Codimension Two Bifurcations

in a Ring of Identical Cells with Delayed Coupling

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Support: NSERC

Motivation

Many physiological systems have rings of similar neurons.

- Ability to synchronize
- Ability to respond differently to different inputs
- Coupling has time delays

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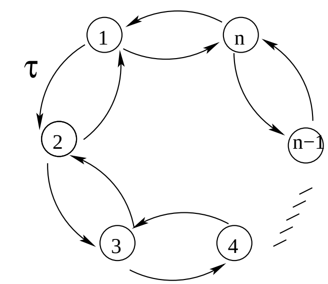

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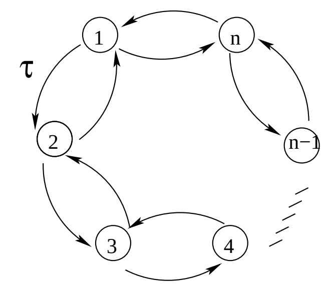

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- Elements, delays, coupling are identical $\Rightarrow$ **symmetry**

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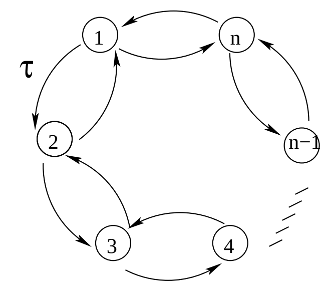

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Tool: Equivariant Bifurcation Theory

Background on Equivariant Bifurcation Theory

Let Γ be a group. The system $\mathbf{x}' = \mathbf{f}(\mathbf{x})$ is called Γ–**equivariant** if it is invariant under the action of any member, γ, of the group:

$$\mathbf{x}' = \mathbf{f}(\mathbf{x}) \Leftrightarrow (\gamma\mathbf{x})' = \mathbf{f}(\gamma\mathbf{x})$$

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Example: Any model for ring of n identical neurons, with x_j the state of the j^{th} neuron, is invariant under

- *permutations:* $x_j \longrightarrow x_{j+1} \bmod n$
- *reflections:* $x_j \longrightarrow x_{n+2-j} \bmod n$

Thus the equations are D_n– equivariant. D_n is the group of symmetries of an equilateral polygon with n sides.

Background on Equivariant Bifurcation Theory

Consequences: Bifurcations of system may be

- *standard* resulting in solutions where symmetry is unchanged
- *equivariant* resulting in solutions where symmetry is reduced (determined by subgroups of Γ)

Equivariant bifurcations are associated with

- repeated roots of the characteristic equation
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References

M. Golubitsky, I. Stewart, and D.G. Schaeffer (1988), *Singularities and Groups in Bifurcation Theory*, volume 2. New York.

W. Krawcewicz and J. Wu (1999), Theory and applications of Hopf bifurcations in symmetric functional-differential equations. *Nonlinear Anal.*, 35(7, Ser. A: Theory Methods):845–870.

Results for Ring of Neurons

Three types of Hopf bifurcation from the quiescent state are possible.

1. **Standard Hopf**: produces one synchronous oscillation
2. **Standard Hopf**: produces one antiphase oscillation (if n even)
3. **Equivariant Hopf**: produces $2(n+1)$ asynchronous oscillations of three types
   (a) travelling wave (2)
   (b) standing wave (n)
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Questions:

1. When do these oscillations occur?
2. Are they stable?

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Answers: Model dependent.

Tools: Analytical and numerical bifurcation analysis for delay differential equations.

Background on Numerical Bifurcation Analysis

- Uses **iterative procedure** to approximate equilibrium points and periodic solutions.
- Can find both stable and unstable solutions.
- By varying parameter and repeating, can follow branches of solutions.
- By approximating eigenvalues/Floquet mulitpliers, can determine stability of solutions.
- Produces:
  - One parameter bifurcation diagrams: plot of norm of solution as a function of a parameter.
  - Two parameter plots of bifurcation curves.

Background on Numerical Bifurcation Analysis

Packages:

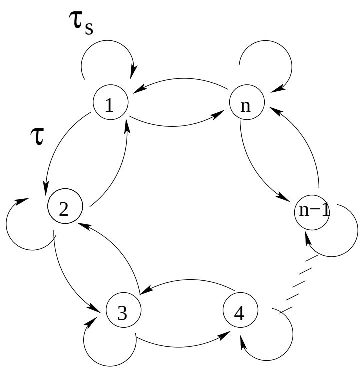
For ODES

- AUTO (E. Doedel et al.)
- Locbif (A. Khibnik et al.)
- Matcont (Y. Kuznetsov et al.)

For DDEs

- DDE-BIFTOOL (K. Engelborghs, D. Roose et al.)

Specific Model: Hopfield-type n-ring



n additive neurons coupled together such that each element receives three time delayed inputs: one from self (τ_s), two from the nearest neighbours (τ)

$$\dot{u}_j(t) = -du_j(t) + af(u_j(t-\tau_s)) + bg(u_{j-1}(t-\tau)) + bg(u_{j+1}(t-\tau)),$$

$$j \mod n$$

$$d > 0,\ \tau_s \geq 0, \tau \geq 0$$

$a \lesseqgtr 0$: Feedback is *inhibitory/excitatory*

$b \lesseqgtr 0$: Coupling is *inhibitory/excitatory*

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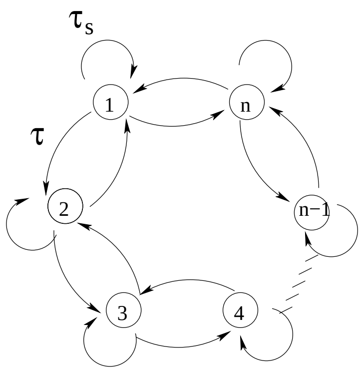

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$$j \mod n$$

$$f(0) = g(0) = 0,\ f'(0) = g'(0) = 1,\ f'(x), g'(x) > 0, x \neq 0$$

$$-\infty < \lim_{x \to \pm\infty} f(x), g(x) < \infty$$

$$f(u) = \tanh(u),\ \ g(u) = \frac{1}{\alpha}\tanh(\alpha u)$$

References

- C.M. Marcus, F.R. Waugh and R.M. Westervelt (1989), *Phys. Rev. A*, 39(1):347-359.
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- S. Guo (2005), *Nonlinearity*, 18:2391-2407.

Single Element

$$\dot{u}_j(t) = -du_j(t) + af(u_j(t - \tau_s))$$

When isolated, each element acts as a simple oscillator and has three possible steady state behaviours.

1. Trivial fixed point, if

$$-d < a < d \quad \text{and} \quad \tau_s \geq 0$$

or

$$a < -d \quad \text{and} \quad \tau_s < \left\{ \frac{1}{\sqrt{a^2 - d^2}} \left[\text{Arccos}\left(\frac{d}{-a} \right) \right] \right\}.$$

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2. Nontrivial fixed point, if

$$0 < d < a.$$

Single Element

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When isolated, each element acts as a simple oscillator and has three possible steady state behaviours.

3. Oscillation about zero, if

$$a < -d \quad \text{and} \quad \tau_s > \left\{ \frac{1}{\sqrt{a^2 - d^2}} \left[\mathrm{Arccos} \left(\frac{d}{-a} \right) \right] \right\}.$$

Bifurcation of the Trivial Solution

Model

$$\dot{u}_j(t) = -du_j(t) + af(u_j(t-\tau_s)) + bg(u_{j-1}(t-\tau)) + bg(u_{j+1}(t-\tau)),$$

clearly admits the trivial solution.

Linearization about the trivial solution:

$$\dot{u}_j(t) = -du_j(t) + au_j(t-\tau_s) + bu_{j-1}(t-\tau) + bu_{j+1}(t-\tau).$$

To investigate stability and bifurcation of the trivial solution, look for solutions: $\mathbf{u} = e^{\lambda t}\mathbf{k}$, $\lambda \in \mathbb{C}$, $\mathbf{k} \in \mathbb{C}^n$.

Bifurcations of the Trivial Solution

Characteristic equation of linearization about trivial solution.

n **odd**:

$$
\begin{aligned}
0 &= \Delta_0(\lambda) \prod_{j=1}^{\frac{n-1}{2}} \Delta_j^2(\lambda) \\
&= (-\lambda - d + ae^{-\lambda\tau_s} + 2be^{-\lambda\tau}) \\
&\quad \prod_{j=1}^{\frac{n-1}{2}} \left(-\lambda - d + ae^{-\lambda\tau_s} + 2be^{-\lambda\tau} \cos\frac{2\pi j}{n}\right)^2
\end{aligned}
$$

Bifurcations of the Trivial Solution

Characteristic equation of linearization about trivial solution.

$n = 2k$ **even**:

$$\begin{aligned} 0 &= \Delta_0(\lambda)\Delta_k(\lambda)\prod_{j=1}^{k-1}\Delta_j^2(\lambda) \\ &= (-\lambda - d + ae^{-\lambda\tau_s} + 2be^{-\lambda\tau})(-\lambda - d + ae^{-\lambda\tau_s} - 2be^{-\lambda\tau}) \\ &\quad \prod_{j=1}^{k-1}\left(-\lambda - d + ae^{-\lambda\tau_s} + 2be^{-\lambda\tau}\cos\frac{\pi j}{k}\right)^2 \end{aligned}$$

Bifurcations of the Trivial Solution

- Simple roots with zero real part of $\Delta_0(\lambda) = 0$ correspond to (standard) bifurcations giving rise to nontrivial *synchronous* solutions, i.e. with $u_j(t) = u_{j+1}(t),\ j \mod n$.

- Simple roots with zero real part of $\Delta_k(\lambda) = 0$ correspond to (standard) bifurcations giving rise to asynchronous solutions with $u_j(t) = -u_{j+1}(t),\ j \mod n$ (*anti-phase*).

- Simple roots with zero real part of the other $\Delta_j(\lambda) = 0$ correspond to equivariant bifurcations giving rise to asynchronous solutions with other symmetries.

Bifurcation Curves

Determine bifurcation curves in terms of the coupling parameters b, τ.

Synchronous pitchfork: $b = \dfrac{d-a}{2}$

Synchronous Hopf: $b = b_0^{\pm}(\omega)$, $\tau = \tau_{H0k}^{\pm}(\omega)$

$$
\begin{aligned}
b_0^{\pm}(\omega) &= \pm\frac{1}{2}\sqrt{d^2 + a^2 + \omega^2 + 2a\omega\sin(\omega\tau_s) - 2ad\cos(\omega\tau_s)} \\
\tau_{H0k}^{\pm}(\omega) &= \begin{cases} \mathcal{T}_{2k}, & d - a\cos(\omega\tau_s) \gtrless 0 \\ \mathcal{T}_{2k+1}, & d - a\cos(\omega\tau_s) \lessgtr 0 \end{cases},
\end{aligned}
$$

where

$$
\mathcal{T}_l(\omega) = \frac{1}{\omega}\left\{\mathrm{Arctan}\left[\frac{-\omega - a\sin(\omega\tau_s)}{d - a\cos(\omega\tau_s)}\right] + l\pi\right\}.
$$

Bifurcation Curves

Determine bifurcation curves in terms of the coupling parameters b, τ.

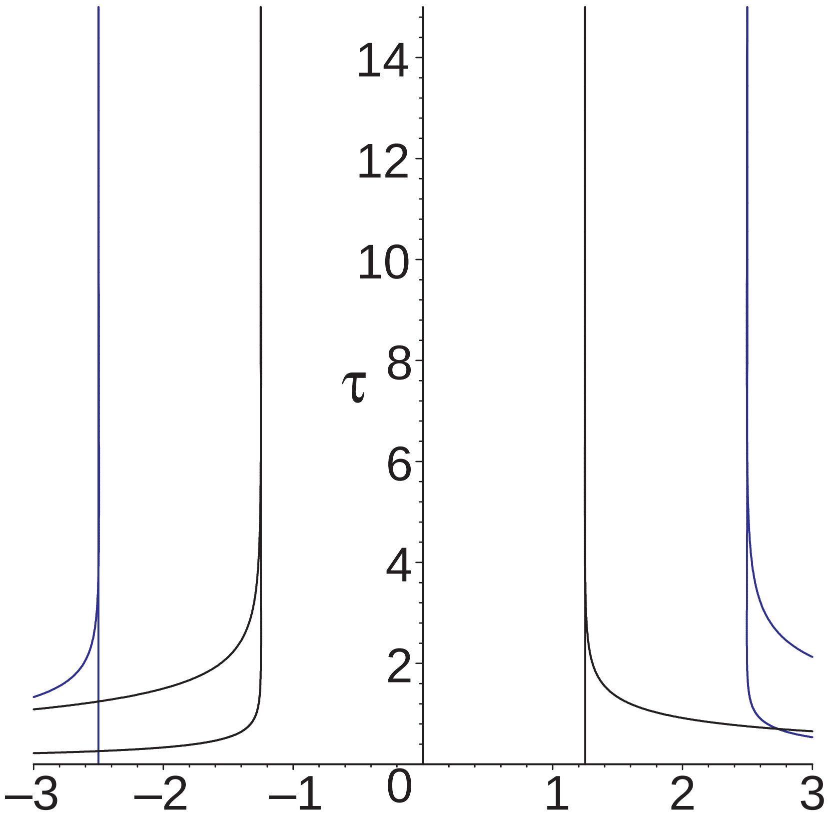
Equivariant pitchfork: $b = \dfrac{d-a}{\cos\frac{2\pi j}{n}}$

Equivariant Hopf: $b = b_j^{\pm}(\omega) = \frac{b_0^{\pm}}{|\cos\frac{2\pi j}{n}|}$, $\tau = \tau_{Hjk}^{\pm}(\omega)$

