Canard dynamics: applications to the biosciences and theoretical aspects

M. Krupa

INRIA Rocquencourt (France)

Collaborators: M. Desroches (INRIA), T. Kaper (BU)

informatiques mathématiques

Outline

1 Canards in two dimensions

2 Mixed-mode oscillations

3 Spike adding in square wave bursters

4 Mixed-mode bursting oscillations

5 Analysis of the canard phenomenon

6 Other directions

Take VdP with α large and constant forcing a

Second order ODE: $$\ddot{x} + \alpha(x^2-1)\dot{x} + x = a$$

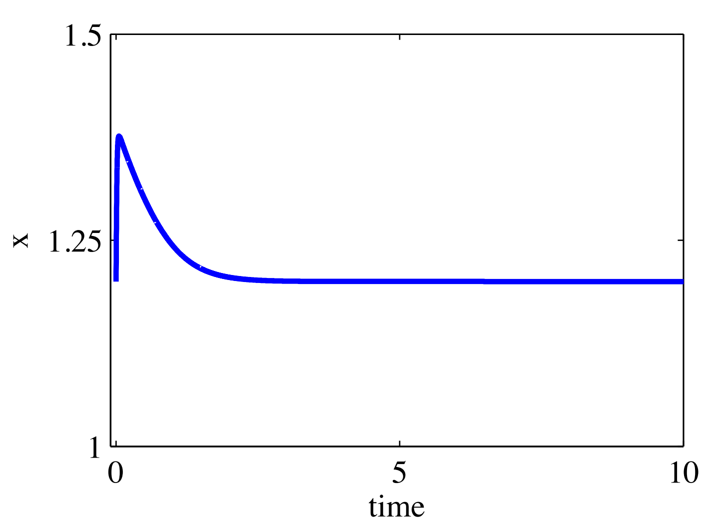
Rewritten as first order system:

$$\varepsilon\dot{x} = y - x^3/3 + x$$
$$\dot{y} = a - x$$

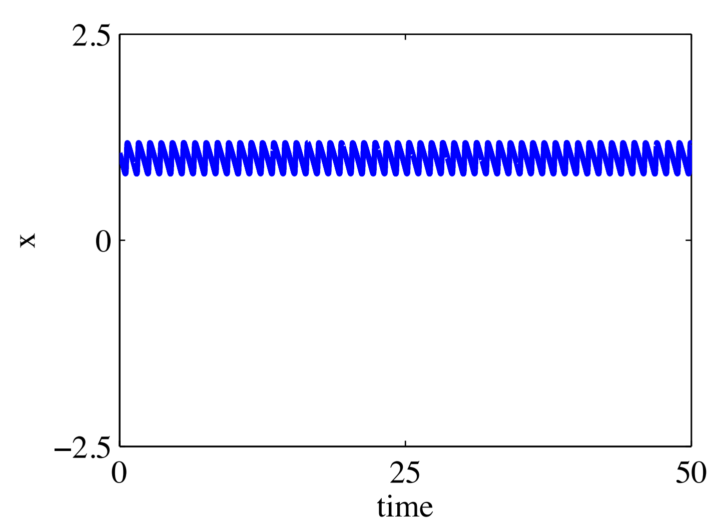
where: $0 < \varepsilon = 1/\alpha \ll 1$

Long-term dynamics of when a is varied:

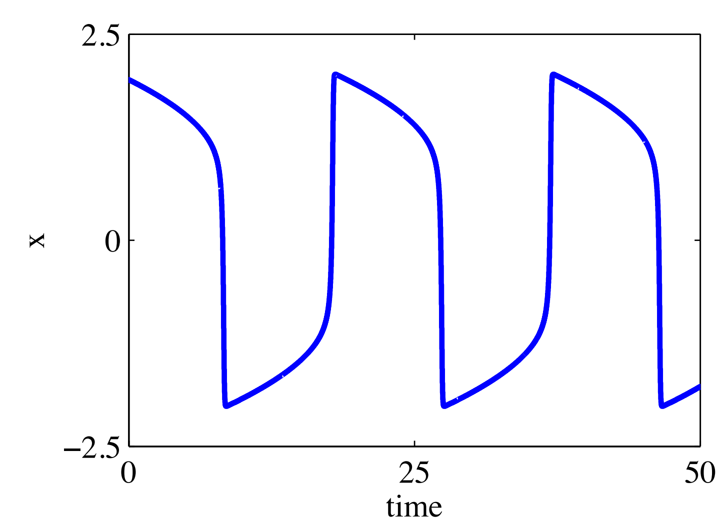
from $a=1.2$



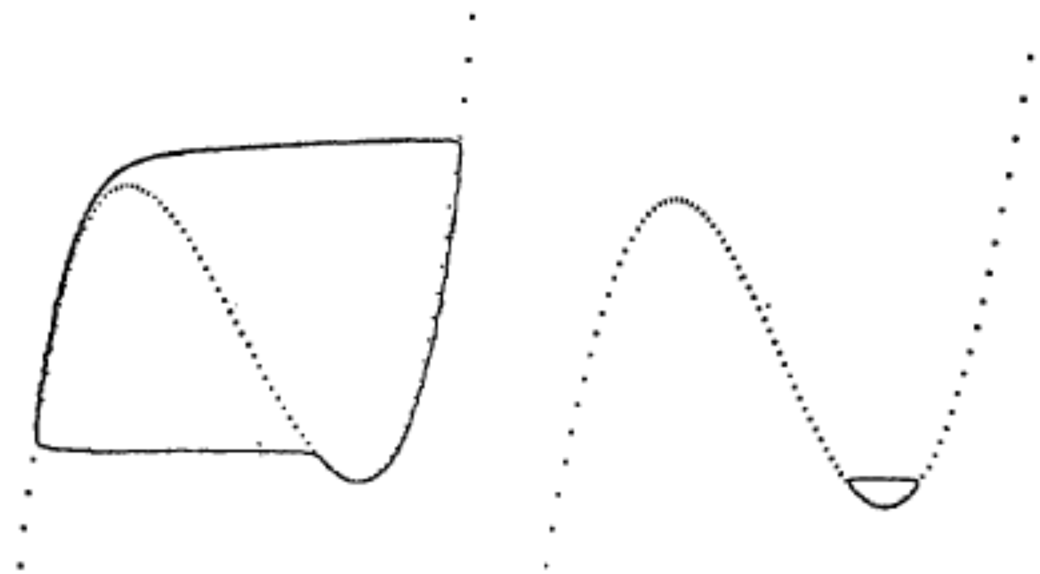
via $a=0.9935$



to $a=0.9934$



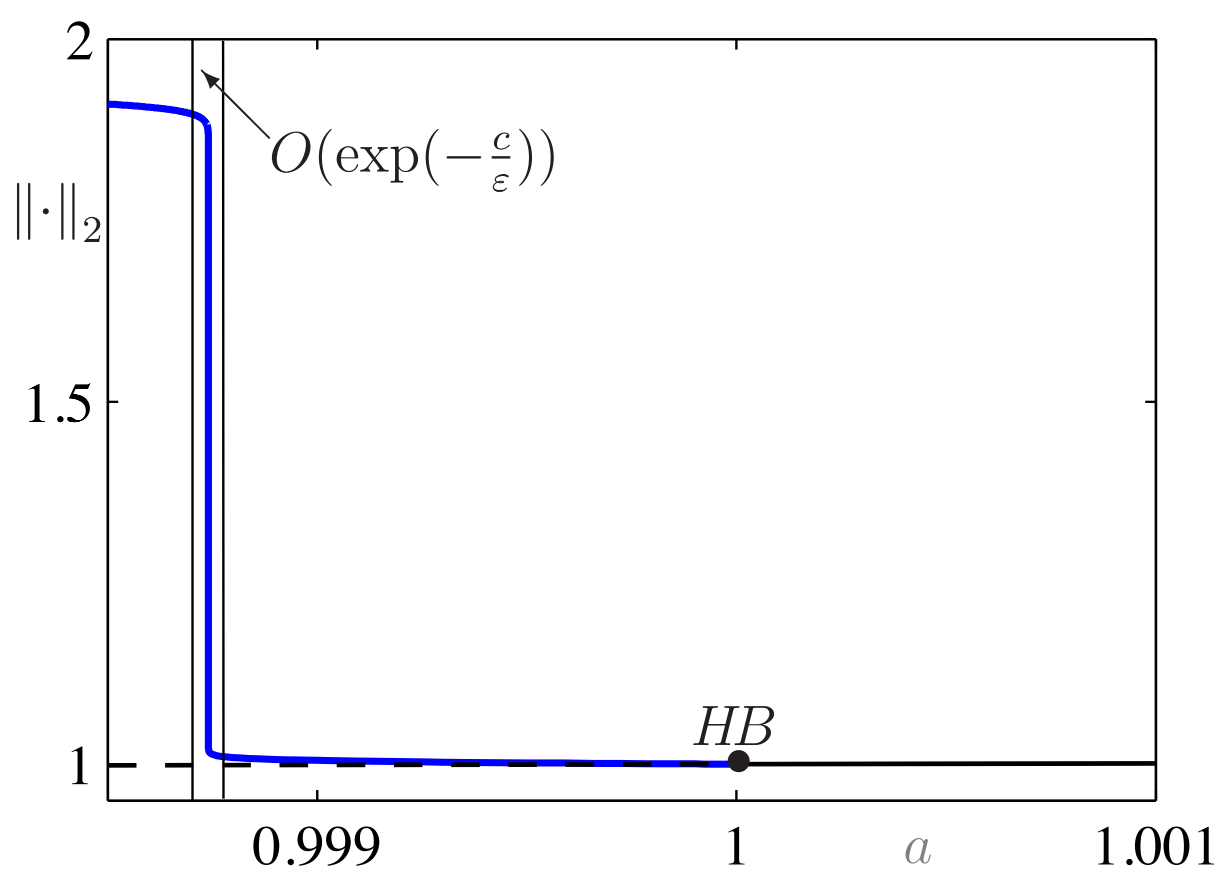
Benoît, Callot, Diener & Diener (1981)



$a = 0{,}998\ 740\ 451\ 2$ $a = 0{,}998\ 740\ 451\ 3$

Van der Pol oscillator

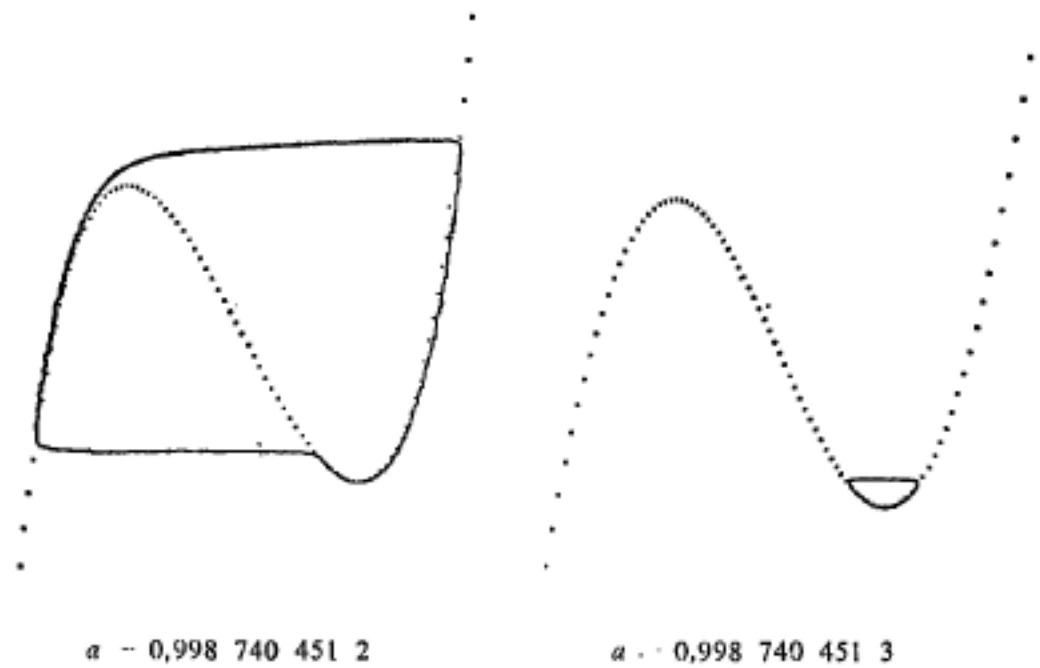
$$\begin{pmatrix} \varepsilon \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} y - x^3/3 + x \\ a - x \end{pmatrix}$$



O(ε)-away from the Hopf point the branch becomes almost vertical

$$\varepsilon = 0.001$$

Benoît, Callot, Diener & Diener (1981)



Van der Pol oscillator

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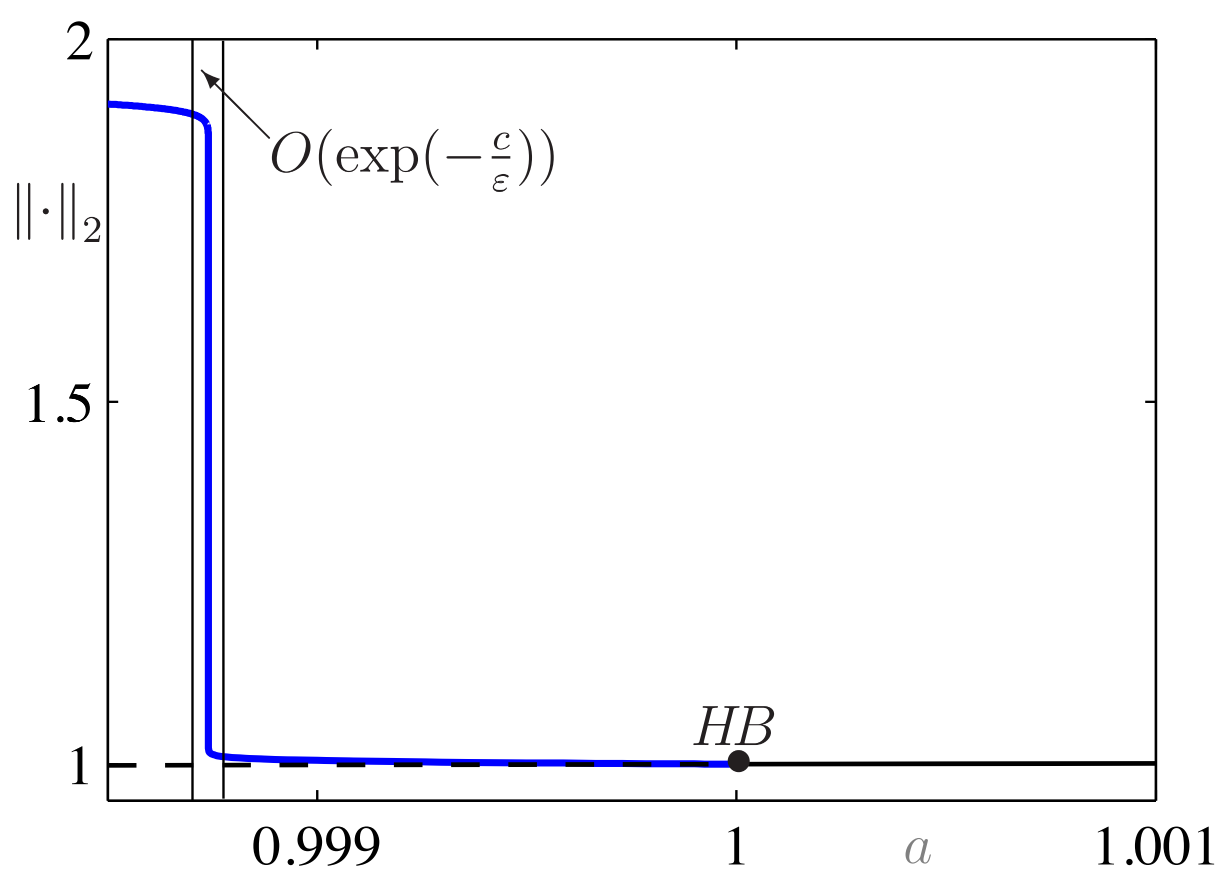

Hopf bifurcation at a=1

O(ε)-away from the Hopf point the branch becomes almost vertical

$$\varepsilon = 0.001$$

Time-scale analysis: from ε > 0 to ε = 0

$\dot{x} \sim O(1/\varepsilon) \Rightarrow x$ is **fast**	$\dot{y} \sim O(1) \Rightarrow y$ is **slow**

Time-scale analysis: from $\varepsilon > 0$ to $\varepsilon = 0$

$\dot{x} \sim O(1/\varepsilon) \Rightarrow x$ is **fast**	$\dot{y} \sim O(1) \Rightarrow y$ is **slow**

Limiting system for the **slow** dynamics:

$\varepsilon > 0$	$\varepsilon = 0$: Reduced sys.
$\varepsilon\dot{x} = y - x^3/3 + x$ $\dot{y} = a - x$	$0 = y - x^3/3 + x$ $\dot{y} = a - x$

Time-scale analysis: from $\varepsilon > 0$ to $\varepsilon = 0$

$\dot{x} \sim O(1/\varepsilon) \Rightarrow x$ is **fast**	$\dot{y} \sim O(1) \Rightarrow y$ is **slow**

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$\dot{y} = a - x$	$\dot{y} = a - x$

Limiting system for the **fast** dynamics:

$\varepsilon > 0$	$\varepsilon = 0$: Layer sys.
$x' = y - x^3/3 + x$	$x' = y - x^3/3 + x$
$y' = \varepsilon(a - x)$	$y' = 0$

Time-scale analysis: from $\varepsilon > 0$ to $\varepsilon = 0$

$\dot{x} \sim O(1/\varepsilon) \Rightarrow x$ is **fast**	$\dot{y} \sim O(1) \Rightarrow y$ is **slow**

Limiting system for the **slow** dynamics:

$\varepsilon = 0$: Reduced sys.
$0 = y - x^3/3 + x$ $\dot{y} = a - x$

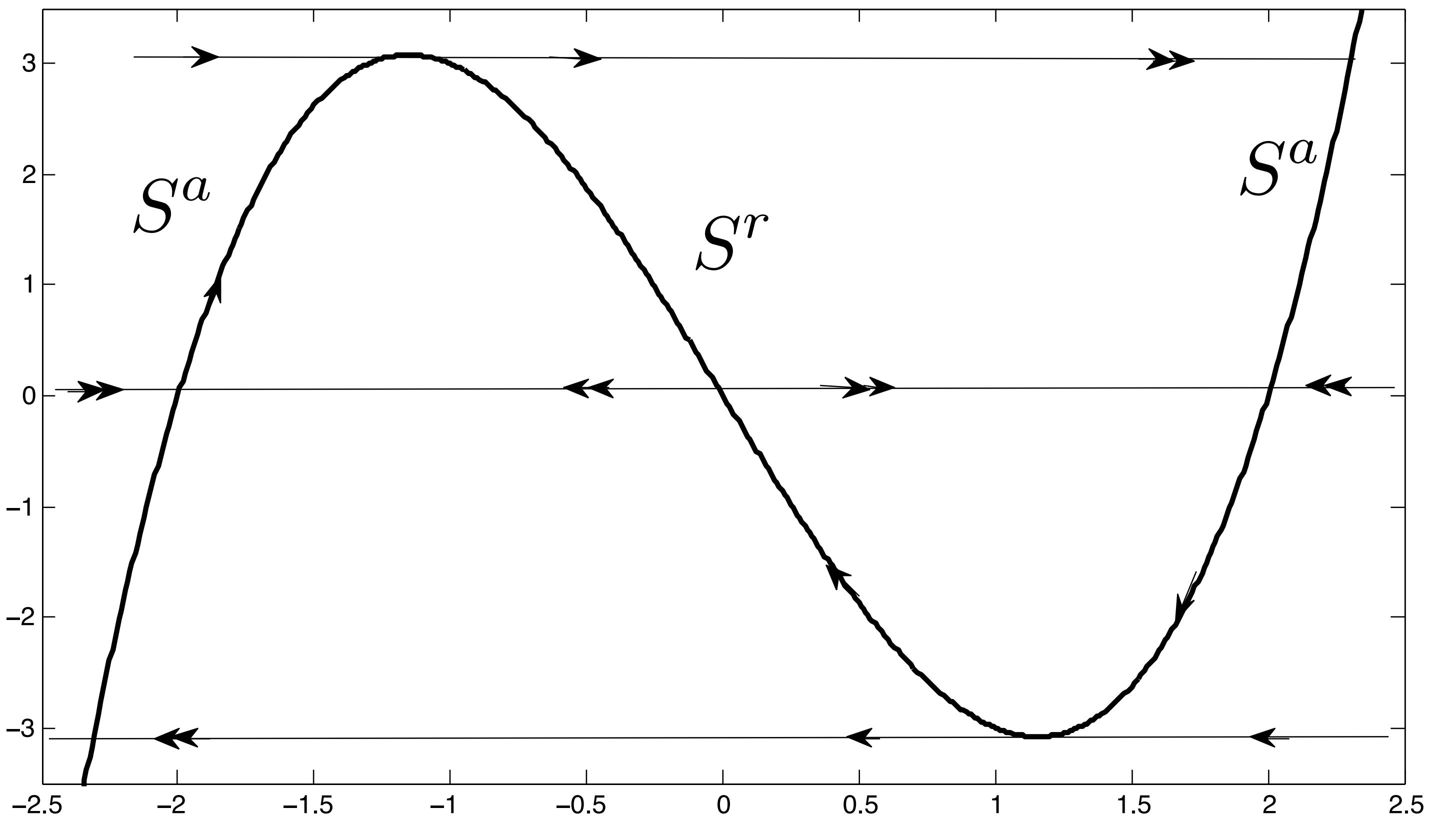
slow subsystem
ODE defined on the cubic $S := \{y = x^3/3 - x\}$

Limiting system for the **fast** dynamics:

$\varepsilon = 0$: Layer sys.
$x' = y - x^3/3 + x$ $y' = 0$

fast subsystem
family of ODEs param. by y   S is a set of equilibria

Time-scale analysis: dynamics from ε = 0 to ε > 0



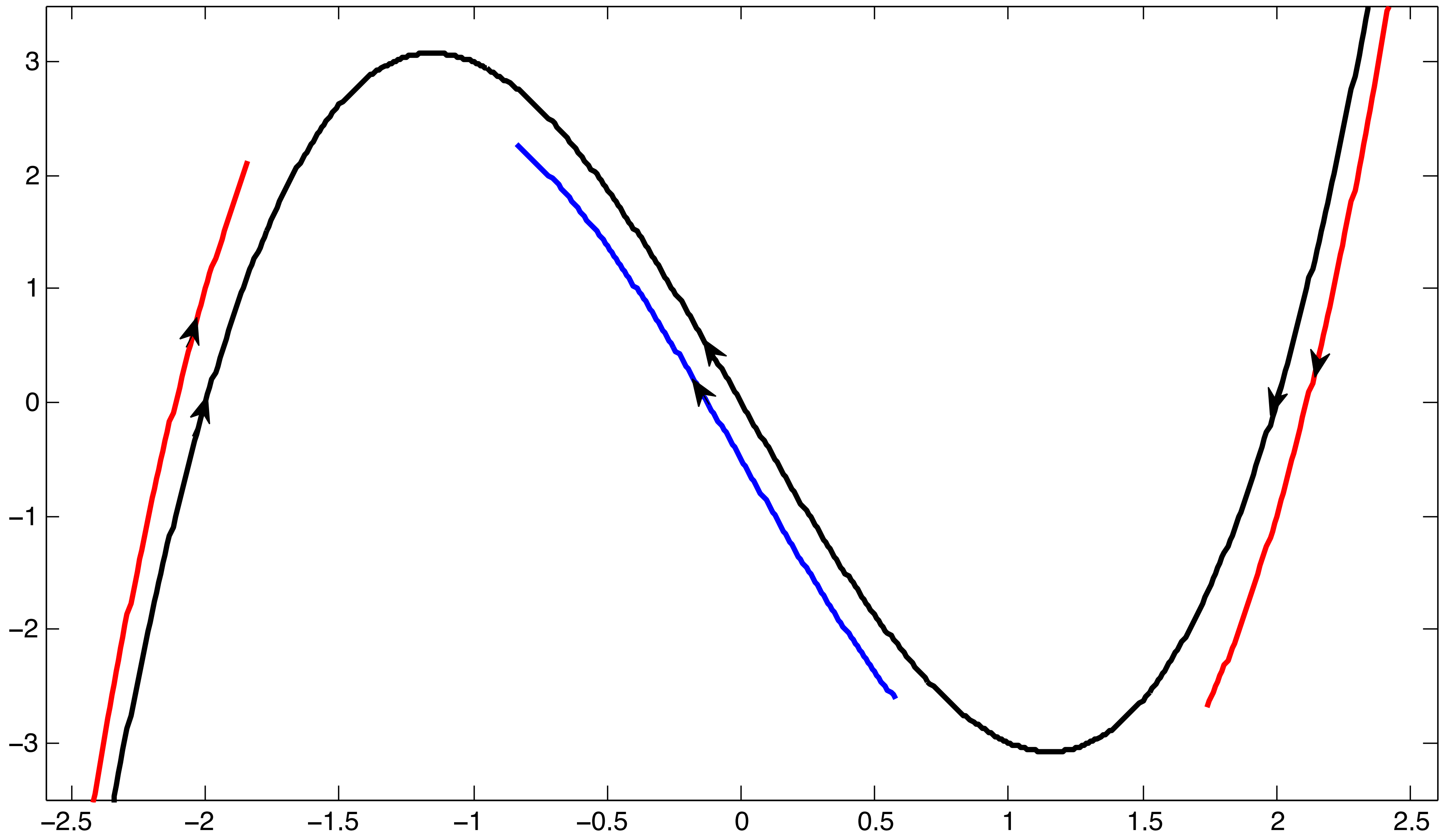
- away from the slow curve S, the overall dynamics is **fast**
- in an ε-neighbourhood of S, the overall dynamics is **slow**

- Transition: bifurcation points of the **fast** dynamics

Note S has 2 fold points ⇒ different stability on each side:

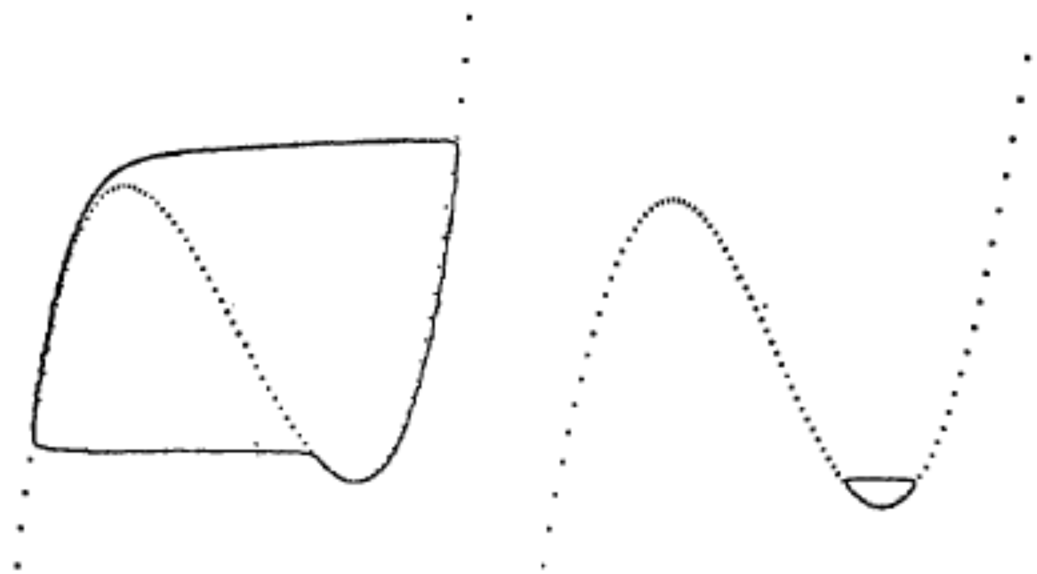
S^a is attracting and **S^r is repelling**

Fenichel theory: dynamics from ε = 0 to ε > 0



For $\varepsilon > 0$ there are Fenichel slow manifolds or rivers

Back to Benoît et al.

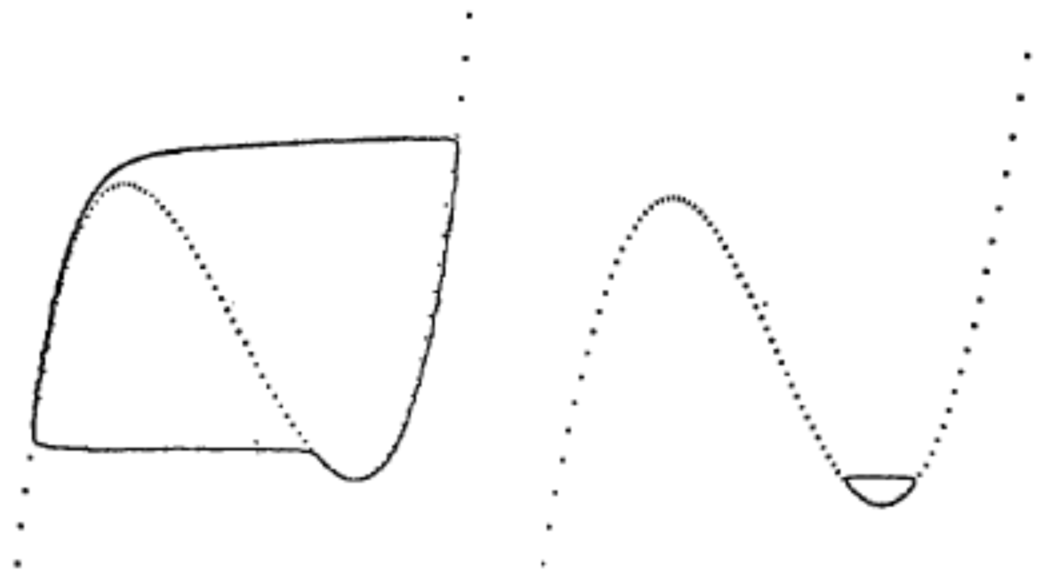


a = 0,998 740 451 2 a = 0,998 740 451 3

- The VdP system has limit cycles which

  ✓ follow the attracting part S of the cubic nullcline S^a...
  ✓ all the way down to the fold point and then ...
  ✓ **continue along the repelling part S^r of S!**

Back to Benoît et al.



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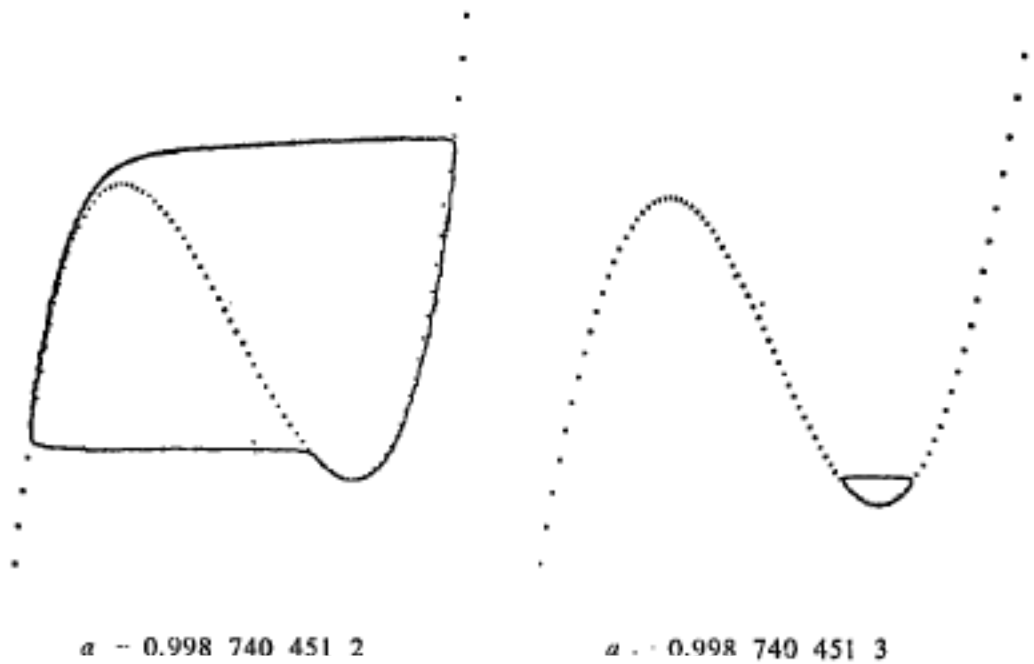
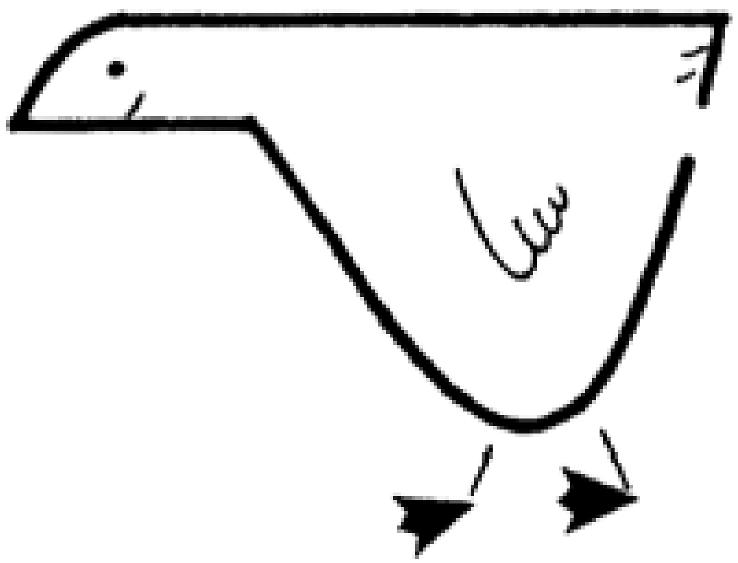
- They have been called **canards** by the French mathematicians who discovered them

Back to Benoît et al.





- The VdP ... s which

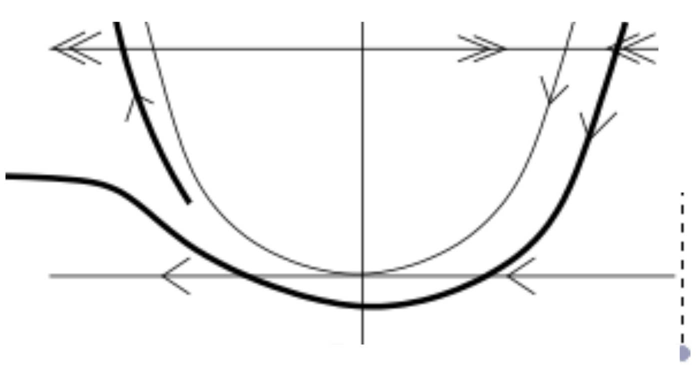
✓ follow the ... ubic nullcline S^a...
✓ all the wa ... nd then ...
✓ **continu ... part S^r of S!**

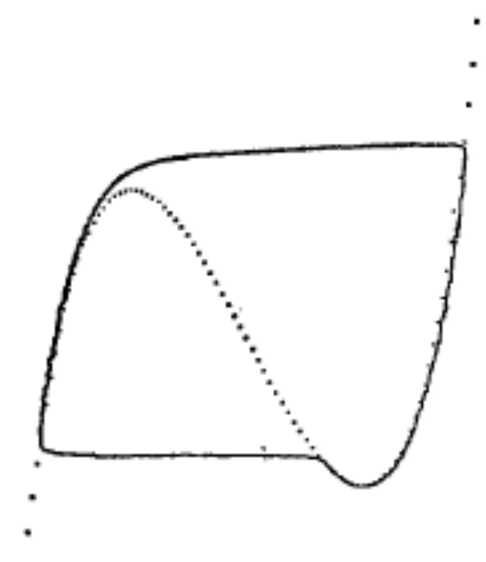
- They have been called **canards** by the French mathematicians who discovered them

Why do canard cycles exist in an exponentially small parameter range?

Answer:

S^r is repelling so to follow it for a time $t = O(1/\varepsilon)$ the solution (cycle) must be exponentially close to it.





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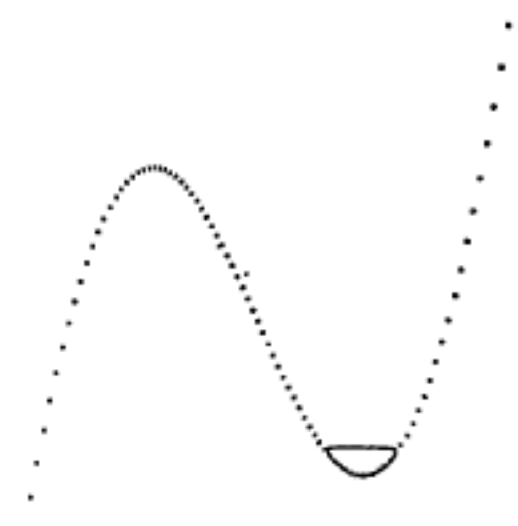

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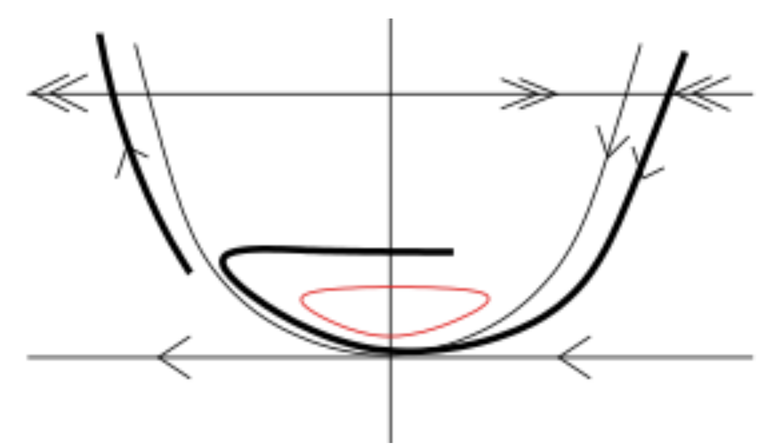


Applications

aerodynamics

Bifurcations and instabilities in the Greitzer model for compressor system surge

MORTEN BRØNS
Mathematical Institute, The Technical University of Denmark, Building 303, DK-2800 Lyngby, Denmark

M. Brøns, Math. Eng. Industry **2**(1): 51-63, 1988

chemical reactions

Canard Explosion and Excitation in a Model of the Belousov–Zhabotinsky Reaction

Morten Brøns*
Mathematical Institute, The Technical University of Denmark, DK-2800 Lyngby, Denmark

and Kedma Bar-Eli
Sackler Faculty of Exact Sciences, School of Chemistry, Tel-Aviv University, Ramat Aviv 69978, Israel
(Received: February 5, 1991)

M. Brøns & K. Bar-Eli, J. Phys. Chem. **95**: 8706-8713, 1991

False bifurcations in chemical systems: canards

BY BO PENG, VILMOS GÁSPÁR† AND KENNETH SHOWALTER
Department of Chemistry, West Virginia University, Morgantown, West Virginia 26506-6045, U.S.A.

B. Peng et al., Phil. Trans. R. Soc. Lond. A **337**: 275-289, 1991

Asymptotic analysis of canards in the EOE equations and the role of the inflection line†

BY MORTEN BRØNS[1] AND KEDMA BAR-ELI[2]
[1] *Mathematical Institute, The Technical University of Denmark, DK-2800 Lyngby, Denmark*
[2] *Sackler Faculty of Exact Sciences, School of Chemistry, Tel-Aviv University, Ramat Aviv 69978, Israel*

M. Brøns & K. Bar-Eli, Proc. R. Soc. London A **445**: 305-322, 1994

Applications (...)

Jeff Moehlis

Canards for a reduction of the Hodgkin-Huxley equations

J. Moehlis, J. Math. Biol. **52**: 141-153, 2006

H.G. Rotstein, N. Kopell, A.M. Zhabotinsky, and I.R. Epstein,

Canard phenomenon and localization of oscillations in the Belousov-Zhabotinsky reaction with global feedback.

J. Chemical Physics, 2003;119:8824-32

4D Hodgkin-Huxley

$$C dv/dt = I - I_L - I_{\mathrm{Na}} - I_K$$

I (applied current) is const

$$I_L = g_L(v - V_L) \quad I_{\mathrm{Na}} = g_{\mathrm{Na}} m^3 h(v - V_{\mathrm{Na}}) \quad I_{\mathrm{K}} = g_{\mathrm{K}} n^4 (v - V_{\mathrm{K}})$$

$x = m,\ h,\ n$ gating variables.

$$dx/dt = \frac{1}{\tau_x(v)} \left(x - x_\infty(v)\right)$$

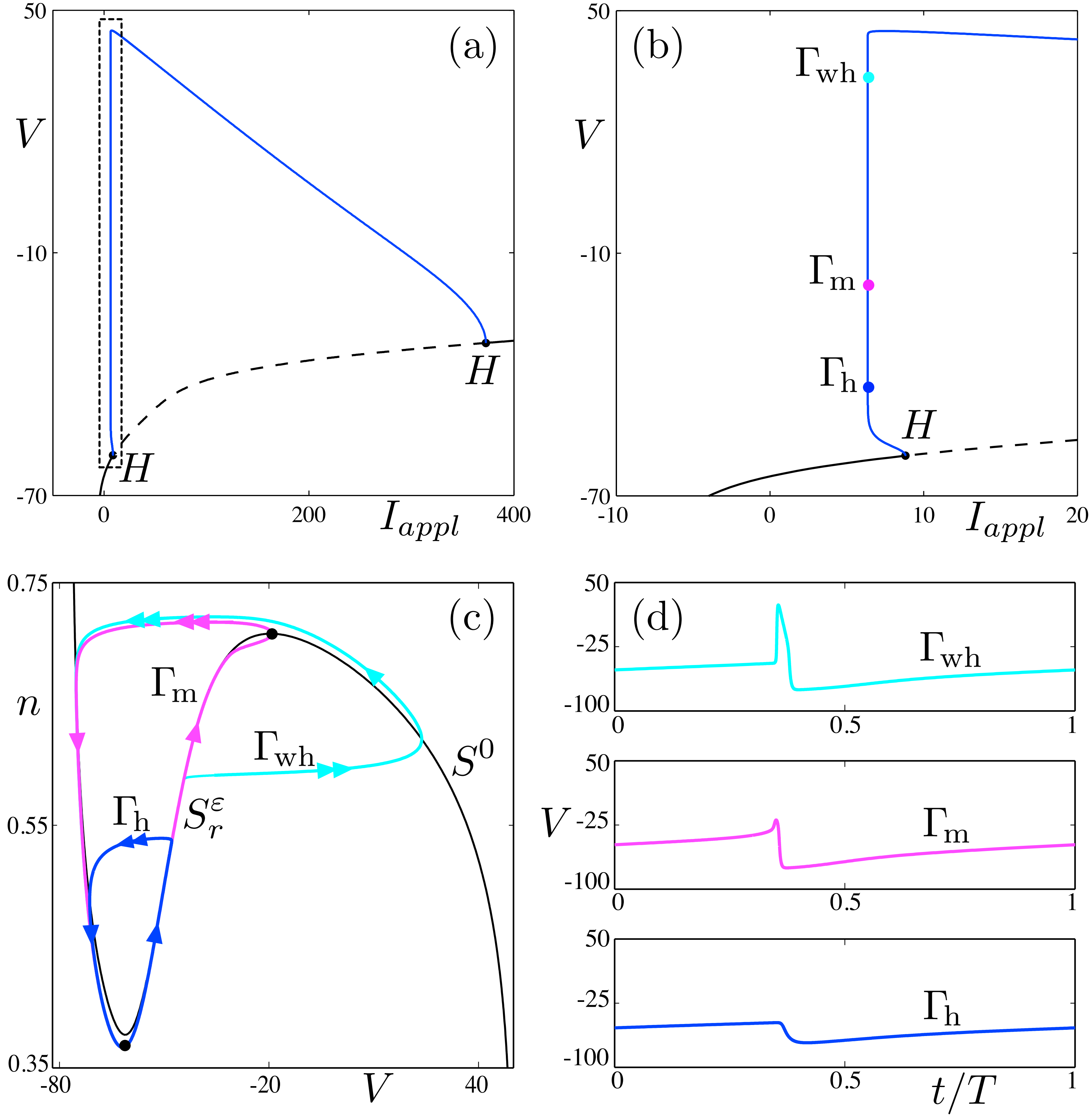
4D $\longrightarrow$ 2D reduction

Known time scale separation: v and m are fast, h and m are slow.

