

Scalar Reduction of a Neural Field Model with Spike Frequency Adaptation

Youngmin Park & Bard Ermentrout

University of Pittsburgh Department of Mathematics

yop6@pitt.edu

November 6, 2017

Introduction: Neural Field Model

We classify the dynamics of bump solutions of the system first studied by Pinto and Ermentrout (2001)

$$\frac{\partial u(\mathbf{x}, t)}{\partial t} = -u(\mathbf{x}, t) + \int_{\Omega} K(\mathbf{x} - \mathbf{y}) f(u(\mathbf{y}, t)) d\mathbf{y} \quad (1)$$

$$+ \varepsilon[ql(\mathbf{x}) - gz(\mathbf{x}, t)],$$

$$\frac{\partial z(\mathbf{x}, t)}{\partial t} = \varepsilon[-z(\mathbf{x}, t) + u(\mathbf{x}, t)], \quad (2)$$

- Periodic boundary conditions on Ω (unit circle or torus).

Introduction: Neural Field Model

We classify the dynamics of bump solutions of the system first studied by Pinto and Ermentrout (2001)

$$\frac{\partial u(\mathbf{x}, t)}{\partial t} = -u(\mathbf{x}, t) + \int_{\Omega} K(\mathbf{x} - \mathbf{y}) f(u(\mathbf{y}, t)) d\mathbf{y} \quad (1)$$

$$+ \varepsilon[ql(\mathbf{x}) - gz(\mathbf{x}, t)],$$

$$\frac{\partial z(\mathbf{x}, t)}{\partial t} = \varepsilon[-z(\mathbf{x}, t) + u(\mathbf{x}, t)], \quad (2)$$

- Periodic boundary conditions on Ω (unit circle or torus).
- K even, periodized Mexican hat on Ω , f sigmoidal.

Introduction: Neural Field Model

We classify the dynamics of bump solutions of the system first studied by Pinto and Ermentrout (2001)

$$\frac{\partial u(\mathbf{x}, t)}{\partial t} = -u(\mathbf{x}, t) + \int_{\Omega} K(\mathbf{x} - \mathbf{y}) f(u(\mathbf{y}, t)) d\mathbf{y} \quad (1)$$

$$+ \varepsilon [qI(\mathbf{x}) - gz(\mathbf{x}, t)],$$

$$\frac{\partial z(\mathbf{x}, t)}{\partial t} = \varepsilon [-z(\mathbf{x}, t) + u(\mathbf{x}, t)], \quad (2)$$

- Periodic boundary conditions on Ω (unit circle or torus).
- K even, periodized Mexican hat on Ω , f sigmoidal.
- $0 < \varepsilon \ll 1$,

Introduction: Neural Field Model

We classify the dynamics of bump solutions of the system first studied by Pinto and Ermentrout (2001)

$$\frac{\partial u(\mathbf{x}, t)}{\partial t} = -u(\mathbf{x}, t) + \int_{\Omega} K(\mathbf{x} - \mathbf{y}) f(u(\mathbf{y}, t)) d\mathbf{y} \quad (1)$$

$$+ \varepsilon [qI(\mathbf{x}) - gz(\mathbf{x}, t)],$$

$$\frac{\partial z(\mathbf{x}, t)}{\partial t} = \varepsilon [-z(\mathbf{x}, t) + u(\mathbf{x}, t)], \quad (2)$$

- Periodic boundary conditions on Ω (unit circle or torus).
- K even, periodized Mexican hat on Ω , f sigmoidal.
- $0 < \varepsilon \ll 1$,
- g, q represent the strength of adaptation and input current, respectively.

Ring Example Solutions

One-dimensional Example Solutions

Two-dimensional Example Solutions

- Analysis of the full neural field model is limited to numerics.

- Analysis of the full neural field model is limited to numerics.
- The neural field model on the two-dimensional domain is especially difficult to analyze.

- Analysis of the full neural field model is limited to numerics.
- The neural field model on the two-dimensional domain is especially difficult to analyze.
- However, all solutions of our neural field model have a well-defined centroid.

- Analysis of the full neural field model is limited to numerics.
- The neural field model on the two-dimensional domain is especially difficult to analyze.
- However, all solutions of our neural field model have a well-defined centroid.
- This property suggests a way to reduce the neural field models to a more tractable system.

