Visualising Random Boolean Network Dynamics: effects of perturbations and canalisation

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Abstract. We have proposed a simple approach to visualising the time behaviour of Random Boolean Networks (RBNs). Here we demonstrate the approach in a variety of cases: examining the effect of state and structure mutations, and examining the effect of canalising functions for $K > 2$ networks.

1 Introduction

Random Boolean networks (RBNs) are a well-studied form of complex discrete dynamical systems [1–5]. Visualisation of the dynamics can aid understanding, but (unlike for 1D Cellular Automata, for example), there has been no satisfactory visualisation of RBN time behaviour. In [6] we proposed a simple approach to visualising the time behaviour of RBNs; here we demonstrate the approach in a variety of cases: examining the effect of state and structure mutations, and examining the effect of canalising functions for $K > 2$ networks.

2 RBNs

A Random Boolean Network (RBN) comprises N *nodes*. Each node i at time t has a binary valued state, $c_{i,t} \in \mathcal{B}$. Each node has K inputs assigned randomly from K of the N nodes (an input may be from the node itself); the wiring pattern is fixed throughout the lifetime of the network. This wiring defines the node's neighbourhood, $\nu_i \in N^K$.

The state of node i's neighbourhood at time t is $\chi_{i,t} \in \mathcal{B}^K$, a K-tuple of node states that is the projection of the full state onto the neighbourhood ν_i.

Each node has its own randomly chosen local state transition rule, or update rule, $\phi_i : \mathcal{B}^K \rightarrow \mathcal{B}$. These nodes form a network of state transition machines. At each timestep, the state of each node is updated in parallel, $c_{i,t+1} = \phi_i(\chi_{i,t})$.

The global dynamics f is determined by the local rules ϕ_i and the connectivity pattern of the nodes ν_i.

Kauffman [3, 4] investigates the properties of RBNs[1] as a function of connectivity K. Despite all their randomness, "such networks can exhibit powerfully

[1] The wiring conditions given here are not stated explicitly in those references. However, in the $K = N$ case, Kauffman [4, p.192] states that "Since each element receives

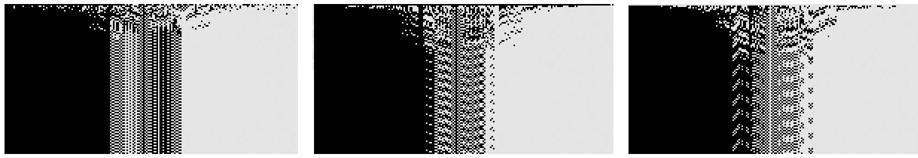

Fig. 1. Visualisation of the time evolution of a $K = 2$ RBN from different initial conditions (half on, half off; all off; all on) with the nodes sorted to expose the frozen core (as described in [6]).

ordered dynamics" [3], particularly when $K = 2$. Kauffman investigates RBNs as simplified models of gene regulatory networks (GRNs). He notes that "cell types are constrained and apparently stable recurrent patterns of gene expression", and interprets his RBN results as demonstrating that a "cell type corresponds to a state cycle attractor" [4, p.467] (in a $K = 2$ network).

Drossel [1] notes that subsequent computer simulation of much larger networks shows that "for larger N the apparent square-root law [of attractor numbers and lengths] does not hold any more, but that the increase with system size is faster".

3 Visualising the dynamics

Good visualisations can aid the understanding of complex systems, and can help generate new questions and hypotheses about their behaviours.

Kauffman [4, p.203] observes that $K = 2$ RBNs "develop a connected mesh, or *frozen core*, of elements, each frozen in either the 1 or 0 state." We can use this result to provide an order for placing the nodes in the visualisation. Nodes frozen in the 1 or 0 state are placed towards the edges of the figure; nodes that are changing state are placed towards the centre: see figure 1. The different transient behaviours and attractors are clearly visible; for example, it is clear that these show three different attractors, with three different periods.

A simple algorithm to achieve this node sorting is described in [6]. It results in the frozen core nodes moving to the edges of the figure, whilst the nodes with cycling states are in the centre. Additionally, the frozen core nodes with shorter transient behaviour are closer to the edges than those with longer transient behaviours. Similarly, nodes with cycling states are sorted according to the amount of time they spend in one state or the other, with those half the time in each state towards the centre. This tends to highlight the attractor structure.

