J. theor. Biol. (1996) **183,** 269–284

Counting and Classifying Attractors in High Dimensional Dynamical Systems

R. J. Bagley and Leon Glass†

Department of Physiology, McGill University, 3655 Drummond Street, Montreal, Quebec, Canada H3G 1Y6

(*Received on* 21 *October* 1994, *Accepted in revised form on* 5 *July* 1996)

Randomly connected Boolean networks have been used as mathematical models of neural, genetic, and immune systems. A key quantity of such networks is the number of basins of attraction in the state space. The number of basins of attraction changes as a function of the size of the network, its connectivity and its transition rules. In discrete networks, a simple count of the numbers of attractors does not reveal the combinatorial structure of the attractors. These points are illustrated in a reexamination of dynamics in a class of random Boolean networks considered previously by Kauffman. We also consider comparisons between dynamics in discrete networks and continuous analogues. A continuous analogue of a discrete network may have a different number of attractors for many different reasons. Some attractors in discrete networks may be associated with unstable dynamics, and several different attractors in a discrete network may be associated with a single attractor in the continuous case. Special problems in determining attractors in continuous systems arise when there is aperiodic dynamics associated with quasiperiodicity or deterministic chaos.

1. Introduction

Discrete Boolean networks have been applied broadly as models of high-dimensional biological systems. Such networks are composed of discrete Boolean elements that we call *automata*. Depending on the context, an automaton might represent a gene (Kauffman, 1969; Thomas, 1973), a neuron (Hopfield, 1982), a class of immune cells (Kaufman *et al*., 1985; Thomas & D'Ari, 1990). Each automaton receives inputs from some subset of the automata in the network and all automata are updated simultaneously. In many applications, the discrete models are thought of as simplified versions of continuous differential equations that would be a more appropriate but less tractable model of the real biological system.

We are concerned with the qualitative features in the dynamics of such systems. Perhaps the most basic qualitative features of a dynamical system are the number and types of different behaviors, often called *attractors*, that are found as time goes to infinity. All initial conditions that evolve to a given attractor constitute its *basin of attraction*. An attractor of a given network might correspond to a memory trace, a pattern of motor nerve activity, a state of an immune network, or a cell type. Consequently, knowledge of the number of attractors and how their respective basins partition the state space is essential to understand the function of the particular system being investigated. For example, in models of neural networks, the number of basins of attraction of a given network might correspond to the number of "memories" that could be stored in it (Hopfield, 1982). In studies of immune networks, the number of attractors might correspond to the numbers of antigens that can be uniquely identified (Segel & Perelson, 1988; Weisbuch & Oprea, 1994).

Although the issue of counting the number of attractors in a given dynamical system is fundamen-

†Author to whom correspondence should be addressed.
E-mail: glass@cnd.mcgill.ca

0022–5193/96/230269 + 16 $25.00/0

tal, the number of definite theoretical results in this area are scattered thinly over a broad range.

(i) Hilbert's sixteenth problem. The problem is to determine the maximum number and position of limit cycles in the ordinary differential equations

$$\dot{x} = f(x,y),\ \dot{y} = g(x,y)$$

where f and g are nth order polynomials (Hilbert, 1902), and the dot represents a derivative with respect to time.

(ii) A Boolean network of N automata in which each automaton receives inputs from each of the automata in the network and realizes a random function on those inputs. This system is described by a random map on a finite state space of 2^N states, see Derrida & Flyvbjerg (1987), Weisbuch (1990), Jaffe (1988), Kauffman (1993) and references therein. In the limit $N \to \infty$ the expected number of cycles is

$$\left(\frac{\log 2}{2}\right) N.$$

(iii) A Boolean network of N automata in which each automaton receives one input. This case was treated by Jaffe (1988). The mean number of cycles grows exponentially like

$$\left(\frac{2}{\sqrt{e}}\right)^{N(1 + o(1))}.$$

(iv) Random Boolean networks of N automata in which each automaton receives inputs from two automata. Numerical results carried out by Kauffman show that the number of attractors increases as $\sqrt{N}$ (Kauffman, 1969, 1993).

(v) Various models of neural networks in which "neurons" are represented by Boolean variables. The state of a neuron at a given time is a Heaviside function of weighted inputs to the neuron at the previous time. An initial condition evolves to one of several attractors. The system could act as a memory device with a low error rate provided the number of attractors $< 0.15N$, where N is the number of neurons (Hopfield, 1982; McEliece *et al.*, 1987; Weisbuch & Fogelman-Soulié, 1985; Weisbuch, 1990).

(vi) Spin glasses. These are physical systems in which localized spins have interaction energies that can take two or more different values. Depending on the temperature, there may be a large number of different configurations that represent local energy minima. This has thermodynamic consequences and may have implications for biological systems (Derrida, 1987b; Mezard *et al.*, 1987; Weisbuch, 1990).

The current work was motivated by a desire to extend earlier results on discrete time and discrete state space systems to systems in which time and state space are continuous. In order to carry this out, we first tried to reproduce Kauffman's results on two input discrete time Boolean networks. This exercise led us to recognize that a simple count of the number of attractors in a given network will not always lead to a clear picture of the dynamics in the network. Moreover, the number of attractors in discrete networks may be different from the number of attractors in analogous continuous networks.

In this paper we address issues concerning counting and classifying attractors in automata networks and in continuous nonlinear equations in high dimensions. In Section 2, we review basic concepts concerning automata networks, and we summarize the numerical methods. Section 3 presents numerical studies on the numbers of basins of attraction in randomly constructed automata networks that have been proposed by Kauffman as models of gene networks. In Section 4 we demonstrate that simple enumeration of the numbers of different attractors in a given network fails to adequately represent the relationships that exist between the different attractors. By considering a particular example, we propose a taxonomic classification of the basins of attraction, and demonstrate the combinatorial basis for the generation of the diversity of the numbers of attractors. Although the results concerning automata networks are relevant to the study of continuous networks, there are many differences between continuous and discrete systems. In Section 5, we discuss the issues associated with counting the attractors in continuous systems, and describe the differences in the dynamics between the continuous and discrete systems.

2. Definitions and Numerical Methods

In a Boolean network, the automata may be in one of two states, designated zero and one. For a network of N automata, there are 2^N possible states for the network. For each automaton, a Boolean rule assigns an output of zero or one to all possible combinations of input automata states in a manner similar to the truth tables of logic. If an automaton has K inputs, its Boolean rule assigns an output to each of the 2^K possible combinations of the input states. Thus, there are 2^{2^K} possible rules for an automaton with K inputs. The dynamics in a Boolean network is represented by the equation

$$X_i(t+1) = B_i(\mathbf{X}(t)) \quad i = 1, 2, \ldots, N, \tag{1}$$

where $X_i(t)$ is the Boolean state, either zero or one, of automaton i at time t, B_i is a Boolean function used to update the state of automaton i, and $\mathbf{X}(t)$ is a Boolean vector giving the states of the N automata in the network.

We study Boolean networks in which the connectivity of the network and the transition rules are chosen at random from those possible. There are possible constraints to this selection procedure. One common constraint is the imposition of a fixed number of inputs per automaton. Another disallows the transition rules of contradiction (all zeros) and tautology (all ones), since these rules are completely insensitive to the state of the individual inputs. Finally, an automaton can have itself as an input—or it can have no self-input.

For each network, once the connectivity and transition rules have been assigned, an initial condition is randomly chosen. Successive states for each automaton are assigned by its transition rule as a function of the state of its inputs. The network is updated synchronously and iterated until a cycle or steady state is reached. A characteristic feature of Boolean networks is that as finite systems, they will eventually cycle. However, since there are 2^N possible states in a network with N automata, for sufficiently large networks, the cycles can be astronomically long.

