Why neuronal dynamics should control synaptic learning rules

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Abstract

Hebbian learning rules are generally formulated as static rules. Under changing condition (e.g. neuromodulation, input statistics) most rules are sensitive to parameters. In particular, recent work has focused on two different formulations of spike-timing-dependent plasticity rules. Additive STDP [1] is remarkably versatile but also very fragile, whereas multiplicative STDP [2, 3] is more robust but lacks attractive features such as synaptic competition and rate stabilization. Here we address the problem of robustness in the additive STDP rule. We derive an adaptive control scheme, where the learning function is under fast dynamic control by post-synaptic activity to stabilize learning under a variety of conditions. Such a control scheme can be implemented using known biophysical mechanisms of synapses. We show that this adaptive rule makes the additive STDP more robust. Finally, we give an example how meta plasticity of the adaptive rule can be used to guide STDP into different type of learning regimes.

1 Introduction

Hebbian learning rules are widely used to model synaptic modification shaping the functional connectivity of neural networks [4, 5]. To ensure competition between synapses and stability of learning, constraints have to be added to correlational Hebbian learning rules [6]. Recent experiments revealed a mode of synaptic plasticity that provides new possibilities and constraints for synaptic learning rules [7, 8, 9]. It has been found that synapses are strengthened if a presynaptic spike precedes a postsynaptic spike within a short (~20 ms) time window, while the reverse spike order leads to synaptic weakening. This rule has been termed spike-timing dependent plasticity (STDP) [1]. Computational models highlighted how STDP combines synaptic strengthening and weakening so that learning gives rise to synaptic competition in a way that neuronal firing rates are stabilized.

Recent modeling studies have, however, demonstrated that whether an STDP type
rule results in competition or rate stabilization depends on exact formulation of the weight update scheme [3, 2]. Sompolinsky and colleagues [2] introduced a distinction between additive and multiplicative weight updating in STDP. In the additive version of an STDP update rule studied by Abbott and coworkers [1, 10], the magnitude of synaptic change is independent on synaptic strength. Here, it is necessary to add hard weight bounds to stabilize learning. For this version of the rule (aSTDP), the steady-state synaptic weight distribution is bimodal. In sharp contrast to this, using a multiplicative STDP rule where the amount of weight increase scales inversely with present weight size produces neither synaptic competition nor rate normalization [3, 2]. In this multiplicative scenario the synaptic weight distribution is unimodal. Activity-dependent synaptic scaling has recently been proposed as a separate mechanism to ensure synaptic competition operating on a slow (days) time scale [3]. Experimental data as of today is not yet sufficient to determine the circumstances under which the STDP rule is additive or multiplicative.

In this study we examine the stabilization properties of the additive STDP rule. In the first section we show that the aSTDP rule normalizes postsynaptic firing rates only in a limited parameter range. The critical parameter of aSTDP becomes the ratio (α) between the amount of synaptic depression and potentiation. We show that different input statistics necessitate different α ratios for aSTDP to remain stable. This lead us to consider an adaptive version of aSTDP in order to create a rule that is both competitive as well as rate stabilizing under different circumstances.

Next, we use a Fokker-Planck formalism to clarify what determines when an additive STDP rule fails to stabilize the postsynaptic firing rate. Here we derive the requirement for how the potentiation to depression ratio should change with neuronal activity. In the last section we provide a biologically realistic implementation of the adaptive rule and perform numerical simulations to show how these parameterizations of the adaptive rule can guide STDP into differentially rate-sensitive regimes.

2 Additive STDP does not always stabilize learning

First, we numerically simulated an integrate-and-fire model receiving 1000 excitatory and 250 inhibitory afferents. The weights of the excitatory synapses were updated according to the additive STDP rule. We used the model developed by Song et al, 2000 [1]. The learning kernel $L(\tau)$ is $A_+ \exp(\tau/\tau_+)$ if $\tau < 0$ or $-A_- \exp(-\tau/\tau_-)$ if $\tau > 0$ where $A_-/A_+$ denotes the amplitude of depression/potentiation respectively. Following [1] we use $\tau_+ = \tau_- = 20 \text{ ms}$ for the time window of learning. The integral over the temporal window of the synaptic learning function ($L$) is always negative. Synaptic weights change according to

$$\frac{dw_i}{dt} = \int L(\tau) s_{pre}(t + \tau) s_{post}(\tau) d\tau , \quad w_i \in [0, \omega_{max}] \quad (1)$$

where $s(t)$ denotes a delta function representing a spike at time $t$. Correlations between input rates were generated by adding a common bias rate in a graded manner across synapses so that the first afferent is zero while the last afferent has the maximal correlation, $C_{max}$.

We first examine how the depression/potentiation ratio ($\alpha = LTD/LTP$) [2] controls the dependence of the output firing rate on the synaptic input rate, here referred to as the effective neuronal gain. Provided that $\alpha$ is sufficiently large, the STDP rule controls the postsynaptic firing rate (Fig. 1A). The stabilizing effect of the STDP rule is therefore equivalent to having weak a neuronal gain.