

Dynamical Systems in Neuroscience

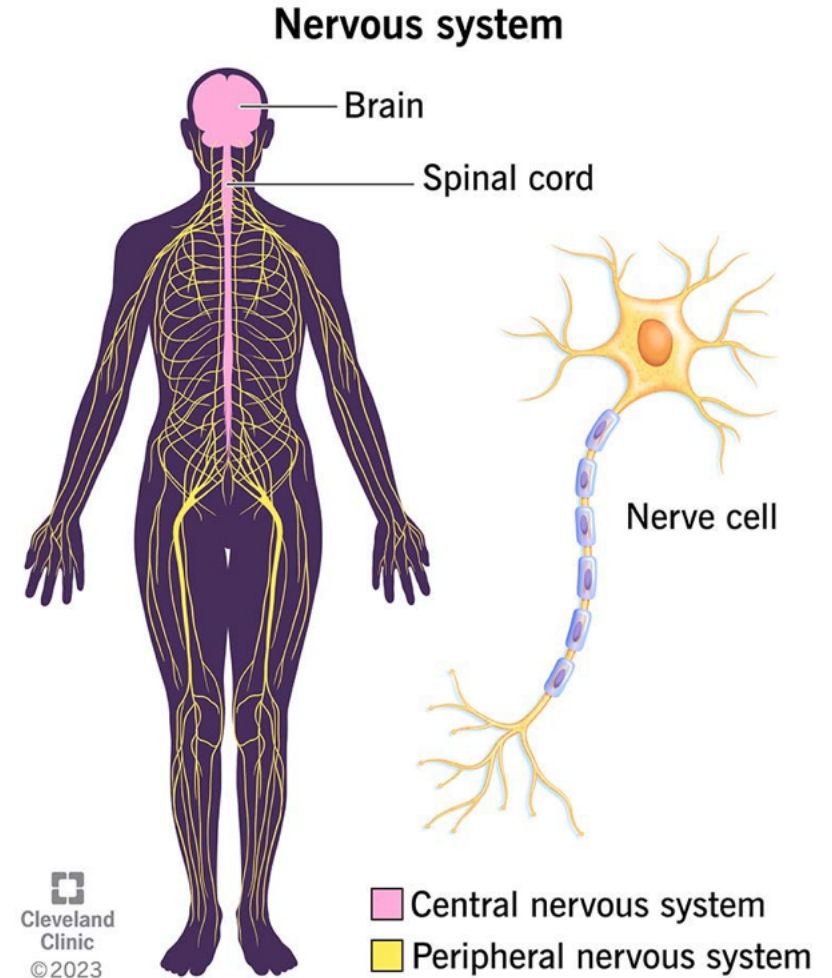
ICTS Summer Course 2026

Textbooks

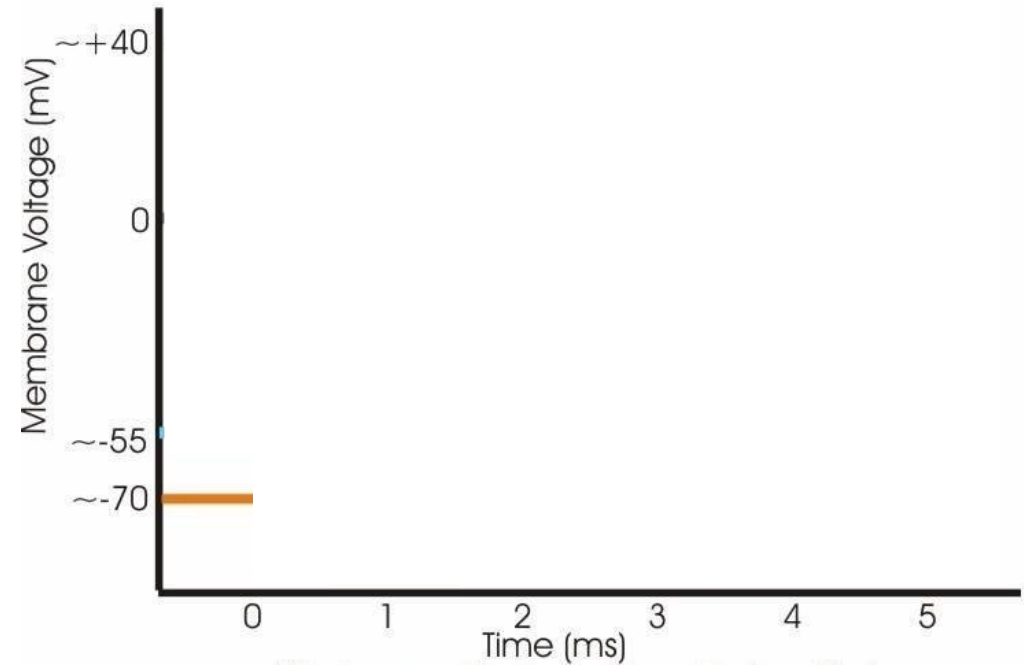
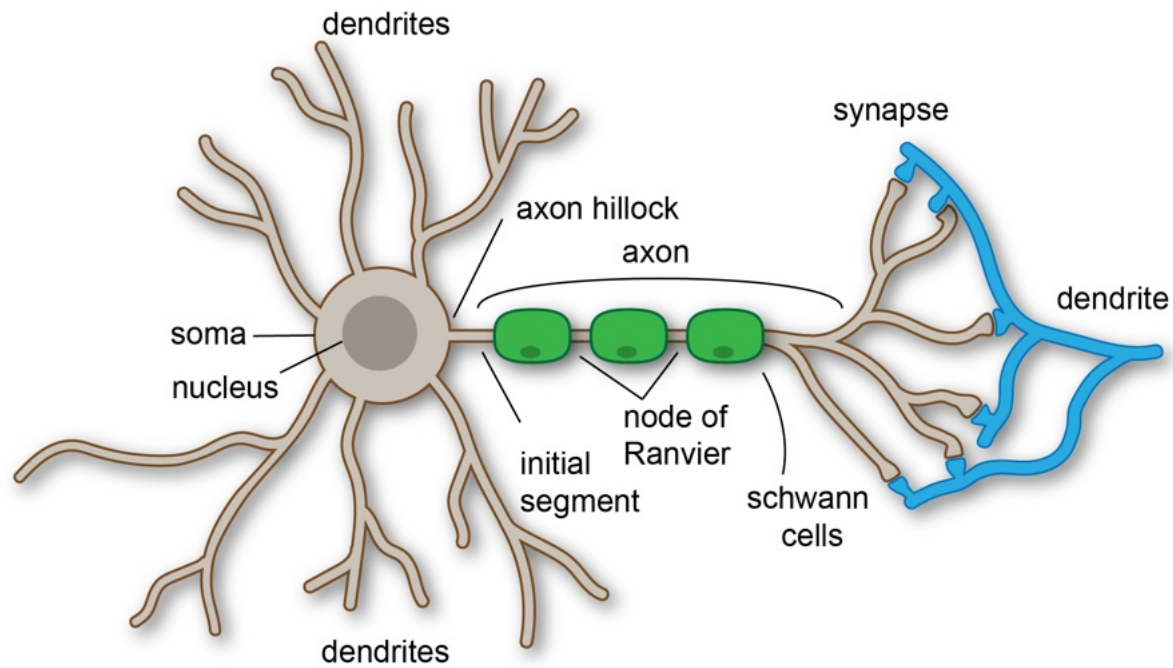
- Nonlinear Dynamics and Chaos - Steven Strogatz
- Chaos in Dynamical Systems - Edward Ott
- Dynamical Systems in Neuroscience - Eugene M. Izhikevich
- Mathematical Foundations of Neuroscience - Bard Ermentrout and David Terman
- Neuronal Dynamics - Gerstner, Kistler, Naud and Paninski

What is neuroscience?

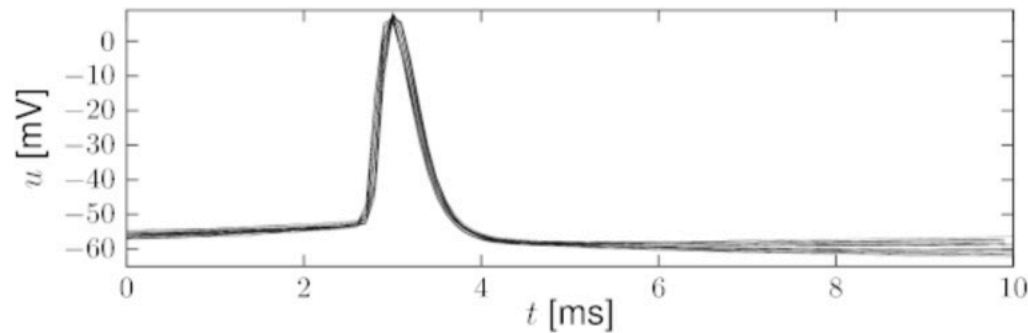
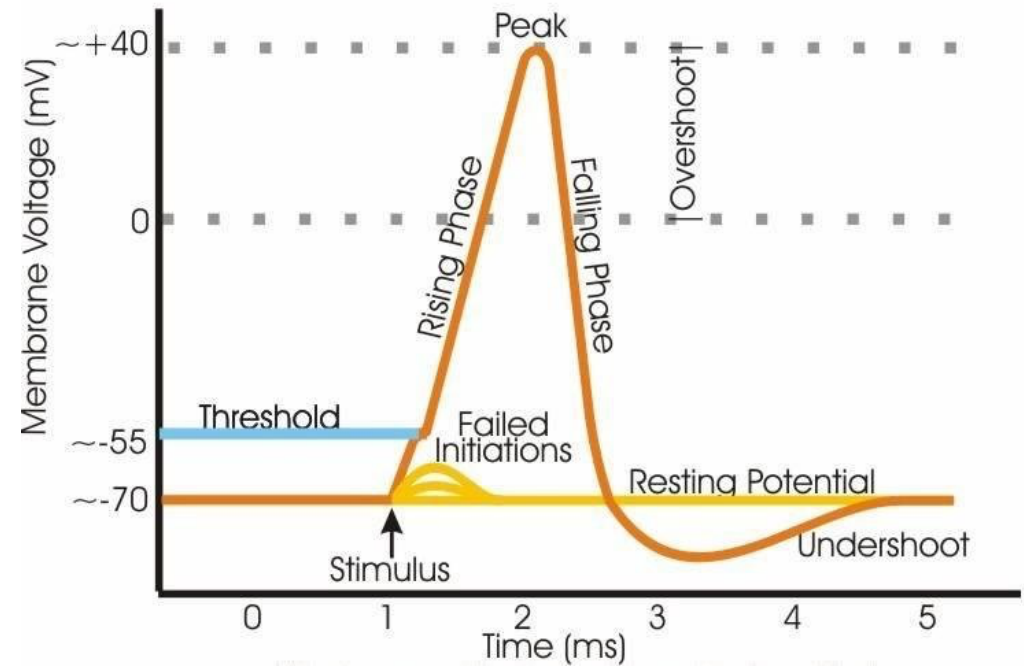
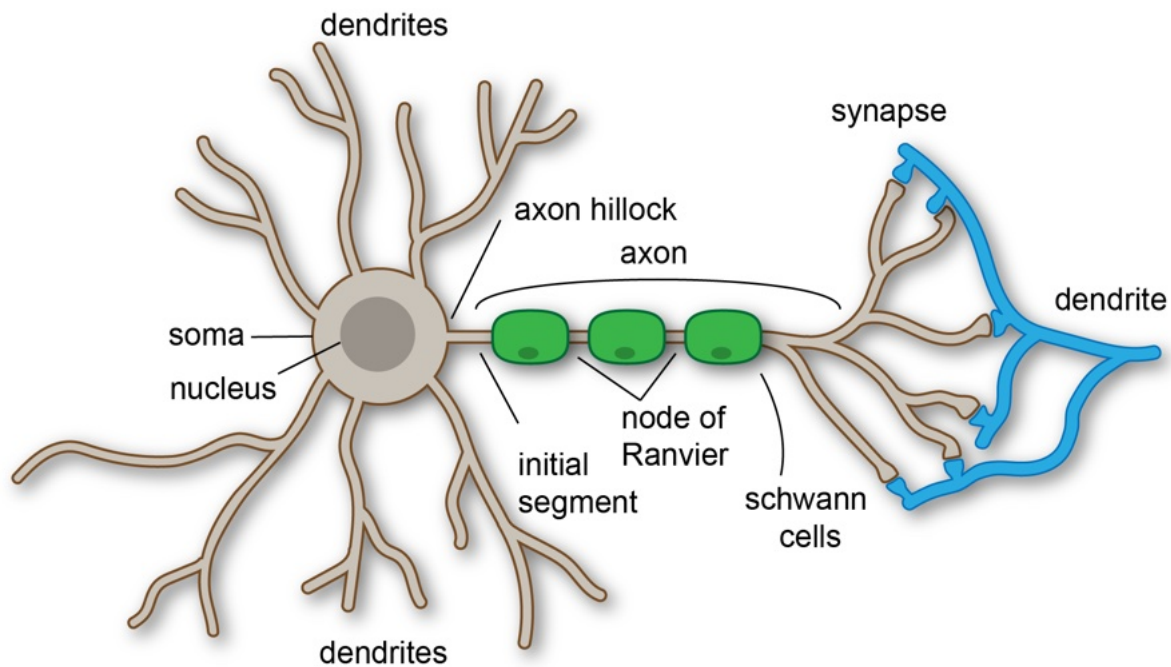
Study of the nervous system



What is a neuron?

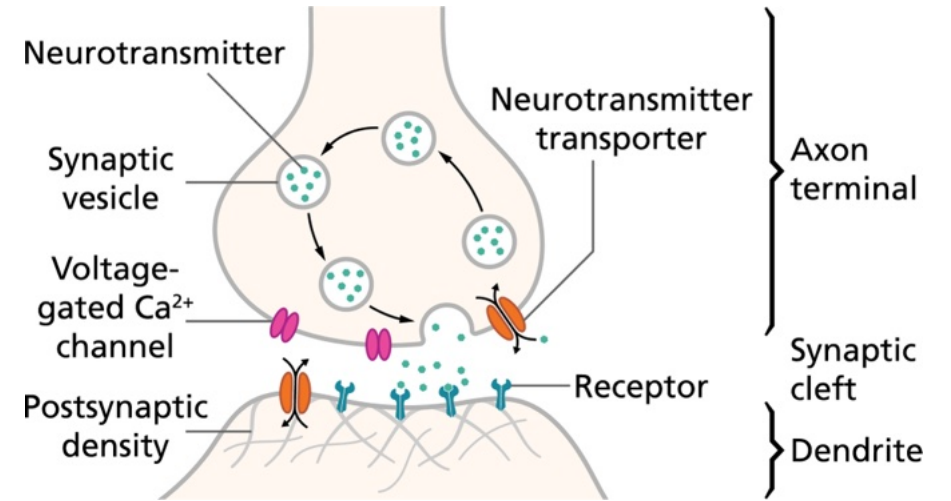
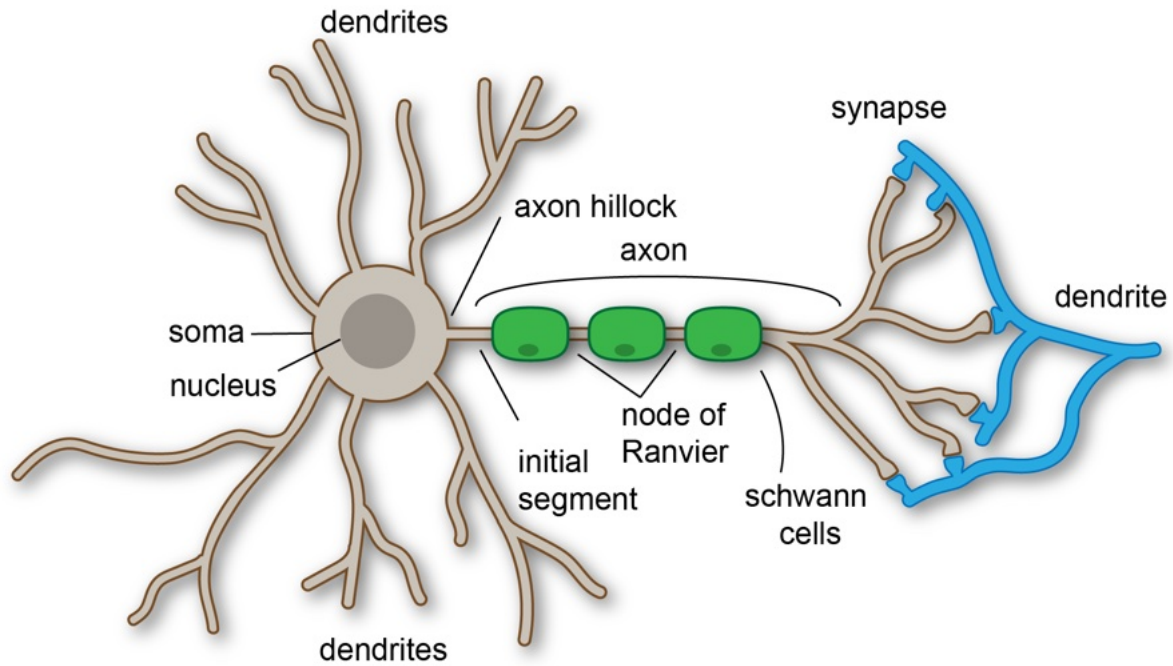


What is a neuron?

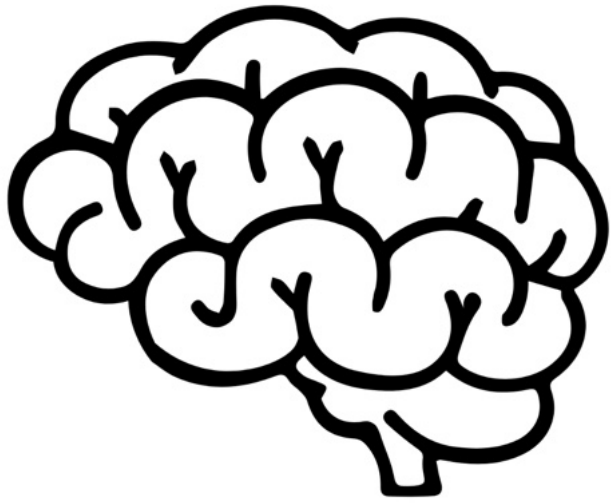


GKND Fig. 1.3

What is a neuron?

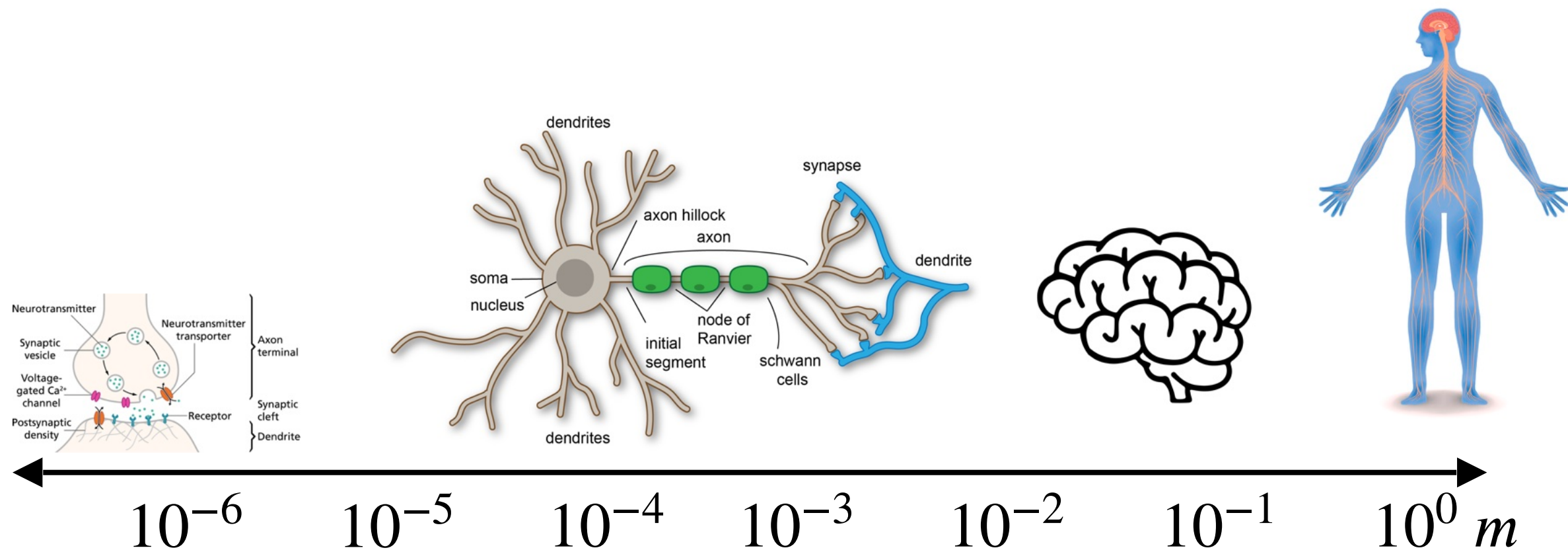


Neurons to neural circuits

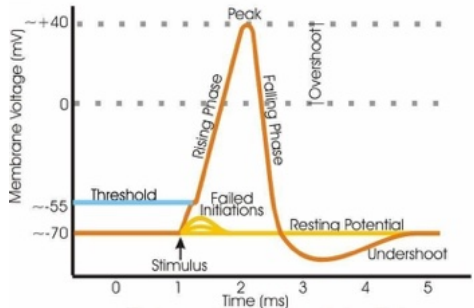


10^{11} neurons
 10^{14} synapses

Relevant lengthscales



Relevant timescales



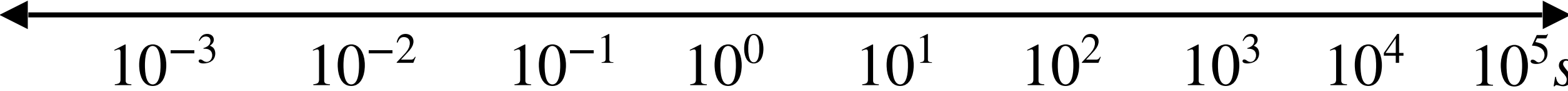
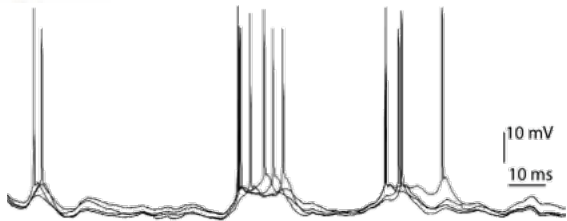
Synaptic plasticity

Sensory perception

Planning, reasoning

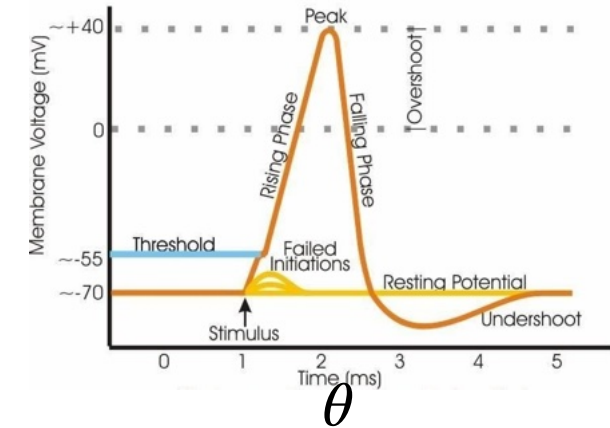
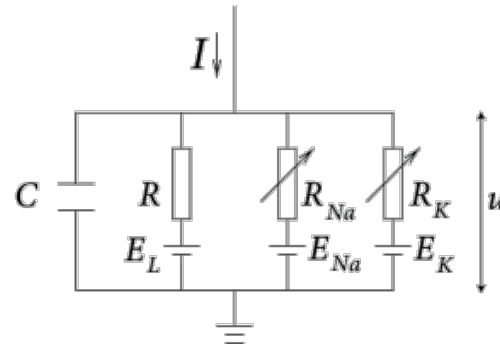
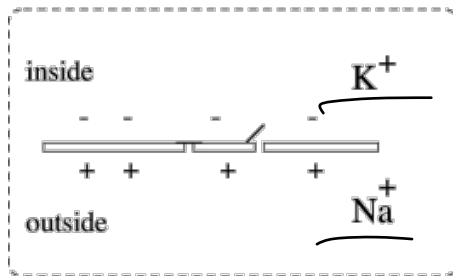
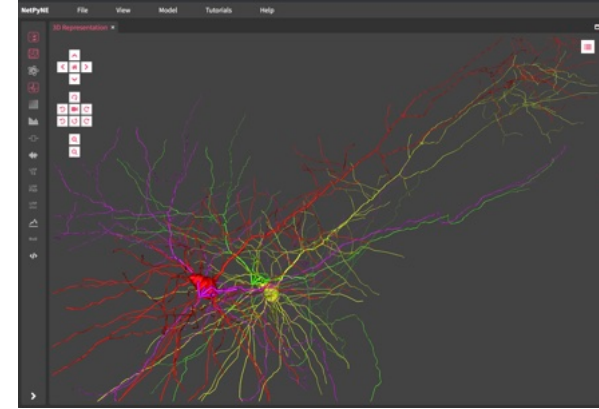
Long-term memory, learning

Short-term memory



Different levels of abstraction

- Model detailed biochemistry and biophysics
- Model individual spikes



$$I = C_m \frac{dV_m}{dt} + \bar{g}_K n^4 (V_m - V_K) + \bar{g}_{Na} m^3 h (V_m - V_{Na}) + \bar{g}_l (V_m - V_l),$$

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

$$\frac{dm}{dt} = \alpha_m (V_m) (1 - m) - \beta_m (V_m) m$$

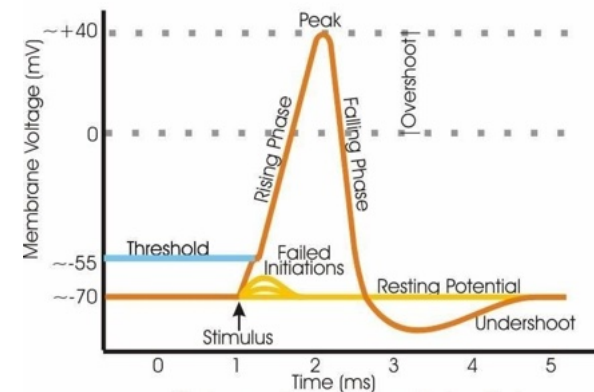
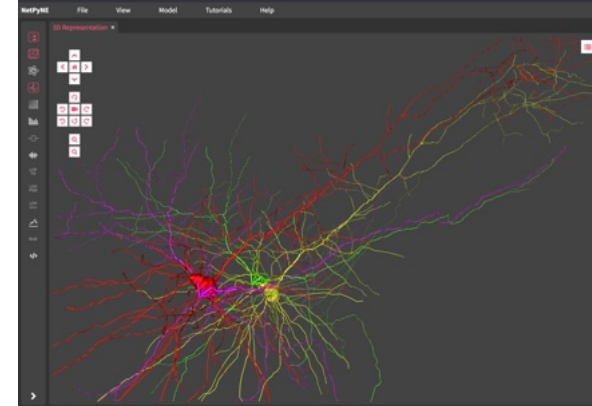
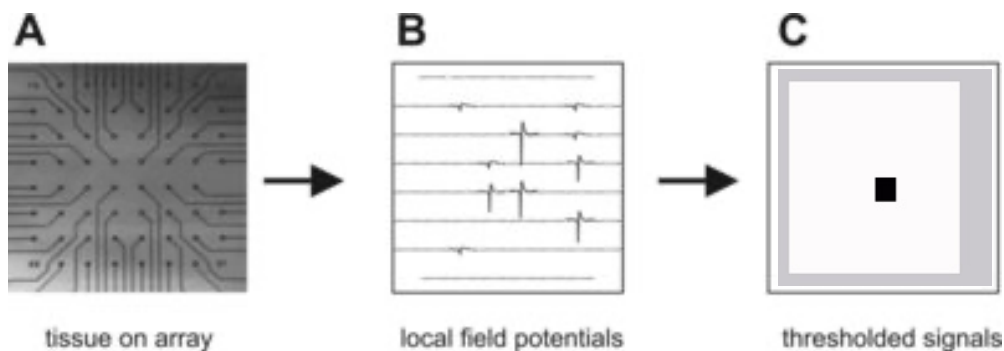
$$\frac{dh}{dt} = \alpha_h (V_m) (1 - h) - \beta_h (V_m) h$$

Hodgkin - Huxley

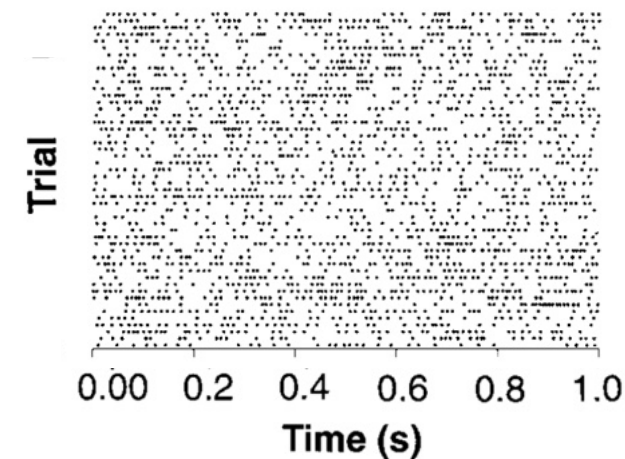
$$\frac{d\theta}{dt} = 1 - \cos \theta + (1 + \cos \theta) I(t),$$

Different levels of abstraction

- Model detailed biochemistry and biophysics
- Model individual spikes
- Model binary neurons

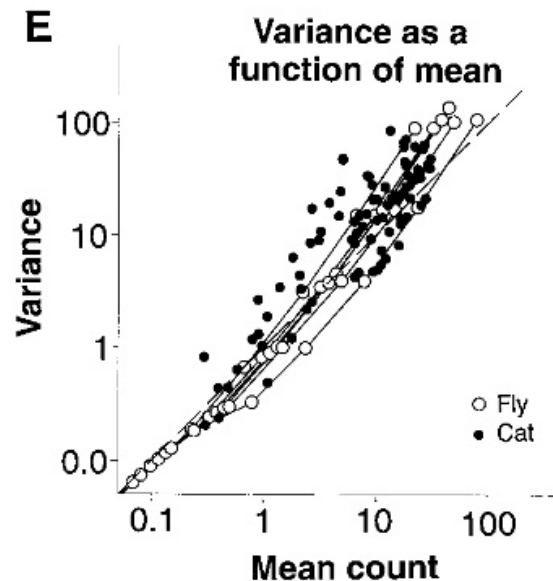
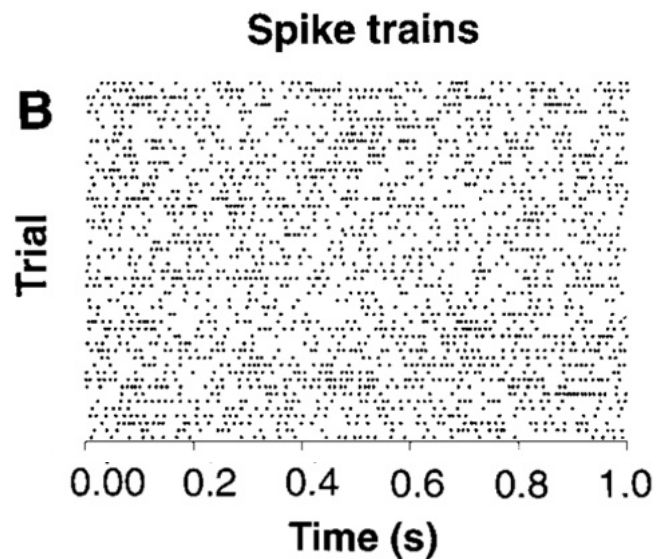


Spike trains



Different levels of abstraction

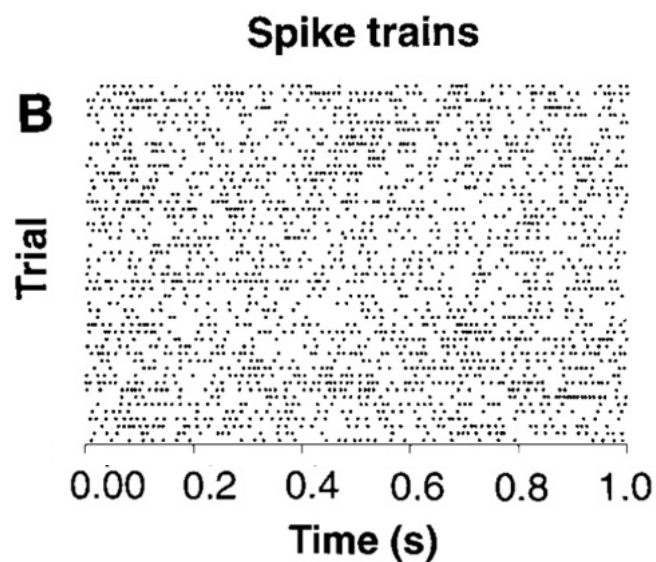
- Neuron spiking can seem stochastic
- Poisson spiking model: neuron action potential spike distribution



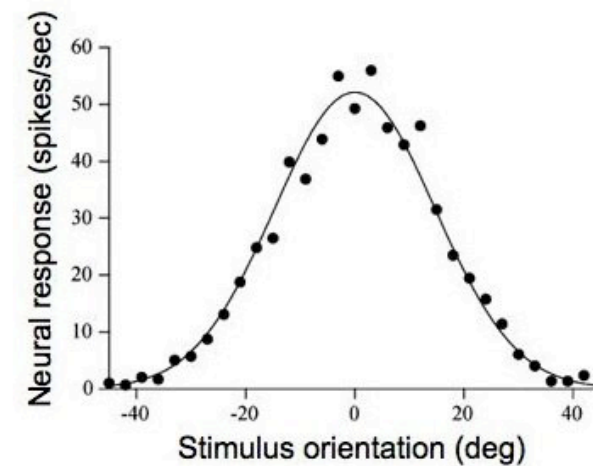
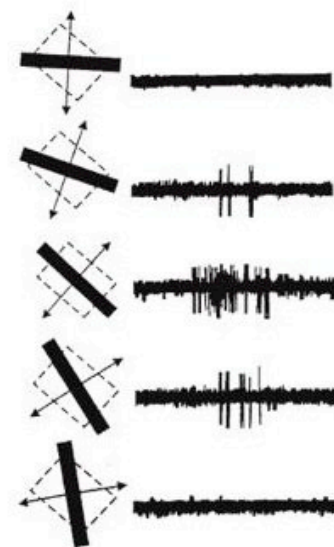
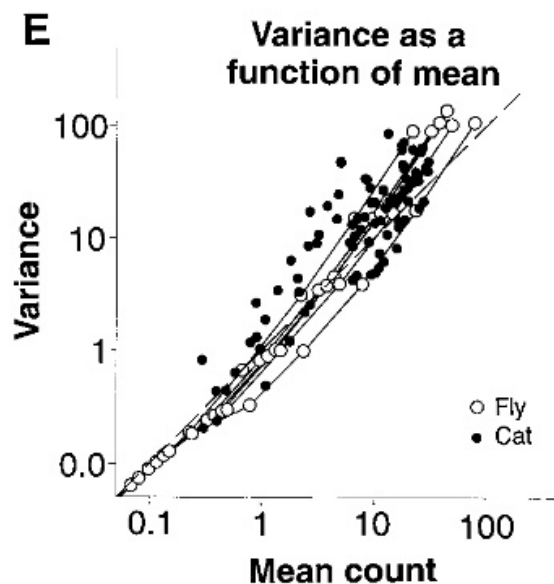
Ruyter van Steveninck et al 1997

Different levels of abstraction

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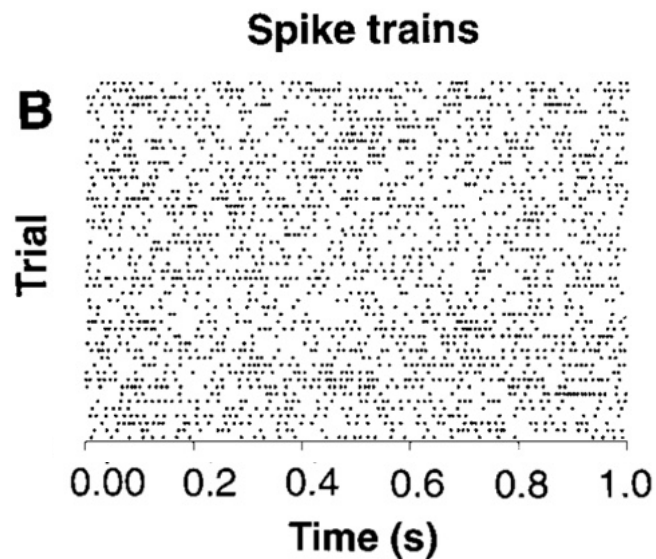
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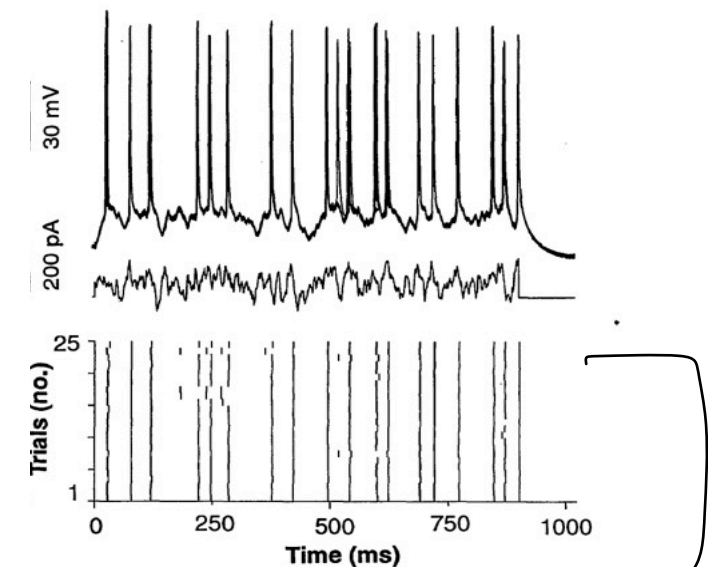
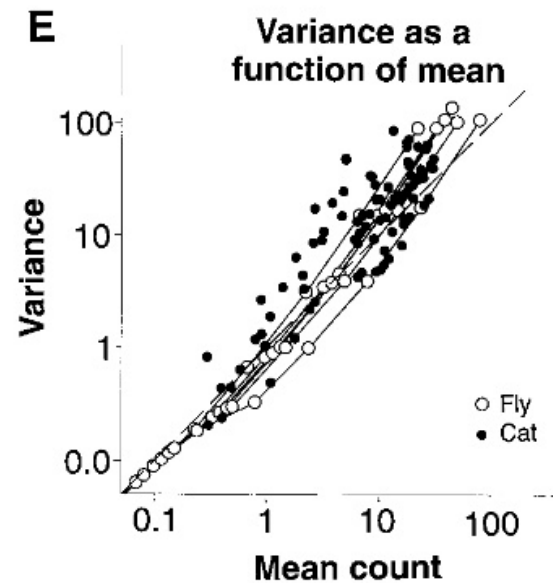
Hubel & Wiesel 1968

Different levels of abstraction

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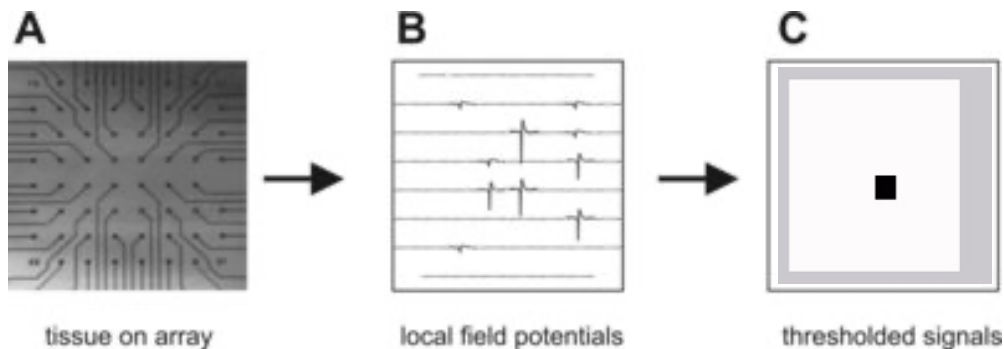
Ruyter van Steveninck et al 1997



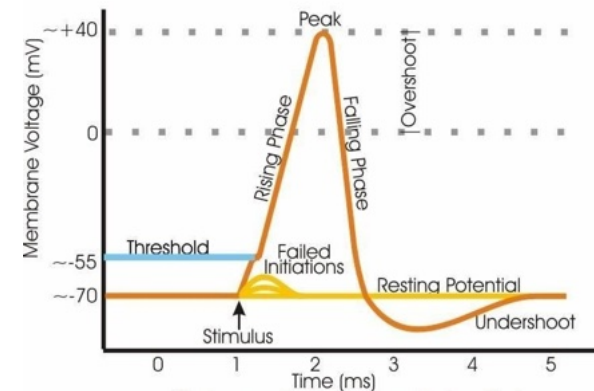
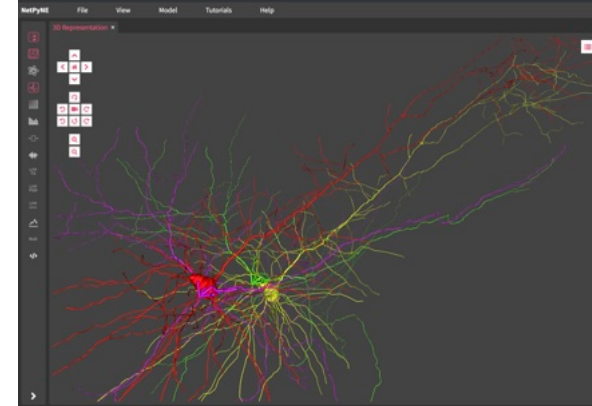
Mainen and Sejnowski 1995

Different levels of abstraction

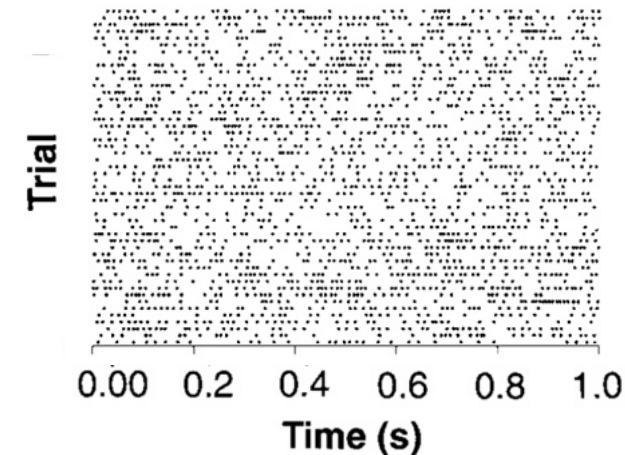
- Model detailed biochemistry and biophysics
- Model individual spikes
- Model binary neurons
- Model firing rate dynamics



$$\frac{\partial s_i}{\partial t} + \frac{s_i}{\tau} = \phi \left[\sum_j W_{ij} s_j + B_i \right]$$

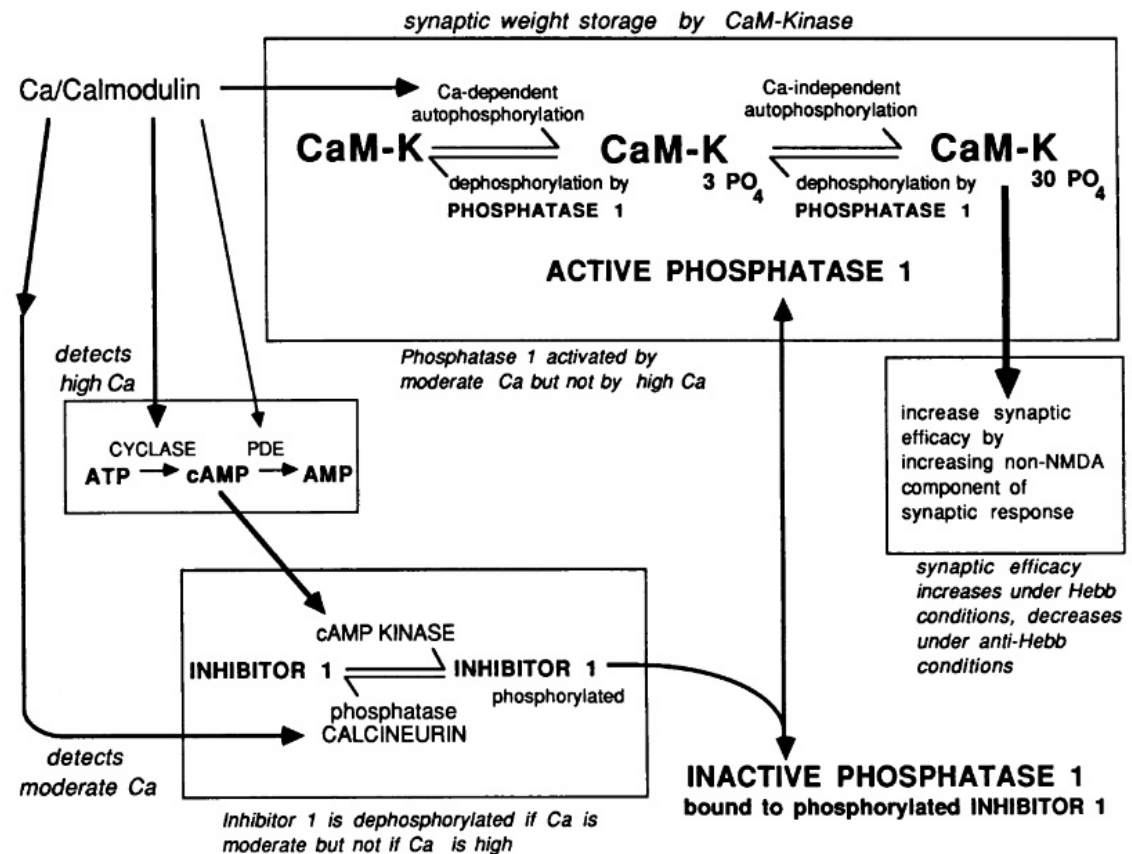
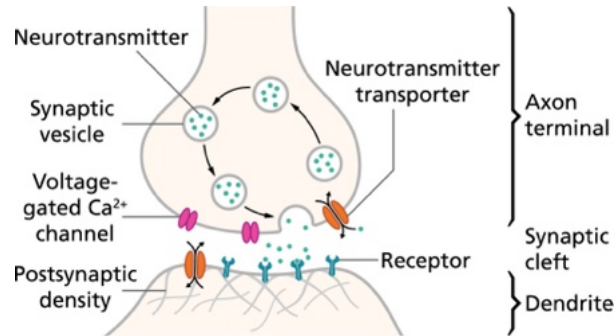


Spike trains



Dynamics of the circuits themselves

Neural plasticity modeled at various levels of abstraction



Proc. Natl. Acad. Sci. USA
Vol. 86, pp. 9574-9578, December 1989
Neurobiology

A mechanism for the Hebb and the anti-Hebb processes underlying learning and memory

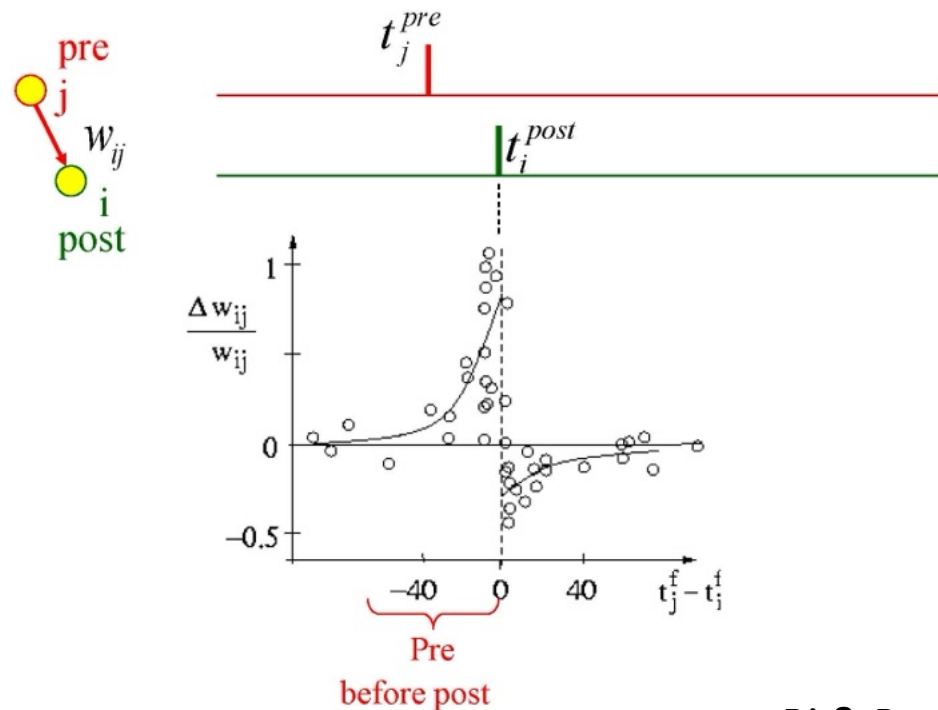
(calmodulin/calcium/calmodulin-dependent protein kinase II/protein phosphatase 1/adenylate cyclase/calcineurin)

JOHN LISMAN

Department of Biology, Brandeis University, Waltham, MA 02254

Dynamics of the circuits themselves

Neural plasticity modeled at various levels of abstraction



The Spike-Timing Dependence of Plasticity

Bi & Poo (1998)

Daniel E. Feldman^{1,*}

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*Correspondence: dfeldman@berkeley.edu

<http://dx.doi.org/10.1016/j.neuron.2012.08.001>

Timescales of plasticity

- STDP ~10 milliseconds
- BTSP ~1-10 seconds
- LTP, LTD ~ 1-1000 minutes
- Neurodevelopment ~ hours to months
- Evolutionary?

Nonlinear dynamical systems

Nonlinear dynamical systems

- Broad goal:
Understand and analyze nonlinear dynamics **without** solving the entire system

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$$\frac{dx}{dt} = \sigma(y - x),$$

$$\frac{dy}{dt} = x(\rho - z) - y,$$

$$\frac{dz}{dt} = xy - \beta z.$$

$$\sigma = 10, \rho = 28, \text{ and } \beta = \frac{8}{3}$$

Nonlinear dynamical systems

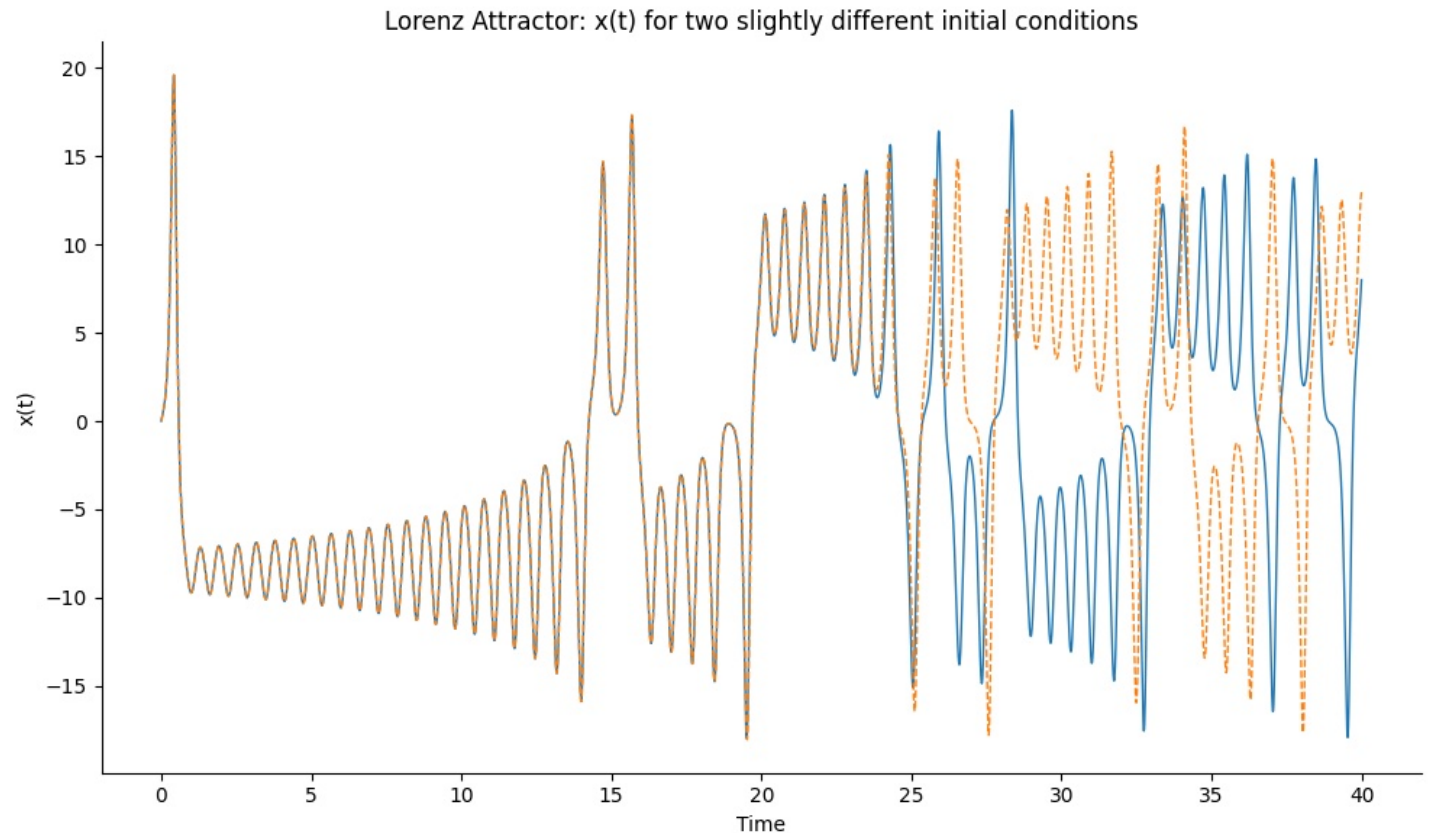
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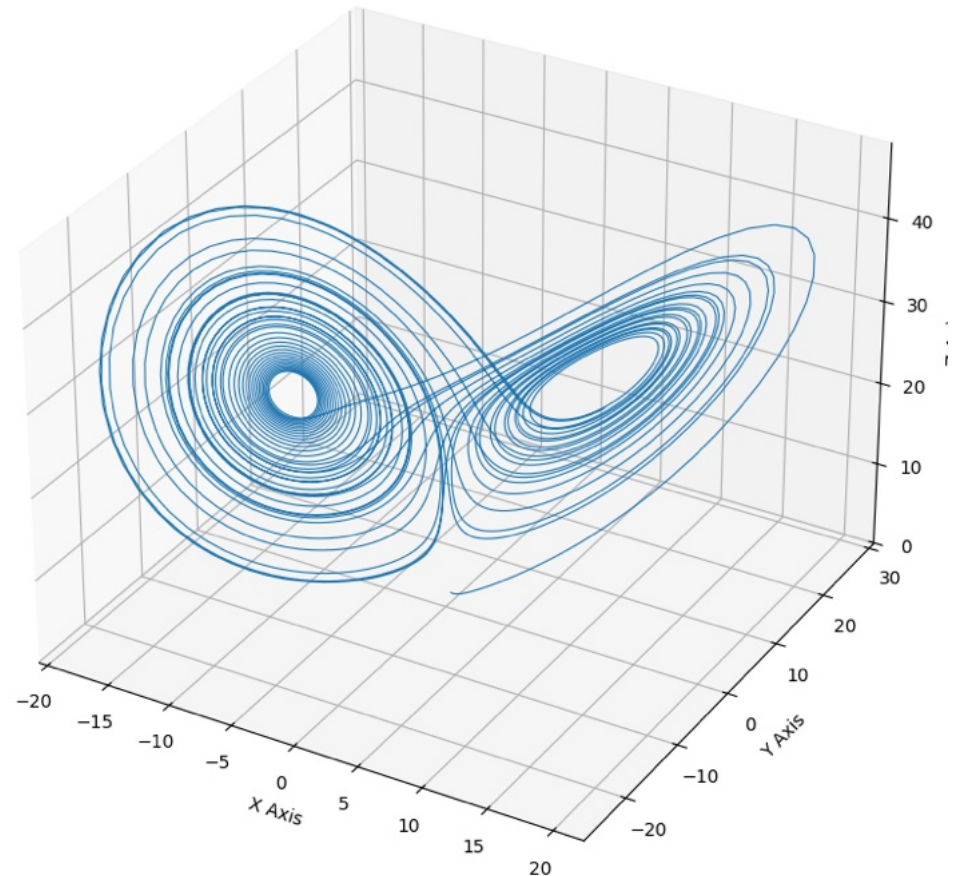
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Lorenz Attractor (3D)



Nonlinear dynamical systems

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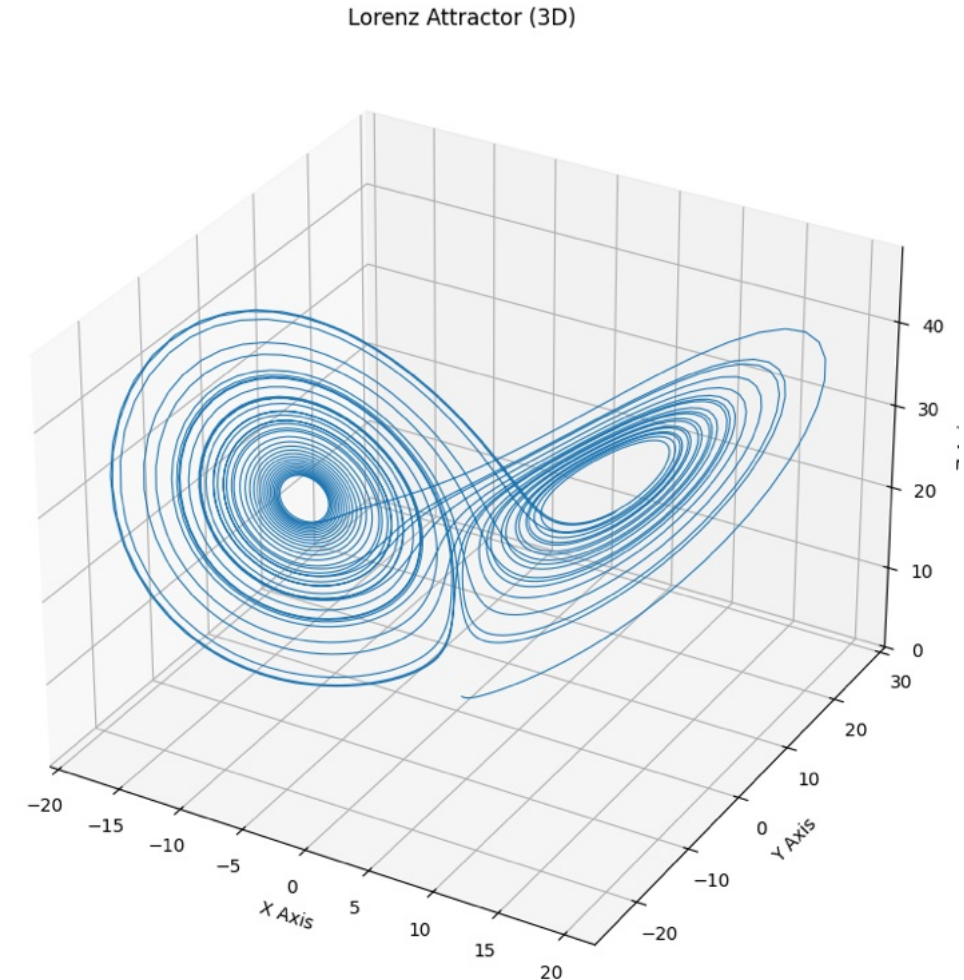
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Edward Lorenz



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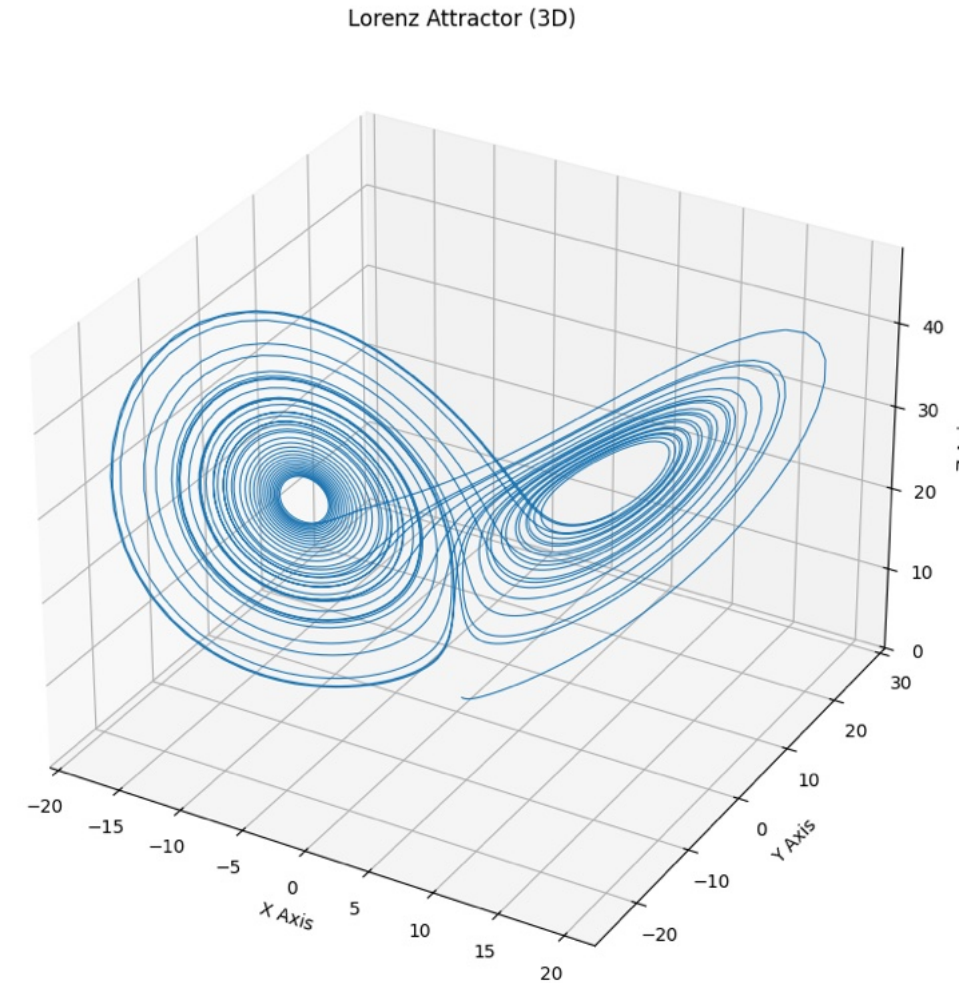
Edward Lorenz



Ellen Fetter



Margaret Hamilton



What is a Dynamical System?

