

# Neural networks with space-dependent delays

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**The University of  
Nottingham**

In collaboration with:  
Markus Owen

# Evans functions for integral neural field equations with Heaviside firing rate functions

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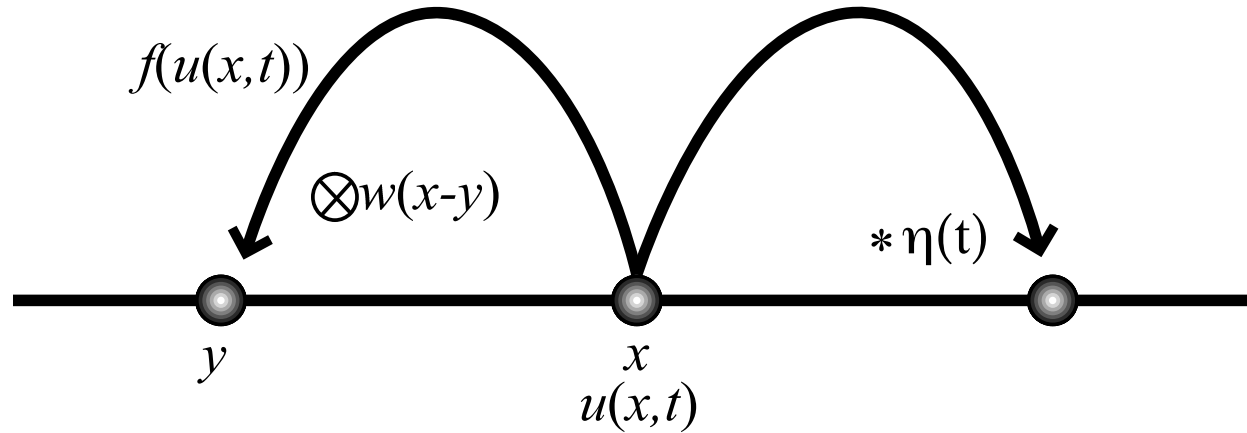
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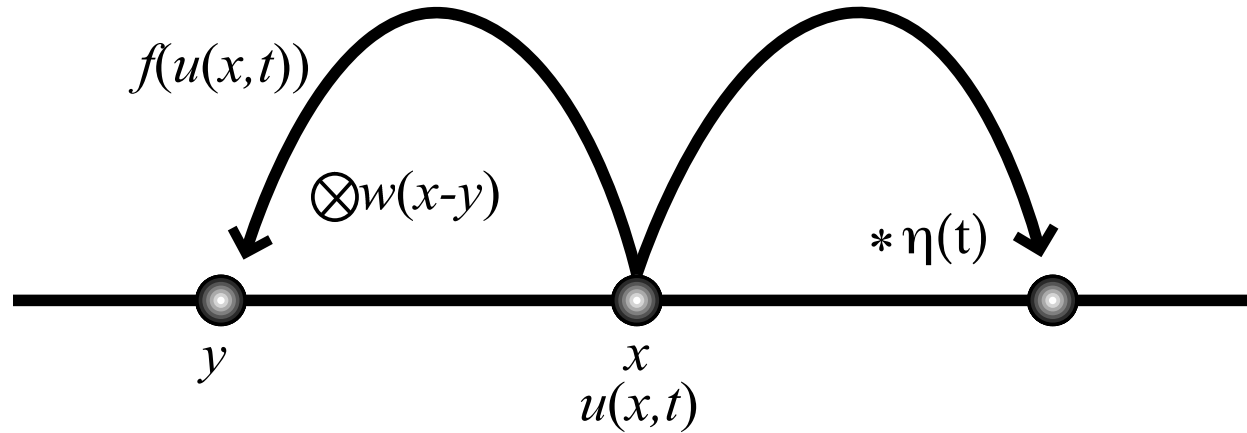
# Firing Rate Model



- ▶ Slow synapses (spike train  $\rightarrow$  firing rate)

$$\frac{1}{\alpha} \frac{\partial u(x,t)}{\partial t} = -u(x,t) + \int_{-\infty}^{\infty} dy w(y) f \circ u(x-y,t) - ga(x,t)$$
$$\frac{1}{\epsilon} \frac{\partial a(x,t)}{\partial t} = -a(x,t) + u(x,t).$$

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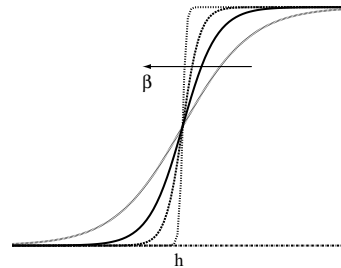


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- ▶ Firing rate derived from model or fit to real data



# A scalar integral equation

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- ▶ Heaviside firing rate  $f(u) = \Theta(u - h)$

$$q(\xi) = \int_0^{\infty} \eta(s) \psi(\xi + cs) ds,$$

where

$$\psi(\xi) = \int_{-\infty}^{\infty} dw(y) \Theta(q(\xi - y + c|y|/v) - h)$$

# Linear stability

► Linearise about the steady state:  $U(\xi, t) = q(\xi) + u(\xi, t)$ , and Taylor expand

$$u(\xi, t) = \int_{-\infty}^{\infty} dy w(y) \int_0^{\infty} ds \eta(s) f'(q(\xi - y + cs + c|y|/v)) \\ \times u(\xi - y + cs + c|y|/v, t - s - |y|/v)$$

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▶ Bounded smooth solutions  $u(\xi, t) = u(\xi)e^{\lambda t}$  generates the eigenvalue equation  $u = \mathcal{L}u$ :

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- ▶ Let  $\sigma(\mathcal{L})$  be the spectrum of  $\mathcal{L}$ . TW is linearly stable if

$$\max\{\operatorname{Re}(\lambda) : \lambda \in \sigma(\mathcal{L}), \lambda \neq 0\} \leq -K,$$

for some  $K > 0$ , and  $\lambda = 0$  is a simple eigenvalue of  $\mathcal{L}$ .

We shall take it that linear stability implies nonlinear stability.

