Interoception and the Neurovisceral Axis as a Modal Basis for Computational Neuroecology

Jesse Bettinger[1,2,*]

[1]*Center for Process Studies; 1325 N. College Avenue; Claremont, California, 91711*

[2]*The Johns Hopkins University, Center for Talented Youth; 5801 Smith Avenue; #400 McAuley Hall; Baltimore, Maryland 21209*

Abstract: The defining parameters of neuroecology stand to benefit from a phenomenological expansion that includes the role of *affect* qua *interoception* as entailing a multimodal storehouse for specialized signal processing and brain architecture within the *neurovisceral* axis. The relationship between the gut and the brain represents an integral axis of communication drawing from the ecosystem of the microbiome as an environment for nerve-cell processes reflecting our habits of living and the influence of the luminal environment in higher-ordered cognition. This is shown to apply in both feedforward and inferential models of interoception. A surplus of evidence in recent years indicates that interoception and interoceptive awareness play a key role in influencing adaptive behavioral strategies, cognition, homeostatic regulation, decision-making, social relations and action. The groundwork for this expansion has already been positioned by preliminary efforts to offer a physiological basis for computational neuroecology and emotion qua *somatic markers*. Building off of their maiden report, this paper develops the richer neuroscientific landscape underwriting somatic markers in the context of the neurovisceral axis qua interoception and biological intuition. In the process we encounter an evolutionarily-rare and morphologically-specialized type of neuron conjectured to provide an advantage for social processing that eclipses the rudimentary notion of somatic markers, alone, and thereby enriches the descriptive landscape of neuroecological phenomena. Finally, we examine the inherent signal processing dynamics in cortical laminar layers as rendered in a newly-fashioned predictive coding account of interoception as a “limbic workspace theory” that interfaces with sensory signals between agranular and granular cells. Advances in predictive coding models and the free-energy principle stand poised to provide a unified model of neural signal processing encompassing sensory coding as well as adaptation in neurons, mood and behavior.The incorporation of *interoceptive inference* sheds critical light on anticipatory (feedback) signal-processing mechanisms in the brain. This suggests that an incorporation of *interoceptive affect*-in combination with cognition and adaptation-will shed critical light on further efforts to organize the driving epistemic structure and phenomenology associated with neuroecology.

Keywords: Neuroecology, Neuroethology, Interoception, Neurovisceral axis, Intuition, Affect and cognition, Predictive coding, Free-energy principle, Von Economo neurons.

1. INTRODUCTION

As the study of adaptive variation in cognition and the brain, neuroecology represents a burgeoning interdisciplinary niche combining anatomical and systems neuroscience with *neuroethology* (brain translations of biological stimuli into natural behavior), *neuromorphology* (the structure of the nervous system), behavioral ecology, and evolutionary biology [1]. What appears missing, however, is a corollary consideration for the influence of specialized *affective* processing on cognition, behavior and evolutionary adaptation. The groundwork for this has already been positioned by the preliminary efforts of [2] in offering a physiological basis for computational neuroecology and emotion qua "somatic markers"[3-5].

> Damasio’s ‘somatic marker hypothesis’ proposes that core (primary) consciousness arises via non-verbal representations of how an organism’s internal state is affected by the perception of an external object, where this representational process helps to place the perceived object in a salient spatiotemporal context [23]. Damasio’s framework includes an ‘as-if body loop’ which involves simulation of interoceptive data, providing a connection to the predictive self-modelling concepts. [Seth, 2009]

Building off their maiden report [2], this paper develops the richer landscape underwriting somatic markers in the neurovisceral axis qua interoception [6-9] and biological intuition.

We agree with the basic premise of [2] that “*communicated somatic markers can correspond to individual benefits*” [2] however, find it necessary to develop somatic markers in the capacity of interoception and the neurovisceral axis, as an evolutionarily specialized and adapted pathway, operating in a regulatory capacity alongside Bayesian computational dynamics. When taken together we are able to account in full for the neuroecological criteria

---

[*]Address correspondence to this author at the Center for Process Studies; 1325 N. College Avenue; Claremont, California, 91711;
Tel: (719) 237 5472; Fax: (909) 621 2760;
E-mail: jesse.bettinger@alumni.cgu.edu

E-ISSN: 2409-3564/16

outlined in this edition. Applying current neuroanatomical and predictive coding models of interoception to somatic markers, we are able to develop a more rigorous portrait of the neuroscientific parameters entailing neuroecology and its close links with integrative neuroscience in terms of cognition and the neural circuits that govern behavior.

The conceptual foundation of *neuroethology* rests on the notion that nervous systems are embodied [10]. Significantly, James and Lange develop emotion precisely as an embodied element of the internal milieu predicated on homeostasis. This has since been applied to designate the biological foundation for interoception and emotion [6-9]. This line of reasoning is also consistent with recent *embodiment* views of cognition [37-39] suggesting that affective states are incorporated into the conceptual knowledge we use to categorize objects and events in the world [33]. As embodied and socially responsive, interoception provides a basis for the emergence of adaptive behavior from the coupling of brain, body and environment [1]. This presupposes the active integration of sensory signals motivated from prior action repertoires as a basis for perception underwriting adaptive behavior. We set this preliminary stage to secure the motivation for including interoception within the horizon of neuroecology.

Comparative neuroanatomical blueprints of brain-gut exchange provide clues that natural selection worked in favor of the development of a specialized pathway in higher primates for the purpose of facilitating a rich social complexity of information qua interoceptive and affective, communicative axes [see 8, 9]. In the process, we encounter an evolutionarily-specialized morphological type of neuron: the *von Economo* neuron—found in the cortical area of the intéroceptive axis-and geared towards the fast integration and diffuse transmission of simple signals throughout the brain [11, 12]. This is conjectured to provide an advantage for social processing that functionally eclipses the rudimentary notion of somatic markers, thereby enriching the neuroecological landscape. Specifically, von Economo neurons are found precisely in the interoceptive cortices at the top of the afferent, neurovisceral axis and are also implicated in the role of intuitive, social decision-making, just like somatic markers.

In what follows, we turn our attention to detailing the major elements of interoception as coincide with the driving challenge of this special edition: namely, *to uncover causal relations between brain architecture and signal dynamics with behavioral strategies subsumed in cognition and adaptation*. We begin by advocating for the role of cognition in contiguity with affect and emotion, and suggest this takes place most prominently within *interoception*. In detailing this modality, we uncover specific neurovisceral and cortical laminar architectures [9, 13, 14], along with corresponding signal processing dynamics in the insula, shown to causally-confer behavioral influences on the order of cognition, affect, emotion, decision-making, attention, action and motivation.

After substantiating this appeal, we turn to approximate models of “Bayesian brain” dynamics in top-down inferential procedures qua active inference [15, 16], predictive coding [17-19] and the *minimization of variational free energy*[20]. These provide intuitive, computational signal-processing mechanisms for ongoing behavioral adaptations underwriting action, perception, cognition and affect. Finally, we examine the proposal of inherent signal processing dynamics in cortical laminar layers, as rendered in [13, 14], by a top-down predictive coding account interfacing with bottom-up sensory interoceptive afferent signals between agranular and granular cells. Combining these accounts orchestrates an updated foundation for the neuroecological landscape centering on interoception.

Antonio Damasio eloquently proposed the notion of *somatic markers* as arising from the association of emotional and affective (feeling) states with visceral and other body responses to certain situations [4]. Underwriting this proposal is the idea that affective reactions can guide future planning and expedite decision making [3]. For example, somatic markers may elicit the “undeliberated inhibition of a response learned previously ... [or] the introduction of a bias in the selection of an aversive or appetitive mode of behavior” [9; see also 3, 4]. The evolutionary advantage of simplifying decision-making based on past repertoires of action and contextual behavior provides clear fitness in a social setting.

The relationship between the gut and the brain represents an integral axis of communication drawing from the ecosystem of the microbiome--as an environment for nerve-cell processes reflecting our habits of living, plus the influence of the luminal environment in higher-ordered cognition--as communicated through packets of feelings from the body: so-called *somatic markers.* Developing the enhanced, affective panorama of neural architecture and signaling dynamics underwriting somatic markers allows us to mature the neuroecological discourse set forth in [2], and in the process, broaden the parameters to include interoception as a faculty critical to cognitive and adaptive neural processing.

2. COGNITION & AFFECT

"Psychoanalysts since Freud have known that emotions affect cognitions without the person being aware of the mechanism" [21].

The contribution of neuroecology to psychology and neuroscience can be traced through the insight it provides on the influence of selective pressures on the evolution of cognition and brain structure across genotypes and within phenotypes.

Increasing evidence suggests that cognition and affect operate in contiguity. Linked to theory of mind [22]; social cognition [23-25]; empathy [26, 27]; emotion [19]; body ownership and sense of self [19, 28], *interoception* provides a multi-modal platform and behavioral interface for adaptation that leverages both affect and cognition. The integrative role between cognitive, sensorimotor, social-emotional and olfacto-gustatory systems has moreover been hypothesized in numerous other studies analyzing links between sensation, affect and cognition [29; see also 6, 30-32]. Recently, Chanes and Barrett suggest that "*in every conscious moment, all modalities are represented, but the type of content that is prioritized may determine whether we categorize the experience as emotion, perception, or cognition*"[14]. Additionally, Duncan and Barrett [33] propose that affect proceeds more like a cognitive faculty with the difference being phenomenal rather than ontological. Thus, echoing [14], there is no such thing as a "non-affective thought."

This motivates the notion of an adaptive basis for cognition and affect based on an *enactivist*, embedded approach [34, 35]. Enactivist theories of perception represent cognition as arising from the dynamical interactions between an organism and its environment [36], making it well-suited to neuroecological needs.

3. INTEROCEPTION

From an evolutionary and adaptive perspective, interoceptive awareness evolved from the afferent limb of the evolutionarily ancient, hierarchical homeostatic system that maintains the integrity of the body's internal operating systems [7], in order to leverage the physiological milieu of the body that guides elements of cognition and adaptive decision-making, as well as affect and behavior.

