Dynamical systems in neuroscience

Pacific Northwest Computational Neuroscience Connection
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What do I mean by a *dynamical system*?

- Set of *state variables*
- Law that governs *evolution* of state variables in time
- Often takes the form of *differential equations*

ex:
$$\frac{dV}{dt} = V\left(a - V\right)\left(V - 1\right) - w + I$$
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state variables

parameters

Dynamical systems arise as models for single neurons

ex: Hodgkin-Huxley equations

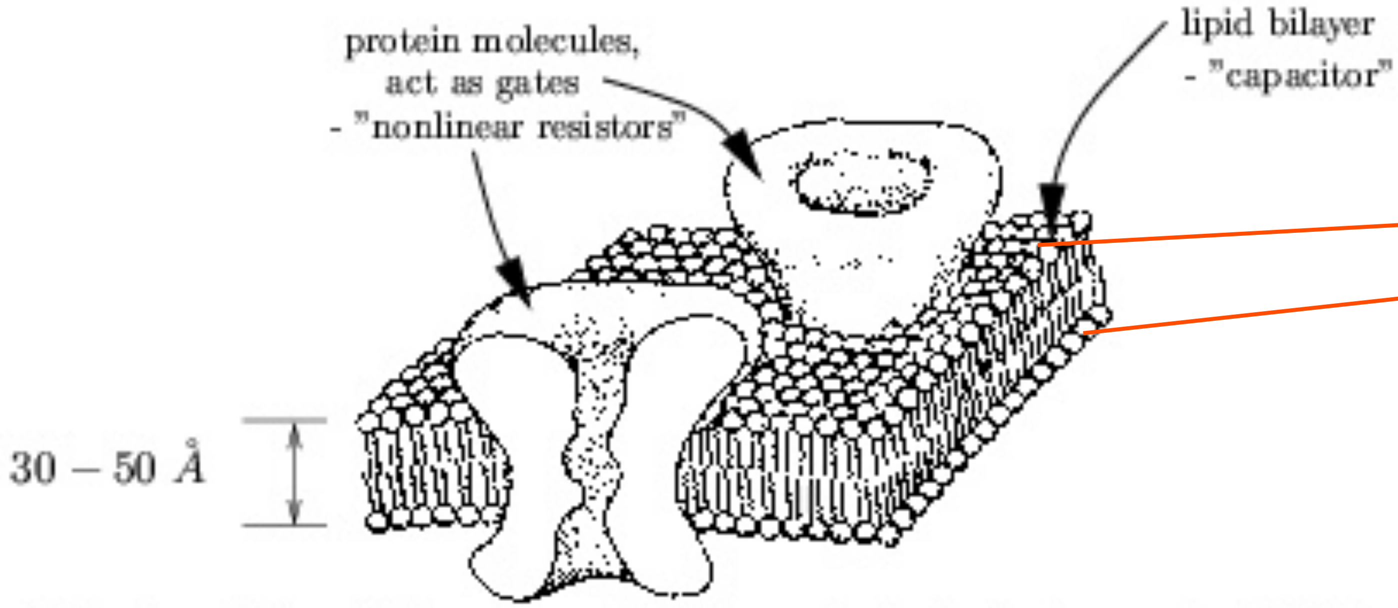
$$C\frac{dV}{dt} = I - g_K n^4 \left(V - E_K\right) - g_{Na} m^3 h \left(V - E_{Na}\right) - g_L \left(V - E_L\right)$$

$$\frac{dn}{dt} = \left(n_\infty\left(V\right) - n\right) / \tau_n\left(V\right)$$

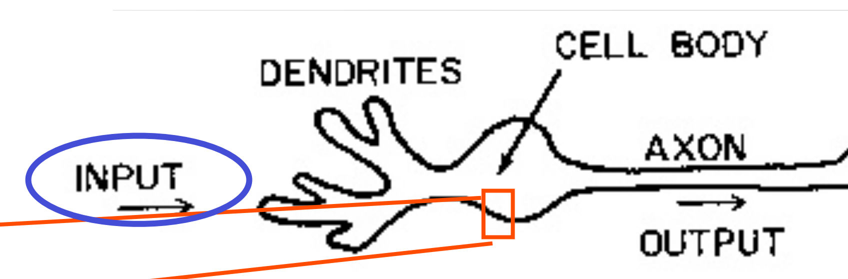
$$\frac{dm}{dt} = \left(m_\infty\left(V\right) - m\right) / \tau_m\left(V\right)$$

$$\frac{dh}{dt} = \left(h_\infty\left(V\right) - h\right) / \tau_h\left(V\right)$$

Hodgkin and Huxley's circuit model of a neuronal membrane:



from *Biophysics of Computation: Information Processing in Single Neurons*, by C. Koch, 1999



from *Mathematical Aspects of Hodgkin-Huxley Neural Theory* by J

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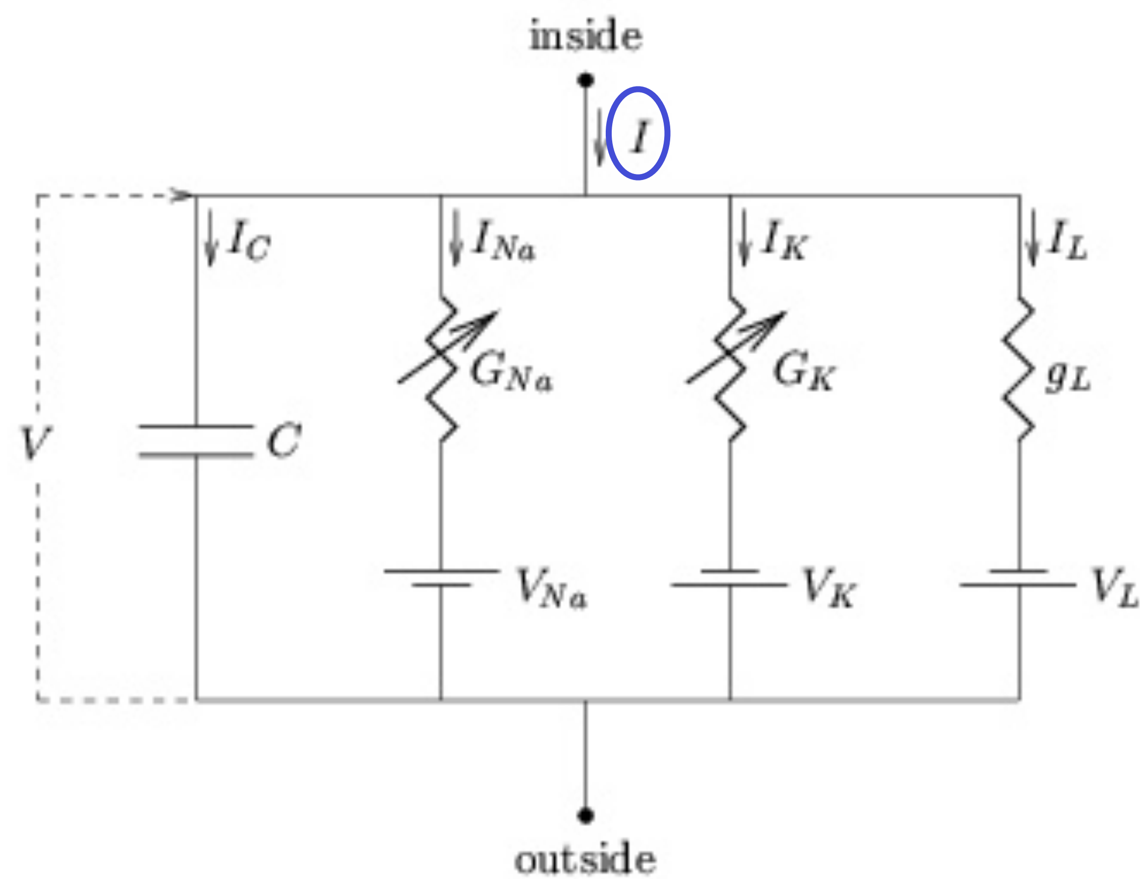

$$\frac{dV}{dt} = [I - \bar{g}_{Na} m^3 h (V - V_{Na}) - \bar{g}_K n^4 (V - V_K) - g_L (V - V_L)]/C,$$

$$\frac{dn}{dt} = \alpha_n(V)(1-n) - \beta_n(V)n,$$

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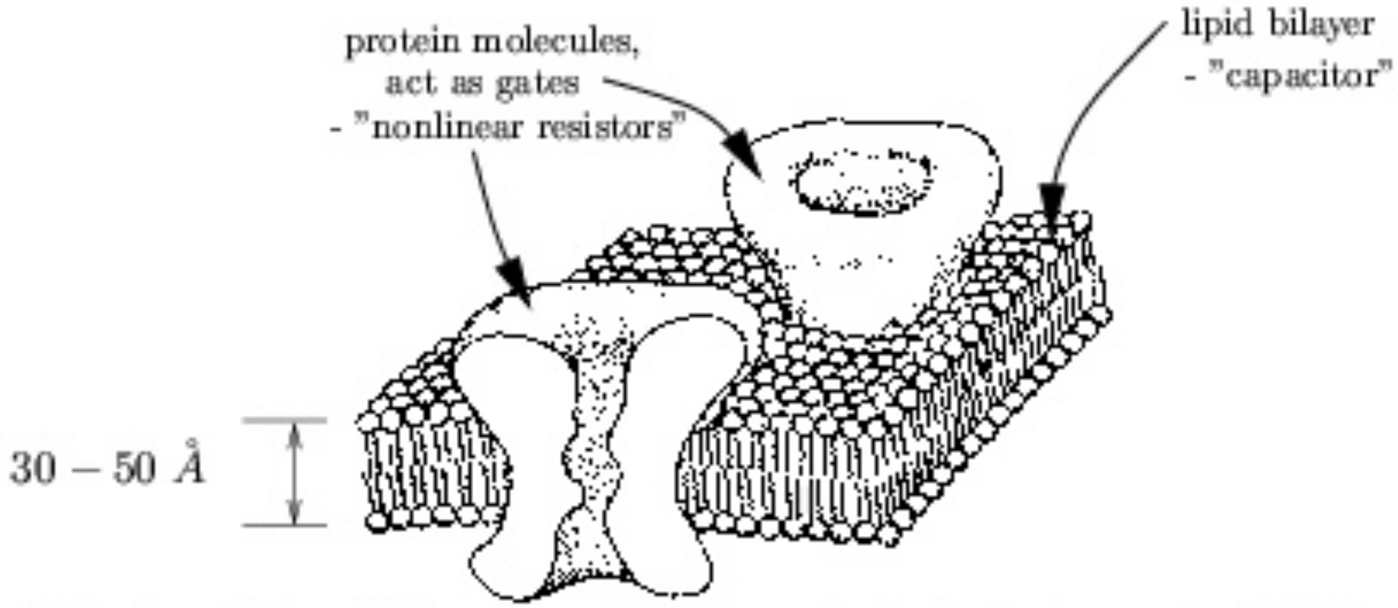

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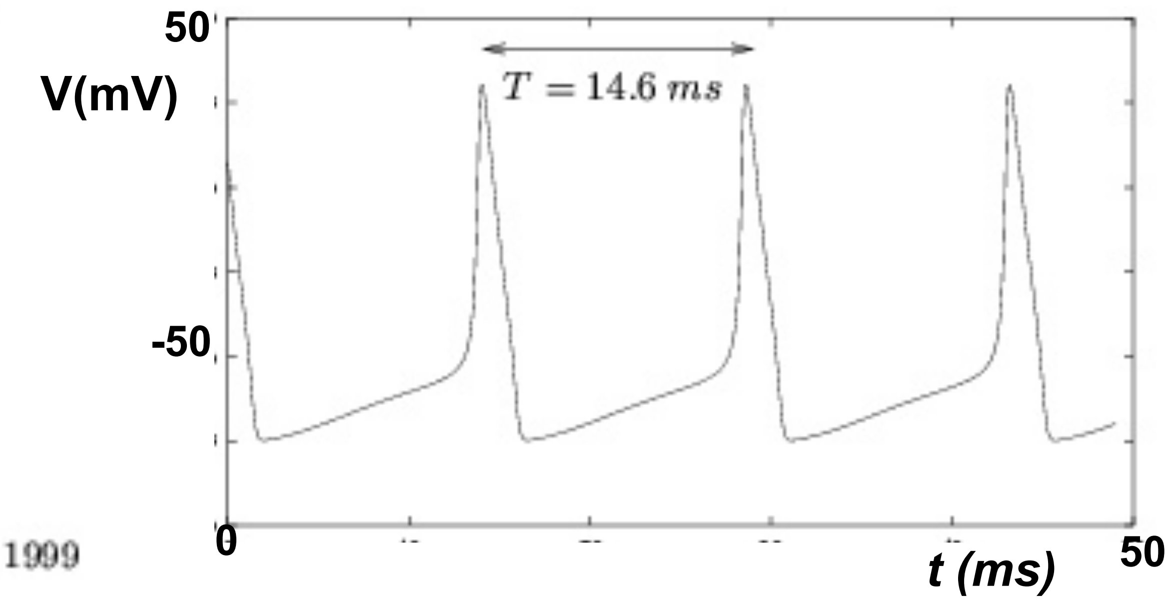
Voltage response to input current 10μA/cm²



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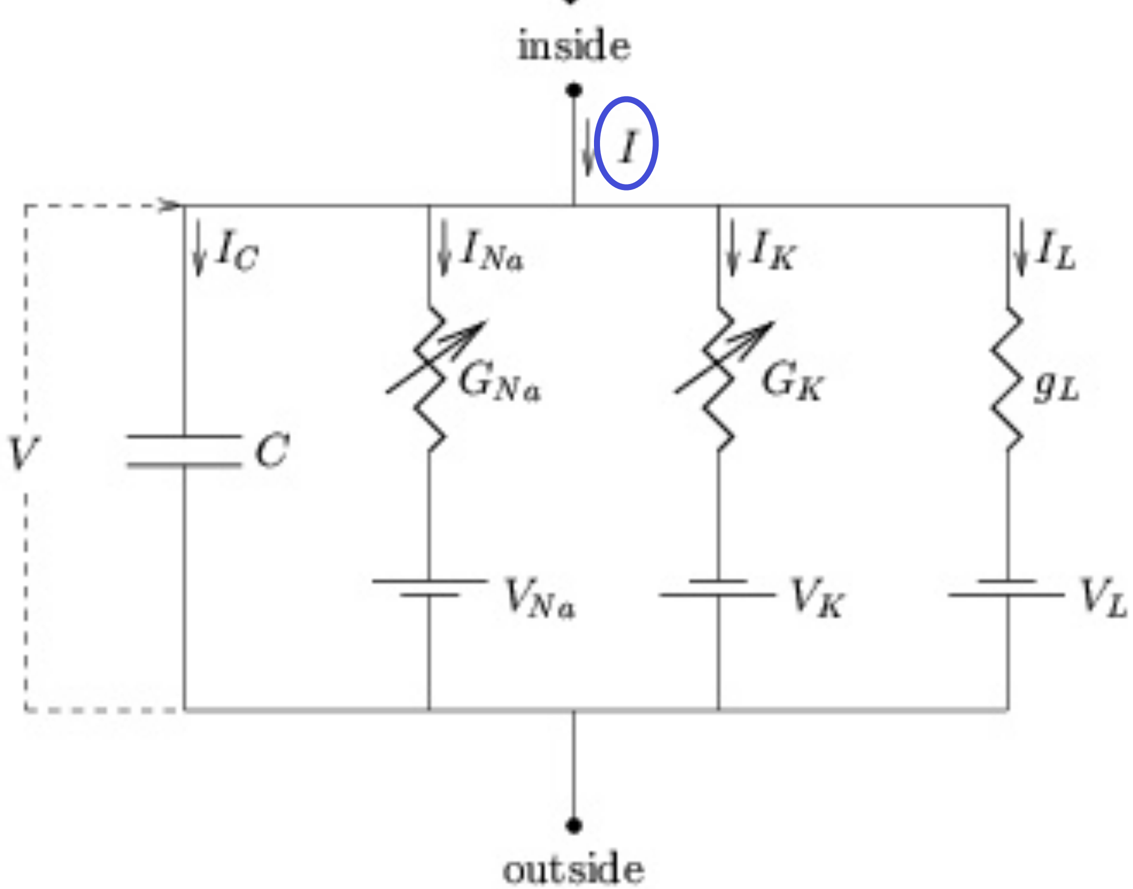

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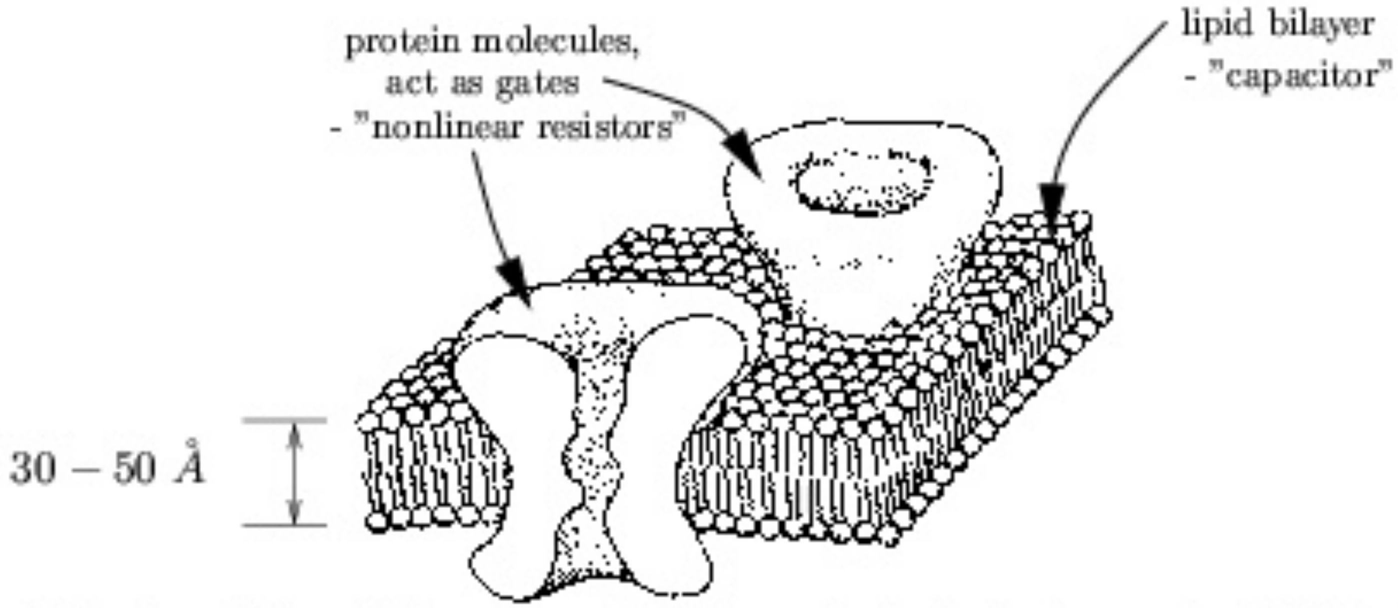

