Interoception in emotional experience
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Purpose of review
Many theories of emotion have postulated a close relationship of the feedback of physiological changes and their perception with emotional experience. This paper reviews recent advances in theory and brain-imaging research on this topic of interoception and describes a hypothetical model of the potential mechanisms.

Recent findings
Research from patients with spinal-cord injuries and pure autonomic failure suggests that emotion-related peripheral autonomic changes are not necessary for emotional experience. However, in support of a role for centrally integrated feedback from the whole body, imaging studies found that activations in areas commonly associated with interoception and emotion (anterior insula and anterior cingulate) were correlated with individual differences in interoception (heartbeat detection) and trait measures of emotion. Because recent theory distinguishes between two levels of emotional experience (phenomenology and awareness), this paper proposes a hypothetical model of the effects of interoception on phenomenology and awareness. This model classifies interoception into the central representation of feedback from the whole body, the perception of actual physiological changes as well as the perception of illusory changes.

Summary
Consistent with recent theories of emotion, evidence from brain imaging supports the notion that centrally integrated feedback from the whole body plays a role in emotional experience. Because research on neural correlates of emotional experience is at an early stage, the hypothesized model of potential causal links between interoception and emotional experience might serve as a helpful guide to future research.

Keywords
brain imaging, consciousness, emotional experience, interoception

Introduction
Emotion is commonly described as involving changes in experience (feeling, affect), autonomic nervous system activation, expressive behaviour, and instrumental behaviour. For example, feeling afraid, increases in heart rate, a fearful face, and running away, respectively, are typically regarded as signs of fear. Within this perspective, autonomic changes in emotion prepare the body for imminent behaviour that is adaptive to the situation [1]. An energizing autonomic response (fight-or-flight) is thus typical in response to threat, whereas a dampening autonomic response (autonomic soothing) is typical in response to safety [2]. Autonomic changes can also have expressive effects [2]. For example, facial blushing can be a sign of embarrassment. In addition, peripheral autonomic changes, and more generally, physiological feedback from the whole body and its perception (interoception) have been postulated to play an important role in emotional experience [3–10]. As the term ‘interoception’ is used interchangeably to refer to the representation of physiological feedback as well as its perception, the present paper discusses both of these aspects in reviewing current theory and research on the role of interoception in emotional experience. In compliance with journal policy, this paper mainly uses references that appeared in 2004 or later.

Peripheral autonomic changes: historical perspective
In 1884, William James [3] argued that ‘our feeling of . . . (peripheral autonomic) changes as they occur IS the emotion’ (pp. 189–190). Because in 1885, Carl Georg Lange [6] proposed a similar view, the theory known as the James–Lange theory posits that for an emotional experience to occur, peripheral autonomic changes are necessary (i.e. if removed, emotional experience disappears) and sufficient (i.e. changes per se result in emotional experience).

Peripheral autonomic changes: contemporary studies
Although early evidence suggested that spinal-cord injuries impair emotional experience, more recent, improved studies found little, if any, impairment in patients and no relationship with the degree of autonomic reduction associated with the level of lesion [11*]. Similarly, patients with pure autonomic failure (who suffer from a selective degeneration of autonomic neurons) cannot generate autonomic changes and thus lack feedback of autonomic changes; nonetheless, they showed only minor
impaired in emotion [12*,13]. These findings argue against the James–Lange theory of emotion. However, it has been suggested that because lesions do not eliminate physiological feedback from all sources, the remaining channels (e.g. facial feedback in spinal-cord patients) might suffice for emotional experience [14]. However, this argument might not be falsifiable because if peripheral changes were taken to refer to any kind of physiological processes (e.g. neurotransmitter activation in the brain), the James–Lange theory would simply be a monist theory of the mind–body relationship, in that emotional experience (mind) results from a physiological process (body). In sum, because research suggests that a substantial reduction in peripheral autonomic changes has a minimal effect on emotional experience, this argues against their necessary role in emotional experience. However, as discussed below, there could still be a role for the central representation of feedback from the whole body in emotion [5,7,8,15].

Heartbeat detection

Successors to James and Lange [3,6] have retained the notion that physiological feedback plays an important role in emotion [4,5,7–9,16]. For example, it might not be the mere occurrence of peripheral changes but their perception that affects emotional experience [16]. Sensitivity to interoceptive processes has commonly been indexed with objective measures of people’s ability to detect their own heartbeats. In these tasks, participants are instructed to detect their heartbeats without feeling for their pulse. Typically, participants count their heartbeats silently or judge the temporal relationship between their heartbeats and tones that are triggered by heartbeats [17]. Research supports the fact that heartbeat detection is associated with emotional experience. For example, when students were shown film clips targeting different emotions, individuals who could detect their heartbeats (assessed separately) reported experiencing more intense emotions than poor detectors. In contrast, good and poor detectors did not differ significantly in physiology (heart rate and electrodermal activity) [18]. Furthermore, good heartbeat detectors showed more arousal focus [19*]. This trait indexes how much individuals are sensitive to the implied degree of experienced activation and deactivation (arousal) of emotion words in describing emotional experiences in daily life.

