Knowing your own heart: Distinguishing interoceptive accuracy from interoceptive awareness

Sarah N. Garfinkel [a,b,*], Anil K. Seth [b,c], Adam B. Barrett [b,c], Keisuke Suzuki [b,c], Hugo D. Critchley [a,b]

[a] Psychiatry, Brighton and Sussex Medical School, UK
[b] Sackler Centre for Consciousness Science, University of Sussex, UK
[c] Department of Informatics, University of Sussex, UK

ABSTRACT

Interoception refers to the sensing of internal bodily changes. Interoception interacts with cognition and emotion, making measurement of individual differences in interoceptive ability broadly relevant to neuropsychology. However, inconsistency in how interoception is defined and quantified led to a three-dimensional model. Here, we provide empirical support for dissociation between dimensions of: (1) *interoceptive accuracy* (performance on objective behavioural tests of heartbeat detection), (2) *interoceptive sensibility* (self-evaluated assessment of subjective interoception, gauged using interviews/questionnaires) and (3) *interoceptive awareness* (metacognitive awareness of interoceptive accuracy, e.g. confidence-accuracy correspondence). In a normative sample ($N = 80$), all three dimensions were distinct and dissociable. Interoceptive accuracy was only partly predicted by interoceptive awareness and interoceptive sensibility. Significant correspondence between dimensions emerged only within the sub-group of individuals with greatest interoceptive accuracy. These findings set the context for defining how the relative balance of accuracy, sensibility and awareness dimensions explain cognitive, emotional and clinical associations of interoceptive ability.

Interoception is the body-to-brain axis of sensation concerning the state of the internal body and its visceral organs (Cameron, 2001; Sherrington, 1948). Interoception is distinguishable from exteroception (perception of the external environment) and proprioception (reflecting the position of the body in space) (Sherrington, 1948). Some models expand the definition of interoception to accommodate other motivationally-important physiological signals (e.g. pain, cutaneous light 'sensual' touch and thermal sensations) (Craig, 2002). Interoceptive ability is relevant to 'peripheral' theories of emotion that propose a basis for emotional feeling states in the central representation and perception of changes in bodily physiology (Lange & James, 1967). It follows that individuals who are more attuned to bodily responses experience emotions with heightened intensity (Wiens, Mezzacappa, & Katkin, 2000). Renewed interest in interoception parallels a growing appreciation that cognition is also embodied, and that cognitive and emotional processes are biased by extracerebral changes, captured for example in the somatic marker hypothesis (Damasio, Tranel, & Damasio, 1991). Correspondingly, neuroscientists, psychologists and physiologists have focused efforts on characterizing how and when internal bodily signals might guide cognition, with recent work demonstrating that enhanced interoceptive accuracy can improve memory (Garfinkel, Barrett, et al., 2013; Garfinkel, Tiley, O'Keeffe, & Critchley, 2013; Werner, Peres, Duschek, & Schandry, 2010) and decision making (Dunn, Galton, et al., 2010; Werner et al., 2013).

Despite this historic and recent interest in interoception, the literature to date remains inconsistent in the methods used to assess interoceptive ability (Medford & Critchley, 2014). Firstly, interoceptive accuracy (1) is gauged via paradigms to objectively quantify individual differences in behavioural performance. Heartbeat detection tasks dominate these methods used to determine individual differences in interoceptive accuracy. This focus is largely pragmatic: heartbeats are distinct and frequent internal events that can be easily discriminated and measured. Heartbeat detection procedures usually require either an individual to count the number of times they perceive their heart beating during

* Corresponding author at: Clinical Imaging Science Centre, Brighton and Sussex Medical School, University of Sussex, Falmer BN1 9RR, UK. Tel.: +44 01273 67 8584.
E-mail address: s.garfinkel@bsms.ac.uk (S.N. Garfinkel).

specified time periods ("Heartbeat Tracking" e.g. Schandry, 1981), or instead to report the timing of individual heartbeats, through tapping or through perceived synchrony of the heartbeats with external stimuli ("Heartbeat Discrimination" e.g. Brener & Kluvitse, 1988; Katkin, Reed, & Deroo, 1983; Whitehead, Drescher, Heiman, & Blackwell, 1977). Measured interoceptive accuracy tends to be greater when assessed using the heartbeat tracking task, relative to heartbeat discrimination (Schulz, Lass-Hennemann, Sutterlin, Schachinger, & Vogele, 2013), and the two methods likely involve different processes, with the former dependent on internal monitoring mechanisms, while the latter may require simultaneous multimodal integration of internal and external information. Indeed, while some studies found these two heartbeat detection procedures to be correlated in individuals (e.g. Hart, McGowan, Minati, & Critchley, 2013; Knoll & Hodapp, 1992), this relationship is not always tight, nor observed in small samples (e.g. Phillips, Jones, Rieger, & Snell, 1999; Schulz et al., 2013). In addition, factors such as stress (Schulz et al., 2013) differentially affect performance on these two heartbeat discrimination and tracking procedures, reinforcing the perspective that they are founded on distinct (as well as potentially shared) underlying processes.

Secondly, an individual's personal account of how they experience internal sensations represents an alternative mode of interoception. This 'sensibility' (2) can be assessed using subjective measures that index both the individual's belief in their interoceptive ability and the degree to which they feel engaged by interoceptive signals (e.g. Ernst et al., 2013; Terasawa, Shibata, Moriguchi, & Umeda, 2013; Wiebking et al., 2011). The quantification of interoceptive sensibility can take two forms. The first approach is to use self-report questionnaires (e.g. Autonomic Perception Questionnaire, Mandler, Mandler, & Uviller, 1958; Body Perception Questionnaire, Porges, 1993), and the second approach is to score subjective aspects (e.g. confidence in interoceptive accuracy) during the performance of a specific interoceptive task. Self-report questionnaire measures of interoception are useful in measuring individual differences in perceived sensitivity across a range of internal bodily changes but do not inherently address whether this subjective interoceptive sensibility is accurate (i.e. actually relates to the strength of viscerosensory 'input', or corresponds to objective measures of accuracy on interoceptive tests). Indeed, self-report measures can reflect biases in subjective thresholds, irrespective of interoceptive accuracy. Thus, a strategy adopted in some studies is to combine measures of interoceptive accuracy (e.g. heartbeat perception task performance), with a measure of subjective confidence in performing the task (Ehlers, Breuer, Dohn, & Fiegenbaum, 1995). When averaged, the subjective confidence score provides an index of interoceptive sensibility for that particular axis of interoceptive signalling. These confidence measures can be combined with mean task accuracy (Khalsa et al., 2008) to highlight the relationship between subjective (perceived) and objective (actual) interoceptive ability. Importantly, more sophisticated analytic approaches (e.g. receiver operating characteristic (ROC) curves or trial-by-trial confidence – accuracy correlations) can also be applied to quantify explicitly how well confidence predicts accuracy within a given individual. This third interoceptive construct provides a measure of metacognitive awareness of interoceptive ability, and therefore, by current standards (Barrett, Dienes, & Seth, 2013), the most precise definition of interoceptive awareness (3) (Garfinkel & Critchley, 2013).

