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1 Interoceptive rhythms in the brain

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10 11 12 13 14 15 16 Abstract

17
18 Sensing internal bodily signals, or interoception, is fundamental to maintain life. However,
19 interoception should not be viewed as an isolated domain, as it interacts with exteroception,
20 cognition and action to ensure the integrity of the organism. Focusing on cardiac, respiratory
21 and gastric rhythms, we review evidence that interoception is anatomically and functionally
22 intertwined with the processing of signals from the external environment. Interactions arise at
23 all stages, from the peripheral transduction of interoceptive signals to sensory processing and
24 cortical integration, in a network that extends beyond core interoceptive regions. Interoceptive
25 rhythms contribute to functions ranging from perceptual detection up to sense of self, or
26 conversely compete with external inputs. [Renewed interest for](#) interoception revives long-
27 standing issues on how the brain integrates and coordinates information in distributed regions,
28 by means of oscillatory synchrony, predictive coding or multi-sensory integration. Considering
29 interoception and exteroception in the same framework paves the way for biological modes of
30 information processing [specific to living organisms](#).

34 Introduction

35 The heart beats, the lungs fill, the stomach contracts: the organism is alive. All three organs
36 constantly send information up to the brain where it is sensed and processed. This central
37 monitoring or interoception^{1,2} mostly takes place unconsciously, **but also** occasionally **gives**
38 **rise** to interoceptive conscious **percepts in humans**³. The overall function of interoception is to
39 process internal bodily parameters, to keep the organism alive by regulating (homeostasis) and
40 anticipating (allostasis) bodily needs, in a loop of interoceptive perception – interoceptive
41 control analogous to the (exteroceptive) perception-cognition-action loop. However, the
42 interoceptive and exteroceptive loops should not be considered in isolation: interoception is
43 tightly intertwined with the processing of the external environment, interacting with all stages
44 of the exteroceptive loop. Such close interactions make sense from an evolutionary perspective:
45 because interoception relates to vital functions, it is likely to constitute a driving force for
46 exteroception, action and cognition. For instance, feeding behavior stems from physiological
47 needs, but foraging for food also involves sensory sampling of the external environment,
48 attentional orienting and memorization, as well as deciding whether to explore new venues or
49 to exploit resources at the current location. Both interoception and exteroception thus contribute
50 to the same overall function. Here we focus on the interplay between interoception and
51 exteroception, rather than on how interoception contributes to the regulation of bodily state,
52 reviewing both the human and animal literature at the system and cognitive levels.

53
54 The organization of core interoceptive pathways has been reviewed in detail⁴⁻⁶ and we only
55 briefly summarize it here. Core interoceptive pathways begin with chemo-, thermo- and
56 mechano- receptors within the body. Peripheral information is relayed up to the central nervous
57 system through the cranial nerves, including the vagus and glossopharyngeal nerves, and
58 visceral sensory nerves such as the splanchnic, phrenic and cardiac nerves traveling through the
59 spinal cord (Figure 1, right). Both pathways target the major interoceptive relays in the
60 brainstem, the nucleus tractus solitarius⁷ (NTS) and parabrachial nucleus⁸ (PBN). These nuclei
61 project in turn to other subcortical structures including hypothalamus, amygdala and directly or
62 indirectly to neuromodulatory nuclei, as well as to several nuclei of the thalamus,
63 ventroposterior medial and lateral nuclei⁹ but also paraventricular nucleus¹⁰. Cortical targets
64 are reached after a thalamic relay or through direct projections from PBN to cortex¹¹. The main
65 known cortical targets are the posterior granular insula, which has a viscerotopic organization⁹,
66 as well as the cingulate motor areas¹² and somatosensory cortices¹³.

67
68 We focus here on the cardiac, respiratory and gastric rhythms in both human and animal studies.
69 The three rhythms are transduced via mechanoreceptors, can be easily measured non-invasively,
70 and their respective periods, from a few hundreds of ms to ~20s, are short enough to match
71 fluctuations in perception and cognition. In the first part of the review, we consider each rhythm
72 in turn, from its generation and mechano-transduction to cortical targets, and describe the
73 olfactory, somatosensory, proprioceptive and vascular pathways which complement core
74 interoceptive pathways. The influence of bodily rhythms on brain and behavior comes in
75 different forms, and reveals contributions to a range of functions, from perceptual detection up
76 to the self, but also competition with external inputs. The cortical network impacted is spatially
77 extensive, mostly consistent across the three rhythms, and includes cortices not classically
78 considered to be interoceptive. Finally, we present the three candidate mechanisms of
79 integration of bodily rhythms with external inputs or ongoing brain activity, namely oscillatory
80 synchrony, predictive coding and multi-sensory integration, which underlie, sometimes
81 implicitly, the interpretation of experimental studies.

82
83

84 Cardiac interoception

85

86 *Functions and pathways*

87 The heart provides the necessary force for blood circulation. It contains its own autonomous
88 pacemaker (Figure 1) generating the cardiac cycle (Figure 2B), characterized by the alternation
89 of contraction (or systole, of a relatively fixed duration) and relaxation (or diastole, of more
90 variable duration) of the atria and ventricles. Both descending pathways and local self-
91 regulating neural mechanisms further regulate heart rate and heart contraction, often in
92 coordination with respiration (e.g., inspiration accelerates the heart) and vascular control. This
93 results in a cardiac contraction typically every ~900 ms in adult healthy humans and every ~100
94 ms in mice.

95

96 Heartbeats are transduced by mechanoreceptors and relayed through core interoceptive
97 pathways (Figure 1, right). Mechanoreceptors sensitive to the transient increase in blood
98 pressure are located in the heart itself, but also in the carotid, the aortic arch or pulmonary
99 vessels. Those baroreceptors discharge at each cardiac cycle¹⁴, with various latencies depending
100 on receptor location and subtype¹⁵. The carotid and aortic baroreceptors are the most studied
101 since they are involved in the so-called baroreflex^{16,17}, going through nucleus tractus solitarius
102 to regulate heart rate and blood pressure. Other cardiac mechanoreceptors inform about the
103 occurrence of a cardiac contraction, independently of pressure changes, with large inter-species
104 differences in the proportion of the different types of mechanoreceptors¹⁸.

105

106 A number of other pathways exist for cardiac interoception (Figure 1, left). First, cardiac
107 contractions are transduced into neural signals through proprioceptive or tactile peripheral
108 receptors which detect the pulsatility of blood vessels¹⁹⁻²¹ or the change in thoracic volume.
109 Second, some pathways recently discovered in rodents might also contribute. Astrocytes [play](#)
110 [many roles](#), and it appeared recently that astrocytes can function as intracranial
111 baroreceptors^{22,23}, in turn modulating brainstem neurons involved in blood flow sympathetic
112 control in anesthetized rats²³ and inducing firing in cortical neurons in acute brain slices²². Pulse
113 transduction from vessels might even occur directly in pyramidal cells²⁴, since those cells
114 express the PIEZO2 channel, a mechanosensitive channel transducing membrane tension into
115 electrical and biochemical signals²⁵. While the last two mechanisms might profoundly alter
116 current views of pulse-to-brain communication and suggest novel computational roles for
117 hemodynamics²⁶, the involvement of those mechanisms in freely moving animals as well as in
118 humans remains to be demonstrated.

119

120 *Cardiac parameters: heart-rate variability, temporal contingencies and heartbeat* 121 *evoked responses*

122 Under normal condition, the heart rate is irregular. Heart rate variability is the consequence of
123 descending influence of cortical regions^{27,28} down to the heart. Changes in heart rate and heart-
124 rate variability are well-established phenomena, in particular under threat²⁹ or fear³⁰. In
125 perceptual and cognitive paradigms, cardiac cycle duration is also systematically modified³¹⁻³⁶
126 with a small but consistent change of cardiac cycle duration induced by stimulus presentation
127 and target detection. We review in more depth two other aspects of heart-brain communication:
128 the influence of temporal contingencies ([or relationships](#)) between heartbeats and external
129 stimuli or action, and the cognitive relevance of the transient neural response evoked by each
130 heartbeat.

