

Updating Schemes in Random Boolean Networks: Do They Really Matter?

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Abstract

In this paper we try to end the debate concerning the suitability of different updating schemes in random Boolean networks (RBNs). We quantify for the first time loose attractors in asynchronous RBNs, which allows us to analyze the *complexity reduction* related to different updating schemes. We also report that all updating schemes yield very similar critical stability values, meaning that the “edge of chaos” does not depend much on the updating scheme. After discussion, we conclude that synchronous RBNs are justifiable theoretical models of biological networks.

Introduction

Random Boolean Networks (RBNs) have been useful tools for modelling and studying the functional and computational requirements and possibilities of life (Kauffman, 1993). They are simple and general. Their advantage is that one does not need to assume any previous functionality. Exploring different parameters of the network, such as number of nodes and connections, one can find regions in the parameter space where computation, such as the one required by life, is very probable. This region is characterized by being stable enough to keep information, but flexible enough to transmit, manipulate and transform it. Not too frozen and ordered, but not too variable and chaotic. That is why it has been referred to as the *edge of chaos*.

There has been a debate on whether RBNs should have a synchronous or asynchronous, deterministic or non-deterministic, updating scheme (Harvey and Bossomaier, 1997; DiPaolo, 2001; Gershenson, 2002; Gershenson et al., 2003). We attempt to close this debate in this paper motivated by the results presented within.

In the next section, we present the background of RBNs and different updating schemes. Then, we show results of experiments which include the quantification of loose attractors, and also present results related to the stability of different RBNs. The main discussion follows from these results. Concluding remarks close the paper.

Background

RBNs are a generalization of cellular automata (CA), where the functionality of each node is not restricted to its neighbourhood. The state (zero or one) of the n nodes of a RBN depends on the states of k other nodes connecting to each. Which nodes affect which (the connectivity) is initially generated at random. The way nodes affect each other (the functionality) is determined by logic lookup tables, which are also initially randomly generated. We can bias the connectivity to achieve different topologies, such as scale-free (Aldana, 2003). We can bias the functionality as well, and this will result in different network properties (Derrida and Pomeau, 1986). The RBNs we study have homogeneous topology and no functional bias, as this is the standard in the literature.

We have proposed a classification of RBNs according to their updating scheme (Gershenson, 2002). We have seen that the updating changes considerably the properties of the same networks, such as number of attractors and attractor lengths, and also affects drastically the shapes of the basins of attraction. The change of updating scheme also affects drastically the behaviour of models based on RBNs or CA (Bersini and Detours, 1994).

Classical RBNs (**CRBNs**) (Kauffman, 1969) have synchronous updating: all nodes at time $t + 1$ take into account nodes at time t for their updating. Since the dynamics are deterministic, and the state space is finite, sooner or later a state will be repeated, and the network will have reached an *attractor*. If it consists of only one state, it will be a *point* attractor. Otherwise, it will be a *cycle* attractor. CRBNs have been widely studied (Wuensche, 1997; Aldana-González et al., 2003).

Asynchronous RBNs (**ARBNs**) (Harvey and Bossomaier, 1997) have asynchronous and non-deterministic updating. A node is randomly chosen and the network updated. There are point attractors, but no cycle attractors due to the non-determinism. However, not all states are revisited. We can identify as *loose* attractors the regions of the state space which capture the dynamics of the network. Until now, loose attractors had been ignored in statistical studies, including

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ours.

Generalized Asynchronous RBNs (GARBNs) (Gershenson, 2002) are similar to ARBNs but semi-synchronous: each time step they select randomly which nodes to update synchronously. Therefore, at a time step some of the nodes can be updated, only one, or even all of them.

Deterministic Asynchronous RBNs (DARBNs) (Gershenson, 2002) introduce two parameters per node, p and q , which allow asynchrony in a deterministic fashion. A node is updated if the modulus of p over time equals q . The set of all p 's and q 's can be seen as the *context* of the network (Gershenson et al., 2003). The context is initially randomly generated, where p 's can take integer values between one and $maxP$, and q 's between zero and $maxP - 1$. DARBNs have point and cycle attractors.

