Introduction

In this perspective paper, we aimed to provide i) an overview of the current theoretical constructs and measurements of interoception, and ii) a useful framework for the complex relationships between interoception and self-awareness. To prepare this paper, we have conducted a literature search on Web of Science using the following keywords: (“interocepti*” (title) AND “self-awareness” OR “minimal self” OR “sense of agency” OR “body ownership” (topic)) and identified 79 relevant papers (Supplementary Materials). Among the identified articles, we found 5 previous reviews (published from 2013 to 2021) which summarized the relationships between interoception and self-awareness in the general population (Seth, 2013; Quattrocki and Friston, 2014; Ceunen et al., 2016; Palmer and Tsakiris, 2018; Musculus et al., 2021). After reviewing the identified article and reviews, we proposed a theoretical framework which encompasses self-awareness, interoceptive awareness, neuroplasticity, and biofeedback. We propose that a four-domain interoceptive intervention approach (cardiac, respiratory, thermal and muscular interoception) may be efficient and effective for training interoceptive abilities, which might in turn alleviate psychopathologies.

The anatomical and physiological origins of interoception

Interoception refers to the processing and integration of inner physiological sensory signals by the central nervous system (Craig, 2009). Anatomically, ascending sensory inputs from internal organs and milieu (cardiovascular, respiratory, and gas-
tric signals) travel via the spino-thalamo-cortical pathway of the vagus nerve (Craig, 2002). These afferent signals are then transmitted to the brainstem nuclei including the nucleus of the solitary tract and the periaqueductal grey, and are further projected to the thalamus, insula, amygdala, and anterior cingulate cortex (Critchley and Harrison, 2013). Specifically, interoceptive sensory signals ascend through a three-level pathway (Figure 1). The vagus nerves are the longest and most complex cranial nerves in humankind, rooted in the solitary nucleus, the dorsal nucleus and nucleus ambiguous. The vagus nerves comprise many branches, including the laryngeal branch, the cardiac branch, the pulmonary plexus, the celiac plexus, and the esophageal plexus, etc. Besides controlling visceral movements, these complex vagal innervations collect sensory information from the chest and abdominal cavity, which constitute the “brainstem level” of interoception. At a higher (second) level, the interoceptive signals are integrated with exteroceptive and proprioceptive signals in the diencephalon (dorsal thalamus), involving the ventral posterior medial, ventral posterior lateral, anterior, and reticular nuclei. The bidirectional neural connections between diencephalon (dorsal thalamus) and other brain areas (e.g., amygdala) are important structures to constitute the “sub-cortical level” of interoception. The top, “cortical level” of interoception involves the insula and the anterior cingulate cortex, which integrate the interoceptive signals with sensory information originated from other sensory cortices, resulting in the sense of “how do I feel” (Craig, 2009).

Interoception is crucial for maintaining homeostasis, or the dynamic physiological equilibrium of the body. Homeostasis refers to the control of body temperature, blood pressure, acidity and alkalinity balance, and glucose levels, etc., and is essential for survival. The autonomic nervous system (aka the peripheral section of the visceral nervous system) is the key center for regulating homeostasis, consisting of sympathetic and parasympathetic innervations, which complement each other. The cranial plexus of the parasympathetic innervations encompasses cranial nerves III, VII, IX, and X (vagus). Therefore, interoception can be thought as part of the feedback system to detect body responses to external stimuli. Moreover, interoception underlies an individual’s subjective feelings, emotional awareness, and most importantly “selfhood” (i.e., whom we think we are) (Craig, 2009; Palmer and Tsakiris, 2018). In essence, self-awareness or selfhood involves the sense of agency and body ownership (Seth and Tsakiris, 2018). The former depicts an

![Figure 1](https://example.com/figure1.png)

**Figure 1.** The three anatomical levels of interoception as internal signals travel from visceral organs (heart, lungs, intestines, etc.) by the vagus nerves, then transmitted to the brainstem nuclei (solitary tract and the periaqueductal grey), and further to the dorsal thalamus, insula, amygdala, and anterior cingulate cortex.
individual’s feeling of generating and controlling over his/her own actions; the latter refers to the perceptual status of one’s own body, a feeling that “my body belongs to me” (Tsakiris, 2017). Both sense of agency and body ownership are grounded in the body (hence the term “bodily-sel”)(Baumeister, 1999).

Herein, interoceptive signals serve as both sensors and effectors to self-awareness. For example, galloping heartbeats can be sensed and interpreted as responses to one’s own action (e.g., brolly-hop from a plane), and thus contribute to the formation of the sense of agency. Moreover, the cardiac branch of vagus nerve can regulate and decelerate one’s heartbeats under an individual’s voluntary will, and thus reinforce the sense of body ownership. To serve both the functions of sensors and effectors, one has to turn his/her attention “inwards”, to focus on visceral sensations like heartbeats and breathing rhythms. The phenomenon as such can be termed “interoceptive awareness”.

