Equiv. circuit

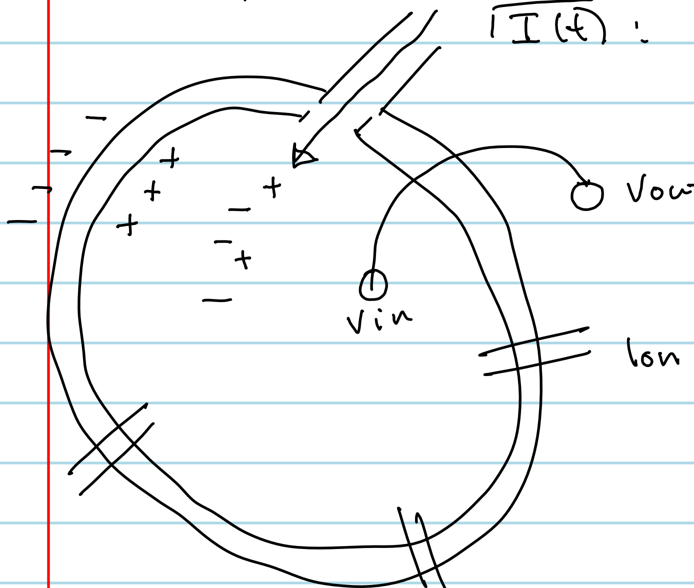
model of single neuron dynamics

· Gerstner, Fig. 1.6, 2.2

INPUT e.g.

$I(t)$: current (net + charge), from dendrite (OR experimenter)

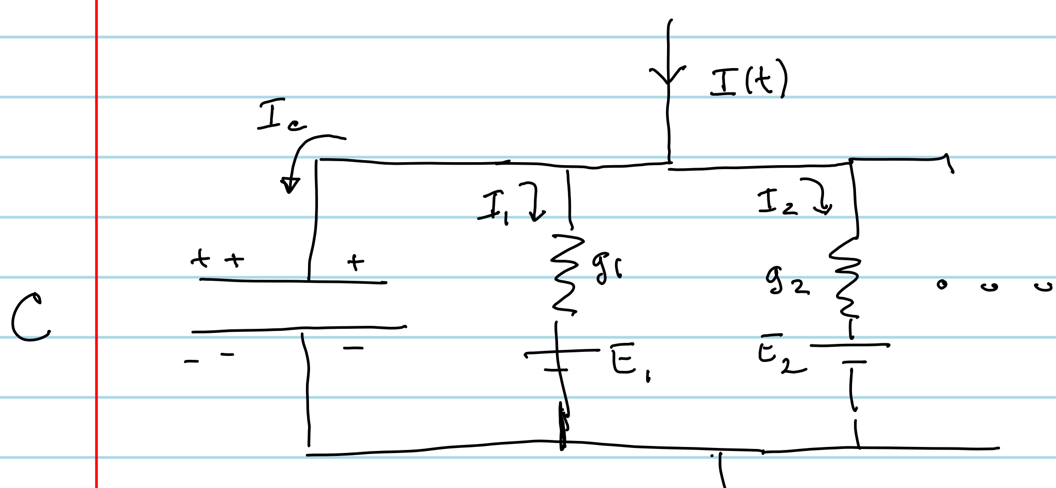
(1)



$V = V_{in} - V_{out}$, voltage

(u in text)

(2)

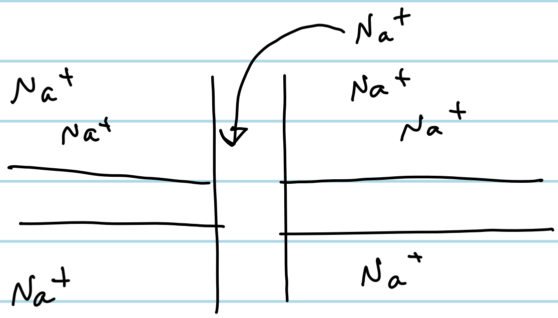


IN

OUT

① Capacitor: $I_c = C \dfrac{dV}{dt}$

② Ion channel: $I_1 = g_1 (V - E_1)$



- passes specific ions only, eg Na^+
- conductance g: "how open it is"

- Two "forces" drive current:
  (1) Diffusion: is there more Na^+ inside or outside
  (2) Voltage V, which pushes on charges

  E_1 is "reversal" potential where these balance.

- Repeat for other channels. Pass different ions $\longrightarrow$ different E_k

- $I(t) = I_c(t) + \sum_k I_k(t)$

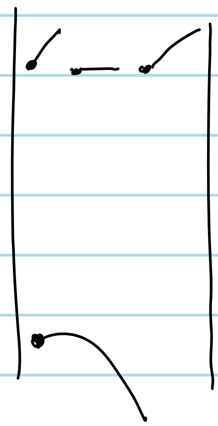
$$I(t) = C\frac{dV}{dt} + \sum_k g_k (V - E_k) \quad \ldots \text{so} \ldots$$

(1) $$C\frac{dV}{dt} = I(t) + \sum_k g_k (E_k - V)$$

AND...

g_k also evolve dynamically over time.

(2) $$g_k(t) = x_k(t)^{\alpha_k} \, y_k(t)^{\beta_k} \cdot \bar{g}_k$$



$x_k(t)$: fraction of "type x" gates in open position

α_k = # of such gates

$y_k(t)$, similar

opening and closing is voltage dependent:

(3) $$\dot{x}_k = \frac{x_k^{\infty}(v) - x_k}{\tau_k^x(v)}$$, similar for y_k.

