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 τ 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_{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.

Solution.

Integrating $(U(t)e^{t/\tau})' = (U'(t) + U(t)/\tau)e^{t/\tau}$ from $t = t_0$ to $t = T$:

$$[U(t)e^{t/\tau}]_{t_0}^{T} = \int_{t_0}^{T} (U'(t) + U(t)/\tau)e^{t/\tau}\mathrm{d}t.$$

Substituting Equation 1 into the brackets on the RHS and expanding the LHS:

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

Multiplying both sides by $e^{-T/\tau}$:

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

Problem 1.2: Response to sinusoidal input **4 points**

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

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

Solution.

Substituting the current into Equation 2:

$$U(T) = U(t_0)e^{(t_0-T)/\tau} + \frac{I_0}{C}\int_{0}^{T} \sin(2\pi\omega t)e^{(t-T)/\tau} \mathrm{d}t.$$

Using the integral given in the hint, with change of variables $a = T$, $b = \tau$, $c = 2\pi\omega$:

$$\begin{aligned}
U(T) &= U(t_0)e^{(t_0-T)/\tau} + \frac{I_0}{C}\left[\tau\ e^{(t-T)/\tau} \frac{-2\pi\omega\tau\cos(2\pi\omega t) + \sin(2\pi\omega t)}{1 + (2\pi\omega\tau)^2}\right]_0^T \\
&= U(t_0)e^{(t_0-T)/\tau} + \frac{I_0}{C}\left[\left(\tau\frac{-2\pi\omega\tau\cos(2\pi\omega T) + \sin(2\pi\omega T)}{1 + (2\pi\omega\tau)^2}\right) - \left(\tau e^{-T/\tau}\frac{-2\pi\omega\tau}{1 + (2\pi\omega\tau)^2}\right)\right] \\
&= U(t_0)e^{(t_0-T)/\tau} + \frac{I_0}{C}\tau^2\left(\frac{2\pi\omega e^{-T/\tau} - 2\pi\omega\cos(2\pi\omega T) + 1/\tau\sin(2\pi\omega T)}{1 + (2\pi\omega\tau)^2}\right) \\
&= U(t_0)e^{(t_0-T)/\tau} + \frac{I_0}{C}\left(\frac{2\pi\omega e^{-T/\tau} - 2\pi\omega\cos(2\pi\omega T) + 1/\tau\sin(2\pi\omega T)}{1/\tau^2 + (2\pi\omega)^2}\right)
\end{aligned}$$

Using the trigonometry identity given in the hint with $A = 1/\tau$ and $B = -2\pi\omega$:

$$U(T) = U(t_0)e^{(t_0-T)/\tau} + \frac{I_0}{C}\frac{2\pi\omega e^{-T/\tau} + \sqrt{1/\tau^2 + (2\pi\omega)^2}\sin\big[2\pi\omega T - \tan^{-1}(2\pi\omega\tau)\big]}{1/\tau^2 + (2\pi\omega)^2},$$

since $\tan(-x) = -\tan(x)$.

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:

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

Solution.

Substituting $t_0 = -\infty$ and noting that $e^{-\infty} = 0$:

$$U(T) = \int_{-\infty}^{T} \frac{I_{\text{stim}}(t)}{C} e^{(t-T)/\tau} \mathrm{d}t.$$

Since $T - t \geq 0$ for all $t \in [-\infty, T]$ (limits of integral), only the right-most sub-function of Equation 3 is relevant. Substituting it in with change of variables $t \to T - t$, we obtain the solution Equation 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 $I_{\text{stim}}(t)$ is simply the convolution of the function $G(t)$ and the current: $U(T) = (G * I_{\text{stim}})(T)$. Find the late-time response of the system to an impulse at $t = 0$: $I_{\text{stim}} = \delta(t)$. What is the significance of $G(t)$? What role does it play for arbitrary input $I_{\text{stim}}(t)$?

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 $t = t_i$.

Solution.

An impulse at $t = 0$ is given by the Dirac delta function $\delta(t)$. Substituting $I_{\text{stim}} = \delta(t)$ into Equation 4:

$$\begin{aligned} U_\delta(T) &= \int_{-\infty}^{T} G(T-t)\delta(t) \mathrm{d}t \\ &= G(T) \end{aligned}$$

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

Thus, $G(T)$ is simply the response of the system to an impulse at $t = 0$, known as the impulse response function. Note that in Equation 3, the impulse response function is defined by two sub-functions with the time domain separated at $t = 0$ as for $t < 0$ the system does not yet respond to an input at $t = 0$ (the system is *causal*), the response only starts at $t = 0$.

