Chapter 2
Previous Work on Boolean Networks

Abstract This chapter summarizes both previous theoretical and expeirmental work on Boolean networks. I distinguish between synchronous and autonomous Boolean networks in Sect. 2.1 and introduce Boolean network models and preceding experimental work with electronic circuits in Sects. 2.2 and 2.3.

2.1 Synchronous and Autonomous Boolean Networks

A Boolean network is a composition of nodes that can be in one of two Boolean states—either “on” or “off”, “1” or “0”—and links that connect the nodes [1, 2]. The network dynamics is determined by Boolean functions of the Boolean states, processing delays, and, especially, the updating method of the Boolean states.

I distinguish between two forms of Boolean networks depending on the updating method: *synchronous* and *autonomous Boolean networks*. Synchronous Boolean networks evolve in discrete time steps, mathematically described by iterated maps and experimentally realized with clocked logic circuits. The processing delays are then given by one iteration step of the map. Autonomous Boolean networks evolve in continuous time, mathematically described by differential equations or Boolean delay equations and experimentally realized with unclocked logic circuits. The processing delays in autonomous Boolean networks originate from processing times of the nodes and propagation delays along the links.

One important example for an autonomous Boolean network is a synthetic biological circuit termed the “repressilator,” which is similar to naturally occurring biological circuits that function as biological clocks [3]. This circuit includes three transcriptional repressors that inhibit each other in a cyclic way, leading to oscillations [4, 5].

A simplified network topology of the repressilator is shown in Fig. 2.1. It consists of three autonomous nodes connected in a directional ring as shown in Fig. 2.1a. In this example, each node executes the inversion Boolean function, hence, it adjusts its Boolean state to be the opposite of the state of the input node, which is referred to as inhibition in a biological context. The specific dynamics of the network depends on the underlying modeling framework and corresponding parameters, which I discuss

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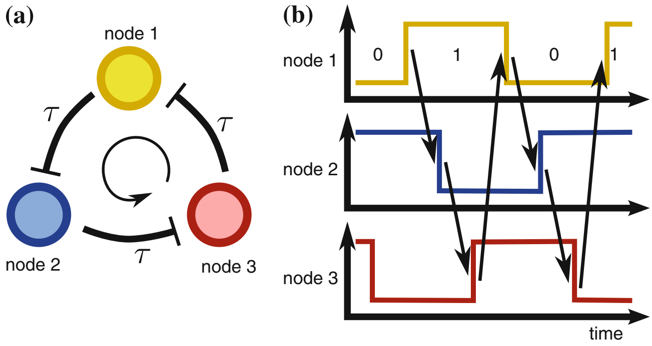

Fig. 2.1 **a** Example of an autonomous Boolean network with three nodes. Each node inhibits one neighbor as indicated by *arrows*. b Schematic of the resulting dynamics. The Boolean states are indicated by “0” and “1” in the first waveform

below, but, for large enough processing delays, the states of the nodes oscillate. This oscillation is a result of an odd number of inversion operations and processing delays of the nodes, as illustrated in Fig. 2.1b. A transition in the first node results in a transition in the second node after one processing delay; after three processing delays, the first node displays another transition, resulting in an oscillation period of six processing delays.

2.2 Boolean Network Models

In this section, I describe three standard Boolean network models, known as Kauffman networks, Boolean delay equations, and piecewise-linear differential equations by Glass and collaborators. The first assumes synchronous operation and the latter two autonomous operation.

2.2.1 Kauffman Networks

In 1969, Kauffman popularized a synchronous Boolean network description for genetic control circuits, where genes are approximated as Boolean nodes that switch between active (“on”) and inactive (“off”) and links that describe the interactions of genes via Boolean functions. The nodes change their Boolean states at fixed time steps in synchronous temporal evolution. This is mathematically described with a map, where one time step corresponds to the node processing delay.

