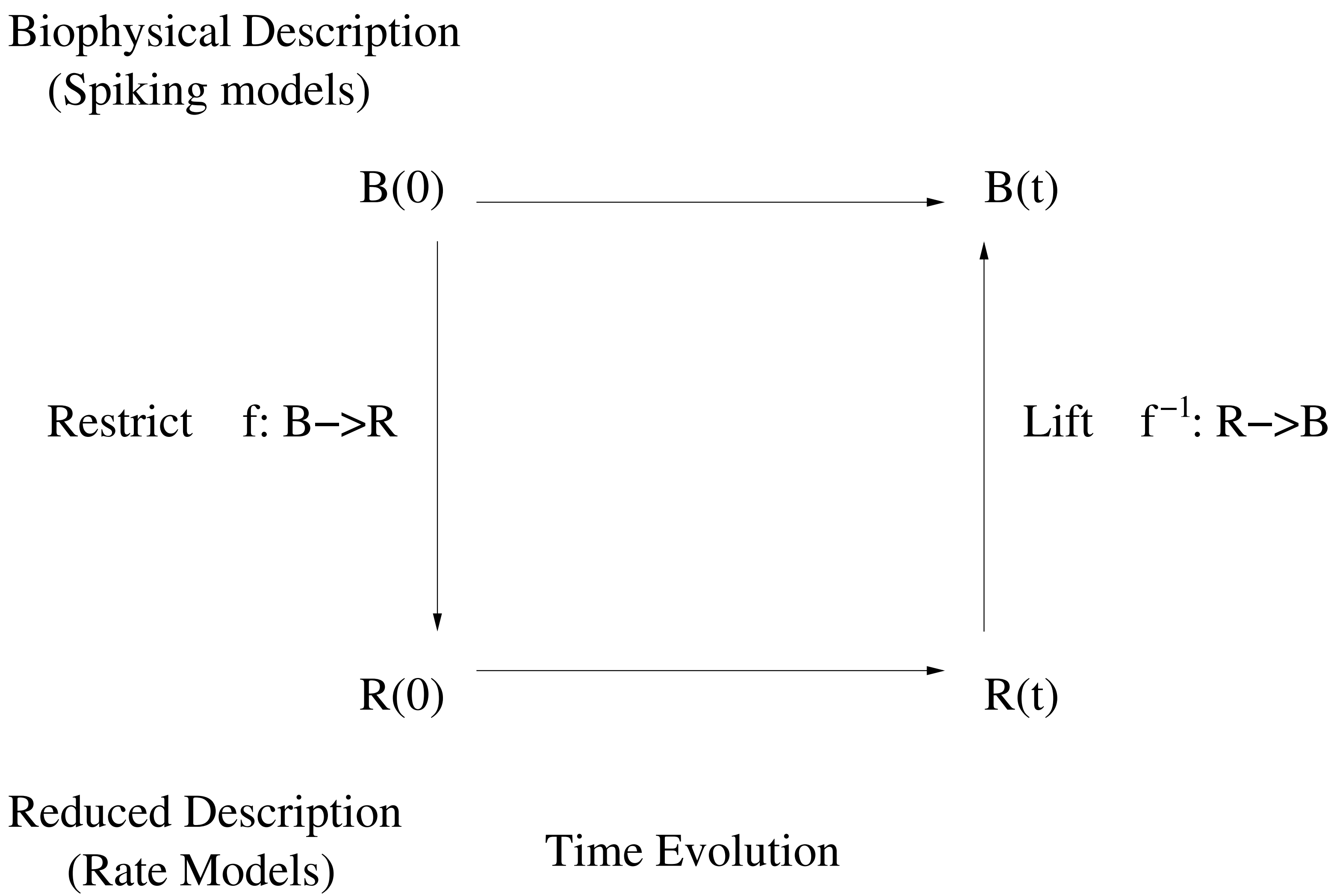
Localized Pulses in Neural Networks

C.C. Chow

NIH

Program


Biophysical Description
(Spiking models)
B(0)
B(t)
Restrict f: B−>R
Lift f^{-1}: R−>B
R(0)
R(t)
Reduced Description
(Rate Models)
Time Evolution

Localized persistent activity

- Short term working memory is correlated to persistent states of neural activity
- Possible analogue in neural network equations are localized self-sustaining ‘pulse’ or ‘bump’ solutions.
- Show existence and stability of pulses and find properties
- Compare and contrast bumps in rate models to spiking models

Integrate-and-Fire Network

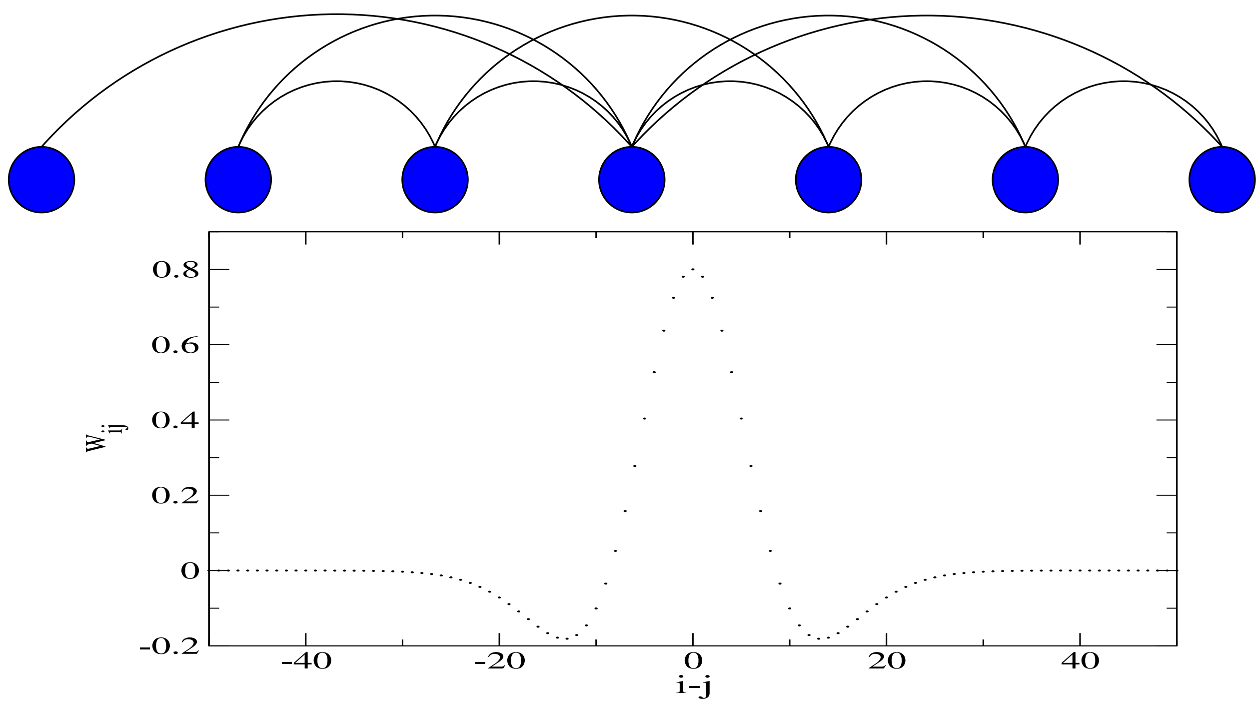
$$\frac{dv_i}{dt} = I - v_i + \sum_j w_{ij} s_j(t),\ \ s_j(t) = \beta \exp(-\beta t)$$

Neuron fires and resets when v reaches threshold

Integrate-and-Fire Network

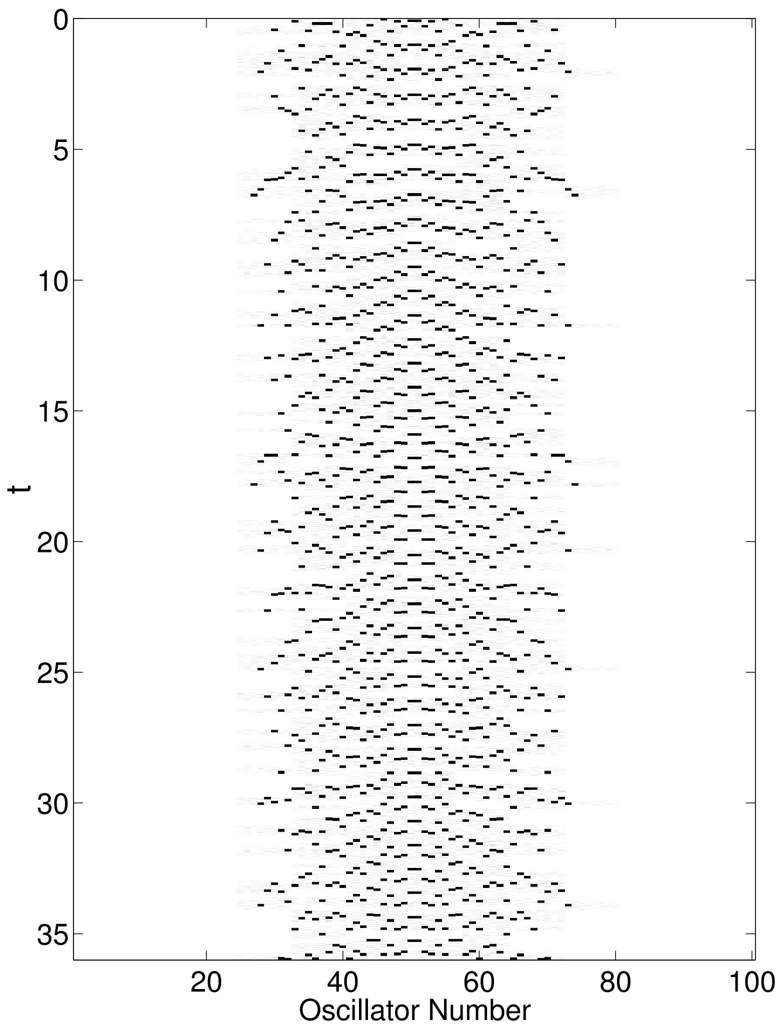
$$\frac{dv_i}{dt} = I - v_i + \sum_j w_{ij} s_j(t), \;\; s_j(t) = \beta \exp(-\beta t)$$

Neuron fires and resets when v reaches threshold



Localized persistent state (pulse)

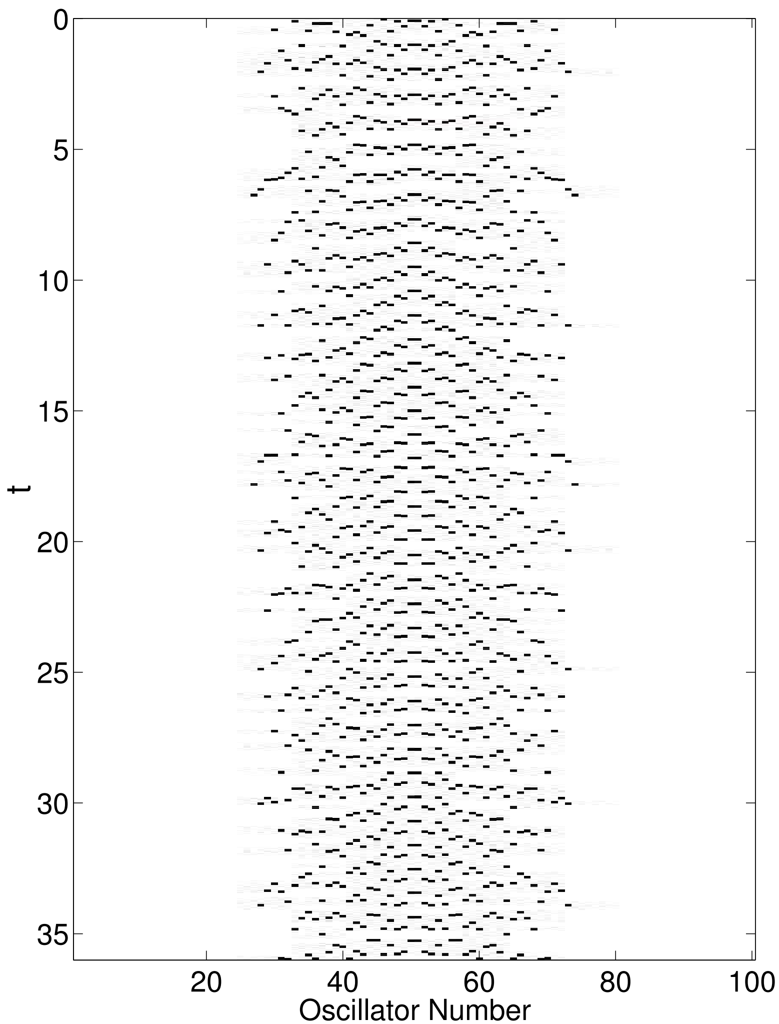
Simulation



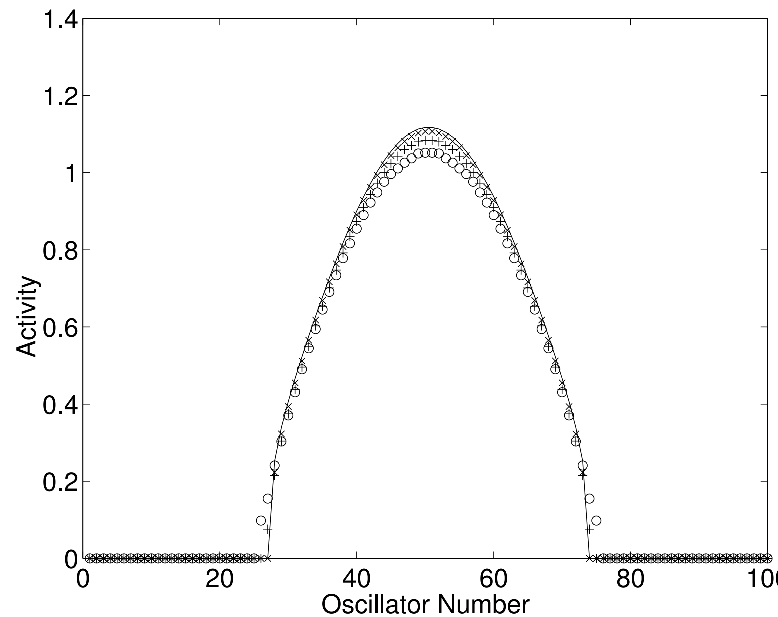
Laing and Chow, 2001

Localized persistent state (pulse)

