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Propagation of spiking regularity and double coherence resonance in feedforward networks

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We investigate the propagation of spiking regularity in noisy feedforward networks (FFNs) based on FitzHugh-Nagumo neuron model systematically. It is found that noise could modulate the transmission of firing rate and spiking regularity. Noise-induced synchronization and synfire-enhanced coherence resonance are also observed when signals propagate in noisy multilayer networks. It is interesting that double coherence resonance (DCR) with the combination of synaptic input correlation and noise intensity is finally attained after the processing layer by layer in FFNs. Furthermore, inhibitory connections also play essential roles in shaping DCR phenomena. Several properties of the neuronal network such as noise intensity, correlation of synaptic inputs, and inhibitory connections can serve as control parameters in modulating both rate coding and the order of temporal coding.

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Multi-layer FFNs are related to functional groups of neurons where information is transmitted from one group to the next. It is a generic framework to characterize the propagation of neural code. Since much information in neural systems is carried by interspike intervals time series, the propagation of spike regularity in the brain is an essential problem. We investigate the effects of noise on the propagation of spike regularity in FFN. Noise-induced synchronization and synfire-enhanced coherence resonance are observed during the propagation. Furthermore, double coherence resonance phenomenon is found in FFNs due to the interaction of correlated synaptic input and noise.

neuronal discrete stochastic excitatory or inhibitory inputs can also induce a maximal regularity in a single FitzHugh-Nagumo neuron model, which is called double coherence resonance.⁷ However, whether this phenomenon exists in the neuronal network with more realistic synapse and topology and whether there are differences are still unknown.

In recent years, influences of network topologies on coherence resonance have been widely studied. It is found that linear coupling of oscillators enhances signal propagation.^{8,10-12} Array-enhanced coherence resonance is found in an array of coupled FitzHugh-Nagumo neurons.^{8,9} For more complex coupling, optimal configuration of network exists when predefined topology structures are given¹³⁻¹⁶ or self-organized connections are developed based on spike-timing-dependent plasticity (STDP) learning rules.¹⁷

Multilayer feedforward network (FFN) structure, which is one of the most extensively studied network structure, can characterize the properties of spiking activities in propagation.¹ Each layer in this network is related to a functional group of neurons, and information is transmitted from one group to the next.¹⁸ Rate coding and temporal coding that both exist in this framework are related to desynchronized states and the synchronized states (synfire chain activity) in the networks, respectively.^{1,19} Precisely timed sequential firings of neurons which are associated with temporal coding in FFN are observed in a number of neural systems.²⁰⁻²² Propagation of rate code is also found to be associated with neuronal spatial coherence^{23,24} and could be propagated robustly in feedforward network by synchronized states based on Hodgkin-Huxley(HH) neurons.^{25,26}

Most of the studies about FFN focus on the propagation of firing rates and the spatial coherence in each layer. Evolution of temporal regularity and the relations between the spatial coherence and temporal regularity in FFN have not been well investigated systematically, especially in noisy conditions.

I. INTRODUCTION

The propagation and processing of neural code in an excitable system of oscillators are essential elements in neuronal network.¹ Effects of noise on signal propagation in excitable systems are also broadly studied, and varieties of phenomena induced by noise have been found.²

Coherence resonance (CR), which refers to the coherent oscillation induced only by noise, is one of the widely studied phenomena in excitable systems. The system achieves optimized regulation of spiking by noise with a finite strength.³ Spiking regularity of neuronal oscillations is often associated with the origin of many cognitive tasks, such as memory formation, neural coding, and perception.^{4,5} Experimental evidence of CR has also been reported in the cat's somatosensory system.⁶ In addition to noise, correlation of

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This paper is structured as follows. First, we investigate the propagation of firing rate and regularity in noisy FFN based on FitzHugh-Nagumo (FHN) model. Then, noise-induced synchronization and evolution of coherence resonance through multi-layers are studied. Furthermore, double coherence resonance of the combination of synaptic input correlation and noise intensity is found in the networks. Influences of inhibitory connections on double coherence resonance are also investigated. Finally, the discussion and conclusion are given.

