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Self-organization of a neural network with heterogeneous neurons enhances coherence and stochastic resonance

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Most network models for neural behavior assume a predefined network topology and consist of almost identical elements exhibiting little heterogeneity. In this paper, we propose a self-organized network consisting of heterogeneous neurons with different behaviors or degrees of excitability. The synaptic connections evolve according to the spike-timing dependent plasticity mechanism and finally a sparse and active-neuron-dominant structure is observed. That is, strong connections are mainly distributed to the synapses from active neurons to inactive ones. We argue that this self-emergent topology essentially reflects the competition of different neurons and encodes the heterogeneity. This structure is shown to significantly enhance the coherence resonance and stochastic resonance of the entire network, indicating its high efficiency in information processing. © *2009 American Institute of Physics*. [DOI: 10.1063/1.3076394]

The topology presented in a neural network exerts significant impacts on its function. Traditionally, a predefined topological structure is adopted in neural network modeling, which may not reflect the true situation in real-world networks such as the brain network. In this paper we propose a self-organized network (SON) whose synaptic connections evolve according to the spike-timing dependent plasticity (STDP) mechanism. Specifically, we study how the heterogeneity of neurons will influence the dynamical evolution and the emergent topology of the network. We find that our network obtained from STDP learning can significantly enhance the coherence resonance (CR) and stochastic resonance (SR) of the entire network. This result may have important implications on how the brain network is able to achieve a high efficiency in information processing by encoding the inherent heterogeneity in its topology.

I. INTRODUCTION

Complex neural systems from either living biological entities or biophysical models have attracted great attention in recent years. Neural networks of various topologies have been investigated, such as globally coupled networks,[1] small-world networks,[2,3] and scale-free networks.[4] Specifically, instead of a prior imposition of a specific topology, it is more reasonable to consider self-organized neural networks, which have been broadly studied in Refs. 5–10. The self-organization is usually managed through STDP, which is a form of long-term synaptic plasticity both experimentally observed[11] and theoretically studied.[12,13] We note, however, that most network models in previous work did not take into account the heterogeneity of neurons, a feature ubiquitous for real neural networks. For example, neurons located near the canard region exhibit complex behaviors in the presence of noise,[14–16] where they are more sensitive to external signals and thus enhance information transfer in biological systems. Neurons having different dynamical activities will lead to the network heterogeneity, which can trigger competitions between individuals and play an important role in the CR (Ref. 17) and phase synchronization.[18] Moreover, in fact, the evolution of the synaptic connectivity or the network structure is closely related to the intrinsic heterogeneous dynamics of neurons.

In this paper the network connection is evolved according to the STDP rule over a set of heterogeneous neurons. The heterogeneity is introduced into the network by choosing the key parameter from a uniform distribution covering a wide variety of neuronal behavior. We start from a network with global constant connections among neurons subject to a common input signal in a noisy background. At this time the neurons are in different states and fire at various frequencies. We find that with the STDP rule, the initial global connection among neurons is self-organized into a particular topology that eventually gives rise to synchronous spiking behavior, during which the competitions are mainly caused by the heterogeneous dynamics of each neuron rather than the initial conditions or different external inputs, as studied in Refs. 5–7. After the reorganization, the active cells tend to have high out-degree synapses and low in-degree synapses, while the inactive ones are just the opposite. This self-emergent topology essentially reflects the relationships of influence and dependence among the heterogeneous neurons and thus achieves energy consumption. In order to test the efficiency of this SON in signal processing, we have made comparisons to three other networks of different topologies in terms of CR and SR, which have been analyzed in various neural networks recently.[16,17,19,20] We show that the network obtained from the STDP learning achieves a higher efficiency in information transfer.

