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Power-law spectrum and small-world structure emerge from coupled evolution of neuronal activity and synaptic dynamics

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Abstract. A co-evolutionary neuronal network model based on previous ones is proposed, and both functional and structural properties are numerically calculated. Recent experiments have revealed power-law behavior in electrocorticogram (ECoG) spectrum related with synaptic plasticity and reorganization. In the present neuronal network model, the network starts its evolution from the initial configuration of random network which is the least biased and without special structure, and the interaction rules among neurons are modified from both models by Bornholdt's and Arcangelis' groups to simulate the process of synaptic development and maturation. The system exhibits dynamic small-world structure which is the result of evolution instead of the assumption beforehand. Meanwhile, the power spectrum of electrical signals reproduces the power-law behavior with the exponent 2.0 just as what is experimentally measured in ECoG spectrum. Moreover, the power spectrum of the average degree per neuron over time also exhibits power-law behavior, with the exponent 2.0 again over more than 5 orders of magnitude. Different from previous results, our network exhibits assortative degree-degree correlation which is expected to be checked by experiments.

1. Introduction

In living organisms, information processing is generally performed by large networks of interacting neurons with huge complexity[1]. However, the level of the complexity exceeds what can be coded by the observed number of genes. So, evolving principles is quite important in network construction. Self-organization and adaptation processes are thought to exist throughout the lifetime of a network, with learning as its major function. It has been reported that, self-organized criticality (SOC) universally exists in natural phenomena [2–9]including neural networks [1, 10–24]. In most studies, the neural network in the brain is supposed to be a small-world (SW) one [25, 26]. Many neural network models have been applied to or based on it. In this paper, we argue that SOC and SW should emerge simultaneously in the same process since no evidence shows that their appearance should be one after another. And we propose a co-evolutionary model to support this opinion.

Based on self-organization of degree of connectivity, Bornholdt et al. [27] have proposed a neural network model. In their model, the network topology changes slowly according to a local

rewiring rule motivated by Hebbian [28], activity-dependent synaptic development, i.e., neighbor neurons whose activities are correlated would develop a new connection, and uncorrelated neighbors tend to disconnect. It is a co-evolutionary process, as the node states and their correlations update simultaneously. As a result, robust self-organization of the network towards the order-disorder transition occurs, which is independent of initial conditions, robust against thermal noises, and dose not require fine tuning of parameters.

Recently, by taking into account the brain plasticity, Arcangelis, Perrone-Capano, and Herrmann (APH) [29] proposed another neural network model. This model is based on an electrical network on a square lattice with the features of threshold firing and activity-dependent synapse strengths. The system exhibits an avalanche activity in a power-law distribution. The power spectrum of the electrical signal could reproduce the $1/f$ power-law behavior observed in experimental EEG spectra.

These two models, Bornholdt and APH ones, are distinct from each other, but they both exhibit the feature of SOC. And they are both consistent with Bak's [30] guess that the brain should be critical, not subcritical or supercritical. Actually, SOC is an important discovery in statistical physics[30], and has been found in many complex systems. For instance, earthquakes, forest fires and etc.. Under general conditions, these dynamical systems, consisting of many interacting elements, can organize themselves into a critical state in which power-law distribution of avalanche sizes and $1/f$ noise in power spectrum in time-series appear simulaneously, and the dynamical response of the system to external environment gets its maximal level in such non-equilibrium steady states. In particular, these features emerge without any significant tuning of the system from the outside, that is to say, variable parameters in the model could be changed widely without affecting the emergence of critical behavior.

All the typical features of SOC have been observed in the Bornholdt and APH models. Like many other models, the initial topologies of their neural networks are supposed to be biased ones, e.g., square lattice or SW. However, there is no evidence so far supporting their assumptions. Here, we ague that, neural network should evolve from a random network, which has less artificial and biased rules. Structural and functional features, observed in experiment, should emerge simultaneously during the same single co-evolutionary process.

