Reduction of neurons to phases

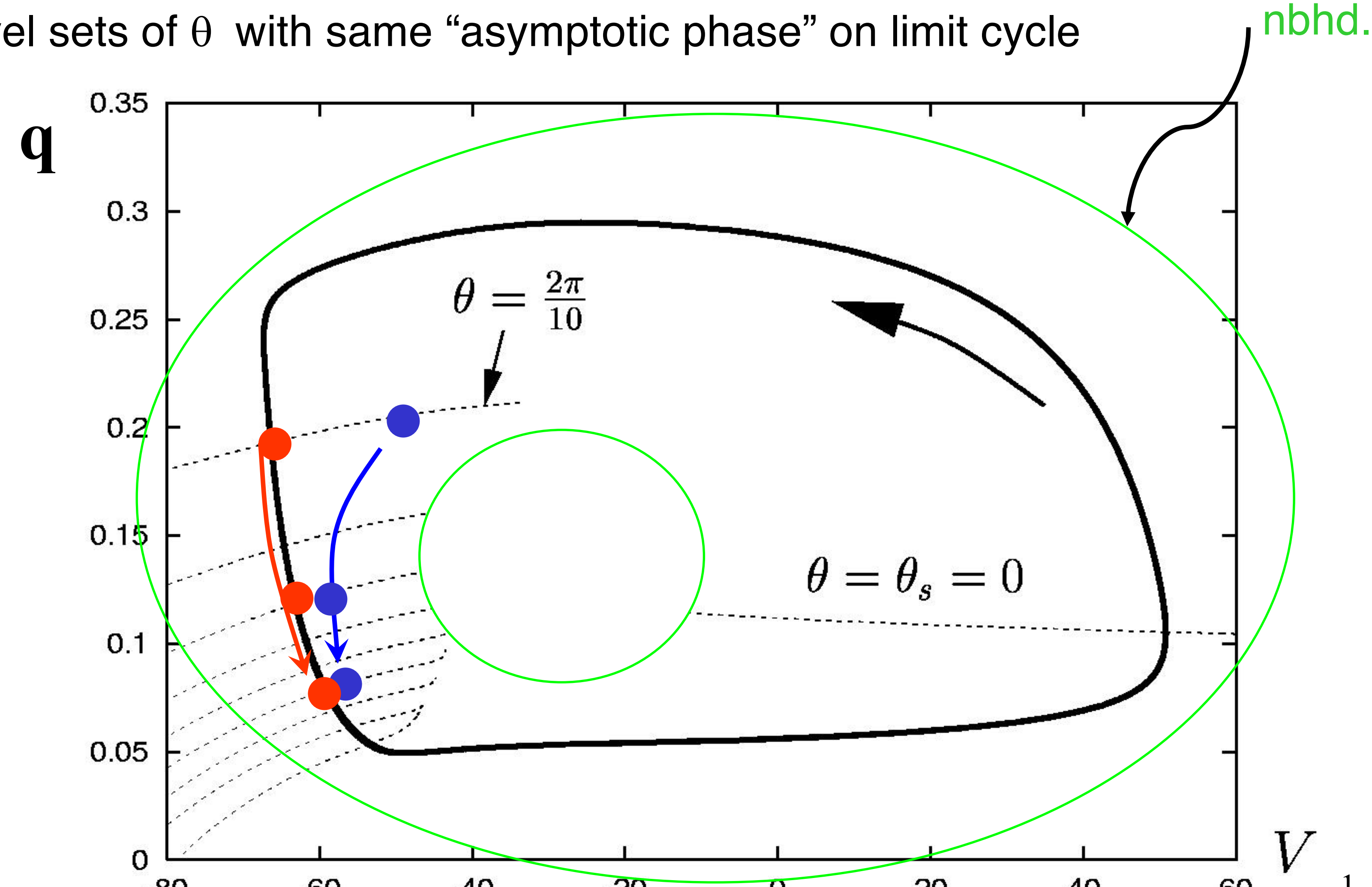
[Coddington and Levinson, 1955, Winfree, 1974, Guckenheimer, 1985]

In nbhd. of limit cycle, define variable $\theta(x)$ such that:

$$\frac{d\theta}{dt} = \omega \text{ along trajectories, where } \omega = \frac{2\pi}{T}$$

Strategy: start on limit cycle itself, where say V(θ)=V(ωt).

