

# Searching for Rhythms in Asynchronous Random Boolean Networks

Ezequiel A. Di Paolo

GMD—German National Research Center for Information Technology  
Schloss Birlinghoven, Sankt Augustin, D-53754, Germany  
Ezequiel.Di-Paolo@gmd.de

## Abstract

Many interesting properties of Boolean networks, cellular automata, and other models of complex systems rely heavily on the use of synchronous updating of the individual elements. This has motivated some researchers to claim that, if the natural systems being modelled lack any clear evidence of synchronously driven elements, then asynchronous rules should be used by default. Given that standard asynchronous updating precludes the possibility of strictly cyclic attractors, does this mean that asynchronous Boolean networks, cellular automata, etc., are inherently bad choices at the time of modelling rhythmic phenomena? In this paper we focus on this subsidiary issue for the case of Asynchronous Random Boolean Networks (ARBNs). We find that it is rather simple to define measures of *pseudo-periodicity* by using correlations between states and sufficiently relaxed statistical constraints. These measures can be used to guide an evolutionary search process to find appropriate examples. Success in this search for a number of cases, and subsequent statistical studies lead to the conclusion that ARBNs can indeed be used as models of coordinated rhythmic phenomena, which may be stronger precisely because of their built-in asynchrony. The methodology is flexible, and allows for more demanding statistical conditions for defining pseudo-periodicity, and constraining the evolutionary search.

## Introduction

Cellular automata, coupled-map lattices, Boolean networks, and a number of variants of these classes have been the centre of copious research effort. The aims of this research have been mainly focused on two distinct directions: a piece of work will, in general, study these entities in themselves, as classes presenting interesting properties from a formal viewpoint, and also possibly from a practical one, or it will use some version of these entities as a modelling tool applied to a scientific end. One may be interested in the properties of cellular automata *per se* as a universal class, or one may use cellular automata to model some biological phenomenon such as morphogenesis. We hurry to

stress that there is much overlap and cross-fertilization between these two directions, but that the distinction holds nonetheless.

Significant contributions from the first route to the second sometimes occur when the limitations of a class of formal entities are exposed. Modellers can assimilate this knowledge, and choose their modelling tools and techniques accordingly. In recent years, much evidence has been gathered suggesting that many of the initially interesting features of the above mentioned classes for modelling complex systems have depended crucially on the use of a synchronous rule for updating the atomic elements. In contrast, the implementation of asynchronous updating rules has tended to produce trivial, rather than complex, behaviour.

In this paper we will be concerned with a subsidiary aspect of one such demonstration of the effects of asynchrony, (Harvey & Bossomaier, 1997). However, the scope of our worries is more general and the results presented here could be applied more widely. As will be described below, Harvey and Bossomaier (1997) show that asynchronous updating introduces radical changes in the long term behaviour of random Boolean networks. In the asynchronous case, the typical number of different attractors per network is smaller than in the synchronous case, and these seem to be mainly of the fixed point type, suggesting much larger basins of attraction. As a further difference, the expected number of point attractors will not depend on the size of the networks. These findings cast doubts on some interpretation made when using random Boolean networks to model genetic regulatory networks, (e.g., Kauffman, 1969, 1993). In passing, the authors draw the correct conclusion that it is not possible for such networks to exhibit non-stationary cyclic long term behaviour due to the randomness of the updating scheme.

A large number of biological systems produce rhythms which arise from the complex interaction of many elements, and are not due to the existence of an external clock that orchestrates the behaviour of

*Copyrighted Material*

these basic constituents, (a variety of examples can be found in Winfree, 1980). For instance, patterns of global rhythmic activity have been observed in ant nests, (Franks, Bryant, Griffiths, & Hemerik, 1990; Cole, 1991b), while the behaviour of individual ants in isolation is not rhythmic in itself (Cole, 1991a). This phenomenon has been successfully modelled using continuous maps that interact asynchronously, (Sole, Miramontes, & Goodwin, 1993).

If, as has been rightly argued, asynchronous updating should be the modeller's default choice, should we conclude that the impossibility of exhibiting cyclic attractors means that asynchronous Boolean networks are inappropriate for modelling rhythmic phenomena such as the above? This question has not been addressed explicitly by Harvey and Bossomaier (1997), or by authors drawing similar conclusions for cellular automata, (e.g., Ingerson & Buvel, 1984; Bersini & Detours, 1994). It seems that the limitations of asynchronously driven systems regarding cyclic behaviour should prompt the modeller to discard them at an early stage as good tools for studying rhythm in biological, and other complex systems.

