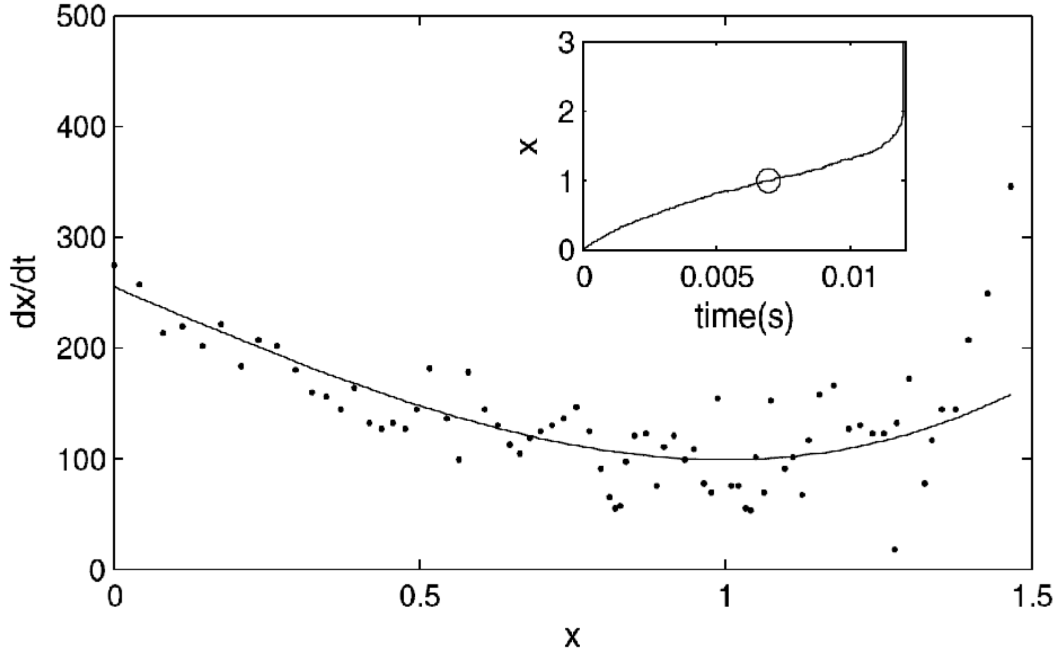
Positive-Feedback Neuron

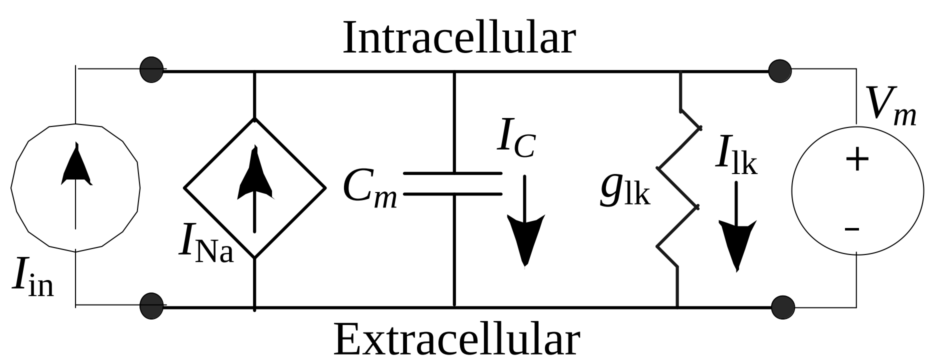


A cortical fast-spiking interneuron's phase-plot, computed from its membrane voltage trace (insert) [Izhikevich07]

Has an inflection in its membrane-voltage trace

Spike frequency increases sublinearly at high rates

Membrane-voltage equation



The inward currents (I_{in} plus I_{Na}) equal the outward currents (I_{lk} plus I_C)

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

$$\Leftrightarrow \tau_m \frac{dx}{dt} + x = r + \frac{1}{3} x^3 \quad \text{where} \quad \tau_m = \frac{C_m}{g_{lk}},\ x = \frac{V_m}{V_{th}},\ r = \frac{I_{in}}{g_{lk} V_{th}}$$

