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Review article

Interoceptive technologies for psychiatric interventions: From diagnosis to clinical applications

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ABSTRACT

Interoception—the perception of internal bodily signals—has emerged as an area of interest due to its implications in emotion and the prevalence of dysfunctional interoceptive processes across psychopathological conditions. Despite the importance of interoception in cognitive neuroscience and psychiatry, its experimental manipulation remains technically challenging. This is due to the invasive nature of existing methods, the limitation of self-report and unimodal measures of interoception, and the absence of standardized approaches across disparate fields. This article integrates diverse research efforts from psychology, physiology, psychiatry, and engineering to address this oversight. Following a general introduction to the neurophysiology of interoception as hierarchical predictive processing, we review the existing paradigms for manipulating interoception (e.g., interoceptive modulation), their underlying mechanisms (e.g., interoceptive conditioning), and clinical applications (e.g., interoceptive exposure). We suggest a classification for interoceptive technologies and discuss their potential for diagnosing and treating mental health disorders. Despite promising results, considerable work is still needed to develop standardized, validated measures of interoceptive function across domains and before these technologies can translate safely and effectively to clinical settings.

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1. Introduction

Interoception—the perception of internal bodily signals—plays an important role in driving emotion and decision-making processes (Allen and Friston, 2018; Khalsa et al., 2018; Petzschner et al., 2021), which may lead to severe impairments when dysfunctional in psychopathology (Khalsa et al., 2018; Maisto et al., 2021; Murphy et al., 2017). The study of interoception is therefore essential to the fields of cognitive neuroscience and psychiatry (Owens et al., 2018; Paulus et al., 2019). However, the manipulation of interoception in the laboratory remains a challenge, due to the invasiveness of current methods and the lack of standardized methods (Garfinkel et al., 2022; Nord and Garfinkel, 2022; Khalsa et al., 2018). The historical emphasis on the brain as the sole substrate for cognition and the corresponding instrumentation (e.g. single-person brain scanners) has led to an underestimation of the role of spinal and peripheral signals (see glossary) in shaping human behavior. Early attempts to manipulate body perception include the studies of Razran (1961) in interoceptive conditioning (see glossary and subsection 2.4.). Valins (1966) introduced the notion of "misattribution of arousal", where controlled manipulation (e.g. false auditory heart rate) leads subjects to misinterpret the cause of their physiological arousal. Later, Cacciopo introduced the concept of somatovisceral illusions (Cacioppo et al., 1992), whereby stimulation leads to cognitive interpretation and emotional response. In clinical settings, interoceptive exposure is a well-validated intervention for generalized anxiety disorders (Furer and Walker, 2005; Schmidt and Trakowski, 2004), which consists in the controlled induction of the somatic symptoms ordinarily associated with a threat response to train the patient to self-regulate. These methods provide an exciting opportunity for neuroscience and psychiatry—see e.g., (Nord and Garfinkel, 2022) and (Weng et al., 2021). Despite these advancements, there remains a significant gap in the comprehensive understanding of these methods, stemming from the distinct research approaches in psychology, physiology, psychiatry, and engineering. This article endeavors to bridge this gap, elucidating the intricate interplay between interoceptive mechanisms, hierarchical predictive processing, and their potential implications for mental health disorders. Previous attempts have been made to systematically examine "interoceptive technologies" (e.g., Schoeller et al., 2019; Weng et al., 2021). While these articles focus on affective neuroscience research, here in contrast, we place the emphasis on clinical applications, specifically exploring the potential of technologies that manipulate interoceptive channels in diagnosing and treating mental health disorders. To this end, we review the existing paradigms for manipulating interoception the laboratory (e.g., interoceptive modulation), their underlying mechanisms (e.g., interoceptive conditioning), and clinical applications (e.g., interoceptive exposure) and suggest a general classification for interoceptive technologies into three abstract classes—1) artificial sensations, 2) interoceptive illusions, and 3) emotional augmentation—depending on their potential for intervening on interoception.

We approach this problem through the lens of predictive processing (PP), a theoretical framework in which the brain actively generates predictions about the environment and bodily states to continuously adapt to a changing world (Rao and Ballard, 1999; Bastos et al., 2012; Shipp, 2016; Marshall et al., 2018). In PP, minimizing prediction errors (see glossary) is essential for maintaining homeostasis and adaptive behaviors. Crucially, to achieve accurate predictions, the brain needs to incorporate information from both the environment (a.k.a., exteroception) and internal bodily states (a.k.a., interoception), leading to the formation of a sense of self (Allen and Tsakiris, 2019; Tsakiris, 2016). The relevance of interoceptive technologies for psychopathology can be framed as follows. If healthy psychology can be equated with optimal inference about the state of the world (and our bodies), it follows that psychopathology can be characterized as false inference (also known as dysfunctional beliefs in clinical psychology, or maladaptive schema). These false inferences can be based on (i.e., adaptations to) past experiences, traumas, cultural influences, or irrational thought patterns. They often involve cognitive distortions such as generalizations, overgeneralizations, jumping to conclusions, magnifying or minimizing events. At the extremes, this amounts to inferring things are there when they are not (e.g. hallucinations and delusions) or inferring things are not there when they are (e.g. agnosia and spatial neglect). From a psychological perspective, false inference in many mental health disorders has been accounted for by aberrant attention or salience (Kapur, 2003; Lawson et al., 2014; Parr et al., 2018a; Powers et al., 2015). In a Bayesian inference perspective, dysfunctional salience amounts to aberrant precision control (see glossary), where precision denotes the confidence placed in prediction errors (mirroring the reliability of the stimulation that causes them) within the hierarchy of information processing (see glossary)—i.e. a high precision will favor bottom-up ascending prediction errors while a low precision will bias perception towards top-down prior beliefs. We detail further the relationship between precision, prediction errors, and dysfunctional beliefs in the first section of the article. An increasing body of evidence indicates that *bodily signals are crucial in driving precision control* (Ainley et al., 2016; Uraguchi et al., 2022; Sennesh et al., 2022) and disruption of interoceptive signals can lead to false thinking and maladaptive behavior (Murphy et al., 2017; Khalsa et al., 2016; Nayok et al., 2023; Berner et al., 2019; Feinstein et al., 2022). This speaks to the importance of exploring reliable body-based interoceptive interventions for mental health disorders and the potential for tailoring specific interventions based on the patient's life history, mental health disorders, and symptoms. It has also been suggested that the dysregulation of bodily signals in psychopathology may offer an important way forward in terms of phenotyping in psychiatry and neuroscience (Torregrossa et al., 2019).

With the goal of providing a shared nomenclature for multidisciplinary research into interoceptive processes, this article provides a primer on interoception and its role in hierarchical predictive processing (reviewed in Section 2), reviews the current state of the art in interoceptive technologies (Section 3), and their clinical applications (Section 4). Examples for such technologies include: a) artificial sensations that directly influence bodily signals, b) interoceptive illusions that modulate the context to influence interoception, and c) systems of emotional augmentation. It is important to note that these categories are conceptual abstractions intended to aid in the understanding and discussion of current and future interoceptive interventions. A common thread is the role of precision in shaping the hierarchical predictive processing of interoceptive signals, as exposed in the first section of the article. By manipulating precision, experimenters can *modify the weight given to sensory inputs and interoceptive priors*, thereby influencing perception, emotion, and behavior. However, while the three categories differ fundamentally in their mechanisms of action, targets of intervention, and potential clinical applications, they are not mutually exclusive and may overlap in practice. For example, stimulating artificial sensations may indeed activate low-level receptors but could also affect higher-level cognitive and emotional processes, e.g., as in the case of patient expectations during the breath-holding test. Proper blinding and control procedures would be needed to truly isolate and directly manipulate those components. These categories therefore serve as heuristic tools, providing a framework to guide both research and clinical applications, but they should not be understood as concrete, isolated phenomena. They are meant to be refined or redefined as our understanding of interoceptive mechanisms and technologies advance further. Table 1.

2. A primer on interoception and its role in emotion

2.1. What is interoception?

Interoception refers to the process by which the body's internal physiological signals are detected and integrated within the brain. Physiologically, interoception comprises various streams or channels (thermoception, respiratory, cardiovascular, chemosensory, gastrointestinal, circadian, rectogenital) transducing bodily signals (e.g., thermal, biochemical, mechanical changes) into electrical (i.e., neural) or chemical (i.e., hormonal) information, integrated within the brain into a coherent representation (see Table 2). One can classify interoceptive systems according to either (1) the classes and channels of information (e.g., respiratory, cardiovascular, gastrointestinal, genitourinary, endocrine, etc). (2) the receptor cells and generation of signals (e.g., mechanoreceptors, chemoreceptors, thermoreceptors, osmoreceptors, humoral receptors, etc.), or (3) the various afferent pathways (autonomic/neural vs. humoral [immune or endocrine]) (Carvalho and Damasio, 2021; Quadt et al., 2018). For instance, interoceptive systems can be classified in terms of organ systems (e.g., cardiovascular vs. rectogenital) and within each system, we can invoke the type of receptors (e.g., baroreceptors, chemoreceptors present in blood vessels [e.g., carotid body/sinus] and heart chambers) and the afferent pathways (i.e., involved afferent fibers, etc.). For the sake of simplicity, and with an eye for engineering, we highlight in Table 2 the specific channels of information, their respective set points, sensors, fibers, and their measurement instruments.

Table 1
Glossary of technical terms.

Prediction error: In the context of active inference, prediction error refers to the discrepancy or mismatch between the predictions generated by a model and the observed sensory outcomes. From a neurobiological perspective, prediction error is thought to be encoded by the activity of neurons in various brain regions, particularly those involved in reward processing and learning. For example, the dopaminergic system, which includes neurons in the substantia nigra and ventral tegmental area, plays a crucial role in signaling reward prediction errors. Dopamine neurons release dopamine in response to unexpected outcomes, contributing to the learning and updating of generative models used in active inference.

Active inference: Active inference is a framework for understanding perception and action as processes that minimize prediction errors through the active selection of sensory information. From a neurobiological standpoint, active inference involves the hierarchical integration of multiple brain systems. The prefrontal cortex, which is involved in decision-making and cognitive control, plays a key role in generating predictions and selecting actions to minimize prediction errors. The parietal cortex assimilates sensory information with internal models, while motor areas, such as the motor cortex and basal ganglia, execute motor commands based on the predictions and action plans generated by active inference.