→ $\dot{\bar{x}} = F(\bar{x})$ Autonomous D.S.

$$\begin{cases} \dot{x}_1 = F_1(x_1, \dots, x_n) \\ \dot{x}_2 = F_2(\dots) \\ \vdots \\ \dot{x}_n = F_n(x_1, \dots, x_n) \end{cases}$$

Non-Aut. D.S. → $\dot{\bar{x}} = F(\bar{x}, t)$

$$\mathcal{S} = \begin{pmatrix} \bar{x} \\ t \end{pmatrix} \quad \dot{\mathcal{y}} = \begin{pmatrix} F(\bar{x}) \\ 1 \end{pmatrix}$$

$\dot{t} = 1$

$$\dot{\bar{x}} = A\bar{x}$$

1) Time explicit ←

2) Higher order Deriv. ←

3) Implicit Dyn ←

4) Neural Fields]

5) Discrete systems]

$$\ddot{x} = -x \quad \begin{pmatrix} \dot{x} \\ y \end{pmatrix} = \begin{pmatrix} y \\ -x \end{pmatrix}$$

$y = \dot{x}$

$$\dot{x} = F(x) \leftarrow$$

$$\dot{x} = F(x, t) \quad]$$

F is cts

DF or F' is cts

Implicit

$$F(\dot{x}, x, t) = 0$$

$\dot{\bar{x}} = A \bar{x}$ (non-normal dynamics \leftarrow V.V. Interesting)

$$\bar{x}(t) = c_1 e^{\lambda_1 t} \hat{e}_1 + c_2 e^{\lambda_2 t} \hat{e}_2 + \dots$$

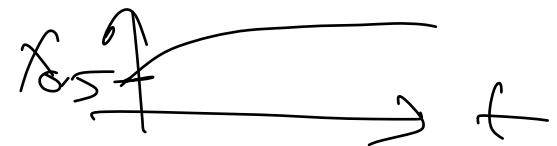
1D Flows

$$x(0) = 0.5$$

$$\dot{x} = F(x) = -x(x-1)(x-2)$$

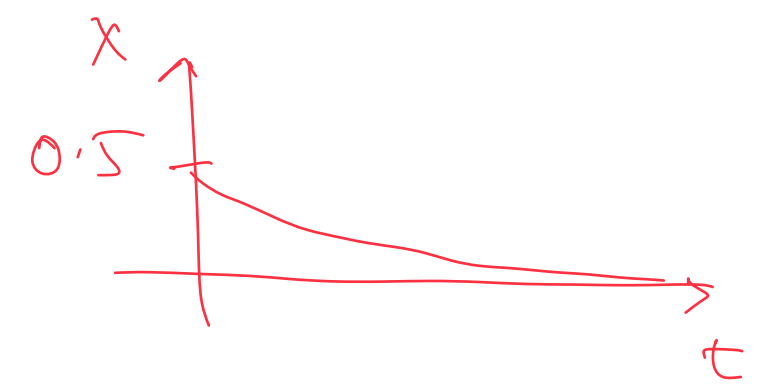
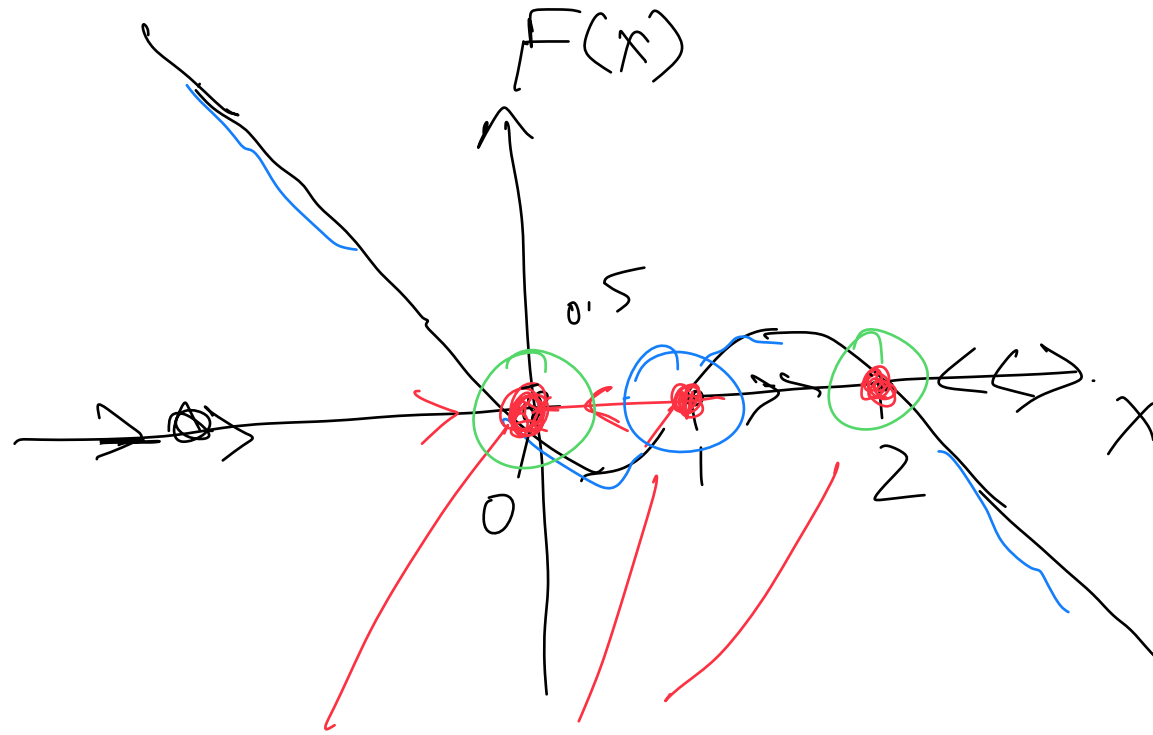
$$\int \frac{dx}{x(x-1)(x-2)} = dt \rightarrow t = -\frac{1}{2} \ln x + \ln(x-1) - \frac{1}{2} \ln(x-2) + C$$

$$x = \underline{\hspace{2cm}}$$



$$\dot{x} = -x(x-1)(x-2) + \boxed{\varepsilon \sin x}$$

$$= F(x)$$



Stable $\rightarrow F' < 0$
 Unstable $\rightarrow F' > 0$

Fixed PT
 $\rightarrow F(x_*) = 0$

$$x = x_* + \varepsilon$$

$$\begin{aligned} \dot{x} &= F(x) \\ x_* + \varepsilon &= F(x_* + \varepsilon) \\ \varepsilon &= F(x_*) + F'(x_*) \cdot \varepsilon \\ \varepsilon &= F'(x_*) \varepsilon \end{aligned}$$

$$\dot{x} = F(x)$$

$$x(0) = x_0$$

Can be multiple
F.P. depending on
init. cond.

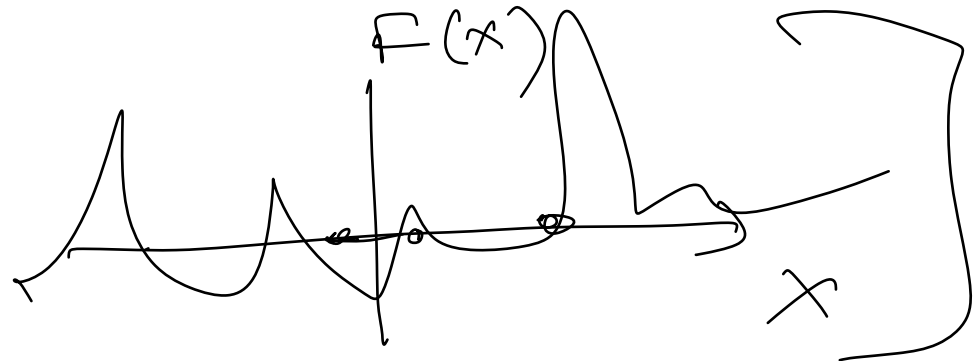
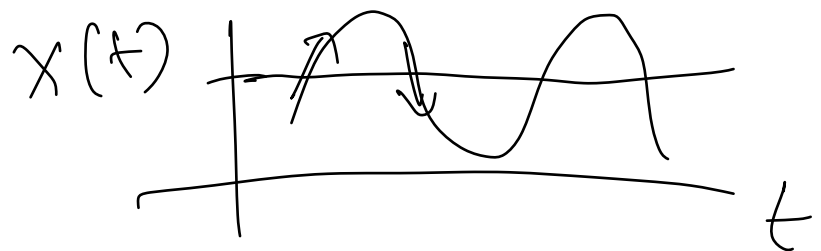
What happens ~~at~~ as $t \rightarrow \infty$

- 1) $x(t) \rightarrow x^*$
- 2) $x(t) \rightarrow \infty$

(goes to a F.P.)

or $x(t) \rightarrow -\infty$

~~Periodic $x(t+T) = x(t)$~~

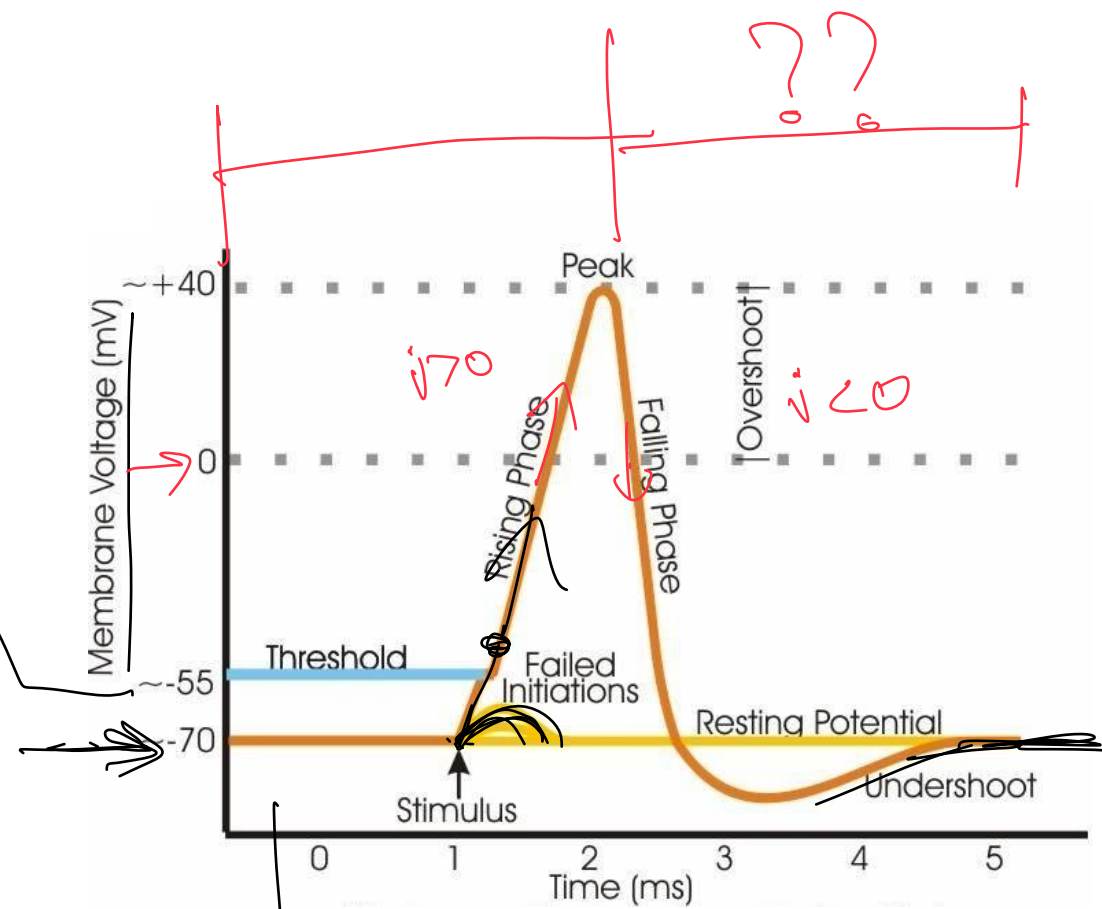


1 D Flow

↳ cannot have periodicity

Unstable F.P.

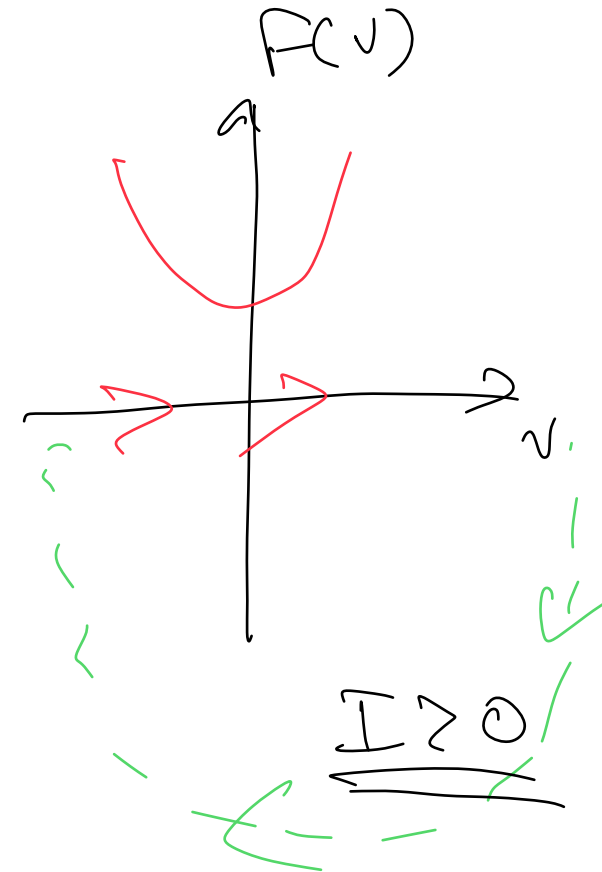
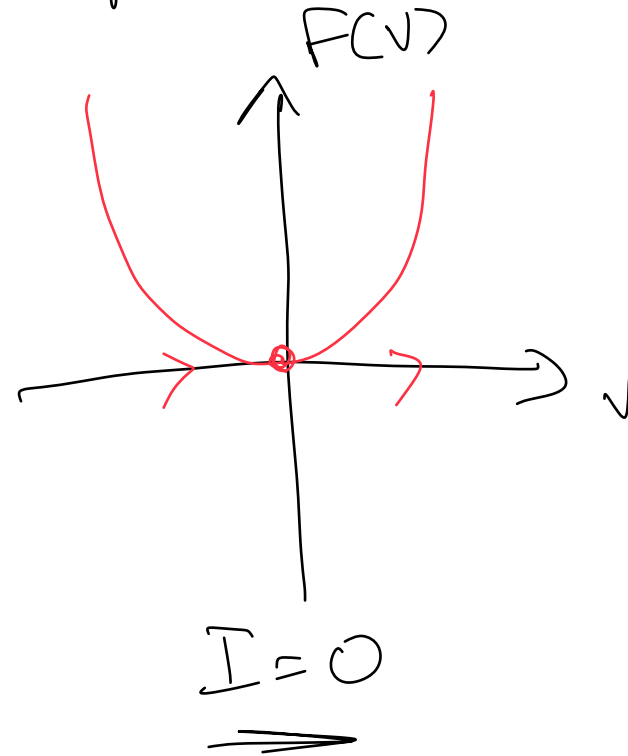
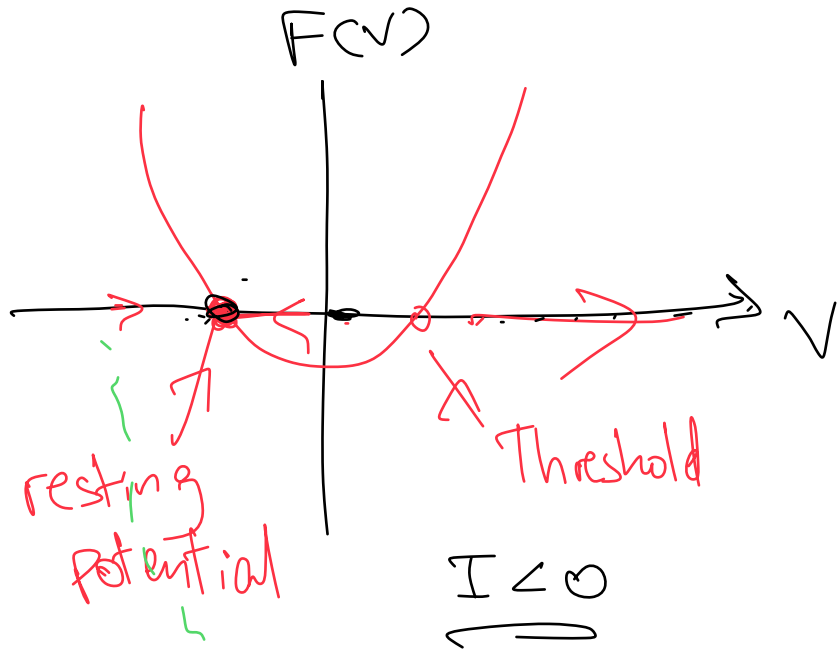
Stable Fixed Pt



Quadratic Integrate and Fire Neuron

GKND § 5.3; lz. § 3.3.8

$$\dot{V} = F(V) = V^2 + \frac{I}{\tau} \rightarrow \text{Inputs}$$



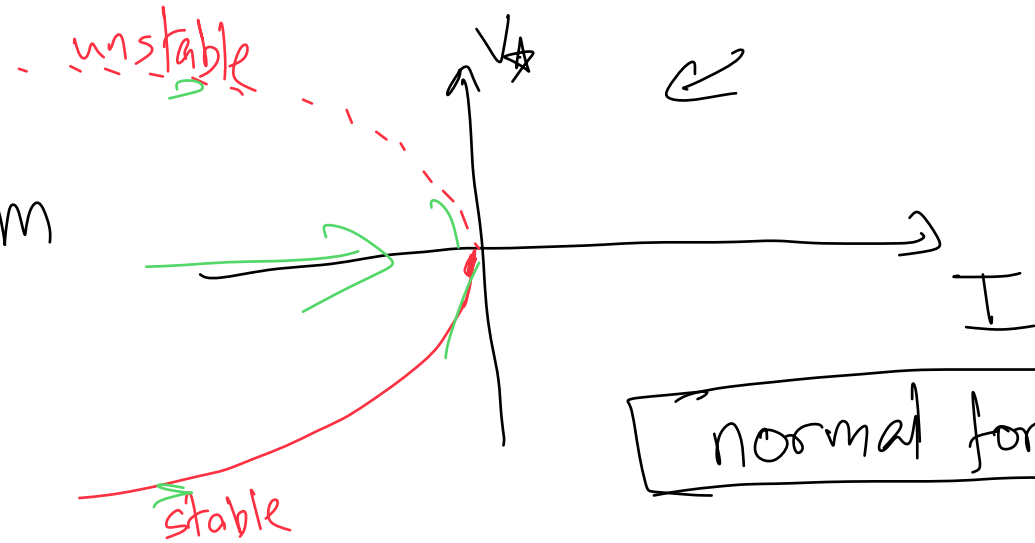
F.P. $\rightarrow V_* = \pm \sqrt{-I}$

Kind of like an extra dim

No. F.P

EIF

Bifurcatⁿ Diagram



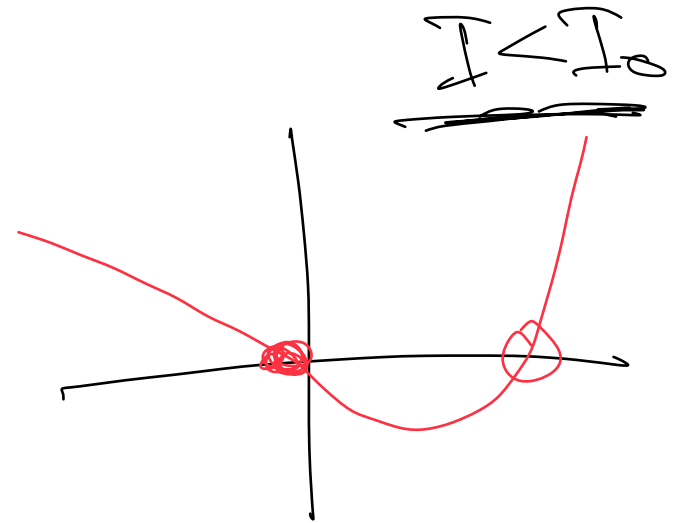
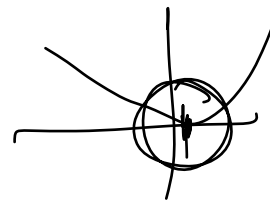
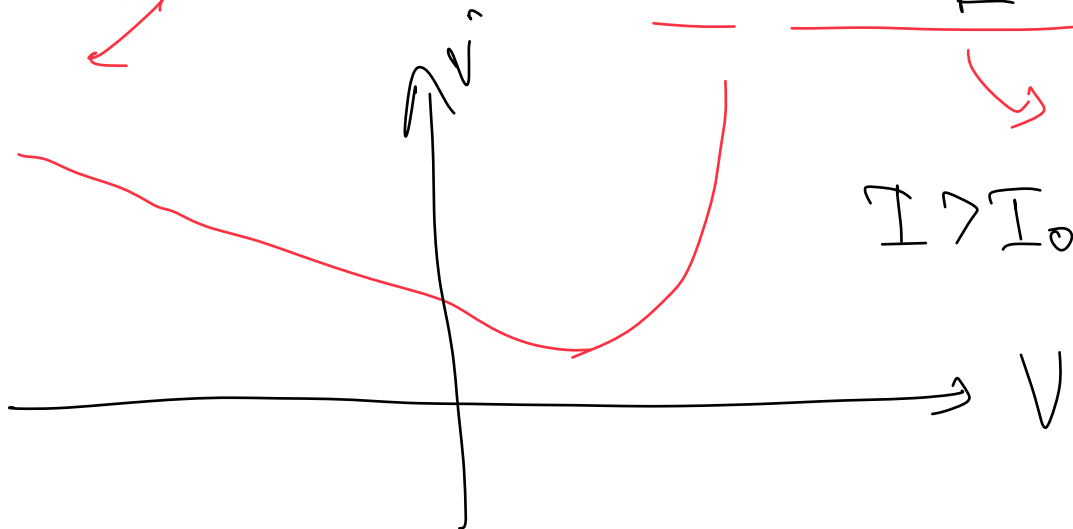
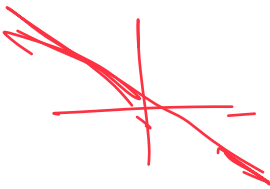
$$\dot{v} = v^2 + I$$

"Saddle Node Bifurcatⁿ"

normal form of an S.N. Bif.

Exponential Int. & Fire Neuron (EIF) GKND § 5.2

$$\dot{v} = -\underbrace{(v - v_0)} + R \exp\left(\frac{v - v_0}{R}\right) + \underbrace{I}$$



~~$\dot{\theta} = F(\theta)$~~

$$\dot{\theta} = F(\theta)$$

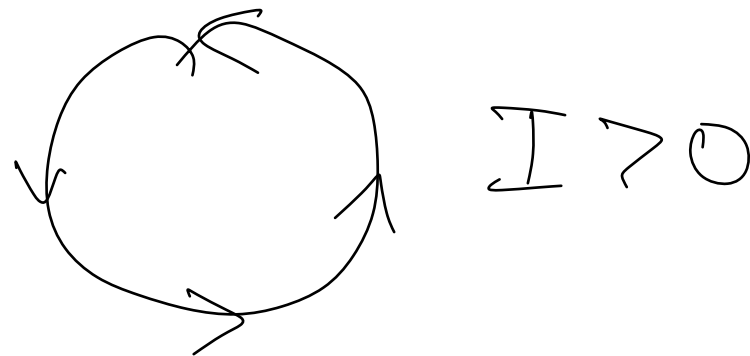
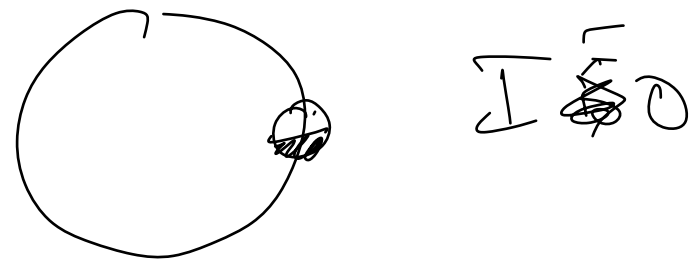
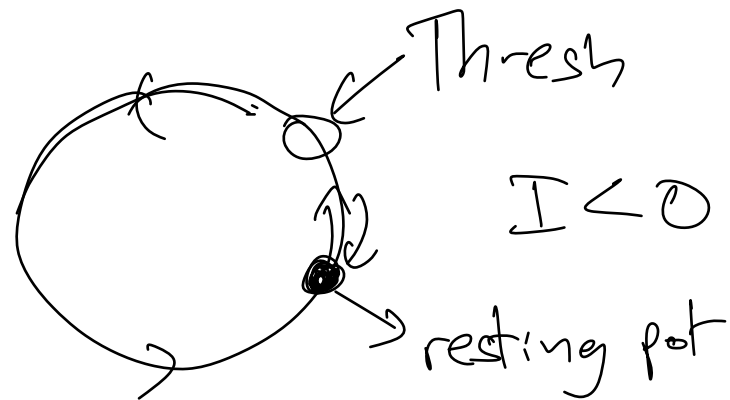
Theta Neuron Model

$$\dot{\theta} = 1 - \cos\theta + (1 + \cos\theta)I$$

12. ~~§~~ 3.38

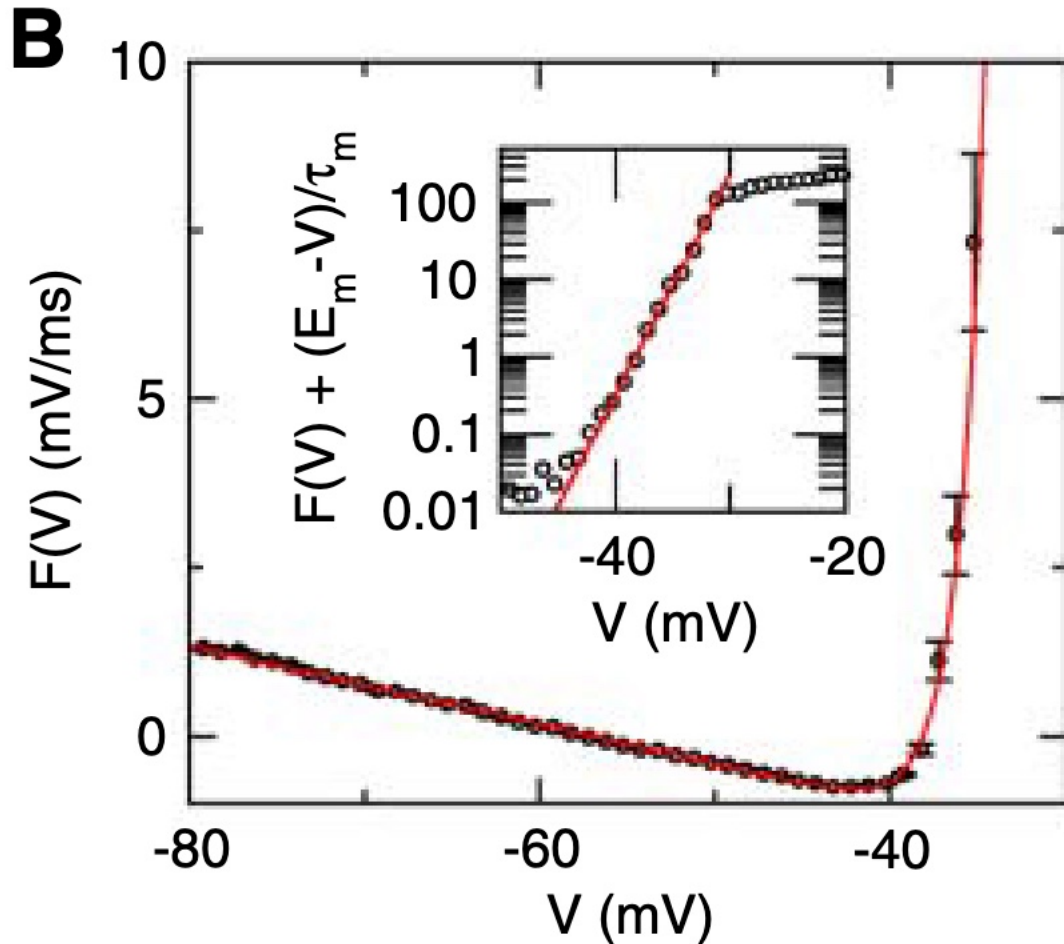
Saddle
Node Bif
on an
Invariant
Cycle
(SNIC)

\mathbb{R}^2
 \mathbb{S}^1

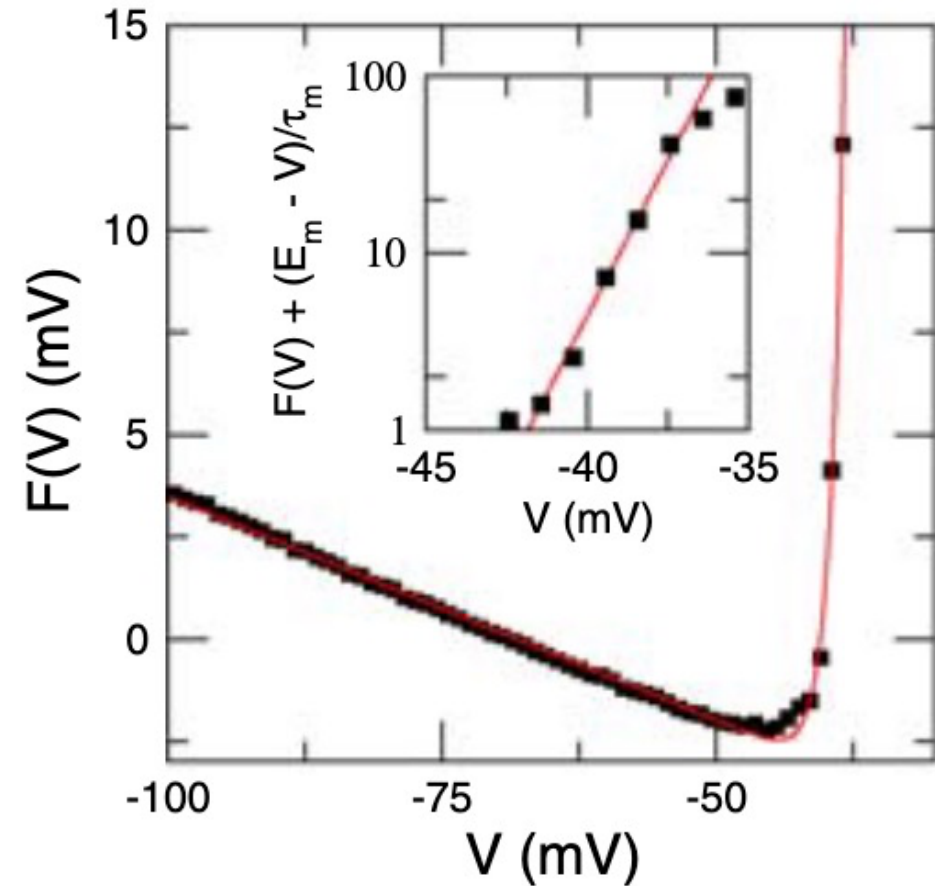


Exponential Integrate and Fire neuron

[Badel et al. Biol Cybern \(2008\)](#)



Pyramidal cell



Interneuron

Transcritical Bifurcation

Avalanche Dyn

$a \rightarrow$ fraction of active neurons

$a \in [0, 1] \rightarrow a=0$ is an absorbing boundary condition

$a=0$ is a F.P. \leftarrow unstable

$\dot{a} = -a + \lambda a(1-a)$ growth \propto active frac
 \propto available frac

$$\frac{da}{dt} = a(\lambda-1) - \lambda a^2$$

$$\tau = \lambda t$$

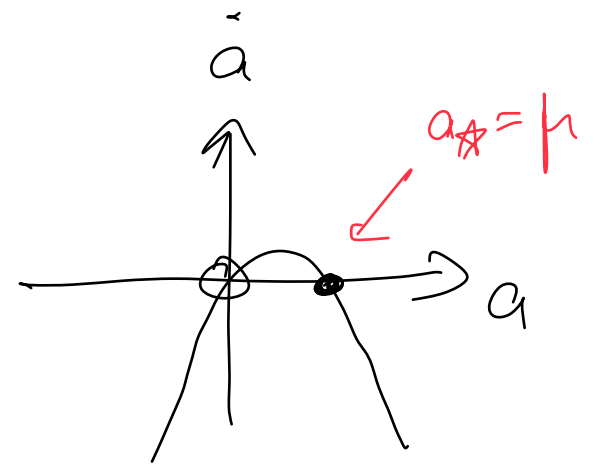
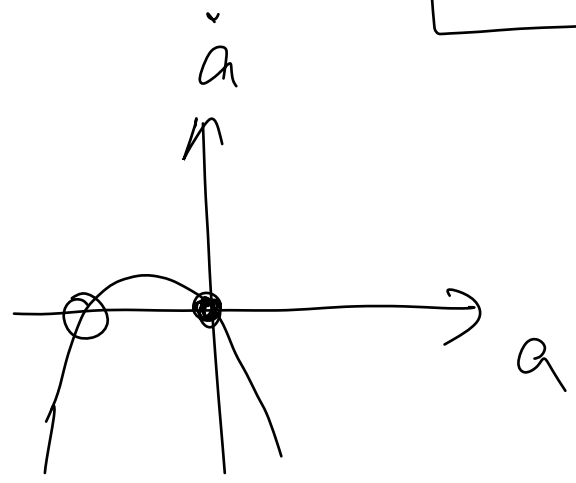
$$\frac{da}{\lambda dt} = a \left(\frac{\lambda-1}{\lambda} \right) - a^2$$

$$\dot{a} = a \left(\frac{\lambda-1}{\lambda} \right) - a^2$$

$$\dot{a} = a \underbrace{\begin{pmatrix} \lambda - 1 \\ \lambda \end{pmatrix}}_{\mu} - a^2$$

$$\dot{a} = \underbrace{\mu}_{\uparrow} a - a^2$$

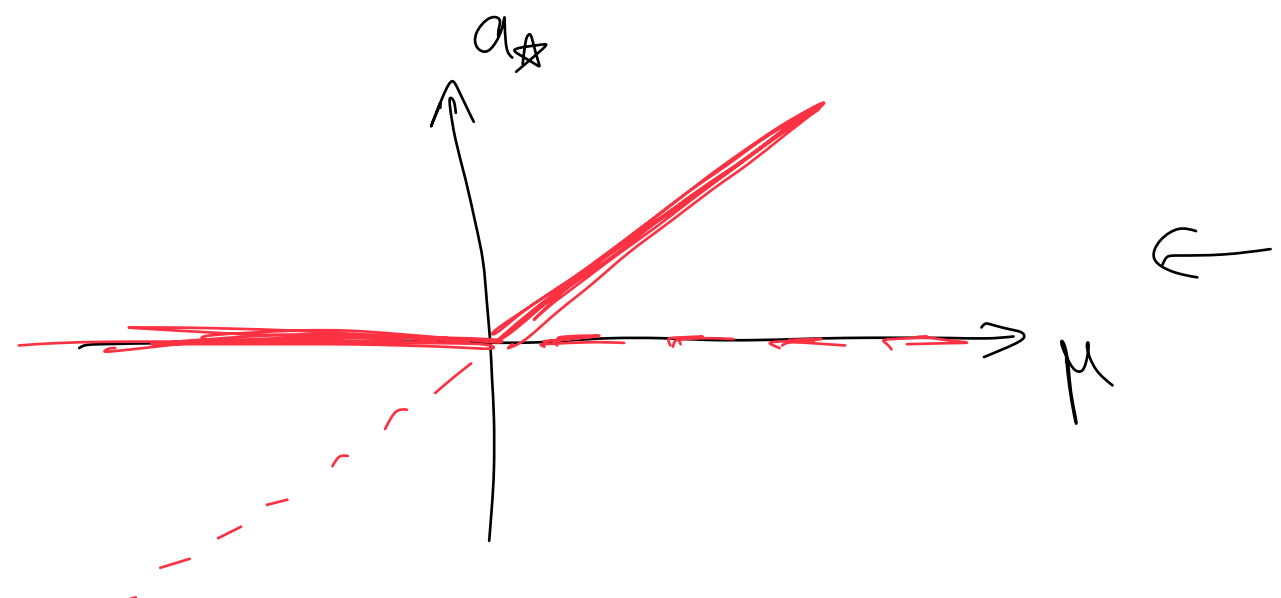
$$\lambda \approx 1 + \mu$$



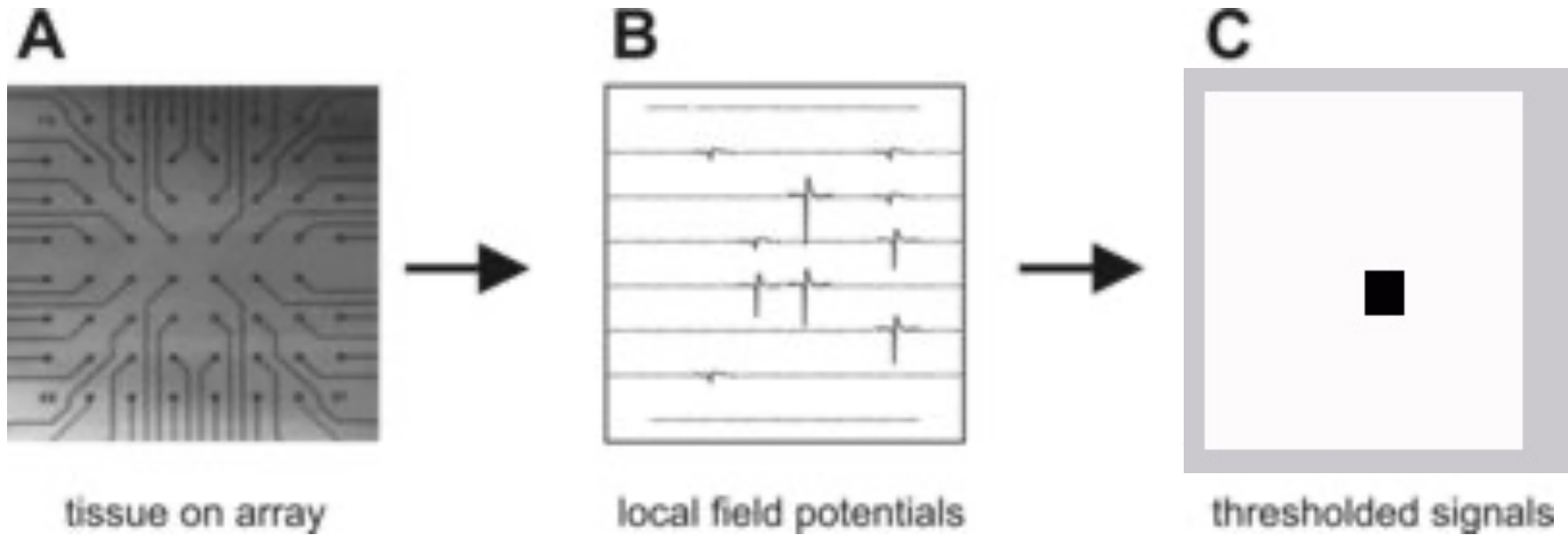
Transcritical Bifurcation

$\mu < 0$

$\mu > 0$



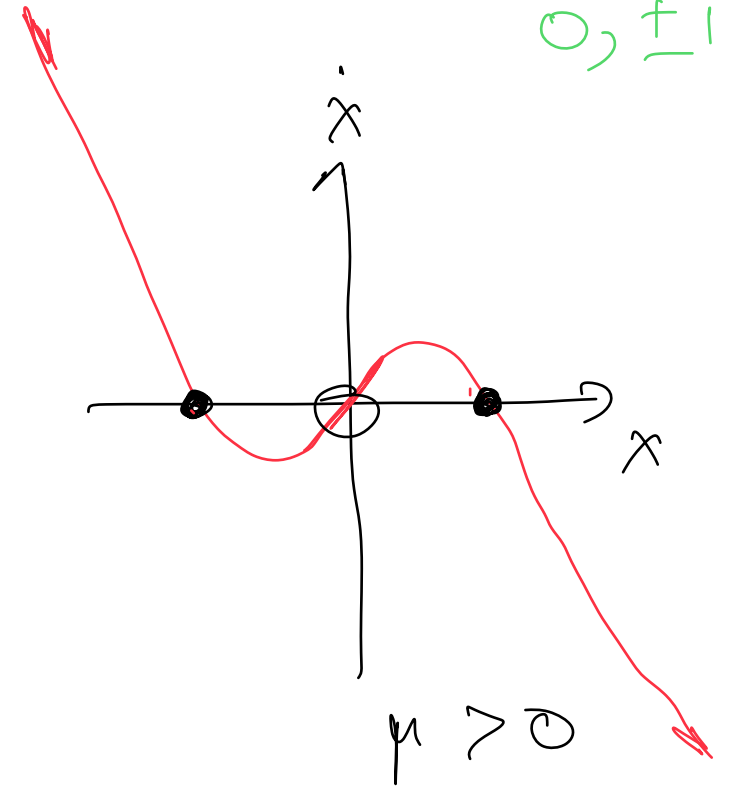
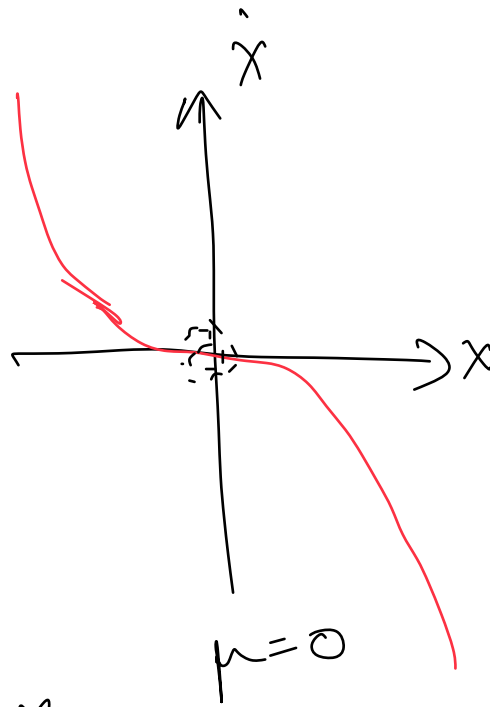
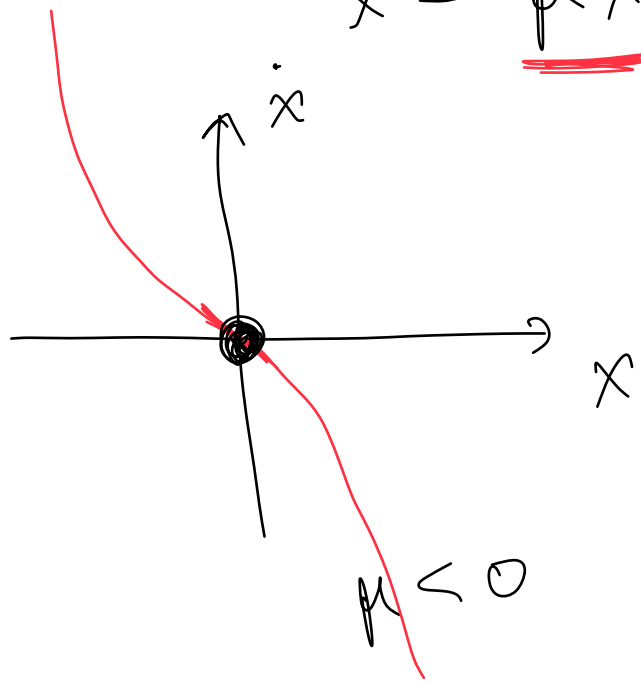
Avalanche Dynamics



J. Beggs (2007)

Pitchfork Bifurcation

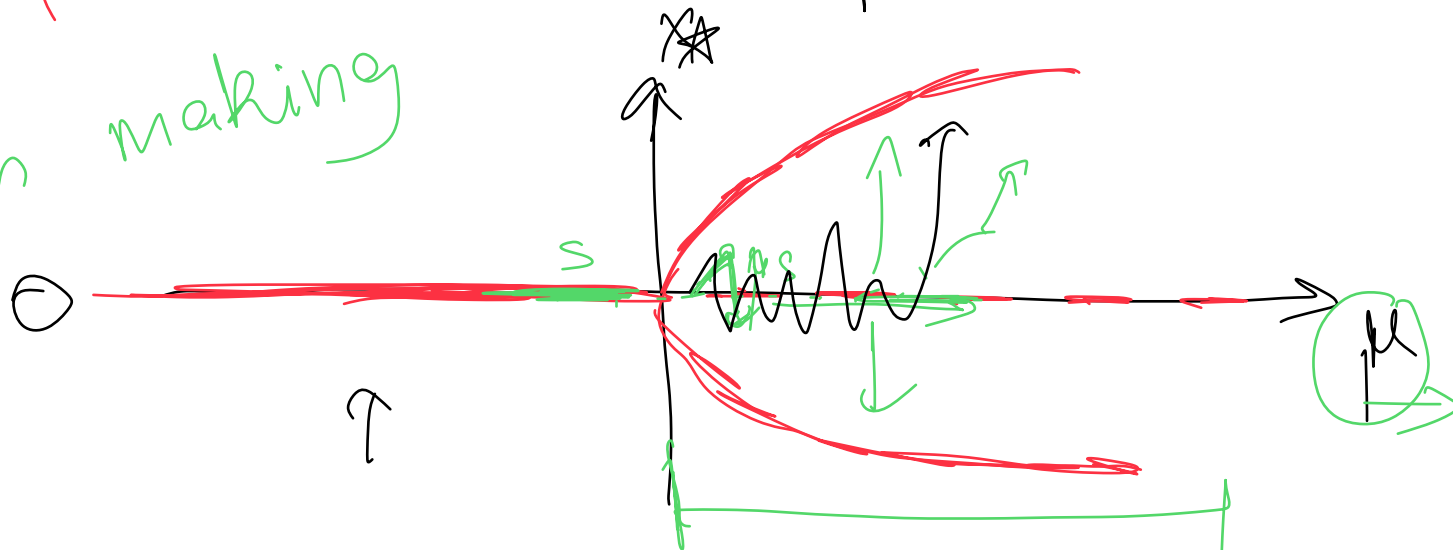
$$\dot{x} = \mu x - x^3$$

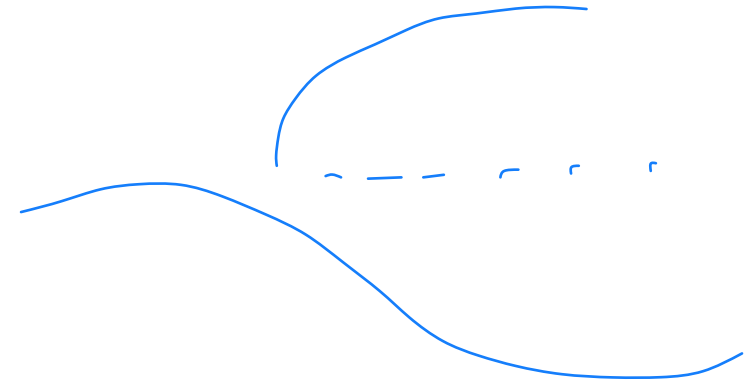
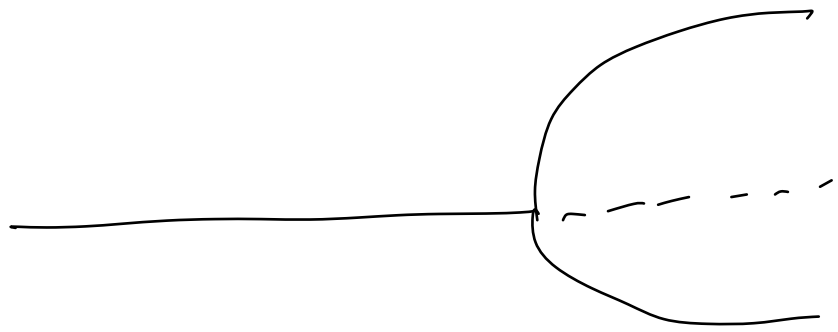


$$\mu x - x^3$$

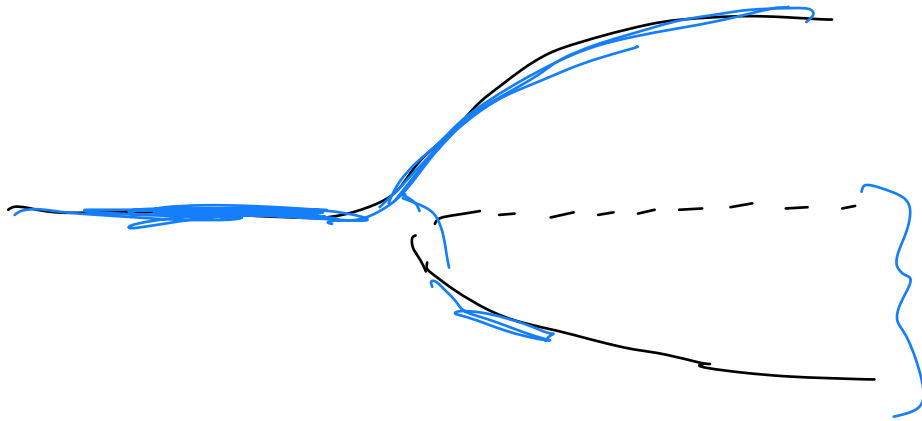
$$+x - \frac{x^3}{0, \pm 1}$$

2-choice decision making



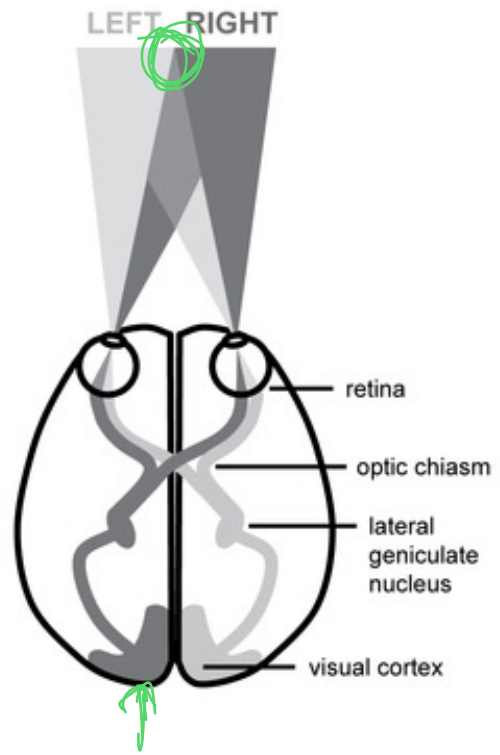


$$\dot{x} = \mu x - x^3 + \underbrace{f(x)}$$

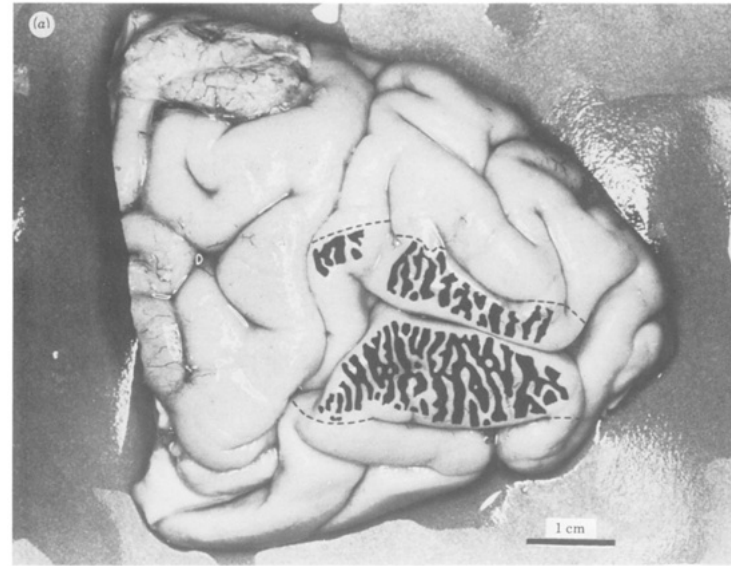
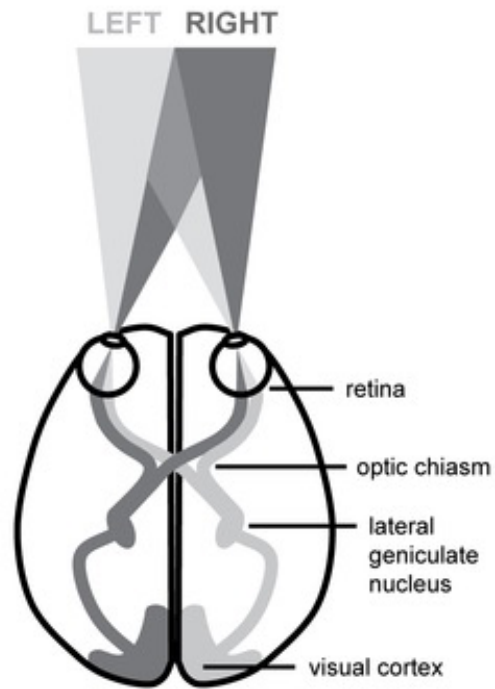


} S.N. Bif.

