M2 Biology **15/10/18**

TD2: Models of Neurons II

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`https://github.com/Elieoriol/2021_UlmM2_ThNeuro/tree/master/TD2`

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.

1.1 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?

   A disadvantage of this method is that as the firing rate of the neuron increases, the neuron spends a greater proportion of its time in the refractory period with the membrane potential at its low reset value. Therefore, the mean membrane potential decreases with increased input in such a model, in contrast to the behavior of real neurons.

1.2 Refractory conductance

A solution closer to biology is to add a large conductance g_K at spike time, producing an outward hyperpolarizing current. In real neurons, such a late current can most often be related to potassium channels.

2. Explain why a large conductance can replace the LIF reset mechanism. Propose a differential equation for g_K to enable the neuron to spike again after the refractory period. Does this model solve the previous problem?

Note: This is a first step towards the Hodgkin-Huxley model of spiking neurons. The difference resides in that instead of roughly adding a decaying conductance at spike time, this conductance is made non-linearly voltage-dependent: when the membrane potential reaches high values, this conductance becomes large and brings the potential down.

1.3 Raised threshold

A third alternative could be to consider that the neuron does not really go into a refractory period but instead becomes less prone to spiking by raising its threshold.

3. By analogy with the previous method, can you think of a way to implement a raised threshold method?
4. **num** Implement numerically the three previous methods.

2 Non linear models

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

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

$$\begin{aligned} \frac{\mathrm{d}V}{\mathrm{d}t} &= V^2 + b \\ \text{if } V > V_{peak} &\text{ , then } V \to V_{reset} \end{aligned} \tag{1}$$

We consider here the potential V and the quantity b to be adimensional (through normalization for instance). b can be a function of time (a varying current), but we consider it constant for the moment.

5. Would you describe V_{peak} as a threshold?

2.1 $b > 0$

6. Describe the behavior of the neuron in this case.

2.2 $b < 0$

7. Can you characterize the steady states of the neuron? Plot the graph of these steady states against b.
8. Depending on V_{reset} and $b < 0$, what are the different behaviors of the neuron regarding excitation?

2.3 Bifurcation diagram

9. Plot the bifurcation diagram of the system, in the V_{reset} and b space.
10. We consider $V_{reset} > \sqrt{|b|}$. Can you compute the period of the oscillations? We note that the solution of the differential equation in this case is:

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

with $t_0 = \dfrac{1}{2\sqrt{|b|}} \log\left(\dfrac{V_{reset} - \sqrt{|b|}}{V_{reset} + \sqrt{|b|}}\right)$.

2.4 Analogy with "theta neurons"

The theta model is described by the following equation:

$$\frac{\mathrm{d}\theta}{\mathrm{d}t} = 1 - \cos\theta(t) + [1 + \cos\theta(t)] \cdot I(t) \tag{2}$$

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

11. Show that for $I < 0$ there are two equilibria for the system, a stable and an unstable one. Show that if θ is not initially equal to the unstable equilibrium, it converges to the stable equilibrium.

12. In the case $I > 0$, show that there is no equilibrium. Conclude that the trajectories are periodic orbits with regular spiking.

13. Can you see a link with the quadratic model? What happens when $I = 0$?