Interoceptive hierarchy: The interoceptive hierarchy refers to the hierarchical organization of neural processing related to bodily sensations and signals. At lower levels of the hierarchy, primary interoceptive areas receive sensory input from the body, such as the insular cortex and somatosensory cortex. Higher levels of the interoceptive hierarchy involve association areas and prefrontal regions, which integrate interoceptive signals with cognitive and emotional processes. The hierarchical organization allows for the construction of increasingly abstract representations of bodily states. Neurobiologically, the interoceptive hierarchy is characterized by the connectivity between these brain regions and the flow of information through interoceptive pathways.

Interoceptive conditioning: A form of classical conditioning that involves pairing an interoceptive stimulus (the conditioned stimulus (CS)) with an aversive stimulus (the unconditioned stimulus (US)). Through repeated pairings, the interoceptive CS acquires the capacity to elicit anticipatory defensive responses similar to those provoked by the US.

Interoceptive modulation: The act of deliberately altering interoceptive signals without necessarily forming new conditioned associations. Here we use the term artificial sensation to refer to the product of interoceptive modulation, specifying the engineered outcome of such modulation typically induced by an experimenter.

Interoceptive exposure: A clinical intervention used to systematically expose individuals to anxiety-inducing bodily sensations in a controlled environment, aiming to reduce fear and improve symptom management. Utilizing principles of fear extinction and habituation, IE employs both natural and artificially-modulated sensations to help individuals confront and gradually adapt to discomfort, primarily in the context of anxiety disorders.

Interoceptive signals: Interoceptive signals are sensory information originating from within the body that provide feedback about bodily states such as heart rate, respiration, temperature, and hunger. These signals are transmitted through specialized pathways, including the autonomic nervous system and specific sensory pathways. Neurobiologically, interoceptive signals are processed by dedicated brain regions involved in interoception, such as the insular cortex and anterior cingulate cortex. These regions integrate interoceptive signals with other cognitive and emotional processes, contributing to the generation of predictions and the computation of prediction errors.

Interoceptive model: The interoceptive model is a generative model that generates predictions about internal bodily states based on incoming interoceptive signals and prior knowledge. Neurobiologically, the construction and updating of interoceptive models involve the activity of brain regions implicated in interoception, such as the insular cortex and anterior cingulate cortex. These regions, along with other interconnected regions, contribute to the integration of interoceptive signals with prior beliefs or expectations, allowing for the generation of accurate predictions and the requisite computation of prediction errors.

Precision control: Precision control refers to the process of adjusting or modulating the precision assigned to predictions or prediction errors, based on the level of confidence or uncertainty they are afforded. From a neurobiological perspective, precision control involves the modulation of synaptic efficacy (i.e., postsynaptic gain or excitation-inhibition balance) to optimize the processing and integration of sensory information. This modulation is thought to be mediated by neuromodulatory systems, such as the noradrenergic and cholinergic systems, which regulate the gain afforded to — and ensuing salience of — sensory signals. Additionally, the balance of excitation and inhibition in neural circuits contributes to precision control, enabling context sensitive weighting of prediction errors and prior expectations (in a way that can be read as establishing the right attentional set).

2.2. *Interoception as hierarchical predictive processing*

In recent decades, the classic Helmholtzian idea about the brain behaving as a prediction engine has resurfaced under the umbrella term of predictive processing (PP). Within a hierarchical model of sensory integration, the brain entails a predictive model in which ascending prediction errors are conveyed to higher levels to update expectations about the state of the world (Fig. 1). These expectations in turn provide descending predictions to lower hierarchical levels. At any level, signals are compared with top-down predictions to form a prediction error—informing expectations at the higher level (Bastos et al., 2012; Parr et al., 2018a; Rao and Ballard, 1999; Shipp, 2016). This process of belief updating continues until prediction error is minimized throughout the hierarchy; thereby furnishing posterior expectations at higher levels of abstraction that provides the best account of sensory input at the lowest level. This formulation of perceptual synthesis in the brain is arguably one of the most influential accounts in cognitive neuroscience. However, it does not say much about action. The framework of "active inference" (see glossary) extends the predictive processing account of brain function by hypothesizing that the same imperatives underlie both perception and action; namely, resolving uncertainty or minimization of prediction errors. For further reading, we refer the reader to the rich literature on the role of forward (i.e., generative) models in the motor system (Bhushan and Shadmehr, 1999, 1998; Wolpert and Miall, 1996). In the domain of interoception, the predictions of visceromotor and autonomic sensations can be regarded as providing set points for motor and autonomic reflexes, i.e., homeostasis (Friston et al., 2011; Parr et al., 2018b; Pezzulo et al., 2015; Seth and Friston, 2016). At higher levels, interoceptive inference concerns the maintenance of these physiological variables on a wider spatiotemporal frame, a process known as *allostasis* (Tschantz et al., 2022).

Notably, early life experiences play an essential role in shaping interoceptive processes (Hechler, 2021; Corcoran et al., 2023). During development, interoceptive signals shape the infant brain's understanding of its own physiological needs and responses—and their communication to the caregiver (Murphy et al., 2017; Lockwood and Perris, 2012; Filippetti, 2021; Burleson and Quigley, 2021; Fotopoulou et al., 2017). In turn, the caregivers' responses to the infant's interoceptive signals, such as hunger, discomfort, or emotional distress, establish regulatory patterns that underwrite the infant's ability to interpret and respond to bodily signals (Lockwood and Perris, 2012;

Table 2

Classification of 4 interoceptive systems based on human physiology (i.e. set points, receptor fields, fibers), technology (e.g. sensors and effectors), and measurement instruments. Note that each system is susceptible to the influence of cycles: e.g. infradian (e.g. deep sleep, rapid eye movement sleep), circadian (e.g. sleep-wake, temperature, hunger control via ghrelin/leptin, diurnal cortisol), and ultradian (e.g. menstrual cycles in women). We extracted the data from (Berntson and Khalsa, 2021; Chen et al., 2021; Felten et al., 2016; Khalsa et al., 2018). EEG: electroencephalography. MEG: magnetoencephalography. HR: heart rate. BP: blood pressure. ASD: autism spectrum disorder. GAD: generalized anxiety disorder. CN IX: glossopharyngeal nerve.

System	Human physiology	Technology	Measurement Interoception Task
Thermoception	**Receptor fields & fibers:** free nerve endings (Aδ and C fibers) projecting to spinal lamina I. **Set point:** 37° Celsius	**Sensors:** thermometer, CASE IV system; whole-room calorimeter **Peripheral actuator:** Peltier elements, room temperature	**The Dynamic Thermoception Task (DTT) (** Crucianelli et al., 2021**):** participants are stroked (on the forearm and palm in random order) with a thermode at reference temperatures of 30°, 32°, or 34 °C and are instructed to verbally indicate when they feel the same temperature again. The temperature is then increased or decreased in discrete steps until the reference temperature is reached or the maximum/minimum temperature is reached. **The Static Thermoception Task (STT) (**Heldestad et al., 2010a, 2010b**):** participants hold a response button and press it when they perceive a change in temperature. Warm and cold trials are presented, and the temperature changes at a rate of 1 °C/s.
Respiratory	**Receptor fields:** chemoreceptors sense and respond to partial pressures of arterial oxygen and carbon dioxide as well as blood pH. **Set point:** during normal unlabored breathing (i.e. eupnea), PaCO2 is maintained within a few mmHg of ~35 mmHg	**Sensors:** motion sensors (IMU), microphone, thermal camera at the nose, oxygen sensors, bioimpedance-based respiration sensors **Center actuator:** many substances can impact respiratory and heart rates. In the laboratory, the most widely used systems to affect cardiovascular changes are the CO2 and caffeine challenges. See also the respiratory resistance sensitivity task (Nikolova et al., 2022)	**The respiratory resistance sensitivity task (RRST):** Participants are shown a breathing visual and instructed to take two conscious breaths, one with standard resistance and one with altered resistance (breathing mask). They then rate which breath felt more difficult and indicate their confidence in their rating.Nikolova et al. (2022) **The Filter Detection Task (FDT),** developed by Harrison et al. (2021), combines an established interoceptive breathing task with a hierarchical model for analyzing signal detection data. It allows researchers to distinguish between decision bias and interoceptive sensitivity, enabling the comparison of metacognitive performance relative to interoceptive sensibility. **The respiratory occlusion discrimination task (RODT)** (Van Den Houte et al. 2021) measures individuals' ability to discriminate between different lengths of respiratory occlusions
Cardiovascular	**Receptor fields:** baroreceptors involving PIEZO1 and PIEZO2 ion channels (i.e., in the aorta and carotid arteries). **Fibers:** information from baroreceptors *(*i.e. in the carotid sinus) about increased arterial pressure travel the afferent axons of CN IX that project to the caudal nucleus solitarius, leading to decreased blood pressure and reflex bradycardia. Information from chemoreceptors in the carotid body, reporting CO2 levels (i.e. hypoxic state), travel along afferent axons of CN IX that project to the medullary caudal nucleus solitarius (Felten et al., 2016). **Set point:** the normal resting adult human heart rate is 60–100 beats per minute. Normal systolic blood pressure is about 130 mmHg	**Sensors:** heartbeat evoked potentials captured by EEG/MEG, stethoscope, electrodes (EEG, MEG), ultrasound, microphones, motion sensors	**Heartbeat Detection Task (HBDT)** (Dale and Anderson, 1978; Schandry, 1981)**:** Participants are instructed to silently count their heartbeats between two verbal signals. The experimenter records the heartbeat frequency using a Biopac MP150 Heart Rate oximeter connected to a Windows laptop. A 5-minute baseline is recorded, followed by three experimental trials of varying lengths. **Phase Adjustment Task (PAT)** (Plans et al., 2021)**:** Tones are presented at the participant's heart rate, but out of phase with heartbeats. Participants adjust the phase relationship between tones and heartbeats until they perceive them to be synchronous using a dial. **CARdiac Elevation Detection (CARED) Task (** Ponzo et al., 2021**):** The CARED task aims to capture objective interoceptive accuracy and attention over an extended period. Participants wear a smartwatch collecting continuous heart rate data, and notifications are sent according to a predefined algorithm. Participants indicate whether their heart rate is higher than usual and report their confidence, while avoiding confounds from high-intensity activities or emotional states.
Gastrointestinal	Gastrointestinal humoral receptors, involving leptin/ghrelin/cholecystokinin; hunger contractions regulate food intake; secretion of saliva by salivary glands: basal - 800 – 1500 mL/day; vomiting, gastric motility, EGG phase and frequency	**Sensor:** electrogastrography, salivaomics	**Water Load Tes (**Van Dyck et al., 2016**):** The water load test is a diagnostic procedure used to evaluate gastric emptying and stomach motility by having the patient rapidly consume a predetermined amount of water, usually around 500 mL, and then monitoring for symptoms like fullness or nausea.

