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The functional role of cardiac activity in perception and action

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ABSTRACT

SKORA, L.I., J.J.A. LIVERMORE and K. Roelofs. The functional role of cardiac activity in perception and action. NEUROSCI BIOBEHAV REV X(X) XXX-XXX, 2022. Patterns of cardiac activity continuously vary with environmental demands, accelerating or decelerating depending on circumstances. Simultaneously, cardiac cycle affects a host of higher-order processes, where systolic baroreceptor activation largely impairs processing. However, a unified functional perspective on the role of cardiac signal in perception and action has been lacking. Here, we combine the existing strands of literature and use threat-, anticipation-, and error-related cardiac deceleration to show that deceleration is an adaptive mechanism dynamically attenuating the baroreceptor signal associated with each heartbeat to minimise its impact on exteroceptive processing. This mechanism allows to enhance attention afforded to external signal and prepare an appropriate course of action. Conversely, acceleration is associated with a reduced need to attend externally, enhanced action tendencies and behavioural readjustment. This novel account demonstrates that dynamic adjustments in heart rate serve the purpose of regulating the level of precision afforded to internal versus external evidence in order to optimise perception and action. This highlights that the importance of cardiac signal in adaptive behaviour lies in its dynamic regulation.

1. Introduction

Throughout the course of a day, the heart is likely to slow down and speed up many times – whether we wait at the traffic lights, skip a key while playing the piano, exercise, meditate, get scared or startled. The pattern of cardiac activity has long been known to vary with environmental demands, modulated by sympathetic and parasympathetic activity to accelerate or decelerate adaptively, depending on circumstances (Graham and Clifton, 1966; Obrist, 1968; Sokolov, 1963; Vila et al., 2007). In the psychophysiological literature this has been examined in various circumstances, including orientation to novel stimuli, reorienting after errors are made, and defensive responses to threat. Elegantly tuned by sympathetic and parasympathetic influences, cardiac activity adaptively shapes both perception and action tendencies.

Recent years have seen considerable advances in our understanding of the impact of internal bodily signals on a range of higher-order processes, from perception, information sampling, memory, emotion, all the way to consciousness and the sense of self (Azzalini et al., 2019; Critchley and Garfinkel, 2015; Seth, 2013). Due to the relative ease of measurement, a lot of focus has been placed on the heart as an index of autonomic function, both in terms of *frequency* patterns such as the heart rate (HR) or heart rate variability (HRV), as well as the psychological correlates of the *phases* of the cardiac cycle. The most attention has perhaps been given to the latter, with evidence showing that action, perception, and cognition vary across the phases of the cardiac cycle. Yet, a comprehensive understanding of cardiac activity (both frequency and phase) in the context of its adaptive function and importance for higher-order processes is limited.

While those two fields have largely been separate, the literatures on cardiac frequency and cardiac cycle effects can be usefully combined to inform a modern functional account of the heart's role in perception and action. Here, we provide an overview of cardiac cycle effects to show that each heartbeat produces a neural signal which interferes with

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perceptual processes, but may facilitate action. We then use examples of threat, anticipation, and error commission to show that transient cardiac deceleration serves as a way to attenuate this interference during environmentally challenging events, in order to support external perception, adaptation, and appropriate behaviour. We close by providing an account rooted in Bayesian inference, where such dynamic adjustments in heart rate serve the purpose of setting the level of precision afforded to sensory accumulation in order to optimise perception and action.

2. The cardiac cycle

The heart has a continuous oscillatory rhythm, maintained by complex electrophysiological activity. Each beat is generated by electrical impulses of the autorhythmic pacemakers, primarily the sinoatrial (SA) node and the atrioventricular (AV) node. These electrical waves are propagated in the cardiac tissue and induce contractions to eject blood into the aorta, thus regulating the heartbeat (Ma et al., 2017). The rate of oscillations – the RR or beat-to-beat interval (see Fig. 2) or, more commonly, the heart rate – is adaptively controlled to respond to changes in environmental factors and the energy demand of the body in order to maintain homeostasis (Qu et al., 2014). This adaptive control comprises of both centrally-guided feedforward regulation (e.g. stimulus-induced demands on the cardiovascular system, such as mobilisation for a fight), and feedback or reflexive regulation (e.g. changes in heart rate to adjust blood pressure) (Dampney, 2016).

Each cardiac cycle consists of two main phases: systole and diastole (see Fig. 2). At ventricular systole, the ventricles of the heart contract and the blood is ejected into the aorta. At this point, blood pressure peaks, and the stretch-responsive baroreceptors located in the vessel walls of the aortic and carotid arteries fire, signalling the timing and strength of cardiac contraction (Craig, 2009; Critchley and Harrison, 2013). As such, baroreceptor activation shows an oscillatory pattern paralleling the pulse pressure wave, with an increase in firing rate approximately 90–390 ms after the R-wave and maximal neural transmission 200–250 ms after the R-wave (Brownley et al., 2000; Dembowsky and Seller, 1995; Donadio et al., 2002; Eder et al., 2009). As a result, baroreceptor load is maximal at systole (Duschek et al., 2013). In contrast, during ventricular diastole the blood is not being ejected and the baroreceptors are inactive.