131

132 *Temporal contingencies between heartbeats and external stimuli*

133 The predictability of the temporal [relationship](#) between heartbeats and external stimuli has been
134 explicitly studied in experiments where external stimuli are repeatedly presented at a fixed
135 latency after each heartbeat. This rationale extends the logic of both exteroceptive multi-sensory
136 integration and predictive coding, where temporal contingencies play an important role, to the
137 integration of interoceptive and exteroceptive signals. A series of studies rooted in the
138 predictive coding framework showed two-ways interactions, with the processing of heartbeats
139 in the central nervous system modulated by temporally congruent, predictable auditory
140 stimuli^{37,38}, and the processing of either auditory³⁹ or visual⁴⁰ stimuli attenuated when
141 synchronized with the heartbeat. Sensitivity to temporal contingencies is also revealed in
142 behavior: both infants⁴¹ and monkeys⁴² spend less time looking at a stimulus moving in
143 synchrony with their heartbeats. The sense of body ownership in bodily illusions is enhanced
144 when the virtual hand⁴³, face⁴⁴ or body⁴⁵ is illuminated synchronously with the participant's
145 own heartbeats, in line with the idea that the integration of interoceptive and exteroceptive
146 might be key to the sense of self in humans⁴⁶⁻⁴⁹.

147
148 Another line of studies revealed that a broad range of perceptual, motor, cognitive and
149 emotional functions depend on whether an external stimulus or an action occurs early or late in
150 the cardiac cycle (Figure 2E). This line of studies is rooted in the hypothesis that baroreceptor
151 activation during systole would induce a generalized cortical inhibition. Indeed, the sustained
152 stimulation of carotid sinus baroreceptors induces immobility and sleep in dogs and monkeys⁵⁰
153 and the appearance of slow waves in cats and dogs⁵¹, an effect which could be mediated by the
154 noradrenergic locus coeruleus⁵². In humans, artificially boosting baroreceptor activation
155 reduces pain sensation⁵³. It was therefore hypothesized that the cortex is transiently inhibited
156 during each systole, resulting in pulsed inhibition. Pain consistently decreases during systole⁵⁴⁻
157 ⁵⁶, which might account for the enduring popularity of the pulsed inhibition hypothesis⁵⁷.
158 However, findings are more mixed when it comes to other modalities. In the somatosensory
159 domain, findings are mostly congruent with the pulsed inhibition hypothesis^{35,36,58,59}; in
160 audition, findings are mixed, with both positive⁶⁰⁻⁶³ and null findings^{64,65}; and in vision, mostly
161 null results are reported for emotionally neutral stimuli^{33,66,67}. Finally, as opposed to the pulsed
162 inhibition hypothesis, action would be facilitated during systole compared to diastole⁶⁸⁻⁷³, but
163 again this finding is not consistent across studies^{74,75}.

164
165 A number of factors might account for such mixed findings. Given the anatomical convergence
166 of interoceptive and somatosensory pathways, somatosensation might differ from vision and
167 audition. Both the measure (ECG, pulse at different locations) and temporal definition of systole
168 and diastole vary from one study to the other, whether stimuli are at or above threshold might
169 also make a difference, and a variety of statistical approaches has been used (Box 1). Finally,
170 and probably more crucially, in some experiments stimuli are delivered randomly and their
171 position in the cardiac cycle is determined *a posteriori*, while in others the timing of stimuli is
172 controlled on line to fall at a specific moment in the cardiac cycle. [This might](#) lead not only to
173 subtle differences in heart rate^{31-34,36} but also to the development of expectancy processes when
174 temporal contingencies are predictable⁷⁶, [for instance learning to expect an external stimulus](#)
175 [200 ms after the heartbeat](#) (Box 1). Understanding the mechanisms at play in cycle effects might
176 be important to better understand brain-body interactions, as further detailed in the section
177 entitled “Integrating bodily rhythms to brain dynamics: candidate mechanisms”, but detailed
178 neurophysiological evidence might be difficult to obtain in rodents given their very fast heart
179 rate. Besides, it remains to be determined whether cycle effects have an impact on perception
180 and cognition outside the highly constrained laboratory settings imposing the temporal
181 alignment of external stimuli and heartbeats.

182

183 *Heartbeat-evoked responses*

184 Heartbeat-evoked responses (HERs) correspond to the transient neural activity observed when
185 averaging neural data locked to heartbeats (Figure 2C). HERs were initially assumed to reflect
186 baroreceptor activity^{77,78}, but they could arise from any of the pathways described above for
187 cardiac interoception. So far, cardiac parameters themselves such as heart rate or stroke volume
188 seem to have only a limited influence on HERs' variability⁷⁹⁻⁸¹. Compared to responses evoked
189 by exteroceptive stimuli, HERs' recording and analysis require extra caution (Box 1). In
190 humans HERs are observed (Figure 3) in somatosensory cortex^{49,59,82,83}, ventromedial
191 prefrontal cortex^{33,83-85} and posterior cingulate/ventral precuneus^{59,84-87}, insula and frontal
192 operculum^{85,88-91}, as well as (mostly right) parietal lobule^{33,59,83} and extrastriate visual cortices
193⁹¹.

194

195 Turning attention inwards and explicitly attending to one's own heartbeats consistently
196 modulates HERs⁹²⁻⁹⁸. Whether and how the attentional modulation of HERs translates into a
197 more accurate conscious percept of heartbeats^{92,94,99} is currently being re-examined (see, e.g.¹⁰⁰)
198 since behavioral procedures to measure the conscious perception of heartbeats are being
199 revised^{101,102}. Beyond attentional modulations, HERs have been related to three different
200 frameworks that we will discuss in turn: emotions, predictive coding, and self and
201 consciousness. Because bodily changes have long been associated with emotions, HERs have
202 been studied in the context of the somatic marker hypothesis¹⁰³. HERs depend on the valence
203 of emotional stimuli presented^{90,104,105} as well as on mood^{88,106} and arousal¹⁰⁷. In such
204 paradigms cardiac parameters also change¹⁰⁸, making it difficult to know whether HERs vary
205 because cardiac parameters change, or because heart-brain communication is altered – echoing
206 the long-standing debate on the interplay between bodily changes and emotions. By analogy
207 with exteroception, HERs have been viewed not as sensory responses *per se*, but as prediction
208 errors signaling the discrepancy between the predicted and observed signal. HERs are
209 modulated by cardiac-driven prediction of auditory stimuli³⁷, by the predictability of outcome
210 states¹⁰⁹ and expected emotional content¹⁰⁵.

211

212 Last, HERs have also been related to the self. Indeed, the organism which has to be fed,
213 protected and regulated can be considered as the simplest biological definition of the self¹¹⁰.
214 In line with this hypothesis, HERs do reflect self-relatedness during mind-wandering^{84,85}, the
215 strength of body ownership during bodily illusions^{44,86} and self-other distinction in mental
216 imagery⁸⁷, and contribute to the stability of decisions based on subjective preferences⁸³. Finally,
217 subjective experience, the hallmark of consciousness, requires the existence of a subject of
218 experience⁴⁷, a minimal form of self which might be biologically grounded in bodily
219 signals^{47,111}. HERs could index the subject of conscious experience, since they predict the
220 likelihood of the conscious detection of a visual³³ or somatosensory⁵⁸ stimulus at threshold,
221 covary with subjective pain perception¹¹², and reliably index residual consciousness in post-
222 comatose patients¹¹³. Interestingly, patients suffering from depersonalization/derealization
223 disorders, who experience a detachment from their own sensations, body and emotions, do not
224 show the modulation of HERs by interoceptive attention¹¹⁴.