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II. NEURON MODEL AND STDP DESCRIPTION

The network used in this paper is composed of N FitzHugh–Nagumo neuron models[21] described by

$$\varepsilon \dot{V}_i = V_i - V_i^3/3 - W_i + I_{\mathrm{ex}} + I_i^{\mathrm{syn}},$$

$$\dot{W}_i = V_i + a - b_i W_i + D\xi_i, \tag{1}$$

$$I_i^{\mathrm{syn}} = -\sum_{1(j\neq i)}^{N} g_{ij} s_j (V_i - V_{\mathrm{syn}}),$$

where $i=1,2,\ldots,N$. a, b_i, and ε are dimensionless parameters with ε small enough ($\varepsilon \ll 1$) to make the membrane potential V_i a fast variable compared to the slow recovery variable W_i. ξ_i is the independent Gaussian noise with zero mean and intensity D that represents the noisy background, and I_{ex} stands for the externally applied current. I_i^{syn} is the total synaptic current through neuron i, where the dynamics of the synaptic variable s_j is governed by

$$\dot{s}_j = \alpha(V_j)(1-s_j) - \beta s_j,$$

$$\alpha(V_j) = \alpha_0/(1+e^{-V_j/V_{\mathrm{shp}}}). \tag{2}$$

Here the synaptic recovery function $\alpha(V_j)$ can be taken as the Heaviside function. When the presynaptic cell is in the silent state $V_j<0$, s_j can be reduced to $\dot{s}_j=-\beta s_j$; otherwise s_j jumps quickly to 1 and acts on the postsynaptic cells. The synaptic conductance g_{ij} from the jth neuron to the ith neuron will be updated through STDP that will be shown later. Note that in this paper both the excitatory and inhibitory synapses are considered. The type of synapse is determined by the synaptic reversal potential V_{syn}, which we set to be 0 and -2 for excitatory and inhibitory synapses, respectively.

In this model, b is a critical parameter that can significantly influence the dynamics of the system. For a single neuron free from noise, the Andronov–Hopf bifurcation occurs at $b_0=0.45$. For $b>b_0$, the neuron is in the rest state and is excitable; for $b<b_0$, the system has a stable periodic solution generating periodic spikes. Between these two states, there exists an intermediate behavior, known as canard explosion.[22] In a small vicinity of $b=b_0$, there are small oscillations near the fixed point before the sudden elevation of the oscillatory amplitude. In our system, b_i is uniformly distributed in [0.45, 0.75]. Hence each neuron when uncoupled has a different activity when subject to external input and noisy background, and neurons with b located near the bifurcation point are prone to fire in a much higher frequency than the others [see Fig. 1(d)].

According to the experimental report on STDP,[11] there are no obvious modifications of excitatory synapses onto inhibitory postsynaptic cells after their repetitive and relative activities. Hence, we set inhibitory synaptic conductance and excitatory-to-inhibitory synaptic conductance to be constants. The remaining excitatory synapses are updated by the STDP modification function F, which selectively strengthens the pre- to postsynapse with relatively shorter latencies or stronger mutual correlations while weakening the remaining synapses.[6] The synaptic conductance is updated by

