Synaptic regulation on various STDP rules

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October 17, 2003

Abstract

An additive rule of spike-timing-dependent synaptic plasticity (STDP) automatically achieves synaptic competition and activity regulation, where synaptic balance is moderately regulated to control the post synaptic activity[7]. On the other hand, asymmetrically multiplicative STDP rules can not achieve the synaptic competition nor the synaptic regulation [8, 5]. These works suggest that synaptic efficacy dependence in updating rule is relevant for synaptic competition and activity regulation. There is another possible factor relevant for activity regulation. Various types of spike pair-to-pair interactions on STDP have been found [3, 6]. It is not clear what type of rules can achieve activity regulation and how it is related to synaptic competition. Here we demonstrate various types of updating rules and show that symmetry in synaptic efficacy dependence is relevant for activity regulation, and that activity regulation is independent from competition.

1 Introduction

A cortical neuron receives thousands of synaptic contacts from other neurons. So slight increase of presynaptic activity level causes drastic increase of postsynaptic activity. This property induces significant instability in recurrent networks. One of the solutions to avoid the instability is inhibitions balanced to excitations. It is, however, not so easy to preserve the balance through development stage.

Song et al. demonstrated that a spike-timing-dependent synaptic plasticity (STDP) can automatically achieve synaptic regulation even for random firing presynaptic neurons[7]. For a change of presynaptic activity level, the balance of excitatory synapses are shifted to regulate the postsynaptic activity (Fig. 1A). It also achieves competition among received synapses. Synapses are clustered into two groups: strong one or weak one (Fig. 1A). Synaptic competition is an important function so that a neuron might achieve and preserve a selectivity. The result is important, because a simple local synaptic updating rule can achieve the two important properties, synaptic competition and regulation, simultaneously and automatically.

However, their STDP rule is not so feasible for experimental results. They adopted an additive synaptic updating rule. It requires explicit upper and lower boundaries to avoid sign flip or divergence of synaptic strength. So they assumed hard boundaries, but it is slight artificial. On the other hand, it is found in hippocampal culture that the size of synaptic depression(LTD) is proportional to the current efficacy(constant percent change), while the size of potentiation is almost constant[1]. Such an asymmetrically multiplicative rule automatically induces natural bound[8].

van Rossum et al.[8] applied the multiplicative rule only for the depression (LTD) and demonstrated that the rule achieves neither competition nor regulation arise under the same situation as Song et al.[7]. Synapses exhibit an unimodal distribution, and the postsynaptic activity increases drastically for slight increase of firing rate of excitatory presynaptic neurons(Fig. 1B). It is known that the result is the same even if synaptic potentiation (LTP) rule also obeys a multiplicative rule[5].

Spike pair-to-pair interactions can be also possible relevant factors in addition to efficacy dependence. There has been reports of various types of spike pair-to-pair interactions on STDP. Froemke and Dan showed evidences suggesting that one spike suppresses the STDP effect on the next spike for successive spikes[3]. Sjöström et al. showed evidences suggesting that a LTP pair cancels the LTD pair just before[6]. It is unknown how the spike pair-to-pair interactions affects activity regulation.

These results provide open questions about the synaptic competition and regulation effects:

1. Do they originate in additivity?

2. Do they originate in symmetry between LTP-LTD rules?

3. Are they cooperative? Is it possible that only one causes without the other?

4. How the pair-to-pair suppressive interactions affects regulation?

In order to answer the last question, we examine the effect of suppressing rule to the additive STDP rule[7] and to the asymmetrically multiplicative rule[8] under the same situations as [7]. In order to answer the other questions, we apply a sigmoidal efficacy dependence for synaptic potentiation(LTP) to show that the identical model exhibits regulation without competition, competition without regulation, both regulation and competition, and neither competition nor regulation by slight change of parameters.

2 Model

Let us consider the same situation as [7] except for the STDP rule. Consider a model neuron receiving synapses from 1,000 excitatory neurons and 200 inhibitory ones. The presynaptic excitatory neurons fire independently at a constant rate λ^{pre} (Poisson process). The presynaptic inhibitory neurons also fire independently at a constant rate λ^{inh}. A presynaptic spike signal causes conductance-based postsynaptic current. The postsynaptic neuron fires obeying the leaky integrate-and-fire model depending on presynaptic spikes.

