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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<sup>1,2</sup> mostly takes place unconsciously, **but also** occasionally **gives**  
38 **rise** to interoceptive conscious **percepts in humans**<sup>3</sup>. 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 detail<sup>4-6</sup> 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 solitarius<sup>7</sup> (NTS) and parabrachial nucleus<sup>8</sup> (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 nuclei<sup>9</sup> but also paraventricular nucleus<sup>10</sup>. Cortical targets  
64 are reached after a thalamic relay or through direct projections from PBN to cortex<sup>11</sup>. The main  
65 known cortical targets are the posterior granular insula, which has a viscerotopic organization<sup>9</sup>,  
66 as well as the cingulate motor areas<sup>12</sup> and somatosensory cortices<sup>13</sup>.

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 cycle<sup>14</sup>, with various latencies depending  
100 on receptor location and subtype<sup>15</sup>. The carotid and aortic baroreceptors are the most studied  
101 since they are involved in the so-called baroreflex<sup>16,17</sup>, 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 mechanoreceptors<sup>18</sup>.

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 vessels<sup>19-21</sup> 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<sup>22,23</sup>, in turn modulating brainstem neurons involved in blood flow sympathetic  
112 control in anesthetized rats<sup>23</sup> and inducing firing in cortical neurons in acute brain slices<sup>22</sup>. Pulse  
113 transduction from vessels might even occur directly in pyramidal cells<sup>24</sup>, since those cells  
114 express the PIEZO2 channel, a mechanosensitive channel transducing membrane tension into  
115 electrical and biochemical signals<sup>25</sup>. While the last two mechanisms might profoundly alter  
116 current views of pulse-to-brain communication and suggest novel computational roles for  
117 hemodynamics<sup>26</sup>, 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<sup>27,28</sup> down to the heart. Changes in heart rate and heart-  
124 rate variability are well-established phenomena, in particular under threat<sup>29</sup> or fear<sup>30</sup>. In  
125 perceptual and cognitive paradigms, cardiac cycle duration is also systematically modified<sup>31-36</sup>  
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<sup>37,38</sup>, and the processing of either auditory<sup>39</sup> or visual<sup>40</sup> stimuli attenuated when  
141 synchronized with the heartbeat. Sensitivity to temporal contingencies is also revealed in  
142 behavior: both infants<sup>41</sup> and monkeys<sup>42</sup> 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 hand<sup>43</sup>, face<sup>44</sup> or body<sup>45</sup> 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 humans<sup>46-49</sup>.

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 monkeys<sup>50</sup>  
153 and the appearance of slow waves in cats and dogs<sup>51</sup>, an effect which could be mediated by the  
154 noradrenergic locus coeruleus<sup>52</sup>. In humans, artificially boosting baroreceptor activation  
155 reduces pain sensation<sup>53</sup>. It was therefore hypothesized that the cortex is transiently inhibited  
156 during each systole, resulting in pulsed inhibition. Pain consistently decreases during systole<sup>54-  
157 56</sup>, which might account for the enduring popularity of the pulsed inhibition hypothesis<sup>57</sup>.  
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<sup>35,36,58,59</sup>; in  
160 audition, findings are mixed, with both positive<sup>60-63</sup> and null findings<sup>64,65</sup>; and in vision, mostly  
161 null results are reported for emotionally neutral stimuli<sup>33,66,67</sup>. Finally, as opposed to the pulsed  
162 inhibition hypothesis, action would be facilitated during systole compared to diastole<sup>68-73</sup>, but  
163 again this finding is not consistent across studies<sup>74,75</sup>.

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<sup>31-34,36</sup> but also to the development of expectancy processes when  
174 temporal contingencies are predictable<sup>76</sup>, [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<sup>77,78</sup>, 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' variability<sup>79-81</sup>. 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<sup>49,59,82,83</sup>, ventromedial  
191 prefrontal cortex<sup>33,83-85</sup> and posterior cingulate/ventral precuneus<sup>59,84-87</sup>, insula and frontal  
192 operculum<sup>85,88-91</sup>, as well as (mostly right) parietal lobule<sup>33,59,83</sup> and extrastriate visual cortices  
193<sup>91</sup>.