Baroreceptor signal is transmitted to the brain along the glossopharyngeal and vagus nerves, terminating at the brainstem nuclei, particularly the nucleus tractus solitarii (NTS) and the parabrachial nucleus (PBN). The NTS is the primary visceral receiving site, and a key region involved in cardiac homeostasis through controlling baroreceptor and cardiac reflexes, thus managing blood pressure and heart rate (Berntson and Cacioppo, 2007). The hypothalamus, rostrolateral ventral medulla (RVLM) and periaqueductal gray (PAG), among others, are also implicated at the early stages of autonomic control (Benarroch, 2012; Card and Sved, 2011; Cechetto and Shoemaker, 2009). The signal is further relayed to distributed subcortical and cortical regions via thalamic projections, with the hippocampus and the insular, anterior cingulate cortex (ACC), medial prefrontal and somatosensory cortices receiving the inputs, as well as other subcortical structures, including the cerebellum, hypothalamus, striatum, and the amygdala, which project to further cortical regions (Azzalini et al., 2019; Berntson and Cacioppo, 2007; Cechetto and Shoemaker, 2009; Critchley and Harrison, 2013; Oppenheimer and Cechetto, 2016; Shoemaker et al., 2012). Consequently, cardiac signals reach a broadly distributed network, including regions implicated in direct cardiac and general homeostatic/allostatic control, intermediate areas involved with interoceptive/somatovisceral representations, as well as areas classically considered to be involved in higher-order processes, such as the prefrontal cortices or the striatum.

While signalling of each heartbeat through firing baroreceptors is vital to successful up- and down-regulation of blood pressure and heart rate in response to situational demands (Stauss, 2002), this signal also

constitutes a mechanical source of noise in the brain. The heart's pulsating cycle of systole and diastole causes synchronous pulsation of the blood vessels, cerebrospinal fluid, and the brain tissue itself, observable in the electrocardiogram (EEG) (Kern et al., 2013; Stern and Engel, 1995) and magnetic resonance imaging (MRI) (Wagshul and Madsen, 2011). Each heartbeat also causes a large electrical artefact related to the muscle contraction during ventricular systole, called the cardiac field artefact (CFA), occurring concurrently with the R-peak of the QRS complex of the electrocardiogram (ECG) (Dirlich et al., 1997; Kern et al., 2013). Aside from the pulsatile movements of the blood vessels and the brain, each heartbeat also causes minuscule movements of the eyeballs, and even the entire body (Kim et al., 2016).

### 2.1. The cardiac cycle and neuronal excitability

On a functional level, early proposals suggested that oscillating cardiovascular activity also affects central cortical excitability, formulated as the baroreceptor hypothesis (Lacey and Lacey, 1958, 1970). According to this view, afferent neural signals from the baroreceptors occurring at systole attenuate cortical excitability and degrade concurrent processing in the brain, such as processing of external stimuli, independently of changes in blood pressure or blood flow Elbert and Rau, 1995 (Lacey and Lacey, 1970). This notion has been validated experimentally, showing that neck-cuff baroreceptor stimulation leads to globally reduced cortical excitability (Duschek et al., 2013; Elbert and Rau, 1995; Makovac et al., 2015; Rau et al., 1993; Rau and Elbert, 2001), and, consequently, to decreased muscle tone (Dworkin et al., 1994), dampened pain sensitivity (Droste et al., 1994), and reduced startle reflex (Nyklíček et al., 2005). This evidence suggests that baroreceptor afferents cause an attenuation of concurrent brain activity, manifested as a general inhibitory effect on neuronal excitability, in a systematic fashion (Dembowsky and Seller, 1995; Duschek et al., 2013).

Formally, neuronal excitability may determine neural gain linked to sensory responses (Kolasinski et al., 2017). Gain refers to the mapping between input and output (I/O) signals, corresponding to the probability or strength of output given an amount of input, and is frequently modelled using a sigmoidal function (see Fig. 1). This function models properties of individual neurons, ensembles and entire regions of the brain (e.g. in cortical excitability). The slope of the I/O function corresponds to a (multiplicative) gain on the input – increased gain manifests in increased output for high-strength input, and conversely, decreased output for low-strength input – a more deterministic (less stochastic) mapping between input and output.

Gain modulation is a property of neural firing, but directly translates into a computational account of sensory processing – increased gain means that processing of attended or salient stimuli is boosted, while that of unattended or non-salient ones is attenuated (Eldar et al., 2013). At a whole-brain level, gain modulations may act across sensory modalities in this manner (e.g. enhancing high-precision exteroceptive sensory signals while attenuating low-precision interoceptive ones). In this mode of action, gain modulation is critical for flexible and adaptive neural responses to ever-changing inputs, and might contribute to attention, learning, sensory processing, and multimodal integration (Ferguson and Cardin, 2020). Consequently, the inverse relationship found between baroreceptor activity and cortical excitability may reflect a modulation of global gain, and thus the contrast between low and high-signal modalities, or modulation of the strength of the internal signal and thus the balance of exteroceptive and interoceptive signal precision. This latter mechanism is explored further in Section 4.