Then define level sets of θ with same "asymptotic phase" on limit cycle



Following Brown, Moehlis, Holmes

Neural Comp 04

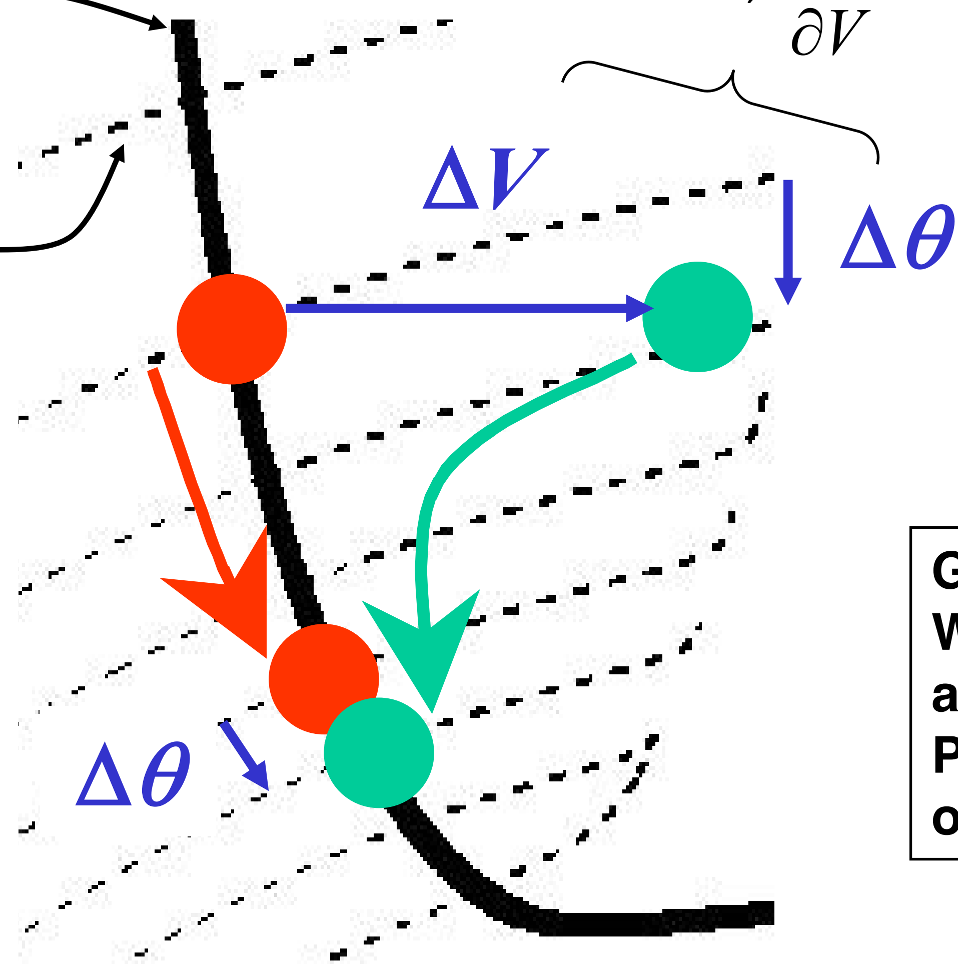
Finding z(θ) .

Asymptotic phase property of field $\theta(\boldsymbol{x})$ gives nice way to calculate

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

$$\to \frac{\partial\theta}{\partial V}$$

standard way to calculate partial deriv. -- must know $\theta(\boldsymbol{x})$ in nbhd. of lim cycle.



BUT! Easier to wait and measure $\Delta\theta$ as difference in asym. phase

Glass and Mackey, Winfree, Ermentrout and Kopell, Izhikevich, Park and Kim, and others

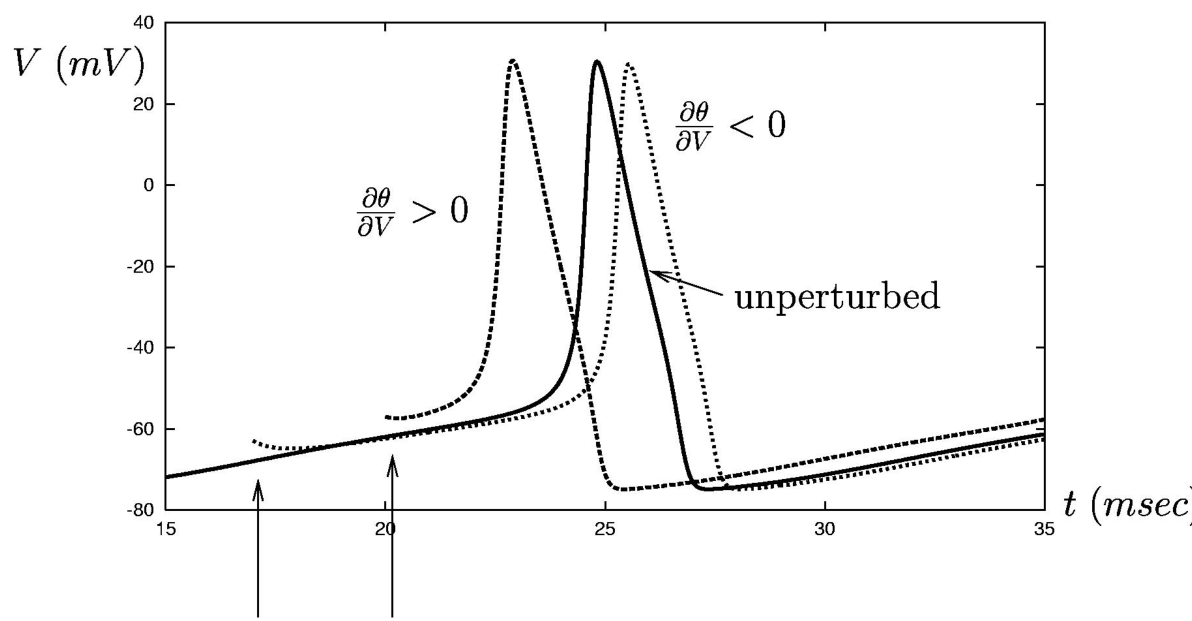
Finding z(θ) .