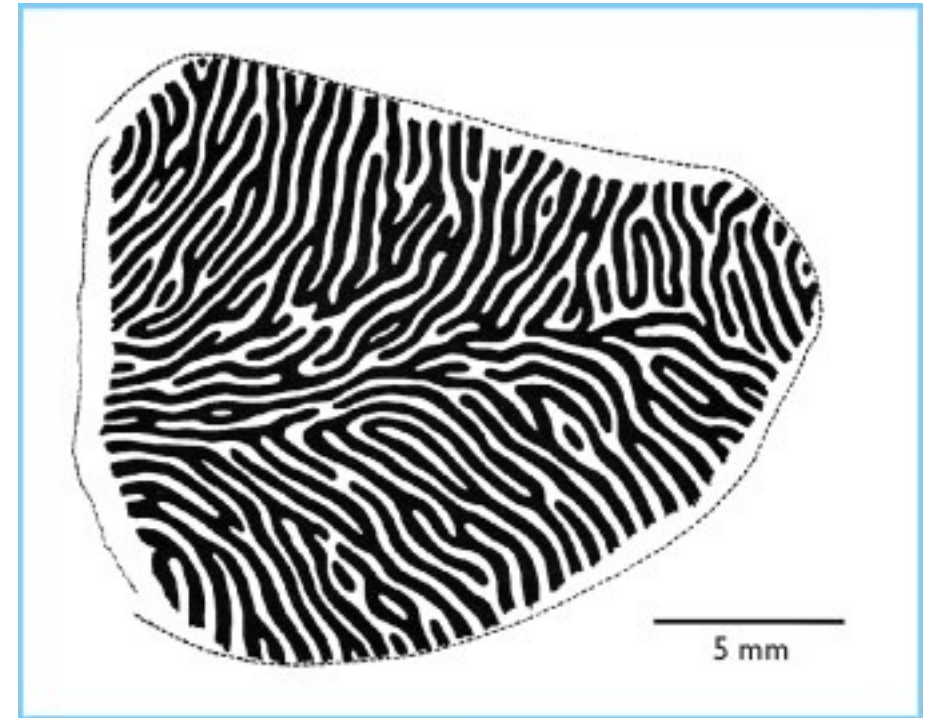
Ocular dominance columns



Ocular dominance columns

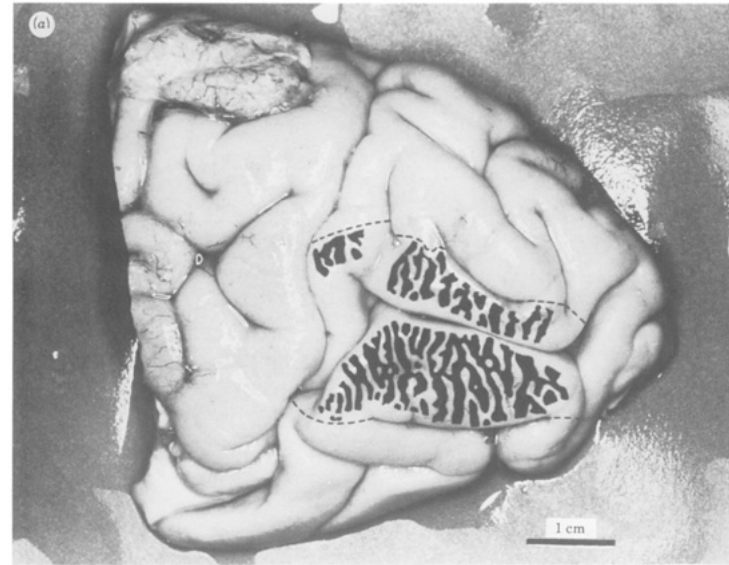
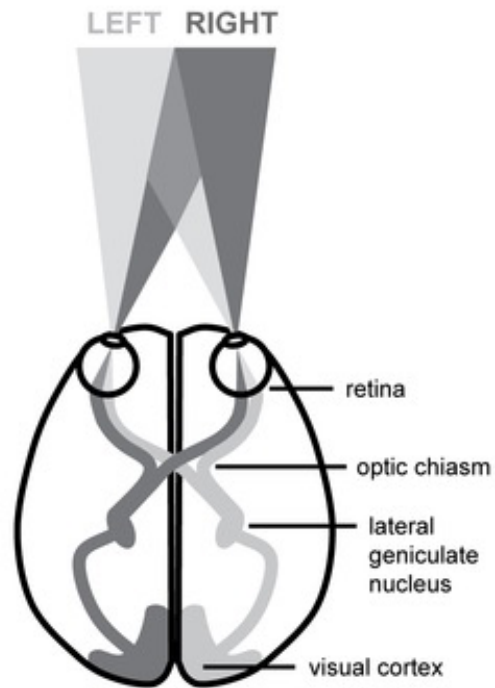


[Horton & Hedley-Whyte \(1984\)](#)

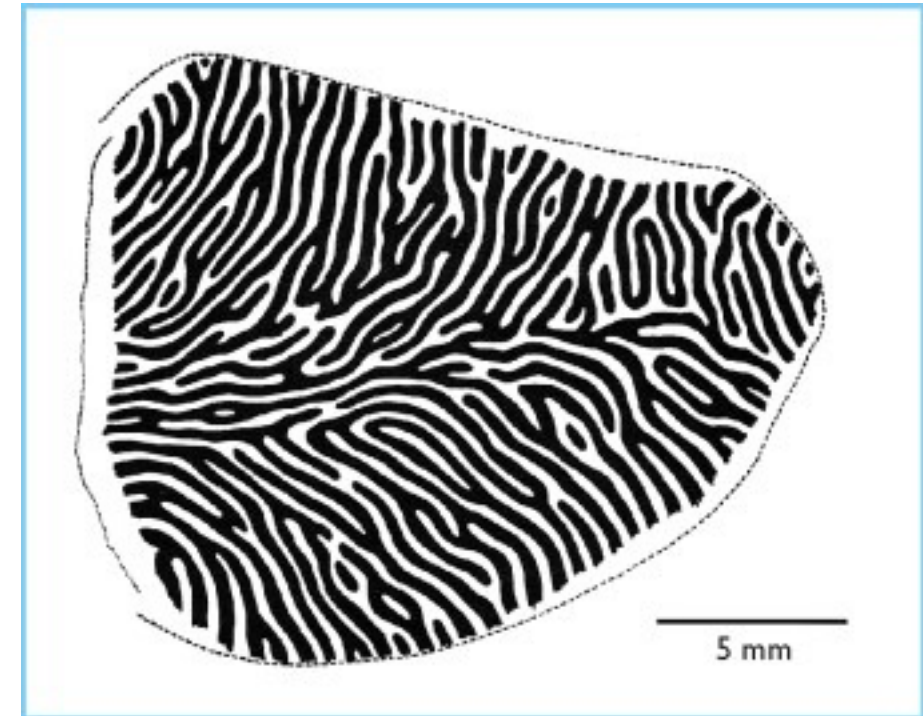


[Hubel & Wiesel 1977](#)

Ocular dominance columns



[Horton & Hedley-Whyte \(1984\)](#)



[Hubel & Wiesel 1977](#)

Proc. Natl. Acad. Sci. USA
Vol. 94, pp. 9944–9949, September 1997
Neurobiology



A model of ocular dominance column development by competition for trophic factor

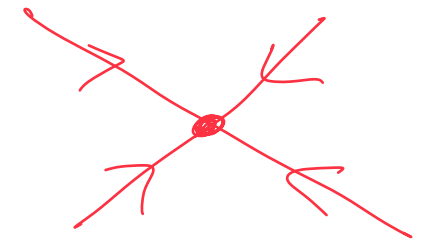
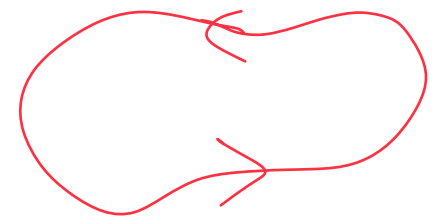
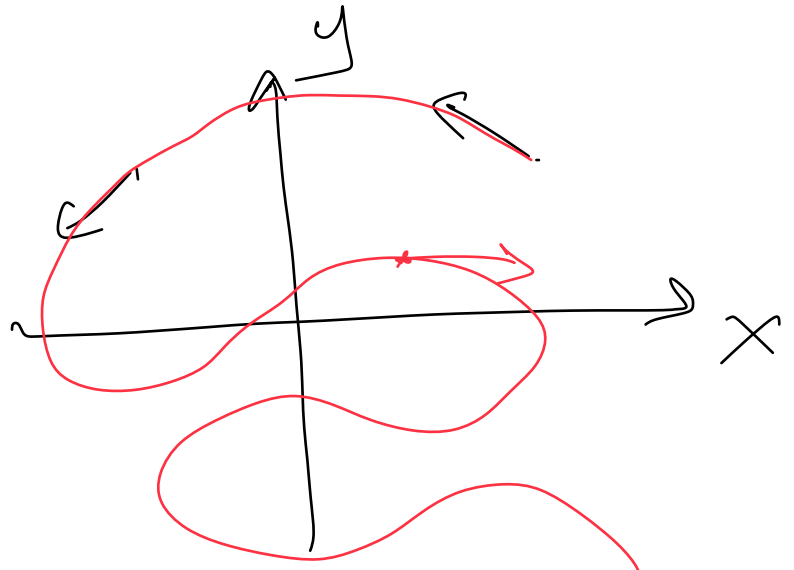
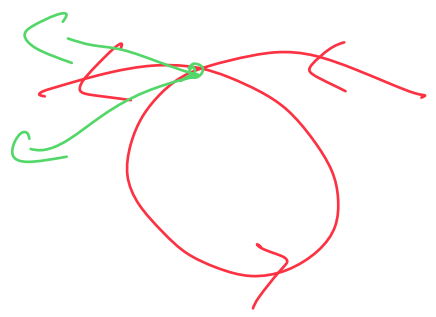
ANTHONY E. HARRIS^{*†‡§}, G. BARD ERMENTROUT^{†¶}, AND STEVEN L. SMALL^{*†‡}

^{*}Intelligent Systems Program, [†]Center for the Neural Basis of Cognition, and Departments of [‡]Neurology and [§]Mathematics and Statistics, University of Pittsburgh, Pittsburgh, PA 15261

2D Flows

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} F_1(x, y) \\ F_2(x, y) \end{pmatrix}$$

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



- Go to infinity
- Go to a F.P.
- Go to a periodic Orbit

→ Poincare-Bendixson Theorem ←

$$\begin{cases} \dot{x} \\ \dot{y} \end{cases} = F(x, y)$$

$$x = 0, y = 0 \Rightarrow F(x^*, y^*) = 0$$

Jacobien

$$x = x^* + \xi$$

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} =$$

$$\begin{pmatrix} \frac{\partial F_1}{\partial x} & \frac{\partial F_1}{\partial y} \\ \frac{\partial F_2}{\partial x} & \frac{\partial F_2}{\partial y} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

eigen values

$$\lambda_1, \lambda_2 \rightarrow$$

$$\text{stable F.P.} \iff \begin{cases} \operatorname{Re}[\lambda_1] < 0 \\ \operatorname{Re}[\lambda_2] < 0 \end{cases}$$

unstable \rightarrow all other cases

$$F(x^*, y^*) = 0$$

$$\begin{cases} F' > 0 & \text{unstable} \\ F' < 0 & \text{stable} \end{cases}$$

$$x = x^* + \xi$$

$$\dot{\xi} = F' \cdot \xi$$

$$J = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

$$\text{Tr}[J] = T$$

$$\text{Det}[J] = \Delta$$

$$\det[\lambda \mathbb{1} - J] = 0$$

$$\det \begin{bmatrix} \lambda - a & b \\ c & \lambda - d \end{bmatrix} = 0$$

$$\lambda^2 - (a+d)\lambda + (ad-bc) = 0$$

$$\lambda^2 - \text{Tr}[J]\lambda + \text{Det}[J] = 0$$

$$\lambda^2 - T\lambda + \Delta = 0$$

↳

$$\lambda = \frac{T \pm \sqrt{T^2 - 4\Delta}}{2}$$

Elements of Applied Bifurcation Theory

25/5/26

- Textbook

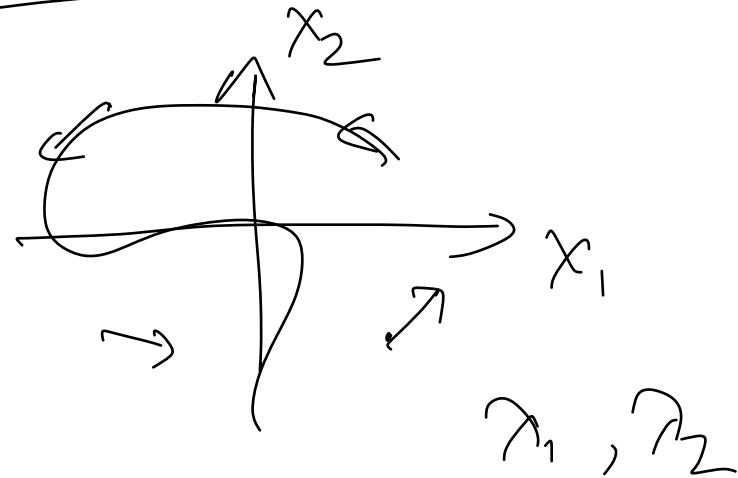
Kuznetsov

2D FLOWS

$$\dot{\bar{x}} = \bar{F}(\bar{x})$$

$$\bar{x}_* \rightarrow \bar{F}(\bar{x}_*) = 0$$

$$\bar{x} = \bar{x}_* + \begin{pmatrix} x \\ y \end{pmatrix}$$



$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} =$$

$$\begin{pmatrix} \partial F_1 / \partial x & \partial F_1 / \partial y \\ \partial F_2 / \partial x & \partial F_2 / \partial y \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

$$\lambda^2 - \lambda T + \Delta = 0$$

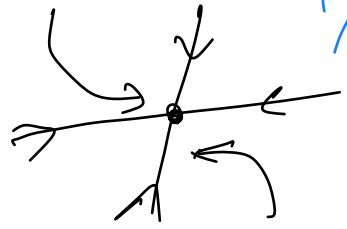
$$\lambda^2 - \lambda T + \Delta = 0$$

$$\lambda = \frac{T \pm \sqrt{T^2 - 4\Delta}}{2}$$

stable focus/spiral

λ_1, λ_2

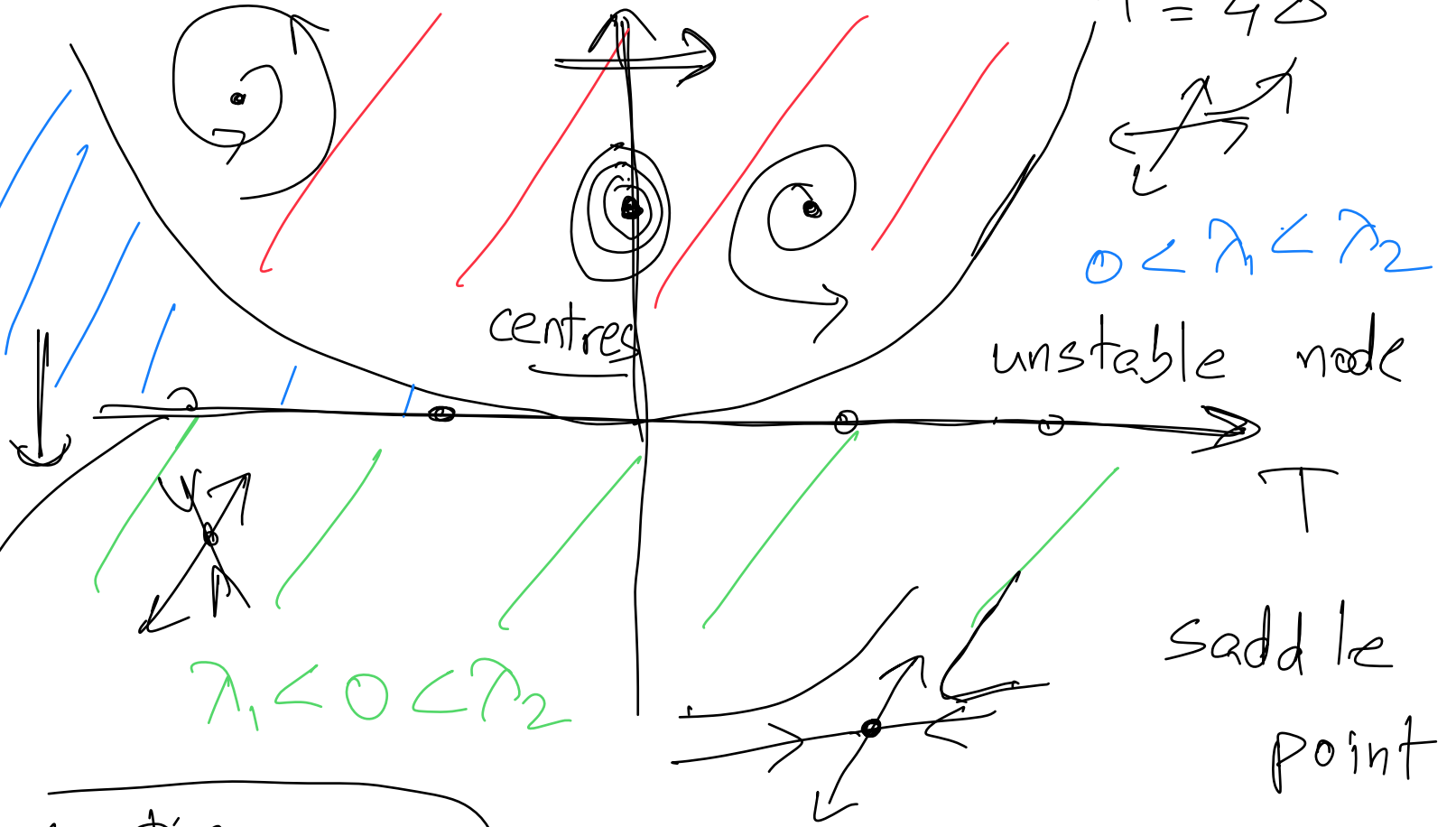
unstable focus/spiral



stable

node

$$\lambda_1 < \lambda_2 < 0$$



$$T^2 = 4\Delta$$

$$0 < \lambda_1 < \lambda_2$$

unstable node

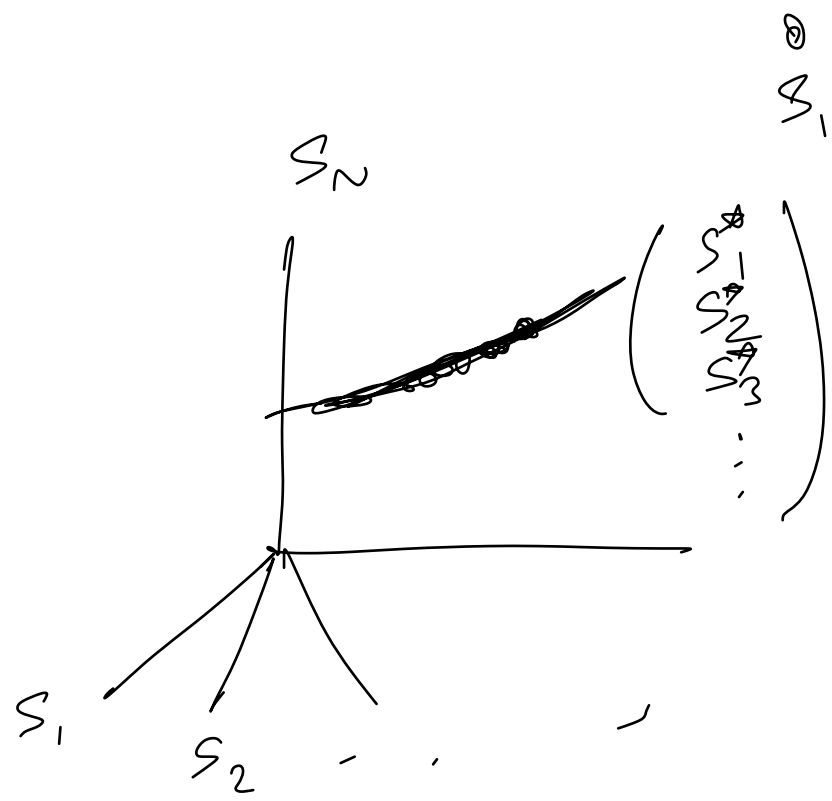
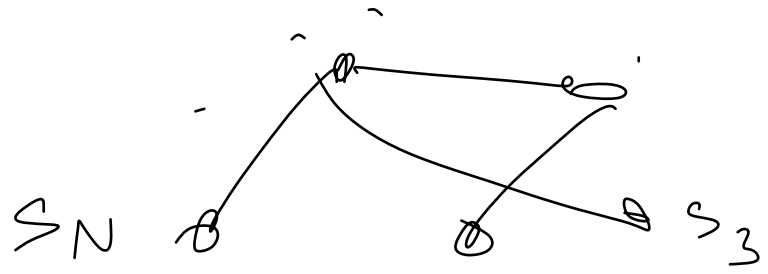
saddle point

centres

$$\lambda_1 < 0 < \lambda_2$$

Continuous Attractor

non-isolated F.P.



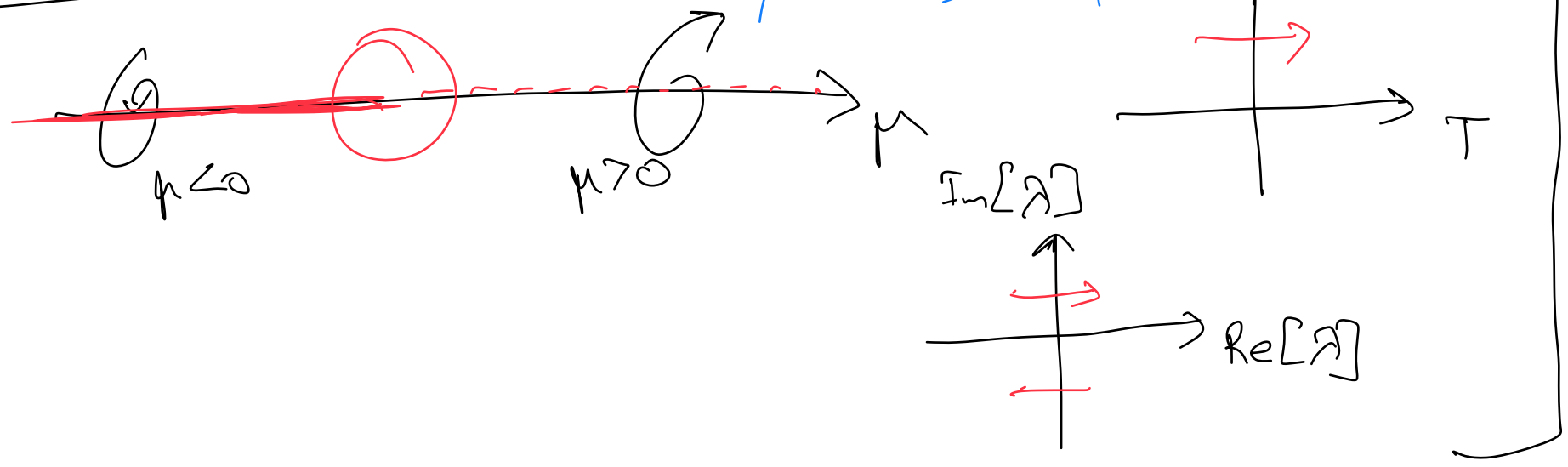
cts. attr

repr.

cts variable

Hopf Bifurcation

Strogatz § 8.2 / Iz. § 6.14

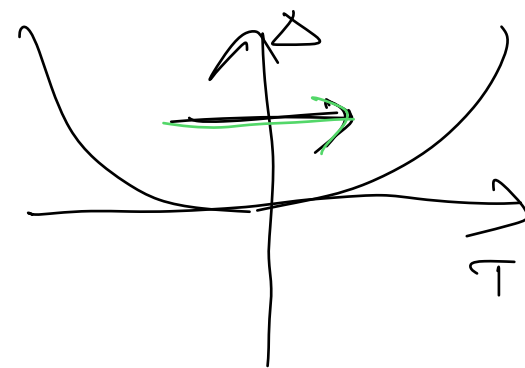


Normal form

$$\begin{cases} \dot{x} = \underline{\mu} x + \omega y + (ax - by)(x^2 + y^2) \\ \dot{y} = \underline{-\omega x + \mu y} + (bx + ay)(x^2 + y^2) \end{cases} \quad \mu, \omega, a, b \in \mathbb{R}$$

$(x, y) = (0, 0)$ is a F.P. $J = \begin{pmatrix} \frac{\partial F_1}{\partial x} & \frac{\partial F_1}{\partial y} \\ \frac{\partial F_2}{\partial x} & \frac{\partial F_2}{\partial y} \end{pmatrix} \Big|_{(0,0)} = \begin{pmatrix} \mu & \omega \\ -\omega & \mu \end{pmatrix}$

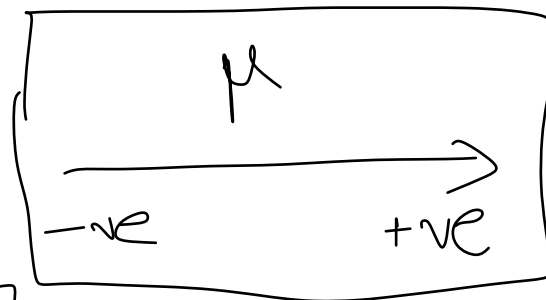
$$J|_{(0,0)} = \begin{pmatrix} \mu & \omega \\ -\omega & \mu \end{pmatrix} \rightarrow \begin{aligned} T &= 2\mu \\ \Delta &= \mu^2 + \omega^2 \end{aligned}$$



$$\lambda_{1,2} = \frac{T \pm \sqrt{T^2 - 4\Delta}}{2}$$

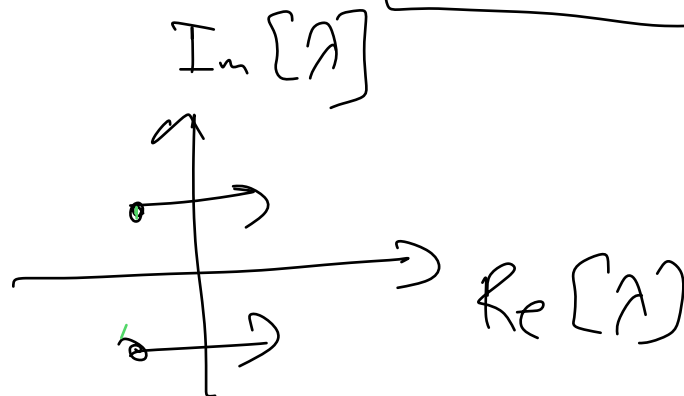
$$\Delta > 0$$

$$= \frac{2\mu \pm \sqrt{4\mu^2 - 4\mu^2 - 4\omega^2}}{2}$$



$$= \mu \pm \sqrt{-\omega^2}$$

$$= \mu \pm i\omega$$



$$(x, y) \rightarrow (r, \theta)$$

$$r^2 = x^2 + y^2$$

$$2r\dot{r} = 2x\dot{x} + 2y\dot{y}$$

$$\dot{r} = \frac{x\dot{x} + y\dot{y}}{r} = \mu r + a r^3$$

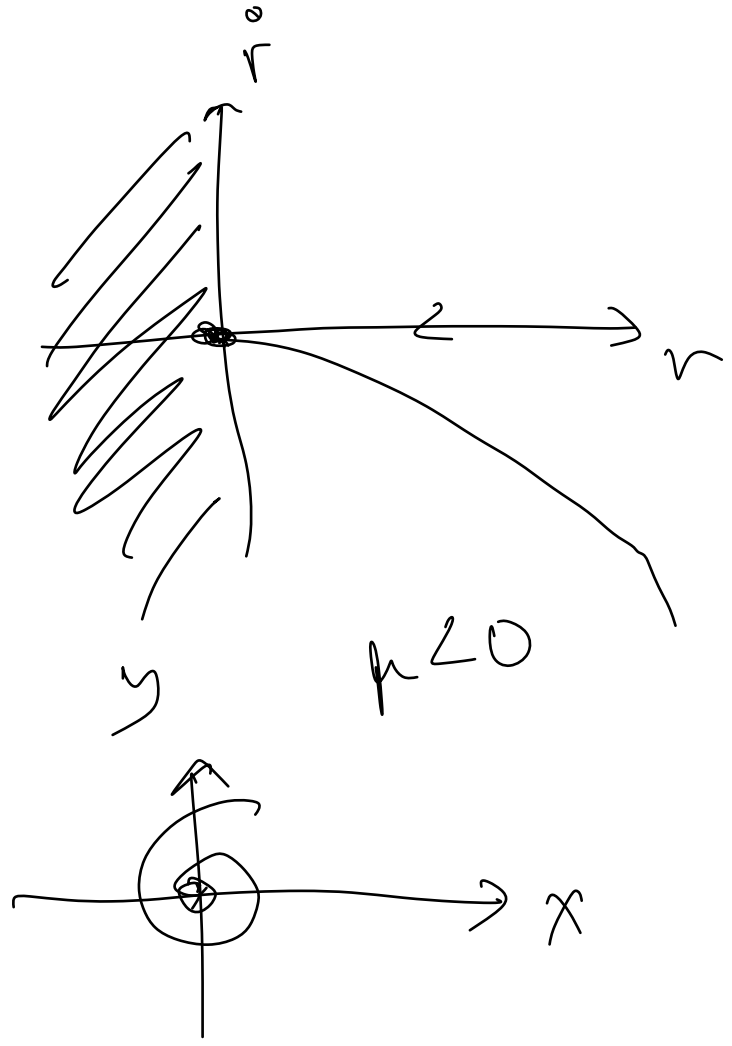
$$\theta = \tan^{-1}\left(\frac{y}{x}\right)$$

$$\dot{\theta} = \frac{1}{1 + y^2/x^2} \left(\frac{x\dot{y} - y\dot{x}}{x^2} \right) = \frac{x\dot{y} - y\dot{x}}{r^2} = \omega + br^2$$

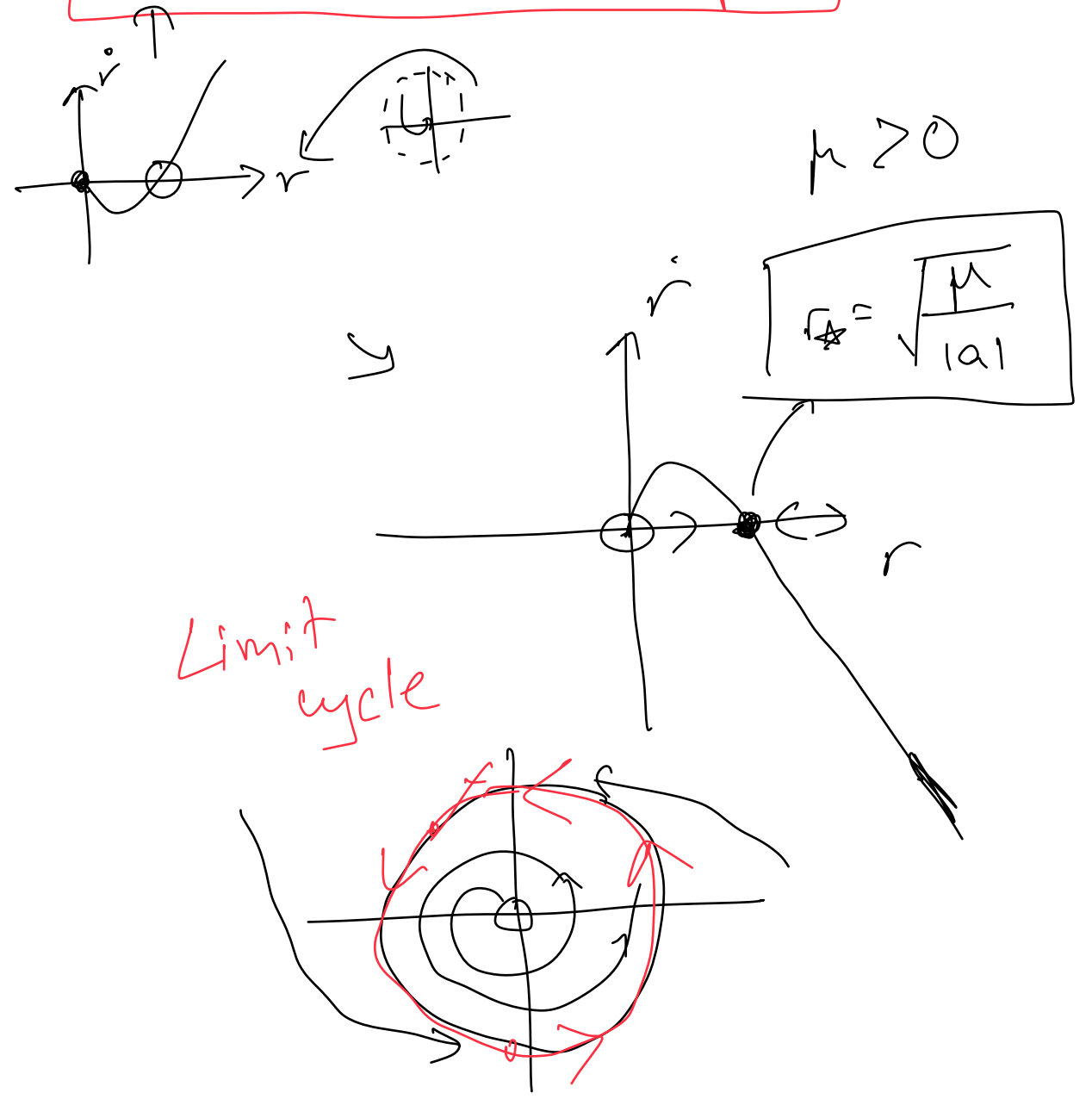
$$\begin{cases} \dot{r} = \mu r + ar^3 \\ \dot{\theta} = \omega + br^2 \end{cases} \leftarrow$$

$a < 0$

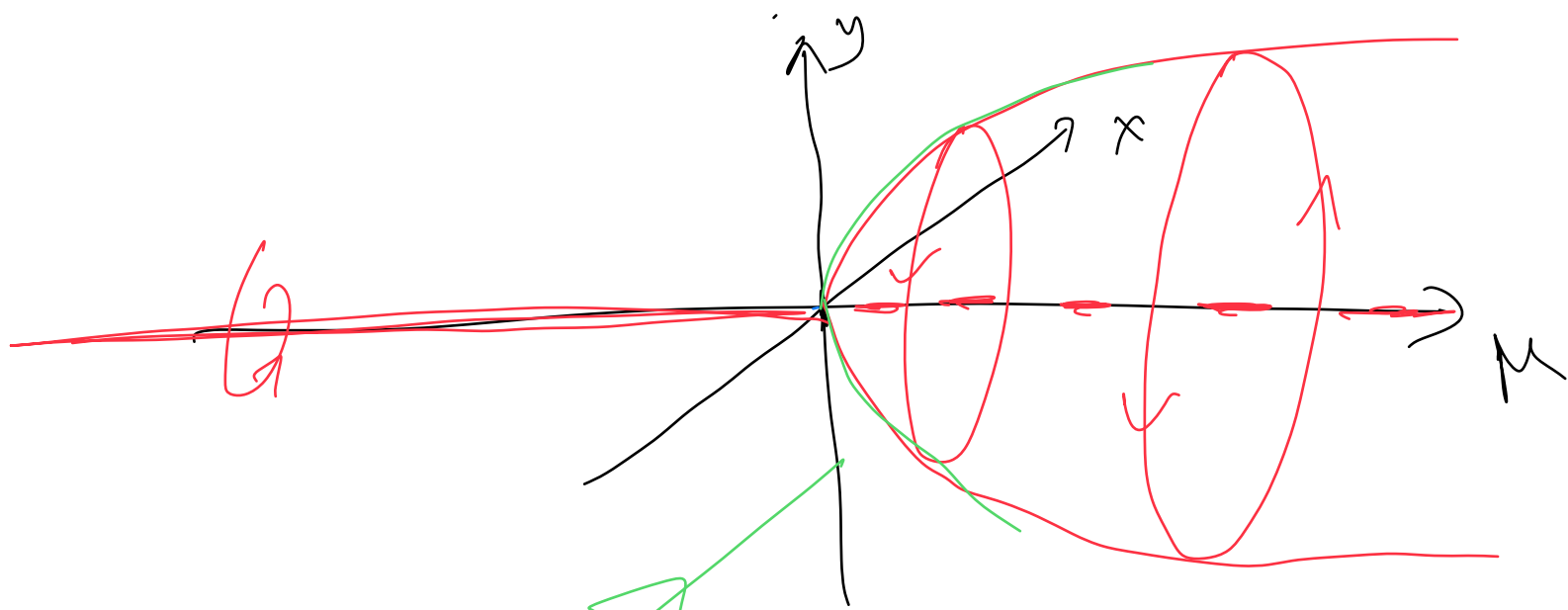
super critical
Hopf
Bif.



$a > 0 \rightarrow$ subcritical Hopf



Limit
cycle



Bifurcat^{ns}
of
Hopf

$\sim \sqrt{\mu}$

$$\dot{\vec{x}} = F(\vec{x}, \mu)$$

\equiv

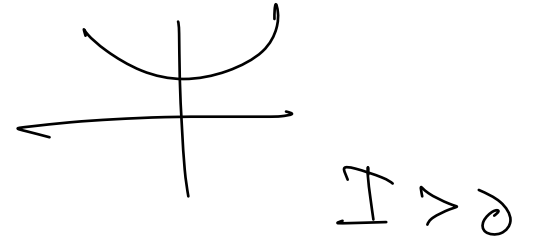
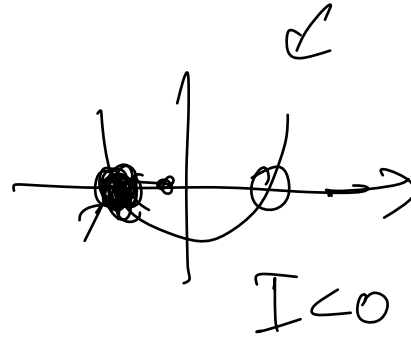
$$\dot{\vec{x}} = F(\vec{x}, \bar{\mu} + \varepsilon)$$

Fitz Hugh - Nagumo Model (FHN)

→ Bonhoeffer van der Pol Oscillator

$$\text{SIF} \rightarrow \dot{V} = V^2 + I$$

→



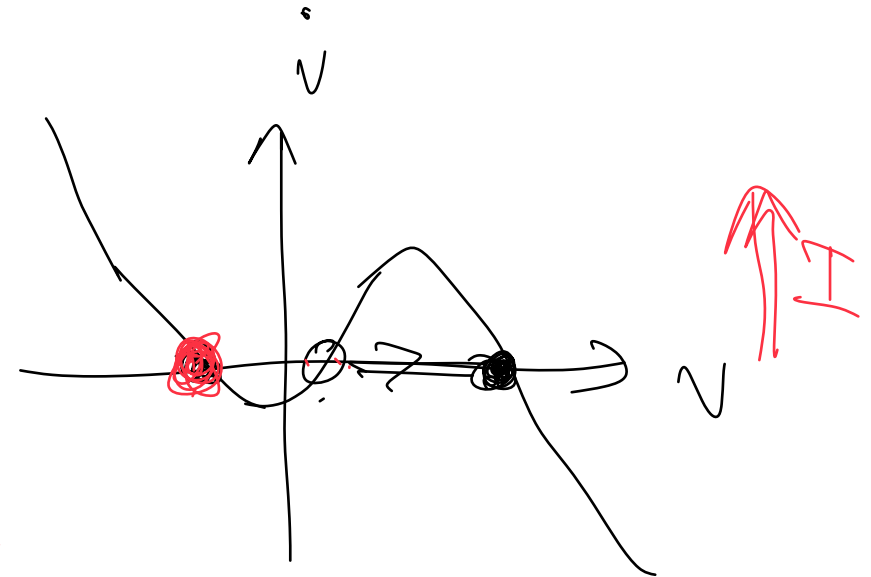
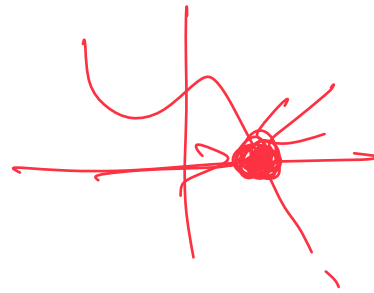
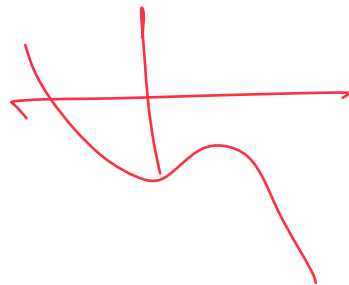
V → threshold for firing ←

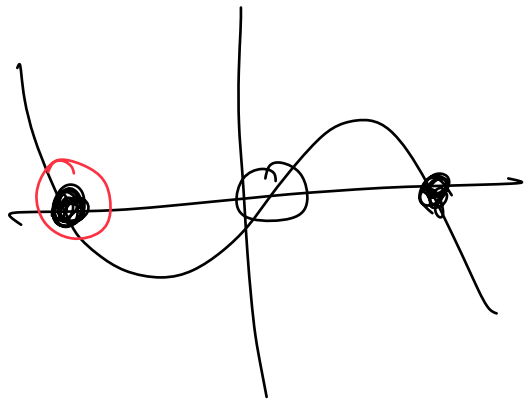
→ Reset V

→ V does not go to ∞ ←

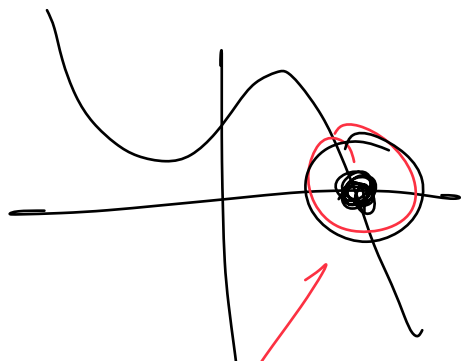
$$\dot{V} = V - \frac{V^3}{3} + I$$

$I \downarrow$

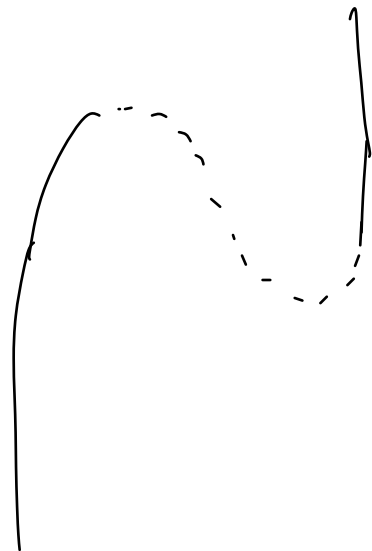
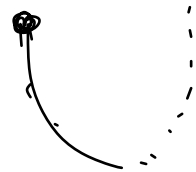
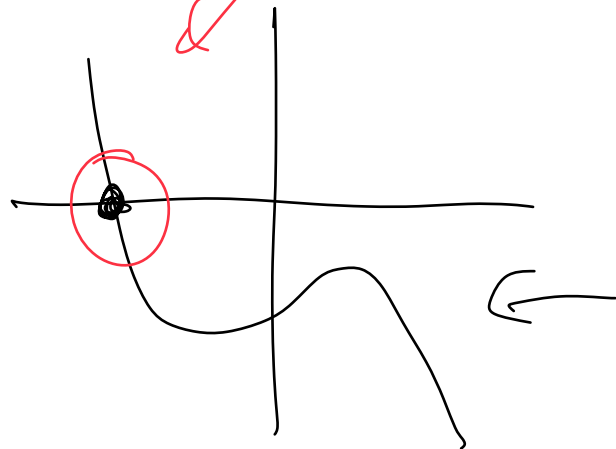




$I \uparrow$



$I \downarrow$



$$\dot{V} = V - \frac{V^3}{3} + I - W$$

$W \uparrow \rightarrow$ if V is high \leftarrow
 W inc.

\rightarrow ~~reset~~ reset if V is small \leftarrow

$$\dot{W} = \tau(V - bW + a)$$

$$\tau \ll 1$$

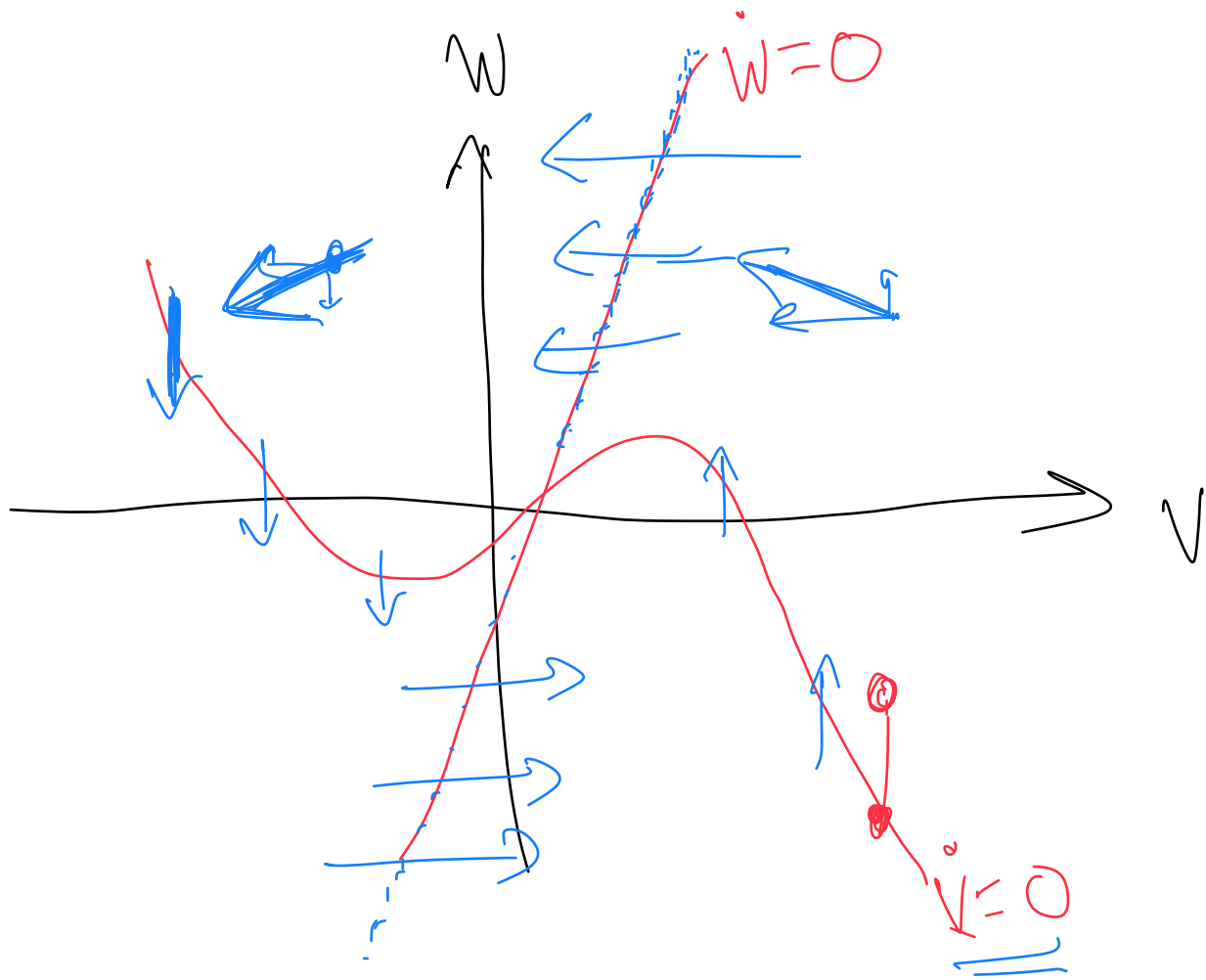
FHN

$\tau \ll 1$

$0 < b < 1$

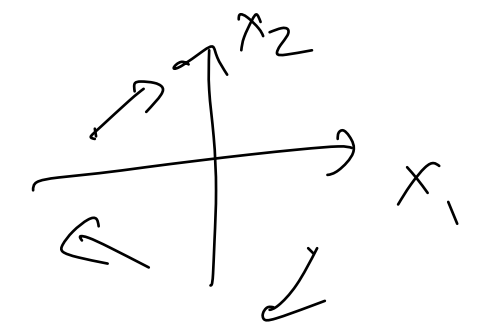
$$\dot{v} = v - \frac{v^3}{3} - w + I$$

$$\dot{w} = \tau (v - bw + a)$$



29-5-2026

$$\dot{x} = F(x)$$



nullclines

$$\dot{v} = 0$$

$$v - \frac{v^3}{3} - w + I = 0$$

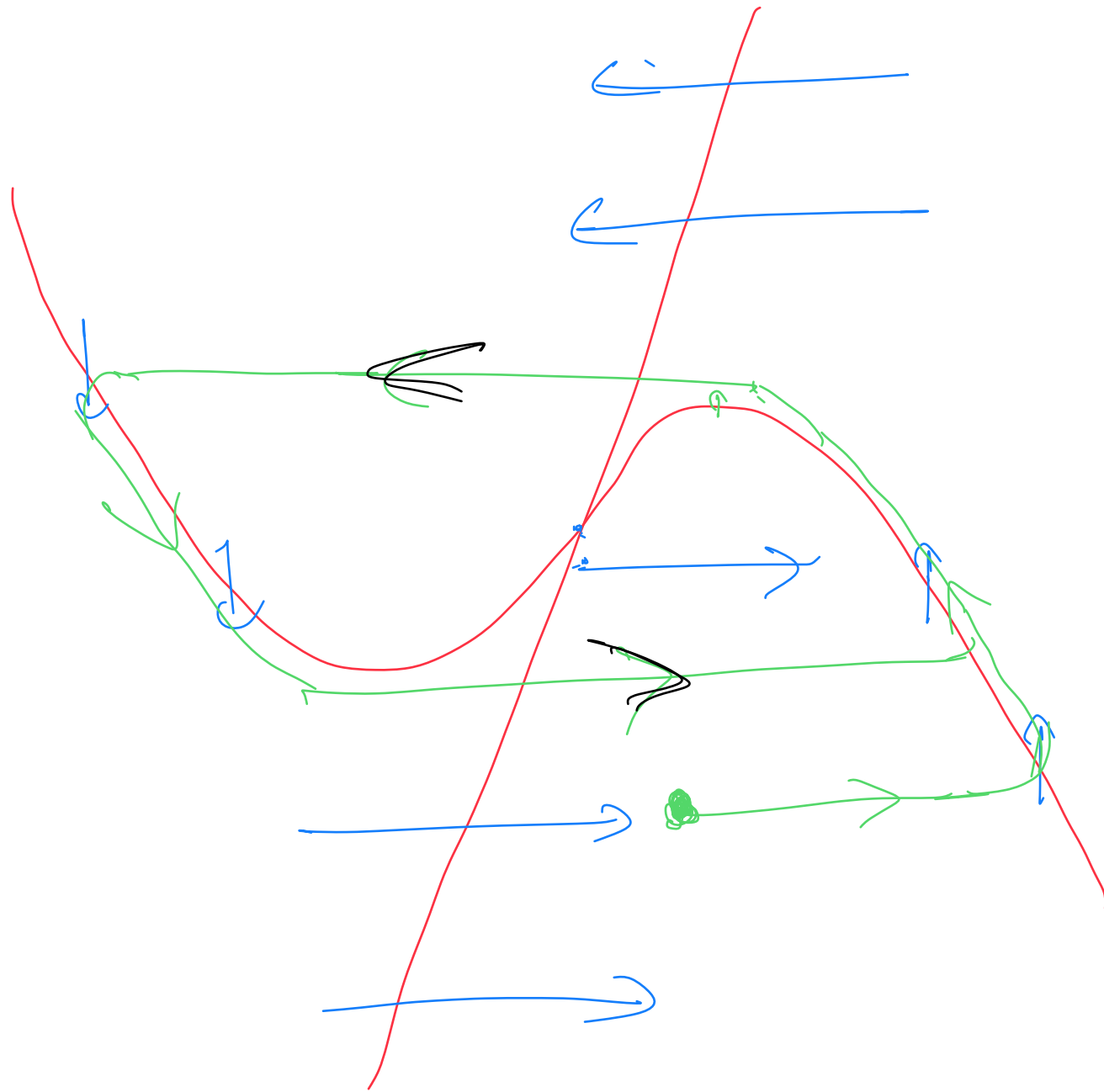
$$w = v - \frac{v^3}{3} + I$$

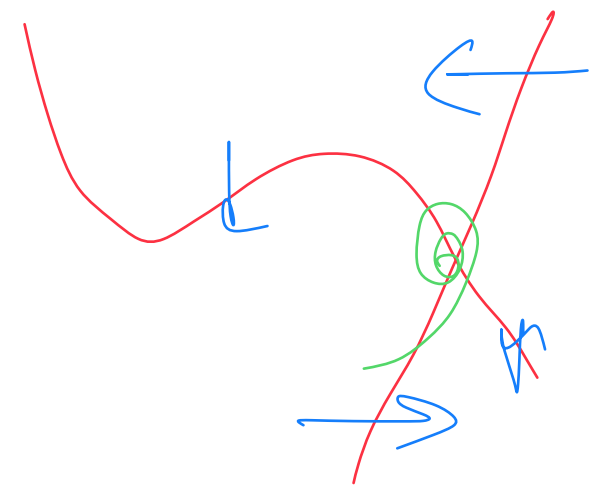
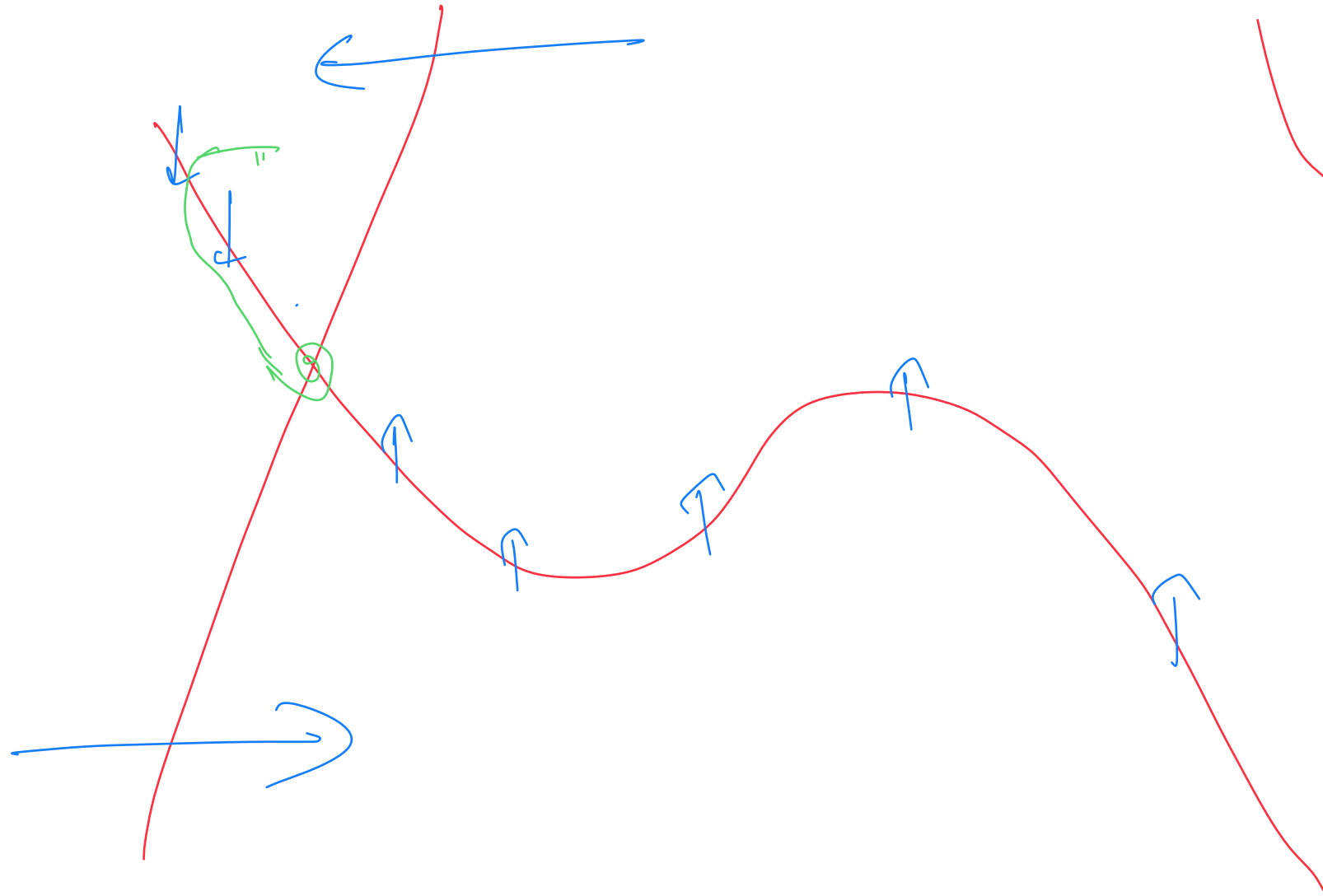
$$\dot{w} = 0$$

$$v - bw + a = 0$$

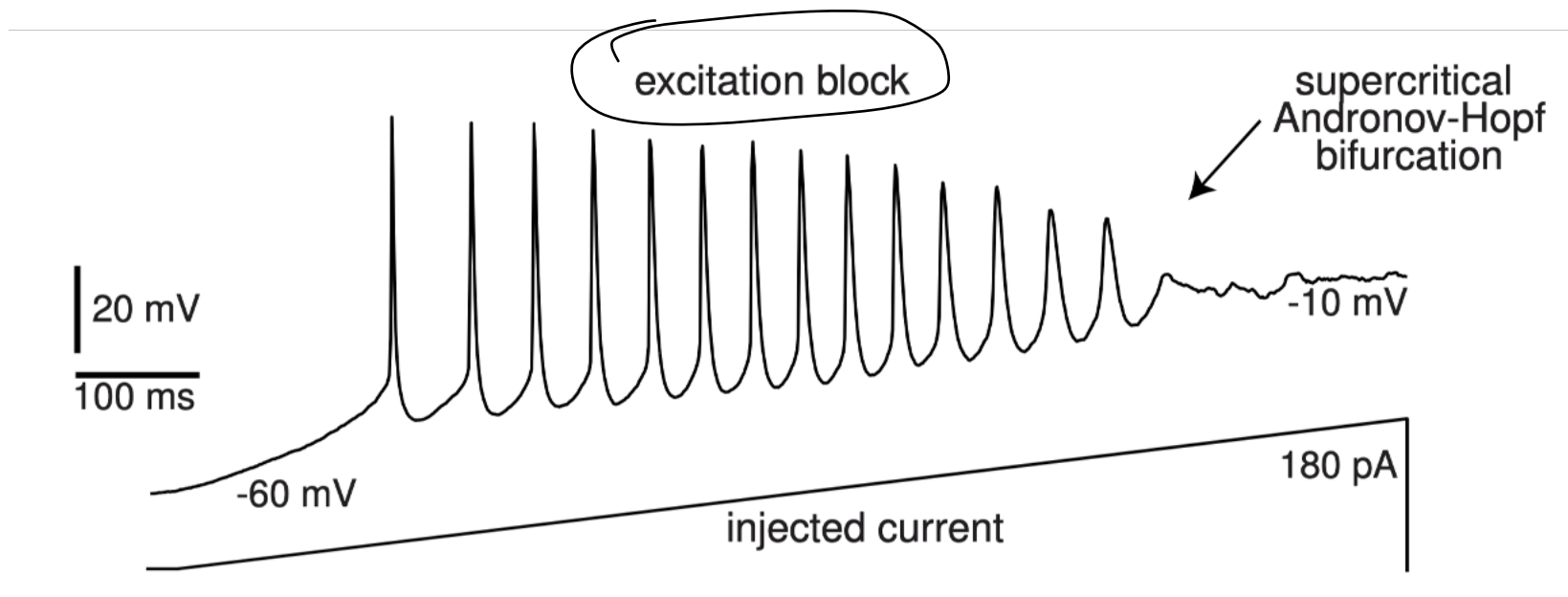
$$w = \frac{v}{b} + \frac{a}{b}$$

12. § 4.2.6
Strogetz § 7.5

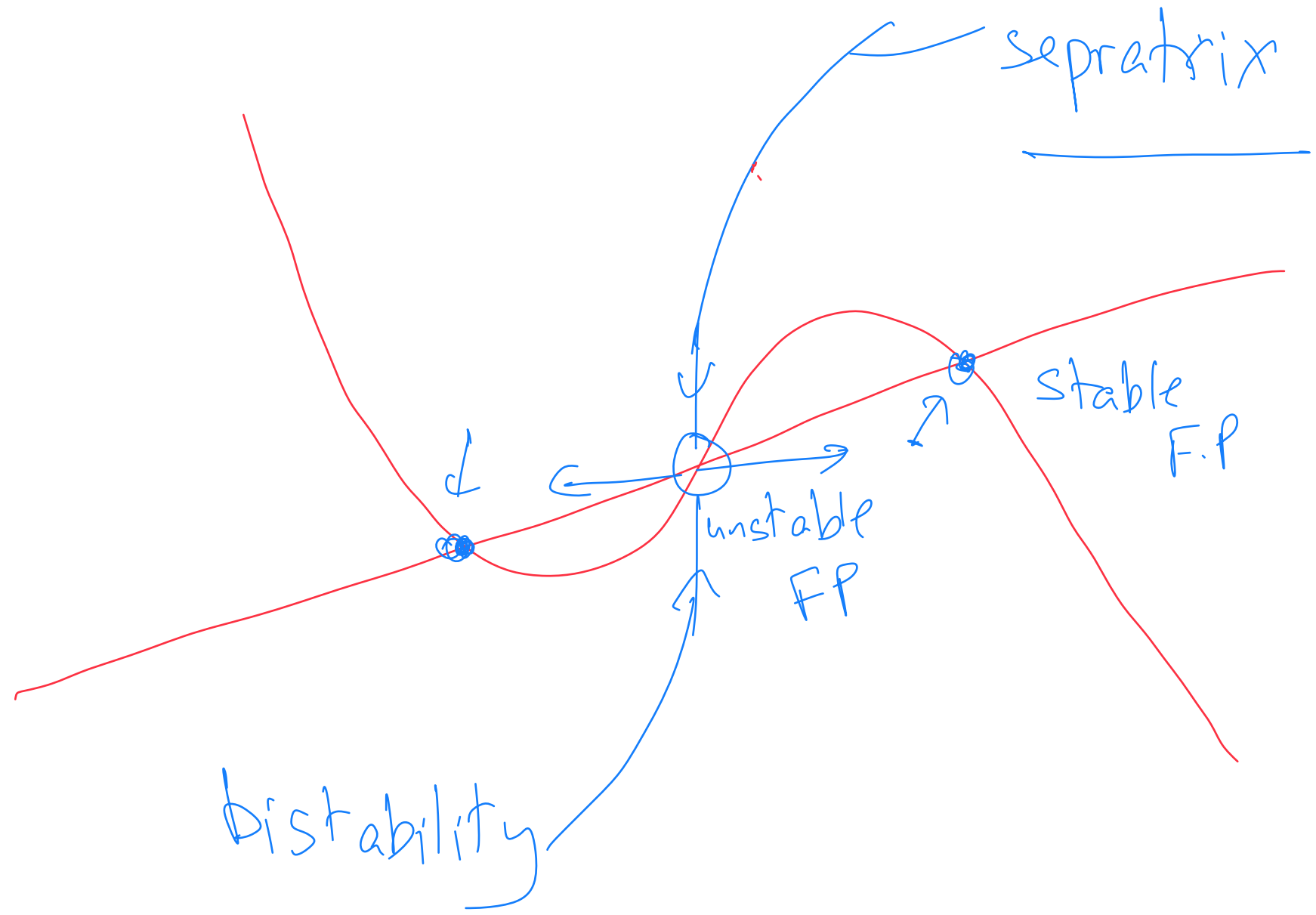




12. → Ch 4



$b > 1$



$$\tau < 1$$

$$0 < b < 1$$

$$\dot{v} = v - \frac{v^3}{3} - W + I$$

$$\dot{w} = \tau (v + a - b w)$$

$$J = \begin{pmatrix} 1 - v^2 & -1 \\ \tau & -\tau b \end{pmatrix} \Big|_{v^*, w^*}$$

