3 Spike-Timing Dependent Plasticity (STDP)

3.1 STDP

(Video 3.1) Now we shall implement some long-term plasticity. Spike-Timing dependent Plasticity (STDP) is a type of neuronal activity-dependent synaptic plasticity, in which the strength of a synapse increases or decreases depending on the time difference between a spike from the presynaptic and a spike from the postsynaptic neuron (from now on we refer to these spikes as pre-spikes and post-spikes, respectively). While different subtypes of STDP can be found in the literature [1], the most widely observed and discussed variety is "Hebbian" or asymmetric STDP, which entails long-term potentiation (LTP) after a pre-post spike pair, and long-term depression (LTD) of the synaptic weight after a post-pre spike pair. Excitatory synapses in the hippocampus and cortex are subject to LTP and LTD via Hebbian STDP [2,3].

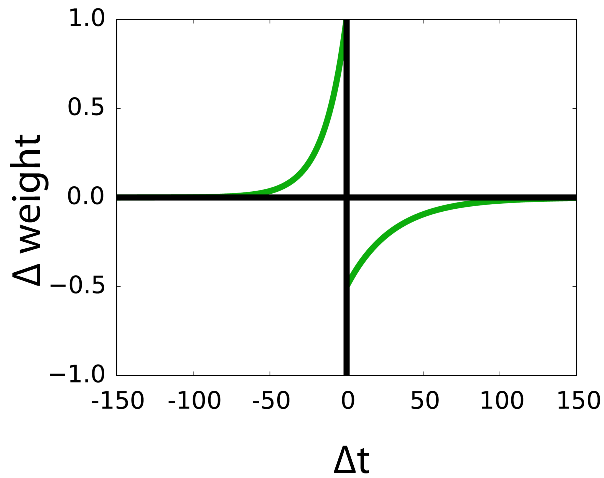

Figure 1: The STDP "window". Left curve, LTP. Right curve, LTD. The value Δt here is the time difference pre-spike - post-spike. When reading literature, keep in mind that some authors switch the sign of Δt.

The dependence on the difference in spike timing can be modeled by an exponentially decaying shape (Fig. 1). The change in the excitatory synaptic strength (weight) w_e therefore obeys:

$$\Delta w_\mathrm{e} = \begin{cases} A_\mathrm{LTP} \exp(\frac{\Delta t}{\tau_\mathrm{LTP}}) & \forall \Delta t < 0 \\ A_\mathrm{LTD} \exp(-\frac{\Delta t}{\tau_\mathrm{LTD}}) & \forall \Delta t > 0 \\ 0 & \forall \Delta t = 0 \end{cases} \tag{1}$$

Fig. 1 uses τ_LTP = 17 ms, A_LTP = 1.0, τ_LTD = 34 ms, and A_LTD = - 0.5. These values, leading to a perfect compensation of LTP by LTD in terms of window area, are frequently used, though other values are possible. There are two major ways to numerically implement STDP in models: all-to-all and nearest-neighbour. The names refer to whether every pre-spike is matched to every post-spike, or only neighbouring spikes are matched, for example a pre-spike is matched to the closest post-spikes only. In this course, use the nearest-neighbour implementation of STDP. This means that only the spike time difference between a pre-spike and its closest post-spike (and vice-versa) is implemented. You can do this using a buffer variable that stores the time of the last spike.

Using the single LIF neuron model from unit 1.4 (without refractory period or SRA), leave out the inhibitory inputs for simplicity, or set their synaptic weight to zero. Reduce the number of excitatory inputs to only 2 and apply the STDP rule, as shown in the figure and the equations above, in these two synapses. Importantly, set A_{LTP} to 0.05 and A_{LTD} to -0.025, such that the change in weight is slow enough for us to see the evolution of the weights. Note also that if the initial weight in combination with the input firing rate and the number of inputs is too weak, there will be no post-spikes. Without post-spikes, STDP is not activated and the weight will remain unchanged, so in this model the syanptic drive must be strong from the start of the simulation to see any effect of STDP. Here, use an initial value of w_{e} 1 for each synapse, and apply two Poisson inputs with firing rate 5 Hz. Plot the value of the weight changing over time.

You should now see that the weights are growing in an unlimited fashion. As a result of the growing weight, the postsynaptic neuron will demonstrate an increasing firing rate. This problem is dealt with in later units, for now just put a maximum weight value $w_{\mathrm{max}} = 6$, above which the weight cannot increase. Uncontrolled growth of synaptic weights is a property of pure additive STDP models in excitatory synapses: since the pre-post spike combination is related to potentiation, STDP rewards causality in the case of an excitatory synapse. The increased excitatory weight then enhances the probability that the pre-spike causes a post-spike, and hence a positive feedback loop is created. Therefore, the weight will mostly undergo LTP and little LTD, despite the integral of the STDP window being 0. Possible mechanisms that the brain employs to limit this positive feedback have been frequently addressed in the last decade in modeling studies concerned with STDP.

Now add another Poisson input with an excitatory synapse with STDP, and set the firing rate of this input to be higher, 8 Hz. You now have two inputs with STDP, one with a higher and one with a lower firing rate (5 and 8 Hz). What do you see in the weights? If it works well, the weight from the 8 Hz input should "win the race".

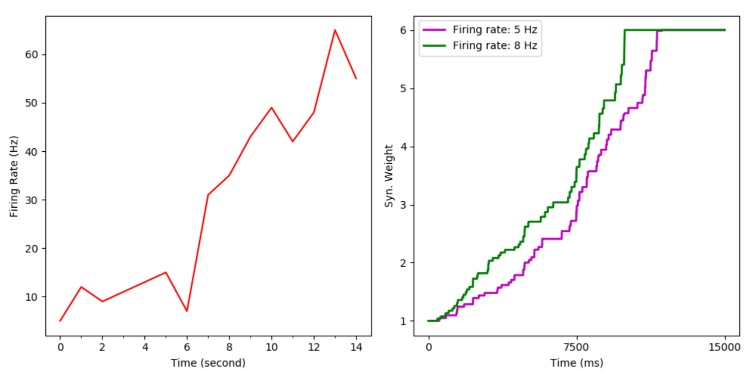

Figure 2: A LIF neuron with Poisson inputs and STDP in two excitatory input synapses with different firing rates (5 and 8 Hz). Left: The neuron is getting increasingly depolarised over time, resulting in more and more output spikes. Right: The cause of the increase in spiking is the growth in excitatory synaptic weights. Importantly, the synaptic weight of the strongly firing input (8 Hz) increases faster than that of the more weakly firing input (5 Hz).

References

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2. G. Q. Bi and M. M. Poo, "Synaptic modifications in cultured hippocampal neurons: dependence on spike timing, synaptic strength, and postsynaptic cell type.," *The Journal of neuroscience : the official journal of the Society for Neuroscience*, vol. 18, pp. 10464–72, dec 1998.

3. L. J. F. M. Markram, H and B. Sakmann, "Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs," *Science*, vol. 275, pp. 213–215, 1997.