How interoception can be measured: the multi-domain approach

Broadly speaking, interoception involves the sense of physiological condition of the “entire body” (Craig, 2002), not limiting to visceral regions, but extending to sensations of temperature and muscle tone (Murphy et al., 2018). Given the different and many modalities of interoceptive receptors, it has been difficult to comprehensively measure interoception. According to Garfinkel et al. (2016), three dimensions of interoception should be considered in the phenomenal context, regardless of modalities: i) interoceptive accuracy (i.e., performance on interoceptive behavioral tests, measured as accuracy rates), ii) interoceptive sensitivity (i.e. subjective beliefs regarding one’s ability to process internal signals, measured using self-reported questionnaires or confidence ratings), and iii) interoceptive awareness (i.e., personal insight into interoceptive aptitude). Notably, the third dimension of “interoceptive awareness” does not fully concur with what we proposed as the ability to allocate attention to interoceptive signal processing. Rather, Garfinkel et al.’s (2016) framework defined interoceptive awareness as a calculable discrepancy between objective accuracy and subjective sensitivity. More recently, a variant of Garfinkel et al.’s (2016) tripartite model was proposed, highlighting the need to distinguish between interoceptive accuracy and interoceptive attention, both of which can be measured using subjective, self-report questionnaires and objective, performance-based tasks (Murphy et al., 2018). Within this model, interoceptive insight reflects the extent to which beliefs and performance are related, and thus can be measured alongside with interoceptive accuracy and interoceptive attention.

Multiple domains of interoceptive signals have been identified and measured, among which the cardiac interoceptive accuracy is the most widely studied, due to its easy applicability. Heartbeat perception is central to research on interoception, which is traditionally defined as the perception and sensation of the internal bodily signals (Musculus et al., 2021). In fact, increased heart rate has long been associated with panic attack and general anxiety disorder, the “prototypical disease” of interoceptive malfunction (Caspi et al., 2014). Most existing paradigms measure interoceptive accuracy in terms of an individual’s ability to detect their own heartbeat. For instance, the Heartbeat Discrimination Task (Katkin et al., 1983) and the Heartbeat Tracking Task (Schandry, 1981) are now considered as conventional paradigms. The Heartbeat Discrimination Task requires participants to detect real-time cardio-audio asynchrony, and the Heartbeat Tracking Task requires participants to silently count their heartbeats and give verbal reports during several time intervals. Whilst tasks involving only the cardiac domain are extensively used, their validity, reliability, and suitability for research has been questioned (Khalsa et al., 2009). In short, confounding factors such as resting heart rate, body mass index, and blood pressure can all interfere measurements for interoception, and have seldom been accounted for in the extant literature. Although the cardiac interoceptive domain can be a good indicator of general interoceptive ability for an individual, it remains insufficient to reflect the complex construct of interoception.

Recently, attempts have been made to study interoceptive accuracy of other sensory channels apart from cardiac rhythms (see Table 1 for detailed descriptions). Specifically, interoceptive tasks for studying respiratory output, muscular effort, and taste sensitivity have recently been developed, and applied to people with high- and low-levels of autistic and alexithymic traits (Murphy et al., 2018). Additionally, Van Den Houte et al. (2021) developed a novel task to measure interoceptive accuracy of the respiratory domain. The Respiratory Occlusion Discrimination Task tapped into an individual’s ability to detect small differences in lengths of short respiratory occlusions. Van Den Houte et al. (2021) suggested that it was feasible to precisely manipulate the interoceptive signal experimentally in the respiratory domain. Moreover, among all the interoceptive domains, the respiratory domain is the one most strongly subjected to willful (cortical) control. In fact, willful control of the breathing rate has been widely adopted in relaxation exercise, meditation and mindfulness therapies (D’Antoni et al., 2022).

In relation to self-awareness, interoception has been measured by way of “body illusions”. In an interoceptive task, participants experienced a rubber hand as part of their own body, by stroking of their own hand while viewing simultaneous stroking of the rubber hand. The results showed that participants were less likely to experience the rubber hand as their own body, if they had a higher interoceptive ability. This interesting finding suggested that a more accurate interoception underlies more ac-