$$\tau = 1 - v^2 - \tau b$$



$$\tau < 0$$

if

$$v < -1 \text{ or } v > +1$$

$$\tau > 0$$

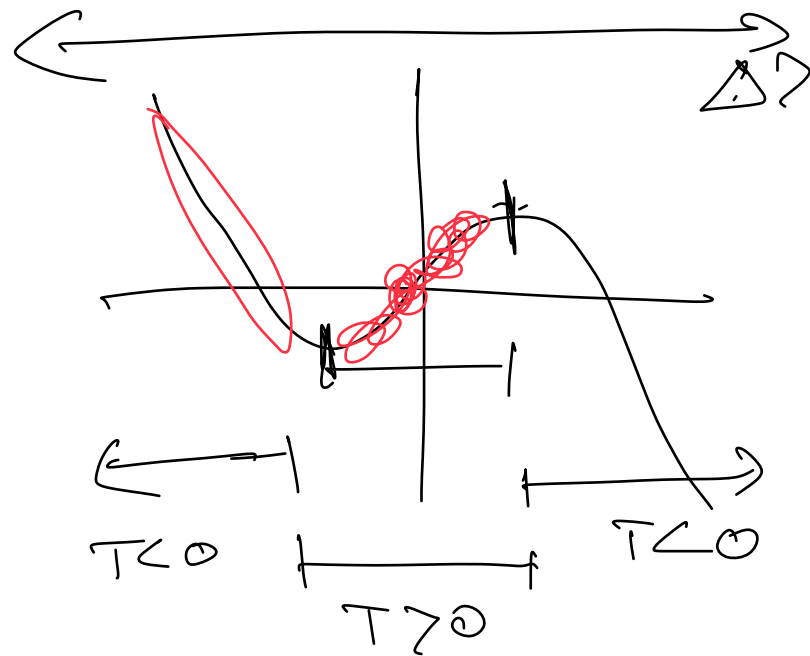
if

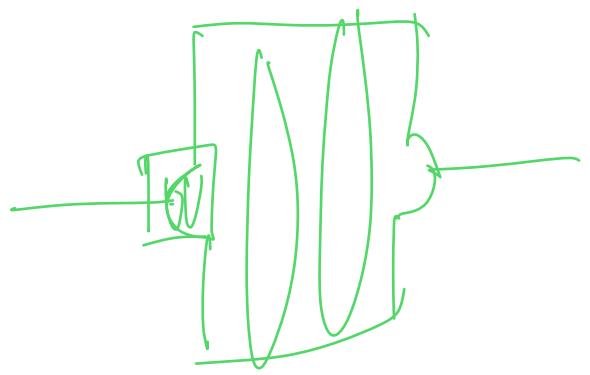
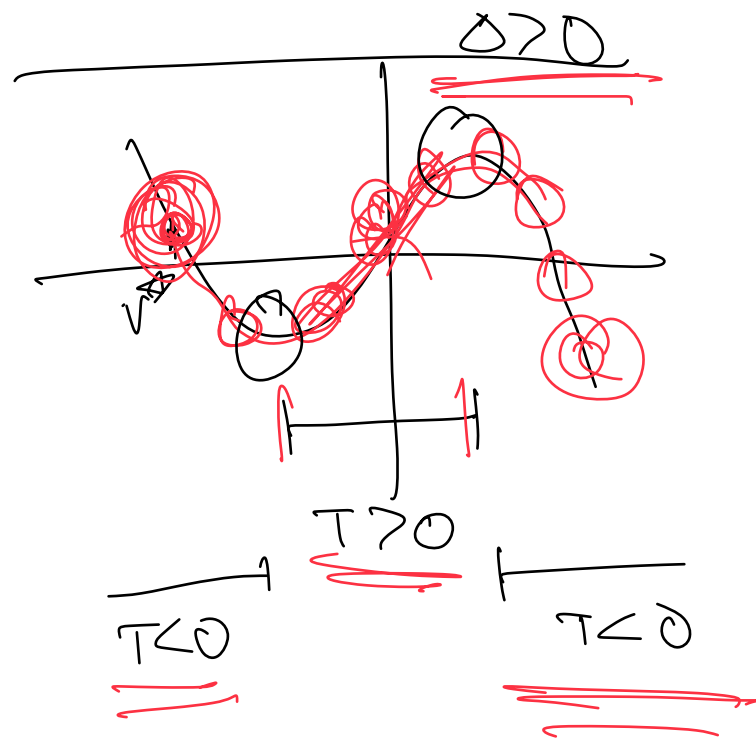
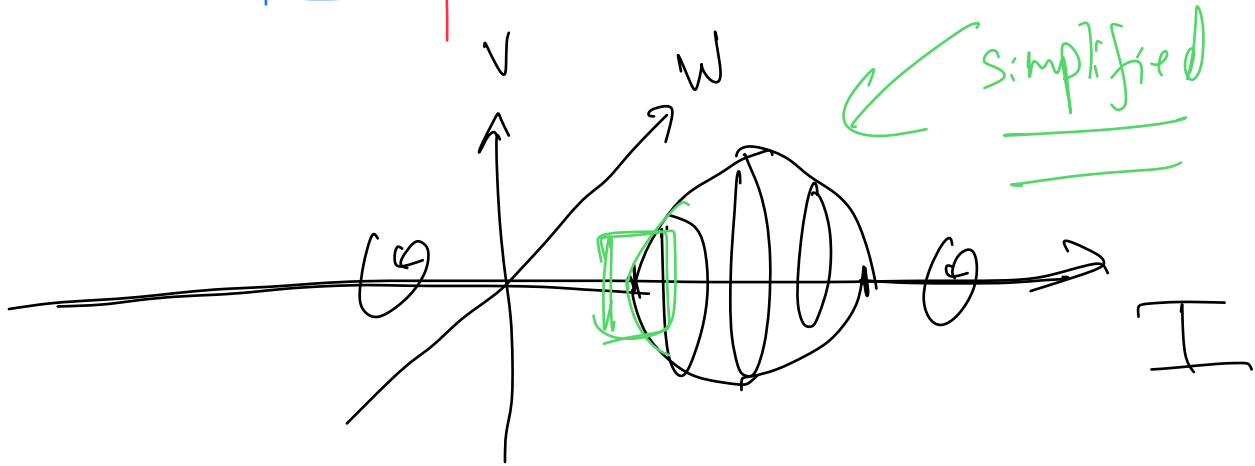
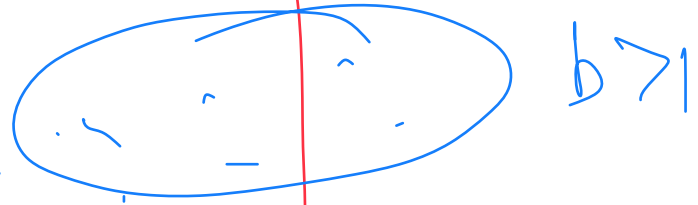
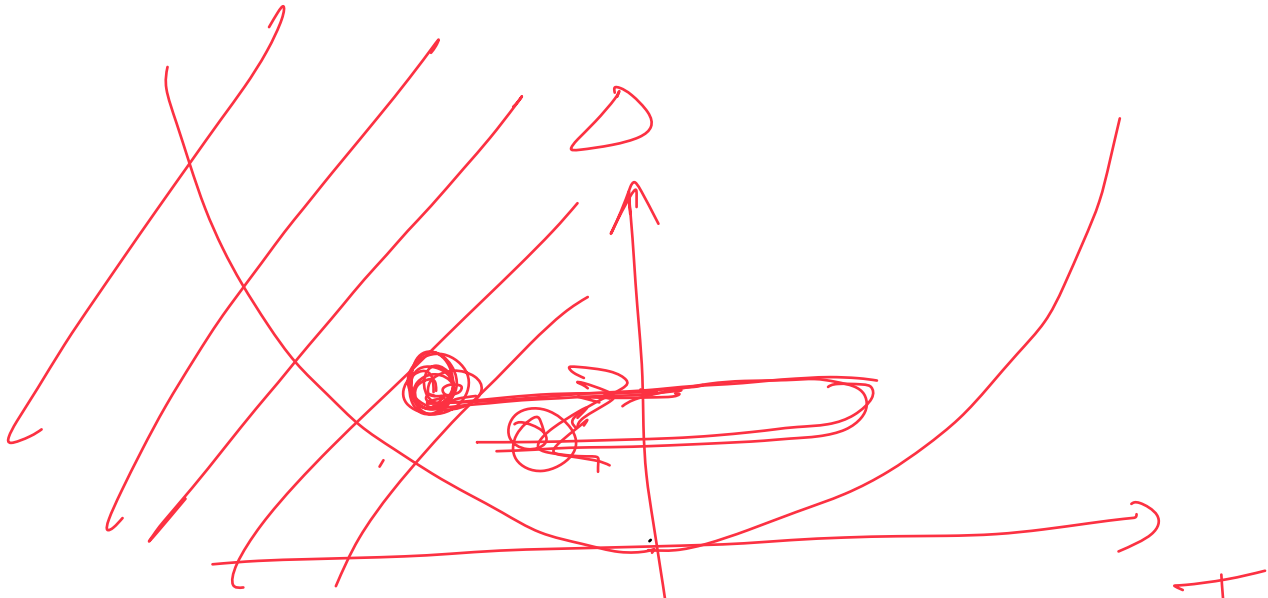
$$-1 < v < 1$$

$$\Delta = (1 - v^2)(-\tau b) + \tau$$

$$\tau (1 - b - b v^2)$$

$$= \tau (1 - b(1 - v^2)) > 0$$





Limit cycles — Perturbations

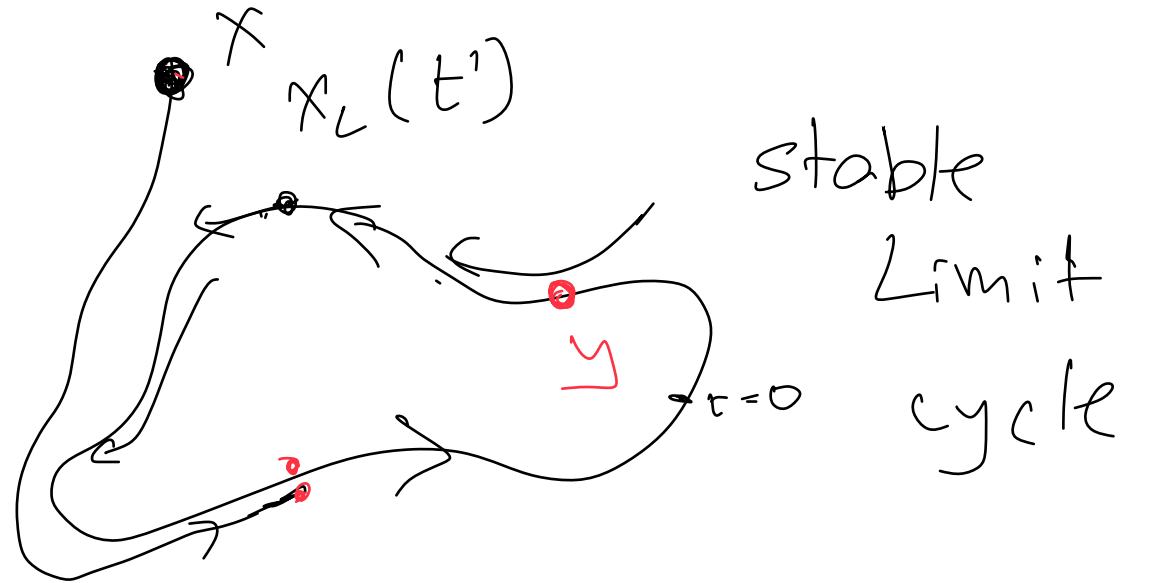
"Phase Reduction"

$$\dot{\bar{x}} = \bar{F}(\bar{x})$$

$$\bar{x}_L(t+T) = \bar{x}_L(t)$$

$$\Omega = 2\pi/T$$

E&T Ch 9, 12. Ch. 10

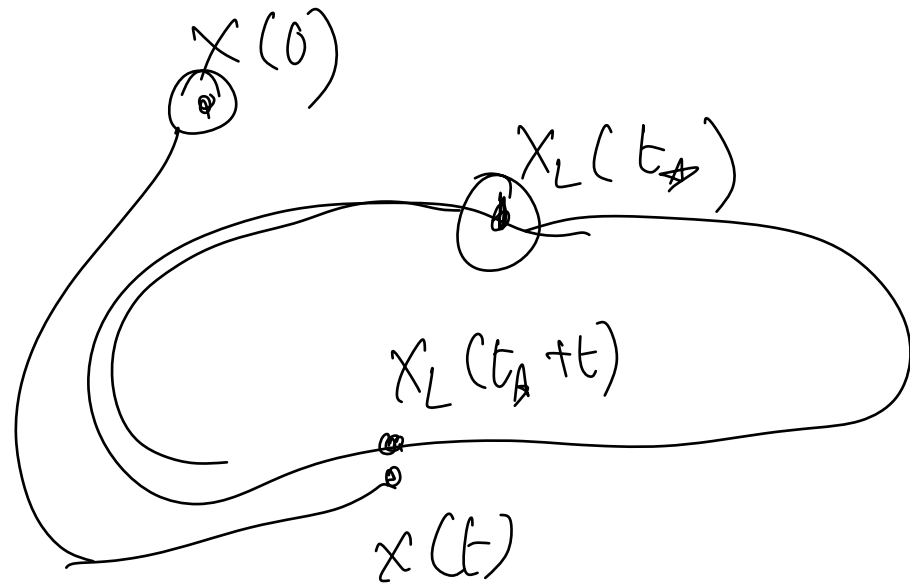


$$\Theta(\underline{x}_L(t)) = \Omega t \pmod{2\pi}$$

Extend definitⁿ of Θ to all \bar{x}

If $\lim_{t \rightarrow \infty} \|x_L(t_A + t) - \underline{x(t)}\| = 0$]

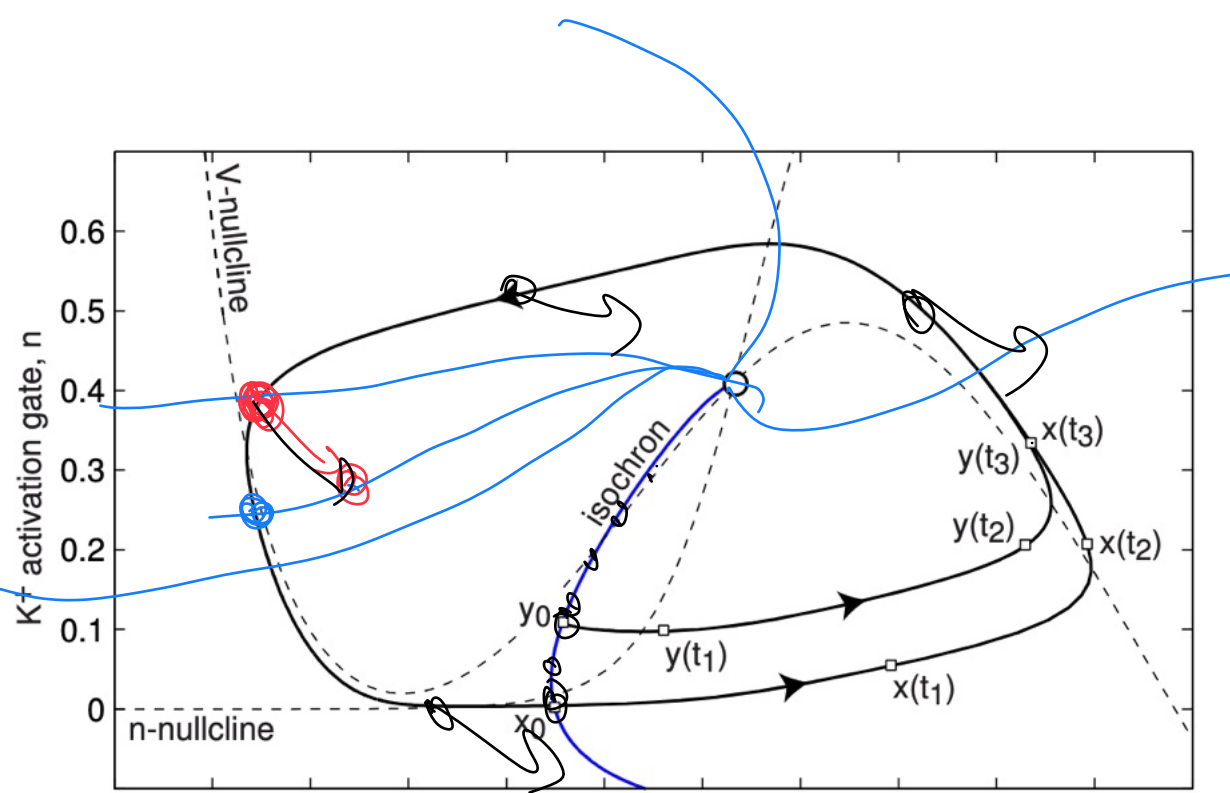
then $\Theta(x(0)) = \Theta(x_L(t_A))$



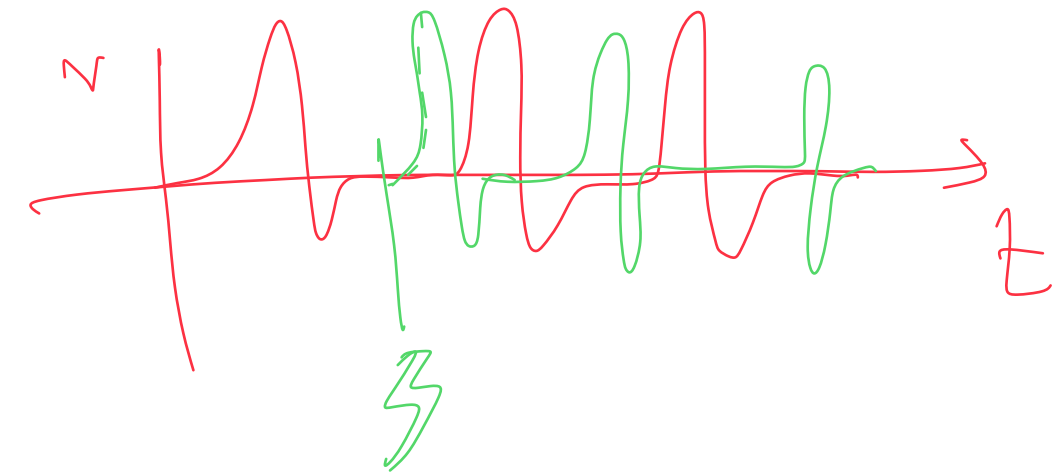
Isochrons ($I_{Na,p} + I_K$)

Isochron \rightarrow level set of Θ

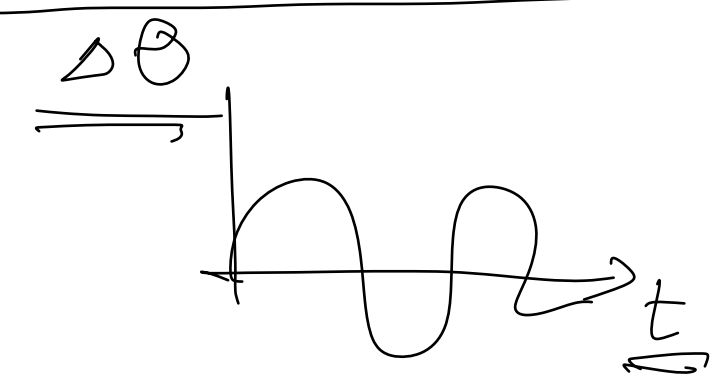
$$\Theta(\vec{x}) = C$$



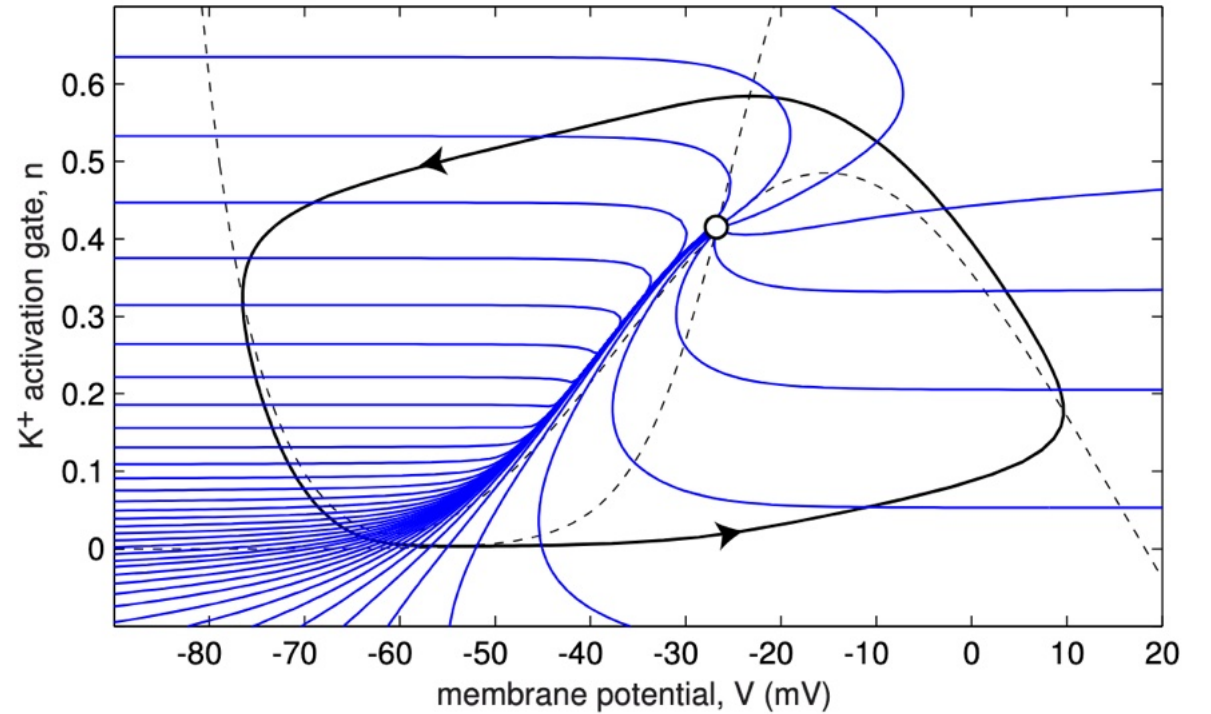
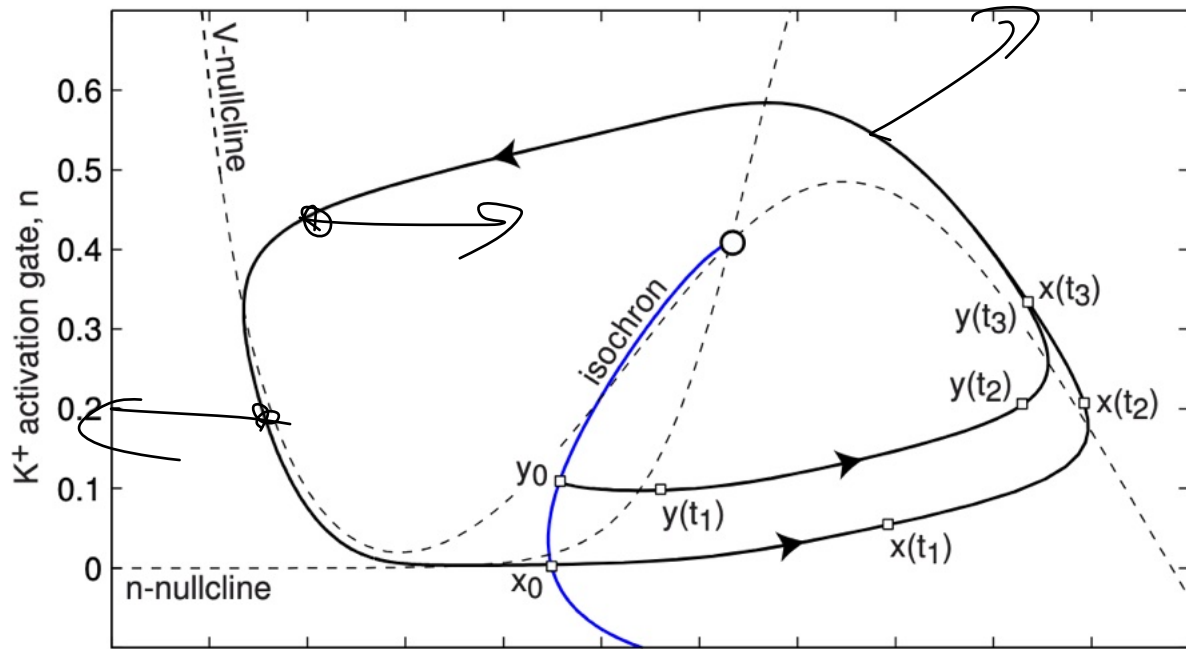
Izhikevich Fig. 10.2



\rightarrow Phase Response Curve

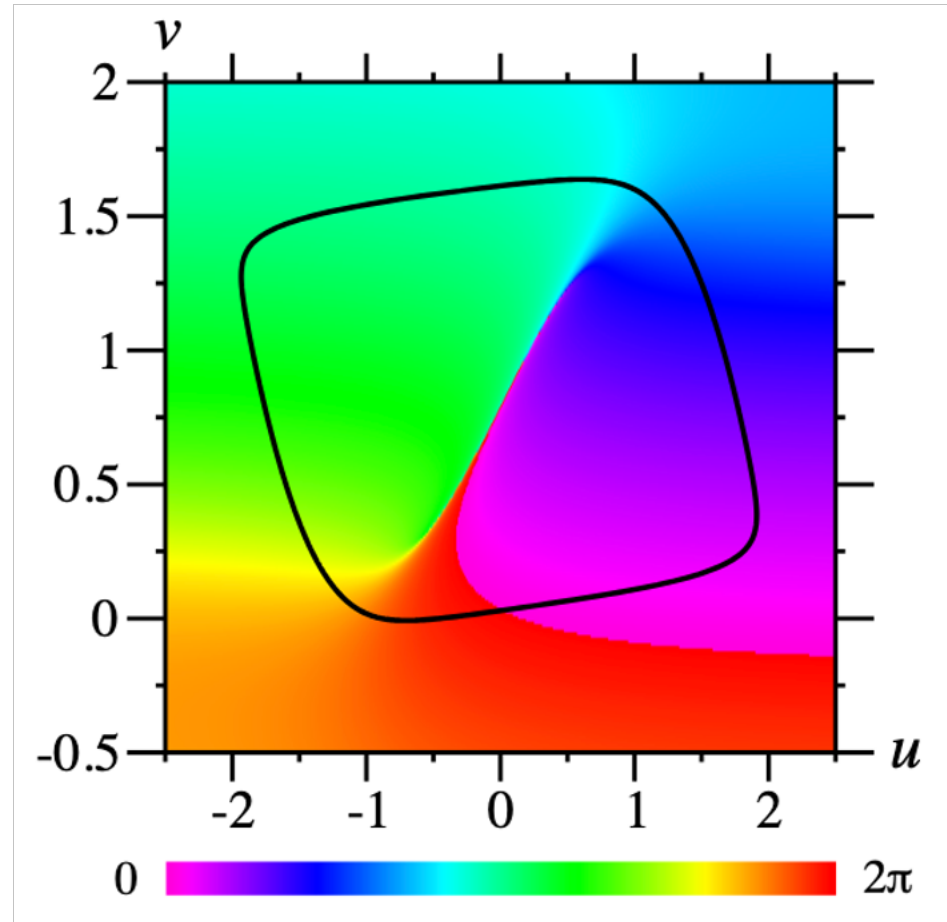


Isochrons ($I_{Na,p} + I_K$)



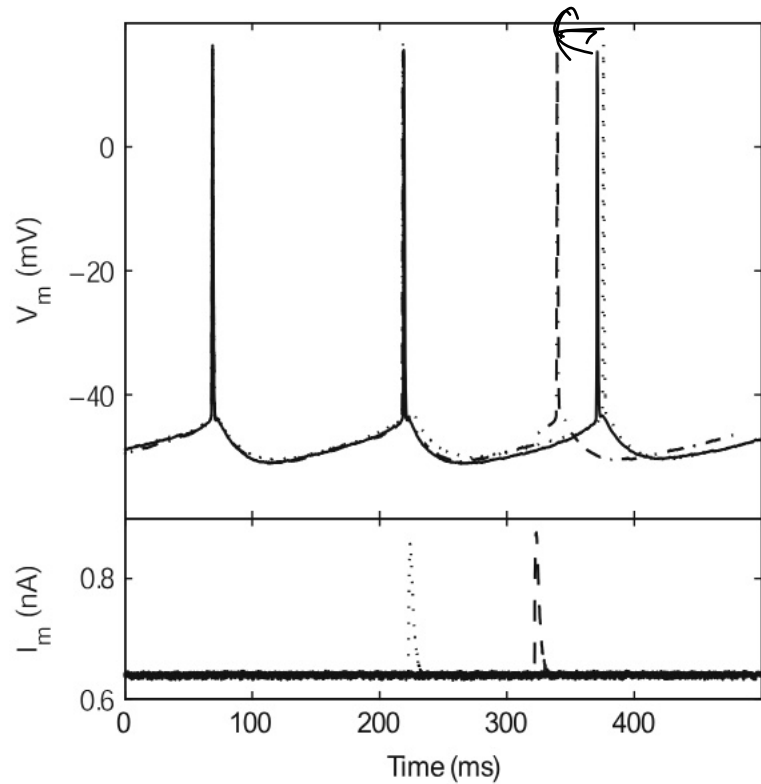
Izhikevich Fig. 10.2

Isochrons (FHN)



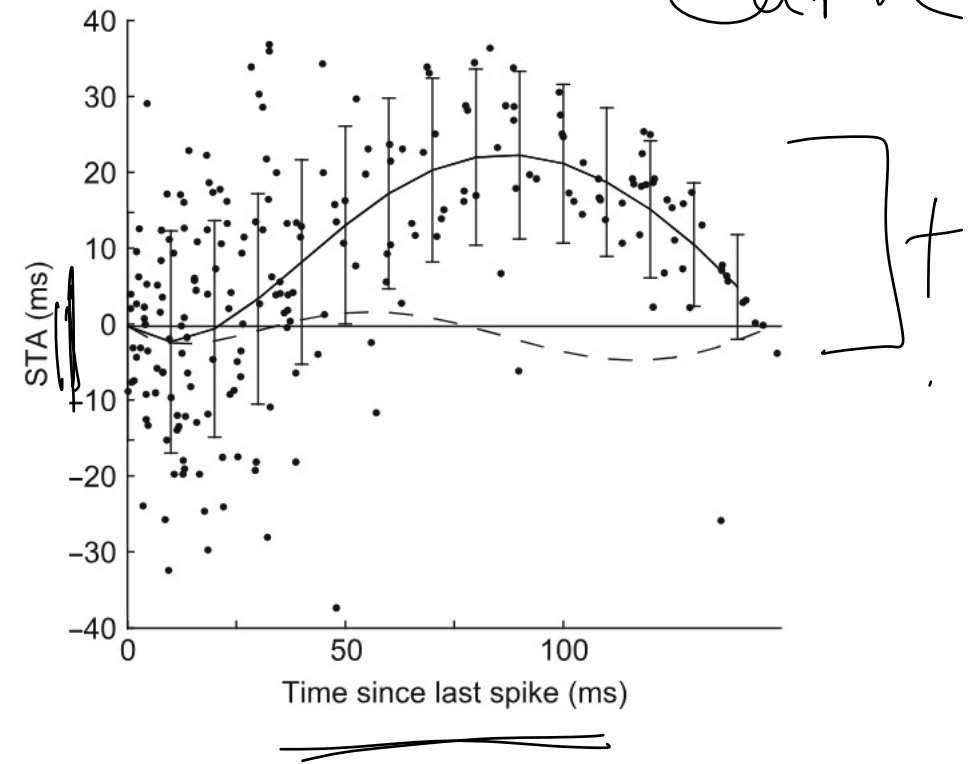
Nakao, H. (2016) 'Phase reduction approach to synchronisation of nonlinear oscillators', *Contemporary Physics*, 57(2), pp. 188–214.

PRC in neurons



Netoff et al (2005)

Phase Response
Curve



$$\left[\frac{d\theta(x)}{dt} = \Omega \right.$$

$$\left. \nabla\theta \cdot \dot{x} = \Omega \right.$$

$$\left. \nabla\theta \cdot \bar{F} = \Omega \right]$$

$$\theta(x_c(t)) = \Omega t \pmod{2\pi}$$

$$\dot{x} = F(x)$$

$$\dot{x} = F(x) + \epsilon p$$

$$\nabla\theta \cdot \dot{x} = \underbrace{\nabla\theta \cdot F}_{=} + \epsilon \nabla\theta \cdot p$$

$$\left[\frac{d\theta}{dt} = \Omega + \epsilon \nabla\theta \cdot p \right]$$

$$\boxed{Z(\theta)}$$

Phase Response Curve

Let $Z(\theta) = \nabla\theta$

$$\frac{d\theta}{dt} = \Omega + \vec{Z}(\theta) \cdot \vec{p}$$

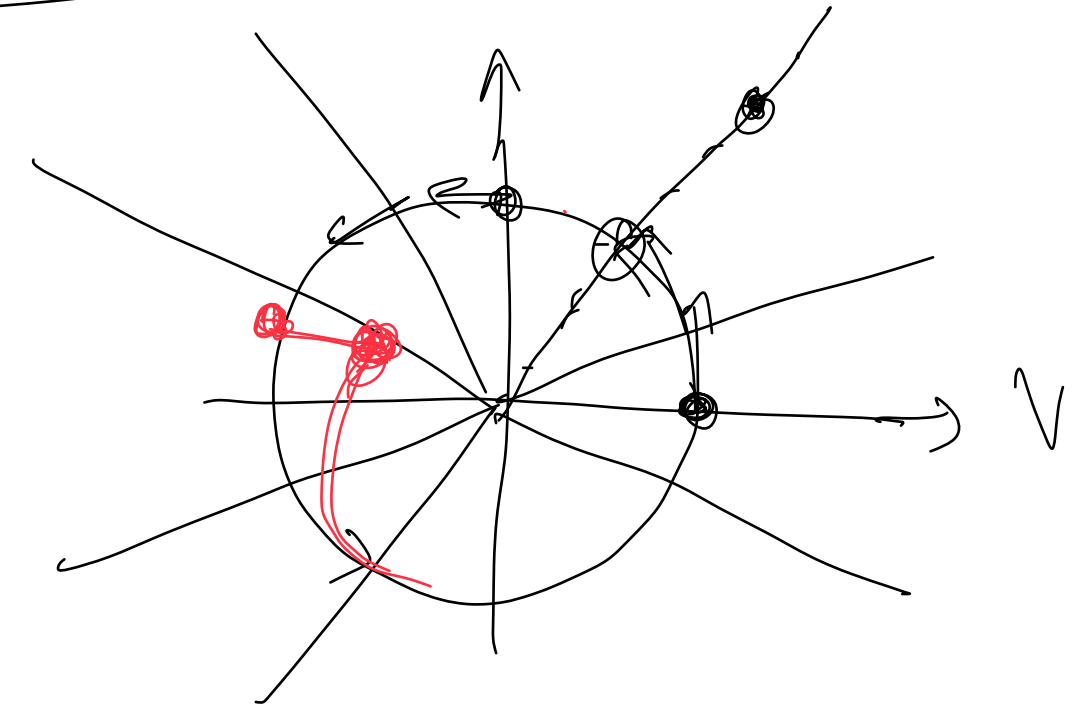
$$\frac{d\theta}{dt} = \Omega$$

$$\vec{Z}(\theta) \cdot \vec{v}$$

$$\left. \begin{aligned} \dot{r} &= \mu r - r^3 \\ \dot{\phi} &= \omega \end{aligned} \right\}$$

ϕ

$$\vec{Z}(\theta) = \begin{pmatrix} -\sin \theta \\ \cos \theta \end{pmatrix}$$

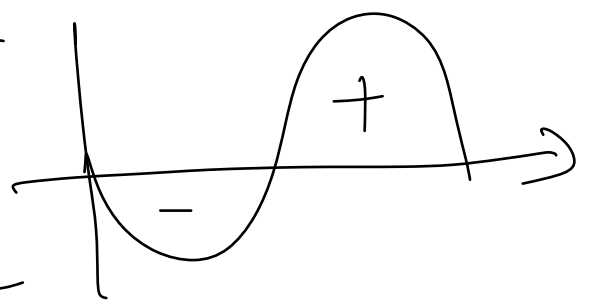


$$\vec{Z}(\theta) \cdot \vec{v} = -\sin \theta$$

Mopf. oscillator

PRC

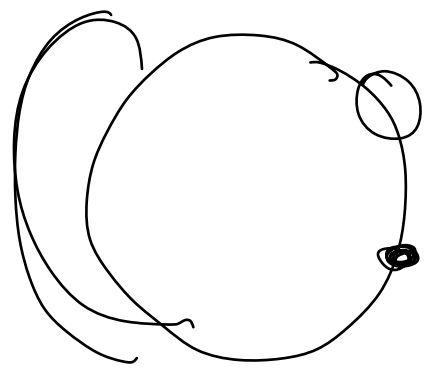
Type II
Neuron/PRC



Biphasic PRC

⊙

Synr.
easily



SNIC



Type I
Neuron PRC



$\epsilon \ll 1$

$$\dot{\bar{x}} = \bar{F}(\bar{x}) + \epsilon \bar{p}$$

$$\rightarrow \frac{d\theta}{dt} = \Omega + \bar{Z}(\theta) \cdot (\epsilon \bar{p}) \quad \leftarrow Z(\theta) = \bar{\nabla} \theta \quad \leftarrow \theta(\bar{x})$$

$$\dot{x}_i^0 = \underline{F(x_i)} + \sum p_i(x_1, \dots, x_N)$$

$$= \underline{F(x_i)} + \epsilon \sum_j g_{ij}(x_i, x_j)$$

$$\dot{\theta}_i = \Omega + \epsilon \underbrace{\sum_j Z_i(\theta_i) g_{ij}(x_i(\theta_i), x_j(\theta_j))}_{g_{ij}(\theta_i, \theta_j)}$$

$$\left[\begin{aligned} \dot{\theta}_i &= \Omega + \varepsilon \sum Q_{ij}(\theta_i, \theta_j) \\ Q_{ij}(\theta_i, \theta_j) &= Q_{ij}(\theta_i, \theta_i + \Delta\theta) \end{aligned} \right]$$



$$H_{ij}(\Delta\theta) = \frac{1}{2\pi} \int_0^{2\pi} Q_{ij}(\theta, \theta + \Delta\theta) d\theta \leftarrow \text{average over fast timescale}$$

$$\dot{\theta}_i = \Omega + \varepsilon \sum H_{ij}(\theta_j - \theta_i) \leftarrow \text{Kuramoto - Daido form}$$

$$\begin{aligned} H_{ij}(\Delta\theta) &= \sum a_{ij}^{is} \sin(\Delta\theta) + b_{ij}^{ic} \cos(\Delta\theta) \\ &= c_{ij}^{is} \sin(\theta_j - \theta_i + \alpha_{ij}^{is}) \leftarrow \text{Kuramoto - Sakaguchi} \end{aligned}$$

$$\text{if } g_{ij}(x_i, x_j) = g_{ij}(x_i - x_j) \leftarrow \text{Diffusive coupling} \Rightarrow H_{ij}(0) = 0$$

$$H_{ij} = \sin(\theta_j - \theta_i)$$

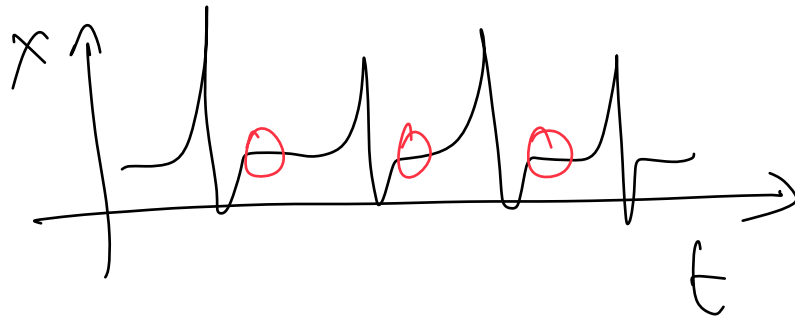
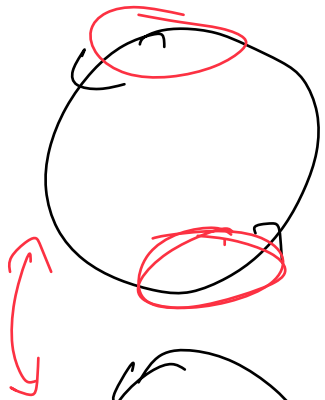
$$\dot{\theta}_i = \Omega + \sum_j c_{ij} \sin(\theta_j - \theta_i)$$

← Kuramoto model

↑ Exc. approx

~~Exact~~ if L.C. were near a Hopf. Bifⁿ

$$\dot{\theta} = \Omega$$



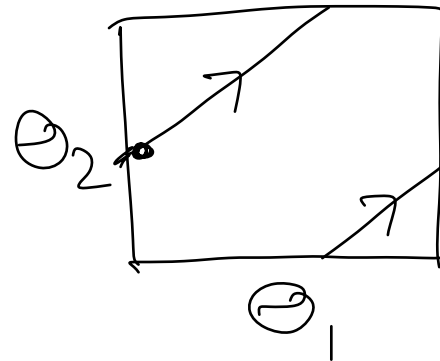
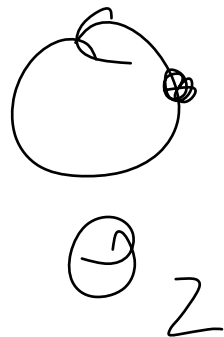
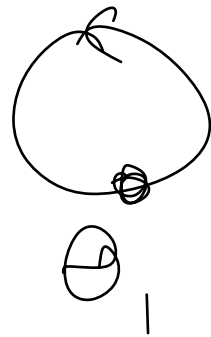
$$\dot{\theta}_1 = \omega + \underline{K_1} \sin(\theta_2 - \theta_1)$$

$$\dot{\theta}_2 = \omega + \underline{K_2} \sin(\theta_1 - \theta_2)$$

If $K_1 = K_2 = 0$

$$\dot{\theta}_1 = \omega$$

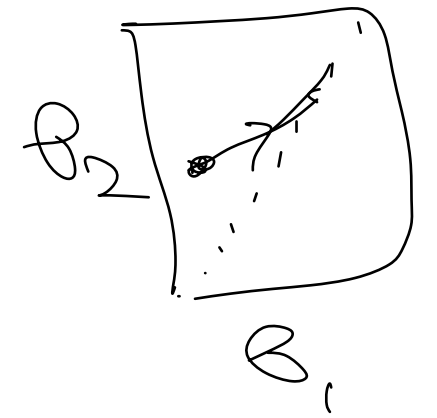
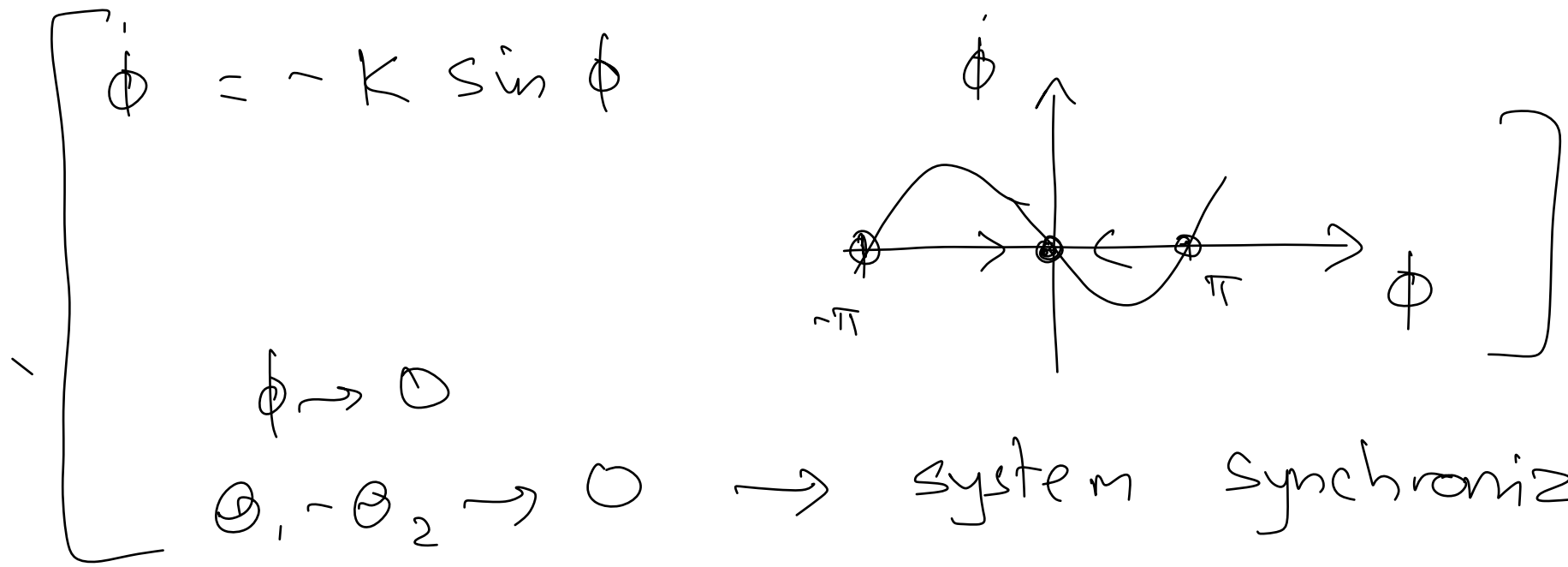
$$\dot{\theta}_2 = \omega$$



$$\phi = \theta_1 - \theta_2$$

$$\dot{\phi} = K_1 \sin(\theta_2 - \theta_1) - K_2 \sin(\theta_1 - \theta_2)$$

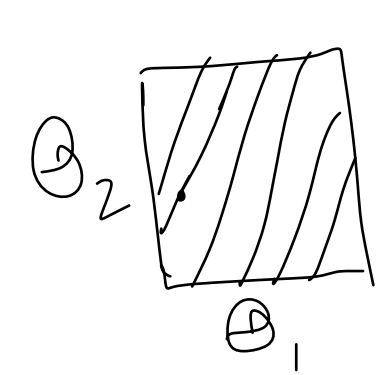
$$\dot{\phi} = (K_1 + K_2) \sin(\theta_2 - \theta_1) = -(K_1 + K_2) \sin \phi \quad \left[\leftarrow \right]$$



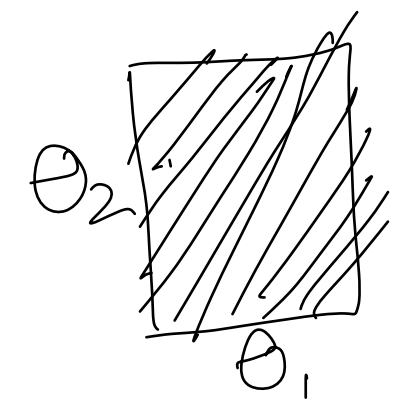
$$\dot{\theta}_i = \omega_i + K \sum \sin(\theta_j - \theta_i)$$

if $\omega_1/\omega_2 \in \mathbb{Q}$

$$\begin{cases} \dot{\theta}_1 = \omega_1 \\ \dot{\theta}_2 = \omega_2 \end{cases}$$



$\omega_1/\omega_2 \notin \mathbb{Q}$



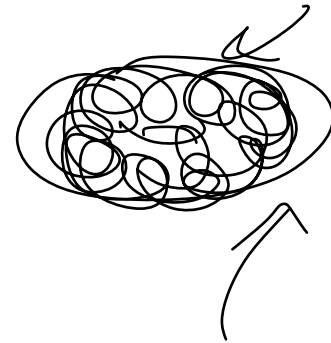
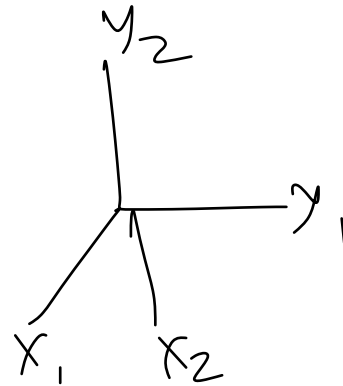
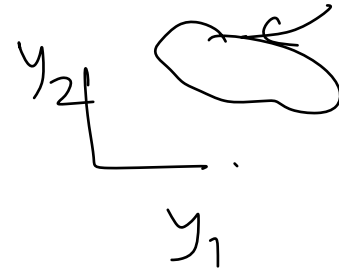
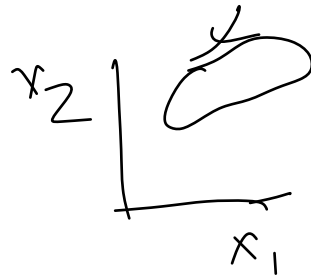
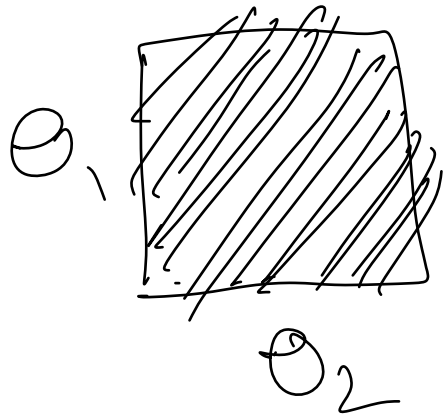
~~P.P.~~
 Quasiperiodic attractor

$$\dot{\theta}_1 = \omega_1$$

$$\dot{\theta}_2 = \omega_2$$



$$\dot{\vec{x}} = \vec{F}(\vec{x}) \quad \vec{x} \in \mathbb{R}^2$$



Strogatz § 8.6 Ed. 1 or 2

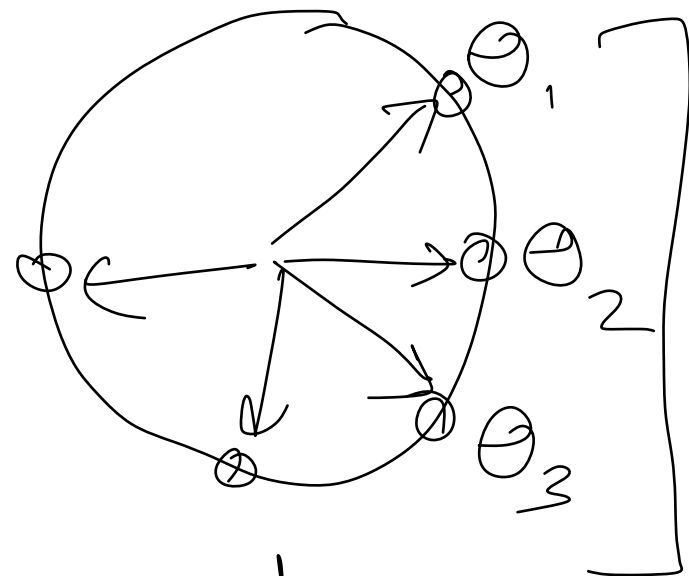
§ 13

Ed 3

for 2 osc. coupled.

$$\dot{\theta}_i = \omega_i + \frac{1}{N} \sum \sin(\theta_j - \theta_i)$$

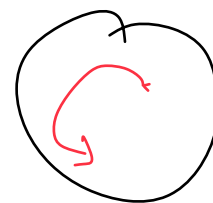
if $\theta_j = \theta_i \pm \pi$
 $\rightarrow \theta_i$ goes faster
 slower



Order parameter

$$Z = \frac{1}{N} \sum e^{i\theta_i}$$

$|Z| \rightarrow 0 \Rightarrow$ a sync.
 $\rightarrow 1 \Rightarrow$ sync.



$$\begin{aligned} \theta_i &= \omega_i + \frac{K}{2} \sum_j \sin(\theta_j - \theta_i) \\ &= \omega_i + \frac{K}{2} \sum_j \operatorname{Im} \left[e^{i(\theta_j - \theta_i)} \right] \\ &= \omega_i + K \operatorname{Im} \left[\sum_j e^{i\theta_j} \cdot e^{-i\theta_i} \right] \end{aligned}$$

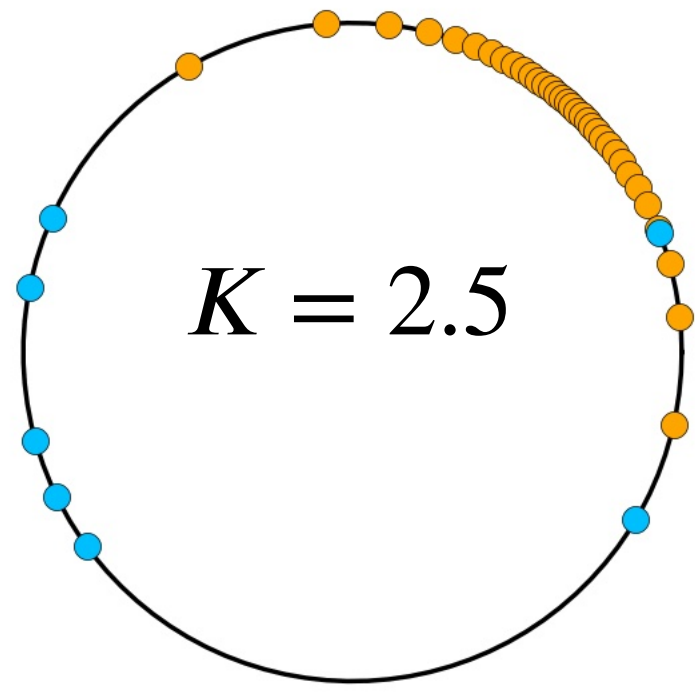
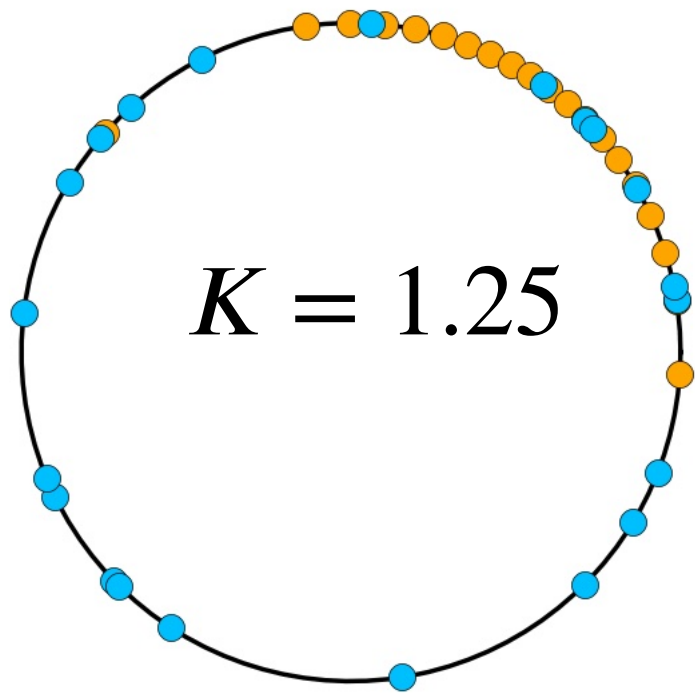
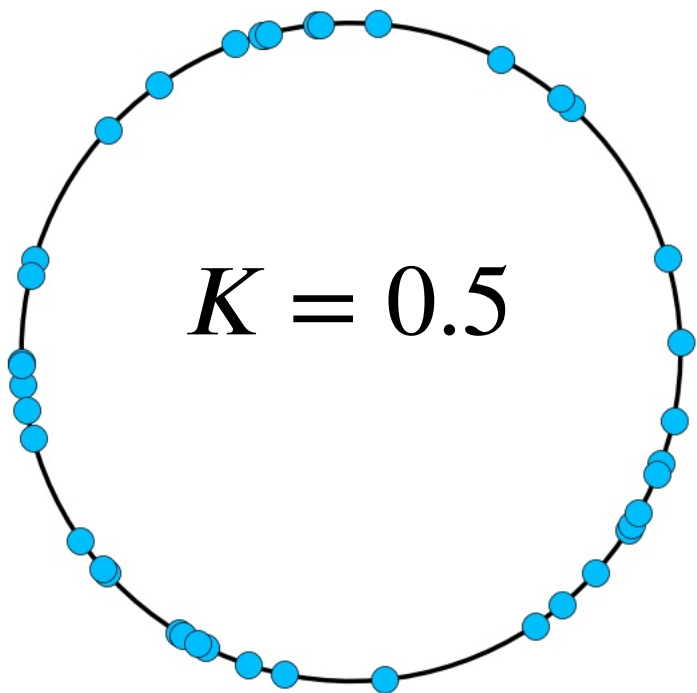
$$\begin{aligned} \theta_i &= \omega_i + K \operatorname{Im} \left[z \cdot e^{-i\theta_i} \right] \\ &= \omega_i + K \operatorname{Im} \left[e^{i\psi} \cdot e^{-i\theta_i} \right] \end{aligned}$$

$$\theta_i = \underbrace{\omega_i}_{\text{oppose synch.}} + \underbrace{Kr \sin(\psi - \theta_i)}_{\text{promotes synch.}}$$

$$\rightarrow z = r e^{i\psi}$$

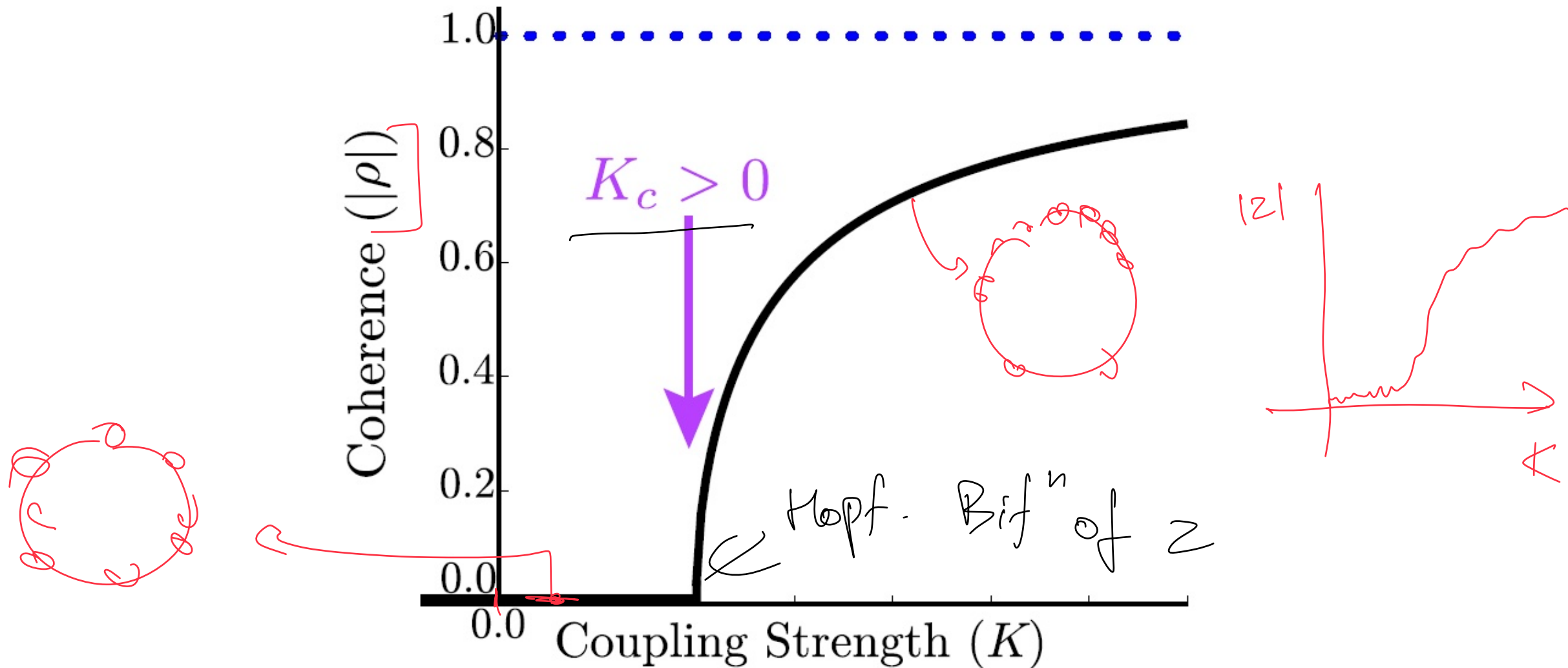
Strogatz CH13
 [Ott § 6.5]

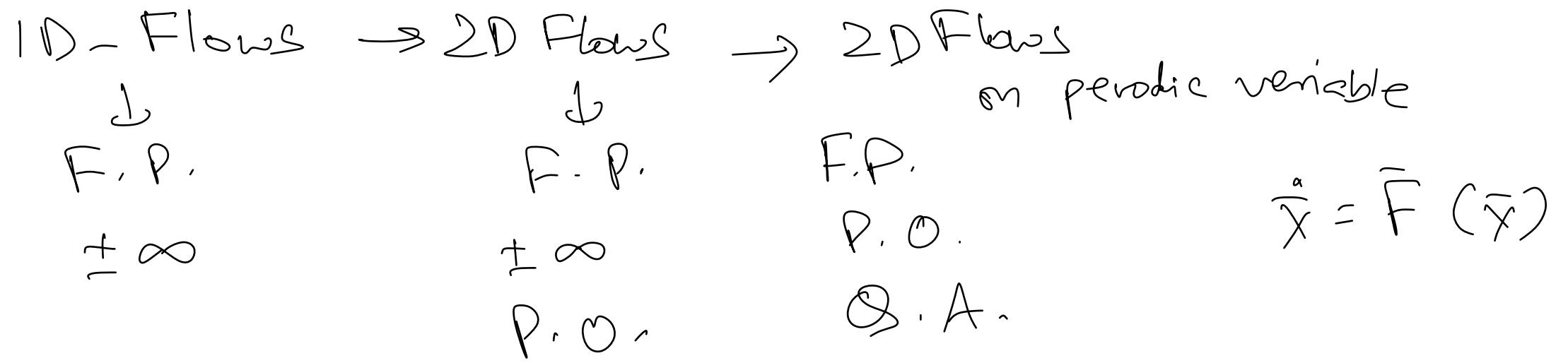
$$\omega_i \rightarrow \omega_i - \langle \omega_i \rangle$$



- Entrained Population
- Free-running Population

$\rho = z$





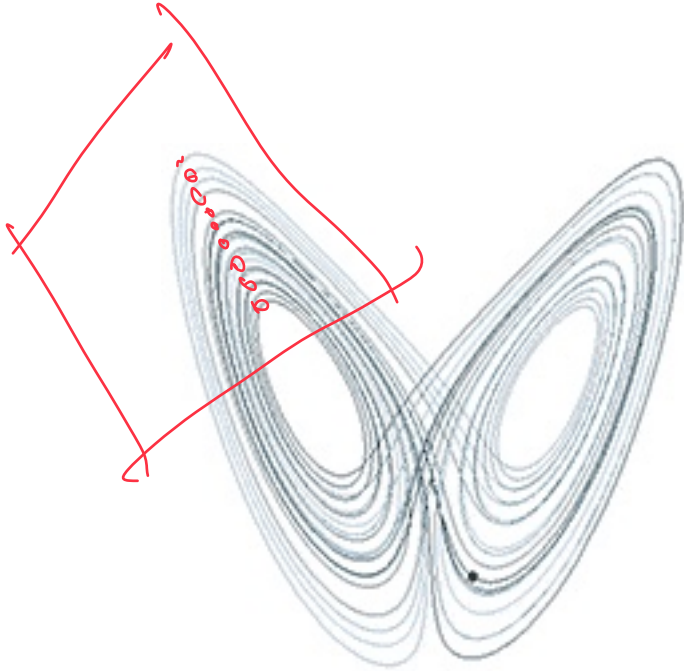
Chaotic attractor → Need 3 or more dim.

