SCIENCE CHINA
Technological Sciences

Special Topic: Neurodynamics
• Article •

May 2014 Vol.57 No.5: 936–946
doi: 10.1007/s11431-014-5534-0

Dynamics of electric activities in neuron and neurons of network induced by autapses

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Received January 22, 2014; accepted March 4, 2014

The effect of autapse on adjusting the membrane of potentials of neuron is described by imposing a time-delayed feedback on the membrane of neuron in a close loop type, and the Hindmarsh-Rose (HR) neuron under autapse is investigated. Firstly, the electric activity of single HR neuron under electric autapse and chemical autapse is investigated. It is found that quiescent neuron is activated due to appropriate time delay and feedback gain in the autapse, and the autapse plays an important role in waking up neuron. The parameter region for periodic, chaotic activity of neuron under autapse is calculated in a numerical way, and transition from spiking to bursting is observed by increasing the feedback gain and time delay carefully. Furthermore, the collective electric activities of neurons in a ring network is investigated and abundant electric activities are observed due to the competition between the autapse and the time-delayed coupling between adjacent neurons in the network, and time delay in coupling between neurons also plays an important role in enhancing synchronization in the network.

time delay, bifurcation, Lyapunov exponent, neuron, network

Citation: Qin H X, Ma J, Jin W Y, et al. Dynamics of electric activities in neuron and neurons of network induced by autapses. Sci China Tech Sci, 2014, 57: 936–946, doi: 10.1007/s11431-014-5534-0

1 Introduction

Neuron is a basic unit in neuronal system, i.e. electric activity of single neuron, and the collective activities of neurons are associated with physical behaviors due to the regulating action from central nervous system. More importantly, it is attractive to explore the brain science by using nonlinear analysis based on some experimental results [1–8]. It is confirmed that cells could be classified as two types, neuron and neuroglia. It was ever thought that neuroglia and glia just had only a passive, supporting role and protected the neurons like a sheath, while new evidences show that they can make crucial contributions to the formation, operation and adaptation of neural circuitry [9–12]. Indeed, it is attractive to detect and explain the potential mechanism on information processing in brain activity and energy encoding [13–15]. Most of researchers prefer to detect and analyze the electric activity of neuron and collective behaviors of neurons in the network, and several theoretical models [16–20] are presented to reproduce main properties of realistic neurons. For example, Hindmarsh and Rose [20] presented a simplified mathematical model to describe the electric activity of neuron, which is often called Hindmarsh-Rose model. It is found that the HR neuron model can generate multi-type dynamic behaviors, such as quiescent, periodic and chaotic activities in appropriate parameter region. Particularly, transition of electric activity from quiescent to periodic spiking, to bursting and chaotic discharging emerges by increasing the intensity of external forcing current carefully. Physical behaviors often depend on the coopera-

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tion of neurons in the neuronal systems. The complex dynamics of electric activities of neurons is often associated with the control and transition of electric activities of neurons, parameter estimation, and synchronization [21] of chaotic neurons, whose the electric activities are chaotic. For example, ref. [22] suggested that a delayed self-feedback scheme could effectively suppress the chaos in Hindmarsh-Rose neuron model. Ref. [23] investigated the possibility of bursting synchronization of neurons due to chemical synapses coupling.

Within the neuron models, stochastic and/or coherence resonance is often observed under optimized noise or controllable bifurcation parameters [24–34]. More interestingly, stochastic and/or coherence resonance (SR, CR) also emerges in the network of excitable media and the ordered state could be observed due to time-delay or external forcing under SR or CR. For example, SR is observed in a small-world network of excitable media induced by pacemaker [35]. Ref. [36] reported the coherence resonance in a noisy Hodgkin-Huxley network. Ref. [37] observed multiple stochastic resonances in scale-free network induced by time delay. Gu et al. [38] reported a multiple spatial coherence resonance induction of spiral waves with a stochastic signal in a square lattice network model composed of type I morris-lecar (ML) neurons. Furthermore, the ordered spatial pattern such as spiral wave emerges in the network of neurons, which regulate the collective behaviors of neurons like a pacemaker. For example, ref. [39] argues that blocking or poisoning in partial ion channels in local area of network plays as defects, and accounts for the appearance of spiral wave in the network. The dynamics of spiral wave in the network is often dependent on the topology connection, poisoning degree and noise [40–45]. For example, ref. [40] confirms that the formation mechanism of multi-armed spiral wave in the network is associated with the symmetric breaking up of target waves.

Most of the previous work ever thought that electric coupling as gap junction between neurons could be an effective way to realize communication among neurons, though chemical coupling via neurotransmitter can also change the synchronization between neurons. In fact, the most attractive connection in neurons could be the autapse, a self-synapse or a specialized connection between a neuron and itself, which is useful for transmitting electrical signals [46–53]. More generally, adjusting autapse on the membrane potential is often described by imposing a self-feedback current on the membrane of neuron with time delay. Signals can be transmitted between neurons due to synapse coupling, and autapse is often classified as two types according to the transmitter media, one is electric autapse and the other is called chemical autapse. The dynamics of neuron can be changed by autapse under certain feedback gain or time delay [53,54], and sleep neuron starts to oscillate from initialized quiescent state under negative feedback under appropriate time delay [48]. Furthermore, autapse can also induce transition of the firing pattern in bursting neurons [55].

In this paper, the dynamics of Hindmarsh-Rose neuron under autapse is investigated in detail. The transition of quiescent state to spiking, bursting and chaotic state is simulated carefully by selecting the time delay and feedback gain, the bifurcation analysis. The distribution of the largest Lyapunov exponents in the two-parameter space(time delay vs. feedback gain) is calculated. Finally, the effect of autapse on the collective behaviors of neurons in ring network is also investigated.