194

195 Turning attention inwards and explicitly attending to one's own heartbeats consistently  
196 modulates HERs<sup>92-98</sup>. Whether and how the attentional modulation of HERs translates into a  
197 more accurate conscious percept of heartbeats<sup>92,94,99</sup> is currently being re-examined (see, e.g.<sup>100</sup>)  
198 since behavioral procedures to measure the conscious perception of heartbeats are being  
199 revised<sup>101,102</sup>. 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 hypothesis<sup>103</sup>. HERs depend on the valence  
203 of emotional stimuli presented<sup>90,104,105</sup> as well as on mood<sup>88,106</sup> and arousal<sup>107</sup>. In such  
204 paradigms cardiac parameters also change<sup>108</sup>, 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 stimuli<sup>37</sup>, by the predictability of outcome  
210 states<sup>109</sup> and expected emotional content<sup>105</sup>.

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 self<sup>110</sup>.  
214 In line with this hypothesis, HERs do reflect self-relatedness during mind-wandering<sup>84,85</sup>, the  
215 strength of body ownership during bodily illusions<sup>44,86</sup> and self-other distinction in mental  
216 imagery<sup>87</sup>, and contribute to the stability of decisions based on subjective preferences<sup>83</sup>. Finally,  
217 subjective experience, the hallmark of consciousness, requires the existence of a subject of  
218 experience<sup>47</sup>, a minimal form of self which might be biologically grounded in bodily  
219 signals<sup>47,111</sup>. HERs could index the subject of conscious experience, since they predict the  
220 likelihood of the conscious detection of a visual<sup>33</sup> or somatosensory<sup>58</sup> stimulus at threshold,  
221 covary with subjective pain perception<sup>112</sup>, and reliably index residual consciousness in post-  
222 comatose patients<sup>113</sup>. 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 attention<sup>114</sup>.

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 vocalization<sup>115</sup>. 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-Bötzing complex<sup>116</sup> and  
236 surrounding nuclei located in the ventral medulla<sup>117</sup>. 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 respiration<sup>118-120</sup>, with the detection of airflow  
240 by mechanoreceptors in the olfactory bulb<sup>121</sup>. 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<sup>122,123</sup>, and lung movement<sup>124</sup> is relayed by the vagus nerve  
243 and influences hippocampal activity<sup>125</sup> *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 thalamus<sup>126</sup> and the neuromodulatory locus coeruleus<sup>127</sup>.  
247 Such non-olfactory pathways could account for some of the respiratory patterns observed at the  
248 cortical level<sup>128</sup>.

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 activity<sup>129</sup> 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 humans<sup>120</sup> and rodents<sup>119,130</sup> where it is distinct from the theta rhythm<sup>131,132</sup>.  
262 Respiration also modulates neural activity in medial prefrontal cortex in rodents<sup>130,133-135</sup>, 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<sup>136,137</sup>. The coupling between nasal respiration and neural  
266 activity in limbic regions is also associated with the modulation of memory  
267 performance<sup>120,138,139</sup> and of emotional ratings in humans<sup>120</sup>, and it influences freezing behavior  
268 in mice<sup>134,135</sup>.

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<sup>137,140</sup> and in different parts of the rodent *or cat* somatosensory cortex: the whisker barrel  
274 cortex<sup>118,141</sup>, trunk<sup>122,123</sup> and nose<sup>142</sup> representation. In humans, the detection of faint tactile  
275 stimuli is facilitated at the beginning of expiration<sup>36</sup>. Second, coupling between respiration and  
276 neural activity has also been observed in motor regions in both rodents<sup>141</sup> and humans<sup>137</sup>. The  
277 link with motor activity is also revealed by enhanced cortico-muscle coherence<sup>143</sup> and startle  
278 reflex responses<sup>144</sup> during expiration, but more voluntary movement initiation<sup>75,140</sup> during