II. DESCRIPTION OF A FEEDFORWARD NETWORK

Information of stimulus is transmitted from one group to another in the brain.²¹ Multi-layer feedforward network structure is the general framework for the studies of spatial-temporal coding in sensory organs.²² The FHN model is a simplified form of the famous model by Hodgkin and Huxley. It has essential neuronal properties such as threshold and refractoriness.²⁷ A neural feedforward network of FHN neurons is constructed as shown in Fig. 1. There are 200 neurons in each layer without recurrent connections. Each neuron receives synaptic inputs from the neurons in the previous layer with probability P . The network model is described as follows:

$$\begin{aligned} \varepsilon \frac{dx_{ij}}{dt} &= x_{ij} - \frac{x_{ij}^3}{3} - y_{ij} + I_{ij}^{syn}(t), \\ \frac{dy_{ij}}{dt} &= x_{ij} + a - by_{ij} + \zeta_{ij}(t), \\ I_{ij}^{syn}(t) &= - \sum_{k=1}^{N_{syn}} g_{syn} \alpha(t - t_{i-1,k}) (x_{i,j} - V_{syn}). \end{aligned} \quad (1)$$

Here, the layer indices are $i = 1, 2, 3 \dots n$, and the neuron indices in each layer are $j = 1, 2, 3 \dots N$ with $N = 200$. x_{ij} and y_{ij} denote the membrane potential and recovery variable, respectively, in each neuron. $I_{ij}^{syn}(t)$ is the total of synaptic current of neuron j in layer i . $\alpha(t) = (t/\tau)e^{-t/\tau}$, where τ denotes the synapse time constant, and N_{syn} is the total number of coupling by synapse from the previous layers. Here, the conductance of the synapse is $g_{syn} = 0.04$ and $\tau = 0.3$ in

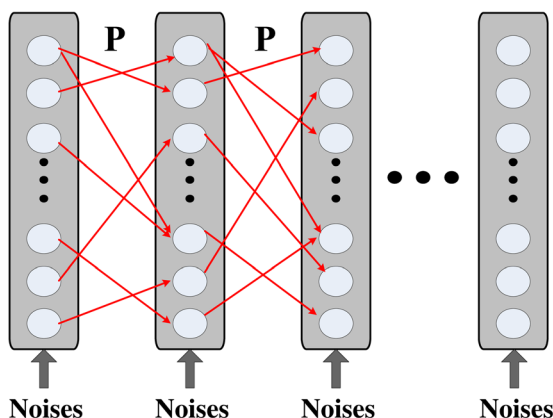


FIG. 1. (Color online) A schematic of multilayer feedforward network with 200 FHN neurons in each layer. P denotes the connection probability between the nearby layers.

this paper unless mentioning specifically. The values of N_{syn} are determined by linking probability P and are identical for all neurons. The type of synapses is determined by the synaptic reversal potential V_{syn} . For excitatory synapses $V_{syn} = 0$, and for inhibitory synapses $V_{syn} = -2$.

In single FHN model without inputs, the Andronov-Hopf bifurcation occurs at $a = 0.7$.^{28,29} When $a < 0.7$, the neuron is in excitable states, and when $a < 0.7$, periodic oscillations are generated. Canard phenomenon can be observed near $a = 0.7$. Here, $\varepsilon = 0.08$, $a = 0.75$, and $b = 0.45$.

$\zeta_{ij}(t)$ indicates that the network is in noisy circumstances, and they are assumed to be independent Gaussian white noise with zero mean and correlation. In many cited papers, it is shown that important features like coherence resonance and stochastic resonance apparently do not depend on to which equation noise is added.² Therefore, we only add the noise in the second equation. $\langle \zeta_{i,j}(t) \zeta_{i,j}(t') \rangle = 2D\delta(t - t')$, where D represents the noise intensity. The numerical integration is done by Euler method with a time step of 0.005.

Average cross correlation K of firing times of neurons is applied to measure the synchronization of one layer in the network,

$$K = \frac{1}{N(N-1)} \sum_{j=1}^N \sum_{m=1, m \neq j}^N K_{j,m}(\delta), \quad (2)$$

where $K_{j,m}(\delta)$ is defined as

$$K_{j,m}(\delta) = \frac{\sum_{i=1}^k X_j(i)X_m(i)}{\left[\sum_{i=1}^k X_j(i) \sum_{i=1}^k X_m(i) \right]^{1/2}}. \quad (3)$$

First, transform the spiking binary series into spiking train after dividing the time series into k bins. δ represents the length of the bins. If there is a spike in the i th bin X , $X(i) = 1$, otherwise, $X(i) = 0$. When $K = 1$, the layer is in a synchronized state, and when $K = 0$, the layer is desynchronized.

