Local and global synchronization transitions induced by time delays in small-world neuronal networks with chemical synapses

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Abstract Effects of time delay on the local and global synchronization in small-world neuronal networks with chemical synapses are investigated in this paper. Numerical results show that, for both excitatory and inhibitory coupling types, the information transmission delay can always induce synchronization transitions of spiking neurons in small-world networks. In particular, regions of in-phase and out-of-phase synchronization of connected neurons emerge intermittently as the synaptic delay increases. For excitatory coupling, all transitions to spiking synchronization occur approximately at integer multiples of the firing period of individual neurons; while for inhibitory coupling, these transitions appear at the odd multiples of the half of the firing period of neurons. More importantly, the local synchronization transition is more profound than the global synchronization transition, depending on the type of coupling synapse. For excitatory synapses, the local in-phase synchronization observed for some values of the delay also occur at a global scale; while for inhibitory ones, this synchronization, observed at the local scale, disappears at a global scale. Furthermore, the small-world structure can also affect the phase synchronization of neuronal networks. It is demonstrated that increasing the rewiring probability can always improve the global synchronization of neuronal activity, but has little effect on the local synchronization of neighboring neurons.

Keywords Synchronization · Time delay · Neuronal network · Small-world

Introduction

Synchronization in biological neuronal systems has attracted extensive attention over the last few years and a series of meaningful phenomena have been observed (Pikovsky et al. 2001; Acker et al. 2003; Steriade 1997). Many experimental and theoretical works have demonstrated that the synchronization of neuronal activity is of particular important for brain functions (Fries et al. 1997, 2002; Gray 1994). It is shown that well-coordinated global synchronization of neuronal spike trains play a vital role in the neuronal signaling and information processing and transmitting across different areas of brain cortex (Singer 1993; Singer and Gray 1995). Globally synchronized activities involving widespread populations of neurons in neocortex are associated with the execution of complex sensorimotor tasks and have been proposed to participate in the ‘binding’ of sensory attributes during perceptual synthesis (Chawla et al. 2001). On the other hand, recent experiments in monkey visual cortex also demonstrate the synchrony among γ activities (30–90 Hz) in local areas and its important role in perceptual modulation (Eckhorn et al. 2004). Moreover, the phenomenon of zero-lag synchronization between distant cortical areas is reported to rely on local connectivity, such as a specific network motif (Gollo et al. 2014). Motivated by above observations, it is necessary to explore the generation mechanisms underlying the variety of neuronal synchrony.

To elucidate this question, a large amount of studies have been carried out to investigate the temporal coherence and spatial synchrony of different neuronal ensembles. For instance, synchronization and propagation of bursts has been studied in networks of coupled map neurons and the underlying mechanism for this synchronization was explained (Tanaka et al. 2006). Furthermore, the effects of

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mutual chaotic phase synchronization in ensembles of map-based bursting oscillators have been investigated (Ivanchenko et al. 2004; Batista et al. 2009). More recently, Batista have studied synchronization in clustered networks of bursting neurons and given bounds for the smallest coupling strength needed to achieve global synchronization (Batista et al. 2012). All these studies demonstrate that the interplay between the intrinsic dynamics of the constituent neurons and their complex structure of connectivity strongly affects the synchronization and oscillatory behavior of the resulting network. However, the exact conditions under which can large neuronal ensembles synchronize their spiking or bursting activity are in general not fully understood.

Recent developments in the quantitative analysis of complex networks, mostly revealed by anatomical, electroencephalographic (EEG), and neuroimaging data, demonstrate that many biological neuronal networks present the typical properties of small-world networks, the short path length of which is associated with a high level of local clustering (Watts and Strogatz 1998). Up to now, small-world topology has been found in the brain's structural and functional systems both at the whole-brain scale of human neuroimaging and at a cellular scale in non-human animals (Bullmore and Sporns 2009; van der Heuvel et al. 2008; Reijneveld et al. 2007). Sporns (Sporns et al. 2000) have described small-world topological properties, and investigated the relationship between topology and complex dynamics, in brain networks. Experimental studies indicate that small-worldness might be a conserved property of brain networks over different species and spatial scales (Bullmore and Sporns 2009; Bassett and Bullmore 2006). Modeling studies show that, compared with regular networks, neuronal systems with small-world connectivity are easier to get synchronization. Increasing the number of shortcut links between long-range units can largely enhance the synchronization degree of small-world networks (Han et al. 2008). Moreover, the significant role of small-world topology on the resonance dynamics of excitable neural media has been explored (Perc 2007; Ozer et al. 2009; Gao et al. 2001).

