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Input synchrony and spike-timing dependent plasticity

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Abstract. The influence of a weight-dependent spike-timing dependent plasticity (STDP) rule on the temporal evolution and equilibrium state of a certain synapse is investigated. We show that under certain conditions, a spike-induced rate-learning scheme could be achieved. Through studying the situation when a single Hodgkin-Huxley neuron is driven by a large ensemble of input neurons, we find that synchronized firing of a sub population of input neurons may be important to information processing in the nervous system. Using simulations, we show that the temporal structure of the spike trains of these synchronized input neurons can be transmitted reliably; further, synapses from these neurons will increase stably due to the STDP rule and this may provide a mechanism for learning and information storage in biologically plausible network models.

PACS. 87.18.Sn Neural networks – 87.16.Xa Signal transduction – 87.17.Aa Theory and modeling; computer simulation

In real nervous systems, information is encoded and transmitted *via* spatiotemporal patterns of action potentials fired by each neuron; and the synaptic weights between neurons can be modified by these firing events. This mechanism, which is referred to as synaptic plasticity, is believed to be responsible for learning, memory and adaptation in neural circuits. Hebb proposed a rule that describe this mechanism qualitatively [1], and has been verified and implemented by substantial experimental and modeling studies. Hebbian plasticity has come to mean synaptic specific modification of synaptic weights that is dependent on correlations between pre and postsynaptic activity [2].

Recent experiments [3–5] revealed a new Hebbian type synaptic plasticity that depends on the precise timings of pre and postsynaptic action potentials. It has been found that presynaptic firing that precedes postsynaptic firing or depolarization can increase the synaptic efficacy; whereas reversing this temporal order will result in the decrease of the synaptic efficacy. This form of synaptic modification, which is referred to as spike-timing dependent plasticity (STDP) has been investigated by several studies in models of long-term plasticity [6], temporal difference learning [7], and competitive Hebbian learning [8]. A common problem encountered by all synaptic plasticity schemes is stability–there must be a nonlinear mechanism to keep the synaptic weights from increasing without bound. It has been found that STDP alone can not achieve a stable modification of synaptic weights, hard bounds must be introduced artificially [8], and synaptic efficacies are driven to these bounds, which is not very biologically plausible. Other studies [9,10], which incorporate a weight-dependent mechanism of synaptic modification amplitude in addition to STDP, show that a unimodal distribution of synaptic efficacies could be achieved and this namely weight-dependent STDP is intrinsically stable. Thus we adopt the weight-dependent STDP rule as the basis of our study. We investigate the temporal evolution and equilibrium states of a synapse that is subjected to STDP and find that under certain conditions, a spike-induced rate-learning rule could be achieved. Further, we explore the situation when a single HH neuron is driven by a large population of input neurons via excitatory synapses, and these synapses modify according to the STDP rule. We find that independent inputs is not very meaningful to information processing; whereas synchronized firing of a sub population of input neurons may be important to information transmission and adaptation in neural circuits.

Recent experiments show that both the degree and sign of synaptic modification depend on the precise temporal order of pre and postsynaptic action potentials [3–5]. The time window for this spike timing-dependent plasticity (STDP) is shown in Figure 1. Experiments also suggest that the amount of synaptic modification is smaller for relatively stronger synapses, given that $\Delta t > 0$; when $\Delta t < 0$, the amount of change for each pair of spikes is fixed. For convenience, let $0 < w < 1$, and the STDP rule