---

(1) - (3) are the famed Hodgkin - Huxley (Nobel!) equations for the spike.
For us, "ground truth."

FORM:

(4) $$\frac{dV}{dt} = f_v(V, \vec{x}) + I(t)$$ where, abusing notation, $\vec{x} = \begin{pmatrix} x_1 \\ \vdots \\ y_1 \\ \vdots \end{pmatrix}$

$$\dot{x}_j = f_j(V, x_j)$$

- Simulate ... HH.m

let $I(t) = \bar{I}$, constant

(increase from 6, see spikes eventually occur.)

- ~~BUT...~~ look at parameters ... zoo of possibilities!

WHAT DO WE CARE ABOUT MOST?

↑ lec 1 '18, '20

(RATE CODING)

Q1) How does FIRING RATE depend on s. stats. of I(t)?

(coding slides... up to RATE CODING)

HH_fI.m.

- do we always get these rapid transients?

(TEMPORAL CODING)

... : doesn't seem that great for "graded" coding of mean inputs – what else can happen?

(Q2) What temporal features of I(t) drive ~~single~~ spikes?

· Next: Bifurcation theory gives windows into this.

(Q3) How can we derive reduced models of neural spiking that can be fit to data...

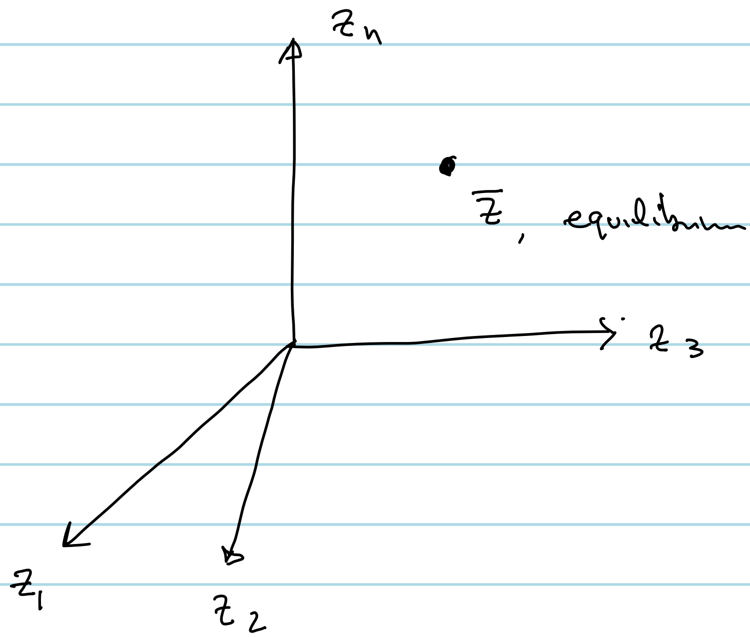
and capture dynamics in "natural" environment.

→ Bifurcations and Type I, Type II neurons: ←

$$\dot{\vec{z}} = \vec{f}(\vec{z}, I) \quad ; \quad \vec{z} = \begin{pmatrix} V \\ \vec{x} \end{pmatrix}$$

$$\vec{f} = \begin{pmatrix} f_V(V, \vec{x}, I) \\ \vec{f}_x(V, \vec{x}) \end{pmatrix}$$

IDEA: State space



$I = I_{cr}$ bif^n value

- At spike onset, equilibrium disappears... and something else happens!
- Idea of Bifurcation theory... Taylor-Expand $\vec{f}$ near $\bar{z}$.
- Primary results (AMATH 575, 502...) ...

... After coord. change,

Are only ~4 "generic" qualitatively distinct forms of this Expansion,

when transition from stable limit cycle to periodic orbit.

lec 1 '16

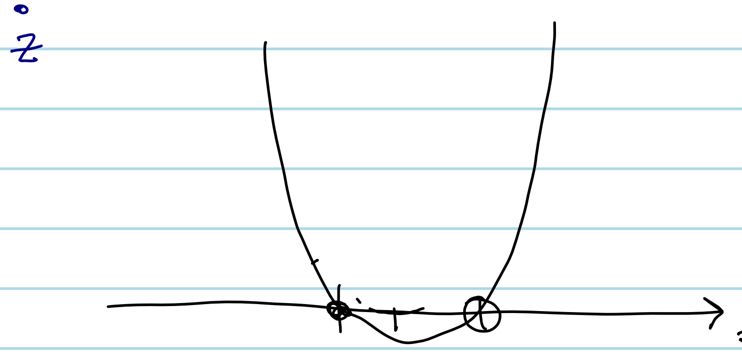
Two of these recur again and again:

Type I: SADDLE NODE BIF^{N}:

Dynamics in neighborhood of $\bar{z}$ are topologically equivalent to (i.e., there is a change of coordinates to normal form):

