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Review Article

Neurophysiological Mechanisms and Structural Pathways of Interoceptive Processing in the Human Insular Cortex

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Abstract

Interoception refers to the physiological process by which the nervous system senses, interprets, and integrates internal visceral signals, providing a foundational baseline for homeostatic regulation and emotional awareness. This review synthesizes current functional neuroimaging, cytoarchitectonic, and electrophysiological literature focused on the human insular cortex as the primary central terminal for interoceptive pathways. Visceral afferents carrying metabolic, cardiovascular, and gastrointestinal data travel via the vagus nerve and spinothalamic tracts to the posterior insula. This region displays a granular cytoarchitecture optimized for primary sensory decoding. From the posterior insula, signals are processed through a functional gradient moving toward the agranular anterior insula. This anterior zone integrates visceral signals with cognitive and environmental inputs. Von Economo neurons, located selectively in the anterior insula, support the rapid transmission of these integrated interoceptive states to the anterior cingulate cortex. Electrophysiological findings highlight the heartbeat-evoked potential (HEP) as a reliable index of cortical interoceptive processing, with fluctuations in HEP amplitude corresponding directly to insular blood-oxygen-level-dependent (BOLD) signals. Understanding these structural and functional pathways provides insight into clinical autonomic imbalance conditions, including anxiety, depression, and somatoform disorders where central interoceptive mapping is altered.

Keywords: Interoception; Insular cortex; Von Economo neurons; Autonomic homeostasis; Heartbeat-evoked potential.

1. Introduction

How does the brain know what the body feels from within? Unlike vision or hearing, which sample a world outside the skin, interoception samples the continuous, largely silent traffic of the viscera — the stretch of the gut, the quickening of the heart, the shift in blood pressure, temperature, glucose, inflammation and airway resistance. The term, introduced in its modern sense by Charles Sherrington and revived by A. D. (Bud) Craig, denotes the sense of the physiological condition of the entire body (Craig, 2002; Craig, 2003). It is not a single channel. It is a family of afferent streams that must be decoded, prioritised, predicted and, only sometimes, made conscious.

The insular cortex, hidden within the lateral sulcus beneath the frontal, parietal and temporal opercula, has emerged as the principal cortical hub for that work. It is the only cortical region that receives direct thalamic relay of small-diameter, interoceptive afferents and that also participates, through dense reciprocal connections, in salience detection, emotion, decision-making and social cognition (Craig, 2009; Gu et al., 2013; Uddin et al., 2017). Damage, stimulation or dysregulation of the insula therefore does more than blunt a sensory modality; it alters how a person experiences hunger, pain, anxiety, disgust, empathy and even the sense of self.

This review asks a deliberately anatomical question with functional consequences: by what structural pathways do visceral signals reach the insula, how does insular cytoarchitecture transform them, and how does electrophysiology make that transformation measurable in living humans? We organise the answer around three claims that recur across the literature. First, interoceptive afferents converge on the posterior insula through vagal and spinothalamic routes, with a thalamic relay that preserves modality and laterality. Second, the insula is organised along a posterior-to-anterior gradient, from granular primary representation to dysgranular integration to agranular awareness and control, supported by distinctive cell types including Von Economo neurons (VENs) in the anterior insula and anterior cingulate cortex (ACC). Third, the heartbeat-evoked potential (HEP) provides a temporally precise, clinically tractable index of this gradient in action, complementing the spatial precision of functional magnetic resonance imaging (fMRI).

We begin with afferent anatomy, move through cytoarchitecture and connectivity, examine the HEP and related measures, and close with clinical translation and open questions. Where evidence

is convergent we say so; where it is contested — notably on lateralisation, on the causal role of VENs, and on whether insular hyper- or hypoactivation characterises anxiety and depression — we make the disagreement explicit. The goal is not to reduce interoception to the insula alone, but to show why no account of interoception, homeostasis or feeling can bypass it.