Functional imaging of heartbeat detection

The neural correlates of heartbeat detection were recently studied with functional magnetic resonance imaging [20**,21]. In the first study [20**], tones were triggered by individual heartbeats and were presented in series of 10 tones at one of two delay intervals (0 or 500 ms). In the heartbeat detection task, participants were instructed to judge the temporal relationship between their own heartbeats and tones. Because the two tone conditions were identical except for the different delays between heartbeats and tones (0 or 500 ms), participants could distinguish between the conditions only if they could detect their own heartbeats. Also, within each series, one of the 10 tones differed slightly in pitch. In separate conditions, participants were instructed to attend either to the relationship between heartbeats and tones (heartbeat detection) or to the pitch of the tones (pitch detection). When participants attended to their heartbeats (rather than the pitch of the tones), activations included anterior cingulate and bilateral anterior insula. When a performance measure of participants’ ability to discriminate between the two tone conditions during the heartbeat detection trials was computed, activation in a region in the right anterior insula and frontal operculum correlated with heartbeat detection. In addition, voxel-based morphometry found that the volume of grey matter in this region correlated with heartbeat detection and (in a different sample) with self-reported body awareness; however, heartbeat detection and the self-report measure were uncorrelated. Also, heartbeat detection and right anterior insula activation correlated with trait anxiety. In another study [21], participants were instructed to count either their own heartbeats silently (no tones were presented) or the number of tones (independent from heartbeats). Although the study apparently did not control for potentially confounding variables (e.g. presentation of tones, task difficulty), results were comparable. Attention to heartbeats activated the insular cortex, and activation in the anterior insula correlated with accuracy in counting heartbeats. However, in addition, intercorrelations among activation in the anterior cingulate, heartbeat detection, trait anxiety, and neuroticism were obtained. Taken together, such studies suggest relationships between heartbeat detection, negative affect, and activation in the anterior insula and anterior cingulate. Consistent with insula activation, another study found that the heartbeat-evoked electrical brain potential was largest right centrally and correlated with perception performance [22*].

These findings support the notions that interoception (heartbeat detection) plays a role in emotion [16], and that the anterior insula and anterior cingulate are involved in interoception and emotion [5,8,10,15]. In particular, Craig [5,15,23] proposed that physiological feedback from the whole body is mapped in the dorsal posterior insula and remapped in the right anterior insula via a lamina-1 thalamocortical pathway. Findings are thus consistent with a role of the right anterior insula in interoception. Although the insula and anterior cingulate have also been postulated to play a role in emotion, it is unclear whether the role of the anterior cingulate is afferent or efferent [5,8,15,24]. However, because findings were obtained in a non-emotional context (attention to heartbeats), they suggest that activations not only in
the anterior insula [25] but also in the anterior cingulate are insufficient for emotional experience.

**Heartbeat detection: an index of awareness?**

Although heartbeat detection is commonly treated as an index of conscious perception (awareness) of interoceptive processes, two questions remain. First, despite its face validity, heartbeat detection might index something other than interoception. For example, research suggests that heartbeat detection is associated with lower heart rate and less heart rate variability at rest [26], greater cardiac reactivity to stress as well as greater facial expressiveness [19*]. However, although confounding effects in heartbeat detection cannot be ruled out completely, anterior insula activations in heartbeat detection [20**,21] are consistent with a process involving interoception [5,15]. Second, it is unclear if heartbeat detection indexes awareness. In support of this, participants in heartbeat detection tasks often report that they are merely guessing, and actual performance on heartbeat detection tasks is uncorrelated with self-rated performance [27]. Therefore, heartbeat detection might index the mapping of interoceptive processes rather than their awareness in regions such as the anterior insula and anterior cingulate. However, in support of awareness, a recent study [28*] found that right insula activation correlated with experiences of the paradoxical heat illusion.

**Brain imaging of emotional experience**

Recent findings [20**,21] are important in understanding the neural mechanisms of emotion. However, it is difficult to design studies that isolate neural mechanisms specific to emotional experience. For example, emotional experience is often confounded with the perceptual input (e.g. picture presentation) [29*,30], and depends on people’s evaluation (appraisal) of the situation [31–34]. Although research on this topic is progressing [35**], empirical evidence is limited [36**,37], in particular with regard to the role of interoception in emotional experience. Therefore, the remainder of this paper discusses recent advances in the conceptualization of emotional experience, and describes a hypothetical model of potential mechanisms that link different interoceptive processes with emotional experience.

**Two levels of emotional experience**

Many theories of emotion are unclear about what it feels like to have an emotional experience [38]. For example, the James–Lange theory does not reveal anything about the content of emotional experience. Current theories of emotional experience distinguish two levels [38–42], similar to two-level models of conscious experience [43–45]. For example, patients with blindsight report the absence of visual phenomenology (first level), whereas patients with Anton syndrome are unaware that they are blind (second level) [38]. First-level experience thus refers to non-reflective phenomenology, whereas second-level experience refers to awareness.

