Effect on information transfer of synaptic pruning driven by spike-timing-dependent plasticity

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Effect of spike-timing-dependent-plasticity-driven synaptic pruning on information transfer

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Spike-timing-dependent plasticity (STDP) is an important driving force of self-organization in neural systems. With properly chosen input signals, STDP can yield a synaptic pruning process, whose functional role needs to be further investigated. We explore this issue from an information theoretic standpoint. Temporally correlated stimuli are introduced to neurons of an input layer. Then synapses on the dendrite, and thus the receptive field, of an output neuron are refined by STDP. The mutual information between input and output spike trains is calculated with the context tree method. The results show that synapse removal can enhance information transfer, i.e. that "less can be more" under certain constraints, which stress the balance between potentiation and depression dictated by the parameters of the STDP rule, as well as the temporal scale of the input correlation.

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Self-organization is an important characteristic of cortical neural networks that determines the connectivity structure, in addition to genetic factors [1, 2]. Neural network structure co-evolves neural dynamics under the stimulation of sensory inputs via various synaptic learning mechanisms, among which a ubiquitous and important mode is spike-timing-dependent plasticity (STDP) [3, 4]. STDP determines the evolution of synaptic weights according to the coincidence of pre- and post-synaptic action potentials, and in doing so also modulates neural activity. It is intriguing to know how this synaptic evolution, which is based on the relative timing between pre- and post-synaptic spikes, influences information transfer in neural networks. It has been shown that several STDP-like synaptic plasticity laws can be obtained from abstract information optimization principles [5–7]. Hennequin et al. have also shown that STDP based on triplets of spikes can give close-to-optimal information transmission in adaptive neurons [8]. Nonetheless, the link between information transfer and the co-evolution of structure and dynamics caused by STDP remains loose, as does the relation between information transmission and the temporal scale of the input correlation.

A basic effect of the co-evolution of structure and dynamics caused by STDP is synaptic pruning. It is well known that the brain has a very dense population of synaptic connections just after birth and most of these connections are subsequently pruned over time [9]. This is reflected by the deletion of synapses whose strength falls below a certain threshold. STDP has been postulated as a mechanism for synaptic pruning, as it can yield a bimodal distribution of synaptic weights, where the majority of synapses are driven toward the minimum weight [4]. Based on this effect, fully connected STDP-driven networks can be refined, to provide non-trivial topological characteristics, such as scale-free degree distribution [10, 11], feed-forward structure [12], and the significance profile coinciding with realistic neural networks [2]. Besides topological benefits, a further question concerns the functional role of an STDP-driven pruning process: what is it good for? For example, it is recently reported that the removal of synaptic connections can be used to systematically improve and optimize synchronization properties in networks [13], i.e. the conclusion, "less can be more", is already established for network synchronization. A natural question, then, is whether the same conclusion applies to information transmission.

To address this question, we focus on the basic components of a feed-forward neural network: synaptic inputs on the dendrite of a single neuron, and the receptive field of that neuron. Temporally correlated stimuli are utilized for neurons of the input layer, mimicking sensory receptors, and STDP synapses are introduced to the dendrite of the output layer. The mutual information between input and output spike trains is calculated with the context tree method [14, 15], which exhibits comparatively low bias on finite data sets and outperforms common alternative procedures. The process of synaptic pruning is studied under different parameter configurations. The results show that synapse removal can enhance information transfer under certain constraints, which stress the balance between potentiation and depression dictated by the parameters of the STDP rule, as well as the temporal scale of the input correlation.

The studied network is composed of an input layer with N neurons and a single output neuron. The neurons are modeled by Leaky Integrate-and-Fire (LIF) dynamics. The membrane potential V_j of the conductance based LIF neuron with index j is governed by

$$C_m \frac{dV_j}{dt} = g_L(V_{rest} - V_j) + g_j(t)(E_{ex} - V_j) \ . \tag{1}$$

The values of parameters we used are the same as in [4], where $C_m = 200$pF is the membrane capacitance, $g_L = 10$nS is the leak conductance, $V_{rest} = -70$mV is the resting potential (leak reversal potential), and $E_{ex} = 0$mV is the excitatory reversal potential. When the membrane potential reaches the threshold value $V_{th} = -54$mV, the neuron emits an action potential, and then the depolarization is reset to the reset potential $V_{reset} = -60$mV after a refractory period $\tau_{ref} = 1$ms during which the potential is insensitive to stimulation.