In Kauffman’s description, N Boolean nodes interact via their Boolean states X_i, according to the Boolean map

$$X_i(t+1) = \Lambda_i(X_{i_1}(t), X_{i_2}(t), \ldots, X_{i_K}(t)), \quad i = 1, \ldots, N, \tag{2.1}$$

where $\Lambda_i(\cdot) : \{0,1\}^K \to \{0,1\}$ are Boolean functions with inputs from K nodes in the network [2, 6]. The Boolean functions, which are associated with the genetic interaction, are picked at random because they were (and still are) unknown. Kauffman assumed that the Boolean functions are evaluated simultaneously in discrete time steps t. Under these conditions, this Boolean network model is known as *Kauffman N-K networks* or simply *Kauffman networks*.

Mathematically, such a Boolean map description is a finite-state machine or cellular automaton, with a phase space composed of 2^N states and rules for the transition between states [7, 8]. The finite number of states means that every trajectory will at some point reach a previously visited state. From there, since the dynamics is deterministic, the trajectory will fall into a limit cycle.

To characterize the dynamics, distance measures tailored for Boolean systems are needed. This is especially necessary to characterize the complexity of the dynamics, such as the divergence of nearby orbits [9]. A widely used Boolean distance measure is the *Hamming distance* from coding theory, which reads for two network states $\{X_i\}_{i=1}^N$ and $\{Y_i\}_{i=1}^N$ with Boolean states $X_i, Y_i \in \{0,1\}$,

$$h = \sum_{i=1}^{N} |X_i - Y_i| \,. \tag{2.2}$$

The Hamming distance corresponds to the number of nodes in the network that differ in their Boolean states.

For Kauffman networks, the Hamming distance can under certain conditions increase exponentially over time calculated between two initially close network states, i.e. consider a small perturbation of the network dynamics by switching the Boolean states of a few nodes. These networks satisfy hence the sensitivity to initial conditions of chaotic systems [10]. On the other hand, because Kauffman networks are finite-state machines, all orbits are closed and periodic, which violates one condition for deterministic chaos. I discuss deterministic chaos and its requirements in detail in Sect. 4.1. The periods can, however, be as long as $T = 10^{150}$ iterations for N-K networks of $N = 10^3$ nodes and in-degrees of $K = N$ [2].

Kauffman networks can display a dynamical transition to such long trajectories with exponential growth of the Hamming distance. The dynamical instability has implications for biology because Kauffman proposed that different attractors in Boolean networks correspond to different cell types of organisms [2]. Specifically, this dynamical instability in biological systems has been hypothesized to be the cause for some types of cancer. Furthermore, researchers have proposed that a method of controlling this dynamical instability could be a route towards curing cancer [10].

Kauffman's description of genetic interaction is appealing from a network point of view because it reduces complex interacting systems, especially genetic circuits, to systems involving only network topology and Boolean functions. But, it also neglects several aspects of the physical system that could be important for the dynamics. For example, Boolean descriptions neglect continuous-variable (non-Boolean) interactions that account for the amplitude of the dynamics. Furthermore, Kauffman's description does not include continuous-time interactions and finite transmission delays between nodes. Time delays have been proven to play a crucial role for the dynamics in many systems because they lead to an infinite-dimensional phase space. For example, time delays can dictate the periodicity of oscillations and stabilize and destabilize fixed points and periodic orbits [11–17].

2.2.2 Boolean Delay Equations

Ghil and Mullhaupt introduced Boolean delay equations as an autonomous Boolean network model [18]. The Boolean state of the node X_i evolves according to the Boolean delay equation

$$X_i(t) = \Lambda_i(X_{i_1}(t-\tau_{i,1}), X_{i_2}(t-\tau_{i,2}), \ldots, X_{i_N}(t-\tau_{i,N})), \quad i = 1, \ldots, N, \tag{2.3}$$

which has a similar structure as Kauffman networks in Eq. (2.1) with the Boolean function Λ_i on the right hand side. However, the resulting dynamics can be very different from Kauffman networks because it includes continuous-time updating and time delays $\tau_{i,j}$, which correspond to the transmission times along the links. Boolean delay equations can be used to model genetic circuits [19].