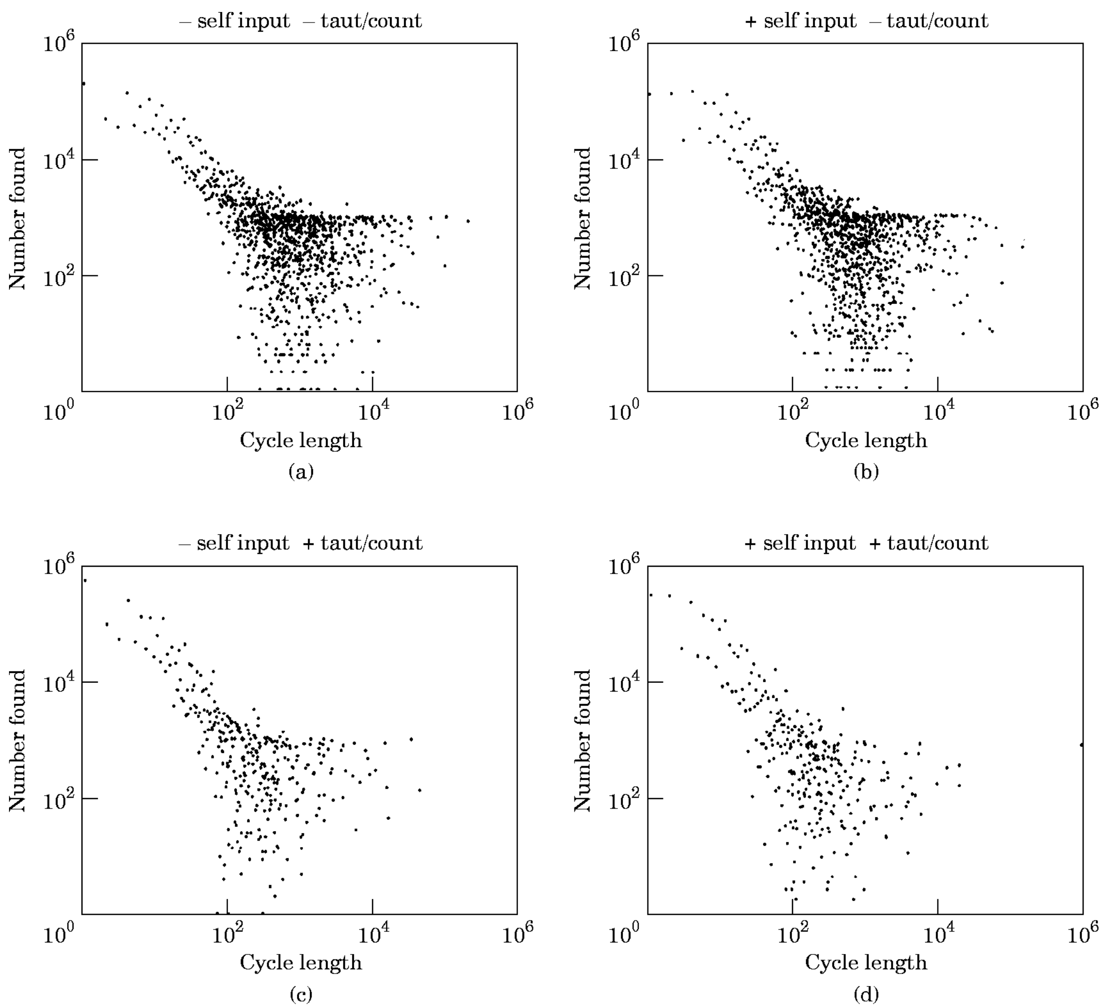

FIG. 1. Cycle lengths for random Boolean networks with 128 automata and two inputs per automata for 2000 different random networks and 1000 random initial conditions. Each point represents the number of networks out of the 2×10^6 trials having the specified cycle length. Each of the four different classes of network is shown in a separate panel. (a) No self-input. No tautology and contradiction. (b) Self-input. No tautology and contradiction. (c) No self-input. Tautology and contradiction. (d) Self-input. Tautology and contradiction. Including tautology and contradiction in the transition rules results in more short cycles and fewer long cycles.

If two different initial conditions lead to an identical cycle, the two different initial conditions lie in the same basin of attraction.

In this paper we consider two input random networks. Numerical simulations were performed on four subsets of Boolean networks. These are the same as those initially considered by Kauffman (1969).

Subset 1: tautology and contradiction allowed; self-input allowed.
Subset 2: tautology and contradiction allowed; self-input not allowed.
Subset 3: tautology and contradiction not allowed; self-input allowed.
Subset 4: tautology and contradiction not allowed; self-input not allowed.

Computations were carried out in a similar fashion to the one employed by Kauffman (1969). Boolean networks and initial conditions were generated randomly using a pseudo-random number generator. Continuous nonlinear equations were integrated using a fourth order Runge-Kutta integration scheme. Piecewise linear equations were integrated using methods considered previously (Glass & Pasternack, 1978b).

3. Counting Attractors

Boolean networks are an ideal system to study the number of the basins of attraction. It is easy to compute dynamics in Boolean networks and distinguishing between different cycles is unambiguous. A previous study of random Boolean networks modeling genetic regulatory systems (Kauffman, 1969; 1993) reported a numerical estimate of the number of basins of attraction for two input networks consisting of N automata. In this model, genes are represented as Boolean automata. On the basis of numerical computation, Kauffman conjectured that both the median cycle length and the number of attractors increases only as $\sqrt{N}$, a striking result when one considers the number of possible states in very large networks. Our first step is to recompute these results and reconsider the issues involved.

The results of randomly sampling among Boolean networks are presented in Figs 1–5. Improvements in the speed and availability of computation have allowed us to improve the sampling somewhat. Where feasible, 2000 networks were iterated from 1000 different initial conditions, for all four connectivity subsets defined above. Figure 1 presents scatter diagrams of the cycle lengths found for the four subsets for networks of $N = 128$ automata. The addition of tautology and contradiction considerably simplifies the dynamics. A bulk statistic, the median, is presented in Fig. 2a on cycle length statistics for networks of $N = 32$, 64, 128, 256 automata. The figure reveals a smooth relationship with increasing N. However, though the median cycle length for networks with tautology and contradiction show the conjectured relationship to $\sqrt{N}$, networks without these transition rules do not.

After examination of the distribution of cycle lengths in Fig. 1 (which are typical), one can see that the median has merit as a representative number. The distributions are heavily skewed towards smaller lengths. Numerically, the median tends to converge to a small interval after only a few samples. The distributions have however very long tails, something not intimated by the median.

A second candidate for the representative cycle length is the mean which in these systems is much

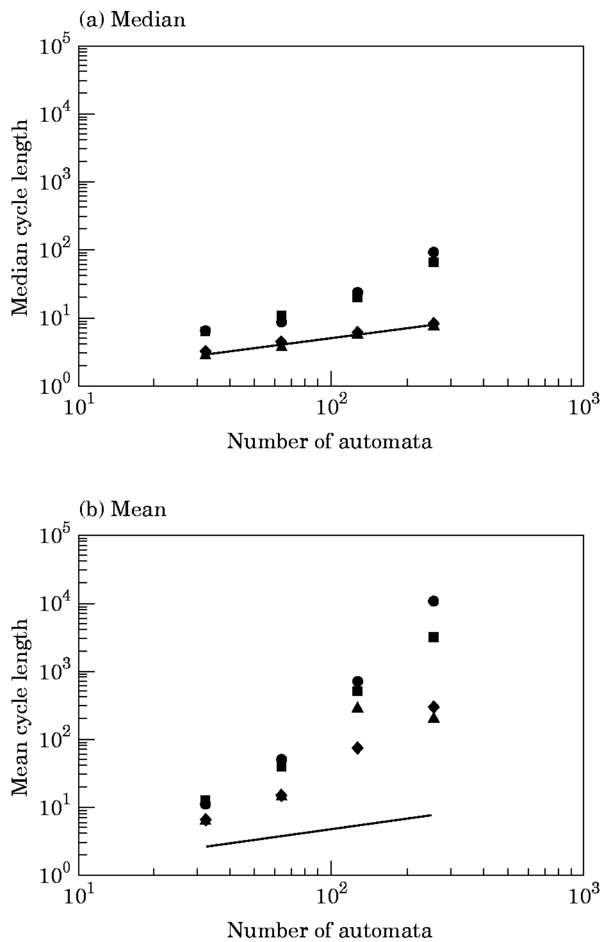

FIG. 2. The (a) median and (b) mean cycle length for the simulations presented in Fig. 1. The curve $y = \sqrt{x}/2$ has been added for reference. The median cycle length is $\propto \sqrt{N}$ only when tautology and contradiction are used. ● − self input − taut/cont; ■ + self input − taut/cont; ◆ − self input + taut/cont; ▲ + self input + taut/cont; ······ $y = \alpha x^{\alpha}$, $\alpha = 1/2$.

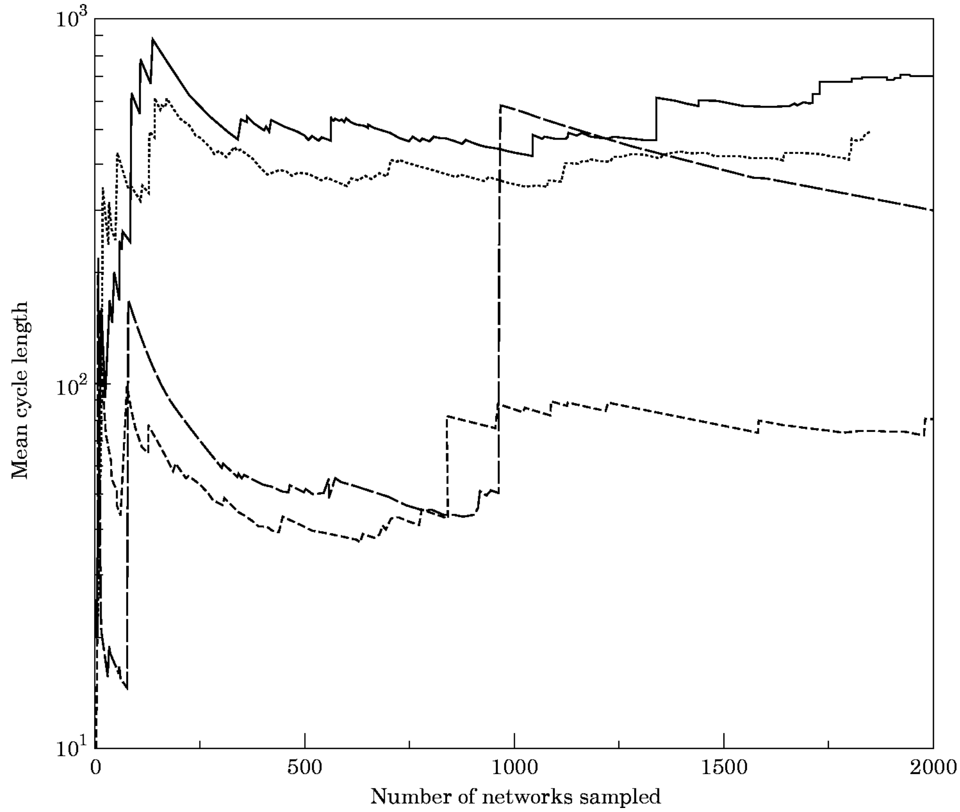

FIG. 3. The mean cycle length for networks of $N = 128$ automata as a function of the number of networks sampled for the same networks represented in Fig. 2. Each network was sampled 1000 times. The data point representing the mean cycle length for 128 automata in networks with self input and tautology and contradiction in Fig. 2 is caused by a single network with a cycle length 521220. 992 out of 1000 initial conditions led to this attractor. —— − self input − taut/cont; ······ + self input − taut/cont; – – – − self input + taut/cont; — — + self input + taut/cont.

