Dynamic behaviors in directed networks

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Motivated by the abundance of directed synaptic couplings in a real biological neuronal network, we investigate the synchronization behavior of the Hodgkin-Huxley model in a directed network. We start from the standard model of the Watts-Strogatz undirected network and then change undirected edges to directed arcs with a given probability, still preserving the connectivity of the network. A generalized clustering coefficient for directed networks is defined and used to investigate the interplay between the synchronization behavior and underlying structural properties of directed networks. We observe that the directedness of complex networks plays an important role in emerging dynamical behaviors, which is also confirmed by a numerical study of the sociological game theoretic voter model on directed networks.

Research of complex systems which brings complex networks into focus has been an intensive and successful area in physics and other disciplines [1,2]. Within the complex network research community, dynamic behaviors in complex networks have been drawn much attention. Among a variety of collective dynamic behaviors, synchronization is the one of the most popular research topics [3–5], and it has been shown that the connection topology of complex networks greatly influences the degree of synchronization [2,6]. Recently, the question of how to increase the synchronizability via weighted and asymmetric couplings has been pursued intensively [7]. Especially, it has been shown that the synchronization is enhanced significantly when the couplings from old to young vertices are more abundant than from young to old, indicating the importance of the directedness of complex networks [8]. As a good and real example of synchronization, the synchronous firing of action potential in neuronal networks has been studied [9]. In Ref. [10], the Hodgkin-Huxley (HH) model [11] has been simulated on the Watts-Strogatz network [12], which has revealed that the underlying small-world network structure enhances synchronization substantially. Different from real biological neuronal networks, where synaptic couplings connecting two neurons are naturally directed, it has been assumed that the synaptic couplings are undirected. In contrast, the neuronal network of the nematode *Caenorhabditis elegans* (*C. elegans*) has been analyzed and 90% of synaptic couplings have been shown to be directed [13]. In other words, only 10% of synaptic couplings are bidirectional.

In the present paper, we fully consider the directions of edges and investigate in a systematic way how the directedness of complex networks changes collective dynamical behaviors. Both the HH model in biology and the sociological voter model are studied on directed model networks, and it is unanimously found that as the more bidirectional edges are changed to unidirectional ones the system as a whole exhibits a worse ordering behavior. We believe that the conclusion should hold in a variety of different natural and social systems since the sparser bidirectional edges are the less efficient the information flow becomes.

The directed small-world network in the present study is constructed as follows: (1) The Watts-Strogatz undirected network is first built in the same way as in Ref. [12]. In detail, starting from the locally connected network of one-dimensional lattice with the connection range 15 corresponding to the average degree $\langle K \rangle = 30$, each edge is picked and then randomly rewired with the probability P to other randomly chosen vertex. The size N of the network is defined as the total number of vertices and we use $N=400$ below. (2) Each edge built above has both directions, one incoming and the other outgoing, and thus we substitute each undirected edge as two arcs with opposite directions (we in this work call a directed edge as an arc). Each pair of arcs is visited one by one, and then with the probability α, the direction of randomly chosen one arc in the given pair is reversed. It should be noted that the network resulting from the above procedure is a directed network and double links connecting the same two vertices are also allowed. We believe that double edges exist not only in a biological neuronal network, where two neurons can have two synaptic couplings, but also in a sociological network, where two individuals can have two different ways of information transfer. In the viewpoint of dynamics in this work, the two arcs connecting the same two vertices are equivalent to one arc with double weights. Consequently, the resulting network from the above procedure is a directed network with double arcs allowed (or double weights allowed), characterized by two parameters P and α. When $\alpha=0$, the network is identical to the WS undirected network, whereas for the other limiting case of $\alpha=1$, all edges in the network become directed. By changing the parameter α from zero to unity, one can systematically change the density of directed edges, while still preserving the average degree $\langle K \rangle$ (both the number of arcs per vertex and the number of directly attached vertices per vertex are conserved). It should be noted that if directions of arcs are not taken into account the directed network at any α has exactly the same structure as the undirected one.