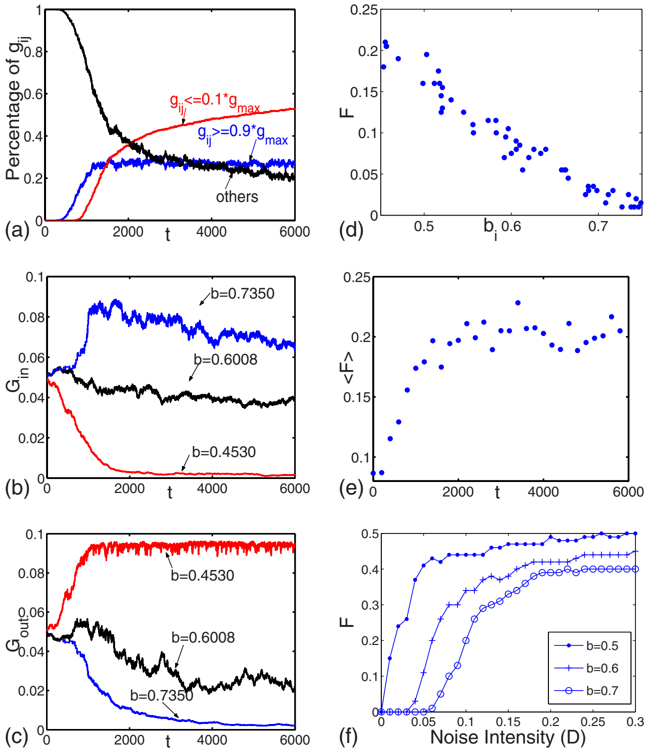

FIG. 1. (Color online) Evolution of the network structure. (a) Percentage of synapses at three value levels: $g_{ij} \leq 0.1 g_{\max}$ (red line), $g_{ij} \geq 0.9 g_{\max}$ (blue line), and the others (black line). [(b) and (c)] The average in-degree and out-degree synapses of three neurons with a different excitability, which is controlled by b. The red line represents the more excitable one with $b=0.4530$, the blue line shows the less excitable one with $b=0.7350$, and the black line is the one with medial excitability $b=0.6008$. (d) The initial firing rate (F) distribution of individual cells with different b for the first 200 s. (e) The average firing rate ($\langle F\rangle$) of all cells during the learning process. (f) Influence of noise intensity (D) on the firing rate of single neuron with different values of b.

$$\Delta g_{ij} = g_{ij} F(\Delta t), \tag{3}$$

$$F(\Delta t) = \begin{cases} A_+ \exp(-\Delta t/\tau_+) & \text{if } \Delta t > 0 \\ -A_- \exp(\Delta t/\tau_-) & \text{if } \Delta t < 0, \end{cases} \tag{4}$$

where $\Delta t = t_i - t_j$ and $F(\Delta t)=0$ if $\Delta t=0$. τ_+ and τ_- determine the temporal window for synaptic modification. A_+ and A_- determine the maximum amounts of synaptic modification. Experimental results suggest that $A_-\tau_- > A_+\tau_+$, which ensures the overall weakening of synapses. Here, we set $\tau_-=\tau_+=2$, $A_+=0.05$, and $A_-/A_+=1.05$, as used in Ref. 6. Only the excitatory-to-excitatory synapses are modified by this learning rule and are restricted to the range $[0, \; g_{\max}]$, where $g_{\max}$ is the limiting value. Other parameters used in this paper are $a=0.7$, $\varepsilon=0.08$, $\alpha_0=2$, $\beta=1$, $V_{\mathrm{shp}}=0.05$, and $g_{\max}=0.1$. The other parameters are given in each case. Numerical integration of the system is done by the explicit Euler–Maruyama algorithm,[23] with a time step of 0.005.

III. SELF-ORGANIZATION OF NEURAL NETWORK

We consider a network of $N=60$, which consists of 50 excitatory and 10 inhibitory neurons. All the neurons are bidirectionally and globally coupled at the beginning, and we assign $g_{\max}/2$ and $3g_{\max}/2$ to excitatory and inhibitory synapses, respectively. The whole network is subject to an external current ($I_{\mathrm{ex}}=0.1$) and noisy background ($D=0.06$) as a learning environment. The influence of noise intensity (D) on the firing rate of single neuron with different values of b is shown in Fig. 1(f).

We now check how the network structure evolves during the learning process. As shown in Fig. 1, after competition, most of the synaptic connections converge to either 0 or the maximum $g_{\max}$ from the initial value $g_{\max}/2$ [see Fig. 1(a)]. This structure becomes stable after about 6000 s. From Figs. 1(b) and 1(c) we can see how the average in-degree synapses G_{in} and out-degree synapses G_{out} of different cells evolve in this competition. For the active cell, such as the one with $b_i=0.4530$, it fires so frequently that it is more likely to activate the others and thus strengthen its out-degree synapses G_{out} to $g_{\max}$ while weakening its in-degree synapses G_{in} to 0. This exactly reflects that such neurons are highly dominant and therefore less dependent on the others, while for the inactive cells (e.g., $b_i=0.6008$ and 0.7350), they typically need large G_{in} to be excited and have small G_{out} due to their low influence. This contributes to the sparse connection of the network and benefits energy consumption. Figure 1(d) shows the initial firing rate distribution of each neuron with different b. The firing rate of the whole network plateaus after about 1500 s when the number of synapses with $g_{ij}\geq 0.9g_{\max}$ equals to that of the synapses with $g_{ij}\leq 0.1g_{\max}$ [Fig. 1(e)]. So the following update of the synapses is in fact a refining procedure that further weakens those unnecessary connections.