225

226

227 Respiration

228

229 *Functions and pathways*

230 The main, vital function of respiration is to allow for gaseous exchanges in the lung for blood
231 oxygenation, but respiration is also used for sniffing and odor sampling, and the precise
232 temporal regulation of air flow is fundamental for swallowing and vocalization¹¹⁵. In some
233 species (e.g., dogs), respiration also plays a role in temperature regulation. As opposed to the
234 heart or the stomach, which both generate their own pacemaker electrical activity, breathing
235 patterns are generated within the central nervous system, in the pre-Bötzinger complex¹¹⁶ and
236 surrounding nuclei located in the ventral medulla¹¹⁷. Another distinctive feature of respiration
237 is that it can be voluntarily controlled (Box 2).

238 *So far, experimental data reveal that* the influence of breathing on brain activity, particularly in
239 the limbic system, appears mostly due to nasal respiration¹¹⁸⁻¹²⁰, with the detection of airflow
240 by mechanoreceptors in the olfactory bulb¹²¹. However other pathways exist, with potentially
241 different cortical targets. Diaphragm stretch and contraction are relayed by the phrenic nerve
242 up to primary somatosensory cortex^{122,123}, and lung movement¹²⁴ is relayed by the vagus nerve
243 and influences hippocampal activity¹²⁵ *via intermediate nuclei*. Chest expansion/contraction
244 might also be detected by the skin and relayed by somatosensory pathways. Finally, the pre-
245 Bötzing complex projects directly to a number of subcortical structures, including the
246 interoceptive NTS and PBS as well the thalamus¹²⁶ and the neuromodulatory locus coeruleus¹²⁷.
247 Such non-olfactory pathways could account for some of the respiratory patterns observed at the
248 cortical level¹²⁸.

249 Coupling between the respiratory rhythm and neural activity has been mostly determined by
250 analyzing the modulation of neural firing or brain rhythms (see Box 1 on experimental
251 challenges with other methods) with the phase of respiration, either by searching for brain
252 activity at respiration frequency, or by extending to brain-body rhythm interactions the rationale
253 of phase-amplitude coupling, where the phase a low frequency brain rhythm modulates the
254 amplitude of a higher frequency rhythm (Figure 2D). Behavior might depend on the strength of
255 such coupling, or show differences between inspiration and expiration (Figure 2E).

256

257 *Nasal respiration and limbic system*

258 The influence of nasal respiration on brain activity¹²⁹ has long been documented in the olfactory
259 bulb and olfactory piriform cortex, but it extends well beyond olfactory structures. Modulation
260 of neural activity by respiration has been observed in limbic regions, most notably in the
261 hippocampus in both humans¹²⁰ and rodents^{119,130} where it is distinct from the theta rhythm^{131,132}.
262 Respiration also modulates neural activity in medial prefrontal cortex in rodents^{130,133-135}, a
263 region considered to be analogous to the anterior cingulate cortex in humans. The involvement
264 of large portions of the limbic system (amygdala, hippocampus, insula, cingulate) is confirmed
265 in human intra-cranial recordings^{136,137}. The coupling between nasal respiration and neural
266 activity in limbic regions is also associated with the modulation of memory
267 performance^{120,138,139} and of emotional ratings in humans¹²⁰, and it influences freezing behavior
268 in mice^{134,135}.

269

270 *Respiration and neural activity in other regions*

271 The coupling between respiration and brain activity is far from being confined to the limbic
272 system. First, respiratory-related activity is observed in the somatosensory cortex, both in
273 humans^{137,140} and in different parts of the rodent *or cat* somatosensory cortex: the whisker barrel
274 cortex^{118,141}, trunk^{122,123} and nose¹⁴² representation. In humans, the detection of faint tactile
275 stimuli is facilitated at the beginning of expiration³⁶. Second, coupling between respiration and
276 neural activity has also been observed in motor regions in both rodents¹⁴¹ and humans¹³⁷. The
277 link with motor activity is also revealed by enhanced cortico-muscle coherence¹⁴³ and startle
278 reflex responses¹⁴⁴ during expiration, but more voluntary movement initiation^{75,140} during

279 inspiration. Reaction times in various auditory and visual tasks vary along the respiratory
280 cycle¹⁴⁵. Third, respiration is also coupled to neural activity in the visual system^{128,141,146} and
281 influences visual performance^{140,146,147}. Respiration-locked modulations were also reported in
282 the human posterior cingulate cortex^{140,148}. Finally, a whole-brain investigation in humans
283 during resting-state reveals an even larger array of regions coupled with respiration, including
284 nodes of the default, saliency and dorsal attention networks as well as cerebellum¹⁴⁸. From a
285 more cognitive perspective, the strength of bodily illusions is enhanced when the virtual avatar
286 either breathes¹⁴⁹ or is illuminated¹⁵⁰ in synchrony with the participant's respiration.

287
288 The directionality of the coupling is not always resolved in the experiments described above:
289 is coupling due to an entrainment of neural activity by respiration, or to a neural command
290 altering respiration rate and depth¹⁵¹? For instance, stimulation^{152,153} of the motor cortex in
291 humans elicits twitches in the diaphragm, and in cats respiration-related activity in the
292 hippocampus can drive respiratory changes¹⁵⁴. The coupling between respiratory cycles and
293 neural activity might also be due to neuromodulation. While there is no direct evidence for this
294 yet, the selective manipulation of the projection of the pre-Bötzinger complex to the locus
295 coeruleus leads to both slower respiration rate and less active exploration behavior in mice¹²⁷.

296
297 In the experimental literature on respiration, the interpretation most often put forward is that
298 beyond olfactory sampling, respiration-entrained oscillations would play a role in the large-
299 scale coordination of neural dynamics, and may contribute to optimizing perception, emotion
300 and cognition. This interpretation echoes the role ascribed to oscillatory synchrony in general,
301 but results could also be interpreted in other frameworks, a point we will develop further in the
302 section entitled "Integrating bodily rhythms to brain dynamics: candidate mechanisms".

303
304

305 Gastric interoception

306

307 *Functions and pathways*

308 The stomach mixes and grinds food during digestion. It senses a rich variety of stimuli, some
309 related to stomach content¹⁵⁵⁻¹⁵⁷, others, upon which we focus, related to gastric electrical
310 activity or mechanical distortion^{158,159}. Like the heart, the stomach generates its own
311 rhythm^{160,161}, with cycles lasting about 20s in both humans and rodents. The rhythm is
312 intrinsically generated by non-neuronal pacemaker cells, the Interstitial Cells of Cajal^{162,163},
313 which contact both smooth muscles and vagal afferents. The gastric rhythm is continuously
314 generated but during digestion, under the pressure of gastric content, its amplitude increases
315 and it coordinates the contractions of the stomach smooth muscles. Gastric rhythm amplitude
316 and frequency can be modulated by both local influences from the enteric nervous system and
317 descending influences from the central nervous system^{164,165}, with descending projections from
318 insula, medial prefrontal cortex, motor and somatosensory cortices¹⁶⁶.