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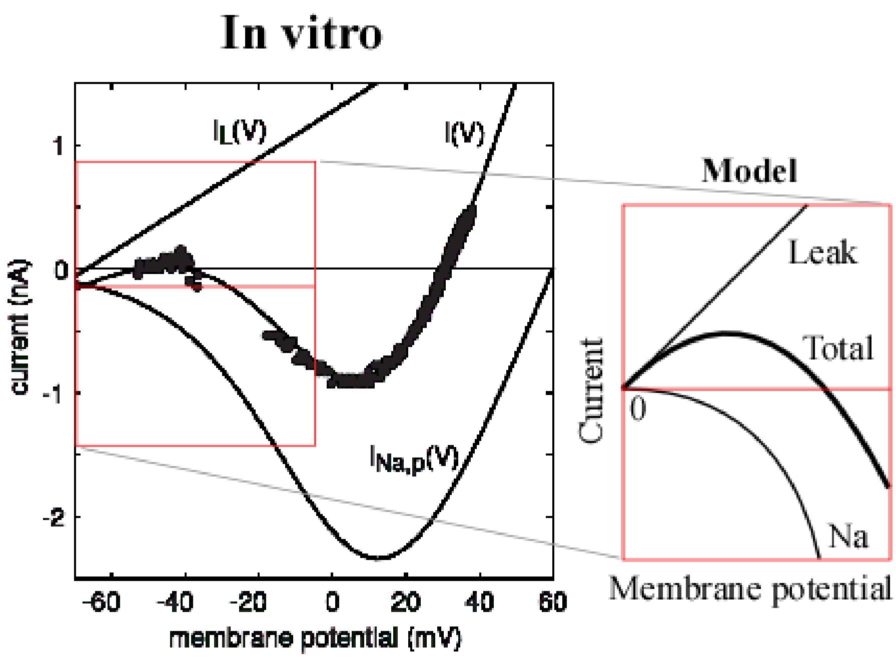
Comparison



Matches neuron's behavior in -70 to -5mV range (rat cortex L5 pyramidal cell) [Izhikevich07]

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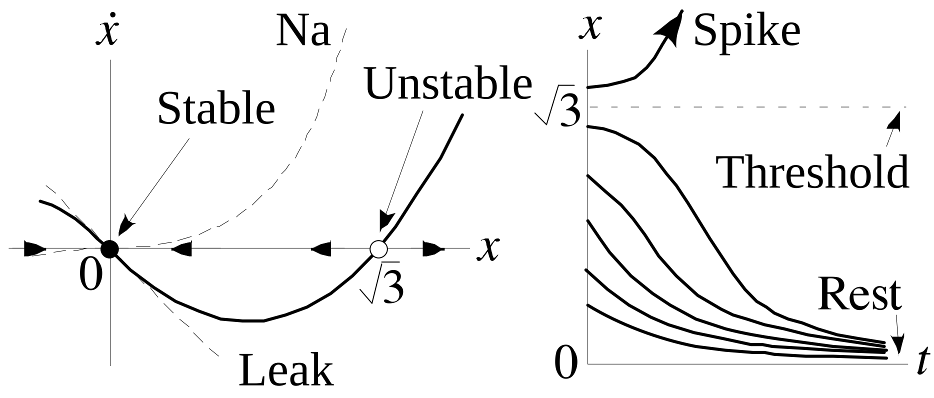
Fixed points: Rest and threshold



Two equilibria (left), corresponding to rest and threshold (right); r is set to zero

We solve the membrane-equation for the derivative. It is proportional to the net current (Input + Na – Leak):

$$\frac{dx}{dt} = r + \frac{1}{3} x^3 - x \text{ where } \tau_m \equiv 1 \quad (\text{time is in units of } \tau_m)$$

Plotting the derivative versus x for $r = 0$ reveals two fixed points:

Rest: A stable point at $x = 0$ — x moves toward 0 ($\dot{x} > 0$ when $x < 0$ and $\dot{x} < 0$ when $x > 0$).