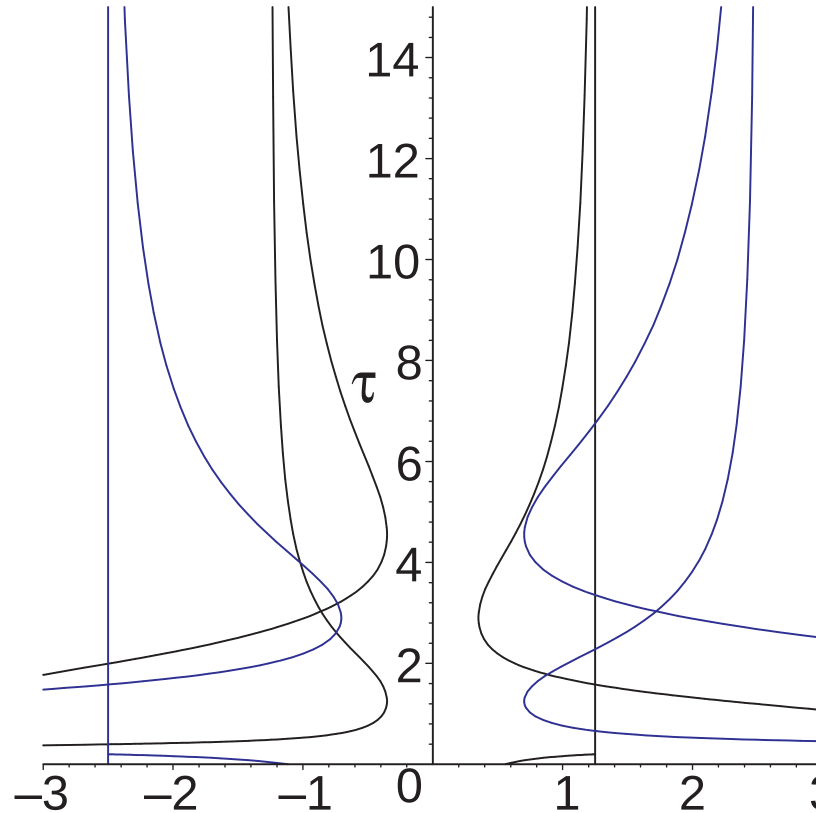
$$\tau_{Hjk}^{\pm}(\omega) \quad = \quad \begin{cases} \mathcal{T}_{2k}, & d - a\cos(\omega\tau_s) \gtrless 0 \quad j = 1, 2, \ldots, \left[\frac{n-1}{4}\right] \\ \mathcal{T}_{2k+1}, & d - a\cos(\omega\tau_s) \lessgtr 0 \\ \mathcal{T}_{2k+1}, & d - a\cos(\omega\tau_s) \gtrless 0 \quad j = \left[\frac{n}{4}+1\right], \ldots, [\\ \mathcal{T}_{2k}, & d - a\cos(\omega\tau_s) \lessgtr 0 \end{cases}$$

Y. Yuan and S.A. Campbell (2004), *JDDE* 16(1), 709-744.

Bifurcation Curves $n = 3$, $d = 1,\ a = -1.5$

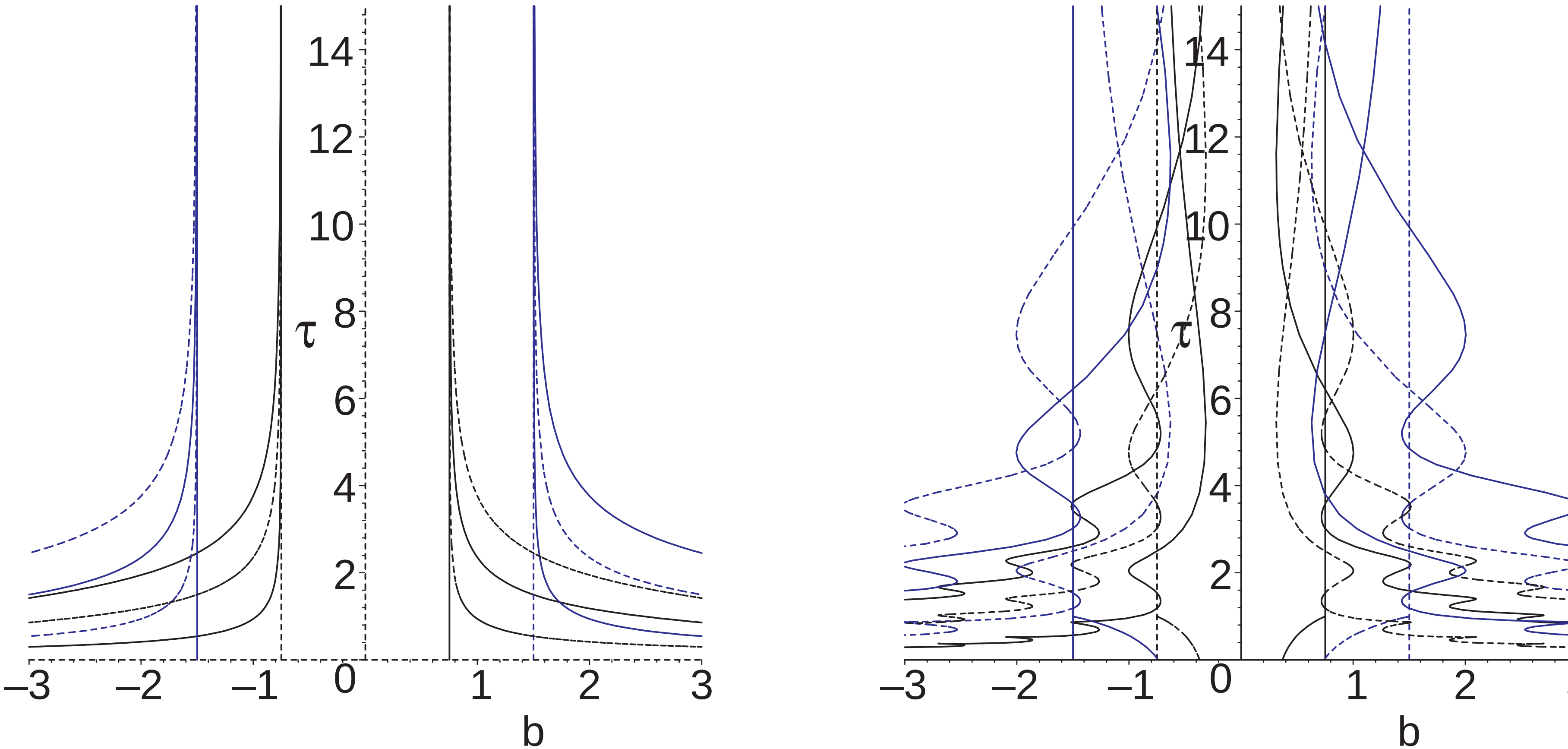


$\tau_s = 0.3$



$\tau_s = 1.0$

Bifurcation Curves $n = 6$, $d = 1,\ a = -0.5$



$\tau_s = 0.7$ $\qquad$ $\tau_s = 5.0$

Criticality of Synchronous Bifurcations

From analysis of existence of equilibria.

- Synchronous pitchfork bifurcation (at $b = \frac{d-a}{2}$) is always supercritical
- For n even, standard pitchfork bifurcation (at $b = \frac{a-d}{2}$) is always supercritical.

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- For n even, standard pitchfork bifurcation (at $b = \frac{a-d}{2}$) is always supercritical.

From centre manifold analysis.

- Synchronous Hopf bifurcation is super/subcritical if

$$a(\tau_s - \tau)(\omega \sin(\omega\tau_s) - d\cos(\omega\tau_s)) - \tau(d^2 + \omega^2) - d \lessgtr 0.$$

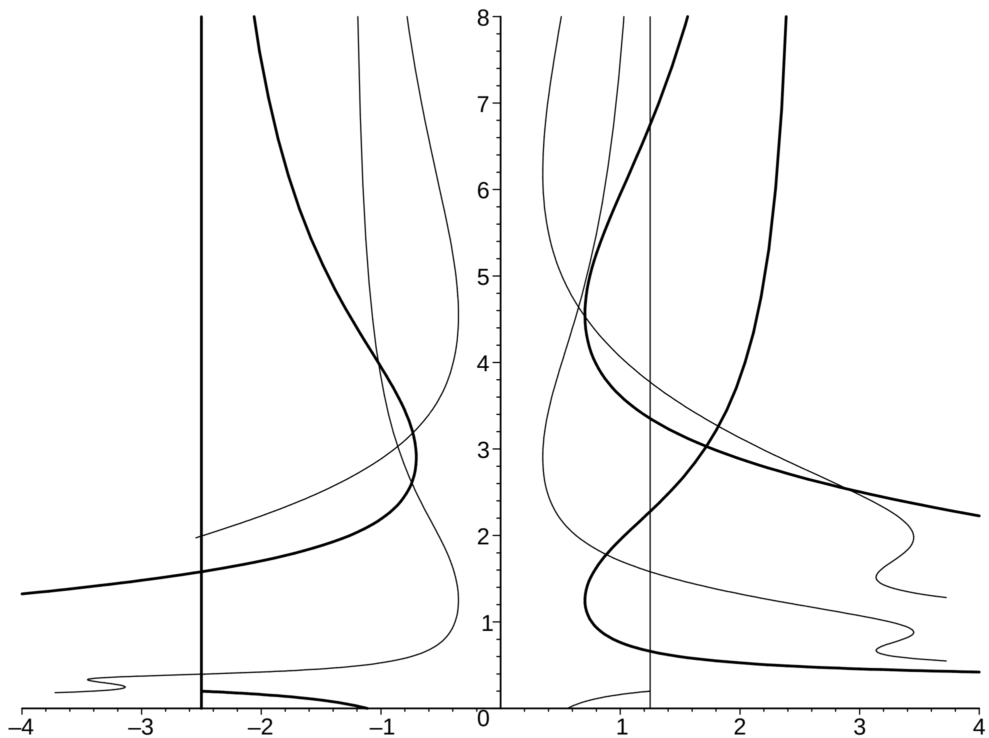
- For n even, Hopf bifurcation to anti-phase oscillations is super/subcritical under the same conditions.

  Y. Yuan and S.A. Campbell (2004), *JDDE* 16(1), 709-744.

Criticality of Synchronous Bifurcations

Example: $n = 3, d = 1, a = -1.5$

Theoretical Result: All branches of synchronous and antiphase Hopf bifurcation are supercritical everywhere for $\tau_s \leq 1.2$.



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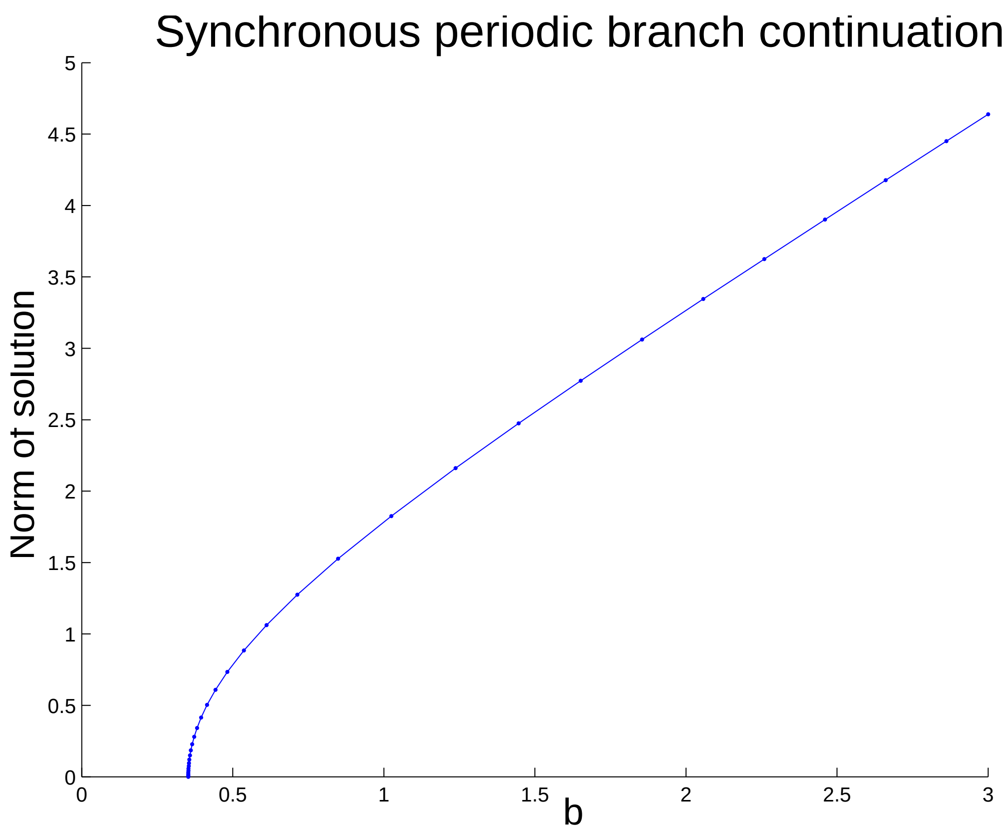
Numerical Result: $\tau_s = 1, \tau = 2.9591$



