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 ($I_{k}$ plus $I_{C}$)

\[
C_m \frac{dv_m}{dt} + g_{lk} V_m = I_{in} + I_{Na} \quad \text{where} \quad I_{Na} = \frac{1}{3} \left( \frac{v_m}{v_{th}} \right)^2 g_{lk} V_m
\]

\[
\tau_m \frac{dx}{dt} + x = r + \frac{1}{3} x^3 \quad \text{where} \quad \tau_m = \frac{C_m}{g_{lk}}, \quad x = \frac{v_m}{v_{th}}, \quad r = \frac{I_{in}}{g_{lk} v_{th}}
\]

Comparison

![In vitro diagram](image)

Matches neuron’s behavior in -70 to -5mV range (rat cortex L5 pyramidal cell) [Izhikevich07]
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 ($Input + Na - Leak$):

$$\frac{dx}{dt} = r + \frac{1}{3} x^3 - x$$

(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.

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 $\sqrt{3}$.

**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.

**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:

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

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

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

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

\[
r + \frac{1}{3} - 1 = 0 \Rightarrow r_{th} = \frac{2}{3}
\]

Model membrane-voltage traces

Spikes sooner with increasing input current—once minimum is exceeded
Spike frequency

Theory (green) holds above 1 nA ($r = 3.3$)—five times the 0.2 nA minimum ($r = 2/3$).

The period $T$ is obtained as:

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

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

$$= \frac{2}{3 \pi} \tau_m \frac{r}{r^{3/2}}$$

This result produced the green fit; the red one is a refined theory.
Next lecture: Adaptive neuron

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