Harshaw, 2008). Fairhurst et al. (2014) observed that 9-month-old infants exhibited a decrease in heart rate when caregivers lightly and moderately stroked them at a speed of approximately 3 cm per second. This speed aligns with the response rate of unmyelinated C-tactile fibers, which are responsible for transmitting interoceptive information (Löken et al., 2009). These early experiences with caregivers form the basis for the development of cognitions, which guide the child's perception and interpretation of bodily sensations throughout life.

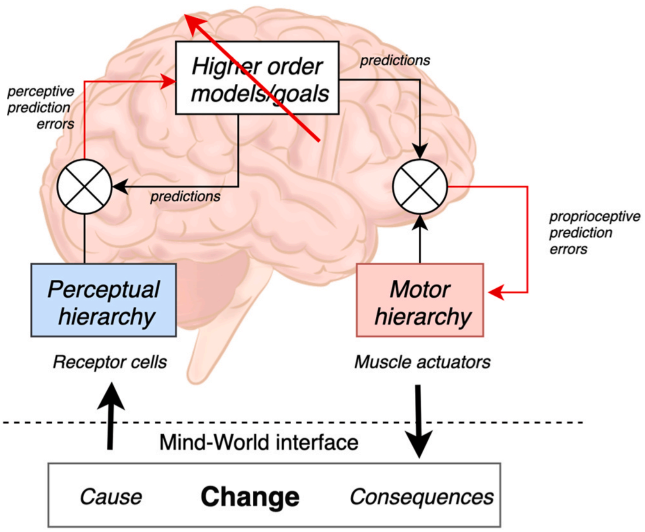

Fig. 1. Perception models changes in states of the world detected by receptor cells (e.g., in the retina) along afferent fibers and the perceptual hierarchy. In this control diagram, ⊗ denotes a comparator. The red arrows denote inference and learning in engineering terms (i.e., driven by prediction errors) that compare (descending) predictions with (ascending) sensations. Cognition and higher-order processing attempt to predict sensory input and future states of the world based on available (generative) models, minimizing prediction error. Action organizes the motor hierarchy in an attempt to actively control the efferent consequences of ongoing events; Namely, by modifying causes anticipated through perceptual means, thereby altering the system dynamics to make them more predictable (i.e., less surprising). Though not specified in this diagram, perception can be further subdivided into interoception and exteroception; respectively, modeling changes in the internal and external world. Emotion—and related notions of selfhood—usually arise via predictive processing of interoceptive sensations, often known as interoceptive inference (Seth, 2013; Seth and Friston, 2016).
Adapted from (Schoeller et al., 2021).

Disruptions or mismatches in interoceptive signaling during this critical period can lead to the installment of what has been referred in Schema Therapy as early maladaptive schemas (Pilkington et al., 2020), as originally conceived by Young et al. (2003). For example, if caregivers consistently fail to respond appropriately to the infant's distress signals, the child may develop a mal-adaptive schema that their bodily signals are not reliable indicators of their needs being met, potentially leading to difficulties in self-regulation, both in the short term and in the long term when the child develops autonomy from the caregivers (Cassidy, 1994; Young, 2003; Lockwood and Perris, 2012). By providing consistent and responsive feedback to the child's interoceptive signals, caregivers contribute to the establishment of adaptive interoceptive schemas, fostering the child's ability to understand and regulate their internal states on their own. However, the disruption of these early interoceptive experiences can have long-lasting effects on the ability to accurately interpret and respond to bodily signals, ultimately leading to the development of mental disorders (Cassidy, 1994; Pilkington et al., 2020). Despite the essential role of early life experiences in shaping interoceptive processes, there is a notable lack of studies investigating dysfunctional interoception and maladaptive interoceptive schema in children and adolescents. For a recent topical review on altered interoception and mental health problems in children, see Hechler (2021).

2.3. *Interoception and emotion*

Even though interoception mostly occurs below the level of conscious awareness—e.g., cardiac, thermal, or respiratory regulation is below conscious control, unless years of training, acquired skills, or technological augmentation such as biofeedback systems—bodily signals have long been considered to be central for the emergence of emotions and feelings. William James famously argued "A purely disembodied human emotion is a nonentity" (Ellsworth, 1994). Experimental studies manipulating interoception typically concern the emotion of fear and the process of fear extinction (see review in 3.1.1) but how does interoception give rise to conscious feelings?

Historically, hypotheses about emotion construction date back to William James and Wilhelm Wundt, but in modern times, the hypothesis can be traced to work by Mandler in the 1980s (Mandler, 2003), Schachter & Singer (Schachter and Singer, 1962), Russell (Russell, 2021), and more recently, Feldman-Barrett (Barrett, 2017, 2006; Barrett and Simmons, 2015). In this view, emotions are a high-level construct or inference that provides *a simple explanation for concurrent sensations* (Barrett, 2017; Barrett and Simmons, 2015; Seth and Friston, 2016). Interoception figures in an important way in this kind of emotional inference, in the sense that being in an emotional state, e.g., 'I am anxious', will predict the consequences of being 'anxious' (why I may feel such or such changes). These consequences will, almost inevitably, include interoceptive sensations (e.g., gut feelings, some thermal changes, accelerated heart rate) that accompany the reallocation of attention towards bodily sensations or changes in the external world (Barrett, 2017; Barrett and Simmons, 2015; Craig, 2013, 2002; Seth and Friston, 2016). In turn, bodily sensations will usually feed back into the associated emotional state — e.g., throat sensation or dyspnea as both correlation and cause of fear and anxiety (Benke et al., 2017).

To make sense of this bidirectionality, Barrett (2017) introduced the distinction between interoceptive feeling (continuous) and emotion (discretized). According to Barrett's theory, the brain is constantly monitoring the body's physiological state and generating interoceptive feelings that provide information about bodily sensations such as heart rate, breathing, and digestion. These interoceptive feelings are continuous and vary in intensity and quality, but they are not inherently emotional, though they can be used as threat of pain in the case of unconditioned interoceptive stimuli (De Peuter et al., 2011). The brain can interpret interoceptive information in different ways depending on the context, past experiences, and cognitive appraisals, leading to the creation of discrete emotional states such as anger, fear, joy, and sadness. In fact, the integration of interoceptive and exteroceptive information is fundamental to the emergence of self-awareness (Suzuki et al., 2013). Emotions are not directly caused by interoceptive signals but are constructed by the brain to make sense of the ongoing stream of interoceptive information given external circumstances.

2.4. *Interoceptive conditioning*

Interoceptive inference is an essential link between emotional states and their attached bodily sensations (a.k.a., somatic markers) and technologies manipulating interoceptive signals may provide novel insight for nosology, diagnosis, and intervention in psychopathology. **"Interoceptive conditioning"** (IC) has been studied as a pivotal mechanism in emotional learning, as the associative pairing of internal bodily cues (conditioned stimulus (CS)) with emotionally or physiologically significant events (unconditioned stimulus (US)) (Van Diest, 2019; Gramsch et al., 2014; De Peuter, 2011; De Cort et al., 2012). Over time and through repetitive pairing, these internal cues can autonomously evoke emotional or physiological responses, laying the groundwork for complex emotional behaviors and self-regulation (De Peuter et al., 2011). For example, inhalation of CO2 can serve as an aversive US that causes unpleasant bodily sensations like breathlessness and heart pounding. When an odor CS is repeatedly paired with CO2 inhalation, the odor alone starts to elicit the same defensive reactions even without CO2, demonstrating interoceptive conditioning (Fannes et al., 2008). IC has been studied in drug tolerance (Wise et al., 2008; Bevins and Murray, 2011), eating disorders (Davidson, 1993; Oldershaw et al., 2011), pain (De Peuter et al., 2011), fatigue (Meagher, 2010), and anxiety disorders (Paulus and Stein, 2010; Deacon et al., 2013a, 2013b).

Table 3
Interoception and Psychopathology: This table provides a general overview of different interoceptive channels, corresponding measurement instruments, and their associations with mental health disorders.