Stability of Synchronous Periodic Solutions

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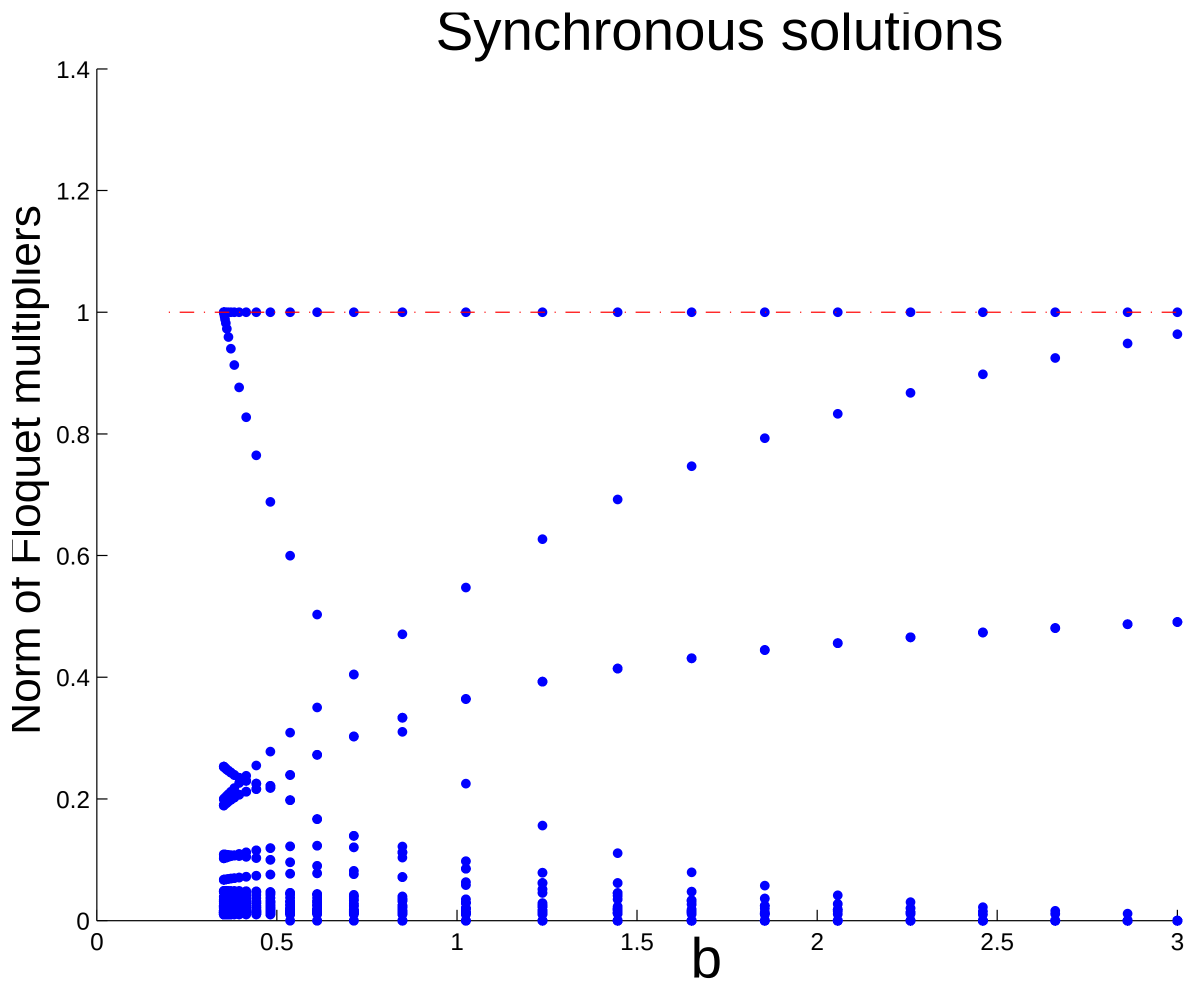

Criticality of Equivariant Hopf

Theorem
Let $m = 1 + \tau(1+\omega^2) - a(\tau - \tau_s)(\cos(\omega\tau_s) - \omega\sin(\omega\tau_s))$. There exists $2(n+1)$ branches of asynchronous periodic solutions of period p_j near $\frac{2\pi}{\beta_{Hj}}$ bifurcated from the zero solution of the system:

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(1) 2 phase-locked oscillations: $x_i(t) = x_{i+1}(t \pm \frac{j\,p_j}{n})$ for $i(\mod n)$; when $m < 0$, they are supercritical and orbitally asymptotically stable; when $m > 0$, they are subcritical and orbitally unstable;

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(2) n unstable mirror-reflecting waves: $x_i(t) = x_{n+2\,k-i}(t)$ for $i(\mod n)$ and $k = 1,\, 2,\, \cdots,\, n$; when $m < 0$, they are supercritical, whereas when $m > 0$, they are subcritical;

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(3) n unstable standing waves: $x_i(t) = x_{n+2\,k-i}(t - \frac{\omega}{2})$ for $i(\mod n)$ and $k = 1, 2, \cdots, n$; when $m < 0$, they are supercritical, whereas when $m > 0$, they are subcritical;

Criticality of Equivariant Hopf

Proof

Uses centre manifold reduction and equivariant bifurcation theory.

Reference

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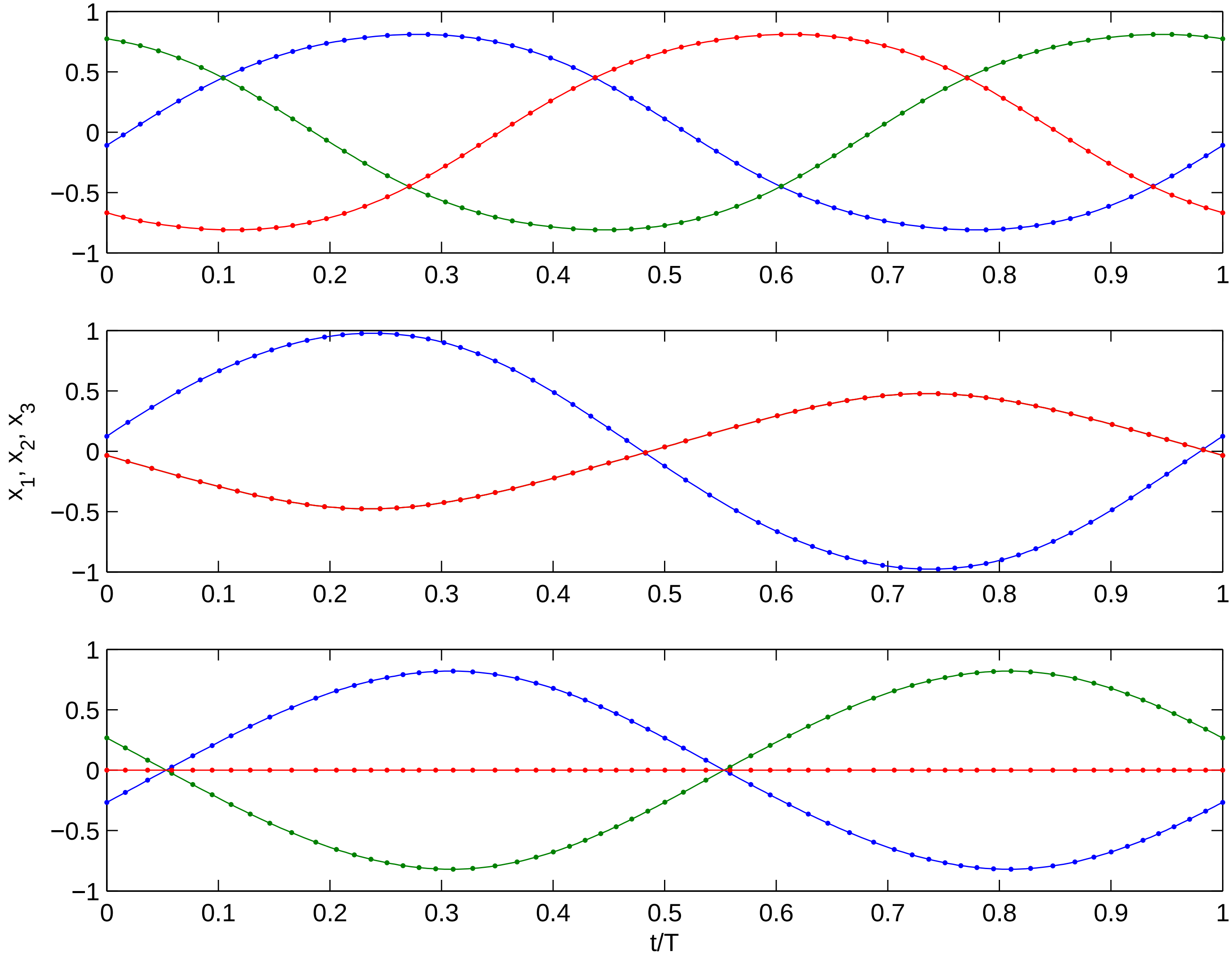
Periodic Solutions from Equivariant Hopf

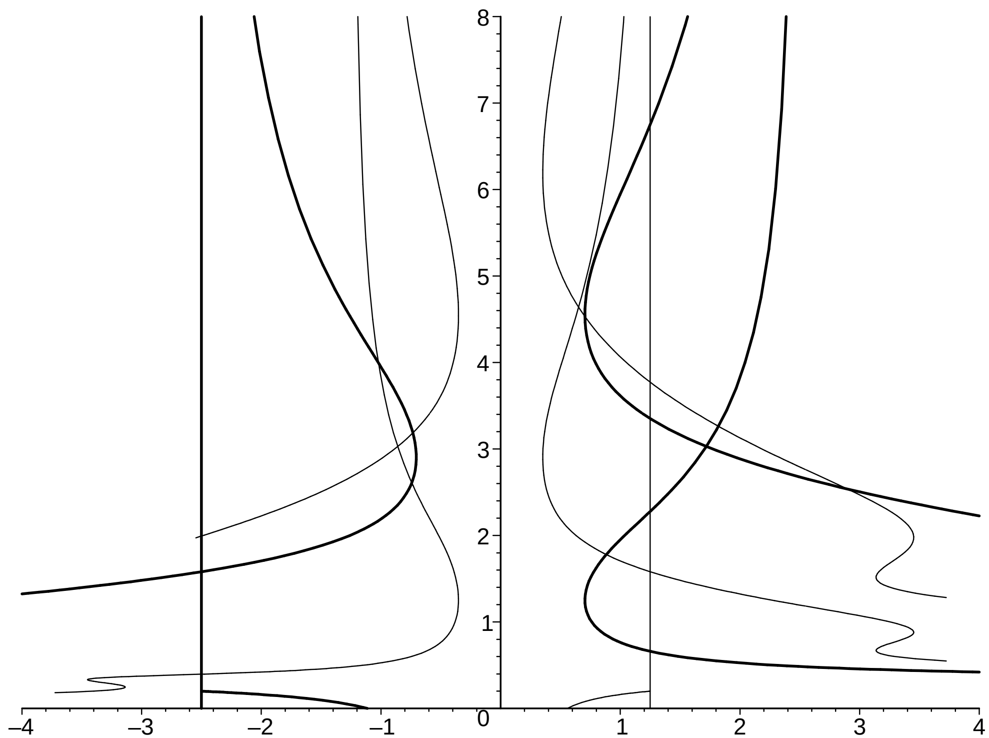
$$n = 3, d = 1, a = -1.5, \tau_s = 1, \tau = 0.73125, b \approx 1.5$$



Criticality of Equivariant Hopf

Example 1: $n = 3, d = 1, a = -1.5, \tau_s = 1$,
$f(u) = g(u) = \tanh(u)$

Theoretical Result: Bifurcations are always supercritical.



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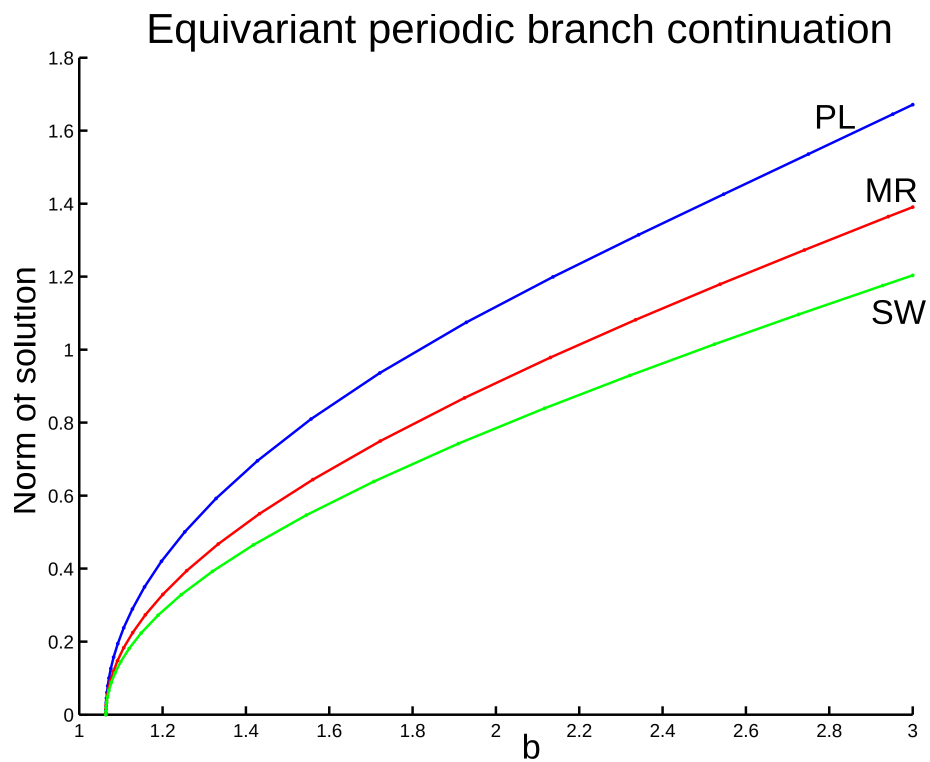