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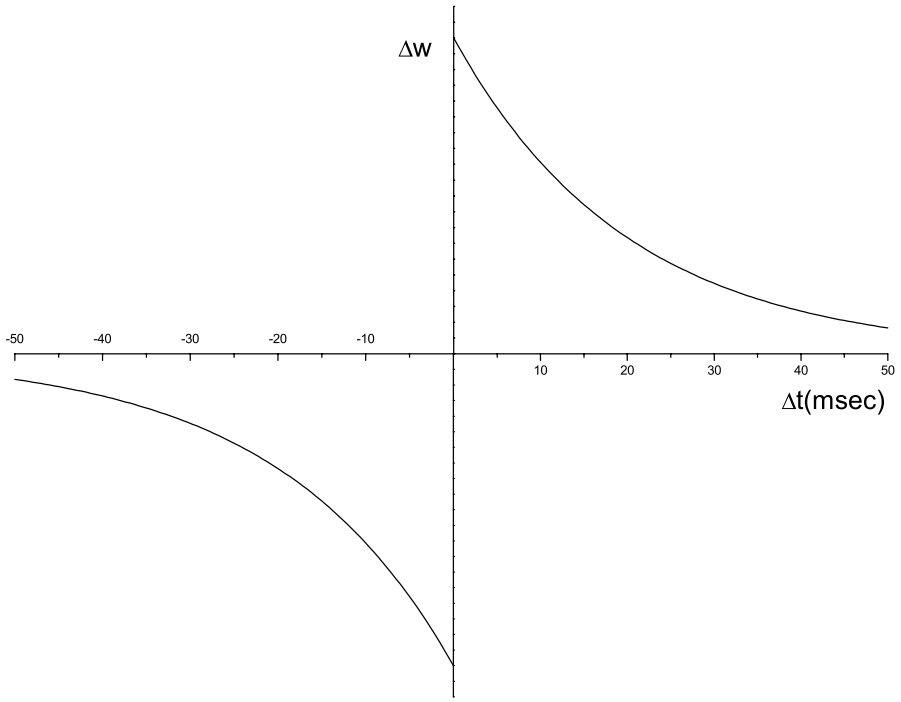

Fig. 1. The time window for STDP. Δw is the amount of synaptic modification for a pair of pre and postsynaptic spikes. Δt is the time of the postsynaptic spike minus the time of the presynaptic spike, *i.e.* $\Delta t = t_{post} - t_{pre}$.

can be written as

$$\Delta w = \begin{cases} \lambda(1-w)\exp(-\Delta t/\tau_1) & \Delta t > 0 \\ -\lambda k \exp(\Delta t/\tau_2) & \Delta t < 0 \end{cases} \quad (1)$$

$\lambda \ll 1$ sets the scale of synaptic change for each pair of spikes. $k > 0$ control the amount of decrease which is fixed. In our simulations, $\lambda = 0.01$. τ_1, τ_2 are the time constants for strengthening and weakening respectively. Some experiments report that τ_1 is roughly the same as τ_2 [4], others report that τ_2 is larger [11]. As we will see in the following study, there isn't significant difference between these two situations. Another assumption made by our study and most other modeling studies on STDP is that the pairing events of pre and postsynaptic spikes are independent, *i.e.* the effect of multiple pre and postsynaptic spikes is just the linear sum of all spike pairs.

Now we consider the temporal evolution of a given synapse subjected to the STDP rule given above for various pre and postsynaptic firing activities. The input and output spike trains are independent homogeneous Poisson processes with mean firing rates r_{in}, r_{out} respectively. Because $\lambda \ll 1$, that is, the amount of change is small for each step, so the rate of synaptic change on a time scale of $\frac{1}{\lambda}$ is proportional to

$$v = r_{in} r_{out}[(1-w)\tau_1 - k\tau_2]. \quad (2)$$

When $v = 0$, *i.e.* the synapse reaches a stable state, we have $(1-w)\tau_1 = k\ \tau_2$, so that

$$w = 1 - k\tau_2/\tau_1. \quad (3)$$

From equations (2) and (3) we can see that whether τ_1 is the same as τ_2 doesn't make a critical difference, the properties of temporal evolution and the equilibrium state are the same for both cases, so we only consider the case when $\tau_1 = \tau_2 = 20$ msec, as suggested by experimental data.

