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Improvement of signal transmission through spike-timing-dependent plasticity in neural networks

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Abstract. We explore the effects of spike-timing-dependent plasticity (STDP) on weak signal transmission in a noisy neural network. We first consider the network where an ensemble of independent neurons, which are subjected to a common weak signal, are connected in parallel to a single postsynaptic neuron via excitatory synapses. STDP can make the signal transmission more efficient, and this effect is more prominent when the presynaptic activities exhibit some correlations. We further consider a two-layer network where there are only couplings between two layers and find that postsynaptic neurons can fire synchronously under suitable conditions. Both the reliability and timing precision of neuronal firing in the output layer are remarkably improved with STDP. These results indicate that STDP can play crucial roles in information processing in nervous systems.

PACS. 87.18.Sn Neural networks – 87.17.Aa Theory and modeling; computer simulation

1 Introduction

Neurons can discharge action potentials by integrating input currents, and information is represented by these firing events. The synapses through which neurons communicate with one another provide passage for information transmission. Synaptic efficacy can be altered by neuronal activity, which is known as synaptic plasticity. Hebb once proposed that the correlation between pre- and postsynaptic activity could induce synaptic modification [1], which has widely been thought to be the mechanism for learning and memory.

Recent experimental studies [2] have reported a new kind of synaptic plasticity, i.e. spike-timing-dependent plasticity (STDP), where both the direction and degree of synaptic modification depend on the temporal relationship between pre- and postsynaptic activity. Modeling studies have also explored the mechanisms for STDP and its functions [3]. Under some conditions, long-term potentiation occurs when a single presynaptic spike precedes a postsynaptic one, while the reverse order of activity produces long-term depression. Furthermore, there is a sharp conversion from maximal strengthening to maximal weakening of synapses when the timing difference of spikes changes sign around 0. Such a mechanism can lead to synaptic competition, which is required for any form of pattern formation, and may be important when information is coded in the timing of individual action potentials [4]. STDP may also make a synapse adjust to an optimal strength for neural synchronization. It has been shown that STDP indeed allows synchronization over a wide range of frequency mismatches and makes it more robust against noise [5]. However, what roles STDP plays in signal transmission and timing coding remains elusive when considering cortical neurons are subjected to large numbers of random synaptic inputs.

Motivated by the aforementioned considerations, here we explore whether signal transmission can be enhanced through STDP in a noisy neural network. The network is composed of an ensemble of presynaptic neurons, which receive a common subthreshold signal, plus a single postsynaptic neuron coupled with all presynaptic neurons via excitatory synapses. Meantime, each neuron is subjected to an independent Gaussian noise. By numerical simulations, we find that the average value of synaptic weight is closely related to the level of correlation among presynaptic activity. The more correlated the neurons exhibit, the larger this value is. STDP can make the signal transmission more efficient in the presence of synchronized presynaptic activity. Such an effect is more prominent when the signal frequency is within the range of 30−90 Hz. We also consider a two-layer network and find that most postsynaptic neurons can fire simultaneously even though presynaptic neurons exhibit weak correlation. Both the reliability and timing precision of spiking in the output layer are remarkably improved due to an increment in synaptic weight. That is, the synaptic weights are adapted to enhance the accuracy of timing coding. This makes it

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possible that precise spatiotemporal firing patterns can be exploited to encode a stimulus accurately, even in a noisy environment.

2 Model and method

We first consider the network where a group of Hodgkin-Huxley (HH) model neurons are connected in parallel to a single postsynaptic neuron. The dynamic equations for the network are presented as follows:

$$C_m\frac{dV_i}{dt} = -g_{Na}m_i^3h_i(V_i - V_{Na}) - g_Kn_i^4(V_i - V_K) - g_l(V_i - V_l) + I_0 + I_i^{syn}(t) + s_i(t) + \varepsilon_i(t), \quad (1)$$

$$\frac{dm_i}{dt} = \alpha_m(V_i)(1 - m_i) - \beta_m(V_i)m_i, \quad (2)$$

$$\frac{dh_i}{dt} = \alpha_h(V_i)(1 - h_i) - \beta_h(V_i)h_i, \quad (3)$$

$$\frac{dn_i}{dt} = \alpha_n(V_i)(1 - n_i) - \beta_n(V_i)n_i, \quad i = 1...N + 1. \quad (4)$$