Interspike intervals (ISI) are often used to characterize the features of neural signals. The regularity of ISI is quantified by the sharpness of the ISI distribution R . R^j is calculated as $R^j = \langle T_k^j \rangle_t / \sqrt{\text{Var}(T_k^j)}$. T_k^j is ISI time series of the

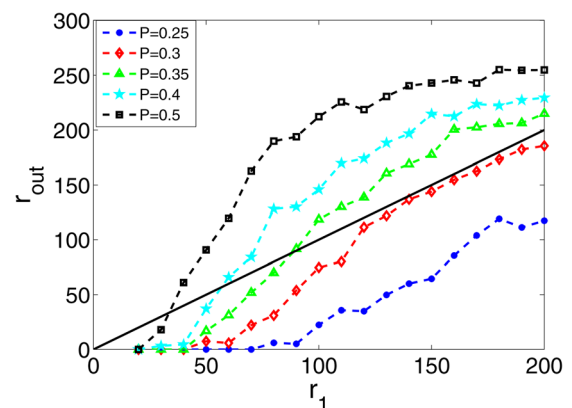


FIG. 2. (Color online) Output of firing rate r_{out} (layer 8 as a whole) versus the input firing rate r_1 (layer 1 as a whole) in the FFN without noise.

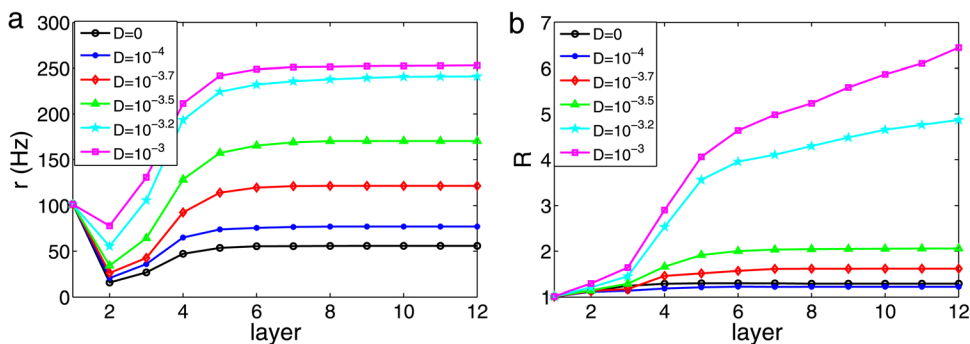


FIG. 3. (Color online) Effects of noise on propagation of firing rate and spiking regularity in the multi-layers with $P = 0.3$. (a) Average firing rate r in each layer (as a whole) of FFN with different noise intensities D . (b) Propagation of spiking regularity R in each layer of FFN with different D .

neuron j . Here, $j = 1, 2, \dots, N$ is the index of neurons in one layer of N neurons. $\langle \cdot \rangle_t$ denotes the average value over time, and $Var(T_k^j)$ denotes the variance of the ISI time series of neuron j . R is obtained by averaging R^j of all neurons in one layer.

III. PROPAGATION OF FIRING PATTERNS IN NOISY FFNs

To investigate the propagation of firing rate and regularity through the FFN, we generate a set of Poisson spike trains with a firing rate r_1 . These spike trains are taken as the output of the neurons in layer 1 of the FFN.

The propagation of different firing rates in the network is shown in Fig. 2. It indicates that the output firing rates r_{out} of the FFN (layer 8) with different P have a nonlinear dependence on the firing rates in the first layer. Therefore, the firing rates could be propagated in FFN based on FitzHugh-Nagumo neurons. The optimal P for basically linear propagation is shown to be $P = 0.3$. It is also found that the network with high P is more sensitive to lower input firing rates r_1 but less sensitive to the variation of input rate when r_1 is higher.

Noise is used to reflect thermal fluctuation, ion channel activities, and the uncorrelated synaptic input received from excitatory and inhibitory neurons outside the FFN. Transmissions of both rate code and spike timing based code are found to be sensitive to noise intensity. The firing rate and the spiking regularity R in each layer of the noisy FFN tend to increase with D as shown in Figs. 3(a) and 3(b). These phenomena can be explained by the following mechanisms. The introduction of noise makes each layer more sensitive to the presynaptic inputs. So, the mean firing rate of the noisy layer becomes a little higher. The firing rhythm becomes more close to their intrinsic frequencies, and the firing pat-

terns become more regular. Then, this effect is amplified by the multi-layers.

