Complex Oscillations: Mixed Modes and Bursting

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Introduction

Dynamical systems theory as framework for organizing empirical time series data

- Upsurge in 1970's: chaos in fluids, lasers, chemical reactions
- Bifurcation diagrams for dependence of attractors on parameters
    - Routes to chaos
    - Bifurcations of codimension two in multi-parameter studies

Recent work uses theory of multiple time scale systems to provide context for explaining complex oscillations

Outline

- Examples of empirical observations
- Analysis of bursting: $n \to n + 1$ spikes
- Local behavior of slow-fast systems yielding MMOs

Belousov-Zhabotinksii Reaction

Hudson, Hart, Marinko (1979) J. Chem. Phys. 71:1601-1606
Homogeneous stirred tank reactor varying flow rate

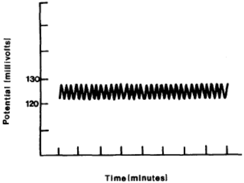


FIG. 11. Recording from bromide ion electrode; T = 25 °C; flow rate = 5.42 ml/min; Ce^{+3} catalyst.

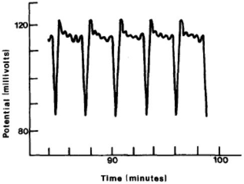


FIG. 9. Recording from bromide ion electrode; T = 25 °C; flow rate = 4.81 ml/min; Ce^{+3} catalyst.

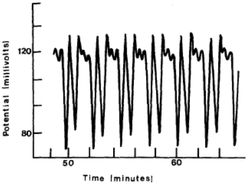


FIG. 12. Recording from bromide ion electrode; T = 25 °C; flow rate = 3.99 ml/min; Ce^{+3} catalyst.

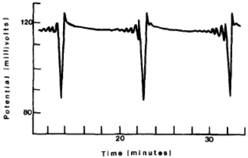
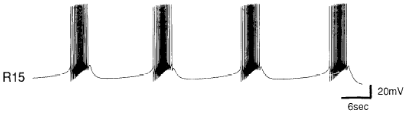


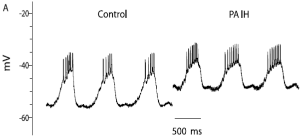
FIG. 10. Recording from bromide ion electrode; T = 25 °C; flow rate = 5.37 ml/min; Ce^{+3} catalyst.

Bursting and MMOs in Neurons

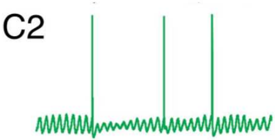
Aplysia R15 Cell (Alevois et al. 1991)



Stomatogastric PD Neuron (Zhang et al. 2003)

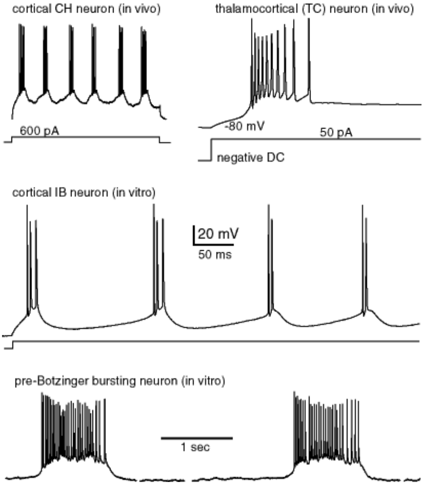


Inferior olive subthreshold oscillations (Khosravani et al. 2007)



More Bursting Neurons

Izhikevich: Scholarpedia



Multiple Time Scales in Bursting

Hodgkin-Huxley equations describe action potential

- ODEs have membrane potential and “gating” variables of channels
- Time constant of sodium current activation $\sim$ 1msec
- Time constants of sodium inactivation and potassium currents $\sim$ 10msec

Slower calcium currents underlie bursting in R15

- First models by Richard Plant
- Rinzel: first explicit connection with slowly varying systems

Bursting viewed as alternation between stable equilibria and stable periodic orbits in fast subsystems

Classification of Bursting: Individual Neurons

Biological perspective (Rinzel)

- Characterize slow currents
- Membrane potential of equilibria vs. spike burst minima
- Interspike intervals (increasing, decreasing, “parabolic“)
- Amplitudes of spikes