2 Model and Scheme

The dynamic equations of Hindmarsh-Rose are often described by [20]

$$\begin{cases} \dfrac{\mathrm{d}x}{\mathrm{d}t} = y - ax^3 + bx^2 - z + I_{\mathrm{ext}} + I_{\mathrm{aut}}, \\ \dfrac{\mathrm{d}y}{\mathrm{d}t} = c - dx^2 - y, \\ \dfrac{\mathrm{d}z}{\mathrm{d}t} = r[s(x - x_0) - z], \end{cases} \tag{1}$$

where x describes the membrane, y denotes the recovery variable and z is selected as adaption slow current, I_{ext} is the external forcing current. Parameters in this model are marked as a, b, c, d, r, s, x_0, and they are often selected as a=1.0, b=3.0, c=1.0, d=5.0, s=4.0, r=0.006, x_0=1.56. The electric activity of this model shows chaotic state under appropriate external forcing current [56]. I_{aut} denotes the transmembrane current induced by autapse, whose schematic diagram is shown in Figure 1.

2.1 Electric autapse

According to the schematic diagram for the autapse in Figure 1, electric autapse often inputs current across the membrane with time-delay (τ) and certain gain (g). Positive and negative feedback with time delay can be switched to each other in realistic neurons, and the dynamics on membrane potential can be detected by introducing additive forcing current in the neuron circuit I_{aut}, whose flow direction of the forcing current is associated with the sign selection of feedback gain in eq. (2) below,

$$I_{\mathrm{aut}} = g(x(t-\tau) - x(t)), \tag{2}$$

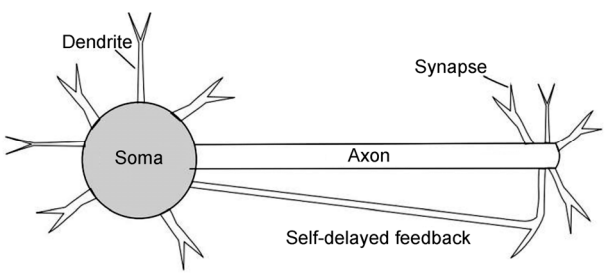

Figure 1 Schematic diagram for the autapse [51].

where g, and τ represent the feedback gain and time delay in the course of feedback, respectively. Generally, negative feedback begins to act on the membrane with positive gain g being used and the electric activity used to be close to stable state. Positive feedback on the membrane potential is generated when negative gain coefficient is used, and neuron can be activated or the electric activities are enhanced.

2.2 Chemical autapse

In the case of chemical synapse coupling, the adjustment of membrane potential and feedback effect depends on the releasing of chemical neurotransmitter, and the effect on membrane potentials of neuron is quantificationally detected as follows:

$$I_{\text{aut}}(t) = g(x(t) - V_{\text{syn}})S(t-\tau), \tag{3}$$

$$S(t-\tau) = 1/\{1+\exp[-\lambda(x(t-\tau)-\theta)]\}, \tag{4}$$

where g is the intensity of chemical coupling, V_{syn} is reversal potential in synapse. It denotes excitable synapse for V_{syn}=2 and inhibitory synapse for V_{syn}=–2. Within a ring network of Hindmarsh-Rose neuron, the dynamics equations are often given with

$$\begin{cases} \dfrac{\mathrm{d}x_i(t)}{\mathrm{d}t} = y_i(t) - ax_i(t)^3 + bx_i(t)^2 - z_i(t) + I_{\text{ext}} + I_{\text{aut}} \\ \qquad\qquad + D(x_{i+1}(t-\tau_1) + x_{i-1}(t-\tau_1) - 2x_i(t)), \\ \dfrac{\mathrm{d}y_i(t)}{\mathrm{d}t} = c - dx_i(t)^2 - y_i(t), \\ \dfrac{\mathrm{d}z_i(t)}{\mathrm{d}t} = r[s(x_i(t) - x_0) - z_i(t)], \end{cases} \tag{5}$$

the subscript i represents the position of neuron in the network, D is the coupling intensity between adjacent neurons, τ_1 describes the time delay when signal is transmitted from a neuron to an adjacent one. Firstly, the dynamics of single neuron under autapse is investigated. Then the collective behaviors of neurons in the network will be studied by imposing the autapse on all the neurons.

3 Numerical results and discussion

In this section for numerical studies, the fourth Runnge-Kutta algorithm is used to calculate the nonlinear equations with time delay, and time step is selected as h=0.01, initial values for the variables are selected as (3.0, 0.3, 0.1), whose neuron keeps quiescent state and the external forcing current is under threshold for excitable state. In realistic neuronal systems, a large number of neurons are of-ten connected directly (neighbour neurons) or indirectly. For the sake of simplicity, it is applicable to detect the collective behaviors in a round-about way based on a ring network. The node number of the network is fixed at N=100, and it makes i+1=1 at i+1>N, and i —1=N at i–1<1 in numerical way.

3.1 Electric autapse on electric activity of neuron

It is found that the neuron begins to discharge in rhythm with increasing the external forcing current to certain threshold (about I_{ext}~1.1) even without autapse being considered. To show the distinct effect of electric autapse, the external forcing current I_{ext} is less than the threshold, for simplicity, I_{ext}=1.0 is used. Then the feedback gain and time delay are changed carefully to detect control parameter region for transition of electric activity by analyzing the time series for membrane potentials. In a quantitative way, the distribution for discharge frequency in certain period about 1000 time units is recorded in the two-parameter space g–τ, and I_{ext}=1.0, 1.37 is investigated, respectively.

