THEORETICAL NEUROSCIENCE

TD2: MODELS OF NEURONS II

All TD materials will be made available at `https://github.com/yfardella/Th_Neuro_TD_2025`.

Previously, we studied the most basic model for firing neurons: the LIF. In this tutorial, we will extend the LIF model to include post-synaptic refractoriness and firing rate adaptation, while also underlying its limits. We then introduce a more realistic model that can account for a larger repertoire of neural behaviours, the quadratic integrate-and-fire (QIF). Unlike the LIF, this model is described by a nonlinear ODE: we will give tools for understanding the dynamics of such systems without the need of explicitly solving the ODE.

1 Extending leaky integrate-and-fire

1.1 Refractory Period

Additional rules can be added to account for other observed features of real spikes, also called action potentials. One of the observed features is a refractory period; immediately after a spike the neuron cannot produce another spike for a short period of time called the refractory period. The refractory period can be included in models of neurons in a number of ways.

One way is forced voltage clamp: the voltage is fixed at its reset value following a spike for the duration of the refractory period τ_{ref}.

1. What is the maximal firing rate f with this method ?

> The maximal firing rate f is obtained when the neuron fires immediately after the refractory period, therefore
> $$\max f = \frac{1}{\tau_{ref}}.$$

Other ways of incorporating the refractory period include adding a refractory conductance (adding a large conductance g_k at spike time to produce an outward hyperpolarising current) and raising the threshold (rising the threshold value after a spike, so that the neuron is less prone to spiking).

1.2 Firing Rate Adaptation

A well-known property of neurons is adaptation. For instance, driven by an injected current, a decrease in time of the firing rate of a neuron to a steady-state value can be observed.
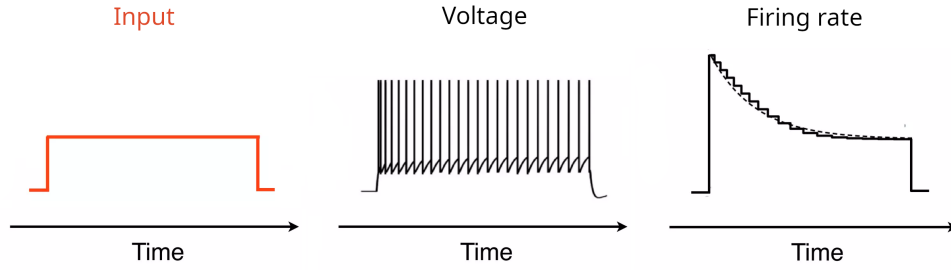
Figure 1: Example of firing rate adaptation in response to injecting a step current.

We are going to model this phenomenon by considering the effect of ion channels which open whenever a neuron fires a spike and let in negative current, such that

$$\tau_m \frac{dV(t)}{dt} = -V(t) - W(t) + I, \tag{1}$$

where, after each spike occurring at V_{th}, W is increased by W_R and V is reset to 0. Between spikes, W decays back to zero with time constant τ_w

$$\tau_w \frac{dW(t)}{dt} = -W(t). \tag{2}$$

1.2.1 Neglecting decay

We make a first approximation that W is **constant** between spikes. A constant current $I_{syn} > V_{th}$ is injected into the neuron.

2. Discuss qualitatively what happens after the first spike.

> After the first spike, W increases by W_R. The steady-state value $V^* = I_{syn} - W$ is shifted to $V^* = I_{syn} - (W + W_R)$, making it closer to V_{th}.

3. At which value W does the model stop spiking? Show that the total number of spikes emitted is roughly $(I_{syn} - V_{th})/W_R$.

> After several spikes, the steady-state may end up below V_{th}, in which case the neuron stops spiking. This happens for
>
> $$I_{syn} - W < V_{th} \Leftrightarrow W > I_{syn} - V_{th}.$$
>
> Starting from $W = 0$, $W = kW_R$ after k spikes, thus the limit is reached for
>
> $$k > \frac{I_{syn} - V_{th}}{W_R}.$$

4. Compute the duration of an inter-spike interval (ISI) as a function of W in that interval.

> In an interval, W is constant and equation (1) is a first-order linear equation. The solution to the ODE is (see previous tutorial)
>
> $$V(t) = (-W + I)(e^{t/\tau_m} - 1)e^{-t/\tau_m}, \text{ taking } t_0 = 0 \text{ and } V_0 = 0.$$

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Then we can compute the ISI interval T

$$V(T) = V_{th} \Leftrightarrow (-We^{T/\tau_m} + W + Ie^{T/\tau_m} - I)e^{-T/\tau_m} = V_{th}$$
$$\Leftrightarrow e^{-T/\tau_m}(W - I) - W + I = V_{th}$$
$$\Leftrightarrow e^{-T/\tau_m} = \frac{I - W - V_{th}}{I - W}$$
$$\Leftrightarrow T = \tau_m \log\left(\frac{I - W}{I - W - V_{th}}\right).$$

1.2.2 Taking decay into account

It is no longer possible to ignore the decay W if the ISI becomes comparable to the time constant of the decay τ_w.