# Travelling fronts

▶  $q(\xi) > h$  for  $\xi > 0$

$$\psi(\xi) = \begin{cases} \int_{-\infty}^{\xi/(1-c/v)} w(y) dy & \xi > 0 \\ \int_{-\infty}^{\xi/(1+c/v)} w(y) dy & \xi < 0 \end{cases}$$

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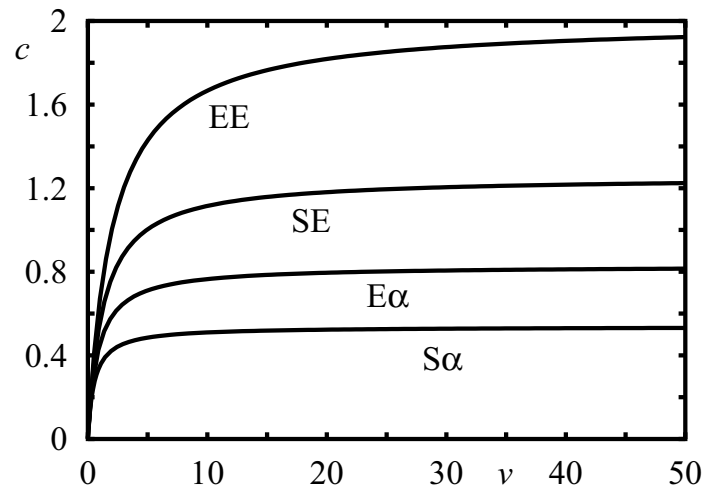
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- ▶ eg  $w(x) = e^{-|x|}/2$ ,  $\eta(t) = \alpha e^{-\alpha t}$ :



$c \sim v$  for small  $v$ .

# Evans function for travelling front

▶  $f(u) = \Theta(u - h)$ , so  $f'(q) = \delta(q - h)$ :

$$u(\xi) = \int_{-\infty}^{\infty} dy w(y) \int_{q(\xi - y + c|y|/v)}^{q(\infty)} \frac{dz}{c} \eta(q^{-1}(z)/c - \xi/c + y/c - |y|/v) \\ \times e^{-\lambda(q^{-1}(z)/c - \xi/c + y/c)} \frac{\delta(z - h)}{|q'(q^{-1}(z))|} u(q^{-1}(z))$$



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▶ Self-consistent condition (at  $\xi = 0$ ) has a non-trivial solution if  $\mathcal{E}(\lambda) = 0$ , where

$$\mathcal{E}(\lambda) = 1 - \frac{1}{c|q'(0)|} \int_{-\infty}^{\infty} dy w(y) \eta(y/c - |y|/v) e^{-\lambda y/c}$$

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▶ For our example front is stable (ES:  $\lambda = -\alpha + ipc$ ) since

$$\mathcal{E}(\lambda) = \frac{\lambda}{\frac{c}{\sigma} + \alpha \left(1 - \frac{c}{v}\right) + \lambda}$$

$v \rightarrow \infty$  to recover the result of Linghai Zhang [DIE, 16, (2003), 513-536]

# A model with linear recovery

► Spike frequency adaptation

$$Qu(x, t) = (w \otimes f \circ u)(x, t) - ga(x, t), \quad Q_a a(x, t) = u(x, t)$$

Notation

$$(w \otimes f)(x, t) = \int_{-\infty}^{\infty} w(y) f(x - y, t - |y|/v) dy$$
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► Integrated form  $u = \eta * w \otimes f \circ u - g\eta_b * u$  where

$$(\eta * f)(x, t) = \int_0^t \eta(s) f(x, t - s) ds, \quad \eta_b = \eta * \eta_a$$

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- ▶ Re-arrange:  $[1 + g\eta_b *]u = \eta * w \otimes f \circ u$  giving TW:

$$q(\xi) = \int_0^{\infty} \eta_c(z) \psi(\xi + cz) dz$$

$$\eta_c(t) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \widehat{\eta}_c(k) e^{ikt} dk, \quad \widehat{\eta}_c(k) = \frac{\widehat{\eta}(k)}{1 + g\widehat{\eta}_b(k)}$$

# Fronts

▶ Evans function  $\mathcal{E}(\lambda) = 1 - \mathcal{H}(\lambda)/\mathcal{H}(0)$ :

$$\mathcal{H}(\lambda) = \int_0^\infty dy w(y) \eta_c(y/c - y/v) e^{-\lambda y/c}$$

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$$\eta_c(t) = \frac{\alpha}{k_- - k_+} \left\{ (1 - k_+) e^{-k_+ t} - (1 - k_-) e^{-k_- t} \right\}$$

$$k_\pm = \frac{1 + \alpha \pm \sqrt{(1 + \alpha)^2 - 4\alpha(1 + g)}}{2}$$



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$q(0) = h$  gives an implicit expression for the front speed as

$$cm_- = \frac{1}{2} \left[ 1 + \alpha - \frac{\alpha}{2h} \pm \sqrt{\left(1 + \alpha - \frac{\alpha}{2h}\right)^2 - 4\alpha \left(1 + g - \frac{1}{2h}\right)} \right] \quad c > 0$$

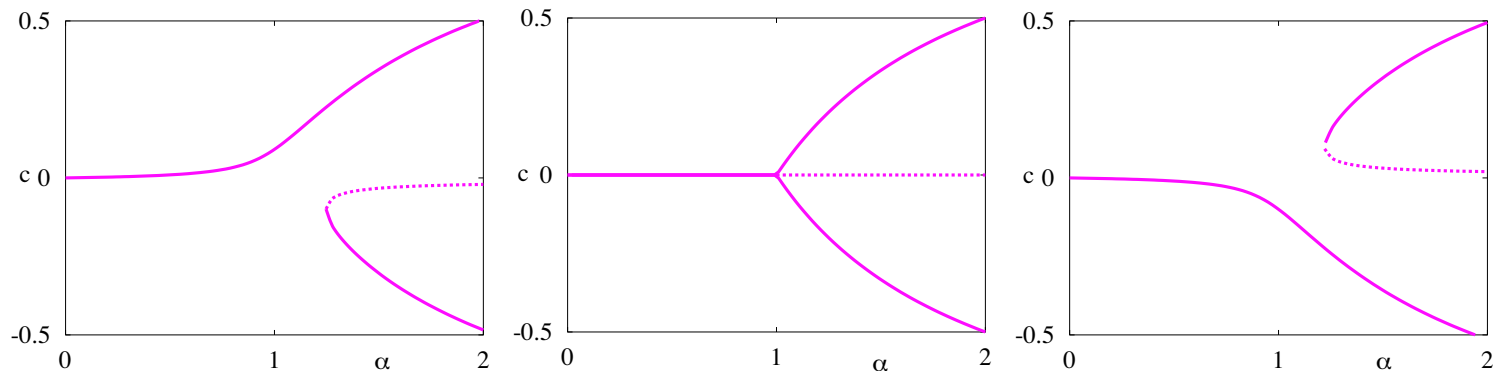
$$cm_+ = \frac{1}{2} \left[ 1 + \alpha - \frac{\alpha}{2h^*} \pm \sqrt{\left(1 + \alpha - \frac{\alpha}{2h^*}\right)^2 - 4\alpha \left(1 + g - \frac{1}{2h^*}\right)} \right] \quad c < 0$$

