Plasticity-induced characteristic changes of pattern dynamics and the related phase transitions in small-world neuronal networks*

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Phase transitions widely exist in nature and occur when some control parameters are changed. In neural systems, their macroscopic states are represented by the activity states of neuron populations, and phase transitions between different activity states are closely related to corresponding functions in the brain. In particular, phase transitions to some rhythmic synchronous firing states play significant roles on diverse brain functions and disfunctions, such as encoding rhythmical external stimuli, epileptic seizure, etc. However, in previous studies, phase transitions in neuronal networks are almost driven by network parameters (e.g., external stimuli), and there has been no investigation about the transitions between typical activity states of neuronal networks in a self-organized way by applying plastic connection weights. In this paper, we discuss phase transitions in electrically coupled and lattice-based small-world neuronal networks (LBSW networks) under spike-timing-dependent plasticity (STDP). By applying STDP on all electrical synapses, various known and novel phase transitions could emerge in LBSW networks, particularly, the phenomenon of self-organized phase transitions (SOPTs): repeated transitions between synchronous and asynchronous firing states. We further explore the mechanics generating SOPTs on the basis of synaptic weight dynamics.

Keywords: spatiotemporal pattern, self-organized phase transition, small-world neuronal network, spike-timing-dependent plasticity

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1. Introduction

Pattern formation and pattern dynamics have been widely studied in both the experiments and theoretical models of many disciplines: physics, chemistry, and biology.[1,2] In neural systems, spatiotemporal patterns of neuron activities are closely related to various kinds of functions, such as information processing, movement control, learning, and memory, etc.[3,4] Several typical patterns of neuron population activities were observed in local areas of the cortex, for example, rhythmical synchronous firing,[5,6] sequential firing,[7] spiral waves,[8,9] plane waves,[8,9] and irregular waves. In particular, neural activity patterns could be temporally switched among spiral waves, plane waves, and irregular waves.[8,9] So far, most of the previous traditional studies on pattern dynamics in excitable systems have focused on fixed connection weights, and there have been no temporal transitions among different typical activity states.

In this paper, the effect of the dynamical changes of synaptic weights on activity states of neuronal networks is considered since synaptic plasticity is widely observed in different brain areas. Spike-timing-dependent plasticity (STDP), as a kind of long-term plasticity and a kind of Hebbian learning based on neuron spikes, is one of the greatest progresses in neuroscience in the last two decades.[10,11] Its phenomenological model, named the STDP learning rule, has been built by theoretical neuroscientists, and is widely applied for studying learning and memory in neural networks.[12–15] In STDP neural networks, rhythmical synchronous firing patterns could be generated when trained by repeated spatiotemporal stimuli,[16,17] and irregular synchronous firing patterns could be generated under stochastic stimuli.[18] However, so far none of the works reported that rhythmical synchronous firing patterns could be generated in a self-organized way under stochastic stimuli or transient stimuli, especially, self-organized transitions between a rhythmical synchronous firing state and a non-synchronous firing state. Transitions between rhythmical synchronous firing states and non-synchronous firing states play an important role in the function and disfunction in brains, such as in the encoding of rhythmical external stimuli,[6] tonic motor control in the cerebellar cortex,[19–22] and the generation of epileptic seizures.[5,23,24]

Phase transitions towards the critical states of avalanches have been reported in neural networks with adaptive interactions in a self-organized way, but there was only an avalanche state in the network and no discussion on the dynamical change of network activity states.[25] The phenomenon of self-organized phase transitions between firing rate patterns was found in artificial neural networks under the Hebbian learning rule, where the self-organized transitions served as the information processing for associative memory.[26] Nonetheless, unlike the STDP learning rule based on neuron spikes, its Hebbian learning rule based on firing rates is just a hypothesis and has no straight biological evidence. Hence, here we discuss

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phase transitions of activity states in electrically coupled and lattice-based small-word (LBSW) neuronal networks (abbreviated as LBSW networks) under the STDP learning rule. It had been discovered by previous studies that LBSW networks without STDP have only three activity states: the synchronous firing state (SF state), the wavelet turbulence state (WT state), and the global rest state (GR state).[27,28] However, by applying STDP on all electrical synapses, the network dynamics could be quite different to that in no-STDP cases. LBSW networks under STDP could generate various kinds of phase transitions between activity states including known and novel transitions: the transition from WT state to SF state (WT-to-SF transition), the transition from SF state to WT state (SF-to-WT transition), the transition from SF state to GR state (SF-to-GR transition), and more interestingly, the repeated transitions between WT states and SF states, the so-called self-organized phase transitions (SOPTs). SOPTs cannot appear in excitable networks without plastic weights, and they could be presented as rapid intermittent transitions at large STDP learning rates. Moveover, we analyze the mechanics of SOPTs on the basis of synaptic weight dynamics, and find that the WT-to-SF transition is triggered by the previously accumulated weight variation; whereas the SF-to-WT transition is driven by the transient activity perturbation.

2. Model

2.1. Network structure

The neural network is composed of $N = L^2$ FitzHugh–Nagumo neurons (FHN neurons) with electrically coupled synapses. We consider that the network has a two-dimensional (2D) lattice-based small-world structure (see Fig. 1(a)), which has both nearest-neighbor connections (NNCs) and long-range connections (LRCs).