319
320 Different forces (distension, contraction, stroking) applied to the stomach wall activate both the
321 vagal¹⁶⁷⁻¹⁶⁹ and the spinal splanchnic^{170,171} nerves, which then follow the core interoceptive
322 pathways presented in Figure 1. In humans, whole-brain imaging studies during experimentally-
323 induced gastric distention show responses in the somatosensory cortices, anterior cingulate
324 cortex, hippocampus, insula, ventromedial prefrontal cortex and occipital cortex¹⁷²⁻¹⁷⁷, a pattern
325 similar to the network activated by gastric stimulation in rats¹⁷⁸. The involvement of occipital
326 cortex has also been observed in sleeping cats¹⁷⁹, where the electrical stimulation of the stomach
327 elicits firing in early visual cortices.

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Coupling between the gastric rhythm and spontaneous brain activity in an extensive network

Outside the acute phase of digestion, the stomach only occasionally contracts, but the gastric rhythm is still generated. Neural activity coupled with the gastric rhythm is observed in a quite extensive network in both the human^{180,181} brain during resting-state and in the anesthetized rodent¹⁸² brain. The so-called gastric network includes all exteroceptive cortices as well as motor regions, some default-network regions but very few transmodal, cognitive regions¹⁸¹. The directionality of interactions remains to be firmly established, but in humans part of the coupling observed corresponds information flowing **from** stomach to brain¹⁸³. In rodents, sectioning the vagus nerve reduces stomach-brain coupling except in somatosensory cortex¹⁸², a pattern reminiscent of the spinal pathways connecting stomach to somatosensory cortex¹².

The gastric network has been recently discovered¹⁸⁰ and little is known about its functional role. It does not appear to be modulated by moderate fasting in humans¹⁸¹, but the combination of more stringent diet control and fasting/feeding intervention alters the gastric network in anesthetized rats¹⁸². In humans, the network predicting weight loss overlaps with the gastric network¹⁸⁴, and weight concern and body shame are associated with decreased gastric-brain coupling¹⁸⁵. Beyond diet and body-related aspects, given the extent of the gastric network, the gastric rhythm has been proposed to orchestrate brain dynamics between the different modules of the external senses and action, bypassing higher-level regions¹⁸¹, but this hypothesis has not been experimentally tested so far. Finally, gastric activity has also been related to arousal: neural responses to gastric stimulation in the visual cortex are larger during sleep than wakefulness¹⁷⁹.

Bodily rhythms are observed in an extensive cortical network

Figure 3 presents a graphical summary of the findings reported in the previous three sections. Obviously, this figure comes with cautionary notes. We collapsed results from animal and human studies with potential issues regarding homologies between species (see e.g. ¹⁸⁶). For cardiac interoception, we plotted heartbeat-evoked responses only, which correspond to responses to an interoceptive input, while for the respiratory and gastric rhythms, the directionality might be either ascending (e.g. gastric stimulation) or undetermined (coupling). Finally, sampling biases depend on technique and species, with both whole-brain and local studies in humans and mostly local studies in animals. Bearing those limitations in mind, Figure 3 shows that despite the variety of possible pathways (Figure 1), effects (Figure 2) and experimental challenges (Box 1), the resulting network is mostly consistent across species, rhythms and recording methods.

First, Figure 3 confirms the known involvement of limbic regions (insula, amygdala/hippocampus, cingulate cortex) in interoceptive processing. Note that we did not distinguish between the posterior interoceptive insula with its viscerotopic organization^{9,187} from more anterior insular regions. Second, cardiac, respiratory and gastric influences on somatosensory cortex are also confirmed. Whether they stem from core interoceptive pathways and/or tactile and proprioceptive pathways, and in which proportion, remains to be determined, and whether somatosensory cortex is viscerotopically organized is an open question. Thirdly, and more surprisingly, there is a consistent link between the respiratory and gastric rhythms and neural activity in visual, auditory, and (pre)motor cortices. The anatomical origins of

377 interoceptive signals in exteroceptive cortices are not known. They might result from
378 intracortical projections from interoceptive to exteroceptive cortices, but the interplay might
379 also be subcortical. For instance, the parabrachial nucleus, which receives visceral inputs, also
380 projects to the main thalamic relay of visual information, the lateral geniculate nucleus¹⁸⁸⁻¹⁹⁰,
381 and has functional links with auditory pathways, as revealed by its role in vocalization-
382 respiration coupling^{191,192}. The parabrachial nucleus might also act on sensory cortices through
383 neuromodulation⁸. The coupling with motor and premotor cortices, which appear quite common
384 for the respiratory and gastric rhythms, might include a descending influence, since anatomical
385 evidence points to a visceromotor role of those regions^{166,193}.

386
387 Finally, in humans, the two core midline nodes of the default network, ventro-medial prefrontal
388 cortex and posterior cingulate cortex/ventral precuneus, appear coupled to bodily rhythms, with
389 all three rhythms consistently found in posterior cingulate cortex, and mostly heartbeat-evoked
390 responses in ventro-medial prefrontal cortex. Another key region, comprising the anterior insula,
391 frontal operculum and inferior-frontal gyrus is a node of the saliency network. All three regions
392 are cortical hubs, i.e. regions with a dense anatomical and functional connectivity with other
393 networks¹⁹⁴. Reports in the parietal lobe are both scarce and scattered, some relating to the
394 lateral node of the default network and others to dorsal parietal regions. To the best of our
395 knowledge, no animal study has investigated those regions yet. It is also worth noting that so
396 far, cognitive prefrontal regions seem quite disconnected from bodily rhythms.

397
398 In conclusion, the cortical network influenced by cardiac, respiratory and gastric rhythms is
399 quite extensive, comprising not only expected interoceptive limbic regions but also sensory and
400 motor regions, as well as some connectivity hubs of the default and salience networks. This
401 calls for a refined anatomical characterization of interoceptive routes, from transduction site to
402 cortical target, and a better understanding of the functional role of interoceptive signals in both
403 exteroceptive cortices and connectivity hubs.

404
405

406 Integrating bodily rhythms to brain dynamics: candidate mechanisms

407

408 How are bodily rhythms integrated with ongoing brain dynamics and exteroceptive or cognitive
409 processing? This question has been considered in the light of three different frameworks –
410 oscillatory synchrony, predictive coding and multisensory integration – which were initially
411 devised for exteroception. We present each candidate mechanism in turn below, and discuss
412 how it was adapted to cardiac, respiratory and gastric inputs (Figure 4). The three frameworks
413 are not mutually exclusive (see, e.g. ¹⁹⁵), but they influence experimental paradigms and color
414 the interpretation of findings, sometimes implicitly.

415

416 *Extending oscillatory synchrony to brain-bodily rhythms interactions: the scaffolding* 417 *hypothesis*

418 Oscillatory synchrony between brain regions is thought to play a role in the coordination of
419 large-scale brain dynamics and in between-area communication^{196,197}. Because increasing
420 membrane potential makes firing more likely, synchronous oscillations would open or close
421 windows of communication between potentially distant groups of neurons. In its original
422 version, oscillatory synchrony is independent from bodily rhythms and would emerge from
423 neural interactions^{196,197}. The scaffolding hypothesis states that because the temporal structure
424 of neural activity in different regions reflects that of the cardiac, respiratory and gastric rhythms,
425 those regions can be considered to be synchronized. This framework has mostly been put

426 forward for respiration¹²⁹ and the gastric rhythm^{180,183}. In this view, bodily rhythms act as
427 carrier waves, imposing temporal windows of more or less excitability (Figure 4A). Whether
428 respiration is deep or shallow, or whether the heart ejects a small or large volume of blood could
429 be of little importance, as long as a rhythmic pattern is generated in different brain areas. The
430 scaffolding hypothesis is thus relatively disconnected from actual bodily physiological states.