Calculating 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 $I = 10\mu A/cm^2$:

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



perturb with 5 mV stim.

Jeff Moehlis

Have phase dynamics … that you could directly derive from the laboratory !

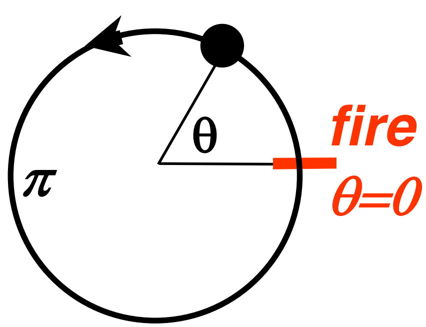
Glass and Mackey, Winfree

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

natural frequency

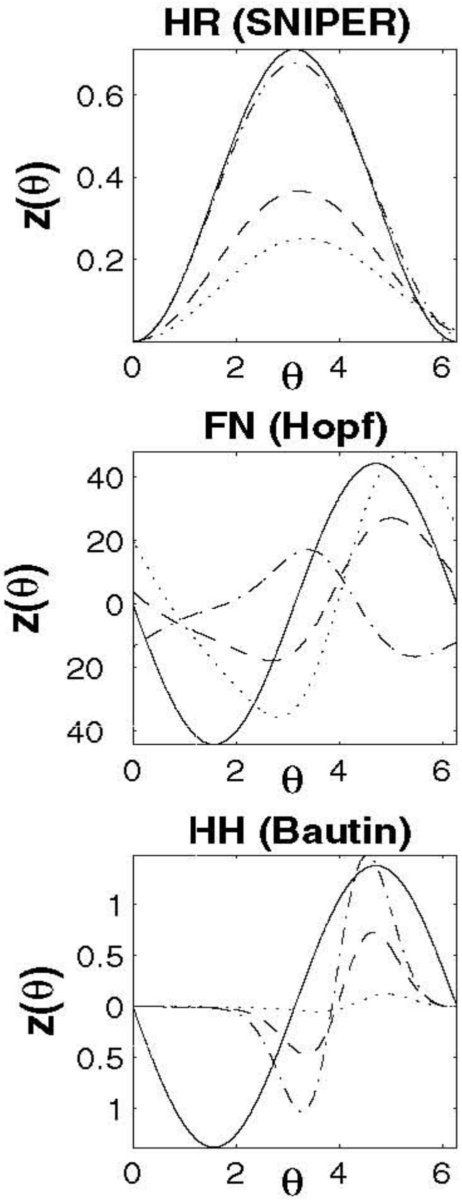
phase response curve (phase sensitivity curve)

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



Phase response curves for different neurons look very different!

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



Hodgkin-Huxley

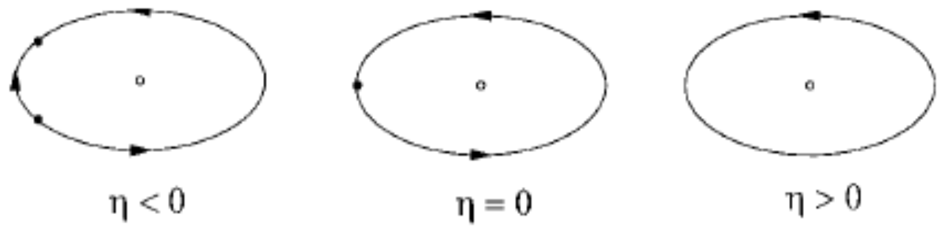
Following Brown, Moehlis, Holmes

Neural Comp 04

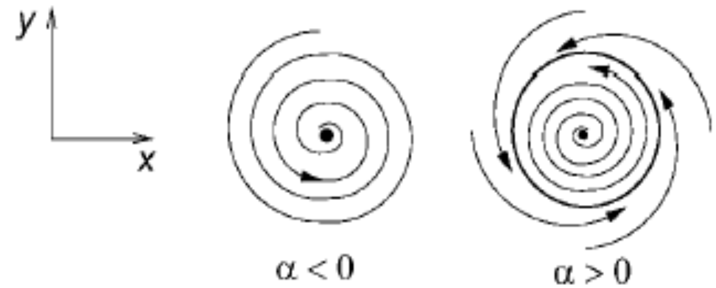
These differences follow from the underlying normal forms

Type I

SNIPER (Ermentrout, 1996)

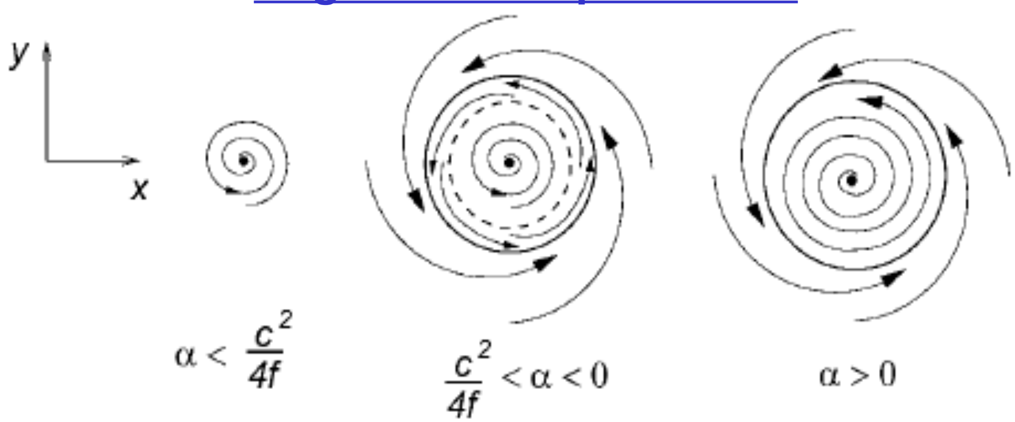


Hopf (Erm. + Kopell, 1984)

