Learning Temporal Patterns by Redistribution of Synaptic Efficacy

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Abstract

Recent experiments have shown that neocortical synapses exhibit both short-term plasticity and spike-timing dependent long-term plasticity. It has been suggested that changes in short-term plasticity are mediated by a redistribution of synaptic efficacy. Here we propose a simple model of the interaction between spike-timing dependent plasticity and short-term plasticity. We show that the model captures the synaptic behavior seen in experiments on redistribution of synaptic efficacy. Results from our simulations suggest that spike-timing dependent redistribution of synaptic efficacy offers neocortical neurons a potentially powerful mechanism for learning spatiotemporal patterns in the input stream.

Key words: synaptic plasticity, dynamic synapses, spike timing, sequence learning

1 Introduction

How does the brain learn and encode spatiotemporal patterns and sequences? Data from recent *in vitro* experiments [1–3] suggest some possible mechanisms. First, neocortical synapses have been shown to be dynamic: postsynaptic responses are not simply a function of the presynaptic firing rate multiplied by a synaptic "weight" but rather, reflect the short-term history of input spike trains. Second, paired firing of pre- and postsynaptic neurons tends to redistribute total synaptic efficacy, so that a synapse responds much more strongly to the first presynaptic event than to subsequent events in a spike train [2]. Third, long-term synaptic plasticity appears to follow a temporally asymmetric spike-timing dependent learning rule: a synaptic connection is strengthened if a presynaptic spike occurs slightly before a postsynaptic spike, and is weakened in the opposite case [3,4].

These experimental results raise three important questions that motivate our study: (1) What is the role of dynamic synapses in cortical information processing? (2) What is the relationship between spike-timing dependent plastic-

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ity (STDP) and the redistribution of synaptic efficacy observed in dynamic synapses? and (3) How does STDP in conjunction with dynamic synapses allow cortical neurons to learn spatiotemporal input patterns? With respect to question (1), dynamic synapses have been identified as a possible mechanism for gain control of cortical activity [1], used as memory buffers for "remembering" a history of presynaptic stimulation [5], and used to model irregular bursts of activity in the cortex [6]. With respect to questions (2) and (3), STDP has been suggested as a mechanism for learning temporal sequences and delays [7–10], although without taking dynamic synapses into account.

Here, we propose a model for STDP in dynamic synapses and show using simulations that it reproduces the basic experimental results on redistribution of synaptic efficacy. We then demonstrate how neocortical neurons can learn spatiotemporal input patterns by using STDP to adapt dynamic synapses. This relates our work to previous research on networks that allow explicit modification of synaptic delays [11], and networks of radial basis function (RBF) neurons for temporal clustering [12] (see also [13]). While short-term plasticity and STDP have both been studied in isolation, our simulation results demonstrate that these mechanisms operating together allow single neurons to extract temporal information from their input spike trains.

2 Methods

In our simulations, we used a leaky integrate-and-fire neuron with short-term synaptic depression modeled as:

$$d_t^{syn} = \begin{cases} f^{syn} d_{t-1}^{syn} & \text{if presynaptic spike received} \\ d_{t-1}^{syn} + \frac{\alpha}{\tau_d}(d_0 - d_{t-1}^{syn}) & \text{if no presynaptic spike received} \end{cases} \tag{1}$$

Here d_t^{syn} represents a fractional amount of excitatory neurotransmitter available to synapse syn at time t, with d_0 a constant value of 1, α an integration rate of 0.7 msec, and τ_d a constant value of 50. Parameter f^{syn} is the fraction of neurotransmitter remaining at synapse syn after a presynaptic spike. Higher values of f correspond to weaker short-term depression. In our simulations, f is initially set to 1 for all synapses (no depression). More sophisticated models of synaptic depression could also be used (e.g. [1]), but the simpler model described above suffices for the purposes of this study.

The novel component of our model is the interaction between short-term depression and STDP. We assume that STDP modifies not only the peak synaptic conductance g_{peak}^{syn} but also the depression parameter f^{syn} as follows:

$$\Delta g_{peak}^{syn} = \beta \mathbf{w}^{\mathrm{T}} \mathbf{s}^{syn} \tag{2}$$