2.2. Neuron and synapse model

The dynamics of a single FHN neuron is described as follows:[27–29]

$$\begin{aligned} \dot{u}_i &= -\frac{1}{\varepsilon}u_i(u_i-1)\left(u_i-\frac{v_i+b}{a}\right)+I_i, \\ \dot{v}_i &= f(u_i)-v_i, \end{aligned} \tag{1}$$

where u_i is the normalized membrane potential of neuron i, v_i is the recovery variable of neuron i, representing the effect of somatic ion currents. Function $f(u_i)$ is set to: $f(u_i) = 0$ for $u_i < 1/3$; $f(u_i) = 1 - 6.75u_i(u_i-1)^2$ for $1/3 \le u_i \le 1$; and $f(u_i) = 1$ for $u_i > 1$. Parameter ε is the ratio of the temporal scales of variables u and v; and parameters a and b control the excitatory threshold of the FHN neuron. Parameter set $\varepsilon = 0.04$, $a = 0.84$, and $b = 0.07$ can guarantee that the neuron is in the rest state without excitable stimuli. I_i is the synaptic current of neuron i. The dynamics of the electrical synaptic current I_i is $I_i = g\sum_j W_{ij}(u_j - u_i)$, where g is the maximum conductance for all synapses and W is the connection matrix containing all electrical synapses (both NNCs and LRCs). W_{ij} represents the unidirectional connection weight from neuron j to neuron i, which is governed by STDP.

Equations are integrated by the Eular method with time step $\delta t = 0.02$ and the no-flux boundary condition is used.

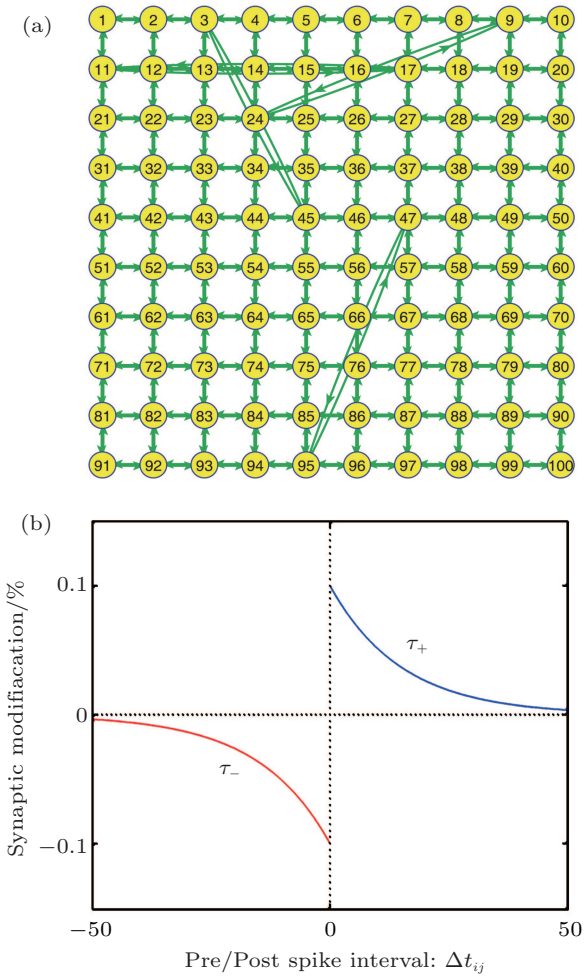


Fig. 1. (color online) Schematic figures for LBSW network structure and the STDP learning rule. (a) A partial structure of an LBSW network. All neurons have connections with their nearest-neighbor neurons and they also randomly link long-range neurons with a probability p. (b) A typical STDP learning rule. The STDP function shows the modification of a synaptic weight is a function of the relative timing of pre- and postsynaptic spikes.[10,11]

2.3. STDP rules

It has been reported that electrical synapses have long-term plasticity,[22,30,31] but the detailed features of the electrical synaptic plasticity has hardly been understood and so far there has been no commonly accepted model for it. In the network model studied here, we assume that electrical synaptic plasticity is governed by a spike-timing-dependent plasticity (STDP), a long-term plastic phenomenon being observed on chemical synapses in many cortical areas, with the synaptic weight adjusted by the relative spike timing of the presynaptic

neuron and the postsynaptic neuron.[10,11] STDP is widely believed to be the basis of the experimentally observed forms of long-term synaptic modification.

In the present study, we mainly adopt the following phenomenological STDP learning rule[12–15]

$$dW_{ij}(t) = \begin{cases} \dfrac{W_{\max} - W_{ij}(t)}{W_{\max}} A_+ \exp\left(\dfrac{-\Delta t_{ij}}{\tau_+}\right), & \text{if } \Delta t_{ij} > 0, \\ 0, & \text{if } \Delta t_{ij} = 0, \\ -\dfrac{W_{ij}(t)}{W_{\max}} A_- \exp\left(\dfrac{\Delta t_{ij}}{\tau_-}\right), & \text{if } \Delta t_{ij} < 0, \end{cases} \tag{2}$$

where A_+ and A_- are the learning rates of facilitation and depression, respectively, and τ_+ and τ_- are the corresponding time constants. Δt_{ij} is the time difference between a spike of the postsynaptic neuron i and an arrival spike of the presynaptic neuron j. The schematic diagram of STDP is shown in Fig. (1(b)). The modified amplitudes of facilitation and depression are dependent on the current weight values ($(W_{\max} - W_{ij}(t))/W_{\max}$ and $W_{ij}(t)/W_{\max}$ in Eq. (2)), and this STDP rule therefore is called a multiplicative STDP rule (M-STDP).[14,15] Without the weight-dependent term in Eq. (2), the STDP rule is called the additive STDP rule (A-STDP).[12,15] M-STDP is believed by some researchers to be more realistic than A-STDP,[13] thus the results shown in the paper are under the condition of M-STDP.