Note, however, that the precise order of the nodes depends on the various initial states chosen. In all the examples given here, for simplicity, the network

an input from all other elements, there is only one possible wiring diagram". This implies that multiple connections from a single node are not allowed in a true RBN (otherwise more wiring diagrams would be possible) whereas self connections are allowed (otherwise K would be restricted to a maximum value of $N - 1$). Subsequent definitions (for example [1]) explicitly use the same conditions as given here.

was run only from the all zeroes and from the all ones state to determine the sort order. In figure 1, it can be seen that in the all ones initial state (middle column) the central node is always on, whilst in the all zeroes initial state (right column) it is always off. (This implies it is a node with a self-connection.) Hence, when these two cases are combined, it is on for an average of half the time, and so ends in the centre.

4 Examples

In this section, we explore some different aspects of RBNs, using this visualisation approach to expose the relevant features.

We use Tufte's "small multiples" [7] technique, which "allows the viewer to focus on changes in the data", by displaying an array of RBNs that can be readily compared.

The aim is to use the visualisation to prime intuition and aid understanding of RBNs' rich dynamics, and to provoke hypotheses about the detailed behaviour. Any such hypotheses would need to be investigated in a rigorous manner.

4.1 Perturbing RBN state

Here we visualise the stability of $K = 2$ networks to perturbations of their state.

Kauffman [3] defines a *minimal perturbation* to the state of an RBN as flipping the state of a single node at one timestep. Flipping the state of node i at time t is equivalent to changing its update rule at time $t-1$ to be $c_{i,t} = \neg\phi_i(\chi_{i,t-1})$. Such a perturbation leaves the underlying dynamics, and hence the attractor basin structure, the same, it merely moves the current state to a different position in the state space, from where it continues to evolve under the original dynamics: it is a transient perturbation to the state.

Kauffman [3] describes the *stability* of RBN attractors to minimal perturbations: if the system is on an attractor and suffers a minimal perturbation, does it return to the same attractor, or move to a different one? Is the system *homeostatic*? (Homeostasis is the tendency to maintain a constant state, and to restore its state if perturbed.)

Kauffman [4] describes the *reachability* of other attractors after a minimal perturbation: if the system moves to a different attractor, is it likely to move to any other attractor, or just a subset of them? If the current attractor is considered the analogue of "cell type", how many other types can it *differentiate* into under minimal perturbation?

Kauffman's results pick out the $K = 2$ networks as having interesting behaviour under minimal perturbation (high stability so a perturbation usually has no effect; low reachability so when a perturbation moves the system to another attractor, it moves it to one of only a small subset of possible attractors).

Visualisations of the effect of minimal perturbations are shown in figure 2, for perturbations of cycling nodes, and of frozen core nodes.

