

Rhythmic and non-rhythmic attractors in asynchronous random Boolean networks

Ezequiel A. Di Paolo *

School of Cognitive and Computing Sciences, University of Sussex, Brighton, BN1 9QH, UK

Received 10 April 2000; received in revised form 27 November 2000; accepted 15 December 2000

Abstract

In multi-component, discrete systems, such as Boolean networks and cellular automata, the scheme of updating of the individual elements plays a crucial role in determining their dynamic properties and their suitability as models of complex phenomena. Many interesting properties of these systems rely heavily on the use of synchronous updating of the individual elements. Considerations of parsimony have motivated the claim that, if the natural systems being modelled lack any clear evidence of synchronously driven elements, then random asynchronous updating should be used by default. The introduction of a random element precludes the possibility of strictly cyclic behaviour. In principle, this poses the question of whether asynchronously driven Boolean networks, cellular automata, etc., are inherently bad choices at the time of modelling rhythmic phenomena. This paper focuses on this subsidiary issue for the case of Asynchronous Random Boolean Networks (ARBNs). It defines measures of *pseudo-periodicity* between states and sufficiently relaxed statistical constraints. These measures are used to guide a genetic algorithm to find appropriate examples. Success in this search for a number of cases, and the subsequent statistical analysis lead to the conclusion that ARBNs can indeed be used as models of co-ordinated rhythmic phenomena, which may be stronger precisely because of their in-built asynchrony. The same technique is used to find non-stationary attractors that show no rhythm. Evidence suggests that the latter are more abundant than rhythmic attractor. The methodology is flexible, and allows for more demanding statistical conditions for defining pseudo-periodicity, and constraining the evolutionary search. © 2001 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Random Boolean Networks; Random asynchronous updating; Modelling; Genetic algorithms; Rhythmic phenomena

1. Introduction

It is generally argued that modelling techniques such as cellular automata, Boolean networks, and other variants, are uniquely fitted to address

issues of spatio-temporal complexity in areas as diverse as morphogenesis, gene regulation, immune networks, and population dynamics. However, much evidence has been gathered suggesting that many of the initially interesting features of these formal classes have depended crucially on the use of a synchronous rule for updating the atomic elements. In contrast, the implementation

* Fax: +44-1273-671320.

E-mail address: ezequiel@cogs.susx.ac.uk (E.A. Di Paolo).

of asynchronous updating rules has tended to produce trivial, rather than complex, behaviour.

The by now almost classic example is the work by Nowak and May (1992) on spatial patterns in a population of players of the Prisoner's Dilemma. The complex spatial patterns obtained in their model, which suggest interesting implications with respect to the polymorphic conviviality of cooperators and defectors, depend critically on the use of a synchronous updating scheme. When random asynchrony is introduced no spatial pattern appears, and the much gloomier picture of global defection as the only stable strategy results, (Huberman and Glance, 1993)¹.

A number of other studies have arrived at similar conclusions from cellular automata (Bersini and Detours, 1994; Ingerson and Buvel, 1984; Ruxton and Saravia, 1998; Schönfisch and de Roos, 1999) random Boolean networks (Harvey and Bossomaier, 1997), and even continuous-state systems such as coupled-map lattices (Abramson and Zanette, 1998; Bohr et al., 1999; Jiang et al., 1999; Lumer and Nicolis, 1994; Rolf et al., 1998). The methodological lesson that can be derived from these cases is that the choice of an updating rule plays a crucial role in the behaviour of the model, and, unless one can advance sufficient reasons to the contrary, random asynchronous updating is 'more physical'. This is because, in the lack of better knowledge about the system being modelled, random asynchronous updating is the most parsimonious default choice when the states of the system are modelled as discrete. It only makes sense to model a system as discrete if the transitions between states can be assumed to occur at a much more rapid timescale than then the typical scale of observation (and other timescales of relevance). Effectively, transitions are considered as almost instantaneous. In such cases it is highly unlikely that the transition of any two elements occurs simultaneously (in effect the probability is 0 if we take transitions as

strictly instantaneous). This means that elements should be updated in sequence. The less biased ordering for this sequence is a random ordering, and so random asynchronous updating, rather than parallel orchestration by an external clock, is justified as a default choice. This caveat is especially relevant for studies of local or global synchronisation of individual elements in such systems, as their results would be undermined should they depend heavily on the use of an unjustified synchronous updating scheme.

This paper is concerned with a subsidiary aspect of the effects of random asynchrony in the long-term behaviour of multicomponent systems with discrete states such as random Boolean networks: the possibility of finding attractors with marked rhythms without the use of synchronous updating.

