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Towards a comprehensive assessment of interoception in a multi-dimensional framework

Chatrin Suksasilp, Sarah N. Garfinkel *

Institute of Cognitive Neuroscience, UCL, UK

A R T I C L E I N F O

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A B S T R A C T

Interoception has historically been assessed using behavioural tests of accuracy, self-report measures or through the characterisation of neural signals underlying interoceptive processing. More recent conceptualisations of interoception incorporate interoceptive attention and higher-order measures related to the interpretation of interoceptive signals. At present, these interoceptive dimensions are largely assessed in isolation, yet this fails to capture the complexity of interoception. Comprehensive assessment across interoceptive dimensions can determine the full operation of general interoceptive function. Current work suggests that these interoceptive processes may be dissociable across dimensions and bodily axes, with differential mapping to cognitive and emotion processing. To characterise differences in interoceptive profiles, all interoceptive dimensions can be assessed within individuals, both within a single bodily axis (e.g., cardiac) or across bodily axes. Future work can better delineate how these interoceptive measures correspond to different types of processing. Comprehensive interoceptive assessment can help isolate selective interoceptive disruptions in different clinical conditions.

1. Introduction

Initial accounts of interoception focused on the sensory nerve receptors (termed ’interoceptors’; Sherrington, 1952) and the resultant ‘neural sensing’ of bodily signals (Cameron, 2001; Sherrington, 1952). Predicated on models which view interoception within a multi-dimensional framework (e.g., Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015), contemporary definitions of interoception highlight the sensing, interpretation and integration of signals originating from within the body across both conscious and unconscious levels of processing (Khalsa et al., 2018). This received view of interoception requires its comprehensive assessment to extend beyond a single measure (e.g., behavioural accuracy) and to instead incorporate the multi-dimensional processing of interoception across neural, behavioural, self-report, attentional, and higher order measures.

This paper outlines a comprehensive multi-dimensional framework for assessing general functioning and individual differences in interoception, building on earlier dimensional approaches (e.g., Critchley & Garfinkel, 2017; Garfinkel et al., 2015; Khalsa et al., 2018), where interoceptive ‘dimension’ is used interchangeably with ‘level of processing’. Specifically, the dimensional approach to interoception is extended here to incorporate lower levels of processing, including visceral, neural (hereby referring to the central nervous system), and preconscious levels, along with higher-order interpretational dimensions (Fig. 1, Table 1). An overview of current methodologies for assessing general functioning and individual differences in these interoceptive dimensions will be outlined. Studies reviewed will predominantly centre on cardiovascular, gastric, and respiratory bodily axes, where bodily ‘axis’ denotes a specific organ system together with its peripheral innervation and central control mechanisms. This focus reflects the current emphasis within the literature; however, work in other bodily axes will also be discussed. Despite each dimension offering particular insight into individual differences in interoception that may relate differently to cognitive processing, emotional constructs and clinical status, these dimensions are, at present, largely assessed in isolation. Concurrent assessment of dissociable interoceptive dimensions will aid understanding of whether specific interoceptive processing corresponds to, and influences, aspects of emotion and cognition. Interoceptive assessment across multiple dimensions can also inform about the nature of selective interoceptive disturbances in distinct clinical conditions, highlighting the potential benefits of comprehensive interoceptive assessment for advancing research into altered mechanisms and potential treatment targets. Assessing interoception across levels and bodily axes may also clarify whether

* Correspondence to: Institute of Cognitive Neuroscience, UCL, Alexandra House, 17–19 Queen Square, Bloomsbury, London WC1N 3AZ, UK.
E-mail address: s.garfinkel@ucl.ac.uk (S.N. Garfinkel).

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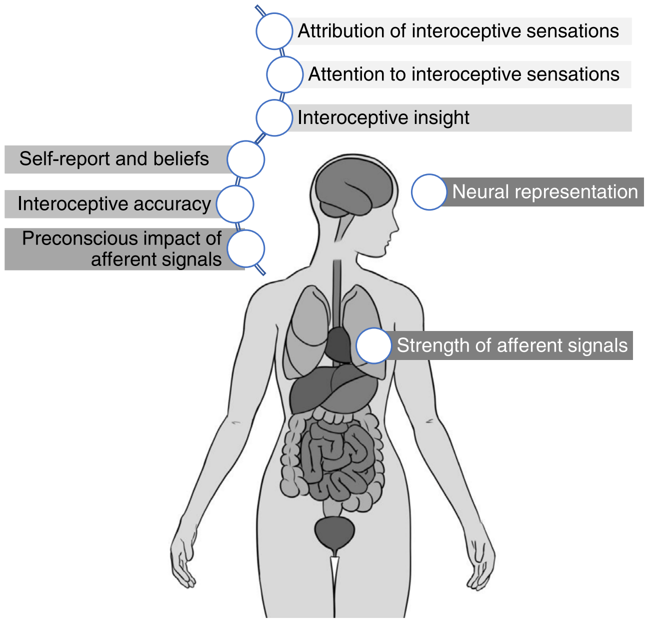

Fig. 1. Dimensions of interoception. Full characterisation of interoception incorporating the (central) neural representation of afferent signals; the strength and nature of afferent signals; the preconscious impact of afferent signals; interoceptive accuracy ascertained through behavioural tests; measures of conscious and unconscious beliefs about interoceptive aptitude, experiences, and sensations; interoceptive insight, a metacognitive measure denoting the correspondence of self-report (e.g. confidence) and behavioural (e.g. accuracy) measures; attention to interoceptive sensations (e.g. relative to exteroceptive attention); and attribution of interoceptive sensations, such as perceived threat.