The synaptic weight variable $W(t)$ is initially set to 0.5 for all connections and is subject to an M-STDP learning rule. The weight variables are then changed over time and in the range of $[10^{-5}, W_{\max}]$, where $W_{\max} = 1$. $gW_{i,j}(t)$ is the effective maximal synaptic conductance at time t.

In the present paper, we consider N (50×50) neurons in 2D regular lattices, and we randomly add bidirectional long-range connections (LRCs) to generate a small-world structure. By defining p as the probability of adding a bidirectional LRC between two neurons, then the total number of LRCs $N_{\rm LRC}$ equals pN^2, $N_{\rm LRC} = pN^2$, so the mean degree of LRCs of a neuron P (LRCs degree) is also proportional to p ($P = 2pN$). We randomly choose $N_{\rm LRC}$ LRCs between non-connected neurons. Throughout the paper, g and P are the two central parameters adjusted for studying the behaviors of phase transitions.

3. Numerical results

In comparison with the results of LBSW networks without STDP,[27,28] the LBSW networks with STDP could have very different patterns of activity states in the parameter space of maximum conductance g and LRC degree P, and different transitions between activity states. In the following subsections, we firstly discuss the different activity states between STDP networks and non-STDP networks, and then consider what and how different kinds of transitions could be generated. In the next section we will analyze the mechanism of self-organized phase transitions (SOPTs) by considering the dynamical relation of synaptic strength patterns and network activity patterns.

3.1. Effects of STDP on oscillatory probabilities

We generate $N_{\rm trial}$ networks with random LBSW topology and random initial variables for different parameter sets of the maximum conductance g and LRCs degree P, and then evaluate the oscillatory probabilities of the asymptotic states of $N_{\rm trial}$ networks with and without STDP. As shown in Fig. 2, in the g–P parameter plane, the parameter region where STDP networks could generate oscillation is smaller than that of non-STDP networks. This implies that STDP is not favorable to network oscillation.

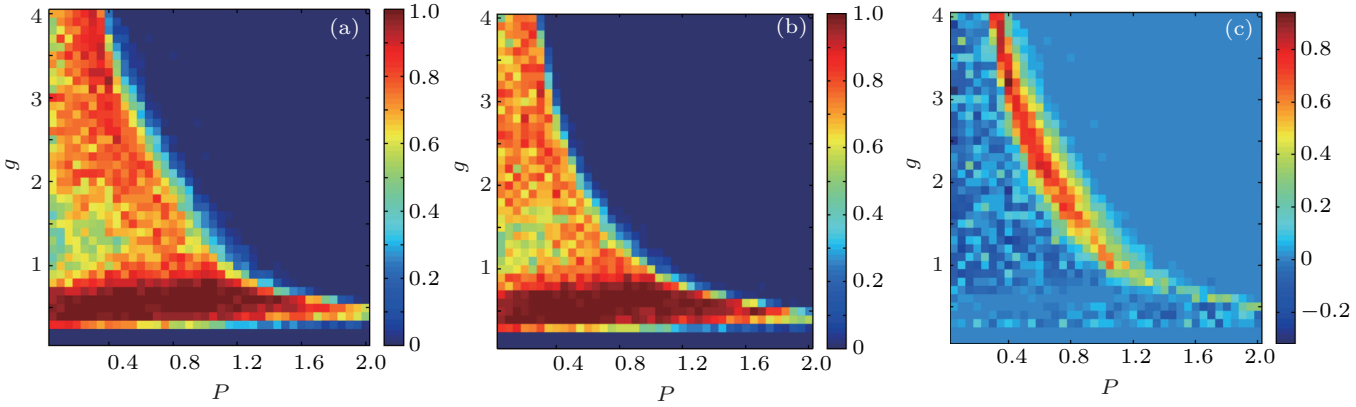


Fig. 2. (color online) Difference of oscillatory probabilities of LBSW networks without and with STDP. P is the mean degree of LRC of a neuron (LRC degree), and proportional to the bidirectional LRC probability p, $P = 2pN$; g is the maximum conductance of all synapses. (a) Oscillatory probabilities of non-STDP networks. The color bar represents different levels of oscillatory probabilities. (b) Oscillatory probabilities of STDP networks. (c) Difference of oscillatory probabilities between non-STDP and STDP networks, i.e., oscillatory probabilities of non-STDP subtracted by that of the corresponding STDP networks. It is shown that the parameter region where STDP networks could generate oscillations is smaller than that for non-STDP networks. Network parameter set: $N = 2500$; total simulation time $T_{\rm total} = 1500$, trial number with randomly generated topology and random initial variables $N_{\rm trial} = 50$, the gradient of maximum conductance $\Delta_{\rm g} = 0.1$, the gradient of the mean degree of LRCs $\Delta P = 0.05$, the range of maximum conductance $g \in [\Delta_{\rm g}, 4]$, the range of the mean degree of LRCs $P \in [\Delta P, 2]$, the scanning number of P and g is 40×40, the duration time of judging the asymptotic state $T_{\rm judge} \in [1450, 1500]$. STDP parameters: learning rates of facilitation and depression $A_+ = A_- = 0.05$, time constants of facilitation and depression $\tau_+ = \tau_- = 2$.

