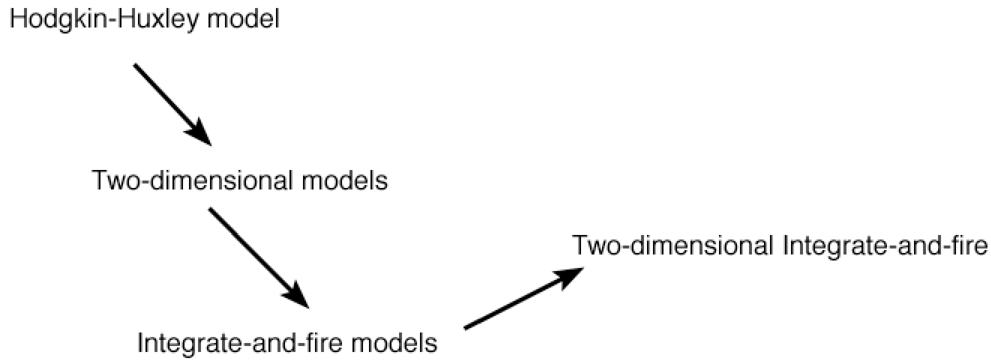
Neuron Model Reduction → Integrate-and-fire



00_title.psd

Neuron Model Reduction

Hodgkin-Huxley model

$$C\dot{V} = I - \overbrace{g_K n^4 (V - E_K)}^{I_K} - \overbrace{g_{Na} m^3 h (V - E_{Na})}^{I_{Na}} - \overbrace{g_L (V - E_L)}^{I_L}$$

$$\begin{aligned}
\dot{n} &= (n_\infty(V) - n)/\tau_n(V) \\
\dot{m} &= (m_\infty(V) - m)/\tau_m(V) \\
\dot{h} &= (h_\infty(V) - h)/\tau_h(V)
\end{aligned}$$

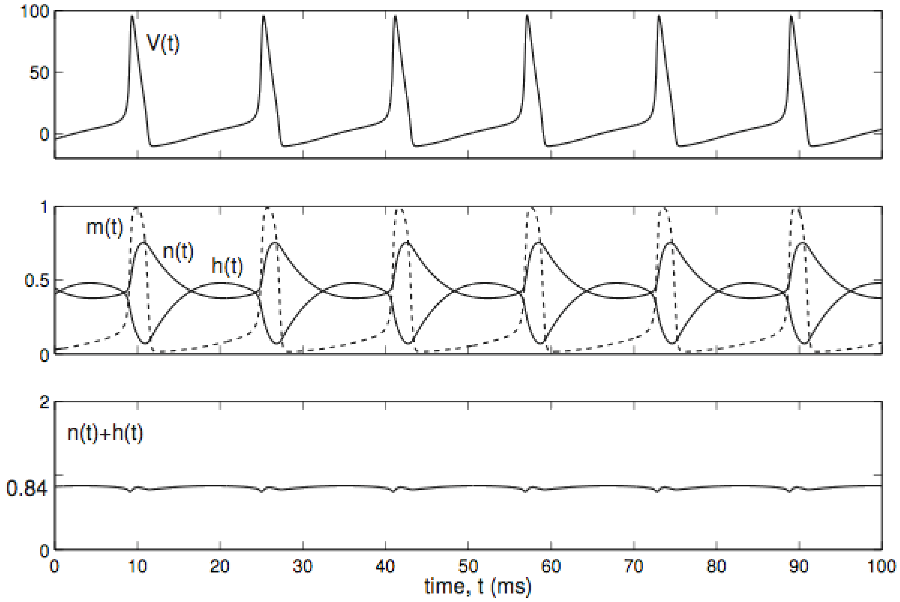
(Izhikevich, 2007)

01_reduceHH.psd

Neuron Model Reduction

Krinskii & Kokoz(1973) have shown that there is a relationship between two of the gating variables:

$$n(t) + h(t) \approx 0.84$$

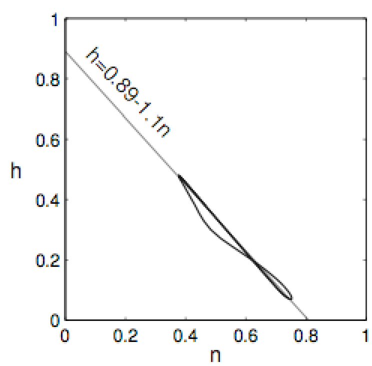


(Izhikevich, 2007)

02_reduceHH nh.psd

Neuron Model Reduction

Plotting the variables on the (n,h) plane:



$$h = 0.89 - 1.1n$$

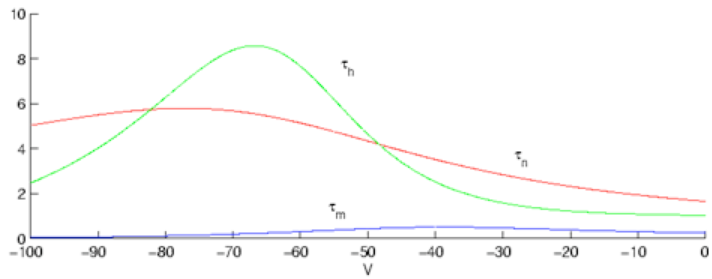
We can use this relationship in the voltage equation to reduce the Hodgkin-Huxley model to a three-dimensional system.

(Izhikevich, 2007)

03_reduceHH nhPlane.psd

Neuron Model Reduction

Next, assume that the activation kinetics of the Na+ current is instantaneous: $m = m_\infty(V)$



Then, the Hodgkin-Huxley model reduces to a two-dimensional system:

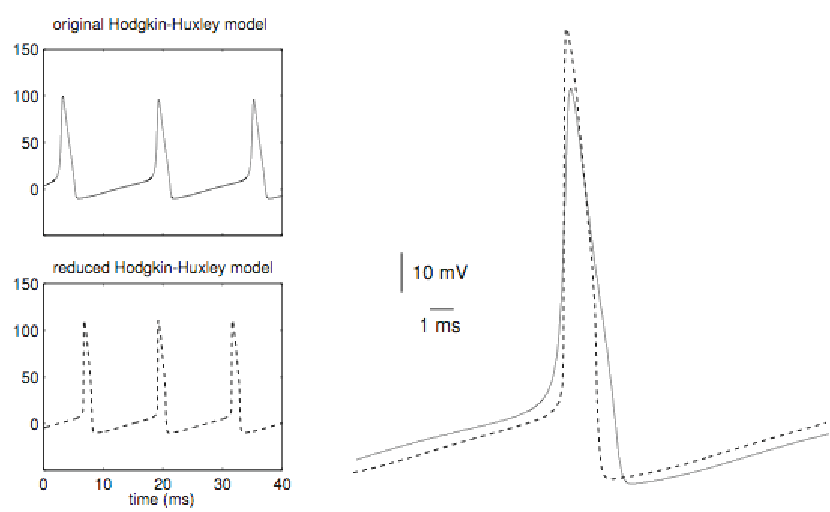
$$
\begin{aligned}
C\dot{V} &= I - \overbrace{g_{\mathrm{K}} n^4 (V - E_{\mathrm{K}})}^{I_{\mathrm{K}}} - \overbrace{g_{\mathrm{Na}} m_\infty^3(V)(0.89 - 1.1n)(V - E_{\mathrm{Na}})}^{\text{instantaneous } I_{\mathrm{Na}}} - \overbrace{g_{\mathrm{L}}(V - E_{\mathrm{L}})}^{I_{\mathrm{L}}} \\
\dot{n} &= (n_\infty(V) - n)/\tau_n(V)
\end{aligned}
$$

(Izhikevich, 2007)

04_reduceHH m_inf.psd

Neuron Model Reduction

$$
\begin{aligned}
C\dot{V} &= I - \overbrace{g_{\mathrm{K}} n^4 (V - E_{\mathrm{K}})}^{I_{\mathrm{K}}} - \overbrace{g_{\mathrm{Na}} m_\infty^3(V)(0.89 - 1.1n)(V - E_{\mathrm{Na}})}^{\text{instantaneous } I_{\mathrm{Na}}} - \overbrace{g_{\mathrm{L}}(V - E_{\mathrm{L}})}^{I_{\mathrm{L}}} \\
\dot{n} &= (n_\infty(V) - n)/\tau_n(V)
\end{aligned}
$$



Action potentials in the original (top) and reduced (bottom) Hodgkin- Huxley model (I=8) are similar.

