THE INFLUENCE OF INTEROCEPTIVE SIGNALS ON THE PROCESSING OF EXTERNAL SENSORY STIMULI

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Interoception refers to the set of physiological and cognitive processes involved in sensing, interpreting, and integrating information that arises inside the body, providing a continuous mapping of our ever-fluctuating internal milieu across conscious and unconscious levels (Khalsa et al., 2018). It can be distinguished from exteroception (sensation of the environment) and proprioception (sensation of the body in space). While far more research has focused on how external stimuli are represented by the brain, research on interoception focuses on the effect of ever-fluctuating afferent bodily signals on brain processes. Importantly, these so-called interoceptive signals do not only inform the brain about the state of the body but also influence how we relate to our environment, that is, they influence our perception of the world. In this chapter, we focus on this latter facet, with special emphasis on the way the cardiovascular system modulates the processing of external stimuli. First, we outline the historical roots of interoception. Second, we describe how changes inside the body are consciously perceived, and such signals influence perception of external stimuli. Thirdly, we describe the physiological pathway of the heart-brain axis and its impact on stimuli processing. Fourth, we review the link between afferent bodily signals and the neural encoding of subjective values and discuss what is known about the way interoception affects hedonic coding of sensory objects. Lastly, we consider current challenges of the field and how these can be overcome.

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A brief history of the study of interoceptive signals on cognition

"The stability of the organism's internal landscape (*milieu intérieur*) is the condition for the free and independent life" (Bernard, 1878). Although 150 years old, these words resonate well with our current understanding of the way the integrity of living organisms rests upon upholding a homeostatic equilibrium. A few years after Bernard, William James (1884) and Carl Lange (1885) proposed that our emotional experiences originate from responses in the body that accompany the perception of external events. In contrast, Walter Cannon (1927) and Philip Bard (1928) proposed that stimulating neurons in the central nervous system was sufficient to elicit feelings and physical reactions in a simultaneous manner. This debate regarding the cause of emotions—body states vs brain activity—has continued to this day.

By the turn of the 20th century, Charles Sherrington (1906) coined the term *interoceptor* to describe the presence of an internal bodily surface dedicated to the monitoring of changes within the body. By the time Sherrington and Edgar Adrian received the Nobel Prize for their discoveries regarding the functions of neurons, Cannon further elaborated Bernard's notion of a *milieu intérieur* in what he termed *homeostasis*, intended to describe self-regulating processes that promote survival by maintaining the stability of the organism (Cannon, 1939). During this first half of the twentieth century, most studies in interoception were conducted in the Soviet Union, with Pavlov's work on learnt reflexes and interoceptive processes in preparation for digestion the most famous. However, some of these works remained unnoticed until later decades, when Soviet psychophysiology became more appreciated by international audiences.

The advent of operant conditioning and the discovery of various types of interoceptors laid the foundation for our present understanding of interoception. Novel paradigms in cardioception such as the *heartbeat detection task* allowed scientists to estimate how much interoceptive information reaches awareness (Schandry, 1981). Later, the development of neuroimaging techniques allowed neuroscientists to map the brain activity correlated with these tasks (Craig, 2002), and new theories such as the Somatic Marker Hypothesis stressed how subjective value computations integrate bodily representations to form decision values (Damasio, 1999, 1994). Since then, the field of interoception has grown, matured, and diversified. The number of studies has grown exponentially and our understanding of the interaction between interoceptive mechanisms and external perception has improved significantly. The current chapter reviews this body of work and moves beyond the

recognised role of interoception for homeostasis, providing insight into the role that afferent interoceptive signals play in the computation of perception, valuation, and reasoning.

Conscious interoception mediates stimulus processing

Interoception is multifaceted, it comprises distinguishable dimensions and different physiological systems (cardiovascular, gastrointestinal, hormonal, circulatory) acting across conscious and unconscious levels (Khalsa et al., 2018; Quigley et al., 2021). Yet, the primary physiological focus of most interoception studies is the cardiovascular system. This is likely due to the emergence of early evidence for a modulatory effect of the carotid sinus on central and autonomous nervous processes (Koch, 1932; Kreindler, 1946), and the methodological ease of monitoring discrete regular events (i.e. heartbeats) that can be recorded via noninvasive tools, e.g., electrocardiogram (ECG), pulse oximeters, or wearable heart rate monitors.