$$
\begin{aligned}
\tau_{\mathrm{m}}\frac{dv}{dt} &= v_{\mathrm{rest}} - v + \sum_{i\in\mathrm{Exc.}} g_i(v_{\mathrm{exc}} - v) + \sum_{i\in\mathrm{Inh.}} g_i(v_{\mathrm{inh}} - v) \\
& \quad v > v_\theta \overset{\mathrm{spike}}{\Longrightarrow} v = v_0. \\
\frac{dg_i}{dt} &= -\frac{g_i}{\tau_g} + g_0 w_i \sum_j \delta(t - t_j^{\mathrm{pre}-i}),
\end{aligned}
$$

where $g_0 w_i$ denote the peak conductance for the i-th synapse, and g_0 is the scale factor of peak conductance, and w_i is normalized synaptic weight. Excitatory synaptic weight w_i changes depending on the relative timings of postsynaptic spikes to the corresponding presynaptic spikes(STDP), while inhibitory one is constant, $g_0 w_i \equiv g_{\mathrm{inh}}$(const.). In the present simulations, the parameters are fixed to the same as [7]: $\lambda^{\mathrm{inh}} = 10\mathrm{Hz}$, $v_{\mathrm{rest}} = v_{\mathrm{inh}} = -70\mathrm{mV}$, $v_{\mathrm{exc}} = 0\mathrm{mV}$, $v_\theta = -54\mathrm{mV}$, $v_0 = -60\mathrm{mV}$, $\tau_{\mathrm{m}} = 20\mathrm{ms}$, $\tau_g = 5\mathrm{ms}$, $g_0 = 0.015\mathrm{ms}^{-1}$, $g_{\mathrm{inh}} = 0.05\mathrm{ms}^{-1}$.

	LTP $M(w)$	LTD $\hat{M}(w)$	boundary
Song et al.(2000)	1	1.05	[0, 1]
van Rossum et al.(2000)	1	w	none
Rubin et al.(2001)	$1-w$	w	none
present work	sigmoid	w	none

Table 1: Synaptic efficacy dependence in STDP rules.

Excitatory weight w_i changes for all pairs of presynaptic and postsynaptic spikes,

$$\begin{aligned} \Delta w &\propto \sum_{j,k} S(t_j^{\rm pre} - t_{j-1}^{\rm pre}, t_k^{\rm post} - t_{k-1}^{\rm post}) W(w, t_k^{\rm post} - t_j^{\rm pre}) \ , \\ W(w,\Delta t) &= \begin{cases} M(w) e^{-|\Delta t|/\tau_+}/\tau_+ & (\Delta t > 0) \\ -\hat{M}(w) e^{-|\Delta t|/\tau_-}/\tau_- & (\Delta t < 0) \end{cases} \ , \\ S(\Delta t^{\rm pre}, \Delta t^{\rm post}) &= \left(1 - e^{-\Delta t^{\rm pre}/\tau_h}\right)\left(1 - e^{-\Delta t^{\rm post}/\hat{\tau}_h}\right) \ , \end{aligned}$$

where the factor S represents the suppressing effect proposed by Froemke and Dan[3]. Non-suppressing STDP rule corresponds to the case: $\tau_h \to 0$ and $\hat{\tau}_h \to 0$. The non-suppressing STDP rules in the previous works[7, 8, 5] correspond to the various patterns of the functions $M(w)$ and $\hat{M}(w)$ (Table1). STDP rules with exponential timing dependence are described as the following differential equations,

$$\begin{aligned}
\frac{dh}{dt} &= \frac{1-h}{\tau_h} - h\sum_j \delta(t - t_j^{\mathrm{pre}}), \\
\frac{d\hat{h}}{dt} &= -\frac{1-\hat{h}}{\hat{\tau}_h} - \hat{h}\sum_k \delta(t - t_k^{\mathrm{post}}), \\
\frac{da}{dt} &= -\frac{a}{\tau_+} + h\sum_j \delta(t - t_j^{\mathrm{pre}}), \\
\frac{d\hat{a}}{dt} &= -\frac{\hat{a}}{\tau_-} + \hat{h}\sum_k \delta(t - t_k^{\mathrm{post}}), \\
\frac{dw}{dt} &= c\left(\frac{M(w)\hat{h}a}{\tau_+}\delta(t - t^{\mathrm{post}}) - \frac{\hat{M}(w)h\hat{a}}{\tau_-}\delta(t - t^{\mathrm{pre}})\right).
\end{aligned}$$

The parameters are fixed to the same as [7]: $\tau_+ = \tau_- = 20$msec, $c = 0.1$. For the suppressing rule(Fig. 1CD), the suppressing time scales are fixed to the fitting values in [3]: $\tau_h = 28$ms, $\hat{\tau}_h = 88$ms. In the other cases(Fig. 1AB, Fig. 2), the rules are non-suppressing type: $\tau_h = \hat{\tau}_h = 0$.

