CHAOS **22**, 043150 (2012)

Impact of connection delays on noise-induced spatiotemporal patterns in neuronal networks

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(Received 13 September 2012; accepted 5 December 2012; published online 28 December 2012)

In the present work, we investigate the nontrivial roles of independent Gaussian noise and time-delayed coupling on the synchronous dynamics and coherence property of Fitz Hugh–Nagumo neurons on small-world networks by numerical simulations. First, it is shown that an intermediate level of noise in the neuronal networks can optimally induce a temporal coherence state when the delay in the coupling is absent. We find that this phenomenon is robust to changes of the coupling strength and the rewiring probability of small-world networks. Then, when appropriately tuned delays with moderate values are included in the coupling, the neurons on the networks can reach higher ordered spatiotemporal patterns which are the most coherent in time and almost synchronized in space. Moreover, the tuned delays are within a range, and the period of the firing activity is delay-dependent which equals nearly to the length of the coupling delay. This result implies that the higher ordered spatiotemporal dynamics induced by intermediate delays could be the result of a locking between the period-1 neuronal spiking activity and the delay. The performance of moderate delays in enhancing the ordered spatiotemporal patterns is also examined to be robust against variations of the network randomness. © *2012 American Institute of Physics*. [http://dx.doi.org/10.1063/1.4772999]

It is well known that time delays and noise perturbations are two ubiquitous features of coupled nonlinear neurons. Recently, dynamical processes in complex neuronal networks under the influences of noise and delays have fueled studies across diverse fields of research. Much works in the literature have reported that these two essential ingredients could play subtle roles in shaping the neuronal firing patterns. The phenomena, such as noise-induced or -enhanced synchronization, stochastic or coherence resonance, delay-induced multiple coherences, are perhaps the most outstanding examples of this fact. Now, this subject is still fascinating. Such frequently emerging complex patterns as well as the underlying mechanism are far from being fully understood at the present time. The objective of this paper is to explore this issue by elaborating significant effects of independent Gaussian noise and time-delayed coupling on the temporal coherence and spatial synchronization in complex neuronal networks. We consider the case of stochastic Fitz Hugh–Nagumo (FHN) neurons on small-world networks and reveal that noise and time delays in electrical coupling could remarkably affect the neuronal dynamics in two aspects. One is that the neuronal networks can exhibit a temporal coherence state at intermediate noise strength when the time delay is vanished in the coupling. The other is that when appropriately tuned delays, which are in a range of intermediate values, are present, the neuronal networks can demonstrate higher ordered spatiotemporal patterns which are the most coherent in time and nearly synchronized in space. Note that both firing synchronization and temporal coherence are important for information processing in the brain. Hence, the present results could be beneficial to researchers for a better understanding of information processing in real neuronal systems.

I. INTRODUCTION

Noise perturbations are inevitably present in real systems. It can influence the dynamical property in different ways. Intuitively, noise is often associated with some kind of destructive forces not desirable, as especially resulting in a large intermittent loss of synchronization.[1] Surprisingly, when noisy fluctuations are introduced to nonlinear systems, they can interact with the systems nonlinearities to render counter-intuitive effects through stochastic resonance,[2] coherence resonance,[3] etc.

Particularly, in neuronal systems, noise arises from many different sources in neurons, such as a quasi-random release of neurotransmitter by the synapses, a random switching of ion channels, and most importantly random synaptic input from other neurons.[4,5] How noise influences the dynamical property is currently a vibrant topic in theoretical neuroscience.[6] Much attention has been paid to the various effects induced by noise in different neuronal networks. For example, in globally coupled networks of Hodgkin-Huxley (H-H) neurons,[7] it was examined that not only coherence of the networks can be

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optimized by additive noise but also synchronization between different neurons can be induced by appropriate noise. Spatial coherence resonance was also revealed when additive temporally and spatially uncorrelated Gaussian noise was introduced in spatially extended H-H networks.[8] In small-world networks of FHN neurons, Okyu Kwon *et al.* further confirmed that coherence resonance can be enhanced by spatially correlated noise.[9] When the coupled elements are nonidentical, synchronization induced by independent external noise was reported in a lattice of coupled FHN neurons.[10] In a square lattice of coupled Rulkov maps,[11] an intermediate noise was found to make ordered spatial patterns emerge, which can propagate through the neurons in the form of beautiful circular waves. More interestingly, the pacemaker-driven stochastic resonance was described in noisy excitable small-world networks,[12] where we can find that there exists an optimal intensity of spatiotemporal noise by which the correlation between the pacemaker frequency and the temporal output of the whole array is maximal.