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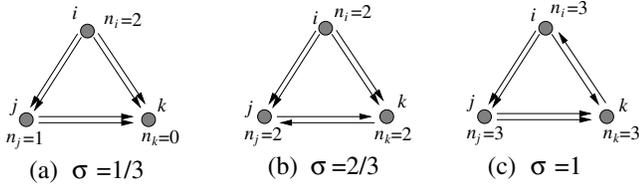
FIG. 1. Definition of the influence σ of a triad. We define n_i for the vertex i as the number of vertices which can get a message from i. A path connecting itself [e.g., $i \rightarrow j \rightarrow k \rightarrow i$ in (c)] is also counted. In (a), i can send its message both to j and k and we assign the number $n_i = 2$ for i; $n_j = 1$, $n_k = 0$ are similarly assigned. In (b), $n_i = n_j = n_k = 2$, since, e.g., j can send a message to k and then can get it back from k. In (c), $n_i = n_j = n_k = 3$ since everyone gets a message from everyone. The influence σ for a given triad (i, j, k) is defined as $\sigma = (n_i + n_j + n_k)/9$.

We first investigate structural properties of our directed network and measure the characteristic path length and the clustering coefficient. The former, denoted as l and defined by $l^{-1} \equiv \sum_{i \neq j} d_{ij}^{-1} / N(N-1)$ with the shortest path length d_{ij} connecting vertices i and j, is computed in the same way as for an undirected network [14]. The shortest paths should be computed with the direction taken into account, and accordingly, $d_{ij} \neq d_{ji}$ for a directed network.

The clustering coefficient for an *undirected* network has usually been defined as [12]

$$C^{(0)} \equiv \frac{1}{N} \sum_i C_i^{(0)},$$

$$C_i^{(0)} \equiv \frac{2E_i}{k_i(k_i - 1)}, \qquad (1)$$

where E_i is the number of edges in the set of neighbors of the vertex i. If all neighbor vertices of i (with the degree k_i) are connected to each other, $E_i = k_i(k_i - 1)/2$ and thus $C_i^{(0)} = 1$.