431
432 In this framework, the rhythmic pattern of neural activity related to bodily rhythms is important
433 as it would **open or close windows of communication**. Experimentally, there are only few
434 studies detailing whether different brain regions are coupled to a bodily rhythm with the same
435 phase or different ones, and they are not congruent: the phase alignment of respiratory-driven
436 neural activity seems rather good¹²⁸, whereas the areas coupled to the stomach are organized
437 along a gradient of phases¹⁸⁰, more suggestive of a traveling wave than near-zero phase-lag
438 synchrony. While the frequency of intrinsic brain rhythms tends to be conserved by evolution¹⁹⁸,
439 this is not the case for bodily rhythms: both the cardiac and respiratory rhythms of mice are
440 about 8 to 12 times faster than those of humans, while gastric frequency is relatively similar
441 across species¹⁹⁹. It is not yet known whether between-organs and between-species differences
442 in frequency have functional consequences for coupling between bodily rhythms and brain or
443 behavior. Finally, an enduring question regarding the role of oscillatory synchrony is how the
444 brain determines which groups of neurons should be synchronized²⁰⁰. So far, synchronization
445 by bodily rhythms does not offer any satisfying answer to this question. Still, the possibility
446 that vascular pulsatility is directly transduced by astrocytes and/or pyramidal cells^{22,23} opens
447 new leads: the combination of an increased local metabolic demand due to firing, and of the
448 temporal tagging due to vessel pulsatility, may generate a novel means to achieve flexible yet
449 relevant neuronal coordination.

450

451 *Interpretation of self and consciousness related findings as well as cycle effects under* 452 *the scaffolding hypothesis*

453 In its original formulation, oscillatory synchrony solves the binding problem, i.e. how
454 distributed neural activities are flexibly combined to generate an object representation¹⁹⁶, and
455 could thus contribute to the unity of conscious experience. However, conscious experience has
456 other properties⁴⁷, such as first person perspective, i.e. an egocentric viewpoint on the world,
457 and intrinsic mineness, i.e. the fact that a conscious percept belongs to the observer, and that
458 the observer **rarely** fails to perceive it as his or her own experience – **at least in healthy human**
459 **adults**. These properties pertain to the subject of experience, **requiring a self-centered viewpoint**
460 whose neural definition could be rooted in the neural representation of bodily signals. More
461 precisely, the pieces of information which are bound together in a conscious experience are not
462 only scattered in different areas, they are also expressed in **different frame of references**, for
463 instance **eye-centered** in early visual regions up to more complex cognitive spaces²⁰¹. Because
464 visceral signals are **constantly present and distributed across** many areas, they could facilitate
465 the alignment and coordination of different systems of coordinates by providing common
466 reference points, corresponding to the same input expressed in each frame of reference⁴⁹,
467 accounting both for the first-person perspective and intrinsic mineness of conscious experience
468 (Figure 4B). **Note that under this hypothesis, visceral signals play a coordination role to align**
469 **external senses in an egocentric framework, rather than contribute to an explicit sense of bodily**
470 **self**. This extension of the binding-for-consciousness hypothesis to integrate bodily signals can
471 accommodate the various findings on the link between the neural monitoring of bodily signals
472 and self and consciousness, **but it remains speculative**.

473

474 The scaffolding hypothesis also allows one to interpret the differential processing of external
475 stimuli in systole/diastole, or during inspiration/expiration in a rather straightforward manner:

476 cycle effects would be a consequence of the existence of temporal windows of enhanced and
477 dampened sensory sampling (e.g.¹⁴⁶), by analogy with previous work on intrinsically generated
478 oscillatory synchrony and visual attentional sampling²⁰². Another interpretation of cycle effects
479 is rooted in the literature on nasal respiration, where inspiration corresponds to olfactory
480 sensory intake²⁰³. Given the evolutionary importance of olfaction in guiding behavior, the
481 influence of (nasal) respiration on brain activity might have spilled over and be generalized to
482 non-olfactory guided cognition^{140,146} – a similar reasoning could hold for the gastric rhythm,
483 which might derive from the evolutionary ancient rhythms of “floating stomachs” such as
484 jellyfishes. Cycle effects have also been interpreted in the predictive coding framework, further
485 detailed in the next paragraph.

486
487

488 *From rhythms to allostatic regulations, emotions and self: the extended predictive* 489 *framework*

490 Because rhythms are predictable, bodily-entrained neural oscillations²⁰⁴ could help align phases
491 optimal for sensory processing with the expected timing of stimulus inputs. This logic seems
492 particularly relevant for nasal respiration, where the respiratory-induced neural rhythm would
493 be aligned with olfactory sensory intake. By extension, the response to a tactile stimulus would
494 be inhibited during systole because the timing of the heartbeat has been predicted and the
495 response to tactile stimuli inhibited. The fact that at least some cycle effects need a prolonged
496 period of synchronization between bodily rhythms and external inputs argues in favor of
497 predictive coding¹³⁹. The extended predictive framework can also easily accommodate the link
498 with motor behavior, with various actions initiated at the best moment given internal state – for
499 instance sniffing, synchronized with inhalation, corresponds to external sensory intake, whereas
500 shooting precision would benefit from an initiation away from the small bodily displacement
501 induced by heartbeats⁷². This logic has been formalized for both cardiac^{57,205} and respiratory²⁰⁶
502 cycle effects, with the rationale that interoceptive inference and exteroceptive inference are
503 most precise at different moments of the cycle.

504

505 More generally, because interoception senses bodily states, it is involved in reactive
506 homeostatic regulations, but also allostatic regulations, i.e. anticipating bodily needs given the
507 external environment and planned behavior – such as salivating in anticipation of food
508 consumption. Allostatic regulations can be expressed in an extended predictive coding
509 framework, where the brain constantly generates and updates not only a model of the external
510 environment, but also of the organism state²⁰⁷ (Figure 4C). This framework might work at short
511 time scales (e.g., from one respiration cycle to the next), but is best suited for longer time scales
512 (minutes, hours), with for instance predictions about future physiological states in insular
513 cortex²⁰⁸. Beyond allostasis, the predictive coding framework proposes that estimating the most
514 likely cause of changes in internal bodily parameters, given a certain exteroceptive context,
515 gives rise to emotional feelings²⁰⁹⁻²¹¹, with a particular role for anterior cingulate and anterior
516 insular cortices to generate visceral predictions²¹². Emotional feelings relating to actual or
517 mentally simulated changes in the body have been proposed as a basis of the (emotional) self¹¹⁰.
518 Alternatively, having a predictive model of the (interoceptive, proprioceptive, somatosensory)
519 body could be the basis of the self²¹⁰ (Figure 4D). In this interpretation, actual and predicted
520 bodily states matter, but the rhythmic nature of inputs and associated neural activity is only one
521 parameter among others that can be predicted.

522

523 *Extero- and interoceptive multi-sensory integration*

524 Another line of interpretation considers that exteroceptive and interoceptive processing
525 converge, in an extended multisensory integration framework⁴⁸. Multisensory integration

526 (Figure 4E) requires the convergence of both intero- and extero-ceptive information onto the
527 same neurons, as shown for instance for bladder and tactile inputs in primary somatosensory
528 cortex²¹³ or at earlier subcortical stages²¹⁴. Inputs are then combined in a super-additive (resp.
529 sub-additive) manner, i.e. presenting simultaneously the two inputs would lead to larger (resp.
530 smaller) responses, as compared to the sum of the responses to each input presented
531 separately²¹⁵. For instance, the inhibition of the neural response to tactile stimuli during systole
532 could be interpreted as a multisensory competition between tactile and baroreceptor inputs in
533 somatosensory cortex⁵⁹. Multisensory integration has been proposed to underlie the bodily self
534 (Figure 4F), as suggested by experimentally-induced bodily illusions. Such illusions arise from
535 congruent or incongruent visuo-tactile stimulation²¹⁶ but are also further modulated by the
536 visual illumination of the virtual body in synchrony with heartbeats⁴³⁻⁴⁵ or respiration^{149,150}.
537 Bodily parameters are relevant in this framework, but the rhythmic pattern of inputs is
538 presumably of little importance. The intraparietal sulcus would play a major role in the
539 integration of external and internal inputs⁴⁸, but this hypothesis remains to be demonstrated
540 experimentally, and so far, this region has seldom been reported to be coupled to bodily rhythms
541 (Figure 3).