Previously, the terms 'interoceptive awareness' and 'interoceptive sensitivity' have been typically treated as synonymous and interchangeable, without deep consideration as to whether the mode of evaluation indeed assesses objective interoceptive accuracy, metacognitive awareness, or subjective sensibility, though recently the term 'interoceptive accuracy' is increasingly used to refer to interoceptive behavioural performance (Ceunen, Van Diest, & Vlaeyen, 2013). To formalize these conceptual issues, we recently proposed a three dimensional construct of interoception that distinguishes between these levels of interoceptive processing (Garfinkel & Critchley, 2013). Here, the term interoceptive sensitivity, which we now unambiguously call *interoceptive accuracy*, is used to define the process of accurately detecting and tracking internal bodily sensations. This is an objective empirical measure of behavioural performance, which is distinct from subjective measures. This objective-subjective distinction is established within human behavioural psychology (e.g. Cheesman & Merikle, 1984, 1986; Dienes & Berry, 1997; King & Dehaene, 2014; Seth, Dienes, Cleeremans, Overgaard, & Pessoa, 2008; Snodgrass & Shevrin, 2006). The subjective, self-evaluated characterological trait (from questionnaire measures) to be interoceptively focused is defined as *interoceptive sensibility*, following prior literature (Terasawa et al., 2013). Lastly, in the present manuscript we retain the use of the term *interoceptive awareness* to refer to the correspondence between objective interoceptive accuracy and subjective report, i.e. metacognition. Here, this is implemented as a quantified measure of the degree to which accuracy of (objective) heartbeat detection is predicted by subjective confidence in the task judgement, e.g. using area under an ROC curve (Barrett et al., 2013; Fleming, Weil, Nagy, Dolan, & Rees, 2010; Galvin, Podd, Drga, & Whitmore, 2003; Garfinkel & Critchley, 2013). A high level of interoceptive awareness reflects the ability (i.e. meta-awareness) of an individual to *know* when he/she is making good or bad interoceptive decisions, on the level of interoceptive behavioural accuracy. These three distinct facets of interoception are depicted in Table 1.

The present paper responds to a clear need to better differentiate between objective, subjective and metacognitive aspects of interoception (Ceunen et al., 2013; Garfinkel & Critchley, 2013), and serves as the first experimental test of these distinctions within a single study. Empirically, we determine the extent to which interoceptive accuracy, interoceptive sensibility and interoceptive awareness interrelate across a large normative sample of healthy individuals. We focus on heartbeat discrimination and tracking, which provide two objective tests of *interoceptive accuracy*. We establish empirically the extent of *interoceptive awareness* across the sample, and further test the hypothesis that these awareness levels are different between individuals who score high or low on *interoceptive accuracy*. We also formally characterize the relationships between *interoceptive accuracy*, *sensibility* and *awareness* using a stepwise linear regression analysis that incorporates a forward selection procedure to test the hypothesis that explanatory variance will be partitioned between the different interoceptive dimensions, as predicted by our model. We extend this regression approach to test our prediction that interoceptive accuracy is the basic construct underlying other aspects of interoception (Garfinkel & Critchley, 2013), predicting that we will formally show dependence of sensibility and awareness on interoceptive accuracy (and a corresponding weakening of relationships if interoceptive sensibility or interoceptive awareness are considered as dependent variables).

We use correlational analyses to detail whether the three dimensions of interoception show different relationships depending on the task used to measure interoceptive accuracy (heartbeat tracking vs. heartbeat discrimination). Lastly, we test whether distinct relationships emerge in individuals classified as high or low on interoceptive accuracy. This extends the notion of a primacy of interoceptive accuracy to suggest that relationships between the three different dimensions of interoception may emerge only when an objective accuracy threshold is surpassed. Thus, individuals scoring high (compared to low) on interoceptive accuracy would show significantly stronger correspondence across objective, subjective and metacognitive interoceptive dimensions.

Table 1
Three distinct dimensions of interoception, as initially proposed by Garfinkel and Critchley (2013), and further refined in the present manuscript.

	Interoceptive accuracy	Interoceptive sensibility	Interoceptive awareness
Definition	Objective accuracy in detecting internal bodily sensations	Self-perceived dispositional tendency to be internally self-focused and interoceptively cognisant	Metacognitive awareness of interoceptive accuracy
Example	Can you accurately report when your heart is beating?	To what extent do you believe you focus on and detect internal bodily sensations?	Do you "know" whether you are accurately or inaccurately assessing your heart-timing?
Mode of assessment	Assessed via objective tests of interoceptive accuracy	Assessed via subjective self-report measures probing perceived aptitude	Relationship between objective performance (interoceptive accuracy) and awareness of performance
Example	Behavioural performance accuracy during heartbeat detection/mental tracking tasks	Questionnaires, such as Porges Body Perception Questionnaire, or global self-report measures such as average confidence	Area under ROC curves mapping confidence onto accuracy

1. Method

1.1. Participants

Healthy volunteer participants were recruited from staff and students of the University of Sussex, and Brighton and Sussex Medical School. Eighty participants took part in all experimental procedures. Demographic data were collected for sex, age and body mass index. Each participant provided written informed consent, with all procedures approved by the local ethics committee at the Brighton and Sussex Medical School.

1.2. Materials and procedure

1.2.1. Interoceptive accuracy

Two measures determined objective interoceptive accuracy: a heartbeat discrimination task (e.g. Katkin et al., 1983) and a heartbeat tracking task (Schandry, 1981).

Heartbeat discrimination tasks typically involve the presentation of a periodic external stimulus (e.g. tones, lights); participants state whether this external stimulus is synchronous or asynchronous with their own heart. Our heartbeat discrimination task required the participant to judge whether a series of ten auditory tones were synchronous with his/her heartbeat; this procedure was repeated 15 times to form 15 trials. Each participant was provided with the following instructions: '*You will hear ten tones. Please can you tell me if the tones are in or out of sync with your heartbeat*'. Each trial consisted of 10 tones presented at 440 Hz and having 100 ms duration, triggered by the participant's heartbeat. Under the synchronous condition, tones were generated at the beginning of the rising edge of the pulse pressure wave. Under the asynchronous condition, a delay of 300 ms was inserted, adjusting for the average delay (~250 ms) between the R-wave and the arrival of the pressure wave at the finger (Payne, Symeonides, Webb, & Maxwell, 2006). This setup delivered tones around 250 ms or 550 ms after the R-wave, which correspond to maximum and minimum synchronicity judgements respectively (Wiens & Palmer, 2001). At the end of each trial, the participants responded by stating whether the series of tones were either *synchronous* or *asynchronous* with her/his heartbeats. In both conditions, the tones were presented at the same rate (i.e. either on the heartbeat or time-shifted), hence participants could not use the tempo of tones or other knowledge about their heart rate to guide responses: phase synchrony of tones and heartbeats served as the only informative cue.

In the heartbeat tracking task, participants were given the following instructions: 'Without manually checking, can you silently count each heartbeat you feel in your body from the time you hear "start" to when you hear "stop"'. This task was repeated six times to form six trials, using time-windows of 25, 30, 35, 40, 45 and 50 s, presented in randomized order. For each trial, an accuracy score was derived: $1 - (|nbeats_{real} - nbeats_{reported}|)/((nbeats_{real} + nbeats_{reported})/2)$: Resulting accuracy scores were averaged over the 6 trials, yielding an average value for each participant (Hart et al., 2013). The inclusion of reported values ($nbeats_{reported}$) within the denominator mitigated against overestimating performance accuracy in people showing high variance, particularly when more heartbeats were reported than occurred.

1.2.2. Confidence judgments

At the end of each trial ($N = 15$ for heartbeat discrimination and $N = 6$ for heartbeat tracking), the participant immediately rated his/her confidence in their perceived accuracy of response. This confidence judgement was made using paper/pencil marked on a continuous visual analogue scale (VAS) that was 10 cm long. One end was marked "Total guess/No heartbeat awareness" while the other end was labelled "Complete confidence/Full perception of heartbeat".

1.2.3. Interoceptive sensibility

The awareness section of the Porges Body Perception Questionnaire was completed (Porges, 1993). This subscale incorporates 45 bodily sensations (e.g. stomach and gut pains) and participants indicated their awareness of each sensation using a five point scale ranging from 'never' to 'always'. In addition, a measure of interoceptive sensibility pertaining just to self-perceived heartbeat detection was also derived from the mean confidence during both heartbeat discrimination and heartbeat tracking tasks (i.e. averaged over experimental trials to produce a global measure of mean confidence). Thus two measures of interoceptive sensibility were used; one relating to a spectrum of internal bodily sensations (Porges Body Perception Questionnaire) and one pertaining just to the heart (mean confidence ratings).

