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Interoception, network physiology and the emergence of bodily self-awareness

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ABSTRACT

The interplay between the brain and interoceptive signals is key in maintaining internal balance and orchestrating neural dynamics, encompassing influences on perceptual and self-awareness. Central to this interplay is the differentiation between the external world, others and the self, a cornerstone in the construction of bodily self-awareness. This review synthesizes physiological and behavioral evidence illustrating how interoceptive signals can mediate or influence bodily self-awareness, by encompassing interactions with various sensory modalities. To deepen our understanding of the basis of bodily self-awareness, we propose a network physiology perspective. This approach explores complex neural computations across multiple nodes, shifting the focus from localized areas to large-scale neural networks. It examines how these networks operate in parallel with and adapt to changes in visceral activities. Within this framework, we propose to investigate physiological factors that disrupt bodily self-awareness, emphasizing the impact of interoceptive pathway disruptions, offering insights across several clinical contexts. This integrative perspective not only can enhance the accuracy of mental health assessments but also paves the way for targeted interventions.

1. Introduction

Self-awareness is the conscious processing of one's own feelings, actions, and autobiographical memories (Morin, 2011), which allow us to understand ourselves in relation to our context. More specifically, bodily self-awareness refers to the self-identification with one's body and sensory information, the experience of a first-person perspective and the ability to self-locate in space (Blanke, 2012). As such, it involves the integration of multiple sensory modalities, from bodily sensations, such as touch and proprioception, to the understanding of one's physical appearance and capabilities. Thus, it is important to understand to what extent signals coming from within the body interact with external sensations and neural networks to contribute to our bodily self-awareness, and therefore, it is the core objective of this review.

To what extent do signals coming from within the body, and their interaction with external sensations and neural networks, contribute to our bodily self-awareness? Interoception—concerning the physiological mechanisms for sensing, integrating, interpreting, and regulating signals within the self (Chen et al., 2021)—may indeed have a significant impact on bodily self-awareness. Various theoretical proposals have suggested that interoceptive mechanisms operating beneath consciousness play a crucial role in the emergence of self-awareness and related cognition, encompassing influences in perceptual awareness across different sensory modalities (Azzalini et al., 2019). These mechanisms, operating outside of awareness, are proposed as essential for maintaining physiological balance and can influence cognitive as well as emotional processes (Blanke and Metzinger, 2009; Candia-Rivera, 2022; Damasio, 1999; Park and Tallon-Baudry, 2014; Qin et al., 2020; Salamone et al., 2021; Sattin et al., 2020; Thompson and Varela, 2001).

Interoceptive mechanisms also allow us to consciously perceive

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bodily cues like heartbeat, respiration, hunger, and pain, which are closely linked with self-awareness. Those mechanisms are traditionally assessed through behavioral tests (e.g., accuracy on detecting heartbeats) and self-reports (e.g., confidence on the performance at detecting heartbeats), but also by assessing further dimensions, including interoceptive attention and metacognitive assessments (Suksasilp and Garfinkel, 2022). These conscious interoceptive signals appear to be altered in certain conditions in which bodily self-awareness is disrupted (Pollatos et al., 2008). In this direction, phenomenological experience would be implicitly related to the generation of a first-person perspective (Park and Tallon-Baudry, 2014)—where bodily signals are actively involved in constituting the sense of self in a physical body.

In the realm of bodily self-awareness, embodiment—the concept that cognition is deeply intertwined with bodily experiences and actions—emphasizes the idea that our bodies play a fundamental role in shaping our thoughts, perceptions, and emotions (Longo et al., 2008). This perspective highlights the close connection between the mind and body, suggesting that our understanding of ourselves emerges from our embodied experiences. Embodiment also refers to the critical role of the body and its activities in cognitive processes. It encompasses how anatomical features influence perception, the impact of bodily actions on cognition, and mental representations related to the body (Goldman and Vignemont, 2009). Embodiment entails the integration of multiple sensory modalities, including vision, touch, proprioception, and interoception (Craig, 2002; Giummarra et al., 2008; Herbert and Pollatos, 2012), to form a comprehensive understanding of the self within the environment. Embodied cognition and interoception are, therefore, connected through the integration of bodily sensations and internal physiological states in shaping cognitive processes and experiences. This process involves the dynamic formation of cortical and subcortical networks, orchestrating the intricate interplay between sensory inputs and motor responses (Crucianelli et al., 2024; Grivaz et al., 2017). However, the precise mechanisms underlying this complex integration remain elusive, posing a challenge to unravel the complexities of embodied cognition.

Initially, interoception was closely linked to homeostasis, the body's ability to maintain internal stability and equilibrium (Craig, 2002). However, later research has expanded this understanding to include the concept of allostasis (Sennesh et al., 2022), which refers to the adaptive processes the body employs to achieve stability through change. Unlike homeostasis, which seeks to maintain a constant internal environment, allostasis recognizes that the body's optimal functioning may require flexible adjustments in response to varying internal and external demands (Burleson and Quigley, 2021; Kleckner et al., 2017). In this direction, cardiac activity has been associated with brain precision for perception and action (Skora et al., 2022). In particular, signaling from the heart seems to have a central role in this regard, as studies on brain-heart interactions have shown that ascending cardiac inputs shape brain dynamics, behavior, and subjective experience (Azzalini et al., 2019; Candia-Rivera, 2022). For example, neural firing rates have been linked to cardiac cycle durations (Kim et al., 2019), cardiac phase impacts active exploration behavior (Galvez-Pol et al., 2020), and neural responses to heartbeats are predictive of subjective visual perception (Park et al., 2014).

In recent years, research has increasingly highlighted the key role of interoceptive inputs—internal signals from within the body—in shaping our processing of exteroceptive information, stimuli from the external environment (Candia-Rivera, 2022; Engelen et al., 2023b; Park and Blanke, 2019). This growing recognition underscores the importance of examining how interoceptive and exteroceptive signals are integrated to gain a deeper understanding of cognitive processes. For instance, under postural threat (risk of falling), participants feel less stable and more fearful when provided with false fast heart rate feedback (Hill et al., 2024). Gastrointestinal feedback can also modulate our perceptions, by ultimately conditioning food preferences (Sclafani and Ackroff, 2012). Therefore, interoception appears to strongly influence various cognitive functions, including our perception, decision-making, and emotional responses. Indeed, research has shown that individuals with disrupted interoception may experience altered emotional experiences and impaired decision-making (Critchley and Garfinkel, 2018). Consequently, studying the mechanisms underlying the integration of these internal and external signals offers valuable insights into how the nervous system processes and interacts with the world. This exploration not only enhances our understanding of sensory and emotional experiences but also informs about self-related cognition and its implications for mental health (Salvato et al., 2020; Suzuki et al., 2013).

This review aims at assembling the physiological and behavioral evidence linking bodily self-awareness to interoceptive mechanisms. First, we review bodily self-awareness disturbances, emphasizing their malleable nature and the apparent key role of interoceptive signals, based on research that has linked those signals with self-consciousness and multisensory integration (Heydrich and Blanke, 2013). Next, we outline the representation of bodily self-awareness in the brain and the overlap between these and interoceptive (sub)cortical networks, followed by an overview of the depth of interoceptive influence on cognition, perception, and action. Lastly, we propose different strategies to investigate these mechanisms through network physiology frameworks, analyzing the interactions between different physiological systems in the body.