Originally entailing only visceral sensations arising from the inner organs, *interoception* represents the ability to sense our interior physiological conditions [6, 7] within an active monitoring of the body [41]. This is accomplished by detecting small changes in the coding and perception of body-tissue physiology including: muscles, skin, joints, and viscera [42]. As Herbert *et al*. explain, these "*bodily sensations are intrinsically tied to life, represent relevant signals for survival and well-being, and underlie mood, emotional state, and fundamental cognitive processes*" [40]. Comparative neuroanatomy reveals that hominoids have developed a distinct cortical image of homeostatic afferent activity reflecting each aspect of the physiological condition of all tissues of the body [7].

Visceral information proves especially important to the physiological regulation of the whole organism, as well as in providing a component of behavioral regulation (qua ingestion of food, cardiac autonomic balance, emotional parameters, differential endocrine allostatic responses) and emotional awareness [4, 43-45]. The ability of visceral afferent information to reach awareness and affect behavior represents a hallmark of bottom-up interoception models, pointing to a constant mixing of body-relevant signals with external stimuli to influence motivated behavior [6-9].

This activity is built up through the innervated differential activity of thin-diameter (Aδ and C) primary afferent fibers ascending the neurovisceral axis to a primary target in the posterior insular cortex (PIC). This specifies a ubiquitous information channel [46] actively representing the ever-changing milieu of physiological conditions of the body [6]. In humans, these body representations are then re-mapped from PIC into the mesial insula (MIC) where they are integrated with emotional, cognitive, and motivational information from a network of corollary brain regions [48] before final expression in AIC. This remapping of interoceptive signals in AIC has been proposed to underpin a primary form of self-awareness that also participates the distinction between 'self' and 'other' required for intuitive social interactions [19, 28, 49].

As such, interoceptive awareness represents the end-product of an integration process entailing autonomic, visceral, and immunological (neurocrine and endocrine) signals that collectively situate how we perceive a transient sense for the physiological conditions and differential microbial levels of the body underwriting mood, emotions [see 14, 29, 43], sense of well-being [35], influence on social cognition [4], decision making [36], and intuition [5]-which in ensemble can be taken as representation of "the material me" [7, 50]. This capacity allows for the adaptive ability to respond intuitively to social signals and patterns, as well as providing a rich landscape for empathic interfacing and comparative inference underwriting theory of mind and the principle of affect sampling.

4. TWO CAUSAL MODELS FOR INTEROCEPTION: FEEDFORWARD & FEEDBACK

Stemming out of the maintenance of optimal, internal survival parameters in the body, converging evidence indicates two models for *interoceptive awareness*: a conventional, bottom-up approach in functional neuroanatomy of the *neurovisceral axis* [6, 7, 9, 54, 55], and a recently developed top-down model a la the 'Bayesian brain' axioms [20, 51-53] and *predictive coding* [50, 56, 57-60].

Where bottom-up approaches explain perception in terms of classical, feed-forward feature detection, top-down approaches operate on the basis of inferential, generative (feedback) models [15, 61]. Within these two standards we identify characteristic neural and cortical architectures enabling specific communicative capabilities and processes. In addition, we encounter specialized signal processing pathways and operations tailored to interoceptive awareness, emotion, adaptive intuition and cognition.

In the feed forward model, this entails the neurovisceral axis and insular processing dynamics, plus the *von Economo* neurons, whereas the feedback model includes the Bayesian brain hypothesis comprising *predictive coding*, *active inference* and the *free-energy principle*. Both models propose that the action center of processing takes place in the insular cortex. We briefly review both these models and their key components.

4.1. FEEDFORWARD (Bottom-Up)

Interoceptive awareness in the bottom-up regime models internal activity through an evolutionarily-specialized afferent signal pathway in the neurovisceral axis projecting to the posterior insula (PIC) for further processing and rendering into subjectivized states, transmitted moment-to-moment via '*drops'* [62] of affect finally contextualized in the anterior insula. This includes the role of VENs that project values and can advance predictions rapidly via intrinsic morphological adaptation and functional capacity.

4.1.1. The Neurovisceral Axis

The neurovisceral axis represents a bottom-up, sensory-driven operation built on the neuroanatomy of ascending, homeostatic lamina I (spinal and vagal) pathways leveraging primary afferent (A and C) fibers to bring interoceptive sensations to the brain [9].

The neuroanatomical architecture and corresponding signal dynamics of the neurovisceral axis represents an "unparalleled relationship" [9] of multi-scale, reflexively communicating (afferent and efferent) interoceptive circuits between the microbial ecosystem of the enteric nervous system and gastrointestinal tract, with the higher cortices of the central nervous system. These internal, physiological circuits operate in a supervisory capacity through which viscerosensory afferents are transmitted up to the brain, "*allowing the organism to homeostatically regulate its internal state and giving rise to awareness of bodily feelings like pain, touch and temperature*" [63] required for preserving healthy internal conditions [64].

Primary afferent fibers ascend two pathways, spinal and vagal, to the posterior insular cortex where these signals undergo a multimodal integration of information following a posterior to anterior gradient [8] that transforms them into moment-to-moment affective reports in the AIC. These states, representing *somatic markers*, provide a basis for decision-making as well as an influence on behavior, cognition and attention-plus a direct influence on low-level affective, adrenal and physiological activity [65].

The brain-gut axis is responsible for maintaining the balance and regulation of body systems in participation with the cerebral, autonomic, and enteric nervous systems-and for generating moment-to-moment interoceptive images of the *internalmilieu* (physiological homeostasis) of the human body [7-9, 66, 67], constantly relaying internal needs to subjective awareness [6, 68]. This phylogenetically new pathway conveys homeostatic afferent activity directly to thalamocortical levels in primates. In non-primates this pathway is rudimentary, if at all [7]; however, in all mammals, integrated homeostatic afferent information from the parabrachial nucleus reaches the anterior cingulate and insular cortices by way of the medial thalamic nuclei and the parvicellular ventropostero-medial nucleus of the thalamus [6, 7, 69-71]. This allows us to recognize the evolution of interoceptive dynamics generally (in all mammals) as well as uniquely reflected in adaptations of the neurovisceral axis in primates and humans.As Mayer notes, "*the engagement of circuits outside of the gut wall integrates interoceptive and exteroceptive information to optimize the homeostatic regulation of intestinal function*" [9]. At the widest scale, owing to the fact that the rudiments of the enteric nervous system have been found throughout the animal kingdom, including in insects and snails [9], it is suggested that the ganglia that eventually formed the higher cortices throughout the animal kingdom originated in more-primitive, enteric circuits [75].

To summarize, interoceptive signals result from changes in the viscera, muscles and skin. These signals ascend the neurovisceral axis via primary afferents in the lamina-1 pathway-plus vagal afferents in the nucleus tractus solitarius (NTS), parabrachial nucleus and the thalamus-before arriving to the (laminar) granular layer IV in the posterior insular cortex, where they are received as a raw distribution of signals and information, and collectively in some character tone, which is to take Damasio's *somatic markers* as the raw and unprocessed "*initial feeling*" of a collection of primary afferent fibers.

4.1.2. Interoceptive Insular Dynamics (Bottom-Up)

Brain activity obtained in neuroimaging data during interoceptive and emotional awareness uniformly correlates with pronounced differential activation of the insula [8, 72-74, 76, 77, 87] and anterior cingulate cortex, where spinal and vagal (afferent) neurovisceral pathways culminate. Craig elaborates the identification of a meta-representation of interoceptive activity fostering the subjective sense of embodied emotional awareness in the *right* anterior insular cortex (rAIC) [6, 88]. "The insula constitutes a functionally and cytoarchitectonically diverse region of cortex with subregions involved in gustatory and olfactory processing, somatosensation, interoception, motivation and the maintenance of homeostasis" [84; see also 6, 9, 82, 85, 86]. The insula is unique in that it is situated at the interface of cognitive, homeostatic, affective and sensory systems of the human brain, providing a link between stimulus-driven processing and brain regions involved in monitoring the body's *internal milieu* [78; see also 8, 79]. Differential insular activity has also been reported in processing attention to sensory stimuli like touch, and in distinguishing between awareness of one's heartbeat to an external rhythm [67, 80].

Computationally, the insula can be regarded as a multimodal integration region for evaluating the emotional and motivational salience of certain stimuli, providing an interface between external information and internal motivational states [6, 9, 81-83]. In humans, the insula has reentrant connections with the frontal, parietal and temporal lobes; the cingulate gyrus; plus subcortical structures such as the amygdala, brainstem, thalamus and basal ganglia [89]. These connections serve as an anatomical foundation for the integration of autonomic, viscerosensory, visceromotor and limbic functions.

Further, a posterior-to-anterior gradient in the insular cortex has been recognized in which physical features of interoception are processed in the posterior insula, followed by a subsequent integration of those (primaryafferent) signals with cognitive and motivational information in the middle insula [8, 72, 73], before a final re-representation of the interoceptive/affective moment in the anterior insula. It is here in the agranular, anterior insula where we also find the evolutionarily rare, von Economo neurons.

4.1.3. Von Economo Neurons

The development of the specialized neurovisceral pathway in the hominoid brain represents a response to selection pressures resulting in enhanced fitness qua social information processing [8, 9] and theory of mind. This specialization is anatomically evinced in the evolutionarily-adapted *von Economo* neurons (VENs): a rare morphological-type of neuron (found at the cerebral apex of the neurovisceral circuit) characterized by a large, fusiform soma tapering into a single, apical axon on one pole, and a single dendrite on the other [11]. Surprisingly, VENs appear in only three brain regions (the anterior insular cortex, anterior cingulate cortex, and dorsolateral prefrontal cortex) of a select handful of species (humans; African and Asian great apes; pachyderms and select cetaceans) [90-93]. Each brain region in which VENs are found is integral to a host of functions that render higher-executive, social, emotional, and episodic dispositional capacities, placing them securely within a neuroecological characterization.

Over a few months in 2009, I successfully recruited to my (original) dissertation committee, the CalTech neuroanatomist (and leading researcher associated with VENs): John Allman. During this time we would meet to hike together up Mt. Baldy, in Southern California, along with his two dogs: Luna and Lunita, while discussing these neurons and their role in interoception; their peculiar correlation of high (*post mortem*) cell-counts with old age and longevity; and to consider novel techniques for indirect, *in vivo* cell-counting approximations--while hiking up to a large tree where we would sit to have lunch and talk more.

