The dynamics of critical Kauffman networks under asynchronous stochastic update

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We show that the mean number of attractors in a critical Boolean network under asynchronous stochastic update grows like a power law and that the mean size of the attractors increases as a stretched exponential with the system size. This is in strong contrast to the synchronous case, where the number of attractors grows faster than any power law.

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Random Boolean networks were introduced in 1969 by Kauffman [1, 2] as a simple model for complex systems consisting of units that interact via directed links. They are used to model social and economic networks [3, 4], neural networks, and gene or protein webs [5].

A random Boolean network (RBN) is a directed graph with $N$ nodes each of which takes a Boolean value $\sigma_i \in \{0, 1\}$. The number $k$ of incoming edges is the same for all nodes, and the starting points of the edges are chosen at random. Usually these models are updated synchronously, $\sigma_i(t + 1) = c_i(\sigma_{d_{i,1}}(t), \ldots, \sigma_{d_{i,k}}(t))$, where the Boolean coupling function $c_i$ of node $i$ is chosen at random among a given set of functions and $d_{i,j}$ denotes the $j$-th input of node $i$. The configuration of the system $\sigma \equiv \{\sigma_1, \ldots, \sigma_N\}$ thus performs a trajectory in configuration space. Critical networks are of special interest [6]. Their dynamics is at the boundary between a frozen phase where initially similar configurations converge, and a chaotic phase where initially similar configurations diverge exponentially.

However, synchronous update is highly improbable in real networks, and it is used under the tacit assumption that going to asynchronous update will not modify the essential properties of the system [6]. But there are good reasons to doubt the validity of this assumption. For instance, for cellular automata it is well-known that some of the self-organization is an artifact of the central clock [6]. For RBNs there is also recent evidence that deviations from synchronous update modify considerably the attractors of the dynamics [6, 7].

In this paper, we investigate a version of the model where at each computational step one node is chosen at random and is updated. A model with this asynchronous stochastic updating scheme is often called Asynchronous RBN (ARBN) [10, 12, 13], while the Classical synchronous RBN is referred to as CRBN. ARBNs are mostly studied numerically with the focus on various measures of stability [14, 15, 16, 17, 18]. ARBNs were observed to be capable to generate an ordered behavior, but the detailed properties of attractors have not been studied yet.

We will show mostly analytically that the number of attractors changes completely when going from CRBNs to ARBNs. For CRBNs, attractors are cycles in configuration space, and their number was recently shown numerically [1, 10, 20, 21, 22] and analytically [23, 24] to grow faster than any power law with the network size $N$. In contrast, we will show in the following that for asynchronous stochastic update the mean number of attractors grows as power law while their size increases like a stretched exponential with $N$. As the dynamics is no longer deterministic, an appropriate definition of an attractor must be given. An attractor is a subset of the configuration space such that for every pair of configurations on the attractor there exists a sequence of updates that leads from one configuration to the other. In such an attractor is called “loose attractor”. Starting from a random initial configuration, the system will eventually end up on an attractor.