Note that another important feature of element interactions is that they involve time delays. Moreover, delays can affect the dynamical property significantly.[13–15] In neuronal systems, time delays are due to the finite speed at which action potentials propagate across neuron axons as well as time lapses occurring in both dendritic and synaptic processing.[16] Similar to noise-induced diverse effects in neuronal networks, a few of studies have been done regarding the important roles of time delays in shaping neuronal dynamics. In diffusively electrically coupled neuronal networks, it was shown that synchronizability can be enhanced by time delays, i.e., synchronization in neuronal networks with time-delayed coupling was achieved at lower coupling strength compared to that with instantaneous coupling.[17] Mahdi Jalili also reported that spike phase synchronization in networks of coupled Hindmarsh-Rose neurons could be enhanced by introducing time delays in the excitatory and inhibitory coupling.[18] Moreover, time delays, whether in electrical connections via gap junctions or chemical synaptic connections, have displayed its subtle roles in synchronization transitions.[19–22] For instance, on scale-free networks of modified H-H neurons,[19] there exists transitions from bursting synchronization to intermittent multiple spiking synchronization upon increasing delays. On small-world networks of the Rulkov maps, delays were revealed to induce a transition from zigzag fronts to clustering anti-phase synchronization and further to regular in-phase synchronization.[21] And on attractively and repulsively coupled scale-free neuronal networks that were locally modeled by the Rulkov maps,[22] the synchronization of bursting oscillations was found undulating intermittently as the delay was increased. In interneuronal networks that were coupled by delayed inhibitory and fast electrical synapses,[23] one can find that not only two coupling modes can play a crucial role by the synchronization of the networks, but also delayed inhibitory synapses can induce a transition from regular to mixed oscillatory patterns at a critical value. Alex Roxin *et al.* reported that delays in large networks of neurons can give rise to a wealth of bifurcations and phase diagram including oscillatory bumps, traveling waves, lurching waves, standing waves, etc.[24] With respect to the resonant behavior of interacting neurons, time-delayed coupling was revealed to induce multiple stochastic resonances as well as multiple temporal coherences in an intermittent fashion.[25–27]

As mentioned above, much information has been published concerning the remarkable effects of noise and delays on the firing dynamics in different kinds of neuronal networks. Note, however, that this subject incorporates not only noise and time delays but also the network topology and the local dynamical behavior. How a spatiotemporal pattern in the neuronal networks is influenced by the combined ingredients as well as the underlying mechanism is not yet fully understood until today. In this study, we mainly explore the interplay of independent Gaussian noise and time-delayed coupling on the coherence performance and synchronous property of electrically coupled FHN neurons on small-world networks.

This work is structured as follows. In Sec. II, the model of stochastic FHN neurons on small-world networks is presented. Our main results are given in Sec. III, followed by the conclusions in Sec. IV.

II. MATHEMATICAL MODEL AND SETUP

We consider an ensemble consisting of N coupled FHN neurons, which is a paradigmatic model of an excitable system such as nerve pulses, or the firing activity of electroreceptor cell of an electric fish.[28] The model reads

$$\varepsilon\frac{du_i(t)}{dt} = u_i(t) - \frac{1}{3}u_i^3(t) - v_i(t) + g\sum_{j=1}^{N} A_{ij}(u_j(t-\tau) - u_i(t)), \tag{1}$$

$$\frac{dv_i(t)}{dt} = u_i(t) + a + D\xi_i(t), \tag{2}$$

where, with reference to neurophysiology, u_i and v_i are the fast voltage variable and the slower recovery variable of the *ith* neuron, respectively. $\varepsilon \ll 1$, representing the small time scale ratio of v_i to u_i, is fixed at $\varepsilon = 0.01$ throughout this work. $g\sum_{j=1}^{N} A_{ij}(u_j(t-\tau) - u_i(t))$ denotes electrically synaptic connection via gap junctions. τ is the time delay through the electric synapse between neuron i and neuron j, and the coefficient g stands for the global coupling strength. The coupling structure in Eq. (1) is given by the connectivity matrix A, defined by $A_{ij} = A_{ji} = 1$ if neuron i and j are connected, and 0 otherwise. $\xi_i(t)$ is an independent Gaussian white noise with zero mean and intensity D for each element. a controls the dynamics of an isolated unit. If $|a| > 1$, the neuron has only a stable fixed point corresponding to its quiescent state, while for $|a| < 1$ a limit cycle appears. The quiescent neuron ($|a|$ slightly larger than 1.0) is excitable because it produces a firing pulse when perturbed away from the fixed point by external stimuli. We fix $a = 1.005$ to make the neuron excitable. A periodic pacemaker of the form $f\cos(\Omega t)$ with $f = 0.01$ and $\Omega = \pi$ is introduced to an arbitrary *ith* element of the networks. This external stimulus is subthreshold ensuring that action potentials cannot be triggered if noise is not taken into account.