The synaptic conductance $g_j(t)$ is determined by

$$g_j(t) = g_m \sum_{i=1}^{n} w_{ij}(t) \sum_k f(t - t_i^k) \ , \tag{2}$$

where n is the number of stimulus sources (for neurons of the input layer), or the number of input neurons (for the output neuron), g_m is the maximum value of synaptic conductance, w_{ij} is the weight of the synaptic connection from the ith neuron (or stimulus source) to the jth neuron, and t_j^k is the timing of the kth spike of the jth neuron. Here, we use an α-function [16] $f(x)$ with latency (transmission delay) τ_d and synaptic time constant $\tau_{ex} = 2$ms:

$$f(t) = \begin{cases} \frac{t - \tau_d}{\tau_{ex}^2} \exp(-\frac{t - \tau_d}{\tau_{ex}}) & \text{if } t > \tau_d \\ 0 & \text{otherwise.} \end{cases} \tag{3}$$

In our study, the weights of the synaptic connections between neurons of the input layer and the output neuron are modified by the STDP rule. STDP is a form of experimentally observed long-term synaptic plasticity, where
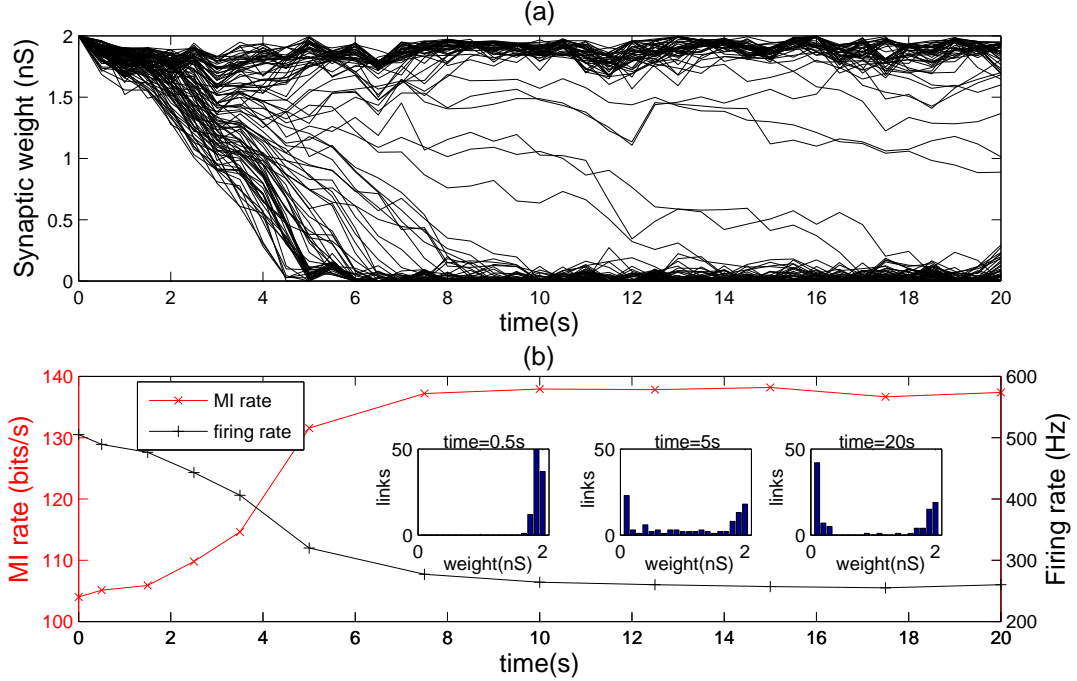
FIG. 1. The pruning process on the dendrite of an output neuron in simulations with: $f_s = 30Hz$, $f_n = 10Hz$, $\alpha = 0.55$, and $T_{max} = 125ms$. (a) Evolution of the peak conductances of all the STDP synapses. (b) The mutual information (MI) rate and the average firing rate at different stages of the pruning process. Inset: The final distribution of peak synaptic conductances in three different stages of the dendrite evolution: 0.5s, 5s, and 20s.