4D $\rightarrow$ 3D reduction: $m = m_\infty(v)$

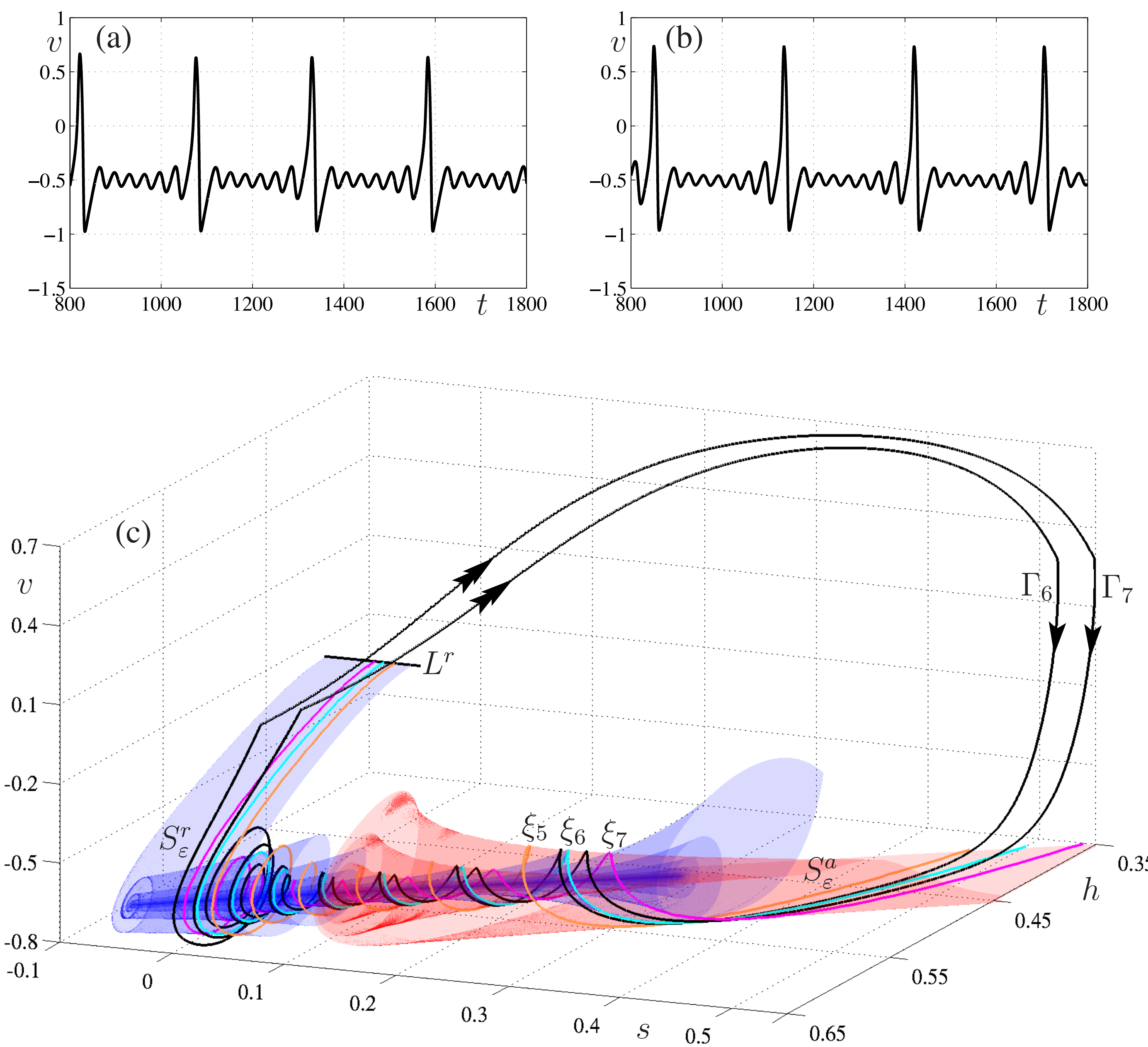
3D $\rightarrow$ 2D reduction (Rinzel): $h(t) = 0.8 - n(t)$

2D Hodgkin-Huxley

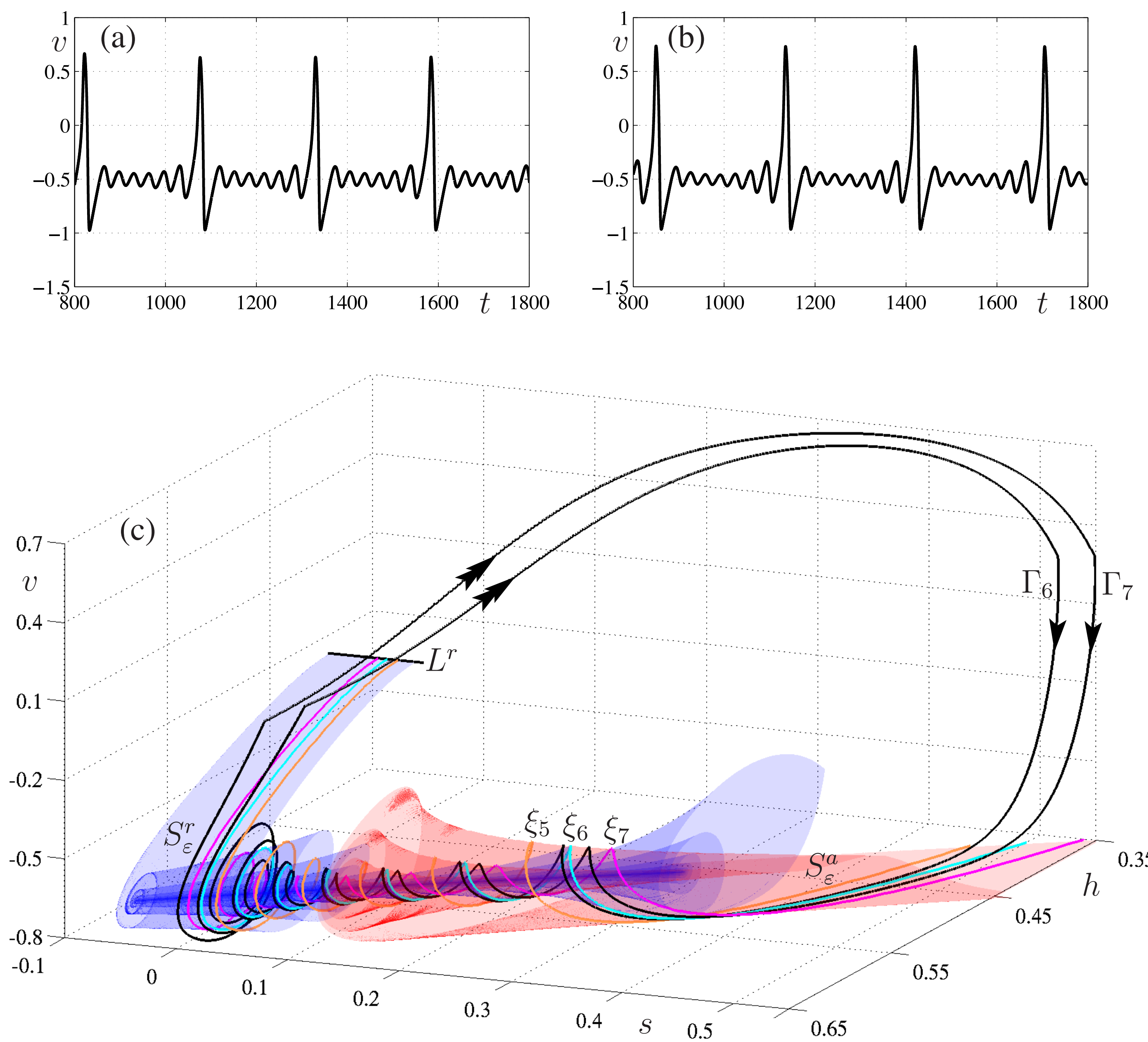


Canard explosion with a drift

Mixed mode oscillations



Mixed mode oscillations



M. Brons, M. Krupa and M. Wechselberger. Mixed mode oscillations due to the generalized canard phenomenon. *Fields Inst. Comm.* 49, 39-63 (2006)

M. Krupa, N. Popovic and N. Kopell. Mixed-mode oscillations in three timescale systems--a prototypical example. *SIAM J. Appl. Dyn. Sys.* **7**, 361-420 (2008)

Applications, mixed mode oscillations

H. Rotstein, T. Oppermann, J. White, and N. Kopell

The dynamic structure underlying subthreshold oscillatory activity and the onset of spikes in a model of medial entorhinal cortex stellate cells.

J. Comput. Neurosci., 2006

J. Rubin and M. Wechselberger

Giant squid-hidden canard: the 3D geometry of the Hodgkin–Huxley model

Biol Cybern (2007) 97:5–32

M. Krupa, N. Popovic, N. Kopell and H. G. Rotstein.

Mixed-mode oscillations in a three timescale model of a dopamine neuron.

Chaos, **18**, p. 015106 (2008)

Review:

M. Deroches, J. Guckenheimer, B. Krauskopf, C. Kuehn, H. Osinga, M. Wechselberger.
Mixed-mode oscillations with multiple time scales.

SIAM Rev. **54** (2012) 211-288.

Spike adding canard explosion and mixed-mode bursting oscillations MMBOs

References:

D. Terman, Chaotic spikes arising from a model of bursting in excitable membranes, SIAM Journal on Applied Mathematics 51 (5) (1991) 1418–1450.

J. Guckenheimer, C. Kuehn, Computing slow manifolds of saddle type, SIADS **8**, 854-879 (2009)

M. Desroches, T. J. Kaper and M. Krupa, Mixed-mode bursting oscillations: Dynamics created by a slow passage through spike-adding canard explosion in a square-wave burster. *Chaos* **23**(4), pp. 046106 (2013).

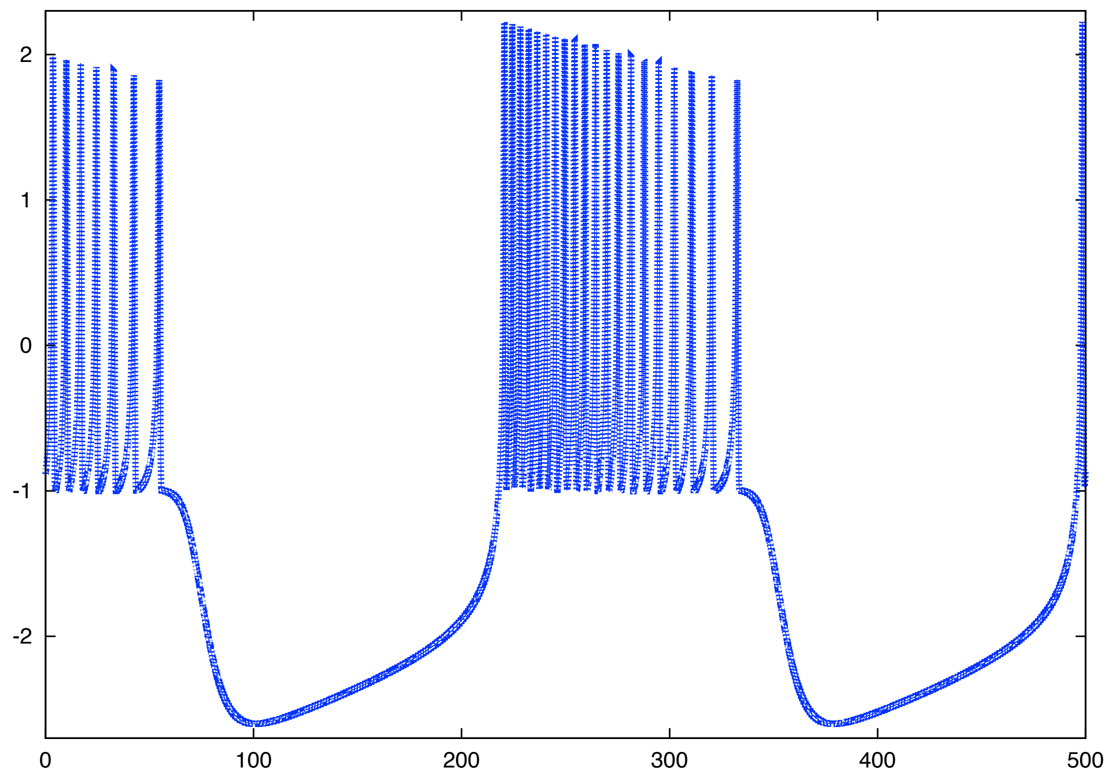
Square wave burster

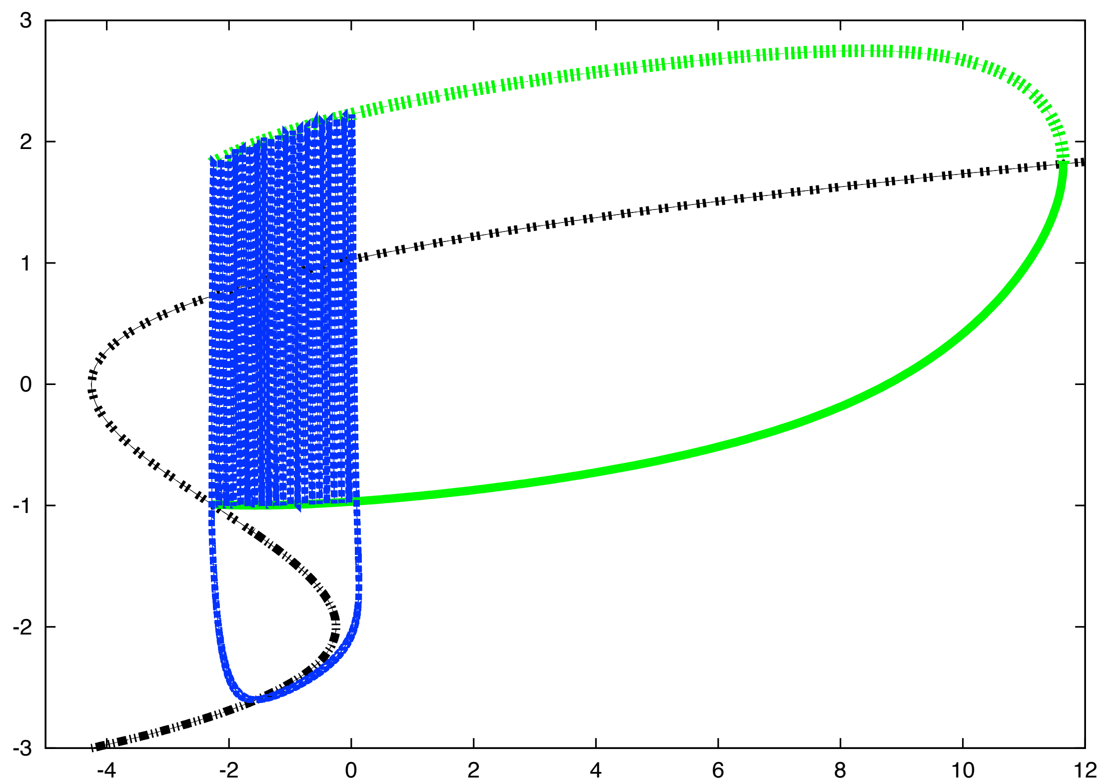
Context: Morris-Lecar type system (extra slow variable):

$$
\begin{aligned}
v' &= I - 0.5(v+0.5) - 2w(v+0.7) - 0.5(1+\tanh(\frac{v-0.1}{0.145}))(v-1) \\
w' &= 1.15(0.5(1+\tanh(\frac{v+0.1}{0.15}) - w)\cosh(\frac{v-0.1}{0.29}) \\
I' &= \varepsilon(k-v)
\end{aligned}
$$

Two fast and one slow variable

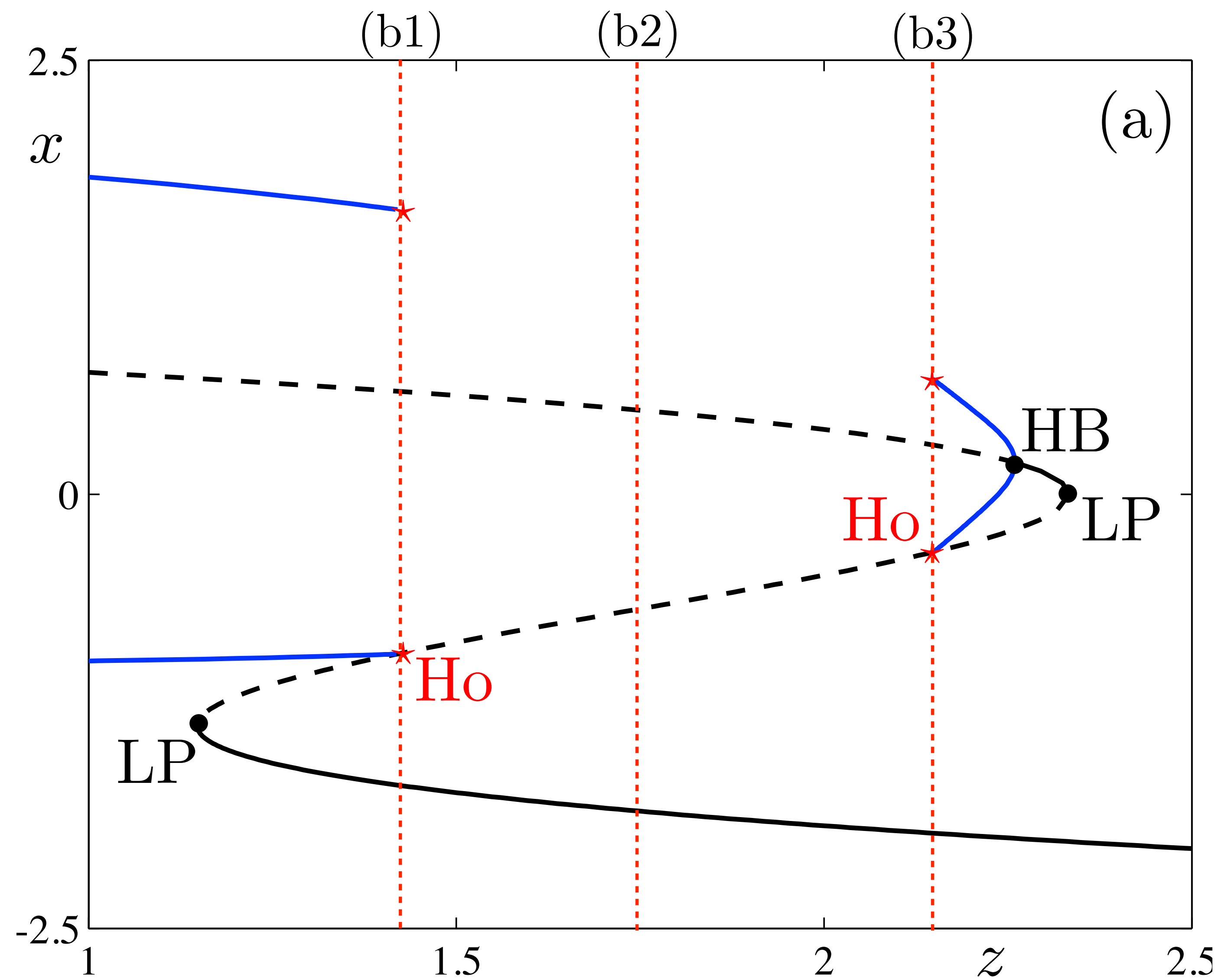
Bursting (square wave burster)





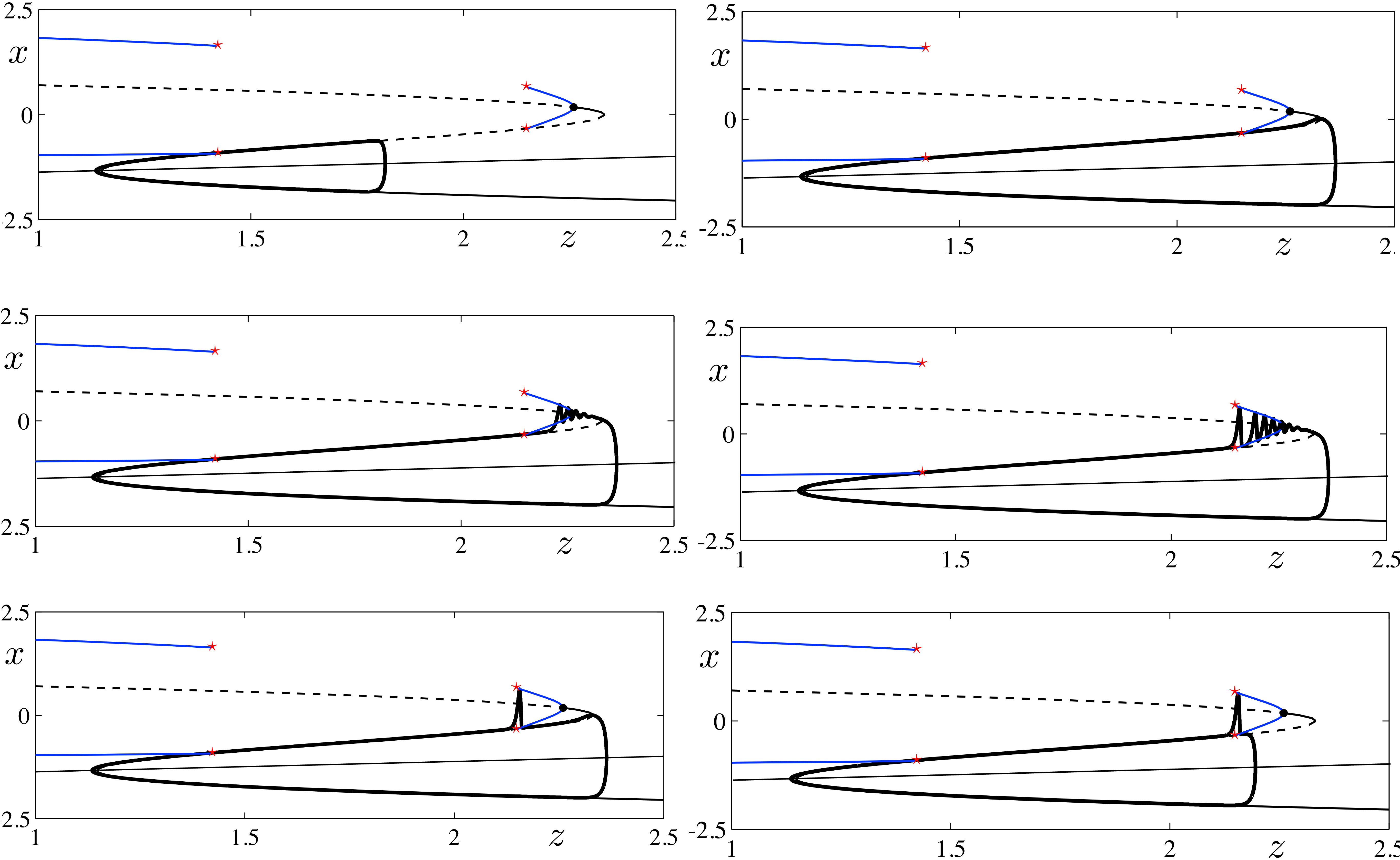
The Hindmarsh-Rose burster

$$x' = y - ax^3 + bx^2 + I - z$$
$$y' = c - dx^2 - y$$
$$z' = \varepsilon(s(x - x_1) - z)$$