The results in Figure 2 show that a quiescent neuron begins to discharge and becomes excitable with increasing the time delay under stronger negative feedback on the membrane. In the case for excitable case, the electric activity of neuron is also enhanced due to the autapse effect. To measure the dependence of electric activity on the time delay and

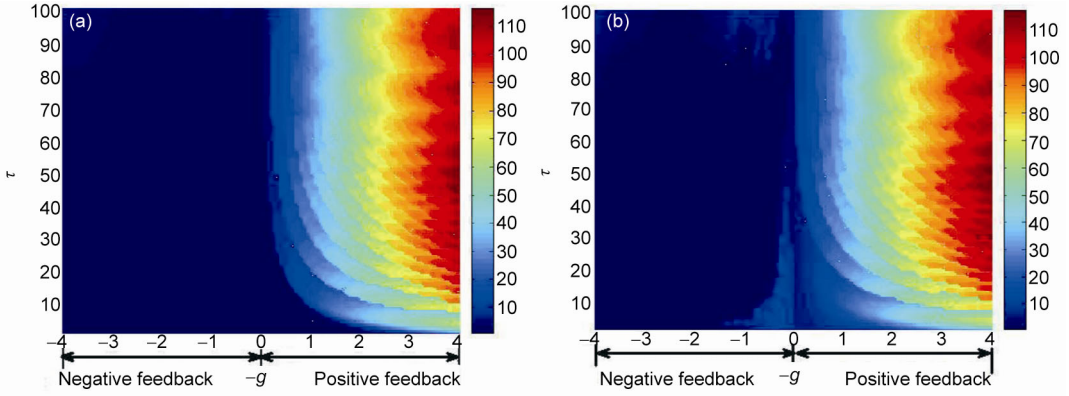

Figure 2 Distribution for discharge frequency under electric autapse shown in eq. (2) in certain period about 1000 time units. (a) For I_{ext}=1.0; (b) for I_{ext}=1.37.

feedback gain, two groups of parameters are selected from Figure 2 to observe the evolution of membrane potential of single neuron. For example, I_{ext}=1.0, g=–0.5 (positive feedback), and the time delay τ is selected by 13, 15, 17, 19, respectively. The numerical results confirm that quiescent neuron is activated and waked up with increasing the time delay due to positive feedback, and the results are independent of the time when the electric autapse begins to work on the neuron. It just indicates that appropriate time delay plays an active role in waking up or exciting the quiescent neurons. Furthermore, the effect of feedback gains (g=–0.6, –0.8, –1.0, –1.2) under the fixed time delay (τ = 9) are also checked under I_{ext}=1.0, respectively. The numerical results confirm that quiescent neuron is activated under appropriate positive feedback (negative feedback gain) at certain time delay. That is to say, the transition of electric activity of neuron is much dependent on the autapse, and these results are consistent with the ones as shown in Figure 2(a). It indicates that appropriate electric autapse is active in waking up quiescent neurons. More interestingly, it is important to detect the transition of electric activity from spiking to bursting and chaotic state due to the effect of electric autapse. In this case, I_{ext}=1.37 is selected for generating spiking state, then two groups of time delay, feedback gain are selected to observe the transition of electric activity from spiking to bursting state. We investigated the case for g=−1.5, –2.5, –3.0, –4.5 at the fixed time delay τ=12, I_{ext}= 1.37; and the case for τ=20, 40, 60, 80 at the fixed feedback gain g=−1.5, I_{ext}=1.37. The numerical results confirm that transition from spiking to bursting could be observed under appropriate time delay or feedback gain, these results just show that autapse plays an important role in regulating the electric activity of neurons. Furthermore, the bifurcation diagram of interval interspike vs. time delay in the electric autapse is also calculated to discuss the effect of autapse on the membrane potential of neurons. In the numerical studies, the case for I_{ext}=1.37, 2.23, τ – [0–60] is plotted in Figures 3, 4, respectively.

The results in Figures 3, 4 confirm that electric activity of neuron goes through spiking, multi-period and chaotic states with increasing the time delay in the electric autapse.The critical time delay for transition is decreased under positive feedback ($-g$>0) with bigger gain being used. Then the distribution of the largest Lyapunov exponents in the two-parameter region is calculated in Figure 5.

The results in Figure 5 show that positive Lyapunov exponents are found for chaotic state under appropriate time delay and feedback gain in electric autapse, these results agree with the bifurcation analysis in Figures 3 and 4.

3.2 Chemical autapse on electric activity of neuron

The dynamics of neuron is also dependent on the chemical synapse, and it is interesting to investigate the effect of chemical autapse on the membrane potential. With the chemical autapse current shown in eq. (3), here, λ=10, θ=–0.25 [52]. In a statistical way, the discharge frequency with certain transient period about 1000 time units is calculated in the two-parameter space $-g-\tau$ at the fixed external forcing current I_{ext}=1.0, and the case for V_{syn}=–2, V_{syn}=–2, is calculated, respectively. The results are plotted in Figure 6.

The results in Figure 6 show that quiescent neurons are

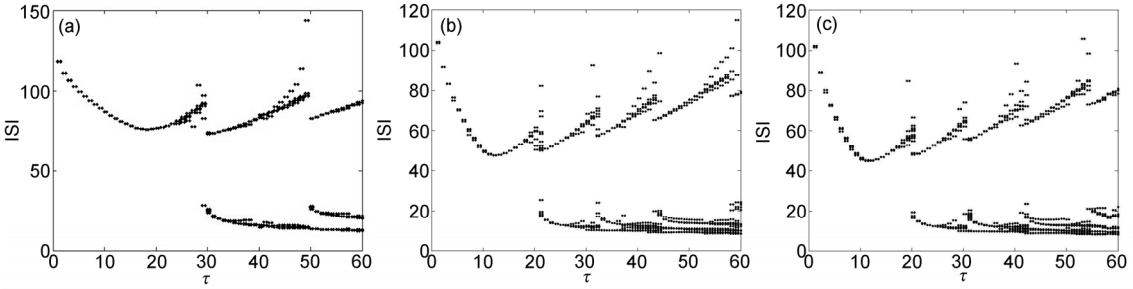

Figure 3 Bifurcation diagram vs. time delay in electric autapse, at I_{ext}=1.37, (a) g=–0.4, (b) g=–0.75, (c) g=–0.8(positive feedback).