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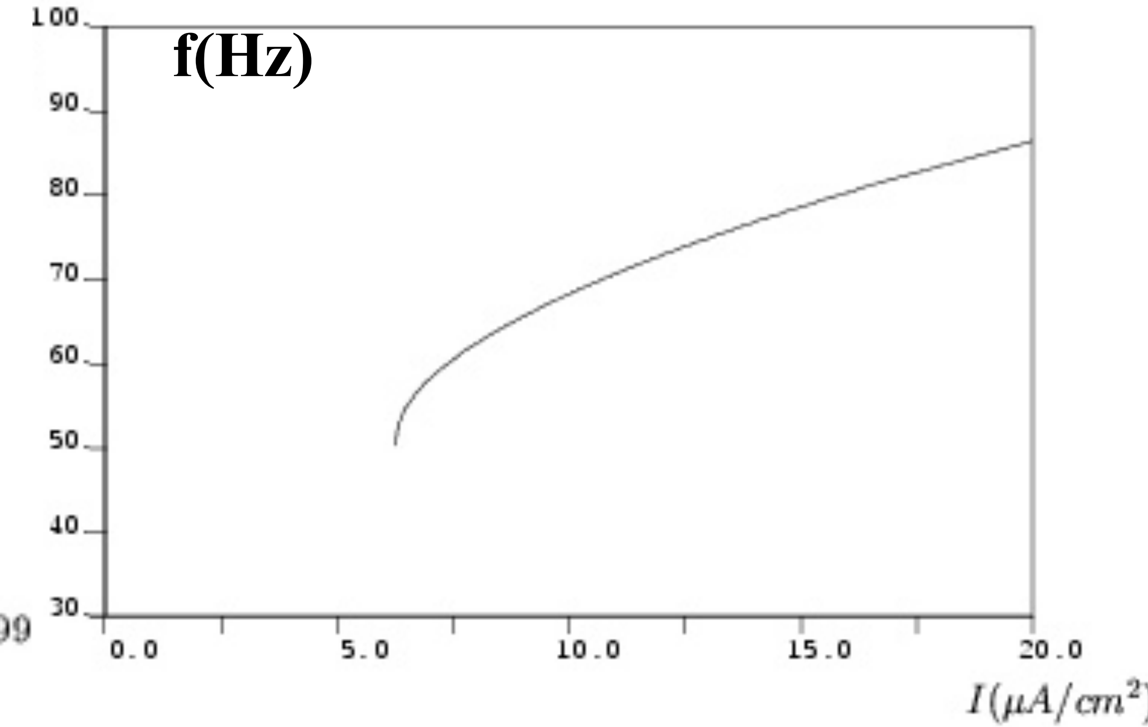

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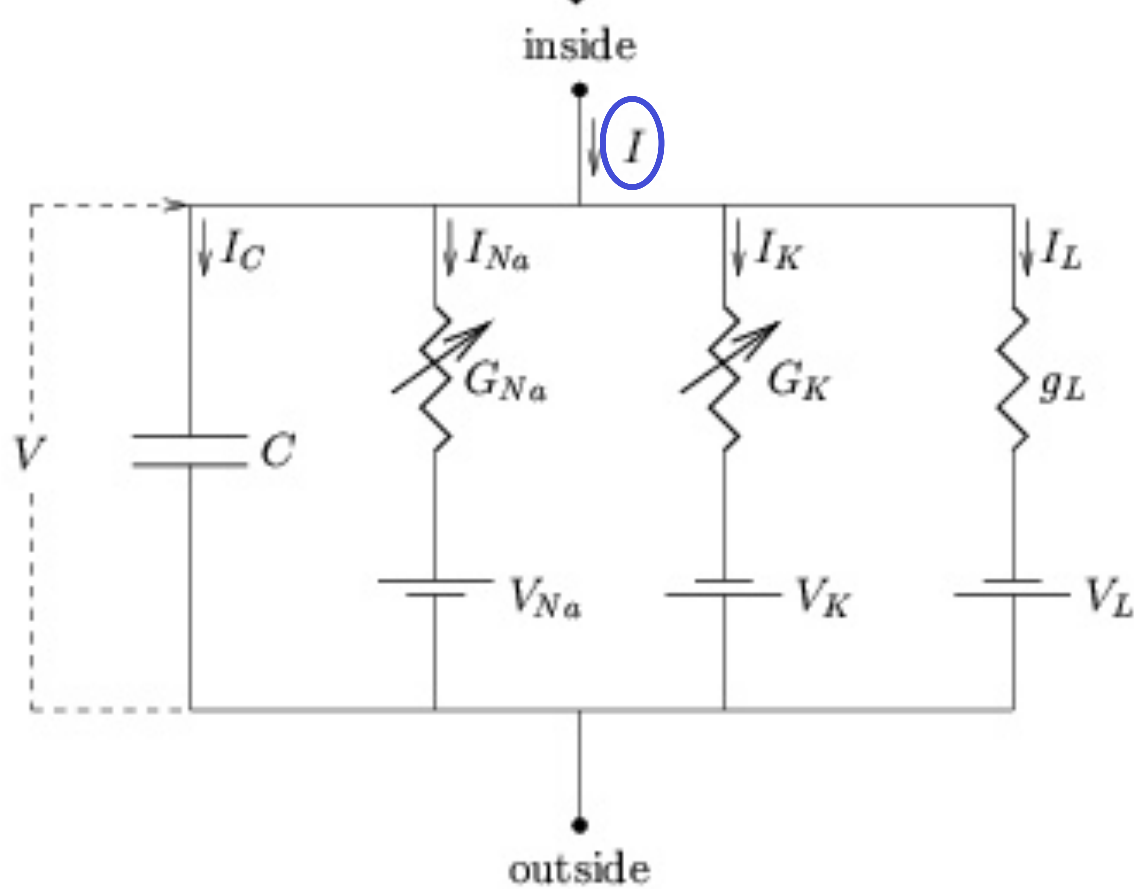

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$$\frac{dm}{dt} = \left(m_\infty(V) - m\right) / \tau_m(V)$$

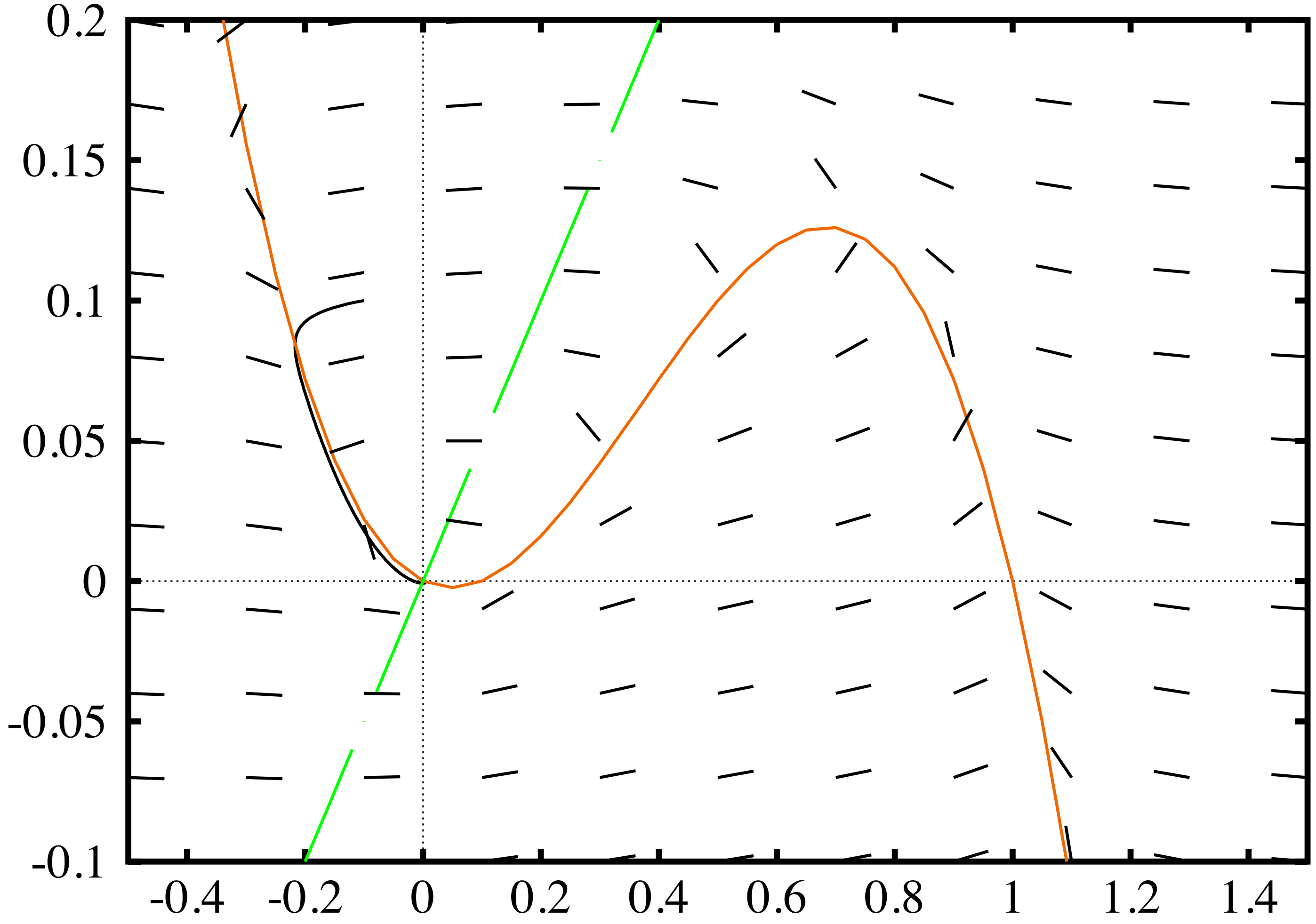
$$\frac{dh}{dt} = \left(h_\infty(V) - h\right) / \tau_h(V)$$

$$\Rightarrow \frac{d\mathbf{V}}{dt} = \mathbf{F}\left(\mathbf{V}\right)$$

$$\mathbf{V} = \left(V, n, m, h\right)$$

Basic question: can I get info about solutions by analyzing $\mathbf{F}\left(\mathbf{V}\right)$?