### Table 1. Tasks of interoceptive accuracy in cardiac, gastric and respiratory domains.

<table>
<thead>
<tr>
<th>Interoceptive domain</th>
<th>Task names</th>
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<tbody>
<tr>
<td>Cardiac interoception</td>
<td>Heartbeat Discrimination Task (Katkin et al., 1983); Heartbeat Tracking Task (Schandry, 1981); Phase Adjustment Task (Plans et al., 2020)</td>
</tr>
<tr>
<td>Gastric interoception</td>
<td>Gastric (e.g., stomach, colon) motility detection and intensity rating (e.g., Zaman et al., 2016); Water load test and the two-step water load test (Van Dyck et al., 2016)</td>
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<tr>
<td>Respiratory interoception</td>
<td>Respiratory Resistance Threshold task (Harver et al., 1993); Respiratory Occlusion Discrimination Task (Van Den Houte et al., 2021)</td>
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curate representations of the self (Tsakiris et al., 2011). Another study combined electrocardiography, electroencephalography, and virtual reality, and found that heartbeat-evoked potentials in the posterior cingulate cortex (an “interoceptive hub”) were linked to changes in body ownership induced by the full-body illusion (Park et al., 2016).

It is likely that multiple domains of interoception may represent distinct interoceptive aspects. Although different interoceptive domains may have shared neuroanatomical underpinnings, they may tap into different high-level functions like self-awareness and homeostasis. The feasibility of generalizing the empirical findings of one interoceptive domain to another has not yet been attested. Future research should study multiple domains of interoception independently.

Atypical interoception as a risk factor for psychopathology

The growing evidence for interoceptive impairments in psychiatric disorders has attracted much attention. Altered interoceptive ability has been found in many psychiatric and neurological disorders, including anxiety and panic disorders (Krautwurst et al., 2014; Critchley et al., 2018), eating disorders (Khalsa et al., 2018; Berner et al., 2019), major depressive disorder (Harshaw, 2015), schizophrenia (Ardizzi et al., 2016) and autism spectrum disorder (Quattricki and Friston, 2014; Schauder et al., 2015; Palser et al., 2018). A recent review comprehensively summarized previous research on interoception, and its potential implications to mental health (Brewer et al., 2021). However, the majority of studies on interoception only focused on the cardiac domain. Moreover, the findings of cardiac interoceptive ability in psychiatric disorders were inconsistent, with different studies showed either increased, decreased or typical interoceptive accuracy or sensibility, even among the same clinical diagnostic entities. Given the multidimensional nature of interoceptive ability, clinical groups may show impairment in different domains or dimensions of interoception, which cannot be readily identified using one single measure of cardiac-related task. The divergence of prior findings may also be related to individual differences within each diagnostic groups. For example, genetic factors, environmental effects (e.g., trauma exposure), and physical health status may influence the specific patterns of interoceptive difficulties.

The physiological condition of the body has long been proposed as the basic substrate for feelings and emotions (Palmer and Tsakiris, 2018). Therefore, alexithymia (i.e., inability to identify and express own emotions and feelings) has been found to link to atypical cardiac interoception in psychiatric patients (Herbert et al., 2011). Alexithymia itself is a neurodevelopmental symptom commonly found in the general population, occurring in the absence of neurological trauma (i.e., primary alexithymia, or congenital alexithymia, as intrinsic neurodevelopmental phenotype), but can also be acquired following traumatic brain injury (i.e., secondary alexithymia, Hogeveen et al., 2016). Alexithymia was found to correlate negatively with perception of taste and muscular effort, while positively correlated with increased reliance on external cues for gauging respiratory output (Murphy et al., 2018). Similarly, a previous study reported that alexithymia was associated with reduced perception of thermal sensation (Borhani et al., 2017). This relationship between altered interoception across multiple domains and the increased alexithymia level may shed light as to how altered interoception may evolve to psychopathologies. For instance, interoception contributes to emotion experience, and is involved in recognizing and expressing one’s own emotions. If interoception becomes impaired, emotion processing would become defective, resulting in alexithymia (Craig, 2009). The interactive relationship between altered interoception, emotion problems, and alexithymia can be found in different clinical conditions (Brewer et al., 2021). We consider alexithymia as a “mediator” and “consequence” of interoceptive malfunctions. As a mediator, alexithymia may be an intervention target for cognitive behavioral training to improve one’s interoception. Taken together, interoceptive deficits may be related to impaired self-awareness and atypical emotional processing.