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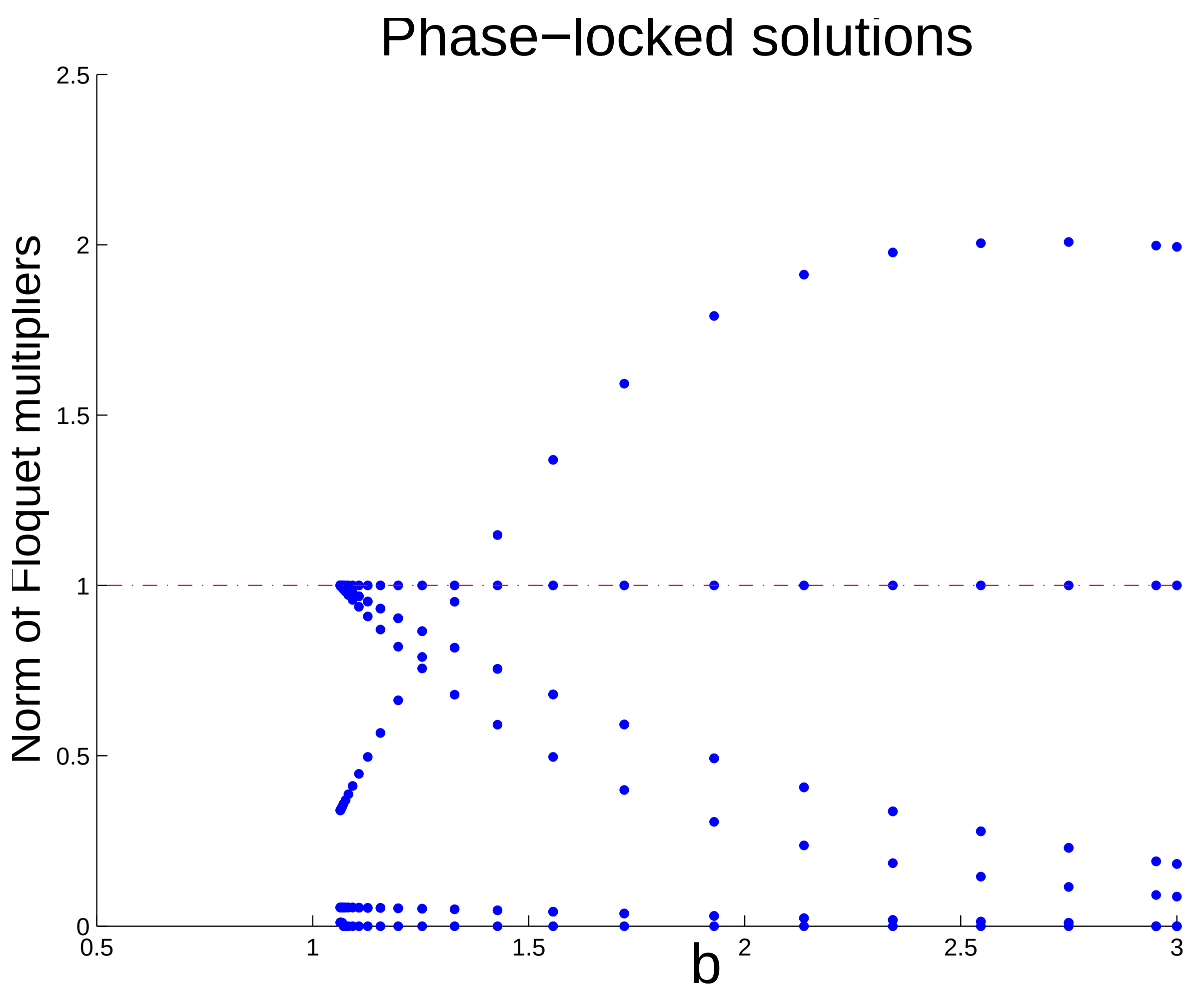

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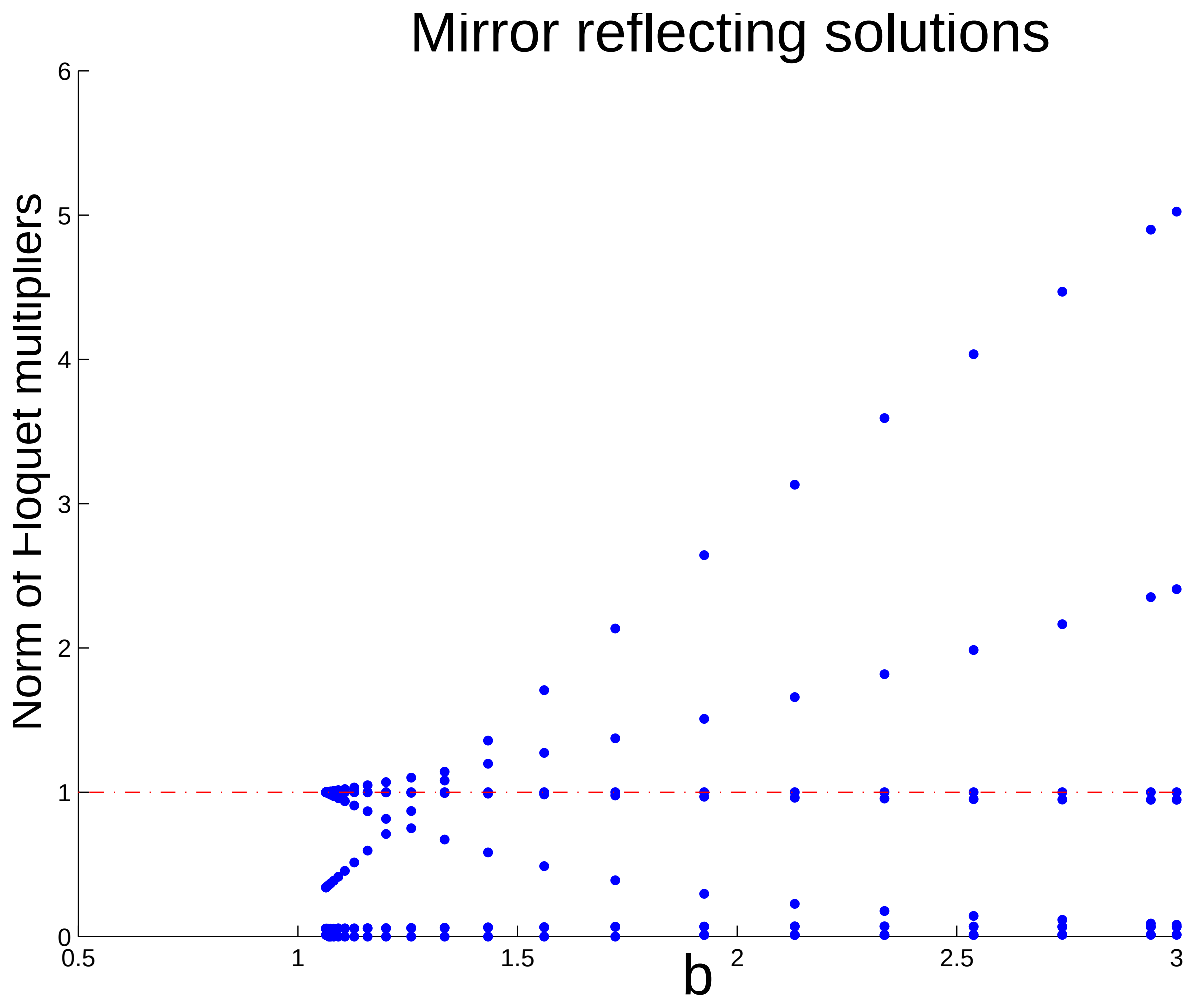

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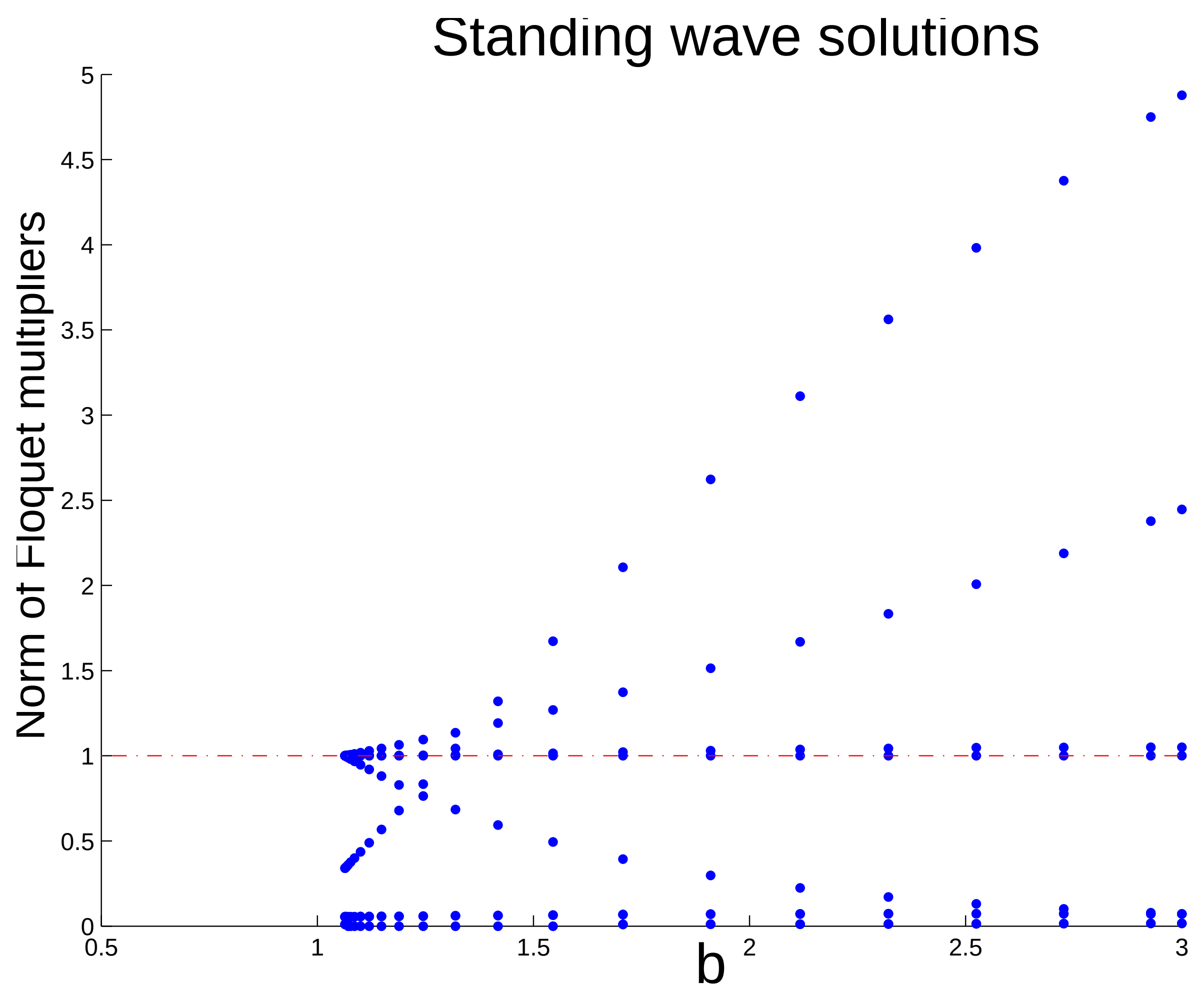
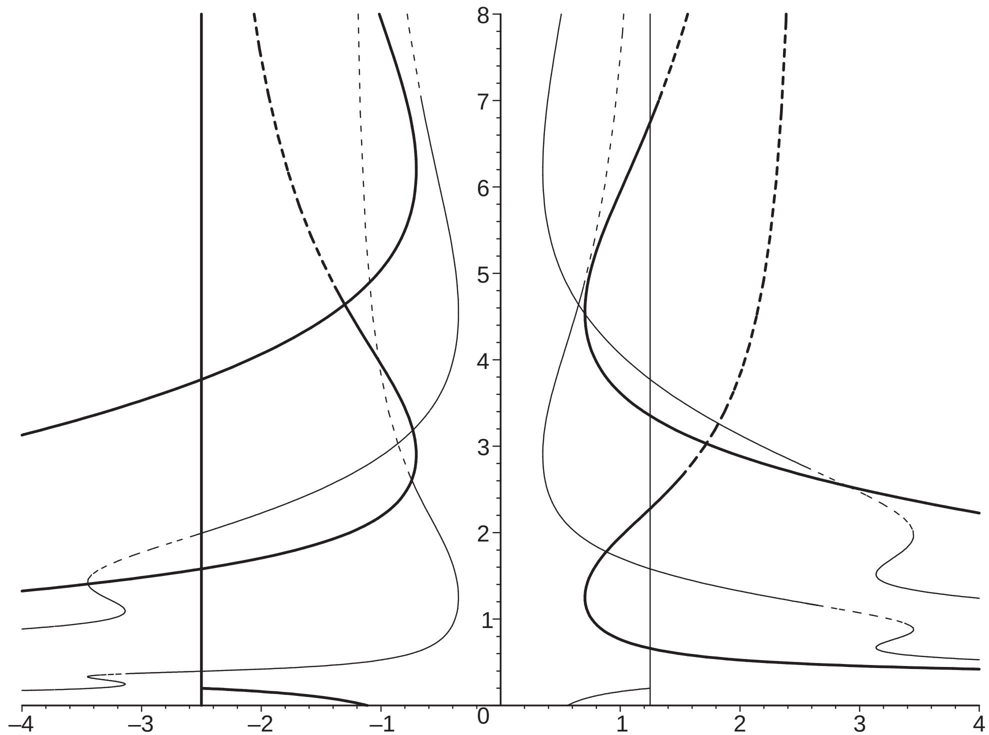


Criticality of Equivariant Hopf

Example 2: $n = 3, d = 1, a = -1.5, \tau_s = 1,$
$f(u) = \tanh(u), g(u) = \frac{5}{2}\tanh(\frac{2}{5}u)$
Theoretical Result: $m > 0$ for ω small, then undergoes sign change.



