Heteroclinic chains in a neural network model

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joint work with Carlos Aguilar, Pascal Chossat, Frédéric Lavigne and Elif Köksal

C. Aguilar, P. Chossat, M. Krupa and F. Lavigne. Latching dynamics in neural networks with synaptic depression. *PloS One* **12** (8), e0183710 (2017).

Motivation

Attractor network models: concepts are represented as attracting steady states

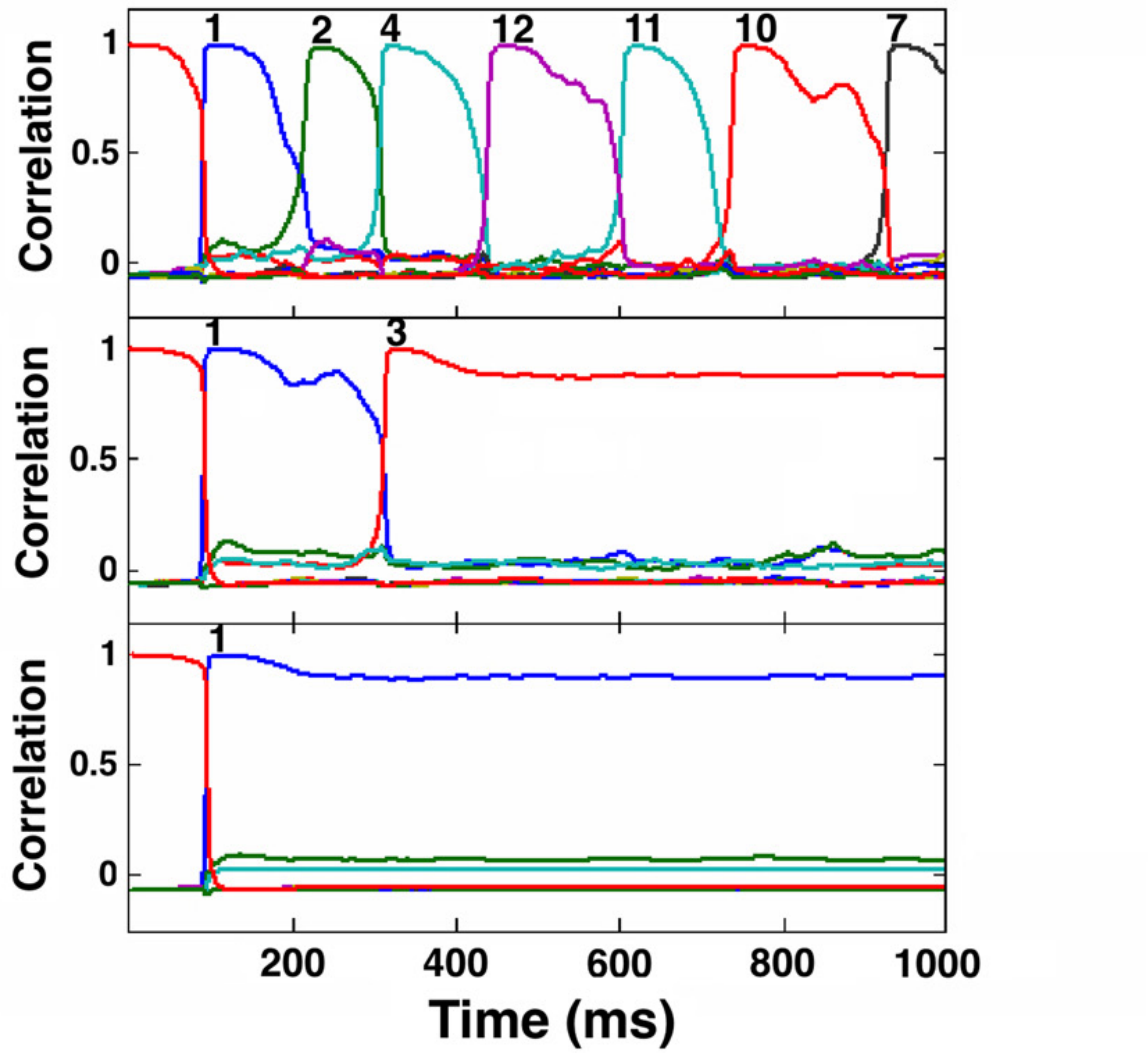
Latching dynamics: sequential activation of concepts. A possible mechanism allowing for transition from one state to the next is fast synaptic depression.

- the system converges to a stable steady state, corresponding to a concept maintained as a long transient by mutual activation of neurons
- these states are only transiently stable and lose stability due to synaptic depression
- the trajectory converges to the next steady state Treves, *Cognitive Neuropsych.* (2005)

Priming: the ability of the brain to more quickly activate a target concept in response to a related stimulus (prime) CAT —> DOG

- in our model prime-target relations are reflected by non-zero entries in the connectivity matrix

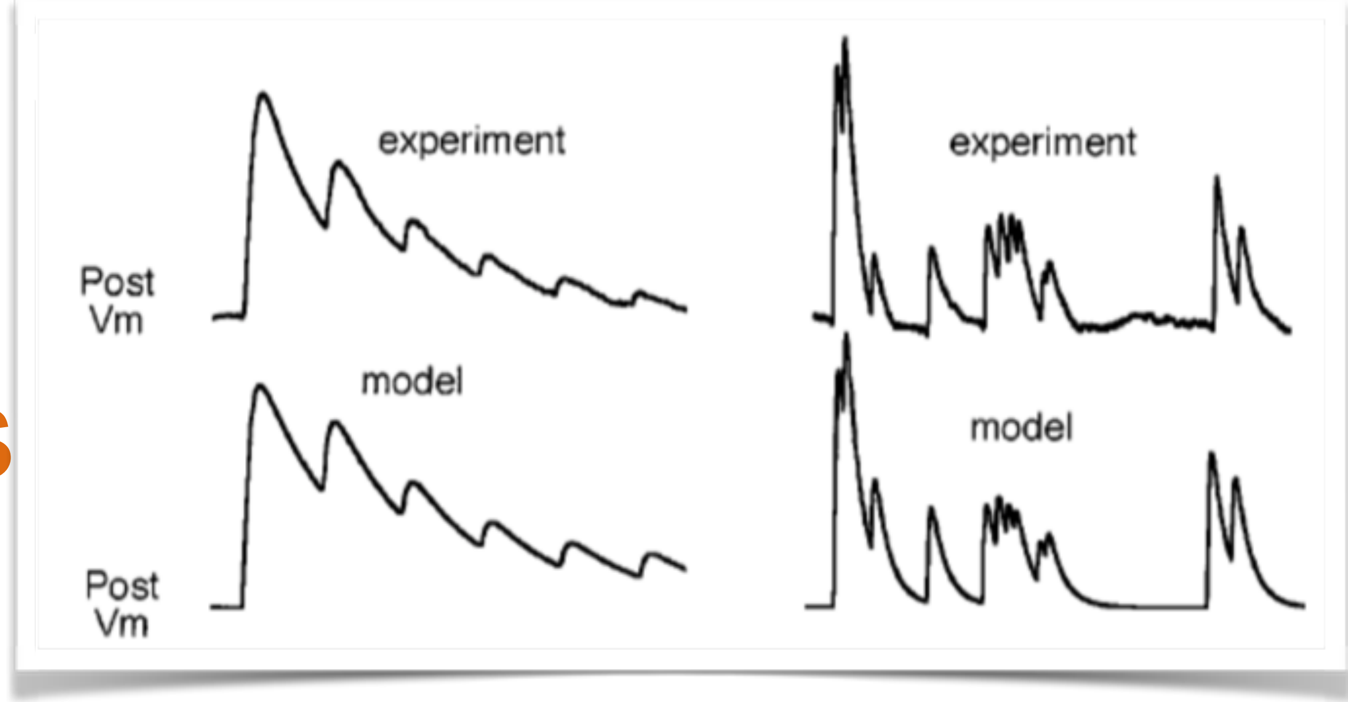
Latching dynamics



Lerner et al
(*Cognitive Science*, 2012)

Synaptic depression:

Synaptic depression refers to the weakening of the synaptic transmission caused by the depletion of the synaptic resources



Tsodyks and Markram, *PNAS* (1997)

Our model

$$\dot{x}_i = x_i(1-x_i)\left(-\mu x_i - I - \lambda\sum_{j=1}^{N} x_j + \sum_{j=1}^{N} J_{ij}s_i x_j\right) + \sigma, \qquad i = 1,\dots,N$$

$$\dot{s}_i = \frac{1-s_i}{\tau_r} - U x_i s_i$$

x_i - firing rate variable, $x_i \in [0,\ 1]$

s_i - synaptic variable, $s_i \in [0,\ 1]$

(J_{ij}) - matrix of excitatory connections, $J_{ij} \geq 0$

σ is a noise term adapted to preserve the invariance of the cube $[0,\ 1]^N$

Note: The excitatory connections weaken while a neuron is active.

