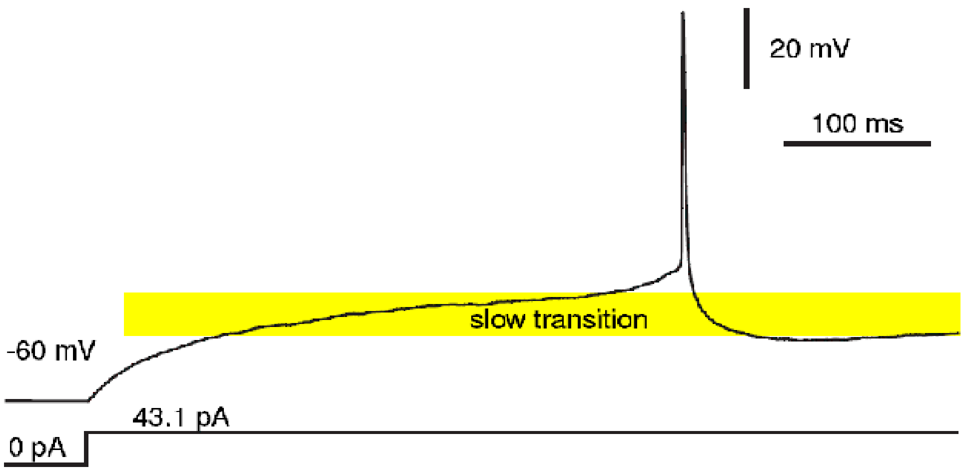
1 of 9

Integrate-and-Fire Neuron



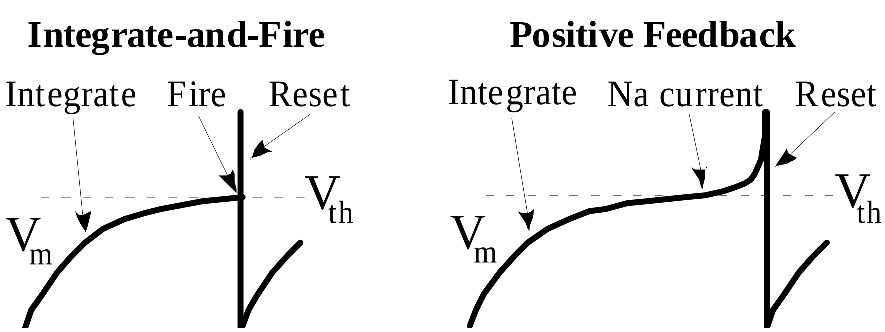
Layer 5 pyramidal cell from rat visual cortex [Izhikevich07]

A minimum current is required for spiking

Spike frequency increases linearly at high rates

2 of 9

Integrate-and-Fire Model



Neurons spike when an inward Na current overcomes an outward leak current

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).

3 of 9

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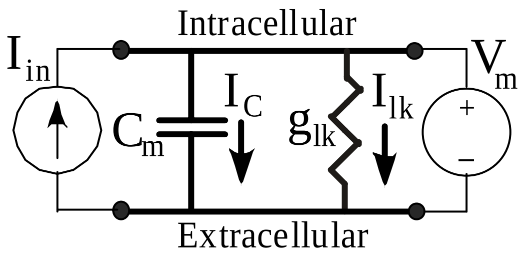
Membrane-Voltage Equation



Current–Voltage Relations

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

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

Capacitor models membrane; conductance models leak

In[1]:=

$$I_C + I_{lk} = I_{in}$$

$$\Longleftrightarrow C_m \frac{dV_m}{dt} + g_{lk} V_m = I_{in}$$

$$\Longleftrightarrow \tau_m \frac{dV_m}{dt} + V_m = V_\infty \quad \text{where} \quad \tau_m = \frac{C_m}{g_{lk}} \quad \text{and} \quad V_\infty = \frac{I_{in}}{g_{lk}}$$

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

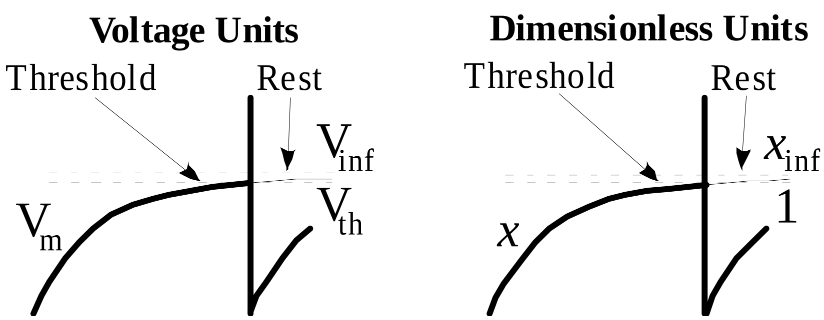
The membrane voltage is reset when it reaches threshold:

$$V_m[t_n] := V_{rst}$$

Here t_n is the time the spike occurs.

|◂ ◂ ▸ ▸| 4 of 9

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]:=

$$\tau_m \frac{dx}{dt} + x = x_\infty \quad \text{where} \quad x_\infty = \frac{V_\infty}{V_{th}}$$

Note that x_∞ must exceed 1 for spiking to occur.