The relationship between the connection probability P and output firing patterns (layer 8) in the noisy FFN is investigated systematically and shown in Fig. 4. r value denotes the average firing rate of certain layer as a whole. It is found that the firing rates increase with the linking probability P for a fixed D . Furthermore, the output firing rates have positive correlations with the level of noise intensity D for all coupling probability P (Fig. 4(a)). For a lower noise intensity D , the temporal regularity R increases with the linking probability P . It is interesting that when D becomes higher, the regularity R first increases with the linking probability P and then decreases after the peak values. The noise also facilitates the propagation of the neural code in network with relatively lower connections probability.

IV. DOUBLE COHERENCE RESONANCE IN NOISY FFNs

A. Propagation of spiking regularity in noisy FFNs

Then, we focus on the effects of noise on the propagation of spiking regularity and synchronized firing (spatial coherence) and the relations between them more systematically from the perspective of coherence resonance. Here, noise is the only external stimulus of the homogenous FFN in this section (layer 1 is also stimulated by noise).

Spiking regularity of each layer in noisy FFN is shown in Fig. 5. Each point in the heat map represents the degree of temporal regularity R of the layer in noisy environments. Similar to the coherence resonance in single FHN neuron, the optimal noise intensity for regular spiking is near $D = 0.03$ in the first layer. Then, the spikes become gradually regular when they are transmitted through the multi-layers with lower noise intensity as shown in Figs. 5(a) and 5(b).

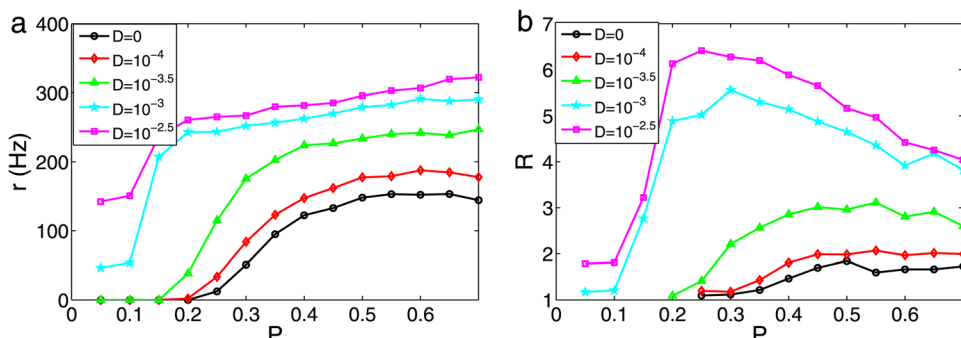


FIG. 4. (Color online) Effects of noise and linking probability on firing rate and spiking regularity. (a) Firing rates r versus linking probability with different noise intensities. (b) Spiking regularity R versus linking probability with different noise intensities.

