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Review Article

Arousal coherence, uncertainty, and well-being: an active inference account

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Abstract

Here we build on recent findings which show that greater alignment between our subjective experiences (how we feel) and physiological states (measurable changes in our body) plays a pivotal role in the overall psychological well-being. Specifically, we propose that the alignment or 'coherence' between affective arousal (e.g. how excited we 'feel') and autonomic arousal (e.g. heart rate or pupil dilation) may be key for maintaining up-to-date uncertainty representations in dynamic environments. Drawing on recent advances in interoceptive and affective inference, we also propose that arousal coherence reflects interoceptive integration, facilitates adaptive belief updating, and impacts our capacity to adapt to changes in uncertainty, with downstream consequences to well-being. We also highlight the role of meta-awareness of arousal, a third level of inference, which may permit conscious awareness, learning about, and intentional regulation of lower-order sources of arousal. Practices emphasizing meta-awareness of arousal (like meditation) may therefore elicit some of their known benefits via improved arousal coherence. We suggest that arousal coherence is also likely to be associated with markers of adaptive functioning (like emotional awareness and self-regulatory capacities) and discuss mind–body practices that may increase coherence.

Keywords: Arousal; Coherence; Active Inference; Interoception; Affect

Introduction

Under the active inference framework (Friston 2010, 2013), survival is achieved through inferences about the causes of sensations and about how to optimally act in order to maintain preferred states. The ability to detect changing levels of uncertainty in these inferences is critical for optimally adapting and learning in dynamic environments (Note: For the brain, the environment includes both the body and the external world.) In the present paper, we discuss how subtle changes in our bodies [measurable changes in autonomic nervous system (ANS) arousal, like heart rate and pupil dilation] and interoceptive inferences thereof relate to changes in uncertainty. We suggest how that (interoceptive) integration of these signals, particularly in affective arousal and meta-awareness of arousal, may impact our capacity to optimally adapt and thrive.

Interoception refers to the bidirectional relationship between the brain and the body through which an organism senses, interprets, and integrates signals from within itself (Desmedt et al. 2023). It is argued to be the foundation of both mental and physical health (Tsakiris and Critchley 2016, Khalsa et al. 2018, Quadt et al. 2018, Herbert et al. 2020). Recently cast in terms of active inference (Barrett and Simmons 2015, Allen and Friston 2018), interoception (i.e. perceiving embodied conditions) and allostasis (i.e. adaptively enacting embodied changes) have been proposed to be inextricably linked, at the very core of the brain's inferential processing (Kleckner et al. 2017, Katsumi et al. 2022). To put it simply, whatever else your brain is doing it is also regulating and tracking the (inferred) states of your body (i.e. your ANS, among other systems; Barrett 2017), and these inferences contextualize other inferences, like what we attend to or are motivated toward. As we will discuss later, inferences about allostatic-interoceptive conditions and rhythms may also be central to how changes in uncertainty are processed in the brain–body system (e.g. Allen 2020, Allen et al. 2020, 2022).

Most interoceptive-allostatic processing happens outside conscious awareness. For example, you do not need to be aware of your ANS for it to keep beating your heart. At the conscious level, what we need mostto know about allostatic-interoceptive inferences (i.e. anticipated consequences for allostasis) are proposed to be mostly experienced implicitly, as changes in lower-dimensional

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affects (Barrett 2017). Affects, typically (but not exclusively; e.g., Panksepp 2011, Solms and Panksepp 2012.) described in terms of feelings of pleasure or displeasure (valence) and high or low arousal, are basic features of consciousness (Wundt 1902, Damasio 1999). They have long been considered some form of mental 'representation' of bodily signals (James 1884, Wundt 1902, Barrett and Russell 1999, Damasio et al. 2000, Barrett and Simmons 2015, Seth and Friston 2016), though the exact relationship remains subject to debate. Under recent active interoceptive inference accounts, affect is thought to guide the predictive system (via precision weighting) to improve; by representing anticipated consequences for allostatic efficiency (Barrett and Simmons 2015, Seth and Friston 2016, Barrett 2017) or fluctuations in error dynamics (Kiverstein et al. 2020), inferences about valence (basically, confidence in how well your system thinks it is set up to handle life; Hesp et al. 2021) can guide gradual overall model improvement across time. While these formulations of affect as inference focus primarily on valence, here we focus on arousal.

Affective arousal is a low-dimensional inference, phenomenologically felt as low or high energy, activation, and/or tension. It can be either pleasant or unpleasant and inform higher-level inferences, for example in the 'construction' of emotional experience (Barrett 2017). As we will discuss later, affective arousal is suggested to serve orienting function, responding to important error signals, and shaping how much they are felt/integrated into conscious affective feelings (Solms and Friston 2018). For example, we can see this in the bidirectional information flow between heart and brain during emotional processing. After initiating the experience, the coupling of heart and brain activity—particularly ascending heart-to-brain signalling—is moderated by self-reported affective arousal (Candia-Rivera et al. 2022). At least in emotional experiences, confidence (precision) over signals arising from the ANS may be modulated by affective arousal.

Autonomic arousal refers to changes in the activation of the ANS, mediated by both sympathetic and parasympathetic branches of the ANS. For example, pupil dilation is impacted by both the pupil sphincter, under parasympathetic control, and the pupil dilator, under sympathetic control (Barbur 2003). In this paper, we refer to increasing autonomic arousal, without specifying whether the increase is driven by increasing sympathetic or decreasing parasympathetic tone. Under Active Inference ANS states are hidden to the brain, both inferred and enacted through a veil of inferences. As we will discuss, changes in uncertainty are inherently impacted by and reflected in the hidden dynamics of the ANS e.g., pupil dilation trackstrial-by-trial changes in prediction errors, environmental volatility, and learning rates; Nassar et al. 2012, Browning et al. 2015, Lawson et al. 2017), and inferences thereof. The extent to which arousal responses track changes in uncertainty also predicts better ability to learn in dynamic environments (de Berker et al. 2016). Uncertainty defines the degree of confidence (or precision; Feldman and Friston 2010) with which a prediction can be made, based on available information, and it determines when to update beliefs. Accurately inferring the dynamics of the ANS may help the system to represent, respond to and enact changes in uncertainty (cf. interoceptive self-inference; Allen et al. 2020), and to learn the statistical regularities (in its predictive model) of the environment more optimally.

