Exercise Sheet 6: Integrate-and-Fire Neuron

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1. Integrate-and-Fire Neuron

We consider the integrate-and-fire neuron with differential equation:

$$\tau \frac{\mathrm{d}V(t)}{\mathrm{d}t} = E_L - V(t) + RI(t)$$

Whenever the voltage reaches a threshold, $V \geq V_{\text{th}}$ is set back to the equilibrium potential $V = E_L$

a). Consider a constant current $I(t) = I_0$. How large must I_0 be so that the neuron starts spiking?

Let us solve the integrate-and-fire neuron's differential equation in this case:

$$\begin{aligned}
& \tau \frac{\mathrm{d}V(t)}{\mathrm{d}t} = E_L - V(t) + RI_0 \\
\Longleftrightarrow \quad & \frac{\mathrm{d}V(t)}{\mathrm{d}t} = \frac{E_L + RI_0}{\tau} - \frac{V(t)}{\tau} \\
\Longleftrightarrow \quad & \frac{\mathrm{d}V(t)}{\mathrm{d}t} + \frac{1}{\tau} V(t) = \frac{E_L + RI_0}{\tau} \\
\Longleftrightarrow \quad & \frac{\mathrm{d}V(t)}{\mathrm{d}t} \mathrm{e}^{t/\tau} + \frac{1}{\tau} V(t) \, \mathrm{e}^{t/\tau} = \frac{E_L + RI_0}{\tau} \mathrm{e}^{t/\tau} \\
\Longleftrightarrow \quad & \frac{\mathrm{d}}{\mathrm{d}t} \left[V(t) \, \mathrm{e}^{t/\tau} \right] = \frac{E_L + RI_0}{\tau} \mathrm{e}^{t/\tau} \\
\Longleftrightarrow \quad & V(t) \, \mathrm{e}^{t/\tau} = \frac{E_L + RI_0}{\tau} \tau \, \mathrm{e}^{t/\tau} + \text{const} \\
\Longleftrightarrow \quad & V(t) \, \mathrm{e}^{t/\tau} = (E_L + RI_0) \, \mathrm{e}^{t/\tau} + \text{const} \\
\Longleftrightarrow \quad & V(t) = (E_L + RI_0) + \text{const} \times \mathrm{e}^{-t/\tau}
\end{aligned}$$

And with $V(0) = E_L$:

$$E_L = E_L + RI_0 + \text{const} \iff \text{const} = -RI_0$$

Therefore:

> $$V(t) = E_L + RI_0 \left(1 - \mathrm{e}^{-t/\tau}\right)$$

As a result:

$$\begin{aligned} & V(t) \overset{\text{eventually}}{\geq} V_{th} \\ \iff & \underbrace{\lim_{t\to+\infty} V(t)}_{= E_L + RI_0} \geq V_{th} \qquad \text{(as } V \text{ is monotonous before spiking)} \\ \iff & E_L + RI_0 \geq V_{th} \\ \iff & I_0 \geq \frac{V_{th} - E_L}{R} \end{aligned}$$

> *Thus, for the neuron to start spiking, it is necessary that:*
>
> $$I_0 \geq \frac{V_{th} - E_L}{R}$$

This is illustrated by the following plot, where we set

- $R \overset{\text{def}}{=} 10 \text{ M}\Omega$
- $E_L \overset{\text{def}}{=} -70 \text{ mV}$ (reversal potential)
- $\tau \overset{\text{def}}{=} 10 \text{ ms}$
- $V_{th} \overset{\text{def}}{=} -63 \text{ mV}$

as a result of which $\frac{V_{th} - E_L}{R} = 0.7 \text{ nA}$:

