Advanced Topics in Theoretical Neuroscience: Bifurcation Analysis

Why is this relevant?

- **Stability**: is the behavior of my system going to change dramatically if some parameter changes a little?
- **Dynamics**: If you care about dynamics of a system, then understanding how fixed points, etc. change is important.
- **Inform hypotheses about mechanisms**: Observing temporal dynamics can tell you something about how the system operates.

Takeways from today:

- Learn how to read a bifurcation diagram
- Know where to look if you have to do this (Hint: there is software so its relatively easy!)
- Remember that identification of fixed points isn't always complete picture!

Outline

- **Part 1:** Review of some basic concepts from dynamical systems
- **Part 2:** Bifurcations: definition, types, and properties
- **Part 3:** Examples in Neuroscience literature:
  - A Recurrent Network Mechanism of Time Integration in Perceptual Decisions
  - Dynamical mechanisms of how an RNN keeps a beat

Part 1: Quick Review

Dynamical System

$$\dot{V}_1 = F(V)$$

$$\dot{V}_3 = F(V)$$

$$\vdots$$

$$\dot{V}_N = F(V)$$

Fixed Points are given by solving (simultaneously):

$$\dot{V}_1 = 0$$

$$\dot{V}_2 = 0$$

$$\vdots$$

$$\dot{V}_N = 0$$

Stability of fixed points are determined by eigenvalues:

for $\lambda_i \in \{\lambda\}_{j=1}^{N}$

$Re(\lambda_i) < 0$ attracting

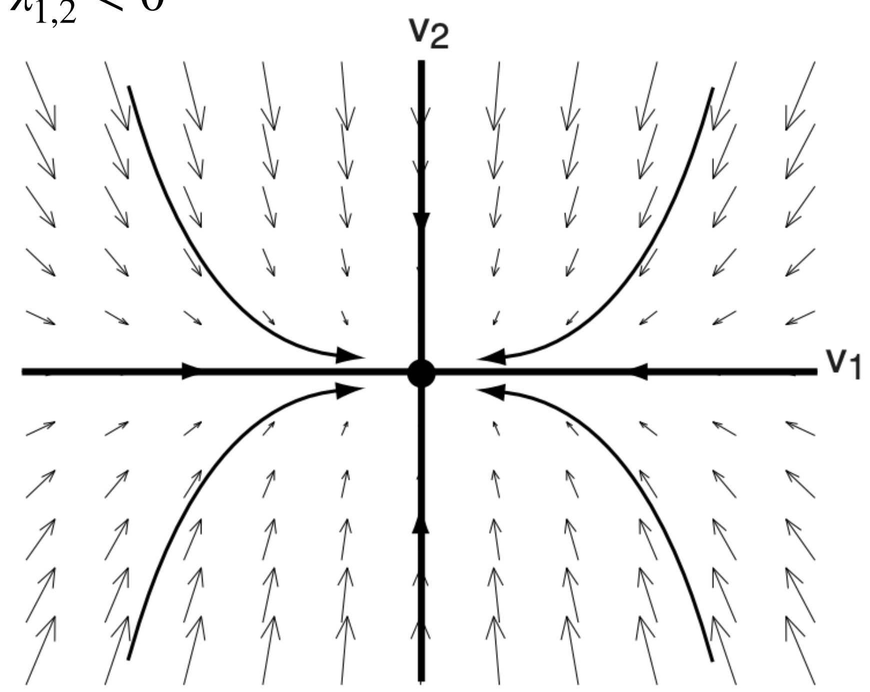
$Re(\lambda_i) > 0$ repelling

$Im(\lambda_i) \neq 0$ oscillating

Part 1: Quick Review

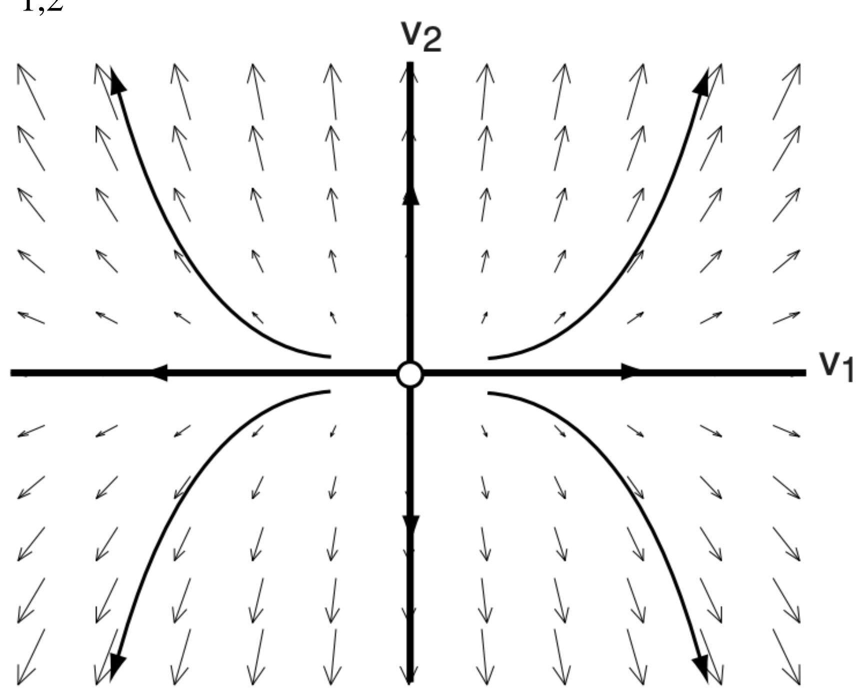
Example dynamics in 2D:

$\lambda_{1,2} < 0$



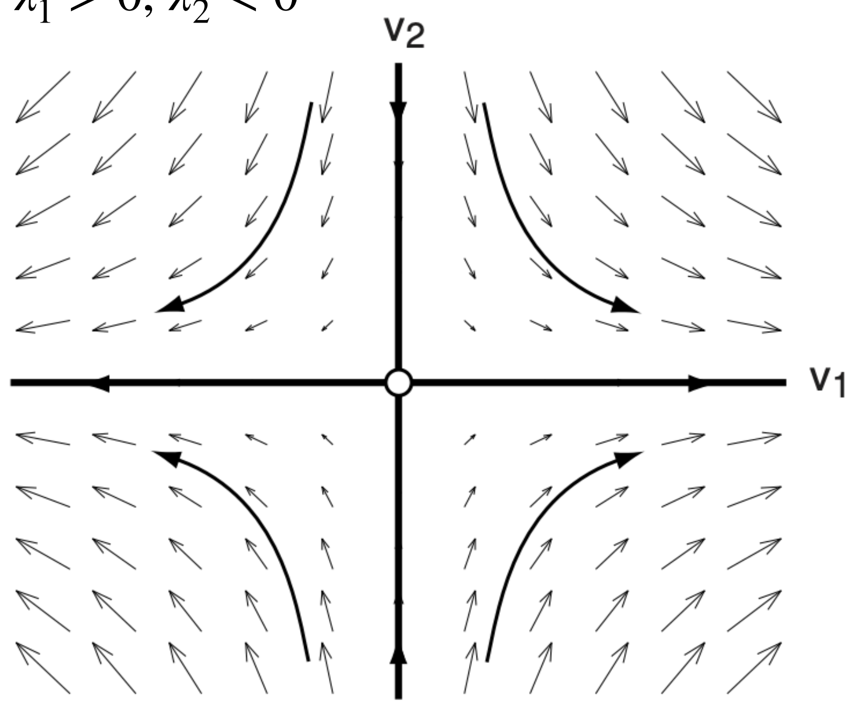
stable node

$\lambda_{1,2} > 0$



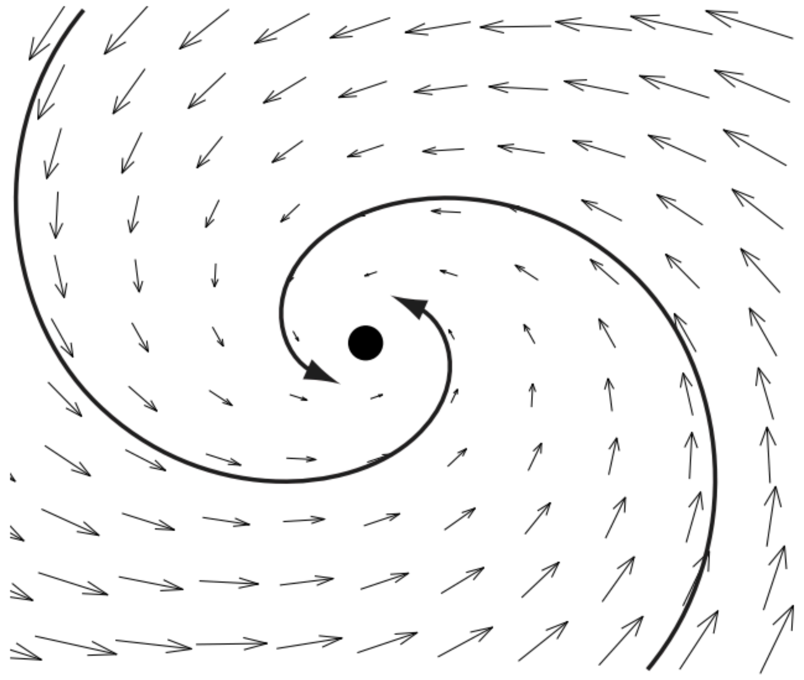
unstable node

$\lambda_1 > 0,\ \lambda_2 < 0$



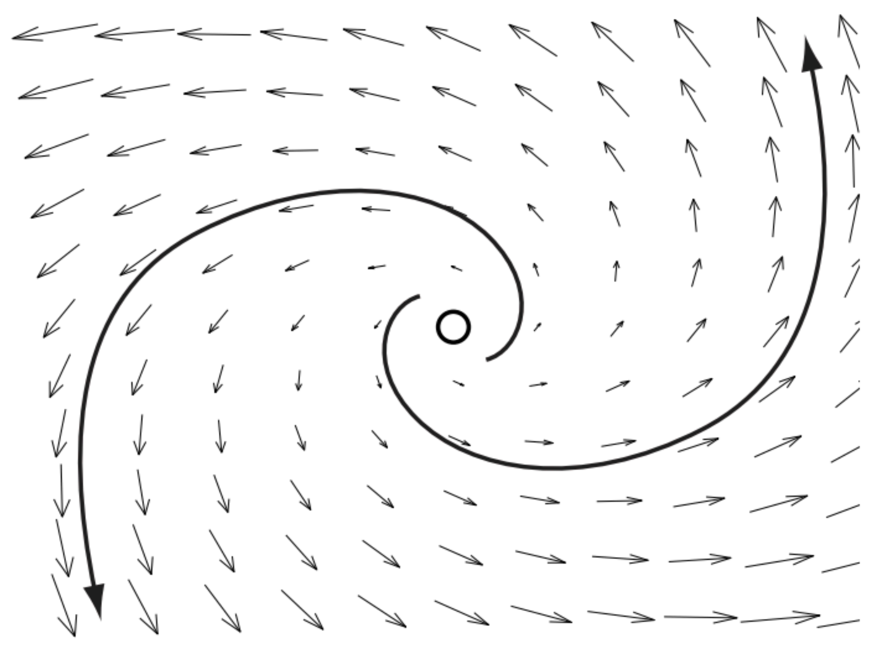
saddle

$\lambda_{1,2} = -a \pm bi,\ \ a > 0$



stable focus

$\lambda_{1,2} = a \pm bi,\ \ a > 0$



unstable focus

Part 1: Quick Review

A **phase portrait** is a geometrical representation of the system's dynamics

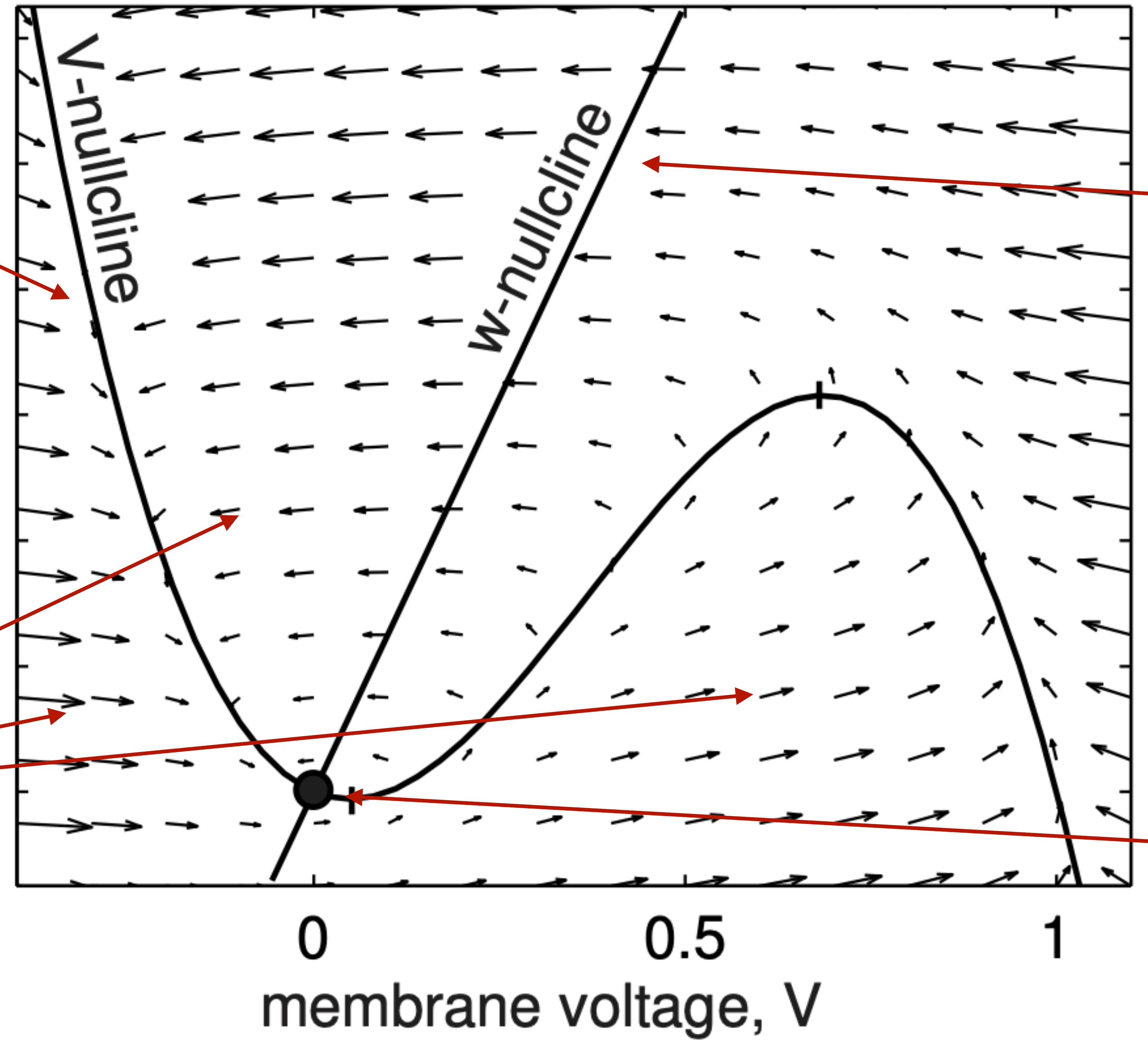
A phase portrait includes:

- Fixed points, flow fields and nullclines.
- The V_j-nullcline is the set of points where V_j' vanishes and separates R^n into a collection of regions in which the V_j-components of the vector field point in either the positive or negative direction.

