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Fast regular firings induced by intra- and inter-time delays in two clustered neuronal networks

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In this paper, we consider two clustered neuronal networks with dense intra-synaptic links within each cluster and sparse inter-synaptic links between them. We focus on the effects of intra- and inter-time delays on the spiking regularity and timing in both clusters. With the aid of simulation results, we show that intermediate intra- and inter-time delays are able to separately induce fast regular firing−spiking activity with a high firing rate as well as a high spiking regularity. Moreover, when both intra- and inter-time delays are present, we find that fast regular firings are induced much more frequently than if only a single type of delay is present in the system. Our results indicate that appropriately adjusted intra- and inter-time delays can significantly facilitate fast regular firing in neuronal networks. Based on a detailed analysis, we conjecture that this is most likely when the largest value of common divisors of the intra- and inter-time delays falls into a range where fast regular firings are induced by suitable intra- or inter-time delays alone. *Published by AIP Publishing.*
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In neuronal systems, time delays are inherently present due to the finite propagation speeds and time lapses occurring by dendritic and synaptic processes. Time delays depend on many factors, including the length of the axon, the conduction velocity of the action potential, and cumulative interactions from synapses, to name but a few. These factors may lead to different time lags between connected neurons. Since regular spiking activity is important and has been observed in many cortical areas, we here therefore consider two different time delays, namely, intra-time delay and inter-time delay, in a clustered neuronal network. The presented results indicate that appropriately adjusted intra- and inter-time delays can significantly facilitate fast regular firing in the considered neuronal network.

I. INTRODUCTION

In biological neuronal systems, neuronal information is transferred among different neurons relying on their dendrites and axons. Dendrites bring information to the cell body and axons take information away from the cell body. So, what is the information in neuronal systems? As is well known, neuronal information is embodied in electrical impulses generated by neurons. Thus, analyzing the statistical properties of electrical impulses' trains, which are also called spike trains, is the basis for understanding the working mechanisms of complex neuronal systems.

In neuronal systems, the regularity of the interspike intervals (ISIs) is one of the important statistical properties of the spike trains. This is because of its close relationship with one of the neuronal coding strategies, the spike-time coding. There, the fine temporal structure of a spike train sparsely encodes information about the temporal structure of the stimulus. For simplicity, we call the regularity of the interspike intervals as *spiking regularity* in this paper.

Due to the importance of the spiking regularity in neuronal systems, lots of literature studies are presented to discuss it not only experimentally[1–4] but also theoretically and numerically.[5–13] Cortical neurons are thought to generate action potentials with irregular interspike intervals. In recent experimental studies, it has been revealed that regular spiking activity appears in the suprachiasmatic nucleus,[1] the association and motor-like parietal regions,[2] and the inferior colliculus.[3] Moreover, regularly firing neurons in the inferior colliculus are reported to have a weak interaural intensity difference sensitivity.[4] In theoretical and numerical studies, researchers are mostly interested in investigating influences of different factors on the spiking regularity of neuronal systems, such as noise, time delay, heterogeneity, etc. Noise has great influences on firing dynamics of neuronal system.[14–24] According to the different sources of randomness, noise in neuronal systems can be classified as synaptic noise[25] and

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channel noise.[26] For spiking regularity, Gong *et al.*[5] revealed that non-Gaussian colored synaptic noise could optimize the spiking regularity of random neuronal networks when neurons are connected with each other with a smaller probability. For channel noise, it has been found that different channel noises have different effects on the spiking regularity of neuronal systems.[6–12] Sodium channel noise enhances spiking regularity of neuronal systems, while in contrast, potassium channel noise decreases it.

The occurrence of time delay is due to the time for signals to transmit in the neural pathways, and it is pervasive in neural information processing. Time delay also has great influences on firing dynamics of neuronal systems.[27–33] For spiking regularity, it is revealed that a moderate time delay can make the electrically coupled neuronal network reach to higher spiking regularity.[34] In the chemical coupling case, it is found that appropriately tuned delays in inhibitory synapses could prompt the spiking regularity of the neuronal networks frequently.[35] Moreover, it was also revealed that time delay could not only induce both spiking synchronization[36] and burst synchronization[37] but also enhance synchronization.[38] Meanwhile, it is known that it could induce various synchronization transitions[39–47] in different kinds of neuronal systems. For stochastic or coherence resonance, it was found that time delay also has important effects on these dynamical behaviors.[35,48,49] Except for synchronization and stochastic resonance or coherence resonance, time delay can have great influences on firing patterns of neuronal systems as well.[50–52]

In the cortex, neurons are connected to each other through millions of synapses and then form a complex network. It has been revealed that neuronal networks have clustered structure properties.[53,54] It means that the complex neuronal network is composed of certain subnetworks with internal and external connectivity. In the language of complex network, neurons inside a subnetwork are connected to the neurons within the same subnetwork through internal connections (called intra-links) but also to some from the other different subnetworks through external connections (called inter-links). According to the above contents, we see that time delays exist in the propagation of neuronal information not only inside a subnetwork but also between different subnetworks. Hence, the intra- and inter-time delays will both influence the firing dynamics of neuronal systems. However, how these two types of time delays interplay with each other to affect firing dynamics of neuronal systems has not been studied.

In this paper, we will devote to investigate combined effects of intra- and inter-time delays on the spiking regularity of a clustered neuronal network with regular subnetworks. The local dynamics of the considered network is simply modeled by FitzHugh-Nagumo (FHN) neuronal models,[55,56] and all neurons are subjected to a subthreshold signal and to external noise. The remainder of this paper is organized as follows. The mathematical model of the neuronal network is constructed by means of FHN neurons in Sec. II. Measures to quantify the spiking regularity of neuronal network are introduced in Sec. III, and our main results are presented in Sec. IV. Finally, discussions and summary are given in Secs. V and VI.

II. MATHEMATICAL MODEL

We apply here the FitzHugh-Nagumo (FHN) neuronal models as the basic blocks in the studied clustered neuronal network. The mathematical equations are described as follows:

$$\begin{aligned}\varepsilon \dot{x}_{I,i}(t) &= x_{I,i}(t) - x_{I,i}^3(t)/3 - y_{I,i}(t) + I_{ext}(t)\\ &\quad + g_{intra}\sum_j A_I(i,j)[x_{I,j}(\tau_1) - x_{I,i}(t)]\\ &\quad + g_{inter}\sum_J\sum_j B_{I,J}(i,j)[x_{J,j}(\tau_2) - x_{I,i}(t)], \qquad (1)\\ \dot{y}_{I,i}(t) &= x_{I,i}(t) + a + D\xi_{I,i}(t),\end{aligned}$$

where the subscript pairs (I, i) represent the i-th neuron in the I-th cluster. x is the action potential and is a fast variable, and y represents the slow recovery variable. The parameter ε is a small parameter which allows us to separate the fast and slow variables. The parameter a controls the local dynamics of a single FHN neuron. In the absence of the external current I_{ext} and the noisy term $D\xi_{I,i}(t)$, the single FHN neuron is in the excitable state for $|a| > 1$ and it generates firing spikes for $|a| < 1$. Here, we set $a = 1.005$, such that an isolated FHN neuron is in an excitable state in the absence of external current I_{ext} and noisy external force $D\xi_{I,i}(t)$. In Eq. (1), D is the intensity of $\xi_{I,i}(t)$ which is assumed to be Gaussian delta-correlated with zero mean: $\langle\xi_{I,i}(t)\rangle = 0$, $\langle\xi_{I,i}(t)\xi_{I,i}(t')\rangle = \delta(t - t')$ and are independent from each other.