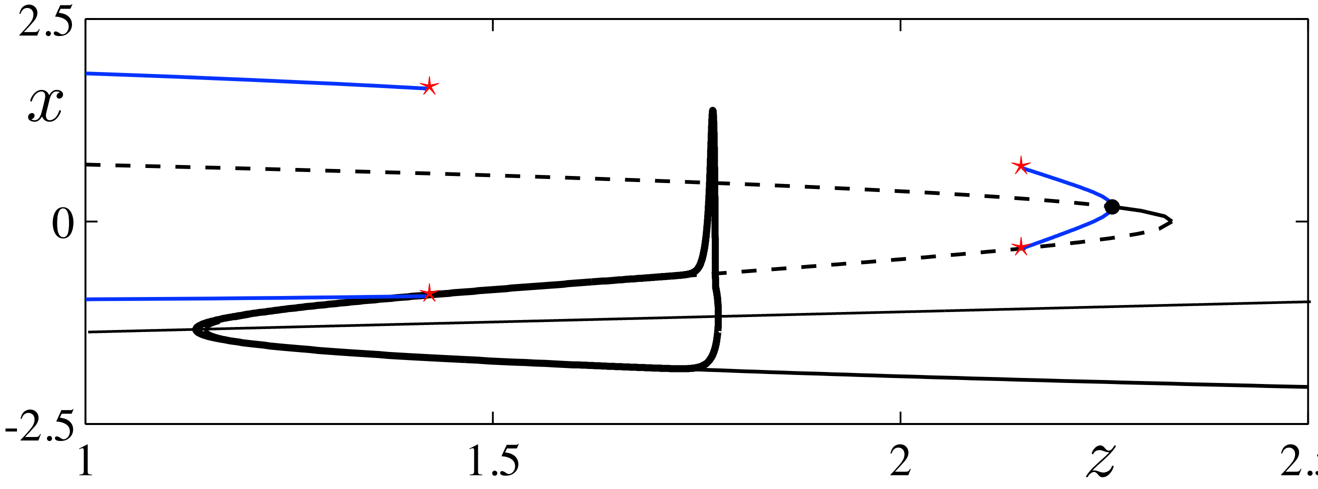


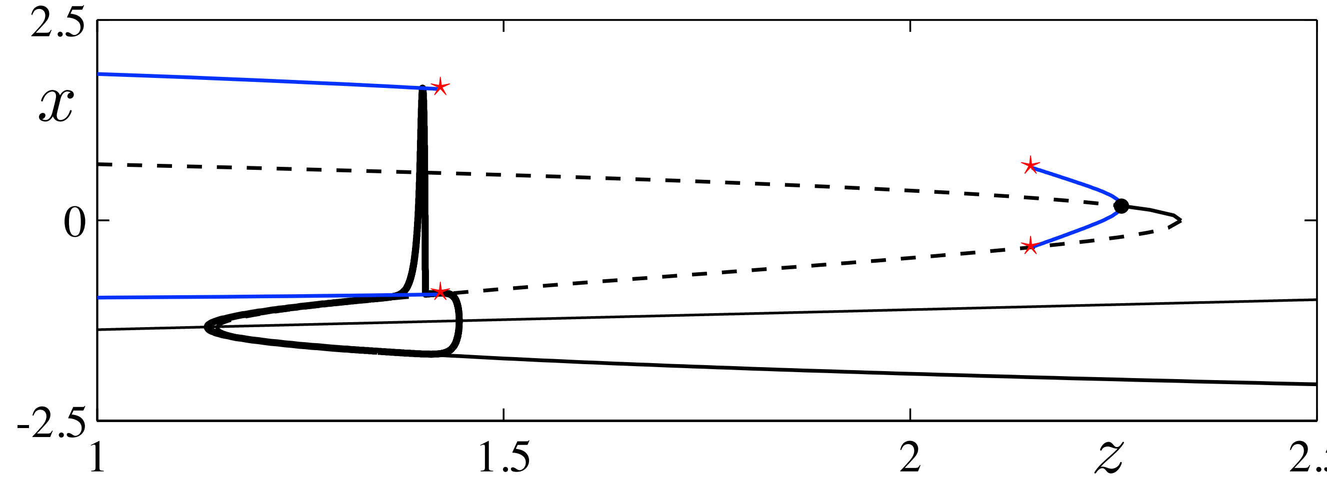
Bifurcation diagram
fast system

Spike-adding via canards

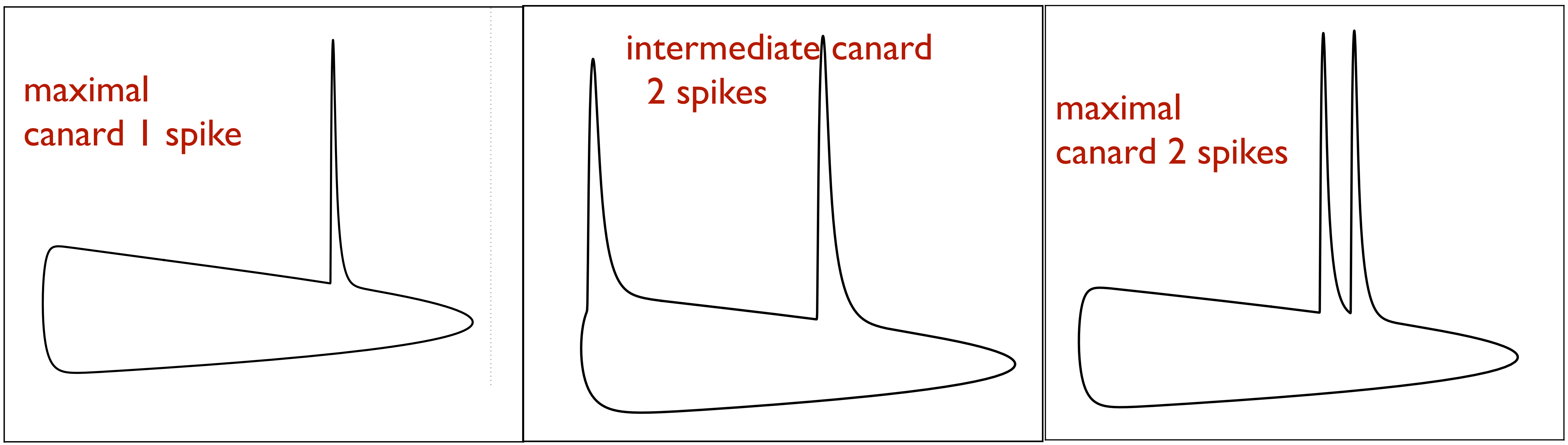


Spike-adding via canards (cont)

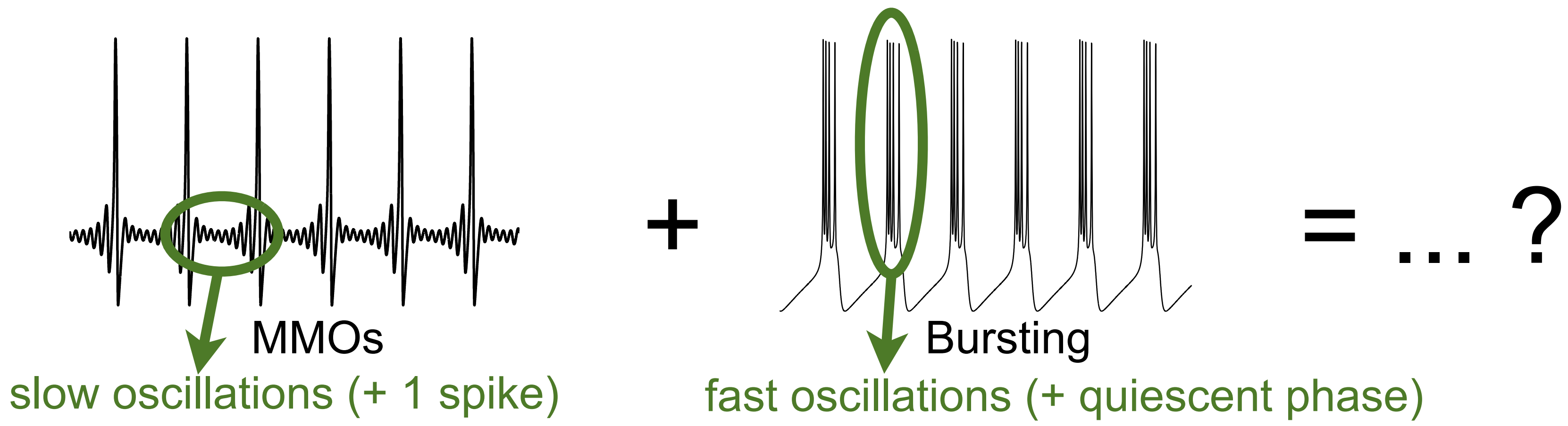




Adding a spike within canard explosion



Combination of MMO and bursting (II)



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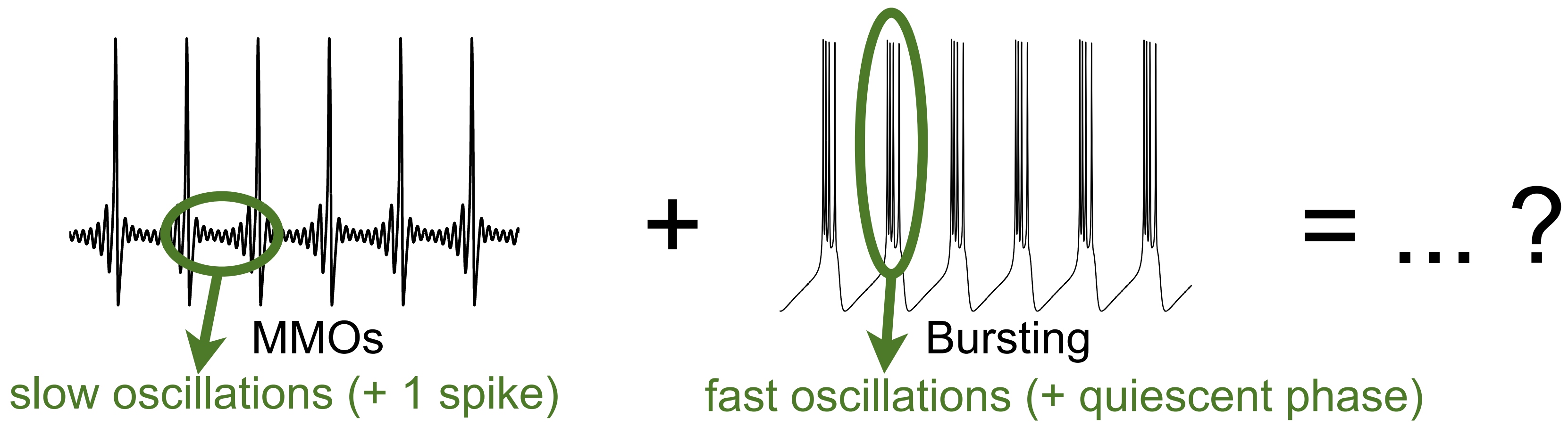
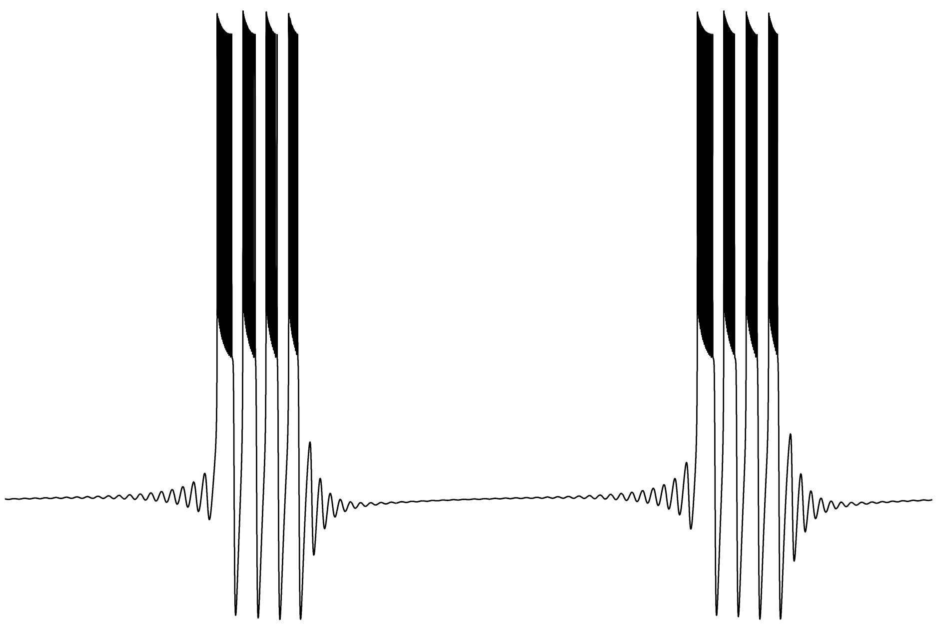


- different time scales, **fast and slow** complex oscillations

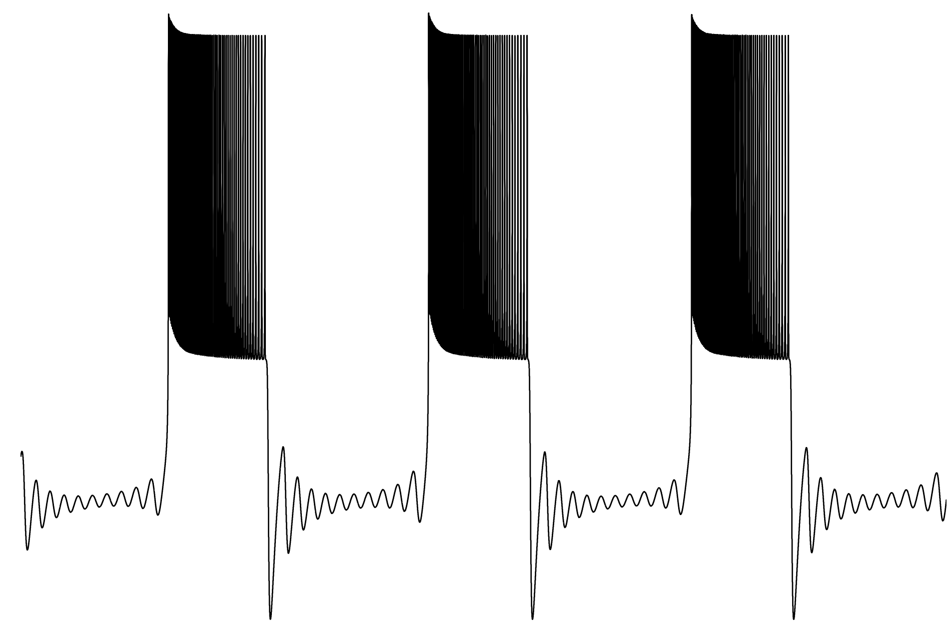
➟ **Minimal system: 2 fast & 2 slow variables**

"MMOs + Bursting" = "Mixed-Mode Bursting Oscillations (MMBOs)"

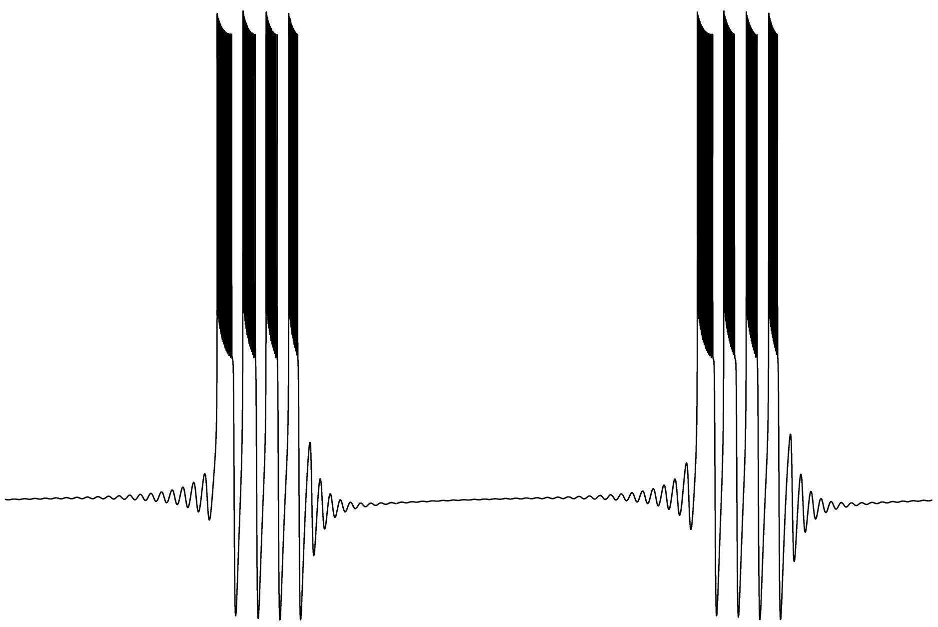


← 2 fast variables →

← 2 slow variables →

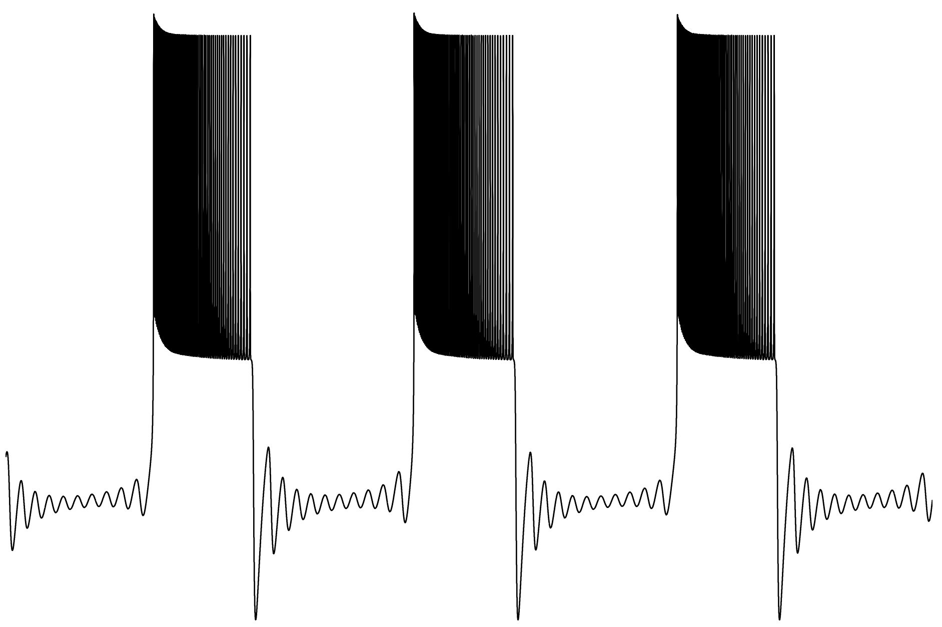


“MMOs + Bursting” = “Mixed-Mode Bursting Oscillations (MMBOs)”



← 2 fast variables →

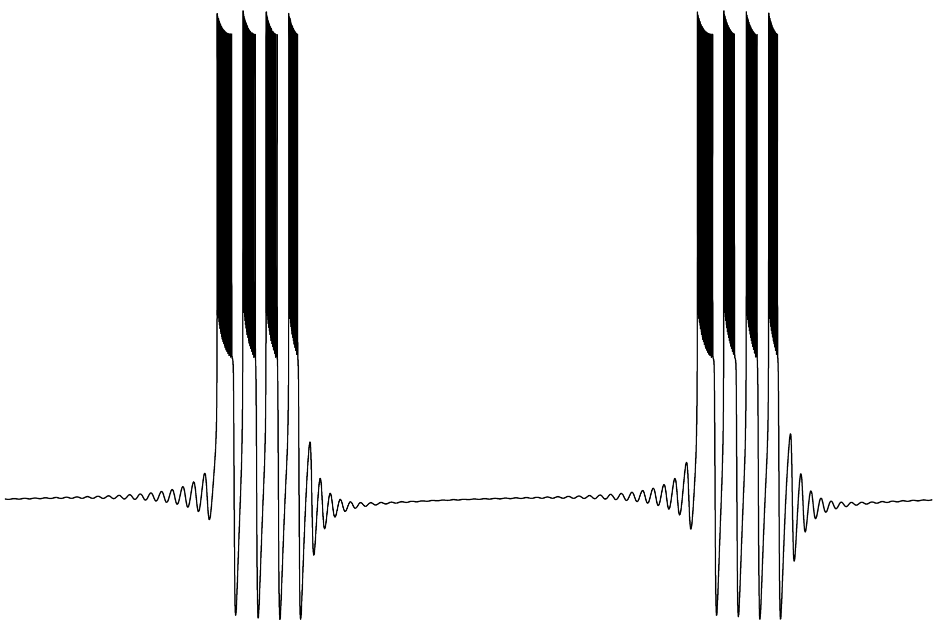
← 2 slow variables →



➟ **2 fast:**

$$
\begin{aligned}
\varepsilon_1 \dot{x}_1 &= f_1 \\
\varepsilon_2 \dot{x}_2 &= f_2
\end{aligned}
$$

“MMOs + Bursting” = “Mixed-Mode Bursting Oscillations (MMBOs)”



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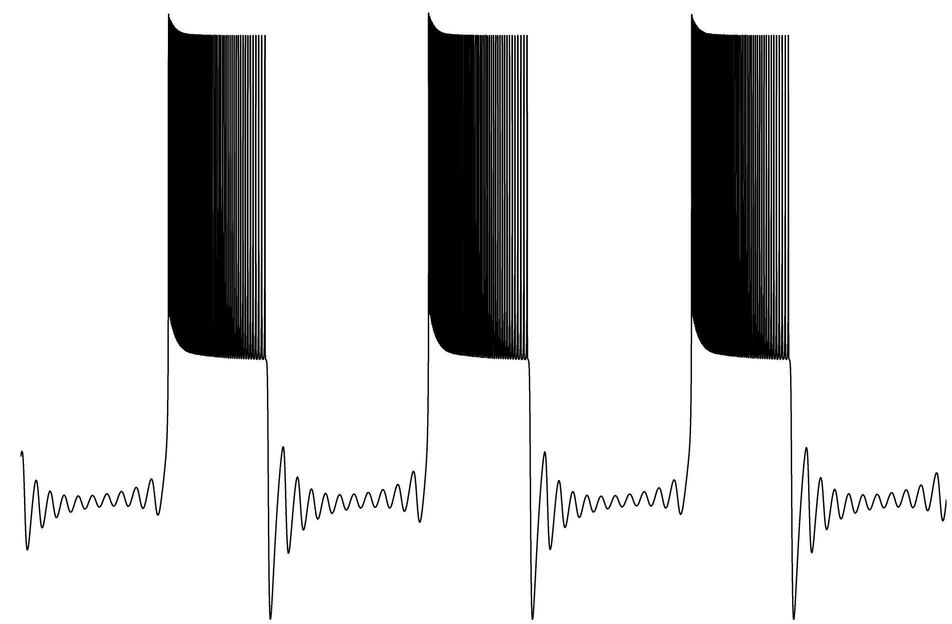
← 2 slow variables →

