Perceptual Mechanism of Interoception: On Roles of Attention in Modulating Uncertain Interoceptive Signals

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Abstract

This thesis presents an in-depth investigation into the perceptual mechanisms of interoceptive awareness, with a primary focus on the role of interoceptive attention. A series of experiments builds upon the predictive coding framework, demonstrating the role of attention in optimizing relative precision (inverse variance) of sensory signals and predictions, across all sensory modalities. The first experiment, using fMRI, investigates the neural basis of interoceptive attention. The results reveal a dissociation between brain regions for interoceptive focus and perceptual accuracy. Importantly, the primary interoceptive area (posterior insula) remains inactive. In contrast, dorsal middle insula activations are linked to interoceptive attention, while the dorsal right anterior insula is tied to individual interoceptive accuracy, suggesting that interoceptive awareness relies more on attentional modulation of sensory precision than analyzing sensory features, as hypothesized by predictive coding. In the second experiment, a comparative analysis of attention to cardiac versus gastric sensations uncovers unique activation patterns in the brain. Cardiac attention primarily activates the right anterior insula, whereas gastric attention involves additional areas like the occipitotemporal visual cortices. Importantly, the middle insula distinctly activates for cardiac and gastric attention but the posterior insula not as in the first experiment, further elaborating the role of attention in interoceptive awareness. In addition to investigations on the neural basis of interoceptive attention, my research extends to the interaction between interoception and exteroception in a unified perceptual system proposed in the predictive coding. Specifically, the third experiment explores how auditory externalization of heartbeats, achieved through real-time biofeedback, influences interoceptive attention and heartbeat perception. The findings indicate that subjective attribution of externalized heartbeat sounds significantly alter participants' heartbeat perception, highlighting the impact of predictive process on interoceptive awareness. The fourth experiment assesses the effect of external auditory stimuli on interoceptive awareness. Results show that auditory distractions can diminish both the accuracy and confidence in heartbeat perception tasks, illustrating attentional modulation of the relative precision can be hindered by external sensory inputs. Finally, the fifth experiment examines the opposite of the fourth experiment, if heightened interoceptive signals via attention affect visual perception and metacognition. This study concludes that

a focused attention on heartbeat sensations leads to more cautious visual perceptual confidence, while not affecting visual accuracy, substantiating the role of attention in optimising the relative precision across all sensory modalities. Overall, the present findings support the inductive hypotheses derived from predictive coding, collectively elucidating the role of attention in modulating relative precision across all sensory modalities, thereby advancing our understanding of how the brain navigates and integrates exteroception and interoception.

Introduction

Humans experience various changes within the body, which contribute to our sense of physical condition and influence mood and emotional states. These internal senses, encompassing everything from the rhythmic beating of the heart to the subtle shifts in stomach fullness, fall under the broad spectrum of interoception. Interoception, a term that has seen evolving definitions and interpretations, refers to the process by which the nervous system senses, interprets, and integrates signals originating from within the body, thereby providing a continuous stream of information about our physiological state (Khalsa et al., 2018; Chen et al., 2021). This intricate process, once overlooked in the shadow of external sensory systems, has now emerged as a vital area of research, shedding light on its crucial role in maintaining bodily homeostasis, guiding behavior, and even shaping emotional experiences. Recent advancements in cognitive science have revolutionized our understanding of interoceptive processing, unearthing its complex neural pathways and highlighting its interconnectedness with cognitive and emotional processing (Critchley and Garfinkel, 2018; Azzalini et al., 2019; Tallon-Baudry, 2023). This new understanding highlights the importance of internal bodily signals in the holistic functioning of the human mind and body, elevating interoception from a peripheral player to a central orchestrator in the symphony of human perception and experience.

However, despite these advancements, a systematic investigation focusing specifically on the mechanisms underlying conscious experience of interoception (i.e., interoceptive awareness) remains relatively unexplored. This gap in research highlights the need to dissect the neural underpinnings and cognitive implications of interoceptive awareness more thoroughly. To address this need, I have embarked on a research journey that centers on unraveling the intricacies of the perceptual mechanism, particularly in terms of interoceptive attention and multisensory processing. This thesis is the culmination of six years of research I conducted in the Department of Psychology at Hokkaido University.

The opening section of this thesis commences with a brief examination of the neural foundations underlying interoception. Following this, the historical evolution of interoception research is traced from its early conceptual stages. Subsequently, I consolidate the numerous taxonomies that have emerged within

contemporary literature, particularly focusing on interoceptive awareness. This categorization is succeeded by a synthesis of the methodologies employed in empirical studies spanning various domains of interoceptive awareness. These surveys collectively establish a structural framework for comprehending the inherent diversity and complexity within interoceptive awareness, setting the stage for an in-depth exploration of its perceptual mechanisms.

Then, I highlight the difficulties when attempting to apply conventional perceptual models from cognitive psychology to the realm of interoceptive awareness. It points out the limitations of such models in encapsulating the unidentifiability of sensory features of interoceptive sensations and perceptual uncertainty in interoceptive awareness. To bridge this gap, the following part proposes a potential model of interoceptive awareness, grounded in the principles of Bayesian brain hypothesis, a powerful framework offering a unified perceptual system. This model posits that perceptual experiences is not a mere passive reception of sensory signals but an active, inferential process, where the brain anticipates, interprets, and assigns meaning to these signals based on past experiences and contextual cues.

The core of this thesis is a series of empirical experiments conducted to validate inductive hypotheses regarding the role of attention in shaping interoceptive awareness, derived from the Bayesian framework. These experiments investigate how focusing on internal bodily signals can modulate the way individuals perceive them and interact with the external environment. By investigating the characteristics of attention that facilitates interoceptive awareness, the present study aspires to unravel the mechanisms governing how we interpret the internal states of our bodies and, in turn, how interoceptive information exerts its influence over other perceptions and higher-order cognitive functions. The findings from these experiments are expected to provide valuable insights into the perceptual mechanisms of interoceptive awareness, further advancing our understanding of this complex and multifaceted construct. Some of these studies have been published elsewhere (Haruki and Ogawa, 2021, 2023b, 2023a; Haruki et al., 2023).

Neural Origins of Interoception

In this section, I will provide a brief review of the physiological systems and neural pathways underpinning interoception, the process by which the nervous system senses, interprets, and integrates signals originating from within the body. The intricate journey of interoceptive afferent begins at the periphery with the initial sensing mechanisms, detecting various changes in internal bodily states. From here, I will explore the visceral sensory pathways, crucial conduits through which this sensory information travels to reach the central nervous system. Attention will be given to the role of the brainstem, a pivotal site for the collection and initial integration of interoceptive signals. I will then synthesize how these signals are further relayed and processed through thalamic projections, a key step in the modulation and refinement of interoceptive signals. An important part of this review will be dedicated to cortical processing, delving into the intricate neural mechanisms at play within the brain's cortical regions. Here, the focus will be on the anatomical and functional aspects of the insular cortex, which have been identified as critical areas in the processing and conscious awareness of interoceptive signals. While much of our understanding of these pathways has been derived from animal studies, recent advancements in neuroimaging and neurological research have shed light on the corresponding cortical activations in humans. By integrating these findings, this review aims to provide a holistic understanding of the complex and multi-layered interoceptive afferents, elucidating how our bodies communicate internal states to the brain.

Interoceptive Sensors

Peripheral and central sensing in interoception is the foundational mechanism by which the body detects and responds to its internal physiological states, encompassing a diverse array of sensory transducers that monitor various aspects of the body's internal environment. These include chemoreceptors, mechanoreceptors, thermal and humoral receptors, each specialized to detect specific types of internal stimuli.

Chemoreceptors, for instance, play a pivotal role in interoceptive signalling by detecting a wide array of chemical states and substances within the body, thereby contributing significantly to the regulation of essential physiological functions. One of the most significant roles of chemoreceptors is in the regulation of respiratory and cardiovascular systems. For instance, carotid body chemoreceptors are highly sensitive to partial pressures of carbon dioxide (pCO2) and oxygen (pO2), as well as to the hydrogen ion concentration (pH) level of blood. They are instrumental in modulating respiratory rates and heart rhythms in response to fluctuating levels of these gases, ensuring that tissue oxygenation remains within optimal limits (Buckler, 2015). This chemosensitivity is thought to be mediated by specific ion channels, such as the Twik-related acid-sensitive K+ channels 1 and 3 (TASK1/TASK3), which respond to acidosis and changes in O2 levels. In addition to these classic roles, chemoreceptors also contribute significantly to metabolic regulation. Central and peripheral glucoreceptors, which detect glucose levels in the body, are vital for energy homeostasis, influencing feeding behavior, and energy expenditure (Li et al., 2019; Ren et al., 2019). Moreover, the gustatory system's chemoreceptors, primarily involved in taste perception, also contribute to interoceptive processes. These receptors, located in the oral cavity and the gastrointestinal tract, are tuned to various tastant molecules and play a dual role in recognizing external stimuli (as part of the exteroceptive system) and signaling internal metabolic states, thus influencing feeding decisions and digestive processes (Barretto et al., 2015; Steensels and Depoortere, 2018). These multifaceted functions of chemoreceptors underscore their critical role in a wide array of physiological processes, from basic metabolic regulation to complex behaviors such as feeding, thereby demonstrating their integral contribution to the body's internal monitoring and regulatory systems.

These receptors are strategically positioned in various organs and tissues to detect mechanical forces and translate them into biological signals that the body can interpret and act upon. A prime example of this is seen in the cardiovascular system, where baroreceptors play a crucial role. Located within the walls of major blood vessels like the aorta and carotid arteries, these mechanoreceptors are sensitive to changes in blood pressure. They continuously monitor the stretching of vessel walls, which corresponds to the blood pressure within them. When blood pressure rises, the increased stretch of these vessels activates baroreceptors, triggering a cascade of neural signals to the brain. This feedback leads to adjustments in heart rate, vascular resistance, and cardiac contractility, ultimately aiding in maintaining stable blood pressure levels (Suarez-Roca et al., 2021). The mechanosensitivity of these receptors is notably influenced by PIEZO1 and PIEZO2 ion channels, which are integral to the process of converting mechanical stimuli into electrical signals (Zeng et al., 2018; Stocker et al., 2019). The presence of these channels in various tissues, including the lungs, bladder, and gastrointestinal tract, further highlights the expansive role of mechanoreceptors in monitoring internal physiological states beyond cardiovascular regulation. The activation of mechanoreceptors in response to stretching or pressure changes is a critical component of the body's internal feedback system, allowing for the real-time regulation of various functions such as blood flow, respiration, and digestive processes.

Thermoreceptors and nociceptors, as integral components of the body's interoceptive system, perform specialized functions in detecting temperature variations and potential harmful stimuli, respectively (Craig, 2018). The skin is innervated by both cold-sensitive and warm-sensitive afferent neurons, each responding to distinct thermal ranges and stimuli. Cold-sensitive afferent neurons in the skin display activity at temperatures between approximately 10 and 42°C. They are activated by innocuous cold stimuli, inhibited by warm stimuli, and are generally mechanoinsensitive. In primates, these neurons have small-diameter myelinated (Aδ) fibers, whereas in non-primate mammals, they possess unmyelinated (C) fibers. In contrast, warm-sensitive afferent neurons, which have a lower density of innervation compared to cold-sensitive afferents, show ongoing activity at temperatures ranging from about 38 to 48°C. They are activated by warm stimuli, inhibited by cold stimuli, and also are mechanoinsensitive, with C fibers (Schepers and Ringkamp, 2010; Vriens et al., 2014; Tan and Knight, 2018). Deep somatic tissues and viscera are also innervated

by thermosensitive afferent neurons, most of which are warm-sensitive and mechanoinsensitive, typically with unmyelinated axons. However, these neurons have been relatively less studied, with some investigations focusing on regions like the upper gastrointestinal tract, liver (both vagal afferents), dorsal abdominal wall, and skeletal muscle (Simon et al., 1986; Jänig, 2018). Warm sensitivity in the spinal cord is potentially mediated by cutaneous afferent neurons excited by spinal cord warming, indicating a complex interplay between external and internal thermal sensing. (Tan and Knight, 2018; Avril and Chevet, 2019; Crucianelli and Ehrsson, 2023).

Nociceptors, specialized sensory neurons in the field of interoception, play a critical role in detecting and responding to potentially harmful stimuli, signaling the sensation of pain. These receptors are adept at recognizing a wide range of noxious stimuli, including extreme temperatures, mechanical damage, and chemical irritants (Dubin and Patapoutian, 2010). Found in skin, joints, muscles, and internal organs, nociceptors are essential for initiating protective reflexes and behaviors, alerting the body to potential injury or damage. These receptors are predominantly associated with Aδ and C fibers. Aδ fibers, known for their relatively fast conduction speeds, are primarily involved in the sensation of acute, sharp pain, often acting as the first warning sign of injury or harm. C fibers, on the other hand, are slower-conducting fibers that contribute to the sensation of dull, lingering pain, crucial for the ongoing awareness of tissue damage or other pathological states (Olausson et al., 2010). The activation of nociceptors occurs in response to various types of noxious stimuli, including extreme temperatures, mechanical damage, and chemical irritants. These receptors are highly sensitized by biochemicals such as prostaglandins, which are often released during tissue injury and inflammation. This sensitization enhances the pain signal, ensuring that the body takes notice and reacts appropriately to avoid further harm (Avril and Chevet, 2019).

Humoral receptors in interoception are crucial for detecting and responding to various hormonal signals, playing important roles in the body's internal chemical monitoring and regulation. These receptors, sensitive to a wide range of hormones, mediate numerous physiological responses that are integral to maintaining homeostasis. For example, in the gastrointestinal tract, humoral receptors are key in regulating food intake through their response to hormones like leptin, ghrelin, and cholecystokinin (Andermann and Lowell, 2017; Quigley et

al., 2021). Leptin, produced in relation to adipose mass, primarily in adipocytes and intestinal enterocytes, exerts a hunger-suppressing effect via its receptors in the arcuate nucleus of the hypothalamus. This hormone plays a pivotal role in energy balance and metabolic regulation. Conversely, ghrelin, originating from gastrointestinal enteroendocrine cells, stimulates hunger and influences a broad range of energy homeostatic processes through its receptors in the hypothalamus. This dual hormonal regulation exemplifies the nuanced control of feeding behavior and energy balance mediated by humoral receptors (Suarez et al., 2019). Furthermore, humoral receptors extend their influence beyond the gastrointestinal system, encompassing broader aspects of physiological regulation. For instance, adrenal hormones like epinephrine, adrenomedullin, and cortisol interact with various receptor sites throughout the body, eliciting diverse responses including excitatory/sympathetic effects and cardiovascular actions (Gordan et al., 2015). The extensive distribution and variety of hormonal receptors, including those on immune cells, underscore their pivotal role in modulating numerous bodily functions. These receptors not only respond to endocrine signals but also contribute to the regulation of immune function, influencing inflammatory reactions and immune responses, as seen in pathways like the vagal anti-inflammatory pathway (Pavlov et al., 2018). These interplays are essential for orchestrating a coordinated response to various internal states, ensuring the maintenance of physiological equilibrium.

Afferent Interoceptive Pathways

The afferent interoceptive pathways are crucial in the field of interoception, responsible for the transmission of sensory signals from internal organs to the central nervous system. Two primary conduits in this intricate system are the cranial pathways and the spinal pathways, both of which play pivotal roles in conveying interoceptive information, including somatosensory and visceral sensations (Saper, 2002; Berntson and Khalsa, 2021).

The cranial pathways, sometimes referred to as the parasympathetic afferent system, primarily carries mechanoreceptor and chemosensory information. This system includes visceral sensory inputs from four cranial nerves: the trigeminal, facial, glossopharyngeal, and vagus nerves, each contributing to the transmission of visceral sensations from various regions of the head, neck, and internal organs (Contreras et al., 1982; Altschuler et al., 1989). Particularly, the vagus nerve extends from the brainstem and is pivotal in conveying sensory information from the thoracic and abdominal viscera (Neuhuber and Berthoud, 2021). It is responsible for a wide range of sensory inputs including afferent signals related to organ function and metabolic status. Predominantly consisting of unmyelinated C fibers and thinly myelinated Aδ fibers, facilitate the transmission of a diverse array of information. The C fibers, which form the majority of the vagus nerve's afferent fibers, are responsible for the slow transmission of ongoing or chronic states, such as organ stretching and chemical composition changes within the body. As such, the vagus transmission plays an important role in regulating various autonomic functions and perceiving the continuous status of internal organs (Saper, 2002).

Conversely, the spinal pathways, an integral part of the body's sensory network, is responsible for conveying both visceral and somatosensory information from the periphery to the central nervous system. In the context of visceral transmission, spinal pathways play a crucial role in transmitting sensations from internal organs in the lower body, such as the bladder and colon (Grundy et al., 2019). These afferents predominantly consist of C fibers, allowing them to respond to chemosensory and mechanosensory stimuli. Somatosensory information, encompassing sensations such as cutaneous, thermoception, and nociception, is also transmitted via the spinal pathways (Craig, 2002; Crucianelli and Ehrsson, 2023). These sensations are primarily processed in the dorsal horn

of the spinal cord, where different types of sensory inputs are integrated. Lamina I of the dorsal horn is particularly noteworthy for its role in nociception and thermoception. It is here that nociceptive and thermoreceptive signals, carried by both Aδ and C fibers, are first relayed and processed. These fibers convey information about potentially damaging or harmful stimuli, triggering immediate protective responses. The processing in the dorsal horn involves not just the relay of sensory signals but also their modulation, which is crucial for the perception of pain and temperature (Todd, 2010).

Collection and Integration of Interoceptive Signals in Brainstem

The brainstem, a crucial node in the neural network of interoception, plays a sophisticated role in processing and integrating signals from the body's visceral organs. This processing begins as interoceptive signals, transmitted via the vagus and spinal sensory pathways, reach the brainstem's intricate substructures. Each component of the brainstem—the medulla oblongata, pons, and midbrain—engages in specific functions, shaping the body's response to internal states (Saper, 2002; Craig, 2003; Neuhuber and Berthoud, 2021).

In the medulla oblongata, the nucleus of the solitary tract (NTS) serves as a central hub for interoceptive inputs, particularly from the vagus nerve. The NTS integrates visceral sensory information with inputs from other critical areas like the area postrema, which is involved in detecting blood-borne signals and toxins, and the dorsal motor nucleus of the vagus, which regulates autonomic outputs. This integration enables the NTS to modulate basic physiological functions such as gastrointestinal motility, heart rate, and respiratory rhythm (Blessing and Benarroch, 2012; MacDonald and Ellacott, 2020). The role of NTS extends to coordinating with other brainstem structures to fine-tune autonomic responses, ensuring a balanced homeostatic state.

Adjacent to the NTS, the reticular formation, spanning the medulla, pons, and midbrain, plays a pivotal role in maintaining consciousness and regulating the sleep-wake cycle. It receives and integrates visceral sensory signals, contributing to the body's overall state of alertness and readiness to respond to internal changes. The reticular formation's extensive network of neurons allows it to interact with various brainstem nuclei, modulating their activity in response to visceral inputs. In the pons, the locus coeruleus, a nucleus critically involved in stress and arousal responses, receives and processes interoceptive information. It is particularly responsive to changes in cardiovascular (Schreihofer and Sved, 2011) and respiratory functions (Del Negro et al., 2018), modulating the body's response to stressors and influencing the overall level of arousal. The parabrachial nucleus, another key structure in the pons, acts as a relay station between the NTS and higher brain regions, including the thalamus and limbic system (Kaur and Saper, 2019). The midbrain, particularly the periaqueductal gray (PAG), is integral to the modulation of pain and autonomic functions. It receives inputs from both the NTS and spinal tracts, and its interaction with the

hypothalamus and limbic structures integrates the physiological and emotional aspects of visceral sensations. The PAG is central to the body's pain modulation system, influencing the perception of visceral pain and orchestrating responses to it (Terpou et al., 2019).

Thalamic Projections in Interoceptive Signal Processing

After intricate processing in the brainstem, interoceptive signals project to the thalamus, a central structure for further integration and modulation. As the brain's relay station, the thalamus receives extensive inputs from the brainstem's substructures, including the NTS, PAG, and the reticular formation. These projections make the thalamus a pivotal hub for processing and distributing interoceptive information to various limbic structures, each contributing uniquely to the body's responses to internal states.

Within the thalamus, the ventral posterolateral (VPL) and ventral posteromedial (VPM) nuclei take center stage in processing interoceptive signals originating from the brainstem (Craig, 2004; Studtmann et al., 2023). These nuclei primarily handle somatosensory information, including visceral sensations, and convey it to the cerebral cortex. VPL receives inputs from the spinothalamic tract, conveying sensory information about pain, temperature, and touch from the body. These signals, processed in VPL, are then relayed to the somatosensory cortex, where they integrate with bodily awareness and homeostasis. Similarly, VPM receives inputs primarily from the trigeminothalamic tract, conveying sensory information from the facial region, including tactile and visceral inputs from the head and neck area. VPM integrates these facial visceral sensations with other somatosensory inputs, contributing to a comprehensive perception of internal states (Blomqvist et al., 2000).

The medial geniculate nucleus (MGN) and lateral geniculate nucleus (LGN) of the thalamus, usually associated with auditory and visual processing, respectively, also play a part in integrating interoceptive signals (Lopez and Blanke, 2011). MGN, primarily processing auditory information, integrates these signals within the context of auditory stimuli, particularly in emotionally charged situations involving sound or speech. LGN, primarily focused on visual processing, also receives interoceptive inputs, adding context to visual information and facilitating a more comprehensive understanding of the environment in relation to internal states (Craig, 2004).

The ventral posterolateral (VPL) and ventral posteromedial (VPM) nuclei of the thalamus play a critical role in the processing of interoceptive signals transmitted from the brainstem. These nuclei are primarily responsible for conveying somatosensory information, including visceral sensations, to the cerebral cortex

(Morel et al., 1997; Studtmann et al., 2023). The VPL nucleus receives extensive inputs from the spinothalamic tract, which carries sensory information from the body, particularly concerning pain, temperature, and touch. These signals, once processed in the VPL, are then relayed to the somatosensory cortex, where they are integrated and interpreted in the context of bodily awareness and homeostasis (Blomqvist et al., 2000). Similarly, the VPM nucleus receives inputs primarily from the trigeminothalamic tract, conveying sensory information from the facial region. This includes not just tactile sensations but also visceral inputs from the head and neck area, which are crucial in the overall perception of internal states, such as oral and nasal sensations. The VPM nucleus thus plays a key role in integrating facial visceral sensations with other somatosensory inputs, contributing to a comprehensive perception of the body's internal state (Craig, 2004). Both the VPL and VPM nuclei, through their respective inputs, provide a detailed mapping of the body's internal and external environments. They are instrumental in distinguishing between different types of sensory stimuli, ensuring that visceral sensations are accurately perceived and contextualized within the broader somatosensory framework.

Cortical Processing of Interoceptive Signals: Focus on the Insula

The cortical regions, particularly the insular cortex, plays a pivotal role in the higher-order processing of interoceptive signals, representing a crucial phase where sensory inputs are integrated with cognitive and emotional contexts. The insular cortex, located deep within the lateral sulcus of the brain, is uniquely positioned to serve as a primary cortical region for interoception. It receives initial cortical inputs related to interoceptive signals from the thalamus and acts as a critical integrative hub, where these signals are not only perceived but also linked with the individual's emotional states (Oppenheimer and Cechetto, 2016; Evrard, 2019). This integrative function allows for the perception of internal bodily states, such as hunger, pain, temperature, and visceral discomfort, transforming them into subjective experiences that can be consciously perceived and emotionally felt (Craig, 2009; Gu et al., 2013; Critchley and Garfinkel, 2017).

The posterior insula is a critical region for the initial cortical processing of interoceptive signals, and its neural pathways play a pivotal role in this function. These pathways facilitate the transmission of raw sensory data from the body to the insula, setting the stage for subsequent higher-order processing (Frot et al., 2014; Evrard, 2019). A primary pathway involves afferent connections from the thalamus, specifically from the VPL and VPM nuclei. The VPL and VPM provide the posterior insula with detailed sensory inputs such as temperature, pain, and tactile information, which are crucial for the conscious perception of the body's internal state. This direct thalamic input enables the posterior insula to act as the first cortical recipient of visceral and somatosensory information, facilitating primary processing and initial interpretation of these signals (Craig, 2002). The posterior insula also maintains significant connections with the primary and secondary somatosensory cortices (Cloutman et al., 2012). Structurally, the posterior insula exhibits a granular cytoarchitecture suited for direct sensory processing (Morel et al., 2013).

The middle insula, serving as a transitional and integrative zone within the insular cortex, plays a crucial role in bridging the primary interoceptive processing of the posterior insula with the more advanced integrative functions of the anterior insula. Anatomically, the middle insula acts as a neural crossroads, featuring a mixture of granular and agranular layers (Morel et al., 2013). This unique composition facilitates its role in refining and contextualizing the raw sensory

information received from the posterior insula. The middle insula has been shown to possess distinct neuroanatomical connections that enable it to process and relay interoceptive information between different insular regions (Cloutman et al., 2012; Lacuey et al., 2016). Functionally, the middle insula is pivotal in advancing the processing of basic interoceptive signals into more elaborated perceptual experiences. It integrates the primary sensory information with emotional, motivational, and cognitive components, contributing to a more comprehensive perception of the body's internal states (Afif et al., 2010a; Yu et al., 2018). This integrative process is crucial for transitioning from the mere sensation of bodily states to their subjective interpretation and relevance within an individual's emotional and cognitive framework.

The anterior insula, a highly evolved and multifaceted region of the brain, plays a pivotal role in the perceptual experience of interoception. Its complex anatomy, including a distinction between the ventral and dorsal parts, enables it to integrate and interpret a wide range of sensory, emotional, and cognitive information, making it a crucial component in the human experience of the internal bodily state (Deen et al., 2011).

The dorsal anterior insula is more closely connected with higher-order cognitive regions, such as the prefrontal cortex, and is involved in more complex processing of interoceptive information (Kurth et al., 2010; Cloutman et al., 2012). This area has been suggested as responsible for the conscious awareness of bodily states, turning raw interoceptive data into a coherent perceptual experience (Craig, 2009; Seth et al., 2011; Gu et al., 2013). On the other hand, the ventral anterior insula, characterized by its dense connections with limbic structures, is central to the emotional aspect of interoception. It is intricately connected to the amygdala, orbitofrontal cortex, and anterior cingulate cortex, forming a key part of the brain’s emotional network (Cloutman et al., 2012). These connections facilitate the ventral anterior insula’s role in assigning emotional significance to interoceptive signals, influencing how bodily sensations are subjectively experienced and emotionally interpreted (Barrett and Simmons, 2015). Anatomically, the anterior insula exhibits a unique cytoarchitecture, featuring a transition from agranular to dysgranular zones as one moves from ventral to dorsal regions. This gradation reflects its functional spectrum, ranging from basic emotional processing in the ventral areas to more complex integrative functions in the dorsal areas (Morel et al., 2013).

History of Interoception Research

In this section, I briefly introduce the history of interoception research, tracing its origins and evolution through a variety of classic studies. This journey begins with the prehistory of interoception, a period marked by foundational observations and concepts which laid the groundwork for the modern understanding of interoceptive awareness. Then, the exploration of interoception within the realm of classic theories of emotion is described. In this era, researchers began to recognize and elucidate the role of interoceptive signals in emotional experiences, shaping early understanding of how bodily sensations influence emotional states of living beings. Another distinct, but important exploration was conducted in the mid 20th century, the examination of conditioning and autonomic responses. In this field, seminal research shed light on the dynamic relationship between internal physiological states and external behavioral expressions. Throughout these studies, the focus was predominantly on the functional implications of interoception, such as its role in physiological regulation and emotional processing, rather than on the direct perceptual experience of these internal signals. This historical overview aims to provide a comprehensive understanding of how the concept and study of interoception have evolved, highlighting key milestones and contributions that have shaped the field.

Prehistory of Interoception

In the nascent stages of scientific inquiry, investigation about interoception was intertwined with broader physiological and psychological studies, yet its distinct identity as a separate field was still emerging. During the 19th century, pioneering figures laid the groundwork, exploring the intricate nexus between bodily sensations and emotional experiences (Vaitl, 1996; Ceunen et al., 2016).

Gustav Fechner, esteemed for his trailblazing efforts in psychophysics, introduced the concept of "perceptual threshold," marking the onset of quantitative sensory perception analysis. While Fechner's work was not explicitly focused on interoception, his methods for measuring perceptual thresholds became crucial for evaluating sensitivity to internal bodily states (Vaitl, 1996). Concurrently, Charles Darwin, famed for his evolutionary theories, highlighted the significance of emotional expressions linked to physiological responses. His seminal book, "The Expression of the Emotions in Man and Animals," acknowledged the complex interplay between emotional experiences and bodily sensations, foreshadowing the concept of interoception. In parallel, William James and Carl Lange, independently yet simultaneously, contributed significant theories on the nature of emotions. James, with his eponymous peripheral theory of emotion, posited that physiological reactions precede and influence emotional experiences, thus integrating the body within the realm of emotional perception (James, 1884). This concept resonated with early notions of interoception, emphasizing the physical embodiment of emotions. Carl Lange, similarly, hypothesized that distinct physiological responses underpin emotions, laying groundwork for the physiological aspects of interoception (Lange, 1885). Despite these early advancements, the formal establishment of interoception as a distinct academic discipline was yet to occur.

The exploration of interoception, as a scientific concept, traces its origins to the early 20th century, with Sir Charles Sherrington playing a pivotal role in its initial conceptualization. In his groundbreaking work, "The Integrative Action of the Nervous System," published in 1906, Sherrington introduced a framework for understanding the sensory systems of the body (Sherrington, 1906). His primary focus was on differentiating between sensations arising from within the body (interoception) and those from the external environment (exteroception), thereby establishing a foundational classification that would guide subsequent

research in the field.

Sherrington's initial description of interoception centered on what he termed "interoceptive reflex arcs" and "interoceptive receptor fields," which laid the groundwork for understanding how the body perceives its internal state. Another of Sherrington's key contributions was his emphasis on the concept of "afferent" and "efferent" pathways. Afferent pathways refer to sensory signals traveling from the periphery, such as the internal organs, toward the central nervous system. These pathways play a crucial role in conveying interoceptive information. Efferent pathways, on the other hand, are responsible for transmitting signals from the central nervous system to various parts of the body, including effectors like muscles and glands. Interestingly, while Sherrington's work laid the foundation for the concept of interoception, he did not use the term "interoception" itself in his initial publications. It was only in the 1940s that the term began to appear in scientific literature, marking a shift in the academic recognition and exploration of the concept (Airapetyantz and Bykov, 1945; Ceunen et al., 2016).

During this early phase, interoception was primarily associated with the sensory perception of the viscera—the internal organs of the body. For example, Edwin Boring conducted a pioneering investigation about internal bodily sensations. He studied the alimentary canal's sensation and thermal sensitivity of the stomach, marking initial strides in recognizing the potential perceptual qualities of visceral processes (Boring, 1915). While this research was primarily grounded in the gastrointestinal domain (also see (Hertz et al., 1908), it laid a crucial foundation for later studies explicitly aimed at unraveling the complexities of interoception. Regrettably, despite these forays into the realm of interoceptive research, empirical investigations specifically measuring individual ability in perceiving the internal bodily states ceased in the early to middle 20th century. This hiatus in research left a significant gap in understanding, with theoretical speculations on interoception and its ties to emotion not being matched by empirical evidence.

Interoception in Classic Theories of Emotion

In the context of emotional experience and its physiological underpinnings, the contributions of William James and Carl Lange, often referred to collectively as the James-Lange theory, stand out. This theory postulated that physiological arousal precedes the experience of emotions, suggesting a direct link between bodily sensations and emotional states (James, 1884; Lange, 1885). The theory fundamentally posited that the perception of bodily changes, as they occur in response to stimuli, is integral to the experience of emotions. This idea, although groundbreaking, was not without its detractors. Walter Cannon, a prominent figure in the field, critiqued this theory, arguing that the physiological evidence for differential interoception - the ability to perceive distinct internal bodily states - was insufficient (Cannon, 1927). His work largely contributed to the diminishment of interest in interoceptive processes as they relate to emotions.

Cannon's arguments were based on the premise that the body's internal responses were too undifferentiated to account for the vast array of emotional experiences. His critique, combined with the lack of substantial empirical evidence at the time, led to a period where the study of interoception, particularly in relation to emotional processes, was considerably neglected. This period of neglect continued until the latter part of the 20th century, when the theory of emotions underwent a renaissance.

The reevaluation of the role of interoception in emotions can be largely attributed to the work of Stanley Schachter. Schachter's theory of emotions, which focused on the cognitive interpretation of general physiological arousal, reignited interest in the field (Schachter and Singer, 1962). Central to Schachter's theory was the idea that while physiological arousal was necessary for emotional experience, it was not sufficient on its own. According to Schachter, cognitive processes were also required to interpret this arousal in the context of the environment, leading to the experience of specific emotions. This theory opened up new avenues for exploring the interplay between interoceptive awareness and emotional processing, although it did not directly address the perceptual mechanisms of interoception itself.

Classic Research on Autonomic Responses

There was paralleling important branch of research relevant to interoception in this era—the classical conditioning of autonomic responses. Classical conditioning studies, significantly influenced by Ivan Pavlov's early 20th-century work (Pavlov, 1927), initially focused on externally observable behaviors. Pavlov's experiments, demonstrating the conditioning of salivary responses in dogs, established that a neutral stimulus, when consistently paired with an unconditioned stimulus, could ultimately elicit a conditioned response. This principle, while initially applied to overt behaviors, gradually extended to include autonomic responses such as heart rate and glandular secretions, thereby creating a bridge to interoceptive processes (Razran, 1961).

Eugeniy N. Sokolov's work further enriched this field by exploring the orienting response, a concept pivotal in understanding the interaction between external stimuli and autonomic reactions (Sokolov, 1963). Sokolov's research elaborated on the neural mechanisms underlying how individuals respond to and process novel stimuli, providing crucial insights into the conditioning of autonomic responses. His work illuminated the ways in which physiological reactions, including those within the realm of interoception, could be influenced and modified through experience and exposure to environmental cues. However, these early conditioning studies, including those by Sokolov, primarily focused on the physiological changes rather than the subjective awareness or perception of these changes from an interoceptive standpoint. The central theme was on the physiological alterations themselves, not on the conscious perception of these changes, which is the essence of interoception.

Despite this initial separation in focus, the principles discovered in classical conditioning research laid the groundwork for understanding how bodily states could be influenced through learning and association. Neal E. Miller's mid-20th-century work on biofeedback and instrumental conditioning of autonomic responses exemplifies this, demonstrating the potential for conscious control over previously involuntary bodily functions (Miller, 1969). This breakthrough highlighted the possibility of intentional modulation of autonomic processes, a concept integral to interoception.

The principles of classical conditioning, enriched by Sokolov's and Miller's findings, were foundational in developing psychophysiology, a field investigating

the interplay between physiological processes and psychological states. The realization that autonomic responses could be conditioned and interact with cognitive and emotional processes opened new pathways in understanding the bidirectional relationship between mind and body. Contemporary interoception research often draws upon these early conditioning studies, expanding them to explore how awareness and modulation of internal bodily states can influence psychological well-being and behavior (Thayer and Sternberg, 2006; Thayer and Lane, 2009; Damasio and Carvalho, 2013; Barrett and Finlay, 2018).

It was not until the 1970s that the perceptual mechanisms underlying interoception and its relation to other cognitive and emotional functions began to be investigated. This delay can be attributed to several factors. Primarily, the technological and methodological limitations of the time made it challenging to study internal bodily sensations in a detailed and controlled manner. Additionally, the dominance of behaviorist paradigms in psychology, which focused on observable behaviors rather than internal processes, contributed to the neglect of internal sensation studies. In the following section, I will synthesize the methodologies for measuring interoception in experimental conditions.

Terminology and Methodology in Current Interoception Research

In this section, I aim to clarify and synthesize the current taxonomy of interoception, an area that has historically been characterized by a considerable degree of ambiguity, complexity, and sometimes confusion. The landscape of interoception research encompasses a diverse array of terms and concepts, including interoceptive awareness, attention, accuracy, sensibility, insight, and so on, each contributing uniquely to understandings of how we perceive and utilize internal bodily states. This exploration then extends to the specific domains of interoception research, highlighting the various bodily systems and sensations that fall under its purview, such as cardiac, respiratory, and gastric interoception, along with thermoception, affective touch, and pain. Accompanying this discussion of the different facets of interoception, particularly focusing on conscious experience related to the internal bodily signals (i.e., interoceptive awareness), I will introduce and evaluate the methodologies employed to measure interoceptive awareness behaviorally in laboratories. These methodologies not only vary depending on the specific interoceptive domain being investigated but also reflect the evolving nature of the field, incorporating both traditional and innovative approaches to better understand the nuances of our internal bodily experience. Through this quick overview, the section seeks to bring order and clarity to the multifaceted field of interoception research, providing a solid foundation for future explorations into our inner sensory world.

Taxonomy of Interoception in Human Study

To clarify the early confusion surrounding interoception and its study, a comprehensive taxonomy is essential, differentiating between various components of interoception.