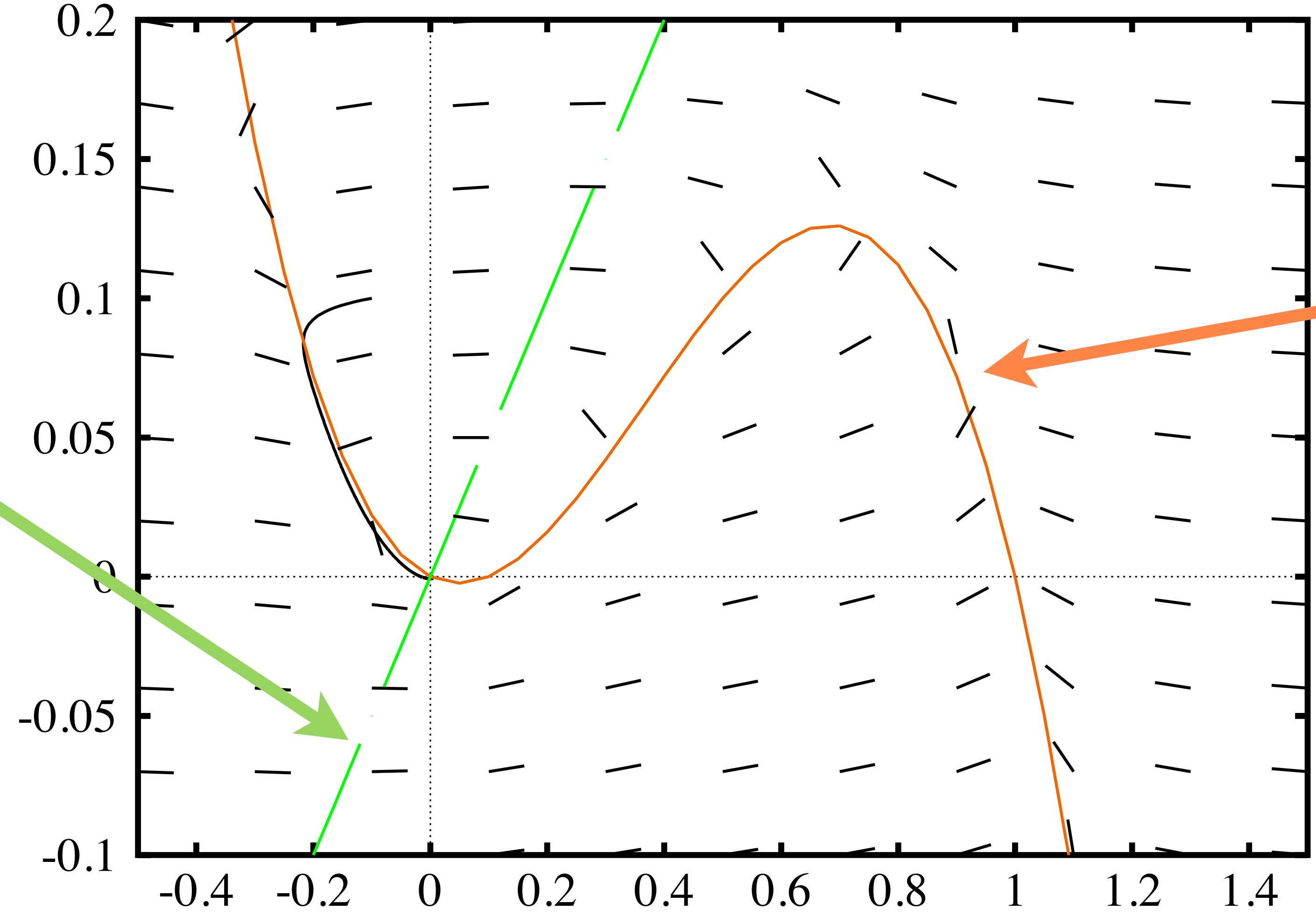
Phase plane analysis



$$\frac{dV}{dt} = V\left(a - V\right)\left(V - 1\right) - w + I$$

$$\frac{dw}{dt} = bV - cw$$

Phase plane analysis: Nullclines



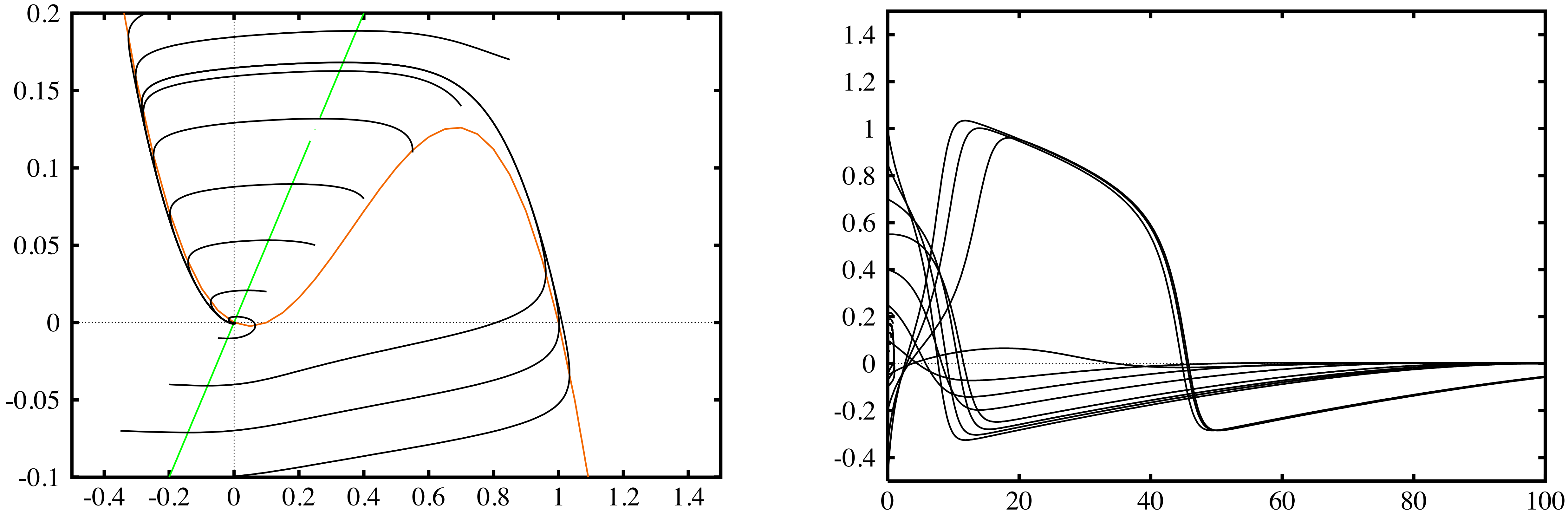
$$\frac{dw}{dt} = 0$$

$$\frac{dV}{dt} = 0$$

$$\frac{dV}{dt} = V(a-V)(V-1) - w + I$$

$$\frac{dw}{dt} = bV - cw$$

Phase plane analysis: Equilibria and stability

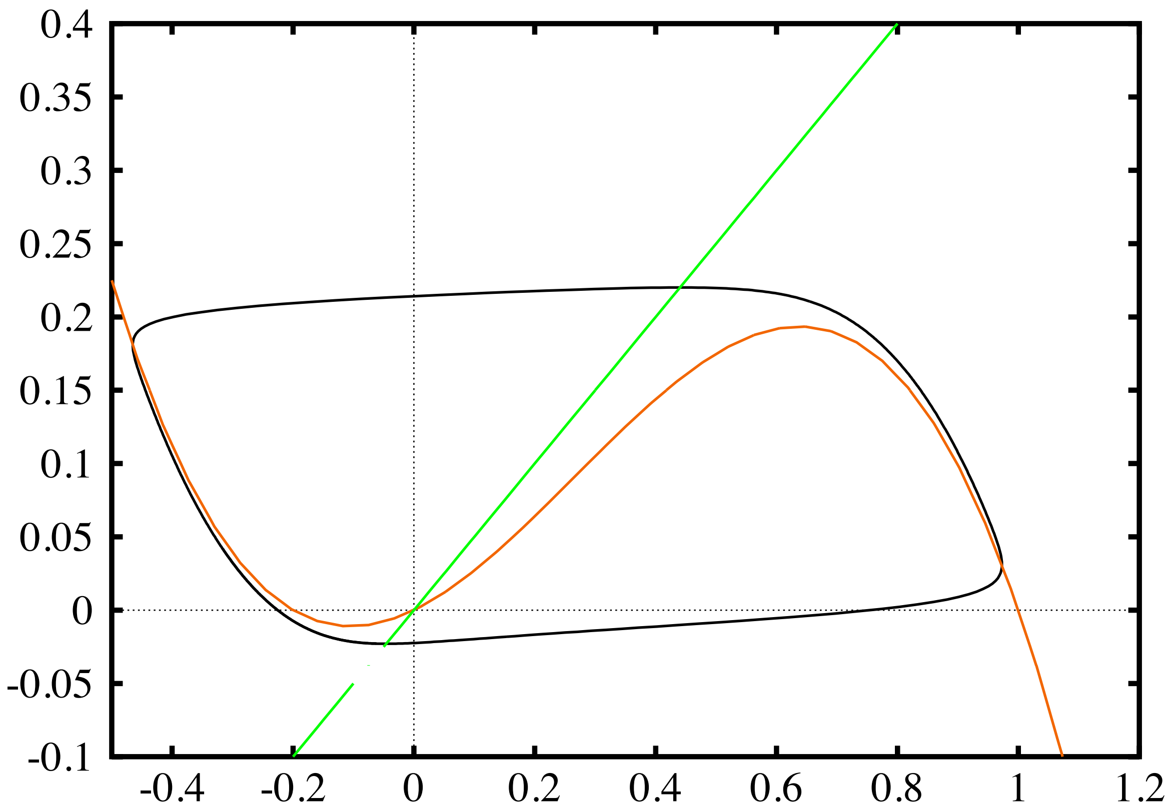


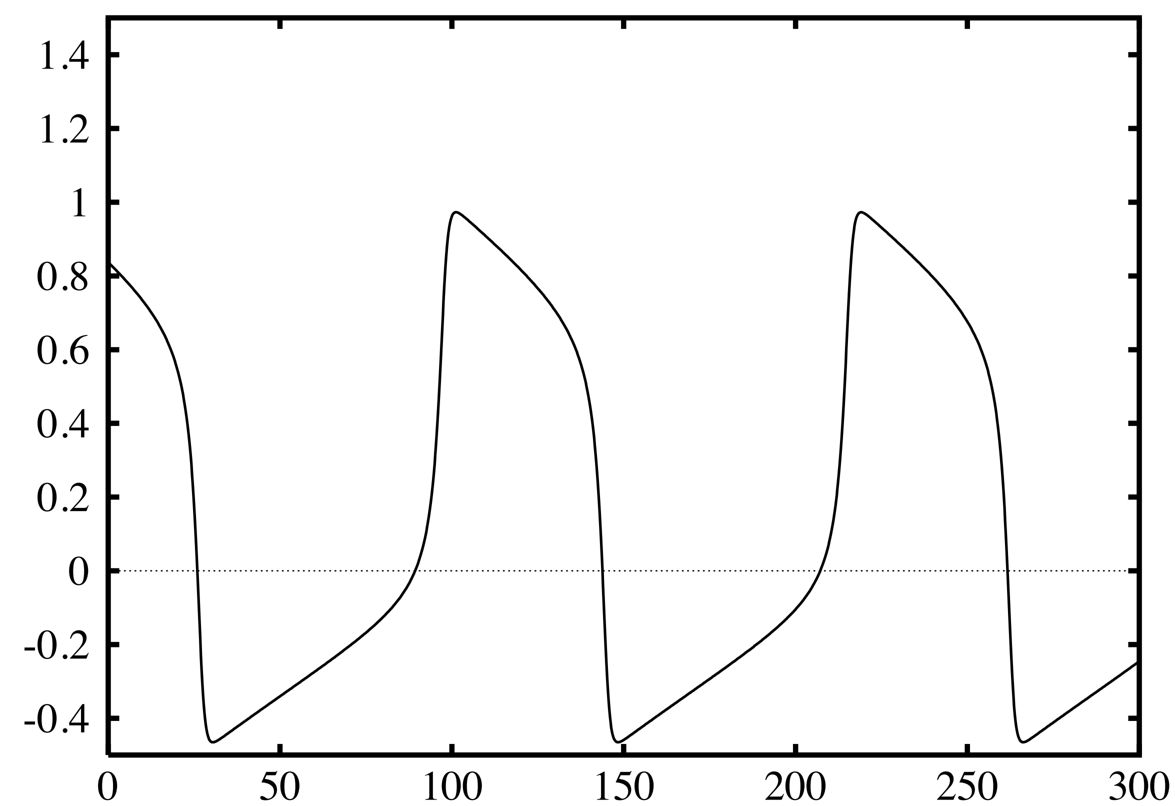
$$\frac{dV}{dt} = V(a - V)(V - 1) - w + I$$

