9.641 Neural Networks
Problem Set 1

(Due Feb. 10, Thursday before class)

The **integrate-and-fire neuron** is a simple model of spiking behavior that sacrifices biophysical realism for mathematical simplicity.

1. Single neuron model

   First, let's consider an isolated neuron into which we inject a current I_{app}. Below threshold, the membrane potential V obeys the differential equation

   $$C\frac{dV}{dt} = -g_L(V - V_L) + I_{app} \tag{1}$$

   If V reaches a threshold V_θ, then the neuron is said to spike, and V is instantaneously reset to a value of V_0, where $V_0 < V_\theta$.

   (a) Analytically determine the threshold current I_θ (or rheobase) below which the neuron is inactive, and above which the neuron fires repetitively. The sign of I_θ should depend on whether V_θ is above or below V_L.

   (b) Experimentally determine I_θ and compare it to the value you found analytically. In MATLAB, a system $\frac{dy}{dt} = f(y)$ can be simulated by choosing the initial conditions $y(1)$ and then repeatedly performing the Euler integration step $y(t+1) = y(t) + dt\frac{dy}{dt}(t)$.
   Use the following values for your simulations: $V_L = -74mV$, $g_L = 25nS$, $V_\theta = -54mV$, $V_0 = -60mV$, $C = 500pF$. Plot a trace of the membrane potential V, one for I right below and one for I right above I_θ.

   (c) If I_{app} is held constant in time above threshold, the neuron fires action potentials repetitively, as you should have observed in your simulations. Find the relationship between the frequency of firing f and I_{app}.

   (d) Show that f behaves roughly linearly for large I_{app} and can be approximated by

   $$f \approx \frac{\left[I_{app} - g_L(V_{1/2} - V_L)\right]^+}{C(V_\theta - V_0)} \tag{2}$$

   with $V_{1/2} = (V_\theta + V_0)/2$. Explain in words the reason for this linearity. [*Hint:* Use the Taylor series expansion $[log(1+z)]^{-1} \approx 1/z + 1/2$.]
   Plot your results from (c) and (d) together and compare them.

2. Modeling synapses

   A synapse is modeled by a variable conductance g in the postsynaptic neuron. A spike in the presynaptic neuron causes an increase of the conductance according to $g := g + \frac{\alpha}{\tau}$. Between spikes, g decays exponentially: $\frac{dg}{dt} = -\frac{g}{\tau}$. So a synapse is a leaky integrator, counting spikes but forgetting them over time periods longer than τ. The area under the exponential caused by a single spike is given by the parameter α.

Under certain conditions this can be approximated by $\tau \frac{dx}{dt} + x \approx f$, where x is proportional to g and f is the frequency of incoming spikes.

Simulate the time course of the conductance of a synapse for $f = 25\text{Hz}$ for different τ. For what values of τ is this approximation valid? Illustrate your answer with two plots.

3. From synapses to current

   In practice, neurons are a part of networks and receive input currents through synapses instead of an electrode. For a neuron i receiving inputs from neurons j, this can be written as:

$$C_i \frac{dV_i}{dt} = -g_{Li}(V_i - V_L) - \sum_j g_{ij}(V_i - V_{ij}) \tag{3}$$

   Show that equation (3) can be simplified to the form of equation (1), describing a neuron with leak conductance g_L receiving an external current I_{app} if the synaptic conductances g_{ij} are changing slowly (meaning they are constant for a small interval dt). Determine I_{app} and g_L analytically in terms of g_{ij}, V_{ij}, V_L and g_{Li}.

4. From spikes to rates

   We are now ready to derive a nonspiking model of a neuron. To do that, we will assume that all neurons have the same membrane capacitance C, the same time constant τ and that conductances are changing slowly (meaning they are constant for a small interval dt).

   Using the results of 1, 2 and 3, show that equation (1) can be approximated by

$$\tau \frac{dx_i}{dt} + x_i \approx f\left(b_i + \sum_j W_{ij} x_j\right) \tag{4}$$

   Starting with the approximation in (2), plug in the approximated f-I relationship from 1(d). Then, substitute I_{app} and g_L with the expressions you found in (3). Assuming all time constants are the same, all synapses emanating from a single neuron have the same temporal behavior, because they are driven by the same spike train, and decay at the same rate. This yields $x_j = \frac{g_{ij}}{\alpha_{ij}}$. Finally, identify b_i and W_{ij} in terms of α_{ij}, g_{Li}, V_L, $V_{1/2}$ and V_{ij}.