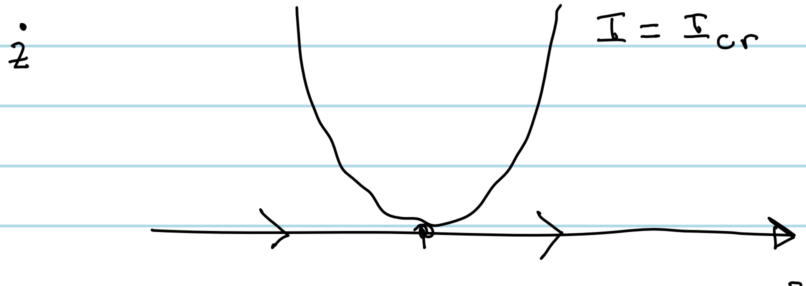
$$\dot{z} = z^2 + (I - I_{cr})$$

[Technically, guaranteed when $Df(\bar{z})$ has single 0 ev^{t}, and $\frac{\partial^2 f_v(\bar{z})}{\partial^2 v} \neq 0$, and $\frac{\partial f_v(\bar{z})}{\partial I} \neq 0$, where $f_v(\bar{z})$ is RHS of V eq^{n} (+) above w/ all $\dot{V}, \dot{x}$ at equilibrium].
Point: easy + "generic" to satisfy.