All the functions and parameter values are the same as in reference [6]. That is, $C_m = 1\ \mu\text{F/cm}^2$, $V_{Na} = 50$ mV, $V_K = -77$ mV, $V_l = -54.4$ mV, $g_{Na} = 120$ mS/cm^2, $g_K = 36$ mS/cm^2, $g_l = 0.3$ mS/cm^2, and $\alpha_m(V) = 0.1(V + 40)/(1 - e^{-(V+40)/10})$, $\beta_m(V) = 4e^{-(V+65)/18}$, $\alpha_h(V) = 0.07e^{-(V_i+65)/20}$, $\beta_h(V) = 1/(1 + e^{-(V+35)/10})$, $\alpha_n(V) = 0.01(V + 55)/(1 - e^{-(V+55)/10})$, and $\beta_n(V) = 0.125e^{-(V+65)/80}$. All the currents are in units of μA/cm^2. Numerical integration of these equations is performed by a second-order stochastic algorithm and the time step is 1000/32768 ms.

I_0 is a constant bias taken as 1 μA/cm^2. The term $\varepsilon_i(t)$ represents a Gaussian white noise with

$$\langle\varepsilon_i(t)\rangle = 0, \langle\varepsilon_i(t_1)\varepsilon_j(t_2)\rangle = 2D\delta_{ij}\delta(t_1 - t_2), \quad (5)$$

where D is referred to as noise intensity and is in units of $\mu\text{A}^2/\text{cm}^4$. The presynaptic neurons are independent of any other (with $I_i^{syn}(t) = 0$) and are subjected to a subthreshold periodic signal, $s_i(t) = A\cos(2\pi f_s t)$, which can be regarded as the input generated by the local field potential. The signal frequency is $f_s = 50$ Hz unless specified otherwise, while the signal amplitude is always set to $A = 1\ \mu$A/cm^2. In contrast, the postsynaptic neuron only receives synaptic inputs from all presynaptic neurons. $I_{N+1}^{syn}(t)$ is defined as [5]

$$I_{N+1}^{syn}(t) = -\frac{1}{N}\sum_{j=1}^{N} g_j(t)s_j(t)(V_{N+1}(t) - E_{syn}). \quad (6)$$

$V_{N+1}(t)$ represents membrane voltage of the postsynaptic neuron, and E_{syn} is the synaptic reversal potential taken as 0 mV. $g_j(t)$ is the synaptic weight of the jth synapse and is in units of mS/cm^2, while $s_j(t)$ is the corresponding fraction of open synaptic channels and obeys first-order kinetics

$$\frac{ds_j(t)}{dt} = \alpha[1 - s_j(t)]H(V_j(t)) - \beta s_j(t) \quad (7)$$

with $H(V_j(t)) = [1 + \tanh(5V_j(t))]/4$, $\alpha = 10$ ms^{-1}, and $\beta = 0.2$ ms^{-1}. Here we assume that the normalized concentration of the postsynaptic transmitter-receptor complex, $H(V_j(t))$, is an instantaneous and sigmoid function of the presynaptic membrane potential [7]. The number of presynaptic neurons is set to $N = 500$.

We call a synapse static if g_j remains constant over time. Otherwise, through STDP $g_j(t)$ changes by an additive update rule [5], i.e.,

$$\Delta g_j(t) = M\text{sgn}(\Delta t_j)\exp(-r|\Delta t_j|) \quad (8)$$

with $M = 0.1$ mS/cm^2, $\Delta t_j = t_{post} - t_{pre}^j$ being the time difference between post- and presynaptic spikes, and $r = 0.15$ ms^{-1}. Figure 1a depicts the amount of unitary synaptic modification against Δt_j. Clearly, there is no strength change when the time difference is large enough. In contrast, a sharp conversion from potentiation to depression of synaptic efficacy occurs within few milliseconds. This indicates that synapses are most sensitive to the timing of spikes. Throughout the paper the initial value of each synaptic weight is set to 0.1. Since these synaptic connections are excitatory, the lower bound of $g_j(t)$ is 0, while its upper bound is set to 0.3. Note that a single presynaptic spike alone cannot trigger the postsynaptic neuron to fire.