Derivation of the Phase Equations

To reduce the neural field, we consider slow timescale shifts in the bump solution,

$$\begin{aligned} U(\mathbf{x}, \tau, \varepsilon) &= U_0(\mathbf{x}, \tau) + \varepsilon U_1(\mathbf{x}, \tau) + O(\varepsilon^2) \\ &= u_0(\mathbf{x} + \boldsymbol{\theta}(\tau)) + \varepsilon U_1(\mathbf{x}, \tau) + O(\varepsilon^2) \end{aligned}$$

where $\tau = \varepsilon t$, and u_0 is the translation-invariant steady-state solution. This ansatz is amenable to the method of multiple timescales Keener (1988).

Derivation of the Phase Equations

Substituting this power series into the neural field model, we get:

$$\begin{aligned} 0 &= -U_0(\mathbf{x}, \tau) + \int_{\Omega} K(\mathbf{x} - \mathbf{y}) f(U_0(\mathbf{y}, \tau)) d\mathbf{y} \\ (L_0 U_1)(\mathbf{x}, \tau) &= \frac{\partial U_0(\mathbf{x}, \tau)}{\partial \tau} - qI(\mathbf{x}) + g \int_0^{\tau} e^{-(\tau-s)} U_0(\mathbf{x}, s) ds, \end{aligned}$$

where

$$(L_0 v)(\mathbf{x}) = -v(\mathbf{x}) + \int_{\Omega} K(\mathbf{x} - \mathbf{y}) f'(U_0(\mathbf{y})) v(\mathbf{y}) d\mathbf{y}.$$

Derivation of the Phase Equations

The linear operator L_0 has a nontrivial nullspace spanned by $\partial_i u_0(\mathbf{x})$, $i = 1, 2$, so we can not immediately say that there exists a solution to the equation

$$(L_0 U_1)(\mathbf{x}, \tau) = \frac{\partial U_0(\mathbf{x}, \tau)}{\partial \tau} - qI(\mathbf{x}) + g \int_0^\tau e^{-(\tau-s)} U_0(\mathbf{x}, s) ds.$$

Derivation of the Phase Equations

Recall the Fredholm Alternative which states that the equation

$$(L_0 v)(\mathbf{x}) = b(\mathbf{x})$$

has a bounded solution if and only if

$$\langle v_i^*(\mathbf{x}), b(\mathbf{x}) \rangle = 0$$

for $i = 1, 2$, where v^* is in the nullspace of the adjoint L^* , and $\langle \cdot, \cdot \rangle$ is the natural inner product,

$$\langle u(\mathbf{x}), v(\mathbf{x}) \rangle = \int_{\Omega} u(\mathbf{x}) v(\mathbf{x}) \, d\mathbf{x}.$$

Derivation of the Phase Equations

the operator L_0 has an adjoint

$$(L^*v)(\mathbf{x}) = -v(\mathbf{x}) + f'(u_0(\mathbf{x})) \int_{\Omega} K(\mathbf{x} - \mathbf{y})v(\mathbf{y}) d\mathbf{y},$$

with a nullspace spanned by $v_i^*(\mathbf{x}) = f'(u_0(\mathbf{x}))\partial_i u_0(\mathbf{x})$, $i = 1, 2$.

For there to exist a solution to

$$(L_0 U_1)(\mathbf{x}, \tau) = \frac{\partial U_0(\mathbf{x}, \tau)}{\partial \tau} - qI(\mathbf{x}) + g \int_0^{\tau} e^{-(\tau-s)} U_0(\mathbf{x}, s) ds,$$

we take v_i^* to be orthogonal to the right hand side.

Phase Equations

Rearranging terms of the inner product yields

$$\frac{d\theta_i}{d\tau} = qJ_i(\boldsymbol{\theta}) - g \int_0^\tau e^{-(\tau-s)} H_i(\boldsymbol{\theta}(s) - \boldsymbol{\theta}(\tau)) ds, \quad i = 1, 2,$$

where

$$\begin{aligned} J_i(\boldsymbol{\theta}) &= \int_{\Omega} f'(u_0(\mathbf{x} + \boldsymbol{\theta})) \partial_i u_0(\mathbf{x} + \boldsymbol{\theta}) l(\mathbf{x}) \, d\mathbf{x}, \\ H_i(\boldsymbol{\theta}) &= \int_{\Omega} f'(u_0(\mathbf{x})) \partial_i u_0(\mathbf{x}) u_0(\mathbf{x} + \boldsymbol{\theta}) \, d\mathbf{x}, \end{aligned}$$

and $\boldsymbol{\theta} = (\theta_1, \theta_2)$, $\tau = \varepsilon t$.

Qualitative Dynamics on the 1D Domain

- We can simplify the 1D neural field model if we choose a cosine kernel $K(x) = A + B \cos(x)$.

