Introduction

This note is about the dynamics of a single neuron, it will cover one of the simplest such models: the leaky integrate and fire model.

Electrical properties of a neuron

The potential inside a neuron is lower than the potential on the outside; this difference is created by ion pumps, small molecular machines that use energy to pump ions across the membrane seperating the inside and outside of the cell. One typical ion pump is Na+/K+-ATPase (Sodium-potassium adenosine triphosphatase); this uses energy in the form of ATP, the energy carrying molecule in the body, and through each cycle it moves three sodium ions out of the cell and two potassium ions into the cell. Since both sodium and potassium ions have a charge of plus one, this leads to a net loss of one atomic charge to the inside of the cell lowering its potential. It also creates an excess of sodium outside the cell and an excess of potassium inside it. We will return to these chemical imbalances later. The potential difference across the membrane is called the **membrane potential**. At rest a typical value of the membrane potential is $E_L = -70$mV. It is useful to remember that the excessive sodium is outside the cell and potassium inside; I think of islands which are surrounded by salty water.

Spikes

So the summary version of what happens in neuons is that **synapses** cause a small increase or decrease in the voltage; **excitatory synapses** cause an increase, **inhibitory synapses** a decrease. This drives the internal voltage dynamics of the cell, these dynamics are what we will learn about here. If the voltage exceeds a threshold, say $V_T = -55$ mV there is a nonlinear cascade which produces a **spike** or **action potential**, a spike in voltage 1-2 ms wide which rises above 0 mV before, in the usual description, falling to a reset value of $V_R = -65$ mV, the cell then remains unable to produce another spike for a **refractory period** which may last about 5 ms. We will examine how spikes are formed later, this involves the nonlinear dynamics of ion channels in the membrane; first though we will consider the integrate and fire model which ignores the details of how spikes are produced and simplifies the voltage dynamics.

The bucket-like equation for neurons

We will now try to extend the bucket-like equation we looked at before so that it applies to neurons. First off we replace h, the height of the water, by V the voltage in the cell and C will be replaced by C_m, the capacitance of the membrane, the amount of electrical charge that can be stored at the membrane is C_mV. The amount of electrical charge is the analogue of the volume of water. Thus, voltage is like height, charge is like the amount of water.

The leak is a bit more complicated, because of the chemical gradients, that is the effects of the differing levels of ions inside and outside the cell along and their propensity to diffuse, the voltage at which there is no leaking of charge is not zero, it is $E_L = -70$mV, roughly. This is an important aspect of how neurons behave, and one we will encounter again looking at the Hodgkin-Huxley equation: you might at first expect that if the voltage inside the cell was, say, -60 mV then even if there was a high conductivity for potassium at the membrane, the potassium ions would stay in the cell: they are positive ions after all and so a negative voltage means the electrical force is attracting them to the inside of the cell. However, this isn't quite what happens, there is a high concentration of potassium inside the cell and because of the random motion of particles associated with temperature, these have a tendency to diffuse, that is to increase the entropy of the situation by spreading out. It takes a force to counteract this. This is the reversal potential, E_L, the voltage required for zero current even if there is some conductivity.

G is now G_m, a conductance, measuring the porousness of the membrane to the flow of ions. The leak current is $G_m(V - E_L)$, as above, we actually divide across by it, and write $R_m = 1/G_m$, the resistance. Finally, we write $\tau_m = C_m/G_m$ to get

$$\tau_m \frac{dV}{dt} = E_L - V + R_m I \tag{1}$$

I might end up being synaptic input, but traditionally we write the equation to match the *in vivo* experiment where I is an injected current from an electrode, so we write I_e, 'e' for electrode. tau_m is a time constant, using the notation of dimensional analysis we have $[\tau_m] = T$. To check this note that the units of capacitance are charge per voltage: $[C_m] = QV^{-1}$, the units of resistance is voltage per current $[R_m] = VI^1$ and current is charge per time, $[I] = QT^{-1}$ so $[C_m R_m] = T$, time.

The equation above leaves out the possibility that there are other non-linear changes in the currents through the membrane as V changes. This is a problem since there are other non-linear changes in the currents through the membrane as V changes. The equation above leaves these out, in fact, the nonlinear effects are strongest for values of V near where a spike is produced, so one approach is to use the linear equation unless V reaches a threshold value and then add a spike 'by hand'. This has the effect of changing the voltage to a reset value, this mimics what happens in the neuron, or in the Hodgkin Huxley model which we will look at next and which includes the full non-linear dynamics which makes the spike. Anyway, in summary

- V satisfies
$$\tau_m \frac{dV}{dt} = E_L - V + R_m I_e \tag{2}$$
- If $V \geq V_T$ a spike is recorded and the voltage is set to a reset value V_R.

The reset value, the voltage after the spike is often set equal to the leak potential. This is the **leaky integrate and fire model**, a surprisingly old model first introduced in [**?**]. It lacks lots of the details important in the dynamics of neurons, but is useful and often used for modeling the behavior of large neuronal networks or for exploring ideas about neuronal computation in a relatively straight-forward setting.