In this paper, we propose a co-evolutionary model starting its evolution from a random network, developed from Bornholdt and APH models. By analyzing its structural properties , we found that, two power-law behaviors emerge in the co-evolutionary process, i.e., power spectra of the electrical signals and average degree per node over time. In the following, we will first introduce some variables and detailed mechanisms appeared in Bornholdt and APH models. Then, we propose our modified model. At last, numerical results will be discussed and compared with experimental ones.

2. Model

2.1. Bornholdt model

In Bornholdt model, links between nodes is represented by W_{ij}, which is randomly drawn from a uniform distribution $W_{ij} \in [-1, 1]$. The couplings between neuron is and js are asymmetric, i.e., $W_{ij} \neq W_{ji}$. The asymmetry has its fundamental significance. First, the transfer of signals though synapse is unidirectional. Second, the neural system must be robust against noises and meanwhile must be sensitive to inputs [31]. In previous studies, a winner-less competition (WLC) principle [32] was proposed. According to this principle, the non-symmetric links could be used to deal with the contradiction of signals and noises. The key point is that, signals and noises have different features, and they influence the dynamics of the system in different ways [31].

For each neuron in the network, it has its own state $\sigma_i = \pm 1$, which will update according to a stochastic Little dynamics [27] based on inputs received from its neighbor neurons in last

time step:

$$\Pr ob[\sigma_i(t+1) = +1] = g_\beta(f_i(t))$$
$$\Pr ob[\sigma_i(t+1) = -1] = 1 - g_\beta(f_i(t)), \tag{1}$$

$$g_\beta(f_i(t)) = \frac{1}{1 + e^{-2\beta f_i(t)}}, \tag{2}$$

$$f_i(t) = \sum_{j=1, j \neq ij}^{N} W_{ij}\sigma_j(t) + \theta_i, \tag{3}$$

where β is the inverse temperature and θ_i is the threshold. Here $\theta_i = -0.1 + \gamma$ and γ is a small random noise term from a Gaussian distribution with the width of $\varepsilon = 0.1$ and the mean of $\mu = 0$. These terms are introduced from the slow fluctuations observed in biological neural systems [27, 33].

In Bornholdt model, the quantity $C_{ij}(\tau)$ is defined as the average correlation of a pair (i,j) of neurons over a time interval τ:

$$C_{ij}(\tau) = \frac{1}{\tau + 1} \sum_{t=t_0}^{t_0+\tau} \sigma_i(t)\sigma_j(t). \tag{4}$$

This could be used as an order parameter to guide the topology rewiring. If the activities of two neighboring neurons are on average highly (anti)correlated, $C_{ij}(\tau)$ will be large and the two neurons will set up a link. Otherwise, the link will be removed. Obviously, it is a local rewiring rule. The updates of node states couple with their correlations, and this leads to a co-evolutionary process between node dynamics and network connections. As pointed out by Bak et al. [30], such kind of simple local interactions could spontaneously induce complexity.

2.2. APH model
Arcangelis et al. [29] proposed a neuronal firing model. The neurons are simply imposed on a square lattice. Therefore, there is a neuron on each site and bonds on the lattice acts as couplings between neurons. Each neuron (node) has its own potential V_j at site j, and each synapse (link) has its own conductance g_{ij}. When the potential is above a threshold, i.e., $V_i > V_{\max}$, the neuron fires. It will generate an action potential and distribute its charges to its connected neighbors according to (for the notations, j is the nearest neighbor of i, and k belongs to j who has the potential of $V_j < V_i$)

$$v_j(t+1) = v_j(t) + v_i(t)\frac{I_{ij}(t)}{\sum_k I_{ik}(t)}, \tag{5}$$

with

$$I_{ij} = (V_i - V_j) \cdot g_{ij}. \tag{6}$$

Once a neuron fires, it will go into a refractory period for a time step, and can not receive charges from other firing neurons until getting out of this period. This could ensure that action potential would not reverberate in the network. The electrical activity is represented by the total current flowing in the network. Supposing the potential of neuron i is equal to or large than v_{max} at time t, it fires follows Eq. (5), then the conductance of links with non-zero current is changes as follows:

$$g_{ij}(t+1) = g_{ij}(t) + \delta g_{ij}(t) \tag{7}$$

with $\delta g_{ij}(t) = k\alpha i_{ij}(t)$ (k, unit constant; α, a tunning parameter). Once the avalanche of firing is over, the bond with non-zero conductance is reduced by $\Delta g = \sum_{ij} \delta g_{ij}(t)/N_b$, N_b is the number of bound with $g \neq 0$. This corresponds to a pruning process of links which mimics the brain development.