3.2. Effects of STDP on network activity states

By classifying the asymptotic states of the above networks under different parameter sets of g and P, it is also found that STDP has a large effect on network activities. In the g–P plane, there are four distinct regions of asymptotic states of non-STDP networks (see Fig. 3(a)): the synchronous firing state (SF state), the wavelet turbulence state (WT state, asynchronous firing state), the global rest state (GR state), and the coexistenting states of WT and SF (CO state). This is similar to the observation in Ref. [27] where LBSW networks were generated by adding unidirectional LRCs.

In STDP networks (see Fig. 3(b)), it is also found that there are four distinct regions of asymptotic states, but the region of the SF state becomes much smaller and the region of the CO state becomes much larger, indicating STDP does not favor the SF state but favors the CO state. In Fig. 3(c), differences of the asymptotic states between STDP and non-STDP networks are plotted, which shows that the asymptotic network states of non-STDP networks are significantly changed in a large parameter region by considering STDP. There are five large regions classifying different relationships between the asymptotic states of non-STDP networks and STDP networks: The green region is no transition which means that STDP and non-STDP networks have identical types of dynamic patterns; the dark red region (labeled by (i) in Fig. 3(c)) is the transition region from the SF state of the non-STDP case to the GR state of the STDP case (abbreviated as SF-to-GR transition region); the other three large transition regions are the SF-to-CO transition region, the WT-to-CO transition region, and the CO-to-WT transition region (labeled by (ii), (iii), and (iv) in Fig. 3(c) respectively). Moreover, the part of the green region surrounded by the above three regions ((ii), (iii), and (iv) in Fig. 3(c)) is a special region, called the CO-to-CO region (not labeled), where time-dependent transitions between the SF state and WT state may occur in STDP networks. All those observations imply that single STDP networks could undergo very rich plasticity-induced transitions between activity patterns by varying the parameters g and P.

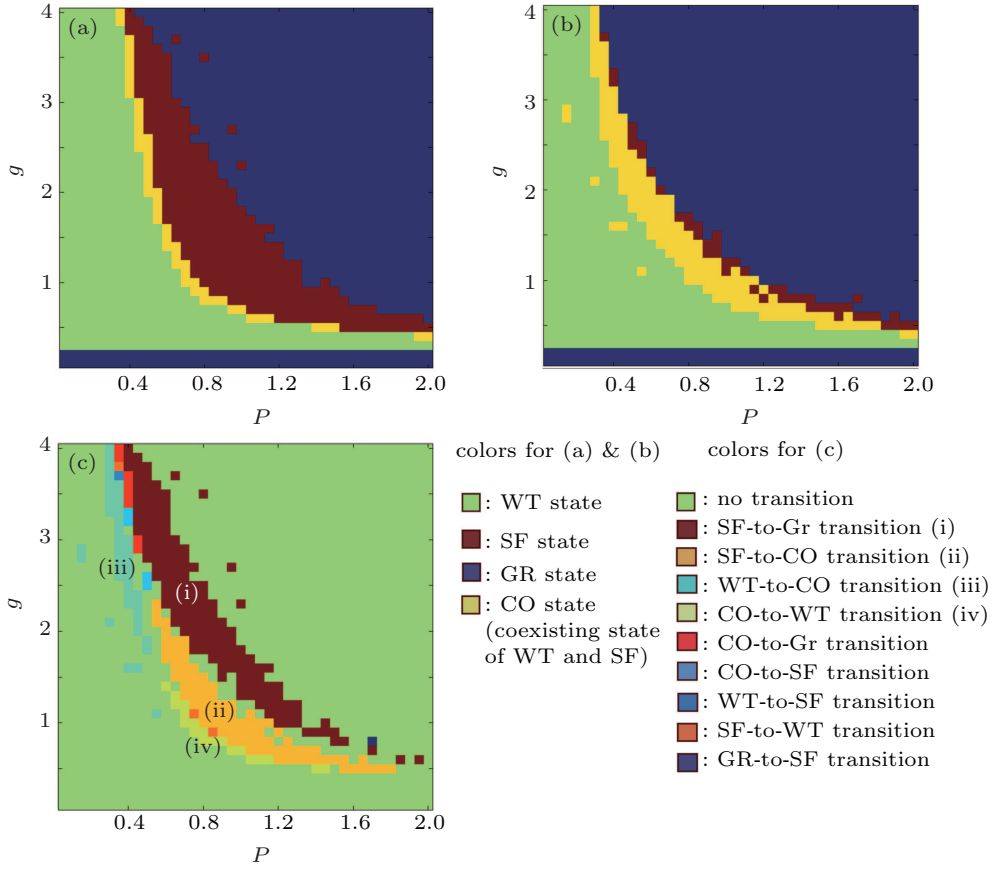


Fig. 3. (color online) Difference between the asymptotic states of LBSW networks without and with STDP. The asymptotic states are calculated from the data of networks in Fig. 2. (a) Asymptotic states of non-STDP networks. There are four typical parameter regions of asymptotic states: the wavelet turbulence state (WT state), the synchronous firing state (SF state), the global rest state (GR state), and the coexistent states of WT and SF (CO state). (b) Asymptotic states of STDP networks. By comparing panel (b) with panel (a), it is easy to find that the region of the SF state in STDP networks becomes much smaller and the region of the CO state in STDP networks turns out to be much larger. Therefore, STDP is not in favor of the SF state but is in favor of the CO state in the parameter space. (c) Asymptotic state differences between non-STDP and STDP networks. There are four large transition regions of asymptotic states from non-STDP networks to STDP networks. In panel (c), the green region represents the no transition region; the dark red region (labeled by (i)) is the transition region from the SF state to GR state (abbreviated as SF-to-GR transition region); The other three large transition regions are the SF-to-CO transition region, the WT-to-CO transition region, and the CO-to-WT transition region (abbreviated as (ii), (iii), and (iv) in the figure respectively). The parameter set is the same as in Fig. 2. The criterion for being in the SF state: If the mean voltage of all neurons in a network $\langle u(t)\rangle$ is no less than the threshold of SF state (here we use $u_{\mathrm{SF,thres}} = 0.8$) during the judgement period $T_{\mathrm{judge}} \in [1450, 1500]$, the asymptotic state of the network is classified as the SF state.