Simulation



Average firing rate



Laing and Chow, 2001

Mean field approach

- Neuronal dynamics if neuron last fired at $t = s$

$$v_i(t) = I(1 - e^{-(t-s)}) + u_i(t) - u(s)e^{-(t-s)}$$

with neuronal input

$$u_i(t) = \sum_{l \in \text{spikes}} \sum_{j \in \text{neurons}} w_{ij}\epsilon(t - t_j^l)$$

where

$$\epsilon(t) = \beta \frac{e^{-\beta t} - e^{-t}}{\beta - 1}$$

- Can rewrite as

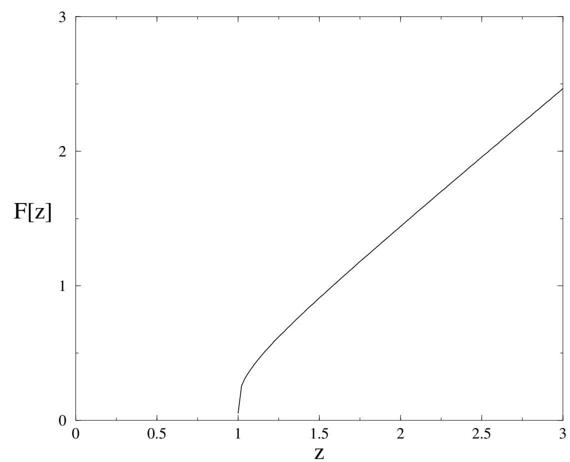
$$u_i(t) = \sum_j w_{ij} \int_0^\infty \epsilon(s) A_j(t-s) ds$$

where $A_j(t) = \sum_l \delta(t - t_j^l)$ is the “activity" of neuron j

- u_i is almost constant if input is uncorrelated (or if synapses are slow)
- Average of A_i is the firing rate of neuron i given u_i, i.e. $A_i = f[u_i]$

- For integrate-and-fire neuron:

$$f[u] = 1/\ln\left[\frac{I+u}{I+u-1}\right]$$

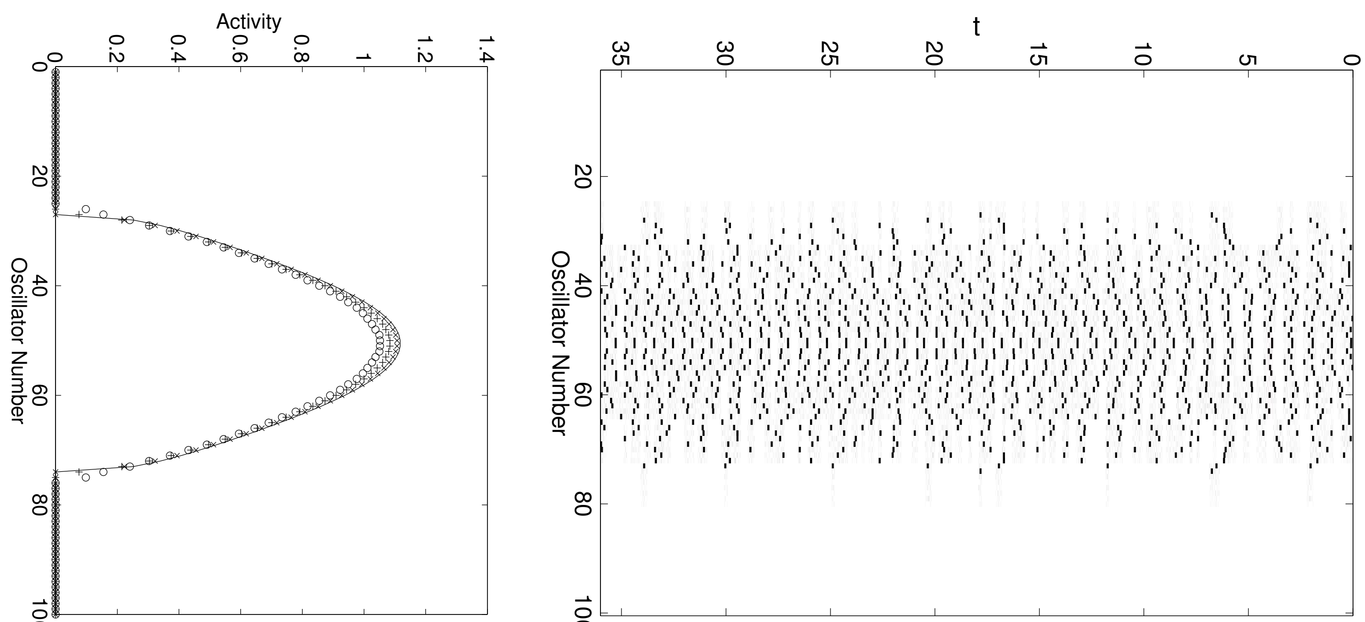


- $f[u]$ is the ‘gain function’

- This gives the mean field equations

$$u_i = \sum w_{ij} f[u_j], \quad A_i = f[u_i]$$

- Matched simulations of integrate-and-fire network (with Carlo Laing)



Dynamics

- Suppose inputs are slowly varying: $A_i(t) \simeq f[u_i(t)]$,

$$u_i(t) = \sum_j w_{ij} \int_{-\infty}^{t} \epsilon(t-s) f[u_j(s)] ds$$

- If $\epsilon(t) \sim \exp(-t/\tau)/\tau$ then

$$\tau \frac{du_i(t)}{dt} = -u_i + \sum_j w_{ij} f[u_j]$$

(..., Wilson-Cowan, Cohen-Grossberg, Amari, Ermentrout,...)

- Breaks down if not slowly varying (Gerstner, van Hemmen) –Spike response formalism

- Coarse-grain in space

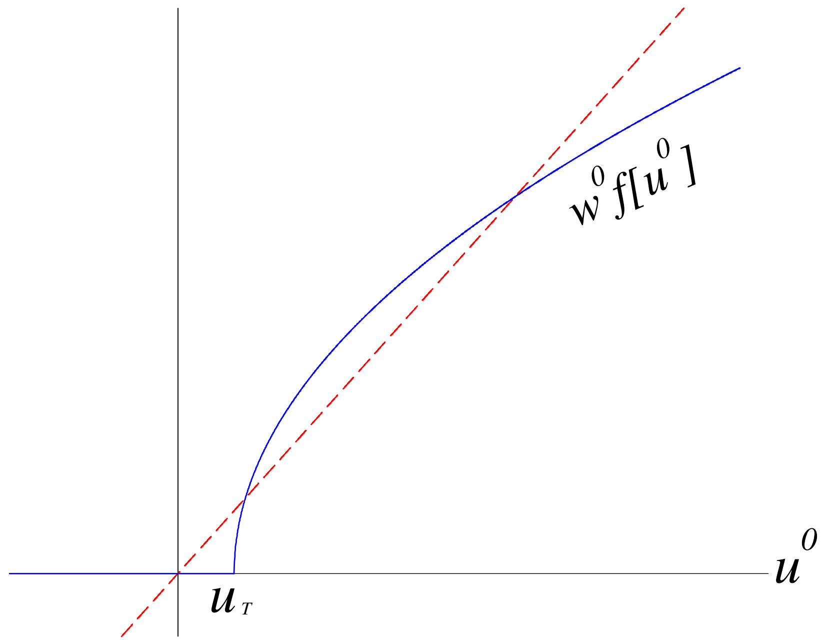
$$\tau \frac{\partial u(x,t)}{\partial t} = -u(x,t) + \int_{\Omega} w(x-y) f[u(y,t)] dy$$

- Stationary solutions obey

$$u(x) = \int_{\Omega} w(x-y) f[u(y)] dy$$

Constant stationary solutions

- Suppose $\int_\Omega w(x-y)dy = w^0$, constant solutions $u_i = u^0$ satisfy $u^0 = w^0 f[u^0]$

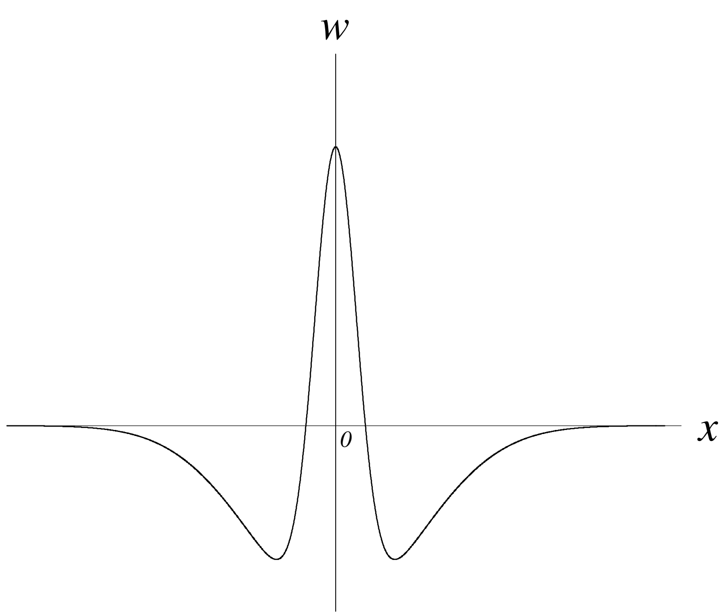


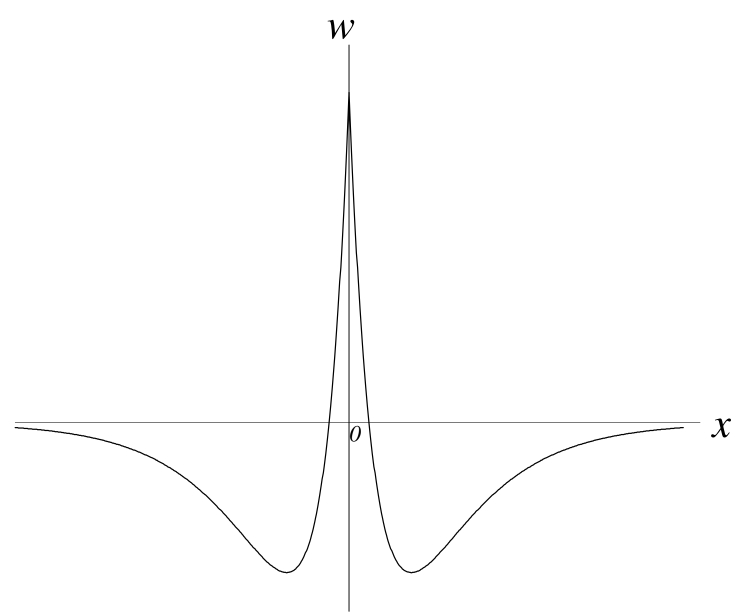
- Multiple stationary solutions possible (analogue of memory)

Localized pulse solutions

$$u(x) = \int_{\Omega} w(x-y) f[u(y)] dy$$

- Spatially dependent weights
  e.g. 'Mexican Hat' 'Wizard Hat'

