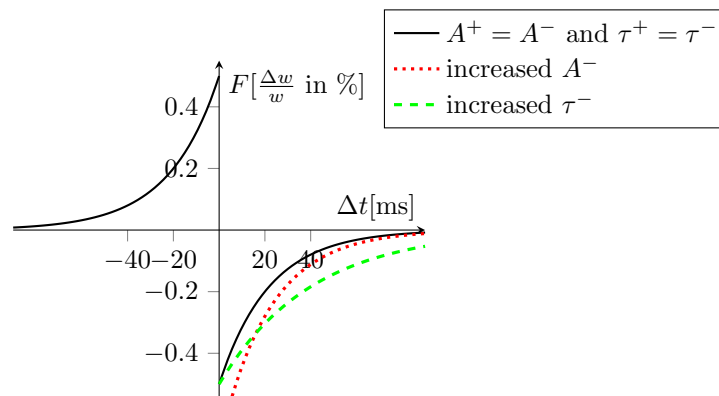


Solution 9.1: Spike timing dependent plasticity

1. If you only strengthen the synaptic weights, they will have very large values over time even if the neurons involved do not fire correlated. It is therefore also necessary to have mechanisms to decrease the synaptic weight.
2. The function $F(\Delta t)$ approaches the y -axis from the left (where $\Delta t \rightarrow 0$) at 0.5%. Since $\lim_{\Delta t \rightarrow 0} \exp(\Delta t / \tau^+) = 1$, we can conclude that $A^+ = 0.5\%$. It remains to estimate τ^+ . For that, we observe that $F(-20) = 0.2\%$ and fill in the values in the definition of $F(\Delta t)$ to obtain $0.2 = 0.5 \exp(-20\text{ms}/\tau^+)$. Rearranging shows $\tau^+ = -20\text{ms} / \ln(0.2/0.5) = 21.8\text{ms}$.
3. Increasing A^- or τ^- achieves the desired effect. In both cases, the area under the right part of the curve is bigger than on the left part (the integral of $F(\Delta t)$).



4.
 - In the ‘regular firing mode’ with strong excitation, if there are many inputs firing frequently, the post-synaptic neuron will have no chance to react to individual inputs – it is already operating with its maximal firing rate, which is limited by the time needed for the neuron to recover from the last spike (refractory period). The resulting timing of the spikes of the post-synaptic neuron does not have any particular correlation to any of its inputs anymore. As a result, there are roughly equal numbers of presynaptic action potentials before and after each postsynaptic spike. Thus, we have a uniform distribution of the Δt ’s. If the synaptic weight should decrease in such a situation, the integral of $F(\Delta t)$ has to be negative, exactly as in question 3 above.
 - In the ‘balanced mode’, there is a causality between the firing of the post-synaptic neuron and the input activity. Because action potentials occur preferentially after a random fluctuation, there tend to be more excitatory presynaptic spikes before than after a postsynaptic response. We would expect to see many negative Δt ’s, thus increasing the synaptic weight.
 - Such a synapse is regulating the mean output activity of the post-synaptic neuron. If it is firing too often, the synaptic weights get decreased; if it is firing only rarely, the synaptic weights get increased. As stated by Song *et al.* (2000), Nat Neurosci: “The STDP rule achieves a steady-state distribution of peak synaptic conductances when the excess of presynaptic action potentials before postsynaptic firing compensates for the asymmetry in areas under the positive and negative portions of the STDP modification curve.”

Solution 9.2: Predictive Coding with STDP

1. The synapse S1 will be strengthened, since N2 fires shortly after N1. On the other hand, S2 will be weakened.

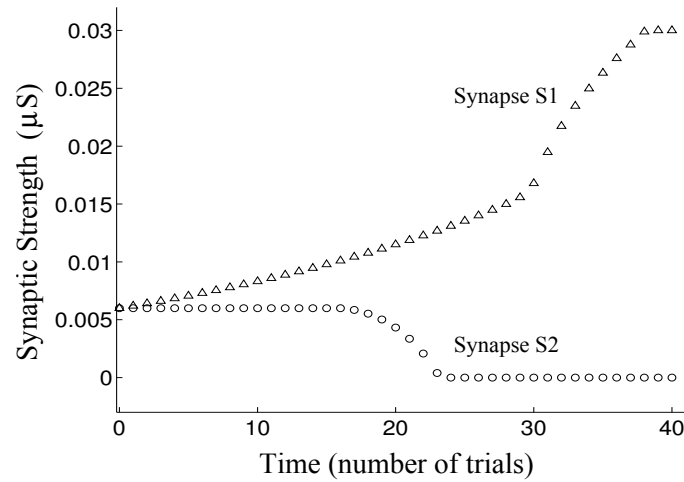


Figure 1: Time course of the maximal synaptic conductance of S1 and S2; taken from Rajesh P. N. Rao and Terrence J. Sejnowski (2001), Spike-Timing-Dependent Hebbian Plasticity as Temporal Difference Learning, *Neural Computation*; 13, 2221-2237.

2. In the beginning, I2 fires before N2 and therefore causes N2 to fire. After the learning, however, S1 is strong enough to excite N2 which in turn inhibits I2. The input 2 can not cause I2 to fire anymore.
3. Without the inhibitory connections, N2 would fire twice: Once because it is stimulated by N1, and a second time for the actual input 2.
4. Both S1 and S2 would get strengthened. This renders the learning of causality impossible, since now an occurrence of input 2 can also excite N1. Further, as pointed out in the previous exercise, the synapses would lose their ability to regulate the mean firing rate of the post-synaptic neurons. The whole system might get unstable and excite itself in an infinite loop.