279 inspiration. Reaction times in various auditory and visual tasks vary along the respiratory  
280 cycle<sup>145</sup>. Third, respiration is also coupled to neural activity in the visual system<sup>128,141,146</sup> and  
281 influences visual performance<sup>140,146,147</sup>. Respiration-locked modulations were also reported in  
282 the human posterior cingulate cortex<sup>140,148</sup>. 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 cerebellum<sup>148</sup>. From a  
285 more cognitive perspective, the strength of bodily illusions is enhanced when the virtual avatar  
286 either breathes<sup>149</sup> or is illuminated<sup>150</sup> 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 depth<sup>151</sup>? For instance, stimulation<sup>152,153</sup> 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 changes<sup>154</sup>. 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 mice<sup>127</sup>.

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".

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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 content<sup>155-157</sup>, others, upon which we focus, related to gastric electrical  
310 activity or mechanical distortion<sup>158,159</sup>. Like the heart, the stomach generates its own  
311 rhythm<sup>160,161</sup>, 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<sup>162,163</sup>,  
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<sup>164,165</sup>, with descending projections from  
318 insula, medial prefrontal cortex, motor and somatosensory cortices<sup>166</sup>.

319  
320 Different forces (distension, contraction, stroking) applied to the stomach wall activate both the  
321 vagal<sup>167-169</sup> and the spinal splanchnic<sup>170,171</sup> 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 cortex<sup>172-177</sup>, a pattern  
325 similar to the network activated by gastric stimulation in rats<sup>178</sup>. The involvement of occipital  
326 cortex has also been observed in sleeping cats<sup>179</sup>, 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<sup>180,181</sup> brain during resting-state and in the anesthetized rodent<sup>182</sup> brain. The so-called gastric network includes all exteroceptive cortices as well as motor regions, some default-network regions but very few transmodal, cognitive regions<sup>181</sup>. The directionality of interactions remains to be firmly established, but in humans part of the coupling observed corresponds information flowing **from** stomach to brain<sup>183</sup>. In rodents, sectioning the vagus nerve reduces stomach-brain coupling except in somatosensory cortex<sup>182</sup>, a pattern reminiscent of the spinal pathways connecting stomach to somatosensory cortex<sup>12</sup>.

The gastric network has been recently discovered<sup>180</sup> and little is known about its functional role. It does not appear to be modulated by moderate fasting in humans<sup>181</sup>, but the combination of more stringent diet control and fasting/feeding intervention alters the gastric network in anesthetized rats<sup>182</sup>. In humans, the network predicting weight loss overlaps with the gastric network<sup>184</sup>, and weight concern and body shame are associated with decreased gastric-brain coupling<sup>185</sup>. 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 regions<sup>181</sup>, 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 wakefulness<sup>179</sup>.

### *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. <sup>186</sup>). 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<sup>9,187</sup> 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 nucleus<sup>188-190</sup>,  
381 and has functional links with auditory pathways, as revealed by its role in vocalization-  
382 respiration coupling<sup>191,192</sup>. The parabrachial nucleus might also act on sensory cortices through  
383 neuromodulation<sup>8</sup>. 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<sup>166,193</sup>.

