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RESEARCH ARTICLE

Sensory Processing

Sensitivity to changes in rate of heartbeats as a measure of interoceptive ability

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Abstract

Individuals vary in their ability to perceive, as conscious sensations, signals like the beating of the heart. Tests of such interoceptive ability are, however, constrained in nature and reliability. Performance of the heartbeat tracking task, a widely used test of cardiac interoception, often corresponds well with individual differences in emotion and cognition, yet is susceptible to reporting bias and influenced by higher-order knowledge, e.g., of expected heart rate. The present study introduces a new way of assessing cardiac interoceptive ability, focusing on sensitivity to short-term, naturalistic changes in frequency of heartbeats. At rest, such heart rate variability typically reflects the dominant influence of respiration on vagus parasympathetic control of the sinoatrial pacemaker. We observed an overall tendency of healthy participants to report feeling fewer heartbeats during increases in heart rate, which we speculate reflects a reduction in heartbeat strength and salience during inspiratory periods when heart rate typically increases to maintain a stable cardiac output. Within-participant performance was more variable on this measure of cardiac interoceptive sensitivity relative to the “classic” heartbeat tracking task. Our findings indicate that cardiac interoceptive ability, rather than reflecting the veridical monitoring of subtle variations in physiology, appears to involve more interpolation wherein interoceptive decisions are informed by dynamic working estimates derived from the integration of afferent signaling and higher-order predictions.

NEW & NOTEWORTHY This study presents a new method for evaluating cardiac interoceptive ability, measuring sensitivity to naturalistic changes in the number of heartbeats over time periods. Results show participants have an overall tendency toward sensing fewer heartbeats during higher heart rates. This likely reflects the influence of changing heartbeat strength on cardiac interoception at rest, which should be taken into account when evaluating cardiac interoceptive ability and its relationship to anxiety and psychosomatic conditions.

heart rate variability; interoception; metacognition; psychophysics

INTRODUCTION

Biological activity in both brain and body, as hosts of our minds, supports and shapes psychological processes. A continuous stream of information from the body informs the brain about our current and changing state physiological functioning and of physical integrity, often independently of immediate perceptual awareness (1). Interoception describes the sense through which signals originating from within the body, especially its visceral organs, are carried, represented, integrated, and interpreted within the nervous system, across unconscious and conscious levels (2). Interoception is essential to the regulation of the internal milieu of the body, conveying to the brain the feedback that informs reflexive homeostatic control and allostatic adaptation (3, 4). Interoception thus encompasses a multidimensional spectrum of signal processing, from physiological responses and their proximate neural representations, to the perception and awareness of these interoceptive signals and associated feelings (2, 4, 5). Overall, discrete interoceptive signals are rarely

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consciously accessible (2). For exteroceptive sensations (e.g., somatosensory touch acuity), an individual's self-report, or discriminatory accuracy is tightly coupled to subjective confidence in the perception (6). In contrast, for interoception, measures of perceptual accuracy vary across interoceptive axes and between individuals, corresponding loosely with subjective ratings of confidence or experience (e.g., in questionnaire reports of interoceptive sensitivity). On experimental tests of interoceptive ability, e.g., heartbeat detection tasks, the correspondence between trial-by-trial accuracy and confidence can be quantified mathematically as interoceptive metacognition (insight). This metacognitive index also often diverges from measures of interoceptive task accuracy (7).

In addition to its critical role in physiological regulation (1, 8), interoception is implicated in normative emotion responses (9–12), and the expression of specific clinical symptoms, including those of anxiety (6, 13). In the present study, we sought to optimize the reliability of measuring interoceptive ability across individuals and populations. Our approach aimed for a more comprehensive understanding of how and why measures of interoceptive accuracy deviate from subjective and metacognitive measures of insight, with further implications for emotion and embodied cognition.

Cardiac Interoception Tasks

The cardiac signal (i.e., the heartbeat coincident with ventricular systole) stands out as a repetitive and discrete physiological event, allowing it to be recorded with some precision (14). Moreover, heartbeats are vital and salient; their frequency and strength changes with emotion and action, when they can breach the threshold for conscious perception and contribute to affective feelings. Consequently, interoception research has tended to focus on the heartbeat. The heartbeat tracking (HBT) task, conceptualized by Schandry (15), is a relatively straightforward procedure. Based on the notion that some people have greater sensitivity than others to their heartbeats, the task aims to quantify interoceptive ability from how well an individual can detect their own heartbeats at rest. The participant focuses attention on his/her heart and counts the number of heartbeats felt within given time periods (without directly palpating a pulse or using other external strategies). Performance is generally calculated as the error rate between reported and actual number of heartbeats (15). One alternative cardiac interoception task, similarly motivated, is the heartbeat discrimination (HBD) task (16, 17). This task also requires an interoceptive focus at rest; on individual trials, which consist of runs of heartbeats, the participant judges if a phasic exteroceptive stimulus (e.g., auditory tone or flashing light) is played either synchronously or delayed with respect to each heartbeat. Synchronicity judgements over repeated trials allow computation of performance accuracy, e.g., the percentage of correct trials, or as d'. The HBT and HBD tasks have dominated approaches to measure individual differences in cardiac interoceptive ability/accuracy, which has been presumed to be a relatively stable constitutional trait. Both tasks carry face validity, reinforced by well-documented links to other cognitive and emotional factors (6, 13, 18–21). Previous studies have investigated cardiac interoception through respiration-induced changes in cardiac activity, such as during slow breathing rhythms (22, 23), breath-holding (24), as well as altered cardiac and breathing sensation through bolus isoproterenol infusions (25). This study, however, aims to investigate cardiac interoceptive ability in the context of resting-state cardiovascular activity.

Limitations of Current Cardiac Interoception Tasks

Despite wide use, both the HBT and HBD tasks are not without controversy. Specifically, performance accuracy in the HBT task is influenced by levels of general intelligence, and relatedly by prior knowledge of one's heart rate (14, 26–30). Thus, performance accuracy scores may track average heart rate rather than simply the veridical number of heartbeats within individual trials (31, 32). Furthermore, although the HBT task was designed as a measure of resting cardiac sensitivity, the reported number of heartbeats is observed to remain fairly constant across conditions (such as postural change) that evoke changes in heart rate: e.g., when the participant is lying down, sitting, or standing (33). Similarly, one study provided preliminary evidence to suggest that changes in heart rate induced by an implanted pacemaker did not reliably change patients' reported number of heartbeats on the HBT task (34).

Another point of contention is that, when performing the HBT task, people overall tend to underreport their number of heartbeats, and high accuracy scores thus appear to be, in part, related to a bias toward reporting a higher number of felt heartbeats (31, 32). Since weak and diffuse interoceptive sensations (including heartbeats at rest) are generally not felt unless attention is focused and distraction removed, underreporting is perhaps expected. People are overall likely to fail to register some heartbeats even when attending to the inherently noisy cardiac signal (35). However, it has also been argued that the tendency of participants to under- or (less commonly) overreport heartbeats by itself does not reliably predict HBT task performance (36). In contrast, successful completion of the HBD cannot be guided by higher-order knowledge of heart rate. However, this task is inherently more difficult, requiring multimodal integration of interoceptive and exteroceptive information, thus utilizing other processes (including general intelligence) in addition to interoception (7). HBD performance typically divides populations bimodally (some that can and most that cannot do the task), hence larger number of trials are needed for more fine-grained stable measures of individual differences (37), limiting its application.

Despite such criticism, these HBT and HBD interoceptive tests remain widely used. Interoceptive accuracy, as measured through the HBT task shows high test-retest reliability across time (38). HBT performance is also repeatedly shown to predict measures of cognition and emotion that fit with a priori theory-driven hypotheses (39). However, despite heuristic value and ease of implementation, HBT task limitations cannot be ignored.