5. Can you explain why? Is it possible for the neuron to stop spiking?

> In that case the decay of W during the interval becomes significant and W cannot be considered constant anymore. This necessarily happens at some point because as we have seen previously, the neuron necessarily stops spiking if W is considered constant (corresponding to an infinite ISI); this approximation cannot hold all along.

We therefore consider that the system has reached its steady-state (equilibrium) firing rate and fires spikes with a period T.

6. Compute the time course of W between two successive spikes, assuming that immediately after the first two spikes $W(t = 0) = W_0$.

> Solving equation (2), we get
> $$W(t) = W_0 e^{-t/\tau_w}.$$

7. Show that W_0 is given by
$$W_0 = \frac{W_R}{1 - \exp(-T/\tau_w)}. \tag{3}$$

> At the steady-state, W decays from W_0 until a spike is emitted at $t = T$. W_R is added to W and the stationary condition is
> $$W(t = T^-) + W_R = W_0.$$
> Having $W(t = T^-) = W_0 e^{-T/\tau_w}$, we find the desired result.

8. **Bonus:** we assume that $T \ll \tau_w$, such that W can be approximated by its average value during the whole inter-spike interval. Show that the period of spike emission is given by
$$T = \tau_m \log\left(\frac{I - W_R \tau_w/T}{I - W_R \tau_w/T - V_{th}}\right). \tag{4}$$

If $T \ll \tau_w$ then W does not vary much - we can therefore approximate it by its average value

$$\langle W \rangle_{ISI} = \frac{1}{T} \int_0^T W(t)dt = \frac{1}{T} \int_0^T W_0 e^{-t/\tau_w} dt = \frac{\tau_w}{T} W_0(1 - e^{-T/\tau_w}) = \frac{\tau_w}{T} W_R.$$

Using question (4), we therefore have

$$T = \tau_m \log \left(\frac{I - \langle W \rangle_{ISI}}{I - \langle W \rangle_{ISI} - V_{th}} \right) = \tau_m \log \left(\frac{I - W_R \tau_w / T}{I - W_R \tau_w / T - V_{th}} \right).$$

9. **Bonus:** show that, as the injected current increases, the neuron firing rate $r(I)$ behaves as

$$r(I) \sim aI, \tag{5}$$

with $a = (\tau_w W_R + \tau_m V_{th})^{-1}$. How does this compare to an integrate-and-fire neuron without firing rate adaptation?

T can be rewritten as

$$T = -\tau_m \log \left(1 - \frac{V_{th}}{I - W_R \tau_w / T} \right).$$

Using the Taylor expansion, we have that for a high current I,

$$T \approx \frac{\tau_m V_{th}}{I - W_R \tau_w / T} \iff TI \approx \tau_m V_{th} + \tau_w W_R.$$

Therefore

$$r(I) = \frac{1}{T} \sim \frac{I}{\tau_m V_{th} + \tau_w W_R}.$$

Without firing rate adaptation, i.e. setting $W_R = 0$ in the previous calculations (one could also do all the calculations again), we have

$$r(I) \sim \frac{I}{\tau_m V_{th}}.$$

Adaptation corresponds to the reduction of the firing rate by a term proportional to the gain W_R of the inhibitory current times its decay constant τ_w. The higher the gain and the larger the decay constant, the stronger adaptation is, effectively reducing the firing rate.

2 Quadratic integrate-and-fire (QIF) neurons

Linear models cannot reproduce all the behaviours of biological neurons. We propose to study a nonlinear model of neurons and show how it can display a richer repertoire of behaviours.

The model we consider is the quadratic integrate-and-fire (QIF) model

$$\frac{dV(t)}{dt} = V(t)^2 + b, \text{ if } V > V_{th} \text{ then } V = V_{reset}, \tag{6}$$

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with b that can be a function of time (e.g. a varying current), but we consider it constant for the time being.