The coupled neurons in Eqs. (1) and (2) are placed on complex networks with small-world topology,[29] which can be generated as follows: starting from a one-dimensional regular lattice of $N = 100$ neurons with periodic boundary condition and $k = 4$ nearest neighbors, and then rewiring each edge at random with a probability p. The final degree of randomness of the networks is determined by the rewiring probability p. The appropriate values of p $(0 < p < 1)$ correspond to complex networks with small-world properties. The main parameters p, D as well as τ and g are to be varied below.

III. THE RESULTS

In this section, we first discuss effects of noise perturbations on the coherence property of the neuronal networks when time delay τ in Eq. (1) is absent. Then, we introduce time delay in the coupling and explore how the delay influences the noise-induced spiking activity.

A. Temporal coherence induced by independent Gaussian noise

First, we describe how temporal coherence manifests itself in the networks as effects of independent Gaussian white noise when $\tau = 0$. Hence, the noise intensity D is taken as a control variable. We numerically integrate Eqs. (1) and (2) by the Euler method with a time step of 0.001 and obtain the spatiotemporal evolutions for all coupled neurons on the networks. Figure 1 shows some typical space-time plots for different noise levels when setting the coupling strength $g = 1.0$ and the rewiring probability $p = 0.04$. In Figure 1, from the top panel to the bottom one, the noise levels are increasing $D = 0.03, 0.05, 0.2, 0.6, 1.5$ successively. Results presented in Figure 1 indicate that for weak noise (see panels (a) and (b)) the output spike trains look random, but the interspike intervals (ISIs) vary substantially. Interestingly, at moderate noise (see panel (c)), the spiking is rather regular, and the ISIs do not differ much. Finally, at large noise intensity (see panels (d) and (e)), the spiking is much more frequent than those in the other cases, but the ISIs are more irregular again. Clearly, the spiking behavior on the neuronal networks reaches a most regular state at intermediate noise intensity of $D = 0.2$.

To quantify the regularity of the firing activity, the coefficient of variation (CV) λ_i,[3,30] defined as the ratio of the standard deviation of the ISIs to its mean, i.e.,

$$\lambda_i = \sqrt{Var(T_k^i)}/\langle T_k^i \rangle_t, \; i = 1, 2, ..., N \tag{3}$$

is introduced for the ith neuron. Here, $T_k^i = \tau_{k+1}^i - \tau_k^i$ denotes the spike interval and $\langle . \rangle_t$ implies average over time. The parameter λ_i characterizes the spiking coherence of the neuron, and smaller values of λ_i mean more regular spikes. This quantity is of biological significance because it is related to the timing precision of the information processing in neuronal systems.[31] A coherence factor λ for the whole neuronal networks is also estimated via averaging λ_i over all coupled neurons. It is evident that the better the collective spike regularity in time, the smaller the coherence parameter λ, especially, a strictly periodic spiking corresponds to $\lambda = 0$. The temporal coherence on the networks manifests itself by a minimum of the coefficient of variation λ vs. noise intensity D.

The dependence of λ on D is described in Figure 2. The results are obtained by averaging over 30 independent realizations for each set of parameter values to guarantee an appropriate statistical accuracy with respect to small-world configurations and numerical calculations. Figure 2(a) shows that, as D is increased, λ first descends and reaches a

