Some mathematics

A first order differential equation

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

$$\tau\frac{df}{dt} = g(t) - f(t) \tag{1}$$

where $f(t)$ is some function of t we are interested, $g(t)$ is some outside *driving function* and τ is a constant. One example we will examine is the integrate and fire equation:

$$\tau_m\frac{dV}{dt} = E_l - V(t) + g_l I(t) \tag{2}$$

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 $g_l I(t)$ 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 df/dt, there is no d^2f/dt^2 term for example, and linear because there are no non-linear f terms, no f^2 or anything like that. First order linear differential equations can be solved, or, at least the solution can be written as an integral. The solution uses an *integrating factor*: the trick of simplifying the equation by multipling across by

$$\lambda = e^{t/\tau} \tag{3}$$

This gives

$$\tau e^{t/\tau}\frac{df}{dt} + e^{t/\tau}f = e^{t/\tau}g(t) \tag{4}$$

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

$$\tau\frac{d}{dt}\left(e^{t/\tau}f\right) = e^{t/\tau}g(t) \tag{5}$$

We integrate both sides

$$\tau e^{t/\tau}f(t) = \int_0^t e^{t'/\tau}g(t')dt' + A \tag{6}$$

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

$$f(t) = e^{-t/\tau}\left[\frac{1}{\tau}\int_0^t e^{t'/\tau}g(t')dt' + f(0)\right] \tag{7}$$

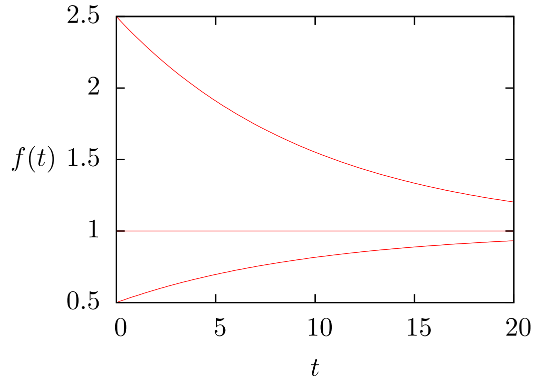

Figure 1: Two examples of $f(t)$ decaying towards $\bar{g}$. Here $\bar{g} = 1$ and $\tau = 10$; in the top curve $f(0) = 2.5$ whereas in the other $f(0) = 0.5$.

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

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

$$f(t) = \bar{g}\left[\frac{1}{\tau}e^{-t/\tau}\int_0^t e^{t'/\tau}dt'\right] + f(0)e^{-t/\tau} = \bar{g}\left(1 - e^{-t/\tau}\right) + f(0)e^{-t/\tau} \quad (8)$$

or

$$f(t) = \bar{g} + [f(0) - \bar{g}]e^{-t/\tau} \quad (9)$$

It is easy to understand this solution:

$$\tau\frac{df}{dt} = \bar{g} - f(t) \quad (10)$$

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

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

What happens if $g(t)$ isn't constant; well some of the same logic applies, the sign of df/dt means that the solution is trying to get to $g(t)$ but the difference is now that $g(t)$ might change before it gets there. Actually looking at

$$f(t) = e^{-t/\tau}\left[\frac{1}{\tau}\int_0^t e^{t'/\tau}g(t')dt' + f(0)\right] \quad (11)$$