We propose that quantifying the higher-order dependencies between the brain and other organs can reveal the physiological foundations of bodily self-awareness. In particular, we highlight how interoceptive mechanisms interact with other sensory modalities, such as vision, touch, and proprioception. Multiple sensory events can result in complex, time-varying engagements with neural networks (Senkowski and Engel, 2024), which potentially form the basis of bodily self-awareness. While the exploration of interoceptive mechanisms in consciousness has been previously emphasized (Azzalini et al., 2019; Candia-Rivera, 2022; Park and Blanke, 2019), this article highlights the need to study complex systems by considering higher-order dependencies, as proposed by frameworks of network physiology incorporating visceral activities (Bashan et al., 2012). Importantly, these approaches acknowledge that the brain forms functional networks that dynamically change based on context (Park and Friston, 2013). Furthermore, this perspective has significant implications for biomarker development and future clinical applications (e.g. treatment of self-related disorders: schizophrenia, depersonalization-derealization disorder).

2. Disturbances of bodily self-awareness

Our bodily self-awareness is part of what defines us as an individual and can be easily malleable in many contexts. For some authors, the integration of information stands as a hallmark in consciousness research (Palmer and Ramsey, 2012), highlighting the importance of understanding how disparate pieces of sensory input come together to form a coherent experience. Despite advances in neuroscience and cognitive science, unraveling how the brain seamlessly combines inputs from various sensory modalities to generate a unified perceptual experience continues to present a challenging frontier in the study of consciousness (Deroy et al., 2016). Sensory integration involves the coordination of various sensory systems—such as somatosensory, auditory, and visual systems—while also processing bodily, self-related information through other systems (Azañón et al., 2016; Giummarra et al., 2008; Herbert and Pollatos, 2012). These include proprioceptive, interoceptive, vestibular, and motor systems (Ventre-Dominey et al., 2003), which work together to provide a comprehensive representation of the body by combining both outgoing (efferent) and incoming (afferent) information (Tsakiris et al., 2005).

Altered bodily self-awareness can manifest in various conditions, ranging from temporary states to chronic disorders. Temporary alterations often arise from acute events like sensory deprivation, extreme stress, or intense meditation practices, where individuals may experience dissociation from their physical form—such as disembodiment of specific body parts, the sensation of reduplication or phantom embodiment of an amputated body part (Giummarra et al., 2008). Among the conditions related to a temporary disruption in bodily self-awareness there is *asomatognosia,* associated with the experience of a temporary perception of disappearance of corporeal awareness (Arzy et al., 2006). Patients experiencing *autoscopic phenomena* perceive illusions of one's own body, being *out-of-body experiences* the most common, where they feel a sense of vestibular detachment and the impression of seeing the world and the self from a distant perspective (Blanke, 2004).

Conversely, chronic changes in bodily self-awareness may arise, for example, following brain damage that disrupts multisensory integration (Candini et al., 2022), as well as in psychiatric disorders such as schizophrenia (Hur et al., 2014) or anorexia nervosa (Frost-Karlsson et al., 2022; Pollatos et al., 2008). Chronic alterations in bodily self-awareness are prevalent in conditions such as *depersonalization disorder*, where individuals consistently perceive distortions or detachment from their bodies over extended periods (Sierra and David, 2011). Symptoms of depersonalization include feelings of disembodiment, disrupted emotional processing, uncertainty regarding past events, and an overall lack of a sense of reality (Sierra and David, 2011). In particular, this condition has been presented as a systematic dysregulation of interoceptive (Saini et al., 2022) and autonomic mechanisms (Michal et al., 2013; Owens et al., 2015; Phillips and Sierra, 2003; Schoenberg et al., 2012; Sierra et al., 2002).

Among other disrupted bodily self-awareness disorders we can find patients with *somatoparaphrenia*, who believe that their limb belongs to someone else (Halligan et al., 1995), while those with *body integrity identity disorder* believe that a healthy limb should be amputated as it is not perceived as owned by themselves (Berger et al., 2005; Lenggenhager et al., 2015). Importantly, these symptoms can appear in patients with absence of clear anatomical alteration causing them (First and Fisher, 2011). In the *alien hand syndrome* patients experience that one limb performs purposeful acts autonomously (Biran et al., 2006). The *supernumerary phantom limb phenomenon* consists in perceiving to have additional limbs, as duplicates or "shadows" (Hari et al., 1998).

Pharmacologically induced alterations can occur with substances like psychedelics, which can temporarily disrupt typical bodily perception, leading to experiences such as depersonalization or out-of-body sensations (Ho et al., 2020). All these variations in bodily self-processing underscore the complex interplay between psychological, neuronal, and pharmacological factors in shaping our perception of self and body.

Perceptual illusions of bodily awareness can be induced through functional adaptations, prosthetic embodiment, and changes in afferent sensory feedback (Giummarra et al., 2008). Illusory bodily awareness—the sensation of one's body being altered or replaced by another object or entity, can be induced by illusory sensory inputs. For instance, the rubber limb paradigm shows that bodily perception can be manipulated with visuo-tactile synchronous stimulation (Botvinick and Cohen, 1998; Ehrsson et al., 2004). This illusory bodily awareness can be further manipulated to even distort the localization of pain, implying that the distorted perception of various sensory modalities can also distort proprioception (Capelari et al., 2009). Such perceptual illusions can even concern the whole body, as in the case of full-body illusions. Individuals experience an altered sense of bodily self, including changes in self-location and self-identification (Blanke and Metzinger, 2009). It is curious that patients with depersonalization disorder do not experience these illusions as healthy individuals do, often lacking the typical sense of ownership over their body (Yamamoto and Nakao, 2022). This dissociative condition disrupts the integration of sensory and emotional experiences, leading to a disconnection from oneself and the external world, altering the way they perceive reality.

When sensory information becomes incoherent or contradictory across modalities, the illusory bodily awareness tends to dissipate (Carruthers, 2008), restoring the individual's awareness of their actual body. These phenomena demonstrate the importance of partial sensory coherence in maintaining the illusory bodily awareness and highlight the complex interdependencies between sensory modalities. This is further underscored in cases of altered bodily self-awareness, such as the sense of disownership towards one's own body part, which cannot solely be attributed to a specific brain structure in charge of ownership; it may also involve the integration of multisensory information and more complex physiological processes (de Vignemont, 2011; Ionta et al., 2011; Lenggenhager et al., 2007).

Bodily self-awareness, though innate and often taken for granted, is subject to alterations in various ways, revealing its inherent malleability and complexity. While typically a seamless aspect of human experience, the diverse conditions explored demonstrate the multifaceted nature of bodily self-awareness. Whether influenced by sensory illusions, physiological mechanisms, or cognitive processes, the volatility of our bodily self-awareness underscores the dynamic interplay between mind and physiological activity. Understanding the underlying dynamics of these alterations not only sheds light on the mechanisms of bodily self-awareness but also highlights the remarkable adaptability of human consciousness.

3. Neural correlates of bodily self-awareness

Bodily self-awareness is a multifaceted phenomenon that weaves together various dimensions, collectively shaping our perception of self and body (Christoff et al., 2011). Some primary dimensions appear within bodily self-awareness, although highly intertwined: self-identification (ownership), self-location, self-attribution (agency) and first-person perspective (Blanke, 2012; Longo et al., 2008). Exploring the mechanisms behind these dimensions not only helps us understand how we perceive our bodies but also provides insights into fundamental questions about selfhood and consciousness. In this section, we give an overview into the neural underpinnings of these dimensions, exploring how they contribute to our sense of self and body perception. The comprehensive understanding of these neural underpinnings can shed light on the network dynamics involved in dissociable phenomena, and the potential overlaps with interoceptive networks, further understanding the neural processes involved in an incoherent sense of self.