Logical or Boolean networks have been used as models of genetic regulation (Kauffman, 1969, 1974, 1993; Thieffry and Romero, 1999; Thomas, 1973, 1978), immune responses (Kaufman et al., 1985, 1999; Muraille et al., 1996; Thieffry and Thomas, 1995), constraints on evolution (Volkert and Conrad, 1998), and developmental processes, both specific (Mendoza and Alvarez-Buylla, 1998; Sánchez et al., 1997) and idealised (Dellaert and Beer, 1994). Theoretical treatment of Boolean networks often makes a distinction between synchronous and asynchronous cases (Glass, 1975; Glass and Kauffman, 1973; Thomas, 1991; Thomas et al., 1995). The distinction is inspired by the need to use logical tools to explore complex continuous dynamics qualitatively. Transitions between states in synchronous networks are allowed to be arbitrary in terms of the Hamming distance between two contiguous states, but this introduces an artificial element of orchestrated updating not usually found in continuous extended systems (Glass, 1975). In contrast, (non-random) asynchronous networks incorporate knowledge about the continuous system (which may be empirically derived) in the form of typical time delays between transitions in order to determine which element should be updated next (the one with the shortest delay or higher first derivative). This causes consecutive states in the network evolution to differ in at most the state of one single element.

¹ In (May et al., 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.

Other studies, however, concentrate not on modelling specific continuous systems, but on understanding the generic features of random Boolean systems for which there is no prior knowledge about time delays (Bagley and Glass, 1996; Bastolla and Parisi, 1998a,b; Kauffman, 1969, 1993). In these cases the updating is performed synchronously. It has been argued (Harvey and Bossomaier, 1997) that this form of updating remains artificial even for this more general purpose, unless one can justify the existence of a driving clock. As a consequence, the default alternative to asynchronous updating using known time lags should be *random* asynchronous updating in which all time lags have a same mean value, but with different actual values between elements and at different time steps. As argued above, this choice fits well with the decision of modelling the system as having discrete states. Harvey and Bossomaier (1997) have shown that the use of random asynchronous updating drastically changes the overall behaviour of random Boolean networks as a class, thus casting doubts on well known interpretations made when using them as models of genetic regulation, especially with respect to cell differentiation and the lengths of cell division cycles, (Kauffman, 1969, 1993). See also (Bagley and Glass, 1996).

An important aspect of the use of random asynchronous updating is the impossibility of the system to exhibit non-stationary cyclic behaviour due to the randomness of the updating scheme. If random asynchronous updating should be the modeller's default choice in the absence of any knowledge about specific time delays, should it be concluded that asynchronous Boolean networks are inappropriate for modelling rhythmic phenomena?

Rhythmic behaviour can indeed be found in genetic regulatory networks if time delays are taken into account. For instance, regulatory processes in gene expression have been shown to participate in the generation of circadian rhythms in *Drosophila*, (e.g. Myers et al., 1996; Weitz, 1996; Young, 1998). Feedback loops in this case depend on delays occasioned by the build-up, reaction, and decay of gene products outside the nucleus.

Also a large number of 'non-Boolean' biological systems produce rhythms that arise from the complex interaction of many elements, and are not due to the existence of an external clock that orchestrates their behaviour (see Winfree, 1980). For instance, patterns of global rhythmic activity have been observed in ant nests, (Franks et al., 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 with no in-built delays in the updating of elements (Solé et al., 1993).

Could rhythmic behaviour also be found in asynchronous systems which are Boolean and do not include in-built time delays that specify the order of update? This question has not been addressed explicitly so far. It seems that the limitations of randomly driven systems regarding strictly 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 randomly updated asynchronous Boolean networks can be characterised by marked rhythms. In order to do this, a way of defining and measuring pseudo-periodic behaviour will be used to guide a genetic algorithm in the search for cases that exhibit this behaviour. At the same time, the method can be used to search for long term behaviours that are far from being rhythmic and yet they are different from the purely random systems.

2. 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 functions 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 the nodes².

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. The word ‘asynchronous’ here refers to a random updating scheme (uniform average time delays), and will be used in this sense throughout the rest of the paper. In this scheme the next node in the network to be updated is chosen with uniform probability independently of previous updates (which means that after N single updates some nodes may remain un-updated and others may have been updated more than once). 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 than in the synchronous case, a finding in accordance with previous observations by Ingerson and Buvel (1984) and Bersini and Detours (1994) for cellular automata (which in particular cases may be thought of as a special sub-class of Boolean networks). The average number of different attractors in an ARBN tends to be small when compared with the synchronous case, and does not depend on the size of the networks. These observations invalidate, if asynchrony is used, Kauffman’s (Kauffman, 1969, 1993) conclusions about the significance of the supposedly intrinsic order of large, sparsely connected 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, therefore, possibly for the same reasons. A similar comparison has been made between the length of cell division cycles and the typical length of cyclic attractors. These analogies,

² More general classes are obtained when K indicates the average number of connections to each node.

however, rely critically on the applicability of synchronous updating to the real case, which remains to be justified.