Table 1
(Glossary) Definitions of the dimensions referred to in this paper are provided below.

Dimension	Definition
Neural representation	Central nervous activity associated with interoceptive processing, including the coupling of central activity with afferent physiological signals.
Strength of afferent signals	The strength and nature of signals originating from the periphery that communicate interoceptive states to the central nervous system.
Preconscious impact of afferent signals	The effect of fluctuations in afferent signals on their central neural representation and the processing of external stimuli.
Interoceptive accuracy	Correct and precise monitoring i.e. the correspondence between objectively measured physiological events and individuals' reported experience of those events, ascertained through behavioural tests.
Self-report and Interoceptive Beliefs	Measures of beliefs, both available to and beyond conscious access, concerning individuals' interoceptive sensations and experiences. Includes self-report measures, such as questionnaires and confidence ratings, and task-based measures of (implicit) prior beliefs thought to influence interoceptive perception.
Interoceptive insight	Metacognitive evaluation of experience/performance e.g., the correspondence between accuracy during an interoceptive task, and (self-reported) perceived accuracy or confidence during the task.
Interoceptive attention	Observing internal bodily sensations. Includes purposefully attending to interoceptive sensations when instructed, as well as habitual tendency to attend to interoceptive sensations, relative to exteroceptive sensations.
Attribution of interoceptive sensations	Interpretation of interoceptive sensations and their causes, such as perceived threat.

interoception can be viewed as a unitary construct with dimensions, addressing a core assumption in interoception research.

2. Central neural representation

Neural approaches to interoception take different forms, including measurement of afferent signals expressed in brain, (central) neural activation while attending to interoceptive sensations, and neural correlates of interoceptive accuracy.

For the neural representation of afferent signals, cardiac interoception research has focused on the heartbeat-evoked potential (HEP), the electrophysiological brain response that reflects cortical processing of individual heartbeats. The HEP is typically computed using scalp electroencephalography (EEG) via the event-related potential time-locked to participants' heartbeats (Park & Blanke, 2019; Schandry et al., 1986). The HEP signal is altered in individuals with changes in emotion processing; HEP amplitude has been found to distinguish people with anxiety, depression, and borderline personality disorder from healthy comparisons (Müller et al., 2015; Pang et al., 2019; Terhaar, Viola, Bär, & Debener, 2012). HEP amplitude increases with attention to the heart (Hodossy et al., 2021; Petzschner, Weber, Wellstein, Paolini, Do & Stephan, 2019). It has also been suggested that HEP amplitude reflects a precision-weighted prediction error for individual heartbeats, or the mismatch between the brain's prediction and incoming sensory evidence, which is proposed to drive learning under a predictive processing framework (Ainley, Apps, Fotopoulou, & Tsakiris, 2016; Petzschner et al., 2019). HEP studies to date have been highly heterogeneous in the preprocessing and measurement of HEP, as well as in how to remove the cardiac field artifact (Park & Blanke, 2019). As a result, HEP effects have been found in varying directions, locations, and time-windows following the heartbeat (for a review and meta-analysis, see Coll et al., 2020). It remains unclear what computational or physiological variables HEP amplitude encodes, and therefore what altered HEPs reflect in clinical populations.

In the gastric axis, rhythmic brain activity in the right insula and bilateral occipito-parietal regions, recorded using magnetoencephalography, is coupled to the infra-slow rhythm of gastric activity, recorded using electrogastrography (EGG). The phase of gastric activity has been shown to constrain the amplitude of the alpha rhythm (phase-amplitude coupling), explaining 8% of alpha variance (Richter, Babo-Rebelo, Schwartz, & Tallon-Baudry, 2017). In another report, stomach stimulation using ingestible vibration capsules produced electrophysiological responses in parieto-occipital regions near the midline, 300–600 ms after stimulation onset. These responses, dubbed 'gastric-evoked potentials' showed dose dependent increases in activity (Mayeli et al., 2021a). Both the degree of phase-amplitude coupling between gastric and central neural activity, and the amplitude of gastric-evoked potentials, represent potential individual differences measures of how gastric afferent signals are represented centrally.

Respiration modulates central neural activity, exhibiting phase-amplitude coupling with higher frequency neural oscillations. Studies in epilepsy patients using intracranial EEG via subdural electrode implants demonstrate that respiratory phase modulates gamma power in the frontal, parietal, and temporal cortex, as well as several bands in the piriform cortex, amygdala, and hippocampus (Zelano et al., 2016). Phase-amplitude coupling effects occurred when patients breathed through the nose, but not through the mouth, suggesting that effects are driven by sensory input from the mechano-sensitive olfactory sensory neurons in the nose (Varga & Heck, 2017).