Qualitative Dynamics on the 1D Domain

- We can simplify the 1D neural field model if we choose a cosine kernel $K(x) = A + B \cos(x)$.
- This choice allows us to write the solutions as

$$\begin{aligned}u(x, t) &= a_0(t) + a_1(t) \cos x + a_2(t) \sin x, \\z(x, t) &= b_0(t) + b_1(t) \cos x + b_2(t) \sin x.\end{aligned}$$

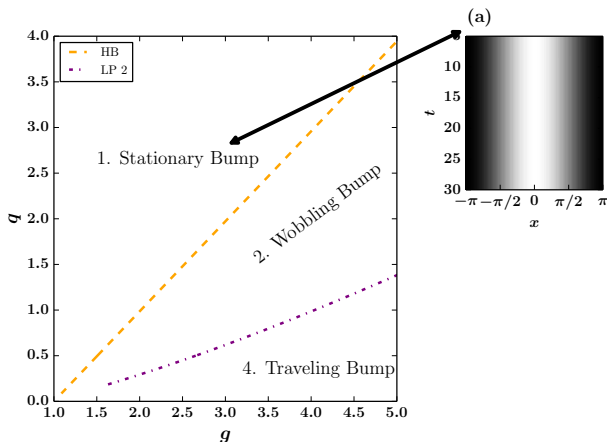
Qualitative Dynamics on the 1D Domain

- We can simplify the 1D neural field model if we choose a cosine kernel $K(x) = A + B \cos(x)$.
- This choice allows us to write the solutions as

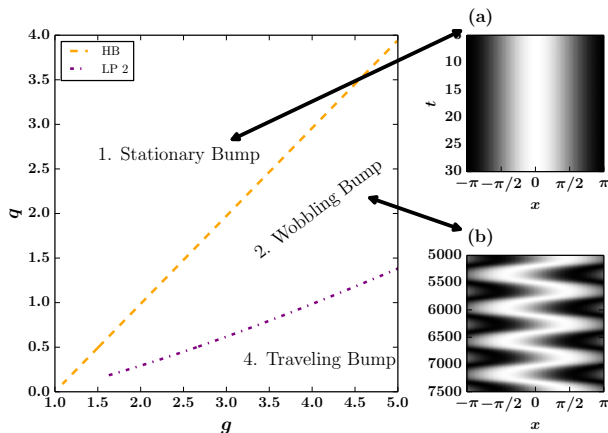
$$\begin{aligned}u(x, t) &= a_0(t) + a_1(t) \cos x + a_2(t) \sin x, \\z(x, t) &= b_0(t) + b_1(t) \cos x + b_2(t) \sin x.\end{aligned}$$

- Plugging these solutions into the neural field equations gives us the ODEs for the coefficients.