Indeed, the large axonal size of VENs, plus the morphological simplicity of their dendritic architecture, suggests a specialization for the rapid transmission of information over long distances throughout the brain [11, 12, 94, 95]. This also suggests a role in processing information across sensory modalities in a distributed neural network [11]. As such, VENs are tailored to swiftly render complex and highly-integrated (multimodal) information into a compressed, *simple* signal sent diffusely throughout the brain for immediate awareness and cognitive appraisal strategy in response to affective signaling. We consider regarding these 'simple' signals qua Damasio's *somatic markers* [3, 66]. In addition, VENs express dopamine, serotonin and vasopressin receptors [12, 96], all of which represent neurotransmitters involved in emotion regulation. Von Economo neurons in layer 5b of the anterior cingulate cortex (ACC) have also been shown to be particularly involved in the rapid transmission of signal processes pertaining to *self-experience*, *social decision-making*, *empathy*, *intuition*, and *social bonding* [158]. As Allman explains:

> Intuition is a form of cognition in which many variables are rapidly evaluated in parallel and compressed into a single dimension. This compression facilitates fast decision-making. Typically we are not aware of the logical steps or assumptions underlying this process although intuition is based on experience- dependent probabilistic models. Instead we experience the intuitive process viscerally. Intuition operates largely in the social domain but can also be applied to purely physical situations [as in physics]. Intuition is plastic; it is not instinct, although instinctive feelings may contribute to it. Emotional value judgments contribute to both intuition and deliberation. [12]

During our discussions John made clear that while the morphological adaptation and associated chemical and wiring requirements of VENs suggest an adapted, functional role in the processing, compression and distribution of neurovisceral information-with many degrees of freedom-throughout the brain; still, a formal, functional physiology remains unrealized. Speculating to these ends, Damasio's theory of somatic markers [3] proposes that the monitoring of sensations arising from the gut is crucial to adaptive decision-making. He suggests this provides a biological basis for gut feelings (biological intuition) qua higher-cognitive social instincts and complex decision-making [12] transmitted through somatic markers. Such an identification of somatic markers with VENs also links interoception and the neurovisceral axis, and thereby strongly encourages, at any rate, the motivation of [2] to implicate somatic markers within a computational account of neuroecology.

4.2. Feedback (Top-Down)

"The brain's default mode of interacting with the world is via continuous, intrinsic predictive activity that is more-or-less constrained by sensations coming from the world and the body" [13].

Throughout the ages a handful of thinkers have maintained that perception involves the integrated admixture of pure sensation with unconscious inference. In earliest known roots, this dates back to Alhazen, Rev. Thomas Bayes, Herman von Helmholtz and Charles Sanders Peirce [97-100]. More recently, about thirty years ago Jaynes [101] used Bayesian probability to model mental processes. Over the last few decades the paradigm of bottom-up (accumulative, sensory-driven) neural processing has been augmented by rigorous computational work in top-down systems advancing the logic of *spontaneous activity* [102] *a-la* the *default mode network*; *executive control network*; *resting-state activity*; *predictive coding* [18, 19] and the *free-energy principle* [17, 103], predicated on Bayesian probabilistic operations.

Whereas bottom-up processes are mostly stimulus-driven, top-down processes are steered by value-driven task demands. This comparison details a conjunction updating neurocognitive models to neuroecological ones [102], and advances the dichotomy of top-down and bottom-up processing from an *either/or* to a *both / and* logic. As Friston explains, "*feedforward architectures on their own are not sufficient. […] Feedback connections mediating internal or generative models of how sensory inputs are caused are essential*" [103]. Various other commentaries [*e.g.*, 104-107] also advocate for an interactive paradigm where the integration of top-down and bottom-up information proves crucial for identifying a general organizational principle of the brain [15, 16, 108, 113] and consciousness [109-112].

4.2.1. The Bayesian Brain, Predictive Coding & Free Energy Principle

Theoretical and computational advances in the logical models underwriting neural processing stand poised to advance our understanding of the relationship between brain architecture and signal dynamics through the implementation of applied **Bayesian brain** axioms [20, 99, 113, 114, 115]. In the Bayesian brain hypothesis, the brain represents sensory information probabilistically-in the form of conditional probability distributions-where the probability for a hypothesis can be updated as more evidence/information accrues over experience. Key examples of functional models within top-down paradigms include *predictive coding* [116] and the *free-energy principle* [17].

Predictive coding is predicated on the principle that "*an organism should maintain well-adapted predictive models of its own physical body and of its internal physiological condition*" [19]. The goal of predictive coding is to build models that maximize successful predictions and approach optimalitybyfine-tuning predictions. As Bialek explains:

> The ability to make accurate predictions of future stimuli and the consequences of one's actions are crucial for the maintenance of internal parameters that are key to endogenous survival, as well as to exogenous survival qua social navigation and efficient, appropriate decision-making [117].

Taken as such, predictive coding provides an integrated model accounting for both top-down and bottom-up approaches to cognition and affect. Two principles spearhead the predictive coding programme; first, that the brain continuously generates models of the world through activity in the nervous system that reflects a process of fitting internally-generated predictions with external stimuli [118, 119]. The second principle states that predictions are transferred from hierarchically higher levels of laminar processing to lower ones, whereas signals traveling in the opposite direction encode prediction errors [120; see also: 116, 121, 122].

Within this functional architecture, *top-down* signals convey predictions and *bottom-up* signals convey prediction errors [18, 123, 124]. Top-down predictions involve expectations spanning multiple spatial and temporal scales [125]. This means that the brain anticipates the causes of incoming sensory signals in the form of predictions with the intent of generating increasingly more-optimized models about the sources of those signals. In a complementary sense, top-down, higher-level cortical processes try to predict, or "explain away" [126], the bottom-up sensory information conveyed by lower-level brain regions [20, 103]. This means that it is only the *difference* between the predicted and actual sensory inputs (prediction errors) that is communicated along the cortical hierarchy, back up to multimodal representations in agranular sensory (limbic) cortices [14]. Unexplained elements of the sensory signal are *"pushed upward so as to select new top-down hypotheses that are better able to accommodate the present sensory signal*" [125].

In this sense, predictive coding constrains signals in an *abductive* procedure [100, 127] that down-regulates all predictable signals to leave only the *surprises*. This ensures constant adaptation in a neural and synaptic modeling capacity through the acquisition of new information about unfamiliar states (obtained through prediction-errors, anomalies, surprises) to update generative models and synaptic weights. Such model adjustment and fine-tuning through synaptic precision weighting and gain modulation supplies constant learning and adaptation to the system, striving towards optimality qua minimization of variational free-energy and optimization of allostatic responses [128] for the maintenance of survival parameters.

Even though predictive coding models found initial success in application to vision, exteroception and proprioception, it seems the best application for Bayesian inference comes by virtue of its role in underwriting affective and emotional awareness in the *interoceptive*, neurovisceral axis [see *e.g*. 19, 128], where the goal of predictive processing is to maintain dynamic equilibrium within the body's optimal internal parameters for survival through a minimization of surprises.

Within *interoceptive* predictive coding, bottom-up prediction errors-comprising the signals of primary afferent fibers arriving in PIC-are largely constrained by top-down the predictions [19, 129]. Prediction error can be regarded as *free energy* such that minimizing variational free energy is effectively the same as minimizing prediction error [17, 103]. The goal of this process is to minimize the discrepancy between the brain's prediction and incoming sensory signals (prediction errors); therefore, in order to maximize survival, organisms must avoid surprising states.

The **free-energy principle** [17, 18] states that any self-organizing system maintaining equilibrium with its environment must also minimize its free energy [17]. This implicates every aspect of the brain, from neural activity to synaptic connection strengths, as a process that minimizes variational free energy [130]. Where variational free energy measures the probability of sensory inputs based on the brain's model of how those inputs were caused [130]. This framework assumes that "*the brain uses internal hierarchical models to predict its sensory input and suggests that neural activity (and synaptic connections) try to minimize the ensuing prediction-error, or Helmholtz free-energy*" [131]. This represents a mathematical formulation of how adaptive systems resist a natural tendency to disorder [see 132-136]. Free energy (surprise) can be suppressed by ***a)*** changing sensory input, ***b)*** acting on external states, or ***c)*** by modifying internal states through perception [130; see also 16, 17] and allostasis [128].

Appliedto interoception, the minimization of variational free-energyis predicated on Bayesian probabilistic operations entailing an inferential, predictive-coding scheme that constantly adapts aspects of its model of the system to best reflect the causes of incoming (feedforward) sensory inputs from the neurovisceral axis [130]. This corresponds to the maintenance of essential biological variables-like blood pressure and heart rate-within optimal parameters [56]. Within this construct, we leverage a computational appeal to the free-energy principle qua **minimization of variational free energy** (*variational Bayes*, or *ensemble learning)* [20, 130] to motivate a case for enabling perpetual neural adaptation. This suggests that "*the brain's architecture constructs a vast repertoire of functional states as a generative model of the world […] shaped by the organism's history and tailored to its allostatic needs and motivational goals*" [14].

These principles incorporate the cost of obtaining information as well as the cost of making complex decisions [137, 138]; therefore, validating such theories could help establish frameworks to compare behavior not only in different species and tasks, but also at multiple scales from: single cells [139], neurons and intracellular pathways, to emergent phenomena at the population level, such as the distribution of blood flow in the brain that anticipates future stimuli [140]. Under this model, adaptive changes in neural representation can be viewed as a predictive computation about the properties of stimuli to be received in the near future. By properly allocating neural responses through mechanisms such as adjusting the neural gain in single neurons [141, 142] or the distribution of the preferred stimulus values for different neurons [143-145], neurons can more accurately encode future stimuli in order to provide more reliable information.