Novel Interoceptive Task and the Cardiac Signal

The present study aimed to develop a new technique to assess individual differences in interoceptive ability. We based our approach on the established HBT protocol, but our aim was to separate genuine discriminability from reporting bias. We applied a new analysis strategy that focused on sensitivity to changes in the number of heartbeats between (shorter) trials. A healthy heart does not beat at an unchanging pace, but instead manifests natural rhythmic fluctuations, such that the cardiac interbeat intervals change continuously over time. These changes, known as heart rate variability (HRV), arise from the dynamics of homeostatic regulation that work to maintain stable cardiac output in response to changing conditions (posture, action, emotion) and metabolic demand. HRV is proximately regulated through the baroreflex, where fluctuations in heart rate are matched with changes in blood pressure to maintain stable cardiac output (40). In short, stronger cardiac higher-pressure ejection of blood into the aorta and carotid arteries cause arterial baroreceptor to discharge. This signal, conveyed to brainstem, triggers compensatory vagal parasympathetic slowing of the subsequent heartbeat. Conversely, a weaker arterial baroreceptor signal, indicating lower ventricular ejection pressure, permits acceleration of the subsequent heartbeat (41–43). Thus, there is a constant interplay between heartbeat strength in terms of blood pressure and cardiac ejection on the one hand and heart rate on the other. The mechanical effect of breathing helps contribute to these changes and dominates variability in resting heart rate measures: inspiration results in decreased pleural pressure as the chest expands and increased abdominal pressure, which together lower right atrial pressure facilitating venous return to the right heart. Left ventricular stroke volume decreases due to increase in pulmonary blood volume, lowering stroke volume and aortic blood pressure (44). The baroreflex causes a decrease in vagal parasympathetic drive that evokes an increase in heart rate to maintain overall stable cardiac output (45, 46). These respiration-related changes in heart rate and strength of heartbeats (ejected blood pressure) cause the heart rhythm naturally fluctuate, giving rise to the naturally occurring HRV, dominated by respiratory sinus arrhythmia (47). In contrast, in nonrest states of cardiovascular arousal, evoked by exercise or a variety of stressors, the baroreflex is suppressed, inhibiting vagal parasympathetic outflow and disinhibiting sympathetic cardiovascular drive to enable heart rate, stroke volume, and blood pressure to rise together.

Natural changes in HRV occur over the course of trials of the standard HBT task, with the aforementioned beat-by-beat fluctuations in heart rate as well as heartbeat strength through fluctuations in cardiac output and blood pressure. If an individual is particularly sensitive to individual heartbeats, then this sensitivity will be closely mirrored in performance, i.e., the reported number of heartbeats experienced over different time-intervals. A participant may also be sensitive to their heartbeat, but may be tracking the strength of individual's heartbeats; as cardiac strength can decrease with an increase in HRV, this could give rise to "counterintuitive" reports of a decrease in heartbeats as more heartbeats occur. In contrast, if the individual is less sensitive to feeling their own heartbeats, or interpolates across fluctuations in interbeat variability to produce a number that approximates more to their average heart rate, then the report will be more consistent over trials when compared with veridical tracking of individual heartbeats in the context of HRV.

Hypothesis

As preregistered (https://osf.io/vz35q), we hypothesized that participants with high interoceptive sensitivity, hence greater sensitivity to changes in the number of heartbeats, can be identified through the slope of a linear regression of reported beats against actual beats per minute (heart rate) across trials of a modified HBT task. Crucially, this task indexes interoceptive sensitivity as a function of cardiac counting speed change in relation to change in heart rate due to natural fluctuations at rest. Specifically, sensitivity to changes in heartbeats was operationalized as a slope significantly different from zero and we predicted that this slope could either be negative or positive.

Standard measures of cardiac interoception are based on indexing heartbeat detection during "rest" (i.e., nonexercise or similar arousal states) on the presupposition that each heartbeat is equal in strength. This leads to the supposition that an increased number of heartbeats would be reported as "felt" with increasing heart rate at rest. Such a prediction would be reflected in a positive slope in the relationship between heart rate and sensed heartbeats. In contrast, a negative slope would still indicate a sensitivity to heart rate, but a sensitivity that itself varies reliably with heart rate through a reduced ability to detect heartbeats during increases in naturally fluctuating HRV at rest. This could potentially reflect a reduced salience of individual heartbeats arising as a consequence of relatively weaker heartbeats (that are more difficult to detect) at higher heart rates induced by resting HRV. The detectability of heart rate may depend on the blood pressure (48). The volume of blood pumped per unit time (cardiac output) will depend on the pressure at which it is pumped and the heart rate. Thus, in the homeostasis of cardiac output, heart rate and pressure are traded against each other. This may introduce (over small time periods) a negative intraindividual correlation between heartbeat detection and heart rate under resting conditions.

The estimate of the raw slope is not biased by restrictions in range, that is, variations in HRV will not affect the expected magnitude of the slope (though the standard error of the slope will be larger, the smaller the range). It is only the ability to discriminate heartbeats at different heart rates that will lead to a nonzero slope. An ideal slope would be 1, which means the reported heart rate on average matches actual heart rate for every heart rate. Given noise, a sample of measurements from a population slope of 1 could yield an estimate either a bit more or a bit less than 1, of course. A systematic slope greater than 1 may arise if hypothetically a person treated different phases of the cardiac cycle as separate heart beats. Bias in reporting (i.e., a tendency to give high or low numbers regardless of the actual heart rate) will affect the intercept of the raw regression (as well as the mean reported heart beat). A perfect judgment would be represented as a slope of 1 and an intercept of 0, whereas an intercept greater or lower than 0 would indicate a tendency to over- or underestimate their number of heartbeats, respectively.

To summarize, both a strong positive and a negative slope would indicate sensitivity to heart rate change. A positive slope would suggest participants track the amount of individual heartbeats, where an increase in counting speed corresponds to an increase in the rate of individual heartbeats. A negative slope would indicate that participants might be sensitive to another physiological index, such as heartbeat strength, manifesting as a decrease in counting speed with an increase in heartbeats due to, for example, "weaker, faster heartbeats" at rest. Finally, a slope of 0 would indicate no/poor heart rate sensitivity, where participants' reports of heartbeats would have no meaningful relationship to changes in heart rate.

METHODS

Participants

A total of 100 participants (76 females) between the age of 18 and 33 yr (mean = 23.01, SD = 3.73) were recruited for the experiment. Participants had a mean body mass index (BMI) of 22.52 (SD = 3.51), and 85 were right-handed. Inclusion criteria included no history of neurological, psychiatric, or heart conditions, and not being on any psychoactive or asthma medication. The participant number was estimated based on a power analysis of pre-existing data that determined the minimal standard error needed to achieve moderate evidence (Bayes factor) for *H1* over *H0* (see APPENDIX A). Baseline physiological data were missing from two participants due to corrupt saving of files, and another three were excluded due to too much noise and movement artifacts within physiological recordings. This resulted in useable baseline data from 95 participants. All participants gave their written informed consent. The study was reviewed and approved by the University of Sussex Sciences & Technology Cross-Schools Research Ethics Committee.

Materials

Electrocardiogram (ECG) recording used CED hardware and software (Cambridge Electron Design, Cambridge; 1408 signal converter and 1902 amplifier, with software Spike2 v. 7.18). The ECG signals was sampled at 1,000 Hz. R-waves were identified via an interactive threshold in the Spike2 software recording. Data analysis was undertaken in the R environment, v. 4.0.2 (49), and MATLAB R2020a (The MathWorks, Inc., Natick, MA); task scripts were programmed and run in Python (v. 2.7.16). Baseline heart rate and noninvasive instantaneous blood pressure recordings were made using a Finometer (Finapres Medical Systems, Model 1 v. 1.01, Amsterdam, The Netherlands) using a finger cuff; analysis of beat-to-beat blood pressure, with accompanying software BeatScope Easy (v. 02.10 build 004, Finapres Medical Systems, Amsterdam, The Netherlands), was used to extract recorded data.

Experimental Procedure

Novel HBT procedure optimized for sensitivity to heartbeat change.

To test the main hypothesis of sensitivity to changes in heartbeats, each participant completed a modified heartbeat tracking (HBT) task, which we had optimized for slope analyses (described in the section *Novel Interoceptive Task and the Cardiac Signal*) measuring changes of number of counted heartbeats as a function of resting HRV. Each participant sat in front of a computer screen with a straight back and both feet on the floor with arms relaxed. The participant was instructed to pay attention to their heart and count heartbeats, without using their hands or other means to feel their pulse that might affect their performance. In the interoceptive condition, each trial started with a clear auditory signal, where the participant was required to close their eyes and start silently count felt heartbeats. After a set period of time (of which 80% of all trials were 20 s in duration, 10% were 18 s, and 10% were 22 s, randomly intermixed), another clear tone was played, marking the end of the trial. The participant then opened their eyes, to report: *1*) how many heartbeats they counted, and *2*) how confident they were that their report was correct, rated on a four-point confidence scale with accompanying descriptions: Level one was "I did not sense my heartbeats; I am completely guessing about the number of beats"; level two was "I sensed something about my heart, but I had no idea what I was counting, and I have no confidence at all in my counting"; level three was "I sporadically or faintly picked up on my heartbeat; my counting is based on something, but it may be off by a small margin"; and level four was "I clearly sensed my heartbeat, and have full confidence in my count." In an exteroceptive condition, the participant was instructed to count how many faint auditory tones were being played through the speakers over the course of individual trials of equivalent length to the interoceptive condition. The participant then rated their confidence (similar to the interoceptive condition). For the purpose of adjusting the within-individual difficulty of the exteroceptive task to the interoceptive task, the volume of the tones was adjusted through an active staircase procedure, where the difficulty of the exteroceptive task was calculated as 1 − error rate between reported and actual number of stimulus occurrences (i.e., number of heartbeats or played tones). Across participants, the interoceptive and exteroceptive conditions were presented in an alternating order across a total of 12 blocks (with 6 for each condition), with the first condition being randomly picked for each participant. Each block contained 10 trials, for a total of 120 trials (with 60 trials for each condition). This modified HBT task took ~60 min to complete. Each participant started the task with a short training block consisting of the exteroceptive condition that served both to familiarize participants with the task, and to staircase the exteroceptive task difficulty to a level where participants had an initial hit-rate of ~70% (between 55% and 85%) through the staircasing procedure described earlier in this section. The training block continued until a hit-rate of between 55% and 85% had been maintained for two consecutive trials, for a maximum of 20 trials.