3.1. Self-identification

Self-identification refers to the sense of possessing one's body, encompassing the feeling that our limbs and organs belong to us (Tsakiris et al., 2007). The coding of self-identification involves a network of brain regions including the inferior temporal and occipital lobes, bilateral inferior parietal lobes involving the postcentral and supramarginal gyri, precentral gyri, right inferior and superior parietal lobes, and insular cortices (Salvato et al., 2020). Some specificity has been shown in brain regions associated with multisensory integration, encompassing the superior parietal, posterior parietal, temporo-parietal, temporo-occipital, premotor and insular cortices (Grivaz et al., 2017). Among all, three brain regions appear as leading self-identification: the temporo-parietal junction, the extricate body area (temporo-occipital cortex) and insula. The temporo-parietal junction is involved in the processing of body-related information (Blanke and Arzy, 2005; Leube et al., 2003). The extrastriate body area is involved in visual information processing of human bodies and body parts (Downing et al., 2001), and for coupling proprioceptive and visual inputs (Chan et al., 2004). The insula responds distinctly to multisensory signals, indicating that it is functionally partitioned to process different sensory modalities (Craig, 2002), such as tactile, vestibular, and interoceptive inputs. Altogether, recent evidence highlights the relevance of fronto-parietal projections in bodily representations and body ownership (Casula et al., 2022; Moro et al., 2023).

Although bodily self-awareness has been primarily described from the cortex, further subcortical structures including the putamen, amygdala, thalamus, hippocampus and the cerebellum are also involved in these mechanisms (Crucianelli et al., 2024). Neuroimaging studies have identified specific cerebellar regions, such as lobules VI and VIIa (Guterstam et al., 2013), consistently activated during body ownership illusions. The cerebellum's involvement in body ownership may include detecting multisensory synchrony, supporting multisensory recalibration, and generating or detecting multisensory prediction errors. However, the exact functional role of different cerebellar regions in body ownership remains unclear.

3.2. Self-location

Self-location refers to the experience of being a body with a given location within the environment (Serino et al., 2013). Electrophysiological studies of the mammalian hippocampus and its connections have identified neurons that encode position and orientation, including place cells, grid cells, head direction cells, boundary vector cells, and self-motion cells (Barry and Burgess, 2014; Moser et al., 2008). These spatial representations are informed by environmental sensory information, but more importantly, by self-motion cues, which can occur even in absence of external cues (Quirk et al., 1990). Two proposed mechanisms explain how self-motion information influences neuronal spatial representations. One described how continuous attractor networks contribute to the smoothly-perceived transitions in facing direction, by calibrating internal models based on error correction and environmental cues (Zugaro et al., 2003). Another one described how oscillatory interference models use theta rhythms to modulate the firing of place and grid cells, which is believed to act as a velocity-sensing system (Jeewajee et al., 2008).

In humans, the brain regions identified as coding self-location include the intraparietal sulcus, retrosplenial cortex, posterior cingulate cortex, and hippocampus (Guterstam et al., 2015), with the intraparietal sulcus constructing egocentric representations of self-location, and the posterior cingulate and retrosplenial cortices involved in integrating egocentric and allocentric spatial representations. The temporo-parietal junction and the right middle-inferior temporal cortex, including the extrastriate body area, are implicated in both, the coding of self-location and self-identification (Ionta et al., 2011), by reflecting changes in self-location and identification induced by updated (illusory) sensory information. More recently, the anterior precuneus (superior parietal cortex) has been described in the processing of the subjective experience of the body, being responsible of dissociative changes in physical and spatial domains (Lyu et al., 2023). The nervous system also integrates information from sensory-motor interactions to define the peripersonal space—the immediate area around the body where sensory and motor information integrates to guide interactions with the environment (Serino, 2019).

The perception of self-location appears to be a dynamic process that is not homogeneously distributed across the entire body nor exclusively localized to a single body part (Alsmith and Longo, 2014), being the upper face and upper torso more susceptible to our focus. The complexity of self-location perception highlights the importance of considering dynamic interactions between bodily cues and the brain in shaping our subjective experience of where I am.

3.3. Self-attribution

Self-attribution, that involves the recognition of bodily sensations and actions as originating from oneself, distinguishing them from external stimuli or other individuals (Tsakiris and Haggard, 2005). Self-attribution involves the interplay of multiple cortical regions to process sensory and cognitive information. Sense of ownership influences self-attribution through various non-motoric cues. These cues are processed in partially distinct circuits and then within fronto-parietal networks, which seem to ground the implementation of self-attribution (Villa et al., 2022). Self-attribution in social contexts with emotional valence content is encoded in the posterior precuneus, where self-attributed positive versus negative contexts showed activation in the anterior precuneus, while negative versus positive contexts showed activation in the bilateral insular cortex (Cabanis et al., 2013). The attribution of actions to oneself caused activation of the anterior insula, while the attributing of actions to another person was associated with activation in the inferior parietal cortex, suggesting its role in representing movements in an allocentric coding system applicable to both self and other actions (Farrer and Frith, 2002). The premotor cortex plays a key role in self-attribution, as demonstrated by the rubber hand illusion paradigm and touch synesthesia (Blakemore et al., 2005; Ehrsson et al., 2004). Meanwhile, the somatosensory cortex is involved in attributing seen touch to felt touch (Schaefer et al., 2006). Illusory self-attribution of body parts activates a left-hemispheric network involving ventral premotor cortex, intraparietal sulcus, and lateral occipitotemporal cortex, showing that self-attribution inference mechanisms rely on a hierarchical propagation of prediction errors (Limanowski and Blankenburg, 2015).

3.4. First-person perspective

First-person perspective refers to the centeredness of one's own experience upon one's own body, operating in an egocentric frame of reference, and allowing self-other distinctions (Vogeley and Fink, 2003). The posterior parietal cortex and premotor cortex play a role in coding an egocentric frame of reference (Avillac et al., 2005; Vallar et al., 1999). In the establishment of distinction of self, others and the environment the nervous system integrates information from proprioceptors and tactile inputs (Schütz-Bosbach et al., 2009). The neural correlates of first-person perspective and third-person perspective involve a vast network of occipital, parietal, and prefrontal areas, being the mesial superior parietal and right premotor cortex focused in third-person perspective, and activations in mesial prefrontal cortex, posterior cingulate cortex, and superior temporal cortex bilaterally engaged the first-person perspective (Vogeley et al., 2004).

The distinction between self-other touch is crucial for delineating the boundaries of bodily self-awareness and understanding how we perceive ourselves in relation to others. The distinction between self-other touch encompasses brain areas as the somatosensory cortex, insula, superior temporal gyrus, temporo-parietal junction, supramarginal gyrus, and prefrontal cortex (Boehme et al., 2019; Eddy, 2016; Qin et al., 2020). Importantly, the right temporo-parietal area plays a role in distinguishing between self and other-generated actions (Leube et al., 2003). More differences in self-other touch can be found in the cerebellum, striatum, parahippocampal gyrus and amygdala (Boehme et al., 2019). In particular, the cerebellum contributes to emotional processing and embodying emotions, including affective touch (Boehme et al., 2019; Petrosini et al., 2022). Finally, the integration of ascending inputs from spinal pathways indicates specific brain mechanisms to generate behavioral responses during affective processing (Marshall, 2022), including self-other touch distinctions (Boehme et al., 2019).