Ghil and Mullhaupt are especially interested in the dynamics of a particular Boolean network given by the Boolean delay equation

$$X(t) = X(t-\theta_1) \oplus X(t-\theta_2) \oplus \cdots \oplus X(t-\theta_\delta), \tag{2.4}$$

which includes $\delta \geq 2$ time delays θ_i with $0 < \theta_\delta < \cdots < \theta_2 < \theta_1 = 1$ [18]. The operator $\oplus$: $\{0, 1\} \times \{0, 1\} \rightarrow \{0, 1\}$ denotes the "*exclusive or*" (*XOR*) operation that maps two Boolean inputs that have combined $2^2 = 4$ possible states, namely 00, 01, 10, and 11, to one Boolean output. This mapping is uniquely defined by a *look-up table* that connects all possible Boolean input combinations (here, a total of four) to one Boolean output value. Specifically, Fig. 2.2a shows the look-up table for the XOR logic operation. Equation (2.4) includes $\delta - 1$ XOR operations with two inputs each, which is equivalent to a single generalized δ-input XOR operation.

The Boolean delay equation (Eq. 2.4) is visualized with a circuit diagram in Fig. 2.2b for $\delta = 2$, where I use the standard graphical representation of an XOR logic gate. It can be seen that the XOR logic operator is subject to two delayed feedback lines.

This Boolean delay equation (Eq. 2.4) leads to aperiodic dynamics, when the delays $\{\theta_i\}_{i=1}^{\delta}$ are incommensurate, for all initial conditions except $x(t) \equiv 0$ [18, 20]. On the other hand, the initial condition $x(t) \equiv 0$ $(t \in (-1, 0])$ leads to a stable fixed point, where the output and the input of the Boolean function stays at the low Boolean value.

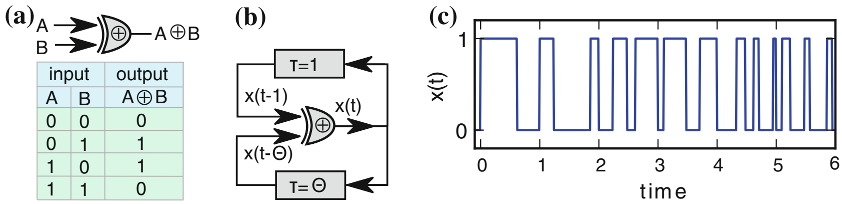

Fig. 2.2 **a** Look-up table and a variation on the ANSI/IEEE Std 91-1984 representation for an XOR logic gate. The look-up table determines the Boolean output of the logic gate for every possible combination of Boolean inputs. **b** Illustration of the circuit that is represented by the Boolean delay equation (2.4) with $\delta = 2$ delays. The delayed feedback lines are represented by *wire connections* and *rectangles*. **c** The solution $x(t)$ of Eq. (2.4) with delays of $\theta_2 = (\sqrt{5} - 1)/2$ and $\theta_1 = 1$; the dynamics are initialized with one transition at time $t = 0$

The resulting dynamics is shown in Fig. 2.2c for an initial function that includes one initial transition at time $t = 0$ and $\delta = 2$ delays of $\theta_2 = (\sqrt{5} - 1)/2$ and $\theta_1 = 1$ in Eq. (2.4). The figure shows that with each time unit (corresponding to the delay $\theta_1 = 1$), the number of transitions increases. In fact, this increase follows a power law in time as reported by Ghil and collaborators [18, 20]. Because these increasingly fast dynamics result in an unlimited growth of frequency over time, Zhang and collaborators referred to that effect as an inevitable *ultraviolet catastrophe* [21].

This complex behavior is not practically observed in nature because the information-transmitting wires (or media) and the processing element (the XOR logic operator) have, when physically realized, a maximum operation frequency. Hence, they cannot transmit or generate signals above a certain frequency. For electronics, this effect is known as low-pass filtering. A maximum operation frequency also exists in biological systems, such as biological genes.

