



Spike-timing-dependent synaptic plasticity: from single spikes to spike trains

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Abstract

We present a neurobiologically motivated model of a neuron with active dendrites and dynamic synapses, and a training algorithm which builds upon single spike-timing-dependent synaptic plasticity derived from neurophysiological evidence. We show that in the presence of a moderate level of noise, the plasticity rule can be extended from single to multiple pre-synaptic spikes and applied to effectively train a neuron in detecting temporal sequences of spike trains. The trained neuron responds reliably under different regimes and types of noise.

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1. Introduction

Recently, there has been a substantial advance in the neurophysiological studies on synaptic plasticity, mainly exploring a function of the relative timing between the pre- and post-synaptic spikes (reviewed in [1,8]). Consequently, research in computational modelling has build upon that and derived synaptic plasticity rules capable of tuning neurons to respond to specific spatio-temporal input patterns [2–6]. However, most of these models operate on single pre-synaptic spikes or temporal differences of less than 100 ms. In this paper we present a computational interpretation of a synaptic plasticity rule for the task of detecting temporal sequences of onset times of spike trains. In order to achieve this, we have developed a model of a neuron with active dendrites and dynamic synapses with the necessary functional properties of spatio-temporal integration of incoming spike trains.

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2. Processing with active dendrites and dynamic synapses

The model presented in this paper is an extension of the integrate- and-fire neuron with active dendrites presented in [4]. Here we will describe it briefly and concentrate on the extended functionality of the added dynamic synapses.

The neuron receives input spikes via sets of synapses \mathcal{S}^i , each attached to a particular dendrite i . The total post-synaptic current I_s^i into i is described by:

$$\tau_s \frac{d}{dt} I_s^i(t) = -I_s^i + \sum_{j \in \mathcal{S}^i} c^{ij} \sum_{t^{(f)} \in \mathcal{F}^j} \rho(\Delta t^{(f)}) \delta(t - t^{(f)}),$$

where synaptic connection j at dendrite i has strength c^{ij} and \mathcal{F}^j is the set of pre-synaptic spike times received at the synapse. The dynamics of the synapse is modelled after [7], but here it is described by a function $\rho(\cdot)$ which depends on the normalised time $\Delta t^{(f)}$ between the current and the earliest spikes in \mathcal{F}^j :

$$\rho(\Delta t^{(f)}) = \mu e^{-[(\Delta t^{(f)} - \tau_{ds})/\sigma]^2}$$

with time constant $\tau_{ds} = 1 - c^{ij}$ and scaling constants σ and μ .

Furthermore, the current I_d^i passing through the dendrite to the soma is:

$$\tau_d^i \frac{d}{dt} I_d^i(t) = -I_d^i + R_d^i I_s^i(t).$$

Here, the time constant τ_d^i and membrane resistance R_d^i are dependent on the post-synaptic current into dendrite i and define the active properties of the dendrite.

Finally, the soma membrane potential u_m is:

$$\tau_m \frac{d}{dt} u_m(t) = -u_m + R_m(I_d(t) + \bar{I}_s(t)),$$

where $I_d(t) = \sum_i I_d^i(t)$ is the total current from the dendritic tree. The current from dendrite i generates part of the potential at the soma u_m^i , which we will call *partial membrane potential*. If pre-synaptic input arrives only at dendrite i then $u_m^i = u_m$.

Fig. 1 shows two cases of a response of a neuron to a couple of spike trains with different onset times. In both cases the total synaptic weight is the same, however the response at the soma is substantially different. With appropriately adjusted weights, the neuron is able to compensate for the delay of one of the spike trains, by delaying the increase of the membrane potential of the earlier one. The result is almost synchronous peaks of the partial membrane potentials, and a significantly higher potential generated at the soma.

3. Synaptic plasticity

The task of the plasticity algorithm is to adjust the weights of the neuron, so that for a particular set of spike trains, it is able to synchronise the peaks of the partial membrane potentials, and therefore maximise the response of the soma membrane