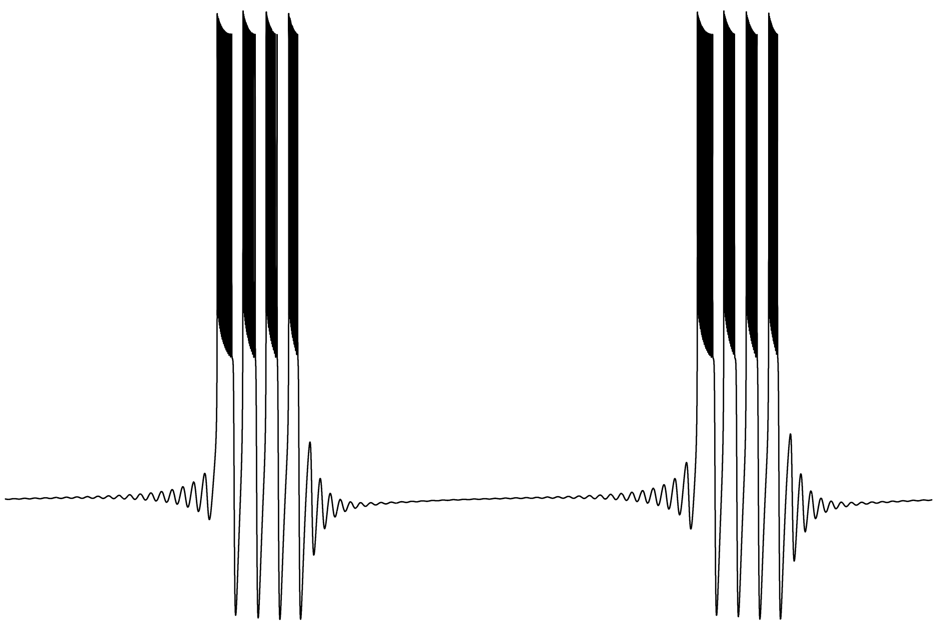


➟ **2 fast:**

➟ **2 slow:**

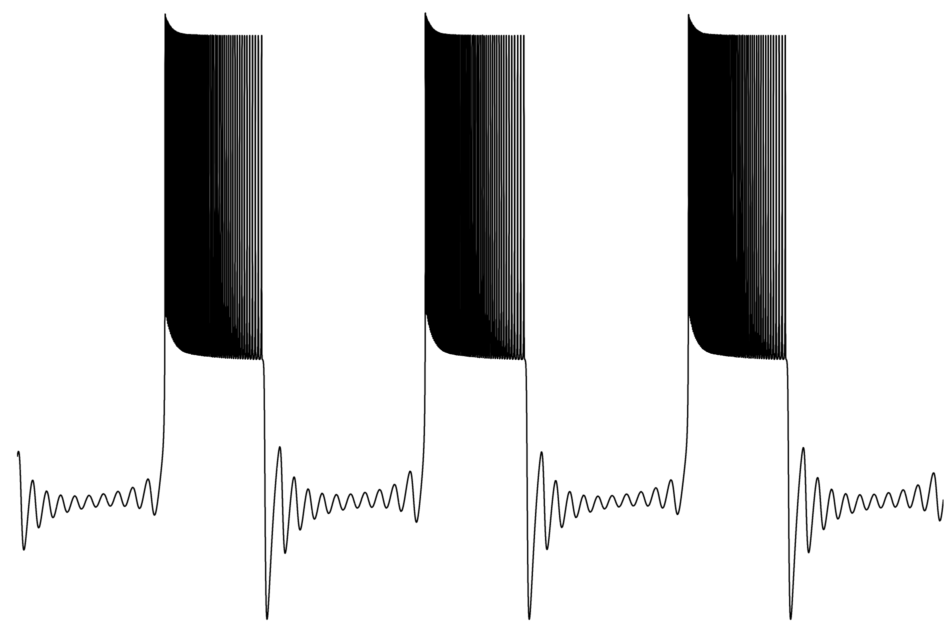
$$
\begin{aligned}
\varepsilon_1 \dot{x}_1 &= f_1 \\
\varepsilon_2 \dot{x}_2 &= f_2 \\
\dot{y}_1 &= g_1 \\
\dot{y}_2 &= g_2
\end{aligned}
$$

“MMOs + Bursting” = “Mixed-Mode Bursting Oscillations (MMBOs)”



← 2 fast variables →

← 2 slow variables →



MMOs

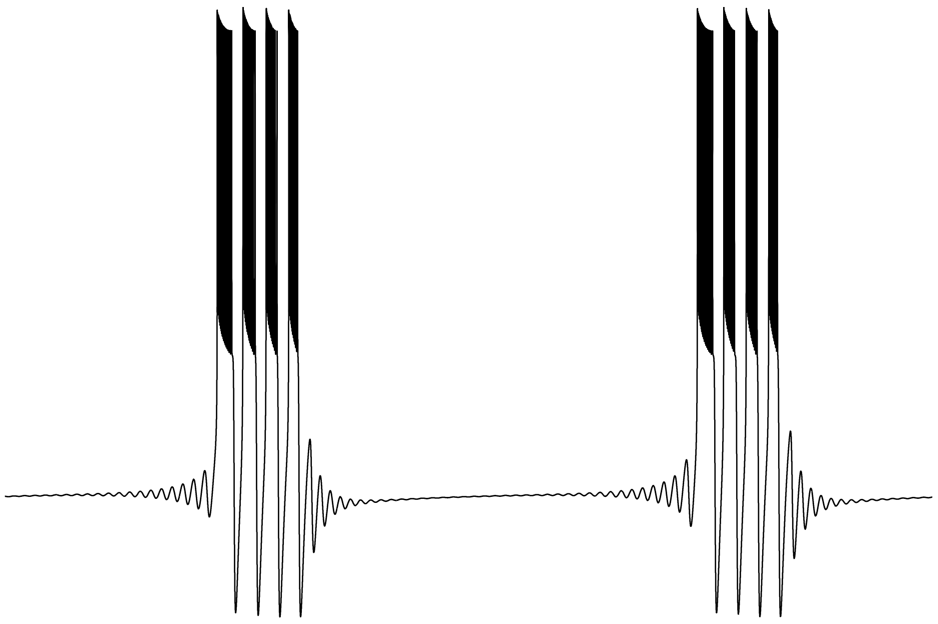
➟ 2 fast:

$$\varepsilon_1 \dot{x}_1 = f_1$$
$$\varepsilon_2 \dot{x}_2 = f_2$$

➟ 2 slow:

$$\dot{y}_1 = g_1$$
$$\dot{y}_2 = g_2$$

“MMOs + Bursting” = “Mixed-Mode Bursting Oscillations (MMBOs)”



← 2 fast variables →

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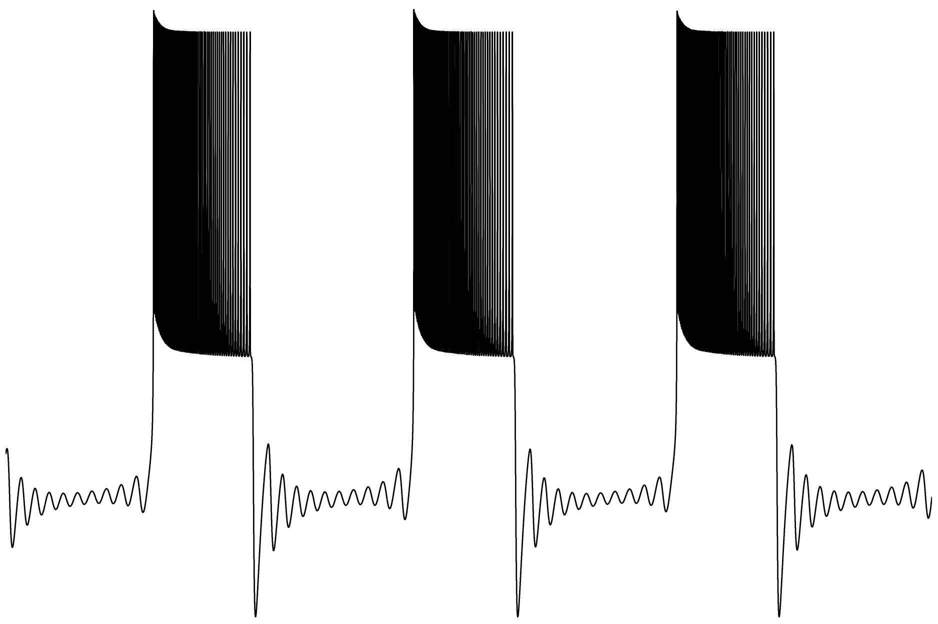


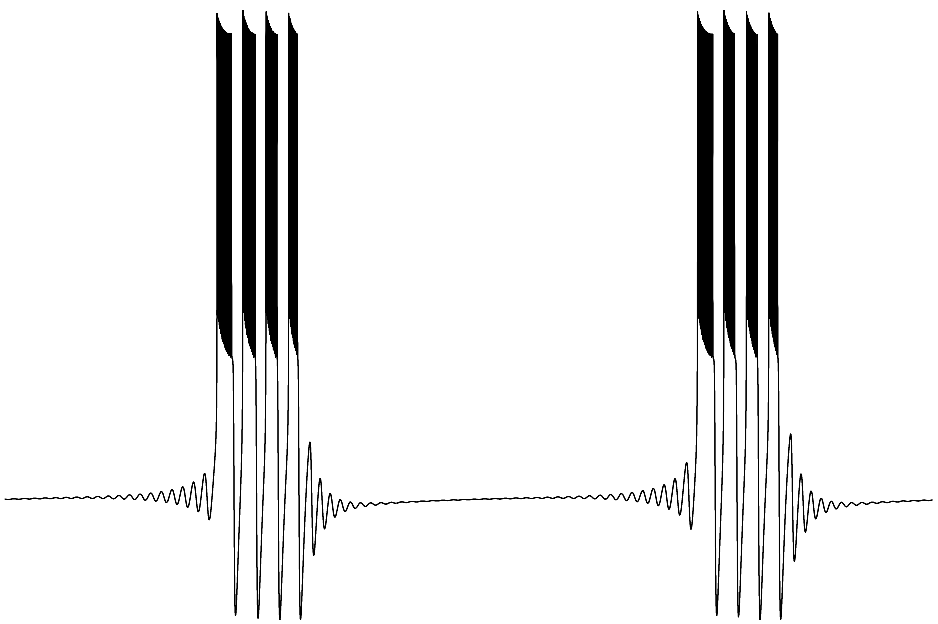
➟ **2 fast:**

➟ **2 slow:**

$$\begin{aligned} \varepsilon_1 \dot{x}_1 &= f_1 \\ \varepsilon_2 \dot{x}_2 &= f_2 \\ \dot{y}_1 &= g_1 \\ \dot{y}_2 &= g_2 \end{aligned}$$

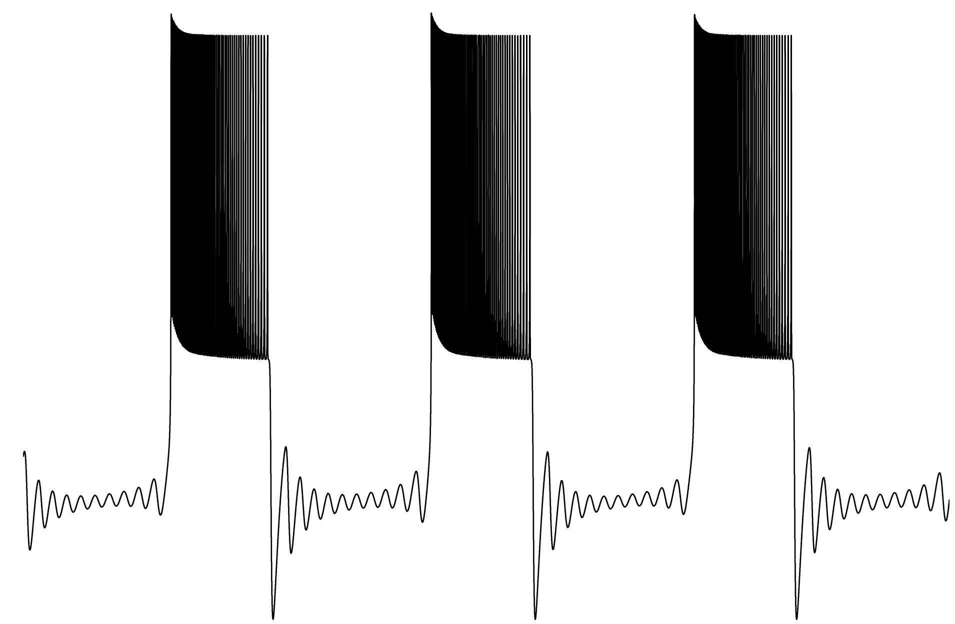
MMOs

“MMOs + Bursting” = “Mixed-Mode Bursting Oscillations (MMBOs)”



← 2 fast variables →

← 2 slow variables →



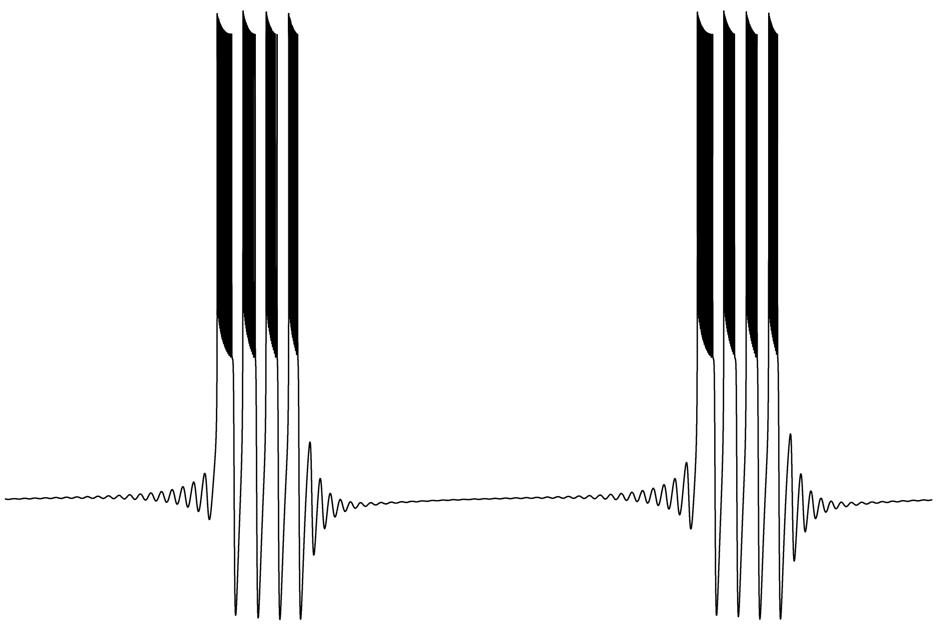
➟ **2 fast:**

➟ **2 slow:**

$$\begin{aligned} \varepsilon_1 \dot{x}_1 &= f_1 \\ \varepsilon_2 \dot{x}_2 &= f_2 \\ \dot{y}_1 &= g_1 \\ \dot{y}_2 &= g_2 \end{aligned}$$

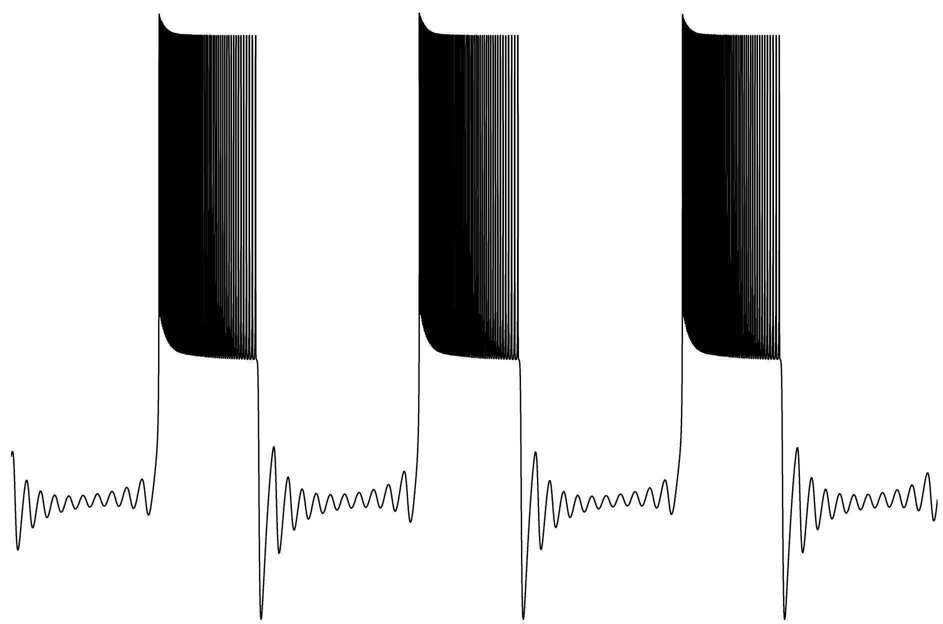
Bursting

“MMOs + Bursting” = “Mixed-Mode Bursting Oscillations (MMBOs)”



← 2 fast variables →

← 2 slow variables →



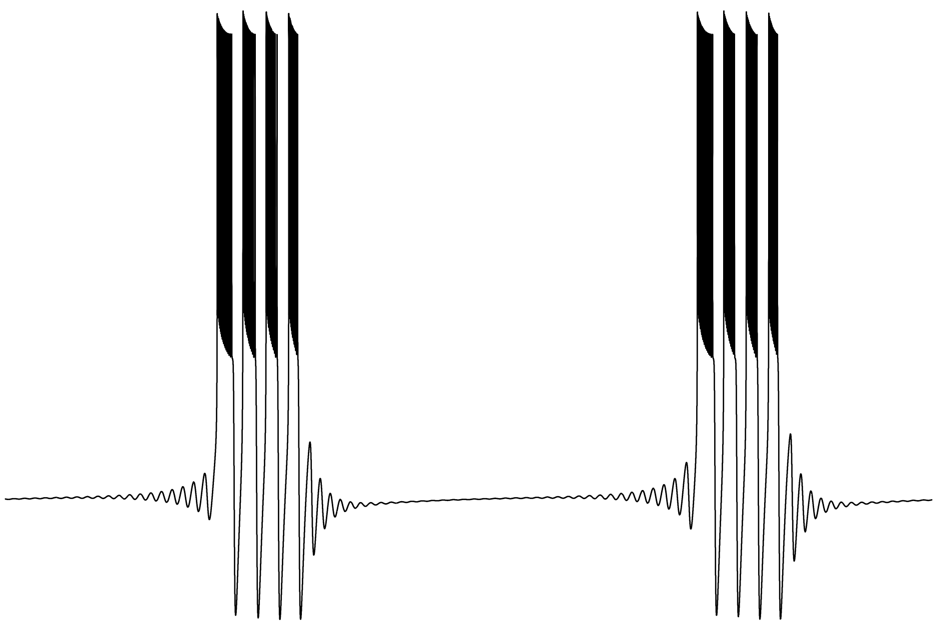
➟ 2 fast:

➟ 2 slow:

$$\varepsilon_1 \dot{x}_1 = f_1$$
$$\varepsilon_2 \dot{x}_2 = f_2$$
$$\dot{y}_1 = g_1$$
$$\dot{y}_2 = g_2$$

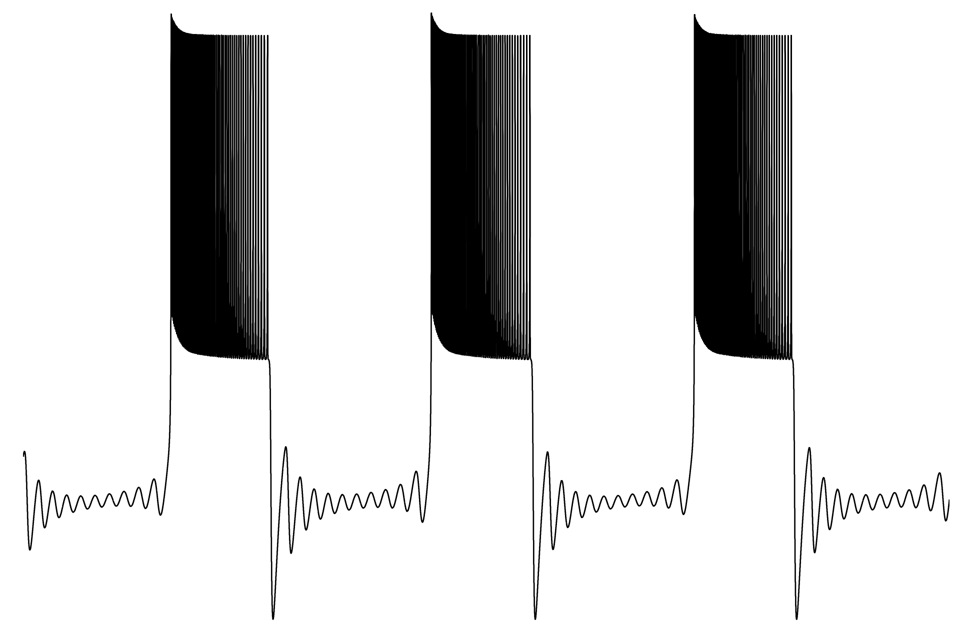
Bursting

“MMOs + Bursting” = “Mixed-Mode Bursting Oscillations (MMBOs)”



← 2 fast variables →

← 2 slow variables →



➟ **2 fast:**

➟ **2 slow:**

$$
\begin{aligned}
\varepsilon_1 \dot{x}_1 &= f_1 \\
\varepsilon_2 \dot{x}_2 &= f_2 \\
\dot{y}_1 &= g_1 \\
\dot{y}_2 &= g_2
\end{aligned}
$$

➟ Combine theories ... and questions:

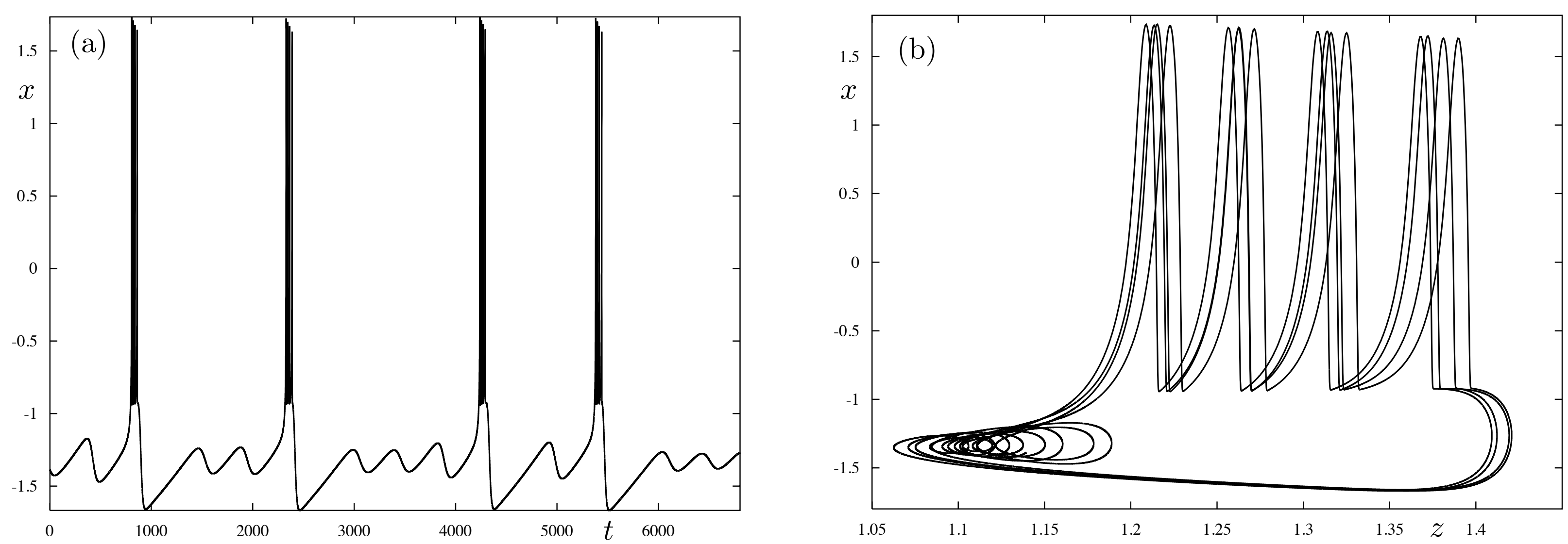
what patterns of oscillations ?

what organising centres ?

