Rhythmic and Non-rhythmic Attractors in Asynchronous Random Boolean Networks

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Abstract

In multi-component, discrete systems, such as Boolean networks and cellular automata, the updating scheme 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

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 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 & Glance, 1993)".

A number of other studies have arrived at similar conclusions for cellular automata (Bersini & Detours, 1994; Ingerson & Buvel, 1984; Ruxton & Saravia, 1998; Schönfisch & de Roos, 1999) random Boolean networks (Harvey & Bossomaier, 1997), and even continuous-state systems such as coupled-map lattices (Abramson & Zanette, 1998; Bohr et al., 1999; Jiang et al., 1999; Lumer & 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 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 transitions of any two elements occur 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 justied as a default choice. This caveat is especially relevant to studies of local or global synchronization of individual elements in such systems as their results would be undermined should they depend heavily on the use of an unjustied 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 nding 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; Thiery & Romero, 1999; Thomas, 1973, 1978), immune responses (Kaufman et al., 1985, 1999; Muraille et al., 1996; Thiery & Thomas, 1995), constraints on evolution (Volkert & Conrad, 1998), and developmental processes, both specic (Mendoza & Alvarez-Buylla, 1998; Sanchez et al., 1997) and idealised (Dellaert & Beer, 1994). Theoretical treatments of Boolean networks often make a distinction between synchronous and asynchronous cases (Glass, 1975; Glass $&$ 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 articial 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 & Glass, 1996; Bastolla & Parisi, 1998a, 1998b; Kauffman, 1969, 1993). In these cases the updating is performed synchronously. It has been argued (Harvey & 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

general arguments about what can be expected from ARBNs as a class. The word `asynchronous' here refers to a random updating scheme

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 $\emph{pseudo-perb}$ with pseudo-period P . A time index j is defined which is incremented by one 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

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.

- Sole, R. V., Miramontes, O., & Goodwin, B. C. (1993). Oscillations and chaos in ant societies. J. $theor.~Biol.,~161,~343-357.$
- Thieffry, D., & Romero, D. (1999). The modularity of biological regulatory networks. BioSystems, $50, 49{-}59.$
- Thieffry, D., & Thomas, R. (1995). Dynamical behaviour of biological regulatory networks II. Immunity control in bacteriophage lambda. Bull. Math. Biol., 57, 277-297.
- Thomas, R. (1973). Boolean formalization of genetic control circuits. *J. theor. Biol.*, $\frac{1}{2}$, 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 loopcharacteristic 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. New York: Springer.
- Young, M. W. (1998). The molecular control of circadian behavioral rhythms and their entrainment in Drosophila. Annu. rev. Biochem., $67, 135-152$.

 $\overline{0}$ 0.2 0.4 0.6 0.8 1 0 10 20 30 40 50 60 70 AC(k) k Autocorrelation Target

Figure 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.

(b)

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N

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

(a)

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

Autocorrelation Target 1 0.8 0.6 AC(k) 0.4 0.2 1111 0 <u>LEEEEEEEEEEEEEEEEEEEEEEE</u> ------0 10 20 30 40 50 60 70 k

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

(b)

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