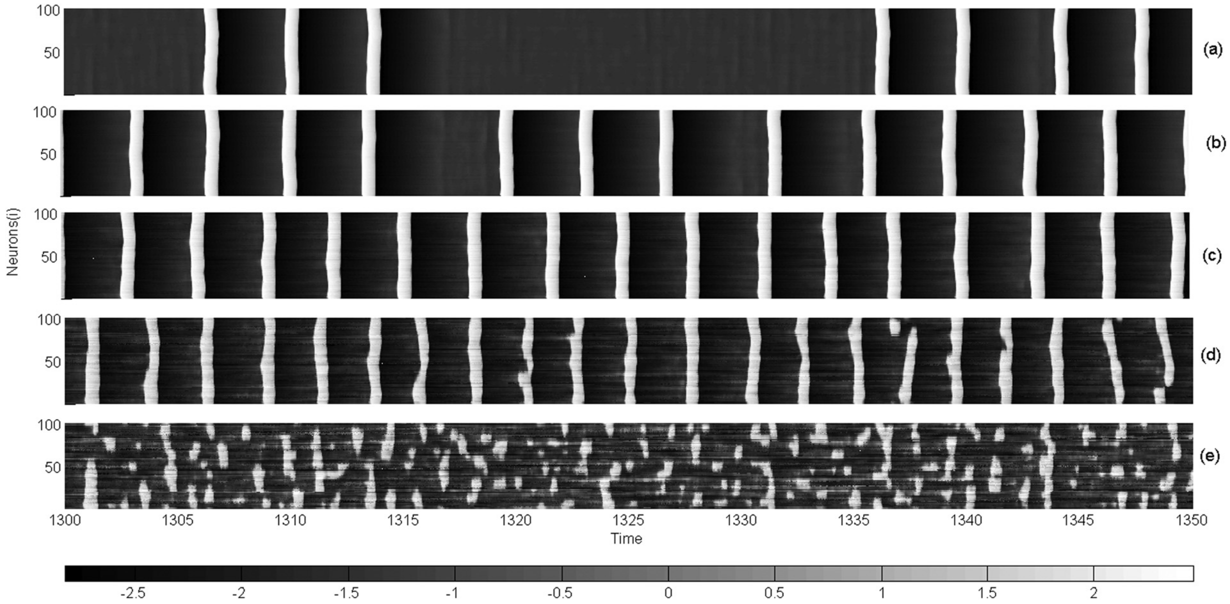

FIG. 1. The space-time plots of coupled neurons on the networks for different noise levels when $\tau = 0$, $g = 1.0$, and $p = 0.04$. Form top to bottom, D is in turn 0.03, 0.05, 0.2, 0.6, 1.5.

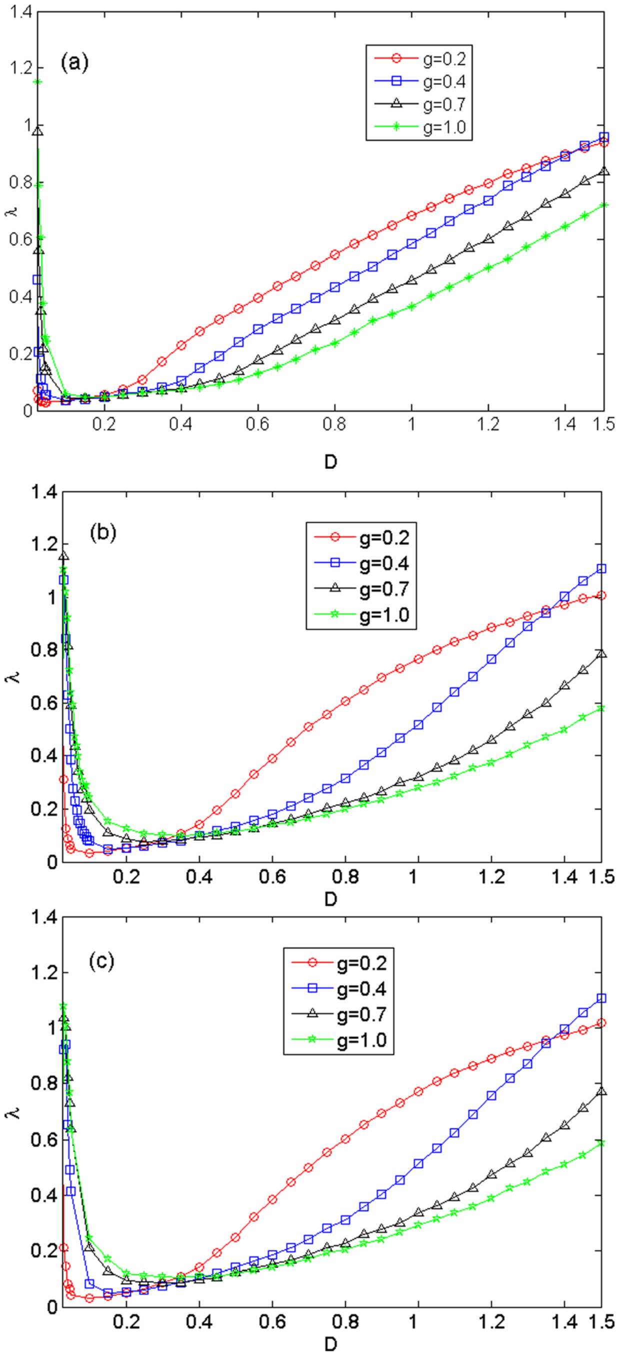

FIG. 2. The dependence of the coefficient of variation λ on the noise intensity D for different values of g and p: (a) $p = 0.04$, (b) $p = 0.5$, and (c) $p = 0.7$.

