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 separating 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, like islands which are surrounded by salty water, as in Fig. 1.

Spikes

The summary version of what happens in neurons 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 $v_\theta = -55$ mV there is a nonlinear cascade that 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.

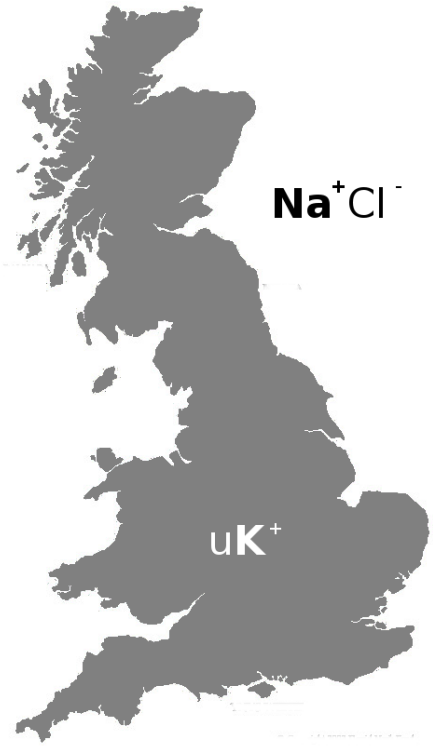

Figure 1: A cartoon to help you remember that there is more sodium outside the cell and more potassium inside.

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 $x(t)$, the height of the water, by $v(t)$ 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 $C_m v$. 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.

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. It turns out that the normal Ohm's law applies around the reversal potential so that the current out of the cell is proportional to $v - E_L$.

G is now G_m, a conductance, measuring the porousness of the membrane to the flow of ions. It gives the constant of proportionality for the leak current: the leak current out of the cell is $G_m(v - E_L)$. We actually divide across by the conductance, and write $R_m = 1/G_m$, the resistance. Finally, we write $\tau_m = C_m/G_m$ to get

$$\tau_m \dot{v} = E_L - v + R_m i(t) \tag{1}$$

$i(t)$ might end up being synaptic input, but traditionally we write the equation to match the **in vivo** experiment where t is an injected current from an electrode, so we write i_e, "e" for electrode. τ_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 $v(t)$ changes. This is a problem since, in general, the conductance (inverse: resistance) of voltage-gated ion channels depend on $v(t)$, introducing nonlinear dependence. In fact, the nonlinear effects are strongest for values of v near where a spike is produced.

The **leaky-integrate-and-fire** model handles this spiking nonlinearity in a particularly simple way: It uses the linear equation unless v exceeds a threshold value v_θ. Above threshold, a spike is added 'by hand', and the membrane voltage is changes to a **reset** value v_r to mimic the neuron returning to a hyperpolarized voltage after the spike is complete. To summarise:

- Below the threshold voltage v_θ, the membrane voltage $v(t)$ satisfies $\tau_m \dot{v} = E_L - v + R_m i_e(t)$
- Above threshold ($v \geq v_\theta$), a spike is recorded and the voltage is set to a reset value $v(t) \leftarrow v_r$.

A common choice for v_r is the leak potential. The **leaky integrate and fire model** is surprisingly old, and was first introduced in [1]. It lacks important details in the dynamics of neurons, but is useful and often used for modelling the behaviour 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:

$$v(t) = (E_L + R_m i_e) + [v(0) - (E_L + R_m i_e)]e^{-t/\tau_m} \tag{2}$$

We can write Equation (2) in terms of a steady-state voltage $v_\infty = E_L + R_m i_e$ as

$$v(t) = v_\infty + [v(0) - v_\infty]e^{-t/\tau_m}. \tag{3}$$

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, for example us-

ing a forward exponential Euler update

$$\begin{aligned} v_{t+\Delta} &\leftarrow \alpha v_t + (1-\alpha)v_\infty(t) \\ \alpha &= e^{-\Delta/\tau_m} \\ v_\infty(t) &= E_L + R_m i_e(t). \end{aligned} \tag{4}$$

An example in given in Fig. 2.

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

$$\tau_m \dot{v} = E_L - v + R_m i_e \tag{5}$$

so the equilibrium value for constant i_e, the value where v stops changing, is

$$\bar{v} = E_L + R_m i_e \tag{6}$$

Now if this value $v_\infty > v_\theta$ then as the neuron voltage increased towards its equilibrium value, v_∞, it would reach the threshold, v_θ, and spike. Hence, if $v_\infty > v_\theta$ the neuron will spike repeatedly. However if $v_\infty < v_\theta$ then the neuron will not spike for that input because it will never reach threshold.