Meanwhile, g_{intra} and g_{inter} are the coupling strengths for neurons inside the cluster and neurons between the two clusters, respectively. The matrix $A_I = [A_I(i,j)]$ is a connectivity matrix for the I-th cluster, $A_I(i,j) = 1$ if neuron i is connected to neuron j inside the I-th cluster, $A_I(i,j) = 0$ otherwise, and $A_I(i,i) = 0$. The matrix $B_{I,J} = B_{I,J}(i,j)$ is also a connectivity matrix, but this matrix represents the connections between neurons which belong to different clusters: $B_{I,J}(i,j) = 1$ if the i-th neuron in the I-th cluster is connected to the j-th neuron in the J-th cluster, $B_{I,J}(i,j) = 0$ otherwise. In the two coupling items, the parameters τ_1 and τ_2 represent time delay for neurons inside a cluster and neurons between the two clusters, respectively. In the following, we call τ_1 and τ_2 as intra- and inter-time delay.

Finally, we give an illustration of the network structure used in this paper. It consists of $N = 300$ neurons, which are grouped into $M = 2$ clusters, i.e., each cluster contains $n = 150$ neurons.[57,58] For each cluster, the neurons are arranged on a ring with each neuron connecting to its $2k$ nearest neighbors. Thus, each cluster is regular and has the same coupling matrix A_I. Additionally, links between neurons from different clusters exist with probability p, i.e., $B_{I,J}(i,j) = 1$ with probability p and $B_{I,J}(i,j) = 0$ with probability $1 - p$. Here, we just consider bidirectional coupling cases, i.e., $A_I(i,j) = A_I(j,i)$, $B_{I,J}(i,j) = B_{I,J}(j,i)$ for $i \neq j$ and assume that $A_I(i,i) = 0$, $B_{I,J}(i,i) = 0$. An example of the considered network topology is shown in Fig. 1.

The other parameters in Eq. (1) are set as: $\varepsilon = 0.01$, $g_{intra} = g_{inter} = 1.0$, $D = 0.4$, $k = 2$, and $p = 0.04$. The external current $I_{ext}(t)$ is taken as $f\cos(\omega t)$ with $f = 0.01$ and

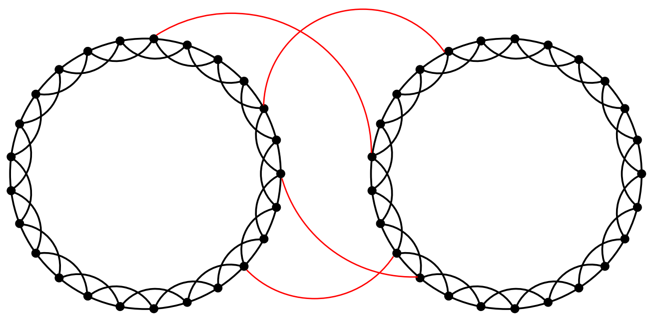

FIG. 1. Schematic presentation of the considered network architecture. The whole network contains 50 neurons, which are grouped into 2 subnetworks. Within each subnetwork, each neuron connects to its four nearest neighbors. The neurons between two different subnetworks are connected with each other with probability $p = 0.005$.

$\omega = \pi$. When the parameters take these values, the firing activity of the neuronal network is regular without time delays. Next, the intra-time delay τ_1 and inter-time delay τ_2 are taken as the control parameters to investigate their effects on the spiking regularity of the considered neuronal network.

III. SPIKING REGULARITY AND TIMING

The measure R is introduced to characterize the spiking regularity and is expressed as

$$R = \frac{1}{\frac{1}{N}\sum_{i=1}^{N} R_i}. \tag{2}$$

Here, N is the total number of neurons in the neuronal network. R_i is the inverse of the coefficient of variation which quantifies the regularity of spike timing in a neuron. R_i is defined as

$$R_i = \frac{\langle T_{i,k}\rangle}{\sqrt{\langle T_{i,k}^2\rangle - \langle T_{i,k}\rangle^2}}, \tag{3}$$

where $T_{i,k} = t_{i,k+1} - t_{i,k}$ represents the inter-spike interval with $t_{i,k}$ denoting the time of the occurring of the k-th spike of the i-th neuron; $\langle T_{i,k}\rangle$ and $\langle T_{i,k}^2\rangle$ denote the mean and the mean squared inter-spike intervals, respectively. Spiking times are defined by the upward crossing of the membrane potential x past a certain value x_{th} (here, x_{th} is taken as 0 mV). For a

