Acknowledgments. None.

Financial support. This work received no specific funding.

Competing interests. The authors declare no competing interests.

References

Anderson, M. L. (2010). Neural reuse: A fundamental organizational principle of the brain. *Behavioral and Brain Sciences*, *33*(4), 245–266.

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, *59*(1), 617–645.

Bavelier, D., & Neville, H. J. (2002). Cross-modal plasticity: Where and how?. *Nature Reviews Neuroscience*, *3*(6), 443–452.

Buehlmann, C., Mangan, M., & Graham, P. (2020). Multimodal interactions in insect navigation. *Animal Cognition*, *23*, 1129–1141.

Desai, R. H., Reilly, M., & van Dam, W. (2018). The multifaceted abstract brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1752), 20170122. https://doi.org/10.1098/rstb.2017.0122

Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M. A. R., Kram, R., & Lehman, S. (2000). How animals move: An integrative view. *Science*, *288*(5463), 100–106. https://doi.org/10.1126/science.288.5463.100.

Dürr, V., & Schilling, M. (2018). Transfer of spatial contact information among limbs and the notion of peripersonal space in insects. *Frontiers in Computational Neuroscience*, *12*, 101. https://doi.org/10.3389/fncom.2018.00101.

Ernst, M. O., & Bülthoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences*, *8*(4), 162–169.

McFarland, D., & Bösser, T. (1993). *Intelligent behavior in animals and robots*. MIT Press.

McNamee, D., & Wolpert, D. M. (2019). Internal models in biological control. *Annual Review of Control, Robotics, and Autonomous Systems*, *2*(1), 339–364.

Merel, J., Botvinick, M., & Wayne, G. (2019). Hierarchical motor control in mammals and machines. *Nature Communications*, *10*(1), 5489.

Schilling, M., Paskarbeit, J., Ritter, H., Schneider, A., & Cruse, H. (2021). From adaptive locomotion to predictive action selection–cognitive control for a six-legged walker. *IEEE Transactions on Robotics*, *38*(2), 666–682

Webb, B. (2004). Neural mechanisms for prediction: Do insects have forward models?. *Trends in Neurosciences*, *27*(5), 278–282. http://dx.doi.org/10.1016/j.tins.2004.03.004.

Complex brains allow functioning in a complex environment by using information

Cameron Rouse Turner[a]*, Thomas J.H. Morgan[b] and Thomas L. Griffiths[a]

[a]Computational Cognitive Science Lab, Department of Psychology and Department of Computer Science, Princeton University, Princeton, NJ, USA and [b]Institute of Human Origins, Arizona State University, Tempe, AZ, USA
c.rouse.turner@princeton.edu
tomg@princeton.edu
thomas.j.h.morgan@asu.edu

*Corresponding author.

doi:10.1017/S0140525X25100782, e96

Abstract

Collating the neural traits possessed by taxa provides valuable evidence about brain evolution. However, to get the full scientific benefit, we must pair it with an understanding of the selection pressures driving brain complexity. This can be achieved by considering the heterogeneity of the animal's environment alongside the reliability of information. A complex environment selects for a complex brain.

A greater understanding of the emergence of complex brains can be reached by considering the evolutionary function of cognition. Coombs and Trestman provide a tremendous overview of the distribution of neural traits across animals. However, their focus on collating traits leads them to a proposal about how complex brains emerge based on the animal's form, but says little about the selection pressures driving brain elaboration. With regard to Tinbergen's (1963) four questions, their mode of explanation is phylogenetic, emphasizing the evolutionary history of organismal form. We propose that this account suffers from the absence of a functional explanation and suggest that the *environmental complexity hypothesis* provides a complementary theory about the adaptive purpose of nervous systems (Godfrey-Smith, 1998; Levins, 1968; Sol, 2009; Turner, Morgan, & Griffiths, 2024) .

We argue that brain complexity is expected to coevolve alongside sophisticated sensors and effectors, but that this must be a worthwhile metabolic investment to be favored. Coombs and Trestman relay that animals with complex brains have traits such as high-resolution eyes and flexible limbs. However, since these metabolically costly additions must pay-for-themselves in terms of fitness, this raises the question of their adaptive value (Sterling & Laughlin, 2015) . Indeed, as we describe below, a toy model illustrates that a greater number of sensors and effectors implies more connections between them (Fig. 1). This is analogous to noting that a house with many switches and lights must have a lot of wire in the walls. Let s be the number of sensory receptors, a the number of motor neuron effectors, and h_i the number of interneurons in the connecting hidden layer i of a neural network with n layers. Therefore, the total number of connections is $sh_i + \sum_{i=1}^{n-1} h_i h_{i+1} + h_n a$. Now conveniently assume h_i can be characterized by an average, with layers being uncorrelated. This makes it easy to see that inter-brain connections increase with the typical number of neurons within a layer (width $\bar{h}$) or number of layers (depth n): $E[\sum_{i=1}^{n-1} h_i h_{i+1}] = (n-1)\bar{h}$. A well-known result in artificial neural network theory is that as connections increase as the network becomes richer in the ways it can map inputs to outputs (namely the Vapnik-Chervonenkis dimension bound; Bartlett & Maass, 2003) . We turn this idea on its head to argue that animals

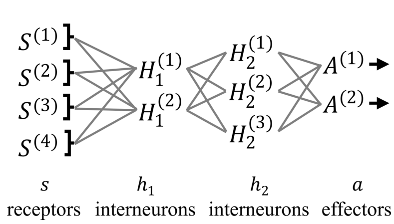

Figure 1 (Turner et al.). An example fully-connected feed-forward neural network with two hidden layers ($s = 4, h_1 = 2, h_2 = 3, a = 2$).

have more connections in order to detect fine-grained patterns and allow intricate responses. Formally, the brain complexity should be an increasing function of sensory and motor system complexity (e.g. $\partial\bar{h}(s)/\partial s$ for all s). Natural brains have many reciprocal connections both between and within layers making the reality far messier. Nonetheless, our toy model demonstrates that complex brains are only useful alongside complex bodies, so the co-occurrence of traits found by Coombs and Trestman is precisely what we should expect. However, this conclusion only intensifies the issue of explaining *why* these systems were elaborated by natural selection in the first place.