Deterministic Generalized Asynchronous RBNs (DGARBNs) (Gershenson, 2002) are the semi-synchronous counterpart of DARBNs: they update synchronously all nodes which fulfill the condition $p \bmod t == q$.

Mixed-context RBNs (MxRBNs) (Gershenson et al., 2003) are non-deterministic in a particular way: They are DGARBNs with m "pure" contexts (sets of p 's and q 's), and each P time steps, one context is chosen randomly.

We have recently studied the sensitivity to initial conditions of different types of RBNs (Gershenson, 2004), and we found out that the updating scheme almost does not affect the phase transition between "ordered" and "chaotic" regimes of the networks.

Experiments

For our experiments we used a software laboratory we have been developing for this purpose. It is an open source project, available at <http://rbn.sourceforge.net>.

Loose attractors

An attractor can be seen as a part of the state space which a dynamical system has a high probability of reaching¹. In deterministic systems this can be precisely defined, since from one state the dynamics will follow to only one another state. However, in non-deterministic systems several states can follow from one state. The state transitions can be analysed carefully for specific systems, but this becomes intractable for large families of networks. Therefore, we can approximate with simulations loose attractors in RBNs as the part of the state space which is reached after some time.

Here we consider for the first time in statistical analysis the existence of loose attractors. We believe that their study is very important, since they reflect the complexity reduction which non-deterministic RBNs can achieve. The algorithm we devised to find them is as follows: We first let run the

¹In a system with random state transitions, a loose "attractor" would be equal to the whole state space. As we will expose, this is not at all the case of non-deterministic RBNs: the set of their "preferred" states is significantly smaller than the state space.

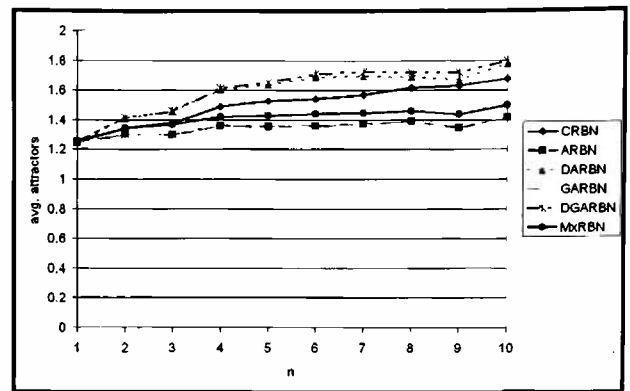


Figure 1: Average number of attractors for $k=1$

network from an initial state for it to reach an attractor (we used more than 10000 time steps). Then, if the state is already in an attractor we have previously found, we begin again with a different initial state. If not, we create a new attractor composed of that state, and the states which we obtain following the dynamic of the network are added to the attractor (omitting states which were already visited). This search for states in an attractor lasts until a maximum search period is reached (we used 3000 iterations). After this, another initial state is chosen and the algorithm is run again. After all the possible initial states of a network, or a certain number, have been explored, there might be some overlapping attractors, since the state of a loose attractor might be missed at first by the algorithm, but then it would construct a redundant attractor over it. Therefore, a trimming process takes place, in which repeated states are sought in different attractors, and if found, the attractors are merged, removing redundant states.

The algorithm is general enough so that any type of attractor (point, cycle, loose) can be detected with it, though it is redundant and computationally expensive. The trimming of the attractors is necessary only for non-deterministic networks (ARBN, GARBN, and MxRBN). Notice that for these networks the sequence of states in the found attractors does not indicate necessarily the actual possible state sequences. The algorithm cannot handle networks of $n > 20$ in a computer with 1Gb RAM. The best supercomputer now would not achieve $n = 30$. Probably the algorithm could be optimized. Also, an analytical solution would be very helpful to explore loose attractors further, but this is not an easy task.