(Izhikevich, 2007)

05_reduceHH 2dim copy.psd

Neuron Model Reduction:
Method of Equivalent Potentials

Systematic method of reducing complex, conductance-based Hodgkin-Huxley-type models (Kepler et al.1992).

$$\begin{aligned} C\dot{V} &= I - I(V, x_1, \ldots, x_n) \\ \dot{x}_i &= (m_{i,\infty}(V) - x_i)/\tau_i(V)\ , \qquad i = 1, \ldots, n\ , \end{aligned}$$

Convert each gating variable to an *"equivalent potential"*: $\boxed{x_i = m_{i,\infty}(v_i)}$

Inverting the definition, $v_i = m_{i,\infty}^{-1}(x_i)$, we express the model in terms of equivalent potentials:

$$\begin{aligned} C\dot{V} &= I - I(V, m_{1,\infty}(v_1), \ldots, m_{n,\infty}(v_n)) \\ \dot{v}_i &= (m_{i,\infty}(V) - m_{i,\infty}(v_i))/(\tau_i(V)\, m'_{i,\infty}(v_i)) \end{aligned}$$

The new coordinates expose many patterns among the equivalent voltage variables that were not obvious in the original, gating coordinate system.

Preserves important aspects of the original dynamics

(Izhikevich, 2007)

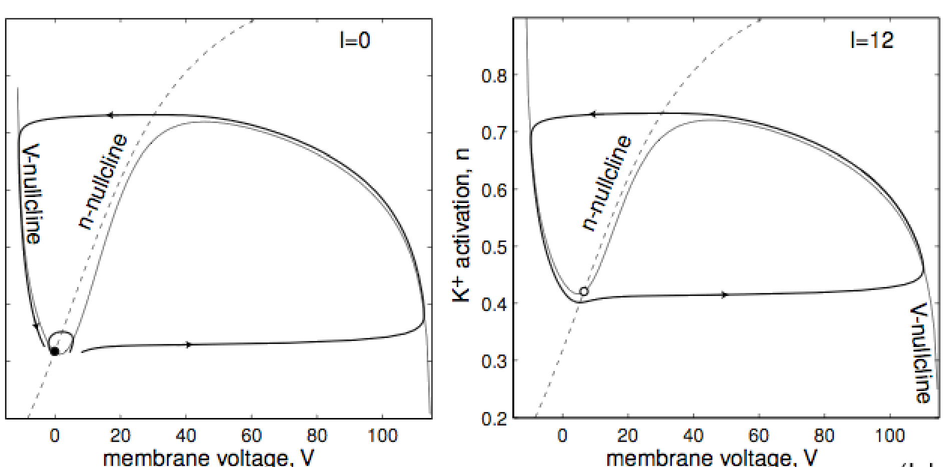
06_reduceHH eqPot.psd

Neuron Model Reduction: Nullclines

$$\begin{aligned} C\,\dot{V} &= 0 = I - \overbrace{g_K n^4 (V - E_K)}^{I_K} - \overbrace{g_{Na} m_\infty^3(V)(0.89 - 1.1n)(V - E_{Na})}^{\text{instantaneous } I_{Na}} - \overbrace{g_L(V - E_L)}^{I_L} \\ \dot{n} &= 0 = (n_\infty(V) - n)/\tau_n(V) \end{aligned}$$

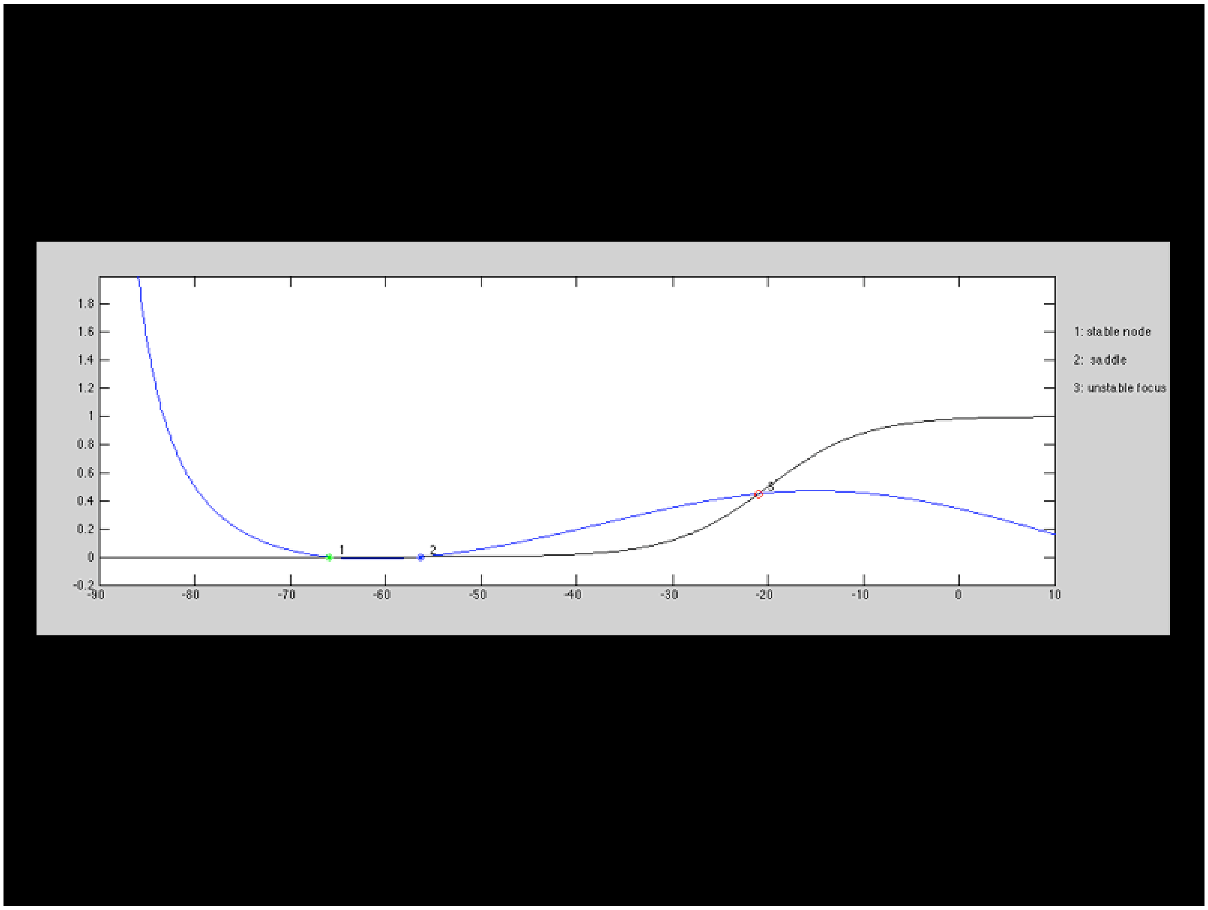
The V-nullcline can be found by solving the equation:

$$I - g_K n^4 (V - E_K) - g_{Na} m_\infty^3(V)(0.89 - 1.1n)(V - E_{Na}) - g_L(V - E_L) = 0$$