We use a coherence measure K to quantify the level of correlation among presynaptic neurons. If a long time interval T is divided into small bins of τ and two spike trains are given by $X(l) = 0$ or 1 and $Y(l) = 0$ or 1, with $l = 1, 2, ..., m$ $(T/m = \tau)$, then a coherence measure for the pair is defined as [8]

$$K_{ij}(\tau) = \frac{\sum_{l=1}^{m} X(l)Y(l)}{\sqrt{\sum_{l=1}^{m} X(l)\sum_{l=1}^{m} Y(l)}}. \quad (9)$$

The population coherence measure K is obtained by averaging K_{ij} over all pairs of presynaptic neurons. Here τ is taken as 2 ms.

The output signal-to-noise ratio (SNR) is defined as $10\log_{10}(S/B)$ with S and B representing the signal peak and the average amplitude of background noise at the input signal frequency in the power spectrum of membrane potential, respectively [9]. An average over 50 different realizations of noise is taken to obtain reported values.

3 Results and discussion

In the absence of input signal, the presynaptic neurons discharge spikes independently owing to the independent Gaussian white noise. The mean time-averaged synaptic weight, $g_s = \frac{1}{N}\sum_{j=1}^{N}\langle g_j(t)\rangle_t$, is used to characterize the average steady-state value of synaptic weight (a long transient is discarded for computing g_s). Figure 1b plots g_s

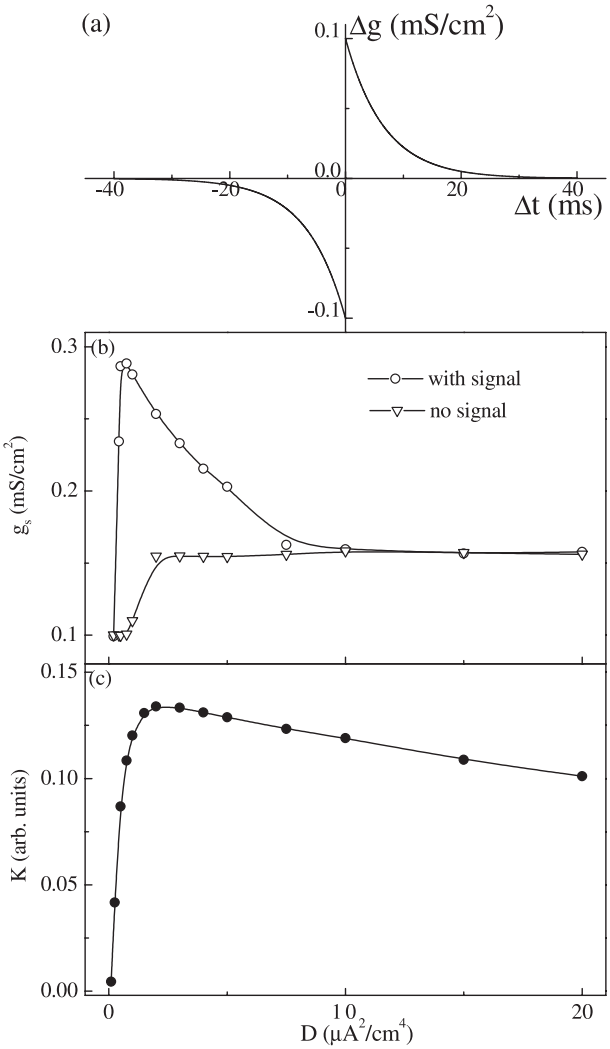

Fig. 1. (a) The amount of unitary synaptic modification vs. the time difference between a single pair of pre- and postsynaptic spikes. (b) g_s vs. noise intensity D in the absence or presence of input signal. (c) The coherence measure K vs. D. The signal frequency is $f_s = 50$ Hz.

versus noise intensity D. When D is small, the postsynaptic neuron is primarily evoked to fire by noise, and the firing rate is very low. The time differences between the pre- and postsynaptic spikes are often quite large. As a result, the modification of synaptic strength is slight, and g_s is nearly equal to 0.1. But as D is larger than 2, the pre- and postsynaptic neurons fire more frequently. Thus there are many spikes located within a short time window, and the impact of STDP becomes more prominent. The synaptic efficacies are potentiated or depressed smartly and randomly. Consequently, g_s is stable around 0.15, which is half the upper bound of synaptic weight, over a wide range of noise intensities.