$$\Delta f^{syn} = -\gamma \mathbf{w}^{\mathrm{T}} \mathbf{s}^{syn} \tag{3}$$

where $\mathbf{w}$ is the vector representing the temporally-asymmetric learning win-
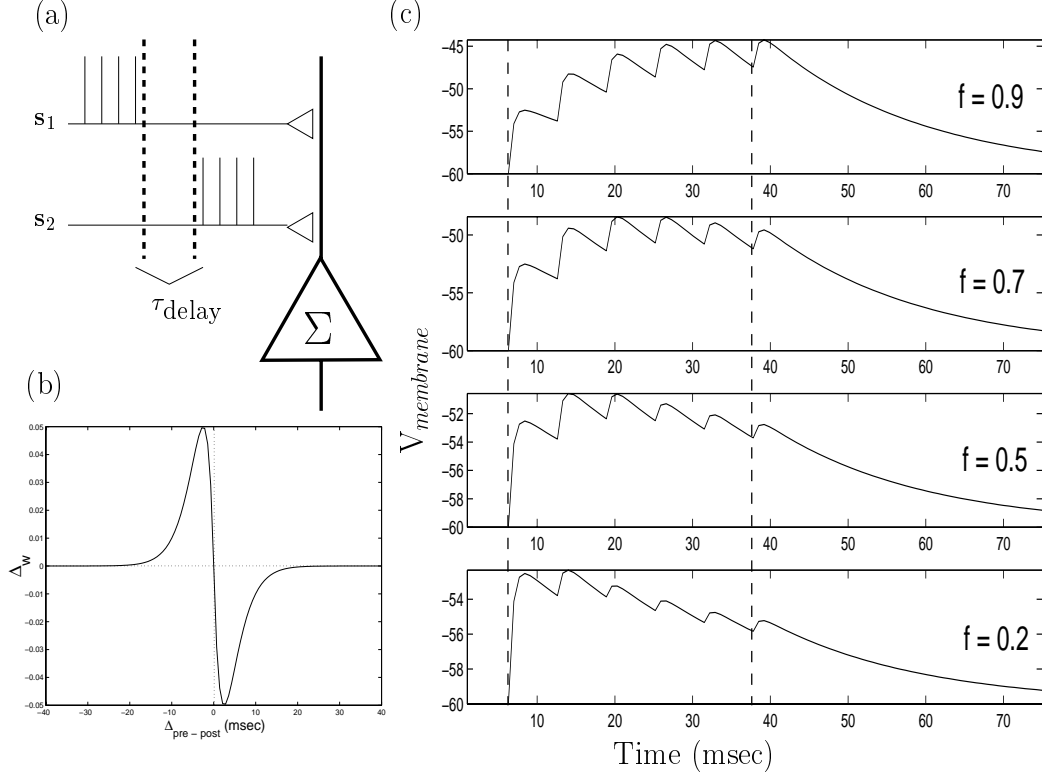
Fig. 1. **Learning Paradigm and Redistribution of Synaptic Efficacy in the Model:** (a) A single neuron receives 2 or more spike trains spaced some time τ_{delay} apart. The objective is to learn a specific temporal pattern of spike trains. (b) A temporally asymmetric learning window updates both the peak conductance g_{peak} and the depression parameter f for each synapse according to the relative timing of pre- and postsynaptic spikes. (c) The four plots depict postsynaptic responses in the model to a fixed input spike train as a function of the depression parameter f ($= f^{syn}$ in the text). Decreasing f causes the synapse to respond much more strongly to earlier presynaptic events. Note also the gradual decrease in the overall magnitude of the responses, which is compensated for during learning by increases in g_{peak} (see Equation 2). This compensatory effect enhances stability and implements a redistribution of synaptic efficacy.

dow (Fig. 1 (b), based on [3,4]), $\mathbf{s}^{syn}$ is the vector of presynaptic spikes to synapse syn, and β and γ are gain factors (for our simulations, we used $\beta = 0.052$ and $\gamma = 0.26$). Thus, updates to g_{peak} and f are assumed to be of complementary signs, so that an increase in synaptic depression is compensated for by an increase in peak conductance. It is precisely this compensation that causes redistribution of synaptic efficacy in the model (see Fig. 1 (c)).

To study the role of STDP and short-term depression in learning temporal patterns, we considered the simple case of a single integrate-and-fire neuron with two synapses. The goal was to investigate whether the neuron could learn to become selective for a specific input pattern by adapting its dynamic synapses. At the onset of each trial, one of the synapses received a train of in-

put spikes (Fig. 1 (a)) at a fixed rate r_1. After a delay τ_{delay}, the other synapse received a train of input spikes also at a rate r_2. Each spike train lasted for a specific duration (35 msec in the simulations). The model is parameterized with resting potential V_{rest} = -60 mV and threshold $V_{threshold}$ = -40 mV. Peak conductance of each synapse before training was $g_{peak} = 0.07$ nS, with a maximum peak conductance $g_{max} = 0.2$ nS. We trained the neuron by stimulating it using input spike trains as described above for 100 trials (each lasting 210 msec), sufficient to allow synaptic parameters to converge. The specific input parameters used were: $r_1 = r_2 = 150$ Hz with $\tau_{delay} = 15$ msec.

