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Interoception and emotion

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Influential theories suggest emotional feeling states arise from physiological changes from within the body. Interoception describes the afferent signalling, central processing, and neural and mental representation of internal bodily signals. Recent progress is made in conceptualizing interoception and its neural underpinnings. These developments are supported by empirical data concerning interoceptive mechanisms and their contribution to emotion. Fresh insights include description of short-term interoceptive effects on neural and mental processes (including fear-specific cardiac effects), the recognition of dissociable psychological dimensions of interoception, and models of interoceptive predictive coding that explain emotions and selfhood (reinforced by structural anatomical models and brain and experimental findings). This growing grasp of interoception is enriching our understanding of emotion and its disorders.

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Introduction

Human emotions encompass characteristic feelings states that are proposed to draw upon interoception, that is the processing and central representation of afferent internal bodily signals [1]. Emotions reflect psychophysiological modes that themselves track and steer the redirection of physiological and psychological resources to adapt behaviour. The physiological expression of emotion includes changes within internal organ systems, driven by autonomic nervous responses usually independently of volitional control. Interoceptive signals vary in motivational immediacy, yet they include information for homeostatic reflexes and for allostatic control, and include feedback of physiological changes induced by emotions. People refer to internal bodily sensations when describing their emotional experiences, with some consistency [2]. This categorical association is likely reinforced by cultural consensus, translating perceived interoceptive responses into a social language that supports emotional understanding of self and others. However, the same interoceptive responses may be categorised emotionally in different ways [3]. The choice of descriptor can reflect how bodily arousal signals are interpreted emotionally (churning or butterflies in stomach; heart missing or skipping a beat). Nevertheless, the coupling of physiological changes to emotional experience is central to theoretical proposals arguing for an interoceptive basis to emotional feelings.

Neural organization

Interoception refers conventionally only to afferent processing of signals that originate within the body and which refer to the state of the body. Interoception is distinct from proprioception (the processing of skeletomotor and vestibular information about position or movement of the body) and the (proximate and distant) sensing of the environment through touch, taste, smell, sight and hearing. Interoception encompasses different classes/channels of information, distinguished by the generation of the signal (mechanoreceptive organ-stretching, chemoreception) and by afferent pathway (neural, humoral). There is crosstalk between specific channels of interoceptive information, and with exteroceptive information, at multiple nodes of the neuraxis (autonomic ganglia, spinal cord, medulla, pons hypothalamus, thalamus, basal ganglia (including amygdala) and cortex) [4]. The perceptual characteristics of different interoceptive sensations are determined by both afferent channel and signal strength. Generally, interoceptive sensations are diffusely localisable compared to somatomotor and somatosensory (including most pain) sensations. In some cases, interoceptive information is overshadowed by, or inseparable from, exteroceptive cues, for example sensations of respiration from chest wall muscle proprioceptors and upper airway somatosensation lie in the perceptual foreground relative to interoceptive signals from alveolar tissue or blood gases. In some motivationally-relevant states, interoceptive information is amplified or overtaken by the recruitment of exteroceptive pathways, for example the pain of cardiac ischaemia felt in the chest wall and upper arm [5].

Following arguments made by Craig, recent literature accommodates broad definitions of interoception, anchored less to internal physiology [6••]. These often include most bodily signals and general feeling states as interoceptive ('intero-perception' [7,8]). There is some

tension between classic physiological definitions and more experiential notions of interoception linked to older notions of vitality and coenaesthesia [7] that might arise from high level cross-modality integration removed from the body afferents. Craig's own definition of interoception is nevertheless grounded on a combination of anatomy and motivational content [6••]: Information relevant to homeostatic control, physiological needs (hunger, thirst, heat, pain) and organ integrity signals are carried centrally by unmyelinated and lightly myelinated afferents that mostly ascend spinal laminar 1 spinothalamic tract. This suggests a dedicated interoceptive-motivational pathway. However, this same spinal tract contains exteroceptive touch (*e.g.* tickle, itch) and skin temperature fibres. Thus defining interoception in terms of nerve fibre type and sensory tract broadens the definition of interoception beyond its conventionally more constrained (internal physiological) boundaries.