In the presence of input signal, the firings of presynaptic neurons are modulated by the signal. At very low noise level, there almost exists no postsynaptic firing and thus g_s equals 0.1 (see Fig. 1b). For moderate noise intensity, most of presynaptic firing events occur around the maxima of the signal, showing a high coherence with the signal. That is, the presynaptic neurons discharge spikes with some correlation. Figure 1c plots K versus D. Obviously, there exists an optimal noise level for neural synchronization. Since each synaptic input is subthreshold, the synchronous inputs can more easily trigger the postsynaptic neuron to fire. Such a causality between pre- and postsynaptic spikes makes their time differences relatively small and thus induces considerable potentiation of synaptic efficacy. The increment in synaptic weight causes the postsynaptic neuron more prone to discharge spikes in a short time interval after receiving synaptic inputs. This further induces strengthening of synaptic weight. Such a positive feedback process makes g_s approach 0.3, its upper bound, when $D = 0.8$. When noise intensity becomes large, both the presynaptic and postsynaptic neurons fire more randomly, and thus g_s is around 0.15 when $D \geq 10$. Here we see that the change of synaptic weight is closely related to the degree of presynaptic correlation.

We also plot the histograms of the fraction of synaptic weight taking different steady-state values in Figure 2. In the absence of input signal, for small noise intensity the values of g_j are close to 0.1 (see Fig. 2a). As D increases, the distribution spreads between two limiting values (0 and 0.3), while the peak located at 0.3 becomes higher but that at 0.0 gets lower. In contrast, in the presence of input signal, the histogram first exhibits a unimodal feature, and the only peak is first located around 0.1 and then shifts rightwards to be around 0.3 when $D \geq 0.5$ (see Fig. 2b). But as noise intensity is further increased, the distribution becomes broad and the peak height evidently drops. For $D > 10$ the histogram also exhibits a bimodal feature with two peaks located at 0 and 0.3, respectively. These are in agreement with the result shown in Figure 1b.

When synaptic weight varies through STDP, the firing activity of the postsynaptic neuron shows more correlation with the input signal than that of presynaptic neurons over a range of noise intensities. For $D = 1$, for example, the postsynaptic neuron fires spikes nearly periodically at the same frequency as the signal (see Fig. 3a), implying that the postsynaptic neuron can effectively detect and transmit the periodic signal. But in the case of static synapses, postsynaptic firings exhibit distinctive skipping and are nearly as noisy and variable as those of presynaptic neurons. To characterize this quantitatively, Figure 3b depicts the output SNR. Each curve exhibits a typical feature of stochastic resonance (SR) [9], that is, the SNR goes through a maximum with increasing D. In other words, the signal can be transmitted more efficiently when noise intensity is within an appropriate range. This verifies that noise indeed plays a critical role in weak signal processing. On the other hand, through STDP the SNR of the postsynaptic neuron is improved evidently for $0.5 \leq D \leq 7.5$, compared to that of presynaptic neurons. In addition, it is always much larger than that in the case of static synapses.

Such an effect results from the increment in synaptic weight induced by the correlated presynaptic activity. This means that the signal transmission is indeed enhanced with STDP, which is of significant biological

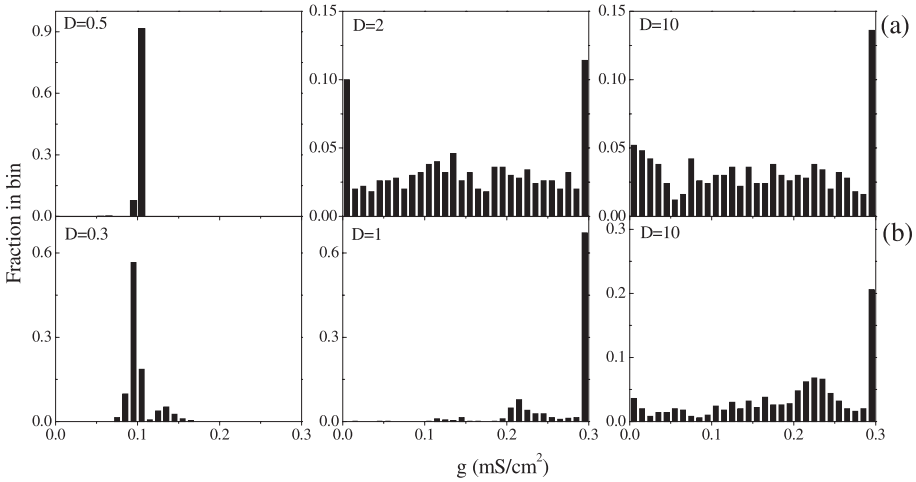

Fig. 2. Histograms of the fraction of synaptic weight taking different values for $D = 0.5$, 2, and 10 without input signal (a) and for $D = 0.3$, 1, and 10 with input signal (b), respectively. The signal frequency is $f_s = 50$ Hz.