larger than the median and increases with a power of N (Fig. 2b). However, the convergence of the mean can be quite slow. Figure 3 shows the value of the computed mean with each increase in the sample for all four network subsets. One network consisting of 128 automata (about the 1000th sampled) in the subset of networks that has both tautology and self-input had a very long cycle length. This led to the apparently inconsistent value for the mean cycle length in Fig. 2 for networks with 128 automata and both tautology and self-input.

A subtlety in interpreting Fig. 2 is that an individual cycle will be counted for each initial condition in its basin of attraction. The long cycle mentioned above was of length 521 220, and 992 of 1000 initial conditions sampled were in this basin of attraction, accentuating its distorting effect. Another way of calculating the mean would only count the cycle length of a particular basin of attraction once, regardless of how many states are in its basin. Our choice reflects the probability of a given cycle length resulting from the random choice of one initial state, one connectivity, and one set of transition rules from their respective spaces.

The number of basins of attraction for the sample of networks of 128 automata are shown in Fig. 4. The presence of self-inputs tends to increase the diversity in behavior. The effect of excluding tautology and contradiction is more complicated. There are fewer networks with very few basins, and also fewer networks with very many basins (Fig. 5) leading to a decrease in the mean number of the basins of attraction. The median number of basins of attraction increases approximately as the square $\sqrt{N}$ as conjectured in Kauffman (1969), but more data is needed to determine if the relationship holds as the number of automata increases further. The mean increases more rapidly than $\sqrt{N}$ for large N.

In the numerical determination of the mean cycle length there is a significant chance that a very long cycle will be encountered; this probability increases with network size. Similarly, as the size of the network grows, more initial conditions are needed to sample the different basins of attraction.

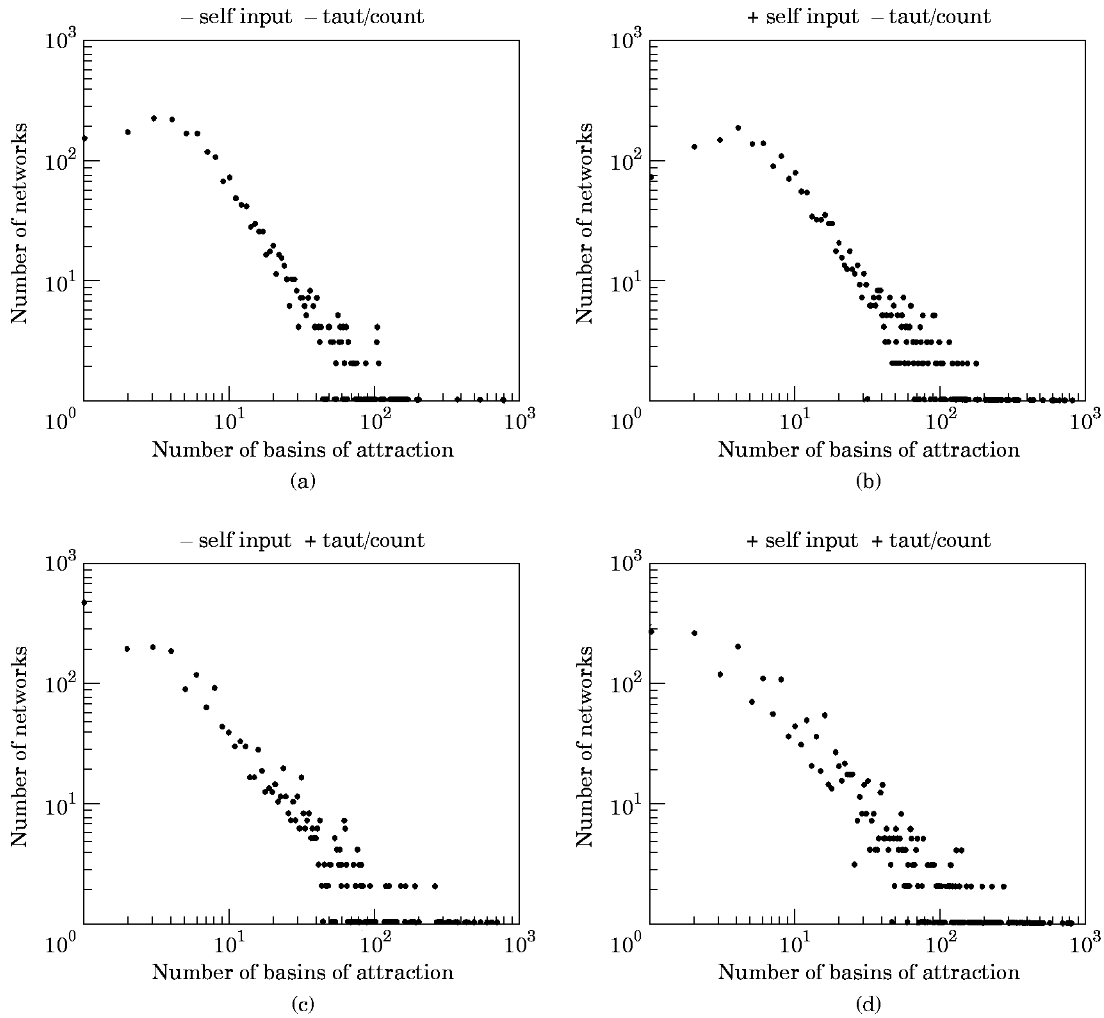

FIG. 4. The number of basins of attraction per network, for the same networks in Fig. 1. Excluding tautology and contradiction results in fewer networks with only one basin, and fewer networks with many basins.

Consequently, the mean numbers of basins computed here are approximate, and are probably lower than the "true" values, especially for the larger networks.

In a discussion of gene regulation, Kauffman (1969) equates a cycle in the Boolean network with the cell cycle and argues that very long cycles would not be a suitable representation of a cell's dynamics. Thus, his proposal of the median as the representative cycle length. But more generally there is no compelling reason for preferring the median as a descriptor of Boolean network dynamics.

In summary, numerical study of random Boolean networks reproduce many early results of Kauffman (1969), but also reveal difficulties in estimating the cycle length. We will now consider additional complications associated with counting the number of different attractors in a given network. Different attractors may arise as a consequence of the discrete updating scheme, and would not necessarily be different in more realistic continuous representations of the same network connectivity. In addition, different attractors in the same network may show striking similarities. These points are important in the interpretation of the results of the computations in automata networks, and are discussed in the remainder of this paper.

4. Classifying Attractors

In this section we demonstrate methods that can be used to classify the attractors in synchronous Boolean networks. For illustrative purposes we consider a randomly connected two input per automata network with 25 automata that had an unusually large number (384) of attractors. However, we shall see that these attractors are related to each other.

In order to determine all the basins for this network initial conditions were generated until no further

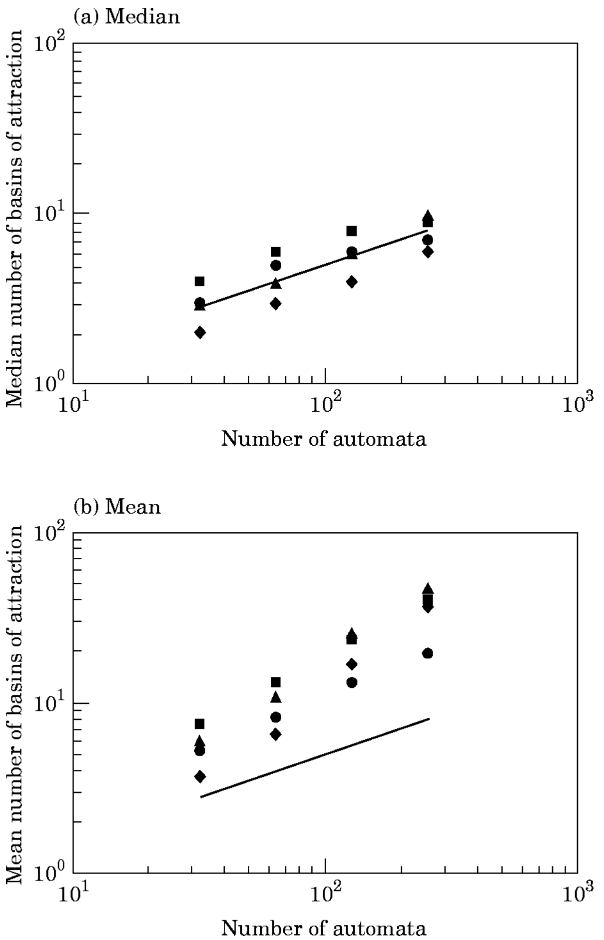

FIG. 5. The (a) median and (b) mean number of basins of attraction per network for the same networks in Fig. 1. inputs per automata plotted against network size. The curve $y = \sqrt{x}/2$ has been added for reference. ● − self input − taut/cont; ■ + self input − taut/cont; ◆ − self input + taut/cont; ▲ + self input + taut/cont; ······ $y = \alpha x^{\alpha}$, $\alpha = 1/2$.