1.3. Data analysis

1.3.1. Interoceptive awareness

Interoceptive awareness during the heartbeat discrimination task was quantified using receiver operating characteristic (ROC) curve analysis (Green & Swets, 1966) of the extent to which confidence predicted accuracy. ROC analysis determines the strength with which a binary response (here confidence measured by VAS) mirrors a binary state variable (here correct or incorrect asynchrony judgement during heartbeat discrimination) at all possible detection thresholds. For each detection threshold, one computes the hit rate (here the proportion of correct trials on which confidence was 'high') and the false alarm rate (here the proportion of incorrect trials on which confidence was 'high'). The ROC curve plots the hit rate vs. the false alarm rate over all the possible detection

thresholds. The area under the ROC curve gives a precise measure of the extent to which confidence reflects accuracy, independent of the participant's overall propensity to report high confidence. Thus this provides a measure specifically of *interoceptive awareness*. For the heartbeat tracking task, on which responses were not binary, the within-participant Pearson correlation, r, between confidence and accuracy provided an alternative index of interoceptive awareness.

We undertook a median split of participants to investigate whether individuals distinguished by high and low interoceptive accuracy differed in their sensibility and awareness measures of interoception. When indexing by heartbeat tracking, high accuracy heartbeat trackers were those with an accuracy score of 0.70 and above ($N = 40$, mean = 0.83, Std. = 0.08), while low accuracy trackers had an accuracy score of 0.69 or below ($N = 40$, mean = 0.49, Std. = 0.16), values comparable to previous median split analyses (Tsakiris, Tajadura-Jimenez, & Costantini, 2011). For heartbeat discrimination, determining group membership via a median split resulted in fewer subjects classified as high-accuracy heartbeat detectors, with an accuracy score of 0.65 and above ($N = 30$, mean = 0.79, Std. = 0.11). Low-accuracy detectors had an accuracy score of 0.60 and below ($N = 50$, mean = 0.48, Std. = 0.11).

1.3.2. Statistical analyses

To determine the relative presence or absence of interoceptive awareness (i.e. metacognition) at the group level (i.e. collapsed across all participants), one-sample t-tests were used to establish whether confidence-accuracy correlations differed significantly from zero, and whether the area under the confidence-by-accuracy ROC curve differed significantly from 0.5 (chance) performance. This latter analysis was also performed separately in individuals with high and low interoceptive accuracy. Independent t-tests assessed whether interoceptive awareness and sensibility were higher in individuals who performed high on interoceptive accuracy relative to low performers, testing our hypothesis that the strongest relationships between subjective and metacognitive interoceptive dimensions would emerge in individuals with greatest (objective) interoceptive accuracy.

A stepwise forward linear regression analysis was conducted across all measures, collapsed across the two tasks, to examine our specific prediction that interoceptive accuracy would partly, perhaps independently, relate to subjective sensibility and metacognitive awareness dimensions. Firstly, the analysis was conducted with interoceptive accuracy as the dependent variable, with measures of interoceptive sensibility (BPQ and mean heartbeat task confidence) and interoceptive awareness, as predictor variables. Secondly, this regression analysis was repeated using interoceptive awareness as the dependent variable; our hypothesis that interoceptive accuracy serves as the base (central) construct predicted that, in this analysis, the statistical relationship between the three interoceptive measures would be greatly diminished.

Pearson's correlations were also employed to explore relationships between all objective, subjective and awareness measures of interoception, independently for the two objective tests, and separately in individuals classified as high and low on interoceptive accuracy. Adjusted thresholds for rejecting the null hypothesis were computed separately for the two clusters of Pearson's correlational analyses, using false discovery rate (FDR) implemented in Matlab 2012a. For the first cluster of correlational analyses, which collapsed across heartbeat tracking and discrimination tasks, the FDR corrected p-values were adjusted to reflect the ten key correlations of interest which either (a) compared the same interoceptive dimension across the two heartbeat detection tasks (e.g. interoceptive accuracy during heartbeat tracking vs. heartbeat discrimination), or (b) compared distinct axes of interoception within the same task (e.g.

interoceptive accuracy during heartbeat discrimination vs. interoceptive awareness during heartbeat discrimination). Analyses in which variables and/or task were not aligned (e.g. interoceptive accuracy during heartbeat tracking with interoceptive awareness during heartbeat discrimination) were excluded. For completeness, the full matrix of these correlational analyses is included in Table 2. FDR was also used to adjust p-values for multiple comparisons for the 12 Pearson's correlational analyses conducted separately for tasks and median-split (high/low in interoceptive accuracy) groups. Throughout the paper, FDR adjusted p-values were used to protect against spurious Type-1 errors and guide interpretation of results. Unadjusted p-values are also included in order to provide the reader which a comprehensive set of values that can inform future hypothesis testing.

2. Results

2.1. Demographic data

In the total sample of $N = 80$, 50 were males (62.5%) and 30 were females (37.5%). Age was recorded for $N = 76$ participants [mean = 25.1 years, Std. = 4.44]. A subset of representative participants ($N = 24$) also provided body mass index [mean = 22.14 kg m^{-2}, Std. = 3.04]. These age and BMI values approximate to those from other healthy samples in published studies of interoception (Pollatos, Gramann, & Schandry, 2007).

2.2. Interoceptive accuracy

The group as a whole performed above chance for objective performance accuracy, as assessed with heartbeat discrimination [$t(79) = 4.80$, $p < 0.001$] and with heartbeat tracking [mean = 0.66 Std. = 0.21]. We noted a considerable inter-individual variation in interoceptive accuracy (for both tasks), that enabled us to meaningfully explore associations with measures of interoceptive awareness (Fig. 1a) and interoceptive sensibility (Fig. 1b).

2.3. Interoceptive awareness

Metacognitive interoceptive awareness, derived from confidence–accuracy correlations (i.e. Pearson's r) during heartbeat tracking, significantly differed from zero at the overall group level [$t(79) = 5.03$, $p < 0.001$, p-FDR = 0.006]. There was no significant difference in interoceptive awareness between individuals rated high and low on interoceptive accuracy during heartbeat tracking [$t(78) = -1.28$, $p = 0.21$]. In contrast, interoceptive awareness, measured using ROC curve analysis of heartbeat discrimination task data, did *not* reach above-chance significance across the whole group [$t(79) = 1.61$, $p = 0.11$]. However, interoceptive awareness for good heart-beat discriminators did differ from chance [$t(29) = 2.30$, $p = 0.029$, p-FDR = 0.087], whereas poor heart beat discriminators demonstrated no significant interoceptive awareness [$t(49) = -0.04$, $p = 0.97$].

2.4. Determining the relationships between different measures of interoception

2.4.1. Regression analyses

Individual differences in mean interoceptive awareness were significantly related to interoceptive accuracy score across all participants (dependent variable: mean accuracy collapsed across the two objective heartbeat perception tasks) [$t = 3.31$, $\beta = 0.35$, $p = 0.001$]. Interoceptive sensibility (measured by average confidence, and included in step two of the stepwise regression analysis), also predicted mean accuracy [$t = 2.15$, $\beta = 0.22$, $p = 0.035$], independently of mean interoceptive awareness [$t = 3.30$, $\beta = 0.34$,

Table 2
Correlation matrix to demonstrate the relationships between the three distinct facets of interoception during heartbeat tracking and heartbeat discrimination. In each cell, the first number corresponds to the r value, and the second number denotes the p value.