2. Methods: How This Review Was Assembled

This is a narrative, anatomically structured review, not a systematic review or meta-analysis. Literature was identified through searches of PubMed, Scopus, Web of Science and Google Scholar for combinations of interoception, insular cortex, insula cytoarchitecture, Von Economo neurons, heartbeat-evoked potential, vagus nerve, spinothalamic tract, salience network and autonomic homeostasis, supplemented by backward citation tracking from landmark papers by Craig (2002, 2009), Critchley et al. (2004) and Garfinkel et al. (2015). Priority was given to human neuroimaging, intracranial electrophysiology, cytoarchitectonic and clinical studies, with animal work used only where human data are unavailable — for example, on VEN phylogeny and on vagal afferent anatomy. Classic papers are retained because later work refines rather than replaces them.

Interpretive caution is warranted. Interoception is measured in at least three dissociable ways — interoceptive accuracy (performance on heartbeat detection or counting), interoceptive sensibility (self-reported tendency to notice bodily signals) and interoceptive awareness (metacognitive correspondence between accuracy and confidence) — and these dimensions do not always correlate (Garfinkel et al., 2015). Studies that conflate them can produce apparently contradictory insular findings. Throughout, we specify which dimension a cited study used when that distinction matters.

3. Afferent Pathways: From Viscera to Posterior Insula

3.1 Two complementary highways

Visceral information reaches the brain by two major routes that are complementary rather than redundant. The vagus nerve (cranial nerve X) carries predominantly parasympathetic afferents — roughly 80% of vagal fibres are afferent — from the heart, lungs, gut and other viscera to the nucleus tractus solitarius (NTS) in the medulla. The spinothalamic tract, and in particular its lamina I component, carries sympathetic and nociceptive afferents — small-diameter Aδ and C fibres signalling temperature, pain, itch, visceral distension and metabolic state — from the spinal cord to the brainstem and thalamus (Craig, 2002; Craig, 2003; Berntson & Khalsa, 2021). Together they provide a near-continuous readout of homeostatic state.

From the NTS, vagal signals relay via the parabrachial nucleus and the ventromedial nucleus of the thalamus (VMpo / VMb in primate nomenclature) to the dorsal posterior insula. Lamina I spinothalamic signals converge on the same thalamic territory. This convergence is important: the posterior insula is not a vagal cortex or a spinal cortex, but a site where parasympathetic and sympathetic streams are first brought into a common cortical map. Thalamic lesions and functional connectivity studies confirm that the posterior insula is the obligatory cortical terminal for this relay in humans (Craig, 2009; Evrard, 2019).

3.2 Why the posterior insula is primary

The posterior insula receives this input in a granular cortex that resembles other primary sensory cortices in its laminar organisation — a well-developed layer IV, dense thalamocortical input and relatively local, modality-specific processing (Morel et al., 2013; Evrard, 2019). It responds to cardiac, respiratory, gastric, thermal and nociceptive stimulation with short latency and with a degree of somatotopic and viscerotopic organisation, though that organisation is coarser and more overlapping than in somatosensory cortex. In other words, the posterior insula does what primary visual or somatosensory cortex does for exteroception: it creates a first, faithful, body-centred map.

That map, however, is not yet a feeling. Patients with posterior insular lesions can show preserved autonomic reflexes with impaired interoceptive awareness, and stimulation of the posterior insula can evoke visceral sensations without the rich affective quality that anterior insular stimulation evokes. The distinction matters clinically: a signal can be represented without being felt, and felt without being accurately interpreted.

Table 1. Cytoarchitectonic and functional organisation of the human insula.

Subregion	Cytoarchitecture	Dominant inputs	Proposed function
Posterior insula	Granular, layer IV prominent	VMpo thalamus; vagal + spinothalamic	Primary interoceptive decoding
Mid / dysgranular insula	Dysgranular, transitional	Posterior insula; somatosensory; amygdala	Re-representation, integration
Anterior insula	Agranular, VENs in layer V	Mid-insula; prefrontal; ACC; limbic	Awareness, salience, control
Frontoinsular cortex	Agranular, VEN-rich	Anterior insula; ACC	Rapid relay to ACC, social-emotional

Legend: Organisation synthesised from Craig (2009), Morel et al. (2013), Gu et al. (2013) and Evrard (2019). Boundaries are graded, not sharp; dysgranular cortex forms a transitional zone. ACC, anterior cingulate cortex; VENs, Von Economo neurons.