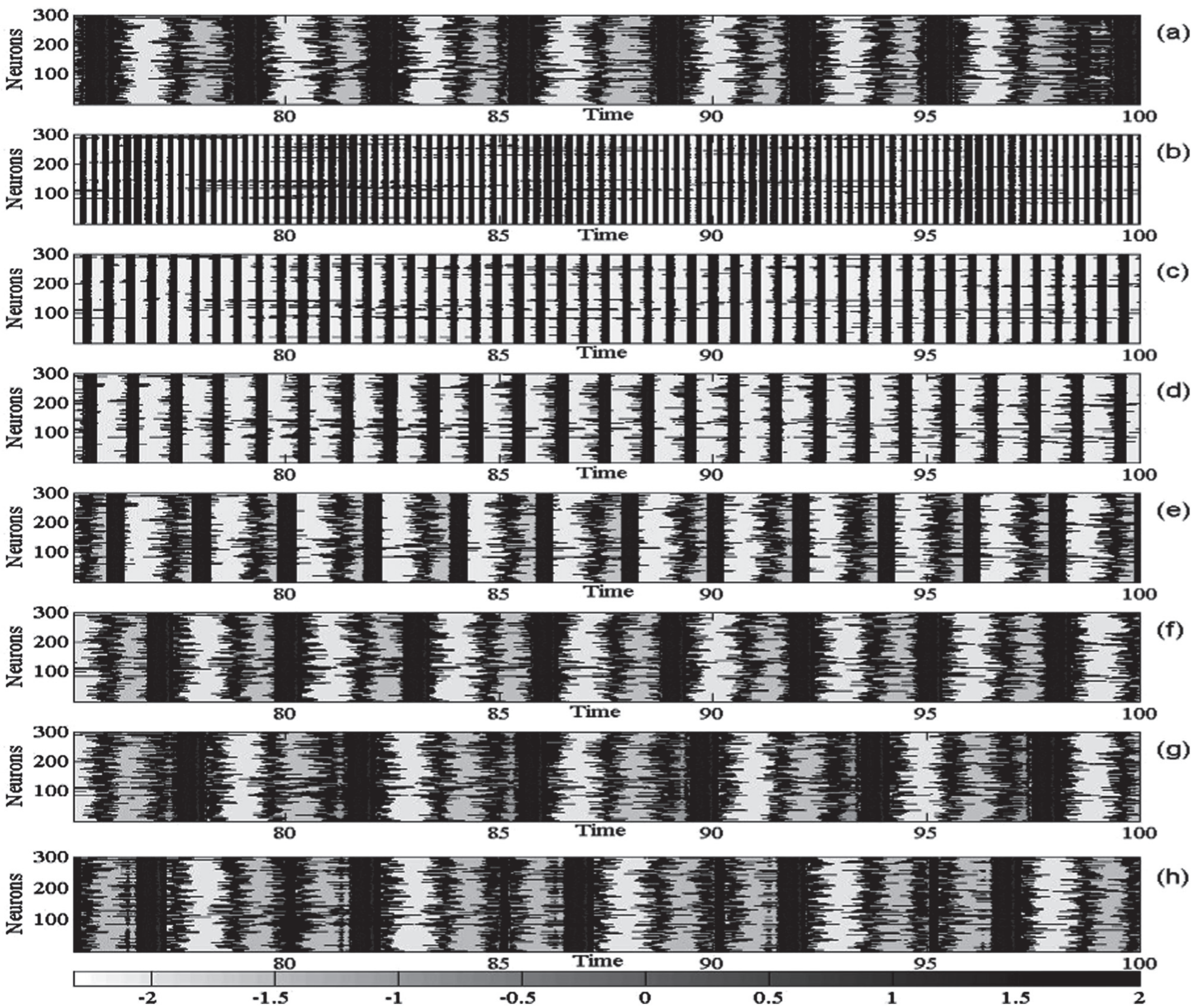

FIG. 2. Spatiotemporal patterns of the neuronal network with $\tau_2 = 0$ for various values of τ_1. The colorbar of values of the membrane potential $x_{I,i}$ is shown at the bottom. (a) $\tau_1 = 0$, where the neuronal network shows regular ISIs. (b) $\tau_1 = 0.25$, the spiking regularity is lower. The patterns become ordered again when τ_1 increases further as shown in (c) $\tau_1 = 0.5$, (d) $\tau_1 = 1.0$, (e) $\tau_1 = 2.0$, (f) $\tau_1 = 3.0$, (g) $\tau_1 = 4.0$. While for $\tau_1 = 5.0$, the spatiotemporal pattern shows non-equivalent interspike intervals (h).

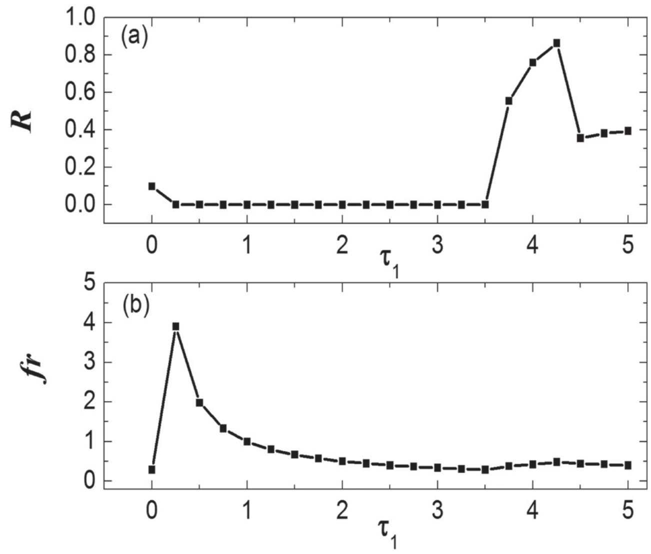

FIG. 3. Dependence of spiking regularity R (a) and the mean firing rate fr (b) with respect to the intra-time delay τ_1 when $\tau_2 = 0$. Values of the other parameters are not changed. The line is just a guide to the eye. The obtained results indicate that there exist some intermediate intra-time delays, at which the clustered neuronal networks exhibit fast regular firing activity.

single FHN neuron studied here, its membrane potential is nearly from -2.0 to 2.0. When its membrane potential is approximately larger than -1.0 (refer to Ref. 59), a spike is generated instantaneously. Thus, the corresponding spiking time can be determined by setting a threshold value of the membrane potential in a wide range $(-1.0, 2.0)$ without altering the results. As mentioned previously, spiking regularity of a single neuron characterizes the regularity of the neuron's inter-spike intervals. If the inter-spike intervals of a neuron are more consistent, then we argue that the neuron has higher spiking regularity. Thus, for the neuronal network's spiking regularity as quantified by Eq. (2), we see that higher spiking regularity of the whole neuronal network corresponds to a smaller value of R. Meanwhile, if the neuronal network has higher spiking regularity, then each neuron inside the neuronal network has more equivalent inter-spike intervals, which then results in much ordered spatiotemporal patterns.

In order to quantify the fast and slow firings of neuronal systems, we need to introduce another measure, the mean firing rate fr as

$$fr = \left\langle \frac{1}{N} \sum_I \sum_i \theta[x_{I,i}(t) - x_{th}] \right\rangle_t , \quad (4)$$

where $x_{th} = 0.0$ is the firing threshold determined by the action potential of the FHN neuron. Notably, $\theta(x)$ is the Heaviside function with $\theta(x) = 1$ if $x \geq 0$ and $\theta = 0$ if $x < 0$. The bracket $\langle\rangle$ indicates the average over the whole iteration time T.

IV. NUMERICAL SIMULATIONS

In this section, we will discuss effects of the intra- and inter-time delay on the spiking regularity numerically. We use the first-order Euler method to integrate Eq. (1). In order to avoid inaccurate simulations and numerical instability of the simulations, a small time step 0.0005 is applied in our stimulations. There is noise in the studied system, and the neuronal network is also generated with some randomness (connections between neurons from different subnetworks exist with probability p.). So, the numerical results exhibited in the following are averaged over 20 independent realizations.