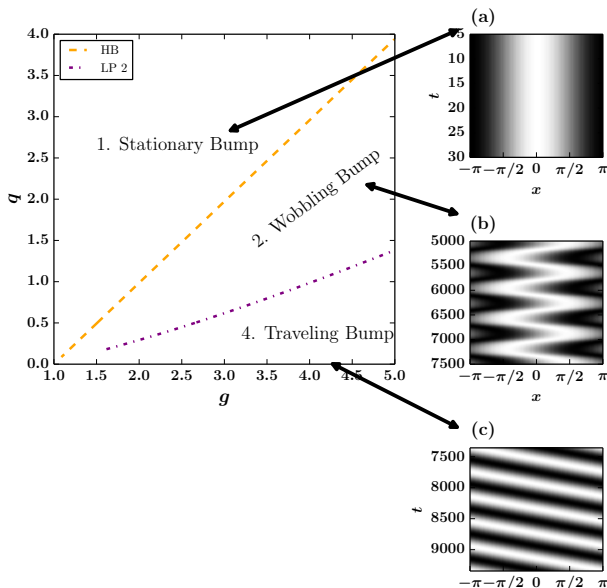
Qualitative Dynamics on the 1D Domain



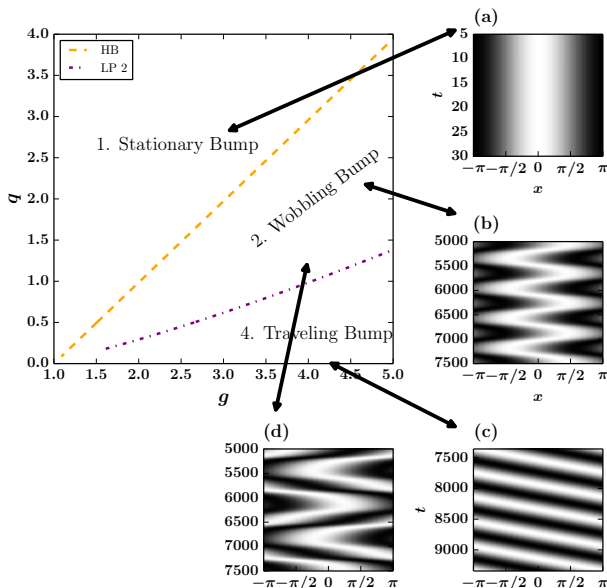
Qualitative Dynamics on the 1D Domain



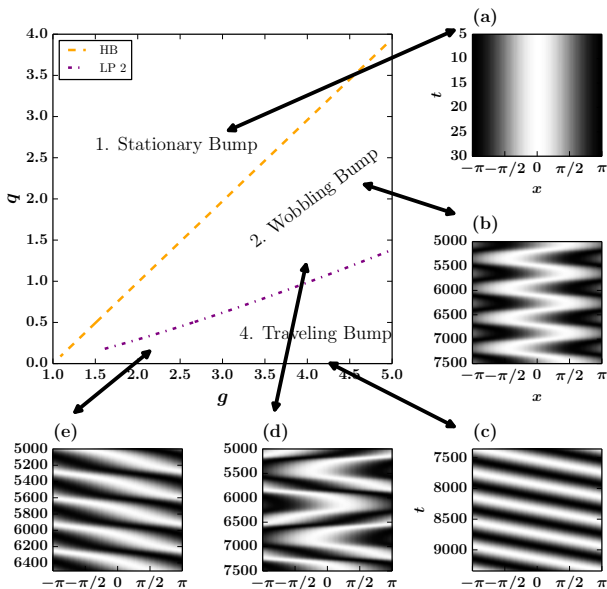
Qualitative Dynamics on the 1D Domain



Qualitative Dynamics on the 1D Domain



Qualitative Dynamics on the 1D Domain



One-dimensional Domain: Equivalent Phase Equation

If $K(x) = A + B \cos(x)$, then $H(x) = \sin(x)$.

$$\begin{aligned}\frac{d\theta}{d\tau} &= qJ(\theta) - g \int_0^\tau e^{-(\tau-s)} H(\theta(s) - \theta(\tau)) ds \\ &= -q \sin(\theta) - g[\cos(\theta)S(\tau) - \sin(\theta)C(\tau)],\end{aligned}$$

where

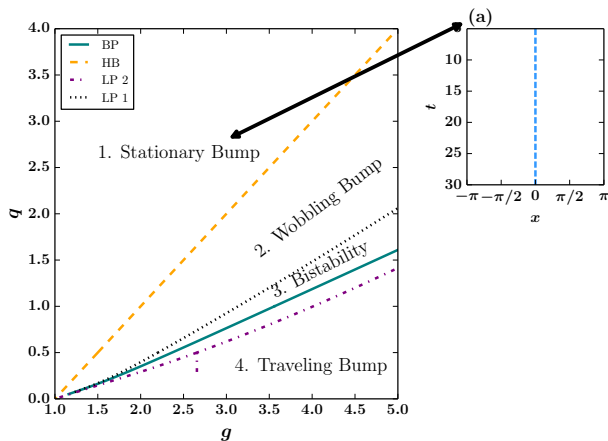
$$S(\tau) = \int_0^\tau e^{-(\tau-s)} \sin \theta(s) ds, \quad C(\tau) = \int_0^\tau e^{-(\tau-s)} \cos \theta(s) ds$$

One-dimensional Domain: Equivalent Phase Equation

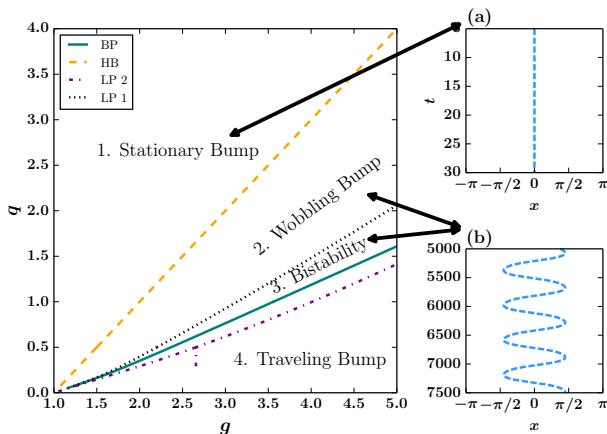
So the phase model has equivalent form,

$$\begin{aligned}\frac{d\theta}{d\tau} &= -q \sin(\theta) - g[\cos(\theta)S(\tau) - \sin(\theta)C(\tau)] \\ \frac{dS}{d\tau} &= -S(\tau) + \sin \theta, \\ \frac{dC}{d\tau} &= -C(\tau) + \cos \theta.\end{aligned}$$