Not all the attractors found in ARBNs are of the fixed point type. Harvey and Bossomaier (1997) refer to those that are not as ‘loose attractors’. These 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 subset, then the state that follows after asynchronous updating will also belong to sub-set. Cyclic attractors, like those found using synchronous updating, cannot be found in ARBNs. If an ARBN had a non-stationary cyclic attractor, then two consecutive states in this attractor should differ in at least the state of one single node. Since a time step is defined as N random updates, there is a probability of $(1 - 1/N)^N$ that the node that should have changed its state remains without being updated. Therefore, the two consecutive states would not necessarily differ in the state of this node as required. Notice that the proof does not work for other forms of random asynchronous updating, which guarantee that all the nodes will be updated after N single node updates³.

3. Defining pseudo-periodicity

The observation that ARBNs cannot produce cyclic attractors is strictly true but only of relative significance for the modelling of rhythmic behaviour. The reason 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,

³ 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 itself with a rule that specifies that, whatever the value of other nodes, its own value must change. Since the updating scheme guarantees that the node will be updated, it will flip its value at every time step giving rise to a cycle of period 1.

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. A more general view of rhythmic behaviour should be adopted 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.

The 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 correspond to 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*⁴ with pseudo-period P . A time index j is defined which is incremented by 1 unit after N random updates to single nodes (i.e. one time step equals N individual updates), but pseudo-periodicity will not be defined as 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 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:

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

⁴This 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.

where $s_i^*(j)$ is the scaling of $s_i(j)$ onto $[-1, 1]$. Highly correlated states will be taken to mean also highly similar states from the point of view of the system's operation or their functional significance. This is an assumption that need not be true in general, as discussed in the last section. A global measure of the behaviour of the network is given by average correlation between states and their k 'th successors, averaging over M successive states with $M \gg N$:

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

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 simply called *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 have a distinct peak value for k close to $P(P \ll M)$.

4. Evolving rhythms

To search for pseudo-periodic ARBNs a target autocorrelation function is proposed, and simple genetic algorithm is used as a search method to find networks approximating this target. ARBNs are described using a binary genotype which encodes their connectivity and the Boolean functions for each node. Any network with parameters N and K can be encoded in a genotype of length G :

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

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 a number of time steps between 500 and 1000, 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 estimated for $k = 0, 1, \dots, 2N - 1$ by averaging for all the states in the run (except the last $2N$ ones).

The fitness of a network is calculated for each trial as $1 - D$, where D is the normalised distance between the network's autocorrelation, and a target autocorrelation. Fitness scores are averaged over the trials, and the value of one standard deviation (S.D.) is deducted to benefit low variability between the trials. Point mutation, uniform crossover, and a rank-based selection scheme with elitism are used, (Mitchell, 1996). The rate of mutation per locus μ is chosen in accordance to the genotype length so as to have a probability of no mutation in a given genotype, $(1 - \mu)^G$, within the range [0.6, 0.8]. The size of the population is of 90 networks. The search method mildly benefits networks with rapid transients as statistics are taken from the beginning of each trial run. However, simple modifications to the search algorithm could avoid this if necessary (for instance, by estimating autocorrelation only after a certain number of time steps).

It is important to choose an adequate target autocorrelation function for the search to succeed. This target need not correspond to any realisable network. Instead, its definition has been guided by considerations of evolvability. In all the cases presented here the choice has been to define a target autocorrelation using steps between the values of 0 and 1. States will be highly correlated around the chosen pseudo-period P and its multiples, 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 typical pseudo-periodic ARBNs can be expected to necessarily exhibit this balance in their autocorrelation functions. In particular, the extreme case in which all the possible transitions between states are such

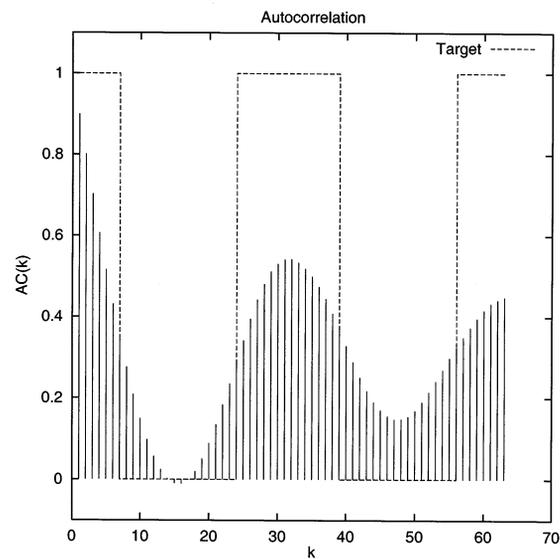
that the Hamming distance between them is always 1 will exhibit, for large N and $P \ll N$, both pseudo-periodicity and a relatively constant, high autocorrelation. This means that the method will only be able to search for a subset of pseudo-periodic ARBNs.