$$\frac{dw}{dt} = bV - cw$$

a=.1, b=.01, c=.02, I=0

Phase plane analysis: Equilibria and stability



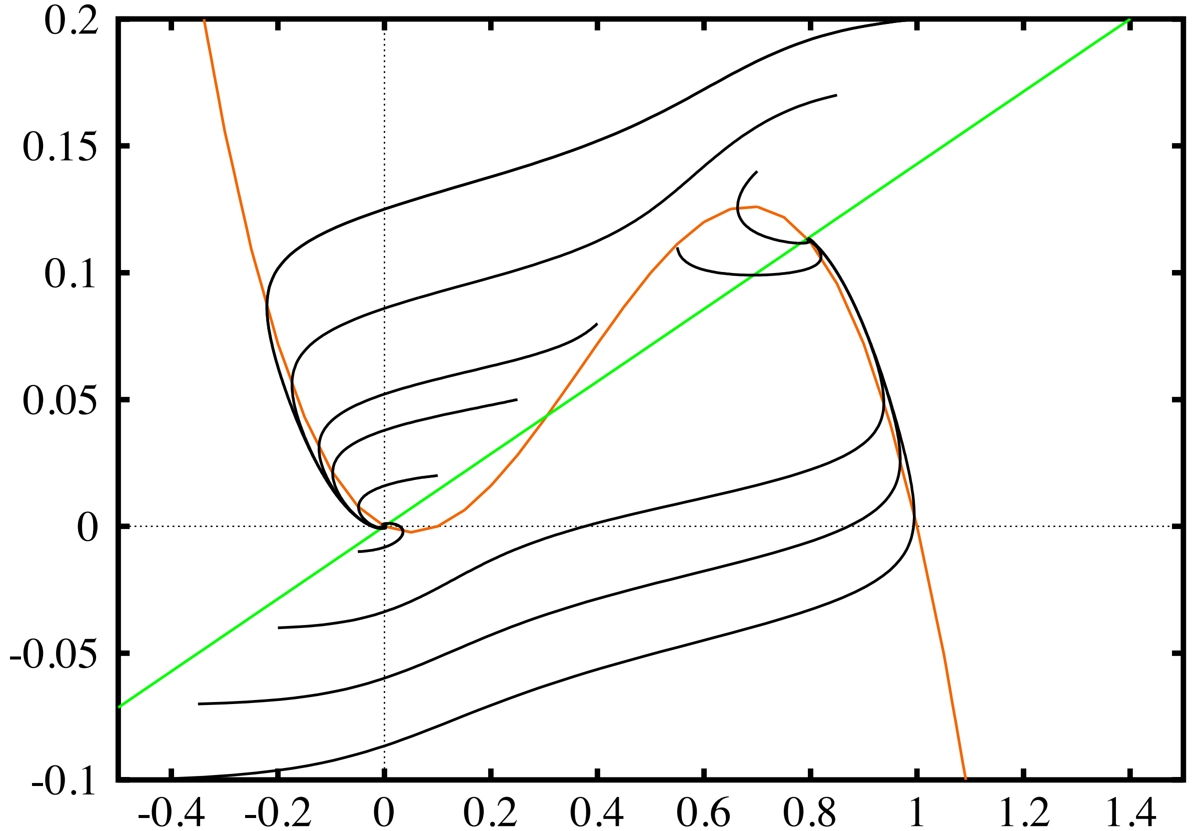


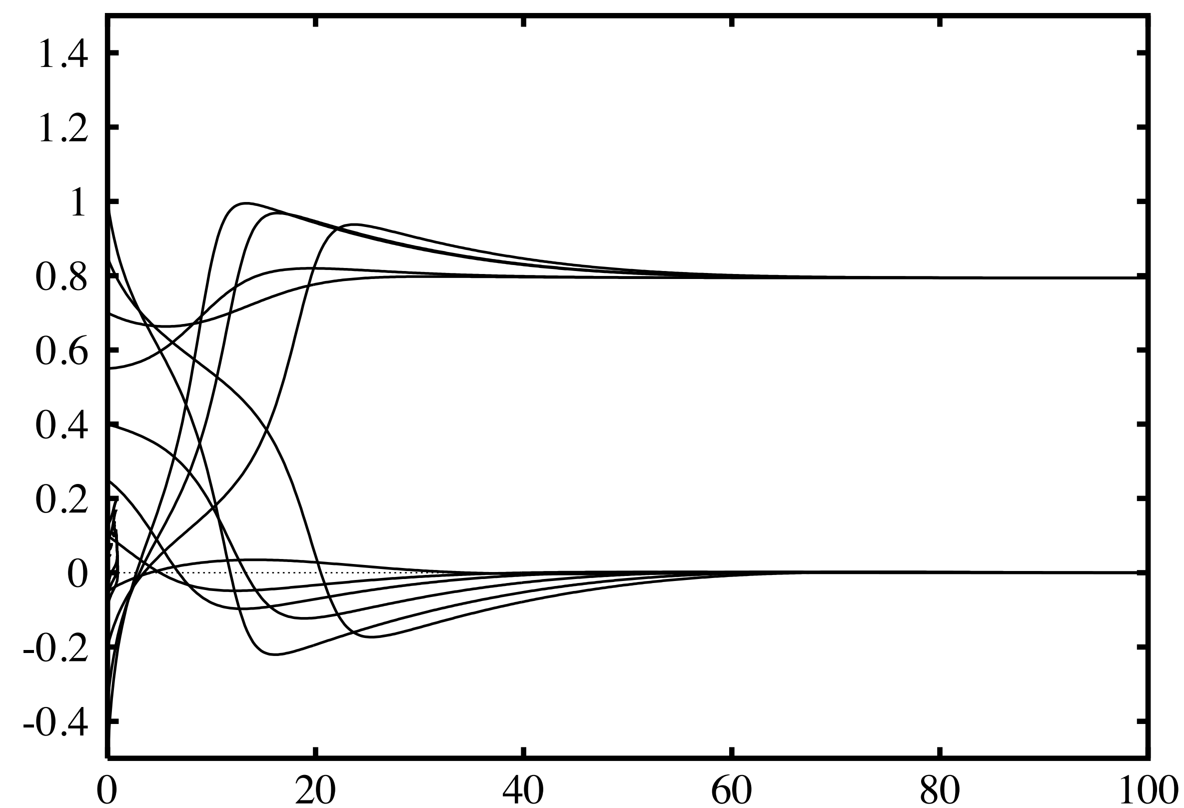
$$\frac{dV}{dt} = V(a-V)(V-1) - w + I$$

$$\frac{dw}{dt} = bV - cw$$

a=.2, b=.01, c=.02, I=0

Phase plane analysis: Bistability



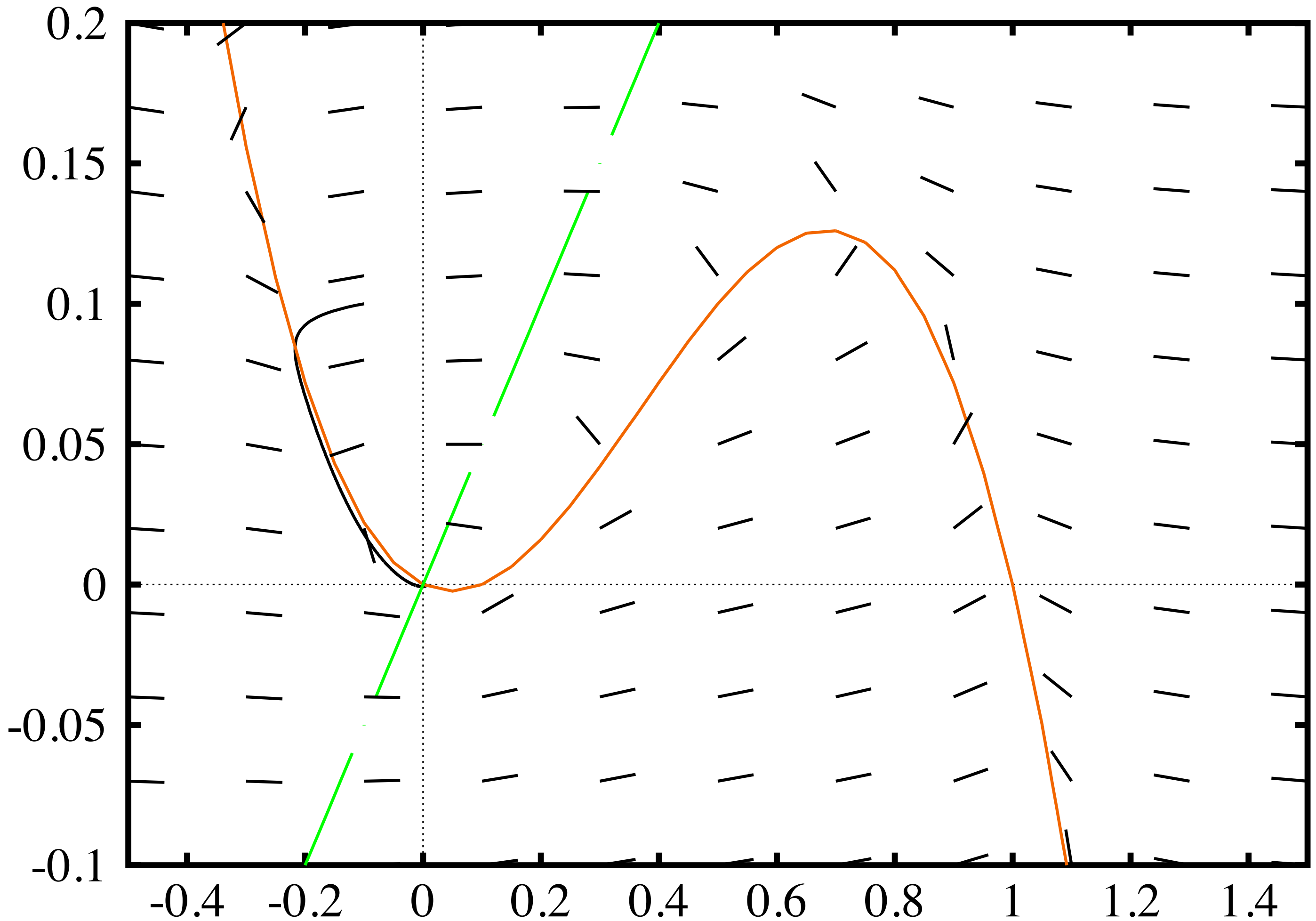


$$\frac{dV}{dt} = V(a - V)(V - 1) - w + I$$

$$\frac{dw}{dt} = bV - cw$$

a=.1, b=.01, c=.07, I=0

Bifurcations: a qualitative change in behavior

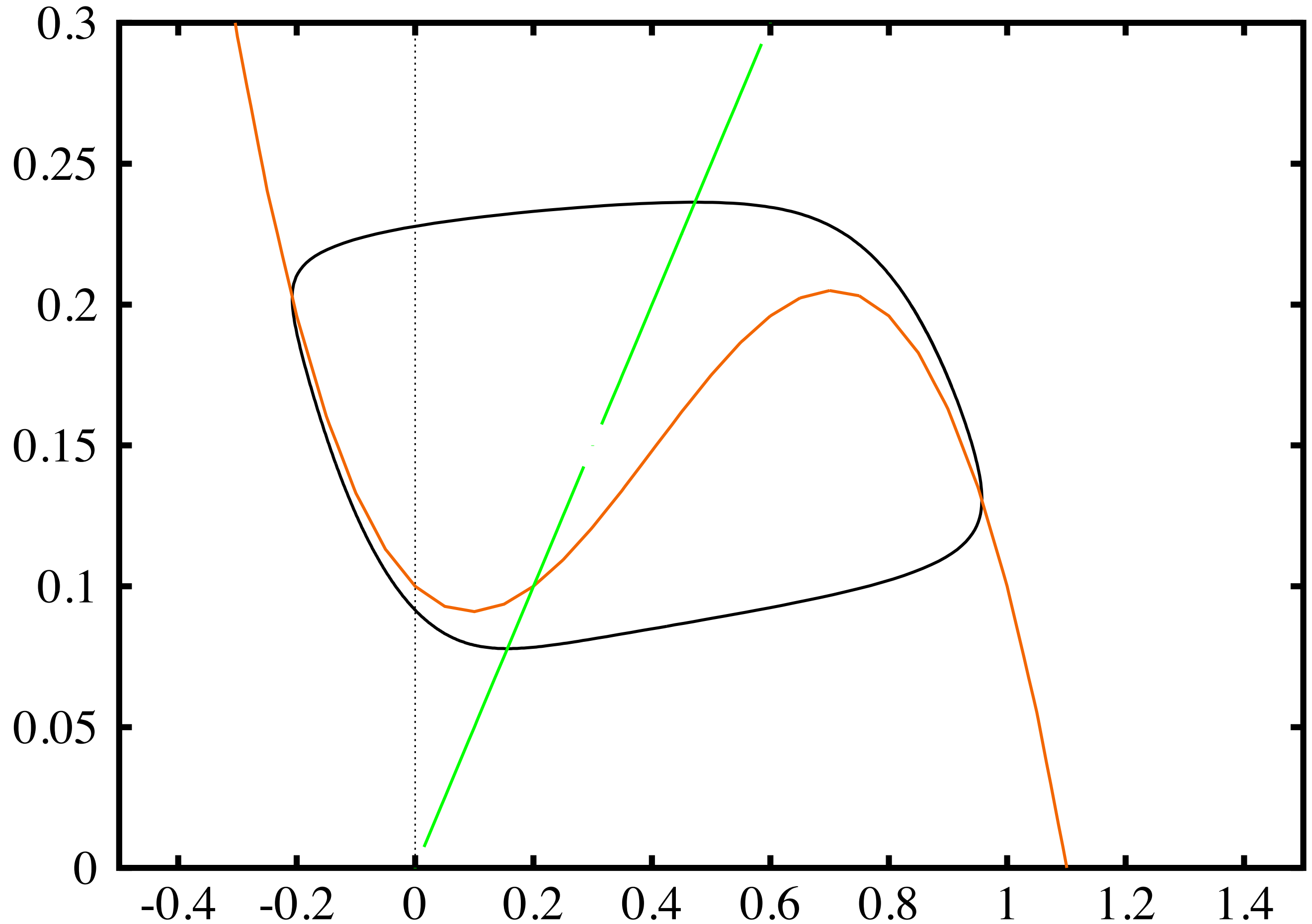


$$\frac{dV}{dt} = V(a - V)(V - 1) - w + I$$

$$\frac{dw}{dt} = bV - cw$$

$$I = 0$$

Bifurcations: a qualitative change in behavior

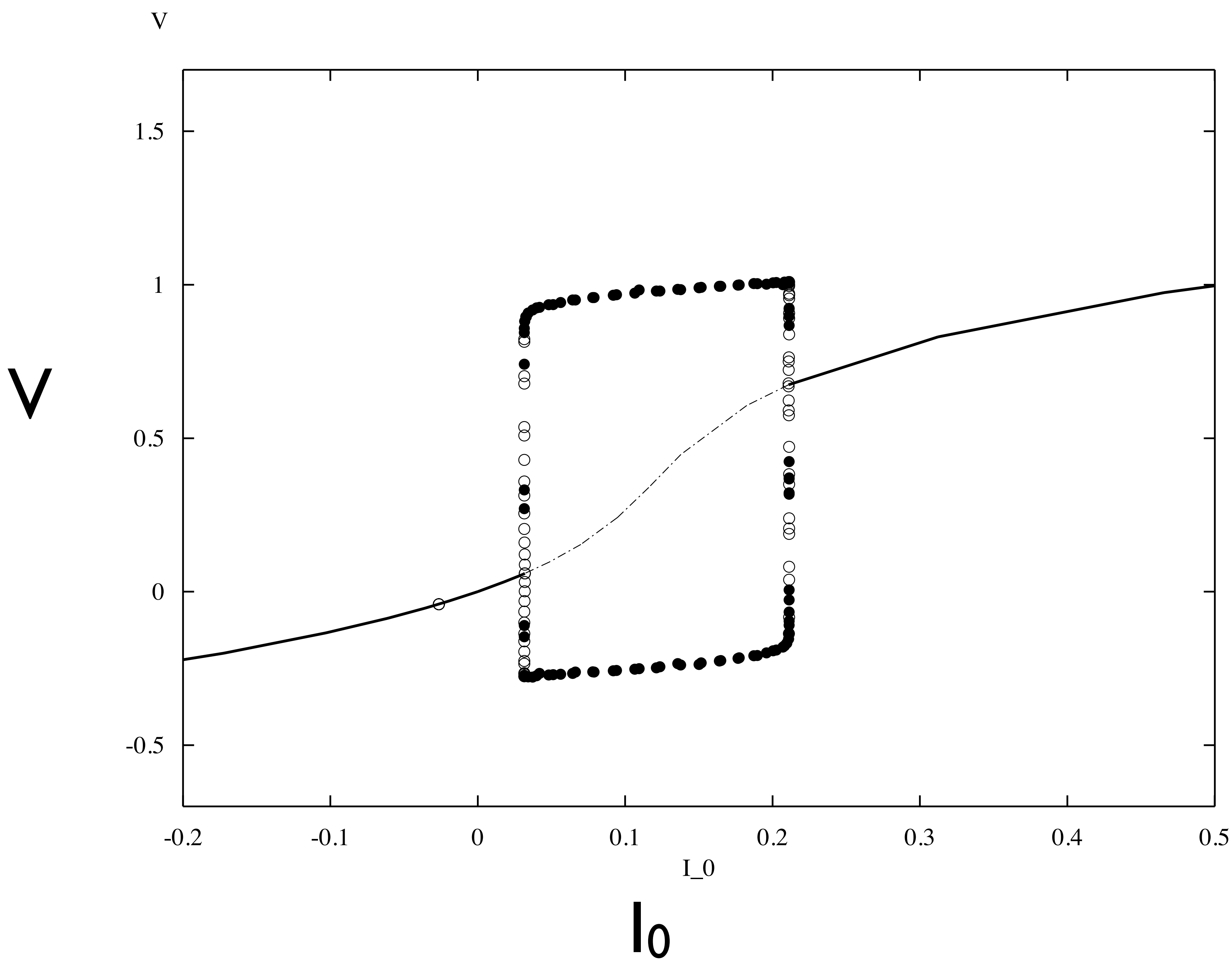


$$\frac{dV}{dt} = V\left(a - V\right)\left(V - 1\right) - w + I$$

$$\frac{dw}{dt} = bV - cw$$

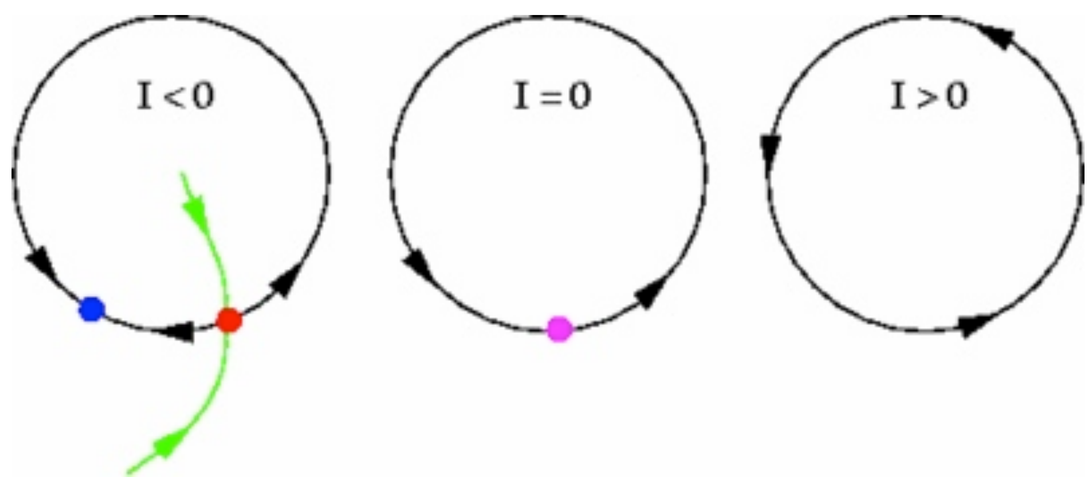
$$I = 1$$

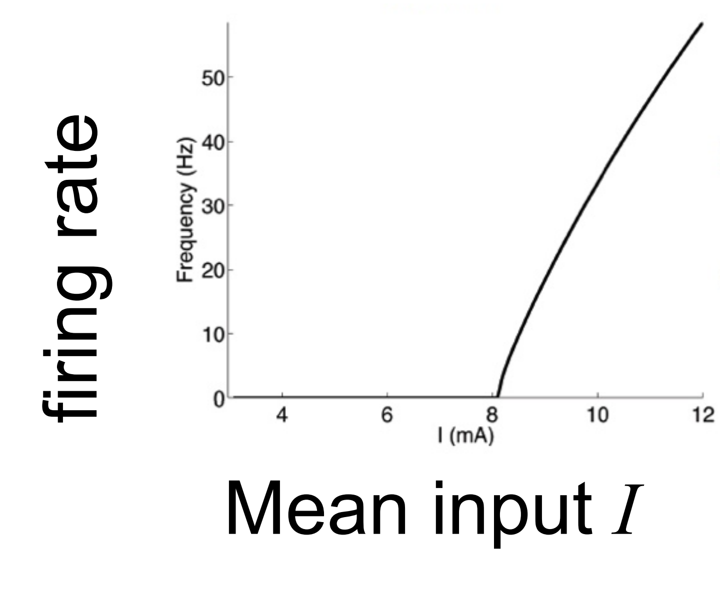
Bifurcation diagrams: an example



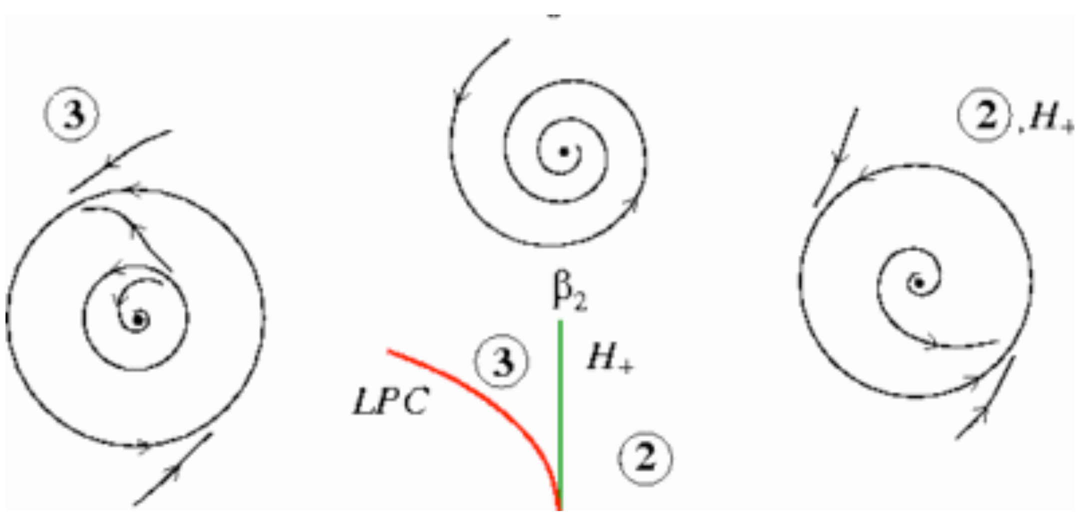
Two types of bifurcations:
Type I vs. Type II (or Class 1 vs. Class 2)

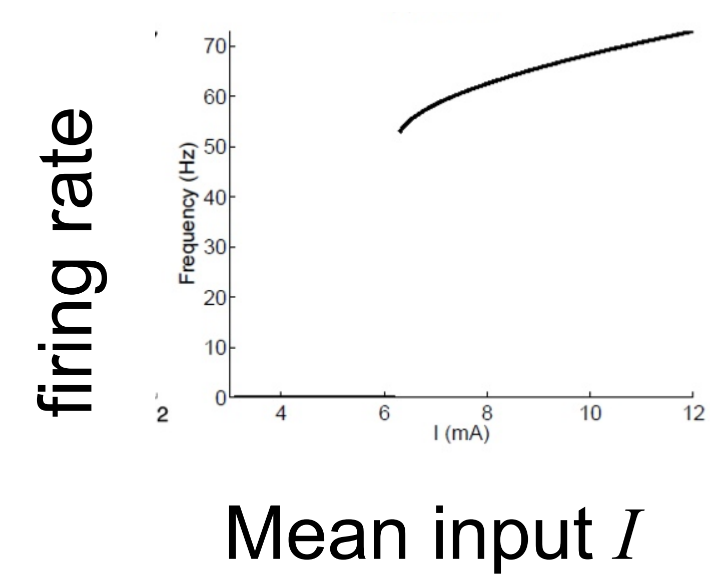
saddle node on invariant circle "Class 1 excitability"





subcritical Hopf: "Class 2 excitability"



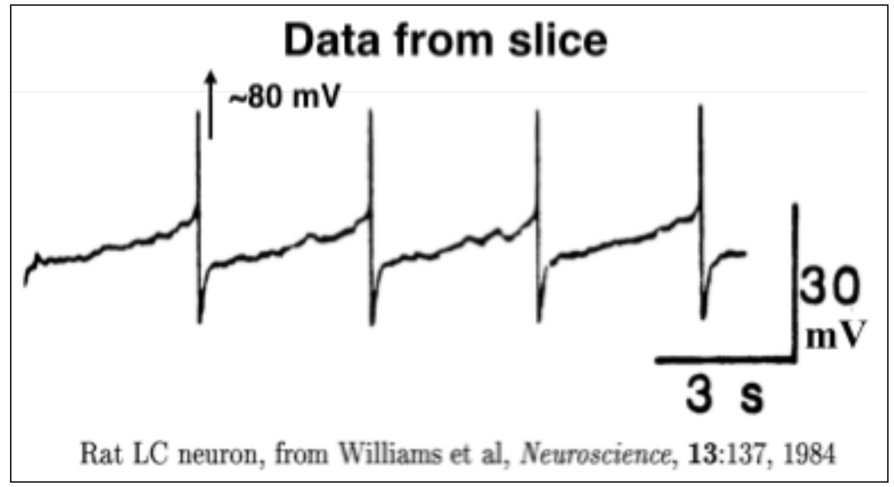


Some simplified models

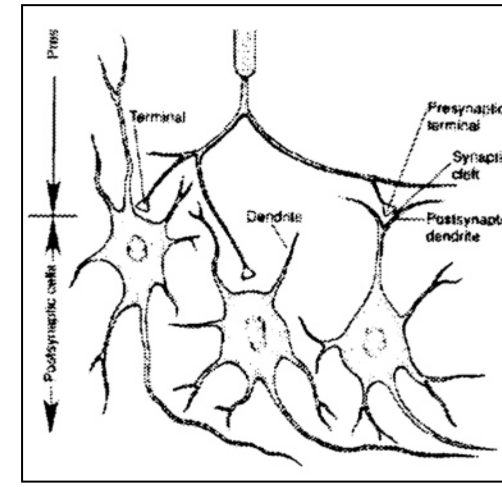
- Phase model
- Integrate-and-fire
- Firing rate models

Reduction of neurons to phases:

1. Brain recordings: voltage spikes via ionic currents



Rat LC neuron, from Williams et al, *Neuroscience*, **13**:137, 1984

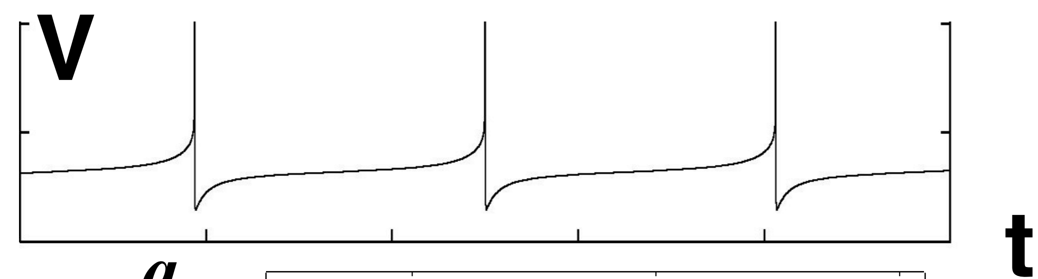


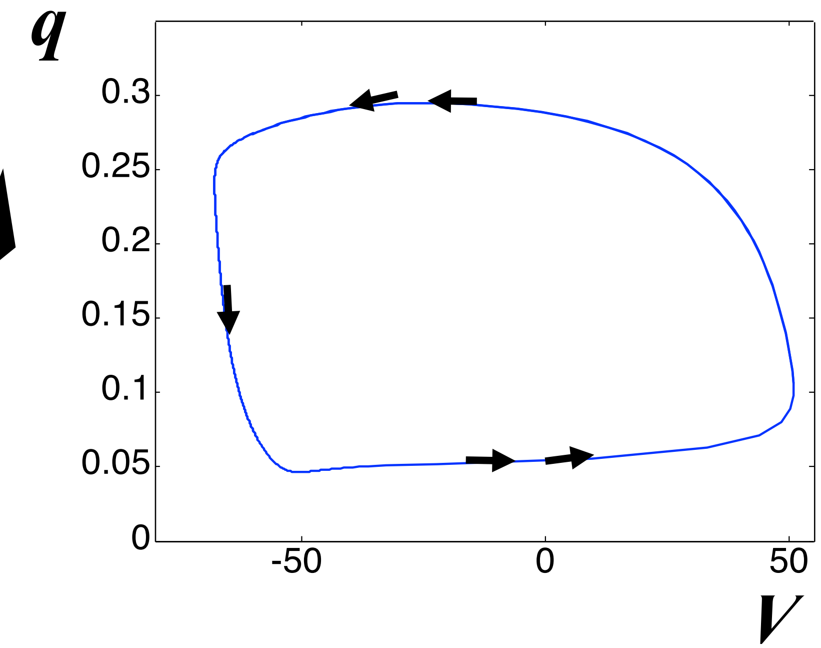
2. Nonlinear oscillator eqn. for each neuron

$$
\begin{aligned}
\dot{v}_i &= [I_i^b - g_{Na} m_\infty(v_i)^3(-3(q_i - B b_\infty(v_i)) + 0.85)(v_i - v_{Na}) \\
&\quad - g_K q_i (v_i - v_K) - g_L(v_i - v_L) + I_i^{ext}]/C \\
\dot{q}_i &= (q_\infty(v_i) - q_i)/\tau_q(v_i)\,.
\end{aligned}
$$

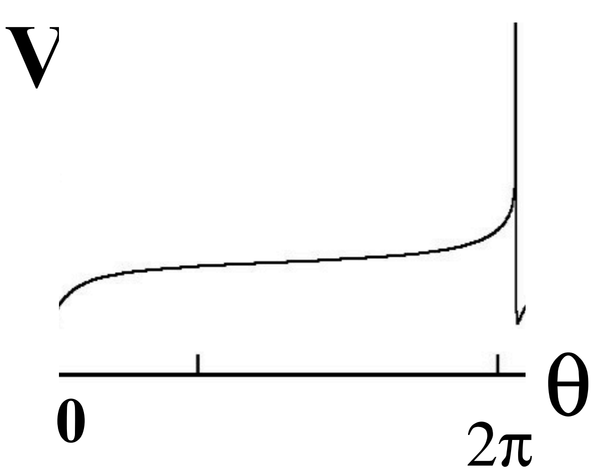
V = voltage
q = conductance

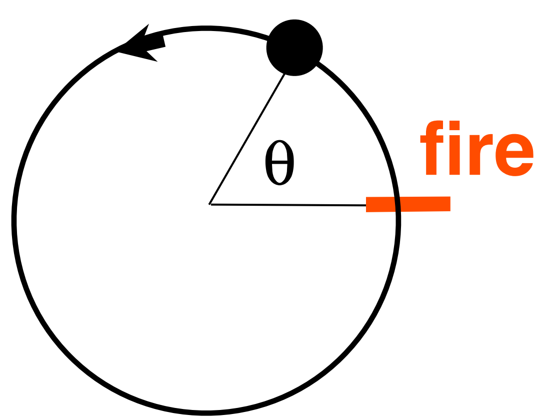
e.g Rose and Hindmarsh, *1989.*
Hodgkin and Huxley, etc.