Within the modified HBT task, the average task duration of 20 s was used as it allows for ~4 compete respiratory cycles given that human adults breathe at around 12 breaths/min while at rest (50), with some variance given when in the respiratory cycle each trial started. The slight trial duration variance of ±2 s in 20% of the trials being used to keep the duration somewhat unpredictable to discourage participants from reporting a static number of heartbeats for all trials and instead try to report on their actual number of heartbeats.

HBD task.

In addition to the modified HBT task, a subset of participants (n = 47) also completed the heartbeat discrimination (HBD) task, where an external tone is presented synchronously or asynchronously to the participant's own heartbeats. This was done as an exploratory test to investigate how well our modified HBT task aligned with the HBD task. All 47 participants performed the HBD task on the same day, immediately after the main HBT task. For each trial, an externally generated tone was played 10 times, triggered by the ECG R-wave. In the synchronous condition, the tones were presented ∼250 ms after the R-waves (at early systole, approximately at the ECG T-wave and the ventricular ejection period, when the heart is beating). In the asynchronous condition, the tones were presented ∼550 ms after the R-waves (late diastole, between heartbeats). At the end of each trial, the participant was required to judge whether the tone was presented synchronously or asynchronously with their heartbeats via a button press response, and then report how confident they are in their report on a four-point confidence scale (as used previously). The synchronous and asynchronous conditions were presented in a randomized order, with 30 trials per condition, for a total of 60 trials. The HBD task took ∼15 min to complete. The number of trials was determined based on a power analysis on pre-existing data (see APPENDIX A).

Baseline physiological measures.

To obtain a baseline measure of cardiovascular activity to compare to explore how they affect modified HBT task performance, each participant also went through a baseline physiological recording period before the heartbeat perception tasks, during which heart rate and beat-to-beat blood pressure were monitored using a Finometer measuring arterial pressure through a finger cuff connected to the intermediate phalanx of the left middle finger in turn connected to a height correction unit. Specifically, this was informed by an "active stand" autonomic test procedure with concurrent noninvasive beat-to-beat monitoring of arterial blood pressure: The participant rested in a sitting position for approximately 2 min before the recording started. In the first stage (prestand) of the baseline recording, the participant was asked to lie back in a supine position and relax and try not to move while heartbeats and blood pressure was measured for 5 min. In the second stage (poststand) after 5 min of recording, the participant was asked to stand upright and face the wall, and stand still for another 3 min. After 3 min had passed, the recording ended and the Finometer wrist and finger cuffs were removed. This baseline physiological data was used for estimating each individual's baseline physiology and reactivity of the autonomic and cardiovascular systems to physiological influences with postural change.

Preprocessing

All ECG recordings from the tasks were visually inspected for signal noise resulting from electrical interference, movement artifacts, or equipment failure. This stage also enabled detection of any extrasystole ectopic beats. Inspection was performed by a trained researcher. Trials where the ECG R-waves could not be discerned from signal noise were excluded from all following analyses. For the HBD task, in trials where signal noise caused irregular stimulus presentation where tones were not presented for ten consecutive heartbeats without disruption, those trials were excluded from the analyses.

Analyses

For the main hypothesis testing, analyses are interpreted with respect to Bayes factors (B), though P values are provided as well (51). A B of above 3 is commonly taken to indicate "moderate" (52) evidence for the alternative hypothesis ($H1$) over the null hypothesis ($H0$); thus by symmetry a B below 1/3 indicates moderate evidence for $H0$ over $H1$. Bs between 3 and 1/3 indicate that the data collected do not sensitively distinguish $H0$ from $H1$. Thus, we report that there was no effect only when $B < 1/3$. Also by convention a B between 10 and 30 (or between 1/10 and 1/10) can be regarded as strong; and between 30 and 100 (or between 1/100 and 1/30) as very strong. $B_{N(0,\ x)}$ refers to a Bayes factor in which the predictions of $H1$ were modeled as a normal distribution with an SD of x, where x scales the size of effect that could be expected, or half the plausible maximum (see Ref. 53). The distribution represents the prediction that the effect could go in either direction. $B_{H(0,\ x)}$ refers to a Bayes factor in which the predictions of $H1$ were modeled as a half-normal distribution with an SD of x; the half-normal distribution represents the prediction of an effect in only one direction. To indicate the robustness of Bayesian conclusions, for each B, a robustness region is reported (54), giving the range of scales that qualitatively support the same conclusion (i.e., evidence as supporting $H0$, or as supporting $H1$, or there not being much evidence at all), notated as: $RR_{concluson}$ [$x1$, $x2$] where $x1$ is the smallest SD that gives the same conclusion and $x2$ is the largest. "Conclusion" means "$B < 1/3$," or "$B > 3$," or "$1/3 < B < 3$."

Novel interoceptive task: sensitivity to heartbeat change.

$Sens_{HB}$, or sensitivity to change in number of heartbeats, is the core measure for testing our main hypothesis. $Sens_{HB}$ was calculated from the modified HBT task as the raw slope from a linear regression of reported beats per minute (BPM) against actual BPM, using the formula $Y = \alpha + \beta X$, where Y is the reported BPM, X is the actual BPM, α is the intercept, and β is the slope (see Fig. 1). In terms of modeling $H1$ for a Bayes

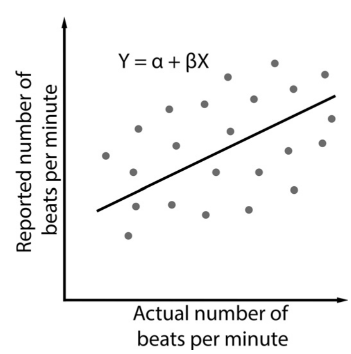

Figure 1. Plotting heart rate sensitivity. Illustration of a linear model plotted between actual and reported beats per minute, where α (the intercept) signifies the bias (i.e., base number of beats per minute reported when the actual number is zero) and β (the slope) used as an interoceptive accuracy estimate based on the slope ($Sens_{HB,}$ sensitivity to change in number of heartbeats).

factor, as the ideal slope, and hence the maximum that could be plausibly expected, is 1 reported as beat per actual beat in every minute, the SD of a normal distribution was set to half, that is, 0.5. A negative slope signifies an inverse adjustment of reported heartbeats relative to actual changes in heartbeats, where the participant reports fewer heartbeats as the actual number of heartbeats increase. A perfect correspondence of reported heartbeats relative to actual heartbeats is represented by a slope of 1. A hypothetical slope greater than 1 would arise if participants regarded, e.g., each of systole and diastole as separate heartbeats.

$Sens_{tones}$, or sensitivity to change in number of exteroceptive tones, was calculated as a control measure from the exteroceptive condition in the modified HBT task. The raw slope from a linear regression of reported and actual number of exteroceptive tones was calculated, using the same formula as for $Sens_{HB}$. The model of *H1* was the same as for the interoceptive case, for comparability.

$Bias_{intercept}$ in the form of a tendency to over- or underreport the number of heartbeats or exteroceptive tones was estimated for the interoceptive condition. The measure signifies their bias in number of reported heartbeats, where a perfect judgement would be represented as a slope of 1 and an intercept of 0, whereas an intercept greater or lower than 0 would indicate a tendency to over- or underestimate their number of heartbeats, respectively. Expected bias depends on participants' beliefs about average heart rate. Where people to be informed that average heart rate is ~80 BPM and they consequently relied on this information, if the slope were zero the intercept would be 80 BPM, reflecting this preexisting knowledge rather than discriminability. Fixing this as the mean reported heart rate, a positive slope would reduce the intercept, with an ideal slope of 1 reducing the intercept to 0. Thus, for the Bayes factor, *H1* for the intercept was modeled as a half-normal with an SD of 80/2. *H1* was modeled for comparability. With the intercept being expected to strongly correlate with the slope, mean reported BPM was also used as a second bias estimate ($Bias_{BPM}$) for comparison.

Traditional measures of interoception.

