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# Analyzing spike-timing-dependent plasticity in recurrent neuronal networks

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*A mathematical framework is being used to investigate the learning dynamics induced by a class of biologically realistic synaptic plasticity rules in recurrently connected neuronal networks.*

Computational tasks, such as object recognition and sound localization, rely on specific, highly organized neuronal structures in the brain. A representation of this kind of network organization is the neuronal map, where neighboring neurons are sensitive to external stimuli that possess some similarity.[1,2] To achieve this, the pairwise connections between neurons, called synapses, form a specific architecture. This underlying synaptic circuitry is not in place at birth, but is acquired during the first years of life. The development of synaptic connectivity relies on both neurogenerative mechanisms (e.g. creation of synapses) and activity-dependent plasticity that strengthens or weakens existing synapses.[3] Here we focus on the latter type of plasticity model, which may also be applied to represent external stimuli in a short-term memory context.[4]

In recent papers, we have examined how synaptic plasticity can generate network structure among recurrently connected neurons stimulated by external (input) spike trains.[5] Our model focuses on an abstract and generic network topology with plastic connections that are trained over a single learning epoch. Our motivation is to understand how a plasticity model, which accounts for some important features observed in physiology for a single synapse, works in networks of neurons.

Recent experiments with glutamatergic synapses showed that changes in their strength due to pre- and postsynaptic activity crucially depends upon spike-timing at the scale of milliseconds.[6–8] Such spike-timing-dependent plasticity (STDP) has been demonstrated to have important theoretical implications in capturing short-time information within spike trains.[9,10] Over ten years after the proposition of the first model, many refinements of STDP have been studied both experimentally and theoretically.[11] However, a lack of analytical results in *recurrent* neuronal architectures persisted until recently, even for the 'original' STDP model.

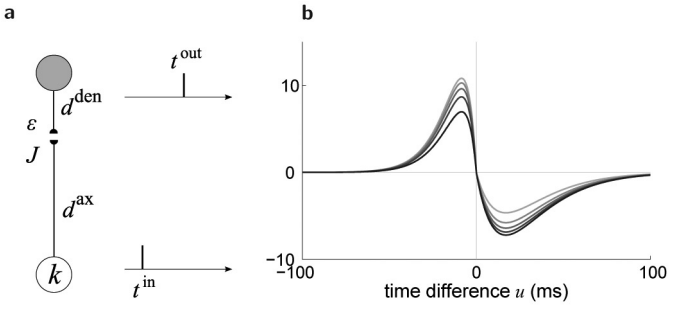


***Figure 1.*** *Single synaptic connection equipped with weight-dependent spike-timing-dependent plasticity (STDP). (a) Detail of a synapse described by its weight strength J, post-synaptic response kernel $\epsilon$, and axonal and dendritic delays $d^{\text{den}}$ and $d^{\text{ax}}$, respectively. The right arrows represent the pre- and post-synaptic spike trains with one spike each at respective times $t^{\text{in}}$ and $t^{\text{out}}$. (b) Example of typical weight-dependent STDP learning window W(J,u). The variable u is the spike-time difference at the synaptic site: $u = t^{\text{in}} + d^{\text{ax}} - t^{\text{out}} - d^{\text{den}}$. When a presynaptic spike arrives sufficiently early with respect to the postsynaptic spike such that $u \leq 0$, the synapse is strengthened; otherwise, it is weakened. Darker lines indicate stronger values for J, which implies less potentiation and more depression. This occurs when using weight-dependent STDP.*

We have developed a mathematical framework with the aim of obtaining insight into the learning dynamics of recurrently connected neurons. Our model focuses on two main physiological observations, as described in Figure 1(b): the dependence both on the timing of pairs of pre- and postsynaptic spikes, and on the current value of the synaptic strength.[7] The Poisson neuron model is used to describe the effects of the synaptic parameters in Figure 1(a), since it allows us to carry out mathematical analysis of the learning dynamics.[10,12] Functional