Changes in uncertainty also play a fundamental role in driving affective arousal (Majumdar et al. 2023), and here, we unpack whether the capacity to accurately represent and account for changes uncertainty dynamics in higher affective arousal may involve interoceptive inferences over autonomic arousal. Though the exact nature of the relationships between autonomic and affective arousal is a matter of debate, they do tend to covary, and there does appear to be a privileged relationship between them. For example, emotions associated with high affective arousal relate to increases in autonomic arousal (i.e. increased heart rate; Ketonen et al. 2023), regardless of their valence (Kreibig 2010). It is also clear that beliefs (about affective and interoceptive states) impact this relationship. For example, self-reported affective arousal is better predicted by beliefs about interoceptive states (e.g. beliefs about heart rate) than actual physiological (autonomic) changes (Blascovich 1990, 1992, Wild et al. 2008, Trotman et al. 2019). Through precision optimization, affective arousal is likely to play a role in integrating ('optimizing') interoceptive inferences about autonomic arousal.

We will suggest that inferred affective arousal informs inferences about inferred physiological arousal, and vice versa, and that this relationship plays a role in the brain's capacity to track changing levels of uncertainty and to harness these changes in adaptive updating of model beliefs. Practically speaking, dysfunction in the coupling between autonomic arousal and affective arousal may reflect a wider dysfunction in representing changing levels of uncertainty, leading not only to learning deficits but also to emotional dysfunction.

Dysfunctional interoceptive beliefs—particularly an inability of the brain to update its beliefs about the body in the face of errors—have previously been proposed as an important transdiagnostic factor within mental and emotional disorders (Paulus et al. 2019, Smith et al. 2020a). In the present paper, we look deeper at the role that affective arousal may play in the ability (or inability) to update beliefs about the body in the face of change and the implications of this ability for adaptive functioning and other indicators of well-being. We also extend our understanding of arousal to incorporate the implications of meta-awareness, and how a higher level of self-reflective awareness of changes in felt affective arousal, may impact awareness, regulation, and ultimately coherence between lower-level representations of arousal.

Please note we are not saying that autonomic arousal is 'necessary' for self-reported affective arousal and nor does autonomic arousal account for 'all' changes in self-reported affective arousal. The same is also true—though perhaps more obviously—in reverse. Changes in affective or meta-awareness of arousal are neither necessary for, nor account for, all changes in autonomic arousal. For example, changes in affective arousal can be felt even when changes in autonomic arousal are pharmacologically suppressed (Ali et al. 2017). However, critically, this pharmacological suppression also blocks pupillary and cardiac responses to changes in uncertainty, increases the effects of prior beliefs on behaviour, and reduces learning when the environment changes (Lawson et al. 2021). We will argue that the strength of the relationship between changes in self-reported affective and autonomic arousal is reflective of a kind of 'affective-interoceptive integration' and plays an important role in adaptive learning under conditions of changing uncertainty. On the other hand if affective arousal is not informed by physiological arousal, then affective inferences will be unable to optimally adapt to changes in uncertainty dynamics.

We begin with an informal (non-mathematical) introduction to the active inference framework, with an emphasis on the embodiment of survival imperatives and on the optimization of uncertainty in interoceptive inferences. We discuss recent literature highlighting that uncertainty (or its inverse, precision) is both impacted by and estimated according to changes in autonomic arousal conditions. We then discuss affective arousal, in terms of its impact orienting feelings, through belief updates in response to changes in uncertainty. We then extend these two levels of arousal to include a third level, namely, meta-awareness (cf. Schooler et al. 2011, Sandved-Smith et al. 2021) of arousal. Experience (i.e. feeling affective arousal) is not necessarily the same as being able to access or report on that experience (Amir et al. 2023). The capacity to report on experiences of affective arousal entails this higher (meta-aware) level of inference 'about lower-level arousal'. Because these high-order inferences are also informed by inferences about the contextual and learned reliability of affective and downstream autonomic signals, meta-awareness may be more or less attuned with actual changes in lower-order arousal. Meta-awareness both determines (controls) and is determined by (emerges from) these lower-order levels and the interplay between them. Crucially, meta-awareness of arousal is also the conscious integrative level of representation that permits an organism to make informed choices about how to monitor and manage lower-order sources of affective arousal.

Put simply, we will suggest that when subjectively reported affective arousal and autonomic arousal (e.g. heart rate and pupil dilation) correlate positively over time (arousal coherence), the organism is more accurately tracking changes in its uncertainty, at multiple levels of interoceptive and affective processing, impacting its capacity to appropriately adapt to change, and to be well. We discuss the implications of this coherence in terms of the veracity and responsiveness of precision estimates, interoceptive abilities, emotional awareness, self-regulation, and well-being. Among several other concrete predictions, we suggest that certain practices may improve the veracity of meta-awareness (and opacity) of arousal. We suggest that these practices may elicit some of their known benefits by supporting interoceptive-affective integration or coherence between affective feelings and physiology. We argue that the otherwise unconsidered role of higher-order meta-awareness of arousal (e.g. in the case of mindfully intervening to monitor and regulate arousal levels) may be key to improving arousal coherence, to training the capacity to adaptively learn about and intentionally regulate arousal and ultimately to more functionally adaptive responses to changing uncertainty.

Everything is inference

Brains have no direct access to the world. Instead, they interact with the world through bodies, receiving sensory signals that can often be ambiguous, noisy, and multifaceted. So, how do brains form a meaningful representation of the world and guide adaptive actions based on these unclear signals? The active inference framework (Friston 2009, 2010, 2013) posits that everything our brain does—including perception, learning, and action—is the result of inferences which minimize 'variational free energy'. Every perception or action is a hypothesis tested against the unfolding reality. When predictions match the actual sensory inputs, everything is fine. But to the extent that there is mismatch (and there always is), there is uncertainty. Put very simply, variational free energy is grounded in Bayesian probability theory and quantifies the mismatch or uncertainty between current beliefs about the state of the world (including the body) and their true state, and the brain is always trying to reduce this 'free energy' through perception and action.

Like previous formulations applying Bayesianism to the brain (e.g. predictive coding; Rao and Ballard 1999), the active inference framework conceptualizes brains as instantiating generative models. These models encode and/or generate probabilistic expectations about the causal structure of the environment (the likelihood of states) and about how observations are generated (the relationships between observations and states). Key to this encoding is 'precision', the inverse variance (width) of the probability distribution of expectations (Feldman and Friston 2010). Beliefs about precision can be considered a kind of higher-order prediction, a prediction not about states themselves but about the uncertainty of (or confidence in) the model in relation to these states. Precision acts to selectively enhance (or attenuate) signals according to their relative confidence. The sum of precision-weighted prediction errors, akin to 'variational free energy' (assuming Gaussian distributions), can thus be understood as a kind of sum of generalized noteworthy and/or trustworthy prediction errors.