2.1 Case $b > 0$.

10. Describe the behaviour of the system in this case.

> We have that $V(t)^2 + b > 0$, therefore the system is oscillating.

11. **Bonus:** show that the solution to equation (6) is

$$V(t) = \sqrt{b} \tan\left(\sqrt{b}(t + t_0)\right), \quad \text{with } t_0 = \frac{1}{\sqrt{b}} \arctan\left(\frac{V_0}{\sqrt{b}}\right). \tag{7}$$

and compute the period of the oscillations.

> Usually, nonlinear ODEs cannot be solved explicitly. However, for equation (6), using the separation of variables method yields an explicit solution
>
> $$\frac{dV(t)}{dt} = V(t)^2 + b \iff \frac{dV(t)}{V(t)^2 + b} = dt,$$
>
> integrating both sides we have
>
> $$\int_{V(0)=V_0}^{V(t)} \frac{1}{V^2 + b} dV = \int_{t=0}^{t} 1 ds \iff \frac{1}{b} \int_{V_0}^{V(t)} \frac{1}{(V/\sqrt{b})^2 + 1} dV = t.$$
>
> Using the change of variables $y = \frac{V}{\sqrt{b}} \Rightarrow \frac{dy}{dV} = \frac{1}{\sqrt{b}}$
>
> $$\frac{1}{b} \int_{V_0}^{V(t)} \frac{1}{(V/\sqrt{b})^2 + 1} dV = \frac{1}{\sqrt{b}} \int_{y(0)=V_{reset}/\sqrt{b}}^{y(t)=V(t)/\sqrt{b}} \frac{1}{y^2 + 1} dy = \frac{1}{\sqrt{b}} \left[\arctan(y) \right]_{y(0)=V_0/\sqrt{b}}^{y(t)=V(t)/\sqrt{b}}$$
>
> $$= \frac{1}{\sqrt{b}} \left(\arctan\left(V(t)/\sqrt{b}\right) - \arctan\left(V_0/\sqrt{b}\right) \right).$$
>
> Therefore, we have
>
> $$t = \frac{1}{\sqrt{b}} \left(\arctan\left(V(t)/\sqrt{b}\right) - \arctan\left(V_0/\sqrt{b}\right) \right) \iff V(t) = \sqrt{b} \tan\left(\sqrt{b}(t + t_0)\right),$$
>
> with
>
> $$t_0 = \frac{1}{\sqrt{b}} \arctan\left(\frac{V_0}{\sqrt{b}}\right).$$
>
> Setting the initial condition $V_0 = V_{reset}$, the period T of an oscillation is given by
>
> $$T = \frac{1}{\sqrt{b}} \left(\arctan\left(V(T)/\sqrt{b}\right) - \arctan\left(V_0/\sqrt{b}\right) \right)$$
>
> $$= \frac{1}{\sqrt{b}} \arctan\left(\frac{V_{th} - V_{reset}}{\sqrt{b} + V_{th}V_{reset}/\sqrt{b}}\right) < \frac{\pi}{2\sqrt{b}}.$$

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2.2 Case $b < 0$.

12. Find the fixed points (equilibria) of the system in this case, study their stability.

> Finding the fixed points of the system means finding when equation (6) is equal to zero
> $$\frac{dV}{dt} = V^2 + b = 0 \Leftrightarrow V_\pm^* = \pm\sqrt{-b} = \pm\sqrt{|b|}.$$
> The stability is determined by looking at the sign of the derivative of equation (6) with respect to V evaluated at its fixed points $V_\pm^*$. Denoting $f(V) := V^2 + b$, we have
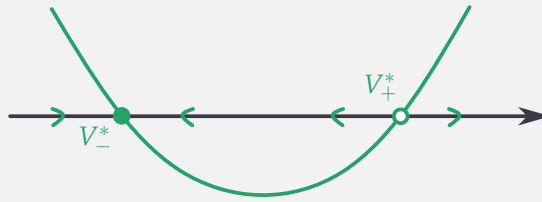> $$f'(V) = \frac{df(V)}{dV} = 2V,$$
> and therefore
> $$f'(V_-^*) = -2\sqrt{|b|} < 0 : \text{the fixed point} V_-^* = -\sqrt{|b|} \text{ is stable,}$$
> $$f'(V_+^*) = 2\sqrt{|b|} > 0 : \text{the fixed point } V_+^* = \sqrt{|b|} \text{ is unstable.}$$
> Another way of understanding and representing the steady-state of the system as well as their stability is summarised in the figure below.
>
>
>
> The green line represents dV/dt, and its intersections with 0 give us the steady-states $V_\pm^*$ of the system. Furthermore, let $V \in [V_-^*, V_+^*]$; since dV/dt is negative in this interval, V will decrease towards V_-^*. Conversely, let $V \in]-\infty, V_-^*]$ (resp. $V \in [V_+^*, \infty[$); since dV/dt is positive in this interval, V will increase towards V_+^* (resp. ∞).