Example phase plane for FitzHugh-Nagumo model

Solved by setting $\dot{V} = 0$

(V-nullclines separate $\mathbb{R}^2$ into regions where vector field points either to the left or to the right)



Solved by setting $\dot{w} = 0$

(w-nullclines separate $\mathbb{R}^2$ into regions where the vector field points upward or downward)

fixed point

Describes local flow from any initial condition

FitzHugh-Nagumo model

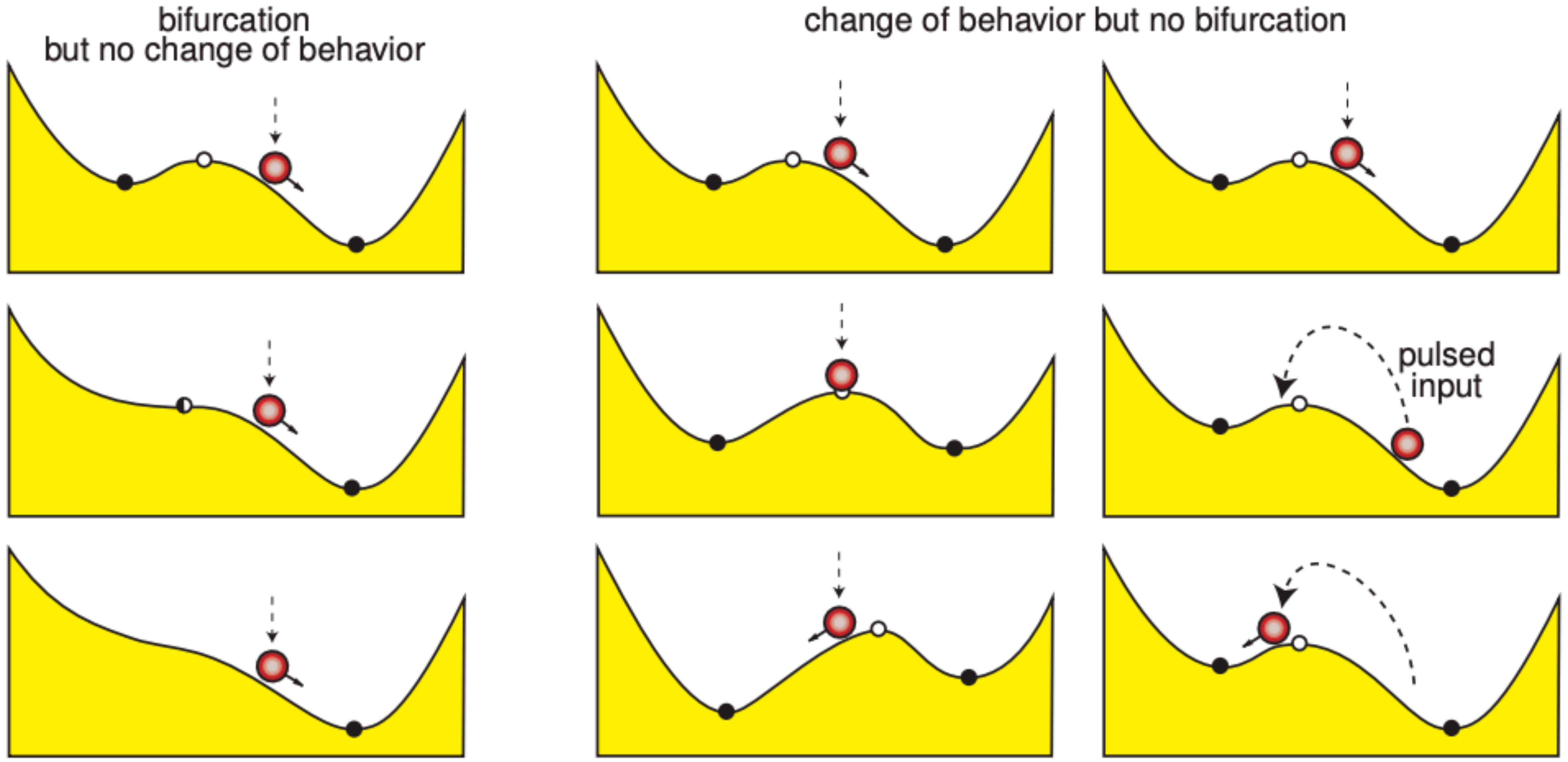
$$\dot{V} = V(a - V)(V - 1) - w + I$$
$$\dot{w} = bV - cw$$

Part 2: Bifurcations

Part 2: Bifurcations

A **bifurcation** is a qualitative, topological change of a system's phase space.

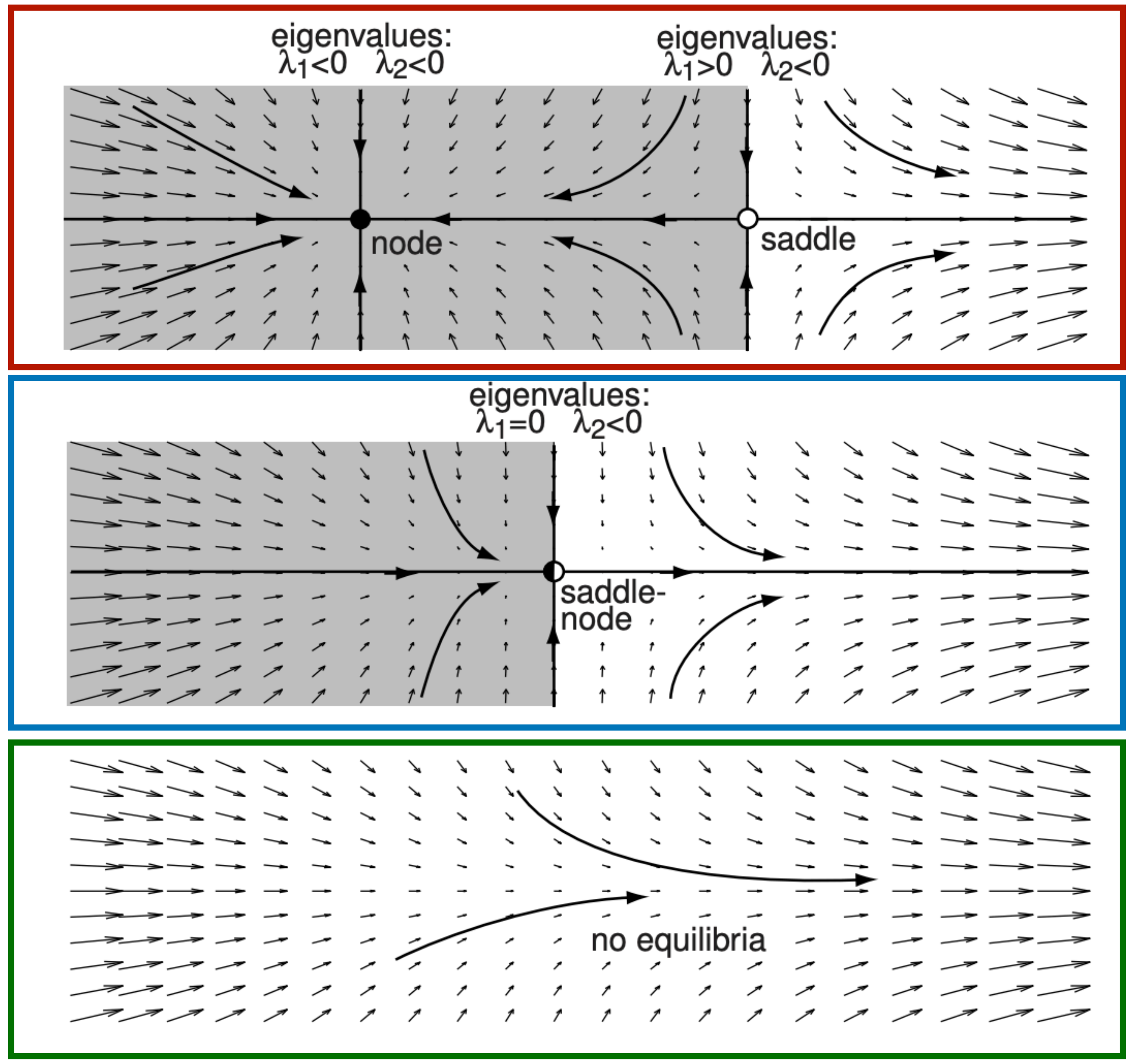
For instance:
- the change in the stability of a fixed point
- a change in the number of fixed points
- appearance or disappearance of oscillations.



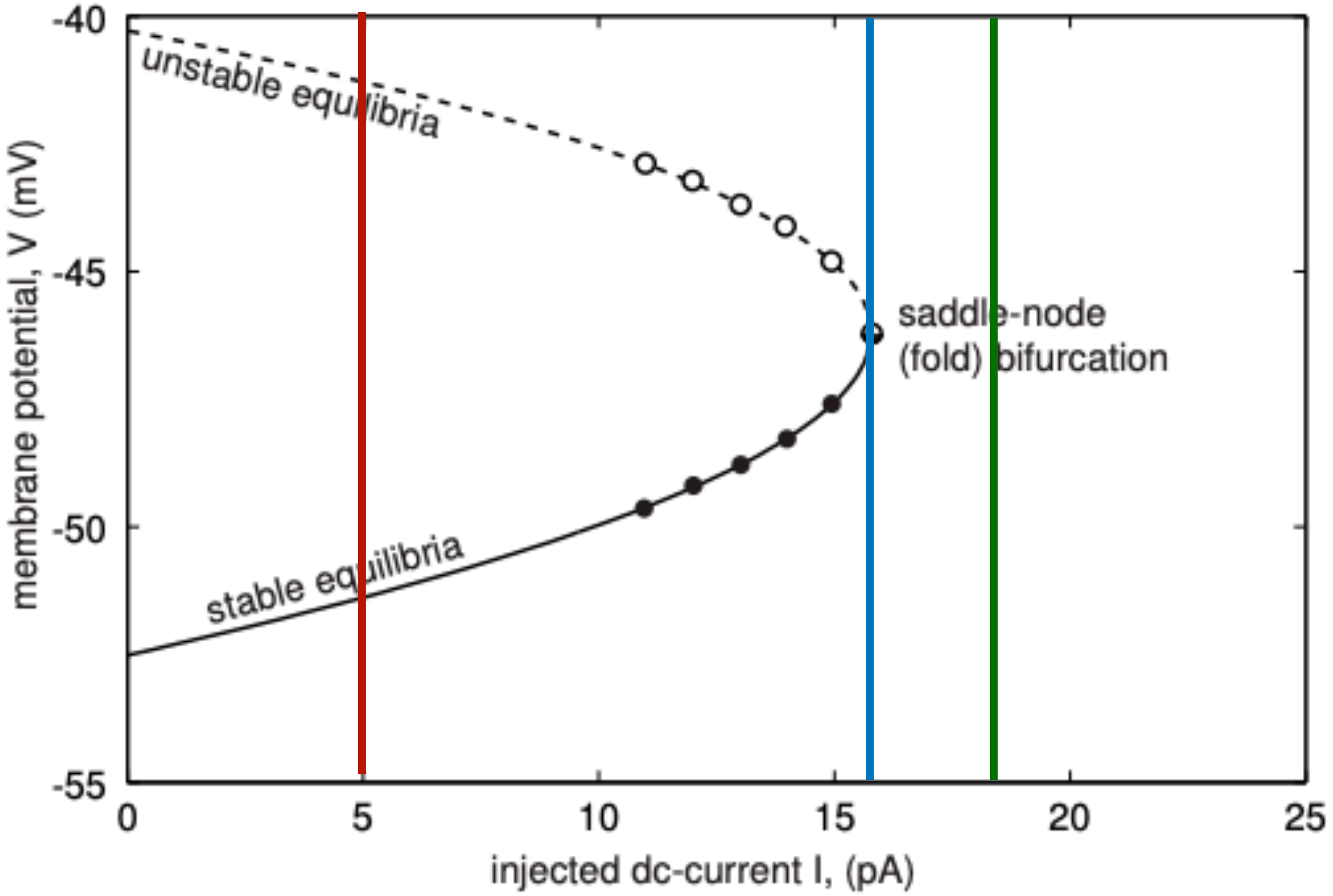
Part 2: Common Bifurcations

Saddle-node bifurcation

(⟵Bifurcation parameter inc)



Bifurcation Diagram showing saddle-node bifurcation

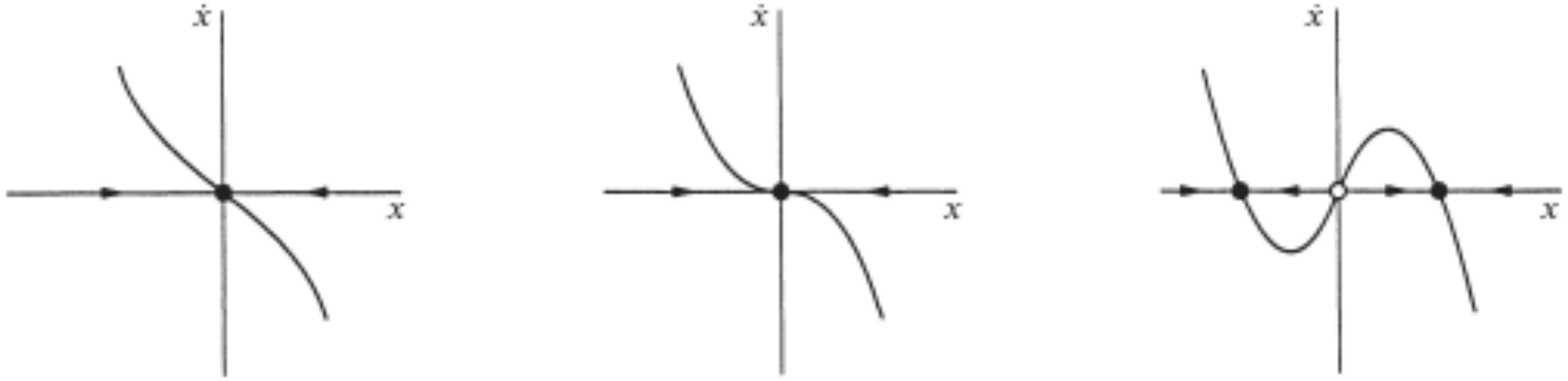


(Bifurcation parameter inc. ⟶)

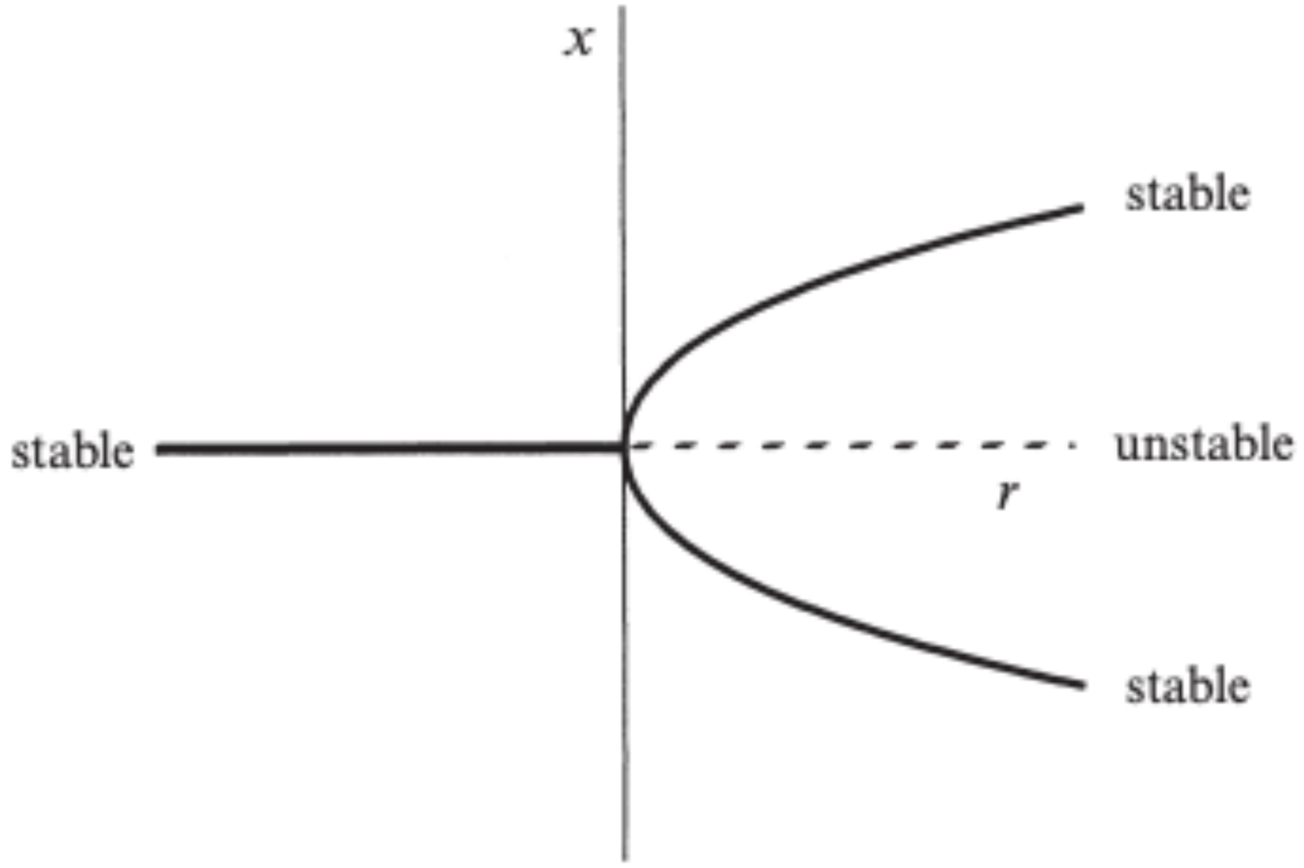
local bifurcation occurs when a parameter change causes the stability of an equilibrium (or fixed point) to change

