Optimal Spike-Timing Dependent Plasticity for Precise Action Potential Firing

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Abstract

Synaptic connections can adapt so that the postsynaptic neuron generates an action potential at a desired firing time defined by the onset of a temporally inaccurate fuzzy teaching signal. We use a modelling framework to show that the optimal strategy of weight adaptation results in a two-phase learning window similar to that of Spike-Timing Dependent Plasticity (STDP). The temporal form of the optimal potentiation window reflects the time course of an excitatory postsynaptic potential. The duration of the optimal depression window reflects the duration of the teaching input.

Key words: Spike-Timing Dependent Plasticity, Temporal code, Spiking neurons, Optimal learning rule

1 Introduction

Synaptic connections between neurons change depending on the activity of pre- and postsynaptic neurons in agreement with Hebb's principle [8]. Recent experimental advances have made it possible to study long-term modification of synapses as a function of the exact timing of pre- and postsynaptic action potentials [11, 3]. See [2] for a review. The result of this 'Spike-Timing Dependent Plasticity (STDP)' for excitatory synapses can be summarised in form of a time-window of sensitivity ('Learning window') with two phases: if the presynaptic spike arrives at the synapse *before* the postsynaptic action potential, the synapse is potentiated; if the timing is reversed the synapse is

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depressed [11, 3, 4]. The two-phase learning window is reminiscent of a temporal contrast or temporal derivative filter and suggests that STDP is sensitive to the temporal features of a neural code. Indeed, theoretical studies have shown that, given a two-phase learning window, synaptic plasticity can lead to a stabilisation of synaptic weight dynamics [12, 10] while the neuron remains sensitive to temporal structure in the input [5, 9, 13, 6]. For a review, see [7].

In order to further elucidate the computational function of STDP, we ask in this paper the following question: What is the ideal form for a learning window of synaptic plasticity in order to generate action potentials of the postsynaptic neuron with high temporal precision? More precisely we are interested in the following problem (c.f. Fig. 1a). Suppose that, in a particular behavioral task or as part of a given temporal code, neuron i should fire an action potential in a 2 ms interval starting at time $t_i^{\rm des}$. How helpful, then, is the spike of a presynaptic neuron j which arrives at time t_j at the synapse for supporting firing of the postsynaptic neuron immediately after time $t_i^{\rm des}$?

2 The model

Neuron Model. The postsynaptic neuron i under consideration receives input from several presynaptic neurons (c.f. Fig. 1a.).

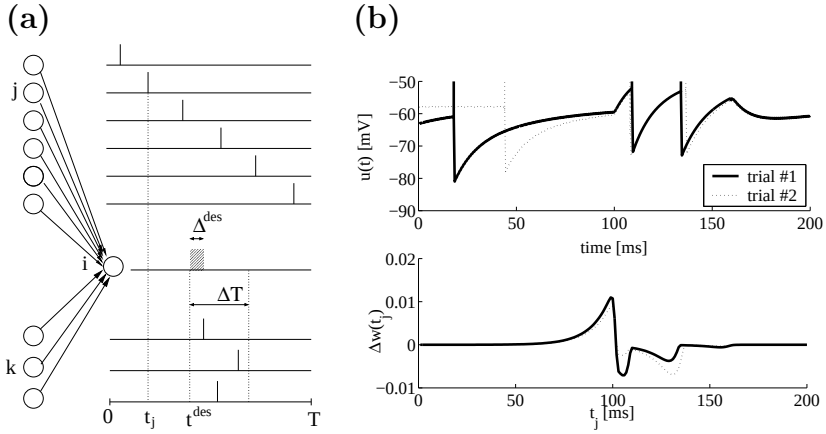

Fig. 1. **(a)**. $N_{\rm pre} = 200$ neurons firing at time $t_j = j \cdot \Delta t$, $\Delta t = 1$ ms and $N_{\rm teach} = 60$ additional ('teaching') ones firing in the interval $[t_i^{\rm des}, t_i^{\rm des} + \Delta T]$ are converging to a single postsynaptic neuron. **(b) top**. Two sample traces of the membrane potential when the 'teaching signal' starts at $t_i^{\rm des} = 100$ ms and stops at $t_i^{\rm des} + \Delta T = 160$ ms. Here $w_j = 1$, $\forall j = 1 \ldots NI + NT$. **(b) bottom** The two corresponding learning windows given by Eq. (5) with $\lambda = \Delta^{\rm des}/\Delta T = 0.0\bar{3}\ldots$.