Nevertheless, Craig's work on the central anatomy of interoceptive processing indicates a hierarchical neural organization and convergence of signals from spine and vagus nerve towards cortical representations within insular cortex [6••,9]. Within the brain, different interoceptive channels share common regional neural substrates that likely permit integrative processing towards (predictive) representations that might ultimately direct adaptive behaviour [10]. However, not all signals are integrated with other modialties: Organ-specific and signal-selective afferent representations are present in insular cortex and associated 'interoceptive' cortical regions [4]. Plausibly, representational and perceptual organization of neurally-transmitted interoceptive information may resemble that observed for taste and flavour processing (not least through adjacent insular cytoarchitecture): In the granular way that cortical representation of different tastes can be distinguished and combined to permit identification of foods, the discrete and patterned representation of bodily responses likely informs different states of subjective experience that contribute to emotion-specific feelings.

Quantifying individual differences in interoception

Bodily changes and their interoceptive signalling help constitute emotional feelings and behaviours. Hence, the emotional 'style' of individuals may reflect differences in their sensitivity to interoceptive signals. Approaches to quantify interoceptive differences include the use of questionnaires and the use of behavioural tests that either exploit natural fluctuations in internal physiological signals, or that manipulate organ physiology experimentally [5,11••,12]. For practical reasons, heartbeat detection tasks are widely used measures for quantifying individual differences in interoceptive ability. These test an individual's ability to perceive their own heartbeats at rest, by counting, tapping or by judging heartbeat timing relative to an external stimulus. The psychometric limitations of these tasks are well-described [13,14•]. However, with necessary caution, data from these methods show face-validity, and the tests maintain wide application, if applied appropriately [15]. Correspondingly, hypotheses regarding how interoceptive ability might contribute to symptoms, or inform motivational decision-making, are often borne out [16]. Until recently, there were discrepancies in how interoceptive sensitivity or ability was measured and described. The term 'interoceptive awareness' was often used to refer to both questionnaire measures and task performance, since these both require judgements. However, a leap forward came from the proposed partitioning of interoception along three dimensions [11••,17,18]. This framework argued that a distinction should be made between objective measures of interoception (*i.e.* interoceptive performance, *e.g.* behavioural score on heartbeat detection tasks) and subjective measures of interoception (how well a person thinks he/she perceives interoceptive signals, *e.g.* on self-rated confidence on heartbeat detection, or by self-reported questionnaires). Moreover, a measure of metacognitive interoceptive awareness (insight) could be derived from the correspondence between actual objective performance and subjective sense of interoceptive ability. These 'psychological dimensions of interoception' were shown to be dissociable from each other. Moreover, the degree of alignment between subjective and objective dimensions can predict emotion states and affective psychopathology [19•]. This dimensional model of interoception can be extended further to incorporate lower level measures of afferent neural traffic (quantifying afferent signal strength, *e.g.* through heartbeat evoked potentials [20••]), and the preconscious impact of interoceptive signals on sensory processing (*e.g.* modification of startle response [21•,22] or augmentation of threat processing [23••,24,25]). 'Higher' interoceptive dimensions beyond metacognition can encompass executive processes, including flexible switching of interoceptive attention (Table 1).

Different sensory channels of interoception

A focus on cardiac afferent signalling has dominated studies of interoception. Afferent signals from other visceral organs have tended to attract specific attention in pathological conditions, for example respiration in asthma (and other obstructive airway disorders), and the stomach and bowel in eating and gastrointestinal disorders. Surprisingly, there is generally weak correspondence between measures of cardiac and respiratory interoceptive accuracy [18]. Respiratory sensation, notably dyspnoea, is largely an interoceptive feeling, since dyspnoea induced through respiratory load (or abnormal O_2/CO_2 levels) does not depend on chest muscle feedback. Moreover, training to improved sensitivity in one axis may not improve another. For example meditative practice generally has little impact on cardiac interoceptive performance (although see Ref. [26•]), yet experienced

Table 1

Dimensions of human interoception

Dimensional level	Nature	Index
Afferent signal	Neural	Visceral afferent nerve recording Intracranial recording Heartbeat evoked potential Respiratory evoked potential Neuroimaging
Preconscious impact on other processes	Behavioural, neural	Cardiac modulation of eyeblink startle Cardiac modulation of fear Respiratory modulation of memory
Accuracy	Objective behavioural performance score	Heartbeat detection tasks Respiratory resistance load detection Water Load task Balloon dilation of stomach/colon
Sensibility	Subjective self-report	Confidence measures on interoceptive tasks Questionnaires probing interoceptive sensitivity
Metacognitive	Correspondence between subjective self-report and objective performance accuracy	Receiver Operating Characteristic (ROC) curves between task performance and rated confidence Correlational measures of task and confidence scores Trait measures, for example correspondence between task performance and body perception questionnaire score
Executive	Behavioural	Shifting from interoceptive to exteroceptive attention, for example within dual tasks or between tasks.