2.2. Correlates of the cardiac cycle

Recent evidence points to a differential effect of the cardiac phases on a host of higher-order processes, largely in line with the predictions of the baroreceptor hypothesis. Presentation at systole (where baroreceptor load is maximal), compared to diastole (when they are quiet) has
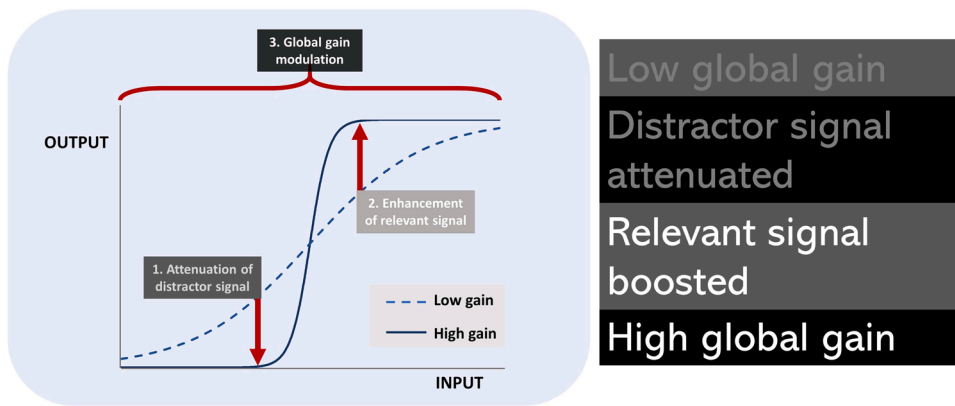
Fig. 1. Left: Gain control and output. Output strength and stochasticity can be altered through (1) attenuation of irrelevant signal, (2) enhancement of relevant signal, or (3) increase in global gain (acting as both 1 and 2) – where relevance is ultimately shaped by fitness demands of the organism's current internal and external environment. Right: illustration of gain through image contrast. Low gain results in lower salience of the signal (here, the words), making discrimination of signal from irrelevant background (respectively the text and the box, both shades of grey) more difficult. The middle two boxes show examples of attenuated background (black box, grey text) and boosted signal (grey box, white text), both of which increase the contrast and the ease of discriminating signal. Finally, in the case of high gain, both sides are modulated in such a way that

contrast is at a maximum (black box, white text), and the problem is easiest.

been shown to attenuate stimulus detection and perception across visual, auditory, and sensorimotor domains (Al et al., 2020; Cohen et al., 1980; Edwards et al., 2009; Grund et al., 2021; Motyka et al., 2019; Salomon et al., 2016; Sandman, 1984; Saxon, 1970; Walker and Sandman, 1982), memory for words (Garfinkel et al., 2013), pain perception (Edwards et al., 2001; McIntyre et al., 2008; Wilkinson et al., 2013), and startle responses (Schulz et al., 2009a, 2009b, 2020). Early EEG evidence also showed attenuated auditory and visual potentials at systole, proposed to reflect dampened attentional processing (Sandman, Walker, and Berka, 1982; Walker and Sandman, 1982). However, contrary results have been reported for visual selection, where the selection efficiency of target among distractors and attentional inhibition of masking stimuli appear enhanced at systole compared to diastole (Pramme et al., 2016, 2014). The evidence around emotional perception is also mixed – while Garfinkel and colleagues (Garfinkel et al., 2014) found that both detection and rated intensity of fearful face images were enhanced at systole, a later study by Leganes-Fonteneau et al. (2020) also showed increased rated intensity but a reduction in visual search accuracy for fearful faces (although an increased accuracy for happy and disgust expressions). Nonetheless, it has been noted that affective value of the stimuli may modulate their relationship with cardiac phase (Allen et al., 2019). As such, those findings point to most forms of non-affective perception being negatively affected at the time of heightened neural noise associated with each heartbeat (systole), compared to a relative improvement in processing at diastole, when the noise is reduced.

While stimuli in the environment do not naturally occur in a manner time-locked to the phases of the cardiac cycle, self-paced or exploratory behaviours also appear to be differentially affected by systole and diastole. Systole is associated with more spontaneous active movements, including a greater number of saccades compared to fixations, which occur predominantly at diastole (Galvez-Pol et al., 2020; Ohl et al., 2016). Similarly, self-paced exploratory actions occur more at systole than diastole (Kunzendorf et al., 2019; Palser et al., 2021, but see Herman and Tsakiris, 2020). However, the enhancing effect of systole has not been found in a reward-guided information sampling (Herman and Tsakiris, 2021), implying that the facilitatory effects of systole may have more to do with spontaneous motor activity or active, rather than passive, sensory sampling (this may also explain previously mentioned enhanced selection accuracy among distractors during systole; Pramme et al., 2014). Supporting this notion, systole is also associated with stronger hand muscle activity in a pinch task (Al, Stephani et al., 2021), enhanced inhibitory motor control (Rae et al., 2018), as well as enhanced rifle shooting performance (Konttinen et al., 2013). Indeed, corticospinal and motor excitability has been found to be higher during systole than diastole (Al et al., 2021; Potts and Li, 1998). Those results suggest that the systolic phase may be conducive to action over

perception.