In the realm of human research pertaining to interoception, interoceptive awareness assumes a pivotal role within its taxonomical framework. This conceptualization was originally introduced by Garner and colleagues, originally intending to assess eating disorder symptom severity (Garner et al., 1983). More recently, it has been defined to encompass any or all of the various interoception features and phenomena that are amenable to conscious self-report (Mehling et al., 2012; Khalsa et al., 2018; Azzalini et al., 2019). As a result, this subcategory within the overarching concept of interoceptive awareness encompasses a multitude of facets pertaining to human interoception. These include perceptions of internal bodily states, attention directed towards these states, the accuracy of these perceptions, subjective sensibility about bodily sensations, and metacognitive insight. Early explorations in this field often conflated all these facets with the overarching construct of interoceptive awareness (e.g., (Pollatos et al., 2005; Matthias et al., 2009; Dunn et al., 2010; Herbert et al., 2011), highlighting the need to disentangle and clarify the specific dimensions of interoception under consideration (Ceunen et al., 2013; Khalsa et al., 2018; Murphy et al., 2019a). Complicating matters further, a seminal study provided by Sarah Garfinkel and colleagues that sought to categorize human interoception into three distinct subdomains regarded interoceptive awareness as a metacognitive capacity pertaining to interoception (Garfinkel et al., 2015). This conflation introduces some ambiguity into the discourse (Forkmann et al., 2016; Leganes-Fonteneau et al., 2019; Mulcahy et al., 2019). To mitigate this ambiguity, I suggest that the metacognitive aspect be denoted as "interoceptive insight" or simply "interoceptive metacognition" (Khalsa et al., 2018; Livermore et al., 2022; Lernia et al., 2023), as expounded upon in the subsequent section on interoceptive insight.

Another crucial element of this research is interoceptive attention, which encompasses both the processes involved and the individual's ability to engage with it. Interoceptive attention can manifest in two primary modes: it may be triggered involuntarily through stimulus-dependent or 'bottom-up' mechanisms

(von Leupoldt et al., 2008; Hassanpour et al., 2018), or it can be intentionally directed in a goal-oriented or 'top-down' manner such as when individuals consciously focus on their internal bodily sensations (Farb et al., 2013a; Simmons et al., 2013; Petzschner et al., 2019). This aspect holds paramount significance as nearly all behavioral tasks necessitate participants to attend to their bodily sensations, either implicitly or explicitly. Therefore, it is imperative to emphasize the importance of disentangling the attentional process from interoceptive awareness (Haruki and Ogawa, 2021). However, it is worth noting that the investigation of interoceptive attention has remained relatively unexplored, primarily due to the inherent challenges in measuring attention. Recently, Jenny Murphy and colleagues developed a questionnaire aimed at assessing individual differences in interoceptive attention ability (Murphy et al., 2019a), although it comes with certain limitations regarding its accessibility and accuracy. Furthermore, it is essential to distinguish between attentional style, which pertains to an individual's dispositional tendencies towards engaging with bodily sensations and is relevant to interoceptive sensibility, and the specific attentional processes under consideration (Mehling, 2016; Gibson, 2019). As a key concept in my current research, the significant emphasis will be placed on interoceptive attention in the following sections.

Interoceptive accuracy and sensitivity represent the most extensively studied concepts in interoception research. They pertain to an individual's perceptual ability to correctly detect and respond to their own bodily signals (Ceunen et al., 2013; Garfinkel et al., 2015; Khalsa et al., 2018). While these terms are sometimes used interchangeably, it is important to note a nuanced difference between them: accuracy typically relates to tasks that have a clearly defined correct answer such as the number and frequency of heartbeats, whereas sensitivity is more aligned with the detection of thresholds related to stimulus intensity. The concept of interoceptive accuracy and sensitivity has played a central role in the expansion of the literature in this field, showing considerable individual differences. Notably, researchers have sought to establish correlations between interoceptive accuracy and emotional responses, drawing from classical theories of emotion (Schandry, 1981; Harver et al., 1993; Ehlers et al., 1995; Critchley et al., 2004). However, recent meta-analyses have revealed that such correlations are limited in scope (Desmedt et al., 2022). There is a growing recognition that studies have occasionally overemphasized or overly relied on this specific aspect of interoception (Murphy et al., 2020; Chen et al., 2021). To advance the field and

provide a more comprehensive perspective, it is imperative to dissociate the measurement of accuracy and sensitivity from the broader construct of interoceptive awareness.

Another aspect that has been extensively studied is interoceptive sensibility, an individual's self-perceived dispositional tendency to focus on interoceptive stimuli in their daily life. Assessments of this trait inherently require the evaluation of self-perceived tendencies over extended time spans. This is commonly achieved by asking individuals to reflect on their autobiographical experiences and respond to questions such as, 'To what extent do you believe you focus on and detect internal bodily sensations?' (Shields et al., 1989; Porges, 1993; Garfinkel et al., 2015). Interoceptive self-report scales involve the ability to reflect upon one's autobiographical experiences of interoceptive states, make judgments about these experiences, and describe them through verbal or motor responses. This aspect is typically assessed experimentally using various instruments or scales, with a range of options available (Mehling et al., 2012; Khalsa and Lapidus, 2016). Within this level of analysis, it is possible to identify multiple constructs. For instance, researchers may explore discrepancies between an individual's self-report of their interoceptive experiences and reports from a partner who knows the participant well and has had ample opportunities to interact with and observe them in various situations. This approach, commonly used in neurological samples (Barrash et al., 2011), offers a means to investigate the intricacies of interoception from different perspectives. Interestingly, researchers have consistently revealed the lack of correlation between interoceptive accuracy and sensibility, suggesting them as reflecting distinct aspects of interoceptive awareness (Garfinkel et al., 2015; Khalsa et al., 2018), though the exact mechanism of the differences is largely untested.

Interoceptive insight represents a metacognitive measure that elucidates the relationship between an individual's subjective experience and their behavioral performance. This burgeoning field of interoception focuses on understanding the interplay between perceptual ability and subjective beliefs. Typically, this is evaluated by assessing the correspondence between the accuracy of an individual's performance and their confidence in that performance on specific tasks (Garfinkel et al., 2015; Murphy et al., 2019b). For instance, in a study involving experienced meditators, despite not exhibiting differential interoceptive accuracy in a heartbeat detection task compared to non-meditators,

they reported differences in interoceptive self-report. Specifically, they indicated that the task was easier, and they perceived their performance as improved relative to non-meditators (Khalsa et al., 2008, 2020).

As quickly reviewed, interoceptive awareness is a multifaceted construct that necessitates precision in research design and methodological approaches. Researchers must explicitly define the specific aspects of interoceptive awareness they are investigating and the methods employed to measure them. It is important to note that individual scores on different dimensions of interoceptive awareness, such as accuracy and sensibility, often do not exhibit significant correlations with each other. In the following part of this section, I will synthesize insights from different domains of interoception to develop a more holistic perspective on interoceptive awareness. Integrating findings from diverse areas of research within interoception can lead to a richer understanding of how individuals perceive, interpret, and respond to their internal bodily signals. This synthesis of knowledge can contribute to the advancement of our comprehension of interoceptive awareness as a complex and multifaceted phenomenon.

Cardiac Interoception

Cardiac Interoception represents one of the most extensively studied facets within the realm of interoception research. This focus is primarily due to the relative ease with which individuals can perceive cardiac signals and the straightforward nature of recording these signals. The heart, as a visceral organ, provides a distinct and rhythmic physiological signal that is both frequent and detectable, making it an ideal candidate for the study of interoceptive processes.

In the late 1970s, researchers in the field of psychology began developing behavioral tasks to measure an individual's interoceptive accuracy or sensitivity, which refers to the ability to correctly perceive internal bodily sensations. A pioneering method in this domain is the heartbeat counting task, introduced by Rainer Schandry (Schandry, 1981). This task, which continues to be widely utilized in contemporary interoception research, requires participants to count their heartbeats over a specified period (Herbert et al., 2010; Garfinkel et al., 2015; Desmedt et al., 2018; Santos et al., 2023). The effectiveness of this task in assessing interoceptive accuracy is determined by comparing the number of heartbeats a participant counts against the actual number recorded via physiological monitoring tools like electrocardiograms (ECG) or photoplethysmograms (PPG) . A typical heartbeat counting task involves multiple trials, usually ranging from three to six, with each trial lasting anywhere from 25 to 55 seconds. A fascinating aspect of the heartbeat counting task is the considerable variability in scores observed across different individuals (Van der Does et al., 2000; Garfinkel et al., 2015; Ainley et al., 2020). Some participants demonstrate remarkable accuracy in detecting their heartbeats, while others struggle significantly, sometimes failing to detect any heartbeat sensations during the counting phase. This variation highlights the diverse range of interoceptive abilities present in the population.

Despite its widespread use and historical significance, the heartbeat counting task has not been without criticism. One of the primary concerns raised pertains to the influence of an individual's knowledge or preconceptions about their cardiac rhythm, which could potentially skew the results (Ring and Brener, 1996; Ring et al., 2015; Murphy et al., 2018b; Desmedt et al., 2020). Additionally, the task's reliance on cognitive skills such as counting and estimation introduces confounding variables that might affect the accuracy of interoceptive assessment

(Ring and Brener, 2018). These cognitive elements could potentially overshadow the pure sensory perception aspect of interoception, thereby complicating the interpretation of the results (Zamariola et al., 2018). However, researchers have found that providing strict instructions and carefully controlling experimental conditions can mitigate some of these confounding effects (Ehlers et al., 1995; Desmedt et al., 2018, 2020). By doing so, the task can more accurately reflect an individual's genuine interoceptive attention towards bodily sensations, distinguishing it from other methods that might blend interoceptive and exteroceptive modalities. In comparison to other interoceptive tasks, the heartbeat counting task holds a unique advantage (Ainley et al., 2020; Zimprich et al., 2020; Haruki and Ogawa, 2023b). While other methods might involve synchronization with external sensory cues or rely on external indicators to infer internal bodily states, the heartbeat counting task demands a more focused and pure form of interoceptive attention. This distinct focus on internal sensations, devoid of external stimuli or cues, offers valuable insights into the nuanced ways individuals perceive and process internal bodily signals.

In recent years, variations of the heartbeat counting task have been developed to address its limitations and deepen our understanding of interoception. The heartbeat tapping task, for instance, requires participants to tap in sync with their heartbeats. This variation aims to reveal the timing participants actually perceive their heartbeats, addressing a primary shortcoming of the counting task (Zaki et al., 2012; Canales-Johnson et al., 2015). However, this method is not without its limitations. The act of tapping can create a rhythmic perception that may overshadow the actual sensation of the heartbeat, and motor commands involved in tapping might interfere with attentive processes. Another approach originated from the counting task is the interoceptive attention task. This variant dispenses with counting and instead asks participants to focus solely on the sensations of their heartbeats (Simmons et al., 2013; Avery et al., 2015; Kerr et al., 2016; Salamone et al., 2021). Often employed in MRI studies, this task seeks to uncover the neural underpinnings of interoceptive attention. By eliminating the counting aspect, researchers can more effectively isolate and analyze the attentional mechanisms at play in interoceptive processing.

In the evolving field of interoception research, the heartbeat discrimination task has emerged as another influential method, offering a unique approach to understanding how individuals perceive their internal bodily states. This task

typically involves presenting participants with a set of external stimuli that are either synchronized or asynchronous with their cardiac cycle. Participants are then asked to discern whether these external stimuli align with their heartbeats (Katkin et al., 1981; Harver et al., 1993; Wiens et al., 2000; Garfinkel et al., 2015). One of the task's major strengths lies in its compatibility with the framework of signal detection theory, which allows for a sophisticated analysis of participants' responses considering trial-by-trial perceptual confidence. Additionally, this method effectively mitigates the influence of beliefs about heart rate and strategies related to counting, which can confound other interoceptive measures (Brener and Ring, 2016).

Despite its advantages, the heartbeat discrimination task is also not without limitations. Primarily, it is a challenging task, and many participants struggle to perform above chance level (Brener and Ring, 2016). The task's success depends on the integration of both external and internal signals, and crucially, it does not facilitate the use of selective interoceptive attention (Haruki and Ogawa, 2023b). Furthermore, the duration of each trial in this task often exceeds 10 seconds, which complicates the acquisition of a sufficient number of trials needed for a robust signal detection analysis (Sorkin et al., 2001; Maniscalco and Lau, 2012). The task's length also makes it difficult to integrate with other measurement techniques due to time constraints in experimental settings. Another critical point often overlooked in early studies is the timing of heartbeat perception, which typically occurs during cardiac systole, approximately 300 milliseconds after the detection of R-peaks on an ECG (Brener and Ring, 2016).

While the heartbeat counting and discrimination tasks have dominated interoception research for over four decades, recent studies have begun exploring alternative approaches that actively incorporate subjective beliefs about heartbeats. This shift is partly driven by critiques of the counting task's limitations. Ryan Smith and colleagues, for instance, have innovatively combined Bayesian modeling with the heartbeat tapping task (Smith et al., 2020, 2021). Their approach sheds light on the role of belief in heartbeat perception and its individual differences. Similarly, another group has developed a heart rate discrimination task that presents stimuli dynamically across trials, adjusted to the participant's current heart rate (Legrand et al., 2022). Using Bayesian modeling, this method estimates psychometric perceptual and metacognitive curves. These curves provide insights into participants' abilities to update and monitor cardiac

beliefs under various conditional manipulations.

These newer paradigms represent a significant advancement in cardiac interoception research. They offer fresh perspectives on how individuals perceive and interpret their heartbeats, accounting for the influence of subjective beliefs and cognitive processes. However, while these models have broadened our understanding of cardiac interoception, they also reveal a gap in our comprehension of the pure perceptual mechanisms underlying interoception. The integration of belief and perception in these tasks, though insightful, may obscure the raw sensory experience of interoception. This aspect underscores a continuing challenge in the field: to develop methods that can isolate and accurately measure the pure perceptual experience of interoceptive signals.

Respiratory Interoception

Respiratory interoception is associated with the awareness and interpretation of respiratory functions, particularly the sensations arising from the bronchial tract or thorax. This domain of interoception is characterized by its direct relation to physiological processes like breathing, and its interplay with psychological states, often highlighted in practices like meditation. In meditation, heightened attention to breath can lead to increased respiratory interoceptive awareness, facilitating a deeper understanding of the mind-body connection (Farb et al., 2013b).

A key tool in studying respiratory interoception is the airway resistance task, where participants asked whether an external load was added to the airway in sync with a breath cycle (Harver et al., 1993). Historically, this was not a primary focus in interoceptive research around the 2000s. However, recent advancements have integrated this paradigm into the broader context of interoceptive awareness, emphasizing aspects such as perceptual accuracy, sensibility, and metacognition (Garfinkel et al., 2016; Harrison et al., 2021). These contemporary studies have expanded the understanding of how individuals perceive and interpret respiratory resistance, contributing significantly to the field of interoceptive research. Additionally, recent methodologies have introduced airway resistance-free approaches to assess respiratory interoception. One such innovative method is the breath detection task. In this task, participants are asked to determine whether a presented breathing curve is delayed or synchronized with their own breathing rhythm (Wang et al., 2019). This approach represents a significant shift from traditional methods, focusing more on the synchronization of external stimuli with internal respiratory rhythms, thus providing a nuanced understanding of respiratory perception.

Despite its importance, respiratory interoception has been less studied compared to cardiac interoception. Interestingly, studies have shown that there is no significant correlation between the scores of respiratory sensitivity and cardiac accuracy (Garfinkel et al., 2016), suggesting that these two modalities of interoception operate distinctly. However, it is worth noting that both forms of interoception may evoke similar neural activations (Caseras et al., 2013; Wang et al., 2019), indicating some common underlying neural mechanisms in the perception of internal bodily states.

Gastric Interoception

Gastric interoception encompasses the body's ability to sense and interpret signals originating from the stomach and gastrointestinal tract. Characterized by sensations related to hunger, fullness, and digestive activities, gastric interoception plays a crucial role in regulating food intake, energy balance, and overall well-being. It involves a sophisticated interplay between neural and hormonal signals, allowing individuals to respond appropriately to their body's nutritional needs.

The initial exploration into gastric interoception heavily relied on methods involving gastric distention, typically achieved through balloon ingestion. This technique involved inflating a balloon inside the stomach to induce sensations of fullness or discomfort, thereby allowing researchers to study the body's response to gastric stretching (Geliebter, 1988; Geliebter et al., 1988; Wang et al., 2008). However, this method often proved uncomfortable for participants, which significantly limited progress in understanding gastric interoception. The discomfort and invasiveness associated with balloon ingestion posed ethical and practical challenges, hindering extensive research in this field.

To overcome these challenges, recent advancements have seen the adoption of the water load test as an alternative method for investigating gastric interoception. This approach requires participants to drink water until they reach a point of satiety or fullness, with the critical aspect being that they remain unaware of the volume they have consumed. By measuring individual differences in the volume of water required to achieve satiety, researchers can gain insights into gastric interoceptive sensitivity (Jones et al., 2003; Herbert et al., 2012; van Dyck et al., 2016; Ferentzi et al., 2019). This method is less invasive and more comfortable for participants, facilitating more extensive research and a deeper understanding of gastric interoception.

A significant breakthrough in the study of gastric interoception came with the development of a new paradigm by introducing the use of a vibrating capsule to stimulate the gut (Mayeli et al., 2023). This groundbreaking technique marks a departure from traditional methods, offering a non-invasive and innovative approach to studying the stomach's sensory responses. The vibrating capsule, when ingested, provides controlled and measurable stimulation to the gastric system. This method aligns with the principles of signal detection theory,

allowing for a more precise and objective measurement of gastric interoceptive responses. By quantifying the detection and perception of gut stimuli, this approach paves the way for more nuanced and detailed research into gastric interoception, expanding our understanding of how the body perceives and responds to internal gastrointestinal signals.

Thermoception

Thermoception, the sensory perception of temperature, extends beyond traditional somatosensory classifications to embrace an interoceptive role, aligning with contemporary physiological and neuroanatomical research. This broader view of thermoception encompasses not just the detection of external temperature changes but also the monitoring of internal body states, essential for homeostatic balance. Thermoceptive signals, distinct from those of tactile and proprioceptive sensations, are relayed via Aδ and C fibers, and follow specialized spinothalamocortical pathways to the posterior insular cortex, a key pathway in interoceptive signalling (Craig, 2002; Crucianelli and Ehrsson, 2023). This neural architecture underscores thermoception's significance in bodily awareness and emotional states, positioning it firmly within the realm of interoception.

In measuring thermoception, researchers employ precise experimental techniques to control and apply thermal stimuli to the skin (Craig et al., 2000). Subjective experiences of these stimuli are typically assessed using rating scales or sophisticated detection and discrimination tasks, complemented by physiological measurements such as changes in skin temperature and autonomic responses. A novel approach in this area is the thermal matching task, where participants identify a moving thermal stimulus amidst varying temperature ranges (Heldestad et al., 2010; Crucianelli et al., 2022). This task is pivotal in exploring the intricate relationship between thermal discrimination, thermal comfort, and tactile pleasantness, offering a comprehensive understanding of thermoception. By altering stimulus parameters like speed, temperature, and target skin areas, researchers can unravel the complex interplay between thermal perception and affective responses.

Despite the anatomical evidence supporting the classification of thermoception as an interoceptive modality, its perceptual accuracy appears to function independently of other interoceptive channels. This notion was recently reinforced by Vabba and colleagues' innovative use of an infrared light bulb, a method that presents thermal changes without accompanying tactile sensations (Vabba et al., 2023). Their findings revealed a lack of correlation between thermoceptive and cardiac accuracy, underscoring the distinct nature of these interoceptive pathways. Another intriguing avenue in thermoception research in the realm of interoception is the thermal grill illusion (Craig and Bushnell, 1994;

Bach et al., 2011). In this paradigm, participants experience a unique thermal sensation when presented with interleaved warm and cool stimuli, a method that deceives the brain into perceiving an entirely different temperature. This illusion not only highlights the complex processing of thermal information in the nervous system but also opens up new possibilities for exploring the intricate relationships between various interoceptive modalities and their respective perceptual accuracies.

Affective Touch

Affective touch, characterized by gentle, caress-like tactile sensations, emerges as a compelling aspect of interoception, distinguished by its profound impact on emotional and social processing. This unique form of touch is mediated by specialized C afferents, primarily located in the hairy skin, which are optimally activated by slow, nurturing strokes mimicking human touch (Vallbo et al., 1999). Notably, the affective touch pathway diverges significantly from classical somatosensory channels, as it predominantly processes emotional and homeostatic information rather than discriminative details about external tactile stimuli. The neural trajectory of these signals, from their origin in the skin to their processing in key interoceptive brain regions such as the insula and cingulate cortices, underscores their interoceptive nature (Craig, 2003; Davidovic et al., 2019; Crucianelli and Ehrsson, 2023). This pathway emphasizes the affective, rather than the discriminative, aspect of touch, aligning affective touch more closely with internal bodily states and emotions rather than with external sensory exploration.

In empirical research, measuring tactile sensitivity and its affective component involves innovative methodologies that not only assess the physical detection of touch but also capture its emotional resonance. One such approach employs the use of specialized stimulators capable of delivering touch at C-optimal speeds, thus selectively activating the C fibers responsible for affective touch. Participants' responses to these stimuli are then evaluated both in terms of their sensory detection thresholds and the emotional valence they ascribe to the touch, using scales that measure perceived pleasantness or discomfort (Pawling et al., 2017; Davidovic et al., 2019). This dual assessment allows researchers to distinguish between mere tactile sensation and its affective interpretation, revealing how affective touch contributes to emotional states as a modality of interoception.

Interestingly, a recent study has shed light on the complex interplay of different modalities within interoception, revealing that the perceptual accuracy of affective touch is distinct and uncorrelated with the accuracy of other interoceptive modalities, including cardiac perception and thermoception, as well as tactile pain perception thresholds (Crucianelli et al., 2022). This finding highlights the unique processing pathway and function of affective touch in the

broader landscape of interoceptive perception. However, in an intriguing twist, the study also found that perceptual confidence in affective touch shows a notable correlation with confidence in thermoception. These findings suggest that while the accuracy of different interoceptive modalities may operate independently, there could be a shared underlying mechanism or cognitive process that governs the confidence level in one's perceptual judgments across these different sensory domains. This intersection of perceptual confidence might be indicative of a more generalized aspect of interoceptive awareness or metacognition, which transcends the specific sensory characteristics of each modality.

Pain as Interoception

Pain perception, encompassing both somatic and visceral pain, plays a pivotal role in the domain of interoception. Interoception, the sense of the internal state of the body, is vital for maintaining bodily homeostasis and wellbeing. Somatic pain, originating from external stimuli impacting the skin, muscles, and skeletal system, serves as a critical alert system, warning of potential tissue damage. Visceral pain, arising from internal organs, is often less precise but equally significant, signaling internal bodily disturbances. Both forms of pain, with their distinct qualities, contribute to the broader interoceptive awareness, helping individuals respond appropriately to internal and external threats to the body's integrity (Cervero, 2009; Paine et al., 2009; Werner et al., 2009). These types of pain are integral to interoception due to their direct link to the body's physiological status. While somatic pain often relates to immediate physical threats, visceral pain reflects the deeper, often more complex status of internal organ health. Both are essential for survival, driving behavioral and emotional responses to maintain balance within the body.

In the realm of cognitive psychology and experimental medicine, the methodology to study pain perception has evolved significantly. Traditional methods include threshold testing, where the minimum intensity of a stimulus that is perceived as painful is determined (Werner et al., 2009). This approach has been widely used to understand variations in pain sensitivity among individuals and under different conditions. Psychophysical techniques, such as pain rating scales, allow individuals to report their subjective experience of pain intensity and quality. Experimental paradigms in pain research often involve controlled induction of pain using thermal, mechanical, or electrical stimuli, providing insights into pain processing mechanisms (Dubin and Patapoutian, 2010; Craig, 2018). Behavioral studies focus on the individual's response to pain, such as withdrawal reflexes or decision-making processes in pain avoidance.

Somatic and visceral pain, while both integral to interoception, exhibit notable similarities and differences. Both somatic and visceral pain involve complex neurological pathways that converge in certain areas of the brain (Jarrahi et al., 2015; Van Oudenhove et al., 2020). The neurologic pain signature, a multivariate brain measure, responds robustly to both types of pain. This indicates a shared neurobiological basis for processing and perceiving pain, irrespective of its

somatic or visceral origin. Somatic pain is typically well-localized and correlates more directly with the intensity of external stimuli, making it easier to study and quantify. Visceral pain, in contrast, is often diffuse, poorly localized, and its perception can be influenced by a range of internal factors, making it more challenging to study empirically (Saper, 2002; Grundy et al., 2019). Interestingly, research has shown that pain thresholds in healthy populations do not correlate with other interoceptive accuracy measures like cardiac and thermoceptive accuracy, nor with affective touch sensitivity (Crucianelli et al., 2022). This suggests that pain perception operates somewhat independently within the interoceptive system. However, in chronic pain patients, pain severity shows a positive correlation with cardiac accuracy but a negative correlation with cardiac perceptual confidence. This indicates that chronic pain might alter interoceptive processing, possibly due to prolonged exposure to pain altering the body's internal monitoring and regulatory mechanisms.

Limited Perceptual Model of Interoceptive Awareness

In the preceding sections, I have navigated through the intricate neural pathways conveying interoceptive signals, traced the historical evolution of interoception research, scrutinized the methodologies and terminologies that define this field. This journey has illuminated the multifaceted nature of interoception, yet, a pivotal aspect remains conspicuously underexplored: the perceptual mechanism that underpins interoceptive awareness. My exploration thus far has laid the groundwork, unveiling the complexity and depth of interoceptive processes. However, as I delve deeper, a pivotal question emerges: how do these processes converge to shape interoceptive awareness, encompassing various phenomena such as heartbeat perception, breathlessness, warmth, hunger, and more? It is this enigmatic interplay between interoceptive signals and the resulting perceptual experiences (i.e., interoceptive awareness) that lies at the heart of my research interest.

In the first place, it is undeniable that everyone experiences interoceptive awareness in their daily lives, which informs us about the state of our bodies, including hydration, fatigue, hunger, and signs of unwellness. These common perceptions play a crucial role in enabling us to act adaptively, thereby ensuring our survival (Quigley et al., 2021; Sennesh et al., 2022). Given its pivotal role in guiding behavior in response to fundamental bodily needs, it is likely that interoceptive awareness evolved early in the animal kingdom (Carvalho and Damasio, 2021), alongside the development of cortical complexity and other perceptual systems such as vision and hearing. Therefore, it sounds natural to focus attention on the perceptual mechanisms of interoceptive awareness in humans, alongside other sensory systems.

However, this area has only begun to receive significant research attention recently and only a few frameworks have been offered. Crucially, as I venture further into this realm, it becomes increasingly evident that traditional perceptual models in experimental psychology, which have admirably elucidated exteroceptive processes, encounter challenges when applied to interoceptive awareness. In this light, the Bayesian framework emerges as a promising candidate. Its principles of perception as an inferential process, integrating prior knowledge with sensory information, align well with the perceptual properties of interoceptive awareness. Therefore, in this section, my objective is to highlight

the incompatibility of existing perceptual models in cognitive psychology when applied to interoceptive awareness.

To this end, I will first provide an overview of the unique perceptual properties of interoceptive awareness, drawing contrasts with exteroception. Following this, I will look at the established perceptual models for visual perception in cognitive psychology, emphasizing their limitations in adequately explaining interoceptive processes. A key focus of this discussion will be on the role of attention in interoceptive awareness. Diverging from models that view attention primarily as a selective filter, in the context of interoception, attention operates more as a flexible and individualized optimizer of sensory information, tuning in to the specific requirements of internal bodily perception. This exploration aims to shed light on the distinct mechanisms at play in interoceptive awareness and the need for more tailored models in cognitive psychology to understand it effectively.

Perceptual Properties of Interoceptive Awareness

Interoceptive awareness, with its unique perceptual properties, presents distinct challenges to models of perception. The following paragraphs delve into these incompatibilities, contrasting them with the more stable and external nature of exteroceptive stimuli.

The spatial distribution of interoceptive sensores presents a unique challenge in understanding interoceptive awareness, particularly when it comes to specifying sensory features. This is because interoceptive sensors are widely dispersed throughout the body (Berntson and Khalsa, 2021), unlike in exteroceptive systems where sensors are localized and restricted to specific organs. In exteroceptive stimuli such as vision or hearing, the source of a stimulus is typically external and can often be precisely located. For instance, in the visual system, the spatial origin of light hitting the retina is clearly defined (Schwartz, 1977), allowing for a straightforward mapping from stimulus to perception. Similarly, in auditory perception, sound waves enter the ear, travel through the ear canal, and vibrate the eardrum. These vibrations are passed through the middle ear bones (ossicles) to the cochlea, wherein the mechanical vibrations are translated into electrical signals, which are then transmitted to the auditory nerve (Shamma and Micheyl, 2010). Interoceptive signals, in contrast, emanate from within the body and often lack this distinct spatial specificity. The perception of hunger, for instance, is not localized to a specific point but is rather a holistic experience that can be challenging to pinpoint spatially. Pain, too, can be a nebulous experience, with its source sometimes difficult to identify precisely. These sensations are perceived through a complex network of interoceptive receptors and neural pathways that do not conform to a singular spatial origin, leading to a less clear-cut pathway from stimulus to awareness (Petersen et al., 2014, 2015b; Berntson and Khalsa, 2021; Quigley et al., 2021).

The complexity of interoceptive neural pathways mirrors the spatial distribution of internal bodily sensations from various organs, offering a stark contrast to exteroceptive processing. In exteroception, such as vision, distinct primary sensory areas in the cortex are dedicated to processing specific features of sensations (Liang et al., 2013). In contrast, the neural pathways for interoception are markedly more complex and less linear. As discussed in "Neural Pathways of Interoception," interoceptive sensations are conveyed via both sympathetic and

parasympathetic pathways and are integrated as early as the brainstem level, before reaching cortical areas. Furthermore, while the insula (particularly the dorsal posterior part) is often considered the primary interoceptive cortex due to its role in receiving initial cortical input for interoceptive signals (Evrard, 2019), interoceptive awareness is not solely dependent on it. Remarkably, research has shown that individuals can maintain interoceptive awareness even with bilateral insula damage (Khalsa et al., 2009). This fact is in sharp contrast with the case of exteroception, where damage to primary sensory cortices typically results in a significant decrease in sensory awareness (Tong, 2003).

The inherent high degree of perceptual uncertainty in interoceptive awareness is another aspect that sets it apart from exteroception. Here, perceptual uncertainty refers to the variability or inconsistency in recognizing and interpreting sensory information, where individuals might be aware of certain sensations but remain unaware or interpret the same or similar sensations in different ways (Diamond, 2019). This differs from perceptual sensitivity, which is the ability to consistently detect sensory stimuli. In this sense, perceptual uncertainty in exteroception typically correlates with perceptual sensitivity, as identifying a certain visual object at night can be more difficult. Conversely, interoceptive awareness is innately vague, fluctuating, and open to interpretation (Craig, 2009; Harshaw, 2015; Chen et al., 2021; Quigley et al., 2021). For example, discomfort in the abdominal area (i.e., high perceptual sensitivity) could be interpreted as hunger, indigestion, or even anxiety, depending on various factors such as previous experiences, current emotional state, and environmental cues (Critchley and Garfinkel, 2017). This variability can be partly attributed to the primary role of interoception, which is to inform us about our internal bodily state, as opposed to exteroception that primarily serves to convey external information (Quigley et al., 2021; Sennesh et al., 2022). Both systems are crucial for survival, aiding in appropriate behavioral selection, yet they operate on fundamentally different principles. Later in the subsection “Role of Attention as a Core Debate”, I will explore the prerequisites of the perceptual model for interoceptive awareness, focusing on the aspects of uncertainty and its interplay with interoceptive attention.

Perceptual Models in Experimental Psychology

In the sphere of experimental psychology, the conventional perception models have been predominantly centered on an information processing (IP) approach, drawing a parallel between human cognition and the functions of a computer. This paradigm has been pivotal in shaping the understanding of cognitive processes, particularly in relation to the exteroceptive senses such as vision and audition. The IP approach metaphorically represents the mind as an intricate processor, akin to a computer system, responsible for receiving, encoding, processing, and outputting information (Marr, 1976; Simon, 1979; Palmer and Kimchi, 1986). Such an analogy, while simplifying the complexities of human cognition, has been instrumental in formulating a structured perspective on mental processes, allowing them to be viewed and analyzed in a systematic and sequential manner. This framework posits that cognitive processes can be broken down into discrete, sequential stages, with each stage involving specific cognitive operations . These stages range from the initial perception of stimuli to the formation of memories and decision-making. This modular view of cognition has been fundamental in experimental psychology, as it allows for the dissection and analysis of complex mental activities into more manageable and understandable components. This approach to cognitive processes as distinct and sequential stages has been central to developing experimental methodologies and theoretical models within cognitive psychology.

In critiquing the perceptual models operationalized in the IP approach, it becomes evident that while these models have significantly advanced our understanding of cognitive processes, they possess inherent limitations when applied to interoceptive awareness. One primary critique is that these models are predominantly visual and auditory centric, heavily drawing upon and tailored to the characteristics of exteroception (Banks and Krajicek, 1991). The perceptual cycle model developed by Ulric Neisser, for instance, proposes a dynamic and cyclical process of perception where an individual actively explores and updates their perceptual schema based on environmental cues (Neisser, 1976). However, its emphasis on the modular and sequential stages of processing, and the necessity to explore and sample the environment to form perceptual schemas, is not easily applicable. The nature of interoceptive awareness is such that one cannot "explore" internal bodily states in the same way one can visually scan an environment. This limitation is further compounded by the inability of this model

to account for the perceptual uncertainty of interoceptive awareness, where the same or similar bodily signals do not result in a coherent percept, depending on lots of factors (Paulus and Stein, 2010; Paulus et al., 2019).

Similarly, more specialized models for object recognition struggle to encapsulate perceptions of the internal bodily sensations. To give an example, Anne Treisman's feature integration model posits that different sensory features of an object (such as color, form, orientation) are coded in specialized modules or "maps" and integrated to form a coherent perception (Treisman and Gelade, 1980). The model's focus on identifiable features of stimuli and their integration into a unified percept falters in the context of interoceptive awareness, where it is often challenging to identify distinct features or components of internal bodily sensations (Saper, 2002). The spatial distribution of sensations related to such as heartbeat or gastrointestinal discomfort defy the clear-cut categorization of sensory features assumed by this model (Petersen et al., 2014). Other models that advocate the decomposition of percepts into abstract components are similarly constrained. These models, effective in dissecting visual objects into geometric shapes or abstract components for recognition (Biederman, 1987; Marr, 2010), are less equipped to handle the fluid and often ambiguous nature of interoceptive signals. The inability to establish fixed abstract components or geometric structures for bodily sensations, which can fluctuate and change over time, marks a significant departure from the requirements of these models (Ainley et al., 2016).

A common shortcoming across these perceptual models is their dependency on perceptual cues and a lack of explanation for perceptual uncertainty, both of which are critical in understanding interoceptive awareness (Ainley et al., 2016; Khalsa et al., 2018). Unlike exteroceptive stimuli, which often provide clear and distinct cues for perception, interoceptive signals are not always accompanied by such definitive cues. Moreover, interoceptive awareness is subject to a high degree of perceptual uncertainty, wherein lots of factors including ongoing emotional states, physiological conditions, and past experiences would affect the perceptual experience. I will further discuss the problem of perceptual uncertainty in terms of the role of interoceptive attention in the following paragraphs. In essence, while these perceptual models have significantly advanced our understanding of cognitive processes related to exteroception, their application to interoception is limited. Their exteroceptive-centric approach,

reliance on identifiable perceptual cues, and structured processing stages do not align with the characteristics of interoceptive awareness. This misalignment calls for the development of models or the adaptation of existing ones to better encompass the unique characteristics of interoceptive awareness.

Role of Attention as a Core Debate

As I have discussed, the perceptual uncertainty in interoceptive awareness is not indicative of flaws in the perceptual system; rather, they illuminate the probabilistic and individualized nature of how sensory information from within our body is processed and interpreted. This understanding necessitates a crucial reevaluation of the role of attention in interoceptive awareness, urging us to move beyond the conventional view of attention as a mere filter or prioritizing mechanism for sensory information.

To comprehend the perceptual uncertainty associated with interoceptive awareness, let's take the example of perceiving one's own heartbeat. Heartbeat perception can typically occur in two primary forms: spontaneous and volitional. Spontaneous heartbeat perception is a prime illustration of perceptual uncertainty, as individuals become aware of their heartbeat pulsations suddenly, without conscious effort. This awareness, or lack thereof, can be influenced by a variety of factors, such as emotional state or physiological changes (Schandry et al., 1993; Iodice et al., 2019). Volitionally perceiving one's heartbeat, as often required in experimental settings, involves a volitional focus on internal bodily sensations (Schandry, 1981; Simmons et al., 2013; Garfinkel et al., 2015). A notable phenomenon here is that, although the interoceptive sensation (i.e., heartbeats) remains constant, its perception tends to diminish over time, particularly between approximately 50 and 100 seconds (Schauder et al., 2015; Zamariola et al., 2018). This phenomenon also exemplifies perceptual uncertainty in interoceptive awareness and is not usually observed in exteroceptive modalities such as vision or hearing.

Furthermore, the individual differences in interoceptive awareness add another layer of complexity. While some individuals might be accurately aware of their internal bodily states, detecting subtle changes in their heartbeat or respiratory rate, others might be less accurate to such sensations unless they are pronounced (Herbert et al., 2012; Garfinkel et al., 2015; Khalsa et al., 2018). Importantly, the perceptual uncertainty and individual differences cannot be attributed to deficiencies in the perceptual system. Instead, they underscore the need for an approach that accounts for probabilistic adjustments in sensory information, tailored to individuals. In this context, rethinking the role of attention becomes essential, as it shifts from being a mere filter or prioritizing

mechanism to a dynamic and individualized process that optimizes sensory information.

