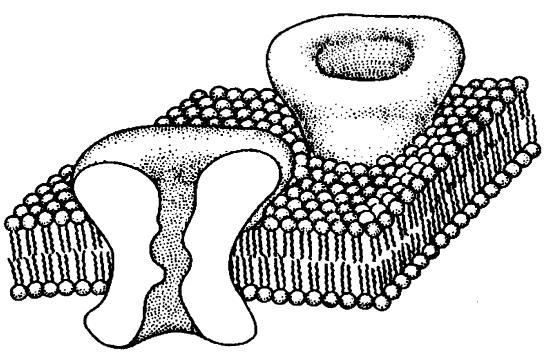
Solving the RC circuit **Adrienne Fairhall Jan 2014**

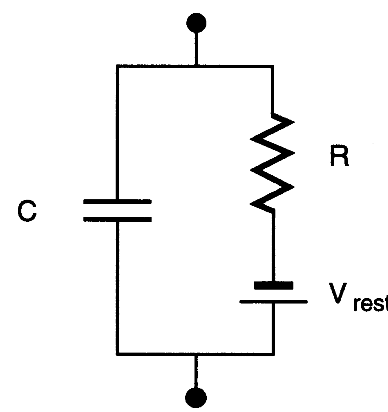
In understanding the dynamics of neural function, the fundamental unit of computation is the single neuron. In this course we will be developing some mathematical tools to analyze the way in which neurons transform incoming information into a sequence of action potentials, or spikes.

RC circuit

We will start with the passive membrane. This is like a neuron with no active channels, only "leak" channels that allow ions to enter in a non-specific way across the lipid bilayer, which separates the exterior from the interior. We can develop an equation for the way in which the passive membrane responds by treating it as an electrical circuit. The passive membrane "neuron" model has three components:

1. A capacitor, with capacitance C, due to the way charges can accumulate across the lipid bilayer;
2. a battery, expressing the resting voltage difference E which results from the difference in concentration of ions between the interior and exterior of the cell; and
3. a resistor, with resistance R, through which ions can pass and carry current across the membrane.





The current through the capacitor can be found from the definition of the capacitance as

$$C = \frac{Q}{V},$$

where Q is the charge that accumulates on the capacitor and V is the voltage across the capacitor. As current is the time derivative of the charge, we can derive the current across the capacitor,

$$I_C = C\,\frac{dV}{dt}. \qquad (1)$$

The current across the resistor is given by Ohm's law:

$$I_R = \frac{V - V_{rest}}{R}, \qquad (2)$$

where *V* is the same voltage drop, applied across the other arm of the circuit. Now we use Kirchhoff's laws to equate the currents that flow across the membrane, including any external current I_{ext}, and arrive at the following:

$$C\,\frac{dV}{dt} = -\frac{V - V_{rest}}{R} + I_{ext}. \qquad (3)$$

This is an inhomogeneous first order linear differential equation: linear, because every term that involves the variable V is linear in V; inhomogeneous because there is a driving term I_{ext} that doesn't depend on V. To understand the dynamics of such a system, it is useful to make some changes of variables. From now on in these notes, we will always think of voltage relative to the resting voltage, so we will drop the V_{rest} term (that is the same as redefining V to be $V - V_{rest}$; but don't forget that when we go back to Hodgkin-Huxley we will have to reinstate the battery voltages as each ion has its own! We multiply by R and collect terms to get a new form of the equation that exposes its two fundamental properties:

$$\tau\,\frac{dV}{dt} = -V + V_\infty, \qquad (4)$$

where here $V_\infty = RI_{ext}$. The time constant $\tau = RC$ is the typical timescale for change in the system. The steady state value V_∞ can be inferred by setting the time derivative to zero in Eq. (4) and solving for V. This is the value that V will attain eventually if I_{ext} is held constant.

Let's solve this equation. First, let's turn it back into a homogeneous equation by making a (second) change of variables $V' = V - V_\infty$. Then $\frac{dV'}{dt} = \frac{dV}{dt}$, and we have

$$\tau\,\frac{dV'}{dt} = -V'. \qquad (5)$$

We can solve this equation by separation of variables: moving all the terms in V to the same side, and all the terms in t to the other side, and integrating:

$$\int_{V'(0)}^{V'(t)} \frac{dV'}{V'} = \int_0^t -\frac{dt'}{\tau}.$$

This gives

$$\ln\big(V'(t)\big) - \ln\big(V'(0)\big) = -t/\tau,$$

$$\ln\left(\frac{V'(t)}{V'(0)}\right) = e^{-t/\tau},$$

$$V'(t) = V'(0)e^{-t/\tau}.$$

This solution shows that without any inputs, the voltage will decay exponentially with time constant τ. Now let's put back in our constant input, and replace V' with $V - V_\infty$.