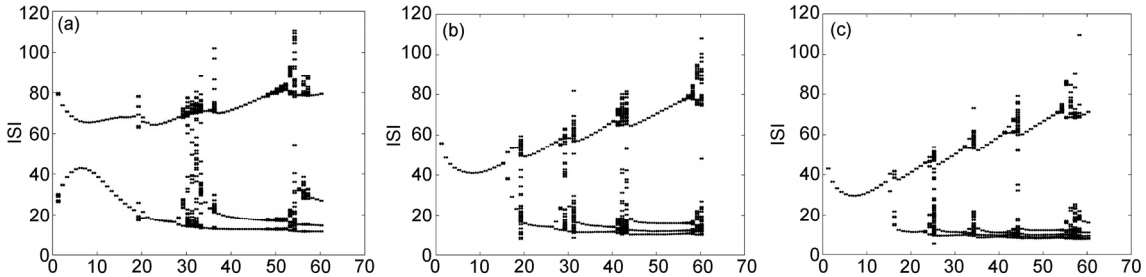

Figure 4 Bifurcation diagram vs. time delay in electric autapse, at I_{ext}=2.23, (a) g=–0.2, (b) g=–0.4, (c) g=–0.7(positive feedback).

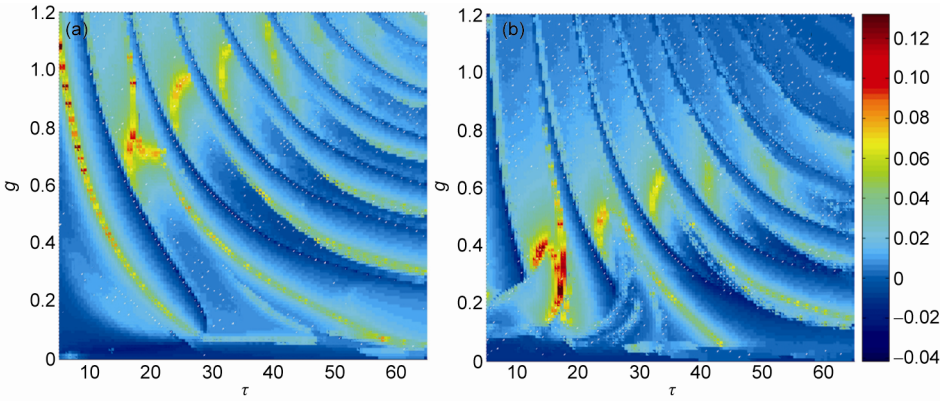

Figure 5 Distribution of the largest Lyapunov exponents in the parameter space τ vs. g, for (a) I_{ext} =1.37, (b) I_{ext} =2.23.

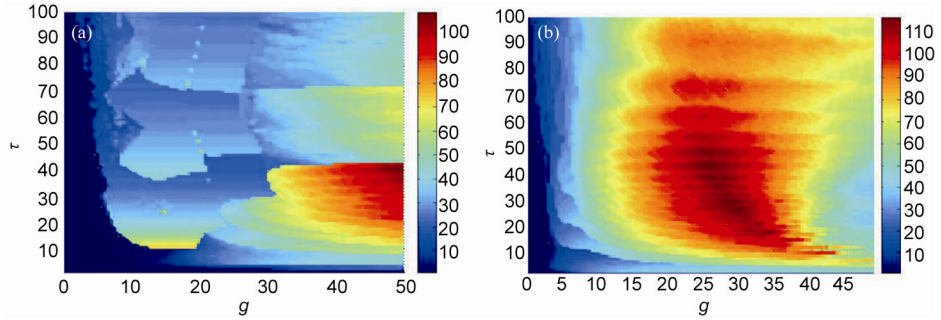

Figure 6 Distribution for discharge frequency under chemical autapse shown in eq. (3) in certain period about 1000 time units, I_{ext}=1.0. (a) For V_{syn}= –2; (b) for V_{syn}=2.

waked up by selecting appropriate feedback gain and time delay in chemical autapse. In the case of excitable synapse (V_{syn}=2), neuron presents rapid discharge rhythm in bigger area indicating that neuron is much easier to be excited than the case for inhibitory synapse being considered. For a clear view of the time delay effect in chemical autapse on electric activity, the feedback gain is fixed at g=0.5, I_{ext}=1.0, V_{syn}=2, time series for membrane potentials under different time delays (τ=30, 50, 80, 100) are calculated, and the numerical results show that electric activity of neuron could be changed only when a bigger time delay is used while the neuron is not much sensitive to the chemical autapse. The case for inhibitory autapse as g=0.5, I_{ext}=1.0, V_{syn}=−2 is also investigated, but it has found that quiescent neuron fails to be activated under smaller feedback gain even if the time delay is increased to a value about 400 time units. Surely, we have to detect the effect of feedback gain in the chemical autapse, for example, I_{ext}=1.0, τ=10, V_{syn}=−2, then different feedback gains (g=1, 10, 15, 20) are tested to find the dependence of chemical autapse. The numerical results show that quiescent neurons could also be excited by chemical inhibitory autapse when bigger feedback gain is used. The potential mechanism could be that stronger feedback imposes stronger positive feedback on the membrane and the inhibitory effect of synapse could be decreased greatly. Another case is to detect the transition from spiking to bursting induced by chemical autapse. For simplicity, I_{ext}= 1.0, τ=10, V_{syn}=2, and different feedback gains are used to observe the transition of electric activity from spiking state to bursting state. The extensive numerical results confirm that distinct transition of spiking to bursting occurs by increasing the feedback gain beyond certain threshold. Compared with the electric and chemical autapses on the electric activity of neuron, it is found that neuron is more sensitive to the electric autapse while chemical autapse keeps dull only when larger feedback gain or time delay is available. The potential mechanism could be that they change the membrane potential of neuron in different ways, and electric autapse prefers a direct electric coupling, while chemical autapse turns to chemical neurotransmitter well.

Above all, the effect of autapse on a single neuron is investigated, and it can predicate that the collective behaviors of neurons in network could be changed by the autapse as well. Therefore, it is interesting to detect the occurrence of electric activities of neurons and transition from spiking to bursting in the network of neurons according to the description as shown in eq. (5). As mentioned above, chemical autapse has distinct impact on the membrane potential only when larger feedback gain and/or time delay are available. Therefore, in the case for collective behaviors of networks induced by autapse, we just focus on the electric autapse on the network while the chemical autapse is left out.

