A Minimal Model of the Evolution of Self-Organisation

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The development of multicellular organisms provides a stunning example of how self-organisation has been harnessed by evolution. Starting from a single cell, a complex form develops with internal differentiation and functional coherence at multiple scales. No overall blueprint or external hand guides this process. Instead, much like a simple model of flocking, high-level organisation arises from individual cells responding to local cues produced by other cells doing the same.

Multicellular development is clearly subject to evolutionary change, but much of evolutionary theory ignores development, and self-organisation with it (see Amundson (2005) for a history). There are, however, claims that self-organisation makes organisms more evolvable (Kirschner and Gerhart, 1998), that it influences the path of evolutionary change (Newman, 2018), or helps explain how evolutionary novelties arise (Moczek, 2011). These issues are still under debate, often falling under the call for a an "extended" evolutionary synthesis Pigliucci (2007).

Here, I attempt to make some headway on this debate using a model-based approach. My aim is to (a) produce a modelling framework that captures key features of both evolution and development with minimal complexity, (b) generate simple examples that display properties typically attributed to self-organisation, (c) describe and display in detail all stages of development and evolutionary history, and (d) provide analytical tools to understand and measure within the model what precisely self-organisation adds to our understanding of the evolutionary process. In this talk, I shall focus on showing some progress with (a), (b), (c), and gesture at some ideas for (d).

The model uses a evolvable Boolean gene regulatory network to provide transition rules for a 2d cellular automaton. Development takes place over discrete time-steps, with the state of each cell updated by both its internal state and output from its neighbours at the prior time-step. Evolution takes place in asexual, non-overlapping populations, and fitness is determined by assessing one or more cell outputs across the grid of cells. Networks are selected for the next generation with a probability proportional to their fitness.

Despite the simplicity of the model, it produces gene networks that generate patterns that are robust to noise, that can regenerate after ablation, and that are capable of producing stable patterns under novel or noisy conditions. The simplicity of the model means the resulting gene networks and associated state space can be readily visualised both over developmental and evolutionary time.

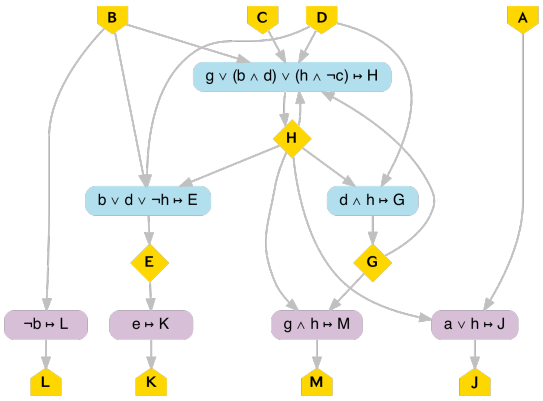

Figure 1 – A gene network evolved to conditionally produce two stripes when stimulated on one edge using product A (see step 1 in fig. 2).

In the talk, I focus on a single experiment where I evolve a small grid of cells to conditionally express two vertical stripes. One successful gene network is shown in fig. 1. The gene network shows products (yellow) that are either input into the network, or generated by regulatory (blue) or structural (purple) genes. One of the inputs, A, is an external stimulus that provokes the stripe pattern (without it, no pattern forms). The other inputs into the network are derived from the outputs of the neighbouring cells. For example, input D is active when there are three or more neighbouring cells that have K active in the previous time step. The network was selected to produce a stable stripe pattern in product M, as shown in fig. 2 (see bottom row).

Despite having evolved in a fixed-size grid, this pattern scales to grids with larger widths, producing a repeated pattern of stripes. The pattern is also stable un-

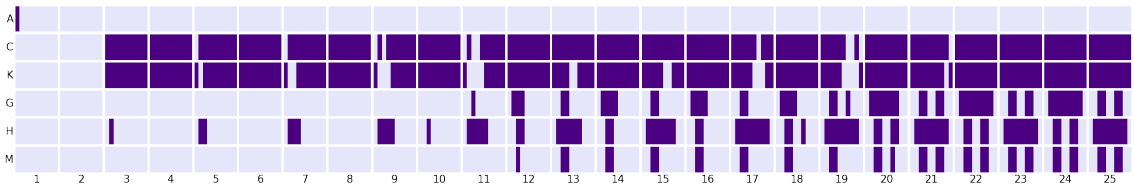

Figure 2 – The first 25 developmental time steps showing the activation of just six products: An external stimulus A, an input, C, derived from the surrounding cells output of K, two regulatory products, G and H, which maintain internal cell state, and the output M, which produces the pattern upon which fitness is judged.

der ablation: if the cells from either the left or right side are reset, the pattern regenerates. Though the pattern produced by product M is stable, many other products settle into cyclic attractors, as can be seen in fig. 2.

Most surprising is that this same network can produce a wide variety of stable 2-dimensional stripe-like patterns by randomly introducing noise (turning products on or off) across the grid of cells for initial set of time steps. fig. 3 shows a pattern where noise was added for the first ten time steps. The result is a pattern of coencentric stripes that grows until they intersect, then the pattern eventually stabilises.

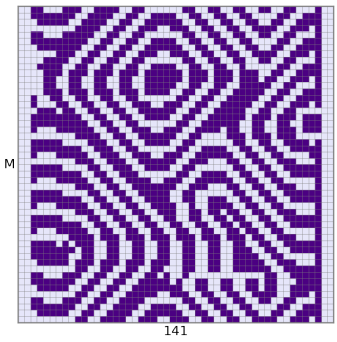

Figure 3 – A stable pattern, at step 141, produced by the random introduction of noise in a larger grid, using the same genetic network shown in fig. 1.

Other evolved networks that succeed in producing the simple stripe pattern respond differently. Rather than repeating stripes, they continuen to produce two small stripes at each side, or the stripes may even expand in size as the grid size changes. These patterns are sometimes robust to large quantities of noise, consistently reforming the same pattern, though they might take hundreds of time steps to get there. So a single simple selective task is capable of producing a wide variety of novel patterning that is only exposed under conditions never selected for.

I do an initial analysis of the dynamics of selected examples, building a graph of the combined state space explored by all cells during development and during exposure to novel stimuli. In some cases, the cells remain locked into just a few cyclic attractors which are accessible to one another via a simple nudge from one of the inputs. I show some parallels with ideas about the development of cell types and modern interpretations of Waddington's "epigenetic landscape" (Bhattacharya et al., 2011).

Finally, I track the evolution of one of these patterns, and show it occurs predominately through neutral change in the gene regulatory model. It looks less like hill-climbing, and more like wandering through a department store with elevators, providing an interesting contrast to some recent work on "differentiable cellular automata" (Mordvintsev et al., 2020).

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