4. The Posterior-to-Anterior Gradient

The most durable model of insular function is Craig's posterior-to-anterior gradient (Craig, 2009; Craig, 2011). In this model, a primary interoceptive representation in the posterior insula is re-represented, first in the mid-insula and then in the anterior insula, with each step adding integration, context and access to consciousness. The gradient is not a conveyor belt — there are dense reciprocal connections and parallel routes — but it captures a robust pattern in meta-analyses: posterior insula activity tracks stimulus intensity and bodily state; mid-insula activity tracks integration of interoceptive with exteroceptive and emotional signals; anterior insula activity tracks subjective feeling, salience and the anticipation of bodily change (Gu et al., 2013; Chang et al., 2013; Uddin et al., 2017).

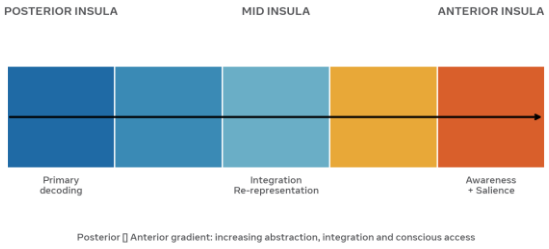


Figure 1. The posterior-to-anterior insular gradient.

Legend: Schematic synthesis, not a histological section. Posterior granular cortex decodes visceral input; dysgranular mid-insula re-represents it; agranular anterior insula integrates it with cognition, emotion and context to support conscious feeling and salience detection. Adapted from concepts in Craig (2009) and Gu et al. (2013).

4.1 Mid-insula: the integrator

The dysgranular mid-insula is often under-described, yet meta-analytic clustering places it at the centre of interoceptive processing across tasks (Chang et al., 2013; Uddin et al., 2017). It receives posterior insular input and connects strongly with

somatosensory cortex, amygdala and striatum. Functionally, it appears to bind “what the body is doing” to “what it means for action” — for example, integrating cardiac signals with pain, taste or respiratory load. Recent work on hemispheric divergence suggests that ventral dysgranular mid-insula may be a convergent site where top-down (attentional, predictive) and bottom-up (afferent) interoceptive processing meet, with the balance shifting in psychiatric disorders (Nord et al., 2021; Hassanpour et al., 2023).

4.2 Anterior insula: feeling, salience and awareness

The anterior insula, especially on the right, is where interoception becomes reportable feeling. Right anterior insular activity correlates with interoceptive accuracy on heartbeat detection tasks, with subjective intensity of disgust, pain, craving and empathy, and with awareness of errors and risk (Critchley et al., 2004; Craig, 2009; Gu et al., 2013). It is a core node of the salience network, together with the dorsal ACC, switching between the default-mode network (internally directed cognition) and the central executive network (externally directed attention) according to homeostatic relevance (Menon & Uddin, 2010; Uddin, 2015). When the body signals urgency — a racing heart, breathlessness, nausea — the anterior insula helps reallocate attention and resources accordingly.

Lateralisation deserves nuance. The right anterior insula is often dominant for sympathetic, arousing, aversive interoception, while the left anterior insula has been linked more to parasympathetic, affiliative and gustatory processing, but the pattern is task-dependent and not absolute. Bilateral recruitment is common, and individual differences are large. Reviews that treat “right insula = feeling” as a law overstate a tendency.