For a directed network, however, the above definition of the clustering coefficient needs to be changed. In this paper, a quantity σ_a (we call it the influence) is defined for the triad a composed of three vertices $a = (i, j, k)$ as follows: (1) Count the number n_i of vertices (including itself) who can get a message from i. For example, in Fig. 1(a), i can send its message to j and k, and thus we assign $n_i = 2$. In the same way, $n_j = 1$ and $n_k = 0$ are obtained in Fig. 1(a). On the other hand, in Fig. 1(b), $n_j = 2$ is assigned since j can send a message to k and then get it back from k. In Fig. 1(c), $n_i = n_j = n_k = 3$ since a message from anyone will be eventually delivered to everyone. (2) Since $n_i \leq 3$, we normalize to obtain $\sigma_{a=(i,j,k)} \equiv (n_i + n_j + n_k)/9$ so that $0 \leq \sigma_{a=(i,j,k)} \leq 1$. In Fig. 1, (a) $\sigma = (2+1+0)/9 = 1/3$, (b) $\sigma = (2+2+2)/9 = 2/3$, and (c) $\sigma = (3+3+3)/9 = 1$, are found, respectively. Although the examples of triad connections in Fig. 1 have an identical number of arcs (six arcs), it is clear that the standard definition of the clustering coefficient cannot capture the difference. We define the clustering coefficient $C^{(d)}$ for a *directed* network as
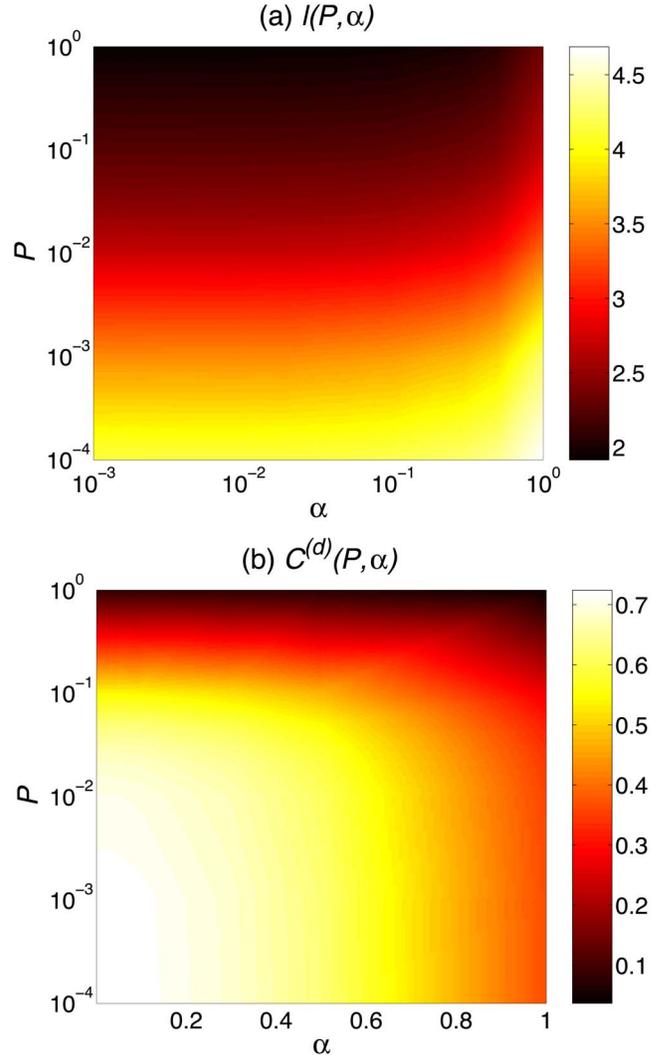
FIG. 2. (Color online) Density plots for (a) the characteristic path length l and (b) the clustering coefficient $C^{(d)}$ in the plane of the rewiring probability P and the probability α of making directed arcs. Note that P is in a log scale while α is not in (b). As P is increased, both l and $C^{(d)}$ are found to decrease consistent with Ref. [12]. When $P = 10^{-2} - 10^{-1}$, the network has short path length together with large degree of clustering, manifesting the small-world behavior. As more edges become directed arcs, i.e., as α is increased, l becomes larger while $C^{(d)}$ becomes smaller, weakening the small-world behavior. The network of the size $N = 400$ at the average degree $\langle K \rangle = 30$ has been used.

$$C^{(d)} \equiv \frac{1}{N} \sum_i C_i^{(d)},$$

$$C_i^{(d)} \equiv \left(\frac{1}{E_i} \sum_{a=1}^{E_i} \sigma_a \right) C_i^{(0)} = \frac{2}{k_i(k_i - 1)} \sum_{a=1}^{E_i} \sigma_a, \qquad (2)$$

where $a = 1, 2, \ldots, E_i$ is the index for triads connected to the vertex i, and σ_a is the influence defined above and shown in Fig. 1. Since $0 \leq \sigma_a \leq 1$, we get $\sum_a \sigma_a \leq E_i$ and consequently $C_i^{(d)} \leq C_i^{(0)}$ and $C^{(d)} \leq C^{(0)}$.

Figure 2 displays (a) $l(P, \alpha)$ and $C^{(d)}(P, \alpha)$ as density

plots. At a fixed value of α, the increase of P results in smaller l and $C^{(d)}$, consistent with the result for the undirected network in Ref. [12] corresponding to $\alpha=0$. The intermediate region of P has short characteristic path length but with a relatively high degree of clustering, manifesting the so-called small-world behavior [12]. In contrast, as the network has more directed arcs (i.e., as α is increased), the small-world behavior becomes weaker: The path length is increased and the clustering coefficient becomes smaller. The structural changes related with the changing bidirectional edges to unidirectional arcs are naturally expected to be reflected in dynamic properties of the system on networks. As more edges are changed to directed arcs, the path connecting two vertices becomes longer, and the spread of information within local neighbors becomes less efficient. We believe that our generalization of the clustering coefficient to capture the difference between directed and undirected networks can be very useful in similar studies. In Ref. [15], a vector called the triad census has been proposed to measure the frequencies of 16 isomorphism classes of all possible directed coupling structures of three vertices. Among them seven correspond to complete 3-graphs like in Fig. 1. Although it should be possible to use the concept of the triad census [15] to characterize the clustering property of directed networks, we believe that our suggestion of the clustering coefficient is practically much more useful and convenient.