Latching dynamics and heteroclinic chains

Recall:

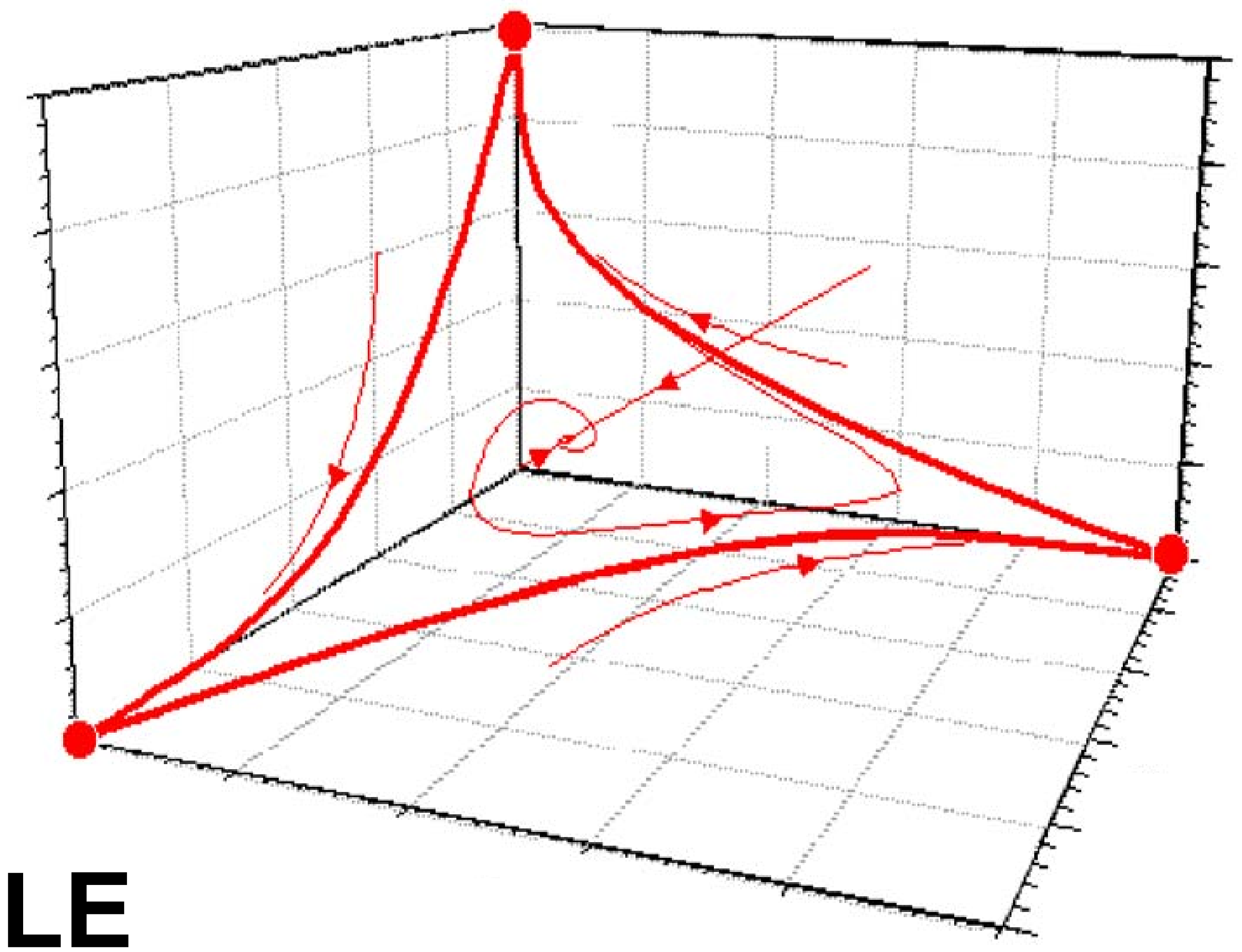
-the learned patterns are some of the vertices of the cube $[0,\,1]^N$

-the spaces defined by $x_i = 0$ or $x_i = 1$ are invariant

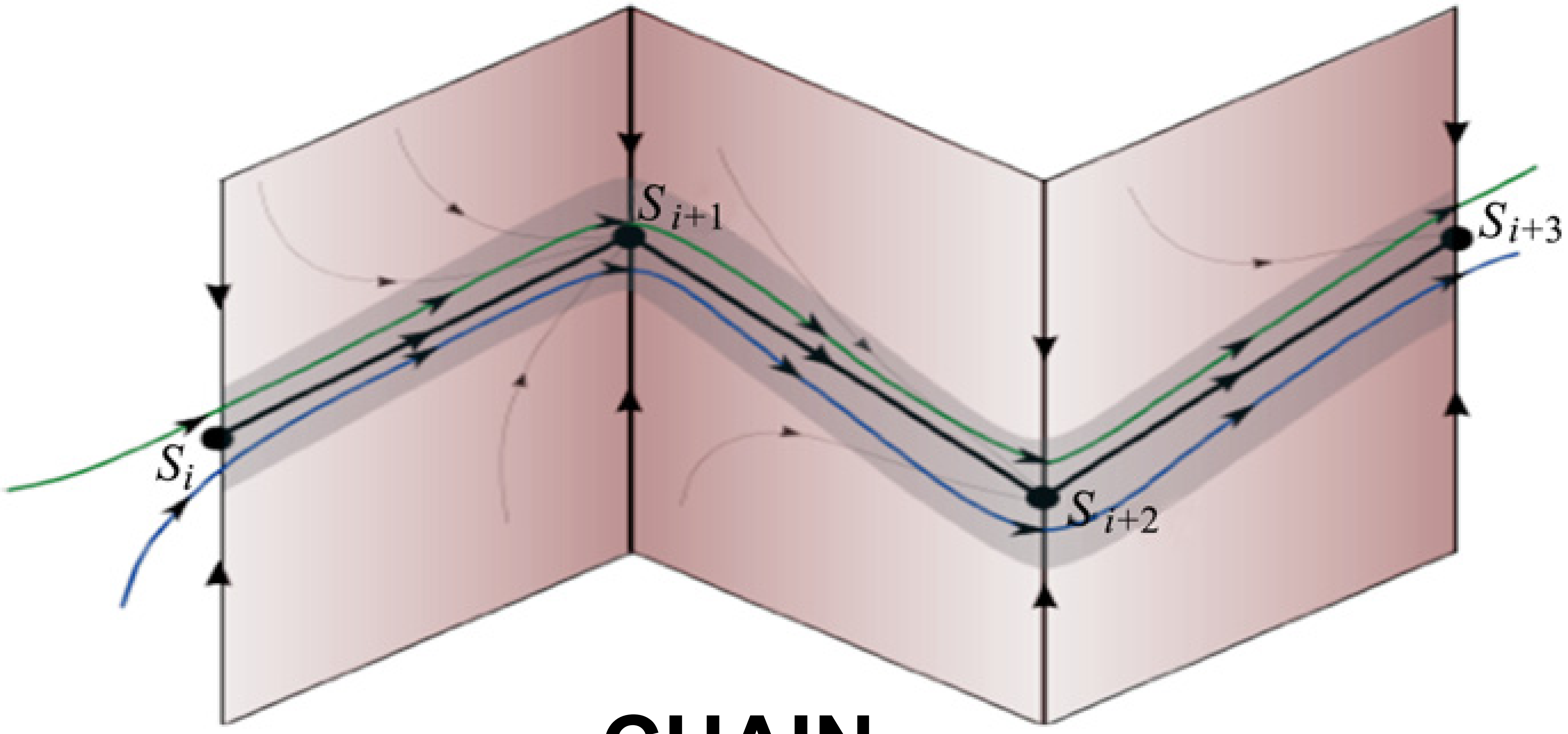
-hence latching dynamics must follow the invariant spaces

We study **heteroclinic chains** as a model of latching dynamics.