This model is easy to solve; if I_e is constant we have already solved it above up to messing around with constants:

$$V(t) = E_L + R_m I_e + [V(0) - E_L - R_m I_e]e^{-t/\tau_m} \tag{3}$$

If I_e is not constant it may still be possible to solve the equation, but in any case the equation can be solved numerically on a computer. An example in given in Fig. **??**.

One thing to notice is that there are no spikes for low values of the current. Looking at the equation

$$\tau_m \frac{dV}{dt} = E_L - V + R_m I_e \tag{4}$$

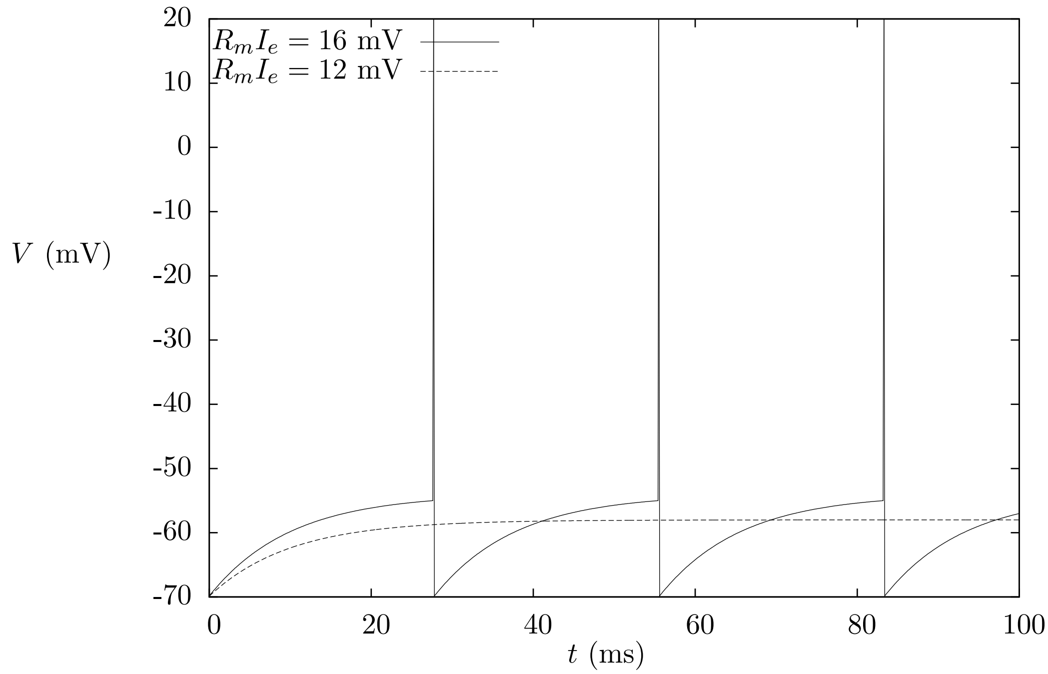

Figure 1: An integrate and fire neuron with different inputs. For $R_m I = 12$mV the voltage relaxes towards the equilibrium value $V = E_L + R_m I_e = -58$ mV. It never reaches the threshold value of $V_T = -55$mV. For $R_m I = 16$ mV the voltage reaches threshold and so there is a spike; the spike is added by hand, in this case by setting V to 20 mV for one time step. The voltage is then reset. Here $\tau_m = 10$ ms.

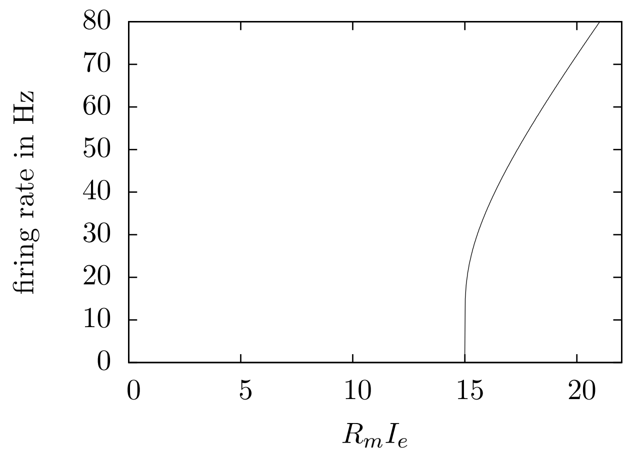

Figure 2: The firing rate, that is spikes per second, for the integrate and fire neuron with different constant inputs with $\tau_m = 10$ ms, $V_T = -55$ mV and both the leak and reset given by -70 mV. Notice how there is no firing until a threshold is reached and after that the firing increases very quickly.

so the equilibrium value for constant I_e, the value where V stops changing, is

$$\bar{V} = E_L + R_m I_e \tag{5}$$

Now if this value $\bar{V} > V_T$ then the neuron would spike before it got there, if $\bar{V} < V_T$ then the neuron will not spike for that input. We won't do it here, but, in fact, since we can solve the equations for constant I_e we can work out the $f - I$ curve, the relationship between the firing rate and the input current. It is plotted in Fig. **??**.

References

[1] Lapicque, L. (1907). Recherches quantitatives sur l'excitation lectrique des nerfs traite comme une polarisation. J. Physiol. Pathol. Gen, 9:620–635.