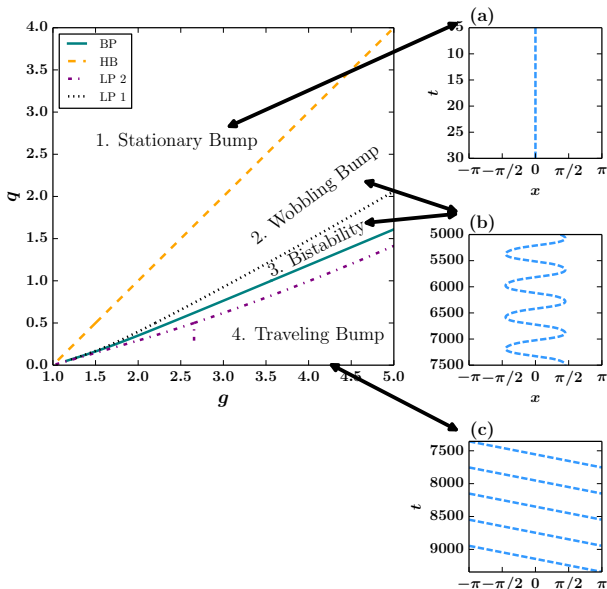
Numerical Results on the 1D Domain: Phase Equation



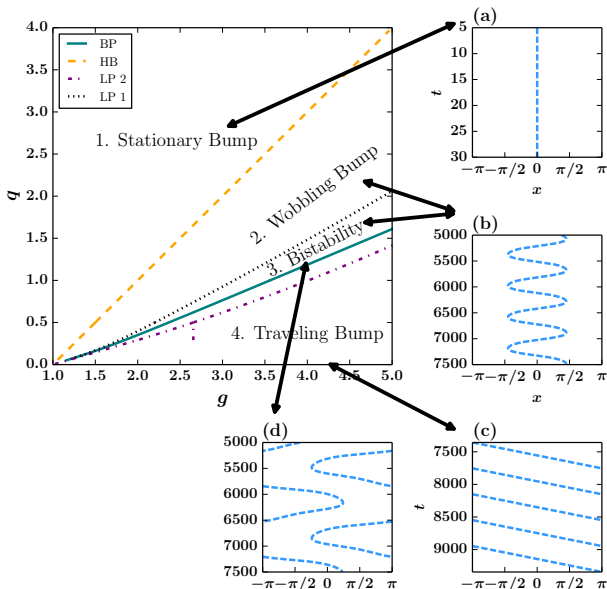
Numerical Results on the 1D Domain: Phase Equation



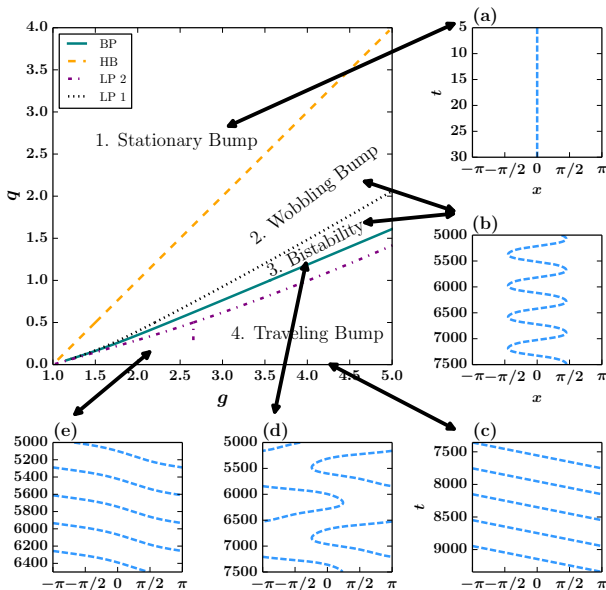
Numerical Results on the 1D Domain: Phase Equation



