

A Maximum Likelihood Approach to Spike-Timing Dependent Plasticity

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Abstract

The aim of this study is to derive a spike-timing dependent learning rule. The particularity of our model is that the learning rule is obtained from an optimal probabilistic point of view. The idea is to maximise the probability of getting a given postsynaptic spike train with respect to the synaptic strength. A simple situation with a single presynaptic spike (PrS) and a postsynaptic spike (PoS) is discussed. The resulting weight adaptation is compared with the experimental results.

Keywords: Spike-Timing Dependent Plasticity, Hebbian Learning, Maximum Likelihood, Spike Response Model, Depolarizing Afterpotential.

1 Introduction

Since synaptical changes are assumed to underly memory and learning processes, a crucial question is to determine what causes those changes and what is the law describing this adaptation process. Among the enormous number of models, there are mainly two categories: rate-based and spike-based learning rule. In this paper, we want to present a new way to derive a spike-time dependent learning rule.

Until now, the existing models are either phenomenological [9] or pseudo-mechanistic [1]. Our model is derived from a probabilistic point of view in the sense that the learning rule should optimise the likelihood of observing a postsynaptic spike train with a desired timing, given the postsynaptic membrane potential.

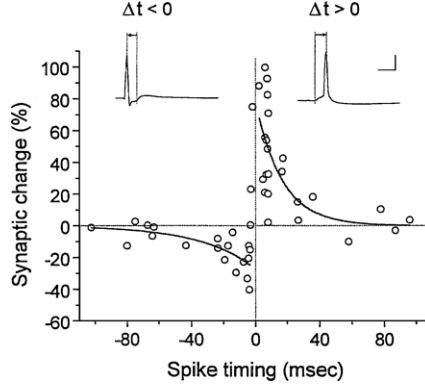


Fig. 1. Critical window for synaptic modifications. Long-term potentiation (LTP)/long-term depression (LTD) were induced by correlated pre- and postsynaptic spiking at synapses between hippocampal glutamatergic neurons in culture. Figure from [4].

A significant part of the synaptic plasticity models are based on Hebb's postulate [8], which basically says that the adaptation of the synaptic weights is driven by a simultaneous activity of the pre- and the postsynaptic neuron. This simultaneity has to be defined in a time window. Recent experiments [3] have shown the influence of a pair of a PrS and PoS on the synaptic strength (figure 1).

The aim of this paper is to show that it is possible to reproduce a similar learning window as a result from an optimal learning rule. Recently Barber [2] studied this question with neurons discrete in time. Here we want to extend this study to the continuous case and discuss the results in relation with the experiments of Bi and Poo [3].

2 Spike Response Model

For the sake of simplicity, let us consider here a single presynaptic neuron j and a postsynaptic neuron i . Those two neurons are considered as Poisson neurons, i.e their firing times depend only on the present value of the membrane potential. Let w be the synaptic weight between those neurons. Finally, let $\{t_j^f\}$ and $\{t_i^f\}$ denote respectively the pre- and postsynaptic firing times.

The fundamental hypothesis in this article is to assume that the instantaneous firing rate of the postsynaptic neuron is given by an increasing function of the membrane potential $u(t)$:

$$\rho(t) = g(u(t)). \quad (1)$$

This instantaneous firing rate can be also termed as escape rate [7]. The mem-

brane potential model we take is the Spike Response Model (SRM). The simplest SRM is called SRM₀ [6] and defines the membrane potential $u(t)$ as follow:

$$u(t) = u_{\text{rest}} + \eta(t - \hat{t}_i) + w \sum_{f'} \epsilon(t - t_j^{f'}), \quad (2)$$

where $\eta(s)$ is a kernel describing the action potential, $\epsilon(s)$ is the kernel representing the excitatory post-synaptic potential (EPSP) and \hat{t}_i is the last firing time of neuron i , i.e. $\hat{t}_i = \max\{t_i^f | t_i^f < t\}$. As we will see in section 4, $\eta(s)$ will only characterise the potential after the repolarisation. The goal is now to maximise the probability that the postsynaptic spike train $S_i(t) = \sum_{f'} \delta(t - t_i^{f'})$ has been generated by the instantaneous firing rate $\rho(t)$.

3 Calculation of the likelihood \mathcal{L}

In order to calculate the likelihood of a spike train given $\rho(s)$, let us first recall that the interval distribution $P(t_i | \rho(s))$ for a Poisson process is given by

$$P(t_i | \rho(s)) = \rho(t_i) \exp \left(- \int_0^{t_i} \rho(t) dt \right). \quad (3)$$

If we consider an interval $I = [0, T]$, the probability density of having M given spikes at time $\{t_i^f\}$, $t_i^f < t_i^{f+1}$, and no other spikes in this interval is given by

$$P(\{t_i^f\} | \rho(s)) = \prod_f \rho(t_i^f) \exp \left(- \int_0^T \rho(t) dt \right). \quad (4)$$

Now we can define the log-likelihood $\mathcal{L}(\{t_i^f\} | u(s))$ of the postsynaptic spike train $S_i(t)$ given the membrane potential $u(s)$ by simply taking the logarithm of $P(\{t_i\} | g(u(s)))$:

$$\mathcal{L}(\{t_i^f\} | u(s)) = \sum_f \log(g(u(t_i^f))) - \int_0^T g(u(t)) dt. \quad (5)$$