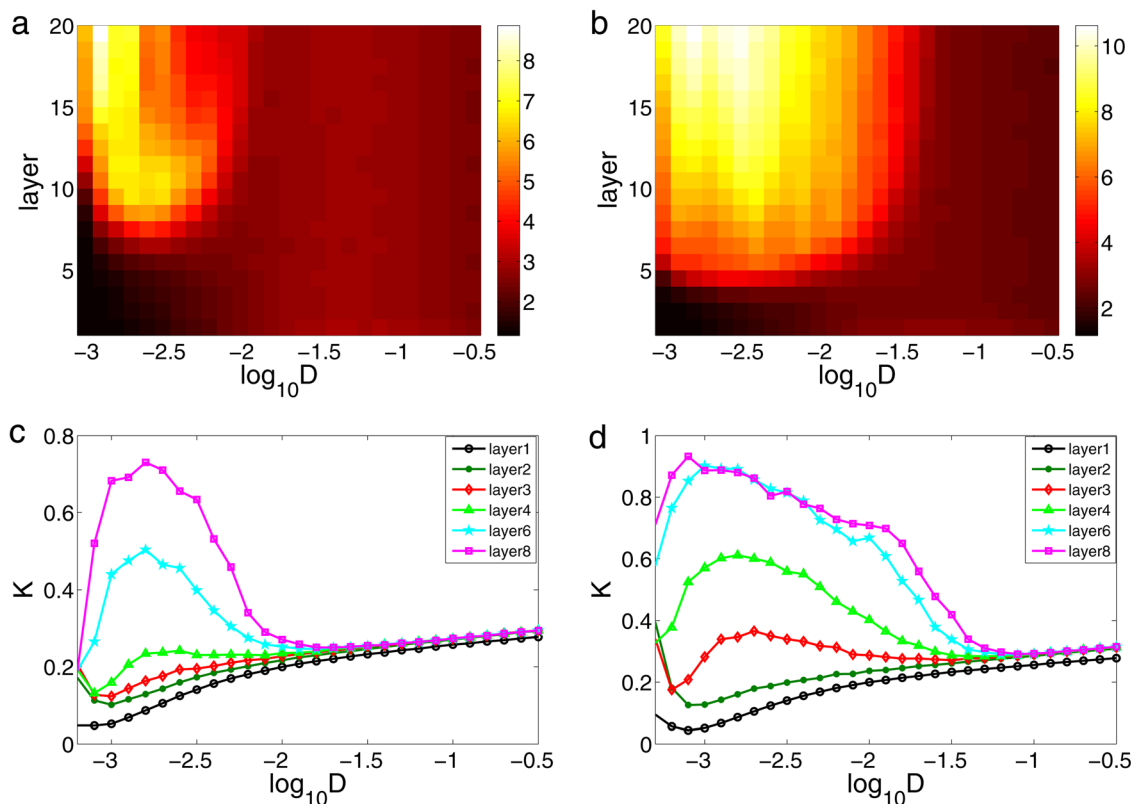


FIG. 5. (Color online) Propagation of spiking regularity and synchrony in the noisy multi-layer network. (a) Spiking regularity R as a function of layers and noise intensity D with $P = 0.2$. (b) Spiking regularity R as a function of layers and noise intensity D with $P = 0.4$. (c) Synchronized states in different layers with $P = 0.2$. (d) Synchronized states in different layers with $P = 0.4$.

Coherence resonance phenomenon can be observed in each layer of the FFN. The maximal value of R becomes higher as the signals are transmitted through layers until being saturated. Furthermore, it is found that the optimal noise intensity for regular firing in the final layer is much lower than these of the first several layers. It makes the regular spiking much easier to be achieved with the help of network structure.

By comparing Fig. 5(a) with Fig. 5(b), a larger parameter range of noise intensity for regular spiking can be observed when the connection probability P is higher. The optimal noise intensity for maximal regularity also shifts slightly with the variation of P value in general.

The regularity R becomes saturated because the network achieves synchronization and transmits signals by synchronized firing in spite of the presence of noise when the noise intensity is relatively low as shown in Figs. 5(c) and 5(d). In order to study this problem in detail, different firing patterns of FFN with different noise intensities are shown in Figs. 6(a)–6(c). When $D < 10^{-3}$, neurons fire so sparsely that the spiking pattern cannot be propagated (Fig. 6(a)). For medium level of noise intensities, the synchronized states are gradually achieved in spite of noise (Fig. 6(b)). So, the spiking patterns can be propagated robustly. Interestingly, an optimal noise intensity for the maximal spatial coherence K is found for some layers in this noise range in which maximal temporal regularity is also achieved. When the noise intensity becomes larger, neurons in each layer fire irregularly, because noise corrupts both temporal regularity and spatial

coherence (Fig. 6(c)). It is also shown that the temporal regularity and the noise-induced synchronization in FFN are correlated to some extent. In noisy condition, synchronization makes the transmission of firing patterns more robust to noise. So, the noise-induced synchronization can enhance the temporal regularity of firing pattern. As the firing patterns of the network basically do not vary qualitatively after layer 8, we take the output of layer 8 as the output of FFN in the following studies.