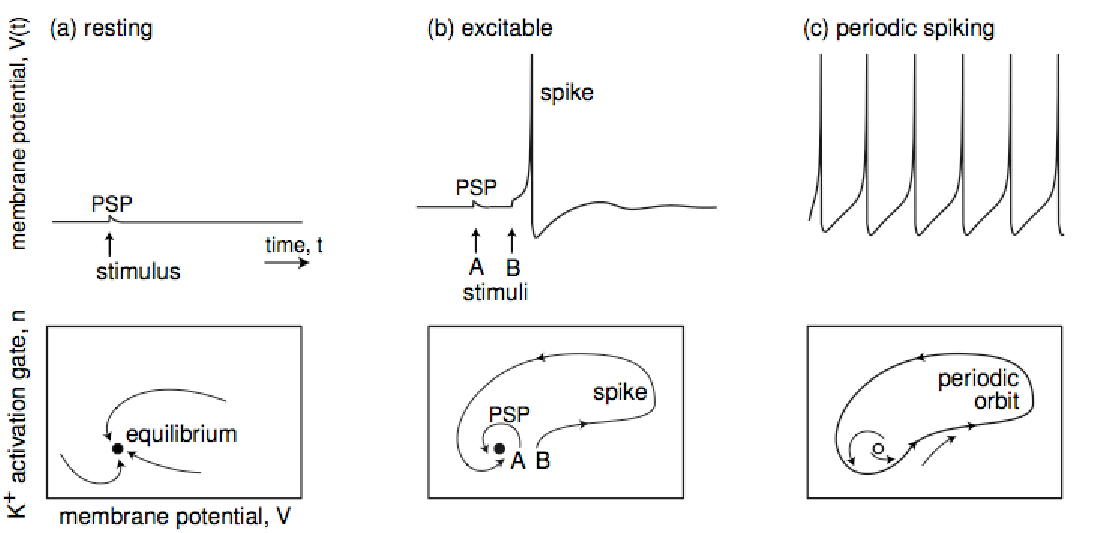
(Izhikevich, 2007)

07_reduceHH nullclines.psd



08_reduceHH simul.psd

Phase Portraits

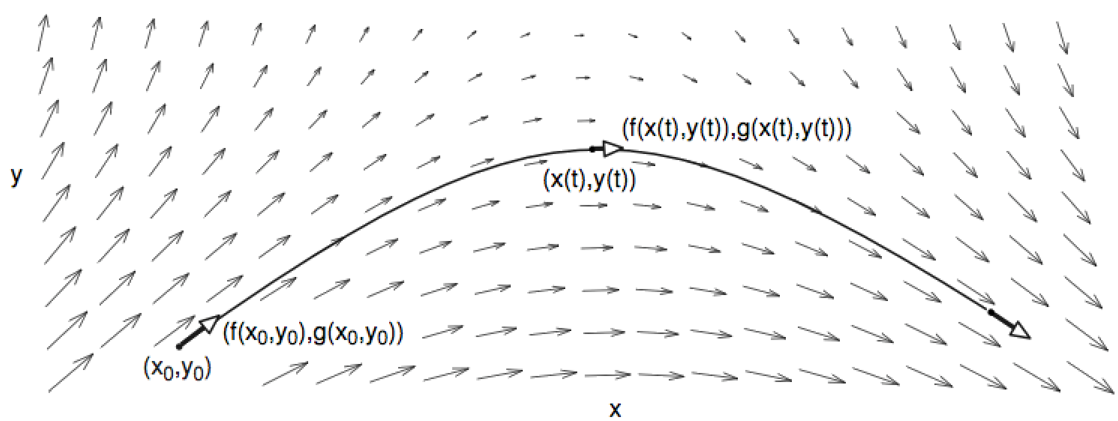


(Izhikevich, 2007)

09_phase.psd

Phase Portraits

$$\begin{aligned} \dot{x} &= f(x,y) \\ \dot{y} &= g(x,y) \end{aligned}$$

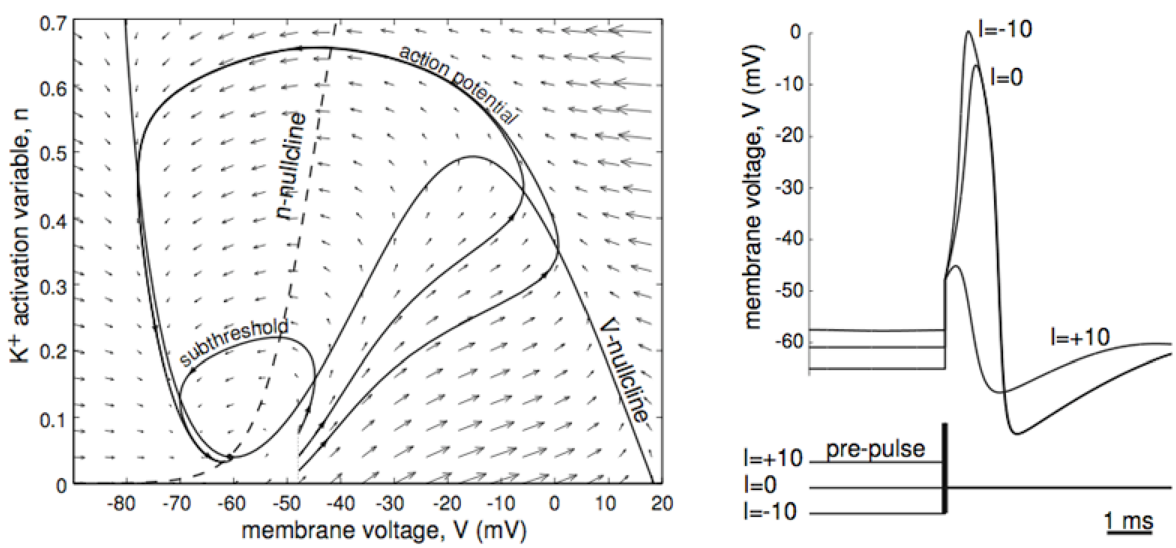


(Izhikevich, 2007)

10_phase2.psd

Phase Portraits

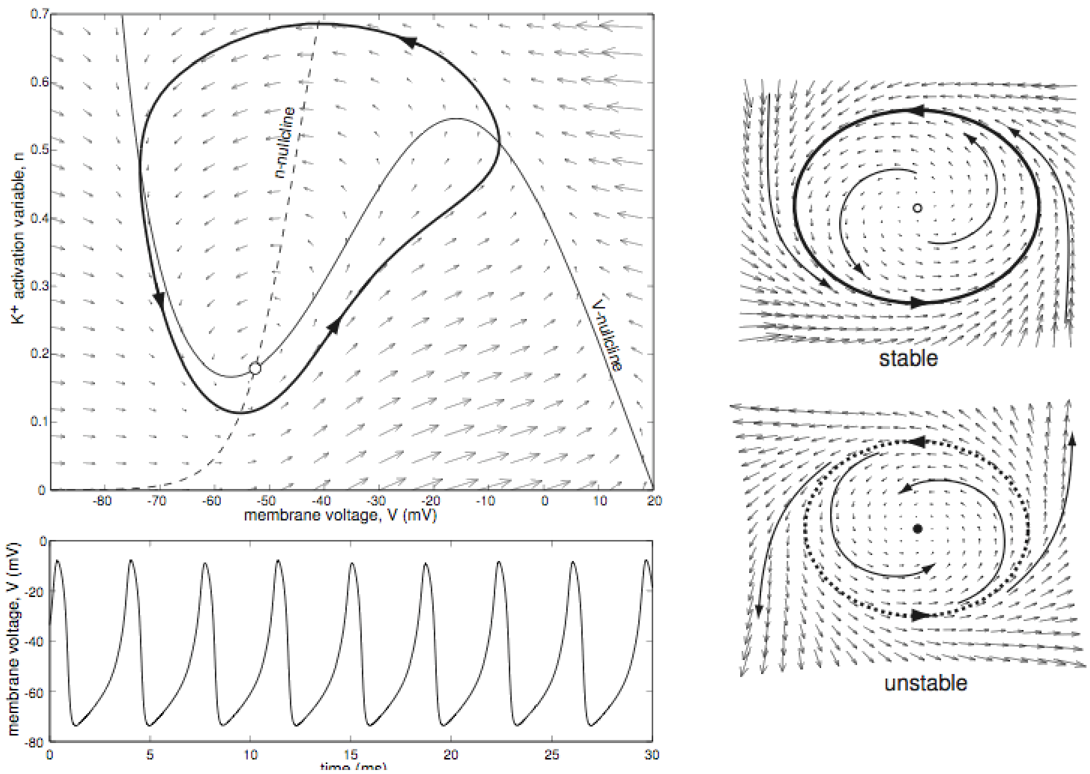
Not exactly all-or-none.