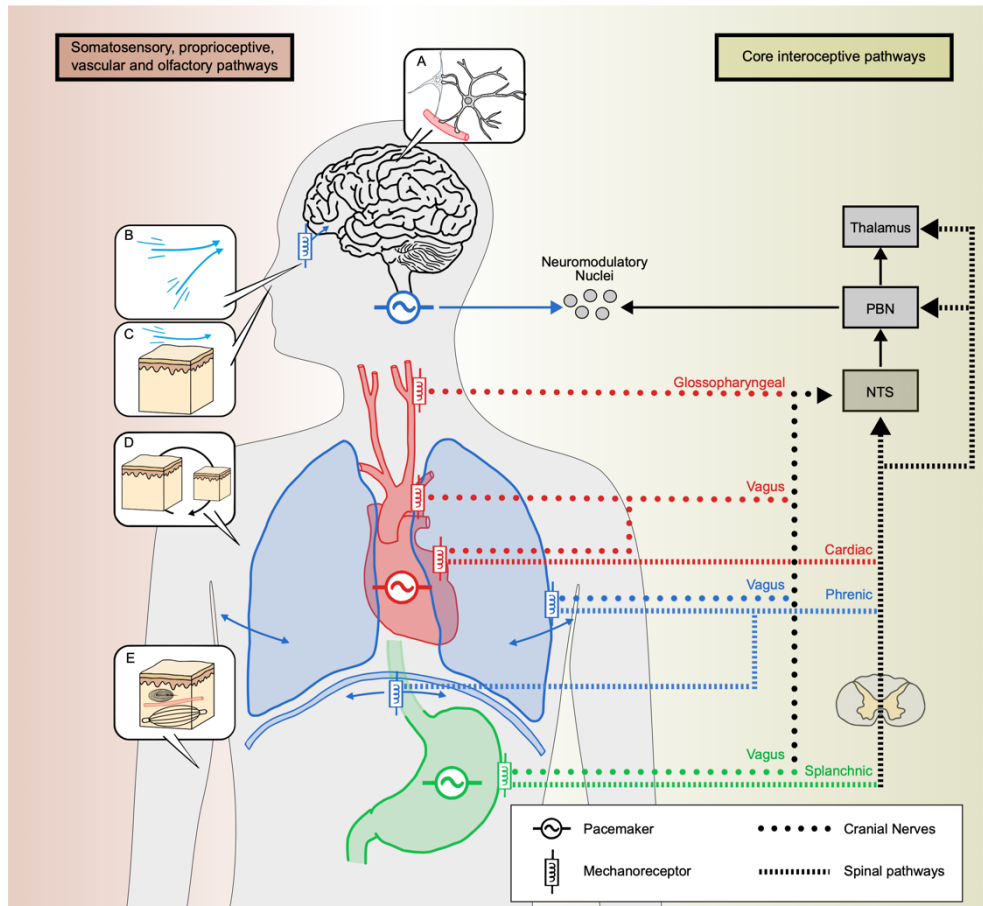
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544 Concluding remarks and open questions

545

546 The anatomical extent of the coupling between bodily rhythms and neuronal activity as well as
547 the range of sensory and cognitive functions impacted open many questions about underlying
548 mechanisms. The integration of interoceptive signals with other sources of information revives
549 central questions on the nature of the neural code, from integration of multisensory information
550 by convergence to oscillatory synchrony and predictive coding. Arousal, loosely defined as a
551 brain-body activation state, is rarely put forward as an explanatory framework in the literature
552 we reviewed, and its role should be reconsidered. Interoception also imposes novel biological
553 constraints. The most obvious ones are related to functions, i.e. the integration of interoception
554 and exteroception related to the survival of the organism, but interoception also suggests novel
555 physiological routes for information processing which would not exist *in silico*, for instance the
556 pulsatility of the vascular system that might be detected within the central nervous system. A
557 more biological stance on information processing might be key to understand the neural code
558 as well as to tackle the difficult questions of self and consciousness, and of animal vs. human
559 consciousness.

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569 **Figure 1. Cardiac, respiratory and gastric rhythms generation and mechanosensory**

570 **signaling: core interoceptive pathways (right) and somatosensory, proprioceptive,**

571 **vascular and olfactory pathways (left).** The heart and the stomach contain their own

572 autonomous electrical pacemaker whereas respiratory cycles are centrally generated in the

573 ventral medulla. Organ contractions are sensed by mechanoreceptors located in the viscera wall

574 itself, including the diaphragm for the respiratory system. Pressure changes occurring at each

575 heartbeat are also detected by baroreceptors located in large vessels such as the carotid and the

576 aortic arch. Viscera-related activity is transmitted to the CNS via two main afferent pathways,

577 that is cranial nerves (vagus and glossopharyngeal) directly entering the brainstem and cardiac,

578 phrenic and splanchnic nerves traveling through the spinal cord (spinal pathways). Both

579 pathways directly or indirectly target major interoceptive relays such as the NTS, PBN - which

580 in turn project to neuromodulatory nuclei – and several nuclei of the thalamus. Organs activities

581 are also sensed through other pathways (left). (A) In the CNS, astrocytes directly detect changes

582 in cerebral intravascular pressure and activate pyramidal neurons, which presumably could also

583 be directly depolarized following pressure changes via PIEZO2 channels. (B) The airflow during

584 respiration can also be sensed by tactile receptors, as well as (C) by mechanoreceptors

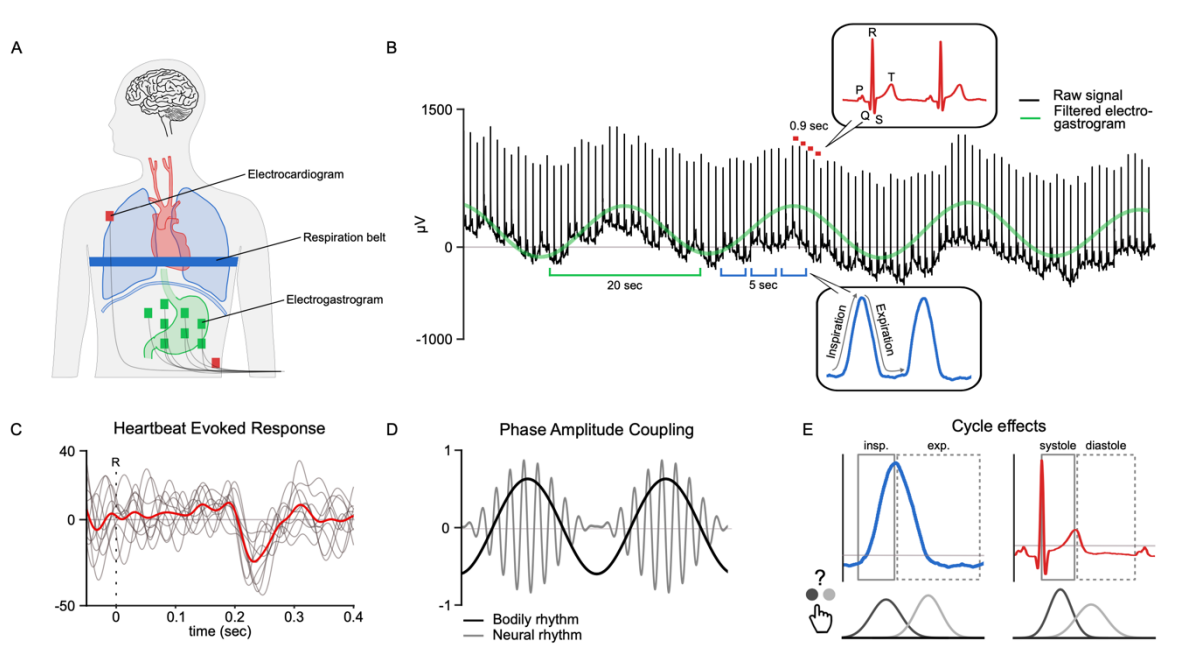
585 in the olfactory bulb. (D) Changes in organs' volume (i.e., chest expansion/contraction) can be

586 detected by the skin, and (F) vessel pulsatility by both tactile and proprioceptive pathways.