Activity in different organs has been coupled to central neural activity using fMRI to reveal brain mechanisms of interoceptive integration. A sliding window analysis to explore coupling of high frequency heart rate variability with neural activity, demonstrates central representation in the posterior insula (Nguyen, Breakspear, Hu, & Guo, 2016). A gastric network in the brain based on the delayed connectivity with the slow electrical rhythm generated in the stomach is comprised of key identifiable regions including somatosensory cortices, dorsal precuneus and occipital cortex (Rebollo, Devauchelle, Béranger, & Tallon-Baudry, 2018). These techniques for investigating the coupling of organ activity to brain activity are distinct, yet complementary, to fMRI paradigms that explore central neural activation during interoceptive behavioural tasks. Here, activity underlying attention to visceral interoceptive sensations is contrasted to activity underlying exteroceptive processing, demonstrating differences in clinical conditions such as depression in the dorsal mid-insula cortex (Avery, Drevets, Moseman, Bodurka, Barcalow, & Simmons, 2014). Such paradigms do not reveal whether bodily signals are being detected veridically; attention does not equate to accuracy. Experiments that correlate brain activation during interoception with a measure of interoceptive accuracy reveal a relationship between the right anterior insula and interoceptive accuracy in the cardiac axis (Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004). Rectal stimulation can be differentiated from anal stimulation, using a catheter placed at different points within the anal verge, with the former relating to interoception and the latter providing a somatosensory control condition. Insula activity was observed following both anal and rectal stimulation (Hobday, Aziz, Thacker, Hollander, Jackson, & Thompson, 2001), though it is worth noting that this procedure fails to differentiate the affective reaction from the brain activity elicited by the stimulation.

These studies illustrate the many techniques for examining interoceptive processing through its expression in brain signals. These techniques typically use an event-related approach, or the mathematic coupling of organ activity with neural activity to determine localised patterns of co-activity. These approaches can provide insight into brain regions underlying both interoceptive attention and interoceptive accuracy. Together, these methods have the potential to reveal nuanced individual differences in the central processing of interoception.

3. Strength of afferent signals

The central nervous system receives ascending communication of afferent interoceptive signals from the periphery via sensory transducers, such as mechanoreceptors, chemoreceptors, and osmoreceptors (Berntson & Khalsa, 2021; Jänig, 1996). Visceral afferent signals are principally communicated to the brain via the vagus nerve, where viscerosensory inputs are carried to a neural 'hub' in the nucleus of the solitary tract, followed by the parabrachial nucleus with subsequent projections to key central areas such as the thalamus and anterior cingulate (Critchley & Harrison, 2013; see Fig. 1). While the nature of the afferent signals themselves do not fall under the strict definition of interoception, their strength and variability can influence interoceptive processing, such as their neural representation and the accuracy with which they are perceived. Their measurement and inclusion in analysis models may thus further inform both assessing normative interoceptive function and identifying loci of interoceptive impairment (i.e., in the diminished generation of autonomic signals themselves, reducing neural sensing or impairing perception via measures of interoceptive accuracy).

Individual differences in the strength and nature of afferent signals might also contribute to emotional experience and clinical symptoms, given evidence that phasic fluctuations in cardiac, respiratory, and gastric signals modulate emotional processing (Azzalini et al., 2019; Critchley & Harrison, 2013). For instance in depression, altered cardiovascular function including attenuated heart rate, heart rate variability, and blood pressure responses (Carroll, Phillips, Hunt, & Der, 2007; Koch, Wilhelm, Salzmann, Rief, & Euteneuer, 2019), might drive emotional symptoms together with impaired interoceptive accuracy and diminished insula activity during interoceptive attention (Avery et al., 2014).

Afferent signal strength can be (indirectly) assessed by externally measuring physiological variables that activate sensory transducers at specific visceral organs. The state of cardiovascular arousal is communicated to the brain in bursts of activity by baroreceptors, stretch sensitive receptors that are stimulated by the ejection of blood at systole with each 'heartbeat'. Baroreceptors therefore transiently activate during the cardiac cycle, signalling the timing and strength of individual heartbeats via the vagus and glossopharyngeal nerves (Berntson & Khalsa, 2021; Min et al., 2019; Zeng et al., 2018). When these signals are elevated, they can trigger the slowing of the next heartbeat and peripheral vasodilation, lowering blood pressure. Physiological variables that correlate with arterial stretch, such as systolic and diastolic blood pressure, pulse pressure wave amplitude, or cardiac output, may serve as markers of cardiac signal strength with bearing on different measures of interoception. For relevant measurement guidelines, see Sherwood, Allen, Fahrenberg, Kelsey, Lovallo, and Van Doornen (1990) and Shapiro et al. (1996).

In the gastric axis, the stomach contains vagal and spinal mechanoreceptors that activate during stomach contraction or distension by ingested food (Berthoud et al., 2001). EGG can measure myoelectrical activity at the stomach to track the frequency and amplitude of gastric muscle contractions (Harrison, Gray, Gianaros, & Critchley, 2010). For a technical overview of recording and analysing EGG data, see Yin and Chen (2013), and while there is no universally agreed standardised procedure to date, see Wolpert et al. (2020) for a recent proposal.

In the respiratory axis, *Piezo2* mechanoreceptors transduce changes in lung volume to support normal breathing (Nonomura et al., 2017), and convey this sensory information to the brain via vagal sensory neurons (Lee & Yu, 2014). Lung volume can be indirectly estimated by measuring chest and abdomen displacements using a range of techniques (e.g., piezoelectric, pneumatic, inductance-based). The most accurate of these is respiratory inductance plethysmography, which relies on insulated coils strapped over the thorax and abdomen, that vary in electrical induction with displacement (for an overview of methods and relevant measurement guidelines, see Ritz et al., 2002). To assess timing of the respiratory cycle, a pressure sensor mounted in a nasal cannula can measure nasopharyngeal airflow (Zelano et al., 2016), indexing activation of mechano-sensitive olfactory sensory neurons (Grosmaitre, Santarelli, Tan, Luo, & Ma, 2007). However, sensing nasopharyngeal airflow during exhalation occurs via somatosensory receptors in the nasal mucosa, and thus can be classified as principally exteroceptive.