13. Depending on V_{reset} and $b < 0$, describe the three different behaviours of the system.

> Three different behaviours can occur depending on the value of V_{reset} relatively to the unstable fixed point V_+^*
>
> - $V_{reset} < \sqrt{|b|}$: after a reset, the system decays back to the stable fixed point V_-^*. However, a sufficiently high perturbation can drive it above the unstable point and make it emit a single spike. The system is excitable.
>
> - $V_{reset} = \sqrt{|b|}$: after a reset, the system lies on the unstable point V_+^*. A small perturbation can either drive it to spiking or to the stable fixed point V_-^*.
>
> - $V_{reset} > \sqrt{|b|}$: after a reset, the system displays periodic oscillations as in the case $b > 0$. However, a strong (inhibitory) perturbation could set it on the stable fixed point, where it would require a strong (excitatory) perturbation to restart oscillatory spiking. The system is bistable.

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The following figure (called a bifurcation diagram) summarises all the behaviours of the system we have studied above (cases $b > 0$ and $b < 0$).
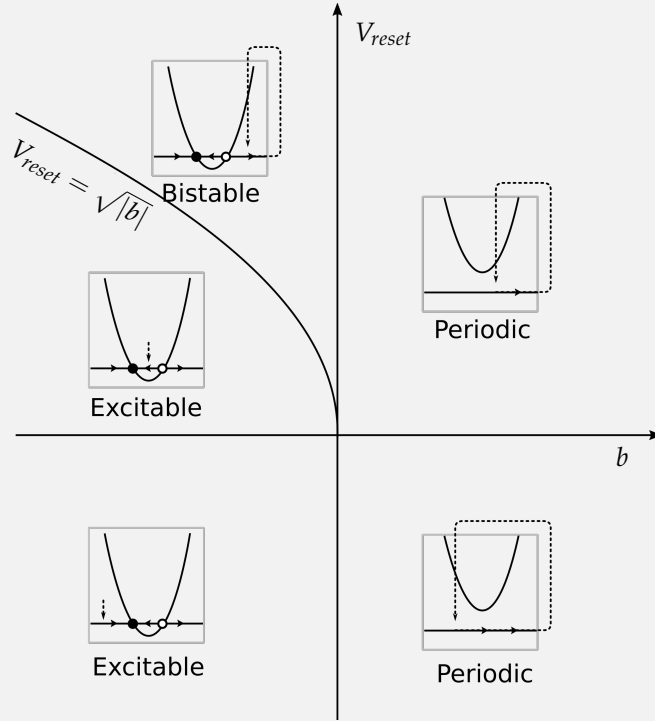
14. **Bonus:** considering that $V_{reset} > \sqrt{|b|}$, show that the solution to equation (6) is

$$V(t) = \sqrt{|b|} \frac{1 + \exp\left(2\sqrt{|b|}(t + t_0)\right)}{1 - \exp\left(2\sqrt{|b|}(t + t_0)\right)}, \quad \text{with } t_0 = \frac{1}{2\sqrt{|b|}} \log\left(\frac{V_0 - \sqrt{|b|}}{V_0 + \sqrt{|b|}}\right). \qquad (8)$$

and compute the period of the oscillations.

Using again the separation of variables method, we have

$$\int_{V(0)=V_0}^{V(t)} \frac{1}{V^2 - |b|} dV = \int_{t=0}^{t} 1 ds.$$

We apply a partial fraction decomposition to obtain

$$\frac{1}{V^2 - |b|} = \frac{1}{(V - \sqrt{|b|})(V + \sqrt{|b|})} = \frac{1}{2\sqrt{|b|}(V - \sqrt{|b|})} - \frac{1}{2\sqrt{|b|}(V + \sqrt{|b|})}.$$