In biological neural systems, the information transmission delay is ubiquity, the cause of which is mainly attributed to the time needed for the conduction of a nerve impulse from one neuron to the next across a synapse. In synapses with a chemical transmission mechanism the synaptic delay can last from 0.3 to 0.5 ms to several tens of milliseconds (Kandel et al. 1991), determining the dynamics and functions of neuronal networks. It has been demonstrated that the time delay can play many different key roles, such as introducing stable oscillations (Bélair et al. 1996), enhancing neural synchrony (Dhamala et al. 2004; Manju Shrii et al. 2012), and shaping spatiotemporal

order (Gong et al. 2012; Roxin et al. 2005; Yang et al. 2012), as well as inducing multiple stochastic resonances (Yu et al. 2013; Wang et al. 2009). Particularly, the effects of time delay on the synchronization among neurons have been extensively studied, and many interesting phenomena have been reported. It is shown that, as the delay increases, regions of irregular and regular propagating excitatory fronts related to the synchronization transitions appear intermittently in excitable small-world and scale-free neuronal networks (Pérez et al. 2011; Wang et al. 2008, 2009, 2010). However, most work has focus on the effect of time delay on the collective dynamics of the whole network; less attention has been given to its impact on the synchronization properties of locally connected neurons, i.e., local synchronization.

In this paper, we extend this subject by studying the effects of time delay on the local and global synchronization in small-world networks of chemically coupled map-based neurons. We consider both excitatory and inhibitory coupling types. We aim to explore the dependence of local and global synchronization transitions in small-world neuronal networks on the information transmission delay and other network parameters. Accordingly, the remainder of this paper is organized as follows. In “[Mathematical model and methods](#)”, we describe the mathematical model of the time-delayed small-world neuronal network with chemical synapses. Local and global synchronization transitions induced by the time delay are investigated in “[Results](#)”. Finally, a brief conclusion of this paper is given in “[Conclusions](#)”.

Mathematical model and methods

In small-world networks, the temporal evolution of each neuron with chemical synapses can be described by a two-dimensional map (Rulkov 2001):

$$x_i(n+1) = \frac{\alpha}{1+x_i^2(n)} + y_i(n) - I_i^{syn}(n) \quad (1)$$

$$y_i(n+1) = y_i(n) - \beta x_i(n) - \gamma, \quad (2)$$

where $x_i(n)$ and $y_i(n)$ are fast and slow dynamical variable of the map, respectively. Small values of parameters $\beta = \gamma = 0.001$ determine a slow temporal evolution of $y_i(n)$. The parameter α determines the spiking-bursting activity of the neuron. Here, we first set $\alpha = 2.3$, such that each individual neuron exhibits spike excitations with the natural period $T_0 = 850$. n is the discrete time index. $I_i^{syn}(n)$ is the synaptic current of neuron i , and take the form

$$I_i^{syn}(n) = g_c(x_i(n) - v) \sum_{j=1}^N \varepsilon_{ij} \Gamma(x_j(n)) \quad (3)$$

g_c is the coupling strength. v is the synaptic reversal potential, whose value determines the types of synapse: inhibitory or excitatory. For the inhibitory synapses, we choose $v = -1.8$; whereas for the excitatory synapses, $v = 1.8$. The matrix $\varepsilon = (\varepsilon_{ij})$ is an connectivity matrix: $\varepsilon_{ij} = 1$ if neuron i is connected to neuron j , $\varepsilon_{ij} = 0$ otherwise, and $\varepsilon_{ii} = 0$. The delayed synaptic coupling function is modeled by the sigmoidal function

$$\Gamma(x_i(n)) = 1 / (1 + \exp\{-\lambda[x_j(n - \tau) - \Theta_s]\}) \quad (4)$$

where Θ_s is the threshold, above which the postsynaptic neuron is affected by the presynaptic one. Here, we take $\Theta_s = -1.0$. $\lambda = 30$ represents a constant rate for the onset of excitation or inhibition. τ is the information transmission delay among neurons.