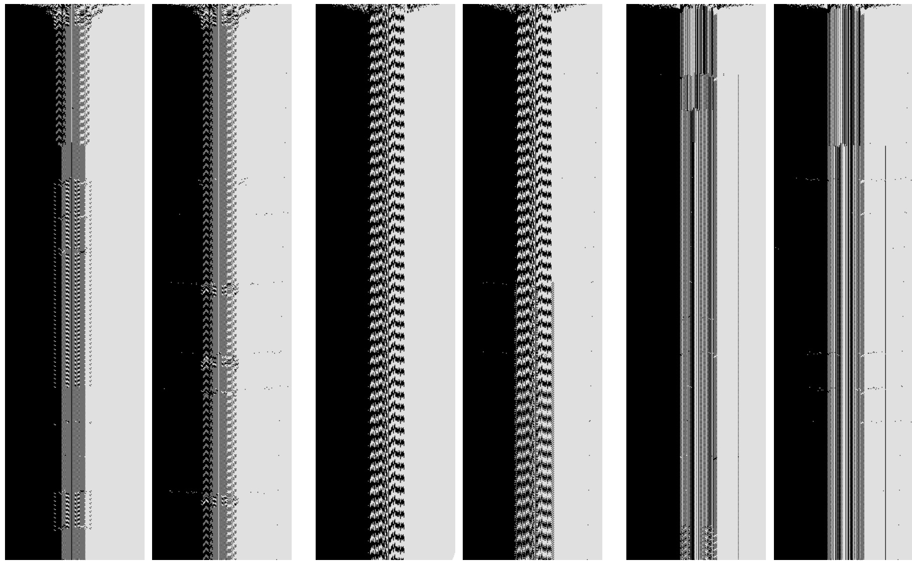

Fig. 2. Visualisation of the time evolution of three typical $K = 2$ RBNs (two runs of each), with $N = 200$, 800 timesteps, and initial condition all nodes "off". After 100 timesteps, a node is flipped once every 50 timesteps. For the left run of each pair, a node is flipped near the centre; for the right run, a node flipped in the frozen core.

These visualisations demonstrate that $K = 2$ RBNs are remarkably stable to minimal perturbations. They also suggest further possible properties: (a) a perturbation to a frozen core node is more likely to preserve the attractor than a perturbation to a cycling node; (b) a perturbation to a frozen core node tends to have longer transient behaviour than a perturbation to a cycling node.

4.2 Perturbing RBN structure

Here we visualise the stability of $K = 2$ networks to perturbations of their structure.

Kauffman [3] defines a *structural perturbation* to an RBN as being a permanent mutation in the connectivity or in the boolean function. So a structural perturbation at time t_0 could change the update rule of node i at all time $t > t_0$ to be ϕ_i' or change the neighbourhood of node i at all time $t > t_0$ to be ν_i'. Since the dynamics is defined by all the ϕ_i and ν_i, such a perturbation changes the underlying dynamics, and hence the attractor basin structure: it is a permanent perturbation to the dynamics, yielding a new RBN.

Such a perturbation could have several consequences: a state previously on an attractor cycle might become a transient state; a state previously on a cycle might move to a cycle of different length, comprising different states; a state might move from an attractor with a small basin of attraction to one with a

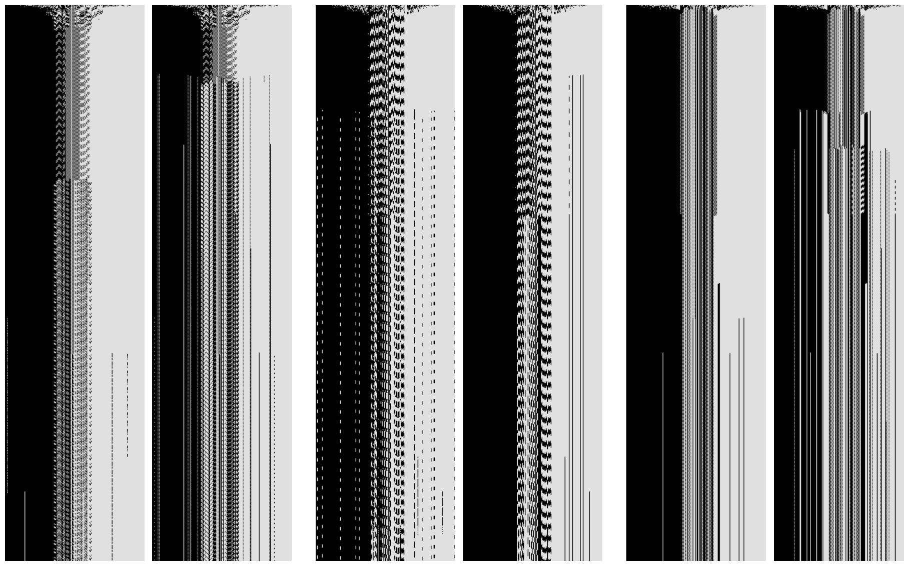

Fig. 3. Visualisation of the time evolution of three typical $K = 2$ RBNs (two runs of each), with $N = 200$, 800 timesteps, and initial condition all nodes "off". After 100 timesteps, the structure of one randomly chosen node is mutated once every 50 timesteps. For the left run of each pair, one of the node's inputs is randomly reassigned; for the right run, the node's boolean function is randomly changed.

large basin; a state might move from a stable (homeostatic) attractor to an unstable attractor; and so on.