3.3 Electric autapse on electric activities of network

For simplicity, it is thought that each neuron is imposed the same autapse, and the feedback current due to coupling between adjacent neurons is given with

$$I_{\text{transm}} = D(x_{i-1}(t-\tau_1) + x_{i+1}(t-\tau_1) - 2x_i(t)). \quad (6)$$

At first, we investigate the case that time delay in coupling between adjacent neurons (τ_1=0), N=100, τ=50, D=0.3, the first neuron is imposed external forcing current as I_{ext}= 1.0 while the other neurons are in absence of external forcing currents, so that all the neurons keep quiescent without autapse being considered. Then different feedback gains as g= −0.5, g=−1, g=−2 will be used to detect the dynamics by analyzing the time series of membrane potentials of neurons (i=1, i=50, i=100) in the network, and the results confirm that quiescent neurons are easier to activate, and then the electric activities pass through periodic firing, and step into bursting state when bigger feedback gain is used in the network. In the network, the electric activity of each neuron is also changed by the additive current due to adjacent coupling. More generally, neurons in the network become synchronized when the coupling intensity exceeds certain threshold, and an ordered state can be reached. In fact, the electric activity of each neuron depends on the cooperation and competition between the autapse and adjacent coupling, the effect of autapse may dominate the change of The electric activity of each neuron when the adjacent coupling intensity is weak. In a realistic neuronal system, finite time delay exists in the network when signal transmits from one neuron to other neurons in the process of mutual coupling. Therefore, it is important to consider the effect of time delay in coupling between adjacent neurons. For simplicity, we test the case for τ_1=10, N=100, D=0.3, τ=50, the sampled time series of three neurons (i=1, 50, 100) are calculated at the fixed feedback gain g= −0.5, g=−1.0, g=−2.0, and the results are shown in Figure 7.

The results in Figure 7 confirm that quiescent neurons in the network can still be activated to generate spiking, bursting states under appropriate electric autapse even time delay in the coupling between two adjacent neurons is considered in the network. All the neurons in the network become excitable to pass through spiking, or bursting electric activities with increasing the intensity of feedback gain in the electric autapse. That is to say, quiescent neurons in the network still be waked up and start to generate spiking, bursting by increasing the feedback gain in the electric autapse even if time delay in coupling between adjacent neurons is considered. More interestingly, the collective behaviors of neurons should be cared, and the spatiotemporal pattern measured by the distribution of membrane potentials of neurons in the spatiotemporal region is calculated, and the results for τ=50, D=0.3, g=−0.5, g=−1.0, g=−2.0 are plotted in Figure 8.

The results in Figure 8 show that all the neurons in the ring network are activated under higher feedback gain, and time delay (τ_1) in coupling between adjacent neurons facilitates complete synchronization of network. The excitation of neuron is greatly dependent on the feedback gain, the first neuron is activated due to electric autapse and subthreshold forcing current (I_{ext}=1.0), then the adjacent neurons are also waked up due to mutual coupling defined in eq. (6) with stronger feedback gain in autapse being used. It is found that the subthreshold forcing current on the first neuron also plays an important role in exciting the neurons in the network, which makes forcing in diversity, and the synchronized neurons are violated by the electric signal generated from the first neuron due to mutual adjacent coupling. When time delay in the adjacent coupling is considered, the

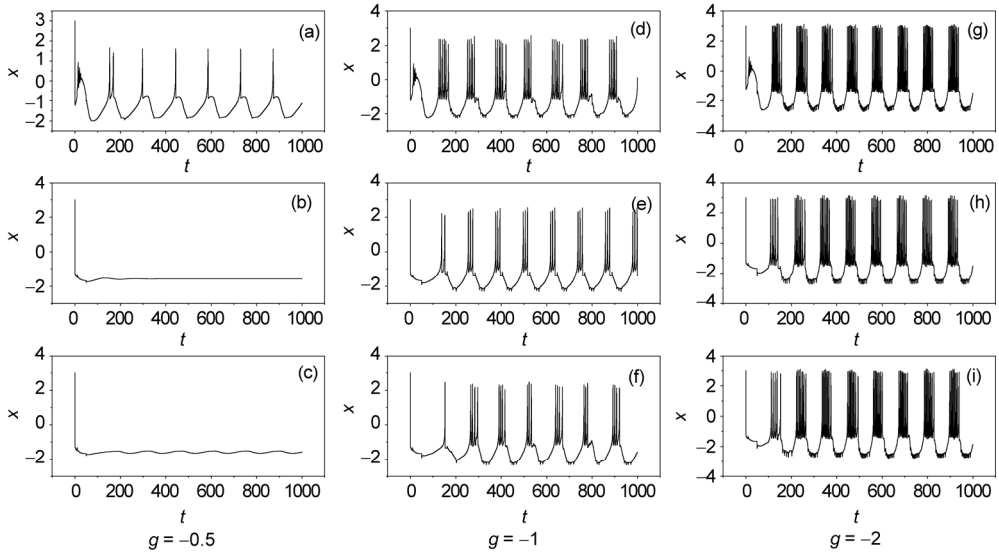

Figure 7 Time series of membrane potentials of single neuron (i=1, i=50, i=100) under electric autapse, only the first neuron (i=1) is imposed external forcing current as I_{ext}=1.0, while no external forcing current is imposed on other nodes in the network, τ_1=10, τ=50, D=0.3. (a) g=−0.5, i=1; (b) g=−0.5, i=50; (c) g=−0.5, i=100; (d) g=−1.0, i=1; (e) g=−1, i=50; (f) g=−1, i=100 ; (g) g=−2.0, i=1; (h) g=−2.0, i=50; (i) g=−2.0, i=100.

continuous electric pulse generated from the first neuron along the network is suppressed by mutual coupling under appropriate time delay τ_1, thus synchronization of network could be realized (Figure 8(f)). Then the effect of the subthreshold forcing current on the wave propagation along the ring network is also investigated by imposing subthreshold forcing current on all the neurons, and all the results are shown in Figure 9.