This need for a revised understanding of attention becomes evident when considering the traditional models of attention, which reveal significant limitations in the context of interoceptive awareness. Historically, typical models of attention have been viewed as a selective process. For instance, Donald Broadbent's filter model, conceptualized in 1958, describes attention as a filter that selects information based on its physical characteristics before processing it for meaning (Broadbent, 1958). This model implies a limited capacity within our cognitive system to process incoming information, suggesting that only a specific subset of stimuli is selected for further processing. Anne Treisman's attenuation model, developed later, proposes that unattended information is not entirely blocked but is instead weakened (Treisman, 1960). This model acknowledges that occasionally, unattended information can penetrate the filter, particularly if it is highly salient or personally relevant. Such models collectively highlight the capacity limitation of attention, suggesting that our cognitive resources are finite, and as a result, only a portion of the available information can be processed thoroughly at any given time (Eriksen and Yeh, 1985; Yantis and Johnson, 1990). In these frameworks, attention functions as a mechanism that selectively processes certain stimuli while disregarding others, influenced by both sensory-driven (bottom-up) and memory-driven (top-down) processes. However, as discussed before, there is a demand for a redefinition of attention's role, at least in the context of interoceptive awareness.

Again, the reimagining of attention's role in interoceptive awareness arises from an understanding that it encompasses much more than the mere selection or prioritization of external stimuli. This broader perspective sees attention as a dynamic, flexible, and individualized process, deeply involved in how we interpret and sense the states within our own bodies. Moreover, attention should be described as a hierarchical entity capable of modulating sensory noise in addition to perceptual uncertainty. This is because interoceptive sensations are received simultaneously with other sensory information, and one of the roles of attention is to relatively prioritize one input over another (Apps and Tsakiris, 2014; Ainley et al., 2016; Allen and Tsakiris, 2018). This redefined role of attention also acknowledges the significance of the brain's predictive coding in interoceptive awareness. The predictive coding framework, operationalized in Bayesian Brain

theorem, suggests that the brain constantly generates and updates models of the world, where attention weighs the likelihood of different interpretations of sensory data. It constantly calibrates and refines the brain's predictions in response to any discrepancies between what is expected and what is actually perceived. This ongoing adjustment process would be what gives rise to the perceptual uncertainty. In the following section, I will focus on the efficiency of this framework for interoceptive awareness.

Interoceptive Awareness in Bayesian Framework

In the previous section, I introduced unique characteristics of interoceptive awareness, focusing particularly on the challenges associated with identifying stimulus features and the complexities of perceptual uncertainty. This exploration included a critical assessment of how typical perceptual models in experimental psychology, especially those developed with a focus on visual and auditory perception, fall short in adequately addressing these aspects of interoceptive awareness. Building upon this foundation, in this current section, I aim to introduce and explore the Bayesian Brain framework as a promising alternative for applying to interoceptive awareness. This framework, originally developed in computational neuroscience for exteroception, reimagines perception not as a passive reception of sensory data but as an active inferential process. Here, perception is understood as the brain's attempt to make sense of sensory input based on a continuous interplay between incoming data and pre-existing knowledge (Rao and Ballard, 1999; Knill and Pouget, 2004). A crucial element within this framework is the role of attention, which is redefined as a dynamic and integral component in the processing of sensory information. Attention in this context is seen as an active process of selecting and weighting sensory inputs, modulating them in accordance with the brain's predictions and the individual's current needs or goals (Feldman and Friston, 2010; Clark, 2013). This is particularly pertinent to interoceptive awareness, where attention needs to navigate and prioritize among multiple internal signals, often in the presence of competing external sensory inputs.

In the past decade, researchers have increasingly begun to frame interoceptive processing within the Bayesian Brain framework. While not exclusively tailored to interoceptive awareness, this framework has been specifically applied to explain aspects such as emotional awareness and body regulation (Seth et al., 2011; Sterling, 2012; Pezzulo et al., 2015; Petzschner et al., 2021). However, the application of these principles can also extend to explaining the perceptual properties of interoceptive awareness. For instance, the perception of a rapid heartbeat might be interpreted differently based on contextual factors and individual expectations, such as whether one is experiencing anxiety or has just completed physical exercise (Paulus et al., 2019).

The primary objective of this section is to demonstrate how the Bayesian

framework effectively encapsulates the unique features of interoceptive awareness that were highlighted in the previous section. By applying this framework, we can begin to formulate inductive hypotheses that offer deeper insights into the workings of interoceptive awareness. These hypotheses could potentially lead to a more comprehensive understanding of how we perceive and interpret our internal bodily states.

Predictive Coding: The Implementation of Bayesian Process

The implementation of the Bayesian framework in cognitive neuroscience, particularly through the paradigm of predictive coding, marks a significant shift in the understanding of perception. This approach has conceptualized perception not as a direct interpretation of sensory inputs, but as an active inferential process where the brain continually generates and updates predictions about sensory input (i.e., perceptual inference). These predictions are hierarchically organized and are continuously compared against actual sensory data (Knill and Pouget, 2004; Friston and Kiebel, 2009; Summerfield and Egner, 2009). The essence of predictive coding lies in its ability to capture the dynamic nature of perception, where the brain constantly anticipates incoming sensory information based on previous experiences and current contextual cues.

A critical aspect of predictive coding is the hierarchical nature of the predictive processes, which posits that higher cognitive levels generate predictions about lower-level sensory inputs (Friston, 2012). These predictions cascade down the hierarchy, where they are compared with actual sensory inputs at each level. The discrepancies between predictions and actual sensory inputs, known as prediction errors, are then propagated upwards to update and refine the predictions. This recursive process results in a refined perceptual experience, constantly shaped by a blend of prior expectations and new sensory evidence (Hohwy, 2012). Furthermore, prediction and prediction errors are represented as probabilistic values, embodying the inherent variance in both the external environment and the internal model of the world. Importantly, within predictive coding, the inverse variance of each signal is represented as precision (Feldman and Friston, 2010; Clark, 2013; Jiang et al., 2013). Precision is afforded to each signal based on its reliability and contextual relevance, playing a crucial role in the weighting of prediction errors. This aspect of the framework addresses how the brain distinguishes between reliable and unreliable sensory inputs, allocating more weight to those deemed more precise. This probabilistic approach to handling sensory information and prediction errors underpins the flexible and adaptive nature of perception.

Attention, in this framework, is reconceptualized as a modulator of sensory precision, rather than a selective filter or spotlight, as traditionally viewed in the perceptual models discussed in experimental psychology (Feldman and Friston,

2010; Hohwy, 2012; Ransom et al., 2017). Here, attention dynamically adjusts the precision afforded to sensory signals, effectively amplifying or attenuating the influence of prediction errors on perceptual updating. This redefinition of attention shifts the focus from a mechanism that selects specific stimuli for processing to one that adjusts the relative importance of sensory inputs based on their predicted relevance and reliability. In this way, attention in predictive coding is closely intertwined with the probabilistic nature of perception, playing a vital role in determining how sensory information is integrated and weighted in the construction of perceptual experience .(Itti and Baldi 2009)

This perspective of attention as a modulator of sensory precision in predictive coding contrasts with its portrayal in the models, where attention acts as a gatekeeper, selectively allowing certain stimuli to pass through for further processing. In predictive coding, attention is more about calibrating the brain's perceptual predictions by adjusting sensory precision, the importance of sensory inputs, ensuring that perception is both context-sensitive and adaptable to changing environments or internal states. This view of attention aligns with the overall premise of the Bayesian framework, emphasizing the brain's role as an active constructor of perception, continuously shaping and reshaping perceptual experience based on a complex interplay of predictions, sensory inputs, and attentional modulation.

Reaching the Perceptual Properties of Interoceptive Awareness

The Bayesian framework, particularly through predictive coding, offers a compelling perspective on the perceptual mechanism of interoceptive awareness, addressing the limitations encountered in traditional perceptual models in cognitive psychology. Perception in predictive coding is seen as an iterative process where the brain constantly generates and updates internal models of the body's state (Ainley et al., 2016). These models hierarchically predict various physiological parameters ranging from central factors like blood pressure, blood gases, energy status, and hydration levels to peripheral sensory inputs, including the activity of mechanoreceptors in blood vessels, chemoreceptors in the kidneys and liver, and nociceptors in body tissues. They continuously update based on changing circumstances and environmental factors, as well as current alterations in interoceptive signals. This enables them to predict and subsequently regulate the body's status within a specific range, functioning as a benchmark for maintaining homeostasis (Petzschner et al., 2021; Unal et al., 2021). When actual bodily sensations deviate from these expected models, prediction errors occur. For instance, if the body experiences an unexpected increase in blood pressure or sensation in the stomach, these would constitute prediction errors. The brain then updates its internal models to account for these discrepancies, leading to a revised perception of the body's state (Ainley et al., 2016).

This updating process in response to prediction errors can explain the perceptual uncertainty characteristic of interoceptive awareness. Since bodily sensations can often be imprecise and spatially distributed, the brain's model of what to expect can vary significantly from the actual sensation experienced. This variance can lead to a state of perceptual uncertainty, where the individual is unsure of how to interpret the internal signals they are receiving (Diamond, 2019; Allen et al., 2022). For example, a sudden increase in heart rate might be interpreted as anxiety, excitement, or simply a response to physical exertion, depending on the internal models, or the context and the individual's previous experiences and expectations. As such, the Bayesian approach, through predictive coding, provides a framework to understand how these interpretations are formed and why they might differ from person to person (Paulus et al., 2019).

Interoceptive sensations, such as those related to heartbeat, hunger, or respiratory status, are inherently imprecise and lack identifiable sensory features,

primarily due to the biological imperative of maintaining homeostasis – a constant internal bodily state (Pezzulo et al., 2015; Allen and Tsakiris, 2018). This is contrasting to that exteroceptive stimuli often present clear and distinct sensory inputs from such as the retina and cochlea. Therefore, due to the relatively low precision of interoceptive sensations, especially when an individual is at rest and bodily arousal levels are low, becoming consciously aware of these signals poses a significant perceptual challenge (Ainley et al., 2016; Paulus et al., 2019). Such phenomena require a "weighting" of imprecise interoceptive sensations, which is equivalent to the role of voluntary attention in predictive coding. Empirical research has demonstrated that the focused attention on bodily sensations can enhance interoceptive awareness, even in states of low bodily arousal (Critchley et al., 2004; Petzschner et al., 2019; Haruki and Ogawa, 2023a). This enhancement is presumably due to the modulation of interoceptive attention, which, under the Bayesian framework, is conceptualized as adjusting the precision (or the expected reliability) of interoceptive sensations. According to Ainley and colleagues (2016), this form of attention specifically increases the weighting of interoceptive prediction errors, thereby amplifying the perceptual signal of otherwise subtle bodily sensations. In other words, by anticipating a higher precision of interoceptive sensations, the brain becomes more attuned to these signals, making them more salient in consciousness (Ainley et al., 2016).

Inductive Hypothesis from the Predictive Coding Accounts of Interoceptive Awareness

The discussion thus far makes a compelling case for adopting predictive coding as a model for interoceptive awareness. This model stands out as more useful compared to other perceptual models, as it posits that without predictive coding processes, interoceptive awareness cannot be fully captured. Conversely, with predictive coding, numerous functional hypotheses can be derived and tested. By examining these hypotheses, we can not only validate the framework's applicability but also open new horizons in perceptual research.

One initial hypothesis pertains to the significant impact of predictions on interoceptive awareness. Given the inherent impreciseness of interoceptive sensations, the influence of predictions is likely to be more pronounced than in exteroception. For instance, studies on heartbeat perception demonstrate how subjective expectations significantly influence individuals' ability to perceive their heartbeat, revealing that individual differences in prior expectations about interoceptive sensations, such as heart rate, could lead to variations in perceptual accuracy (Desmedt et al., 2020; Körmendi et al., 2021). Furthermore, training to perceive heartbeats with auditory cardiac feedback improves perception ability, suggesting that the brain's predictive models (Meyerholz et al., 2019). This suggests that the brain's predictive models, which integrate past experiences and current context, play a pivotal role in shaping interoceptive awareness.

Moreover, under predictive coding, precision holds relative value across all sensory signals, implying interactions between interoceptive sensations and exteroception. Notably, studies have shown that heartbeat pulsations can interfere with both visual and tactile sensations (Mirams et al., 2012; Al et al., 2020; Galvez-Pol et al., 2022b). This cross-modal interaction underscores the intertwined nature of sensory modalities in perceptual processing, as predicted by the predictive coding model. For example, Galvez-Pol and colleagues demonstrated that precisely predictable interoceptive sensations, like heartbeat pulsations, can suppress visual information processing, highlighting the brain's prioritization of sensory signals based on their predicted precision and relevance (Galvez-Pol et al., 2020).

These examples support the hypothesis that in predictive coding, the brain continuously adjusts its perceptual models, balancing interoceptive and

exteroceptive inputs based on their relative precision and contextual relevance. This dynamic process potentially offers a more comprehensive understanding of how interoceptive awareness is shaped and modulated, not only by internal bodily states but also in relation to external sensory experiences. Validating these hypotheses could significantly enhance our understanding of perceptual mechanisms, particularly in the context of interoceptive awareness, and contribute to broader perceptual and cognitive research.

Objective and Overview of the Current Experiments

I have devoted considerable effort to discussing predictive coding as a viable model for explaining the perceptual properties of interoceptive awareness. Recent empirical research supports inductive hypotheses derived from predictive coding, particularly underscoring the importance of predictions in interoceptive awareness and the influence of interoceptive sensations on exteroceptive senses. This growing body of evidence has further provided support for this perceptual model. However, there remain unexplored areas, most notably the role of attention in interoceptive awareness. Within predictive coding, attention is conceptualized as modulating the precision of sensory signals. This modulation is vital for tuning the brain's responses to relevant internal and external stimuli. To this end, I have designed experiments to investigate inductive hypotheses in the predictive coding that remain uninvestigated, thereby aiming to further validate this model and extend our understanding of the perceptual system to the realm of interoception.

The initial area of exploration in my research, categorized under the section “Neural Underpinnings of Attention in Facilitating Interoceptive Awareness”, focuses on investigating the neural mechanisms underlying attention that facilitate interoceptive awareness within the framework of predictive coding. This investigation is particularly crucial as previous studies, while following similar experimental paradigms, often failed to adequately separate the concepts of attention and perceptual accuracy in the realm of interoceptive awareness (Simmons et al., 2013; Avery et al., 2014; Kerr et al., 2016; DeVille et al., 2020). These studies, though insightful, have not comprehensively examined the critical phenomenon where even when interoceptive input remains constant, an enhanced level of interoceptive awareness is achieved. Moreover, there is a substantial individual difference in the interoceptive awareness, in addition to variational interpretations of similar inputs within individuals, both indicating a high level of perceptual uncertainty in interoceptive awareness (Herbert et al., 2012; Garfinkel et al., 2015; Harrison et al., 2021). These observations point to the pivotal role of attention, in an individualized and contextualized manner. To address this research gap, my study involves conducting two functional magnetic resonance imaging (fMRI) experiments. These experiments are designed to advance our understanding of the interplay between interoceptive attention and awareness, and how these processes are represented and managed in the brain.

The primary objective is to identify and map the specific neural activities that are associated with the attentional modulation of sensory precisions and clarity of interoceptive percepts, even in situations where the sensory inputs themselves remain unchanged. The findings from these fMRI experiments are expected to offer valuable insights into the neural mechanisms of attention and their role in shaping our conscious experience of bodily states, thereby enriching the field of cognitive neuroscience.

The second line of investigation in my research, which falls under the section "Interoceptive Awareness Affected by Other Sensory Modalities", delves into the interaction between interoceptive awareness and exteroceptive inputs, also resulting in a high degree of perceptual uncertainty. Within the framework of predictive coding, perception is an outcome of perceptual inference, where the brain assigns precision weighting to sensory signals from all modalities (Hohwy, 2012; Clark, 2013). This theoretical foundation suggests that exteroceptive inputs, such as those from auditory or visual sources, could significantly influence the processing of interoceptive information, and vice versa. Predictive coding stands out among other models by offering a comprehensive understanding of how different sensory modalities can interact, leading to either interference or facilitation within a unified perceptual system (Friston and Kiebel, 2009; Hohwy, 2017). In this context, my research explores the dynamics of how interoceptive awareness is affected by external sensory inputs. The first study focused on the impact of auditory feedback related to cardiac activity on interoceptive attention and how this interaction influences overall interoceptive awareness. This experiment was designed to determine if and how external auditory stimuli related to one’s own heartbeat could enhance or alter the perception of internal bodily states. In contrast, the second study investigated the potential interference effect of auditory distractions on interoceptive awareness. This was done to assess whether external auditory stimuli unrelated to bodily functions could disrupt or modify the perception of internal bodily signals. Both studies aimed to evaluate whether external sensory inputs can lead to perceptual outcomes that are not readily explained by other models treating distinct sensory modalities and their further integration, thereby challenging and expanding our understanding of sensory processing. The findings from these investigations are expected to contribute significantly to our knowledge of sensory integration and the interdependence of different sensory modalities. By examining the influence of exteroceptive stimuli on interoceptive awareness, these studies shed light on

the complex mechanisms through which our brain integrates and interprets sensory information from both the external environment and our internal bodily states.

The final aspect of my research, categorized under "Precision Weighting of Interoceptive Signals and Its Effect on Exteroception", ventures into testing the implications of enhanced precision in interoceptive signals, as proposed by the predictive coding model. This segment investigates whether the principle of precision weighting, a cornerstone of predictive coding, can be extended to general perceptual processes (Hohwy, 2012; Clark, 2013; Allen and Tsakiris, 2018). The focus here is on examining the effects of artificially increasing the precision of interoceptive sensations and assessing their subsequent impact on visual decision-making and metacognitive abilities. This study is designed to test the hypothesis that interoceptive signals, when their precision is heightened, can exert a measurable influence on the processing of other sensory modalities, particularly visual perception. In this experiment, participants were engaged in dot motion tasks that were unrelated to the primary visual tasks. The aim was to observe how manipulating the relative precision of interoceptive sensations affected their performance and decision-making in visual tasks. This approach allowed for the direct testing of the influence of interoceptive signals on visual perceptual systems and metacognition. If it is found that visual perceptual decision-making and metacognitive systems are indeed influenced by enhanced interoceptive signals, such a discovery would have profound implications. It would challenge and potentially require significant revisions to existing models in the fields of object recognition and perceptual processing, which have traditionally considered sensory modalities as largely independent in their processing (Massaro and Cowan, 1993). By exploring the interaction between increased precision in interoceptive awareness and visual perception, the study provides empirical evidence to support the idea of a more integrated sensory processing system. This could lead to a reevaluation of how sensory information is prioritized and integrated in the brain, offering new perspectives on perceptual processing and the brain’s adaptive mechanisms.

The overarching goal of these research areas is to substantiate the inductive hypotheses inherent in the predictive coding framework. By focusing on the complex interplay between interoceptive and exteroceptive sensations and how they are processed and integrated by the brain, my experiments are positioned

at the cutting edge of research in this field. This endeavor is not just about validating the predictive coding model; it's about pushing the boundaries of our current understanding of how this model can be applied to explain phenomena in interoceptive awareness. Furthermore, this body of research opens up new pathways for comprehending perception as a holistic and dynamic process. It underscores the notion that perception is not just a straightforward response to sensory stimuli but is significantly shaped by a complex interplay of internal bodily sensations and external environmental inputs. This integrative approach highlights the flexible and interconnected nature of sensory processing, where internal states can influence the perception of external stimuli and vice versa. By adopting this comprehensive perspective, the research contributes to a deeper understanding of cognitive processes, potentially leading to innovative approaches in both theoretical models and practical applications in fields such as psychology, neuroscience, and even clinical practice.

Neural Underpinnings of Attention in Facilitating Interoceptive Awareness

Research Backgrounds

The "Neural Underpinnings of Attention in Facilitating Interoceptive Awareness" section of my thesis delves into the specific neural mechanisms that are engaged during volitional attention to interoceptive signals. This inquiry is particularly focused on the role of attention as conceptualized within the predictive coding framework, where attention dynamically modulates the precision of sensory signals, rather than simply selecting or filtering them, thus allowing the flexible interpretation of sensations (Feldman and Friston, 2010). This process involves a recalibration of the relative importance of these signals and predictions about them, optimised by the brain's attentional mechanisms (Summerfield and de Lange, 2014). A crucial aspect of this investigation involves noting that, although interoceptive signals like heartbeat sensations remain relatively stable during rest, focusing attention on these signals is hypothesized to increase their importance or precision. As a result, specific brain regions involving attentional processes are expected to become activated, without manifested activation in the primary sensory area (Jiang et al., 2013).

In this context, my research aims to identify the specific brain regions that are activated when attention is directed towards certain sensations related to interoceptive awareness, such as the heartbeat and stomach. This involves using functional magnetic resonance imaging (fMRI) to visualize brain activity in response to focused interoceptive attention. The hypothesis is that regions beyond the dorsal posterior insula, namely the primary interoceptive area (Oppenheimer and Cechetto, 2016; Evrard, 2019), particularly those associated with higher-order cognitive functions and attention modulation, such as the anterior insula, will show increased activation. This would suggest that these areas are integral to recalibrating how interoceptive signals are processed and interpreted, aligning with the predictive coding model's assertion of attention as a modulator of sensory precision.

The initial experiment in this research series (Experiment 1) is designed to test the hypothesis that focused attention optimises the relative precision of

interoceptive sensations, thus facilitating interoceptive awareness as an ongoing perceptual experience (Ainley et al., 2016; Petzschner et al., 2019). A key aspect of this study involves contrasting attention directed towards internal bodily sensations related to heartbeat, with attention focused on external auditory stimuli. The study further seeks to disentangle attention and perceptual accuracy in interoceptive awareness, even when sensory inputs itself remain constant. By doing so, I aim to localize brain regions related to interoceptive attention and accuracy as a critical grounding of the predictive coding model, aligning with the assertion that attentional modulation of the relative sensory precisions, rather than sequential processing of sensory features, is required for interoceptive awareness.

Previous research related to Experiment 1 has consistently implicated the right anterior insula as a pivotal region in interoceptive awareness, often associated with sympathetic bodily responses (Craig, 2009; Seth et al., 2011; Gu et al., 2013). However, the insula's multifaceted role, lateralization, and the specific involvement of its subregions in interoceptive processing have not been fully elucidated. While the involvement of the right anterior insula in interoceptive awareness is well-documented, emerging evidence from attention paradigms involving interoception points to a more intricate involvement of the insula. Notably, a meta-analysis focusing on heart attention paradigms identified consistent activation in bilateral dorsal middle insula regions against a right-lateralization in interoceptive attention (Schulz, 2016). However, the precise degree of this lateralization and the specific functional roles of different insula subregions in interoceptive awareness remain to be fully understood. In response to this gap, my research employs detailed neuroimaging to scrutinize the subdivisions within the insula and their activity patterns during tasks requiring interoceptive attention. This approach is aimed at clarifying the lateralization and localization within the insula during interoceptive awareness. Moreover, by correlating activation patterns in insula subregions with individual differences in interoceptive accuracy scores, the study seeks to elucidate how variations in insula activity correspond to individual differences in interoceptive accuracy.

The second experiment in my research series (Experiment 2) builds upon the initial exploration by investigating how attention influences various interoceptive modalities, specifically focusing on cardiac and gastric sensations. This study is

grounded in the hypothesis that the brain differentially processes signals from these distinct internal states. According to the predictive coding framework, the differences in brain activations would be more pronounced in regions involved in modulating sensory precision, as opposed to the primary sensory areas typically engaged in basic signal processing (Summerfield and Koechlin, 2008; Jiang et al., 2013). This experiment aims to ascertain if focused attention on specific interoceptive sensations, such as heartbeats or stomach signals, elicits distinct patterns of brain activation. Importantly, I focus on the distinctness in the primary interoceptive area (dorsal posterior insula) and more anterior part of the insula, thereby contributing to a shift in the role of attention from the traditional view of modular sensory feature processing to a modulatory player of relative precisions across sensory modalities.

Previous research in the field has predominantly concentrated on cardiac interoceptive awareness, often overlooking other bodily sensations such as gastric signals (Lutz et al., 2019; Dobrushina et al., 2021). This research limitation has consequently restricted theoretical advancements in understanding how the brain encodes different types of bodily signals. To address this gap, the present Experiment 2 conducts a direct neural comparison between cardiac and gastric interoceptive awareness. A critical region of focus in this experiment is the insula, as well as Experiment 1. The expectation is that different subregions of the insula will demonstrate modality-specific activations; specifically, the activation in the dorsal posterior insula or primary interoceptive area would not be distinguished while regions relevant to attentional modulation of sensory precisions might show distinct activation patterns. This hypothesis aligns with the predictive coding model, which posits that attention modulates the precision of sensory inputs based on their relevance and importance to the body's current state (Ainley et al., 2016). To achieve a thorough understanding of the insular cortex's role in interoceptive awareness and its differential encoding of various interoceptive modalities, this study employs a combination of multivoxel pattern analysis and basic neural activation comparisons (Norman et al., 2006). By integrating these neuroimaging techniques with the theoretical framework of predictive coding, this experiment aims to significantly enhance our understanding of the neural mechanisms underlying interoceptive awareness. It seeks to contribute to the broader understanding of sensory processing within the brain, particularly emphasizing how attention and the brain’s predictive capabilities shape our perception of internal bodily states.

Experiment 1

Introduction

The information arising from within our body can contribute to various cognitive functions; for example, an increased heart rate might be indicative of mind-body stress and an empty stomach can motivate an individual to eat. The term “interoception” encompasses a broad range of concepts regarding internal state, including the senses and processes associated with the nervous system and the interpretation of signals originating from within the body (Critchley and Harrison, 2013; Critchley and Garfinkel, 2017; Azzalini et al., 2019). Interoception is a comprehensive and multi-dimensional concept; thus, studies on interoception should describe which specific aspect of interoception is being discussed. Recent studies have attempted to find some distinct aspects of conscious experience of interoception (i.e., interoceptive awareness), by proposing various dimensions across interoceptive awareness, such as attention (the process of focusing on one’s internal bodily environment), accuracy (the ability to correctly perceive changes arising from within the body), and sensibility (the subjective tendency to feel one’s body states) (Ceunen et al., 2013; Garfinkel et al., 2015; Murphy et al., 2019a). Typically, interoceptive accuracy is measured using a behavioral task, such as the heartbeat counting task, and sensibility is assessed via a questionnaire regarding interoceptive awareness. Accuracy and sensibility can be considered as distinct concepts because both vary greatly between individuals and seldom correlate with each other (Garfinkel and Critchley, 2013; Garfinkel et al., 2015). In contrast, attention seems to be a general aspect; therefore, the interoceptive attention paradigm is often employed as a task that records brain activity pertaining to interoceptive awareness (Pollatos and Schandry, 2004; Wiebking et al., 2010); however, unlike accuracy and sensibility, an objective evaluation of interoceptive attention is difficult. Since each aspect of interoceptive awareness is measured in different ways and has different properties, it is important to distinguish the aspects from each other when discussing interoception to avoid misunderstandings.

The autonomic nervous system relays bodily signals to the central nervous system; for interoceptive processing, the insular cortex is involved at the cortical level due to its importance in processing and representing such afferent signals. Bodily information is relayed through subcortical regions, such as the brainstem, hypothalamus, and thalamus, through the lamina I spinothalamic and

vagus/glossopharyngeal cranial pathways and are projected principally to the posterior insula and primary somatosensory area (Craig, 2002, 2003; Oppenheimer and Cechetto, 2016). It has been proposed that bodily information in the posterior insula is transmitted forward along the rostrocaudal axis, integrated with other sensory inputs in the middle insula, and finally re-represented in the anterior insula to be consciously available (Craig, 2009; Frot et al., 2014).

These models assume that each subdivision of the insular cortex has a unique role. According to a large-scale meta-analysis on the functions of the insular cortex (Kurth et al., 2010), the subdivisions of the insula were activated by different task domains, such as the activation of the dorsal anterior region by the cognitive domain (such as attention, memory, and speech), the ventral anterior region by the social-emotional domain (such as emotion and empathy), and the dorsal middle posterior region by the sensorimotor domain (such as somatosensory and motor functions). In addition to the differences in anatomical location, a neural asymmetry in the insula has been suggested, wherein the positive emotions are associated with activation in the left anterior and mid-insula, while negative emotions activate the bilateral anterior and mid-insula (Duerden et al., 2013; Strigo and Craig, 2016). These functional specializations may be related to differences in their structural connections with the other regions. While the posterior insula is connected to the parietal region, including the postcentral gyrus, the dorsal anterior insula is connected to the frontal operculum, and the ventral anterior insula to the limbic regions (Cerliani et al., 2012; Cloutman et al., 2012). The insular cortex seems to have a wide variety of functions between the hemispheres and along the rostrocaudal and ventrodorsal axes. Careful consideration on the structure-function variety of the insula would be needed in the literature regarding interoceptive awareness, which posits that the insula is the core region.

Although empirical works suggest that the right anterior insula is central to interoceptive awareness, there is little information regarding its multidimensionality and the laterality and variations of the insula. Many neuroimaging studies have emphasized the general involvement of the right anterior insula in interoceptive awareness, revealing that a single aspect of interoception, such as the subjective intensity rating of interoceptive sensation and the interoceptive accuracy (IAc) index, was related to the activity of the right

anterior insula (Craig et al., 2000; Critchley et al., 2004; Pollatos et al., 2007; von Leupoldt et al., 2008; Caseras et al., 2013). These studies may support the view of sympathetic bodily re-representation that occurs exclusively in the right anterior insula, but others implicitly challenge this notion. That is, studies employing the interoceptive attention paradigm have often reported the activation of the bilateral middle insula (Wiebking et al., 2010; Avery et al., 2014; Haase et al., 2016; Stern et al., 2017; Failla et al., 2020). A meta-analysis on interoceptive attention (especially heart attention) found that the cluster was consistently activated in the bilateral (but somewhat right-lateralized) dorsal middle insula (Schulz, 2016). Although right insula dominance in relation to autonomic input asymmetry has been suggested (Craig, 2008; Zaki et al., 2012), to the best of our knowledge, no study has specifically examined the extent of laterality in interoceptive awareness.

Indeed, the neural activity in the insula is associated with an origin of interoceptive awareness; however, some incongruencies are present about its detailed localization. We believe that these inconsistencies could be because prior studies did not thoroughly investigate both the structure-function variety of the insular cortex and the distinct interoceptive modalities. In particular, we suspected that the patterns in which the insular cortex is involved in terms of interoceptive attention and accuracy are different, as implied by Schulz (2016). Therefore, we performed two experiments on the same day: the behavioral heartbeat counting task to measure an individual's IAc index and a functional magnetic resonance imaging (fMRI) scanning during interoceptive attention. We then thoroughly examined the differences in activities among the subdivisions of the insula during interoceptive attention to assess the extent of laterality and localization in the insula. Additionally, we identified the exact region of the insula that is related to the differences in individual IAc scores. Two to four functional divisions of the insula have been confirmed in prior large-scale meta-analyses (Kurth et al., 2010; Deen et al., 2011; Cauda et al., 2012; Chang et al., 2013), but these studies did not effectively divide the dorsal region, which might be associated with interoceptive awareness, into its four distinct anatomical gyri (Türe et al., 1999; Morel et al., 2013; Faillenot et al., 2017). Thus, we used the anatomical divisions of the insula as regions of interest (ROI) while assuming that a distinct anatomical gyrus may be uniquely associated with interoceptive attention. Based on previous results, we hypothesized that the right middle insula would show the highest activation during interoceptive attention (Zaki et al., 2012; Simmons et al., 2013; Schulz, 2016), and that it would be associated with

IAc scores (Critchley et al., 2004; Pollatos et al., 2007; Caseras et al., 2013), which might be distant from the activation peak coordinate associated with interoceptive attention.

Materials and Methods

Participants. We recruited 29 healthy, right-handed volunteers to participate in this study. One participant was excluded from the analysis because the scanning suddenly stopped due to defects during the experimental run, yielding incomplete data. Thus, the final analysis included 28 participants (12 women; age, 19–28 years). Written informed consent was obtained from all the participants. The handedness of each participant was assessed using a modified version of the Edinburgh Handedness Inventory in Japanese (Hatta and Nakatsuka, 1975). The study was conducted in accordance with the Declaration of Helsinki. The ethics committee of Hokkaido University approved the experimental protocol.

Heartbeat counting task. A heartbeat counting task, outside the fMRI scanner, was used to assess each participant's interoceptive accuracy (Schandry, 1981); this task was performed on the day of the fMRI experiment. After obtaining signed consent forms, a pulse oximeter (IWS920, Tokyo Devices; Tokyo, Japan) was placed on the participants' left ring finger while they sat on a chair. To avoid feeling a pulse, they were instructed to place their arms on the desk and not to lean back in their chair. Before the task started, the apparatus was set in an appropriate position so that the participant could not sense their bloodstream outside their body (e.g., via their finger on the pulse oximeter, wrists on the desk, or buttocks on the chair). The experimenter verbally instructed the participants to "count each heartbeat you feel in your body especially around the heart, from the time you hear the cue sound to when you hear the same sound again, and then tell me how many heartbeats you felt." The experimenter also told the participants, "do not estimate the number of heartbeats; if you feel nothing, please tell me so." This was done to ensure that participants only counted sensations felt inside their body and did not estimate the number of heartbeats, as this would affect the IAc (Desmedt et al., 2018; Ring and Brener, 2018). Subsequently, the participants were given 2 min of rest to control their levels of arousal, which was followed by the task trial. The participants performed three task trials with different time windows (25 s, 35 s, 45 s) after a short training trial (10 s). The order of the time windows was randomized for each participant before the trial began. The IAc index was individually calculated using the following formula (Pollatos et al., 2008; Tsakiris et al., 2011):

$$IAc\ index = 1 - \left(\frac{|Recorded\ Number\ of\ Heartbeats - Counted\ Number\ of\ Heartbeats|}{Counted\ Number\ of\ Heartbeats}\right)$$

According to this calculation, the IAc could range from 0 to 1. Scores closer to 1 indicated small differences between the subjectively counted heartbeats and objectively measured heartbeats.

MRI data acquisition. All scans were performed on a Siemens (Erlangen, Germany) 3-T Prisma scanner with a 20-channel head coil at Hokkaido University. Using T2*-weighted echo-planar imaging (EPI), 237 scans were acquired per session, with a gradient echo EPI sequence. The first three scans acquired within each session were discarded to allow for T1 equilibration. The scanning parameters used were as follows: repetition time (TR), 2000 ms; echo time (TE), 30 ms; flip angle (FA), 90°; field of view (FOV), 192 x 192 mm; matrix, 94 x 94; 32 axial slices; and slice thickness, 3.500 mm, with a 0.875-mm gap. Thus, the voxel size was 2.042 x 2.042 x 4.375 mm. T1-weighted anatomical imaging with an MP-RAGE sequence was performed using the following parameters: TR, 2300 ms; TE, 2.32 ms; FA, 8°; FOV, 256 x 256 mm; matrix, 256 x 256; 192 axial slices; and slice thickness, 1 mm without a gap.

fMRI procedure. The general procedure was based on several previous studies (Wiebking et al., 2010, 2015; Simmons et al., 2013; Kuehn et al., 2016), which were modified for our interests. One session consisted of two condition trials: a heart attention condition (interoception) and a control tone condition (exteroception). Each heart and tone condition trial was performed nine times in one session. Each condition trial was composed of a heart/tone attention task block, a concentration rating block (4 s), and a rest block (8 s). In an attention task block, the duration was 12 s, 14 s, or 16 s, with each task presented three times for a total of nine times. Heart and tone trials were alternated throughout the whole session for a total of 18 times. The presentation order within each trial was randomized before the session began, in which there could be an appearance of identical durations on consecutive task trials. The total experiment consisted of four sessions, with both the heart and tone condition trials performed 36 times in total. Participants were equipped with MRI-compatible headphones and watched the screen via a mirror inside the scanner. After each session, the participants were given a break of approximately 2 min.

Before the first session began, the volume of the tone sound used as a target was individually adjusted in accordance with previous studies (Kuehn et al., 2016). While a dummy EPI scan was running, the experimenter gradually decreased the volume of the tone sound, while the participants gave feedback so that the tone

sound was just perceivable. This was done to ensure that the task difficulty level was comparable between the heart attention and tone attention tasks. These adjusted low-volume tone sounds were presented during both the heart attention and tone attention blocks. The duration of the sounds was 200 ms, and the intervals corresponded to each participant's mean beat-to-beat interval that was recorded during the prior heartbeat counting task, while being jittered by 200 ms, to control for habituation effects (Wiebking et al., 2010).

In the heart attention task, the participants were instructed to silently count each heartbeat by focusing on their heart and feeling their heartbeat-related sensations. Estimating the number of heartbeats was prohibited as with the heartbeat counting task, which was performed outside the MR scanner. Very low-volume tone sounds were delivered through the headphones. The participants were instructed to ignore them and to focus only on their heart to prevent estimation of the number of their heartbeats from the frequency of the tones, although they were not informed of what the sound intervals meant. A previous study found that tone sounds analogous to heart rate did not facilitate heartbeat detection under explicit instructions (Zaki et al., 2012).

In the subsequent concentration rating tasks, the participants self-reported about how well they felt they had concentrated in the previous blocks, using a scale from one (poor) to four (good) by pressing buttons with their right hand. This was done to ensure participants' attention in the prior task trials (Simmons et al., 2013; Avery et al., 2014). They did not have to report the number of counted heartbeats, and no feedback about the correctness of their response was provided.

In the rest block, a fixation crossbar was presented in the center of the screen, no sound stimulation was played, and the participants were told to watch the bar. Preparing for the next task block was prohibited.

In the tone attention task, the participants counted each tone by concentrating on the sounds presented via a headphone. They reported on their concentration following the same procedure similar to that in the heart attention trial. Because the experimental situations were equal between the two task conditions (e.g., the scanning noise and low-volume tone sounds), the only difference noted was where the participants would focus their attention (heart: on their heartbeats, tone: on the tone sounds). This allowed us to estimate the focal brain activity for

interoceptive and exteroceptive attention by subtracting the effects of confounders included in both attention tasks.