3 Results

Our first set of simulation results demonstrate how the combination of STDP with short-term plasticity can reproduce the experimental results on redistribution of synaptic efficacy. Recall that pairing a presynaptic spike with a postsynaptic spike that occurs a few milliseconds later causes a decrease in f^{syn} in our model (Equation 3). Fig. 1 (c) shows the effect of decreasing f^{syn} on the postsynaptic responses to a fixed input spike train. Decreasing f^{syn} causes the synapse to respond much more strongly to earlier presynaptic events than to subsequent events in a spike train, moving the peak response to closer to the onset of the input spike train. This is accompanied by a gradual decrease in the overall magnitude of the responses, which is compensated for during learning by increases in g_{peak} (see Equation 2). This compensation stabilizes the learning process and captures the synaptic behavior seen in experiments on redistribution of synaptic efficacy.

Our second set of simulation results demonstrate that single neurons using short-term depression and STDP are capable of learning temporal input patterns. Fig. 2 (a) shows how a neuron that is stimulated by two spatiotemporally-separated input spike trains (as described in the Methods section) can redistribute its synaptic efficacies to recognize and fire in response to the temporal order of the input spike trains. Note that the neuron's output is also predictive, in the sense that it learns to fire soon after the onset of the second spike train before receiving the spike train in its entirety.

Fig. 2 (c)-(f) contrast the adjustment of both f and g_{peak} with adjustment of g_{peak} alone. Again, the neuron whose synapses use short-term depression (Fig. 2 (c),(d)) learns to recognize the input sequence. More importantly, the neuron does not respond to a different ordering of the inputs. By contrast, a neuron that modifies its g_{peak} values over time, but not its f values (which remain fixed at $f = 1$) repeatedly spikes on both the training sequence and on a different ordering of the sequence (Fig. 2(e),(f)).

This example illustrates how redistribution of synaptic efficacy allows a neuron to become selective for specific input patterns by introducing an asymmetry in synaptic excitation over time. In turn, this asymmetry leads to temporal
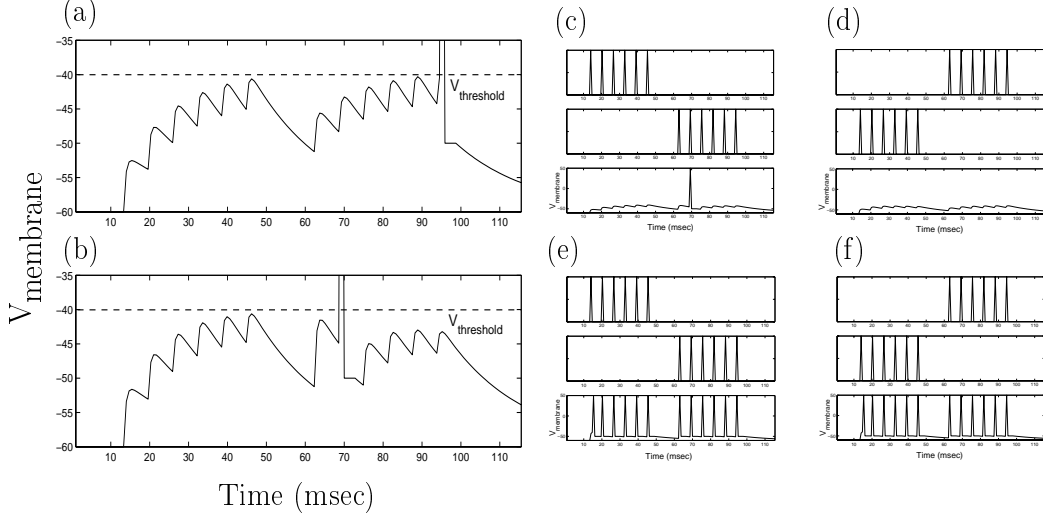
Fig. 2. **Learning Temporal Patterns using Redistribution of Synaptic Efficacy:** (a) Before training, the neuron responds to the sequence by emitting a single spike near the end of the sequence. (b) After training, the neuron still encodes the sequence using a single spike, but the spike is now generated earlier in time, soon after onset of the second spike train. (c) A model neuron that adjusts both the depression parameter f and peak conductance g_{peak} using STDP spikes when presented with a temporal sequence used in training. (d) The same neuron does not fire when presented with a sequence that reverses the order of inputs in the training sequence. Note that the firing rate remains the same and only the temporal order is changed. (e,f) A model neuron that only adjusts peak conductance g_{peak} (as in traditional models) responds vigorously and indiscriminately to both the training sequence as well as the reverse-order sequence.

selectivity: the neuron will fire only if the input spike trains generate a set of appropriately aligned EPSPs (according to the learned f and g_{peak} values) that push the membrane potential above spiking threshold.

4 Conclusion

Our simulation results suggest a computational role for STDP and short-term depression in making cortical neurons selective for specific spatiotemporal stimuli. For example, in the case of moving visual stimuli, our model predicts the development of direction selectivity (Fig. 2 (c),(d)), an important property of neurons in the visual cortex (see also [14]). The question of how our neuron-level model of temporal pattern learning fits into network-level models of sequence learning [7,9,15] remains a subject of ongoing investigations.

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