The small-world network can be obtained by starting from a ring-like network with regular connectivity containing $N = 200$ vertices, each one connecting to its $K = 6$ nearest neighbors. Each link is then randomly rewired with probability p . By increasing the probability p , the architecture of the network is tuned between two extremes: regular ($p = 0$) and random ($p = 1$) networks. For $0 < p < 1$, the resulting network have small-world properties, characterized by a distinctive combination of short characteristic path length, comparable with that of a random network, and high clustering coefficient, just like a regular network (Watts and Strogatz 1998). The time delay τ and rewiring probability p are two main parameters to be investigated in this paper.

In order to quantitatively characterize the synchronization degree of spiking neurons on small-world networks, we introduce the phase of neuron i as:

$$\phi_i(n) = 2\pi k + 2\pi \frac{n - n_k}{n_{k+1} - n_k}, (n_k < n < n_{k+1}) \quad (5)$$

where n_k is the time of the k th firing of neuron i and $n_{k+1} - n_k$ is the inter-spike interval. Thus, the neuronal phase $\phi_i(n)$ increases linearly between the firing moments n_k and n_{k+1} , and gains a 2π growth over each inter-spike interval.

To measure the phase synchronization between neuron i and the set of its neighbors $v(i)$, we calculate the quantity (Pérez et al. 2011):

$$s_i(n) = \frac{1}{k_i} \sum_{j \in v(i)} \sin^2\left(\frac{\phi_i(n) - \phi_j(n)}{2}\right), \quad (6)$$

where k_i represents the degree of neuron i , i.e., the number of neurons connected to neuron i . Then, the local phase synchronization of the network is measured by the order parameter S^{loc} , which is defined as

$$S^{loc} = \frac{1}{t} \sum_{n=1}^t \left(\frac{1}{N} \sum_{i=1}^N s_i(n) \right), \quad (7)$$

where t is the period of numerical integration. To measure the global phase synchronization, we first calculate the synchronization degree of neuron i with the rest of the network as (Pérez et al. 2011)

$$s'_i(n) = \frac{1}{N} \sum_{j=1}^N \sin^2\left(\frac{\phi_i(n) - \phi_j(n)}{2}\right), \quad (8)$$

Then, by averaging over all units, we obtain a global order parameter S^{glob} , described as

$$S^{glob} = \frac{1}{t} \sum_{n=1}^t \left(\frac{1}{N} \sum_{i=1}^N s'_i(n) \right). \quad (9)$$

It is evident that the order parameters S^{loc} and S^{glob} are zero if the phases of the neurons are equal, i.e., in-phase synchronization, and unity if they differ by π , termed as anti-phase synchronization. When the phases of the neurons are randomly distributed, i.e., out-of-phase synchronization, the order parameters take an intermediate value of 0.5.

Results

In what follows, we present the effects of information transmission delay τ and rewiring probability p on the synchronization of small-world neuronal networks with chemical coupling. We first consider the network with excitatory coupling and the rewiring probability $p = 0.1$. Results presented in Fig. 1 illustrates the spatiotemporal dynamics of neurons that are evoked by different values of τ . As one can see, when $\tau = 0$, $\tau = 850$ and $\tau = 1,700$, the neuronal spiking is clearly synchronous, while this synchronized state disappears for $\tau = 400$, $\tau = 1,200$. For inhibitory coupling, similar transitions of spiking synchronization can also occur for appropriate time delays (not shown here). It can thus be concluded that the information transmission delay plays a pivotal role in the synchronization of neuronal networks by either enhancing or destroying the synchrony of neuronal activity.