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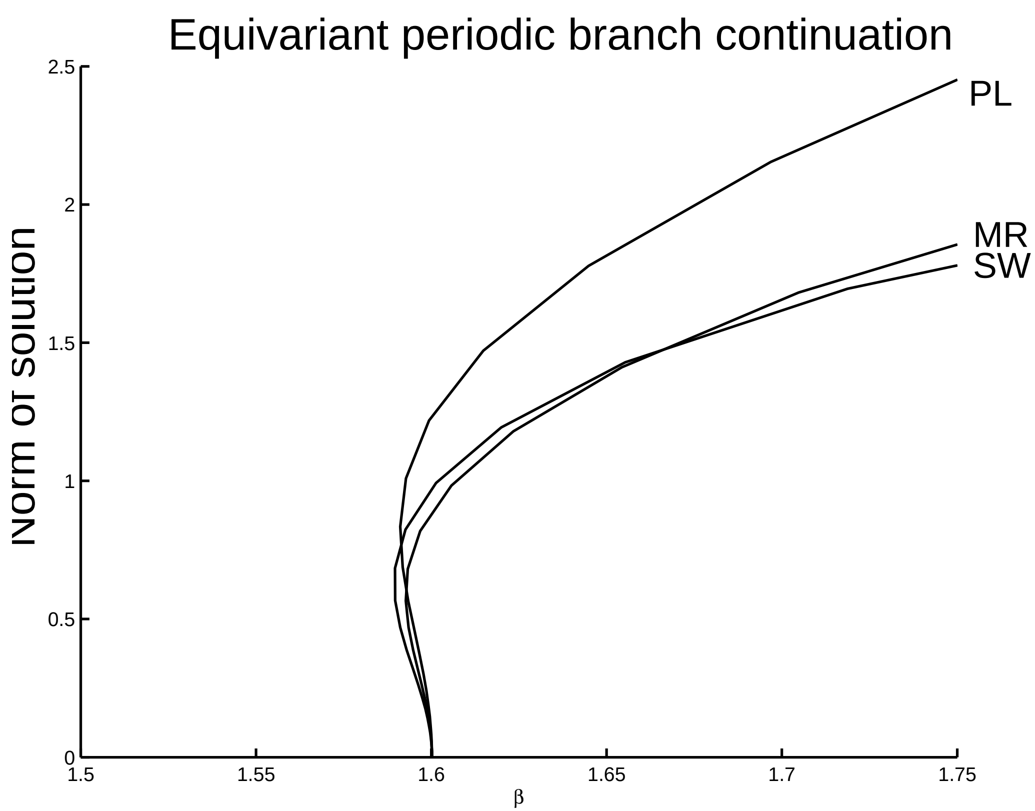
Numerical Result: $\tau = 2.8$



Criticality of Equivariant Pitchfork

Theorem: The trivial solution undergoes a D_n equivariant pitchfork bifurcation along $b = \frac{d-a}{\cos \frac{2\pi j}{n}}$ giving rise to $4n$ branches of equilibria:

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- $2n$ branches of standing wave equilibria, $(\pm x^*, 0, \mp x^*, \dots)$ and permutations, where x^* satisfies

  $$-x^* + a\tanh(x^*) + b\tanh(-x^*) = 0;$$

  these branches are alway supercritical;

Criticality of Equivariant Pitchfork

Theorem: The trivial solution undergoes a D_n equivariant pitchfork bifurcation along $b = \frac{d-a}{\cos\frac{2\pi j}{n}}$ giving rise to $4n$ branches of equilibria:

- $2n$ branches of standing wave equilibria, $(\pm x^*, 0, \mp x^*, \ldots)$ and permutations, where x^* satisfies

$$-x^* + a\tanh(x^*) + b\tanh(-x^*) = 0;$$

  these branches are alway supercritical;

- $2n$ branches of mirror reflecting equilibria, $(\pm x^*, \pm y^*, \pm x^*, \ldots)$ and permutations, where x^*, y^* satisfy

$$\begin{aligned} -x^* + a\tanh(x^*) + b\tanh(x^*) + b\tanh(y^*) &= 0 \\ -y^* + a\tanh(y^*) + 2b\tanh(x^*) &= 0; \end{aligned}$$

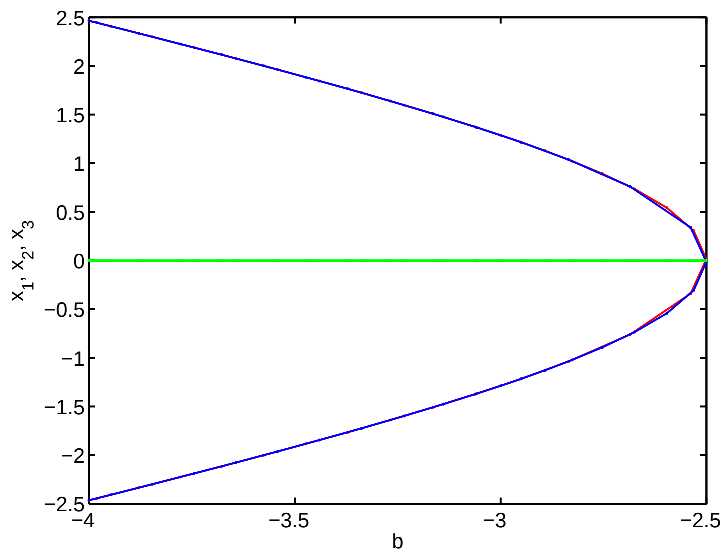
  these branches may be sub- or supercritical.

Criticality of Equivariant Pitchfork

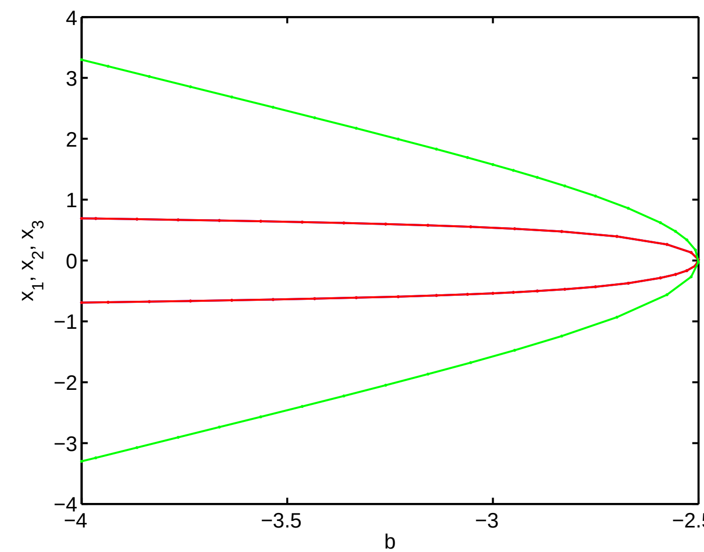
Using numerical continuation software DDE-BIFTOOL.

Example: $n = 3, d = 1, a = -1.5, \tau_s = 1, \tau = 1$,

$f(u) = g(u) = \tanh(u)$



Standing wave equilibria



Mirror reflecting equilibria

Codimension Two Bifurcations

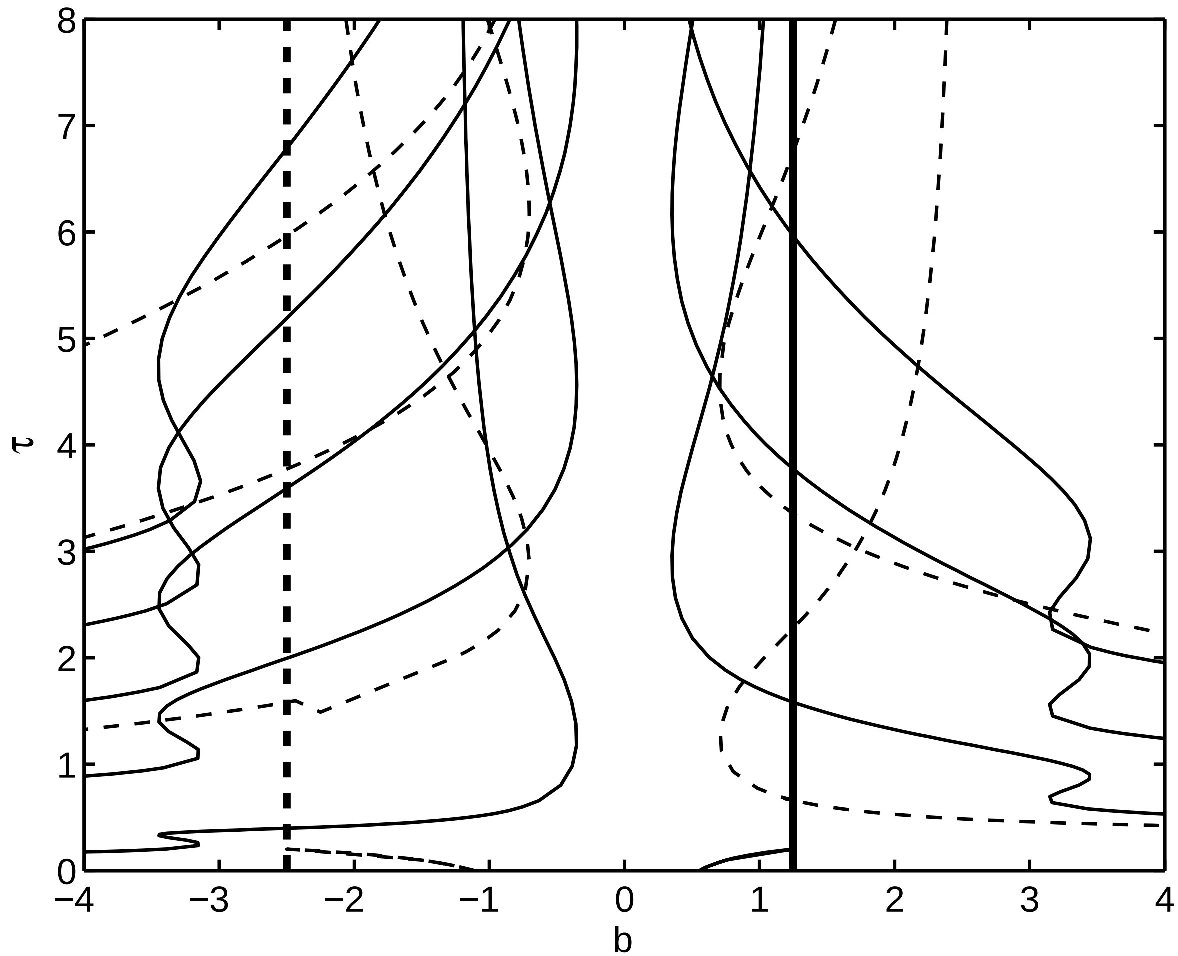
Generically, need two parameters for such points to occur.
Examples: Points in parameter space where characteristic equation has

- double zero root (Bogdanov-Takens)
- one zero root and a pair of pure imaginary roots (steady state/Hopf interaction)
- two pairs of pure imaginary roots (Hopf/Hopf interaction)

Occur where two codimension one bifurcation curves intersect.

Codimension Two Bifurcations

Model with $n = 3$



Codimension Two Bifurcations – Synchronous Hopf/Pitchfork

Theoretical Result: There exist two secondary bifurcations emanating from the codimension two bifurcation point.

