The bucket-like equation for neurons

We will now try to extend this bucket-like equation so that it applies to neurons. First off V is now voltage 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.

The charge 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 $E_L = -70\text{mV}$, 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, the voltage required for zero current even if there is some conductivity. The leak potential takes into account a mixture of a reversal potential and the effect of the ion pumps.

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.

This 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 is the **leaky integrate and fire model**.

- 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 V_R.

This model is easy to solve; if I_e is constant we have already solved it above up to messing around with constants. 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. Basically you divide time up into small steps, assume I_e is constant for each small step and use the analytic constant-input equation to get from one time step to another. Alternatively the equation can be solved using a numerical approach to solving differential equations, such as the Euler method, or Runge Kutta, or, as mentioned when discussing the bucket equations, by using the constant-input current solution to evolve across small time steps. An example in given in Fig. **??**.

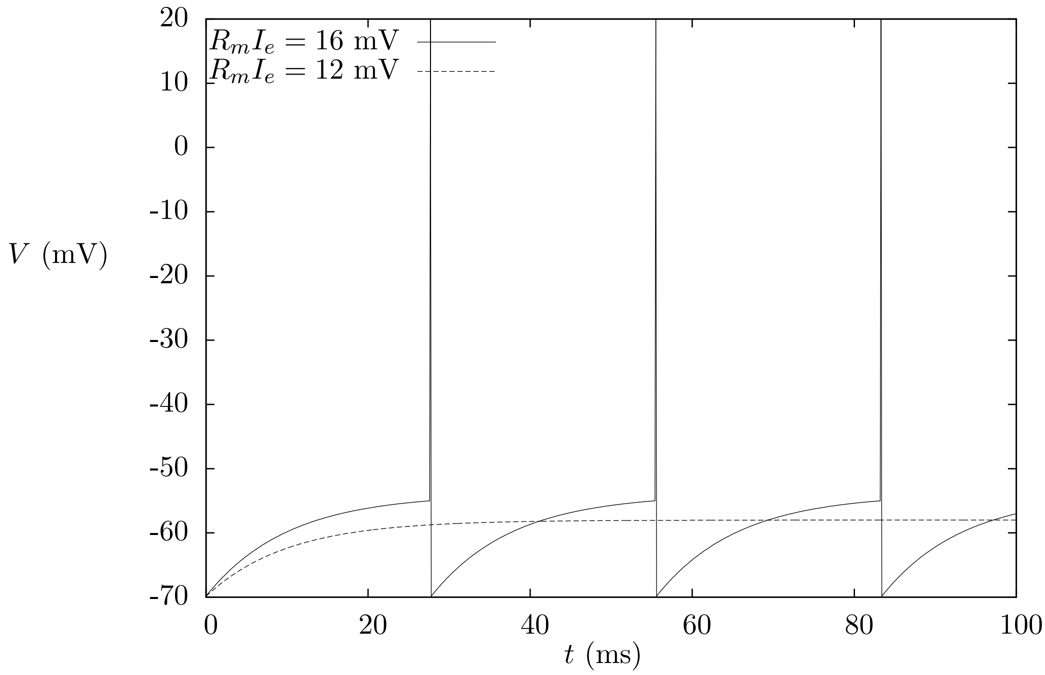

Figure 1: An integrate and fire neuron with different inputs. For $R_m I = 12$mV the voltage relaxes towards the equilibrium value $V = E_L + R_m I_e = -58$ mV. It never reaches the threshold value of $V_T = -55$mV. For $R_m I = 16$ mV the voltage reaches threshold and so there is a spike; the spike 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.