By minimizing 'variational free energy', the model updates its beliefs over the question of current experience. These (approximately Bayesian) updates minimize both the sum of discrepancies (between what is expected and what is observed) and the magnitude of change in beliefs required (maximizing accuracy while minimizing complexity; Friston 2009), thus maintaining a pragmatically true and computationally tractable model of the (hidden) world. The result of these updates is known as 'state estimation' or perceptual inference. The process of minimizing variational free energy operates across multiple nested layers, where higher-level beliefs both guide and are simultaneously refined by inferences at lower levels. Higher levels of the hierarchy generate a cascade of descending predictions, with each level aiming to best explain the process that gives rise to the observations at the level immediately below. This hierarchical structure can be described in terms of increasing conceptual (Smith et al. 2019, Heins et al. 2020), temporal (Friston et al. 2017), or parametric depth (Hesp et al. 2021, Sandved-Smith et al. 2021). In other words, higher-level inferences inform lower-level ones, with lower-level outcomes feeding back to inform subsequent higher-level belief updates. For instance, basic perceptual inference (or state estimation) is both informed by and informs higher-level inferences about how states are expected to change over time. These expectations about state transitions are further informed by (and inform) even higher-level inferences about the action policy, or the sequence of state transitions, that the agent is most likely to be following.

When it comes to action selection, the most likely policy must be 'expected to' minimize free energy in subsequent observations. Like the process of state estimation, by minimizing variational free energy, prior beliefs about action policies are updated, or 'selected', accounting for both the anticipated consequences of action (quantified by 'expected free energy') and the incoming evidence for the perceptual priors (quantified by variational free energy). These updates then descend to shape precision-weighted expectations (i.e. probability distributions) of subsequent state transitions and state estimations. In other words, through action, expected free energy is minimized, in anticipation, and in reverse. Unlike perceptual inference, where errors can lead to adjustments in expectations by moving 'upward' through cognitive processes, active inference involves expectations 'descending' or influencing lower levels of processing. This descending influence can lead to actions like physical movements or covert mental (e.g. precision) adjustments, such as focussing attention, all aimed at minimising future surprises or uncertainties (i.e., the free energy 'expected' in future sensory observations). Through cycles of perceptual and active inferences, free energy can be continually, dynamically, and proactively minimized, both by changing the model and by acting to change the input.

Active inference reveals the architecture of bidirectional information flow, between the brain and its environment, between expectations of the future and observations in the moment, and between action and perception. It is these bidirectional relationships that result in the synergistic whole. Each new observation from the (bodily or ambient) environment enables beliefs about states to be updated. Beliefs about action policies and precision can then be updated, and these revised beliefs are then used to select actions and sample new observations, and the cycle repeats. This bidirectionally causal perception-action cycle allows the model to adaptively seek out (Friston 2010, 2013) and self-fulfil (Friston 2011) the evidence for its own existence (Hohwy 2016).

Uncertainty dynamics in embodied active inference

Living organisms are 'embodied' inference machines. This means that they carry expectations about their survival. These expectations (or 'prior preferences'), shaped by phylogenetic (Allen and Tsakiris 2018) and ontogenetic (Veissière et al. 2019) evolution, are privileged in the inferential architecture (Pezzulo et al. 2015, Allen and Tsakiris 2018). Simply put, our brains expect us to be in states conducive to survival and they act accordingly. For instance, our brain maintains that body temperature should stay within certain limits. Through interoceptive and allostatic inferences, the brain can closely monitor and control internal bodily states (cf. Seth and Friston 2016), minimizing deviations from (homeostatic) expectations both in the moment (e.g. through autonomic reflexes) and (e.g. through learned relationships between proprioceptive/exteroceptive events and likely interoceptive trajectories) proactively before they arise (this is allostasis; Sterling and Eyer 1988, Pezzulo et al. 2015, Stephan et al. 2016). Through interoceptive-allostatic inferences, which are posited to be at the core of this predictive architecture, our actions and perceptions are always closely tied to our survival instincts.

Importantly, however, interoceptive inferences need not necessarily be concerned only with maintaining homeostatic states. Minimizing expected free energy is equivalent to maximizing expected Bayesian model evidence (Friston 2010), which includes both extrinsic (or instrumental) and epistemic terms (Friston et al. 2015, 2016, 2023, Parr and Friston 2017). Maximizing the extrinsic value of policies encodes their alignment with prior preferences (like 'preferred' homeostatic or goal states), while maximizing epistemic value also encodes the 'expected information gain' under predicted outcomes (mutual information expected between hidden states and observations). The precision-weighted balance between these two imperatives helps the organism avoid getting stuck in suboptimal conditions and promotes continual learning and improvement, leading to long-term (epistemic) uncertainty reduction that ultimately maximizes extrinsic value (see also Kiverstein et al. 2019, Tschantz et al. 2020).

Here, we also consider how interoceptive inferences monitor and mitigate sources of uncertainty via the dynamics of the ANS. [Note, the primary neurotransmitters of the branches of the ANS, noradrenaline (sympathetic) and acetylcholine (parasympathetic; LeBouef et al. 2023), are also proposed to act as neuromodulatory precision systems in the brain (Parr and Friston 2017).] Fluctuations in ANS activity can cause changes in model uncertainty, both in lower-order sensory motor inferences and in higher-order meta-cognitive representations (Allen et al. 2016). For example, the rhythmic contraction of the heart muscle (systole) causes pulsatile blood flow across the retina, affecting the certainty with which the brain can rely on incoming (visual) signals. There is also a substantial literature demonstrating how baroreceptor firing (arising from vagal afferents to the brain) influences cognition and behaviour (i.e. Allen et al. 2016, Critchley and Garfinkel 2018, Azzalini et al. 2019).

The 'interoceptive self-inference' model (Allen et al. 2020, 2022) proposes that by inferring expected autonomic conditions, active inference agents can better estimate changes in expected uncertainty (e.g. caused by increased sensory noise) and thus modulate the expected precision of incoming signals (the impact of sensory errors on belief updates and action selection) accordingly. This may explain why changes in the frequency or rhythm of autonomic cycles impact higher-order estimates of uncertainty. For example, why heart rate increases are associated with changing confidence in exteroceptive judgements; Allen et al. 2016). ANS dynamics are intertwined with uncertainty and used in inferences about uncertainty throughout the hierarchy. Put simply, by interoceptively (self-)inferring what the heart (or other activity of the ANS) is going to do and when, the brain can improve its overall sensitivity to changes in bodily mediated uncertainty dynamics, and account for these expected fluctuations through optimizing precision.