2.3. Our co-evolutionary model
It is noticeable that the coupling strength W_{ij} in Bornholdt model plays a similar role as the conductance g_{ij} in APH model in the network evolution process. Here, these two models are combined together by replacing g_{ij} in APH model with the absolute value of W_{ij} in Bornholdt one. Based on the combination of the firing mechanism in APH model and the network evolution process from Bornholdt one, we start from a random network.

The random network we start with has a link probability p, i.e., each pair of neurons can be connected with probability p. The average degree of the network, K, is defined as the average number of nonzero degree of each node (include both incoming and outgoing links). This means our initial network has an average degree $K = pN$, where N is the total number of neuron in the system. Then, the whole model is presented as follows,

(1) Start with a random network with link probability p and a random initial system state with the vector $\vec{\sigma}(0) = (\sigma_1(0), ..., \sigma_N(0))$. The neuron potentials are uniformly distributed between $V_0 - 1$ and V_0.

(2) For each neuron i, choose a random threshold $\theta_i = -0.1 + \gamma$, where γ is a small random noise term from a Gaussian distribution of width $\varepsilon = 0.1$ and mean $\mu = 0$.

(3) Starting from the initial state, calculate the new system state applying Eqs. (1-3) using parallel update. Iterate this for τ time steps. Here we set the inverse temperature to be $\beta = 25$ [27].

(4) For each neuron i, randomly choose neuron j from its neighbors and the neighbors' neighbors (the first and second nearest neighbors). Determine the average correlation $C_{ij}(\tau)$ over the τ time steps according to Eq. (4).

(5) If $C_{ij}(\tau)$ is larger than a given threshold α, node i receives a new link W_{ij} from j with a weight chosen randomly from the interval $W_{ij} \in [-1, 1]$. Note that, weights are asymmetric (here we make the absolute value of W_{ij} as the conductance from i to j. Positive and negative represent excitation and inhibition, respectively). If $C_{ij}(\tau) < \alpha$, the weight of the link W_{ij} is set to be zero.

(6) For each neuron i, if $V_j < V_i$ (where j is the neighbor of i) and they are both out of refractory periodthen i can discharge to j according to Eqs. (5-6). After that, i goes into the refractory period and $V_i = 0$.

(7) Go to step 2 and iterate, using the current state of the network as a new initial state.

To summarize, based on Bornholdt and APH model, we developed a co-evolutionary neural network model. As mentioned above, in our model, the small-world topology should be the result of co-evolution, not a given assumption. We adopt the random network as the initial state, since this kind of network has less biased rules and has no deterministic regular pattern. With less biased and artificial factors, the system could exhibit the effect of co-evolution and SOC more naturally. In detail, nodes' states and interactions should evolve coupled with each other. The coupled evolution process should make a dynamically stable structure and functional properties emerge simultaneously. In addition, this process should be self-organized.
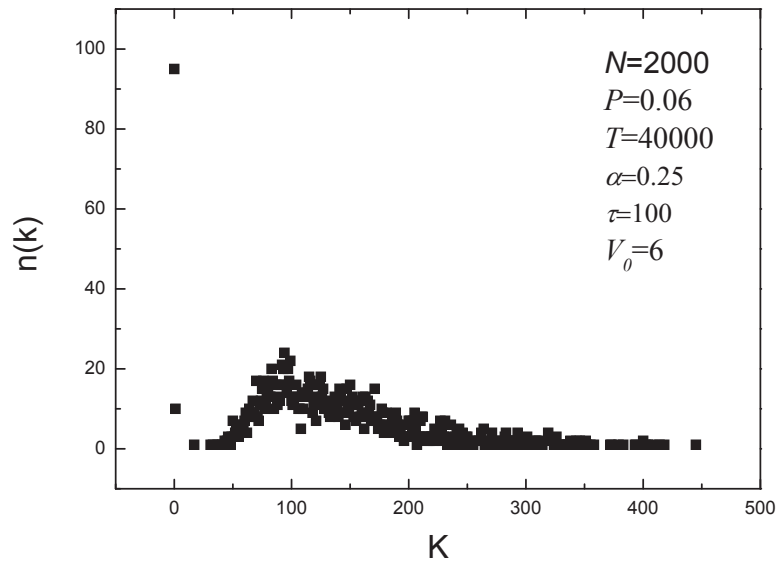
Figure 1. Distribution of degree K for a system with 2000 nodes evolved for $T = 40000$ time steps. The degree of a node is defined as the number of its neighbors, and in this paper it includes both incoming and outgoing links. The initial state is a random network with probability $p = 0.06$. Other parameters: $V_0 = 6$, averaging time window $\tau = 100$, correlation threshold $\alpha = 0.25$.