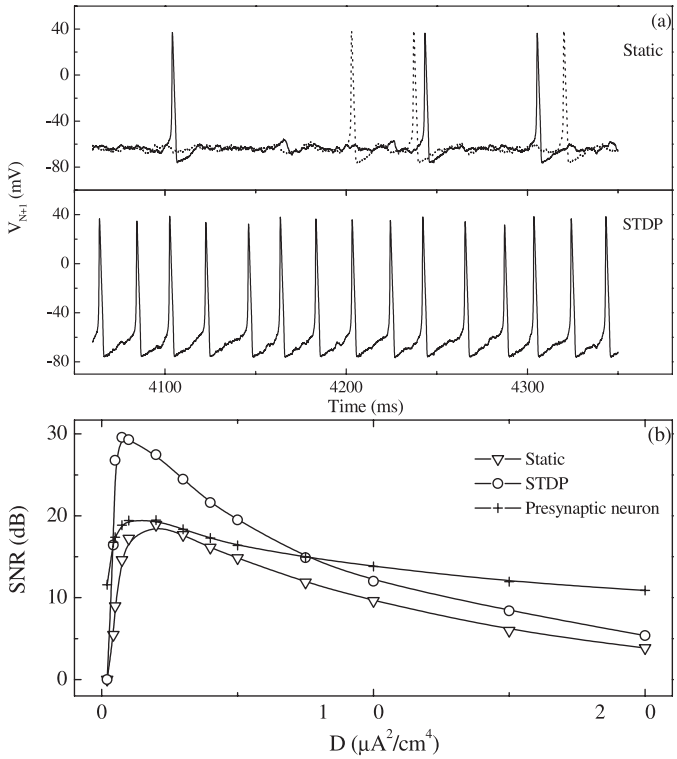

Fig. 3. (a) The time course of membrane potential $V_{N+1}(t)$ in the cases of static and dynamic synapses, respectively. The dotted line is for some presynaptic neuron. The noise intensity is $D = 1$. (b) The SNRs corresponding to the above cases vs. noise intensity. The signal frequency is $f_s = 50$ Hz.

implication. The results also imply that synchronized activity can propagate rapidly across neural networks when STDP is taken into account [10]. We may as well assume that the postsynaptic neuron acts as a coincidence detector and prefers to relaying synchronized activity, as suggested in reference [11]. In brief, synapses may be able to detect and transmit information, to the extent associated with the level of correlation among presynaptic activity, through dynamical modification of their strength.

Such an enhancement of signal transmission also holds for various signals, especially when the signal frequency is within the range of 30−90 Hz. The SNR takes a relatively large value for these signals in both static and dynamic synapses cases (see Fig. 4a). As discussed above, the correlation of presynaptic activity plays a significant role in this effect. Figure 4b plots the coherence measure K versus the signal frequency. Clearly, the presynaptic neurons discharge spikes with more correlation for the signals in the same frequency sensitivity range. As a result, g_s takes a relatively large value (see Fig. 4c). This selective improvement origins from the fact that HH neurons are more sensitive to the signals with frequencies located in this range, owing to the resonance effects between the periodic signal and the subthreshold oscillation of membrane potential [12]. The resonance makes neurons respond selectively to the signals at preferred frequencies. This, together with STDP, remarkably improves the capability of neurons to transmit these signals efficiently. Such a selective enhancement may be one of the basic principles of signal processing in the nervous system.

