting painful vs harmless stimulation affects recorded and reported heart beats differently, that is, whether expecting painful (relative to harmless) stimulation increases a cardioceptive illusion of perceived heart rates that is not reflected in real (recorded) heartbeats.

Experiment 2

Participants

Twenty-four healthy volunteers (mean age 25.41, SD = 4.31, 16 women) recruited from Gabriele D'Annunzio University and the wider community participated in the study after written informed consent was obtained. Participants were asked to either not drink coffee or smoke cigarettes in the 60 minutes preceding the experiment. Sensitivity analysis with G*Power 3.1 (Faul, Erdfelder, Lang, & Buchner, 2007) revealed that a sample size of 24 provides 0.80 power to detect effects with Cohen's $d = 0.59$ (SESOI of $\delta = 0.41$). Two additional participants were excluded from the experiment. One additional participant was excluded due to sub-standard performance (see *Exclusion Criteria*). Another was excluded because of missing data. Information about the purpose of the study was provided only after the experimental tests were completed. The experiment was conducted in accordance with the Declaration of Helsinki. Ethical approval from the local ethics board was obtained.

Exclusion criteria

Exclusion criteria were identical to Experiment 1. Participants were excluded (*n*=1) if their individual average of either reported or recorded beats during both conditions (i.e., Predictive Safe vs. Predictive Pain) exceeded 3 SD relative to the mean of the group for each of the four conditions (i.e., average of perceived beats over predictive pain/safe condition, average of recorded beats over predictive pain/safe condition). Moreover, participants were excluded if they could not reach the desired pain threshold, demonstrating an abnormal level of sensitivity relative to the electrical stimulation.

Apparatus and Stimuli

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

Procedure

Participants were received and briefed by the experimenter, gave their consent, and proceed to the montage of the ECG, once their skin was cleaned. As in Experiment 1, participants' cardiac interoception was assessed at rest, through a modifiedversion of the Heartbeat Counting Task (Dale and Anderson, 1978, Schandry, 1981). Each trial started with a neutral visual cue presented on the screen. Participants were instructed to start silently counting their own heartbeat once a visual start cue (a red circle appearing on top of theneutral image) appeared, until its disappearance. After a brief training session (15 s), the actualtask started. It consisted of six different time intervals of 10, 15, 20, 25, 35, 40, and 45 s, presented in a random order across participants. Participants were asked to rate verbally the number of heartbeats counted at the end of each interval. The experimenter annotated, for eachtrial, the number of counted beats. Throughout, participants were not permitted to take their pulse, and no feedback on the length of the counting phases or the quality of their performancewas given.

After completing this task, participants underwent the same psychophysical procedure as in Experiment 1 to determine, for each participant, the low- and high- intensity pain stimulus that

would then be administered over the experiment. Once the intensity of high- and low-stimulations were established, participants were instructed about the experiment proper.

Participants were informed that, over the experiment, they would be exposed to different levels of intensity of the cutaneous electrical stimulation, administered through the electrodes previously attached to their wrist, as established over the calibration procedure. They were also informed that their task over the experiment was to silently count their heartbeats and report the number out loud over different time windows, marked by the appearance and disappearance of a red circle presented at the centre of the screen. Importantly, this start visual cue appeared over two different experimental phases, that is, a baseline phase - wherein a neutral image was presented on the screen - and a predictive phase – wherein, depending on which of two warning visual cues (i.e. Predictive safe warning cue vs. Predictive pain warning cue) was shown on the screen, they could predict the intensity of the upcoming electrical stimulation (Figure 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 vary the duration of the time intervals participants had to count for. In contrast to the key presses in Experiment 1, constant time intervals would create the danger that participants would learn the counts they reported and simply memorize and repeat these counts in subsequent trials, instead of counting their actual heartbeats.