A presynaptic spike from neuron j evokes an excitatory postsynaptic potential (EPSP) of amplitude w_j and time course $\epsilon(t - t_j)$ where t_j denotes the spike arrival time at the synapse. We approximate the EPSP time course by a double exponential $\epsilon(s) = \epsilon_0 \left[e^{-s/\tau_m} - e^{-s/\tau_s}\right]$ with a membrane time constant of $\tau_m = 10$ ms and a synaptic time constant of $\tau_s = 0.7$ ms which yields an EPSP rise time of 2 ms. We set $\epsilon_0 = 1.3$ mV such that $\max(\epsilon(s)) = 1$ mV.

There are two groups of presynaptic input. The first group is a set of delayed spikes so that each spike arrives at a different synapse. In total, we have $N_{\rm pre} = 200$ neurons in the first group. The second group is the teaching signal. Neurons tart to fire at the desired time $t_i^{\rm des}$ and stop $\Delta T = 60$ ms later.

The membrane potential of the postsynaptic neuron i (two sample traces shown on Fig. 1b) is influenced by the EPSPs of all presynaptic neurons (Spike Response Model, [7]) and given by

$$u_i(t) = u_{\rm rest} + \sum_{j=1}^{N_{\rm pre}} w_j \epsilon(t-t_j) + \underbrace{\sum_{k=N_{\rm pre}+1}^{N_{\rm pre}+N_{\rm teach}} w_k \epsilon(t-t_k)}_{u_{\rm teach}(t)} + \sum_f \eta(t-t_i^{(f)}) \quad (1)$$

where $u_{\rm rest} = -70$ mV is the resting potential; the first sum runs over all $N_{\rm pre}$ input neurons. The second sum is the contribution of the teaching input $u_{\rm teach}(t)$ which is generated by the EPSPs arising from a second set of $N_{\rm teach}$ synapses; $\eta(t-t_i^{(f)})$ is the spike-afterpotential generated by an action potential at time $t_i^{(f)}$. We take $\eta(t-t_i^{(f)}) = \eta_0 \exp(-(t-t_i^{(f)})/\tau_m + \eta_h \exp(-(t-t_i^{(f)})/\tau_h$ where $\eta_0 = -10$ mV is the standard reset and $\eta_h = -10$ mV mimics the contribution of a h-current with $\tau_h = 40$ ms.

In order to account for the 'synaptic noise' generated by stochastic spike arrival from excitatory and inhibitory presynaptic neurons which are not modelled explicitly, we adopt the following procedure [7]. Action potentials of the post-synaptic neuron are generated stochastically by an inhomogeneous Poisson process with an instantaneous firing rate $\rho(t)$ that depends non-linearly upon the membrane potential (see Fig. 2a for the PSTH generated by this process)

$$\rho(t) = f(u_i(t)). \quad (2)$$

We take an exponential to describe the escape across a noisy threshold, i.e, $f(u) = \rho_0 \exp \frac{u-\vartheta}{\Delta u}$ where $\vartheta = -50$ mV is the formal threshold, $\Delta u = 2$ mV is the width of the threshold region, and $\rho_0 = 1/\text{ms}$ is the sensitivity at threshold. Other choices of the escape function f are possible with no qualitative change of the results. For $\Delta u \to 0$, $\tau_s \to 0$ and $\eta_h = 0$, the model is identical to the deterministic leaky integrate-and-fire model.

