The Relationship Between Spike-Timing-Dependent Plasticity (STDP) and Sliding Threshold (BCM) Synaptic Modification

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We demonstrate that BCM learning rule follows directly from STDP when 1) pre- and post-synaptic spike trains are generated by independent random processes, and 2) only nearest-neighbor spike interactions are taken into account.

There has been an increased interest in a novel type of synaptic plasticity - *spike-timing-dependent plasticity* (STDP), in which potentiation or depression occurs depending on the temporal order of the pre and postsynaptic spikes; see Fig. 1a. However, it is not clear how STDP relates to the best studied form of synaptic plasticity – classical LTP and LTD. The two kinds of plasticity must be somehow related, since it is believed that they are based on the same biophysical mechanism. Here we consider different implementations of STDP and compare them with a standard LTP/LTD implementation called the Cooper or BCM (Bienenstock-Cooper-Munro) synapse. In the BCM formulation, one considers instantaneous firing rates rather than individual spikes. Synaptic input that drives postsynaptic firing to high levels results in an increase in synaptic strength, whereas input that produces only low levels of postsynaptic firing results in a decrease (Fig. 1b). The threshold firing rate, the crossover point between potentiation and depression, is itself a slow function of postsynaptic activity, moving so as to make potentiation more likely when average activity is low and less likely when it is high. Considerable experimental evidence for this kind of plasticity has been obtained in neocortex, at some of the same synapses at which evidence for STDP

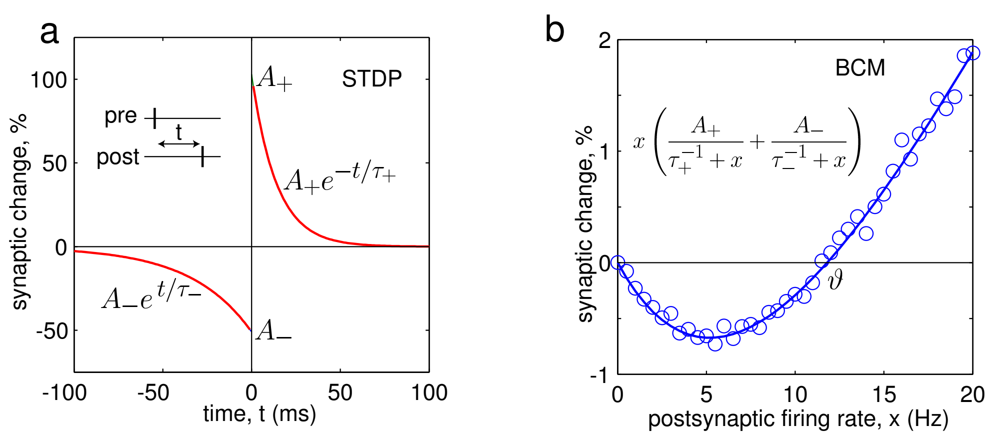

Figure 1: a. The STDP curve. b. The resulting BCM function; circles denote numerical simulation of STDP with 100,000 Poisson spikes.

has also been obtained. Even so, it is not obvious how the BCM plasticity and STDP are related or even if they are compatible. Consider, as an illustration, the extreme case in which all spikes of the postsynaptic neuron occur after those of the presynaptic one. This will always result in potentiation by an STDP rule, but could result in either depression or potentiation by the BCM rule, depending on exact value of the postsynaptic firing rate. Below we compare the two kinds of plasticity more closely, in a more biologically-realistic regime, that of uncorrelated or weakly correlated presynaptic and postsynaptic neurons that fire in a nearly Poisson manner.

When the postsynaptic spike train is a Poisson process with firing rate x, then the postsynaptic probability density, i.e., the probability to observe a spike with certain delay, becomes exponential, $xe^{\pm xt}$. Because of the shape of the STDP curve, high (low) firing rate x results in predominately small (large) intervals and hence in facilitation (depression). The expected magnitude of synaptic modification per 1 presynaptic spike has the form

$$\begin{aligned} C(x) &= \overbrace{\int_0^\infty A_+ \, e^{-t/\tau_+} \, xe^{-xt} \, dt}^{\text{average potentiation}} + \overbrace{\int_{-\infty}^0 A_- \, e^{t/\tau_-} \, xe^{xt} \, dt}^{\text{average depression}} \\ &= x \left(\frac{A_+}{\tau_+^{-1} + x} + \frac{A_-}{\tau_-^{-1} + x} \right) \end{aligned} \tag{1}$$

depicted in Fig. 1b. Apparently, it coincides with the Cooper synapse in the sense that low activity results in depression and large activity results in potentiation.

The parameters of STDP can be related to the biophysical processes underlying plasticity. In particular, τ_+ depends on the kinetics of NMDA receptors, which in turn depend on their subunit composition. It has been shown by Mark Bear and colleagues that a low level of postsynaptic activity due to light deprivation increases the ratio of NR2B to NR2A subunits, which in turn increases the time constant of NMDA receptors by up to 20%. As one can check, increasing τ_+ by as little as 10% results in sliding the threshold of BCM by a factor of two, which is in agreement with Kirkwood and Bear's experimental data.

Using a handful of reasonable assumptions we have generated a simple equation that links the parameters of STDP to the BCM formulation of LTP/LTD, and thereby built a more intuitive picture of how these forms of plasticity are related.

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