4 Learning rule

The goal of our study is to find a learning rule which tends to optimise the weights w in order to maximise the likelihood of getting postsynaptic firing times given the instantaneous firing rate. This means that those weights must evolve in the direction of the gradient of \mathcal{L} :

$$w^{\text{new}} = w + \kappa \frac{\partial \mathcal{L}}{\partial w}, \quad (6)$$

with

$$\frac{\partial \mathcal{L}}{\partial w}(\{t_i^f\}|u(s)) = \sum_f \sum_{f'} \epsilon(t_i^f - t_j^{f'}) \frac{g'(u(t_i))}{g(u(t_i))} - \int_0^T g'(u(t)) \sum_{f'} \epsilon(t - t_j^{f'}) dt \quad (7)$$

and κ is the learning rate. Since $g(u(t)) = \exp(\beta(u(t) - \theta))$ is a reasonable choice [7], we can use it to evaluate the gradient of \mathcal{L} for a pre- and a postsynaptic spike train:

$$\frac{\partial \mathcal{L}}{\partial w}(\{t_i^f\}|u(s)) = \beta \sum_f \sum_{f'} \epsilon(t_i^f - t_j^{f'}) - \beta \int_0^T g(u(t)) \sum_{f'} \epsilon(t - t_j^{f'}) dt. \quad (8)$$

Let us now study the restricted case with only a single pair of PrS and PoS. With $\beta = 1$, we get:

$$\frac{\partial \mathcal{L}}{\partial w}(t_i|u(s)) = \epsilon(t_i - t_j) - \int_0^T \exp(u(t) - \theta) \epsilon(t - t_j) dt. \quad (9)$$

In order to represent the gradient of the log-likelihood function \mathcal{L} (figure 2), it is necessary to determine specific kernels for $\eta(s)$ and $\epsilon(s)$. For simplicity sake, we choose

$$\eta(s) = \eta_0 e^{-\frac{s}{\tau_\eta}} \Theta(s), \quad \epsilon(s) = \epsilon_0 e^{-\frac{s}{\tau_\epsilon}} \Theta(s), \quad (10)$$

where Θ is the usual Heaviside step function with $\Theta(s) = 1$ for $s > 0$ and $\Theta(s) = 0$ else. If $\eta_0 > 0$, the neuron exhibits a depolarizing afterpotential (DAP). In reverse, if $\eta_0 < 0$, it exhibits a hyperpolarizing afterpotential (HAP).

It is interesting to note that the qualitative shape of this learning window is similar to the one obtained by Bi and Poo [3] only in presence of DAP

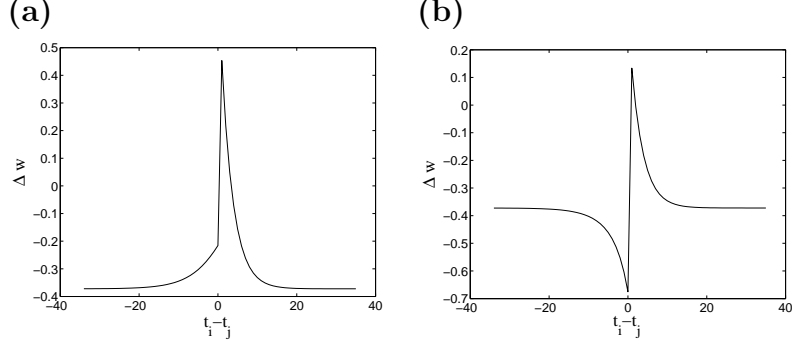


Fig. 2. First step of the adaptation of weights $\Delta w = w^{\text{new}} - w = \frac{\partial \mathcal{L}}{\partial w}$. The parameters for this simulation are : $w = 0.2, \theta - u_{\text{rest}} = -2, \beta = 1, \epsilon_0 = 1, \tau_\epsilon = 3, \tau_\eta = 5$. The amplitude of the spike-afterpotential is given by $\eta = -1$ (DAP) for **(a)** and $\eta = 1$ (HAP) for **(b)**. Note the different vertical scales.

which could be consistent with DAP observed by Connors et al. in neocortical neurons [5].

5 Discussion

One can note that a major difference between the result of Bi and Poo and our model is the negative offset. This offset is related to the integral of the kernel $\epsilon(s)$. Indeed, if the PoS occurs a long time after the PrS and if $w \simeq 0$, the first term of equation (9) can be neglected and the membrane potential can be approximated by its resting potential in the range where $\epsilon(t - t_j)$ is significant:

$$\frac{\partial \mathcal{L}}{\partial w} \simeq \exp(u_{\text{rest}} - \theta) \int_0^\infty \epsilon(s) ds. \quad (11)$$

This is of course valid only if $T \gg t_j$. In fact, this offset is related to the probability of not having a spike at time $t \neq t_i$ (c.f. last term of eq. (3)).

One can also note that the shape of the positive peak on figure 2b is given by the kernel $\epsilon(s)$ (c.f. first term of eq. (9)). This is due to the choice of an exponential for the function $g(u)$.

Let us note that the we are looking at the gradient of the likelihood function \mathcal{L} and not at the optimal solution given by $\frac{\partial \mathcal{L}}{\partial w} = 0$. Indeed, it is straightforward to notice that there is no fix point for w if $t_i < t_j$.

We have shown a new framework for deriving a spike-time dependent learning

rule. The interesting feature of this learning rule is the similarity to the one obtained by Bi and Poo. This similarity is valid only in presence of DAP. The duration of the DAP determines the width of the negative phase of the learning window.

As a consequence we could speculate that the form of the learning window changes according to the type of neuron since in this framework the learning window strongly depends on the spike-afterpotential.

It is of course possible to make the model more complex by not using the SRM_0 model but more realistic models. Even if our study was restricted to a single pair of PrS and PoS, equation (8) remains totally general for spike trains and is also valid for an entire neural network.

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