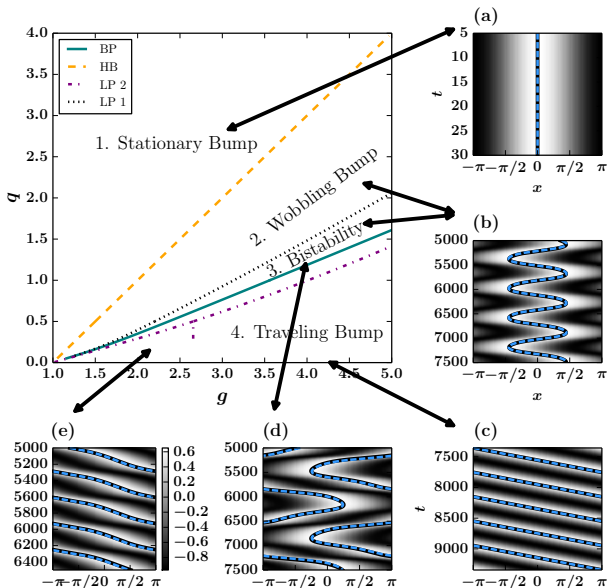
Numerical Results on the 1D Domain: Phase Equation



Numerical Results on the 1D Domain: Phase Equation



Numerical Results on the 1D Domain: Phase Equation



Analytical Results on the 1D Domain: Oscillations

First, existence of a Hopf bifurcation: Let $\theta = 0 + \varepsilon e^{\lambda\tau}$. Plug this expansion into the phase to get an equation for λ .

$$\lambda^2 + \lambda[1 - qJ'(0) - gH'(0)] - qJ'(0) = 0$$

Generally, $J'(0) < 0$ and $H'(0) > 0$, so there exists a Hopf bifurcation when

$$g^* = \frac{1 - qJ'(0)}{H'(0)}.$$

with q sufficiently large.

Existence and stability of oscillations follows from a normal form analysis.

Analytical Results on the 1D Domain: Traveling Solutions

Suppose $q = 0$ and $g > 0$ and let $\theta(\tau) = \nu\tau$. Plugging in to the phase equation with $H(x) = \sin(x)$ yields

$$\begin{aligned}\nu &= -g \int_0^\infty e^{-s} H(-\nu s) ds \\ &= g \int_0^\infty e^{-s} \sin(-\nu s) ds \\ &= \frac{g\nu}{1 + \nu^2}.\end{aligned}$$

So $\nu = \pm\sqrt{g-1}$

Qualitative Dynamics on the Two-dimensional Domain

We apply a similar transformation with the neural field model on two-dimensions.

- Take a Fourier truncation of the kernel,

$$K(\mathbf{x}) = k_{00} + k_{10} \cos(x_1) + k_{01} \cos(x_2) + k_{11} \cos(x_1) \cos(x_2),$$

which allows us to rewrite the neural field equations on the 2D domain into a system of 18 ODEs.

Qualitative Dynamics on the Two-dimensional Domain

We apply a similar transformation with the neural field model on two-dimensions.

- Take a Fourier truncation of the kernel,

$$K(\mathbf{x}) = k_{00} + k_{10} \cos(x_1) + k_{01} \cos(x_2) + k_{11} \cos(x_1) \cos(x_2),$$

which allows us to rewrite the neural field equations on the 2D domain into a system of 18 ODEs.

- Although the numerics are more tractable and compatible with AUTO, we are unable to generate a two parameter bifurcation diagram.

2D Domain: Approximation of the Phase Equations

$$\frac{d\theta_i}{d\tau} = qJ_i(\boldsymbol{\theta}) - g \int_0^\tau e^{-(\tau-s)} H_i(\boldsymbol{\theta}(s) - \boldsymbol{\theta}(\tau)) ds, \quad i = 1, 2,$$

- To generate bifurcation diagrams, we use the simplest nontrivial Fourier truncation of H_i ,

$$H_1^F(\theta_1, \theta_2) = \sin(\theta_1)(h_{10} + h_{11} \cos(\theta_2)).$$

2D Domain: Approximation of the Phase Equations

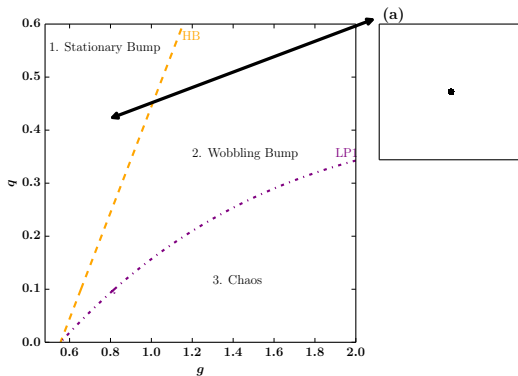
$$\frac{d\theta_i}{d\tau} = qJ_i(\boldsymbol{\theta}) - g \int_0^\tau e^{-(\tau-s)} H_i(\boldsymbol{\theta}(s) - \boldsymbol{\theta}(\tau)) ds, \quad i = 1, 2,$$

- To generate bifurcation diagrams, we use the simplest nontrivial Fourier truncation of H_i ,

