Travelling waves in biology: Lecture 4

Bumps, breathers, and waves in a neural network with threshold accommodation

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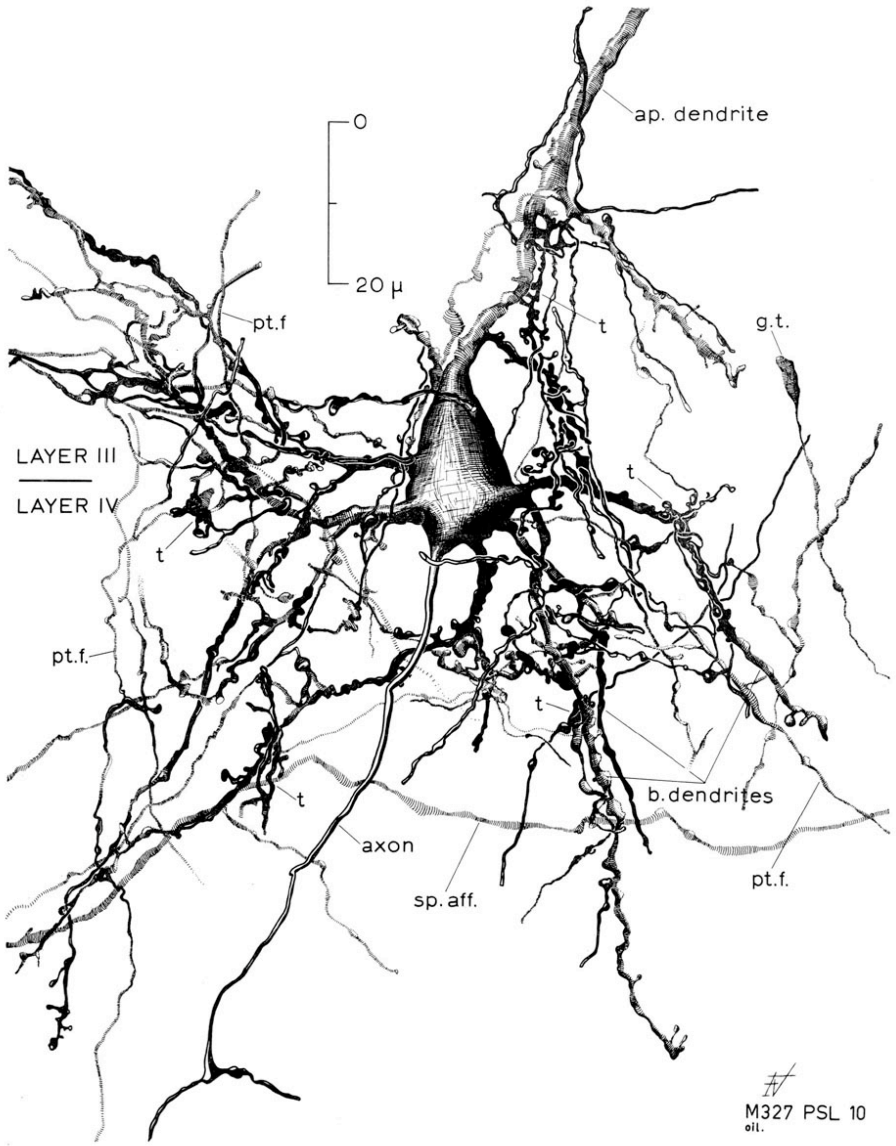
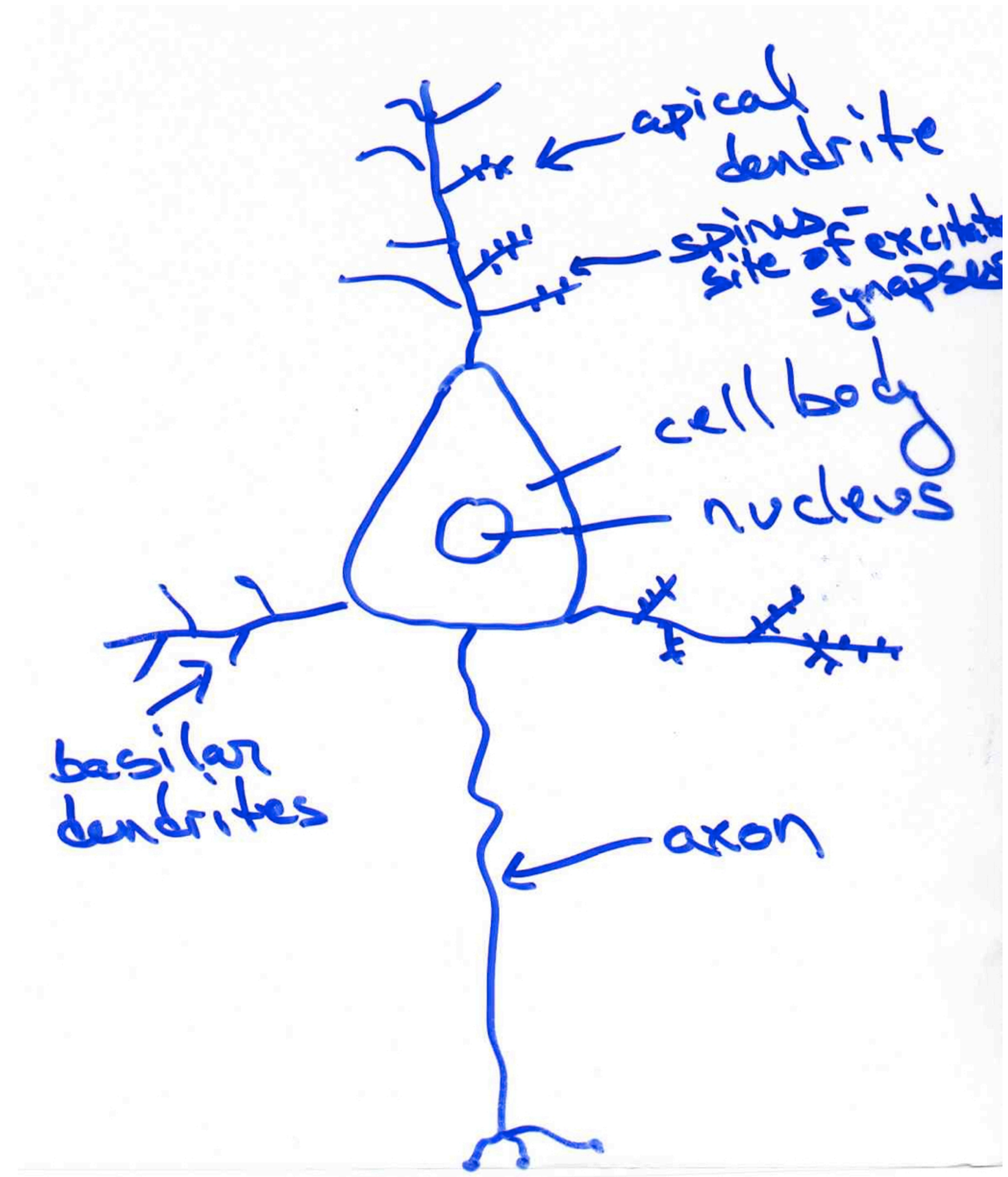
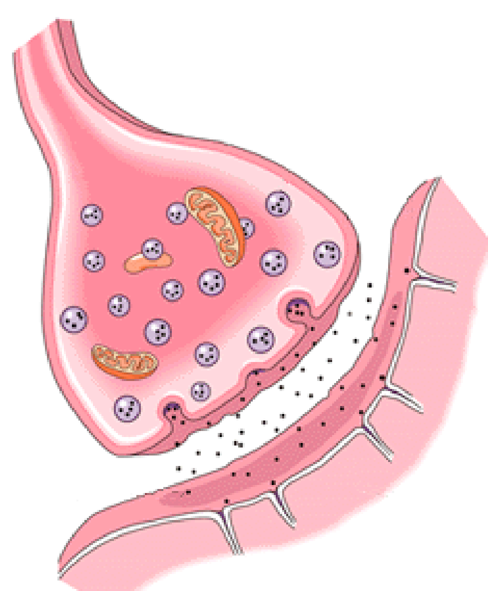
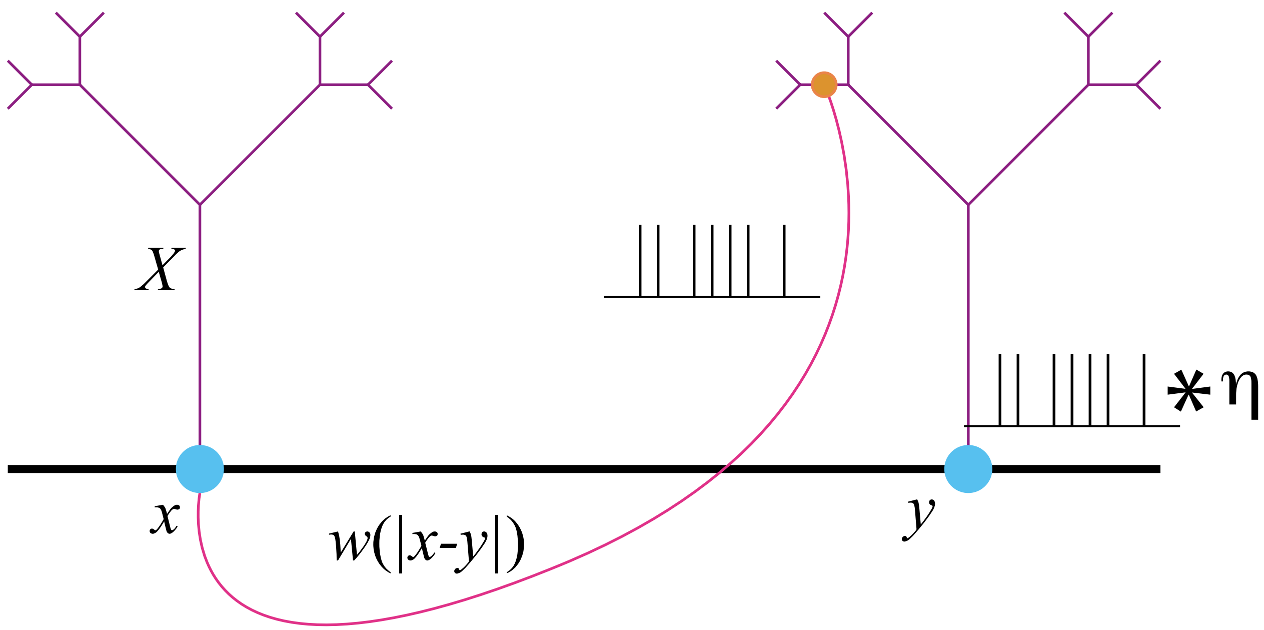
Neurons: pyramidal cells







Neural Field Model



Slow synapses:
spike train → firing rate f

$$f(u) = H(u)$$

Wilson and Cowan (1972, 1973), Amari (1977)

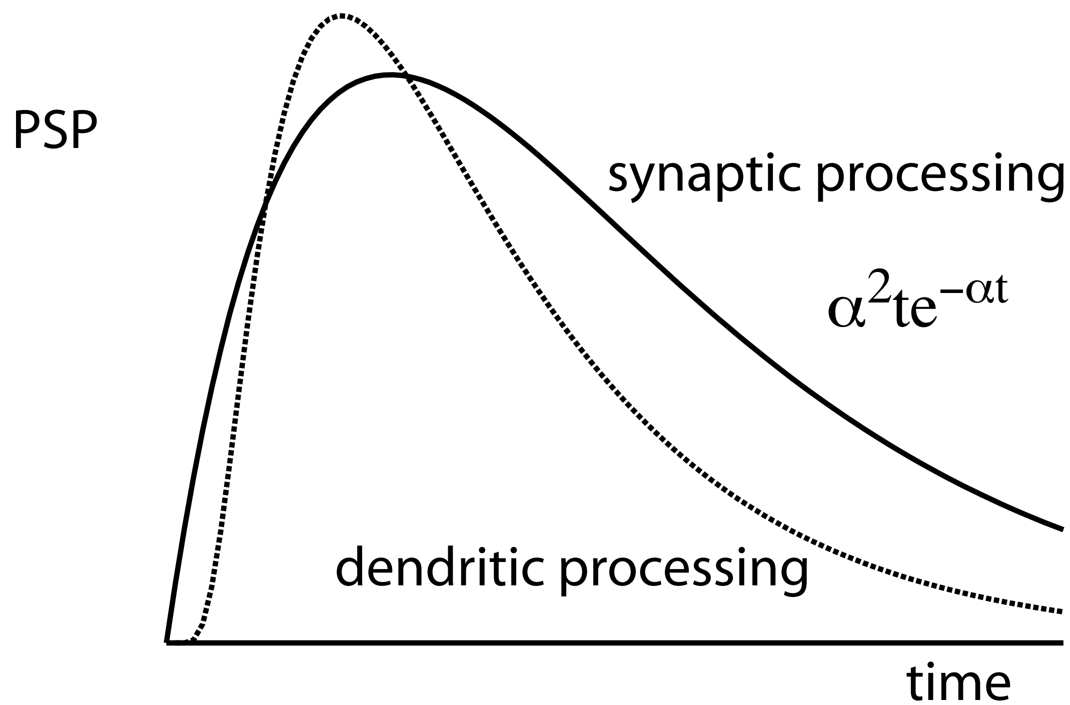
$$u(x,t) = \int_{-\infty}^{\infty} w(x-y) \int_{-\infty}^{t} \eta(t-s) f(u(y,s)-h) \mathrm{d}s\mathrm{d}y$$

Hill (1936), "... the threshold rises when the *local potential* is maintained ... and reverts gradually to its original value when the nerve is allowed to rest."