synapses are modified by repeated pairings of pre- and postsynaptic action potentials, and the sign and the degree of the modification depend on their relative timing. A synapse is strengthened when the presynaptic neuron fires shortly before the postsynaptic one, and weakened when this temporal order is reversed. The weight modification Δw_{ij} is described by the following equations:

$$\Delta w_{ij}(\Delta t) = \begin{cases} \lambda \exp(-|\Delta t|/\tau_+) & \text{if } \Delta t \geq \tau_d \\ -\lambda\alpha \exp(-|\Delta t|/\tau_-) & \text{if } \Delta t < \tau_d. \end{cases} \tag{4}$$

w_{ij} is constrained within the range $[0, 1]$, which ensures that the peak synaptic conductance $g_m w_{ij}$ is always positive and can not exceed the maximum value $g_m = 2.0nS$. Δt is the temporal difference between the occurrence of the postsynaptic action potential and the arrival of the presynaptic action potential, i.e. $\Delta t = t_j - (t_i + \tau_d)$, where t_j is the spike time of the postsynaptic neuron j, τ_d is the delay time of the spike transmission from neuron i to neuron j, and t_i is the spike time of the presynaptic neuron i. λ is the learning rate. The time constants τ_+ and τ_- control the width of the time window(s). Here, an asymmetric time window ($\tau_+ = 16.8ms$ and $\tau_- = 33.7$ms) is used for STDP, which provides a reasonable approximation of the synaptic modification observed in experiment [3]. α, together with τ_+ and τ_-, introduces a possible asymmetry between the scale of potentiation and depression. Note that the definition of α here is slightly different from the standard definition of the α term in [4], where it was defined as the ratio of integrated depression and potentiation in the learning window. As argued in [4], in order to obtain a stable competitive synaptic modification, which means that uncorrelated pre- and postsynaptic spikes produce an overall weakening of synapses, the integral of $\Delta\omega_{ij}$ in STDP expression should be negative. A negative integral requires $(\alpha\tau_-/\tau_+) > 1.0$.

It has been repeatedly reported that STDP can drive a globally connected network to a steady bimodal distribution of synaptic weights if the neurons are stimulated by partially correlated spike trains [4, 10]. Here, we utilize a similar strategy to simulate the synaptic pruning process. Neurons of the input layer are stimulated by temporally correlated spike trains and independent stochastic spike trains, representing input signal and noise respectively. A simple method is utilized to generate temporally correlated inputs, which makes it easier to manipulate the temporal scale of the input correlation: We take a single Poisson spike process of mean rate f_s, and then offset the specific timing of each spike within this process by a single, independent value T_d for each of the one hundred input neurons, where T_d is drawn randomly from a uniform distribution in the range $[1ms, T_{max}]$. In this way, the temporal correlation scale is

determined by the parameter T_{max}. In addition, 100 stochastic Poisson spike processes with equal mean firing rate of f_n are also introduced as noise to the input neurons. This stimulation scheme combined with the aforementioned negative integral of the STDP rule induces net weakening of synapses, while the additive nature of the STDP rule generates a bimodal distribution of synaptic weights [17] (see fig. 1a,b).

To study the influence of the pruning process on information transfer, we calculate the mutual information between input and output corresponding to the state of synaptic weights at different temporal 'snapshots' during their STDP-driven evolution. In this paper, we only focus on the general performance of the refined dendrite on information transfer, and try to eliminate the impact of other specific factors. Thus when we calculate the mutual information, the synaptic weights of the dendrite are fixed to the weight distribution at that time, and uncorrelated stimuli are adopted. We focus on the rates of information that the refined network can transfer, more specifically, the statistical significance of how the responses of the output neuron vary with different stimulations of the input layer. Based on this standpoint, we utilize a classical method [18–20] to calculate the mutual information.