3. Results and Discussions

3.1. Structural properties produced by our co-evolutionary model

We simulate our model on a random network with $N = 2000$ (number of nodes), $\alpha = 0.25$ (correlation threshold), $\tau = 100$, $V_0 = 6$ and $p = 0.06$. After 40000 time steps, there are 95 neurons being separated from the network. They become isolated nodes ($K = 0$). The distribution of degree, for the final state, is shown in Fig. 1. It is reasonable that a few nodes become isolated, or in other words, dead. From the neurological point of view, during the brain's evolving, there are a number of reasons that could lead to the death of neurons, such as termed apoptosis, environmental toxins, genetic diseases etc. [34–36].

Ignoring those isolated nodes, the distribution of degree, as we can see, is similar to Poisson distribution. One thing should be noted that the degree of a node includes both the incoming and outgoing links, and this rule is also applied to the calculations of clustering coefficient and distribution of $K_{nn}(K)$. Figure 2 presents the clustering coefficient of each node (except the nodes with $K = 0$). The clustering coefficient of a node is defined as the ratio of the number of connections in the neighborhood of this node to the number of connections when the neighbors are fully connected with each other. From this value, we could see whether the neighbor of a node tends to connect with other neighbors of the same node. As shown in Fig. 2, most clustering coefficients range in (0.10, 0.35). Their average is 0.19, which is relatively high for a network. From the distribution of the degree and the clustering coefficient, we can conclude that, the final state is a small-world network.

To understand the network structure deeply, we calculate the distribution of $K_{nn}(K)$ (shown in Figure 3), which is the average degree of the neighbors of the nodes whose degree is equal to K. The whole curve exhibits an upward trend, indicating that the nodes with small degree tend to connect with the nodes also with small degree, and large ones to large ones. So, the network exhibits positive degree-degree correlation. This result can not be proved by the current
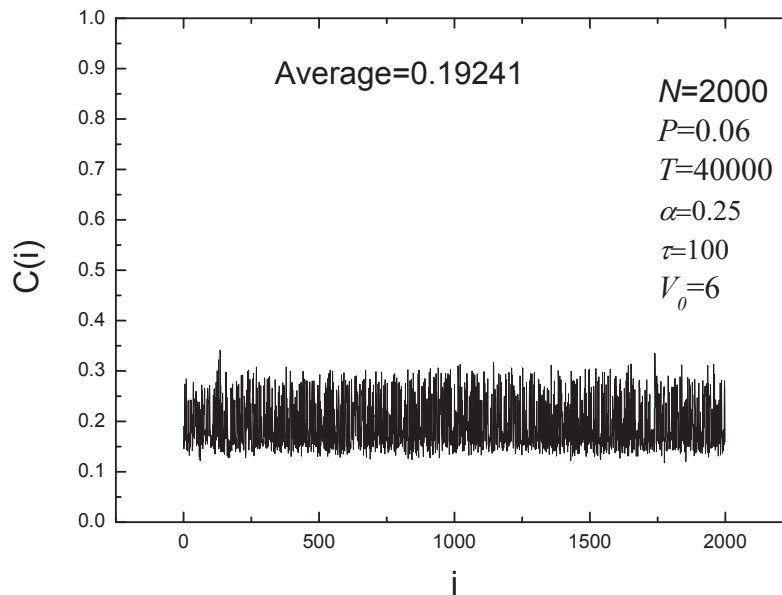
Figure 2. Clustering coefficient $C(i)$ of each node ($i = 1 \sim 2000$, except the nodes with $K_i = 0$). The clustering coefficient of a node is defined as the ratio of the number of connections in the neighborhood of this node to the number of connections when the neighbors are fully connected with each other. The average value of the clustering coefficients is 0.19241.