	Heartbeat tracking	Awareness heartbeat tracking (R)	Mean confidence heartbeat tracking	Heartbeat discrimination	Awareness heartbeat discrimination (ROC)	Mean confidence heartbeat discrimination	Awareness portion of BPQ
Heartbeat tracking	1						
Awareness heartbeat tracking (R)	.200 .075	1					
Mean confidence heartbeat tracking	.282** .011	.065 .569	1				
Heartbeat discrimination	.316** .004	.266* .017	.208 .064	1			
Awareness heartbeat discrimination (ROC)	.277* .013	-.103 .362	.138 .223	.204 .070	1		
Mean confidence heartbeat discrimination	.211 .061	-.009 .937	.711** .000	.114 .315	.072 .527	1	
Awareness portion of BPQ	.064 .571	-.209 .063	.162 .151	-.006 .959	.162 .150	.065 .569	1

Key	Colour	Format style
** Below FDR corrected threshold * Significant at uncorrected threshold	Heartbeat tracking Heartbeat discrimination Questionnaire (BPQ)	**Objective measure of interoception** Awareness (metacognitive) measure of interoception *Subjective measure of Interoceptive sensibility*

$p = 0.001$]. The questionnaire measure of general interoceptive sensibility, assessed using the BPQ, was rejected from both regression models [$t = 1.09$, $\beta = 0.12$, $p = 0.23$; $t = 0.81$, $\beta = 0.09$, $p = 0.42$]. Thus, self-rated sensibility across a range of internal bodily sensations did not independently predict objective measures of interoceptive accuracy on either task, beyond what was also accounted for by interoceptive awareness and heartbeat-specific interoceptive

sensibility. Interoceptive accuracy was thus significantly and independently associated with both interoceptive awareness and axis-specific interoceptive sensibility, but not by a more general measure of interoceptive sensibility. As a control, when the regression model was changed so that interoceptive awareness was entered as the dependent variable, it was still predicted by interoceptive accuracy, but not by the general (questionnaire;
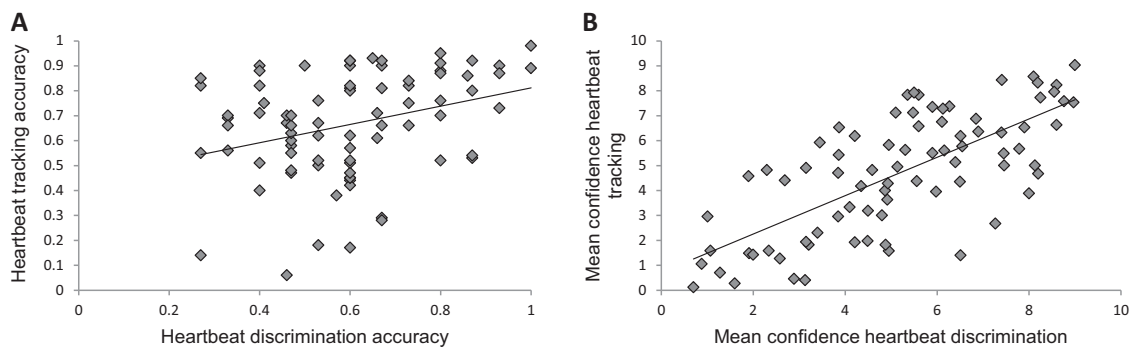
Fig. 1. Correlation between two objective measures of interoceptive accuracy, determined using heartbeat tracking (silent counting of heartbeats in specified time windows) and heartbeat discrimination (judging whether a series of tones are synchronous or asynchronous with heartbeats) (A). Mean confidence, a measure of interoceptive sensibility, derived separately from these two tasks, were also significantly interrelated (B).
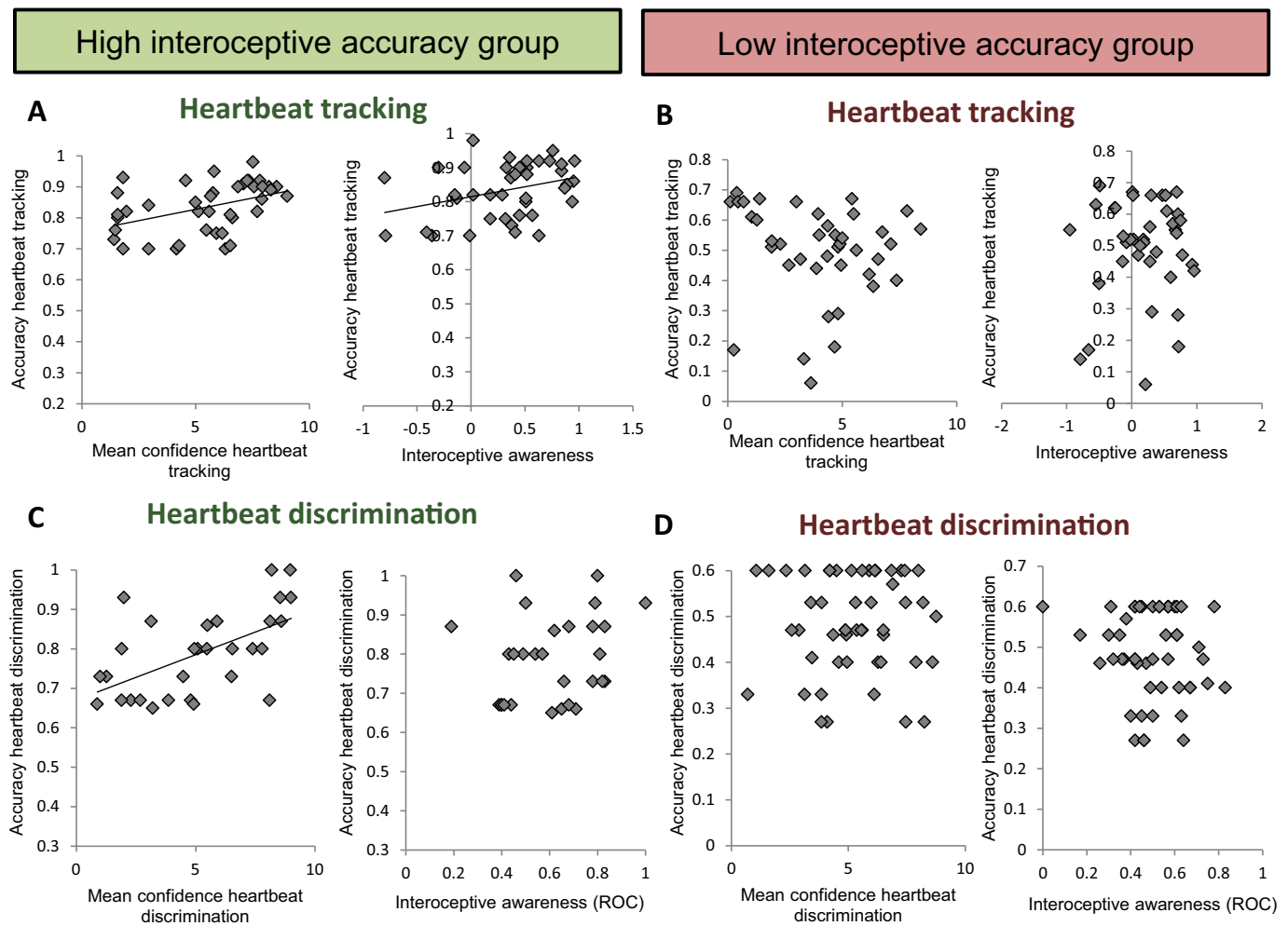
Fig. 2. A correlation between objective interoceptive accuracy and mean confidence was only present in individuals with high interoceptive accuracy during both the heartbeat tracking and heartbeat discrimination tasks. In addition, interoceptive awareness (metacognition) only correlated with heartbeat tracking in the high interoceptive accuracy group. Together, these findings support the hypothesis that relationships between the distinct dimensions of interoceptive awareness are more likely to manifest amongst individuals with high interoceptive accuracy.

$t = -1.45$, $\beta = -0.15$, $p = 0.15$) or specific scores of interoceptive sensibility (heartbeat confidence, $t = -0.411$, $\beta = -0.045$, $p = 0.68$).

2.4.2. Correlational analyses

The two objective tests of interoceptive accuracy, heartbeat discrimination and heartbeat tracking, were significantly correlated [$r = 0.317$, $p = 0.004$, p-FDR $= 0.02$] (see Fig. 1A). The two measures of mean confidence were also highly correlated [$r = 0.711$, $p < 0.001$, p-FDR $= 0.01$] (see Fig. 1B). Interestingly, the two interoceptive awareness measures (derived from confidence-accuracy correlations and area under ROC curve) were not significantly related.

The relationships between our other measures of interoception were much weaker and principally subthreshold significance when the two interoceptive tasks were analyzed separately (see Table 2 for a correlation matrix).