The top-down computational feedback procedure can be applied to interoceptive signal-processing dynamics such that bottom-up signals represent the contents being predicted by the active, top-down mechanism. In this way, interoceptive predictions indicate a pattern of activity that represents the expected interoceptive sensations. Interoceptive perception is largely a construct of adaptive beliefs and models kept in check by the actual state of the body. "*Percepts emerge via a recurrent cascade of top-down predictions that involve expectations spanning multiple spatial and temporal scales*" [125]. The associated neural processing for interoceptive perception is linked to the differential activation of *a)* anterior insula and visceromotor signals to the hypothalamus and brainstem; *b)* sends indirectly via subgenual ACC; and *c)* indirectly through multimodal integration network in MIC and primary somatosensory area (S1). As de-Wit explains:

> Inferences about the sensory consequences of homeostatic budgeting are implemented as upcoming visceromotor commands constrained by error signals resulting from the failure of previous predictions to accurately account for incoming interoceptive sensations. [146]

This ensures homeostasis both directly via autonomic regulation and indirectly by shaping actions through influences on decision-making [56]. As such, interoceptive inference contributes to physiological homeostasis by influencing value-based decision-making. This neatly places the somatic marker hypothesis within an embodied predictive coding context [128]. As Gu (*et al*) explain:

The joint involvement of AIC and SI in integrating top-down and bottom-up information suggests that a possible "somatic marker" signal (Damasio, 1996) is activated when the processing of affective visual stimuli is guided by certain top-down requirements. Such signal might be subsequently conveyed to control regions such as ACC and prefrontal cortex for appropriate behavioral output. [57]

For instance, Craig proposes "a parallel specialization of ACC for the support and facilitation of motivational behavior, where ACC receives interoceptive information via an ancillary medial lamina 1 pathway" [7,67].

4.2.2. Interoceptive Insular Dynamics (Top-Down)

Seth and Critchley [50] propose that the AIC also represents the convergence zone between top-down and bottom-up processing where a predictive coding procedure actively minimizes surprise by leveraging the free-energy principle to elicit a constraining effect within interoceptive awareness. As such, interceptive awareness is largely attributed to the constraining element of predictive coding on incoming (neurovisceral) signals, such that only anomalies are made salient for awareness and attention. In this way, feedback signaling reflects an "*explaining-away*" [126] of values in order to render only those that remain unexplained: the anomalies, surprises, or prediction errors. To these ends, the goal of predictive coding is for the brain to *abductively* [147] infer the causes of interoceptive sensations in a Bayesian capacity qua '*inference to the best approximation*' [127]. Here, the insula processes current feeling states linked to interoception, predicted feeling states, prediction error and cognitive evaluation of risk and uncertainty [74], allowing for an evaluation and adaption of the prediction.

> The joint involvement of AIC and SI in integrating top-down and bottom-up information suggests that a possible "somatic marker" signal [3] is activated when the processing of affective visual stimuli is guided by certain top-down requirements. Such signal might be subsequently conveyed to control regions such as ACC and prefrontal cortex for appropriate behavioral output.

When taken together, the top-down and bottom-up models of interoception suggest a two-way causal convergence of signals proposed to meet in the AIC, where bottom-up interoceptive signals are inferentially assessed against top-down predictions based on expectation values within homeostatic parameters [7, 19] and previous synaptic weighting encoded in combination with Edelman's '*perceptual categorization'* interfacing with the reentrant '*value-category memory*' to abductively resolve outliers to predicted values for enhanced salience in the AIC/ACC salience network.

4.2.3. Cortical Laminar Processing and the EPIC Model

In response to early suggestions that the AIC was solely responsible for intéroceptive predictive coding, Barrett and Simmons [13] consider that such an important procedure wouldn't be left to only one region of the brain, and instead represents a paradigm example of a larger dynamic exhibited in cortico-cortical and limbic cellular processing. Tracing the free-energy principle and predictive coding through current theoretical and computational channels, they clarify notion of a causal relationship between corticocortical connections interfacing in the laminar layers of the brain [13] to provide a neural basis for the incipient processing underwriting *interoception*, *perception*, *behavior* and *action*. This includes the role of adaptive models leading to cognitive and behavioral strategies informing allostatic responses and adaptive model refining. To these ends, Barrett and Simmons develop the "EPIC" model (**e**mbodied **p**redictive **i**nteroceptive **c**oding) to provide "*a systematic variation of laminar structure of the cortex that integrates a structural theory of corticocortical connections with the principle of predictive coding to propose an interoceptive system in the brain*" [13].

Both the insular processing and EPIC models of interoceptive predictive coding ensure significant outlier signals are made salient in attentional awareness for appraisal and allostatic response. In the bottom-up approach, this information is made salient through dual activation of the AIC and ACC (salience network). Alternatively, in the predictive coding [19, 103] and EPIC [13] models, salience comes from the differential gain adjustment of superficial agranular signals onto deep-layered, granular cells (interoceptive signals, prediction errors) based on generative models.

Within the insula, we consider the nuances of a tripartite cytological organization and multimodal information processing dynamics. The insula can be subdivided into a posterior, medial and anterior region corresponding with granular, dysgranular and agranular cell-types, respectively.

Chanes and Barrett [14] claim that the insular gradient dynamics of interoceptive information processing could generalize to all corticocortical processing. Specifically, they model limbic cortices at the highest layer of processing in the cortex, projecting predictions from less-laminated, agranular cortical regions onto superficial layers of highly-granulated (and laminated) cortices [14]. This updates agranular limbic cortices-like the AIC-such that they are no longer simply reacting to stimuli from the world, but are actually *anticipating* it. For instance, den Ouden gathers evidence supporting the putamen as a gating mechanism between motor procedures and sensory expectations based on predictive and efficient coding in brain [148].

Together, this identifies an alternative to classical notions of perception as simply a bottom-up enterprise of evidence accumulation and feature detection, suggesting instead that interoceptive awareness of perceptual content also results from descending limbic predictions contextualized from hierarchically-organized generative models reflecting the expected state of sensory signals from the body and constrained against ascending interoceptive sensations [19].

CONCLUSION

Précis

The purpose of the present edition is to develop neuroecology in the capacity of a causal relationship between brain architecture and corresponding signal dynamics with distinct behavioral strategies subsumed under cognition and adaptation. We consider that cognition and adaptation alone, however, are not enough to provide a sufficient basis for neuroecology without also including the important role of*affect* on behavior. By revising the definitional parameters of neuroecology to include affect qua interoception and the neurovisceral axis, we provide a more rigorous and intuitive foundation for future experimental approaches and conceptual foundations.

Building off the preliminary groundwork established in [2] for a computational neuroecology of somatic markers provides the necessary platform for this present work; however, it also leaves much to be developed. Specifically, it becomes essential to elaborate somatic markers within the neuroanatomical and cellular context of interoception and the neurovisceral axis. This article identifies feedforward (bottom-up) and feedback (top-down) models of interoceptive processing in the corollary context of the neurovisceral axis, homeostasis, intuition (as gut-feelings), von Economo neurons, predictive coding, the free-energy principle and precision weighting.

Feedforward interoceptive signaling confers the existence of a common phylogenetic platform exhibiting evolutionarily-specialized and adaptive mechanisms in the human and in primates. This includes a biological basis for 'gut intuition' as well as enhanced affective awareness pathways of internal states of the body through the thalamus. This operates on the implicit ontological claim that "*perception follows sensation and therefore bodily feelings originate in the body*" [13]. However, such a line of reasoning has led to subsequently incomplete theories of interoceptive awareness when weighed against evidence for predictive modulation predicated on top-down approximations of Bayesian inferential modeling.

In the feedback approach, affect, qua subjective feeling states of emotion, is seen as the result of interoceptive predictive coding arising from "*actively-inferred, generative models on the causes of interoceptive afferents*" [19]. Here, interceptive awareness is computationally attributed to the constraining element of predictive coding on incoming (neurovisceral) signals, such that only anomalies are made salient for awareness and attention. In addition to embodiment theories, this approach also generalizes '*appraisal*' theories [149, 150] that consider emotions as emerging from cognitive evaluations of physiological changes. The fact that interoception and the brain-gut axis are predicated on homeostasis (qua balance and maintenance of optimal survival parameters) demonstrates a solid link to adaptive and regulatory systems within the body in terms of modeling the internal milieu. This follows the idea from Ashby that "every good regulator of a system must also be a model of that system" [151].

From a top-down perspective, generative models of a system are adaptively appealing given their constant optimization of expectations and predictions in response to new, incoming data. The mechanism in which they realize this optimization is through the minimization of (variational) free energy in conjunction with a fine-tuning of synaptic and precision weighting and gain modulation of lower sensory neurons in cortical laminar layer processing. This secures a constant adaptation in the organism aimed at *optimization* [20] within modeling and predictions about the external world, including influences on our internal worlds (physiology, cognition). This suggests an ecological principle at work in top-down processing to the extent that expectations can exert an influence on perception and the processing of bottom-up stimuli.

The neurovisceral axis enables a modelling of intuitive decision making based on the representation of affective, somatic markers [152] predicated on gut responses working in concert with the evolutionarily rare and morphologically specialized von Economo neurons (VENs), found only in species with a highly complex social structure and sense of self - and most pronounced by far in the human brain [12, 153]. Also of note, in a top-down capacity Friston [154] provisionally implicates VENs in a 'privileged' role for sending advanced predictions from the insula to the amygdala and hypothalamus [see also 155].

In another sense, the parameters of neuroecology are closely related to "integrative neuroscience," where both epitomize top-down and bottom-up phenomenological models as well as theoretical and philosophical foundations for explicit hierarchical and functional integration in the brain [156]. In addition, integrative neuroscience provides an express focus on the brain as an adaptive system [157], focusing on the functional organization of brain systems across hierarchical levels leading to species-typical behaviors [156]. We propose developing this connection further in the future.

Closing Remarks

The goal of this special edition is to "uncover the causal relations between brain architecture and signal dynamics with behavioral strategies subsumed in cognition and adaptation." This paper provides substantive support for an expansion of the defining parameters of neuroecology to include an affective processing dimension-qua interoception-as an essential and complimentary basis to accompany cognitive and adaptive components. To wit, interoception provides a paradigmatic modality precisely combining neural and cortical brain architecture and signal dynamics within underwriting cognitive and adaptive behavioral strategies such as decision-making, problem solving, cognition; memory, recall and computation. These behavioral strategies are causally related to the brain architecture and signal dynamics in computational and predictive top-down models, and in neuroanatomical and physiological bottom-up models. The common denominator of these relationships can be harnessed within the multimodal context of interoception.