(Izhikevich, 2007)

11_phase3.psd

Phase Portraits: Limit Cycles



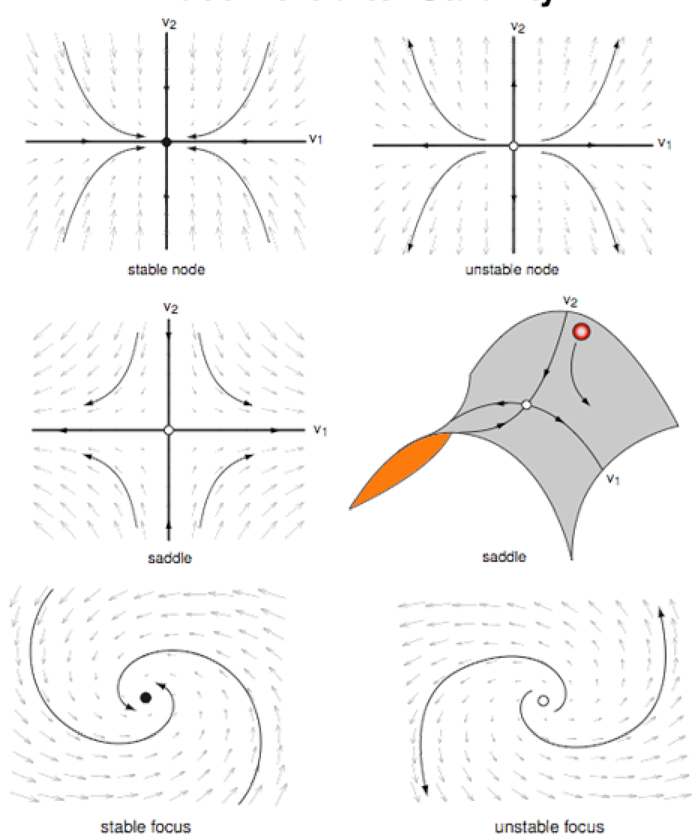
(Izhikevich, 2007)

12_phase cycle.psd

Phase Portraits: Stability

$\lambda_1 = -1$
$\lambda_2 = -3$

$\lambda_1 = +1$
$\lambda_2 = +3$



$\lambda_1 = +1$
$\lambda_2 = -1$

$\lambda = -3 \pm i$

$\lambda = +3 \pm i$

(Izhikevich, 2007)

13_phase stable .psd

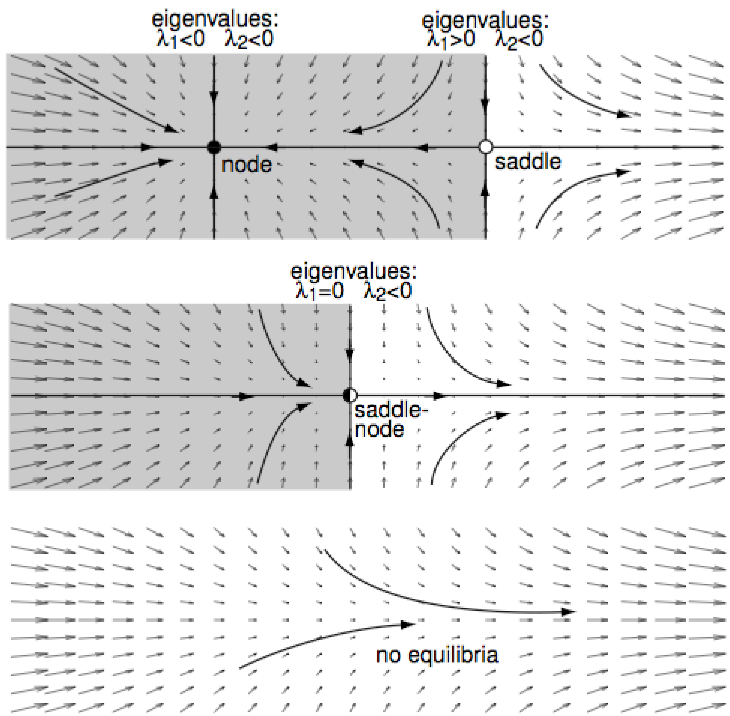
Phase Portraits: Stability

Stability is determined by the eigenvalues of the Jacobian at the fixed point.

$$\dot{x} = f(x,y)$$
$$\dot{y} = g(x,y)$$

<u>Jacobian</u>

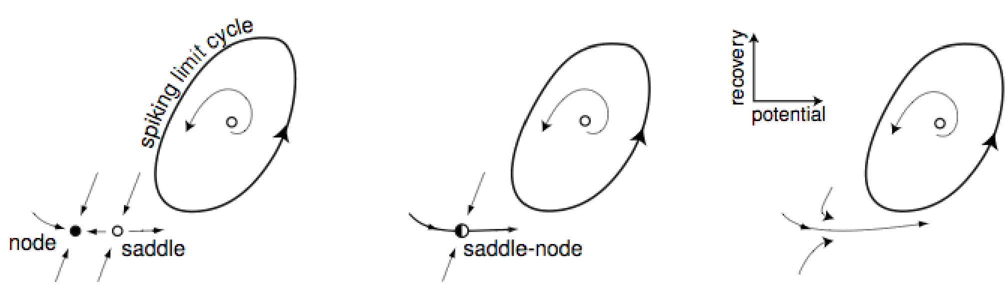
$$\begin{pmatrix} \frac{\partial f}{\partial x}(x_0,y_0) & \frac{\partial f}{\partial y}(x_0,y_0) \\ \frac{\partial g}{\partial x}(x_0,y_0) & \frac{\partial g}{\partial y}(x_0,y_0) \end{pmatrix}$$



(Izhikevich, 2007)

14_phase eval.psd

Bifurcations

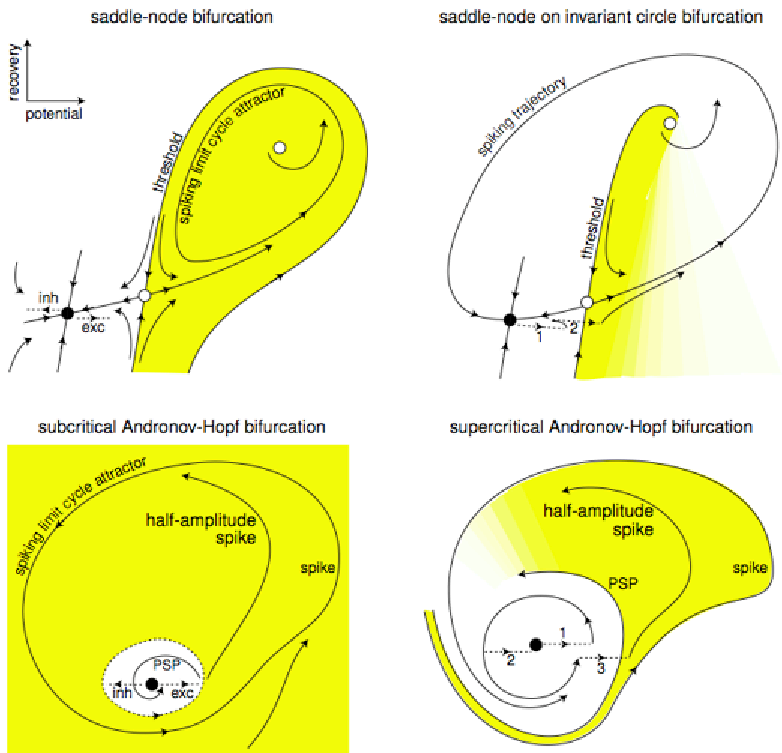


saddle-node bifurcation

(Izhikevich, 2007)