Interoceptive channel	Psychopathology
Cardioception	Anxiety & Panic disorder: Ehlers 1995, 1992 found that patients with panic disorder had superior heartbeat perception compared to controls. Antony 1995 found no differences in heartbeat awareness at rest between panic disorder patients, social phobia patients, and non-anxious subjects, but all groups became more aware of cardiac sensations following exercise. Does 2000 reanalyzed multiple studies and found that accurate heartbeat perception was more prevalent in panic disorder patients compared to healthy controls, but no differences were found between panic disorder patients and other anxiety disorders.
	Substance use disorder: D'Souza 2018 found that low HRV was associated with greater severity of drug and alcohol symptoms in individuals with substance use disorders. Moon 2023 reviewed several studies and found that substance users generally had decreased resting HRV compared to healthy controls, and lower HRV was associated with stress, craving, and greater symptom severities. Tür 2017 reported cardiac complications, including high-degree AV-node conduction block and occlusive ST segment elevated myocardial infarction, associated with substance use, particularly synthetic cannabis and ecstasy. Frishman 2003 provided a broader overview of cardiovascular manifestations of substance abuse, including alcohol, amphetamines, heroin, cannabis, and caffeine.
	Post-traumatic stress disorder: Individuals with PTSD may have dysregulated heart rate interoception, characterized by altered HRV and autonomic dysregulation in response to trauma-related cues. Rabellino 2017 found that individuals with PTSD showed decreased high-frequency HRV during both sub- and supraliminal exposure to trauma-related cues. Hauschildt 2011 also found lower HRV in individuals with PTSD compared to controls, indicating decreased parasympathetic activity and inflexible response regulation. Cohen 1998 demonstrated that individuals with PTSD exhibited autonomic dysregulation at rest, which may explain their lack of autonomic response to trauma-related cues. Shalev 1998 found that elevated heart rate shortly after trauma was associated with the later development of PTSD.
	Major depressive disorder: Terhaar 2012 found that depressed patients had reduced accuracy in perceiving their own heartbeats compared to healthy controls. Terhaar 2012 and Pollatos 2004 both found that depressed patients had reduced amplitude of heartbeat evoked potentials. However, Dunn 2007 found that severely depressed individuals performed similarly to healthy controls in a heartbeat perception task, contradicting the expected findings.
	Eating disorders: Pollatos 2008 found that patients with anorexia nervosa displayed decreased interoceptive sensitivity compared to healthy controls (HBDT). However, Eshkevari 2014 found no significant difference in interoceptive sensitivity between individuals with eating disorders and healthy controls.
Respiroception	Panic and anxiety disorder: Biddle 1989 and Tiller 1987 both discuss how individuals with anxiety disorders may have altered perceptions of breathlessness, even in the absence of respiratory disease. Wilhelm 2001 further explores the role of dysregulated breathing in panic disorder, functional cardiac disorder, and chronic pain, highlighting the efficacy of respiration-focused treatment. Note that Stein 1995 found that patients with panic disorder exhibit irregular breathing patterns during sleep, which may be related to altered brainstem sensitivity to CO2.
	Obsessive-compulsive disorder: Han 2000 found that individuals with anxiety and somatoform disorders, including OCD, exhibited breathing instability and modulation of respiratory frequency and end-tidal CO2 concentration. Orepic 2022 explored the impact of interoceptive signals, particularly respiration, on self-voice perception and found that participants were better at discriminating self-voice from others' voices during the inspiration phase of the respiration cycle.
	Substance use disorder: Tiller 1987 found that patients with anxiety disorders had less sensitive perceptions of resistive loads during inspiration compared to normal subjects. Mustafaoglu 2022 found that patients with substance use disorders had lower lung function, respiratory muscle strength, and exercise capacity compared to non-smokers. Berk 2015 found that adolescents with substance use disorders exhibited hypersensitivity to aversive interoceptive stimuli, specifically in the insular cortex.
	Eating disorders: Bogaerts 2005 found that individuals with high negative affectivity (NA) were less accurate in perceiving respiratory volume, especially in distressing contexts. Tiller 1987 found that patients with anxiety disorders had reduced sensitivity in perceiving resistive loads during inspiration. Biddle 1989 highlighted the role of respiratory perception in panic disorder symptoms.
Thermoception	Panic and anxiety disorder: Fischer 2021 found that individuals with social anxiety disorder and panic disorder exhibited altered thermoregulatory responses, such as increased sweating and altered skin temperature. Federici 2019 demonstrated that panicogenic drugs and stimuli induced changes in thermoregulation related to hot flushes and chills in rats. Septiadi 2019 showed that there were differences in facial temperatures measured using thermal imaging among individuals with varying levels of anxiety.
	Mood and affective disorders: Raison 2015 proposes that afferent thermosensory signals contribute to well-being and depression, and activating warm thermosensory pathways may have therapeutic potential in the treatment of affective disorders. Salerian 2008 hypothesizes that brain temperature may influence mood, with lower temperatures being beneficial for depressive disorders and higher temperatures possibly associated with mania. Avery 1982 found that patients with affective disorder had higher nocturnal temperatures during depression compared to recovery and controls. Jain et al., found a difference in anhedonic depression in terms of aesthetic chills (Jain et al., 2023)
	Substance use disorder:Firth (1991) found that cocaine use is associated with thermoregulatory abnormalities, potentially due to hypothalamic damage. Levine 2012 found that drug utilization, including drugs associated with abnormal thermal homeostasis like amphetamines and cocaine, was prevalent among patients admitted for heatstroke. Dharmarajan 2001 highlights the risk of drug-related hyperthermia in the elderly, particularly those taking multiple medications.Gomez (2014) discusses how drugs can induce hyperthermia and produce specific clinical syndromes.

In the context of hierarchical predictive processing, IC can be computationally modeled as the updating of the brain's existing beliefs or "priors" with new sensory "likelihoods" to generate updated beliefs or "posteriors." These posteriors then inform future emotional and physiological reactions. In this model, the role of "artificial sensations" is paramount. The artificially generated interoceptive signals—ranging from artificial heartbeats to simulated thermal sensations— serve as controlled likelihoods. While interoceptive conditioning has been demonstrated through stimuli like CO2 inhalation, new wearable technologies allow more precise and customizable modulation of interoceptive signals. For instance, devices using haptic feedback or electrical muscle stimulation can present interoceptive stimuli directly to the body in consistent, repeatable ways to condition emotional responses (a phenomenon we explore in the next section under the umbrella term of "Emotional Augmentation"). Wearable sensors can also monitor physiological signals, allowing interoceptive stimuli to be delivered contingently based on an individual's internal state. Such technologies are essential to research the mechanisms of interoceptive conditioning and developing robust, personalized novel clinical applications for mental health disorders across interoceptive channels (Table 3).

3. Interoceptive technologies: intervening on bodily signals

Numerous systems and methods exist to intervene on bodily signals and induce affective, cognitive, or behavioral changes (Table 4, Fig. 2). These aim to modulate the interoceptive system, which monitors the physiological state of the body and contributes to the generation of subjective experiences such as emotions, feelings, and bodily sensations. In this section, we distinguish three categories of such interoceptive technologies, namely artificial sensations, interoceptive illusions, and emotional augmentation, which are illustrated in Fig. 2 and each reviewed in the following subsections.

1. **Artificial sensations:** low-level, bottom-up, interoceptive stimulation at the level of the receptor cells, which result in controlled

Table 4
A review of interoceptive technologies at various levels of the interoceptive hierarchy.

Interoceptive technology & definition	Studies
Artificial sensation Low-level, direct stimulation of interoceptive signals.	**Breathing load paradigm:**Van Diest et al. (2005);Biddle et al. (1989);Tiller et al. (1987); Berk et al. (2015);Benke et al. (2017);Berner et al. (2019); Tural et al., 2021; Van den Hout, 1984; Van Diest, 2005 **C-Tactile Stimulation:**Crucianelli et al. (2013);Di Lernia et al. (2018b), (2018a), (2020); Triscoli et al. (2017);von Mohr et al. (2018) **Others:** Cafeine challenge (Benke et al., 2015), Visceral sensations (Craske et al., 2011), cardiorespiratory stimulation (Hassanpour et al., 2016), baroreceptors (Jain et al., 2023)
Interoceptive illusion Manipulation of contextual influences on interoception, altering the precision weighting of some interoceptive expectations at intermediate levels by means of exteroceptive cues	**False Heart Rate Feedback:**Valins (1966); Stern et al., 1972; Woll et al., 1979; Aspell et al. (2013);Iodice et al. (2019); Azevedo et al., 2017; Heydrich et al. (2018) **Thermal Illusion:**Craig and Bushnell (1994);Janssen et al. (2016);Poguntke et al. (2019) **Other:** Inter-individual differences in susceptibility to bodily illusions (Cutts, 2019); Neural activity predisposes susceptibility to a body illusion (Hsu, 2022); VR Breathing Avatar causes respiration entrainment (Czub et al., 2019); Rubber-hand illusion [not interoceptive per se] (Suzuki et al., 2013; van Stralen et al., 2014),Windlin et al. (2019).
Emotional augmentation Temporally precise stimulation of interoceptive signals based on contextual cues. Mix of artificial sensation, interoceptive illusion, and exteroceptive stimulation.	Haar et al. (2020); Di Lernia and Riva (2023); Pezzulo et al. (2018); von Mohr et al. (2017); Costa et al. (2016); de Rooij et al. (2017); Sra et al. (2019); Craske et al. (1997); Solcà et al. (2018)

stimulation of the autonomic network (Di Lernia et al., 2018a, 2018b; Riva et al., 2019, 2017).

2. **Interoceptive illusions:** intermediate-level, interoceptive modulation, provided by contextual cues (interoceptive or exteroceptive), altering top-down predictions concerning the current state of the body and the most likely causes of interoceptive signals (Iodice et al., 2019; Pezzulo et al., 2018; Parrotta et al., 2023).
3. **Emotional augmentation:** the combination of bottom-up artificial sensations with top-down interoceptive illusions and contextual cues. These can either already be imbued with personal significance, or acquire significance in the process (Schoeller et al., 2019).

3.1. Artificial sensations: direct, bottom-up, interoceptive modulation

Interoceptive fibers collect and convey various inputs, including subtle changes in muscle contraction, hormonal, endocrine, and immunological responses, along with metabolic activity. The first, most basic, level of interoceptive engineering is that of bottom-up interoceptive modulation at the signal level, which we refer to here as artificial sensations — i.e., stimuli directly influencing the interoceptive system at the receptor cell; effectively allowing the experimenter to induce a percept. There are few techniques to induce low-level modulations, and their effects on the brain and behavior are manifold. We start by reviewing the literature on “interoceptive modulation” and the current state of the art in technologies to allow experimenters to induce artificial sensations for interoceptive modulation. We then review in more detail two streams of research on artificial sensations: 1) CO2-induced fear by respiration-based stimulation, and 2) C-tactile-induced safety by affective touch.

3.1.1. State of the art in interoceptive modulation

Interoceptive modulation refers to the act of deliberately altering interoceptive signals without necessarily forming new conditioned associations. Since the original studies of Razran in the 1960s (Razran, 1961), several researchers have explored interoceptive modulation by means of controlled, artificial induction of sensations. For example, Christiane Pané-Farré (Benke et al., 2017) studied dyspnea and suffocation fear using inspiratory resistive loads and breathing occlusion tools. Other non-invasive techniques involve the use of stimuli that induce interoceptive sensations, such as balloons, internal shocks, or internal thermal probes, as conditioning stimuli and/or responses. In more invasive designs, procedures such as the distension of the visceral esophagus, stomach, and rectum through balloon inflation (Zaman et al., 2016) have also been used to induce interoceptive sensations (Razran, 1961). These can also serve as unconditioned stimuli in fear conditioning study as in the work of Sigrid Elsenbruch (Gramsch et al., 2014) with painful rectal distensions, or as tools to assess the multimodal fear response to interoceptive modulation (Benke et al., 2017). Notably, the mere imagination of interoceptive sensations in adolescents with chronic (primary) pain elicited a multimodal fear response (Opdensteinen, K. et al., in press). Studies in interoceptive modulations are essential to improve existing “interoceptive exposure paradigms”, see for example the work of Michelle Craske on irritable bowel syndrome and panic disorders (Craske et al., 2011, 1997), and Alfons Hamm and colleagues on anxiety (Melzig et al., 2011). Interoceptive exposure is discussed in more detail in the final section of the article, which deals with clinical applications for these research streams.