B. Double coherence resonance in noisy FFNs

Double coherence resonance (DCR) means a maximum coherence occurs for an optimal combination of P and D . For FFN, connection probability P , which denotes the input correlation of neurons in the same layer, is an important factor for signal propagation. The spiking regularities in the 8th layer as a function of noise intensity D and linking probability P are shown by heat map in Fig. 7(a). It is shown that there exists a maximum R for all connection probability P and noise intensity D . When P value is low, the maximum coherence cannot be attained, because signals cannot be propagated by in-layer synchronized firings. When P value is medium, the spikes with maximum coherence are propagated by synchronization with relatively lower noise intensity (Fig. 6(b)). As P value becomes larger, the maximal spiking regularity decreases. The details of its firing patterns are shown in Fig. 6(d). That is because the irregular firing patterns which violate the relative refractory period of the

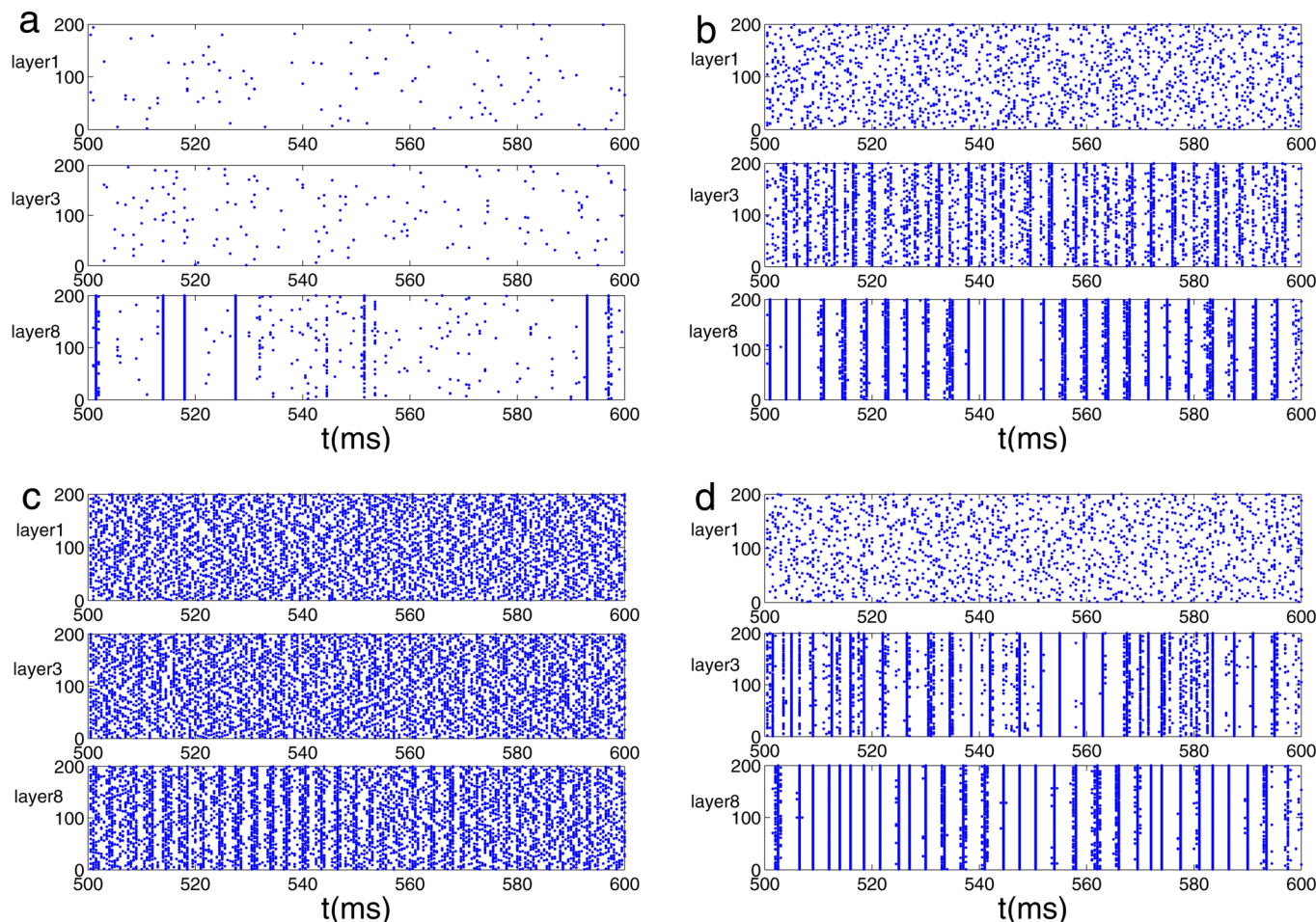


FIG. 6. (Color online) Comparison of raster plots in the FFNs with different noisy intensities and connections. (a) Network with lower noise intensity ($D = 10^{-3.3}$) and connection probability $P = 0.4$. (b) Network with medium noise intensity ($D = 10^{-2.8}$) and $P = 0.4$. (c) Network with higher noise intensity ($D = 10^{-1.4}$) and $P = 0.4$. (d) Network with noise intensity $D = 10^{-2.8}$ and $P = 0.8$.

neuron can be propagated robustly by in-layer synchronization due to the high correlation of synaptic inputs. Here, temporal regularity and spatial coherence are not positively correlated when P value becomes relatively large (comparing Fig. 7(a) with Fig. 7(b)).