ARBNs have been successfully evolved for $N = 16, 32, 64$ and $K = 2, 3, 4$ using target periods of $P = N/2, N, 2N$. Shorter target periods have been attempted without success so far. The number of generations has ranged from 1000 to 5000 depending on parameter values, often obtaining reasonably good results after about 500 generations.

Figs. 1 and 2 correspond to an evolved network with $N = 32, K = 2$, and $P = 32$. Fig. 1(a) shows the first 1000 steps in the evolution of the network starting from a random initial condition. Al-



(a)



(b)

Fig. 1. Evolved ARBN with $N = 32, K = 2$, and a target period $P = 32$. (a) Evolution for 1000 time steps; (b) autocorrelation. The dashed line shows the target autocorrelation.

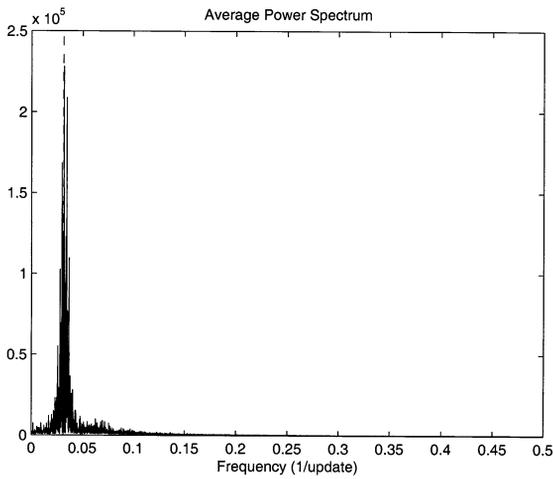


Fig. 2. Power spectrum for evolved network corresponding to Fig. 1 averaged over variations in the state of individual nodes for 10 000 steps. The frequency corresponding to the target period is shown with a vertical dashed line.

though some nodes are frozen most of the time, the remaining ones form distinct patterns which appear with a marked rhythm. Comparisons with the behaviour further downstream show that the form of the pseudo-periodic attractor is stable which is a result not directly implied in the constraints used to perform the evolutionary search, which condition only the form of the autocorrelation.

The autocorrelation function is shown in Fig. 1(b), together with the target autocorrelation (dashed line), the range of which goes from $k = 0$ to $k = 63$. This function has been calculated by averaging over $M = 10\,000$ steps. It has been found to be same over 10 different runs starting from different random initial conditions. It shows a clear peak of considerable width at around $k = 32$.

Further evidence of rhythmic behaviour in this network can be obtained by calculating the power spectrum (using Fast Fourier Transform) for each node in the network. This is shown in Fig. 2 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 $1/P = 0.03125$.

The following figures show other evolved ARBNs and their autocorrelation averaged over 10 000 consecutive states. Fig. 3 and Fig. 4 show two evolved networks with $N = 16$ and $K = 4$, with periods $P = 16$ and $P = 32$, respectively, (in the latter case the range of the autocorrelation and the target function has been doubled). Fig. 5 and Fig. 6 show two evolved networks with $N = 64$ and $K = 2$, with respective periods of $P = 64$ and $P = 32$.

It is important to notice that in all the cases shown each successive peak in the autocorrelation 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.