In Fig. 2a, we plot the local and global synchronization coefficients S^{loc} and S^{glob} versus the time delay τ for excitatory coupling. Numerical results show that, as the delay increases, three minima of S^{loc} and S^{glob} approximately appear at $\tau = 850$, $\tau = 1,700$, and $\tau = 2,550$. It is proved that the delay-induced transitions to synchronized neuronal activity indeed appear intermittently as the delay increases. Importantly, all these synchronization transitions roughly occur at integer multiples of the spiking period of individual neurons. For inhibitory connections, similar synchronization transitions also occur, but at the odd multiples of the half of the firing period of neurons (Fig. 2b). This difference is mainly result from phase slips

Fig. 1 Spatiotemporal plots obtained for different time delays. *a* $\tau = 0$, *b* $\tau = 400$, *c* $\tau = 850$, *d* $\tau = 1,200$, *e* $\tau = 1,700$. The color coding is linear, white depicting -2 and black depicting 0.1 values of $x(n)$. Other parameter values are $g_c = 0.01$ and $p = 0.1$

Fig. 2 Dependence of the local and global synchronization parameter S^{loc} and S^{glob} on the time delay τ for **a** excitatory coupling and **b** inhibitory coupling. Other parameter values are $g_c = 0.01$ and $p = 0.1$. (Color figure online)

induced by the time delay. Indeed, the delay-induced multiple synchronization states of neuronal activity are due to an intricate interplay between the inherent dynamics of constituting neurons and the locking between the delay time and the oscillatory period of neuronal spiking (Pérez et al. 2011; Wang et al. 2008, 2009, 2010). On the other hand, for both coupling types the local synchronization transition is more profound than the global synchronization transition, as the value of S^{glob} is no larger than 0.5. That is to say, the small-world neuronal network cannot get overall anti-phase synchronization, which can only be achieved by locally connected neurons with appropriate time delays.

In order to generalize the above obtained results, we calculate the value of the local and global synchronization parameters in a two-dimensional parameter space: time delay τ versus coupling strength g_c (Fig. 3). At a local level, for both excitatory and inhibitory coupling, there exists some narrow-banded regions with small values of $S^{loc} \sim 0$, where

in-phase synchronization of neuronal activity is realized, as shown in Fig. 3a and c. For excitatory coupling, these regimes are approximately located at $\tau \approx mT_0$; while for inhibitory connections, they appear for $\tau \approx (2m + 1)T_0/2$. However, parameters outside these tongue-like regions will unfortunately impair the local synchrony, leading to out-of-phase ($S^{loc} \sim 0.5$) even anti-phase synchronization ($S^{loc} \sim 1$). In the latter case, neighboring neurons fire with a phase difference of π between them. This phenomenon occurs at $\tau = (2m + 1)T_0/2$ for excitatory coupling, while happens at $\tau = mT_0$ for inhibitory connections. In conclusion, all these observations demonstrate that the neuronal activity enters and exits the in-phase synchronous regions in an intermittent fashion as the delay increases. The different is the delay times at which these synchronization transitions occur.

At a global scale, the phase synchronization depends on the type of synapses. For excitatory synapses, the local in-

Fig. 3 Contour plots of the synchronization parameter $S^{loc}[S^{glob}]$ in dependence on the time delay τ and the coupling strength g_c for **a**, **b** excitatory coupling and **c**, **d** inhibitory coupling

Fig. 4 Dependence of the local and global synchronization parameter $S^{loc}[S^{glob}]$ on the time delay τ for different coupling strength g_c : **a**, **b** excitatory coupling and **c**, **d** inhibitory coupling. (Color figure online)

Fig. 5 Dependence of the local and global synchronization parameter S^{loc} and S^{glob} on the rewiring probability p for **a** excitatory coupling ($\tau = 850$) and **b** inhibitory coupling ($\tau = 450$). (Color figure online)