We investigate effects of intra- or inter-time delays on the spiking regularity of the two clustered neuronal networks separately in Secs. IV A and IV B. Then, we turn to study their interactional effects. With the obtained results, we get some insights on the combined effects of intra- and inter-time delay on the clustered neuronal network's spiking regularity.

A. Effects of intra-time delay on spiking regularity

Firstly, we consider the effect of intra-time delay τ_1 on the spiking regularity of the studied neuronal network [expressed by Eq. (1)], i.e., $\tau_2 = 0$. The spatiotemporal patterns for eight different values of τ_1 are presented in Fig. 2. In this figure, τ_1 increases from 0.0 to 5.0. When $\tau_1 = 0$, the spatiotemporal pattern is ordered and the interspike intervals of each neuron are almost the same [Fig. 2(a)]. Thus, the spiking regularity of the neuronal network is at a high level for $\tau_1 = 0$. If we increase τ_1 from 0.0 to 0.25, the obtained results are shown in Fig. 2(b). Even though the interspike intervals are almost equidistant, they become narrower than the ones for $\tau_1 = 0$. This means that intra-time delays could increase the neuronal network's mean firing rate without decreasing its spiking regularity. It shows that τ_1 could increase the mean firing rate without destroying the spiking regularity of the neuronal network. What happens if τ_1 increases further? Can the mean firing rate of the neuronal network increase further without destroying the spiking regularity?

In order to find answers to these questions, we give the results for much larger values of τ_1 as 0.5, 1.0, 2.0, 3.0, and 4.0, as exhibited in Figs. 2(c)–2(g). From them, we can see that the interspike intervals are still almost equivalent, but become broader and broader when τ_1 increases. This indicates that the neuronal network's spiking regularity maintains at a high level but the mean firing rate of the neuronal network decreases by increasing τ_1. Therefore, the intra-time delay can be controlled not only to excite the neuronal firing but also to suppress it but without destroying the spiking regularity.

At this moment, we may wonder whether the mean firing rate of the neuronal network will decrease further, and the firing activity will be still regular for much larger intra-time delays. For seeking answers to this question, we increase the intra-time delay further. As shown in Fig. 2(h), where $\tau_1 = 5.0$, the interspike intervals for each neuron are not always the same as in the above cases. It indicates that spiking regularity of the neuronal network for $\tau_1 = 5.0$ decreases. Thus, R of the neuronal network does not always stay at a high level by introducing intra-time delays. While for the mean firing rate, we cannot clearly see if it decreases or increases with the spatiotemporal pattern. By introducing a measure for the mean firing rate fr, we find that it does not change much when τ_1 takes large values, as shown by Fig. 3, which will be stated in detail in the followings.

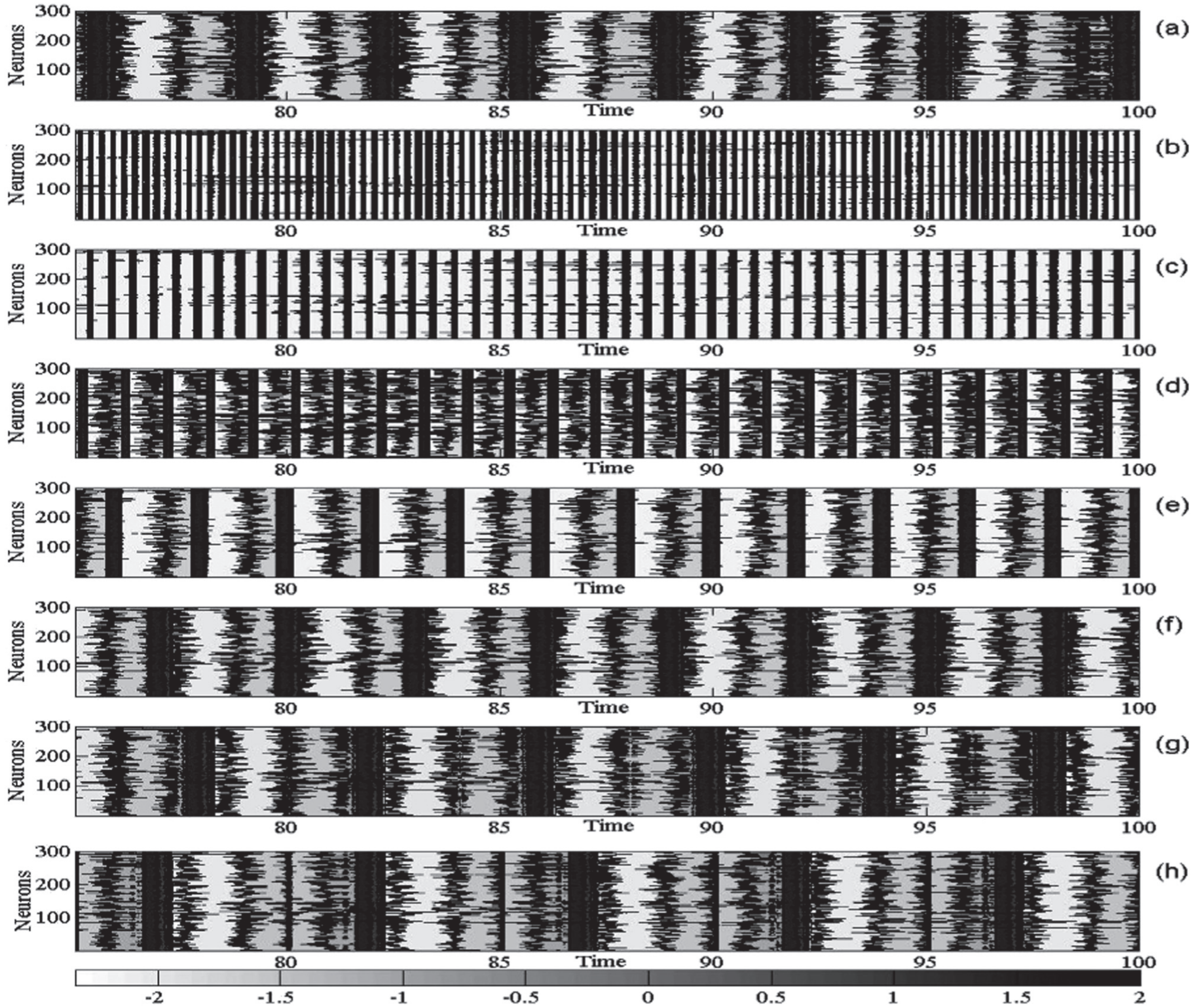

FIG. 4. Spatiotemporal patterns of the neuronal network with $\tau_1 = 0$ for various values of τ_2. The colorbar of values of the membrane potential $x_{I,i}$ is shown at the bottom. (a) $\tau_2 = 0$, where the neuronal network shows regular ISI intervals. (b) $\tau_2 = 0.25$, the spiking regularity is lower. The patterns become ordered again when τ_2 increases further as shown in (c) $\tau_2 = 0.5$, (d) $\tau_2 = 1.0$, (e) $\tau_2 = 2.0$, (f) $\tau_2 = 3.0$, (g) $\tau_2 = 4.0$. While for $\tau_2 = 5.0$, the spatiotemporal pattern shows non-equivalent interspike intervals (h).