Preprocessing of the fMRI data. Image preprocessing was performed using SPM12 software (Welcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm). All functional images were initially realigned to adjust for motion-related artifacts. Volume-based realignment was performed by co-registering images using rigid-body transformation to minimize the squared differences between volumes. The realigned images were then spatially normalized using the Montreal Neurological Institute (MNI) template based on the affine and non-linear registration of co-registered T1-weighted anatomical images (normalization procedure of SPM). They were resampled into 3-mm-cube voxels with sinc interpolation. Images were spatially smoothed using a Gaussian kernel of 6 x 6 x 6 mm full-width at half-maximum. Low-frequency noise was removed using a high-pass filter with a cut-off period of 128 s, and serial correlations among scans were estimated using an autoregressive model implemented in SPM12.

Statistical analysis of fMRI data. A first-level general linear model (GLM) analysis was performed to estimate the brain activity related to bodily and auditory attention. Both the heart and tone blocks per session were modeled as separate boxcar regressors that were convolved with a canonical hemodynamic response function, and both the rest and concentration rating blocks were used as the baseline. For each participant, four contrast images were created: heart vs. baseline, tone vs. baseline, heart vs. tone, and tone vs. heart.

Subsequently, we implemented three types of group analyses. First, we performed a random-effects analysis using one-sample *t*-tests. Whole-brain activity in the first-level contrast images of heart vs. tone and tone vs. heart was independently analyzed to confirm the selective activation for each heart and tone attention. The voxel-level threshold was set to a *p*-value of < .05 and corrected for false discovery rate (FDR). Clusters corrected for FDR ($p < .05$; corresponded to more than 15 voxels) were reported as activated areas.

Secondly, we conducted another group analysis to explore the insular activity related to interoceptive attention in more detail. We adopted the anatomical image of the insular subdivisions published in Hammersmith brain atlases (Brain Development, www.brain-development.org) as the ROI. These images were

constructed as a 3D probabilistic atlas using *in vivo* T1 MR images, including anatomical structures commonly noted in the human insula: the anterior short gyrus (ASG; the most dorsal anterior portion of the insula, left: 6212 mm^3; right: 6096 mm^3), middle short gyrus (MSG; the dorsal mid-anterior portion; left: 4127 mm^3; right: 4629 mm^3), posterior short gyrus (PSG; the dorsal mid-posterior portion, left: 5531 mm^3; right: 5223 mm^3), anterior inferior cortex (AIC; the ventral anterior portion, left: 7599 mm^3; right: 7625 mm^3), anterior long gyrus (ALG; the dorsal posterior portion, left: 6817 mm^3; right: 6568 mm^3), and posterior long gyrus (PLG; the ventral posterior portion, left: 6785 mm^3; right: 6612 mm^3) (Faillenot et al., 2017). These six ROIs were adopted separately from both hemispheres; a total of 12 ROIs were used to compare the activation among the insular cortex. Thereafter, the effects of both the heart and tone conditions were individually estimated as a beta weight among the insular subdivisions based on the first-level results. A repeated-measures analysis of variance (ANOVA) was performed on these beta values with hemisphere (left/right) and location (ASG, MSG, PSG, AIC, ALG, PLG) as the within-factors. Additionally, we assumed that some confounding effects, such as counting numbers, could be introduced in the heart attention condition. To remove such effects, we computed the difference between the tone attention and heart attention conditions for each ROI individually. Thereafter, a repeated-measures ANOVA was performed on these differences, with hemisphere and location as the within-factors.

In the third group analysis, we conducted a correlation analysis between the hemodynamic response and the individual ability to perceive the internal state, or the IAc index. The second-level contrast image of the heart vs. baseline was created, which modeled the individual IAc index as a covariate of interest. This was then masked using the bilateral insular cortex image parcellated in the Anatomical Automatic Labeling (AAL) brain atlas, which was because the correlation between IAc and the insula activity have been reported in prior studies (Critchley et al., 2004; Pollatos et al., 2007; Tan et al., 2018). A one-sample *t*-test under the insula mask was performed to identify the exact region whose activity correlated with IAc. The threshold was set to a *p*-value of $< .005$ (uncorrected). Also, we checked whether the activation of insula subdivisions obtained in our ROI analysis was correlated with IAc. Pearson's correlation coefficient between individual IAc and beta values of the 12 ROIs during heart attention was calculated.

Results

Heartbeat counting task. The mean IAc score for all participants was 0.59 (*SD* = 0.24). No significant sex-specific difference was found ($t_{(25.04)}$ = -0.10, p = .92), and the IAc scores did not show a significant correlation with age or heart rate during the counting task (r = -.30, p = .12; r = -.27, p = .15, respectively).

fMRI. Whole-brain analysis revealed that, compared with the brain regions activated with the tone attention task, the heart attention task induced significant activation of several brain regions, including the bilateral frontal operculum, middle insula, precentral gyrus, middle cingulate cortex, and supplementary motor area (Table 1; Figure 1). None of the significantly activated regions during the tone attention task were comparable to those activated during the heart attention task, with the current threshold.

Repeated-measures ANOVA on the beta estimate values across the insular subdivisions suggested functional differences across the insular cortex (Figure 2). The main effect of location was significant in the heart attention task ($F_{(5, 135)}$ = 29.35, p < .001, η^2_p = .52), but the main effect of hemisphere and the interaction between them was not statistically significant ($F_{(1, 27)}$ = 0.00, p = .99, η^2_p < .001; $F_{(5, 135)}$ = 1.57, p = .17, η^2_p = .06), suggesting no lateralization of interoceptive attention. Multiple comparison using Shaffer's modified sequentially rejective Bonferroni procedure on the differences among the insular subdivisions revealed the strongest activation in the MSG (adjusted p-values < .005); the results also indicated that the ASG and PSG showed higher activation than the AIC, ALG, and PLG regions (adjusted p-values < .002; adjusted p-values < .001, respectively). In the tone attention condition, the main effect of location and the interaction between the location and hemisphere was significant ($F_{(5, 135)}$ = 4.09, p = .002, η^2_p = .13; $F_{(5, 135)}$ = 2.51, p = .032, η^2_p = .09), but the main effect of hemisphere showed no statistical significance ($F_{(1, 27)}$ = 0.03, p = .88, η^2_p = .001). A simple effect analysis showed significant difference between the activity of the left ALG (M = 0.02, SD = 0.13) and the right ALG (M = -0.01, SD = 0.15) ($F_{(1, 27)}$ = 11.87, p = .002, η^2_p = .31). A multiple comparison of the locations activated during the tone attention task indicated that the ASG was more strongly activated than the AIC (adjusted p = .001).

As a supplementary analysis, we subtracted the beta values acquired during the tone attention tasks in the 12 insula ROIs from those acquired during the heart

Anatomic region	Voxels	MNI coordinates			*t*-value
		x	y	z	
Heart attention > Tone attention					
L Rolandic operculum	120	-54	2	8	7.71
Dorsal mid-insula		−36	2	8	6.23
Precentral gyrus		−57	5	26	5.86
R Rolandic operculum	39	57	2	5	7.60
L Supplementary motor area	46	−9	−1	59	6.84
L Middle cingulate cortex	72	−9	8	35	6.79
R Supplementary motor area		3	5	47	6.31
R Supplementary motor area	15	9	-4	65	6.02
Tone attention > Heart attention					
No voxel has activated					

Table 1. Anatomical regions, peak voxel coordinates, and t-values of observed activations. The peak-level threshold was set to p < .05 (FDR-corrected) and the cluster size was also corrected for FDR.

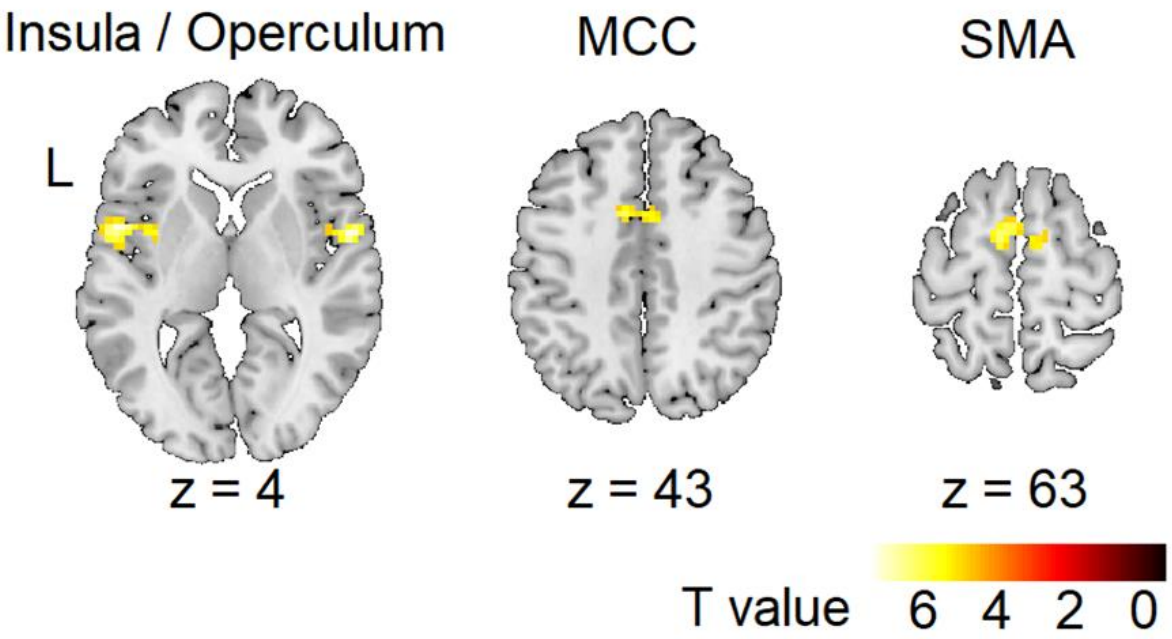

Figure 1. Activated brain regions in the heart attention condition compared to the tone attention condition. Activation was reported with a threshold *p*-value of < .05, corrected for multiple comparisons for the false discovery rate (FDR) with an extent threshold *p*-value of < .05. L, left hemisphere; MCC, middle cingulate cortex; SMA, supplementary motor area. MNI coordinates of the activated foci are reported in Table 1. Figures are displayed in the axial slices with z denoting locations in the MNI coordinates.

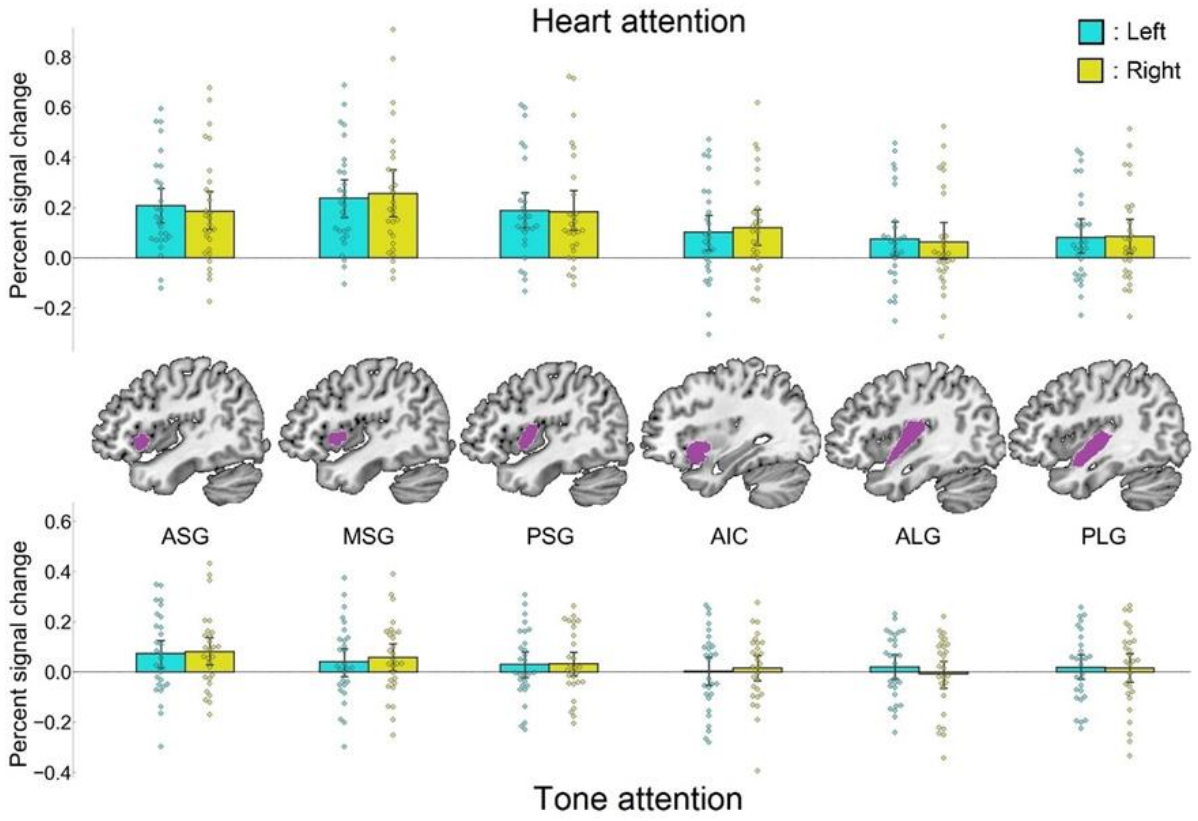

Figure 2. The averaged effects of each task condition among the subdivisions of the insular cortex. The Y values (percent signal change) correspond to the beta values acquired. The upper and lower six columns are associated with the subdivision of the insula shown in the center. Each point that overrayed on the barplots corresponds to the raw data of each participant. Error bars indicate 95% confidence interval. ASG, anterior short gyrus; MSG, middle short gyrus; PSG, posterior short gyrus; AIC, anterior inferior cortex; ALG, anterior long gyrus; PLG, posterior long gyrus.

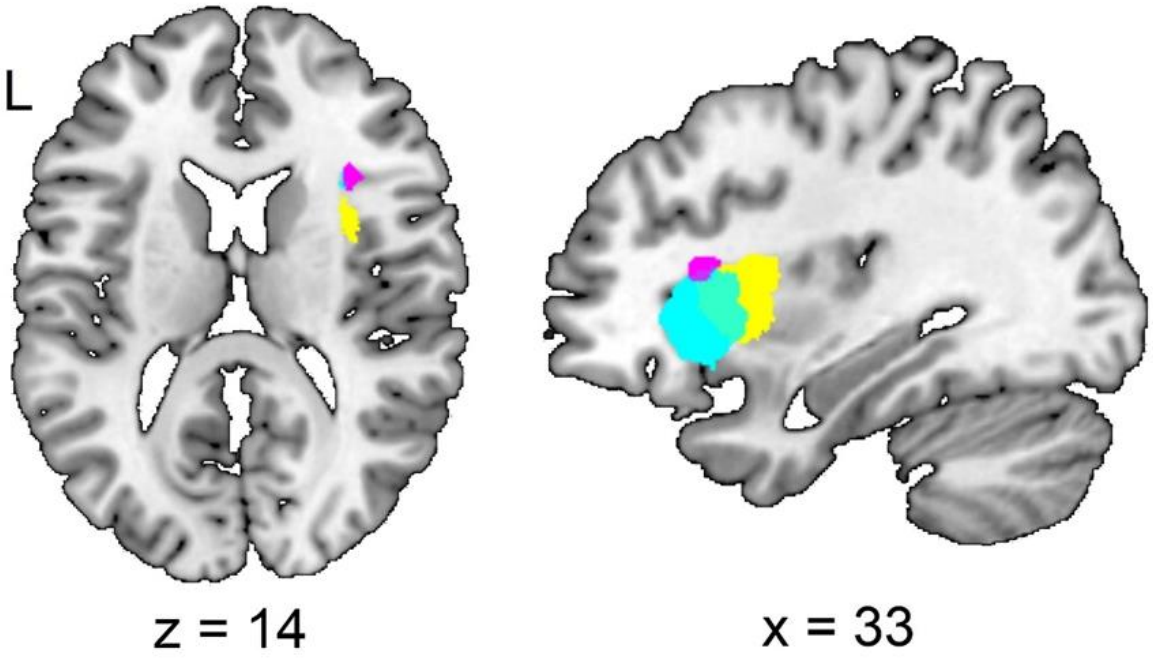

Figure 3. The region showed an activation that correlated with the interoceptive accuracy index. Only the right dorsal anterior insula/frontal operculum (purple cluster, MNI coordinates: x = 33, y = 21, z = 14) was associated with individual interoceptive accuracy. The ASG (cyan) and the MSG (yellow) that were used in our ROI analysis are shown in the overlay as a reference. Figures are displayed as axial slice with z and sagittal slice with x, with the letters denoting locations in the MNI coordinates.

attention tasks. Repeated-measures ANOVA with these values indicated a significant main effect of location ($F_{(5, 135)}$ = 9.40, p < .001, η^2_p = .26), but no significant main effect of hemispheres and the interaction between them ($F_{(1, 27)}$ = 0.00, p = .95, η^2_p < .001; $F_{(5, 135)}$ = 1.02, p = .41, η^2_p = .03, respectively). Since only the effect of location was significant, we checked whether the values of each location were higher than zero by repeating the one-sample *t*-tests. As a result, at a threshold of p < .05 (Bonferroni-corrected), the ASG, MSG, and PSG regions were significantly activated during the heart attention task, even after subtracting the activations during the tone attention task; however, the AIC, ALG, PLG regions were not activated (ASG: $t_{(55)}$ = 3.36, uncorrected p = .001, Cohen's d = 0.63; MSG: $t_{(55)}$ = 5.33, p < .001, d = 1.01; PSG: $t_{(55)}$ = 4.49, p < .001, d = 0.85; AIC: $t_{(55)}$ = 2.51, p = .02, d = 0.47; ALG: $t_{(55)}$ = 1.55, p = .12, d = 0.30; PLG: $t_{(55)}$ = 2.57, p = .01, d = 0.49).

Subsequently, we modeled each participant's IAc index as a covariate of interest into a second-level GLM analysis to investigate the relationship between the IAc and the observed activation. This analysis revealed a positive correlation between the right dorsal anterior insula/frontal operculum (x = 33, y = 21, z = 14, 162 mm^3) activity and the IAc (Figure 3). However, we could not find a significant correlation between IAc index and beta values of the 12 anatomical ROIs ($|rs|$ < .12, details are exhibited in Supplementary material).

Discussion

Using a well-documented heartbeat counting task and an fMRI paradigm related to interoceptive awareness, this study aimed to clarify the sensitive brain activation pattern, especially in the insular cortex, with regard to the two dimensions of interoceptive awareness: attention and accuracy. First, compared with the tone attention task, the heart attention task activated the bilateral frontal operculum, middle insula, precentral gyrus, middle cingulate cortex, and supplementary motor area. Previous studies have reported that these areas are activated during interoceptive attention (Pollatos et al., 2007; Avery et al., 2014; Stern et al., 2017; Tan et al., 2018). By comparing the activation among the insular subdivisions during the heart attention task, we found, for the first time, that the MSG showed the highest activation, followed by the ASG and PSG. Moreover, the current study found no lateralized activation across the insula in the heart attention task, although some previous studies have argued in favor of right insular dominance in overall interoceptive awareness (Craig, 2009; Critchley and Harrison, 2013). Finally, we found a strong association between an individual's ability to correctly perceive heartbeats (IAc index) and right dorsal anterior insula/frontal operculum activity during the heart attention task. This is in line with previous knowledge that individual interoceptive accuracy scores correlate almost exclusively with the right anterior insula activity during an interoceptive attention task (Critchley et al., 2004; Pollatos et al., 2007; Caseras et al., 2013).

The differences in activation across the anatomical locations of the insular cortex observed in this study confirm and extend the findings of previous studies. During the heart attention task, the ASG, MSG, and PSG were more activated than the other ventral and posterior portions of the insula (AIC, ALG, and PLG). This indicates the involvement of the dorsal middle-anterior insula in interoceptive attention (Kurth et al., 2010; Terasawa et al., 2013; Araujo et al., 2015), suggesting that these insular regions are strongly associated with processing and representing the internal state of one's own body. In addition, we identified for the first time that among the anatomical locations of the brain, the MSG shows the highest activation during the heart attention task. Human insular subdivisions have variable structural connections with other cortical areas, such that the ASG and MSG have a connection with the frontal area, and the AGL and PLG, with the primary somatosensory area (Cerliani et al., 2012; Cloutman et al., 2012). Therefore, it is plausible that our heart attention task did not activate the long gyri (posterior portions of the insula) because any explicit interoceptive

sensation, such as palpitation or pain, was absent during the experiment.

Previous studies have revealed that electrical stimulation of the MSG and PSG evoked a number of bodily responses, including somatosensory, visceral, and pain sensations (Afif et al., 2010b; Yu et al., 2018). The current activation of the MSG and PSG may therefore be considered as a reflection of the bodily representation. In particular, the representation associated with heartbeats could be in the PSG because another study reported that stimulation of the PSG often induced bradycardic effects (Chouchou et al., 2019). Although the ASG stimulations elicited few bodily responses in these studies, the current heart attention paradigm significantly activated the bilateral ASG region even after subtracting the confounding effects like counting numbers and the presented tone sounds. A previous meta-analysis has shown that the ASG is involved in cognitive processes such as working memory (Kurth et al., 2010) in addition to its structural connection with the frontal area. Hence, the current ASG activity may reflect a more cognitive aspect of interoceptive attention, such as searching for heart-related sensations and focusing attention on the internal milieu.

These findings can be incorporated into the results of psychiatric research on interoceptive awareness. For example, (Avery et al., 2014) reported that during interoceptive attention, patients with major depressive disorder exhibited lower activity in the bilateral dorsal mid-insula (especially the mid-posterior, comparable to the PSG) than healthy subjects. They also found that left mid-insula activity was negatively correlated with depression severity and the degree of somatization in the depressed group. Another study has shown that the dorsal anterior insula (corresponding to the ASG, MSG, and PSG) exhibited lower activation in depressed patients than in healthy controls and depression-remitted populations (Wiebking et al., 2015). Taken together, depressed individuals may have an attenuation in bodily representation in the MSG and PSG. In addition, aberrant somatosensation could be represented in the left PSG of people with depression.

This study also highlighted important insights into the laterality of the insula. There was no significant difference in insular activity between the hemispheres regarding interoceptive attention, even after subtracting the effects from possible confounders, which does not support our hypothesis. Previous fMRI studies have suggested right insular dominance in interoceptive awareness (Zaki et al., 2012; Simmons et al., 2013), which supports the forebrain asymmetry of

sympathetic/parasympathetic processing (Craig, 2005, 2009). Other studies have reported that the bilateral insula is involved in interoceptive attention tasks; however, none of these studies directly compared the activation between the right and left insula(Wiebking et al., 2010; Haase et al., 2016; Failla et al., 2020). Regarding the asymmetry in autonomic input to the insula, the results of the current study imply that a representation of body states is established by the cooperation of sympathetic activities on the right middle-anterior insula and by parasympathetic activities on the left. This may be supported by the fact that there is a bidirectional information exchange between the left and right insula, especially in the middle and anterior portions (Lacuey et al., 2016).

The activity in the most dorsal region in the right anterior insula was positively correlated with the IAc index measured by the heartbeat counting task. This is in line with many studies that employed a behavioral task to measure individuals' abilities to perceive their own heartbeats (Critchley et al., 2004; Pollatos et al., 2007; Caseras et al., 2013; Kuehn et al., 2016; Tan et al., 2018). This lateralization regarding interoceptive accuracy was once interpreted as right anterior insula dominance for the representation of bodily arousal and interoceptive awareness overall (Gray and Critchley, 2007; Critchley and Harrison, 2013). However, this explanation might be inadequate because recent studies have revealed that the anterior insula can be divided into two distinct functional regions: the ventral portion involved in the affective process and the dorsal portion in the cognitive process (Cauda et al., 2011, 2012; Deen et al., 2011). In addition, the right dorsal anterior insula and frontal operculum are proposed as the core structures for cognitive processing, such as attentional control and salience detection (Dosenbach et al., 2007; Eckert et al., 2009; Menon and Uddin, 2010; Touroutoglou et al., 2012). Thus, the consistent relationship between the activity of the individual IAc and right dorsal anterior insula might be distinct from that of the bilateral middle-anterior insula during general interoceptive attention. This suggests that the right dorsal anterior insula plays a key role in gaining an accurate perception of internal bodily states via top-down attention, such as filtering body signals from noise. Nonetheless, it is also possible that the higher the activity of the right dorsal anterior insula while focusing on heartbeats, the more sympathetic bodily arousal is re-represented there (Gray and Critchley, 2007), facilitating conscious perception of heartbeats. If this were true, the individual IAc index would be associated with the quality of the bodily re-representation rather than with attentional processes. Although conclusion

cannot be inferred from the present results alone, it is likely to be true in one of these two cases. Clarifying the role of right anterior insula in accurate, not for general interoceptive awareness is needed to orient the future researches aiming at their individual differences.

Limitations of this study. The current study has several limitations. First, we stated that insular involvement in interoceptive attention and accuracy could be dissociable. However, the task administration for interoceptive attention and accuracy differed because we employed a heart attention task using fMRI; moreover, the heartbeat counting task was performed outside of the MRI scanner. An individual IAc score is known to be temporally stable (Ehlers et al., 1995; Ferentzi et al., 2018), and we tried to make the two heartbeat counting tasks comparable with strict instructions, but it is still possible that there were differences in postures or task environments. Second, we introduced tone stimuli during both heartbeat and tone attention tasks to make both conditions more comparable for the subtraction analysis. Whereas the presentation of auditory stimuli during interoceptive attention task was commonly used in the previous studies (Critchley et al., 2004; Kuehn et al., 2015), this could, however, cause multisensory integration even when the participants attended to interoceptive signals. Although the volume of tone was adjusted so small that participants had to pay much attention to perceive, subliminal auditory stimuli might affect the pattern of brain activation elicited by their attention to the heart. Thus, our interoceptive attention paradigm might be somewhat different from the pure attention to interoceptive signals and might cause the absence of significant activity in the posterior insula. Third, in our ROI analysis, we used structural subdivisions of the insula that were constructed using probabilistic mapping, which can have several overlaps with each other by nature. This would cause an increase in the activation similarity between two adjacent ROIs. Therefore, it may be inappropriate to declare that the MSG of the insula was the most involved in interoceptive attention, although the current analysis obtained clearly significant results.

Conclusion. In conclusion, our findings elaborate and extend previous knowledge regarding the relationship between interoceptive awareness and the insular cortex. Recent studies have uncovered multiple aspects of interoceptive awareness, and critically, the current study revealed the different involvement of the subdivisions of the insula in interoceptive attention and accuracy. Specifically,

interoceptive attention was associated with activation in the bilateral mid-anterior insula. On the other hand, interoceptive accuracy—the correct perception of any change in the body—was positively correlated with the activity of the dorsal margin of the right anterior insula, which is considered as the center of attentional control. Identifying the distinct relationship between each aspect of interoception and the subdivisions of the insular cortex would facilitate the understanding of the nature of interoceptive awareness and the function of the insula in further detail.

Experiment 2

Introduction

Subjective experiences of internal bodily states are referred to as interoceptive awareness (Khalsa et al., 2018), and such senses indicate ongoing physiological changes and guide adaptive behavior (Paulus et al., 2019; Quigley et al., 2021). Although interoceptive awareness serves multiple functions, depending on its source e.g., thirst, hunger, heartbeat perception, it remains unclear how subjective differences in interoceptive awareness are represented in the human brain (Azzalini et al., 2019). We used functional magnetic resonance imaging (fMRI) to focus on the brain activations accompanying attention to cardiac (related to the heartbeat) and gastric (related to the stomach) sensations that elicit interoceptive awareness of different body organs, which have been suggested to serve different functional roles.

Considering the types of situations where people become aware of their heartbeat, the heartbeat signals and cardiac interoceptive awareness inform changes in physiological arousal (Paulus et al., 2019). In experimental settings, accelerated false cardiac feedback i.e., exaggerated cardiac interoceptive awareness, has been found to alter the emotional salience of neutral faces (Gray et al., 2007) and perceived physical effort (Iodice et al., 2019) by enhancing physiological arousal. Similarly, gastric interoceptive awareness, such as fullness or hunger, modulates foraging and feeding behavior. In fact, people with eating disorders show altered gastric function and interoceptive awareness (Walsh et al., 2003; van Dyck et al., 2021), which may cause their abnormal eating behavior. Despite considerable differences in their functional roles, extant research has failed to establish whether cardiac and gastric interoceptive awareness are differently represented in the brain.

The invasive procedures needed to manipulate bodily signals have limited detailed functional brain mapping of interoceptive awareness. The brain regions responding to changes in visceral signals and interoceptive awareness have been studied using physical stimulation of viscera (Lu et al., 2004; Jarrahi et al., 2015) or pharmacological disturbance (Hassanpour et al., 2016, 2018) during fMRI scanning. However, such paradigms are difficult to combine in a single study because of invasiveness and the requirement of specific instruments, e.g., a

barostat or an intravesical infuser. In addition, these brain activations would reflect the participant's discomfort and anxiety, induced by the abnormal sensations, and thus may not be appropriate for mapping interoceptive awareness of different organs. Another way to map interoceptive awareness is to use an interoceptive attention paradigm—asking participants to direct their attention toward sensations originating from the body. Importantly, although exteroceptive information, such as cutaneous sensations, may contribute to interoceptive awareness (Khalsa et al., 2009), interoceptive attention has been found to elicit interoceptive awareness and robust activations of brain regions, including the insula, middle cingulate cortex, and supplementary motor area (Caseras et al., 2013; Tan et al., 2018; Haruki and Ogawa, 2021). In particular, researchers have consistently associated activation of the right anterior insula with interoceptive attention (Zaki et al., 2012; Simmons et al., 2013) and objective accuracy of heartbeat perception (Critchley et al., 2004; Pollatos et al., 2007; Caseras et al., 2013). These results appear to support an influential neuroanatomical model of interoceptive awareness, where the posterior insula receives the initial cortical input of visceral signals while awareness of internal bodily states is represented in the right anterior insula (Craig, 2009, 2011; Evrard, 2019).

Previous studies using the interoceptive attention paradigm suffer from the limitation of having extensively used heartbeat attention, eliciting cardiac interoceptive awareness, over other bodily sensations. Even when attentional focus on gastric sensations was deployed, direct comparison within the modality of interoceptive attention has not been discussed (Simmons et al., 2013; Kerr et al., 2016; DeVille et al., 2020). Therefore, it is still unclear whether the neural encodings of interoceptive awareness of different bodily signals differ, limiting theoretical advances in this field. To address this issue, we directly compared the neural activations for cardiac and gastric interoceptive awareness using the interoceptive attention paradigm in a healthy population. We hypothesized that attention to cardiac and gastric sensations, and thus their interoceptive awareness, would elicit distinct neural activations, which would be modulated according to their functional roles. That is, cardiac attention might activate the regions underlying physiological arousal, while brain areas that modulate feeding and foraging behavior might show enhanced activation in gastric attention. Moreover, we considered that the insula, the most relevant region for interoceptive awareness (Craig, 2009; Critchley and Harrison, 2013), would show

a subregion-specific representation of cardiac and gastric interoceptive awareness. To test this idea, we performed a region of interest (ROI) analysis, focusing on the insula, by combining multivoxel pattern analysis (MVPA) with a basic comparison of neural activation.

Materials and Methods

Participants. A total of 35 right-handed people participated in the experiment (15 women). One participant (a woman) requested an interruption of the experiment, yielding incomplete data. Of the remaining participants, the data of three (one man and two women) were excluded from the analysis because their maximum head movement was more than 3 mm during the experiment. Thus, the final analysis included 31 participants (12 women) who were 21.61 ± 2.45 years of age on an average (range: 20 to 31). Their handedness was assessed by a modified version of the Edinburgh Handedness Inventory for Japanese participants (Hatta and Nakatsuka, 1975). The sample size deemed sufficient for determining brain activation was based on previous studies that used a similar task for interoceptive attention(Wiebking et al., 2015; Haruki and Ogawa, 2021). Written informed consent was obtained from all participants. This study was carried out in accordance with the Declaration of Helsinki and all its amendments. The Ethics Committee of the Center for Experimental Research in Social Science, Hokkaido University approved the experimental protocol.

Task procedures. To quantify brain activation for cardiac and gastric interoceptive awareness noninvasively, we asked participants to perform an established interoceptive attention task in an MRI scanner. We used a task procedure that elicited robust brain activation for interoceptive awareness (Simmons et al., 2013; Kerr et al., 2016; DeVille et al., 2020), which was modified to suit our purpose i.e., to perform MVPA, and to increase statistical power. The present task had a simple block design that had three conditions with resting periods: heart attention (for cardiac interoceptive awareness), stomach attention (for gastric interoceptive awareness), and visual attention (for control). Participants were asked to focus on sensations from their heartbeat or stomach, or visual stimuli, and to be aware of the slight sensations for each condition (Figure 4). In the heart and stomach attention trials, the words “HEART” and “STOMACH” were presented for 10 s each on the screen to allow participants to realize which sensation they were focusing on. In the visual attention trial, the word “TARGET” was presented on the screen for 10 s, with the color of the word gradually and slightly fading from black to gray. The color changed every 1.5 s for a total of five times. Therefore, in each task trial, participants directed their attention to a particular, vague sensation without a

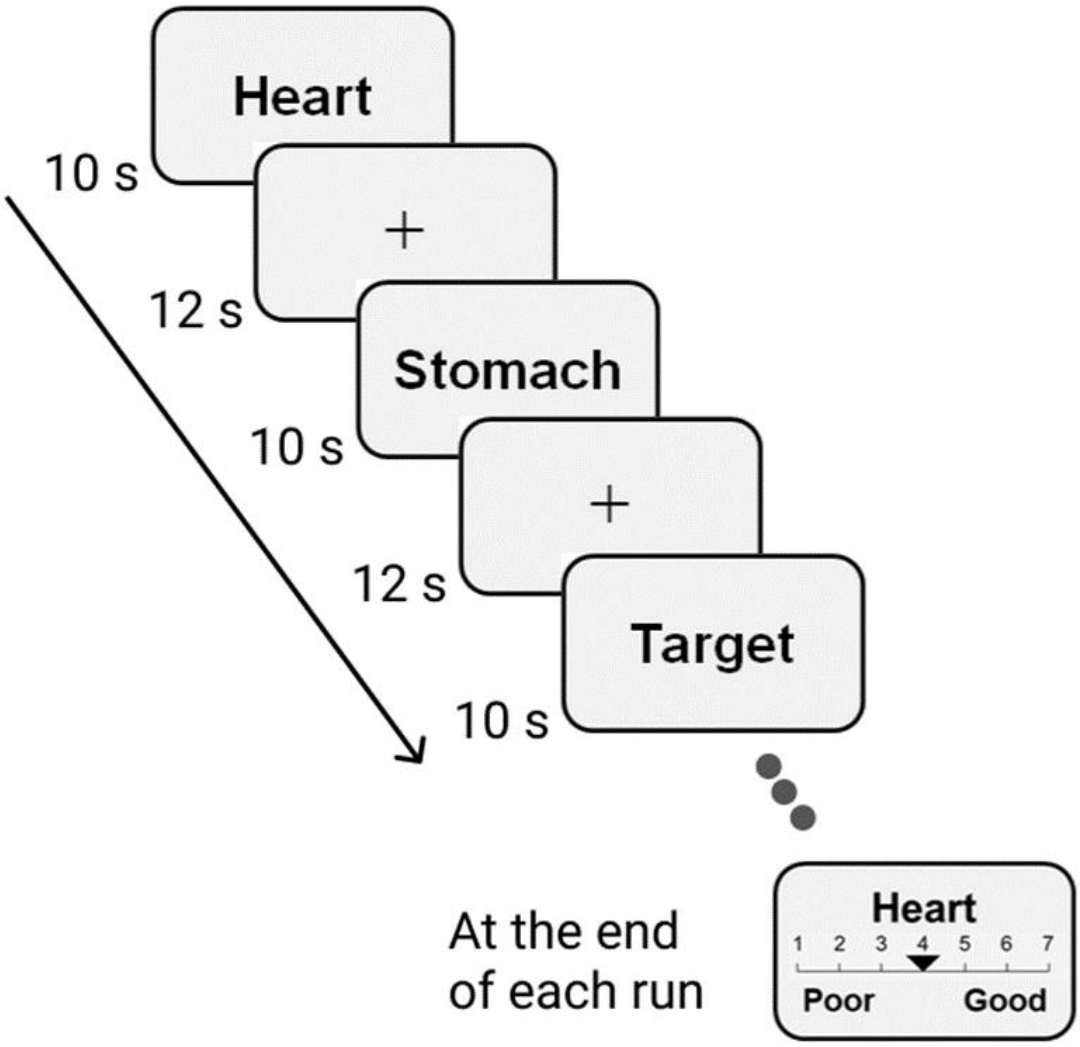

Figure 4. An example of the time course of the functional magnetic resonance imaging (fMRI) task is depicted. Our block design fMRI task included three types of task trials (heart attention, stomach attention, and control visual attention) that lasted 10 s each, followed by rest (12 s). Participants were asked to focus on sensations arising from the heart, stomach, and color changes in the word, according to the type of task. At the end of each run, participants rated the subjective intensity of the sensations for each condition using a Likert scale ranging from 1 (not intense at all) to 7 (extremely intense).

salient stimulus. During the rest period, participants watched a fixation crossbar for 12 s with their eyes open. Preparing for the next task trial was prohibited.

