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A long-standing, open question in biology is how populations are capable of rapidly adapting to novel environments, a trait called evolvability. A major contributor to evolvability is the fact that many biological entities are modular, especially the many biological processes and structures that can be modeled as networks, such as metabolic pathways, gene regulation, protein interactions, and animal brains. Networks are modular if they contain highly connected clusters of nodes that are sparsely connected to nodes in other clusters (Wagner et al., 2001; Leicht and Newman, 2008). Despite its importance and decades of research, there is no agreement on why modularity evolves (Wagner et al., 2001). Intuitively, modular systems seem more adaptable, a lesson well-known to human engineers, because it is easier to rewire a modular network with functional subunits than an entangled, monolithic network (Kashtan and Alon, 2005). However, because this evolvability only provides a selective advantage over the long-term, such selection is at best indirect and may not be strong enough to explain the level of modularity in the natural world (Wagner et al., 2001).

Modularity is likely caused by multiple forces acting to various degrees in different contexts (Wagner et al., 2001), and a comprehensive understanding of the evolutionary origins of modularity involves identifying those multiple forces and their relative contributions. The leading hypothesis is that modularity mainly emerges due to rapidly changing environments that have common subproblems, but different overall problems (Kashtan and Alon, 2005) (Modularly Varying Goals: MVG). It is unknown how much natural modularity MVG can explain, however, because it unclear how many biological environments change *modularly*, and whether they change at a high enough frequency for this force to play a significant role.

We investigate an alternate hypothesis that has been suggested, but heretofore untested, which is that modularity evolves not because it conveys evolvability, but as a byproduct from selection to reduce connection costs in a network (Fig. 1, Striedter (2005)). Modularity of networks is
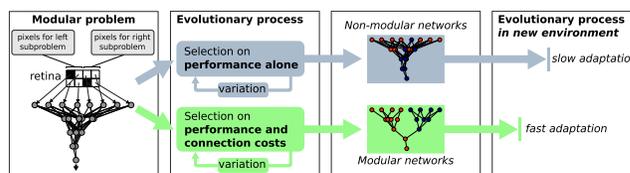

Figure 1: Main hypothesis. Evolving networks with selection for performance alone produces non- modular networks that are slow to adapt to new environments. Adding a selective pressure to minimize connection costs leads to the evolution of modular networks that quickly adapt to new environments.

measured with the Q score (Leicht and Newman, 2008).