In line with the enactive implications of active inference, the same bodily mediated precision mechanisms (e.g. autonomic mechanisms like cardiac regulation) may also be used to optimize action in response to changes in expected sensory uncertainty. That is, certain dynamics of the ANS may be enacted (though active inference) to respond to changes in uncertainty, because of the learned impacts of those dynamics on uncertainty and precision. One recent proposal suggests that heart rate changes (like respiratory cycles and gastric waves) are central in shaping the precision dynamics and fine-tuning the balance between perception and action, according to situational demands (Skora et al. 2022). Under perceptual uncertainty, heart rate slows, increasing the amount of time and predictability of time spent in diastole and, by extension, the amount of and predictability of opportunities for high-precision sensory sampling (Corcoran et al. 2021). The implication is that active interoceptive self-inference may not only predict (monitor) autonomic conditions and 'account for' their effects on sensory precision but also enact (control) autonomic changes to 'utilize' these expected effects in future inferences. Interoceptive self-inferences help agents to monitor and control their precision trajectories 'through' monitoring and controlling their interoceptive (particularly autonomic) rhythms (see Allen et al. (2020, 2022) for more detailed accounts).

Autonomic conditions also respond to 'unexpected' changes in uncertainty. For instance, while baseline pupil dilation has been shown to reflect expected uncertainty (roughly the inverse of expected precision), rapid changes in pupil dilation are also momentarily evoked by uncertainty that is not expected (i.e. violations of precise expectations, volatility, or surprise; Dayan and Yu 2003, Nassar et al. 2012, Browning et al. 2015, de Berker et al. 2016, Reimer et al. 2016, Harris et al. 2022, Pajkossy et al. 2023). The magnitude of these momentary autonomic deviations (i.e. from baseline to evoked pupil dilation, reflecting estimates of expected to unexpected uncertainty) suggests that the process generating observations has changed. Prior estimates may no longer be reliable. Depending on the magnitude or consistency of these deviations, they may drive belief updates about expected uncertainty. These updates will depend on the level of confidence assigned to interoceptive beliefs relative to error signals or interoceptive precision.

Interoceptive precision estimates are vital for the uncertainty dynamics in embodied active inference to operate effectively. Under sudden changes in autonomic conditions, the precision of interoceptive error signals usually increases—facilitating updated estimates of these states. For example, precise tracking of heartbeats improves during heightened physiological arousal (i.e. Smith et al. 2020a, 2020b, 2021), enabling more rapid updating of expected autonomic states. As described earlier, inferred autonomic states helps to shape precision estimates throughout the inferential hierarchy. If an agent fails to update precision estimates in line with changing bodily signals (i.e. despite surmounting error signals), it may subvert precision weighting mechanisms throughout the hierarchy. Indeed, failure to adapt interoceptive precision in response to autonomic changes has been associated with poorer mental and physical health outcomes, including depression, anxiety, and substance use disorders (Smith et al. 2021).

In the next section, we discuss how affective arousal may assist in adaptively updating interoceptive precision estimates by acting as an orienting function, enabling the system to focus on particularly strong indicators of changes, and guiding the system in when to prioritize updates of interoceptive precision.

Affective arousal and precision optimization

Under the active inference framework and other implementations of predictive coding, affective states have been associated with inferences about the causes or consequences of interoceptive conditions (i.e. Seth 2013, Barrett and Simmons 2015, Seth and Friston 2016), or with changes in prediction error dynamics or uncertainty (i.e. Joffily and Coricelli 2013, Kiverstein et al. 2019, Hesp et al. 2021). Through the lens of deep active inference, affect is proposed to represent changes in 'lower-level' uncertainty. The experience is an abstraction—a minimal form of meta-cognition over changes in how well the model is doing at life (subjective model fitness) across time (Hesp et al. 2021). Being 'tuned' by this higher-level affective abstraction of fitness guides the system to become a better predictor over time. For example, the feeling of momentary subjective happiness is thought to signal that the model is improving in its predictions (i.e. that prediction errors are reducing across time). This feeling can thus be used to guide overall improvement (Miller et al. 2022).

When affective arousal is discussed in the current active inference literature (often in passing), it is generally suggested to be inferred based on unexpected or unexplained changes, such as residual interoceptive (Barrett and Simmons 2015) or homeostatic (Solms and Friston 2018) errors. Inferences about affective arousal are proposed to be evaluative, resulting from the magnitude of changes in uncertainty (e.g. Solms and Friston 2018, Solms 2019, Hesp et al. 2021), and also directive, acting to fine-tune the precision of certain ascending error signals, according to those evaluations (i.e. shifts in expected free energy associated with homeostatic deviations; Solms and Friston 2018). Rather than proposing a specific computational account for affective arousal here, we instead draw on the ideas offered in previous perspectives under the active inference framework.

Under active inference accounts, affective arousal has been proposed to serve as a signal for the need to learn or adapt in response to significant changes in interoceptive-allostatic uncertainty (Barrett and Simmons 2015). It orients belief updates towards reliable cues of affective states (Hesp et al. 2021)—including, presumably, interoceptive-allostatic errors—through precision optimization (Solms and Friston 2018). Surprisingly, large or unrelenting deviations (e.g. homeostatic errors (Solms and Friston 2018) or residual interoceptive errors (Barrett and Simmons 2015)) can serve as evidence for high (or increased) affective arousal. Inferences about affective arousal optimize the precision of those ascending signals, upregulating those that are expected to resolve future uncertainty. In non-affective domains, this might be considered bottom-up attention/salience. That is, affective experiences (like valence or other affective qualities resulting from homeostatic deviations) are proposed to be aroused or to consciously change (Solms and Friston 2018, Solms 2019), only when there is a need to prioritize or learn from changing conditions. The arousal into consciousness (or in reverse, attenuation) of affective stimuli and qualities—and we suggest, particularly interoceptive changes—may also play an important role in monitoring and regulating changes in uncertainty.