Evolution invests in complex brains to allow animals to cope with a heterogeneous and changing environment. Investment in cognition is hypothesized to occur when the environment presents many states that vary drastically in their outcomes for fitness depending on the animal's actions, so that the environment is complex (Turner et al., 2024) . Further, there must be reliable information indicating states, such that the animal can often use cues to produce an appropriate action. For instance, consider the evolution of the special-purpose eyes that allow comb jellies (*Copula sivickisi*) to hunt bioluminescent plankton (Garm et al., 2016). First, the comb jellies' environment is complex because plankton exist in patches, and substantial energy is lost if these patches are not found. Second, bioluminescent light reliably indicates the location of plankton. Therefore, conditions favor investing in systems for detecting, processing, and propelling toward information indicating plankton.

Considering adaptive function in terms of environmental complexity and the reliability of information allows us to deepen our understanding of the evolution of complex brains. For instance, Coombs and Trestman note that the Cambrian was marked by the emergence of image-forming eyes and more flexible appendages. The environmental complexity hypothesis suggests further theorizing. Perhaps rising ambient light due to ocean oxygenation during the Cambrian enabled predators and prey to reliably detect each other, while the behavior of other species created a complex environment with high-stakes interactions. Analyzing environmental complexity provides an understanding of why lineages move from simple to complex brains, which is significant for interpreting Coombs and Trestman's history of morphological forms.

Understanding how evolutionary function and morphological mechanisms interact remains a particular challenge for theory on the evolution of nervous systems. Another way to categorize the mode of explanation employed by Coombs and Trestman is as *internalist*. That is, their study implies traits must be bundled together to be successful, creating an internal influence on the course of evolution (Sterelny, 1997) . For instance, nondirectional photoreceptors provide the conditions that favor directional pit eyes. By contrast, the environmental complexity hypothesis is *externalist*, and it focuses on selection coming from the environment. However, a subtle point is that what is considered "the environment" actually arises from how an organism interacts with the world around it; what states an animal can detect, their available actions, and what constitutes a reward. These factors are in fact determined by the bundle of traits possessed by a lineage and evolve over time. Therefore, theory on nervous systems faces the same issue as evolutionary theory broadly: combining internalist and externalist explanations (Laland et al., 2015) . This unresolved tension puts particular strain on the study of brains because their very purpose is to respond to the external world.

Acknowledgements. None.

Financial support. We thank the Templeton World Charity Foundation for supporting this research (grant number 20648).

Competing interests. None.

References

Bartlett, P. L., & Maass, W. (2003). Vapnik-Chervonenkis dimension of neural nets. In M. A. Arbib (Ed.), *The handbook of brain theory and neural networks*. MIT Press.

Garm, A., Bielecki, J., Petie, R., & Nilsson, D. E. (2016). Hunting in bioluminescent light: Vision in the nocturnal box jellyfish Copula sivickisi. *Frontiers in Physiology*, *7*, 99. https://doi.org/10.3389/fphys.2016.00099

Godfrey-Smith, P. (1998). *Complexity and the function of mind in nature*. Cambridge University Press.

Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Müller, G. B., Moczek, A., Jablonka, E., & Odling-Smee, J. (2015). The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20151019. https://doi.org/10.1098/rspb.2015.1019

Levins, R. (1968). *Evolution in changing environments*. Princeton University Press.

Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters*, *5*, 130–133. https://doi.org/10.1098/rsbl.2008.0621

Sterelny, K. (1997). Where does thinking come from? A commentary on Peter Godfrey-Smith's Complexity and the function of mind in nature. *Biology & Philosophy*, *12*, 551–566. https://doi.org/10.1023/A:1006572119820

Sterling, P., & Laughlin, S. (2015). *Principles of neural design*. MIT Press.

Tinbergen, N. (1963). On aims and methods in ethology. *Zeitschrift für Tierpsychologie*, *20*, 410–433. https://doi.org/10.1111/j.1439-0310.1963.tb01161.x

Turner, C. R., Morgan, T. J. H., & Griffiths, T. L. (2024). Environmental complexity and regularity shape the evolution of cognition. *Proceedings of the Royal Society B: Biological Sciences*, *291*, 20241524. https://doi.org/10.1098/rspb.2024.1524

On bodies, brains, and behaviour (and a little bit of magic)

Nathaniel R. Farndale Wright[a]* and Nicola S. Clayton[b]

[a]Department of Psychology, School of Biological Sciences, University of Cambridge, UK and [b]Department of Psychology, School of Biological Sciences, University of Cambridge, UK
nrfw2@cam.ac.uk
nsc22@cam.ac.uk
https://www.psychol.cam.ac.uk/ccl

*Corresponding author.

doi:10.1017/S0140525X25100666, e97

Abstract

The impact the body has upon complex cognitive capabilities has long challenged cognitive scientists. Insights into the complex interplay between how we see, what we see, and how we interpret what we think we saw and remembered are offered by a surprising source: the effects magicians create.

Coombs and Trestman (C&T) name six "pivotal traits," which correlate with complex cognitive capabilities across vertebrate, coleoid cephalopod mollusc, and euarthropod lineages. These