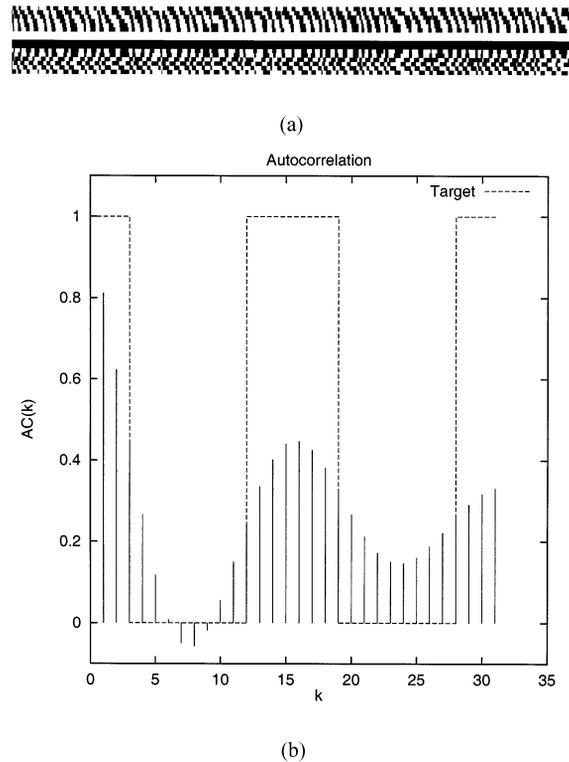


Fig. 3. Evolved ARBN with $N = 16$, $K = 4$, and a target period $P = 16$. (a) Evolution for 1000 time steps; (b) autocorrelation.

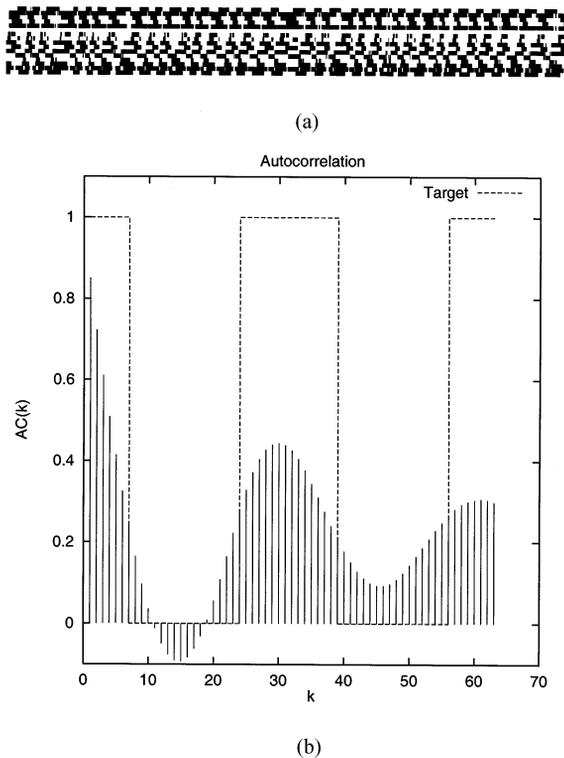


Fig. 4. Evolved ARBN with $N = 16$, $K = 4$, and a target period $P = 32$. (a) Evolution for 1000 time steps; (b) autocorrelation.

5. Non-rhythmic non-stationary attractors

How widespread are rhythmic attractors within the class of non-stationary attractors in ARBNs? This is not an easy question to answer, but it is possible to use the preceding method to find out whether at least some non-stationary attractors in ARBNs are non-rhythmic. One way of doing this is by evolving networks under the criterion that their attractors be highly de-correlated. In other words, by asking the autocorrelation function to be as close to 0 as possible.

Results are shown in Fig. 7 and Fig. 8, which correspond to a network with $N = 32$, $K = 2$ and null target autocorrelation. It is possible to observe a rapid, possibly exponential, decay in the autocorrelation (calculated over 10 000 time steps), and a continuous power spectrum. These properties differ both from the marked pseudo-periodic cases (e.g. Figs. 1 and 2), and the uni-

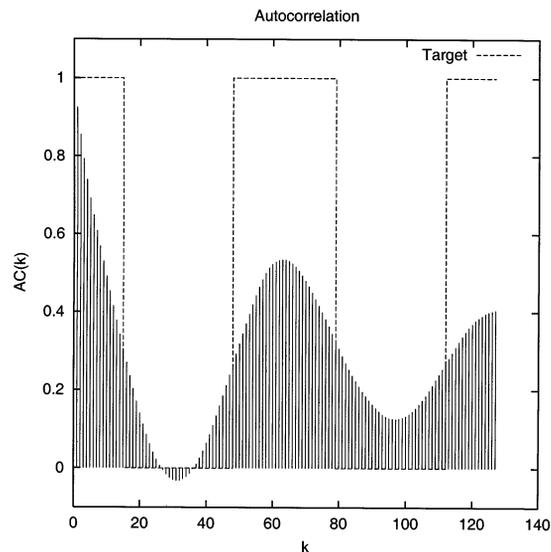
form spectrum and instantaneous decay in autocorrelation that one would expect from pure white noise. For other parameter values the results are qualitatively the same.

It is a contentious issue whether this kind of behaviour in a noisy, discrete-state system deserves to be called 'chaotic-like' or 'pseudo-chaotic', but the statistical features of the autocorrelations and the power spectra are suggestive enough (see for instance Drazin, 1992, pp. 264–277).