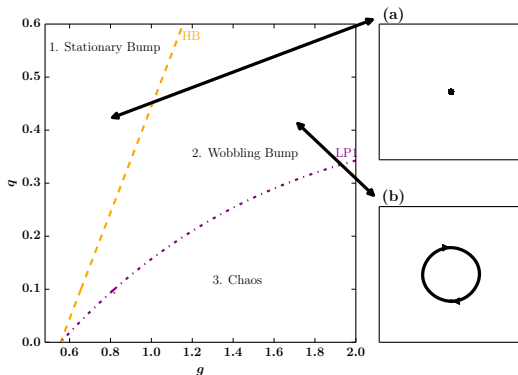
$$H_1^F(\theta_1, \theta_2) = \sin(\theta_1)(h_{10} + h_{11} \cos(\theta_2)).$$

- We can then rewrite the phase equations as a system of 10 ODEs and generate bifurcation diagrams using AUTO.

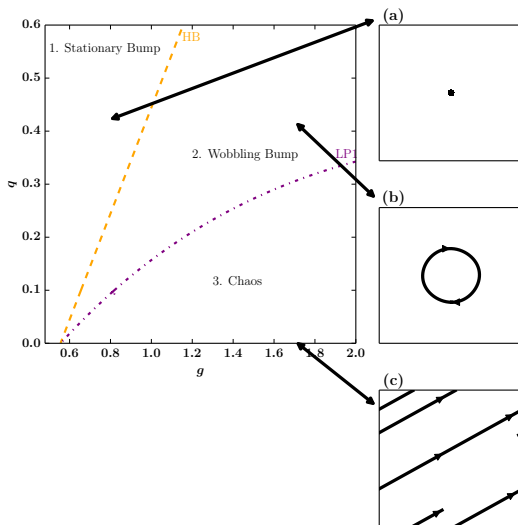
Numerical Results on the 2D Domain: Phase Equation



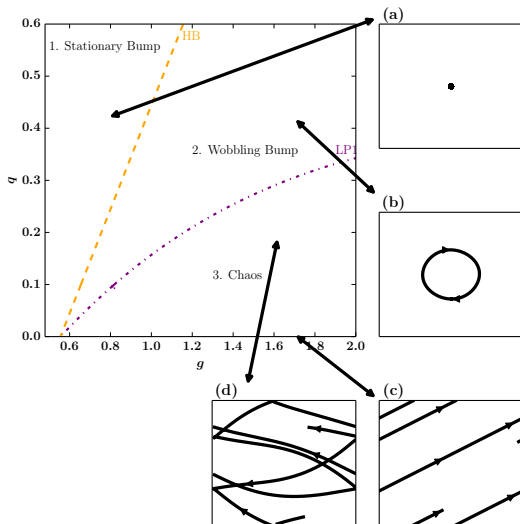
Numerical Results on the 2D Domain: Phase Equation



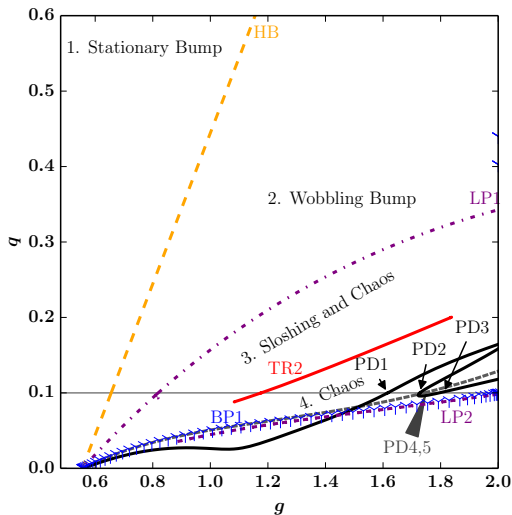
Numerical Results on the 2D Domain: Phase Equation



Numerical Results on the 2D Domain: Phase Equation



Numerical Results on the 2D Domain: Phase Equation



Analytical Results on the 2D Domain

Let $q = 0$ and consider the ansatz $\theta_1(\tau) = \nu_1\tau$ and $\theta_2(\tau) = \nu_2\tau$. Constant velocity bump solutions exist if ν_1, ν_2 simultaneously satisfy

$$\begin{aligned}\nu_1 &= g \int_0^\infty e^{-s} H_1(\nu_1 s, \nu_2 s) ds, \\ \nu_2 &= g \int_0^\infty e^{-s} H_2(\nu_1 s, \nu_2 s) ds.\end{aligned}$$

If we take $H_i = H_i^F$, we can solve for ν_1, ν_2 explicitly.