Note also that though the Dirac delta function can be defined as (a distribution/test function) as $\int_{-\infty}^{\infty} f(x-\alpha)\delta(x)\mathrm{d}x = f(\alpha)$ where the integral is over the whole real line $x \in (-\infty, \infty)$, one simply needs to make sure that the limits of the integral $x \in (a, b)$ enclose $x = 0$ to obtain $\int_a^b f(x-\alpha)\delta(x) = f(\alpha)$. The result we derived just above thus stands with the condition $T \geq 0$.

Now, substituting an arbitrary input $I_{\text{stim}}(t) = \sum_i \alpha_i(t_i)\delta(t - t_i)$ into Equation 4:

$$\begin{aligned} U_\delta(T) &= \int_{-\infty}^{T} G(T-t)\left[\sum_i \alpha_i(t_i)\delta(t-t_i)\right]\mathrm{d}t \\ &= \sum_i \alpha(t_i)\int_{-\infty}^{T} G(T - t_i + t_i - t)\delta(t-t_i)\mathrm{d}t \\ &= \sum_i \alpha(t_i)G(T-t_i) \end{aligned}$$

Thus, Equation 4 is thus telling us that the response of the system to any arbitrary input I_{stim} is a weighted linearly sum of the functions $G(T)$, whose weights $\alpha(t_i)$ and shifts in time $T - t_i$ are determined by the decomposition of the input into Dirac delta functions. Note the same holds for arbitrary *continuous-time* input (i.e. decomposing the input as $I_{\text{stim}} = \int \alpha(t_i)\delta(t - t_i)\mathrm{d}t$).

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 $U_g(T) = U_f(T + \tau_0)$.

Solution.

Linearity:
RTP: We are required to show that if $U_f(T)$ is the response to input $I_{stim}(t) = f(t)$ then $U_{\alpha f+\beta g}(T) = \alpha U_f(T) + \beta U_g(T)$.

Starting with the left-hand side, substituting $I_{\text{stim}} = \alpha f(t) + \beta g(t)$ and $G(T - t) =$

$1/Ce^{(t-T)/\tau}$ as $T - t \geq 0$ for $t \in (-\infty, T]$ into Equation 4:

$$
\begin{aligned}
U_{\alpha f+U_\beta f}(T) &= \int_{-\infty}^{T} G(T-t)\big[\alpha f(t) + \beta g(t)\big]\mathrm{d}t \\
&= \alpha \int_{-\infty}^{T} G(T-t) f(t)\mathrm{d}t + \beta \int_{-\infty}^{T} G(T-t) g(t)\mathrm{d}t \\
&= \alpha U_f(T) + \beta U_g(T).
\end{aligned}
$$

Thus, the system is linear due to the linearity of integration.

Time-invariance:
RTP: That if $g(t) = f(t+\tau_0)$, then $U_g(T) = U_f(T+\tau_0)$.

The response of the system to input $I_{\mathrm{stim}}(t) = f(t)$ is $U_f(T) = \int_{-\infty}^{T} G(T-t)f(t)\mathrm{d}t$, while that to $I_{\mathrm{stim}}(t) = g(t) \equiv f(t+\tau_0)$ is $U_g(T) = \int_{-\infty}^{T} G(T-t)f(t+\tau_0)\mathrm{d}t$. A change of time variables to $x = t + \tau_0$ in $U_g(T)$ means:

$$
\begin{aligned}
\frac{\mathrm{d}x}{\mathrm{d}t} = 1 \quad &\Longrightarrow \quad \mathrm{d}t = \mathrm{d}x \\
x_i = t_i + \tau_0 \quad &\Longrightarrow \quad x_i = -\infty + \tau_0 = -\infty \\
x_f = t_f + \tau_0 \quad &\Longrightarrow \quad x_f = T + \tau_0
\end{aligned}
$$

Making these substitutions into $U_g(T)$ we get

$$
\begin{aligned}
U_g(T) &= \int_{-\infty}^{T+\tau_0} G(T+\tau_0-x)f(x)\mathrm{d}x \\
&\equiv U_f(T+\tau_0)
\end{aligned}
$$

Thus, the same input pushed forward in time by τ_0 (i.e. $g(t) = f(t+\tau_0)$) produces the same membrane potential response but pushed forward in time by τ_0 (i.e. $g(t) = f(t+\tau_0)$). This is exactly what it means for the system to be time-invariant.

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

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

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

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:

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

as well as the trigonometric identity given in Problem 1.2.

Solution.