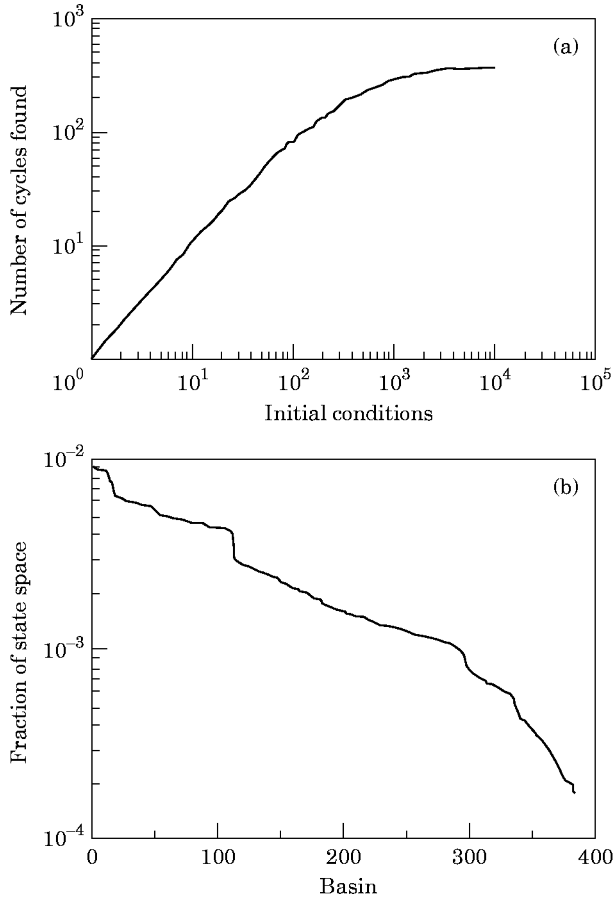

FIG. 6. (a) The number of basins of attraction a network of 25 automata as a function of the number of initial conditions sampled. 384 basins of attraction were present, the last sampled at 10632th initial condition. (b) The fraction of state space associated with each attractor based on 10^5 initial conditions. $K = 2$; $N = 25$ for (a) and (b).

attractors were found. In Fig. 6, the number of distinct periodic orbits is plotted against the number of initial conditions, showing that the finding of new basins saturates. After several recomputations of this curve, the same 384 basins were consistently found after $\sim 10^4$ initial conditions were iterated. If any basins have escaped count, they comprise a negligible portion of the state space.

In a first attempt to find a means of grouping cycles, individual cycles were reduced to a schema (see Table 1) that distinguishes periodic orbits on the basis of which of the automata have frozen to a fixed value (Weisbuch & Stauffer, 1987). Thus, cycles may be represented by the same schema if the same automata are frozen to the same fixed values. In this example, the 384 basins of attraction fall into 12 schemata, with a large degree of homology between schemata (Table 2). What is not shown is that the individual

TABLE 1.
The generation of a schema from a periodic cycle of a Boolean network with six automata

1	1	1	0	1	0
1	0	1	0	0	1
1	1	0	0	0	0
1	0	0	0	0	0
1	1	1	0	1	1
1	0	0	0	1	0
1	*	*	0	*	*

The states of the automata are displayed from left to right, and the six steps of the cycle progress from top to bottom. Beneath the cycle is the schema. The first and fourth automata are frozen into the one and zero states respectively. The other automata are assigned the symbol * indicating that the individual automata exhibited a cycle length greater than one.

TABLE 2.
The twelve schemata derived from the 384 cycles found for one network of 25 automata

A	56	1	*	1	1	*	*	1	1	*	*	0	*	0	1	0	0	1	*	*	1	*	0	*	0	1
B	20	1	*	1	1	*	*	1	1	*	*	*	*	*	1	*	0	*	*	*	*	*	*	*	*	1
C	192	1	*	1	*	*	*	1	1	*	*	*	*	*	1	*	*	*	*	*	*	*	*	*	*	1
D	48	1	*	1	*	*	*	1	1	*	*	*	*	*	1	*	0	*	*	*	*	*	*	*	*	1
E	4	1	*	*	*	*	*	1	1	*	*	*	*	*	1	*	*	*	*	*	*	*	1	*	*	1
F	4	1	*	*	*	*	*	1	1	*	*	*	*	*	1	*	0	*	*	*	*	*	*	*	*	1
G	24	1	*	1	1	*	*	1	1	*	*	*	*	*	1	*	*	*	*	*	*	*	*	*	*	1
H	8	1	*	*	*	*	*	1	1	*	*	*	*	*	1	*	*	*	*	*	*	*	*	*	*	1
I	4	1	*	1	1	*	*	1	1	*	1	0	0	0	1	0	0	1	*	1	1	*	0	0	0	1
J	4	1	*	1	1	*	*	1	1	*	*	*	*	*	1	*	*	*	*	*	*	*	1	*	*	1
K	16	1	*	1	*	*	*	1	1	*	*	*	*	*	1	*	*	*	*	*	*	*	1	*	*	1
L	4	1	*	1	1	*	*	1	1	*	0	0	1	0	1	0	0	1	*	0	1	*	0	1	0	1

The first column is a label for each schemata, the second indicates the number of periodic orbits which are grouped under the schemata which follows.

cycles grouped within a single schema also show a large degree of homology. The resemblances in the set of schemata, and the fact that some schemata tend towards more frozen states than others, suggests a taxonomic classification of the schemata. In Fig. 7, the schemata are arranged in a tree. As one descends in the tree, automata become progressively fixed. Each schema in the tree has more fixed elements than the schema immediately above it. Once a given automaton is fixed it remains fixed to the same value in all the schemata beneath it. In most instances schema connected by a line differ in the state of only a single automaton. If more automata than a single one become fixed as one descends in the tree, this number is indicated in Fig. 7.

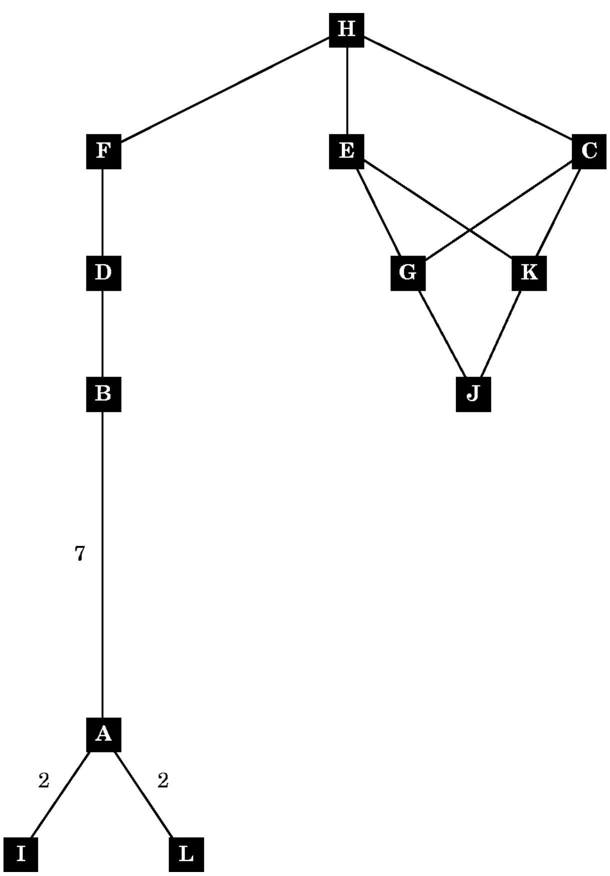

FIG. 7. A taxonomic representation of the schemata in Table 2. As one descends from the top of the tree to the bottom, automata get fixed (see the text).

An alternative way to group the cycles of a network is by the cycle length of each automaton (Weisbuch & Stauffer, 1987). With the same data used to generate the schemata in Table 2, 21 schemata with this alternative definition were found (see Table 3). Note that the number of cycles grouped under each schema (the second column) is often a multiple of some of the individual cycle lengths. This arises because many cycles differ only in the phase of the oscillations of the individual automata. Between two such cycles, all of the individual automata have identical sequences of on and off states, but one or several automata in one cycle are not synchronized in the same way as in the other. In such instances, the cycles are qualitatively identical. Such an occurrence is diagrammed in Table 4.

The fact that automata cycles which vary in synchrony may be of different lengths leads to a simple way for generating periodic orbits of many different lengths for the network as a whole, often longer than the period of any of its constituent automata (Weisbuch & Stauffer, 1987; Weisbuch, 1990). In Table 4, no single automaton has a cycle length larger than 3, yet the cycle length of the network is six. Note in Table 3 that orbits for the network as a whole are often much larger than the cycle length of any individual automaton.