We have

$$\int_{V_0}^{V(t)} \frac{1}{V^2 - |b|} dV = \int_{V_0}^{V(t)} \frac{1}{2\sqrt{|b|}(V - \sqrt{|b|})} - \frac{1}{2\sqrt{|b|}(V + \sqrt{|b|})} dV$$

$$= \frac{1}{2\sqrt{|b|}} \int_{V_0}^{V(t)} \frac{1}{V - \sqrt{|b|}} - \frac{1}{V + \sqrt{|b|}} dV$$

$$= \frac{1}{2\sqrt{|b|}} \left[\log\left(V - \sqrt{|b|}\right) - \log\left(V + \sqrt{|b|}\right) \right]_{V_0}^{V(t)}$$

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$$= \frac{1}{2\sqrt{|b|}} \left[\log \left(\frac{V - \sqrt{|b|}}{V + \sqrt{|b|}} \right) \right]_{V_0}^{V(t)}$$

$$= \frac{1}{2\sqrt{|b|}} \left(\log \left(\frac{V(t) - \sqrt{|b|}}{V(t) + \sqrt{|b|}} \right) - \log \left(\frac{V_0 - \sqrt{|b|}}{V_0 + \sqrt{|b|}} \right) \right).$$

Therefore, we have

$$t = \frac{1}{2\sqrt{|b|}} \left(\log \left(\frac{V(t) - \sqrt{|b|}}{V(t) + \sqrt{|b|}} \right) - \log \left(\frac{V_0 - \sqrt{|b|}}{V_0 + \sqrt{|b|}} \right) \right)$$

$$\Leftrightarrow \frac{V(t) - \sqrt{|b|}}{V(t) + \sqrt{|b|}} = \exp \left(2\sqrt{|b|}t + \log \left(\frac{V_0 - \sqrt{|b|}}{V_0 + \sqrt{|b|}} \right) \right)$$

$$\Leftrightarrow V(t) = \sqrt{|b|} \frac{1 + \exp \left(2\sqrt{|b|}(t + t_0) \right)}{1 - \exp \left(2\sqrt{|b|}(t + t_0) \right)},$$

with

$$t_0 = \frac{1}{2\sqrt{|b|}} \log \left(\frac{V_0 - \sqrt{|b|}}{V_0 + \sqrt{|b|}} \right).$$

Setting the initial condition $V_0 = V_{reset}$, the period T of an oscillation is given by

$$T = \frac{1}{2\sqrt{|b|}} \left(\log \left(\frac{V_{th} - \sqrt{|b|}}{V_{th} + \sqrt{|b|}} \right) - \log \left(\frac{V_{reset} - \sqrt{|b|}}{V_{reset} + \sqrt{|b|}} \right) \right).$$

3   Bonus: Theta neurons

The theta model is described by the following ODE

$$\frac{d\theta(t)}{dt} = 1 - \cos \theta(t) + (1 + \cos \theta(t))I(t). \tag{9}$$

We consider that a spike is emitted when θ reaches the value π.

15. Show that for $I > 0$, there is no equilibrium. Conclude that the trajectories are periodic orbits with regular spiking.

We have that

$$I > 0 \Rightarrow -1 + I > -1 \Rightarrow (\cos \theta)(-1 + I) > -1$$
$$\Rightarrow (\cos \theta)(-1 + I) + 1 + I > -1 + 1 + I > 0.$$

Therefore, $d\theta/dt$ is always strictly positive, meaning there is no equilibrium and the system oscillates.

16. Show that for $I < 0$, there are two steady-states for the system, one stable and one unstable.

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Let $I < 0$. Then

$$\frac{d\theta}{dt} = 1 - \cos\theta + (1 + \cos\theta)I = 0 \Leftrightarrow \cos\theta = \frac{1+I}{1-I},$$

which has two distinct solutions because $\cos(\theta) = \cos(-\theta)$. Let $\theta_*^{\pm}$ denote these two fixed points and $f(\theta) := 1 - \cos\theta + (1 + \cos\theta)I$. Then

$$f'(\theta) = (\sin\theta)(1 - I), \text{ with } 1 - I > 0,$$

meaning the stability of $\theta_*^{\pm}$ is determined by the sign of $\sin\theta_*^{\pm}$. Since $\theta_*^- = -\theta_*^+$ and $\sin(-\theta) = -\sin(\theta)$, we necessarily have that one fixed point is stable and the other unstable.

17. Show that this model is equivalent to the QIF model.

We have seen that the dynamics of the theta model are the same as those of the QIF model. We can explicitly show that both models are equivalent: indeed, the change of variables $V = \tan\theta$ transforms the QIF model into the theta model.