experiment, but a recent experimental breakthrough shows the possibility, i.e., using brainbow technology, developed by Jean Livet et al [37], one could visualize synaptic circuits by genetically labeling neurons with multiple and distinct colors. In the level of anatomical connections between cortical areas, degree-degree correlation was observed in the latest experimental results [38].

3.2. Functional properties of the network
Figure 4 shows the total current as a function of time, which is the sum of current every time step flowing in the system. At the beginning of evolution, the current is very large, but unstable. Then, it declines rapidly, and after 3300 time steps the current reaches a minimum. After that, it slightly increases, and then oscillates stably. Figure 5 shows the details of the current signal in a short period. Like the ECoG in experiment [39], they vary in the same way. According to the time interval of the experimental ECoG signal [39], every time step in our model stands for 4 ms. If we make it as the sampling period, the corresponding sampling frequency will be 250 Hz. Then we can get the power spectrum (the square of the amplitude of the Fourier transform as a function of frequency) of the current with this sampling frequency (log-log scale for horizontal and vertical coordinates). Surprisingly, it exhibits power-law behavior over more than 5 orders of magnitude. On the left of the figure, the curve shows flat head, and on the right, it show peaks on the tail. These features agree quite well with the experimental results [39]. In particular, the slope (-2.01789) of the curve (Fig. 6), which is the exponent of the function, matches the experimental slopes ranging between -2.27 and -1.54 and with their mean as -1.97[39]. They both exhibit power-law, a feature of SOC. It should be noted that, according to scale-free properties of the power law distribution, the difference of axiss scale does not affect the shape and slope of the curve.
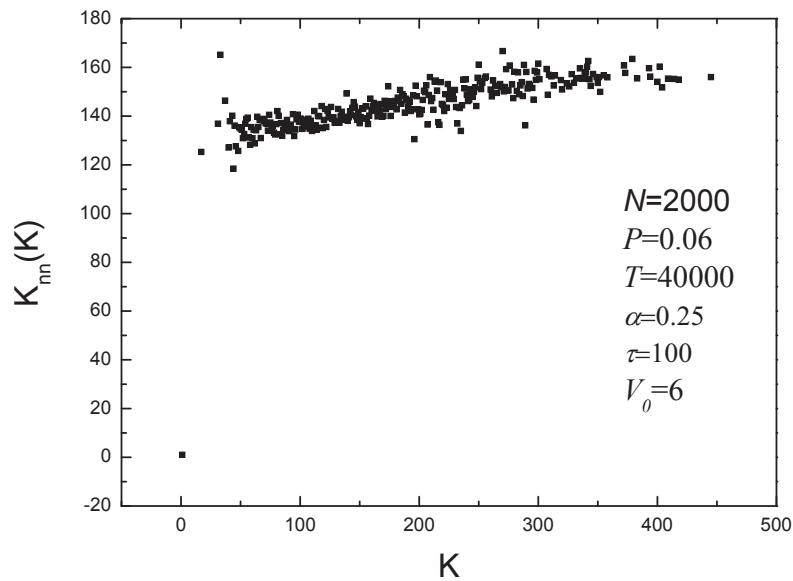
Figure 3. Distribution of $K_{nn}(K)$, which is the average degree of the neighbors of the nodes whose degree is equal to K. An upward trend indicates a positive degree-degree correlation, i.e., the nodes with small (or large) degree tend to connect with the nodes also with small (or large) degree.
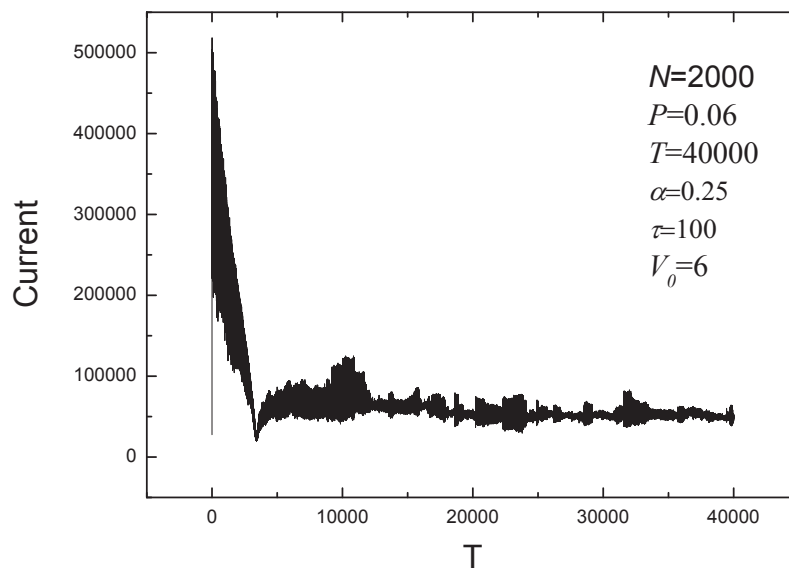