Here we consider the following weight dependence,

$$\begin{aligned}
M(w) &= \mathrm{ltanh}(\kappa(w - \varepsilon - 1)) + 1, \\
\hat{M}(w) &= w,
\end{aligned}$$

where the function $\mathrm{ltanh}(x)$ is a sigmoidal function with wide linear range shown in Fig. 2A defined as the following equation,

$$x = \left(\tanh^{-1}(\mathrm{ltanh}(x)) - \mathrm{ltanh}(x)\right)^3 + \mathrm{ltanh}(x).$$

3 Results

We can see in Fig. 1 that the suppressing effect enhances competition and regulation slightly. But it does not make qualitative changes. It is not so relevant as the efficacy dependence.

Through the simulation using the sigmoidally efficacy-dependent LTP rule, we can find in Fig. 2 that all 4 patterns of competition and regulation can causes by slight change of parameters, $(\kappa, \varepsilon) = (0.5, 0)$, $(1.5, -0.1)$, $(0.98, 0.01)$, $(1, 0.01)$. The results show that competition and regulation are not specific for additive rule, and that they are not cooperative. So we can find that the mechanisms of competition and regulation are independent. We can easily find that the number of LTP-LTD-balanced points determines the rough shape of synaptic distribution(competitive or not). The results also suggest that regulation needs the condition that efficacy dependence of LTP and LTD should be almost symmetric in a range.

Now summarize the answers for the initial questions,

1. Do competition and regulation originate in additivity? — NO.

2. Do they originate in symmetry between LTP-LTD rules?

   — Symmetry is necessary for regulation.

3. Are they cooperative? — NO.

4. How the pair-to-pair suppressive interactions affects regulation?

   — Slight enhancement. Not so relevant.

4 Discussion

Steady synaptic distribution can be calculated from the integral equation derived from the Fokker-Plank equation[2]. The method can be applied for the non-suppressive cases. So it also leads to the necessary conditions for competition or regulation about efficacy dependence.

There is another important factor. In this paper, all-to-all pairs of pre-and-post spikes are considered for STDP. But there is another simple rule that only nearest neighbor pairs are considered for STDP. This difference is not so relevant in the case that the time scales of STDP window are not so different between LTP and LTD[2]. But in the case that the time scales of STDP window are far different between LTP and LTD, the nearest neighbor rule has different firing rate dependence from the all-to-all rule[4]. If the time scale of STDP window for LTD is far longer than LTP one, then the nearest neighbor rule is considered to suppress the activity regulation.

Acknowledgments

This research was partially supported by the Ministry of Education, Science, Sports and Culture, Grant-in-Aid for Scientific Research on Priority Areas, No.15016022, 2003.

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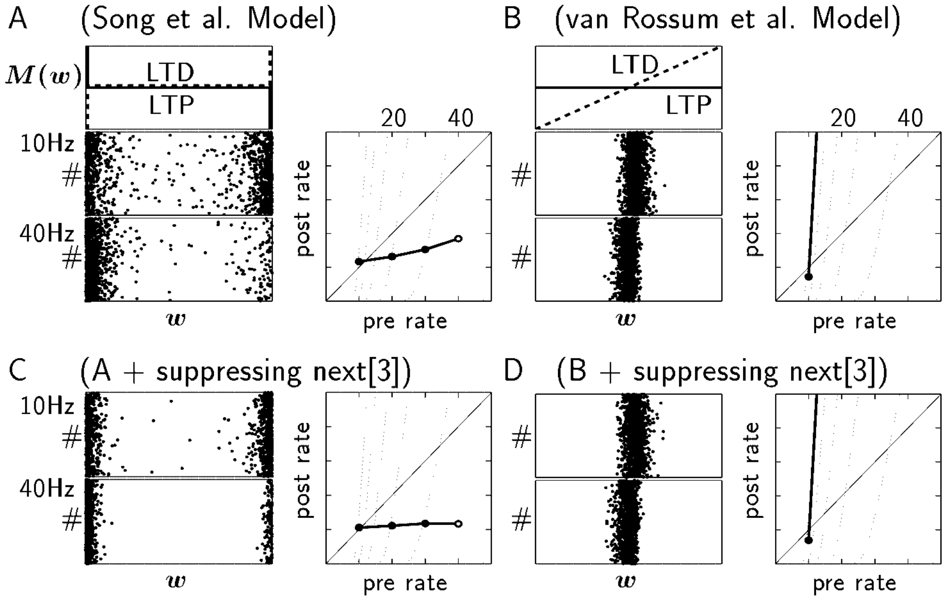