5. Von Economo Neurons: A Fast Lane to the Cingulate

Within the agranular anterior insula — and its frontoinsular subdivision — and the ACC lies a distinctive cell type: the Von Economo neuron (VEN), first described by Constantin von Economo in 1926. VENs are large, spindle-shaped, bipolar projection neurons in layer V (and layer III), with a thick apical and basal dendrite, a large axon and relatively sparse dendritic branching compared with neighbouring pyramidal cells (Allman et al., 2010; Evrard et al., 2012). Their morphology suggests speed and fidelity over local computation: a large, fast-conducting neuron suited to relaying a distilled signal over long distance with minimal delay.

Phylogenetically, VENs are concentrated in humans, great apes, elephants, cetaceans and some other large-brained, socially complex species, and are sparse or absent in most other primates — though recent work has identified VEN-like cells in macaques, complicating a simple “human-only” story (Evrard et al., 2012; Allman et al., 2010). Their selective distribution in the frontoinsular cortex and ACC, two regions that co-activate in salience, empathy, error awareness and social pain, has led to the hypothesis that VENs support rapid, intuitive social-emotional signalling: the “gut feeling” that guides a decision before deliberation catches up.

Direct causal evidence in humans remains limited — VENs cannot be selectively stimulated non-invasively — so the claim must be phrased carefully. What is established is anatomical: VENs project to the ACC and to other salience-network targets, and VEN density is altered in conditions where salience and social cognition are disrupted, including frontotemporal dementia, autism and schizophrenia (Allman et al., 2010; Brüne et al., 2011). What is plausible, and consistent with connectivity and lesion data, is that VENs provide a high-speed frontoinsular–cingulate relay by which an integrated interoceptive state in the anterior insula is broadcast to the ACC for action selection, autonomic adjustment and conscious appraisal. The insula–ACC loop is therefore not merely anatomical proximity; it is a functional circuit for turning feeling into doing.

6. Electrophysiology: The Heartbeat-Evoked Potential

If fMRI shows where interoception is processed, electrophysiology shows when. The heartbeat-evoked potential (HEP) is an event-related potential time-locked to the cardiac R-peak, typically measured with electroencephalography (EEG) or magnetoencephalography (MEG) in a window roughly 200–600 ms after the heartbeat (Schandry et al., 1986; Pollatos & Schandry, 2004; Park & Blanke, 2019). It is not the cardiac artefact — careful artefact correction is essential — but a cortical response to cardiac afferent signalling. Dipole source localisation places its generators in the insula (especially right insula), ACC, prefrontal cortex and secondary somatosensory cortex (Pollatos et al., 2005; Kern et al., 2013).

HEP amplitude is modulated by attention to the heart, by interoceptive accuracy, by emotional state and by clinical status. Individuals with higher interoceptive accuracy tend to show larger HEP amplitudes; patients with atrial fibrillation show attenuated HEP, localised to the right insula; and focused-ultrasound modulation of the posterior insula reduces HEP amplitude, providing causal evidence for a posterior insular contribution (Coll et al., 2021; Kern et al., 2013; Legon et al., 2024). HEP also tracks predictive processing: when a heartbeat is expected but omitted, or when interoceptive and exteroceptive signals are integrated, HEP reflects prediction error — the mismatch between what the brain predicted the body would do and what it sensed (Ainley et al., 2016; Petzschner et al., 2019).

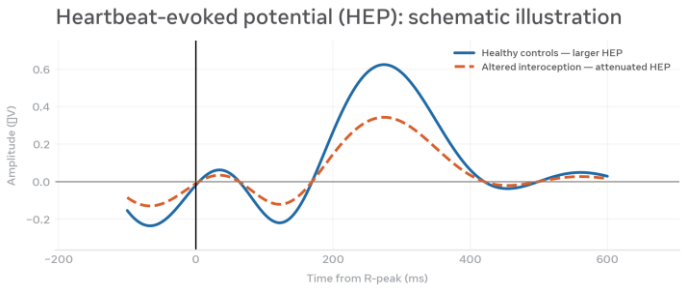


Figure 2. Heartbeat-evoked potential (HEP).

