Optimal Hebbian Learning: A Probabilistic Point of View

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Abstract. Many activity dependent learning rules have been proposed in order to model long-term potentiation (LTP). Our aim is to derive a spike time dependent learning rule from a probabilistic optimality criterion. Our approach allows us to obtain quantitative results in terms of a learning window. This is done by maximising a given likelihood function with respect to the synaptic weights. The resulting weight adaptation is compared with experimental results.

1 Introduction

Since synaptic changes are most likely to underly memory and learning processes, it is crucial to determine the causes and underlying laws 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. Existing models of spike-timing dependent plasticity are either phenomenological [12] or, in contrast, 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 at the location of the synapse.

A significant part of the synaptic plasticity models are based on Hebb's postulate [14]:

> When an axon of cell A is near enough to excite cell B or repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased.

In fact models rephrase this postulate by saying that the adaptation of the synaptic weights is driven by a simultaneous activity of the pre- and the post-synaptic neuron. This simultaneity has to be defined in a time window. Recent
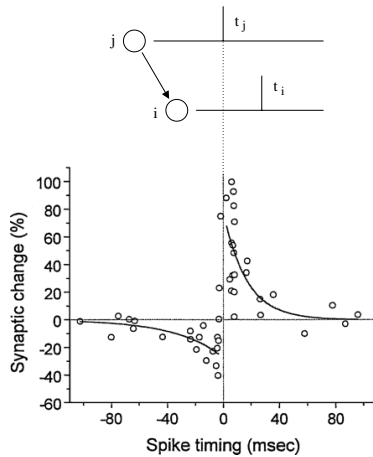
Fig. 1. Critical window for synaptic modifications. Long-term potentiation (LTP)/long-term depression (LTD) were induced by correlated pre- and postsynaptic spiking at synapses between hippocampal glutamatergic neurons in culture. Figure adapted from [4].

experiments [3] have shown the influence of a pair of a single pre- and postsynaptic spike on the synaptic strength (figure 1).

The aim of this paper is to show that it is possible to get 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 $u(t)$:

$$\rho(t) = g(u(t)). \tag{1}$$

This firing rate can be also termed escape rate [11]. The membrane potential model we take is the Spike Response Model (SRM). The simplest SRM is called SRM_0 [9] and defines the membrane potential $u(t)$ as follow:

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

where, in our case, $\eta(s)$ is a kernel describing the spike-afterpotential, $\epsilon(s)$ is the kernel representing the excitatory post-synaptic potential (EPSP) and $\hat{t}_i$ is the last firing time of neuron i, i.e. $\hat{t}_i = \max\{t_i^f | t_i^f < t\}$. 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 firing rate $\rho(t)$.

3   Calculation of the Likelihood $\mathcal{L}$

In order to calculate the likelihood of a spike train given a firing rate, it is useful to first make a time discretization before coming back to the continuous case. Let $\bar{\rho}(t)$ be the discretised version of $\rho(t)$ on the interval $I = [0, T]$ where $\bar{\rho}(t) = \rho(t_n)$, $\forall t \in [t_n, t_n + \Delta t]$ and $t_0 = 0$, $t_N = N\Delta t = T$.

The probability that a neuron produces a spike at time $t \in [\tilde{t}, \tilde{t} + \Delta t]$ given its firing rate $\bar{\rho}(s)$ is simply given by the probability of spiking between $\tilde{t}$ and $\tilde{t} + \Delta t$ multiplied by the probability of not spiking at any other time:

$$\bar{P}(t \in [\tilde{t}, \tilde{t} + \Delta t] | \bar{\rho}(s))\Delta t = \bar{\rho}(\tilde{t})\Delta t \prod_{t_n \neq \tilde{t}} (1 - \bar{\rho}(t_n)\Delta t)$$ (3)

To extend this result to the case of M spikes, we need to define $\mathbf{t} = (t^1, \ldots, t^M)$ a M-dimensional time variable ordered chronologically, i.e. $t^f < t^{f+1}$. Let $\tilde{\mathbf{t}}$ be the M desired firing times and $\Omega(\tilde{\mathbf{t}}) = \prod_n [\tilde{t}_n, \tilde{t}_n + \Delta t]$ a M-dimensional bin. The probability of firing at the M given times $\tilde{\mathbf{t}}$ is

$$\bar{P}(\mathbf{t} \in \Omega(\tilde{\mathbf{t}}) | \bar{\rho}(s))\Delta t^M = \prod_f \bar{\rho}(\tilde{t}^f)\Delta t^M \prod_{t_n \neq \tilde{t}^f} (1 - \bar{\rho}(t_n)\Delta t)$$

$$= \prod_f \frac{\bar{\rho}(\tilde{t}^f)\Delta t^M}{1 - \bar{\rho}(\tilde{t}^f)\Delta t} \prod_n (1 - \bar{\rho}(t_n)\Delta t)$$

$$= \prod_f \frac{\bar{\rho}(\tilde{t}^f)\Delta t^M}{1 - \bar{\rho}(\tilde{t}^f)\Delta t} \exp\left(\sum_n \log(1 - \bar{\rho}(t_n)\Delta t)\right).$$ (4)