$$V(t) - V_\infty = (V(0) - V_\infty)e^{-t/\tau},$$

or

$$V(t) = (V(0) - V_\infty)e^{-\frac{t}{\tau}} + V_\infty\,. \qquad (6)$$

Let's check: at time t = 0, the exponential is equal to 1 and the V_∞'s cancel, leaving $V(0)$. As $t \to \infty$, the exponential term goes to zero, and we are left with V_∞. So the solution starts out at $V(0)$ and approaches V_∞ exponentially, either increasing or decreasing depending on the difference between the initial condition and where the system is trying to head to.

Time-varying inputs

Now we'd like to handle the case that the input current is varying in time: $I_{ext} = I(t)$. This is the generic case for a neuron receiving dendritic inputs from many other neurons firing in a network. We can't use separation of variables as we did last time because now the equation is inhomogeneous (meaning there is a term that doesn't depend on V) and also time-varying, so we can't absorb the constant into V the way we did last time. The key to solving the equation in this case is to notice that we can use what is called an "integrating factor". Let's multiply V by the factor $e^{t/\tau}$. Now, by the chain rule, the derivative of the *combination* is

$$\frac{d}{dt}\left(Ve^{\frac{t}{\tau}}\right) = \frac{dV}{dt}e^{\frac{t}{\tau}} + \frac{1}{\tau}Ve^{\frac{t}{\tau}}. \tag{7}$$

So multiplying the original equation 4, $\tau\,\frac{dV}{dt} = -V + RI(t)$, by the integrating factor, we get

$$\tau e^{\frac{t}{\tau}}\,\frac{dV}{dt} = -Ve^{\frac{t}{\tau}} + RI(t)e^{\frac{t}{\tau}}; \tag{8}$$

and now we can define a new variable W = $Ve^{\frac{t}{\tau}}$ and use Equation (8) to rewrite Equation (4) as

$$\tau\,\frac{dW}{dt} = RI(t)e^{\frac{t}{\tau}}. \tag{9}$$

What was the point of this? Now the only place our new variable *W* appears is on the left hand side, and we can simply integrate both sides to solve for it:

$$[W]_0^t = \frac{1}{\tau}\int_0^t dt'\,RI(t')e^{\frac{t'}{\tau}}. \tag{10}$$

The notation $[W]_0^t$ means that we evaluate W at the two endpoints of the integration. Now let's put V back in:

$$V(t)e^{\frac{t}{\tau}} - V(0) = \frac{1}{\tau}\int_0^t dt'\,RI(t')e^{\frac{t'}{\tau}},$$

$$V(t) = V(0)e^{\frac{-t}{\tau}} + \frac{1}{\tau}\int_0^t dt'\,RI(t')e^{\frac{-(t-t')}{\tau}}. \tag{11}$$

Filtering

This is a very fundamental equation that illustrates a very important point. Leaving out the initial condition, which simply decays exponentially away over time, we can express the solution in the general form:

$$V(t) = \int_0^t dt'\,I(t')K(t-t'), \tag{12}$$

where in this case, the function K(t), known as the *kernel*, is $\frac{1}{\tau}e^{\frac{-t}{\tau}}$. This form is known as a *convolution*. This is the same as acting on the current *I(t)* with a linear filter given by *K(t)*. What does this mean? I find it a little more intuitive if we make a change of variables to $s = t - t'$, so that Equation (12) becomes

$$V(t) = \int_0^t ds\,RI(t-s)K(s). \tag{13}$$

At any time *t,* we can find out what the voltage is by taking a *weighted sum* of the previous current inputs at times *s* relative to the time right now, *I(t-s).* The weights are given by the value of the kernel function K at *s*.

What does it do to *I(t)* to run it through this exponential filter? Because each value of the voltage is a weighted sum of the recent current values, where the weights are all positive and decay as one goes backward in time, the output voltage is like a local average of the input, where the effective averaging window size is of order the time constant τ. So we would expect the output to be smoother than the inputs *I(t)*. In fact, this form of K is a low-pass filter, that is, slow frequencies in I(t) make it into V(t) much more effectively than high frequencies. This is because high frequencies, components of the input that oscillate quickly, average out. Which frequencies get through while others are damped? Hopefully it is intuitive that frequency components that oscillate quickly relative to the time constant are reduced in size, while those that oscillate slowly relative to τ aren't much affected by the filtering.