Our strategy to construct and analyse a 4D slow-fast system with MMBOs

- start from a **burster** (Hindmarsh-Rose in our case)
- add a **slow variable**
- similarly to the MMO case, we want MMBOs to be the result to a **slow passage** through a canard explosion

➠ we will construct a ***slow passage through a spike-adding canard explosion***



$$x' = y - ax^3 + bx^2 + I - z$$
$$y' = c - dx^2 - y$$
$$z' = \varepsilon(s(x - x_1) - z)$$

Hindmarsh-Rose

$$I' = \varepsilon(k - h_x(x - x_{\text{fold}})^2 - h_y(y - y_{\text{fold}})^2 - h_I(I - I_{\text{fold}}))$$

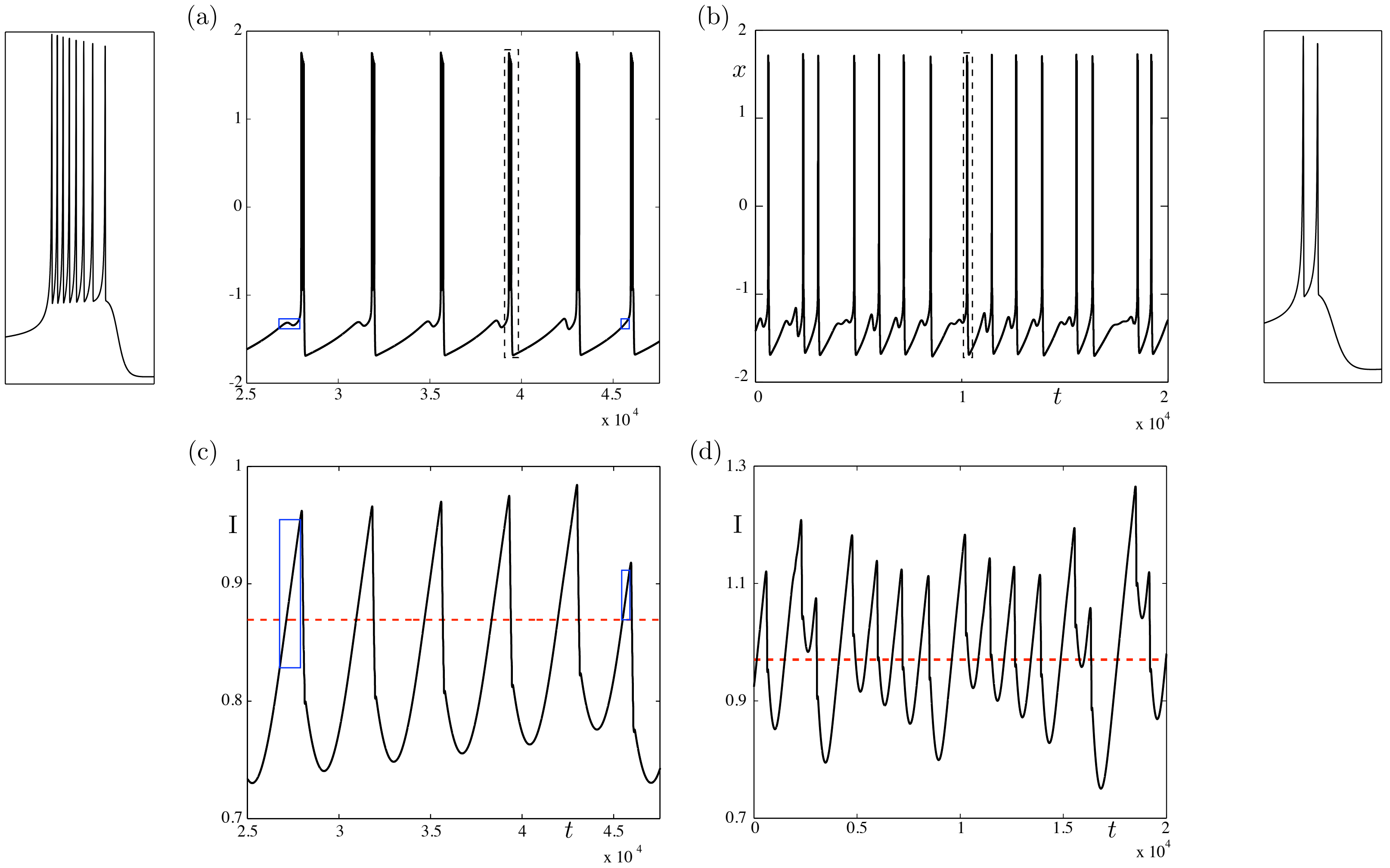
Understanding MMBOs as a slow passage

$$x' = y - ax^3 + bx^2 + I - z$$
$$y' = c - dx^2 - y$$
$$z' = \varepsilon(s(x - x_1) - z)$$
$$I' = \varepsilon(k - h_x(x - x_{\text{fold}})^2 - h_y(y - y_{\text{fold}})^2 - h_I(I - I_{\text{fold}}))$$

Controlling the number of SAOs using folded node theory

$$x' = y - ax^3 + bx^2 + I - z$$
$$y' = c - dx^2 - y$$
$$z' = \varepsilon(s(x - x_1) - z)$$
$$I' = \varepsilon(k - h_x(x - x_{\text{fold}})^2 - h_y(y - y_{\text{fold}})^2 - h_I(I - I_{\text{fold}}))$$

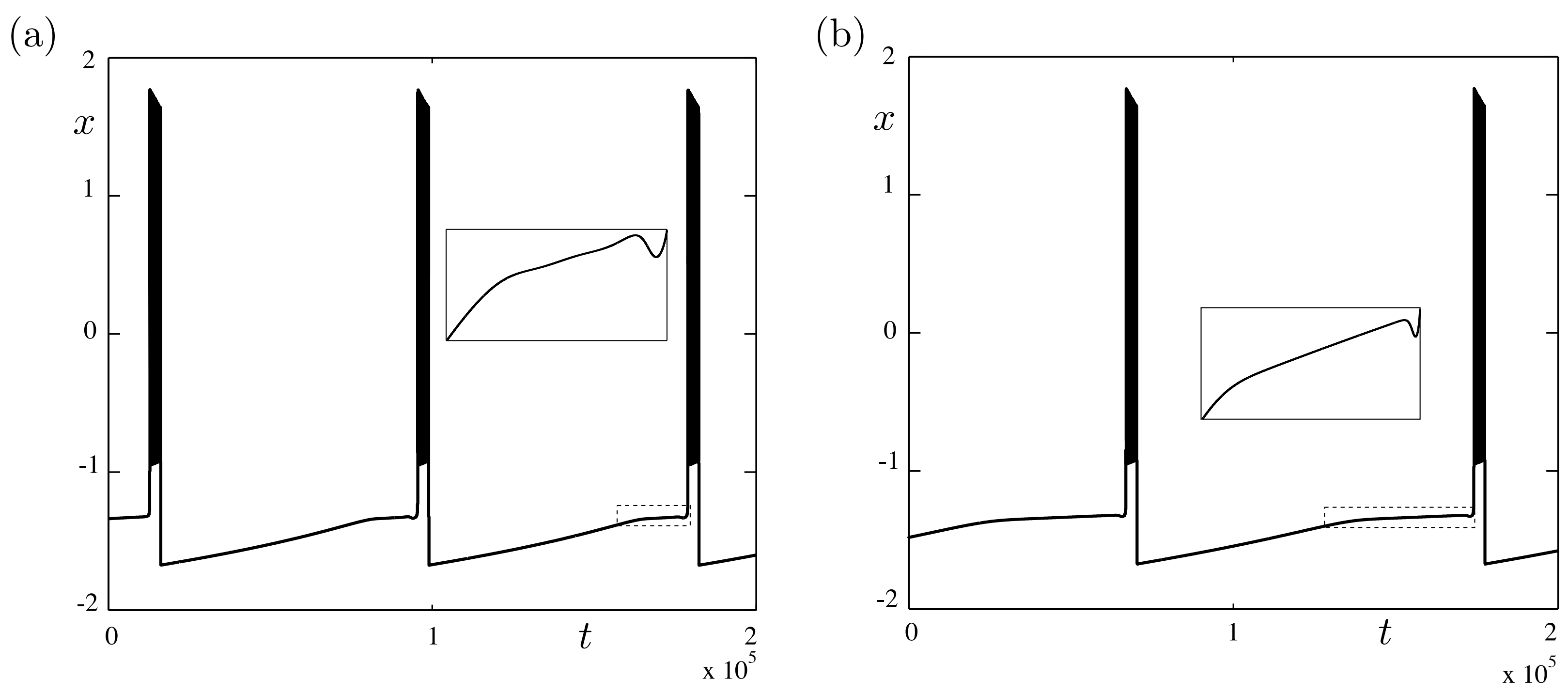
$\varepsilon = 10^{-4}$ $\varepsilon = 10^{-3}$



Reducing the value of epsilon to match theoretical formulas

$$x' = y - ax^3 + bx^2 + I - z$$
$$y' = c - dx^2 - y$$
$$z' = \varepsilon(s(x - x_1) - z)$$
$$I' = \varepsilon(k - h_x(x - x_{\text{fold}})^2 - h_y(y - y_{\text{fold}})^2 - h_I(I - I_{\text{fold}}))$$

$$\varepsilon = 10^{-5}$$



Analysis: canard phenomenon and MMOs

Naive approach: rescaling

We first translate the singularity to the origin:

$$\dot{x} = y - x^2 - \frac{1}{3}x^3$$

$$\dot{y} = \lambda - x \qquad \lambda = a - 1$$

Now rescale:

$$x = \sqrt{\varepsilon}\bar{x}, \qquad y = \varepsilon\bar{y} \qquad \lambda = \sqrt{\varepsilon}\bar{\lambda}$$

Rescaled equations (we drop the bars):

$$\dot{x} = \sqrt{\varepsilon}(y - x^2 - \frac{1}{3}\sqrt{\varepsilon}x^3)$$
$$\dot{y} = \sqrt{\varepsilon}(\lambda - x)$$

After time rescaling:

$$\dot{x} = y - x^2 - \frac{1}{3}\sqrt{\varepsilon}x^3$$
$$\dot{y} = \lambda - x$$

What is the problem?

$$x = \sqrt{\varepsilon}\bar{x}, \qquad y = \varepsilon\bar{y} \qquad \lambda = \sqrt{\varepsilon}\bar{\lambda}$$

If $(\bar{x}, \bar{y})$ were assumed uniformly bounded with respect to ε then the corresponding neighborhood in (x, y) is $O(\varepsilon)$ in size.

Too small for Fenichel theory!

Possible approaches:

Nonstandard analysis

E. Benoît, J.-L. Callot, F. Diener and M. Diener, *Chasse au canard*, Collectanea Mathematica **32** (1-2): 37-119, 1981.

Classical analysis, using stretch variables

W. Eckhaus, *Standard chase on French Ducks*, Springer LNM Vol. **985**: 449-494, 1983

Blow-up

F. Dumortier and R. Roussarie, *Canard cycles and center manifolds*, Memoirs of the American Mathematical Society **121**(577), 1996.

M. Krupa and P. Szmolyan, *Relaxation oscillations and canard explosion*, Journal of Differential Equations **174**(2) 312-368, 2001.

Blow-up

Singular coordinate transformation:

$$\Phi : \mathbb{R}^+ \times \mathbb{S}^4 \mapsto \mathbb{R}^4$$

$$x = r\bar{x}, \quad y = r^2\bar{y}, \quad \varepsilon = r^2\bar{\varepsilon}, \quad \lambda = r\bar{\lambda}$$

-it contains the rescaling

-it covers a neighborhood of fixed size (wrt to ε)

Charts of the blow-up, i.e. charts of the sphere, correspond to parts of the phase space

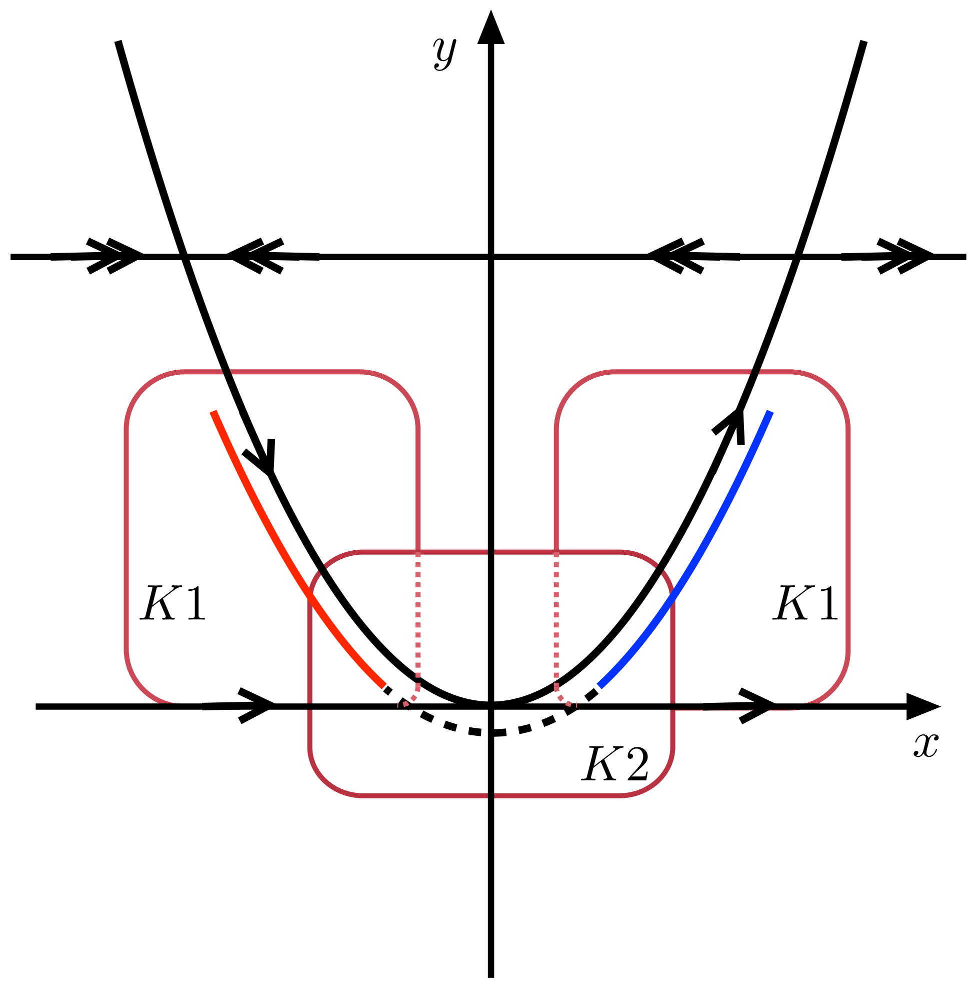


Chart *K1* connects to the slow flow

Chart *K2* is the rescaling

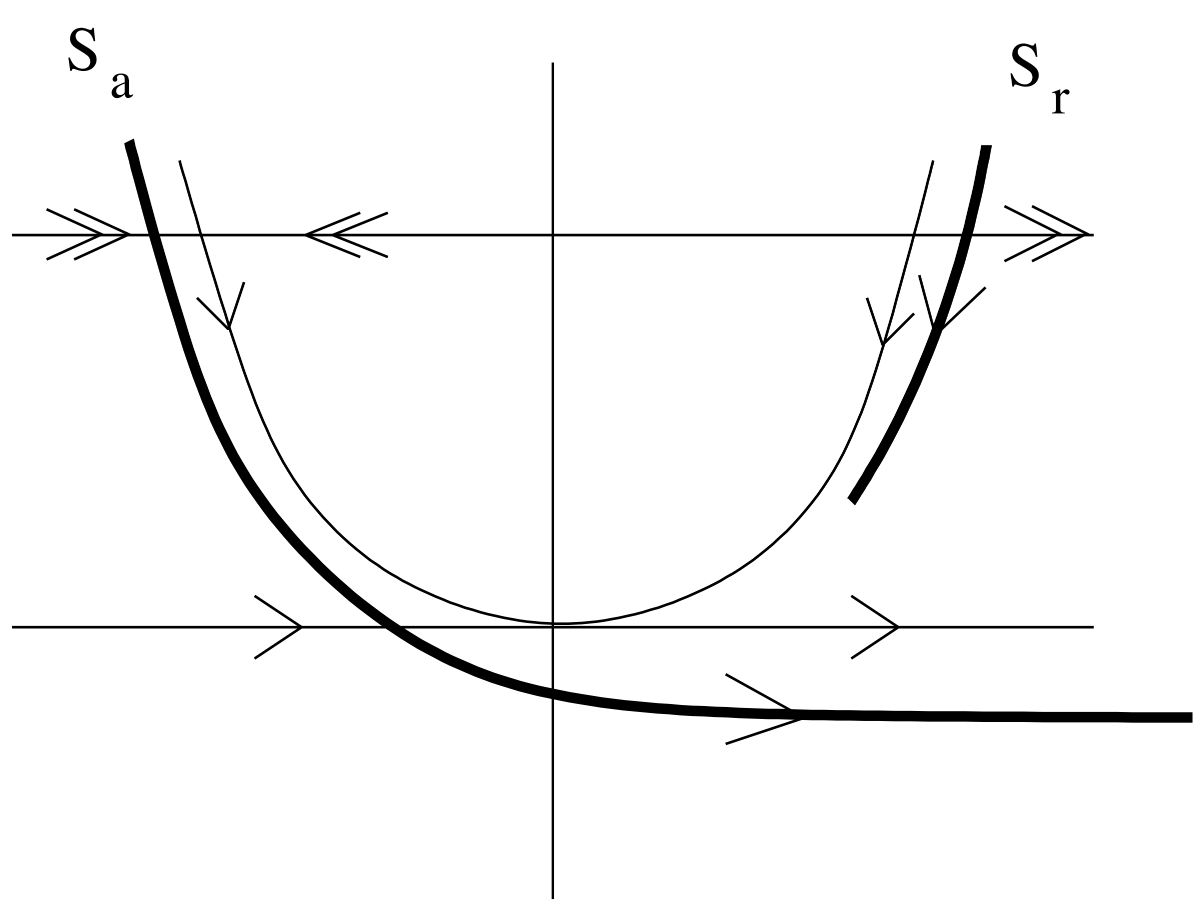
Chart *K3* connects to the fast flow

2D problems lead to 3D problems

Case 1: Simple fold

$$\varepsilon \dot{x} = -y + x^2$$

$$\dot{y} = g(x, y), \qquad g(0,0) < 0.$$

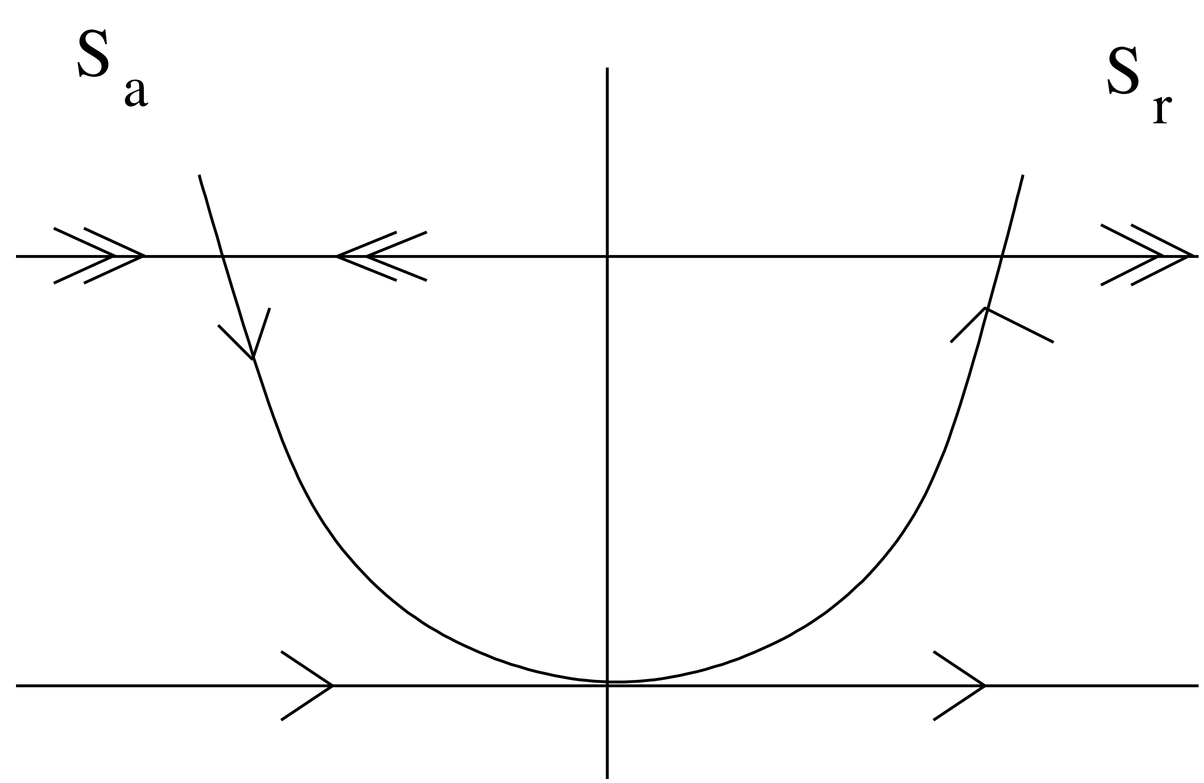


Case II: canard point

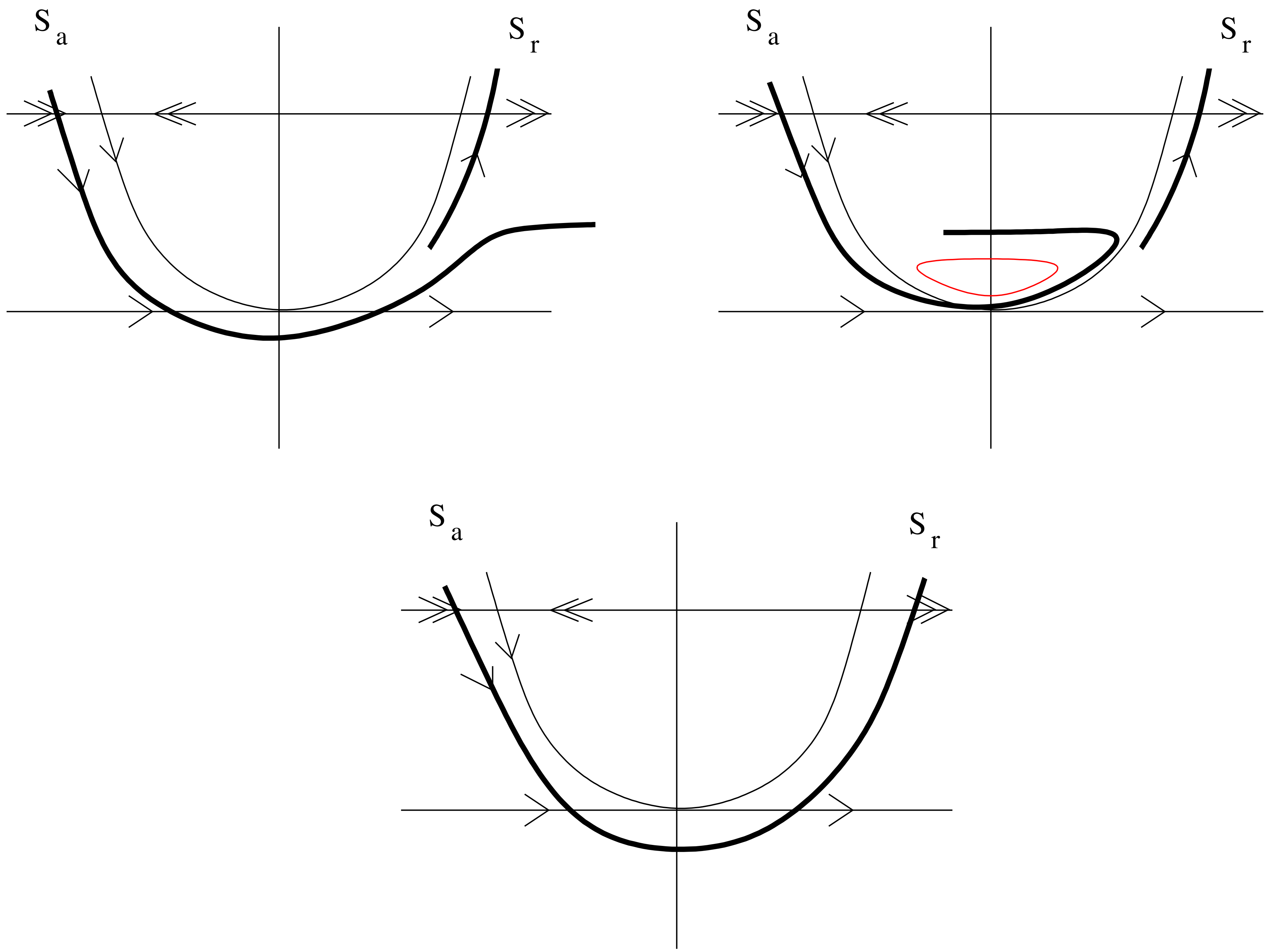
Canard point is a degenerate fold defined by the condition $g(0,0) = 0$ The following equations give an example:

$$\varepsilon \dot{x} = -y + x^2$$

$$\dot{y} = x - \lambda \qquad \lambda \approx 0$$



Unfoldings of a canard point, $\varepsilon > 0$



Case III: folded node (two slow one fast dimensions)

$$\varepsilon \dot{x} = -y + x^2$$

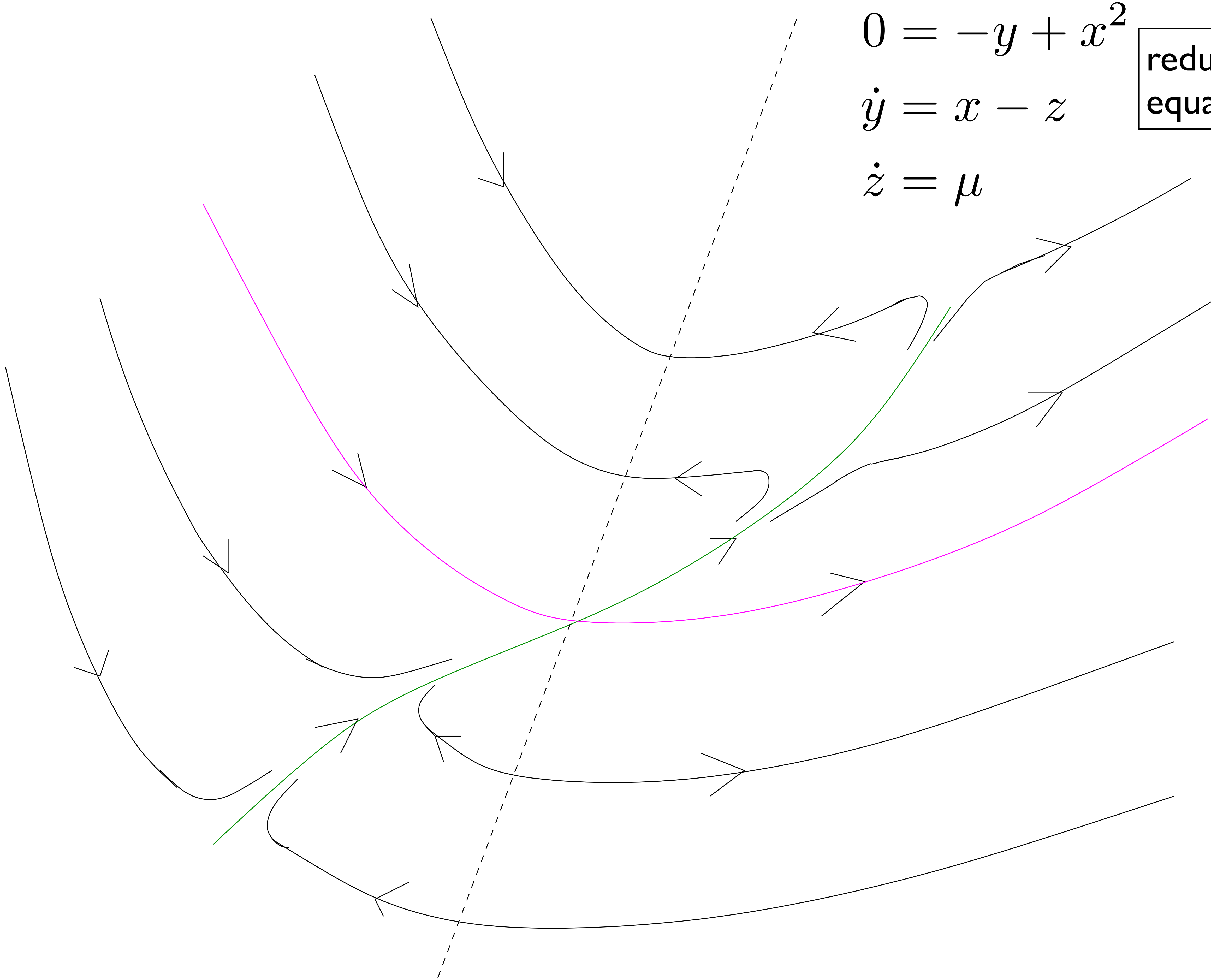
$$\dot{y} = x - z$$

$$\dot{z} = \mu$$

The slow subsystem

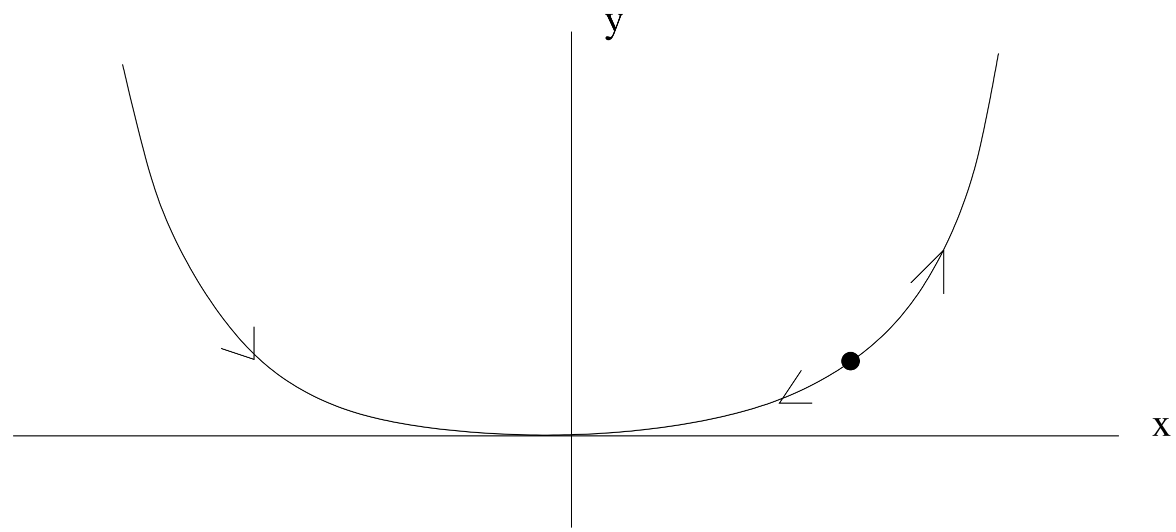
$$0 = -y + x^2$$
$$\dot{y} = x - z$$
$$\dot{z} = \mu$$