where  $h^* = 1/(1 + g) - h$  and  $m_\pm = v/(c \pm v)$ .

$v \rightarrow \infty$  to recover the result of Bressloff and Folias [preprint (2004)]

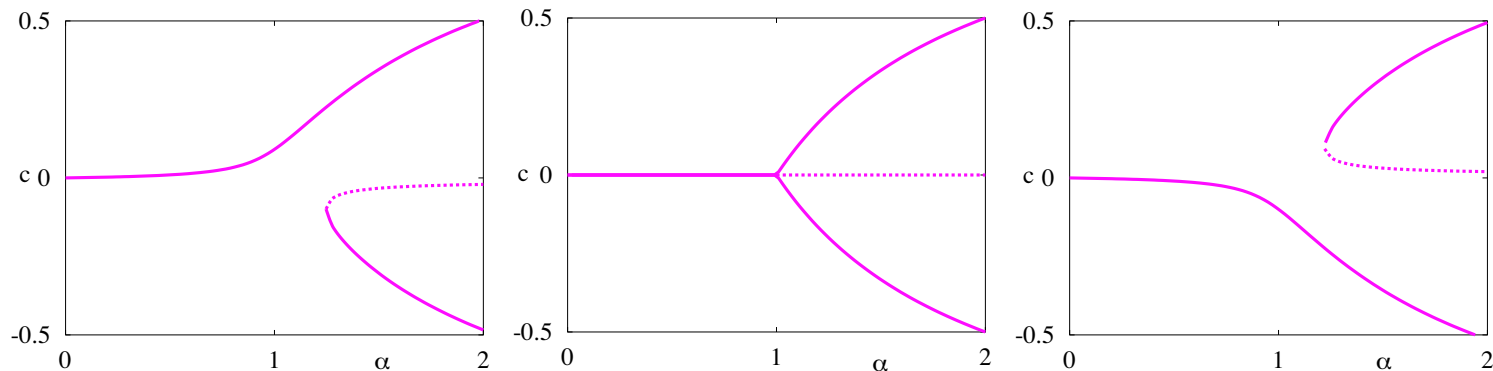
# Front bifurcations

If  $g = g_c$ , where  $2h(1+g_c) = 1$ , there is a front for all  $\alpha$  with speed  $c = 0$ . At a critical value of  $\alpha$  this stationary front undergoes a pitchfork bifurcation leading to a pair of fronts traveling in opposite directions. If this critical condition is not met then the pitchfork bifurcation is broken:



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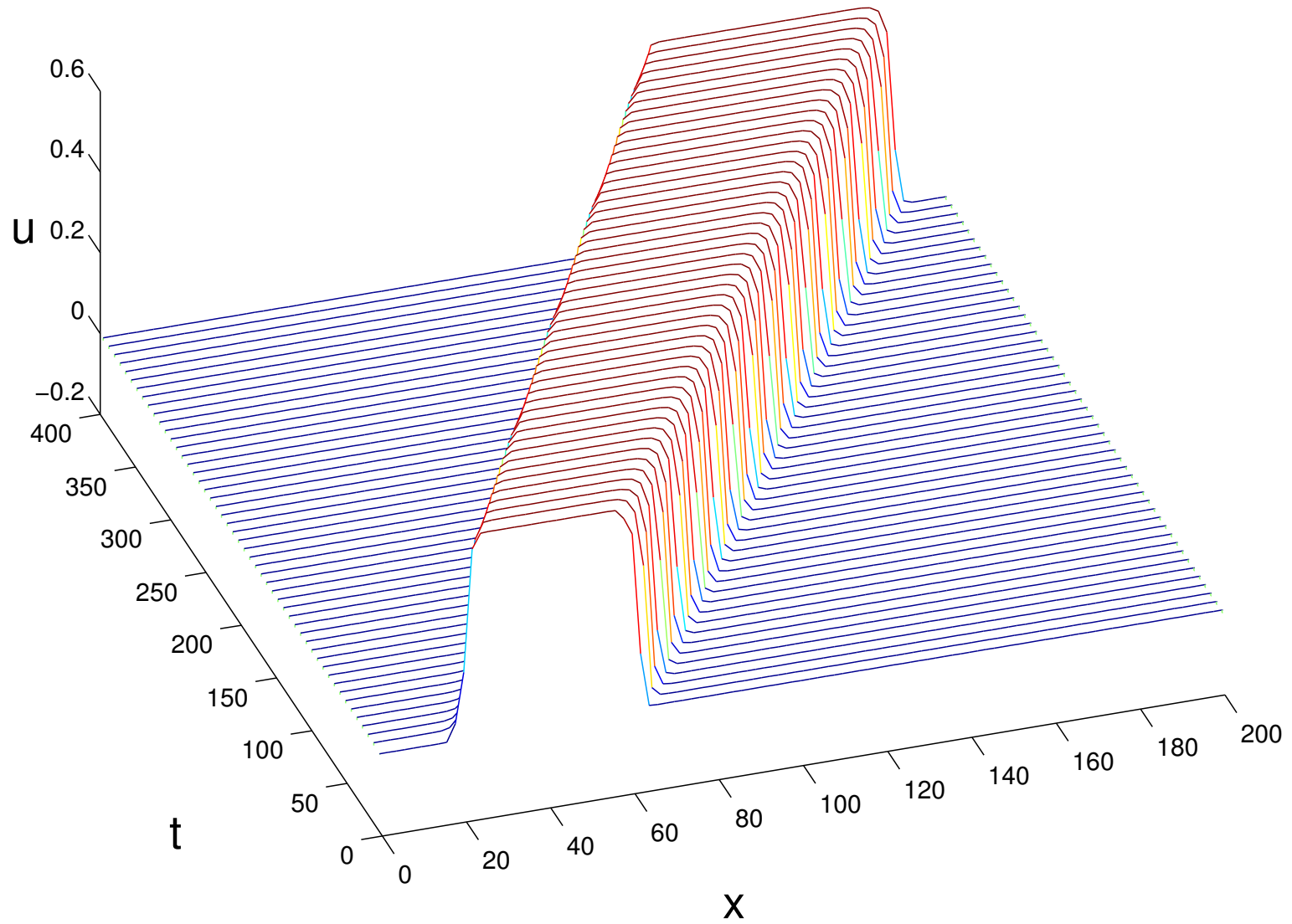