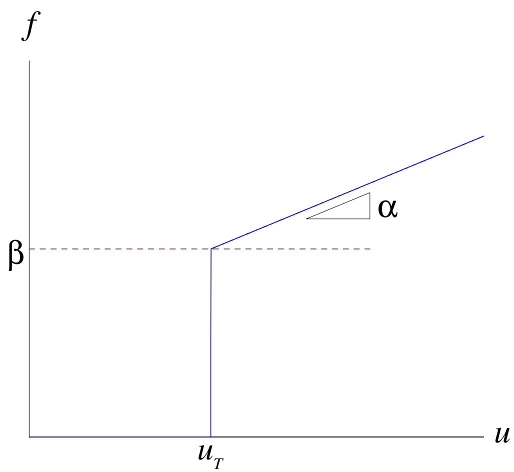


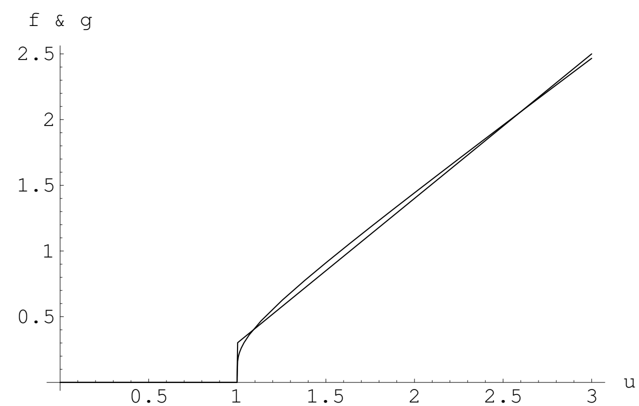


$$w(x) = Ae^{-ax^2} - Be^{-bx^2} \quad w(x) = Ae^{-a|x|} - Be^{-b|x|}$$

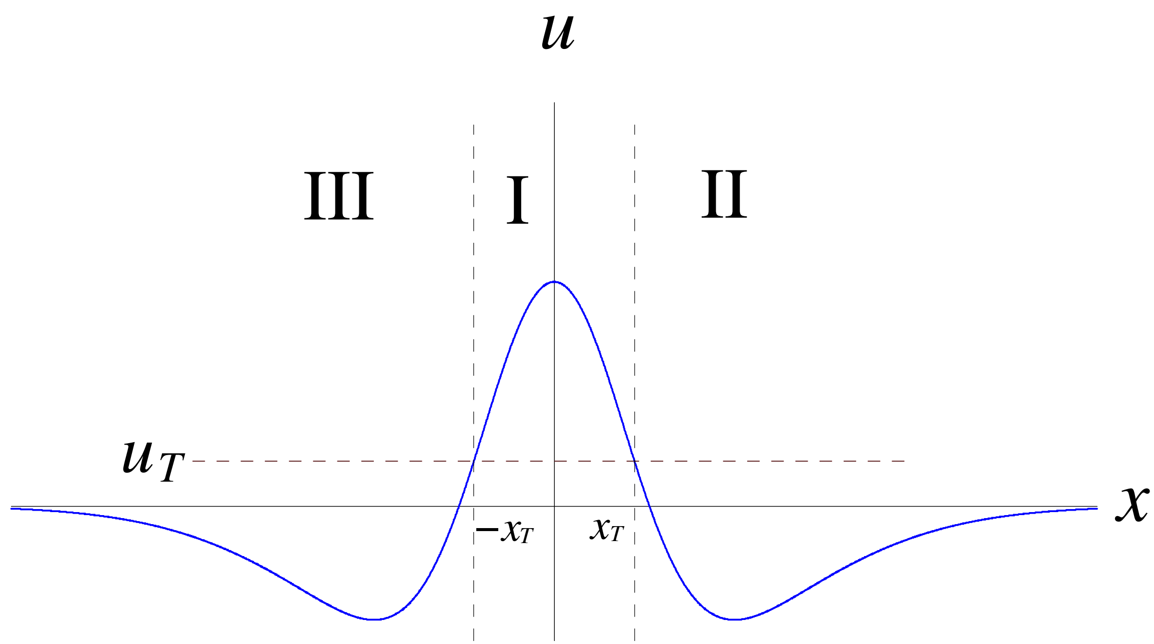
- Consider ‘jump linear’ gain function to represent integrate-and-fire gain

$$f[u] = [\alpha(u - u_T) + \beta]\, H(u - u_T)$$





- Find pulse solutions of the form



- $u(x_T) = u_T$

Project to Low Dimension

- Strategy is to transform to ODE and solve
- Fourier transform deconvolves integral operator

$$u(x) = \int_{-\infty}^{\infty} w(x-y) f[u(y)] dy$$

to

$$F[u] = F[w]F[f[u]]$$

with

$$F[\cdot] = \int e^{isx} \cdot dx, \; F^{-1}[\cdot] = \frac{1}{2\pi} \int e^{-isx} \cdot dx$$

- For $w(z) = Ae^{-a|z|} - Be^{-b|z|}$

$$F[w] = \frac{2aA(s^2+b^2) - 2bB(s^2+a^2)}{(s^2+a^2)(s^2+b^2)}$$

- Rearrange to obtain

$$(s^2+a^2)(s^2+b^2)F[u] = 2ab(Ab-Ba)F[f]+2(aA-bB)s^2F[f]$$

- Inverse transform

$$
\begin{aligned}
u'''' - (a^2+b^2)u'' + a^2b^2u &= 2ab(bA-aB)f[u] \\
&+ 2(aA-bB)\Big\{ f[u(x_T)]\left[\delta'(x-x_T)+\delta'(x+x_T)\right] \\
&\quad + f'[u(x_T)]u'(x_T)\left[\delta(x-x_T)+\delta(x+x_T)\right] \\
&\quad + \left[f''[u(x)](u')^2 + f'[u(x)]u''\right]_{u\geq u_T}\Big\}
\end{aligned}
$$

- Piecewise linear 4th order ODE
- Choice of coupling allows for projection to low dimension

Pulse solution must satisfy:

1. Boundary conditions
   $u(x) > u_T, \ -x_T < x < x_T$
   $u'(0) = u'''(0) = 0$
   $u(\pm\infty) = 0$ and derivatives
2. Matching conditions at $x = x_T$

$$
\begin{aligned}
u(x_T^+) &= u(x_T^-) = u_T \\
u'(x_T^+) &= u'(x_T^-) \\
u''(x_T^+) &= u''(x_T^-) + 2(aA - bB) f[u(x_T^-)] \\
u'''(x_T^+) &= u'''(x_T^-) + 2(aA - bB) f'[u(x_T^-)] u'(x_T^-)
\end{aligned}
$$

- Solutions have the form

$$I : u(x) = C(e^{\omega_+ x} + e^{-\omega_+ x}) + D(e^{\omega_- x} + e^{-\omega_- x}) + U_0$$

$$II : \quad u(x) = Ee^{-ax} + Fe^{-bx}$$

$$III : \quad u(x) = Ee^{ax} + Fe^{bx}$$

where

$$U_0 = \frac{2(\beta - \alpha u_T)(bA - aB)}{ab - \alpha(bA - aB)}, \quad \omega_\pm = \left[\frac{R \pm \sqrt{\Delta}}{2}\right]^{1/2}$$

$$R = a^2 + b^2 + 2\alpha(aA - bB), \quad \Delta = [R^2 - 4a^2b^2 + 8\alpha ab(bA - aB)]$$

- Solution structure changes as $\omega_\pm$ changes

Matching Conditions

$$Ee^{-ax_T} + Fe^{-bx_T} = u_T$$

$$C(e^{\omega_+ x_T} + e^{-\omega_+ x_T}) + D(e^{\omega_- x_T} + e^{-\omega_- x_T}) + U_0 = Ee^{-ax_T} + Fe^{-bx_T}$$

$$\omega_+ C(e^{\omega_+ x_T} - e^{-\omega_+ x_T}) + \omega_- D(e^{\omega_- x_T} - e^{-\omega_- x_T}) = -aEe^{-ax_T} - bFe^{-bx_T}$$

$$\omega_+^2 C(e^{\omega_+ x_T} + e^{-\omega_+ x_T}) + \omega_-^2 D(e^{\omega_- x_T} + e^{-\omega_- x_T}) = a^2 Ee^{-ax_T} + b^2 Fe^{-bx_T} - 2\beta(aA - bB)$$

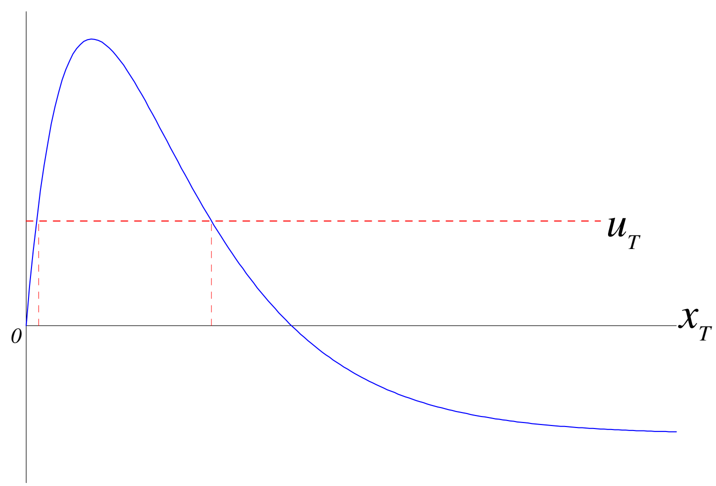
$$\omega_+^3 C(e^{\omega_+ x_T} - e^{-\omega_+ x_T}) + \omega_-^3 D(e^{\omega_- x_T} - e^{-\omega_- x_T}) = - a^3 Ee^{-ax_T} - b^3 Fe^{-bx_T} + 2\alpha(aA - bB)[aEe^{-ax_T} + bFe^{-bx_T}]$$

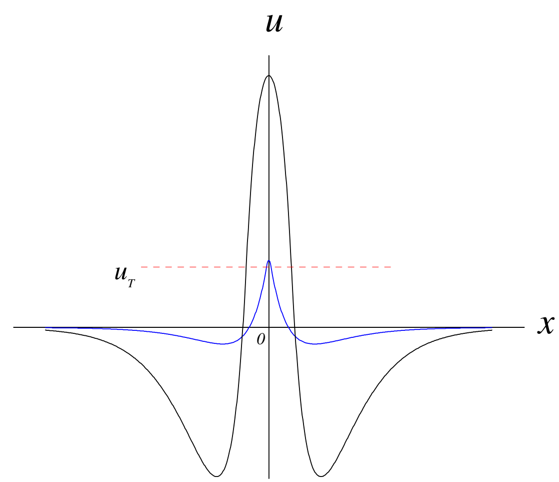
- Pulse exists if solution can be found (5 eq'ns, 5 unknowns)
- Solve 'linear system' for coefficients C, D, E, F and obtain existence condition $\Phi(x_T) = u_T$
- Simple for $\alpha = 0$, unwieldy otherwise

Amari's Solution: $\alpha = 0$

- $f[u] = H[u - u_T]$ with $w(z) = Ae^{-a|z|} - Be^{-b|z|}$
- Existence Condition ($u_T = \int_{-x_T}^{x_T} w(x-y)dy$)

$$\Phi(u_T) \equiv \frac{A}{a}(1 - e^{-2ax_T}) - \frac{B}{b}\left(1 - e^{-2bx_T}\right) = u_T$$

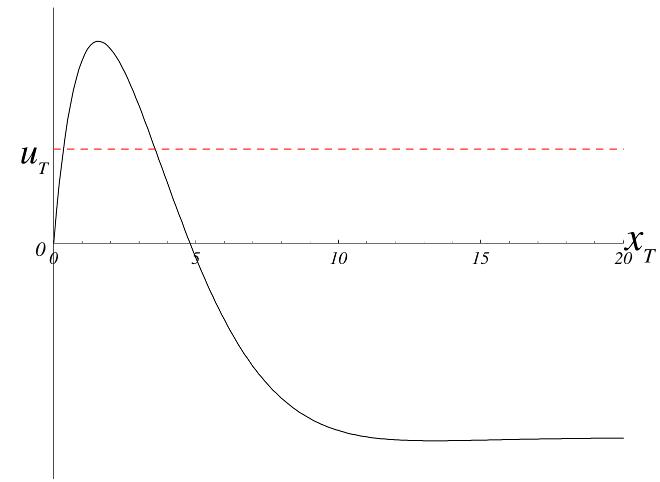


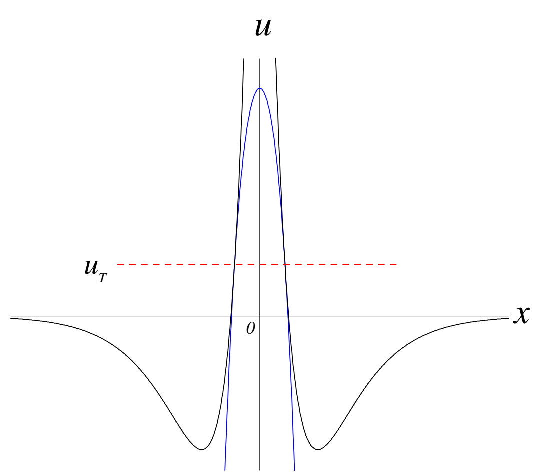


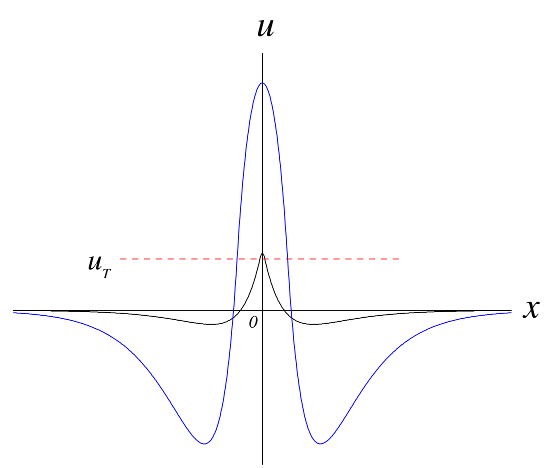
- Two pulse solutions (small and large)
- Only large one is linearly stable

