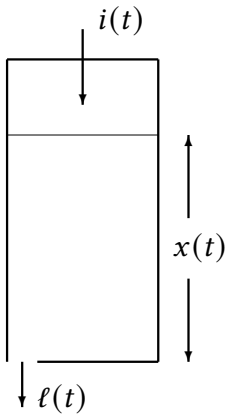
Equation for leaky buckets

These notes are about a simple but very useful model of spiking neurons: the integrate and fire model. First, though, we consider the dynamics of a leaky bucket of water. These dynamics are very similar to those seen in the integrate and fire model.

Buckets of water

In the simplest model of neurons their voltage dynamics is similar to the dynamics of a bucket with a leak and the class of equations that apply in this case will also be applied to synapses, for example.



Consider a bucket with straight sides which is filled to a height x with water. Imagine the water leaks out of a hole in the bottom. The rate the water leaks out depends on x; the larger x is the larger the pressure at the bottom is and hence the faster the water pours out. In other words

$$\ell(t) \propto x(t) \tag{1}$$

or

$$\ell(t) = Gx(t) \tag{2}$$

where G is a constant which will depend on the size of the hole and complicated things like the viscosity of water. Of course, we are ignoring lots of complicated stuff, like turbulence and so forth, but since we are interested in the equation rather than the amount of water in a bucket, this is fine.

Imagine water also pours in the top at a rate $i(t)$. This means the total rate of change of the amount of water is $i - Gx$.

Now, x is the height of the water not the volume: the volume is Cx where C is the cross-sectional area of the bucket. The rate of change of the volume is therefore

$$C\dot{x} = i - Gx \tag{3}$$

or

$$\dot{x} = \frac{1}{C}\left[i - Gx\right] \tag{4}$$

or perhaps most usefully

$$\tau\dot{x} = Ri - x \tag{5}$$

where $R = 1/G$ and, more interestingly, $\tau = C/G$.

The τ is called "tau" because it is a timescale. This can be checked in two ways, first, in this equation on the right hand side there is a x, a length, and Ri that must also be a length. In fact, from $\ell = Gx$ we can see that R converts flow rates like ℓ and i to heights. This implies the left hand side must also be a height and τ is therefore a timescale to balance the 'per time' from the derivative. We can also check directly. From the equation defining G we can see $[G] = L^2/T$ and from we know $[C] = L^2$ so $[\tau] = [C]/[G] = T$.

This is an equation we know how to solve; we saw it at the start of the course when learning about differential equations. This same equation will appear when we look at the dynamics of neuron and for similar reasons, something, water in the case of the bucket, charge in the case of a neuron, is being added to a leaky container.

Constant input

This equation can be solved analytically if the current flowing in is constant, but we won't try that calculation here since it only works for this specific special case, normally we have to solve numerically, using a computer. The

solution is

$$x(t) = [x(0) - Ri]e^{-t/\tau} + Ri \tag{6}$$

This makes sense, when $x = Ri$ then the equation says $\dot{x} = 0$ so this is an equilibrium point, a value where everything stops changing. The dynamics describe the systems as decaying exponentially to the equilibrium.

As for actually finding the solution, that can be done a few different ways, I would usually solve it by ansatz, that is by guessing the solution and checking I am right, so I would substitute in

$$x(t) = A + Be^{rt} \tag{7}$$

with A, B and r constants to get

$$Br\tau e^{rt} = Ri - A - Be^{rt} \tag{8}$$

and the solution follows by matching up the terms to give A and r so, equating the coefficients of the exponential I get $r = -1/\tau$ and $A = Ri$. To find B you just look at the initial condition, the value when $t = 0$. Another common approach to these equations is the integrating factor, this avoids knowing a good guess as the most of ansatz requires, here you rewrite the equation

$$\dot{x} + \frac{1}{\tau}h = \frac{R}{\tau}i \tag{9}$$

and notice that multiplying by $\exp(t/\tau)$ allows you to write the left hand side as a product:

$$\partial_t \left(he^{t/\tau} \right) = \tfrac{R}{\tau} ie^{t/\tau} \tag{10}$$

Next you integrate both sides. There are still other approachs, for example, using Laplace transforms.

These dynamics are intuitive: The more water there is in the bucket, the higher the pressure will be at the leak and the quicker the water will pour out. If there is just the right amount of water the rate the water pours out the leak will precisely match the rate it pours in, this is the equilibrium. If there is more water than required for equilibrium it will pour out faster than the flow coming in, if there is less, it will pour out slower. Either way, as time passes the height of the water will reach the equilibrium. The plot in Fig. 1 illustrates this.