We have found that the steady-state values of synaptic weight are closely associated with the degree of presynaptic correlation. On the other hand, since synaptic weight can be modified through STDP with a high precision on the order of milliseconds, it is of interest to examine its influence on spike timing. To this end, we extend the current network into a two-layer network. In this structure, each neuron of the output layer receives synaptic inputs from all neurons in the input layer, and there exists no coupling between the neurons within the same layer. Each layer can be regarded as a functional group. The number of neurons in each layer is still $N = 500$. Here we assume that synaptic weight varies only when time is larger than 4110 ms. It is worth comparing different neural activity before and after the application of STDP.

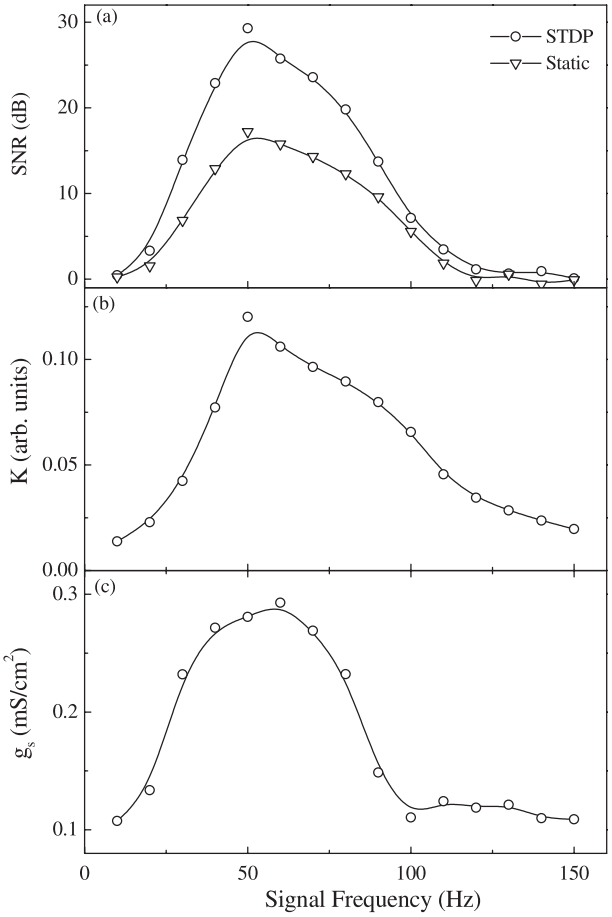

Fig. 4. Noise intensity $D = 1$. (a) The SNR of the postsynaptic neuron vs. signal frequency in the presence or absence of STDP. (b) The coherence measure K and (c) g_s vs. the signal frequency with STDP.

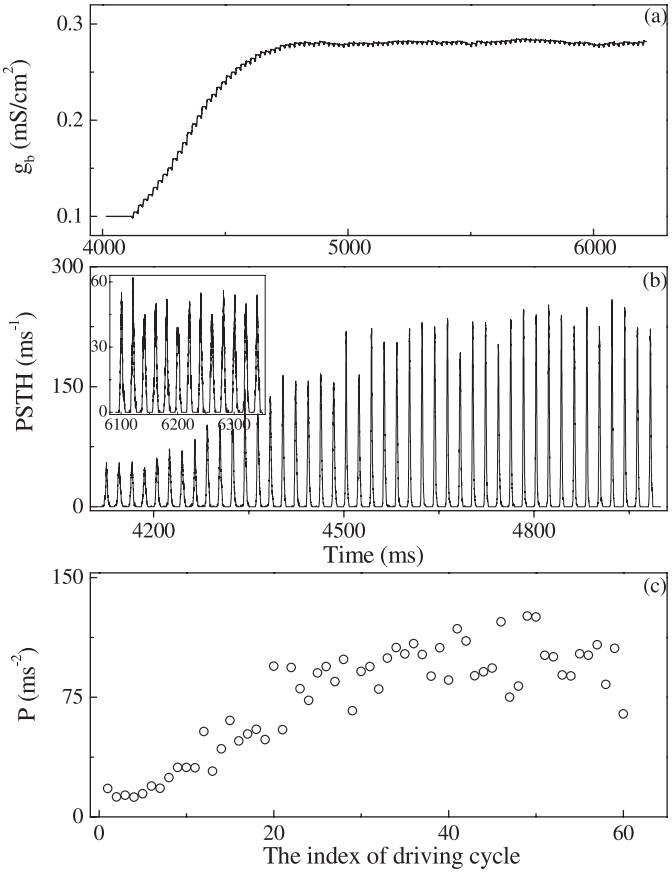

Fig. 5. Noise intensity $D = 1$. (a) g_b and (b) PSTH vs. time. The inset is that for the input layer. (c) The spike timing precision vs. the index of driving cycle. The signal frequency is $f_s = 50$ Hz.