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References:

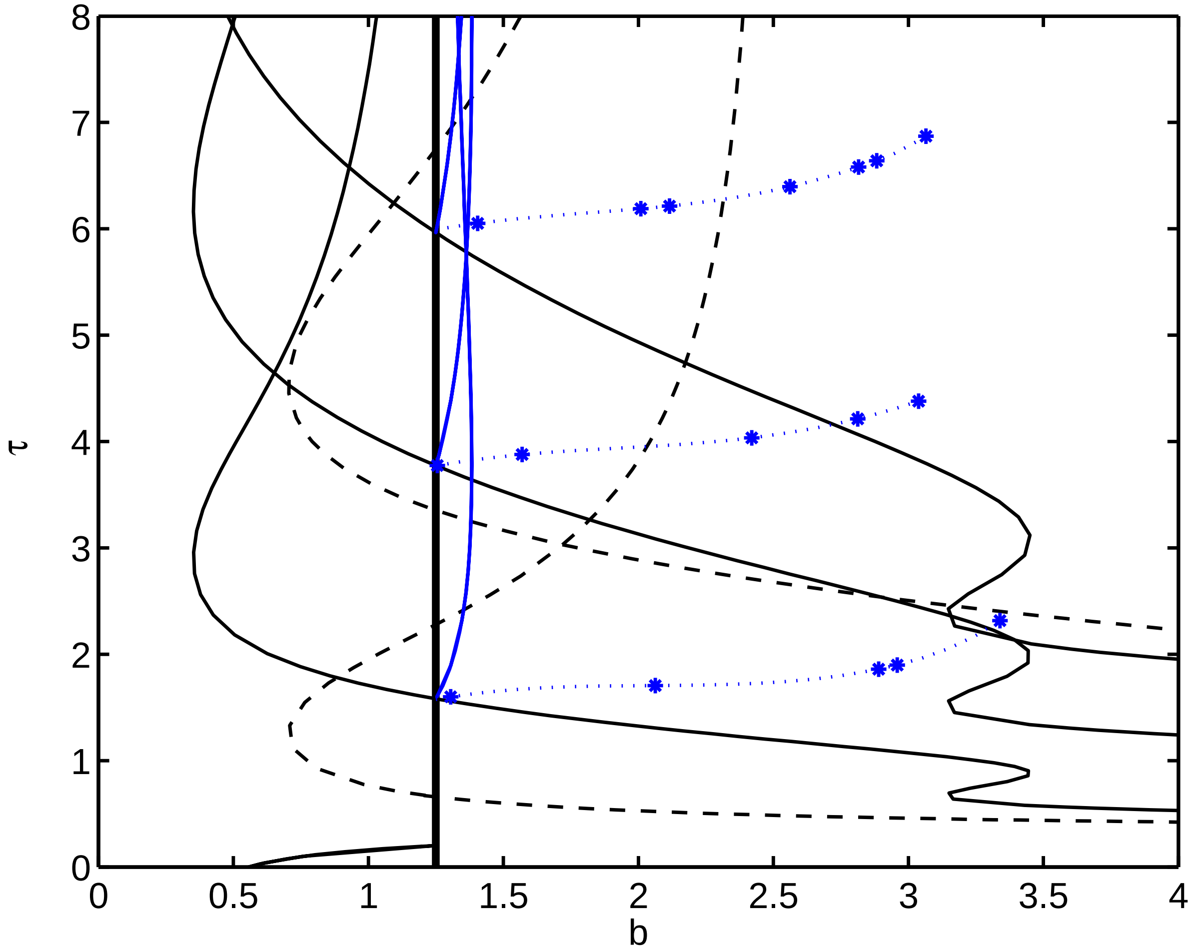
J. Guckenheimer and P.J. Holmes (1983), *Nonlinear Oscillations, Dynamical Systems and Bifurcations of Vector Fields* (Chapter 7), Springer-Verlag.

Y.A. Kuznetsov (1995), *Elements of Applied Bifurcation Theory*, (Chapter 8) Springer-Verlag.

Codimension Two Bifurcations – Synchronous Hopf/Pitchfork

Numerical Result: Using DDE-BIFTOOL

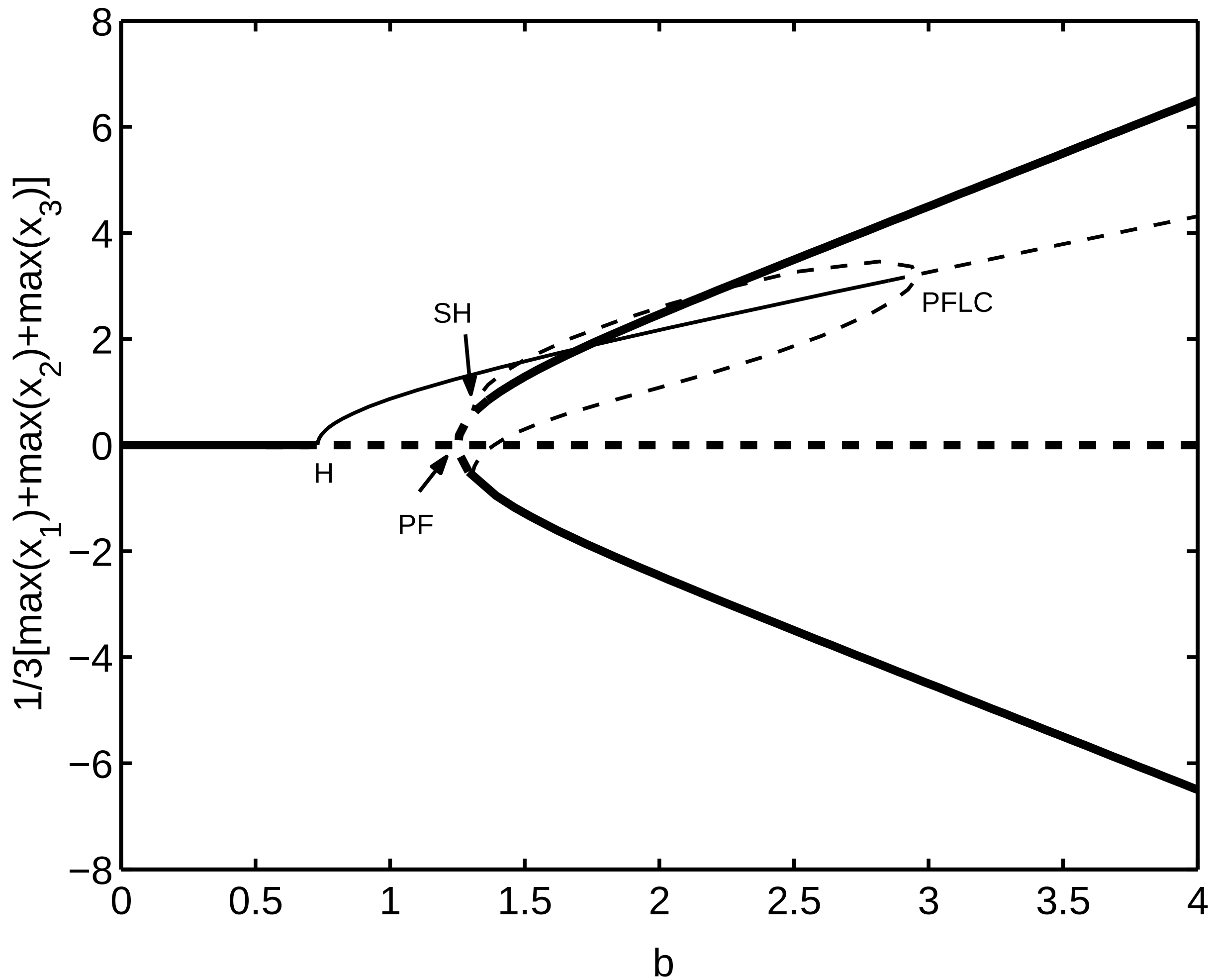
Example: $n = 3, d = 1, a = -1.5, \tau_s = 1$



Codimension Two Bifurcations – Synchronous Hopf/Pitchfork

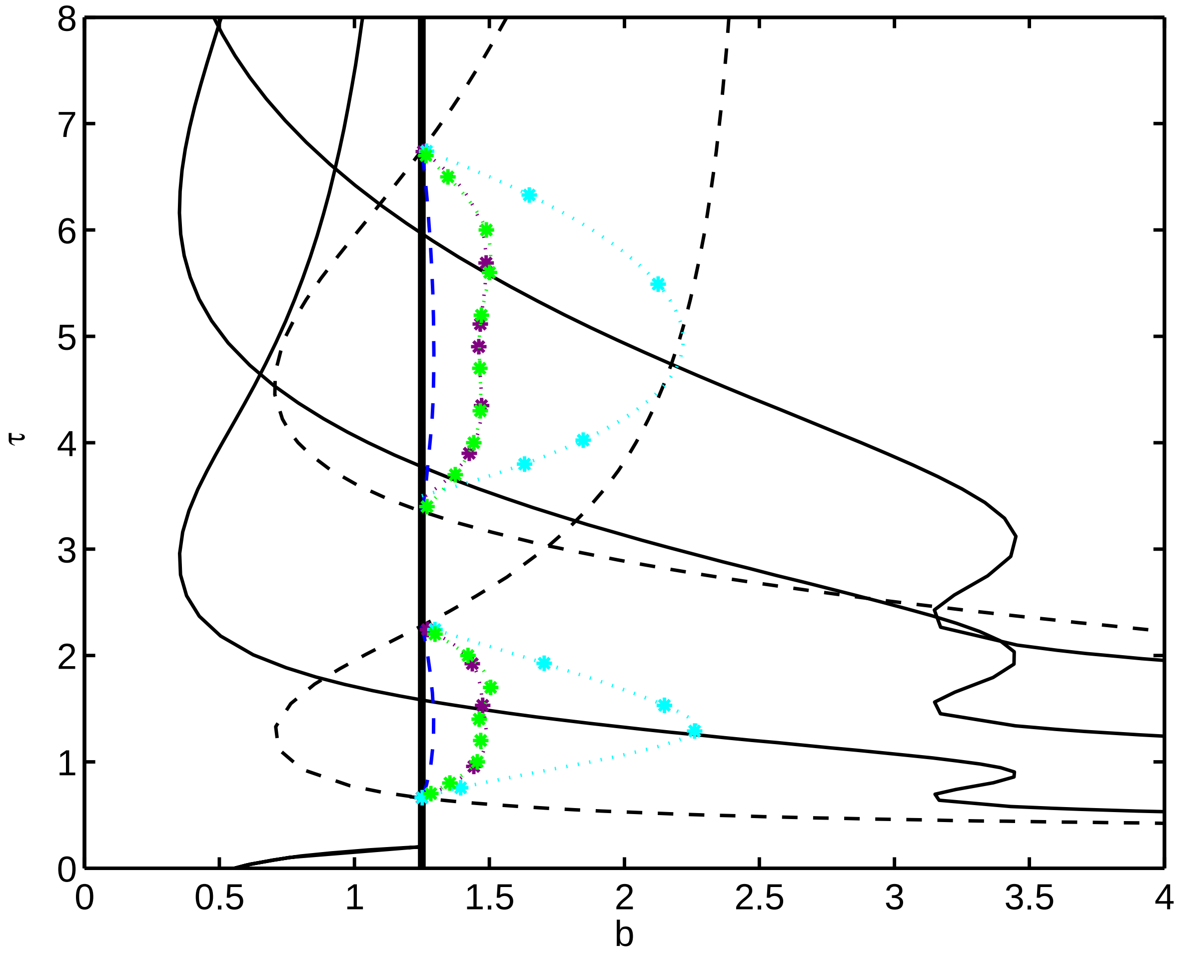
Numerical Result: Using DDE-BIFTOOL

Example: $n = 3, d = 1, a = -1.5, \tau_s = 1, \tau = 1.8$



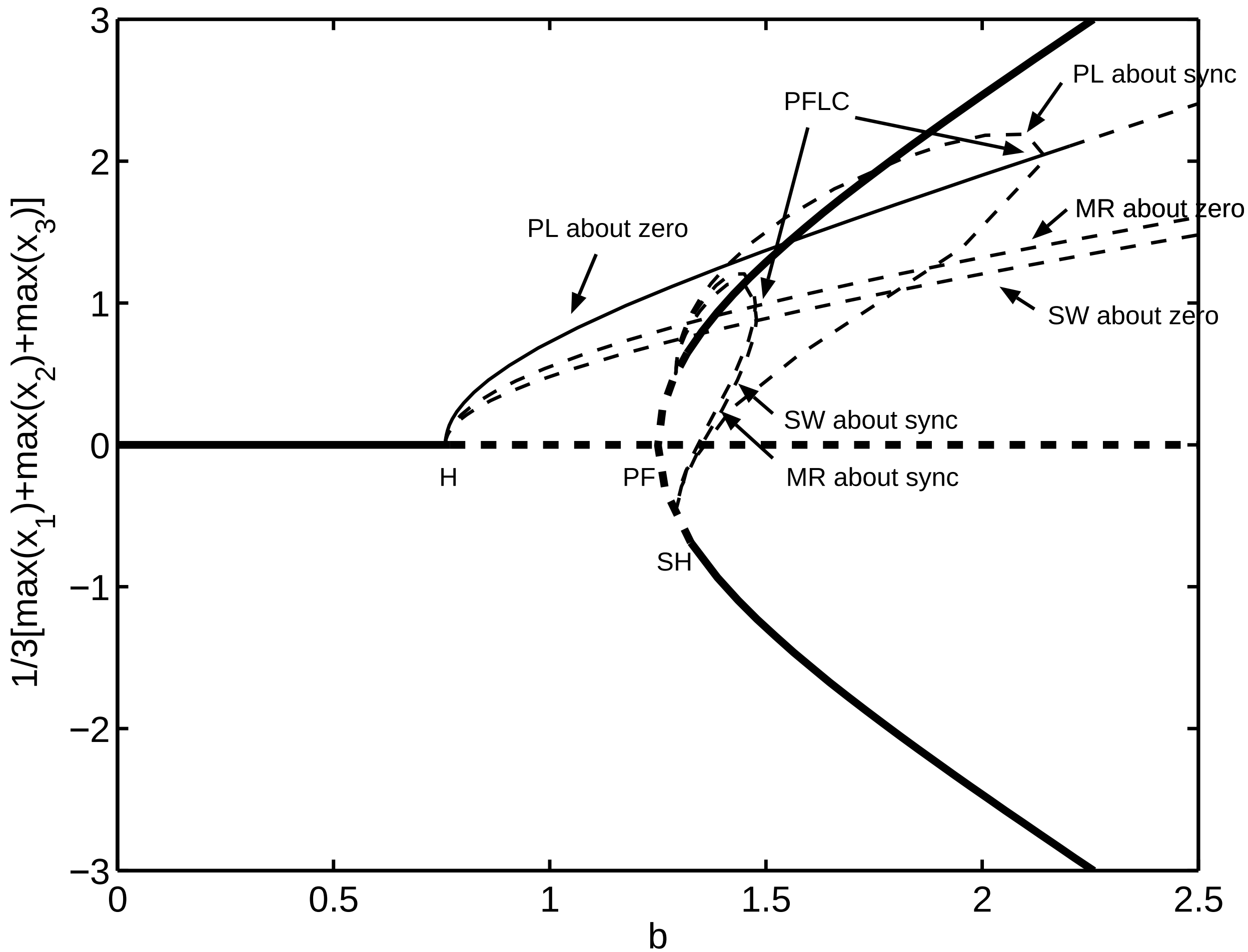
Bifurcation Interactions – Equivariant Hopf/Synchronous Pitchfork