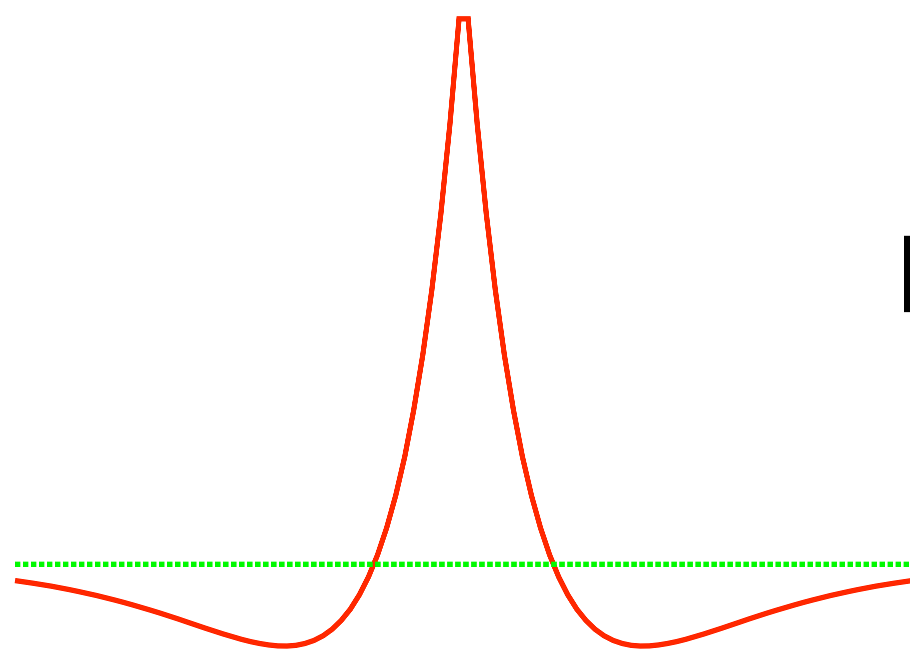
$$h_t = -(h - h_0) + \kappa H(u - \theta)$$

Network ingredients

Synaptic/dendritic processing



Network anatomy



Mexican-Hat

$$w(x) = (1 - |x|)e^{-|x|}$$

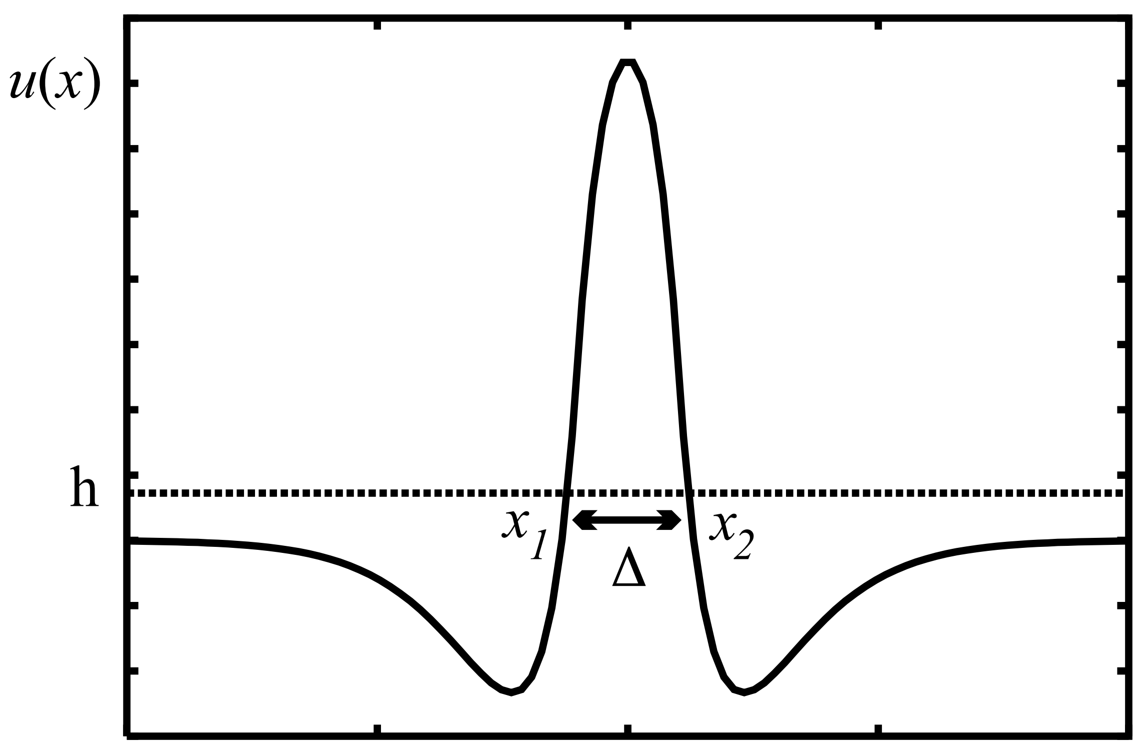
Behaviour without accommodation

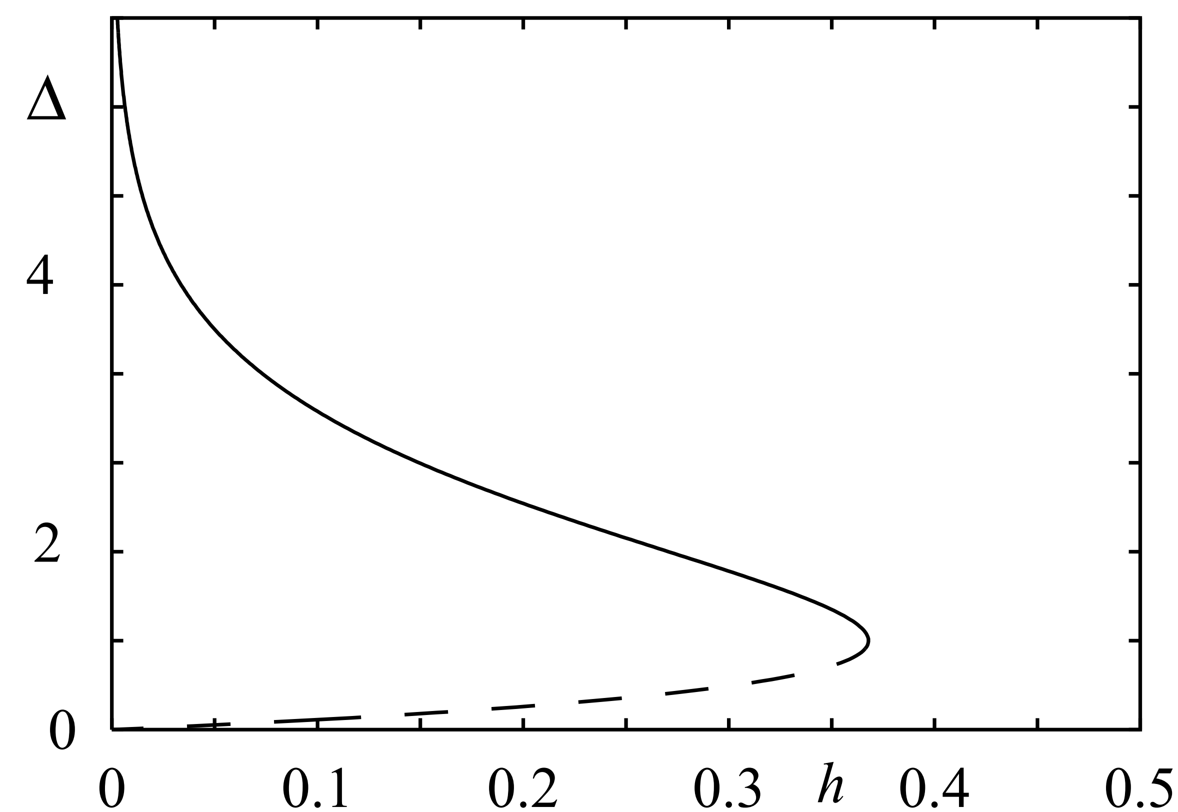
Time-independent solutions : $u(x) = \int_{\mathbb{R}} w(x-y) f(u(y)-h) \mathrm{d}y$

One-bump spatially localised solution

$$q(x) = \int_{x_1}^{x_2} w(x-y) \mathrm{d}y$$

$q(x_{1,2}) = h$ gives $\Delta \mathrm{e}^{-\Delta} = h$ where $\Delta = x_2 - x_1$





Stability

Examine eigenspectrum of the linearization about a solu

Solutions of form $u(x)\mathrm{e}^{\lambda t}$ satisfy $\mathcal{L}u(x) = u(x)$

$$\mathcal{L}u(x) = \tilde{\eta}(\lambda)\int_{-\infty}^{\infty} w(x-y)f'(q(y)-h)u(y)\mathrm{d}y$$

For Heaviside firing rate

$$f'(q(x)-h) = \delta(q(x)-h) = \frac{\delta(x-x_1)}{|q'(x_1)|} + \frac{\delta(x-x_2)}{|q'(x_2)|}$$

so

$$u(x) = \frac{\tilde{\eta}(\lambda)}{|w(0)-w(\Delta)|}[w(x-x_1)u(x_1) + w(x-x_2)u(x_2)]$$

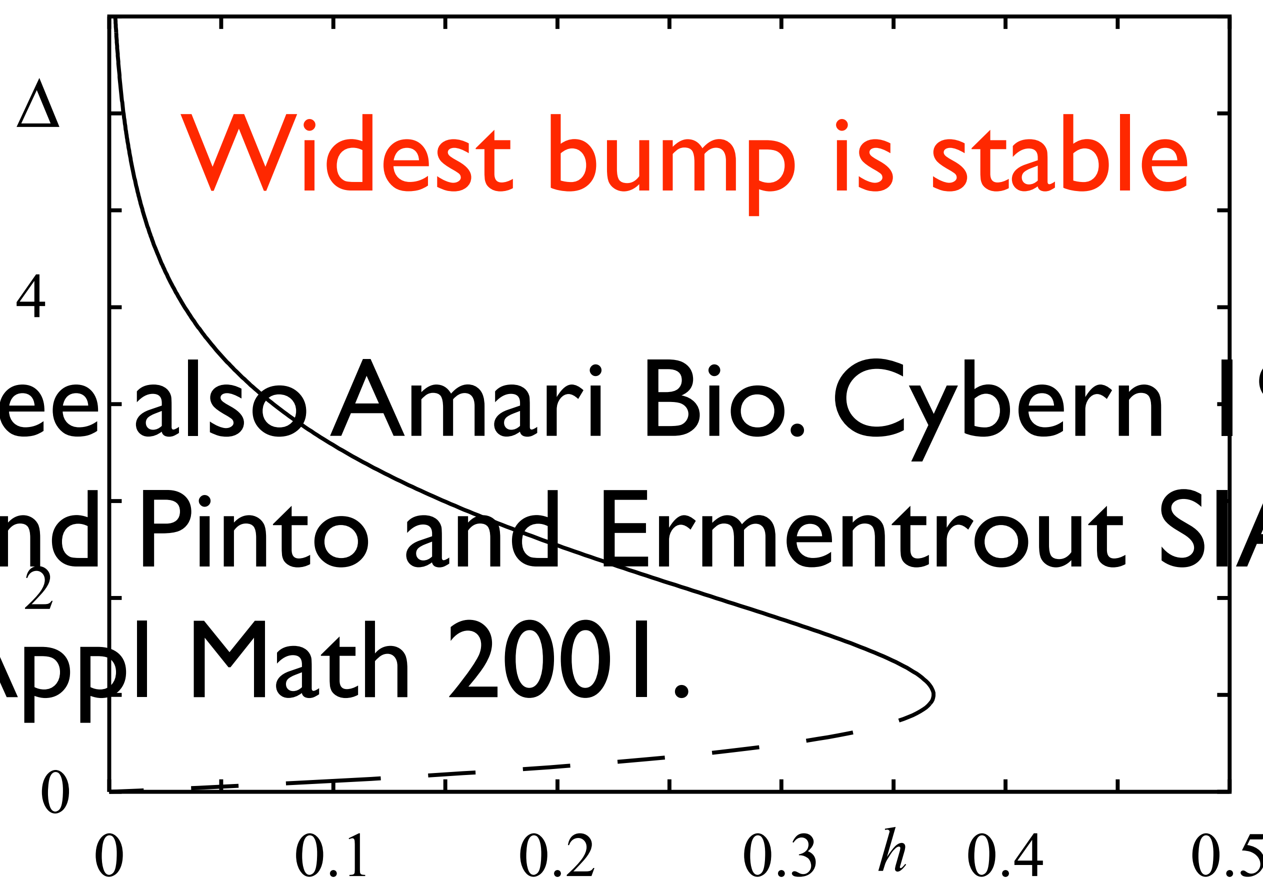
If $u(x_{1,2}) = 0$ then $u(x) = 0$ for all x. Matrix eqn :

$$\begin{bmatrix} u(x_1) \\ u(x_2) \end{bmatrix} = \mathcal{A}(\lambda) \begin{bmatrix} u(x_1) \\ u(x_2) \end{bmatrix}, \qquad \mathcal{A}(\lambda) = \frac{\tilde{\eta}(\lambda)}{|w(0) - w(\Delta)|} \begin{bmatrix} w(0) & w(\Delta) \\ w(\Delta) & w(0) \end{bmatrix}$$

Non trivial solutions if

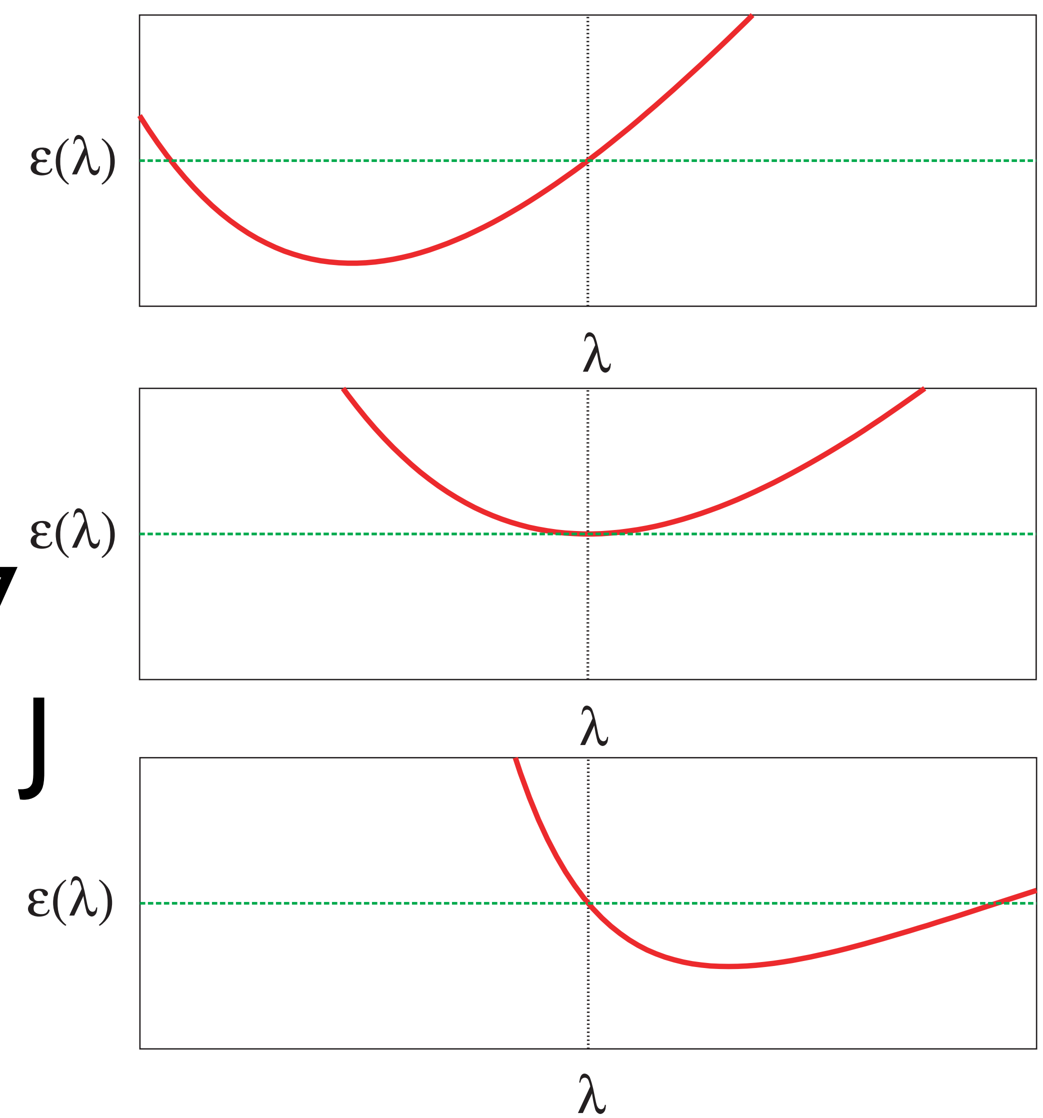
$$\mathcal{E}(\lambda) = |\mathcal{A}(\lambda) - I| = 0$$

Solutions stable if $\text{Re}(\lambda) < 0$



Widest bump is stable

See also Amari Bio. Cybern 1977 and Pinto and Ermentrout SIAM J Appl Math 2001.