3.3. Phase transitions

There are three activity states of an LBSW network: the SF state, WT state, and GR state. By adding STDP to a non-STDP network, the network state could be switched from one state to another, this phenomenon is called 'phase transitions'.[26] Those transitions are induced by STDP. Here we find that these kinds of transitions could be generated in networks with parameters g and P belonging to the transition regions in Fig. 3. In addition, highly frequent and time varying transitions could occur in a network with parameters g and P belonging to the region of the CO state in Fig. 3(b).

To investigate the phase transitions of network activities effected by STDP, we add STDP on an LBSW network when its state is converged to a stable state, and find three types of phase transitions: the SF-to-WT phase transition (Fig. 4(a) and Fig. 4(c)), the WT-to-SF phase transition (Fig. 4(b) and Fig. 4(c)), and the SF-to-GR phase transition (Fig. 4(b)). Moreover, the SF-to-WT phase transition can easily be observed in the CO-to-WT transition region and the CO-to-CO region in Fig. 3(c); the WT-to-SF phase transition easily occurs in the WT-to-CO transition parameter region and the CO-to-CO region in Fig. 3(c).

It is very interesting that the state of an LBSW network under a large STDP learning rate could be rapidly switched between the SF state and the WT state (Fig. 4(c)). These irregular occurrences of the SF state are a kind of intermittent phase transition. Particularly, there is no change of control parameter during the period of repeated state transitions, so we call this kind of transition a self-organized phase transitions (SOPTs). In realistic neural systems, there are many kinds of activity of the transitions of neuron populations, for example, the local field potential (LFP) could be frequently in up and down states (temporally switched between a high value and a low value of mean voltage), and the neuron population in the up state of LFP fires more frequently than in the down state.[7]

A phase transition in a general system is defined as the typical state of the system when changed to another one by altering the external conditions or control parameters. The phase transition considered here also could be driven by changing the network parameters (STDP parameters). In Fig. 4(a) and Fig. 4(b), the control parameters of these transitions could be regarded as the changed STDP learning rate (abruptly change STDP learning rate from 0 to 0.05). However, due to the special dynamical relationship of connection weights and network activities induced by STDP, SOPTs could be generated without modification of STDP parameters (Fig. 4(c)); this is a special typical transition behavior induced by the self-interplay of weight dynamics and activity dynamics.[25,26]