In each trial, the neutral cue was presented first. After a randomly selected time window (4, 5, 6, or 7 seconds), a red circle appeared on top of the neutral cue, instructing participants to silently count their heartbeats. The counting time window (presentation of the red circle) could last for 10 s, 15 s, 20 s, and 25 s (randomly selected for each trial). Once the red cue disappeared, participants reported out loud the number of counted beats, and the experimenter noted it down. In the baseline phase, the neutral cue remained on the screen for a randomly selected amount

of time (3, 9, 15, and 21 seconds), based on the previous amount of time allocated to the counting time window (the baseline phase always lasted 35 seconds totally). Then, the warning cue appeared. Depending on whether knives vs. flowers were presented, participants could generate a reliable expectation of the upcoming high- or low-intensity cutaneous electrical stimulation. After a randomly selected time interval (4, 5, 6, or 7 seconds), the red circle (i.e., start visual cue) appeared again on top of the warning cue, informing participants to silently count their heartbeats. Analogously to the neutral baseline phase, the red circle could be presented for 10 s, 15 s, 20 s, and 25 s (randomly selected for each trial). Then, the red cue disappeared instructing participants to report out loud the number of counted beats. After the red cue disappeared, the warning cue remained on the screen for 2 seconds, giving participantsnenough time to tell the experimenter the number out loud. After that, the electrical cutaneous stimulation was delivered, marking the end of the trial.

Between trials, a pause screen was shown for 30 seconds, in order to enable participants to recover from the electrical stimulation and 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 comprised 16 trials. No catch trials were needed and included in Experiment 2, as the length of the time windows over the predictive phase was different in each trial.

As in Experiment 1, at the end of Experiment 2, participants completed the State-Trait Anxiety Inventory (STAI) and filled out a brief questionnaire aimed at collecting their beliefs about the hypotheses of the study and a subjective report of their expectations about their heartbeat variation in relation to the expectation of a threat, as well as in response to a painful stimulus.

Data Analysis

As for Experiment 1, data analysis was conducted by extracting, for each participant and each of the two phases (baseline phase, prediction phase), the number of reported and recorded beats.

These counts were transformed into frequency, separately for the baseline and the predictive phases. The frequency of recorded and reported beats were computed for the whole time window, starting with the presentation of the red cue and terminating with its disappearance, both for the predictive and baseline phase, respectively. Like in Experiment 1, the percentage change of frequency was then calculated for each individual trial (i.e., % signal change = (frequencyPREDICTION - frequencyBASELINE)*100 / frequencyBASELINE), and averaged across conditions. Data analysis was conducted on individual %change of frequency values, which provided a directional measure of whether the expectation of a threat or a harmless event, relative to a neutral phase, elicited a decrease or increase in the frequency of either reported or recorded beats. No change in the predictive phase relative to baseline would produce a value of 0. Positive and negative values denote an increase or a decrease in the beats' frequency over the predictive phase relative to the baseline, respectively. Each participant's % change in beat frequency values was then entered into a 2 x 2 repeated measures analysis of variance (ANOVA), with Type of Beat (Reported vs. Recorded) and Pain Expectation (Pain vs. Safe) aswithin-participants factors. As a replication of Experiment 1, we expected perceptual judgments to be shaped towards the expectation of an increased heart rate during the anticipation of a threat.Participants should then *report* a higher number of beats when they are exposed to cues that threaten a high-intensity pain stimulus (i.e., Predictive Pain warning cue), relative to when they are expecting a low-intensity pain stimulus (i.e., Predictive Safe warning cue). Moreover, we expect this effect to be reduced for the recorded beats, as these biases should represent perceptually instantiated expectations and not a reflection of the real cardiac state. Interactions with Type of Beat will therefore reveal whether the expectation of a threatening stimulus induces a modulation uniquely in the real (i.e., Recorded Beats) or in the perceived (i.e., Reported Beats) cardiac state.

Experiment 3

Participants

Twenty-four healthy volunteers (mean age 25.9, SD = 3.6, 16 women) recruited from Gabriele D'Annunzio University and the wider community participated in the study after written informed consent was obtained. Exclusion criteria were 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 use of drugs. Participants were asked to either not drink coffee or smoke cigarettes in the 60 minutes preceding the experiment. Two additional participants were excluded due to sub-standard performance based on the study exclusion criteria (see Exclusion Criteria). Sensitivity analysis with G*Power 3.1 (Faul, Erdfelder, Lang, & Buchner, 2007) revealed that a sample size of 24 provides 0.80 power to detect effects with Cohen's d = 0.59 (SESOI of $\delta = 0.41$). Information about the purpose of the study was provided only after the experimental tests were completed. The experiment was conducted in accordance with the Declaration of Helsinki. Ethical approval from a local ethics board was obtained.