One hundred 1.5s long spike trains with mean firing rate f_s are generated by independently truncating from a single Poisson spike train. These spatio-temporal spike patterns are then repeated one thousand times at regular intervals, interleaved among one hundred 1500s long stochastic Poisson stimuli, whose mean firing rates are also f_s. Thus, the input signal at each synapse is composed of alternating repeated spike segments and stochastic spike segments, each lasting 1.5s. In addition, noise is provided to each synaptic input as a stochastic Poisson spike process with a mean firing rate of f_n. In response to the segments of time varying stochastic stimuli, the spike train of the output neuron varies, and this variability can be quantified by the entropy per unit time of the spike train H_{total}. As for the repeated spike pattern, a similar, but not identical, sequence of spikes can be obtained. The trial-to-trial variability in the responses to the repeated stimulus is given by the conditional or noise entropy H_{noise}. Then the mutual information that the output spike train provides about the input signal is the difference between these entropies, $I_{info} = H_{total} - H_{noise}$. In this paper, all estimates of entropy (H) and information (I) are reported as entropy or information rates in units of bits per sec. To achieve a direct estimator of the entropy rate, we adopt a well-known algorithm proposed in [14, 15], which combines context tree weighting algorithm with local Bayesian entropy estimators. It makes few assumptions about the underlying neural dynamics and has been shown to exhibit comparatively low bias on finite data sets.

Based on the measure of mutual information, we can compare the information transmission of different phases during the pruning process. An example is shown in fig. 1. At the beginning of simulations, peak conductances of all STDP synapses between the input layer and the output neuron are initialized to the maximum value $g_m = 2.0nS$. Then synapses afferent on the dendrite of the output evolve to a steady state. A large proportion of STDP synapses decrease rapidly to the minimum synaptic conductance, while most of the rest approach the maximum value. This can be regarded as a pruning process. Toward the end of simulations the distribution of peak synaptic conductances becomes bimodal and remains almost constant except for tiny fluctuations. We take snapshots at certain intervals, that reflect momentary states of the afferent synaptic weights. Then the information rates that different snapshots can transfer are calculated using the aforementioned method. The results in fig. 1b show that the mutual information rate increases as the firing rate decreases during the pruning process. In particular, the upslope of the information curve has a significant inverse relationship with the depression of synaptic weights and the down slope of the firing rate curve. The distributions of the peak synaptic conductances corresponding to three stages (the low point, the rising step and the plateau) of the information curve are also shown in fig. 1, which indicates that synapse removal contributes to improving information transfer in neural network.

The effect of "less can be more" in neural information transfer is not hard to predict in extreme cases. It is shown that the choice of maximum synaptic conductance can have a significant effect on weight distributions [17], and may subsequently affect information transfer. When the peak conductances of all synapses are so large that the spike interval of the output neuron reaches the refractory period, one could obtain no information about the input stimuli. On the other hand, if the dendrite becomes so sparse that the output neuron spikes rarely, its response is also trivial. Therefore, there exists a tradeoff, which corresponds to the maximum rate of information transmission. Furthermore, it is interesting to examine which properties of STDP modify the information transfer performance by modulating the level of synaptic pruning. The information transfer rate corresponding to the final steady state of the dendrite is examined in different configurations. We investigate two key parameters related to the performance of STDP: One is the ratio between potentiation and depression, and the other is the maximum delay T_{max} used in the generation of temporally correlated stimuli. Moreover, to study the generality of these results with respect to the input firing rate, various input firing rates and signal to noise ratio (SNR) values are also examined.