Most interoceptive processes, such as the monitoring of one's psychophysiological state, unfold at the unconscious level and often reach awareness only when the system is compromised (e.g., pain, thirst). The study of this facet of interoception is usually focused on the effect of afferent bodily signals upon the processing of external stimuli and brain function. At the conscious level, numerous studies have examined the ability to notice bodily states and fluctuations, mostly in the cardioception domain. Three dimensions of conscious interoception have dominated this research: (i) *Interoceptive sensibility*, which refers to the subjective experience of internal sensations as measured by self-reports. (ii) *Interoceptive sensitivity*, which refers to the objective measure of interoception, and involves testing of the capability to perceive bodily changes in behavioural tasks. (iii) *Interoceptive awareness*, which refers to metacognitive insights about the two former dimensions, is most often operationalized as the distance between one's beliefs and the person's actual ability to perceive inner body states (see Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015; Murphy, Catmur, & Bird, 2019). Below we briefly review findings that this body of works has produced with respect to the role these dimensions play in the processing of external stimuli.

Interoceptive sensibility

One way to examine the conscious processing of interoceptive signals is by using self-report questionnaires that allow for an assessment of participants' experience with bodily sensations (interoceptive sensibility), as well as how this sensitivity is related to other cognitive

domains. The choice of a self-report questionnaire depends largely on the research question, for example noticing vs. body listening or dissociating adaptive vs. maladaptive interoception (see the Body Perception Questionnaire (Porges, 1993), the Multidimensional Assessment of Interoceptive Awareness (Mehling et al., 2018, 2012), or the Interoceptive Sensory Questionnaire (Fiene et al., 2018).

Self-report measures have shown that participants with a heightened interoceptive sensibility might experience more anxiety, and this is more likely to occur when they have difficulties in identifying and describing emotions. The lack of attributing interoceptive signals to emotional states predisposes participants to anxiety-related characteristics (Palser et al., 2018). This in turn may intensify the attribution of negative valence to stimuli, as well as exacerbate a negative narrative when processing external events. In this way, self-reports allow us to quickly obtain information about the interoceptive-mediated valuation of external stimuli. Relatedly, Paulus, Feinstein, and Khalsa (2019) highlighted two scenarios in which the negative appraisal of stimuli can be mediated by maladaptive interoceptive mechanisms. In the first scenario, people who are exposed to threatening stimuli experience high levels of arousal. If the situation is positively resolved, future related events should be perceived as less hazardous, decreasing sympathetic engagement. However, if people fail to update their beliefs, similar scenarios will continue to elicit heightened visceral responses. In the second scenario, people extrapolate physiological responses from the original context to other situations. Both scenarios involve persistent non-veridical perception that negatively affects the regular function of the viscera, which eventually feeds back to the central nervous system where it affects the assessment of external stimuli. In sum, if one's set point (i.e., optimal bodily state) is missattuned, the representation of interoceptive signals becomes imprecise, and the valuation of external stimuli does not necessarily meet the most appropriate behaviour (Linson et al., 2020; Paulus et al., 2019).

Interoceptive sensitivity

Another way to examine the conscious processing of interoceptive signals is by using lab-based tasks that allow obtaining more objective measures. This usually involves asking participants to notice bodily changes while their physiological rhythms are being recorded (e.g., counting heartbeats while the ECG is recorded). Then, the difference between participants' subjective reports and the objective quantification of their bodily changes are compared against each other. The difference between these measures provides an objective

estimate of interoceptive sensitivity. This allows for "profiling" of participants, ranking them on a continuum from poor to good interoceptors, and relating this individual variance to other measures and tasks. For example, good interoceptors display larger electrodermal responses to unfair offers in the context of the ultimatum game (Dunn et al., 2012), have better memory recall for words encoded during the systolic phase of the cardiac cycle (i.e., hearts' contraction pumping the blood, Garfinkel et al., 2013), exhibit greater sympathetic reactivity during mental stress and subjective arousal during emotional picture viewing (Herbert et al., 2010), and display higher reinforced learning of emotional faces (Pfeifer et al., 2017). Good cardioception has also been associated with stronger expectancy for unconditioned stimuli (Zaman et al., 2016), better learning with the corresponding modulation of hippocampal activity (Stevenson et al., 2018), and higher sensitivity to negative affect but lower accuracy in recognising faces depicting fear and sadness (Georgiou et al., 2018). A recent study, combining both objective and subjective measures of interoception, have shown that participants with better cardiac interoceptive awareness and insight are able to withhold actions and respond slower in a Go/NoGo task, while the opposite pattern was observed for participants with poorer interoception (Rae et al., 2020). This suggests that precise afferent input may support sensorimotor decisions. In contrast, noisier signalling could prompt hasty responses to external stimuli.