On the branch with  $c = 0$  and  $g = g_c$  (defining a stationary front) we find that ES:  $\lambda = -k_{\pm} + ipc$  and

$$\mathcal{E}(\lambda) = \lambda \frac{(\lambda + k_+ + k_- - k_+k_-)}{(\lambda + k_+)(\lambda + k_-)},$$

which has zeros when  $\lambda = 0$  and  $\lambda = \alpha g_c - 1$ . Hence, the stationary front changes from stable to unstable as  $\alpha$  is increased through  $1/g_c$ .

# Front bifurcations: simulations



# Pulses

►  $q(\xi) > h$  for  $\xi \in (0, \Delta)$  and  $q(\xi) < h$  otherwise.

$$\psi(\xi) = \begin{cases} \mathcal{F}\left(\frac{-\xi}{1+c/v}, \frac{\Delta-\xi}{1+c/v}\right) & \xi \leq 0 \\ \mathcal{F}\left(0, \frac{\xi}{1-c/v}\right) + \mathcal{F}\left(0, \frac{\Delta-\xi}{1+c/v}\right) & 0 < \xi < \Delta \\ \mathcal{F}\left(\frac{\xi-\Delta}{1-c/v}, \frac{\xi}{1-c/v}\right) & \xi \geq \Delta \end{cases}$$

where

$$\mathcal{F}(a, b) = \int_a^b w(y) dy.$$

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The dispersion relation  $c = c(\Delta)$  is then implicitly defined by the simultaneous solution of  $q(0) = h$  and  $q(\Delta) = h$  ( $\Delta > 0$ ). Linearising around the traveling pulse solution and proceeding as before we obtain an eigenvalue equation of the form  $u = \mathcal{J}_c u$ , where

$$\mathcal{J}_c u(\xi) = A_c(\xi, \lambda)u(0) + B_c(\xi, \lambda)u(\Delta)$$

$$A_c(\xi, \lambda) = \frac{1}{c|q'(0)|} \int_{\frac{\xi}{1-c/v}}^{\infty} dy w(y) \eta_c(-\xi/c + y/c - y/v) e^{-\lambda(y-\xi)/c}$$

$$B_c(\xi, \lambda) = \frac{1}{c|q'(\Delta)|} \int_{\frac{\xi-\Delta}{1+c/v}}^{\infty} dy w(y) \eta_c((\Delta - \xi)/c + y/c - |y|/v) e^{-\lambda(y-(\xi-\Delta))/c}$$

Demanding that the eigenvalue problem  $u = \mathcal{J}_c u$  be self-consistent at  $\xi = 0$  and  $\xi = \Delta$  gives the system of equations

$$\begin{bmatrix} u(0) \\ u(\Delta) \end{bmatrix} = \mathcal{A}_c(\lambda) \begin{bmatrix} u(0) \\ u(\Delta) \end{bmatrix}, \quad \mathcal{A}_c(\lambda) = \begin{bmatrix} A_c(0, \lambda) & B_c(0, \lambda) \\ A_c(\Delta, \lambda) & B_c(\Delta, \lambda) \end{bmatrix}$$

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Nontrivial solution if  $\mathcal{E}(\lambda) = 0$ , where

$$\mathcal{E}(\lambda) = \det(\mathcal{A}_c(\lambda) - I)$$

which we recognise as the Evans function for a pulse.