$IAcc_{classic}$ is a classical measure of interoceptive accuracy in the HBT task, and was included to compare our novel measure to traditional HBT task performance estimates. $IAcc_{classic}$ was calculated from the HBT task as the average error rate between actual and reported number of heartbeats, using the classical interoceptive accuracy formula (15):

$$IAcc_{classic} = 1 - \frac{1}{n}\sum \frac{|(HB_{actual} - HB_{reported})|}{HB_{actual}}.$$

$EAcc_{classic}$ was calculated from the HBT task as the average error rate between actual and reported number of exteroceptive tones, using the same formula as for $IAcc_{classic}$. An ideal score is 1; maximum underreporting (saying the heart rate was 0) would give a score of 0.

Interoceptive confidence (IC) for the HBT task (IC_{HBT}) and for the HBD task (IC_{HBD}) was measured as the averaged trial-based confidence scores.

Exteroceptive confidence (EC_{HBT}) for the HBT task was measured as the trial-based confidence scores.

Interoceptive awareness (IAw_{HBT}, i.e., metacognitive insight into one's own objective performance) was calculated from the interoceptive condition of the HBT task as the raw slope (β) between $IAcc_{classic}$ and IC_{HBT} coded as "guess" (i.e., confidence level of 1) versus any other level of confidence (55). A total of 25 participants had to be excluded from the IAw_{HBT} analysis as they did not give a single confidence report either above 1 or below 2 across the entire task, and thus a slope could not be calculated.

Exteroceptive awareness (EAw_{HBT}) was calculated from the interoceptive condition of the HBT task as the raw slope (β) between $EAcc_{classic}$ and EC_{HBT}. A total of nine participants had to be excluded from the EAw_{HBT} analysis as they did not give a single confidence report either above 1 or below 2 across the entire task, and thus a slope could not be calculated.

The results of secondary analyses of the exteroceptive HBT task condition are reported in APPENDIX B only for brevity.

d-Prime (*d*′) was used as the sensitivity/accuracy index from the HBD task, following signal detection theory (56), calculated as the standardized difference between the mean of the signal-to-noise distribution, compared against the standard deviation of signal-to-noise distribution.

Meta-*d* (57) was used as the measure of metacognition interoceptive awareness/insight for the HDB task. Following signal detection theory (56), it calculates the *d*′ (*type 1*) accuracy that would be expected, assuming maximum metacognitive sensitivity. Given each subject's actual *type 2* performance data, one can obtain the underlying *type 1* sensitivity that is expected if the subject is ideal in placing their confidence ratings. Thus, meta-*d* is compared with accuracy to assess metacognitive relative to the idea value.

Physiological measures.

For the purpose of comparing (novel and traditional) interoceptive measures, physiological measures at rest were also obtained. Resting HRV was calculated from the root mean square of successive differences (RMSSD) in the interbeat intervals during the 5 min of supine rest using the MATLAB package HRVAS (Heart Rate Variability Analysis Software) (58). A 5-min resting period is generally considered sufficient for acquiring a stable baseline blood pressure recording, as shorter period may result in an unstable baseline, and there are no significant change between 5 and 10 min of supine rest (59). For variation in heart rate during the heartbeat counting task, the standard deviation of heart rate across all trials was also used.

Heart rate variability (HRV_{rest}) from the baseline Finometer recording was calculated as the root mean square of successive differences (RMSSD) of cardiac interbeat intervals using the MATLAB package HRVAS (Heart Rate Variability Analysis Software) (58).

Stroke volume (SV) was calculated from the resting-state data as the amount of blood (in milliliter) the heart pumps with each beat.

Baroreflex sensitivity (BRS) from the baseline Finometer recording was calculated using a sequence technique (60) which entails identifying sequences of three or more contiguous heartbeats during which there is a progressive increase or decrease in systolic blood pressure (SBP) followed by a reduction or increase in interbeat intervals (IBI). Each sequence gives mean corrected values of SBP and related IBI, where the slope from a linear regression of these values gives an estimate of global BRS (BRS_{global}).

Ultra-short-term heart rate variability (HRV_{short}) was calculated as the standard deviation of the interbeat intervals of each trial of the modified HBT task.

Split-trial reliability.

A split-trial task reliability analysis was performed to test the reliability of the modified HBT task in terms of both $IAcc_{classic}$ and $Sens_{HB}$ scores across trials. For each participant, all trials were divided into odd and even (30 trials each), including all output of each trial. For each participant, the $Sens_{HB}$ and $IAcc_{classic}$ scores were once again calculated for both the odd and even trials, resulting in two scores of each for every participant. Across all participants, correlational analyses were conducted between odd and even trial mean $IAcc_{classic}$ scores, as well as between odd and even trial $Sens_{HB}$ scores. The ideal raw regression slope is 1, so *H1* for the raw regression slope was modeled using a half-normal distribution with SD = 0.5.

Data and Code Availability Statement

All data obtained in this study, pre-existing data used in the power analysis, modified HBT and HBD task code, and analysis code can be found at the project's Open Source Framework site (https://osf.io/gfc62/).

RESULTS

Novel Interoceptive Task: Sensitivity to Heart Rate Change

Twelve trials across four participants from the modified HBT task were excluded due to noise in the ECG recordings. In terms of the main hypothesis of a relationship across trials of the HBT task between heart rate and number of reported heartbeats, the mean $Sens_{HB}$ score was -0.22 (SD = 0.62), this differed from zero at the group level $t(99) = -3.48$, $P < 0.001$, $B_{N(0,0.5)} = 60.65$, $RR_{B>3}[0.03, 11.20]$, suggesting that participants were overall sensitive to trial-by-trial changes in heartbeats. Importantly, we observed across participants an average negative slope; participants tended to report fewer heartbeats as their heart rate increased. In comparison, we observed a mean $IAcc_{classic}$ of 0.56 (SD = 0.20) (see Fig. 2).

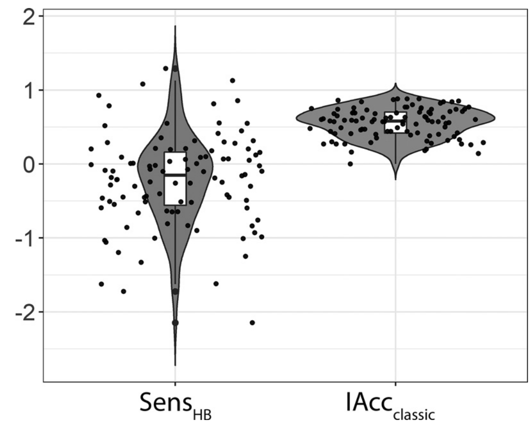

Figure 2. Heartbeat tracking (HBT) task violin plots showing sensitivity to change in number of heartbeats ($Sens_{HB}$) and classical measure of interoceptive accuracy in the HBT task ($IAcc_{classic}$) values from all 100 participants (76 females and 24 males). The violin curves indicate the data density. The dots indicate the individual data points. The boxplots within the violin curves indicate the median (thick line within the box), lower and upper quartiles (*bottom* and *top* ends of box), and the whiskers indicate the minimum values within the lower quartile minus 1.5 times the interquartile range and the maximum values within the upper quartile plus 1.5 times the interquartile range, respectively.

Relationship to Traditional Measures of Interoception

To compare performance across the novel measure of interoceptive sensitivity with traditional interoceptive measures taken from the modified HBT task, correlational analyses estimated only a small possible relationship between $Sens_{HB}$ and $IAcc_{classic}$ scores {$r(98) = 0.056$, CI = [-0.14, 0.25]}; and likewise for the relationship between either interoceptive accuracy and interoceptive metacognitive insight, between $Sens_{HB}$ and IAw_{HBT}: $r(73) = -0.09$, CI = [-0.31, 0.14], or between $IAcc_{classic}$ and IAw_{HBT}, {$r(73) = -0.19$, CI = [-0.40, 0.04]} (see Fig. 3). $Bias_{intercept}$ was positively correlated in the sample with $IAcc_{classic}$ {$r(98) = 0.20$, $P = 0.045$, $b = 46.64$, SE = 22.94, $B_{N(0,80)} = 1.86$, $RR_{1/3<B<3}[0, 546.6]$}, although the Bayes factor (B) indicated only anecdotal evidence for this effect. $Bias_{intercept}$ was strongly negatively correlated with $Sens_{HB}$ {$r(98) = -0.95$, $P < 0.001$, $b = -69.12$, SE = 2.37, $B_{N(0,80)} > 100$, $RR_{B>3}[\approx 0, \infty]$}. Thus, the bias to over or underreport heartbeats was related to interoceptive accuracy quantified both by the classic measure and, particularly, our new slope-based index. Specifically, underreporting is related to a higher $IAcc_{classic}$ score, and overreporting bias is inversely related to positive slope scores. For fixed means, the negative relation between intercept and slope for a regression line follows mathematically. So for additional comparison, $Sens_{HB}$ was also compared with $bias_{BPM}$ as an additional estimate of bias not confounded by the regression, revealing evidence for no correlation {$r(73) = -0.09$, $P = 0.432$, $b = -0.02$, SE = 0.03, $B_{N(0,80)} < 0.01$, $RR_{B<1/3}[0.12, \infty]$}, though $bias_{BPM}$ did correlate with $IAcc_{classic}$ {$r(98) = 0.92$, $P < 0.001$, $b = 67.69$, SE = 2.96, $B_{N(0,80)} > 100$, $RR_{B>3}[0.20, \infty]$}. The estimate of the correlation between $bias_{intercept}$ and IAw_{HBT} was $r(73) = 0.06$, CI = [-0.17, 0.28], and between $bias_{BPM}$ and IAw_{HBT}, $r(73) = -0.08$, CI = [-0.30, 0.15] (see Fig. 3).