3. Coordinate change → phase





Winfree '74, Guckenheimer '75, …

Reduction of neurons to phases:

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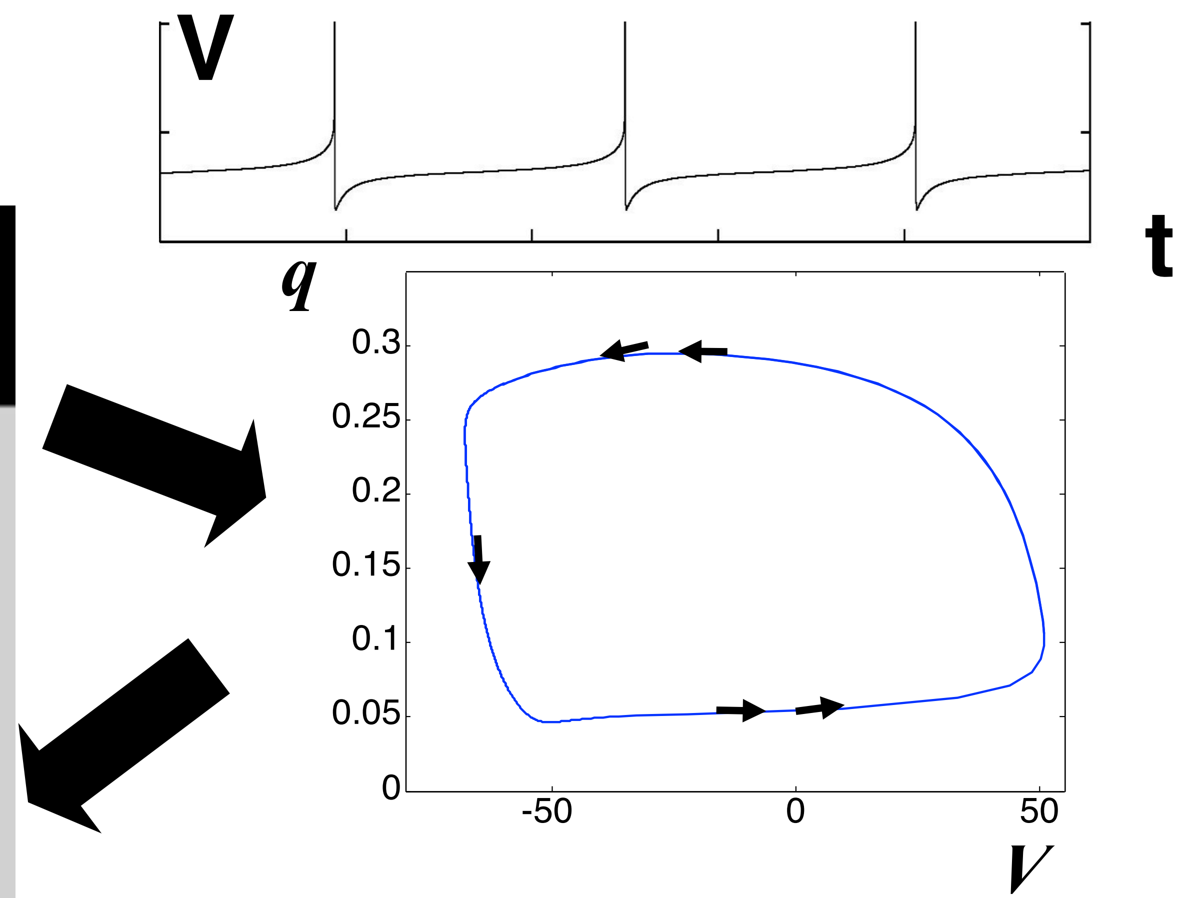

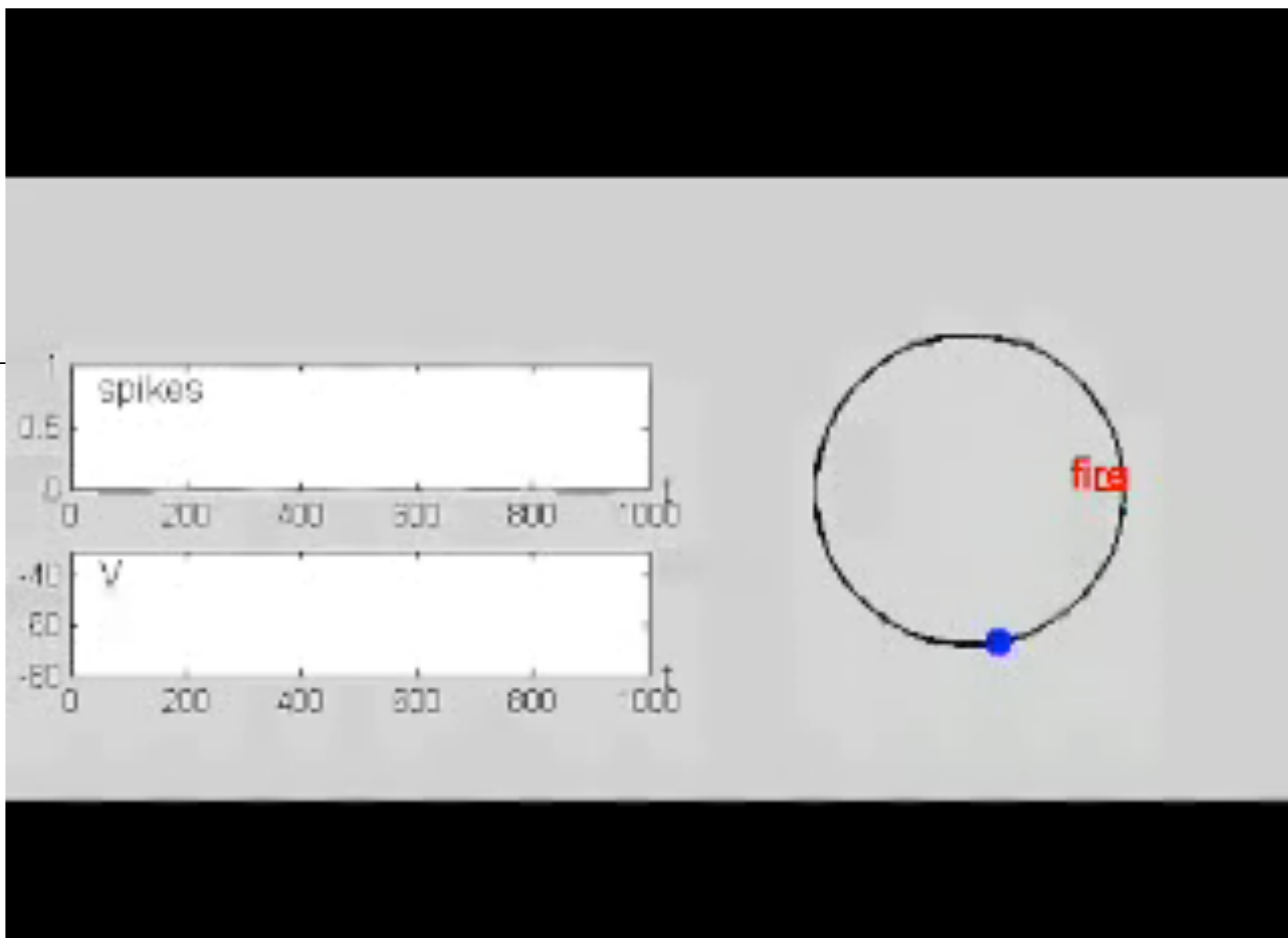

Winfree '74, Guckenheimer '75, …

Goal: simple phase description

natural frequency

$$\frac{d\theta}{dt} = \omega$$

- Let $\mathbf{x} = \begin{pmatrix} V \\ q \end{pmatrix}$. Then we have defined coordinate change so that:

$$\frac{d\mathbf{x}}{dt} = \mathbf{F}(\mathbf{x}) \quad \rightarrow \quad \frac{d\theta}{dt} = \omega$$

where $\mathbf{F}(\mathbf{x})$ is 'original' neural vectorfield giving oscillations at freq. ω.

Goal: simple phase description

natural frequency

$$\frac{d\theta}{dt} = \omega + \cdots$$

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- We're actually interested in effects of additional currents: $J(\mathbf{x},t)$ "perturbation"

$$\frac{d\mathbf{x}}{dt} = \mathbf{F}(\mathbf{x}) + \begin{pmatrix} J(\mathbf{x},t) \\ 0 \end{pmatrix} \quad \rightarrow \quad \frac{d\theta}{dt} = \frac{\partial\theta}{\partial\mathbf{x}} \cdot \left[\mathbf{F}(\mathbf{x}) + \begin{pmatrix} J(\mathbf{x},t) \\ 0 \end{pmatrix} \right]$$

$$\frac{d\theta}{dt} = \omega + \boxed{\frac{\partial\theta}{\partial V}} \; J(\mathbf{x},t)$$

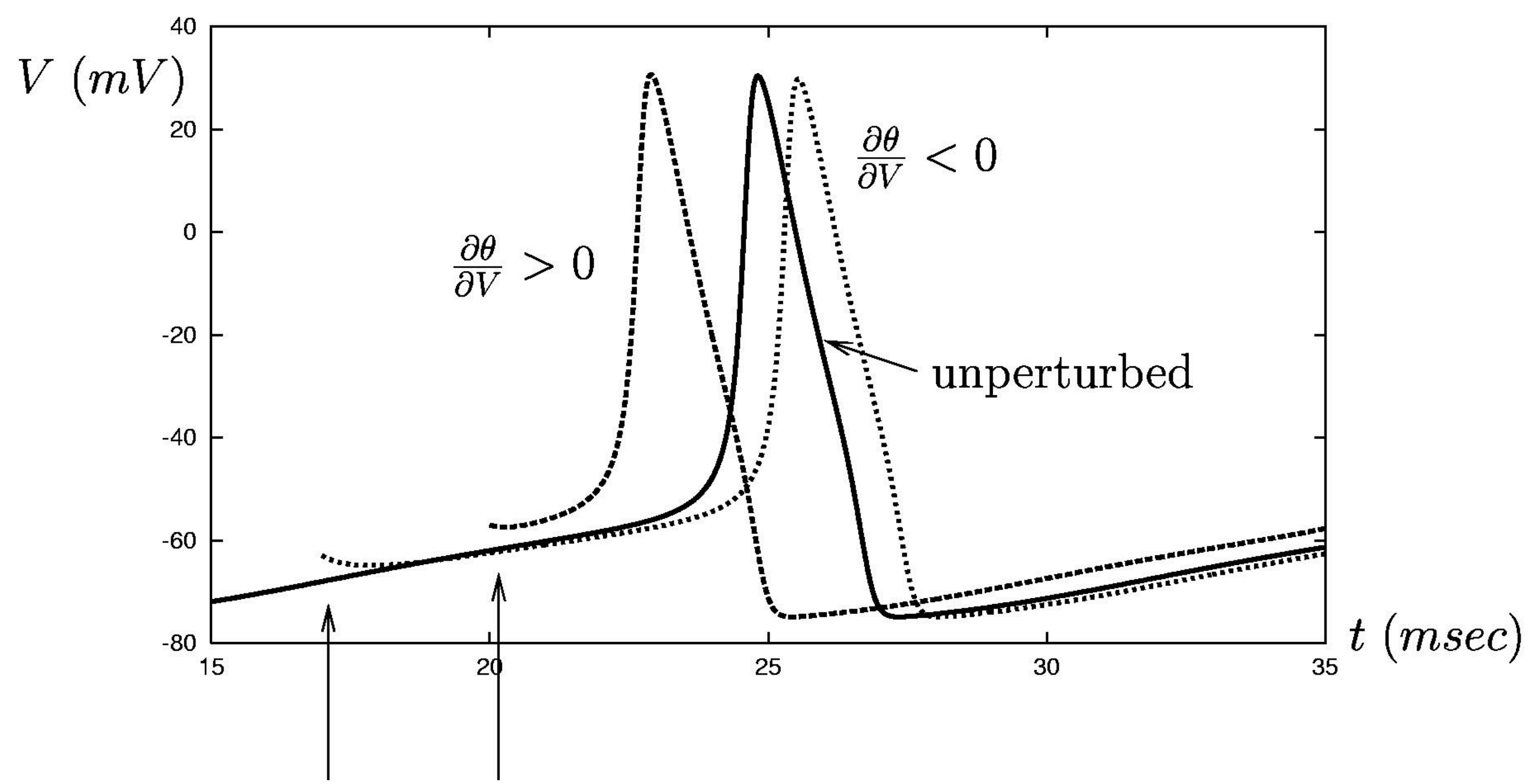
Finding $\partial\theta / \partial V = z(\theta)$, the phase response curve:

- Perturb an uncoupled neuron with a brief voltage stimulus ΔV at different times in its cycle, parameterized by θ
- Measure the resulting phase-shift $\Delta\theta$ with respect to the unperturbed system

For Hodgkin-Huxley neurons with $I = 10\mu A/cm^2$:

$$\boxed{z(\theta) = \lim_{\Delta V \to 0} \frac{\Delta\theta}{\Delta V}}$$

NOTE: this technique often used in lab experiments!

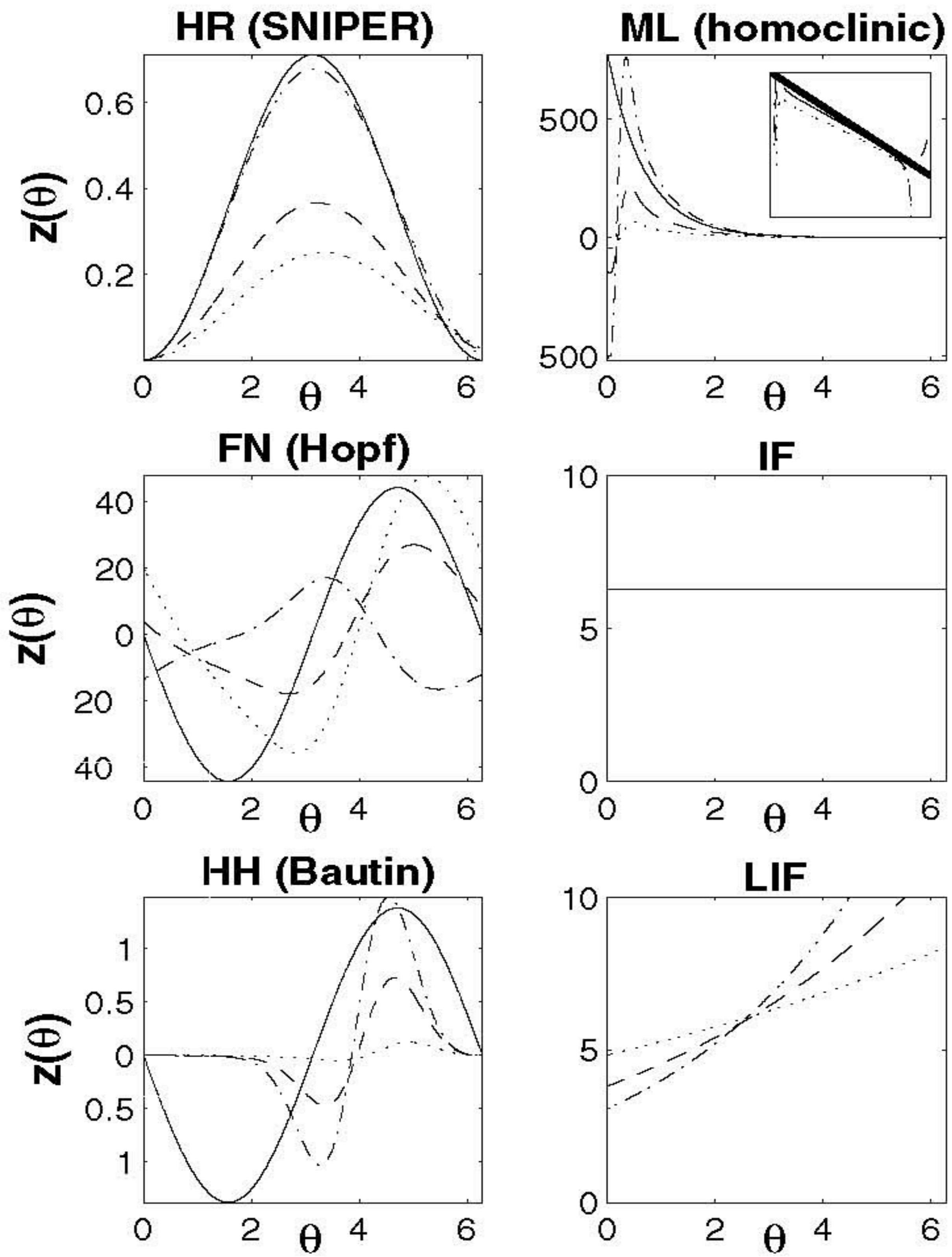


perturb with 5 mV stim.

Thanks to Jeff Moehlis

Phase response curves for different neurons look very different!