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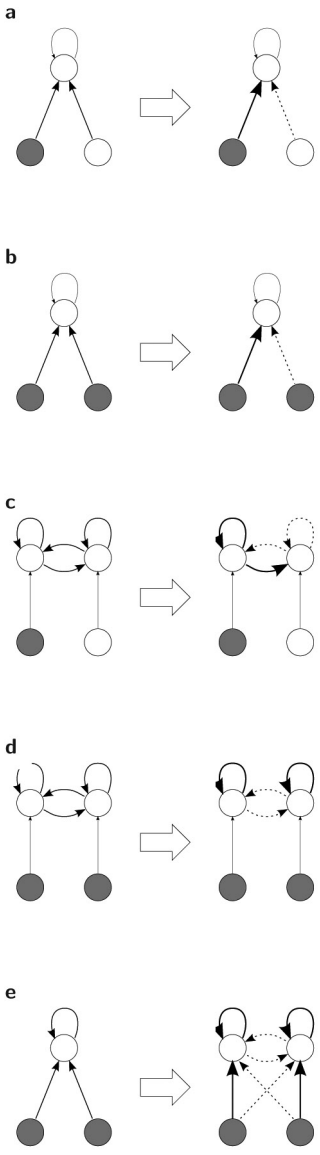


***Figure 2.*** *Desirable self-organization schemes for a network (top circles) stimulated by two correlated pools of external inputs (bottom circles). The diagrams represent the connectivity before and after learning (indicated by the block arrows). For initial configurations, thin arrows represent fixed connections while thick arrows denote plastic connections. After learning, very thick (resp. dashed) arrows indicate potentiated (depressed) weights. Configurations in (a), (b), (c & d) and (e) correspond to the first, second, fourth and fifth papers in the series,*[5] *respectively.*

pathways are represented by input pools of spike trains that exhibit narrow temporal correlations, although our framework is suited to incorporate arbitrary input configurations. In practice, we use stochastically generated input spike trains that have fixed firing rates and spike-time cross-correlations. The key to predicting the weight evolution lies in describing how the recurrent connectivity constrains the neuronal activity (firing rates and correlations) and, consequently, the learning dynamics.

In a recurrently connected neuronal network, the weight evolution is determined by an interplay between the STDP parameters, neuronal properties, input correlation structure, and network topology. The degree of competition between individual weights can be tuned using weight-dependent STDP.[5, 13] Typically, the strong synapses experience less potentiation and more depression than weak synapses, cf. Figure 1(b). Such a weight dependence also shapes the asymptotic distribution of the weights after a learning epoch, which can result in unimodal or bimodal weight distributions.[5, 13, 14] Our results show how STDP can represent the structure of the input spike-time correlations in the weight structure of the network, as illustrated in Figure 2. In each situation, correlated pathways (filled bottom circles) are represented in the emerging reinforced connectivity. In configuration (b), only one of the two identical pools wins the competition, each with 50% probability. Inconfiguration (e), the initially homogeneous network (top circle) splits into two groups, each specialized to one of the two similar input pathways. Our series of papers describe conditions on the postsynaptic response (involving synaptic delays) and STDP learning window required to obtain the 'desirable' weight evolution for recurrent connections presented in (c–e). These self-organization schemes can be seen as basic dynamical ingredients for the emergence of neuronal maps in more elaborate network architectures.[1]

In summary, STDP naturally generates rich learning dynamics, namely a mixture of stability for the output neuronal firing rate and competition between individual incoming weights. STDP can reproduce weight specialization schemes obtained with elaborate rate-based plasticity rules that rely on rate correlations, implying slower time scales.[15, 16] STDP has led to a re-evaluation of our understanding of Hebbian learning,[17] in particular by discriminating between rate-based and spike-based contributions to synaptic plasticity for which temporal causality plays a crucial role. It is not yet clear, however, how rich the class of stimuli signals is that STDP can process. Similarly, the unsupervised learning algorithm performed by STDP through the weight dynamics is still only partially understood. Our future research aims to establish links between such physiological learning mechanisms and the more abstract

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domain of machine learning, thereby expanding our understanding of the functional role of synaptic plasticity in the brain.

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