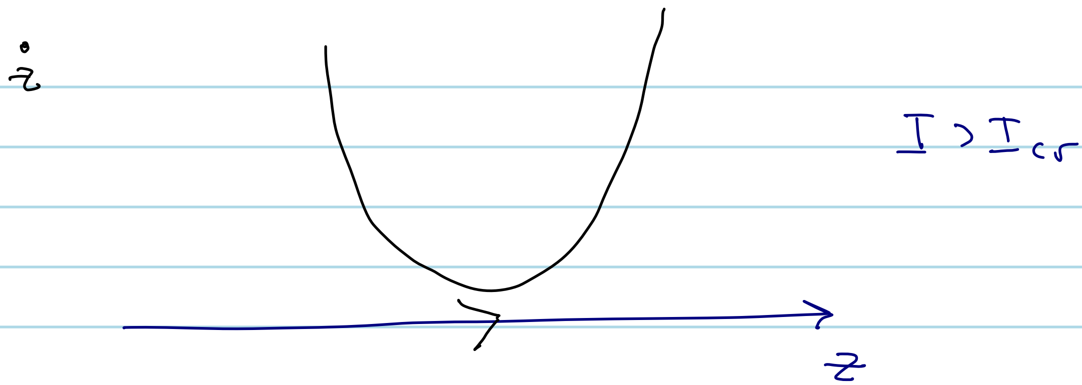


$I < I_{cr}$

spike onset direction z

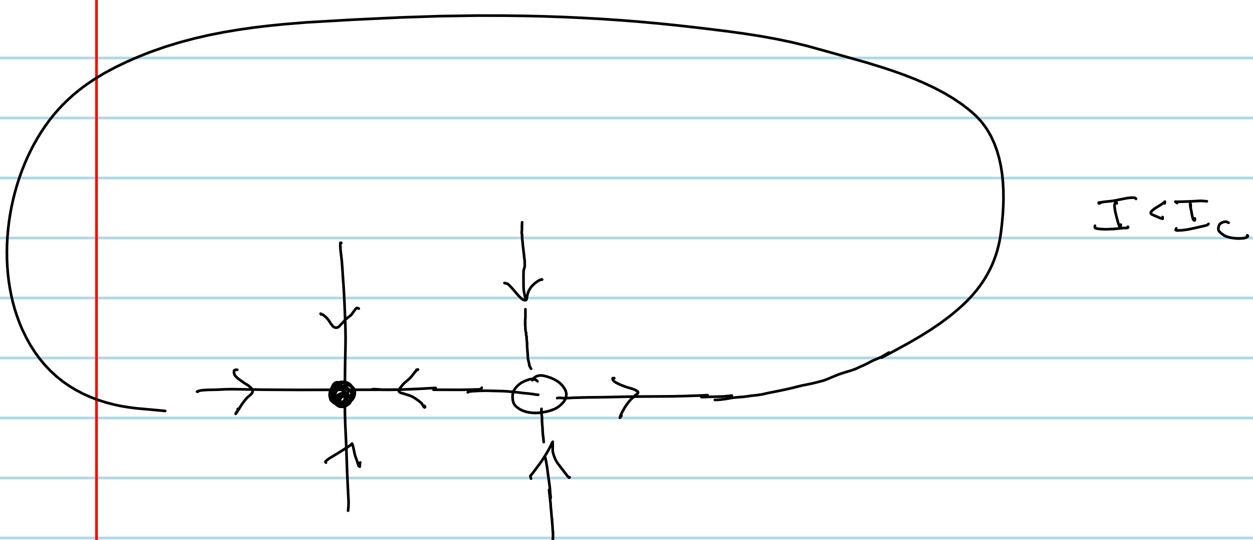


$I = I_{cr}$



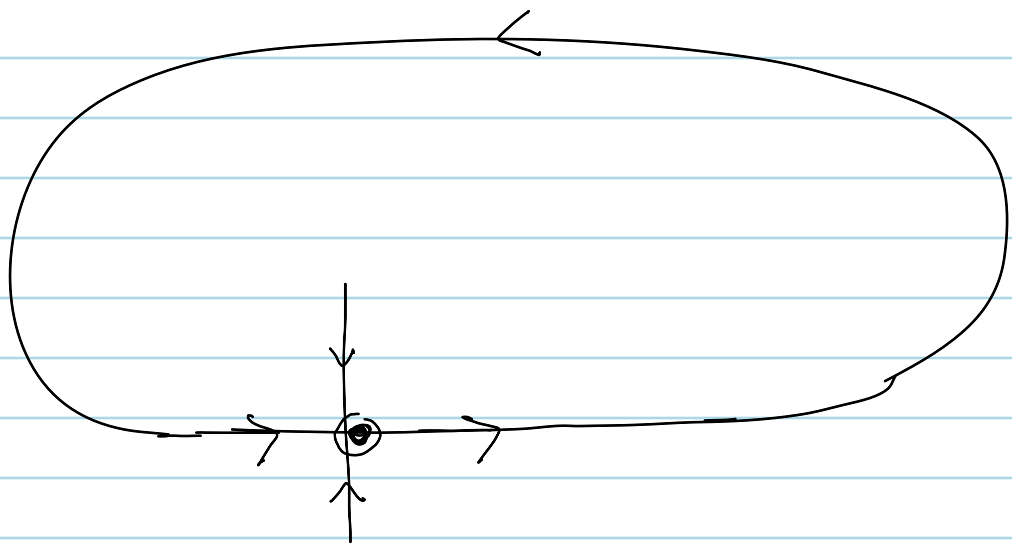
Produces trajectories blasting $\rightarrow$ lg. values of z, <u>BUT</u> ...
How does this produce a <u>spike</u> ?

If exist "return dynamics" – Saddle Node on Invariant Circle.

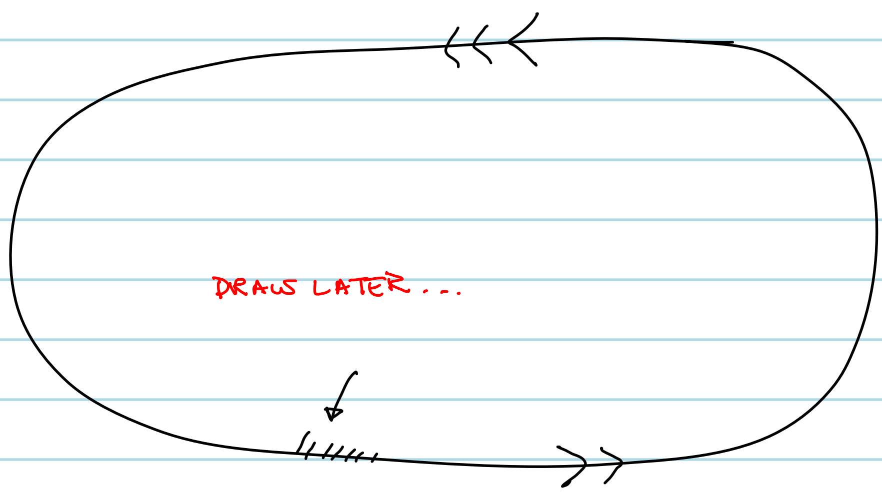


<u>Think:</u> common to have trajectories connect like this ...
follow traj out of saddle – makes sense get sucked to stable point from both ends.

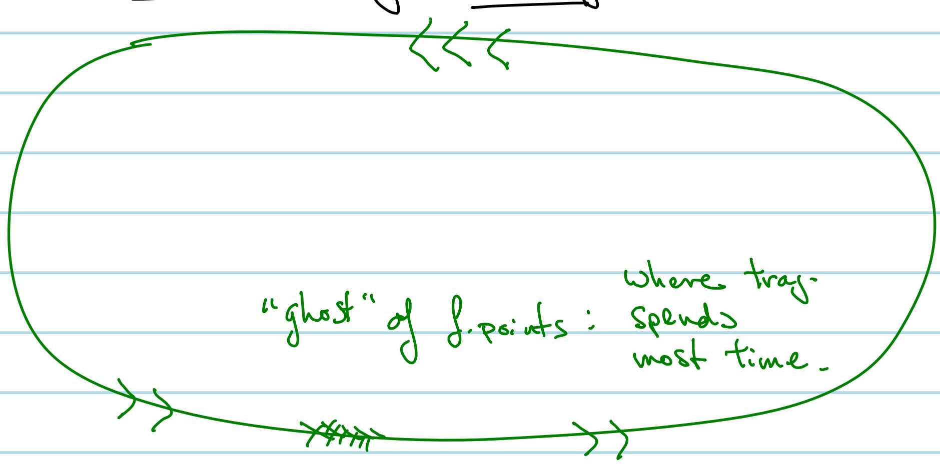
[invariance whole circle, etc. – <u>Actually</u>, invariance makes sense wrt the below ...]



Persists as $I > I_c$



What is period of (spiking) orbit?



$\dot{z} \approx z^2 + (I - I_c)$

W'20 Lec 2

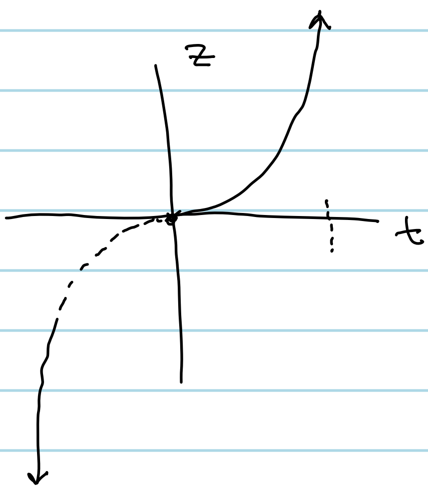
Solve ODE here.