It will be shown that this would be a hasty conclusion, and that the long term behaviour of some asynchronous random Boolean networks can be characterized by marked rhythms. In order to do this, we will provide a simple way of defining and measuring pseudo-periodic behaviour, and use this measure to guide an evolutionary algorithm in the search for cases exhibiting this pseudo-periodicity.

### Asynchrony as the default modelling choice

The work by Nowak and May (1992) on spatial patterns in a population of players of the Prisoner's Dilemma is by now almost a classic in the growing literature on the role of artefacts in simulation models. The complex spatial patterns obtained in their model, which suggest interesting implications regarding the polymorphic conviviality of cooperators and defectors, depend critically on the synchronous updating scheme they use. When asynchrony is introduced no spatial pattern appears, and the much gloomier picture of global defection as the stable strategy results, (Huberman & Glance, 1993)<sup>1</sup>. But this is not the only example from which a similar lesson can be learned.

Abramson and Zanette (1998) show that asyn-

<sup>1</sup>In (May, Bonhoeffer, & Nowak, 1995) the original choice of synchronous updating is defended by saying that it may be appropriate for some biological situations. This is, no doubt, true, although they fall short of justifying that such is indeed the case for the situation they are modelling.

chronous updating in globally coupled logistic maps suppresses much of the complexity of the synchronous case. The state of each site results from a sum of the application of a logistic map to the previous state and a global coupling term reflecting the mean activities of all the other sites. In the case of synchronism, as the strength of the coupling increases so does the complexity of the global behaviour from partially ordered to turbulent regimes. With asynchronous updating, complexity *decreases* as the coupling between maps is made stronger. Abramson and Zanette (1998) argue that this is a significant difference, and concur with Rolf, Bohr, and Jensen (1998) in that, unless one can advance sufficient reasons to the contrary, asynchronous updating is "more physical".

Analogous results have been reported for the case of cellular automata, (e.g., Ingerson & Buvel, 1984; Bersini & Detours, 1994), and Boolean networks (Harvey & Bossomaier, 1997). The latter authors suggest that the assumption of synchrony is perhaps made "most dangerous" when it is associated with the idealisation that individual elements can be safely modelled as having discrete states, (the "Boolean idealisation" as they call it). This is interesting, although the above example of coupled maps (in which elements are "non-Boolean") suggest that the dangers may in fact be more widespread.

The methodological lesson we can derive from these and other cases is that, in the absence of knowledge about specific time delays, orchestration by an external clock should not be the default choice when modelling complex systems of many interacting elements. This is especially relevant to studies addressing phenomena related to local or global synchronization, or entrainment in such multicomponent systems.

### Attractors in asynchronous random Boolean networks

A Boolean network is an array of nodes, each of which can have any one of two states (0 or 1). Each node is connected to other nodes in the network. By computing a Boolean function of their states, a new state for the node is determined. Random Boolean networks form a class of networks in which the links between nodes and the Boolean function are specified at random. They are divided into subclasses depending of the total number of nodes ( $N$ ), and the number of links that influence each node ( $K$ ), which is assumed here to be the same for all nodes<sup>2</sup>.

Boolean networks have been used as models of different biological phenomena including morphogenesis,

<sup>2</sup>More general classes are obtained when  $K$  indicates the average number of connections to each node.

and immune response. The most well known use of random Boolean Networks has been as models of genetic regulation (Kauffman, 1969, 1993). They have also served to model idealised developmental processes, (Dellaert & Beer, 1994). In the majority of cases, synchronous methods have been used to update the network.

Harvey and Bossomaier (1997) have studied asynchronous random Boolean networks (ARBNs) by exploring the nature of their attractors using numerical experiments, and by presenting some general arguments about what can be expected from ARBNs as a class. In contrast with their synchronous cousins, ARBNs have a significant trend to evolve towards fixed point attractors suggesting that these attractors have much larger basins of attraction in the asynchronous case, a finding in accordance with previous observations by Ingerson and Buvel (1984), and Bersini and Detours (1994) on cellular automata (which in particular cases may be thought of as a special sub-class of Boolean networks). The average number of point attractors in an ARBN tends to be small when compared with the synchronous case, and does not depend on the size of the network. These observations would invalidate, if asynchrony were to be used, Kauffman's (1969, 1993) conclusions about the significance the supposedly intrinsic order of genetic regulatory networks. Kauffman has argued that different cell types in multicellular organisms correspond to different attractors of the genetic regulatory network, and that the number of cell types is roughly related to the size of the genome in the same way as the number of different attractors in a Boolean network is related to its size  $N$  for low  $K$  (roughly,  $\sqrt{N}$  for  $K = 2$ ), and, consequently, possibly for the same reasons. A similar comparison is made between the length of cell division cycles and the typical length of attractors. But these analogies rely critically on the applicability of synchronous updating to the real case which remains to be justified.