Understanding the normal distinction between self, other, and environment lays the groundwork for exploring how alterations in this perception can manifest and how different brain networks may be implicated in these disruptions. The experience of bodily detachment often arises from a breakdown in the integration of somatosensory, proprioceptive, visual, and vestibular information (Blanke, 2004). In cases where individuals have lost a limb, the brain areas responsible for movement and sensation adapt to the incongruity between intention and sensory feedback, leading to phenomena such as phantom limb sensation and pain (Flor et al., 2006). Furthermore, studies employing brain imaging techniques have indicated heightened activity in the prefrontal cortex, particularly in regions associated with the contextualization and appraisal of emotionally significant information, among individuals experiencing dissociative symptoms (Phillips and Sierra, 2003). These findings underscore the multifaceted nature of disruptions in bodily self-awareness and the diverse neural mechanisms implicated in such alterations.

The intricate interplay between cortical, subcortical, and peripheral mechanisms likely contributes to our perception of self and body ownership. Transitioning to the exploration of peripheral and interoceptive mechanisms offers a holistic understanding of how bodily self-awareness emerges from the complex interactions within and beyond the brain.

4. Interoceptive mechanisms, from perceptual awareness to embodiment

Interoceptive mechanisms are crucial for understanding bodily self-awareness as internal bodily signals are constantly integrated with external sensory inputs. These mechanisms enable individuals to perceive and interpret sensations such as heartbeat, respiration, and visceral states, forming a foundational basis for interoceptive self-awareness. By integrating interoceptive signals with sensory feedback from the environment, the nervous system can develop a coherent sense of their own bodies within their surroundings. Moreover, interoceptive processes contribute to the formation of self-related cognition and emotional states (Babo-Rebelo et al., 2016a; Candia-Rivera et al., 2022b; Engelen et al., 2023a; Salamone et al., 2021), influencing the perception of self and the world (Park et al., 2016). The neural processing of cardiac inputs has been associated with perceptual awareness across various sensory modalities and self-related cognition (Azzalini et al., 2019). Therefore, these interoceptive inputs may play a crucial role in defining, for instance, an individual's perspective and egocentric reference frame (Baiano et al., 2021; Park and Blanke, 2019; Tallon-Baudry et al., 2018). Thus, a comprehensive understanding of bodily self-awareness necessitates an exploration of interoceptive mechanisms and their interactions with other sensory modalities.

Experimental efforts have investigated the physiological mechanisms that define the self, through the analysis of brain relationships with interoceptive inputs. The degree of self-relatedness of spontaneous thoughts was reflected in the amplitude of heartbeat-related responses in specific brain regions within the default network (Babo-Rebelo et al., 2016a). Specifically, the posterior cingulate cortex and ventral precuneus encoded the self as an active agent in self-related thoughts (subjective self or "I" dimension), while the ventromedial prefrontal cortex was associated with the self as the object of the thought or introspection (objective self or "Me" dimension) (Babo-Rebelo et al., 2016a). Subsequently, those results were further replicated with intracranial recordings in epileptic patients (Babo-Rebelo et al., 2016b). These findings demonstrate differentiated heart-brain mechanisms that allow the distinction between self-related and non-self-related thoughts. Furthermore, heartbeat-evoked responses differed between self- and other-imagination, in the anterior precuneus, mid-cingulate, supplementary motor area, and the ventromedial prefrontal cortex (Babo-Rebelo et al., 2019). Self-other distinction prior to emotion processing has been shown encoded as well in the heartbeat-evoked responses in the frontal operculum and visual cortices (Engelen et al., 2023a). Heartbeat-evoked responses can reflect own name perception, and in turn hearing one's own name alters heartbeat evoked potentials, through two separate neural mechanisms in the right and left temporo-parietal junction respectively (Zhang et al., 2023). Altogether, those findings suggest that neural monitoring of cardiac signals may play a role in establishing a body-centered reference frame that the brain uses to identify thoughts and other neural processes as self-related (Babo-Rebelo and Tallon-Baudry, 2018).

Research on embodiment highlights the importance of visual, somatosensory, and vestibular inputs (Giummarra et al., 2008). However, until recently, the significance of interoceptive mechanisms has been largely overlooked, especially concerning the effects of focal brain damage on multisensory integration. For instance, case reports have shown that lesions in the insular cortex impair interoceptive signal processing, while subcortical lesions affect exteroceptive processing (Couto et al., 2015). Here, the concept of interoceptive-exteroceptive integration plays a key role (Fig. 1), as sensory information—such as visual, auditory, tactile, proprioceptive, chemosensory and vestibular inputs—interacts alongside visceral mechanisms. These visceral mechanisms involve an inter-organ crosstalk, often detected through dynamic changes in cardiovascular and cardiorespiratory activities during different cognitive and behavioral contexts (Widjaja et al., 2013). Visceroceptive processes sense these changes (Brener, 1977), therefore providing a transient feedback of the physiological state of the body. This unified physiological architecture enables smooth communication between internal and external sensory cues, ultimately contributing to bodily self-awareness and conscious cognition. In the subsequent paragraphs, we overview the results elucidating interactions between interoception and other sensory modalities. These findings shed light on how interoceptive mechanisms intertwine with processes from different sensory modalities, contributing to our understanding of bodily self-awareness, even in the absence of one of these modalities (Miall et al., 2021).

There has been a noted connection between visual awareness and cardiac dynamics. For instance, visual detection is influenced by the phase of the cardiac cycle (contraction versus relaxation), e.g. (Salomon et al., 2016), while neural responses to heartbeats can predict visual detection of a faint visual grating (Park et al., 2014). In line with these findings, lesions in anterior insula can disrupt the effect found on visual detection based on the cardiac cycle (Salomon et al., 2018). Besides these effect of cardiac afferents on visual awareness, visually presented information about the cardiac rhythm can also influence body ownership (Heydrich et al., 2018; Suzuki et al., 2013). Furthermore, active sampling in visual search has also been shown as being coupled with the cardiac cycle (Galvez-Pol et al., 2020).

Similarly to vision, detection of somatosensory stimuli and tactile action are also coupled to the phase of the cardiac cycle (Edwards et al., 2009; Motyka et al., 2019), and neural responses to heartbeats are predictive of somatosensory detection, suggesting that interoceptive inputs are integrated during conscious perception (Al et al., 2021, 2020). Notably, somatosensory pathways can mediate conscious cardiac interoception (Khalsa et al., 2009). The extent of intertwining between these mechanisms is evident in the altered tactile processing observed in individuals experiencing full-body illusions induced by cardio-visual synchrony (Heydrich et al., 2018). Similarly to the case of active visual sampling, during an active tactile discrimination task, individuals tend to modify their sensory sampling behavior based on the cardiac cycle, as they spend more time sensing during cardiac systole—a period characterized by relatively lower tactile perceptual sensitivity (Galvez-Pol et al., 2022). Lastly, multisensory integration appears enhanced during cardiac contractions (Saltafossi et al., 2023), especially in the cases of audio-tactile and visuo-tactile integration, suggesting that heartbeat signaling may influence somatosensory inputs during cardiac relaxation, ultimately affecting multisensory integration. Building on these results, it has been suggested that combining coherent multisensory stimuli with visual interoceptive feedback in virtual environments can enhance bodily self-awareness and control in immersive scenarios (Macruz et al., 2024).