2.4.3. Median split analyses

2.4.3.1. Heartbeat tracking.
Among the high accuracy heartbeat trackers, mean confidence correlated with objective interoceptive accuracy ($r = 0.43$, $p = 0.006$, p-FDR $= 0.036$) (Fig. 2A). Within the low accuracy group, we observed no significant correlation between this subjective measure of task-specific sensibility and objective interoceptive accuracy ($r = -0.13$, $p = 0.42$) (Fig. 2B). Thus, mean confidence successfully predicted mean interoceptive accuracy

only in those individuals who objectively showed high interoceptive accuracy. This was also expressed in interoceptive awareness, which was significantly related to interoceptive accuracy only in the high interoceptive accuracy group [$r = 0.33$, $p = 0.038$] (Fig. 2A). General interoceptive sensibility (BPQ) approached significance ($r = 0.28$, $p = 0.078$) across these individuals. Interestingly, no interoceptive sensibility or awareness measure correlated with objective heartbeat tracking performance in low accuracy heartbeat trackers ($r < 0.5$, $p > 0.4$).

2.4.3.2. Heartbeat discrimination.
Similar effects were observed for heartbeat discrimination: Among high accuracy heartbeat discriminators, mean confidence was significantly correlated with heartbeat discrimination performance ($r = 0.56$, $p = 0.001$, p-FDR $= 0.012$) (Fig. 2C). However, there was no significant correlation with the other measure of interoceptive sensibility, nor with interoceptive awareness. In the low heartbeat discrimination group, heartbeat discrimination performance did not correlate with any measure ($r < -0.12$, $p > 0.40$) (Fig. 2D).

3. Discussion

Our study was motivated by conceptual and methodological variability within the study of interoception. Previous studies

frequently conflate distinct aspects of interoception, namely objective behavioural performance on interoceptive tasks, trait-based self-reported belief about interoceptive aptitude (i.e. interoceptive sensibility), and interoceptive awareness. The frameworks for understanding interoception and its interaction with cognitive and emotional processes are becoming more refined (e.g. Craig, 2004; Critchley, Eccles, & Garfinkel, 2013; Podsiadlo et al., 2009; Seth, 2013; Seth, Suzuki, & Critchley, 2011). These motivate a need for well specified and differentiated empirical measures of interoceptive performance. We therefore used two heartbeat-dependent objective tests of interoceptive accuracy alongside subjective confidence judgements of performance and a self-reported questionnaire rating, to examine the interrelatedness of objective, subjective and awareness measures of interoception.

Our first main observation was that interoceptive accuracy was related to both interoceptive awareness and subjective interoception, as assessed via mean confidence during the heartbeat detection tasks. It is noteworthy that interoceptive awareness was independent of (i.e. did not predict) interoceptive sensibility. This endorses the notion that interoceptive accuracy is the central construct underpinning other interoceptive measures. Our second key observation, in many ways a test of construct validity, was that performance accuracy on the (objective) heartbeat discrimination and (objective) heartbeat tracking tasks were correlated, as were the two mean confidence ratings. However, it is interesting to note that the measures of interoceptive awareness derived from each of the two tasks were not correlated, highlighting differences in conscious monitoring of interoceptive performance that may originate in distinct demand characteristics intrinsic to these tasks. This observation has implications for future studies measuring interoceptive ability.

Across this non-clinical sample of young adults, our data also support distinctions between actual interoceptive accuracy, subjective interoceptive sensibility (mean confidence pertaining to heart and Porges Body Perception Questionnaire) and metacognitive interoceptive awareness of performance. By illustrating this potential for independence, our empirical findings are consistent with our proposed model that defined three distinct dissociable dimensions of interoception (Garfinkel & Critchley, 2013). Importantly, we observed relationships between these dimensions only in people with high interoceptive accuracy, for whom mean confidence and interoceptive awareness were related to performance of the heartbeat tracking task. This is consistent with our hypothesis regarding the primacy of accurate interoception, such that a correspondence between the dimensions would emerge only after a basic accuracy threshold is overcome, which is more likely for individuals showing high objective measures of interoceptive accuracy. Similarly, for the heartbeat discrimination task (which produced lower measures of accuracy than the tracking task), the correlation between confidence and accuracy was apparent in the high interoceptive group only, but not across the whole sample, which again accorded with our specific prediction that relationships between different dimensions of interoception are stronger in individuals with high interoceptive accuracy.

Mental processes can be dissected in terms of the relationship between observed behaviour and awareness. Behaviour and awareness may closely correlate or markedly diverge, often depending on context, as seen in the examples of emotion (Lane, 2008), knowledge and perception (Dienes & Perner, 1999; Seth et al., 2008). This distinction is also reflected across brain networks, wherein distinct patterns of functional brain connectivity correlate with objective performance and subjective beliefs (Barttfeld et al., 2013). With respect to interoception, we hypothesize a similar dissociation of neural substrates encoding discrete bodily changes, including individual heartbeats, putatively in regions such as right anterior insula (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004), and

those underlying the perception, interpretation, and use of such information in the context of other cognitive, motivational, and affective processes, potentially anterior cingulate cortex (Medford & Critchley, 2014) and orbitofrontal areas (Fleming, 2012; Kepecs, Uchida, Zariwala, & Mainen, 2008). Cameron (2001) suggests that the concurrent engagement of central arousal mediated by the reticular system is a likely basis for why only a relatively reduced amount of interoceptive information reaches conscious awareness. Stimulation of the reticular formation can facilitate conduction of exteroceptive and proprioceptive information to the cortex, yet might inhibit interoceptive information flow (Cameron, 2001). It has been previously noted that self-reported heartbeat awareness (using questionnaires) tend not to be strongly correlated with actual (experimentally measured) heartbeat awareness (e.g. Mcfarland, 1975; Whitehead et al., 1977), such that a preoccupation with internal bodily sensations and a belief in one's own interoceptive accuracy does not necessary predict actual interoceptive ability. Deviations between subjective (arguably a more cortical) questionnaire ratings of interoceptive sensibility and interoceptive accuracy are also reported in clinical populations (Garfinkel, Tiley, et al., 2013). We reinforce and extend these observations by systematically dissociating the three dimensions of interoception, and characterizing interoceptive awareness and sensibility in relation to task demand and individual differences in accuracy.

Objective interoceptive accuracy in heartbeat detection does not appear to be enhanced with training in body awareness (though see Schaefer, Egloff, Gerlach, & Witthoft, 2014). Experienced meditators do not differ from non-meditators in heartbeat detection accuracy, yet consistently rate their performance accuracy to be higher (Khalsa et al., 2008). Thus, meditative experience increases a trait measure of confidence in interoceptive ability, which in turn (as much due to under-confidence in non-meditators) increases measured awareness through better correspondence between overall perceived performance accuracy with actual performance (Khalsa et al., 2008). Dissociation between the effects of interoceptive accuracy and awareness is also apparent from interventional studies designed to enhance selectively one dimension of interoception: Heartbeat feedback training, a manipulation to enhance interoceptive awareness, can change the style of decision-making (when people performed the 'ultimatum game') yet at the same time, individual differences in interoceptive accuracy do not affect overall outcome (Lenggenhager, Azevedo, Mancini, & Aglioti, 2013).

While we observed significant relationships between interoceptive accuracy, sensibility and awareness when we collapsed data across heartbeat tracking and discrimination tasks, significant correlations were largely absent when analyses were performed separately for each of the tasks. Thus, the process of increasing statistical power across the group and diluting variance intrinsic to the separate interoceptive tests seems to drill into a fundamental property (putatively representational accuracy) shared across the three dimensions of interoception. The power to detect an effect is also influenced by the number of trials. While our experiment was sufficiently powered to determine interoceptive accuracy, it may have had less than ideal sensitivity for the assessment of metacognition measures (published experiments assessing metacognitive ability typically involve more trials per participant; Green & Swets, 1966; Howard, Bessette-Symons, Zhang, & Hoyer, 2006). Future research should ensure adequate power to determine all objective, subjective/sensibility and awareness measures of interoception, and potentially test even larger samples to identify discrete subgroups of participants. For example, those individuals displaying heightened interoceptive ability across all interoceptive dimensions might be more appropriately compared to participants who show selective deficits, e.g. reduced metacognitive awareness of interoception in the presence of intact interoceptive accuracy. Our median split analysis revealed much stronger correspondence

between interoceptive accuracy and confidence/awareness in a subset of highly interoceptively accurate individuals. Our proposal is that this is due to a threshold effect in interoceptive accuracy (i.e. a minimal level of basic representational fidelity is required). This view is also supported by another recent study in which we found that objective measures of body ownership, assessed in a virtual-reality 'rubber hand illusion' paradigm, were modulated by individual interoceptive accuracy only for those participants with high accuracy, again as determined by a median split (Suzuki, Garfinkel, Critchley, & Seth, 2013).