One may find that although $\lambda \ll 1$ can guarantee $w + \Delta w < 1$ when the synaptic modification is positive *i.e.* $\Delta t > 0$; there are not sufficient constraints to ensure $w + \Delta w > 0$ when $\Delta t < 0$. This problem could easily be solved by making the weight decrease, in this case, proportional to w, *i.e.*

$$\Delta w = -\lambda k w \exp(\Delta t/\tau_2)\ \Delta t < 0. \quad (4)$$

Similarly, the equilibrium value of a synapse subjected the STDP rule of this version is:

$$w = \frac{1}{1 + k\tau_2/\tau_1}\,. \quad (5)$$

Actually, in our simulations, we find that the qualitative behaviors of the temporal evolution of a synapse subjected to STDP are the same for both equations (1) and (4), as we shall see in the following study (Fig. 2), if $0 < k < 1$ and k is not too close to 1, the fluctuation of the synaptic weight will not make it decrease below zero. Thus, we adopt equation (1) because the form of the equilibrium value of w is more concise and a fixed amount of decrease is what neurobiologists found in their experiments [5].

We ran simulations for different initial values of w, and different values of parameter k. To ensure that the results

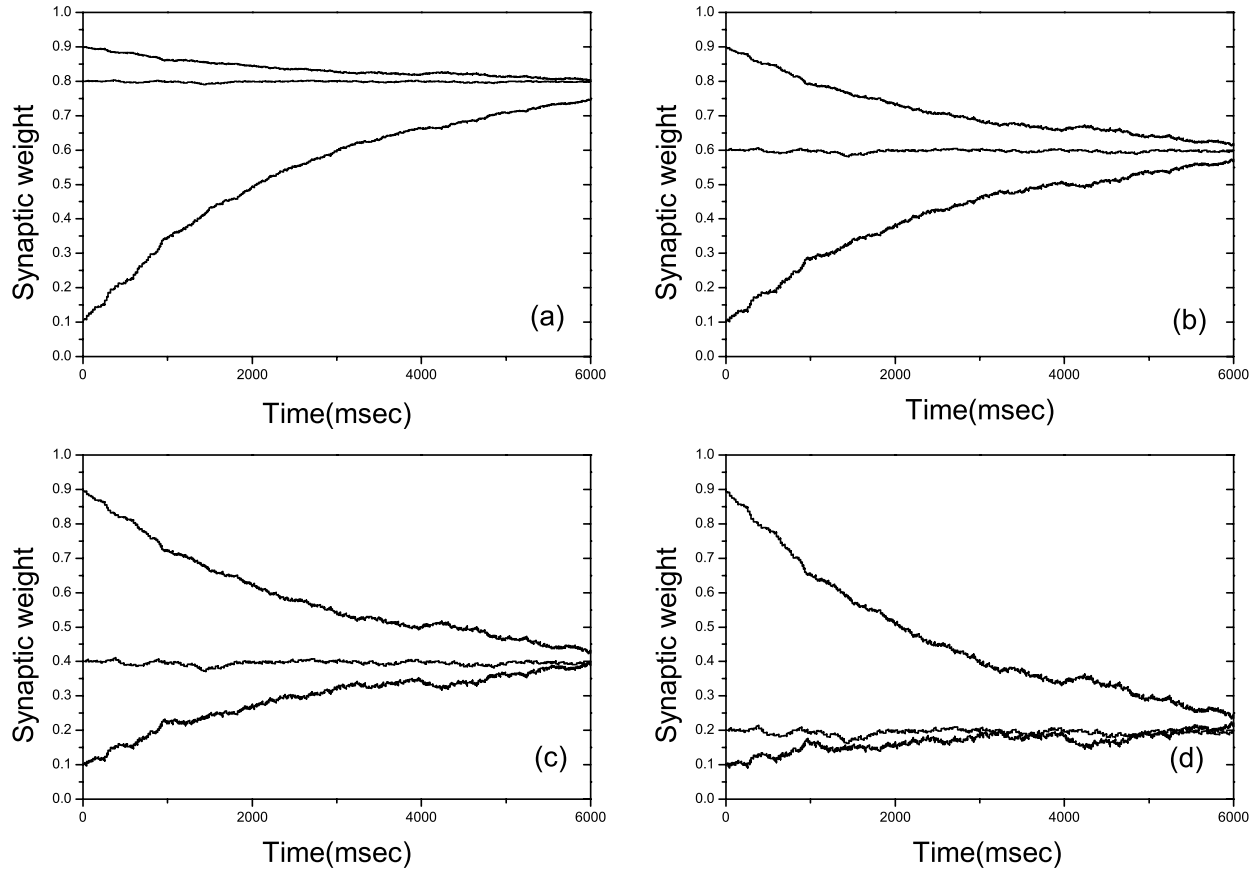

Fig. 2. Temporal evolution of a synapse with different initial values and different values of parameter k when the pre and postsynaptic firing activities are independent Poisson processes with the same mean firing rate of 50 Hz. (a) $k = 0.2$. (b) $k = 0.4$. (c) $k = 0.6$. (d) $k = 0.8$.

do not depend on initial conditions, each set of parameters is ran for over two trails and there is no qualitative difference between these trials. The result is shown in Figure 2. We find that equations (2) and (3) describe the behavior of the system quite well. We notice that if k is small, such as $k = 0.1$, the equilibrium value of w is nearly the upper limit, and this can result in a rate-based learning