3.1.2. Panicogenic hypercapnia (‘artificial’ panic attacks)

Several protocols exist to perturbate cardiorespiratory mechanisms such as the acute hyperventilation challenge test (Sardinha et al., 2009), the breath-holding test (Nardi et al., 2002), or the caffeine challenge (Charney et al., 1985; Benke et al., 2015). These are typically used to induce fear, worry, and panic. Interestingly, both healthy and panic patients experience behavioral, physiologic, and biochemical reactions to carbon dioxide (Nardi et al., 2004; Woods et al., 1988). The acute hyperventilation challenge (~30 breaths/min for 4 min) is another technique to provoke CO2-induced ‘artificial’ panic attacks (also known as panicogenic hypercapnia) in both healthy and anxious patients (Tural and Iosifescu, 2021; Van den Hout and Griez, 1984). Conversely, induced hypocapnia (cardiac coherence) is a well-known treatment of acute or chronic anxiety disorders as hypercapnia activates the noradrenergic hormonal stress response in anxiety. Panic attacks typically begin with a surprising onset of intense fear or terror, associated with many autonomic, especially cardiorespiratory symptoms (Roy-Byrne et al., 2006). In contrast to healthy controls, study participants with panic disorder develop a panic-like reaction within minutes after breathing a gas containing 5 % CO2 (Drury, 1919). These reactions are similar to those induced by stimulation with similar anxiomimetic effects, e.g., caffeine. Oral administration of caffeine (10 mg/kg) produces significantly greater increases in anxiety, nervousness, fear, nausea, palpitations, restlessness, and tremors in panic disorder patients compared with healthy participants (Charney et al., 1985). Interestingly, interindividual differences in susceptibility to the CO2 tests have been found to lead to different autonomic responses; speaking to the need for personalized approach. Nardi *et al.* (Nardi et al., 2004) described the clinical features of hyperventilation-induced panic attacks in patients with panic disorder and compared them with their spontaneous panic attacks. They found that artificially induced panic attacks were similar to organic, spontaneous panic episodes. However, in those that did not develop panic-like reactions after hyperventilating, the

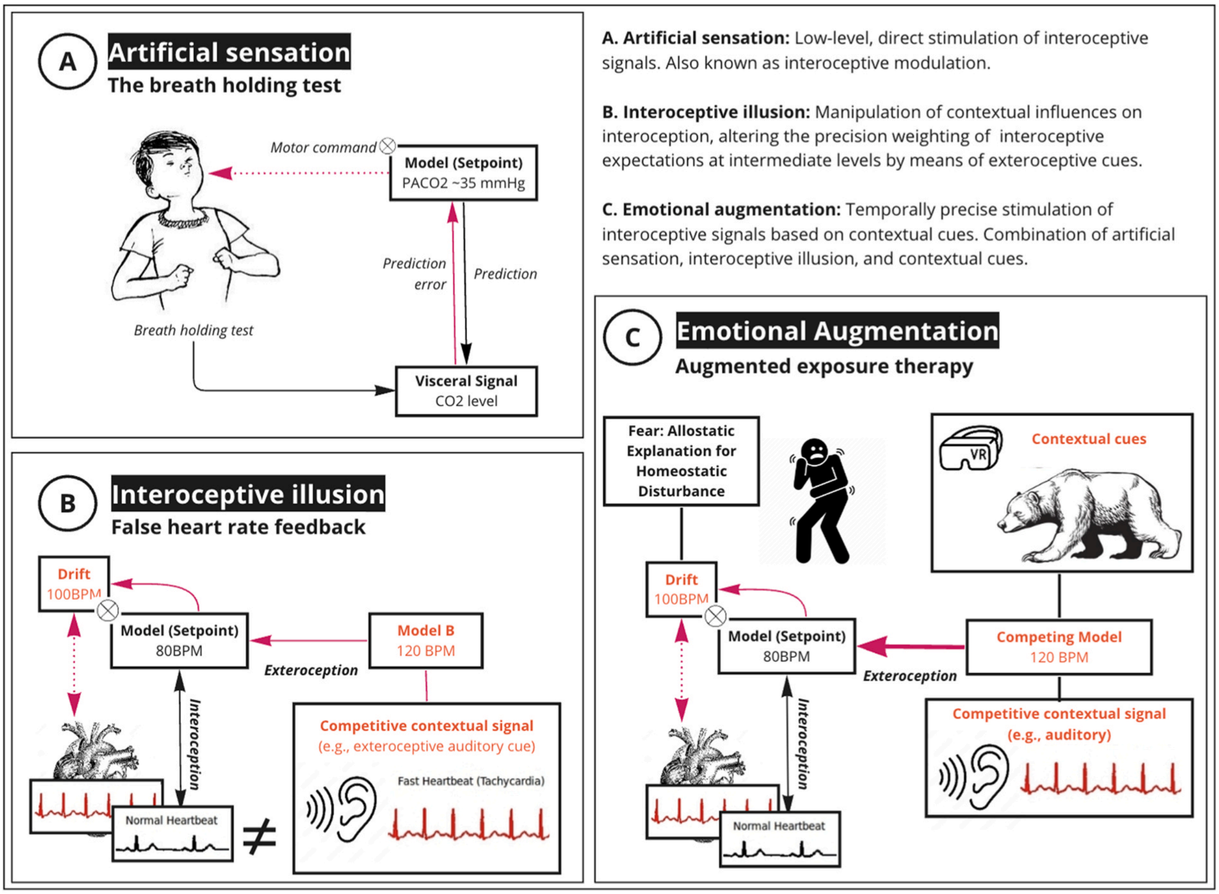

Fig. 2. Overview of interoceptive technologies: A) the breath holding test as an artificial sensation, whereby some bodily signal is directly manipulated, B) false heart feedback as interoceptive illusion, where contextual cues generate a perceptual drift (here the illusion that the heart beats faster at a faster-than-expected rate), C) the therapeutic alliance as entrainment, where the patient's heart rate slows down as the therapist's is increasing, leading both to tend towards some average value, D) augmented exposure therapy as emotional augmentation, similar to B but with additional exteroceptive cues having personal significance to the individual (e.g. eliciting the trauma-related memory) favoring an emotional explanation for the interoceptive drift.

spontaneous panic attacks were accompanied by thermal changes (e.g. chills and hot flashes) and less often by respiratory symptoms such as shortness of breath, choking sensation, chest pain/discomfort, paresthesia or fear of dying. Patients who panicked during the test more often had a family history of mental disorders, were older at onset of the disorder, and more often had a history of depressive episodes (Nardi et al., 2004). Hence, this suggests that artificial sensations may hold potential for discriminating patients, pathologies, and perhaps treatment responses beyond mere interoceptive exposure (as discussed in the final section of the manuscript).

3.1.3. C-tactile stimulation (affective touch)

Even though affective touch falls outside the strict definition of interoception used in this manuscript, new evidence suggests that the C-tactile pathway provides unique neural access to interoceptive processing and control over internal bodily states (Crucianelli et al., 2013; Quigley et al., 2021; Craig, 2003; Di Lernia et al., 2018a; Godron, 2013; Triscoli et al., 2017). While slow, dynamic touch stimulation of C-tactile afferents relies on contact with the external surface of the skin (an exteroceptive process), the effects of affective touch extend to internal bodily systems usually associated with interoceptive channels (e.g., temperature, pain) and interoceptive cortical structures (Gordon, 2013), thereby providing a unique neural access to interoceptive processing. The ability of externally-stimulated C-tactile fibers to modulate internal bodily states highlights the close interaction between skin-based touch and underlying physiological systems. At this level, Aδ and C polymodal afferent fibers collect and convey a wide range of inputs. These fibers report to the Lamina I spinothalamocortical pathway (Craig, 2003) and, through this, to the insula and the interoceptive matrix. They can also report subtle changes in muscle contraction (Wilson et al., 2002), hormonal, endocrine, and immunological response, along with metabolic activity (Craig, 2002). Interestingly, this afferent system differentiates in free tactile arborization on the skin, creating a secondary touch system with deep involvement in different psychophysiological pathways (Olausson et al., 2016). As underlined by Craig, "some C-fibers are exquisitely sensitive to light (sensual) touch" (Craig, 2003; Vallbo et al., 1999).

Going beyond the strict definition of interoception presented here, some authors redefined affective (sensual) C touch as primarily interoceptive input, insofar as affective touch is primarily processed by the left insula rather than the somatosensory cortex (Gordon et al., 2013). As C fibers collect a broad range of sensations "they include cells selectively responsive to Aδ nociceptors (first, sharp pain), C-fiber nociceptors (second, burning pain), Aδ cooling-specific thermoreceptors (cool), C-fiber warming-specific receptors (warmth), ultra-slow histamine-selective C-fibers (itch)" and among these they also differentiate in tactile C-fibers exquisitely sensitive to a peculiar type of tactile stimulation (Craig, 2003). As noted by Quigley and colleagues, "the accessibility of C-tactile afferent nerve endings and their fibers in mammalian hairy skin, a pathway that mediates affective touch and shares anatomical features with classical interoceptive afferents, may provide an externally accessible experimental channel for the manipulation of interoceptive signaling in healthy humans" (Quigley et al., 2021). From this perspective, the skin assumes a new role in interoceptive processing, where “according to some views grounded on anatomical and physiological evidence, skin-mediated signals such as affective touch, pain, and temperature have been redefined as interoceptive” (Crucianelli, 2023), therefore suggesting that affect touch could be considered an interoceptive submodality along with cardiac sensation, thermosensation, and nociception (Crucianelli et al., 2022).