Let us first consider a set of nodes arranged in a loop. Such loops occur as relevant components of critical networks. Nontrivial dynamics occurs only if the two constant Boolean functions are omitted, the remaining Boolean functions being “copy” ($\oplus$), and “invert” ($\ominus$). A loop with $n$ inversions $\ominus$ can be mapped bijectively onto a loop with $n – 2$ inversions by replacing two $\ominus$ with two $\ominus$ and by inverting the state of all nodes between these two couplings. It is therefore sufficient to consider loops with zero inversions (“even” loops) and loops with one inversion (“odd” loops). The position of the $\ominus$-coupling in the odd loop is called the twisted edge. For synchronous update, each configuration is on a cycle in configuration space and occurs again at most after $N (2N)$ time steps for even (odd) loops. The number of cycles increases therefore exponentially with $N$. In contrast, most configurations are transient in the asynchronous case, and only two (one) attractors are left. The reason for this is that a domain of neighboring nodes that have the same value increases or decreases with probability $1/N$ per computational step. The domain size therefore performs a random walk, and for an even loop no domain is left after of the order of $N^3$ updates. The attractors are the two fixed points. For an odd loop, the nodes of a domain change their state at the twisted edge, and the total number of domain walls is therefore odd. The attractor contains only one domain wall that moves around the loop, and the attractor comprises $2N$ configurations. The dynamics on such a loop is closely related to the Glauber dy-
dynamics of a one-dimensional Ising chain with cyclic boundary condition at temperature $T = 0$, where the domains also shrink and grow with a fixed rate and where the equal-time correlation function obeys a scaling form $C(r, t) = f(r^2 t^{-1})^{24}$. The dynamics of an odd loop can be mapped onto the dynamics of an Ising chain with one negative coupling. It is a frustrated system in which not all bonds can be satisfied simultaneously. To conclude, by going from synchronous to asynchronous update, the number of attractors of a loop is reduced from an exponentially large number to 1 or 2. This was also pointed out in 21, where a different asynchronous updating rule is used.

Let us next consider critical networks with connectivity $k = 1$, where the Boolean coupling functions are again “copy” and “invert”. Relevant nodes are those nodes whose state is not constant and that control at least one relevant element 21. They determine the attractors of the system. In 28, exact results for the topology of $k = 1$ networks are derived, and in 21, it is shown that the number of attractors of a critical $k = 1$ network increases faster than any power law. The number of relevant nodes scales as $\sqrt{N}$, and they are arranged in of the order of $\ln(N)$ loops. The remaining nodes sit on trees rooted in these loops. Under asynchronous update, each loop has at most two attractors. The nodes on trees rooted in even loops are frozen because the loop is on a fixed point. The nodes on trees rooted in odd loops can assume any combination of states, since one can find to each possible state of a tree a sequence of updates that generates it. Since each loop is even or odd with equal probability, the mean number of attractors of networks with $n$ relevant loops is

$$\frac{1}{2^n} \sum_i \binom{n}{i} 2^i = \left(\frac{3}{2}\right)^n \approx \left(\frac{3}{2}\right)^{\ln(N/2)},$$

which is a power law in $N$. The number of nodes in trees is of the order of $N$. On average, half of the trees are rooted in odd loops. Consequently the mean attractor size increases exponentially with $N$.

Finally, we investigate the most frequently studied critical networks with connectivity $k = 2$, where each of the 16 possible Boolean coupling functions is chosen with equal probability. All nodes apart from the order of $N^{2/3}$ nodes are frozen. This follows for instance from the factor $e^3$ in the last term of Eqn. (9) of 23, which implies that only the fraction $N^{-1/3}$ of all nodes undergo a non-frozen sequence of states in time. Numerical support for this result is presented in 20.

The number of relevant nodes scales as $N^{1/3}$ 20, and only a fraction $N^{-1/3}$ of these relevant nodes have two relevant inputs. This last statement follows from the evaluation of Eqns. (6) and (9) in 23 in saddle-point approximation, where the width of the first term in the direction perpendicular to the line of maxima is of the order $N^{-2/3}$, implying that of the order $N \cdot N^{-2/3} = N^{1/3}$ nodes have 2 nonfrozen inputs. Consequently, the proportion $N^{-1/3}$ of nonfrozen nodes (whether they are relevant or not) have 2 nonfrozen inputs. This result, together with the other just mentioned features of the model is confirmed by (unpublished) studies of our group.

The other relevant nodes have one relevant input (as the second input comes from a frozen node). The remaining non-frozen nodes (of the order of $N^{2/3}$) are on trees rooted in relevant nodes. Just as for the $k = 1$ networks, there are of the order of $\ln(N)$ independent relevant components 21. In contrast to the $k = 1$ networks, these components are not always simple loops, but may contain several nodes with two relevant inputs. In order to obtain results for the number of attractors of the networks, we have to investigate the attractors of such relevant components.