Mathematical perspective

- Bifurcations that initiate and terminate of burst
- Izhikevich: 4×4 matrix of possibilities
- Asymptotics of interspike intervals fit to bifurcations

What are bifurcations *between* bursting orbits

Morris-Lecar as Model System

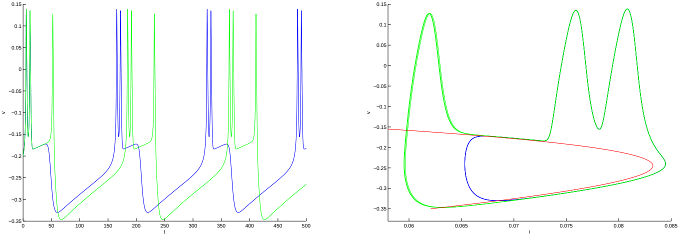
$$\dot{v} = i - 0.5(v + 0.5) - 2w(v + 0.7) - 0.5(1 + tanh(\frac{v - 0.1}{0.145})(v - 1)$$

$$\dot{w} = 1.15(0.5(1 + tanh(\frac{v + 0.1}{0.15}) - w)cosh(\frac{v - 0.1}{0.29})$$

$$\dot{i} = \varepsilon(k - v)$$

- Model derived from studies of barnacle muscle
- Slow equation is ad hoc
- Asymptotics of interspike intervals identify slow-fast transitions
- Terman: analysis of transitions from $n \to n + 1$ spikes/burst

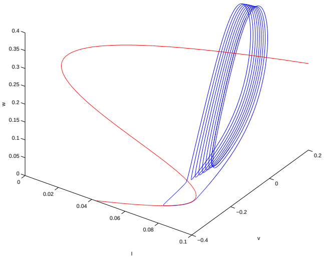
Bursting Oscillation

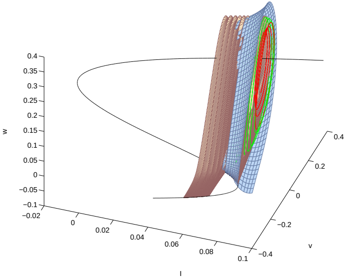


Bistable system with periodic orbits having 2/3 spikes per burst

Bifurcation diagram of Morris-Lecar model

Trajectories of full and ”frozen“ system



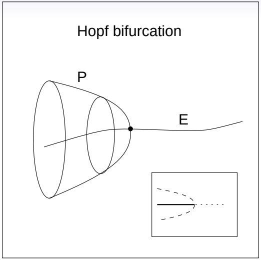


Death of Periodicity

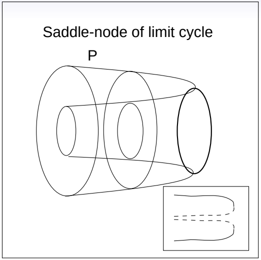
Dynamical mechanisms for death of oscillations

- Hopf bifurcation
- Saddle-nodes of limit cycles
- Equilibrium saddle-node in limit cycle
- Homoclinic bifurcation

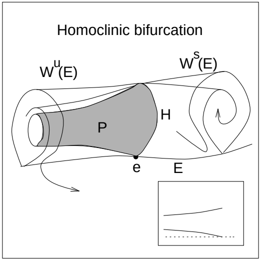
SNIC's and Homoclinic bifurcation have unbounded periods