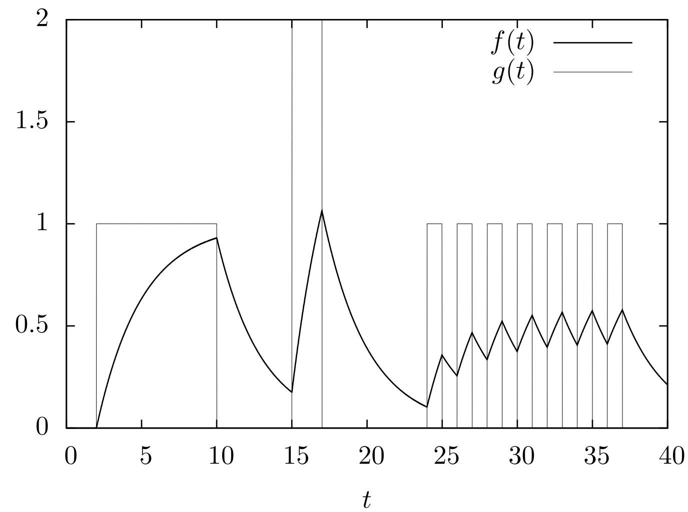

Figure 2: This shows how the response $f(t)$ filters the input $g(t)$; the differntial equation has $\tau = 3$ and an input $g(t)$ which varies as shown above; the code used to calculate $f(t)$ is `filtered_input.py`.

lets consider the function

$$T(t) = \frac{1}{\tau} e^{-t/\tau} \int_0^t e^{t'/\tau} g(t') dt' \tag{12}$$

and do a change of variable $t' = t - s$ so

$$T(t) = \frac{1}{\tau} \int_0^t e^{-s/\tau} g(t-s) ds \tag{13}$$

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

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

$$T(t) \approx \frac{1}{\tau} g(t) \int_0^t e^{-s/\tau} ds = g(t)\left(1 - e^{-t/\tau}\right) \tag{14}$$

and substituting back in we get

$$f(t) \approx g(t) + [f(0) - g(t)] e^{-t/\tau} \tag{15}$$

Two first order differential equation

Differential equations can be coupled; here is an example of a nearly homogeneous pair of coupled equations

$$\tau_f \frac{df}{dt} = \bar{f} - f - w \tag{16}$$

$$\tau_w \frac{dw}{dt} = \bar{w} - w \tag{17}$$

There are lots of ways to solve this equation; one approach is to rewrite it as a matrix equation and find the eigenvectors, another is to convert it into a second order equation and solve that; the first way is more general but the second is quicker. Let's start by making the equation homogeneous and going from there, so let

$$f' = f - \bar{f} + \bar{w} \tag{18}$$

$$w' = w - \bar{w} \tag{19}$$

giving

$$\tau_f \frac{df'}{dt} = -f' - w' \tag{20}$$

$$\tau_w \frac{dw'}{dt} = -w' \tag{21}$$

Actually having the prime on f and w gets annoying so we'll drop the prime for convenience.

$$\tau_f \frac{df}{dt} = -f - w \tag{22}$$

$$\tau_w \frac{dw}{dt} = -w \tag{23}$$

Now, differentiate the first equation to get

$$\tau_f \frac{d^2 f}{dt^2} = -\frac{df}{dt} - \frac{dw}{dt} \tag{24}$$

Since

$$\frac{dw}{dt} = -\frac{1}{\tau_w} w \tag{25}$$

we can substitute back in for w:

$$\tau_f \frac{d^2 f}{dt^2} = -\frac{df}{dt} + \frac{1}{\tau_w} w \tag{26}$$

From the original df/dt equation we have

$$w = -f - \tau_f \frac{df}{dt} \tag{27}$$

and using this to get rid of the w we have

$$\tau_f \frac{d^2 f}{dt^2} = -\frac{df}{dt} - \frac{1}{\tau_w} f - \frac{\tau_f}{\tau_w}\frac{df}{dt} \tag{28}$$

Finally, multiplying across by τ_w and fiddling around a bit we have

$$\tau_w \tau_f \frac{d^2 f}{dt^2} + (\tau_w + \tau_f)\frac{df}{dt} + f = 0 \tag{29}$$

This second order equation is solved by ansatz, that is by guessing; we guess

$$f(t) = e^{rt} \tag{30}$$

and substitute back in

$$\tau_w \tau_f r^2 + (\tau_w + \tau_f) r + 1 = 0 \tag{31}$$

which has two solutions $r = -1/\tau_f$ and $r = -1/\tau_w$ so

$$f(t) = Ae^{-t/\tau_f} + Be^{-t/\tau_w} \tag{32}$$

and substituting back into

$$\tau_f \frac{df'}{dt} = -f' - w' \tag{33}$$

give an equation for w'.