The above results show that in discrete networks there can be a rich combinatorial structure that is not reflected in a simple count of the numbers of attractors.

TABLE 3.
A different schema for the same network in Table 2

1	24	12	1	6	1	1	6	6	1	1	4	4	1	4	1	1	1	1	1	6	4	1	4	1	4	1	1
2	16	8	1	2	1	1	2	2	1	1	4	8	4	8	4	1	4	1	4	2	8	4	4	4	8	4	1
3	4	4	1	2	1	1	2	2	1	1	4	2	1	2	1	1	1	1	1	2	2	1	4	1	2	1	1
4	32	24	1	6	1	12	6	6	1	1	4	8	4	8	4	1	4	4	4	6	8	4	4	4	8	4	1
5	32	24	1	6	1	12	6	6	1	1	4	8	4	8	4	1	4	1	4	6	8	4	4	4	8	4	1
6	4	56	1	14	14	14	14	14	1	1	4	8	2	8	2	1	2	2	2	14	8	2	4	1	8	2	1
7	4	56	1	14	14	14	14	14	1	1	4	8	2	8	2	1	2	1	2	14	8	2	4	2	8	2	1
8	80	8	1	2	1	4	2	2	1	1	4	8	4	8	4	1	4	8	4	2	8	4	4	4	8	4	1
9	16	8	1	2	1	1	2	2	1	1	4	8	4	8	4	1	4	4	4	2	8	4	4	4	8	4	1
10	8	56	1	14	14	14	14	14	1	1	4	8	2	8	2	1	2	4	2	14	8	2	4	4	8	2	1
11	16	8	1	2	1	4	2	2	1	1	4	8	4	8	4	1	4	4	4	2	8	4	4	4	8	4	1
12	24	4	1	2	1	1	2	2	1	1	4	4	1	4	1	1	1	1	1	2	4	1	4	1	4	1	1
13	64	24	1	6	1	12	6	6	1	1	4	8	4	8	4	1	4	8	4	6	8	4	4	4	8	4	1
14	8	8	1	2	1	1	2	2	1	1	4	8	2	8	2	1	2	4	2	2	8	2	4	4	8	2	1
15	4	12	1	6	1	1	6	6	1	1	4	2	1	2	1	1	1	1	1	6	2	1	4	1	2	1	1
16	4	4	1	2	1	1	2	2	1	1	4	1	1	1	1	1	1	1	1	2	1	1	4	1	1	1	1
17	16	8	1	2	1	4	2	2	1	1	4	8	4	8	4	1	4	1	4	2	8	4	4	4	8	4	1
18	4	8	1	2	1	1	2	2	1	1	4	8	2	8	2	1	2	2	2	2	8	2	4	1	8	2	1
19	2	12	1	6	1	1	6	6	1	1	4	1	1	1	1	1	1	1	1	6	1	1	4	1	1	1	1
20	16	8	1	2	1	4	2	2	1	1	4	8	4	8	4	1	4	8	4	2	8	4	4	1	8	4	1
21	4	8	1	2	1	1	2	2	1	1	4	8	2	8	2	1	2	1	2	2	8	2	4	1	8	2	1

The first column is a numerical index, the second indicates the number of periodic orbits which fall within the following schemata, and the third column indicates the length of the cycles found. The length of the cycle for each individual automata in the network of 25 automata is given.

5. From Discrete to Continuous Models

Though discrete dynamical systems are relatively easy to compute, continuous descriptions of regulatory networks in the biological sciences are undoubtedly a more appropriate mathematical framework. Variables in biological systems are usually continuous and there are few mechanisms for synchronous updating of the state. There have been a number of studies that have tried to relate the dynamics in logical networks with associated continuous equations based on them (Thomas & D'Ari, 1990; Thomas, 1991). Our approach is based on (Glass & Kauffman, 1973; Glass, 1975a; Glass, 1975b).

A natural generalization of eqn (1) to the continuous domain is

$$\dot{x}_i = B_i(\mathbf{X}(t)) - x_i,\ i = 1, 2, \ldots, N, \tag{2}$$

where x_i is a continuous variable, the time t is continuous, and B_i is once again a Boolean function that depends on the Boolean vector $\mathbf{X}(t)$. However, the Boolean variable X_i, now depends on the value of the continuous variable x_i by the rule

$$X_i(t) = H(x_i - \theta_i),$$

where H is the Heaviside function $H(u) = 0$ for $u < 0$, $H(u) = 1$ for $u \geq 0$, and θ_i is a constant that we call the threshold.

Starting at some initial condition, designate the first time a variable crosses its threshold as t_1. There will be evolution until a second variable crosses its thresholds at t_2 and so forth. The set of threshold crossing times is $\{t_1, t_2, \ldots, t_k\}$. Then by integrating eqn (2), we find for each variable x_i,

$$x_i(t) = x_i(t_j)e^{-(t-t_j)} + a_i(\mathbf{X}(t)) \times (1 - e^{-(t-t_j)}),\ t_j < t < t_{j+1}, \tag{3}$$

where a_i is either zero or one; the value at any time depends on the current logical state $\mathbf{X}(t)$. Since the

TABLE 4.
Two different periodic orbits from the same ten automata network

0	1	0	1	1	0	1	0	0	1	0	1	1	0	1	0	1	1	0	0
1	1	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	1
0	1	0	0	1	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0
0	1	1	1	1	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0
1	1	0	1	0	0	1	1	0	0	0	1	1	1	0	1	1	1	0	1
0	1	1	0	1	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0
3	1	2	3	3	3	2	3	1	3	3	1	2	3	3	3	2	3	1	3

The schemata at the bottom of the table give either the fixed state for each automaton, or the cycle length for each automaton. Using this schema, both cycles are the same.

current value of a_i depends on the logical state, for each variable, the solution is a continuous function with discontinuities in the slope that arise as a consequence of input variables crossing their respective thresholds. Thus, in eqn (2), each variable is governed by a linear equation and is a piecewise exponential function asymptotically approaching either one or zero. In the N-dimensional phase space, the trajectories are straight lines that have corners on the thresholds. A variety of modifications of eqn (3) have been studied. For example, Glass and Pasternack (1978b) considered the case in which a_i is no longer restricted to be a Boolean variable, but could be any real finite number whose sign was not a function of X_i. Also, the Boolean functions can be smoothed to make steep continuous nonlinear functions (Glass & Kauffman, 1973; Glass & Pasternack, 1978*a*; Thomas & D'Ari, 1990). Equation (2) is a generalization of Hopfield models of neural networks (Lewis & Glass, 1992) so that this class of equations in its various incarnations is relevant in different fields.

Here are two problems that appear to be of some interest:

(i) Given some subset of eqn (2), e.g. all networks with N variables and two inputs, what is the expected numbers of basins of attraction?
(ii) Given a particular logical network (1), can one predict the dynamics in the analogous continuous eqn (2) without integrating it but simply based on its logical structure?

Since in the continuous equations, in general only one variable will change at a given time a natural geometrical representation of the logical structure of (1) and the flows in (2) can be achieved by a directed graph on an N-dimensional hypercube (Glass, 1975a, b). For the case of no self-input, each edge on the graph of the N-dimensional hypercube is directed in a unique orientation. Two vertices on a graph are called adjacent if they share a common edge.

The logical structure can be exploited to identify stable and unstable steady states and limit cycles in N dimensional networks (Glass & Pasternack, 1978b; Plahte *et al*., 1994; Snoussi & Thomas, 1993; Mestl *et al*., 1995). For example, a vertex in the directed graph in which all edges from adjacent vertices are directed towards it is associated with a stable steady state in both the discrete (1) and continuous (2) representations of the same network. Similarly, cycles on the directed graph representation of a given logical network are stable (or unstable) if all (no) adjacent vertices are directed towards the cycle. In some instances stable limit cycles can be predicted in the continuous eqn (2) based solely on the presence of a stable cycle in the discrete system and in the associated directed graph (Glass & Pasternack, 1978b; Mestl *et al*., 1995). These observations enable one to generate a method to classify two different networks. Two networks are in the same equivalence class if their directed graph representations on the N-dimensional hypercube are equivalent under a symmetry operation of the N-dimensional hypercube. For example, for $N = 3$, there are 112 different classes which are enumerated in Glass (1975b). However, these methods have not yet been extended to higher dimensions and other means to count and classify the attractors in high dimensions are needed.

Consider a network in high dimensions. Provided (i) the system can be decomposed into subnetworks, (ii) there is at most a single stable limit cycle in only one of the subnetworks, and (iii) the remaining subnetworks only display steady states, the discussions concerning the combinatorial structure of the network presented above applies. In these cases the number of stable attractors in the continuous systems will be of the same order as the number of attractors in the discrete analogue. However, in continuous systems it is also possible to find aperiodic dynamics as a consequence of either quasi-periodicity (the presence of two incommensurate cycles in a single system) or deterministic chaos. Since eqn (2) can display both stable limit cycles (Glass & Pasternack, 1978b) and deterministic chaos (Sompolinsky *et al*., 1988; Lewis & Glass, 1992; Mestl *et al*., 1996), in high dimensional systems it is possible to find combinations of quasi-periodicity and chaos in specific examples. We illustrate some of the issues that arise in systems that have aperiodic dynamics in two examples.