$$\frac{dz}{dt} = z^2 + (I - I_c)$$

$$\int_{z(0)=0}^{z(t)} \frac{dz}{z^2 + (I - I_c)} = \int_0^t dt$$

$$\frac{\tan^{-1}\left(\frac{z}{\sqrt{I-I_c}}\right)}{\sqrt{I-I_c}} = t$$

$$z(t) = \tan\left[t\left(\sqrt{I-I_c}\right)\right] / \sqrt{(I-I_c)}$$



$$z(t^*) = \infty$$

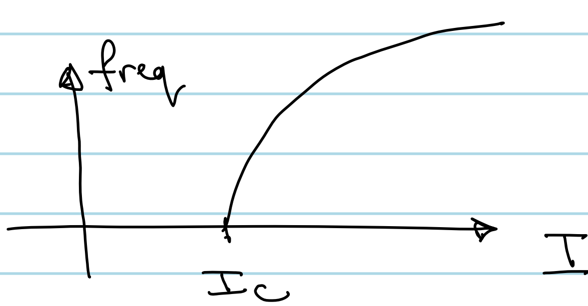
$$t^* \cdot \sqrt{I-I_c} = \pi/2$$

$$t^* = \pi / 2\sqrt{I-I_c} \longrightarrow$$

AND...
"comes in" from $-\infty$.

$$T = \frac{\pi}{\sqrt{I-I_c}} \quad \text{or} \quad \text{freq} \sim \sqrt{I-I_c}$$

Answer to Q1!



* FINITE *
ONSET
FREQ.

- Fact (Gerstner see 5.3.1):

Change of coordinates via $z(t) = \tan\left(\frac{\phi(t)}{2}\right) \longrightarrow$

$$\dot{\phi} = [1-\cos\phi] + (I - I_c)[1+\cos\phi]$$

Ermentrout + Kopell: Canonical Type I model or "Theta Model"...

Very convenient for simulation (smooth!) + visualization.

Type II: Hopf Bifurcation:

[$Df(\vec{z})$ has a pair of purely imaginary ev's when $I = I_{cr}$, and other derivative $\neq 0$ conditions]

$\longrightarrow$ Dynamics equivalent to...

$$\dot{z}_1 = (I - I_{cr}) z_1 - \omega z_2 + (z_1^2 + z_2^2)(-z_1 - b z_2)$$

$$\dot{z}_2 = \omega z_1 - (I - I_{cr}) z_2 + (z_1^2 + z_2^2)(-z_2 + b z_1)$$

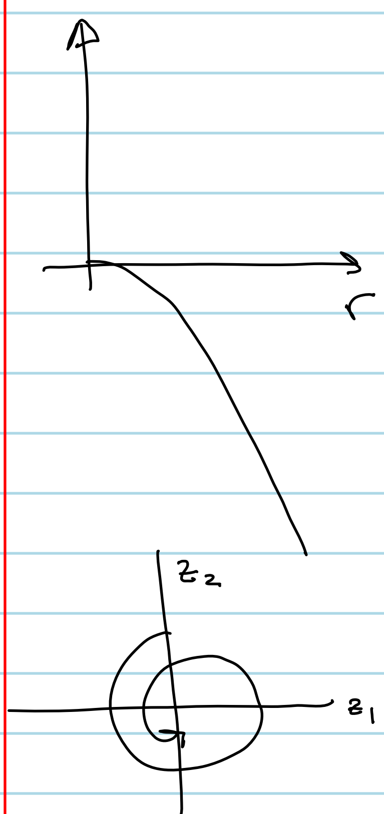
OR, in radial coordinates...