Another approach to this pair of equations which we won't explore here is to write them as a matrix equation:

$$\frac{d}{dt}\begin{pmatrix} f' \\ w' \end{pmatrix} = \begin{pmatrix} -1/\tau_f & -1/\tau_f \\ 0 & -1/\tau_w \end{pmatrix}\begin{pmatrix} f' \\ w' \end{pmatrix} \tag{34}$$

As important as seeing how to solve these differential equation is understanding the phase dynamics; recall how in case above with just one differential equation we could see that the equation had a stable equilibrium, well we can do the same thing here. First consider the equation

$$\tau_w \frac{dw}{dt} = -w \tag{35}$$

If $w = 0$ this means that $dw/dt = 0$; this is called a nullcline and, in $f - w$ space it is a line not a point. The system isn't in equilibrium along the nullcline because df/dt isn't zero but it is stable in the sense that if we are above $w = 0$ then $dw/dt < 0$ and if it is below $dw/dt > 0$ and so, as before, the system will approach the nullcline. In fact there is also a df/dt nullcline given by $f = -w$; this is a diagonal line in $f - w$ space; it is also stable, if $f > -w$, that is if we are to the right of the nullcline, then $df/dt < 0$ and we move to the left, and the converse for $f < -w$. Hence, we always move towards the nullclines;

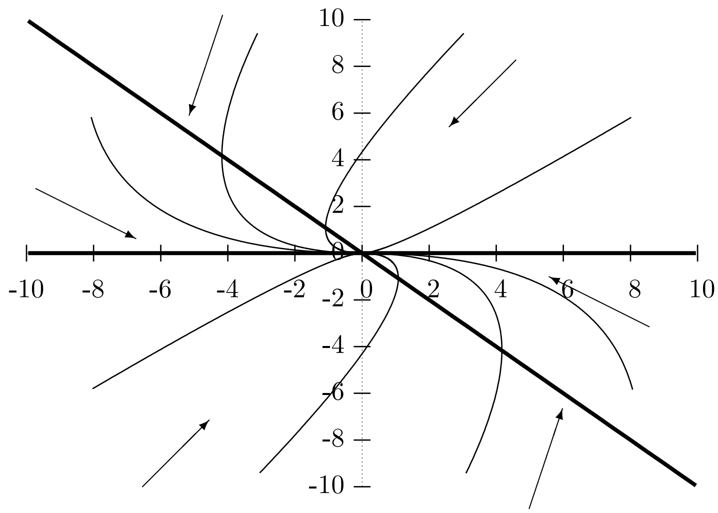

Figure 3: This shows some of the trajectories in $f - w$ space; the horizontal axis is f, the vertical is w. The nullclines are the two curves in bold. All the trajectories approach the equilibrium point, as they cross the $f = -w$ nullcline their tangent is vertical because on this line $df/dt = 0$; $\tau_f = 2$ and $\tau_w = 1$. The arrows are included for illustrative purposes, the direction of the trajectories could also be decided using the two rules described in the text based on the signs of the derivatives. The programme used to plot the trajectories `two_d.py`.

furthermore, the two lines cross at $f = w = 0$ and this is a stable equilibrium point.

The trajectories for an example system are shown in Fig. 3; this is a plot in $f - w$ space so it doesn't tell us how quickly the system will move along the trajectories, only their shape. To see the exact shape of the trajectories we need to solve the differential equations, but to guess roughly what they do we can use the nullclines and the logic above that describes what sign the derivatives have in the different areas as the $f - w$ space is divided up by the nullclines. Later we will use this sort of analysis to understand the behaviour of systems where the nullclines aren't straight because the differential equations are not linear.