Fig. 6 Contour plots of the synchronization parameter S^{loc} [S^{glob}] in dependence on the time delay τ and the rewiring probability p for **a**, **b** excitatory coupling and **c**, **d** inhibitory coupling

phase synchronization observed for some values of the delay also occur at a global scale (Fig. 3b). While for inhibitory ones, this synchronization, observed at the local scale, disappears at a global scale (Fig. 3d). It is indicated that global in-phase synchronization cannot be achieved in small-world neuronal networks with inhibitory chemical coupling. However, in previous studies of global synchronization in neuronal networks with electrical synapses, it is shown that the neural networks with purely inhibitory

synapses can even get synchronization for some particular values of time delay (Wang and Chen 2011). The reason for this difference may be the stronger synchronization ability of electrical synapses compared with chemical ones. Chemical coupling acts only when the presynaptic neurons is spiking, whereas electrical coupling connects neurons at all times. Hence electrical synapses can make the dynamics of neurons stay much closer during the non-spiking epoch, leading to the more profound synchronization (Yu et al.

Fig. 7 Dependence of the local and global synchronization parameter S^{loc} and S^{glob} on the time delay τ for **a** excitatory coupling and **b** inhibitory coupling. Other parameter values are $\alpha = 4.1$, $g_c = 0.01$ and $p = 0.1$. (Color figure online)

Fig. 8 Dependence of the local and global synchronization parameter S^{loc} and S^{glob} on the rewiring probability p for **a** excitatory coupling ($\tau = 350$) and **b** inhibitory coupling ($\tau = 800$). (Color figure online)

2013). Furthermore, the coupling strength between neurons strongly affects the synchronous spiking transition in small-world neuronal networks. As shown in Fig. 4, with the increase of coupling strength, the synchronization degree of the ensemble is enhanced for both excitatory and inhibitory coupling types. It is thus indicated that increasing the coupling intensity can always induces the transition from non-synchronization to synchronization.

To gain more insights into the dependence of synchronous spiking transition in small-world neuronal networks on the rewiring probability, we plot the variation of S^{loc} and S^{glob} with respect to p , as shown in Fig. 5. It can be seen that, for each kind of synapses, S^{glob} decreases monotonously and finally reach a constant with the increase of p . It is indicated that the nonsynchronous neuronal activity can transit to regular synchronization and finally saturate as p approaches the random network limit. To make an overall inspection, the dependence of S^{glob} on both p and τ is presented in Fig. 6b and d. It is shown that the small-world neuronal network can transit to in-phase

synchronization as p increases. From Fig. 5, we can also see that S^{loc} changes much less profoundly as p is varied, thus implying no clear effect of small-world topology on the local synchronization of the neuronal network. Results of S^{loc} versus both p and τ are shown in Fig. 6a and c. It is evident that S^{loc} undergoes no significant changes as p increases, which fully support our above assessment. In sum, global synchronization transitions on small-world neuronal networks can also be induced by the variation of rewiring probability p .

Finally, the local and global synchronization is investigated in the bursting small-world neuronal network. Here α is set to be 4.1 so that each neuron in the network bursts with the natural period $T_0 = 350$. In Fig. 7, we plot the synchronization coefficients S^{loc} and S^{glob} versus the time delay τ for excitatory and inhibitory coupling, respectively. It is shown that, for both coupling types, the information transmission delay can induce synchronization transitions of bursting neurons in small-world networks: the synchronous state emerges at $\tau \approx mT_0$ for excitatory coupling

and $\tau \approx (2m + 1)T_0/2$ for inhibitory coupling. The observed results are similar with that obtained in spiking neuron networks. In addition, the variations of S^{loc} and S^{glob} with respect to p are presented in Fig. 8. It is shown that, with the increase of p , S^{glob} decreases monotonously and finally reach a constant, while S^{loc} increases much less profoundly. It is demonstrated that increasing the rewiring probability can always enhance the global synchronization of neuronal activity, but has little effect on the local synchronization of neighboring neurons, which is in accord with the results shown in Fig. 5. From the results above, it can be concluded that the transitions of the local and global synchronization also occur in the bursting small-world neuronal network with time delay.