reduced equations

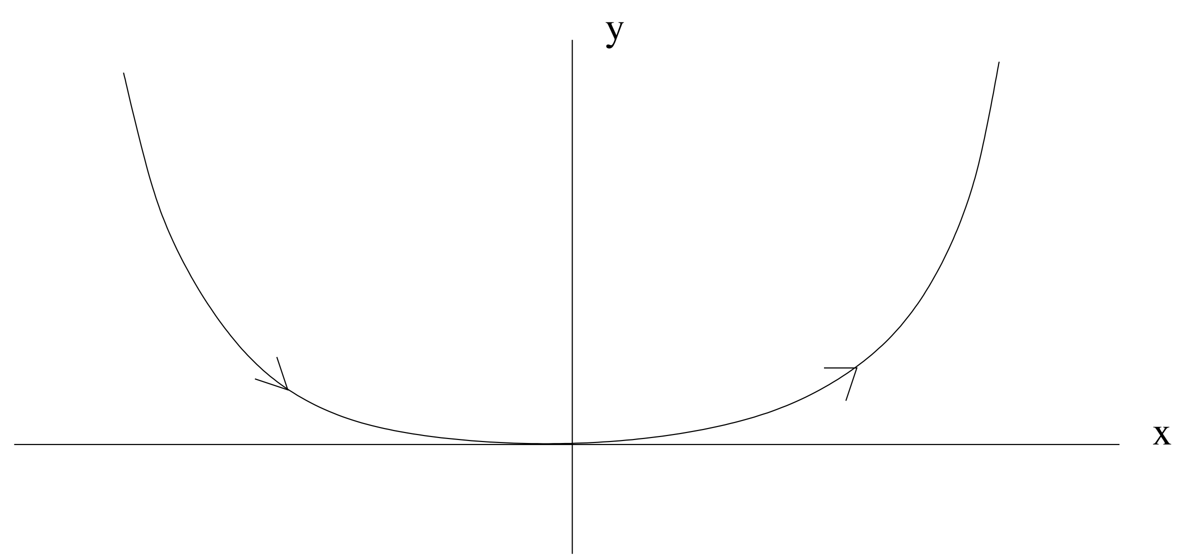


Explanation: λ unfoldings of a canard point

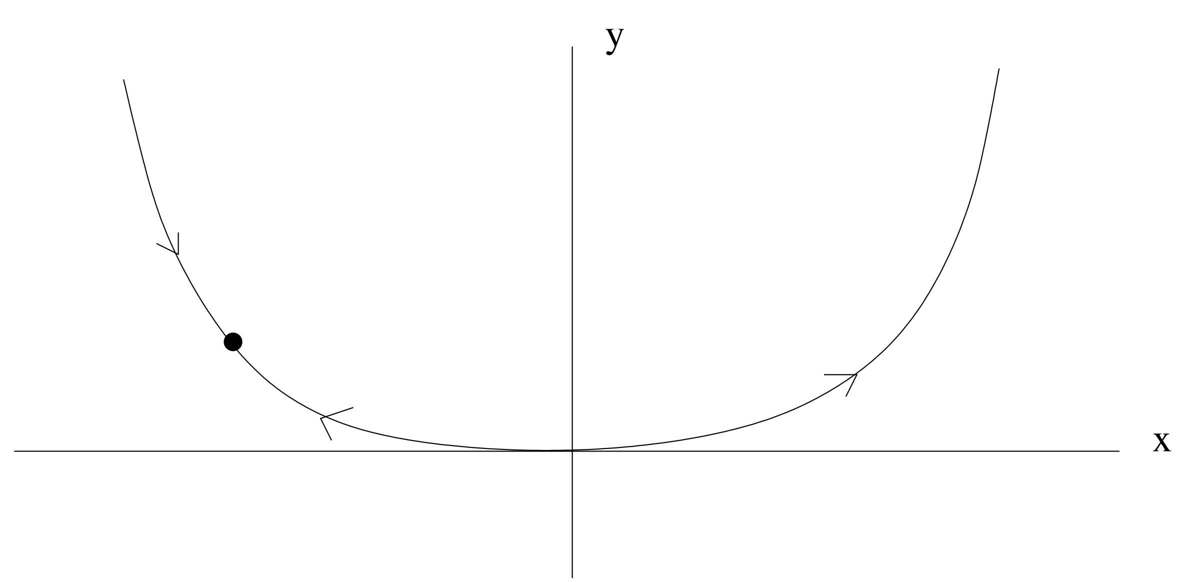
$\lambda > 0$



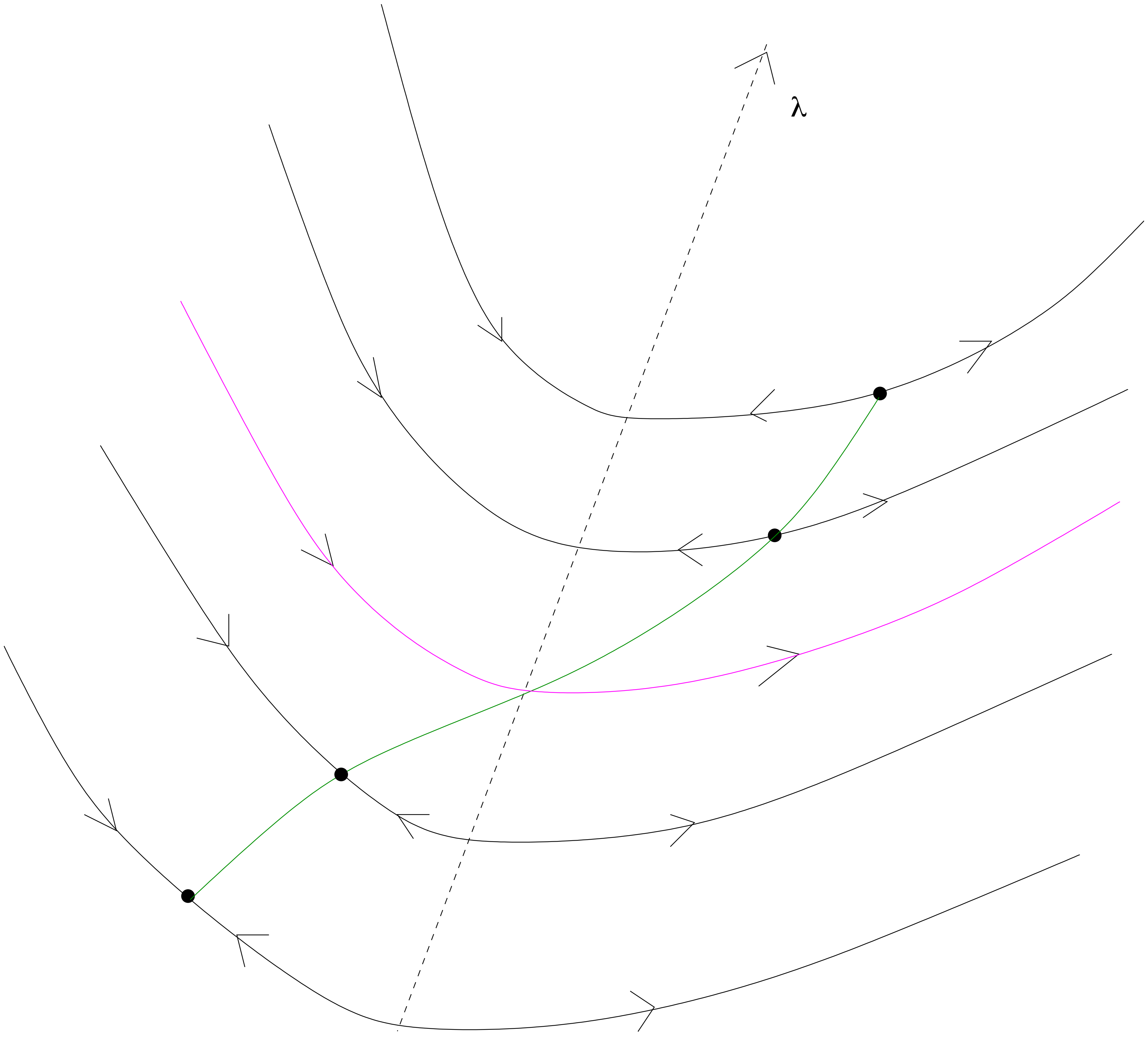
$\lambda = 0$



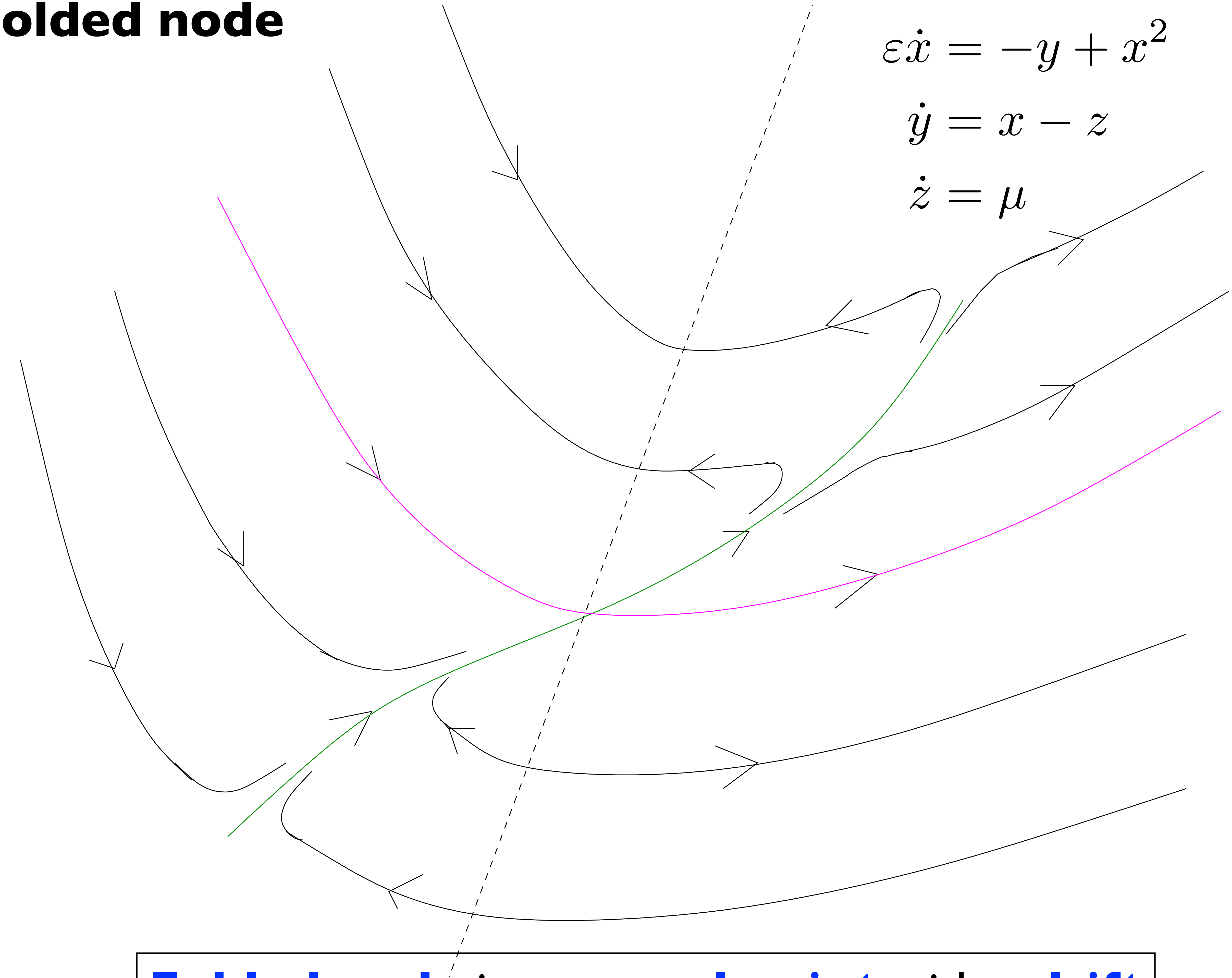
$\lambda < 0$



Explanation: λ unfoldings of a canard point



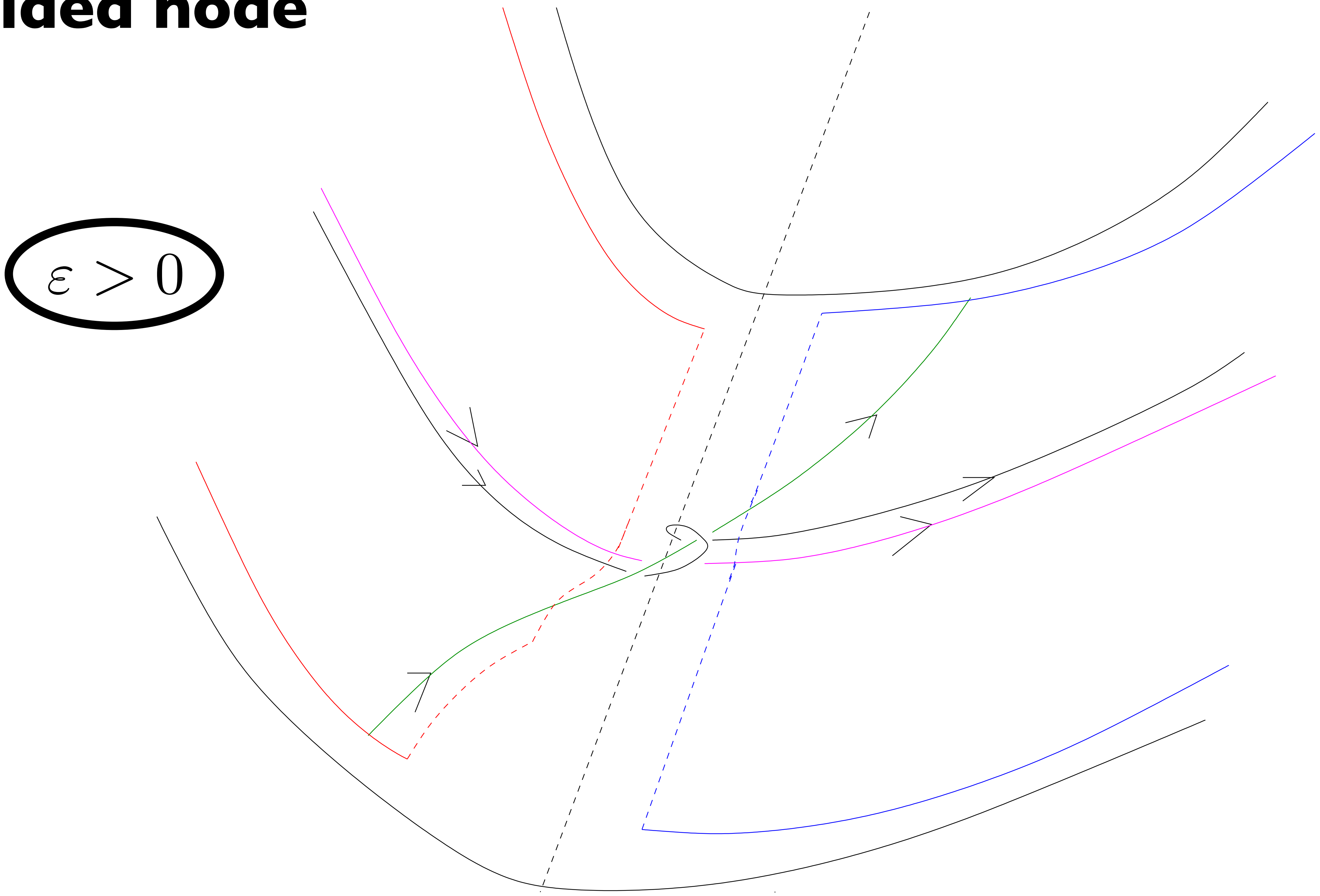
Folded node



$$\varepsilon \dot{x} = -y + x^2$$
$$\dot{y} = x - z$$
$$\dot{z} = \mu$$

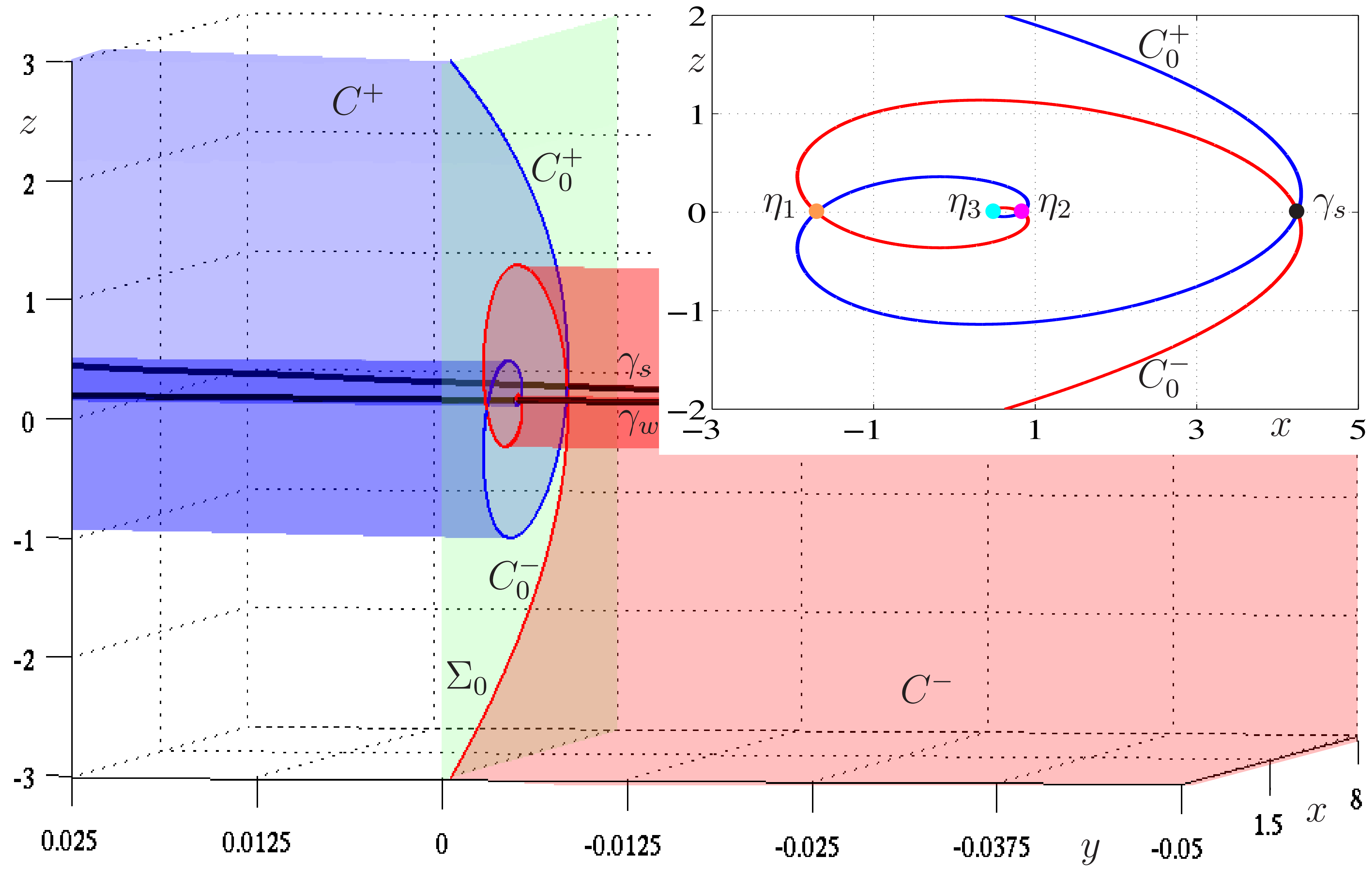
Folded node is a **canard point** with a **drift**

Folded node



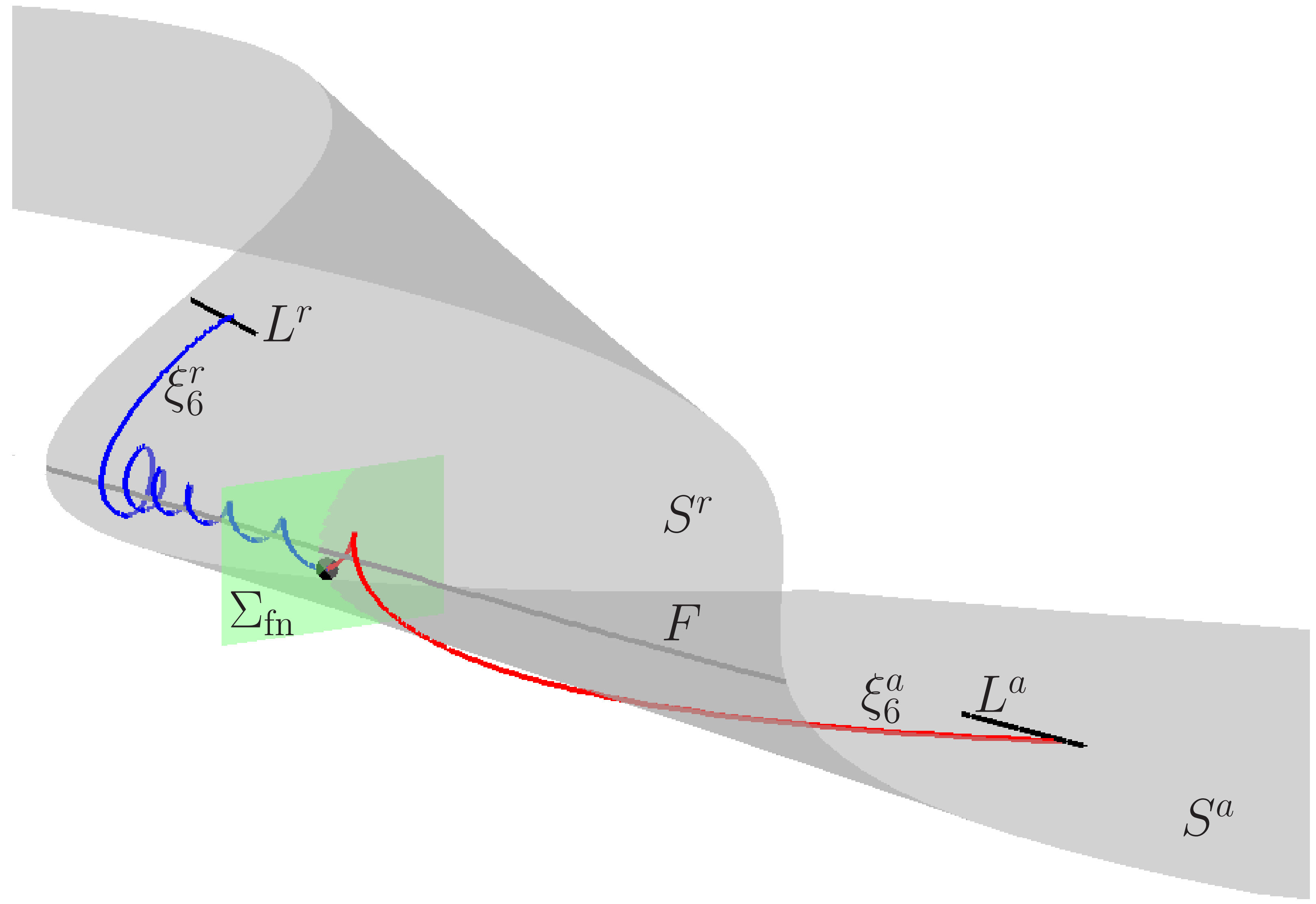
The green trajectory and the magenta trajectory are called **primary canards**
The black trajectory is a **secondary canards**

Computed slow manifolds and canards



computed by Mathieu Desroches

Secondary canard obtained by continuation



computed by Mathieu Desroches

Selected references on folded node

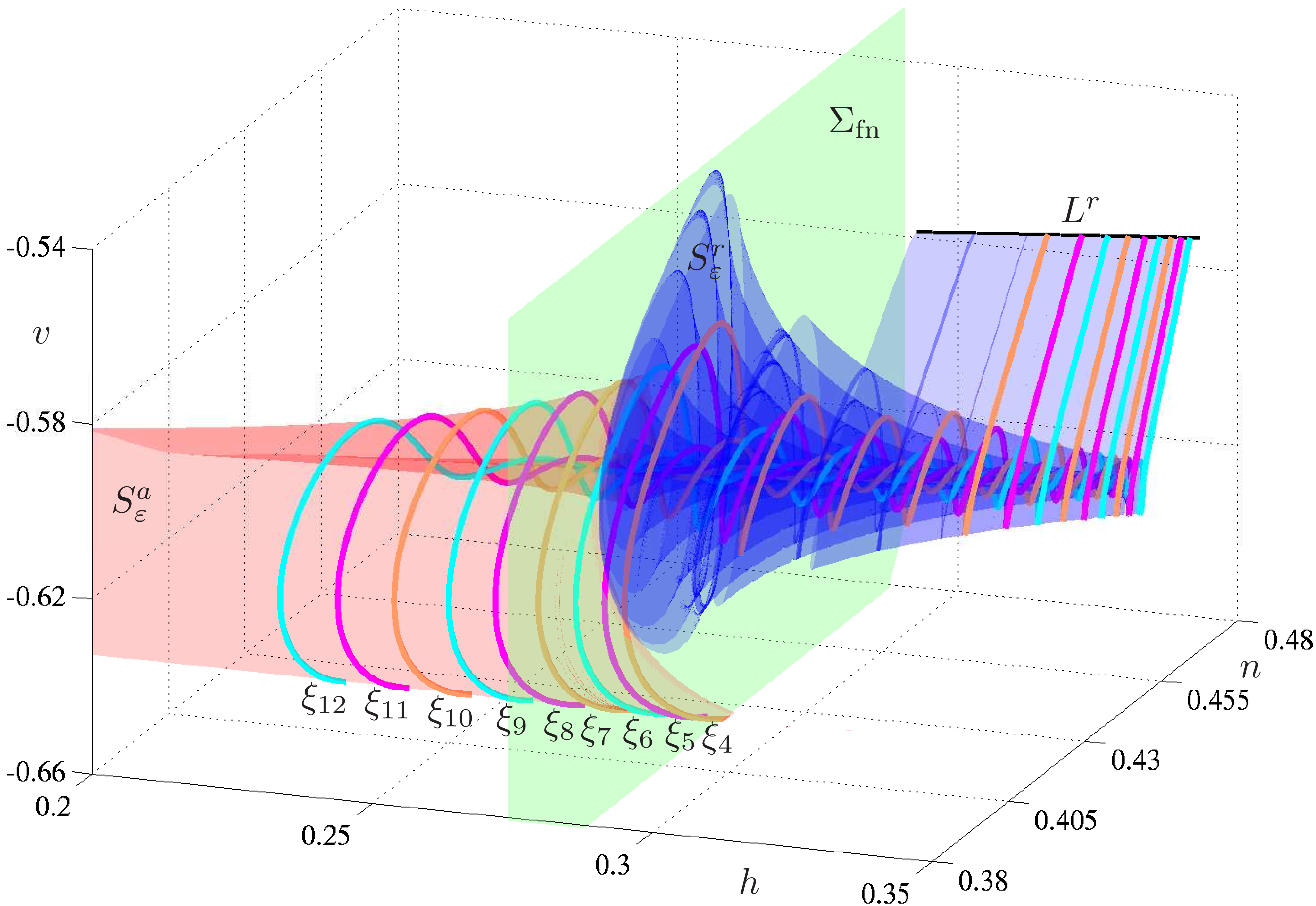
E. Benoît, *Canards et enlacements*,
Publications Mathématiques de l'IHES **72**(1): 63–91, 1990.

P. Szmolyan and M. Wechselberger, *Canards in* $\mathbb{R}^3$,
Journal of Differential Equations **177**(2): 419-453, 2001.

M. Wechselberger, *Existence and bifurcations of canards in* $\mathbb{R}^3$ *in the case of the folded node*,
SIAM Journal on Applied Dynamical Systems **4**(1): 101-139, 2005.

M. Brøns, M. Krupa and M. Wechselberger, *Mixed-mode oscillations due to the generalized canard phenomenon*, in Bifurcation Theory and spatio-temporal pattern formation, Fields Institute Communications vol. **49**, pp. 39-63, 2006.

Multiple secondary canards



Computed by M. Desroches

References on secondary canards

M. Wechselberger, *Existence and bifurcations of canards in* $\mathbb{R}^3$ *in the case of the folded node*, SIAM Journal on Applied Dynamical Systems **4**(1): 101-139, 2005.

M. Krupa, N. Popovic and N. Kopell, *Mixed-mode oscillations in the three time-scale systems: A prototypical example*, SIAM Journal on Applied Dynamical Systems **7**(2): 361-420, 2008.

M. Krupa and M. Wechselberger, *Local analysis near a folded saddle-node singularity*, Journal of Differential Equations **248**(12): 2841-2888, 2010.

M. Krupa, A. Vidal, M. Desroches and F. Clément, *Multiscale analysis of mixed-mode oscillations in a phantom bursting model*, SIAM Journal on Applied Dynamical Systems (2012)

Torus canards: transition from spiking to bursting

(related to discrete canards?)

Early work by Izhikievich, *SIAM Review*, **43**, 315-344, 2001.

Canonical system:

$$\dot{z} = (u + i\omega)z + 2z|z|^2 - z|z|^4 + \ldots$$
$$\dot{u} = \varepsilon(a - |z|^2) + \ldots$$

Canard explosion for amplitude equations

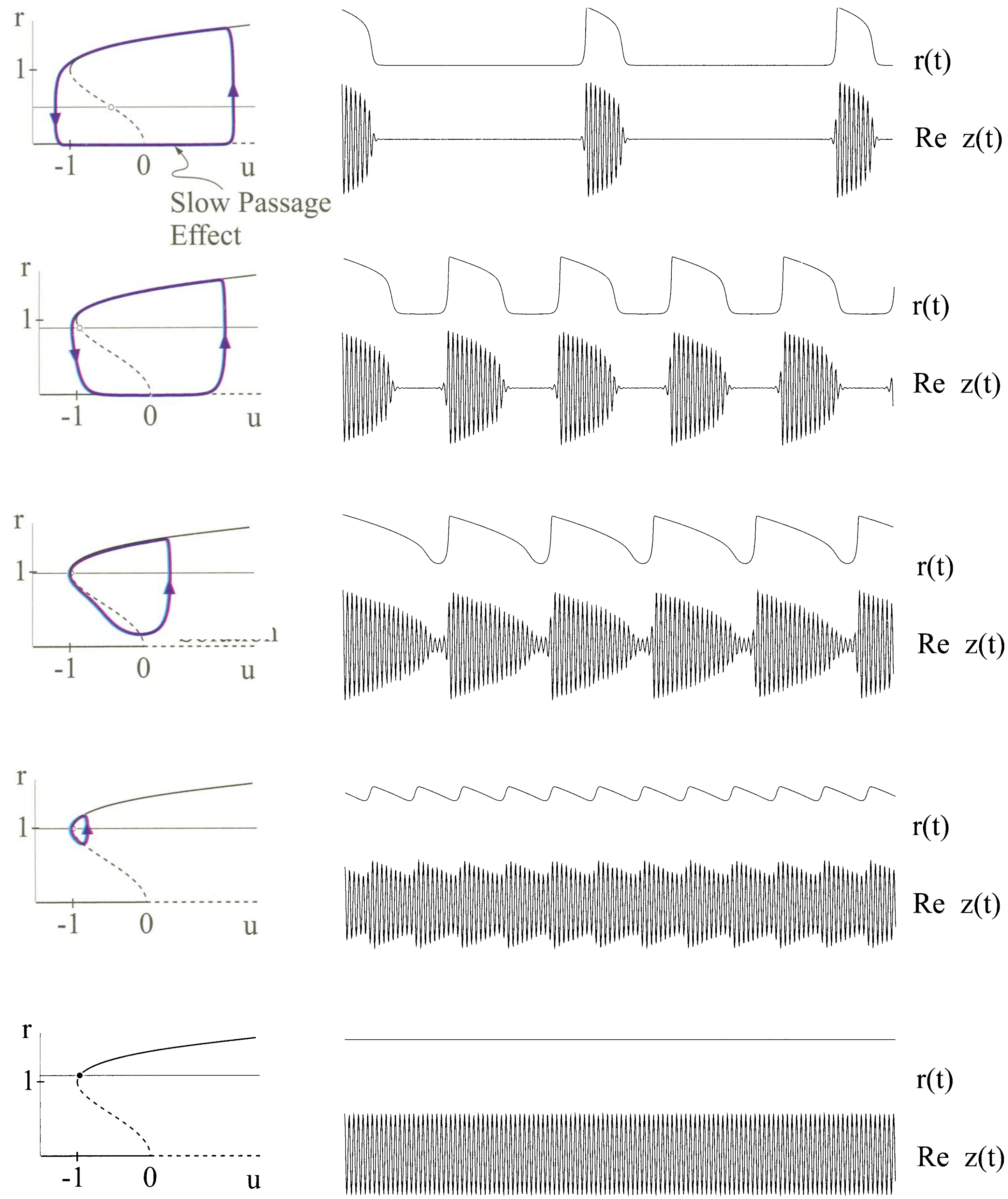
Transition from bursting to spiking

bursting: relaxation oscillation

modulated spiking: canard with head

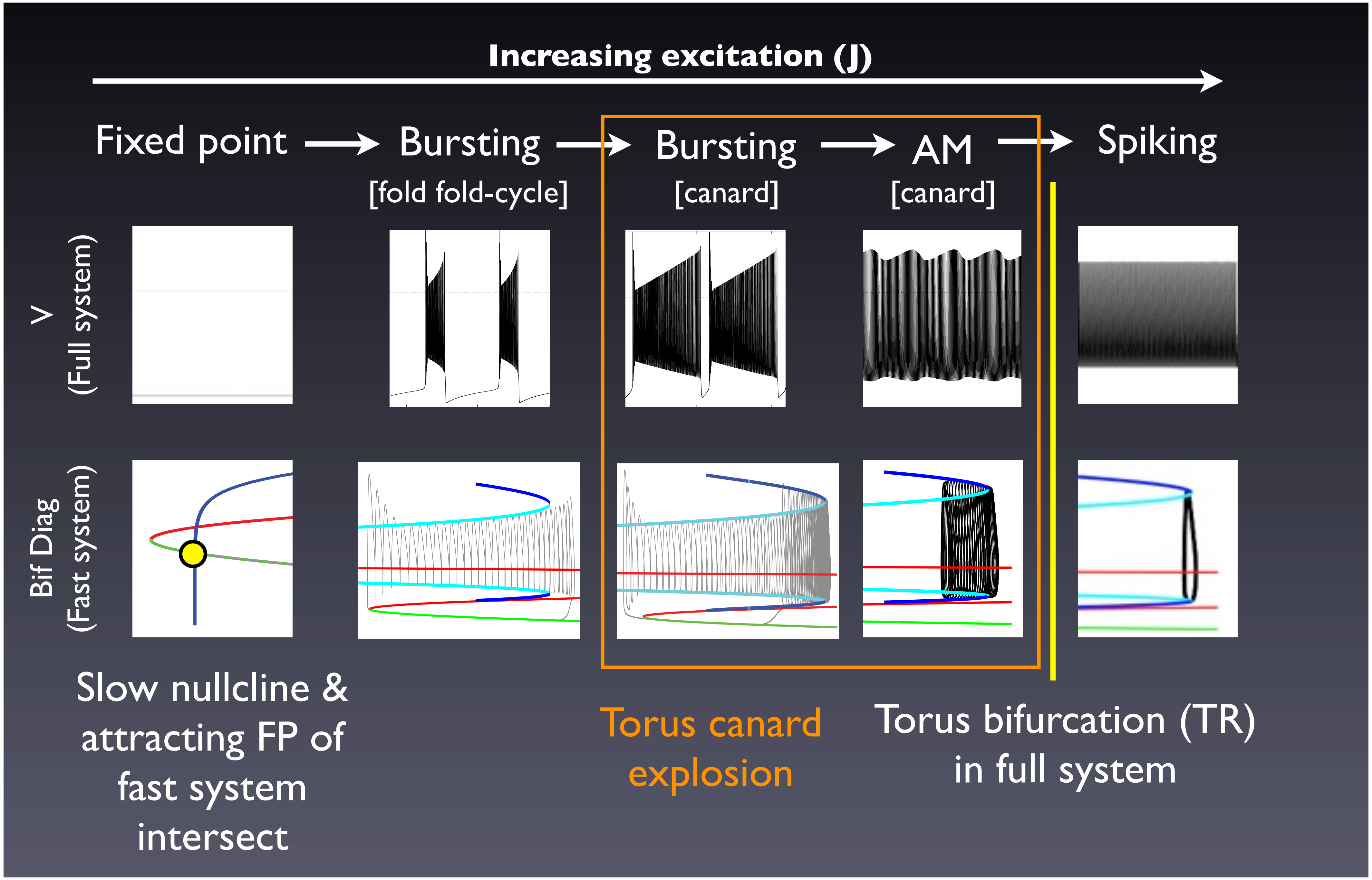
modulated spiking: small canard

fast spiking



Activity of a Purkinje cell

Burke, Barry, Kramer, Kaper, Desroches



Other directions

- Extensions to infinite dimensions, delay eqs, PDES

  Krupa, Touboul

- Fine aspects of the dynamics, e.g. chaotic MMOs

  Krupa, Popovic, Kopell, *SIADS* 2008

- Systems with more than two timescales

  Krupa, Vidal, Desroches, Clémént, *SIADS* 2012

- Noise driven canards

  Touboul, Krupa, Desroches, submitted 2013

- Networks of canard oscillators, synchronization
- Canards in boundary value problems
- Torus canards?