In order to study the effect of directedness of networks on dynamic cooperative behaviors in detail, we first study the Hodgkin-Huxley (HH) model in neuroscience on the directed network structure built as described above. The HH model is the one of the most representative models describing dynamics of a neuronal system. Originally, based on the result of physiological experiments of a neural system of a squid, the HH model equations have been proposed to describe the membrane action potential [11,16,17]. In the present work, we use the HH coupled differential equations in Ref. [10] but with parameters obtained from physiological experiments of neurons in the part CA3 in hippocampus which plays an important role in learning and memory [18]. In detail, the membrane capacitance per unit area $C_m=1.0\ \mu\text{F/cm}^2$ and the external current density $I^e=0.9\ \mu\text{A/cm}^2$ are used, and maximum conductances for the leakage channel, the sodium, and the potassium ionic channels, are $g_L=0.15\ \Omega^{-1}/\text{cm}^2$, $g_{\text{Na}}=50.0\ \Omega^{-1}/\text{cm}^2$, $g_{\text{K}}=10.0\ \Omega^{-1}/\text{cm}^2$, respectively (see Ref. [10] for HH coupled equations). The synaptic current between presynaptic and postsynaptic neurons is treated in the same way as in Ref. [10]. In this work, a direct current is injected into $40(=N/10)$ contiguous neurons between the onset (100 ms) and the offset (1000 ms) times, and the sixth-order Runge-Kutta method with the time step $\Delta t=0.01$ ms is used to integrate HH equations. In order to get better statistics, 500 independent runs are performed and then averaged over different network realizations.

We below use the synchronization order parameter in Refs. [3,5] to study the interplay between the dynamic synchronization behavior and the underlying directed network structure. We denote $t_{i,n}$ as the nth firing time of the neuron i, and define the corresponding phase variable $\theta_i(t)$ as
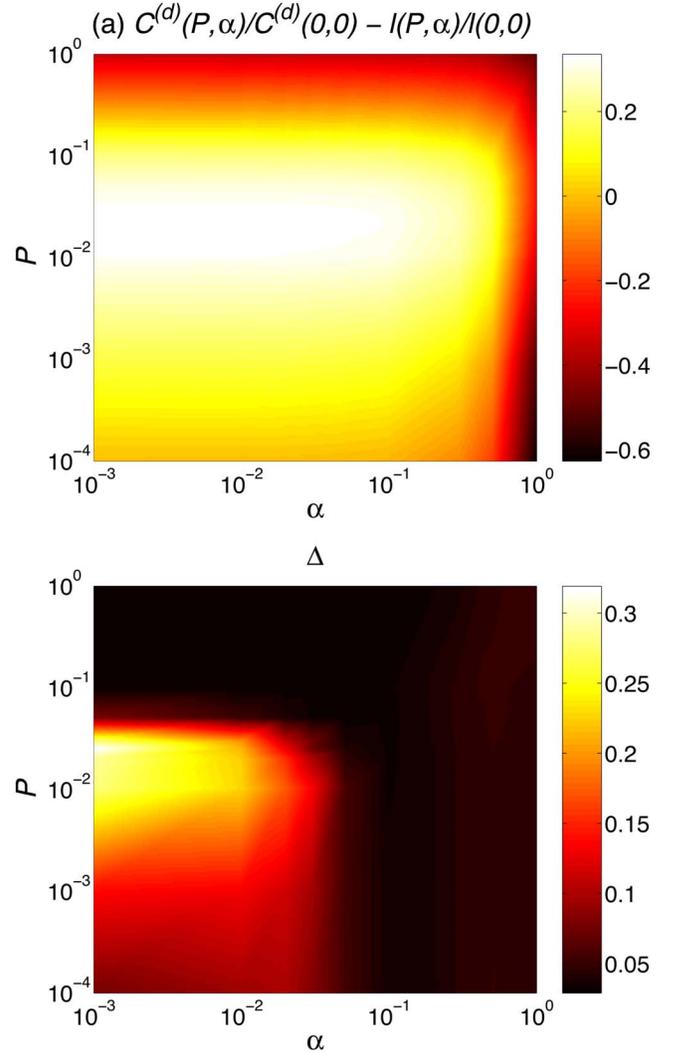
FIG. 3. (Color online) Density plots for (a) the small-world property measured by $C^{(d)}(P,\alpha)/C^{(d)}(0,0)-l(P,\alpha)/l(0,0)$ and (b) the synchronization order parameter $\Delta(P,\alpha)$ computed for the Hodgkin-Huxley model in the α-P parameter space. As either α of P becomes larger the network loses both the structural small-world property and the dynamical synchronizability.