Robust Heteroclinic Chains/Cycles/Networks



CYCLE



CHAIN

- robust for structure preserving perturbations (inv. planes or symmetry)
- cycles/chains can be dynamically attracting
- weak breaking of the structure $\Rightarrow$ trajectories shadow cycle/chain
- noise $\Rightarrow$ random distribution of passage times
- cycles/chains between non-equilibrium attractors may exist

Historical perspective

Models of intermittency in biology and physics dating back to the early 80s (May-Leonard, Busse-Heikes)

Applications to neuroscience dating back to the early 2000s by Rabinovich and collaborators, using heteroclinic chains (transients)

Mathematical explorations dating back the work of dos Reis (70s), Guckenheimer and Holmes, Hofbauer and Sigmund (80s)
see Krupa *J. Nonl. Sci.* 1997 for a review of early work

Recent review concerning neuroscience applications: Rabinovich et al, *Physics of Life Reviews* 2012

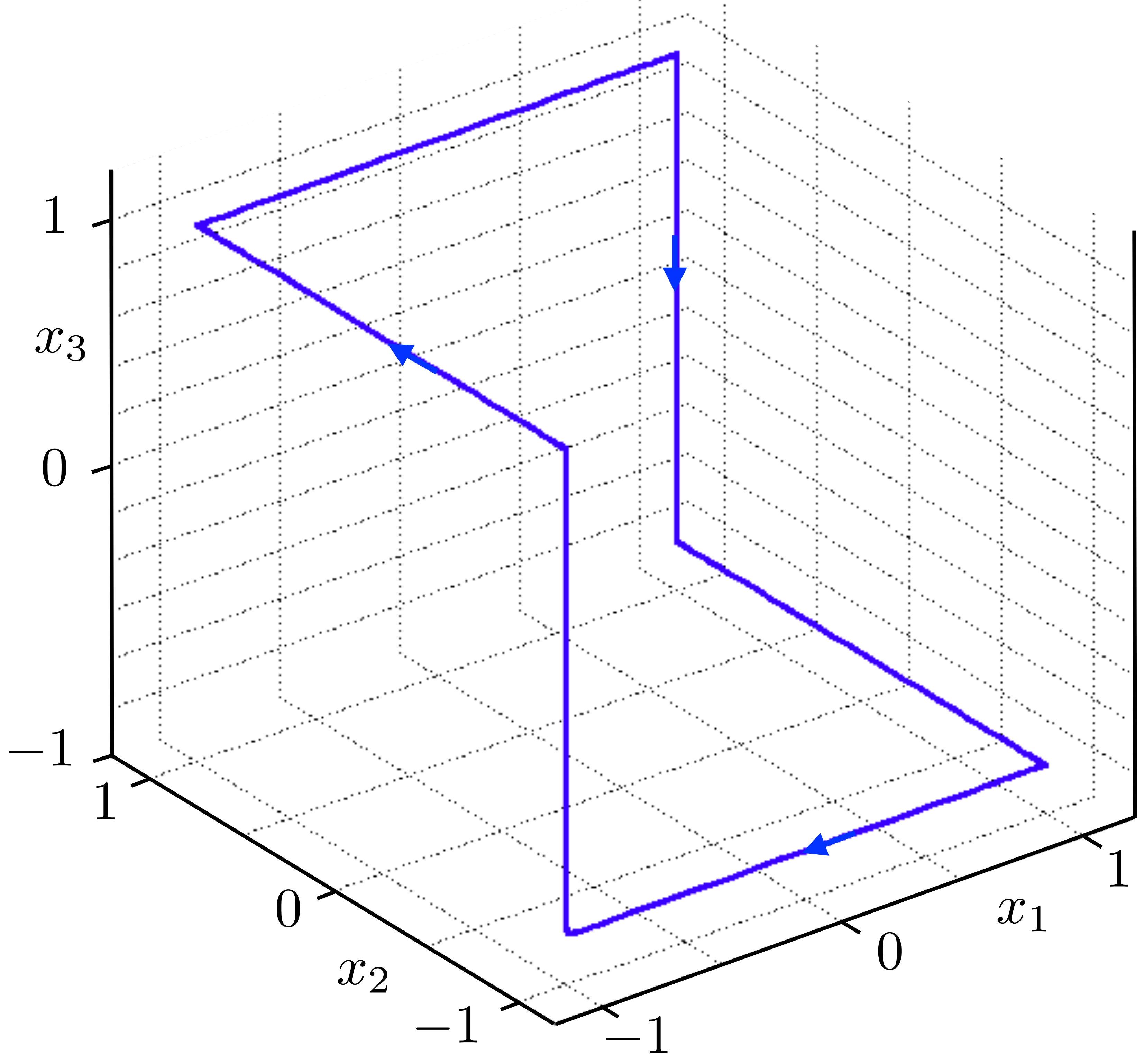
Heteroclinic cycles in Hopfield networks

Chossat, K., *J. Nonl. Sci.* 2016

-we considered a Hopfield network with the pseudo-inverse learning rule

Personnaz et al. *Phys. Rev. A* (1986)

-we proved that this rule was well suited for storing robust chains/cycles



a cycle along the edges of $[-1,1]^N$

Question: can a similar learning rule be implemented by neurons?

A heteroclinic chain joining learned patterns with two active neurons

Postulate: there are $p = N - 1$ learned (stable) patterns:

$$\xi^1 = (1,1,0,\ldots,0),\ \xi^2 = (0,1,1,0\ldots,0)\ \ldots\ \xi^P = (0,\ldots,0,1,1)$$

structure of the chain

$$\begin{tikzcd}
\xi^1 \arrow[dr] & & \xi^2 \arrow[dr] & & \cdots \arrow[dr] & & \xi^P \\
& \hat{\xi}^1 \arrow[ur] & & \hat{\xi}^2 \arrow[ur] & & \hat{\xi}^{P-1} \arrow[ur] &
\end{tikzcd}$$

where

$$\hat{\xi}^1 = (0,1,0,\ldots,0),\ \hat{\xi}^2 = (0,0,1,0\ldots,0),\ldots,\hat{\xi}^{P-1} = (0,\ldots,0,1,0)$$

are saddle type steady states providing the mechanism of transition

Example continued

What can we say about the connectivity matrix *J* ?

Note! The linearisation at the vertices of $[0,1]^N$ is diagonal

Hence explicit expressions for eigenvalues are available.

Using the postulated properties of the chain and the eigenvalue expressions we derive the following conditions:

$$\text{(i) } J_{i,i+1} < J_{i+1,i+2}, \; i = 1, \ldots n-1 \text{ (upper diagonal elements are increasing)}$$

$$\text{(ii) } I + \lambda < J_{32} \quad , \quad I + 2\lambda > J_{p,p+1}$$

$$\text{(iii) } I + 2\lambda + \mu < \min_{i=1,\ldots,p} (J_{i,i} + J_{i,i+1}), \quad I + 2\lambda + \mu < \min_{i=2,\ldots,p+1} (J_{i,i} + J_{i,i-1}).$$