Conclusions

In this paper we have studied the dependence of local and global synchronization transitions in small-world neuronal networks with chemical synapses on the information transmission delay and the wiring probability. The obtained numerical results show that, for both excitatory and inhibitory coupling types, the synaptic time delay can always induce synchronization transitions in small-world neuronal networks. It can either enhance or destroy the synchrony of neuronal activity. In particular, regions of in-phase and out-of-phase synchronization of connected neurons appear intermittently as the delay increases. In addition, for excitatory coupling, all these synchronization transitions occur approximately at integer multiples of the firing period of individual neurons; while for inhibitory coupling, they appear for the odd multiples of the half of the firing period of neurons. More importantly, the local synchronization transition is more profound than the global synchronization transition, depending on the type of synapses. For excitatory synapses, the local in-phase synchronization observed for some values of the delay also occur at a global scale; while for inhibitory ones, this synchronization, observed at the local scale, disappears at a global scale. Furthermore, it is found that the small-world topology can also affect phase synchronization transitions of neuronal system. Irrespectively of the coupling type, increasing the rewiring probability can always enhance the global synchronization of neuronal activity, but has little effect on the local synchronization of neighboring neurons. In conclusion, the information transmission delay and rewiring probability can perform significant but different roles in the synchronization of small-world neuronal networks.

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References

- Acker CD, Kopell N, White JA (2003) Synchronization of strongly coupled excitatory neurons: relating network behavior to biophysics. *J Comput Neurosci* 15:71–90
- Bassett DS, Bullmore E (2006) Small-world brain networks. *Neuroscientist* 12:512–523
- Batista CAS, Batista AM, de Pontes JAC, Lopes SR, Viana RL (2009) Bursting synchronization in scale-free networks. *Chaos, Solitons & Fractals* 41:2220–2225
- Batista CAS, Lameu EL, Batista AM, Lopes SR, Pereira T, Zamora-Lopez G, Kurths J, Viana RL (2012) Phase synchronization of bursting neurons in clustered small-world networks. *Phys Rev E* 86:016211
- Bélair J, Campbell SA, van den Driessche P (1996) Frustration, stability, and delay-induced oscillations in a neural network model. *SIAM J Appl Math* 56(1):245–255
- Bullmore E, Sporns O (2009) Complex brain networks: graph theoretical analysis of structural and functional systems. *Nat Rev Neurosci* 10:186–198
- Chawla D, Friston KJ, Lumer ED (2001) Zero-lag synchronization dynamics in triplets of interconnected cortical areas. *Neural Networks* 14:727–735
- Dhamala M, Jirsa VK, Ding MZ (2004) Enhancement of neural synchrony by time delay. *Phys Rev Lett* 92:074104
- Eckhorn R, Gail AM, Bruns A, Gabriel A, Al-Shaikhli B, Saam M (2004) Different types of signal coupling in the visual cortex related to neural mechanisms of associative processing and perception. *IEEE Trans Neural Networks* 15:1039–1052
- Fries P, Roelfsema P, Engel A, König P, Singer W (1997) Synchronization of oscillatory responses in visual cortex correlates with perception in interocular rivalry. *Proc Natl Acad Sci USA* 94:12699–12704
- Fries P, Schroeder J, Roelfsema P, Singer W, Engel A (2002) Oscillatory neuronal synchronization in primary visual cortex as a correlate of stimulus selection. *J Neurosci* 22:3739–3754
- Gao Z, Hu B, Hu G (2001) Stochastic resonance of small-world networks. *Phys Rev E* 65:016209
- Gollo LL, Mirasso C, Sporns O, Breakspear M (2014) Mechanisms of zero-lag synchronization in cortical motifs. *PLoS Comput Biol* 10:e1003548
- Gong Y, Wang L, Xu B (2012) Delay-induced diversity of firing behavior and ordered chaotic firing in adaptive neuronal networks. *Chaos, Solitons Fractals* 45:548–553
- Gray CM (1994) Synchronous and oscillations in neuronal systems: mechanisms and functions. *J Comput Neurosci* 1:11–38
- Han F, Lu Q, Wiercigroch M, Ji Q (2008) Chaotic burst synchronization in heterogeneous small-world neuronal network with noise. *Int J Non-Linear Mech* 44:298–303
- Ivanchenko MV, Osipov GV, Shalfeev VD, Kurths J (2004) Phase synchronization in ensembles of bursting oscillators. *Phys Rev Lett* 93:134101
- Kandel ER, Schwartz JH, Jessell TM (1991) *Principles of Neural Science*. Elsevier, Amsterdam
- Manju Shrii M, Senthilkumar DV, Kurths J (2012) Delay coupling enhances synchronization in complex networks. *EPL* 98:10003
- Ozer M, Perc M, Uzuntarla M (2009) Stochastic resonance on Newman-Watts networks of Hodgkin-Huxley neurons with local periodic driving. *Phys Lett A* 373:964–968
- Perc M (2007) Stochastic resonance on excitable small-world networks via a pacemaker. *Phys Rev E* 76:066203