Each condition of the task trial was presented five times per run: a single run included a total of 15 task trials and 15 rest periods. The order of the task trials was pseudo-randomized, but the same trial was not presented three times in succession. At the end of each run, participants rated the subjective intensity of the sensations (heart, stomach, and visual) throughout the run using a Likert scale ranging from 1 (not intense at all) to 7 (extremely intense). An approximately 5.5 min run was repeated five times; thus, we obtained 25 data points (125 volumes) for each condition per participant. This procedure was designed to include a larger number of trials than those of previous studies (Kerr et al., 2016; DeVille et al., 2020) because we needed a sufficient number of task trials to perform MVPA. Before the first run began, all participants underwent a resting-state scan that lasted for 5 min, which was not analyzed in the present study. Stimuli were presented on a liquid crystal display and projected onto a custom-made viewing screen. Participants took a supine position in the scanner and viewed the screen via a mirror. Participants experienced a practice trial and filled its intensity report (for each condition), to learn how to perform the task and report the subjective intensity, before entering the MRI scanner. Through the practice trials, we verbally confirmed that the participants successfully directed their attention to each sensation depending on the condition.

MRI acquisition. All scans were performed on a Siemens (Erlangen, Germany) 3-Tesla Prisma scanner with a 64-channel head coil at Hokkaido University. T2*-weighted echo planar imaging (EPI) was used to acquire a total of 168 scans per run, with a gradient echo EPI sequence. The first three scans within each session were discarded to allow for T1 equilibration. The scanning parameters used were as follows: repetition time (TR), 2,000 ms; echo time (TE), 30 ms; flip angle (FA), 90°; field of view (FOV), 192 × 192 mm; matrix, 94 × 94; 32 axial slices; and slice thickness, 3.500 mm, with a 0.875 mm gap. Thus, the voxel size was 2.042 × 2.042 × 4.375 mm. T1-weighted anatomical imaging with an MP-RAGE sequence was performed using the following parameters: TR, 2,300 ms; TE, 2.32 ms; FA, 8°; FOV, 256 × 256 mm; matrix, 256 × 256; 192 axial slices; and slice thickness, 1 mm without a gap.

Preprocessing of fMRI data. All image preprocessing was performed using

SPM12 software (Wellcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm). All the functional images were initially realigned to adjust for motion-related artifacts. Volume-based realignment was performed by co-registering images using rigid-body transformation to minimize the squared differences between volumes. The realigned images were then spatially normalized with the Montreal Neurological Institute template based on the affine and non-linear registration of co-registered T1-weighted anatomical images. They were resampled into 3-mm-cube voxels with sinc interpolation. The images were spatially smoothed using a Gaussian kernel of 6×6×6 mm full width at half-maximum. The images used for MVPA were not smoothed to avoid blurring the information in the multi-voxel activity pattern.

Statistical analysis. *Subjective intensity of the sensations.* We used R (version 4.0.3) for all our statistical inferences, except with functional imaging data. First, we tested whether the subjective intensity of the sensations differed between the modalities (cardiac, gastric, and visual). A linear mixed-effects (LME) model analysis, implemented in the lme4 package (Bates et al., 2015), was performed. With all the data obtained (N = 465, 3 trial types for 5 runs for 31 participants) as the dependent variable, we modeled the type of sensation as the fixed effect. Random intercepts and slopes for the effects of participants, and random intercepts for the runs, were modeled as random effects, ensuring the maximal random structure for our models (Barr et al., 2013). The LME allowed us to avoid averaging the values across five runs compared to the traditional analysis of variance (ANOVA) (Baayen et al., 2008). The parameters were estimated using the restricted maximum likelihood method, with the degrees of freedom estimated using the Satterthwaite method.

Whole-brain activation. We first evaluated the brain regions activated under each condition (heart attention, stomach attention, and visual attention) using a generalized linear model (GLM). An individual-level GLM included three regressors of interest for each condition as a separate box-car function that was convolved with the canonical hemodynamic response function. The rest period was used as a baseline. To reduce motion-related artifacts, six motion parameters were included as nuisance regressors. By combining the three conditions, we obtained six contrast images (heart attention compared to stomach attention, heart compared to visual, stomach compared to visual, and their opposite contrasts) for each participant. We then performed a group-level

random effects analysis for these images using a one-sample t-test. Through these statistical inferences, we directly compared the activation for each condition across the whole brain.

Moreover, we performed a group-level analysis of covariance (ANCOVA) to exclude the effect of the subjective ratings of stimulus intensity on brain activation. This was because we considered that the differences in subjective intensity could affect the brain activation pattern, independently of the object of attentional focus. Using the image of interoceptive attention, contrasted to the visual control, we modeled individual subjective ratings for each condition, averaged for five runs, as covariates. Then ANCOVA, excluding the effects of subjective rating as nuisance, was performed. By doing so, we assessed the brain activations of cardiac attention, contrasted with visual attention, without the effect of individual differences in subjective heartbeat intensity; and gastric attention, contrasted with visual, without the subjective intensity of stomach sensation. Furthermore, we explored variations in brain activation as a function of subjective intensity; a regression analysis with subjective intensity as a covariate of interest was performed using the same model used in the ANCOVA. For all the analyses, the voxel-level threshold was set to $p < .001$ (uncorrected), and the cluster-level threshold was set to $p < .05$, corrected for family-wise error (FWE).

ROI analysis of the subregions of the insula. We tested whether cardiac and gastric interoceptive awareness at the voxel level were differently represented in the subdivisions of the insula. In particular, we first performed MVPA, which allowed us to investigate more sophisticated neural representation than did conventional analysis (Norman et al., 2006), suspecting that conventional analysis might fail to detect activation differences in the insula. The ROIs were defined as the anatomical subdivisions of the insula in the Hammersmith brain atlases (Brain Development, www.brain-development.org). These images were constructed as a 3D probabilistic atlas using in vivo T1 MR images, including anatomical structures commonly seen in the human insula: the anterior short gyrus (ASG; the most dorsal anterior portion of the insula), middle short gyrus (MSG; the dorsal mid-anterior), posterior short gyrus (PSG; the dorsal mid-posterior), anterior inferior cortex (AIC; the ventral anterior), anterior long gyrus (ALG; the dorsal posterior), and posterior long gyrus (PLG; the ventral posterior) (Faillenot et al., 2017). Importantly, these ROIs have been confirmed to show a subregion-

specific activation pattern for heart attention (and, therefore, cardiac interoceptive awareness) (Haruki and Ogawa, 2021).

The MVPA for heart and stomach interoceptive attention was performed with a two-class classifier based on a linear support vector machine (SVM) implemented in LIBSVM (http://www.csie.ntu.edu.tw/~cjlin/libsvm/). We first created another individual-level GLM, apart from the whole-brain analyses that included 15 task trials as independent regressors per run with six motion parameters as nuisance regressors. By doing so, we obtained parameter estimates of all the voxels in each ROI, for a total of 75 trials per participant, labeling them as heart, stomach, or visual, depending on the condition of each trial. We then trained SVM to classify the identity of the brain activation pattern of heart and stomach interoceptive attention using these parameter estimates as inputs to the SVM. Individual-level classification accuracy was estimated with a five-fold "leave-one-out" cross-validation to avoid overfitting. This procedure uses inputs in four runs as training data, and inputs in one remaining run as test data, which was repeated five times for all possible combinations. The averaged classification accuracy across five repetitions of the tests was computed for each ROI for each participant, independently. We used a default hyperparameter (a fixed regularization parameter C = 1). The parameter estimates of the trial were not used as inputs to the classifier. One-sample t-tests were performed to test whether the activation patterns for heart and stomach interoceptive attention in each subregion were classifiable using SVM. That is, we tested whether the computed classification accuracy was higher than the chance level (50%) at the group level, separately for each ROI. Because we used 12 ROIs (six anatomical regions for both hemispheres), the calculated p values were corrected for Benjamini and Hockberg's false discovery rate (FDR; (Benjamini and Hochberg, 1995).

We also compared the differences in the averaged activations in the ROIs among each condition because we suspected that the classification accuracy calculated by MVPA could merely reflect the mean signal change in the ROIs. First, the mean signal changes in each ROI were extracted for each participant, separately for the heart and stomach attention conditions. Then, we performed a repeated-measures ANOVA on these values with the conditions (heart and stomach) and anatomical locations (the ASG, MSG, PSG, AIC, ALG, and PLG) as within-factors, independently for each hemisphere. Multiple comparison correction for post-hoc

analyses was performed using Shaffer's modified sequentially rejective Bonferroni procedure implemented in R. The combined use of MVPA and direct comparisons of the averaged signal change allowed detailed investigation of how interoceptive awareness specific to the cardiac and gastric domains are represented in the human insula.

Furthermore, we tested whether the averaged activation for interoceptive and exteroceptive attention differed in the insula, using a similar procedure for cardiac and gastric interoceptive attention. We extracted mean signal changes for interoceptive attention, the averaged activation across heart and stomach attention, and exteroceptive attention (visual attention) in each ROI. Then repeated-measures ANOVA, with the condition (interoceptive and exteroceptive) and the anatomical location as within-factors, was performed separately for each hemisphere.

Results

Subjective intensity of the sensations. We performed an LME model analysis for the subjective ratings of the intensity of each sensation. The LME included the type of stimuli (heart, stomach, and visual) as the main factors; random intercept and slope for the effects on the participants and random slope for the sequence of runs, were modeled as random effects. The subjective intensity of visual stimuli was rated the highest (marginal mean contrasted to heart = 0.90, $t_{30.00}$ = 4.51, p < .001) and that of the stomach the lowest (marginal mean = -0.41, $t_{30.00}$ = -2.22, p = .03) among the three stimuli (Table 2).

Whole-brain activation for cardiac and gastric attention. We directly compared whole-brain activation across the three conditions (heart attention, stomach attention, and visual attention as the control). We found that stomach attention that elicited gastric interoceptive awareness activated larger brain areas, including the occipitotemporal visual cortices, bilateral primary motor, primary somatosensory, left orbitofrontal, and bilateral posterior hippocampus. In contrast, the right dorsal anterior insula extending to the frontal operculum only showed higher activation in heart attention i.e., selectively for cardiac interoceptive awareness (Figure 5A, Table 3). In particular, the medial visual area that was enhanced during gastric interoceptive attention largely overlapped with the “gastric network”, that showed a temporal coupling with the gastric basal rhythm (Figure 5B) (Rebollo and Tallon-Baudry, 2022). Moreover, by comparing the heart and stomach conditions to the visual control, we found that cardiac and gastric interoceptive attention activated similar brain regions, including the insula, frontal operculum, parietal operculum, middle cingulate, and supplementary motor area; the results were highly comparable to previous studies (Caseras et al., 2013; Tan et al., 2018; Haruki and Ogawa, 2021). A notable exception was that the hippocampus and medial visual areas were activated only in stomach attention (Figure 6A). The visual control condition, contrasted with the heart and stomach conditions, activated brain regions critical for visual attention, such as the middle frontal gyrus, superior parietal lobule, posterior thalamus (geniculate nucleus), and lateral visual association area (Dosenbach et al., 2007; Mayer et al., 2007), supporting the validity of our experimental design (Figure 6A). Furthermore, we confirmed that the brain activation elicited by cardiac and gastric interoceptive attention was almost unaffected by differences in subjective stimulus intensity by performing an

Predictor	Marginal mean	S.E.	95% CI for marginal means		e.d.f.	t	*p*
			Lower	Upper			
(Intercept)	4.71	0.16	4.33	5.09	31.00	24.69	< .001
Stomach compared to Heart	-0.41	0.18	-0.77	-0.04	30.00	-2.22	.034
Visual compared to Heart	0.90	0.20	0.50	1.29	30.00	4.51	< .001

Table 2. Subjective intensity of sensations in each condition. The linear mixed-effects model included the condition as the fixed effect. The random structure was maximal for appropriate inference: random intercept and slope for the effect of the participants, and random intercept for the effect of the run sequence, were modeled as random effects. S.E., standard error for marginal means; CI, confidence interval; e.d.f., estimated degrees of freedom

Location	Voxels	MNI coordinates			T value
		x	y	z	
Contrast: cardiac attention > gastric attention					
R Dorsal anterior insula	48	33	17	2	4.65
Frontal operculum		54	11	8	4.39
Dorsal anterior insula		30	26	2	3.72
Contrast: gastric attention> cardiac attention					
L Secondary visual area	3793	-12	-73	-13	8.42
R Primary visual area		9	-82	5	8.29
Secondary visual area		18	-79	5	8.06
L Middle temporal gyrus	211	-60	-31	-4	6.71
Superior temporal gyrus		-57	-7	-7	4.64
Middle temporal gyrus		-54	-19	-7	4.29
L Lateral orbitofrontal cortex	95	-42	26	-16	6.21
		-36	38	-16	5.29
		-51	26	-4	3.99
L Primary motor cortex	67	-48	-7	29	5.90
R Primary motor cortex	41	48	-7	35	5.88
L Primary sensory area	116	-12	-25	59	5.50
		-3	-37	68	4.57
		-18	-37	68	4.26
L Fusiform gyrus	181	-51	-58	-13	5.31
		-48	-46	-13	4.52
		-36	-61	-13	4.18
L Primary motor cortex	47	-36	-25	53	5.18
		-39	-22	65	3.71
L Dorsomedial prefrontal cortex	96	-12	62	17	5.14
		-18	59	29	5.00
		-9	59	5	4.93
L Medial orbitofrontal cortex	52	-3	47	-13	5.11
		-3	56	-10	4.45
L Frontal eye field	50	-21	32	53	5.05
		-12	35	44	4.72
R Premotor area	50	33	-22	53	4.88
		33	-10	68	4.80

		33	-25	62	4.46
L Dorsolateral prefrontal cortex	42	-54	26	23	4.47
		-39	26	14	3.98
		-48	29	5	3.72

Contrast: cardiac attention> visual attention

L Frontal operculum	578	-51	5	5	8.98
Dorsal anterior insula		-33	5	8	6.56
Supramarginal gyrus		-57	-31	26	6.54
R Supplementary motor area	652	9	-1	68	8.90
L Supplementary motor area		-9	-7	68	8.69
		18	-13	65	5.67
R Frontal operculum	199	48	-1	8	8.81
		60	2	11	5.83
Dorsal anterior insula		36	8	11	5.09
R Primary somatosensory area	112	24	-40	68	6.33

Contrast: gastric attention> visual attention

R Supplementary motor area	950	9	-7	59	8.45
L Supplementary motor area		-9	-7	71	8.13
R Primary somatosensory area		24	-40	68	7.41
L Frontal operculum	490	-51	2	8	7.07
		-45	-4	2	6.51
Dorsal anterior insula		-33	2	11	6.06
R Frontal operculum	151	48	-1	8	7.02
		60	2	11	5.28
		60	5	20	5.21
R Posterior hippocampus	94	33	-40	-4	6.55
		33	-49	2	5.09
		36	-31	-10	4.70
R Secondary visual area	1011	12	-88	23	6.48
L Secondary visual area		-6	-94	20	5.97
		0	-85	23	5.83
L Angular gyrus	161	-48	-73	29	5.87
		-36	-61	23	5.20
		-36	-82	35	4.66
R Visual association area	63	18	-61	-4	4.34
		21	-64	-16	3.58

Contrast: visual attention > cardiac attention

R Visual association area	4302	33	-82	-7	10.86
Secondary visual area		27	-91	2	10.27
L Secondary visual area		-33	-91	2	10.04
R Frontal operculum	849	45	11	29	7.73
Premotor area		45	5	53	6.79
Dorsolateral prefrontal cortex		45	35	20	5.81
R Dorsal posterior thalamus	309	18	-31	2	6.72
		-24	-28	-1	5.52
		9	-28	-1	5.52
R Medial orbitofrontal cortex	132	21	32	-13	6.58
Frontal pole		36	50	-10	5.36
Lateral orbitofrontal cortex		45	41	-13	4.37
L Primary motor area	52	-45	-10	35	5.13
		-45	5	32	4.70
R Frontal eye field	116	3	35	47	5.00
		6	26	56	4.88

Contrast: visual attention > gastric attention

R Fusiform gyrus	1495	27	-79	-1	10.36
Visuomotor area		27	-49	44	9.02
Secondary visual area		24	-88	-4	8.66
L Secondary visual area	812	-33	-91	2	9.88
		-27	-91	-4	9.43
		-27	-97	8	7.86
R Premotor area	996	45	2	53	7.99
Frontal operculum		45	11	29	7.83
Dorsolateral prefrontal cortex		45	35	20	5.96
L Cerebellum	204	-9	-76	-40	6.94
		-6	-76	-31	5.90
		-6	-73	-19	5.38
R Dorsal thalamus	124	6	-13	5	6.80
		6	-28	-1	5.53
L Superior parietal cortex	149	-24	-61	56	6.56
		-24	-61	47	5.95
R Frontal eye field	173	12	35	38	5.61
		9	23	56	5.58

		6	29	44	4.89
L Cerebellum	65	-15	-40	-43	5.28
		3	-31	-31	4.77
		-9	-37	-37	4.43
R Frontal pole	52	39	44	-4	4.42
		36	53	-7	4.41

Table 3. Anatomical regions, peak voxel coordinates, and t-values of observed activations. The peak-level threshold was set to $p < .001$ and the cluster size was also corrected for an extent threshold of $p < .05$ (corrected for family-wise error). L, left hemisphere; MNI, Montreal Neurological Institute; R, right hemisphere

ANCOVA excluding the effect of the subjective ratings of stimulus intensity. The results of the ANCOVA were fairly comparable to the brain activation obtained with cardiac and gastric interoceptive attention contrasted with that in visual control (Figure 6B, 6C). There was no brain activation covarying with the subjective intensity rating even at a more moderate threshold (cluster-level $p < .05$, uncorrected). All results are reported with a voxel-level threshold of $p < .001$ (uncorrected) with cluster size correction for p values < .05 (FWE).

Multivoxel pattern classification for cardiac and gastric attention in the insula. We performed MVPA using an SVM classifier that distinguished the activation patterns in the insula in heart and stomach conditions. Activation patterns in the anatomical subregions of the insula (Faillenot et al., 2017, Figure 7A) were used as inputs to the SVM. We found that classification accuracy in the left PSG, which corresponds to the dorsal middle insula, was significantly higher than the chance level (50%) (mean classification accuracy = 56.32, $t_{30} = 3.39$, $d = 0.61$, corrected p-value for FDR = .024), suggesting that the region had distinct representation for cardiac and gastric interoceptive awareness. The right ASG (mean = 53.48, $t_{30} = 2.56$, $d = 0.46$, corrected $p = .089$), left ASG (mean = 54.26, $t_{30} = 2.28$, $d = 0.41$, corrected $p = .089$), and left MSG (mean = 53.42, $t_{30} = 2.34$, $d = 0.42$, corrected $p = .089$) showed a marginally significant classification accuracy above the chance level; all corresponded to the dorsal mid-anterior insula. The other subdivisions of the insula, such as the posterior or ventral subdivisions, showed no significant classification accuracy above the chance level (corrected ps > .27, ds < 0.30) (Figure 7B).

Comparison of the signal change for cardiac and gastric attention in the insula. We directly compared the signal change in the insular subregions for cardiac and gastric interoceptive attention. Averaged parameter estimates were extracted from the insular ROIs independently for heart and stomach conditions, i.e., 12 values for each condition. We then conducted a repeated-measures ANOVA, with the anatomical location and condition as the within-factors, independently for each hemisphere. The results indicated that, in both hemispheres, the main effects of anatomical location and the interaction between location and condition were significant (left, $F_{5, 150} = 56.37$, $\eta^2_p = .65$, $F_{5, 150} = 8.87$, $\eta^2_p = .22$; right, $F_{5, 150} = 39.18$, $\eta^2_p = .57$, $F_{5, 150} = 15.42$, $\eta^2_p = .34$; all ps < .001), but the main effect of the condition was not (left, $F_{1, 30} = 0.07$, $\eta^2_p = .00$; right, $F_{1, 30} = 0.15$, $\eta^2_p = .01$; $p > .70$) (Figure 7C), replicating the results of a previous study

(Haruki and Ogawa, 2021). Post-hoc analysis of the left ROIs revealed that the ALG (corresponding to the dorsal posterior insula) showed a marginally significant activation that was higher for gastric attention than for cardiac attention ($F_{1, 30}$ = 3.83, corrected p = .059). Post-hoc analysis of the right ROIs also revealed that the right ASG and MSG exhibited higher activation for cardiac attention than for gastric attention ($F_{1, 30}$ = 5.93, corrected p = .021; $F_{1, 30}$ = 6.57, corrected p = .016, respectively) while a marginally significant activation, higher for gastric attention, was found in the ALG ($F_{1, 30}$ = 4.13, corrected p = .051).

Furthermore, we found differences in the averaged activation between interoceptive and exteroceptive attention; the ANOVA on activations in the left insula revealed significant effects of anatomical location ($F_{5, 150}$ = 52.71, p < .001, η^2_p = .64), and the interaction between condition and location ($F_{5, 150}$ = 13.45, p < .001, η^2_p = .31). Post-hoc analysis showed that the left MSG and PSG were more activated by interoceptive attention ($F_{1, 30}$ = 7.38, p = .011, η^2_p = 20; $F_{1, 30}$ = 18.70, p < .001, η^2_p = .38, respectively). The ANOVA on the right insula activation revealed significant effects from anatomical location ($F_{5, 150}$ = 41.02, p < .001, η^2_p = .58), and interaction between condition and location ($F_{5, 150}$ = 12.23, p < .001, η^2_p = .28), as well. We found that exteroceptive attention activated the right ASG more than interoceptive attention did, by post-hoc analysis ($F_{1, 30}$ = 10.28, p = .003, η^2_p = .26).

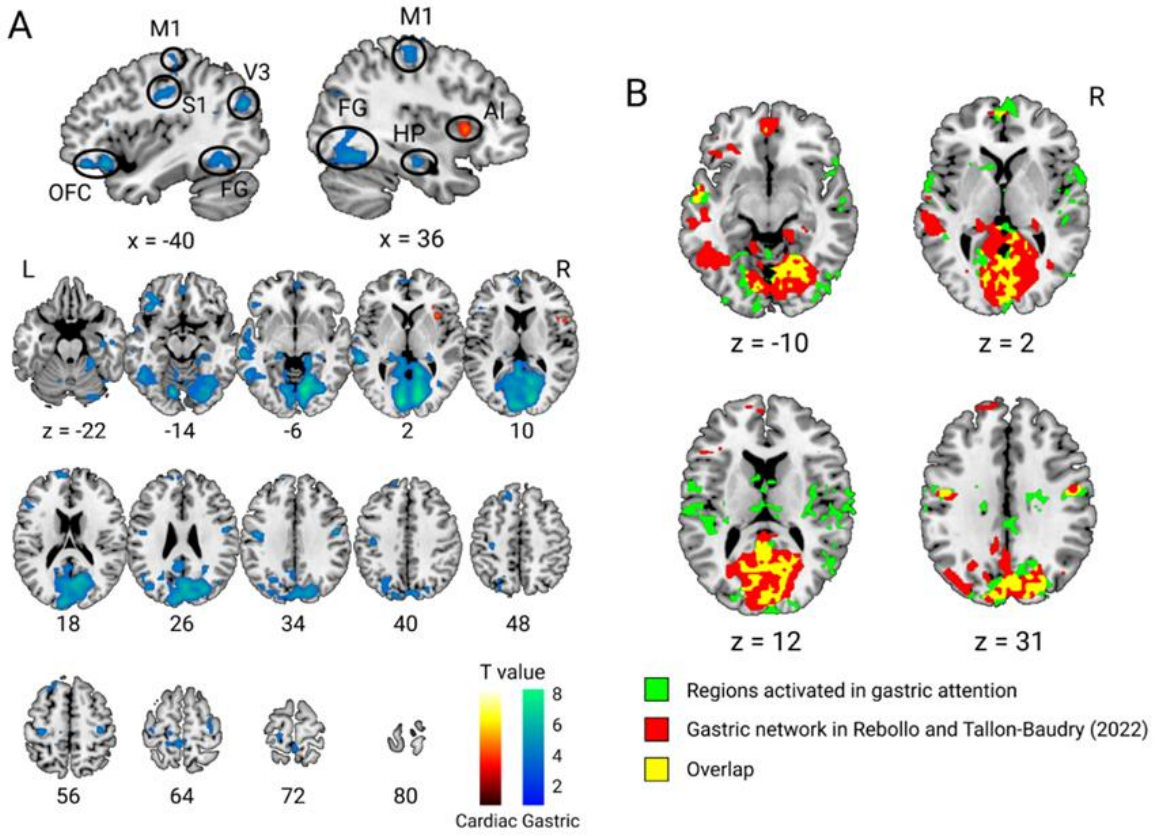

Figure 5. Whole-brain activation for cardiac and gastric attention. A). Significant activation in cardiac attention contrasted with gastric attention (warm color) and vice versa (cold color) are depicted with a height threshold of $p < .001$ (uncorrected) and an extent threshold of $p < .05$ (corrected for family-wise error, corresponding to more than 42 voxels). Sagittal views show that attention to cardiac and gastric sensations activated the brain region relevant to each interoceptive awareness. The sensorimotor regions (S1: primary sensory, M1: primary motor, V3: visual area 3, FG: fusiform gyrus), orbitofrontal cortex (OFC), and hippocampus (HP) showed enhanced activation in gastric attention, while the right anterior insula (AI) was activated in cardiac attention. B). The internally extended visual area that was activated in gastric attention largely overlapped with the brain regions that have been shown to couple with the gastric basal rhythm (Rebollo and Tallon-Baudry, 2022; https://neurovault.org/collections/9985/). L, left hemisphere; R, right hemisphere. All figures are shown in axial slices with z and sagittal slices with x denoting locations in the Montreal Neurological Institute coordinates.

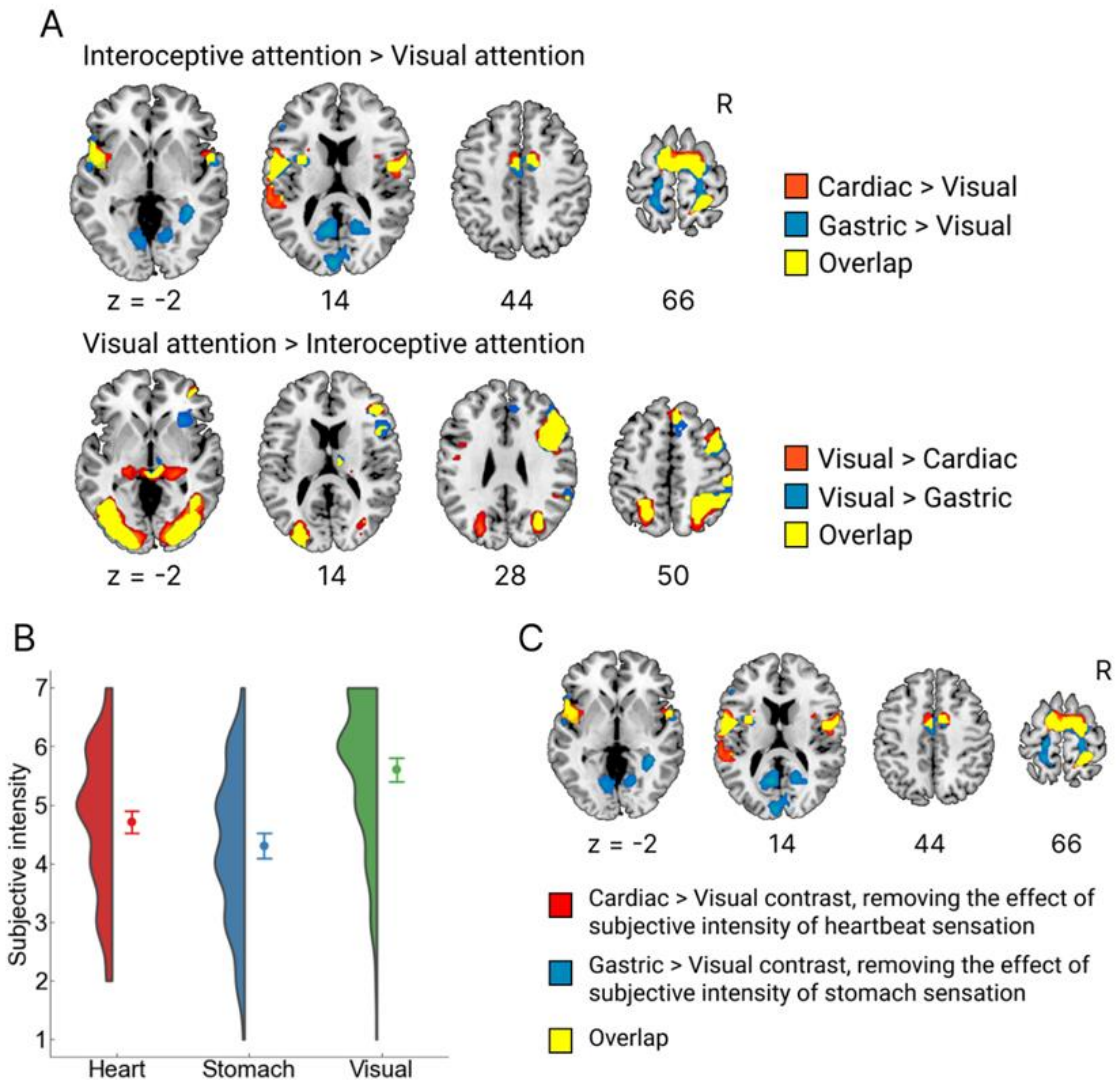

Figure 6. Brain activation for cardiac and gastric attention compared with the control. A). When compared with the visual attention condition, cardiac and gastric attention showed similar activation patterns, such as activations in the insula and supplementary motor areas and deactivations in the right middle frontal, superior parietal, posterior thalamus, and lateral visual association areas. However, activations in the medial visual cortex and hippocampus were found only in gastric attention, compared with visual attention. The height threshold was set to $p < .001$ (uncorrected) with an extent threshold of $p < .05$ (corrected for family-wise error), corresponding to more than 52 voxels. B). The distribution and mean scores of the subjective reports of stimulus intensity are plotted separately for each condition. Participants reported the intensity at the end of the scanning runs for each condition, yielding 155 datasets (31 participants for 5 runs) for each condition. Our maximal linear mixed-effects model analysis revealed that the visual stimulus (slight change in word color) was rated the most intense (regression coefficient compared to heart = 0.90,

$t_{30.00}$ = 4.51, p < .001) and the stomach sensation was rated the least intense (regression coefficient = -0.41, $t_{30.00}$ = -2.22, p = .034). Error bars show the 95% confidence intervals while the half-violin plot represents the kernel density estimation. C). The brain activation underlying cardiac and gastric interoceptive awareness did not vary as a function of the subjective report of the stimulus intensity. We performed the analysis covariance that excluded the effect of the subjective reports from brain activation, revealing almost the same activation patterns compared with the activations reported in A). The height threshold was set to p < .001 (uncorrected) with an extent threshold of p < .05 (corrected for family-wise error), corresponding to more than 52 voxels. R, right hemisphere. All figures are shown in axial slices with z denoting locations in the Montreal Neurological Institute coordinates

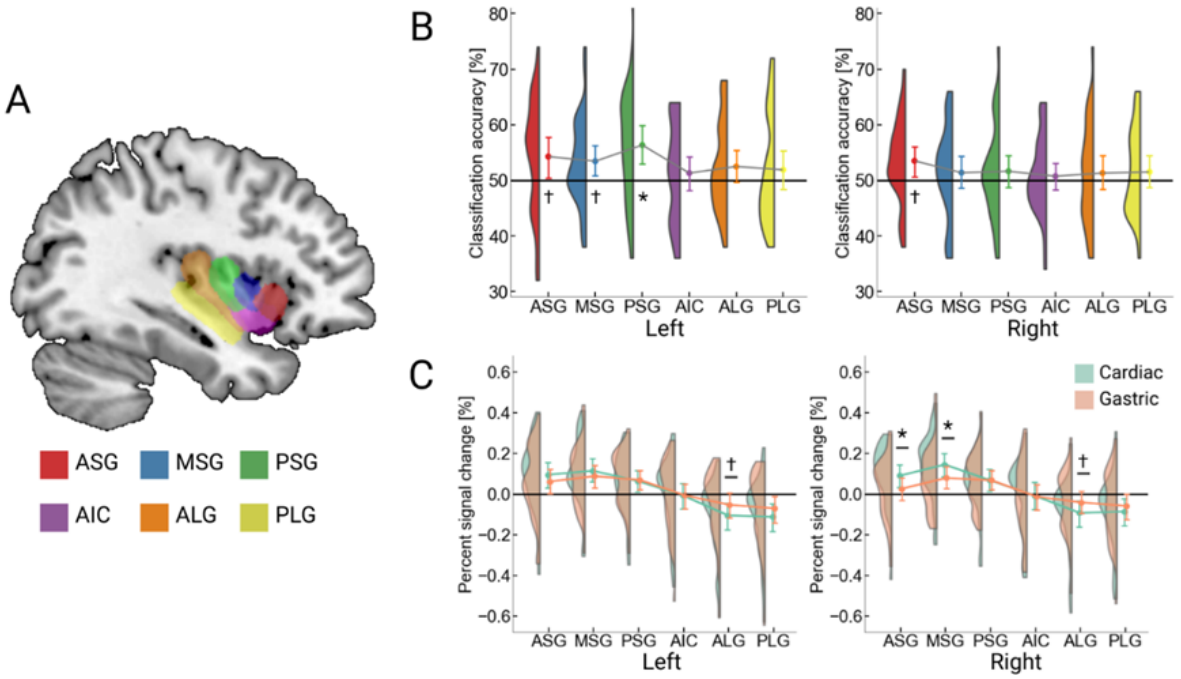

Figure 7. Comparison of activations for cardiac and gastric attention in the subdivisions of insula. A). The anatomical subdivisions of the insula (Faillenot et al., 2017) are presented. We adopted six regions (the anterior short gyrus: ASG, middle short gyrus: MSG, posterior short gyrus: PSG, anterior insular cortex: AIC, anterior long gyrus: ALG, and posterior long gyrus: PLG) for both hemispheres. B). The results of multivoxel pattern analysis are depicted, with the left panel showing the results of the left insula subdivisions and the right panel showing the right insula. The left MSG exhibited significantly higher classification accuracy above the 50% chance level. A marginally significant classification accuracy i.e., $p < .1$, was observed in the right ASG, left ASG, and left MSG. The point plot represents the mean classification accuracy with a 95% confidence interval, while the half-violin plot represents the kernel density estimation. C). The results of direct comparison of the signal strength between cardiac and gastric attention are plotted. Post-hoc analysis of repeated-measures analysis of variance revealed that the right ASG and MSG showed significantly higher activation in cardiac than gastric attention. There was a marginally significant effect that implies stronger activation in gastric than cardiac attention in the left ALG and right ALG. The point plots represent the mean signal change, with 95% confidence interval, while the half-violin plot represents the kernel density estimation (green for cardiac, orange for gastric attention). * $p < .05$; † $p < .10$ (corrected for false discovery rate).

Discussion

Our results empirically showed that cardiac and gastric interoceptive awareness had similar but distinct neural substrates. Direct comparisons of brain activations revealed that interoceptive attention to heart and stomach sensations activated similar brain regions, including the insula, frontal operculum, parietal operculum, middle cingulate, and supplementary motor area, in contrast to the control visual attention. However, compared to gastric attention, cardiac attention activated the right anterior insula extending to the frontal operculum more; gastric attention enhanced activations in the occipitotemporal visual cortices, bilateral primary motor, primary somatosensory, left orbitofrontal, and bilateral posterior hippocampus. Moreover, our MVPA-based ROI analyses revealed that the left middle-anterior insula had distinct neural representations for cardiac and gastric interoceptive attention.

Previously, heartbeat perception has been studied as a representative of interoceptive awareness in general, suggesting the right anterior insula as the most relevant region for the generation of subjective experiences of internal bodily states (Craig, 2009; Critchley and Garfinkel, 2017). We, however, found that cardiac attention activated the right anterior insula more than gastric attention did, suggesting that the right anterior insula may predominantly code cardiac interoceptive awareness, rather than interoceptive awareness arising from other sources e.g., gastric. In line with this idea, the most consistent activation in the right insula has been found by a meta-analysis focusing on cardiac interoceptive attention (Schulz, 2016). Furthermore, previous studies have found a robust correlation between individual accuracy of heartbeat perception and heightened activation of the right anterior insula (Critchley et al., 2004; Pollatos et al., 2007; Caseras et al., 2013; Haruki and Ogawa, 2021), but this was not the case for awareness of breathing (Wang et al., 2019) or skin conductance (Baltazar et al., 2021). The activation dominance of the right anterior insula may be explained by the functional roles of cardiac interoceptive awareness: people can notice increased arousal with heartbeat perception (Paulus et al., 2019). The right insula appears essential to perceive arousal as resection of the region causally diminishes physiological and emotional arousal (Terasawa et al., 2021; Holtmann et al., 2022). Moreover, presenting accelerated cardiac feedback increases perceived physiological arousal (Story and Craske, 2008) and, more importantly, activates the right anterior insula (Gray et al., 2007; Kleint et al., 2015). These

findings, in conjunction with the present results, imply that cardiac interoceptive awareness closely involves physiological arousal and thus activates the right anterior insula by merely focusing on cardiac sensation. To sum up, the relationship between the right anterior insula and interoceptive awareness appears stronger in cardiac interoceptive awareness than in other modalities; such dominance of the cardiac domain may reflect the functional role of cardiac interoceptive awareness, which informs physiological arousal.