15_bifurcations.psd

Bifurcations

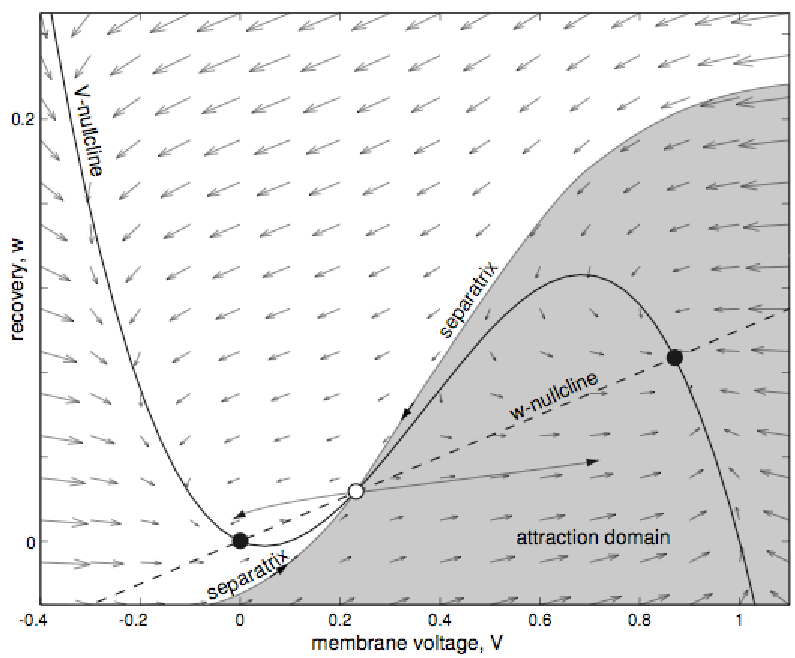


(Izhikevich, 2007)

16_bifurcations2.psd

FitzHugh-Nagumo Model

$$\dot{V} = V(a-V)(V-1) - w + I$$
$$\dot{w} = bV - cw$$

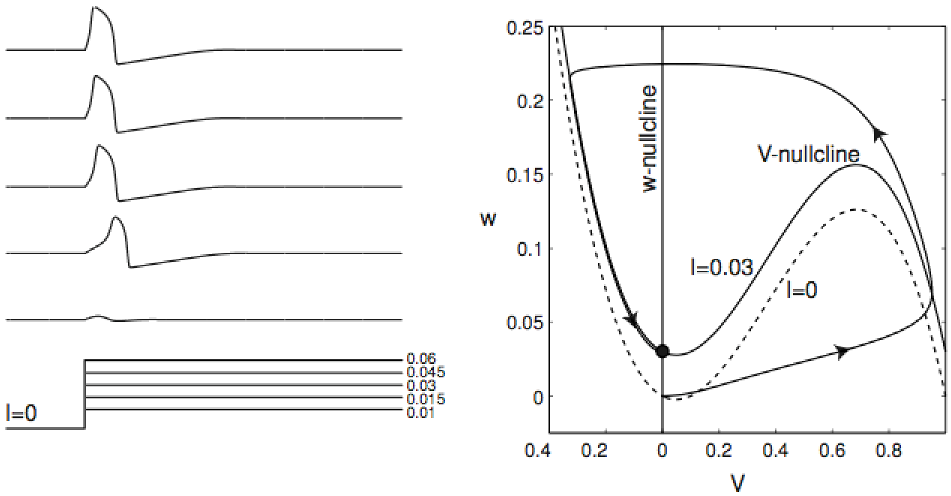


(Izhikevich, 2007)

17_Fitzhugh.psd

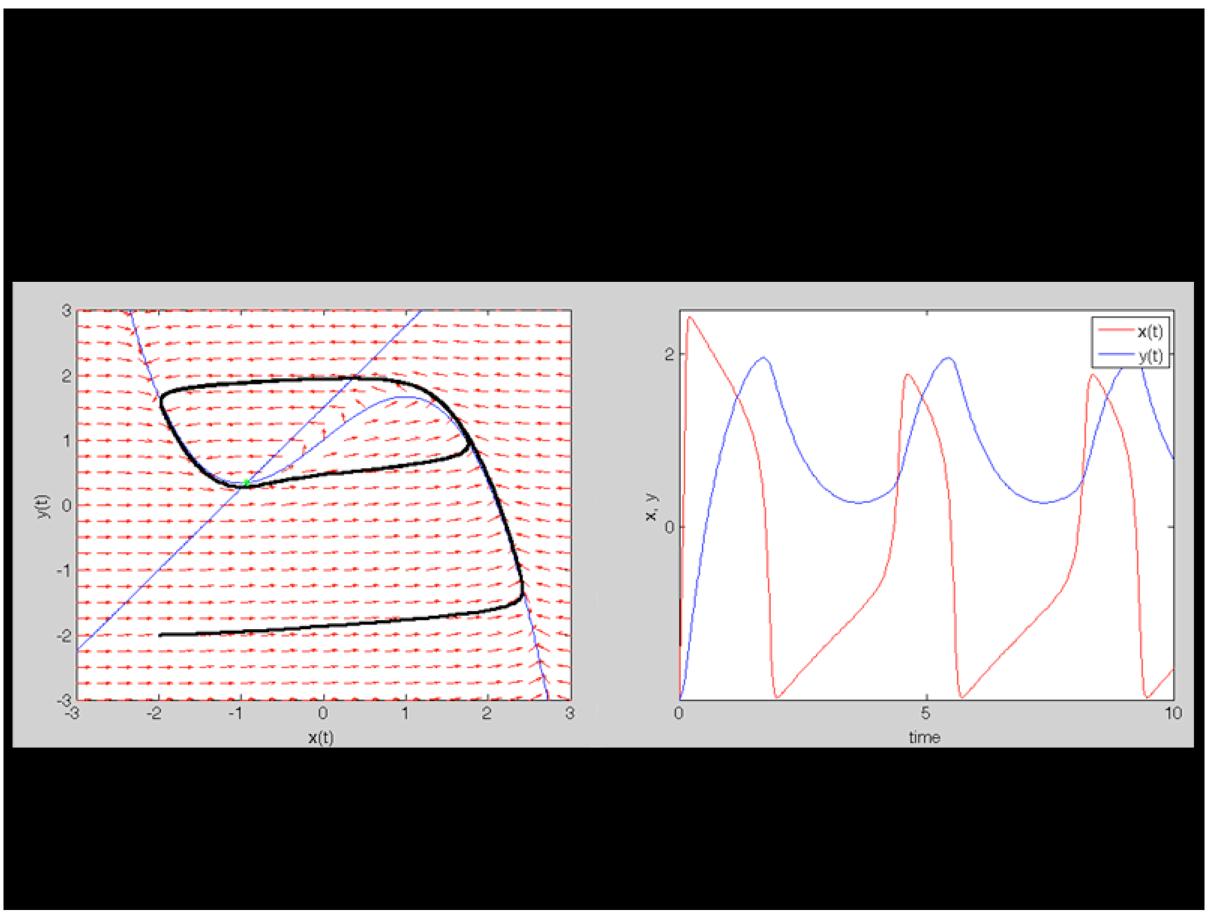
FitzHugh-Nagumo Model

$$\begin{aligned}\dot{V} &= V(a-V)(V-1) - w + I \\ \dot{w} &= bV - cw\end{aligned}$$