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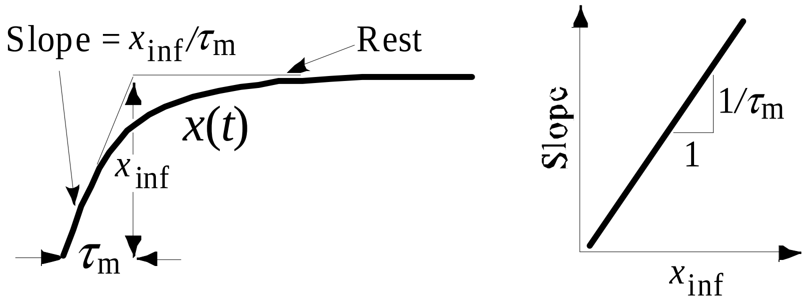
Determining the Time-Constant



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

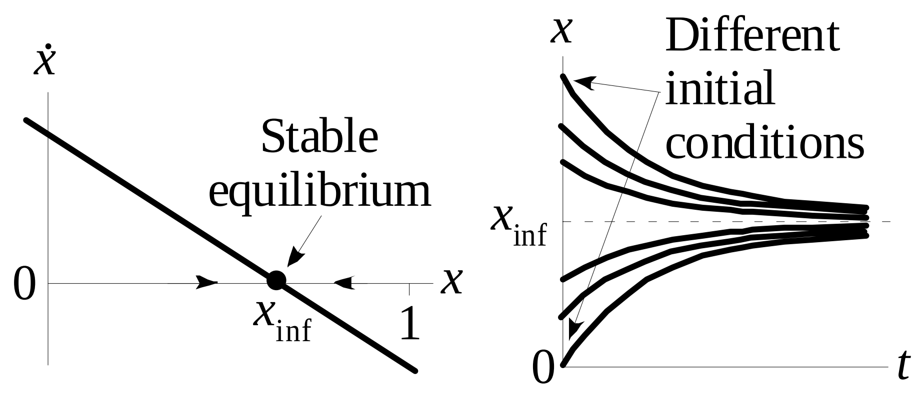
For $x \ll x_\infty$, we have

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:

$$\frac{dx}{dt} = \frac{x_\infty - x}{\tau_m}$$

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

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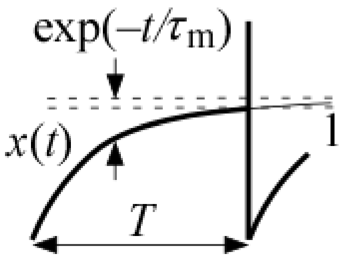
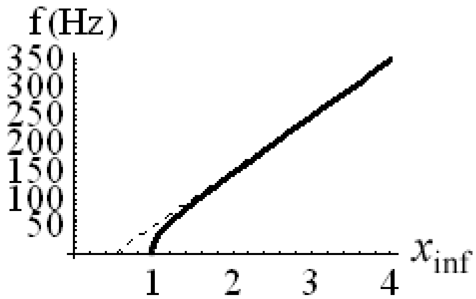
That is, the derivative's sign is such that x returns to x_∞ when perturbed.

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 $x(0) = 0$:

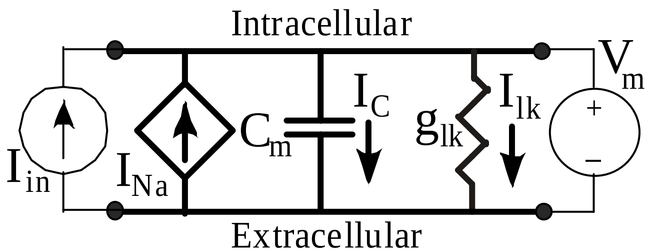
$$x[t] = x_\infty + (0 - x_\infty)\, e^{-t/\tau_m} = x_\infty \left(1 - e^{-t/\tau_m}\right)$$

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

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

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

Sodium Channels



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

The sodium current is modeled as:

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

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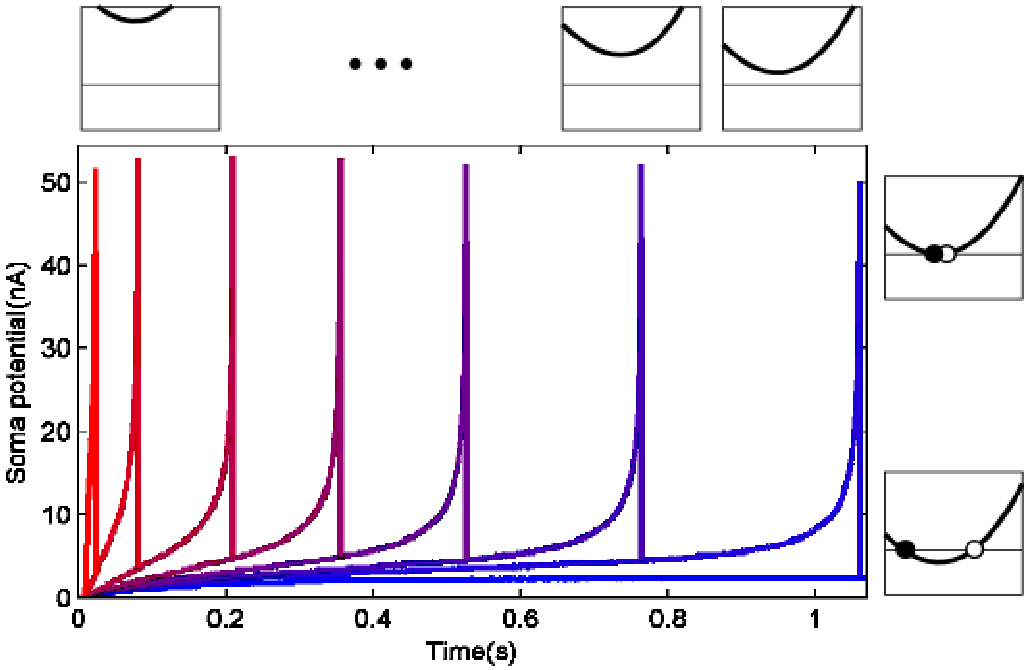
I_{Na} causes V_m to increase, which then causes I_{Na} to increase further (positive-feedback).

Positive-Feedback Neuron



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