Some mathematics

A first order differential equation

Many of the differential equations we come across in neuroscience are inhomogeneous first order differential equations

$$\tau \frac{\mathrm{d}x}{\mathrm{d}t} = -x + u(t) \tag{1}$$

where $x(t)$ is a time-varying quantity we are interested in and $u(t)$ is some outside *driving function*.

One example we will examine is the integrate and fire equation:

$$\tau_m \frac{\mathrm{d}v}{\mathrm{d}t} = E_l - v(t) + g_l \cdot i(t) \tag{2}$$

where $v(t)$ is the voltage inside a neuron, and the driving function is made up of two parts E_l, the so called reversal potential and $g_l \cdot i(t)$ which represents current coming into the cell, for example, through an electrode if the cell being modelled is being experimented on, or because of signals from other neurons.

Another example is the gating equation which represents the opening and closing of ion-channels, little gates in the membrane of the cells and a third example is the equation for synaptic conductance. In each of these examples the underlying equation is the same, or nearly the same, and so we will look at it now in the abstract without considering the application.

These are called first order linear differential equations, first order because the highest derivative is $dx/\,\mathrm{d}t$, there is no $d^2x/\,\mathrm{d}t^2$ term for example, and linear because there are no non-linear x terms, no x^2 or anything like that.

First order linear differential equations can be solved, or, at least the solution can be written as an integral.

Solution using an integrating factor

In these notes we will review the use of an *integrating factor* to integrate Equation (1). Other approaches include using Laplace transforms or remembering that first-order linear ODEs tend to have solutions of the form $c \cdot \exp(at)$ and using this form as an ansatz.

Start by re-writing Equation (1) in the form

$$\frac{\mathrm{d}x}{\mathrm{d}t} + \frac{1}{\tau}x = \frac{1}{\tau}u(t) \tag{3}$$

The integration factor simplifies (3) by multiplying it across by $e^{t/\tau}$; This gives

$$e^{t/\tau}\frac{\mathrm{d}x}{\mathrm{d}t} + \frac{1}{\tau}e^{t/\tau}x = \frac{1}{\tau}e^{t/\tau}u(t) \tag{4}$$

The clever bit, now, is to notice that the two terms on the left hand side can be rewritten in product form

$$\frac{\mathrm{d}}{\mathrm{d}t}\left(e^{t/\tau}x(t)\right) = \frac{1}{\tau}e^{t/\tau}u(t) \tag{5}$$

Moving τ over to the left-hand side and integrating both sides, we obtain

$$\tau e^{t/\tau}x(t) = \int_0^t e^{\tilde{t}/\tau}u(\tilde{t})\,\mathrm{d}\tilde{t} + c \tag{6}$$

where c is some integration constant. Setting $t = 0$ shows that $c = \tau x(0)$ and, hence, dividing across by the stuff in front of $x(t)$

$$\begin{aligned} x(t) &= e^{-t/\tau}\left[\frac{1}{\tau}\int_0^t e^{\tilde{t}/\tau}u(\tilde{t})\,\mathrm{d}\tilde{t} + x(0)\right] \\ &= x(0) + \frac{1}{\tau}\int_0^t e^{-(t-\tilde{t})/\tau}u(\tilde{t})\,\mathrm{d}\tilde{t} \end{aligned} \tag{7}$$

Hence, $x(t)$ is written as an integral, if we can do the integral we have solved the equation.

The easiest case is obviously $u(t) = \bar{u}$ a constant:

$$\begin{aligned} x(t) &= \bar{u}\left[\frac{1}{\tau}e^{-t/\tau}\int_0^t e^{\tilde{t}/\tau}\,\mathrm{d}\tilde{t}\right] + x(0)\,e^{-t/\tau} \\ &= e^{-t/\tau}x(0) + (1 - e^{-t/\tau})\bar{u} \\ &= \bar{u} + [x(0) - \bar{u}]e^{-t/\tau} \end{aligned} \tag{8}$$