(Izhikevich, 2007)

18_Fitzhugh spk.psd



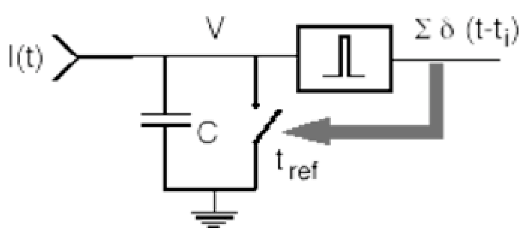
19_fitzhughSimul.psd

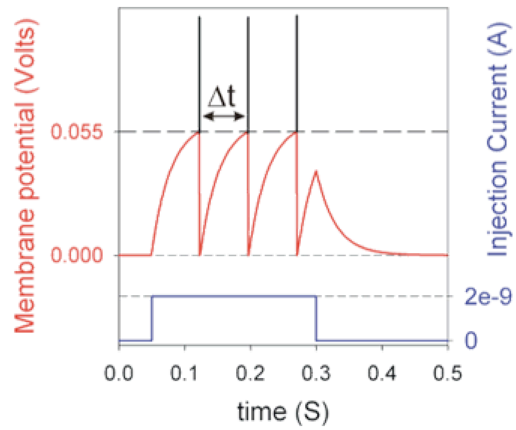
Integrate-and-Fire Model

One-variable, linear in V, with a threshold and reset to represent spikes.

$$c_m \frac{dV}{dt} = -\bar{g}_L (V - E_L) + \frac{I_e}{A}$$

If $V > V_{th}$, then $V = V_{reset}$





(Dayan & Abbott, 2001)

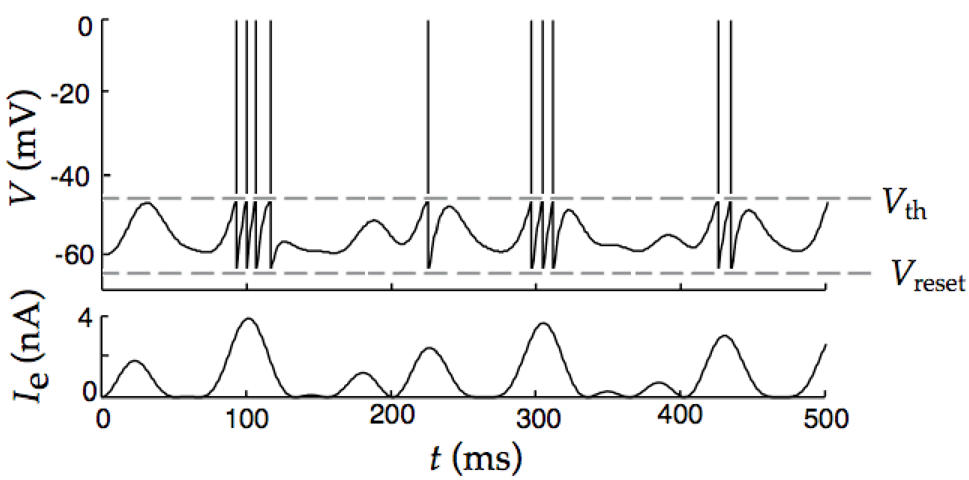
20_IF.psd

Integrate-and-Fire Model

Multiply equation by the specific membrane resistance to obtian the time constant.

$$\tau_m \frac{dV}{dt} = E_L - V + R_m I_e$$

If $V > V_{th}$, then $V = V_{reset}$



(Dayan & Abbott, 2001)

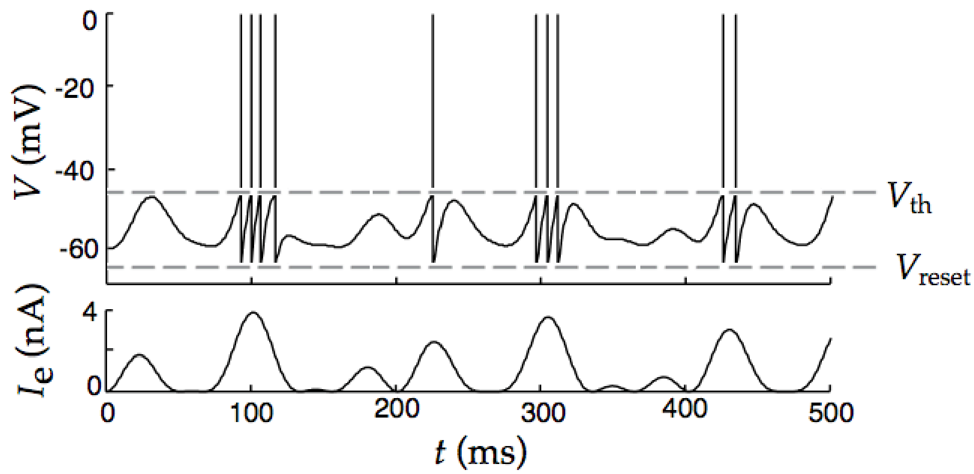
21_IF2.psd

Integrate-and-Fire Model

Multiply equation by the specific membrane resistance to obtian the time constant.

$$\tau_m \frac{dV}{dt} = E_L - V + R_m I_e$$

If $V > V_{th}$, then $V = V_{reset}$



(Dayan & Abbott, 2001)

22_IF2b.psd

Integrate-and-Fire Model

If the injected current is time-independent, then the equation can be integrated to find analytic solutions for the firing rate.

$$\tau_m \frac{dV}{dt} = E_L - V + R_m I_e \qquad \text{If } V > V_{th}\text{, then } V = V_{reset}$$

Integrate from time=0, to time=t:

$$V(t) = E_L + R_m I_e + (V(0) - E_L - R_m I_e)\exp(-t/\tau_m)$$

If the neuron fired an action potential at t = 0, then $V(0) = V_{reset}$
The next action potential will occur when the membrane potential reaches the threshold.

$$V(t_{isi}) = V_{th} = E_L + R_m I_e + (V_{reset} - E_L - R_m I_e)\exp(-t_{isi}/\tau_m)$$

By solving this for the interspike intercal (isi)we can determine the rate for constant current:

$$r_{isi} = \frac{1}{t_{isi}} = \left[\tau_m \ln\left(\frac{R_m I_e + E_L - V_{reset}}{R_m I_e + E_L - V_{th}}\right)\right]^{-1} \approx \left[\frac{E_L - V_{th} + R_m I_e}{\tau_m (V_{th} - V_{reset})}\right]_+$$

Linear, for large current injections.