↳ If Flows

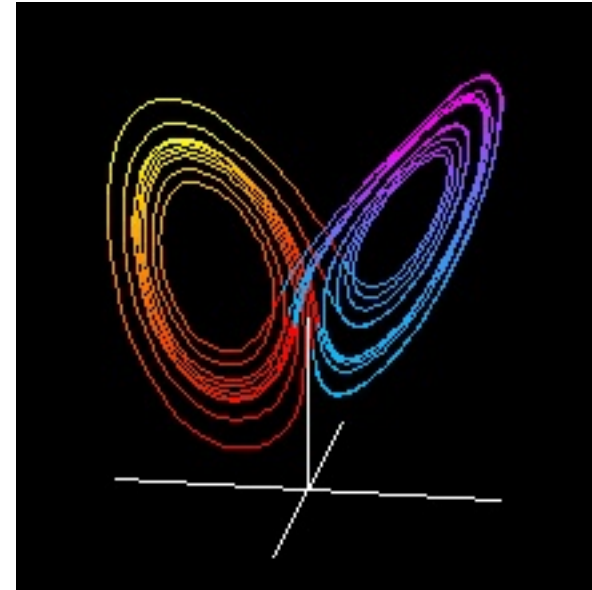
→ 1D Map → enough for
class

Lorenz Model

$$\begin{aligned}\dot{x} &= \sigma(y - x) \\ \dot{y} &= rx - y - xz \\ \dot{z} &= xy - bz\end{aligned}$$



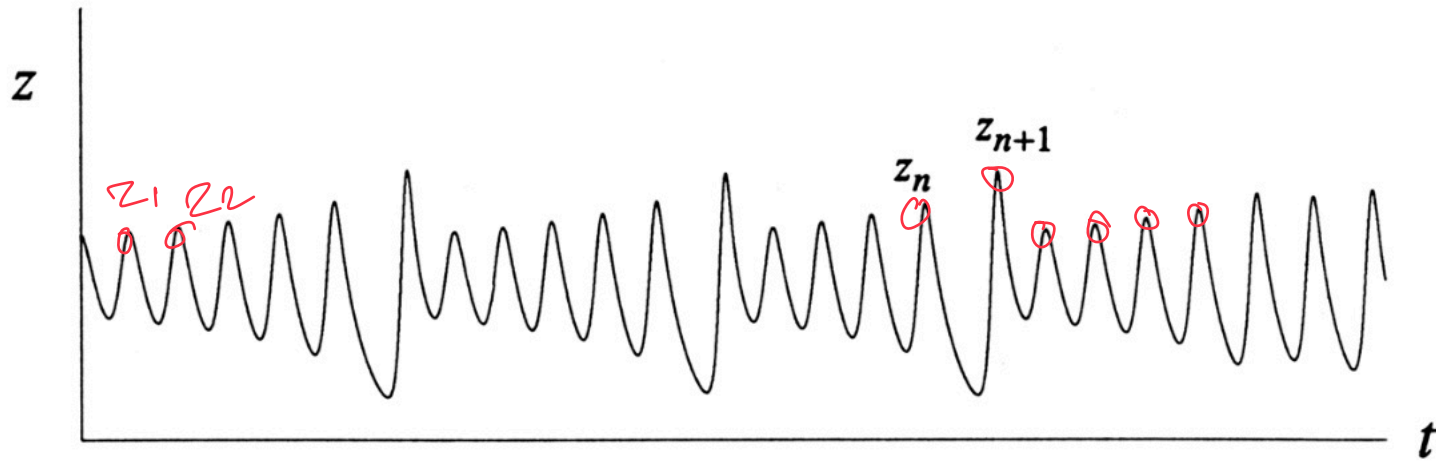
Wikipedia



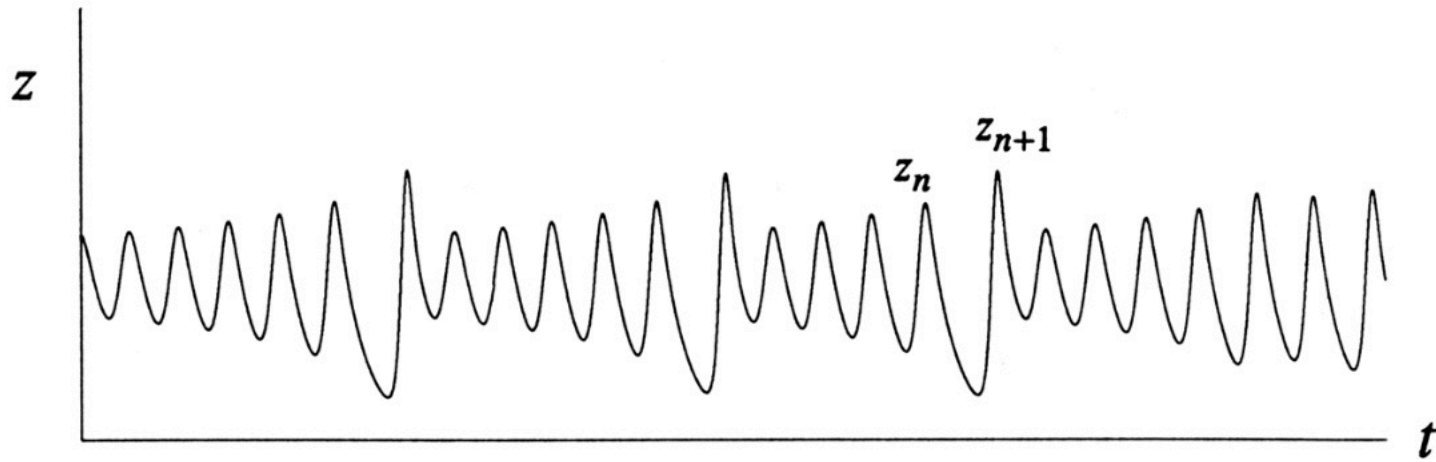
[Source](#)

See also: https://itp.uni-frankfurt.de/~gros/Vorlesungen/SO/simulation_example/

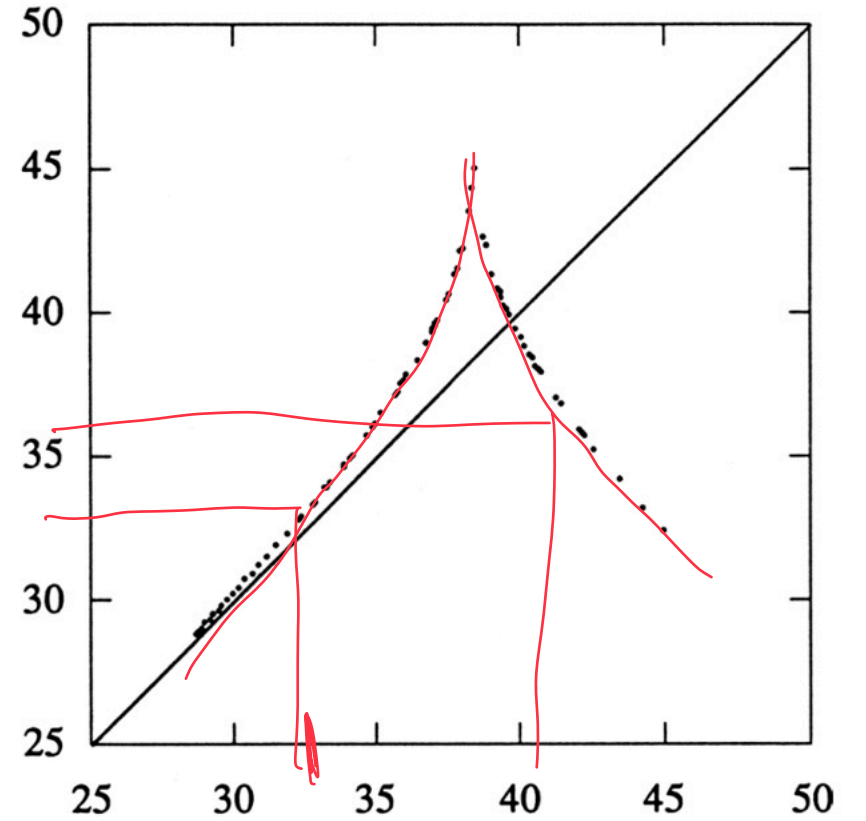
Lorenz Model z return map



Lorenz Model z return map



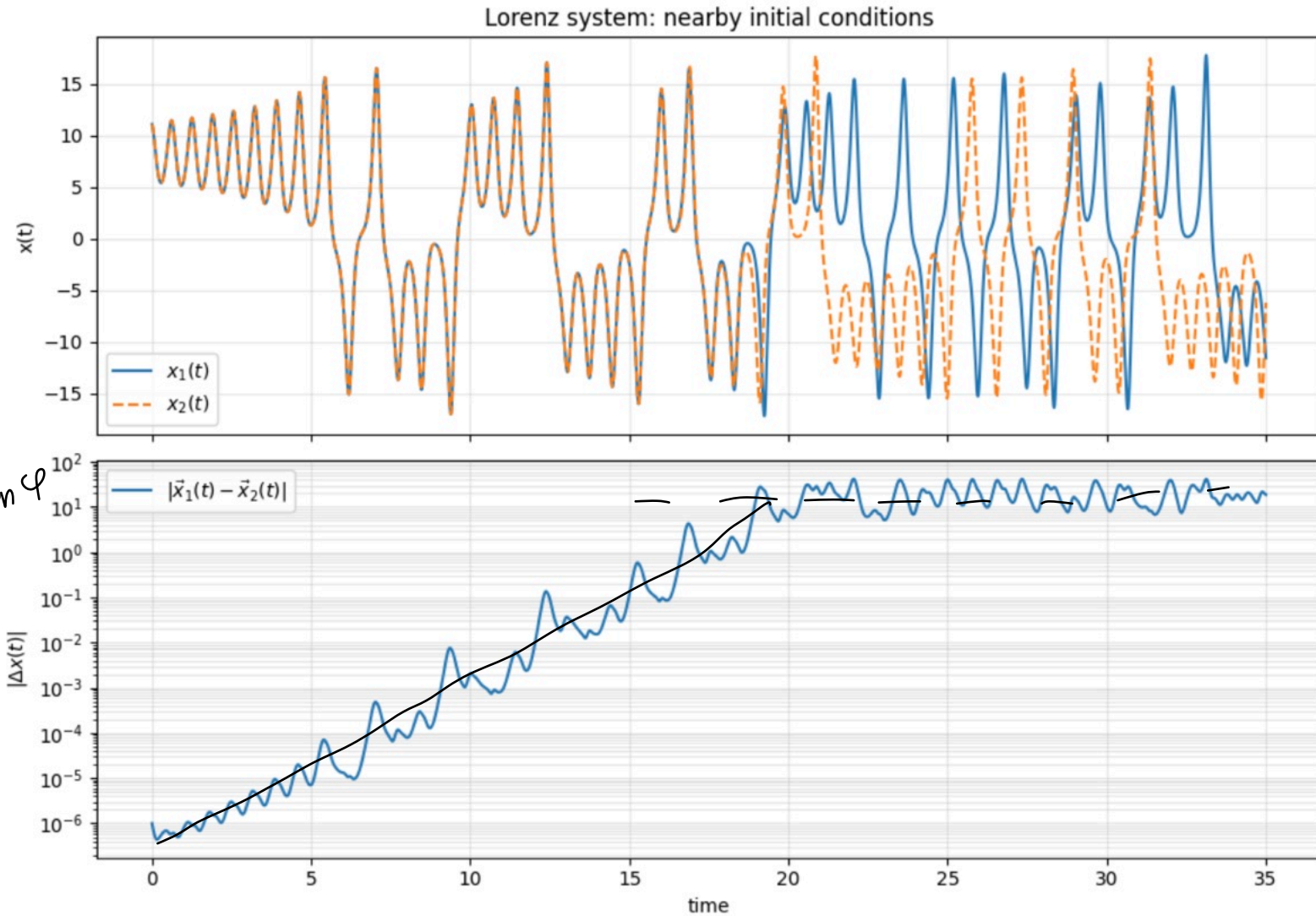
z_{n+1}



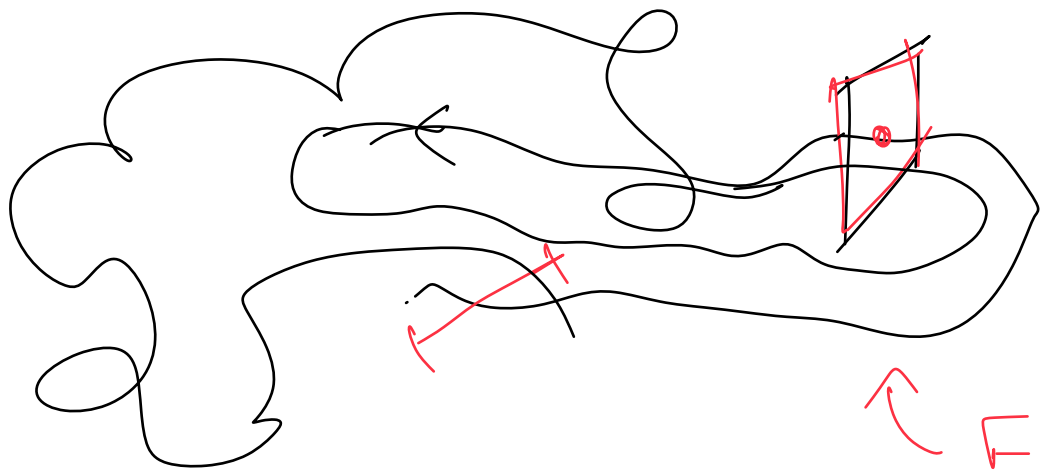
z_n

Dynamical System
in discrete time } Map

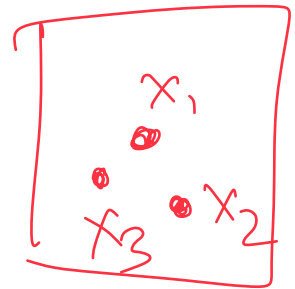
Lorenz Model



Chaos
↓
Exp. divergence
but
bounded



Flow



Map

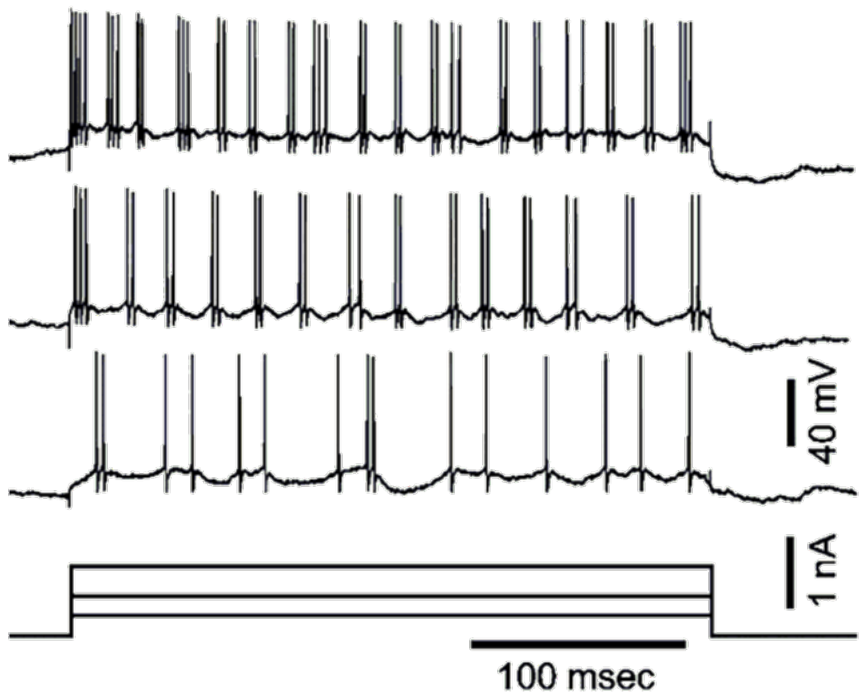
Poincare' Section

Bursting neurons

Est Ch 6

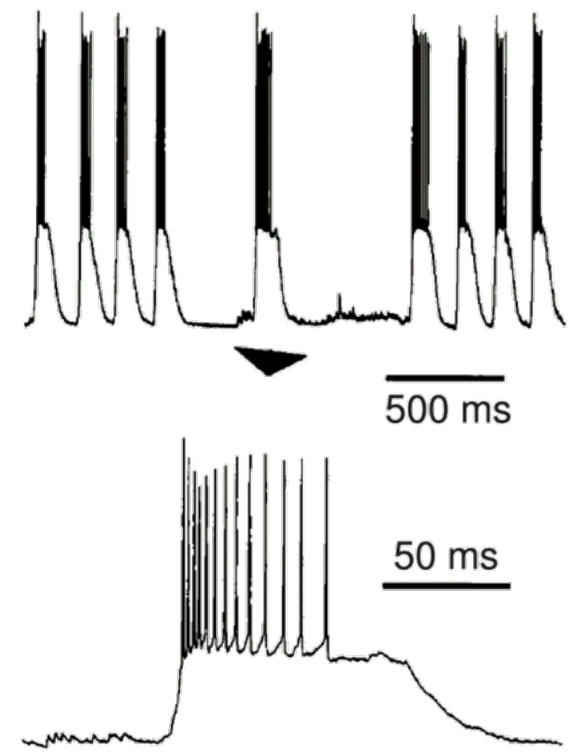
+ 12. Ch 9

(a) cortical chattering neuron

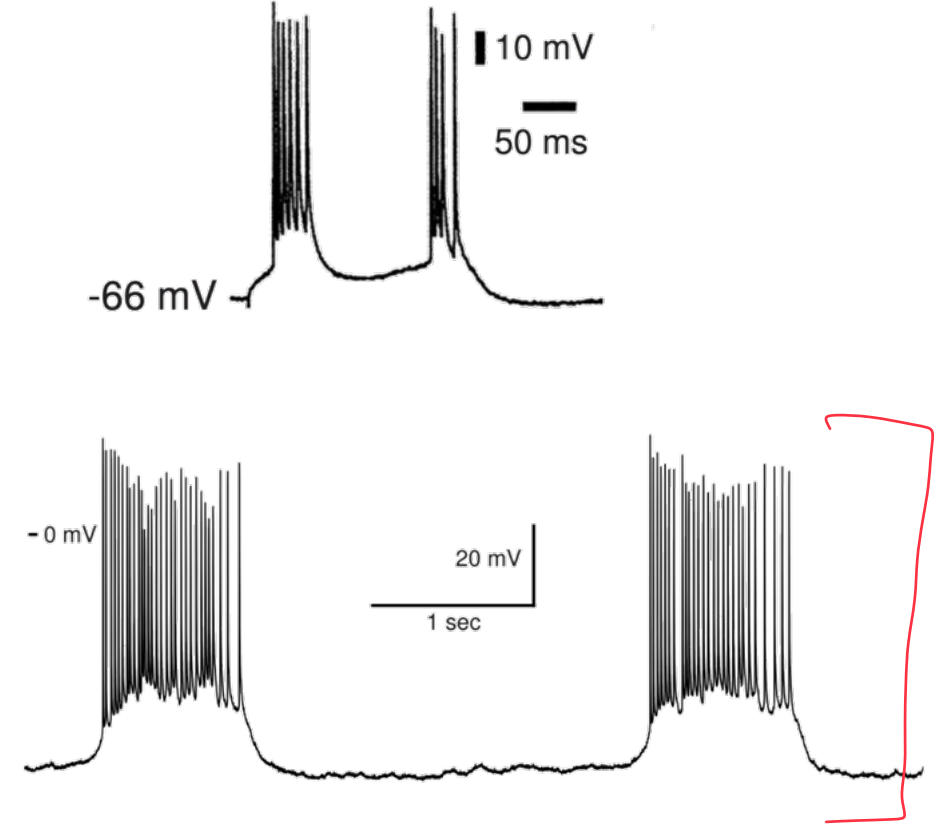


Iz. Fig. 9.1

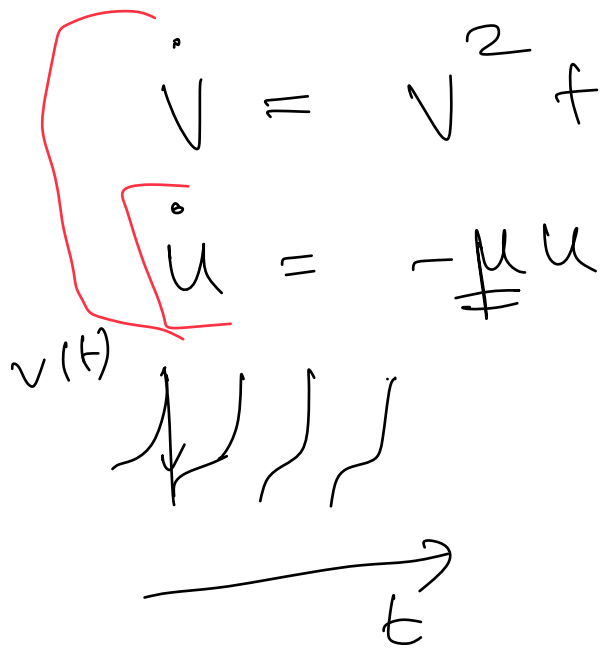
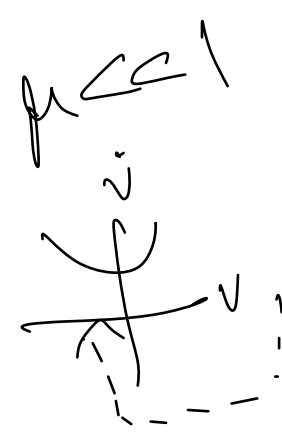
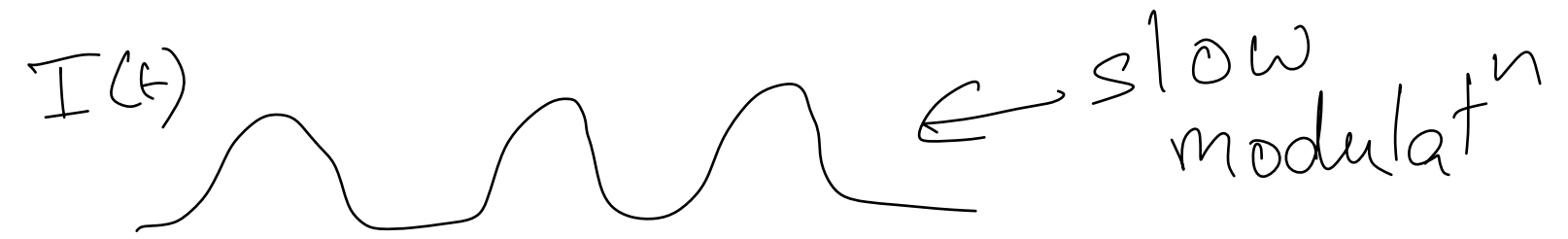
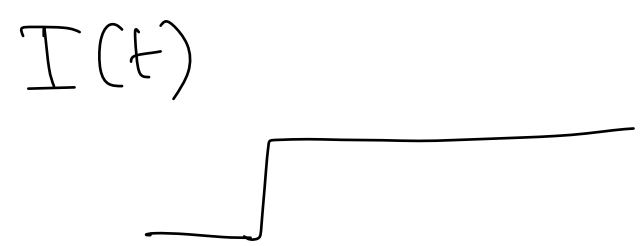
(d) thalamic reticular neuron



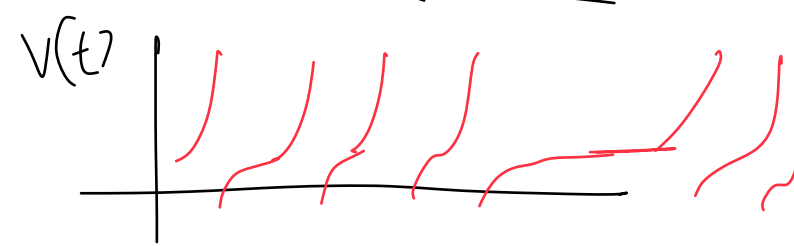
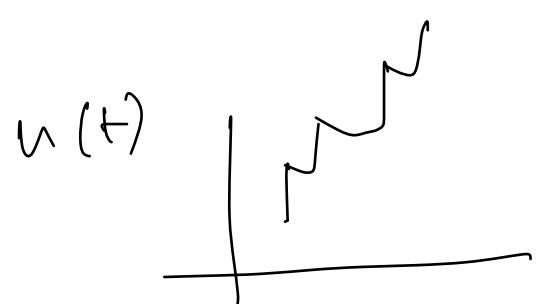
(f) hippocampal pyramidal neuron



Iz. Fig. 9.27



Resetting
 if $v \rightarrow \infty$
 reset $v \rightarrow 1$
 $u \rightarrow \underline{u + d}$

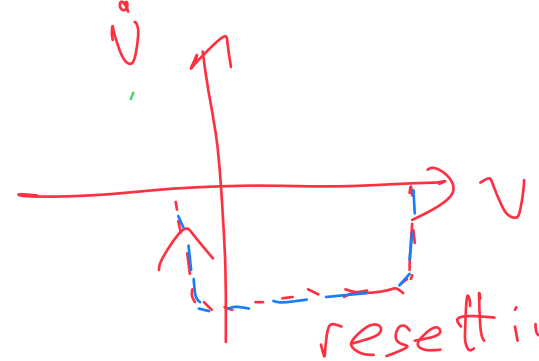


$$\dot{v} = v^2 + I - u$$

$$u = -\mu h$$

$$\mu \ll 1$$

@ $v \rightarrow \uparrow$
 reset $u \rightarrow \underline{u+d}$



\rightarrow 3d Flow

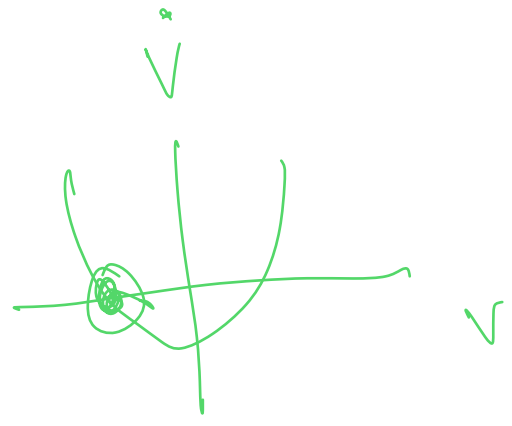
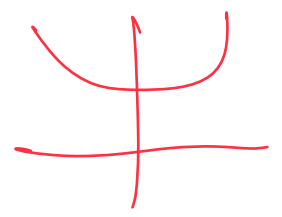
Fold-Homoclinic

Bursting neuron

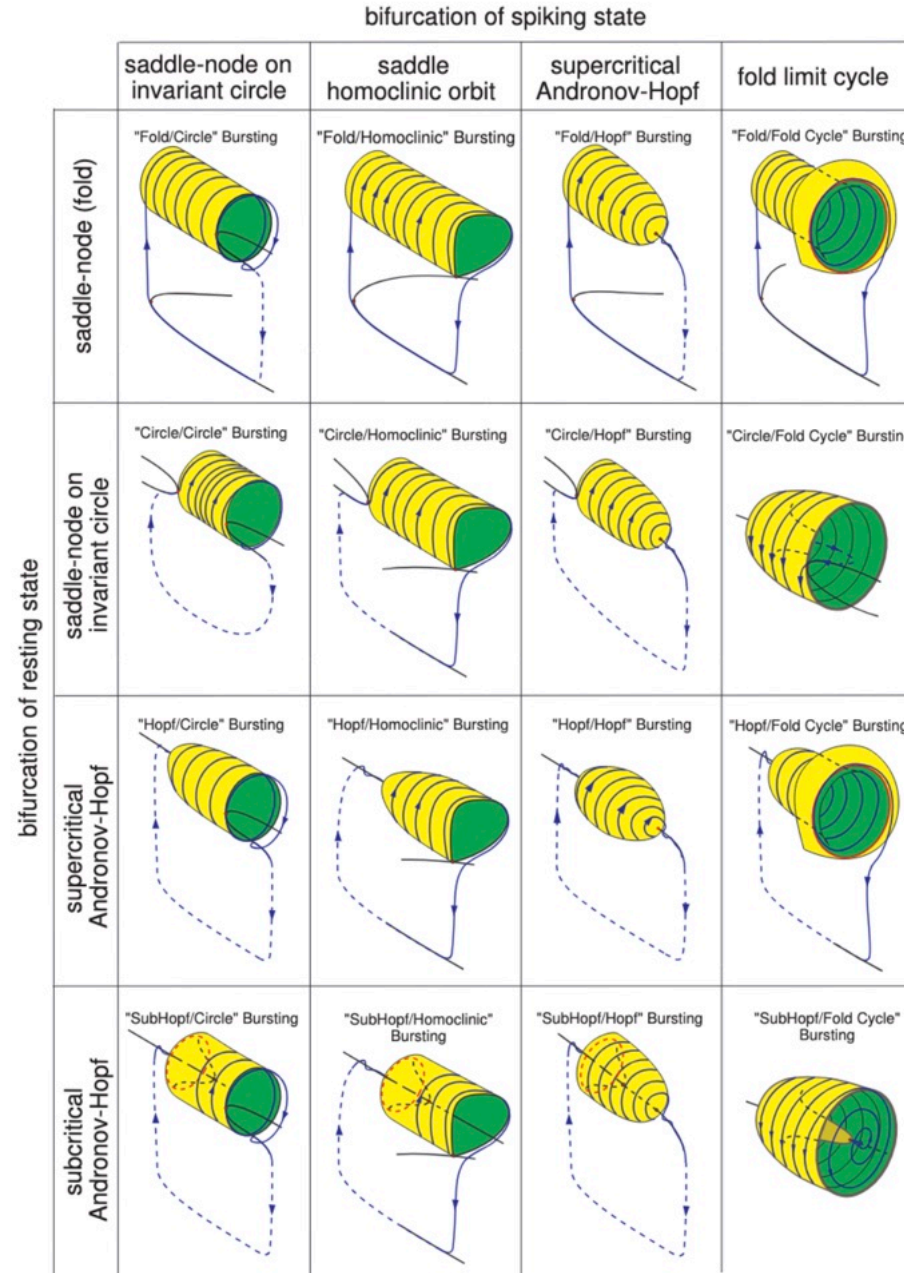


$$u(0) = 0$$

$$I > 0$$

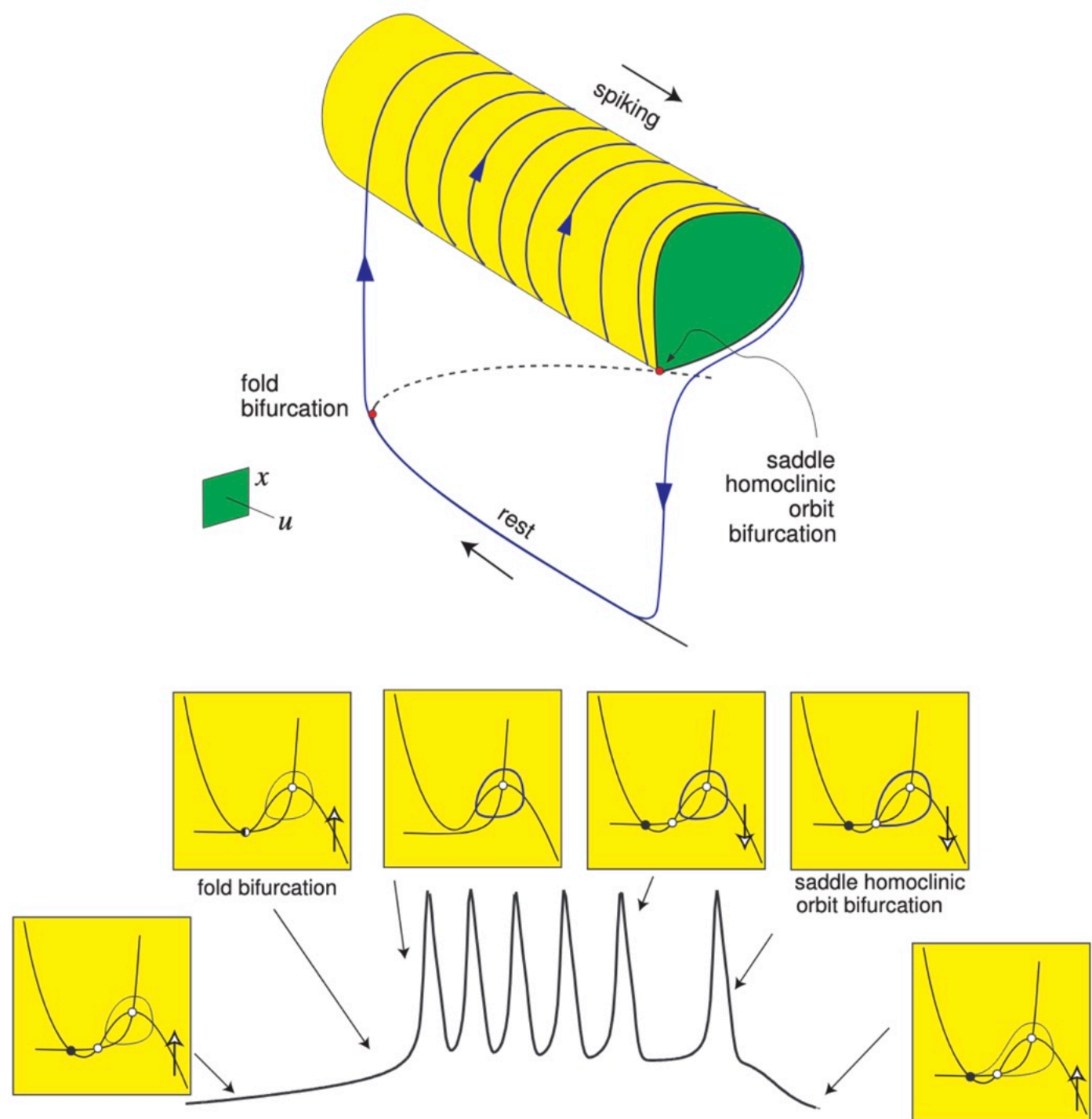


Zoo of bursting neurons

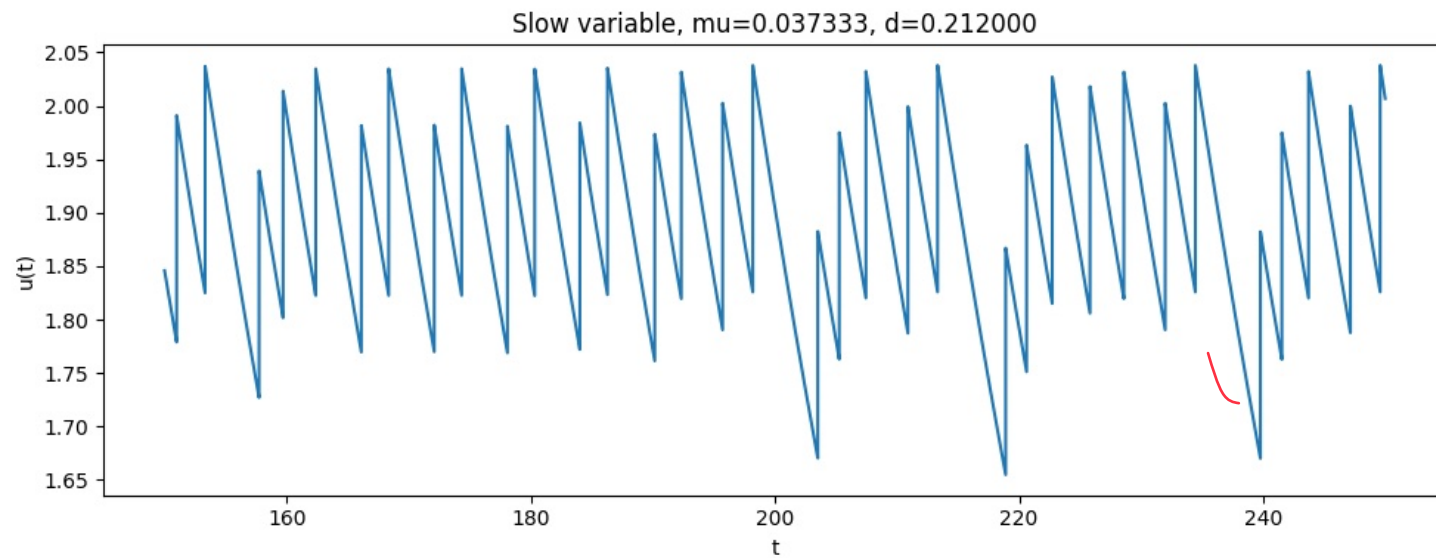
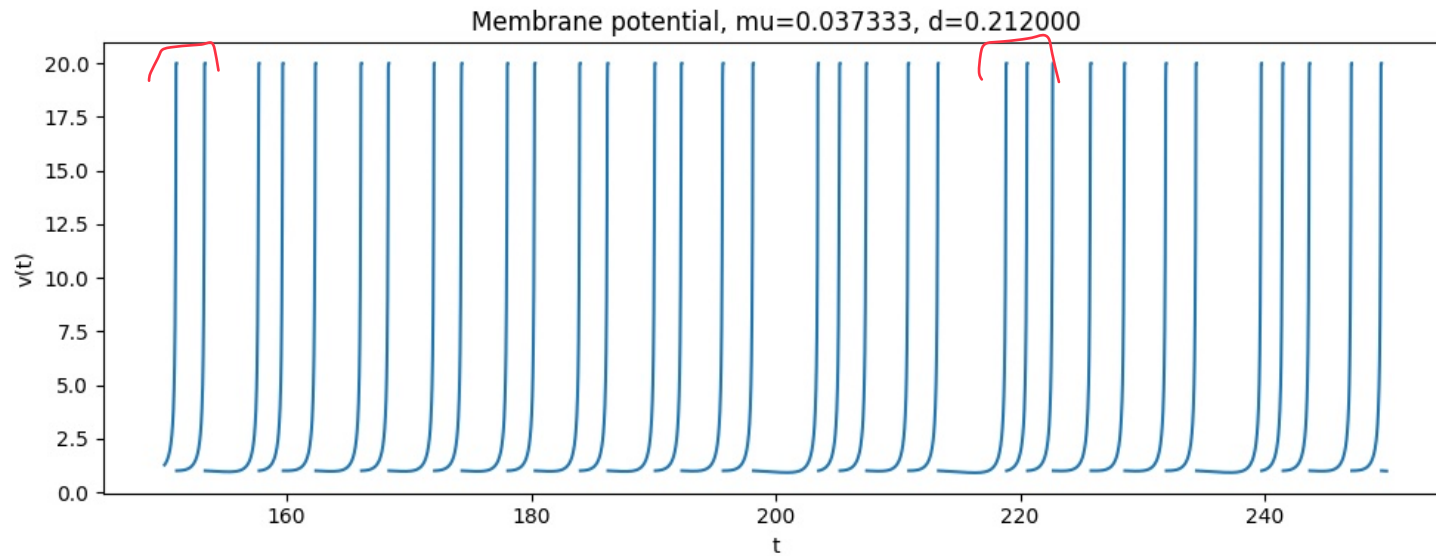


Iz. Fig. 9.24

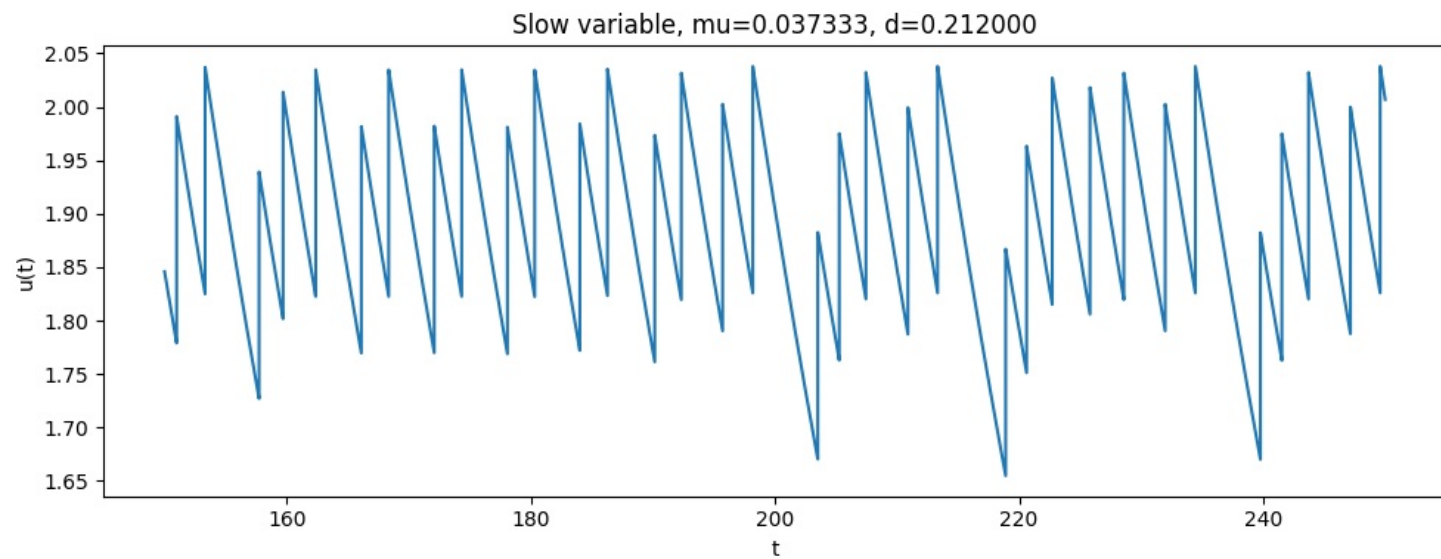
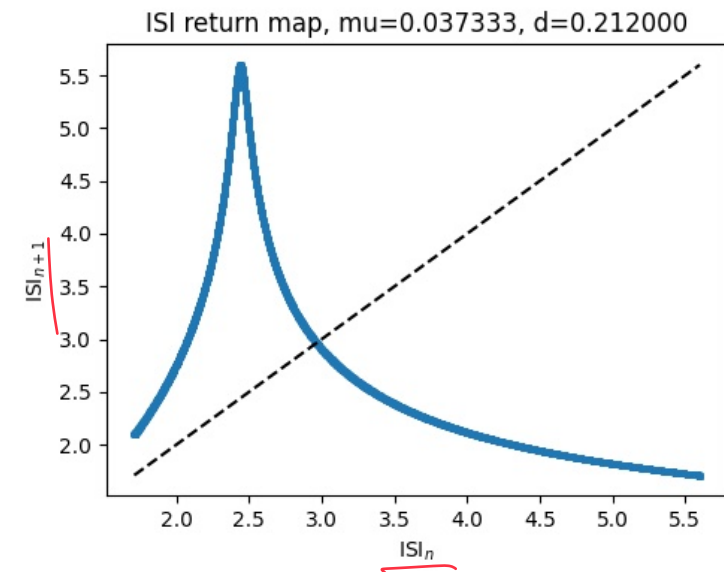
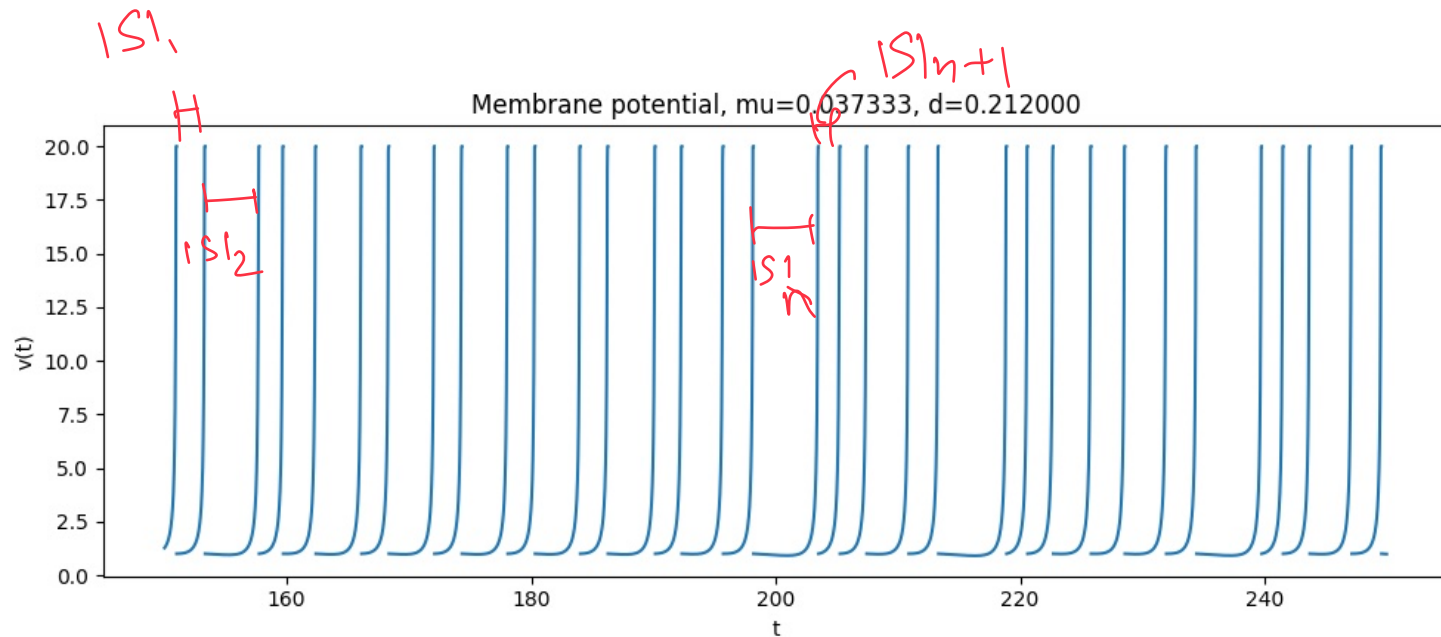
Fold-homoclinic bursting neuron



Canonical Fold-homoclinic bursting neuron

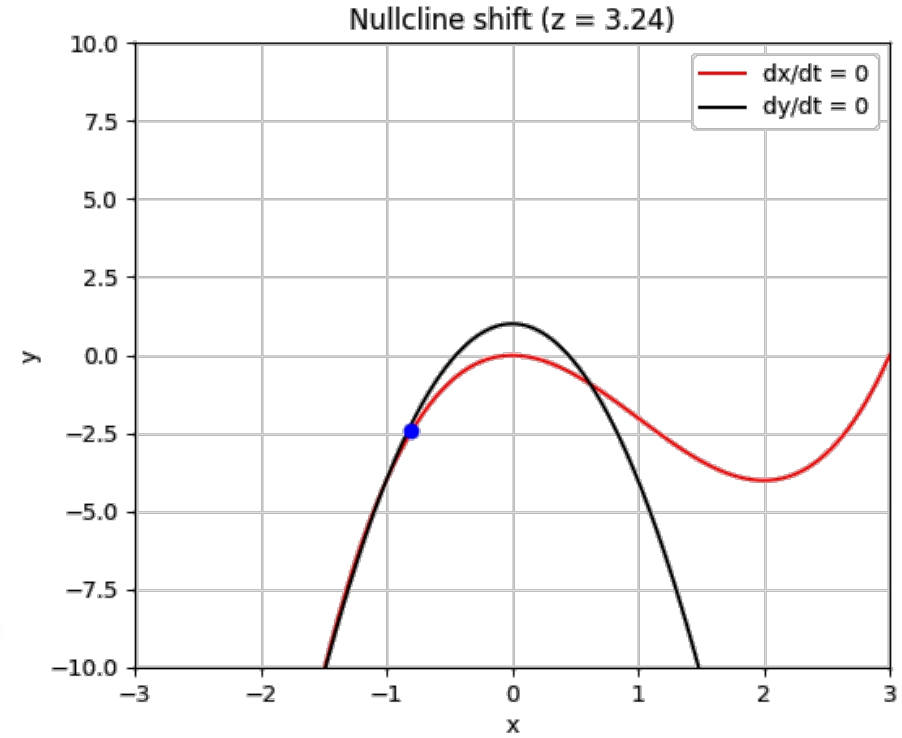
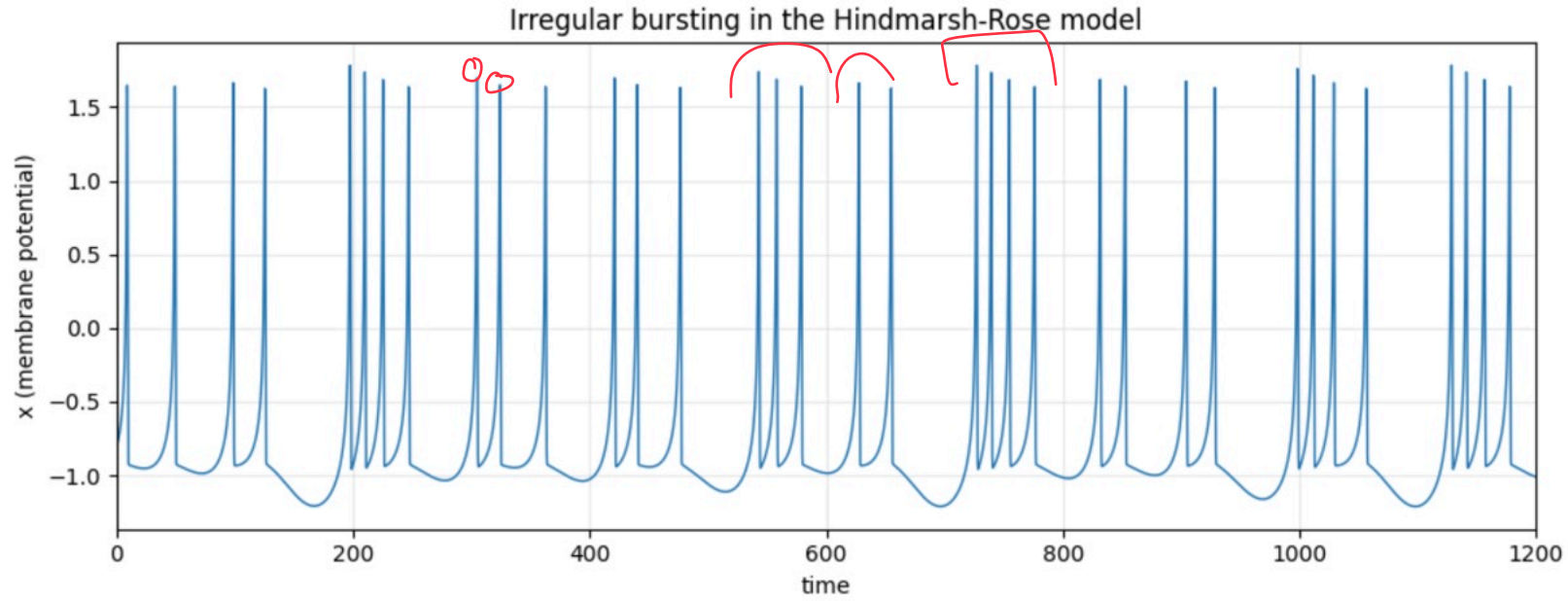


Canonical Fold-homoclinic bursting neuron

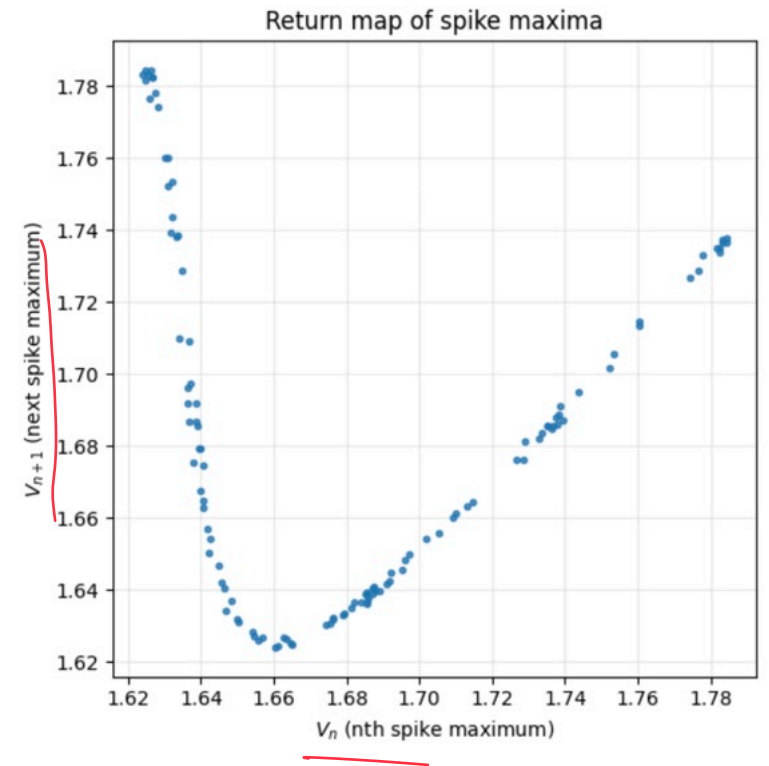
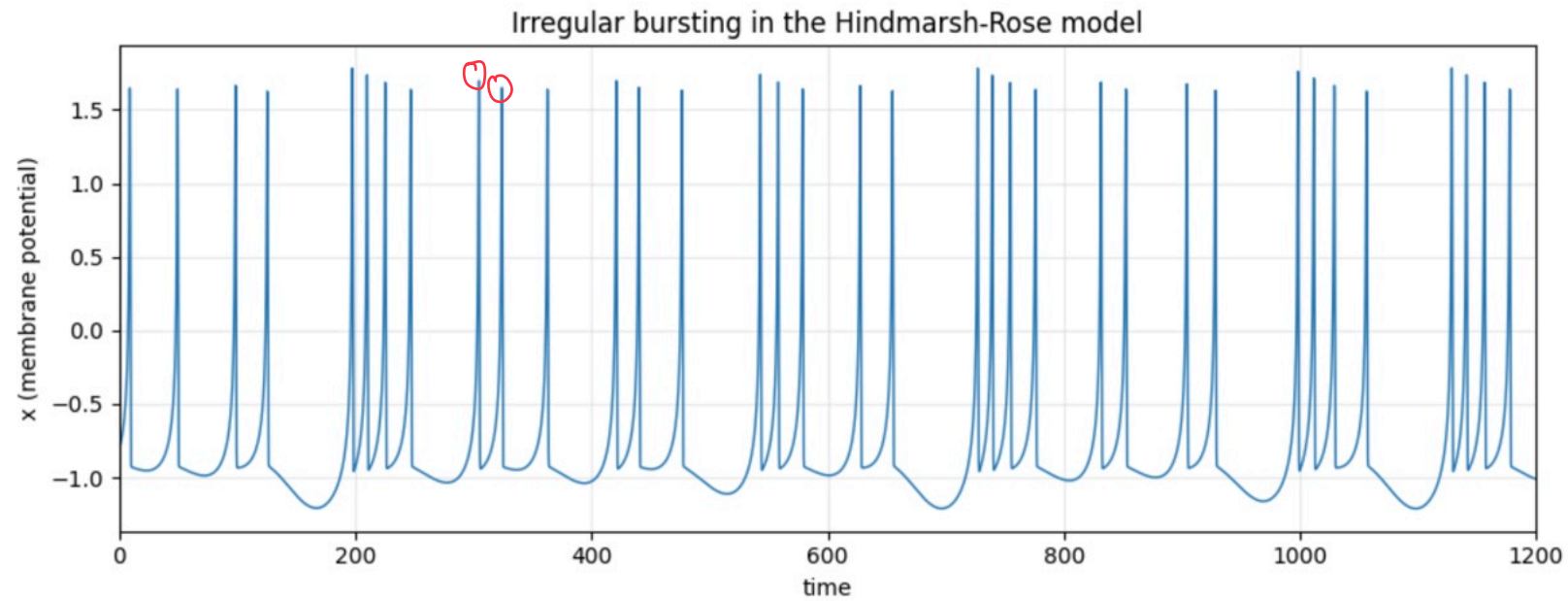