In short, Harvey and Bossomaier (1997) contribute to the methodological lesson drawn in the previous section. Asynchronous updating should be the default choice when Boolean networks are used as modelling tools, unless there is sufficient justification for considering synchrony as characteristic of the phenomenon being modelled.

Not all the attractors found in ARBNs are of the fixed point type. Those that are not have been termed "loose attractors", which can be broadly defined as the sub-set of states of the network with more than one element such that, if a given state belongs to this sub-set, then the state that follows after asynchronous updating will also belong to the sub-set. Cyclic attractors,

like those found using synchronous updating, cannot be found in ARBNs. The proof is simple for standard random updating (random selection with replacement of the node to be updated, i.e., each node is updated at random with uniform probability independently of previous updates). If we suppose that the network has a cyclic attractor which is not a fixed point, then there must be two consecutive states in this attractor differing in at least the state of one single node. Since a time step is *defined* as  $N$  random node updates, there is a non-zero probability that the node that should have changed its state remains without being updated. Therefore, the two consecutive states will not differ in the state of this node as required. Notice that the proof does not work for other forms of asynchronous updating which guarantee that all nodes will be updated after  $N$  single node updates<sup>3</sup>.

### Autocorrelation and pseudo-periodicity

Using standard random updating (as will be used in this paper), is it possible for these 'loose' attractors to show marked rhythms? This question must be answered on two fronts simultaneously. On the one hand, one should specify what is meant by 'rhythm' in this case, and, on the other, one should try to find a way of using this criterion to search for cases that qualify.

Strictly speaking, the observation that ARBNs cannot produce cyclic attractors is true but only of relative significance for the researcher interested in rhythmic behaviour, for instance, in biology. This is mainly because the definition of periodicity for deterministic systems does not conform well with the relaxation of the assumption of an external driving clock. Effectively, in order to say that cyclic attractors cannot be found in ARBNs, one must take back the discarded external clock, this time not as a driving, but as a measuring device. This is achieved by using a system-independent time scale for defining when a new state of the whole network has occurred. We must therefore adopt a view of rhythmic behaviour which focuses more on the operational relationships between the states of the system — for instance, by noticing regularities in the ordering and/or statistical properties of patterns — and less on the externally measured individual duration of the states.

<sup>3</sup>As a simple counterexample, suppose that all nodes in the network but one fixate on a given state, and will remain unchanged independently of how the update is performed, and suppose that the remaining node is connected to a number of the other nodes, and to itself with a rule that specifies that, whatever the value of the other nodes, its own value must change. Since the updating scheme guarantees that the node will be updated, it will flip its value every time step.

Self	Self - 1	Self + 1	New Value
0	0	0	0
0	0	1	0
0	1	0	1
0	1	1	0
1	0	0	1
1	0	1	0
1	1	0	1
1	1	1	1

Table 1: Update rules for hand-built example of pseudo-periodic ARBN.

The real measure of rhythmic behaviour in this case will be a measure of how patterns occurring at different instants in the history of a system relate to one another. For the case of ARBNs in particular it is possible to devise a variety of simple measures based on correlations between states occurring at different points during the evolution.