(Dayan & Abbott, 2001)

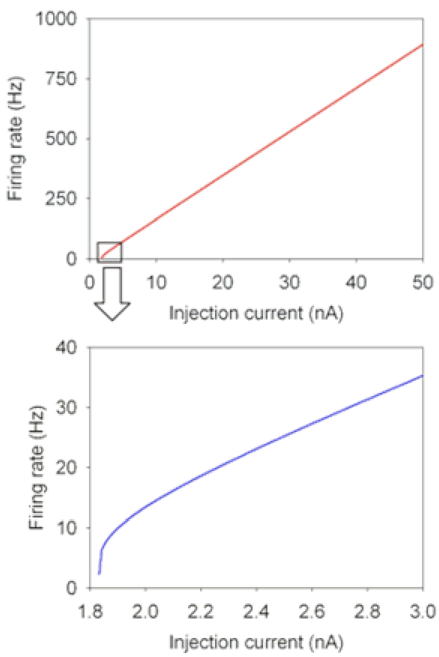
23_IF2 solu.psd

Integrate-and-Fire Model: Problems

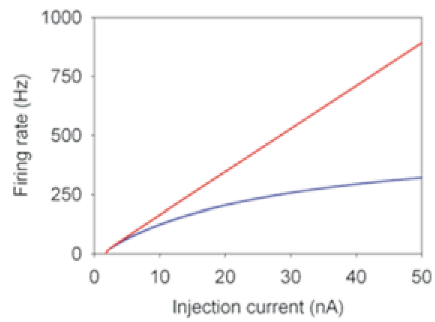
Simplifications results in inaccuracies when predicting spike rates.

Real neurons:

(1) Respond Nonlinearly to weak input



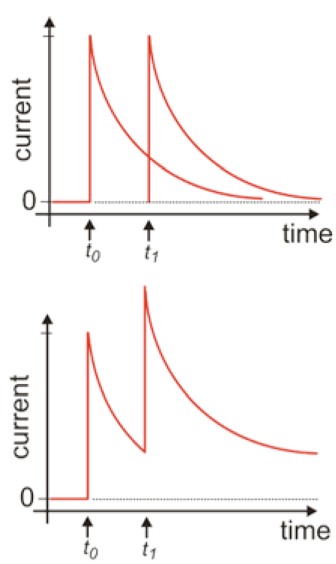
(2) Have an absolute ractory period



24_IF2 problems.psd

Integrate-and-Fire Model: Synaptic Currents

Synapses are represented similarly to conductance-based models.



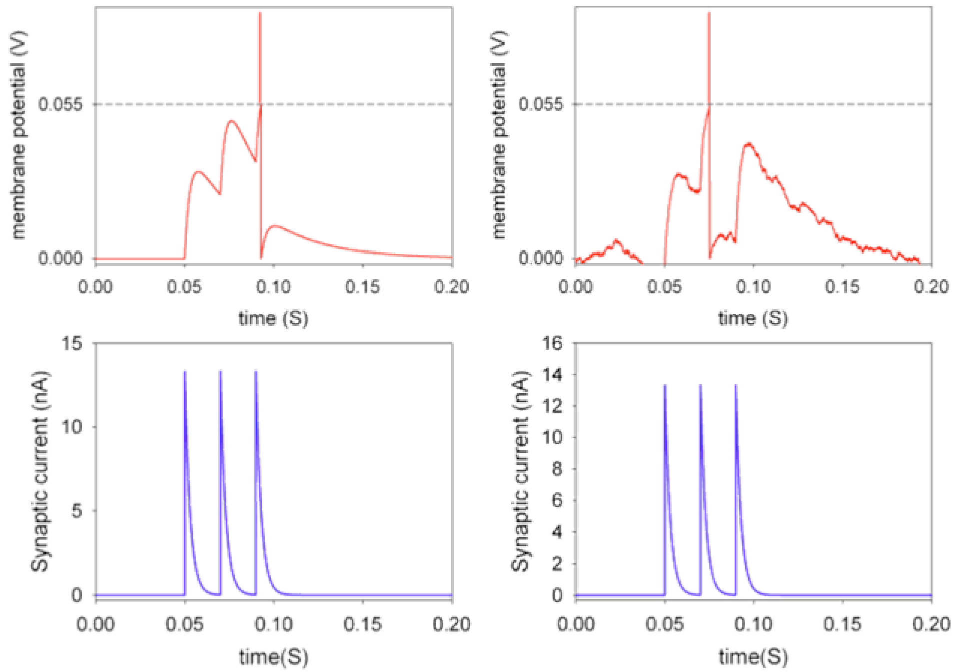
- Multiple PSCs add arithmetically
- Formally, if $\mathcal{F}$ is the set of afferent spike times at the neuron, and I_s is now the *total* synaptic current, then for synapses with strength w.

$$I_s(t) = \sum_{t_i \in \mathcal{F}} \frac{w}{\tau_s} e^{-(t-t_i)/\tau_s}$$

25_IF2 syns.psd

Integrate-and-Fire Model: Noise

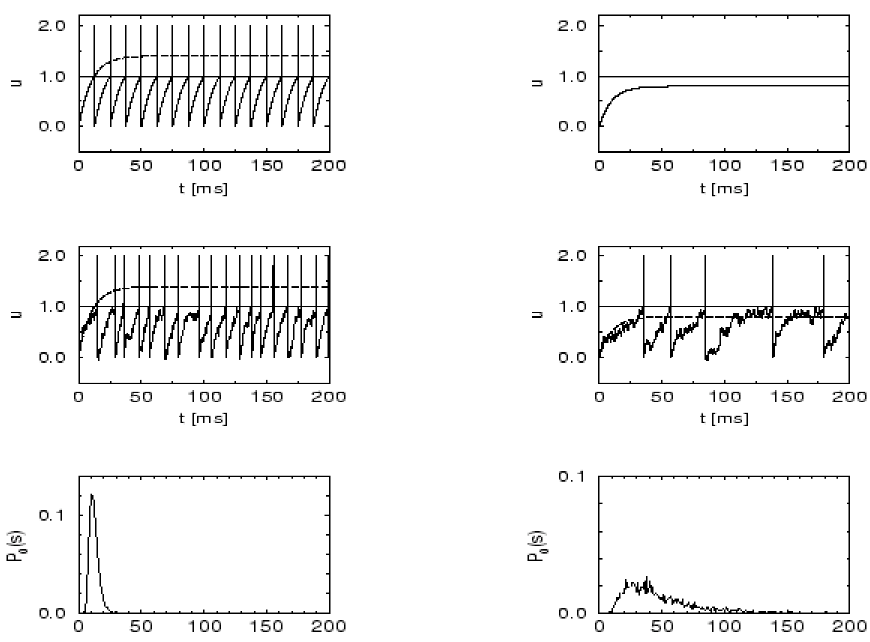
Sources of noise: channel noise, synaptic noise, threshold noise



26_IF2 syns noise.psd

Integrate-and-Fire Model: Noise

Sources of noise: channel noise, synaptic noise, threshold noise

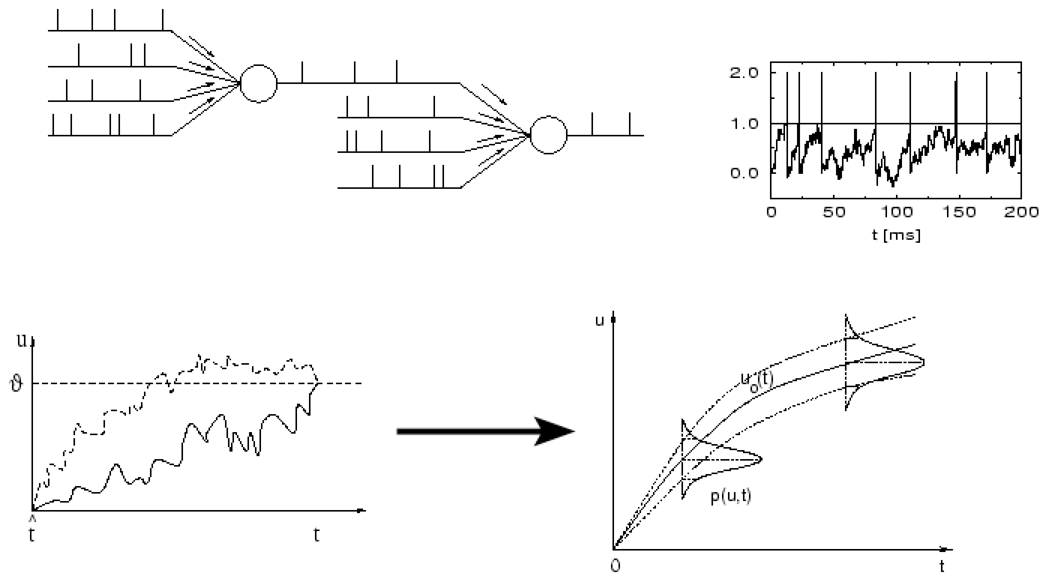


(Gerstner, 2002)