Evans functions

Evans function for integral neural field equations with

Arbitrary synaptic footprints
Arbitrary synaptic response
Space dependent delays
[For a Heaviside]

Usual properties for $\mathcal{E}(\lambda)$

$\mathcal{E}(\lambda) = 0$ iff λ is an eigenvalue of $\mathcal{L}$

Order of the roots = multiplicity of eigenvalues

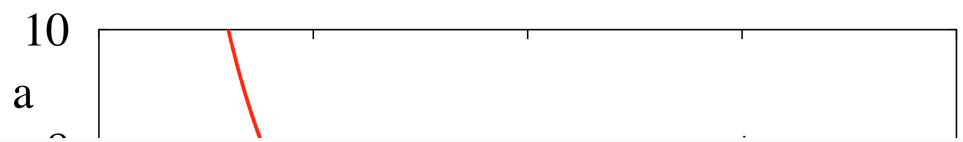
$\mathcal{E}(\lambda)$ is analytic

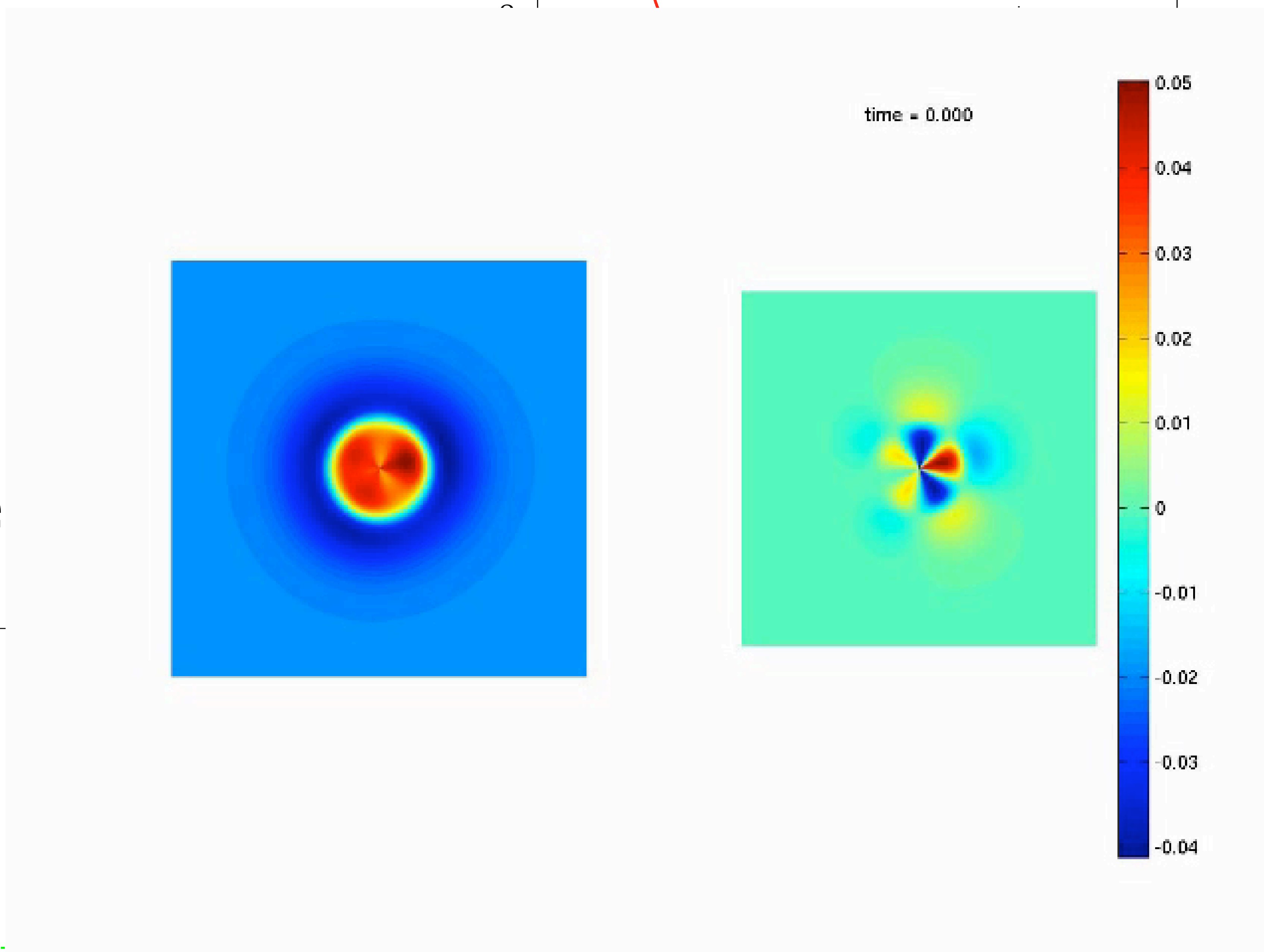
Essential spectrum in left half plane, so not a problem.

T Kapitula, N Kutz and B Sandstede. The Evans function for nonlocal equations. Indiana University Mathematics Journal 53 (2004)1095-1126
S Coombes and M R Owen (2004) Evans functions for integral neural field equations with Heaviside firing rate function SIAM Journal on Applied Dynamical Systems, Vol 34, 574-600.
D J Pinto, R K Jackson and C E Wayne (2005) Existence and stability of traveling pulses in a continuous neuronal network, *SIAM Journal on Applied Dynamical Systems* **4**, 954-984.

Stability in 2D

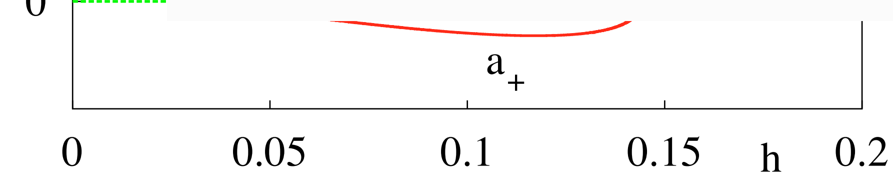
2D Wizard-Hat, radially symmetric one-bump

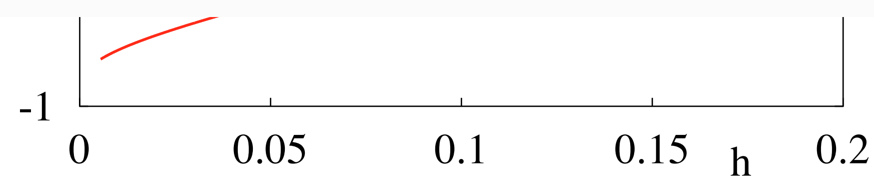


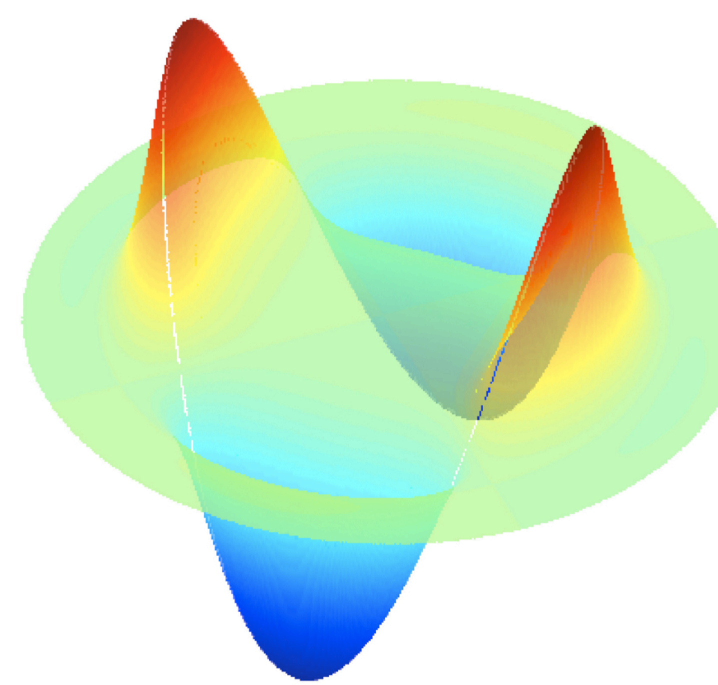


Eigenfunction suggests bump splits into two

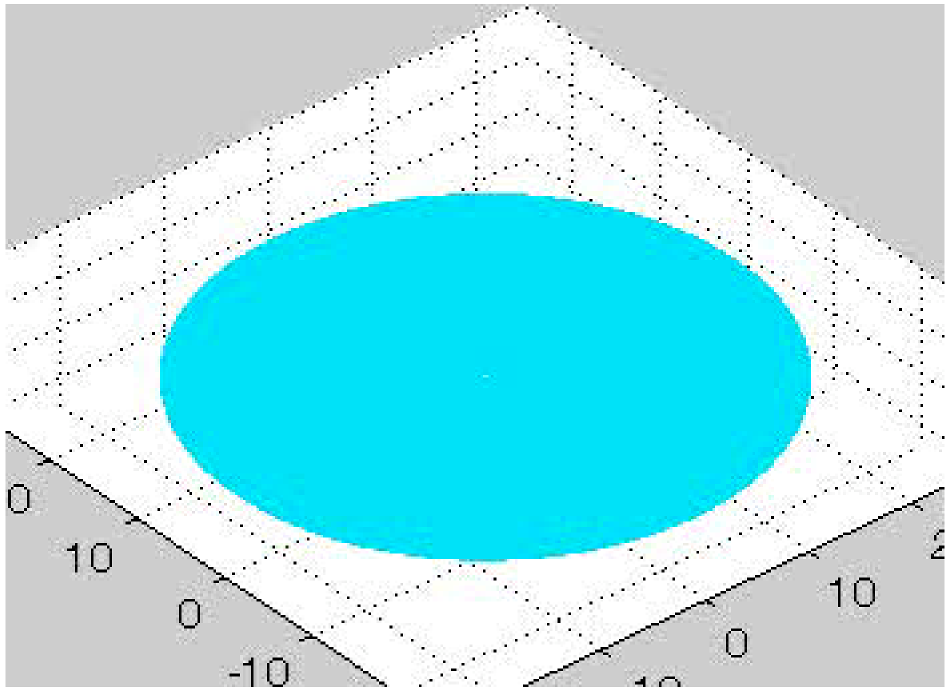
Pe … nt where $m \in \mathbb{Z}$







Bill Troy @ Pittsburgh



$$\frac{1}{\alpha}\partial_t u(\mathbf{r},t) = -u(\mathbf{r},t) + \int_{\mathbb{R}^2} \mathrm{d}\mathbf{r}\, w(|\mathbf{r}-\mathbf{r}'|) f\circ u(\mathbf{r}',t) - g a(\mathbf{r},t)$$

$$\partial_t a(\mathbf{r},t) = -a(\mathbf{r},t) + u(\mathbf{r},t)$$

Rotational bifurcation

following Moskalenko, Liehr, and Purwins, Europhys Lett, 2003

Linearising around time-independent solution $q(\mathbf{r})$ gives

$$\partial_t \psi(\mathbf{r},t) = \mathcal{L}[\overline{\psi}]\psi, \quad \psi = \begin{bmatrix} u(\mathbf{r},t) \\ a(\mathbf{r},t) \end{bmatrix}, \quad \overline{\psi} = \begin{bmatrix} q(\mathbf{r}) \\ q(\mathbf{r}) \end{bmatrix},$$

From invariance of the full system under rotation there exists a Goldstone mode $\psi_0 = \partial_\theta \overline{\psi}$

$$\mathcal{L}\psi_0 = 0.$$

Destabilisation when one of the other modes exactly coincides with ψ_0 under parameter variation. Parameter degeneracy means a generalised eigen-fn ψ_1 of $\mathcal{L}$ appears:

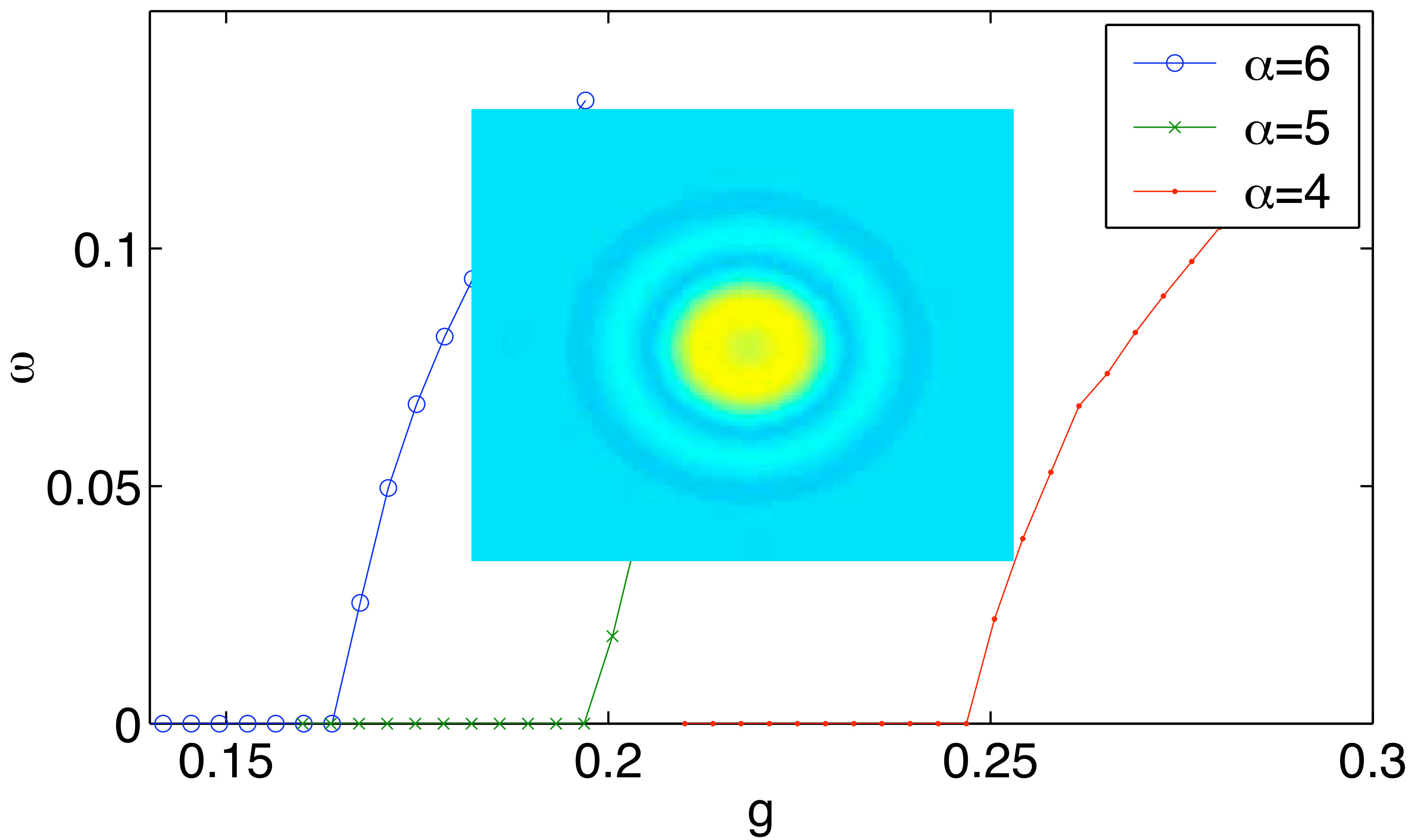
$$\mathcal{L}\psi_1 = \psi_0.$$

Solvability condition: $\langle \psi_0^\dagger \mid \psi_0 \rangle = 0, \qquad \mathcal{L}^\dagger \psi_0^\dagger = 0.$

Nice result that $\psi_0^\dagger$ can be expressed in terms of ψ_0

Bifurcation condition $0 = (\alpha g - 1) \left\langle f'(q)(\partial_\theta q)^2 \right\rangle$

$$\boxed{g_{\text{rot}} = \alpha^{-1}}$$



more eye candy

Threshold Accommodation

$$u(x,t) = \int_{-\infty}^{\infty} w(x-y) \int_{-\infty}^{t} \eta(t-s) f(u(y,s)-h) \mathrm{d}s\mathrm{d}y$$

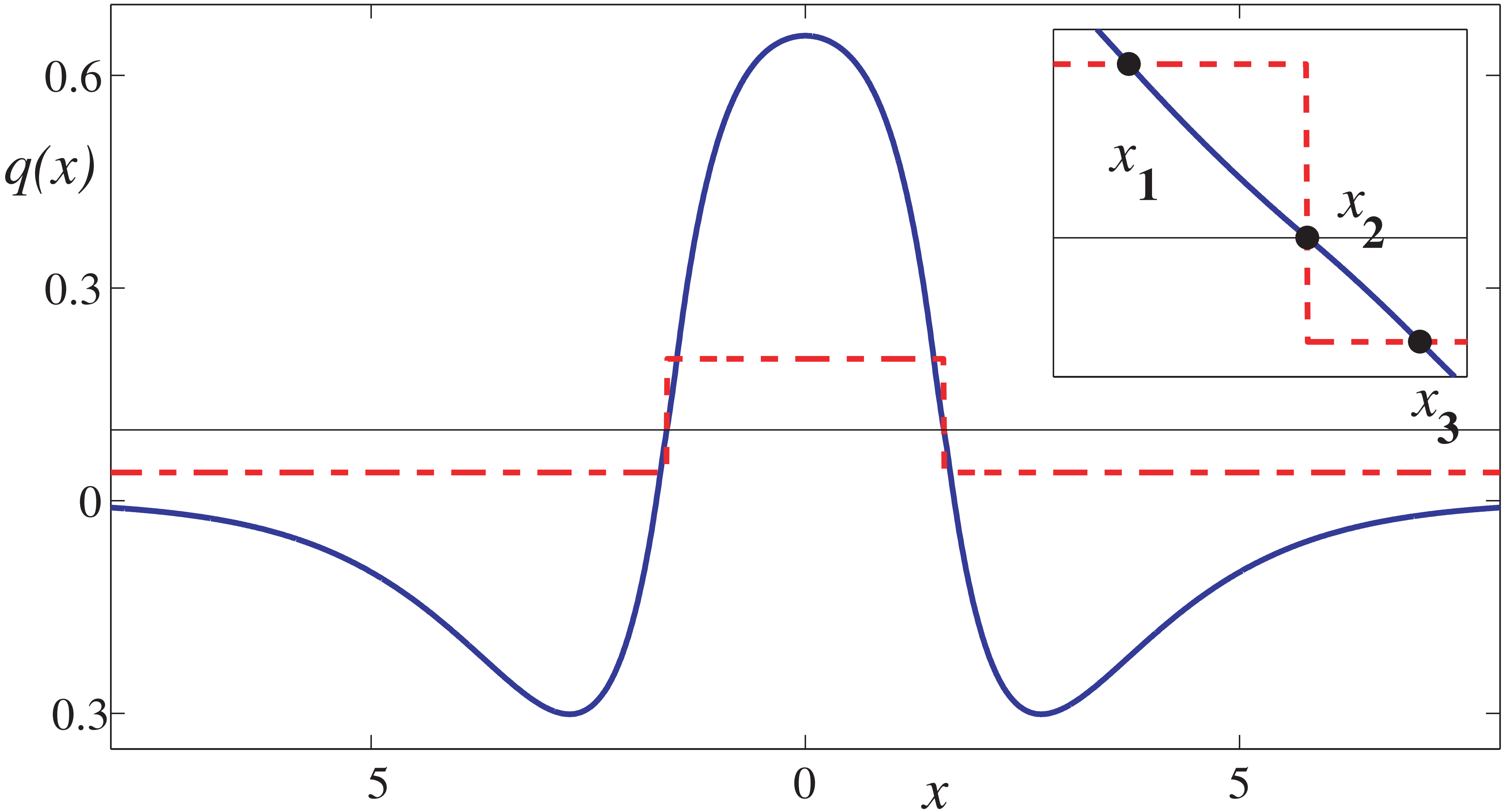
Hill (1936), "... the threshold rises when the *local potential* is maintained ... and reverts gradually to its original value when the nerve is allowed to rest."

$$h_t = -(h - h_0) + \kappa H(u - \theta)$$

Time-independent solutions $(u,h) = (q(x), p(x))$

$$(w \otimes f)(x,t) = \int_{-\infty}^{\infty} w(y) f(x-y,t) \mathrm{d}y$$

$$q = w \otimes H(q-p), \qquad p = \begin{cases} h_0 & q < \theta \\ h_0 + \kappa & q \geq \theta \end{cases}$$



An explicit solution may be constructed as

$$q(x) = \left(\int_{-x_3}^{-x_2} + \int_{-x_1}^{x_1} + \int_{x_2}^{x_3} \right) w(x-y) \mathrm{d}y$$

The unknowns x_1, x_2, x_3 are found by the simultaneous solution of

$$q(x_1) = h_0 + \kappa, \qquad q(x_2) = \theta, \qquad q(x_3) = h_0$$

Windows of existence: It appears that for κ less than some critical value there is only ever one solution of this type.

Bump Stability I

Perturbations: $(u(x), h(x))e^{\lambda t}$ $\qquad$ $\tilde{\eta}(\lambda) = \int_0^\infty \mathrm{d}s \eta(s) \mathrm{e}^{-\lambda s}$

$$u(x) = \tilde{\eta}(\lambda) w \otimes H'(q(x) - p(x))[u(x) - h(x)]$$

$$\lambda h(x) = -h(x) + \kappa H'(q(x) - \theta) u(x)$$

Hence $\dfrac{u}{\tilde{\eta}(\lambda)} = w \otimes H'(q - p) \left[1 - \dfrac{\kappa}{1+\lambda} H'(q - \theta) \right] u$

Within the convolution

$$H'(q(x) - p(x)) = \sum_{y = \pm x_1, \pm x_3} \frac{\delta(x - y)}{|q'(q^{-1}(y))|}$$

$$H'(q(x) - \theta) = \frac{1}{\kappa} \sum_{y = \pm x_2} \frac{\delta(x - y)}{|q'(q^{-1}(y))|}$$

Bump Stability II

$$\frac{u(x)}{\widetilde{\eta}(\lambda)} = \sum_{j=1}^{6} A_j(x,\lambda) u_j$$

where the A_j are defined in terms of $w(x), q'(x), x_{\pm 1}, x_{\pm 2}, x_{\pm 3}$

Demanding non-trivial solutions gives the Evans function

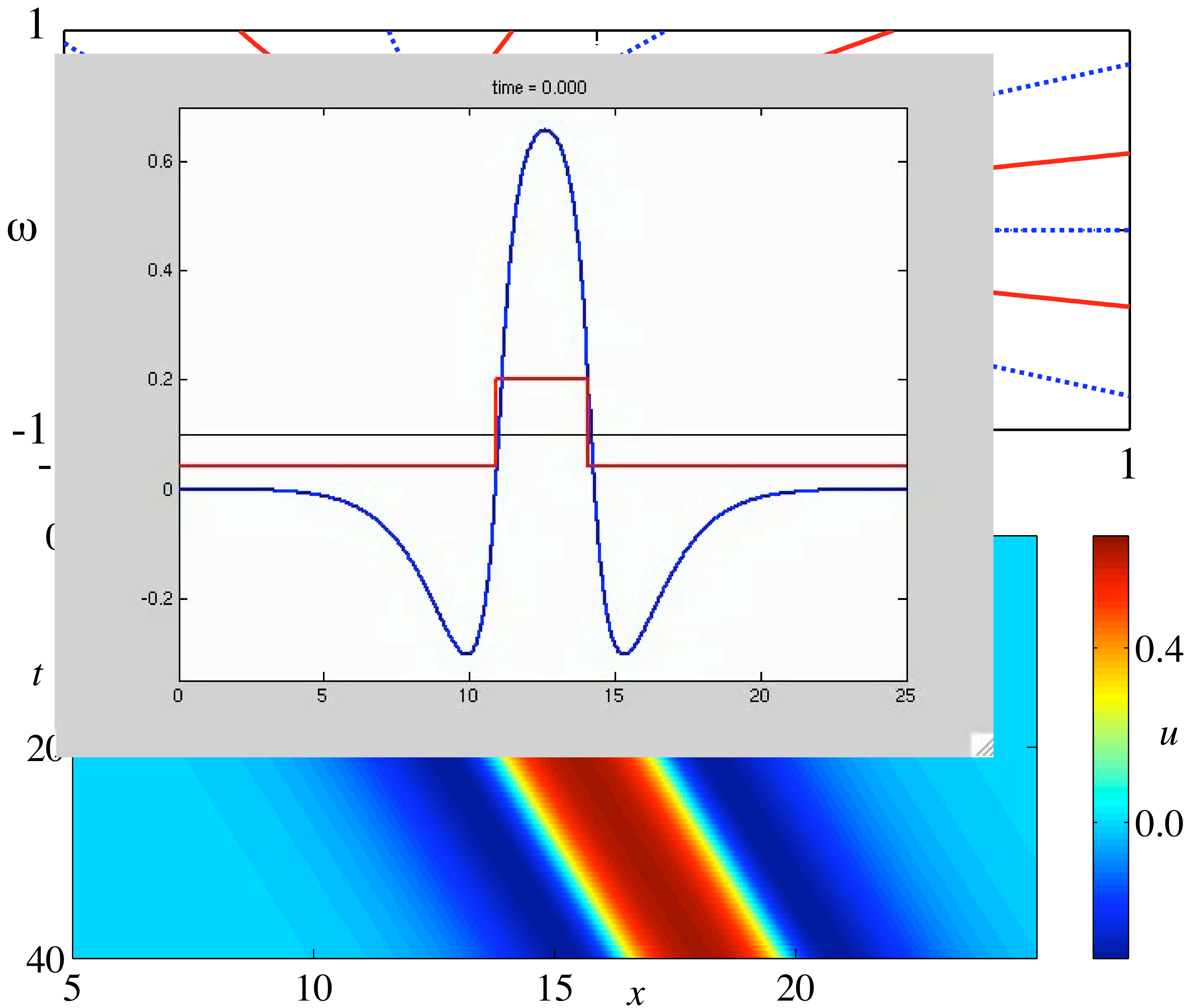
$$\mathcal{E}(\lambda) = |\mathcal{A}(\lambda) - I| = 0, \qquad \mathcal{A}(\lambda)_{ij} = \widetilde{\eta}(\lambda) A_j(x_i, \lambda)$$

One natural way to find the zeros of $\mathcal{E}(\lambda)$ is to write $\lambda = \nu + \text{i}\omega$ and plot the zero contours of **Re** $\mathcal{E}(\lambda)$ and **Im** $\mathcal{E}(\lambda)$ in the (ν, ω) plane. The Evans function is zero where the lines intersect.