[Ermentrout and Kopell, Van-Vreeswick, Bressloff, Izhikevich, Moehlis, Holmes, S-B]



Hodgkin-Huxley

Leaky Integrate and Fire

With phase dynamics …

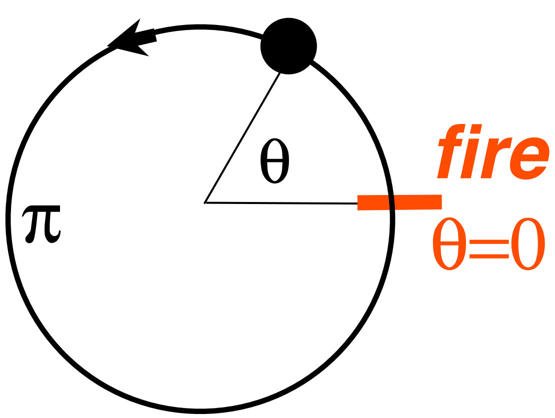
$$\frac{d\theta}{dt} = \omega + z(\theta) \times \left[I_{syn}(t) \right]$$

natural frequency

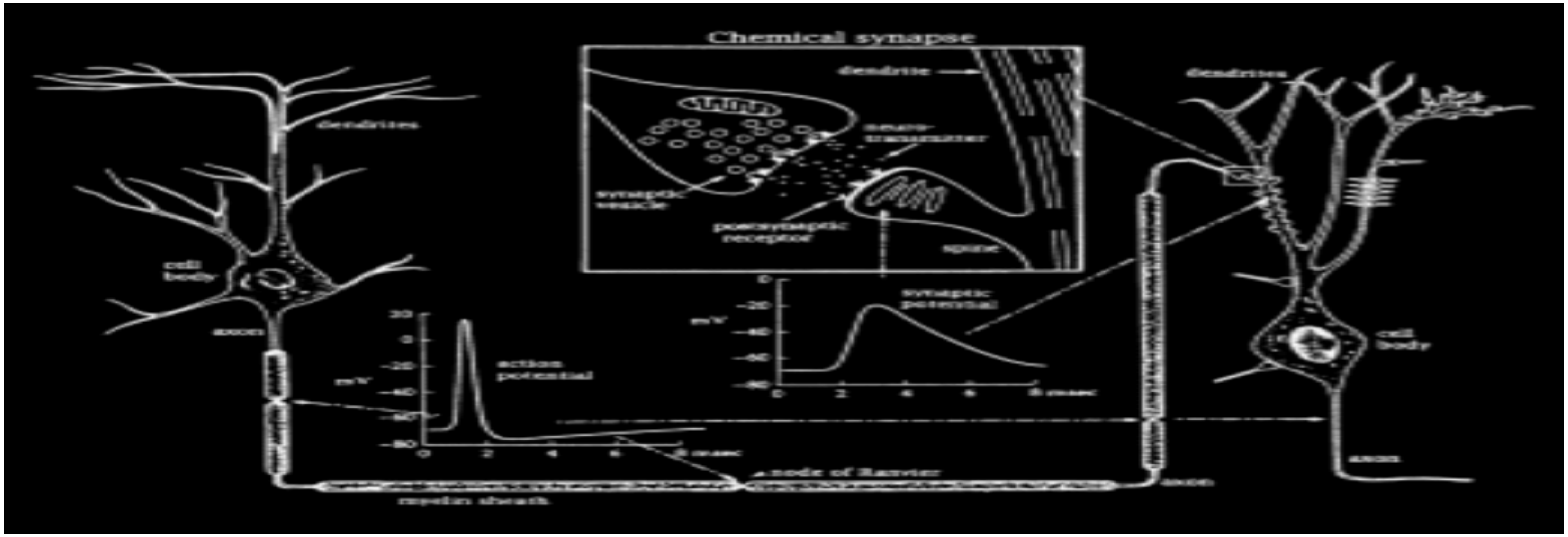
phase response curve

(phase sensitivity curve)

$$\boxed{z(\theta) = \lim_{\Delta V \to 0} \frac{\Delta \theta}{\Delta V}}$$



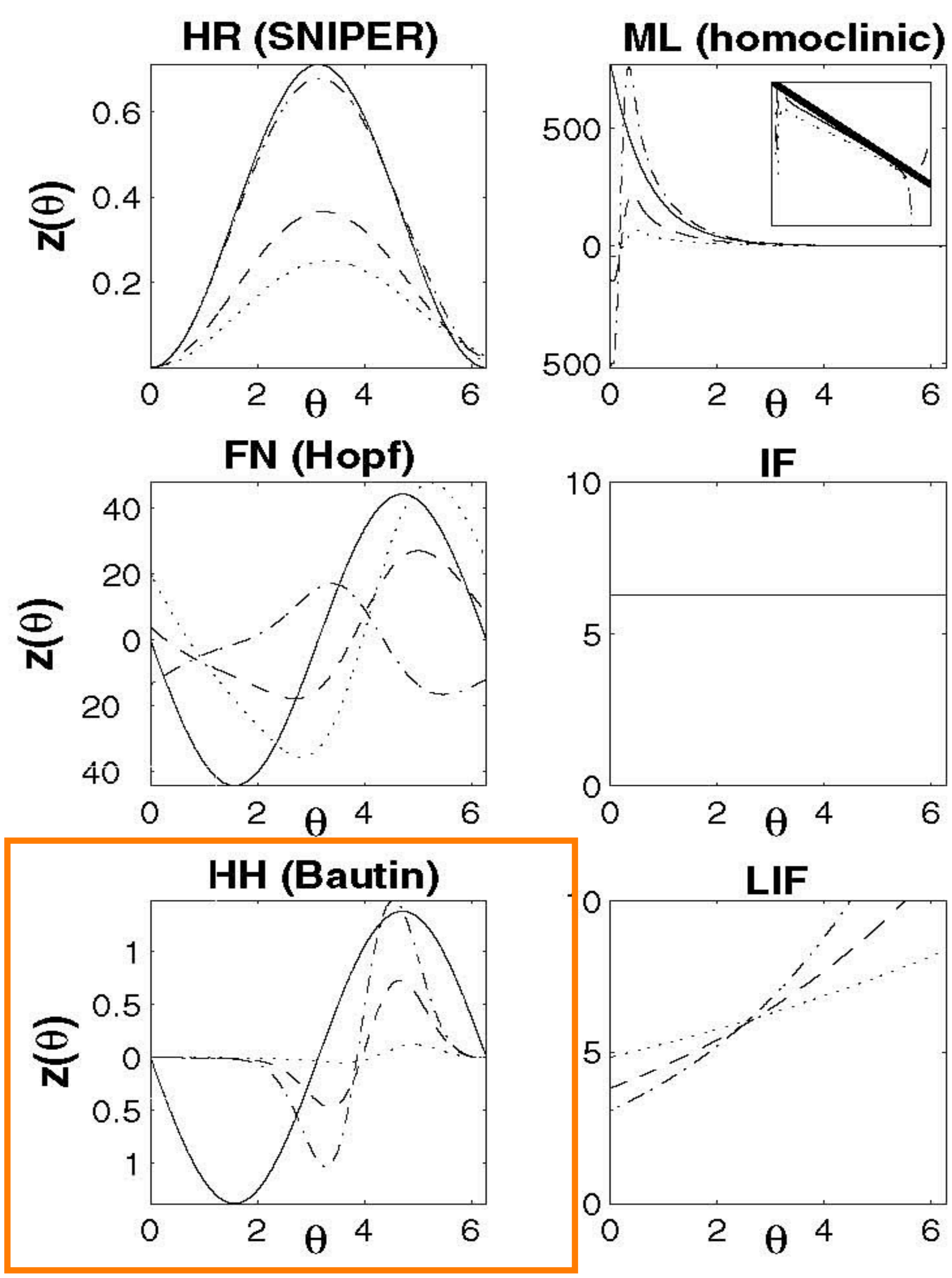
We can study synchrony in “network” of two coupled neurons



$\mathbf{I_{syn}(t)}$

$$\frac{d\theta_1}{dt} = \omega + z(\theta_1) * h\delta(t - t_2^j)$$
$$\frac{d\theta_2}{dt} = \omega + z(\theta_2) * h\delta(t - t_1^j)$$

For example, Hodgkin-Huxley...



$$C\frac{dV}{dt} = I - g_K n^4 \left(V - E_K\right) - g_{Na} m^3 h \left(V - E_{Na}\right) - g_L \left(V - E_L\right)$$

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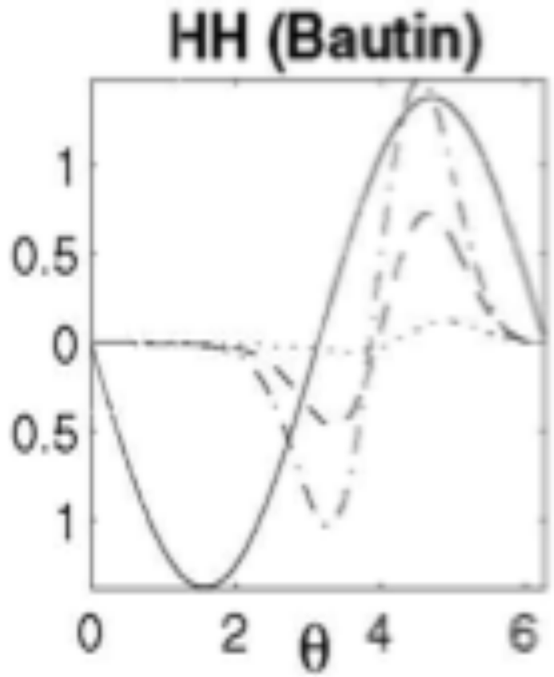
The Hodgkin-Huxley model

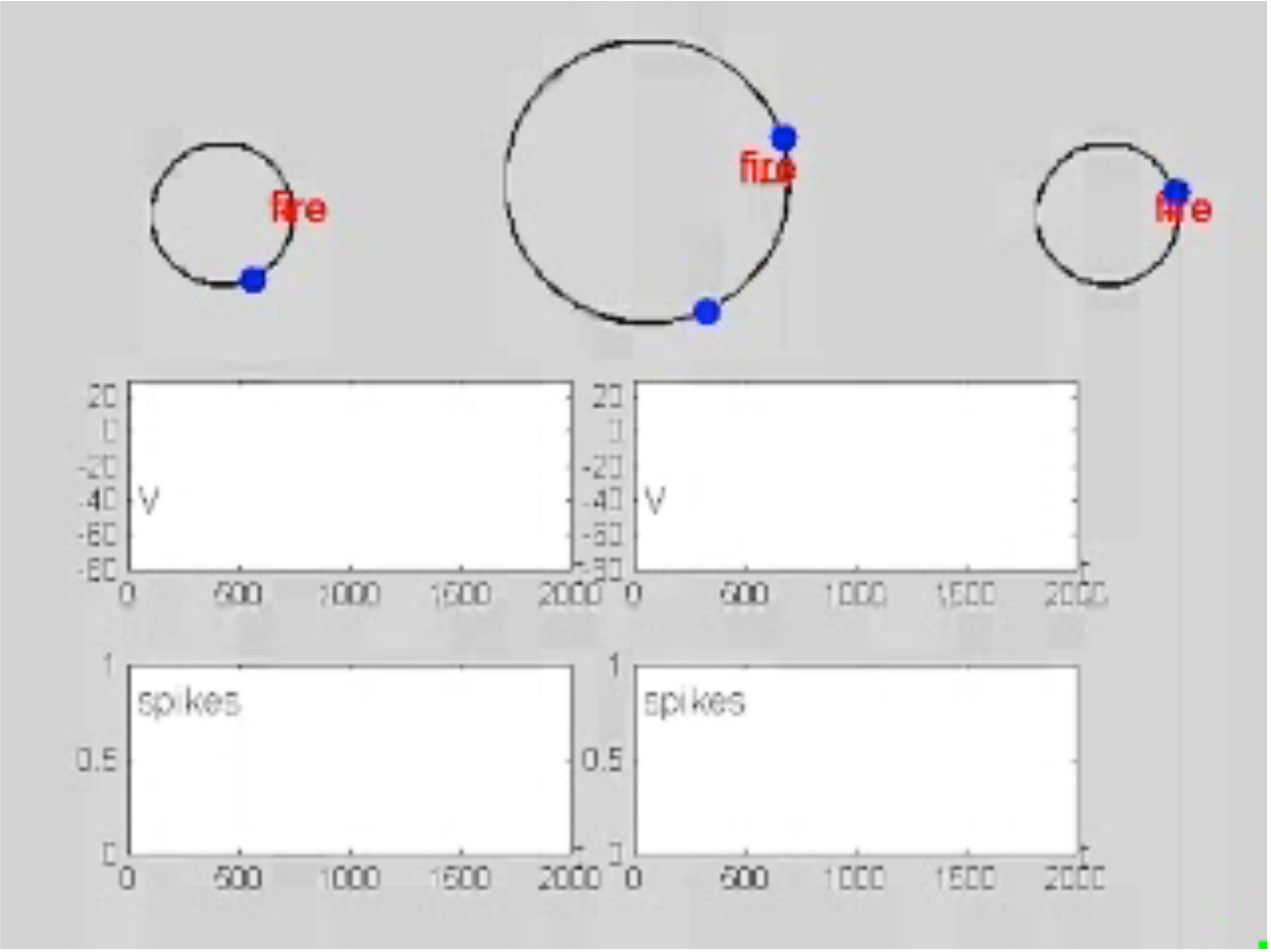
PRC

z(θ)



$$\frac{d\theta_1}{dt} = \omega + h * z(\theta_1)\delta(t - t_2^j)$$

$$\frac{d\theta_2}{dt} = \omega + h * z(\theta_2)\delta(t - t_1^j)$$



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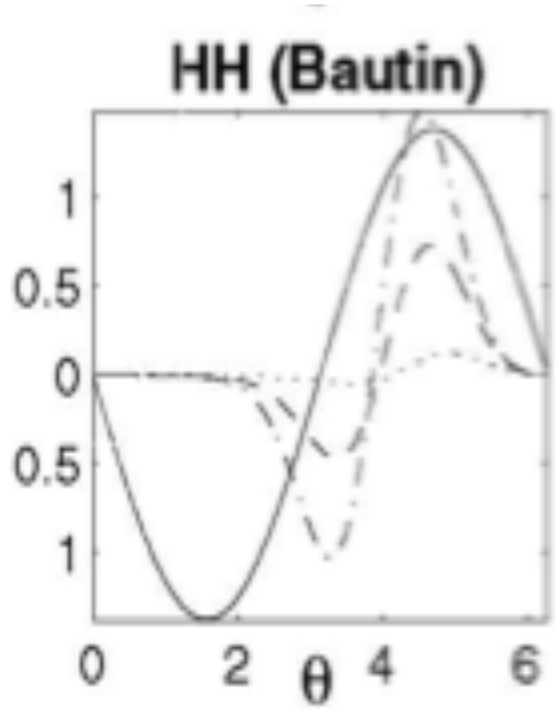


$$\frac{d\theta_1}{dt} = \omega + h * z(\theta_1)\delta(t - t_2^j)$$
$$\frac{d\theta_2}{dt} = \omega + h * z(\theta_2)\delta(t - t_1^j)$$

Moral: "Fast" excitatory coupling can synchronize HH neurons …

Analyze via Poincare map between firing times of θ_1

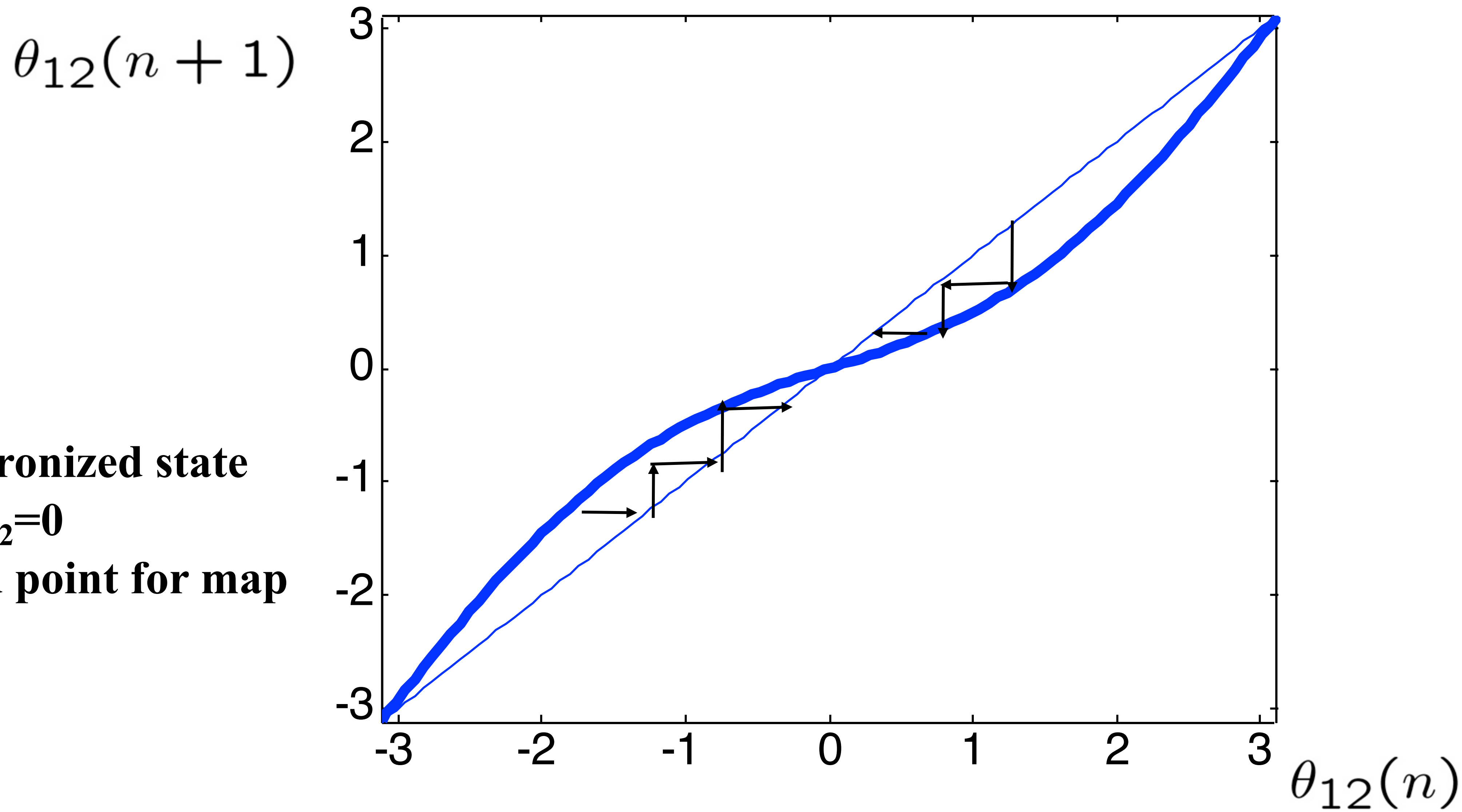
$$\theta_{12} = \theta_1 - \theta_2$$

Nancy Kopell, Bard Ermentrout,
-- "weak coupling theory"

$$\theta_{12}(n+1) \;=\; \theta_{12}(n) + h\,\{z(\theta_{12}(n)) - z(-\theta_{12}(n))\} + \mathcal{O}(h^2)$$