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 networks<sup>194</sup>. 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. <sup>195</sup>), 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<sup>196,197</sup>. 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<sup>196,197</sup>. 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 respiration<sup>129</sup> and the gastric rhythm<sup>180,183</sup>. 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 good<sup>128</sup>, whereas the areas coupled to the stomach are organized  
437 along a gradient of phases<sup>180</sup>, 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 evolution<sup>198</sup>,  
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 species<sup>199</sup>. 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 synchronized<sup>200</sup>. 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<sup>22,23</sup> 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 representation<sup>196</sup>, and  
455 could thus contribute to the unity of conscious experience. However, conscious experience has  
456 other properties<sup>47</sup>, 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 spaces<sup>201</sup>. 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 reference<sup>49</sup>,  
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.<sup>146</sup>), by analogy with previous work on intrinsically generated  
478 oscillatory synchrony and visual attentional sampling<sup>202</sup>. Another interpretation of cycle effects  
479 is rooted in the literature on nasal respiration, where inspiration corresponds to olfactory  
480 sensory intake<sup>203</sup>. 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<sup>140,146</sup> – 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 oscillations<sup>204</sup> 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 coding<sup>139</sup>. 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 heartbeats<sup>72</sup>. This logic has been formalized for both cardiac<sup>57,205</sup> and respiratory<sup>206</sup>  
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 state<sup>207</sup> (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 cortex<sup>208</sup>. 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 feelings<sup>209-211</sup>, with a particular role for anterior cingulate and anterior  
516 insular cortices to generate visceral predictions<sup>212</sup>. Emotional feelings relating to actual or  
517 mentally simulated changes in the body have been proposed as a basis of the (emotional) self<sup>110</sup>.  
518 Alternatively, having a predictive model of the (interoceptive, proprioceptive, somatosensory)  
519 body could be the basis of the self<sup>210</sup> (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 framework<sup>48</sup>. 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 cortex<sup>213</sup> or at earlier subcortical stages<sup>214</sup>. 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 separately<sup>215</sup>. 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 cortex<sup>59</sup>. 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 stimulation<sup>216</sup> but are also further modulated by the  
536 visual illumination of the virtual body in synchrony with heartbeats<sup>43-45</sup> or respiration<sup>149,150</sup>.  
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 inputs<sup>48</sup>, 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).

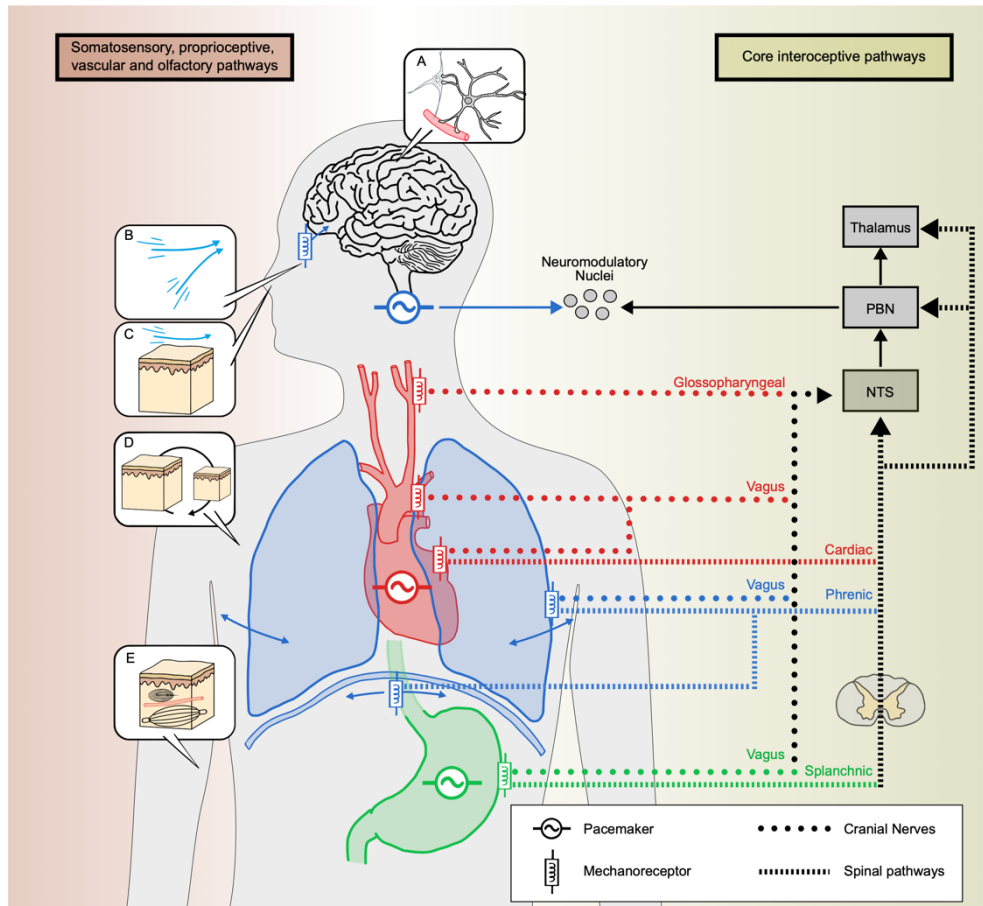
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## 544 Concluding remarks and open questions