Threshold: An unstable point at $x = \sqrt{3}$ — x moves away from $\sqrt{3}$ ($\dot{x} < 0$ when $x < \sqrt{3}$ and $\dot{x} > 0$ when $x > \sqrt{3}$).

That is, if you initialize x above $\sqrt{3}$ (i.e., peg V_m above $\sqrt{3}$ V_{th} and release it), the neuron will spike.

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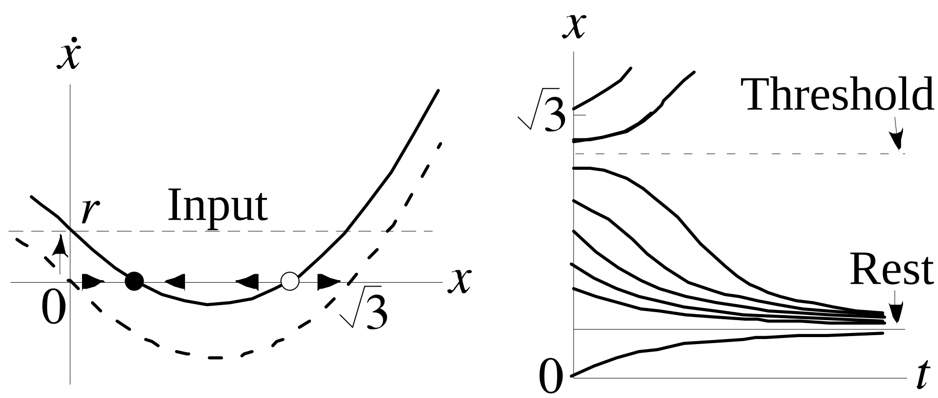
Adding input brings fixed points together



The equilibria move together (left); rest rises and threshold drops (right)

Increasing r shifts the phase-plot up, moving the equilibria closer. That is, the neuron rests at a higher voltage and has a lower threshold — the value above which x must be initialized to get a spike is now less than $\sqrt{3}$.

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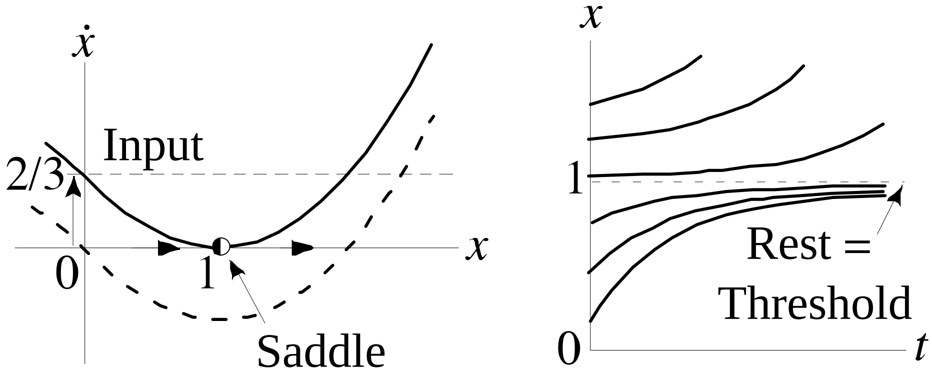
Saddle-node bifurcation



A bifurcation is said to occur when the number (or nature) of fixed-points changes

Eventually, the fixed points come together at $x = 1$. They coalesce into a ***saddle point*** — a fixed-point that is neither stable nor unstable — x may move toward it or away from it, depending on whether x is above or below ($\dot{x} > 0$ when $x < 1$ and $\dot{x} > 0$ when $x > 1$).

This is called a saddle-node ***bifurcation***. When it happens, a neuron that was resting queiscently starts spiking rhythmically. That is, when x is reset to 0, it approaches 1, and sits there (similar to rest). However, with a little nudge (from noise), it takes off, producing a full-blown spike (similar to threshold). Thus, the current level at which the bifurcation occurs is the minimum input required for spiking.