In this paper, perhaps the simplest of these possible measures will be used because it will provide us with the case most similar to deterministic periodic behaviour. Other measures are imaginable, and the methodology used to search for cases that rank high under these measures is, in principle, equally applicable. The chosen measure indicates the degree to which a given state in an ARBN of  $N$  nodes *approximately* recurs after *approximately*  $P \times N$  single node updates. Networks ranking high on the scale defined by this measure will be called *pseudo-periodic*<sup>4</sup>. The meanings of ‘approximately’ must be made clear in both cases. We first define an order index  $j$  which is incremented by one unit after  $N$  random updates to single nodes, but we will not equate periodicity with strict recurrence of states using this index. Instead, the correlation between two states of the network will be used to that end. The state at time  $j$  is denoted by  $S(j)$ , a vector whose components  $s_i(j)$  correspond to the state of each node  $i$  in the network. The correlation between the states at two different times  $j$  and  $j'$  is:

$$C(j, j') = \frac{1}{N} \sum_{i=1}^N s_i^*(j) s_i^*(j'),$$

where  $s_i^*(j)$  is the linear scaling of  $s_i(j)$  into  $[-1, 1]$ . Highly correlated states will be taken to mean also highly similar states from the point of view of the sys-

<sup>4</sup>This term should not be confused with “quasi-periodicity” as used to refer to toroidal attractors with an irrational ratio of frequencies in continuous deterministic systems.



Figure 1: Asynchronous evolution of hand-built example. Initial condition: all nodes but one set to 0.  $N = 32$ ,  $K = 3$ , time increases from left to right; 1000 updates. Black corresponds to 1 and white to 0.

tem’s operation or its global significance. This is an assumption that need not be true in general, as discussed in the last section. A more global measure of the behaviour of the network is given by the correlation function between a state and its  $k$ ’th successor, averaging over  $M$  successive states:

$$AC(k) = \frac{1}{M} \sum_{j=1}^M C(j, j+k),$$

with  $k = 0, 1, 2, \dots$ . For sufficiently large values of  $M$  this function will give an idea of how well correlated, on average, is any given state with a state occurring  $k$  time steps afterwards. In this case, the function will be called simply *autocorrelation*. Notice that a given network may possess different autocorrelation functions depending on how many attractors it has and how much they differ in their statistical properties. A *sufficient* condition for ensuring non-stationary pseudo-periodic behaviour with pseudo-period  $P$  will be to ask that at least one of the autocorrelation functions has distinct peak values for  $k$  close to  $P$  which means high similarity between  $S(j)$  and  $S(j+P)$ .

Let’s consider the following hand-designed example for  $N > 3$  and  $K = 3$ . Each node is connected to the nodes which immediately precede and follow it as indexed (with wrapping-up at the end), and to itself. The Boolean functions are the same for all nodes<sup>5</sup> and are shown in table 1. What these rules say is that if a node is in state 0, then it must remain 0 unless there is a 1 on the preceding node and a 0 in the following node. If a node is in state 1, then it must remain 1 unless there is a 0 in the preceding node and a 1 in the following. With synchronous updating, these rules and connectivity produce travelling waves with period  $P = N$ . For the case of asynchronous updating we find that the evolution of the network can also be characterized by waves with a pseudo-period  $P \cong N$ .

Figure 1 shows an example of the asynchronous evolution of this network, and figure 2 shows the corresponding autocorrelation function averaged over 10000

<sup>5</sup>This example is a particular case of a homogeneous Boolean network. In the general case, as in the rest of the paper, Boolean functions differ from node to node.

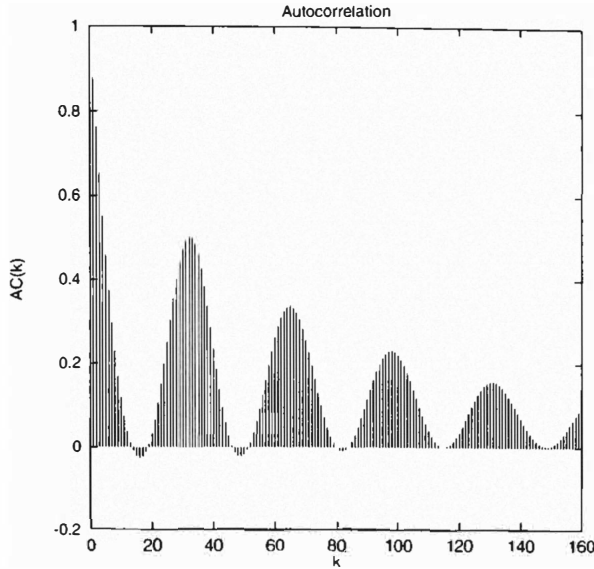


Figure 2: Autocorrelation corresponding to hand-built example as averaged over 10000 consecutive states and over 10 runs.  $N = 32$ ,  $K = 3$ ; peaks in  $k = 0, 32, 65, 99, 132$ .

consecutive states and over 10 runs. Rhythmic behaviour is apparent both by direct observation of the evolution, and from the autocorrelation function. The evolution of the network can be interpreted as a soliton wave with varying width but having a distinctly low variability in speed. The autocorrelation function shows clear peaks near multiples of a pseudo-period of  $P \cong N$ . It is important to notice that each successive peak is a bit lower than the previous one, showing an effect of ‘memory decay’. This is mainly due to the fact that a highly correlated state will recur after *about*  $P$  time steps, and therefore actual recurrence becomes more uncertain the further upstream one moves.