Together, the cardiac cycle literature suggests that systole – the period associated with elevated baroreceptor noise– may impair exteroceptive processing across multiple domains, but enhance action. Conversely, diastole – the quiet baroreceptor period – is associated with reduced action and active sensory sampling, but enhanced perceptual processing, relative to systole. This dissociation may reflect the relevance of baroreceptor signal for perceptual versus active processes, with cortical/motor excitability arbitrating between perception and action through dynamic changes in gain. Importantly, any increase in heart rate is equivalent to an increase in the baroreceptor firing rate and the associated attenuation in cortical excitability, while a decrease in heart rate is associated with a reduced occurrence of baroreceptor noise. This raises the natural question of whether and how this oscillatory pattern and its consequences affect perception and behaviour in natural, extended (i.e. not time-locked) settings.

3. Transient changes in heart rate in adaptive behaviour

Beside heart phase, heart frequency plays a role in perception and adaptive behaviour. In what follows, we briefly describe three phenomena characterised by transient slowing of heart rate (bradycardia): threat-related, anticipation-related, and error-related deceleration. The phenomena provide a useful illustration of adaptive, context-dependent adjustments in cardiac activity. While there has been little research into the functional overlap between them, all manifest in situations requiring enhanced attention to salient events (e.g. external stimuli or own errors) and adaptive adjustments to ongoing behaviour. Crucially, all three are characterised by transient changes in heart rate, with an initial deceleration in response to the salient event, followed by acceleratory recovery, as well as increases in arousal indexed by elevated skin conductance and pupil dilation. This pattern is brought about by parasympathetic and sympathetic activity, operating reciprocally in line with situational demands (Berntson et al., 1993).

3.1. Threat-related cardiac deceleration

Cardiac deceleration in response to threat has been observed in numerous studies in both human and non-human species (for reviews see Livermore et al., 2021; Roelofs, 2017; Vila et al., 2007). It is particularly associated with more distal threat (therefore permitting a greater length of time to choose appropriate actions; Blanchard et al., 2011; Mobbs et al., 2015). Aside from parasympathetically-driven cardiac deceleration, threats cause a co-activation of the sympathetic branch, reflected in increased skin conductance, pupil dilation, and muscle tone, as well as the subsequent heart rate acceleration when the

action decision is made (Hashemi et al., 2019; Klaassen et al., 2021).

Crucially, the magnitude of threat-related deceleration is associated with enhanced information processing and action preparation (Hashemi et al., 2019; Klaassen et al., 2021; Lojowska et al., 2015). Considering the strong selection pressures associated with threat, the enhanced capabilities for preparing and executing effective responses to threat during cardiac deceleration, and the evolutionarily-conserved nature of this response, this naturally implies an adaptive function for cardiac deceleration.

3.2. Anticipation-related cardiac deceleration

Cardiac deceleration has also been observed during anticipation or preparation in non-threatening scenarios, for example following a cue indicating imminent appearance of a stimulus or necessity for a response. Such alerting stimuli induce attentive anticipation, a state characterised by physiological changes reflected in cardiac deceleration, in addition to pupil dilation, skin conductance response, and changes in respiration, spinal reflexes, muscle activity, and electrical potentials (for a review, see Jennings and van der Molen, 2005). Anticipation has been proposed to combine the alerting, orienting, and executive inhibitory functions, acting to inhibit competing processes in the face of an anticipated stimulus in order to prepare the organism for potential response (Jennings and van der Molen, 2005; Jennings et al., 2009; van der Veen et al., 2000).

Behaviourally, the state of attentive anticipation has been related to preparation for action (in this sense, threat-related deceleration could be considered as a subset of this state). Anticipatory heart rate deceleration was found to positively correlate with reaction times (Jennings et al., 1998; Reyes Del Paso et al., 2015), and increased with increasing task complexity (Ribeiro and Castelo-Branco, 2019). Those results suggest that response efficiency is related to the magnitude of inhibitory activity, indexed by cardiac deceleration. Importantly, subsequent action execution – a removal of the inhibitory brake – immediately elicits cardiac acceleration (Jennings & Wood, 1977).

3.3. Error-related cardiac deceleration

Error-related deceleration has been observed to follow immediately after an error in performance (e.g. erroneous approach or perceptual decision), where the heart decelerates more in response to negative feedback than to positive feedback, which elicits faster recovery (Crone et al., 2005, 2003; van der Veen et al., 2004). This error-related deceleration is initiated in anticipation of feedback delivery and continues until after feedback is presented. Importantly, this response is only observed when the feedback carries valid, reliable information about performance accuracy – that is, when the stimulus reliably predicts the outcome, and the feedback reflects the match or mismatch between the actual and expected outcome (Crone et al., 2003; Mies et al., 2011; Skora et al., 2022).

Errors in performance are salient events, which may carry information important for fitness or survival. The accompanying cardiac deceleration is a part of a larger suite of error-related autonomic responses, including elevated skin conductance response (Hajcak et al., 2003) and pupil dilation (Critchley et al., 2005), as well as its electrical signatures, the error-related negativity (ERN or Ne) and positivity (Pe) components in electroencephalography (EEG) (Falkenstein et al., 2000; Overbeek et al., 2005; Walsh and Anderson, 2012). Together, they have been proposed to reflect an internal performance monitoring mechanism (Hajcak et al., 2003; Ullsperger et al., 2014), responding to errors in performance as salient events which necessitate orienting the agent and its internal resources in service of behavioural adjustment.

