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Modeling intrinsic noise in random Boolean networks

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HIGHLIGHTS

- The statistical properties of noise in random Boolean networks (RBNs) are explored.
- The measured noise is intrinsic and results from the discrete dynamics of finite populations.
- A stochastic mean-field model is formulated to mimic the dynamics revealed by a RBN.
- The proposed idea in this paper can be applied to other discrete systems belonging to the category of RBNs.

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ABSTRACT

Noise has crucial effects on biological processes, chemical reactions, and various chaotic systems. This study explores the dynamical properties of noise in random Boolean networks, in which the stochasticity may cause significant deviations from deterministic descriptions. Such noise is intrinsic and results from the discrete dynamics of finite populations. By using methods from statistical physics and nonlinear dynamics, this study illustrates the dynamical characteristics of the inherent noise. Furthermore, a modified mean-field model is formulated to mimic the stochastic dynamics revealed by the discrete systems. The proposed idea of modeling intrinsic noise can be potentially applied to other discrete systems belonging to the category of random Boolean networks.

1. Introduction

Cellular automata (CA), which are typical spatial–temporal systems, often exhibit extremely rich dynamical behaviors [1]. Besides providing easy calculation procedures, CA models well explain microscopic mechanisms that result in macroscopic behaviors of systems. Although CAs are relatively simple sketches of real systems, they usually capture the major characteristics of the systems they mimic. So far, CA has provided simple but useful models for various physical systems [2], including magnetization in solids [3], reaction–diffusion processes [4], fluid dynamics for complex situations [5], growth phenomena [6], traffic flow models [7], and others.

The CAs are generally described in terms of two concepts: evolution rules and interaction configurations. For elementary cellular automata (ECA) proposed by Wolfram [1], the state of a cell is given by the Boolean function $c_n(t+1) = f_n[c_{n-1}(t), c_n(t), c_{n+1}(t)]$, where the subscript n is the site index and the updating rule f_n is identical for all cells. The rule clearly shows that the states of a cell and its two topological neighbors determine the future state of the cell itself. Because of the local coupling configuration, ECA is applicable for solving the problems of one-dimensional crystal growth and fluid flow. Regarding the systems with fewer spatial meanings, such as the spin model with random long-range interactions and cell differentiation processes [8], another category of CA, *i.e.*, Kauffman networks (KNs), was proposed to characterize

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the revealed dynamics. The updating rules f_n of KNs differ among cells, and neighboring cells are randomly chosen from networks. Such models have greatly contributed to biosciences, especially for solving problems in genome dynamics [9].

Besides the above two categories, an intermediate class of CA known as disorder cellular automata (DCA) or random Boolean networks (RBNs) was proposed by Andrecut and Ali in 2001 [10]. The updating functions of RBNs are identical in each cell throughout the system while the coupling configurations are random networks. In addition to its potential applications in biology, RBNs have proven effective for revealing chaotic behaviors in the formulated mean field (MF) model [10]. The MF model can be modified to explore more complex situations, such as heterogeneous networks (since the number of neighbors assigned to a cell is different to another in the network) [11,12], asynchronous updating networks [13], and RBNs with flipping processes in uncertain cells [14,15]. Coupled MF models further give us good predictions of the mutual synchronization emerged in microscopically coupled RBNs [16–19], which is useful for modeling self-organization phenomena in nature [20], especially in transitions from turbulence, through partial synchronization, to global synchronization [21,22]. Moreover, the applications to modeling signal transduction networks have been demonstrated [23].

In fact, the prediction results of MF models agree with the original RBNs when the number of interacting cells approaches *infinite*. Fig. 1 of Ref. [10] shows that discrepancies between the MF model and the original system occur when the number of cells within the system is finite or is very small. Similar discrepancies can be found in coupled RBNs consisting of finite cells [19]. From the perspective of statistics, the deviations from the deterministic descriptions result from inherent stochasticity and the discreteness of the dynamics in finite systems. Because the mechanism is the finite populations of systems, such deviations are therefore referred to as *intrinsic noise* [24]. Similar phenomena have been observed in biological systems, such as gene expression processes in living cells [25]. Moreover, in networks with more than two coupled RBNs, a finite system size may substantially increase the threshold of transition to the emerged synchronous state or may even desynchronize the system [19]. That is, the predictive accuracy of the deterministic MF model is no longer sufficient, and a refined model with an intrinsic noise term is required. Understanding the statistical properties of noise is therefore an important step in statistical modeling.