### Evolving rhythms

Is the above example an unique case? This question can be answered by devising a method for searching for more examples. The idea is to use a target autocorrelation function and a search method that provides us with networks which will approximate this target. We have used a simple genetic algorithm as a search tool. ARBNs are described using a binary genotype which encodes their connectivity and the rules governing how each node is updated. Any network with parameters  $N$  and  $K$  can be encoded in a genotype of length  $G_L$ :

$$G_L = N(K \log_2 N' + 2^K),$$



(a)



(b)

Figure 3: Asynchronous evolution of evolved ARBN with  $N = 16$ ,  $K = 2$  and a target period  $P = 16$ , (see also figure 4). 1000 consecutive states starting from a random initial condition are shown in (a). These can be compared with another 1000 consecutive states occurring later in the same run, (b). The interval between the two figures is of 8000 steps.

where  $N'$  is the first power of 2 greater than or equal to  $N$ . The factor in parentheses corresponds to the number of binary loci necessary to encode  $K$  connections plus one Boolean function of  $K$  arguments. Other encodings are possible.

Individual networks are run for between 500 and 1000 time steps (each time step being equivalent to  $N$  node updates), and for a number of trials (usually between 4 and 10) starting from different random initial conditions. After each trial, the autocorrelation  $AC(k)$  is calculated for  $k = 0, 1, \dots, 2N - 1$  by averaging for all the states in the run (except the last  $2N$ ).

The fitness of a network is calculated for each trial as  $1 - D$ , where  $D$  is the normalized distance between the network's autocorrelation, and the target autocorrelation. Fitness scores are averaged over the trials, and the value of one standard deviation is deducted to benefit low variability between the trials. Point mutation, uniform crossover, and a rank-based selection scheme are used. The rate of mutation per loci is chosen in accordance to the genotype length so as to have a probability of no mutation in a given genotype of about 80%. The size of the population is of 90 networks.

The choice of an adequate target autocorrelation function is crucial for the success of the search. This target need not correspond to any realisable network. Instead, its definition has been guided by considerations of evolvability. Our choice in all the cases presented here has been to define a target autocorrelation using steps between the values of 0 and 1. States will

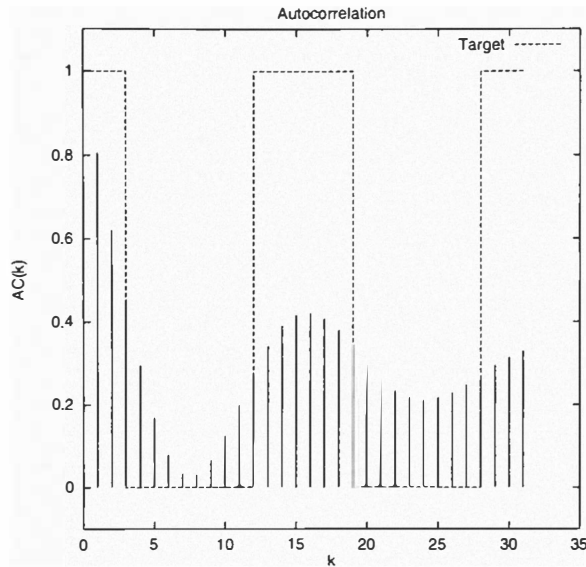


Figure 4: Autocorrelation for an evolved network with  $N = 16$ ,  $K = 2$ , and  $P = 16$ , as averaged over 10000 consecutive states. The dashed line shows the target autocorrelation used in the fitness function.

be highly correlated around the chosen pseudo-period  $P$ , so that a value of 1 is assigned to values of  $k$  in  $[nP - e, nP + e]$ , with  $n = 0, 1, 2, \dots$ . For any other value of  $k$  the autocorrelation is 0. The width of the square peak  $2e$  is carefully chosen so as to strike a balance between the number of values of  $AC(k)$  equal to 0 and those equal to 1. This balance is important in order not to bias the search process, and not because we can expect typical pseudo-periodic ARBNs to necessarily exhibit such balance in their autocorrelation functions.