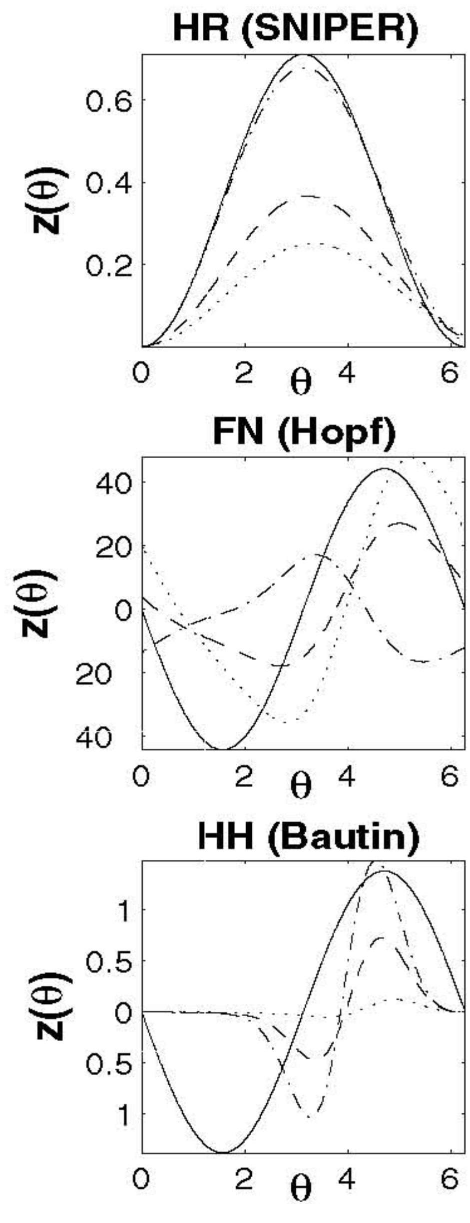


Type II

Degenerate Hopf / Bautin



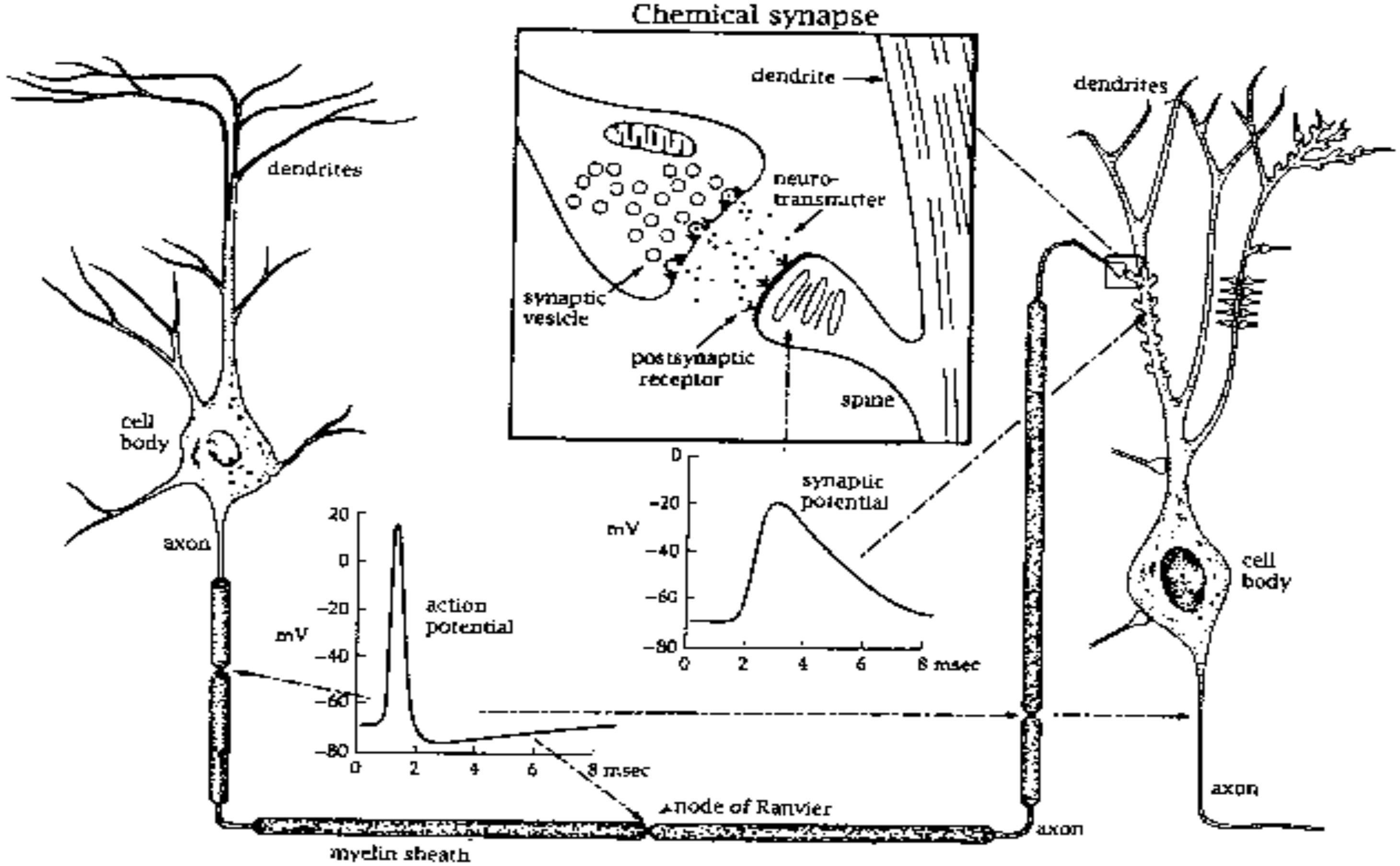
Phase response curves for normal form neuron models