Evolving de-correlated networks has been tried for most of the combinations of parameters mentioned above. In all cases there is a striking difference in the speed with which the genetic algorithm finds good solutions, being the de-correlated cases much easier to find by up to two orders of magnitude in comparison with the pseudo-periodic net-



(a)



(b)

Fig. 5. Evolved ARBN with $N = 64$, $K = 2$, and a target period $P = 64$. (a) Evolution for 1000 time steps; (b) Autocorrelation.

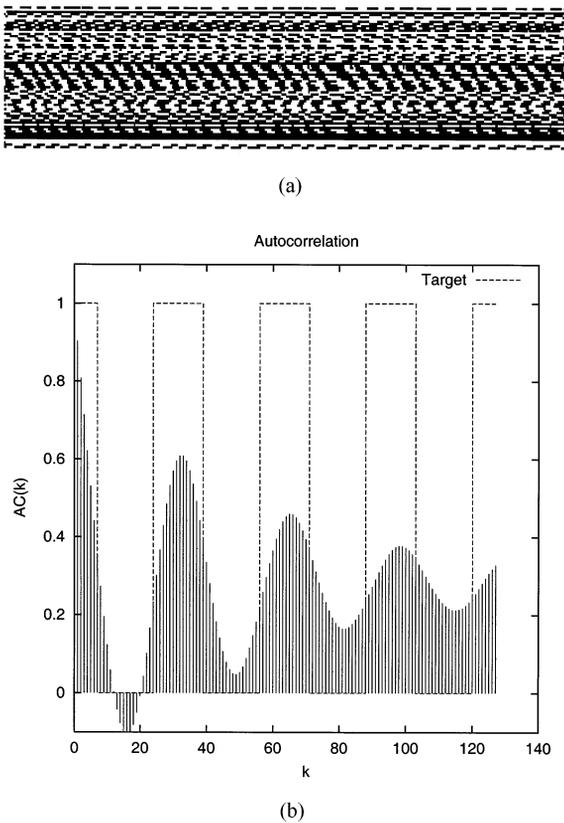


Fig. 6. Evolved ARBN with $N = 64$, $K = 2$, and a target period $P = 32$. (a) Evolution for 1000 time steps; (b) autocorrelation.

works (50–100 generations). This suggests that the space of non-stationary attractors in ARBNs is populated largely by de-correlated attractors and markedly pseudo-periodic attractors of the kind that can be found by the search method are much more rare. Studies are currently underway to test for the existence of pseudo-periodic attractors showing more than one single marked frequency.

6. Conclusion

It is not possible for ARBNs to exhibit strictly cyclic behaviour but this does not mean that they need to be discarded a priori as possible models of rhythmic phenomena since it has been shown that they may be able to capture many features of

interest of such phenomena. No one would hesitate to call a natural system ‘rhythmic’, or even ‘periodic’, if its behaviour exhibited a power spectrum like the one shown in Fig. 2. Precisely, because they do not incorporate synchrony by default, ARBNs, and similar asynchronous systems that are able to show spontaneous rhythmic behaviour, may constitute quite stronger models when compared with models using built-in synchrony from the start.

Pseudo-periodicity can be straightforwardly defined and recognised in ways that can be used to guide an evolutionary search process. Probably a number of other search methods could have worked equally well or better for this task, but success using a genetic algorithm is suggestive of ways in, which, natural selection could have acted

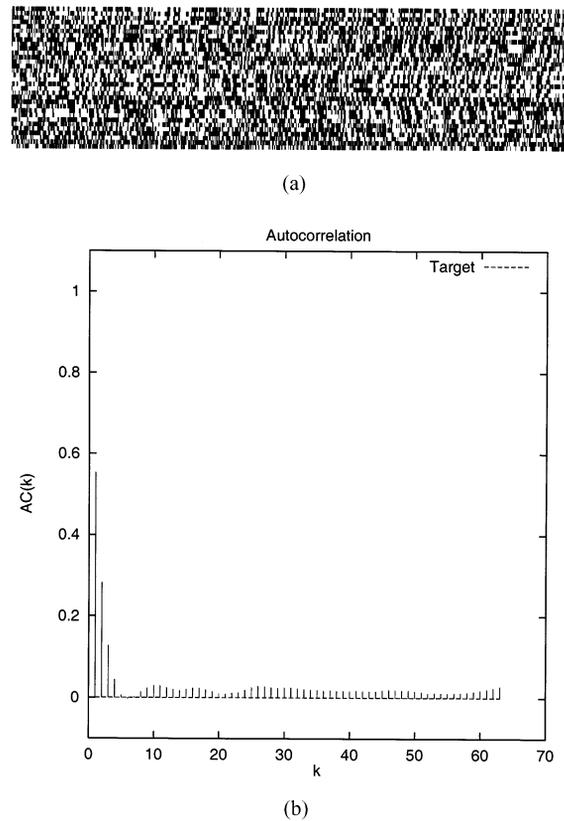


Fig. 7. Evolved ARBN with $N = 32$, $K = 2$, and a null target autocorrelation. (a) Evolution for 1000 time steps; (b) autocorrelation.