rule according to equation (2). Only the product of the pre and postsynaptic firing rate determines the speed of learning, as is show in Figure 3. Plus other reversibility mechanisms such as decay [12], this spike-induced rate-learning rule may have important implications for information storage and retrieval in neural networks.

Now we consider the situation when a single Hodgkin-Huxley neuron is driven by 100 input neurons *via* excitatory synapses which are subjected to the STDP rule. The HH neuron model is described by four differential equations

$$C\mathrm{d}V/\mathrm{d}t = -g_{Na}m^3h(V - V_{Na}) - g_K n^4(V - V_K) - g_L(V - V_L) + g_{syn}(V - V_s) \quad (6)$$

$$\mathrm{d}m/\mathrm{d}t = -(a_m(V) + b_m(V))m + a_m(V) \quad (7)$$

$$\mathrm{d}h/\mathrm{d}t = -(a_h(V) + b_h(V))h + a_h(V) \quad (8)$$

$$\mathrm{d}n/\mathrm{d}t = -(a_n(V) + b_n(V))n + a_n(V) \quad (9)$$

V is the membrane potential of the neuron, g_{syn} is the total conductance of the synapses, V_s is the reversal potential for the excitatory synapses. The term $g_{syn}(V - V_s)$ represents the excitatory postsynaptic current (EPSC) generated by the arrival of input spike trains. The meanings and values of other parameters can be found in [13]. The input spike train from the ith input neuron can be expressed by

$$S_i(t) = \sum_j \delta(t - t_i(j)) \quad (10)$$

where $t_i(j)$ are the spike times of the ith neuron. Then the total synaptic conductance is given by

$$g_{syn}(t) = g_{amp} \sum_i w_i \sum_j F_{syn}(t - t_i(j)). \quad (11)$$

Where w_i is the synaptic weight from the ith input neuron to the HH neuron, g_{amp} is a parameter controlling the amplitude of g_{syn}, $F_{syn}(t)$ is the synapse function which describe a temporal change of the injected synaptic electric current after the arrival of an action potential.

$$F_{syn}(t) = \begin{cases} 0 & t < 0 \\ t/(t_s)^2 \exp(-t/t_s) & t \geqslant 0 \end{cases} \quad (12)$$