Separate analyses explored the relationship between HBD performance with performance on the modified HBT task, using both traditional HBT measures and our novel slope analysis. An exploratory correlational analysis between HBT (heartbeat tracking) and HBD (heartbeat discrimination) task performance was done on a subset of the participants ($n = 47$) who completed both tasks (see Fig. 4), to investigate correspondence in task performance. One hundred twenty trials across 25 participants were excluded due to noise in the ECG recording causing incorrect or irregular stimulus presentation timings relative to the R-peaks. Estimated correlations between $Sens_{HB}$ and HBD task performance in terms of d' or meta-d were only in a small range around zero.

Interoception and Relationship to Baseline Physiology

Correlations between physiological measures and HBT task performance revealed a notable negative correlation

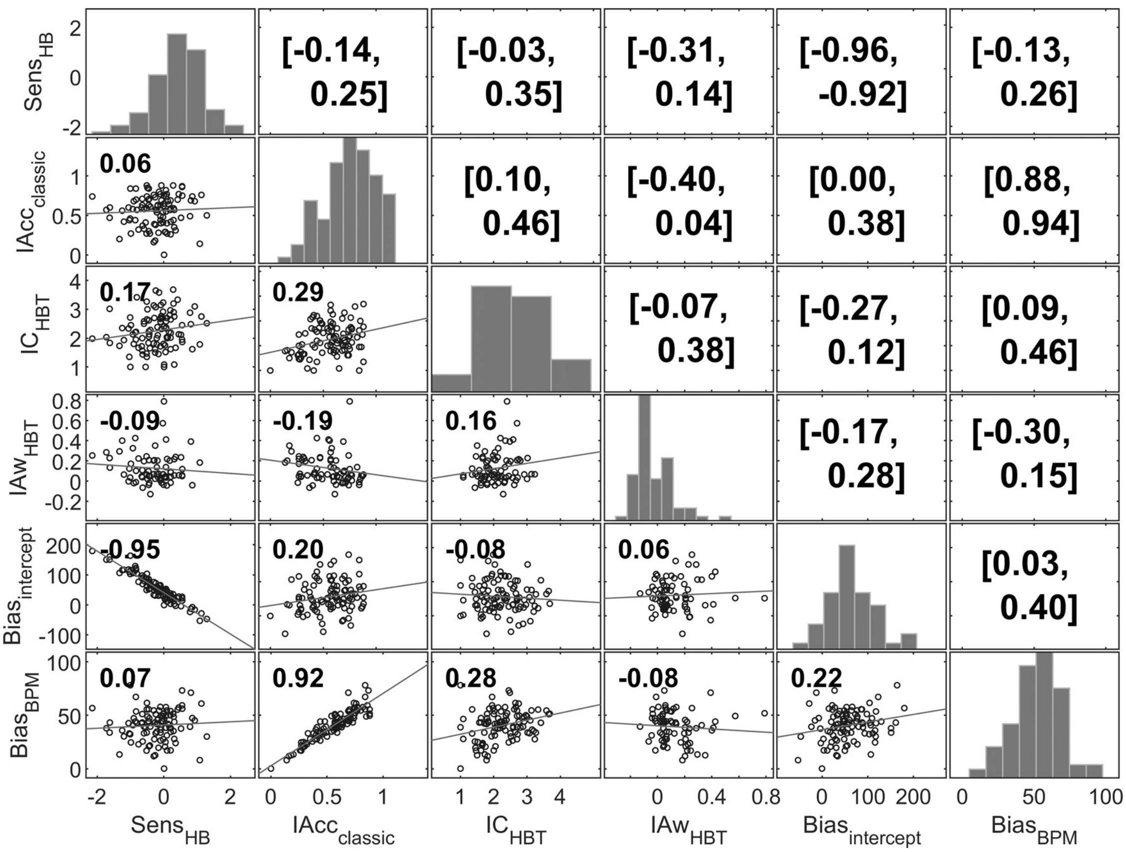

Figure 3. Heartbeat tracking (HBT) task correlogram. Scatter plots of modified HBT task scores from all 100 participants (76 females and 24 males) between row and column variables, and variable distribution along diagonal axis. Each scatter plot of the *bottom* half of the correlogram contains the corresponding correlation coefficient (*r*), and the boxes in the *top* half contain the corresponding confidence intervals (i.e., [*bottom*, *top*]). BPM, beats per minute; HB, heartbeat; HBT, heartbeat tracking; $IAcc_{classic}$, classical measure of interoceptive accuracy; IAw_{HBT}, interoceptive awareness for the HBT task; IC_{HBT}, interoceptive confidence for the HBT task; $Sens_{HB}$, sensitivity to change in number of heartbeats.

between within-task heart rate (HR) and $IAcc_{classic}$ score {$r(98) = -0.26$, CI = [−0.43, −0.06]}, suggesting the $IAcc_{classic}$ measure to be affected by, or related to, participant's heart rate, with higher heart rate being associated with lower $IAcc_{classic}$ scores (see Fig. 5).

Novel HBT Task Split-Trial Reliability Analysis

From the split-trial task reliability analysis testing for consistency of the $Sens_{HB}$ and $IAcc_{classic}$ measures, results showed positive correlations between odd and even trial $Sens_{HB}$ {$r(98) = 0.22$, $P = 0.031$, CI = [0.02, 0.40], $b = 0.21$, SE = 0.09, $B_{H(0,0.5)} = 4.90$, $RR_{B>3}$[0.058, 0.874]} as well as between odd and even trial $IAcc_{classic}$ {$r(98) = 0.99$, $P < 0.001$, CI = [0.982, 0.992], $b = 1.00$, SE = 0.02, $B_{H(0,0.5)} > 100$, $RR_{B>3}[0, \infty]$} (see Fig. 6), signifying task reliability of both accuracy measures, although the B related to the $Sens_{HB}$ measure shows the evidence to be inconclusive. Comparing the correlations using the Silver et al. (61) modification of the Dunn and Clark's (62) z estimated the difference between the correlations to be $z = -16.34$, 95% CI [−0.97, −0.59].

DISCUSSION

This study introduced a new interoceptive accuracy measure, based on how changes in number of counted heartbeats correspond to natural variations in heart rate. Our aim was to characterize this measure systematically, quantify its internal reliability, and evaluate it in comparison to classical measures of interoceptive accuracy (15). The contrast between this new measure and the classical Schandry (15) accuracy calculation sheds light on the nature of cardiac interoception, and particularly the use of the HBT task.

In testing the main hypothesis, our results revealed a negative mean $Sens_{HB}$ score across participants. This indicates that overall, heartbeat counting in the traditional HBT task is indeed affected by changes in the number of heartbeats. This is not in the expected direction for the simplest theory of participant sensitivity to heart rate: Rather, participants tended to report fewer heartbeats on trials with an increase in heart rate (i.e., on trials with a higher number of heartbeats). Nonetheless, this outcome of our rigorous methodology indicates that cardiac interoceptive perception through counting is affected by changes in the number of heartbeats, arguably contradicting previous findings (33, 34). The negative slope may be driven by other physiological changes that accompany increases in heart rate at rest. One plausible mechanism is the changing heartbeat strength (stroke volume) relating to the coupling of the respiratory cycle to the baroreflex: Inspiration decreases pressure in the chest, decreasing left ventricular filling and stroke volume. Lower baroreceptor activation triggers a baroreflexive increase in heart rate; when heartbeats are weaker, interbeat intervals