2.2.3 Piecewise-Linear Differential Equations

To overcome these problems, Glass and collaborators proposed an autonomous Boolean network model with continuous-time, continuous-state differential equations that include Boolean switching terms [22–24]. Specifically, Kauffman networks in Eq. (2.1) are expanded with piecewise-linear differential equations that include a first-order approach to the Boolean levels, according to

$$\frac{dx_i}{dt} = -x_i + \Lambda_i(X_{i_1}(t), X_{i_2}(t), \ldots, X_{i_K}(t)), \quad i = 1, \ldots, N, \tag{2.5}$$

where, similar to Kauffman networks, $\Lambda_i(\cdot) : \{0, 1\}^K \to \{0, 1\}$ are the Boolean functions and $\{X_i\}_{i=1}^N$ the Boolean states. The equation describes the continuous temporal evolution of continuous states $\{x_i\}_{i=1}^N$, which are used to calculate the

Boolean states according to the threshold condition

$$X(t) = \begin{cases} 1, & \text{if } x(t) \geq 0.5, \\ 0, & \text{if } x(t) < 0.5, \end{cases} \tag{2.6}$$

Equation (2.5) is more realistic than Eq. (2.1) to describe physical systems, but it is still a highly simplified model. Glass and collaborators justify this step towards higher complexity with the model's "remarkable mathematical properties that facilitate theoretical analysis" [22, 25]. For example, Eq. (2.5) can be solved analytically with simple exponential functions.

To construct the analytical solution, consider the times $\{t_1, t_2, \ldots, t_k\}$ of switching events when any of the variables x_i crosses the threshold 0.5 and hence the Boolean functions can change values. The solution of Eq.(2.5) is then

$$x_i(t) = x_i(t_j)\mathrm{e}^{-(t-t_j)} + \Lambda_i(X_{i_1}(t_j), X_{i_2}(t_j), \ldots, X_{i_K}(t_j))(1 - \mathrm{e}^{-(t-t_j)}), \tag{2.7}$$

for $t \in \left[t_j, t_{j+1}\right]$ [22].

As an example, I discuss the resulting dynamics for a single variable x in the network with $\Lambda = 0$ for $t < 0$ and $\Lambda = 1$ for $t \geq 0$. Then, the dynamics, shown in Fig. 2.3, approaches the Boolean level of Λ with a rise time of

$$T_{1/2} = \ln(2). \tag{2.8}$$

The figure also shows the corresponding Boolean variable X that switches Boolean states when x reaches 0.5. Due to the finite rise time $T_{1/2}$, the Boolean variable X takes on the value of Λ only after $T_{1/2}$, leading to the effective processing delay $T_{1/2}$.

Mestl and collaborators have investigated the dynamics of Eq. (2.5) for random networks of N nodes with a fixed in-degree of K [24, 26]. They have chosen the Boolean functions of the nodes at random by filling the look-up table with 0's and 1's with a probability p. This probability p is known to produce more complex dynamics the closer it is to 0.5 [27]. They also include a slight variation on the Boolean levels for each gate by ± 0.01 to introduce heterogeneity and thus increase

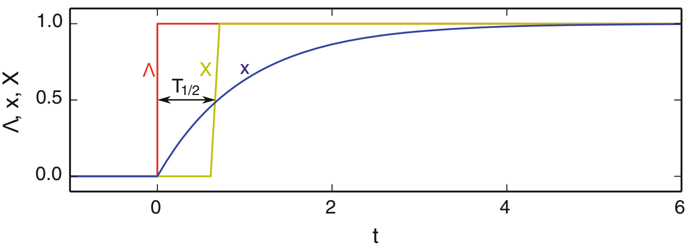

Fig. 2.3 Analytic solution Eq. (2.7) of Eq. (2.5) for a Boolean driving term Λ that switches from 0 to 1 at $t = 0$. Shown are Λ, x, and X and the rise time $T_{1/2}$

the complexity in the dynamics. They have shown that, for $N = 64$, $9 \leq K \leq 25$, and $p = 0.5$, chaos is the usual behavior [22, 24]. It is assumed that chaos occurs for most network realizations when the network is above a certain size and $p \approx 0.5$ [28]. In these studies, the network topologies exclude self-feedback loops and loops that are composed of only two nodes because they can lead to fast oscillations that dominate the dynamics [22].

The solution of this network of N nodes exists in a phase space of N dimensions. An inclusion of time delays in Eq. (2.5), however, will result in a much larger phase space and is hence likely to have a drastic effect on the dynamics. I include such time delays to model the transmission time of the signals between nodes to model experimental dynamics in Sect. 4.3.2.