In fact, we can work out the curve that represents the firing rate as a function of the current. This is the called the f-I curve and is shown in Fig. 3. In the model

$$\tau_m \dot{v} = E_L + R_m i_e - v = v_\infty - v \tag{7}$$

which we can solve from our study of ODEs, it gives

$$v(t) = v_\infty + [v(0) - v_\infty]e^{-t/\tau_m} \tag{8}$$

so if the neuron has spiked and is reset at time $t = 0$ and reaches threshold at time $t = T$, assume $v_r = E_L$ we have

$$\begin{aligned} v(t) = v_\theta &= v_\infty + [v_r - v_\infty]e^{-T/\tau_m} && \text{using assumption } v(0) = v_r \\ &= v_\infty + [E_L - v_\infty]e^{-T/\tau_m} && \text{using definition } v_r = E_l \\ &= v_\infty + [E_L - (E_L + R_m i_e)]e^{-T/\tau_m} && \text{using definition of } v_\infty \\ &= v_\infty - R_m i_e\, e^{-T/\tau_m} \end{aligned} \tag{9}$$

so

$$e^{-T/\tau_m} = \frac{v_\infty - v_\theta}{R_m i_e} \tag{10}$$

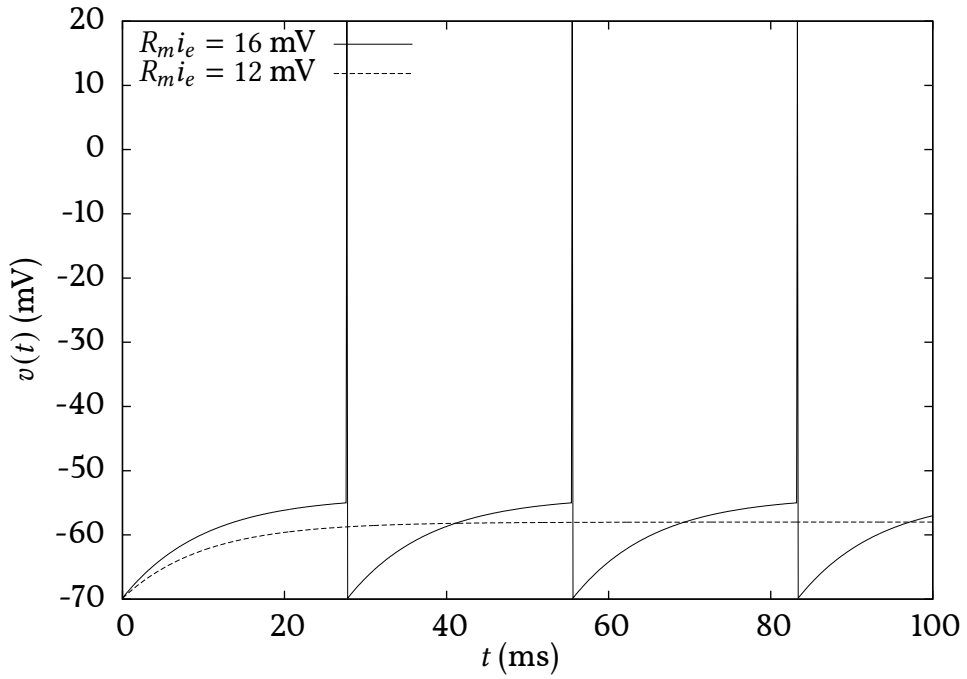

Figure 2: An integrate and fire neuron with different inputs. For $R_m i_e = 12$ mV the voltage relaxes towards the equilibrium value $v = E_L + R_m i_e = -58$ mV. It never reaches the threshold value of $v_\theta = -55$ mV. For $R_m i_e = 16$ mV the voltage reaches threshold and so there is a spike; 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.

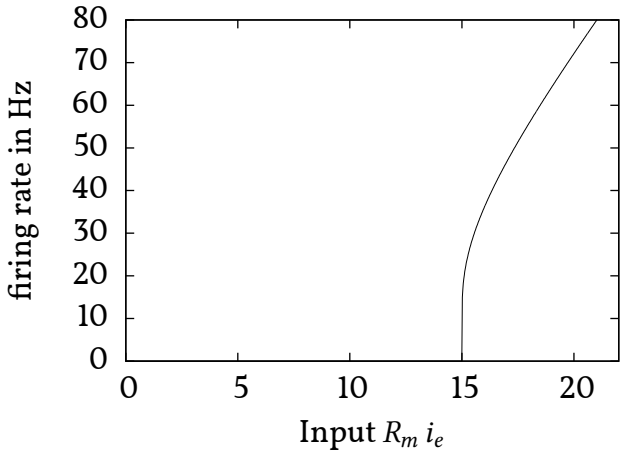

Figure 3: The firing rate, that is spikes per second, for the integrate and fire neuron with different constant inputs with $\tau_m = 10$ ms, $v_\theta = -55$ mV and both the leak and reset given by -70 mV. Notice how there is no firing until a threshold is reached and after that the firing increases very quickly.