Predicated on homeostasis, adaptation, perception and cognition, *interoception*, as the sense of the internal physiological condition of the body, provides a secure basis for contextualizing all of the criteria outlined in the main challenge of this special journal issue. It underwrites the moment-to-moment experience that includes constituents perceived: cognitively, affectively, motivationally, in awareness, attention, salience and learning-as well as from the special faculties of intuition, insight and situational-instinct, all made available through a biological-leveraging of pathways in the bottom-up, neurovisceral axis, whose functional architecture enables enhanced representation of active information. Homeostasis is taken as a key organizing principle of neuroecology.

In the bottom-up model, the development of this specialized pathway in hominoid neurovisceral architecture indicates a response to selection pressures resulting in enhanced fitness qua social information processing [8, 9], cooperationand empathy. Functionally, the brain and gut are in almost-constant communication, sending various neurocrine and endocrine signals back and forth to such an extent that they participate in an overall, neurovisceral axis whose end-products are raised into awareness through the specialized sensory-modality of interoception with attributes of salience, affect and intuition.

Specifically, the gut-brain axis generates moment-to-moment interoceptive maps of the internal milieu (interior condition) of the human body [7-9, 67, 152]. In humans, a meta-representation of this interoceptive activity is represented in the right anterior insula, providing a subjective image of the emotionally aware, material self [8, 9, 19]. This meta-representation of interoceptive activity emerges from the dynamics of this hierarchical, reflexive (neurovisceral) axis with integrated networks of circuitry responsible for maintaining the homeostatic balance of body systems in participation with cerebral, autonomic, and enteric nervous systems. As such, the neurovisceral communication axis renders interoception and gut-feelings against the backdrop of homeostasis, as one of the essential organizing principles of body systems.

As such, interoceptive affect is the result of value-deviations from homeostasis recorded within ascending (spinal and vagal) afferent fibers projecting up to the insula, where they are rendered into feelings that characterize and accompany specific, momentary physiological distinctions in the body. Primary afferent fibers carry details about the internal, visceral states associated with differential activity and responses in body physiology (to sensory and external inputs) across the range of the neurovisceral axis and experientially-contextualizing in the special sense-capacities of *interoception* and *intuition* (gut-feelings) operating alongside top-down motivated conditioning on perception and expectation-values. As Buldeo explains, "*afferent information traveling from the body to the central nervous system enables the body to holistically control or maintain this homeostatic milieu interieur*" [63]. The differential streaming effect and contents of these affective feelings translate into our experience of emotions. This is known as the 'homeostatic model of emotion' [6]. This compliments one of the express goals of neuroecology to contextualize how natural selection acts on the neural mechanisms underwriting cognition and adaptation [1].

We are further able to draw this out through the morphological adaptation of the evolutionarily- and functionally-specialized *von Economo* neurons and their proposed role in difficult problem-solving, social decision-making and intuition, plus sense of humor [12]. These evolutionarily-unique neurons-*found only in the brains of a handful of species all sharing advanced social structures*-add additional cytoarchitectonic and proteomic layers onto the picture of how moment-to-moment affective and interoceptive multi-state dynamics are hypothesized to rapidly confer as packets of intuition transferred from the gut to the brain [91, 153] as *somatic markers* of awareness in consciousness.

Neuroecology adds an additional dimension to neuroethology insofar as establishing critical links between neural processes and "community-level consequences of individual behavior" [160]. In this sense, the rapid and complex processing of social information (tailored by morphology and laminar location of VENs) into simple signals might enable the facilitation of intuitive decision-making. Here, intuitive decision making is based on the interpretive appraisal of affective, 'somatic markers' predicated on gut responses working in concert with the neuro-morphologically adapted VENs, to enable fast-paced decisions based on interoceptive stimuli [159] predicated in the 'supercomputer' of enteric computations-with many degrees of freedom more than in a cognitive capacity.

In the top-down regime, applying the neuroanatomical predictive coding model of [13, 14] to interoception provides a compelling basis for expounding the provisional account of computational neuroecology qua somatic markers, as evinced in [2]. This suggests that the value deviations from predictions, when synthesized in AIC, represent the somatic markers that lead to differential activation of the salience network qua structure forms of contextual repertoires from past experiences. Within this model, the minimization of variational free energy (surprise) is considered more intuitive for physiological states than for environmental states; thus, interoceptive inference appears as a most natural expression of the Bayesian brain, even more than original formulations in exteroceptive contexts like vision [20, 56, 161].

The view that prediction and error-correction provide fundamental principles for understanding neural processing is gaining increasing traction within the cognitive and brain sciences. Predictive coding provides a constantly-adaptive, integrative, regulatory and corrective monitoring capacity on sensory and external signals.

Interfacing top-down and bottom-up neurosignaling dynamics are considered to engage two levels of interoceptive processing: *a)* in the anterior insular cortex, as a multi-modal comparator region [6, 39] and synthesizing platform for interoceptive afferents arriving in the posterior insula from the neurovisceral axis [see 9, 10]; and *b)* in the generalized intracortical (corticocortical processing) of the EPIC model [13] within the laminar architecture and corresponding signal dynamics [38] from agranular to granular cortices (less-laminated to highly-laminated layers) of the Limbic Workspace model of [14].

This suggests that an incorporation of interoceptive affect-in combination with cognition and adaptation-will shed critical light on further efforts to organize the driving epistemic structure and phenomenology associated with neuroecology. Thus, through interoception we are drawn into acquaintance with our inner ecology.

REFERENCES

[1] Sherry DF. Neuroecology. Annu Rev Psychol 2006; 57:167-97. https://doi.org/10.1146/annurev.psych.56.091103.070324

[2] Harrington K, Olsen M and Siegelmann H. Communicated Somatic Markers Benefit Both the Individual and the Species. In 2011 Intl. Joint Conf. on Neural Networks (IJCNN), 2011; 3272-3278

[3] Damasio A, Everitt B and Bishop D. The Somatic Marker Hypothesis and the Possible Functions of the Prefrontal Cortex. Philos. Trans.: Bio Sci 1996; 351(1346): 1413-1420. https://doi.org/10.1098/rstb.1996.0125

[4] Bechara, Antoine, Hanna Damasio and Antonio R. Damasio. "Emotion, decision making and the orbitofrontal cortex." Cerebral cortex, no. 2000; 10(3): 295-307. https://doi.org/10.1093/cercor/10.3.295

[5] Bechara, Antoine, Hanna Damasio, Daniel Tranel and Antonio R. Damasio. "The Iowa Gambling Task and the somatic marker hypothesis: some questions and answers." Trends in cognitive sciences 2005; 9(4): 159-162. https://doi.org/10.1016/j.tics.2005.02.002

[6] Craig, Arthur D. "How do you feel? Interoception: the sense of the physiological condition of the body." Nature reviews neuroscience 3.8 2002: 655-666. https://doi.org/10.1038/nrn894

[7] Craig AD. "Interoception: the sense of the physiological condition of the body." Current opinion in neurobiology 2003; 13.4: 500-505. https://doi.org/10.1016/S0959-4388(03)00090-4

[8] Craig AD. How do you feel - now? The anterior insula and human awareness. Nat. Rev. Neurosci 2009; 10: 5-70.

[9] Mayer, Emeran A. "Gut feelings: the emerging biology of gut–brain communication." Nature Reviews Neuroscience 2011; 12.8: 453-466. https://doi.org/10.1038/nrn3071

[10] Hochner B. How nervous systems evolve in relation to their embodiment: what we can learn from octopuses and other molluscs. Brain Behav Evol 2013; 82:19-30. https://doi.org/10.1159/000353419

[11] Allman J, Hakeem A, Watson K. "Two phylogenetic specializations in the human brain". Neuroscientist 2002; 8(4): 335-46 https://doi.org/10.1177/107385840200800409

[12] Allman JM, Watson KK, Tetreault NA, Hakeem AY. Intuition and autism: a possible role for Von Economo neurons. Trends Cogn Sci 2005; 9:367-373. https://doi.org/10.1016/j.tics.2005.06.008

[13] Barrett, Lisa Feldman, and W. Kyle Simmons. "Interoceptive predictions in the brain." Nature Reviews Neuroscience 16, no. 7 (2015): 419-429. https://doi.org/10.1038/nrn3950

[14] Chanes, Lorena, and Lisa Feldman Barrett. "Redefining the role of limbic areas in cortical processing." Trends in cognitive sciences 2016; 20(2): 96-106. https://doi.org/10.1016/j.tics.2015.11.005

[15] Friston, Karl; Learning and Inference in the Brain; Neural Networks 2003; 16(9): 1325-52. https://doi.org/10.1016/j.neunet.2003.06.005

[16] Friston K, Samothrakis S, Montague R. Active inference and agency: optimal control without cost functions. Biol Cybern. 2012 https://doi.org/10.1007/s00422-012-0512-8

[17] Friston K, Kilner J, Harrison L. A free energy principle for the brain. Journal of Physiology-Paris 2006; 100: 70-87. doi: 10.1016/j.jphysparis.2006.10.001 https://doi.org/10.1016/j.jphysparis.2006.10.001

[18] Friston K. The free-energy principle: a rough guide to the brain? Trends Cogn Sci 2009; 13: 293-301. https://doi.org/10.1016/j.tics.2009.04.005

[19] Seth AK. Interoceptive inference, emotion, and the embodied self; Trends in Cognitive Sciences 2013; 17(11): 565-573 https://doi.org/10.1016/j.tics.2013.09.007

[20] Friston K. The free-energy principle: a unified brain theory? Nat Rev Neurosci 2010; 11, 127- 138. https://doi.org/10.1038/nrn2787

[21] Hoffman Leon MD. "Emotions Affect Cognitions," 23 October 2011. [Online]. Available: https://www.psychologytoday.com/blog/beyond-freud/201110/emotions-affect-cognitions. [Accessed 26 August 2016].