Part 2: Common Bifurcations

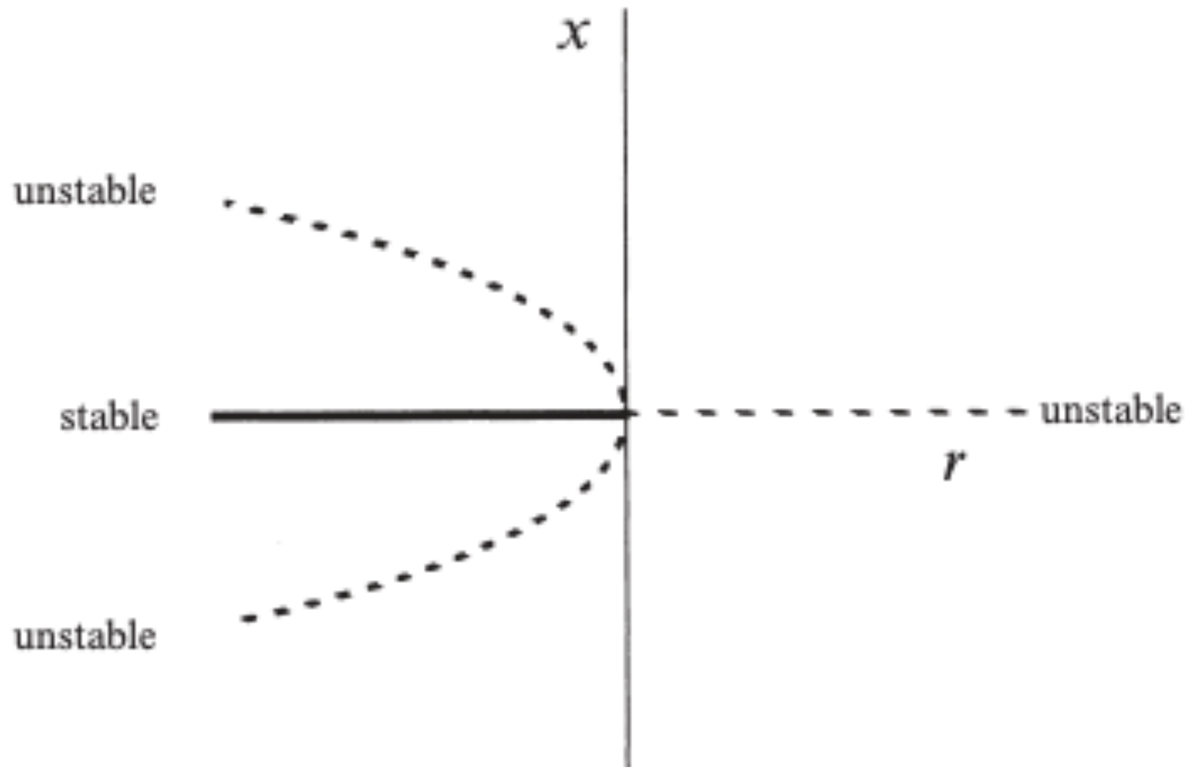
Supercritical Pitchfork bifurcation $(\dot{x} = rx - x^3)$



(a) $r<0$ (b) $r=0$ (c) $r>0$



Subcritical Pitchfork bifurcation $(\dot{x} = rx + x^3)$



These are **local bifurcations**

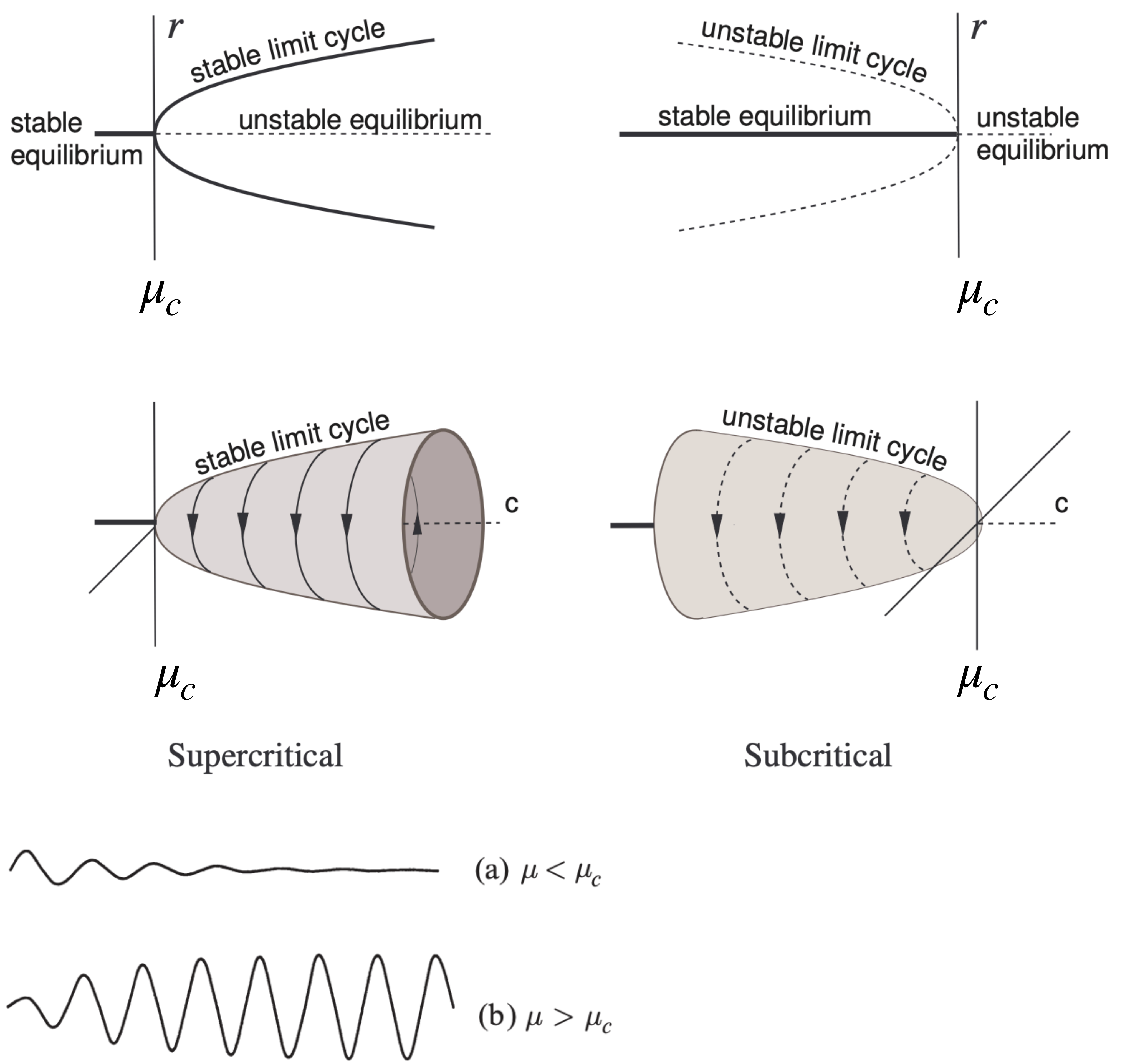
Part 2: Common Bifurcations

Andronov-Hopf bifurcation

- In a **supercritical** Hopf bifurcation, the equilibrium loses stability and gives birth to a stable limit cycle with **vanishing amplitude (non-zero freq.)**

- In a **subcritical** Hopf bifurcation, the unstable limit cycle shrinks to an equilibrium and this causes the equilibrium point to lose stability

- These are **local** bifurcations, complex conjugate eigenvalues simultaneously cross the imaginary axis

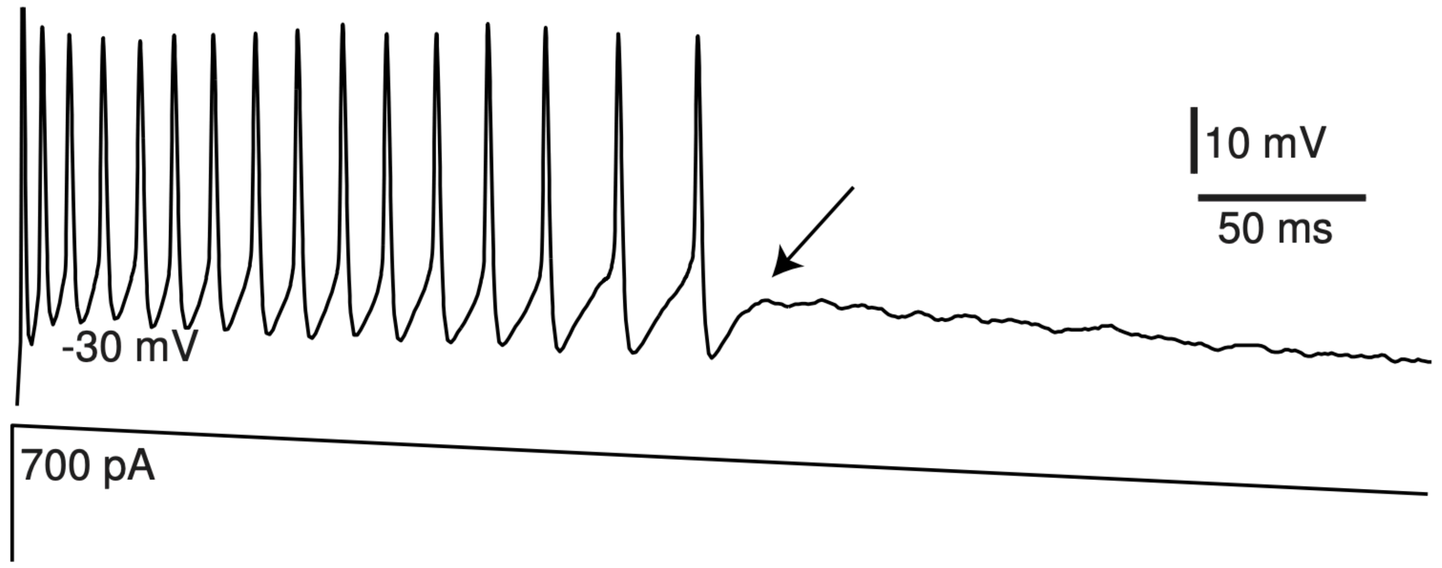


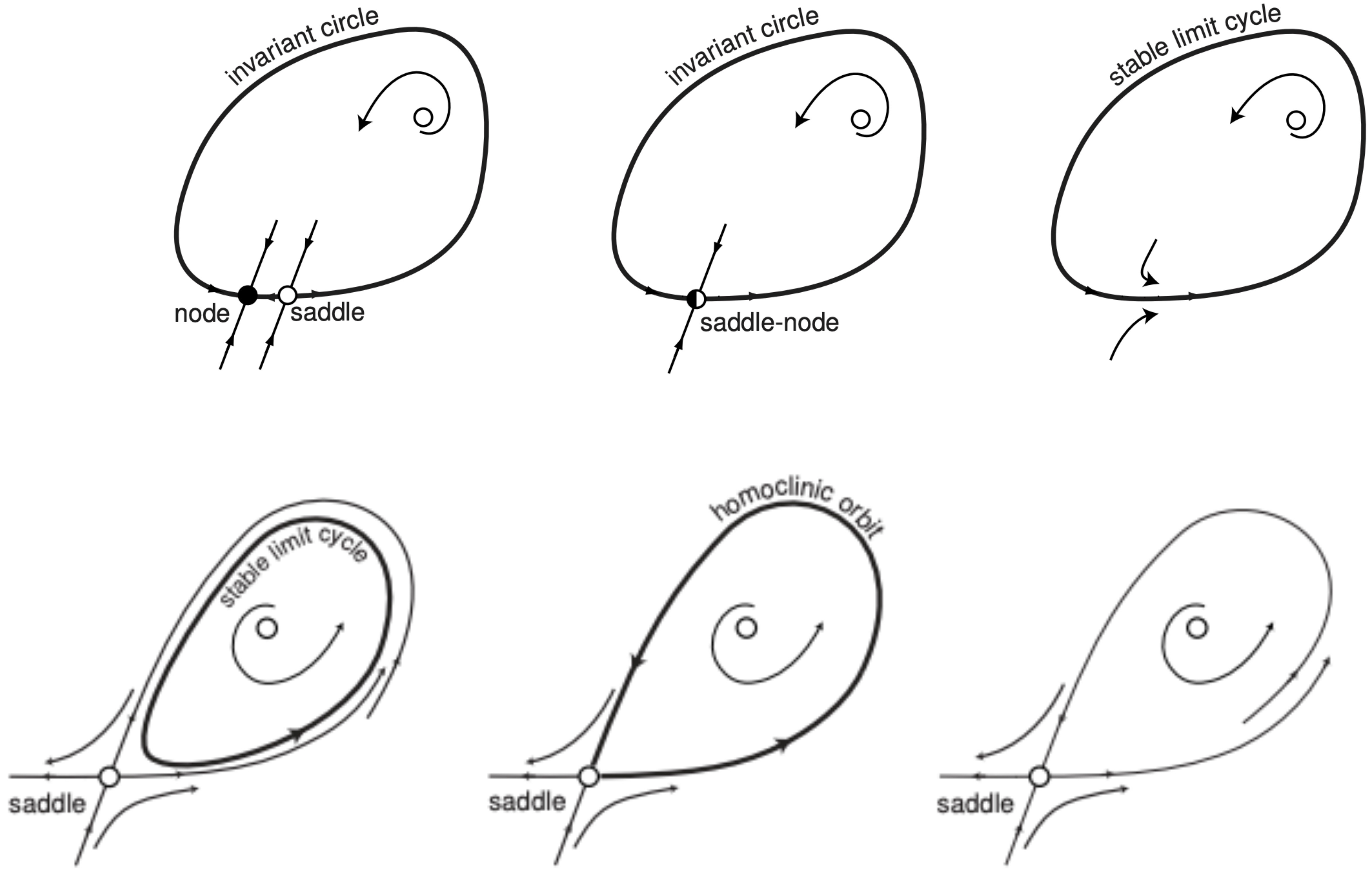
Part 2: Common Bifurcations

Homoclinic bifurcation (infinite period)

- The frequency of oscillations goes to 0 (**infinite perio**d) but the **amplitude remains nonzero**.
- This is an example of **a global bifurcations** occur when 'larger' invariant sets, such as periodic orbits, collide with equilibria

Example oscillations from a single neuron:

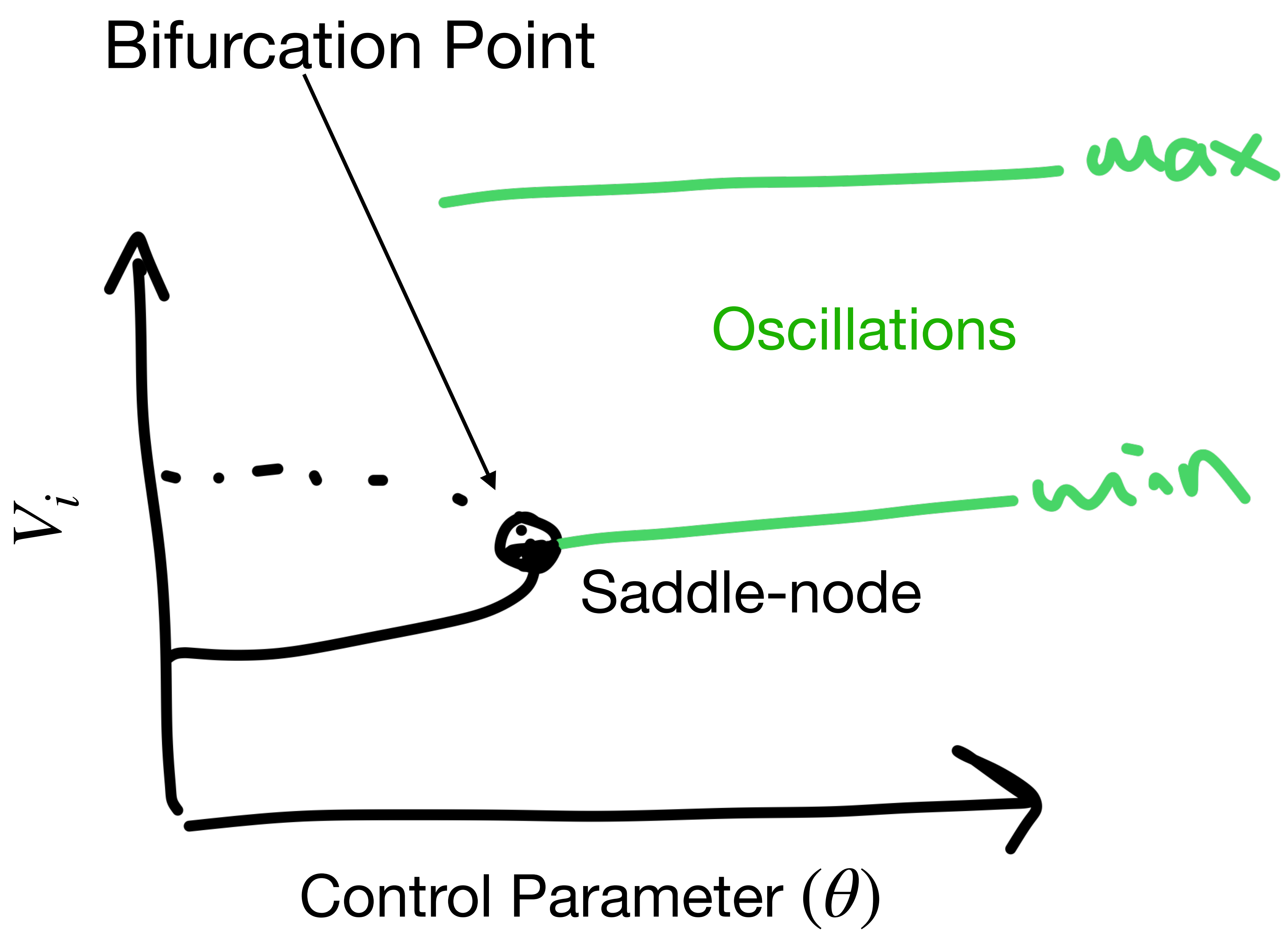


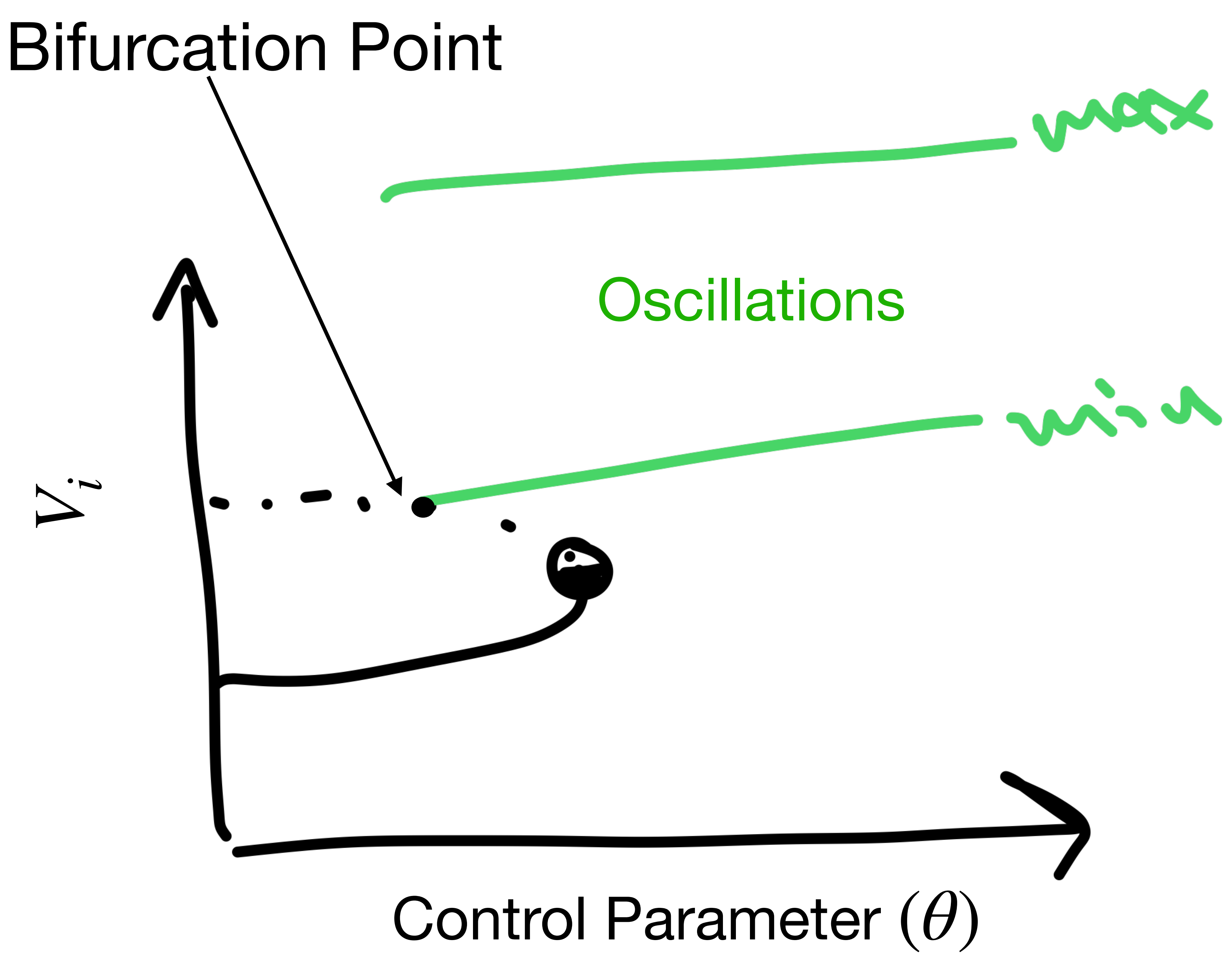


Part 2: Common Bifurcations

Example bifurcation diagrams for Homoclinic bifurcations (infinite period)

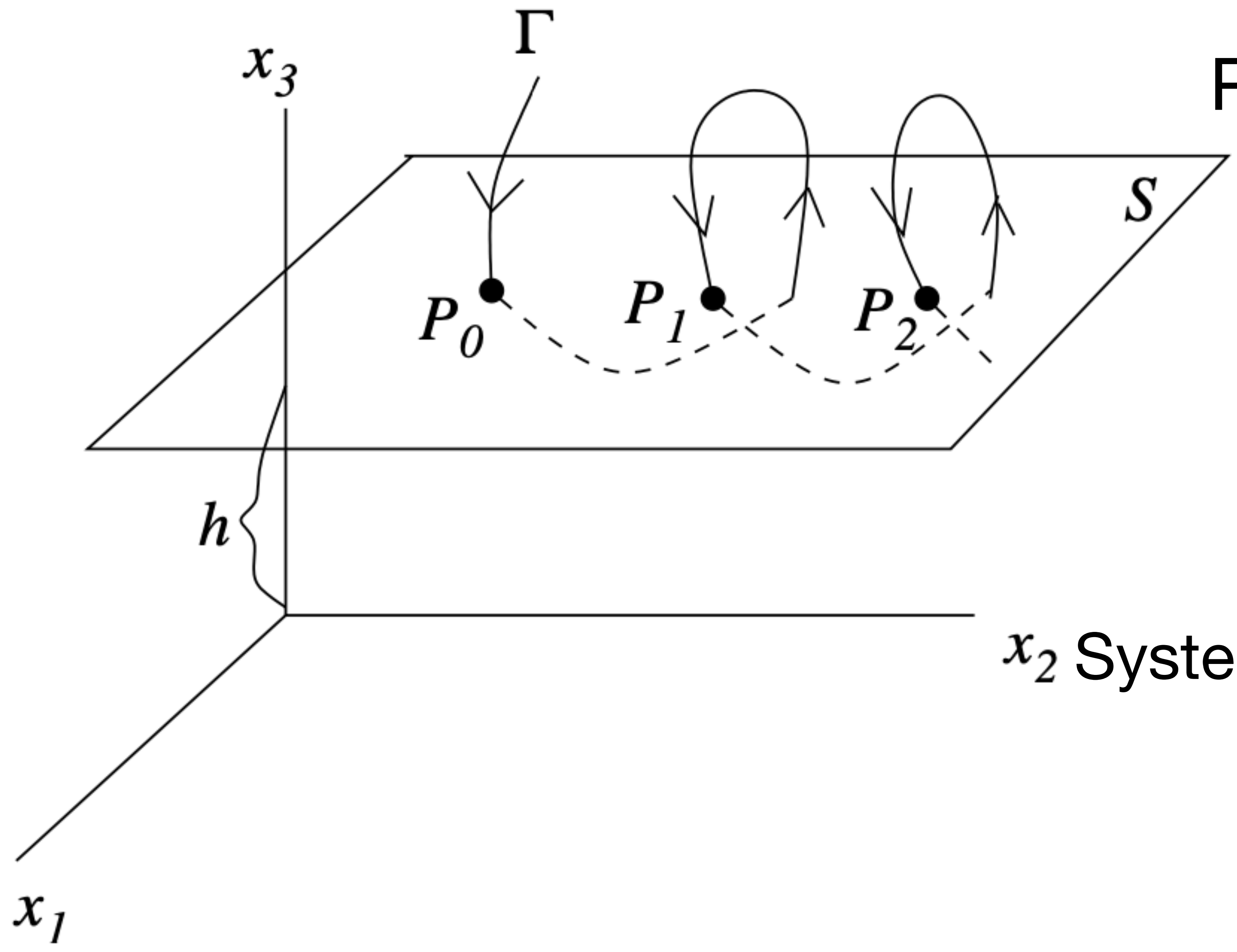
$$\dot{V} = F(V, \theta)$$





Part 2: Common Bifurcations

Solving for Limit Cycles



Poincare Section

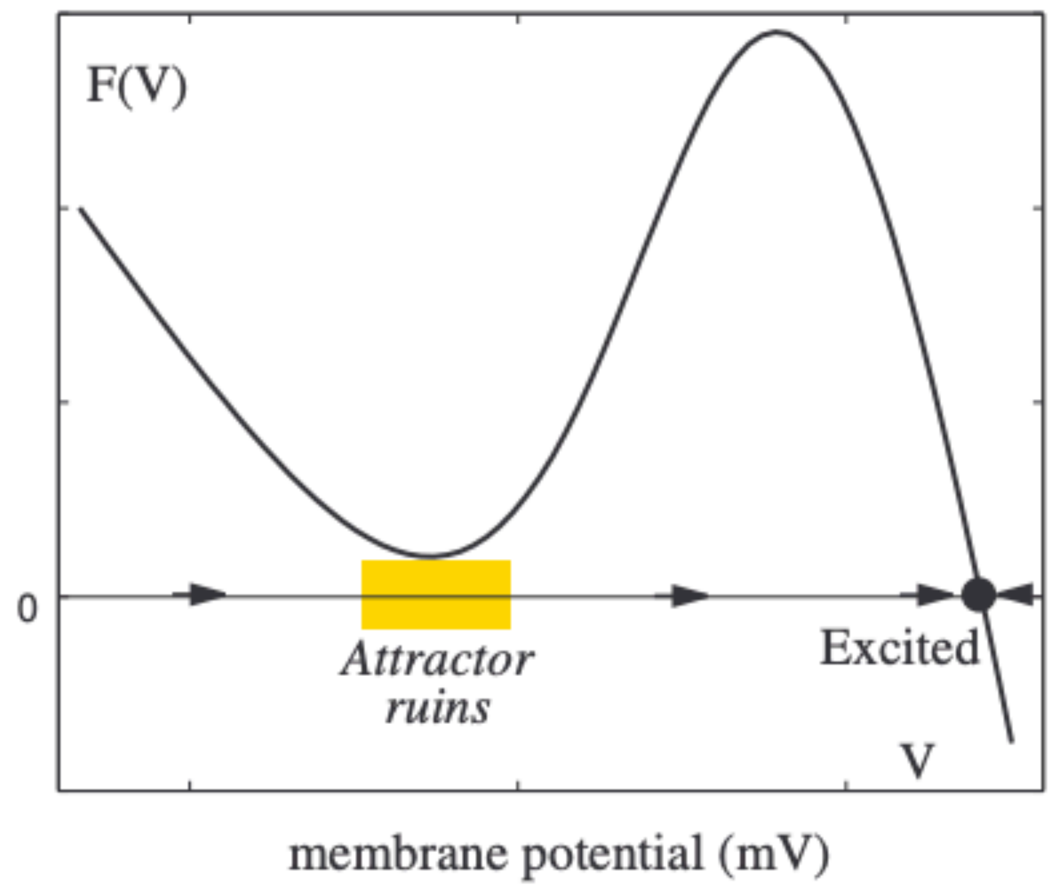
Dim = n-1

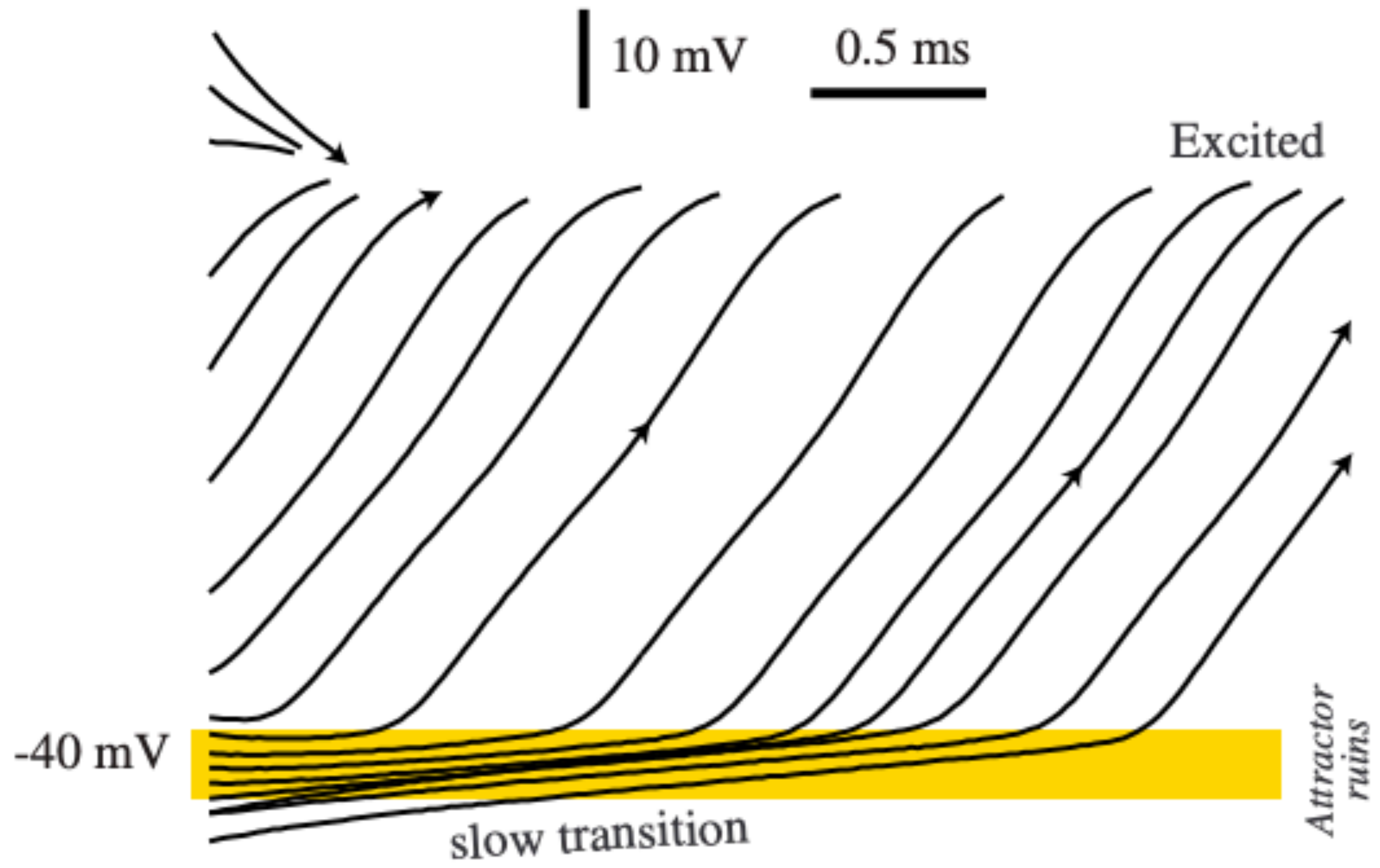
System Dim = n

- Poincare map is a map from the poincare section to itself:
  $P_{k+1} = T(P_k) = T(T(P_{k-1})) = \dots$
- Fixed point of the poincare map is a closed orbit.
- Stability of the closed orbit can evaluated by computing the eigenvalues (floquet multipliers) around the fixed point on the poincare map.
  $|\lambda_i| < 1$ attracting, $|\lambda_i| > 1$ repelling