There is presently limited information about the extent to which interoception concords across different bodily axes. Heartbeat tracking and discrimination tests are assumed to map onto other measures of interoceptive accuracy, for example as evidenced by correlations between performance during heartbeat and gastric detection tasks (Herbert, Muth, Pollatos, & Herbert, 2012; Whitehead & Drescher, 1980). This is in line with recent work which demonstrates a link between interoceptive accuracy and 'intuitive eating', an adaptive measure presumed to reflect an individual's capacity to be guided by sensations of hunger and fullness (Herbert, Blechert, Hautzinger, Matthias, & Herbert, 2013). Certainly, more research is needed to determine the robustness of these relationships (e.g. Whitehead & Drescher, 1980 reported a correlation of $r = 0.51$, $N = 20$) and to establish the degree to which performance on heartbeat detection tests extrapolates to other modalities such as respiration. There is therefore a need for future studies to characterize and compare distinct types of interoceptive accuracy (e.g. respiratory, gastric) alongside heartbeat signals, including both sensibility and awareness measures. This knowledge will enrich our understanding of relationships between accuracy and awareness across a range of visceral bodily signals and have broader clinical relevance. We note also that the correspondence between objective interoceptive performance measures and self-perceived interoception is influenced by the mode of assessment, including choice of questionnaire to assess interoceptive sensibility and objective interoceptive tasks to assess accuracy. Here, our measures of mean interoceptive confidence pertain just to heartbeat signals, thus mirroring measures of interoceptive accuracy and interoceptive awareness. This shared focus on the heart likely accounts for why this subjective sensibility measure yielded closer correspondence to interoceptive accuracy and awareness, when compared to the questionnaire measure of general interoceptive sensibility across different bodily sensations. Also, in the present study, we assessed this more general interoceptive sensibility using the awareness portion of the Body Perception Questionnaire (Porges, 1993). Our finding that this sensibility measure did not positively relate to objectively determined interoceptive accuracy replicates previous research (Fairclough & Goodwin, 2007; Schulz et al., 2013). It remains to be established if other questionnaire measures, such as the Autonomic Perception Questionnaire (Mandler et al., 1958) and Body Awareness Questionnaire (Shields, Mallory, & Simon, 1989), yield closer correspondence to accuracy measures in heartbeat tasks (or tests of other interoceptive axes, e.g. respiratory or gastric cues). Further investigation could help elucidate the extent to which lack of correspondence between interoceptive sensibility and interoceptive accuracy is influenced by the particular methodology used, or reflects an underlying divergence of these two interoceptive constructs.

Our dimensional model provides the foundation and impetus to quantify objective indices of interoceptive performance accuracy against subjective questionnaire measures of interoceptive sensibility, an important development especially given the potential clinical significance of discrepancy between these objective and subjective dimensions. It has been suggested that individuals who are prone to anxiety show an altered interoceptive prediction signal, through which they manifest a heightened discrepancy

between observed and expected bodily states (Paulus & Stein, 2006, 2010). Enhanced interoceptive processing has been documented among individuals with anxiety (Dunn, Stefanovitch, et al., 2010; Pollatos, Traut-Mattausch, Schroeder, & Schandry, 2007; Terasawa et al., 2013), yet this finding has not always been demonstrated (Asmundson, Sandler, Wilson, & Norton, 1993; Craske, Lang, Tsao, Mystkowski, & Rowe, 2001), and may not extrapolate to interoceptive tests using respiration (Bogaerts et al., 2005; van den Bergh et al., 2004). While anxiety patients can manifest a more accurate perception of their interoceptive performance than controls, external factors are more likely to disrupt the extent to which their subjective confidence corresponds with their interoceptive accuracy (Ehlers et al., 1995). An altered interoceptive prediction error signal might derive from discrepancy between the representation of bodily signals and the subjective awareness and evaluation of these signals. Interoceptive error signals may further depend upon representational precision and accuracy of the expected internal state of the body (Seth, 2013; Seth & Critchley, 2013; Seth et al., 2011). These arguments, alongside the present data, further substantiate an emerging theoretical framework of 'interoceptive predictive coding' or 'interoceptive inference' (Gu, Hof, Friston, & Fan, 2013; Seth, 2013; Seth et al., 2011). Here, Bayesian principles of predictive processing (e.g. Clark, 2013) are extended to interoception, such that subjective feeling states (emotions) are proposed to arise from hierarchically-organized probabilistic inference of the causes of interoceptive signals. Importantly, this implies multiple levels of representation of interoceptive sensation and perception which have previously been experimentally and theoretically opaque. The present data from a normative healthy population, and our multidimensional model for interoception, represent important steps towards formalizing this proposed layering of representations underlying interoceptive judgement, plausibly reflecting multiple sources of interoceptive predictions and their independence from veridical interoceptive signals.

Future work should build on integrating these multidimensional theoretical models of interoception and interoceptive predictive coding towards better characterizing the differential contributions of levels of interoceptive representation to clinical psychological and psychosomatic conditions. More generally, an enhanced neurobiological understanding of the underlying neural substrates and interactions will help construct a comprehensive and nuanced understanding of the wider contributions of bodily representation to emotion, cognition, and consciousness.

Acknowledgements

References

Asmundson, G. J., Sandler, L. S., Wilson, K. G., & Norton, G. R. (1993). Panic attacks and interoceptive acuity for cardiac sensations. *Behaviour Research and Therapy*, 31(2), 193–197, pii: 0005-7967(93)90071-2.

Barrett, A. B., Dienes, Z., & Seth, A. K. (2013). Measures of metacognition on signal-detection theoretic models. *Psychological Methods*, 18(4), 535–552. http://dx.doi.org/10.1037/a0033268

Barttfeld, P., Wicker, B., McAleer, P., Belin, P., Cojan, Y., Graziano, M., et al. (2013). Distinct patterns of functional brain connectivity correlate with objective performance and subjective beliefs. *Proceedings of the National Academy of Sciences of the United States of America*, 110(28), 11577–11582. http://dx.doi.org/10.1073/pnas.1301353110

Bogaerts, K., Notebaert, K., Van Diest, I., Devriese, S., De Peuter, S., & Van den Bergh, O. (2005). Accuracy of respiratory symptom perception in different affective contexts. *Journal of Psychosomatic Research*, 58(6), 537–543. http://dx.doi.org/10.1016/j.jpsychores.2004.12.005

Brener, J., & Kluvitse, C. (1988). Heartbeat detection – Judgments of the simultaneity of external stimuli and heartbeats. *Psychophysiology*, 25(5), 554–561. http://dx.doi.org/10.1111/j.1469-8986.1988.tb01891.x

Cameron, O. G. (2001). *Visceral sensory neuroscience: Interoception*. New York, USA: Oxford University Press.

Ceunen, E., Van Diest, I., & Vlaeyen, J. W. S. (2013). Accuracy and awareness of perception: Related, yet distinct (commentary on Herbert et al., 2012). *Biological Psychology*, 92(2), 426–427. http://dx.doi.org/10.1016/j.biopsycho.2012.09.012

Cheesman, J., & Merikle, P. M. (1984). Priming with and without awareness. *Perception & Psychophysics*, 36(4), 387–395. http://dx.doi.org/10.3758/Bf03202793

Cheesman, J., & Merikle, P. M. (1986). Distinguishing conscious from unconscious perceptual processes. *Canadian Journal of Psychology*, 40(4), 343–367.

Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behavioral and Brain Sciences*, 36(3), 181–204. http://dx.doi.org/10.1017/S0140525X12000477, pii: S0140525X12000477

Craig, A. D. (2002). How do you feel? Interoception: The sense of the physiological condition of the body. *Nature Reviews Neuroscience*, 3(8), 655–666. http://dx.doi.org/10.1038/Nrn894

Craig, A. D. (2004). Human feelings: Why are some more aware than others? *Trends in Cognitive Sciences*, 8(6), 239–241. http://dx.doi.org/10.1016/j.tics.2004.04.004, pii: S1364661304001032

Craske, M. G., Lang, A. J., Tsao, J. C., Mystkowski, J. L., & Rowe, M. K. (2001). Reactivity to interoceptive cues in nocturnal panic. *Journal of Behavior Therapy and Experimental Psychiatry*, 32(3), 173–190. pii: S0005-7916(01)00033-7.

Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, 7(2), 189–195. http://dx.doi.org/10.1038/Nn1176

Critchley, H. D., Eccles, J., & Garfinkel, S. N. (2013). Interaction between cognition, emotion, and the autonomic nervous system. *Handbook of Clinical Neurology*, 117, 59–77. http://dx.doi.org/10.1016/B978-0-444-53491-0.00006-7, pii: B978-0-444-53491-0.00006-7

Damasio, A. R., Tranel, D., & Damasio, H. C. (1991). Somatic markers and the guidance of behavior: Theory and preliminary testing. In H. S. Levin, H. M. Eisenberg, & A. L. Benton (Eds.), *Frontal lobe function and dysfunction*. New York: Oxford University Press (pp. xv, 427p.).

Dienes, Z., & Berry, D. (1997). Implicit learning: Below the subjective threshold. *Psychonomic Bulletin & Review*, 4(1), 3–23. http://dx.doi.org/10.3758/Bf03210769

Dienes, Z., & Perner, J. (1999). A theory of implicit and explicit knowledge. *Behavioral and Brain Sciences*, 22(5), 735.

Dunn, B. D., Galton, H. C., Morgan, R., Evans, D., Oliver, C., Meyer, M., et al. (2010). Listening to your heart: How interoception shapes emotion experience and intuitive decision making. *Psychological Science*, 21(12), 1835–1844. http://dx.doi.org/10.1177/0956797610389191

Dunn, B. D., Stefanovitch, I., Evans, D., Oliver, C., Hawkins, A., & Dalgleish, T. (2010). Can you feel the beat? Interoceptive awareness is an interactive function of anxiety- and depression-specific symptom dimensions. *Behaviour Research and Therapy*, 48(11), 1133–1138. http://dx.doi.org/10.1016/j.brat.2010.07.006

Ehlers, A., Breuer, P., Dohn, D., & Fiegenbaum, W. (1995). Heartbeat perception and panic disorder – possible explanations for discrepant findings. *Behaviour Research and Therapy*, 33(1), 69–76. http://dx.doi.org/10.1016/0005-7967(94)E0002-Z

Ernst, J., Boker, H., Hattenschwiler, J., Schupbach, D., Northoff, G., Seifritz, E., et al. (2013). The association of interoceptive awareness and alexithymia with neurotransmitter concentrations in insula and anterior cingulate. *Social Cognitive and Affective Neuroscience*, http://dx.doi.org/10.1093/scan/nst058

Fairclough, S. H., & Goodwin, L. (2007). The effect of psychological stress and relaxation on interoceptive accuracy: Implications for symptom perception. *Journal of Psychosomatic Research*, 62(3), 289–295. http://dx.doi.org/10.1016/j.jpsychores.2006.10.017

Fleming, S. M. (2012). Relating introspective accuracy to individual differences in brain structure (vol 329, pg 1541, 2010). *Science*, 336(6082), 670-670.

Fleming, S. M., Weil, R. S., Nagy, Z., Dolan, R. J., & Rees, G. (2010). Relating introspective accuracy to individual differences in brain structure. *Science*, 329(5998), 1541–1543. http://dx.doi.org/10.1126/science.1191883

Galvin, S. J., Podd, J. V., Drga, V., & Whitmore, J. (2003). Type 2 tasks in the theory of signal detectability: Discrimination between correct and incorrect decisions. *Psychonomic Bulletin & Review*, 10(4), 843–876. http://dx.doi.org/10.3758/Bf03196546

Garfinkel, S. N., & Critchley, H. D. (2013). Interoception, emotion and brain: New insights link internal physiology to social behaviour. Commentary on: "Anterior insular cortex mediates bodily sensibility and social anxiety" by Terasawa et al. (2012). *Social Cognitive and Affective Neuroscience*, 8(3), 231–234. http://dx.doi.org/10.1093/Scan/Nss140

Garfinkel, S. N., Barrett, A. B., Minati, L., Dolan, R. J., Seth, A. K., & Critchley, H. D. (2013). What the heart forgets: Cardiac timing influences memory for words and is modulated by metacognition and interoceptive sensitivity. *Psychophysiology*, 50(6), 505–512. http://dx.doi.org/10.1111/Psyp.12039

Garfinkel, S. N., Tiley, C., O'Keeffe, S., & Critchley, H. D. (2013). Disassociating interoceptive focus and interoceptive accuracy in asperger's syndrome. *Psychosomatic Medicine*, 75(3). A161-A161.

Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.

Gu, X. S., Hof, P. R., Friston, K. J., & Fan, J. (2013). Anterior insular cortex and emotional awareness. *Journal of Comparative Neurology*, 521(15), 3371–3388. http://dx.doi.org/10.1002/Cne.23368

Hart, N., McGowan, J., Minati, L., & Critchley, H. D. (2013). Emotional regulation and bodily sensation: Interoceptive awareness is intact in borderline personality disorder. *Journal of Personality Disorders*, 27(4), 506–518.

Herbert, B. M., Muth, E. R., Pollatos, O., & Herbert, C. (2012). Interoception across modalities: On the relationship between cardiac awareness and the sensitivity for gastric functions. *PLoS ONE*, 7(5.) http://dx.doi.org/10.1371/journal.pone.0036646

Herbert, B. M., Blechert, J., Hautzinger, M., Matthias, E., & Herbert, C. (2013). Intuitive eating is associated with interoceptive sensitivity. Effects on body mass index. *Appetite*, 70, 22–30. http://dx.doi.org/10.1016/j.appet.2013.06.082

Howard, M. W., Bessette-Symons, B., Zhang, Y. F., & Hoyer, W. J. (2006). Aging selectively impairs recollection in recognition memory for pictures: Evidence from modeling and receiver operating characteristic curves. *Psychology and Aging*, 21(1), 96–106. http://dx.doi.org/10.1037/0882-7974.21.1.96

Katkin, E. S., Reed, S. D., & Deroo, C. (1983). A methodological analysis of 3 techniques for the assessment of individual-differences in heartbeat detection. *Psychophysiology*, 20(4), 452-452.

Kepecs, A., Uchida, N., Zariwala, H. A., & Mainen, Z. F. (2008). Neural correlates, computation and behavioural impact of decision confidence. *Nature*, 455(7210), U227–U255. http://dx.doi.org/10.1038/Nature07200

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

King, J. R., & Dehaene, S. (2014). A model of subjective report and objective discrimination as categorical decisions in a vast representational space. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 369(1641) http://dx.doi.org/10.1098/rstb.2013.0204

Knoll, J. F., & Hodapp, V. (1992). A comparison between 2 methods for assessing heartbeat perception. *Psychophysiology*, 29(2), 218–222. http://dx.doi.org/10.1111/j.1469-8986.1992.tb01689.x

Lane, R. D. (2008). Neural substrates of implicit and explicit emotional processes: A unifying framework for psychosomatic medicine. *Psychosomatic Medicine*, 70(2), 214–231. http://dx.doi.org/10.1097/Psy.0b013e3181647e44

Lange, C. G., & James, W. (1967). *The emotions*. New York/London: Hafner Publishing Co (edited by Knight Dunlap – Reprinted).