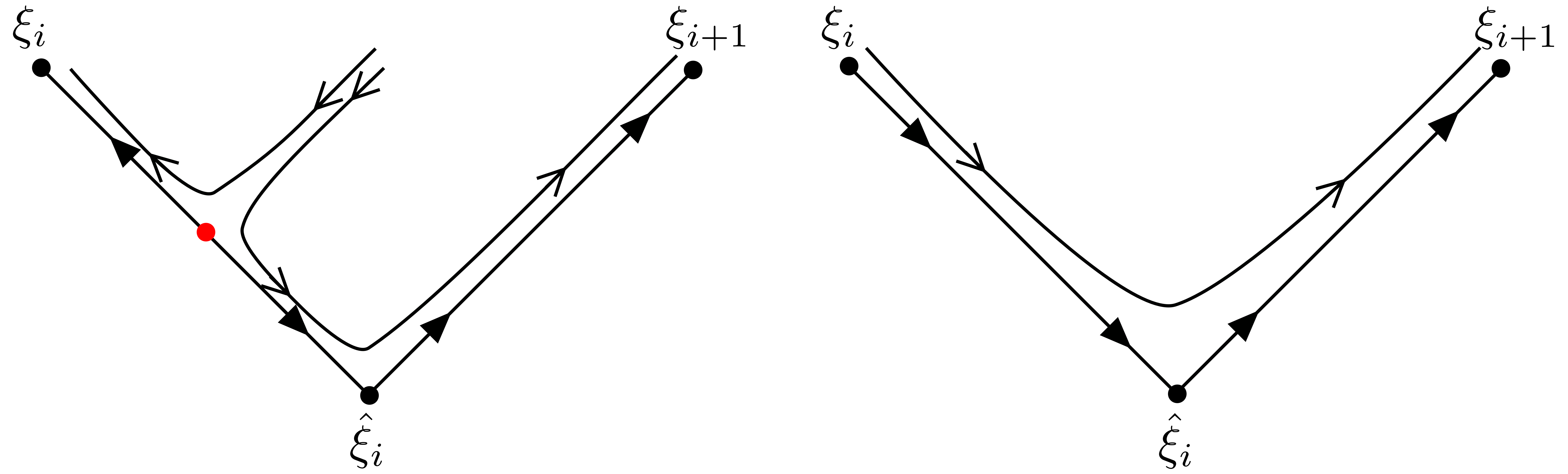
These conditions are necessary but not sufficient

Conclusion for the application: in the present model chains are hard to find.

A picture to keep in mind

$$\begin{tikzcd}[column sep=small]
\xi^1 \arrow[dr] & & \xi^2 \arrow[dr] & & \cdots \arrow[dr] & & \xi^P \\
& \hat{\xi}^1 \arrow[ur] & & \hat{\xi}^2 \arrow[ur] & & \hat{\xi}^{P-1} \arrow[ur] &
\end{tikzcd}$$

This picture gives the idea behind the eigenvalue conditions:

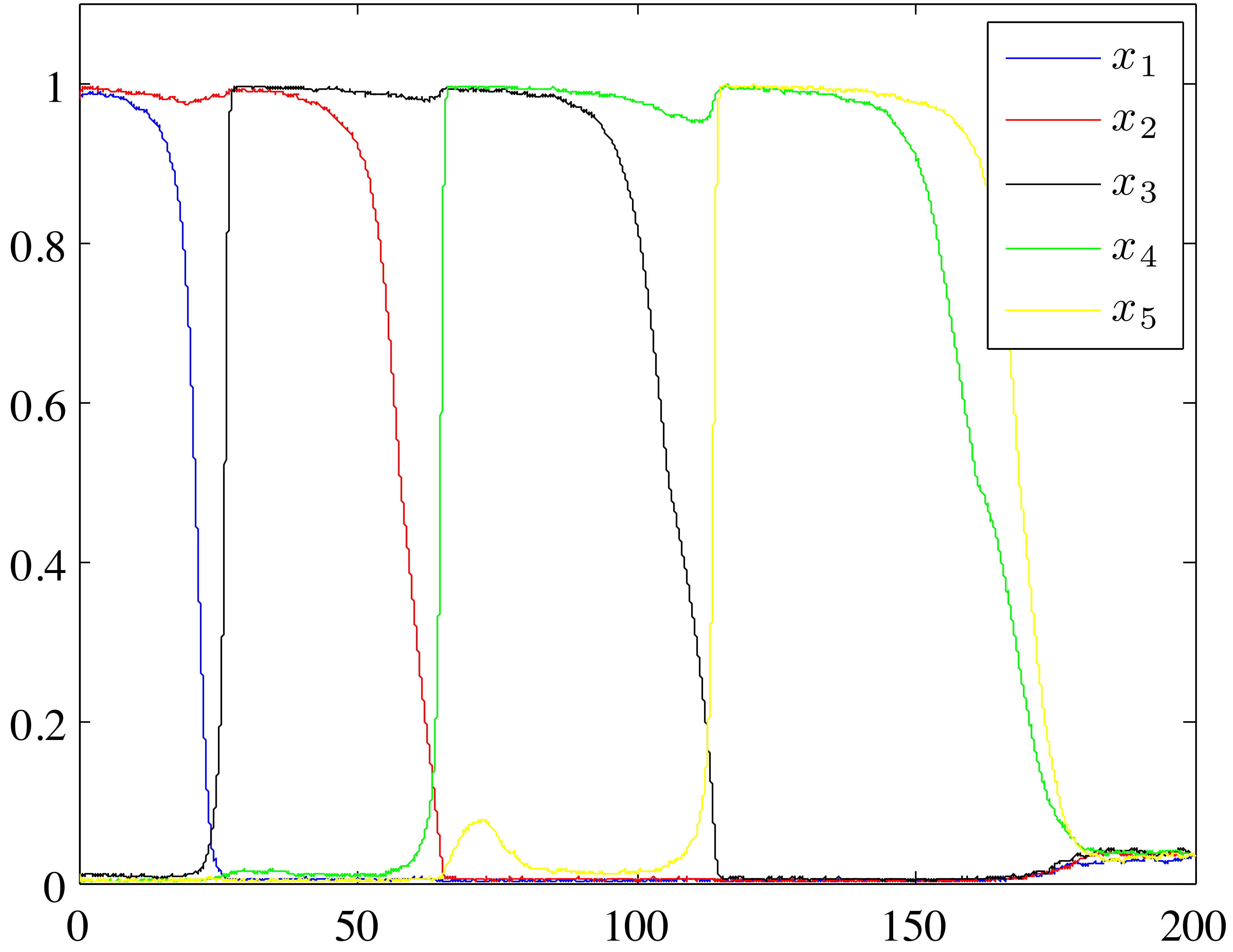


The direction $\xi^i \to \hat{\xi}^i$ must be weaker than the direction $\hat{\xi}^i \to \hat{\xi}^{i+1}$

Numerical example

$$J^{\max} = \begin{pmatrix} 9 & 3 & 0 & 0 & 0 \\ 3 & 10 & 5 & 0 & 0 \\ 0 & 5 & 11 & 6 & 0 \\ 0 & 0 & 6 & 11 & 7 \\ 0 & 0 & 0 & 7 & 11 \end{pmatrix} \qquad N = 5$$

Simulation:



time in ms

Sufficient conditions using slow/fast approach

Intuition: the synaptic variables are slow compared to the firing rate variables

To formalize this we set:

$$\varepsilon = \frac{1}{\tau_r}, \qquad \rho = \tau_r U$$

Now:

$$\dot{x}_k = x_k(1 - x_k)\left(-\mu x_k - I - \lambda \sum_{j=1}^{N} x_j + \sum_{j=1}^{N} J_{kj} x_j\right) + \sigma$$

$$\dot{s}_k = \varepsilon(1 - (1 + \rho x_k)s_k), \qquad k = 1, \ldots, N$$

Within the slow-fast framework we can find necessary and sufficient conditions for the existence of heteroclinic chains

Slow-fast systems review

$$\varepsilon \dot{x} = f(x,y)$$
$$\dot{y} = g(x,y)$$

slow formulation

$$x \in \mathbb{R}^n,\ y \in \mathbb{R}^m$$

$$x' = f(x,y)$$
$$y' = \varepsilon g(x,y)$$

fast formulation

0th order approximations are given by:

$$f(x,y) = 0$$
$$\dot{y} = g(x,y)$$

reduced equation

$$x' = f(x,y)$$
$$y' = 0,$$

layer equation

- The set $S_0 = \{(x,y)\ :\ f(x,y) = 0\}$ is called the critical manifold.
- S_0 is the phase space for the reduced problem and the set of equlibria for the layer problem.