Network structures at learning times of 200 and 6000 s are shown in Fig. 2. The synaptic connection finally becomes sparse with about 50% being 0 and 20% being $g_{\max}$ [Fig. 2(c)]. Figure 2(d) gives a clear picture of the active-neuron-dominant synaptic connections in this network, where strong connections are mainly distributed to the synapses from active neurons (those with small values of b_i) to inactive ones (those with large values of b_i). The reason for generating such a special structure is that, under the same learning environment, active neurons can fire with a high frequency and thus are more likely to act as the precells whose out-degree and in-degree synapses are then strengthened and weakened by STDP, respectively. Such synapse distribution renders the active cells a powerful drive to the inactive ones. Hence, through the STDP learning process, the high level of excitability of those active neurons is fully exploited to trigger the whole network to fire synchronously, which becomes more excitable than the original network [Fig. 1(e)]. It should be noted that when the driving of external applied signal is removed, the sustained synchronous firing after learning will terminate and the whole network returns the normal rest state. Instead of the synchronous activity, the main point of this paper is the reorganized network topology. Its enhancement on coherence and SR will be discussed in the Sec. IV.

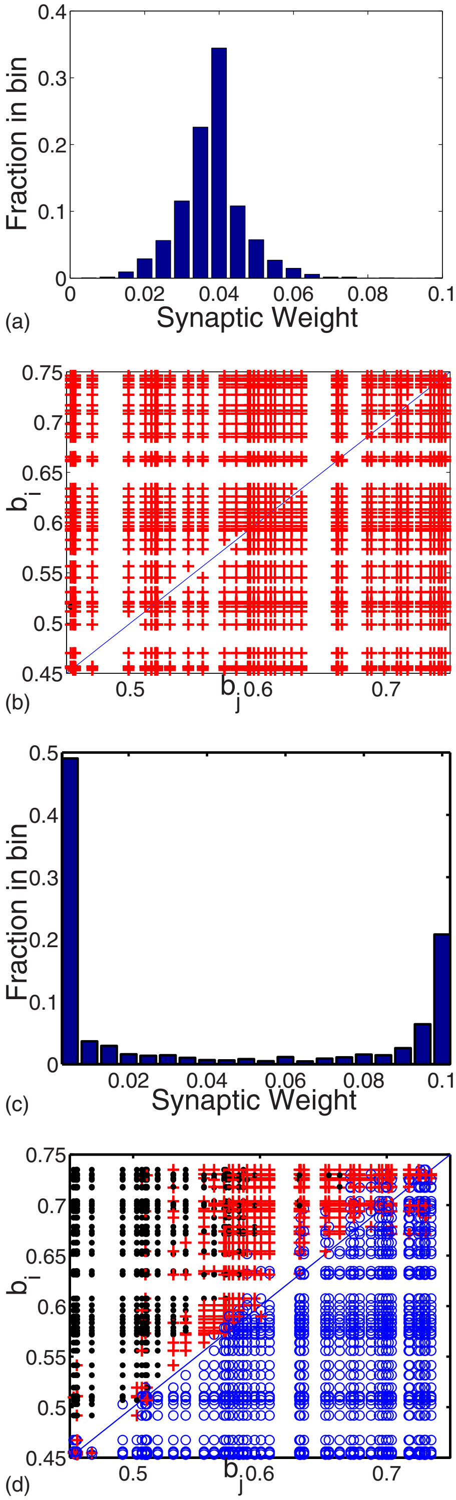

FIG. 2. (Color online) Histogram and distribution of the synaptic matrix G at learning times of 200 and 6000 s. Synapses g_{ij} from cell j to cell i with b_j and b_i, respectively, are plotted. The black dots are the strong synapses satisfying $g_{ij}\geq 0.9g_{\max}$, the blue circles are the weak synapses satisfying $g_{ij}\leq 0.1g_{\max}$, and the red plus signs are intermediate values of synapses.

As the inhibitory synapses are not involved in the update procedure, the size and distribution of the number of excitatory and inhibitory neurons will not influence the formation of final network topology, but just the speed of the convergence process. Also, if the initial excitatory synapses are set to be $g_{\max}$ or randomly distributed in $[0,\ g_{\max}]$, similar results can be obtained but need longer convergence time. Moreover, to ensure that our results do not depend on the specific realization of the uniform distribution of parameter b_i among neurons, we have performed the learning process over several different realizations and find no significant changes of the final network topology.