# A pair of travelling pulses

▶  $Q_a = \partial_t$

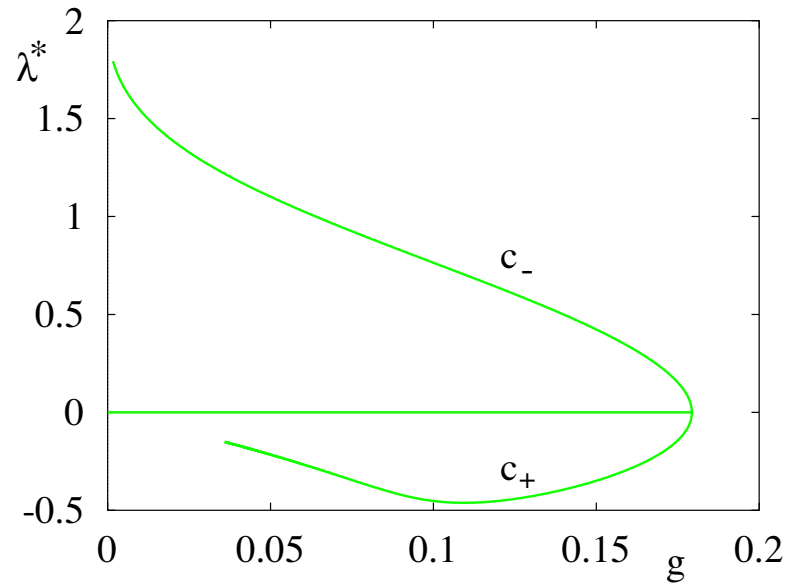
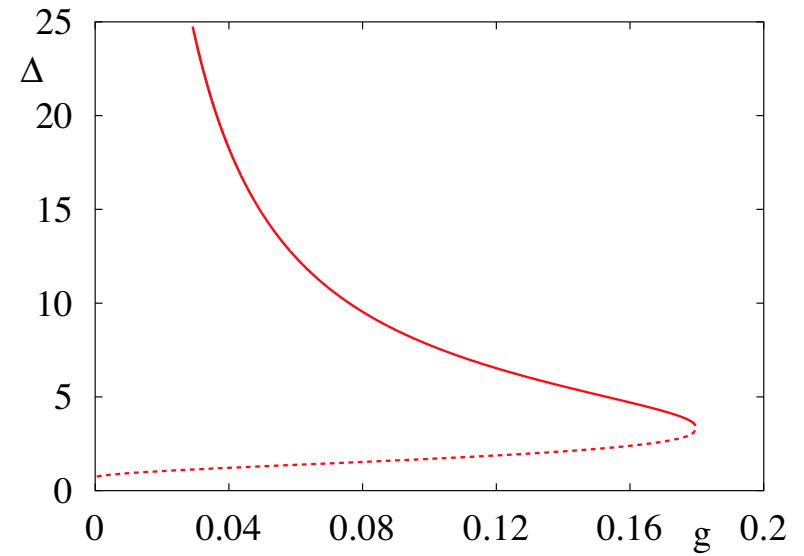
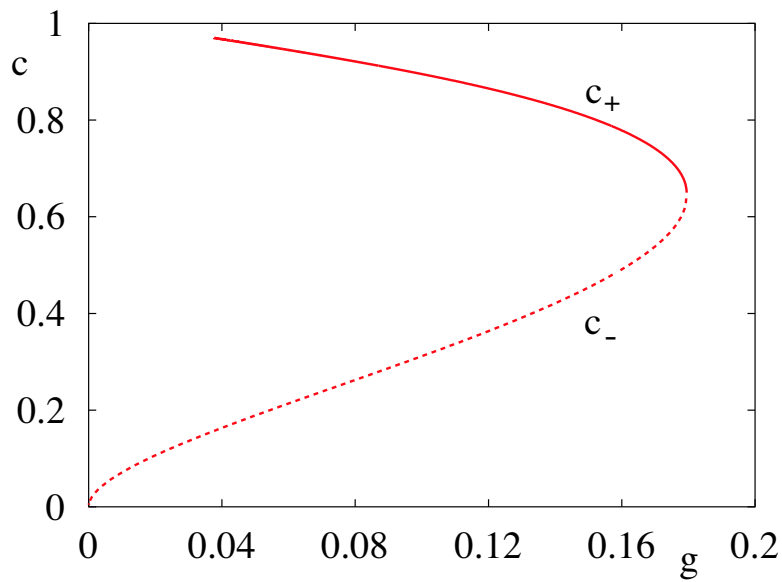
$$\eta_c(t) = \frac{\alpha}{k_+ - k_-} \left\{ k_+ e^{-k_+ t} - k_- e^{-k_- t} \right\}$$

$$k_{\pm} = \frac{\alpha \pm \sqrt{\alpha^2 - 4\alpha g}}{2}$$

▶  $q(0) = h = q(\Delta)$  gives

$$h = \frac{\alpha c (1 - e^{-\Delta})}{2(c^2 + \alpha c + \alpha g)}$$

$$h = \frac{\alpha}{k_+ - k_-} \left\{ e^{-k_- \Delta/c} + \frac{k_-}{2} \left( \frac{e^{-\Delta} - e^{-k_- \Delta/c}}{k_- - c} + \frac{1 - e^{-k_- \Delta/c}}{k_- + c} \right) \right. \\ \left. - e^{-k_+ \Delta/c} - \frac{k_+}{2} \left( \frac{e^{-\Delta} - e^{-k_+ \Delta/c}}{k_+ - c} + \frac{1 - e^{-k_+ \Delta/c}}{k_+ + c} \right) \right\}$$



$v \rightarrow \infty$  to confirm a conjecture of Pinto and Ermentrout [SIAM J Appl Math, 62 (2001), 206-225]

# A model with nonlinear recovery/lateral inhibition

$$Qu(x, t) = (w \otimes f \circ u)(x, t) - g(w_a \otimes a)(x, t) \quad Q_a a(x, t) = f \circ u(x, t)$$

$$u = [\eta * w \otimes -g\eta_b * w_a \otimes] f \circ u$$

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$$u = [\eta * w \otimes -g\eta_b * w_a \otimes] f \circ u$$

► TW

$$q(\xi) = \left( \int_{-\infty}^{\infty} dy w(y) \int_0^{\infty} ds \eta(s) - g \int_{-\infty}^{\infty} dy w_a(y) \int_0^{\infty} ds \eta_b(s) \right) \\ \times \Theta(q(\xi - y + cs + c|y|/v) - h)$$

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## ► Stability: eigenvalue equation of the form $u = \mathcal{L}u - g\mathcal{J}u$ , where

$$\mathcal{L}u(\xi) = A(\xi, \lambda)u(0) + B(\xi, \lambda)u(\Delta)$$

$$\mathcal{J}u(\xi) = C(\xi, \lambda)u(0) + D(\xi, \lambda)u(\Delta)$$

where

$$A(\xi, \lambda) = \frac{1}{c|q'(0)|} \int_{\frac{\xi}{1-c/v}}^{\infty} dy w(y) \eta(-\xi/c + y/c - y/v) e^{-\lambda(y-\xi)/c}$$

$$B(\xi, \lambda) = \frac{1}{c|q'(\Delta)|} \int_{\frac{\xi-\Delta}{1+c/v}}^{\infty} dy w(y) \eta((\Delta - \xi)/c + y/c - |y|/v) e^{-\lambda(y-(\xi-\Delta))/c}$$

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Demanding that perturbations be determined self consistently at  $\xi = 0$  and  $\xi = \Delta$  gives the system of equations

$$\begin{bmatrix} u(0) \\ u(\Delta) \end{bmatrix} = \mathcal{A}(\lambda) \begin{bmatrix} u(0) \\ u(\Delta) \end{bmatrix}, \quad \mathcal{A}(\lambda) = \begin{bmatrix} A(0, \lambda) - gC(0, \lambda) & B(0, \lambda) - gD(0, \lambda) \\ A(\Delta, \lambda) - gC(\Delta, \lambda) & B(\Delta, \lambda) - gD(\Delta, \lambda) \end{bmatrix}$$