587 CNS, central nervous system; NTS, nucleus tractus solitarius; PBN, parabrachial nucleus.

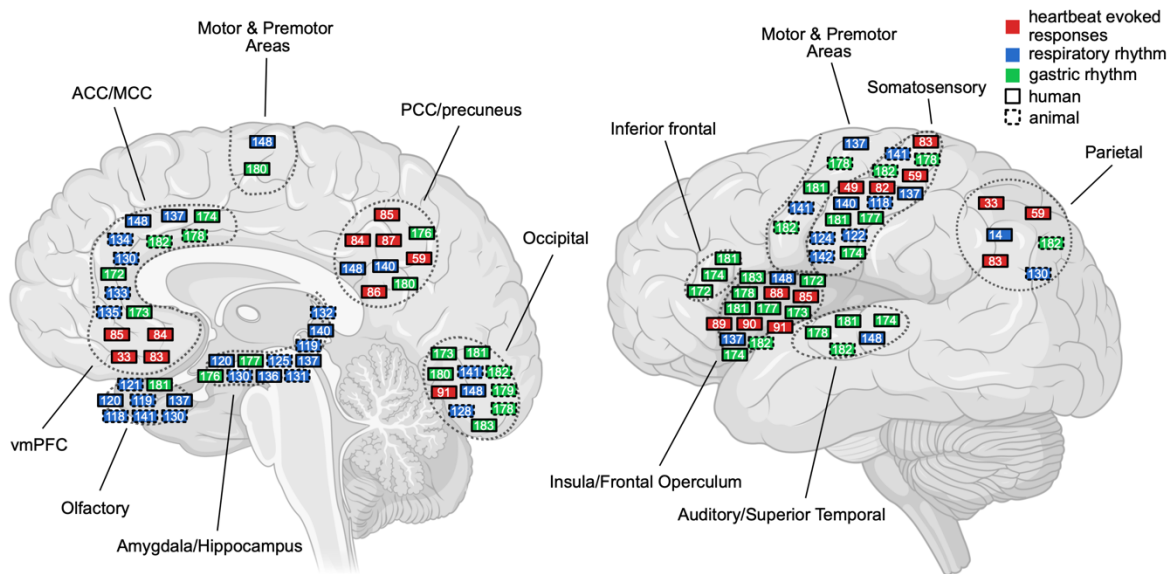
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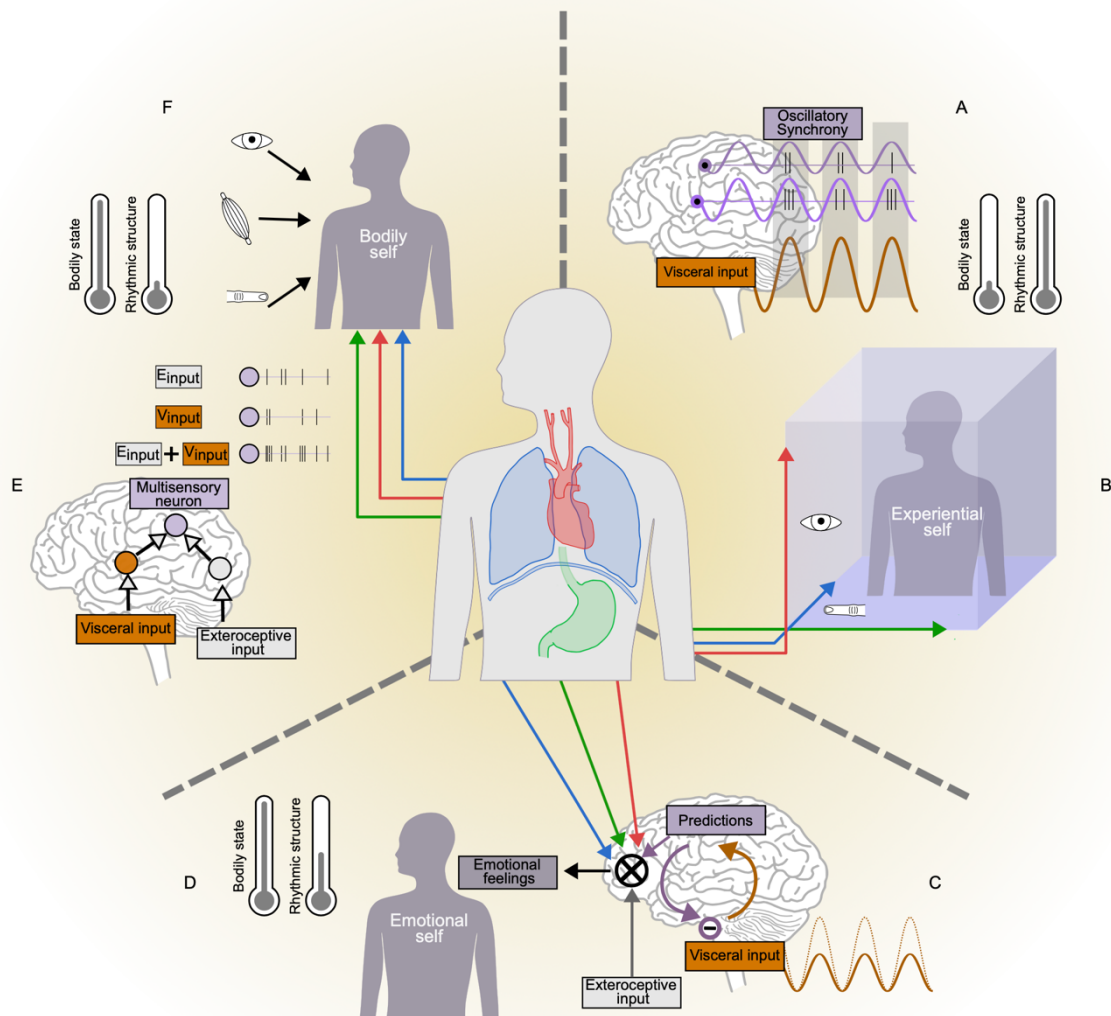
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 591 **Figure 2. Measuring cardiac, respiratory and gastric interoception.** A. Settings in humans
 592 to measure cardiac and gastric¹⁹⁹ rhythms with cutaneous electrodes in humans, and respiratory
 593 rhythm with a belt. B. Example of raw data from an abdominal electrode, showing the slow
 594 gastric rhythm, the faster respiration rate and the heartbeats. C. Intracranial recordings in the
 595 human somatosensory cortex show that each heartbeat evokes a transient neuronal response
 596 (single responses in light gray, aligned to the R peak of the electrocardiogram). Averaging
 597 single responses generates the heartbeat-evoked response (red). D. The influence of bodily
 598 rhythms on neuronal activity can also be measured with phase-phase coupling (not illustrated)
 599 or phase-amplitude coupling, where the amplitude of a neuronal rhythm (light gray)
 600 is modulated according to the phase of the bodily rhythm (black). E. Both the respiration and
 601 cardiac cycles are composed of two phases (respectively inspiration and expiration, systole and
 602 diastole). Cycle effects refer to the different behavioral outcomes in response to exteroceptive
 603 stimuli which are sometimes observed between the two phases.