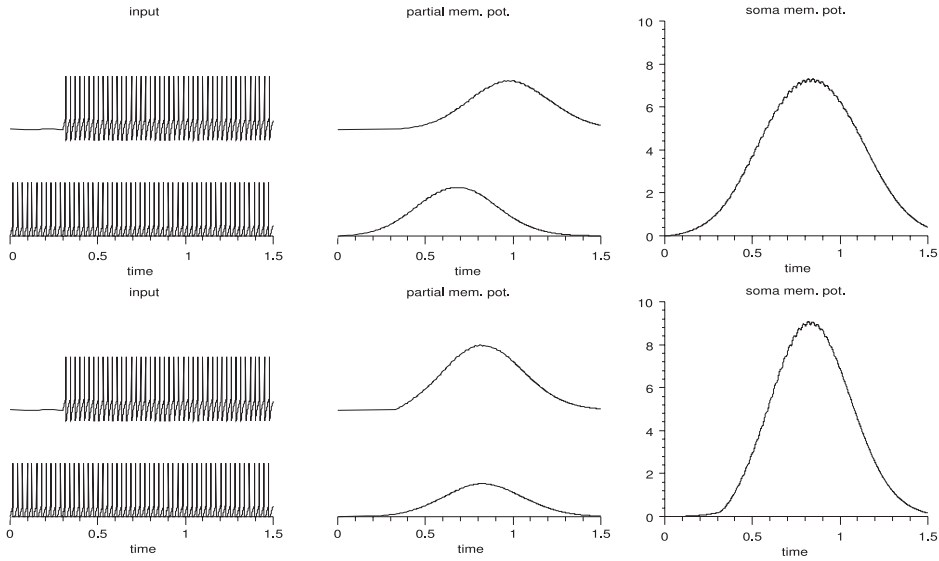


Fig. 1. Integration of multiple spike trains through dynamic synapses with different strength. The onset of one of the spike trains is delayed by 300 ms. Top: Both spike trains arrive at two synapses with strength $c^{1,2}=0.45$ each. Bottom: The first spike train arrives at a synapse with strength $c^1=0.3$, whereas the second arrives at synapse with strength $c^2=0.6$.

potential. Immediately following a post-synaptic spike at time \hat{t} (in a simulation with time step Δt), a synapse j at dendrite i receives an error correction signal:

$$\Delta c^{ij} = \frac{\Delta u_d^i(\hat{t}) - \Delta u_m(\hat{t})}{\sqrt{\Delta t^2 + (\Delta u_d^i(\hat{t}) - \Delta u_m(\hat{t}))^2}},$$

where $\Delta u_d^i(\hat{t})$ and $\Delta u_m(\hat{t})$ are the changes in the partial and total membrane potentials, respectively, just before the post-synaptic spike. The error correction signal has two main contributions: a signal from the dendrite Δu_d^i and a signal from the soma Δu_m . If we remove Δu_m , the rule will implement the following logic: if a post-synaptic spike occurs before the peak of the partial membrane potential (i.e. in the ascending phase of the membrane potential, $\Delta u_d^i > 0$), the synaptic weight will be increased, so that next time the peak will occur earlier, i.e. closer to the post-synaptic spike time. On the other hand, if a post-synaptic spike occurs after the peak of the partial membrane potential, the synaptic weight will be decreased, and the peak delayed.

The Δu_m term has a normalisation effect, its role is to prevent the weights of the synapses from reaching very high values simultaneously, as well as to prevent a total decay in the synaptic strength. Achieving post-synaptic spike-time exactly at the peak of the membrane potential is not always possible, and in most cases undesirable, since it will limit the noise handling capabilities of the neuron. Therefore, if the post-synaptic spike-timing is sufficiently close (for a predefined constant ε) to the peak of the membrane potential, Δu_m is ignored.

Following the error correction signal, the weights are changed according to:

$$c_{\text{new}}^{ij} = \begin{cases} c_{\text{old}}^{ij} + \eta \Delta c^{ij} (1 - c_{\text{old}}^{ij}) & \text{if } \Delta c^{ij} > 0, \\ c_{\text{old}}^{ij} + \eta \Delta c^{ij} c_{\text{old}}^{ij} & \text{if } \Delta c^{ij} < 0. \end{cases}$$

The above algorithm for synaptic plasticity is a local learning rule and it depends on the precise timing of single pre- and post-synaptic spikes. It has been shown to effectively train the neuron to an arbitrary precision, when responding to a temporal sequence of single pre-synaptic spikes [4]. Here, we will examine how this rule can be extended in neural adaptation for spike trains.

One of the main differences in receiving an input as a spike train is that the membrane potential is not a smooth curve, but it contains many local peaks (Fig. 1). If the learning algorithm is directly applied to such an input, it will converge to one of these local peaks and not drive the neuron towards firing close to the global maximum. However, a closer look into the membrane potential curve reveals that (1) during the ascending phase, the local rising of the membrane potential is either steeper, or longer compared to the local decrease; and (2) during the global descending phase, the local decrease is either steeper or longer.

Consequently, if during the global ascending phase, the neuron's firing time fluctuates moderately around a local peak, on average over several iterations, it has a higher probability of coinciding with the local ascending too. Similarly, if the neurons firing time fluctuates moderately around a local peak in the global descending phase, it has a higher probability of coinciding with a local decrease of the membrane potential. Similar arguments apply if instead of fluctuating the post-synaptic spike times, the timing of the single spikes in the input are slightly different, and therefore causing a fluctuation of the timing of the local peaks.