27_IF2 syns noise2.psd

Integrate-and-Fire Model: Noise

Stochastic models compute ISI varaince as a diffusion process



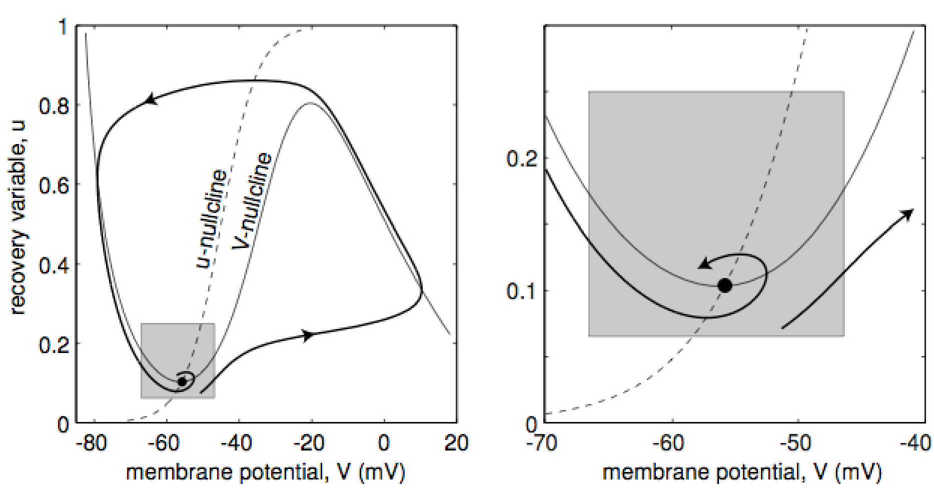
(Gerstner, 2002)

28_IF2 syns noise3.psd

Two-dimensional, Integrate-and-Fire

$$\begin{aligned} C\dot{v} &= k(v - v_r)(v - v_t) - u + I \\ u &= a\{b(v - v_r) - u\} \end{aligned} \qquad \begin{aligned} &\text{if } v \geq v_{\text{peak}}, \text{ then} \\ &v \to c, \ u \to u + d \end{aligned}$$

Fit an parabola to the V-nullcline near the fixed point, and fit a line to the u-nullcline.



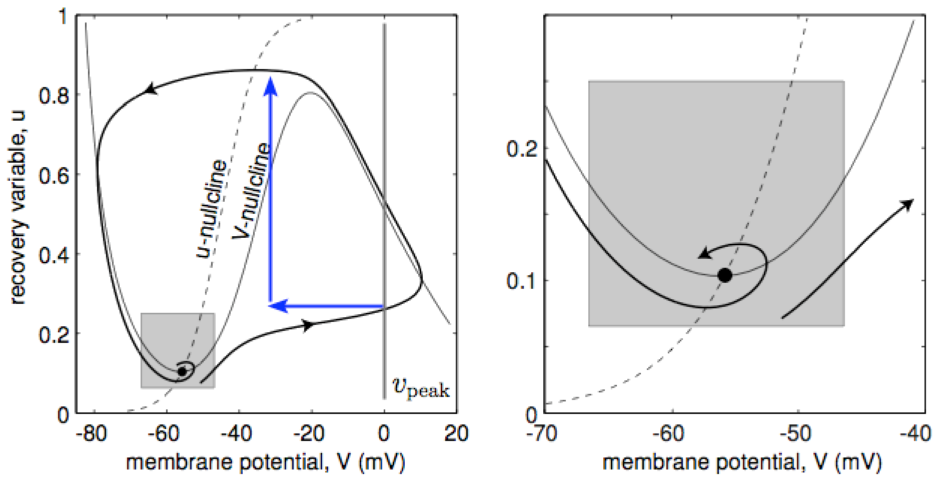
(Izhikevich, 2007)

30_izh.psd

Two-dimensional, Integrate-and-Fire

$$\begin{aligned} C\dot{v} &= k(v-v_r)(v-v_t) - u + I & \text{if } v \geq \quad , \text{ then} \\ u &= a\{b(v-v_r) - u\} & v \to c,\ u \to u + d \end{aligned}$$

Fit an parabola to the V-nullcline near the fixed point, and fit a line to the u-nullcline.

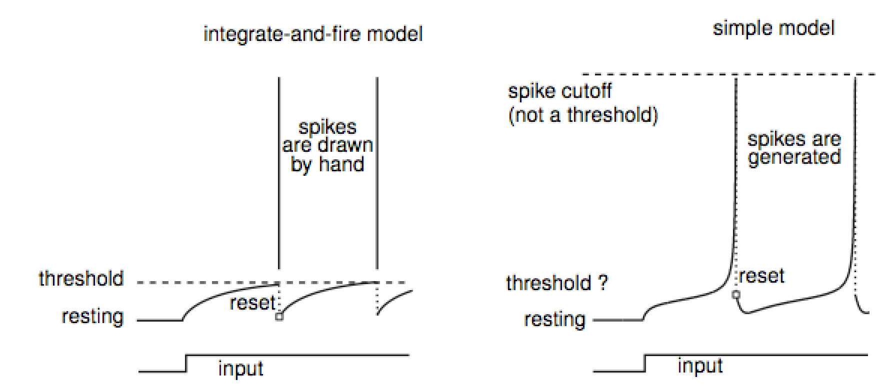


(Izhikevich, 2007)

31_izh2.psd

Two-dimensional vs One-dimensional Integrate-and-Fire

$$\begin{aligned} C\dot{v} &= k(v-v_r)(v-v_t) - u + I & \text{if } v \geq \quad , \text{ then} \\ u &= a\{b(v-v_r) - u\} & v \to c,\ u \to u + d \end{aligned}$$

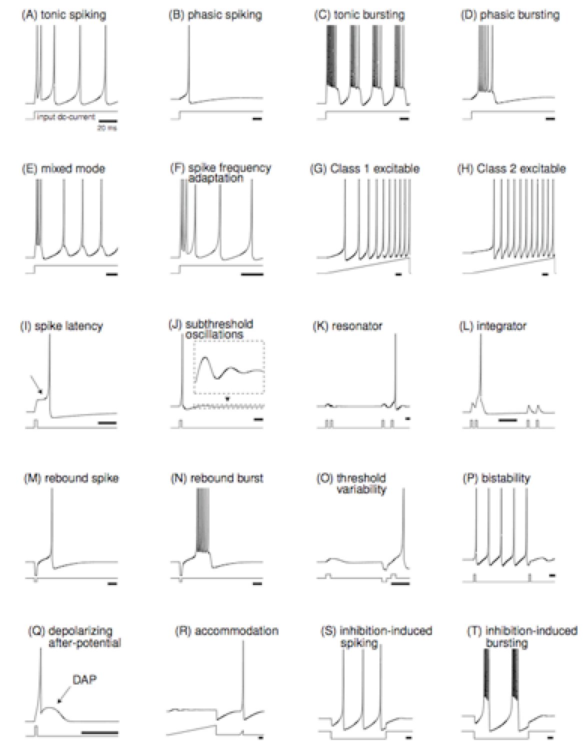


(Izhikevich, 2007)

32_izh-IF.psd

Two-dimensional, Integrate-and-Fire

A remarkable variety of neural properties can be realized with this framework.



(Izhikevich, 2007)

33_izh variety.psd