We can appreciate some of the results of our experiments in Figures 1-6 for $k = 1$ and $k = 3$. The averages are of one thousand networks, exploring at most two thousand initial states. We used $maxP = 7$ for contextual networks (DARBNs, DGARBNs, and MxRBNs). MxRBNs have $m = 2$ pure contexts, randomly chosen at each $P = 100$ time steps. The figures sum point, cycle, and loose attrac-

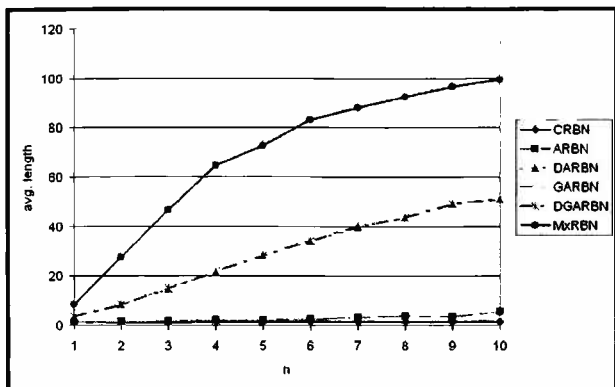


Figure 2: Average length of attractors for $k=1$

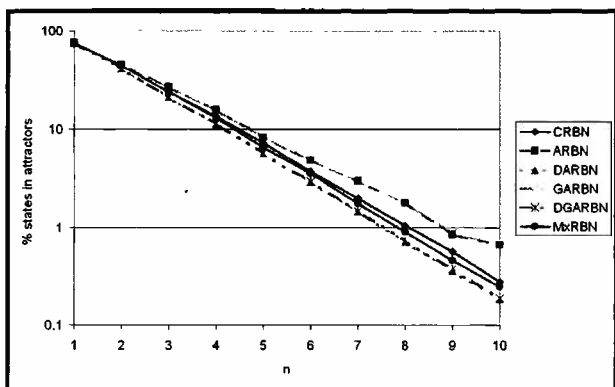


Figure 3: Average percentage of states in attractors for $k=1$

The full data, including standard deviations, and more graphics ($k = 2$) with better resolution are available at <http://homepages.vub.ac.be/~cgershenn/rbn>.

Edge of chaos

We have recently studied the sensitivity to initial conditions of different types of RBNs (Gershenson, 2004). We first created randomly an initial state A, and flip one node to have another initial state B. We run each initial state in the network for ten thousand time steps, obtaining states A' and B'. Then we compare the normalized Hamming distance (1) of the final states with the one of the initial states to obtain a parameter δ (2).

$$H(A, B) = \frac{1}{n} \sum_i^n |a_i - b_i| \quad (1)$$

$$\delta = H_{t \rightarrow \infty} - H_{t=0} \quad (2)$$

If δ is negative, it means that the Hamming distance was reduced. Since the initial distance is minimal ($\frac{1}{n}$), a negative δ indicates that both initial states tend to the same attractor. This implies that the network is stable, in an ordered phase