Hopf bifurcation
P
E

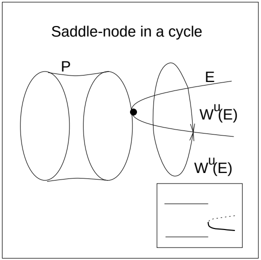
a


Saddle-node of limit cycle
P

b


Homoclinic bifurcation
$W^u(E)$
$W^s(E)$
H
P
e
E

c


Saddle-node in a cycle
P
E
$W^u(E)$
$W^u(E)$

d

Aysmptotics of Interspike Intervals

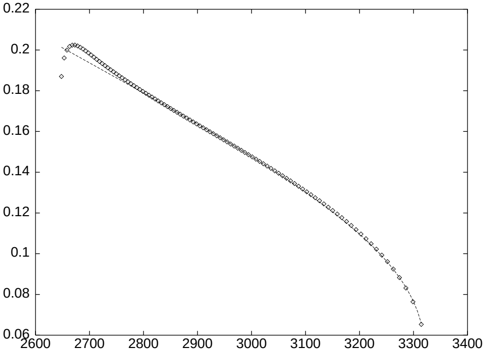
SNIC

- Singular perturbation model: $\dot{x} = \epsilon t + ax^2$
- In slowly varying system, frequency declines like $\epsilon^{1/2}(t_c - t)^{1/2}$
- Final cycle occurs for $(t_c - t) \approx \epsilon^{2/3}$

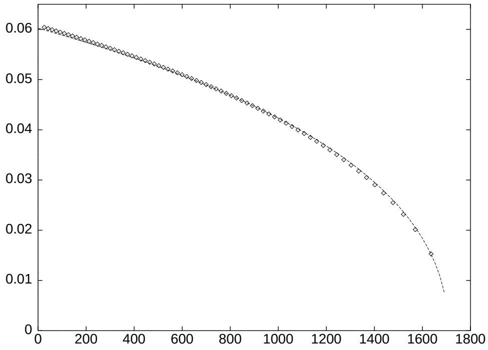
Homoclinic bifurcation

- Homoclinic orbit: trajectory tending to hyperbolic saddle as $t \to \pm\infty$
- Bistability and hysteresis in frozen system
- Frequency proportional to $-1/\ln \epsilon$

Interspike Intervals: Homoclinic Death

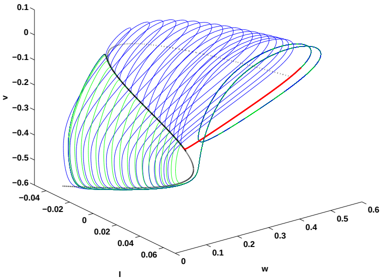


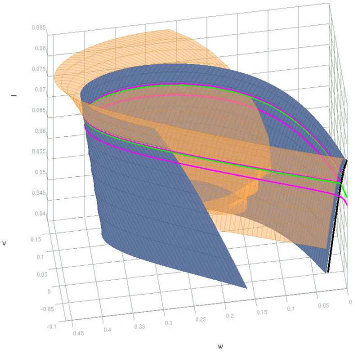
Interspike Intervals: SNIC Death



Computing Slow Manifolds of Saddle Type

Boundary value solver locates slow manifold of ML system





Initial value solver used to compute stable and unstable manifolds

Normally Hyperbolic Slow Manifolds

$$\begin{aligned} \varepsilon \dot{x} &= f(x,y) \qquad x \in R^m \\ \dot{y} &= g(x,y) \qquad y \in R^n \end{aligned}$$

- Critical manifold: $f(x,y) = 0$
- Slow flow: $\dot{y} = g(h(y),y)$ where $f(h(y),y) = 0$
- *Fenichel Theory*: Existence of slow manifolds when $f = 0$ normally hyperbolic
- Uniqueness up to exponentially small terms
- *Candidates*: Singular limits of trajectories
  - Approach along strong stable manifold
  - Follow slow flow on critical manifold
  - Depart along strong unstable manifold

Algorithms for Slow Manifolds of Saddle Type

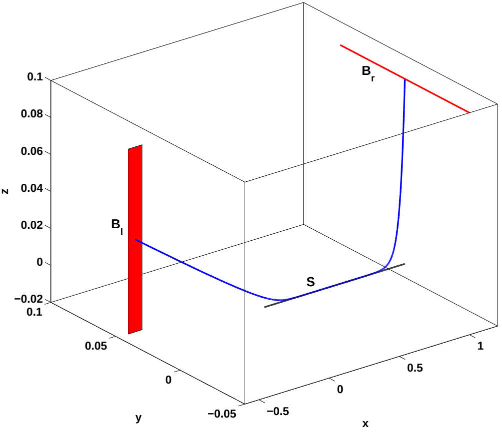
Challenges

- Initial value solvers won't track manifold in forward or backward time
- Boundary conditions yielding points on manifold are unknown
- Manifolds are located distance $O(\varepsilon)$ from critical manifold