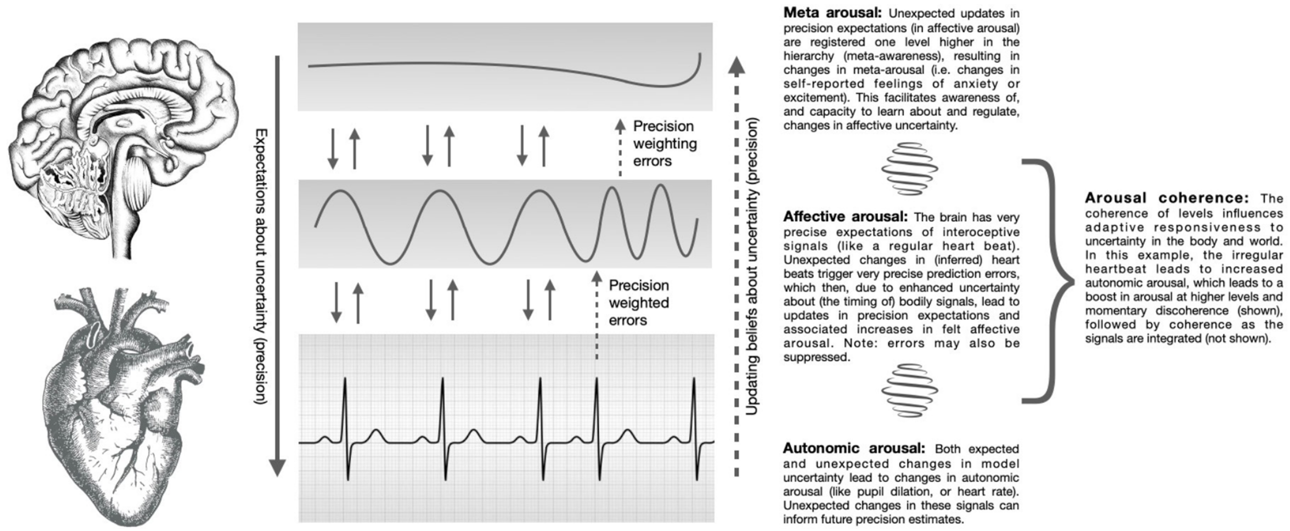
Interoceptive prediction errors and precision may play a unique role in monitoring, responding to, and utilizing changes in uncertainty and precision dynamics. Recall that interoceptive self-inference is proposed as a core mechanism through which organisms implicitly and preconsciously infer and actively shape their own expected precision trajectories (Allen 2020, Allen et al. 2020). If affective states recruit bodily signals (or the outcomes of interoceptive inferences) to model the current state of affairs (Critchley and Garfinkel 2017) and changes in autonomic arousal reflect and enact changes in uncertainty and precision (as discussed earlier in 'Uncertainty dynamics in embodied active inference'), then inferred affective arousal may reflect a (minimally) meta-cognitive mechanism through which the precision and error dynamics of interoceptive self-inference are consciously represented and regulated.

Again, note that we do not mean to imply that affective arousal is 'only' informed by the outcomes of interoceptive predictions. As discussed earlier, affective arousal is also informed by error and uncertainty dynamics not necessarily exclusive to interoception. The precision optimization process reflected that affective arousal is dynamic and continuous, shaped by prior beliefs (like past affect), higher-level beliefs, and other learned contextual factors, and responsive to both external and internal changes, ensuring that the organism remains adaptable and responsive to evolving environmental and physiological conditions. What we are suggesting is that interoceptive self-inferences—particularly concerning changes in ANS arousal—may be one mechanism through which the precision dynamics of affective arousal are monitored and enacted. This relationship is depicted in the bottom half of Fig. 1.

Given beliefs about the (low) reliability of interoceptive errors, ascending error signals may be suppressed, leading to affective arousal that is out of synchrony with the changes in uncertainty encoded by the ANS. On the other hand, if inferred affective arousal is responsive to the magnitude of (particularly unexpected) changes in autonomic arousal, the resulting affectively driven orienting processes will also be more responsive to changes in uncertainty. This suggests a sensitive bidirectional relationship between inferences about autonomic and affective arousal, with both acting as different kinds of device for monitoring and controlling uncertainty through precision, and where the relationship (or integration) between them may be particularly important for maintaining up-to-date uncertainty estimates in affectively oriented processing.

Meta-awareness

Felt affective experiences, as a minimal form of meta-cognition, are proposed to guide actions towards uncertainty reduction over time (Hesp et al. 2021). However, importantly, felt experience (i.e.



Meta arousal: Unexpected updates in precision expectations (in affective arousal) are registered one level higher in the hierarchy (meta-awareness), resulting in changes in meta-arousal (i.e. changes in self-reported feelings of anxiety or excitement). This facilitates awareness of, and capacity to learn about and regulate, changes in affective uncertainty.

Affective arousal: The brain has very precise expectations of interoceptive signals (like a regular heart beat). Unexpected changes in (inferred) heart beats trigger very precise prediction errors, which then, due to enhanced uncertainty about (the timing of) bodily signals, lead to updates in precision expectations and associated increases in felt affective arousal. Note: errors may also be suppressed.

Autonomic arousal: Both expected and unexpected changes in model uncertainty lead to changes in autonomic arousal (like pupil dilation, or heart rate). Unexpected changes in these signals can inform future precision estimates.

Arousal coherence: The coherence of levels influences adaptive responsiveness to uncertainty in the body and world. In this example, the irregular heartbeat leads to increased autonomic arousal, which leads to a boost in arousal at higher levels and momentary discoherence (shown), followed by coherence as the signals are integrated (not shown).

Figure 1. From bottom to top: autonomic arousal fluctuates with sensory and probabilistic uncertainty (cf. de Berker et al. 2016, Allen et al. 2020, 2022). Affective arousal reflects and influences organismic (affectively relevant) uncertainty, which entrains descending precision estimates over interoceptive error signals. In reverse, inferences about affective arousal are also informed by ascending (precision-weighted) interoceptive error signals. Meta-awareness monitors and regulates the precision of affective-level precision estimates, enabling intentional monitoring and regulation of changes in arousal. With increasing meta-awareness of arousal, inferences about affective arousal may become more responsive to subtle changes in ascending interoceptive errors, over time resulting in higher arousal coherence. On the other hand, continually affectively suppressing these interoceptive errors leads to discoherence

phenomenal affective arousal) is not necessarily the same as being able to access or report on that experience (Amir et al. 2023). Here, we extend our conception of arousal beyond autonomic and affective, to a third level of meta-cognitive awareness. We suggest that higher-order meta-cognitive awareness over affective arousal (i.e. reflected in the capacity to explicitly notice and report on current affective arousal experiences) monitors and regulates lower-level inferences about affective arousal. Through learning and deploying action policies to monitor and regulate momentary felt affective arousal, this awareness can facilitate uncertainty reduction over longer timescales.

Meta-cognitive awareness and control (Sandved-Smith et al. 2021) have recently been modelled under deep parametric active inference. Parametrically deep models exhibit a nested, fractal-like structure where each generative model of perception and action exists under an identical structure above it. At higher parametric levels, inferences monitor and regulate lower-level inferences. The ascending signals are related to prediction outcomes across time, and descending signals entrain expected states and their precision. For example, in a model of attention with three levels of parametric depth, third-order meta-awareness both monitors and controls (or entrains the expected states and precisions of) second-order attentional states, which subsequently entrain the expected states and precisions of first-order perception and action (Sandved-Smith et al. 2021).

