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Chaining Distinct Tasks Drives The Evolution of Modularity

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Abstract

I introduce a novel method for evolving modularity in gene regulatory networks. Like previous models of modular evolution, it relies on selecting networks to perform a task consisting of distinct sub-tasks, with the aim of producing modules that perform these sub-tasks. Whilst existing models structure these sub-tasks in parallel and then combine the output, this model chains sub-tasks together, so they must be performed one after another. This task structure resembles the selective constraints undergone in multicellular evolution, where genetic networks must (a) integrate multiple cues to establish what environment they are in, and (b) express a pattern of gene activity on the basis of this environment. I show that the modules produced in these networks exhibit the hallmarks of modularity: existing modules can change independently of others, and modules can also be re-used and combined in various ways.

Extended Abstract

Modularity makes complex systems evolvable—it permits localised changes to be made without impacting the entire system, and it allows already functioning parts in a system to be re-used in novel ways. An important goal then, is to understand the conditions under which modularity can evolve. One way this problem has been explored is through simple models of network evolution, where nodes in the network are thought of as neurons or regulatory genes that compute some function. These nodes are then wired together into a network whose overall behaviour can be evaluated for how close it comes to some target behaviour (such as the computation of a boolean function).

Two recent network models that successfully evolve modularity share a central idea: networks are selected to solve a *modular task*—one that can be broken down into two parallel sub-tasks whose outputs are then combined into a single output (see Figure 1(b)) (Kashtan and Alon, 2005; Clune et al., 2013). When modularity in the network does evolve, it is possible to isolate individual modules that perform the separate sub-tasks. In both these models, additional constraints are required for the networks to reliably evolve modularity. Kashtan and Alon vary the sub-tasks rapidly and independently over time, whilst Clune et al. add a fitness cost to the number of connections in network, demonstrating that both the external selective regime, and costs imposed by internal structure can affect the evolution of modularity.

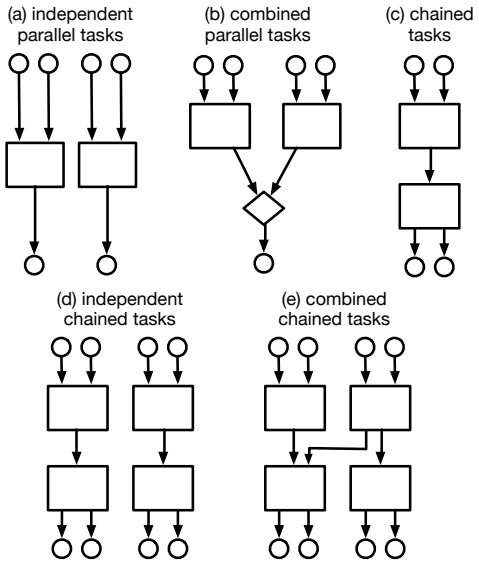

Figure 1: Different modular task definitions that networks can be selected to perform. Successful modular evolution should reflect a similar network structure. Previous models focus on (b). This method first develops (c) as a building block, and then uses it to evolve (d) and (e). Note that chained tasks must coordinate *multiple outputs*.

I explore a novel method for evolving modularity in an existing model of gene regulation (Calcott et al., 2008) that similarly relies on selecting networks to perform a modular task. In this model, however, the sub-tasks are chained together, and must be performed one after another, rather than in parallel (see Figure 1 (c)). The upstream sub-task integrates information from multiple inputs into a single output, and the downstream sub-task uses that information to coordinate several outputs.

I show that this selective regime *alone* is often sufficient to evolve modules in the network that map onto the sub-tasks

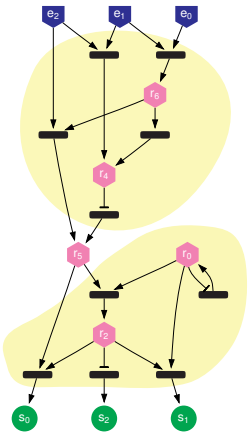

Figure 2: A modular network. Genes are black; environmental cues E_i, regulatory products R_j, and structural output S_k, are colored), showing a positional module and a structural module (which, in this case, produces a cyclic expression pattern). The interface between these two modules is a single regulatory signal (R_5 in this case).

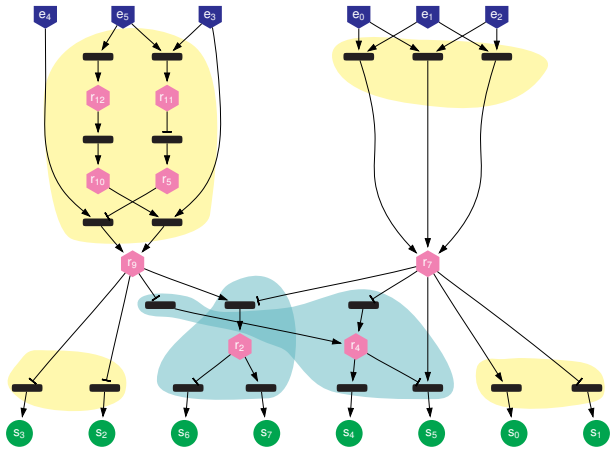

Figure 3: Upstream modules are first produced, along with co-regulated structural genes (in yellow). A second selection regime then co-opts the output from these modules to use in new downstream structural modules (in blue).

defined by the selective problem. I display the structure of the resulting gene networks using 'signaling' diagrams that includes both genes and regulatory products as nodes in the diagram. This emphasises the key role that the mediating regulatory products (transcription factors) play, providing an interface between upstream and downstream modules (see Figure 2).

I then show that these modules exhibit the following behaviour:

- Modules subject to a constant selective regime frequently undergo localised change via drift that affects how they compute the sub-task, but without changing the functional (input/output) profile of the module. This demonstrates a key feature of modularity: changes can be isolated with affecting the entire system.
- It is possible to independently select for modifications in either the upstream or downstream module without affecting the rest of the system. This further demonstrates the ability to isolate change within the system, this time under directional selection rather than drift.
- Lastly, I show that simulations that include multiple instances of these chained modules can be induced to co-opt, or wire together, existing modules to produce new functions (see Figure 1 (d) and (e), and Figure 3). This demonstrates a second key function of modularity, its ability to recombine existing functional parts.

The structure of the chained task that these networks evolve to perform resembles the selective constraints under which multicellularity evolves, where each cell must integrate multiple upstream environmental cues to establish its position, and coordinate a variety of gene expression patterns on the basis of this position. Furthermore, the evolution of co-option in these networks closely resembles (indeed, it was inspired by) recent empirical work on the evolution of morphological novelties, where existing positional signals are co-opted to re-use existing pattern of downstream gene expression. The model results can thus provide some theoretical underpinning to recent attempts to formulate 'principles' of regulatory evolution derived only from empirical observation (Prud'homme et al., 2007).

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