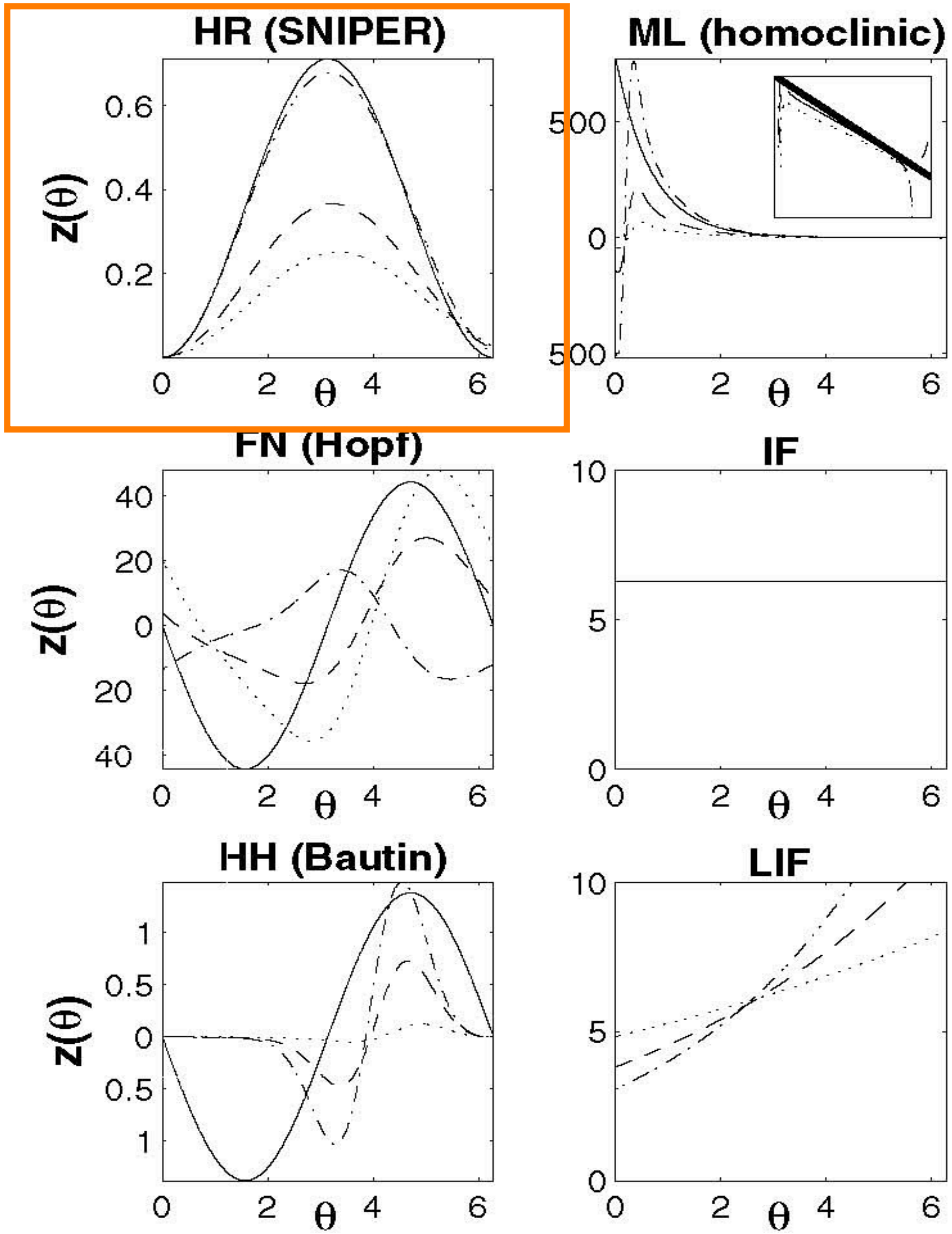
E.g., for HH neuron, $z(\theta) \sim -\sin(\theta)$, so

$$\boxed{\theta_{12}(n+1) \approx \theta_{12}(n) - 2h\sin(\theta_{12})}$$



See: synchronized state
θ_{12}=0
is stable fixed point for map

Let's try Hodgkin-Huxley + A-current



$$C\frac{dV}{dt} = I - g_K n^4 (V - E_K) - g_{Na} m^3 h (V - E_{Na}) - g_L (V - E_L) - g_A a^3 b (V - E_A)$$

$$\frac{dn}{dt} = (n_\infty(V) - n) / \tau_n(V)$$

$$\frac{dm}{dt} = (m_\infty(V) - m) / \tau_m(V)$$

$$\frac{dh}{dt} = (h_\infty(V) - h) / \tau_h(V)$$

$$\frac{da}{dt} = (a_\infty(V) - a) / \tau_a(V)$$

$$\frac{db}{dt} = (b_\infty(V) - b) / \tau_b(V)$$

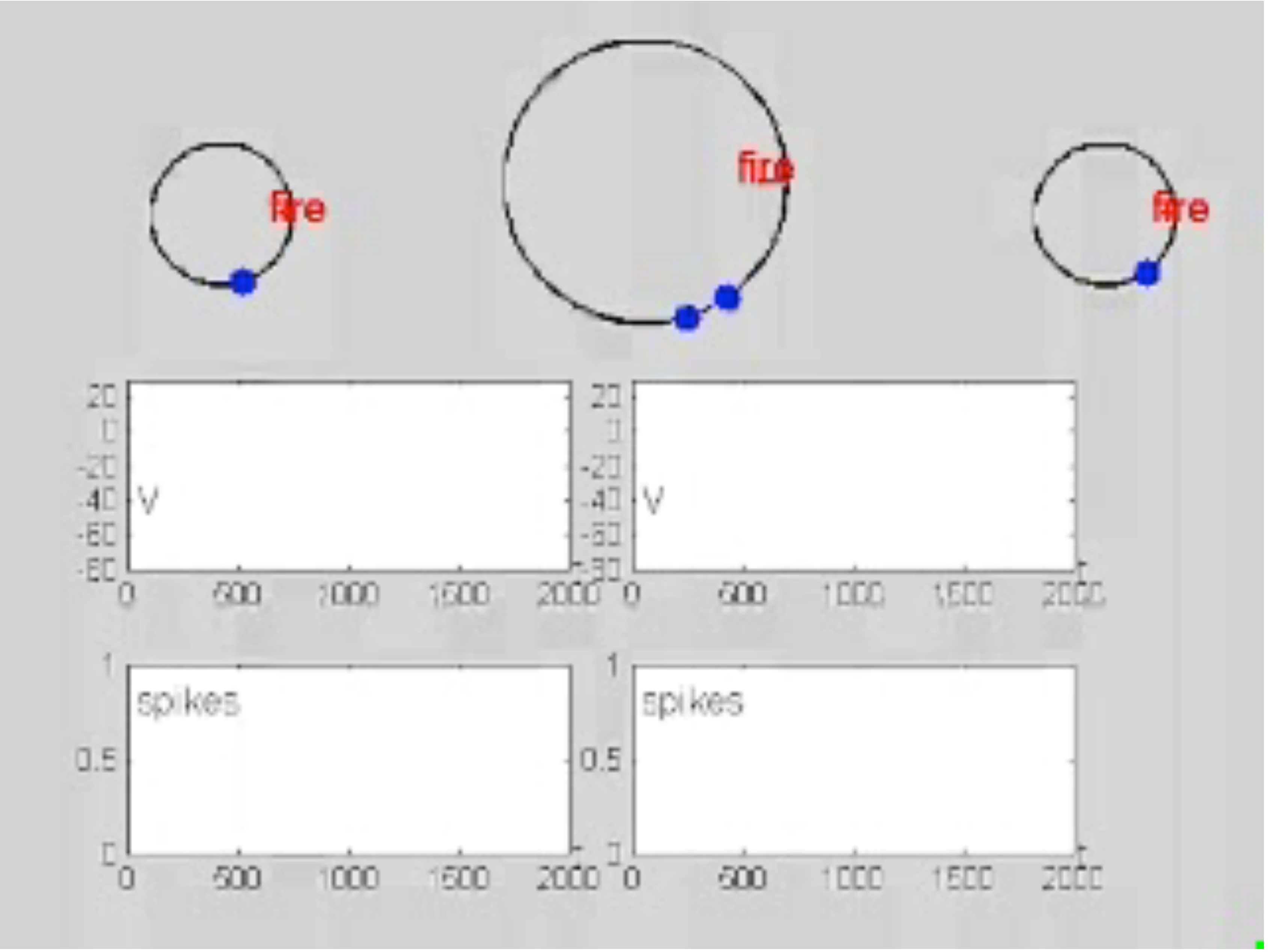
The "Hodgkin Huxley plus A current" model

PRC

z(θ)

$$\frac{d\theta_1}{dt} = \omega + h * z(\theta_1)\delta(t - t_2^j)$$

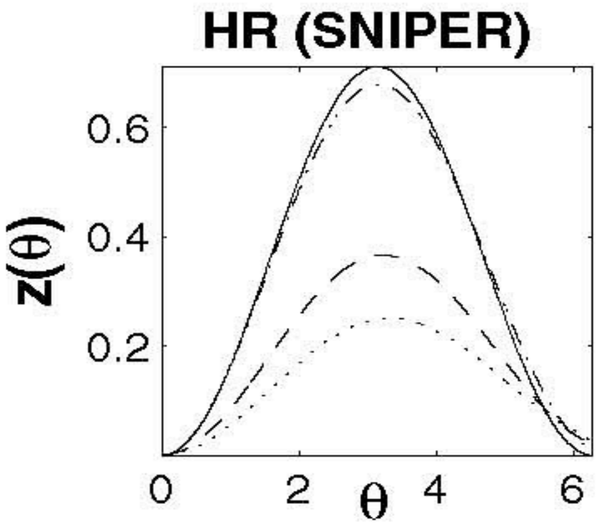
$$\frac{d\theta_2}{dt} = \omega + h * z(\theta_2)\delta(t - t_1^j)$$



The "Hodgkin Huxley plus A current" model

PRC

z(θ)



$$\frac{d\theta_1}{dt} = \omega + h * z(\theta_1)\delta(t - t_2^j)$$
$$\frac{d\theta_2}{dt} = \omega + h * z(\theta_2)\delta(t - t_1^j)$$

Moral: Excitatory coupling actually DEsynchronizes HH neurons with A currents

Stable "anti-synchronized" state

However, inhibition *does* synchronize …

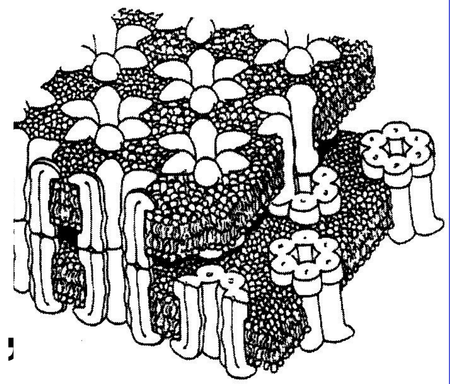
"When inhibtion, not excitation, synchronizes…" Van Vreeswijk et al 1995

Beyond impulse coupling

$$\frac{d\theta}{dt} = \omega + z(\theta)\times\left[I_{syn}(t) \right]$$

$$\frac{d\theta_i}{dt} = \omega + z(\theta_i)\sum_{j=1}^{n} I_j(\theta_j)$$

Brain has gap junctions,



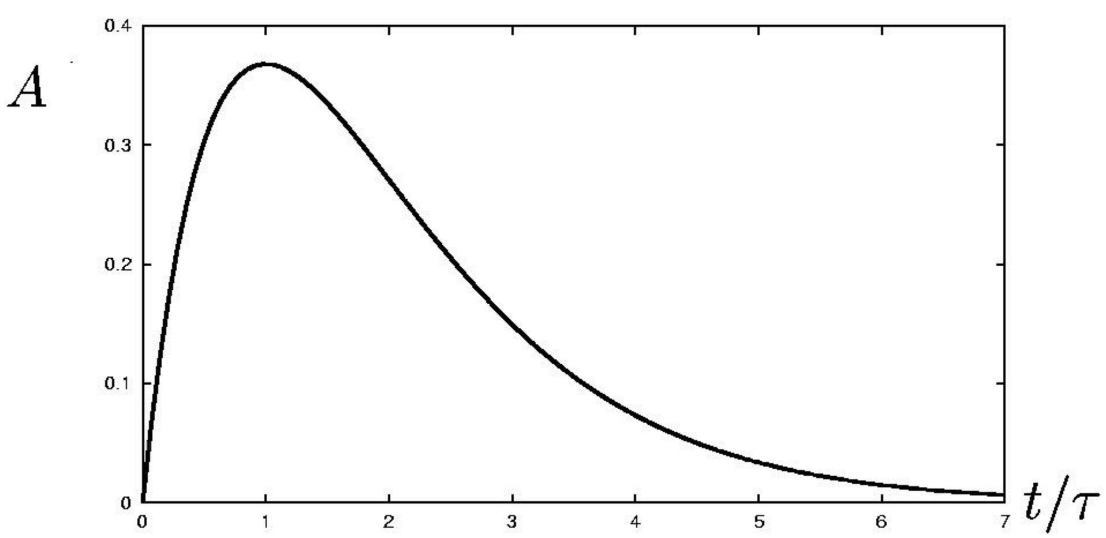
$$\dot{V}_i = \cdots + \frac{\alpha_e}{N}\sum_{j=1}^{N}(V_j - V_i)$$

N = number of neurons

α_e = electrotonic coupling strength

as well as slow chemical synapses.

$$\dot{V}_i = \cdots + \frac{\alpha_s}{N}(V_K - V_i)\sum_{j=1}^{N} A(t - t_j - \tau_d)$$



Kuramoto, Kopell, Ermentrout -- average coupling functions:

$$f_{e,s}(\theta) = \frac{1}{2\pi}\int_0^{2\pi} z(\phi)\, I_{e,s}^{coup}(\theta + \phi)\, d\phi$$

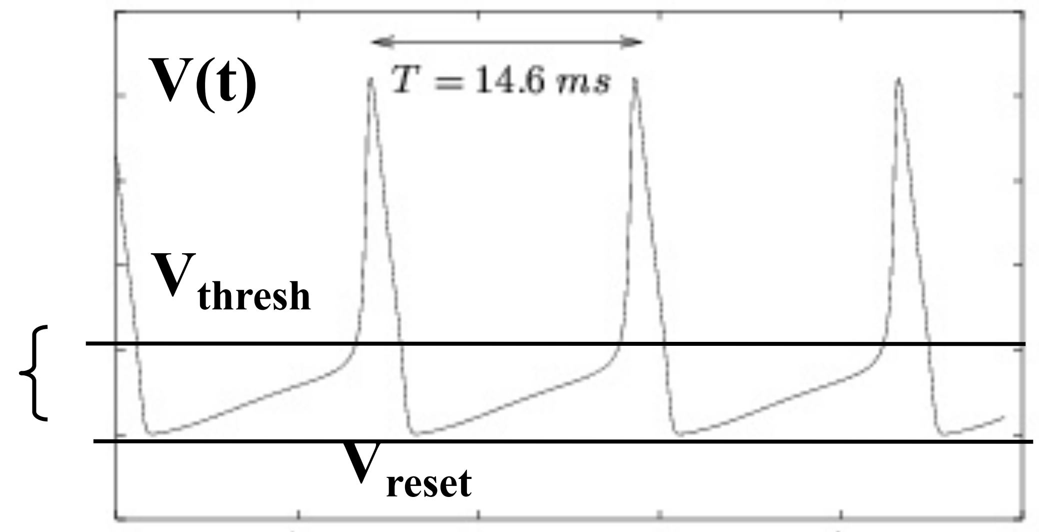
get a system depending on phase differences only

$$\frac{d\theta_i}{dt} = \omega + \underbrace{\frac{\alpha}{N}\sum_j f_e(\theta_j - \theta_i)}_{\text{electrotonic}} + \underbrace{\frac{\beta}{N-1}\sum_{j\neq i} f_s(\theta_j - \theta_i)}_{\text{synaptic}}$$

Integrate-and-fire models

Hodgkin-Huxley

$$\frac{dV}{dt} = [I - \bar{g}_{Na} m^3 h (V - V_{Na}) - \bar{g}_K n^4 (V - V_K) - g_L (V - V_L)]/C,$$

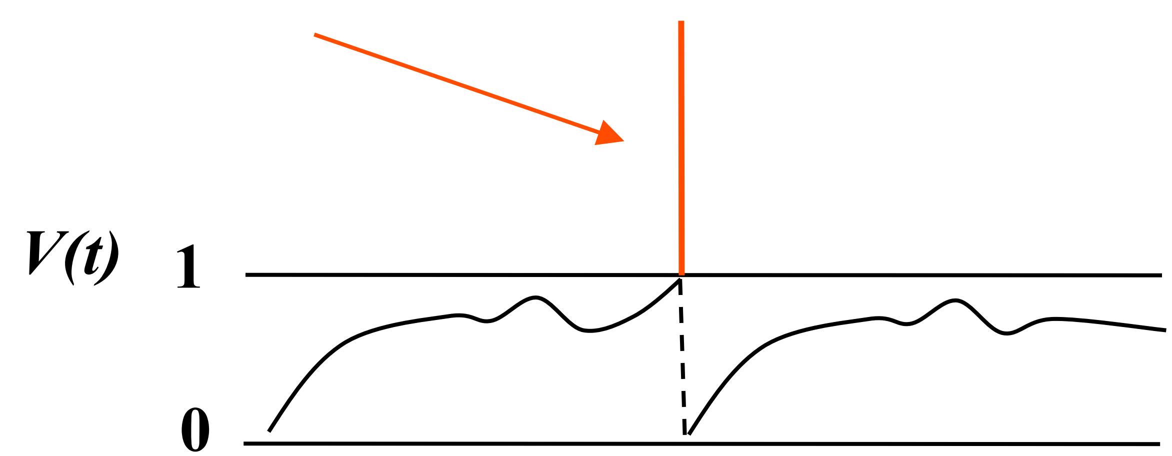


Claim: conductances approx. constant in this range
Above value V_{thresh}, "stereotyped" spike takes over

In range $[V_{reset}, V_{thresh}]$, following rescaling,

$$\tau \frac{dV}{dt} = -V + k_1 + k_2 I \quad ; 0 \leq V \leq 1$$

plus "reset" condition: $V \rightarrow 0$ and spike when passes 1



INTEGRATE – AND – FIRE MODEL OF LAPICQUE
Gerstner, Abbott, others relate to HH

Many variations...