minimum at an optimal noise level of $D = 0.2$ when $g = 1.0$, then it ascends gradually. This characteristic feature characterizes the occurrence of noise-induced temporal coherence in the neuronal networks. In Figure 2(a) we also depict the dependence of λ on D for other coupling intensities such as $g = 0.2, 0.4, 0.7$. For each g, λ passes through a valley at an intermediate noise level. Obviously, the phenomenon of temporal coherence prevails irrespectively of the amplitude of the coupling, except that both the optimal D and the minimum λ shift to slightly smaller values as g is decreased. This result implies that the stronger the coupling, the larger the noise for inducing the occurrence of temporal coherence. Moreover, the coherence is depressed by the coupling.

When the rewiring probability is changed to other values such as $p = 0.5, 0.7$, the variation of λ as a function of D for different g is further presented in Figures 2(b) and 2(c), respectively. One can find that the characteristic feature, which appears to be very similar to the case of $p = 0.04$, also occurs when p is varied. Thus, we can conclude that temporal coherence on the small-world FHN networks is a robust phenomenon, which occurs largely independent of the coupling strength and the rewiring probability of small-world networks.

B. Higher ordered spatiotemporal patterns induced by time delays

In what follows, we investigate how time delays in the coupling influence the above noise-induced spiking dynamics. Hence, time delay τ is taken as a control variable. The parameters of noise level and the coupling intensity are fixed at $D = 0.4$ and $g = 1.0$, respectively.

For different delays, results presented in Figure 3 are some typical space-time plots of coupled neurons on the small-world networks with $p = 0.04$. Clearly, the spatiotemporal behavior shows nicely ordered if $\tau = 0$ (see panel (a)), which is almost coherent in time and nearly synchronized in space. When τ is increased to $\tau = 0.05$, the ordered pattern in both time and space deteriorates substantially, for the reason that a very small delay suppresses the firing activity strongly and thus the spikes appear sparsely and irregularly (see panel (b)). As τ is increased to moderate values, e.g., $\tau = 0.8, 1.0, 1.2$, the performance of temporal coherence becomes the best and spatial synchronization is more enhanced (see panels (c)-(e)), which are higher ordered spatiotemporal patterns than that of $\tau = 0$. With a further increase of τ, e.g., $\tau = 2.0, 3.5$, however, the temporal coherence is apparently lost though the spikes are still nearly synchronized in space (see panels(f) and (g)).

To better investigate the degree of spatiotemporal order on the neuronal networks, a synchronization factor, i.e., the standard deviation $\sigma = [\langle \sigma(t) \rangle_t]$ with

$$\sigma(t) = \sqrt{\frac{\left(\sum_i u_i^2(t)\right)/N - \left(\sum_i u_i(t)/N\right)^2}{N-1}} \tag{4}$$

is introduced. Here $\langle . \rangle_t$ implies the average over time and [.] denotes the average over different network realizations for each p. Obviously, $\sigma(t)$ measures the degree of spatial synchronization of coupled neurons at a fixed time t. Smaller values of σ mean more synchronous firing activity among coupled neurons.

Now, the synchronization parameter σ as well as the coefficient of variation λ is employed to quantitatively characterize the above delay-induced spiking behavior. Figure 4 depicts the dependence of λ along with σ on τ for three different p. From the left panels to the right panels, p equals to 0.04, 0.3, 0.5 successively. For the left panel, i.e., $p = 0.04$, one can see that λ initially increases and passes through a