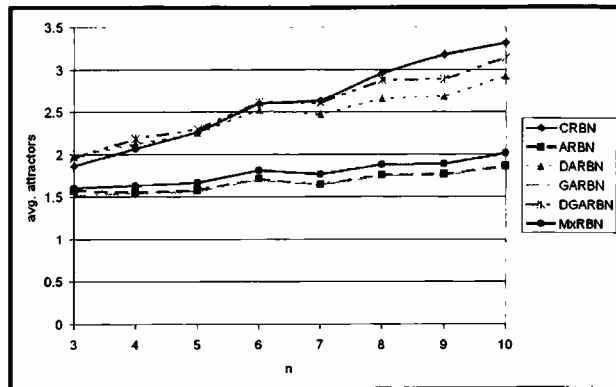


Figure 4: Average number of attractors for $k=3$

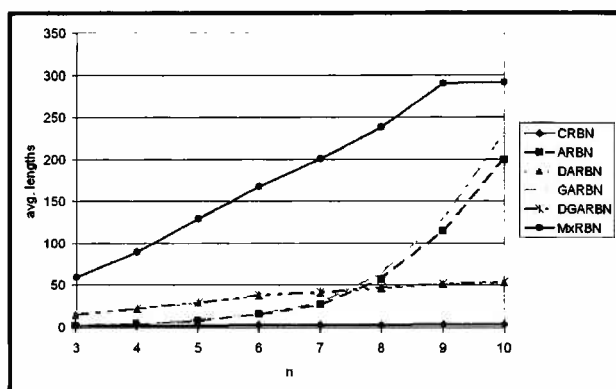


Figure 5: Average length of attractors for $k=3$

A positive δ indicates that the dynamics for very similar initial states diverge. This is a common characteristic of chaos in dynamical systems.

Since the initial states are chosen randomly, the comparison we make is equivalent to see B as a perturbed version of A, and observe if the perturbation affects the dynamics.

To compare the regimes of different types of RBN, we created NN number of networks (200), and evaluated for each NS number of states (200) for all six types of RBN.

We can observe the averages of δ for networks with $n = 5$ in Figure 7. The error bars indicate the standard deviations. We can see that all networks have an average phase transition from ordered to chaotic for values of k between one and three (although the standard deviations indicate us that there can very well be chaotic networks for $k = 2$ and ordered for $k > 2$). They have all a similar “edge of chaos”.

Further results and analysis on the phase transitions of RBNs, including statistics for networks of different sizes, can be found in (Gershenson, 2004).

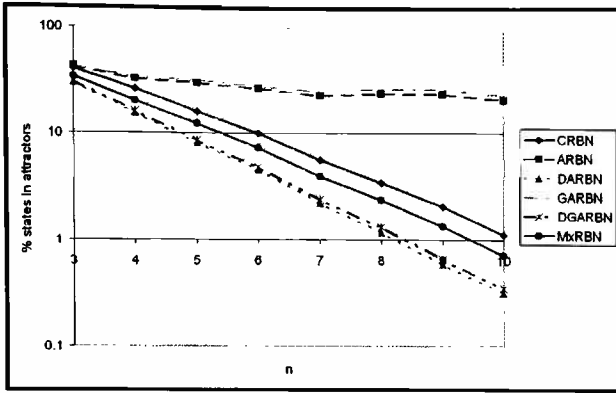


Figure 6: Average percentage of states in attractors for $k=3$

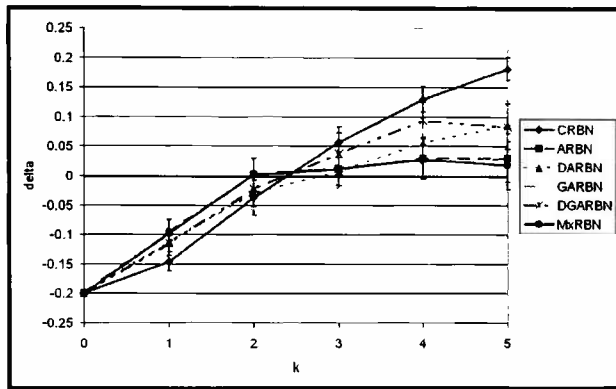


Figure 7: Sensitivities to initial conditions for $n=5$

Discussion

We should say that all the presented data related to attractors have *very* high standard deviations (this is why these are not shown in the figures). This diversity is due to the fact that some networks have only one attractor, others several. Some attractors are of length one (point), while few ones are very long. This makes some networks to have very few states in their attractors and others not so few. This high variance seems to be common in these type of statistical studies (Mitchell et al., 1993).