Nonzero α

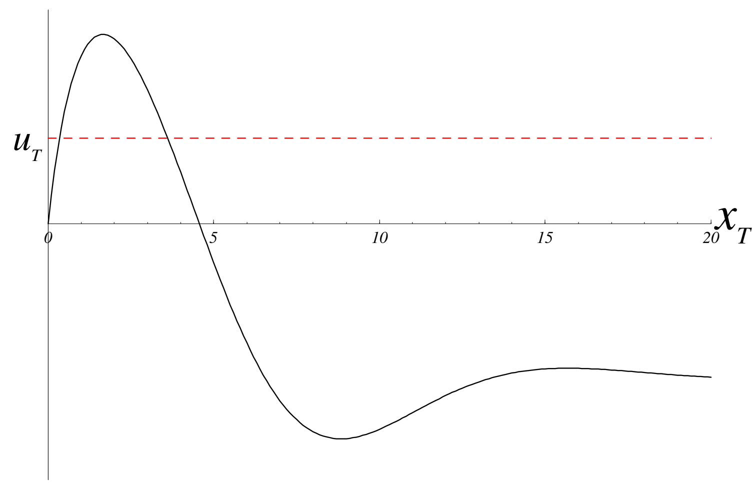
- Examples with $A = 1, B = 0.65, a = 0.32, b = 0.18, \beta = 1$ $\alpha = 0.1$

