# Summary of "The Evolutionary Origins of Modularity"

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## INTRODUCTION

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 [4, 2]. Despite its importance and decades of research, there is no agreement on why modularity evolves [4]. 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 [1]. 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 [4].

Modularity is likely caused by multiple forces acting to various degrees in different contexts [4], 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 [1]. It is unknown how much natural modularity MVG can explain, however, because it unclear if 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 [3].

## Categories and Subject Descriptors

J.3 [**Computer Application**]: Life & medical sciences

## Keywords

Mutation rates, self-adaptive, evolvability, meta-GA


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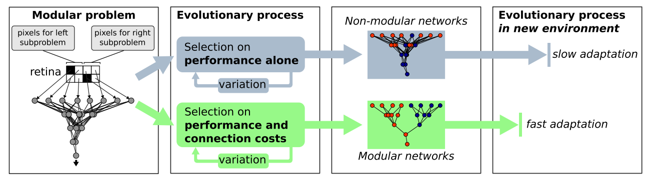


**Figure 1: Main hypothesis. Evolving networks with selection for performance alone produces non-modular networks that are slow to adapt to new environments. Adding a selective pressure to minimize connection costs leads to the evolution of modular networks that quickly adapt to new environments.**

## RESULTS

After 25000 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. $Q = 0.18[0.16,$ $0.19]$, $p = 8{\times}10^{-09}$ using Matlab's Mann-Whitney-Wilcoxon rank sum test, which is the default statistical 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 (Fisher's 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 (Fisher's exact test, $p = 3 \times 10^{-6}$). Fig. 2g,h sheds light on why connection costs cause the evolution of modularity.

## 1. REFERENCES

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