$$k(1 - cos(\theta))$$

$$k_1 sin(\theta - k_2)$$

Use phase response curves to study synchrony in "network" of two coupled neurons



$I_{syn}(t)$

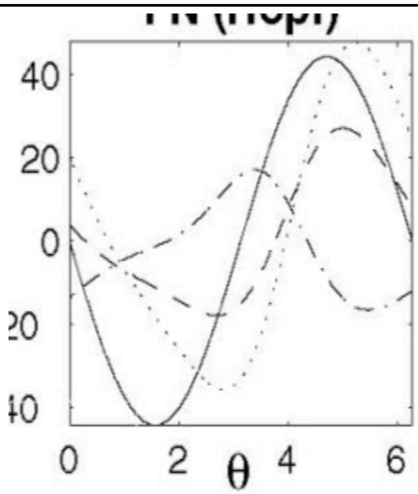
$$\frac{d\theta_1}{dt} = \omega + z(\theta_1) * h\delta(t - t_2^j)$$

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

The Hodgkin-Huxley model

PRC

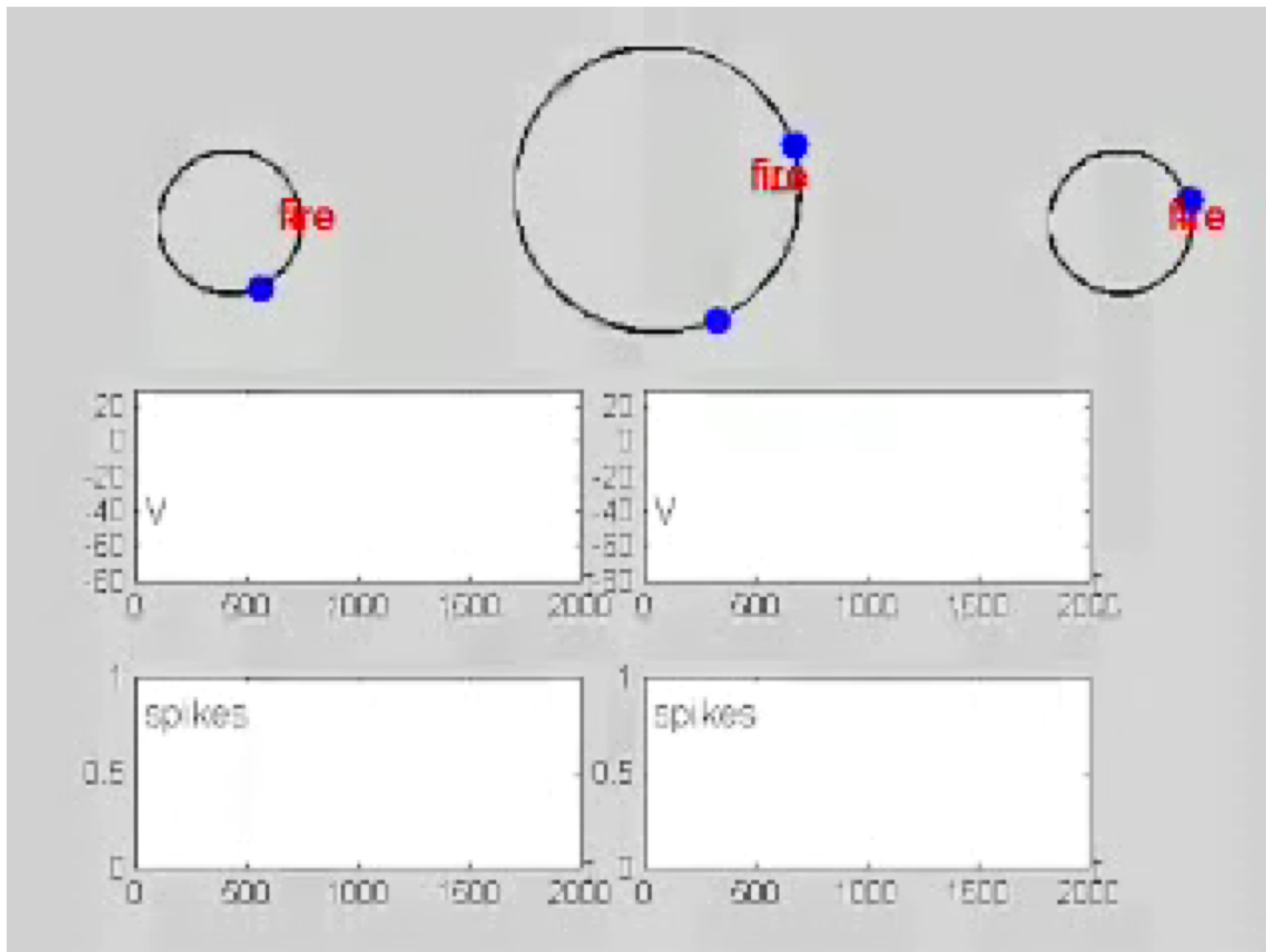
z(θ)