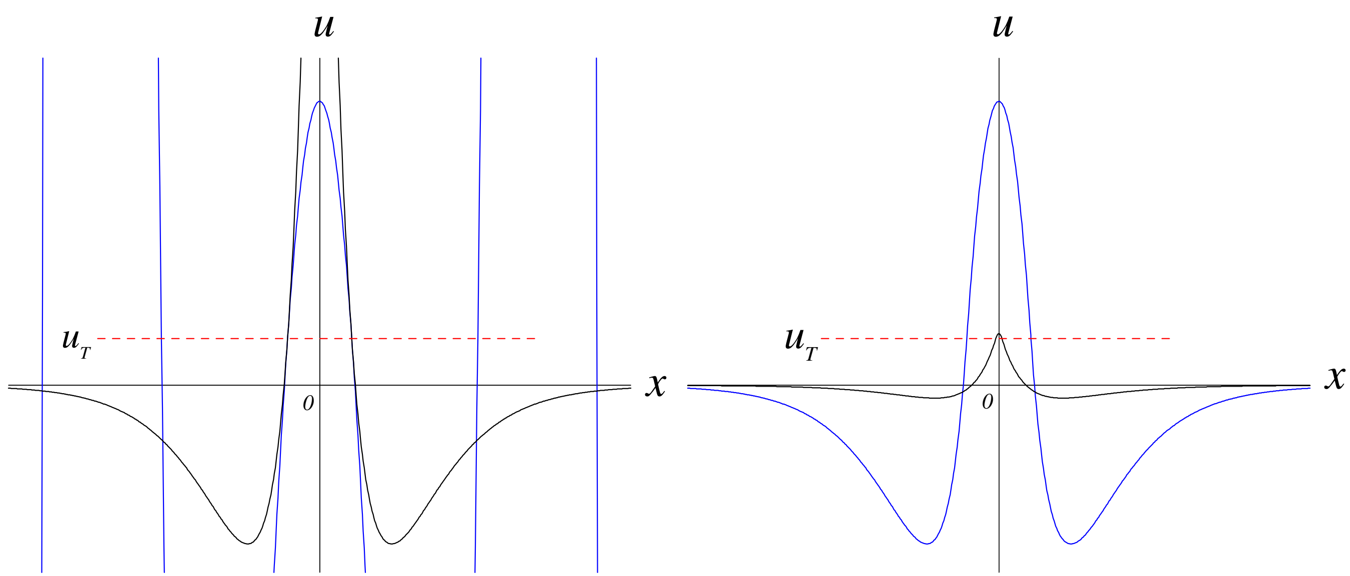




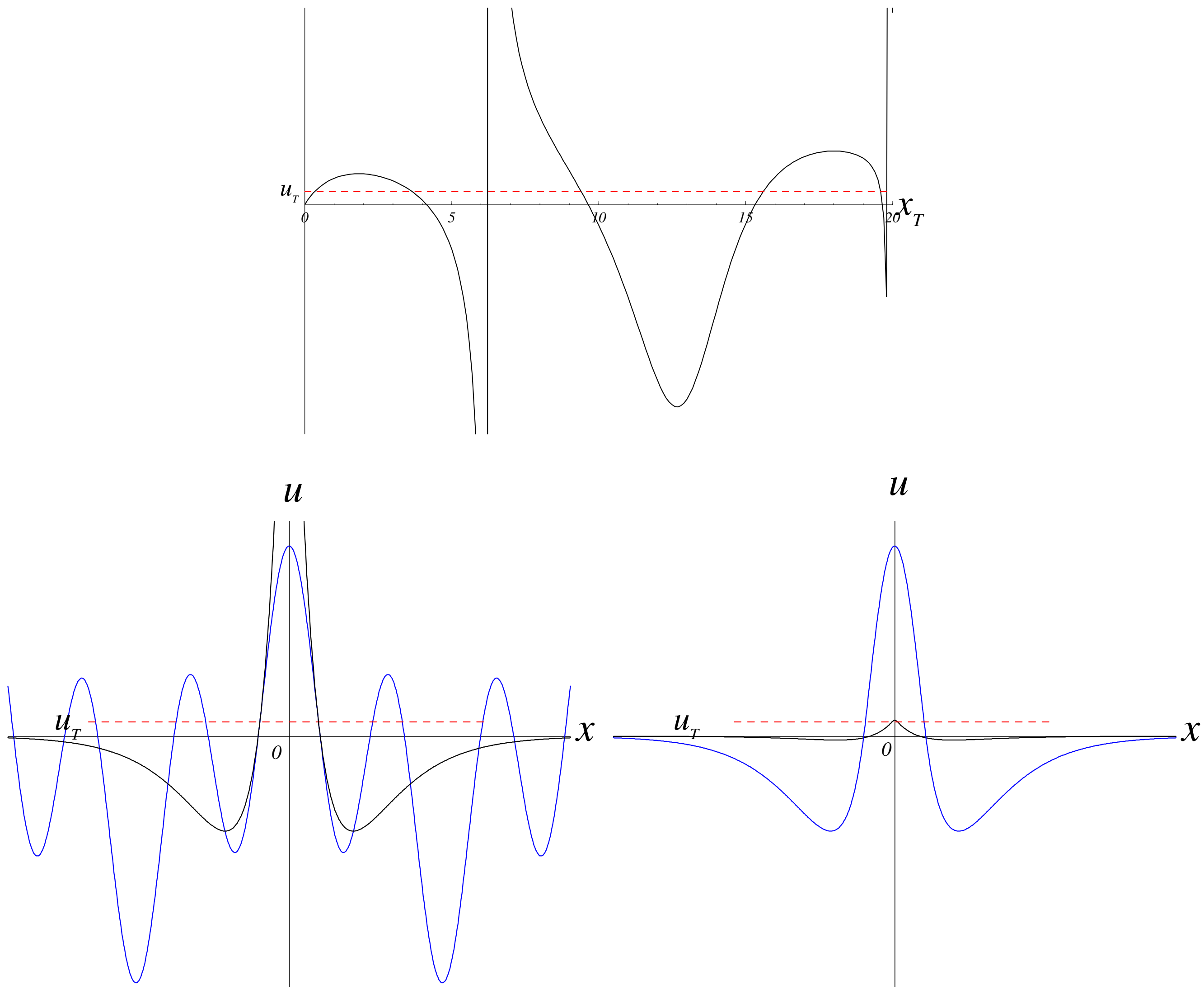


$\alpha = 0.5$





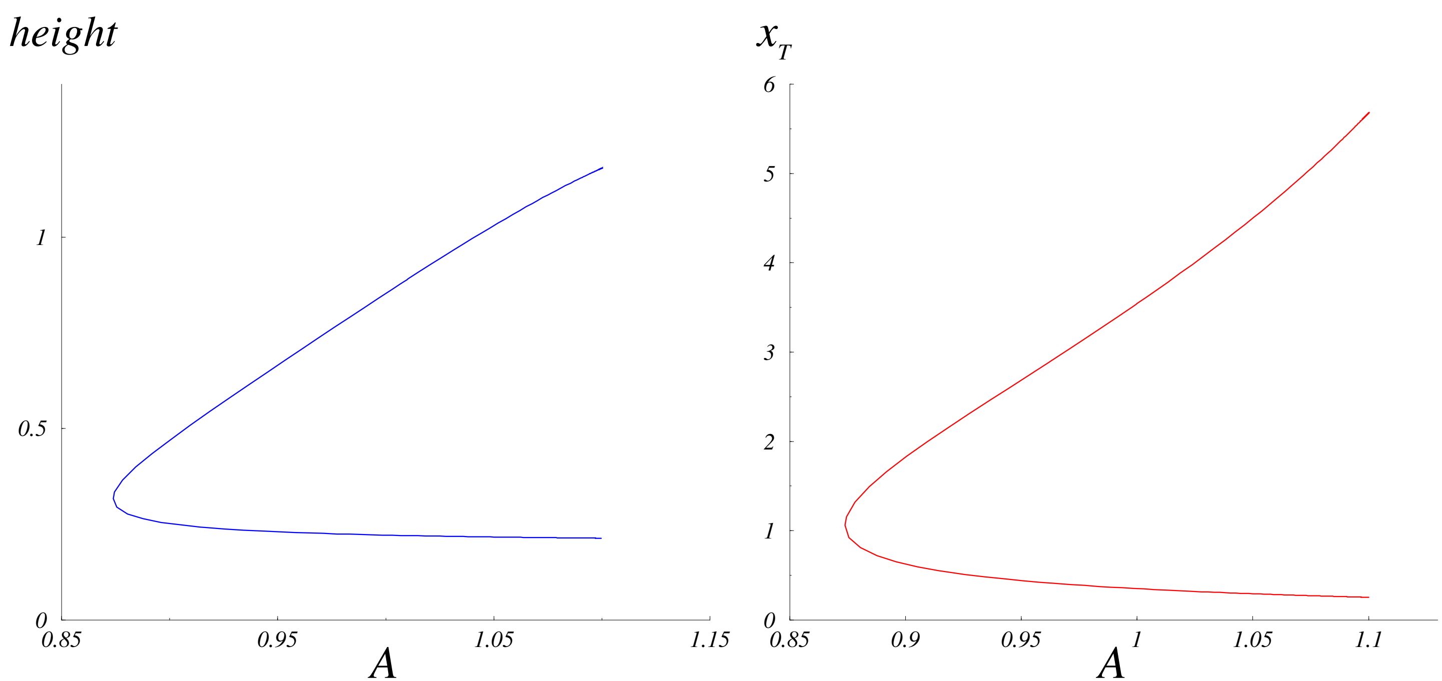
$\alpha = 1.0$



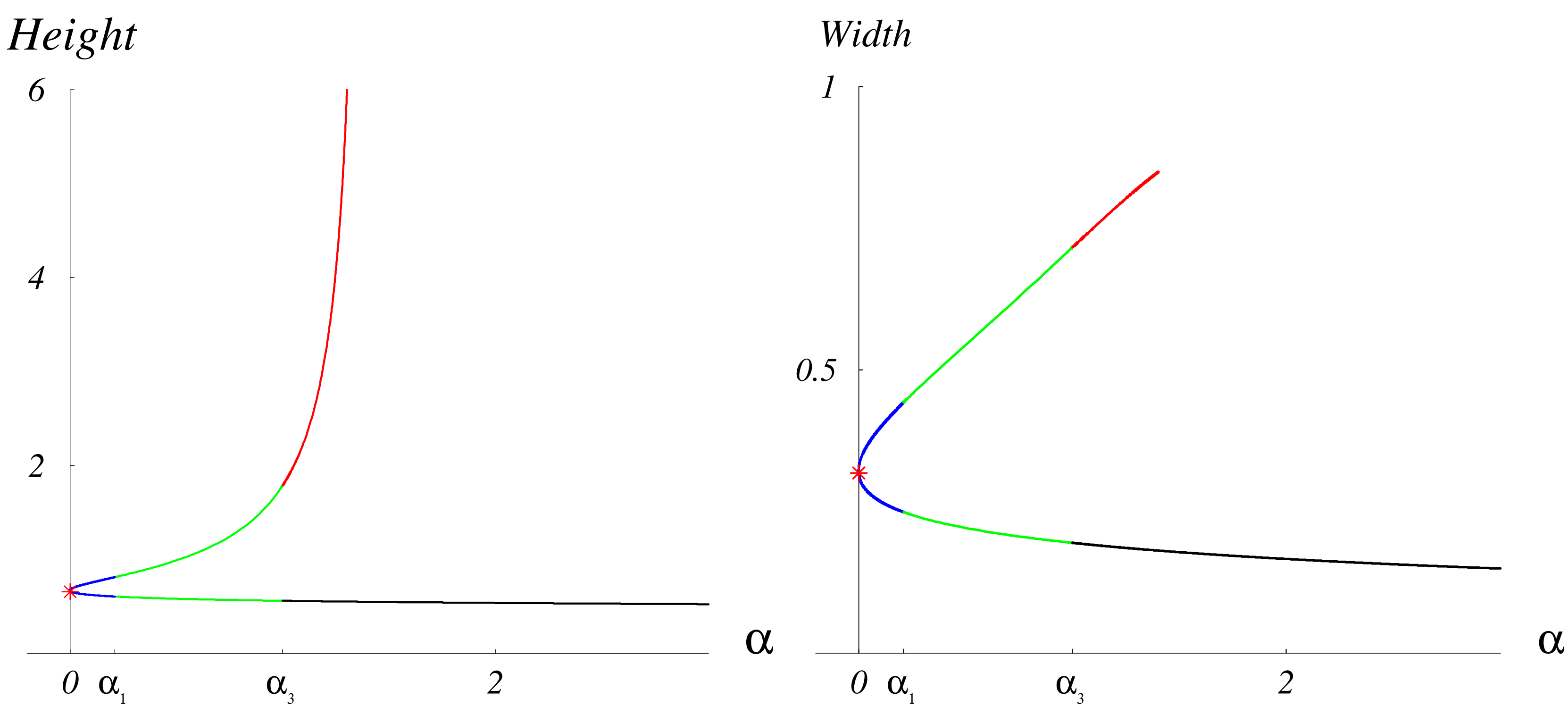
Continuation

- Small bump and large bump annihilate in saddle node

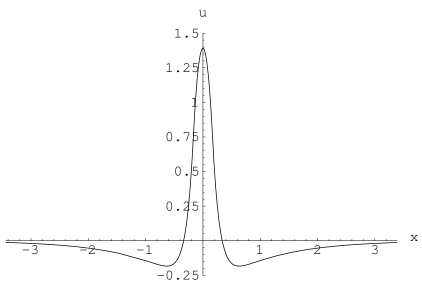
$$\alpha = 0.04$$

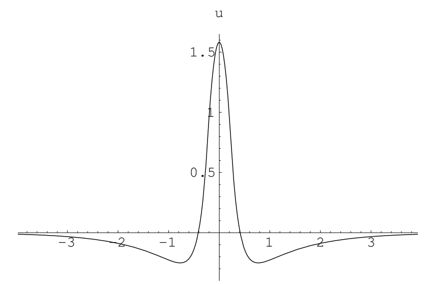


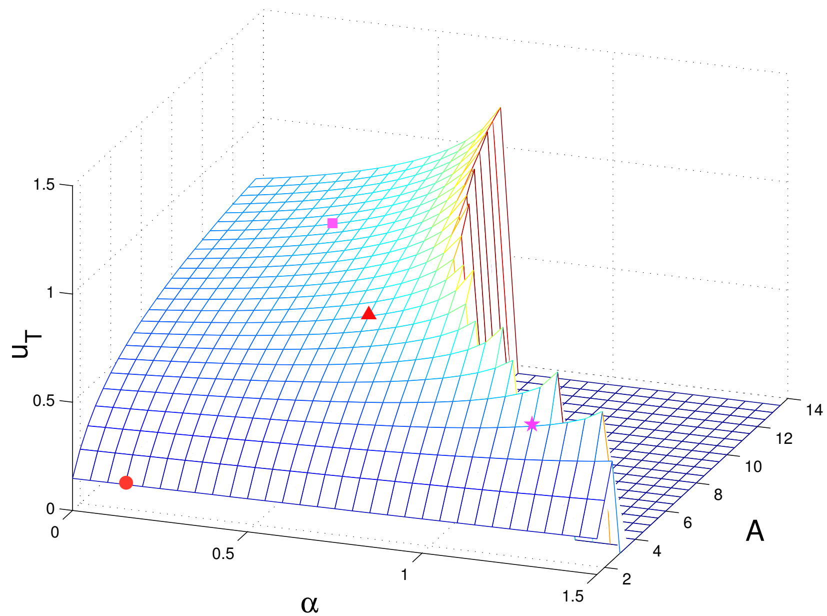
Height goes to infinity at critical α

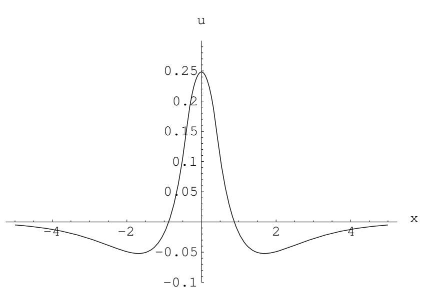


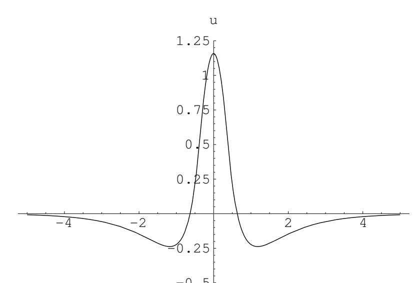
Critical u_T $(A = a)$



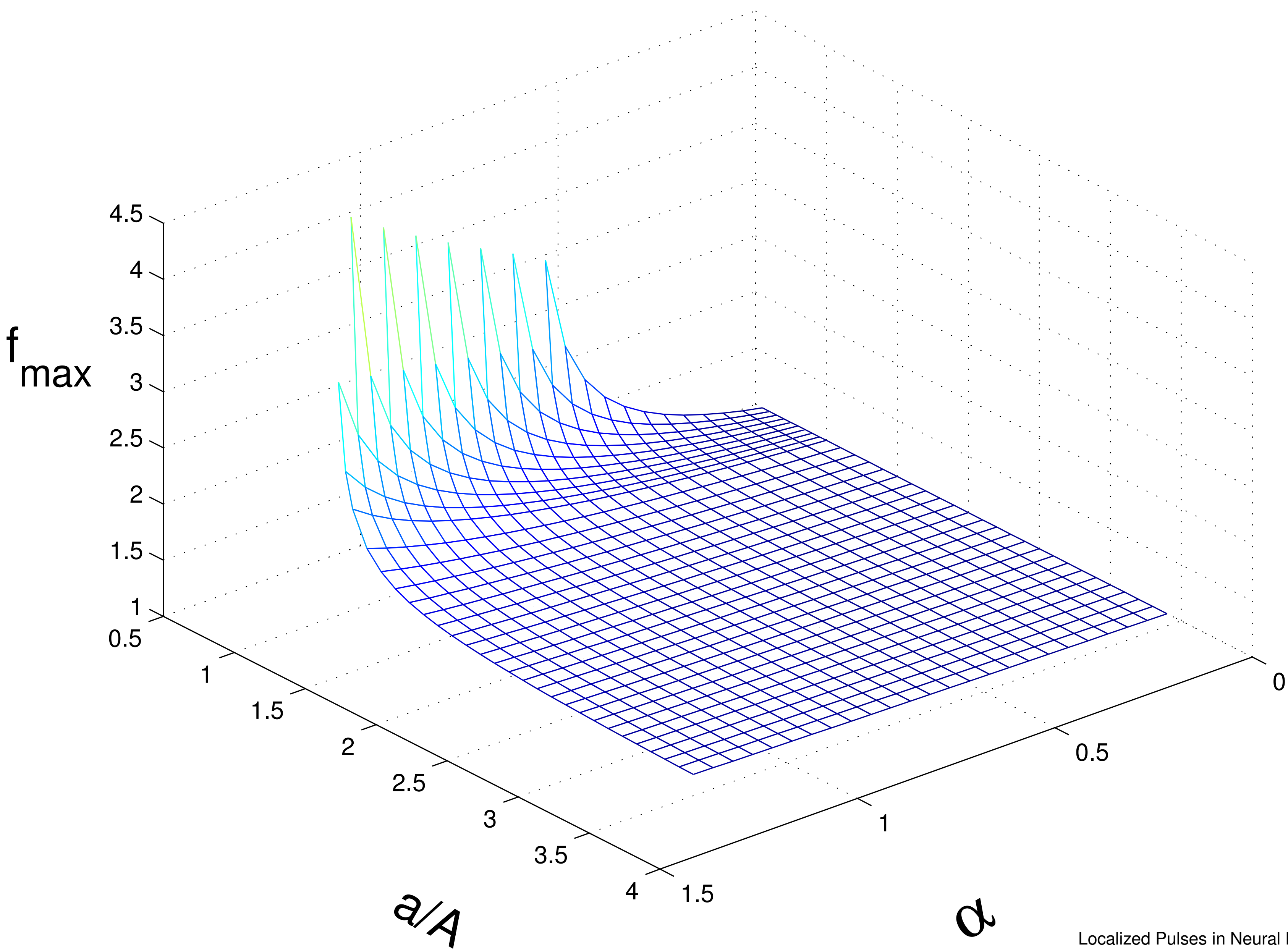




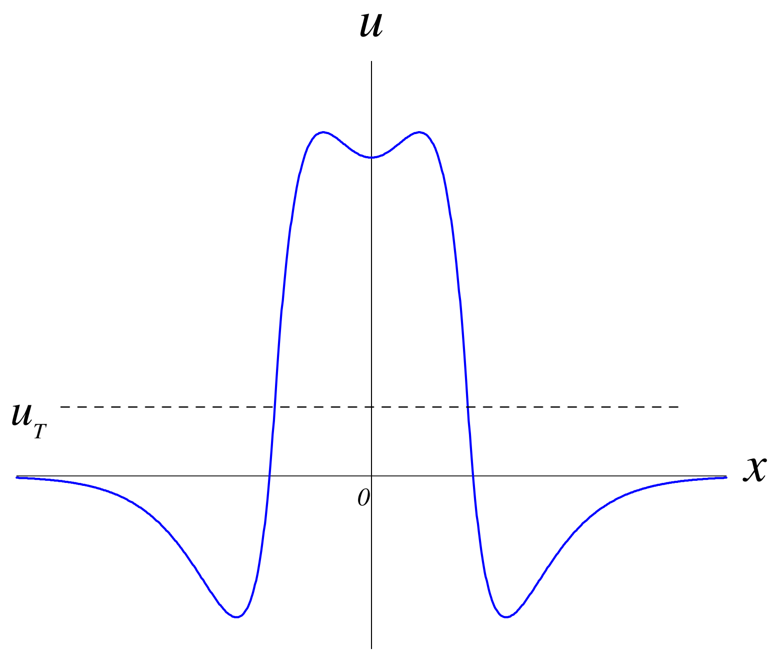


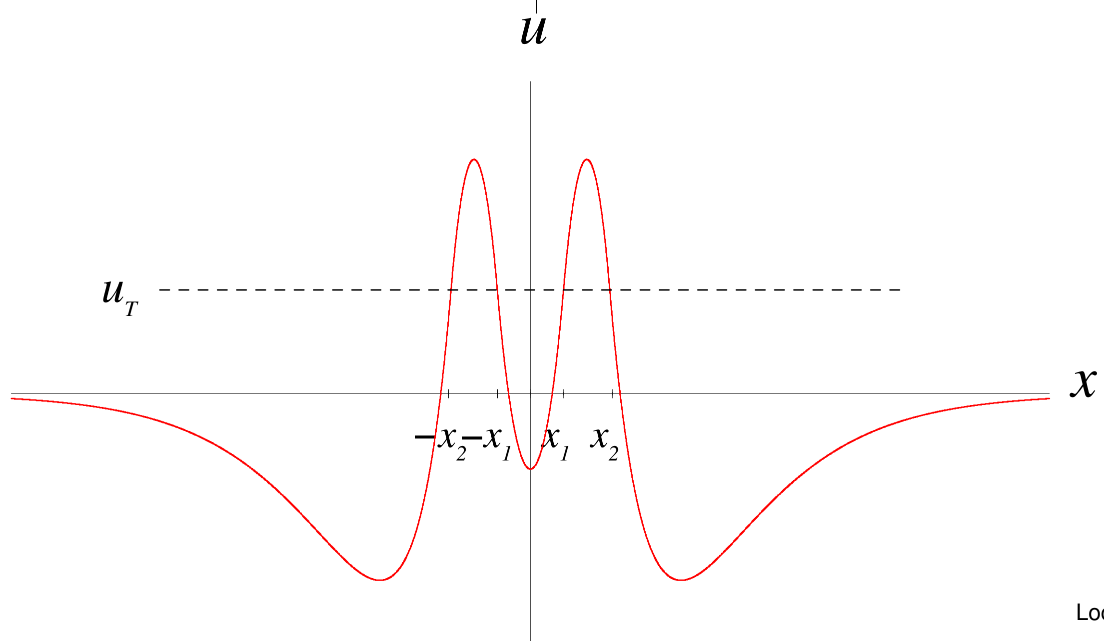


Maximum firing rate

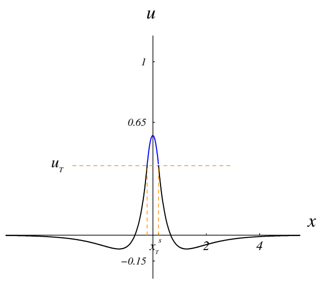


Dimple and Double Pulses

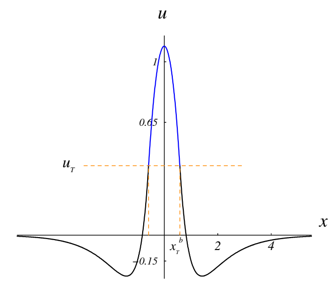




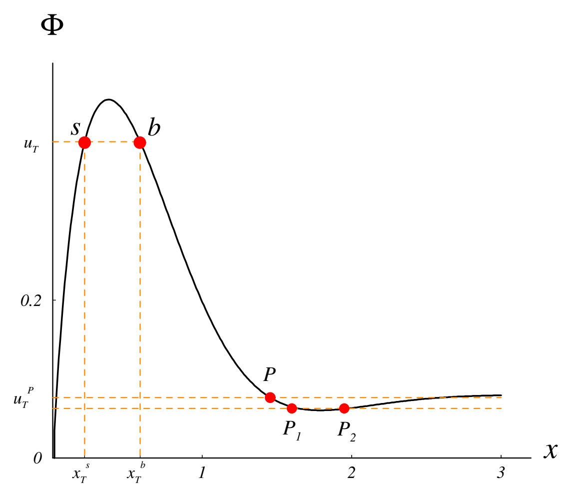
Transitions in u_T ($\alpha = 0.6187$, $A = 2.8$, $a = 2.6$, $B = b = \beta = 1$)

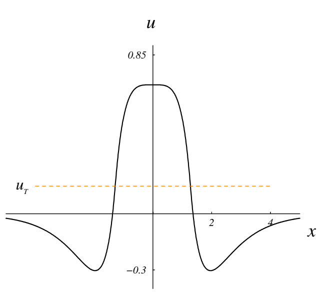


Single-pulse **s**

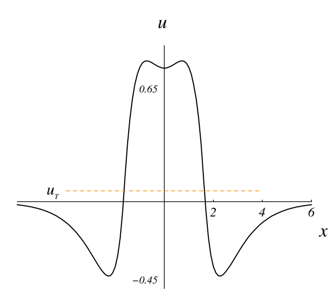


Single-pulse **b**



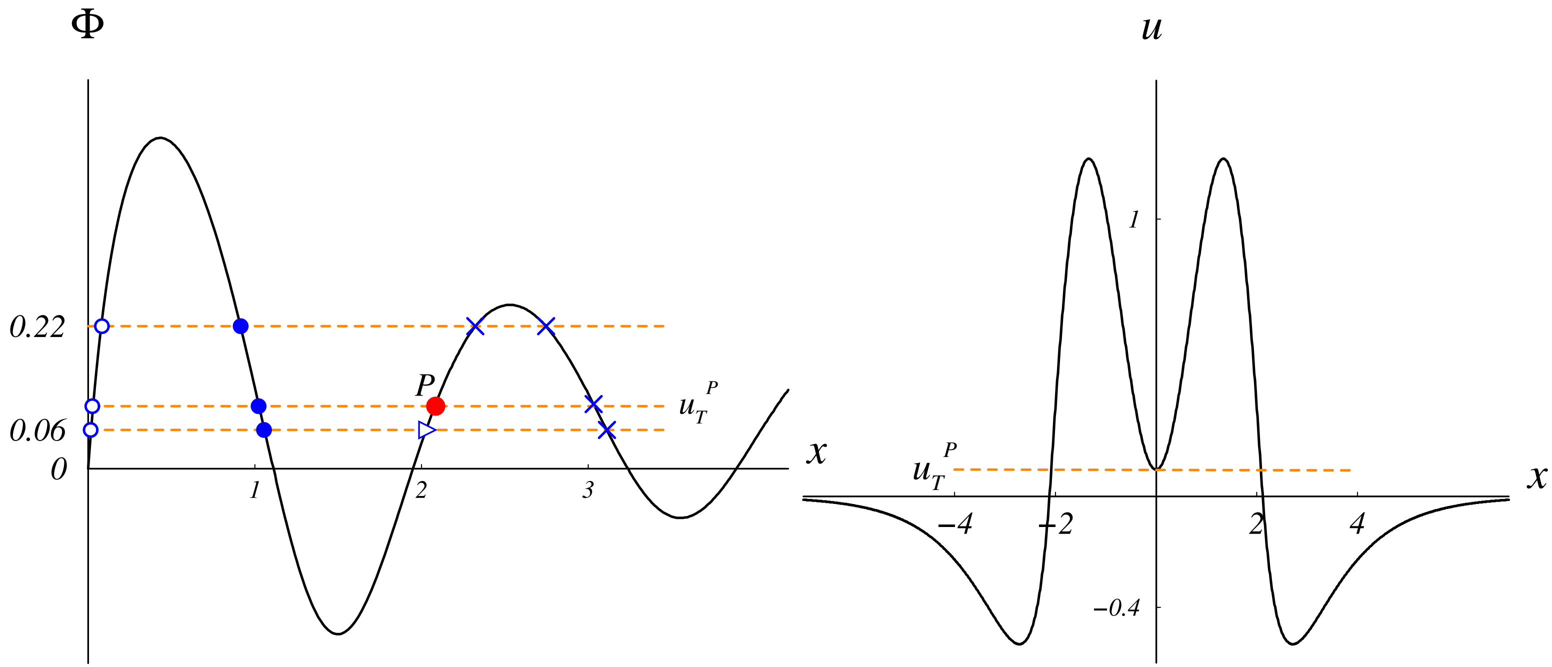


Pulse at transition P



Pulse at P_1

$$A = 2.8,\ a = 2.6,\ \alpha = 0.9987,\ \beta = 1$$



- ○ small single pulse
- ● big single pulse
- ▷ dimple pulse
- × not a valid solution

At P, dimple pulse splits into a double pulse.

Linear Stability

$$u_t = -u + \int_{-\infty}^{\infty} w(x-y) f[u(y,t)] dy$$

- Let $u(x,t) = u_0(x) + v(x)e^{\lambda t}$ and linearize

$$(1+\lambda)v(x) = w(x-x_T)\frac{v(x_T)}{c} + w(x+x_T)\frac{v(-x_T)}{c} + \alpha \int_{-x_T}^{x_T} w(x-y)v(y)dy$$