Fig 2 shows the results of multiple simulations, among which we vary α while keeping other parameters fixed. Every data point denotes the information transfer rate corresponding to the final steady state of the dendrite in each simulation. These results show similar phenomena and arrive at the same conclusion as in the study of pruning process in our initial simulation experiment. Remarkably, the upslope of the information curve falls in the interval $0.47 < \alpha < 0.5$, where the ratio between potentiation and depression ($\tau_+/\alpha\tau_-$) is decreasing from a dominance of
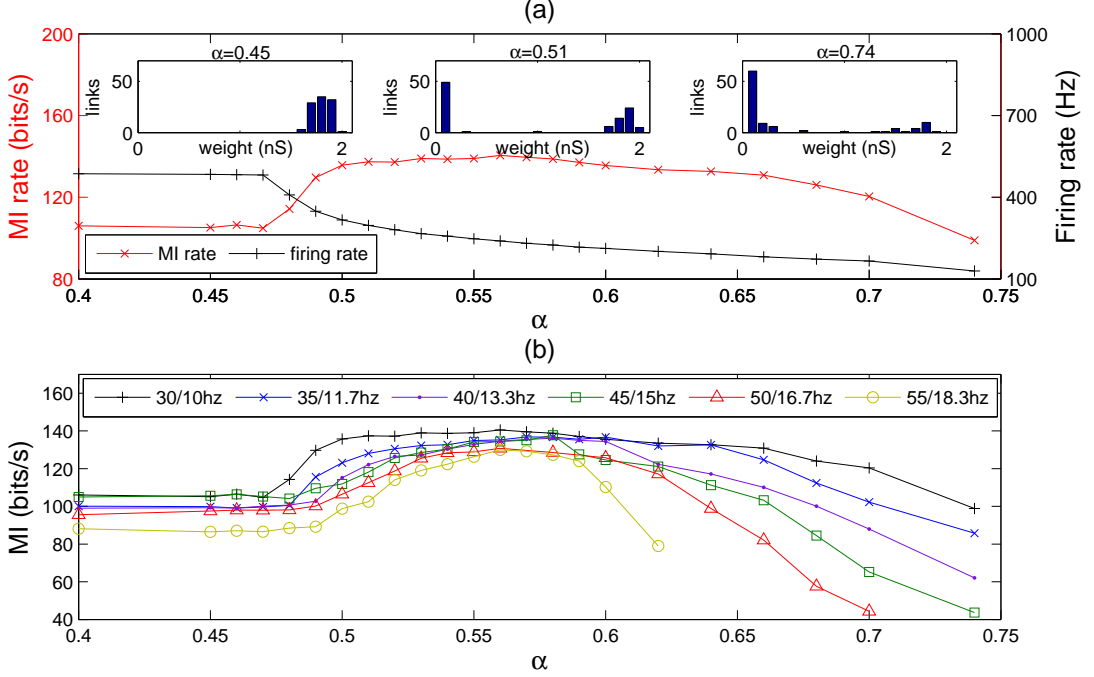
FIG. 2. The mutual information at final steady states in simulations with different α and fixed $T_{max}(= 125\text{ms})$. (a) The case of $f_s = 30Hz$ and $f_n = 10Hz$. Inset: The final distribution of peak synaptic conductances in three different stages of the curve. (b) The results of different f_s/f_n with fixed SNR.

potentiation to balance. If the balance is maintained to a certain extent ($0.5 < \alpha < 0.6$), the information transfer rate is preserved in a plateau. The balance between the integral over potentiation and depression windows of the learning rule can result in the bimodal weight distribution generated by additive STDP. When depression is significantly more prevalent than potentiation, the information transfer rate decreases to a low level, because of the lack of effective synapses.

Next, we study this case with stimuli of different firing rate but fixed SNR (see fig 2b). It is shown that the maximum mutual information value achieved at each firing rate is similar, but there are significant differences in the range of alpha values that provide this maximum information transmission rate - a wider range being achieved at lower firing rates.

Besides alpha, T_{max} can also influence the equilibrium distribution of synaptic weights dictated by the STDP rule. If T_{max} is very small, there will be a high correlation among different inputs and also between input and output, which drives most synapses to approach the maximum weight. Conversely, a large T_{max} can make the time delay between different paths much larger than the time window of STDP, such that the stimuli can be regarded as uncorrelated spike trains, which drives most synapses to approach the minimum weight. The results in fig. 3 show that the T_{max} values (hundreds of ms) which give the greatest information transfer performance are an order of magnitude higher than the optimal STDP time constants (tens of ms). In this range of T_{max}, the number of the synapses with non-trivial weight is within the range [20,30]. As a consequence, the minimum time delay between different paths is within the range [7ms, 20ms], which matches the time window of STDP. Moreover, the influence of T_{max} on information transfer rate also coincides with the aforementioned results (see fig 3a). Next, if we adopt a fixed firing rate f_n for input noise while incrementally increasing the firing rate of input signal f_s, a higher SNR will lead to a larger information transfer rate (see fig 3b).