Figure 4. Total current flowing in the system as a function of time, which is the sum of current every time step flowing in the whole system. After about 3300 time steps, it reaches a stable oscillating state.
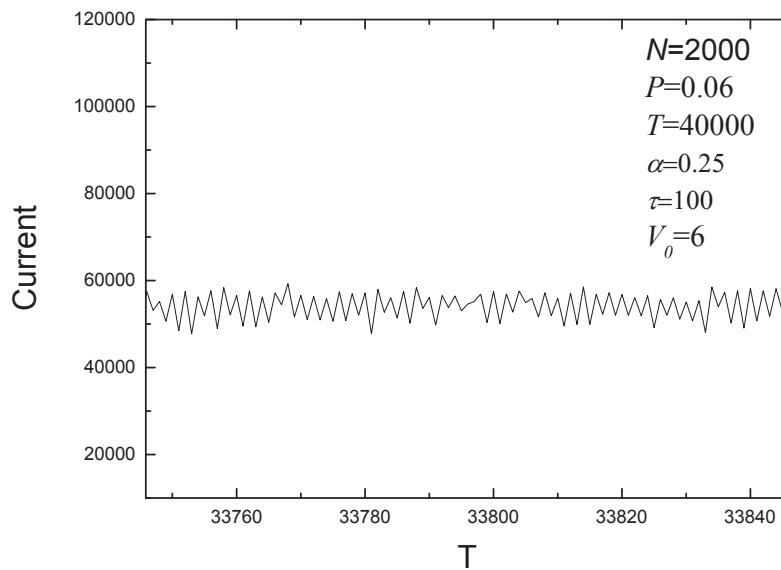
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Figure 5. Local details of the total current shown in Fig. 4 for a short period. Comparing with the experimental ECoG signal [39], every time step in our model is estimated to be 4 ms.
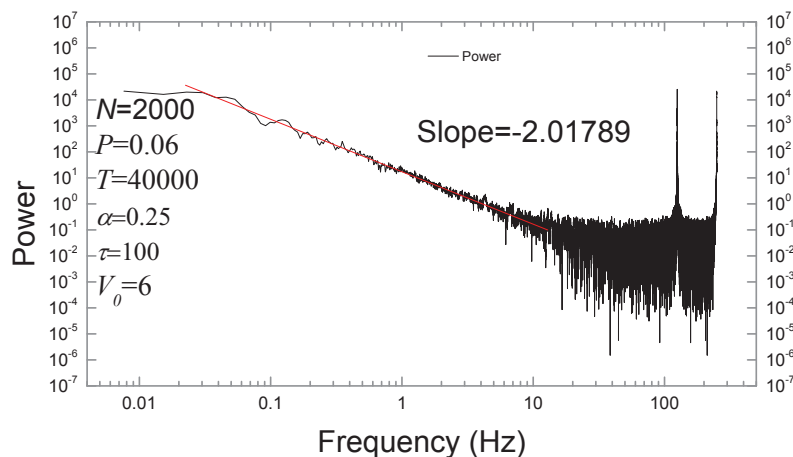