where $c > 0$ is the slope of $u_0(x)$ at $-x_T$

- $\mathrm{Re}\lambda > 0$ indicates instability
- Consider wizard hat coupling and solve eigenvalue problem

Properties of Eigenvalue Problem

$$(1 + \lambda) = L(v)$$

- λ is real
- $\lambda = 0$ is an eigenvalue (translational invariance)
- λ is bounded above by λ_b

$$\lambda \leq 2w_0(\frac{1}{c} + \alpha x_T) - 1 \equiv \lambda_b$$

  where w_0 is the maximum of $|w(x)|$ on $[-x_T, x_T]$
- Eigenfunction $v(x)$ is either even or odd.
- $L(v)$ is a compact operator
- Essential spectrum is in the left half plane

Eigenvalues

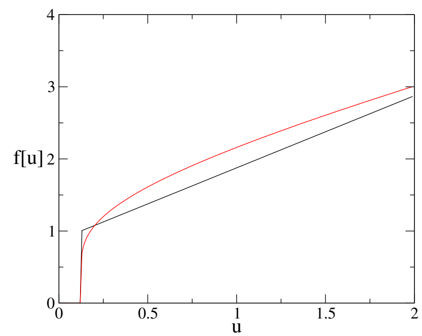
- To evaluate λ explicitly, transform to ODE and solve
- Matching conditions across $\pm x_T$ form linear system of coefficients $M(\lambda) = 0$
- Eigenvalues must satisfy $Det M(\lambda) = 0$
- If there exists $0 < \lambda < \lambda_b$ then the standing pulse is unstable
- Otherwise pulse is stable

Stability Results

- Small pulse is unstable, large pulse is stable
- Can have coexisting stable pulses
- Dimple pulses can be stable and coexist with large pulses
- No stable double pulses for Amari case were found

Compare to spiking models

- Search parameter space using jump-linear gain rate model matched to integrate-and-fire gain rate model

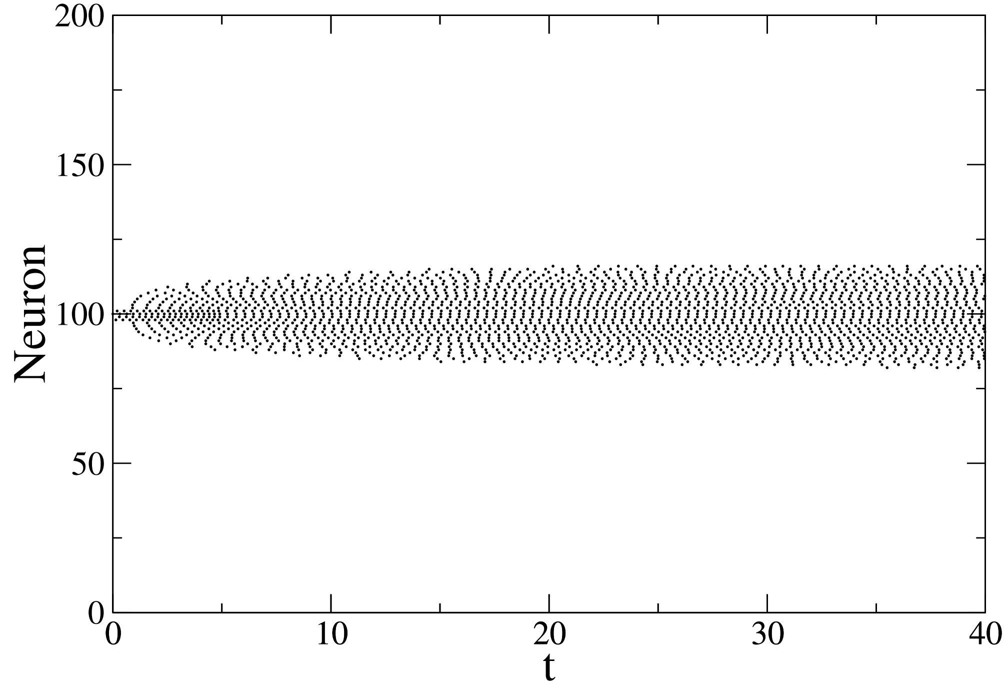


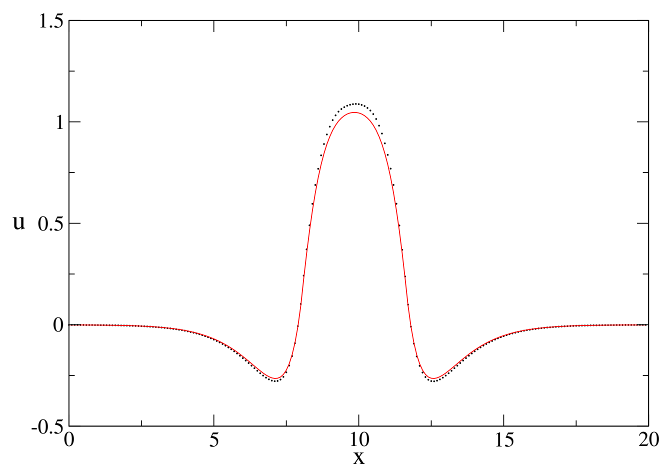
- Simulate in integrate-and-fire spiking model

$$\tau \frac{dv}{dt} = I - v + \sum_j w_{ij} s_j, \quad \frac{ds_j}{dt} = -\beta s_j$$