Boundary Value Strategy

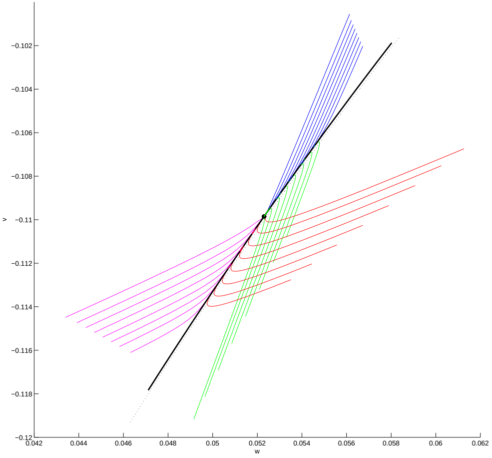
- Choose boundary values (almost) orthogonal to flow
- Include segments of arrival and departure
- Respect transversality to attracting and repelling manifolds of slow manifold
- Use simple collocation scheme

Boundary Conditions for Slow Manifold of Saddle Type



Slow Manifold Accuracy

- Test accuracy by integrating trajectories that straddle numerical slow manifold in attracting and repelling directions
- Distance from slow manifold is $10^{-4} - 10^{-11}$
- Fast instability in both forward and backward directions



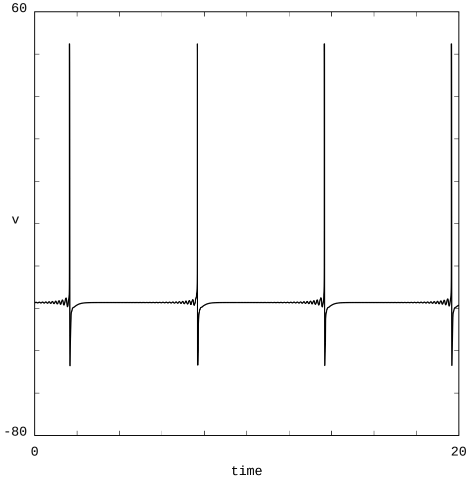
Mixed Mode Oscillations

Multiple mechanisms

- Alternation between two limit cycle families of fast subsystems
- Subcritical Hopf bifurcation produces oscillations of growing amplitude
- "Local” mechanisms that produce small amplitude oscillations
  - Folded nodes
  - Singular Hopf bifurcations

Subcritical Hopf Bifurcation

- Guckenheimer, Harris-Warrick, Peck and Willms study of interspike intervals
- 14 dimensional model of STG LP neuron
- Trajectories funneled toward equilibrium: saddle with complex eigenvalues having small positive real parts



Slow-Fast Systems: "Desingularized" Slow Flow

$$\begin{aligned} \varepsilon \dot{x} &= f(x,y) \\ \dot{y} &= g(x,y) \end{aligned}$$

- Solve $f = 0$ for x except at **folds**: $\det(f_x) = 0$
- Vector (v, w) is tangent to critical manifold if $f_x v + f_y w = 0$
- Derive slow flow tangent to critical manifold with projection parallel to g if
$$-f_x^\dagger f_y g \partial_x + \det(f_x) g \partial_y$$
($f_x^\dagger = 1$ when there is only one fast variable)
- **Normal crossing condition**: $-f_x^\dagger f_y g \neq 0$ on fold
- **Folded Singularities**: failure of normal crossing conditions

Example: Forced van der Pol Equation

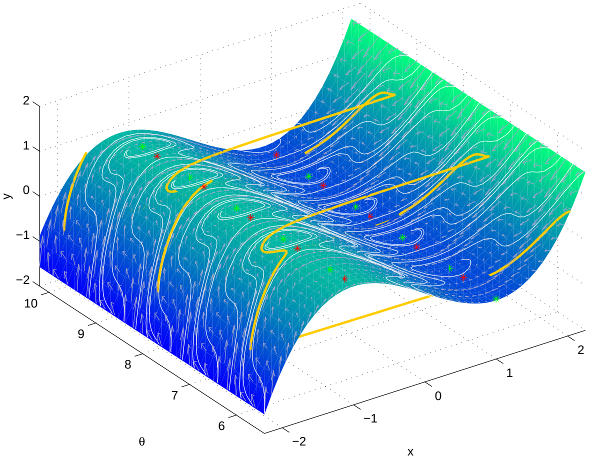
The original system in which dissipative chaos was discovered and analyzed by Cartwright and Littlewood

$$\begin{aligned} \varepsilon\dot{x} &= y + x - \frac{x^3}{3} \\ \dot{y} &= -x + a\sin(2\pi\theta) \\ \dot{\theta} &= \omega \end{aligned}$$