So far, ARBNs have been successfully evolved for  $N = 16, 32, 64$  and  $K = 2, 3, 4$  using target periods of  $P = N/2, N, 2N$ . A few trials with shorter target periods and larger  $N$  have been attempted only with minor success. The number of generations has oscillated between 1000 and 5000, often obtaining good results after about 500 generations<sup>6</sup>.

Figures 3, 4, 5, and 6 correspond to an evolved network with  $N = 16$ ,  $K = 2$ , and  $P = 16$ . Figure 3 shows the first and the last 1000 steps corresponding

<sup>6</sup>The search method implicitly selects networks with rapid transients. Harvey and Bossomaier (1997) have observed that standard asynchronous updating produces the shortest transients, so we do not consider this to be a major problem. However, simple modifications to the search algorithm could avoid this if necessary.

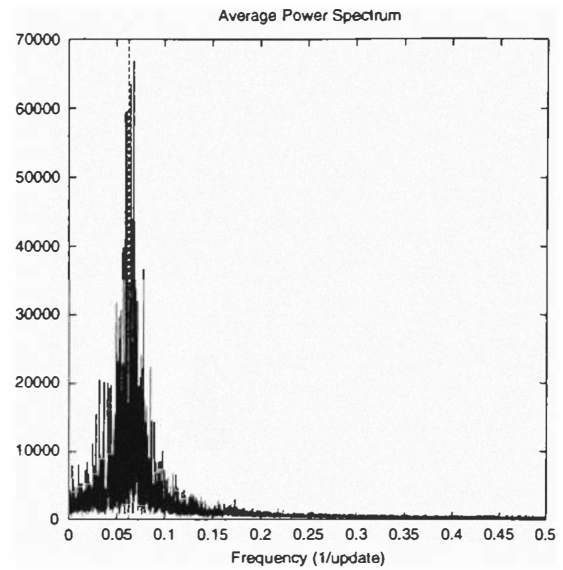


Figure 5: Power spectrum for evolved network corresponding to figures 3 and 4, as averaged over variations in the state of individual nodes. The frequency corresponding to the target period is shown with a vertical dashed line.

to a 10000-step run. Although some nodes are frozen most of the time, the remaining ones form distinct patterns which appear with a marked rhythm. The form of the pseudo-periodic attractor is stable as can be appreciated by comparing both figures. This result is not directly implied in the constraints used for performing the evolutionary search, which condition only the shape of the autocorrelation.

The autocorrelation function is shown in figure 4, together with the target autocorrelation, the range of which goes from  $k = 0$  to  $k = 31$  (dashed line). This function has been calculated by averaging over 10000 steps corresponding to 10 different runs starting from different random initial conditions. It shows a clear, though wide, peak around  $k = 16$ .

Further evidence of the rhythmic behaviour of this network can be obtained by calculating the power spectrum (using Fast Fourier Transform) for each node in the network. This is shown in figure 5 where the  $N$  spectra have been averaged to give an idea of the behaviour of the whole. There is a marked peak corresponding to a frequency near  $1/P = 0.0625$ .

Figure 6 presents a histogram showing the percentage of recurrence of individual states corresponding to the same network, again over a 10000-step run. States

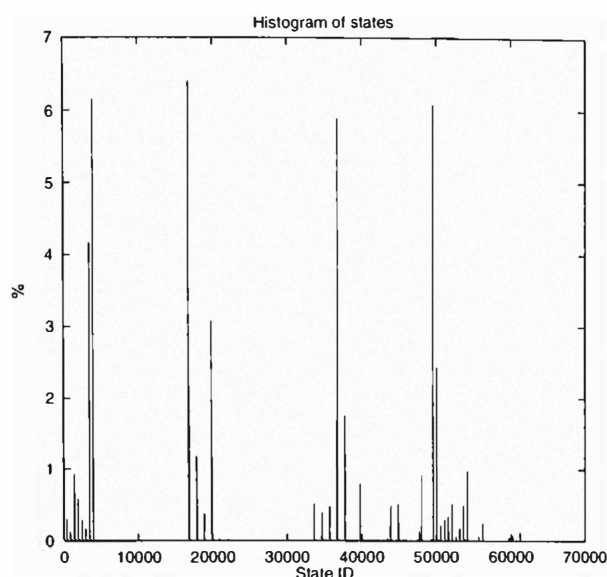


Figure 6: Histogram of states corresponding to the run shown in figure 3. States are labeled by using the integer number that they encode as a binary string. Only about 12 states recur with a frequency greater than 1%.

are identified using the integer number that they encode as binary strings. The number of states that recur in the attractor with a frequency greater than 1% is about 12.