S Coombes and M R Owen 2004 Evans functions for integral neural field equations with Heaviside firing rate function SIAM Journal on Applied Dynamical Systems, Vol 34, 574-600.

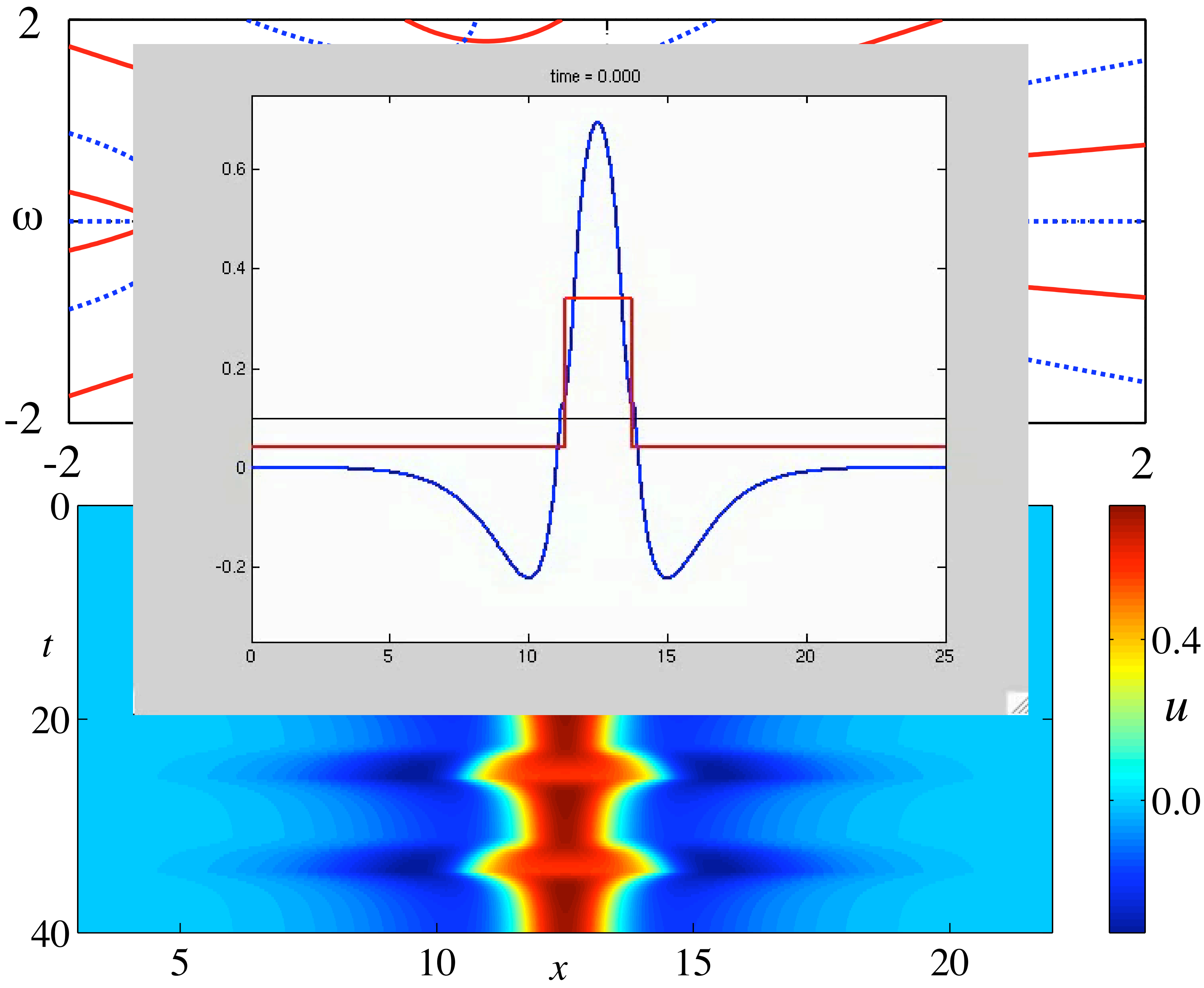
Bump Stability III: $\eta(t) = \alpha e^{-\alpha t}$

Low κ instability on Re axis (increasing α)

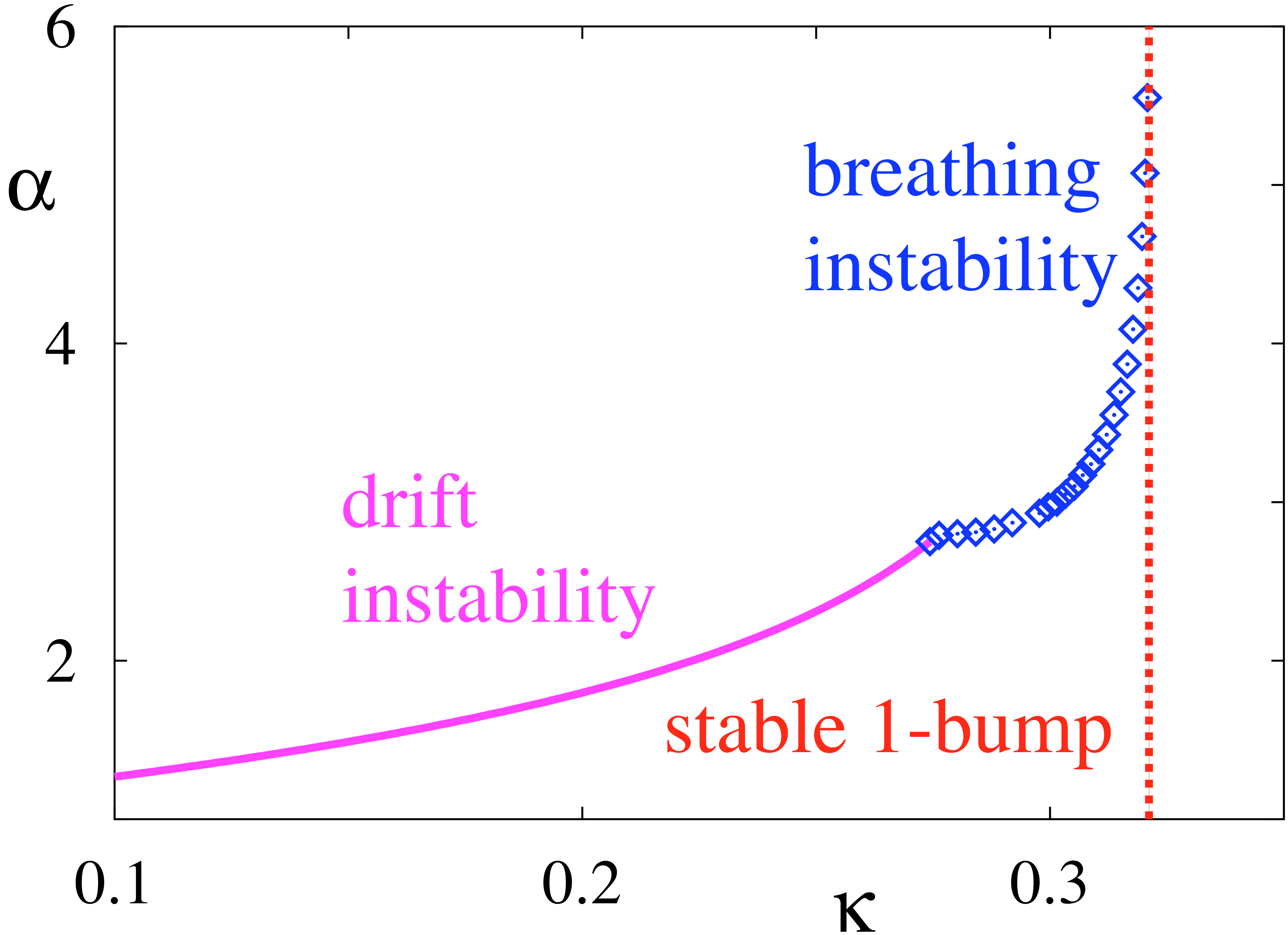


Bump Stability IV

High κ instability on Im axis (increasing α) gives a breather

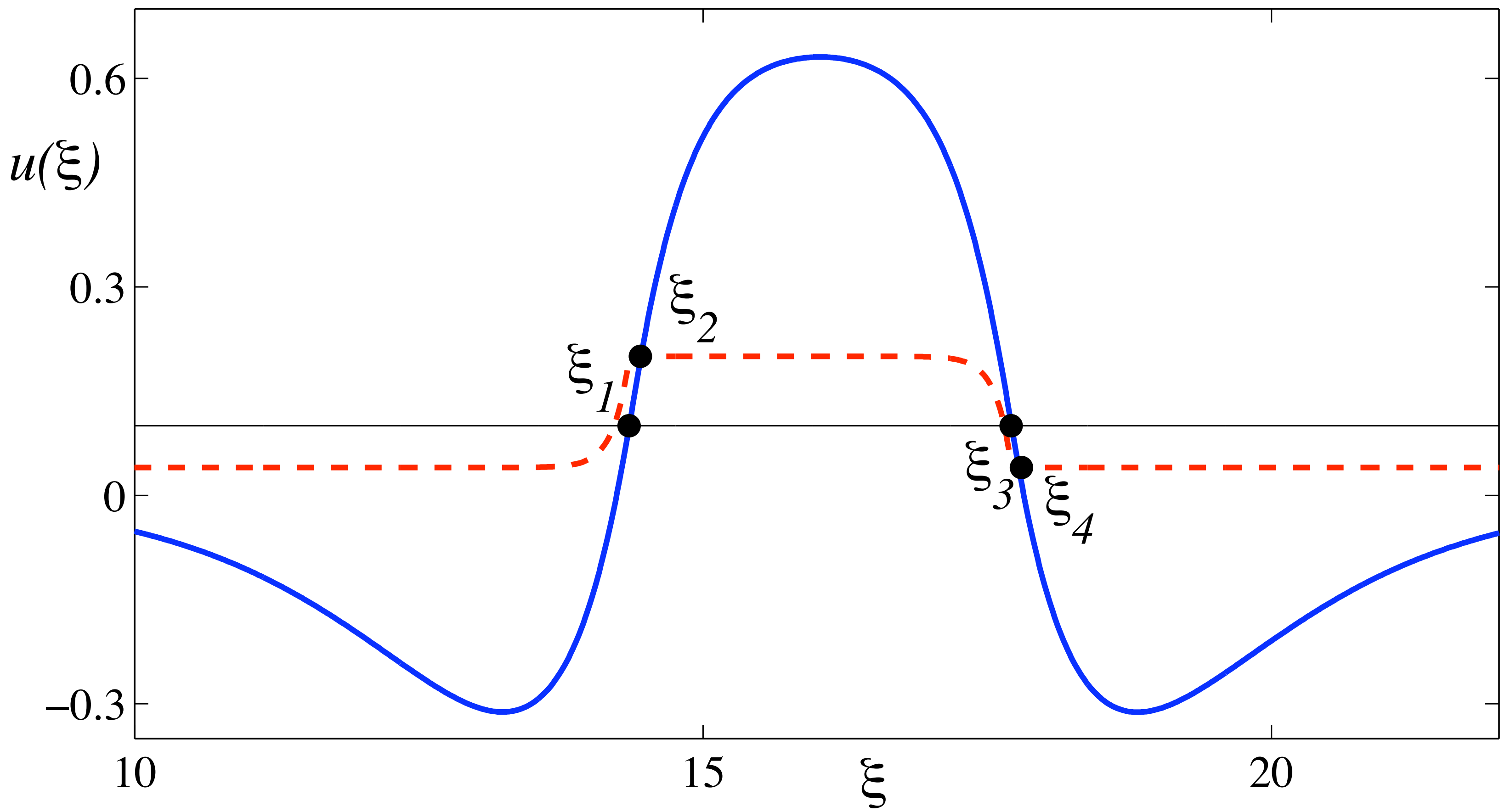


Summary of Bump instabilities



Travelling Pulse I

Introduce travelling wave coordinate $\xi = x - ct$



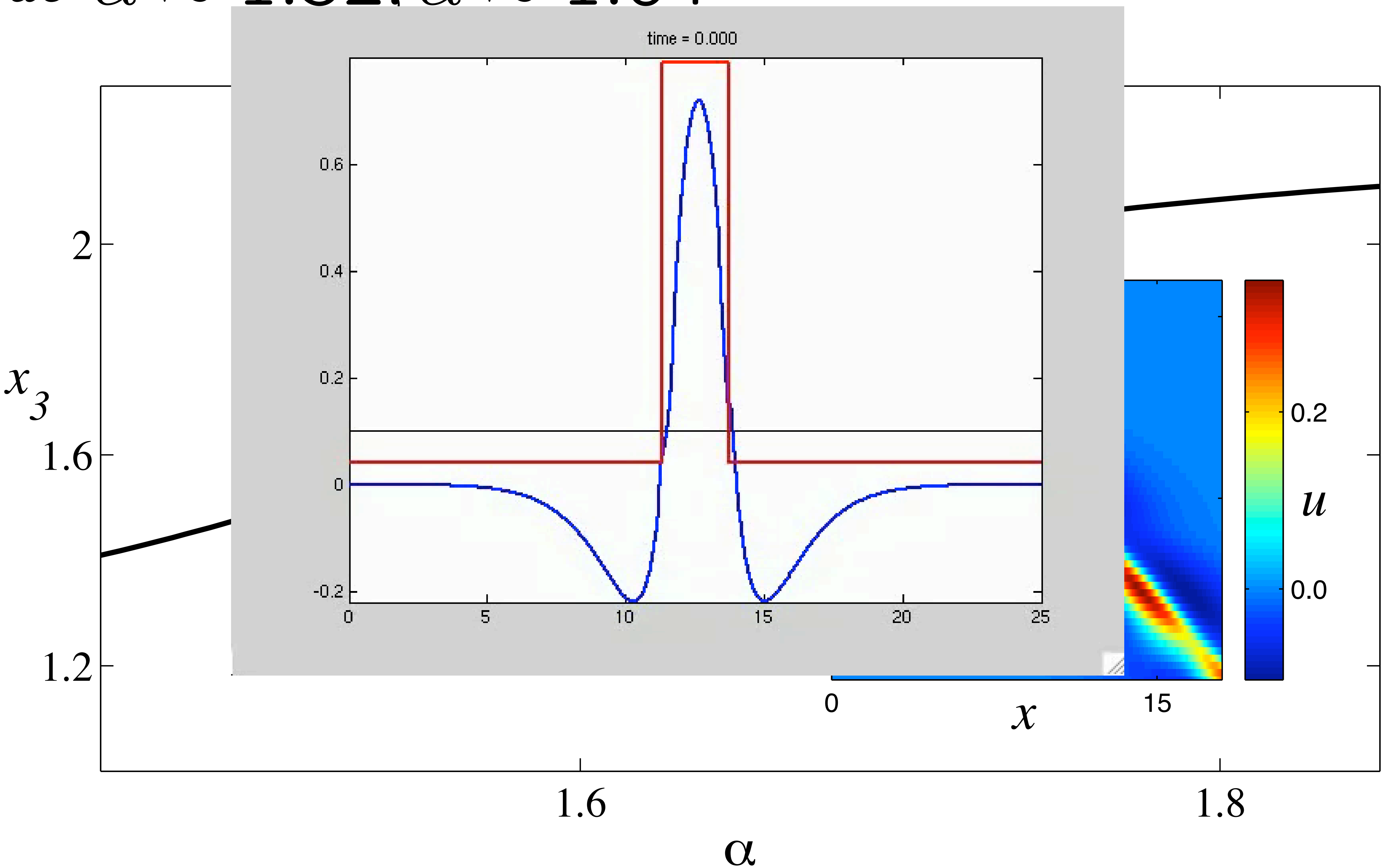
$q(\xi) \geq \theta$ for $\xi \in [\xi_1, \xi_3]$ allows to solve for p

