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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 model?

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.

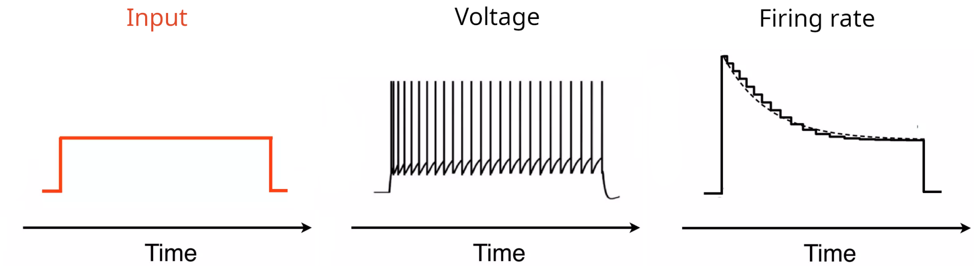

Figure 1: Example of firing rate adaptation in response to injecting a step current.

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.
3. At which value W does the model stop spiking? Show that the total number of spikes emitted is roughly $(I_{syn} - V_{th})/W_R$.
4. Compute the duration of an inter-spike interval (ISI) as a function of W in that interval.

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?

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 $W(t = 0) = W_0$.
7. Show that W_0 is given by

$$W_0 = \frac{W_R}{1 - \exp(-T/\tau_w)}. \tag{3}$$

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

$$T = \tau_m \log \left(\frac{I - W_R \tau_w / T}{I - W_R \tau_w / T - V_{th}} \right). \tag{4}$$

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?

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

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

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.

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

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

and compute the period of the oscillations.

2.2 Case $b < 0$.

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

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

14. **Bonus:** considering that $V_{reset} > \sqrt{|b|}$, show that the solution to equation (6) is

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

and compute the period of the oscillations.

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.
16. Show that for $I < 0$, there are two fixed points for the system, one stable and one unstable.
17. Show that this model is equivalent to the QIF model.