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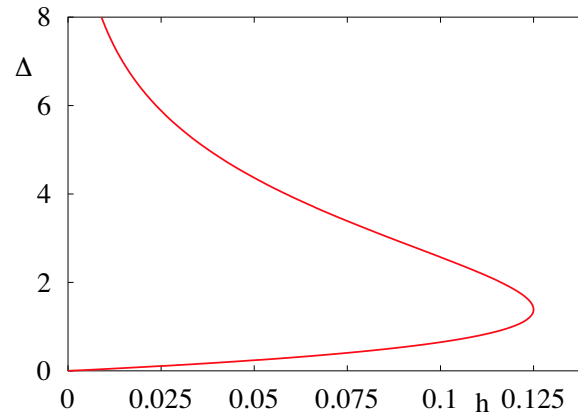
Nontrivial solution if  $\mathcal{E}(\lambda) = 0$ , where the Evans function is

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



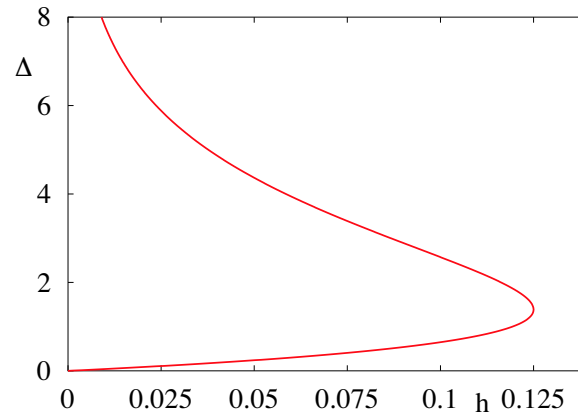
# Dynamic instability of a standing pulse

$$\eta(t) = \alpha e^{-\alpha t}, \quad \eta_a(t) = e^{-t}, \quad w(x) = e^{-|x|}/2, \quad w_a(x) = e^{-|x|/\sigma_a}/(2\sigma_a)$$