Legend: Schematic, not empirical data. The waveform is time-locked to the R-peak (0 ms). Larger positive deflection around 250–400 ms in healthy controls is attenuated when interoceptive processing is altered. Real HEP morphology varies with electrode, task and artefact correction (see Park & Blanke, 2019; Coll et al., 2021).

6.1 HEP and BOLD: complementary, not redundant

A common misunderstanding is that HEP and insular BOLD are interchangeable. They are complementary. BOLD offers millimetre spatial resolution but seconds-level temporal resolution; HEP offers millisecond temporal resolution but limited spatial resolution. Studies combining EEG-fMRI find that trial-by-trial fluctuations in HEP amplitude correlate with BOLD in the insula and ACC, supporting the view that the HEP indexes the cortical receipt and evaluation of cardiac signals that fMRI localises (Park et al., 2014; Park & Blanke, 2019). For clinical use, HEP has practical advantages: it is inexpensive, portable, repeatable and can be recorded at the bedside or in populations who cannot undergo MRI. Its limitations — artefact sensitivity, inter-individual variability and dependence on cardiac physiology — require standardised recording and analysis, a need now addressed by consensus recommendations (Coll et al., 2021).

Table 2. Methods for studying insular interoception: trade-offs.

Method	Spatial resolution	Temporal resolution	What it reveals	Key limitation
fMRI (BOLD)	Millimetres	Seconds	Where insular subregions activate	Slow, indirect, costly
EEG / MEG — HEP	Centimetres (source-localised)	Milliseconds	When cardiac signals reach cortex	Cardiac artefact, variability
Intracranial EEG	Millimetres (implanted)	Milliseconds	Direct insular HEP, causal timing	Invasive, epilepsy patients only
Heartbeat counting / detection	Behavioural	Trial-level	Interoceptive accuracy	Confounded by counting strategy, priors
Self-report (e.g., MAIA)	—	Trait-level	Interoceptive sensibility	Subjective, not accuracy

Legend: MAIA, Multidimensional Assessment of Interoceptive Awareness. No single method captures interoception; convergent use is recommended (Garfinkel et al., 2015; Bornemann et al., 2015).

7. Predictive Interoception and the Insula

A productive reframing of the gradient is predictive: the brain does not passively wait for visceral signals; it predicts them. Under predictive-coding accounts, the anterior insula and ACC generate predictions about bodily state, the posterior insula compares predictions with afferent input, and prediction errors update beliefs and drive autonomic action (Barrett & Simmons, 2015; Seth, 2013; Petzschner et al., 2019). Feeling, in this view, is the brain's best inference about the causes of interoceptive signals, not a direct readout.

This helps explain why identical bodily signals can feel different in different contexts — a racing heart during exercise versus during panic — and why anxiety can arise from amplified interoceptive prediction errors even when peripheral physiology is normal. It also explains why interoceptive training, mindfulness and biofeedback can alter feeling without changing the heart: they change priors, precision weighting and attention, not the viscera alone (Bornemann et al., 2015; Farb et al., 2015). The insula is the anatomical site where prediction, afference and error are most plausibly integrated.

8. Clinical Implications

When insular interoceptive mapping is altered, the consequences are transdiagnostic. The pattern is not a single lesion or a single direction of change, but a set of dissociable alterations that map onto different dimensions of interoception.

8.1 Anxiety

Anxiety is often characterised by interoceptive hypervigilance: heightened attention to cardiac and respiratory signals, catastrophic interpretation of benign bodily change, and anterior insular hyperactivation to interoceptive and threat cues (Paulus & Stein, 2006; Garfinkel et al., 2016). Panic disorder provides the clearest example — a palpitation is felt, predicted as dangerous, and amplified into a cascade of sympathetic arousal. Interoceptive exposure, which deliberately induces bodily sensations in a safe context, works in part by recalibrating insular prediction and appraisal.