$ISI \rightarrow$ Inter spike
Interval

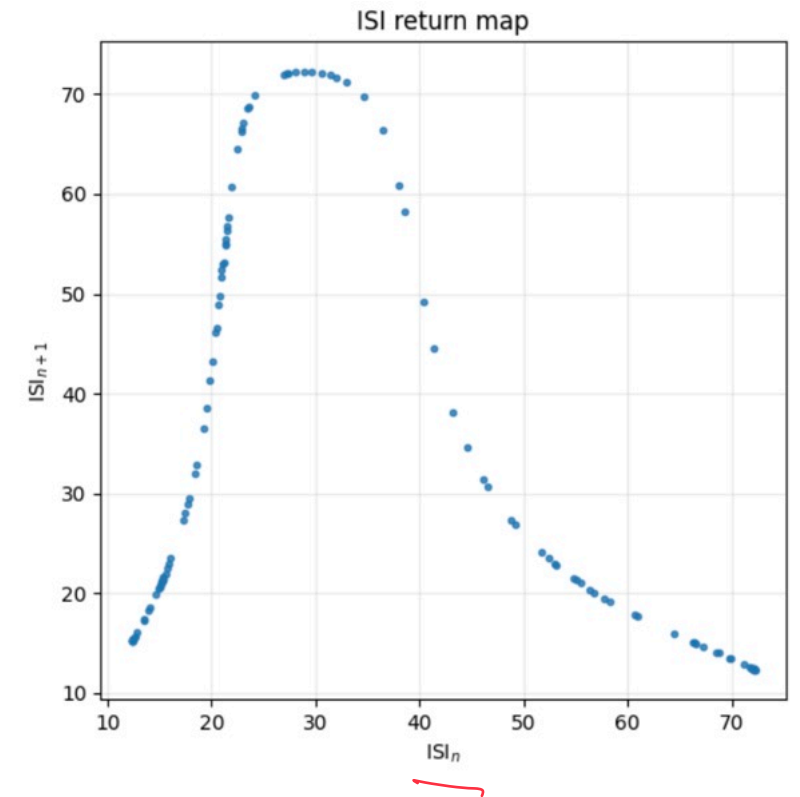
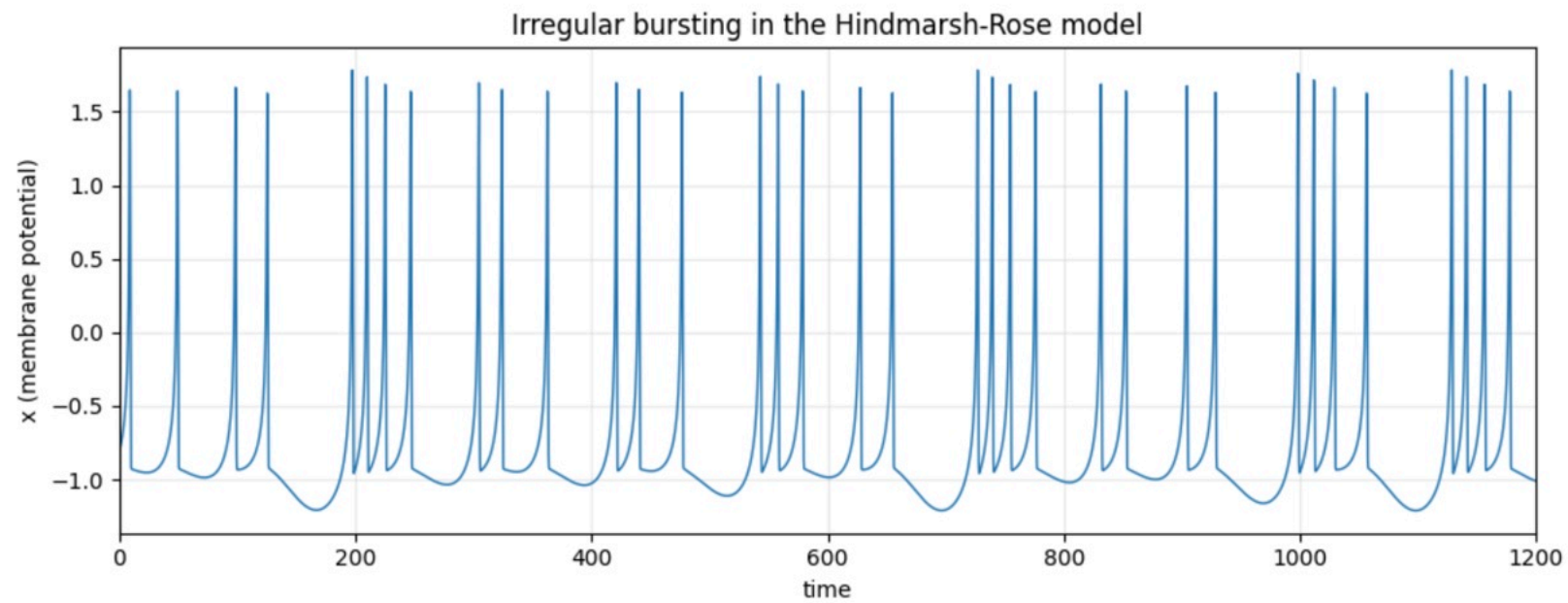
Hindmarsh Rose neuron



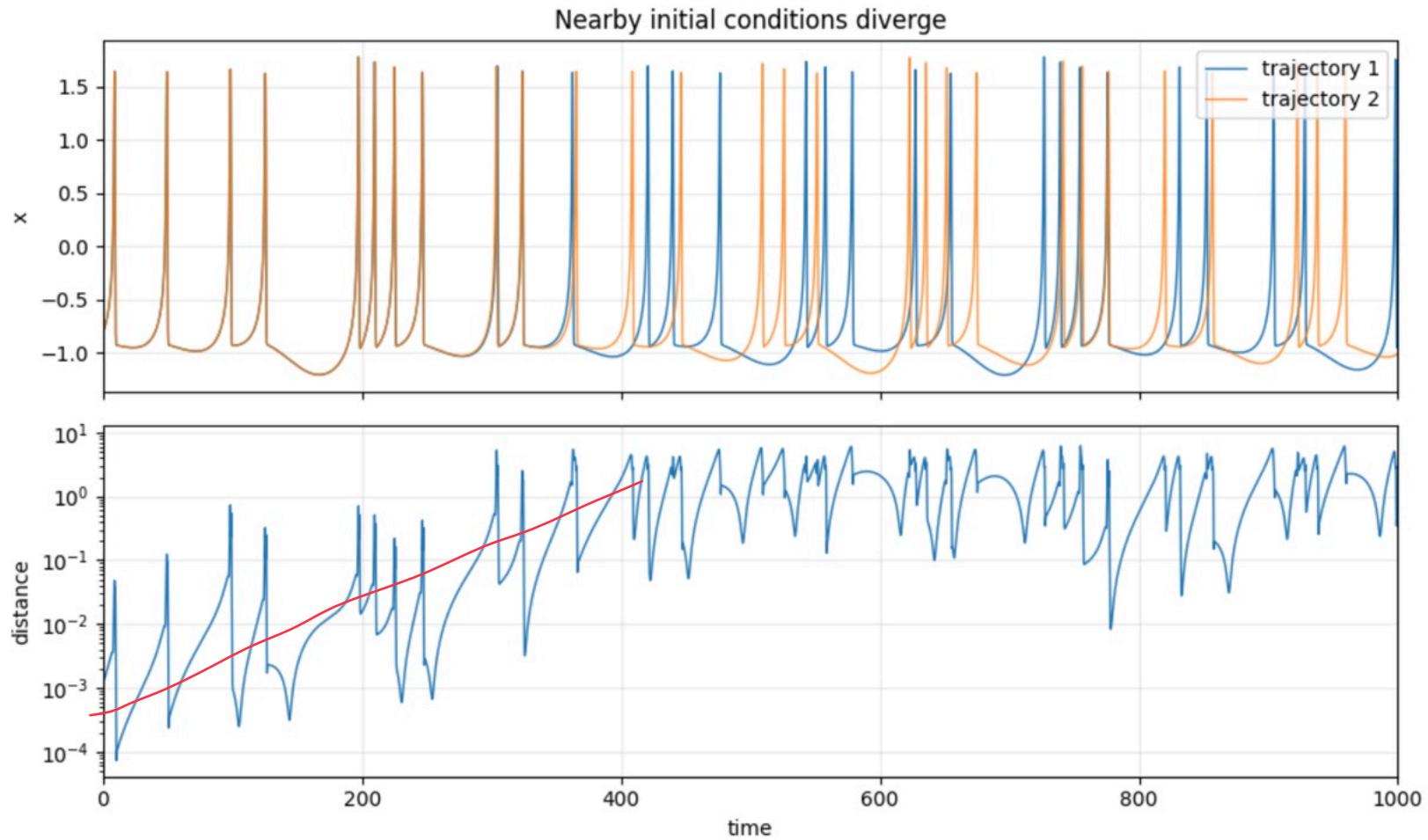
Hindmarsh Rose neuron

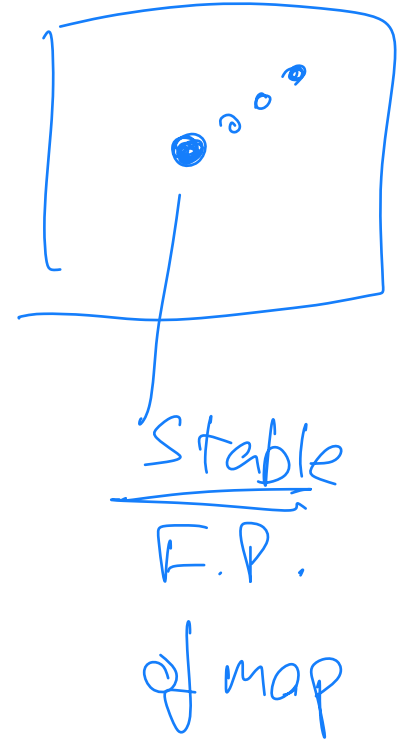
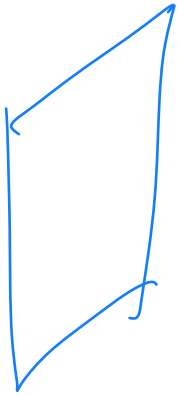


Hindmarsh Rose neuron

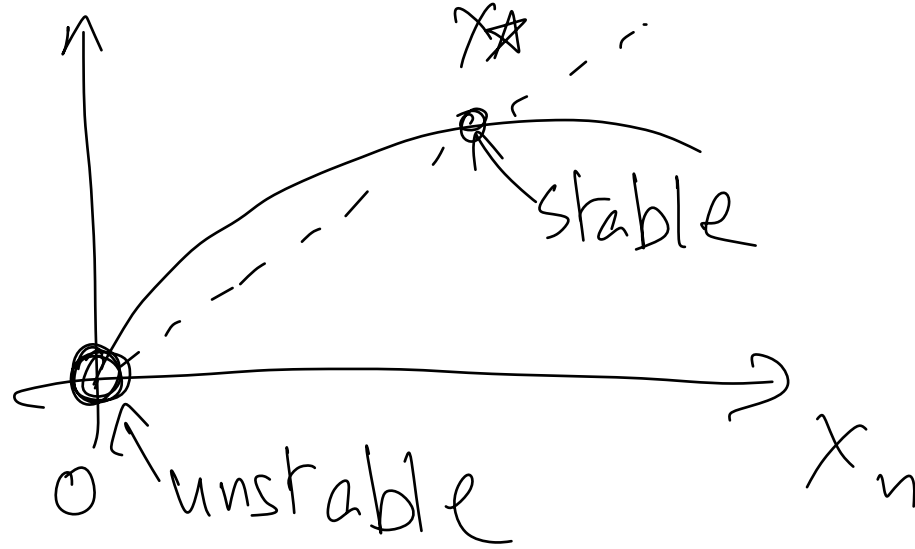


Hindmarsh Rose neuron





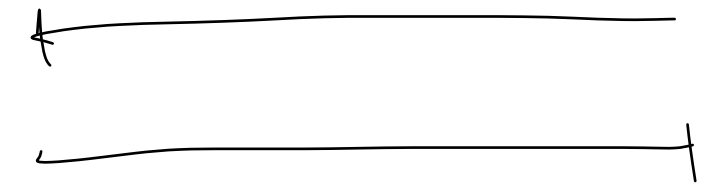
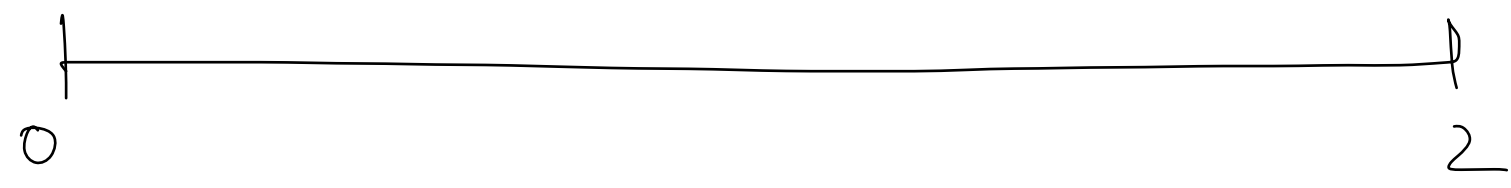
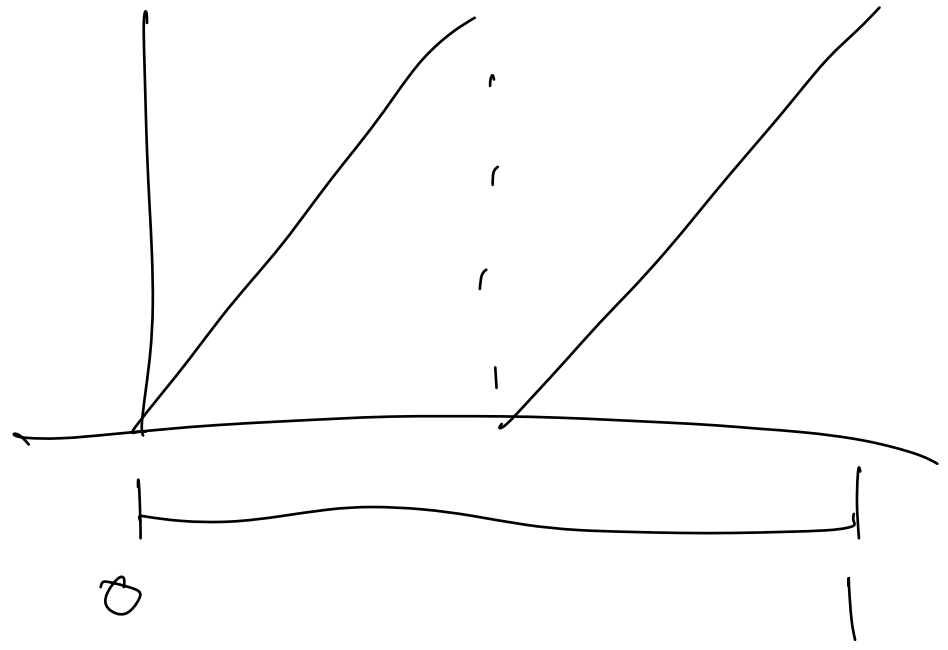
Maps

 x_{n+1} 

04-06-2026

$$\lambda = \lim_{n \rightarrow \infty} \lim_{\epsilon \rightarrow 0} \frac{1}{n} \ln \left| \frac{y_n - x_n}{y_0 - x_0} \right|$$

$$\approx \left\langle \ln |F'(x)| \right\rangle_n = \ln |F'(x_A)|$$

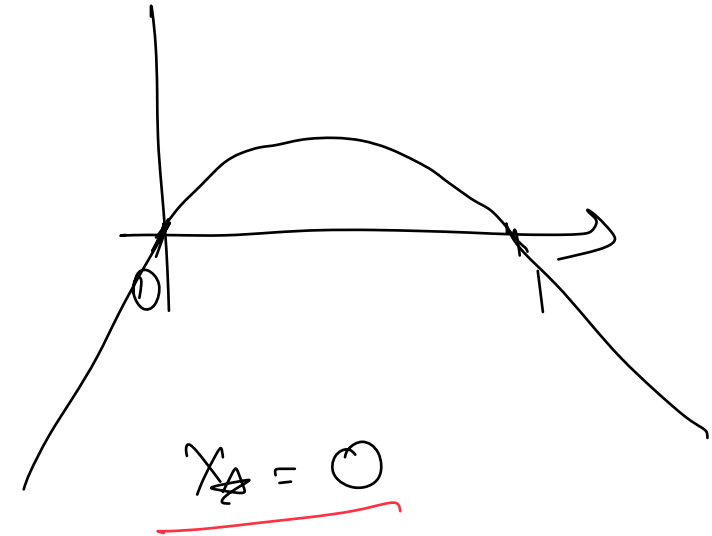
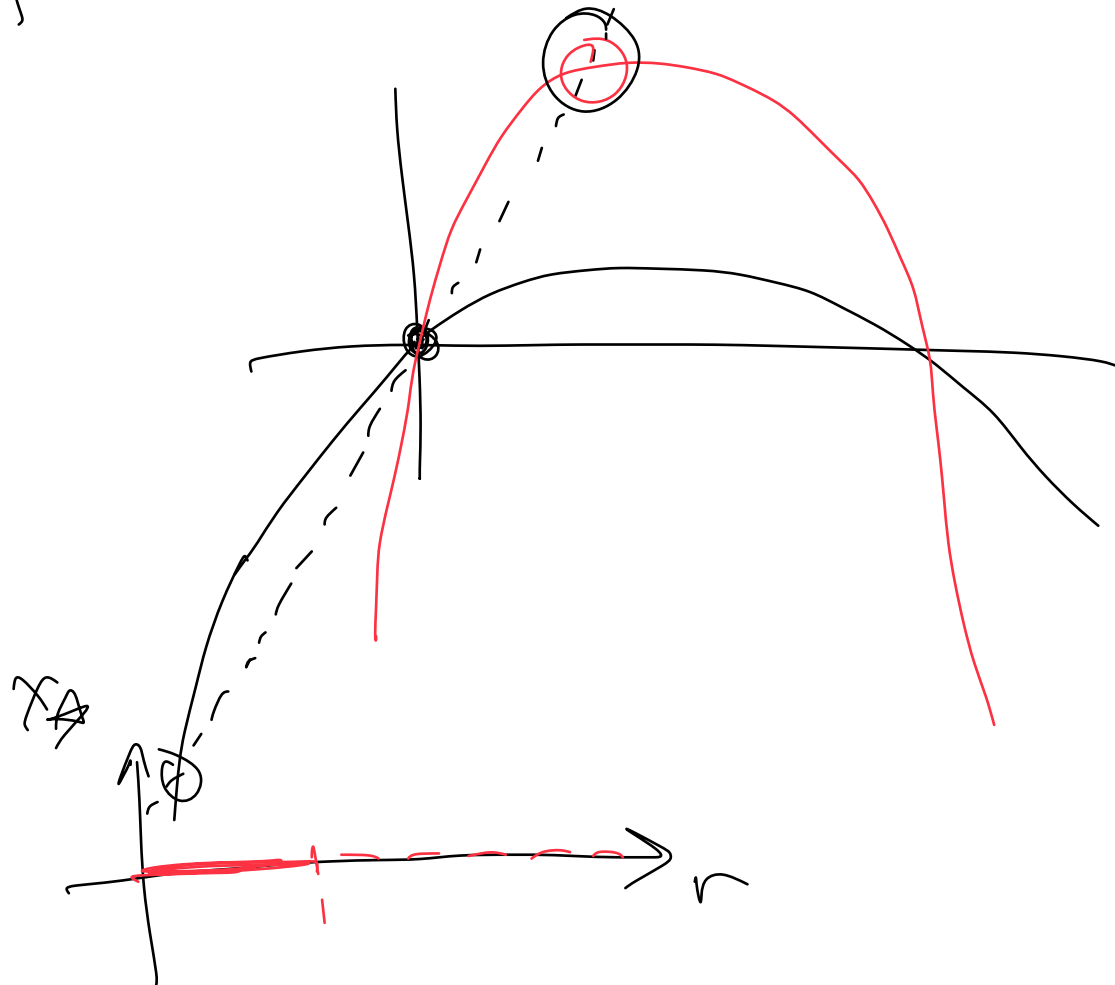


Logistic Map

Strogatz Ch. 10; Ott Ch. 2

$$x_{n+1} = r x_n (1 - x_n) \approx F(x_n)$$

if $r < 1$



$$F' = r - 2r x$$

$$\underline{F'(x=0) = r}$$

stable $r < 1$
unstable $r > 1$

$$x = r x (1 - x)$$

$$\text{if } x \neq 0$$

$$r(1 - x) = 1$$

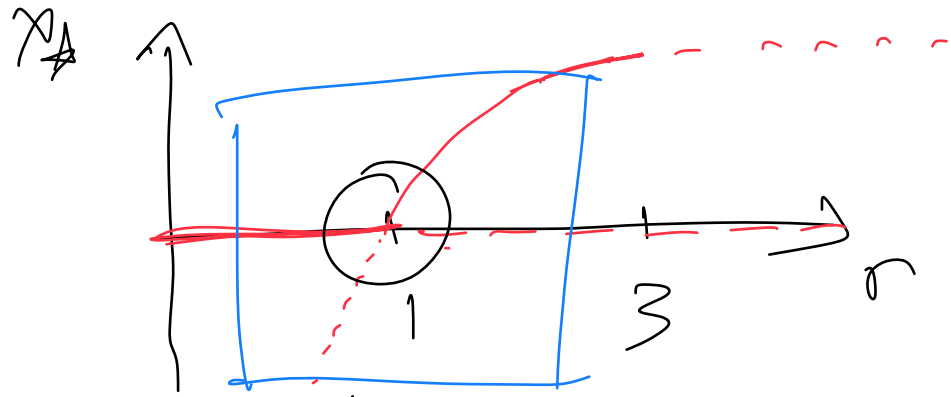
$$x = 1 - \frac{1}{r}$$

$$F' = r - 2rx$$

$$= r - 2r \left(1 - \frac{1}{r}\right)$$

$$= r - 2r + 2$$

$$= \underbrace{2 - r}$$



Transcritical
Bifurcatⁿ

$$x^* = 1 - \frac{1}{r} \rightarrow \text{stable}$$

unstable

$$1 < r < 3$$

$$r > 3$$

$$x_{n+1} = F(x_n) = r x_n (1 - x_n)$$

$$x_{\star} = F(F(x_{\star}))$$

$$x = r [r x (1 - x)] [1 - r x (1 - x)]$$

$$x_{\star}^{1,2} = \frac{r+1 \pm \sqrt{(r-3)(r-1)}}{2r}$$

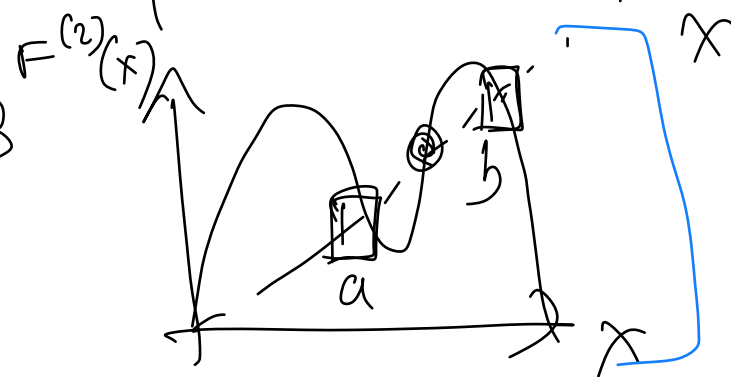
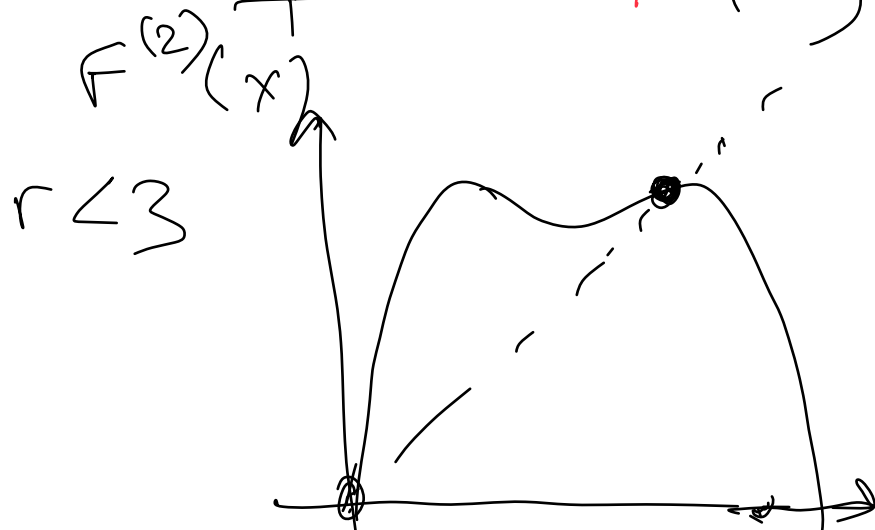
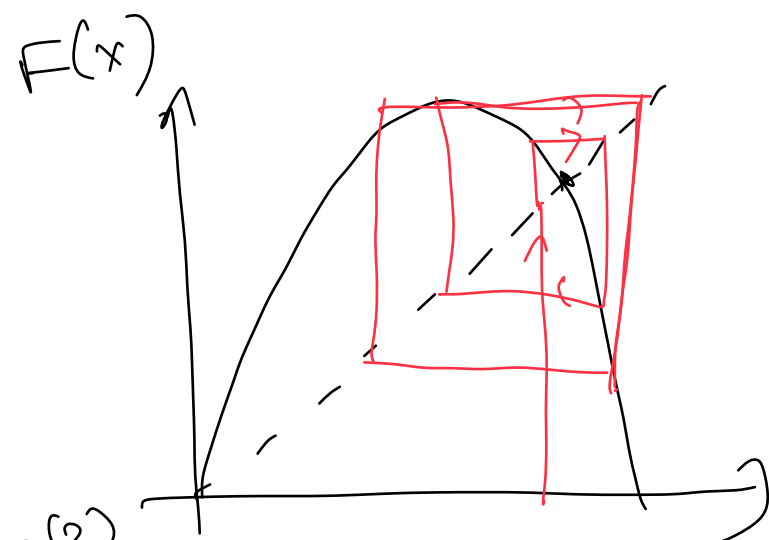
$$r=3 \rightarrow x_{\star}^1 = x_{\star}^2$$

$$r=3+\epsilon \rightarrow (x_{\star}^1 - x_{\star}^2) \sim \sqrt{\epsilon}$$

$$F(a) = b$$

$$F(b) = a$$

$$\Leftarrow F^{(2)}(a) = a \quad r > 3$$



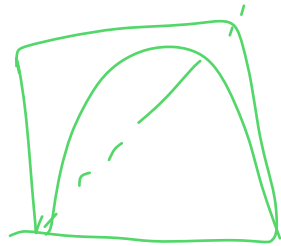
stab. of period 2
orbit

$$F'(x_1) \cdot F'(x_2)$$

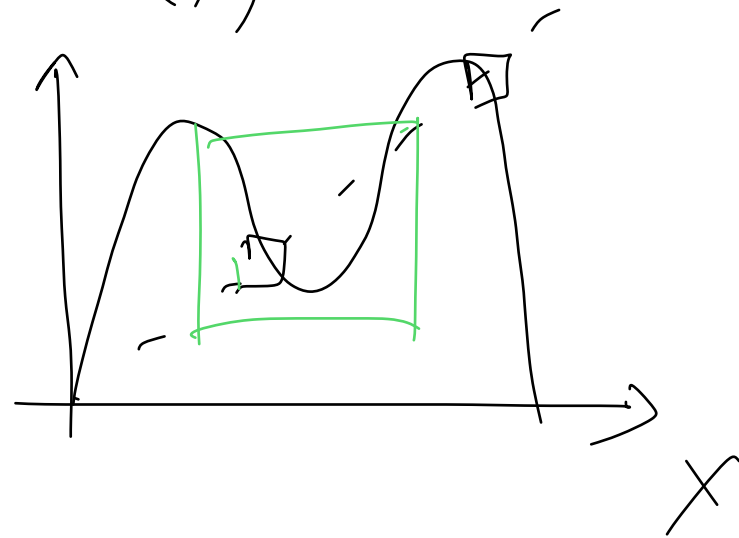
↓

P. 2 orbit
stable

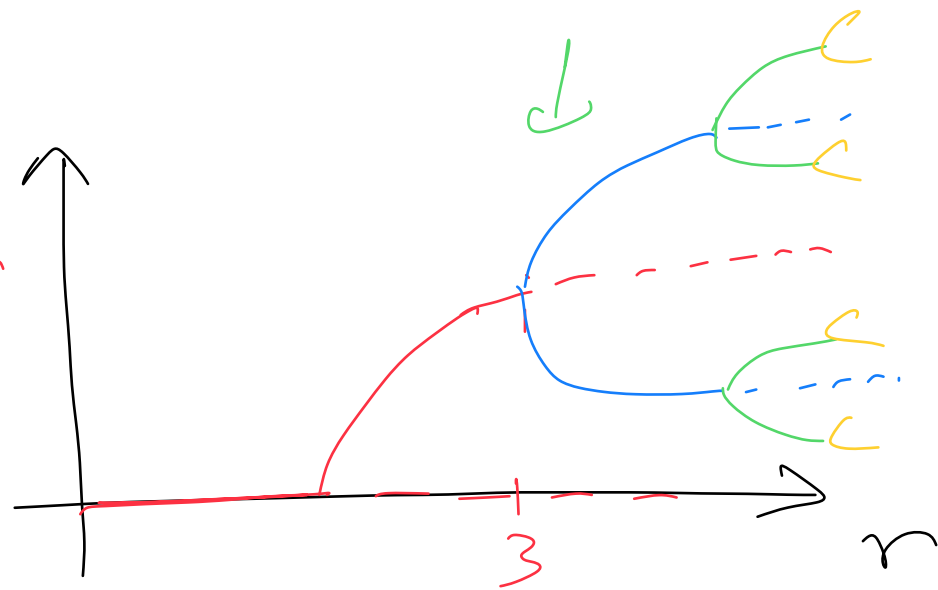
$$3 < r < 1 + \sqrt{6}$$



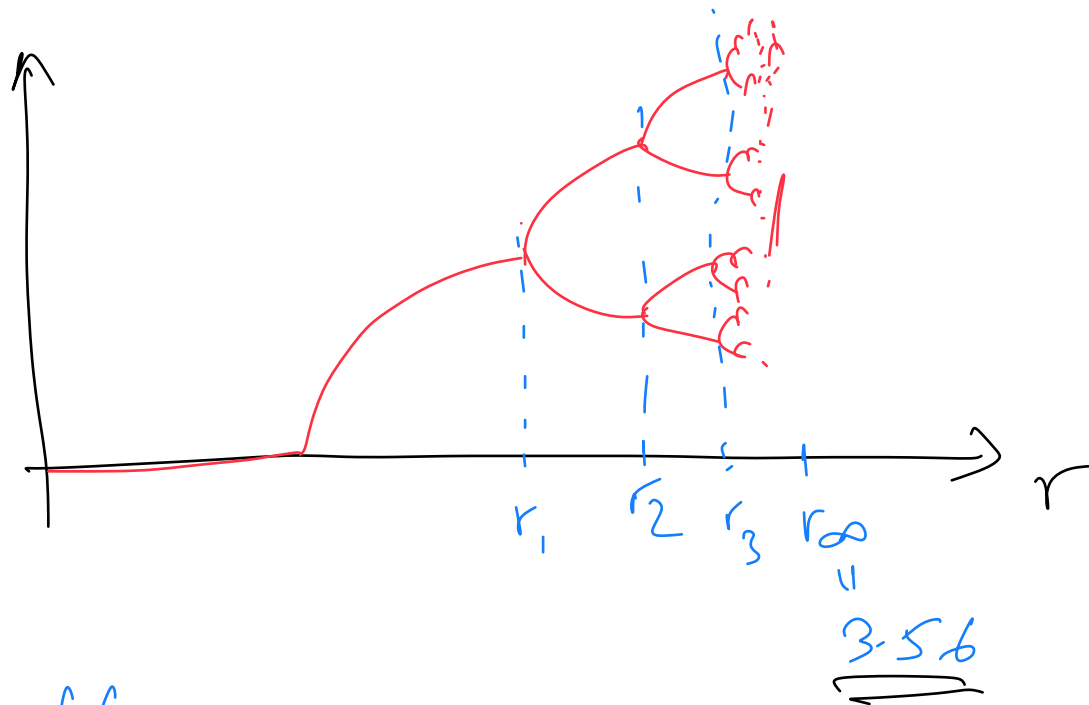
$$F^{(2)}(x)$$



~~Limit pts of x~~



Lim.
pts.



$$\frac{r_m - r_{m-1}}{r_{m+1} - r_m}$$

~ 4.66

Feigenbaum constant

What of

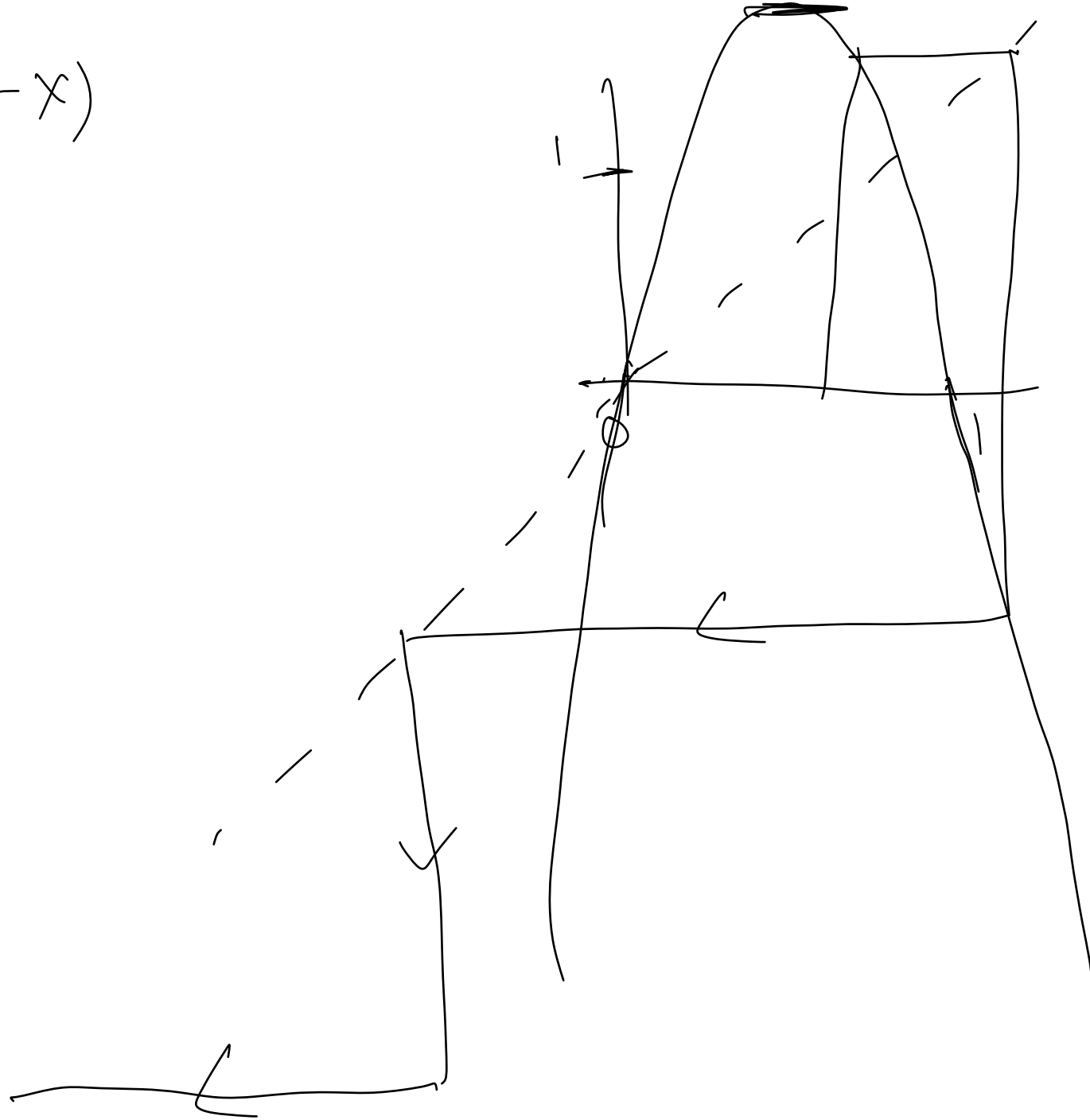
$r_\infty < r < 4$

$$r < r_\infty \rightarrow \lambda < 0$$

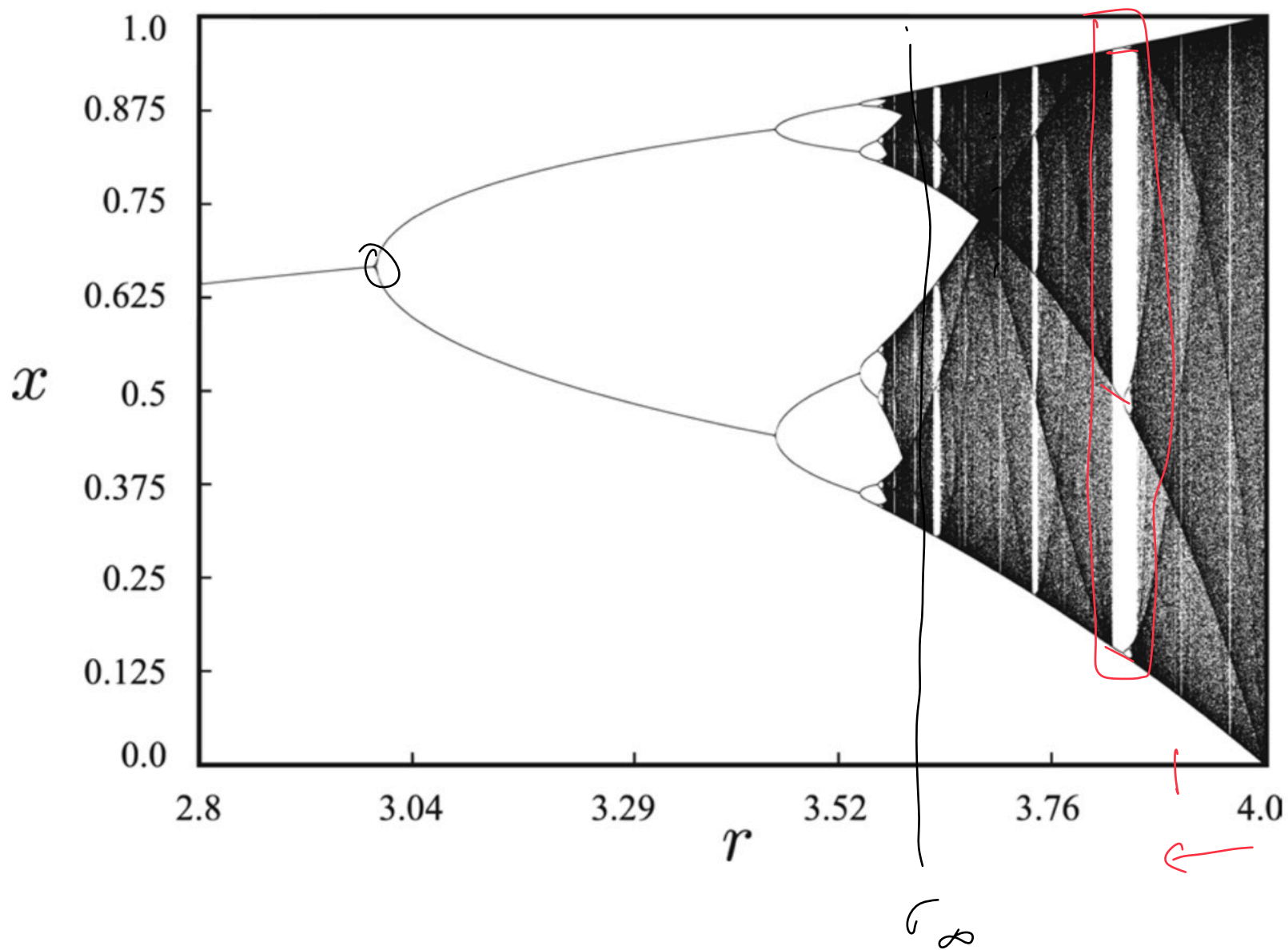
$r > r_\infty \rightarrow$ start of chaos

$$F(x) = r x (1-x)$$

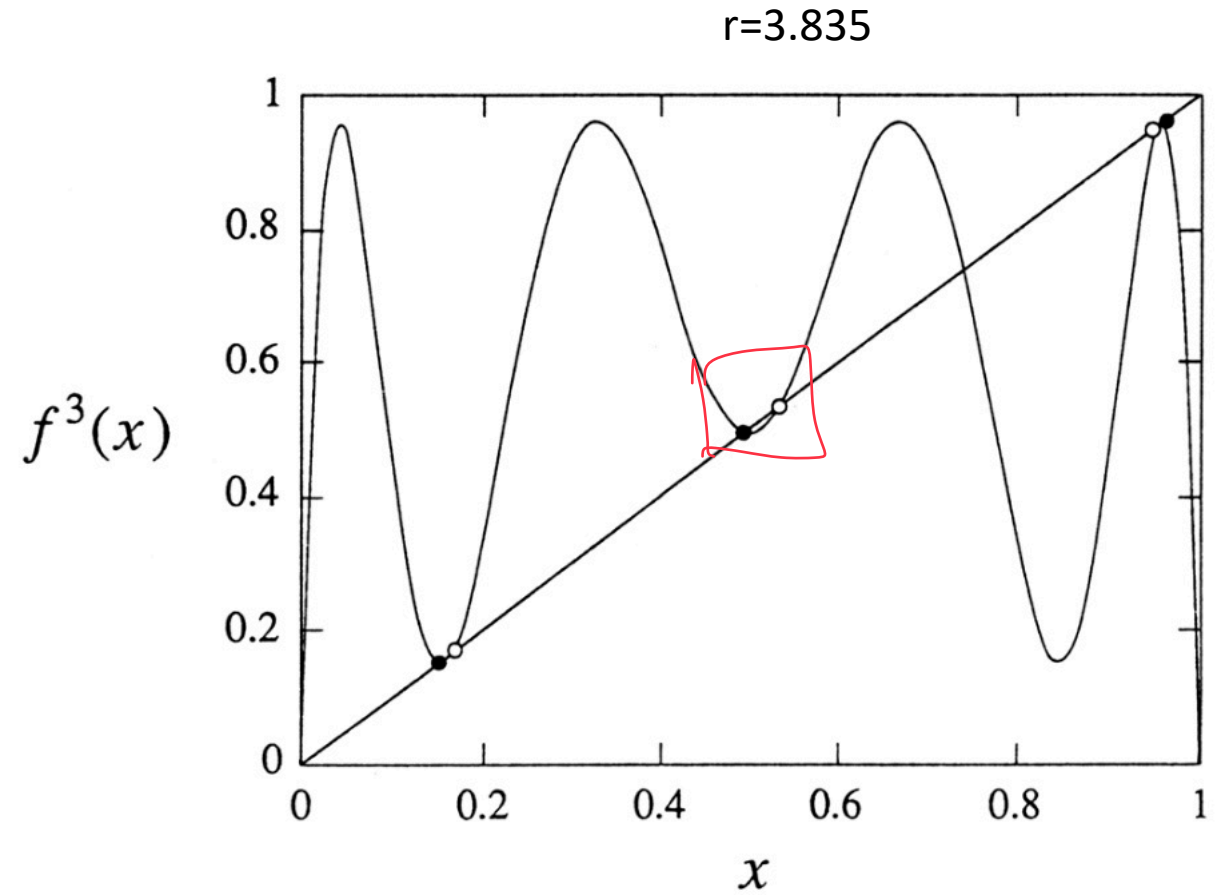
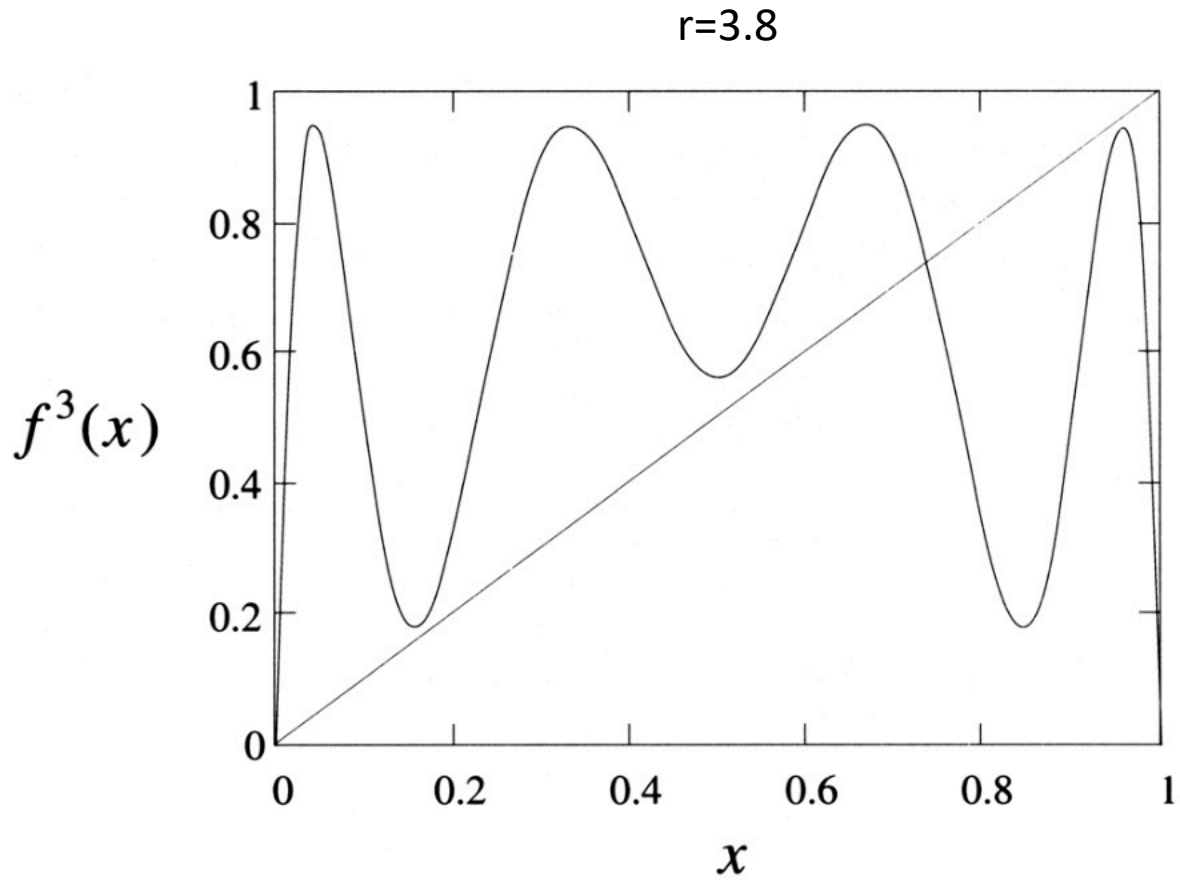
$$r < 4$$



Logistic map (Figs. From Ott Ch 2 + Strogatz Ch. 10)

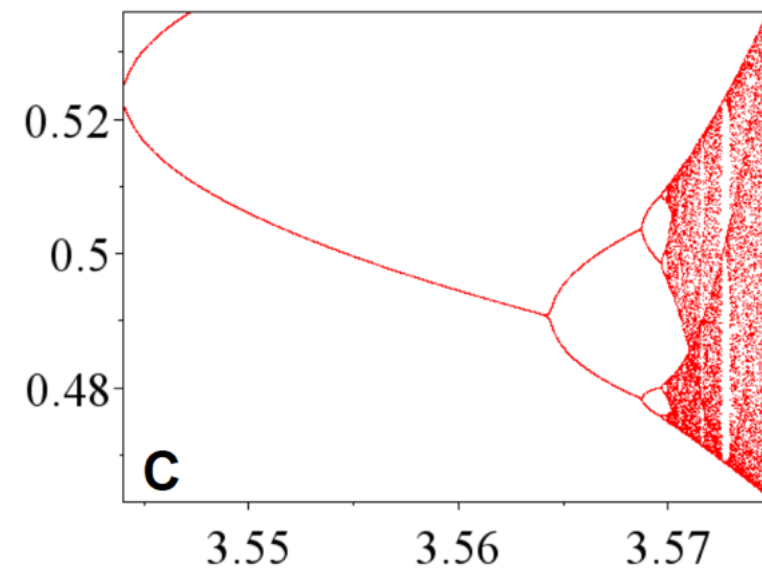
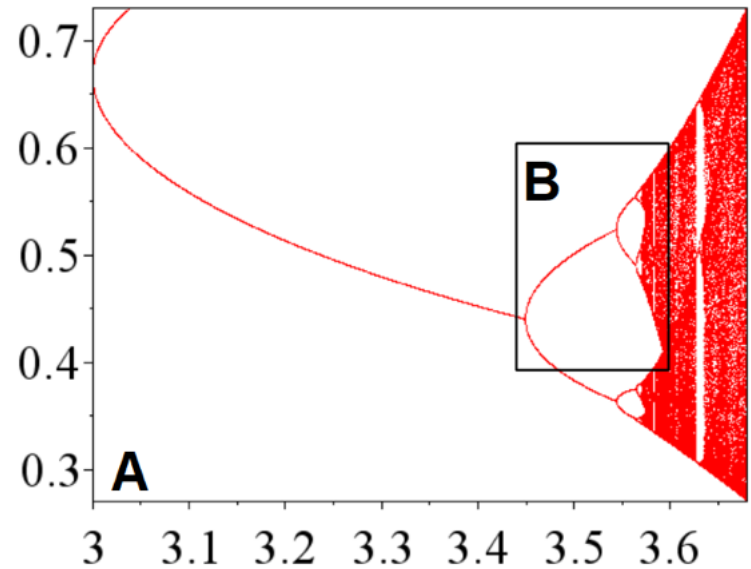
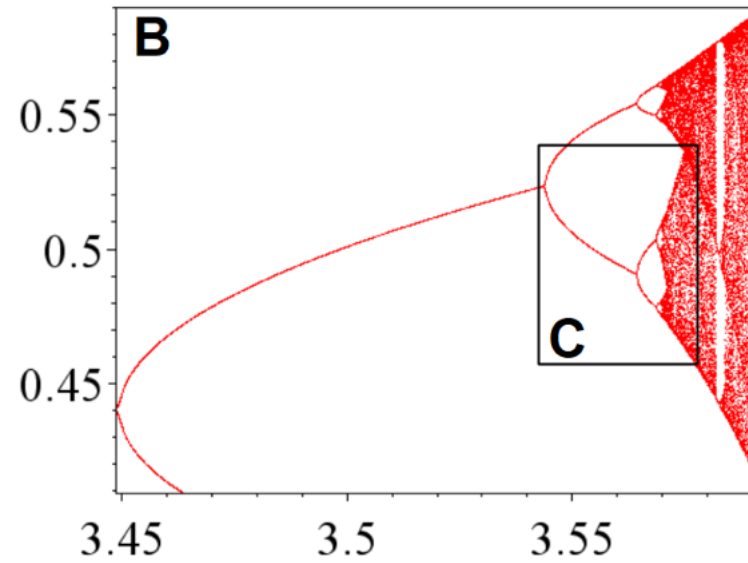
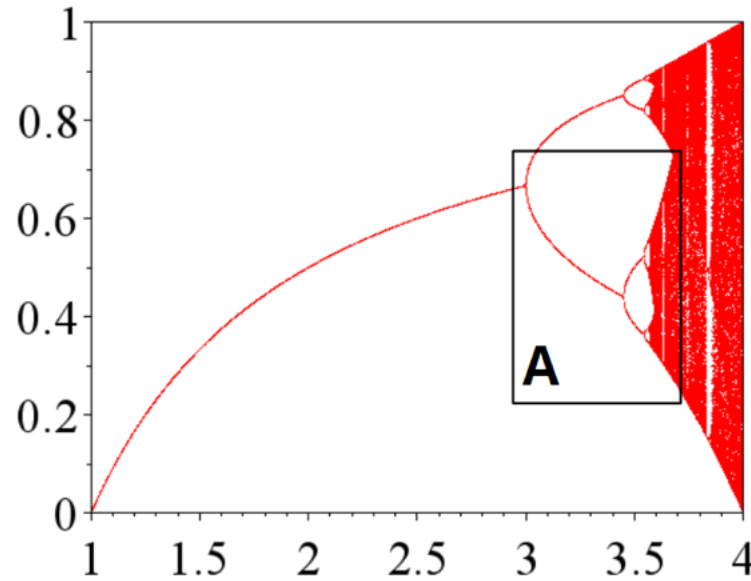


Logistic map

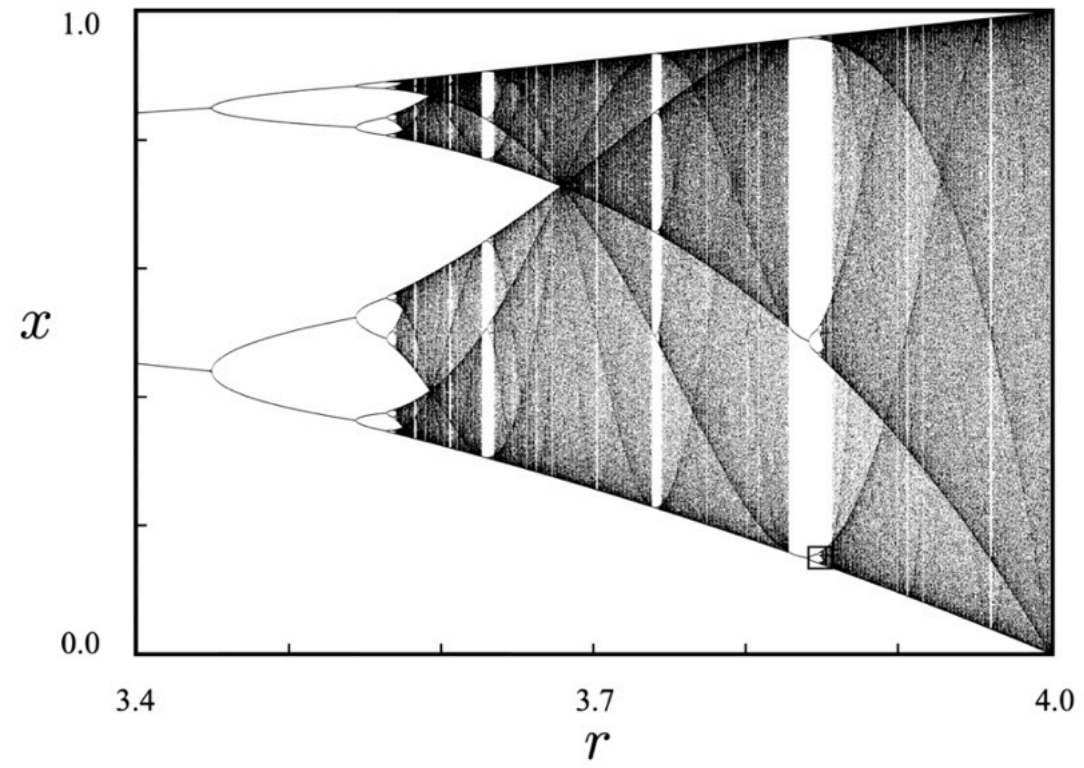


Logistic map

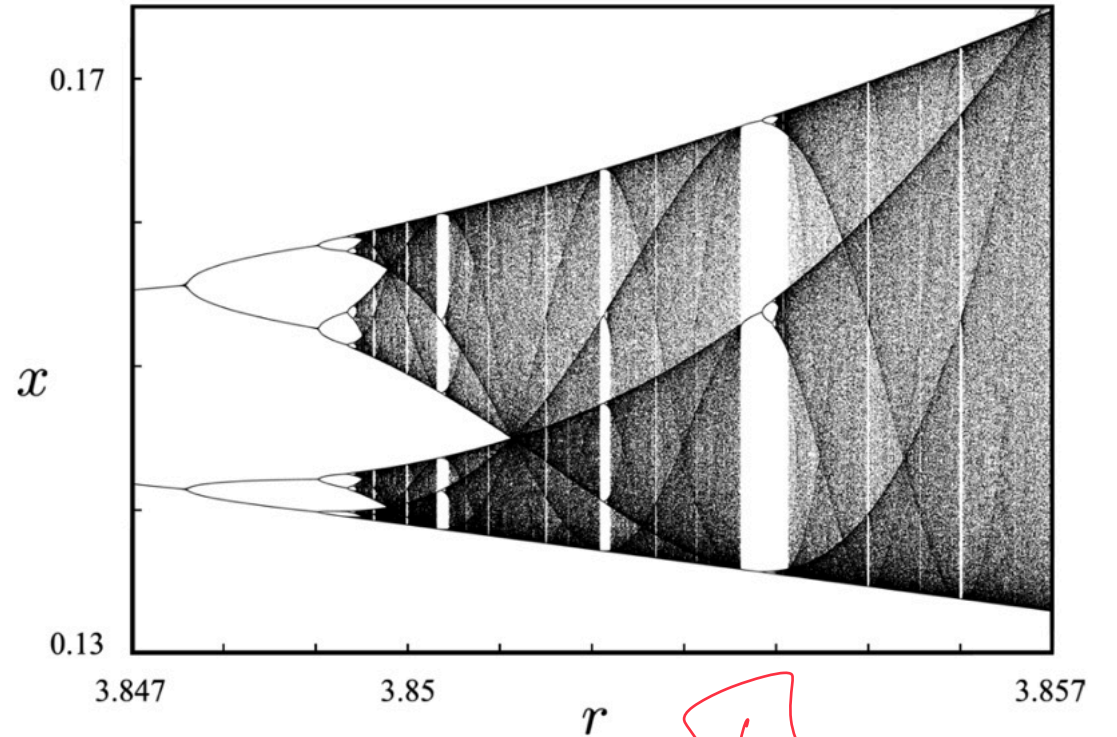
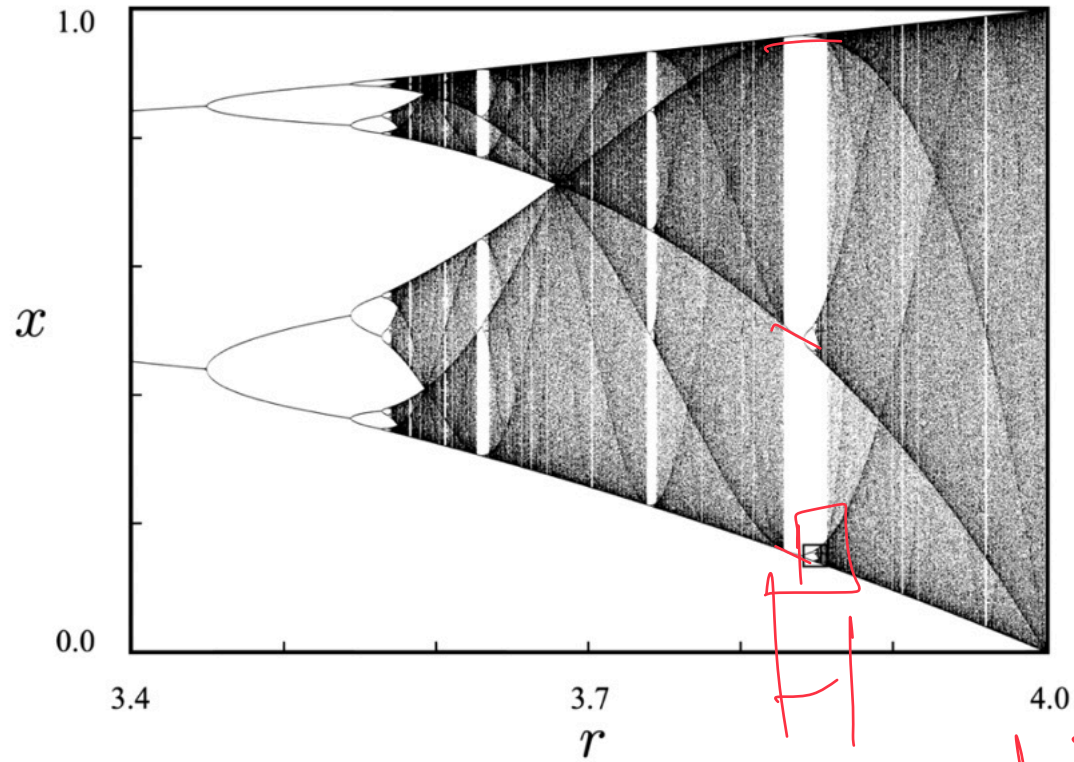
Period doubling route to chaos