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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568

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. Organ 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

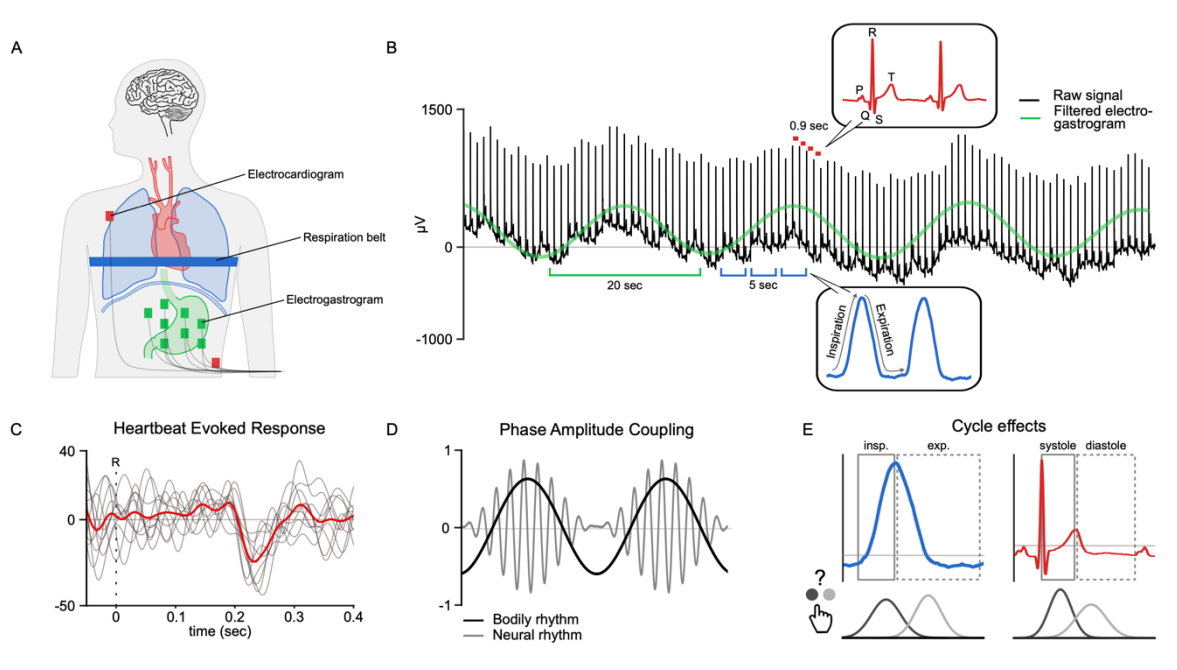
585 in the olfactory bulb. (D) Changes in organs' volume (i.e., chest expansion/contraction) can be

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.