Slow flow

$$\begin{aligned} \theta' &= \omega(x^2 - 1) \\ x' &= -x + a\sin(2\pi\theta) \end{aligned}$$

Phase Portrait: Forced van der Pol Equation



Two Slow Variables: Folded Singularities

Fold curve $f_x = 0$: assume $f_{xx} \neq 0$ and $f_y g = 0$

- Model equations for generic **folded singularities**

$$\begin{aligned} \varepsilon \dot{x} &= y - x^2 \\ \dot{y} &= -z \pm x \\ \dot{z} &= a \end{aligned}$$

- Slow flow

$$\begin{aligned} \dot{x} &= -z \pm x \\ \dot{z} &= 2ax \end{aligned}$$

- Rescale $(x, y, z, t) = (\varepsilon^{1/2} X, \varepsilon Y, \varepsilon^{1/2} Z, \varepsilon^{1/2} T)$ to set $\varepsilon = 1$
- $a < 0$: saddle; $a < 0$: node; $0 < a < 1/8$: focus $1/8 < a$
- Minus sign gives stable equilibrium

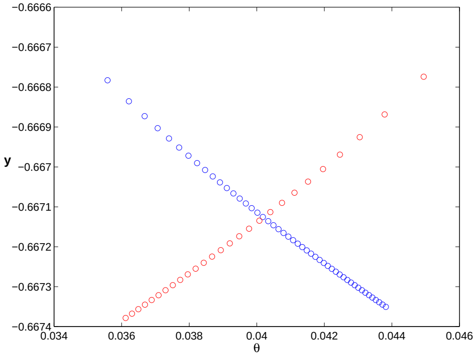
Folded Nodes and Saddles

Analysis of Normal Forms

- Maximal canards are quadratic functions of t
- Saddles: slow stable and unstable manifolds along canard intersect transversally at $z = 0$ with angle $O(\varepsilon)$.
- Nodes
  - Rotations around maximal canard, number increases as $|a|$ decreases
  - Slow flow: linear vector field with sector approaching folded node
  - $|a|$ small gives slowly varying vector fields for (x, y): Wallet "tourbillon"

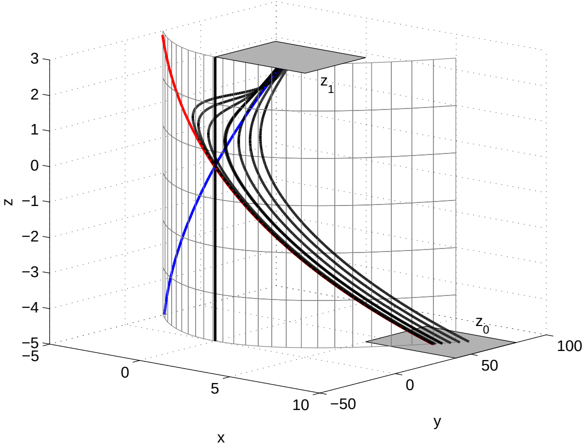
New numerical computations of flow maps

Intersection of Slow Stable and Unstable Manifolds



Intersections of slow stable and unstable manifolds of Forced van der Pol system with plane $x = 1$. Parameters $(a, \omega, \varepsilon) = (4, 1.55, 0.0001)$.