Up to now, we just get a glancing acknowledgment of effects of the intra-time delay on spiking regularity. In order to get a relationship between spiking regularity and the intra-time delay τ_1 more clearly, we calculate variations of the measures R and fr with changing of τ_1. The obtained results are presented in Fig. 3. As shown there, with the increasing of τ_1, R is small when τ_1 is nearly smaller than 3.5 and increases to some large value when τ_1 becomes larger; For the mean firing rate fr, it increases to a very high level for τ_1 just increasing a little to nearly 0.25, then begins to decrease gradually, and finally, it nearly saturates when τ_1 is much larger. Combining the numerical simulation results shown by the two curves in Figs. 3(a) and 3(b), we find that with τ_1 increasing from 0.0 to 5.0, the neuronal network changes from a slow regular firing state to a fast regular state, then via a slow regular state, and finally to a slow irregular state. This indicates that there exist some intermediate intra-time delays, at which the clustered neuronal networks exhibit fast regular firing activity.

B. Effects of inter-time delay on spiking regularity

In this subsection, we will move to discuss effects of the inter-time delay τ_2 on the spiking regularity of the two clustered neuronal networks by setting $\tau_1 = 0$. Similar as discussed in Sec. IV A, some spatiotemporal patterns for different values of τ_2 are presented in Fig. 4. Comparing the results shown in Fig. 4 with the ones in Fig. 2, we find that they have a high degree of similarity. In details, the spatiotemporal pattern changes from an ordered one [Fig. 4(a)] to another ordered one [Fig. 4(b)] with interspike intervals becoming narrower, similar as observed in Figs. 2(a) and 2(b). It indicates that using appropriate inter-time delays ($\tau_2 = 0.25$) could make the neuronal networks more excited but without losing their firing regularity. When we increase τ_2 from 0.25 to larger values 0.5, 1.0, 2.0, 3.0, and 4.0, we find that the interspike intervals for each neuron inside the neuronal network are almost equivalent but become wider and wider as τ_2 increases. The corresponding spatiotemporal patterns for these values

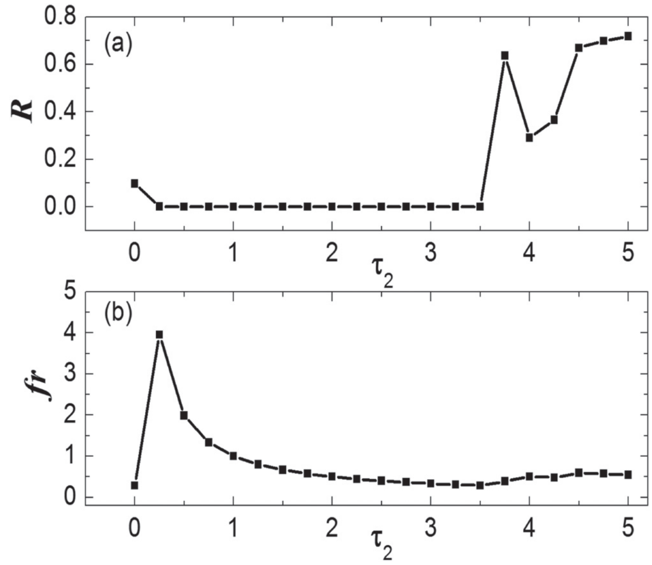

FIG. 5. Dependence of spiking regularity R (a) and the mean firing rate fr (b) with respect to the inter-time delay τ_2 when $\tau_1 = 0$. Values of the other parameters are not changed. The line is just a guide to the eye. The obtained results indicate that there exists some intermediate inter-time delays, at which the clustered neuronal networks exhibit fast regular firing activity.

of τ_2 are exhibited by Figs. 4(c)–4(g), respectively. Namely, introducing a proper smaller τ_2 could make the neuronal network's mean firing rate increasing greatly, and then the fast firing activity could also be suppressed by tuning the inter-time delay to larger values. Thus, we see that the mean firing rate of the neuronal network can also be tuned by the inter-time delay without destroying the spiking regularity. If we increase τ_2 further, for example, to 5.0 as shown in Fig. 4(h), we find that the interspiking intervals for each neuron are not equivalent yet. This means that the spiking regularity could be disturbed when τ_2 is large enough.

Figure 5 presents the dependence of R and fr on the controlled parameter τ_2. From this figure, we see that there exist some intermediate τ_2 (around 0.25) at which the neuronal network's spiking regularity is high and its mean firing rate increases distinguishably. While for larger τ_2, the spiking regularity of the neuronal network becomes fluctuating, but the mean firing rate stays at some smaller value. In other words, the neuronal network exhibits slow and less regular firing activity when τ_2 is large enough.

With the results obtained in Sec. IV A and the current subsection, we infer that the inter-time delay has similar influences as the intra-time delay that we have discussed in Sec. IV A. Then, we reveal that the inter-time delay also has substantial effects on the spiking regularity of the two clustered neuronal networks. Thus, the neuronal network's spiking regularity can be controlled not only by the intra-time delay but also by the inter-time delay.

C. Combined effects of intra- and inter-time delays on spiking regularity

The most interesting topic is to investigate interactional effects between the intra- and inter-time delays on the spiking regularity. Therefore, we will next focus on discussing the interplay of both.