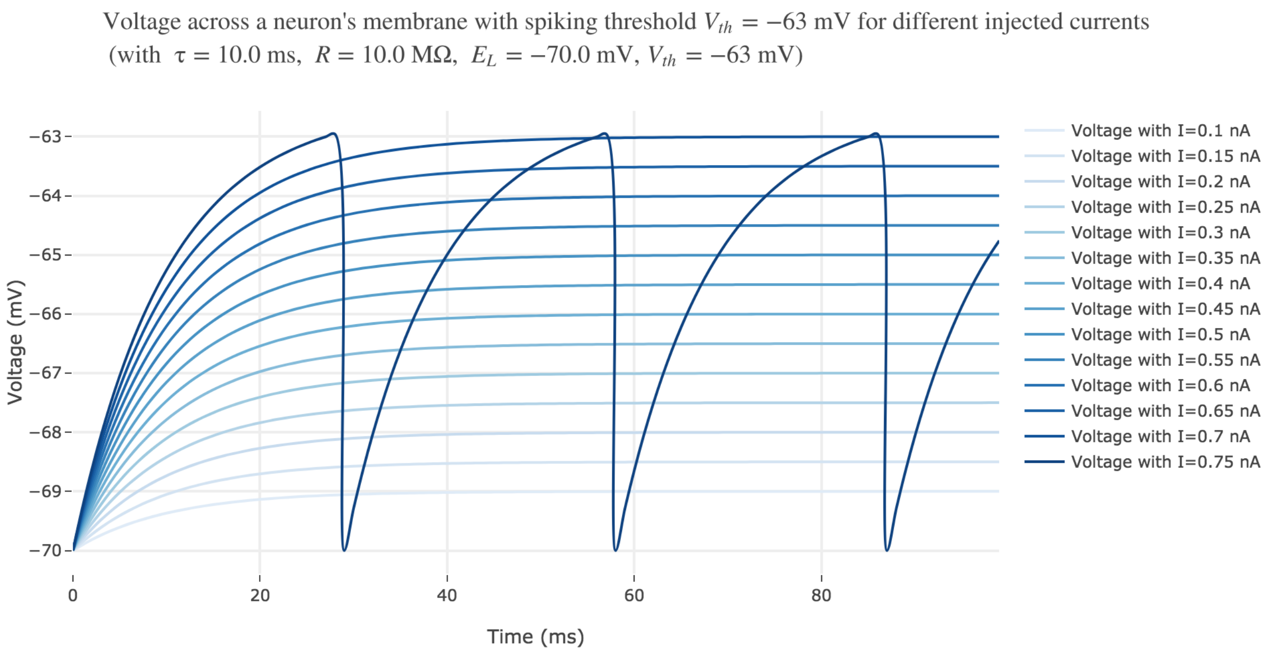

Figure 1.a. - Voltage accross a neuron's membrane with spiking threshold $V_{th} \overset{\text{def}}{=} -63 \text{ mV}$ for different injected currents

b). Let us now consider the case of a current step.

In this case, we turn on a current at time $t = t_0$ and then turn it off after T time units. In other words, the current is given by:

$$I(t) = \begin{cases} 0 \text{ for } t < t_0 \\ I_0 \text{ for } t_0 \leq t < t_0 + T \\ 0 \text{ for } t \geq t_0 + T \end{cases}$$

How large does I_0 have to be, as a function of T, for the neuron to spike? Make a plot of I_0 versus T.

Analogously to what we did in the previous question, we can show that:

- for $t \in [0, t_0]$:

  $$V(t) = E_L + \text{const} \times \mathrm{e}^{-t/\tau}$$

  and since $V(0) = E_L$:

  $$E_L = E_L + \text{const} \iff \text{const} = 0$$

  that is:

  $$V(t) = E_L$$

- for $t \in [t_0, t_0 + T[$:

  $$V(t) = E_L + RI_0 + \text{const} \times \mathrm{e}^{-t/\tau}$$

  and since $V(t_0) = E_L$:

  $$E_L = E_L + RI_0 + \text{const} \times \mathrm{e}^{-t_0/\tau} \iff \text{const} = -RI_0\, \mathrm{e}^{t_0/\tau}$$

  that is:

  $$V(t) = E_L + RI_0 \left(1 - \mathrm{e}^{-(t-t_0)/\tau}\right)$$

- for $t \in [t_0 + T, +\infty[$:

  $$V(t) = E_L + \text{const} \times \mathrm{e}^{-t/\tau}$$

  and since $V(t_0 + T) = E_L + RI_0 \left(1 - \mathrm{e}^{-T/\tau}\right)$:

  $$E_L + RI_0 \left(1 - \mathrm{e}^{-T/\tau}\right) = E_L + \text{const} \times \mathrm{e}^{-(t_0+T)/\tau}$$
  $$\iff \text{const} = RI_0 \left(1 - \mathrm{e}^{-T/\tau}\right) \mathrm{e}^{(t_0+T)/\tau}$$

  that is:

  $$V(t) = E_L + RI_0 \left(1 - \mathrm{e}^{-T/\tau}\right) \mathrm{e}^{-(t-t_0-T)/\tau}$$

Thus:

- for $t < t_0$, the membrane voltage is constant and equal to the equilibrium potential E_L
- for $t_0 \leq t < t_0 + T$, the voltage increases up to $V(t_0+T) = E_L + RI_0\left(1 - \mathrm{e}^{-T/\tau}\right)$
- for $t \geq t_0 + T$, the voltage decreases to $\lim\limits_{t \to +\infty} V(t) = E_L$

so the maximal value reached by V is $V(t_0+T) = E_L + RI_0\left(1 - \mathrm{e}^{-T/\tau}\right)$

> *As a consequence, the neuron spikes if and only if:*
>
> $$\begin{aligned} & V(t_0+T) = E_L + RI_0\left(1 - \mathrm{e}^{-T/\tau}\right) \geq V_{th} \\ \Longleftrightarrow \quad & I_0 \geq \frac{V_{th} - E_L}{R\left(1 - \mathrm{e}^{-T/\tau}\right)} \end{aligned}$$