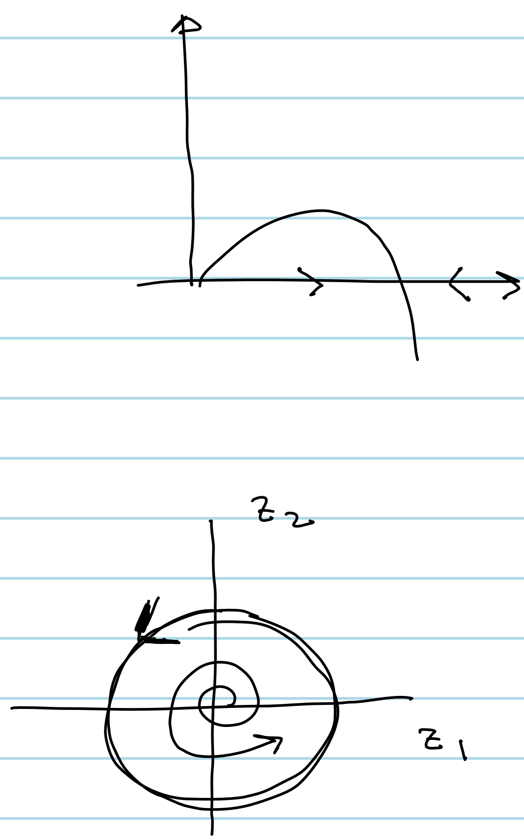
$$\dot{r} = (I - I_{cr}) r - r^3$$

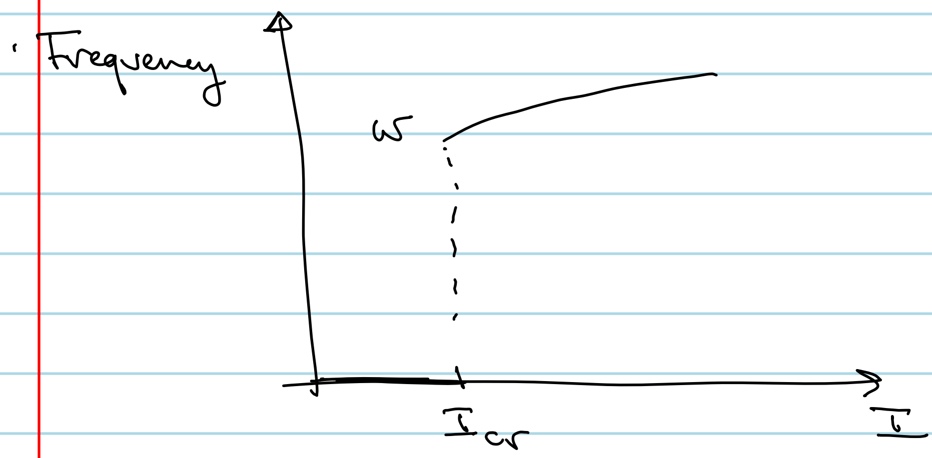
$$\dot{\theta} = \omega + b r^2$$

$I < I_{cr}$ $\qquad\qquad$ $I = I_{cr}$ $\qquad\qquad$ $I > I_{cr}$

$\dot{r}$





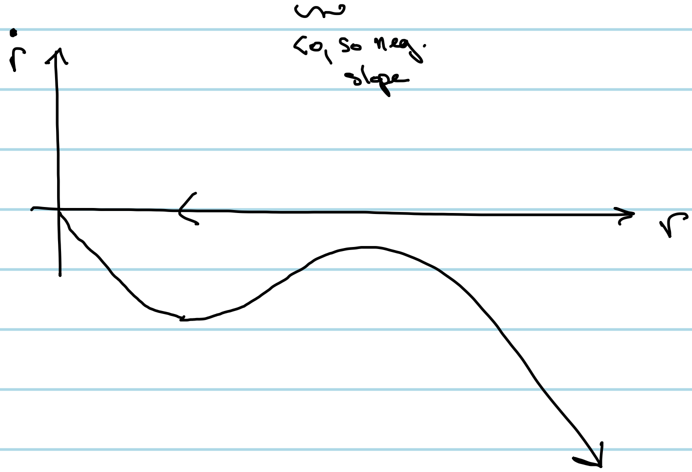


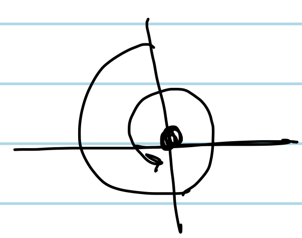
Jump → Nonzero frequency.

DETAIL: HH and other models display "generalized Hopf" or Bautin bifurcation. To capture, need higher-order poly. expansion:

eg. $$\dot{r} = \Big((I - I_{cr}) + \underbrace{\frac{c^2}{4f}}_{<0,\ \text{so neg. slope}} \Big) r + c r^3 + f r^5$$; $f<0$, $c>0$

$I < I_{cr}$



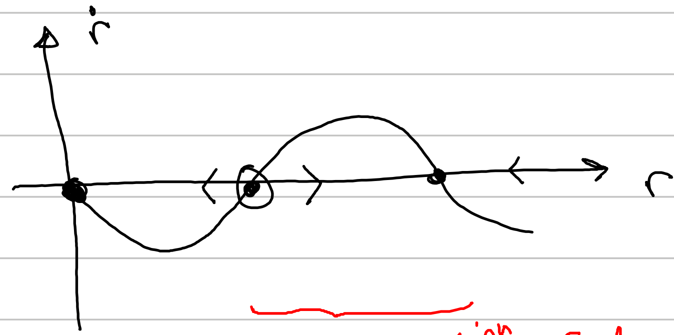


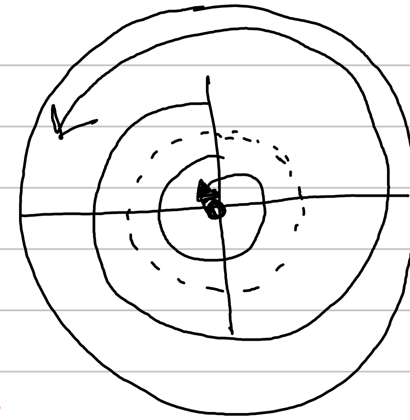
Note: this normal form arises generically in TWO-PARAMETER families of D.S. — 1 param drives subcritical Hopf. The other, the saddle node of l.c. @ Bautin point, both of these branches meet + have the N. Form above.

Both branches in bif'n diagram

$I > I_{cr}$

(I<0 above ✓
I_{cr}!
f<0.)





saddle node bif^n OF lim. cycles
occurs HERE.

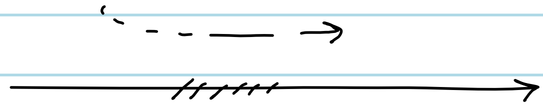
(same property: nonzero frequency).

[sudden appearance of stable + unst. l.c.].

Q2: WHAT KIND OF TEMPORAL INPUTS ELICIT A SPIKE?