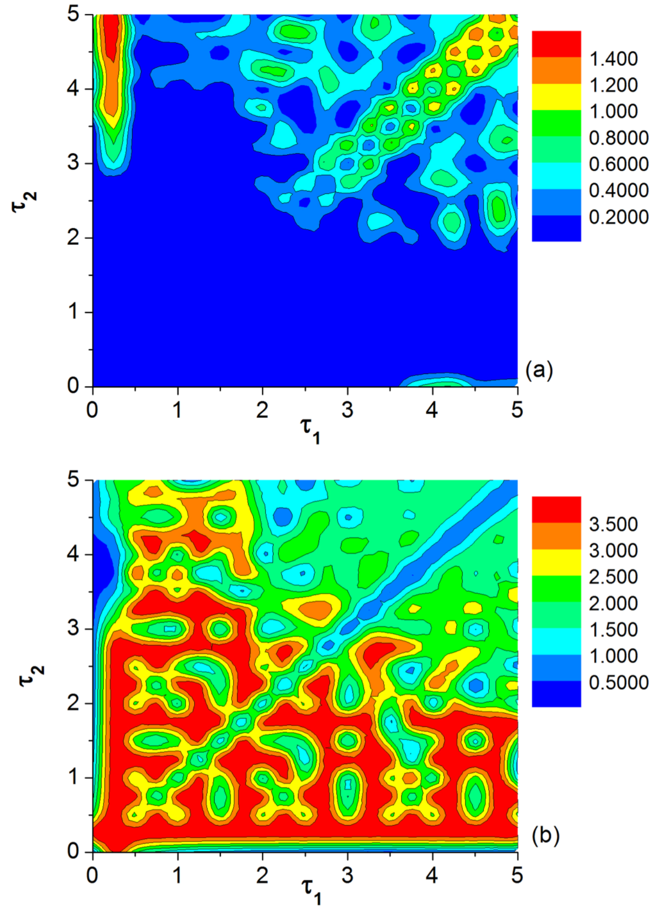

FIG. 6. (a) Dependence of R on the intra-time delay τ_1 and the inter-time delay τ_2 is shown; colorbar of values of R is shown at the right side with blue color indicates regular firings and red color indicates irregular firings. (b) Dependence of fr on the intra-time delay τ_1 and the inter-time delay τ_2 is shown; colorbar of values of fr is shown at the right side with blue color indicates slow firings and red color indicates fast firings.

The dependence of the measures R and fr on the intra-time delay τ_1 and the inter-time delay τ_2 are given in a 2-dimensional parameter space. As exhibited in Figs. 6(a) and 6(b), two beautiful symmetric patterns (colored online) are generated. In this paper, we refer fast regular firings to be the firing activity, which have high spiking regularity and large mean firing rate. Here, we think the firing activity has high spiking regularity if $R < 0.2$ and large mean firing rate if $fr > 3.5$. Through overlapping by the blue-colored areas ($R < 0.2$) in Fig. 6(a) and the red-colored areas ($fr > 3.5$) in Fig. 6(b), we see that fast regular firings arise in several regions in the $\tau_1 - \tau_2$ parameter plane.

By comparing the current results and the results obtained in the former two subsections where $\tau_2 = 0$ (in Sec. IV A) or $\tau_1 = 0$ (in Sec. IV B), we can further get a very important discovery. Here, we take the case where $\tau_2 = 0$, for example, to illustrate this important discovery. As shown in Sec. IV A, fast regular firings can just arise when τ_1 falls into a narrow internal belonging to $(0, 0.3)$. However, as exhibited in Fig. 6, if $\tau_2 > 0$ and takes some appropriate values, fast regular firings could arise in much wider regions of τ_1. For example, when $\tau_2 = 0.25$, the two clustered neuronal networks exhibit fast regular firings from $\tau_1 = 0.0$ to 5.0. It is much wider than

in the case where $\tau_2 = 0$ [see the overlapping of blue-colored area in Fig. 6(a) and red-colored area in Fig. 6(b)]. This indicates that introducing proper inter-time delay could strongly promote the intra-time delay's ability to induce fast regular spiking activity of the two clustered neuronal networks. In the same way, if we compare the current results with the one shown in Sec. IV B, we find that introducing proper intra-time delay could also promote the inter-time delay's ability to induce fast regular firings. Therefore, with the interplay of the intra- and inter-time delays, the two clustered neuronal networks could exhibit fast regular firings frequently.

V. DISCUSSION

With the results shown in Sec. IV, we learn that intra- or inter-time delay could separately induce two clustered neuronal networks to generate fast regular firings, and interactions between these two time delays could further make fast regular firings occurring frequently. In this section, we will try to give some illustrations on the occurrence of time-delay-induced fast regular firings. Note that fast regular firings are referred to the firing activity with the spiking regularity $R < 0.2$ and the mean firing rate $fr < 3.5$ in this paper.

We firstly start from the simple cases where the intra-time delay $\tau_1 = 0$ or the inter-time delay $\tau_2 = 0$. In order to illustrate the occurrence of fast regular firings, we give the interspike interval bifurcation diagram with respect to τ_1 for $\tau_2 = 0$ and τ_2 for $\tau_1 = 0$, respectively, shown in Fig. 7. As exhibited in Fig. 7(a), for much smaller τ_1(nearly smaller than 0.25), the interspike intervals take either multiple values or no value (see the inset figure in Fig. 7 for details). The reason why the interspike intervals take no value is that time delay could make an oscillation death happen in neuronal systems.[60–62] Here, we pay attention to clarify the occurrence of fast regular firing and do not talk much about oscillation death. According to the definition of the spiking regularity measure R, the clustered neuronal network's spiking regularity is worse if the interspike intervals take multiple values.

From Fig. 7(a), it can be seen that the clustered neuronal networks exhibit less regular firing activity for both larger τ_1(nearly larger than 3.5) and smaller τ_1 (nearly smaller than 0.25). While for intermediate τ_1(larger than 0.25 and smaller than 3.5), the interspike intervals are almost equivalent, which indicate the emergence of higher regular firings. Meanwhile, for intermediate τ_1, we find that values of the interspike intervals are nearly equal to it. Therefore, the firing periods of the neurons inside the two clustered neuronal networks are nearly equal to the intra-time delay τ_1 when it takes intermediate values. Then, the mean firing rate of the clustered neuronal network is nearly equal to its reciprocal value. Thereby, the smaller the intra-time delay τ_1 is, the higher the mean firing rate of the clustered neuronal networks is. Because oscillation death could occur in clustered neuronal networks for much smaller τ_1, the mean firing rate could take largest values when τ_1 is around 0.25. Thus, fast regular firings are observed around $\tau_2 = 0.25$ as exhibited by Fig. 3 in the former contents. Thereby, we can also understand the emergence of fast regular

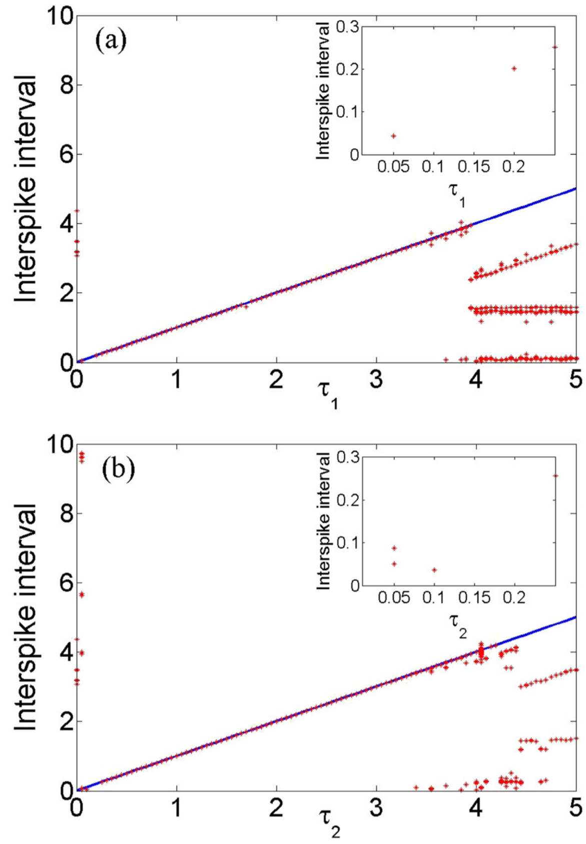

FIG. 7. (a) Interspike interval bifurcation diagram with respect to τ_1 for $\tau_2 = 0$; (b) interspike interval bifurcation diagram with respect to τ_2 for $\tau_1 = 0$. The blue line in each figure indicates the line with $x = y$.