Shaded area denotes the three psychological dimensions described by Garfinkel *et al.* [11••,17,19•].

meditators show improved respiratory interoceptive accuracy [27]. Short-term respiratory afferent signals, like cardiac afferent signals, modify defensive reflexes (notably startle responses [22]) and even nasopharyngeal airflow (an internal, yet mostly exteroceptive, respiratory stimulus) also influences processing of affective information [28••]. Interestingly, at a metacognitve level, respiratory and cardiac interoceptive abilities align [18].

Among tests of gastrointestinal sensitivity, the Water Load test quantifies gastric interoceptive sensitivity from the amount of water ingested freely using an experimental protocol (recently refined [29]). Measures of gastric interoception typically correlate with heartbeat detection accuracy (unlike respiratory interoceptive accuracy) [29]. Signals from the stomach convey emotional impact beyond motivational signals of hunger and fullness, to support other affective states (notably disgust [4]). Moreover, afferent gastric signalling has other central effects, for example 'resting' 0.05 Hz bradygastria can entrain electrocortical rhythms [30].

Gastric signals represent only one aspect of gut-to-brain interoceptive signalling [31–33]. The whole enteric nervous system is coupled neurally to brain, mainly via the vagus nerve and spinal cord. These afferents inform the central neural regulation of gut motility and digestive function. Additional information concerning the chemical and inflammatory environment of the gut and endocrine responses to food intake, are also signalled both neural and humorally to brain [31]. Gastrointestinal information is conveyed along similar pathways as other sources of interoceptive information, to shaping both behaviour and subjective feeling states. Gut hormones can be potent modulators of affect and motivation, and neural signals of hunger and satiety are linked to the systemic and psychological expression of stress and wellbeing [32]. Additionally, the inflammatory status of the bowel and composition of luminal gut bacteria also impact interoceptively on emotional functions [32]. Empirical findings from both basic and clinical science increasingly demonstrate the psychological influences of gut microbiota, even linking the expression of mood disorder to species of colonic microbes [33].