5.1. A CONTINUOUS EQUATION WITH QUASI-PERIODIC DYNAMICS

We now consider the dynamics of a system of continuous differential equations which models a regulatory network with threshold functions that are steep, but are not step functions. The logical network and the associated differential equation were analysed in previous work (Glass & Pasternack, 1978a, b). The system has been chosen to illustrate some of the combinatorial notions in the preceding sections, and to illustrate complications that arise when trying to draw conclusions concerning the numbers of attractors in continuous systems based on an analysis of the associated discrete systems.

Define

$$f(x,\theta,n) = \frac{x^n}{x^n + \theta^n}$$

$$\bar{f}(x,\theta,n) = \frac{\theta^n}{x^n + \theta^n} \tag{4}$$

Consider the ordinary differential equation with nine variables

$$\begin{aligned}
\dot{x}_1 &= \bar{f}(x_2,0.5,6) - x_1\\
\dot{x}_2 &= \bar{f}(x_1,0.5,6) - x_2\\
\dot{x}_3 &= \bar{f}(x_4,0.5,6) - x_3\\
\dot{x}_4 &= f(x_5,0.5,6) - x_4\\
\dot{x}_5 &= f(x_3,0.5,6) - x_5\\
\dot{x}_6 &= \bar{f}(x_7,0.25,4)\bar{f}(x_8,0.25,4) - x_6\\
\dot{x}_7 &= \bar{f}(x_8,0.25,4)\bar{f}(x_9,0.25,4) - x_7\\
\dot{x}_8 &= \bar{f}(x_9,0.25,4)\bar{f}(x_6,0.25,4) - x_8\\
\dot{x}_9 &= \bar{f}(x_6 0.25,4)\bar{f}(x_7,0.25,4) - x_9
\end{aligned} \tag{5}$$

This differential equation is chosen so that there are really three distinct subnetworks. Elements 1 and 2 mutually inhibit each other to give dynamics with two stable steady states; elements 3, 4 and 5 form a feedback inhibition loop that gives a stable limit cycle oscillation with a period of about 3.61, and elements 6, 7, 8, and 9 form an inhibitory network that gives a stable limit cycle oscillation with a period of about 6.1 (Glass & Pasternack, 1978a). Since the periods of the oscillations in the two different oscillating subgroups are not commensurate, the dynamics are quasi-periodic.

To illustrate the dynamics in this system we assume that we do not have access to the state of all the variables, but only the quantity $x_1 + x_3 + x_6$ shown in Fig. 8, and display this quantity for two different initial equations. There are two different asymptotic behaviors which result in an offset in the mean value of this fluctuation.

The best way to think of this system is in a combinatorial manner. There are three subnetworks—one has two stable steady states and each of the other two have one stable limit cycle. Consequently, the number of stable attractors is $2 \times 1 \times 1 = 2$.

This result is different from the discrete description of a system with the same logical structure. For the current case, the Boolean equation of the form of eqn (1) corresponding to eqn (5) is

$$\begin{aligned}
X_1 &= \bar{f}(X_2)\\
X_2 &= \bar{f}(X_1)
\end{aligned}$$

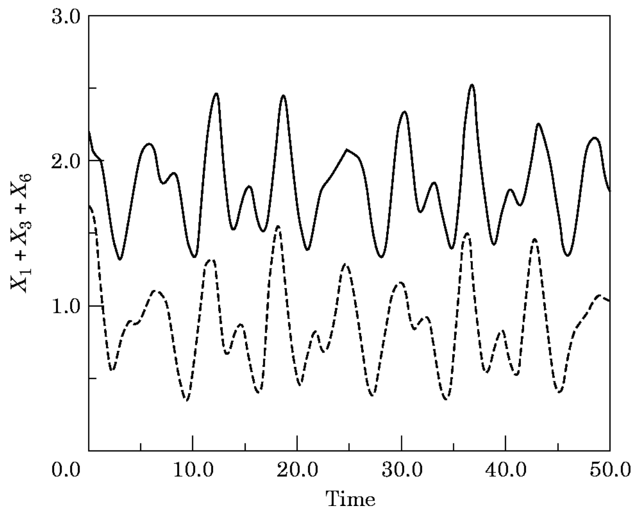

FIG. 8. $x_1 + x_3 + x_6$ for eqn (5) starting from two different initial conditions. In both time series there is quasiperiodic behavior. The two time traces are shifted due to the difference in the steady-state values of x_1.

$$\begin{aligned}
X_3 &= \bar{f}(X_4)\\
X_4 &= f(X_5)\\
X_5 &= f(X_3)\\
X_6 &= \bar{f}(X_7)\bar{f}(X_8)\\
X_7 &= \bar{f}(X_8)\bar{f}(X_9)\\
X_8 &= \bar{f}(X_9)\bar{f}(X_6)\\
X_9 &= \bar{f}(X_6)\bar{f}(X_7)
\end{aligned} \tag{6}$$

where f represents tautology, $\bar{f}$ represents contradiction, and the variables are Boolean variables.

The three subnetworks will show the following behaviors.

(1) The subnetwork composed of elements 1 and 2 has 3 different behaviors: Steady states (10),(01) and the 2-cycle (00→11→00→. . .).
(2) The subnetwork composed of elements 3,4,5 has 2 different behaviors: the 2-cycle (110→001→110→. . .), and the 6-cycle (000→100→101→111→011→010→000→. . .).
(3) The subnetwork composed of elements 6,7,8,9 has 2 different behaviors: the 2-cycle (0000→1111→0000→. . .) and the 8-cycle (1000 → 1100 → 0100 → 0110 → 0010 → 0011 → 0001→1001→1000→. . .).

As with the Boolean networks discussed earlier, the three independent cycles in this example may have an arbitrarily chosen phase with respect to the others.

The total number of different cycles that are found using the methods discussed in Section 2 is 32. This number arises from different behaviors that can occur in each subnetwork, being combined with all possible phases.

Thus, in this example, there is a striking difference between the number of different attractors that are found in the discrete system and in the continuous system.

Part of this discrepancy arises from the introduction of unstable cycles in the Boolean network introduced by the synchronous updating. An unstable cycle can be defined based on the associated directed graph on the N-dimensional hypercube representation, see for example (Glass & Pasternack, 1978*b*). For an unstable cycle, transitions between a state on the cycle and all its adjacent states are directed from the cycle to its adjacent states. Thus, in this context the 2-cycles mentioned above 00→11→00→. . ., (110→001→110→. . .), and (0000→1111→0000→. . .) are all unstable cycles. An unstable cycle as defined here would in general not be found in with asynchronous updating.

The network in this section consisted of three independent subnetworks. Randomly generated connectivities will generate such special connection geometries, but with low probability. The frequency of generating subnetworks in randomly constructed networks with different construction rules and in real biological networks is not well understood.

5.2. CHAOTIC DYNAMICS IN HIGH DIMENSIONS

Deterministic chaos is found in continuous equations based on eqn (2) (Lewis & Glass, 1992; Mestl *et al*., 1996). Unpublished studies (LG) show that in randomly generated networks, chaos is comparatively infrequent in two input networks with no self-input of moderate dimension. The frequency of networks that give chaos increases with the size of the network, but is still less than about 2% for networks of dimension 100. The presence of chaotic dynamics adds further difficulties in the counting of the number of attractors. To illustrate problems that arise, we consider a randomly generated network with 50 automata that display chaotic dynamics. More details concerning the network is given in the Appendix.

In this one network, our results indicate the presence of two attractors. In Fig. 9 the projection of the state space on two variables corresponding to network elements 4 and 22 are shown for a periodic orbit and a chaotic attractor respectively. The periodic orbit was followed for several hundred

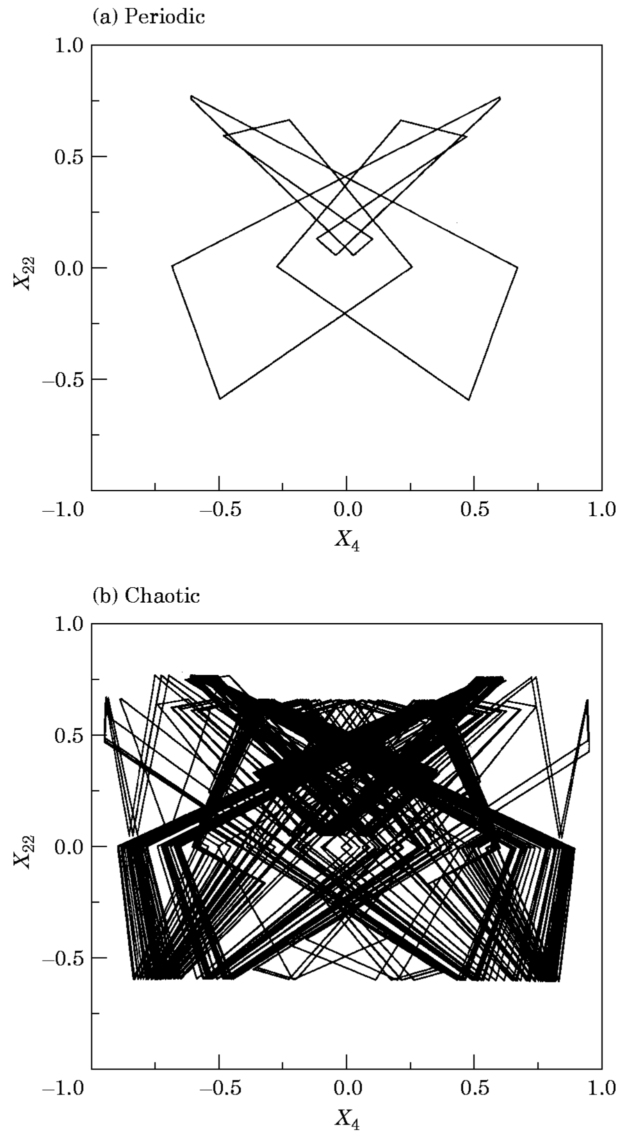

FIG. 9. (a) Periodic and (b) chaotic attractors in the 50 element network given in the Appendix. The projection of the tracetory in the x_4 and x_{22} plane is shown. The periodic orbit was followed for several hundred cycles. The chaotic trajectory was followed for 256×10^4 transitions, of which 10^4 are plotted.

cycles. The chaotic trajectory was followed for 256×10^4 threshold crossings and the dynamics were sensitive to small (10^{-3}) displacements from arbitrary points on the attractor.