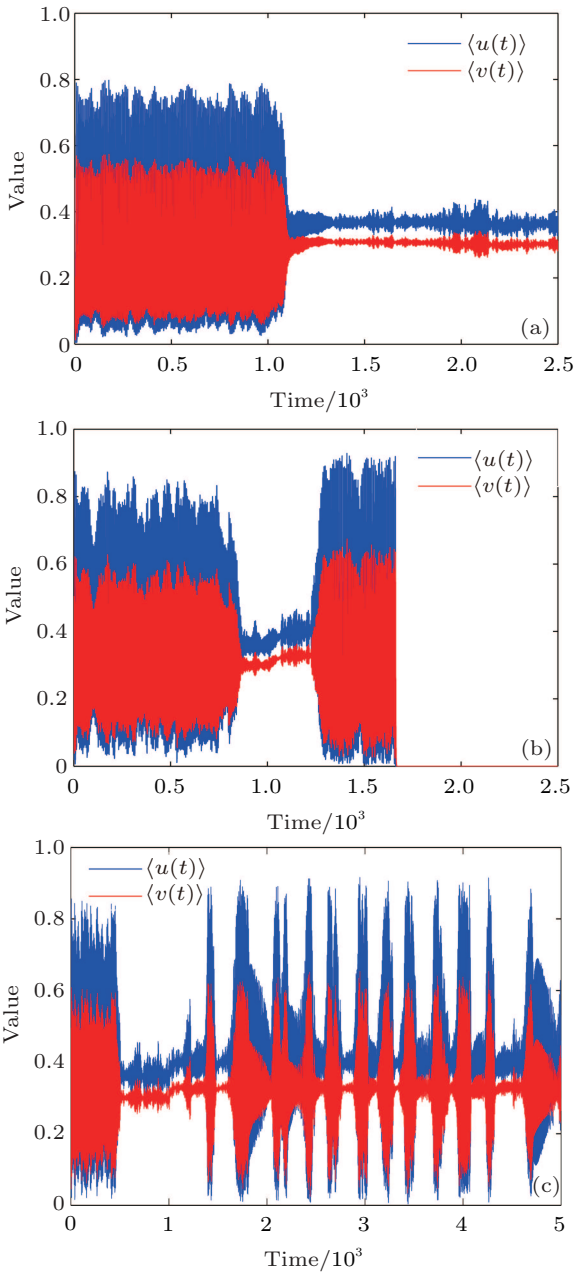


Fig. 4. (color online) Typical phase transitions in LBSW networks by adding STDP. STDP is applied after $t = 1000$, $\langle u(t)\rangle$ and $\langle v(t)\rangle$ are used to judge network activity states. (a) Phase transition in a network whose state is SF state before adding STDP, and there is an SF-to-WT transition after adding STDP. (b) Phase transition in a network whose state is the WT state before adding STDP, and WT-to-SF transition and SF-to-GR transitions occur successively after adding STDP. (c) Intermittent phase transitions. There are rapidly repeated transitions between the SF state and WT state. The parameters g and P of panel (a) are in the region of the CO-to-WT transition, and those of panel (b) and panel (c) are in the region of the WT-to-CO transition in Fig. 3(c). Network parameter: (a) $P = 0.70$, $g = 1.0$, $A_+ = A_- = 0.05$; (b) $P = 0.48$, $g = 2.4$, $A_+ = A_- = 0.05$; (c) $P = 0.48$, $g = 2.4$, $A_+ = A_- = 0.1$. The other parameters are the same as those in Fig. 2.

3.4. Pattern dynamics of network activities under a phase transition

Another measurement of network states is the spatiotemporal activity pattern of all neurons. In Fig. 5, the dynamical change of the network state before and after the SF-to-WT transition is shown by both the mean voltage $\langle u(t)\rangle$ and snap-

shots of spatiotemporal activity pattern in detail. The dynamics of $\langle u(t)\rangle$ in the SF state and WT state are both oscillatory, but the amplitude in the SF state is much larger than that in the WT state (see Fig. 5(a)). As shown in Fig. 5(b), we can see that there is a very high level of synchronized firing at times $t = 503$ and $t = 509$ in the SF state, whereas the network is always in asynchronous firing mode in the WT state (Fig. 5(c)), and the spatiotemporal pattern of the WT state is like wavelet turbulence (the origin of the name 'WT state') and fairly homogeneous in time.

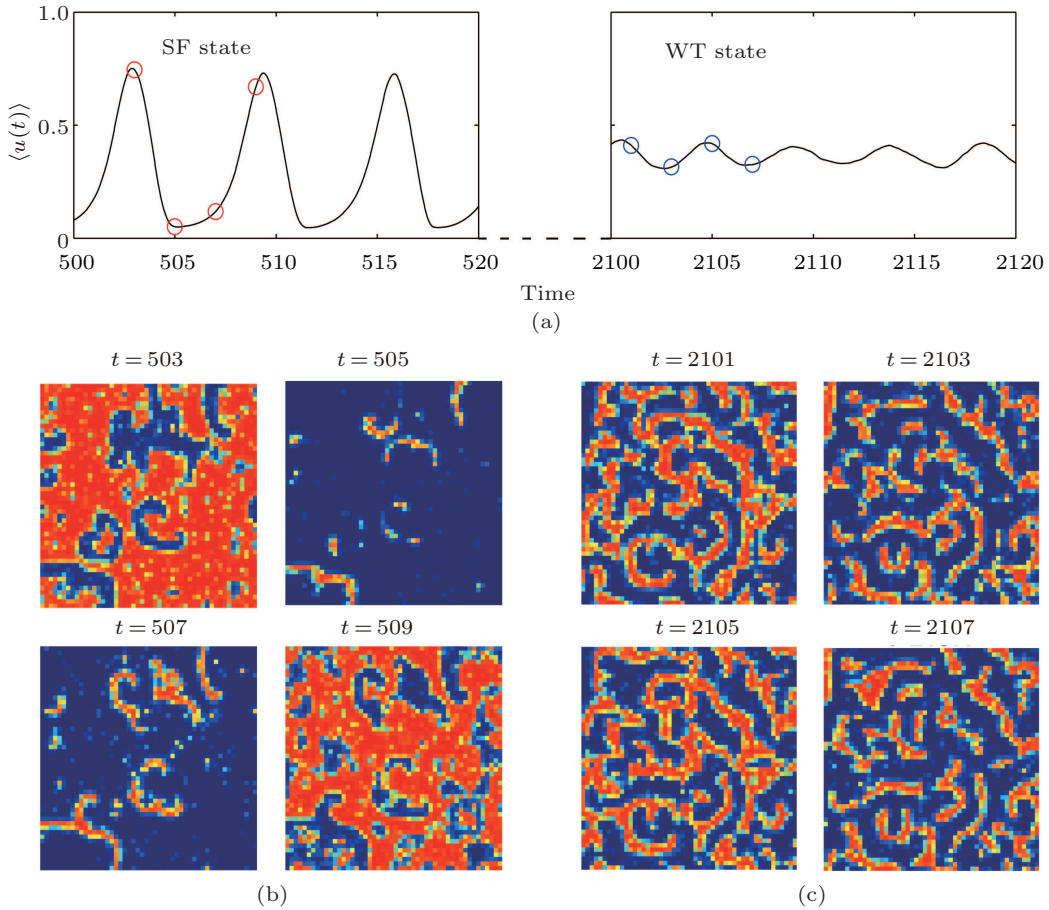


Fig. 5. (color online) Pattern dynamics of the activities of an LBSW network before and after adding STDP. The data are from the results of the network of Fig. 4(a), in which there is an SF-to-WT transition. (a) The amplified local behaviors of $\langle u(t)\rangle$ in both the SF state (left) and the WT state (right). (b) Snapshots of the spatiotemporal patterns of the SF state of all neurons. (c) Snapshots of the spatiotemporal patterns of the WT state of all neurons. The four patterns of panel (b) (panel (c)) are the corresponding patterns at the four circles labeled times in the SF (WT) state of panel (a).