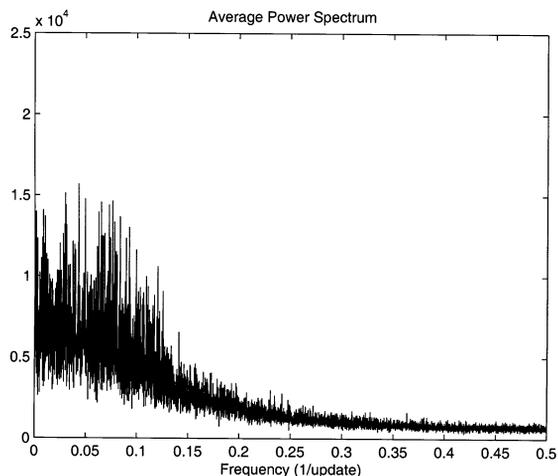


Fig. 8. Power spectrum for evolved network corresponding to Fig. 7 averaged over variations in the state of individual nodes for 10 000 steps.

on natural systems with analogous properties, if rhythmic or co-ordinated behaviour happened to be of some functional value.

The 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 from a functional perspective. In those cases, the correlation definition for the whole state of the network does not work, and it is an open question whether other would. Two speculative solutions could be of some use in such cases. One is the utilisation of *weighted correlations* 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 larger 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 or different pseudo-periods) if it were necessary. It is not clear yet whether these solutions would work in general.

The evolutionary search methodology has been used in an uncommon way in this work in that selective constraints are not put on the specific behaviour or computational capabilities of the networks (see for instance Mitchell et al., 1994) but on more relaxed global statistical constraints. The genetic algorithm also provides complementary information with respect to the evolution of non-rhythmic ARBNs. The relative ease with which this task is achieved suggests that rhythmic attractors are uncommon within the set of non-stationary attractors.

The choice of an adequate updating scheme and the definition of a time step are not independent modelling decisions but must make sense when combined. Observations like this beg the question of which is the most adequate method for defining the passage of time in a way that accords naturally with the type of system being modelled. In this work, a time index has been defined in an intuitive manner in accordance to the size of the system so as to simulate uniform average time delays and independent updating for all nodes. It is believed that such a choice is appropriate since it has not been heavily relied upon to define pseudo-periodicity (variability in the pseudo-period has been allowed to be large). It remains an open issue whether other, 'more physical' time indexes, appropriate for the particular systems in questions, could be defined.

References

- Abramson, G., Zanette, D.H., 1998. Globally coupled maps with asynchronous updating. *Phys. Rev. E* 58, 4454–4460.
- Bagley, R., Glass, L., 1996. Counting and classifying attractors in high dimensional dynamical systems. *J. Theor. Biol.* 183, 269–284.
- Bastolla, U., Parisi, G., 1998a. The modular structure of Kauffman networks. *Phys. D* 115, 219–233.
- Bastolla, U., Parisi, G., 1998b. Relevant elements, magnetization and dynamical properties in Kauffman networks: A numerical study. *Phys. D* 115, 203–218.
- Bersini, H., Detours, V., 1994. Asynchrony induces stability in cellular automata based models. In: Brooke, R., Maes, P. (Eds.), *Artificial Life IV, Proceedings of the Fourth International Conference on Artificial Life*. MIT Press, Cambridge, MA, pp. 382–387.