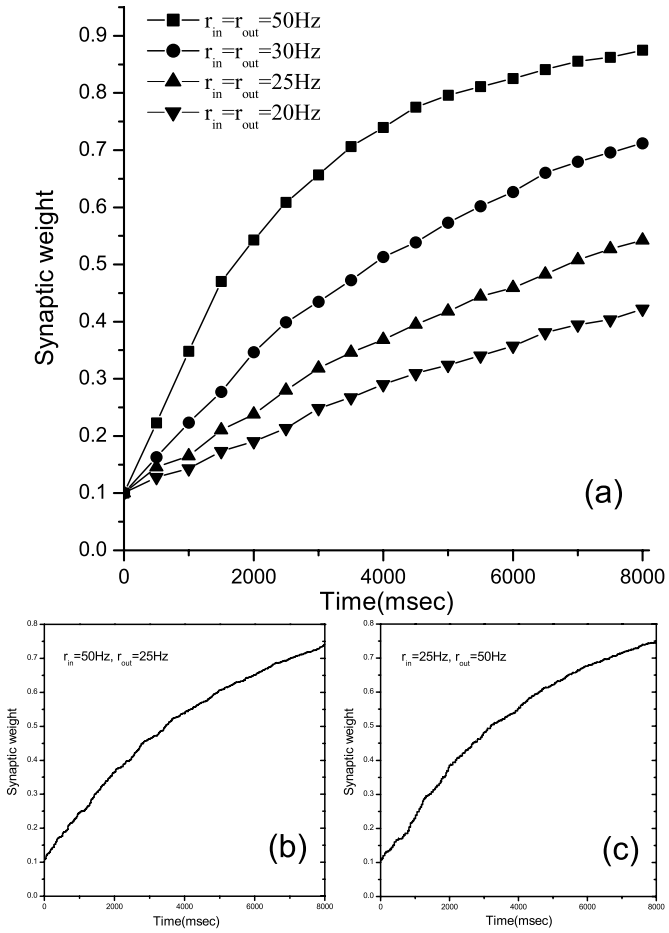

Fig. 3. When $k = 0.1$, the equilibrium value of w is 0.9. This can result in a firing rate-based learning scheme. The temporal evolution of a synapse with initial value 0.1 for different input and output firing rates is shown in (a). Only the product of r_{in} and r_{out} determines the process of learning, this can be seen by comparing (b) with (c).

In our study, $g_{amp} = 0.01$, $V_s = 0$ mV, $t_s = 5$ ms, $k = 0.5$.

We first consider the case when the input neurons fire independently. The firing activity of each input neuron is described by a homogeneous Poisson process with the same mean firing rate of 50 Hz. All the synapses are given an random initial value between 0 and 1. Figure 4 shows the simulation result. We can see that the HH neuron fire rather periodically. This is demonstrated in Figure 5, the interspike interval histogram of the output spike train (ISIH). Thus, there are no correlations between the input and output spike trains, according to our previous study, the synaptic weight will approach the equilibrium value of $1-k = 0.5$. This is confirmed by Figure 6, which plots the temporal evolution of a synapse chosen at random from the 100 synapses. From the simulation results we can see that the situation of independent inputs is rather useless for information transmission and storage. All synapses will become the same and the output spike train is just the same with the activity of a neuron driven by a constant input current.

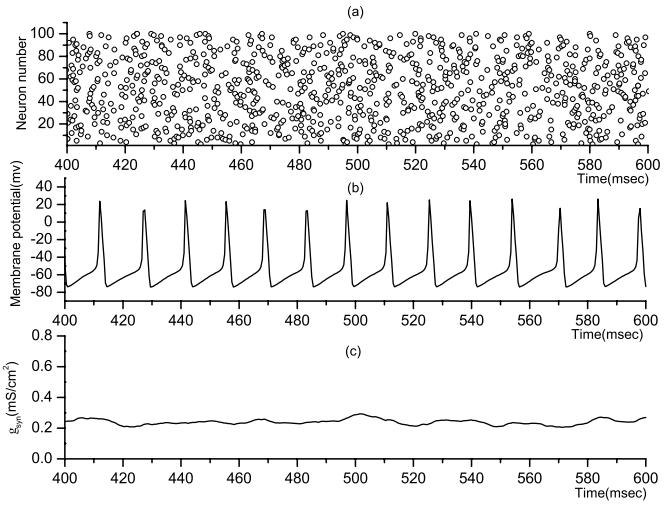

Fig. 4. Response of the HH neuron to independent inputs. (a) The raster that records the firing events of the input neurons. (b) The membrane potential of the HH neuron. (c) The synaptic conductance.