Figure 6. Power spectrum of the simulated total current, which is the square of the amplitude of the Fourier transform as a function of frequency for the current signal. The sampling frequency is 250 Hz, corresponding to 4 ms. Log-log scale is chosen for both horizontal and vertical coordinates. A power-law behavior over more than 5 orders of magnitude emerges. The straight (red) line shows the linear fit for the middle part of the curve.
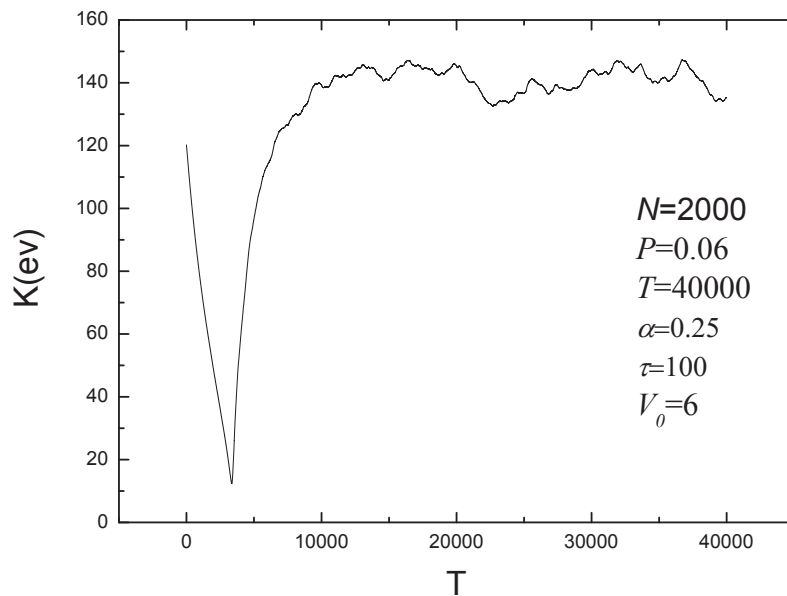
Figure 7. The average degree per neuron changes as a function of time. After about 3200 time steps, it reaches a stable oscillating state, being consistent with the current (Fig. 4).