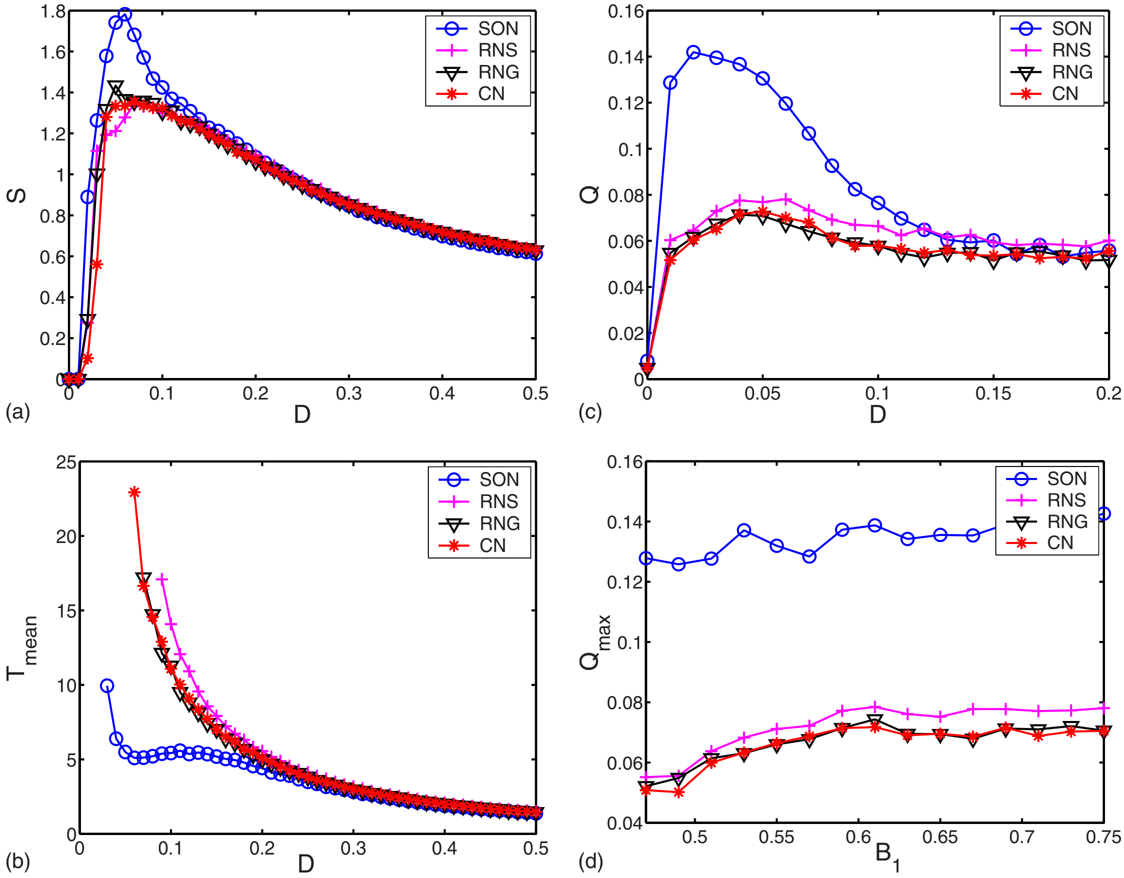

FIG. 3. (Color online) Comparisons of four types of neural networks on [(a) and (b)] CR and [(c) and (d)] SR. SON is the self-organized network obtained via STDP. RNS is the network with the same synaptic distribution as SON but shuffled. RNG is the random network with synapses uniformly distributed in $[0,\ g_{\max}]$. CN is the globally coupled network with constant synapses $g_{\max}/2$. [(a) and (b)] S and T_{mean} vs noise intensity D, respectively. (c) Q vs noise intensity D, where $B_1=0.75$. (d) The influence of inactive cells on SR. $Q_{\max}$ is the maximum of Q. Only cells with parameter $b_i \in [0.45,\ B_1]$ are subject to external signal. This figure is the average result of ten trials.