**First-level emotional experience**

Theories of emotion disagree on whether there are genuine (i.e. potentially free-floating) experiences of fear, anger, disgust, happiness, and so on. Proponents of basic emotions support this view [46], but it is not clear how emotions differ in content. However, Lambie and Marcel [38] included first-level examples like feeling blue (sadness), feeling paralyzed (fear), and experiencing a person as hostile (anger). In contrast, according to the theory of core affect [39] the first level is characterized only by bipolar mental dimensions of valence (pleasure–displeasure) and arousal (sleepy–activated). However, although other theories also apply dimensions, there is disagreement about which model captures the underlying mechanisms of first-level experience (e.g. two unipolar dimensions or two bipolar approach and avoidance dimensions) [47]. Nonetheless, in these dimensional theories, fear and anger might not differ in first-level experience (both with negative valence and high arousal). Instead, basic emotions might be culture-specific social constructs (schemata) that occur on the second level [39].

**Second-level emotional experience**

According to core affect theory [39], second-level experience is a meta-experience that is characterized as the awareness of emotion-related processes (e.g. first-level core affect, behaviour, antecedent event, autonomic changes, facial expression). It is thus an act of self-perception [39] that is affected by attention focus [38]. Although theories differ in detail, they postulate that second-level experience involves an awareness of various aspects of emotional processing. However, it is uncertain to what extent the phenomenology of second-level emotional experience qualifies to be of an emotional nature.

**Decoupling of first and second-level emotional experience**

As in two-level theories of conscious experience, the two levels of emotional experience can be decoupled [38,39]. Similar to experiences of mind wandering (first level) without awareness (second level) [48], introspection suggests that individuals can behave and appear in ways that observers would clearly describe as emotional, even though the individuals themselves are unaware of their emotional state (e.g. repressors) [38]. An unresolved question is whether these individuals experience emotions (first level) without being aware of them (second level), or whether the self-reported absence of phenomenology is accurate [49]. Furthermore, if it is possible that first-level phenomenology is not necessary for second-level experience, individuals might infer emotion
(at the second level) from any changes that they consider emotion relevant. For example, symptoms of sweating and increases in heart rate might be experienced as anger (second level) even in the absence of core affect (first level). Studies of split-brain patients are relevant to this issue. When patients are prompted to laugh (through a signal to the right hemisphere) they confabulate reasons for laughing (through their left hemisphere, which controls language) [50], supporting the notion of an interpreting process [51]. Because it is conceivable that patients might infer (on the second level) that they responded emotionally, this suggests that second-level emotional experience can occur in the absence of first-level phenomenology.

**Interoception and the two levels of emotional experience**

Figure 1 shows a hypothetical model of the effects of interoception on first and second-level emotional experience. This model divides interoception into the central representation of feedback from the whole body (e.g. right anterior insula) [5,20]**, the perception of actual physiological changes, and the perception of illusory changes. Whereas whole-body representation affects only first-level experience, first-level experience and the perception of actual and illusory changes affect second-level experience. Because whole-body representation is centrally integrated, clear emotion-specific autonomic patterns are not expected. In contrast, correlations between autonomic responses and dimensions of first-order emotional experience are expected [39,47]. Although individual differences in interoception (indexed by heartbeat detection) affect first-order experience [20**], this process might not necessarily involve awareness. Note that experiences like feeling blue or experiencing the world as hostile [38] might be non-emotional experiences that are affected by emotional processes [52–54]. In the absence of first-level experience, second-level experience reflects the perception of actual or illusory physiological changes. This perception triggers an attribution process [4,9] according to culture-specific emotion schemata [39]. Interoceptive sensitivity (heartbeat detection) affects this process by allowing better discrimination between actual and illusory changes.

By distinguishing among different aspects of interoception, this model accommodates for findings regarding the relative importance of actual physiological changes, their perception, and false beliefs about their occurrence in normal and pathological conditions of emotion and health [55**,56*,57,58*,59**]. For example, research suggests that the accurate perception of physiological changes plays a greater role in panic than in social anxiety [56*,58**]. Although this model can serve as a guide, future research needs to study potential moderators (e.g. situational context) [60,61], the relative contribution of subcortical and cortical mechanisms [62,63], differences between primary and secondary emotions (e.g. fear and pride, respectively) [64], and the extent of emotional experience in animals [65].

**Conclusion**

This paper discussed theoretical and empirical relationships between interoception and emotional experience. Consistent with theories of emotion, evidence from brain imaging supports the notion that centrally integrated feedback from the whole body plays a role in emotional experience. Incorporating advances in psychological theory, a model was proposed on the potential causal relationships between three aspects of interoception (centrally integrated feedback from the whole body, the perception of actual physiological changes and of illusory changes) and two levels of emotional experience (phenomenology and awareness). This model might serve as a guide for research on the role of interoception in emotional experience.

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