In this paper, the effect of STDP-driven pruning on information transfer has been studied. We have focused on the basic component of a feed-forward network, where neurons of the input layer are stimulated by temporally correlated stimuli and synapses afferent on the dendrite of the output neuron are refined by STDP. For snapshots of the pruning process, we calculated the mutual information between input and output spike trains with the context tree method. It is shown that STDP-driven synaptic pruning can enhance information transfer, i.e. that, in terms of synaptic connections, "less can be more". Moreover, we have studied the influence of various STDP parameters on these results, and found that there are two key factors: the balance between potentiation and depression dictated by the learning rule, and the temporal scale of input correlation matching the time window of STDP. The significance of these
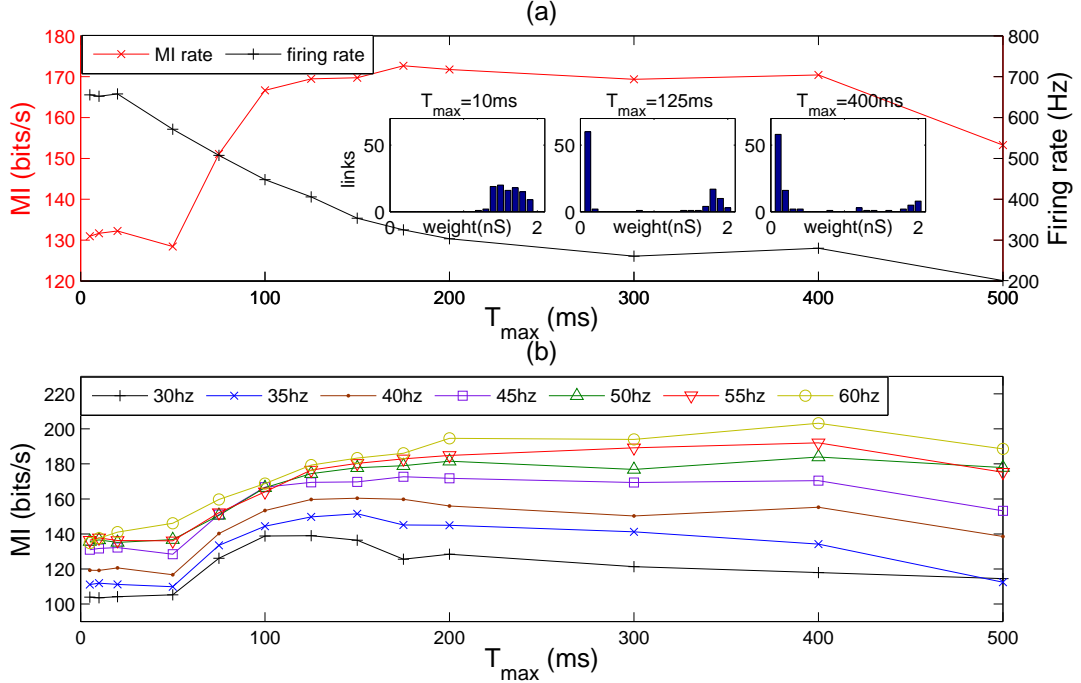
FIG. 3. The mutual information at final steady states in simulations with different T_{max} and fixed $\alpha(= 0.55)$. (a) The case of $f_s = 30Hz$ and $f_n = 10Hz$. Inset: The final distribution of peak synaptic conductances in 3 different stages of the curve. (b) The results of different f_s and fixed $f_n = 10Hz$.

two factors and the function role of synapse removal are both fundamental problems relating to the computational function of neural networks, and this paper has begun to answer them from an information theoretic perspective.

In this study, we have only considered additive STDP, as it has been demonstrated that multiplicative rules generate no pruning [21]. Current experimental data is insufficient to fully support either an additive or multiplicative rule, although some evidence does indicate that synaptic modifications are dependent on the initial weight [22]. This limits the applicability of our results, and further work is required to explore the influence of multiplicative STDP on information transmission. Furthermore, output firing rates in our simulations are generally higher than those observed in vivo, as the scale of input firing rates, number of synaptic inputs, and relative scale of synaptic conductances adopted here differ from those in real cortical neurons. Further simulations with a more realistic neuron model and parameter choices are required to determine how well the results presented apply to real neuronal networks.

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