The Fourier transform of $G(t)$ is:

$$
\begin{aligned}
\hat{G}(\phi) &= \int_{-\infty}^{+\infty} G(t)e^{-2\pi i\phi t}\mathrm{d}t \\
&= \int_{-\infty}^{0} \big[0\big]e^{-2\pi i\phi t}\mathrm{d}t + \frac{1}{C}\int_{0}^{+\infty} \big[e^{-t/\tau}\big]e^{-2\pi i\phi t}\mathrm{d}t \\
&= \frac{1}{C}\int_{0}^{+\infty} e^{-t/\tau}e^{-2\pi i\phi t}\mathrm{d}t \\
&= \frac{1}{C}\int_{0}^{+\infty} e^{-t(1/\tau+2\pi i\phi)}\mathrm{d}t \\
&= -\frac{1}{C(1/\tau+2\pi i\phi)}\Big[e^{-t(1/\tau+2\pi i\phi)}\Big]_{0}^{+\infty} \\
&= \frac{1}{C(1/\tau+2\pi i\phi)}
\end{aligned}
$$

From Lecture 1, the Fourier transform of $I_{\text{stim}}(t) = I_0\sin(2\pi\omega t)$ is:

$$\hat{I}_{\text{stim}}(\phi) = I_0\frac{i}{2}\big(\delta(\phi+\omega) - \delta(\phi-\omega)\big).$$

Since the system response is a convolution $U(T) = (G * I_{\text{stim}})(T)$, then by the convolution theorem: $\hat{U}(\phi) = \hat{G}(\phi)\cdot\hat{I}_{\text{stim}}(\phi)$. Thus, the response of the system can be calculated using the reverse Fourier transform:

$$
\begin{aligned}
U(T) &= \int_{-\infty}^{+\infty} \hat{U}(\phi)e^{2\pi i\phi T}\mathrm{d}\phi \\
&= \int_{-\infty}^{+\infty}\left[\frac{1}{C(1/\tau+2\pi i\phi)}\right]\left[I_0\frac{i}{2}\big(\delta(\phi+\omega)-\delta(\phi-\omega)\big)\right]e^{2\pi i\phi T}\mathrm{d}\phi \\
&= \frac{iI_0}{2C}\int_{-\infty}^{+\infty}\left[\frac{1/\tau-2\pi i\phi}{1/\tau^2+(2\pi\phi)^2}\right]\Big[\delta(\phi+\omega)-\delta(\phi-\omega)\Big]e^{2\pi i\phi T}\mathrm{d}\phi \\
&= \frac{iI_0}{2C(1/\tau^2+(2\pi\omega)^2)}\Big[e^{-2\pi i\omega T}\big(1/\tau+2\pi i\omega\big) - \Big[e^{2\pi i\omega T}\big(1/\tau-2\pi i\omega\big)\Big] \\
&= \frac{iI_0}{2C(1/\tau^2+(2\pi\omega)^2}\left[-2i/\tau\left(\frac{e^{2\pi i\omega T}-e^{-2\pi i\omega T}}{2i}\right)+4\pi i\omega\left(\frac{e^{2\pi i\omega T}+e^{-2\pi i\omega T}}{2}\right)\right]
\end{aligned}
$$

Using the the exponential expressions for sinusoids obtained from Euler's formula and cancelling factors:

$$U(T) = \frac{I_0}{C(1/\tau^2+(2\pi\omega)^2}\Big[1/\tau\sin(2\pi\omega T) - 2\pi\omega\cos(2\pi\omega T)\Big]$$

Using the trigonometric identity given in the hint of Problem 1.2 we obtain the solution:

$$\begin{aligned} U(T) &= \frac{I_0}{C(1/\tau^2 + (2\pi\omega)^2} \left[\sqrt{1/\tau^2 + (2\pi\omega)^2} \sin\big(2\pi\omega T - \tan^{-1}(2\pi\omega\tau)\big) \right] \\ &= \frac{I_0}{C\sqrt{(1/\tau^2 + (2\pi\omega)^2}} \left[\sin\big(2\pi\omega T - \tan^{-1}(2\pi\omega\tau)\big) \right]. \end{aligned}$$

We obtain the same answer when taking the limit $T \to \infty$ of the solution for Problem 1.2, as the exponential transients die out at late-time. Thus, we ultimately find that the late-time membrane potential response $U(T)$ oscillates with the same frequency as the current input, though weighted by amplitude $I_0/C\sqrt{1/\tau^2 + (2\pi\omega)^2}$ and with a phase lag of $\tan^{-1}(2\pi\omega\tau)$). Note, the higher the input frequency ω, the smaller amplitude the bigger the lag is of the membrane response $U(T)$.

Take home notes:

In this sheet, we saw that the linearity of the (sub-threshold) LIF system allowed for easy analytical analysis not possible for the non-linear (and high-dimensional) Hodgkin-Huxley model. As a result, we found that the membrane response could be modelled as a linear, time-invariant system in that the impulse response function $G(T)$ is sufficient to understand how the system reacts to arbitrary input. 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, and the production of a solitary spike during continuous current input. These phenomena require the non-linearity and dimensionality of the Hodgkin-Huxley model.