We also found that the brain regions underlying gastric interoceptive awareness encompassed the visual cortex. The involvement of the visual cortices in attention to stomach sensations appears puzzling, but converging evidence suggests a strong connection between the visual cortex and stomach function. Recently, Rebollo and colleagues found temporally delayed connectivity between brain activity and the intrinsic electrical rhythm generated by the stomach, which included the occipitotemporal visual cortices in addition to the somatosensory and motor areas (Rebollo et al., 2018; Rebollo and Tallon-Baudry, 2022). Crucially, the visual areas activated in the current experiment largely overlapped with the clusters included in the gastric network. Other past research showed that electrical or vibration stimuli on the stomach evoked neural activation in the occipital area in rats (Cao et al., 2019), cats (Pigarev et al., 2013), and even humans (Mayeli et al., 2023). Considering all these reports, it can be suggested that gastric functions are strongly tied to the visual cortex; here, we demonstrated that interoceptive attention to the stomach, which elicits gastric interoceptive awareness, activates the visual cortex even without direct stimulation of the stomach.

The reason for the involvement of the visual area may be that gastric signaling, and its subjective awareness, are closely related to foraging and feeding behavior that requires the integration of visuospatial information with energy status and motor coordination (Kanoski and Grill, 2017; Rebollo et al., 2021a). For example, hungry people would change their sensory sampling and behavior in the external world to maximize the chance of food consumption. The current results support this idea; we observed activation related to gastric attention in the left orbitofrontal cortex, bilateral hippocampus, primary motor cortex, and the visual areas, which are all associated with food intake. For example, the orbitofrontal cortex has been suggested to modulate eating behavior by encoding the nutritional and reward values for food or food cues (Seabrook and Borgland,

2020). A meta-analysis of fMRI studies, including viewing food pictures compared with non-food pictures, indicated that the left orbitofrontal cortex was most consistently activated for visual food stimuli (van der Laan et al., 2011). Furthermore, the role of the hippocampus in controlling food intake and regulating energy status has received considerable attention in the past few years (Suarez et al., 2019; Quigley et al., 2021); recent evidence indicates that the human hippocampus encodes ongoing nutritional states in response to food cues (Jones et al., 2021). Based on these findings, we consider that neural responses to gastric interoceptive awareness could be encoded in relation to food intake, which was activated by focusing on stomach sensations without any stimulation or food-related cues in the present study.

The present ROI analyses revealed that cardiac and gastric interoceptive attention had distinct representations in the insula. Only the right ASG and MSG, corresponding to the dorsal anterior insula, showed higher activation in cardiac than gastric attention; in the right mid-posterior and left insula, there was no activation difference. Nevertheless, we identified the left PSG, corresponding to the dorsal middle insula, in different activation patterns for cardiac and gastric attention. These results elaborate on how interoceptive awareness is represented in the human insula; in particular, we suggest, for the first time, that the left middle insula codes viscera-specific interoceptive awareness. Interestingly, the posterior insula did not show separable activation for cardiac and gastric attention, nor higher activation than baseline. Researchers have considered the posterior insula as the “primary” interoceptive cortex as it receives an initial cortical input of visceral signals (Craig, 2002; Evrard, 2019). The current inactivity of the posterior insula may support its role in encoding ongoing changes in bodily signals (Craig et al., 2000; Meier et al., 2018), rather than a subjective awareness of bodily states. This is because, in the interoceptive attention task, participants must have interoceptive awareness without homeostatic perturbation. Together, our ROI analyses would support the gradual processing of bodily signals in the insula along the posterior-anterior axis (Craig, 2009): the posterior codes physical changes in the signal while interoceptive awareness would be represented in the middle-anterior insula.

Unfortunately, we did not record any physiological data during the fMRI scanning, potentially limiting the current study. Simultaneous recording of electrocardiograms (ECGs) and electrogastrograms would address the

interaction between brain activation and physiological changes evoked by interoceptive attention. However, we believe the lack of physiological recording does not challenge the validity of the present study because past research indicated that cardiac parameters (heart rate and ECG amplitude) did not differ by directing attention between interoceptive and exteroceptive signals (Petzschner et al., 2019). On a related note, previous studies suggested that external processes, such as cutaneous sensations, could affect interoceptive awareness (particularly in the cardiac domain) (Khalsa et al., 2009). Although we asked participants to focus on their internal sensations, we could not completely rule out the possibility that participants felt the heartbeat sensation from their skins. However, in the first place, interoceptive awareness may not arise solely from a single visceral sensation, such as when heartbeat perception is felt with the contraction of blood vessels and beating of the heart or hunger is mediated by both the physical contents of the stomach and a chemical signal. If so, researchers may benefit from isolating the neural substrates of cardiac and gastric interoceptive awareness localized in the present study from visceral topography to reveal the process of (visceral) multisensory integration. Another possible limitation is that the difference in task difficulty in each condition could affect the results. Although we tried to make the difficulty comparable for each condition, the task condition had a significant effect on the subjective intensity of stimulus; the subjective intensity of the visual stimulus was rated the highest while that of the stomach sensation was the lowest. We therefore performed another analysis that excluded the effect of the subjective rating of stimulus intensity, finding that brain activation was almost unaffected by individual differences in the subjective ratings. The results support our original idea that the present brain activation was elicited by the subjects (the heartbeat and stomach sensations) of attentional focus not by the difference in task difficulty. Recording a trial-by-trial fluctuation of the subjective intensity of stimuli would strengthen the present findings that the subjective differences in interoceptive awareness are encoded differently in the brain.

All the participants of this study were healthy adults aged between 20 and 31 whose native language was Japanese. However, we consider the present results to be replicable in other countries in healthy young adults because the brain activations induced by cardiac attention were comparable to that of previous studies conducted in Europe and the U.S. (Caseras et al., 2013; DeVille et al., 2020). The stimulus used in the present experiment was a single word in English;

therefore, we expect the results to be generalizable to healthy young adults as long as they understand the meaning of the word. The participants performed the task while they were lying in a supine position in an MRI scanner. Thus, it could be argued that the differences in brain activation of cardiac and gastric attention may be specific to interoceptive awareness in a supine position. We have no reason to believe that the results depend on other characteristics of the participants, materials, or context.

Interoceptive Awareness Affected by Other Sensory Modalities

Research Background

My research, particularly within the "Interoceptive Awareness Affected by Other Sensory Modalities" section, focuses on unraveling the relationship between interoceptive awareness and exteroceptive inputs. This line of inquiry is anchored in the predictive coding framework, which posits perception as an outcome of perceptual inference, wherein the brain assigns precision weightings to sensory signals from all modalities, indicating a potential for significant interaction between interoceptive (internal bodily states) and exteroceptive (external environmental) information (Hohwy, 2012).

The interaction between interoceptive and exteroceptive inputs is a dynamic process influenced by both predictive mechanisms and attentional modulation. Predictive coding provides a unique lens through which to view the integration of different sensory modalities within a unified perceptual system. This integration can lead to either interference or facilitation effects, depending on how the brain prioritizes and weights these sensory signals (Feldman and Friston, 2010; Ainley et al., 2016; Corcoran et al., 2020). My research explores this dynamic interplay, particularly examining how external sensory inputs, such as auditory stimuli, can influence the awareness of internal bodily states. This research is pivotal in enhancing our understanding of how the brain optimises diverse sensory information via attention, challenging traditional views of sensory processing as isolated within specific modalities.

The first study in this series (Experiment 3) marks a significant stride in exploring the dynamic relationship between attentional enhancement of interoceptive signals and manipulated predictions about them. Central to this experiment is the investigation of how externalized interoceptive cues, particularly auditory feedback correlating with cardiac activity, impact interoceptive attention and awareness. This study is designed to uncover the influence of external auditory stimuli, which are synchronized with an individual's heartbeat, on the perception of internal bodily states. The objective is to understand how these subjective experiences, when influenced by externally presented interoceptive stimuli, can

alter our internal sensory perceptions, expanding on the previous studies that associated prior knowledge about their bodily information with interoceptive awareness (Murphy et al., 2018b; Körmendi et al., 2021). The methodology employed in this experiment is centered around a cardiac feedback paradigm (Gray et al., 2007; Kuřátková et al., 2019). This approach probes how variations in the timing of auditory feedback, in relation to the actual heartbeat, can affect an individual's perceptions of both the heartbeat itself and the externalized sounds. This experimental design directly ties into the overarching thesis that interoceptive awareness is an integrative product, significantly influenced by both external stimuli and subjective experiences. The results from this study are expected to demonstrate that predictive coding extends beyond the neural substrates of attention, encompassing a more comprehensive integration of external cues into the perception of interoceptive awareness.

Specifically, by manipulating the temporal alignment of auditory feedback with actual heartbeats, Experiment 3 seeks to observe the extent to which these externally presented stimuli can influence an individual's perception and judgment of their internal bodily state. This method provides a novel way to assess the malleability of interoceptive awareness, particularly in the context of how external cues, closely matching the timing of intrinsic bodily signals, can modify our perceptions of internal states. It would challenge the traditional notion that perceptions might solely depend on the sequential processing of sensations. The findings from this experiment are expected to contribute significantly to the field of cognitive neuroscience, offering new insights into the complex interplay between external stimuli and internal bodily awareness.

My research further extends into Experiment 4, which examines the potential interference effect of auditory distractions on interoceptive awareness. The primary objective of this study is to determine whether external auditory stimuli, which are unrelated to interoceptive sensations, can disrupt or modify heartbeat perceptions. This inquiry is particularly significant as it might challenge the boundaries of traditional perceptual models by evaluating if and how external sensory inputs lead to perceptual outcomes. The experiment utilizes the heartbeat counting task (Schandry, 1981; Garfinkel et al., 2015), requiring participants to concentrate on their internal interoceptive sensations while facing external auditory distractions. This setup provides an ideal scenario to explore the interplay between interoception and exteroception, particularly the

interference caused by external stimuli on internal bodily awareness. In this experiment, simple tone sounds are introduced as distractors, offering highly precise auditory sensations in contrast to the less precise interoceptive sensations. This contrast is critical in testing the hypothesis that the presence of these precise external auditory sensations could attenuate interoceptive awareness. This approach aligns with the predictive coding framework, which postulates that the brain continuously adjusts the precision of sensory information. Furthermore, the study also hypothesizes that individual differences, such as variations in heart rate variability and subjective sensitivity to interoception, will modulate how these distractor effects impact interoceptive awareness.

Previous findings in this area have provided a foundation for the current study. Research has shown that perceptions are intertwined, with heartbeat pulsations between interoception and exteroception, for instance, known to reduce somatosensory sensitivity and suppress visual information sampling (Al et al., 2020; Galvez-Pol et al., 2020, 2022c). This interplay, in turn, suggests that attentional enhancement of interoceptive sensations is necessary for heightened awareness of internal states, yet it remains vulnerable to interference from precise signals of other sensory modalities. Despite these insights, there is a notable gap in evidence regarding the direct disruption of interoceptive attention and awareness by external distractors. Consequently, this experiment aims to fill this gap by directly investigating the effects of sensory distractors on interoceptive attention and awareness, expanding upon previous research that primarily focused on the differences in attentional mechanisms between interoception and exteroception (Mirams et al., 2012; García-Cordero et al., 2017).

The series of experiments conducted in this research endeavor collectively strive to elucidate a detailed understanding of how interoceptive awareness is influenced by and intertwined with other sensory modalities. The core aim is to explore and illuminate the interactions between internal bodily sensations and external sensory inputs. By rigorously examining these dynamics, the research sheds light on a unified mechanism through which the brain processes and interprets a wide range of sensory information. This approach is pivotal in advancing our understanding of the human cognitive system, particularly within the context of the predictive coding framework. These insights are invaluable in enhancing our comprehension of sensory processing, moving beyond traditional

models that often view each sensory modality as a distinct and separate entity.

Experiment 3

Introduction

In the initial phases of my research, Experiments 1 and 2 provided insights into the neural mechanisms behind the modulation of attention in interoceptive processing. These explorations revealed a complex interplay between the ascension of bottom-up bodily sensations and the crucial descent of top-down predictive signals (Hohwy, 2012; Clark, 2013). Such a dichotomy forms the bedrock of our perceptual experiences, shaping the subjective beliefs about our bodily states, as highlighted by Paulus et al. (2019). This interplay, intricate in its nature, underscores the dynamic balance between the physiological underpinnings of our body and the cognitive interpretations we construct about these sensations.

Building upon this understanding, the Experiment 3, embarks on a more sophisticated exploration, one that probes deeper into the manipulated perceptions and altered beliefs. Inspired by the innovative methodologies in the field of real-time biofeedback, as pioneered by Gray et al. (2007) and Iodice et al. (2019), this experiment investigates the perceptual modulation in interoceptive awareness via external stimuli. Real-time biofeedback, a technique of providing individuals with false feedback about their physiological states, serves as a powerful tool to test the malleability of our interoceptive perceptions. It enables us to observe how external cues, when cleverly disguised as intrinsic bodily signals, can shape and even alter our perceptions of internal bodily states (Story and Craske, 2008; Kleint et al., 2015).

In this experimental framework, I specifically employed a cardiac feedback paradigm. The paradigm involved manipulating the temporal alignment of auditory feedback with the participants' actual heartbeats. Participants were exposed to auditory cues that either synchronized with their heartbeats or were deliberately offset. This manipulation allowed us to observe the extent to which externally presented stimuli could influence an individual's perception and judgment of their internal bodily state. The hypothesis was grounded in the understanding that interoceptive perception is not a static, unidirectional process solely dictated by internal physiological states but is a dynamic interplay influenced by external sensory inputs (Apps and Tsakiris, 2014; Ainley et al., 2016).

The experiment aimed to explore several layers of this interplay. Firstly, it sought to understand how the synchronization or lack thereof between the external auditory cues and the internal rhythm of the heart impacted the perception of one's heartbeat. Secondly, it aimed to investigate the cognitive processes involved in reconciling or differentiating between these external and internal cues. The experiment was particularly focused on understanding how the brain processes and integrates these distinct sources of information, and how this integration or disintegration influences the overall experience of interoception.

The findings from this study are expected to make a significant contribution to our understanding of interoceptive processes. By examining the cognitive and perceptual mechanisms underpinning our sense of internal bodily awareness, and how these can be influenced or altered by external stimuli, the study extends the boundaries of current knowledge in the field of interoception. It provides a unique perspective on the interplay between bottom-up physiological signals and top-down cognitive interpretations, offering a deeper understanding of the subjective nature of bodily awareness. Through this exploration, the study sheds light on the malleability of interoceptive perception and opens up new avenues for understanding the complex relationship between our bodies and our minds.

Materials and Methods

Participants. In this study, we enlisted a diverse cohort of 20 undergraduate students from Hokkaido University, comprising 16 men and 4 women, to participate in our experimental investigation. The age range of these participants was between 19 and 23 years, with a mean age of 21.65 and a standard deviation of 1.09 years. To ensure a comprehensive understanding and voluntary participation, we obtained written informed consent from each participant. This process was crucial for maintaining ethical standards and adhering to the principles outlined in the Declaration of Helsinki, which emphasizes the importance of voluntary participation, informed consent, and the right to withdraw at any time. The study protocol underwent meticulous scrutiny and received approval from the Ethics Committee of Hokkaido University, ensuring that our experimental design and procedures adhered to the highest ethical standards.

Heartbeat Counting Task. Participants completed the heartbeat counting task that assesses individual interoceptive accuracy (Schandry, 1981; Garfinkel et al., 2015) (Figure 8A). This task was conducted in a controlled environment where each participant was comfortably seated at a desk, with both arms resting on the surface of desk. Participants were provided with clear instructions about the task's purpose and process. To ensure precise monitoring of their heartbeats, we equipped each participant with a pulse oximeter, specifically the IWS920 model from Tokyo Devices, attached to their left ring finger. The placement and positioning of the participants were carefully adjusted to prevent any external detection of blood flow, such as through the fingers, buttocks, or back, thereby focusing solely on the internal sensation of their heartbeat. Participants were instructed to silently count the number of heartbeats they perceived within specific time intervals, which varied across four trials: 25, 35, 45, and 55 seconds. This variety in durations was strategically chosen to assess the consistency and reliability of their interoceptive awareness under different time constraints. Participants were explicitly advised against using any external aids such as taking their pulse or estimating the heartbeat count, as these methods could potentially influence their interoceptive accuracy. Following each trial, participants were asked to report their confidence in their performance on a Likert scale ranging from 1 (not at all confident) to 7 (completely confident). This self-assessment provided additional insight into their subjective perception of their interoceptive

abilities.

To calculate the interoceptive accuracy for each participant, we employed a specific formula that took into account their reported heartbeat counts and the actual durations of each trial as follows:

$$Interoceptive\ accuracy = 1 - \left(\frac{|Recorded\ Number\ of\ Heartbeats - Counted\ Number\ of\ Heartbeats|}{Counted\ Number\ of\ Heartbeats}\right)$$

This method allowed us to quantitatively evaluate their accuracy in perceiving internal bodily states. Additionally, we computed the interoceptive confidence as an average score across the four trials, providing a measure of their self-perceived proficiency in the task. The combination of these quantitative and qualitative assessments offered a comprehensive understanding of each participant's interoceptive abilities, laying the groundwork for further exploration of the relationship between interoception and perceptual processes in our subsequent experiments.

Auditory Cardiac Feedback Task. In the Auditory Cardiac Feedback Task, the primary objective was to investigate how individuals perceive externally generated heartbeat sounds and how this perception impacts their overall awareness of their own heartbeat. The task involved presenting participants with artificial heartbeat sounds that were either synchronized or asynchronous with their actual heartbeats (Figure 8A, B). To assess their perception, participants were required to judge whether the presented sound corresponded to "their heartbeat" by comparing it to their bodily sensations. The study aimed to explore potential changes in subjective experiences related to externalized heartbeat sounds and heartbeat perception when manipulating the characteristics of the feedback sounds. The experimental procedure consisted of a single task trial, which included consecutive rest and feedback sessions, each lasting for five minutes. During the rest session, participants were instructed to keep their eyes open, remain still, and refrain from engaging in any specific thoughts. Subsequently, the feedback session commenced with a verbal cue from the experimenter, during which artifactual heartbeat sounds were continuously delivered via headphones. Immediately after the feedback session, participants assessed whether the sounds were synchronized with their actual heartbeats. Additionally, participants provided ratings on the degree of synchronization with their own heartbeats, the perceived strangeness of the sounds, the intensity of

their actual heartbeats, their arousal level during the feedback session, and whether they felt an entrainment of their actual heartbeats by the artificial sounds. A Likert scale ranging from -3 (not at all) to 3 (completely) was employed for these subjective assessments.

The study encompassed three distinct types of task trials: true feedback, accelerated feedback, and other's feedback. In the true feedback session, the presented artifactual heartbeat sound was synchronized with the systole (cardiac ejection) period, a time frame in which individuals are more likely to perceive their heartbeats. The synchronization algorithm followed a previously established method (Suzuki et al., 2013) that estimated the timing of each heartbeat (cardiac R-wave) based on the average period of the preceding ten pulse wave peaks. This calculation was necessary because the cardiac R-wave precedes a pulse waveform peak by approximately 350 ms, and the systole period corresponds to a range of 200–250 ms after the R-wave (Brener and Ring, 2016). In the accelerated feedback session, the presentation of artifactual sounds was achieved by adjusting the estimated timing of each heartbeat to be faster, approximately 130% of the original rate. In the other's feedback session, the sound was presented using the pulse waveform time series of the experimenter's own heartbeat (64 bpm), which had been recorded prior to the experiment. Importantly, participants were unaware of the type of feedback they were receiving or the existence of accelerated and other's feedback conditions. The order of the task trials was pseudo-randomized prior to each participant's involvement in the study.

In addition to collecting subjective reports, the study also incorporated the measurement of individual physiological data during each task trial. Pulse oximetry signals obtained during the trials were subjected to detailed analysis using the HeartPy module in Python (van Gent et al., 2019). The raw pulse waveform was initially preprocessed to eliminate any erroneous peak detections. Subsequently, the peak-to-peak time series data were used to estimate the heart rate and the high-frequency component of heart rate variability (HF-HRV). Root mean square of successive difference (RMSSD) was employed as an index of HF-HRV. Both heart rate and RMSSD were computed for both rest and feedback sessions within each trial. The difference between the rest and feedback session values was utilized as an indicator of the effect of feedback types on individual physiological changes.

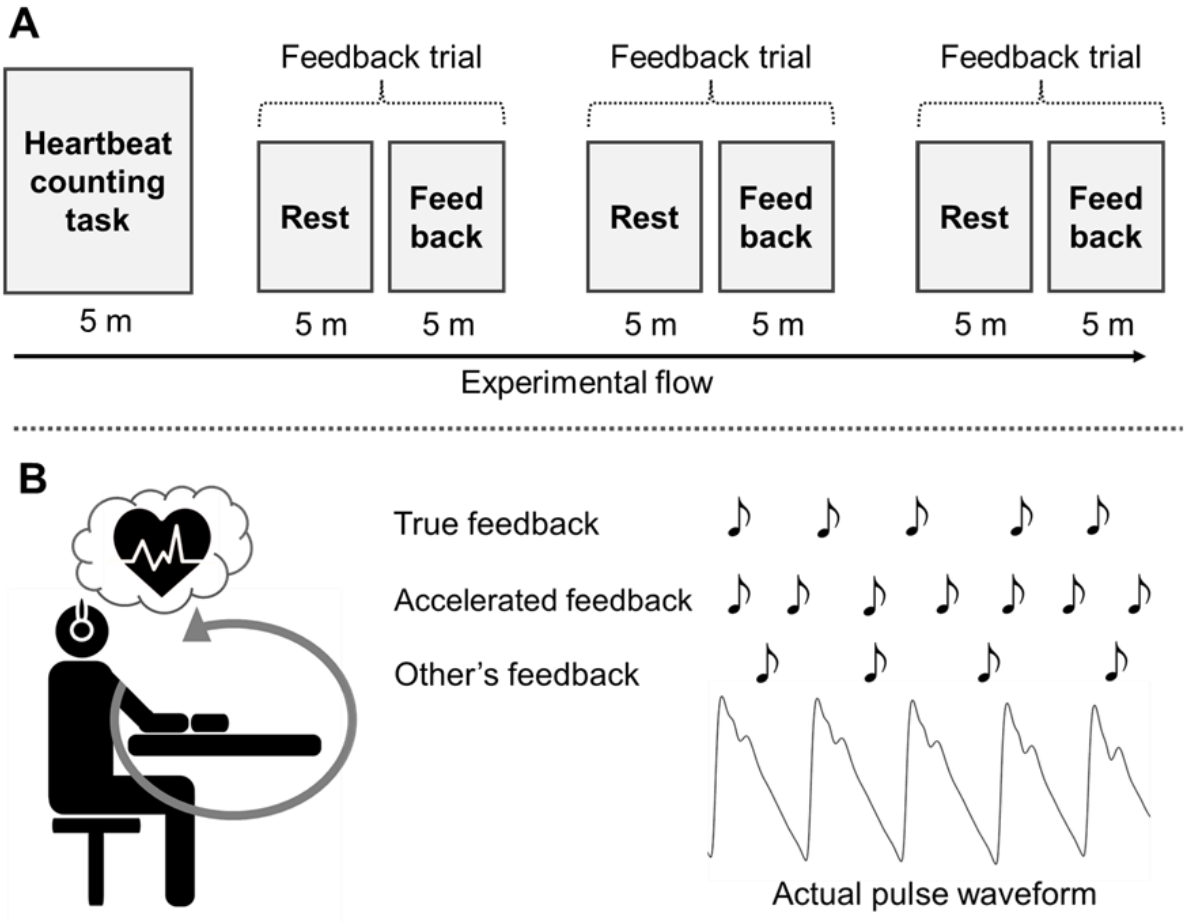

Figure 8. Schematical presentation of the experimental flow and cardiac feedback trial. A) The time course of experimental flow is presented. Immediately after each feedback trial, participants rated subjective experience regarding the artifactual sounds and their heartbeat. The order of the types of feedback (true, accelerated, and other's) was randomized for each participant. B) Example of cardiac feedback task is presented. Phonetic symbols represent the feedback timing in relation to a pulse timing.

Statistical analysis. I used JASP (https://jasp-stats.org/, version 0.16) for the statistical analyses. Firstly, I conducted a generalized linear mixed model (GLMM) analysis with the judgement of the artifactual sound's attribute as a dependent variable (mine or not mine). Specifically, I examined whether the types of feedback or the subjective experience would decide the judgement by comparing three models that differed in independent variables: the first model with the feedback types as an independent variable, the second with subjective ratings of synchronization and strangeness, and the third with the feedback types and subjective ratings of synchronization and strangeness. Random effects included the effects of each participant in these models.

Secondary, I conducted a one-way analysis of variance (ANOVA) for subjective synchronization of the artifactual sounds, the strangeness of the sounds, intensity of the actual heartbeats, feeling of entrainment, arousal, and change in the heart rate and RMSSD with the feedback type as the main factor. Because I performed the ANOVA seven times, a significance level was corrected based on Benjamini and Hochberg's false discovery rate (FDR) (Benjamini and Hochberg, 1995).

Thirdly, I conducted a Bayesian correlation analysis across behavioral outcomes obtained from the auditory cardiac feedback task and heartbeat counting task. All variables were used regardless of the type of feedback task. Pearson's correlation coefficient was calculated for each pair; then, the Bayes factor (BF10) was calculated using a default prior scale of JASP for each coefficient. The Bayes factor is a likelihood ratio of the marginal likelihood of two competing hypotheses (existing/no correlation). Based on Harold Jeffreys's criteria, I considered $BF_{10} > 10$ as strongly supporting the existence of correlation and $BF_{10} < 0.1$ as supporting no correlation.

Results

In our study, the primary aim was to discern the relative contributions of feedback type and subjective experience in shaping participants' judgments about the attribution of artifactual heartbeat sounds. To this end, we conducted a comprehensive analysis comparing three Generalized Linear Mixed Models (GLMMs). The first model (Model 1) considered only the type of auditory feedback (true, accelerated, or other's) as the independent variable. The second model (Model 2) focused on subjective ratings of the synchronization and strangeness of the sounds. The third model (Model 3) combined both the feedback type and subjective ratings as independent variables. Each model included random effects to account for individual differences among participants.

Our analysis revealed that Model 2, which emphasized subjective experiences of synchronization and strangeness, provided the best fit for our data based on Akaike's Information Criteria (Table 4). In this model, both subjective synchronization (Marginal Mean [MM] = 1.89, 95% Confidence Interval [CI] = [1.00, 4.15], p = .001) and strangeness (MM = -0.78, 95% CI = [-2.60, -0.12], p = .03) significantly and independently influenced participants' judgments. Model 3, which included both feedback types and subjective experiences, also showed significant effects for subjective synchronization and strangeness, but no significant influence from the feedback types themselves. Interestingly, Model 1, which only accounted for feedback types, demonstrated a significant contribution from the true feedback condition alone (MM = 1.46, 95% CI = [0.18, 2.86], p = .03). These findings suggest that participants' subjective experiences, rather than the objective timing of feedback, predominantly guided their judgments regarding the sounds.

To further explore the impact of feedback types on subjective experiences, we performed a one-way Analysis of Variance (ANOVA) for each subjective measure. The main effect of feedback type was significant only for the subjective strangeness of the artifactual sounds ($F_{(2, 38)}$ = 9.14, η^2_p = .33, p < .001) (Figure 9). Participants reported feeling significantly stranger about the artifactual heartbeat sounds in both the accelerated and other’s feedback trials compared to the true feedback (accelerated feedback: $t_{(19)}$ = 3.53, Cohen’s d = 0.79, p = .003; other's feedback: $t_{(19)}$ = 3.95, d = 0.88, p < .001). A subsequent GLMM analysis, incorporating both feedback types and judgments of the sound's attributes,

affirmed the significant impact of feedback types on subjective strangeness, even when accounting for participants' judgments.

Moreover, the correlation analysis across all behavioral measures revealed several significant relationships. There was strong evidence for a correlation between subjective synchronization and strangeness (r = -.43, BF_{10} = 45.75), strangeness and arousal (r = .39, BF_{10} = 18.07), and between subjective intensity of actual heartbeats and interoceptive accuracy (r = -.46, BF_{10} = 128.91). A particularly noteworthy correlation was observed between interoceptive accuracy and confidence (r = .61, BF_{10} = 56332.80), suggesting a close relationship between these two aspects of interoceptive processing. However, no strong evidence was found supporting the non-existence of any correlations ($BF_{10} < 0.1$).

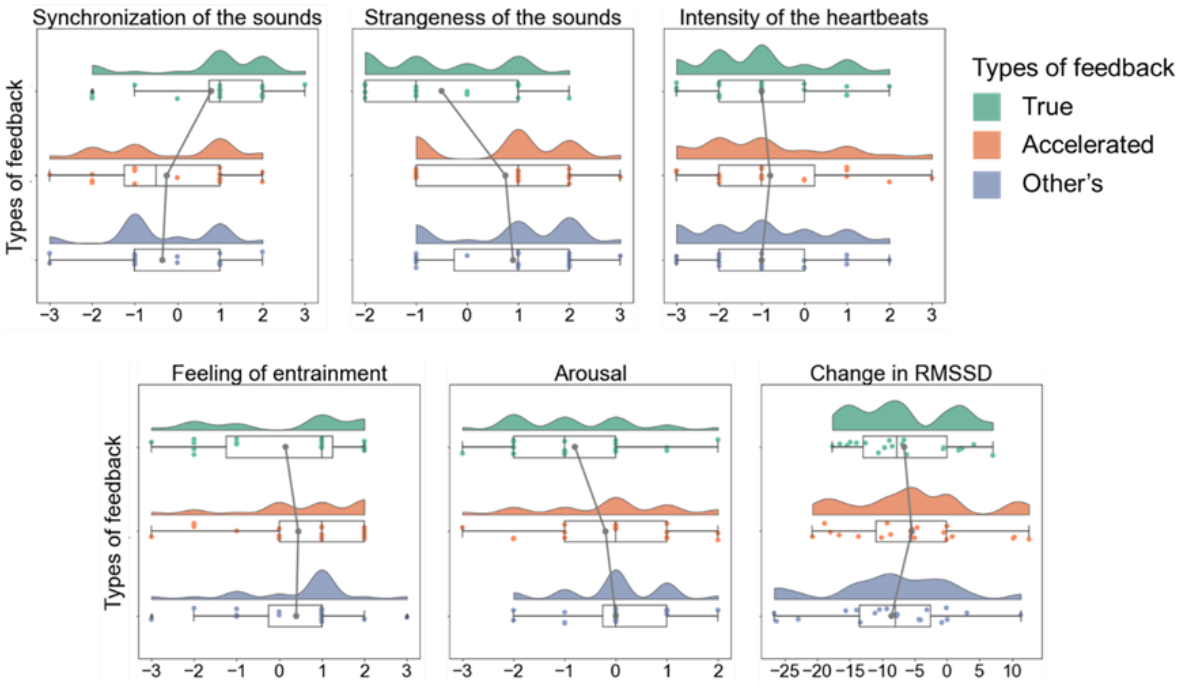

Figure 9. Raincloud plots for the effect of the feedback types for each measurement. Each point represents the raw data for each participant.

Model	AIC	Deviance	χ^2	ANOVA *p*	
Model 1	80.87	72.82			
Model 2	42.56	34.56	38.27	> .001	***
Model 3	46.02	34.02	38.80	> .001	***

Model 2, Model 3 > Model 1

Table 4. The result of GLMM model comparison. The model 1 that did not include subjective experience about the sound showed worse fitting than the model 2 and 3, suggesting that the judgement of the sound's attribution was primarily based on the subjective belief.

Discussion

In the field of interoception research, this study marks an advance in our understanding of the perceptual mechanisms underlying interoception. Rooted in the predictive coding framework (Apps and Tsakiris, 2014; Ainley et al., 2016; Petzschner et al., 2021), the study investigated the complex interplay between externalized interoceptive cues and the actual internal bodily state, particularly focusing on the cardiac rhythm. Utilizing a cardiac feedback paradigm, where auditory feedback timing was intricately manipulated, this investigation sheds light on how external cues can reshape our inferential process about interoceptive states.

First, participants were asked to discern the synchronization of feedback sounds with their heartbeats, coupled with ratings of their subjective experience in relation to these sounds and internal sensations. The findings were revelatory, underscoring the primacy of subjective experience over objective attributes in the perceptual judgment of these sounds. When participants felt a synchrony between the artificial sounds and their heartbeats, coupled with a lesser sense of strangeness, they were more inclined to attribute these sounds as reflective of their heartbeats. This pattern held true even when statistical models factored in the actual attributes of the sounds, thus highlighting the dominant influence of subjective experience in shaping perceptual judgments.

Another key finding of the study was the influence of feedback timing on the perceived strangeness of the sounds. Feedback that was artificially accelerated or represented another's heartbeat was consistently rated as stranger than the true feedback, irrespective of the judgment about the sound's attribute. This observation points to an innate human alignment with one's biological rhythm, where stimuli synchronized with one’s heartbeats are perceived as familiar, transcending conscious awareness of actual synchronization.

This study's results also resonate with prior research which demonstrated the modulating effect of visually externalized cardiac timing on the sense of body ownership (Suzuki et al., 2013). Our study extends this understanding to the auditory domain, showing that auditory feedback, when synchronized with the cardiac rhythm, can similarly influence perceptions of bodily states. These findings challenge the traditional view of interoceptive perception as a mere reflection of internal physiological processes, suggesting instead that it is actively

shaped by external sensory inputs.

The implications of these findings are far-reaching. Firstly, they reveal a deep-rooted human sensitivity to biological rhythms, particularly the cardiac rhythm, suggesting a level of bodily awareness that may operate subconsciously (Thayer et al., 2009; Park and Blanke, 2019). This sensitivity implies a complex, possibly adaptive, mechanism that allows individuals to maintain a consistent sense of bodily self in the face of varying external stimuli (Pezzulo et al., 2015; Gentsch et al., 2019).

Secondly, the study highlights the complex interplay between subjective experience and perceptual accuracy. The preference for subjective familiarity over objective synchrony in judgment making points to a cognitive bias in interoceptive awareness, which could be an evolved trait allowing for a consistent sense of bodily self (Fiacconi et al., 2017). This bias might serve an adaptive function, enabling individuals to navigate a world of fluctuating external stimuli while maintaining a stable internal representation of their bodily state (Allen and Tsakiris, 2018).

Moreover,, the malleability of interoceptive awareness as demonstrated in this study has profound implications for therapeutic interventions. In conditions where distorted interoceptive perception plays a pivotal role, such as anxiety disorders, manipulating external sensory inputs to align with internal bodily rhythms could be a promising therapeutic avenue. This approach could help recalibrate interoceptive perception, potentially alleviating symptoms associated with these disorders.

In conclusion, this study contributes significantly to the field of interoceptive research, offering new insights into the perceptual mechanisms underpinning interoception. It reveals the malleable nature of interoceptive perception and its susceptibility to external sensory influences, highlighting the intricate relationship between internal bodily rhythms and subjective experience. These findings not only deepen our understanding of interoception but also pave the way for novel therapeutic strategies for conditions characterized by distorted interoceptive perception. They call for further research into the cognitive and neurological underpinnings of interoception, which could lead to a more comprehensive understanding of the role of bodily awareness in health and disease.

Experiment 4

Introduction

Interoception refers to the processing of internal bodily information, including the signaling, collection, and perception of sensations arising from within the body (Chen et al., 2021). Specifically, interoceptive awareness, or the perception of one's own internal bodily states, has been a topic of interest for decades in relation to emotional experience and mental health (Critchley and Garfinkel, 2017; Khalsa et al., 2018). Researchers have mentioned the ambiguous and unstable nature of interoceptive awareness compared to exteroception, noting characteristics such as the low magnitude of perceptual intensity and difficulty in sensory attribution (Petersen et al., 2014, 2015a; Ceunen et al., 2016). Although the exact mechanism of interoceptive awareness remains unclear, it has recently been incorporated into an influential theoretical framework, the predictive coding of perception instantiated by bidirectional information passing in the neural hierarchy (Ainley et al., 2016; Stephan et al., 2016; Paulus et al., 2019).

The perceptual properties of interoceptive awareness can be well understood within the framework of perceptual inference, where the brain employs predictions about incoming sensations among all sensory modalities. According to this framework, perception is an inference about the cause of incoming sensations, optimized via attentional modulation of the sensory precision—an inverse variance of predictions and sensory information, i.e., prediction errors, that reflect the uncertainty of each signal (Summerfield and Koechlin, 2008; Clark, 2013; Jiang et al., 2013; Sedley et al., 2016). Attention plays a crucial role in this process, as it can optimize the relative precision of incoming sensations across all sensory modalities to sample the targeted information depending on one's needs (Feldman and Friston, 2010; Hohwy, 2012). Consequently, highly precise sensory information, such as visual or auditory sensations, is more likely to dominate perceptions compared to those with lower precision, like tactile, olfactory, or interoceptive ones.

Interoceptive sensations are inherently imprecise due to biological needs to maintain constant bodily states (Pezzulo et al., 2015; Allen and Tsakiris, 2018), Thus, becoming aware of interoception is particularly challenging when individuals have low levels of bodily arousal, resulting in the perceptual ambiguity compared to exteroception. However, research has shown that

attentional focus on bodily sensations can facilitate interoceptive awareness (e.g., heartbeat perception), even at rest (Critchley et al., 2004; Bornemann and Singer, 2017; Petzschner et al., 2019; Haruki and Ogawa, 2021). This is presumably due to the interoceptive attention, expecting a high precision of interoceptive sensations (Ainley et al., 2016).