Research has uncovered intriguing evidence of pain modulation across the cardiac cycle, suggesting a dynamic relationship between cardiovascular activity and pain processing. These studies have indicated that pain sensitivity varies throughout the cardiac cycle, with peaks in pain threshold occurring during cardiac contraction, and troughs during cardiac relaxation (Edwards et al., 2008, 2001; Wilkinson et al., 2013). Moreover, interoceptive feedback has shown to relieve pain (Gong et al., 2022), lower cardiac awareness has been linked to greater severity of symptoms and lower tolerability of pain in patients suffering from chronic pain (Di Lernia et al., 2016; Pollatos et al., 2012), and pain anticipation can alter interoceptive perception (Parrotta et al.,

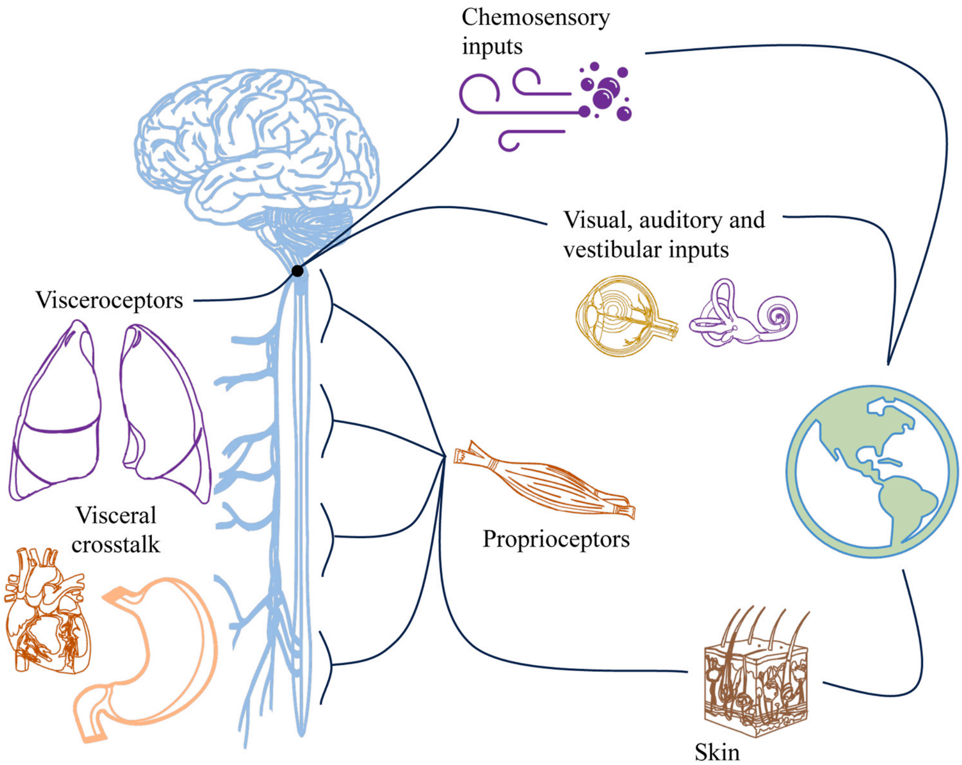

Fig. 1. The figure illustrates the concept of interoceptive-exteroceptive integration, which encompasses multiple physiological mechanisms occurring concurrently. Visual, auditory, tactile, proprioceptive, and vestibular inputs contribute to the exteroceptive component, providing information about the external environment, but also about the body and its relationships with the environment. Meanwhile, visceral crosstalk and visceroceptive mechanisms, integral parts of interoceptive processes, operate in parallel, relaying information about internal bodily states. This integrated system facilitates the seamless interaction between internal and external sensory signals, ultimately contributing to bodily self-awareness and conscious processing.

2024). Further research has suggested that these mechanisms emerge from the interplay between cardiovascular physiology and central processing, which include a suppression of the brain responses to heartbeats (Shao et al., 2011) and cardiac sympathetic modulations to brain delta and gamma brain oscillations (Candia-Rivera et al., 2022a). This was recently supported by neuromodulation of the insula, which affects both pain processing and heart rate variability (Legon et al., 2024). Indeed, sympathetic responses can anticipate pain (Dudarev et al., 2024) and relate to the overall subjective experience of pain (Terkelsen et al., 2004).

The vestibular system is crucial as well for the neural representations of spatial aspects of bodily self-awareness, through mental spatial transformation, self-motion perception, and body representation with respect to multisensory signals from the body (Pfeiffer et al., 2014). Fewer evidence exists on the potential relationships between vestibular and interoceptive mechanisms (Nakul et al., 2020). Vestibular stimulation can evoke changes in autonomic nervous system activity (Radtke et al., 2000) and alterations in vestibular function have been associated with dysregulation of cardiovascular functions (Oh et al., 2015; Yates et al., 2000). As the central processing of the vestibular system has overlaps with those regions related to autonomic regulation, interoceptive inputs may influence vestibular representations (zu Eulenburg et al., 2013) as well as cognitive factors may influence vestibular-autonomic regulation (Yates et al., 2014). Indeed, recent evidence suggested that interoceptive feedback contributed to the feeling of stability while standing on the edge of a raised surface (Hill et al., 2024).

Chemosensation plays a key role as well in embodied interactions. The direct links between interoceptive mechanisms and chemosensation are connected to visceral sensations, such as those associated with food smell, nutrient sensing (Sclafani and Ackroff, 2012), and, although debated, pheromones (Oren et al., 2019). Neural processing of chemosignals is highly specific (Lundström et al., 2008), and its functions include self-awareness through the transient updates of sensory inputs including own smell (Perl et al., 2020), but also social interactions as reported in smell after handshaking (Frumin et al., 2015), attractiveness to smell-alike individuals (Ravreby et al., 2022), and tears' chemosignaling of emotions (Gelstein et al., 2011). Indeed, odors can trigger emotion-specific functional responses linking autonomic responses to brain networks (Rho et al., 2024).

Further evidence demonstrates the complex intertwining of sensory modalities significantly influencing bodily self-awareness. The insula, which converges on interoceptive processing, also plays a role in bodily self-awareness and social cognitive processing. For instance, the posterior insula distinguishes between observing others' somatosensory experiences and one's own (Ebisch et al., 2011), and damage to the right insula disrupts perception of social, affective touch (Kirsch et al., 2020). However, beyond anatomical convergence among there processes, functional convergence has been shown as well. Higher interoceptive awareness enhances the effects of social touch representation (Adler and Gillmeister, 2019), and social touch exerts specific autonomic modulations of cardiac dynamics (Candia-Rivera et al., 2024a), suggesting specificity of certain interoceptive mechanisms with respect to the social component. Improved cardiac interoception correlates with increased perceived self-body closeness and peripersonal space representation (Nakul et al., 2020; Scandola et al., 2020), and a higher interoceptive accuracy predicts narrower peripersonal space boundaries (Ardizzi and Ferri, 2018). A disruption in interoceptive mechanisms appears linked to the feeling of detachment of reality or dissociation, as reported in depersonalization disorder, epilepsy and ketamine use (Kaldewaij et al., 2024; Koreki et al., 2020; Yamamoto and Nakao, 2022). Differences in interoception have been linked to the malleability of body representation, as subjects who experience a stronger rubber hand illusion tend to have lower interoceptive sensitivity (Tsakiris et al., 2011), which was further confirmed in patients with unilateral brain damage (Boccia et al., 2023). Full-body illusion paradigms, like cardio-visual stimulation synchronizing a virtual body illumination with heartbeats, evoke altered states of bodily self-awareness, which is particularly altered in patients with insular resection (Ronchi et al., 2015). These illusions can also occur by synchronizing the virtual body with breathing patterns instead of heartbeats, further reinforcing the role of bodily activities in self-awareness. (Monti et al., 2020). In experiments with full-body and enfacement illusions, changes in neural responses to heartbeats correlate with shifts in bodily self-awareness (Park et al., 2016; Sel et al., 2017). Increased self-focus through mirror self-observation enhances cardiac interoceptive sensitivity (Ainley et al., 2012), while alterations in body ownership affect cardiac interoceptive accuracy (Filippetti and Tsakiris, 2017). But also, self-face recognition is enhanced when perceived during cardiac systole, further highlighting the intertwined nature of interoceptive mechanisms and self-awareness (Ambrosini et al., 2019). In conclusion, it is evident that interoceptive mechanisms are pivotal in both the primary processing of sensory inputs necessary for bodily self-awareness and in higher-order cognitive functions, such as social interactions and meta-representations of the bodily self. Importantly, the interplay between interoception and the self is bidirectional, emphasizing the dynamic and reciprocal nature of this relationship in shaping human experience and cognition (Kaldewaij et al., 2024).