4. Transient cardiac deceleration as a means for attenuating cardiac signal

The three phenomena outlined above illustrate the adaptive value of cardiac deceleration: it occurs during highly salient events, when it is imperative for the organism to orient attention to the external world in order to process the stimulus and its properties, and prepare or adjust behaviour. This notion features in the early cardiac reflexes literature, for example formalised by Lacey and Lacey (, 1970, 1978) as the intake-rejection hypothesis, where cortical excitation/inhibition is modulated by down- or up-regulation of cardiac activity in order to engage or disengage, respectively, with salient stimuli. We highlight that this phenomenon can be understood in terms of adaptive precision modulation under a Bayesian inference approach such as predictive processing, a process theory fruitfully applied to various domains of brain function (Hohwy, 2020). Under this account, cardiac deceleration is a means of adjusting precision of sensory evidence accumulation relative to precision of bodily information, in order to allow the brain to 'work around' the oscillating cardiac signal, and optimise perception and action.

4.1. Physiology of cardiac deceleration

For the purpose of maintaining homeostasis, a continuous stream of information (whether directly perceived or not) communicates the ongoing state of the body to the brain, such as temperature, blood pressure, hydration, or hunger. This stream constitutes internal sensory data important for the survival and fitness of the organism. Consequently, internal sensory data provides a strong anchor determining the processing of external stimuli. Typically, this is an appropriate state of affairs – behaviour can be quickly and efficiently guided to satisfy homeostatic needs, such as finding a pizza irresistible when the blood sugar level is low, but less so when not. Similarly, the cardiac cycle effects outlined earlier illustrate how a natural internal fluctuation can differentially affect not only perception, but also broader cognition and action (see Fig. 2). However, this bodily influence might not always be desirable – for example, in situations where enhanced, unbiased processing of the external world is paramount. The three phenomena outlined earlier are precisely such cases.

One interpretation of cardiac deceleration observed following a threatening stimulus, an anticipatory signal, or one's error in performance, is that it occurs in order to attenuate baroreceptor noise associated with each heartbeat, and thus allows for enhanced processing of the stimulus or preparation/adjustment of action. Similar versions of this idea have been argued by Lacey and Lacey (e.g. 1970), Jennings (1992), and Gray (1982). In order to remove the noise interfering with external perception, the brain slows down the heart, thus reducing the frequency of noisy events – the beats themselves. Physiologically, this is achieved by applying a parasympathetic brake, which rapidly slows down the heart rate (Roelofs, 2017). Once this need is satisfied and it is time to act, parasympathetic withdrawal causes sympathetically-driven cardiac acceleration. Notably, in the absence of the parasympathetic brake, sympathetic arousal signatures may serve as evidence that the stimulus requires immediate action rather than enhanced information gathering, potentially leading to premature or non-optimal action.

Understanding the neuromodulatory mechanisms of autonomic processes may provide insight into their functional roles – while a full treatment of neurotransmitter pathways is beyond the scope of this paper (see Roelofs & Dayan, 2022, for a comprehensive discussion), key functional overlaps are apparent. Autonomic responses are controlled chiefly by cholinergic (parasympathetic) and noradrenergic (sympathetic) pathways, connecting forebrain areas (including ACC and amygdala) with brainstem areas (including PAG, NTS, and RVLM) and onwards to the rest of the body (Benarroch, 2012; Card and Sved, 2011; Roelofs & Dayan, 2022). Importantly, both neurotransmitters are considered integral to neuromodulatory control of gain for optimal
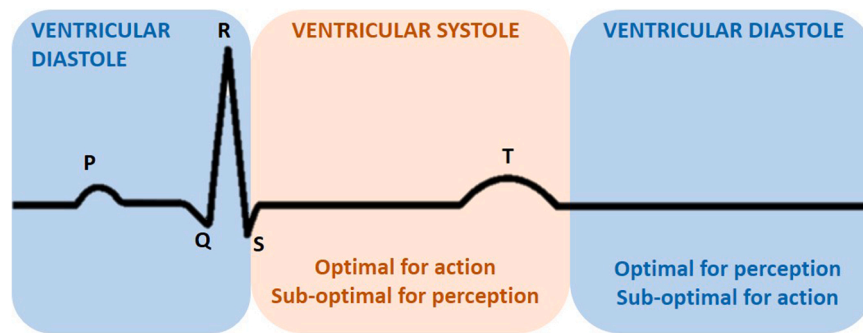
Fig. 2. Schematic illustration of one cardiac cycle and its two main phases, ventricular systole and diastole. The letters indicate the peaks observable in an electrocardiogram, with the R-peak indicating the beat.

control of precision in sensory processing – specifically, gain enhancement (Ferguson and Cardin, 2020; Kang et al., 2014; Moran et al., 2013; Servan-Schreiber et al., 1990; Warren et al., 2016). Thus, the phasic activation of both branches of the ANS can be seen as attuning the brain towards enhanced processing of the sensory environment – succinctly resolving the apparent paradox of heart rate decreases accompanying skin conductance and pupil dilatory increases during threat and error-monitoring, despite activity in each branch being generally reciprocal (Weissman and Mendes, 2021). While it should be noted that centrally-modulated sensory gain does not necessarily imply peripheral involvement, the robust co-occurrence of autonomic activity and sensory upregulation, together with common substrates and functional requirements (during the critical periods for sensory processing that we consider here) are strongly suggestive of an integrated control process using acetylcholine and noradrenaline as its principal modulators.