Despite the clear distinction between periodic and chaotic behavior, by other measures the two attractors are quite similar. These attractors may be represented using a schema similar to those utilized in Section 4. In Fig. 10, the elements which are fixed are represented at the base of the graph in their respective states, zero and one. Elements which are not fixed are represented by an asterisk (*) at the bottom of the

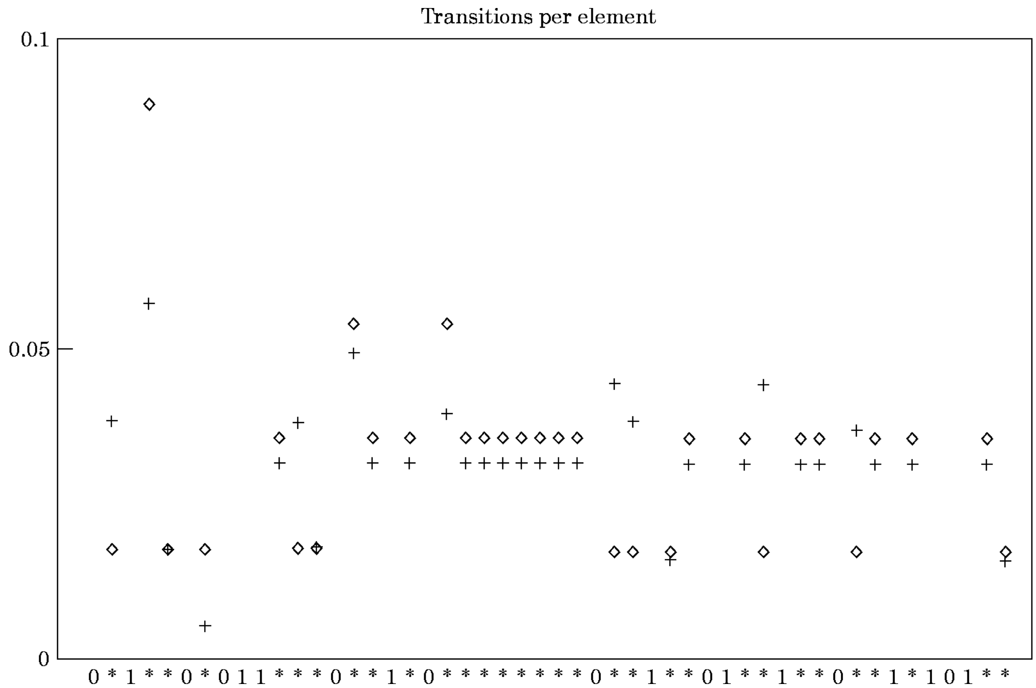

FIG. 10. Schema for representing the chaotic and periodic dynamics in a continuous network in Fig. 9. Each element is either fixed or varying. If an element is fixed, its fixed value is represented at the bottom of the table. If the element is varying, the symbol * is given at the bottom of the graph. For the varying elements, the number of the transitions (from one to zero or from zero to one) made by the element is divided by the total number of transitions is given. Based on simulations with 256×10^4 transitions. Key: T2, Periodic; +, Chaotic.

graph. For elements that are varying, the relative transition frequencies are given. This is determined by counting the number of threshold crossings for a given element in the network and dividing that number by the total number of threhold crossings. The plots for the two attractors are overlayed. The elements which are fixed in the network are identical in both attractors. The relative transition frequencies are similar in both the periodic and chaotic systems. In addition, both periodic and chaotic attractors share symmetries, at least in the variables selected for the projection. Thus, both the state space projections and transition density histograms portray a similar global structure for both attractors. This schema represents a novel method for classifying attractors in continuous systems, and should be useful in analysing systems in which both periodic and chaotic dynamics can both be present in a single network.

6. Discussion

This work has considered problems associated with counting the number of attractors in dynamical systems. In discrete Boolean networks with synchronous updating, the criteria for deciding if two behaviors are the same or different are precise. However, some of the cycles may be unstable; others that are technically different may still be equivalent in many aspects (e.g. the cycles of each element considered separately may be identical). Our comparison of continuous and discrete dynamics for one connectivity underscored these problems by showing that the two stable quasi-periodic attractors in the continuous system represented 32 different asymptotic periodic behaviors in the discrete case.

There are a number of factors that lead to differences between the numbers of attractors in Boolean equations and in continuous equations with the same logical structure. Most significant is that the synchronous updating in the discrete system introduces artifactual attractors not found in the continuous system. However, the issues are subtle. Cycles on the directed graph generated from a given logical equation can be associated with steady states, stable or unstable limit cycles, or chaos in an associated differential equation. In a recent analysis of a continuous equation in four dimensions, there were two stable attractors—a steady state and a chaotic attractor, whereas in the associated Boolean network there was a single periodic attractor (Mestl *et al.*, 1996). As well, there is a possibility for multiple steady states in continuous equations with self-input that do not have corresponding steady states in the discrete equations (Snoussi & Thomas, 1993).

Despite these considerations, our analyses indicate that there are deep connections between the dynamics in a discrete system and its continuous analogues. We believe that the key to the correspondences lies in learning how to interpret the N-dimensional directed graph which is related to both the discrete and continuous descriptions. Several correspondences have been described with respect to the identification of steady states and limit cycles, but identification of chaotic dynamics remains an open question. Although we have still only carried through limited computations in high-dimensional phase space, it is clear that for two-input continuous networks, each network displays a limited number of attractors. Thus, Kauffman's observations of a limited number of attractors of discrete synchronous random Boolean nets with two-inputs, appears to hold for two-input continuous networks. We conjecture that the numbers of attractors in the discrete and continuous equations scales in similar fashion assuming the same restrictions with respect to connectivity and input functions.

We have utilized two different schemata to classify the asymptotic behaviors of Boolean networks. In both classification schemes, a large number of attractors could be assigned to a much smaller number of classes. Although these schemata obscure some important aspects of the dynamics, they nevertheless give equivalence relationships for different attractors that can be useful for developing taxonomic classifications between the different attractors (Fig. 7). The most informative schema to classify attractors of a discrete network is the schema in which the steady state or the cycle length for each element is explicitly given, e.g. Table 3. Although this schema still includes unstable dynamics, it is nevertheless comparable to the schema in continuous systems in which the steady state (for fixed elements) or the transition density for varying elements is explictly given (e.g. Fig. 10). The schema in Fig. 10 can classify and compare attractors in continuous equations that display quasiperiodicity and deterministic chaos.

The current work is related to previous attempts to classify dynamics in logical and continuous networks. Wolfram (1984) has given a classification that identifies discrete cellular automata networks into one of four classes—fixed, periodic, chaotic, and complex. This terminology used by Wolfram (and many others who primarily study discrete networks) is not consistent with usage in other areas of nonlinear dynamics. In the Wolfram definition, "chaos" can occur in a system with a discrete phase space whereas in continuous systems, aperiodicity is always a necessary condition for chaotic dynamics.

There have been other previous approaches to characterize the attractors and in dynamical systems. One involves definition of an energy. This is particularly useful for spin glasses and neural networks that evolve to a steady state. The energy can be used to generate trees relating the different basins of attraction (Rammal *et al*., 1986; Mezard *et al*., 1987). It is not clear if a quantity comparable to the "energy" will be useful for networks which show complex fluctuations in time such as we have here. However, the average value of the Boolean variables (the "magnetization") has been used to characterize the transition from ordered to disordered behavior as a function of changes in the rules used to construct the network (Derrida, 1987a).

Determination of the complete structure of the basins of attraction of both cellular automata and random Boolean networks have been carried out by Wuensche who used inverse mappings to generate the evolution of states throughout state space (Wuensche & Lesser, 1992; Wuensche, 1993). However, determination of the complete structure of the basin of attraction is necessarily limited to comparatively small networks.