Analytical Results on the 2D Domain: Constant Velocity Solutions (Existence)

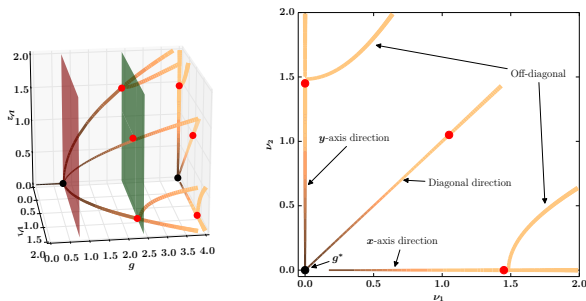


Figure: Existence of traveling bump solutions using the truncated interaction function H_i^F .

Results on the Two-dimensional Domain: Constant Velocity Solutions (Stability)

To study stability of the axial direction, we perturb off the axial solution, $\theta_1(\tau) = \nu\tau + \varepsilon e^{\lambda_1\tau}$ and $\theta_2(\tau) = 0 + \varepsilon e^{\lambda_2\tau}$, which gives us the eigenvalue equations,

$$\Lambda_1(\nu, \lambda) = 1 + \frac{\nu}{\int_0^\infty e^{-s} H_1(\nu s, 0) ds} \int_0^\infty e^{-s} \frac{\partial H_1}{\partial x}(\nu s, 0) \frac{e^{-\lambda s} - 1}{\lambda} ds,$$

$$\Lambda_2(\nu, \lambda) = 1 + \frac{\nu}{\int_0^\infty e^{-s} H_1(\nu s, 0) ds} \int_0^\infty e^{-s} \frac{\partial H_1}{\partial x}(0, \nu s) \frac{e^{-\lambda s} - 1}{\lambda} ds.$$

For a given velocity ν , the eigenvalue λ satisfies $\Lambda_i(\nu, \lambda) = 0$

Results on the Two-dimensional Domain: Constant Velocity Solution (Stability)

With $H_i^F(\theta_1, \theta_2) = \sin(\theta_1)(1 + b \cos(\theta_2))$, where $b = 0.8$, we compute the equations $\Lambda_i = 0$ explicitly as polynomials,

$$0 = \lambda_1^2 + \lambda_1 + 2\nu^2$$

$$0 = \lambda_2^3 + c_2\lambda_2^2 + c_1\lambda_2 + c_0,$$

where

$$c_0 = \frac{(2b-1)\nu^2 - \nu^4}{b+1}, \quad c_1 = \frac{(1+b+(2b-1)\nu^2)}{b+1},$$
$$c_2 = \frac{(2(b+1) - \nu^2)}{b+1}.$$

By the Routh-Hurwitz criterion, small velocity traveling bump solutions are stable. The stability condition fails when $\nu^2 = 2b - 1$.

Results on the Two-dimensional Domain: Constant Velocity Solution (Stability)

Results on the Two-dimensional Domain: Constant Velocity Solution (Stability)

Conclusion of Analysis on the 2D domain

- The phase model qualitatively reproduces the dynamics of the neural field model.
- As in the 1D domain, the phase model allows for a much more straightforward analysis for the existence of particular dynamics
 - Existence of sloshing solutions via a Hopf bifurcation.
 - Existence of constant velocity traveling solutions.
 - Existence and stability of non-constant velocity traveling solutions.

Conclusion

- We successfully reduce the dimensionality of the model to one or two scalar differential equations representing the coordinates of the centroid.
- This reduction places no strong assumptions on the firing rate function or the kernel.
- Using this reduction, we show that it faithfully reproduces the dynamics of the original neural field model, and we use it to rigorously classify the existence and stability of various bump dynamics.

Acknowledgements

- NSF DMS 1712922
- Kreso Josic
- Zack Kilpatrick
- Josh Gold
- G. Bard Ermentrout

Thanks to members of the Pitt math bio group

- Jon Rubin
- Brent Doiron
- Abby Pecoske
- Marcello Codiani
- Jay Pina

and visiting scholars

- Cati Vich (Universitat De Les Illes Balears)
- Aki Akao (Univ. of Tokyo)

James P Keener. *Principles of applied mathematics*. Addison-Wesley, 1988.

D. Pinto and G. Bard Ermentrout. Spatially structured activity in synaptically coupled neuronal networks: I. Traveling fronts and pulses. *SIAM Journal on Applied Mathematics*, 62(1):206–225, January 2001. ISSN 0036-1399. doi: 10.1137/S0036139900346453. URL <http://epubs.siam.org/doi/abs/10.1137/S0036139900346453>.