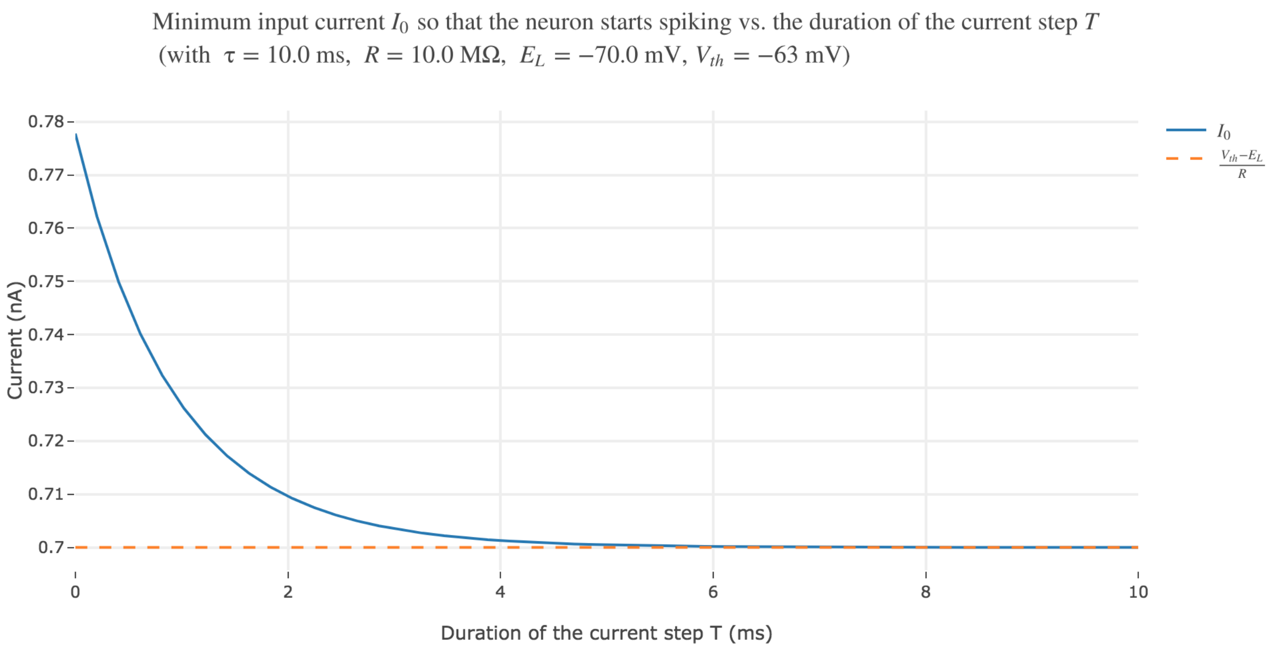

Figure 1.b. - Minimum input current I_0 so that the neuron starts spiking as a function of the duration of the current step (with the same parameters as in the previous question)

c. *Advanced*: Imagine that two current steps of length T are injected with a time delay of Δt. What is the maximum delay Δt between the two steps until an action potential is emitted?

Let us assume that the first current step happens between t_0 and $t_0 + T$ as before: then the second current step occurs between $t_0 + T + \Delta t$ and $t_0 + 2T + \Delta t$ as they are delayed by Δt.

Similarly to what we did in the previous question:

- for $t \in [0, t_0]$:

$$V(t) = E_L$$

- for $t \in [t_0, t_0 + T[$:

$$V(t) \ = E_L + RI_0\left(1 - \mathrm{e}^{-(t-t_0)/\tau}\right)$$

- for $t \in [t_0 + T,\, t_0 + T + \Delta t[$:

$$V(t) \;= E_L + RI_0 \left(1 - \mathrm{e}^{-T/\tau}\right) \, \mathrm{e}^{-(t-t_0-T)/\tau}$$

- for $t \in [t_0 + T + \Delta t,\, t_0 + 2T + \Delta t[$:

$$V(t) = E_L + RI_0 + \text{const} \times \mathrm{e}^{-t/\tau}$$

  and since $V(t_0 + T + \Delta t) = E_L + RI_0 \left(1 - \mathrm{e}^{-T/\tau}\right) \, \mathrm{e}^{-\Delta t/\tau}$:

$$\begin{aligned} E_L + RI_0 \left(1 - \mathrm{e}^{-T/\tau}\right) \, \mathrm{e}^{-\Delta t/\tau} &= E_L + RI_0 + \text{const} \times \mathrm{e}^{-(t_0+T+\Delta t)/\tau} \\ \iff \; \text{const} &= RI_0 \, \mathrm{e}^{(t_0+T+\Delta t)/\tau} \left(\left(1 - \mathrm{e}^{-T/\tau}\right) \mathrm{e}^{-\Delta t/\tau} - 1\right) \end{aligned}$$

  that is:

$$V(t) \;= E_L + RI_0 \left(1 + \mathrm{e}^{-(t-t_0-T-\Delta t)/\tau} \left(\left(1 - \mathrm{e}^{-T/\tau}\right) \mathrm{e}^{-\Delta t/\tau} - 1\right)\right)$$

- for $t \in [t_0 + 2T + \Delta t,\, +\infty[$:

$$V(t) = E_L + \text{const} \times \mathrm{e}^{-t/\tau}$$

  and since $V(t_0 + 2T + \Delta t) = E_L + RI_0 \left(1 + \mathrm{e}^{-T/\tau}\left(\left(1 - \mathrm{e}^{-T/\tau}\right) \, \mathrm{e}^{-\Delta t/\tau} - 1\right)\right)$:

$$\begin{aligned} E_L + RI_0 \left(1 + \mathrm{e}^{-T/\tau}\left(\left(1 - \mathrm{e}^{-T/\tau}\right) \, \mathrm{e}^{-\Delta t/\tau} - 1\right)\right) &= E_L + \text{const} \times \mathrm{e}^{-(t_0+2T+\Delta t)/\tau} \\ \iff \; \text{const} &= RI_0 \, \mathrm{e}^{(t_0+2T+\Delta t)/\tau} \, \left(1 + \mathrm{e}^{-T/\tau}\left(\left(1 - \mathrm{e}^{-T/\tau}\right) \, \mathrm{e}^{-\Delta t/\tau} - 1\right)\right) \end{aligned}$$

  that is:

$$V(t) \;= E_L + RI_0 \, \left(1 + \mathrm{e}^{-T/\tau}\left(\left(1 - \mathrm{e}^{-T/\tau}\right) \, \mathrm{e}^{-\Delta t/\tau} - 1\right)\right) \, \mathrm{e}^{-(t-t_0-2T-\Delta t)/\tau}$$