Example: $n = 3, a = -1.5, \tau_s = 1$



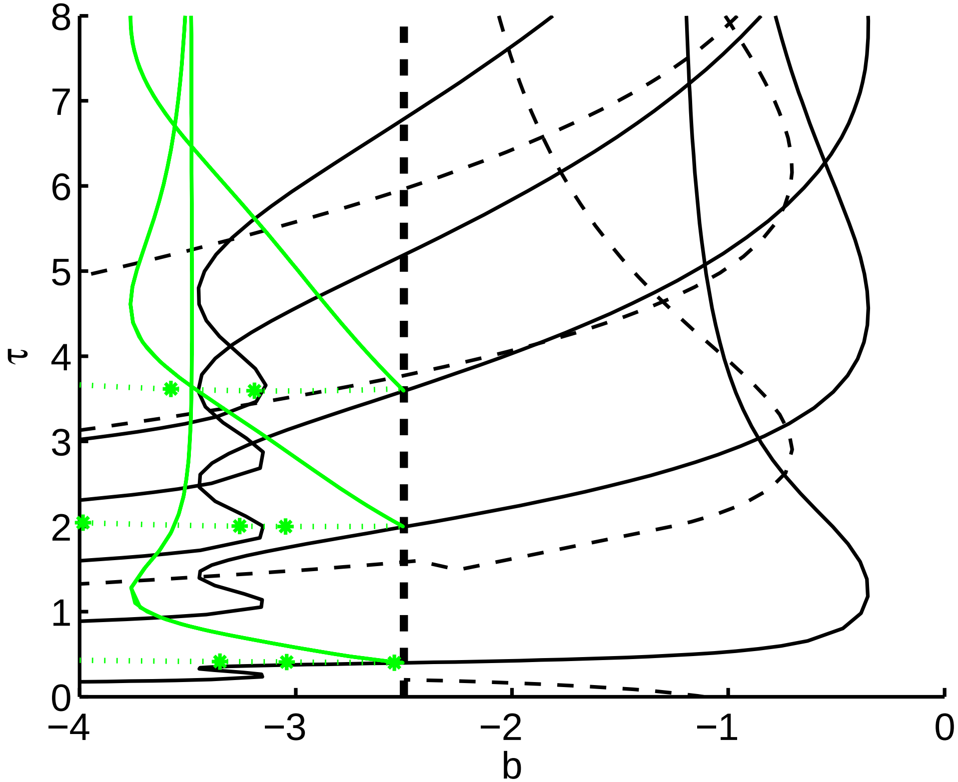
Bifurcation Interactions – Equivariant Hopf/Synchronous Pitchfork

Example: $n = 3, a = -1.5, \tau_s = 1, \tau = 1.5317$



Bifurcation Interactions – Synchronous Hopf/Equivariant Pitchfork

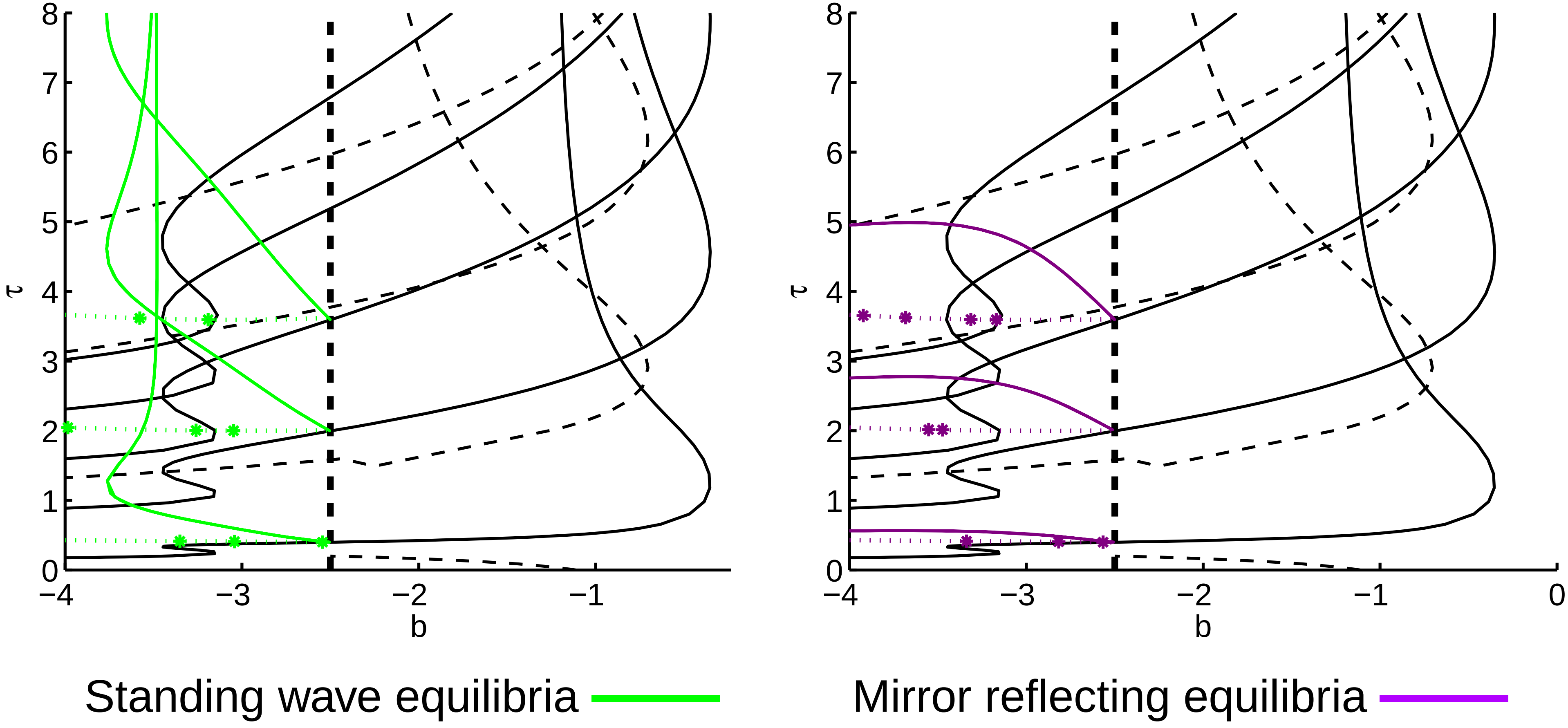
Example: $n = 3, a = -1.5, \tau_s = 1$



Standing wave equilibria

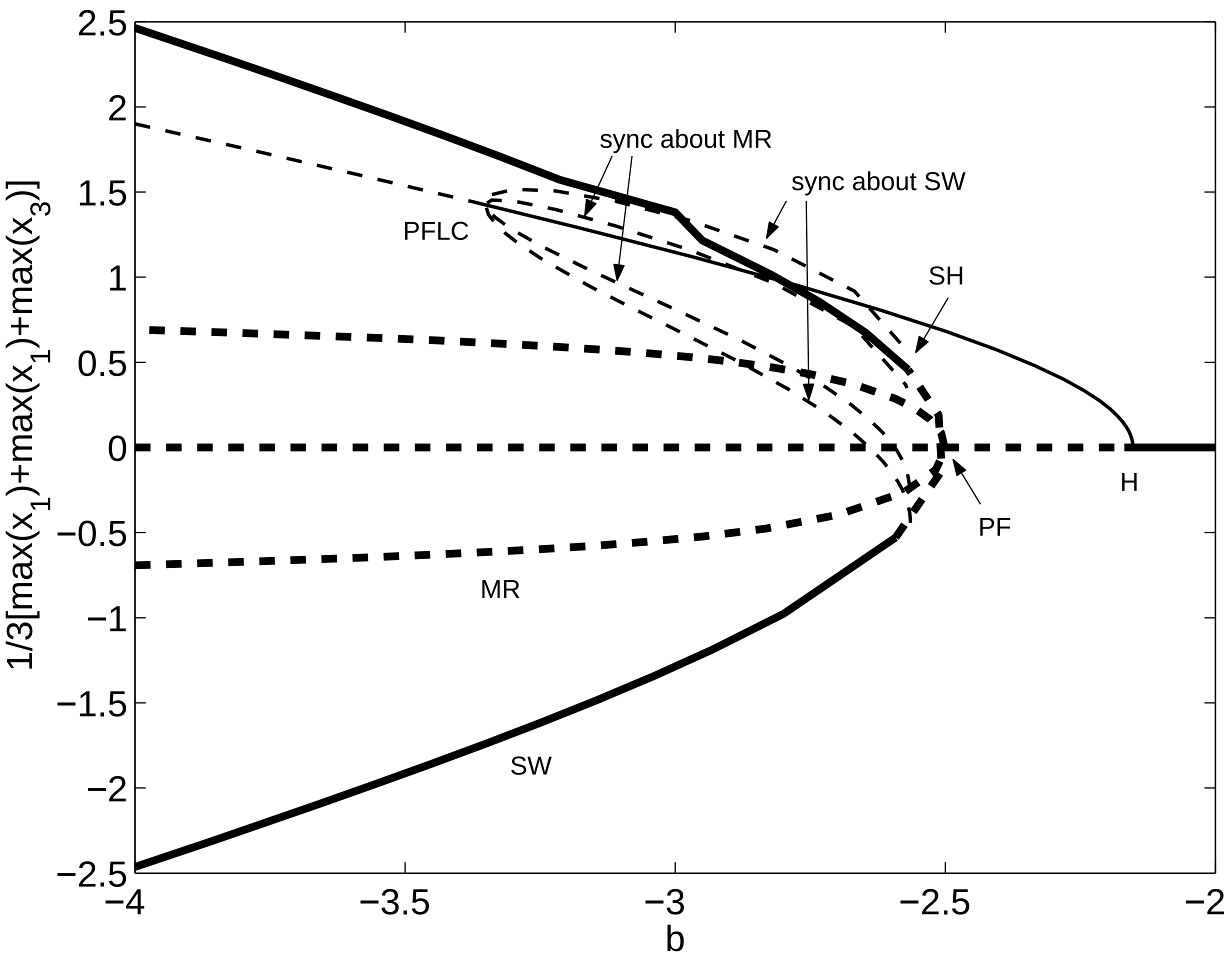
Bifurcation Interactions – Synchronous Hopf/Equivariant Pitchfork

Example: $n = 3, a = -1.5, \tau_s = 1$



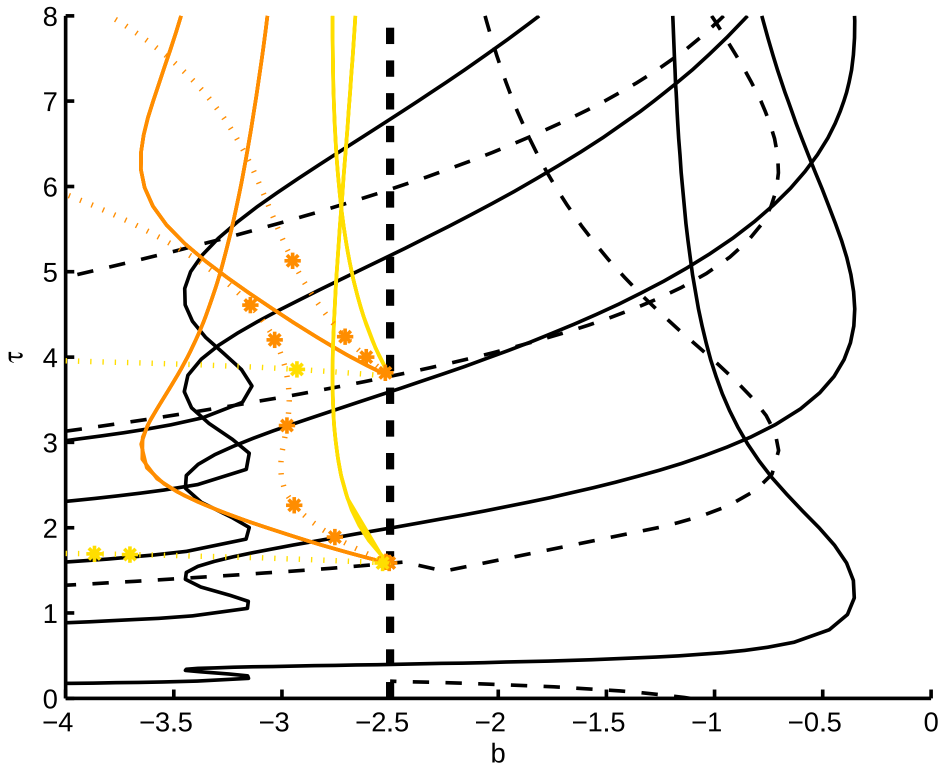
Bifurcation Interactions – Synchronous Hopf/Equivariant Pitchfork