The complex interplay of various sensory modalities underscores the intricate relationship between bodily self-awareness, or more broadly, self-related cognition, highlighting the complexity of human experience. Traditional approaches in neuroscience must be reexamined to capture the complexities of these interactions and better understand their physiological foundations (Westlin et al., 2023). Rather than assuming localized brain regions govern specific cognitive processes, we should acknowledge the distributed nature of neural ensembles across the whole nervous system. Certain events, responses or conditions likely arise from the coordinated activity of diverse neural ensembles, influenced by signals from both internal milieu and the environment (Azzalini et al., 2019). A paradigm-shift towards alternative assumptions is essential for advancing our understanding of the physiological underpinnings of certain behavioral responses and clinical conditions.

5. Unraveling the network physiology of interoceptive mechanisms

In recent years, considerable advances have been made in elucidating the complex brain networks responsible for interoceptive processing (Craig, 2009; Engelen et al., 2023b; Fermin et al., 2023; Kleint et al., 2015; Park et al., 2018; Salvato et al., 2020), shedding light on the potential mechanisms responsible for the way we perceive and interpret bodily cues.

The framework of predictive coding, which posits that the brain generates predictions about incoming sensory information and updates internal models based on the actual input received, has emerged as an explanatory model for how the brain processes interoceptive signals (Barrett and Simmons, 2015; Seth and Tsakiris, 2018). Multisensory integration and the perceptual formation of the self can be understood as well within predictive coding frameworks. Allostatic mechanisms, which regulate the body's internal state, use both current and prior inputs to continuously update these predictions, allowing for adaptive responses to changing environmental conditions (Carruthers, 2008). Models of interoception within the predictive coding framework suggest that precision in interoceptive systems shapes individual differences in interoceptive sensitivity, which are translated into different weights for prior representations and prediction errors (Petzschner et al., 2021). However, bodily inputs can be noisy and subject to transduction delays, especially proprioceptive signals—which allows us to sense the position and movement of our body parts, contributing to our conscious experience of having and controlling a physical body (Dallmann et al., 2021). To quantify and manage the uncertainty introduced by the noisy bodily feedback, the central nervous system may perform a state-of-body estimation by combining multisensory feedback with predictions (McNamee and Wolpert, 2019). With regard to proprioception, the process of matching one's position with an intended movement or action encompass a comparison with the predicted consequences of the action as well (Balslev et al., 2006; Farrer et al., 2003). Existing models of interoception do not allow for predictions concerning how ascending signals and descending regulations differentially contribute to the monitoring and interpretation of bodily signals (Chen et al., 2021). Instead, predictive coding models typically consist in a probabilistic signal processing to compare the actually observed and expected bodily outputs (Farb et al., 2015; Seth et al., 2011).

To uncover the interdependencies between physiological signals, a multisystem modeling approach accounting for multidirectional physiological communication may be required. By quantifying the impact of interoceptive processes on the organization of neural networks, we aim to gain deeper insights into how our neural systems generate physiological dynamics that contribute to our awareness of ourselves as embodied beings. Typical approaches to quantify the relationship between brain dynamics and peripheral signals rely on correlation, directional coupling, co-occurrences, or phase synchronization measures. Different approaches have been proposed to study brain-other organs couplings, including gastric, respiratory and cardiac rhythms (Candia-Rivera et al., 2022b; Kluger et al., 2021; Rebollo et al., 2018). However, previous studies have predominantly focused on the interaction between specific brain or scalp regions and visceral dynamics, disregarding the dynamic nature of brain networks and their role in numerous neural functions (Bashan et al., 2012; Bressler and Menon, 2010; Faes et al., 2022; Park and Friston, 2013). Fewer efforts exist on computational approaches accounting for several types of interactions within brain-other organ systems, coupled and integrated, which can further enlighten the physiological substrates of bodily self-awareness. This could identify the network structure of multisystem interactions, revealing the underlying complex and hierarchical organizations triggered at different physiological and cognitive states.

Complex systems—systems composed of interconnected parts that exhibit a collective behavior not easily inferred from the behavior of the individual parts—frequently display interactions among numerous components that surpass mere pairwise connections (Fig. 2), involving higher-order interactions among various nodes. These interactions can profoundly influence global network properties but are frequently disregarded in conventional analyses. To bridge this gap, methodologies have been devised to evaluate higher-order interactions among multivariate time series, with particular emphasis on assessing the synchronization of physiological dynamics, in which the equilibrium between redundant and synergistic information may signal specific cognitive functions (Scagliarini et al., 2023). Synergy emerges from global interactions within a network, enhancing the efficiency of information exchange through the utilization of interactions between the network's nodes. Conversely, redundancy guarantees the system's robustness but may not fully exploit the available information capacity. These descriptions provide a detailed comprehension of how information flows and is used within complex systems (Luppi et al., 2024). Through these frameworks, low-order descriptors can be derived, offering insights into the individual contributions of variables in shaping high-order circuits (Scagliarini et al., 2023), providing a comprehensive assessment of system dynamics. Building upon the measures of information synergy and redundancy, the complex systems' information can be decomposed to assess physiological causality and instantaneous influences across multiple frequency and time scales (Faes et al., 2022). For instance, spectral representations of different physiological systems can be represented as vectors of state space models— mathematical frameworks used to describe the dynamics of a system—to assess interactions among process groups, both in specific frequency bands and in the time domain.