All the networks mentioned above are connected only by excitatory synapses. Inhibitory connections also widely exist in neural system such as hippocampus and play an essential role in neural coding. Sub-layers which consist of inhibitory neurons are taken into consideration in the following studies. Here, the dynamic properties of inhibitory neurons are the same as the excitatory ones we mentioned

above. P_{inh} is used to represent the ratio of inhibitory neurons in each layer. Here, we investigate the double coherence resonance when $P_{inh} \leq 0.2$, which is the ratio of inhibitory neurons in the mammalian neocortex. The linking probability P values from both excitatory and inhibitory neurons to the neurons in next layer are identical.

Double coherence resonance in noisy FFN with different ratios of inhibitory neurons is shown in Figs. 8(a)–8(c). It is found that inhibitory neurons decrease the maximal regularity of the output firing patterns in the FFN (comparing Fig. 7(a) with Figs. 8(a)–8(c)). The effects of DCR can be better observed by considering the maximal regularity R for

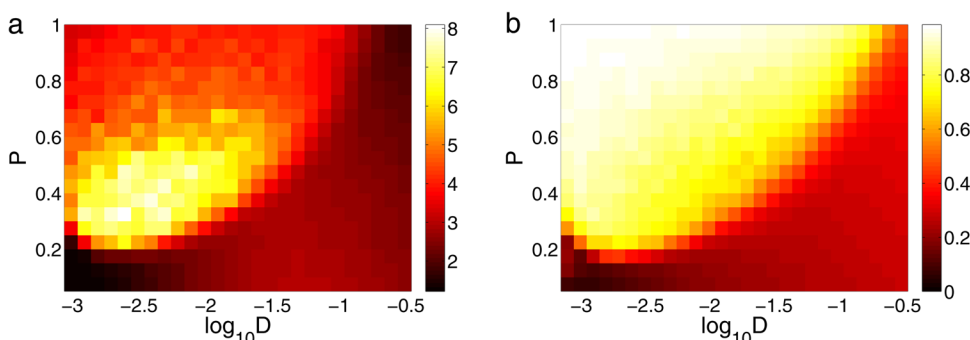


FIG. 7. (Color online) Degrees of average temporal regularity R and spatial coherence K of 8th layer as a function of noise intensity D and linking probability P . (a) The color denotes the value of temporal regularity R . (b) The color denotes the value of spatial coherence K .