Let us first consider relevant components that contain one node with two relevant inputs. These are two loops with one interconnection ($\circ\circ\circ$-component), and a loop with an extra link ($\circ$-component). The dynamics under synchronous update for such components is studied in 23, and it is found that the number of attractors in both systems increases exponentially with the number of nodes. With asynchronous update, the number of attractors becomes very small.

We discuss first two loops with one interconnection. The first loop is independent of the second loop, and its attractor is either a fixed point (if the loop is even), or it has one domain wall moving around the loop. If the first loop is on a fixed point, it provides a constant input to the second loop, which therefore behaves like an even loop, or an odd loop, or a frozen loop. The system can have at most three attractors. If the first loop is odd, if provides a changing input to the second loop, which can therefore have an attractor that contains an arbitrary and fluctuating number of domain walls. Consequently, a loop that has one external input can show one out of four different types of behavior on an attractor:

1. The loop can be at a fixed point 0.
2. The loop can be at a fixed point 1.
3. There is exactly one domain wall which moves around the loop.
4. The number of domain walls in the loop fluctuates.

(Without loss of generality, we have assumed that all coupling functions for nodes with one input are “copy”.)

Now we turn to a loop with an extra link. We can again assume that all coupling functions for nodes with one input are “copy”. If this component has one fixed point (two fixed points), it is (they are) the only attractor(s). This is because one can reach a fixed point from an arbitrary initial state by updating one node after another by going around the loop in the direction of the links. After
at most two rounds the fixed point is reached. Only if the coupling function for the node with two inputs has no fixed point, a more complicated attractor occurs. Without loss of generality, we choose this function to have the output 1 if and only if both inputs are 0. By considering the possible update sequences, one finds that the component can accumulate a large and fluctuating number of domain walls, as illustrated in Fig. 1.

Equipped with these results, we now consider components with several nodes with 2 inputs. We define a section to be a sequence of nodes starting at a node with two inputs and ending right before a node with 2 inputs. Such a sequence can branch and have several end points. Clearly, the number of sections is the number of nodes with 2 inputs; a simple loop is counted as one section. A section is controlled by its first node, which is the one with two inputs. Just as for the loop with one external input, a section can show on an attractor one out of the four different types of behavior listed above. This is because all states that have more than a single domain wall in a given section must be part of the same attractor. We show this by the following argument: Assume that on an attractor there occur two domain walls in a section. The two domain walls can be destroyed by updating all nodes between the two walls, such that the domain enclosed by the walls vanishes. A configuration with no wall on the section (and with the state of all other sections unmodified) is therefore also part of the attractor, and there exists consequently a way back to the configuration with two domain walls on this section. By repeating the same sequence of updates, every even number of domain walls can be created in this section, and odd numbers can be created by moving one domain wall out of the section. If \( s \) is the number of sections, an upper bound for the number of attractors of the component is therefore given by \( 4^s \).

We checked this analytical result by computer simulations. In order to make sure that we capture all attractors, we did a complete search of state space, which can only be done for small networks. Starting from an initial state, we did \( N^3 \) updates before assuming that the system is on an attractor, and we made sure that the results are not changed when the length of the initial time period is varied. All states that can be reached from this last state are on the same attractor as this state. All other states that have been visited are marked as transient states. Then we start with an unvisited state as new initial condition in order to identify further transient states and attractors. We constructed relevant components by starting with one loop of a certain size, and by iteratively inserting additional connections between two randomly chosen nodes. The new connection contains a randomly chosen number of 1 to 4 nodes (such that a section can contain two domain walls in its interior). In these networks, the number of sections, \( s \), is identical to the number of nodes with 2 inputs, \( \mu \). After each insertion, we evaluated the number of attractors for different choices of coupling functions. The procedure was repeated more than 750000 times. The largest number of attractors found in a system is shown in Table I as function of \( s = \max(1, \mu) \).