$q(\xi) \geq p(\xi)$ for $\xi \in [\xi_2, \xi_4]$

$q(\xi_1) = \theta \quad q(\xi_2) = p(\xi_2) \quad q(\xi_3) = \theta \quad q(\xi_4) = p(\xi_4)$

Dynamic instability of pulses

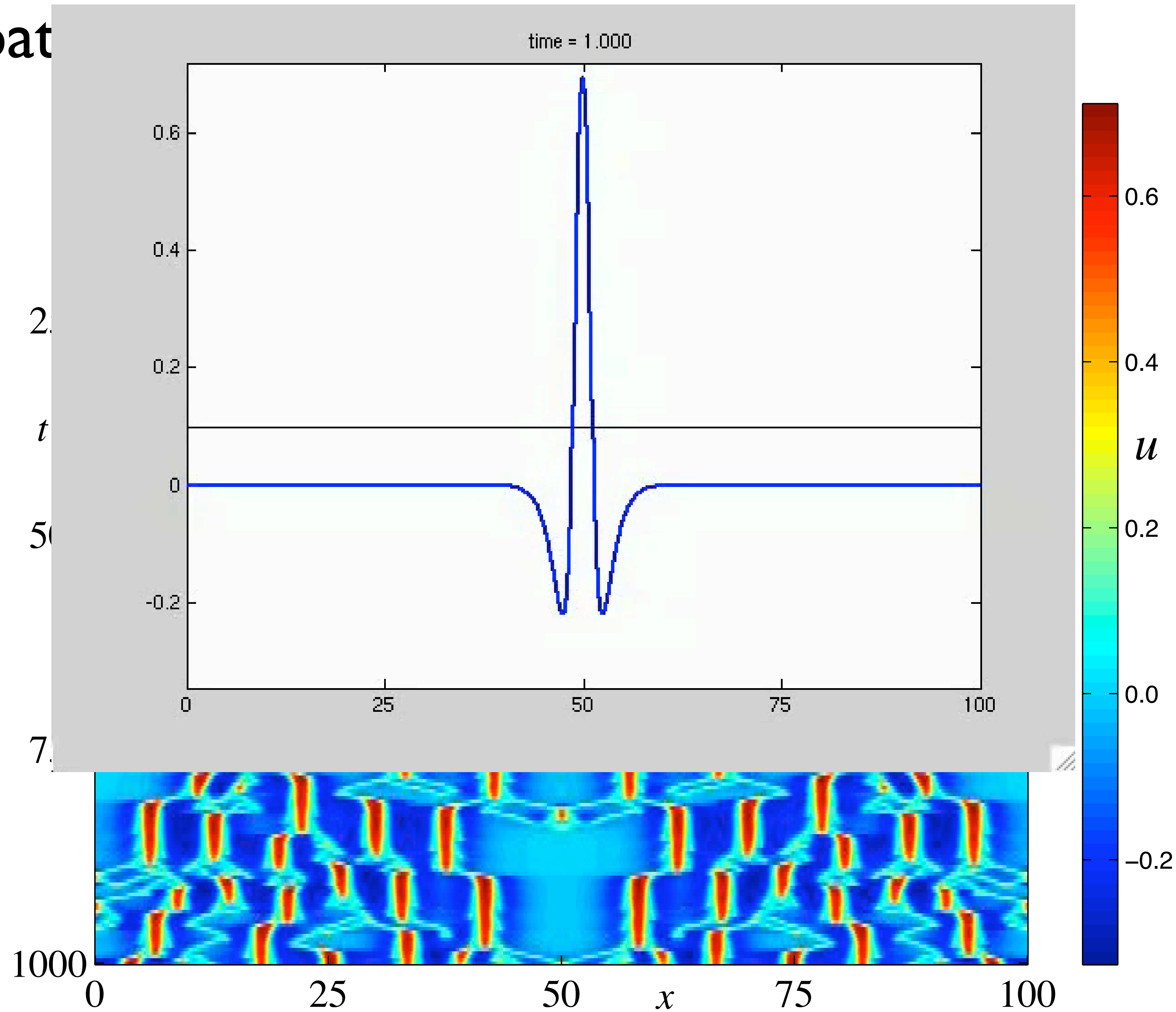
A pair of complex conjugate eigenvalues crosses the Im axis at $\alpha \approx 1.52, \alpha \approx 1.64$



Exact solution (curve); Hopf bifurcations (asterisks); Numerics (points).

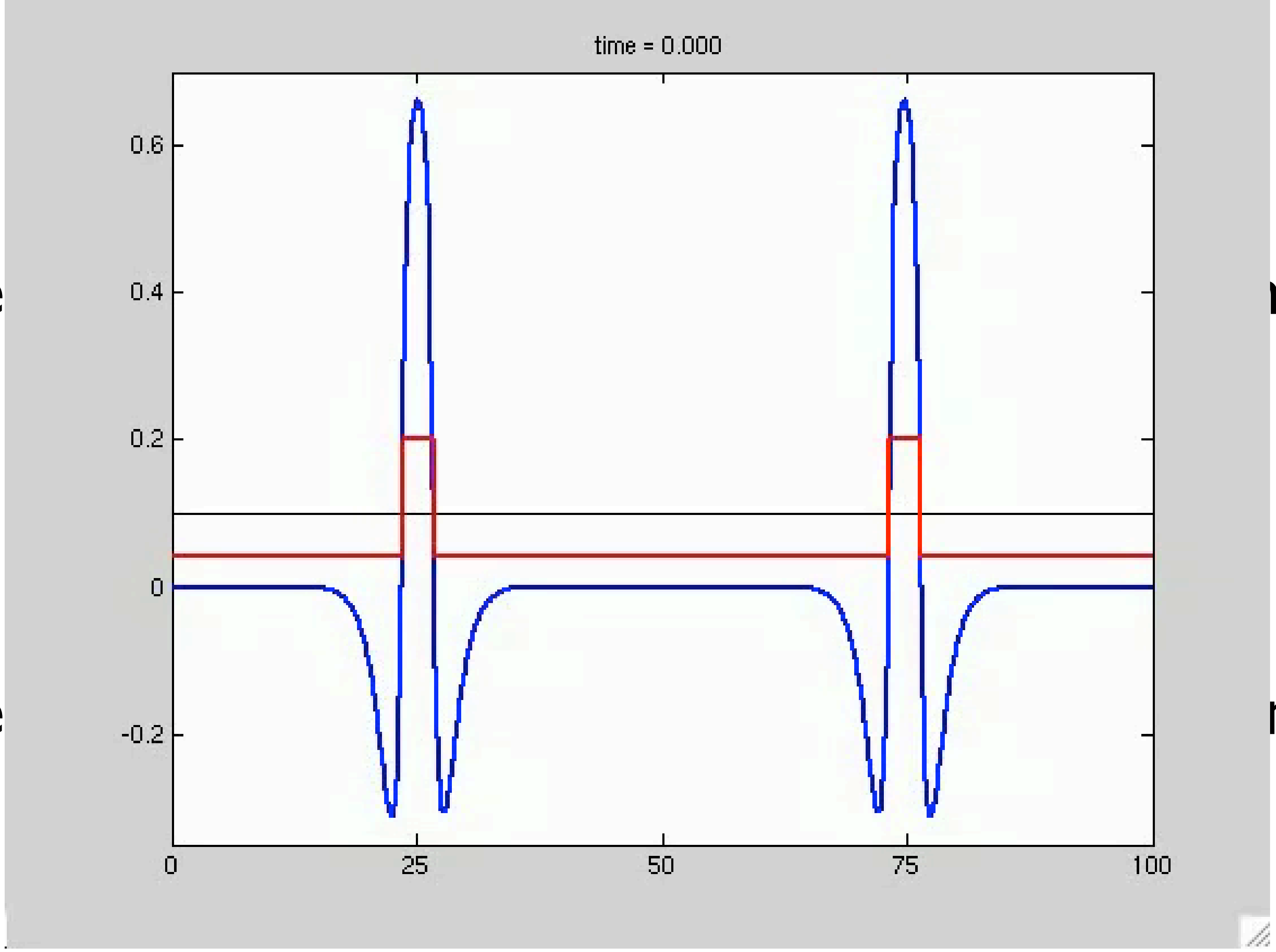
Exotic Dynamics

... including asymmetric breathers, multiple bumps, multiple pulses, periodic traveling waves, and bump-splitting instabilities that appear to lead to spat



S Coombes and M R Owen: Bumps, breathers and waves in a neural network with spike frequency adaptation. PRL, 94, 148102, (2005).

