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Comment

# A plea for "variational neuroethology" Comment on "Answering Schrödinger's question: A free-energy formulation" by M.J. Desormeau Ramstead et al.

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What is life? According to Erwin Schrödinger [13], the living cell departs from other physical systems in that it – apparently – resists the second law of thermodynamics by restricting the dynamical repertoire (minimizing the entropy) of its physiological states. This is a physical rephrasing of Claude Bernard's biological notion of *homeostasis*, namely: the capacity of living systems to self-organize in order to maintain the stability of their internal milieu despite uninterrupted exchanges with an ever-altering external environment [2]. The important point here is that physical systems can neither identify nor prevent a state of high entropy. The *Free Energy Principle* or FEP was originally proposed as a mathematical description of how the brain actually solves this issue [4]. In line with the Bayesian brain hypothesis, the FEP views the brain as a hierarchical statistical learning machine, endowed with the imperative of minimizing Free Energy, i.e. prediction error. Action prescription under the FEP, however, does not follow standard Bayesian decision theory. Rather, action is assumed to further minimize Free Energy, which makes the active brain a self-fulfilling prophecy machine [6]. This is adaptive, under the assumption that evolution has equipped the brain with innate priors centered on homeostatic set points. In turn, avoiding (surprising) violations of such prior predictions implements homeostatic regulation [10], which becomes increasingly anticipatory as learning unfolds over the course of ontological development [5].

But, as is argued by Ramstead et al. [11]: "Although it is highly generalizable, the explanatory scope of the FEP is limited – it only imposes modest constraints on the class of dynamical patterns (i.e. complex adaptive systems) that count as living. The FEP therefore requires a complementary evolutionary (i.e. ultimate) account that explains the specific adaptive solutions responsible for producing different embodied models, along with proximate processes that produce every phenotype." What is missing here is a set of (survival-relevant) ecological problems that are solved by self-organizing nervous systems over evolutionary, developmental and psychobiological timescales. Identifying such ecological problems is the starting point of neuroethology [7], which aims at disclosing the biological constraints under which natural selection operates by studying the species-specific features of animal brains (e.g., the bat's echolocation system). The synthesis of this approach with the FEP is what authors coin *variational neuroethology*.

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In brief, variational neuroethology ambitions to explain the known properties of a species' neurocognitive apparatus in terms of adaptations, i.e. stigmas of a (multi-scale, Free-Energy minimizing, dynamical response to a) given ecological problem. But if it is not to be reduced to evolutionary neuroscience, what does endorsing variational neuroethology actually imply? In what follows, we highlight two simple potential contributions.

First, a strong emphasis is put on the comparative approach, in the aim of detecting phylogenic and/or ontogenic signatures of evolutionary pressure. In particular, inter-species comparisons will be critical for testing quantitative predictions regarding potential relationships between features of species' socioecological niches and neurocomputational adaptations. This resonates with recent appeals to rebalancing the diversity of animal models in neuroscience research [14]. A related issue is the development of statistically-optimal phylogenetic comparative methods. In brief, existing approaches detect adaptations as unlikely observations under null models of covariances between species' lineages [3]. This is problematic however, as the same observations could be even more unlikely under the alternative hypothesis [12]. At the very least, variational neuroethology could provide (alternative) generative models for adaptation effects, the statistical detection of which could then proceed from comparing these models with classical null phylogenetic models.

Second, in promoting the role of nonlinear dynamical phenomena such as *emergence*[1] and *self-organization*,[2] it challenges the common-sense idea that adaptations consist of evolution shaping the nervous system of more or less "passive" species. In line with evolutionary systems theory [1], variational neuroethology rather views adaptations as the outcome of evolutionary pressure on living systems that actively select and/or mold their ecological niche. One may argue that human culture provides an example of emergent and self-organized adaptation, as the human species has to continuously adapt to complex socio-ecological environments inherited from – and carved by – previous Homo Sapiens generations [9]. Variational neuroethology cannot address the question of whether the culturally-accelerated path of the human species will eventually prove to possess adaptive fitness. However, it can be used to identify the conditions under which different forms of social learning, including cultural evolution, can be understood as adaptive solutions to an ecological problem. The difficulty here lies in the fact that social learning may counteract natural phenotypic diversity without improving overall adaptive fitness. Interestingly, human crowds actually seem to exhibit such adverse effects of social influence in collective decision-making tasks [8]. In any case, variational neuroethology may be valuable simply because it provides a principled and systematic account of the impact of reciprocal organism-niche interactions on evolutionary dynamics.

In conclusion, the proposal of Ramstead et al. [11] is a promising avenue for evolutionary neuroscience, provided the field invests the time and effort required for integrating increasingly diverse experimental results with increasingly sophisticated computational models. The success of such endeavor should not be taken for granted, given its demands in terms of academic breadth. But what other alternative does the field have, if it is to self-organize adaptively (Karl Friston, personal communication)?

## References

[1] Badcock P. Evolutionary systems theory: a unifying meta-theory of psychological science. Rev Gen Psychol 2012;16:10–23.
[2] Bernard C. Introduction à l'étude de la médecine expérimentale. Madrid: C. Bailly-Baillière; 1865.
[3] Cornwell W, Nakagawa S. Phylogenetic comparative methods. Curr Biol 2017;27:R333–6.
[4] Friston K. The free-energy principle: a unified brain theory?. Nat Rev Neurosci 2010;11:127–38.
[5] Friston K, FitzGerald T, Rigoli F, Schwartenbeck P, O'Doherty J, Pezzulo G. Active inference and learning. Neurosci Biobehav Rev 2016;68:862–79.
[6] Friston KJ, Daunizeau J, Kilner J, Kiebel SJ. Action and behavior: a free-energy formulation. Biol Cybern 2010;102:227–60.
[7] Hoyle G. The scope of neuroethology. Behav Brain Sci 1984;7:367–81.
[8] Lorenz J, Rauhut H, Schweitzer F, Helbing D. How social influence can undermine the wisdom of crowd effect. Proc Natl Acad Sci 2011;108:9020–5.
[9] Mesoudi A. Cultural evolution: a review of theory, findings and controversies. Evol Biol 2016;43:481–97.

[1] Emergence is the mechanism by which a system acquires entirely novel properties by re-assembling its interacting parts.
[2] Self-organization is a process by which the internal order of a system (usually away from equilibrium) increases spontaneously, without external forcing.

[10] Pezzulo G, Rigoli F, Friston K. Active inference, homeostatic regulation and adaptive behavioural control. Prog Neurobiol 2015;134:17–35.
[11] Ramstead MJD, Badcock PB, Friston KJ. Answering Schrödinger's question: a free-energy formulation. Phys Life Rev 2018;24:1–16 [in this issue].
[12] Rouder JN, Morey RD, Verhagen J, Province JM, Wagenmakers E-J. Is there a free lunch in inference?. Top Cogn Sci 2016;8:520–47.
[13] Schrodinger E. What is life? The physical aspect of the living cell. Cambridge University/Macmillan; 1947.
[14] Yartsev MM. The emperor's new wardrobe: rebalancing diversity of animal models in neuroscience research. Science 2017;358:466–9.