4.2. Bayesian inference and precision weighting

Under predictive processing, information about the world arriving through the senses is continuously interpreted in relation to prior expectations about its causes. The causes are inferred through a probabilistic process, proposed to operate on the principles of Bayesian inference, where incoming sensory information from multiple modalities (understood as statistical likelihood) is combined with the prior predictions to arrive at a best guess (posterior prediction) of the causes of that information (Clark, 2013; Hohwy, 2020). Biologically, predictions are encoded by probabilistic generative models within cortical hierarchies, whereby models at higher (more abstract) levels generate predictions about the content of lower levels (e.g. perceptual features). Incoming sensory signals are compared against these descending predictions to give rise to predictions errors (PEs) at each level of the processing hierarchy, indicating the degree of mismatch between predicted and actual input. PEs are then passed up the hierarchy, allowing to update the higher-level predictions, corresponding to perceptual inference (Kanai et al., 2015; Rao and Ballard, 1999). Alternatively, PEs can be actively minimised by executing an action to change the sensory input to match the predictions, corresponding to active inference, or interoceptive inference in the internal domain (Friston, 2009).

This process is optimised by precision weighting. Precision refers to the reliability assigned to incoming sensory signals or to the prior belief (in statistical terms, it is the inverse variance of the probability distribution – highly precise distributions have little variance). Precision-weighting regulates the interaction between top-down and bottom-up signals, as well as between sensory modalities, such that the inference process is dominated by the signal that is attributed higher reliability and contains less noise (Ernst and Banks, 2002; Shams and Beierholm, 2010; Yon and Frith, 2021) (see Fig. 3). For instance, salient sensory inputs assigned high precision would induce stronger prior belief updates, thus dominating the resulting percept. Conversely, if the prior expectation is assigned higher precision than the sensory stream, it will
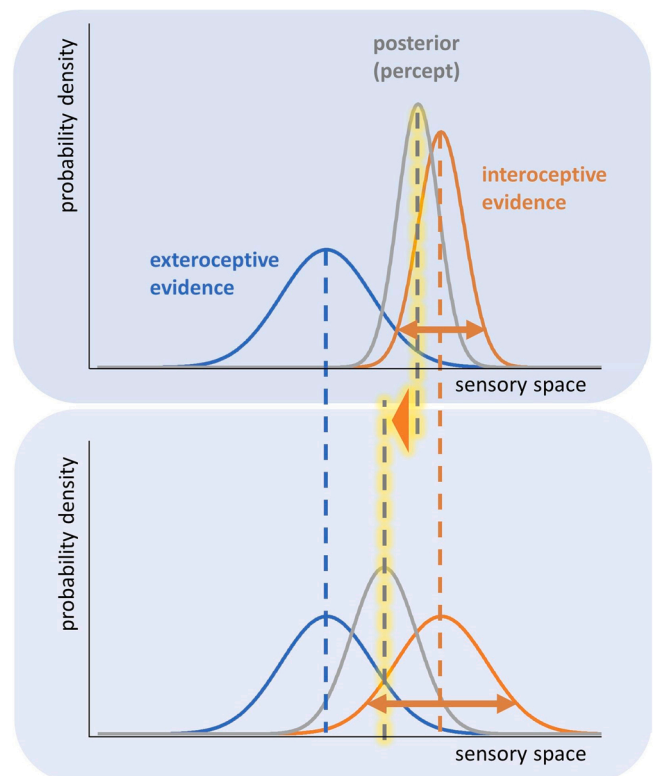
Fig. 3. Two examples of precision weighting. In both diagrams, sensory evidence from interoceptive and exteroceptive signals is combined to form a percept of the situation faced by the organism and determine action tendencies (priors would also be present but are omitted for simplicity). (1) In the upper diagram, the interoceptive signal is afforded a high level of precision, and thus exerts a greater influence than the exteroceptive signal on the resulting percept. An example could be where, in a state of high arousal, one perceives an ambiguous sound as a thief breaking in through the downstairs window, rather than a more likely and less emotionally-weighted scenario, such as the wind moving the window panes. (2) In the lower diagram, the signals are weighted equally and thus exert the same influence. Here, through lowering the interoceptive precision, the percept is steered back towards the exteroceptive channel and further information gathering. Note that the mean of each distribution remains the same in both diagrams: the only change is to the precision, but the percept shifts as a result.

be less affected by the incoming PEs, and will exert a stronger influence over perception. Effectively, precision modulation allows the brain to optimally select the sources of information which should be afforded greater relevance, such that only precise evidence is assimilated at higher-order levels (Kanai et al., 2015). Precision-weighting may be altered either by bottom-up characteristics of the sensory signal (i.e. if it

has a more or less precise distribution), by attention to the signal (an issue we will return to), or by prior predictions coding for the *expected* precision of a given sensory channel, reflected the expected reliability of sensory information over longer timescales (an issue we will not engage with here, but see Allen et al., 2020; Allen et al., 2021; Nikolova et al., 2021). Biologically, precision has been proposed to be encoded by synaptic gain or excitability (post-synaptic responsiveness) of neurons reporting the bottom-up signal (PEs) (Friston, 2008; Moran et al., 2013). Effectively, precision corresponds to gain control in information passing between the levels of the cortical hierarchy (Kanai et al., 2015).

