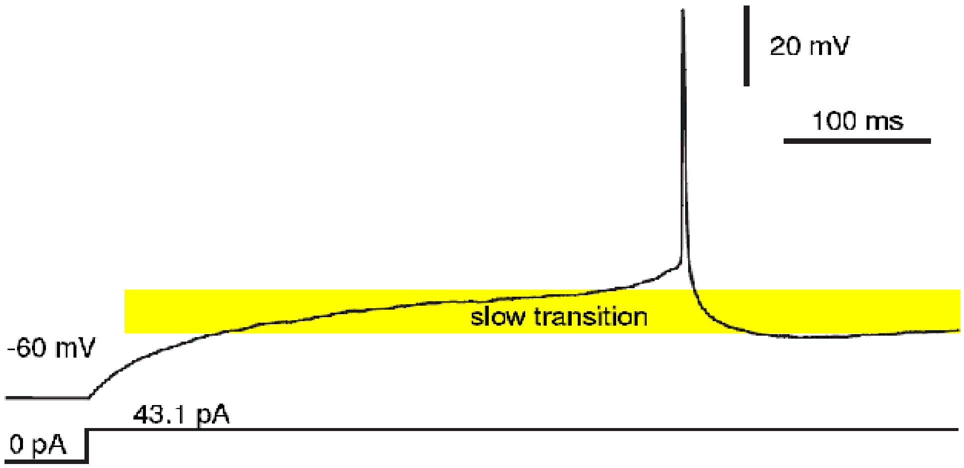
Integrate-and-Fire Neuron

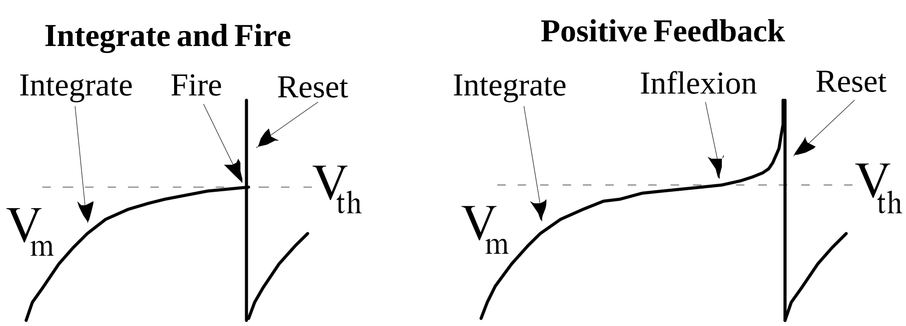


Layer 5 pyramidal cell from rat visual cortex [Izhikevich07].

A minimum current is required for spiking

Spike frequency increases linearly at high rates

Integrate-and-Fire Model



Neurons spike when an inward Na current overcomes an outward leak current (inflexion point).

This model does not include spike generation—the spike is pasted on when V_m reaches V_{th}, the threshold voltage. It only captures the neuron's behavior below threshold (inflexion point).

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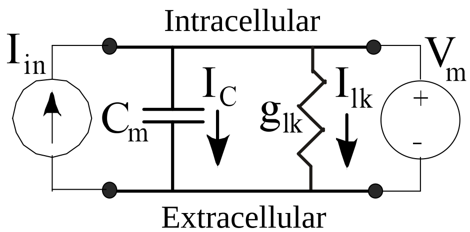
Membrane-Voltage Equation



Current– Voltage Relations

$$I_{lk} = g_{lk} V_m$$

$$I_C = C_m \frac{dV_m}{dt}$$

Capacitor models membrane; resistor models leak.

In[1]:= $I_C + I_{lk} = I_{in}$

$\Longleftrightarrow C_m \dfrac{dV_m}{dt} + g_{lk} (V_m - E_{lk}) = I_{in}$

$\Longleftrightarrow \tau_m \dfrac{dV_m}{dt} + V_m = V_\infty$ where $\tau_m = \dfrac{C_m}{g_{lk}}$, $V_\infty = \dfrac{I_{in}}{g_{lk}}$ and $E_{lk} = 0$

V_m reaches V_{th} only if $V_\infty > V_{th}$. Thus, $I_{in} = g_{lk} V_{th}$ is the minimum current for spiking.

The membrane voltage is reset when it reaches threshold:

$V_m[t] := V_{rst}$ when $V_m[t] = V_{th}$

A spike is declared at this time t ($\equiv t_n$).