Autonomic parameters related to the strength of visceral signals themselves may serve as meaningful additions to models designed to assess the locus of interoceptive impairments.

4. Preconscious impact of afferent signals

There is a growing literature on how afferent signals from various visceral systems, referred to here as 'interoceptive channels', exert a preconscious impact on the processing of external stimuli and neural (central) activity. Here, the timing of stimulus processing in relation to bodily state and body-brain interactions can change the way that stimuli are processed. For example, with each heartbeat, stretch-sensitive baroreceptors located in the aortic arch are activated, conveying to the brain through bursts of activity how fast and strong the heart is beating (Berntson & Khalsa, 2021; Min et al., 2019; Zeng et al., 2018). Procedures for probing the impact of the cardiovascular channel time-lock brief stimulus presentations to bursts of baroreceptor activity (at systole) or in between heartbeats (at late diastole), when baroreceptors, and thus this cardiac channel, are quiescent (Garfinkel & Critchley, 2016). Studies using this methodology have primarily demonstrated inhibitory effects of the cardiovascular channel, in line with the historical view that cardiovascular signals to the brain have an inhibitory or distracting effect, serving to both distract and interfere with perception and cognition (Lacey & Lacey, 1978). When presented at systole, electrocutaneous shocks produce reduced pain sensation (Wilkinson et al., 2013), loud auditory stimuli produce smaller startle responses (Müller et al., 2015; Schulz, Schilling, Vögele, & Schächinger, 2019), and word stimuli are less well remembered relative to when presented at diastole (Garfinkel, Barrett, Minati, Dolan, Seth, &

Critchley, 2013). In contrast, the cardiovascular channel can enhance fear processing: at systole, fearful faces are more easily detected and rated as more intense (Garfinkel, Minati, Gray, Seth, Dolan, & Critchley, 2014), and painful cutaneous shocks produce greater threat learning for stimuli encoded at systole, as indexed using skin conductance response, relative to stimuli encoded at diastole (Garfinkel et al., 2020).

Other procedures involve experimentally manipulating organ physiology to assess the associated change in stimulus processing. Non-invasive, automated neck suction can artificially activate the carotid baroreceptors, reducing pain sensation (Dworkin et al., 1994) and altering both appraisal of, and neural responses to, fearful faces (Makovac et al., 2015).

The impact of the interoceptive channel on stimulus processing appears to distinguish clinical groups from healthy controls. For instance, the systolic effect on startle responses is diminished in individuals with depersonalization-/derealization disorder (Schulz et al., 2016). Cardiac facilitation of fear via the active heart-brain channel is particularly sensitive to individual differences in anxiety (Garfinkel et al., 2020), again demonstrating how individual characteristics can shape interoceptive processing with resultant effects on emotion. To assess the impact of the gastric channel in emotional experience, in particular disgust, initial studies took a correlational approach in which participants viewed films that evoked disgust, while reactive gastric muscle contractions were tracked using EGG. These studies found that self-reported disgust correlated with the magnitude of increase in rapid dysregulated gastric responses or tachygastria (Harrison et al., 2010; Shenhav & Mendes, 2014). Nord, Dalmaijer, Armstrong, Baker, and Dalgleish (2021) extended these findings by pharmacologically manipulating gastric myoelectrical activity during disgust exposure. Disgust response was indexed by oculomotor avoidance, or the reduction in time that participants spent fixating on disgust-inducing images relative to neutral images. Oculomotor avoidance to disgusting images was reduced by repeated exposure when the drug domperidone normalised gastric activity, but not with placebo, demonstrating a causal role of the gastric channel in disgust experience. Emerging minimally-invasive methods to perturb the gastric system, either pharmacologically (Nord et al., 2021) or mechanically (Mayeli et al., 2021a), hold promise for studying gastric channel effects on emotion and cognition.

The respiratory channel also influences cognition and emotion, putatively by modulating higher-frequency neuronal oscillations via coupling effects (Varga & Heck, 2017). Procedures that present stimuli at different times in the respiratory cycle have demonstrated that fearful expressions were more quickly identified, and other visual stimuli more quickly recognised, when presented during nasal inspiration relative to at expiration (Zelano et al., 2016). Conversely, painful shock is perceived as less severe and produced smaller electrophysiological response when delivered during expiration relative to inspiration (Iwabe et al., 2014).

Analysing the timing of stimulus presentation in relation to different internal bodily signatures can provide insight into how these interoceptive channels alter stimulus processing. As well as operating on a moment-to-moment basis, these effects can also provide insights into how chronic or prolonged changes in bodily state might alter and/or prioritise different types of processing.