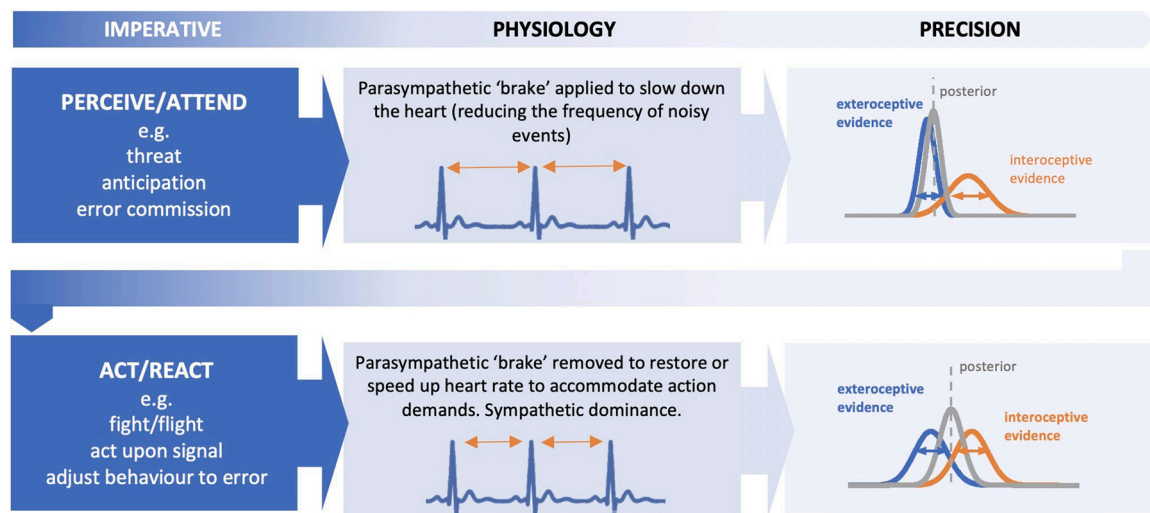### 4.3. Precision adjustment through cardiac regulation

Formally, predictive processing approaches to homeostasis propose that homeostatic loops are controlled by interoceptive inference. Ascending internal signals communicate internal PEs, which are met by top-down hierarchical predictions reflecting the expected state of the organism, where the lower levels provide homeostatic set-points, and the progressively higher levels integrate the interoceptive, proprioceptive and exteroceptive information (Gu and Fitzgerald, 2014; Seth, 2013; Seth and Friston, 2016). Autonomic effectors can be engaged to actively minimise interoceptive PEs, corresponding to low-level homeostatic control (for example, adjusting blood pressure or mobilising glucose reserves if they deviate from their set-points). The higher-level predictions, in contrast, are gradually more removed from the lowest-level sensory information, reflecting longer-term predictions of the interaction between the organism and its environment, allowing for predictive control of homeostatic parameters known as allostasis (for example, engaging with the world to cook a meal before glucose level falls).

This brings us to the key point of our proposal. The adjustment in heart rate allows the brain to set the appropriate level of precision of external evidence accumulation, relative to the precision of the internal signal. When the situation demands high perceptual sensitivity (e.g. accurate visual perception), the relevant sensory channel is assigned high precision, while the precision of the cardiac channel is reduced in order to attenuate the impact of each systole on concurrent processing (see Section 2.2 and Fig. 4). Consequently, the exteroceptive, as opposed to the interoceptive, channel dominates the resulting inference.

Biologically, the parasympathetically-driven reduction in the frequency of baroreceptor events allows exteroceptive (e.g. visual) channels to become more excitable, and therefore more susceptible to external inputs, supporting enhanced attentional/perceptual performance. This account is consistent with the proposals that gain modulation controls precision assigned to PEs competing to update higher-level predictions, permitting the brain to tune into situationally relevant inputs (Feldman and Friston, 2010; Kanai et al., 2015; Moran et al., 2013). Under this view, precision is encoded in terms of excitability of the regions reporting the ascending signal, where higher gain translates into higher precision on the corresponding sensory channel.

Conversely, when the situation demands a shift to action, and rapid, accurate perception is less important, exteroceptive channels no longer need to be assigned higher precision relative to cardiac information. Consequently, the dynamic attenuation of heart rate is no longer required to control assigned precisions through dynamic attenuation of gain. Parasympathetic withdrawal then allows for heart rate acceleration to fulfil action demands, including fight, flight, or behavioural adjustment (see Fig. 4). This very pattern – cardiac deceleration followed by acceleratory recovery – is observed in the three phenomena above. In this fashion, cardiac activity can be dynamically regulated in order to adjust the precision of evidence accumulation when appropriate. Effectively, the brain 'works around' the continuously oscillating cardiac signal to optimise perception and action through a precision-weighting mechanism.