As a consequence, C Tactile stimulation represents an increasingly popular approach for influencing the interoceptive system through artificial sensations. C-tactile artificial sensations trigger a range of interoceptive outcomes including modulation of body ownership (Crucianelli et al., 2013) and social buffering of pain (von Mohr et al., 2018). Specifically, slow (at 1–10 cm/s velocities), light-pressure (< 2.5 mN), dynamic (moving along the skin) touch has been shown to activate C Tactile receptors with a variety of different effects. Interoceptive technologies capable of stimulating the C-Tactile network can be used to modulate the autonomic parasympathetic response (Di Lernia et al., 2018a; Triscoli et al., 2017). In a recent study, eleven minutes of C-Tactile mechanical stimulation reduced chronic pain of approximately 23 % across different pathologies such as neuropathic primary pain, musculoskeletal pain, fibromyalgia, and others (Di Lernia et al., 2020). Although mechanisms of C-Tactile analgesia are still to be completely understood, evidence in humans and animal models suggests that the stimulation of C-Tactile afferents might have an inhibitory effect in the dorsal horn, releasing a protein TAFA4 that has analgesic effects (Yoo et al., 2021), enhance the autonomic parasympathetic system that sustains relaxation and well-being (Di Lernia et al., 2018a), modulate the μ-opioids system response (Nummenmaa et al., 2016; Niikura et al., 2010) and mediate oxytocin release (Wrobel et al., 2011) which has a specific effect on chronic pain (Tracy et al., 2015). In this context, low-level, pre-conscious modulation could rewrite dysfunctional responses to external or internal stimuli. For example, CT stimulation could provide parasympathetic activation in a sympathetic context (e.g. phobic response to non-threatening stimuli).

3.2. *Interoceptive illusions*

3.2.1. *An overview of interoceptive illusion*

Though historically the study of illusions has chiefly been concerned with the domain of exteroception, an increasing number of studies concern the controlled manipulation of physiological variables by false feedback (e.g. real-time visual or auditory cues on breathing or cardiac patterns) or sensory substitution (i.e. changing information from one sensory modality like audition into stimuli of another sensory modality like touch). The effects of these interoceptive illusions can be enhanced with coordinated exteroceptive stimulation. Some examples would be the thermal grill illusion, whereby study participants press their hand against a fake grill with alternating cool and warm portions and experience an illusion of burning heat (Craig and Bushnell, 1994), false auditory heart rate during physical exercise inducing an illusion of effort (Iodice et al., 2019), and false cardiac feedback modulating romantic attraction (Valins, 1966). Parrota et al. (2023) recently showed that exposure to false cardiac feedback alters pain perception and anticipatory cardiac frequency. Sometimes mere exteroceptive stimulation alone is sufficient to elicit such outcome (Makkar and Grisham, 2013). Reminiscent of how mental simulation of interoceptive sensations in chronic pain patients may elicit a fear response (Opdensteinen, K. et al., in press).

As noted above, interoception can also be modulated by indirect means through exteroceptive somesthetic information contradicting interoceptive signals. For example, acoustic feedback about heart rate during effort (Iodice et al., 2019; Valins, 1966), haptic feedback about heart rate during public speech (T Azevedo et al., 2017), and time estimation of interoceptive stimuli (Di Lernia et al., 2018b). Other examples of interoceptive manipulations include visceral illusions during placebo conditions and other contextual manipulations, context-related pharmacologically-induced visceral illusions (Khalsa et al., 2018), direct brain-stimulation induced vestibular illusions (Mazzola et al., 2014), auricular vagal nerve stimulation (Verma et al., 2021), and even corporeal illusions following spinal cord damage (Scandola et al., 2017). A wide range of physiological variables have been manipulated in this way, such as oxygen consumption (Van Diest et al., 2005), thermoregulation (Haar et al., 2020; Janssen et al., 2016; Poguntke et al., 2019), cardiorespiratory pathways (Hassanpour et al., 2016), and others (Aspell et al., 2013; Costa et al., 2016; de Rooij et al., 2017; Heydrich et al., 2018; Schoeller et al., 2019; Solcà et al., 2020, 2018; Suzuki et al., 2013; Windlin et al., 2019).

While these studies are all categorized under the umbrella of ’interoceptive illusions,’ their commonality lies in the manipulation of perceptual experience via precision modulation in hierarchical predictive processing. This induces a divergence between objective physiological states and subjective perceptual experiences, thereby eliciting what can be termed as an “interoceptive false alarm”. In such instances, the individual is not merely ’guessing’ but is perceiving an interoceptive signal that is objectively absent. The extent to which these manipulations result in ’true’ interoceptive illusions varies based on the rigor of satisfying this criterion (a.k.a., interoceptive drift). To further elucidate the underlying mechanisms, the following subsection introduces a model that aims to bring clarity to this complex interplay of factors.

3.2.2. *A Bayesian model of interoceptive illusion*

Interoceptive illusions can be tentatively defined in analogy to proprioceptive illusions (e.g., the rubber hand illusion)—see Maselli et al. (2022). In a standard perceptual inference setup, the participant must infer some hidden variable H (e.g., the position of the hand), based on prior information (e.g., years of visual and proprioceptive evidence that my hand is connected to the rest of my body) and some sensory observations O (e.g., some incoming visual and proprioceptive signals related to my arm). Here, H is the inferred cause of O, i.e., a generative model of O. An illusion implies a situation where H, the "inferred" (subjective) position of the hand differs significantly from the "actual" (objective) position of the hand — whether that inference is reported explicitly (by conscious self-report) or implicitly (by unconscious behavior). In the rubber hand illusion, this can be induced (for example) by providing some false (e.g., visual) feedback, as a direct consequence of the above Bayesian formulation (Allen and Tsakiris, 2019). The inference implies a generative model, a body model or schema, whose two key components are the priors $P(H)$ and a likelihood function $P(O|H)$. Such Bayesian causal inference models of multisensory perception (visual, proprioceptive, and tactile) reproduce the rubber hand illusion accurately and predict the empirical observation that the illusion can occur without tactile simulation and be enhanced by synchronous stroking (see Samad et al., 2015).

We propose that a similar mechanism may be at play in the interoceptive domain. This implies some sort of "interoceptive schema" that is updated in the same Bayesian fashion as described above (i.e., testing hypothesis about hidden cause H against observed sensory outcome O). Imagine that the hidden state H concerns some homeostatic parameters such as hunger, thirst, effort, or fatigue level (i.e., a deviation from homeostatic set point). One can infer H by considering priors and observations—most of which are interoceptive observations (e.g., heart rate), but some of the evidence for H may also come from exteroceptive observations. We saw in Section 2 that the weighting of prediction errors at various levels in the cortical hierarchy is in proportion to their precision, that is, their reliability or predictability (Ainley et al., 2016; Palmer et al., 2019; Parr et al., 2018a; Seth and Friston, 2016). At the lowest hierarchical level, precision scores the confidence placed in sensory information, whereas at higher levels, it mediates the confidence placed in prior beliefs. This precision itself has to be estimated—a process often associated with attention (as a psychological function) and synaptic gain or efficacy (as a physiological structure) (Ainley et al., 2016; Auksztulewicz and Friston, 2015).

Altered precision in interoceptive prediction errors leads to an overestimation of the significance of bodily signals, even when there is no actual threat to homeostatic function. Attentional biases further amplify the salience of bodily signals (e.g., dyspnea and fear of suffocation in anxiety), intensifying distress and preoccupation. Interoceptive illusions can be employed to objectively measure the impact of this dysfunction (Cutts et al., 2019; Hsu et al., 2022). We saw previously that by inducing controlled changes in sensations, such as manipulating breathlessness perception, researchers can assess the subjective and objective responses of individuals with anxiety. Quantifying the drift in perception—during these illusions—provides an objective measure of how the misinterpretation of bodily signals influences perception. This approach offers insights into the specific nature and magnitude of the dysfunction and aids in developing targeted interventions to address and alleviate distress.

This aspect of interoceptive inference also offers a mechanistic overview of how non-interoceptive cues may play a role in interoceptive processing, as the estimation of effort or hunger levels can depend on a combination (or integration) of interoceptive, exteroceptive, and proprioceptive cues, especially in the context of anxiety and panic disorder. We can think of this integration hierarchically, whereby lower levels comprise modular homeostatic predictive coding loops (e.g., in the spine and brainstem), which maintain tightly controlled (i.e., precise) homeostatic set points of temperature, respiration, cardiac pulsation, etc. At higher hierarchical levels, interoceptive information will be primarily relevant for a multimodal self-model. One model of "interoceptive self-inference" (Allen and Tsakiris, 2019) argues that at the most domain-general level (i.e., metacognition), interoceptive states are mostly used to estimate expected precision for both interoception and exteroception (Allen et al., 2018, 2019, 2022).

3.2.3. Interoceptive entrainment

When an incoming “error” sensory signal is sustained, the stimulation may cause a system to adjust its expectations, which may ultimately lead to temporal coordination between false feedback and actual interoceptive activity (Ferrer and Helm, 2013). In the context of interoceptive illusion this corresponds to a situation where the system adapts to the illusion and therefore can no longer be described as such (e.g., the subject’s actual heart rate synchronizes with the false auditory heart rate). This can be compared to the phenomenon known in physiology as “entrainment”, broadly defined in psychophysiology as the synchronization of nervous systems to their environment. The tendency for biological rhythms to entrain to externally perceived rhythms, is under the control of the sympathetic and parasympathetic branches of the autonomic nervous system (J Trost et al., 2017). In humans, entrainment is perhaps most evident in music and dance, where the tempo of a song can directly influence breathing and heart rate, and the heart rates of singers in unison can speed up and slow down synchronously (Vickhoff et al., 2013). Indeed, the paragon of human physiological entrainment is the spontaneous temporal coordination of mother-infant heart rhythms through episodes of interaction synchrony (Feldman et al., 2011). The term “neural entrainment” describes the synchronization of neural activity with repetitive external stimuli (Thut et al., 2011). This synchronization (a.k.a., interoceptive synchromimetism) can be elicited by many stimuli: from rhythmic auditory, visual, and tactile sensory stimulation, to controlled respiration, to magnetic and electrical fields generated by transcranial stimulations (Vosskuhl et al., 2018; Zmeykina et al., 2020). Clayton *et al.* (Clayton et al., 2004) suggested that two or more autonomous oscillating systems must be present to distinguish entrainment from other concepts. For example, in the human body, the periodic firing of neurons and different interoceptive processes including cardiac activity and respiration can be conceptualized as oscillating systems (J Trost et al., 2017).