Taken altogether, current findings suggest that cardiac sensitivity is related to greater perception and memory encoding of emotional stimuli. However, these results should be considered with caution. More consistent research is needed and some studies have also shown that interoceptive signals can inhibit stimulus processing (see e.g., Park, Correia, Ducorps, & Tallon-Baudry, 2014; Salomon et al., 2018). Overall, the question of the relation between interoceptive sensitivity and everyday well-being needs further work. Furthermore, research in atypical interoception, a common denominator in all mental disorders, suggests that either low or amplified functioning in interoceptive sensibility, sensitivity, or awareness could be linked to a maladaptive valuation of stimulus processing (Khalsa et al., 2018).

The influence of afferent bodily signals on the processing of stimuli
As noted above, the primary focus of studies in interoception has been the influence of the cardiac cycle on cognition. To understand the influence of the heart on stimulus perception, below we summarize what is currently known about neural signalling from the heart to the brain, and how these projections modulate cognition.

The heart-brain axis

One of the distinctive features of the heart is that it is endowed with pacemaker properties, i.e., the heart can generate its own intrinsic oscillatory electrical activity. In a single heartbeat two phases are observed: in the *systole* phase the heart contracts and ejects the blood, whereas in the *diastole* phase the heart expands while being filled. Both phases comprise a cardiac cycle, with the R-peak (peak in ECG depicting the contraction at systole) denoting the beginning of a new cycle. During the systolic phase, pressure sensors located in the carotid sinus, coronary arteries, and in the aortic arch (i.e., baroreceptors), detect changes in blood pressure due to the ejection of the blood from the left ventricle. Baroreceptors convey information to the brain about the strength and timing of the heartbeats during the systolic phase while being quiescent during the diastole phase of the cardiac cycle (Critchley and Harrison, 2013). Many studies have observed that neural and behavioural responses to external stimuli vary according to the phase of the cardiac cycle during which they occur (see e.g., Azevedo et al., 2017; Leganes-Fonteneau et al., 2020). This is usually demonstrated by meticulously locking the presentation of stimuli to the systolic or diastolic phase of the cardiac cycle. Many studies have associated the variation in participants' responses along the cardiac cycle with the phasic firing of the baroreceptors. While this is under investigation, it is clear that heartbeats selectively modulate the processing of external stimuli by constantly facilitating, competing with, or inhibiting information processing (see Figure 1 and the following section).

As an intrinsic oscillator, the heart has an inherent nervous system composed of interconnecting, efferent, and afferent ganglionated nerve plexi (a branching network of intersecting nerves). These project through the spinal cord and the vagus nerve to the nucleus of the solitary tract (NTS) and other autonomic nuclei of the brainstem, which in turn allow for dynamic regulation of efferent[1] sympathetic and parasympathetic cardiomotor activity. Interestingly, approximately 80% of the fibres of the vagus nerve are afferent, which makes it more of a listener than a storyteller (as revisited by Wolpert, Rebollo, & Tallon-Baudry, 2020). In the NTS, the convergence of signals from different bodily systems (e.g., cardiac, gastric) projects to viscero-sensitive brain regions such as the thalamus, hypothalamus, amygdala, cingulate cortex, and the insula. The insula is considered a major hub for interoceptive information (Craig, 2009). The posterior insula receives inputs from bodily systems and the anterior part re-represents this information with emotional, cognitive, and