Inflammation and emotional processes

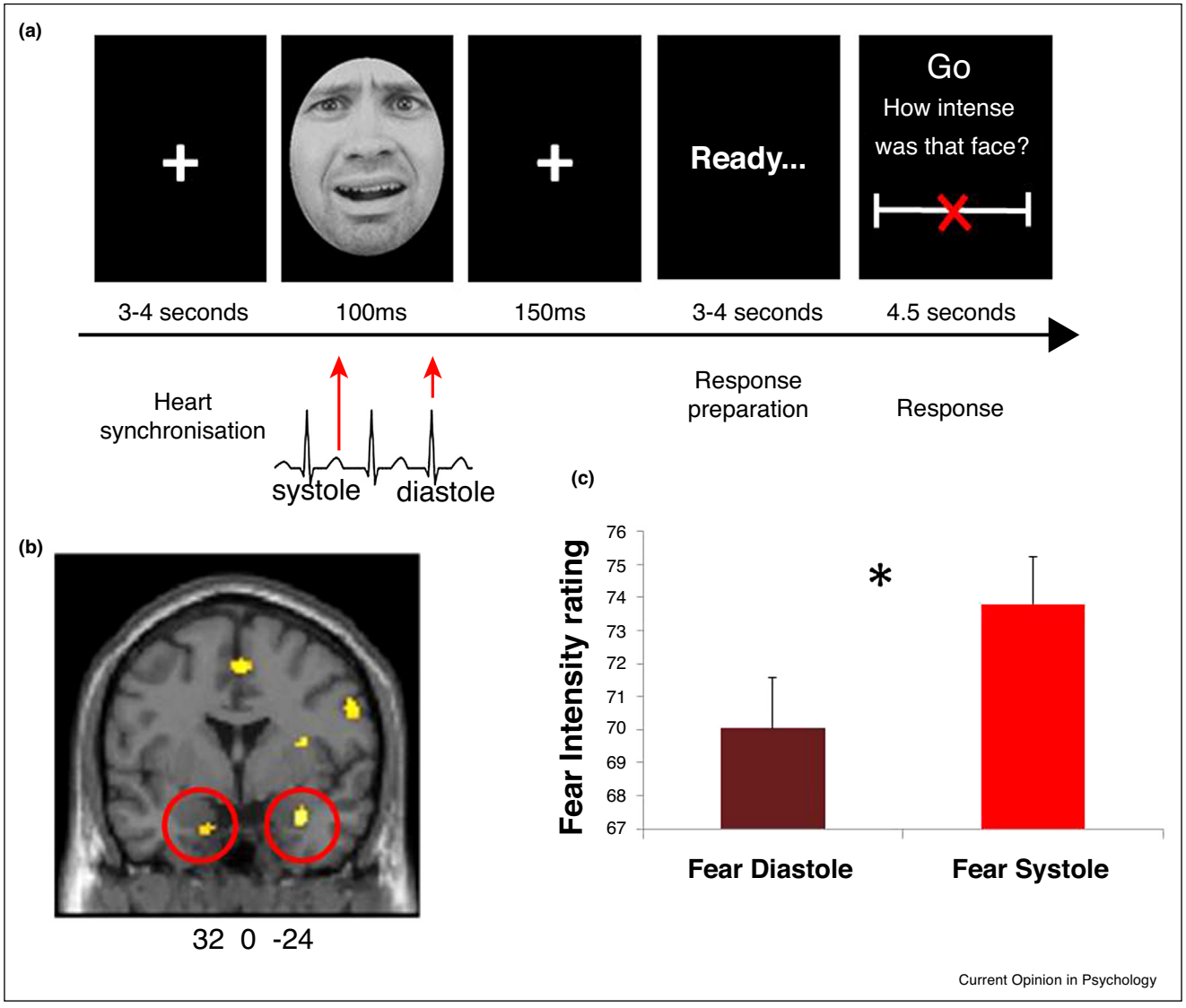
Immune communication from periphery to brain represents a major component of interoception. The signalling of systemic inflammation is communicated to brain via neural (predominantly vagus nerve) pathways, humorally via circulating cytokines, and directly via immune cells. Both acute and chronic states of inflammation influence emotion through a coordinated set of motivational changes conceptualised as 'sickness behaviours'. These include fatigue, anhedonia, social withdrawal and irritability, that is symptoms shared with depression [34]. Interestingly, central signalling of inflammation engages established interoceptive pathways to insula, but can also engage a distinct subcortical response that might better predict development of affective psychopathology [34]. Acute inflammation biases behaviour by changing sensitivity to rewards and punishments, through effects on

insula cortex and dopaminergic ventral striatum [35]. These effects are manifest even before marked shifts in subjective feelings are observed.

Short-term emotional effects of interoceptive signals

The impact of phasic interoceptive signals on emotional processes are perhaps best described for the cardiovascular channel though, as noted above, respiratory and gastric signals modulate brain responses and associated cognitive and perception. Cardiovascular arousal is signalled by arterial baroreceptors in aorta and carotids that fire with each heartbeat as ventricular contraction pumps blood out of the heart. Thus baroreceptors signal the timing and strength of each heartbeat to brainstem via the vagus and glossopharyngeal nerves and inform the reflexive control of blood pressure through the baroreflex. In states of cardiovascular arousal (including emotional stress), the baroreflex is suppressed, allowing heartrate and blood pressure rise together. The impact of this channel of interoceptive information on brain processes can be assessed by exploiting the phasic nature of baroreceptor firing. One can compare responses to brief stimuli presented around systole, when the baroreceptors are active, to responses to stimuli presented at diastole, when the baroreceptors are quiescent. Differences can then be