Figure 1: Synaptic competition and activity regulation in various STDP rules. Reproductions of [7] and [8](A,B) and effects of the suppressing rule[3] on them(C,D). Each figure(A-D) has 4 or 3 plots. (Left-Top in A and B) efficacy-dependence of LTP(solid line) and LTD(dashed line). (Left-Middle) a snapshot of efficacy pattern for excitatory synapses in the case that presynaptic firing rate $\lambda^{\rm pre} = 10$Hz in steady state($t = 10000$sec). (Left-Bottom) a snapshot of efficacy pattern for excitatory synapses in the case that presynaptic firing rate $\lambda^{\rm pre} = 40$Hz in steady state($t = 10000$sec). (Right) postsynaptic firing rate $\lambda^{\rm post}$ for presynaptic firing rate $\lambda^{\rm pre} = 10, 20, 30, 40$Hz in steady state($t = 10000$sec). Background solid line denotes the line $\lambda^{\rm post} = \lambda^{\rm pre}$. Background dotted lines denotes the relationships of $\lambda^{\rm post}$ to $\lambda^{\rm pre}$ in the case that the synaptic efficacy is constant.

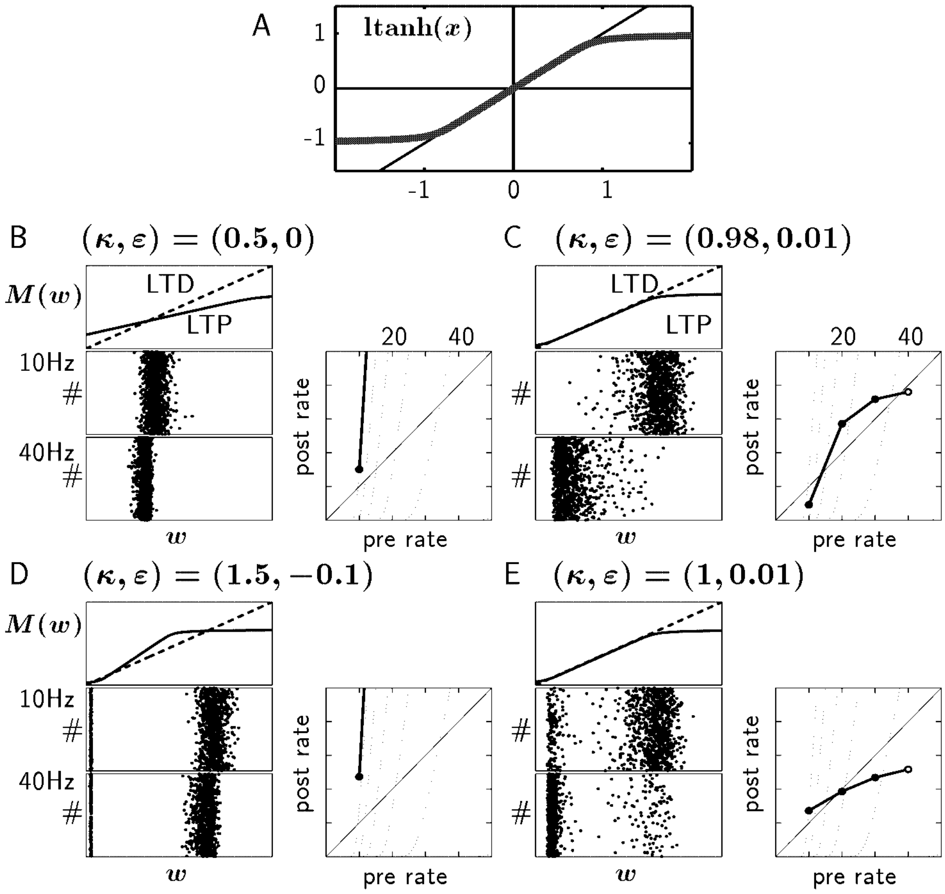

Figure 2: Various patterns of competition and regulation demonstrated on asymmetrical STDP rules with sigmoidally efficacy-dependent LTP and multiplicative LTD. A: The sigmoidal function $\text{ltanh}(x)$ with wide linear range. B–F: Four figures correspond to the cases at the respective parameters: the slope at the flection point κ and the horizontal shift ε of the sigmoidal function. Each plot represents the same quantities as Fig. 1A.