Say Input = $\underbrace{I}_{\text{Sets baseline (above or below } I_c)} + \underbrace{I(t)}_{\text{temporal}}$

Type I / SADDLE NODE:



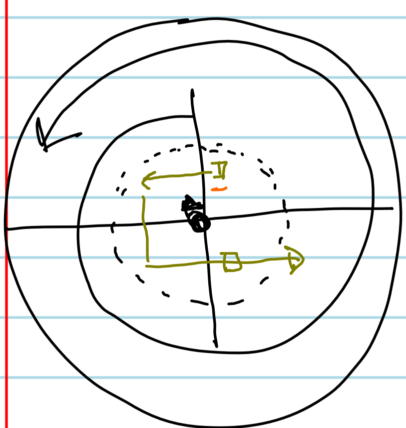
Z

Spike direction

Answer: $\dot{I}(t)$ of one sign ... "push" state through slow region $\longrightarrow$ spike.

"INTEGRATOR"

Type II / Hopf:



(Well-timed) ...

Inputs of BOTH signs can contribute to crossing "circular" threshold...

"Resonator."

[slide]

· Formalize this via PHASE RESPONSE CURVES.

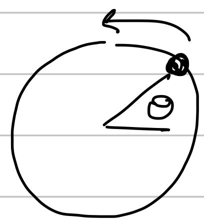
Recall that type I normal forms can be transformed to:

$$\dot{\phi} = [1-\cos\phi] + [I - I_c + I(t)][1+\cos\phi]$$

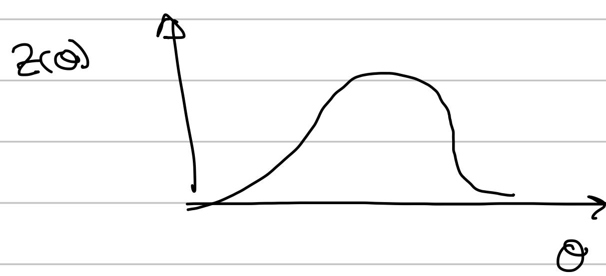
Another coord change $\longrightarrow$

$$\dot{\Theta} = \omega + Z(\Theta)\, I(t)$$

, where $Z(\Theta) = k\,(1-\cos\Theta)$ for some Θ.



$Z(\Theta)$ is PHASE RESPONSE CURVE:



always > 0

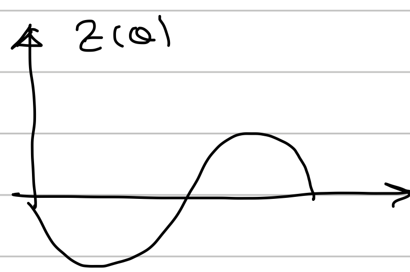
$\longrightarrow$ integrator.

see Brown et al 2004; earlier, Ermentrout + Kopell.

— · —

For type II cells get

$\rightarrow$ $\dot{\Theta} = \omega + Z(\Theta)\, I(t)$, where $Z(\Theta) = k_1 \sin(\Theta - k_2)$



pos. + neg.

$\longrightarrow$

RESONATOR.

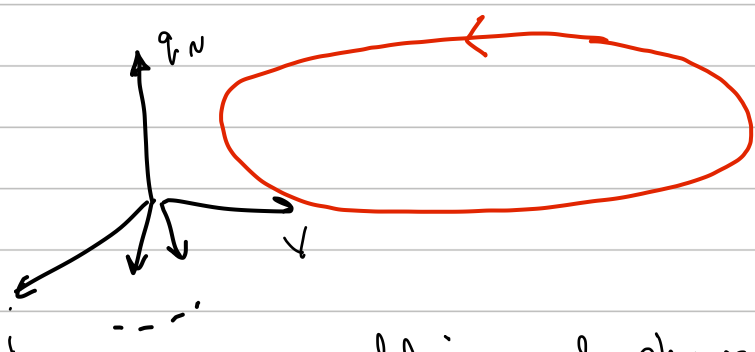
Computing the Phase Response Curve (Brown et al '04):

HAVE: original ODE: $\vec{x} = \begin{pmatrix} V \\ \vec{q} \end{pmatrix}$ voltage
gating variables

$$\frac{d\vec{x}}{dt} = \vec{F}(\vec{x}) + \begin{pmatrix} I(t) \\ \vec{0} \end{pmatrix}$$

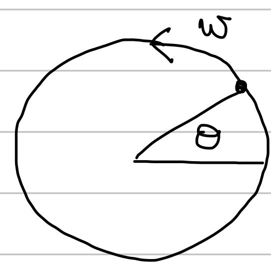
, "extra" input ... could generalize to $I(t, \vec{x})$; "conductance-based input"

<u>Idea:</u> when $I(t) = 0$, have periodic firing w/ period T.



$\dot{\vec{x}} = \vec{F}(\vec{x}) + 0$

define coord. change $\Theta(\vec{x})$ s.t. $\frac{d\Theta}{dt} = \omega$,



where $\omega = \frac{2\pi}{T}$

(angular freq.)