HH (Bautin)

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

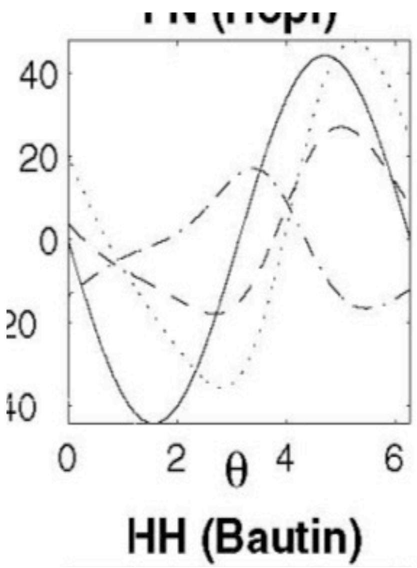
$$\frac{d\theta_2}{dt} = \omega + h * z(\theta_2)\delta(t - t_1^j)$$



The Hodgkin-Huxley model

PRC

z(θ)



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

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

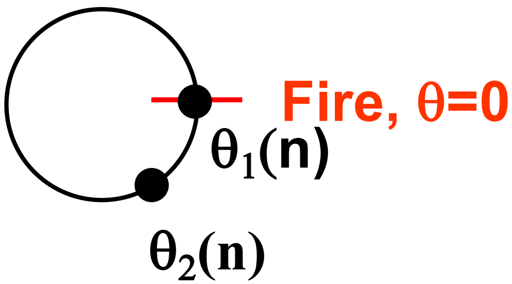
Moral: "Fast" excitatory coupling can synchronize HH neurons …

Analyze via Poincare map between firing times of θ_1

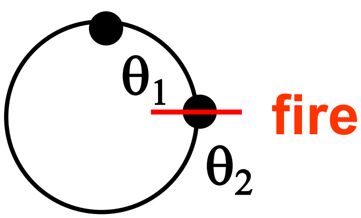
$$\frac{d\theta_1}{dt} = \omega + h * z(\theta_1)\delta(t - t_2^j)$$
$$\frac{d\theta_2}{dt} = \omega + h * z(\theta_2)\delta(t - t_1^j)$$

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

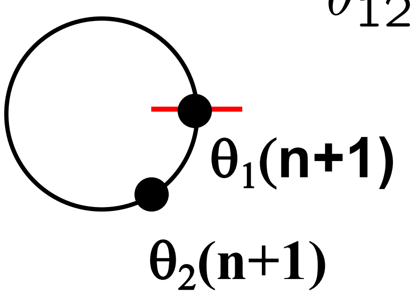
Let $\theta_{12} = \theta_1 - \theta_2$



$$\theta_2 \mapsto \theta_2 + hz\left(-\theta_{12}(n)\right)), \text{ or:}$$
$$\theta_{12}(n) \mapsto \underbrace{\theta_{12}(n) - hz\left(-\theta_{12}(n)\right)}$$



$$\theta_1 \mapsto \theta_1 + hz\,[\overbrace{\theta_{12}(n) - hz\left(-\theta_{12}(n)\right)}]$$