$$\theta_i(t) \equiv 2\pi\frac{t-t_{i,n-1}}{t_{i,n}-t_{i,n-1}}, \qquad (3)$$

via the simplification that $\theta(t)$ $(t_{i,n-1}\leq t\leq t_{i,n})$ increases linearly from 0 to 2π between the two successive firings at $t_{i,n-1}$ and $t_{i,n}$. The synchronization order parameter is then defined as

$$\Delta \equiv \frac{1}{N}\left\langle\sum_{i=1}^{N_{\text{fire}}}e^{i\theta_i(t)}\right\rangle, \qquad (4)$$

where $\langle\cdots\rangle$ represents the time average after achieving a steady state, and N_{fire} is the number of neurons which fired at least twice [otherwise $\theta(t)$ is not defined]. For convenience, we have not included winding number term in Eq. (3); it does not change the value of Δ.

In Fig. 3, we compare (a) the structural small-world prop-

erty and (b) the dynamic synchronization behavior. In order to measure the former in Fig. 3(a), we normalize the clustering coefficient and the characteristic path length and then compute the difference, i.e., $\beta \equiv C^{(d)}(P,\alpha)/C^{(d)}(0,0) - l(P,\alpha)/l(0,0)$. If β has a sufficiently large value, the network has a relatively large clustering coefficient and a relatively short path length, corresponding to the small-world region in Ref. [12]. It is clearly displayed in Fig. 3(a), that as either P or α is increased, the network begins to exhibit the small-world property, which is destroyed eventually when P or α is increased further. The structural importance of the directedness of networks is easily seen here: As more and more edges are changed to directed arcs, the network loses the small-world property. In Fig. 3(b), we show the synchronization order parameter Δ in Eq. (4) in the α-P plane. Although the region with large Δ values is much smaller than the region with the small-world behavior in Fig. 3(a), it is unambiguously shown that the existence of directed arcs prohibits the system from being better synchronized. We believe that if one neglects the directedness of networks in the study of structural and dynamic properties of networks, the results should be taken cautiously. Especially, for a study of neuronal networks, in which much more synaptic couplings are directed than undirected, the conclusion reached by using an undirected network may change significantly if one takes the direction of synaptic couplings into full account.

We next study a sociological game theoretic model called the voter model [19], defined on a directed network, to check the generality of our conclusion drawn above for a biological system. In the voter model, the ith player can have two different opinions $\sigma_i = \pm 1$, and the time evolution of $\sigma_i(t)$ is described as follows: (1) Pick one voter (call her i) in the network randomly. (2) Pick another voter (call her j) randomly among i's incoming neighbors. (3) The voter i changes her opinion to the j's one, i.e., $\sigma_i(t+1) = \sigma_j(t)$. The directedness of a given network enters through the step (2) above: Each voter is influenced only by her neighbor voters connected by *incoming* arcs. We use the random initial condition to start with, and as time proceeds, the system approaches one of two absorbing states characterized by a perfect ordering, i.e., $\sigma_i = 1$ or $\sigma_i = -1$ for all i. In previous studies of voter models, the active bond is defined as the one connecting two voters with different opinions, and the key quantity to measure is the fraction ρ of active bonds given by