![Diagram](image_url)

FIG. 1: A possible sequence of configurations of a loop with a cross-link showing how multiple domain walls are generated. The coupling function of the node \( \bigcirc \) with two inputs is such that only two dark inputs lead to light output, all other combination give black output. After (e) the procedure described by (a) to (d) is repeated to obtain (f) and similarly for (g), (h) and (i).

| \( \mu \) | \( \nu_{\text{max}} \) | \( 4^s \) realizations |
|---|---|---|
| 0 | 2 | 1 |
| 1 | 2 | 4 | 167370 |
| 2 | 4 | 16 | 138541 |
| 3 | 8 | 64 | 110263 |
| 4 | 23 | 256 | 73268 |
| 5 | 25 | 1024 | 40770 |
| 6 | 23 | 4096 | 15727 |

TABLE I: Maximum number of attractors \( \nu_{\text{max}} \) as function of the number of nodes with 2 inputs, \( \mu \), for networks with up to 17 nodes. Networks with higher \( \mu \) are probed less often because if only short links are added there is no node left which has not already two inputs.

This leads us to the conclusion that a network consisting of the order of \( \ln(N) \) relevant components, with component number \( i \) having \( \mu_i \) nodes with 2 inputs, cannot have more than

\[
\nu = 4^{\max(1, \mu_1)} \cdot 4^{\max(1, \mu_2)} \cdot \ldots \cdot 4^{\max(1, \mu_{\ln N})} \leq 4^{\ln(N) + \mu} \tag{2}
\]

attractors. This is a power law in \( N \) if the probability distribution for the value of \( \mu \) becomes independent of \( N \) for
large $N$. Indeed, as we have mentioned above, each of the $N^{1/3}$ relevant nodes has two (randomly chosen) relevant inputs with probability $aN^{-1/3}$ (with some constant $a$). Since this probability is independent for different nodes, the value of $\mu$ is distributed for large $N$ according to a Poisson distribution with a mean $a$.

We thus have shown that in critical $k = 2$ networks with asynchronous stochastic update, the number of attractors grows as a power law in $N$, which is in strong contrast to the synchronous case, where the number of attractors increases like a stretched exponential function.

We conclude with a discussion of the size of attractors in these networks. There are of the order of $N^{2/3}$ nodes on the trees rooted in the relevant components. These nodes in trees can adopt any configuration if the node they are rooted in can switch its state on an attractor. Since a non-vanishing fraction of all relevant nodes switch their states on an attractor, the size of the attractor is of the order of

$$2^{N^{2/3}} = \exp\left(N^{2/3} \ln 2\right).$$

The size of the attractors grows like a stretched exponential function and therefore faster than any power law.

Many of our results hold also for other kinds of stochastic asynchronous update, for instance if a certain (small) fraction of nodes is updated at each step, or if the time interval between two updates of a node is peaked at a value $\tau$ and Gaussian distributed around it. (The latter case describes our system for large $N$, when the network of relevant nodes is coarse-grained such that of the order of $N^{1/3}$ neighboring nodes are replaced by a single node that receives a delayed input from the previous node.) In these modified stochastic models, domain walls on an isolated loop can annihilate, but cannot be created again, leading to the same attractors as with the completely stochastic update. However, the state of the trees rooted in the loops will be dominated by a few domain walls when the distribution of update times becomes narrow, with states with more domain walls occurring rarely. Similarly, relevant loops that receive input from outside, and relevant components with nodes with two inputs will have attractors dominated by few domain walls, and the actual size of attractors becomes in the thermodynamic limit $N \to \infty$ smaller than the size obtained by considering any possible sequence of updates.

The biological implications of these findings are clear and have been pointed out in [27]. Since biological networks do not have a completely synchronous update, the number of attractors should be derived from models with asynchronous update. In [27] it is found numerically that the number of stable attractors increases sublinearly. Attractors are called stable if they do not change when a perturbation is added to a synchronous updating rule. The present paper extends this finding by showing that the number of attractors in critical asynchronous Kauffman models increases as a power law, and we thus regain the original claim by Kauffman - albeit for models with a different update rule than the original one.

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