Figure 1



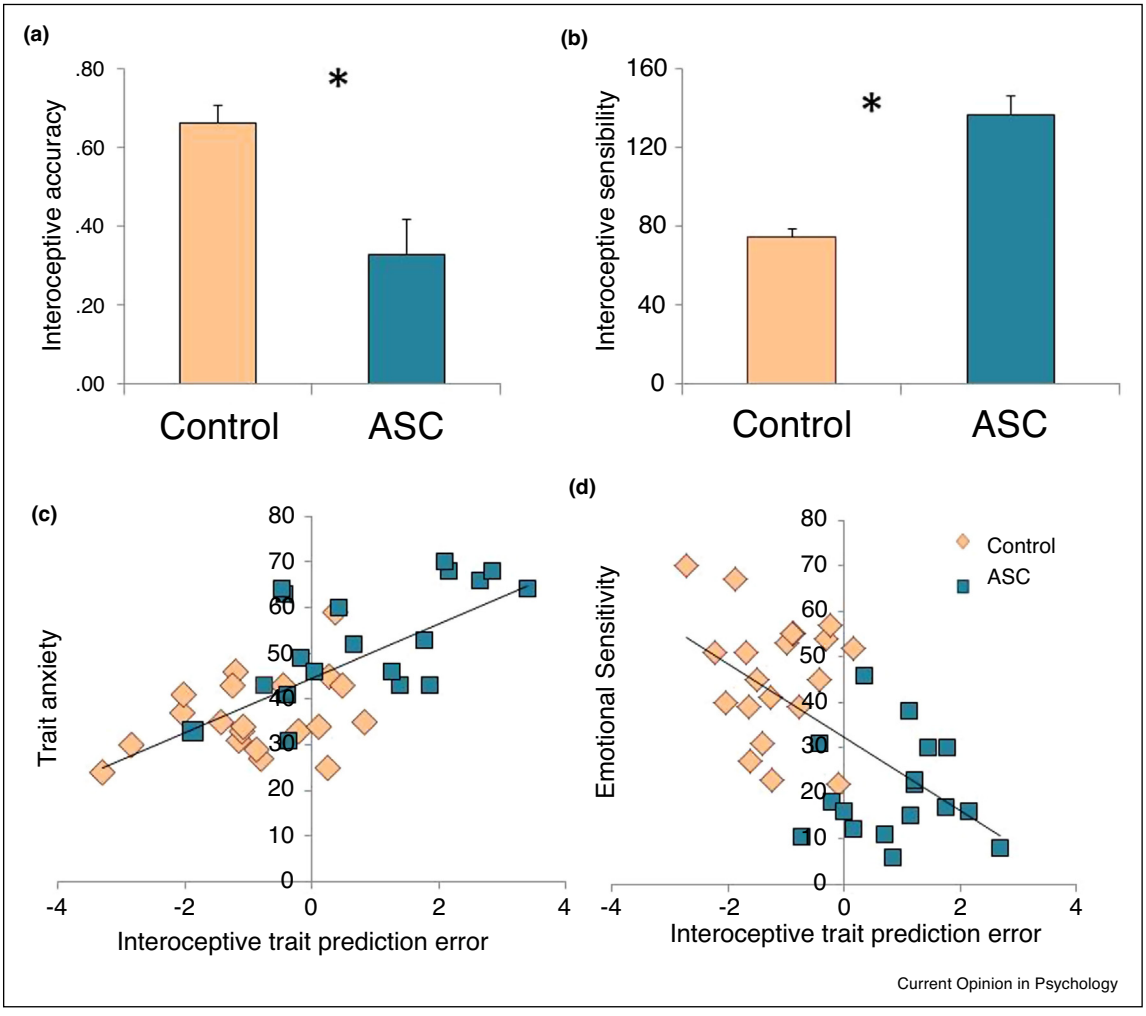
Fear and neutral faces are time-locked to distinct parts of the cardiac cycle to determine how cardiac afferent signals alter neural activity and intensity judgements **(a)**. A cardiac cycle by emotion interaction demonstrated enhanced bilateral amygdala activation in response to fear faces at systole **(b)**. Fear faces presented at systole were also judged as significantly more intense **(c)**.

attributed to the presence versus absence of cardiac interoceptive signals. Historically, such experiments highlight the inhibitory nature of cardiac afferent signals. Interoceptive inhibition is also apparent in suppression of startle responses and attenuation of memory for words encoded at systole [21•,36]. However, these baroreceptor signals amplify threat processing, enhancing the detection and perception of fear signals in others [23••,24,25] (Figure 1). External manipulation of baroreceptor firing also engenders specific fear effects [37]. Similar, but weaker effects are sometimes reported for other emotions, notably disgust [38]. While such cardiac interoceptive effects are particularly observed for threat and fear stimuli [25], the impact of cardiac signals on the encoding of words does not appear to be related to whether the word is emotional [36].