Now we can come back to the continuous case. By taking the limit $\Delta t \to 0$, we have $\bar{\rho}(t) \to \rho(t)$, $\bar{P}(\mathbf{t} \in \Omega(\tilde{t}) | \bar{\rho}(s)) \to P(\mathbf{t} = \mathbf{t}' | \rho(s))$, $\sum_n \log(1 - \bar{\rho}(t_n)\Delta t) \to -\int_0^T \rho(t)dt$ and $1 - \bar{\rho}(\tilde{t}^f)\Delta t \to 1$. Therefore we can define the log-likelihood $\mathcal{L}(\mathbf{t}_i | u(s))$ of the postsynaptic spike train given the membrane potential $u(s)$ by simply taking the logarithm of $P(\mathbf{t} = \mathbf{t}' | \rho(s))$:

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

4 Learning Rule

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

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

with

$$\frac{\partial \mathcal{L}}{\partial w}(\mathbf{t}_i | u(s)) = \sum_f \frac{\frac{dg(u(t_i^f))}{du(t_i^f)} \frac{\partial u(t_i^f)}{\partial w}}{g(u(t_i^f))} - \int_0^T \frac{dg(u(t))}{du(t)} \frac{\partial u(t)}{\partial w} dt$$

$$= \sum_f \sum_{f'} \frac{\epsilon(t_i^f - t_j^{f'})}{g(u(t_i^f))} \frac{dg(u(t_i^f))}{du(t_i^f)} - \int_0^T \frac{dg(u(t))}{du(t)} \sum_{f'} \epsilon(t - t_j^{f'}) dt \tag{7}$$

and κ is the learning rate. Since $g(u(t)) = \exp(\beta(u(t) - \theta))$ is a reasonable choice [11], we can use it to evaluate the gradient of $\mathcal{L}$ for a pre- and a postsynaptic spike train:

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

Let us now study the restricted case with only one pre- and one postsynaptic spike and $\beta = 1$:

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

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

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

$$\epsilon(s) = \epsilon_0 e^{-\frac{s}{\tau_\epsilon}} \Theta(s), \tag{11}$$

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 $\eta_0 < 0$, is 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 which could be consistent with DAP observed by Connors et al. in neocortical neurons [6].
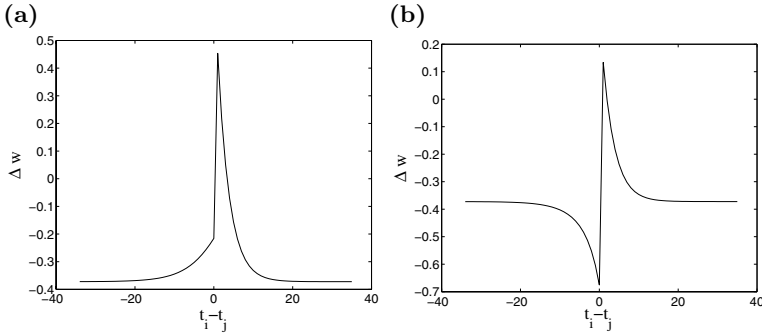
(a)   **(b)**

Fig. 2. First step of the adaptation of weights $\Delta w = w^{\mathrm{new}} - w = \frac{\partial \mathcal{L}}{\partial w}$. The parameters for this simulation are : $w = 0.2, \theta - u_{\mathrm{rest}} = -2, \beta = 1, \epsilon_0 = 1, \tau_\epsilon = 3, \tau_\eta = 5$. The amplitude of the spike-afterpotential is given by $\eta_0 = -1$ (HAP) for **(a)** and $\eta_0 = 1$ (DAP) for **(b)**. Note the different vertical scales.

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 postsynaptic spike occurs a long time after the presynaptic spike 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:

$$\frac{\partial \mathcal{L}}{\partial w} \simeq - \exp(u_{\mathrm{rest}} - \theta) \int_{t_j}^{T} \epsilon(t - t_j) dt$$

$$\simeq - \exp(u_{\mathrm{rest}} - \theta) \int_{0}^{\infty} \epsilon(s) ds. \tag{12}$$

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)). In order to increase the likelihood of not having a spike the weight needs to be reduced.

A possible way to solve the problem of negative bias of Δw is to consider a slightly different scenario where we still impose the postsynaptic spike at a given time, but instead of imposing no spike at all the other times, we choose the desired number of spikes that are allowed to occur stochastically over the period T. This number of spikes has to be related to the spontaneous firing rate.

One can also note that the shape of the positive peak on figure 2a is dominated 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 fixed point for w if $t_i < t_j$. For $t_j < t_i$, there is a fixed point and it is stable since $\frac{\partial^2 \mathcal{L}}{\partial w^2} < 0$.

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 pre- and postsynaptic spike, equation (8) remains totally general for spike trains and is also valid for an entire neural network.

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