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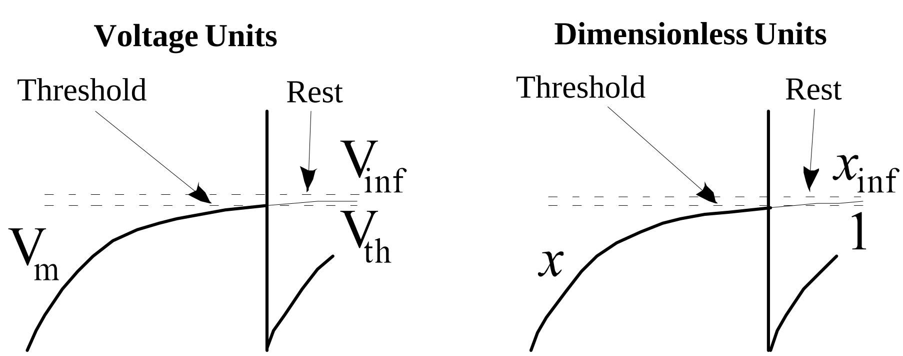
Dimensionless Form



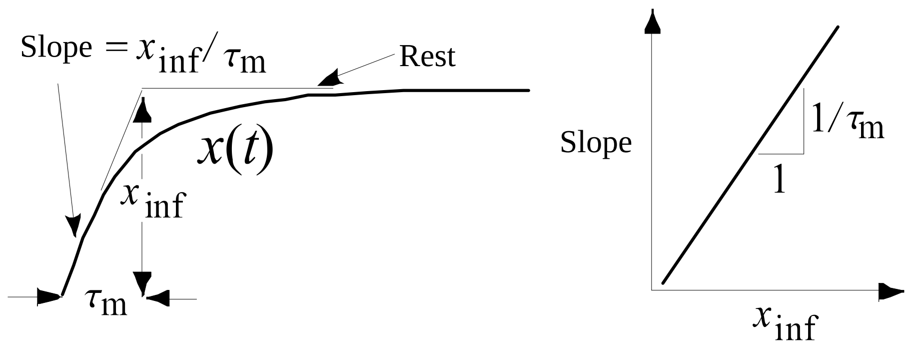
Voltages are expressed as multiples of the threshold voltage.

Dividing both sides by V_{th} and defining $x = V / V_{th}$ yields

In[1]:= $\tau_m \frac{dx}{dt} + x = x_\infty$ where $x_\infty = \frac{V_\infty}{V_{th}} = \frac{I_{in}}{g_{lk} V_{th}}$

Note that x_∞ must exceed 1 for spiking to occur—because the input current must exceed the leak.

Determining the Time-Constant



The initial slope (left) increases linearly with the rest-level (right).

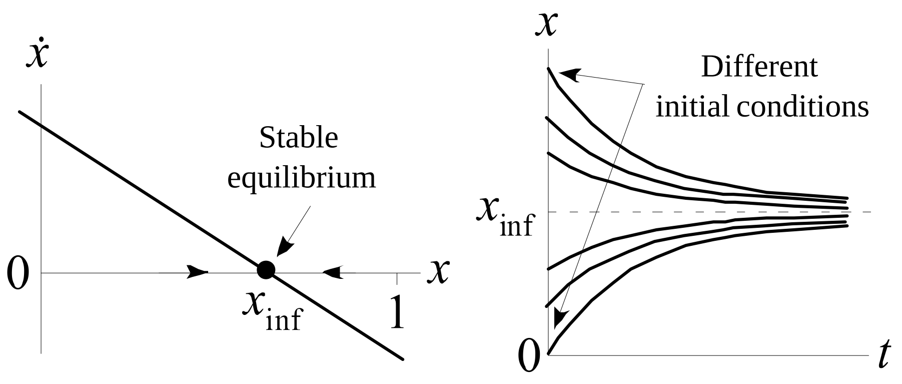
For $x \ll x_\infty$, we have

In[1]:= $\tau_m \frac{dx}{dt} \approx x_\infty \implies \frac{dx}{dt} = \frac{x_\infty}{\tau_m}$

The membrane voltage would take τ_m seconds to reach x_∞ at its initial rate of change.

We determine τ_m in lab by measuring the intial slope for different input currents: Data should fall on a straight-line with slope $1/\tau_m$.