- Pérez T, Garcia GC, Eguíluz VM, Vicente R, Pipa G, Mirasso C (2011) Effect of the topology and delayed interactions in neuronal networks synchronization. *PLoS ONE* 6:e19900
- Pikovsky A, Rosenblum M, Kurths J (2001) Synchronization: a universal concept in nonlinear sciences. Cambridge University Press, Cambridge
- Reijneveld JC, Ponten SC, Berendse HW, Stam CJ (2007) The application of graph theoretical analysis to complex networks in the brain. *Clin Neurophysiol* 118:2317–2331
- Roxin A, Brunel N, Hansel D (2005) Role of delays in shaping spatiotemporal dynamics of neuronal activity in large networks. *Phys Rev Lett* 94:238103
- Rulkov NF (2001) Regularization of synchronized chaotic bursts. *Phys Rev Lett* 86:183–186
- Singer W (1993) Synchronization of cortical activity and its putative role in information processing and learning. *Annu Rev Physiol* 55:349–374
- Singer W, Gray CM (1995) Visual feature integration and the temporal correlation hypothesis. *Annu Rev Neurosci* 18:555–586
- Sporns O, Tononi G, Edelman GM (2000) Theoretical neuroanatomy and the connectivity of the cerebral cortex. *Cereb Cortex* 10:127–141
- Steriade M (1997) Synchronized activities of coupled oscillators in the cerebral cortex and thalamus at different levels of vigilance. *Cereb Cortex* 7(6):583–604
- Tanaka G, Ibarz B, Sanjuan MAF, Aihara K (2006) Synchronization and propagation of bursts in networks of coupled map neurons. *Chaos* 16:013113
- van der Heuvel MP, Stam CJ, Boersma M (2008) Hulshoff Pol HE. Small-world and scale-free organization of voxel-based resting-state functional connectivity in the human brain. *NeuroImage* 43:528–539
- Wang Q, Chen G (2011) Delay-induced intermittent transition of synchronization in neuronal networks with hybrid synapses. *Chaos* 21:013123
- Wang Q, Duan Z, Perc M, Chen G (2008) Synchronization transitions on small-world neuronal networks: effects of information transmission delay and rewiring probability. *Europhys Lett* 83:50008
- Wang Q, Perc M, Duan Z, Chen G (2009a) Delay-induced multiple stochastic resonances on scale-free neuronal networks. *Chaos* 19:023112
- Wang Q, Perc M, Duan Z, Chen G (2009b) Synchronization transitions on scale-free neuronal networks due to finite information transmission delays. *Phys Rev E* 80:026206
- Wang Q, Perc M, Duan Z, Chen G (2010) Impact of delays and rewiring on the dynamics of small-world neuronal networks with two types of coupling. *Phys A* 389:3299–3306
- Watts DJ, Strogatz SH (1998) Collective dynamics of ‘small-world’ networks. *Nature* 393:440–442
- Yang XL, Senthilkumar DV, Kurths J (2012) Impact of connection delays on noise-induced spatiotemporal patterns in neuronal networks. *Chaos* 22:043150
- Yu H, Wang J, Du J, Deng B, Wei X, Liu C (2013a) Effects of time delay and random rewiring on the stochastic resonance in excitable small-world neuronal networks. *Phys Rev E* 87:052917
- Yu H, Wang J, Liu C, Deng B, Wei X (2013b) Delay-induced synchronization transitions in small-world neuronal networks with hybrid electrical and chemical synapses. *Phys A* 392:5473–5480