These frameworks can be simplified to the identification of the brain

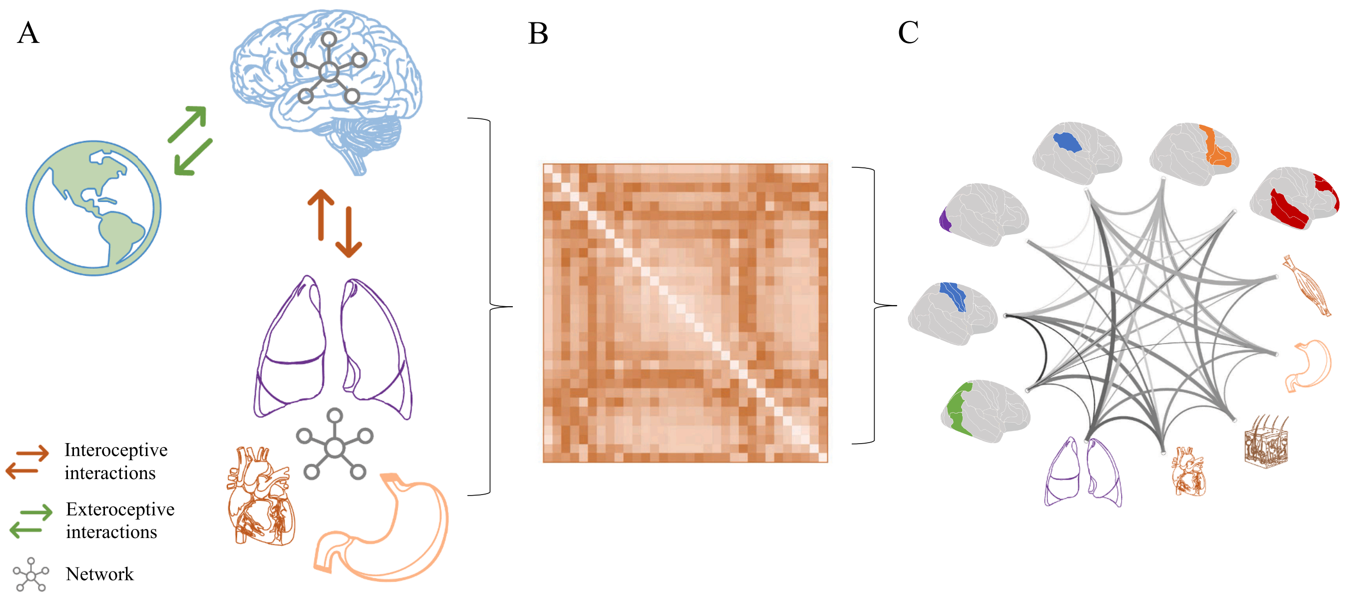

Fig. 2. Illustration of a simplified framework for the (A) integration of interoceptive and exteroceptive information, (B) represented as a pseudo-connectivity framework, (C) and its subsequent representation as a graph depicting interactions between key brain regions and bodily systems. Interoceptive signals (arising from within the body) and exteroceptive signals (arising from the external environment) converge and interact within the nervous system (left), forming a complex network of connections (center). This network is depicted as a graph (right), where nodes represent specific brain regions and bodily systems, and lines? represent the connections and interactions between them. Through these representations we can derive further characterizations of the systems involved to gain insights into the intricate interplay between neural processes and bodily functions, shedding light on the mechanisms underlying perception, cognition, and behavior.

networks associated with changes of a bodily or visceral rhythm (Fig. 3). For instance, by examining the interplay between pair-wise brain functional connectivity and cardiac dynamics (Candia-Rivera et al., 2024d). Through this approach, the framework is simplified by landing the analysis between triads, by quantifying the coupling of pairwise brain region connectivity and cardiac dynamics, with the ultimate goal of identifying the networks associated with cardiac dynamics under different conditions. In self-other touch distinction, this approach revealed that other touch induces changes in the coupling between brain networks and cardiac autonomic activity (Candia-Rivera et al., 2024c). Specifically, there was an increase in the coupling between fronto-parietal brain networks and parasympathetic activity, particularly in the alpha and gamma frequency bands. Conversely, touch progressed, there was a decrease in the coupling between brain networks and sympathetic dynamics across a broad frequency range. These findings highlight the intricate relationship between visceral dynamics and brain organization, shedding light on the neurophysiological mechanisms underlying self-other touch distinction.

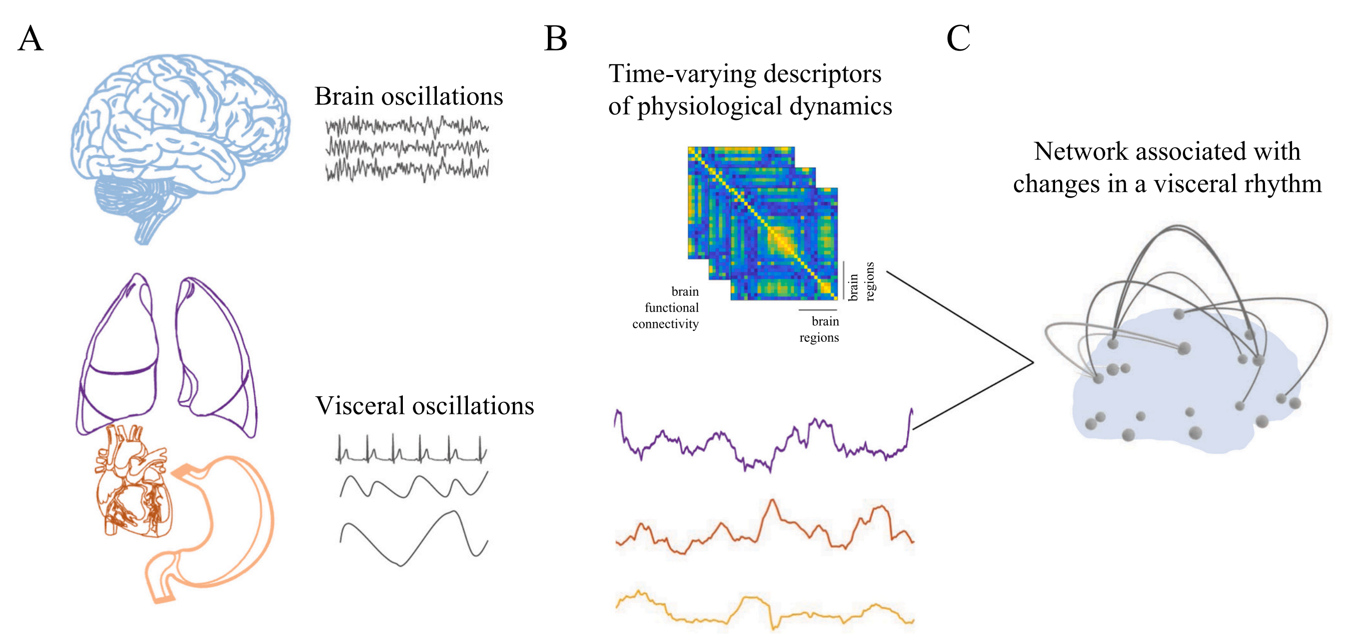

Fig. 3. Frameworks for understanding higher-order interactions within complex physiological systems. In this example, the framework is focused on (A) non-invasive electrophysiological measurements for quantifying relationships between (B) changes in brain functional connectivity, by gathering co-fluctuations between two nodes in the brain as a function of a visceral oscillation, such as cardiac, respiratory or gastric dynamics, to ultimately (C) identifying the entire network of pairwise connections that dynamically synchronize with other organs' dynamics.

Alternatively, when brain regions of interest have not been identified, in a more agnostic manner, another framework provides biomarkers related to large-scale brain-heart interaction by quantifying the dynamics between global brain activity and cardiac dynamics (Candia-Rivera et al., 2024b). This framework showcases how the study of brain-other organs' interactions can be approached in various conditions where global neural dynamics are not fully understood by solely examining the dynamics of specific brain regions. The method quantifies the variations in global network dynamics, focusing on parameters indexing the changes in brain segregation (Rubinov and Sporns, 2010), by providing a holistic quantification of global dynamics and their relationships with the fluctuations in visceral activities.