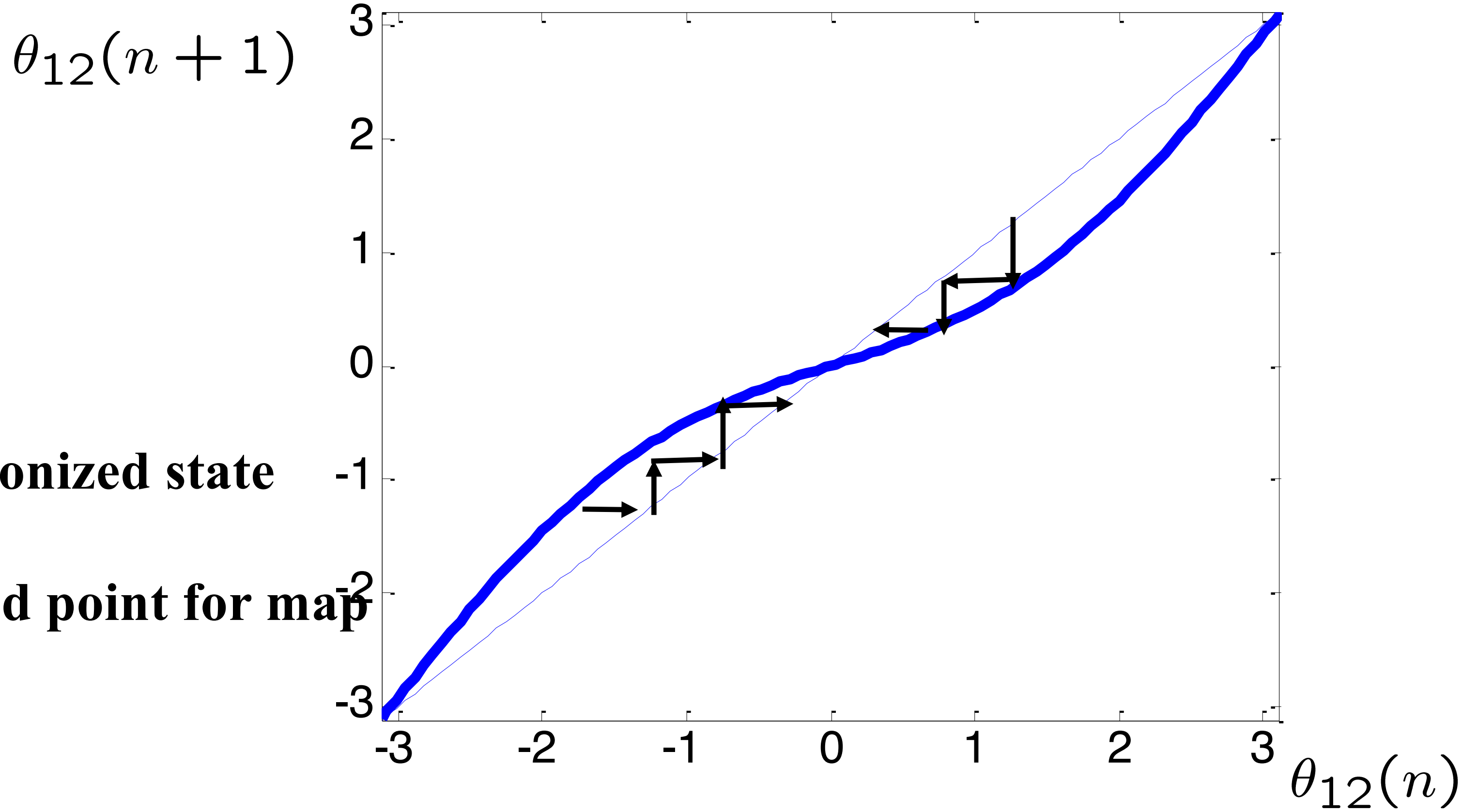
$$\begin{aligned} \theta_{12}(n+1) &= \theta_{12}(n) \\ &\quad -hz\left(-\theta_{12}(n)\right) \\ &\quad +hz\left[\theta_{12}(n) - hz\left(-\theta_{12}(n)\right)\right] \\ &= \theta_{12}(n) + h\left\{z(\theta_{12}(n)) - z(-\theta_{12}(n))\right\} + \mathcal{O}(h^2) \end{aligned}$$

Phase-difference map $\theta_{12} = \theta_1 - \theta_2$

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

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

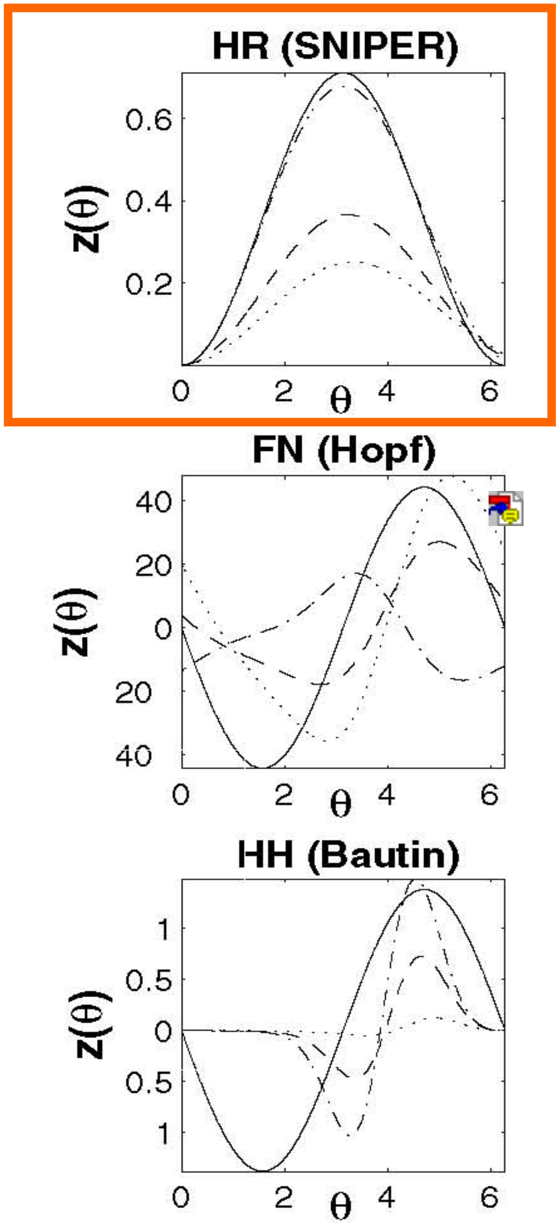
$$\theta_{12}(n+1) \approx \theta_{12}(n) - 2h\sin(\theta_{12})$$