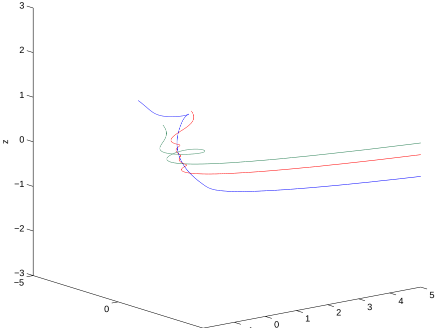
Canard Trajectories at Folded Saddle



Trajectories follow separatrix of folded saddle onto the unstable sheet of the slow manifold and then jump back to the stable sheet

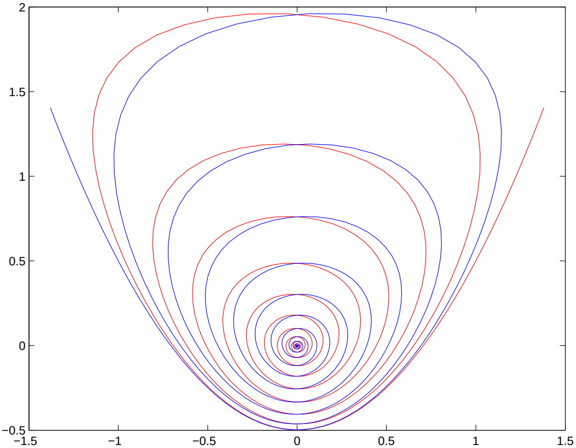
Folded Nodes

Folded nodes induce small scale oscillations of trajectories



Folded node normal form (a=0.03)

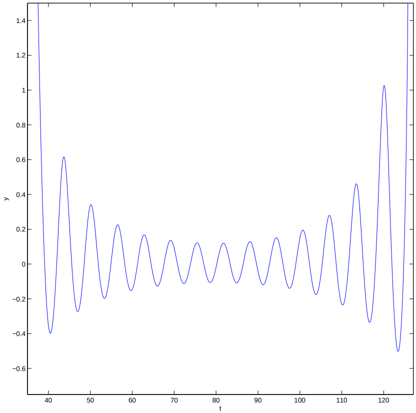
Folded Node Slow Manifold Intersections



Intersection with plane passing through folded node orthogonal to fold curve

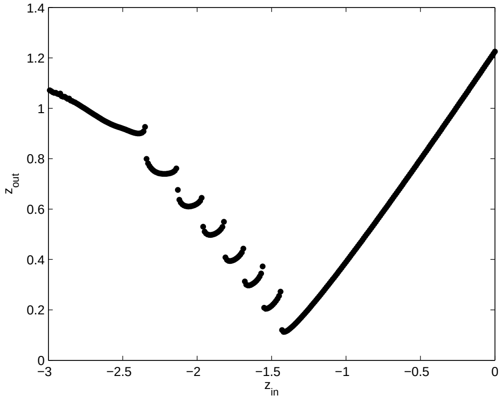
Small amplitude oscillations at folded node

Normal form equation



Three time scales produce more small oscillations

Flow Map past Folded Node



z_{out} vs. z_{in} for segment $(x, y) = (50, 500)$ to $x = -20$, $(a = 0.03)$

Chaotic MMOs via Folded Nodes

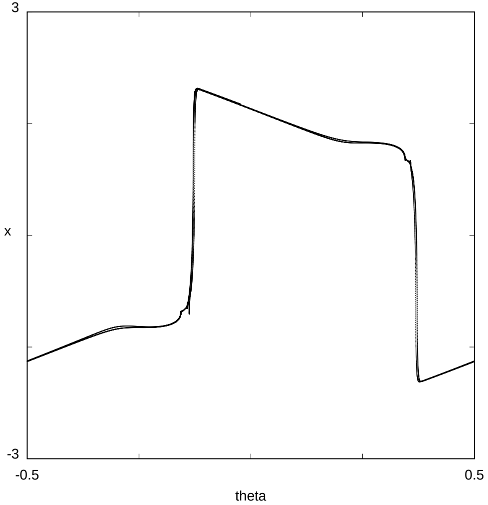
$$\varepsilon\dot{x} = y + x - \frac{x^3}{3}$$
$$\dot{y} = -x + a\sin(2\pi\theta)$$
$$\dot{\theta} = b + \omega\left(1 - \frac{1}{1 + (x^2 - 1)^2}\right)$$