Part 2: Other related phenomena

Example of a ghost:





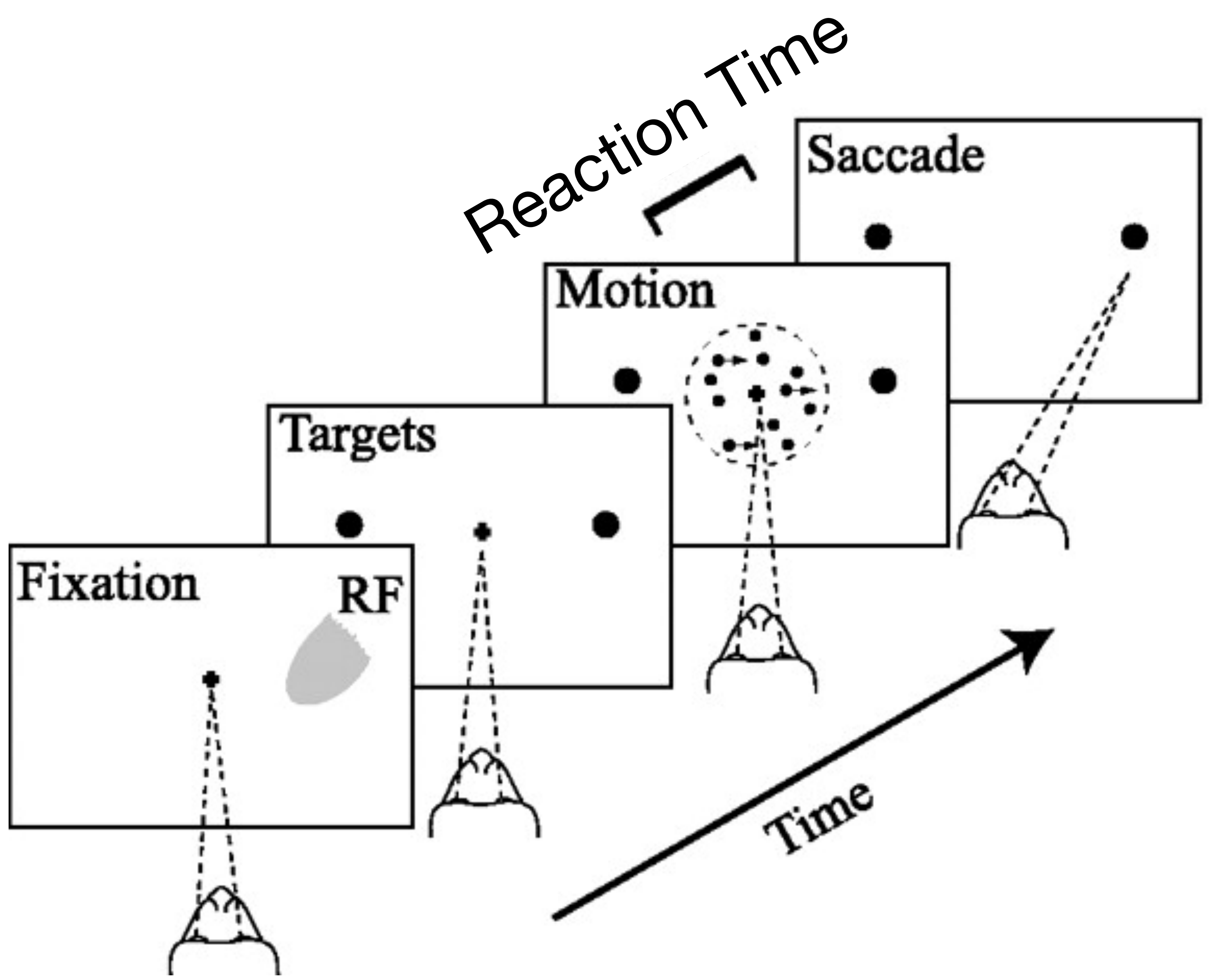
- Even after the attracting fixed points have disappeared, they can continue to influence the flow
- A **ghost** is a bottleneck region that sucks trajectories in and delays them before allowing passage out the other side.
- The **time spent in the bottleneck increases as** $(\mu - \mu_c)^{-1/2}$ where μ_c is the value at which the saddle-node bifurcation occurs.

Part 3: Examples from Neuroscience Literature

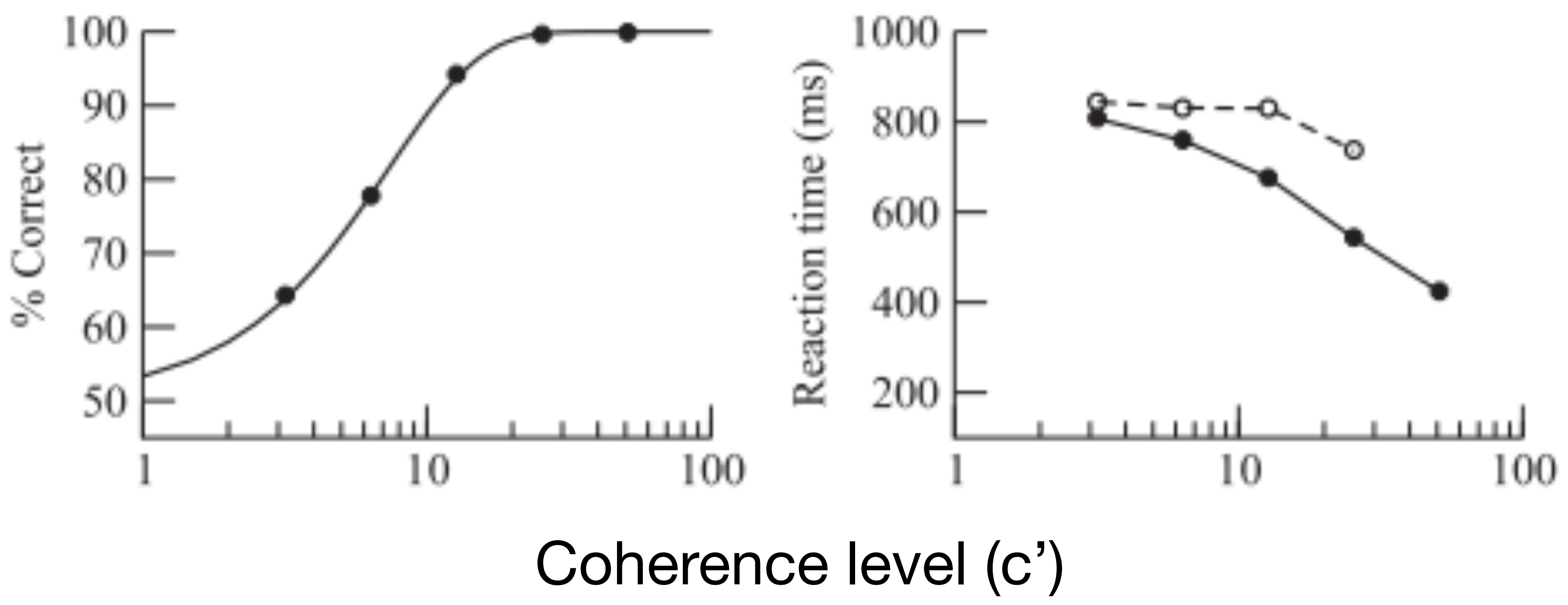
Part 3: Wong and Wang, 2006

A Recurrent Network Mechanism of Time Integration in Perceptual Decisions

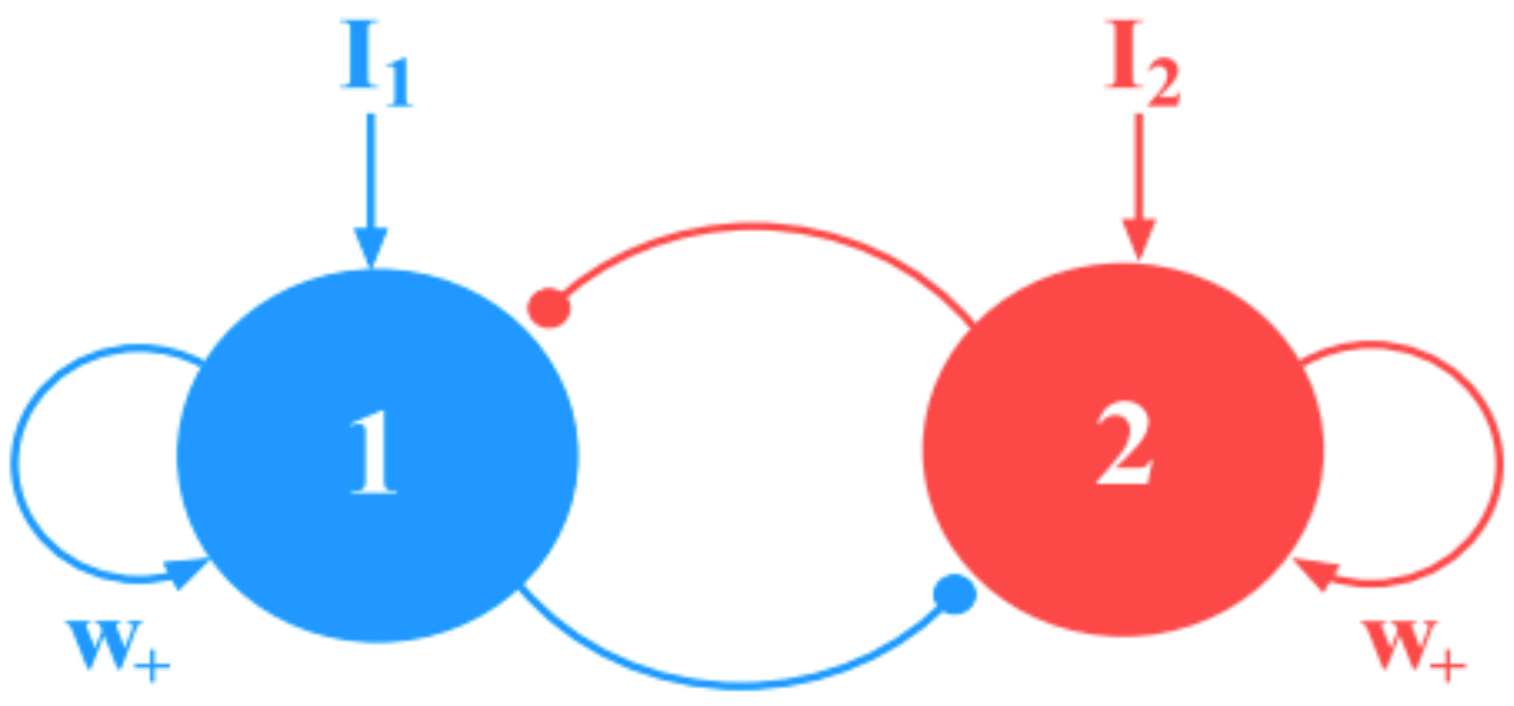
Experimental Setup



Experimental Data



Part 3: Wong and Wang, 2006



Reduced two-variable model

$$\frac{dS_i}{dt} = -\frac{S_i}{\tau_S} + (1 - S_i)\gamma H_i$$

$$H_i = \frac{a x_i - b}{1 - \exp\left[-d\left(a x_i - b\right)\right]}$$

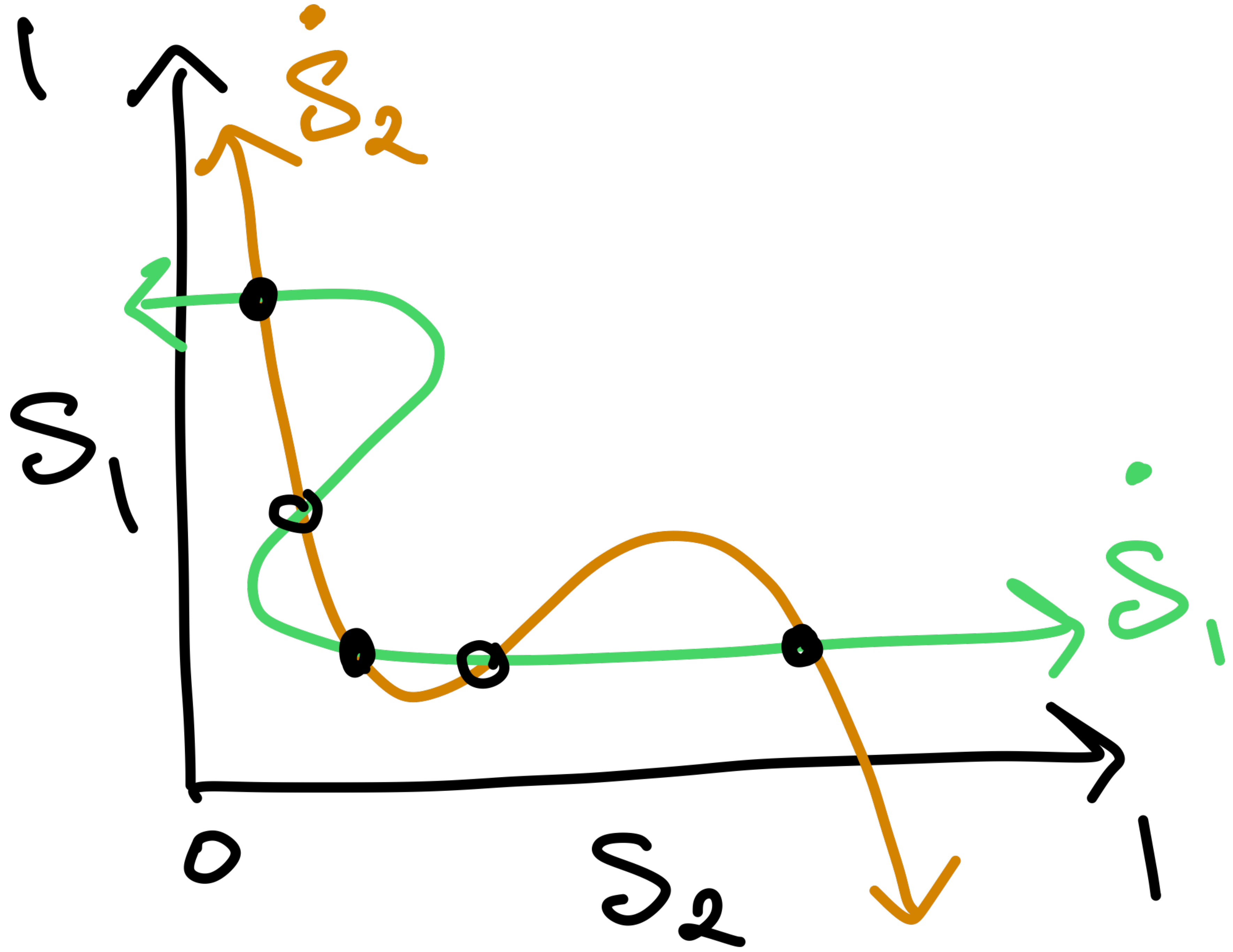
$$x_1 = J_{N,11} S_1 - J_{N,12} S_2 + I_0 + I_1 + I_{\text{noise},1}$$