We depict the temporal evolution of $g_b = \frac{1}{N^2}\sum_{i=1}^{N}\sum_{j=1}^{N} g_{ij}(t)$ in Figure 5a, where $g_{ij}(t)$ represents the synaptic weight between the ith neuron in the input layer and the jth neuron in the output layer. After STDP is applied, g_b increases progressively and is saturated at the value of 0.28. This is consistent with the result shown in Figure 1b.

To explore the impact of STDP on spike timing, we plot the post stimulus time histogram (PSTH) of the output layer in Figure 5b, which shows the number of spikes per millisecond [13]. There is a peak in each driving cycle, and the peak height remarkably rises over time and finally is saturated at a rather large value compared to that of the input layer shown in the inset of Figure 5b. This indicates that most postsynaptic neurons discharge simultaneously. As a result, the reliability of signal transmission is evidently improved through STDP. Based upon the shape of smoothed data set taken from a five-point moving average of PSTH, we can compute the spike timing precision P (in each driving cycle), namely,

$$P_i = H_i/w_i, \tag{10}$$

where H_i is the height of the ith peak in the smoothed PSTH and w_i is the width at H_i/e [13]. Figure 5c displays P against the index of driving cycles. Clearly, the timing precision also increases over time. That is, the temporal structure of spike trains becomes more accurate with STDP, implying that this mechanism is beneficial to temporal encoding. The improvement of timing precision is also sensitive to the signal frequency and noise intensity because it occurs when the synapses are potentiated in response to correlated synaptic inputs (data not shown). Therefore, through STDP postsynaptic neurons can fire synchronously under suitable conditions, and the timing precision is also largely improved.

4 Conclusions

Synchronized activity has been observed in many brain areas and is believed to play functional roles such as pattern segmentation and feature binding [14]. The issue concerning the mechanism underlying synchronization has attracted wide interest. Here we demonstrated that when the spike-timing-dependent synaptic plasticity is taken into account, synchronized activity can be

attained although presynaptic neurons exhibit weak correlations. This is largely different from the case where synchronization origins from the coupling interactions between neurons in the same functional ensemble. Here synchronization just occurs through dynamical modification of synaptic weight. That is, synapses can be adjusted to an optimal value for neural synchronization [5]. Such a mechanism is of potential functional significance, by which familiar stimuli may generate synchronized spike volleys that can be propagated rapidly across neural tissue [10].

On the other hand, through STDP both the reliability and timing precision of firing, on the order of milliseconds, can be enhanced greatly. This is consistent with the report that under certain conditions the spike timing can exhibit a high precision and reproducibility with the temporal resolution being 2−3 ms [15]. In addition, spiking patterns with high temporal fidelity can be propagated stably through cortical networks, which may be important for information transfer in a robust way against background noise [16]. These all suggest that STDP is a significant mechanism in temporal coding and that precise spatiotemporal patterns can be exploited to encode stimuli accurately.

It is worth noting that we introduced hard bounds to keep synaptic weight from increasing without bound. Others have also shown that a weight-dependent mechanism for strength amplitude modification can be introduced more naturally to keep synapses stable [17]. Our preliminary results indicate that the conclusions drawn here qualitatively hold even when the weight-dependent STDP rule is adopted. Further work is in progress.

In addition, Amit and Mongillo have recently used the spike-driven synaptic plasticity model to generate stimulus-selective persistent activity [18]. In their model, the synaptic dynamics is described as a function of pre- and postsynaptic spike rates. This can implement rate-dependent plasticity and exhibit both long-term potentiation and depression. In the context of STDP, however, the steady distribution of synaptic weight is more sensitive to the firing time than to firing rates. It is interesting to compare the signal transmission efficiency with these models.

In summary, we have studied the effects of STDP on signal transmission. Neural information can be transmitted more efficiently through STDP than in the case of static synapses. With STDP both the reliability and timing precision of spiking are profoundly improved. Such an enhancement effect is sensitive to the signal frequency. Therefore STDP can play critical roles in signal processing.

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