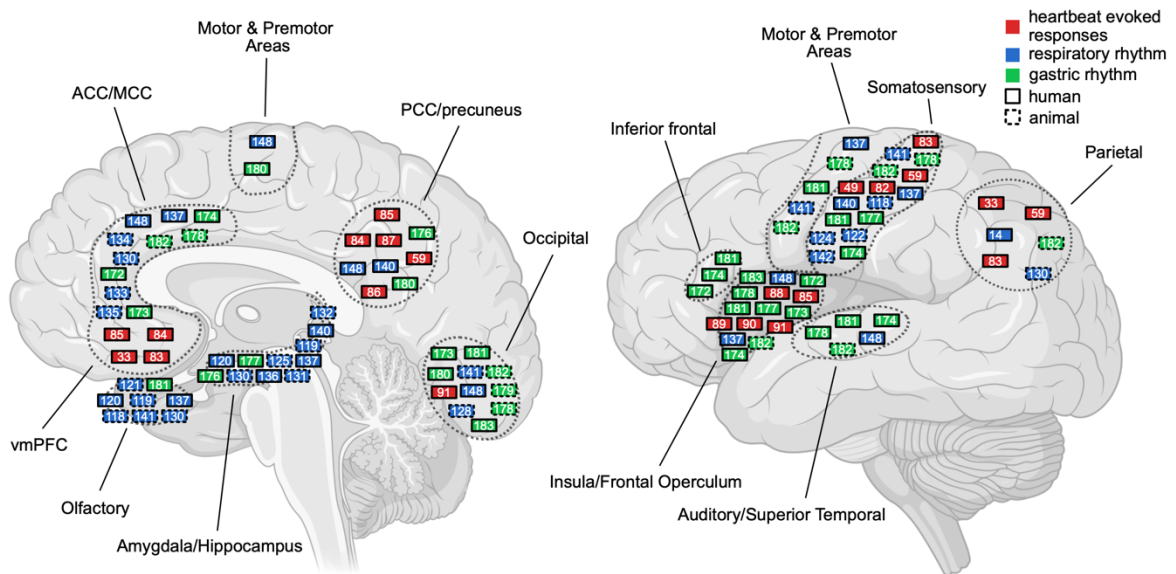
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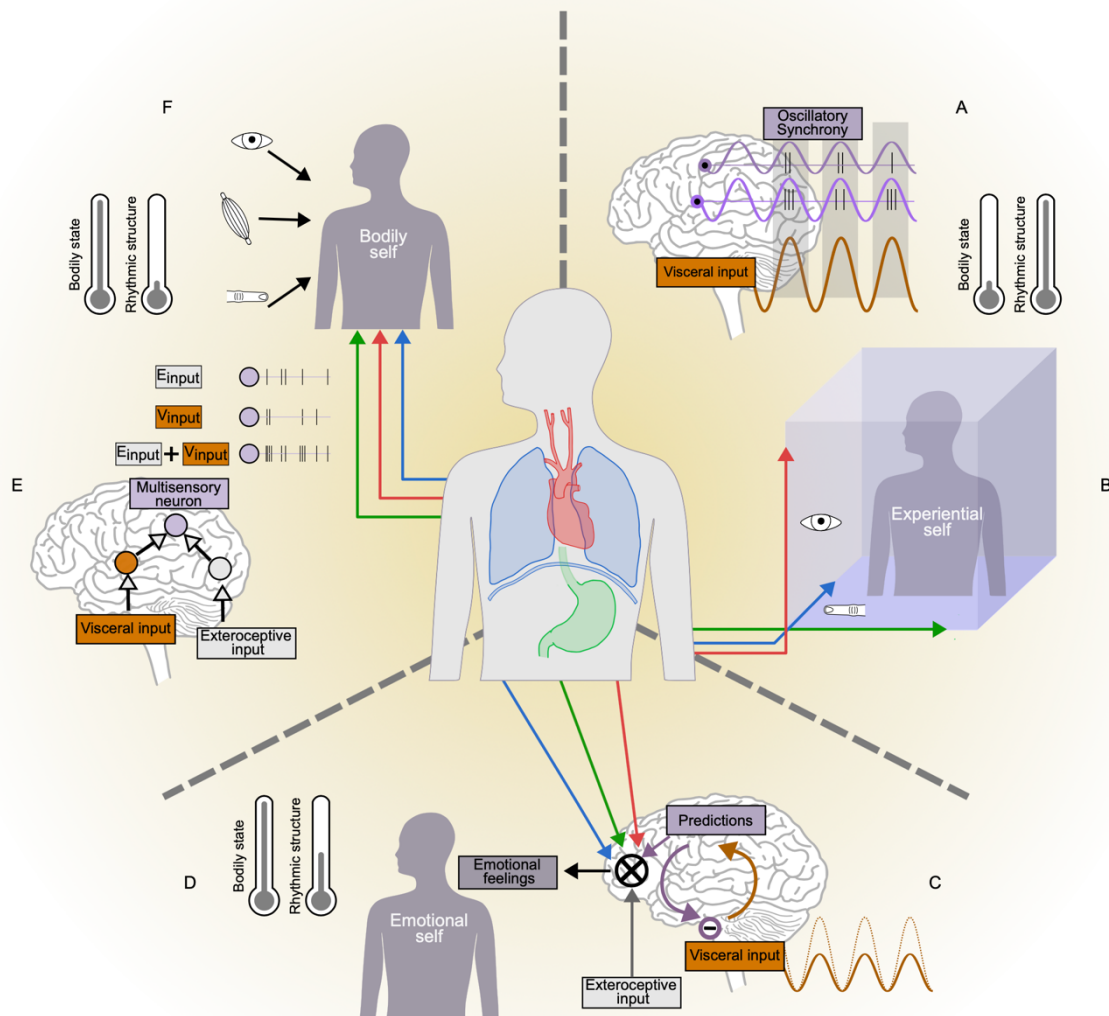
590  
 591 **Figure 2. Measuring cardiac, respiratory and gastric interoception.** A. Settings in humans  
 592 to measure cardiac and gastric<sup>199</sup> rhythms with cutaneous electrodes in humans, and respiratory  
 593 rhythm with a belt. B. Example of raw data from an abdominal electrode, showing 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.