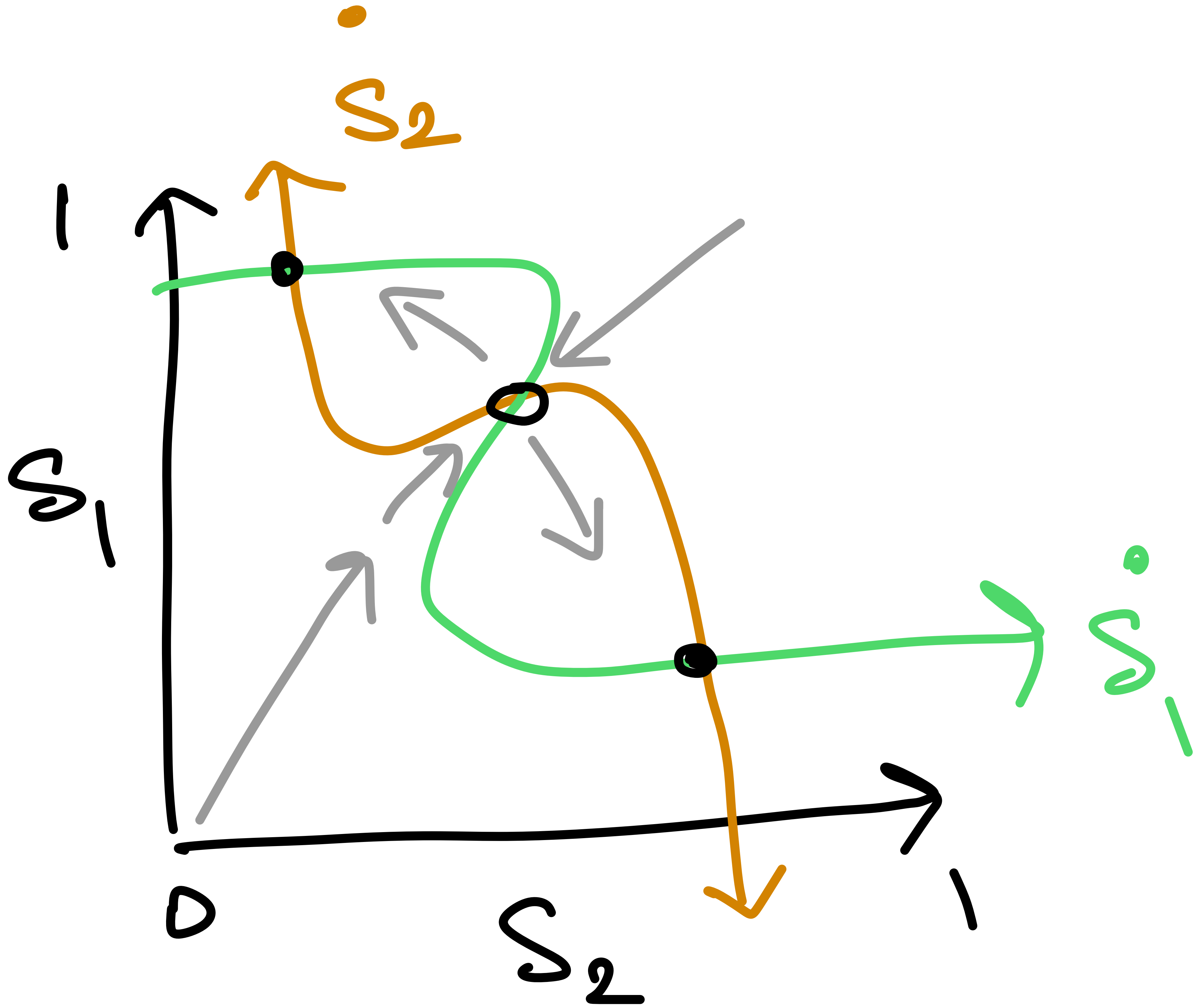
$$x_2 = J_{N,22} S_2 - J_{N,21} S_1 + I_0 + I_2 + I_{\text{noise},2}$$

$$I_i = J_{A,\text{ ext}}\, \mu_0 \left(1 \pm \frac{c'}{100\%}\right)$$

$$\tau_{\text{AMPA}} \frac{dI_{\text{noise},i}(t)}{dt} = -I_{\text{noise},i}(t) + \eta_i(t)\sqrt{\tau_{\text{AMPA}}\, \sigma_{\text{noise}}^2}$$

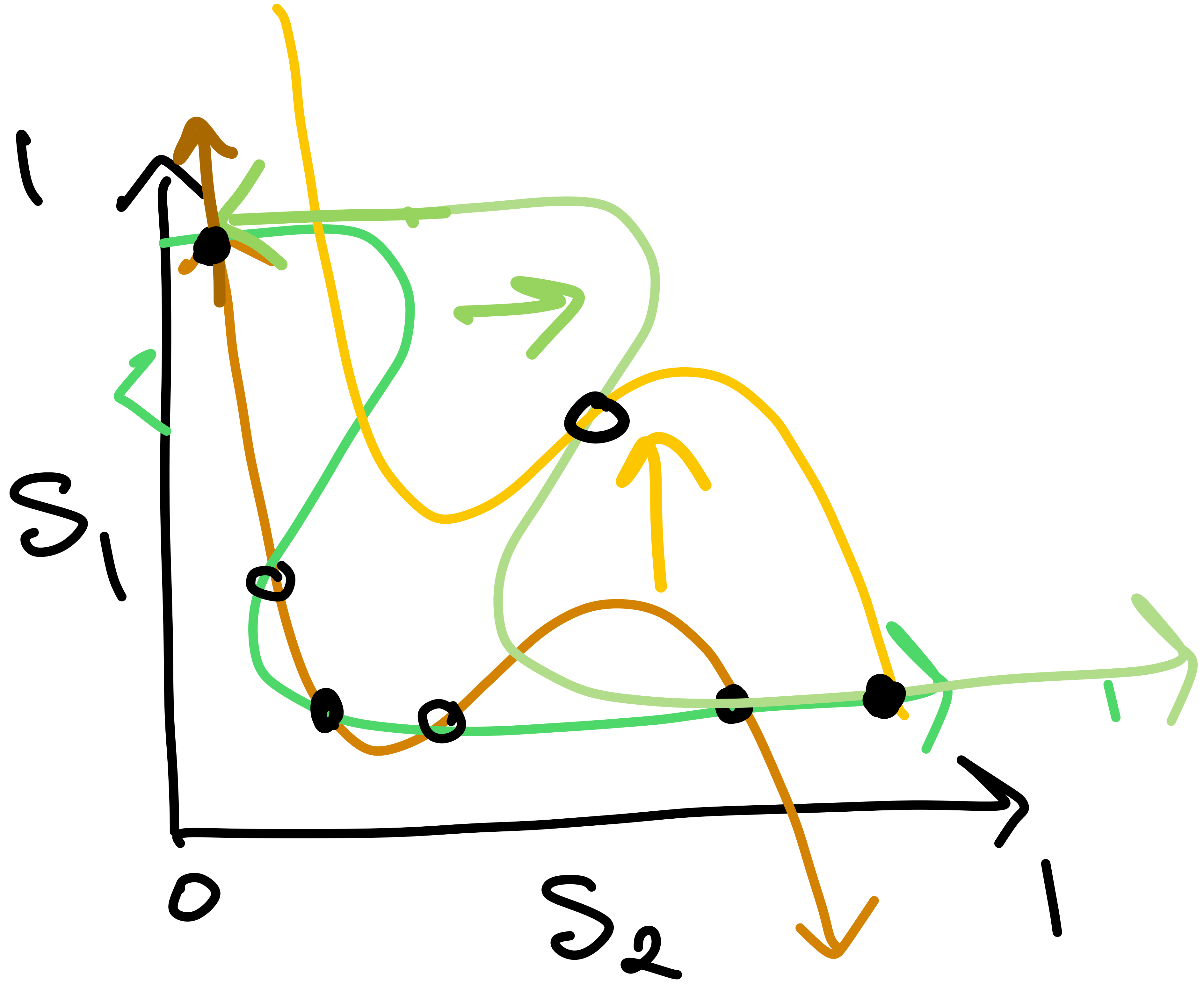
Part 3: Wong and Wang, 2006





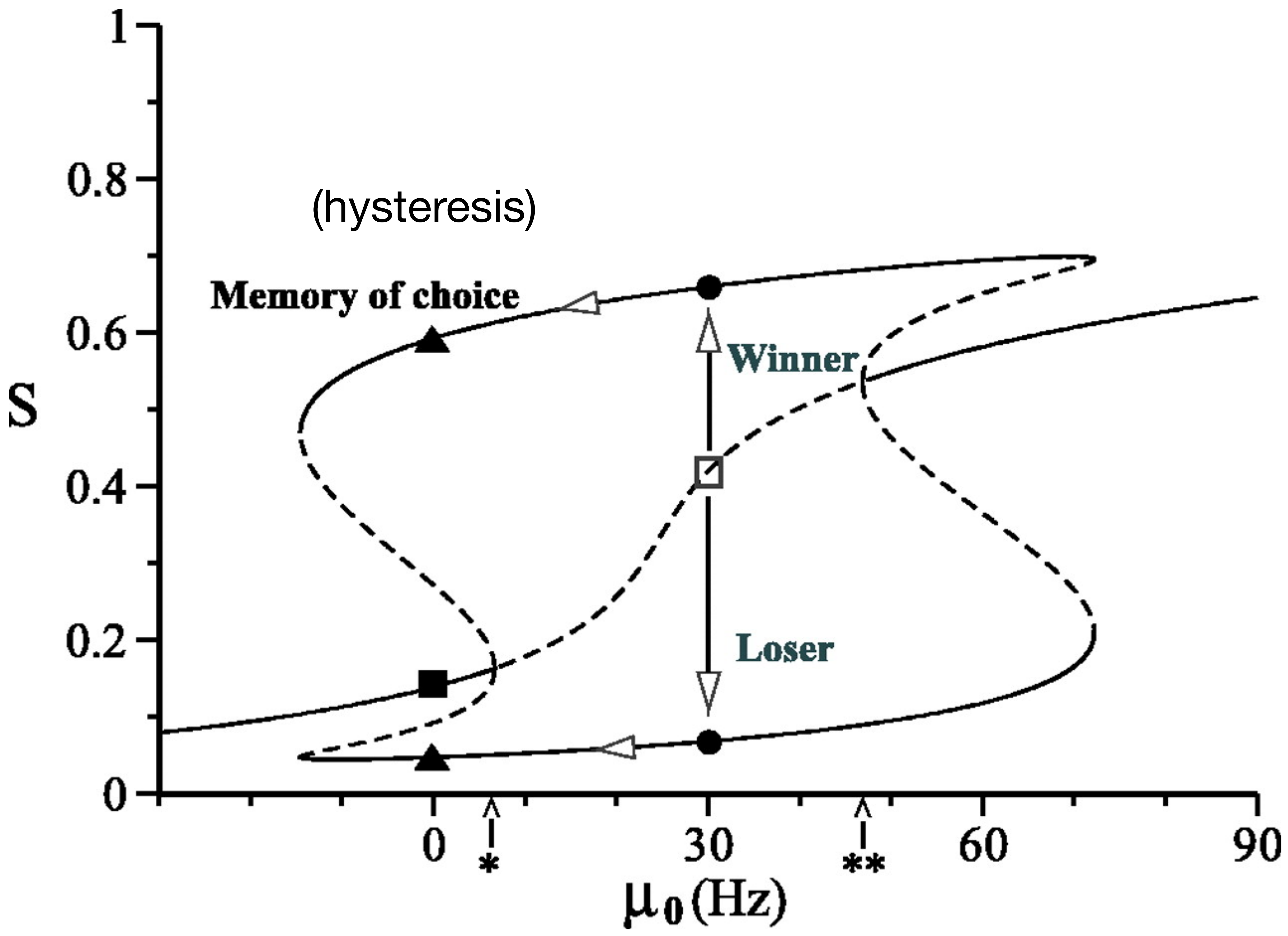
(Adapted from fig. 5 in paper)

Part 3: Wong and Wang, 2006



Phase plane analysis (Adapted from Fig. 4)

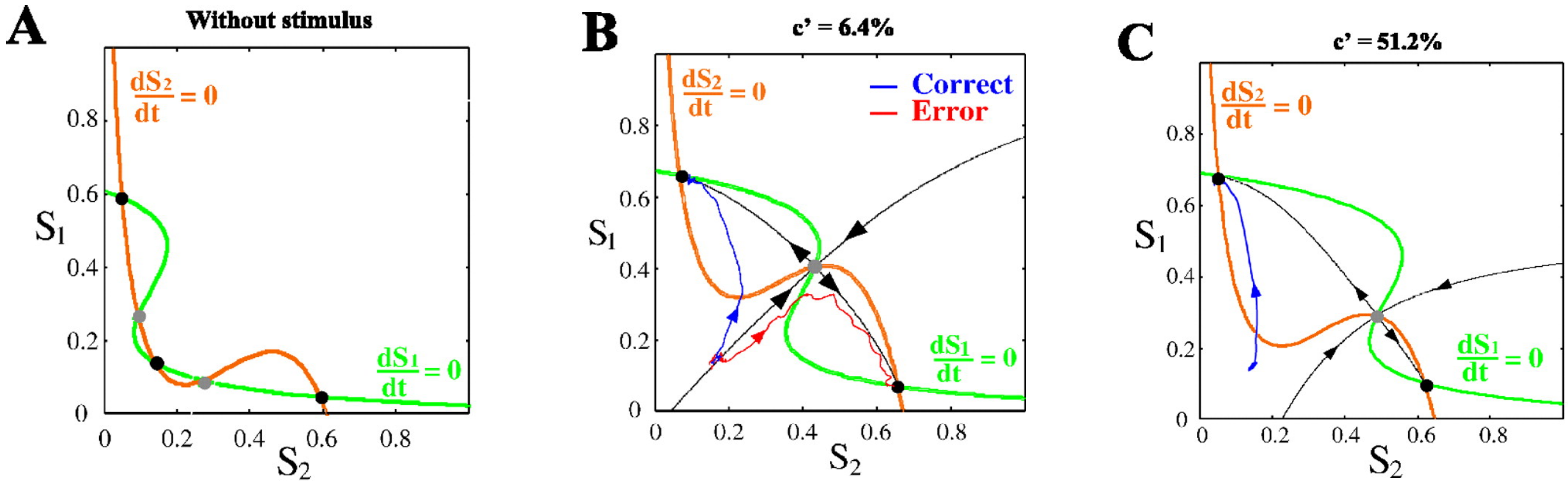
1D Bifurcation Diagram (Fig. 10 from paper)



(Stimulus Strength)