It is easy to understand this solution:

$$\tau\frac{\mathrm{d}x}{\mathrm{d}t} = \bar{u} - x(t) \tag{9}$$

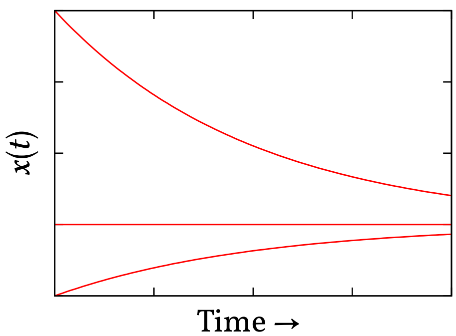

Figure 1: Two examples of $u(t)$ decaying towards $\bar{u}$. Here $\bar{u} = 1$ and $\tau = 10$; in the top curve $u(0) = 2.5$ whereas in the other $u(0) = 0.5$.

has $\mathrm{d}x/\,\mathrm{d}t = 0$ only if $x(t) = \bar{u}$ furthermore if $x(t) > \bar{u}$ then $\mathrm{d}x/\,\mathrm{d}t < 0$ and $x(t)$ decreases towards $\bar{u}$; if $x(t) < \bar{u}$ so $\mathrm{d}x/\,\mathrm{d}t > 0$ then $x(t)$ increases. Since $\mathrm{d}x/\,\mathrm{d}t$ is zero for $x(t) = \bar{u}$ we say this is the equilibrium; since the sign of $\mathrm{d}x/\,\mathrm{d}t$ means that $x(t)$ always approaches $\bar{u}$ we say this solution is stable.

We can see in the solution that $x(t)$ decays exponentially towards $\bar{u}$, where and it does so with a time scale that depends on τ. An example is shown in Fig. 1.

What happens if $u(t)$ isn't constant? Well, some of the same logic applies: the sign of $\mathrm{d}x/\,\mathrm{d}t$ means that the solution is trying to get to $u(t)$ but the difference is now that $u(t)$ might change before it gets there. Actually looking at

$$x(t) = e^{-t/\tau}\left[\frac{1}{\tau}\int_0^t e^{\tilde{t}/\tau}u(\tilde{t})\,\mathrm{d}\tilde{t} + u(0)\right] \tag{10}$$

let us consider the function

$$h(t) = \frac{1}{\tau}e^{-t/\tau}\int_0^t e^{\tilde{t}/\tau}u(\tilde{t})\,\mathrm{d}\tilde{t} \tag{11}$$

and do a change of variable $\tilde{t} = t - s$ so

$$h(t) = \frac{1}{\tau}\int_0^t e^{-s/\tau}u(t-s)\mathrm{d}s \tag{12}$$

then the role of the integral is to filter or smooth out $u(t)$ by averaging it over its past with a exponential window. This is illustrated in Fig. 2.

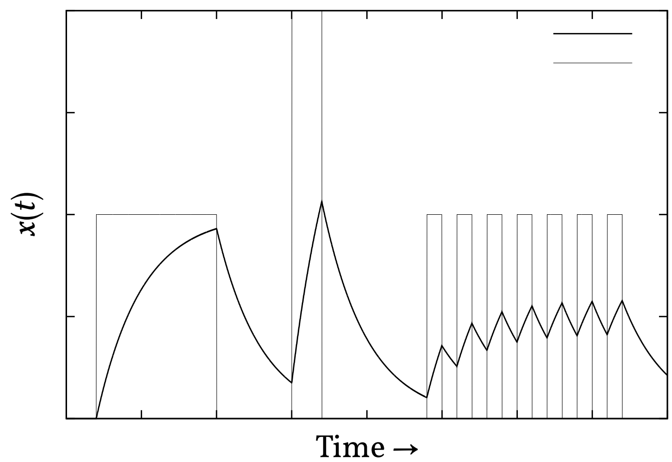

Figure 2: This shows how the response $x(t)$ filters the input $u(t)$; the differntial equation has $\tau = 3$ and an input $u(t)$ which varies as shown above; the code used to calculate $x(t)$ is `filtered_input.py`.

Imagine that $u(t)$ varies slowly compared to the time scale τ, so by the time $u(t-s)$ changes much compared to $u(t)$ then $\exp(-s/\tau)$ is more-or-less zero, then

$$h(t) \approx \frac{1}{\tau}u(t)\int_0^t e^{-s/\tau}\mathrm{d}s = u(t)\left(1 - e^{-t/\tau}\right) \tag{13}$$

and substituting back in we get

$$x(t) \approx u(t) + [u(0) - u(t)]e^{-t/\tau} \tag{14}$$