Thus:

- for $t < t_0$, the membrane voltage is constantly equal to the equilibrium potential E_L
- for $t_0 \le t < t_0 + T$, the voltage increases up to $V(t_0 + T) = E_L + RI_0 \left(1 - \mathrm{e}^{-T/\tau}\right)$
- for $t_0 + T \le t < t_0 + T + \Delta t$, the voltage decreases down to $V(t_0 + T + \Delta t) = E_L + RI_0 \left(1 - \mathrm{e}^{-T/\tau}\right) \, \mathrm{e}^{-\Delta t/\tau}$
- for $t_0 + T + \Delta t \le t < t_0 + 2T + \Delta t$, the voltage increases up to $V(t_0 + 2T + \Delta t) = E_L + RI_0 \left(1 + \mathrm{e}^{-T/\tau}\left(\left(1 - \mathrm{e}^{-T/\tau}\right) \, \mathrm{e}^{-\Delta t/\tau} - 1\right)\right)$
- for $t \ge t_0 + 2T + \Delta t$, the voltage decreases to $\lim\limits_{t \to +\infty} V(t) = E_L$

As

$$V(t_0 + 2T + \Delta t) = V(t_0 + T) + RI_0 \, \mathrm{e}^{-T/\tau} \left(1 - \mathrm{e}^{-T/\tau}\right) \, \mathrm{e}^{-\Delta t/\tau} > V(t_0 + T)$$

the maximal value reached by V is $V(t_0 + 2T + \Delta t)$.

> *As a consequence, the neuron spikes if and only if:*
>
> $$\begin{aligned} & V(t_0 + 2T + \Delta t) \geq V_{th} \\ \iff \quad & E_L + RI_0 \left(1 + e^{-T/\tau}\left(\left(1 - e^{-T/\tau}\right) e^{-\Delta t/\tau} - 1\right)\right) \geq V_{th} \\ \iff \quad & e^{-T/\tau}\left(\left(1 - e^{-T/\tau}\right) e^{-\Delta t/\tau} - 1\right) \geq \frac{V_{th} - E_L}{RI_0} - 1 \\ \iff \quad & \left(1 - e^{-T/\tau}\right) e^{-\Delta t/\tau} \geq e^{T/\tau} \left(\frac{V_{th} - E_L}{RI_0} - 1\right) + 1 \\ \iff \quad & \Delta t \leq -\tau \ln \frac{e^{T/\tau} \left(\frac{V_{th} - E_L}{RI_0} - 1\right) + 1}{1 - e^{-T/\tau}} \end{aligned}$$

2. Integrate-and-Fire with refractory period

Real neurons usually have refractory periods, i.e. for a few milliseconds after an action potential, the neuron will not fire again.

How could you add such a refractory period to the integrate-and-fire neuron?

To add a refractory period Δ, we make the voltage stay constant at the equilibirum potential E_L for a time span Δ whenever it is reset to E_L after reaching the threshold.