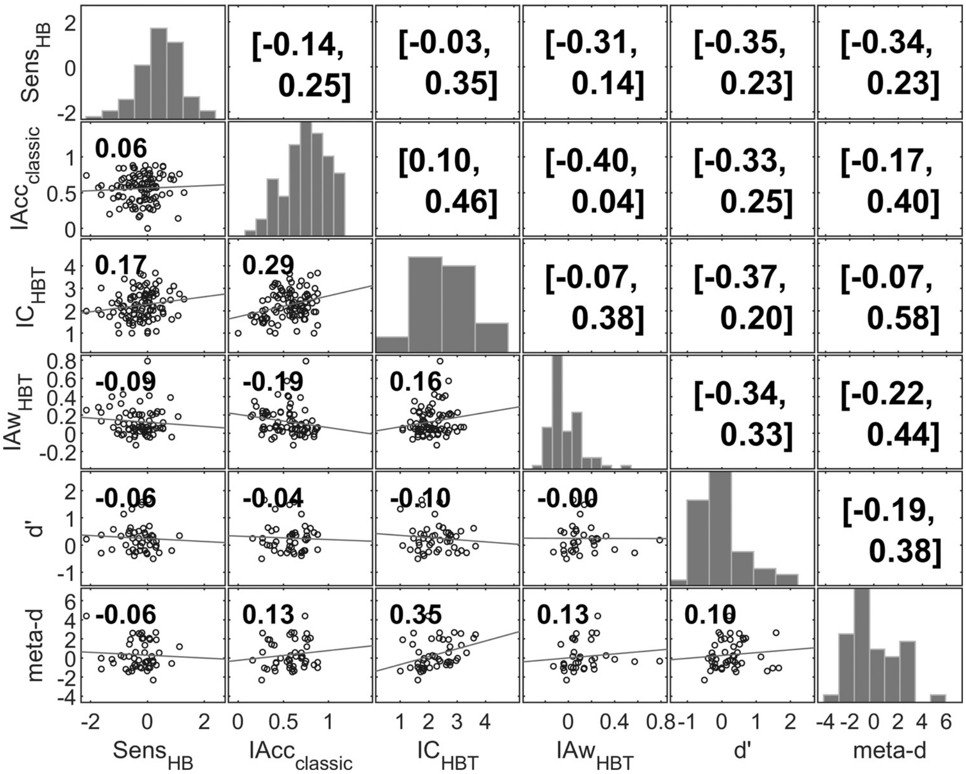

Figure 4. Heartbeat discrimination (HBD) task correlogram. Scatter plots of HBD task and interoceptive HBT task scores from all 100 participants (76 females and 24 males) between row and column variables, and variable distribution along diagonal axis. Each scatter plot of the lower half of the correlogram contains the corresponding correlation coefficient (*r*), and the boxes in the upper half contains the corresponding confidence intervals (i.e., [*bottom*, *top*]). BPM, beats per minute; HB, heartbeat; HBT, heartbeat tracking; $IAcc_{classic}$, classical measure of interoceptive accuracy; IAw_{HBT}, interoceptive awareness for the HBT task; IC_{HBT}, interoceptive confidence for the HBT task; $Sens_{HB}$, sensitivity to change in number of heartbeats.

shorten. This mechanism, interpolated over brief time periods, helps stabilize cardiac output (41–43, 45, 46). In the context of cardiac interoception and the HBT task, instances of increased heart rate occur during periods of weaker heartbeats. This itself could make heartbeats harder to detect. Interpolation over these periods of reduced signal would result in perhaps lower estimated counts of heartbeat occurrence. One interesting related observation in our study is that, rather than the participants simply reporting generally constant value across all trials (as they might if they were for example reporting their average heart rate), performance was instead affected by fluctuations in the frequency of heartbeats coupled reflexively to heartbeat strength. Thus, the observed negative slope between reported and actual heartbeats when performing the task suggests that participants are sensitive to the strength of heartbeats, rather than the overall number of heartbeats.

There are of course other plausible explanations for why phasic increases in heart rate, typically driven at rest by cardiac acceleration during inspiration, may compromise the perception of heartbeats: The active movement of diaphragm and chest wall on inspiration may inhibit cardiorespiratory afferent signaling (likely within brainstem but potentially also at other levels of the neuraxis) or, alternatively, may generate competing respiratory interoceptive signals and sensations that overshadow weaker cardiac signals. Cardiac interoception in states of low arousal may be driven more by the relative strength or salience of heartbeats rather than the amount of heartbeats.

Although the negative mean slope shows a highly significant effect across participants, the split-trial reliability measure showed that the $Sens_{HB}$ measure did show a markedly high amount of noise in its scoring within participants compared with the $IAcc_{classic}$ measure [based on the classical Schandry (15) calculation]. Thus, the measure falls short in reliably identifying people strongly sensitive to changes in their number of heartbeats, which may be due to task difficulty coupled with between-subject variance in heartbeat perception and task performance. Future studies should consider screening for a minimal level of task performance to see if more nuanced trends in $Sens_{HB}$ scores could be found. It is noteworthy, however, that a large number of trials are needed to calculate a reliable slope, and the number of trials is effectively halved during the split-trial reliability measure, meaning the reliability measure risks being less statistically powered relative to the core $Sens_{HB}$ measure.

Directly comparing the two cardiac accuracy measures [traditional Schandry (15) calculation $IAcc_{classic}$ and the slope $Sens_{HB}$ measure] revealed strong evidence against a relation between them. The $IAcc_{classic}$ measure is usually relatively consistent over time (21, 38, 63, 64), in line with the within-subject reliability that we also observed here. This lack of relation could imply $IAcc_{classic}$ scores to be unrelated to the measures ability to detect changes in the number of heartbeats. It remains unclear to what extent this would be due to a limitation of the $Sens_{HB}$ measure, or the $IAcc_{classic}$ measure not being sensitive to changes in cardiac events.

There was also limited correspondence between accuracy and interoceptive metacognitive awareness when comparing accuracy score with metacognitive measures of the HBT task (IAw_{HBT}) and HBD task (meta-d'). However, this was also true for comparisons between awareness and $IAcc_{classic}$ scores. In terms of accuracy, performance in the HBT and HBD tasks may not necessarily correlate (27), hence the observed small relationships are not too unexpected.

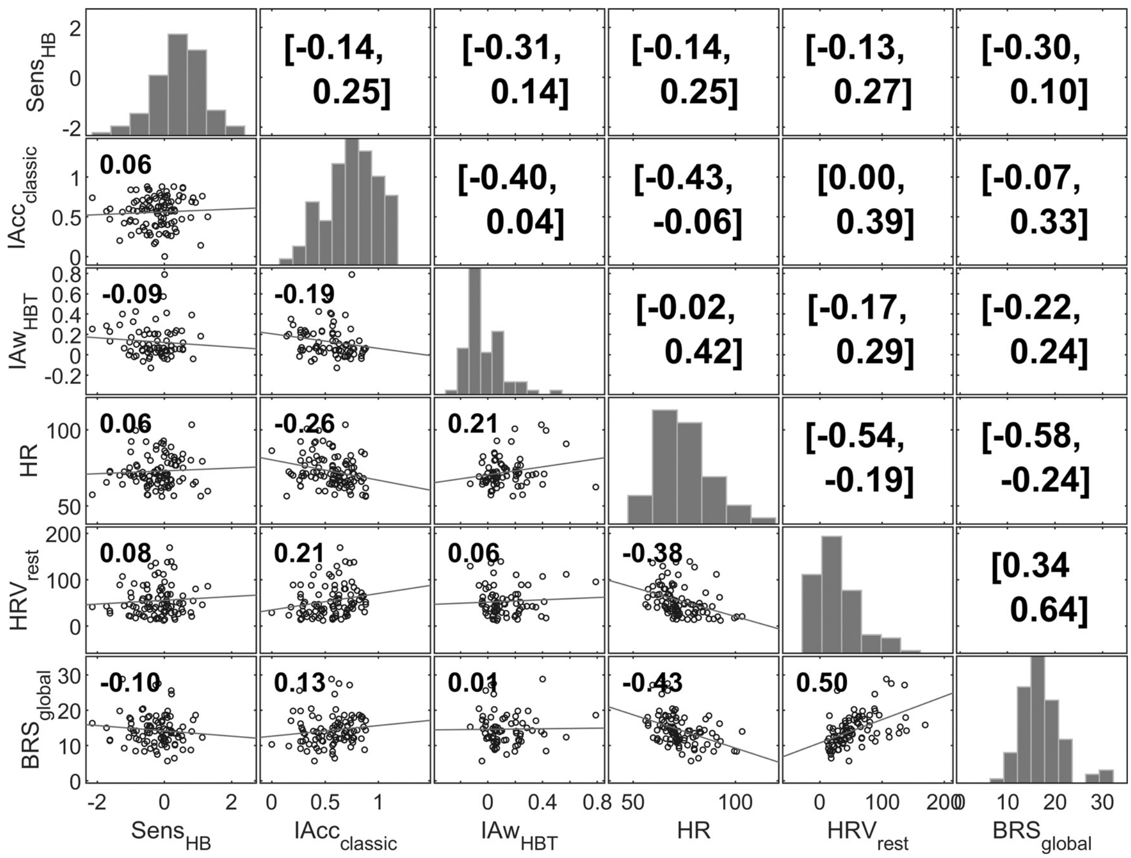

Figure 5. Baseline physiology correlogram. Scatter plots of baseline data and interoceptive heartbeat tracking (HBT) task scores from all 100 participants (76 females and 24 males) between row and column variables, and variable distribution along diagonal axis. Each scatter plot of the *bottom* half of the correlogram contains the corresponding correlation coefficient (*r*), and the boxes in the *top* half contains the corresponding confidence intervals (i.e., [*bottom*, *top*]). BRS$_{global}$, baseline barorflex sensitivity; HR, heart rate; HRV$_{rest}$, baseline heart rate variability; IAcc$_{classic}$, classical measure of interoceptive accuracy; IAw$_{HBT}$, interoceptive awareness for the HBT task; IC$_{HBT}$, interoceptive confidence for the HBT task; Sens$_{HB}$, sensitivity to change in number of heartbeats.