Interaction of interoceptive dimensions and clinical symptoms

Different aspects of interoception interact in how they shape emotional states and behaviours. The impact of phasic cardiac signals may be tempered by other psychological dimensions of interoception. For example individuals that perform well on heartbeat detection tasks (good 'interoceptive accuracy'), are less susceptible to the deleterious impact of cardiac signals at systole signals on memory encoding [36], yet in other contexts show an enhanced processing of self-related signals [39]. Good interoceptive accuracy is generally associated with better affective regulation [40]. Positive shifts in interoceptive accuracy induced by contemplative training are associated with an improved capacity to verbalize emotional states (decreased alexithymia [26•]). Disruption of

Figure 2



Interoceptive accuracy was significantly impaired in the ASC group **(a)** despite ASC individuals having a heightened belief in their own interoceptive aptitude, as reflected by elevated interoceptive sensibility relative to controls **(b)**. The discrepancy between these objective and subjective measures of interoception, termed the interoceptive trait prediction error, correlated with both affective symptoms **(c)** and an index of emotional sensitivity **(d)**.

interoceptive signalling [20••], accuracy [41] and subjective sensibility [42] are observed in clinical disorders that impact on self-focused emotional control. Moreover, the alignment of subjective and subjective components of emotion appears to predict emergence of affective symptoms. For example in people with autism, the degree of 'mismatch' between perceived sensitivity to interoceptive state and observed accuracy in performing an interoceptive task (heartbeat detection) predicts anxiety symptoms and deficits in interpersonal emotional interaction [19•] (Figure 2).

Interoception and expectation

Subjective interoceptive experience 'interoceptive sensibility' can be considered as an expression of a high level model or 'belief' for generating predictions about information coming from inside the body. Thus mismatch between subjective interoceptive sensitivity and objective interoceptive accuracy may be considered as an 'interoceptive trait prediction error signal'. This perspective, and its observed relationship to affective symptoms [19•], is consistent with theoretical work that presents interoception and associated emotional feeling states within a predictive coding framework [3,43,44,45••,46]. The conceptualization of the brain as a 'prediction machine' challenges previous ascription of emotional feelings to cortical representations of viscerosensory afferent information. Instead, there is 'reverberating' causality: Neural encoding of generative (*i.e.* top–down) predictions concerning internal bodily state is expressed in drive to the autonomic nervous system (and in endocrine and immune responses). Efferent autonomic responses can thus be viewed as descending 'interoceptive predictions' through their effects on peripheral physiology [3,43,44,45••,46]. These are met with ascending interoceptive neural signals that cancel predictions and inform (through prediction errors) a revision of the predicted state. Autonomic efferents represent means to probe and actively infer the internal state of the body, and both emotions and feelings arise through the interacting representational cascades of ascending prediction errors and descending bodily predictions (autonomic drive). The interoceptive sensing of internal information can thus be built upon higher predictive representations as shown by the observation that emotional feelings and reactions to interoceptive challenges will conform to 'artificial' categorical priors [47]. Exteroceptive and proprioceptive information also constrain and contextualise such interoceptive processing. Predictive coding models of interoception have explanatory power, both for observations on emotion, extending to self-representation and, interestingly, in accounting for both structural and functional organizational features of the brain, notably insular cortex and its relationship to visceromotor centres [3,48,39,49,43,44,45••,46,50••].

Conclusions

Increasingly evidence describing how interoceptive signals influence emotional and motivational processes make it untenable to dismiss the contribution of bodily physiology to emotions as epiphenomenal. Detailed understanding of these mechanisms is important given their influence on adaptive [16] and maladaptive [51••] motivational decisions and their implications for preventing and managing clinical disorders [19•,20••,21•,34,41,42,46,50••].

Conflict of interest statement

The authors declare no conflicts of interest relation to contents of this paper.

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