$$\rho = \frac{\displaystyle\sum_{i=1}^{N} \sum_{j \in \Lambda_i^{(\text{in})}} (1 - \sigma_i \sigma_j)/2}{\displaystyle\sum_{i=1}^{N} K_i^{(\text{in})}}, \tag{5}$$

where $\Lambda_i^{(\text{in})}$ is the set of incoming neighbors of i, and the incoming degree $K_i^{(\text{in})} \equiv |\Lambda_i^{(\text{in})}|$. The active bond has different signs of the opinion $\sigma_i \sigma_j = -1$, and consequently $(1 - \sigma_i \sigma_j)/2$ takes the value either 1 or 0, depending on the activity of the bond.
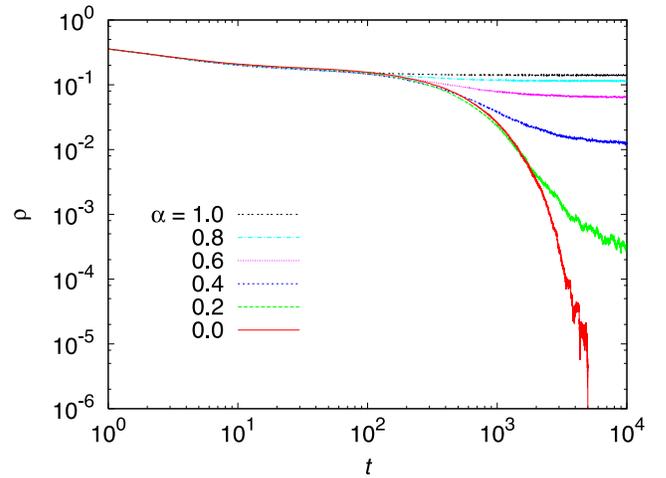
FIG. 4. (Color online) Fraction $\rho(t)$ of active bonds in the voter model on directed networks as a function of time t. From bottom to top, curves correspond to $\alpha = 0.0$, 0.2, 0.4, 0.6, 0.8, and 1.0. As the network becomes more directed, i.e., as α is increased, the ordering towards the absorbing state ($\sigma_i = 1$ or -1 for all i) takes longer time, and the complete ordering becomes impossible for a sufficiently large α even at $t \to \infty$. Directed networks of the size $N = 400$ with $\langle K \rangle = 30$ and the rewiring probability $P = 0.1$ are used as an underlying interaction structure of the voter model.

In Fig. 4, the time evolution of ρ is shown for various values of α at the rewiring probability $P = 0.1$ for the directed network of the size $N = 400$ with the average degree $\langle K \rangle = 30$. It is displayed that as α is increased the convergence of opinions, i.e., $\rho \to 0$, takes longer time, and eventually becomes impossible for large enough values of α. This observation, in parallel to the above finding of the weaker synchronizability of the HH model on directed networks, implies that the existence of directed arcs inhibits an efficient flow of information, making global collective behaviors less plausible to occur.

In conclusion, we have studied dynamic behaviors of the biological neuron model and the sociological voter model on directed networks, built from the standard network model of Watts and Strogatz by changing undirected edges to directed arcs with the probability α. In the process of making directed networks numbers of connected vertices and arcs are not changed, and the characteristic path length does not change significantly in a broad range of α; this suggests that the connectivity is not altered much from the undirected counterpart. Unanimously found is that as the network becomes more directed by the increment of α, a global emergence of collective behaviors (the synchronization in the former and the opinion convergence in the latter models) becomes harder to develop. An extended definition of the clustering coefficient for directed networks has also been suggested, and the dynamic behaviors have been studied in relation with the network structures, captured by the characteristic path length and the clustering coefficient. However, we note that the region of the structural small-world behavior in Fig. 3(a) and the region of the enhanced synchronizability in Fig. 3(b) do not overlap completely. The origin of this discrepancy is

not clear at present and needs further study in the future. We believe that our conclusion of decreased synchronizability of directed networks is very general beyond the model systems studied in this work and that the neglect of the directions of edges in network studies needs to be done very carefully.

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