Nevertheless, one thing we can deduce from the first experiments, is that all network types can perform *complexity reduction*. This means that compared to all the possible states of a network, only few ones are favoured: those in attractors. This property has also been dubbed as “order for free” (Kauffman, 1993). This is more noticeable as k decreases: fewer connections allow more order, and more order implies more complexity reduction². Even when there is an exponential increase of attractor length (states in an attractor) for ARBNs and GARBNS, there is an even higher

²But too much complexity reduction implies no adaptability nor evolvability. That is why we find life at the “edge of chaos”

increase in complexity reduction, since the percentage of states in attractors reduces exponentially with n for low values of k (see Figure 3). ARBNs and GARBNS have also less, but larger attractors, i.e. loose attractors include much more states. We can see that the dynamics of non-deterministic RBNs with low k are very different from random transitions in a state space, because the percentage of states in loose attractors is considerably small (independently of standard deviations). We should notice that MxRBNs, even when non-deterministic, reduce much more complexity than ARBNs and GARBNS, since they have a constrained set of possible attractors, determined by their pure contexts. This tells us that there are many ways in which a network can be constrained in order to have complexity reduction. Other ways include topological or functional bias. It is worth mentioning that this analysis could not have been made without the inclusion of loose attractors in the statistics.

Another property independent of the updating scheme we have found is that networks have almost the same phase transition from an ordered to a chaotic phase. This is, they have very similar “edge of chaos”. This region is interesting, because it is precisely where computation and life can take place (Langton, 1990; Fernández and Solé, 2003). It is flexible and stable enough in order to allow the storage, transmission, and processing of information. Thus, in principle, any updating scheme can be good for modelling life and computation. Moreover, due to the high variances found, evolution has a myriad of parameters to play with in order to find suitable networks. Not only the size and connectivity are important. Also the functionality, topology, updating scheme, and other criteria can be modified to reach an “edge of chaos”. The precise numbers for this do not matter much for theoretical studies, but we know that there is a much higher probability to find it for values $1 < k < 3$ (Gershenson, 2004)³ when there are no functional nor topological biases. We speak about probabilities, but nature selects the convenient configurations of parameters, making them more probable if they are useful in a particular context. This changes the probability space and the constraints of systems. Therefore, in some contexts we can expect to find networks which reached their “edge of chaos” via functional bias, others through topological bias, others through number of connections. But in general, nature would fiddle with all of these parameters in order to find viable networks.

However, it seems that determinism, or at least quasi-determinism, will be favoured by evolution, since RBNs with these types of updating schemes can perform more complexity reduction, as seen in Figure 6. They can have the similar stability than non-deterministic RBNs at the “edge of chaos”, but they will need, in general, less nodes to per-

³In analytical studies n has not been taken into account, but we have found with simulations that the size of the networks does matter, since larger nets seem to have indirect “interferences” which decrease the precise critical value of k as n increases.

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form the same functions. This can be thought in the following way: a non-deterministic network can perform computations and complexity reduction, but in order to cope with the non-determinism, a lot of redundancy is required. And excessive redundancy costs. Contextual RBNs can perform even more complexity reduction because they “throw” information into their context (but they are more complex). We can assume that there are many constraints in nature which prevent “full” non-determinism (where any node can be updated indiscriminately), so in this case, plain ARBNs and GARBNs would not be good models of natural networks. Still, they can be constrained through artificial evolution to show rhythmic behaviour (DiPaolo, 2001). We can also assume other constraints, such as delays (Klemm and Bornholdt, 2003), or limited non-determinism, such as the one of MxRBNs.