2.2.4 Overview of Boolean Network Models

The three standard Boolean network models are summarized in Table 2.1. The Boolean networks interact via discrete states and, in the piecewise-linear differential equations by Glass and collaborators, an additional continuous variable is used for the temporal evolution of nodes. They evolve either in discrete time steps or in continuous time, which determines their type to be either synchronous or an autonomous, respectively.

2.3 Electronic Realizations of Boolean Networks

Central processing units (CPUs) are highly specialized, electronically realized synchronous Boolean networks, similar to Kauffman networks. These systems are finite-state machines where set rules determine the transition from one state to the next every clock cycle, where clock speeds can be as high as several gigahertz. CPUs are the method of choice to perform linear operations at a high rate and are included

Table 2.1 Overview of the three discussed models for Boolean networks

	N-K networks	Boolean delay equations	Glass models
States x	Discrete	Discrete	Discrete/continuous
Time t	Discrete	Continuous	Continuous
Type	Synchronous	Autonomous	Autonomous
Mathematical description	Finite-state machine	Boolean delay equation	Ordinary differential equation

I use the abbreviation ‘Glass models’ for piecewise-linear differential equations by Glass and collaborators [22] in everyday electronic equipment. However, from a fundamental point of view, the physical network problem becomes more interesting when synchronous clocking is removed from the setup and replaced by continuous-time evolution, i.e. the autonomous operation. Especially when the signal transmission times matter, the system's dimensionality increases substantially. Furthermore, the operation frequency increases to the limit of the Boolean nodes. Then, the system can be used for novel network-based computing approaches and other applications.

For fundamental research, unclocked logic circuits can be used to test the validity of autonomous Boolean network models, such as the piecewise-linear differential equations by Glass and collaborators. With this goal, they have built an electronic realization of a Boolean network of five nodes based on unclocked logic gates [29]. In this study, they found qualitative agreement between model and experiment in both periodic and chaotic dynamical states, when parameters used in the simulation are derived from the experimentally measured dynamics. However, they have not shown that the experimental dynamics is indeed deterministic chaos. Furthermore, their dynamics is, with a timescale on the order of tens of milliseconds, rather slow for applications.

2.3.1 Autonomous Boolean Network by Zhang and Collaborators

As an extension, Zhang and collaborators have realized an unclocked logic circuit with a timescale on the order of nanoseconds and have shown that deterministic chaos occurs [21].

Their Boolean network is composed of three nodes with a topology shown in Fig. 2.4a. The system is an electronic circuit that realizes the Boolean nodes with logic gates, specifically two XOR logic gates and one XNOR (inverted XOR) logic gate as shown in Fig. 2.4b. For the physical implementation of this logic design, they use several separate electronic integrated circuits that each execute one logic function and connect them with electronic wires on a printed circuit board as shown in Fig. 2.4c.

Zhang and collaborators find that, depending on the delays in the circuit, the circuit displays either periodic dynamics or chaotic dynamics. Figure 2.5a shows a time series from chaotic dynamics recorded by Zhang and collaborators. The dynamics fluctuates between the Boolean low and high voltage of 0 and 3 V with an irregular timing of transitions. Narrow pulses and dips in the chart do not reach the Boolean voltages because of finite rise and fall times. This non-ideal behavior is due to low-pass filtering of the electronic logic gates, specifically, capacitances in the micro circuits that constitute a logic gate. In addition, amplitude noise is present as can be seen in the graph when the system is close to the Boolean voltage levels. Figure 2.5b shows the power spectrum of this dynamics. It extends from dc to high frequencies of $\sim$1.3 GHz at -10 dB dropoff. This large bandwidth is a characteristic of chaos, which is reassured by the irregularity of the waveform.