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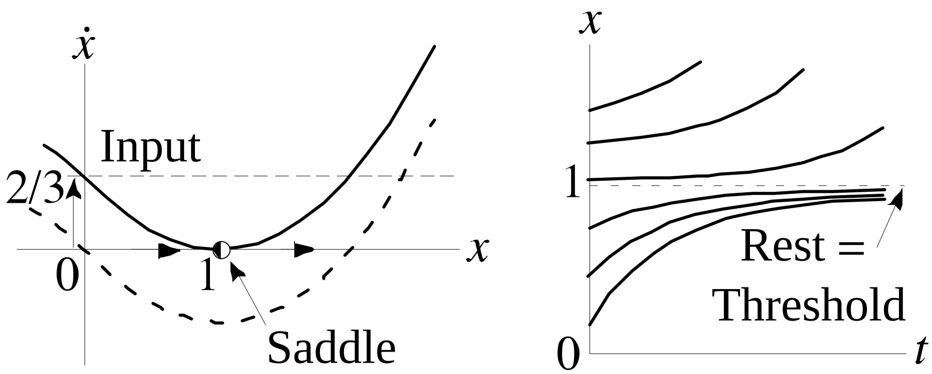
Determining the minimum input



How far up must the phase-plot move for the minimum to touch the x-axis?

For the system $\dot{x} = f(x, r)$, the input r_{th} at which the bifurcation occurs and the membrane voltage x_{th} at which the saddle-point appears must satisfy:

$$f[x_{th}, r_{th}] == 0 \text{ and } f'[x_{th}, r_{th}] == 0$$

First find where $f'(x, r)$, f's derivative with respect to x, is 0:

$$\frac{d}{dx}\left(r + \frac{1}{3}x^3 - x\right) = 0 \implies x^2 - 1 = 0 \implies x_{th} = \pm 1$$

Then find the value of r that makes $f(x_{th}, r)$ equal to 0:

$$r + \frac{1}{3} - 1 = 0 \implies r_{th} = \frac{2}{3}$$

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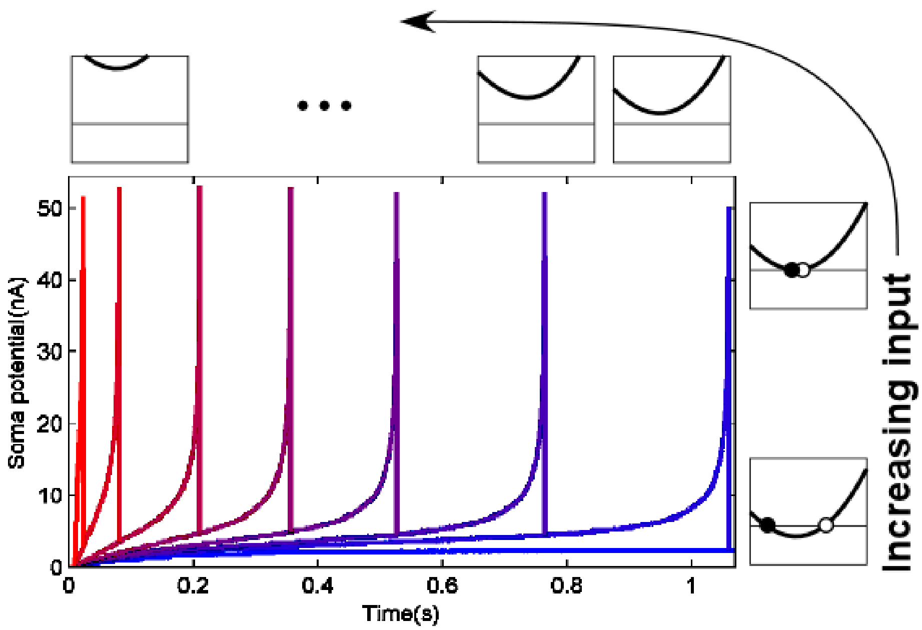
Model membrane-voltage traces