4. Mechanism of phase transitions and SOPTs

As shown in Subsection 3.3, various phase transitions could be induced by STDP, especially, SOPTs. In the following part, we discuss the mechanism of SOPTs on the basis of synaptic weight dynamics.

For different asymptotic states of the networks under STDP as shown in Fig. 3(b), one can see not only a significant difference between their spatiotemporal activity patterns (Fig. 5), but also a distinct difference of their synaptic weight distributions. As shown in Fig. 6, when an STDP network is in the SF state, its corresponding synaptic weight distribution is a kind of unimodal distribution, whereas, if an STDP network is in the WT state, its synaptic weight distribution is a kind of bimodal distribution. This implies that the characteristic changes of the pattern dynamics on synaptic weight distributions could be a crucial measurement for SOPTs of networks under STDP.

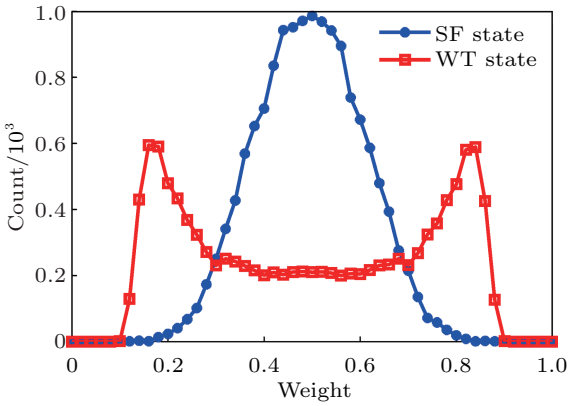


Fig. 6. (color online) Synaptic weight distributions in the SF and WT states of LBSW networks with STDP, which are at the parameter sets $g = 0.5$, $P = 1.9$ (SF), and $g = 0.5$, $P = 0.8$ (WT) in Fig. 3(b), respectively. Weight distributions are calculated by the mean of 20 distributions in final 20 physical time units ($t \in [1480, 1500]$, each time unit for one distribution). The other parameters are the same as those in Fig. 3(b).

In Fig. 7, we analyze the synaptic dynamics of SOPTs in an LBSW network where STDP is added at $t = 500$. Synaptic weight distribution is dynamically changed at different times. In particular, synaptic weight distribution is a distinct bimodal distribution when the network is in the WT state (e.g., $t = 800, 1550$), and is a distinct unimodal distribution when the network is in the SF state (e.g., $t = 1300, 1800, 2300$) (Fig. 7(a)). We define the mean weight of all facilitated synapses $\langle W_f \rangle$ by averaging all synaptic weights that are larger than the initial value $W_{max}/2$, and conversely the mean weights of all depressed synapses $\langle W_d \rangle$ are similarly defined for all weights smaller than $W_{max}/2$. The variations of $\langle W_f \rangle$ and $\langle W_d \rangle$ (Fig. 7(b)) could represent the change of synaptic weight distribution (Fig. 7(a)) and they are strongly correlated to the network activity dynamics (represented by $\langle u(t) \rangle$ and $\langle v(t) \rangle$ in Fig. 7(c)).