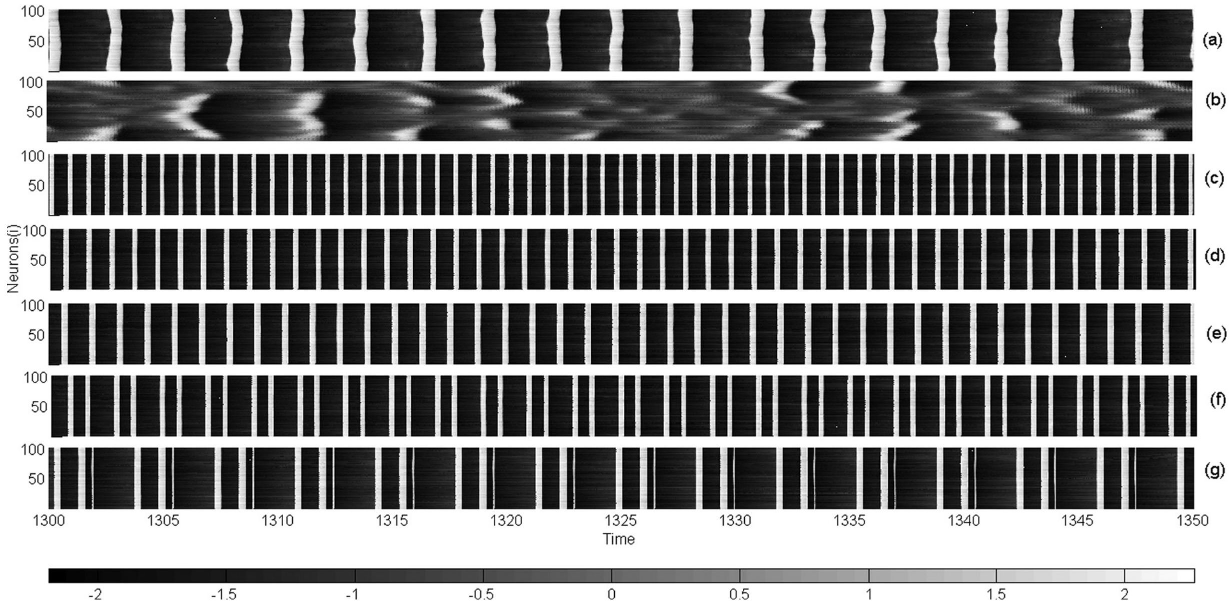

FIG. 3. The space-time plots of coupled neurons on the networks for different delays when $p = 0.04$, $D = 0.4$, and $g = 1.0$. Form top to bottom, τ is in turn $0, 0.05, 0.8, 1.0, 1.2, 2.0, 3.5$.

sharp peak as τ is increased, and then it decreases rapidly, approaching 0 ($\lambda \leq 0.0441$) when τ lies in an intermediate range of [0.1,1.4], after that, λ increases slowly upon further increasing τ. On the same time, the evolution of σ demonstrates almost the same tendency as that of λ, i.e., it rapidly increases at the first increase of τ and arrives at a maximum, and then it decreases to a minimum ($\sigma \leq 0.0142$) when τ lies in a moderate range of [0.5,3.9], further on, it increases very slowly as τ is further increased. Interestingly, λ and σ can simultaneously undergo a minimum at some moderate τ of [0.5,1.4], which implies that there exists appropriately tuned delays lying in a range of intermediate values, in which higher ordered spatiotemporal patterns are observed, i.e., the neurons on the networks are best coherent in time and almost synchronized in space. This confirms the claim, which has been illustrated in Figure 3, that intermediate delays have the ability to induce higher ordered spatiotemporal dynamics. The middle panels for $p = 0.3$ and the right panels for $p = 0.5$ appear qualitatively very similar to the left panels, which implies that delay-induced higher ordered spatiotemporal behavior in the neuronal networks is robust against changes of the rewiring probability.

In addition, through a careful inspection of Figures 3(c)–3(g), it is interesting to find that the collective firing on