After 25,000 generations in an unchanging environment (Fig. 2a), treatments selected to maximize performance and minimize connection costs (P&CC) produce significantly higher performing (Fig. 2c) and more modular networks (Fig. 2d) than treatments maximizing performance alone (PA) ($Q = 0.42$, 95% confidence interval $[0.25, 0.45]$ vs. $Q = 0.18[0.16, 0.19]$, $p = 8 \times 10^{-9}$ using Matlabs Mann-Whitney-Wilcoxon rank sum test). To test whether evolved networks exhibit functional modularity corresponding to the left-right decomposition of the task, we divide networks into two modules by selecting the division that maximizes Q and color nodes in each partition differently. Left-right decomposition is visually apparent in most P&CC trials and absent in PA trials (Fig. 2e,f). Functional modularity can be quantified by identifying whether left and right inputs are in different partitions, which occurs in 56% of P&CC trials and never with PA (Fishers exact test, $p = 4 \times 10^{-11}$). Pairs of perfect sub-solution neurons – whose outputs perfectly answer the left and right subproblems – occur in 39% of P&CC trials and 0% of PA trials (Fishers exact test, $p = 3 \times 10^{-6}$).
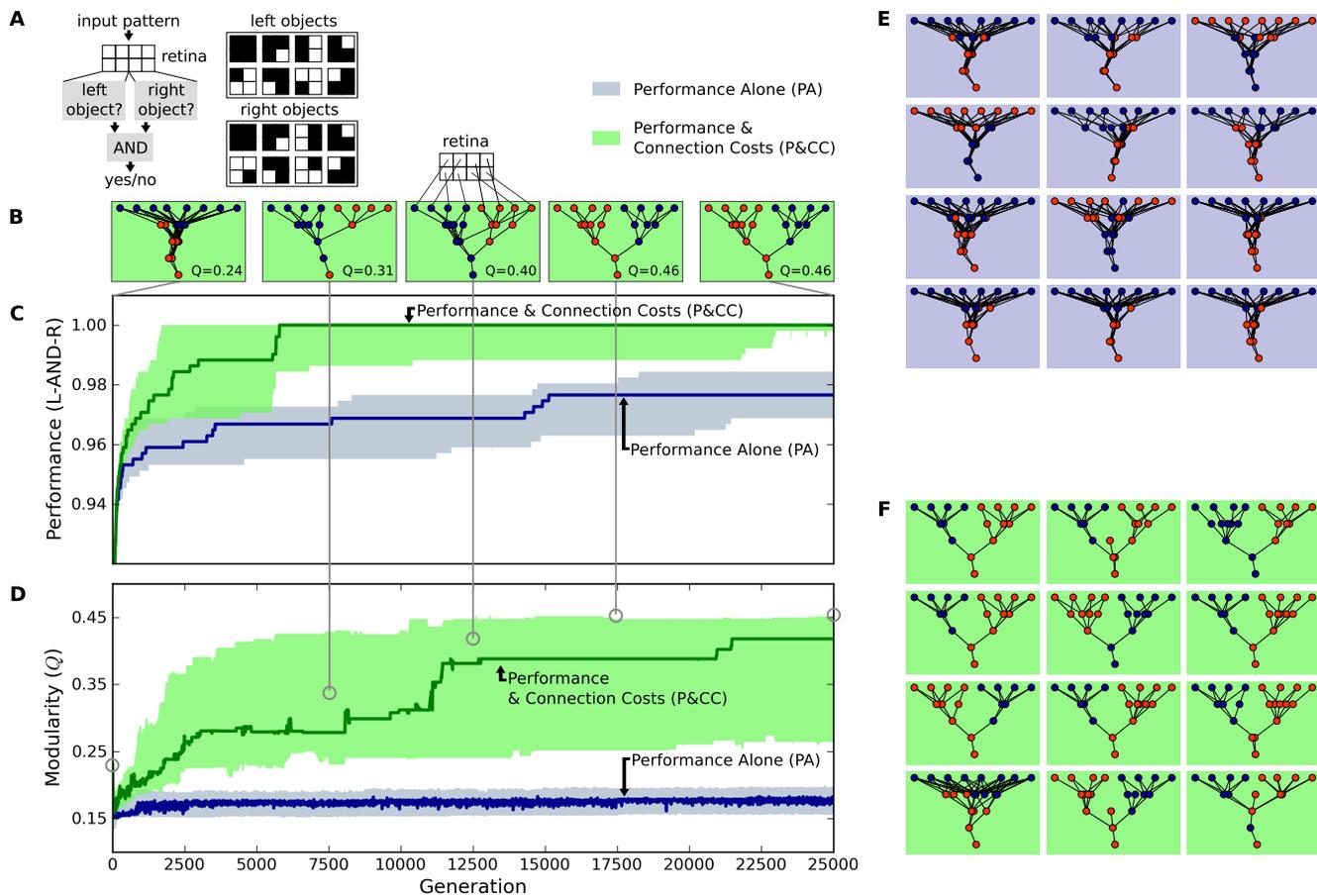
Acknowledgements

Figure 2: **The addition of connection costs leads to higher-performing, functionally modular networks.** **(A)** Networks evolve to recognize patterns (objects) in an eight-pixel retina. The problem is modularly decomposable because whether an object exists on the left and right sides can be separately determined before combining that information to answer whether objects exist on *both* sides (denoted by the AND logic function). **(B)** Networks from an example trial become more modular across evolutionary time with a pressure to minimize connection costs in addition to performance (P&CC). **(C)** Median performance ($\pm$ 95% bootstrapped confidence intervals) per generation of the highest-performing network of each trial, which is perfect only when minimizing connection costs in addition to performance. **(D)** Network modularity, which is significantly higher in P&CC trials than when selecting for performance alone (PA). **(E)** The 12 highest-performing PA networks, each from a separate trial. **(F)** The 12 highest-performing P&CC networks, which are functionally modular in that they have separate modules for the left and right subproblems. Nodes are colored according to membership in separate partitions when making the most modular split of the network (see text).

References

Clune, J., Mouret, J.-B., and Lipson, H. (2013). The evolutionary origins of modularity. *Proceedings of the Royal Society B: Biological sciences*, 280(1755):20122863.

Kashtan, N. and Alon, U. (2005). Spontaneous evolution of modularity and network motifs. *Proceedings of the National Academy of Sciences*, 102(39):13773–13778.

Leicht, E. A. and Newman, M. E. J. (2008). Community structure in directed networks. *Physical review letters*, pages 118703–118707.

Striedter, G. (2005). *Principles of brain evolution*. Sinauer Associates Sunderland, MA.

Wagner, G., Mezey, J., and Calabretta, R. (2001). *Modularity. Understanding the development and evolution of complex natural systems*, chapter Natural selection and the origin of modules. MIT Press.