The results in Figure 9 show that all the neurons can be waked up and neurons begin to oscillate synchronously under subthreshold forcing current and electric autapse, the time delay τ_1 has slight impact on the propagation of wave and synchronization in the ring network because the electric autapse dominates the electric activity of each neuron than the mutual coupling stimuli. The spatiotemporal pattern in the ring network depends on the competition between the electric autapse in each neuron and the time-delayed coupling between adjacent neurons. It deserves to investigate the case that no subthreshold forcing current is imposed on the network, and the results are shown in Figure 10.

The results in Figure 10 show that no travelling wave is developed by electric autapse and all the neurons keep quiescent under smaller feedback gain (g=–0.5) when no subthreshold forcing current is imposed on the network. The neurons become excitable and generate stable electric pulses to develop stable travelling wave in the ring network by increasing the intensity of feedback gain in the electric autapse even no subthreshold forcing current is considered, and the formation, and propagation of travelling wave are independent of the time delay in coupling between adjacent neurons. It seems that the development and propagation of travelling wave mainly depend on the electric autapse and keeps certain robustness to the time delay in coupling between neurons. The potential cause could be that these results are calculated under lower coupling intensity, therefore, this case should be investigated by selecting other coupling intensities between neurons, and the results are shown in Figures 11 and 12.

Comparing the results in Figure 11 with the results presented in Figure 8, we have found that the development of travelling wave much dependent on the intensity of gain in electric autapse under lower coupling intensity D=0.1, and the developed travelling wave induced by higher feedback gain (g=–1.0, –2.0) wave will propagate in a slower speed,

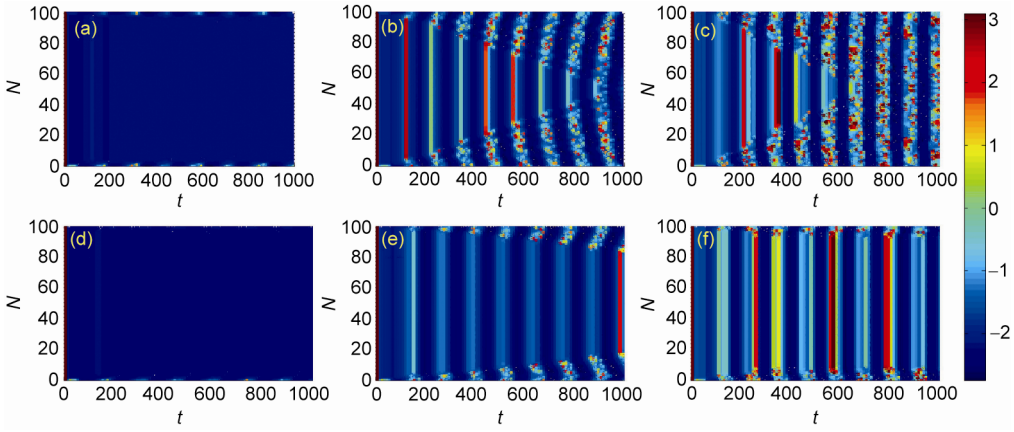

Figure 8 Time series of membrane potentials of all neurons under electric autapse, only the first neuron (i=1) is imposed external forcing current as I_{ext}=1.0, while no external forcing current is imposed on other nodes in the network, τ=50, D=0.3. (a) τ_1=0, g=–0.5; (b) τ_1=0, g=–1.0; (c) τ_1=0, g=–2.0; (d) τ_1=10, g=–0.5; (e) τ_1=10, g=–1.0; (f) τ_1=10, g=–2.0.

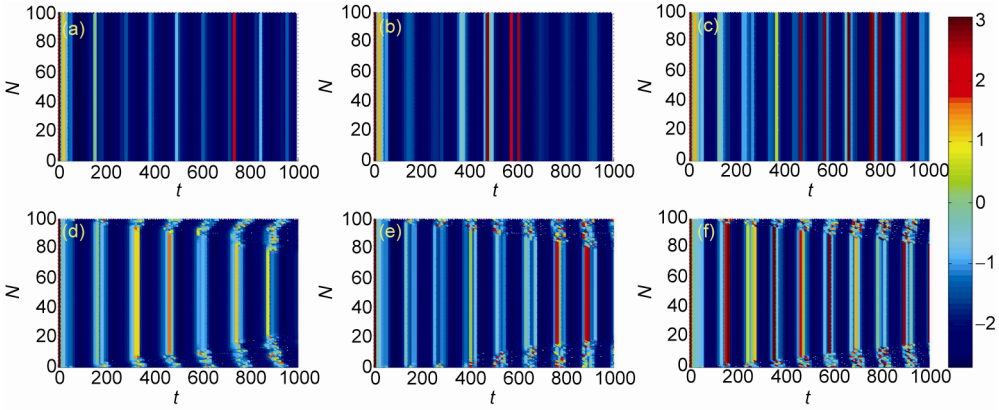

Figure 9 Time series of membrane potentials of all neurons under electric autapse, all the neurons (i=1, 2,···, 100) are imposed subthreshold(external) forcing current as I_{ext}=1.0, τ=50, D=0.3. (a) τ_1=0, g=–0.5; (b) τ_1=0, g=–1.0; (c) τ_1=0, g=–2.0; (d) τ_1=10, g=–0.5; (e) τ_1=10, g=–1.0; (*f*) τ_1=10, g=–2.0.