Interoception is the signaling and processing of physiological signals, and as such estimates of interoceptive ability should be expected to map relatively well onto underlying physiological events. In relation to physiology, within-task heart rate (HR) showed a negative correlation with IAcc$_{classic}$ score, showing that participants with a lower HR tended to display higher accuracy scores, which is in line with IAcc$_{classic}$ being positively correlated with bias$_{intercept}$ (a

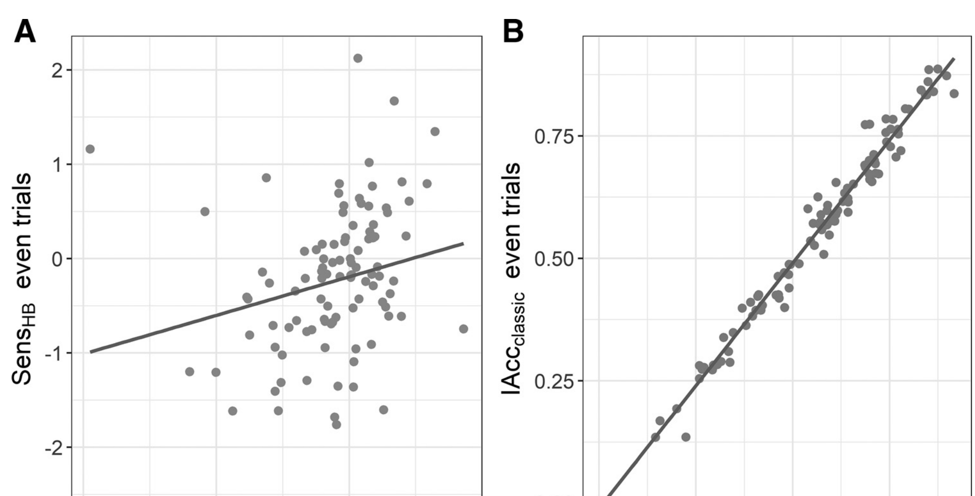

Figure 6. Heartbeat tracking task split-trial task reliability plot. Comparing scores from odd and even trials for each of the 100 participants (76 females and 24 males) showed significant correlation between sensitivity to change in number of heartbeats (Sens$_{HB}$) scores (*A*), and a significant correlation between classical measure of interoceptive accuracy (IAcc$_{classic}$) scores (*B*).

measure showing the baseline tendency to over- or underreport the number of heartbeats). Given that people tend to underreport the number of heartbeats (31, 32), and that lower HR was here associated with greater heartbeat detection accuracy in terms of $IAcc_{classic}$ scores, this would suggest that those with a lower HR either have an easier time perceiving their heartbeats, or that their lower average HR means that their true number of heartbeats is generally closer to their reported number of heartbeats, which would support the view that differences in accuracy are driven by differences in report bias (31).

At the core of this experiment is a reliance on the occurrence of natural heart rate variability (HRV) which gives rise to fluctuations in the number of heartbeats on a trial-by-trial basis. Previous studies have investigated cardiac interoception in the context of manipulated breathing rhythms, with mixed evidence for there being an effect on cardiac interoceptive ability (23, 24). In the current experiment, we focused on cardiac interoception in the context of resting-state respiration and cardiovascular activity. At rest, HRV has a cardiac cycle-length dependence: Higher heart rate yields a shorter IBI, which leaves less opportunity for variation, resulting in an overall lower HRV. In contrast, a slower heart rate yields longer IBI with greater room for variation, resulting in an overall greater HRV (47). For this reason, it can be expected that task performance in the form of sensitivity to changes in the number of heartbeats will be confounded by average HR in virtue of the task being more difficult the lower the HRV, given that there is less variation to pick up on. However, within these data, it could not be determined if there is a relation between baseline HRV (HRV_{rest}) and either $IAcc_{classic}$ or $Sens_{HB}$, or between baseline baroreflex sensitivity (BRS_{global}) and either of the two accuracy measures. However, it is important to note that these HRV and BRS recordings were both taken during rest, as opposed to during task performance. Noninvasive measures of beat-to-beat blood pressure and stroke volume typically involve the application of pressure to the participant's finger to record changes in blood pressure; this approach gives the participant a very clear sensation of their pulse for the duration of the recording, confounding the participant's performance of heart beat detection tasks (65). Future research should aim to better incorporate within-task measures of cardiovascular activity as heartbeat strength and blood flow may play a significant role in heartbeat perception. Indeed, recent research has demonstrated that heartbeat-evoked responses co-fluctuate with beat-to-beat changes in stroke volume (66). In addition, a main limitation of the study is that while respiration is speculated to play a role on heartbeat strength, respiration was not being measured, and thus these are currently only speculations and do not allow for us to draw strong conclusions. Future studies should actively look into the effect of respiration on a trial-by-trial basis, as well as other factors modulating heart rate, on sensitivity to changes in heartbeats to further clarify how heartbeat perception is affected by physiological changes related to the cardiac cycle.

It has previously been illustrated that the HBT task is confounded by participant giving reports based on a priori estimates of their average heart rate rather than reporting on their actual heartbeats (31, 32). This study has attempted to work around this limitation by focusing on trial-by-trial changes in heartbeats. To limit confounding effects of trial duration, the task was designed with limited variance in trial duration, with the average duration of 20 s chosen as it allows for ~4 compete respiratory cycles given that human adults breathe at around 12 breaths/min (50), with some variance given when in the respiratory cycle each trial started. A small variance of ±2 s in 20% of the trials was used to not make the trial duration too predictable to discourage participants from simply reporting a static number of heartbeats for all trials. There is still the risk that participants count at a steady rate that they approximate to their heart rate without actually perceiving their heartbeats. However, this does not explain a negative slope, and so does not explain our results.

These observed findings built on inferences obtained from "threshold" task-based measures of cardiac perception. We highlight how fluctuations in heartbeat strength, accompanying baroreflex-driven vagally mediated heart rate variability at rest, may represent more than a confound in heartbeat detection tasks but a basis for individual difference in cardiac interoception. For example, people may vary in their perceptual sensitivity to the strength of individual heartbeats relative to their timing. There is potential relevance to understanding symptoms such as anxiety: although for most people, the variable strength and inconsistent perception of heartbeats at rest may engender a reduced perceptual weighting of cardiac interoceptive sensations, people with more chronic stress states, the suppressed heart rate variability may lead to a more consistent perception of heartbeats, increasing sensory precision and hence their perceptual salience and impact on emotion states. Our findings thus provide the basis for testable hypothesis linked to expectation and prediction in cardiac interoception (24, 67).

In conclusion, as hypothesized, participants vary in the number of heartbeats counted in a specified timeframe as a function of changes in their heart rate (due to natural fluctuations in heart rate). At the same time, this was arguably in the opposite to the intuitive direction, since participants reported fewer heartbeats as their heart rate increases, a finding that may be driven by changes in heartbeat strength in terms of moment-to-moment changes in blood pressure. Compared with other interoceptive tasks, within-participant performance was marked by a high degree of noise. This inverse slope suggests that participants may be more sensitive to relative strength and salience of heartbeats when performing cardiac interoception tasks, rather than the amount of heartbeats. Future work could usefully track beat-to-beat measures of ventricular ejection strength to test how detection parameters vary. As we observed that the reported number of heartbeats did not increase with increases in heart rate, our findings also suggest that interoceptive monitoring at rest may not be a finely tuned process of tracking and detecting subtle internal events. Rather, available interoceptive information guides estimations that in turn may be partly shaped by higher order beliefs.

APPENDIX A: ANALYSIS ON PRE-EXISTING DATA

The extent that HB counting speed is modulated by subtle changes in heart rate on a trial-by-trial basis was assessed using pre-existing data from 219 healthy participants who performed the HB counting task. Each participant went through six trials of six different trial lengths (25, 30, 35, 40, 45, and 50 s) in a randomized order. For each participant, a general linear regression was plotted between actual and reported beats per minute (BPM).