With a global spike arrival rate of $\nu^{\rm pre} = 1\text{ms}^{-1}$ and a mean efficacy $\langle w \rangle = \frac{1}{N_{\rm pre}} \sum_{j=1}^{N_{\rm pre}} w_j \int_0^\infty \epsilon(s) ds$ and in the absence of a teaching input, neuron i has a spontaneous firing rate ν_0 given by $\nu_0 = [\int_0^\infty P(t) t dt]^{-1}$ where $P(t) = f\left(u_{\rm rest} + \langle w \rangle \nu^{\rm pre} + \eta(t)\right)$ is the probability of having a spike at time t given that the last spike occurred at $t = 0$.

Optimisation. The overall aim of our approach is to increase the probability of spike firing in the interval $A_{\rm in} = [t_i^{\rm des}, t_i^{\rm des} + \Delta^{\rm des}]$ without changing the instantaneous firing rate $\rho(t)$ during the rest of the time [1]. We take $\Delta^{\rm des} = 1$ ms. For the inhomogeneous Poisson process (2), the probability $P_{\rm in}$ that neuron

i fires exactly once in the interval A_{in} is given by $P_{\text{in}} = Q_{\text{in}} \exp(-Q_{\text{in}})$ where

$$Q_{\text{in}} = \int_{A_{\text{in}}} \rho(t) dt. \tag{3}$$

One possible hypothetical solution to increasing P_{in} would be to equally potentiate all excitatory synapses converging onto neuron i. To avoid such an non biological solution, we require that, outside the interval A_{in} the instantaneous firing rate $\rho(t)$ in the *presence* of the teaching input, should be as close as possible to the spontaneous rate ν_0 *without* the teaching input. The above condition is implemented by a quadratic penalty term P_{out}. Denoting by $A_{\text{out}} = [0, t_i^{\text{des}}] \bigcup [t_i^{\text{des}} + \Delta^{\text{des}}, T]$ the whole period of a single trial except the interval A_{in}, we optimise the regularized likelihood L with respect to w,

$$L = P_{\text{in}} - \lambda P_{\text{out}} = Q_{\text{in}} \exp(-Q_{\text{in}}) - \frac{\lambda}{2} \int_{A_{\text{out}}} [\rho(t) - \nu_0]^2 dt \tag{4}$$

where λ scales the relative importance of the penalty term. Maximisation of L can be performed by gradient ascent, i.e., $\Delta w_j = \alpha dL/dw_j$ with a small positive constant α:

$$\Delta w_j = \alpha Q'_{\text{in}} \exp\left(-Q_{\text{in}}\right) \left(1 - Q_{\text{in}}\right) - \alpha\lambda \int_{A_{\text{out}}} [\rho(t) - \nu_0] f'(u_i(t)) \epsilon(t - t_j) dt \tag{5}$$

where $Q'_{\text{in}} = \int_{A_{\text{in}}} f'(u_i(t)) \epsilon(t - t_j) dt$. The update rule for the weight change Δw_j in Eq. (5) will in the following be compared with STDP.

3 Results

For a given realisation of the membrane potential (Fig 1b top), we get the optimal weight change for each presynaptic firing time (Fig 1b bottom) that maximises the likelihood of firing in a 2 ms interval after t_i^{des} from Eq. (5). By simply averaging 1000 of those weight changes, we get changes which are good on average (Fig. 2b). We can see that synapses that have been active a few milliseconds before the desired postsynaptic firing time are potentiated whereas those which have been active after t_i^{des} are depressed.

The first term on the right-hand side of Eq. (5) yields the positive part of the learning window. Its time course is a mirror image of the EPSP. The second term on the right-hand side of Eq. (5) yields the negative part of the learning window. Its width is essentially controlled by the duration of the teaching input, since $\rho(t) - \nu_0 \simeq= 0$ when $u_{\text{teach}} = 0$.