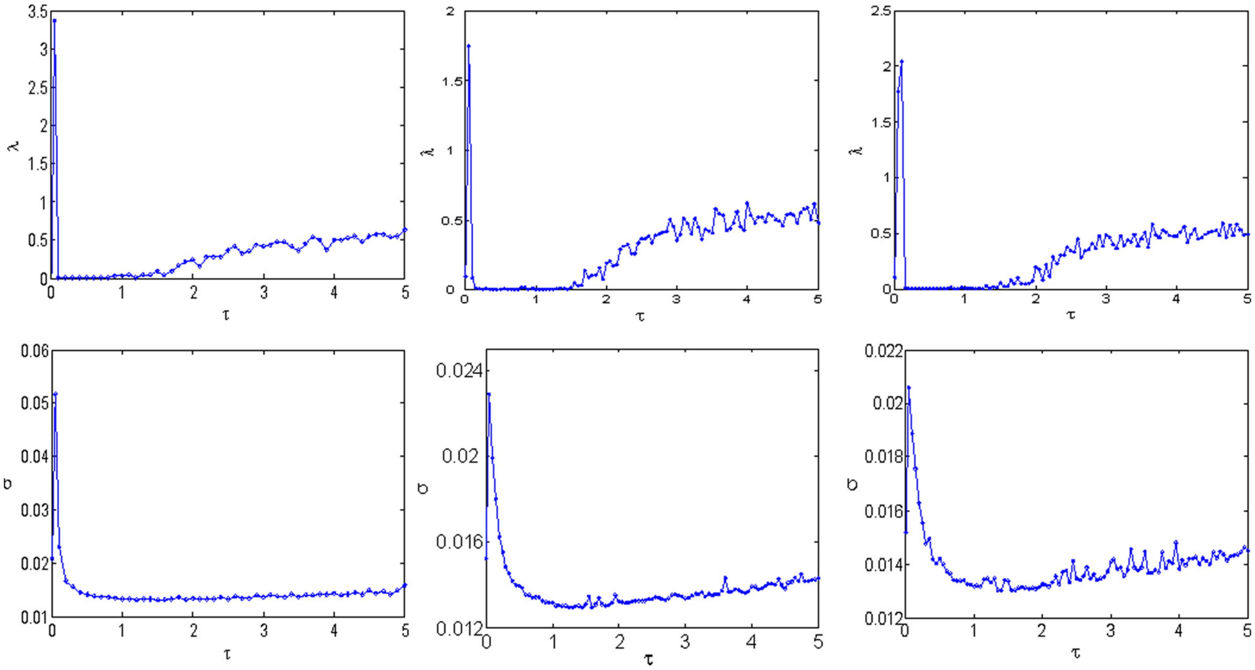

FIG. 4. The dependence of the coefficient of variation λ and the synchronization factor σ on the time delay τ for three different values of p: the left panels for $p = 0.04$, the middle panels for $p = 0.3$ and the right panels for $p = 0.5$.

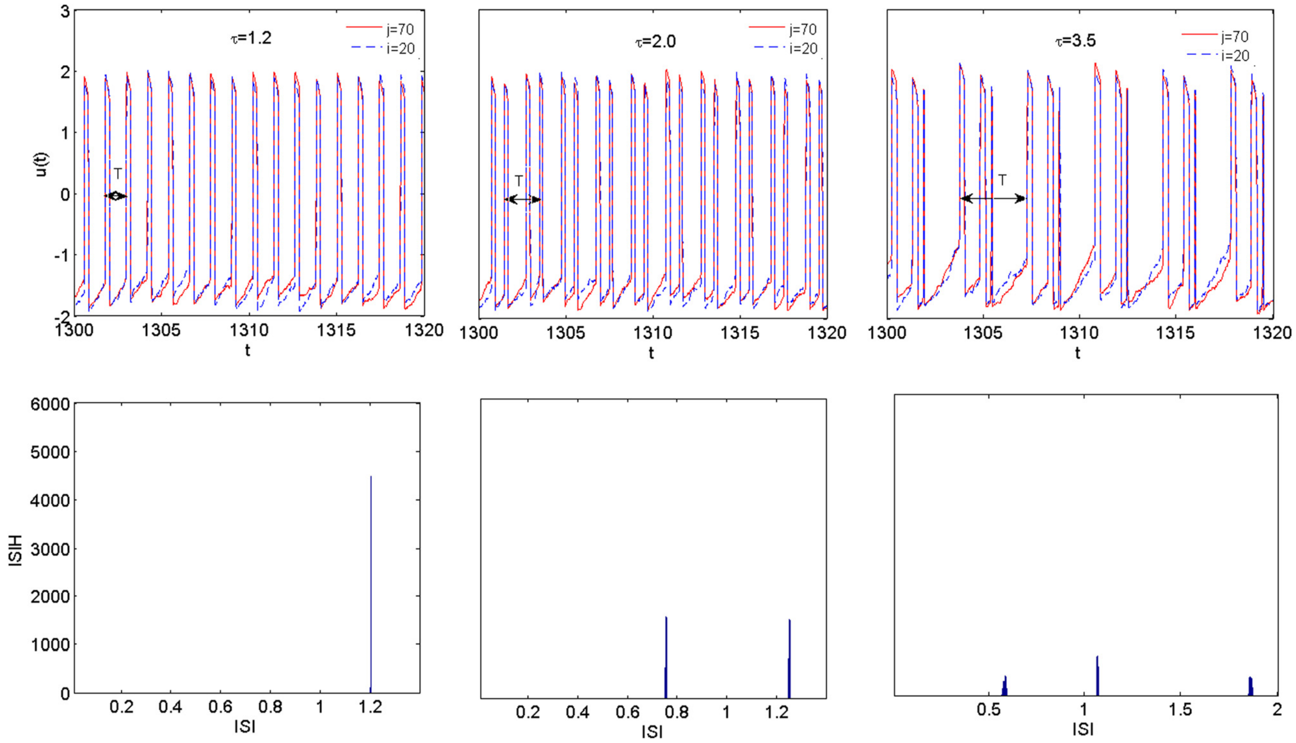

FIG. 5. Time series of two arbitrary neurons $i = 20$ and $j = 70$ on the networks (top panels) and the histogram of interspike intervals of the networks (bottom panels) for different τ: the left panels for $\tau = 1.2$, the middle panels for $\tau = 2.0$ and the right panels for $\tau = 3.5$.