This was performed as proof of principle, on data taken from a design that was not optimized for the present analysis (i.e., only 6 trials of differing length were performed per participant). The analysis yielded an average slope of 0.136 and standard deviation of 2.396 (see Fig. A1). A t test against the null hypothesis (a value of zero representing no effect) showed the effect to be nonsignificant [$t(218) = 0.841$, SE = 0.16, $P = 0.402$]. The maximum slope that could be achieved if people detected their heart rate without error would be 1 BPM/BPM. Thus, setting the model of the hypothesis (*H1*) for a Bayes factor as a half-normal with SD = 0.5 (i.e., half the maximum), gives $B_{H(0,\ 0.5)} = 0.67$, which is insensitive (B >1/3), indicating that more data from each participant is necessary to find strong evidence for an effect. As the standard deviation is expected to shrink according to the square root of number of trials, the trial number was increased 3^2 times, rounded up to 60 trials. Thus, the new expected standard deviation was estimated as $2.396 \times \text{sqrt}(6/60) = 0.76$. *H1* was modeled as a half-normal with an SD of 0.136. Based on a sample mean of 0.136 and standard deviation of 0.76, a sample size of 100 participants would give a Bayes factor of 3.11 if the sample mean were 0.136, which would be enough to give moderate evidence for an effect.

APPENDIX B: HBT TASK INTEROCEPTIVE AND EXTEROCEPTIVE CONDITIONS

Comparing the different accuracy measures of the HBT task, Shapiro–Wilk test showed both the interoceptive ($Sens_{HB}$, $IAcc_{classic}$) and exteroceptive ($Sens_{tones}$, $EAcc_{classic}$) accuracy scores to be normally distributed. Comparing interoceptive and exteroceptive accuracy scores, a paired-sample t test revealed a notable difference {$t(99) = 2.60$, CI = [0.01, 0.06]} between $IAcc_{classic}$ (mean = 0.56, SD = 0.20) and $EAcc_{classic}$ (mean = 0.53, SD = 0.16). There was also as a strong difference {$t(99) = -10.36$, CI = [−0.80, −0.54]} between $Sens_{HB}$ (mean = −0.21, SD = 0.62) and $Sens_{tones}$ (mean = 0.45, SD = 0.27), indicating that participants had significantly better performance in terms of the slope measure in the exteroceptive compared with interoceptive task, suggesting they had an easier time detecting changes in number of auditory tones compared with changes in number of heartbeats (see Fig. B1). Participants did not show a difference in task confidence {$t(99) = 0.39$, CI = [−0.10, 0.15]} between the interoceptive (IC_{HBT}, mean = 2.25, SD = 0.63) and exteroceptive (EC_{HBT}, mean = 2.23, SD = 0.49) conditions. However, they did show greater metacognitive awareness {$t(69) = -9.49$, CI = [−0.38, −0.25]} in the exteroceptive (EAw_{HBT}, mean = 0.47, SD = 0.25) compared with interoceptive (IAw_{HBT}, mean = 0.13, SD = 0.15) condition.

When investigating the relationship between interoceptive and exteroceptive conditions, strong correlations were observed between $IAcc_{classic}$ and $EAcc_{classic}$ {$r(98) = 0.78$, CI = [0.69, 0.85]}, IC_{HBT} and EC_{HBT} {$r(98) = 0.41$, CI = [0.23, 0.56]}, indicating performance accuracy and confidence were related across interoceptive and exteroceptive domains. Meanwhile, the relationship between interoceptive and exteroceptive measures for the slope analysis ($Sens_{HB}$ and $Sens_{tones}$) {$r(98) = 0.15$, CI = [−0.06, 0.32]} and for metacognitive awareness (IAw_{HBT} and EAw_{HBT}) {$r(68) = 0.20$, CI = [−0.03, 0.42]} was not as strong.

APPENDIX C: ULTRA-SHORT-TERM HRV ANALYSIS

Ultra-short-term HRV (HRV_{short}) was calculated for each trial from the standard deviation of the inter-beat-intervals. A total of 12 trials were excluded from this analysis, due to excessive ECG noise. Across all participants, there was a mean trial-by-trial inter-beat-interval (IBI) of 829 ms (SD =

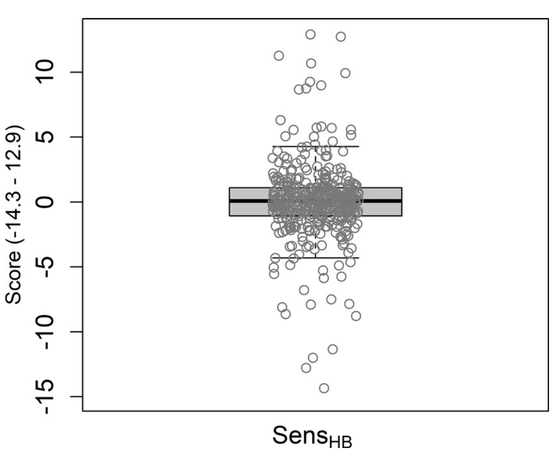

Figure A1. Mean sensitivity to change in number of heartbeats ($Sens_{HB}$). *Y*-axis label signifies the range (min to max) of $Sens_{HB}$ scores from 219 participants. Whiskers correspond to the 1.5 interquartile range of the *bottom* and *top* quartiles. The gray circles indicate individual data points.

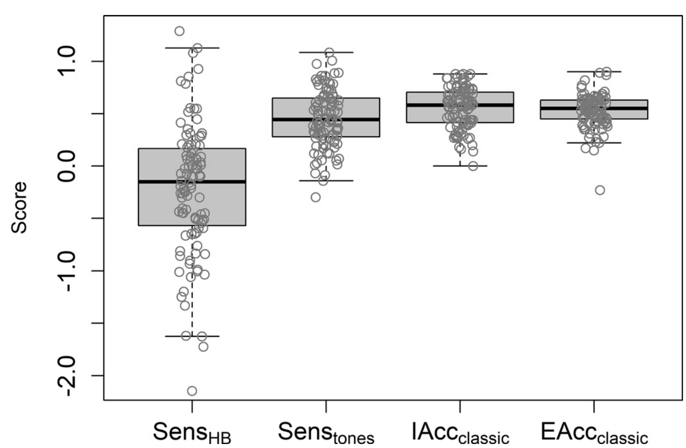

Figure B1. Mean accuracy scores from the heartbeat tracking task in the form of interoceptive and exteroceptive slope (sensitivity to change in number of heartbeats, $Sens_{HB}$, and sensitivity to change in number of exteroceptive tones, $Sens_{tones}$, respectively) and interoceptive and exteroceptive error ratio (classical measure of interoceptive accuracy, $IAcc_{classic}$, and classical measure of exteroceptive accuracy $EAcc_{classic}$, respectively) from all 100 participants (76 females and 24 males). Whiskers correspond to the 1.5 interquartile range of the *bottom* and *top* quartiles. The gray circles indicate individual data points.

114 ms), and a mean HRV_{short} of 53 ms (SD = 19 ms). Mean HRV_{short} correlated strongly with baseline HRV_{rest} calculated as the RMSSD of inter-beat intervals from a 5-min period of rest {$r(92)$ = 0.46, $P < 0.001$, CI = [0.28, 0.60]}, suggesting within-participant consistency between the two HRV measures. There was also a significant negative correlation between trial-by-trial HRV_{short} and heart rate {$r(5982)$ = −0.31, $P < 0.001$, CI = [−0.34, −0.29]}, as well as between mean HRV_{short} and mean HR {$r(98)$ = −0.41, $P < 0.001$, CI = [−0.56, −0.23]}, similar to the relation observed between heart rate and HRV_{rest} (see Fig. 5).

Furthermore, to estimate the trial-by-trial stability of HR and HRV_{short}, their within-participant standard deviation was calculated. The same was also done for the trials of each duration (i.e., 18, 20, and 22 s). The means and standard deviations of these are displayed in Table C1.

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

D.E.O.L., Z.D., and S.N.G. conceived and designed research; D.E.O.L. and G.E. performed experiments; D.E.O.L. and G.E. analyzed data; D.E.O.L. interpreted results of experiments; D.E.O.L. prepared figures; D.E.O.L. drafted manuscript; D.E.O.L., H.D.C., Z.D., and S.N.G. edited and revised manuscript; D.E.O.L., G.E., H.D.C., Z.D., and S.N.G. approved final version of manuscript.

ENDNOTE

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Table C1. *Heart rate variation and ultra-short-term heart rate variability across trials*

	All Trials		18 s Trials		20 s Trials		22 s Trials	
	Means	SD	Means	SD	Means	SD	Means	SD
SD of HR	36.47	12.86	36.23	17.92	36.35	12.89	36.23	16.48
SD of HRV_{short}	19.41	7.68	18.63	10.18	19.57	7.90	16.06	9.70

Means and standard deviation (SD) of the standard deviation of heart rate (HR) and ultra-short-term heart rate variability (HRV_{short}) from all 100 participants (76 females and 24 males) across all trials, and across all trials with a duration of 18 s, 20 s, and 22 s. All values are in the unit of milliseconds.

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