In the current study, we aimed to investigate the perceptual mechanism of interoceptive awareness in terms of the relative precision between interoception and exteroception modulated via attention, by testing the effect of concurrent auditory sensations on interoceptive awareness. Accumulating data support the intertwined perceptual process between interoception and exteroception; for instance, heartbeat pulsations (i.e., easily predictable interoceptive sensations due to its periodicity) reduce somatosensory sensitivity (Al et al., 2020; Galvez-Pol et al., 2022c) and suppress visual information sampling (Galvez-Pol et al., 2020). Given the imprecise interoceptive sensations at rest, it is hypothesized that the attentional enhancement of interoceptive sensations is needed to get aware of interoception and vulnerable to precise signals from other sensory modalities (Ainley et al., 2016). However, there is a dearth of evidence on the disruption of interoceptive attention and awareness. Although one previous study has suggested that heartbeat perception can be disrupted in the presence of tone sounds (Van der Does et al., 2000), this finding was not fully discussed by the authors. To the best of our knowledge, no study has directly investigated the effects of sensory distractor on interoceptive attention and awareness, with previous research having focused on the differences in attentional mechanisms between interoception and exteroception (Mirams et al., 2012; García-Cordero et al., 2017; Petzschner et al., 2019).

We employed the heartbeat counting task (Schandry, 1981; Garfinkel et al., 2015), which necessitates an attentional focus on one's interoceptive sensations over others (Hickman et al., 2020). This makes it appropriate for examining the interference between interoception and exteroception. We irregularly presented simple tone sounds as a distractor, the highly precise auditory sensations relative to the interoceptive ones, to assess the impact of the auditory distractor on interoceptive attention and awareness. Furthermore, we postulated that the magnitude of the distractor effect would be associated with individual differences in the precision of interoceptive predictions and sensations, i.e., the balance of uncertainty between predictions and their errors. To that end, we

measured psychophysiological traits of individuals that may reflect differences in interoceptive predictions, including heart rate variability (HRV) at rest and subjective beliefs about daily experiences of interoception. For example, a more variable heart rate has been linked to greater sensitivity to visual (Hansen et al., 2003) and interoceptive sensations (Lischke et al., 2021), suggesting relatively imprecise interoceptive predictions and imbalance between prediction and sensation in people with higher HRV. Researchers have also found altered neural activations accompanying interoceptive attention in individuals with negative beliefs about interoceptive awareness (Baranauskas et al., 2017; Stern et al., 2017; Petzschner et al., 2019).

Our primary hypothesis posits that the presence of highly precise sensations would attenuate interoceptive awareness. This is crucial for testing the impact of the relative precisions across sensory modalities on interoceptive awareness: a previous study suggested the disrupted interoceptive awareness when presented with a high contrast distractor (Van der Does et al., 2000), whereas static (i.e., low contrast) visual sensations did not diminish interoceptive awareness (Ainley et al., 2013; Isomura and Watanabe, 2020). Furthermore, we hypothesized that the distractor effects on interoceptive awareness would be modulated by individual differences in HRV and subjective sensibility to interoception.

Materials and Methods

Participants. Thirty undergraduate students, ranging in age from 18 to 23 years old (mean age = 20.83 ± 1.44), from Hokkaido University participated in the experiment. The sample consisted of 17 women and 13 men. The sample size (n = 30) deemed the required number of participants (n = 27) for detecting a medium effect size in a within-participant design (Cohen's d = 0.5, α = 0.05, 1-β = 0.80, one-tailed), as calculated using G*Power software (ver 3.1.9.7). Written informed consent was obtained from all participants, and the study was conducted in accordance with the Declaration of Helsinki and all its amendments. The experimental protocol was approved by the Ethics Committee of the Center for Experimental Research of Social Sciences at Hokkaido University.

Experimental setting. The experiment was conducted in a quiet, temperature-controlled room. Participants were seated approximately 80 cm in front of a blank wall and instructed to place their arms on the desk without leaning against either the desk or backrest. Informed consent was obtained prior to the experiment, after which participants were equipped with headphones and pulse oximetry (IWS920, Tokyo Devices; Tokyo, Japan) on their left index fingers. The pulse oximetry sampling rate was 409.6 Hz. To minimize external sensory interference, participants were instructed to adjust the apparatus and their body positions appropriately, such as positioning their finger on the pulse oximeter, wrists on the desk, and buttocks on the chair. We used a pulse oximetry instead for an electrocardiogram to mitigate potential electromagnetic interference arising from the use of headphones. A break of at least two minutes was provided for bodily arousal control prior to the experiment.

Experimental procedure. Following a two-minute interval for physiological stabilization, resting-state photoplethysmography (PPG) signals were obtained via pulse oximetry for a duration of five minutes. Participants were instructed to maintain an open-eyed, still posture and to refrain from actively directing their thoughts during this period. Subsequently, the participants were presented with the heartbeat counting task in both the presence and absence of auditory distractors. Finally, the participants completed the Japanese version of the Multidimensional Assessment of Interoceptive Awareness scale (MAIA; (Shoji et al., 2018)) via an online form accessed through their personal mobile devices.

Resting-state physiological data. We analyzed photoplethysmography (PPG)

data using the HeartPy module in Python (van Gent et al., 2019). to investigate individual differences in heart rate variability (HRV). The preprocessing of PPG data was conducted to avoid erroneous peak detection. A 3rd-order low-pass filter with a cutoff frequency of 5Hz was applied to the raw PPG data. The automated peak detection and interpolation using the default setting of the HeartPy were performed, with manual inspections. Then, heart rate (beats per minute) was calculated based on the preprocessed PPG waveform. We focused on the high-frequency component of HRV (HF-HRV), which reflects rapid changes in heart rate, as our primary metric. To estimate the power spectral density, we employed Welch's method, the default in HeartPy, and defined the HF-HRV frequency band between 0.15 and 0.40 Hz, based on previous literature (Forte et al., 2019). To reduce skewness, we transformed the value of HF-HRV into a natural logarithm (Park et al., 2013).

Heartbeat counting task. In this study, we aimed to investigate the impact of external auditory signals on interoceptive awareness, under the assumption that highly precise auditory sensations may affect perceptual inference. To do this, we utilized a modified version of the heartbeat counting task (Schandry, 1981; Garfinkel et al., 2015) and presented two conditions to participants: a distractor condition (in which auditory distractors were introduced) and a non-distractor (control comparable to previous one) condition. This repeated-measures design enabled us to directly evaluate the effect of tone sounds on interoceptive awareness. Participants were asked to count their own heartbeats for a specified duration while focusing on internal bodily sensations. Immediately afterward, they verbally reported the number of heartbeats they had counted, as well as their level of confidence in their performance and the strength of the heartbeats they felt, on a scale of 1-7. This procedure corresponded to a single trial.

The two conditions differed solely in regard to whether sounds were present during the trial interval. In the distractor condition, a tone sound (1000 Hz, lasting 100 ms) was intermittently delivered through headphones. The inter-stimulus interval fluctuated between 500 and 2000 ms for each sound to prevent the participants from predicting the occurrence of the next tone sound, ensuring that the sensations were highly precise throughout the task. We also intended to present the sound unrelated to participant's cardiac cycles as exteroceptive sensitivity decreases at cardiac systole (Galvez-Pol et al., 2020, 2022c). We confirmed that the volume of distractor sounds was audible and not excessively

loud for each participant prior to beginning of the experiment. The volume was calibrated to approximately 52 dB SPL, which was estimated using the apparatus and a binaural headstand. Participants were explicitly instructed to disregard the tone sounds as they were completely unrelated to their heartbeats.

There were four trials for the non-distractor and distractor conditions, respectively, with durations of 25 s, 35 s, 45 s, and 55 s. Consequently, a total of eight trials were conducted (25 s, 35 s, 45 s, and 55 s for the non-distractor and distractor conditions) for each participant. The trial order was pseudo-randomized, however, the same condition was not repeated three times consecutively. The number of trials and duration of trials were based on previous studies (Herbert et al., 2012; Grabauskaitė et al., 2017), and a recent study revealed that increasing the number of trials would not influence the outcomes of the task (Santos et al., 2023). Participants were instructed to only count the heartbeats that they actually perceived. They were also prohibited from utilizing any strategies unrelated to the detection of heartbeat internally, such as taking their pulse and estimating the number of heartbeats based on time. While these strategies would inflate the score of the heartbeat counting task (Desmedt et al., 2018; Ring and Brener, 2018), it has been found that asking participants to count heartbeats felt for sure and not to estimate the number of heartbeats or time can reduce the confounding effects (Desmedt et al., 2018, 2020). Specifically, Desmedt and colleagues (2020) found a significant correlation between the number of counted beats in the heartbeat counting task and the number of seconds in the time estimation task when allowing the estimation (r = .41), whereas the modified instruction yielded no correlation (r = .08). Participants were instructed to use the same strategy for detecting heartbeats across the two conditions. Participants performed a practice trial (without a distractor for 25 s) prior to the first trial, to ensure that all participants understood how to perform the task according to our instructions.

Based on the participant's reports, we obtained three measures of interoception: interoceptive accuracy, confidence, and intensity for each trial in both the distractor and non-distractor conditions. Interoceptive confidence and intensity were assessed using a 7-point Likert scale that ranged from 1 to 7, while interoceptive accuracy was computed using the following formula:

$$Interoceptive\ accuracy = 1 - \left(\frac{|Recorded\ Number\ of\ Heartbeats - Counted\ Number\ of\ Heartbeats|}{Counted\ Number\ of\ Heartbeats}\right).$$

Questionnaire. We evaluated the self-reported interoceptive sensibility of each participant through the use of the MAIA questionnaire. The MAIA comprised 32 statements describing daily experiences pertaining to interoceptive awareness (e.g., "When I am tense, I notice where the tension is located in my body."). Participants rated the extent to which these statements applied to them on a 5-point Likert scale that ranged from 0 (never) to 5 (always). The MAIA encompasses eight factors: noticing—awareness of uncomfortable, comfortable, and neutral body sensations; not distracting—tendency to not distract oneself from sensations of pain or discomfort; not worrying—tendency to not worry about emotional distress with sensations of pain or discomfort; attention regulation—ability to sustain and control attention to body sensations; emotional awareness—awareness of the connection between body sensations and emotional states; self-regulation—ability to regulate psychological distress by attention to body sensations; body listening—active listening to the body for insight; and trusting—experience of one's body as safe and trustworthy.

Statistical analysis. *The effects of auditory distractor on interoceptive awareness.* We used R (version 4.0.3) for statistical analyses. We conducted a linear mixed effects (LME) model analysis using the lme4 package in R (Bates et al., 2015) to investigate the effects of auditory distractors on interoceptive awareness. LME models can include any variations specific to the participant and types of stimuli or trials as random effects, in addition to any covariates simultaneously. Thus, LME models are more suitable for longitudinal or repeated-measures data than conventional paired t-tests or ANOVA (Baayen et al., 2008). In the current study, the LME models allowed us to avoid averaging observed values (i.e., accuracy, confidence, and intensity) across the participants or trials.

We used all data in our LME models (N = 240, eight trials x 30 participants). Each parameter (interoceptive accuracy, confidence, and intensity) was separately modeled to have one main predictor as a fixed effect (condition: distractor or non-distractor) and random effects (random intercept and slope over participants). The participant's gender, age, number of heartbeats per trial, and duration of the trial were included in the models as covariates. These variables have been associated with the measurements of interoception (Grabauskaitė et al., 2017; Murphy et al., 2018a; Zamariola et al., 2018). Thus, each model was defined as:

$$Interoceptive\ measures \sim Condition + Age + Gender + Number\ of\ heartbeats\ for\ each\ trial +$$

$$Duration\ of\ trial + (1 + Condition|Participants).$$

The expression outside the parentheses indicates fixed effects, whereas the expression inside indicates random effects. In particular, the fixed effect in bold is the main predictor of interest. The effect of predictors was estimated as marginal means and statistically evaluated using the lmerTest package in R (Kuznetsova et al., 2017). The approximations of degrees of freedom and *p*-values were calculated using the Kenward-Rogers method. We performed multiple comparisons correction for the statistical inference, using the Bonferroni method for three models (i.e., α = .05/3 = .017).

The relationship between the distractor effects and individual traits

We tested whether the auditory distractor effects on interoceptive awareness were associated with individual psychophysiological traits that would reflect the balance of relative precisions across interoception and exteroception. To this end, we conducted an exploratory LME analysis to find variables predicting the individual differences in the distractor effect. We first defined Δaccuracy, Δconfidence, and Δintensity as the difference value of the corresponding trials (i.e., the same duration) between the non-distractor and distractor conditions, positing that the values would reflect the distractor effect. The full model was defined as having individual resting-state heart rate, the HF-HRV, each factor of the MAIA, age, gender, the difference in the number of heartbeats between corresponding trials, and the duration of trials as main predictors and having random intercepts and slopes over participants. The final models were constructed by comparing the full model to alternative ones, where the main predictors were successively eliminated (i.e., backward elimination method). Model comparison and selection were based on the Akaike information criterion and log-likelihood ratio testing. These calculations were performed using the "step" function in lmerTest. The final models that best fit our data were as follows:

$$\Delta accuracy \sim HF\_HRV + Not\_Worrying + (1 + HF\_HRV + Not\_Worrying|Participants);$$

$$\Delta confidence \sim Not\_Worrying + (1 + Not\_Worrying|Participants);$$

$$\Delta intensity \sim Not\_Worrying + (1 + Not\_Worrying|Participants).$$

The marginal means of the predictors were estimated and statistically evaluated using the lmerTest package for each model. Bonferronis' multiple comparisons correction was performed for the three models.

Results

The effects of auditory distractor on interoceptive awareness. Descriptive statistics for each measurement are listed in Table 5. The LME models revealed a significant distractor effect on all the measurements of interoception: accuracy, confidence, and intensity (Table 6, Figure 10 and 11), indicating that people perceived their heartbeats less intensely, counted heartbeats less correctly, and felt unconfident regarding their interoceptive awareness when presented with tone sounds. Interoceptive accuracy was lower by an average of 0.13 points in the distractor condition compared to the non-distractor condition ($t_{28.98}$ = -4.42, corrected p < .001, 95% confidence interval (CI) = [-0.19, -0.07]). Interoceptive confidence decreased by an average of 1.15 points in the distractor condition compared to the non-distractor condition ($t_{28.98}$ = -5.32, corrected p < .001, 95% CI = [-1.58, -0.72]). Interoceptive intensity also decreased by 0.76 points in the distractor condition ($t_{28.98}$ = -3.49, corrected p = .006, 95% CI = [-1.20, -0.33]). Note that the scale of interoceptive accuracy ranged between 0 and 1, while confidence and intensity were rated on Likert scales that ranged from 1 to 7. About the effects of covariates (i.e., age, gender, number of heartbeats, and trial duration), only the number of heartbeats and duration of trial (linear) had significant effect in the accuracy model (corrected p = .04 and < .001, respectively) while others were not significant for each model (corrected ps > .14). This implies that a smaller number of heartbeats and shorter trial duration may contribute to marginally improved interoceptive accuracy. However, the present study did not replicate the previously reported effects of age and gender on interoceptive awareness, probably because the variance of age was small (SD = 1.44). Also, the present sample size (n = 30) was not large enough to detect the effect of gender as recent meta-analyses revealed a small effect size of men's superiority in interoceptive accuracy (Desmedt et al., 2022; Prentice and Murphy, 2022).

The modulator of the distractor effects on interoceptive awareness. The exploratory analysis revealed that the distractor effect on interoceptive accuracy was associated with both the individual HF-HRV and tendency to worry about one's body. In contrast, the decline in confidence and intensity was associated only with the tendency to worry (Table 7). The LME model that predicted Δaccuracy indicated that a high level of the HF-HRV and low score on the *not worrying* factor of the MAIA independently contributed to a larger distractor effect on interoceptive accuracy ($t_{10.27}$ = 3.18, corrected p = .03, marginal mean

(MM) = 0.08, 95% CI = [0.04, 0.10]; $t_{13.23}$ = -3.33, corrected p = .02, MM = -0.11, 95% CI = [-0.15, -0.06], respectively). With our multiple comparisons correction using the Bonferroni method, the modulating effects of MAIA score in not worrying factor disappeared for the LMEs predicting Δconfidence and Δintensity ($t_{11.55}$ = -2.72, corrected p = .06, MM = -0.71, 95% CI = [-1.14, -0.28]; $t_{9.91}$ = -2.44, corrected p = .10, MM = -0.65, 95% CI = [-1.09, -0.22]).

	Mean	S.D.	Range
Interoceptive measure			
Accuracy	0.62	0.26	[0.14, 0.99]
Confidence	4.06	1.12	[1.00, 6.25]
Intensity	4.04	1.18	[1.25, 5.75]
Accuracy with distractor	0.49	0.27	[0.00, 0.99]
Confidence with distractor	2.91	1.18	[1.00, 5.50]
Intensity with distractor	3.28	1.24	[1.00, 6.50]
Physiological measure			
HF-HRV	6.06	1.25	[3.77, 8.65]
Psychological measure			
Noticing	2.86	0.74	[1.25, 4.75]
Not-distracting	2.46	0.96	[0.00, 4.33]
Not-worrying	2.07	0.89	[0.33, 4.00]
Attention regulation	2.15	0.70	[0.57, 3.29]
Emotional awareness	2.39	1.00	[0.40, 4.80]
Self-regulation	2.81	0.79	[1.25, 4.00]
Body listening	1.52	1.04	[0.00, 3.33]
Trusting	2.59	1.11	[0.67, 5.00]

Table 5. The descriptive statistics of each measurement. S.D.: standard deviation; HF-HRV: high-frequency component of heart rate variability

Predictor	Marginal mean	S.E.	95% CI for marginal means		e.d.f.	*t*	*Uncorrected p*
			Lower	Upper			
Interoceptive accuracy							
(Intercept)	0.59	0.07	0.46	0.71	27.91	8.85	< .001
Condition Distractor	-0.13	0.03	-0.16	-0.09	28.98	-4.42	< .001
Age	-0.03	0.04	-0.10	0.03	26.78	-0.85	.41
Gender Man	0.08	0.10	-0.11	0.27	26.74	0.79	.44
Number of heartbeats	0.01	0.00	-0.00	0.01	208.73	2.50	.01
Duration of trial linear	-0.05	0.02	-0.08	-0.02	176.02	-3.44	< .001
Duration of trial quadratic	0.03	0.02	0.00	0.06	176.02	2.02	.05
Duration of trial cubic	-0.02	0.02	-0.05	0.01	176.02	-1.62	.11
Interoceptive confidence							
(Intercept)	4.02	0.26	3.54	4.50	29.14	15.69	< .001
Condition Distractor	-1.15	0.22	-1.58	-0.72	28.98	-5.23	< .001
Age	-0.09	0.13	-0.36	0.14	26.32	-0.83	.48
Gender Man	0.09	0.38	-0.60	0.78	26.26	0.25	.80
Number of heartbeats	0.03	0.02	-0.01	0.07	93.44	1.44	.16
Duration of trial linear	-0.03	0.14	-0.30	0.25	176.26	-0.21	.83
Duration of trial quadratic	-0.02	0.14	-0.29	0.26	176.26	-0.12	.91
Duration of trial cubic	-0.10	0.14	-0.37	0.18	176.26	-0.69	.49
Interoceptive intensity							
(Intercept)	4.10	0.28	3.58	4.63	28.88	14.73	< .001
Condition Distractor	-0.76	0.22	-1.20	-0.33	28.98	-3.49	.002
Age	-0.10	0.14	-0.37	0.17	26.44	-0.72	.48
Gender Man	-0.14	0.41	-0.90	0.61	26.37	-0.35	.73
Number of heartbeats	0.02	0.02	-0.01	0.06	127.46	1.21	.23
Duration of trial linear	0.09	0.13	-0.15	0.33	176.16	0.71	.48
Duration of trial quadratic	0.08	0.13	-0.16	0.33	176.16	0.67	.51
Duration of trial cubic	-0.04	0.13	-0.29	0.20	176.16	-0.36	.72

Table 6. Auditory distractor effects on interoceptive measures revealed by linear mixed effects analysis. The marginal means of our main predictor (condition distractor compared to non-distractor), covariates, and intercept are noted for each model. S.E.: standard error for marginal means; CI: confidence interval; e.d.f.: estimated degrees of freedom

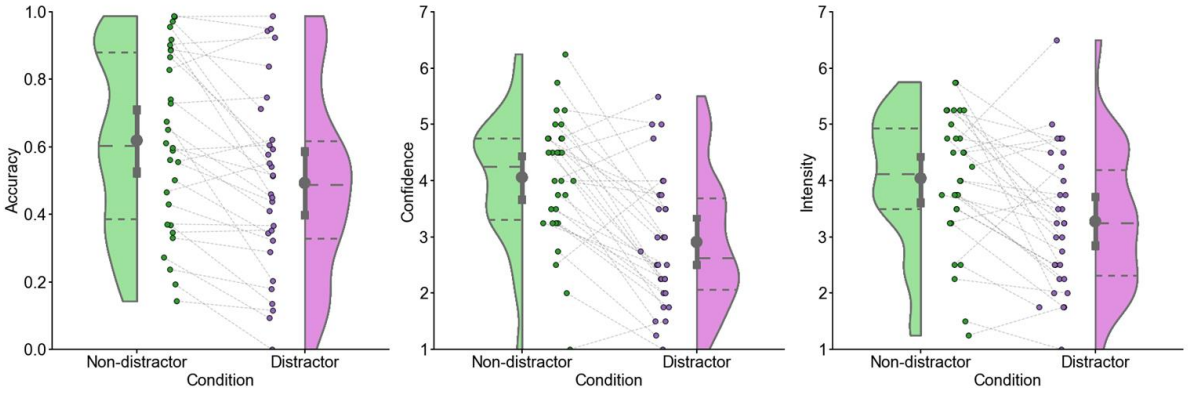

Figure 10. The difference in interoceptive measurements (accuracy, confidence, and intensity) between conditions. Each point corresponds to the averaged score of each participant across four trials. The dash lines are showing the difference in scores acquired by the same participant between conditions. All measurements declined in the distractor condition compared with the non-distractor condition (*p*s < .001) while controlling the effects of participants gender, age, and the number of heartbeats. The data distribution is represented as kernel density with quartile points and point estimates of the group mean. Error bars are showing 95 % confidence intervals.

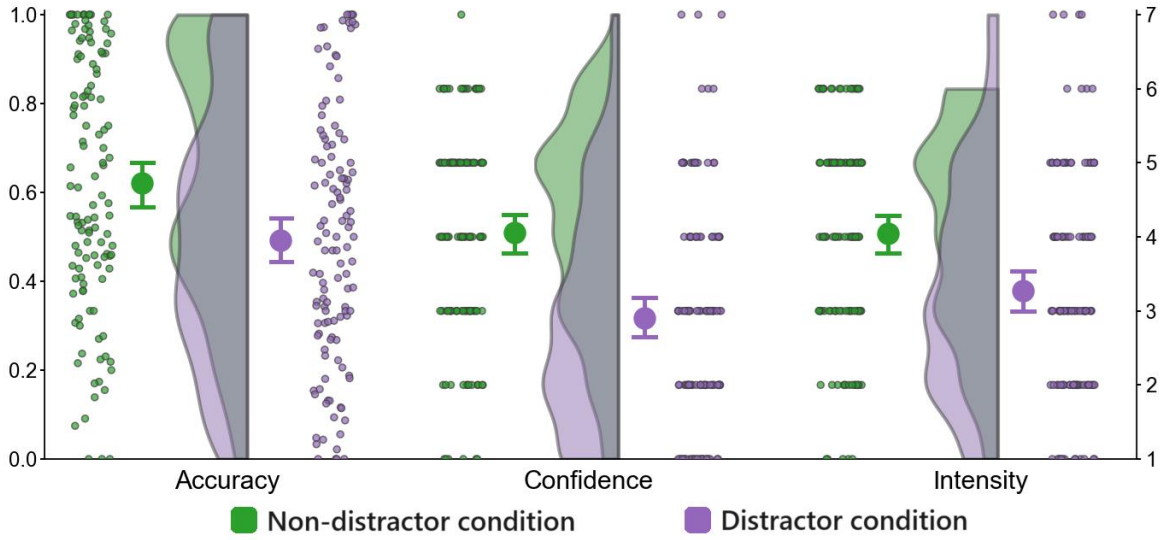

Figure 11. The raw data distribution of all trials obtained from each participant. Note that scores in interoceptive accuracy ranges from 0 (no perception) to 1 (complete heartbeat perception) while that of confidence and intensity was rated using Likert scale from 1 (not confident/intense at all) to 7 (completely confident/intense). Error bars are showing 95 % confidence intervals.

Predictors	Marginal mean	S.E.	95% CI for marginal mean		e.d.f.	*t*	*Uncorrected p*
			Lower	Upper			
Δaccuracy ~ HF-HRV + Not-worrying + (1 + HF-HRV + Not-worrying | Participants)							
(Intercept)	-0.10	0.14	-0.29	0.11	6.71	-0.66	.53
HF-HRV	0.08	0.02	0.04	0.10	10.27	3.18	.005
Not-worrying	-0.11	0.03	-0.15	-0.06	13.23	-3.33	.009
Δconfidence ~ Not-worrying + (1 + Not-worrying | Participants)							
(Intercept)	2.62	0.52	1.78	3.45	8.62	5.07	< .001
Not-worrying	-0.71	0.26	-1.14	-0.28	11.55	-2.72	.02
Δintensity ~ Not-worrying + (1 + Not-worrying | Participants)							
(Intercept)	2.12	0.58	1.15	3.07	10.03	3.65	.004
Not-worrying	-0.65	0.27	-1.09	-0.22	9.91	-2.44	.03

Table 7. Psychophysiological modulators of the distractor effects on interoceptive awareness. The marginal means of the main predictors and intercept are noted for each model. The main predictors for each model were selected using a backward elimination method. S.E.: standard error for marginal means; CI: confidence interval; e.d.f.: estimated degrees of freedom

Discussion

In the current study, we demonstrate that interoceptive awareness is disrupted by auditory signals and that the effect is modulated by individual psychophysiological traits. Participants performed the heartbeat counting task with and without distractor sounds while their resting-state HF-HRV and self-reported interoceptive sensibility were also measured. The results revealed that the auditory distractor diminished all measures of interoceptive awareness including objective accuracy, subjective confidence, and subjective intensity. Notably, individuals with higher rather than lower HF-HRV were more disturbed in interoceptive accuracy when presented with the distractor. Furthermore, a tendency to feel distressed or worried about sensations of pain or discomfort was also associated with larger distractor effects on interoceptive accuracy. These findings would support and extend the predictive accounts of perceptual experiences by suggesting that interoceptive awareness is influenced by the relative precisions of prediction and prediction error across sensory modalities.

The current study revealed a considerable distractor effect of tone sounds on interoceptive awareness, verifying our main hypothesis. These declines in perceptual accuracy and intensity support the intertwined perceptual process between interoception and exteroception, coinciding with the ideas of recent computational framework, predictive coding. The heartbeat counting task requires a selective and sustained attentional focus on sensations from within the body (Hickman et al., 2020), which has been proposed as an up-weighting of interoceptive sensations in the framework of predictive coding (Ainley et al., 2016). In the present distractor condition, a salient and unpredictable sound was delivered continuously. Such auditory sensation would be up-weighted automatically (i.e., exogenous attention), suppressing other sensory signals relatively. Combined with the current results, it is posited that the participants had the diminished heartbeat perception in the distractor condition due to the auditory suppression of interoceptive signals among a cascade of sensory signals.

It is important to note that the current distractor effect would not merely be the results of multisensory cognitive demands. Previous research has demonstrated that dividing attention between the heartbeats and self-relevant visual stimuli (e.g., one's own face or a self-relevant word) did not disrupt, rather actually enhanced heartbeat perception (Ainley et al., 2013; Isomura and Watanabe, 2020).

In these cases, exteroceptive sensations remained consistent and did not have high contrasts, rather potentially augmenting bodily sensations (i.e., emotional response). Considering the fact that presenting low-contrast visual sensations did not interfere with interoceptive awareness, the present distractors would be better understood in terms of the relative precision of sensory signals. Similarly, it may be argued that the present tone sound impeded estimation or reporting of the number of heartbeats, but not the perception itself. However, it is believed that the current result is not a disruption of the cognitive strategy used to perform the heartbeat counting task, as participants were instructed to count heartbeats they undeniably perceived and prohibited from estimating the number of heartbeats (cf. (Desmedt et al., 2020). In fact, the participants perceived their heartbeats less intensely in the distractor condition, which would not occur if the distractors solely disrupted cognitive strategies such as counting or reporting the number. Furthermore, it should be noted that the distractor effect was independent of physiological changes between conditions, as the number of heartbeats during each trial was modeled as a covariate in the statistical model. Taken together, it is plausible that the disrupted interoceptive awareness is the result of perceptual inference, in which the relative precision of exteroceptive prediction error outweighs that of interoceptive ones.

Interestingly, individuals with a higher level of resting-state HRV displayed greater difficulty in accurately perceiving their own heartbeats when a distractor was present. Research has previously linked greater HRV to enhanced abilities in selective and sustained visual attention (Hansen et al., 2003; Siennicka et al., 2019). Based on these findings, it has been proposed that people with greater HRV can better optimize the relative weights of sensory signals for goal-directed behavior (Smith et al., 2017). However, the present study found that individuals with higher HF-HRV exhibited a larger decline in interoceptive awareness when presented with auditory stimuli. These seemingly incompatible findings would be understood in terms of the predictive coding framework: the extent of fluctuations in each heartbeat may correspond to the uncertainty of heartbeat-related predictions. Theoretically, any physiological changes should be predicted very precisely to maintain homeostasis in the neural hierarchy (Pezzulo et al., 2015; Seth and Tsakiris, 2018; Corcoran et al., 2021). It is therefore posited that people with relatively inconsistent heartbeats (i.e., high HRV) may benefit from imprecise interoceptive predictions for outweighing the targeted sensations via top-down attention, compared to those with low HRV. However, the attentional

modulation of the relative precision would be less effective when an unexpected distractor was presented, which may have contributed to the larger perceptual decline in people with greater HRV.

Furthermore, participants with a low score on the MAIA *not worrying* factor, indicating a greater tendency to feel distress or worry about sensations of pain or discomfort, had more disrupted interoceptive accuracy under the auditory distractor. This contextual-dependent alteration of perceptual inference may reflect a different encoding of interoceptive predictions. Research has revealed that people with more negative traits regarding interoceptive awareness exhibited a reduced neural marker of interoception: smaller amplitude of heartbeat-evoked potentials (HEPs) in individuals who are more concerned about their bodily states (Baranauskas et al., 2017; Petzschner et al., 2019). The HEP is a brain potential that occurs around the cardiac systole and has been considered as an indication of cortical processing of interoceptive signals (Babo-Rebelo and Tallon-Baudry, 2018; Park and Blanke, 2019). Notably, it has been posited that subjective beliefs about interoceptive awareness are instantiated in the higher-order internal model that generates predictions (Critchley and Garfinkel, 2017). In particular, negative interoceptive beliefs have been proposed to prolong a vigilant internal model, in which appropriate perceptual inference is restricted (Paulus et al., 2019). In light of these ideas, it is possible that participants who worried about their bodily states may have failed to prioritize interoceptive signals in a noisy environment due to their vigilant internal model.

The current findings may also reconcile a discrepancy in the measurement of interoceptive accuracy. There are two predominant tasks that are used to assess interoceptive accuracy: heartbeat counting, which was used in this study, and heartbeat discrimination. In the heartbeat discrimination task, individuals are asked to determine whether their own heartbeats are in sync with an externally presented stimulus (Katkin et al., 1981; Garfinkel et al., 2015). However, the results of these two tasks are often incongruous, with studies showing that individuals perform worse on the discrimination task and there is no correlation between the two tasks (Schulz et al., 2013; Forkmann et al., 2016), leading to ongoing debate about the validity of both methods. Our finding suggests that interoceptive awareness can be easily disrupted by external stimuli, which may have contributed to the discrepancy between the two methods. That is, individuals may have a poorer interoceptive awareness in the heartbeat

discrimination task than the counting task due to the presence of external stimuli per se. This idea is consistent with the fact that heartbeat discrimination is a difficult task to accomplish, with a large proportion of participants performing at chance level (Brener and Ring, 2016). While the heartbeat discrimination task remains a valuable method in interoception research (for an elegant example of its use, see (Critchley et al., 2004; Bekrater-Bodmann et al., 2020), researchers should be mindful of the potential for perceptual disruption for interoceptive awareness by external stimuli when using this method.

The current experimental procedure had several limitations. Firstly, in the distractor condition, the inter-stimulus interval varied between 500 and 2000 ms in order to present the sounds in an unpredictable and unrelated manner to the cardiac timing of the participants. This procedure resulted in a slight variation in frequency among participants and between trials. However, we believe that this difference was not a significant issue as the relative number of presented tone sounds did not affect the measurements of interoceptive awareness (see Supplementary Material S1). Additionally, it may be argued that the participants accidentally counted the number of presented tones or the task duration, instead of their heartbeats, in the distractor condition. We argue that this idea is unlikely as the participants were instructed to count the number of heartbeats that they felt for certain and to ignore the tone sounds. This is supported by the fact that the actual data distribution of scores in the heartbeat counting task was far from the virtual distribution where participants would have accidentally counted the tone sounds or time (seconds) for their heartbeats (Supplementry Material S2).

All participants in this study were healthy young adults aged 18 to 23, native Japanese speakers. Given prior research in the U.S. indicating auditory interference on interoceptive awareness (Van der Does et al., 2000), we anticipate that our findings are generalizable to healthy young adults in other countries. However, it is worth noting that this distractor effect may not apply to elderly populations, as interoceptive perceptual abilities tend to decline with age (Murphy et al., 2018a). Additionally, participant's bodily position can influence the distractor effect, as it modulates cardiovascular activity and interoceptive awareness (Schulz et al., 2021). In our study, participants completed the task while seated in chairs. Nevertheless, we have no reason to suspect that our results are contingent upon other participant characteristics, materials, or environmental factors.

In summary, we have demonstrated that interoceptive awareness can be readily disrupted by exteroceptive stimuli by introducing distractor sounds in the heartbeat counting task. Furthermore, individual differences in the distractor effect were found to be modulated by psychophysiological characteristics of the individual. These results would support the predictive mechanism of perception encompassing all sensory modalities including interoception. Given the coordination of exteroceptive and interoceptive signals in the basic perceptual experience, it would be valuable to test the multimodality in more complicated situations such as social or emotional perception. For example, recent studies revealed that people can estimate other's heartbeats through vision (Arslanova et al., 2022; Galvez-Pol et al., 2022a), which might be influenced by the precision of their own interoceptive signals (e.g., cardiac cycle) as in the cases of emotional face recognition and perceptual decision-making (Allen et al., 2016; Garfinkel and Critchley, 2016).

Weighted Interoceptive Signals and Its Effect on Exteroception

Research Background

The final segment of my research, titled "Weighted Interoceptive Signals and Its Effect on Exteroception," delves into the hypothesis that enhancing the precision of interoceptive signals, as proposed in the predictive coding model, has a significant impact on exteroceptive perception, with a specific focus on visual cognition. This line of investigation is crucial as it probes whether the concept of precision weighting, a cornerstone of predictive coding, is applicable to broader perceptual processes. The aim is to determine how artificially heightening the precision of interoceptive sensations, such as those associated with heartbeat awareness, can influence visual decision-making and metacognitive abilities.

In the context of predictive coding, attention refers to the brain's mechanism of assigning degrees of importance or confidence to sensory inputs, thereby influencing how these inputs are processed and integrated into our perceptual experience (Feldman and Friston, 2010; Hohwy, 2012). The hypothesis under investigation in this segment of the research posits that increasing the precision of interoceptive signals will affect how visual information is processed and interpreted. This is based on the understanding that the brain does not operate in isolated sensory modalities but integrates information across different senses to form a cohesive percept. One key aspect of this research is to explore the implications of heightened interoceptive precision for visual decision-making. By increasing relative precision of heartbeat sensations via attention, the study aims to assess whether this leads to changes in how visual information is processed, potentially altering decision-making processes. This could manifest in various ways, such as changes in perceptual sensitivity, the confidence with which visual decisions are made, or the efficiency of metacognition, offering insights into how cognitive systems incorporate effects of interoceptive signals within the cognitive framework. Previous studies have established a foundational understanding that increases in bodily arousal can impact visual cognition, thereby hinting at a significant connection between interoceptive states and visual processing (Allen et al., 2016; Hauser et al., 2017; Salamone et al., 2021). These findings set the stage for my investigation, which aimed to further probe this link. Building on

these preliminary insights, the experiment was meticulously designed to test whether directing attention to interoceptive cues before engaging in a visual task could influence visual perception and metacognitive capabilities.

The experimental setup involved participants in a visual detection task, structured in a trial-by-trial sensory manipulation. Here, participants alternated their focus between interoceptive cues, specifically their heartbeat sensations, and exteroceptive stimuli, such as external auditory tones. This design allowed for a systematic exploration of how varying the relative precision of interoceptive versus exteroceptive signals could affect visual perception. In the interoceptive condition, participants concentrated on their heartbeat sensations, which was hypothesized to enhance the precision weighting afforded to these interoceptive signals. Conversely, in the control condition, attention was directed towards auditory tones, serving as an external focus point that would not directly augment interoceptive precision.

The primary objective of this experiment was to investigate the extent to which heightened precision of interoceptive information, achieved through focused heartbeat attention, affected aspects of visual cognition. The investigation was pivotal in expanding our understanding of the predictive coding framework, particularly in exploring the bidirectional influence between interoception and exteroception. The implications of this study extend beyond the confines of traditional sensory processing models. It promises to shed light on the complex mechanisms underlying sensory integration and the multifaceted role of interoception in cognitive processes, proposed within Bayesian theorem (Friston and Kiebel, 2009; Hohwy, 2012). By providing empirical evidence to support the concept of an integrated sensory processing system, this research aligns with the principles of predictive coding. The findings could elucidate how the brain synthesizes and prioritizes information from both internal and external sources, contributing to a more nuanced understanding of human perception and cognition. Moreover, this investigation has potential implications for developing therapeutic strategies in conditions where sensory integration or processing is disrupted, offering a new perspective on the interplay between the body and the brain in shaping our perceptual experiences.