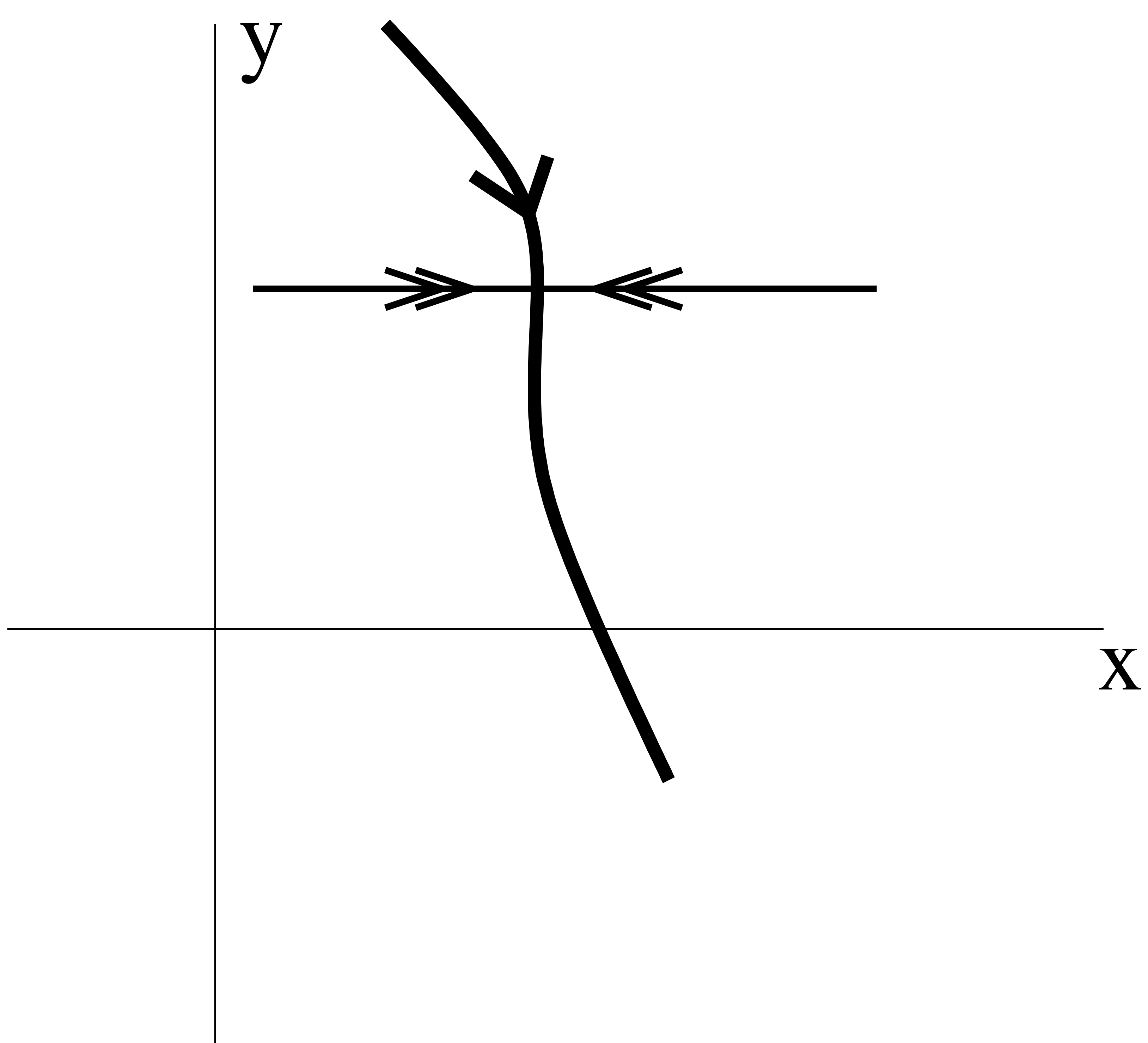
Slow manifolds

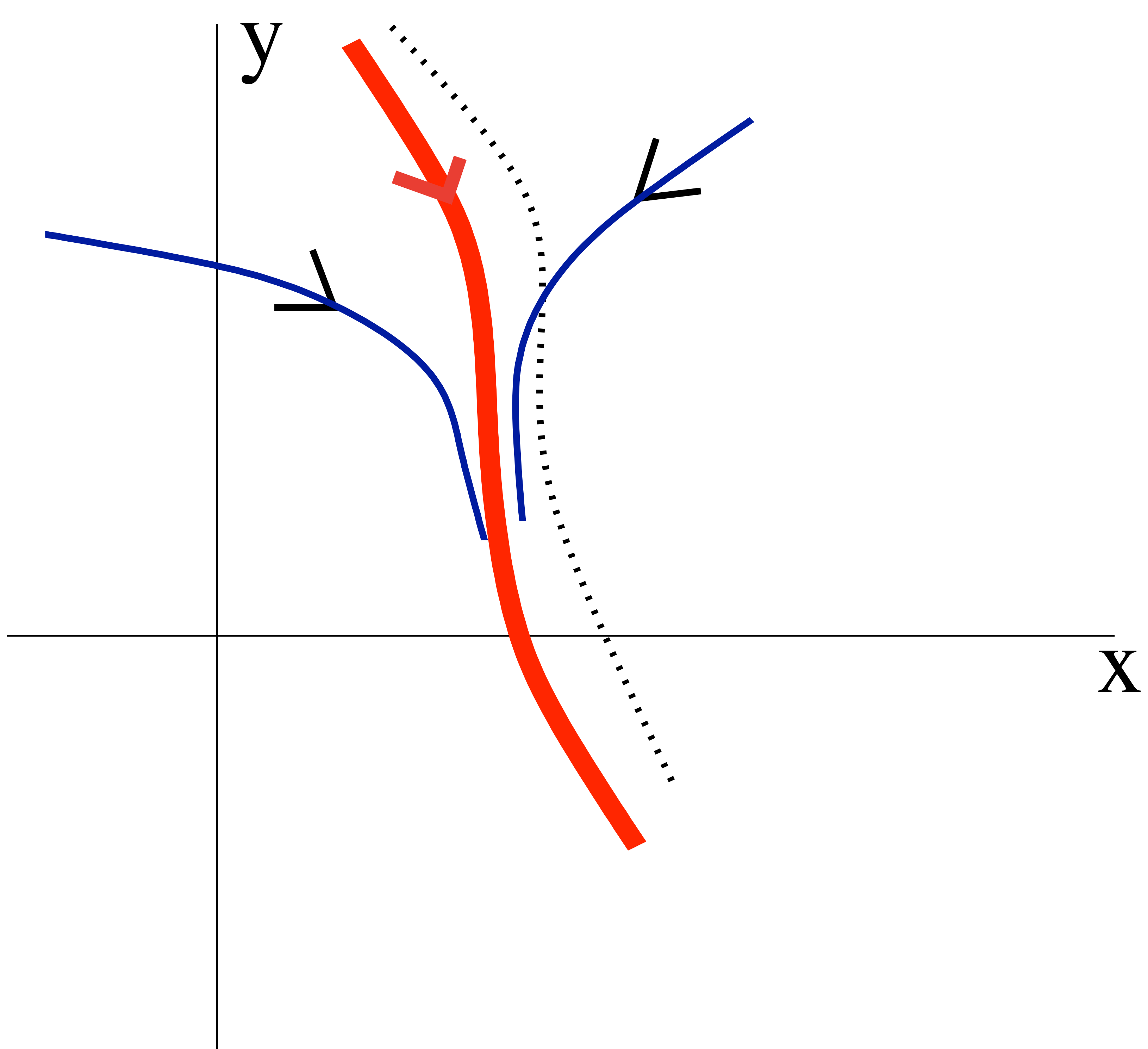
$$x' = f(x, y)$$

$$y' = \varepsilon g(x, y)$$

Theorem (Fenichel, Tikhonov, …)

If a segment of the reduced manifold is normally hyperbolic, then for $\varepsilon > 0$ there exists a nearby slow manifold with the same stability.