Fig. 4. Illustration of the proposed mechanism for the functional role of cardiac signal in adaptive perception and action. To satisfy perception/attention to the external world, such as in cases of threat-, anticipation-, and error-related deceleration, the parasympathetic brake is applied to dynamically slow down the heart rate, thus reducing the frequency of noise-inducing events (baroreceptor activity upon each heartbeat). This allows the brain to set the precision level appropriately, reducing the impact of interoceptive signalling on perception. As such, enhanced precision of exteroceptive evidence is what underlies the instances of enhanced perception reviewed in text. Conversely, when the perceive/attend imperative is satisfied and it is time to act, the parasympathetic brake is removed to restore or accelerate the heart rate to furnish action demands. Importantly, the precision modulations are not fully symmetrical – interoceptive signal is not automatically prioritised

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Indeed, computational models of synthetic cardio-visual integration under an active inference scheme show exactly such attenuation of perceptual sensitivity at each systole (Allen et al., 2019), with context (e. g. relaxed or aroused state) further modulating the need to up- or down-regulate precision of sensory evidence accumulation. Furthermore, empirical evidence to support such an interaction between cardiac deceleration and visual sensitivity was recently provided in an elegant study showing that cardiac deceleration tracks active attention in a binocular rivalry task (Corcoran et al., 2021).

This account is also consistent with evidence showing that attentional processes are typically accompanied by heart rate deceleration, with more attention-demanding or complex task eliciting greater deceleration (De Pascalis et al., 1995; Dehais et al., 2011; Salvia et al., 2012; Zimmer et al., 1990). As mentioned earlier, attention was proposed to constitute a mechanism to increase the relative precision of sensory evidence on the attended sensory channel (Feldman and Friston, 2010). As such, the present account is able to accommodate this evidence in a common scheme – cardiac deceleration accompanies enhanced attention to external stimuli to allow for enhanced precision of sensory evidence associated with the attended sensory channel.

The framework can also provide insights into phenomena characterised by a reduction in perceptual or behavioural performance, such as inattentional blindness/deafness (failure to perceive an unexpected stimulus when attention is engaged elsewhere), mind-wandering (decoupling of attention from processing external or relevant information), or maladaptive perseveration (continuing a response after original stimulation ceases, rendering it irrelevant to the stimulus). In line with the theoretical predictions, those phenomena show an opposing pattern of cardiac activity, with elevated heart rate, as well as heightened alpha power, linked to an impairment in perceptual efficacy or adaptation (for a review, see Dehais, Lafont, Roy, and Fairclough, 2020).

5. Outstanding questions and concluding remarks

The picture emerging from this analysis is that the importance of cardiac signal in adaptive behaviours lies not in the signal itself, but rather in its dynamic regulation. Cardiac deceleration is a reflection of a centrally-driven mechanism geared at reducing the influence of internal signal affecting external processing when efficient exteroception is paramount. This is likely to occur through dynamic and selective modulations in neuronal excitability. We propose that this is achieved in order to adaptively control the level of precision attached to external versus internal information on the principles of precision-weighing under Bayesian inference.

This perspective can provide insight into the general functional involvement of bodily signals in adaptive behaviour, and may be applied to other types of rhythmic bodily activity. Incoming evidence in the domain of respiration shows that perceptual and active processes may be similarly tuned to the respiratory stages of inspiration and expiration, with stronger respiratory phase-locking related to better somatosensory detection performance (Grund et al., 2021) and motion tracking (Takagi et al., 2020), as well as more frequent action initiation during expiration (Park et al., 2020). Another candidate are gastric waves. While respiration is known to be (to some extent) coupled with the heart (Berntson et al., 1993), gastric waves vary based on the current state of the stomach, so it is conceivable that their effects could vary in a similar fashion, i.e. through up- or down-regulation in line with context.

Early evidence from the respiratory domain also points to the coupling between the respiratory cycle and alpha frequency, which may reflect a gating mechanism for optimising exteroceptive processing around the periodic internal signal (Kluger et al., 2021; Varga and Heck, 2017). Oscillatory activity in the alpha frequency range (8–12 Hz) has been proposed to selectively inhibit cortical regions (Hindriks and van Putten, 2013; Jensen and Mazaheri, 2010) – neural deactivation or

inhibition is associated with higher alpha power, while high excitability is linked to low-amplitude alpha oscillations. Alpha-driven inhibition may serve to modulate the system's performance around irrelevant or periodic inputs, such as the oscillatory baroreceptor signal, although this assumption remains to be directly investigated. Nonetheless, recent evidence shows that respiration – itself an internal oscillatory signal – modulates both alpha power and perceptual sensitivity, in line with the notion that internal signals may recruit gating mechanisms to optimise processing in periods of lower or higher excitability (Kluger et al., 2021). Similarly, higher alpha power has been positively associated with respiratory sinus arrhythmia, the variation in heart rate during the respiratory cycle (Duschek, Wörsching, and Reyes del Paso, 2015). Finally, phase-amplitude coupling has also been found between alpha activity and slow gastric rhythm (Richter et al., 2017). Further investigation into neural oscillations coupled to the heart or other internal fluctuations may provide fruitful insights into the functional brain-body interaction.

From a perceptual perspective, while there is ample research into attention and visual processing during cardiac deceleration (especially in threatening scenarios), such evidence is limited for error-related processing, as well as for other perceptual domains (e.g. auditory). The predictive processing-rooted account also opens the door to computational treatment of evidence accumulation during cardiac deceleration and acceleration across the sensorium, as well as its relationship with adaptive learning and decision-making. Together with growing empirical and theoretical literature in interoception, a closer investigation of how the dynamic regulation of bodily signals adaptively shapes information processing can contribute to a fuller understanding of the mechanics and computations behind the brain-body interaction.

Declaration of interest

Acknowledgements

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