8.2 Depression

Major depressive disorder shows a different pattern. Meta-analysis of fMRI interoceptive tasks finds reduced activation in the right dorsal mid-insula and left posterior insula during interoceptive attention in depression, consistent with blunted or noisy interoceptive representation (Nord et al., 2021; Kohn et al., 2023). Subjectively, this can manifest as emotional numbness, disconnection from the body and difficulty using bodily signals to guide decision-making. The contrast with anxiety is instructive: both involve altered insular processing, but one leans toward amplification, the other toward attenuation — and some patients show both, at different times or in different subregions.

8.3 Somatoform, pain and other disorders

Somatoform and functional disorders, chronic pain, eating disorders and addiction all show insular involvement. In chronic pain, posterior and mid-insular sensitisation may amplify nociceptive interoception; in eating disorders, altered gastric interoception and anterior insular responses to taste and fullness may distort hunger and satiety; in addiction, anterior insular activity tracks craving and relapse risk, and insular lesions have famously been reported to abolish the urge to smoke (Naqvi et al., 2007; Simmons et al., 2013). These are not "insula diseases" — they are disorders in which a hub is dysregulated within a wider network — but they illustrate why the insula is a promising target for neuromodulation, interoceptive training and psychotherapy.

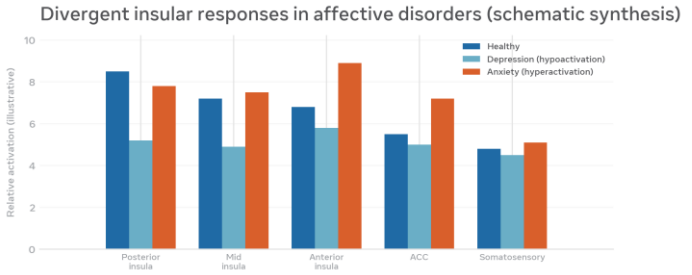


Figure 3. Divergent insular responses in affective disorders.

Legend: Schematic synthesis of meta-analytic trends, not raw data. Depression tends toward reduced mid/posterior insular activation during interoceptive tasks; anxiety tends toward heightened anterior insular / ACC activation. Individual studies vary with task, medication and comorbidity (Nord et al., 2021; Kohn et al., 2023).

9. Future Directions

Four priorities stand out. First, laminar and ultra-high-field fMRI, together with intracranial recordings, should test whether the posterior-to-anterior gradient is laminar-specific and whether distinct insular layers carry predictions versus prediction errors. Second, longitudinal studies should determine whether HEP and insular BOLD predict treatment response — for example, whether normalisation of HEP precedes symptom improvement in anxiety or depression. Third, causal manipulation — focused ultrasound, transcranial magnetic stimulation, vagus nerve stimulation and closed-loop biofeedback — should move from proof-of-concept to controlled trials, with careful attention to which insular subregion is targeted and what outcome is measured. Fourth, diversity matters: most insular interoception research has been conducted in Western, young, healthy samples. Age, sex, culture, cardiovascular health and medication all shape interoception and insular function, and models that ignore them will not generalise.

10. Conclusion

Interoception is not a vague "sixth sense." It is a structured, anatomically grounded system in which vagal and spinothalamic afferents converge on a granular posterior insula, are re-represented in dysgranular mid-insula, and are integrated in an agranular anterior insula whose Von Economo neurons broadcast the result to the anterior cingulate cortex for feeling, salience and action. The heartbeat-evoked potential makes that system visible in time, just as fMRI makes it visible in space. When the system is miscalibrated — amplified in anxiety, blunted in depression, distorted in pain and somatoform disorders — feeling itself is altered, not merely reported differently. Understanding the insular pathways of interoception is therefore not an anatomical curiosity;

it is a foundation for explaining how the brain constructs emotion, regulates the body and, when that construction falters, how it might be restored.

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Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

M. L. Hämäläinen conceived the review, synthesised cytoarchitectonic and neuroimaging literature, and drafted the manuscript. C. H. Kim contributed electrophysiological and clinical sections, revised the manuscript, and serves as corresponding author. Both authors approved the final version.

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