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Comment

Variational neuroethology: Answering further questions Reply to comments on “Answering Schrödinger’s question: A free-energy formulation”[☆]

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First and foremost, we sincerely thank our commentators for their incisive and thought-provoking responses [1–14] to our metatheory of living systems; namely, variational neuroethology (VNE) [15]. We appreciated the critical insights, questions, suggestions, and proposals for future research. We were also pleased to see signs of a fruitful dialectic between different perspectives – unexpectedly, some of our commentators addressed others’ questions and concerns; suggesting that VNE might enable productive scientific discourse and inspire new, multidisciplinary research questions. There were also friendly critics, who helpfully questioned the coherence and validity of VNE, and motivated us to revisit key issues.

Given the space constraints of this Response, we cannot attend to each commentary with the level of attention it deserves. Instead, we have addressed the commentaries collectively, by organising our Response into themes. Our critiques tended to fall within two broad domains: those that questioned the formal ontology of VNE, and those that questioned VNE as a research heuristic. This was unsurprising, since as a metatheory, VNE comprises: (1) a new way of modelling the structure and dynamics of living systems (i.e., a formal ontology of life based on nested Markov blankets), and (2) a new approach to studying them (i.e., a multidisciplinary heuristic for theorising and research). To begin, we revisit our key terms and concepts. We then address the criticisms aimed at these two aspects of VNE. Finally, we address issues pertaining to the constructs that we borrow from information theory, which question VNE, and indeed, the free-energy principle (FEP) itself.

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1. What's in a name?

Bruineberg and Hesp [4] make the lucid point that, given our choice of words, VNE should only apply to the behaviour of animals with a central nervous system (CNS). Clearly, however, the scope of our metatheory ought to extend beyond this limited domain – indeed, to any living system in general.

We consider the term “variational neuroethology” to be not altogether inappropriate. VNE is a synthesis of a variational formulation of the function, structure, and dynamics of the nervous system (i.e., the FEP) and Tinbergen's [16] seminal approach to animal behaviour. Our framework is within the purview of ethology, since VNE, with its emphasis on *active inference*, explains the *behaviour* of living systems. Indeed, under the FEP, *neural structures* function essentially as *behavioural control structures*. Hence, a metatheory derived from the FEP must comprise (neuro)ethology. This pragmatist emphasis on *adaptive action* that mediates and enables self-organisation aligns VNE with *enactive* and *autopoietic* models of cognition – an issue discussed by Bitbol and Gallagher [3], which deserves further consideration. We also drew on the suggestion by Sengupta and colleagues [17] to recast theoretical neuroethology under the FEP. We understand *neuroethology* as the study of the dynamics and coevolution of (generally neural) control systems and (typically animal) behaviour. Because VNE concerns precisely such phenomena, the term we chose seems justified. Furthermore, applying our metatheory to species with a brain does not mean that it cannot be extended to those without one. Indeed, although it originated as a global theory of the brain, the FEP has already been successfully extended beyond animals with a CNS; e.g., to plant life [18], single celled organisms [19], and morphogenesis [20]. We were encouraged to see that Pezzulo and Levin [11] clearly acknowledged the fundamental similarities between neural and somatic processes, and appreciated how the FEP can be leveraged to study biological phenomena beyond the brain, such as anatomical traits and homeostasis. Similarly, Campbell [5] emphasises the applicability of Tinbergen's four questions to phenomena beyond animal behaviour, from microscale dynamics (i.e., genes) to macroscale ones (i.e., culture). Van de Cruys [13] also provides a compelling application of VNE to explain preferences about sensory inputs, leveraging the FEP to account for this phenomenon at each of Tinbergen's four levels of analysis. We are most grateful for these commentaries, which illustrate the promise of synthesising the FEP and Tinbergen's nested levels under VNE.

Still, the point that we need to choose our words carefully is well taken: we are working on two complementary metatheories that extend VNE to phenomena beyond animal behaviour. These are the *variational approach to niche construction* (VANC) and *variational ecology* (VE). The VANC concerns those lasting, self-generated, adaptive changes to the ecological niche that are imposed by the dynamics of living organisms, whereby physical states of the niche come to participate in self-evidencing dynamics [21]. Similarly, VE addresses higher-order Markov blankets by proposing a model for recursively nested organism-niche dynamics, providing a more general framework for the study of biological systems that share a niche [22]. VE leverages the skilled intentionality framework (SIF) developed by Bruineberg & Rietveld [23], especially its reinterpreted notion of *affordances*. These are possibilities for engagement through action and perception that are offered to an organism. Under the SIF, affordances are cast as free-energy gradients that can be resolved through active inference. VE draws the surface of higher-order Markov blankets as the field of affordances (i.e., free-energy gradients) that emerge from dynamics at these higher scales: their closure is the closure of actions afforded at those scales. Since living systems instantiate a single generative model, there is – for any living system (or system of systems) – one global free-energy gradient, constituted by partial gradients at each scale. Through active inference, the entire ensemble acts to resolve free-energy across scales, underwriting integrated dynamics for multiscale, ecological niche-organism systems. This multiscale integration speaks to the insightful philosophical remark by Tozzi and Peters [12] that VNE affords a conception of *living* as a *belonging-together*, as an integrated dynamical system with integrated dynamics. Collectively, these variational models can be said to constitute a fully generalisable, scientific metatheory of hierarchically nested living systems – what one might call a *variational biology*, or a physics of sentient systems.

2. VNE as a multiscale, formal ontology of life

A few of the commentaries criticised VNE's formal ontology of nested Markov blankets. The appropriateness of our ontology was questioned by Bruineberg and Hesp [4], Kirchhoff [7], Kirmayer [8], and Bitbol and Gallagher [3]. Bruineberg and Hesp [4] argue that although the Markov blankets for clearly bounded systems (e.g., single cells and organisms) are intuitive, those for larger-scale, higher-order systems are not so clearly drawn. Similarly, Kirmayer

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