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Lecture 9
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Exercise 9.1: Spike timing dependent plasticity

It is experimentally observed that the relative timing of pre-and post-synaptic action potentials can change the synaptic efficacy. Within a time window of 50ms, presynaptic spikes that precede postsynaptic action potentials produce LTP (strengthening of the synapse), whereas presynaptic spikes that follow postsynaptic APs produce LTD (weakening of the synapse).

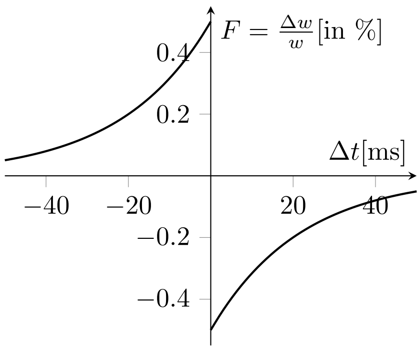

Figure 1: Spike-timing-dependent plasticity (STDP) modification function for a particular synapse, after Song *et al.* (2000).

1. Why is it important – for any learning rule – to have mechanisms for both the strengthening and the weakening of the synaptic weight?

2. Fig. 1 shows the spike-timing-dependent plasticity (STDP) modification function for a particular synapse. $F(\Delta t)$ is the amount of synaptic weight modification observed after a pair of pre- and postsynaptic spikes, as function of $\Delta t = t_{pre} - t_{post}$.

$$F(\Delta t) = \begin{cases} A^+ \exp(\Delta t/\tau^+) & \text{if } \Delta t < 0 \\ -A^- \exp(-\Delta t/\tau^-) & \text{if } \Delta t \geqslant 0 \end{cases}$$

   Estimate the value of the parameters A^+ and τ^+ for the function $F(\Delta t)$ of fig. 1.

3. If two neurons fire completely independently, there is on average as many occurrences where the first one spikes just before the second one does, as there are cases where the opposite happens. Nevertheless, a synapse between two such neurons should be weakened, which will only happen if the integral of the function F is negative, *i.e.* if $A^+\tau^+ < A^-\tau^-$. Draw a weight update function (similar to fig. 1) that ensures that uncorrelated pre- and postsynaptic spikes produce an overall weakening of the synapse.

4. Now consider how a STDP synapse will behave in two different operational regimes of the postsynaptic neuron (‘regular firing mode’, ‘balanced mode’).

   - When excitation is strong so that the mean input to the neuron would bring it well above threshold, the neuron operates in an input-averaging or regular-firing mode. Its firing rate is approximately the inverse of its refractory period. Hence, the precise timing of its individual action potentials is driven by internal dynamics and fairly insensitive to presynaptic spike times (independent of fluctuations in the input).

     On a plot like the given one, where the x-axis describes the time difference Δt between pre- and post-synaptic firing, how are the spikes of a neuron in this regime distributed?

     Given this distribution, what is the requirement on the STDP modification function that guarantees that a synapse will be weakened in this situation?

- When the excitatory synapses are weakened by STDP, the postsynaptic neuron enters a balanced mode of operation in which it generates a more irregular sequence of action potentials that are more tightly correlated with the presynaptic spikes that evoke them. The total synaptic input in the balanced mode is, on average, near or below threshold, so the postsynaptic neuron fires irregularly, primarily in response to statistical fluctuations in the total input.

  On a plot like the given one, where the x-axis describes the time difference Δt between pre- and post-synaptic firing, how are the spikes of a neuron in this regime distributed?
- Is it possible to draw an STDP modification function for which synapses in the first regime are weakened, but synapses in the second regime are strengthened?

  Why would such a learning rule be useful?

Exercise 9.2: Predictive Coding with STDP

In the model neural network in Figure. 2, there are two neurons N1 and N2 that are recurrently connected to each other via excitatory synapses S1 and S2. Neurons I1 and I2 are sensory neurons (here, I stands for input) that immediately fire a single spike after detecting Input 1 or Input 2 respectively. I1 is connected to N1 via a strong excitatory synapse that causes N1 to fire immediately after I1. Similarly, I2 drives neuron N2. N1 and N2 are connected via inhibitory interneurons (red) back to I1 and I2, respectively. These indirect inhibitory connections are strong enough to prevent firing in I1 or I2. We assume that synapses S1 and S2 are plastic and learn according to a standard STDP model (see fig. 1), whereby postsynaptic firing shortly after presynaptic firing causes potentiation, and postsynaptic firing shortly before presynaptic firing causes synaptic depression. S1 and S2 are initially not strong enough to cause postsynaptic spikes on their own. We assume that all other synapses do not change.

Assume that the network is stimulated repeatedly by an input sequence in which first only Input 1 is present, followed by Input 2 after a short 5 ms delay. The time between each presentation of the sequence is long enough to not influence plasticity.

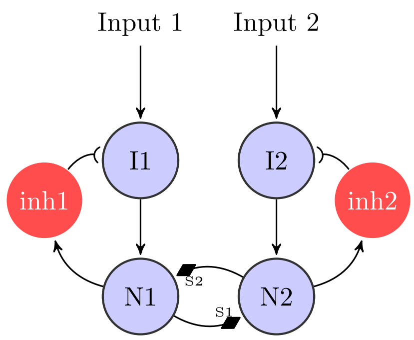

Figure 2: Schematic of a neural network circuit. Each circle represent excitatory (blue/black) and inhibitory (red/white) neurons. The excitatory synapses are represented by arrow heads, inhibitory synapses by parentheses and plastic synapses by diamonds.

1. What effects do you expect at synapses S1 and S2 due to STDP, and why? Plot the approximate development of the synaptic strengths as a function of time.
2. Explain how the spiking pattern of N2 and I2 in response to the stimulus sequence changes over time? How does the network react after learning, if only Input 1, but not Input 2 is presented for a single trial?
3. How would the network after learning react, if the inhibitory connections were removed?
4. Assume that instead of STDP a temporally symmetric (Hebbian) learning rule was used, which potentiates synapses whenever the pre- and postsynaptic neuron fire together within a short time interval (e.g. 10 ms), regardless of the order in which the spikes arrive. What problem would you expect to arise in such a network?