An important methodological issue in researching interoceptive channel effects is that studies which time-lock stimuli to phasic fluctuations in afferent signal (i.e., systole vs. diastole; inspiration vs. expiration) may confound the effects of the afferent signal on stimulus processing from central commands that might alter both. As such, it is important to follow up initial studies to isolate the effect of afferent signals by manipulating them while bypassing the central control of the visceral organ. Some of the studies highlighted so far have done so by perturbing bodily axes: Nord et al. (2021) manipulated gastric activity using a drug known to selectively affect peripheral (but not central) dopamine uptake, resulting in reduced oculomotor disgust responses. Makovac et al. (2015) used non-invasive neck suction to externally activate the carotid baroreceptors while bypassing central control, altering processing of fearful faces. Ingestible vibrating capsules are also a promising tool for isolating interoceptive channel effects in the gastro-enteric organ systems (Mayeli et al., 2021a), as well as resistive load breathing procedures to probe the respiratory axis (e.g., Faull, Jenkinson, Ezra, & Pattinson, 2016; Rieger et al., 2020). Further work employing perturbation techniques will be crucial to establish the causal role of afferent interoceptive signals in modulating cognitive and emotional processes. Interoception research will also benefit from further work to adapt existing perturbation techniques from the psychophysiology literature into procedures that are controlled, experienced as comfortable for participants, and sufficiently repeatable for adequate statistical power while also being accessible to patient populations.

5. Interoceptive accuracy

Interoceptive accuracy refers to the ability to precisely and correctly monitor changes in internal events (Garfinkel et al., 2015; Khalsa et al., 2018). Procedures to quantify interoceptive accuracy generally involve objectively measuring a physiological event while participants report the bodily sensations they experience. Individual difference measures of interoceptive accuracy are then derived from the objective relationship between the physiological measurements and participant report. Multiple tasks exist across visceral axes to produce interoceptive accuracy measures and increasing effort is being devoted to the creation of new tests.

Cardiac accuracy has been the largest focus of interoception research. Historically, approaches have predominantly relied on the heartbeat counting task (HCT) and the heartbeat detection task (HDT). In the HCT, participants report the number of heartbeats felt during a certain time interval without manually feeling their pulse, and accuracy is essentially derived from a ratio of actual to reported heartbeats (Schandry, 1981). In the HDT, participants judge whether sequences of auditory tones are synchronised or delayed relative to their heart beats, producing signal detection indices of sensitivity and bias (e.g., Critchley et al., 2004). Issues in psychometrics and construct validity of both tasks question their utility for interoception research (e.g., Brener & Ring, 2016; Ring, Brener, Knapp, & Mailloux, 2015; Zamariola, Maurage, Luminet, & Corneille, 2018). Method of Constant Stimuli (Yates, Jones, Marie, & Hogben, 1985) and 6-alternative-forced-choice (Brener & Kluvitse, 1988) variants of the HDT overcome some psychometric issues by presenting present auditory tones at multiple delays relative to participants' actual heart beats. Participants then indicate which tones they perceive to be synchronous, with the consistency of delays relating to chosen tones indexing interoceptive accuracy. While these HDT variants require long procedures that can be prohibitive, a recent report has adapted a similar procedure for use with smartphone-camera photoplethysmography and greatly reduced procedure length, allowing for remote measurement of interoceptive accuracy at scale (Plans et al., 2021). Despite this, HDT-style tests cannot be viewed as pure tests of interoception, as performance is additionally dependent on internal-external integration between cardiac sensations and audio-visual stimuli administered in the task. As such, differences in task demands, together with psychometric flaws, contribute to the poor alignment between interoceptive accuracy indices produced by different tasks in the cardiac axis (for a review, see Brener & Ring, 2016).

While cardiac accuracy has been studied the most extensively to date, other approaches to characterise interoceptive accuracy have been adopted in different bodily axes. For example, in the gastric axis, a water loading procedure can quantify interoceptive accuracy by measuring the volume of ingested water required to produce a subjective feeling of satiation as a percentage of maximum gastric volume (Van Dyck, Vögele, Blechert, Lutz, Schulz, & Herbert, 2016).

In the respiratory axis, an added resistive load detection task can assess individual sensitivity to oral breathing resistance by asking participants to judge whether they perceived variable resistive loads compared to free breathing. Accuracy can be indexed with the percentage of correct load detection across trials (Garfinkel, Manassei, Hamilton-Fletcher, In den Bosch, Critchley, & Engels, 2016), or the smallest resistive load that is correctly detected at least 50% of the time (Daubenmier, Sze, Kerr, Kemeny, & Mehling, 2013). A different respiratory task asks participants to estimate their speed of exhalation into a peak flow metre with respect to a standard exhalation; comparing the estimated and actual exhalation speeds can produce error scores to quantify accuracy (Murphy et al., 2018). It is worth nothing that these two respiratory tasks likely involve different types of respiratory sensations: added resistive loads mimic the obstruction of the airways, while the exhalation task involves voluntary generation of effort to contract expiratory muscles. As such, interoceptive accuracies derived from these two tasks may not necessarily align, even though they target the same bodily axis; this is likely true in most, if not all, bodily axes, whereby different behavioural tasks may elicit or access a variety of qualities of sensations, utilising shared and/or potentially distinct mechanisms.

Other bodily axes that have been studied include the urinary axis, where accuracy can be measured using a non-invasive water loading procedure known to produce maximum bladder fullness in around one hour. Intraclass correlations between bladder volumes and self-reported urinary urge during the procedure can index accuracy (Heeringa, van Koeveringe, Winkens, van Kerrebroeck, & de Wachter, 2011). Pioneering work in intestinal interoception has used an inflatable balloon catheter inserted into the colon to gradually distend it, measuring the threshold of distension required to feel pain as an index of sensitivity to intestinal sensations (Whitehead et al., 1990).