IV. CR AND SR

In this section, we investigate the efficiency of the SON obtained via STDP in signal processing by comparing its performance on CR and SR with three other networks, i.e., the network with the same synaptic distribution as SON but shuffled (RNS), the random network with synapses uniformly distributed in $[0,\ g_{\max}]$ (RNG), and the globally coupled network with constant synapses $g_{\max}/2$ (CN). All these four types of network are composed of heterogeneous cells that are bidirectionally coupled and have the same mean value of synapses being about $g_{\max}/2$. Ten trials are conducted for each network.

CR is a noise-induced effect, which describes the occurrence and optimization of periodic oscillatory behavior due to noise perturbations.[14] With an intermediate noise intensity, the system can behave the most regular periodic oscillations. We take S and T_{mean} as the coherence factors of the firing events. They are defined as

$$S=\frac{1}{N}\sum_{i=1}^{N}S_i,\quad S_i=\langle T_k^i\rangle_t/\sqrt{\operatorname{Var}(T_k^i)},\quad T_{\text{mean}}=\frac{1}{N}\sum_{i=1}^{N}\langle T_k^i\rangle_t. \tag{5}$$

$T_k^i=\tau_{k+1}^i-\tau_k^i$ is the pulse internal, where τ_k^i is the time of the kth firing of the ith cell. $\langle\cdot\rangle_t$ denotes average over time. S describes the degree of spiking regularity in neural systems. T_{mean} is the average interspike interval (ISI). Here, $I_{\text{ex}}=0$ and all the cells are in the subthreshold region in the absence of noise. Figure 3(a) shows that the optimal regularity occurs when the noise intensity D equals about 0.06. The corresponding S in SON is much larger than the other networks, indicating the high coherent output of SON. The best performance of SON on CR with intermediate noise intensity $D=0.06$ is shown in Fig. 4(a). The flat curve of T_{mean} near the optimal case [see Fig. 3(b)] reflects that the regular ISIs in SON can exist in a relatively wide range of noise intensity, while due to the inefficient connectivity, the other networks display unsynchronized and inactive activities, causing the small S and large T_{mean} (ISI). This is because, under the driving of the same noise intensity, neurons with different levels of excitability show diverse firing patterns. Only the SON that has a reasonably selected synapse distribution can couple the neurons efficiently and generate regular spiking.

SR describes the cooperative effect between a weak signal and noise in a nonlinear system, leading to an enhanced response to the periodic force. The neuron model is an excitable system, which can potentially exhibit SR.[24] To evaluate SR, we set the periodic input to be $I_{\text{ex}}=B\sin(\omega t)$, with $B=0.1$ and $\omega=0.3$. The amplitude of the input signal is small enough to ensure that there is no spiking for all the neurons in the absence of noise. Also, the frequency ω is much