[22] Ondobaka S, Kilner J, Friston K. The role of interoceptive inference in theory of mind. Brain and Cognition 2015. https://doi.org/10.1016/j.bandc.2015.08.002

[23] Melloni M, Sede-o L, Couto B, Reynoso M, Gelormini C, Favaloro R, Ibanez A. Preliminary evidence about the effects of meditation on interoceptive sensitivity and social cognition. Behavioral and Brain Functions : BBF, 2013; 9: 47. https://doi.org/10.1186/1744-9081-9-47

[24] Garfinkel Sarah N and Hugo D. Critchley; Interoception, emotion and brain: new insights link internal physiology to social behaviour. Commentary on: "Anterior insular cortex mediates bodily sensibility and social anxiety" by Terasawa *et al.*; Soc Cogn Affect Neurosci 2013; 8(3): 231-234. doi: 10.1093/scan/nss140 https://doi.org/10.1093/scan/nss140

[25] Garfinkel SN, Seth AK, Barrett AB, Suzuki K, Critchley HD. Knowing your own heart: distinguishing interoceptive accuracy from interoceptive awareness; Biological Psychology 2015; 104: 65-74. https://doi.org/10.1016/j.biopsycho.2014.11.004

[26] Fukushima H, Terasawa Y, Umeda S. Association between interoception and empathy: evidence from heartbeat-evoked brain potential; Int. J Psychophysiol 2011; 79: 259-265. https://doi.org/10.1016/j.ijpsycho.2010.10.015

[27] Ainley V, Maister L, Tsakiris M. Heartfelt empathy? No association between interoceptive awareness, questionnaire measures of empathy, reading the mind in the eyes task or the director task. Frontiers in Psychology 2015; 6: 554. https://doi.org/10.3389/fpsyg.2015.00554

[28] Tsakiris M, Jiménez AT, Costantini M. Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations. Proceedings of the Royal Society B: Biological Sciences 2011; 278(1717): 2470-2476. https://doi.org/10.1098/rspb.2010.2547

[29] Kurth F, Zilles K, Fox PT, Laird AR, and Eickhoff SB. A link between the systems: functional differentiation and integration within the human insula revealed by meta-analysis. Brain Structure & Function 2010; 214(5-6): 519-534. https://doi.org/10.1007/s00429-010-0255-z

[30] Chen LM. Imaging of pain. Int Anesthesiol Clin 2007; 45: 39-57. https://doi.org/10.1097/AIA.0b013e31803419d3

[31] Dolan RJ. Emotion, cognition, and behavior. Science 2002; 298: 1191-1194. https://doi.org/10.1126/science.1076358

[32] Frith CD, Singer T. The role of social cognition in decision making. Philos Trans R Soc Lond B Biol Sci 2008; 363: 3875-3886. https://doi.org/10.1098/rstb.2008.0156

[33] Duncan S. and Barrett LF. Affect is a form of cognition: A neurobiological analysis Cogn Emot 2007; 21, 1184-1211.

[34] de Bruin L and de Haan S. Enactivism & social cognition: In search of the whole story.Journal of Cognitive Semiotics 2012; 4(1): 225-250.

[35] de Bruin LC, and Kastner L. Dynamic embodied cognition. Phenomenology and the Cognitive Sciences 2012; 11(4); 541-563. https://doi.org/10.1007/s11097-011-9223-1

[36] van Elk M, Slors M, and Bekkering H. Embodied language understanding requires an enactivist paradigm of cognition. Front Psychol 2010; 1: 234. https://doi.org/10.3389/fpsyg.2010.00234

[37] Trehub A. Neuronal models for cognitive processes: Networks for learning, perception, and imagination. Journal of Theoretical Biology 1977; 65:141-69. https://doi.org/10.1016/0022-5193(77)90081-9

[38] Barsalou LW. Being there conceptually: Simulating categories in preparation for situated action. In: Stein NL, Bauer PJ, Rabinowitz M, editors. Representation, memory, and development: Essays in honor of Jean Mandler. Mahwah, NJ: Lawrence Erlbaum Associates, Inc; 2002; 1-15

[39] Barsalou LW, Niedenthal PM, Barbey AK, Ruppert JA. Social embodiment. In: Ross BH, editor. The psychology of learning and motivation. 43. San Diego, CA: Academic Press; 2003a. p. 43-92. https://doi.org/10.1016/s0079-7421(03)01011-9

[40] Herbert Beate M, and Olga Pollatos. "The body in the mind: on the relationship between interoception and embodiment." Topics in cognitive science 2012; 4(4): 692-704. https://doi.org/10.1111/j.1756-8765.2012.01189.x

[41] Arnhart Larry. "Darwinian Conservatism." (Blog Comment of

June 8, 2011: http://darwinianconservatism.blogspot.com/2011/06/bud-craigon-interoception-and.html.)

[42] Dunn Barnaby D, Hannah C Galton, Ruth Morgan, Davy Evans, Clare Oliver, Marcel Meyer, Rhodri Cusack, Andrew D. Lawrence, and Tim Dalgleish. "Listening to Your Heart: How Interoception Shapes Emotion Experience and Intuitive Decision Making." Psychological science 2010; 1835-1844. https://doi.org/10.1177/0956797610389191

[43] Cameron Oliver G, and Satoshi Minoshima. "Regional brain activation due to pharmacologically induced adrenergic interoceptive stimulation in humans." Psychosomatic medicine 2002; 64(6): 851-861.

[44] Naqvi, Ammar, Huzefa Rangwala, Ali Keshavarzian, and Patrick Gillevet. "Network-Based Modeling of the Human Gut Microbiome." Chemistry & biodiversity 2010; 7(5): 1040-1050. https://doi.org/10.1002/cbdv.200900324

[45] Ernst, Jutta, Heinz Böker, Joe Hättenschwiler, Daniel Schüpbach, Georg Northoff, Erich Seifritz, and Simone Grimm. "The association of interoceptive awareness and alexithymia with neurotransmitter concentrations in insula and anterior cingulate." Social cognitive and affective neuroscience 2013: 857-63.

[46] Tsakiris, Manos, Ana Tajadura-Jiménez, and Marcello Costantini. "Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations." Proceedings of the Royal Society of London B: Biological Sciences (2011); 278(1717): 2470-2476. https://doi.org/10.1098/rspb.2010.2547

[47] Damasio, Antonio R, Thomas J. Grabowski, Antoine Bechara, Hanna Damasio, Laura LB Ponto, Josef Parvizi, and Richard D. Hichwa. "Subcortical and cortical brain activity during the feeling of self-generated emotions." Nature neuroscience (2000); 3(10): 1049-1056. https://doi.org/10.1038/79871

[48] Barlassina, Luca, and Albert Newen. "The Role of Bodily Perception in Emotion: In Defense of an Impure Somatic Theory." Philosophy andPhenomenological Research (2014); 3(89): 637-78. https://doi.org/10.1111/phpr.12041

[49] Tajadura-Jiménez, Ana, and Manos Tsakiris. "Balancing the "inner" and the "outer" self: Interoceptive sensitivity modulates self–other boundaries." Journal of Experimental Psychology: General (2014); 2(143): 736. https://doi.org/10.1037/a0033171

[50] Seth, Anil K., and Hugo D. Critchley. "Extending predictive processing to the body: emotion as interoceptive inference." Behavioral and BrainSciences (2013); 3(36): 227-228. https://doi.org/10.1017/S0140525X12002270

[51] Helmholtz, Hermann; "The Facts of Perception" (1878); in Selected writings of Hermann von Helmholtz, ed., with an introduction, by Russell Kahl. Middletown, Connecticut: Wesleyan University Press, 1971.

[52] Dayan, Peter, Geoffrey E. Hinton, Radford M. Neal, and Richard S. Zemel. "The helmholtz machine."Neural computation (1995); 7(5): 889-904. https://doi.org/10.1162/neco.1995.7.5.889

[53] Battaglia PW, Jacobs RA, Aslin RN. Bayesian integration of visual and auditory signals for spatial localization. J Opt Soc Am A Opt Image Sci Vis 2003; 20: 1391-1397. doi: 10.1364/josaa.20.001391 https://doi.org/10.1364/JOSAA.20.001391

[54] Craig AD. "An ascending general homeostatic afferent pathway originating in lamina I." Progress in brain research (1995); 107: 225-242. https://doi.org/10.1016/S0079-6123(08)61867-1

[55] Craig AD. How do you feel? An interoceptive moment with your neurobiological self. New Jersey: Princeton University Press, 2015. https://doi.org/10.1515/9781400852727

[56] Seth Anil K. Response to Gu and FitzGerald: interoceptive inference: from decision-making to organism integrity.Trends in Cognitive Sciences 2014; 18(6): 270-271. ISSN 1364-6613

[57] Gu X, Hof PR, Friston KJ, Fan J. Anterior insular cortex and emotional awareness. J Comp Neurol 2013; 521 (15), 3371-3388. https://doi.org/10.1002/cne.23368

[58] Sel A. Predictive codes of interoception, emotion, and the self. Front Psychol 2014; 4 (5): 189. https://doi.org/10.3389/fpsyg.2014.00189

[59] Scarpelli S, D'Atri A, Gorgoni M, Ferrara M and De Gennaro L. EEG oscillations during sleep and dream recall: state- or trait-like individual differences? Front Psychol 2015; 6: 605. https://doi.org/10.3389/fpsyg.2015.00605

[60] Farb N, Daubenmier J, Price CJ, Gard T, Kerr C, Dunn BD *et al*. Interoception, contemplative practice, and health Front Psychol 2015; 6: 763. doi: 10.3389/fpsyg.2015.00763 https://doi.org/10.3389/fpsyg.2015.00763

[61] Li Min, Baohong Wang, Menghui Zhang, Mattias Rantalainen, Shengyue Wang, Haokui Zhou, Yan Zhang *et al*. "Symbiotic gut microbes modulate human metabolic phenotypes. "Proceedings of the National Academy of Sciences, no 2008; 105(6): 2117-2122. https://doi.org/10.1073/pnas.0712038105

[62] James William. The Principles of Psychology, 2 vols. (1890), Dover Publications 1950; 1: ISBN 0-486-20381-6

[63] Buldeo, Nitasha. "Interoception: A Measure of Embodiment or Attention?." International Body Psychotherapy Journal 2015; 14(1).

[64] Verdejo-Garcia A, Clark L, and Dunn BD. The role of interoception in addiction: a critical review. Neuroscience & Biobehavioral Reviews Rev 2012; 36(8): 1857- 1869 https://doi.org/10.1016/j.neubiorev.2012.05.007

[65] Raison CL, Hale MW, Williams LE, Wager TD, and Lowry CA. Somatic influences on subjective well-being and affective disorders: the convergence of thermosensory and central serotonergic systems. Front Psychol Cogn 2015; 5: 1580. https://doi.org/10.3389/fpsyg.2014.01580

[66] Damasio A. Self Comes to Mind: Constructing the Conscious Brain. New York, NY: Pantheon Books, Random House 2010.