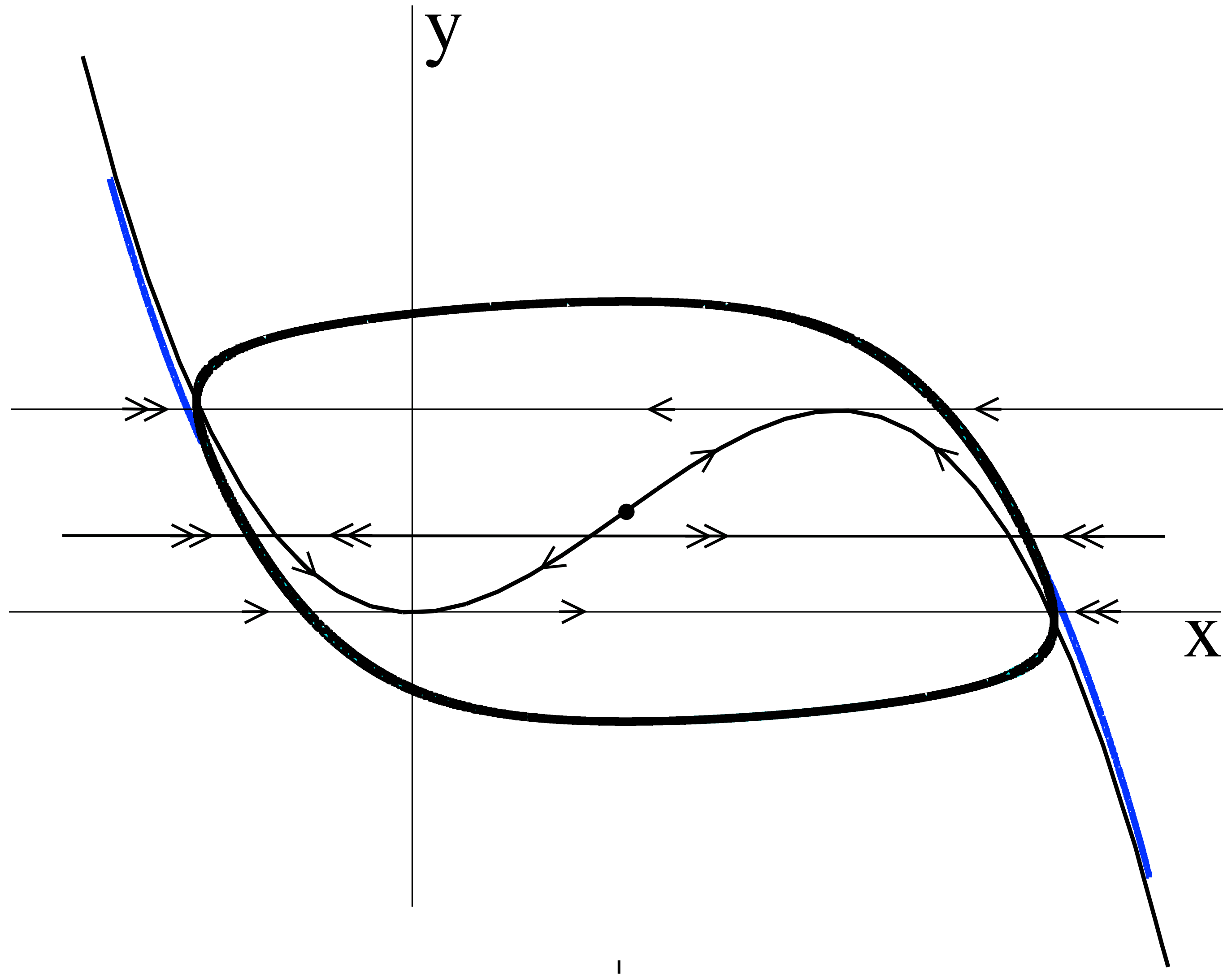
Non-hyperbolic points (dynamic bifurcations)

Slow flow can become unstable at non-hyperbolic points (**dynamic bifurcations**)

Example:

relaxation oscillation (**fold points**)

K., Szmolyan *JDE* 2001

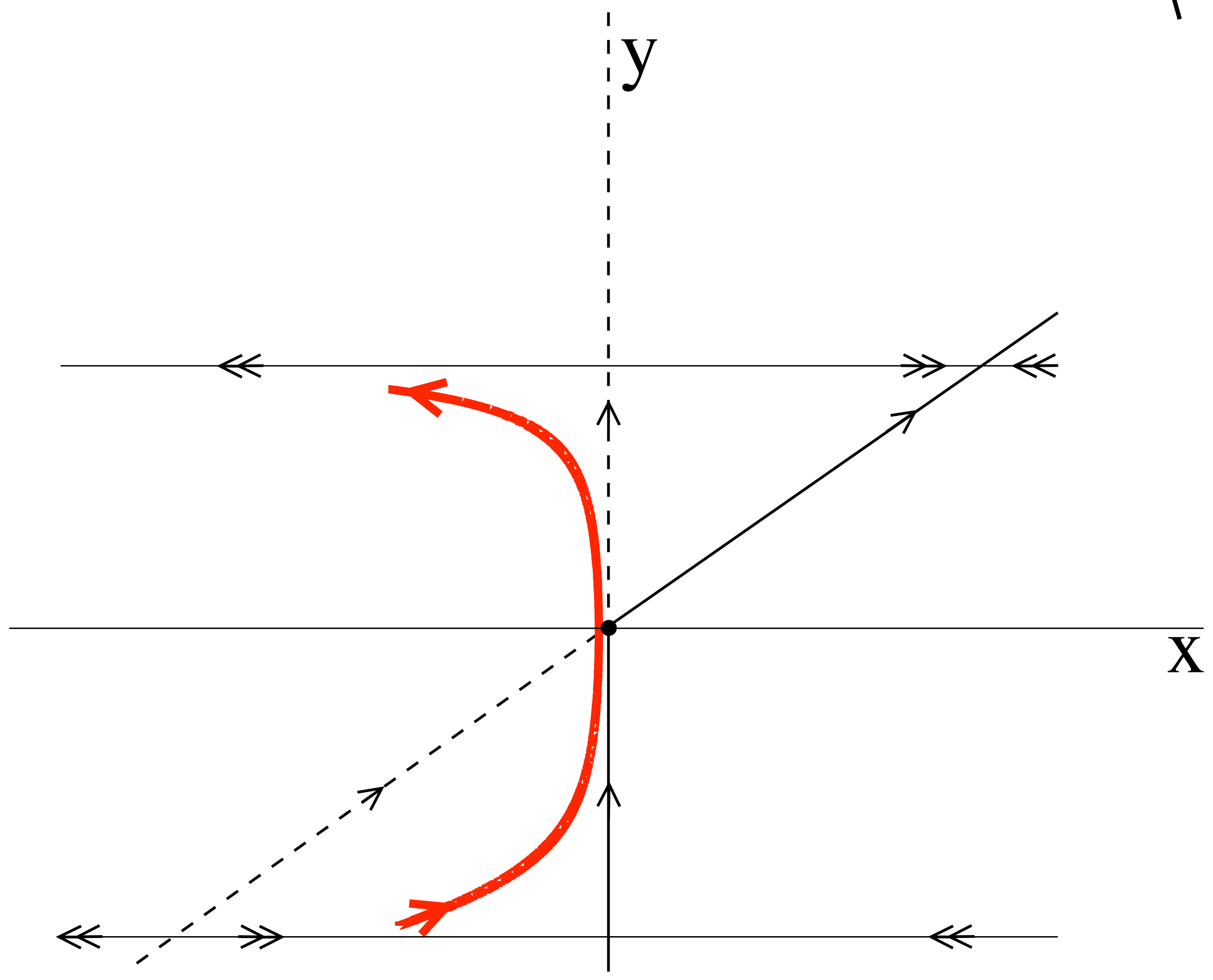


Example (relevant to our problem):

transcritical bifurcation

K., Szmolyan *SIAM J. Math. Anal.* 2001

K., Szmolyan *Nonlinearity* 2001



Slow-fast systems with noise:

Berglund and Gentz, *Springer* 2006

Analysis of the dynamics

(we assume the eigenvalue conditions stated earlier hold)

Earlier results restated in the slow-fast framework:

-each pattern $\xi^k = (\xi_1^k, \ldots, \xi_N^k)$ defines a slow manifold which is attracting for $(s_k, s_{k+1}) \approx (1,1)$ and loses stability in a transcritical bifurcation for smaller s_k or s_{k+1}

-each pattern $\hat{\xi}^k = (\hat{\xi}_1^k, \ldots, \hat{\xi}_N^k)$ defines a slow manifold which is of saddle type for $s_k \approx 1$

Using singular perturbation theory we can derive precise values at which the transcritical bifurcation occurs.