In line with this conceptualization of meta-awareness of attention, we suggest that meta-awareness of arousal may be the result of similar inferences, particularly concerning the contextual and learned reliability of various lower-level sources of affective arousal. This level of representation permits an organism to make informed choices about how to monitor and regulate lower-order sources of affective arousal, through monitoring and entraining changes in precision estimates. This may also include enhancing/attenuating the impact of ascending interoceptive (autonomic) errors upon updates of affective arousal. Meta-awareness of arousal may be both determined by (monitor) and determine (control) the strength and sensitivity of inferred affective arousal to fluctuations in interoceptive inferences.

Recent empirical findings show that ascending heart-to-brain information flow in affective processing (presumably reflective of interoceptive precision) is modulated by self-reported affective arousal. In brief, there is an initial cardiac response (sympathovagal/heartbeat activity) to emotion elicitation that precedes and prompts a specific response in the brain related to affective arousal. This initial response is followed by a continuous interaction between brain and heart. Importantly, self-reported subjective affective arousal specifically influences the strength of the continuous signals flowing from the heart to the brain (Candia-Rivera et al. 2022). In a similar vein, arousal focus—the tendency to emphasize felt changes in affective arousal when reporting emotional experiences—is also associated with stronger interoceptive sensitivity (Barrett et al. 2004). Thus, self-reported (read: meta-aware) experiences of affective arousal also appear to be involved in shaping interoceptive precision.

We propose that meta-awareness of arousal may entrain the precision and expected states of lower-order sources of affective arousal, shaping their responsiveness to ascending sources of error, including interoceptive errors. That is, meta-awareness of arousal monitors and controls the responsiveness of inferred affective arousal to changes in ascending errors. We show an example of this relationship in Fig. 1, specifically for interoceptive/autonomic errors. Facilitating affective arousal that is more responsive to ascending interoceptive errors may allow agents to update and refine their inferred arousal states with more accuracy. As such, meta-awareness of arousal across time may contribute to a more sensitive and responsive relationship between feelings of affective arousal and measurable changes in autonomic arousal. This would not only allow for a more accurate conscious representation of changes in uncertainty, but also, over time, allow for learning about contextual changes in arousal. As a result of this higher-order learning, agents could deploy action policies to create future circumstances which purposely regulate and utilize (changes in) arousal and coherence.

Arousal coherence and well-being

An extension of this is that arousal coherence may also be an inferred state or thing to track in the model's estimations of its own allostatic control. Does my subjective state match up with the (inferred) state of my body? Should I expect it to? Conflict between levels may suggest inefficient allostatic control and self-efficacy (i.e. reduce confidence that the model is a good regulator of action), which may manifest phenomenologically as lower subjective well-being. In contrast, coherence between levels may increase confidence in allostatic control estimates. Phenomenally feeling of allostatic control estimates in subjective well-being may adaptively guide the system—again, through feelings—towards better allostatic control (e.g. prediction error minimization) over time. However, these inferences can become pathological. For example, pathologically inferring low/lost allostatic control and self-efficacy are also thought to be involved in clinical symptoms and phenomenology across fatigue, depression, and depersonalization (Stephan et al. 2016, Deane et al. 2020, Ramstead et al. 2023). In brief, high-level inferences about arousal coherence may inform inferences about allostatic control (i.e. how well the system is doing at budgeting energy resources) and thus impact subjective feelings of well-being. (We thank reviewer 1 for helpfully drawing our attention to this interpretation.) Indeed, stronger arousal coherence (as indexed by the intra-individual relationship between physiologically and affectively aroused states) has previously been associated with higher self-reported psychological well-being (e.g. Sommerfeldt et al. 2019).

While noting that this is an interesting avenue for further consideration, we propose that beyond informing high-level allostatic control estimates and related inferences about well-being, arousal coherence may also be involved in updating precision estimates, with implications for the veracity and adaptability of all affectively informed inferences. Through its role in precision optimization, we suggest that arousal coherence is also likely to be associated with self-awareness and self-regulation and through these to facilitate more adaptive functioning and ultimately well-being. We also suggest that this kind of coherence may shape responsiveness to changing levels of uncertainty in the (bodily and ambient) environment. The focus of our remaining discussion pertains to the functions, implications, and potential measurement of arousal coherence itself (rather than high-level inferences about arousal coherence).

Optimizing affective arousal according to changes (or errors) in inferred autonomic arousal (which we suggest is reflected in arousal coherence) presumably impacts the dynamics of higher-order affectively informed inferences, like inferences about emotions. Dysfunctional emotional perception—particularly perceptions of stress—are associated with various psychiatric symptoms (Thorsén et al. 2022). Keeping emotional perception broadly in tune with embodied changes in uncertainty (i.e. through arousal coherence) may help both by preventing emotion beliefs and perceptions from becoming rigid and by facilitating opportunities for regulation. Indeed, arousal coherence is associated with less use of maladaptive coping strategies, like repressive and suppressive coping, and with significantly higher psychological and physical well-being, particularly seen in lower depression and anxiety (Sommerfeldt et al. 2019).

Importantly, while in most circumstances, integrating interoceptive and affective arousal is presumably adaptive (under conditions of changing uncertainty), this is not necessarily always so (i.e. under stable uncertainty). For example, in cases of unrelenting or overwhelming distress with an inability to resolve it, such as in intense grief or prolonged conflict, it may be more adaptive to be able to dissociate from (or attenuate) overwhelming signals arising from the body (at least for a time). In line with this, repressive and suppressive coping, which have been shown to help with grief adjustment in the short term (Coifman et al. 2007), have also repeatedly been tied to reduced coherence (Coifman et al. 2007, Sommerfeldt et al. 2019, Brown et al. 2020). As we will discuss further later, the capacity to appropriately connect to a coherent mapping of arousal (to promote responsiveness to uncertainty dynamics) and the (higher order) capacity to override momentary discoherence in the short term, where necessary, may both serve important functions.

However, with prolonged discoherence (for example, given sufficient overwhelm) beliefs may form about how valuable bodily signals are, leading to sustained attenuation and an inability to access and utilize these signals. Recent findings suggest that beliefs about the value and safety of bodily signals may also predict this kind of arousal coherence (interestingly though, not explicit interoceptive accuracy), such that the less valuable or more dangerous bodily signals are perceived to be, the lower the coherence between subjective/affective and objective/autonomic markers of arousal (MacCormack et al. 2024). In other words, if one has a strong expectation that bodily signals are unreliable or untrustworthy (learned over longer timescales), one may systematically underweight ascending interoceptive errors in affective arousal. This is likely to have detrimental impacts on well-being.

