

[https://github.com/Elieoriol/2021\\_U1mM2\\_ThNeuro/tree/master/TD3b](https://github.com/Elieoriol/2021_U1mM2_ThNeuro/tree/master/TD3b)

In the following we will consider the parameters:

$C$	$g_l$	$E_l$	$g_K$	$E_K$	$g_{Na}$	$E_{Na}$
$1\mu\text{F}/\text{cm}^2$	$0.3\text{mS}/\text{cm}^2$	$-54.4\text{mV}$	$36\text{mS}/\text{cm}^2$	$-77\text{mV}$	$120\text{mS}/\text{cm}^2$	$50\text{mV}$

## 1 The Hodgkin-Huxley model of spiking neurons

In the leaky integrate-and-fire model, spikes occur as a simple threshold crossing of the voltage variable; the biophysical mechanisms for spike generation are not directly described. In the Hodgkin-Huxley model, spikes are generated by the cooperative activity of two voltage dependent channels (sodium Na and potassium K), which open and close with different time scales. The equation which regulates the time evolution of the membrane potential is given by:

$$C \frac{dV}{dt} = g_l(E_l - V) + g_K n^4 (E_K - V) + g_{Na} m^3 h (E_{Na} - V) + I \quad (1)$$

where the second term on the right-hand-side describes the current due to the K-channel and the third term the current due to the Na-channel.

The channel variables  $h$ ,  $m$ ,  $n$  all follow first-order kinetics, i.e. rate equations of the form

$$\frac{dx}{dt} = \alpha_x(V)(1 - x) - \beta_x(V)x \quad (2)$$

and the open and closing rates,  $\alpha(V)$ , and  $\beta(V)$  are channel-specific and voltage-dependent.

$$\begin{aligned} \alpha_n(V) &= \frac{55 + V}{100(1 - e^{-(55+V)/10})} \\ \beta_n(V) &= e^{(65+V)/80}/8 \\ \alpha_m(V) &= \frac{40 + V}{10(1 - e^{-(40+V)/10})} \\ \beta_m(V) &= 4e^{-(65+V)/18} \\ \alpha_h(V) &= 0.07e^{-(65+V)/20} \\ \beta_h(V) &= \frac{1}{(e^{-(35+V)/10} + 1)} \end{aligned}$$

1. **num** Implement numerically this model with  $I = 10$  using Euler's method.
2. **num** Vary the value of the external input. At which value  $I_C$  does the neuron start firing?
3. **num** What is the value of the firing rate for  $I \sim I_C$ ? How does this differ from a LIF neuron?

## 2 Sub-threshold resonance

From experiments it is observed that some neurons display a resonance of their membrane potential at a particular frequency upon injection of a small oscillating current.

We now consider the behaviour of the Hodgkin-Huxley model close to the leak potential  $V_L$ . The sodium channels are therefore closed and can be ignored.

$$\begin{aligned} C \frac{dV}{dt} &= -g_L(V - V_L) - g_K n^4(V - V_K) \\ \tau_n(V) \frac{dn}{dt} &= -n + n_\infty(V) \end{aligned} \quad (3)$$

1. We suppose that there is an equilibrium point at  $V_{eq}$  and  $n_{eq}$ , where:

$$\frac{dV}{dt} = 0 \quad \frac{dn}{dt} = 0 \quad (4)$$

We aim at studying the stability of this solution. We consider a small perturbation away from the equilibrium, and we analyse its time evolution.

Linearize the equations around this equilibrium point so as to show that the response to a small perturbation  $V(t) = V_{eq} + \delta V(t)$ ,  $n(t) = n_{eq} + \delta n(t)$  follows:

$$\frac{d(\delta V)}{dt} = -a\delta V - b\delta n \quad \frac{d(\delta n)}{dt} = c\delta V - d\delta n \quad (5)$$

where:

$$\begin{aligned} a &= (g_L + g_K n_{eq}^4)/C \\ b &= 4g_K n_{eq}^3(V_{eq} - V_K)/C \\ c &= n'_\infty(V_{eq})/\tau_n(V_{eq}) \\ d &= 1/\tau_n(V_{eq}) \end{aligned} \quad (6)$$

2. Determine the time evolution of the first-order perturbations. Under what conditions will the system return to the equilibrium point when it is perturbed?

We can consider the evolution of the vector  $X = (\delta V, \delta n)$ .

3. Consider the system dynamics close to the equilibrium state. Show that the response to a small oscillating current is:

$$V_0 \exp(i\phi_V) = \frac{I_0(d + i\omega)}{bc + (d + i\omega)(a + i\omega)}$$

4. Does the voltage response necessarily decrease as the input frequency  $\omega$  increases?

For simplicity, consider the case  $a = 0$ . Show that there is resonance if  $bc/d^2 > \sqrt{2} - 1$ .