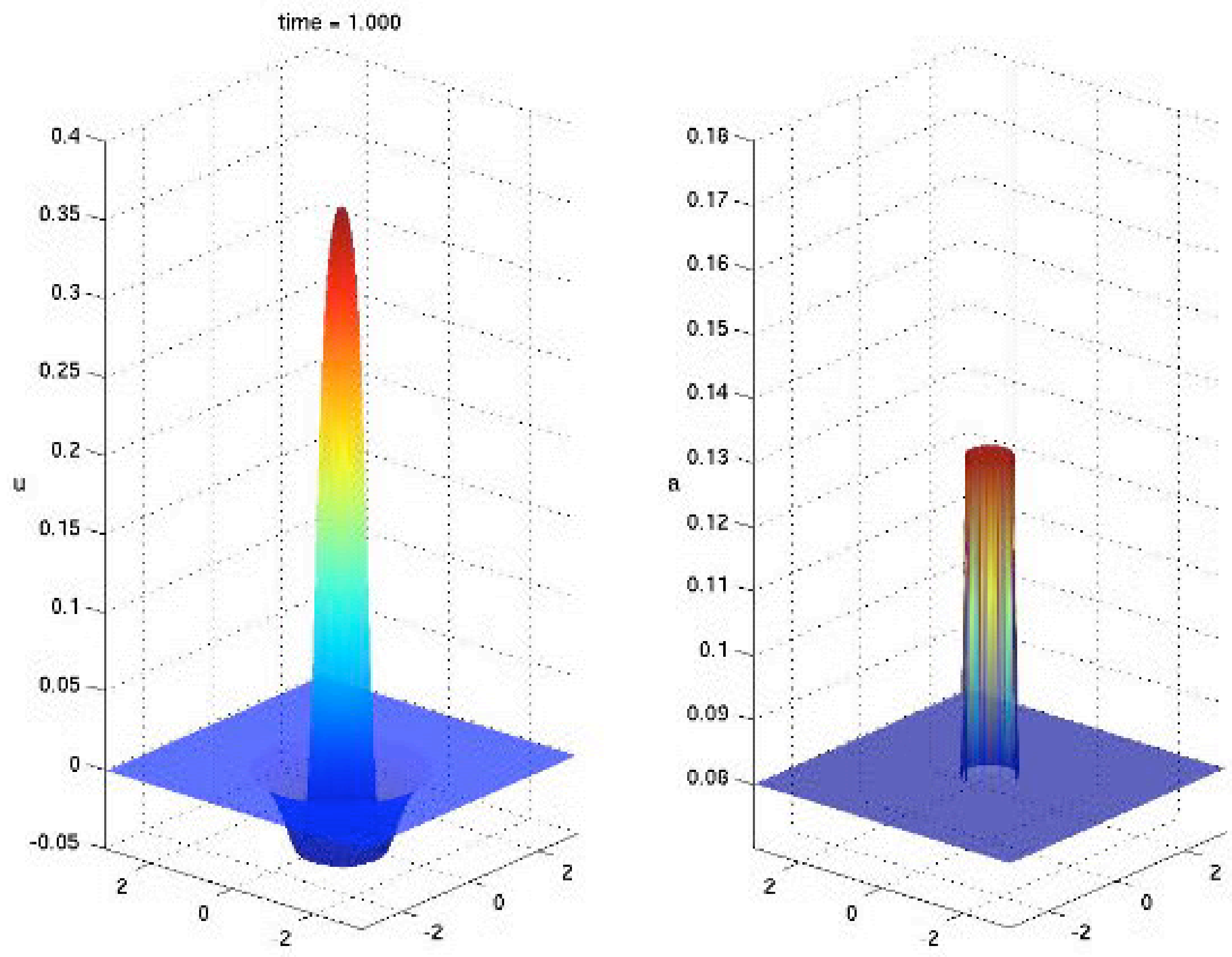
Colliding pulses 1D



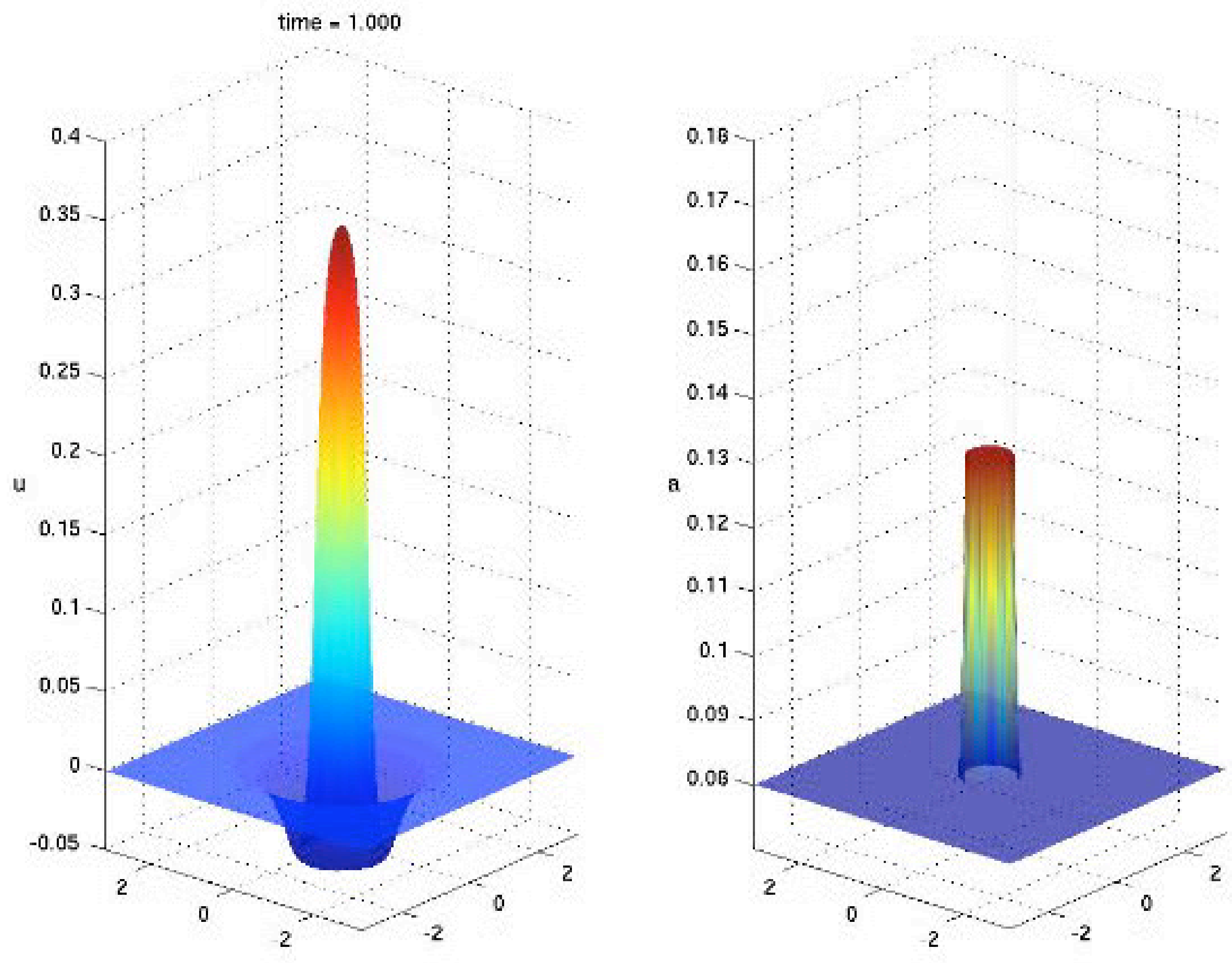
⭐ Pulse … other.

⭐ Pulse … mp.