Kim *et al.* (Kim et al., 2018) used a biofeedback device to enable real-time synchronization of relaxing music to the listener’s pulse. The entrained-tempo condition led to a significantly stronger increase in peripheral blood flow and subjective well-being, suggesting its ability to generate a psychophysiological relaxation response. Czub & Cowal (Czub and Kowal, 2019) used exposure to a breathing avatar in virtual reality (VR) to change the respiration rate of the observer. Specifically, the avatar was first breathing for 60 s in accordance with the observer’s respiration rate. Then, it was either slowing down or speeding up, each condition lasting for 180 s. Their results suggest providing a visual cue can entrain participants’ respiration rates, with a clinically significant outcome. Though they did not observe entrainment per se, another study by Azevedo *et al.* (T Azevedo et al., 2017) used a device able to deliver a slow heartbeat-like vibration to the wrist and found that the stimulation had a calming effect on both physiological measures of arousal and subjective reports of anxiety. Perhaps this trend has the most to benefit from studies of real-world interactions and physiologic synchronization, demonstrating that a collective ritual may evoke synchronized arousal over time between active participants and bystanders (Konvalinka et al., 2011). Dumas & Fairhurst reviewed the multiple types of reciprocity and alignment processes during human interactions, from unconscious physiological coupling to intentional motor coordination and semantic alignment (Dumas and Fairhurst, 2021). In clinical settings, physiological synchronization and behavioral mirroring have been suggested as a mechanism of patient-clinician interaction (Ellingsen et al., 2020) which has yet to be enhanced by technological means.

3.3. Emotional augmentation

The third category of interoceptive technologies combines a blend of interoceptive and exteroceptive stimulation, i.e., a combination of bottom-up and top-down interoceptive stimulation. Emotional augmentation refers to precise temporal and spatial delivery of interoceptive stimulation targeting "somatic markers" of an emotion (Schoeller et al., 2018). This interoceptive augmentation often occurs concurrently with personally significant contextual cues via audiovisual stimulation or Virtual Reality (VR) environments. Perhaps a canonical example of emotional augmentation is the study by Haar et al. (2020), where the team augmented cognitive and affective processing associated with emotional chills (i.e., emotional, psychogenic shivers) by synchronizing thermal stimulation with chills audiovisual stimuli (Fig. 3). They developed Frisson, a thermoelectric device that attaches to the user’s back, mimicking the sensation of an aesthetic chill coursing down the spine in alignment with specific instances in a film or musical piece where similar chills are commonly experienced. The device uses Peltier motors to stimulate thermoreceptors, triggering the sensation of coldness during psychogenic shivers. This results in additional physical evidence for the unconscious belief "I am cold", stimulating rather than augmenting the bodily response. The study revealed that this interoceptive enhancement of emotion intensifies downstream effects of chills, such as pleasure and prosocial behavior (Haar et al., 2020; Schoeller et al., 2018; Schoeller et al., 2019). A similar example shown in (Fig. 3) is a device worn on the neck and uses galvanic vestibular stimulation to modulate nausea during VR experiences, opening up pathways to modulate or influence disgust via vestibular stimulation (Sra et al., 2019). Other devices are built to generate the illusion of effort in VR using electronic muscle stimulation (Lopes et al., 2015). These devices unite physiological sensors with electronic actuators, sensing and modulating the body in a closed-loop manner. This complex loop between device actuation, bodily sensation, cognitive effect, and subsequent change in appraisal of device-induced sensations must be considered in the design of any technology aimed at inducing emotional augmentation. Emerging technologies in this realm can employ a diverse array of solutions, such as trans-auricular vagus nerve stimulation (taVNS) (Paciorek and Soka, 2020), a technique that manipulates interoceptive signaling to enhance interoception and modulate body ownership. Synthetic auditory non-invasive stimulation, termed as "Sonoception", is another technique that aims to alter interoceptive signaling to influence cognitive and affective processing (Riva et al., 2017; Di Lernia, 2023).

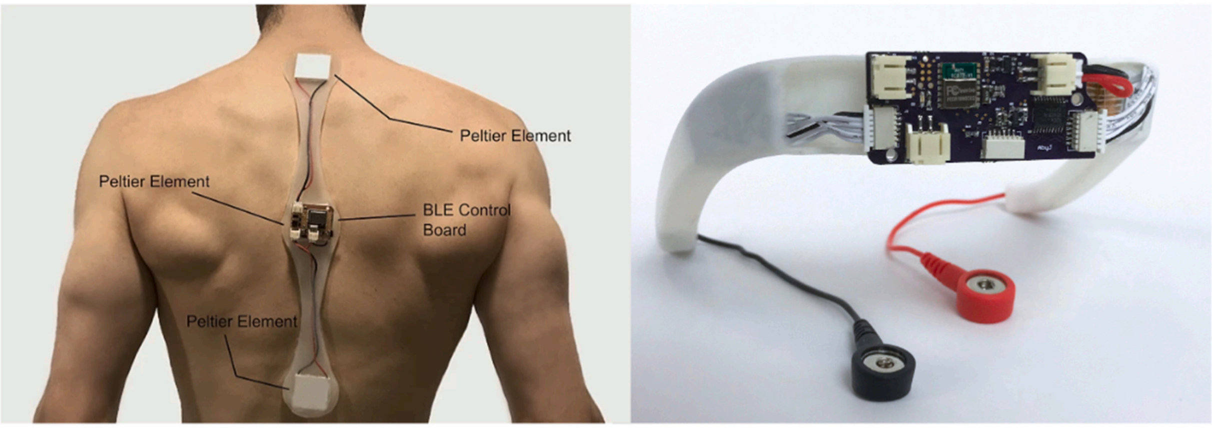

Fig. 3. The Frisson and MoveU devices, designed respectively to enhance aesthetic chills (or psychogenic shivers) and to reduce motion sickness in VR (Haar et al., 2020; Schoeller et al., 2019; Sra et al., 2019).

The downstream effects of these emotions can be manipulated experimentally. For example, the Frisson device seems to enhance ratings of pleasure (associated with dopaminergic discharge during the chills), and prosocial tendencies known to derive from chills (Fukui and Toyoshima, 2014). One core difficulty here is the distinction between an illusory sensation and an organic one: a device-driven chill or nausea experience can transition from one which is mistakenly perceived as internally generated into one which is in fact organic, as illusory nausea begets real nausea (if this distinction remains meaningful). This subtle change is hard to detect with physiologic sensors and would need to be distinguished, which should be a key focus for future work before tools for interoceptive illusion can enter clinical settings. Biofeedback-enhanced VR therapies have been used in exposure-based treatment for anxiety disorders, including phobias and post-traumatic stress disorder (Kothgassner and Felnhofer, 2021). By incorporating real-time physiological responses into the VR environment, individuals can learn to manage and control their anxiety responses. For instance, a person with acrophobia (fear of heights) could gradually adapt to the sensation of being high up in a controlled VR environment, while real-time biofeedback could help them learn to modulate their learned physiological stress responses.

4. Future research directions and clinical applications

If deployed at scale and broadly disseminated, interoceptive technologies may aid in developing and improving clinical interventions. However, considerable work is still needed to ensure the reliability and safety of interoceptive interventions for diagnostic and treatment purposes. In this section we review and suggest two promising leads: 1) the use of artificial sensations as probes to overcome to current limitations of self-reported measures of interoception (Garfinkel et al., 2022) and the domain-specificity of unimodal measures of interoception—i.e., the fact that, for example, improvement in cardioception do not translate into improvement in respiroception (Legrand et al., 2021), and 2) the use of body-based technologies to change bodily priors in conjunction to interventions to change dysfunctional beliefs about the environment, specifically in the context of anxiety disorder.

4.1. Research directions: using artificial sensations as probes

Mounting evidence suggests that interoceptive deficits in the realm of psychopathology manifest most prominently during states of homeostatic perturbation (Khalsa and Lapidus, 2016; Smith et al., 2021). As we saw in the first section, the literature on predictive coding hierarchies in interoception and bodily signals is abundant (Smith et al., 2021), particularly as related to mental health disorders (Petzschner et al., 2021), such as depression (Stephan et al., 2016) and post-traumatic stress disorder (Linson et al., 2020). Within the conceptual framework of active inference, disorders of affect are understood as aberrant precision control, mediated by high-level representations of being in one emotional state or another (Clark et al., 2018; Friston, 2017; Parr et al., 2018b, 2018a). Examples include mood disorders, anxiety disorders, obsessive-compulsive disorder, and possibly other mental health disorders such as autism and post-traumatic stress disorder (Badcock et al., 2017; Kiverstein et al., 2019b; Lawson et al., 2017; Palmer et al., 2017; Peters et al., 2017; Rae et al., 2019). Evidence also suggests that bodily location of emotion is altered and reduced in schizophrenia (Torregrossa et al., 2019). In short, emotional inference and related psychopathologies should be accompanied by characteristic changes in the deployment of precision or attention (Adams et al., 2013; Edwards et al., 2012) that are accompanied by changes in the descending predictions of autonomic states. Because interoceptive predictions constrain autonomic reflexes, one would expect to see the correlates of emotional inference in both the central and peripheral (autonomic) nervous systems. For example, changes in sensory precision triggered by auditory or visual stimuli accompanied by sympathetic arousal would be measurable in terms of changes in the amplitude of evoked potentials; e.g. modulation of the mismatch negativity by emotional set (Chen et al., 2022). Similarly, some mental disorders should be associated with aberrant responses to interoceptive stimuli, such as body maps in schizophrenia (Torregrossa et al., 2019) and nociception in autism (Gu et al., 2015). However, current measures of interoception often fall short as improvements in one domain do not necessarily translate into others (Ferentzi et al., 2018a; Heldestad et al., 2010a, 2010b; Ferentzi et al., 2018b)—see also Section 4.2.4. Interoceptive technologies could bridge this gap by providing a more holistic, real-time assessment of multiple interoceptive domains, thereby enabling targeted interventions.