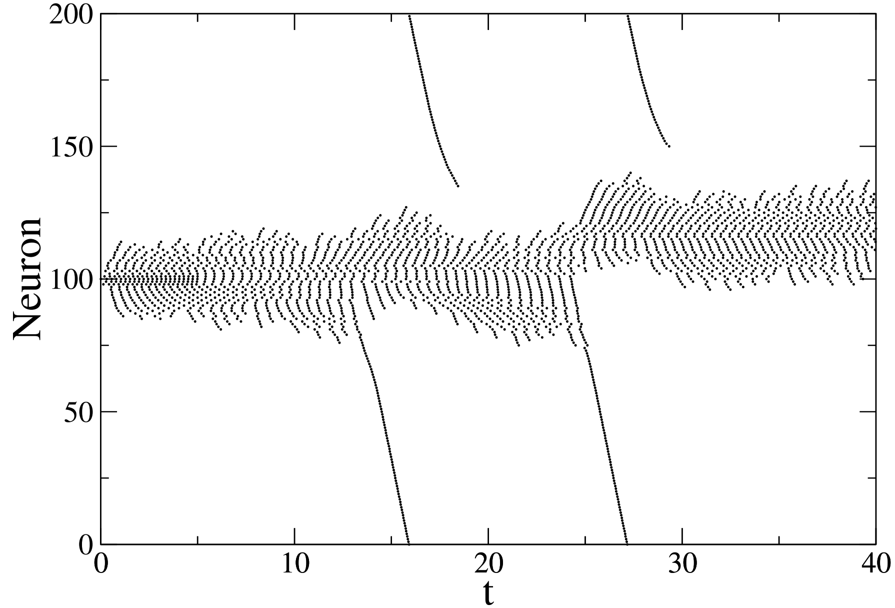
at $v_j = 8$, $v_j \to 0$, $s_j \to s_j + \beta$, $\tau = .2$,
$w_{ij} = (Ae^{-a|i-j|dx} - e^{-|i-j|dx})dx$