Exclusion criteria

As in previous experiments, participants were excluded if their individual raw average of either reported or recorded beats during both conditions (i.e., safe vs. pain) exceeded the mean of the group for each of the four conditions by 3SD. Moreover, participants were excluded if, during the behavioural procedure, they did not manage to reach a level of visual accuracy that matches their counterpart participants in Experiment 1 after 20 trials of behavioural procedure (n=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) that have been modified to adjust the design for the exteroceptive nature of the stimulus. The visual stimulus was a circle drawn with Adobe Photoshop (3.30 cm) that pulsed intermittently at the centre of the screen and overlapped by a black-and-white squared checkerboard (6 cm x 6 cm) gathered from Google Images (https://google.co.uk). In order to create different difficulty levels, the brightness of the circle varied from the 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) (Figure 7).

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 who took part to the interoceptive tapping experiment (Experiment 1). Therefore, the individual level of participants' visual accuracy varied between participants of the exteroceptive tapping task but should be equal to the interoceptive accuracy of the previous group, measured at rest, before

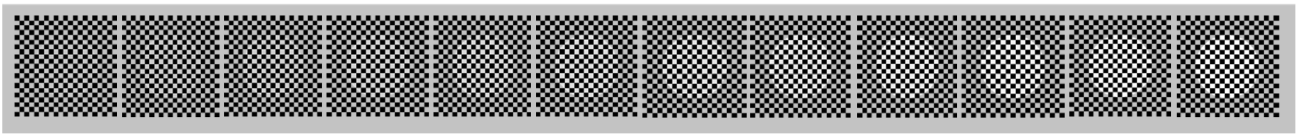

Figure 7. Set of stimuli used in the behavioural phase. Each level of difficulty, associated with a different RGB code of the stimulus, is illustrated. From the left, the circle with the lowest RGB code values is shown (200,200,200), until the right, where the highest RGB code of the stimulus (255,255,255) 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 circle appeared for 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 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 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 then intended to be equal to each participant's interoceptive accuracy ± 1SD (i.e., if the interoceptive accuracy over the entire interval was d' = 1.32 and the SD was 0.078, 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.

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. 5), 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 eachappearance 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 (Figure 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.

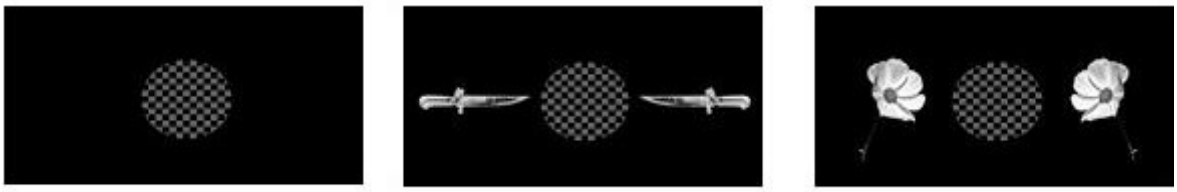

Figure 8. Set of stimuli used in Experiment 3. From the left, 1) The neutral cue that indicates to participants to get ready to start the visual tapping task (i.e., baseline phase) 2) The predictive pain warning cue, that indicates to participants that they will receive the high-intensity cutaneous stimulation 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 showna screen with the instruction to press the spacebar, whenever they were ready to start the next trial (see Figure 5, trial timeline).

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 16.67% 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.

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 frequency was then calculated for each individual trial and each phase (baseline, predictive) separately (% signal change = (frequencyPREDICTIVE - frequencyBASELINE)*100 / frequencyBASELINE). 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 Pain 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 Pain Expectation. Effect sizes and p-values are reported for crucial two-sided tests using JASP software (JASP Team, 2018).

As in Experiment 1, accuracy scores were estimated for each participant based on Heartbeat Detection Task outcomes via signal detection (Thomson et al., 2005), as validated by previous studies (Fittipaldi et al., 2020; Gonzalez Campo et al., 2019). To test whether the difficulty of the exteroceptive (Experiment 1) and the interoceptive (Experiment 3) tapping task was

balanced, a t-test was run between participants' mean accuracy displayed in both tasks only over the experimental baseline phases. The mean accuracy in the experiment was, as for the previous experiments (1) compared over the different experimental phases (Baseline, Predictive Pain, Predictive Safe), to evaluate how the expectancy may affect participants' ability to monitor and report external stimuli, (2) correlated with the size of the potential exteroceptive illusion.

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