Taking the log of both sides we get

$$T = \tau_m \ln \left[\frac{R_m i_e}{v_\infty - v_\theta} \right] \tag{11}$$

Finally, this is the time between spikes, so the frequency is one over this. It is only defined for $v_\infty > v_\theta$, below that there is no spiking and the frequency is zero. The actual gnuplot command used to make the figure was

```
plot [0:22] x>15 ? 1/(.01*log(x/(x-15))) : 0
```

We have been ignoring the refractory period, this can easily be added to the model. The easiest approach is just to adjust the rule for spiking by specifying the voltage remains fixed at v_r for some time, T_r, corresponding to the refractory period. In fact, the refractory period tends to be divided in the **absolute refractory period** when the neuron can't spike at all and a **relative refractory period** when spiking is just harder. Holding v at v_r models an absolute refractory period, to model a relative refractory period a negative current can be added to the equation.

In fact, neurons tend not to have a regular firing rate; they often, for example, show spike rate adaptation. This means that the firing rate decreases even if the incoming current remains constant. As we have seen this isn't modelling in the integrate and fire model, in the integrate and fire model the response to a constant current is a constant firing rate. The model can be extended to include it. For example a slow potassium current could be added, a slow potassium current is a current that would increase every time there is a spike and decrease between spikes. Since a potassium current reduces the voltage inside the cell, it decreases the firing rate; thus, if the cell fires quickly the potassium current increases, decreasing the firing rate until the increase in the potassium when there is a spike balances the decrease between spikes. These slow currents are common, they may help protect the cell from 'exhaustion' by reducing its spike rate for ongoing stimuli and they may play a computation role, helping the brain infer the nature of stimuli across timescales. The 'face of Jesus' illusion demonstrates the existence of these currents.

A simple approach, which would approximate adding a potassium would be to just add a second input u

$$\tau \dot{v} = R_m i_e - v + u \tag{12}$$

where

$$\tau_u \dot{u} = -u \tag{13}$$

where there is an additional rule that $u \leftarrow u + \delta u$ whenever there is a spike. Thus if u is negative it will reduce the equilibrium value of v, reducing the spike rate if the cell is spiking. u will decay towards zero with a timescale τ_u but spiking will change it by δu. In the case we have discussed here, where we want to model a reduction in spiking δu would be negative and τ_u would have a moderate timescale, perhaps 200 ms.

Summary

Chemical gradients mean that current flows across the membranes of the cell are not zero for zero potential There is a reversal potential for each type of ion, this is the value of the potential for which no current flows. For our purposes here we consider the leak potential; at lower voltages most of the channels that allow ions to pass through the membrane are closed, this means

the conductance is near zero. The are some open channels, mostly for potassium and the corresponding reversal potential is called the leak potential E_l while the conductance is g_l. E_l is often take to be somewhere around -80 mV. Using Ohms law the equation for the voltage in a cell is then

$$C_m \dot{v} = g_l(E_l - v) + i_e(t) \tag{14}$$

where C_m is the capacitance of the membrane and $i_e(t)$ is the input current. This is also written

$$\tau_m \dot{v} = E_l - v + R_m i_e(t) \tag{15}$$

where τ_m is a timescale, often around 12–20 ms and $R_m = 1/g_l$. However, this linear equation does not include the nonlinear dynamics that supports spiking, we add spiking 'by hand' with a rule that says if $v > v_\theta$, a threshold value, usually about -55 mV, then there is a spike and the voltage is reset to a reset value v_r often set equal to, or a little greater than, E_l. This is the leaky integrate and fire equation. We know something of what the solutions look like from the leaky bucket equation considered before, but now there are spikes. We can see that if the equilibrium value $v_\infty = E_l + R_m i_e$ is greater than v_θ the neuron will spike regularly, if it is less, it won't spike at all. The equation leaves out the actual spiking dynamics, it also ignores the actual spatial organization of the neuron, treating it as a point. It does not include some other aspects of neuronal spiking like the refractory period and slow currents, though these can be added, at least approximately.

References

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