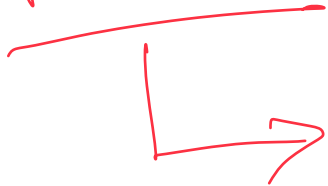
Logistic map



Logistic map



period 3



period 3 implies

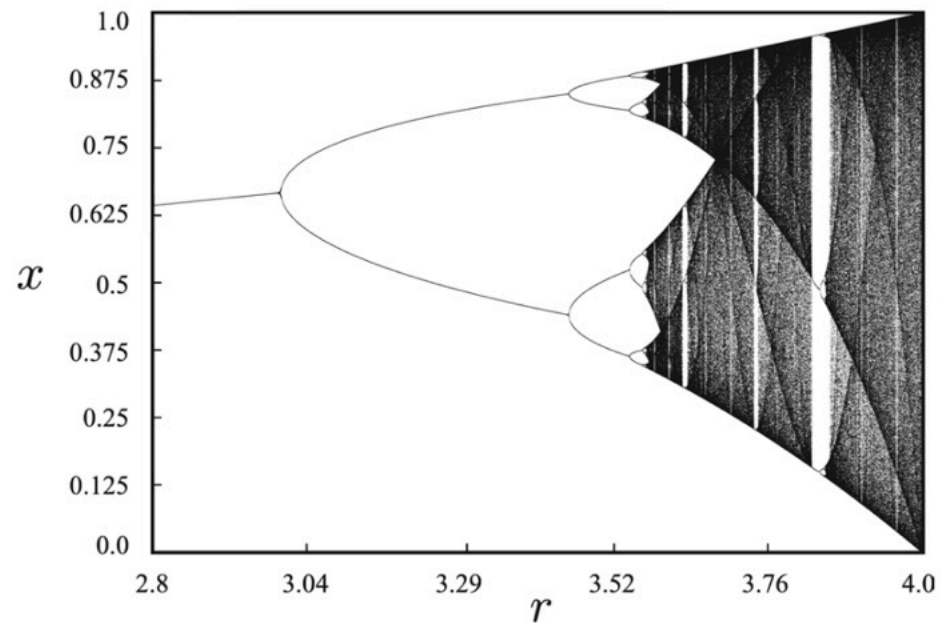
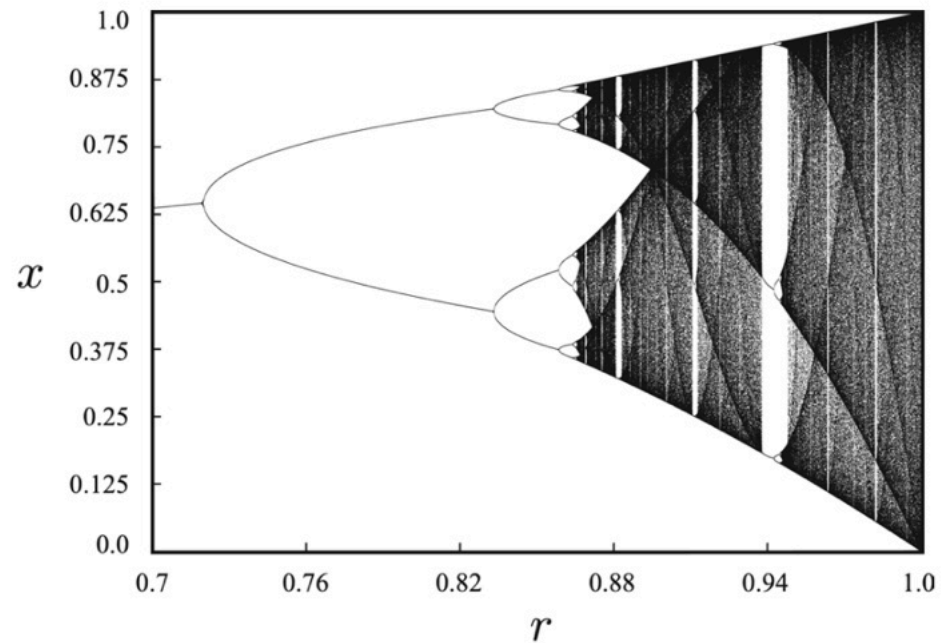
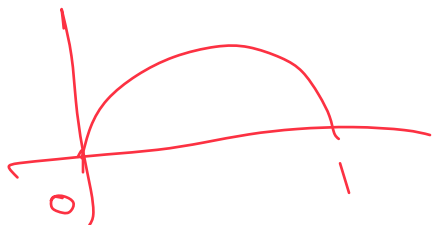
Chaos

Yorke, Li 1975

Sine map vs logistic map

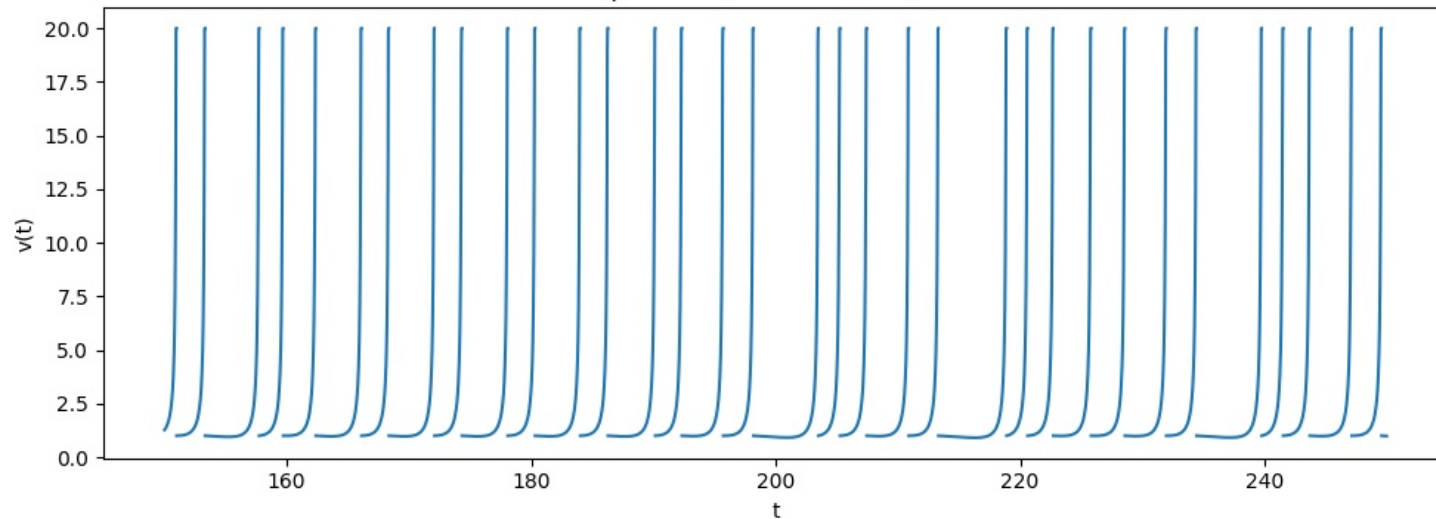
$$x_{n+1} = r x_n (1 - x_n) \rightarrow$$

$$x_{n+1} = \frac{r}{\pi} \sin(\pi x_n) \leftarrow$$

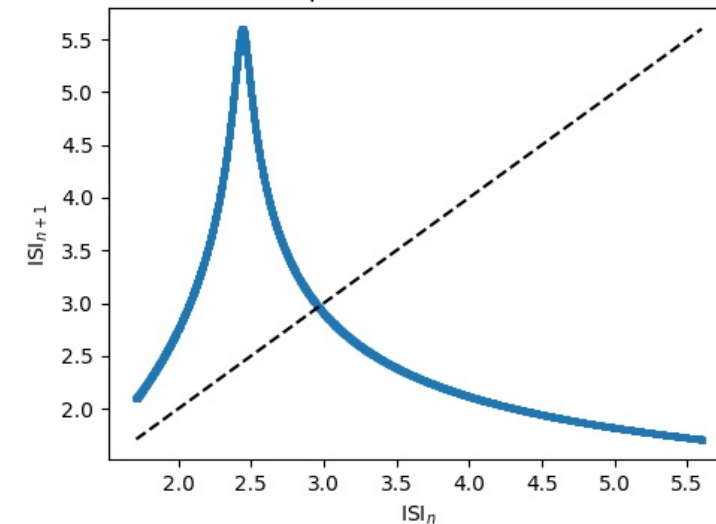


Canonical Fold-homoclinic bursting neuron

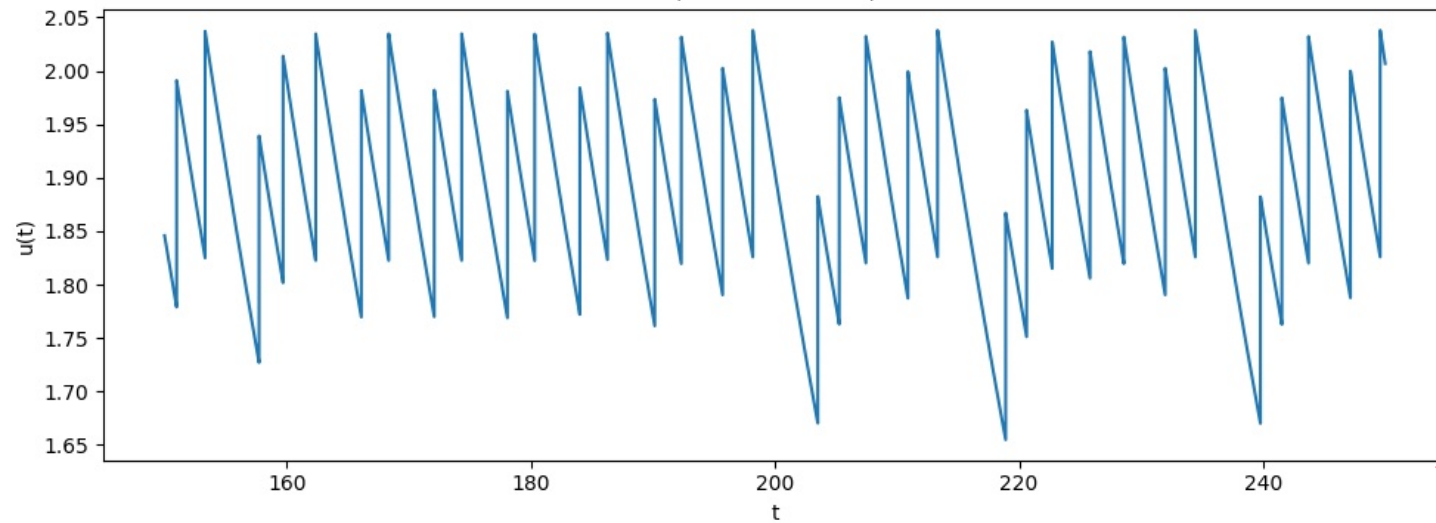
Membrane potential, $\mu=0.037333$, $d=0.212000$



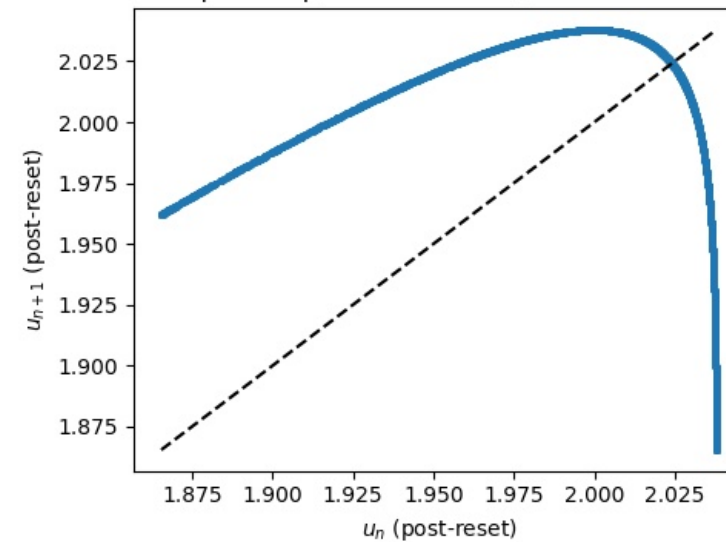
ISI return map, $\mu=0.037333$, $d=0.212000$



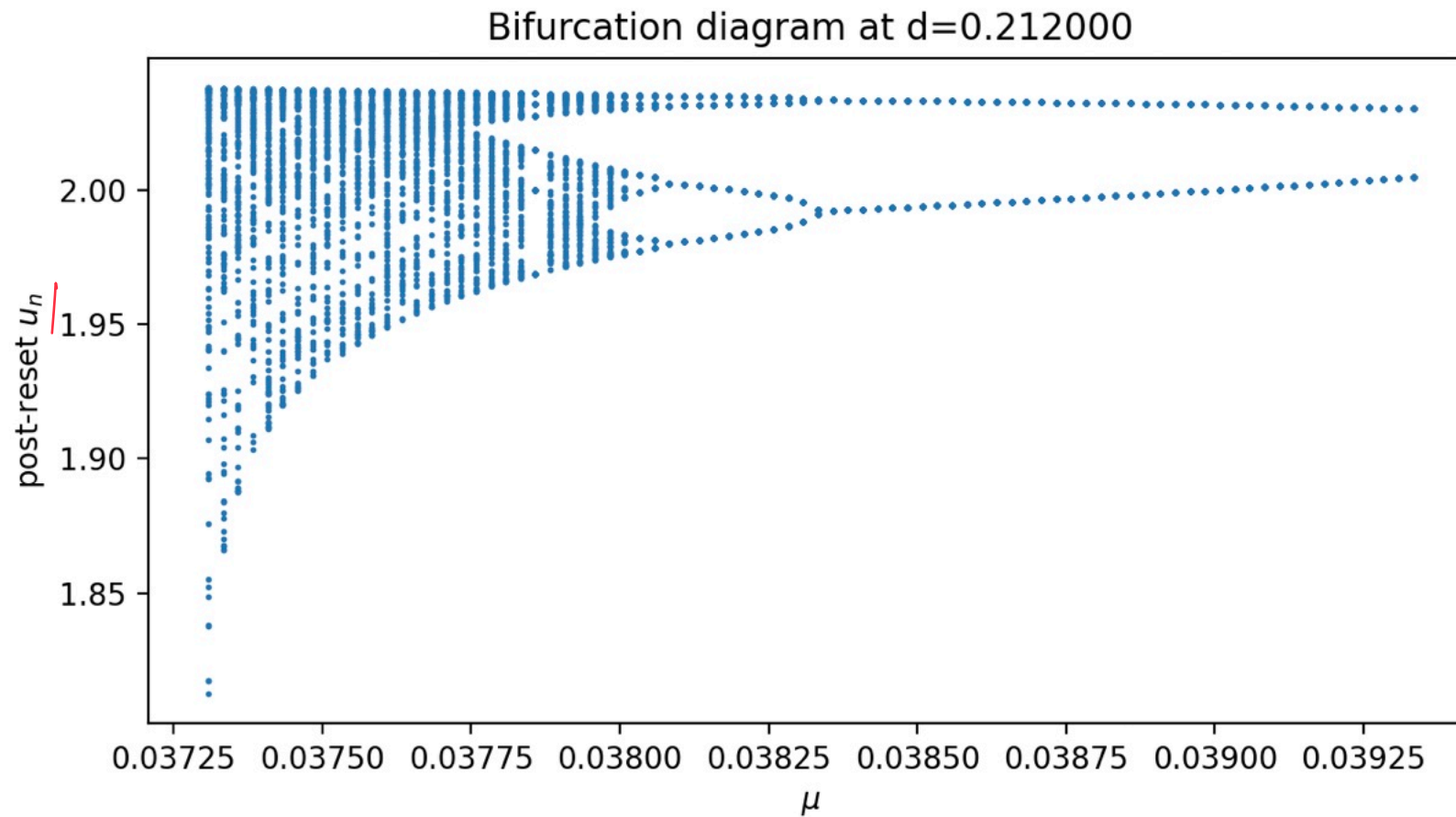
Slow variable, $\mu=0.037333$, $d=0.212000$



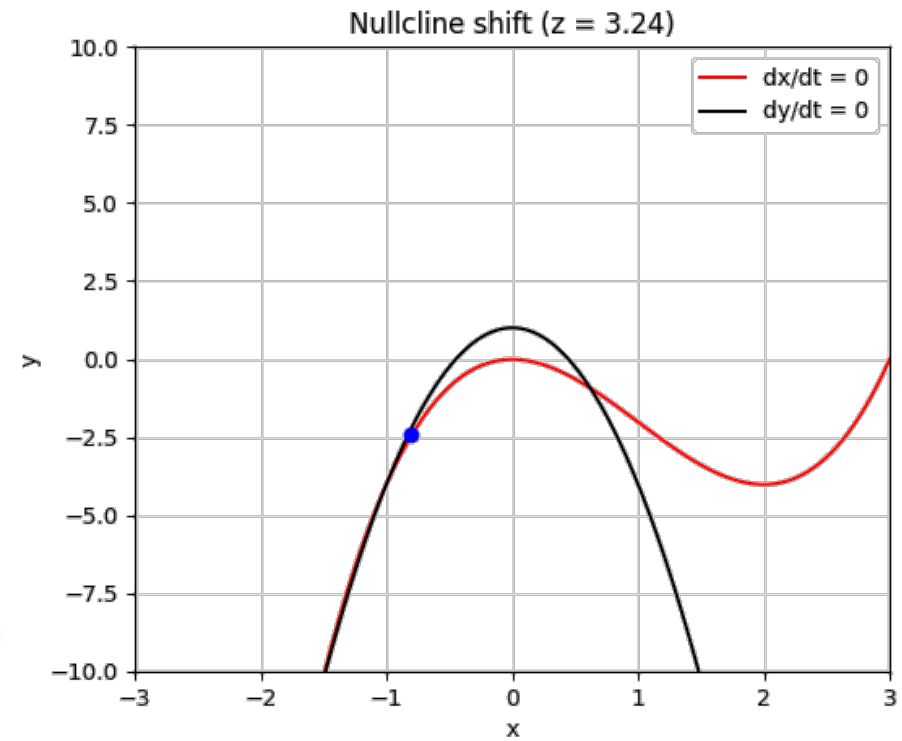
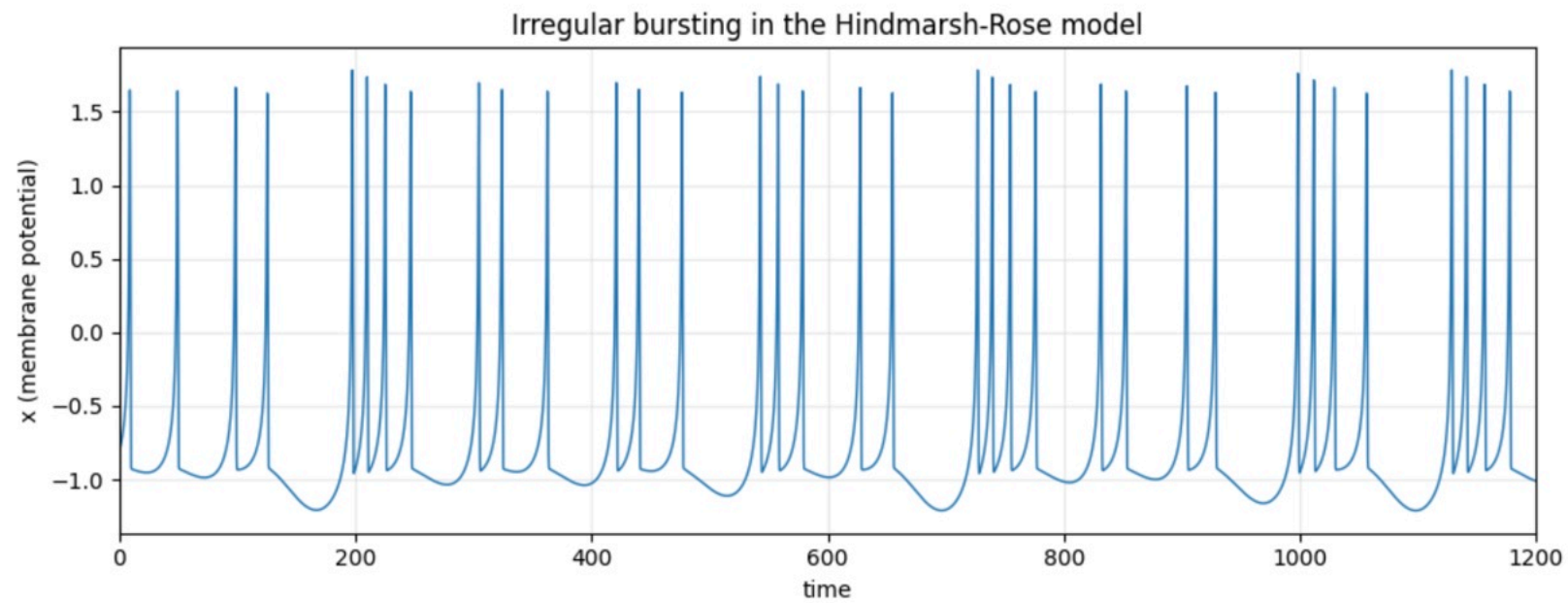
Spike map, $\mu=0.037333$, $d=0.212000$



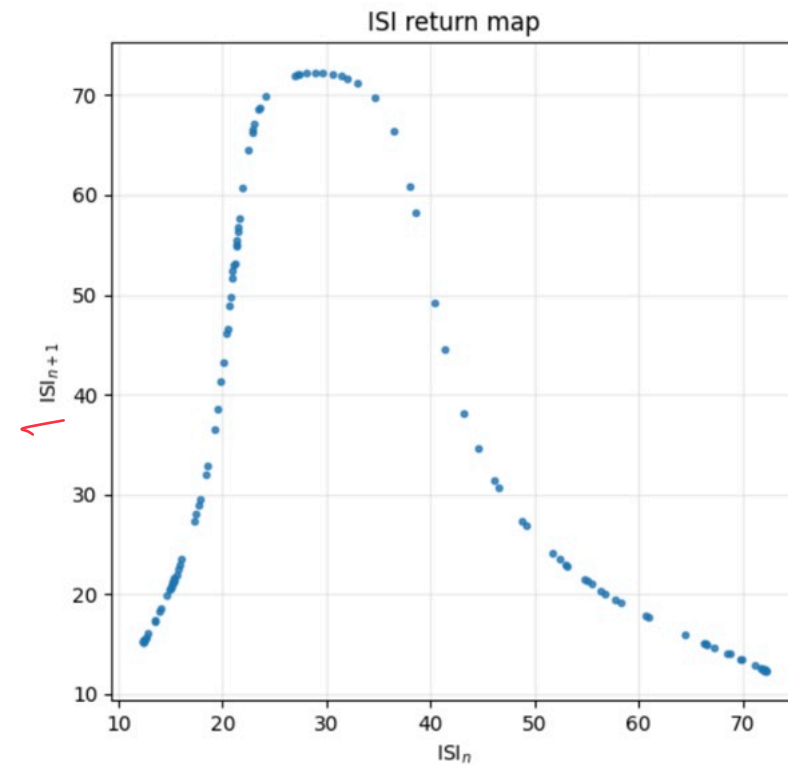
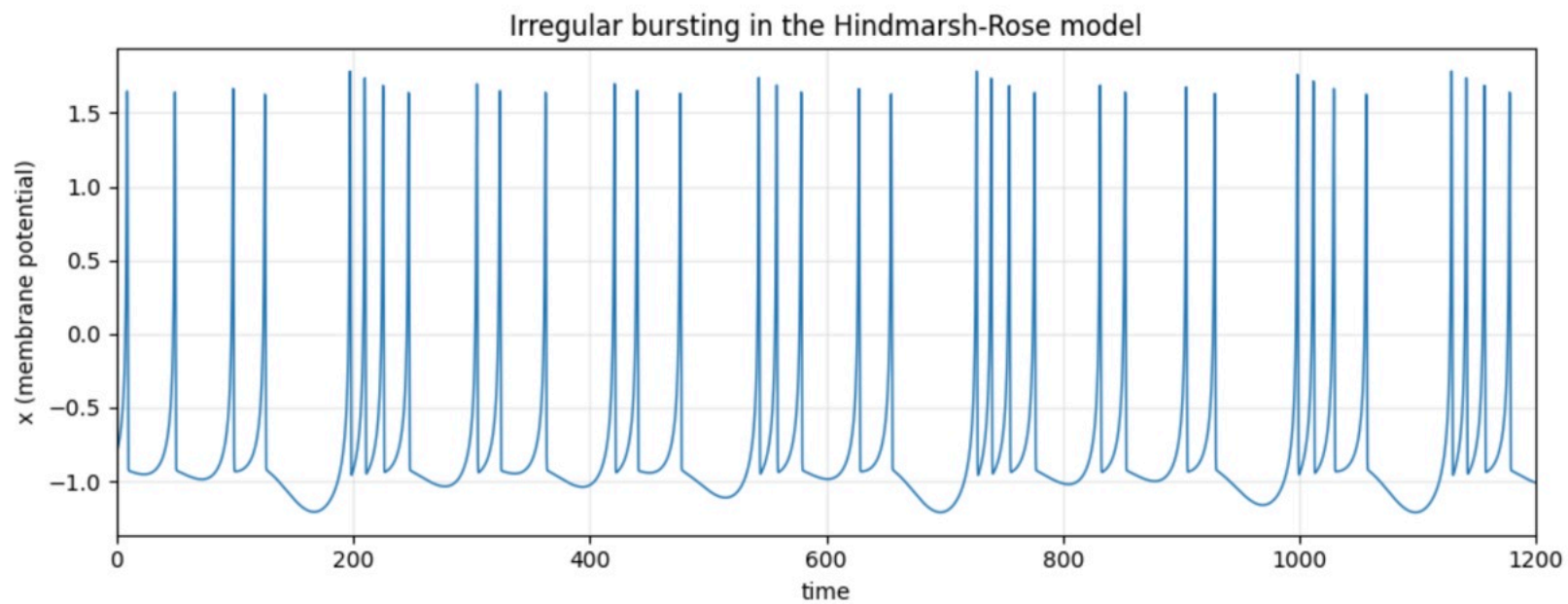
Canonical Fold-homoclinic bursting neuron

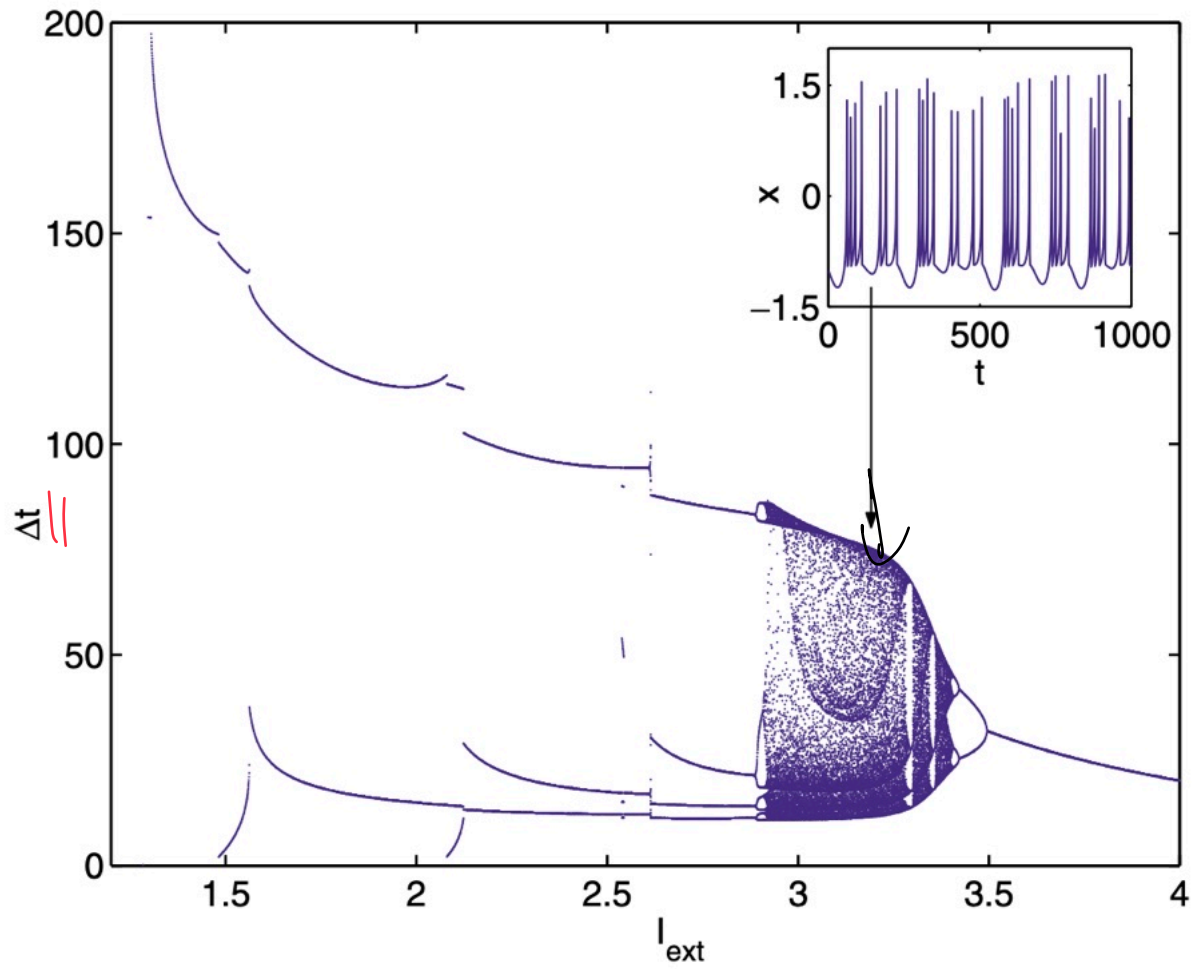


Hindmarsh Rose neuron



Hindmarsh Rose neuron





Transitions to Synchrony in Coupled Bursting Neurons

Mukeshwar Dhamala,¹ Viktor K. Jirsa,^{1,2} and Mingzhou Ding^{1,3}

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(Received 8 September 2003; revised manuscript received 14 November 2003; published 15 January 2004)

Hyperpolarization-Activated Current Induces Period-Doubling Cascades and Chaos in a Cold Thermoreceptor Model

Kesheng Xu¹, Jean P. Maidana¹, Mauricio Caviedes¹, Daniel Quero², Pablo Aguirre² and Patricio Orio^{1,3*}

2.1. Mathematical Model

The basis of our model is the Orio et al. (2012) model that reproduces the static firing patterns of cold thermoreceptors. The equation for the membrane voltage V is:

$$C_m \frac{dV}{dt} = -I_{sd} - I_{sr} - I_h - I_d - I_r - I_l, \quad (1)$$

where C_m is the membrane capacitance; I_d , I_r , I_{sd} , I_{sr} are depolarizing (Na_V), repolarizing (K_{dr}), slow depolarizing ($\text{Na}_P / \text{Ca}_T$) and slow repolarizing (K_{Ca}) currents, respectively. I_h stands for hyperpolarization-activated current, and lastly I_l represents the leak current. Currents are defined as:

$$I_i = \rho(T)g_i a_i (V - E_i) \quad i = d, r, sd, h, l; \quad (2)$$

$$I_{sr} = \rho(T)g_{sr} \frac{a_{sr}^2}{a_{sr}^2 + 0.4^2} (V - E_{sr}), \quad (3)$$

where a_i is an activation term that represents the open probability of the channels ($a_i \equiv 1$), with the exception of a_{sr} that represents intracellular Calcium concentration. Parameter g_i is the maximal conductance density, E_i is the reversal potential and the function $\rho(T)$ is a temperature-dependent scale factor for the current. The activation terms a_r , a_{sd} , and a_h follow the differential equations:

$$\frac{da_i}{dt} = \phi(T) \frac{a_i^\infty(V) - a_i}{\tau_i} \quad i = r, sd, h, \quad (4)$$

where

$$a_i^\infty(V) = \frac{1}{1 + \exp(-s_i(V - V_i^0))}. \quad (5)$$

On the other hand, a_{sr} follows

$$\frac{da_{sr}}{dt} = \phi(T) \frac{-\eta I_{sd} - \kappa a_{sr}}{\tau_{sr}}. \quad (6)$$

Finally,

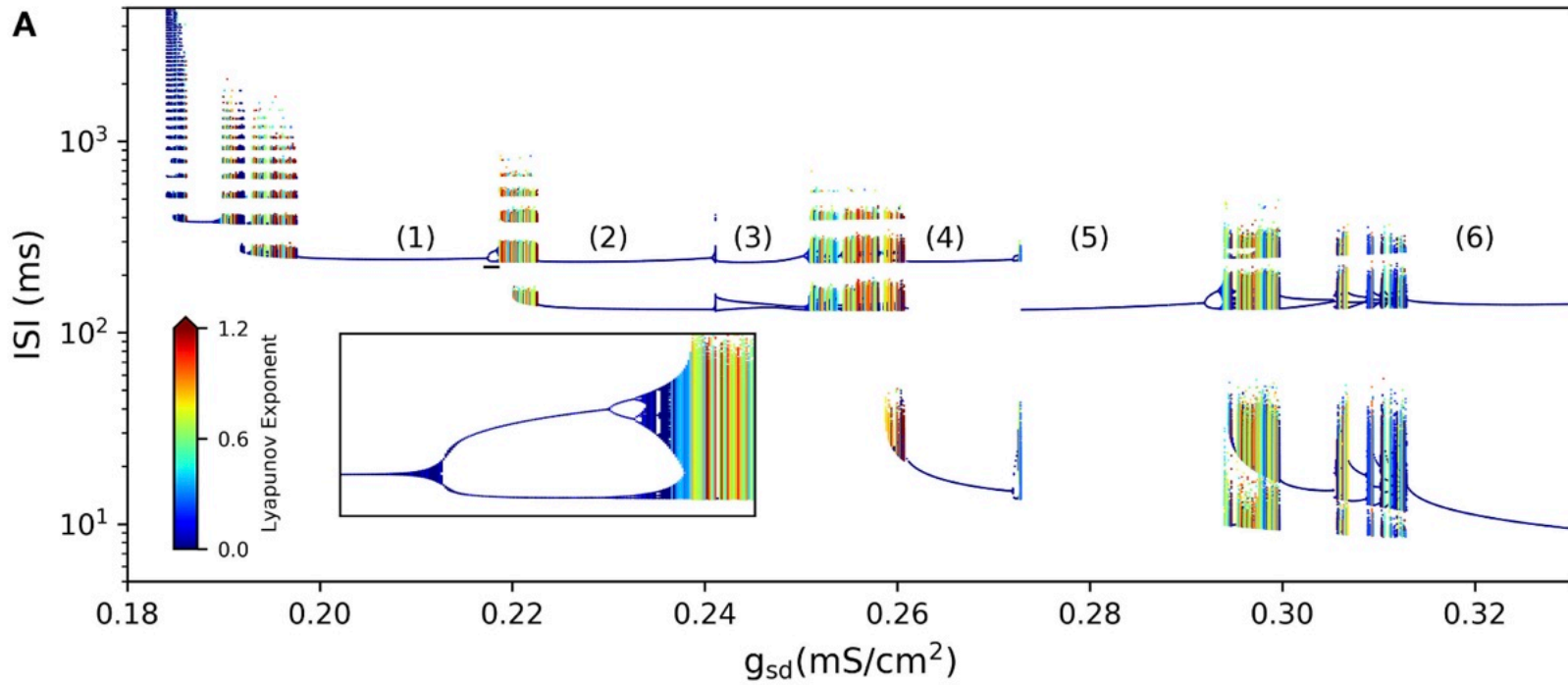
$$a_d = a_d^\infty = \frac{1}{1 + \exp(-s_d(V - V_d^0))}. \quad (7)$$

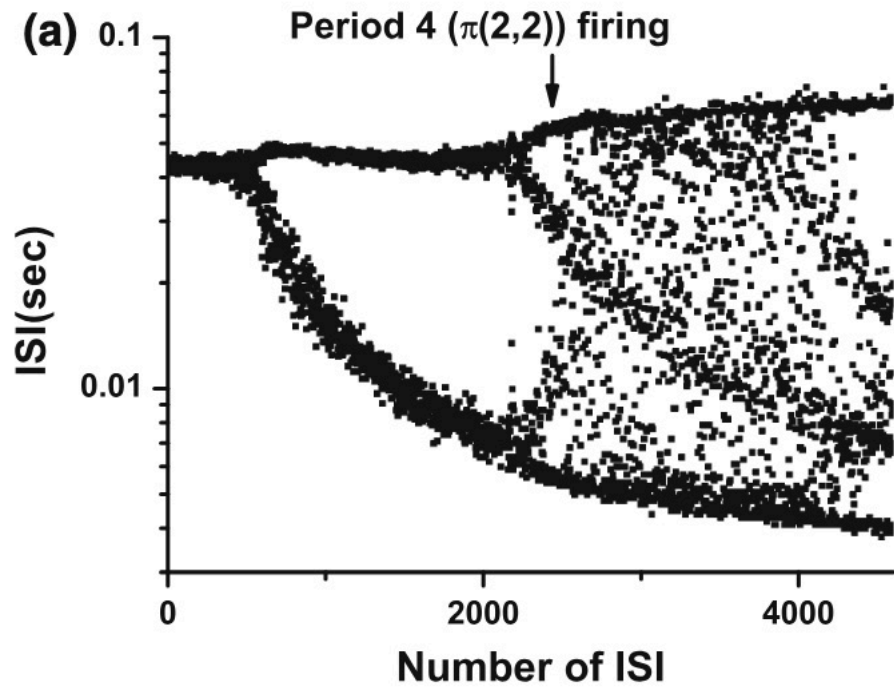
The function $\phi(T)$ in Equations (4) and (6) is a temperature factor for channel kinetics. The temperature-dependent functions for conductance $\rho(T)$ in Equations (2–3), and for kinetics $\phi(T)$ in Equations (4) and (6) are given, respectively, by:

$$\rho(T) = 1.3 \frac{T-25}{10} \quad \phi(T) = 3 \frac{T-25}{10}. \quad (8)$$

TABLE 1 | Parameters of the HB+Ih model.

Parameter	Value	Units
C_m	1.0	$\mu\text{F}/\text{cm}^2$
g_d	2.5	mS/cm^2
g_r	2.8	
g_{sd}	0.21	
g_{sr}	0.28	
g_l	0.06	
g_h	0.4	
V_d^0	-25	mV
V_r^0	-25	
V_{sd}^0	-40	
V_h^0	-85	
κ	0.18	-
η	0.014	$\text{cm}^2/\mu\text{A}$
τ_r	2	ms
τ_{sd}	10	
τ_{sr}	35	
τ_h	125	
S_d	0.25	mV^{-1}
S_r	0.25	
S_{sd}	0.11	
S_h	-0.14	
E_d, E_{sd}	50	mV
E_r, E_{sr}	-90	
E_l	-80	
E_h	-30	





Cogn Neurodyn (2012) 6:89–106
DOI 10.1007/s11571-011-9184-7

RESEARCH ARTICLE

Dynamics of period-doubling bifurcation to chaos in the spontaneous neural firing patterns

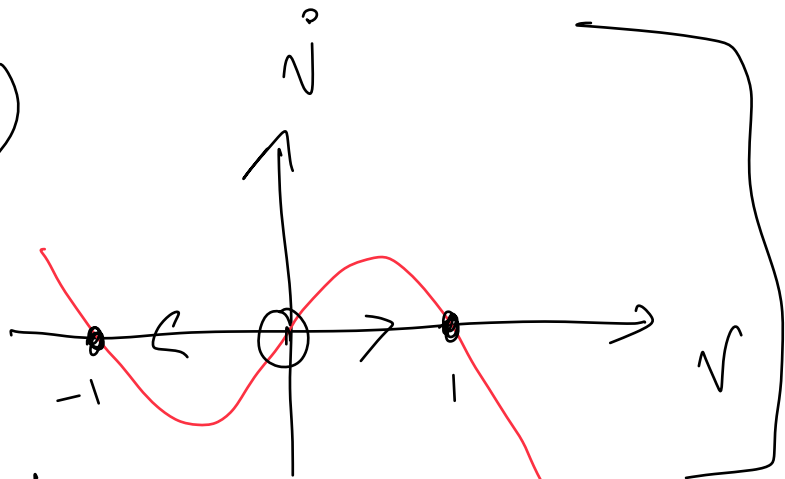
Bing Jia · Huaguang Gu · Li Li · Xiaoyan Zhao

Hopfield Networks

↳ N-neuron model

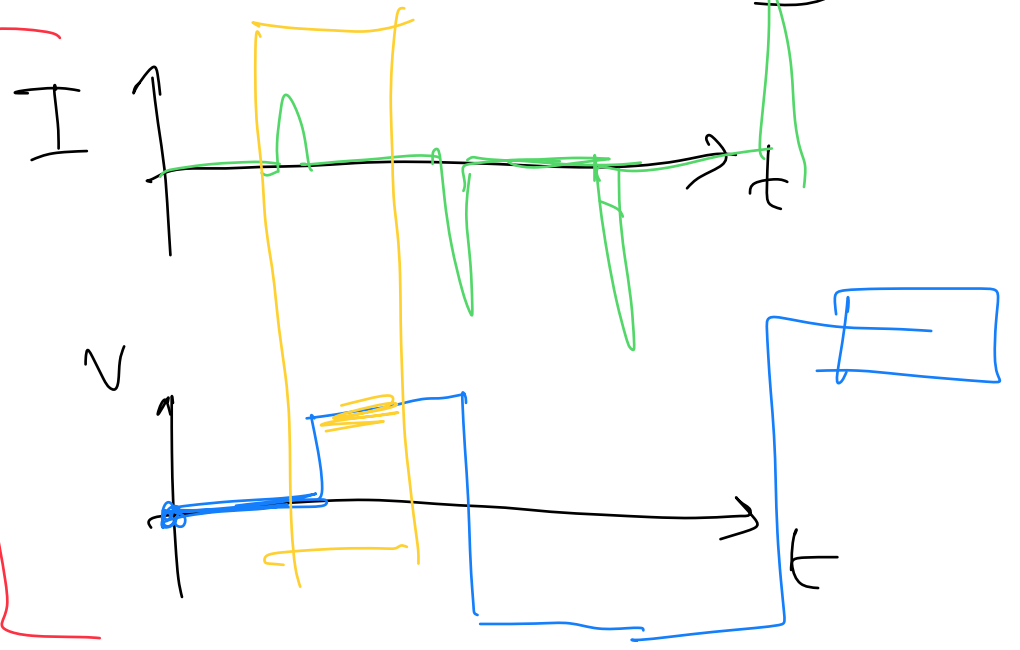
→ Model for associative memory /
content-addressable Memory

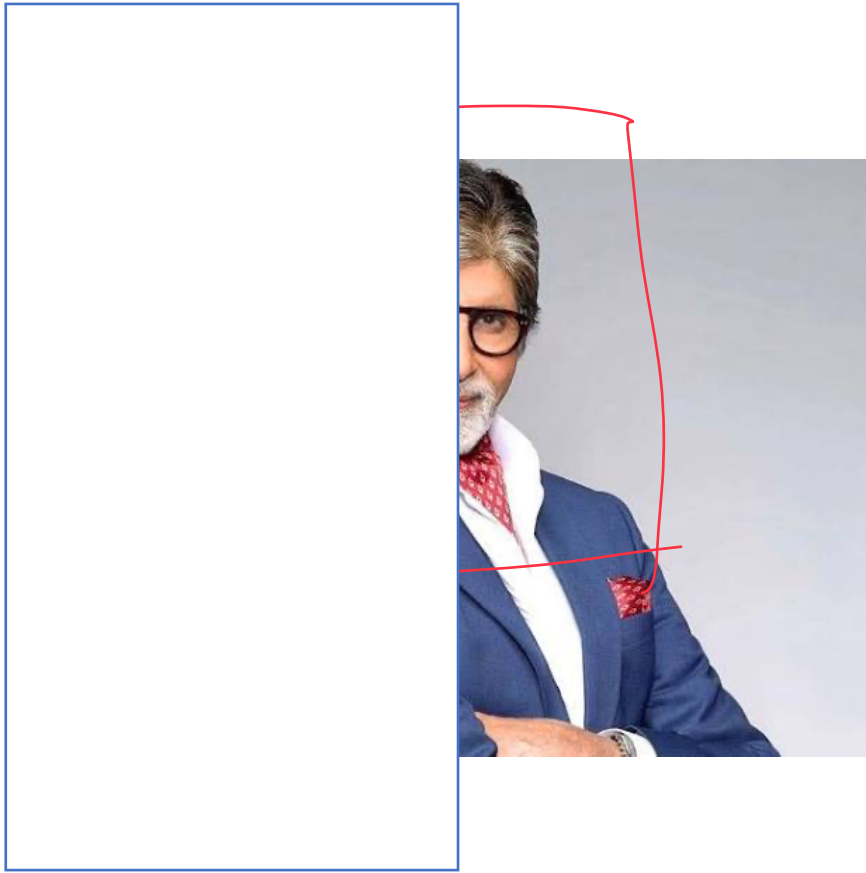
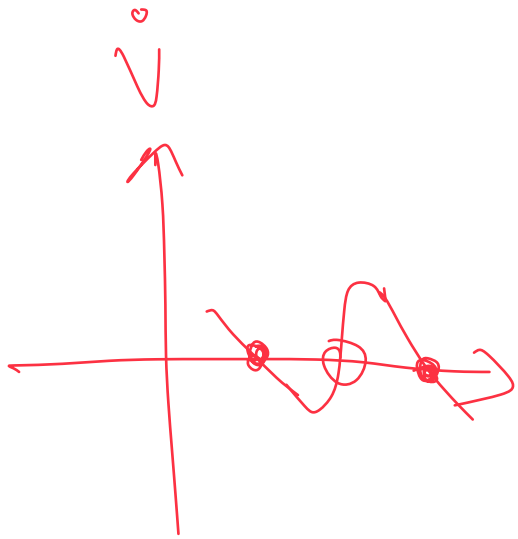
$$\dot{v} = f(v)$$



↳ $s_i = \pm 1$

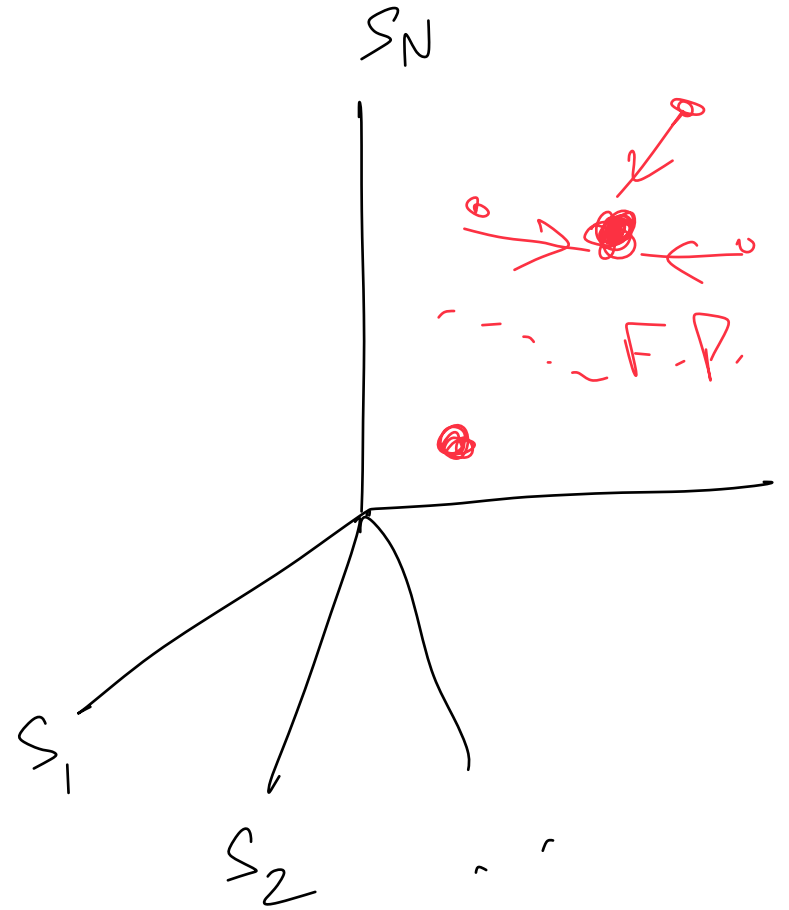
$$s(t) = \text{Sgn}[\text{Inputs}]$$





Exact memory

S_1, S_2, \dots, S_N



$$s_i(t) = \text{sgn}[\text{Inputs}]$$

$$\underline{\underline{= \text{sgn}[h_i(t-1)]}} \leftarrow$$

$$s_i(t) = \text{sgn}\left[\sum_j w_{ij} s_j(t-1)\right] \leftarrow$$

$$s_i \in \{-1, 1\}$$

$$\begin{array}{cc} \uparrow & \downarrow \\ +1 & -1 \end{array}$$

$$H[\vec{s}] = \sum s_i H_{ij} s_j$$

Zero T, Classical
Hopfield \leftrightarrow Ising model

$$s_i(t) = \text{sgn} \left[\sum w_{ij} s_j(t-1) \right]$$

$$[w_{ij} = w_{ji} ; w_{ii} = 0]$$

synchronous updates $\rightarrow \vec{s}(t) = \text{sgn} [W \vec{s}(t-1)]$ Map \leftarrow

asynch updates Pick i
 $s_i(t) = \text{sgn} [\dots]$ N -times Map \leftarrow

$$W = \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$$

$$s(0) = \begin{bmatrix} 1 \\ -1 \end{bmatrix}$$

syn $\rightarrow s(1) = \begin{bmatrix} -1 \\ 1 \end{bmatrix}; s(2) = \begin{bmatrix} 1 \\ -1 \end{bmatrix}$

\rightarrow asynch $\rightarrow s(0) = \begin{bmatrix} 1 \\ 1 \end{bmatrix}$

$0 \cdot (-1) + 1 \cdot 1 = 1 \rightarrow s(1) = \begin{bmatrix} 1 \\ 1 \end{bmatrix} \rightarrow \text{F.P.}$

\hookrightarrow periodic orbit

Energy funcⁿ

$$E[\vec{s}] = -\frac{1}{2} \sum_{i,j} w_{ij} s_i s_j$$

Goal \rightarrow Async. updates reduce $E \uparrow$

$E[\vec{s}] \rightarrow$ Lower bound \leftarrow


Assume updated s_k

$$E = -\frac{1}{2} \sum_{i,j} w_{ij} s_i s_j = \underbrace{-\frac{1}{2} \sum_{\substack{i \neq k \\ j \neq k}} w_{ij} s_i s_j}_{\text{red box}} - \frac{1}{2} \sum_{i \neq k} w_{ik} s_i s_k - \frac{1}{2} \sum_{j \neq k} w_{kj} s_k s_j - \cancel{\frac{1}{2} w_{kk} s_k^2}$$

$$E = C - \frac{1}{2} \sum_{i \neq k} W_{ik} S_i S_k$$

$$-\frac{1}{2} \sum_{j \neq k} W_{kj} S_k S_j$$

↓
 W_{jk}



$$= C - \sum_{i \neq k} W_{ik} S_i S_k$$

$$= C - S_k \underbrace{\sum_{i \neq k} W_{ik} S_i}_{h_k}$$

Recall

$$S_k(t+1) = \text{sgn}[h_k(t)]$$

$$E(t+1) - E(t) = - \left(\underbrace{\sum_i W_{ik} S_i}_{h_k} \right) \left(S_k(t+1) - S_k(t) \right)$$

if $\underline{h_k} > 0 \Rightarrow [S_k(t+1) - S_k(t)] > 0 \Rightarrow \Delta E < 0$
 $h_k < 0 \Rightarrow [S_k(t+1) - S_k(t)] < 0 \Rightarrow \Delta E < 0$

If E changes $\Rightarrow \Delta E < 0$

Either already at F.P.

or E will dec. \rightarrow eventually go to F.P.

How to choose F.P.s?

$\hookrightarrow W_{ij}$?

Single memory \sum

$$\hookrightarrow \xi_i = \text{sgn} \left[\sum_j W_{ij} v_j \right]$$

$$\xi_i \in \{-1, 1\}$$

$$w_i \mapsto \{ -1, 1 \} \quad z_i = \text{sgn} \left[\sum w_{ij} x_j \right] \quad \uparrow$$

$$\underline{w_{ij} = x_i x_j} \quad \Rightarrow \quad \begin{matrix} w_{ij} & w_{ij} & w_{ij} \\ \vdots & \vdots & \vdots \\ w_{ij} & w_{ij} & w_{ij} \end{matrix}$$

$$\Rightarrow \text{sgn} [\quad] = \text{sgn} [z_i] \quad \Rightarrow \quad \text{A.P.}$$

$$W = \sum W^T$$

$$s_i = \text{sgn} \left[\sum w_{ij} s_j \right]$$

$$s(0) = s$$

$$s(1) = \text{sgn} \left[\sum W^T s \right]$$

$$\text{if } \sum^T s > 0$$

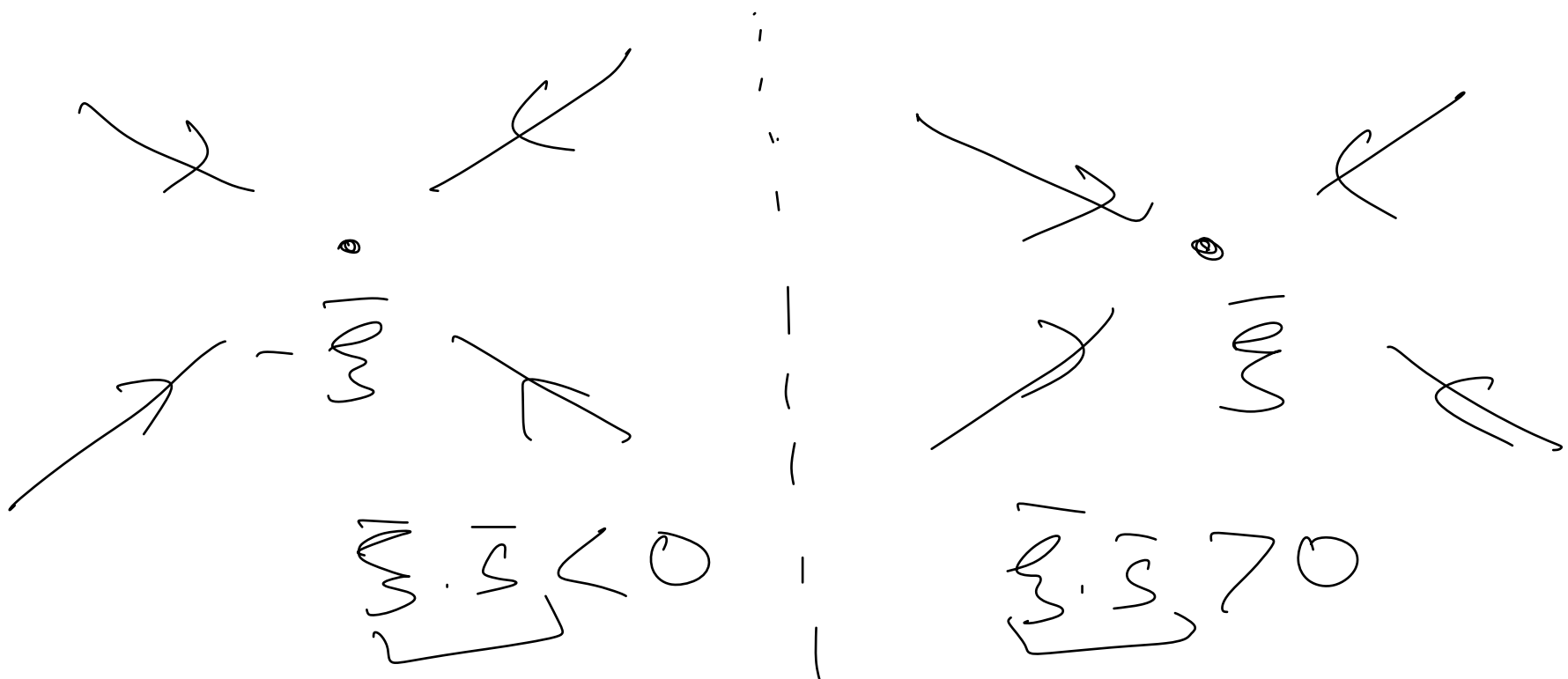
$$= \text{sgn} \left[\sum^T s \right]$$

$$s(1) = \sum$$

$$= \sum$$

$$\text{if } \sum^T s < 0$$

$$s(1) = - \sum$$



spurious fixed pts \rightarrow F.P.s that I didn't store

$\rightarrow w_{ij} = w_i w_j$

Many memories

$$\rightarrow \sum^M$$

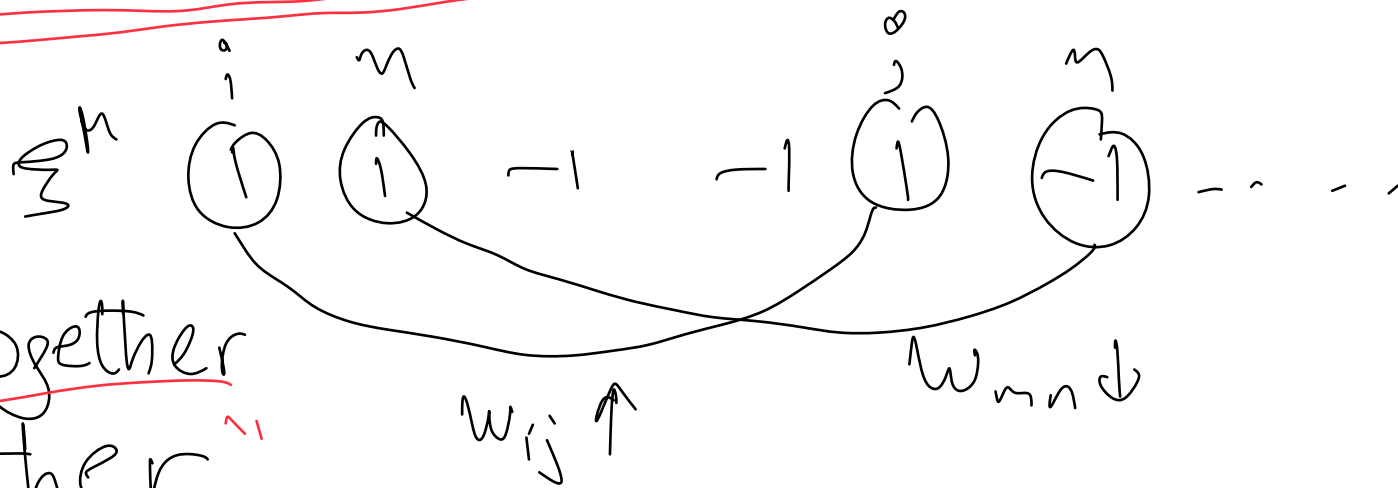
$$w_{ij}(0) = 0$$

$$w_{ij} = \frac{1}{N} \sum_{\mu} \sum_i^M \sum_j^M \rightarrow \Delta w_{ij} = 2 \underbrace{\sum_i^M \sum_j^M}$$

Hebb rule



Neurons that fire together wire together



Examine if Σ^2 is a F.P.