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610 **Figure 3. Bodily rhythms in the brain: an extensive network.** Regions where heartbeats
 611 elicit a response, or where neuronal activity is related to the respiratory and gastric rhythm,
 612 collapsed across studies in humans and animals, mostly rodents. Each number corresponds to
 613 a reference, and indicates the contribution of the region, not to an exact location. We did not
 614 distinguish between posterior and anterior insula, and the border between the most ventral part
 615 of the ACC and vmPFC is difficult to establish. In addition to expected limbic regions, neuronal
 616 activity is related to bodily rhythms in somatosensory, but also visual and auditory cortices, as
 617 well as motor and premotor areas. Two medial nodes of the default network (vmPFC,
 618 PCC/precuneus) and one node of the saliency network (anterior insula, inferior frontal gyrus)
 619 are present. Reports in the parietal lobe are few and anatomically scattered. ACC: anterior
 620 cingulate cortex; MCC: mid-cingulate cortex; PCC: posterior cingulate cortex; vmPFC: ventro-
 621 medial prefrontal cortex.

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 625 **Figure 4. Bodily rhythms in the brain: candidate mechanisms.** The effects of cardiac,
 626 respiratory and gastric rhythms on brain dynamics and cognition can be explained under
 627 different frameworks. (A) Rhythmic visceral signals facilitate synchronization of neuronal
 628 oscillations between remote brain regions and thus promote integration by offering a common
 629 oscillatory scaffold between distributed brain circuits. (B) Visceral signals could facilitate the
 630 integration of signals originating from different systems of coordinates (e.g. eye-centered and
 631 body-centered reference frames) by providing a common frame of reference. (C) Visceral
 632 signals are predicted and suppressed from being consciously perceived to minimize their
 633 interference on brain processing. (D) Interpreting visceral inputs given priors and exteroceptive
 634 context gives rise to emotional feelings, which would in turn constitute the basis of the
 635 emotional self. (E) Exteroceptive and interoceptive sensory inputs are super-additively
 636 combined in multisensory neurons (or sub-additively), and the multisensory integration of
 637 interoceptive and exteroceptive signals build the brain's body representation and the experience
 638 of the bodily self (F). The thermometers symbolize the relative importance of bodily state and
 639 of the rhythmic structure of visceral inputs, for each of the framework.

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642 BOX 1 – Measuring brain responses to visceral activity: Artefacts and 643 pitfalls

644
645 Investigating the influence of internal organs on brain activity is experimentally challenging.
646 First, visceral activity can induce relative motion between sensors and brain, artefactually
647 modulating the data. For instance, both breathing movement and cardiac pulsatility affect
648 magnetic resonance imaging data^{217,218}. Similarly, brain movements occurring at each heartbeat
649 during in vivo recordings modulate action potential waveform²¹⁹ and affect intracranial HER
650 recordings⁸². Moreover, local changes in vascular tone (i.e. vasomotion) or hemodynamic
651 oscillations linked to respiration modulate near-infrared spectroscopy signals²²⁰. Distinguishing
652 artefacts due to motion from the neural activity resulting from the transduction of heart, pulse
653 and respiration signals is an important technical challenge.

654
655 Second, brain electrophysiological sensors might also directly capture distant organs electrical
656 activity. Cardiac electrical activity, as detected by the electrocardiogram, is directly visible in
657 EEG²²¹ and MEG²²² recordings, typically on temporal sensors. This so-called cardiac field
658 artefact can be only partially corrected, and specific experimental design and control analysis
659 are required to extract meaningful information^{49,79,80}.

660
661 Third, the periodic nature of organs' contractions calls for particular attention. It precludes the
662 existence of "baseline activity", since the activity preceding a given cycle also corresponds to
663 the end of the previous cycle. In addition, data analysis involves circular statistics, which
664 probably require more methodological work to identify all pitfalls and caveats^{223,224}.

665
666 Fourth, the experimental paradigm itself might influence visceral rhythms. For instance, the
667 conscious perception of an external stimulus slows down the heart³³, and when stimulus
668 presentation times are predictable, participants tend to inhale and hence increase their heart rate
669 at stimulation onset³⁶. The entrainment of cardiac and respiratory rhythms by experimental
670 variables might account for some of the differences in cycle effects observed between
671 paradigms where stimuli are delivered randomly and their position in the cycle determined *a*
672 *posteriori*, and paradigms where experimenters impose stimulus presentation at a specific
673 moment in the cycle¹³⁹.

674
675 Finally, establishing the directionality of interactions is challenging. Tampering with visceral
676 organs might result in non-ecological, stressful conditions (i.e., ingestion of an inflatable
677 balloon for gastric interoception¹⁷³), and is likely to draw attention to bodily state. More
678 fundamentally, identifying causality in complex systems is intrinsically difficult.

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682 BOX 2 – Fast and slow breathing: respiration can be voluntarily 683 controlled

684 Breathing is automatic, but is tightly regulated for active sniffing, swallowing and vocalization.
685 Emotions are also typically associated with changes in respiratory pattern²²⁵. More subtle
686 changes have recently been observed in non-emotional situations, where participants might
687 spontaneously align their respiratory pattern to the movement generated²²⁶ or to the
688 experimental paradigm^{36,145}, although such behavior is not systematic³³. Respiration, as
689 opposed to cardiac or gastric rhythm, is also under explicit volitional control, which is
690 associated in humans with a limbic circuit including insula and anterior cingulate cortex^{137,227}.

691
692 Fast breathing is generally associated with stress and anxiety, and more precisely to dyspnea,
693 or the feeling of breathlessness. It is a central feature of panic attacks²²⁸ – although respiratory
694 rates increase for positive emotions as well²²⁵. Neuroimaging studies of dyspnea, induced by
695 flow-resistive load or altered O₂/CO₂ content, indicate the involvement of most limbic
696 structures as well as somato-motor regions²²⁹, with an anxiety-dependent engagement of the
697 anterior insula²³⁰. Intracranial EEG confirm those findings and reveal in addition the
698 contribution of occipital regions¹³⁷. Fast breathing increases the coupling between neuronal
699 activity and respiration in the orbitofrontal cortex, insula and amygdala, but does not affect the
700 respiratory influence in somatosensory cortex¹³⁷. Finally, asking participants to inhale or exhale
701 once, as fast as possible, increases motor excitability and finger flexion force²³¹.

702
703 Conversely, controlled, slow breathing is often used in cognitive behavioral therapy and is an
704 important component of increasingly popular practices such as meditation or yoga, which
705 involve a larger repertoire of controlled breathing – fast, slow, left/right nostril breathing,
706 sometimes associated with specific postures and vocalization²³². While there is considerable
707 interest for yoga and meditation as a way to improve mood, sleep and the general sense of well-
708 being²³³, the specific role of respiratory patterns and/or attention to respiration²³⁴ remains
709 difficult to isolate from other components. When practiced in isolation, slow-paced breathing
710 is associated with stress reduction²³⁵ and influences brain activity²³⁶. Still, the literature reveals
711 mixed findings when it comes to pain or emotional feelings^{237,238}. The detailed mechanism of
712 the influence of slow-paced breathing remains to be fully elucidated. It might be mediated by
713 an interplay between the respiratory system and both the cardiac and vascular systems^{235,237},
714 but the hypothesis is still debated²³⁹.

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725

726 Competing interests.

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728 The authors declare no competing interests
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