subjective states. Information from the environment and interoceptive signals seem to be assimilated across this posterior-to-anterior insular gradient (Namkung et al., 2017).
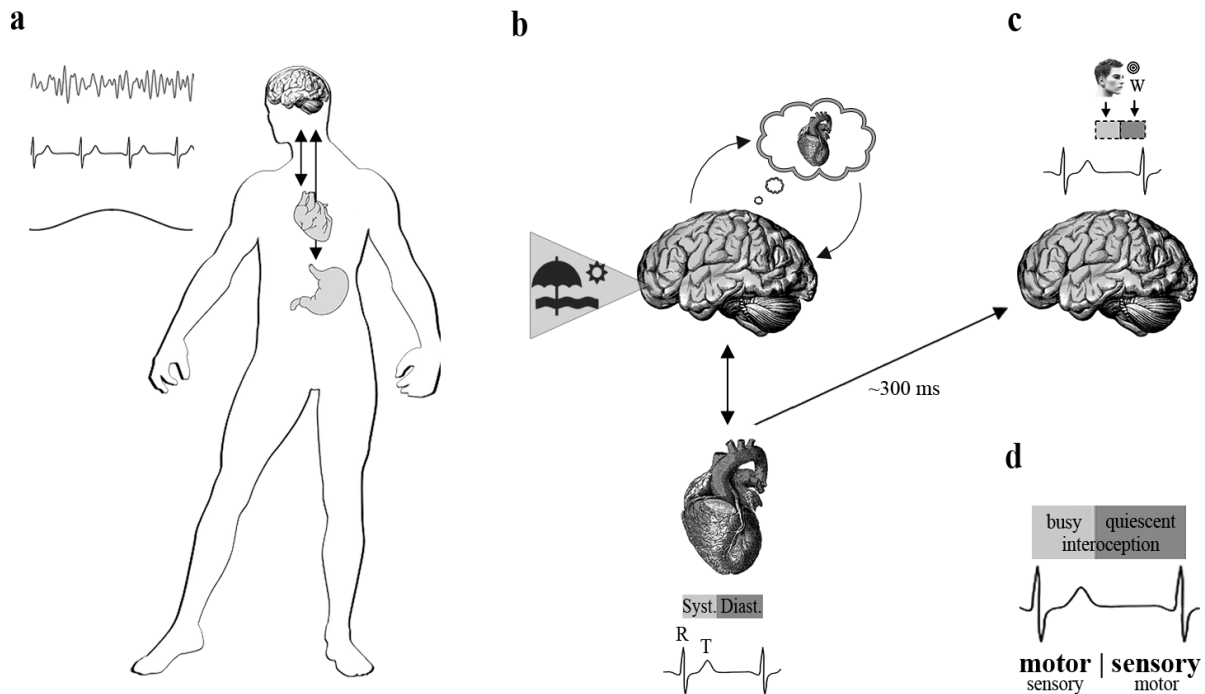

Figure 6.1. Interoceptive processes and their influence on stimulus processing. a) Bodily organs endowed with pacemaker properties interact with the brain via afferent and efferent signals. The activity of the stomach, heart, and brain unfolds at various frequencies. Changes in such a complex oscillatory activity affects one another and influence cognition (Azzalini et al., 2019b). b) The brain's responses to sensory inputs (e.g., external stimuli) not only depend on the stimuli's properties but also on its own internal state at the time when the stimuli are processed. Conscious perception and awareness of one's inner bodily states moderates the perception of stimuli and corresponding physiological correlates (interoceptive sensibility and predictions; Murphy et al., 2019). c) Studies examining the influence of the cardiac cycle on cognition often measure participants' ECG and present stimuli during time windows phase-locked to systole or diastole. In principle, stimulus presentation is shifted in time to account for the time needed for afferent baroreceptor activity and other physiological changes to reach the brain (~300ms). d) An overall trend in studies using cardiac phase-locking, show that motor responses are more prone in the early period of the cycle (systole) whereas sensory processing of stimuli seems enhanced in the later quiescent physiological period (diastole). Icons in all panels are under Creative Commons license CC0 from Pixabay.com.

Effect of cardiac phases on stimulus perception

Many studies have examined the iterative influence of the cardiac cycle upon the perception of stimuli by presenting these during systolic or diastolic phases (Figure 1c). The idea is to exploit these naturally occurring fluctuations to understand how subsequent variations (e.g., bodily arousal, firing of baroreceptors at systole) affect stimulus processing at the neural and behavioural levels. These studies are usually focused on inspecting the processing of emotional or non-emotional stimuli presented at near or suprathreshold perceptual levels.