Although the intrinsic noise may alter the dynamics of RBNs, to our best knowledge a few papers published previously have studied this issue. In fact, the dynamical properties of the intrinsic noise in RBNs are completely unknown. This paper aim to solve this problem by formulating a RBN consisting of a finite number of cells. It is organized as follows. After reviewing the RBN in Section 2, intrinsic noise and its statistical characteristics are further defined. In Section 3, a modified MF model, the stochastic mean-field (SMF) model, is proposed based on statistical analysis. The artificial noise in the SMF model shows good agreement with the noise measured in an actual RBN. Finally, a brief conclusion and suggestions for further works are given.

2. Model description

Consider a disorder cellular automaton consisting of N cells. Each cell C_n within the RBN is presented in two mutually exclusive states, $c_n = 1$ and $c_n = 0$. Here C_n expresses the nth cell in the system whereas c_n expresses the *state* of the nth cell. The subscript $n = 1, 2, \ldots, N$ is the cell index. A cell C_n is randomly assigned a set of neighbors that dominate the trajectory of C_n based on a Boolean rule $\hat{\mathbf{R}}$. The number of neighbors that belong to C_n is labeled by k, which is also known as the *degree* of the network. During each iteration, the neighbors of C_n are re-determined randomly at each step, but the value of k stays invariant. The operator $\hat{\mathbf{R}}$ stands for the evolution rule of RBNs. Here a totalistic rule, the generalized ECA rule 126 is used because of its potential implication in biological evolution and its rich dynamics (especially chaos) [10,11]. The rule is, if the state of C_n and all *neighbors* are 1 or 0, then $c_n = 0$ after the operation of $\hat{\mathbf{R}}$; otherwise, $c_n = 1$. Other totalistic rules such as rule 22 [12] may reveal similar biological implications and chaotic motions. The authors will present an analysis of intrinsic noises revealed by other rules in a future study.

The density of a RBN, *i.e.*, the probability of finding a cell in state 1, can be formulated by a MF model. On the basis of rule 126, the MF model is given by Ref. [10]

$$P(t+1) = f_{\mathrm{MF}}(P(t)) = 1 - P(t)^{k+1} - [1 - P(t)]^{k+1}, \tag{1}$$

where t is the time index, k is the number of neighbors, and $P(t)$ is the density that satisfies $0 \le P(t) \le 1$ for all t. The MF model adequately approximates the density evolution of the realistic RBN *if and only if* the number of cells $N \to \infty$. When N is finite, the deterministic description presented in Eq. (1) is no longer appropriate [19]. Since the deviations between the densities of the MF model and the realistic network results from the discreteness of the RBN dynamics in finite system, the deviations are referred to as *intrinsic noise* and the noise strength is determined by N. In order to avoid confusion, this paper defines the density determined by the realistic RBN as $P_R(t) = \Sigma_{n=1}^{N} c_n(t)/N$ while the density predicted by the MF model is labeled as $P_{\mathrm{MF}}(t)$.

The RBN intrinsic noise can then be defined as follows. Suppose at time t the density of a realistic RBN is given by $P_R(t)$. After the operation of $\hat{\mathbf{R}}$, the density at $t+1$ evolves to $P_R(t+1) = \Sigma_{n=1}^{N} c_n(t+1)/N$ based on rule 126. Alternatively, the density can also be evaluated by the MF model, $P_{\mathrm{MF}}(t+1) = f_{\mathrm{MF}}(P_R(t))$. The measured intrinsic noise, which is the deviation of $P_R(t+1)$ from $P_{\mathrm{MF}}(t+1)$, is formulated as

$$e(t+1) = P_R(t+1) - P_{\mathrm{MF}}(t+1), \tag{2}$$