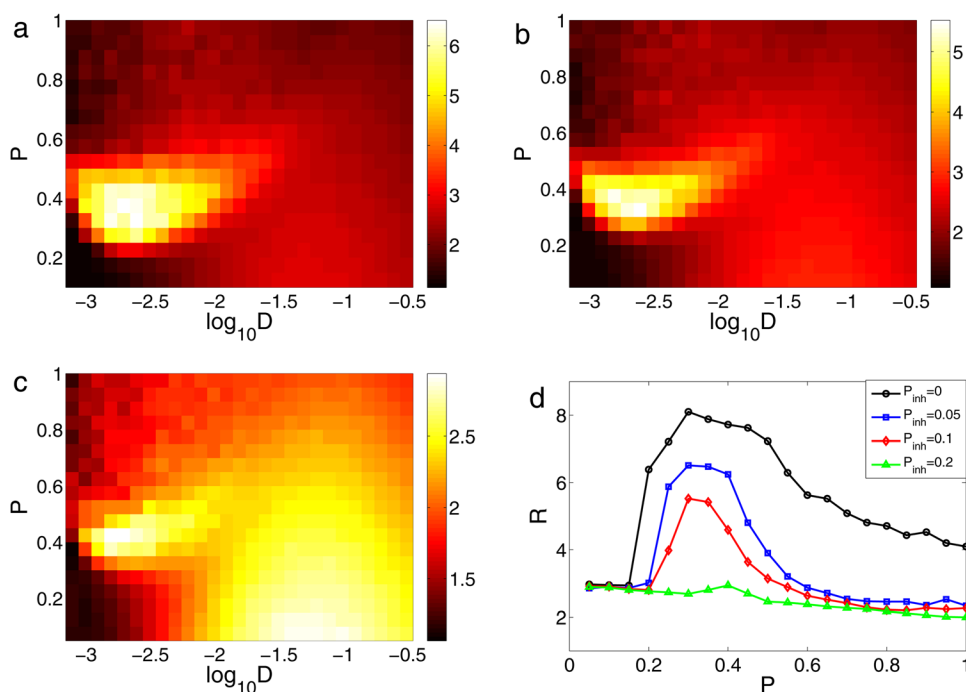


FIG. 8. (Color online) Degrees of average spiking regularity R of 8th layer as a function of noise intensity D and linking probability P with different ratios of inhibitory connections. The color denotes the value of R . (a) $P_{inh} = 0.05$; (b) $P_{inh} = 0.1$; and (c) $P_{inh} = 0.2$. (d) The maximal R value for each P versus linking probabilities P of the FFN with different P_{inh} .

each linking probability as a function of P with different P_{inh} as shown in Fig. 8(d). The optimal configuration of FFN exists at $P = 0.3$ for coherence resonance. Inhibitory connections play a role in decreasing the levels of synchronization and corrupt the temporal regularity.

V. DISCUSSION AND CONCLUSION

Noise, which widely exists in real neuronal networks, can increase the network sensitivity to the input signal and modulate the propagation of both rate code and temporal regularity with the help of the amplification effects of FFN structure.

The relations between noise, synchronization, and spiking regularities are investigated systematically in feedforward networks. Noise-induced synchronization is observed in FFN when noise with medium intensity is added. Propagation of temporal regularity in a neuronal layer is also found to be correlated with the phenomenon of noise-induced synchronization to some extent. These phenomena arise from the competition between noise and the correlated synaptic inputs from the previous layer. When D is low or medium, synaptic inputs play the dominant role, and when D is larger, noise becomes the dominant factor.

The noise-induced synchronization has been widely studied.^{30–32} However, there are differences between our studies. In Ref. 31, the noise is common in each element in the network. In Ref. 32, the synchronization is between the system and the external signal. The mechanisms in Ref. 30 and our study have some similarities. All of them arise from the interactions between the noise and network interactions. Furthermore, the synchronization phenomena are both correlated with temporal regularity of spiking patterns when the noise intensity is medium. However, the network structures in these cases are different. The connections in Ref. 30 are recurrent, while it is feedforward in our research. It

results in different mechanisms about the formation of synchronization.

There are differences in the ways that noise and synaptic input correlation modulate spiking regularity. Noise decreases the spiking regularities mainly by corrupting the synchronized states. However, neurons in the 8th layer are still synchronized when the spiking regularity decreases as the increasing of the synaptic input correlation in relatively lower noise intensity (see Fig. 7). The competition of noise and correlated synaptic inputs results in the double coherence resonance in FFN. The optimal combination of synaptic input correlation and noise intensity induces the maximal spiking regularity.

Kreuz *et al.*⁷ have studied double coherence resonance of a balanced FHN neuron with excitatory and inhibitory pulses in the high-input regime. In our studies, we focus on the network with excitatory synaptic connections and Gaussian white noise. Furthermore, when the network becomes balanced, double coherence resonance phenomena are not obvious, which is different from the results of Kreuz *et al.* That is because inhibitory connections are found to counteract the effects of excitatory connections and make the synchronized states difficult to achieve in feedforward network. So, the spiking regularity is more easily corrupted by noise as the increasing of the inhibitory connections.

Our findings in this paper may be significant in neuroscience. Since much information in neuronal network is carried by ISI time series, noise-induced synchronization and spiking regularity can enhance the order and robustness of neural code in biological information processing. It is also found that propagation of neural coherence can be controlled by modulating input correlation or noise intensity. Input correlation is found to play an essential role in information propagation in brain activities such as attention.³³ This has a nontrivial influence on the propagation of neural code. Therefore, these properties which are generic in neuronal

network can serve as control parameters in modulating rate coding, the order, and timing precision of temporal coding in nervous systems.

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