Depending on the task and stimuli, cardiac phases can both selectively facilitate and inhibit stimulus processing. Systolic modulation of sensory processing has been observed for subjective pain perception and sensitivity to tactile stimuli, which are attenuated during this phase compared to diastole (Wilkinson et al., 2013; Al et al., 2020; Motyka et al., 2019; see also concurrent effects of respiration in Grund et al., 2021). Similarly, the startle reflex, an unconscious defensive response that induces an immediate eyeblink response to sudden or threatening stimuli such as sudden noises or sharp movements, is attenuated by systolic afferent signals (Larra et al., 2020). Startle responses are also modulated by phase respiratory and gastric rhythms (Schulz et al., 2017, 2016). Conversely, enhanced processing at systole has been often linked to negative emotional stimuli such as the detection of fearful faces and memories (Garfinkel et al., 2020; Garfinkel and Critchley, 2016). Likewise, the processing of threatening stimuli associated with racial stereotypes is heightened during systole (Azevedo et al., 2017). Specifically, participants in a first-person shooter task produced more errors ('shooting' un-armed Black *vs.* White targets) during systole. These results may be associated with a cardiac modulation of error monitoring (Bury et al., 2019) and that motor inhibition might be more prone to fail during systole (Makowski et al., 2020; but see Rae et al., 2018).

Overall, current research indicates that there is a putative effect of afferent cardiac signalling on stimulus processing (Critchley and Garfinkel, 2018). However, results seem to vary significantly across experimental manipulations. While more consistent research is needed, it is clear that cardiac afferent signals and concurrent physiological changes moderate cognitive processes by competing for the allocation of attentional and representational resources. This is turn, can reduce or amplify the sensory processing of stimuli. Sensory processes that are concurrent with the systolic phase of the cardiac cycle (the noisy period of the cycle) seem to be reduced, whereas motor behaviour seems facilitated (see the section "Active Sensing" below).

Cardiac-related effects upon the processing of face stimuli

Influential theories of emotion highlight that certain emotions are likely coupled with particular bodily states. For instance, disgust is closely coupled with parasympathetic responses, whereas feelings of anxiety or fear are associated with heightened cardiovascular arousal caused by sympathetic activation. In this context, physiological arousal is often understood as a consequence of top-down processes rather than as a cause of our emotional experience. Yet, several studies have shown that detection and appraisal of facial emotional expressions fluctuate according to the effect of short-term baroreceptors' activity, i.e., a transient increase of visceral arousal.

The modulatory effect of the heart upon the processing of face stimuli varies according to both the emotion displayed and the task employed. In a forewarned reaction time task, facial expressions of disgust, but not sad, happy, or neutral expressions, were judged as more intense when presented in systole. Furthermore, the processing of disgust and happy faces resulted in a more pronounced deacceleration of subsequent heartbeats, a mechanism proposed to facilitate perception and appraisal (Gray et al., 2012). In a rapid serial presentation task, the detection and intensity ratings of fearful faces were found to be higher when these were presented in systole, suggesting that peoples' heartbeats might facilitate conscious processing of briefly presented and emotionally strong stimuli (Garfinkel et al., 2014). The cardiac interaction between processing of fearful faces and cardiac phase correlated with neural activations in several brain regions with the most prominent found in the amygdala, a structure associated with threat processing and the integration of physiological and affective information. Interestingly, regardless of the emotion, the overall effect of the cardiac cycle on emotional processing was found in the anterior insula. In an emotional spatial cueing task, a systolic effect on attentional engagement to fearful faces was found at different spatial frequency ranges. The systolic phase enhanced the processing of fearful facial expressions at low, but not broad or high spatial frequencies (Azevedo et al., 2017), implying that afferent bodily signals modulate the processing of faces by distinctly influencing the magnocellular and parvocellular pathways at the early stages of the visual processing.

More recently, Leganes-Fonteneau et al., (2020) have used an emotional visual search task where participants saw a target emotional face on the screen (fear, happy, sad or disgust) surrounded by five neutral distractors. An interesting point of this task is that allows

capturing attentional processes allocated to the scanning of faces in a crowd, as well as differentiating between the correct detection of the target stimuli (accuracy in the visual search task) and the correct identification of the emotion presented. Respectively, accuracy in the visual search was higher for disgust and happy faces presented during systole, whereas the opposite effect was found for fearful faces. The identification of fearful and sad faces was higher when presented in diastole. Overall, these studies highlight that detection and appraisal of facial emotional expressions are the result of body-brain interactions. The role of cardiac interoceptive signals goes beyond the processing of fearful faces and depends on the core task and emotional expression. Presumably, these effects have been explained as a consequence of afferent baroreceptor signals conveyed through the brainstem via the vagus nerve. However, other physiological changes are concurrent to heartbeats (Davos et al., 2002) and these may instigate the above effects by directly or concurrently affecting key neural substrates for face processing.