firings induced by the inter-time delay τ_2 by analyzing the interspike intervals' bifurcation diagram shown in Fig. 7(b).

Next, we turn our attention to illustrate why introducing proper intra-(inter-) time delays could promote the inter-(intra-) time delay's ability for inducing fast regular firings. For this aim, we set τ_2 as 0.25, 0.5, 0.75, 1.0, 1.25, and 1.5, respectively. Then, we investigate variations of R and fr with respect to τ_1 for these different values of τ_2. The simulation results are presented in Fig. 8.

As shown in Fig. 8, when $\tau_2 = 0.25$ is introduced into the neuronal network, the intra-time delay τ_1 could induce fast regular firings for all multiple values of $\tau_2 = 0.25$. When $\tau_2 = 0.5$ (or $\tau_2 = 0.75, 1.25$), it is found that fast regular firings could emerge when τ_1 is multiples of 0.25 and not multiples of $\tau_2 = 0.5$ (or $\tau_2 = 0.75, 1.25$). For example, when $\tau = 0.75$, as shown in Fig. 8, fast regular firings can be induced by τ_1 just for $\tau_1 = 0.25, 0.5, 1.0, 1.25, 1.75, 2, 2.5, 2.75, 3.25, 3.5, 4, 4.25, 4.75$, and 5.0; fast regular firings cannot be induced by τ_1 for $\tau_1 = 0.75, 1.5, 2.25, 3, 3.75$, and 4.5. Namely, when $\tau_2 = 0.75$, fast regular firings occur for τ_1 being multiples of 0.25 and not multiples of $\tau_2 = 0.75$. While when $\tau_2 = 1.0$, fast regular firings just occur when τ_1 is multiples of 0.25 and not multiples of 0.5 and $\tau_2 = 1.0$. Finally, for $\tau_2 = 1.5$, fast regular firings could emerge when τ_1 is multiples of 0.25 and not multiples of $0.5, 0.75$, and $\tau_2 = 1.5$. With these observations, we can surprisingly find that fast regular firings could occur when the largest value of common divisors of τ_1 and τ_2 is 0.25, at which fast regular firings can be induced by

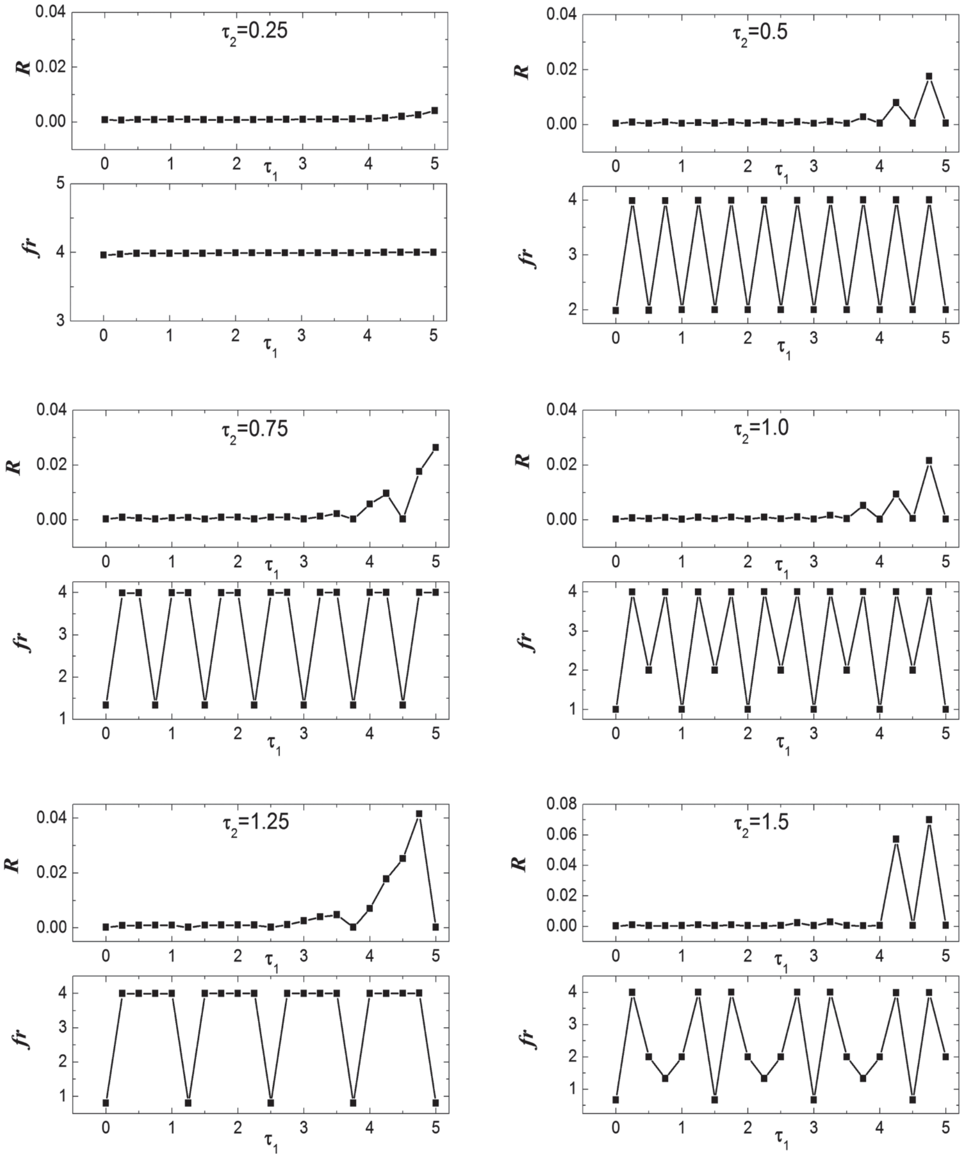

FIG. 8. Dependence of the spiking regularity R and the mean firing rate fr with respect to τ_1 for different values of τ_2. The line is just a guide to the eye. The obtained results indicate that when the largest value of common divisors of intra- and inter-time delays is equal to 0.25 at which fast regular firings could be induced by intra- or inter-time delays separately, then fast regular firings could occur.