The combinatoric basis for comparing behaviors may be applicable in various areas in biology. The taxonomic trees that emerge from our analysis may have correspondences with classifications of cell types and may be related to the differentiation pathways of different cell types (Kauffman, 1993). Cognitive processes such as the formation of a visual image or the recollection of a memory may depend on generation of diversity in a combinatorial manner (Weisbuch, 1990). On a larger scale, the combination of relatively simple behaviors to form many more complicated ones may be one aspect of biological evolution. Thus, combinatoric mechanisms may underly both the function and evolution of a system.

In conclusion, a simple count of the number of basins of attraction offers limited insight into the dynamics of many high-dimensional dynamical systems. What is also required is a notion of relatedness, between basins. We have proposed classification methods that can be used for discrete and continuous high dimensional networks. The dynamic diversity observed in nature might best be analysed by considering the combinatorial generation of complex dynamics.

This work has been partially supported by the Natural Sciences Engineering and Research Council (Canada). In addition, R.B. wishes to thank the International Institute for Applied Systems Analysis, Laxenburg, Austria and the Institut für Molekulare Biotechnologie, Jena, Germany for hospitality while some of this work was performed.

REFERENCES

DERRIDA, B. & FLYVBJERG, H. (1987). The random map model: A disordered model with deterministic dynamics. *J. Physique* **48,** 971–978.

DERRIDA, B. (1987*a*). Phase transitions in random networks of automata. In: *Chance and Matter* (Souletie, J., Vanimenus, J. & Stora, R., eds), Les Houches, 1986. North Holland.

DERRIDA, B. (1987*b*). Valleys and overlaps in Kauffman's model. *Philosoph. Mag. B.* **6,** 917–923.

GLASS, L. & KAUFFMAN, S. A. (1973). The logical analysis of continuous non-linear biochemical control networks. *J. theor. Biol.* **39,** 103–129.

GLASS, L. & PASTERNACK, J. S. (1978a). Prediction of limit cycles in mathematical models of biological oscillations. *Bull. Math. Biol.* **40,** 27–44.

GLASS, L. & PASTERNACK, J. S. (1978b). Stable oscillations in mathematical models of biological control systems. *J. Math. Biol.* **6,** 207–223.

GLASS, L. (1975a). Classification of biological networks by their qualitative dynamics. *J. theor. Biol.* **54,** 85–107.

GLASS, L. (1975b). Combinatorial and topological methods in nonlinear chemical kinetics. *J. Chem. Phys.* **63,** 1325–1335.

HILBERT, D. (1902). Mathematical problems. *Bull. A. M. S.* **8,** 436–479.

HOPFIELD, J. (1982). Neural networks and physical systems with emergent collective computational abilities. *PNAS* **79,** 2554–2558.

JAFFE, S. *Kauffman Networks: Cycle Structure of Random Clocked Boolean Networks*. PhD thesis, Courant Institute, New York University, (1988).

KAUFFMAN, S. A. (1969). Metabolic stability and epigenesis in randomly connected nets. *J. theor. Biol.* **22,** 437–467.

KAUFFMAN, S. A. (1993). *The Origins of Order: Self-Organization and Selection in Evolution*. Oxford: Oxford University Press.

KAUFMAN, M., URBAIN, J. & THOMAS, R. (1985). Towards a logical analysis of the immune response. *J. theor. Biol.* **114,** 527–561.

LEWIS, J. & GLASS, L. (1992). Nonlinear dynamics and symbolic dynamics of neural networks. *Neural Computation* **4,** 621–642.

MCELIECE, R., POSNER, E. C., RODEMICH, E. R. & VENKATESH, S. S. (1987). The capacity of the Hopfield associative memory. *IEEE Transactions on Information Theory* **33,** 461–482.

MESTL, T., PLAHTE, E. & OMHOLT, S. W. (1995). Periodic solutions in systems of piecewise linear differential equations. *Dyn. Stab. Systems* **10,** 179–193.

MESTL, T., LEMAY, C. & GLASS, L. (1996). Chaos in high dimensional neural and gene networks. *Physica* **D.** (in press).

MEZARD, M., PARISI, G. & VIRASORO, M. (1987). *Spin Glass Theory and Beyond*. Singapore: World Scientific.

PLAHTE, E., MESTL, T. & OMHOLT, S. W. (1994). Global analysis of steady points for systems of differential equations with sigmoid interactions. *Dyn. Stab. Systems* **9,** 275–291.

RAMMAL, R., TOULOUSE, G. & VIRASORO, M. (1986). Ultrametricity for physicists. *Rev. Mod. Phys.* **58(3),** 765–788.

SEGEL, L. A. & PERELSON, A. S. (1988). Computations in shape space: A new approach to immune network theory. In: *Theoretical Immunology, Part Two* (Perelson, A. S., ed.), pp. 321–343. Reading, MA: Addison-Wesley.

SNOUSSI, E. H. & THOMAS, R. (1993). Logical identification of all steady states: The concept of characteristic states. *Bull. Math. Biol.* **55,** 973–991.

SOMPOLINSKY, H., CRISANTI, A. & SOMMERS, H. J. (1988). Chaos in random neural networks. *Phys. Rev. Lett.* **61,** 259–262.

THOMAS, R. & D'ARI, R. (1990). *Biological Feedback*. Boca Raton, FL: CRC Press.

THOMAS, R. (1973). Boolean formalization of genetic control circuits. *J. theor. Biol.* **42,** 563–585.

THOMAS, R. (1991). Regulatory networks seen as asynchronous automata: A logical description. *J. theor. Biol.* **153,** 1–23.

WEISBUCH, G. & FOGELMAN-SOULIÉ, F. (1985). Scaling laws for the attractors of Hopfield networks. *Journal de Physique Lettres (Paris)* **46,** 623–630.

WEISBUCH, G. & OPREA, M. (1994). Capacity of a model immune network. *Bull. Math. Biol.* **56(5),** 899–921.

WEISBUCH, G. & STAUFFER, D. (1987). Phase transitions in cellular random boolean nets. *J. Physique* **48,** 11–18.

WEISBUCH, G. (1990). *Complex Systems Dynamics*, volume 2 of *Santa Fe Institute Studies in the Sciences of Complexity: Lecture Notes*. Redwood City, CA: Addison-Wesley.

WOLFRAM, S. (1984). Cellular automata as models of complexity. *Nature* **311,** 419–424.

WUENSCHE, A. & LESSER, M. (1992). *The Global Dynamics of Cellular Automata*, volume 1 of *Santa Fe Institute Studies in the Sciences of Complexity*. Reading, MA: Addison-Wesley.

WUENSCHE, A. (1993). Memory, far from equilibrium: Basins of attraction of random boolean networks. In: *Proceedings*, pp. 1150–1159. ECAL 1993.

APPENDIX

The connectivity and transition rules for the network which generated the chaotic dynamics of Section 5.2 is listed in Table A1. In integrating the equation, the flow in each orthant is directed toward a given vertex of a 50-dimensional hypercube. The hypercube is centered at the origin with edge length of 2. Thus, at any time, each variable is exponentially increasing towards $+1$, or exponentially decreasing towards -1, see Glass & Pasternack (1978b) for more details about integration of these equations.

TABLE A1.
The network which generated the periodic chaotic dynamics of Section 5.2 *is listed*

Element	Inputs		Transition rule $f_A = f(x_B, x_C)$			
A	B	C	00	01	10	11
1	23	44	1	0	0	0
2	15	46	1	0	1	1
3	8	18	1	1	1	0
4	15	22	1	0	0	1
5	2	37	0	0	0	1
6	8	29	0	0	1	1
7	30	13	0	0	1	0
8	20	41	0	1	0	0
9	48	47	1	1	1	0
10	3	24	1	0	1	1
11	49	41	0	0	1	0
12	35	15	0	1	1	0
13	22	42	0	1	0	1
14	39	40	0	0	0	0
15	42	18	0	1	1	0
16	33	29	0	0	1	1
17	12	34	1	0	1	1
18	36	16	1	0	1	1
19	47	10	0	0	1	0
20	27	12	1	0	0	1
21	24	26	0	1	0	0
22	23	36	0	1	1	0
23	31	18	1	0	0	1
24	3	22	0	1	0	1
25	3	43	0	1	0	1
26	43	18	0	1	0	0
27	9	39	0	0	0	1
28	10	34	1	1	0	1
29	4	17	1	1	0	0
30	15	34	1	1	0	0
31	49	6	1	1	1	0
32	50	8	1	0	0	1
33	28	11	0	1	0	1
34	35	17	0	0	0	0
35	21	19	1	0	1	0
36	39	47	0	0	1	1
37	4	39	1	1	0	0
38	48	10	1	1	0	1
39	35	25	0	0	0	1
40	42	45	0	1	0	1
41	5	1	0	1	0	1
42	29	26	1	1	0	0
43	27	3	1	1	1	0
44	35	34	1	1	1	1
45	49	41	1	0	0	0
46	29	8	1	1	1	0
47	2	22	0	0	0	0
48	22	35	1	1	1	1
49	43	36	1	1	0	0
50	12	31	1	0	1	1

The transition rules and connectivity were randomly generated, with the restrictions that all automata had two inputs and no self-inputs. The first column indexes the automata of the network (A), followed by the indices for the two inputs (B,C) in the second and third columns. The transition rule for A as a function of the states of input B and C appears in the last four columns, each of which is headed with the state of the inputs (i.e. 01 implies that $x_B = 0$, $x_C = 1$.)