Note that in Fig. 1b, the synaptic changes Δw_j are plotted as a function of the presynaptic firing times t_j. Even though the graph has the appearance of

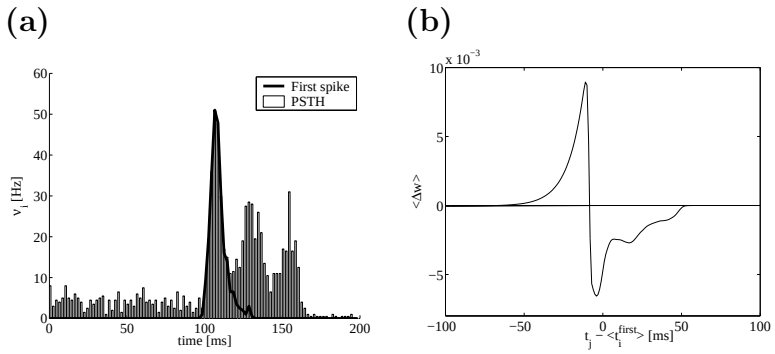

Fig. 2. **(a)** The histogram depicts the PSTH of the postsynaptic neuron after 1000 repetitions. The solid line represents the distribution of the first spikes that occurred after $t_i^{\rm des}$ (onset of the 'teaching signal'). **(b)** This learning window is the average of 1000 individual learning windows like the two of Fig. 1b bottom but horizontally shifted.

a two-phase learning window, it is not a STDP function, since postsynaptic firing times are not made explicit. However since postsynaptic firing is most likely immediately after $t_i^{\rm des}$ (see sharp peak in Fig. 2a), it is possible to convert the results of Fig. 1b into a STDP function, by simply shifting the horizontal scale and plot the weight changes Δw_j as a function of $t_j - \langle t_i^{\rm first} \rangle$, where $\langle t_i^{\rm first} \rangle$ is the mean firing time of the first postsynaptic spike after $t_i^{\rm des}$.

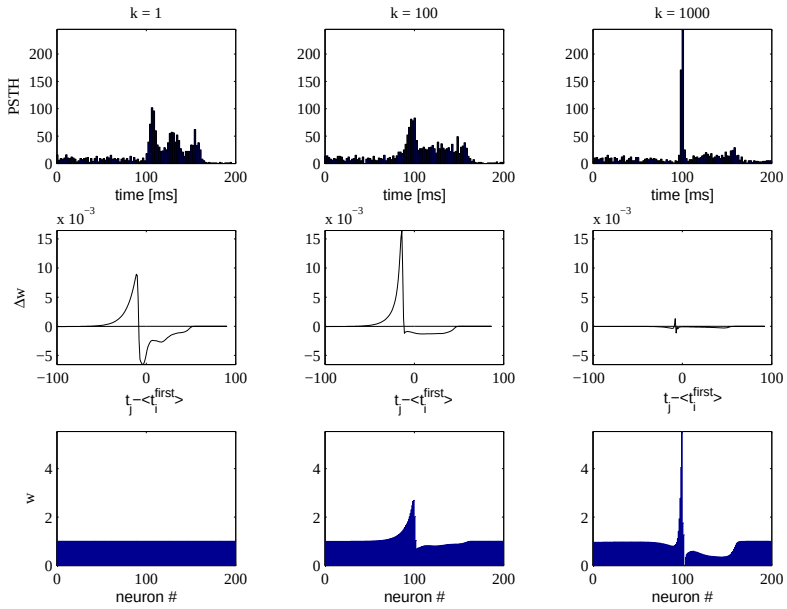

Fig. 3. The iteration of the learning window (second row) induces a change in the distribution of the weights (third row) which causes a modification of the PSTH of the postsynaptic neuron (first row). The three columns correspond respectively to the $k^{\rm th}$ iteration. The learning window of the last column is almost flat which means that the maximisation process has converged.

By maximising L and adapting the weights iteratively by gradient ascent, we end up with the final set of weight values (last column and last row of Fig. 3).

In order to measure the performance in trial k, we consider the probability $\Gamma(k)$ that the postsynaptic neuron emits a spike in the desired interval A_{in}. During the first trial, $\Gamma(1) = 0.03$ while $\Gamma(1000) = 0.53$ for the final state.

4 Conclusions

We have shown in this article that the optimal strategy of weight adaptation to increase to temporal resolution of the postsynaptic AP's results in a learning window which is similar to that of STDP.

The other interesting feature that comes out of this study is also the fact that the STDP learning window is not a fixed quantity, but depends strongly on the trajectory of the membrane potential around the 'teaching signal'.

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