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

Let’s try (as our last example)

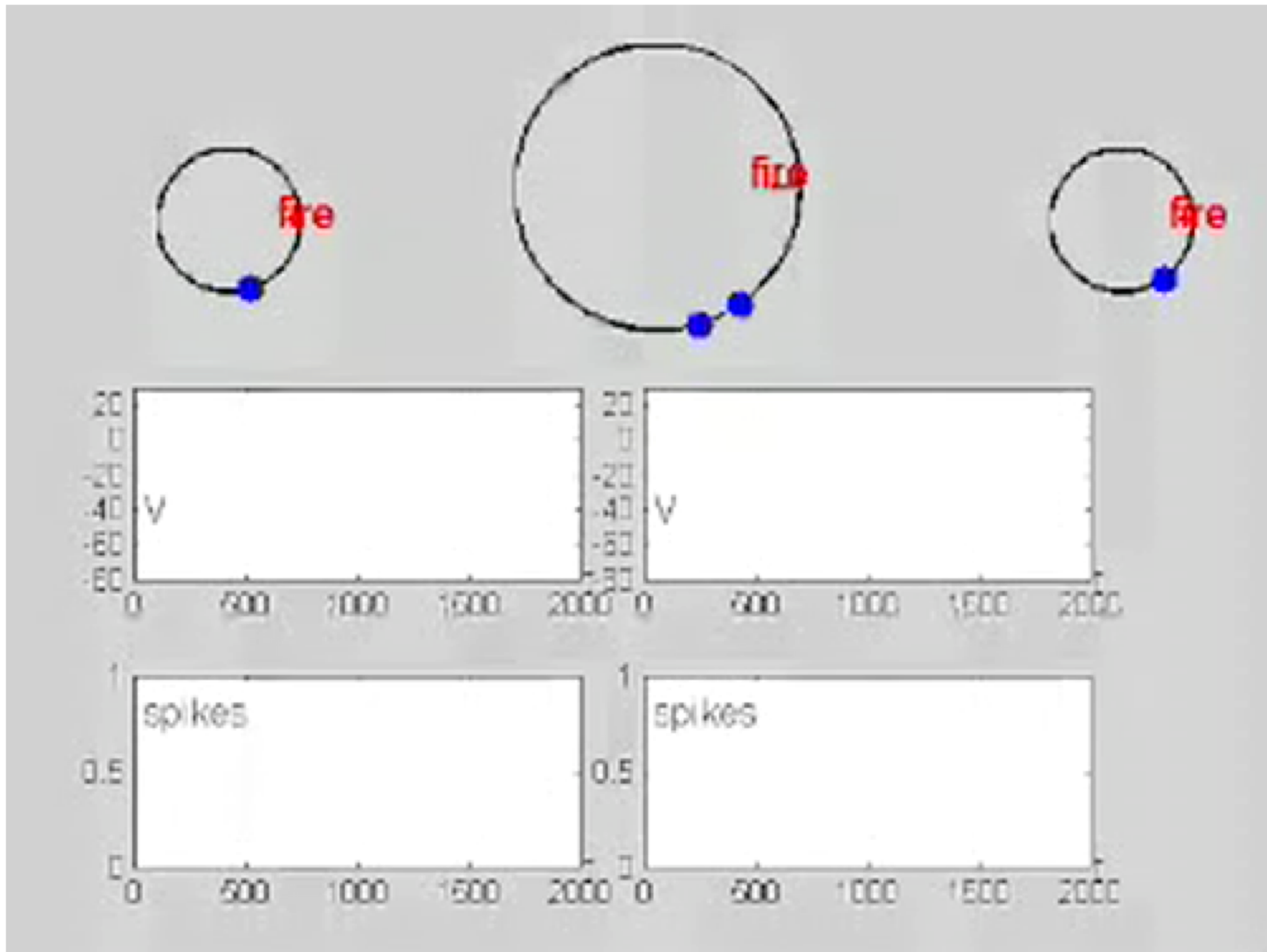
Very common in neural models …



The “Hodgkin Huxley plus A current” model

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

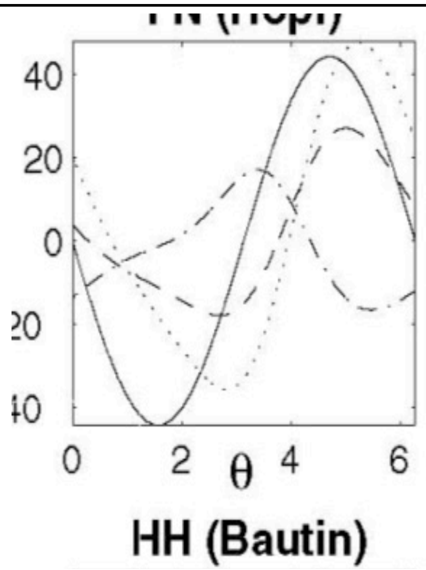
$$\frac{d\theta_2}{dt} = \omega + h * z(\theta_2)\delta(t - t_1^j)$$



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