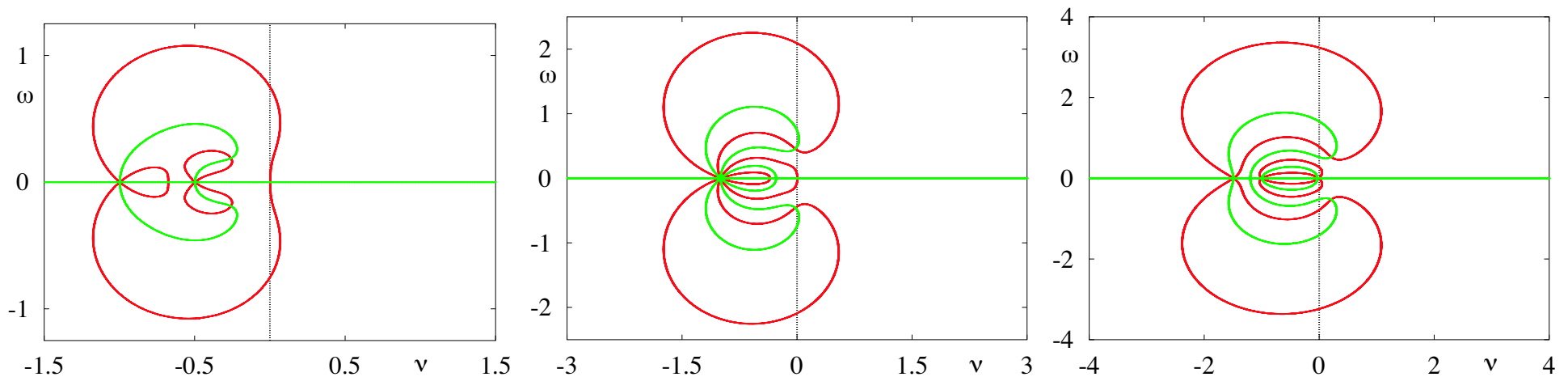


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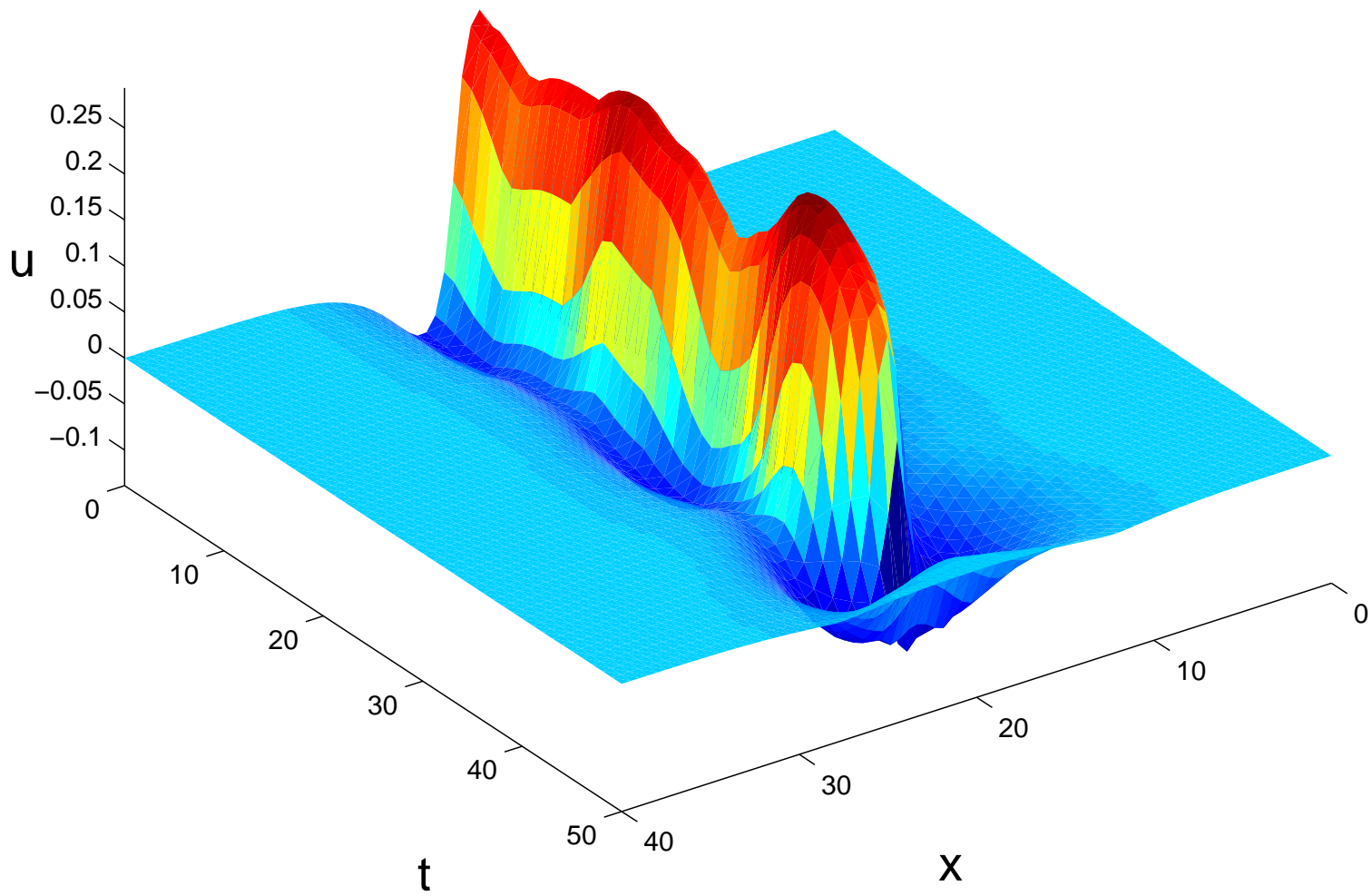
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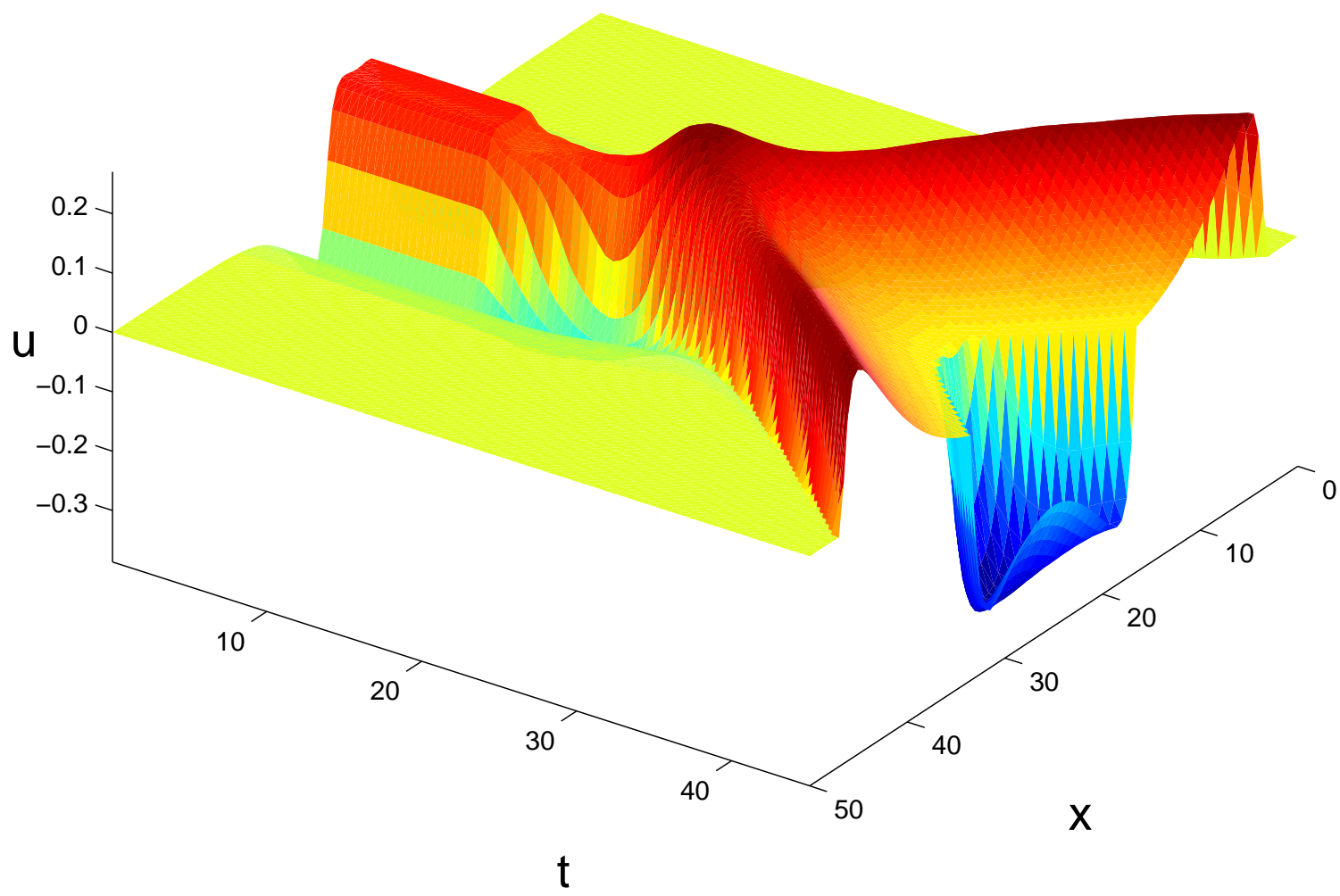


► Let  $\lambda = \nu + i\omega$  and plot  $\text{Re } \mathcal{E}(\lambda) = 0 = \text{Im } \mathcal{E}(\lambda)$



$\nu \rightarrow \infty$  to recover work of Pinto and Ermentrout [SIAM J Appl Math, II]





## Summary

- ▶ Evans function for integral neural field equations with

Arbitrary synaptic footprints

Arbitrary synaptic response

Space dependent delays

[For a Heaviside]

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Order of the roots = multiplicity of eigenvalues

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- ▶ Front, pulse and bump stability for a number of examples

## Further work

- ▶ Anisotropy and inhomogeneity [Bressloff *et al.*]



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- ▶ Anisotropy and inhomogeneity [Bressloff *et al.*]
- ▶ Multi-layered (2D) networks and thalamo-cortical interactions.

$$u(x, t) = \int_{-\infty}^{\infty} w(x - y) \int_{-\infty}^t \eta(t - s) f(v(y, s)) ds dy$$

$$v(h, u) = \frac{v_s u + g h s}{\tau^{-1} + u}$$

$s = 1$  if  $v(h, u)$  crosses  $v_h$  from below and  $s = 0$  if  $v$  crosses  $v_h$  from above.