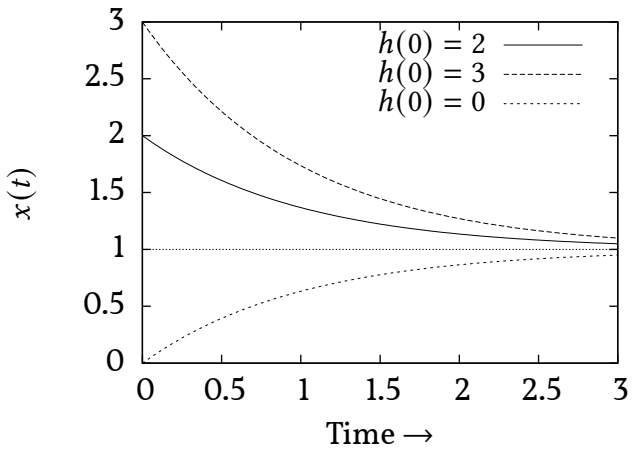


Figure 1: Exponential relaxation. The dynamics described by the "bucket equation" are very common. Here $x(t)$ is plotted with $i = G$, $\tau = 1$ and three different values of $x(0)$. $x(t)$ relaxes towards the equilibrium value, the closer it gets, the slower it approaches.

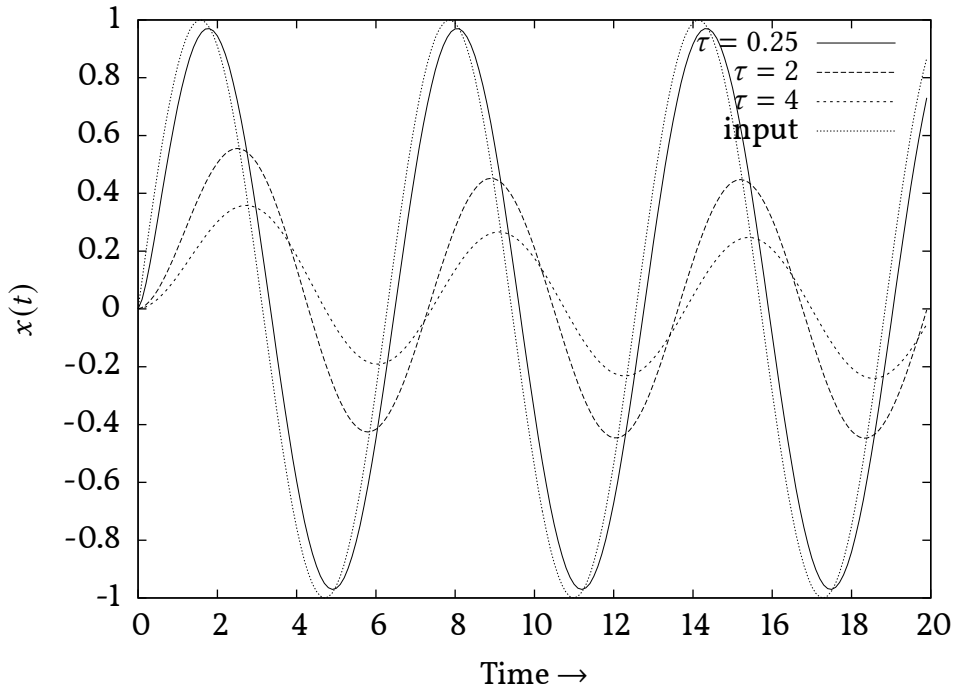


Figure 2: Variable input. Here the input is a sine wave $i(t) = \sin(t)$ and the equation is evolved with $x(0) = 0$ and three different τ values. For $\tau = 0.25$ we see $x(t)$ closely matches the input whereas for larger τ it is smoother and lags behind.

Variable input

We have only discussed constant inputs; the variable input case where i depends on time is harder and although it can sometimes be solved it is often easier just to compute it numerically. We will look briefly at how to do this, but first note that the effect of variable input is that the solution follows the input with a timescale set by τ. For very small τ is chases it quickly, so it is close to the input, but for large τ it lags behind it and smooths it out. This is sometimes described by saying that it **filters** the input. There is an illustration in Fig. 2.