Part 3: Wong and Wang, 2006

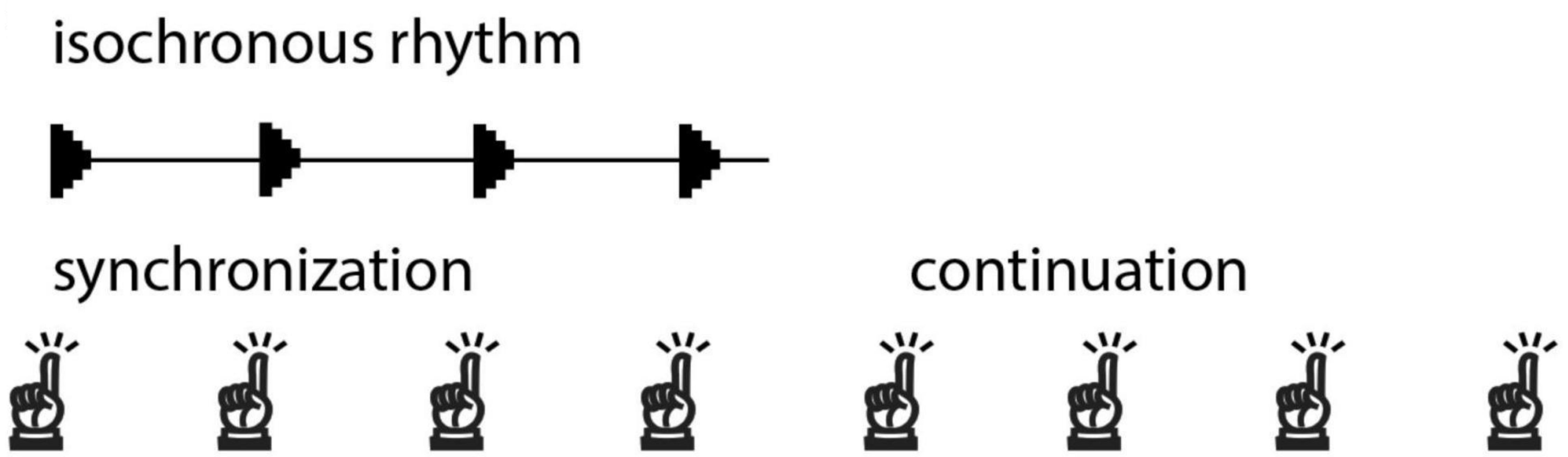
Changing coherence (c’) changes the size of the basin of attraction



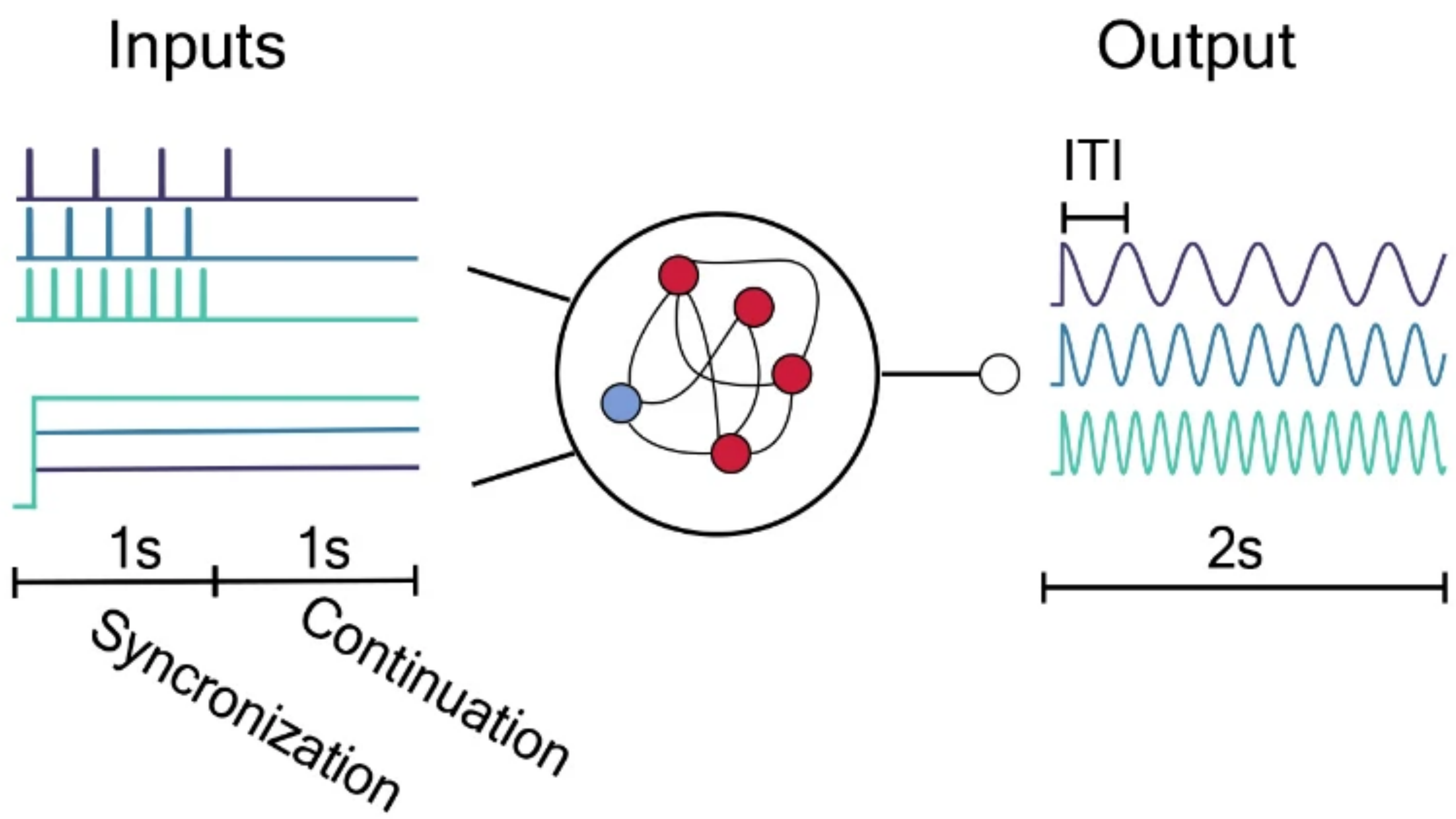
Part 3: Zemlianova et al. 2024

Dynamical mechanisms of how an RNN keeps a beat

Task:



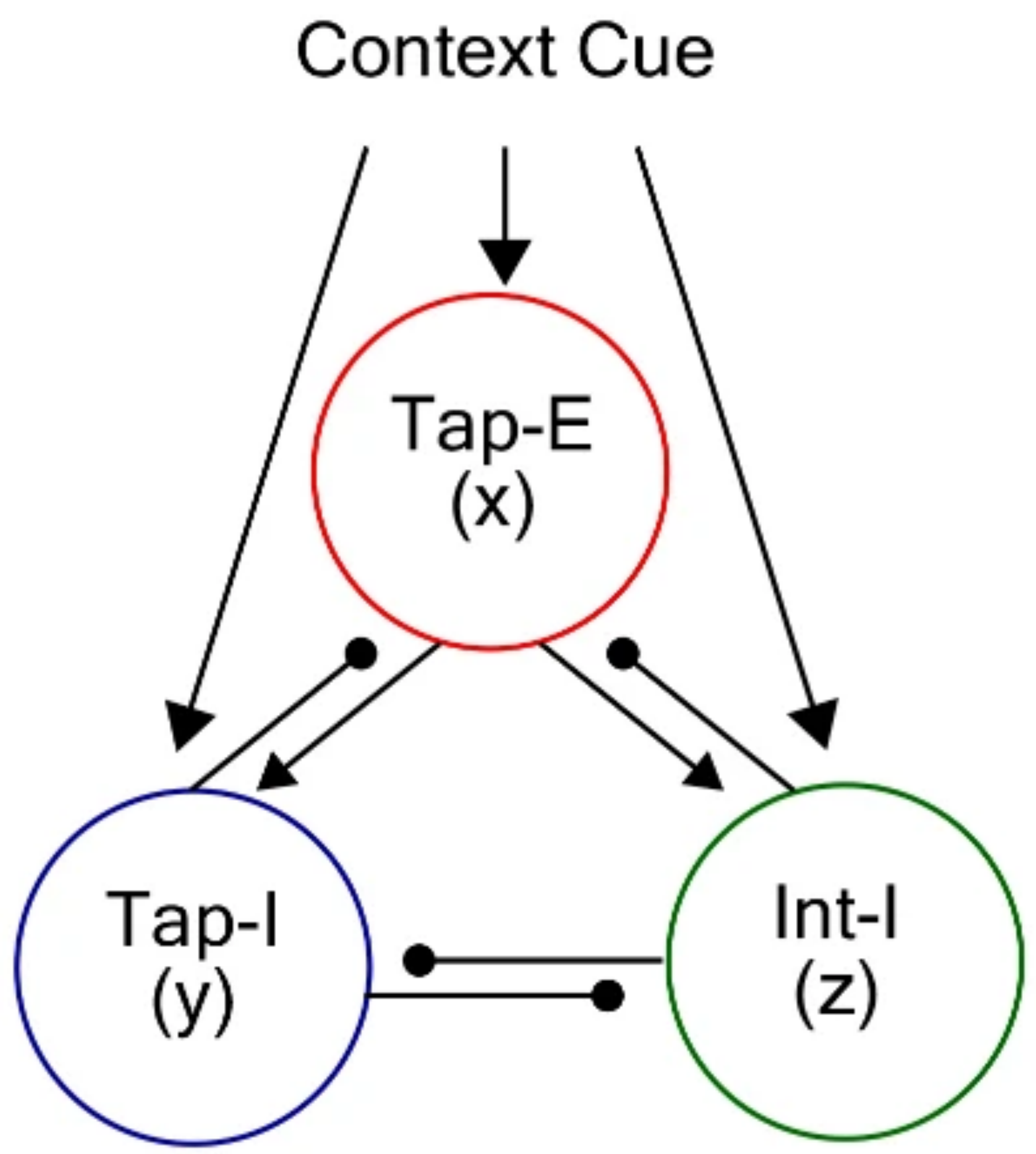
RNN setup:



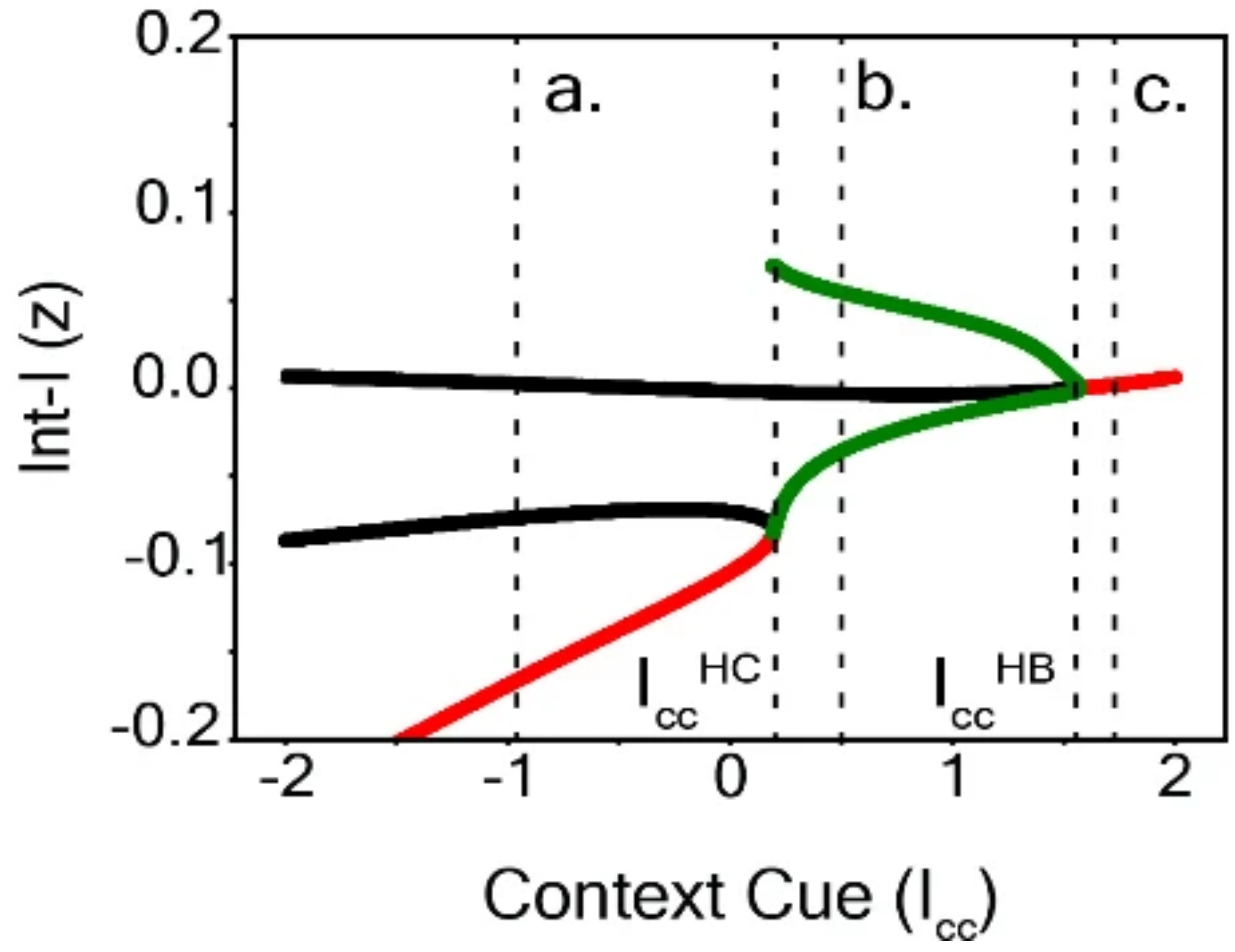
Part 3: Zemlianova et al. 2024

3 var. reduced model

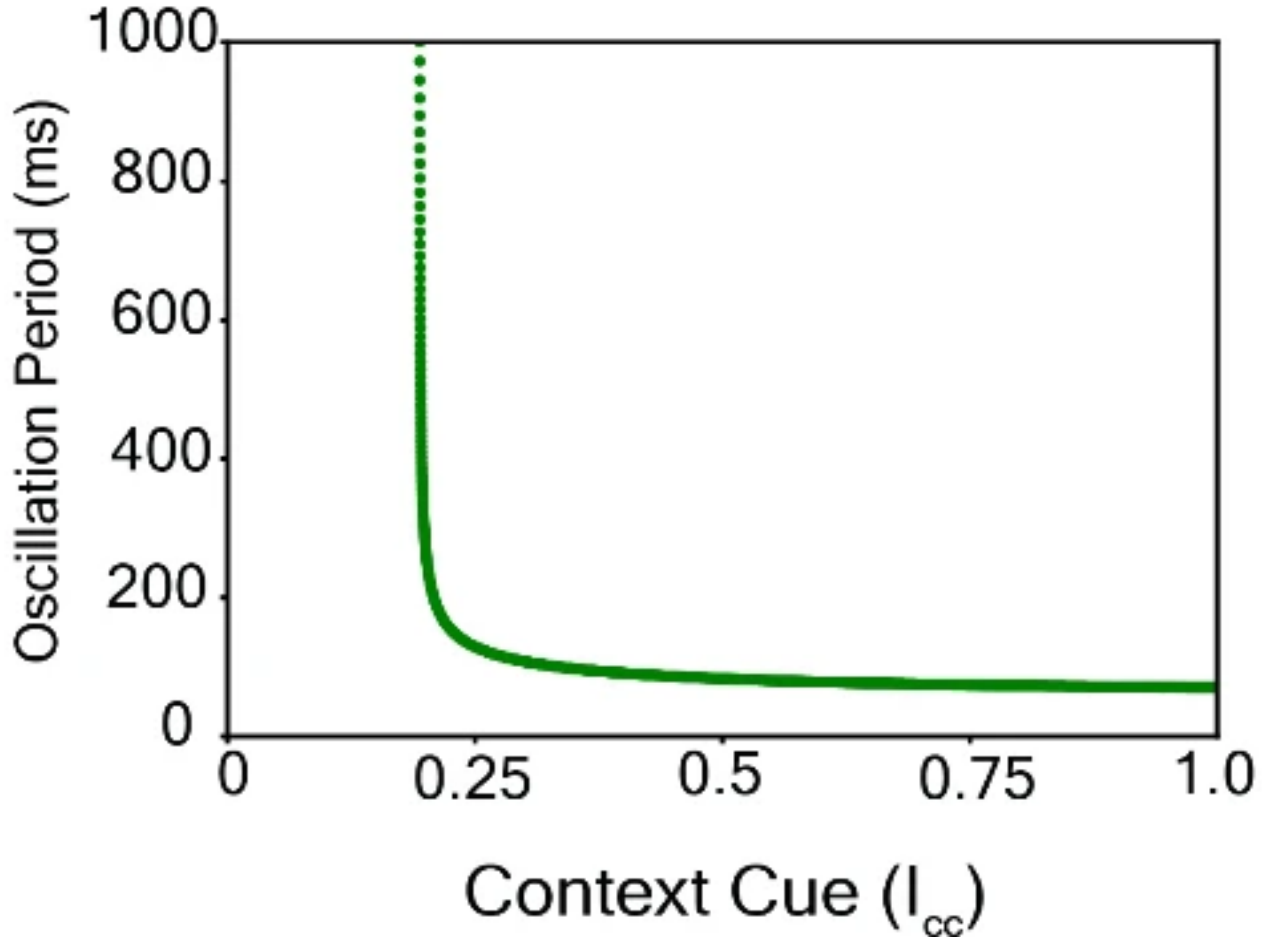
$$\tau_x x' = -x + W_x F(x, y, z) + W_x^{in} I_{cc} + I_{b_x}$$
$$\tau_y y' = -y + W_y F(x, y, z) + W_y^{in} I_{cc} + I_{b_y}$$
$$\tau_z x' = -z + W_z F(x, y, z) + W_z^{in} I_{cc} + I_{b_z}$$