The majority of work in interoceptive accuracy has investigated how accuracy varies between individuals as a trait construct. However, accuracy can also vary within individuals as a state construct. In other words, there may be certain situations that temporarily elevate interoceptive accuracy, such as a stressor or physical exercise; within-individual variability in accuracy may be influenced by perturbations to afferent signals that result from such situations. Early studies have demonstrated that cardiac interoception accuracy is superior when cardiovascular activity is heightened by physical exercise relative to rest (Jones & Hollandsworth, 1981; Schandry et al., 1993). It possible to target state accuracy while modelling trait accuracy using a procedure that assesses accuracy throughout an ecological range of physiological states. This approach can quantify accuracy at any particular state relative to a baseline state or a whole-range aggregate. Ecological approaches to interoceptive assessment are becoming increasingly possible with mobile technology and wearable sensors that can track individuals' physiological states in real time (for an initial report, see Ponzo, Morelli, Suksasilp, Cairo, & Plans, 2021). Work by Khalsa and colleagues has used methods such as a stress induction and inspiratory breath holds to probe altered interoceptive processing in different clinical conditions (e.g., Lapidus et al., 2020; Smith et al., 2021). Perturbing the interoceptive system may offer relevant clinical insights that could potentially be obscured at rest. Studies since the early wave of interoception research have investigated interoceptive accuracy across multiple bodily axes in the same individuals (e.g., Whitehead & Drescher, 1980; Harver et al., 1993); despite this, present interoception research typically studies them in isolation. Pioneering work by Pennebaker pointed to the lack of comparability across organ systems as well as to the lack of convergence of findings using different paradigms within a single organ system; this points to the differential mechanisms (or noise) measured by different interoceptive tasks which could also impede cross-axis correspondence (Pennebaker, Gonder-Frederick, Cox, & Hoover, 1985). Interoceptive accuracy appears to be fractionated across bodily axes (Ferentzi, Bogdány, Szabolcs, Csala, Horváth, & Köteles, 2018). For example, gastric accuracy, but not respiratory accuracy, correlates with cardiac accuracy; despite this, respiratory and cardiac interoception align at the metacognitive level (Garfinkel, Manassei, et al., 2016; van Dyck, Vögele, Blechert, Lutz, Schulz, & Herbert, 2016; Whitehead & Drescher, 1980). The degree of correlation will also depend on the tests administered, and more precise interoceptive tests may reveal greater alignments in accuracy across different bodily axes.

From a general processing viewpoint, assessing interoception across multiple bodily axes can determine whether physiological events in one organ system are more accurately perceived than those of another.

6. Self-report and interoceptive beliefs

This interoceptive dimension comprises both self-report (previously referred to as 'subjective' or 'sensibility') measures, which require participants to report their experiences and beliefs about their interoceptive sensations, and interoceptive beliefs, which can be cast as perceptual priors under a predictive processing framework. Self-report of interoception usually relies on questionnaire-based scales, of which there are a variety purporting to assess different trait-like dimensions. The Interoceptive Accuracy Scale (IAS; Murphy, Brewer, Plans, Khalsa, Catmur, & Bird, 2020) assesses self-reported accuracy, or how accurately individuals believe they perceive bodily signals (also referred to as 'interoceptive sensibility'; Garfinkel et al., 2015). Other scales include items that assess both self-reported accuracy and attention (Shields et al., 1989; Van den Bergh, Bogaerts, Walentynowicz, & Van Diest, 2012). Some self-report scales target a range of interoceptive constructs, such as the Multidimensional Assessment of Interoceptive Awareness (Mehling, 2016; Mehling, Acree, Stewart, Silas, & Jones, 2018), which aims to assess how individuals notice, appraise and regulate interoceptive signals, measures which may be highly relevant in clinical conditions (see Attribution of Signals section). While more research with precise self-report measures is needed (Gabriele, Spooner, Brewer, & Murphy, 2020; Murphy et al., 2020), preliminary work suggests that self-report measures of interoception may not always closely correspond to task-based behavioural measures (e.g. accuracy). This suggests that interoceptive processing may be less accessible to conscious access relative to exteroceptive processing (Garfinkel, Manassei, et al., 2016), rendering it more likely to be susceptible to strongly held interoceptive beliefs. The extent to which they deviate may have implications for clinical symptoms such as anxiety and dissociation (Garfinkel, Tiley, O'Keeffe, Harrison, Seth, & Critchley, 2016; Koreki et al., 2020).

Confidence ratings, or judgements of how accurately an individual performs during a task of interoception, also fall under the category of self-report measures. Confidence ratings differ from questionnaire measures by targeting a state-like belief in the moment, on a trial-by-trial basis (e.g., Garfinkel et al., 2015). Questionnaire measures, on the other hand, may target global beliefs that are more likely trait constructs. It is currently unclear whether trial-by-trial confidence ratings align with questionnaire measures that target accuracy, such as the IAS.

Recent interoception literature has referred to self-report measures as "subjective" and behavioural task measures (e.g., of accuracy and attention) as "objective" (e.g., Garfinkel et al., 2015; Murphy et al., 2019). However, it worth noting that "subjective" self-report measures provide their own valuable insight; these measures present tools for the scientific observation of different levels of interoceptive processing relating to subjective experience, phenomenology and conscious access. Indeed, from a clinical perspective, self-report measures pertaining to individual's beliefs and interpretations concerning their bodily sensations may, in some instances, prove better predictors of clinical status than behavioural or brain-based measures.