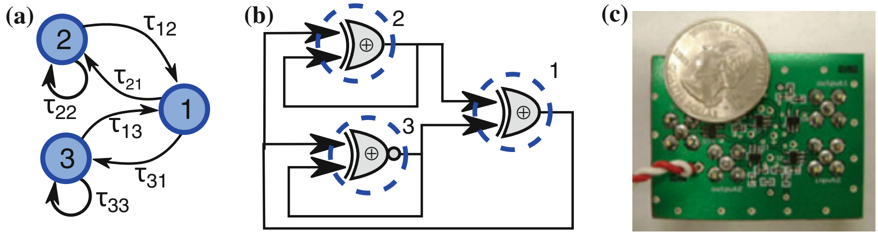

Fig. 2.4 **a** Schematic of the network topology considered by Zhang and collaborators in Ref. [21]. **b** Schematic of the corresponding logic circuit with XOR and XNOR logic gates. The look-up table of an XNOR gate can be obtained by inverting the output row of the look-up table of an XOR gate shown in Fig. 2.2a. **c** Experimental implementation with integrated circuits that perform Boolean operations (logic gates, *black rectangles*) on an electronic circuit board (*photo* by Seth Cohen)

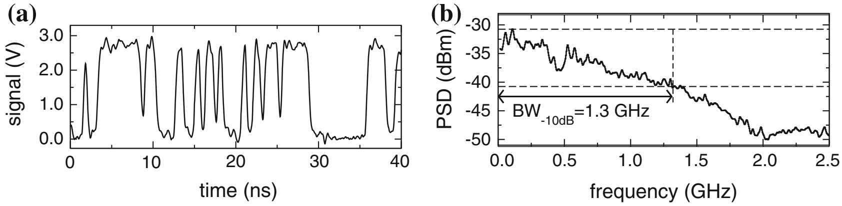

Fig. 2.5 **a** Waveform of Boolean chaos generated by the system described in Fig. 2.4b. **b** Power spectrum of the dynamics with a bandwidth at −10 dB dropoff of 1.3 GHz. The illustrations are taken from Ref. [21]

Zhang and collaborators model Boolean chaos with an extension on Ghil's Boolean delay equations that includes non-ideal attributes of the experiments [21, 30]. Specifically, important effects included in the model are low-pass filtering and a degradation function that includes a rejection of short-pulses and a history-dependent gate delay.

2.3.2 Boolean Chaos

In Sect. 2.2.1, I have discussed that the quantification of complexity in Boolean systems requires a distance measure specialized for Boolean systems, such as the Hamming distance. However, the Hamming distance is a measure for synchronous Boolean systems that does not work for small autonomous Boolean systems. As a solution for autonomous Boolean networks, Zhang and collaborators use a distance measure that is sensitive to the timing of Boolean transitions, termed the *Boolean distance* [18, 21]. It is defined as

$$d\,[x,y]\,(t) = \frac{1}{T}\int_{t}^{t+T} x(t') \oplus y(t'), \tag{2.9}$$

where x and y are two Boolean waveforms that are compared, T indicates an integration interval, which should include on average about five transitions, and $\oplus$ indicates the XOR Boolean function of the Boolean scalars $x(t')$ and $y(t')$ [18, 21]. The result is a contribution to the integral whenever the two waveforms have different Boolean states; specifically, $d\,[x,x] = 0$.

Using the Boolean distance, they calculate the largest Lyapunov exponent Λ of their system, which is a measure for the divergence of close orbits used to quantify chaotic systems, as I introduce in Sect. 4.1.1. They calculate a Lyapunov exponent of $\Lambda = 0.16\,\mathrm{ns}^{-1}$ from the experimental time series of their Boolean oscillator. The positive sign confirms the divergence of close orbits and is usually considered a proof of deterministic chaos.

They show that the complexity and chaoticity of the dynamics is encoded in irregular timing of transitions. Specifically, with the calculation of the Lyapunov exponent, they show that small perturbations in the timing of transitions grow exponentially over time, leading to completely different transition times after a long time [21]. On the other hand, a small perturbation in the voltage from the Boolean level does, in most cases, not affect the dynamics over time.

Zhang and collaborators termed the chaotic dynamics in an autonomous Boolean system *Boolean chaos*. Boolean chaos can possibly be applied to random number generation and chaotic radar (radio detection and ranging) because of the broad power spectrum and the fast time-scale dynamics. Furthermore, Boolean chaos in the experiment also gives fundamental insight into the dynamics generated by autonomous Boolean networks [21].

2.4 Conclusion

In this chapter, I have discussed previous work on Boolean networks. I have destinguished between synchronous and autonomous operation, which results in very different dynamics. In the next chapter, I discuss a new method of realizing experimental autonomous Boolean networks.

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