Slow-fast analysis cont.

Lemma Let $(s_k^{B,1},\ s_k^{B,2}),\ k=1,\dots p$ be the pairs of numbers defined by

$$s_1^{B,1} = \frac{I+\mu+2\lambda}{J_{11}+J_{12}} \qquad s_1^{B,2} = \frac{I+\mu+2\lambda}{J_{11}+J_{12}}$$

$$\begin{pmatrix} -(s_{k-1}^{B,1} - \frac{1}{1+\rho}) & 1 & 0 \\ -\frac{\rho}{1+\rho} & 0 & 1 \\ 0 & J_{kk} & J_{kk+1} \end{pmatrix} \begin{pmatrix} F_B, \\ s_k^{B,1} \\ s_k^{B,2} \end{pmatrix} = \begin{pmatrix} \frac{1}{1+\rho} \\ \frac{1}{1+\rho} \\ I+\mu+2\lambda \end{pmatrix}$$

Then, for each $k=1,\dots p-1$ the transcritical bifurcation is given by

$$s_k = s_k^{B,1}, \quad s_{k+1} = s_k^{B,2}$$

Idea of proof The slow flow is linear and can be solved explicitly.

Slow-fast analysis cont.

Theorem Assume:

(H1) $$1 > s_k^{B,1} > \frac{1}{1+\rho}, k = 1, \dots p-1$$

(H2) For each $k = 1, \dots, p-1$ the conditions on eigenvalues, adapted from the ones introduced earlier by substituting the s_k and s_{k+1} values corresponding to the *k*th transcritical bifurcation, are satisfied.

Then for ε and σ sufficiently small there exists an open set of initial conditions such that the corresponding trajectories follow the heteroclinic chain, as specified earlier.

$$\begin{tikzcd}
\xi^1 \arrow[dr] & & \xi^2 \arrow[dr] & & \cdots \arrow[dr] & & \xi^P \\
& \hat{\xi}^1 \arrow[ur] & & \hat{\xi}^2 \arrow[ur] & & \hat{\xi}^{P-1} \arrow[ur] &
\end{tikzcd}$$

Slow-fast analysis cont.

Idea of proof

(1) The eigenvalue with the precise values of s_k and s_{k+1} guarantee the correct sequence of fast dynamics to pass to the next slow manifold.

(2) There is no delay phenomenon, due to noise. Berglund and Gentz, *Springer* 2006

New idea - transition through neutrally stable points

$$
\begin{tikzcd}
\xi^1 \arrow[dr] & & \xi^2 \arrow[dr] & & \cdots \arrow[dr] & & \xi^P \\
& \hat{\xi}^1 \arrow[ur] & & \hat{\xi}^2 \arrow[ur] & & \hat{\xi}^{P-1} \arrow[ur] &
\end{tikzcd}
$$

where

$$\hat{\xi}^1 = (0, 1, 0, \ldots, 0),\ \hat{\xi}^2 = (0, 0, 1, 0 \ldots, 0), \ldots, \hat{\xi}^{P-1} = (0, \ldots, 0, 1, 0)$$

are neutrally stable steady states providing the mechanism of transition

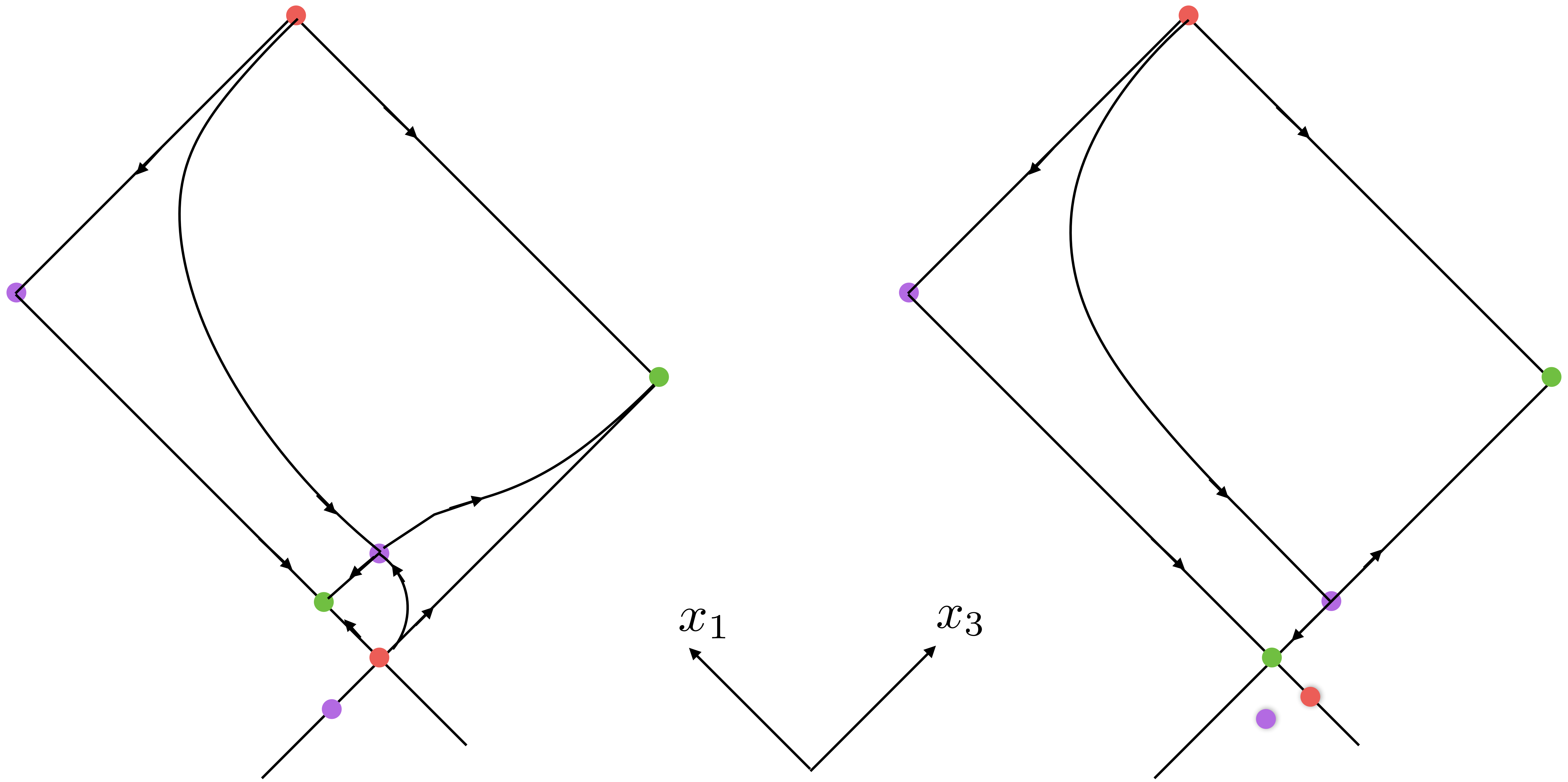
Suitable connectivity matrix

$$J = \begin{pmatrix} 1 & 1 & 0 & 0 & 0 & \dots & 0 \\ 1 & 2 & 1 & 0 & 0 & \dots & 0 \\ 0 & 1 & 2 & 1 & 0 & \dots & 0 \\ \vdots & & \ddots & \ddots & \ddots & & \vdots \\ 0 & \dots & 0 & 1 & 2 & 1 & 0 \\ 0 & \dots & 0 & 0 & 1 & 2 & 1 \\ 0 & \dots & 0 & 0 & 0 & 1 & 1 \end{pmatrix}$$