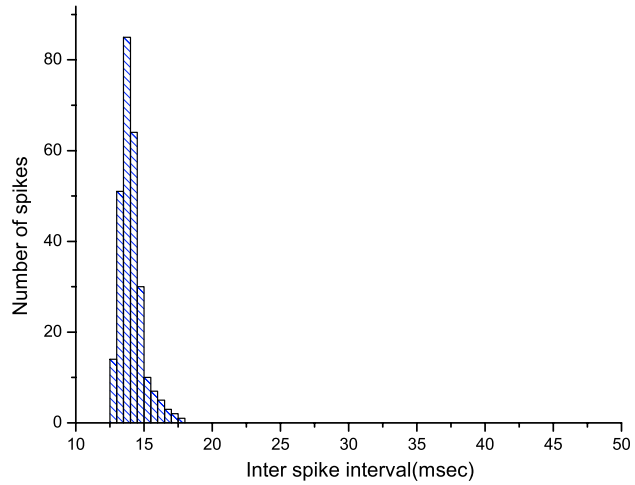

Fig. 5. The interspike interval histogram of the output spike train produced by the HH neuron when driven by independent inputs.

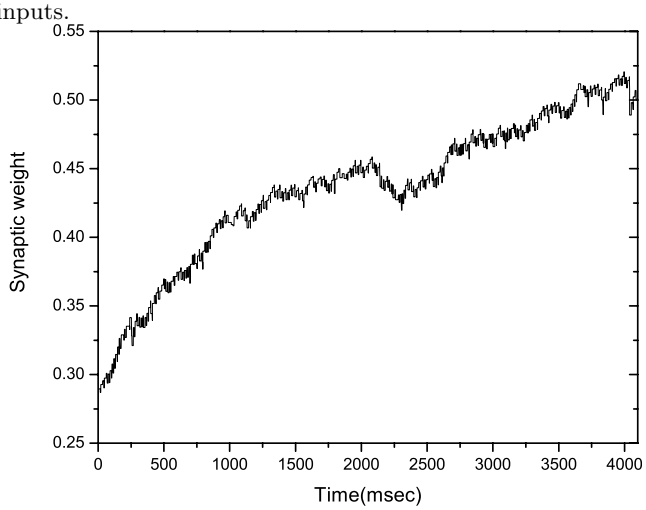

Fig. 6. Temporal evolution of a synapse chosen randomly from the 100 synapses in the situation of independent inputs.