622  
623



624  
 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.

640  
 641

## 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<sup>217,218</sup>. Similarly, brain movements occurring at each heartbeat  
649 during in vivo recordings modulate action potential waveform<sup>219</sup> and affect intracranial HER  
650 recordings<sup>82</sup>. Moreover, local changes in vascular tone (i.e. vasomotion) or hemodynamic  
651 oscillations linked to respiration modulate near-infrared spectroscopy signals<sup>220</sup>. 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 EEG<sup>221</sup> and MEG<sup>222</sup> 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<sup>49,79,80</sup>.

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<sup>223,224</sup>.

665  
666 Fourth, the experimental paradigm itself might influence visceral rhythms. For instance, the  
667 conscious perception of an external stimulus slows down the heart<sup>33</sup>, and when stimulus  
668 presentation times are predictable, participants tend to inhale and hence increase their heart rate  
669 at stimulation onset<sup>36</sup>. 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 cycle<sup>139</sup>.

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 interoception<sup>173</sup>), 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 pattern<sup>225</sup>. More subtle  
686 changes have recently been observed in non-emotional situations, where participants might  
687 spontaneously align their respiratory pattern to the movement generated<sup>226</sup> or to the  
688 experimental paradigm<sup>36,145</sup>, although such behavior is not systematic<sup>33</sup>. 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<sup>137,227</sup>.

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 attacks<sup>228</sup> – although respiratory  
694 rates increase for positive emotions as well<sup>225</sup>. Neuroimaging studies of dyspnea, induced by  
695 flow-resistive load or altered O<sub>2</sub>/CO<sub>2</sub> content, indicate the involvement of most limbic  
696 structures as well as somato-motor regions<sup>229</sup>, with an anxiety-dependent engagement of the  
697 anterior insula<sup>230</sup>. Intracranial EEG confirm those findings and reveal in addition the  
698 contribution of occipital regions<sup>137</sup>. 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 cortex<sup>137</sup>. Finally, asking participants to inhale or exhale  
701 once, as fast as possible, increases motor excitability and finger flexion force<sup>231</sup>.

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 vocalization<sup>232</sup>. While there is considerable  
707 interest for yoga and meditation as a way to improve mood, sleep and the general sense of well-  
708 being<sup>233</sup>, the specific role of respiratory patterns and/or attention to respiration<sup>234</sup> remains  
709 difficult to isolate from other components. When practiced in isolation, slow-paced breathing  
710 is associated with stress reduction<sup>235</sup> and influences brain activity<sup>236</sup>. Still, the literature reveals  
711 mixed findings when it comes to pain or emotional feelings<sup>237,238</sup>. 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<sup>235,237</sup>,  
714 but the hypothesis is still debated<sup>239</sup>.

715  
716

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725

726 Competing interests.

727  
728 The authors declare no competing interests  
729

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