Kauffman [4] relates structural perturbation to the *mutation* of a cell; if there is only a small change to the dynamics, this represents mutation to a "similar" kind of cell.

Visualisations of the effect of structural perturbations are shown in figure 3, for perturbations of input connections, and of boolean functions.

These visualisations appear to show that the effect of an input change is less dramatic than that of a boolean function change. Here no distinction is drawn between changing a cycling node or a frozen node: visualisation of further experiments along these lines could yield interesting conjectures about the stability of these RBNs.

4.3 Canalisation

Here we visualise the effect of canalising functions on the time behaviour of $K > 2$ networks.

Kauffman [4, p.203] defines a canalising function as "any Boolean function having the property that it has at least one input having at least one value (1 or 0) which suffices to guarantee that the regulated element assumes a specific value

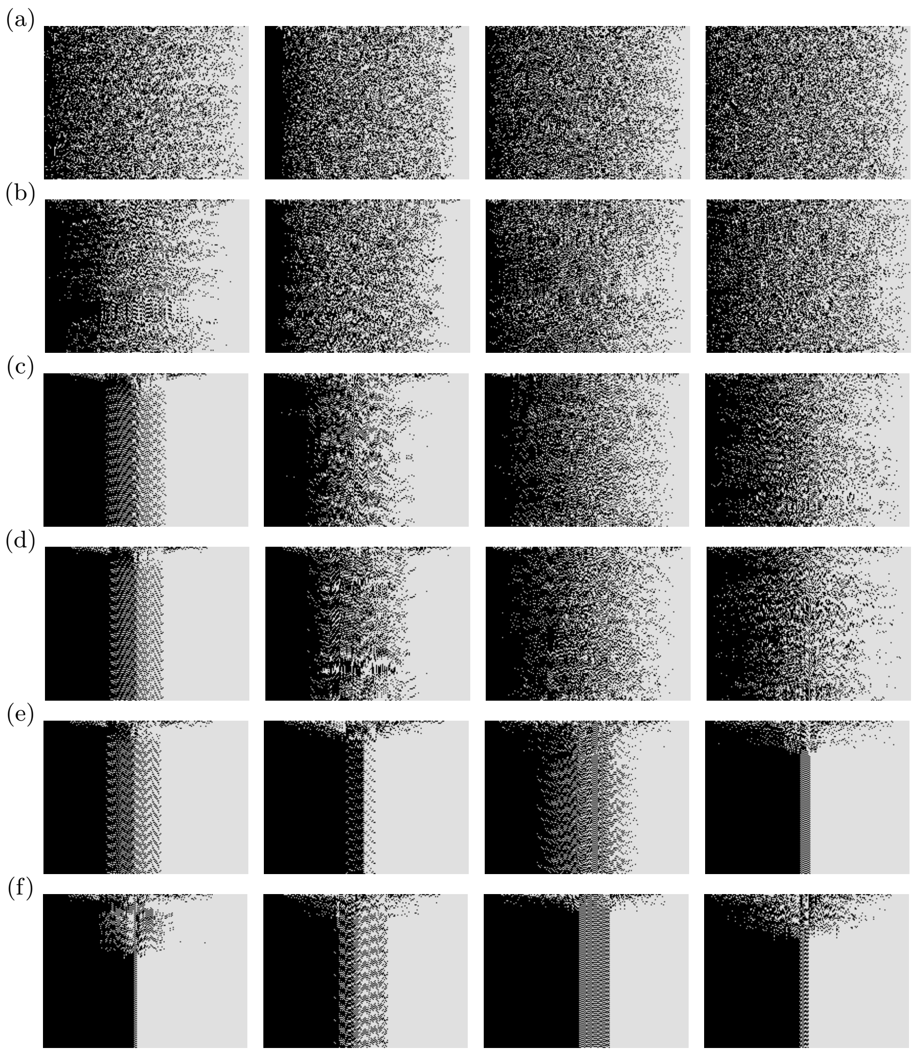

Fig. 4. Visualisation of the time evolution of 24 typical $K = 3$ RBNs, with $N = 200$, and initial condition all nodes "off"; for 150 timesteps; rows have the following number of canalised nodes: (a) 94 = 47.0% (b) 128 = 64.0% (c) 181 = 90.5% (d) 184 = 92.0% (e) 190 = 95.0% (f) 198 = 99.0%