Interceptive interventions

Given the relationship of interoception with self-awareness and emotion processing, effective strategies to improve one’s interoceptive abilities may have important clinical implications. Interoceptive attention and interoceptive awareness can further motivate stimulus-response (conditioned reactions) and willful behaviors. Therefore, self-awareness plays an important role in willful actions. The self is not entirely an interaction of environment and genetics, and once sense of agency and body ownership are both developed, it serves as a willful director of attention. Imaging studies have identified a network involving brain regions in the medial and lateral frontal cortex, as well as the parietal cortex, as being responsible for internally guided behaviors (Krieghoff et al., 2011). Moreover, whereas brain changes can lead to behavioural changes, “neuroplasticity” (a phenomenon that behavioural changes can result in brain changes) has been observed after training in exteroceptive domains, such as audition (Jancke et al., 2001), somatosensation (Godde et al., 2003), and olfaction (Gottfried et al., 2002). Studies on volition in neuroscience have demonstrated that behavioural trainings could alter cortical brain structure (Barnes and Finnerty, 2010). For instance, in a mindfulness intervention study, structural brain images were acquired before and after an 8-week training period. The results found cortical regions involved in interoceptive signal processing demonstrated functional plasticity following breathing monitoring practice (Farb et al., 2013).

A notable example of interoceptive interventions is the contingent cardiac biofeedback training. During cardiac biofeedback, participants received either a visual, acoustic or tactile feedback on their heart activity, through which they were supposed to learn to perceive and influence heartbeats more accurately (Schandry and Weitkunat, 1990). To improve cardiac interoceptive accuracy through cardiovascular feedback training, Meyerholz et al. (2019) divided 100 participants into the contingent (true) feedback group, the non-contingent (false) feedback group, the mindfulness practice group, and the control group. In contingent biofeedback trials, a visually presented animated heart symbol was shown 200 ms after R-wave detection, and participants were asked to press a button after a specified number of heartbeats. Compared with non-contingent cardiac feedback and mindfulness practice, a significant increase of cardiac interoceptive accuracy was observed in the contingent feedback group (Meyerholz et al., 2019). Importantly, this study also pointed out that simply focusing internally could not improve one’s perception of cardiac activity. The “Aligning Di-
mensions of Interoceptive Experience” therapy has been reported in randomized control trials as effective to reduce anxiety symptoms among autistic adults (Quadt et al., 2021). This intervention may improve regulatory control over internal stimuli by feedback from heartbeat detection tasks.

Despite these preliminary promising findings (Farb et al., 2013; Meyerholz et al., 2019; Quadt et al., 2021), future designs of intervention on interoception should cover multiple domains. We recommended a four-domain interoceptive intervention approach, covering the cardiac, respiratory, thermal and muscular domains. The cardiac and respiratory domains represent the “brain-stem level” of interoceptive processing (cranial nerve X) and have relatively strong empirical foundation. The thermal domain represents the “subcortical (thalamic) level” of interoceptive processing, as thermoregulation is the function of diencephalon, where interoceptive and exteroceptive signals from the skin and viscera are converged. Lastly, the muscular level represents “cortical level” of interoception, for interoceptive signals must be integrated with exteroceptive and proprioceptive information to determine and adjust muscles’ tone and movements. For instance, a behavioral task designed to measure muscular interoceptive accuracy called “the muscular effort task” has been put forward by Murphy et al. (2018), in which participants held sealed buckets before indicating whether the weight matched that of a standard weight. This muscular effort task might foreshadow similar design in interoceptive interventions. To our knowledge, no such biofeedback intervention covering different levels of interoception has been developed and validated. Previous studies mainly applied interoceptive training on the cardiac and respiratory domains (Schillings et al., 2022; Smith et al., 2022).

In addition to the interoceptive training, some new paradigms have been developed to assess one’s ability of integrating internal bodily sensations with external environmental stimuli, which is important for an individual to develop self-other boundary and social skills (Yang et al., 2022). For example, in the Interoception-Exteroception Synchronicity Judgement (IESJ) task, interoceptive accuracy is probed by viewing the motion of a heart-shape jumping either synchronously or asynchronously with the participant’s own real-time heart rate, whereas exteroceptive accuracy is measured by judging whether a ball-shape is jumping synchronously or not with a series of sounds. Moreover, as the interoceptive and exteroceptive stimuli (the heart shape and ball shape) are presented on the same screen side-by-side, this paradigm also generates “balancing score”, reflecting the extent of discrepancy between one’s interoceptive and exteroceptive accuracy (Yang et al., 2022). The IESJ may be useful for training one’s ability to balance attention allocation between exteroceptive and interoceptive signals, which in turn may facilitate multisensory integration, self-other distinction and social cognition abilities.

Conclusions

Interoception is important for self-awareness and emotion processing. Altered interoception can be found in different psychiatric disorders, and may contribute to development of psychopathologies, in particular alexithymia. Together, interoception provides a useful framework for transdiagnostic research to explore the plausible underlying mechanisms for psychiatric disorders. This review advocated more research to cover the “brainstem”, “subcortical” and “cortical” levels of interoception, and to investigate different domains of interoception, in particular the cardiac, respiratory, thermal and muscular domains. Interoceptive training may be a viable intervention to alleviate certain types of psychopathologies in psychiatric patients.

References