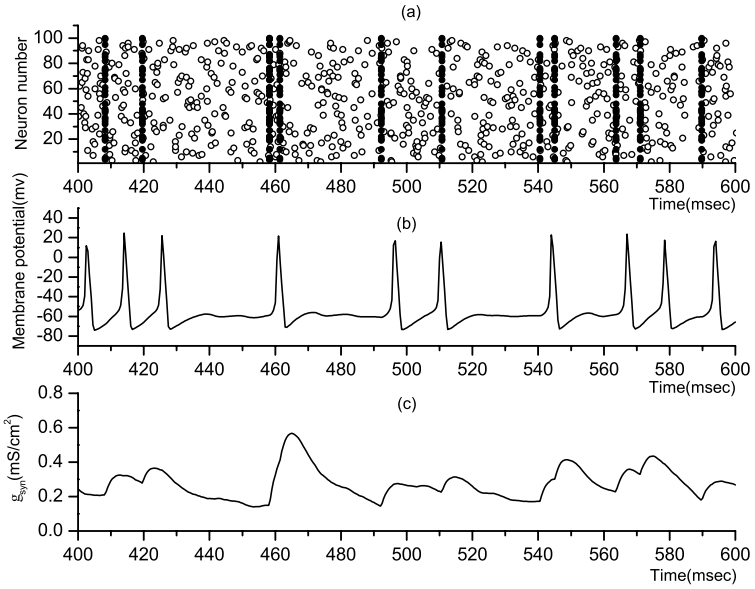

Fig. 7. Response of the HH neuron in the situation when a sub population of input neurons fire synchronously. (a) The raster that records the firing events of the neurons, solid dots represent those neuron which fire synchronously. (b) The membrane potential of the HH neuron. (c) The synaptic conductance.

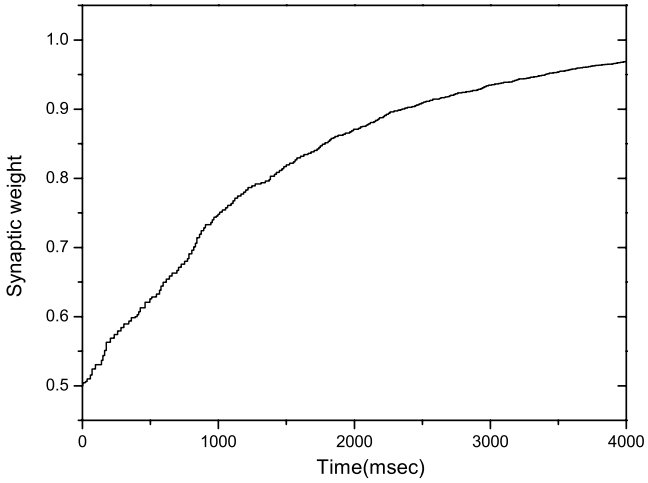

Fig. 8. Temporal evolution of a synapse which is from a synchronous input neuron.

Synchronized firing of cortical neurons is a prevalent phenomenon in the nervous system [14]and is believed to be an important mechanism for information representation and coding. For example, it has been found that synchronous discharge of motor cortical neurons provide a distinct coding variable for movement direction in macaque monkeys [15]. Thus, we consider the case when a sub population of the input neurons fire synchronously. Whether a certain input neuron is within this population is determined by the following process–$z \in [0, 1]$ is a random number, $d \in [0, 1]$, If $z \leq d$, then the neuron is selected in the population. In our simulation, $d = 0.3$. The simulation result is shown in Figure 7. We notice that if there is a temporal coding represented by the ISI of the spike trains of the synchronized input neurons, the information is transmitted reliably by the output spike train, in most cases, there is only a small temporal shift between the spike train of the synchronized input neurons and the output spike train. This correlation result in a different situation of synaptic modification. We plot the temporal evolution of a particularly chosen synapse with initial weight 0.5 in Figure 8. We can see that although for uncorrelated input and output spike trains, 0.5 is the equilibrium value of the synaptic weight, the synapse from the synchronized neuron keep increasing. This may provide a mechanism for information storage and adaptation in the nervous system. Particularly, if k is relatively large, such as 0.9, the equilibrium value of synapses from unsynchronized neurons is relatively small, so synchronized inputs and STDP can result in a competitive learning without introducing other mechanisms such as synaptic scaling [9].

In this paper, we have investigated the influence of a weight-dependent STDP rule on the temporal evolution and equilibrium state of a certain synapse. We have shown that under certain conditions, a spike-induced rate-learning scheme could be achieved. How this mechanism can be implemented in a neural network model for pattern storage and retrieval would be the interest of further studies. In addition, we have found that synchronized firing of a population of neurons may be important to information processing in the nervous system. Using simulations, we find that the temporal structure of the spike trains of these synchronous input neurons can be transmitted reliably. Further, due to the temporal correlation of input and output spike trains, synapses from these synchronous neurons will increase and approach the upper limit stably. This can provide a mechanism for competitive learning and information storage in biologically plausible network models.

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