3.3. Structural properties during co-evolutionary process

Our initial network is a random network consisting of 2000 nodes, and the link probability is 0.06. It is a sparse network. In Bornholdt model [27], the absolute average correlation is studied under different conductivities K. It is found that the correlation is large for networks with small connectivity, and small for networks that are densely connected. This quantity is used as a criterion for rewiring process, and it makes the rewiring rule reach a balance, i.e., links tend to be created at strong correlation, and destroyed at weak correlation. Thus, without global information, the local rewiring rule, synaptic evolving depending on averaged correlation between neurons, could guide the whole network to a convergent state. Figure 7 shows the average degree per neuron changes as a function of time. Obviously, after 3200 time steps, the average degree reached its minimum, being consistent with the current (Fig. 4). This is the time at which 4.8 percent nodes are separated from the network and became isolated nodes. After that, the average degree rises up to about 140 rapidly, and oscillates stably around it. This demonstrates that local rewiring mechanism could control global dynamical properties in a large network [27]. Whether nearby neurons establish a connection between them is only dependent on the degree of correlation between their activities. However, as a result, the entire network could evolve into a stable state. It is a key point of SOC. The final state is not static, and it changes slightly over time. We think it is these slight changes that create a variety of functions of the brain, e.g., learning and memory. To figure out the inherent mechanism imbedded in such changes, we did Fourier transform for the evolution of this average degree, and got its power spectrum (Fig. 8). Interestingly, it exhibits power-law behavior with the exponent 1.95 (close to 2.0) over more than 5 orders of magnitude. And the linear of the middle part of the curve is quite well. Like the current, the average degree changes also show $1/f^2$ noise. This is another evidence and presentation of SOC.
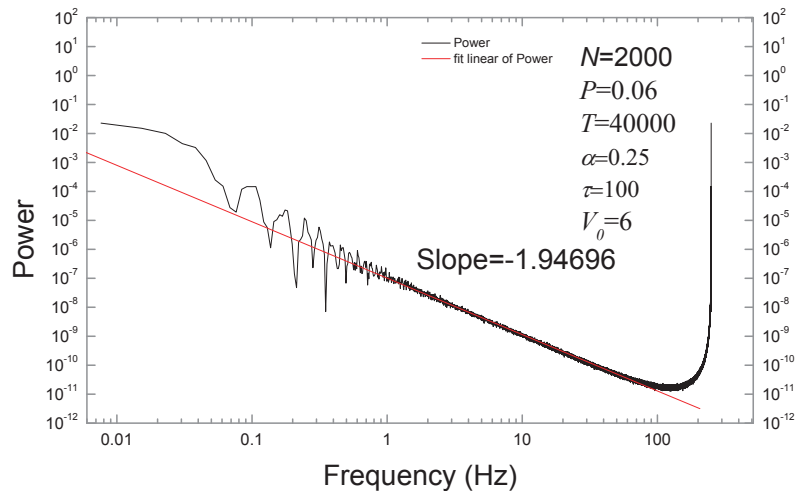
Figure 8. Power spectrum of the average degree per neuron, which is the square of the amplitude of the Fourier transform as a function of frequency for the average degree signal in Fig. 7. The sampling frequency is 250 Hz. Log-log scale is chosen for both horizontal and vertical coordinates. A power-law behavior like that in Fig. 6 is also observed. The straight (red) line shows the linear fit for the middle part of the curve.

3.4. Ranges of parameters

As we mentioned before, for SOC, variable parameters could be changed widely without influencing the emergence of critical behavior. Next we focus on the ranges of parameters in our model. By performing a large number of numerical simulations, we get the following ranges

$$\alpha \sim [0.1, 0.6],$$

$$p \sim [0.06, 1],$$

$$V_0 \sim [1, \infty],$$

in which we can insure the emergences of the properties mentioned above, e.g. the small-world structure and $1/f^2$ noise. The ranges are wide, so the final network relies less on the initial state. As we can see, both of the structural and functional properties could emerge for a quite large range of parameters. For instance, the link probability p of the random network in our model can be taken between 0.06 and 1, i.e., which means the properties of emergence of small world structure and $1/f^2$ noise can exist even from sparsely to fully connected networks. This is strong evidence that the emergent properties are the results of inner co-evolutionary rules instead of fine-tuning of parameters.

Local rewiring rules, as well as the evolution rules of neuron states, are the key mechanisms in Bornholdt and APH models. These mechanisms are essential to produce the self-organized criticality (SOC) properties. Based on them, we developed a co-evolutionary model and applied it to an unbiased network. Unlike previous studies, the small-world structure is the result of evolution instead of the assumption beforehand. At the same time, SOC behaviors do not vanish. In other words, the coupled evolution process makes a dynamically stable structure and functional properties emerge simultaneously. This demonstrates our argument that they should

emerge simultaneously in the same process since no evidence shows that their appearance should be one after another.

4. Conclusion

To summarize, we developed a neural network model with SOC features based on Bornholdt and APH models. Compared with other models, ours co-evolves from a random network with less biased structure. Emergence of SOC behaviors is observed during evolution, and the structural and functional features emerge simultaneously. Different from previous models, small-world topology emerged as a natural result of evolution, not an assumption *apriori*. The currents power spectrum exhibits power-law behavior, which is consistent with experimental results. Interestingly, the spectrum of average degree changes also exhibits power-law behavior, which is expected to be verified by future experiments.

Acknowledgments

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