The rhythmic behaviour of an evolved ARBN with  $N = 32$ ,  $K = 2$ , and  $P = 32$  is shown in figure 7, and the corresponding autocorrelation in figure 8 where a more defined peak around  $P$  can be observed.

Finally, one interesting observation we have gathered from all the cases tested so far is that all the evolved pseudo-periodic ARBNs behave as strictly periodic if they are updated synchronously with periods corresponding to the evolved pseudo-periods. We do not know how generalised is this observation.

### Conclusion

It has been shown that, although they cannot reproduce strictly cyclic behaviour, ARBNs need not be discarded *a priori* as possible models of rhythmic phenomena since they may be able to capture many features of interest of such phenomena. Few people would hesitate in calling a natural system 'rhythmic', or even 'periodic', if its behaviour exhibited a power spectrum such as the one shown in figure 5.

Precisely because they do not incorporate synchrony

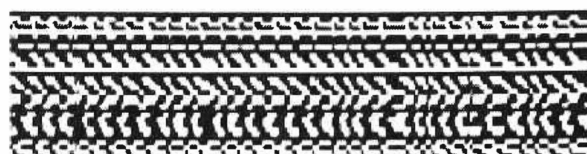


Figure 7: Asynchronous evolution of evolved ARBN with  $N = 32$ ,  $K = 2$ , and a target period  $P = 32$ , for 1000 time steps.

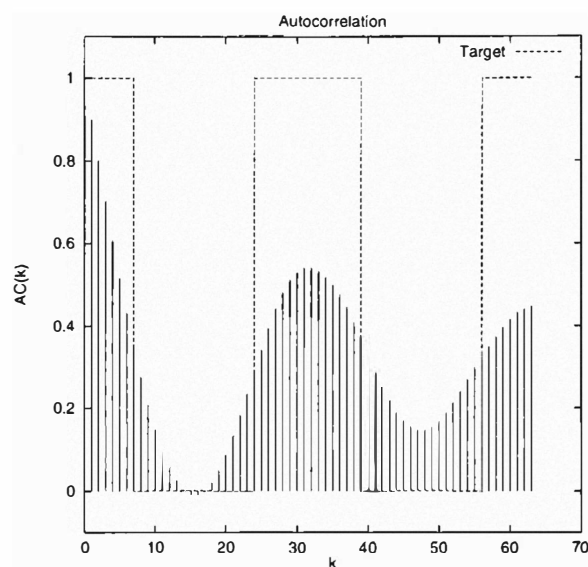


Figure 8: Autocorrelation for ARBN corresponding to figure 7, averaged over 10000 consecutive states. The dashed line shows the target autocorrelation.

by default, ARBNs, and similar asynchronous systems, may constitute quite strong models if they are able to show spontaneous rhythmic behaviour as compared with models using built-in synchrony from the start.

It is possible to provide simple ways for recognizing pseudo-periodicity, and use them to guide an evolutionary search process to find examples. Probably a variety of search processes could have worked equally well or better for this task, but success using a genetic algorithm is suggestive of ways natural selection could have acted on natural systems with analogous properties, if rhythmic or coordinated behaviour happened to be of some functional value.

Before drawing conclusions about the relatively minor success in evolving ARBNs with other pseudo-periods or values of  $N$ , it may be necessary to un-

derstand better the evolutionary task itself, and check whether the choices for encoding and mutation rates could not be improved. As it stands, the evolutionary landscape exhibits a high degree of neutrality (there are many ways of producing functionally equivalent ARBNs), and choice of search parameters would perhaps need some re-consideration in view of this fact.