Then: when $I(t) \neq 0$

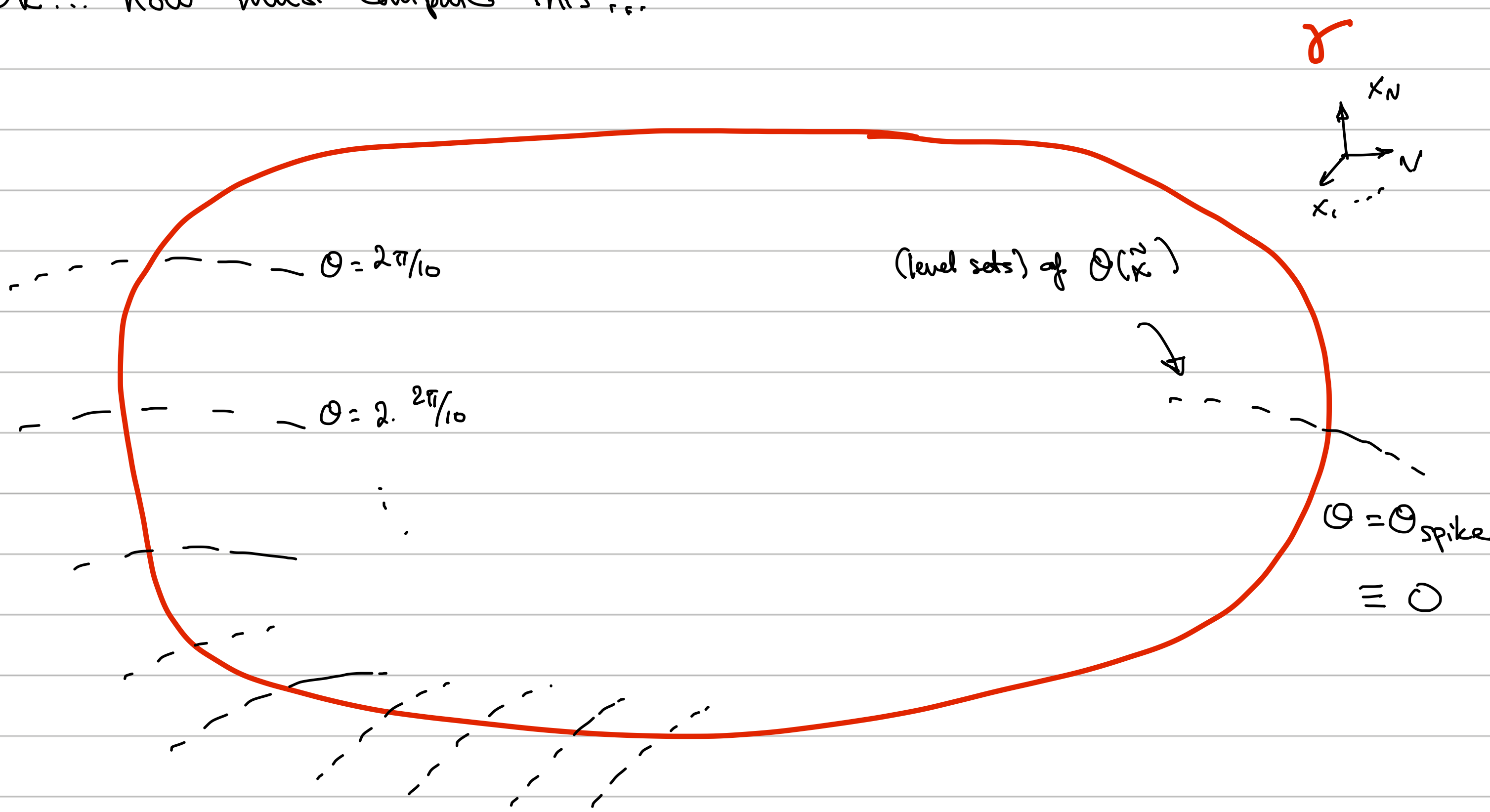
$$\frac{d\vec{x}}{dt} = \vec{F}(\vec{x}) + \begin{pmatrix} I(t) \\ \vec{0} \end{pmatrix} \longrightarrow \frac{d\theta}{dt} = \underbrace{\frac{\partial \theta}{\partial \vec{x}}}_{\nabla_{\vec{x}}\,\theta(\vec{x}) = \left(\frac{\partial\theta}{\partial V}, \frac{\partial\theta}{\partial q_1}, \dots\right)(\vec{x})} \cdot \frac{d\vec{x}}{dt} =$$

$$= \frac{\partial\theta}{\partial\vec{x}} \cdot \left[\vec{F}(\vec{x}) + \begin{pmatrix} I(t) \\ \vec{0} \end{pmatrix}\right]$$

$$= \omega + \frac{\partial\theta}{\partial\vec{x}} \cdot \begin{pmatrix} I(t) \\ \vec{0} \end{pmatrix}$$

$$= \omega + \underbrace{\frac{\partial\theta}{\partial V}}(\vec{x})\, I(t) \qquad (t)$$

OK... now must compute this...



Level sets called Isochrons: Winfree '74, Guckenheimer '75.

· In general, would need to know "whole" field $\theta(\vec{x})$, to compute its derivatives in nbhd. of γ.

$$\frac{\partial \theta}{\partial V}(\vec{x})$$

But, can use ASYMPTOTIC PHASE TRICK ... to get

$$\frac{\partial \theta}{\partial V}(\vec{x})$$ ON for $\vec{x}$ on limit cycle γ.

Let $\vec{x}(\theta)$ be point on γ w/ phase θ.

$$\frac{\partial \theta}{\partial V}\left(\vec{x}(\theta)\right) \equiv z(\theta),$$ phase response curve.

From (+) above, gives $\dot{\theta} = \omega + z(\theta)\, I(t)$.

[Asymptotic Phase + Phase Response curve slides . ppt]