A persistent challenge in modeling physiological interactions is accounting for the interplay across different scales, from molecular to systemic mechanisms (Chen et al., 2017). New discoveries have revealed certain heartbeat sentinel mechanisms at cell membrane level (Jammal Salameh et al., 2024), indicating that the communication pathways between the brain and other organs are still not completely understood. The development of new frameworks to understand large-scale physiological interactions, such as the integration of interoception and exteroception, could greatly enhance our understanding of bodily self-awareness. These complex mechanisms, which are not yet fully uncovered, represent significant challenges and are difficult to study. Consequently, there is a pressing need for more multidisciplinary science partnerships. By advancing our comprehension of the functional connections between the brain and other organs, these efforts may provide valuable insights into the role of these interactions in health and disease.

6. Translational perspectives

Understanding the interoceptive mechanisms underlying bodily self-awareness through fundamental research in neurophysiology lays the foundation for advancements in clinical practice. The translation of physiological mechanisms into biomarkers holds profound significance, particularly in the realm of mental health (Jenkinson et al., 2024), for conditions that cause alterations in self-awareness and pathological (dis) embodiment. The relationship between mental health and bodily triggers has been acknowledged. Indeed, these pathological conditions encompass dissociative symptoms emerging from stress, anxiety, mood, and addictive disorders; altered bodily cues in somatic symptom disorders; or disrupted body image, as observed in eating disorders (Khalsa et al., 2018). Therefore, recognizing dysfunctions in interoceptive mechanisms seems key for further understanding some mental health conditions, however, this has been primarily reported from behavioral evidence and limited physiological insights (Garfinkel et al., 2016). For instance, brain-based biomarkers are yet to efficiently stratify major depressive disorder (Winter et al., 2024). Interestingly, depression is known to emerge together with certain cardiovascular conditions (Penninx, 2017), which has been shown as well in studies of brain-heart interaction (Garcia et al., 2020).

Dissociative symptoms and disorders are marked by disruptions in the experience of the self and the surrounding world, and some insights exist into these disruption through the lens of interoception, with potential use as a transdiagnostic framework (Woelk and Garfinkel, 2024). Studying the neurophysiology of altered bodily self-awareness promises insights into dissociative symptoms such as the ones described in conditions like depersonalization disorder, enhancing our understanding of this complex condition. Thoroughly, Depersonalization Disorder may represent a disordered interoception condition, potentially caused by a disruption in the intricate connection between the sense of self and how the brain interprets internal cues. First, one of the altered regions reported in depersonalization disorder is the insula, a brain region associated with interoceptive processing (Medford et al., 2016). Case reports of depersonalization disorder revealed impaired cardiac interoceptive awareness and lower functional connectivity during an interoception task, indicating altered neural mechanisms and cognitive processes regarding cardiac interoception (Sedeño et al., 2014). Further research confirmed that depersonalization disorder patients exhibit altered cortical processing of cardiac signals during interoception tasks, they fail to show the pattern of heartbeat evoked response modulations demonstrated by healthy participants (Schulz et al., 2015). Additionally, depersonalization disorder may involve a deficient representation of visceral signals at the brainstem level, as evidenced by the absence of cardiac cycle effects on startle responses (Schulz et al., 2016).

Interventions targeting interoceptive pathways may improve dissociative symptoms. For instance, meditation with a sustained interoceptive focus on breath sensations increases the neural activation of interoception networks (Weng et al., 2021). Evidence in depersonalization disorder patients suggests that mindful breathing reduces symptom severity and enhances autonomic regulation (Michal et al., 2013). Altogether, the integration of internal cues into the sense of self underscores their key role in shaping our understanding of identity and perception. This line of research can bridge the gap between fundamental research and clinical intervention, paving the way for targeted therapeutic strategies to alleviate the distressing symptoms of conditions such as depersonalization disorder. Indeed, within the neuromodulation realm, treatments for depression include the use of transcranial magnetic stimulation—the use of magnetic fields to stimulate brain regions—potentially triggering neural excitability and new connections (Iseger et al., 2020). Neuromodulation is usually aimed at the dorsolateral prefrontal and the anterior cingulate cortices, which in turn affect cardiac dynamics. This highlights the importance of including brain-heart interplay measurements in the treatment of human depression.

The clinical translation of fundamental research on the neurophysiology of bodily self-awareness also holds significant implications for consciousness research. By unraveling the intricate interplay between neural processes and subjective experiences of selfhood, such studies offer invaluable insights into the nature of consciousness itself. Understanding how disruptions in these processes manifest in conditions like dissociation not only sheds light on the mechanisms underlying altered states of consciousness but also provides a framework for evaluating disordered consciousness more broadly. Experimental findings suggest that cardiac signals act as an anchor point for self-awareness. However, the physiological evidence suggesting that interoceptive mechanisms are essential for anchoring the self to the body is scarce. The question of whether embodied interactions are necessary for self-awareness has been challenged, also in the absence of bodily self-awareness. For instance, the encoding of the self is possible in the absence of body-environment interactions, as evidenced by cases of brain damage leading to the locked-in syndrome (Laureys et al., 2005). However, it is important to note that even locked-in patients still have interoceptive inputs for example from the beating of their heart, and suggesting they have a history of interactions with the environment which can be recalled during re-experience, imagination or dreaming. Additionally, the potential of neuromodulating peripheral nerves to restore consciousness (Corazzol et al., 2017) underscores the importance of these neural connections in overall conscious processes, including the multifaceted manifestation of brain-heart interactions at different levels of consciousness (Candia-Rivera and Machado, 2023).

Assessing interoceptive mechanisms is a vital indicator of consciousness, shedding light on the emergence of self-awareness and the physiological processes connecting the self to the body. Understanding how interoceptive inputs shape our self-awareness helps define the phenomenological and physiological markers of altered states of consciousness. A comprehensive study of bodily self-awareness should include various physiological dynamics, such as metabolic and multisystem interactions. Translating fundamental research on the neurophysiology of bodily self-awareness into clinical practice offers promising insights into mental health and consciousness studies.

7. Conclusions

At the intersection of neuroscience and cognitive science lies a rich tapestry of research exploring the multifaceted dimensions of self-awareness and their underlying physiological substrates. Exploring this detailed landscape reveals a complex interplay between various cognitive processes and neural mechanisms. Among these, interoception emerges as a central component, intimately intertwined anatomically and functionally with diverse aspects of self-awareness. From the perception of internal bodily states to the shaping of external perceptual experiences, interoception appears to play a foundational role in delineating the boundaries of the self. As we navigate this exploration, it becomes increasingly apparent that understanding the intricacies of self-awareness necessitates a holistic consideration of both internal and external realms, with interoceptive mechanisms serving as a bridge connecting these domains.

Interoceptive signals are crucial for creating our sense of reality and embodied experiences, forming a first-person perspective that anchors subjective experience in a physical body. Disruptions in interoception can cause detachment from the body and abnormal emotion processing. Given its significant role in emotions, interoception is likely central to disembodiment conditions involving disrupted interoceptive mechanisms. The experimental evidence suggests that interoceptive information is essential for embodied cognition and behavior, but it is still unclear which contexts require interoceptive information integration compared to other sensory modalities. It is also unclear to what extent interoceptive signals shape global brain dynamics and whether higher-order interdependencies are necessary to enable bodily self-awareness.

Therefore, the research agenda on bodily self-awareness, and more broadly, consciousness, should focus on the relationship between different sensory information sources and their impact on various cognitive and behavioral processes. This is challenging to achieve, while meta-analyses can serve as intermediate steps towards more complex multilevel studies, research efforts should promote long-term multi-disciplinary research partnerships. Specifically, by incorporating advanced biomedical signal processing to uncover the network physiology behind these processes by quantifying couplings, directionality, and integration within and between physiological systems.

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