- Bohr, T., Jensen, M.H., Rolf, J., 1999. Statistical properties of turbulent dynamical systems. *Phys. A* 263, 155–157.
- 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. Nat.* 137, 244–259.
- Dellaert, F., Beer, R., 1994. Toward an evolvable model of development for autonomous synthesis. In: Brookes, R., Maes, P. (Eds.), *Artificial Life IV, Proceedings of the Fourth International Conference on Artificial Life*. MIT Press, Cambridge, MA, pp. 246–257.
- Drazin, P.G., 1992. *Nonlinear Systems*. Cambridge University 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.
- Glass, L., 1975. Classification of biological networks by their qualitative dynamics. *J. Theor. Biol.* 54, 85–107.
- Glass, L., Kauffman, S.A., 1973. The logical analysis of continuous, non-linear biochemical control networks. *J. Theor. Biol.* 39, 103–129.
- 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*. MIT Press, Cambridge, MA, pp. 67–75.
- 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. *Phys. D* 10, 59–68.
- Jiang, Y., Antillón, A., Escalona, J., 1999. Globally coupled maps with sequential updating. *Phys. Lett. A* 262, 403–408.
- Kauffman, S.A., 1969. Metabolic stability and epigenesis in randomly constructed genetic nets. *J. Theor. Biol.* 22, 437–467.
- Kauffman, S.A., 1974. The large scale structure and dynamics of gene control circuits: an ensemble approach. *J. Theor. Biol.* 44, 167–190.
- Kauffman, S.A., 1993. *The Origins of Order*. Oxford University Press.
- Kauffman, M., Andris, F., Leo, O., 1999. A logical analysis of T cell activation and anergy. *Proc. Natl. Acad. Sci. USA* 96, 3894–3899.
- Kauffman, M., Urbain, J., Thomas, R., 1985. Towards a logical analysis of immune response. *J. Theor. Biol.* 114, 527–561.
- Lumer, E.D., Nocolis, G., 1994. Synchronous versus asynchronous dynamics in spatially distributed systems. *Phys. D* 71, 440–452.
- 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*, Granada, Spain. Springer, Berlin, pp. 749–759.
- Mendoza, L., Alvarez-Buylla, E.R., 1998. Dynamics of the genetic network for *Arabidopsis thaliana* flower morphogenesis. *J. Theor. Biol.* 193, 307–319.
- Mitchell, M., 1996. *An Introduction To Genetic Algorithms*. MIT Press, Cambridge MA.
- Mitchell, M., Crutchfield, J.P., Hraber, P.T., 1994. Evolving cellular automata to perform computations: mechanism and impediments. *Phys. D* 75, 361–391.
- Muraille, E., Thieffry, D., Leo, O., Kauffman, M., 1996. Toxicity and neuroendocrine regulation of the immune response: a model analysis. *J. Theor. Biol.* 183, 285–305.
- Myers, M.P., Wager-Smith, K., Rothenfluh-Hilfiker, A., Young, M.W., 1996. Light-induced degradation of TIMELESS and entrainment of the *Drosophila* circadian clock. *Science* 271, 1736–1740.
- Nowak, M.A., May, R.M., 1992. Evolutionary games and spatial chaos. *Nature* 359, 829–836.
- Rolf, J., Bohr, T., Jensen, M.H., 1998. Directed percolation universality in asynchronous evolution of spatio-temporal intermittency. *Phys. Rev. E* 57, R2503–R2506.
- Ruxton, G.D., Saravia, L.A., 1998. The need for biological realism in the updating of cellular automata models. *Ecol. Model.* 107, 105–112.
- Sánchez, L., van Helden, J., Thieffry, D., 1997. Establishment of the dorso-ventral pattern during embryonic development of *Drosophila melanogaster*: a logical analysis. *J. Theor. Biol.* 189, 377–389.
- Schönfisch, B., de Roos, A., 1999. Synchronous and asynchronous updating in cellular automata. *BioSystems* 51, 123–143.
- Solé, R.V., Miramontes, O., Goodwin, B.C., 1993. Oscillations and chaos in ant societies. *J. Theor. Biol.* 161, 343–357.
- Thieffry, D., Thomas, R., 1995. Dynamical behaviour of biological regulatory networks-II. Immunity control in bacteriophage lambda. *Bull. Math. Biol.* 57, 277–297.
- Thieffry, D., Romero, D., 1999. The modularity of biological regulatory networks. *BioSystems* 50, 49–59.
- Thomas, R., 1973. Boolean formalization of genetic control circuits. *J. Theor. Biol.* 42, 563–585.
- Thomas, R., 1978. Logical analysis of systems comprising feedback loops. *J. Theor. Biol.* 73, 631–656.
- Thomas, R., 1991. Regulatory networks seen as asynchronous automata: a logical description. *J. Theor. Biol.* 153, 1–23.
- Thomas, R., Thieffry, D., Kaufman, M., 1995. Dynamical behaviour of biological regulatory networks — I. Biological role of feedback loops and practical use of the concept of the loop-characteristic state. *Bull. Math. Biol.* 57, 247–276.
- Volkert, L.G., Conrad, M., 1998. The role of weak interactions in biological systems: the dual dynamics model. *J. Theor. Biol.* 193, 287–306.
- Weitz, C.J., 1996. Circadian timekeeping: loops and layers of transcriptional control. *Proc. Natl. Acad. Sci. USA* 93, 14308–14309.
- Winfree, A.T., 1980. *The Geometry of Biological Time*. Springer, New York.
- Young, M.W., 1998. The molecular control of circadian behavioral rhythms and their entrainment in *Drosophila*. *Annu. Rev. Biochem.* 67, 135–152.