The above arguments provide the basis for the generalisation of the learning algorithm for neurons receiving input as spike trains. The additional condition required is a moderate fluctuation of the timings of the pre- or post-synaptic spikes. Indeed, such fluctuations can come in a natural way similar to the real neural systems, as noise in the input spike trains. It is well known that most real neurons receive input spike trains containing irregular spike timing and a level of noise.

4. Experiments

There are many different systems in the brain where recognition of temporal information encoded in incoming spike trains is required. Here, we will present part of an experiment, where we used the model to recognise words based on input of phoneme sequences. This experiment was carried out on four words: “bat”, “tab”, “cab” and “cat”. Each of the words was represented as a sequence from the phonemes: “A”, “B”, “C” and “T”. The active phonemes and the order of their activation defines the word on the input. The neural network consisted of four input neurons (each representing one phoneme) fully connected to four output neurons (each representing one word). The input neurons are standard integrate- and-fire driven by a decaying injection current with a random fluctuation within a predefined range. This fluctuation provided the noise

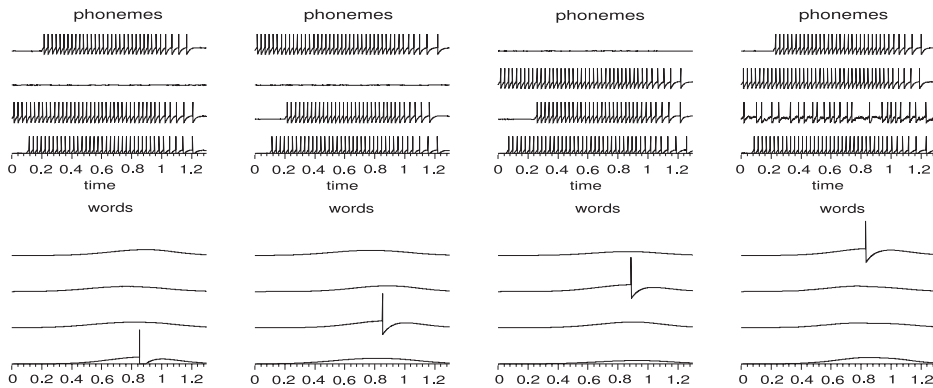


Fig. 2. Processing the words after training (from left to right): “bat” and “tab” as trained; “cab” with variation in the onset times; “cat” with noise in the onset times and random spikes from the non-active phonemes. Top: input neurons representing phonemes “A”, “B”, “C” and “T”; Bottom: output neurons representing the words “bat”, “tab”, “cab” and “cat”.

in the input spikes necessary for the training of the neurons. Thus each phoneme was represented by a decaying spike train of a single neuron, with 100 ms delay between the onset times of successive phonemes. The output units are neurons with dynamic synapses and active dendrites.

Each output neuron was trained to respond to a particular sequence of spike trains. Fig. 2 shows the input and output spikes for the words “bat” and “tab”. The same input neurons are active in both cases, but based on the temporal order of the onset times of the spike trains the output neurons are able to distinguish between the two different inputs.

In the real neural systems there are different sources and types of noise. Although the neurons were trained only with noise in the single spikes within the train, the model exhibits robust behaviour for several different types of noise. The output neurons have reliable response when the onset times of the input spike trains varied by up to 40 ms. Further, the output neurons reliably detected temporal sequences in the presence of relatively high levels of noise from the non-active inputs. Fig. 2 shows such examples for the words “cab” and “cat”.

This experiment does not aim to achieve a speech recognition system, but rather to test and present the properties of the neuron in detecting temporal sequences under different noise conditions. In further successful experiments we applied the model as part of a language communication system of a robot with a larger lexicon. It included further development of the neuron and the synaptic plasticity rule, with the introduction of lateral connections and self-organisation. We achieved a well formed phonotopic map, where words with similar sounds were recognised by neighbouring neurons.

5. Conclusion

The developed model of a novel integrate- and-fire neuron with active dendrites and dynamic synapses performs spatio-temporal integration which is critical for achieving

effective temporal sequence detection in a time scale from 100 ms up to several seconds.

We have been able to extend a neurophysiologically derived synaptic plasticity rule into the case of spike trains, under the single additional condition of moderate noise in the input spikes. It has long been argued that such noise could in fact facilitate the processing and learning in the neurons. The learning paradigm presented here gives a computational interpretation of such a case. In addition, the trained neurons respond reliably under different regimes and types of noise.

We believe that the presented work is a valuable contribution to the computational models processing temporal information and a step towards bridging the gap between the empirical and modelling work on spike-timing-dependent learning on single spikes and learning in spike trains, and potentially further to processing and adaptation in firing rates.

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