The self and the heart-brain axis support subjective preferences

Research in cognitive neuroscience and psychology have long focused on the significance of the body as the ground of the self—the person as the object of its own reflective consciousness. More recently, the study of the self has focused on the importance of the body from within. It has been proposed that regardless of the bodily state, organs endowed with pacemaker properties such as the heart and the stomach could work as constant transmitters that signal the presence of a body to the brain (Azzalini et al., 2019; Tallon-Baudry et al., 2018). Then, the central nervous system would make use of this information to generate a first-person perspective. Compelling evidence for this mechanism comes from observing that the amplitude of brain responses to heartbeats (heartbeat-evoked responses; HER) correlates with the self-relatedness of thoughts in the ventromedial prefrontal cortex (vmPFC; Babo-Rebelo, Richter, & Tallon-Baudry, 2016; Tallon-Baudry, Campana, Park, & Babo-Rebelo, 2018). Relatedly, the amplitude of the HER has been linked to the conscious perception of stimuli presented at near-threshold detection (Al et al., 2020; Park et al., 2014; Park and Blanke, 2019). This suggests that brain responses to heartbeats might regulate the perception of near-threshold stimuli by moderating one's self-consciousness during the perceptual experience.

Following this line of work, it has been proposed that this relationship, between the self and the heart-brain axis, supports the valuation of what we like or dislike. Specifically, it has been

exposed that preference-based decisions about external stimuli such as cultural goods are subjected to the self. For instance, 'do you prefer Forrest Gump or Matrix? Only you know which movie you like best' (Azzalini et al., 2021, p.1). These authors examined participants' brain activity while they were presented with pairs of movie titles. The participants either indicated which movie they preferred or had to discriminate between versions of the title written with different levels of contrast. The results of the study showed that when choosing the participants' preferred movie, HERs signalled the recruitment of self-reflective processes in vmPFC. Conversely, this association was not observed for the contrast discrimination task. Moreover, the interaction between HERs and subjective value encoding reflected the inter-individual variability in choice consistency and the trial-by-trial fluctuations within participants. These results indicate that the neural monitoring of cardiac signals and the neural encoding of subjective values are related to each other. Considering these findings, the sensory valuation of stimuli appears to depend on the novelty of the stimuli and the use/absence of a subjective approach, including possible re-enactments of autobiographical and bodily memories (Galvez-Pol et al., 2020a; Riva, 2018).

The gut-brain axis

The gastrointestinal tract has received increasing attention in recent research on interoception. Similar to the heart, the gut generates its own intrinsic oscillatory electrical activity. The gastrointestinal tract has a rhythm that unfolds in the form of a continuous slow electrical pulse (one cycle every 20 seconds, ~0.05Hz). This rhythm results from the activity of Interstitial Cells of Cajal, peacemaker cells that generate rings of electrical waveforms. These cells mediate between the autonomic nervous system and the muscle layers of the stomach, whereby mechanical changes in smooth muscles can be detected by making contact with vagal sensory neurons along with intramuscular arrays (Powley et al., 2016).

The gastric rhythm can be non-invasively measured via electrogastrography (EGG), which reflects a combination of the gastric rhythm caused by Interstitial Cells of Cajal and of gastric smooth muscle contractions (Wolpert et al., 2020). Importantly, the recording of spontaneous brain activity (non-task-related fluctuating neural activity) has revealed that several brain regions are linked to gastric function (Rebollo et al., 2018). In this so-called gastric network, the gastric phase seems to modulate the neural activity of viscero-sensitive brain areas (somatosensory cortices and parieto-occipital regions). The presence of this gastric network suggests that automatic regulation of basic processes for life such as digestion are linked to

complex patterns of brain activity that affect how people could perceive external stimuli. Evidence for this has been shown in a behavioural task where participants were given a dose of domperidone (an antiemetic moderating gastric rhythm) or a placebo while their oculomotor responses to neutral and disgust images were recorded. The study showed that domperidone did not change the subjective ratings of disgust but decreased oculomotor avoidance following incentivized exposure to disgusting stimuli (Nord et al., 2021). Future work is needed to examine the link between gastrointestinal afferent signals, the brain and subsequent behaviour, as well as to study other aspects of the gut-brain axis that are likely to mediate this link (e.g., microbiota).