J is matrix derived from the Hebbian rule: $J_{ij} = \sum_{k=1}^{N-1} \xi_i^k \xi_j^k$

based on the learned patterns $\xi_1,\, \xi_2, \dots, \xi_{N-1}$

Dynamics of the fast system in the plane $\{x_2 = 1,\ x_k = 0,\ k \geq 4\}$



before the dynamic bifurcation

after the dynamic bifurcation

Results

Coefficient conditions $$\frac{1}{\rho+1} < I+\lambda < 1 < I+2\lambda, \quad I+2\lambda+\mu < 2$$

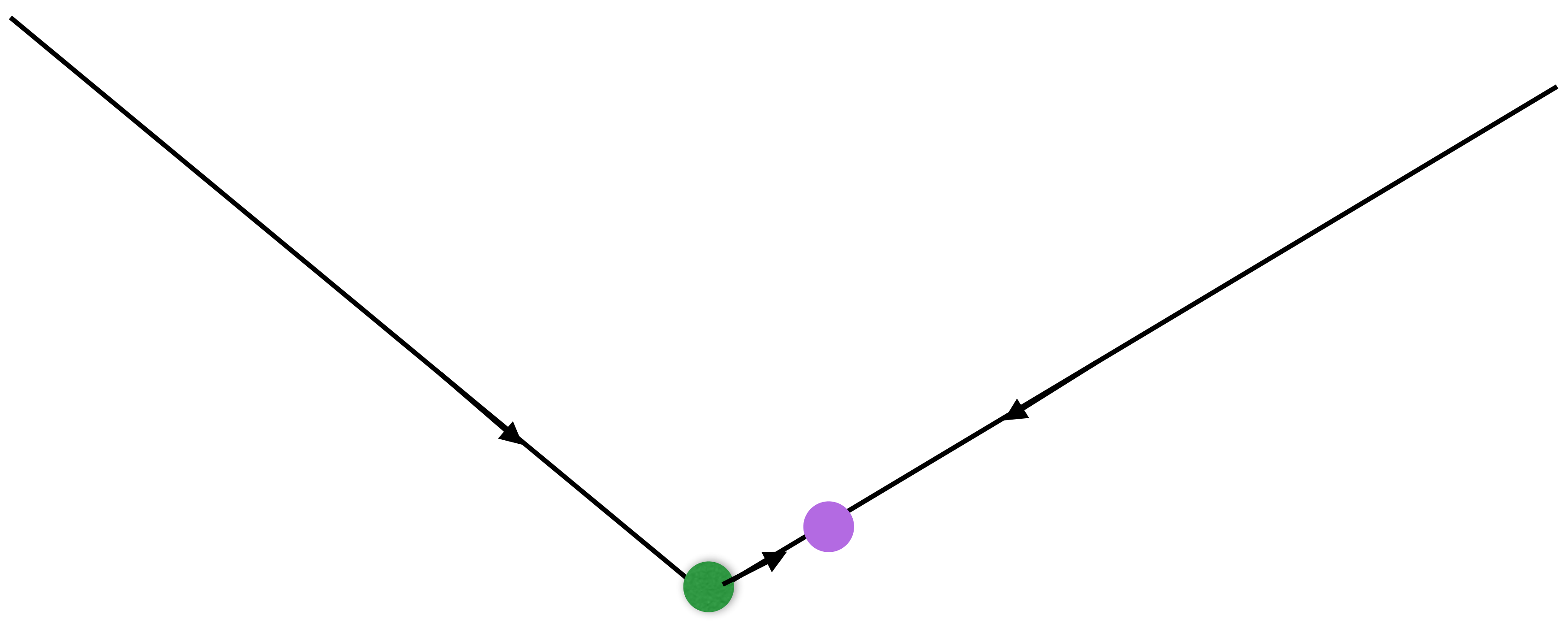
$$\frac{((I+\lambda)(1+\rho)-1)^2+\rho}{\rho(\rho+1)} < \mu+\lambda < 1$$

Theorem All trajectories starting within *O(1)* of ξ_k are attracted to $\hat{\xi}_k$ but pass $O(\varepsilon)$ close to ξ_{k+1}

Conclusion A noisy trajectory is a chain

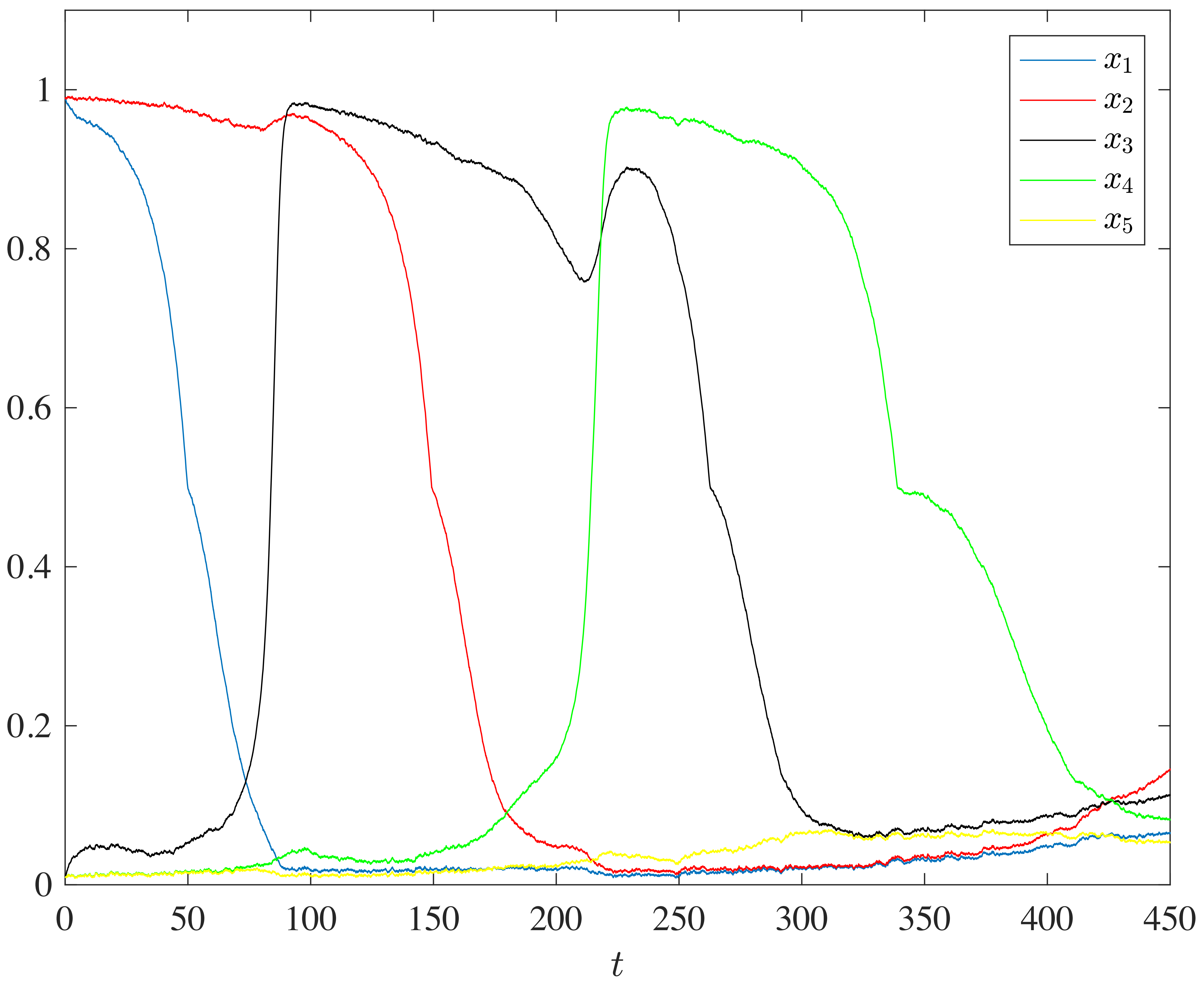
Excitable cycles/chains

Ashwin and Postelthwaite *JNLS* 2016



Passage past the saddle sink pair occurs through the action of noise

Simulation



Goals

- Understand better the excitable case and its perturbations
- Understand the role of noise and the noisy dynamics

  Any noise annoys an oyster but a noisy oyster annoys an oyster most

- Is there a way to connect the two cases?
- Which case is more relevant biologically?
- Look at more general examples

Happy Birthday Jean-Marc!