[67] Critchley HD, Wiens S, Rotshtein P, Öhman A and Dolan RD. Neural systems supporting interoceptive awareness. Nat Neurosci 2004; 7: 189-195. doi: 10.1038/nn1176 https://doi.org/10.1038/nn1176

[68] Harrison NA *et al*. The embodiment of emotional feelings in the brain. J Neurosci 2010; 30: 12878-12884 https://doi.org/10.1523/JNEUROSCI.1725-10.2010

[69] Saper CB: The central autonomic nervous system: conscious visceral perception and autonomic pattern generation. Annu Rev Neurosci 2002; 25: 433-469. https://doi.org/10.1146/annurev.neuro.25.032502.111311

[70] Krout KE, Loewy AD: Parabrachial nucleus projections to midline and intralaminar thalamic nuclei of the rat. J Comp Neurol 2000; 428: 475-494 https://doi.org/10.1002/1096-9861(20001218)428:3<475::AID-CNE6>3.0.CO;2-9

[71] Zhang ZH, Oppenheimer SM: Baroreceptive and somatosensory convergent thalamic neurons project to the posterior insular cortex in the rat Brain Res 2000; 861: 241-256. https://doi.org/10.1016/S0006-8993(00)01990-9

[72] Craig AD. The sentient self. Brain Struct Funct 2010; 214: 563-577. https://doi.org/10.1007/s00429-010-0248-y

[73] Craig AD. Significance of the insula for the evolution of human awareness of feelings from the body. Ann. NY Acad Sci 2011; 1225: 72-82. https://doi.org/10.1111/j.1749-6632.2011.05990.x

[74] Singer T *et al*. A common role of insula in feelings, empathy and uncertainty. Trends Cogn Sci 2009; 13: 334-340 https://doi.org/10.1016/j.tics.2009.05.001

[75] Bullock, Theodore, and Adrian Horridge G. "Structure and function in the nervous systems of invertebrates 1965.

[76] Wiebking C and Northoff G. Interoceptive Awareness and the Insula – Application of Neuroimaging Techniques in Psychotherapy; GSTF International Journal of Psychology J Psych 2014.

[77] Seth AK, Suzuki K and Critchley HD. An interoceptive predictive coding model of conscious presence. Front Psychol 2011; 2: 395.

[78] Bernard, Claude. Introduction à l' étude de la médecine expérimentale. Baillière, 1865.

[79] Menon Vinod, and Lucina Q. Uddin. "Saliency, switching, attention and control: a network model of insula function." Brain Structure and Function (2010); 214(5-6): 655-667. https://doi.org/10.1007/s00429-010-0262-0

[80] Johansen-Berg H and Matthews PM; Attention to movement modulates activity in sensorimotor areas including primary motor cortex; Experimental Brain Research 2002; 142: 13-24. https://doi.org/10.1007/s00221-001-0905-8

[81] Mesulam MM and Mufson EJ. Insula of the old world monkey. III: efferent cortical output and comments on function. J Comp Neurol 1982; 212: 38-52. https://doi.org/10.1002/cne.902120104

[82] Augustine JR. Circuitry and functional aspects of the insular lobe in primates including humans. Brain Res Rev 1996; 22: 229-244. https://doi.org/10.1016/S0165-0173(96)00011-2

[83] Seeley WW, Merkle FT, Gaus SE, Craig AD, Allman JM, Hof PR. Distinctive neurons of the anterior cingulate and frontoinsular cortex: a historical perspective; Cereb Cortex 2012; 22(2): 245-250. https://doi.org/10.1093/cercor/bhr005

[84] Deen B, Pitskel NB, Pelphrey KA. Three systems of insular functional connectivity identified with cluster analysis. Cereb Cortex 2011; 21: 1498-1506. https://doi.org/10.1093/cercor/bhq186

[85] Small DM, Gregory MD, Mak YE, Gitelman D, Mesulam MM, Parrish T. Dissociation of neural representation of intensity and affective valuation in human gustation; Neuron 2003; 39: 701-711 https://doi.org/10.1016/S0896-6273(03)00467-7

[86] Olausson H *et al*. Unmyelinated tactile afferents signal touch and project to insular cortex. Nature Neurosci 2002; 5: 900-904 https://doi.org/10.1038/nn896

[87] Gu X, Hof PR, Friston KJ, Fan J. Anterior insular cortex and emotional awareness. J Comp Neurol 2013; 521(15): 3371-3388. https://doi.org/10.1002/cne.23368

[88] Craig Arthur D, Kewei Chen Bandy D and Eric M. Reiman. "Thermosensory activation of insular cortex." Nature neuroscience 2000; 3(2): 184-190. https://doi.org/10.1038/72131

[89] Flynn FG, Benson DF, Ardila A. Anatomy of the insula functional and clinical correlates. Aphasiology 1999; 13:55-78. https://doi.org/10.1080/026870399402325

[90] Fajardo, Escobar MI, Buriticá E, Arteaga G, Umbarila J, Casanova MF *et al*. "Von Economo neurons are present in the dorsolateral (dysgranular) prefrontal cortex of humans.". Neuroscience Letters 2008; 435 (3): 215-218 https://doi.org/10.1016/j.neulet.2008.02.048

[91] Butti C, Sherwood CC, Hakeem AY, Allman JM, Hof PR. "Total number and volume of Von Economo neurons in the cerebral cortex of cetaceans."The Journal of comparative neurology 2009; 515(2): 243-59 https://doi.org/10.1002/cne.22055

[92] Hakeem AY, Sherwood CC, Bonar CJ, Butti C, Hof PR, Allman JM. "Von Economo neurons in the elephant brain". The Anatomical Record (Hoboken) 2009; 292 (2): 242-248 https://doi.org/10.1002/ar.20829

[93] Allman JM *et al*. The von Economo neurons in frontoinsular and anterior cingulate cortex in great apes and humans. Brain Struct Funct 2010; 214: 495-517 https://doi.org/10.1007/s00429-010-0254-0

[94] Nimchinsky Esther A, Brent A Vogt, John H Morrison and Patrick R Hof. "Neurofilament and calcium-binding proteins in the human cingulate cortex."The Journal of comparative neurology 1997; 384(4): 597-620. https://doi.org/10.1002/(SICI)1096-9861(19970811)384:4<597::AID-CNE8>3.0.CO;2-Y

[95] Nimchinsky EA, Gilissen E, Allman JM, Perl DP, Erwin JM, Hof PR. "A neuronal morphologic type unique to humans and great apes". Proc Natl Acad Sci USA 1999; 96 (9): 5268-73 https://doi.org/10.1073/pnas.96.9.5268

[96] Stimpson CD, Tetreault NA, Allman JM, Jacobs B, Butti C, Hof PR *et al*. Biochemical specificity of von Economo neurons in hominoids; Am. J. Hum. Biol 2011; 23: 22-28 https://doi.org/10.1002/ajhb.21135

[97] Alhazen (Ibn al-Haytham). Critique of Ptolemy. Pines S, trans. Actes X Congrès internationale d'histoire des sciences, Vol I. Ithaca 1962, as referenced in: Sambursky S, ed. Physical thought from the Presocratics to the quantum physicists. New York: Pica Press 1974: 139.

[98] Bayes T. An Essay towards solving a problem in the doctrine of chances. Phil. Trans. Roy. Soc. London 1764; 53: 370-418. https://doi.org/10.1098/rstl.1763.0053

[99] von Helmholtz H 1866. Concerning the perceptions in general, 3rd edn. Treatise on Physiological Optics, Vol. III (translated by J. P. C. Southall 1925 Opt. Soc Am Section 26, reprinted NY: Dover 1962).

[100] Peirce, Charles Sanders. "On the natural classification of arguments." In Proceedings of the American Academy of Arts and Sciences, 1867; 7: 261-287. https://doi.org/10.2307/20179566

[101] Jaynes ET. `How Does the Brain Do Plausible Reasoning?', in Maximum-Entropy and Bayesian Methods in Science and Engineering, 1, GJ. Erickson and CR. Smith (eds.) 1988. https://doi.org/10.1007/978-94-009-3049-0_1

[102] Northoff G. Neuroscience and Whitehead I: Neuro-ecological Model of Brain; Axiomathes 2016: 1-34 https://doi.org/10.1007/s10516-016-9286-2

[103] Friston K. "Functional integration and inference in the brain". Progress in neurobiology 2002; 68(2): 113-43 https://doi.org/10.1016/S0301-0082(02)00076-X

[104] Di Lollo V, Enns JT and Rensink RA. Competition for consciousness among visual events: the psychophysics of reentrant visual processes. J Exp Psychol Gen 2000; 129: 481-507 https://doi.org/10.1037/0096-3445.129.4.481

[105] Rauschenberger R. Reentrant processing in attentional guidance – time to abandon old dichotomies. Acta Psychol (Amst) 2010; 135: 109-111. https://doi.org/10.1016/j.actpsy.2010.04.014

[106] Theeuwes J. Top-down and bottom-up control of visual selection. Acta Psychol (Amst) 2010; 77-99 https://doi.org/10.1016/j.actpsy.2010.02.006

[107] Awh E, Belopolsky AV and Theeuwes J Top-down versus bottom-up attentional control: a failed theoretical dichotomy. Trends Cogn Sci (Regul Ed) 2012; 16: 437-443. https://doi.org/10.1016/j.tics.2012.06.010

[108] Corbetta, Maurizio, Gaurav Patel, and Gordon L Shulman. "The reorienting system of the human brain: from environment to theory of mind." Neuron 2008; 58(3): 306-324. https://doi.org/10.1016/j.neuron.2008.04.017

[109] Dehaene Stanislas, Jean-Pierre Changeux, Lionel Naccache, Jérôme Sackur, Claire Sergent. Conscious, preconscious, and subliminal processing: a testable taxonomy; Trends in Cognitive Sciences 2006; 10(5): 204-211. https://doi.org/10.1016/j.tics.2006.03.007

[110] Tononi G and Koch C. The neural correlates of consciousness: An update. Ann N Y Acad Sci 2008; 1124: 239-261. https://doi.org/10.1196/annals.1440.004

[111] Dehaene S. and Changeux JP. Experimental and theoretical approaches to conscious processing. Neuron 2011; 70: 200-227. https://doi.org/10.1016/j.neuron.2011.03.018

[112] Sarter, Martin, Ben Givens, and John P. Bruno. "The cognitive neuroscience of sustained attention: where top-down meets bottom-up." Brain research reviews 2001; 35(2): 146-160. https://doi.org/10.1016/S0165-0173(01)00044-3

[113] Dayan P, Hinton Neal Zemel. The Helmholtz machine. Neural Comput 1995; 7: 889-904 https://doi.org/10.1162/neco.1995.7.5.889

[114] Battaglia PW, Jacobs RA, Aslin RN. Bayesian integration of visual and auditory signals for spatial localization. J Opt Soc Am A Opt Image Sci Vis 2003; 20: 1391-1397. doi: 10.1364/josaa.20.001391 https://doi.org/10.1364/JOSAA.20.001391

[115] Knill DC, Pouget A. The Bayesian brain: the role of uncertainty in neural coding and computation. Trends Neurosci 2004; 27: 712-719. https://doi.org/10.1016/j.tins.2004.10.007

[116] Rao RPN and Ballard DH. Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. Nat. Neurosci 1999; 2: 79-87 https://doi.org/10.1038/4580

[117] Bialek W: Biophysics Searching for Principles 2013.