As briefly mentioned, our definition of pseudo-periodicity relies on similarity between states using a correlation measure. Such similarity need not correspond to *significant* similarity in the context of a natural system. It is easy to think of many (not necessarily pathological) cases in which alterations to the strict order of single events may produce radically different results. In those cases, our definition does not work, and it is an open question whether others would. Two speculative solutions could perhaps be of some use in such cases. One is the utilization of *weighted correlation* as a measure of similarity. If it is functionally important that certain states recur pseudo-periodically more reliably than others, then they could be assigned a higher weight in the calculation of correlations. The other possible solution is the use of *single element autocorrelation* on which stricter statistical demands could be made on particular nodes (like less variability in pseudo-period) if it were necessary. It is not clear yet whether these solutions would work in general.

Finally, we have also mentioned that the impossibility of reproducing strictly cyclic behaviour depends on the use standard random updating. Other schemes which guarantee that all nodes be updated in a same time step admit some cases of strict cycles. This is not important in itself, but should warn us that these latter forms of updating are perhaps as artificial as synchronous updating, and should not constitute a default choice for the modeller either. Observations like this one open the question of which is the most adequate way of defining the passage of time in a way that accords naturally with the type of systems involved. In this work, a time index has been defined in a intuitive manner in accordance to the size of the system so as to simulate statistically parallel (uniform time delays) and independent updating for all nodes. We believe that such a choice is appropriate since we did not rely heavily upon it to define pseudo-periodicity (variability in the pseudo-period is allowed to be large). It remains an open issue whether other, 'more physical' time indexes, appropriate for the particular systems in question, could be defined.

## References

- Abramson, G., & Zanette, D. H. (1998). Globally coupled maps with asynchronous updating. *Phys. Rev. E*, **58**, 4454–4460.
- Bersini, H., & Detours, V. (1994). Asynchrony induces stability in cellular automata based models. In Brooks, R., & Maes, P. (Eds.), *Artificial Life IV, Proceedings of the Fourth International Conference on Artificial Life*. Cambridge, MA: MIT Press.
- Cole, B. J. (1991a). Is animal behaviour chaotic? Evidence from the activity of ants. *Proc. R. Soc. Lond. B*, **244**, 253–259.
- Cole, B. J. (1991b). Short-term activity cycles in ants: generation of periodicity by worker interaction. *Am. Natur.*, **137**, 244–259.
- Dellaert, F., & Beer, R. (1994). Toward an evolvable model of development for autonomous synthesis. In Brooks, R., & Maes, P. (Eds.), *Artificial Life IV, Proceedings of the Fourth International Conference on Artificial Life*. Cambridge, MA: MIT Press.
- Franks, N. R., Bryant, S., Griffiths, R., & Hemerik, L. (1990). Synchronization of the behavior within nests of the ant *Leptothorax acervorum* I. *Bull. Math. Biol.*, **52**, 597–612.
- Harvey, I., & Bossomaier, T. (1997). Time out of joint: Attractors in asynchronous random Boolean networks. In Husbands, P., & Harvey, I. (Eds.), *Proceedings of the Fourth European Conference on Artificial Life*, pp. 67–75. Cambridge, MA: MIT Press.
- Huberman, B. A., & Glance, N. S. (1993). Evolutionary games and computer simulations. *Proc. Natl. Acad. Sci. USA*, **90**, 7715–7718.
- Ingerson, T. E., & Buvel, R. L. (1984). Structure in asynchronous cellular automata. *Physica D*, **10**, 59–68.
- Kauffman, S. (1969). Metabolic stability and epigenesis in randomly constructed genetic nets. *J. theor. Biol.*, **22**, 437–467.
- Kauffman, S. A. (1993). *The Origins of Order*. Oxford: Oxford University Press.
- May, R. M., Bonhoeffer, S., & Nowak, M. A. (1995). Spatial games and the evolution of cooperation. In Moran, F., Moreno, A., Merelo, J. J., & Chacon, P. (Eds.), *Proceedings of the Third European Conference on Artificial Life*, pp. 749–759. Granada, Spain. Berlin: Springer.
- Nowak, M. A., & May, R. M. (1992). Evolutionary games and spatial chaos. *Nature*, **359**, 836–829.
- Rolf, J., Bohr, T., & Jensen (1998). Directed percolation universality in asynchronous evolution of spatio-temporal intermittency. *Phys. Rev. E*, **57**, R2503–R2506.
- Sole, R. V., Miramontes, O., & Goodwin, B. C. (1993). Oscillations and chaos in ant societies. *J. theor. Biol.*, **161**(3), 343–357.
- Winfree, A. T. (1980). *The geometry of biological time*. New York: Springer Verlag.