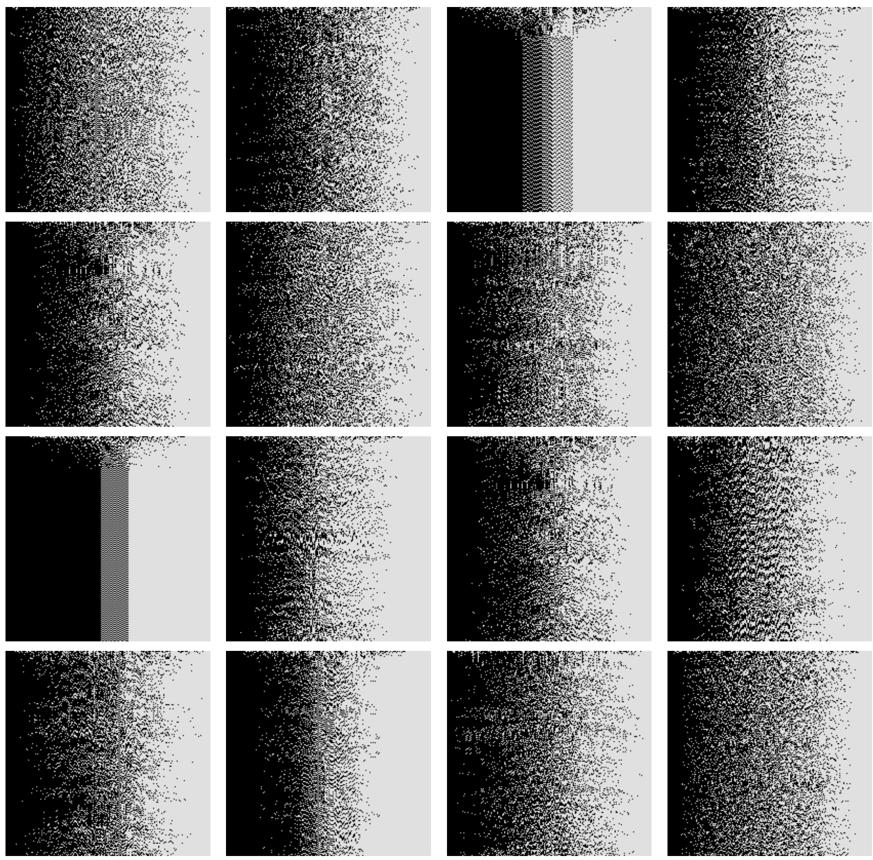

Fig. 5. Visualisation of the time evolution of 16 typical $K = 4$ RBNs, with $N = 200$, and initial condition all nodes "off"; for 200 timesteps; all functions canalising

(1 or 0).” ([1] categorises canalising functions further, into weak, strong, and constant.) Kauffman argues that the canalising functions are important for establishing the frozen core and ordered dynamics of $K = 2$ networks. The proportion of canalising functions decreases rapidly with increasing K . Kauffman [4, p.206] states that “networks with $K > 2$ restricted to canalyzing functions ... [have] orderly dynamics in the entire network”.

Visualisations of the effect of canalising functions on the time behaviour are shown in figures 4 and 5. Clearly for $K = 3$ (figure 4), increasing the proportion of canalising functions does make transients and attractors shorter, and establish an “orderly dynamics”. However, for $K = 4$, even with all functions canalising, change in the chaotic behaviour is evident in only a minority of cases. The effect does not appear to be as strong as Kauffman suggests.

5 Discussion and conclusions

A very simple algorithm allows the time behaviour of RBNs to be visualised in a manner that exposes the transient behaviour, and the structure of the frozen core and cycling nodes. We have used this algorithm to explore various examples of the behaviour of RBNs as certain parameters are varied.

Visualisation of the dynamics helps to prime intuition, and to suggest hypotheses to explore. Some conjectures have been posed; more such conjectures could be generated from larger numbers of examples; some of these may be worthy of further investigation.

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