Active sensing in interoception: Beyond the phase-locked presentation of stimuli

Many of the findings that we have presented here were obtained by deliberately locking the presentation of stimuli to the different phases of the cardiac cycle. However, in our everyday life, the environment does not normally provide us with sensory information phase-locked to our physiological cycles. Instead, we freely and actively sense the stimuli at hand. Interoception studies in active sensing examine whether participants are naturally prone to sample the stimuli in the environment in a particular phase of the bodily cycles. Thesee types of studies get rid of temporal constraints by allowing participants to access the stimuli at their own pace. Simultaneously, participants' behaviour and their physiological rhythms are coregistered (e.g., ECG, breathing, and participants' responses). After data collection, researchers work 'backwards' the data by situating each of the participants access to the stimuli along with the recorded continuous rhythms. Then, they analyse whether participants are more prompt to sample the stimuli, for instance, in the systolic or diastolic phase of the cardiac cycle (Figure 2a,b).

A significant coupling between the active sampling of stimuli and cardiovascular oscillations have been found in various tasks. For instance, in a visual search task comparable to a "spot the difference task," participants' oculomotor behaviour and ECG were recorded while they searched for differences between two bilateral arrays continuously displayed on the screen (Figure 2c; Galvez-Pol et al., 2020b). Across three different analyses, the results showed a significant coupling of saccades, subsequent fixations, and blinks with the cardiac cycle. More eye movements to sample the arrays were generated during systole, which has been reported as the period of the maximal firing of the baroreceptors. Conversely, more ocular fixations were found during the diastole phase (quiescent baroreceptors). Lastly, more blinks

were generated in the later period of the systolic phase. These results show that (*1*) in a more ecological setting, interoceptive and exteroceptive processes adjust to each other; (*2*) the active sampling of external stimuli might occur when more computational resources are available, that is, during quiescent periods of the inner body (Galvez-Pol et al., 2020b). While this latter hypothesis needs further examination, recent research seems to support this idea (see e.g., Kluger et al., 2021).
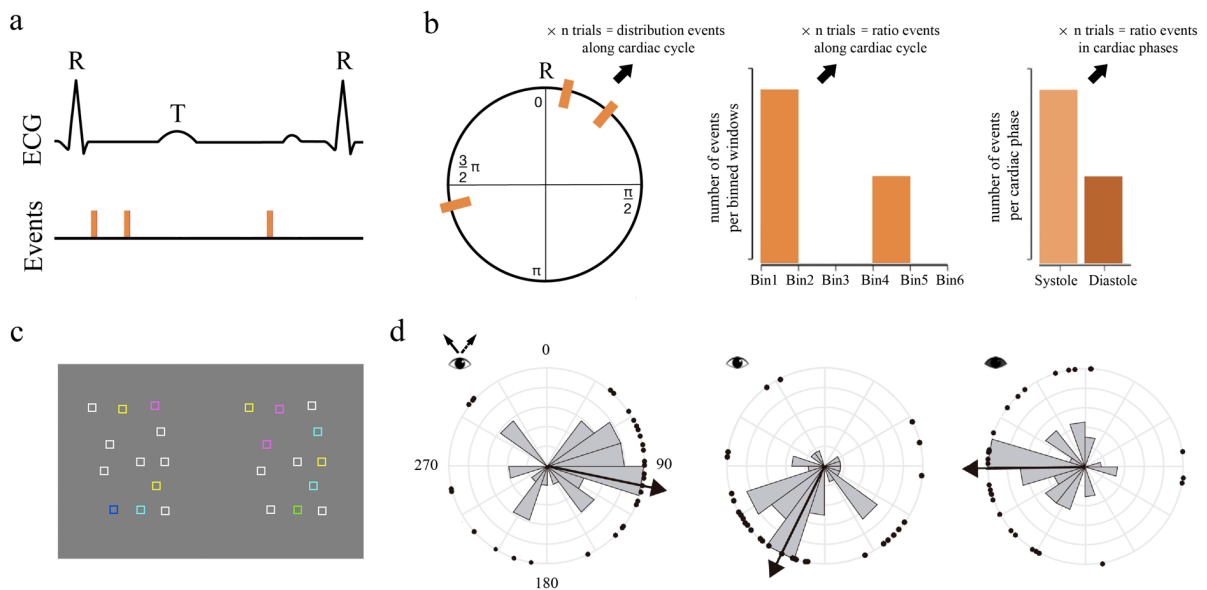