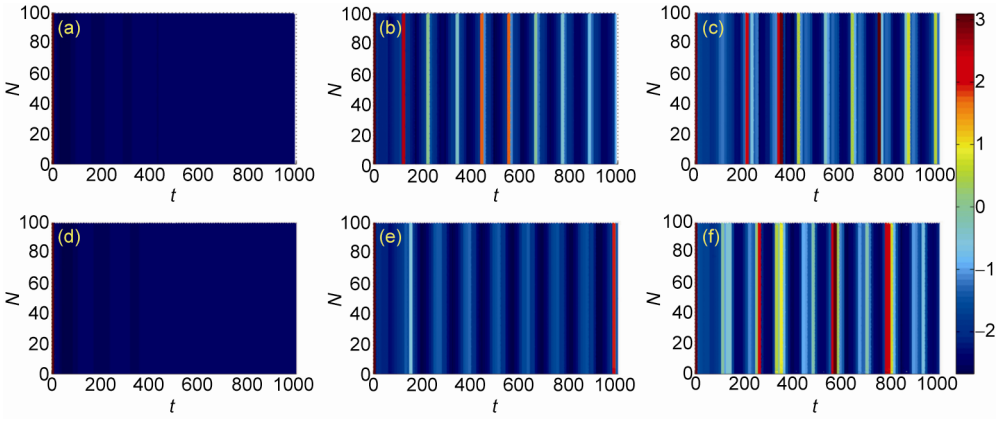

Figure 10 Time series of membrane potentials of all neurons under electric autapse, no subthreshold(external) forcing current is imposed on the network, τ=50, D=0.3. (a) τ_1=0, g=–0.5; (b) τ_1=0, g=–1.0; (c) τ_1=0, g=–2.0; (d) τ_1=10, g=–0.5 ; (e) τ_1=10, g=–1.0; (f) τ_1=10, g=–2.0.

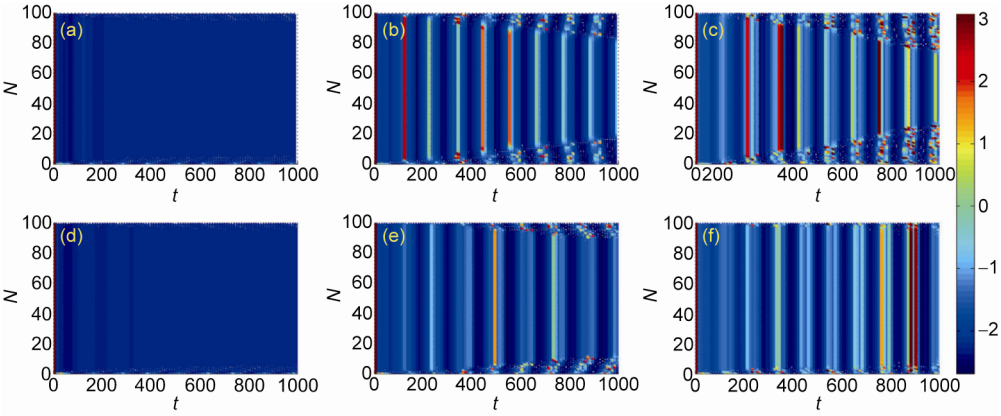

Figure 11 Time series of membrane potentials of all neurons under electric autapse, only the first neuron (i=1) is imposed external forcing current as I_{ext}=1.0, while no external forcing current is imposed on other nodes in the network, τ=50, D=0.1. (a) τ_1=0, g=–0.5; (b) τ_1=0, g=–1.0; (c) τ_1=0, g=–2.0; (d) τ_1=10, g=–0.5 ; (e) τ_1=10, g=–1.0; (f) τ_1=10, g=–2.0.

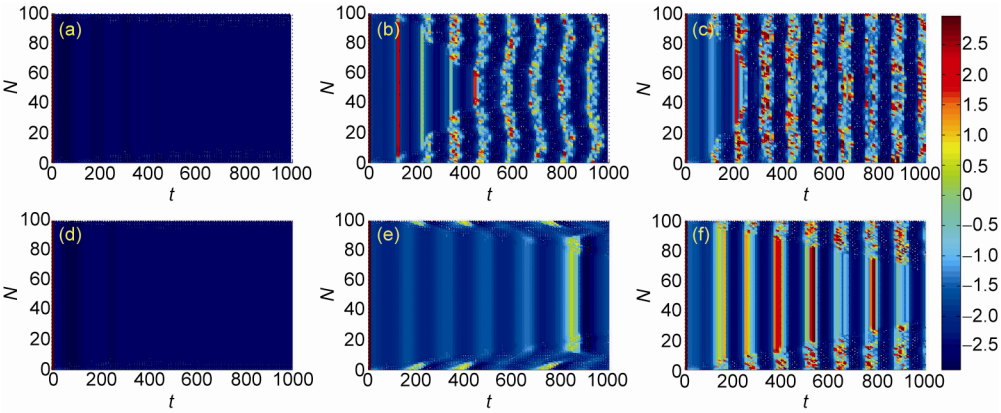

Figure 12 Time series of membrane potentials of all neurons under electric autapse, only the first neuron (i=1) is imposed external forcing current as I_{ext}=1.0, while no external forcing current is imposed on other nodes in the network, τ=50, D=1.0. (a) τ_1=0, g=–0.5 ; (b) τ_1=0, g=–1.0; (c) τ_1=0, g=–2.0; (d) τ_1=10, g=–0.5; (e) τ_1=10, g=–1.0; (f) τ_1=10, g=–2.0.

thus the electric pulse initiated from the first neuron (imposed subthreshold forcing current I_{ext}=1.0) can not reach the farthest neuron (i=50) within 1000 time units. The potential mechanism is that the propagation speed is associat-

ed with the coupling intensity. Comparing the results in Figures 11(b) and (c) with the results in Figures 11(e) and (f), it is also confirmed that synchronization in network is enhanced by considering time delay in coupling between adjacent neurons in the ring network. Furthermore, the case for coupling intensity D=1.0 is also investigated, and the results are shown in Figure 12.