$\tau \frac{dV}{dt} = -V + k_1 + k_2 I \quad ; 0 \leq V \leq 1$
plus "reset" condition: $V \to 0$ and spike when

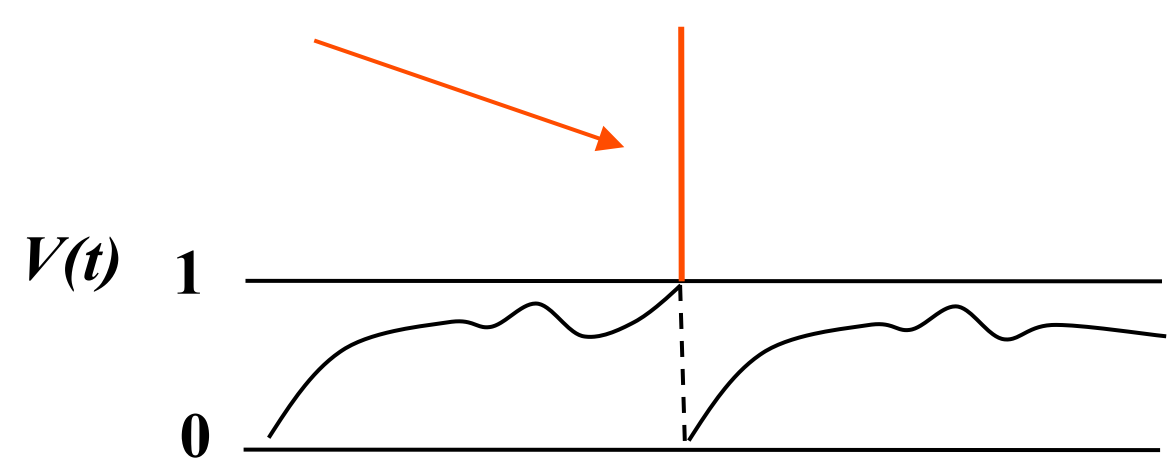
passes 1

$$\frac{dV}{dt} = -V + aV^2; \quad V < V_{thresh}$$

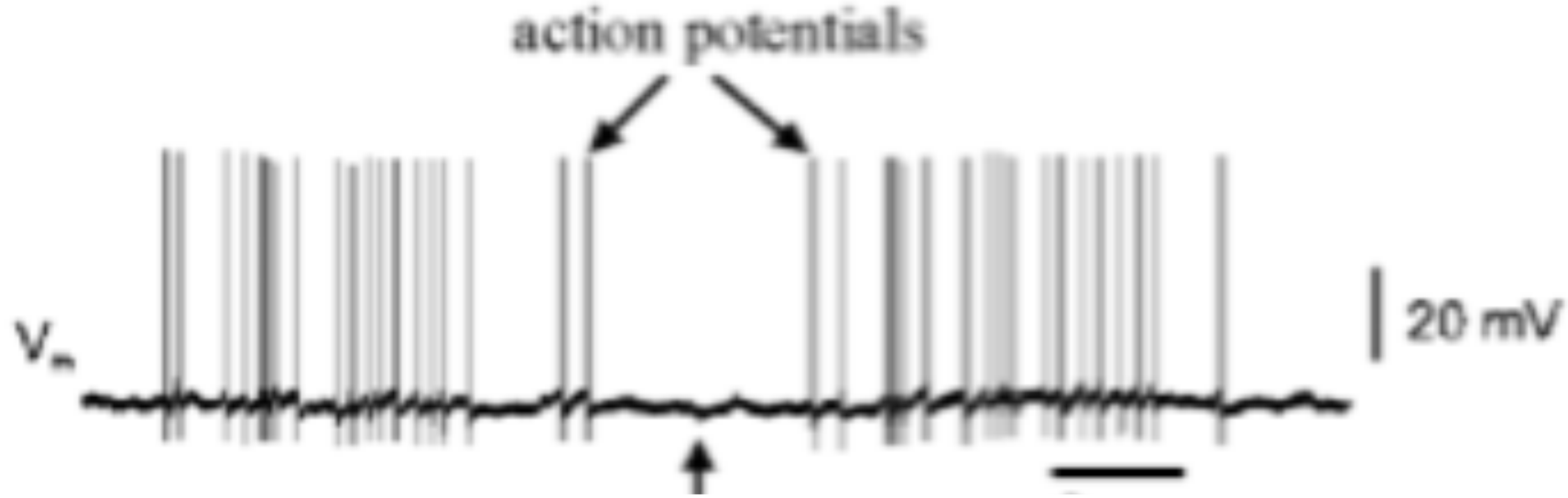
quadratic integrate and fire (QIF)

$$\frac{dV}{dt} = \frac{1}{\tau_m}\left(E_L - V + \Delta_T e^{(V - V_T)/\Delta_T}\right)$$

exponential integrate and fire (EIF)

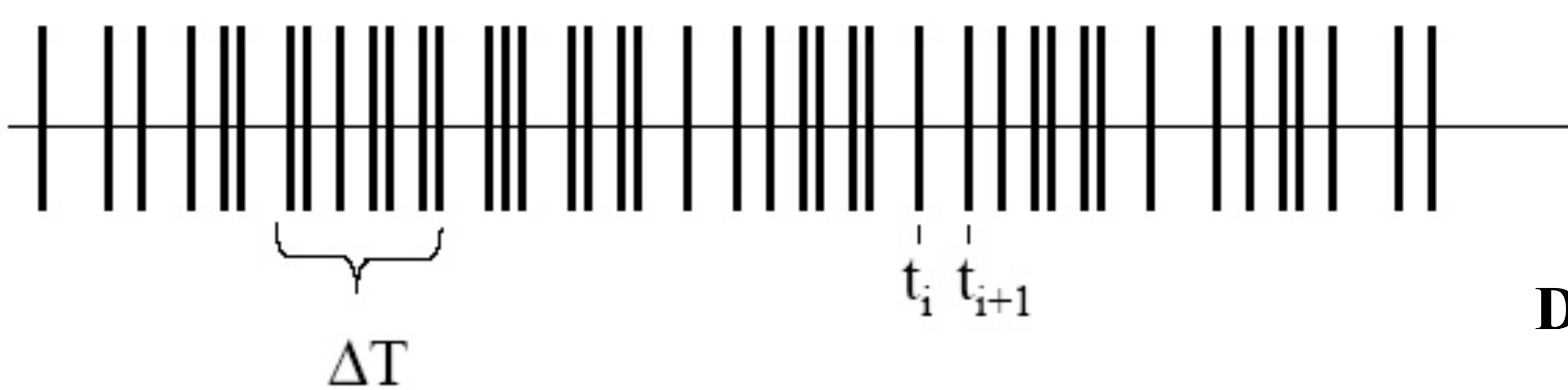


Firing rate models



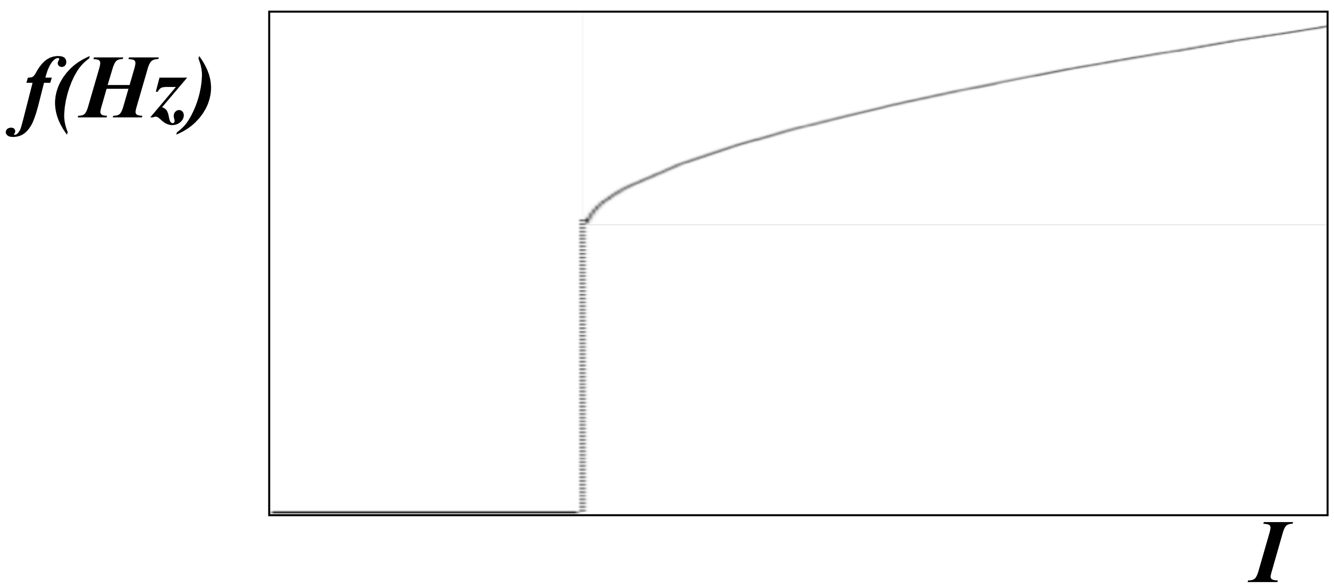
encoding: mean firing rate

$$f(t) = \frac{1}{\Delta T} \int_{t}^{t+\Delta T} \sum_{i=1}^{n_i} \delta(t' - t_i)\, dt'$$

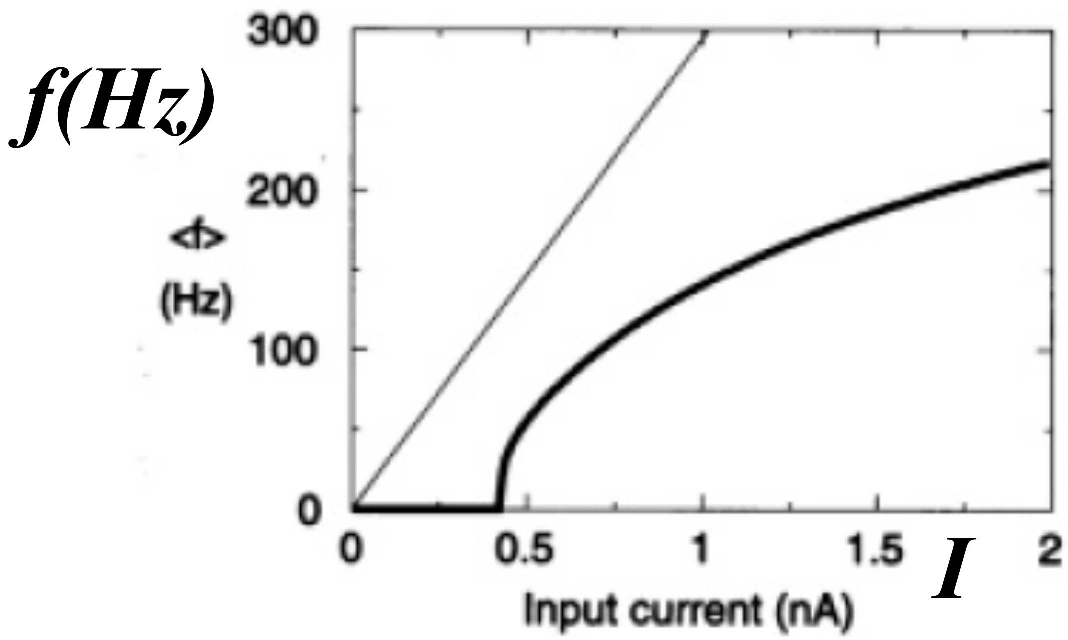


How does firing rate f depends on input current I?
via different firing rate vs. current ("f-I") curves

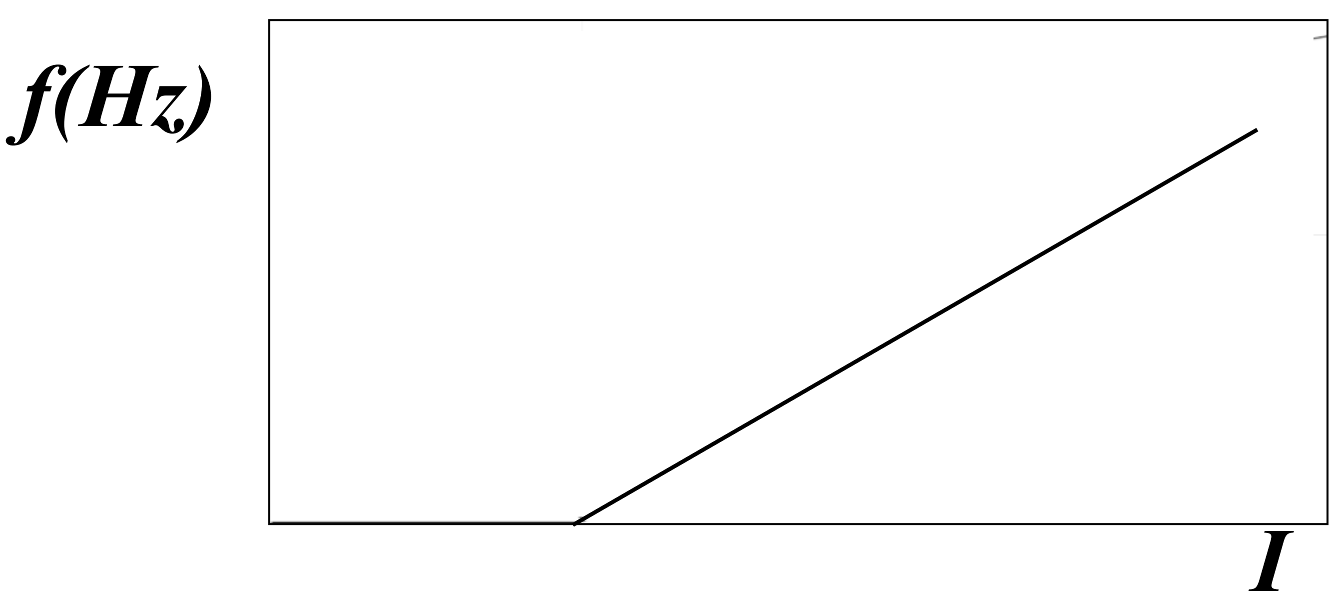
Hodgkin-Huxley



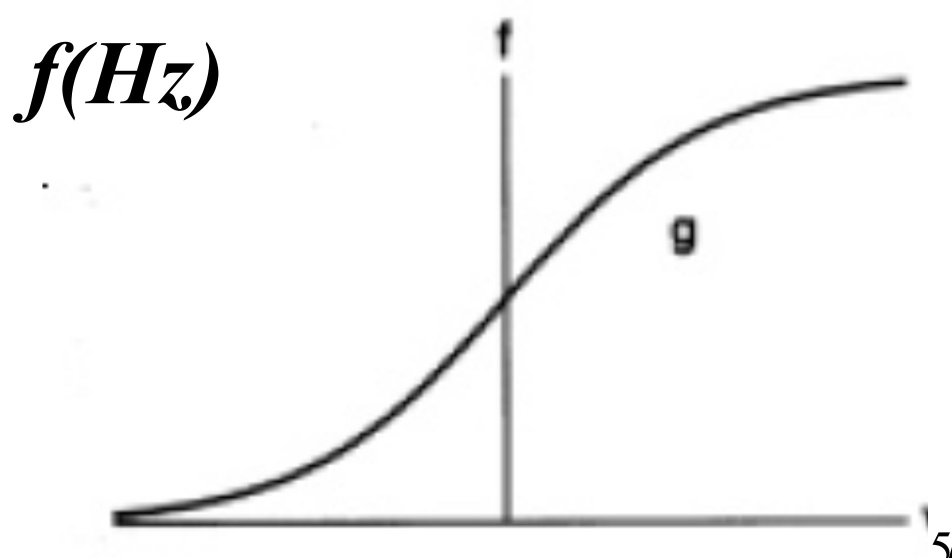
Integrate + Fire



Piecewise linear



Sigmoidal, gain g

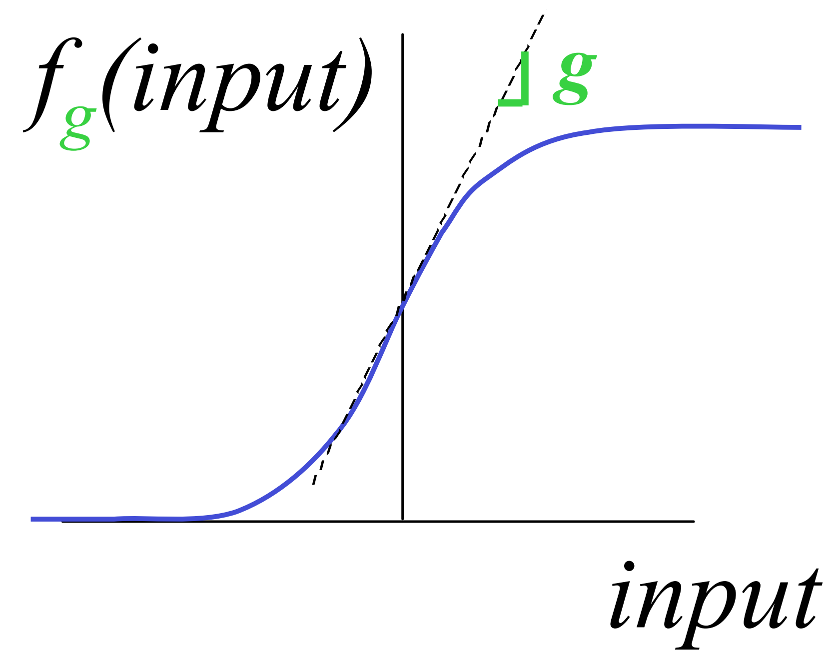


Dynamics?

- Think of neural "units…" described by firing rates y

  which approach equilibrium rates *f(input)* with time constant τ_m.

$$\tau_m \frac{dy}{dt} = -y + f\,(input)$$



- *nonlinearity of input-output function f* allows amazing array of "neural network" computations – Hopfield, Grossberg, Cohen
  – *associative memory: recall and learning*
  – *can encode complex input-output functions*

Computational tools for dynamical systems

- XPP
- AUTO
- MATCONT

References

- Check website later!
- http://depts.washington.edu/compnsci/