Stability: Phase-Plot



The phase-plot (left) explains the neuron's behavior (right)

We solve the membrane-equation for the derivative and plot it versus x:

$$\frac{dx}{dt} = \frac{x_\infty - x}{\tau_m} \Leftrightarrow \frac{dV_m}{dt} = \frac{I_{in} - g_{lk} V_m}{C_m}$$

The plot reveals that the point $x = x_\infty$ is stable: $\dot{x} > 0$ when $x < x_\infty$ and $\dot{x} < 0$ when $x > x_\infty$.

That is, the derivative's sign is such that x returns to x_∞ when perturbed.

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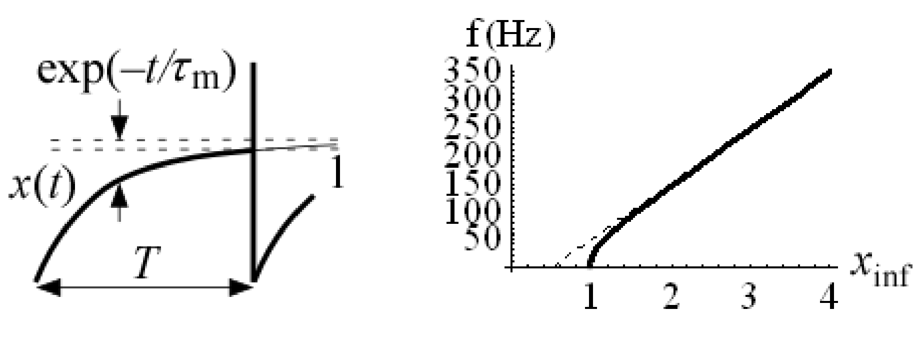
Spike Frequency



The time T when $x = 1$ equals the period; frequency is $1/T$ (plotted for $\tau_m = 10$ ms)

Given steady-state x_∞, time-constant τ_m, and initial condition $x(0) = 0$:

$$x[t] = x_\infty + (0 - x_\infty)\, e^{-t/\tau_m} = x_\infty \left(1 - e^{-t/\tau_m}\right)$$

Setting $x(T) = 1$ and solving for T yields:

$$T = \tau_m \ln\left(\frac{x_\infty}{x_\infty - 1}\right) \Longrightarrow T \approx \frac{\tau_m}{x_\infty - 1/2} \text{ for } x_\infty \gg 1$$

Using the approximation: $1/\ln(1+\epsilon) \approx 1/\epsilon + 1/2$. Thus the spike frequency is

$$f[x_\infty] \approx \frac{1}{\tau_m}\left(x_\infty - \frac{1}{2}\right)$$

> *Question: Does inhibition (i.e., a bigger g_{lk}) have a divisive or a subtractive effect on the firing rate?*

Answer: Rewrite the equation

$$f[I_{in}] \approx \frac{1}{C_m V_{th}}\left(I_{in} - \frac{1}{2} g_{lk} V_{th}\right)$$

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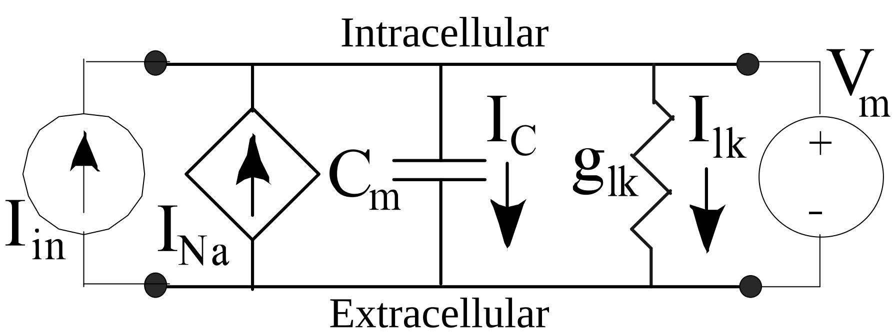
Sodium Channels



An additional (voltage-dependent) inward current I_{Na} models Na channels

The sodium current is modeled as:

In[1]:= $$C_m \frac{dV_m}{dt} + g_{lk} V_m = I_{in} + I_{Na} \quad \text{where} \quad I_{Na} = \frac{1}{3}\left(\frac{V_m}{V_{th}}\right)^2 g_{lk} V_m$$

I_{Na} causes V_m to increase, which then causes I_{Na} to increase further (positive-feedback).

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Positive-Feedback Neuron