The results in Figure 12 confirm that the quiescent network is activated due to the electric autapse and subthreshold forcing current on the first neuron, then the ordered wave is violated by the electric pulse generated from the first neuron, and the pulse propagates along the ring network with higher speed under D=1.0. For example, comparing the results in Figure 12 (D=1.0) and the results in Figure 8 (D=0.3), we have found that the critical time to violate the ordered wave is decreased from 1000 time unites (Figure 8(f)) to 200 time units (Figure 12(c)). In the absence of time delay τ_1 in coupling between adjacent neurons, the network fails to keep synchronized under higher feedback gain when subthreshold forcing current is only imposed on a single neuron in the network thus diversity in forcing occurs. The disorder of ring network is suppressed greatly when time delay τ_1 in coupling between adjacent neurons is considered, and partial synchronization is observed in the ring network(Figures 12(e) and (f)). Finally, the case that no external subthreshold forcing current is imposed on the network is investigated, and the results are shown in Figure 13.

The results in Figure 13 confirm that quiescent neurons are waked up and keep in synchronized with higher feedback gain and coupling intensity being used, and the synchronization state could be violated (Figure 13(f)). In fact, the developed state mainly depends on the cooperation or competition between the electric autapse and adjacent coupling in neurons in absence of external subthreshold forcing current.

Above all, the electric autapse and chemical autapse on the electric activity of single neuron are investigated in detail. It is found that quiescent neurons can be waked up and become excitable by selecting appropriate feedback gain and time delay, and the electric activity of neuron is sensitive to the stimulus from electric autapse, while it responds to the chemical autapse dully except for larger time delay and feedback gain. Furthermore, neuron will pass through spiking, goes into bursting and steps into chaotic state with increasing the feedback gain and time delay. In the case of ring network, electric autapse still plays an active role in waking up the quiescent neurons, and transition from spiking to bursting, spatiotemporal chaos with increasing the feedback gain and time delay in the electric autapse. In a word, the autapse plays an important role in regulating the electric activity of single neuron and types of bifurcation behaviors can be observed. For a single neuron or oscillator, bifurcation analysis provides a feasible but easy way to understand the dynamics of nonlinear oscillator and transition of behavior induced by adjusting controllable bifurcation parameters [57–62]. More generally, the Hindmarsh-Rose neuron model is often used to analyze the bifurcation in electric activity of neuron in analytical [59] or experimental way [62] when complex dynamic behaviors emerge in the system. Practically, the external forcing current is often controllable and used as a bifurcation parameter to detect types of bifurcation. The autapse effect is mapped by introducing a specific intrinsic forcing current in close loop with time-delay. This kind of self-feedback forcing current could induce certain bifurcation by changing the time delay or feedback gain carefully and its potential mechanism could be similar to the case of external quasi-periodic forcing current-induced period-adding bifurcation, while it could be some what different from the periodic pacing-induced bifurcation in a Hindmarsh-Rose neuron without autapse. In the case for network, time delay in mutual coupling between adjacent neurons can facilitate and enhance synchronization of network by decreasing external forcing current in diversity, while it also can violate synchronization of network in the absence of external forcing current on the network.

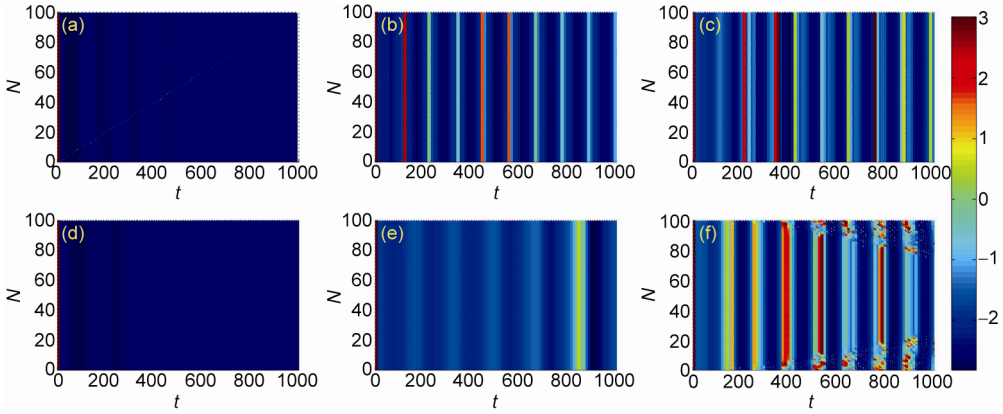

Figure 13 Time series of membrane potentials of all neurons under electric autapse, no subthreshold(external) forcing current is imposed on the network, τ=50, D=1.0. (a) τ_1=0, g=–0.5 ; (b) τ_1=0, g=–1.0; (c) τ_1=0, g=–2.0; (d) τ_1=10, g=–0.5; (e) τ_1=10, g=–1.0; (f) τ_1=10, g=–2.0.

4 Conclusion

The effect of autapse on the neuron is described by introducing a time-delayed forcing current on the membrane potential with certain gain. The electric activity of neuron is much sensitive to the electric autapse, and it responses to the chemical autapse only under larger feedback gain and time delay. The quiescent neuron is much easier to be activated under stronger feedback gain and subthreshold forcing current. The distribution of discharging frequency and largest Lyapunov exponent in the two-parameter space (feedback gain g vs. the time delay τ) indicate that neuron can pass through spiking to bursting and chaotic electric activity by selecting feedback gain and time delay carefully. In the case of ring network, the development and propagation of travelling wave also depend on the feedback gain and time delay in autapse, competition between travelling wave occurs when one neuron is imposed on subthreshold forcing current (other neurons are in the absence of external forcing currents). The regular travelling wave can be suppressed by the pulse wave from a single neuron due to subthreshold forcing current. The time delay in coupling between adjacent neurons often plays an important role in enhancing synchronization of network in the presence of external forcing current, while it also violates the synchronization in the absence of external forcing.

In a word, appropriate autapse is very helpful to waking up quiescent neurons, and driving neurons to pass through spiking, bursting and chaotic activities by increasing the feedback gain and time delay slightly.

This work was supported by the National Natural Science Foundation of China (Grant Nos. 11265008, 11372122, 11072099 and 11365014).

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