Indeed, decoupling between physiological and subjective streams of affective experiences has been proposed to be one of the mechanisms by which early life adversity predicts later life health (Petrova et al. 2021). This decoupling may also help to explain seemingly contradictory lines of thinking about disorders of presence (like depersonalization or dissociation) which have previously been associated with deficits in successful prediction of interoceptive signals (Seth et al. 2012), particularly due to systematic (Saini et al. 2022) and pathological down-regulation of interoceptive error signals (Seth 2013, Seth and Critchley 2013), despite people with these disorders showing normal performance on explicit interoceptive accuracy tasks (Michal et al. 2014). Perhaps disorders of presence are affected by pathological affective down-regulation of interoceptive signals rather than explicit interoceptive attention or regulation.

Interestingly, when interoceptive signals are processed as anticipated, this is proposed to increase the ability to trust body signals (Herbert and Pollatos 2012, Owens et al. 2018), suggesting that arousal coherence may not only reflect but also impact the capacity of a person to trust their bodily signals. Embodied contemplative practices like meditation also emphasize purposeful attention to and acceptance of bodily signals, facilitating meta-awareness and control of arousal states. If maladaptive interoceptive integration is a key factor across many psychological disorders, contemplative practice may work by attenuating these dysfunctions.

In their predictive coding model of mind–body integration, Farb et al. (2015) suggest that non-judgementally attending to or 'sitting with' unexpected feelings of arousal during meditation may reduce over-dependence on top-down expectations and facilitate learning or 'insight' about the self in the environment rather than knee-jerk arousal regulation strategies. Indeed, these practices have been shown to improve elements of self-reported interoceptive sensibility, particularly trust in bodily signals and how the body is used for self-regulation and emotional insight (Bornemann et al. 2015, Lima-Araujo et al. 2022). Interestingly, while meditation practice shows no effect on enhancing explicit interoceptive accuracy measures (Khalsa et al. 2020, Lima-Araujo et al. 2022), it does relate to increased interoceptive sensibility (Lima-Araujo et al. 2022) and to an index of increased arousal coherence (Sze et al. 2010).

Increasing arousal control and coherence

More recent active inference models of meditation (e.g. Laukkonen and Slagter 2021) indicate that one way in which contemplative practices may increase coherence between mind and body generally but also specifically for arousal is by temporarily flattening hierarchically deep processing. By reducing the precision of temporally extended models (e.g. thinking) and increasing the expected precision of here-and-now bodily signals (e.g. through shifting attention to the breath; Lutz et al. 2019), one may increase the coherence between affective and autonomic arousal by tuning expectations more precisely to bodily data (e.g. ANS arousal indicators). Consequently, the organism may become more responsive to unexpected changes in environmental uncertainty through better integration of changes in physiological arousal. Put metaphorically, connecting affective and autonomic arousal through orienting feelings (optimizing precision, Feldman and Friston 2010, Lutz et al. 2019) 'grounds' more abstract beliefs to the more volatile and direct connection that exists between the body and the world. By maintaining a connection between higher-order and lower-order systems of arousal (e.g. through increasing meta-awareness of arousal, like in specific kinds of meditation practices), the organism may be better tuned to uncertainty throughout all levels of the mind (i.e. the generative hierarchy).

Crucially, the capacity to be meta-aware of changes in arousal is also key to Buddhist meditation practice (Britton et al. 2014, Dunne et al. 2019). For example, to achieve 'samatha' (tranquillity, serenity, and/or concentration), one needs to maintain a 'balanced' energy that is neither too aroused [e.g. restless or agitated, known as 'uddhacca' in Pali (the liturgical language of early Buddhism)] nor too drowsy (associated with sloth or 'thīna' in Buddhism). The capacity to consciously monitor arousal states corresponds to the high-order level of inference described earlier. Moreover, in classical Buddhist meditation, this high-order monitoring allows one to consciously apply certain 'antidotes' to shift arousal levels back to balance in a top-down way—e.g. in the case of mental dullness a meditator is encouraged to apply belief ('śraddhā'), aspiration ('chanda'), effort ('vyayama'), and suppleness ('praśrabdhi'). Indeed, a review of evidence showed that meditators do appear to possess meaningful control over their levels of wakefulness and arousal (in some cases even during sleep) with increasing prowess as expertise increases (Britton et al. 2014). Awareness and gradual 'opacification' of arousal processes through practices like meditation may increase the capacity to regulate these states, for example, via reducing autonomic or 'knee-jerk' arousal regulation strategies.

We propose that this is because of the bidirectional relationships between meta-awareness, affective arousal, and autonomic arousal, where meditation exerts its control (initially) through high-order inferential mechanisms, followed by temporal flattening effects described earlier (see also Laukkonen and Slagter 2021 for an extreme example of how meditation can control arousal and wakefulness levels to the point of cessation). An interesting implication of this view is that simple 'awareness' of arousal levels and intentions to affect them (e.g. through determined effort) may have substantial effects on both affective and autonomic arousal levels, possibly helping to both control and integrate uncertainty inferences throughout the system.

Speaking more broadly, any activity that prioritizes awareness of bodily information over other more abstract processes (e.g. yoga, dancing, and other forms of exercise, as opposed to less-embodied contemplative practices, like reciting prayers) may increase coherence between affective, autonomic, and self-reported arousal (cf. Sze et al. 2010), thereby extending already known benefits to the organism's capacity to respond to uncertainty in the world (e.g. possibly improving the capacity to update maladaptive beliefs about uncertainty and to learn under conditions of changing uncertainty; Mrazek et al. 2013, Laukkonen et al. 2020, McGovern et al. 2022).

The kind of interactions that occur between affect and autonomic processes in embodied practices (like meditation and sport) involves a healthy amount of appropriate and intentional attenuation (e.g. ignoring physical distress during intense exercise or meditation in favour of perceptual inference or long-term error reduction). The ideal scenario may therefore be one where the organism can appropriately connect to a coherent mapping of arousal to promote responsiveness to uncertainty dynamics (cf. Miller et al. 2022) while also possessing higher-order (meta) capacities to override autonomic signals (momentary discoherence) in the short term, where necessary. Nevertheless, baseline arousal coherence is likely to remain a useful marker of many factors associated with healthy well-being and is an exciting path for future work. Likewise, the capacity to increase meta-awareness of arousal levels and to direct attention to autonomic changes is promising as a clinical intervention for disorders characterized by arousal discoherence (e.g. dissociation and anxiety) or other common but less severe forms of decoupling. Such interventions may be especially effective when physical movement is included to ensure bottom-up and top-down information processing across all levels of arousal (physiological, affective, and reportable).