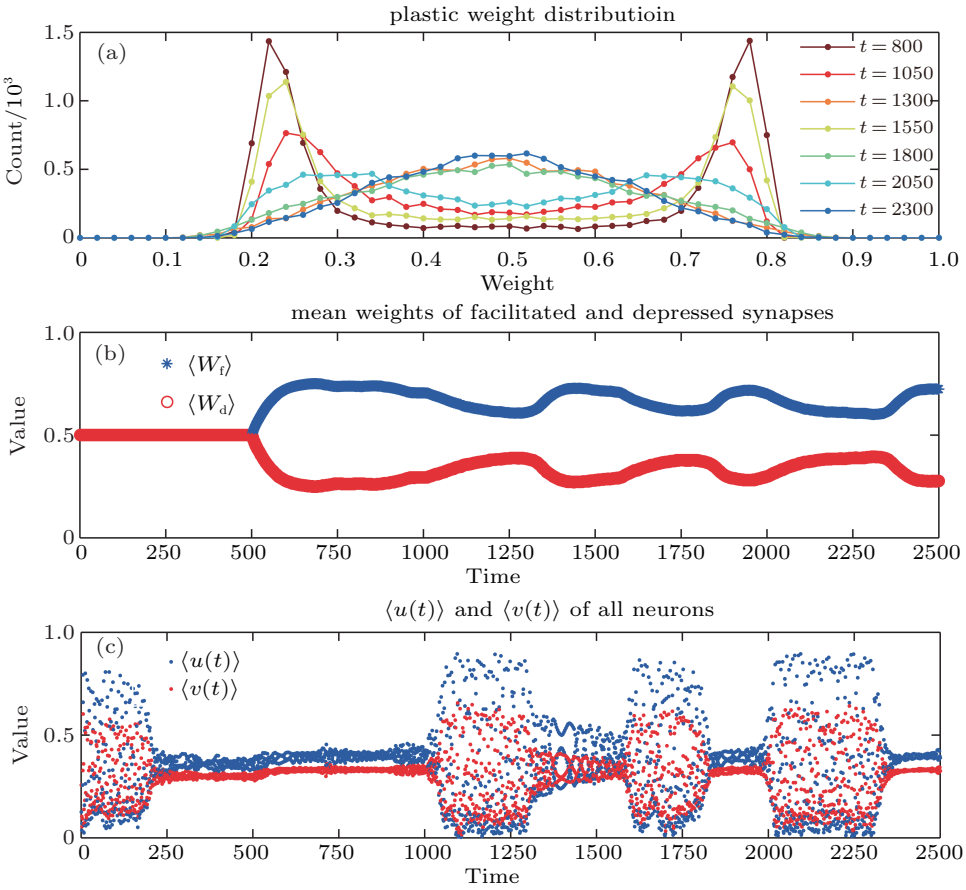


Fig. 7. (color online) Synaptic dynamics and the mechanism of SOPTs in an LBSW network under STDP. STDP is applied after time $t = 500$. (a) Synaptic weight distribution at different times. (b) Mean weights of all facilitated synapses $\langle W_f \rangle$ and all depressed synapses $\langle W_d \rangle$. $\langle W_f \rangle$ ($\langle W_d \rangle$) is defined as the mean weight of all synapses that are larger (smaller) than the initial value $W_{max}/2$, their variations could represent the change of synaptic weight distribution. (c) The corresponding $\langle u(t) \rangle$ and $\langle v(t) \rangle$. Time evolutions of $\langle W_f \rangle$, $\langle W_d \rangle$, $\langle u(t) \rangle$, and $\langle v(t) \rangle$ are shown with the time interval $\delta t = 1$. Parameters: $P = 0.46$, $g = 2.4$, they are in the parameter region of the WT-to-CO transition in Fig. 3(c); $A_+ = A_- = 0.05$; and the other parameters are the same as those in Fig. 3.

Further analysis shows that the WT-to-SF transition is driven by the temporal accumulation of the weight change. For example, in the period of $t \in [800, 1020]$ of Fig. 7, the network is in a WT state and the first WT-to-SF phase transition in the network happens at $t = 1020$ (Fig. 7(c)), whereas $\langle W_f \rangle$ ($\langle W_d \rangle$) had been accumulatively decreasing (increasing) obviously since $t = 900$ (Fig. 7(b)). That is, the changes of the two mean weights occur much sooner than the change of the network state in the process of the first WT-to-SF transition. In the third WT-to-SF transition (around time $t = 2000$) during SOPTs, the changes of the two mean weights are at least 40 physical time units earlier than the change of the network state. Hence, the previously accumulated weight variation triggers the change of the network state in the WT-to-SF transition.

For the mechanism of the SF-to-WT transition, the origin of the transition is triggered by transient activity perturbation. Taking the process of the third SF-to-WT phase transition of Fig. 7 as an example, at the starting time of the transition ($t = 1300$), $\langle W_f \rangle$ and $\langle W_d \rangle$ change almost simultaneously, associated with the decrease of $\langle u(t) \rangle$ (see Fig. 7(b) and Fig. 7(c)). In fact, the weight change is not earlier than the state change at all. Why is this so different to that in the SF-to-WT phase transition? The key reason is that the SF state is less stable than the WT state. This conclusion can be intuitively justified by the observation that in a large parameter region the SF state under non-STDP (Fig. 3(a)) loses stability when loading STDP (see the SF-to-GR and SF-to-CO transition regions in

Fig. 3(c)). When the network is in the SF state, a transient activity perturbation induced by STDP could easily increase the number of neurons firing at the quasi-rest state of the network (e.g., '$t = 505$' in Fig. 5(b)), and then the perturbation would be amplified to drive the system dynamics away from the SF state to to the WT state with a large probability, and finally an SF-to-WT transition may happen.

5. Conclusion and discussion

In summary, we have studied the influences of the plasticity of connection weight on both pattern dynamics and phase transition behaviors in neuronal networks. By assuming STDP on electrical synapses, the LBSW networks under STDP could generate diverse phase transitions between network activity states which cannot happen in non-STDP networks. Especially, self-organized phase transitions could be found in the STDP network without external input. Moreover, there are some other effects of STDP on network activities compared with those of non-STDP networks: smaller parameter regions of both oscillation and the SF state; and the larger region of the CO state. Based on synaptic weight dynamics, we can intuitively understand the mechanics of SOPTs: the WT-to-SF phase transition is triggered by the preceding accumulated weight variation; whereas the SF-to-WT phase transition is driven by the transient activity perturbation.

Results obtained throughout the paper are under the condition of M-STDP. By changing the parameters of M-STDP, we found that the transition between network states hardly happens when the time constants of STDP are too large or the learning rates are too small. We also investigated the effects of A-STDP and found that the network under A-STDP could generate the SF-to-WT transition and the SF-to-GR transition, but fails to generate the WT-to-SF transition.

In this paper, the plasticity of electrical synapses is assumed to STDP, similar to that on chemical synapses. We argue that the hypothesis is reasonable, since the plasticity of electrical coupling could be regulated by the chemical coupling in mixed synapses and the plasticity of electrical synapses could be affected by the activities of nearby chemical synapses.[31] In future, we will investigate the pattern dynamics of LBSW neural networks with chemical couplings under STDP to explore whether SOPTs are general phenomena in STDP networks. Furthermore, since the effect of external stimuli on network dynamics has not been taken into account here, in the next step it is worthwhile to discuss pattern dynamics of activities affected by different kinds of external spatiotemporal stimuli and to explore the function of phase transitions in LBSW plastic networks.

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