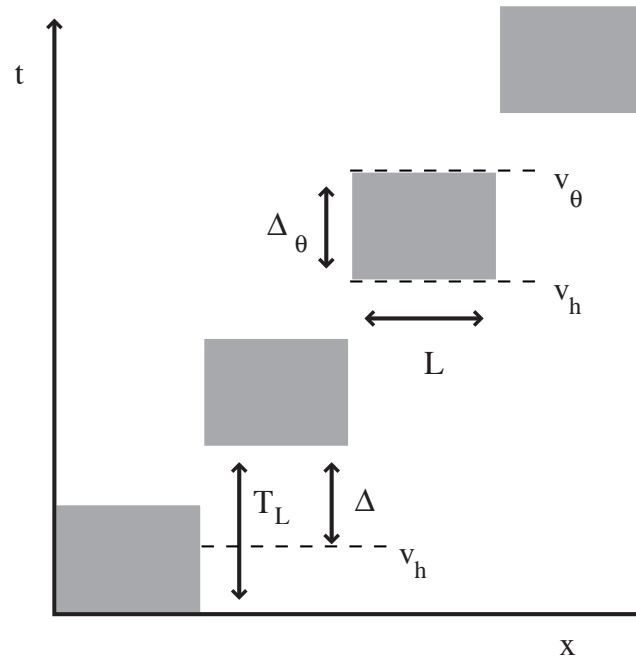
$$\dot{h} = \begin{cases} -h/\tau_h^- & v \geq v_h \\ (1 - h)/\tau_h^+ & v < v_h \end{cases}$$

i.e. a model of a network with a slow T-type calcium current, with an exact solution for a Heaviside.

S Coombes PRE 67 (2003) 041910

# An Inhibitory TC network

►  $w(x) = \Theta(\sigma - |x|)/2\sigma$

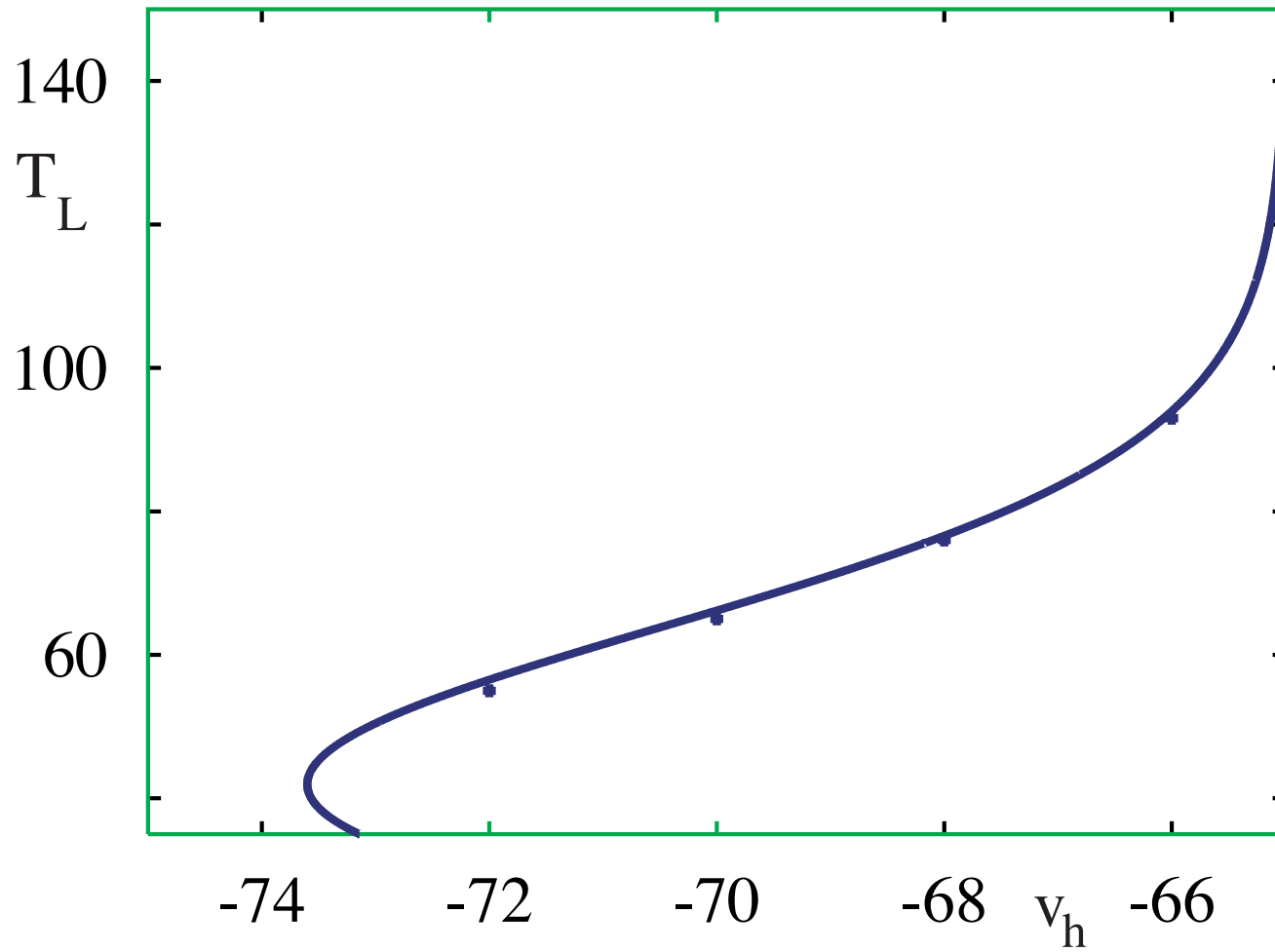


► Solitary lurcher

$$u(x, t) = Q(t, \min(t, \Delta_\theta))W(x)$$

$$Q(t, a) = \int_0^a \eta(t - s)ds, \quad W(x) = \int_x^{x+L} w(y)dy$$

► Closed form solution ...



Slow wave is stable