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Robust Basins, Fragile Attractors: A New View on Biological Network Dynamics

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Extended Abstract

Boolean networks (BNs) are a simple, yet powerful class of models for representing the dynamics of complex biological systems. They were introduced by Kauffman as models of gene regulatory networks [1]. Since then, they have been used to study a wide range of processes, from developmental programs to cell signaling pathways [2]. In a BN, genes and proteins are represented by nodes, and regulatory interactions between genes and proteins are represented by edges between nodes. This gives rise to a dynamical system. Despite their inherent simplicity, biological BN models capture important design principles of gene regulation that have been consistently observed in curated biological systems, such as low connectivity, canalization, and functional bias [3].

The attractors of a biological BN correspond to phenotypes or cell types, and the stability of attractors is a central biological question. Coherence is the biologically most meaningful way to assess this stability. It measures the resilience of *arbitrary* network states to perturbation. Yet, in vivo, biological systems predominantly operate at attractors. For this reason, it is more appropriate to consider attractor-based stability measures, as already envisioned by Kauffman in his first paper on Boolean networks [1]. Here, we formalize and systematically analyze this concept, which we term *attractor coherence*. We compare the coherence of attractors to the coherence of their respective basins, which comprises all states that eventually transition to the attractor.

First, we consider an ensemble of 122 published biological BN models [3], and show that, for moderately large basin sizes, attractors are often less coherent than their basins. That is, when perturbed, a transient state is more likely to remain in its original basin compared to an attractor state. To investigate the causes of this phenomenon, we consider large random network ensembles, in which we vary canalization and bias. We show that higher canalization and bias both lead to larger divergence between these measures. This suggests that biological networks, which possess high levels of canalization and bias, are particularly prone to phenotype-altering perturbations when resting at attractors.

Altogether, our findings align with the broader robustness–adaptability trade-off that has long been discussed in systems biology [4]. Park et al. recently showed that biological networks, when correctly accounting for their abundance of source nodes, are substantially more robust to perturbations than previously appreciated, casting doubt on the criticality conjecture: that biological networks operate at the edge of order and chaos [5]. Our results refine this picture. On one hand, features of biological networks, such as high canalization and bias, enhance robustness at the level of transient dynamics, ensuring that perturbations during the approach to an attractor typically do not alter the eventual outcome. On the other hand, attractors themselves are more prone to phenotypic switching in response to small perturbations. This duality illustrates how biological systems may balance the competing demands of reliable function (robustness) and the capacity to explore alternative states (adaptability).

Ethical considerations: This work relies exclusively on published, expert-curated models and simulated random networks. The research is theoretical in nature and is intended to advance fundamental understanding of robustness and adaptability in biological networks. Eventually, such insights can inform biomedical applications.

References

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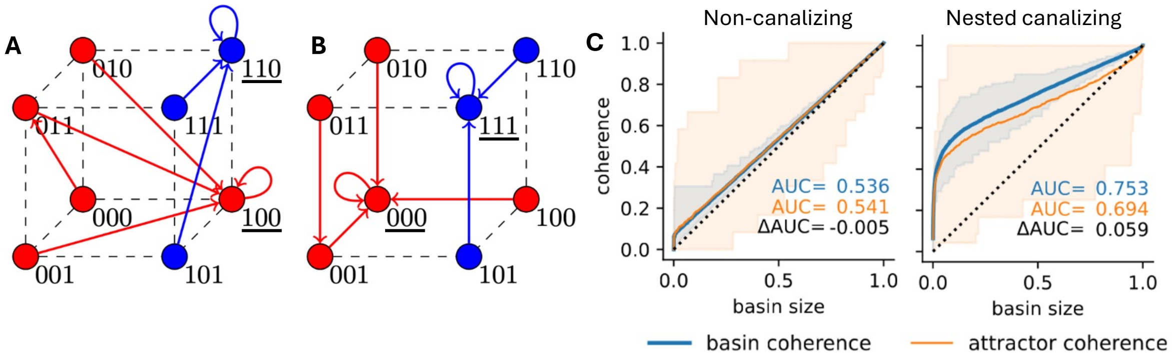

Figure 1: **Attractors in biological canalizing networks are less coherent than their basin of attraction.** (A-B) Example of two 3-node BNs. Both networks have two steady state attractors (underlined) with same basins of sizes 5 (in red) and 3 (in blue), respectively. The two basins are maximally coherent with basin coherences of $2/3$ and $4/9$, respectively. However, the attractor coherences between the two BNs differ wildly. The BN in (A) has steady state attractors 100 and 110, both of which have attractor coherence $1/3$ because only one of each of their three neighboring states is in their basin of attraction. On the contrary, the steady state attractors 000 and 111 of the BN in (B) have much higher attractor coherence of 1 and $2/3$, respectively. (C) For 10,000 random 12-node Boolean networks governed by update rules of in-degree 5 with different levels of canalization (increasing from left to right), the coherence of each attractor (orange) and the coherence of its corresponding basin (blue) are stratified by basin size (x-axis). Shaded areas indicate the range of observed values. Lines depict rolling-window means with moving window size 500 and AUC quantifies the area under the respective lines. Highly canalizing networks, such as biological networks, exhibit higher coherence but the gap between basin and attractor coherence widens.