Example: $n = 3, a = -1.5, \tau_s = 1, \tau = 0.41318$



Codimension Two Bifurcations – Equivariant Hopf/Pitchfork

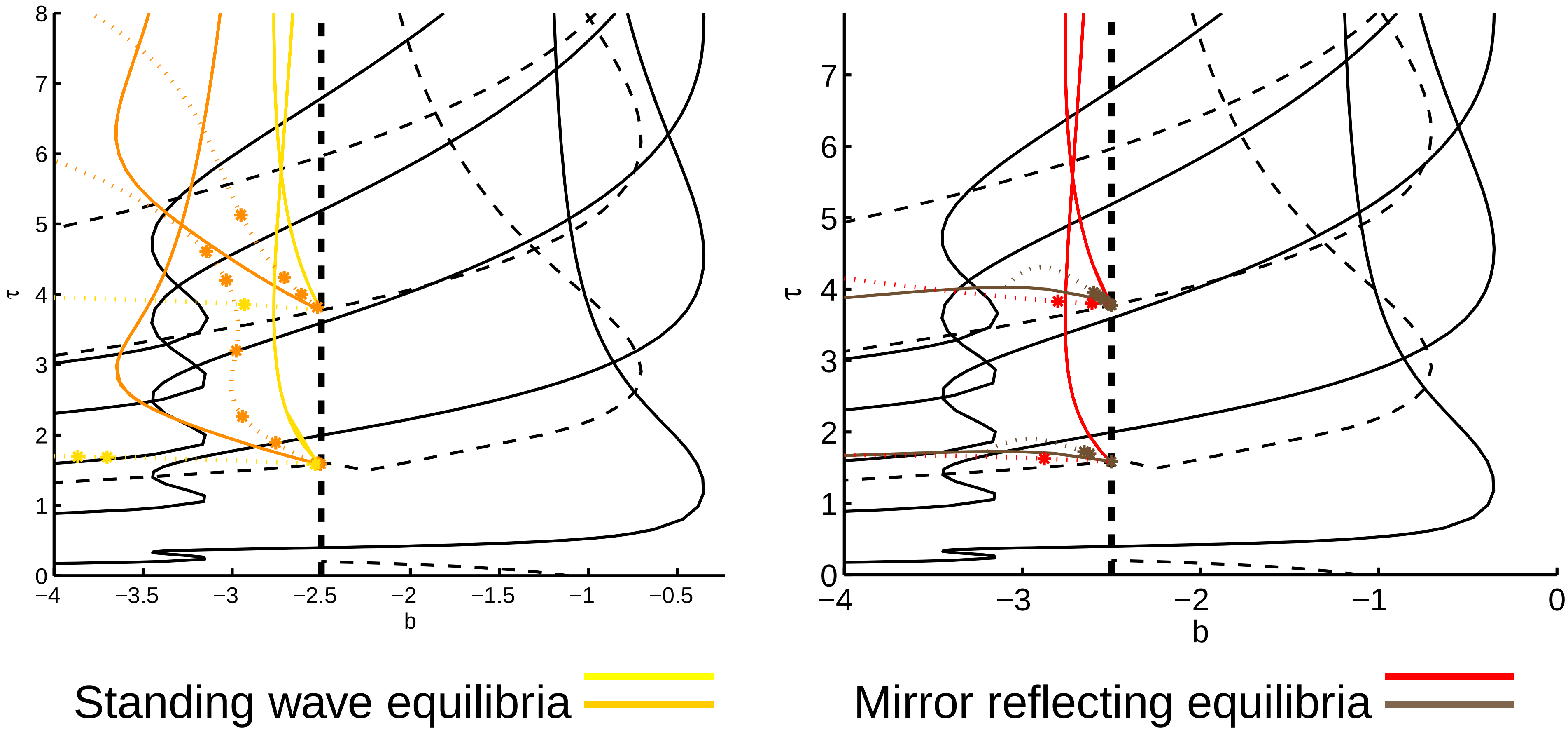
Example: $n = 3, a = -1.5, \tau_s = 1$



Standing wave equilibria

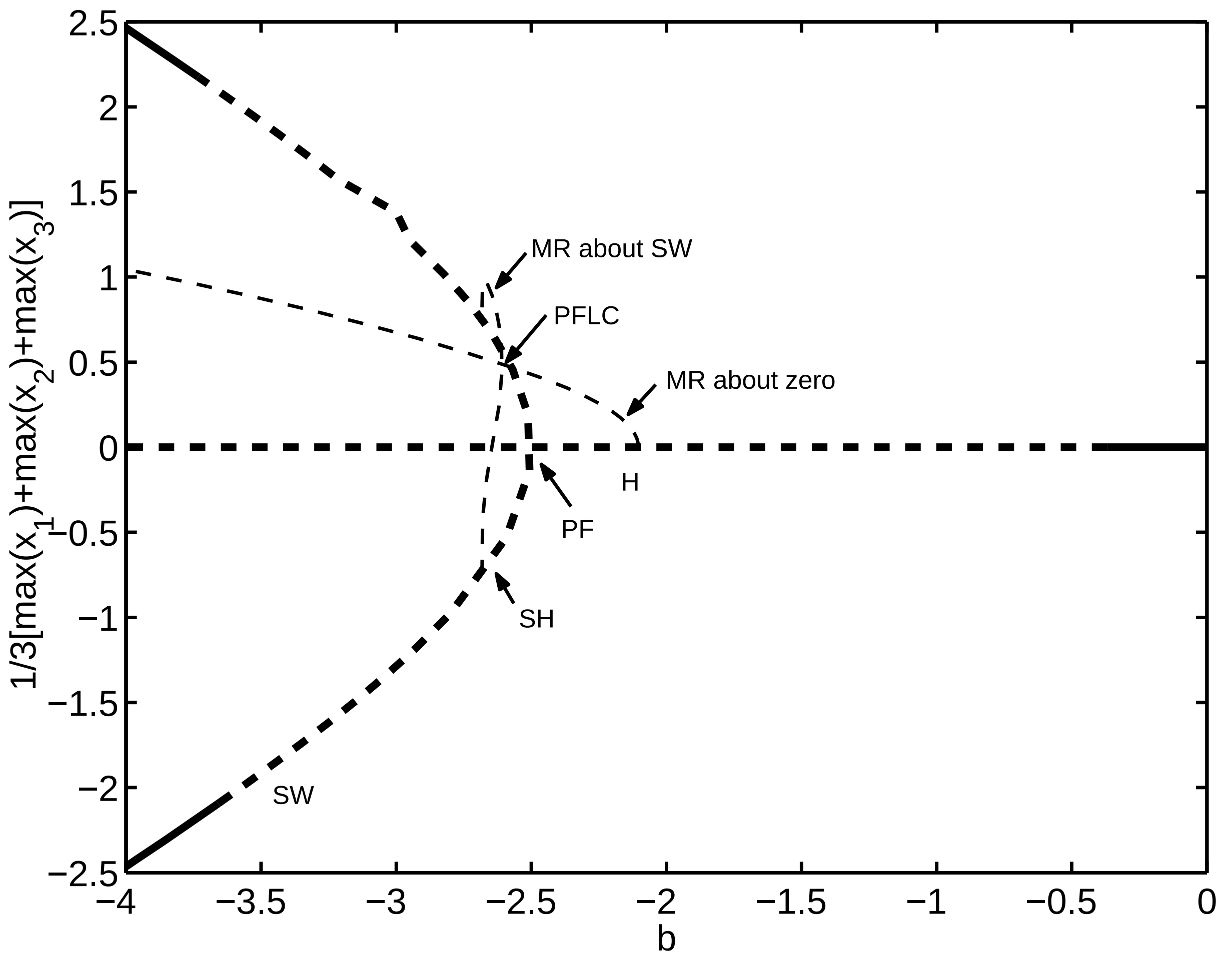
Codimension Two Bifurcations – Equivariant Hopf/Pitchfork

Example: $n = 3, a = -1.5, \tau_s = 1$

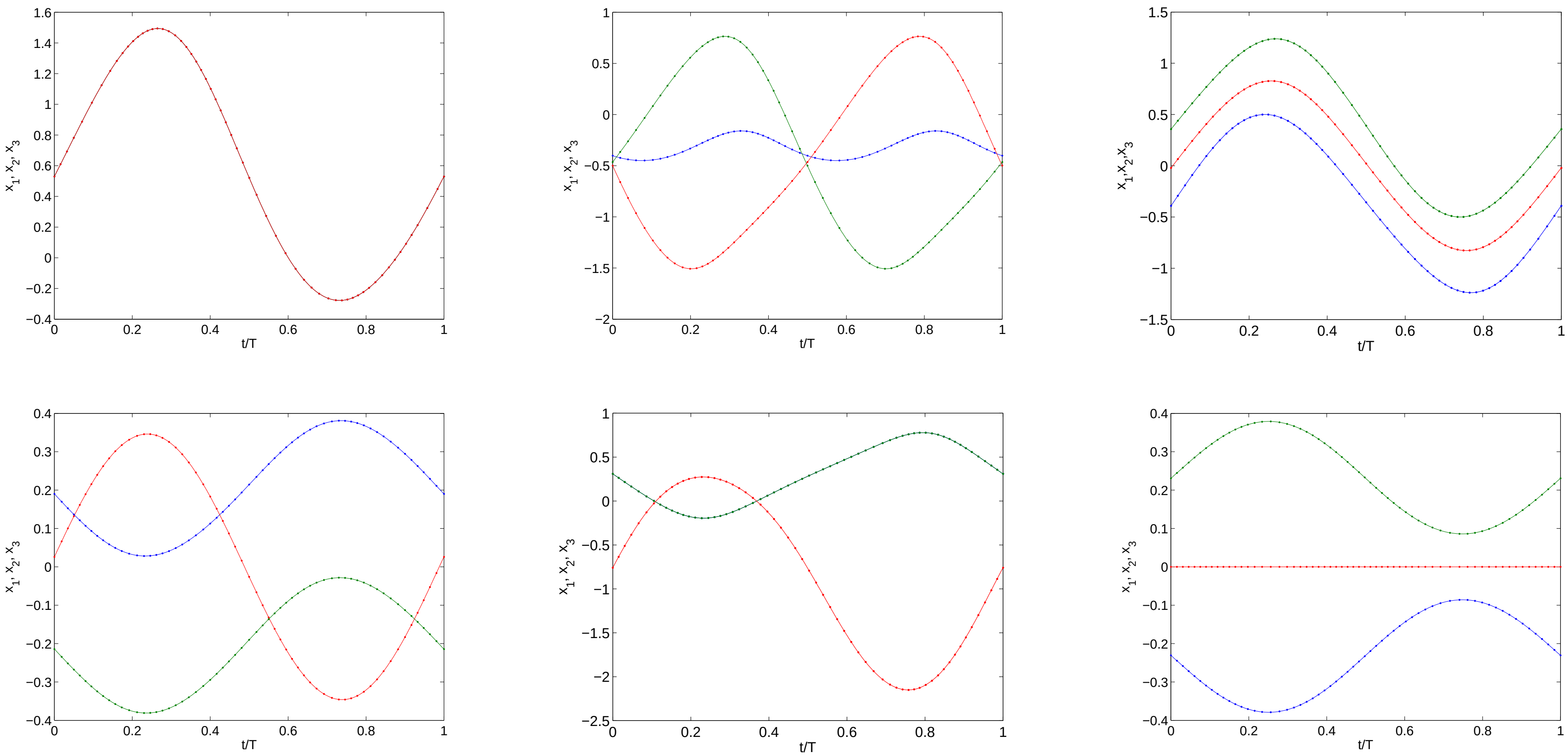


Codimension Two Bifurcations – Equivariant Hopf/Pitchfork

Example: $n = 3, a = -1.5, \tau_s = 1, \tau = 4$



Patterns of Oscillation



Conjectures

Conjecture 1

Consider a codimension two bifurcation point involving a standard pitchfork bifurcation and a D_n equivariant Hopf bifurcation of an equilibrium point. There will be a secondary equivariant Hopf bifurcation emanating from the codimension two point, giving rise to $2n+2$ branches of periodic orbits (n standing wave oscillations, n mirror reflecting oscillations and 2 phase-locked oscillations) about each equilibria produced by the pitchfork bifurcation. There will also be $2n+2$ pitchfork bifurcations of limit cycles emanating from the codimension two point.

Conjectures

Conjecture 2

Consider a codimension two bifurcation point involving a D_n equivariant pitchfork bifurcation and a standard Hopf bifurcation of an equilibrium point. Note that the pitchfork bifurcation gives rise to $2n$ standing wave equilibria and $2n$ mirror reflecting equilibria. There will be $4n$ secondary standard Hopf bifurcations emanating from the codimension two point, giving rise to $4n$ synchronous periodic orbits, one about each of the $4n$ asynchronous equilibria. There will also be $2n$ pitchfork bifurcations of limit cycles emanating from the codimension two point.

Conjectures

Conjecture 3

Consider a codimension two bifurcation point involving a D_n equivariant pitchfork bifurcation and a D_n equivariant Hopf bifurcation of an equilibrium point. There will be $8n$ secondary standard Hopf bifurcations emanating from the codimension two point, giving rise to $8n$ branches of periodic orbits, two about each of the $4n$ equilibria produced by the equivariant pitchfork bifurcation. There will also be $4n$ pitchfork bifurcations of limit cycles.

Conclusions

1. **Symmetry** in model leads to multiple patterns of oscillation.
2. **Delay** in model leads to multiple branches of Hopf bifurcation
3. **Symmetry + Delay** in model leads to multistability

Note: Systems with *different* models for individual neurons still exhibit same bifurcation structure.

N. Burić and D. Todorivic (2003), *Phys. Rev. E*, 67:0066222.

S.A. Campbell, R. Edwards and P. van den Driessche (2004), *SIAM J. Appl. Math.*, 65(1):316-335.

N. Burić, I. Grozdanović and N. Vasović (2005), *Chaos, Sol. & Frac.*, 23:1221-1233.

Future Work/Open Problems

- Effect of small perturbation to symmetry.
- Normal form analysis of codimension two bifurcation points involving equivariant bifurcations.
- Extension to systems with distributed delay.