τ_1 or τ_2 separately. This discovery inspires us to formulate the following conjecture: fast regular firings may occur frequently when the largest value of common divisors of τ_1, τ_2 is equal to a value at which fast regular firings could be induced by intra- or inter-time delays separately. In order to check this conjecture, we set τ_2 as 0.28, 0.56, 0.84, 1.12, 1.4, and 1.68 to investigate variations of spiking regularity R and the mean firing rate fr with respect to τ_1; the simulation results are shown in Fig. 9. From this figure, we also get the conclusion that fast regular firings could be induced by the interplay of the intra-time delay τ_1 and the inter-time delay τ_2 when their largest value of common divisors is 0.28, at which fast regular firings could be induced by intra- or inter-time delays separately.

VI. SUMMARY

Summarizing, in this paper, we have studied effects of intra- and inter-time delays on dynamical characteristics of neuronal firings measured by the spiking regularity and the mean firing rate in two clustered neuronal networks which are locally modelled by FHN neuronal models. Based on our simulation results, we have found that fast regular firings could be separately induced not only by the intra-time delay but also by the inter-time delay. Meanwhile, by introducing appropriate inter-(or intra-) time delays could greatly enhance the ability of intra-(or inter-) time delay to induce fast regular firings. With detailed analyses, we have got deep understanding on effects of intra- and inter-time delays on the spiking regularity and the mean firing rate of the two clustered neuronal networks, especially the interplay effects of intra- and inter-time delays on these firing characteristics. We have found that when the largest value of common divisors of intra- and inter-time delays are equal to a value at which fast regular firings could be induced by intra- or inter-time delays separately, then fast regular firings could occur.

In real neuronal systems, delayed coupling terms between two connected neurons could be described in different mathematical forms. For different synaptic types, such as electrical and chemical synapses, delayed coupling terms could be different.[63] If we consider the cumulative interactions (the coupling is integrated over a time interval τ), an integrative

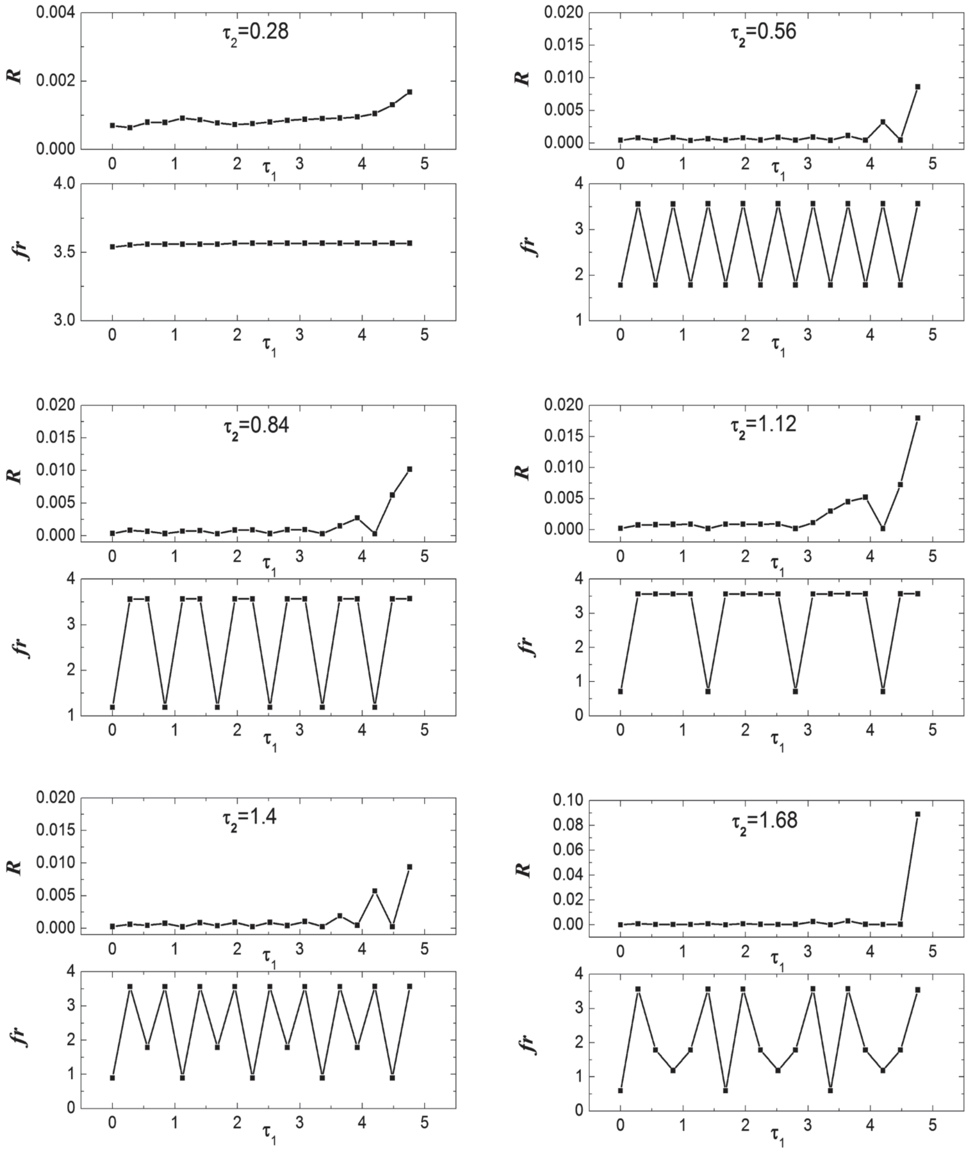

FIG. 9. Dependence of the spiking regularity R and the mean firing rate fr with respect to τ_1 for different values of τ_2. The line is just a guide to the eye. The obtained results indicate that when the largest value of common divisors of intra- and inter-time delays is equal to 0.28 at which fast regular firings could be induced by intra- or inter-time delays separately, then fast regular firings could occur.

time-delay coupling should be considered.[64] Sometimes, time delay is also changing with time.[65] No matter what mathematical forms time delay appears with, time delay always has great influences on the system's dynamical behaviors.[66] Even though effects of time delay on neuronal dynamics have been discussed in many literature studies, its influences on neuronal firings of clustered neuronal networks are not widely studied. Therefore, different from the former works about effects of time delay on neuronal dynamics, we consider intra- and inter-time delays in the clustered neuronal network in this paper and reveal that fast regular firings could be induced frequently through the interplay of these two time delays.

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