Conclusion

Computation of uncertainty is crucial for self-organizing inference machines (like Bayesian brains) to learn about and adapt to dynamic and only-indirectly-observable environments. Affect is part of the mechanism that brains use to become better prediction machines. Where previous work on affective error dynamics has focussed primarily on valence (in terms of patterns of changing uncertainty, i.e. Kiverstein et al. 2019, Hesp et al. 2021, Miller et al. 2022), here we have focussed on arousal in monitoring the magnitude of and enacting changes in uncertainty. We have seen how uncertainty processing is distributed across both affective and autonomic arousal, and the role that affective-interoceptive integration, or *arousal coherence*, may play in responding to changes in uncertainty, both internally and externally. In practice, this means that the correlation between subjective reports of affective arousal and physiological markers of autonomic arousal (i.e. changes in heart rate, respiration, or pupil dilation) might be used to index the capacity to adjust interoceptive precision, particularly in response to changing levels of uncertainty in the bodily and external environment.

Difficulties integrating interoceptive information into higher-order processes are established to have wide-ranging implications, from emotional awareness and regulation (Price and Hooven 2018, Schultchen et al. 2019), to the sense of self (Damasio 2003, Seth et al. 2012), to intuitive (Dunn et al. 2010) and rational decision-making (Kirk et al. 2011), and from the aetiology of several psychiatric conditions (Khalsa and Lapidus 2016), to mental and physical health more broadly (Critchley and Garfinkel 2018, Khalsa et al. 2018, Quadt et al. 2018, Herbert et al. 2020). The emphasis in the present paper is not explicit interoception, like accurately reporting on your heartbeat, but rather 'integrating' certain interoceptive information into felt experience (cf. Solms 2019). We have suggested that the within-person correlation between measures of autonomic and affective arousal may be a useful index of the level of this integration. We also suggested that practicing meta-awareness of changes in arousal (like in meditation) may facilitate improvements in coherence.

If unexpected changes in autonomic arousal (i.e. interoceptive errors) are not effectively integrated into affective arousal over time, then pathological decoupling (discoherence) can occur. If discoherence between arousal systems occurs (e.g. owing to failures to update interoceptive precision, via affective inference), then there are likely to be broad negative outcomes for the organism in the long term, particularly in terms of the ability to update beliefs appropriately in response to fluctuating uncertainty. Updating uncertainty estimates is crucial for well-being, as discussed earlier. Indeed, a range of affective disorders are associated with reduced sensitivity to changes in uncertainty (Pulcu and Browning 2019). Under active inference, failures to update estimates of uncertainty particularly negatively impact the capacity for learning because the system cannot optimally recognize opportunities for reducing uncertainty. Therefore, our take on the role of arousal coherence yields further hitherto untested predictions, as discussed later.

Presumably, difficulties with affectively integrating information about one's own autonomic states will also have negative impacts on emotional awareness and regulation. Dysfunctional affective arousal is suggested as a contributing factor in alexithymia (Bermond 1997, Vorst and Bermond 2001), which is also a risk factor for affective disorders via emotional regulation difficulties (Preece et al. 2022). We suggest that emotional awareness difficulties, like in alexithymia, are likely associated with dysfunctional arousal coherence. Further, if discoherence represents failures to integrate information about uncertainty, we hypothesize that it will be associated with intolerance of uncertainty and psychological inflexibility. Notably, discoherence has also previously been associated with the use of avoidant coping strategies (Sommerfeldt et al. 2019), which are strongly predictive of intolerance of uncertainty (Sahib et al. 2023). Meanwhile, mindfulness, an adaptive and non-avoidant coping strategy, is associated with both increased coherence (Sze et al. 2010) and increased tolerance of uncertainty (Sahib et al. 2023).

Beyond emotional awareness and regulation, arousal coherence is also likely to have implications for autonomic regulation (i.e. recovery from stress), as well as learning under more complex conditions, with changing levels of uncertainty (e.g. safety signal learning). Anxiety has been proposed to reflect rigid learning of uncertainty estimates (McGovern et al. 2022), and individuals with high-trait anxiety (also associated with low arousal coherence index; Sommerfeldt et al. 2019) indeed show difficulties learning in changing environments, with less ability to adjust and update expectancies when environments change between stable and volatile conditions (Browning et al. 2015). Finally, given recent findings that ANS synchrony (e.g. heart rate or respiration co-variation) 'between' individuals is associated with feelings of connectedness, co-operation, and empathy (Levenson and Ruef 1992, Marci et al. 2007, Palumbo et al. 2016, Coutinho et al. 2021), the inability to access or reflect upon changes in one's own autonomic signals consciously (affectively) may contribute to difficulties in social contexts, with possible detriments in empathic abilities, detecting social cues, and diminished feelings such as connectedness.

The relationships between inferences about physiological arousal, affective arousal, meta-awareness of arousal, and uncertainty estimation may be central to understanding not only our emotional experiences but also our capacity to learn and adapt to the world around us. We have seen that physiological (autonomic) and psychological (affective) arousal both respond to shifts in uncertainty, and that changes in inferences about these states influence precision estimates across the inferential architecture. Although multiple factors influence inferred affective arousal, including past affect (cf. Asutay et al. 2021) and higher-order inferences (i.e. meta-awareness of arousal, as discussed earlier), we have proposed that incorporating information about the magnitude of errors or changes in inferred autonomic states into experienced affective arousal is beneficial for maintaining current estimations of uncertainty. Moreover, meta-awareness regarding these arousal processes may play a significant role in the responsiveness of inferred affective arousal to lower-level changes, precluding (or enhancing) the impact of ascending interoceptive errors on updates of affective arousal. Increasing meta-awareness also permits organisms to make decisions about if and how to potentially intervene where there might be decoupling or discoherence between lower-order arousal systems.

Ultimately, we have suggested that the interplay between affective, autonomic, and self-reported arousal within an individual over time may reflect their ability to adapt to evolving uncertainty dynamics. We outlined why, theoretically, this would have profound implications for estimates of uncertainty, for higher-order affective awareness, for self-regulation, and ultimately for well-being. Encouragingly, certain mind–body practices seem to have potential to enhance baseline arousal coherence across all levels, thus improving integration and responsiveness to changes in uncertainty. Nevertheless, future research may also investigate whether it is possible to isolate the level of arousal in the hierarchy where intervention might be most impactful for different conditions. In a world that is increasingly complex and unpredictable, interventions that improve multi-layered arousal coherence (and awareness therein) may offer a promising pathway to help us dance in step with the ever-changing music of uncertainty.

Conflict of interest.

None declared.

Data availability

No data are available as this is purely a conceptual paper.

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