[118] Heekeren HR, Marrett S, Ungerleider LG. The neural systems that mediate human perceptual decision making. Nat Rev Neurosci 2008; 9: 467-479. https://doi.org/10.1038/nrn2374

[119] Bar Moshe. "A cognitive neuroscience hypothesis of mood and depression." Trends in cognitive sciences 2009; 13(11): 456-463. https://doi.org/10.1016/j.tics.2009.08.009

[120] Pourtois G, Rauss K, Vuilleumier P and Schwartz S. Effects of perceptual learning on primary visual cortex activity in humans. Vision Res 2008; 48: 5562. https://doi.org/10.1016/j.visres.2007.10.027

[121] Serences JT. Value-based modulations in human visual cortex. Neuron 2008; 60: 1169-1181. https://doi.org/10.1016/j.neuron.2008.10.051

[122] Grossberg S. Cortical and subcortical predictive dynamics and learning during perception, cognition, emotion and action. Philos Trans R Soc Lond B Biol Sci 2009; 364: 1223-1234. https://doi.org/10.1098/rstb.2008.0307

[123] Alink A, Schwiedrzik CM, Kohler A, Singer W and Muckli L. Stimulus predictability reduces responses in primary visual cortex. J Neurosci 2010; 30: 2960-2966 https://doi.org/10.1523/JNEUROSCI.3730-10.2010

[124] Hesselmann G, Sadaghiani S, Friston KJ and Kleinschmidt A. Predictive coding or evidence accumulation? False inference and neuronal fluctuations. PLoS ONE 2010; 5: e 9926. https://doi.org/10.1371/journal.pone.0009926

[125] Lupyan G, and Clark A. Words and the World: Predictive Coding and the Language-Perception-Cognition Interface. Current Directions in Psychological Science 2015; 24(4): 279-284. https://doi.org/10.1177/0963721415570732

[126] Searle John R, Daniel Clement Dennett and David John Chalmers. The mystery of consciousness. New York Review of Books, 1997.

[127] Hohwy J. The predictive mind. Oxford: Oxford University Press 2013. https://doi.org/10.1093/acprof:oso/9780199682737.001.0001

[128] Gu X and Fitz Gerald THB. Interoceptive inference: homeostasis and decision-making. Trends Cogn Sci 2014; 18: 269-270. https://doi.org/10.1016/j.tics.2014.02.001

[129] Mumford GK, Holtzman SG. Qualitative differences in the discriminative stimulus effects of low and high doses of caffeine in the rat. J Pharmacol Exp Ther 1991; 258: 857-65

[130] Sengupta Biswa, Arturo Tozzi, Gerald K Cooray, Pamela K Douglas, Karl J. Friston; PLoS Biol 2016; 14(3): e1002400.

[131] Carhart-Harris RL and Friston KJ. Brain 2010; 133(4): 1265-1283. https://doi.org/10.1093/brain/awq010

[132] Ashby WR. Principles of the self-organising dynamic system. J Gen Psychol 1947; 37: 125-128. https://doi.org/10.1080/00221309.1947.9918144

[133] Nicolis G and Prigogine I. Self Organisation in NonEquilibrium Systems (Wiley, New York, 1977).

[134] Haken H. Synergistics: an Introduction. NonEquilibrium Phase Transition and Self Organisation in Physics, Chemistry and Biology; 3rd edn (Springer, New York, 1983). https://doi.org/10.1007/978-3-642-88338-5

[135] Kauffman S. The Origins of Order: Self Organization and Selection in Evolution; (Oxford Univ. Press, Oxford, 1993).

[136] Adams RA, Shipp S. and Friston KJ. Predictions not commands: active inference in the motor system. Brain Struct Funct 2013; 218: 611-643. https://doi.org/10.1007/s00429-012-0475-5

[137] Sharpee TO, Calhoun AJ and Chalasani SH. Information theory of adaptation in neurons, behavior, and mood. Current Opinion in Neurobiology 2014; 0: 47-53. https://doi.org/10.1016/j.conb.2013.11.007

[138] Tishby N. Polani D. editors. Information theory of decisions and actions. New York: Springer 2011.

[139] Bray D. Protein molecules as computational elements in living cells. Nature. 1995; 376: 307-312 https://doi.org/10.1038/376307a0

[140] Cardoso MM, Sirotin YB, Lima B, Glushenkova E, Das A. The neuroimaging signal is a linear sum of neurally distinct stimulus- and task-related components. Nat Neurosci 2012; 15: 1298-1306. https://doi.org/10.1038/nn.3170

[141] Wark B, Lundstrom BN, Fairhall A. Sensory adaptation. Curr Opin Neurobiol 2007; 17: 423-429. https://doi.org/10.1016/j.conb.2007.07.001

[142] Maravall M, Petersen RS, Fairhall AL, Arabzadeh E, ziamond ME. Shifts in coding properties and maintenance of information transmission during adaptation in barrel cortex. PLoS Biol 2007; 5: e19. https://doi.org/10.1371/journal.pbio.0050019

[143] Liu YS, Stevens CF, Sharpee TO. Predictable irregularities in retinal receptive fields. Proc Natl Acad Sci USA 2009; 106: 16499-16504.

https://doi.org/10.1073/pnas.0908926106

[144] Fitzgerald JD, Sharpee TO. Maximally informative pairwise interactions in networks. Phys Rev E Stat Nonlin Soft Matter Phys 2009; 80: 031914 https://doi.org/10.1103/PhysRevE.80.031914

[145] Tkacik G, Prentice JS, Balasubramanian V, Schneidman E. Optimal population coding by noisy spiking neurons. Proc Natl Acad Sci USA 2010; 107: 14419-14424. https://doi.org/10.1073/pnas.1004906107

[146] deWit L, Machilsen B and Putzeys T. Predictive coding and the neural response to predictable stimuli. J Neurosci 2010; 30: 8702-8703. https://doi.org/10.1523/JNEUROSCI.2248-10.2010

[147] Wiese Wanja. "Perceptual Presence in the Kuhnian-Popperian Bayesian Brain." In Open MIND. Open MIND. Frankfurt am Main: MIND Group 2014.

[148] Den Ouden HEM, Daunizeau J, Roiser J, Friston KJ and Stephan KE. Striatal prediction error modulates cortical coupling. The Journal of Neuroscience : The Official Journal of the Society for Neuroscience 2010; 30(9): 3210-3219. https://doi.org/10.1523/JNEUROSCI.4458-09.2010

[149] Smith Craig A and Lazarus Richard S. Chapter 23. Emotion and Adaptation. In L.A. Pervin (Ed). Handbook of Personality: Theory and Research 1990: 609-637. New York: Guilford.

[150] Scherer KR, Shorr A and Johnstone T. (Ed.) Appraisal processes in emotion: theory, methods, research. Canary, NC: Oxford University Press 2001.

[151] Conant R and Ashby WR. Every good regulator of a system must be a model of that system. Int J Syst Sci 1970; 1: 89: 97.

[152] Damasio AR. Self comes to mind: Constructing the conscious brain. London: Heinemann 2010.

[153] Watson KK, Matthews BJ, Allman JM. Brain activation during sight gags and language-dependent humor. Cereb Cortex 2007; 17: 314-324. https://doi.org/10.1093/cercor/bhj149

[154] Friston KJ. The fantastic organ. Brain 2013; 136: 1328-1332 90.

[155] Seth AK, Suzuki K and Critchley HD. An Interoceptive Predictive Coding Model of Conscious Presence. Frontiers in Psychology 2011; 2: 395. https://doi.org/10.3389/fpsyg.2011.00395

[156] Grillner S, Kozlov A, Kotaleski JH. "Integrative neuroscience: linking levels of analyses." Current Opinion in Neurobiology 2005; 15(5): 614-621. https://doi.org/10.1016/j.conb.2005.08.017

[157] E. Gordon ed., Harwood (2000) Integrative Neuroscience; ISBN 90-5823-054-6

[158] Parr LA, Waller BM, Fugate J. Emotional communication in primates: implications for neurobiology. Curr Opin Neurobiol 2005; 15: 716-720 https://doi.org/10.1016/j.conb.2005.10.017

[159] Preuschoff K, Quartz SR, Bossaerts P. Human insula activation reflects risk prediction errors as well as risk. J Neurosci 2008; 28: 2745-2752 https://doi.org/10.1523/JNEUROSCI.4286-07.2008

[160] Zimmer R and Derby C. Neuroecology and the Need for Broader Synthesis. Integrative and Comparative Biology 2011; 51(5): 751-755 https://doi.org/10.1093/icb/icr070

[161] Clark A. Whatever next? Predictive brains, situated agents, and the future of cognitive science. Behav Brain Sci 2013; 36: 181-204 https://doi.org/10.1017/S0140525X12000477

Received on 01-07-2016 Accepted on 05-12-2016 Published on 12-05-2017

http://dx.doi.org/10.15379/2409-3564.2017.04