the networks behaves almost periodically, but for intermediate delays $\tau = 0.8, 1.0, 1.2$, the spike trains are period one, and for large delays $\tau = 2.0, 3.5$, the pulse sequences are period two and period three, respectively. More interestingly, the spike period T of the firing activity is delay-dependent, i.e., it equals nearly to the length of the coupling delay, regardless of the magnitude of τ. For a clearer presentation of this phenomenon, Figure 5 depicts vividly the time history of two arbitrary neurons (e.g., $i = 20, j = 70$) and the interspike interval histograms of the neuronal networks for different τ. Left panels are for $\tau = 1.2$, in which the time series of two arbitrary neurons indicates the firing is periodic one, and a sharp peak occurring at about 1.2 in the interspike interval histograms further verifies the spiking period is $T \approx \tau = 1.2$. Middle panels and right panels are for $\tau = 2.0$ and $\tau = 3.5$, respectively. In both cases, from the time series, we can clearly observe that the spiking is period two and period three, respectively. Moreover, the character of two sharp peaks and three peaks in the interspike interval histograms, respectively, reveals the spiking period of the firing activity is $T \approx 2.0$ when $\tau = 2.0$ and $T \approx 3.5$ when $\tau = 3.5$. So, one can conclude that the higher ordered spatiotemporal patterns induced by intermediate delays could be the result of a locking between the period-1 neuronal spiking activity and the delay.

IV. CONCLUSIONS

In this paper, we have numerically studied the influences of independent Gaussian noise as well as time-delayed coupling on the firing behavior of small-world networks, which is locally modeled by the famous FHN neuron describing neuronal dynamics. On one hand, we have found that the neuronal networks could exhibit the phenomenon of temporal coherence at intermediate noise intensity, thereby clearly manifesting the constructive role of noise perturbations in complex networks. This result is also confirmed to be robust to changes of the coupling strength and the rewiring probability of small-world networks. On the other hand, we have revealed that, for appropriately tuned moderate delays lying in a range, higher ordered spatiotemporal patterns are formed which are the best coherent in time and almost synchronized in space. Further analysis of the space-time plots and the interspike interval histograms of the neuronal networks has indicated that the higher ordered spatiotemporal dynamics could be the result of a locking between the period-1 neuronal spiking activity and the delay.

In addition, we point out that that firing synchronization and temporal coherence are of great significance for information processing in the brain. In the literature, some investigations have discussed how to improve the performance of spatial synchronization and temporal coherence simultaneously in neuronal networks. In Refs. 32 and 33, it has been reported that when an optimal number of random shortcuts are introduced to a regular neuronal chain, the coupled neurons can reach a state which is nearly periodic in time and almost synchronized in space. Recently, Wu *et al.* have stated that an appropriate delay can dramatically enhance the temporal coherence and spatial synchronization in noisy neuronal networks, and they also revealed that the optimal delay nearly matches the intrinsic spiking period of the neuronal networks when the coupled delay is excluded.[34] Here, we have suggested that intermediate delays in the coupling can induce higher ordered spatiotemporal patterns in the FHN neuronal networks which are the best coherent in time and almost synchronized in space. The higher ordered spatiotemporal state with delays could exist for intermediate values within a range, and not only for a single value of delay. Moreover, when the higher ordered spatiotemporal patterns appear, the spiking period of the neuronal activity is time-dependent which equals nearly to the length of coupling delay. So, our results are significantly different from previous works.

Finally, note that many complex networks such as biological networks and technological networks are modular, i.e., composed of certain subgraphs with complex connectivity or even networks of networks.[35–39] Time delays are ubiquitous and often significantly affect the dynamical behavior of the networks. How time-delayed coupling influences the neuronal functioning in neuronal networks of subnetworks appears to be challenging and significant, which is one of our interested studies in the future.

ACKNOWLEDGMENTS

This work is partially supported by the National Natural Science Foundation of China (Grant Nos. 10902062 and 11172342). D.V.S. and J.K. acknowledge the support from EU under Project No. 240763 PHOCUS (FP7-ICT-2009-C).

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