Reduced model bifurcation diagram over ctx. cue



Part 3: Zemlianova et al. 2024



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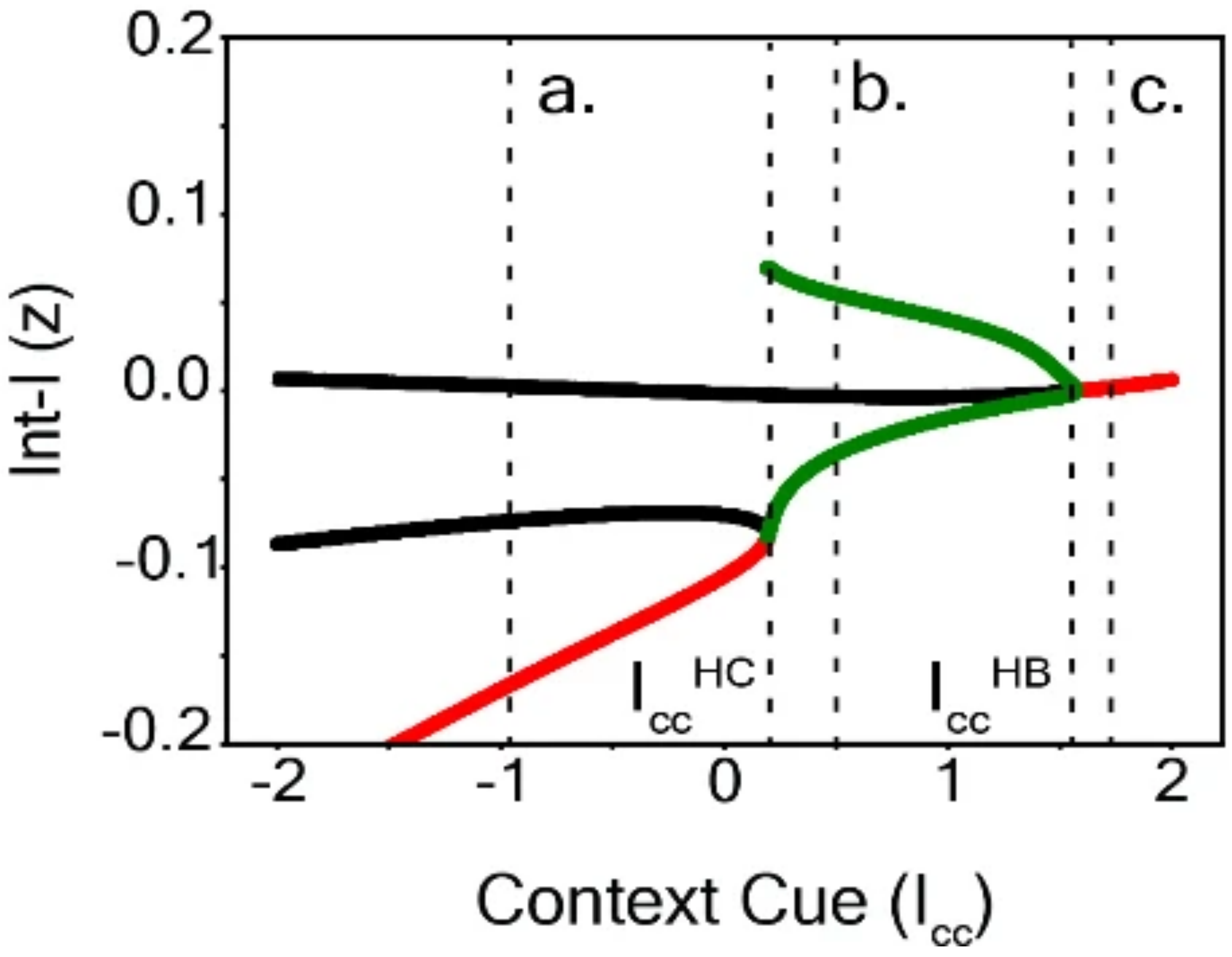
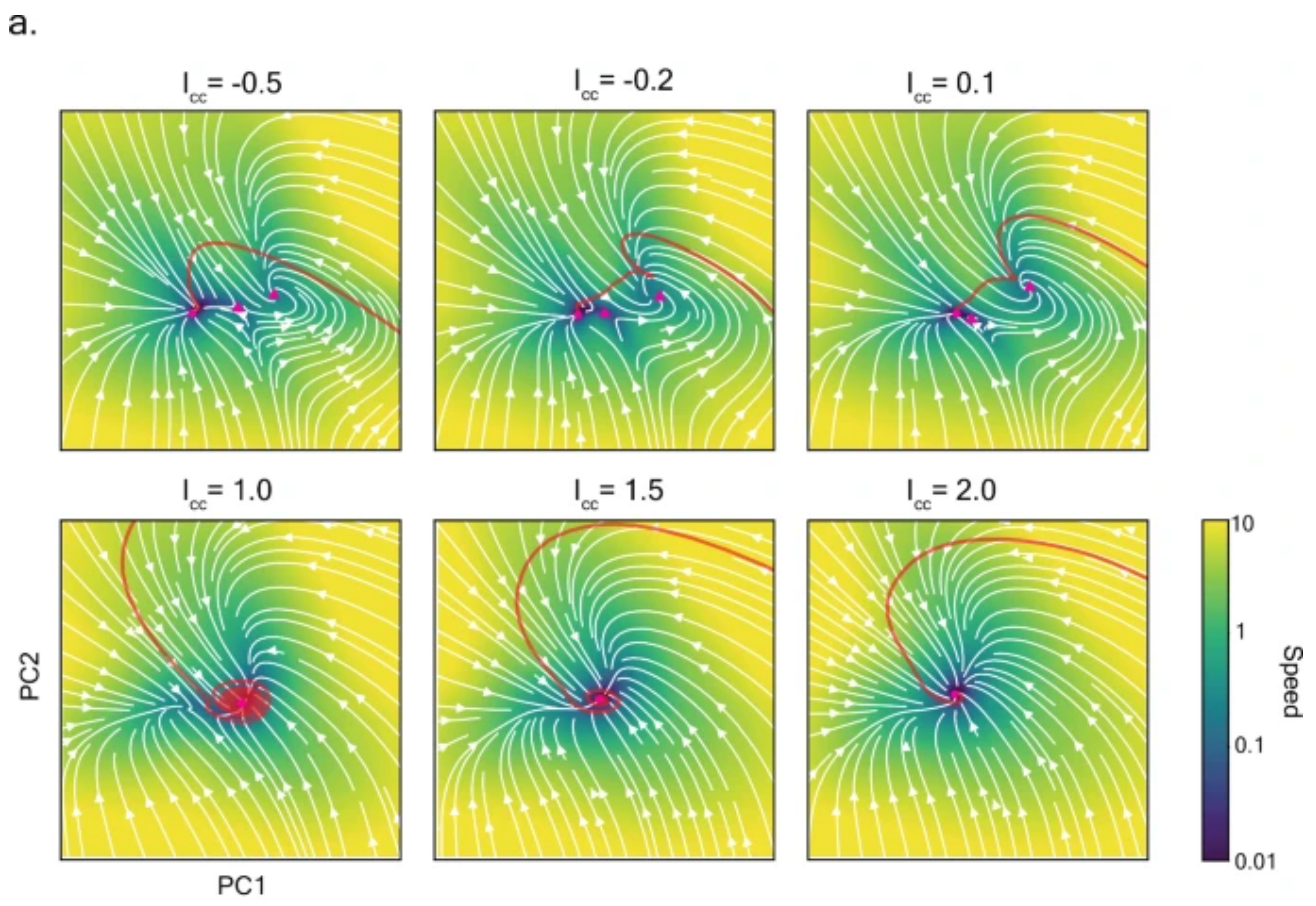
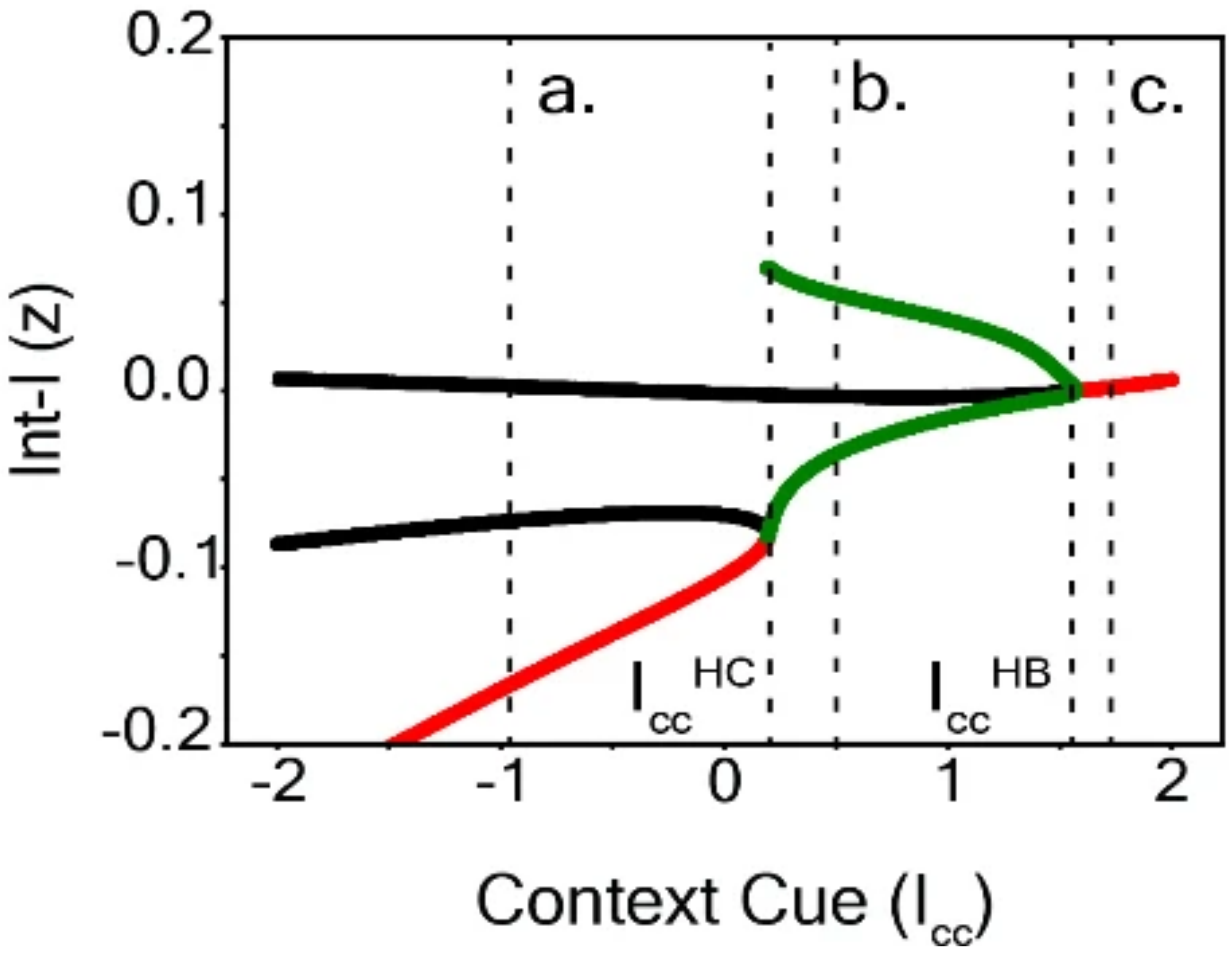


Part 3: Zemlianova et al. 2024

Behavior in high-dim. RNN



Reduced model bifurcation diagram over ctx. cue



Resources

Books:

- Dynamical Systems in Neuroscience by Eugene Izhikevich (lots of applied examples)
  PDF: https://www.izhikevich.org/publications/dsn.pdf
- Elements of Applied Bifurcation Theory by Kuznetsov
  PDF: https://www.ma.imperial.ac.uk/~dturaev/kuznetsov.pdf
- Differential Equations, Dynamical Systems and Intro. to Chaos by Hirsch, Smale, and Delaney (theory medium)
- Nonlinear Oscillations, Dynamical Systems and Bifurcations of Vector fields by Guckenheimer and Holmes (theory heavy)
- Simulating, Analyzing, and Animating Dynamical Systems: A Guide to **XPPAUT** for Researchers and Students by by Bard Ermentrout (instructions on how to use XPPAUT with applied examples)

Software to do the analysis:

- XPPAUT (written by Bard Ermentrout)
  Install here: https://sites.pitt.edu/~phase/bard/bardware/xpp/xpp.html
  (If you want a tutorial on this, find me! And/or use the XPPAUT book)

Papers:

- Neuromechanistic Model of Auditory Bistability
  https://journals.plos.org/ploscompbiol/article?id=10.1371/journal.pcbi.1004555
- Role of mutual inhibition in binocular rivalry
  https://journals.physiology.org/doi/10.1152/jn.00228.2011
- A Recurrent Network Mechanism of Time Integration in Perceptual Decisions
  https://www.jneurosci.org/lookup/doi/10.1523/JNEUROSCI.3733-05.2006
- Recurrent Neural Circuits Overcome Partial Inactivation by Compensation and Re-learning
  https://www.jneurosci.org/lookup/doi/10.1523/JNEUROSCI.1635-23.2024
- Bifurcation analysis of a neural network model
  https://link.springer.com/article/10.1007/BF00203668
- Flexible multitask computation in recurrent networks utilizes shared dynamical motifs
  http://biorxiv.org/lookup/doi/10.1101/2022.08.15.503870
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Supplementary Slides

Relevant Theorems:

Hartman-Grobman Theorem states that the local phase portrait near a hyperbolic fixed point is "topologically equivalent" to the phase portrait of the linearization; in particular, the stability type of the fixed point is faithfully captured by the linearization. This theorem allows us to use the Jacobian of the dynamical system to describe the local behavior.

Andronov & Pontryagi Theorem: A smooth dynamical system is structurally stable in a region D in R2 if and only if (i) it has a finite number of equilibria and limit cycles in D, and all of them are hyperbolic; (ii) there are no saddle separatrices returning to the same saddle or connecting two different saddles in D. (Note that there is no equivalent theorem for n-dimensions.)

Poincare and Benedixon Theorem: If a region R is closed and bounded and $\dot{x}$ is a continuously differentiable function on R with no fixed points, then R contains a limit cycle. This is useful for proving existence of orbits in planar systems. For non-planar systems you have to use other methods such as poincare maps.