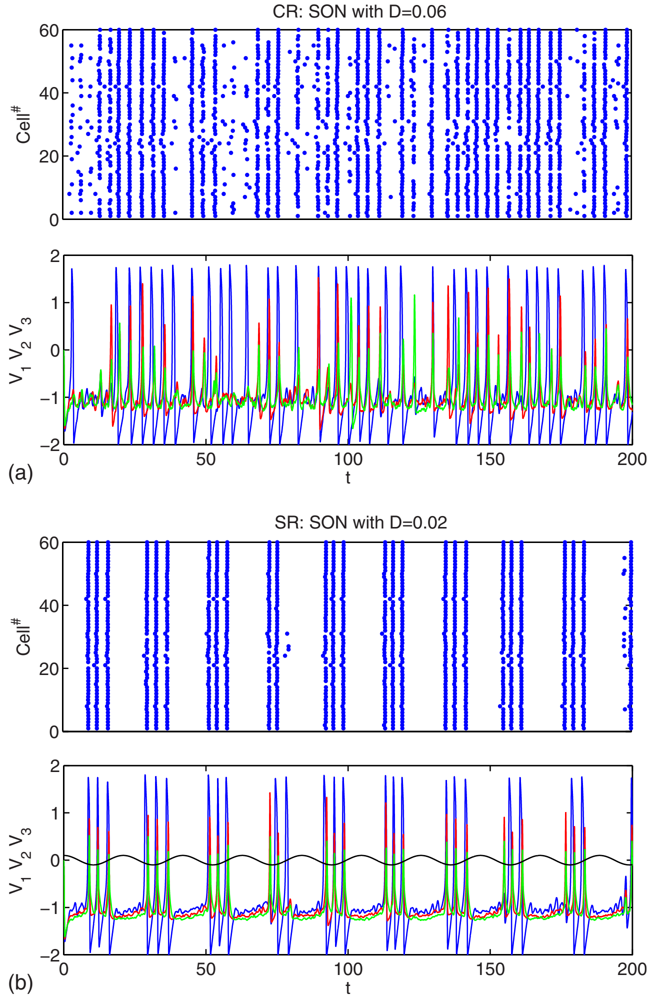

FIG. 4. (Color online) Performance of SON network on CR and SR with intermediate noise intensity $D=0.06$ in (a) and $D=0.02$ in (b). The top figures in (a) and (b) show the spike trains among the first 50 excitatory neurons and the last 10 inhibitory neurons. V_1, V_2, and V_3 represent the membrane potentials of three neurons with different values of b: V_1, $b=0.4530$; V_2, $b=0.6008$; V_3, $b=0.7306$. The black line in (b) (bottom) is the input signal.

slower than that of the neuron's inherent periodic spiking.

Fourier coefficient Q is used to evaluate the response of output frequency to input frequency. It is defined as[25]

$$Q=\sqrt{Q_{\sin}^2+Q_{\cos}^2},\quad Q_{\sin}=\frac{\omega}{2\pi n}\int_0^{2\pi n/\omega}2V_i(t)\sin(\omega t)dt, \tag{6}$$

$$Q_{\cos}=\frac{\omega}{2\pi n}\int_0^{2\pi n/\omega}2V_i(t)\cos(\omega t)dt.$$

Here n is the number of periods $2\pi/\omega$ covered by the integration time. V_i is the average membrane potential among the network. The quantity Q measures the component from the Fourier spectrum at the signal frequency ω. The maximum of Q shows the best phase synchronization between input signal and output firing. Again, SON exhibits greater SR than the other cases [Fig. 3(c)]. In the three other networks that have inefficient connections, active cells fire much more frequently than the periodic driven signal while the inactive ones may be even at the rest state. The active-cell-dominant connection in SON regulates well the network activity and eventually achieves a balanced energy distribution among neurons. The best performance of SON on SR with intermediate noise intensity $D=0.02$ is shown in Fig. 4(b). In order to investigate the importance of active cells, only cells with $b_i\in[0.45,\ B_1]$, where $0.47\leq B_1\leq 0.75$, are subject to the periodic input. Figure 3(d) shows that whether the inactive cells are subject to external signal or not has little effect on SR. This indicates that the contributions of inactive cells to SR are negligible, while the active cells are critical and play a vital role to trigger the whole network response with external signal.

V. CONCLUSION

In this paper, a new type of self-organized neural network with heterogeneous neurons is obtained via STDP learning. The internal dynamics of different neurons is shown to be clearly encoded in the topology of the emergent network after learning. During the STDP learning process, the synaptic strengths of the network are renewed by increasing the influence of active cells over the others and the dependence of inactive cells on the active cells. This process mediates the internal dynamical properties of different neurons and renders the whole network more synchronous and therefore more sensitive to weak input. This effect is clearly reflected from its improved performance on CR and SR. Therefore, we believe that this self-organized heterogeneous neural network is much efficient in signal processing tasks. The network model we proposed may be biologically relevant, considering the highly diversified behaviors of different neurons and the time-varying synaptic connectivity. Our result may be further extended to the study of functional or hierarchical connections in complex brain networks,[26] where heterogeneity is essential for certain brain activities.

Recently STDPs of inhibitory synapses are also observed and investigated.[27,28] This kind of synaptic plasticity has been shown to play an important role in the neuronal function, although the cooperation between these two types of STDP is still unclear. It could be considered by using more physiological neuron and synapse model in the future. For simplicity, we use the excitatory postsynaptic current (EPSC) of AMPA (α-amino-3-hydroxyl-5-methyl-4-isoxazole-propionate) type as is used in Refs. 5–7, which is a kind of fast synaptic current mediated by AMPA receptors.[29] Further advancements on NMDA (N-methyl-D-aspartic acid) receptors, which activate EPSC much slower than AMPA, need to be studied in detail in terms of long-term synaptic plasticity.[30]

ACKNOWLEDGMENTS

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