An emerging frontier in interoception research focuses on top-down expectations or beliefs concerning bodily states and the strength and nature of interoceptive sensations. Under 'Bayesian brain' or 'predictive processing' approaches, interoception is formalised as a process of Bayesian inference that combines top-down prior beliefs represented in the brain with bottom-up afferent sensory signals from the periphery to estimate the bodily state and produce 'felt' interoceptive sensations (Petzschner, Weber, Gard, & Stephan, 2017; Petzschner, Garfinkel, Paulus, Koch, & Khalsa, 2021). Unlike the conscious beliefs targeted by self-report measures, these prior beliefs are most likely beyond conscious access, although they are thought to integrate an individual's implicit and explicit knowledge of the structure and dynamics of bodily states.

Beliefs as perceptual priors form the basis of multiple computational models of interoception and physiological regulation (for an overview, see Petzschner et al., 2021), which provide novel conceptual frameworks for understanding clinical conditions, such as depression and anxiety (Barrett et al., 2016; Paulus et al., 2019), addiction (Keramati, Durand, Girardeau, Gutkin, & Ahmed, 2017), and functional disorders (Edwards, Adams, Brown, Pareés, & Friston, 2012). Applying computational modelling to brain-based and behavioural interoceptive dimensions can produce individual and quantitative markers of central information processing both in normative functioning and in clinical groups, as demonstrated in a growing body of work (e.g., Mayeli et al., 2021a; Smith et al., 2020). Recent work has also developed a behavioural procedure to quantify interoceptive beliefs, that is amenable to both signal detection and predictive processing analyses (Legrand et al., 2021). Research on interoceptive beliefs within a predictive processing framework has the potential to deliver a novel understanding of disease processes in psychiatric and psychosomatic disorders.

7. Interoceptive insight

Assessing the correspondence between behavioural task performance (e.g. accuracy) and self-report (e.g. confidence) can produce metacognitive measures, often referred to as interoceptive awareness (Garfinkel et al., 2015) or insight in the literature (Khalsa et al., 2018). The simplest index of metacognition is the correlation between accuracy and confidence scores from task-based measures ('phi'); however, phi is known to be biased by ceiling or floor task performance and violations of the assumption of normality (Fleming & Lau, 2014). Area Under the Receiver Operating Characteristic (AUROC; Green et al., 1966) can better quantify the degree to which confidence ratings predict accuracy on a trial-by-trial basis, but is similarly confounded by task performance. Overcoming these limitations, the meta-*d'* approach explicitly models the connection between task performance and AUROC to produce un-confounded metacognition estimates (Fleming, 2017).

Under Murphy et al.'s (2020) framework, in which both behavioural and self-report interoceptive measures may tap into either accuracy or attention, there are at least two (potentially dissociable) dimensions of interoceptive insight: correspondence between behavioural and self-report measures of interoceptive accuracy, and between those of interoceptive attention.

8. Interoceptive attention

The study of interoceptive attention has been relatively neglected, though its importance for interoceptive research is being increasingly recognised (Khalsa et al., 2018; Murphy et al., 2020).

Neuroimaging methods, as previously discussed, can assess the impact on brain activity of purposefully attending to one's interoceptive sensations (e.g., Hodossy et al., 2021; Petzschner et al., 2019). However, such procedures only explore interoceptive attention under instruction, whereas habitual tendency to be aware of interoceptive sensations during individuals' everyday lives may be more associated with emotional and clinical constructs. To date, habitual interoceptive attention has primarily been assessed using self-report questionnaire measures, such as the Body Perception Questionnare (Porges, 1993). These self-report measures administered in clinical groups suggest an interoceptive attentional bias associated with different conditions, such as anxiety (Palser, Palmer, Galvez-Pol, Hannah, Fotopoulou, & Kilner, 2018). Future research needs to explore the correspondence between self-report measures of interoceptive attention with behavioural measures assessed in real-time, such as those reliant on experience sampling methods and smartphone technology, both in normal functioning and clinical groups. Like interoceptive accuracy, interoceptive attention may vary not only between individuals as a trait, but also within individuals with respect to physiological state. Speculatively, states in which afferent signals are perturbed from quiescence may temporarily elevate interoceptive attention. Experience sampling methods combined with wearable sensor technology can explore the physiological conditions in which interoceptive sensations most readily reach conscious awareness. It is important that behaviour-based measures of attention (as ascertained via experience sampling methods) are compared with questionnaires that probe self-reported attention to interoceptive signals, to determine whether these attention metrics align (Murphy et al., 2019).

Interoceptive attention can change the amplitude of interoceptive signals in the brain; the magnitude of the heartbeat evoked response (HEP) increases with interoceptive relative to exteroceptive attention (Petzschner et al., 2019). This has important implications for clinical populations who display a heightened bodily focus; an attentional bias to interoceptive relative to exteroceptive cues may drive augmented neural activation to interoceptive signals.