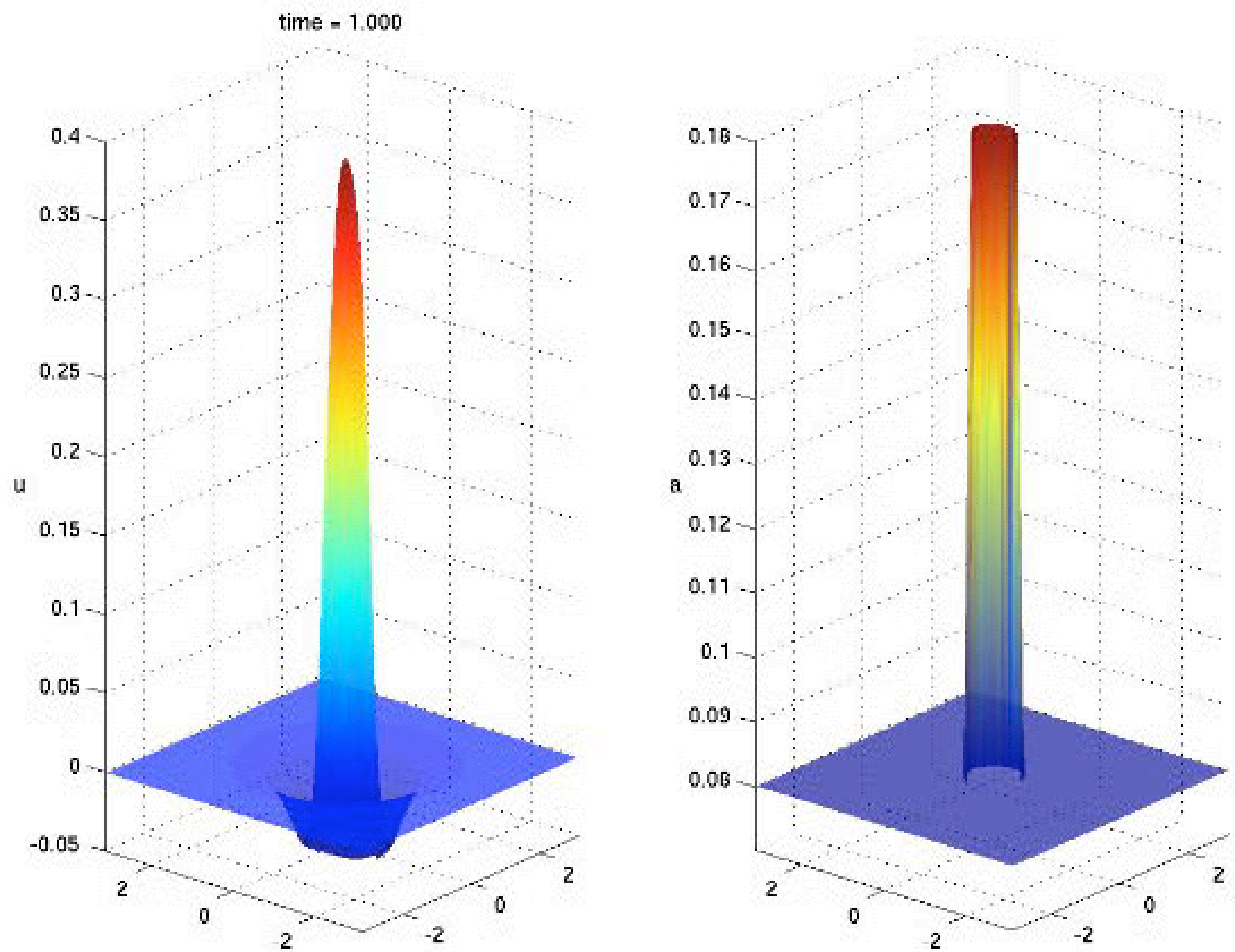
Stable Bump 2D



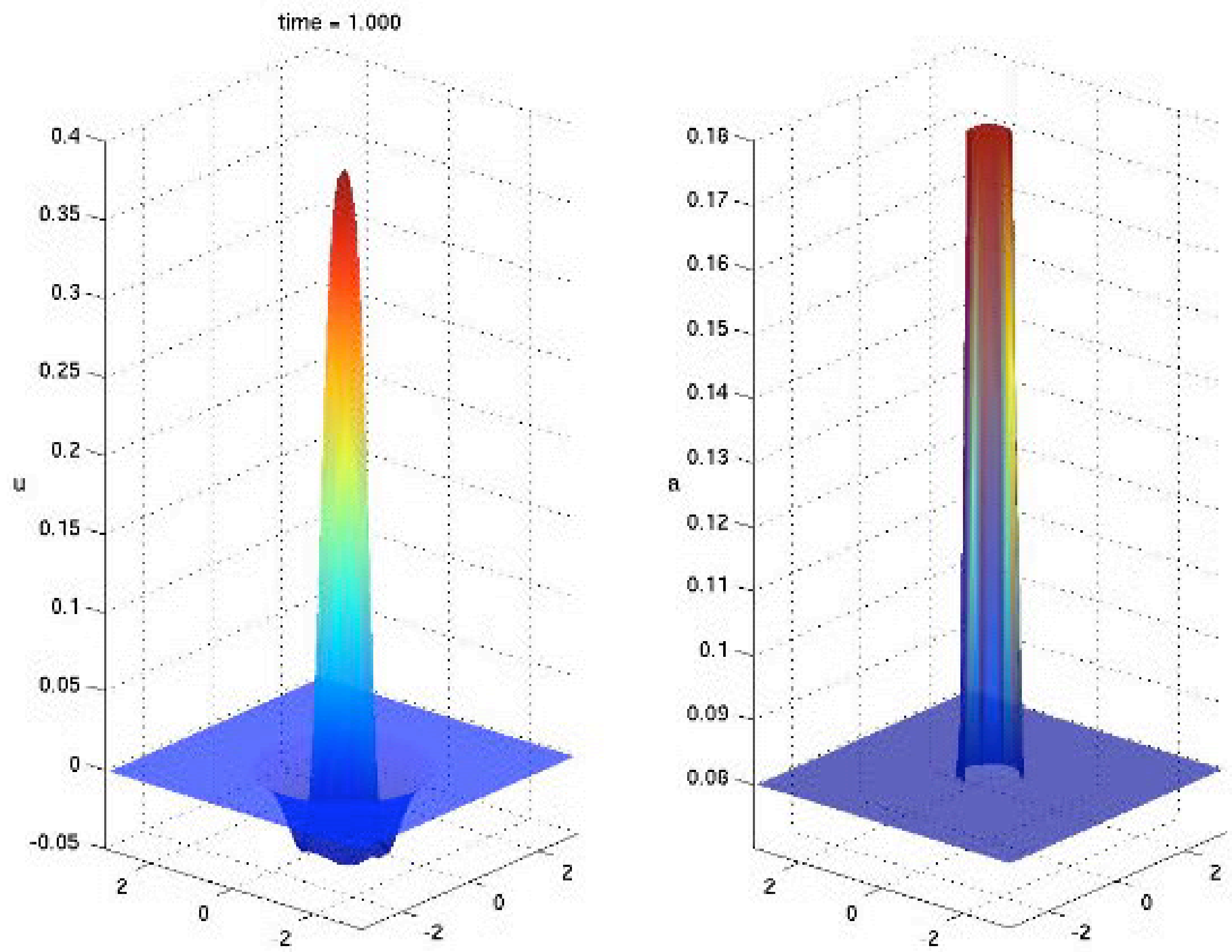
2D: Bump to Breather



2D: Bump to Pulse

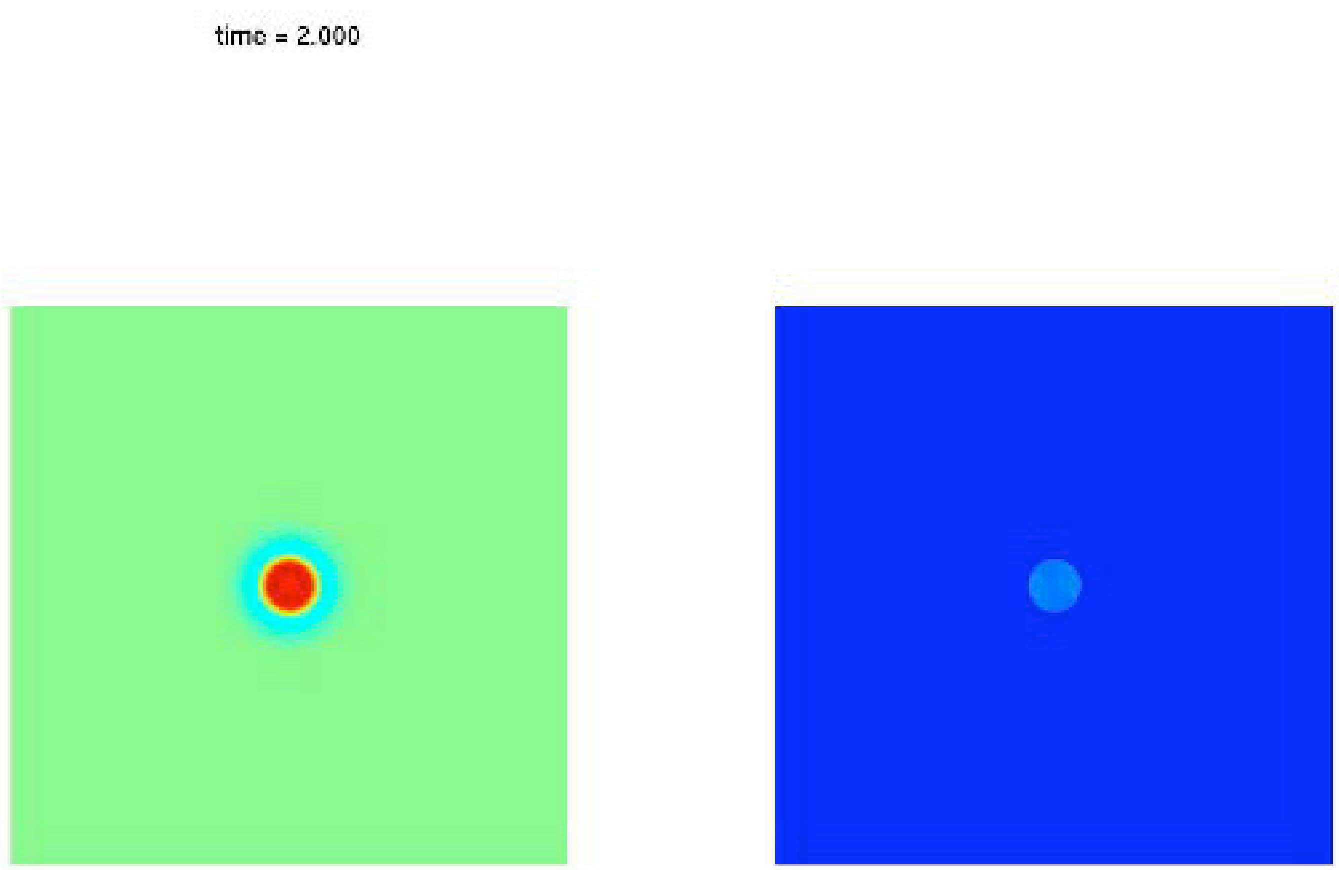


2D: Breathing Pulse

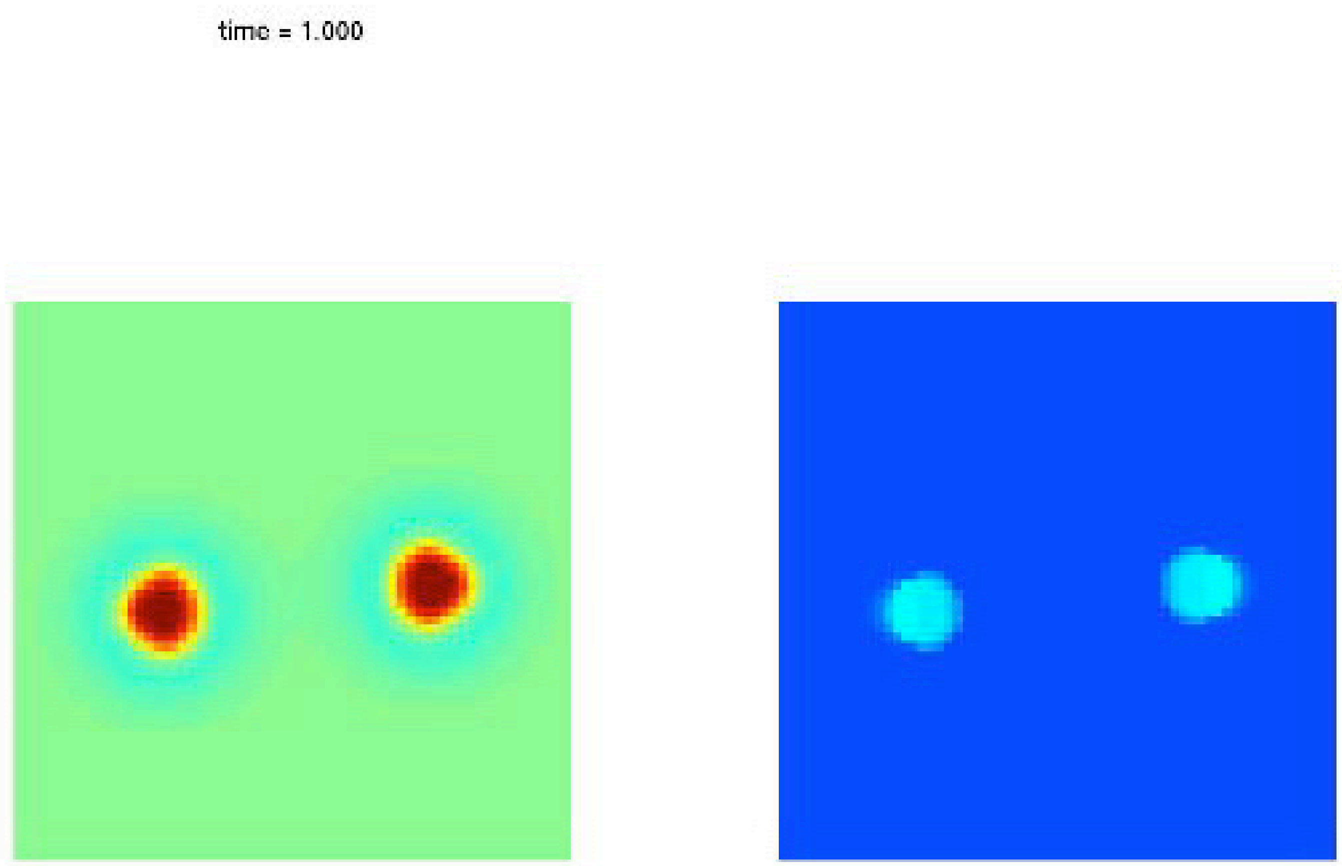


2D: Dimple Bumps

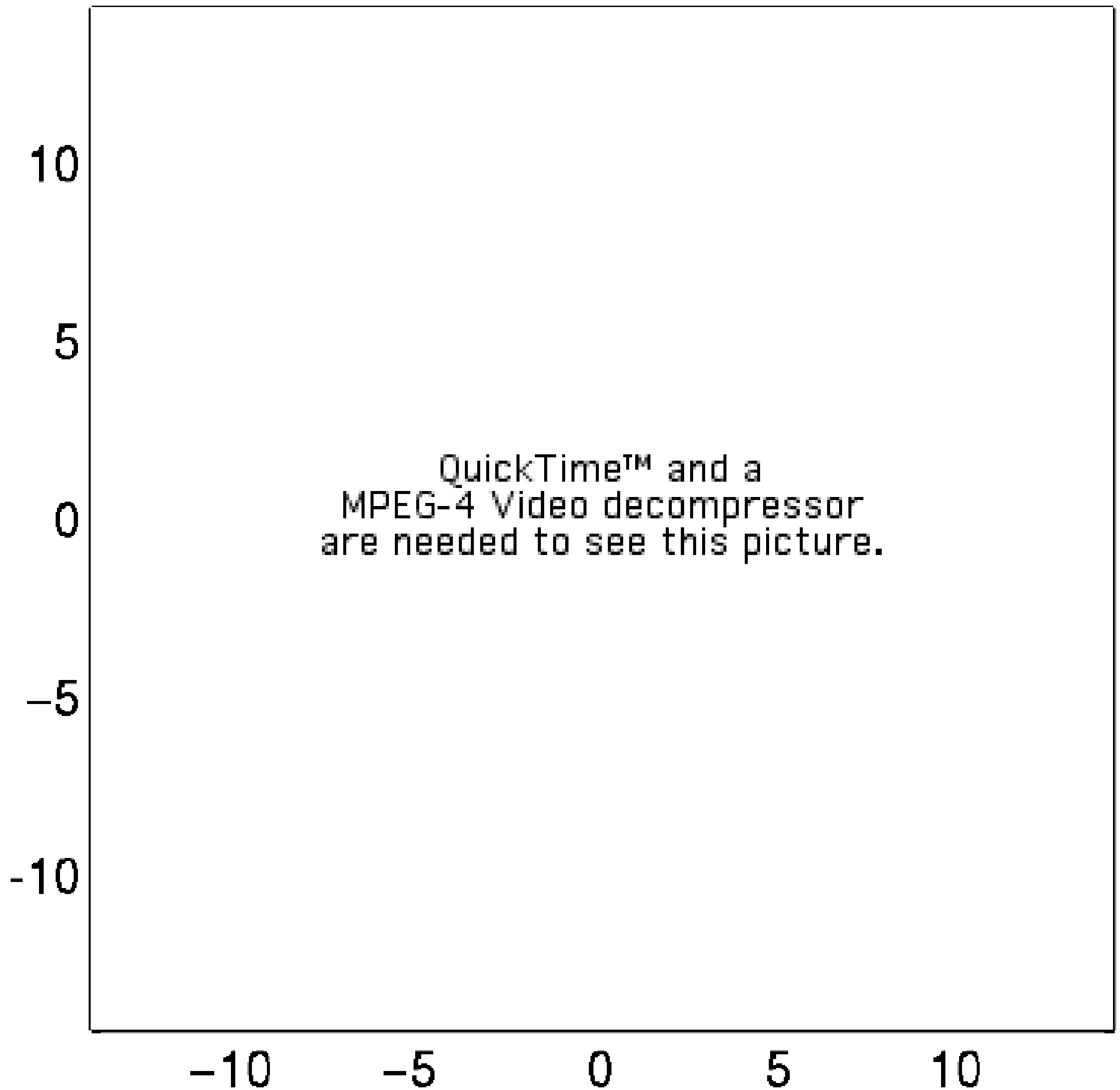
Complex splitting



2D: Collisions



Spirals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5
0
–5
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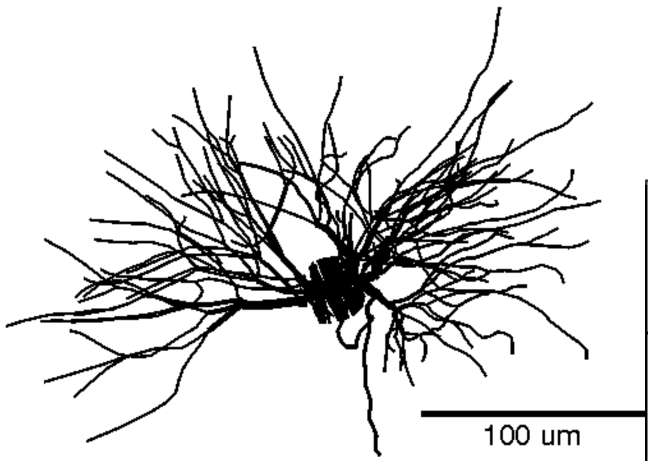
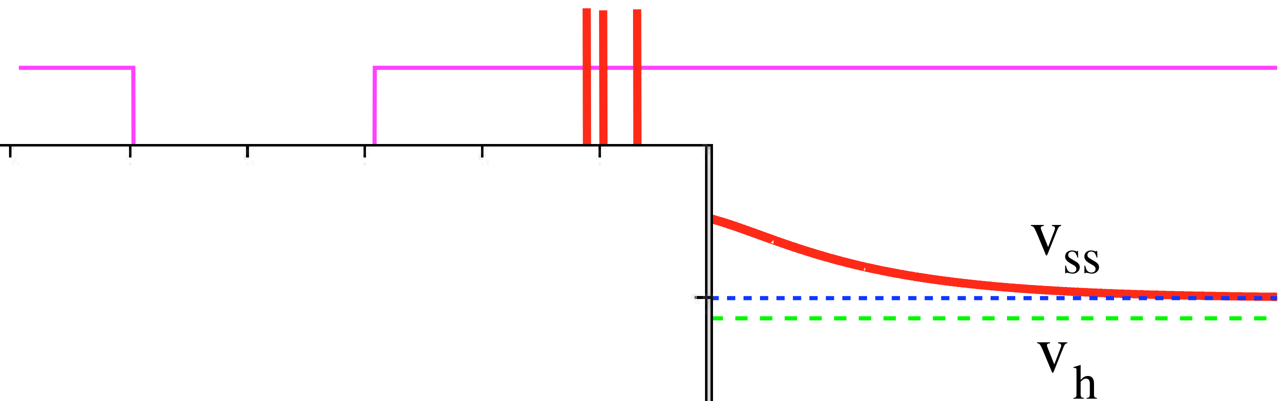
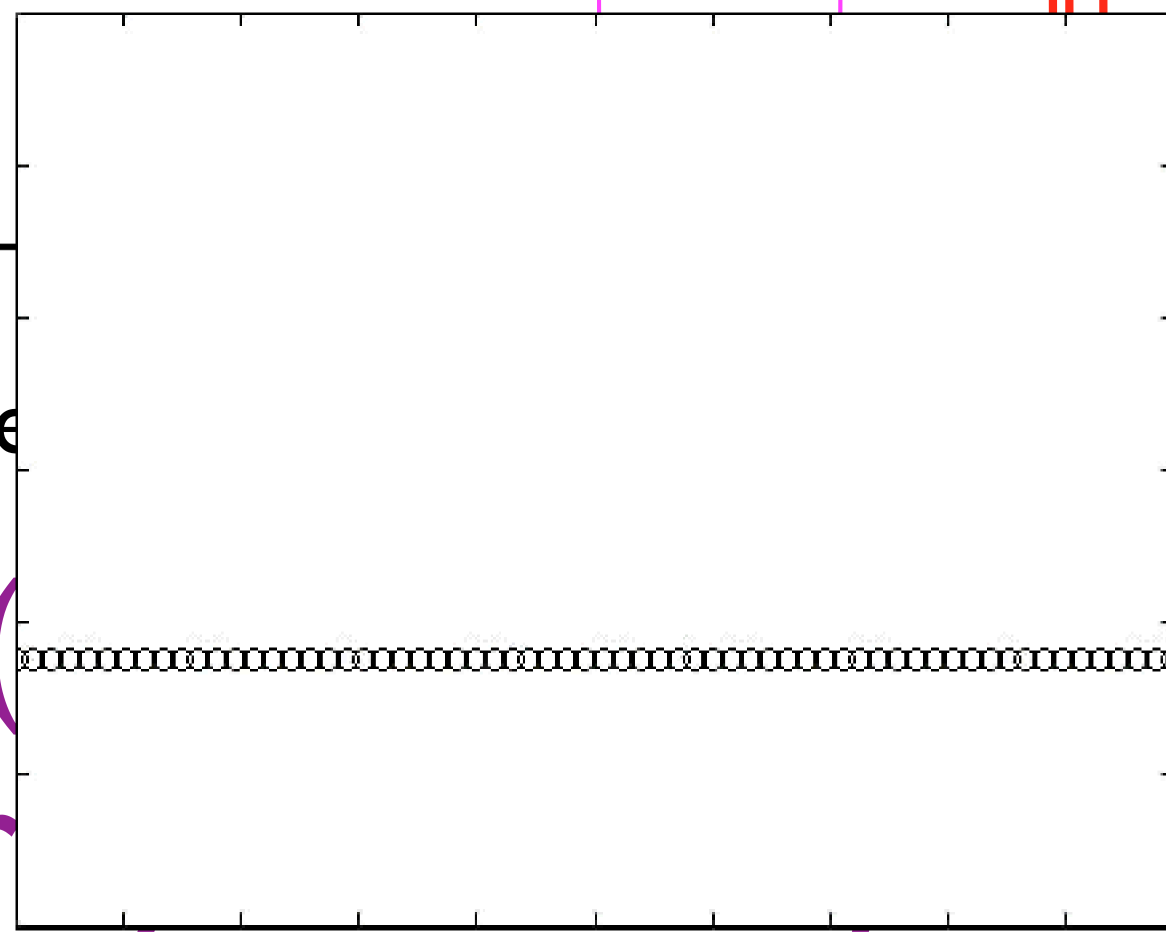
QuickTime™ and a
MPEG-4 Video decompressor
are needed to see this picture.

Post-Inhibitory Rebound (slow current)

Thalamocortical (TC)







Dynamic respons … um conductance.

Stable (… waves in a pur … twork

D H Terman, G B Ermentrout and A C Yew, Propagating activity patterns in thalamic neuronal networks, *SIAM Journal on Applied Mathematics* **61**, 1578-1604 (2001)

S Coombes, Dynamics of synaptically coupled integrate-and-fire-or-burst neurons, *Physical Review E* **67**, 041910 (2003)

and for smooth waves in RE-TC networks see

J Jalics, Slow waves in mutually inhibitory neuronal networks, *Physica D* **192**, 95–122 (2004)

The End!

http://www.maths.nott.ac.uk/~sc/