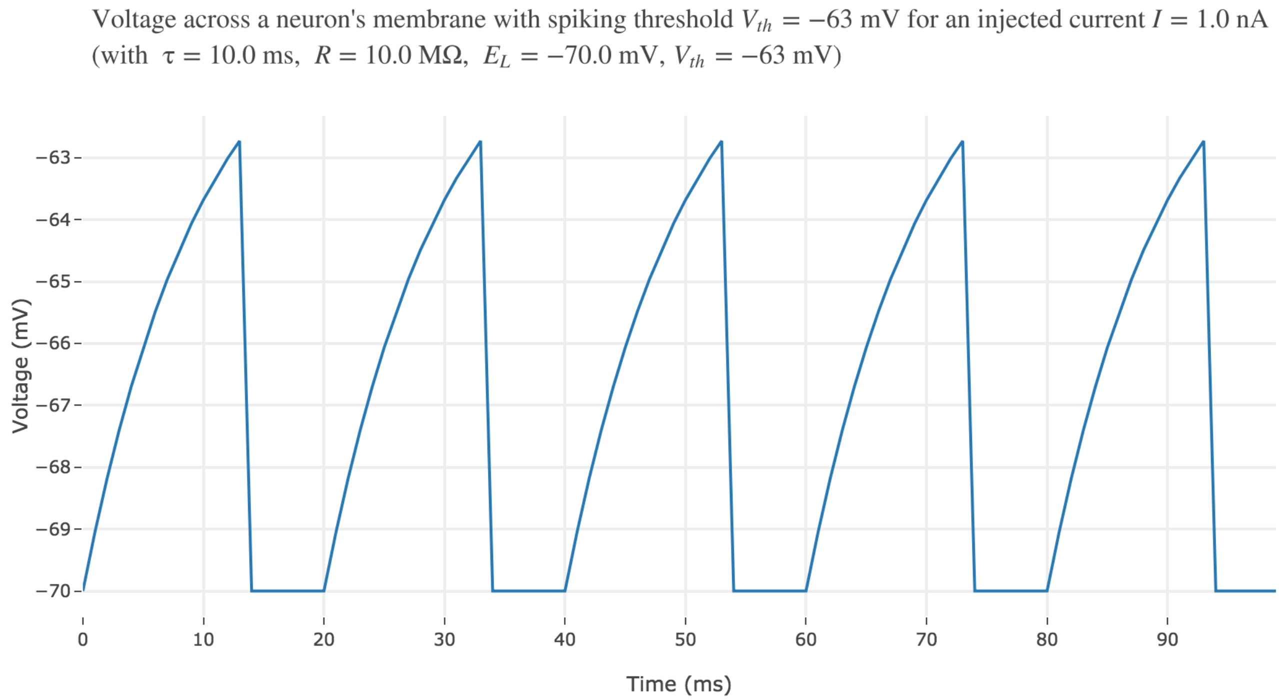

Figure 2.a.1. - Voltage across a neuron's membrane with spiking threshold $V_{th} = -63$ mV and a 5 ms refractory period

Compute the new fI-curve, i.e. the firing rate versus input current curve of the neuron with refractory period. How does it differ from the old one?

Let us denote by T the time to threshold *when there is no refractory period*:

$$\begin{aligned} & \tau \frac{\mathrm{d}V(t)}{\mathrm{d}t} = E_L - V(t) + RI(t) \quad \text{and} \quad V(0) = E_L \\ \iff & V(t) = E_L + RI_0 \left(1 - \mathrm{e}^{-t/\tau}\right) \end{aligned}$$

and by definition of T:

$$\begin{aligned} & V(T) = V_{th} \\ \iff & E_L + RI_0 \left(1 - \mathrm{e}^{-T/\tau}\right) = V_{th} \\ \iff & \mathrm{e}^{-T/\tau} = 1 - \frac{V_{th} - E_L}{RI_0} \\ \iff & T = -\tau \ln\left(1 - \frac{V_{th} - E_L}{RI_0}\right) \\ \iff & T = \tau \ln\left(\frac{RI_0}{RI_0 - V_{th} + E_L}\right) \end{aligned}$$

and the firing rate f is equal to:

$$f \overset{\text{def}}{=} \frac{1}{T} = \left(\tau \ln\left(\frac{RI_0}{RI_0 - V_{th} + E_L}\right)\right)^{-1}$$

So **when there is a refractory period** Δ:

$$T_{ref} = \tau \ln\left(\frac{RI_0}{RI_0 - V_{th} + E_L}\right) + \Delta$$

as a result of which the firing rate is equal to:

> $$f_{ref} \overset{\text{def}}{=} \frac{1}{T_{ref}} = \left(\tau \ln\left(\frac{RI_0}{RI_0 - V_{th} + E_L}\right) + \Delta\right)^{-1}$$

Therefore, compared to f:

- the firing rate f_{ref} is now bounded by $\frac{1}{\Delta}$:

$$f_{ref} = \Bigg(\underbrace{\tau \ln\left(\frac{RI_0}{RI_0 - V_{th} + E_L}\right)}_{\geq 0} + \Delta\Bigg)^{-1} \leq \frac{1}{\Delta}$$

- and it is lower than the firing rate without refractory period f:

$$f_{ref} = \Bigg(\tau \ln\left(\frac{RI_0}{RI_0 - V_{th} + E_L}\right) + \underbrace{\Delta}_{\geq 0}\Bigg)^{-1} \leq \frac{1}{\tau \ln\left(\frac{RI_0}{RI_0 - V_{th} + E_L}\right)} = f$$

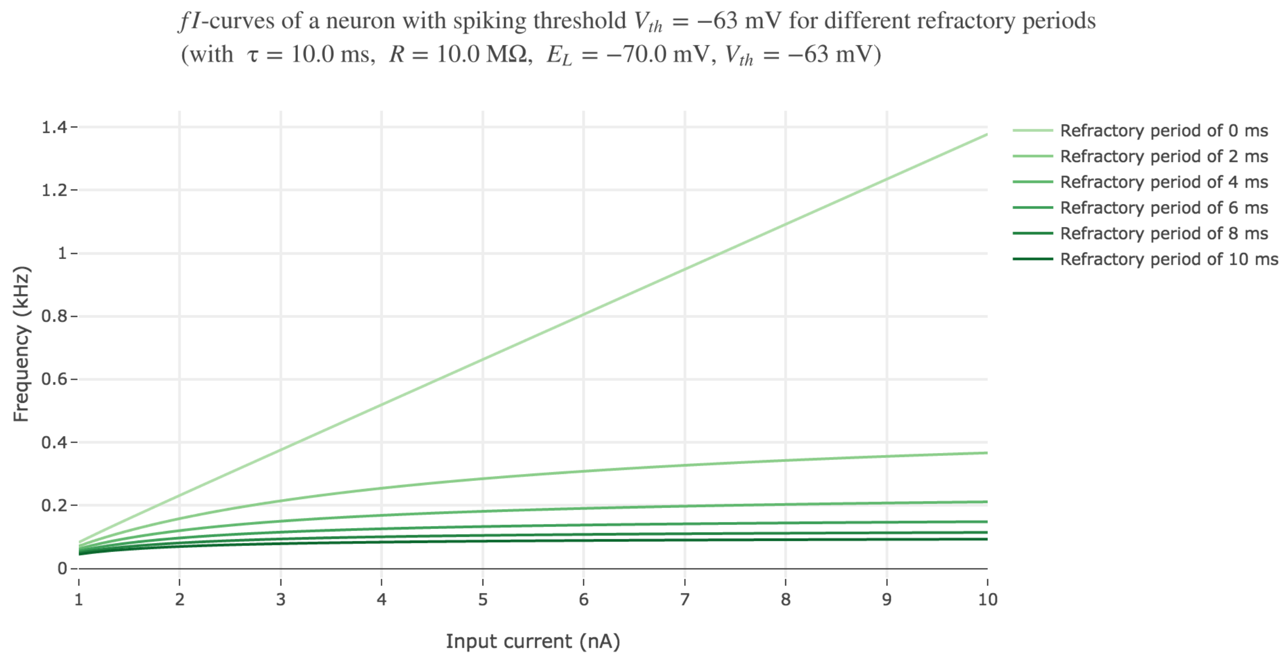

Figure 2.a.2. - fI-curves of a neuron with spiking threshold $V_{th} = -63$ mV for different refractory periods