Entering into the main debate concerning the use of synchronous RBNs as realistic models, we have found that the main difference of ARBNs with classical RBNs was due to non-determinism, not to asynchronicity (Gershenson, 2002). And the determinism of natural networks has just been justified: deterministic or quasi-deterministic networks are more efficient, especially in the case of large networks. There is not a big difference between the properties of DARBNs and CRBNs, and moreover, they can be mapped into one another (Gershenson, 2002). Therefore, for *simplicity*, CRBNs seem to be justifiable models of real networks, if we are interested in theoretical studies of the possibilities of RBNs, such as the ones carried out by Kauffman⁴. This is because even when contextual RBNs can perform even more complexity reduction⁵ than CRBNs, they are harder to study. CRBNs give similar results than DARBNs and DGARBNs, and we should not be interested in the *precise* numbers we obtain. As we have seen, there is a huge variance in RBNs, and different parameters, such as biases or constraints, can change the precise numbers considerably. Another reason for justifying CRBNs is that if we are not assuming any functionally, how could we assume some updating period for a DARBN? Real networks are not fully synchronous, but they are also not fully boolean, nor with homogeneous connectivity. We believe that the synchronous assumption is justifiable for *theoretical* studies, especially compared to plain ARBNs. But if we are interested in modelling a particular network, then the type of synchronicity should be that which resembles more the one of the particular system modelled.

⁴Kauffman used RBNs to explain how there could be so few cell types with so many genes. Indeed, there is a complexity reduction towards few cell types (attractors). But the precise calculation related to the number of genes (roughly known in 1993) and the precise number of expected cell types (attractors) seems more like numerology, since there is a huge variance in RBNs, and real regulatory networks do have topological and functional biases.

⁵This is a bit tricky, because contextual RBNs have much more possible states, since these include the actual phase of the context (Gershenson et al., 2003).

Then we should model a suitable updating scheme, but also a suitable functionality and topology. DGARBNs seem to be a good alternative for this. MxRBNs are also promising, since even when they are non-deterministic, they have enough limits so that they can perform much better complexity reduction than plain ARBNs or GARBNs. Other methods already mentioned are also worth exploring.

The main lesson from the presented data is that there is always a critical region, and that nature *thrives* (selects) towards it, since it is of selective advantage. But in general, it does not matter which updating scheme is being used, since all schemes *have* this region. We can conclude, as it has been stated by others, that life is very probable in our universe (Kauffman, 1993), and almost inevitable in a planet like ours. This contributes to the understanding of the general conditions for life. But this understanding generates further questions. What about environments which do not allow the exploration, selection, or retention of life? They might be too ordered (frozen) or too chaotic (boiling). How abundant are they? Which are the paths from them to a life-supportive environment? Which are the paths *out* of a life-supportive environment? Which are the mechanisms used by an environment to *maintain* or *propagate* its ability to promote life? These are questions which eagerly await exploration.

Conclusions

In the XIXth century, many Latin American countries tried to develop with “order and progress” (It was the lemma of Mexican president Porfirio Díaz, and the Brazilian flag bears the inscription “Ordem E Progresso”). In order to have both, a careful balance is required: too much order does not allow changes, thus progress. Too much progress can destabilize the order. The evolution of life requires the same “order and progress” principle: order to retain acquired characteristics, progress to explore new possibilities. This is the “edge of chaos”. In this paper, we have defended that in random Boolean networks, many parameters influence the precise location of this region, but it exists, and evolution can find it.

Even when interactions in real systems may be non-deterministic, the responses can be at a higher level deterministic, or close to deterministic. It is convenient to have determinism, because of computational reasons: information can be manipulated much easier and with less requirements. We can see that for the same networks, deterministic updating offers much more complexity reduction, therefore, this should be favoured by evolution. We can assume that nature can find cyclic or quasi-cyclic behaviours, varying different parameters, because it did, presumably more than once.

The main criticism to CRBNs was that the synchronicity was not justified (Harvey and Bossomaier, 1997). We believe that synchronicity can be justified with our results, since we have seen that synchronous networks are able to

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compute and to reduce complexity better than asynchronous non-deterministic ones. Therefore, it is expected, and observed, that synchronicity will evolve in living systems. How could this happen, and the precise mechanisms by which asynchronous components can synchronize, are other questions, very interesting ones, and people have been already studying them (Rohlfshagen and DiPaolo, 2004; Strogatz, 2003).

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