# Problem Set 3:
## The Leaky Integrate–and–Fire Neuron

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In the first problem set we looked at the Hodgkin-Huxley model of the neuron. This is the leading example of an *active* model of the membrane potential of the neuron, where the opening and closing of its ionic channels causes the membrane to play an active role in the temporal evolution of the membrane potential. As a result though, the Hodgkin-Huxley equations define a 4-dimensional, non-linear system making analysis difficult. Simpler model can be created by restricting the membrane to play a *passive* role, whose properties (e.g. channel porosity and membrane permeability) don't change with time or membrane potential. An example is the leaky integrate-and-fire (LIF) neuron model, which only keeps the time-/voltage-independent leak current term out of all the channel currents of the Hodgkin-Huxley model. The differential equation can be written as

$$\frac{\mathrm{d}U}{\mathrm{d}t} + \frac{U}{\tau} = \frac{I_{\mathrm{stim}}(t)}{C}, \qquad U(t_0) = b, \tag{1}$$

where $C$ and $\tau$ are constants, and $b$ is the arbitrary initial condition of the membrane potential. Note we've set the resting potential as $U_0 = 0$ for simplicity. In this sheet, we will take the further simplification of having no threshold potential $V_{\mathrm{th}}$ found in the usual LIF model, such that no "synthetic" spikes are produced and the membrane potential is never reset. As a result, however, we will be able to investigate the sub-threshold membrane potential dynamics in response to different inputs $I_{\mathrm{stim}}(t)$.

## Problem 1: The Full Solution — 8 points

### Problem 1.1: The exact solution — 4 points

Integrate Equation 1 from $t = t_0$ to $t = T$ to find the exact solution to the system. You should obtain the following solution:

$$U(T) = U(t_0)e^{(t_0 - T)/\tau} + \int_{t_0}^{T} \frac{I_{\mathrm{stim}}(t)}{C} e^{(t-T)/\tau} \mathrm{d}t. \tag{2}$$

*Hint: Start by noting that $(U(t)e^{t/\tau})' = (U'(t) + U(t)/\tau)e^{t/\tau}$, substitute in Equation 1 and integrate both sides.*

### Problem 1.2: Response to sinusoidal input — 4 points

Obtain the response of the system to a sinusoidal input current $I_{\mathrm{stim}}(t) = I_0 \sin(2\pi\omega t)$ from $t = 0$ to $t = T$.

*Hint: You should find the following integral useful*

$$\int e^{(t-a)/b} \sin(ct)\ \mathrm{d}t = b\ e^{(t-a)/b} \frac{-(b\,c)\cos(ct) + \sin(ct)}{1 + b^2c^2},$$

*as well as this trigonometric identity*

$$A\sin(x) + B\cos(x) = \sqrt{A^2+B^2}\sin\big(x + \tan^{-1}(B/A)\big).$$

# Problem 2: The Solution at Late Times — 8 points

### Problem 2.1: The simplified solution — 3 points

The solution becomes much simpler if we are merely interested in the late-time behaviour $T \to \infty$. Find the late-time solution of Equation 2 by letting $t_0 = -\infty$. By defining the function

$$G(t) = \begin{cases} 0 & \text{if } t < 0, \\ \frac{1}{C}e^{-t/\tau} & \text{if } t \geq 0, \end{cases} \tag{3}$$

you should obtain the following solution:

$$U(T) = \int_{-\infty}^{T} G(T-t) I_{\mathrm{stim}}(t)\mathrm{d}t. \tag{4}$$

### Problem 2.2: The significance of G(t) — *Star problem*

Equation 4 tells us that the late-time response of the membrane potential to current input $I_{\mathrm{stim}}(t)$ is simply the convolution of the function $G(t)$ and the current: $U(T) = (G * I_{\mathrm{stim}})(T)$. Find the late-time response of the system to an impulse at $t = 0$: $I_{\mathrm{stim}} = \delta(t)$. What is the significance of $G(t)$? What role does it play for arbitrary input $I_{\mathrm{stim}}(t)$?

*Hint: Remember that any arbitrary function can be decomposed into a sum of weighted Dirac delta functions* $f(t) = \sum_i \alpha(t_i)\delta(t - t_i)$[1]*, where* $\alpha(t_i)$ *is the weight of the Dirac delta at time* $t = t_i$*.*

### Problem 2.3: Linearity and time-invariance — *Star problem*

Prove both the linearity and time-invariance of the late-time solution given by Equation 4.

*Hint: To prove linearity, it is sufficient to show that that if* $U_f(T)$ *is the response of the system to input* $I_{stim}(t) = f(t)$ *then* $U_{\alpha f + \beta g}(T) = \alpha U_f(T) + \beta U_g(T)$ *is the resonse to input* $I_{stim}(t) = \alpha f(t) + \beta g(t)$*.*

*To prove time-invariance, it is sufficient to show that if the input is pushed in time* $I_{stim}(t) = g(t) \equiv f(t + \tau_0)$*, then* $U_g(T) = U_f(T + \tau_0)$*.*

### Problem 2.4: Late-time solution to the sinusoidal input — 5 points

Show that the Fourier transform of $G(t)$ is

$$\hat{G}(\phi) = \frac{1}{C(1/\tau + 2\pi i\phi)} \tag{5}$$

[1] $f(t) = \int \alpha(t_i)\delta(t - t_i)\mathrm{d}t$ in the continuous case.

Use this solution to determine the late-time response of the system to the same sinusoidal input used in Problem 1.2. Does your solution agree with what you obtained in Problem 1.2?

*Hint: Use the convolution theorem: if $h(t) = (f * g)(t)$, then $\hat{h}(\phi) = \hat{f}(\phi) \cdot \hat{g}(\phi)$, where '$\cdot$' denotes the point-wise product. Use the following relations between trigonometric functions and the complex exponential:*

$$\cos(x) = \frac{e^{ix} + e^{-ix}}{2}, \qquad \sin(x) = \frac{e^{ix} - e^{-ix}}{2}.$$

*as well as the trigonometric identity given in Problem 1.2.*

## Take home notes:

In this sheet, we saw that the linearity of the system allowed for easy analytical analysis not possible for the non-linear (and high-dimensional) Hodgkin-Huxley model. That said, this simplistic model cannot reproduce the interesting phenomena that we saw in the Hodgkin-Huxley model, such as the action potential (without *ad hoc* reset of the membrane potential acting as a spike), the refractory period, the production of a solitary spike during continuous current input, and the rebound spike. These phenomena require the non-linearity and dimensionality of the Hodgkin-Huxley model.