Numerical solutions

Consider a situation where we want to solve

$$\dot{x} = \frac{1}{\tau}(Ri - x), \tag{11}$$

but can't do it analytically—as will be the case for many values of the time dependent input $i(t)$ or, indeed, if $i(t)$ itself is only known numerically.

Forward Euler

The simplest numerical approach is the **forward Euler** method. Say you know the value of $x(t)$ and want to approximate $x(t + \Delta)$ where Δ is a small increment in time. By Taylor expanding $x(t)$ and truncating at first order, we know that

$$x(t + \Delta) = x(t) + \dot{x}(t)\,\Delta + O(\Delta^2). \tag{12}$$

The $O(\Delta^2)$ says there are Δ^2 sized errors in this approximation. These arise because $\dot{x}(t)$ is itself changing but our approximation assumes it is fixed. If we substitute the expression $\dot{x}(t)$ given in right-hand side of Equation (11), we obtain

$$x(t + \Delta) = x(t) + \frac{1}{\tau}[Ri(t) - x(t)]\Delta + O(\Delta^2). \tag{13}$$

A common implementation of forward Euler uses fixed steps in time, with time bins indexed by $n = 0, 1, 2, \ldots$. We can denote this fixed-stepping form of (13) as

$$x_{n+1} \leftarrow x_n + \frac{\Delta}{\tau}(Ri_n - x_n). \tag{14}$$

The "$\leftarrow$" here means "gets" or "assign to", and emphasises that at this point our mathematical equation also serves as pseudo-code for how one might implement fixed-timestep forward Euler in a computer program.

There are more sophisticated approaches like *Runge-Kutta* or *backwards Euler* which are more complex and computational costly for each step, but that are more accurate. In the next subsection, we detail common approach used in computational neuroscience that balances accuracy and simplicity.

Exponential Euler

In the previous subsection, did it seem odd to you that we numerically approximated a solution to (11) using a first-order Taylor expansion, when we already had an *exact* analytic solution for constant input in Equation (6)?

Why not use this exact solution to solve forward Δ time-units into the future, and approximate $i(t)$ as constant over this step?

This approach is known as forward **Exponential Euler**. It leads to the fixed-timestep update

$$x_{n+1} \leftarrow [x_n - Ri_n]e^{-\Delta/\tau} + Ri_n. \tag{15}$$

We can also define $\alpha = e^{-\Delta/\tau}$ to write (15) as

$$x_{n+1} \leftarrow x_n\alpha + (1-\alpha)Ri_n. \tag{16}$$

Forward exponential Euler can be more stable than forward Euler: Since Δ/τ is always positive, $\alpha = e^{-\Delta/\tau}$ is always between 0 and 1. Equation (16) therefore updates x_{n+1} as a **weighted average** of the present x_n and the driving input Ri_n. This avoids overshoot and instability. As an exercise, you may wish to simulate what happens if we choose $\Delta \geq 2\tau$ in forward Euler, and compare this to the behaviour of forward exponential Euler for the same step size. You may encounter code resembling Equation (16) in the source code for computational neuroscience papers in that simulate neuronal membrane voltage.

1 Summary

Water filling a leaky bucket gives a useful example of the dynamics that will describe a neuron. The idea is that the leak is proportional to the height of the water, so we write:

$$\ell(t) = Gx(t) \tag{17}$$

The volume of water is also proportional to the height, so we write:

$$\text{volume} = Cx(t) \tag{18}$$

where G and C are both constants of proportionality, the G will depend in a complicated way on the viscosity of water, the size of the hole, the C is

more straight-forwardly the cross-sectional area of the bucket. Given that the rate of change of volume is given by water coming in minus water going out, an writing $i(t)$ for the inflow:

$$C\dot{x}(t) = i(t) - Gx(t) \tag{19}$$

This can also be written

$$\tau\dot{x} = R \cdot i(t) - x \tag{20}$$

where $R = 1/G$ and $\tau = C/G$ is a timescale. By solving for constant input and discussing the dynamics we see that the solution to this equation 'chases' the input Ri over a timescale corresponding to τ. Finally we look at numerical approaches: for the Euler approximation, the approximate solution at a time $t_n = n\Delta$ is

$$x_n \leftarrow x_{n-1} + \Delta\ \dot{x}|_{t_n} \tag{21}$$

We also introduced forward exponential Euler method for linear first-order systems that track (filter) an input:

$$x_n \leftarrow \alpha x_{n-1} + (1 - \alpha) \cdot \text{input}, \tag{22}$$

where $\alpha = e^{-\Delta/\tau}$.