Figure 6.2. Active sensing of stimuli in interoception. a) ECG depicting one cardiac cycle. Here, two events (e.g., saccades to sample stimuli, keypresses leading to stimuli onset, etc) occurred at the early phase of the cardiac cycle and one at the later phase. b) Schematic of analysis, from left to right, the number of events in this cycle are depicted in phase i) as degrees of each event relative to the concurrent heartbeat, ii) as counted events binned into time windows along the cycle, and iii) as counted events in the systolic or diastolic phases. After *n*-trials, it is possible to compute the frequency of events as a function of phase, the event changing ratio, and their phasic occurrence. c) Active visual sampling task and results. Participants reported the number of boxes differing in colouration between two bilateral arrays by comparing each box in the left array with the homologous box in the right array. d) The succeeding results showed that saccades onset, mean time point of fixations, and blinks onset occurred significantly more often in the early, mid, and later period of the cardiac cycle, respectively. Adapted from Galvez-Pol et al., (2020b).

Beyond ocular sensory sampling, Kunzendorf et al., (2019) found that participants freely generated a keypress leading to the onset of images in a memory task more often during the systolic phase, though it did not influence memory performance. Similarly, Perl et al., (2019) reported that participants preferred to self-initiate the onset of non-olfactory cognitive tests to coincide with the beginning of the inspiratory phase. Also, recently it has been shown that participants tend to initiate actions during the expiration phase of the breathing cycle. Moreover, the neural marker of these self-initiated movements seems to be modulated by the respiratory phase (Park et al., 2020). Overall, active sensing is entrained by cardiorespiratory fluctuations, which indicates the constant incorporation of bodily signals into one's engagement with the stimuli in the environment. However, the behavioural relevance of this entrainment remains unclear.

Future research: a more ecological approach to interoceptive processing

Many of the studies reviewed in this chapter show that perception, reasoning, and emotional experiences vary according to changes inside the body (e.g., heartbeats). Yet, most of this research has been conducted by: (*1*) meticulously locking the presentation of brief stimuli to distinct phases of our bodily cycles; (*2*) adopting an idiosyncratic perspective: physiological bodily signals serve "one's purposes"; or (*3*) somewhat overlooking that humans might relate to stimuli in their environment according to the processing of their physiological signals.

Active sensing paradigms tackle the first limitation (see the section above). Meanwhile, very recent work has shown that dynamic changes inside our bodies can be inferred by others (hence, unfolding a dialectical perspective; Galvez-pol et al., 2021a). Also, recent work has shown that our sense and interpretation of inner bodily signals correlate with how we seek and experience our surrounding environment (Galvez-Pol et al., 2021b). We believe that these lines of research will allow for a better understanding of the physiological mechanisms underpinning sensory processing in real-life scenarios, including work, family life, entertainment, or even art experiences.

Conclusive remarks

In recent years, the field of interoception has grown, matured, and expanded. Exponential growth in the number of studies has produced a better grasp of the relationship between the perception of the outside world and mechanisms inside the body. These studies have shown that our responses to external stimuli not only depend on the stimuli's properties but also on

our internal bodily state at the time when the stimuli are processed. Internal bodily changes (e.g., afferent signalling from the heart and stomach) moderate cognitive processes by competing for the allocation of attentional and representational resources. This in turn might dampen, enhance, or modify the processing of stimuli. While the field is still in development, more consistent methods, paradigms, and integrated theories are needed. Likewise, the consideration of various physiological systems (beyond the cardiac system, e.g., gastrointestinal, hormonal, respiratory) is a promising avenue for developing next-generation studies. Furthermore, we believe that research in interoception should advance towards a more ecological understanding of how humans function in the real world, that is, the ecological niche in which the brain has evolved. In this setting, including interoceptive signals in the study of sensory acquisition in active sensing is a fundamental step towards a more ecological understanding of exteroceptive and interoceptive processes.

Acknowledgments

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[1] *Efferent* neurons carry signals from the central nervous system (i.e., the brain) to the body's muscles, glands, and organs. *Afferent* neurons project signals from sensory receptors and the autonomous nervous system (i.e., the body) to the central nervous system.