Experiment 5

Introduction

In the preceding experiments of this thesis, I explored the dynamic interplay between interoception and exteroception, investigating how one modality can influence the processing of the other. This exploration was grounded in the growing understanding of interoception not just as a passive reception of bodily signals but as an active component in the complex web of sensory integration. Building on this foundation, in experiments 3 and 4, I demonstrated that interoceptive processes are indeed susceptible to modulation by external sensory inputs. This finding aligns with the predictive coding framework, suggesting that such modulations are likely a result of alterations in the hierarchical model the brain uses to interpret sensory data. Extending this line of inquiry, the current Experiment 5 hypothesizes that just as interoceptive awareness can be influenced by exteroceptive stimuli, the converse may also be true – exteroception, particularly visual cognition, could be modulated by preceding interoceptive attention. This hypothesis is rooted in the notion that focusing attention on internal bodily sensations – a key aspect of interoception – enhances their precision in the brain's internal model (Hohwy, 2012; Ainley et al., 2016; Corcoran et al., 2021). Consequently, this heightened interoceptive precision could potentially recalibrate how external stimuli are processed and perceived.

Previous studies have provided preliminary evidence supporting this hypothesis. Research has shown that unexpected increases in bodily arousal can lead to alterations in visual cognition, suggesting a tangible link between interoceptive states and visual processing (Allen et al., 2016; Hauser et al., 2017). Building upon these insights, this experiment aimed to directly test whether directing attention to interoceptive cues before a visual task could influence visual perception and metacognition, as suggested in previous studies (Ernst et al., 2013; Salamone et al., 2021). To this end, a novel trial-by-trial sensory manipulation approach was employed, involving a visual detection task where participants' attention was alternately focused on either their heartbeat sensations or external auditory tones.

The experimental design was designed to parallel conditions where the relative

precision of interoceptive versus exteroceptive signals varied systematically. In the interoceptive condition, participants concentrated on their heartbeat sensations, thereby enhancing the weighting afforded to interoceptive signals (Ainley et al., 2016; Petzschner et al., 2019). Conversely, in the control condition, attention was directed towards auditory tones, serving as an external focus that would not directly augment interoceptive precision. This manipulation allowed for a controlled comparison of how the preceding focus of attention – interoceptive versus exteroceptive – influenced subsequent visual perceptual processing.

The primary objective was to discern whether and how the heightened precision of interoceptive information following focused heartbeat attention impacted visual cognition. Did it lead to changes in how visual stimuli were perceived, in the confidence with which these perceptions were held, or in the accuracy of visual discrimination? These questions lie at the heart of this experiment, probing the intricate relationship between internal bodily awareness and the perception of the external world. In summary, this experiment sought to expand our understanding of the predictive coding framework by exploring the bidirectional influence between interoception and exteroception. It aimed to unravel how attentional focus on internal bodily states could recalibrate the perceptual processing of external stimuli, specifically in the realm of visual cognition. This investigation promised to shed new light on the complex mechanisms underlying sensory integration and the multifaceted role of interoception in cognitive processes.

Materials and Methods

Participants. The experiment engaged 20 undergraduate students from Hokkaido University, comprising eight male and twelve female participants. Their ages ranged narrowly, with a mean age of 19.65 years and a standard deviation of 2.13 years, reflecting a relatively homogenous young adult demographic typically encountered in university settings. Prior to participation, each individual underwent a thorough screening process to ensure suitability for the study, including assessments for any history of neurological or psychiatric conditions, visual or auditory impairments, or any known sensitivities or allergies to experimental equipment. Informed consent was obtained from all participants, adhering to the ethical guidelines laid out by the Ethics Committee of Hokkaido University, which had approved the study protocol. The committee's approval was crucial in ensuring the ethical integrity of the research, particularly concerning participant welfare and data handling procedures. Participants were also briefed on the nature and purpose of the study, ensuring transparency and understanding of their involvement in the research. This briefing included information on the tasks they would be performing, the duration of the experiment, and the confidentiality of their data. To facilitate accurate data collection, participants were equipped with a headphone set and pulse oximetry, devices chosen for their non-invasive nature and reliability in capturing auditory attention and cardiac signals, respectively. The demographic and psychophysical profiles of the participants were meticulously recorded, providing a comprehensive dataset for analyzing the interactions between interoceptive attention and visual cognition within this specific population segment.

Procedure. The procedure for the study was meticulously designed to investigate the influence of interoceptive attention on visual cognition. After an initial briefing session where the participants were informed about the study's objectives, methodology, and their role, they were comfortably seated in a controlled environment optimized for minimal distractions. This setting was crucial to ensure that the participants could focus entirely on the tasks without external interference.

Each participant underwent a brief training session to familiarize themselves with the experimental tasks and equipment. This training included practicing the dot motion discrimination task and familiarization with the sensation of focusing on

heartbeat and tone sounds. The training ensured that participants understood how to perform the tasks accurately and were comfortable with the experimental setup.

The main experimental session commenced with the dot motion discrimination task (Figure 12). This task involved presenting a dynamic visual display of a thousand white dots moving in a random direction on a computer screen for a duration of 250 ms. The motion of the dots was either to the left or the right in relation to vertical lines displayed on the screen. Participants were instructed to identify the direction of motion (left or right) and respond using a designated input device within 1000 ms, starting 500 ms post-presentation of the dots. This timing was critical to assess the immediate perceptual judgment of the participants without allowing excessive deliberation. Following the visual task, participants rated their confidence in their motion discrimination judgment on a Likert scale ranging from 1 (not confident at all) to 4 (completely confident). This self-assessment was integral to measuring the subjective certainty in their perceptual decision-making process.

Two conditions were employed to present a trial-by-trial manipulation of the relative precision of sensory signals. In the interoceptive condition, participants directed their attention to their heartbeat sensations for 6 seconds before the onset of the dot motion, followed by a 1 second blank. This focus was intended to heighten the precision of interoceptive information processing. Conversely, in the control condition, participants focused on tone sounds played through headphones for the same duration. The volume of these tones was individually adjusted to each participant's perceptual threshold, ensuring that they required similar levels of concentration as the heartbeat sensation. This design aimed to control for general attentional effects by providing an auditory attention task parallel to the interoceptive task.

Each session consisted of 72 trials, with an equal split of 36 trials for each condition (interoceptive and control). To avoid any order effects or bias, the trials were randomized. Participants completed two consecutive sessions with a brief 2-minute break in between, allowing for a momentary rest and to prevent fatigue, which could potentially influence their performance and responses.

Statistical analysis. The statistical analysis for this study was conducted with a

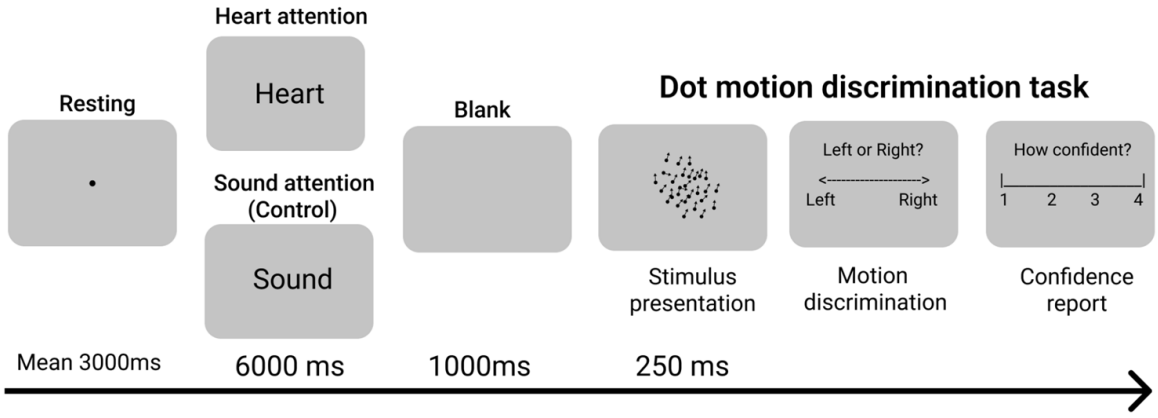

Figure 12. Schematical example of a single trial. The main session involved a dot motion discrimination task. Participants observed a display of a thousand white dots, moving randomly either left or right against vertical lines on a screen, for 250 ms. They had to identify the motion direction using an input device within 1000 ms, starting 500 ms post-presentation. This was immediately followed by a confidence rating on a 1-4 Likert scale. Two conditions were alternated: the interoceptive condition, where participants focused on heartbeat sensations for 6 seconds before dot motion, and the control condition, involving focus on auditory tones for an equivalent duration. This trial-by-trial manipulation assessed the impact of relative precision of interoceptive versus exteroceptive signals on visual perception and confidence judgments.

meticulous approach to ensure precision and reliability in interpreting the experimental data. The analysis began with the application of the signal detection theory, as modified and proposed by Maniscalco and colleagues (2012), implemented using Python programming language. This choice of methodology and software was pivotal for a nuanced analysis that could accommodate the complexities of the perceptual decision-making processes being studied.

Signal detection theory (SDT) provided a robust framework to dissect and quantify the participants' perceptual sensitivity and decision-making strategies. The first step in this analysis involved calculating the discrimination sensitivity, denoted as 'd-prime' (d'), for each participant. The d' metric is a measure of the participant's ability to discriminate between the two motion directions of the dots, reflecting the accuracy of their sensory perception. This calculation was based on the hit rate (correct identification of motion direction) and false alarm rate (incorrect identification), adjusted for the inherent bias in the participant's responses. The d' scores were computed separately for the interoceptive and control conditions, allowing for direct comparison between the two attentional focus scenarios.

Next, the analysis focused on metacognitive efficiency, quantified as the M-ratio. The M-ratio is a crucial metric that represents the ratio of the participant's actual perceptual sensitivity (d') to their metacognitive sensitivity. Metacognitive sensitivity refers to the participant's ability to introspectively assess the accuracy of their own decisions. It is a critical component in understanding the participants' awareness of their cognitive processes, particularly in the context of heightened interoceptive attention. The M-ratio was calculated for each participant and condition, shedding light on how interoceptive attention influenced not only the perceptual decision but also the participant's awareness and confidence in their decision-making.

Additionally, the response bias for confidence ratings, denoted as 'meta-c', was calculated. Meta-c represents the tendency of participants to lean towards a certain level of confidence in their judgments, independent of the actual accuracy of their perceptual decision. This bias is essential in understanding how interoceptive attention might skew the participants' subjective confidence in their perceptual judgments.

Following these individual-level analyses, the data were subjected to a linear

mixed effects model (LMM) to assess the effect of condition (interoceptive versus control) on the perceptual and metacognitive measures. LMMs were chosen for their ability to handle the complexities of repeated measures data and their capacity to model both fixed and random effects, thus accounting for individual differences and potential non-independence of observations within participants.

The model specification in the LMM included the condition as a fixed effect to examine the primary interest of the study: the impact of the interoceptive versus control condition on the participants' perceptual and metacognitive processes. Participant identity was included as a random effect to account for individual variability in baseline perceptual and metacognitive abilities. This random effect structure allowed for the modeling of within-participant correlations across the two conditions, providing a more accurate representation of the data structure. The interaction between condition and session was also examined to explore any potential changes across the two experimental sessions.

Each measure – d', M-ratio, and meta-c – was analyzed separately using this LMM framework. The results from these analyses provided insights into how the manipulation of attentional focus towards interoceptive or auditory stimuli influenced the participants' visual perception, confidence in their perceptual decisions, and metacognitive awareness.

Results

Initially, the analysis focused on the discrimination sensitivity, represented as 'd-prime' (d'), a crucial measure of participants' ability to discern the direction of dot motion. Results indicated that the d' scores did not show significant difference between the interoceptive and control conditions (Interoceptive = 1.51 ± 0.44, Control = 1.49 ± 0.50; p = .67), suggesting that the heightened interoceptive focus did not alter the participants' ability to accurately perceive the motion direction of the dots. This finding was consistent across both experimental sessions, underscoring the stability of perceptual sensitivity regardless of the attentional focus. Metacognitive efficiency, quantified as the M-ratio, was another focal point of the analysis. This ratio, representing the participants' actual perceptual sensitivity relative to their own assessment of decision accuracy, was separately computed for each condition. I found no significant difference in the M-ratio between the interoceptive and control conditions (Interoceptive = 0.95 ± 0.65, Control = 0.89 ± 0.56; p = .47), indicating that the enhanced focus on interoceptive signals did not substantially influence participants' metacognitive awareness of their perceptual decisions.

The third key metric analyzed was the response bias for confidence ratings, known as 'meta-c'. This metric provides insight into participants' tendency towards certain confidence levels in their judgments. The results demonstrated a notable effect in the interoceptive condition, where the meta-c values indicated a more conservative bias in confidence ratings (Interoceptive = 0.29 ± 0.37, Control = 0.13 ± 0.35; regression coefficient = 0.13, t_{39} = 2.16, p = .03) (Figure 13). This finding suggests that participants exhibited a heightened cautiousness or conservatism in their confidence assessments following the interoceptive attention, compared to the control condition where auditory attention was directed. This effect was prominent even after controlling for individual d' and M-ration, using the linear mixed effects model, highlighting the unique influence of interoceptive attention on subjective confidence.

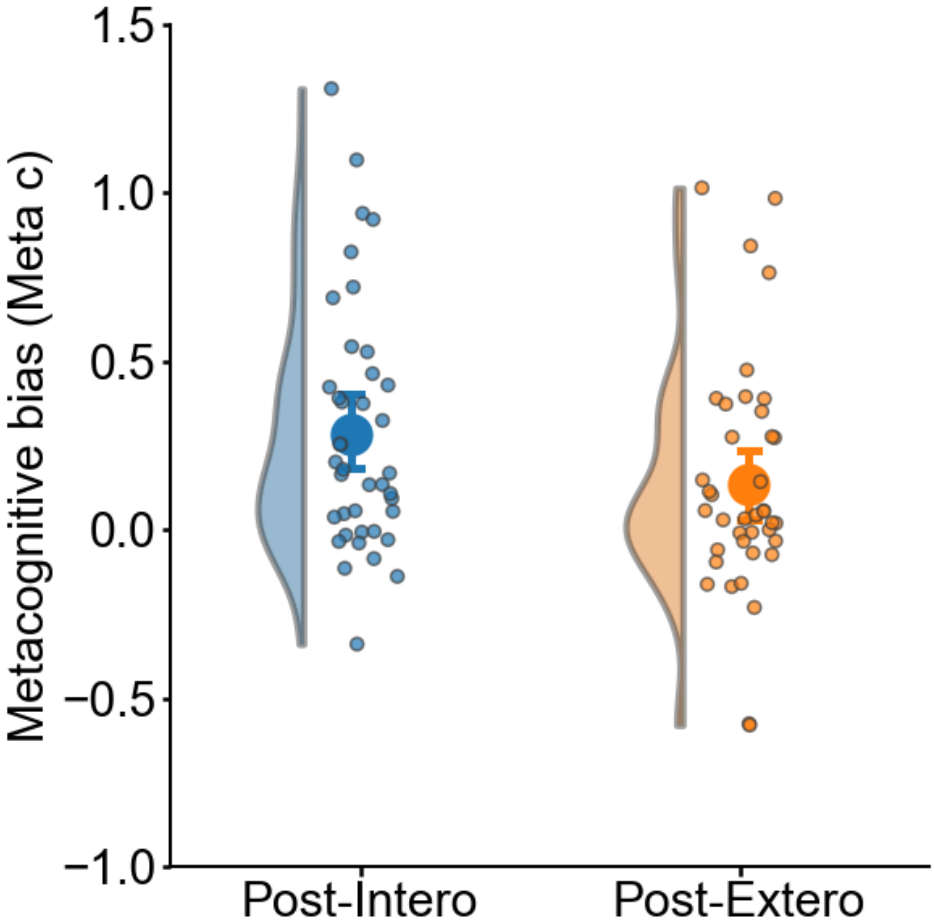

Figure 13. Conservative confidence rating after interoceptive attention. The raincloud plot illustrates the distribution and mean values of the response bias 'meta-c' across conditions. Meta-c measures participants' bias towards certain confidence levels in their judgments. In the interoceptive condition, meta-c values showed a conservative bias (regression coefficient = 0.13, $t_{39} = 2.16$, $p = .03$), indicating heightened cautiousness in confidence assessments post interoceptive attention. This effect persisted even after controlling for individual d' and M-ratio using linear mixed effects models, underscoring the distinct impact of interoceptive attention on subjective confidence compared to the control condition with auditory attention.

Discussion

The present results demonstrate that directing attention to interoceptive cues, specifically heartbeats, influences subjective confidence in visual perception. The increase in conservative bias following interoceptive attention, as indicated by higher meta-c ratings, suggests a recalibration of visual cognition where interoceptive information is afforded with relatively high precision. In contrast, perceptual accuracy and metacognitive efficiency in visual discrimination, as measured by the d' and M-ratio respectively, remained unaffected. This implies that while interoceptive attention affects the metacognitive reappraisal of the preceding perceptual judgments, it does not necessarily alter the accuracy of these judgments.

The concept of relative precision in predictive coding provides a compelling explanation for these observations. According to this framework, the brain constantly updates its internal model based on incoming sensory information, weighting each source by its relative precision or reliability (Hohwy, 2012; Jiang et al., 2013). When attention is focused on interoceptive signals, their precision is increased relative to other sensory modalities, thereby amplifying the influence of bodily signals on the following cognitive processes. It aligns with the notion that internal bodily states can exert a significant influence on the perception of external stimuli, as suggested in previous research (Allen et al., 2016; Hauser et al., 2017; Azzalini et al., 2019). Specifically, the present attentional focus on interoception might induce a shift in the balance of sensory integration, leading to a more cautious approach in confidence judgments regarding external stimuli (Paulus et al., 2019; Allen et al., 2022).

Interestingly, the present interoceptive attention did not impact perceptual accuracy, suggesting a hierarchical, multisensory process among all sensory modalities. The dissociation between visual perception and subjective confidence ascribed to those perceptions would align with the multisensory models of consciousness, wherein the interoceptive signals are integrated with other sensory modalities in higher processes of cognition (Barrett and Simmons, 2015; Allen and Tsakiris, 2018). The current independence of visual perception from effects of the heightened interoceptive signals is suggestive, as interoceptive awareness is easily disrupted by exteroceptive signals (Haruki and Ogawa, 2023b). This disparity might be attributed to the difference in uncertainty

between visual and interoceptive signals (Hohwy, 2012; Apps and Tsakiris, 2014; Ainley et al., 2016). The formulation of such optimised differences in sensory precision will further elaborate on the perceptual inference.

In conclusion, this study sheds light on the interplay between interoceptive and exteroceptive modalities, particularly highlighting the role of attention in modulating this interaction across the modalities. It underlines the importance of considering both interoceptive and exteroceptive processes in understanding perceptual mechanisms. The findings open avenues for further research, particularly in exploring the extent to which interoceptive processes can influence other cognitive domains and how these influences manifest in different perceptual scenarios. The application of predictive coding as a theoretical framework provides a fertile ground for such explorations, offering a comprehensive lens through which the complexities of sensory integration can be understood.

General Discussion

The series of experiments conducted offers a comprehensive exploration into the perceptual mechanisms of interoception. Each study contributes uniquely to our understanding, painting a holistic picture of how interoceptive attention, expectations, and sensory precision interact to realize the perceptual experience of bodily states.

Activations in the Insula for Interoceptive Attention

Experiment 1 in this series represented a significant step forward in understanding the neural basis of attention in enhancing interoceptive awareness, with a specific focus on sensations related to the heartbeat. Utilizing functional magnetic resonance imaging (fMRI), the study aimed to capture and analyze the brain's activity when participants directed their attention to interoceptive sensations. The core hypothesis was that regions beyond the dorsal posterior insula, traditionally recognized as the primary area for interoceptive signals, would demonstrate increased activation (Oppenheimer and Cechetto, 2016; Evrard, 2019). This hypothesis was rooted in the framework of predictive coding, which views attention not just as a selective filter, but as a dynamic modulator of the precision of sensory signals (Summerfield and Koechlin, 2008; Itti and Baldi, 2009; Jiang et al., 2013).

The results from this experiment provided evidence in support of this hypothesis, partly addressing the perceptual uncertainty of interoceptive awareness. When participants focused on their internal bodily sensations, increased activation was observed in regions such as the bilateral middle insula and supplementary motor area, known for their involvement in higher-order cognitive functions and attention modulation (Kurth et al., 2010; Ruan et al., 2018). This finding is crucial as it indicates that these brain regions are actively involved in recalibrating how interoceptive signals are processed and interpreted, going beyond the mere reception of these signals in the dorsal posterior insula (Cechetto and Saper, 1987; Zhang et al., 1998; Saper, 2002; Evrard, 2019). Furthermore, the findings from this experiment lend substantial support to the predictive coding model's concept of attention. According to this model, attention plays a crucial role in adjusting the precision of sensory information, shaping our perception based on the brain's predictions and the actual sensory input. This experiment's results underscore the idea that attention involves a complex process of modulating the precision of

interoceptive signals, thereby influencing how these signals are processed, integrated, and ultimately, how they contribute to the perceptual uncertainty of interoceptive awareness.

Overall, the insights gained from Experiment 1 contribute significantly to our understanding of the brain's processing of interoceptive signals. By demonstrating that areas beyond the dorsal posterior insula are actively involved in this process, and that the brain exhibits a preferential response to interoceptive signals under directed attention, this research challenges existing perceptions of sensory processing. It underscores the importance of considering the predictive coding model in explaining not just interoceptive awareness but potentially other aspects of sensory perception and cognitive processing as well.

Building upon the findings of the first experiment, Experiment 2 investigated how the brain differentiates between various interoceptive modalities, with a specific emphasis on cardiac and gastric sensations. This experiment was designed to validate the hypothesis that different interoceptive modalities would induce distinct patterns of brain activation in regions implicated in the modulation of sensory precision, rather than the primary sensory region, as the physiological inputs remained constant. This hypothesis is critical in the context of the predictive coding framework, which posits that the brain constantly adjusts the precision of certain sensory signals to be perceived.

The results from Experiment 2 provided significant insights into the understanding of interoceptive awareness. The study revealed that directing attention toward specific interoceptive sensations led to unique activation patterns in the brain. Notably, focusing on cardiac sensations primarily activated regions in the right anterior insula, a region associated with processing arousal (Craig, 2009; Oppenheimer and Cechetto, 2016; Hassanpour et al., 2018). In contrast, attention to gastric sensations engaged not only the insular cortex but also additional cortical areas involved in higher-order processing, such as the lateral orbitofrontal area. This finding is pivotal as it underscores the brain’s capacity to process different interoceptive modalities in a distinct and modality-specific manner, especially out of the dorsal posterior insula, or primary interoceptive cortex. These findings challenge the traditional view that sensory processing is modular and uniform across different modalities at the primary sensory area (Cechetto and Saper, 1987). Instead, they support a more dynamic

and integrative approach to perceptions, where the brain's response to various interoceptive stimuli is influenced not only by their primary sensory characteristics but also by the attention-driven modulation of their precision. By revealing the role of attention in modulating the relative precision of interoceptive signals, the study contributes to a more comprehensive understanding of how the brain constructs interoceptive awareness.

In conclusion, the collective findings from these two experiments significantly elaborates on the insular activation related to the role of attention in interoceptive awareness. These studies provide evidence supporting the concept that the brain's approach to sensory perception, including the awareness of internal bodily states, is more dynamic and integrative than stimulus-driven, as previously understood in traditional perceptual models. The implications of these results for the field of cognitive neuroscience are profound, offering perspectives on the mechanisms through which attention and the brain's predictive abilities shape our perception of internal bodily states. By showing how different regions of the insula are selectively activated in response to various interoceptive awareness and how attention modulates them, the present experiments provide valuable insights into the brain’s complex processing of sensory information. This has broad implications for our understanding of various psychological and physiological conditions and opens up new avenues for research into how altered interoceptive processing may contribute to these conditions. Overall, these studies mark a significant step forward in our comprehension of sensory processing and the intricate workings of the human brain.

Relative Precisions Across Sensory Modalities

Experiment 3 in my research series played a crucial role in examining the dynamic interplay between external sensory cues and interoceptive awareness. The focus was on how auditory feedback synchronized with heartbeats influences interoceptive inference. The experiment was designed to show how external stimuli, specifically auditory cues, can integrate with and modulate internal bodily sensations, affecting the process of perceptual inference (Ainley et al., 2016; Hodossy et al., 2021). This exploration is significant as it extends the understanding of interoceptive awareness beyond internal bodily states to include the integration and influence of external stimuli.

The findings of Experiment 3 revealed that participants' subjective experiences, particularly their perceptions of the synchronicity and strangeness of artificially generated heartbeat sounds, significantly influenced their judgments about the source of these sounds. This observation provides valuable insights into how attention and prediction shape interoceptive awareness. It suggests that perceptual inference related to heartbeats is heavily influenced by individuals' subjective interpretations of sensory congruence, rather than solely by the objective attributes of the stimuli. This aligns with the Bayesian perception models, where perception is considered an inferential process based on a combination of sensory data and prior beliefs or expectations (Hohwy, 2012; Clark, 2013). The study thus supports the predictive coding framework by demonstrating that perception, particularly in the context of interoceptive awareness, involves an inferencial process influenced by both internal and external sensory inputs. More specifically, Experiment 3 elaborates on how external stimuli can be integrated into the perceptual inference about the internal state of the body, highlighting the interplay of attention, prior expectations, and cross-modal sensory integration in shaping our awareness of internal bodily states. This is contrasting to the framework of traditional perceptual models, such as those focused on modular sensory processing, as the influence of external stimuli on interoceptive awareness was often overlooked or underemphasized.

Experiment 4 in my series of studies presents a detailed examination of how interoceptive awareness is impacted by external auditory stimuli, offering new insights into the interaction between different sensory modalities. This study aligns with the principles of predictive coding, particularly in its emphasis on how

perceptual inference is influenced by the relative precision of sensory inputs (Hohwy, 2012; Allen and Tsakiris, 2018). The experiment set out to explore the impact of auditory distractors on interoceptive awareness, particularly in the context of heartbeat perception tasks.

The results of Experiment 4 are significant in demonstrating that auditory distractors can indeed disrupt interoceptive awareness. Participants exhibited reduced perceptual accuracy, confidence, and intensity in tasks involving the perception of their heartbeat, suggesting a clear impact of the auditory stimuli on interoceptive processing. This disruption occurred without any changes to the actual physiological status, indicating that the effect was more purely perceptual. These findings underscore the concept of relative precisions assigned to all sensory information, as postulated in predictive coding, where attention plays a pivotal role in determining the weighting of different sensations (Feldman and Friston, 2010; Jiang et al., 2013). In this context, the introduction of auditory distractors appeared to skew the precision weighting in favor of the external auditory stimuli, consequently leading to a diminished interoceptive awareness. Furthermore, this study shed light on the role of individual differences in shaping perception, a factor that is often highlighted in predictive coding models as priors (Summerfield and Koechlin, 2008; Summerfield and Egner, 2009; Diamond, 2019). Differences in factors such as heart rate variability and individual sensibility to bodily sensations were observed to significantly influence the degree to which auditory distractors affected interoceptive awareness. This finding aligns with the concept of individual priors in predictive coding, which posits that personal background and physiological traits can influence how sensory information is processed and perceived. Such individual differences can determine the extent to which external stimuli impact the perception of internal states, thereby highlighting the personalized nature of sensory processing.

In comparing the results of Experiments 3 and 4, a comprehensive picture emerges of how interoceptive awareness is influenced by the interaction and balancing of multiple sensory modalities. These studies collectively illustrate that attention does not operate in isolation but is heavily influenced by the relative precision of both internal and external sensory inputs (Ainley et al., 2016; Allen and Tsakiris, 2018; Corcoran et al., 2021). This finding challenges traditional perceptual models, which often view sensory modalities as operating more independently. The outcomes from these experiments suggest a more

integrated approach to understanding sensory processing, where the brain is continuously balancing and integrating information from various sources to construct a coherent perceptual experience (Ransom et al., 2017, 2020; Nikolova et al., 2022). In conclusion, Experiment 4, along with the findings from Experiment 3, significantly contributes to our understanding of the perceptual mechanisms underlying interoceptive awareness. By highlighting the role of attention in modulating the precision of sensory inputs and demonstrating the impact of external stimuli on the perception of internal bodily states, these studies provide strong empirical support for the predictive coding framework. They also expand our understanding of human perception, emphasizing the importance of considering the interplay between different sensory modalities and individual differences in shaping our perceptual experiences. These insights have important implications for cognitive neuroscience, offering a more nuanced and integrated perspective on how the brain processes and interprets sensory information.

Towards Unified Perceptual System Incorporating Interoceptive Signals

Furthermore, Experiment 5 represented a critical advancement in understanding the interplay between interoceptive sensations and visual perception within the predictive coding framework. The study was designed to validate the hypothesis that an increased precision in interoceptive signals could significantly impact the processing of other sensory modalities, as suggested in the form of arousal interference on exteroceptive sensitivity (Allen et al., 2016; Hauser et al., 2017; Al et al., 2020; Galvez-Pol et al., 2022b). By engaging participants in dot motion tasks that were not directly related to primary visual tasks, the experiment provided a novel platform to assess how altering the precision of interoceptive sensations, specifically heartbeats, affects visual task performance and decision-making processes.

The primary aim of this experiment was to explore whether heightened attention to interoceptive cues could influence subjective confidence in visual perception. The results were revealing: participants who focused more on their interoceptive cues, notably heartbeats, demonstrated a significant shift in their subjective confidence during visual tasks. This was evident in their increased conservative bias in visual judgments, as indicated by higher meta-c ratings. This observation is particularly intriguing as it suggests a recalibration of visual cognition following task-irrelevant interoceptive attention. According to the predictive coding model, this outcome supports the idea that the brain continuously updates its perceptual hypotheses and weightings in response to varying sensory inputs (Feldman and Friston, 2010; Apps and Tsakiris, 2014; Ainley et al., 2016). In this case, enhanced interoceptive precision seems to have influenced the cognitive appraisal process, altering how participants judged their visual perceptions. However, it's noteworthy that while there was a shift in subjective confidence, the accuracy of visual perception or metacognitive efficiency, measured by d' and M-ratio respectively, did not show corresponding changes. This finding is critical as it indicates that while interoceptive attention can alter subjective aspects of visual cognition, it does not necessarily impact the objective accuracy of these perceptions. This result adds a nuanced understanding to the hierarchical nature of the predictive coding, illustrating that sensory modalities can influence each other in complex ways that go beyond mere perceptual layers (Friston and Kiebel, 2009; Friston, 2012).

The results of Experiment 5 not only enhance our comprehension of the predictive coding framework but also suggest the necessity to reevaluate traditional models of sensory processing. These traditional models often view sensory modalities as operating largely independently (Banks and Krajicek, 1991; Massaro and Cowan, 1993). The experiment challenges this view, highlighting the importance of considering the bidirectional influence between interoception and exteroception. It sheds light on the complex mechanisms underlying sensory integration and emphasizes the multifaceted role of interoception in cognitive processes. The findings might call for revisions to existing models in areas such as object recognition and perceptual processing, advocating for a more integrated approach to understanding sensory perception. The experiment underscores the dynamic nature of sensory processing, where internal and external stimuli are continuously and interactively influencing each other, shaping our cognitive experiences and perceptions.

Future Directions in Interoception Research

Recent advancements in our understanding of interoception, particularly through a Bayesian framework, have significantly deepened our comprehension of the interplay between internal bodily states and cognitive-emotional processes (Barrett, 2017; Babo-Rebelo and Tallon-Baudry, 2018; Di Lernia et al., 2018; Seth and Tsakiris, 2018; Petzschner et al., 2021; Unal et al., 2021). This progression aligns with the insights garnered from the current research, which highlights the role of attention in interoceptive awareness and its perceptual uncertainty. In the Bayesian model, the brain is conceptualized as a generator and updater of predictions about internal bodily states, intricately intertwined with cognitive and emotional processing. This perspective has illuminated how the brain interprets interoceptive signals, not merely as passive receivers of bodily information, but as active constructors of perceptual reality based on internal predictions and external feedback (Pezzulo et al., 2015; Ainley et al., 2016; Stephan et al., 2016). By employing a Bayesian approach, researchers have been able to model the brain's inferential processes, revealing how it anticipates, responds to, and learns from interoceptive inputs. This understanding bridges the gap between the physical sensations within the body and the subjective experiences they evoke, offering a more comprehensive view of perceptual experiences.

The influence of interoceptive sensations on higher cognitive functions represents an emerging area of research with significant implications for our understanding of human cognition (Park and Tallon-Baudry, 2014; Azzalini et al., 2019; Rebollo et al., 2021b). Building upon the insights from recent studies, it's evident that visceral synchrony with external stimuli—a core aspect of interoception—plays a crucial role in shaping various cognitive processes such as decision-making and memory. For instance, the temporal alignment between visceral events, such as heartbeats, and exteroceptive inputs has been shown to influence the processing of sensory information (Garfinkel and Critchley, 2016; Al et al., 2020; Galvez-Pol et al., 2022c), suggesting a deep interconnection between our internal bodily state and how we perceive the external world. This interplay offers fertile ground for future investigations, especially in understanding how visceral synchrony might affect attentional processes and information encoding in memory tasks (Garfinkel et al., 2013; Umeda et al., 2016; Terasawa and Umeda, 2017; Messina et al., 2022).

In the context of affective science, research has suggested a direct link between the perception of internal bodily states and the emotional valence attributed to external events (Barrett et al., 2004; Carvalho and Damasio, 2021). This relationship posits that interoceptive processing could be a key factor in both the development and treatment of emotional disorders. For instance, individuals with anxiety or mood disorders often exhibit altered interoceptive awareness and relevant neural activation (Wiebking and Northoff, 2015; Wiebking et al., 2015), which could be contributing to or exacerbating their emotional symptoms (Paulus and Stein, 2010; Stephan et al., 2016). Future research could focus on developing therapeutic interventions that target interoceptive processing, potentially offering new pathways for treating these disorders. Mindfulness and body awareness therapies, which focus on enhancing interoceptive awareness, could be particularly effective in this regard and warrant further exploration (Fischer et al., 2017; Palascha et al., 2021; Heim et al., 2023). There's also a growing interest in how interoceptive signals shape our understanding of complex emotional experiences such as empathy and compassion. Given that these emotions involve an understanding or resonance with others' emotional states, interoceptive awareness might play a crucial role (Schaefer et al., 2012; Ondobaka et al., 2017).

The exploration of the relationship between interoceptive signals and the concept of self represents a burgeoning field that intertwines bodily awareness with our understanding of identity, agency, and spatial orientation. Recent studies suggest that interoceptive signals, by informing us about the internal state of our body, play a crucial role in shaping our sense of self, influencing everything from the first-person perspective to self-agency. A key area of future research in this domain is the investigation of how interoception contributes to the development and maintenance of the first-person perspective (Park and Tallon-Baudry, 2014; Tallon-Baudry et al., 2018). This perspective is fundamental to human experience, encompassing the sense of being an observer within a body that interacts with the external world. Another intriguing avenue is the investigation of interoception’s role in self-perception, particularly in how we distinguish between self-generated and externally generated stimuli (Ainley et al., 2013; Isomura and Watanabe, 2020). This distinction is central to the experience of agency, the sense that we are the ones initiating our actions. Research could focus on how interoceptive signals inform the brain's attribution of actions to the self, potentially illuminating mechanisms underlying disorders

of agency, such as schizophrenia, where this attribution can be distorted.

The sense of body ownership, the feeling that our body belongs to us, is another aspect intimately linked with interoception (Filippetti and Tsakiris, 2017; Salvato et al., 2020). Future studies could delve into how interoceptive processing contributes to this sense, particularly how it integrates with exteroceptive and proprioceptive inputs to construct a coherent body image. This research could have implications for understanding body image disorders and developing more effective treatments for these conditions (Zamariola et al., 2017; Todd et al., 2020). Additionally, interoception's influence on self-related cognitive functions, such as self-referential processing and autobiographical memory, offers a rich field for exploration (Babo-Rebelo et al., 2016; Muir et al., 2017). Researchers could examine how internal bodily states affect the way we recall personal experiences and perceive our identity over time. Such studies could lead to better understanding of conditions like depression and anxiety, where these self-related processes are often altered.

Concluding Remarks

In closing, this thesis represents a significant journey through the largely uncharted territory of interoceptive awareness. The surveys conducted in the initial sections have provided a solid grounding in the neural foundations and historical evolution of interoception research. A critical aspect of this thesis was to challenge and extend beyond applying perceptual models of cognitive psychology to the realm of interoceptive awareness. While highlighting their limitations, I suggested the adoption of the Bayesian brain hypothesis as a foundational model of a unified perceptual model, including interoception. The heart of this thesis lies in the series of empirical experiments that investigated the perceptual mechanisms underlying interoceptive awareness, providing support for inductive ideas derived from the predictive coding framework. This attempt has highlighted the role of interoceptive attention in facilitating interoceptive awareness, by modulating relative precisions across all sensory modalities. It also demonstrated how individual differences in prior predictions and expectancies exert a profound influence on interoceptive awareness. This work provides a foundation for future research aimed at unraveling the intricate dynamics of interoceptive awareness and its implications for various facets of human behavior and mental health, contributing to the broader fields of cognitive neuroscience and psychology.

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With utmost gratitude,

Haruki

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