Modification of Forced van der Pol equation

- $\dot{\theta}$ increases with distance to fold lines
- Folded nodes with increased linking as $b \to 0$ ($a > 1$)

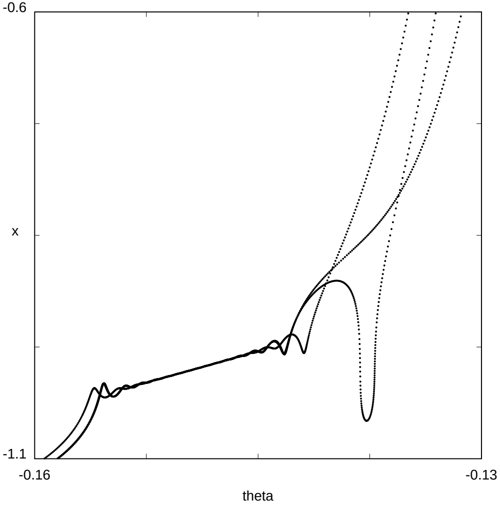
Compare with behavior of flow maps in folded node normal form

Trajectory: Modified Forced van der Pol



$$(a, b, \omega, \varepsilon) = (1.24, 0.001, 0.5, 0.01)$$

Trajectory Detail: Modified Forced van der Pol



$(a, b, \omega, \varepsilon) = (1.24, 0.001, 0.5, 0.01)$

Singular Hopf bifurcation

Truncated normal form

$$\begin{aligned} \varepsilon\dot{x} &= y - x^2 \\ \dot{y} &= z - x \\ \dot{z} &= -\mu - ax - by - cz \end{aligned}$$

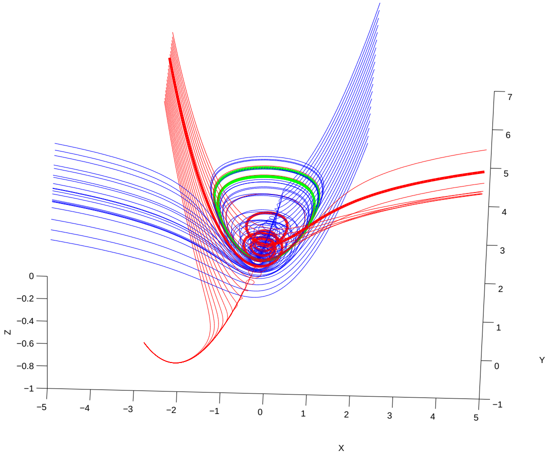
- Hopf bifurcation when $\mu = -(a + c)x - bx^2$ and

$$a + 2xb - 2xc^2 - \varepsilon(2x + 2x^2c + bc) - 2\varepsilon^2 xb = 0$$

- Period-doubling and torus bifurcations of periodic orbits possible
- Important invariant manifolds
  - Stable and unstable manifolds of equilibrium point
  - Attracting and repelling manifolds

Intersecting Invariant Manifolds

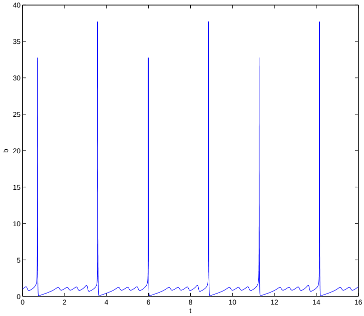
Mixed mode oscillations occur when repelling slow manifold and unstable manifold of equilibrium point intersect



Autocatalator

$$\dot{a} = \mu(\kappa + c) - ab^2 - a$$
$$\varepsilon\dot{b} = ab^2 + a - b$$
$$\dot{c} = b - c$$

- System studied by Petrov et al. and Milik and Szmolyan
- Mixed mode oscillations: periodic and chaotic
- Singular Hopf bifurcation as mechanism



Summary

Complex oscillations are a byproduct of multiple time scales in dynamical systems

- Bursting: alternation between equilibrium and oscillatory behavior
- Mixed modes: alternation between oscillations of large and small amplitude
- Bifurcations of singular limit layer equations locate transitions in slow-fast decomposition of trajectories
- Small oscillations result from local mechanisms
    - Folded nodes
    - Singular Hopf bifurcation