Lenggenhager, B., Azevedo, R. T., Mancini, A., & Aglioti, S. M. (2013). Listening to your heart and feeling yourself: Effects of exposure to interoceptive signals during the ultimatum game. *Experimental Brain Research*, 230(2), 233–241. http://dx.doi.org/10.1007/s00221-013-3647-5

Mandler, G., Mandler, J. M., & Uviller, E. T. (1958). Autonomic feedback – the perception of autonomic activity. *Journal of Abnormal and Social Psychology*, 56(3), 367–373. http://dx.doi.org/10.1037/H0048083

Mcfarland, R. A. (1975). Heart-rate perception and heart-rate control. *Psychophysiology*, 12(4), 402–405. http://dx.doi.org/10.1111/j.1469-8986.1975.tb00011.x

Medford, N., & Critchley, H. D. (2014). Interoception and psychopathology. In A. L. Mishara, P. Corlett, A. Fletcher, A. Kranjec, & M. A. Schwartz (Eds.), *Phenomenological Neuropsychiatry, How Experience Bridges Clinic with Clinical Neuroscience*. New York: Springer, in press.

Paulus, M. P., & Stein, M. B. (2006). An insular view of anxiety. *Biological Psychiatry*, 60(4), 383–387. http://dx.doi.org/10.1016/j.biopsych.2006.03.042

Paulus, M. P., & Stein, M. B. (2010). Interoception in anxiety and depression. *Brain Structure & Function*, 214(5–6), 451–463. http://dx.doi.org/10.1007/s00429-010-0258-9

Payne, R. A., Symeonides, C. N., Webb, D. J., & Maxwell, S. R. J. (2006). Pulse transit time measured from the ECG: An unreliable marker of beat-to-beat blood pressure. *Journal of Applied Physiology*, 100(1), 136–141. http://dx.doi.org/10.1152/japplphysiol.00657.2005

Phillips, G. C., Jones, G. E., Rieger, E. J., & Snell, J. B. (1999). Effects of the presentation of false heart-rate feedback on the performance of two common heartbeat-detection tasks. *Psychophysiology*, 36(4), 504–510. http://dx.doi.org/10.1017/S0048577299980071

Podsiadlo, P., Michel, M., Critchley, K., Srivastava, S., Qin, M., Lee, J. W., et al. (2009). Diffusional self-organization in exponential layer-by-layer films with micro- and nanoscale periodicity. *Angewandte Chemie-International Edition*, 48(38), 7073–7077. http://dx.doi.org/10.1002/anie.200901720

Pollatos, O., Gramann, K., & Schandry, R. (2007). Neural systems connecting interoceptive awareness and feelings. *Human Brain Mapping*, 28(1), 9–18. http://dx.doi.org/10.1002/Hbm.20258

Pollatos, O., Traut-Mattausch, E., Schroeder, H., & Schandry, R. (2007). Interoceptive awareness mediates the relationship between anxiety and the intensity of unpleasant feelings. *Journal of Anxiety Disorders*, 21(7), 931–943. http://dx.doi.org/10.1016/j.janxdis.2006.12.004. pii: S0887-6185(06)00232-5

Porges, S. (1993). *Body perception questionnaire: Laboratory of development assessment*. University of Maryland.

Schaefer, M., Egloff, B., Gerlach, A. L., & Witthoft, M. (2014). Improving heartbeat perception in patients with medically unexplained symptoms reduces symptom distress. *Biological Psychology*, 101, 69–76. http://dx.doi.org/10.1016/j.biopsycho.2014.05.012. pii: S0301-0511(14)00154-9

Schandry, R. (1981). Heart beat perception and emotional experience. *Psychophysiology*, 18(4), 483–488. http://dx.doi.org/10.1111/j.1469-8986.1981.tb02486.x

Schulz, A., Lass-Hennemann, J., Sutterlin, S., Schachinger, H., & Vogele, C. (2013). Cold pressor stress induces opposite effects on cardioceptive

accuracy dependent on assessment paradigm. *Biological Psychology*, *93*(1), 167–174. http://dx.doi.org/10.1016/j.biopsycho.2013.01.007

Seth, A. K. (2013). Interoceptive inference, emotion, and the embodied self. *Trends in Cognitive Sciences*, *17*(11), 565–573. http://dx.doi.org/10.1016/j.tics.2013.09.007. pii: S1364-6613(13)00211-8

Seth, A. K., & Critchley, H. D. (2013). Extending predictive processing to the body: Emotion as interoceptive inference. *Behavioral and Brain Sciences*, *36*(3), 227–228. http://dx.doi.org/10.1017/S0140525X12002270

Seth, A. K., Dienes, Z., Cleeremans, A., Overgaard, M., & Pessoa, L. (2008). Measuring consciousness: Relating behavioural and neurophysiological approaches. *Trends in Cognitive Sciences*, *12*(8), 314–321. http://dx.doi.org/10.1016/j.tics.2008.04.008. pii: S1364-6613(08)00151-4

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

Sherrington, C. S. (1948). *The integrative action of the nervous system*. Cambridge, UK: Cambridge Univ. Press.

Shields, S. A., Mallory, M. E., & Simon, A. (1989). The body awareness questionnaire – reliability and validity. *Journal of Personality Assessment*, *53*(4), 802–815. http://dx.doi.org/10.1207/s15327752jpa5304_16

Snodgrass, M., & Shevrin, H. (2006). Unconscious inhibition and facilitation at the objective detection threshold: Replicable and qualitatively different unconscious perceptual effects. *Cognition*, *101*(1), 43–79. http://dx.doi.org/10.1016/j.cognition.2005.06.006

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

Terasawa, Y., Shibata, M., Moriguchi, Y., & Umeda, S. (2013). Anterior insular cortex mediates bodily sensibility and social anxiety. *Social Cognitive and Affective Neuroscience*, *8*(3), 259–266. http://dx.doi.org/10.1093/Scan/Nss108

Tsakiris, M., Tajadura-Jimenez, A., & Costantini, M. (2011). Just a heartbeat away from one's body: Interoceptive sensitivity predicts malleability of body-representations. *Proceedings of the Royal Society B-Biological Sciences*, *278*(1717), 2470–2476. http://dx.doi.org/10.1098/rspb.2010.2547

van den Bergh, O., Winters, W., Devriese, S., van Diest, I., Vos, G., & de Peuter, S. (2004). Accuracy of respiratory symptom perception in persons with high and low negative affectivity. *Psychology & Health*, *19*(2), 213–222. http://dx.doi.org/10.1080/08870440410001675627

Werner, N. S., Peres, I., Duschek, S., & Schandry, R. (2010). Implicit memory for emotional words is modulated by cardiac perception. *Biological Psychology*, *85*(3), 370–376. http://dx.doi.org/10.1016/j.biopsycho.2010.08.008

Werner, N. S., Schweitzer, N., Meindl, T., Duschek, S., Kambeiz, J., & Schandry, R. (2013). Interoceptive awareness moderates neural activity during decision-making. *Biological Psychology*, *94*(3), 498–506.

Whitehead, W. E., & Drescher, V. M. (1980). Perception of gastric contractions and self-control of gastric-motility. *Psychophysiology*, *17*(6), 552–558. http://dx.doi.org/10.1111/j.1469-8986.1980.tb02296.x

Whitehead, W. E., Drescher, V. M., Heiman, P., & Blackwell, B. (1977). Relation of heart-rate control to heartbeat perception. *Biofeedback and Self-Regulation*, *2*(4), 371–392. http://dx.doi.org/10.1007/Bf00998623

Wiebking, C., de Greck, M., Duncan, N. W., Heinzel, A., Tempelmann, C., & Northoff, G. (2011). Are emotions associated with activity during rest or interoception? An exploratory fMRI study in healthy subjects. *Neuroscience Letters*, *491*(1), 87–92. http://dx.doi.org/10.1016/j.neulet.2011.01.012

Wiens, S., & Palmer, S. N. (2001). Quadratic trend analysis and heartbeat detection. *Biological Psychology*, *58*(2), 159–175. http://dx.doi.org/10.1016/S0301-0511(01)00110-7

Wiens, S., Mezzacappa, E. S., & Katkin, E. S. (2000). Heartbeat detection and the experience of emotions. *Cognition and Emotion*, *14*(3), 417–427.