4.1.1. Aberrant emotional processing

It would be useful to quantify affective stimuli in terms of changes in precision or post-synaptic gain in the central nervous system—and peripheral measures (e.g. pupillary dilation, electrodermal activity, heart rate variability, etc.). Artificial sensations provide an ideal opportunity to elicit emotional inference and quantify central and peripheral responses, for example by using non-invasive electroencephalography (EEG) and the peripheral measures described above. This approach is sometimes referred to as aberrant emotional processing (Sadeh et al., 2014). Perhaps one of the earliest examples of using responses to experimental perturbations was the dexamethasone suppression test which showed early promise in phenotyping depression (Naughton et al., 2014). This test can be thought of as a form of 'stress test' used routinely in cardiology to measure cardiac ability to respond to external stress in a controlled clinical environment. The search for valid 'stress tests' for mental health disorders continues—and speaks to a potential role for artificial sensations and interoceptive illusions.

4.1.2. *The relevance of artificial sensations*

One can imagine several paradigms in which artificial sensations are used to induce emotional processing that would orient the attention paid to interoceptive and exteroceptive sensations. Artificial sensations that do and do not produce psychogenic shivers could potentially be used to assess reward sensitivity in depression (Schoeller et al., 2022, 2023). It could also be used with the prediction that individuals with alexithymia, e.g. Parkinson's disease (Poletti et al., 2012), would not recognize or infer the difference—and fail to show differential event-related responses as measured with EEG. More sophisticated designs could address key questions about the ability of individuals to modulate or attenuate interoceptive precision; e.g. in children with autism (Gu et al., 2015; Lawson et al., 2014; Quattrocki and Friston, 2014; Van de Cruys et al., 2014). Using a mood induction paradigm in conjunction with artificial sensations might reveal the interaction between inferred or recognized emotional states and interoceptive responses to artificial sensations. In this example, artificial sensations would play the role of an experimentally well-controlled delivery of interoceptive stimulation, much like affective touch or noxious stimulation (Gómez et al., 2014; Gu et al., 2015; Krahé et al., 2013). However, the advantage of artificial sensations is that they do not cause pain, do not have any side effects, and can be administered with temporal and spatial (somatosensory) precision.

4.2. *Clinical applications: body-based interventions to modulate precision encoding*

4.2.1. *Artificial sensations for interoceptive exposure*

Interoceptive exposure refers to a clinical intervention that aims to systematically and safely expose individuals to sensations or cues that elicit anxiety or distress (Holtz et al., 2019; Boettcher et al., 2016). This approach is designed to target the fear and avoidance associated with specific interoceptive cues, with the ultimate goal of reducing anxiety and improving symptom management (Boettcher et al., 2016). Leveraging artificial sensations for interoceptive modulation, various IE protocols have been developed, ranging from non-invasive to more invasive designs. These procedures provide a more direct and intense experience of bodily sensations, allowing individuals to confront and tolerate discomfort in a controlled manner. IE as a clinical intervention depends on the specific goals and aims of each individual treatment; however, IE is typically used in the context of anxiety disorders, where it aims to reduce fear and avoidance responses associated with interoceptive cues. The underlying mechanisms involve the principles of fear extinction and habituation (e.g., Gramsch et al., 2014). By repeatedly exposing individuals to interoceptive sensations in a safe and controlled manner, fear and anxiety responses can gradually diminish, leading to symptom reduction and improved coping strategies (Deacon et al., 2013a, 2013b). IE is often used to treat anxiety, panic, and fear (Schmidt et al., 2022; Melzig et al., 2011). Artificial sensations and interoceptive modulation paradigms can help develop novel interoceptive exposure interventions that aim to create a controlled environment in which individuals can experience and gradually habituate to interoceptive sensations that trigger anxiety.

4.2.2. *Mimicking the somatic basis of affective valence*

Pathological anxiety is considered to result in part from a persistent prior belief about one's own inability to manage error (Peters et al., 2017; Stephan et al., 2016). In healthy subjects, this expectation about increasing error is corrected either by updating priors to better fit the actual state of affairs or by engaging regulatory actions that move the individual toward better opportunities for error resolution. In pathological cases, this belief persists even when mental health disorders let the individual maintain a good predictive fit with the environment. Beliefs about volatility produce negative affective reactions which entrains attention towards anxiety-related stimuli in the world, and drives internal anxiety-related thought patterns and rumination—both of which reinforce the anxiety-related prior (Wild et al., 2018). As the priors become increasingly precise, they also become resistant to updating (Paulus et al., 2019; Paulus and Stein, 2006), and the strength of this prior means that there is a loss of top-down inhibitory control over those expectations (Clark et al., 2018). In physiopathologic terms, this could correspond to central (prefrontal cortex) and peripheral (corticotropic and noradrenergic) retrocontrol on subcortical fear circuits (e.g. extended amygdala). Interoceptive augmentation technology—capable of imitating core affective systems related to valence—may help to address such disorders by altering part of the bodily feedback process that adjusts precision on negative expectations through a combination of interoceptive, exteroceptive, and proprioceptive cues.

4.2.3. *Disrupting interoceptive conditioning to facilitate emotional regulation*

The technologies reviewed in the previous section directly and holistically interface with the (vicious) cycle that entrenches the pathological expectations underlying various mental health disorders. A key characteristic of panic attacks is the interoceptive sensation of palpitations (e.g. the sensation of irregular and/or too strong heartbeats), thoracic oppression and respiratory discomfort with a prior error leading to the sensation of being short of breath (dyspnea) and thus imminent death. This in turn induces hyperventilation, hypocapnia and worsen the primary interoceptive symptoms. Here the error in the interoceptive prior triggers the vicious circle of the panic attack. Breathing retraining and IE are among the main components of cognitive and behavioral therapy in panic disorder (Pompoli et al., 2018). With breathing retraining, the patient takes deep and regular breaths and lowers down his respiratory frequency, which reduces hypocapnia and thus interoceptive signals of anxiety such as tachycardia. Evidence suggests that IE is more effective in the treatment of panic disorder compared to breathing retraining (Craske et al., 1997). From an active inference perspective, we can interpret this as augmenting emotional feedback disrupting the attribution of precision that characterizes pathological anxiety. The individual can gradually learn to self-regulate. Success in an otherwise anxiety-provoking situation would increase confidence in managing such situations, and so contribute to a reduction in the pathological belief about their inability to succeed, which is assumed to be the root condition. A review of some research in this direction including VR/AR systems can be found in the fields of regenerative VR (Riva et al., 2021) and transformative experience design (Chirico et al., 2016; Chirico and Gaggioli, 2021; Quesnel and Riecke, 2018; Schoeller et al., 2019).

4.2.4. *The need for reliable measures*

The robustness of interoceptive interventions is critically tied to the utilization of valid and reliable measures for both direct and indirect outcomes. Direct outcomes refer to the immediate effects on interoceptive illusions, such as altered perception of bodily sensations. Indirect outcomes encompass broader interoceptive dysfunctions, including but not limited to symptom alleviation in psychopathological conditions. Rigorous evaluation frameworks must be in place to quantify these outcomes, employing a mix of psychometric scales, physiological biomarkers, and clinician-administered assessments. Randomized controlled trials (RCTs) comparing interoceptive technologies with standard interventions are essential for establishing the diagnostic and therapeutic validity of these approaches. Without these validated metrics, the efficacy and clinical utility of interoceptive interventions ultimately remains to be demonstrated. Perhaps most concerning, unimodal interoceptive tests (as listed in Table 2) only provide quantitative indexes within single specific modalities like cardiac, respiratory, thermal, and gastric domains. However, performance on one test offers limited insight into abilities in other modalities. For example, studies have found minimal correlations between heart rate detection accuracy and pain perception thresholds (Ferentzi et al., 2018a; Heldestad et al., 2010a, 2010b), as well as between heartbeat tracking and respiratory resistance detection (Ferentzi et al., 2018b). This indicates interoceptive abilities do not readily generalize across sensory channels. The lack of correlation across unimodal tests underscores the need for multimodal approaches that assess integration of interoceptive information across bodily systems. As we argued throughout, it is at the stage of multimodal convergence where the brain constructs predictive representations most relevant to homeostasis, subjective feeling states, and sense of bodily self (Tsakiris, 2016).

5. Conclusion

The literature on interoception highlights its significance as a mechanism for prediction and its potential for various clinical interoceptive interventions. We have identified precision-weighting as a key component of interoception and differentiated between three types of interoceptive technologies. Our analysis suggests that these could be used in two distinct areas: one focused on nosology and diagnosis, where artificial sensations could be used to test patient susceptibility to interoceptive illusions; and the other on emotional augmentation, where such technologies could help modulate the precision of predictions and promote beneficial changes in maladaptive beliefs or behaviors.

However, several important gaps remain. First, the developmental aspects in interoceptive technologies require further exploration, despite the significance of understanding emotional regulation and dysregulation beginning in childhood and its persistence into adulthood. This gap relates to the limited research on interoception in children and adolescents (Khalsa et al., 2018; Murphy et al., 2019). To advance our understanding of healthy and pathological interoceptive trajectories over the lifespan, it is crucial to study this developmental period further. For example, research could examine the impact of dysfunctional interoception acquired in childhood from adverse experiences, and use that knowledge to inform targeted clinical interoceptive interventions that promote healthier emotional regulation throughout life.

Additionally, more rigorous evaluation frameworks must be developed to quantify the outcomes of interoceptive interventions, using psychometric scales, physiological biomarkers, and clinician assessments. Well-controlled randomized trials are essential for establishing the diagnostic and therapeutic validity of these technologies compared to standard interventions. Without validated metrics, the efficacy and clinical utility of interoceptive technologies remains unproven.

Further research should explore the neural mechanisms underlying interoceptive technologies and how they may alter brain connectivity patterns that maintain maladaptive psychological states. Identifying neural signatures and connectivity biomarkers associated with clinical improvements would strengthen the theoretical models guiding this emerging field. Interoceptive technologies hold promise for understanding and treating disorders of affect and interoception. However, research must address key developmental, evaluative, and neuroscientific gaps before these tools can be responsibly and effectively translated into clinical practice. Focused efforts in these domains will propel the maturation of interoceptive technologies from lab curiosities into validated and potent interventions.

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Data availability

No data was used for the research described in the article.

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