9. Attribution of signals

Interoceptive sensations can be viewed as benign, ambiguous, or threatening, and individual differences in dispositional styles and affect can influence how they are interpreted. Individuals high in anxiety are biased to process threat, manifesting as an attentional bias to threat (Armstrong & Olatunji, 2012; Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & Van Ijzendoorn, 2007; Van Bockstaele, Verschuere, Tibboel, De Houwer, Crombez, & Koster, 2014) and heightened memory for threat (Herrera, Montorio, Cabrera, & Botella, 2017). This threat sensitivity can also manifest for interoceptive sensations in individuals with anxiety, and panic in particular; attributing bodily sensations to dangerous or life-threatening causes is a key feature of panic disorder (Ehlers, 1993). Negative appraisal of bodily sensations may constitute an important component of anxiety disorders more broadly, on top of any alterations to interoceptive accuracy or preconscious levels. Other clinical groups may also be more likely to attribute interoceptive sensations to a negative or malignant cause and/or interpret these sensations within a negative framework. The interpretation of interoceptive signals may hold particular relevance for individuals with physical, pain and somatoform disorders (Woud, Zhang, Becker, Zlomuzica, & Margraf, 2016). Self-report measures can help ascertain how interoceptive signals are interpreted, such as via the Body Sensations Interpretation Questionnaire (Clark et al., 1997). Behavioural paradigms can manipulate threat context to demonstrate the resultant impact of external exteroceptive context on the perceived threat of interoceptive sensations. The threat relevance of interoceptive sensations can also be manipulated directly via conditioning procedures (Zacharioudakis et al., 2020). Determining individual differences in interoception, including in this higher order attribution/interpretation dimension in patients, may reveal insights relevant for treatment.

10. Towards a comprehensive assessment of interoception

This paper has reviewed methods for assessing in interoception at various levels of processing. These interoceptive measures are largely assessed in isolation at present; however, simultaneously indexing multiple interoceptive levels to comprehensively assess interoceptive profiles can address key issues in interoception research with broad implications for understanding the relevance of different interoceptive mechanisms for emotion and cognition.

Assessment of multiple levels of processing can help reveal how different interoceptive dimensions may interact within the same bodily axis. Individuals with greater cardiac interoceptive accuracy are less susceptible to the systolic inhibition of memory encoding (Garfinkel et al., 2013), and display a higher heartbeat evoked potential in the brain (Pollatos & Schandry, 2004). The impact of a specific interoceptive channel may be moderated by its signal strength, producing individual differences in preconscious impact effect size (Schulz et al., 2016). Current work suggests that these interoceptive dimensions can also dissociate and that such discrepancies may have particular relevance for clinical symptoms, such as anxiety (Ferentzi et al., 2018; Garfinkel, Tiley, et al., 2016) and functional seizures (Koreki et al., 2020). Strongly held interoceptive beliefs in the presence of poor interoceptive accuracy may render individuals particularly vulnerable to interoceptive distortions with implications for the perception of functional symptoms. Thus, in addition to the comprehensive characterisation of interoception across different dimensions, mapping out their divergence may also prove valuable. Future work needs to better delineate how these different measures of interoception, and their divergence, maps on to cognition, emotion, and clinical symptoms. From a general functioning perspective, simultaneously assessing the impact of different interoceptive channels can reveal the mapping between specific bodily axes and emotional processes. Delineating how different interoceptive channels modulate specific types of cognition and emotional experience, and how this may differ in patient populations, represents a future priority for interoception research. Identifying the causal role of interoceptive channels in adverse emotional experience (as in Nord et al., 2021) can lead to the development of body-based intervention strategies for mental health conditions that target peripheral mechanisms.

Studies illustrate the many techniques for examining interoceptive processing through its expression in brain signals. These methods typically use an event-related approach, or the mathematic coupling of organ activity with brain activity to determine localised patterns of coactivity. These approaches can provide insight into brain regions underlying interoceptive processing, interoceptive attention and interoceptive accuracy. Together, these methods all have the potential to reveal nuanced individual differences in the central processing of interoception.

Topographies for visceral (in addition to somatic) signals can exist in the brain on multiple levels, from hindbrain to forebrain. A simple mapping from central neural representation to conscious awareness is neither likely nor expected. For example, pre-conscious neural coupling with cardiac afferent signals is thought to occur in posterior insula (Nguyen et al., 2016) while anterior insula activity underlying cardiac interoception is more available to conscious access (Critchley et al., 2004). The exact measurement of activity in the periphery is in itself an imperfect science, which also impedes the mapping of peripheral to central representations; these methodological limitations pose a challenge to interoception researchers in their quest to determine the correspondence of interoceptive processes across different dimensions.

The framework proposed in this paper can advance other research questions from a general functioning perspective, such as whether sensations from specific bodily axes are more easily consciously detected than sensations from others. How connected are the different bodily axes; can the phasic fluctuation of afferent signals from one bodily axis heighten or interfere with conscious perception of sensations from another? How might interoceptive accuracy correspond to interoceptive attention? More foundational to the field, is interoception best conceptualised as a latent cohesive construct with dimensions, or rather a collection of loosely related processes with no underlying unity? Does the ability to consciously detect interoceptive sensations accurately, or the habitual tendency to be aware of them, transfer across bodily systems? Comprehensively mapping the convergence and divergence of interoceptive processes across dimensions and bodily axes will be critical for addressing these questions to establish the validity and nature of interoception as a construct.

Applied to investigating interoceptive mechanisms of clinical disorders, the framework advanced in this paper falls within the wider approach of computational and cognitive neuropsychiatry, which seeks to specify mental symptoms as departures from healthy psychological function (Corlett & Fletcher, 2014). Comprehensively measuring levels of interoceptive processing can better identify the specific (potentially multiple and interacting) points of departure from the healthy model in clinical populations, advancing our understanding of interoceptive contributions to psychopathology.

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