Spikes sooner wIth increasing input current—once minimum is exceeded

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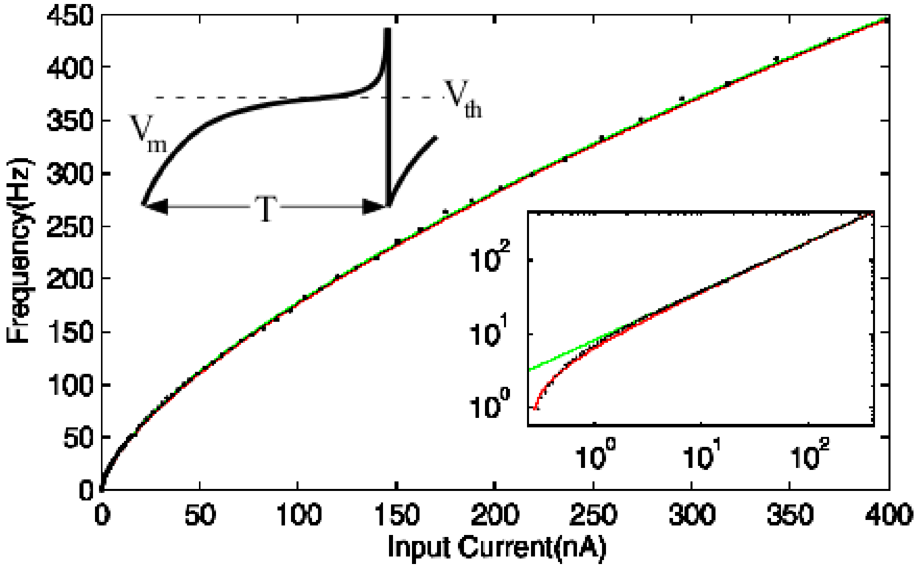
Spike frequency



Theory (green) holds above1nA ($r = 3.3$)—five times the 0.2nA minimum ($r = 2/3$)

The period T is obtained as:

$$\int_0^T dt = \int_0^\infty \frac{dx}{\dot{x}} = \tau_m \int_0^\infty \frac{1}{r - x + x^3/3}\, dx$$

$$\approx \tau_m \int_0^\infty \frac{1}{r + x^3/3}\, dx \quad \text{when} \quad r \gg 1$$

$$\approx \frac{2\pi}{3^{7/6}} \frac{\tau_m}{r^{2/3}}$$

This result produced the green fit; the red one is a refined theory.

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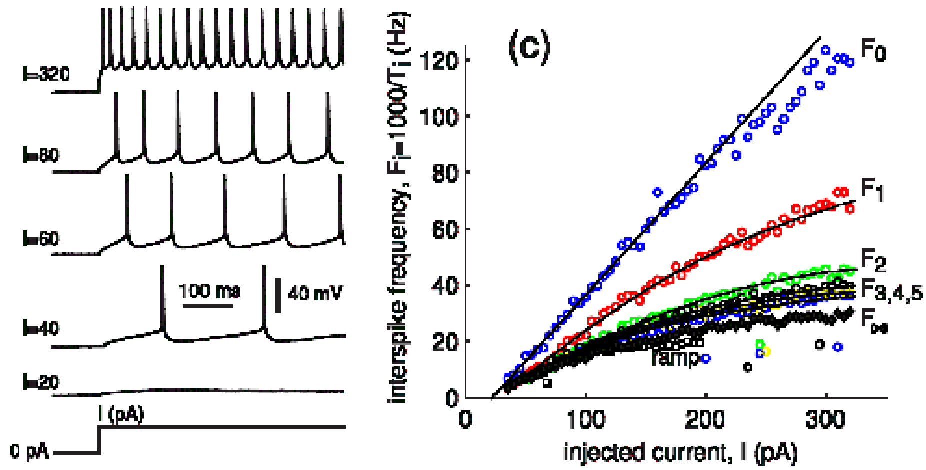
Next lecture: Adaptive neuron



Frequency adaptation (rat cortex L5 pyramidal cell) due to M-current