Want $\|\Sigma^2\| = \text{sgn} \left[\sum_j w_{ij} \Sigma_j^2 \right]$

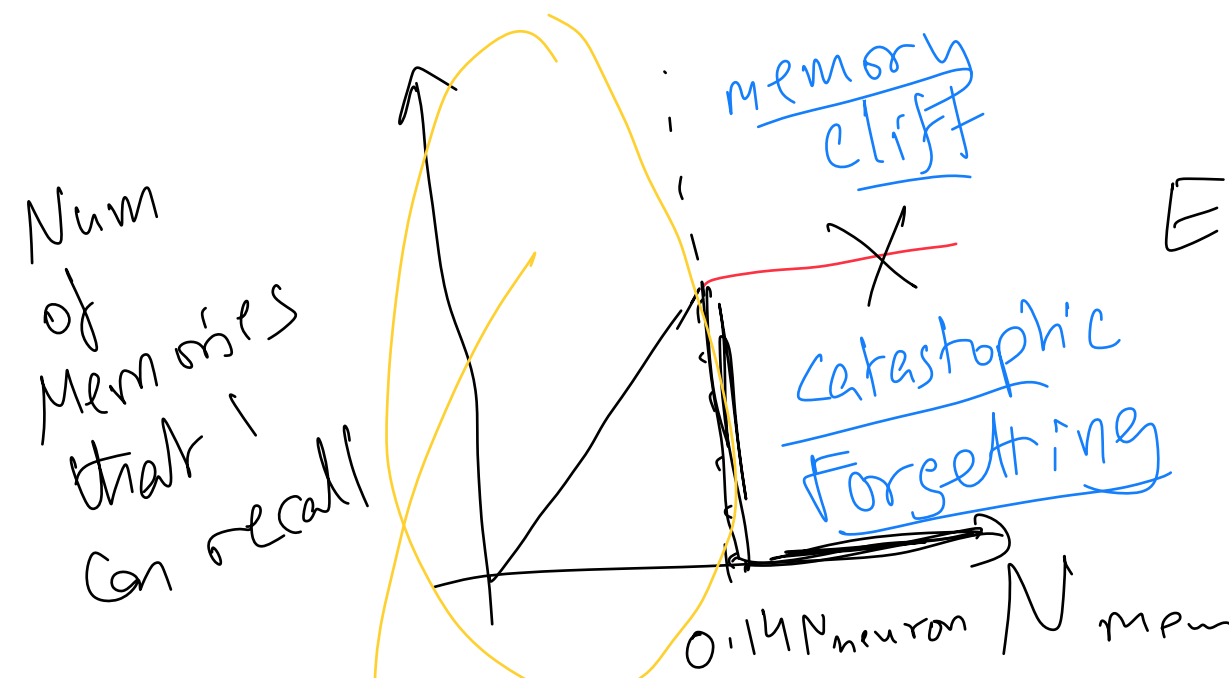
$w_{ij} \Sigma_j^2 = \frac{1}{2} \sum_{\mu \neq j} \frac{w_{i\mu}}{w_{ij}} \Sigma_\mu^2 + \frac{1}{2} \Sigma_i^2$

Want $\|\Sigma^2\| = \frac{1}{2} \left[\Sigma_i^2 + \sum_{\mu \neq i} \left(\frac{w_{i\mu}}{w_{ij}} \Sigma_\mu^2 \right) \right]$

(interference) (cross talk)

Upper bound on number of memories

$$N_{\text{mem}} \lesssim 0.14 \cdot N_{\text{neurons}} \leftarrow$$



~ 1980s

Elizabeth Gardner

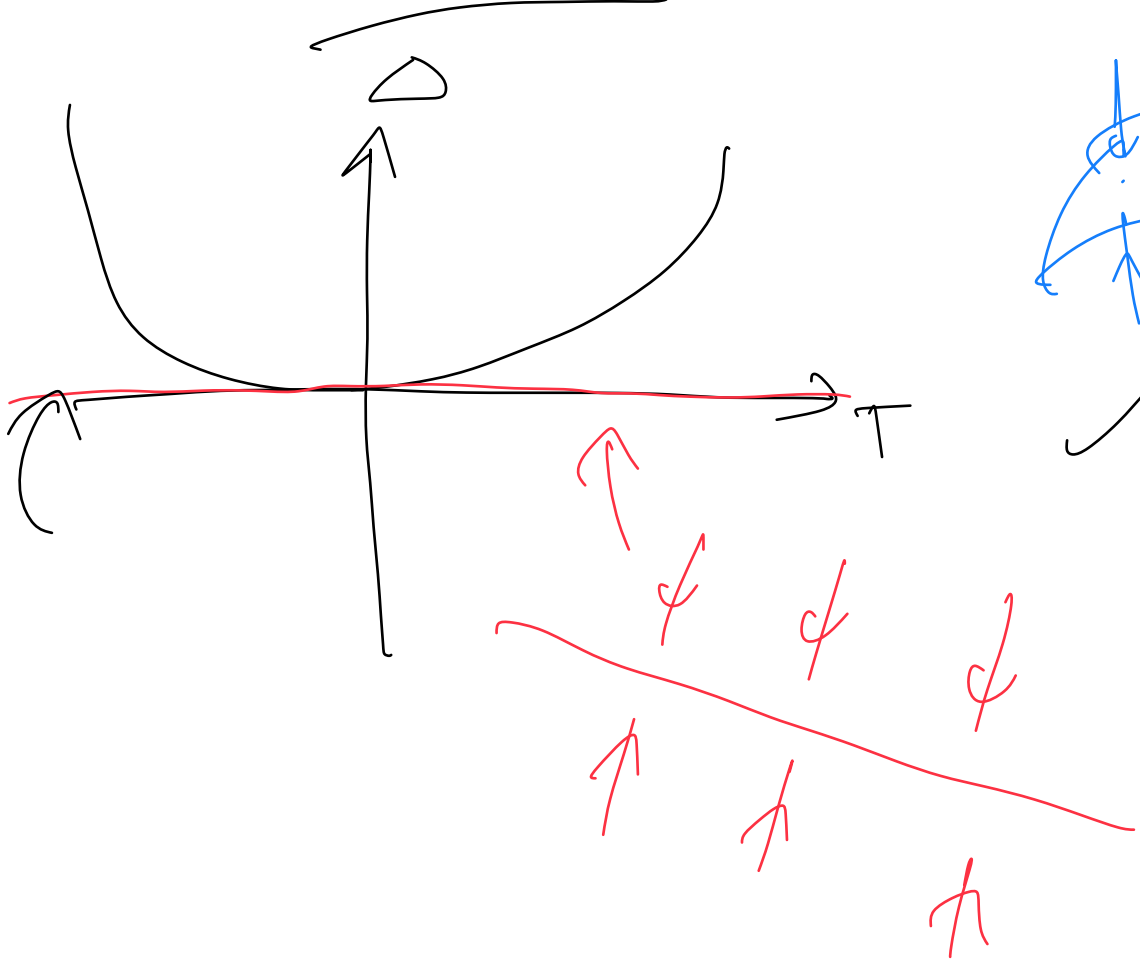
Daniel Amit

H. Sompolinsky

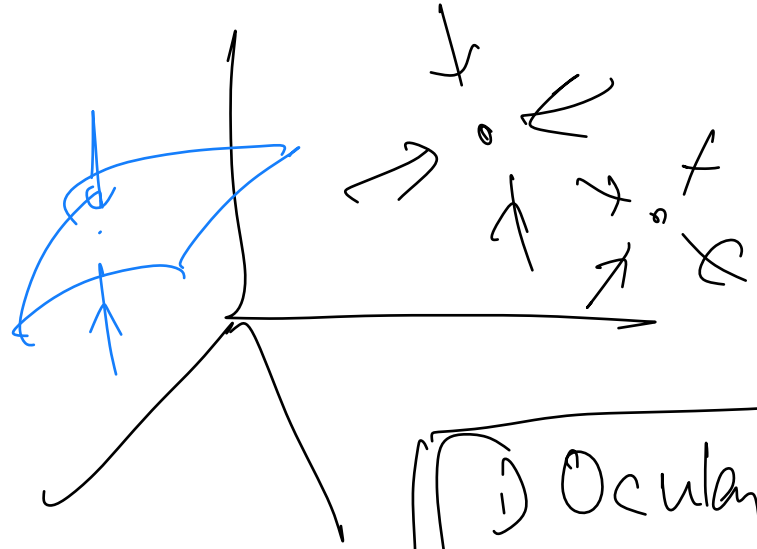
Abu Mostafa

Many spurious F.P.
↳ $\exp(N_{\text{neurons}})$

Continuous Attractor



Hopfield



Discrete attractors

- 1) Ocular Motor Integrator
- 2) Head Directⁿ Cells
- 3) Grid Cells

Ocular motor integrator

RESEARCH ARTICLE | NEUROSCIENCE | ✓

How the brain keeps the eyes still

H. S. Seung [Authors Info & Affiliations](#)

November 12, 1996 | 93 (23) 13339-13344 | <https://doi.org/10.1073/pnas.93.23.13339>

$$\tau \frac{ds_i}{dt} = -s_i + \phi \left[\sum_j W_{ij} s_j + b \right]$$

$$\tau \dot{s} = -s + Ws + b$$

$$\tau \dot{s} = (W - \mathbb{1})s + b$$

$$(W - \mathbb{1})s = -b$$

↳ if $(W - \mathbb{1})$ is singular \rightarrow degenerate solⁿ s

W has an eigenvalue 1

$$Wv = v$$

Ocular motor integrator

RESEARCH ARTICLE | NEUROSCIENCE | ✓

How the brain keeps the eyes still

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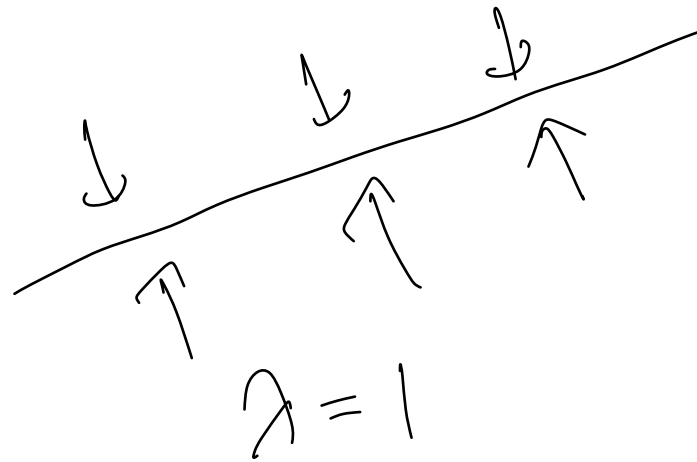
November 12, 1996 | 93 (23) 13339-13344 | <https://doi.org/10.1073/pnas.93.23.13339>

$$Wv = v$$

$$(W - \mathbb{1})s = -b$$

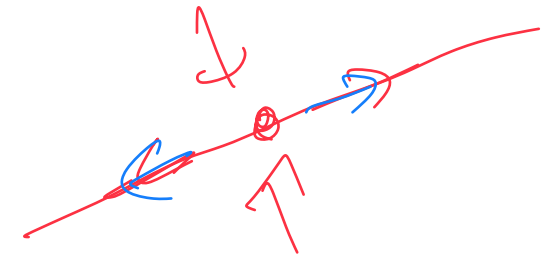
if s_0 is a soln.

$\Rightarrow s = s_0 + \alpha v$ is also a solution

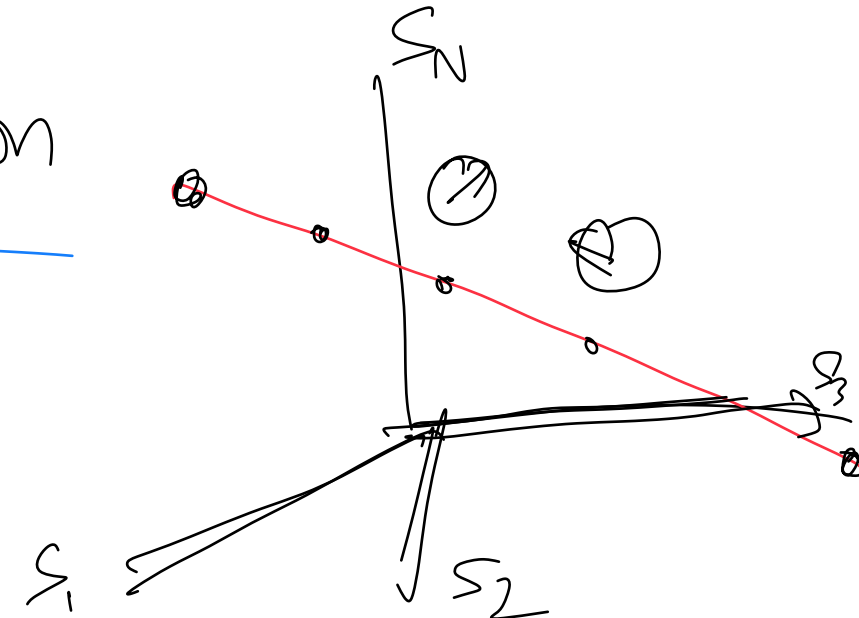
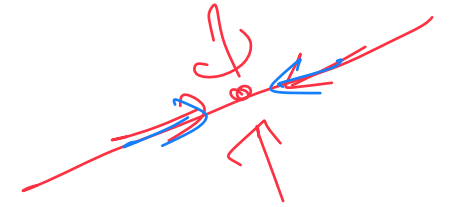


$$\lambda = 1$$

$$\lambda = 1 \pm 10^{-3}$$



$$\lambda \neq 1$$



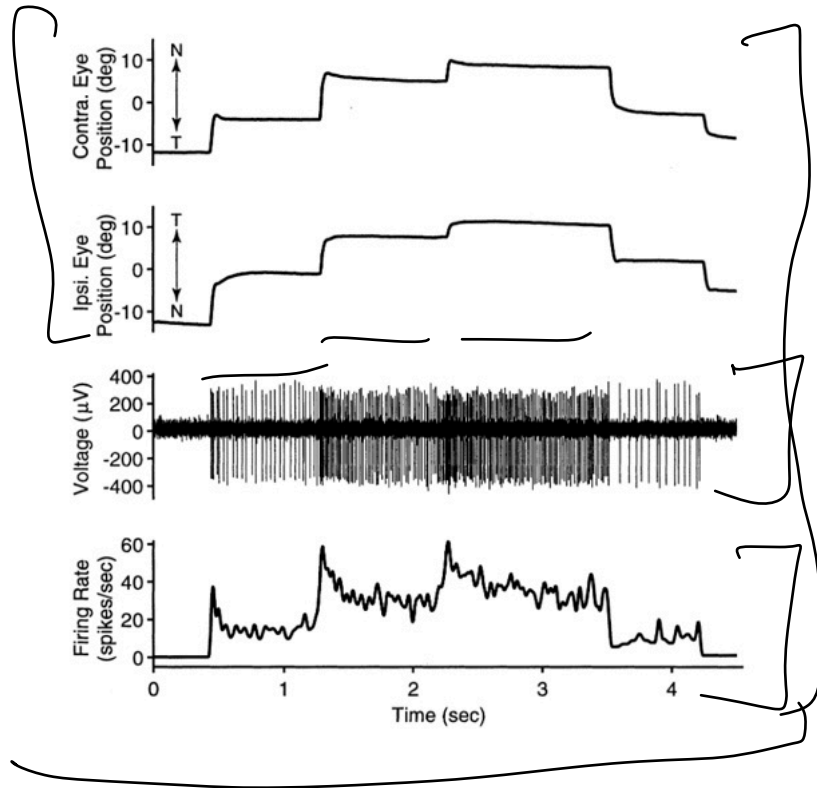
Ocular motor integrator

RESEARCH ARTICLE | NEUROSCIENCE |

How the brain keeps the eyes still

H. S. Seung [Authors Info & Affiliations](#)

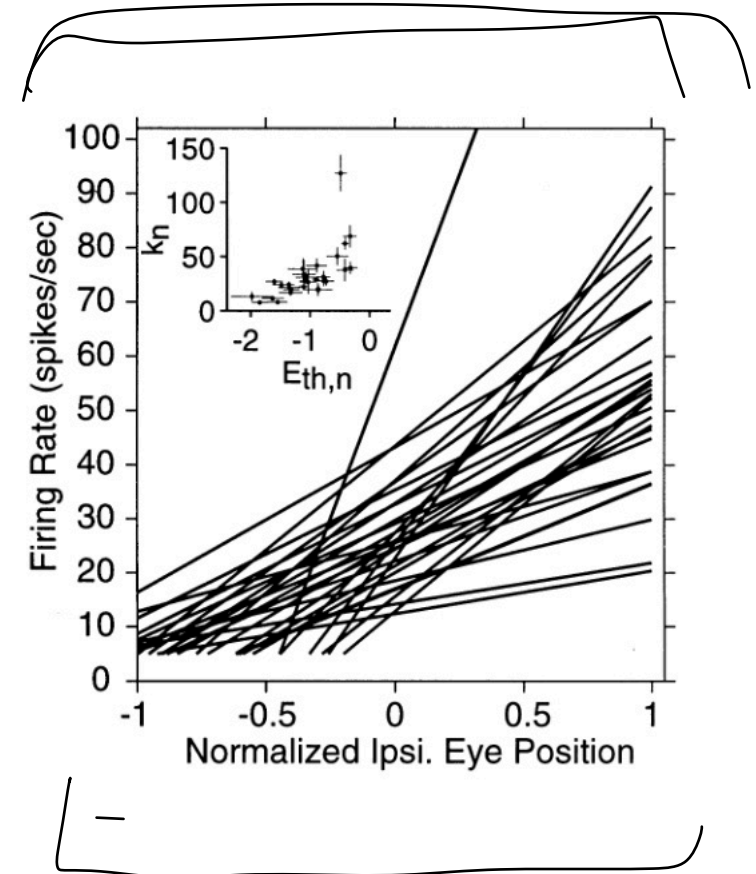
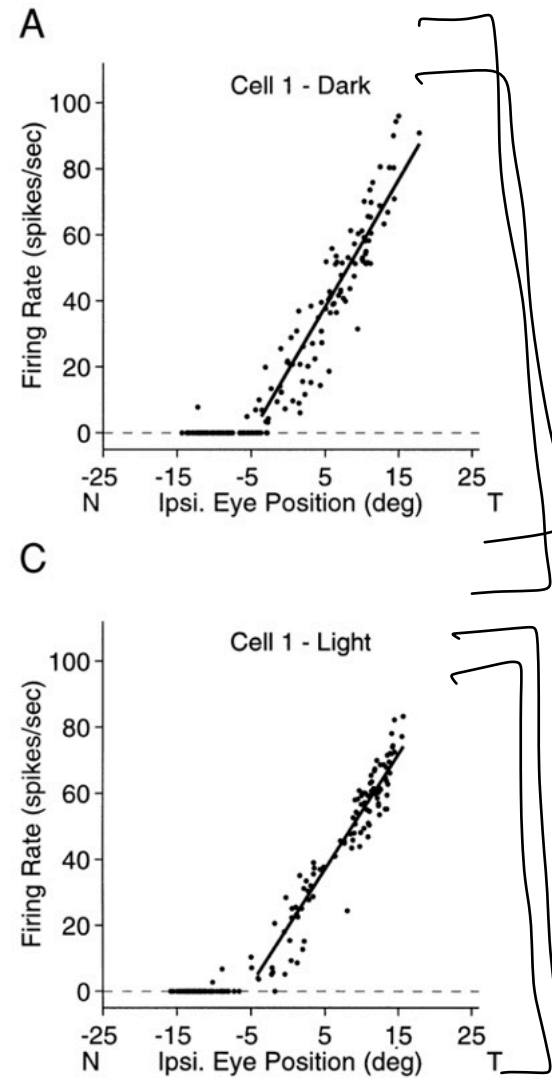
November 12, 1996 | 93 (23) 13339-13344 | <https://doi.org/10.1073/pnas.93.23.13339>



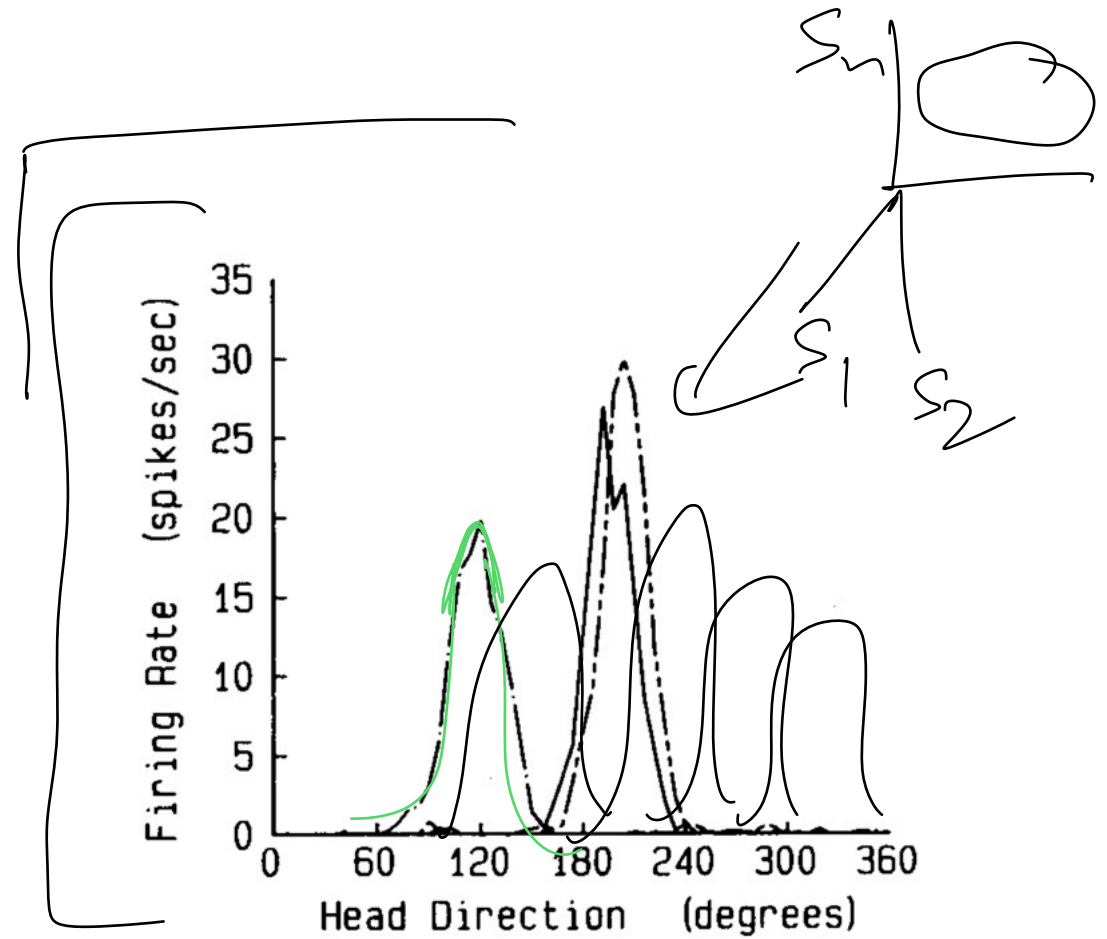
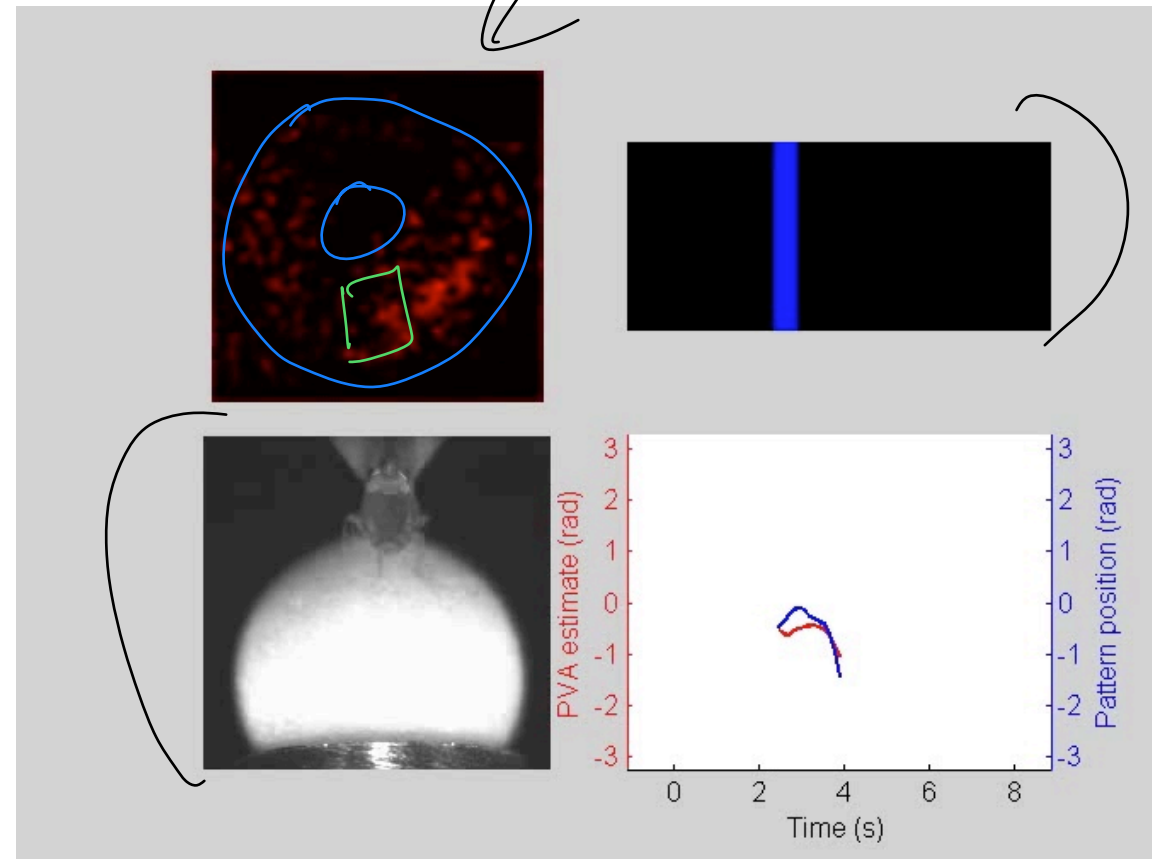
Anatomy and Discharge Properties of Pre-Motor Neurons in the Goldfish Medulla That Have Eye-Position Signals During Fixations

Authors: E. Aksay, R. Baker, H. S. Seung, and D. W. Tank | [AUTHORS INFO & AFFILIATIONS](#)

Publication: Journal of Neurophysiology • Volume 84, Issue 2 • <https://doi.org/10.1152/jn.2000.84.2.1035>



HD cells



Head-direction cells recorded from the postsubiculum in freely moving rats.

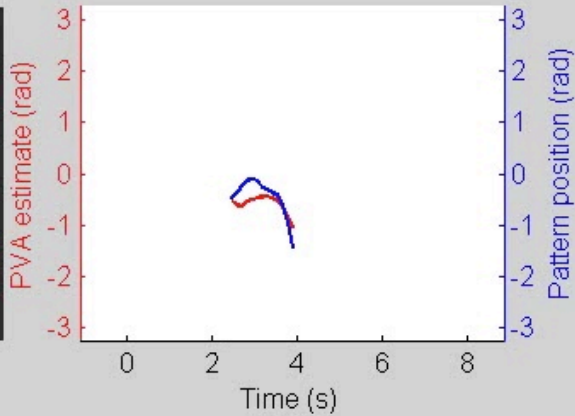
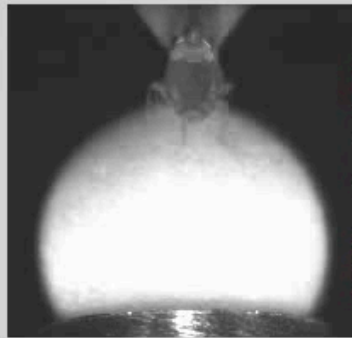
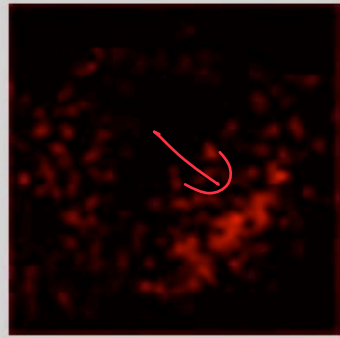
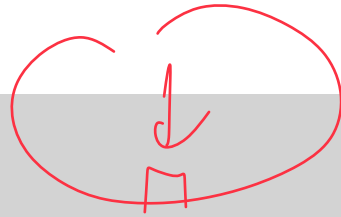
JS Taube, RU Muller, and JB Ranck Jr

Journal of Neuroscience 1 February 1990, 10 (2) 436-447; <https://doi.org/10.1523/JNEUROSCI.10-02-00436.1990>

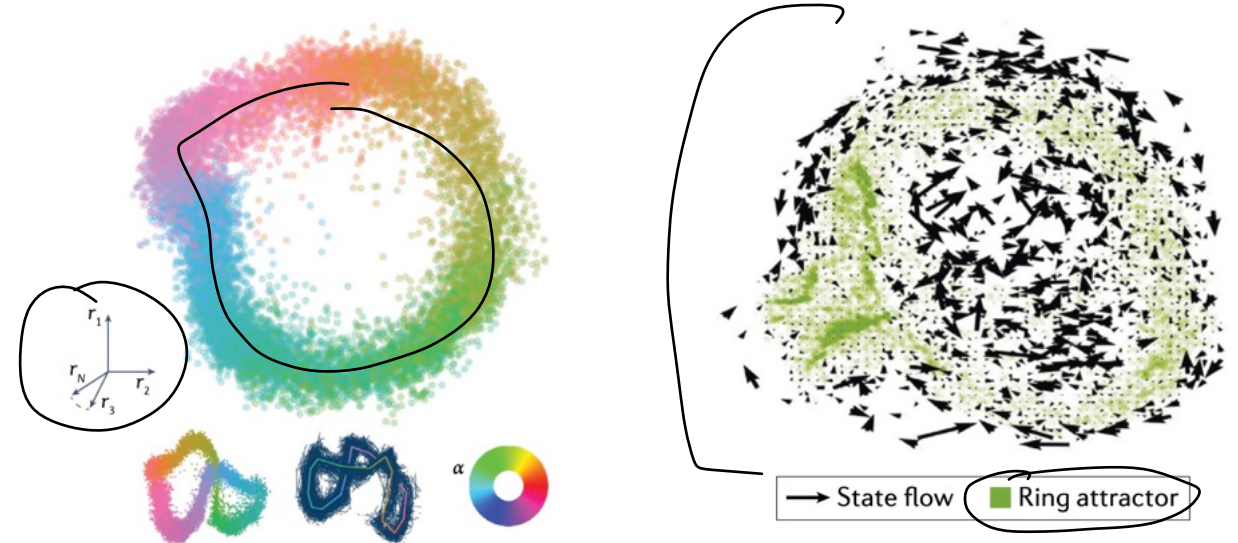
Neural dynamics for landmark orientation and angular path integration

Johannes D. Seelig¹ & Vivek Jayaraman¹

HD cells



$$\vec{x} = \vec{F}(\vec{x})$$



The intrinsic attractor manifold and population dynamics of a canonical cognitive circuit across waking and sleep

[Rishidev Chaudhuri](#) , [Berk Gerçek](#), [Biraj Pandey](#), [Adrien Peyrache](#) & [Ila Fiete](#) 

[Nature Neuroscience](#) 22, 1512–1520 (2019) | [Cite this article](#)

Neural dynamics for landmark orientation and angular path integration

Johannes D. Seelig¹ & Vivek Jayaraman¹

Field Model

$$s(x)$$

$$\tau \frac{\partial s(x,t)}{\partial t} = -s + \phi \left(\int_0^{2\pi} w(x,x') s(x') dx' + B \right)$$

x is on a circle
 $s(x+2\pi) = s(x)$

$$w(x,x') = w(|x-x'|)$$

↳ F.P.s exist.

$s_0(x)$ is a F.P.

$s_0(x+\epsilon)$ will also be a F.P.

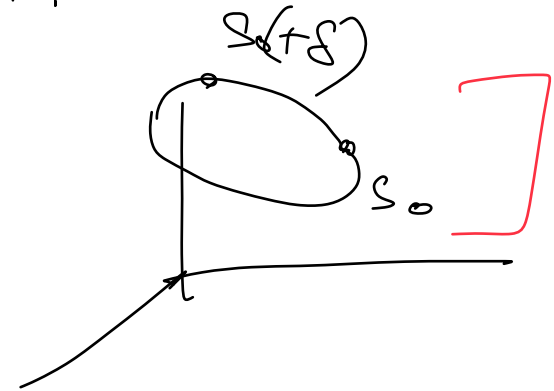
$$\dot{s} = F(s)$$

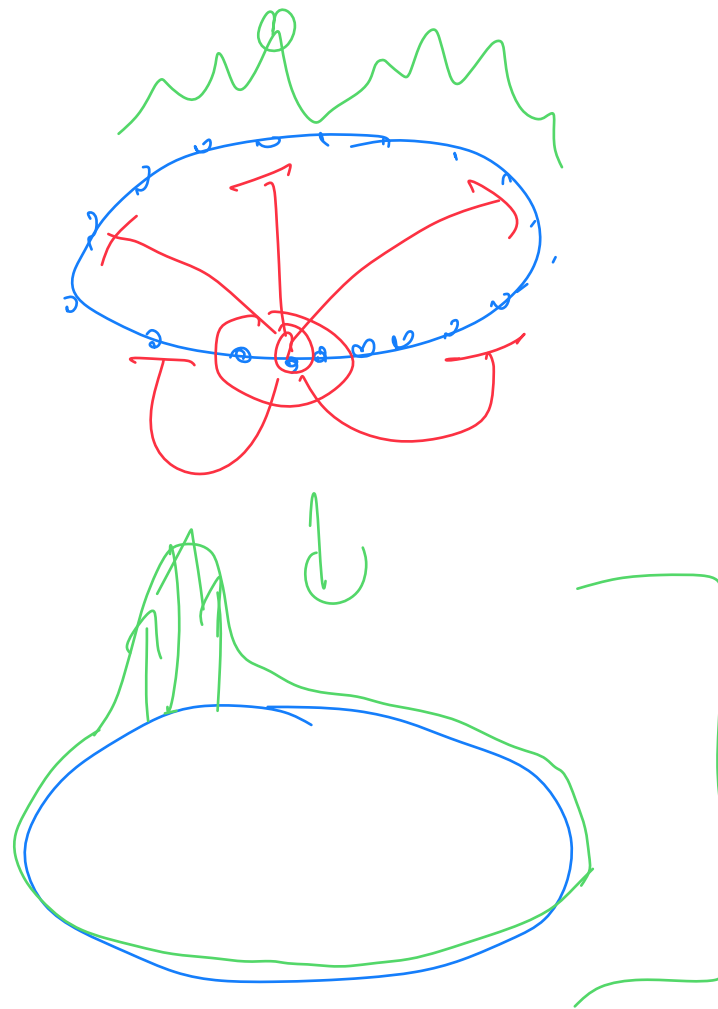
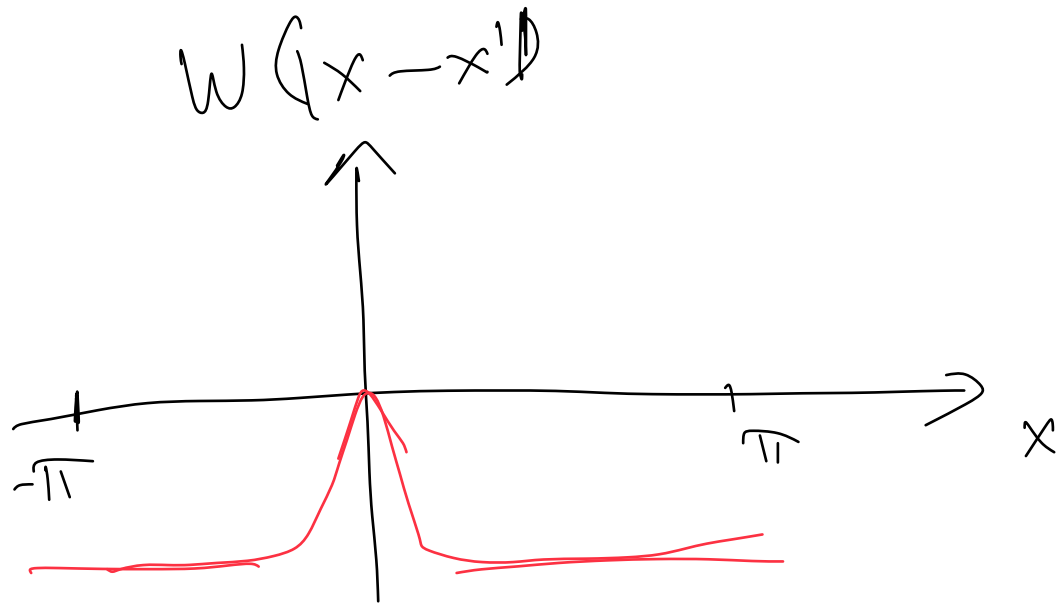
$$x \in \mathbb{R}^n$$

s_i

MD cells with finite neurons
Norman et al 2024

Biswas et al 2026





$$S_0(x) + \varepsilon(x,t)$$

$$\left[\frac{\partial \varepsilon(x,t)}{\partial t} = -\varepsilon + \phi'(L) \int W \varepsilon(x') dx' \right]$$

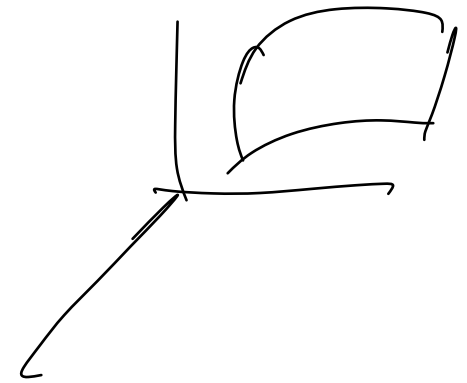
$$\frac{\partial \varepsilon}{\partial t} = \mathcal{L}[\varepsilon(x,t)]$$

\mathcal{L} has a zero e. value

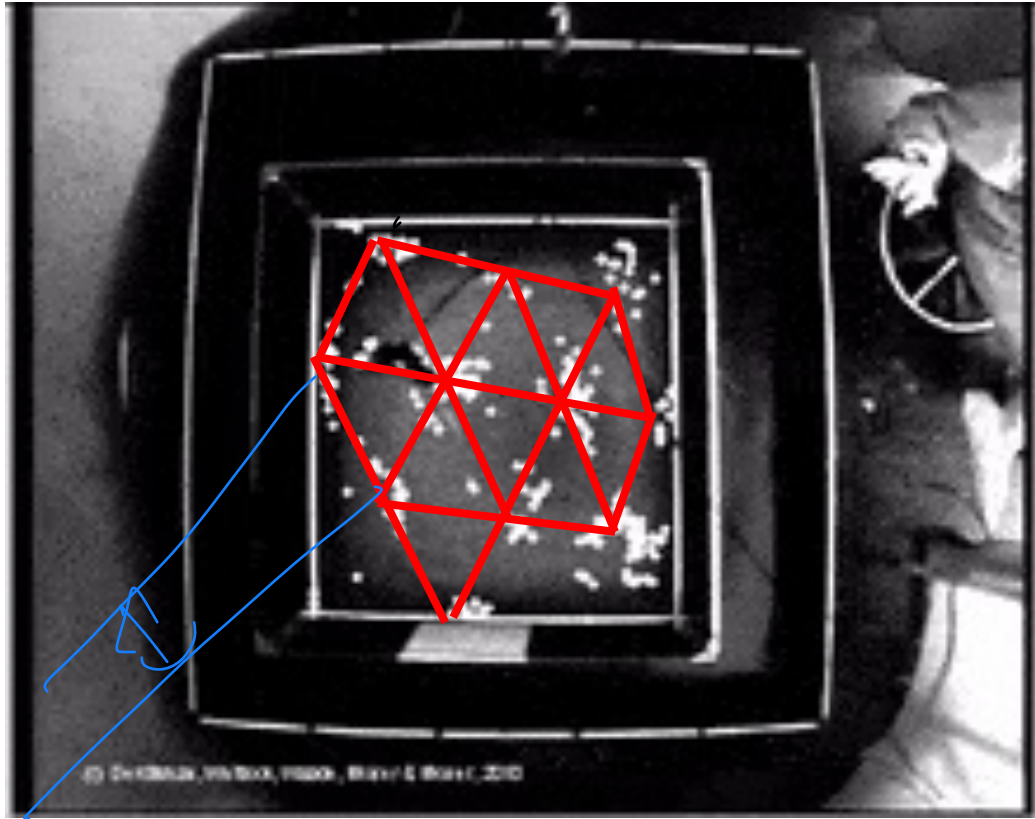
HD cells \rightarrow represent a pt on a circle

\rightarrow circle is neural state space

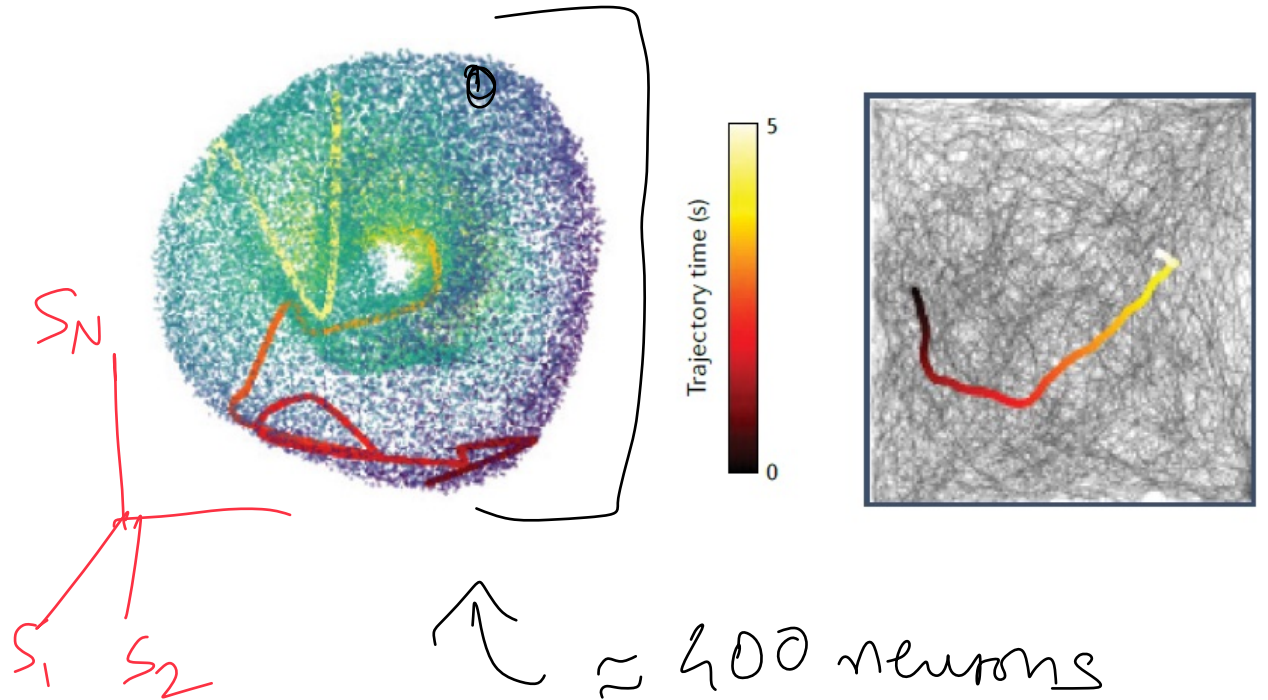
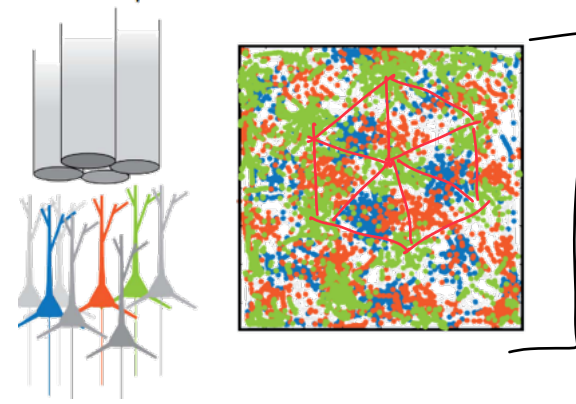
Grid cells \rightarrow represent a pt. on \mathbb{R}^2



Grid cells



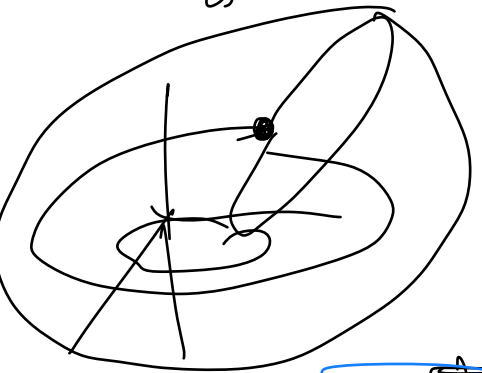
Derdikman et al. 2010



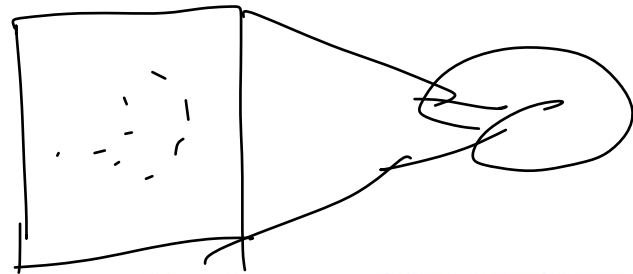
$$s(x)$$

$$\tau \frac{\partial s(x,t)}{\partial t} = -s + \phi \left[\int W(x, x') s(x') dx' + \underline{\underline{B}} \right]$$

$$W(x, x') = \underline{\underline{W(|x-x'|)}}$$

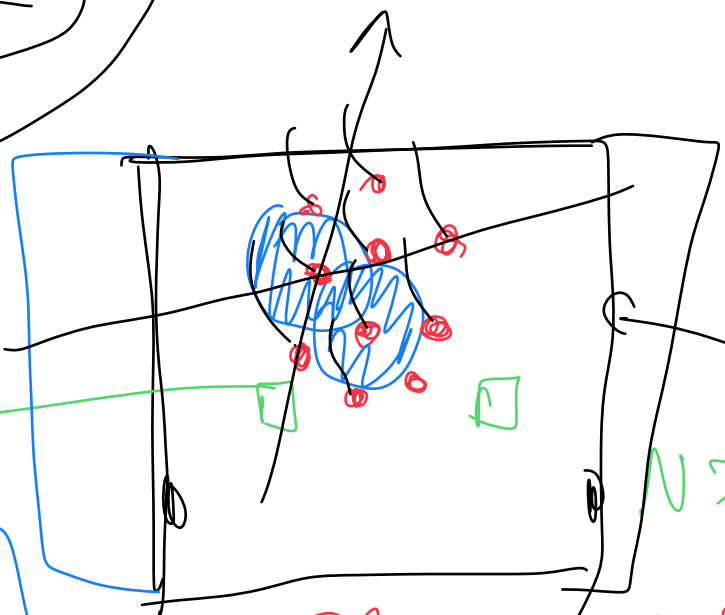
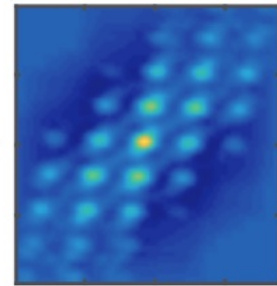
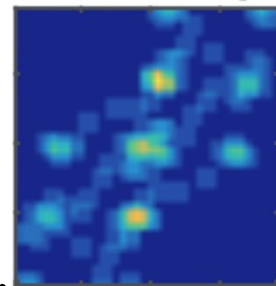


$x \in$

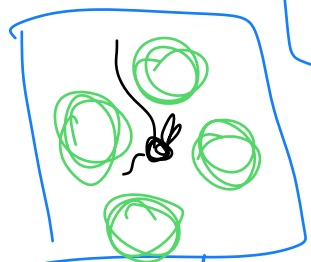


Density
Low  High

Autocorrelogram
grid score=0.92

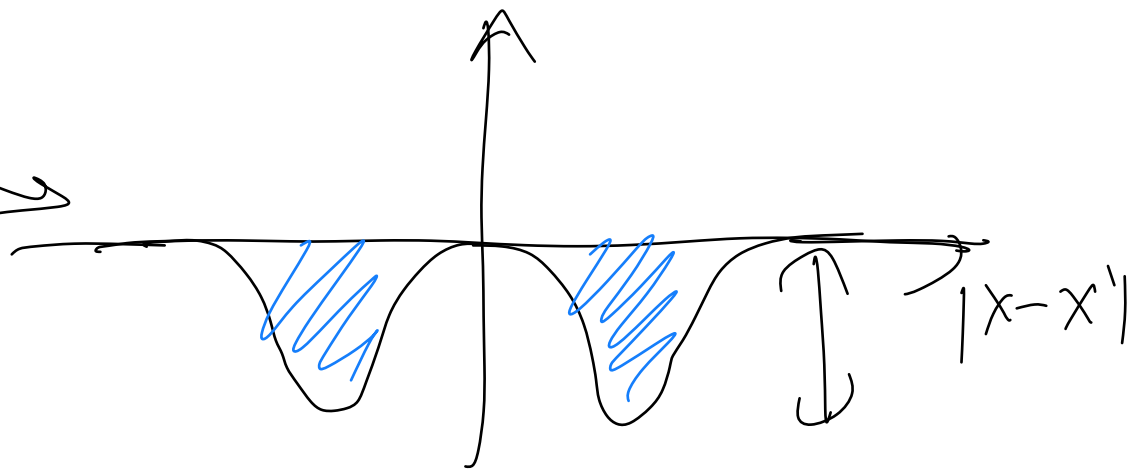


ON neurons



real space \in

$W(|x-x'|)$



$$\frac{\partial S}{\partial t} = -S + \phi \left(\int W(|\bar{x} - \bar{x}'|) S(\bar{x}') d\bar{x}' + B \right)$$

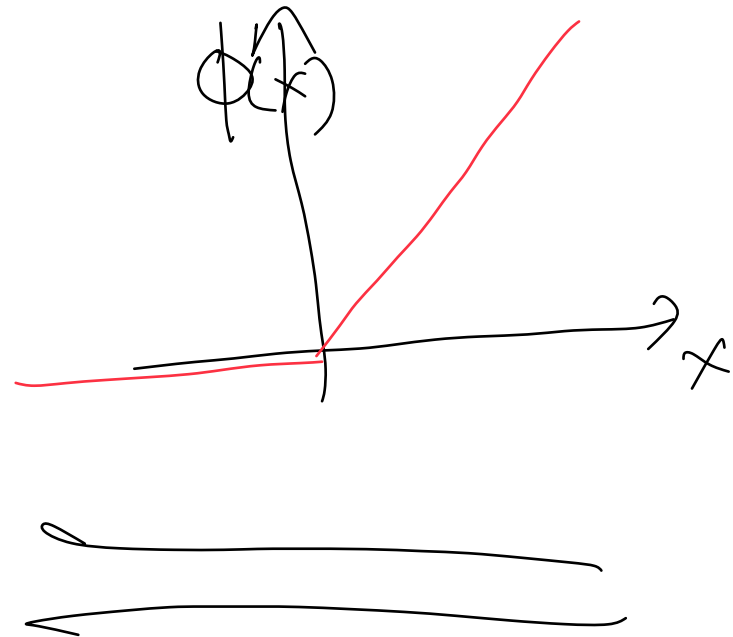
If there is a nontrivial $S_0(\bar{x})$ F.P.

$S_0(\bar{x} + \bar{\xi})$ is also a F.P.

What is the trivial F.P.

$$0 = -S_0 + \phi \left(S_0 \int W + B \right)$$

$$S_0 = \frac{B}{1 - \int W}$$



$$S(x, t) = S_0 + \varepsilon(x, t)$$

$$\tau \frac{\partial \varepsilon}{\partial t} + \varepsilon = \phi'(x) \int W(x-x') \varepsilon(x') dx'$$

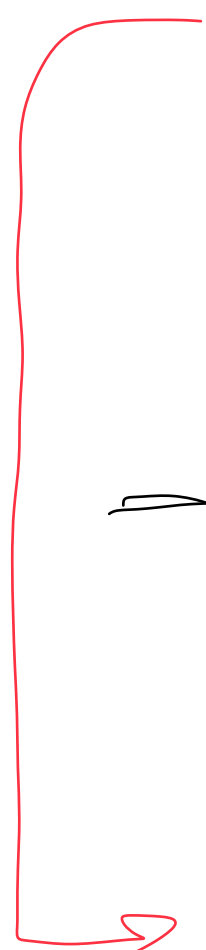
$$\varepsilon(x, t) = \varepsilon \cdot e^{i k x + \alpha(k) t}$$

$$\tau \alpha(k) \varepsilon e^{i k x} + \varepsilon e^{i k x} = \varepsilon e^{i k x} \int W(x-x') e^{i k x'} dx'$$

$$\int W(x-x') e^{-i k (x-x')} dx' = \tilde{W}(k)$$

$$\tau \alpha(k) + 1 = \tilde{W}(k)$$

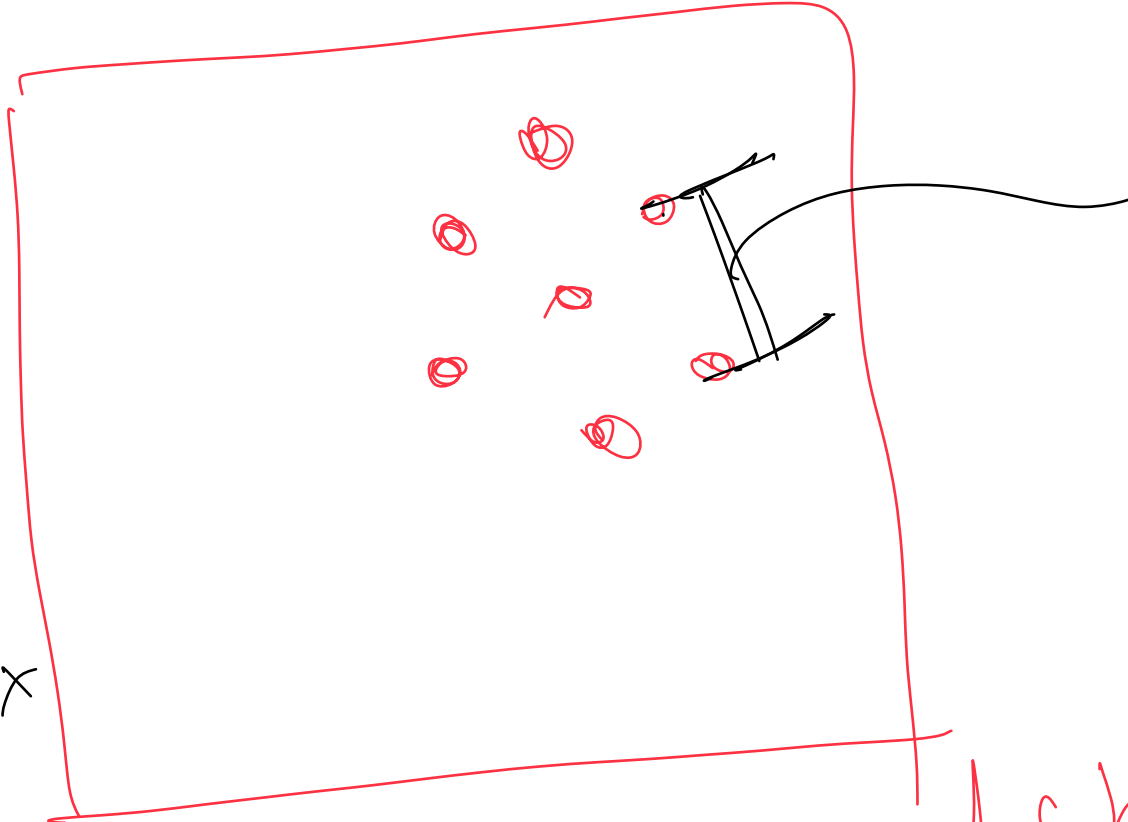
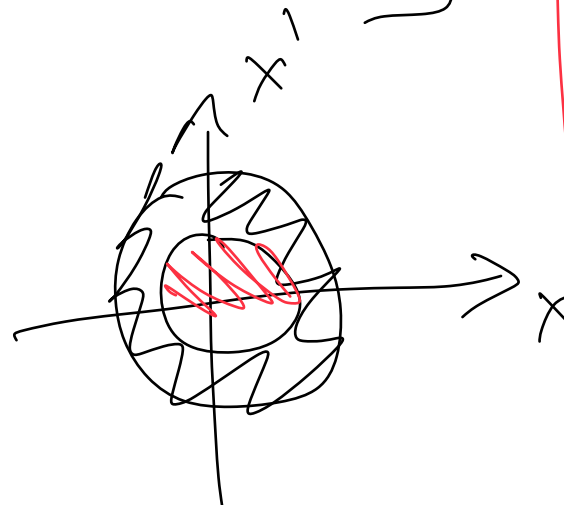
$$\alpha(k) = -\frac{1}{\tau} + \frac{1}{\tau} \tilde{W}(k)$$



Pattern formation

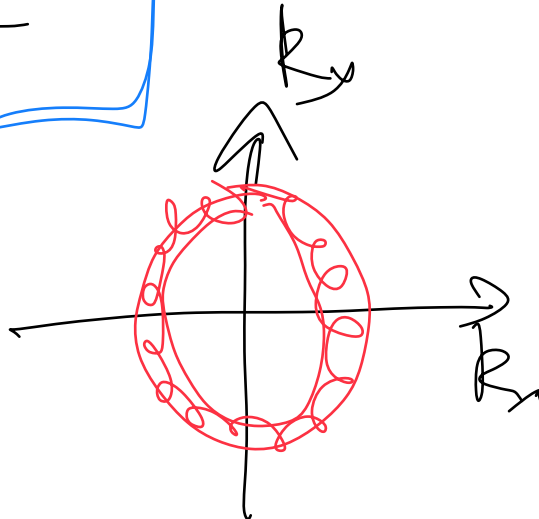
at wavenumber $k^* = \text{arg max} [\tilde{W}(k)]$

Khona Chandren
Fiete
(2025)



neural shell

$$\frac{2\pi}{k^*}$$



Attractors in the Brain

Khona & Fiete (2022)