$$I = 0.786 \; A = 1.8 \; a = 1.6 \; \beta = .5$$

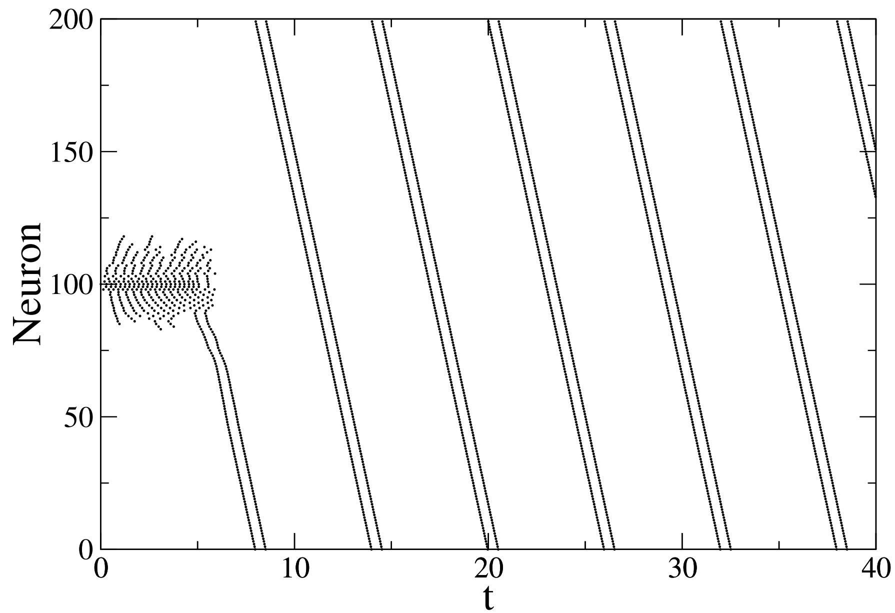




Increase β

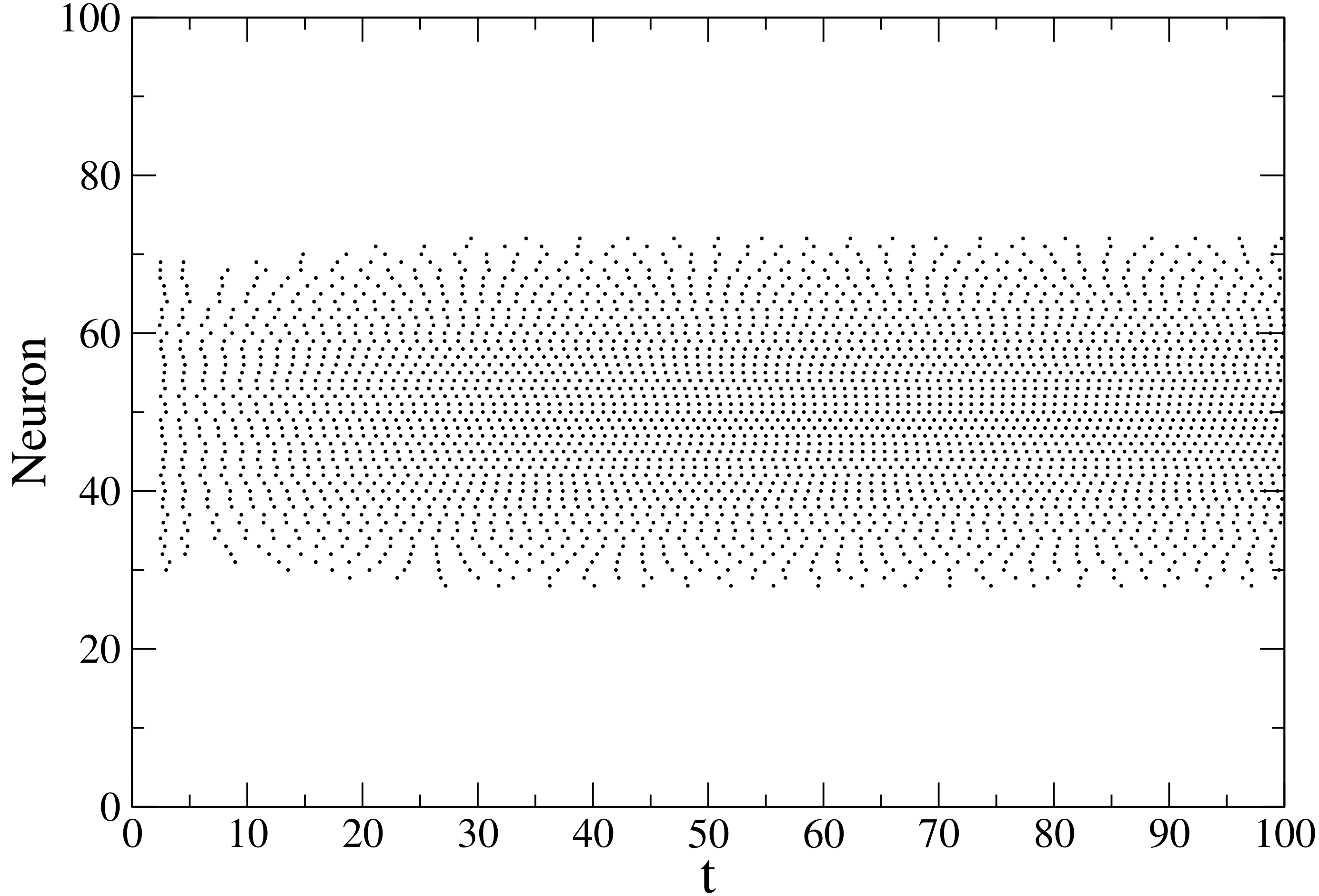


$\beta = 4$

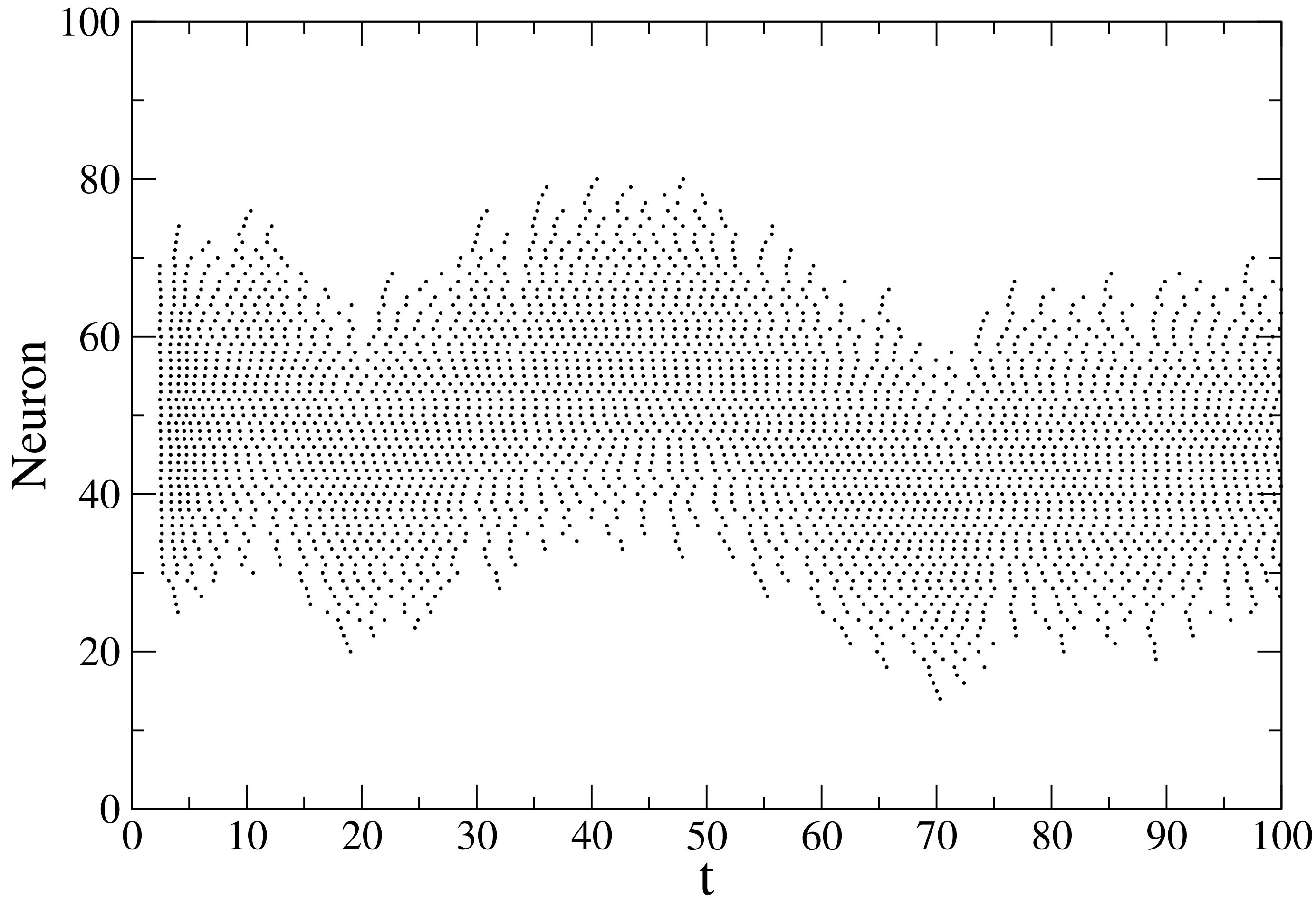


$\beta = 6$

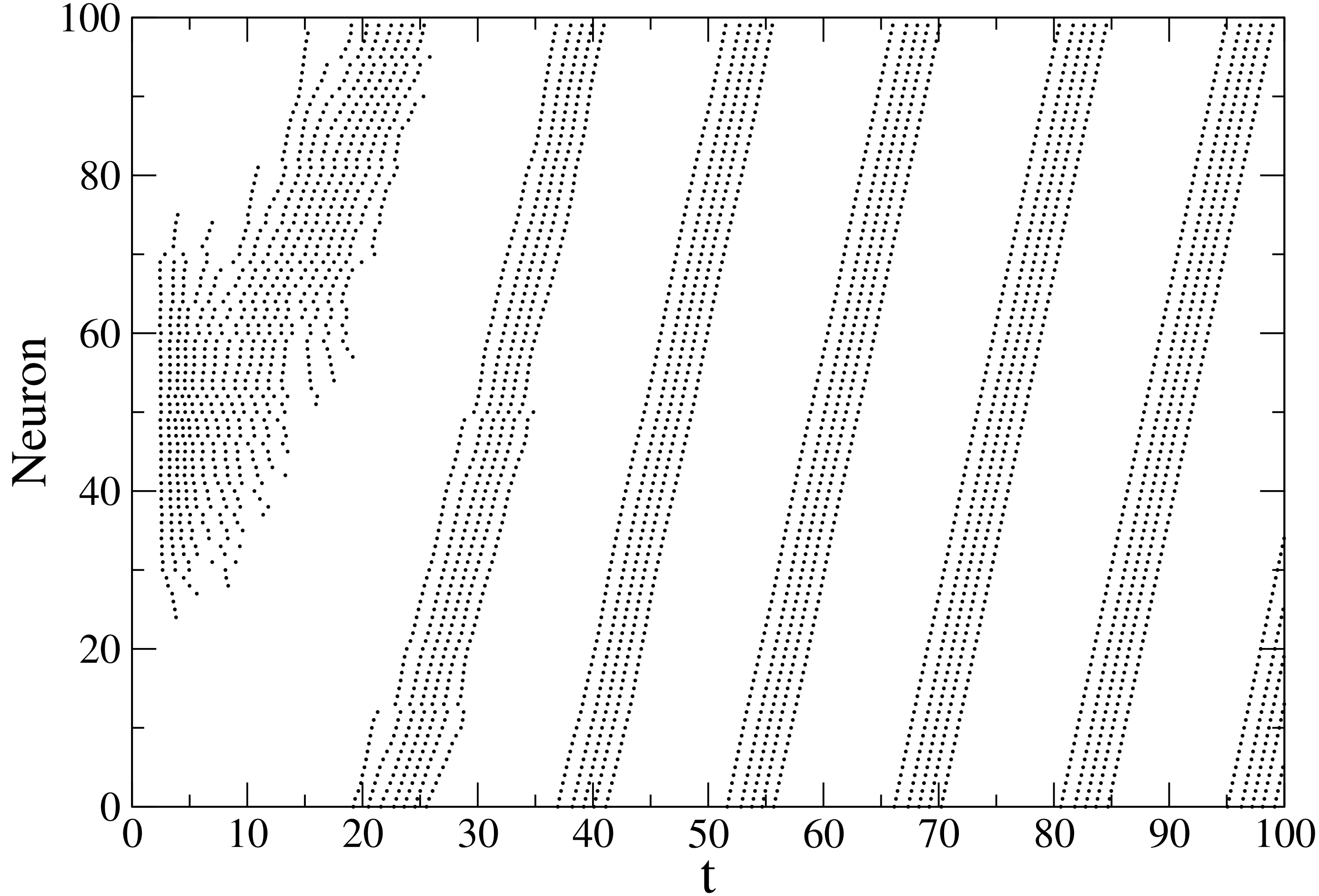
Gaussian weight function: $\beta = 0.3$



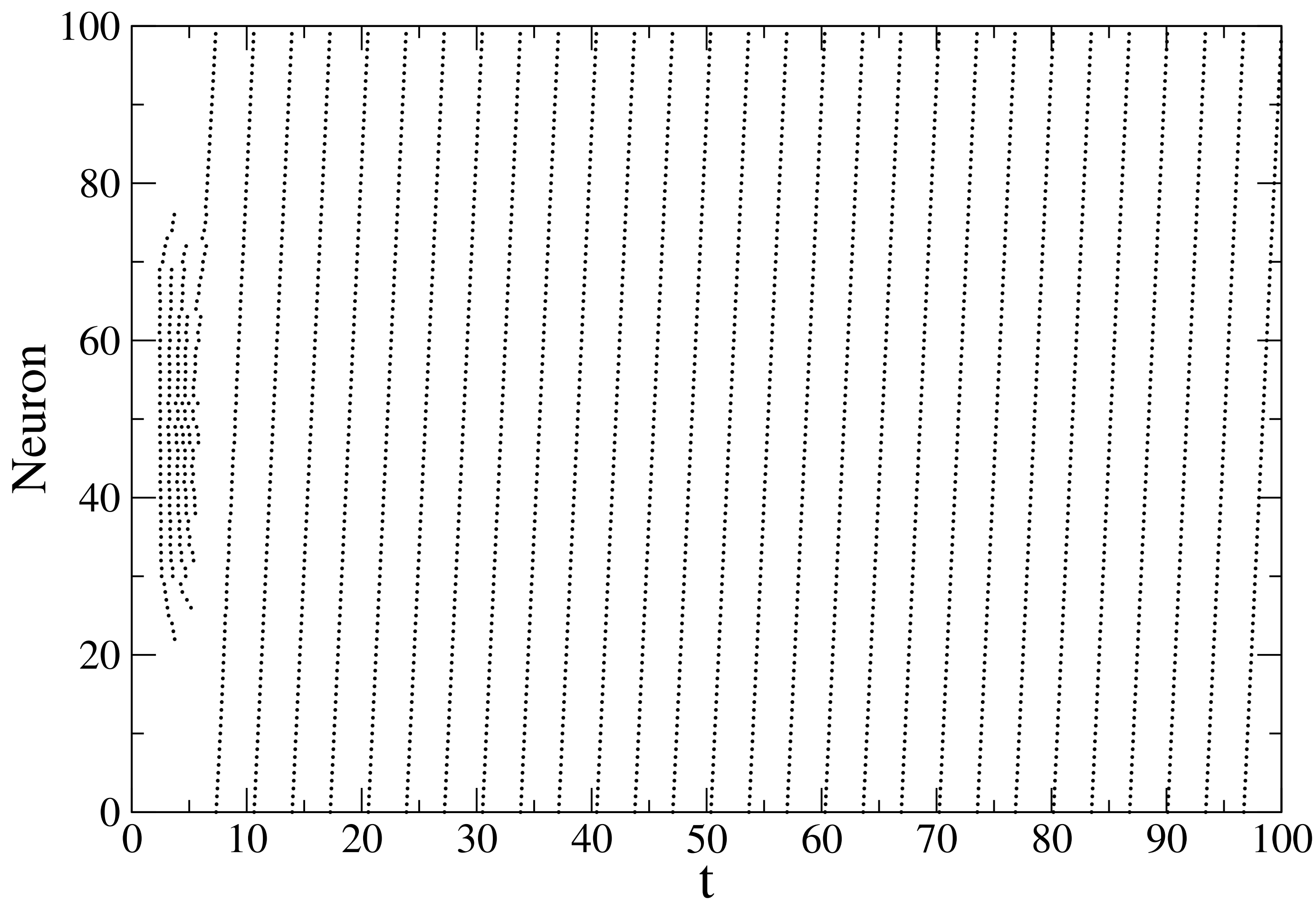
$$\beta = 2.5$$



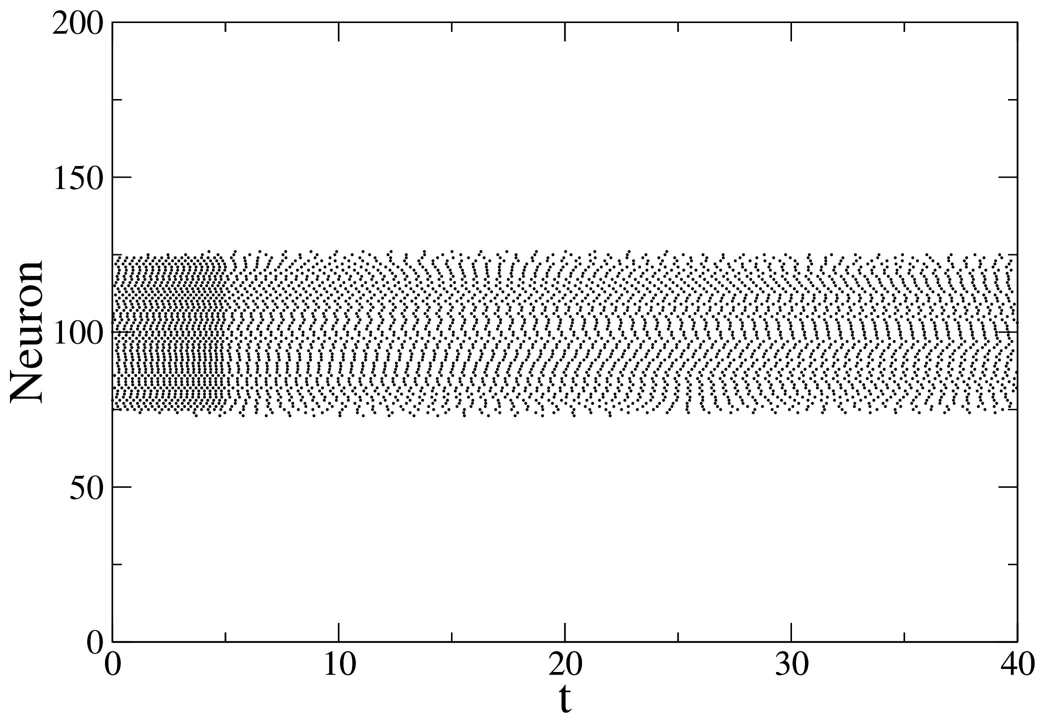
$\beta = 3.5$

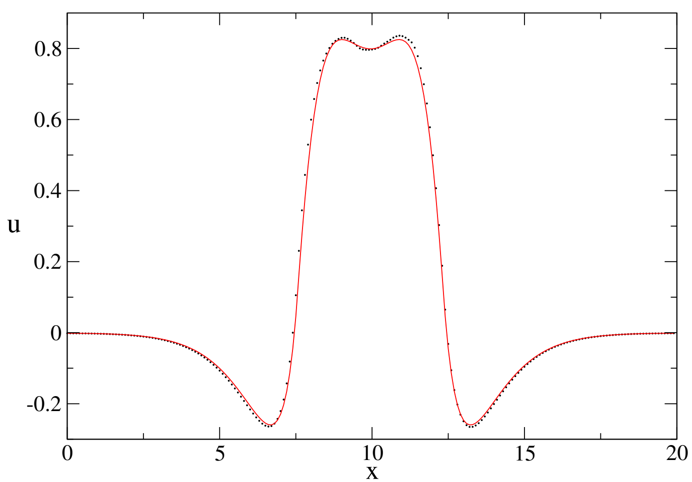


$\beta = 5$



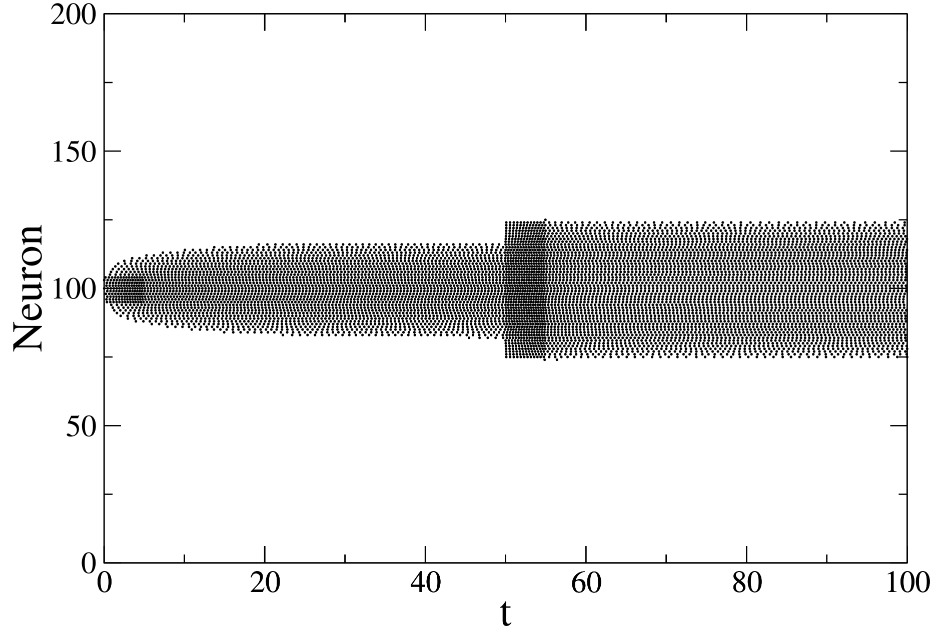
Dimple Bumps (but not really)

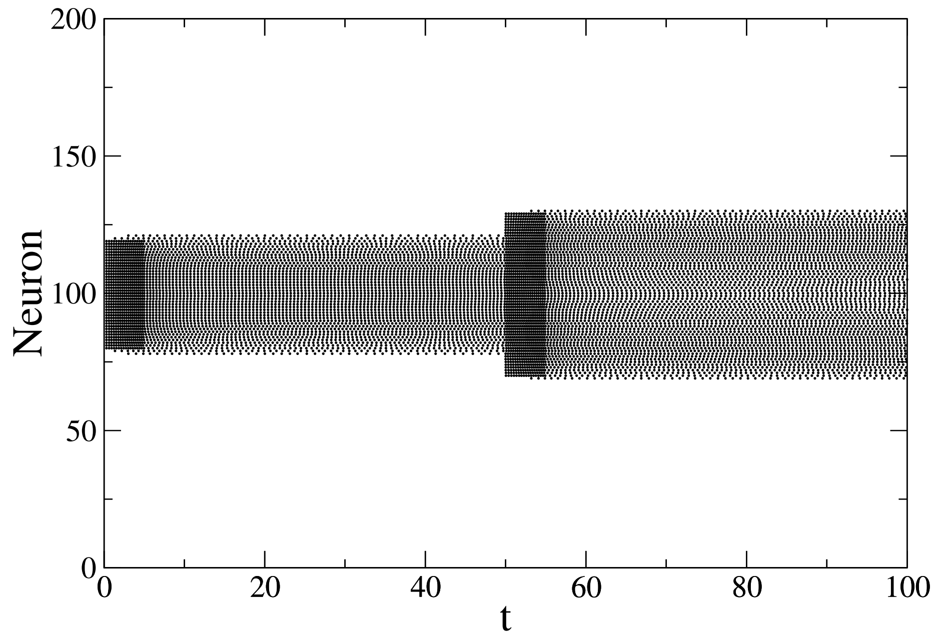




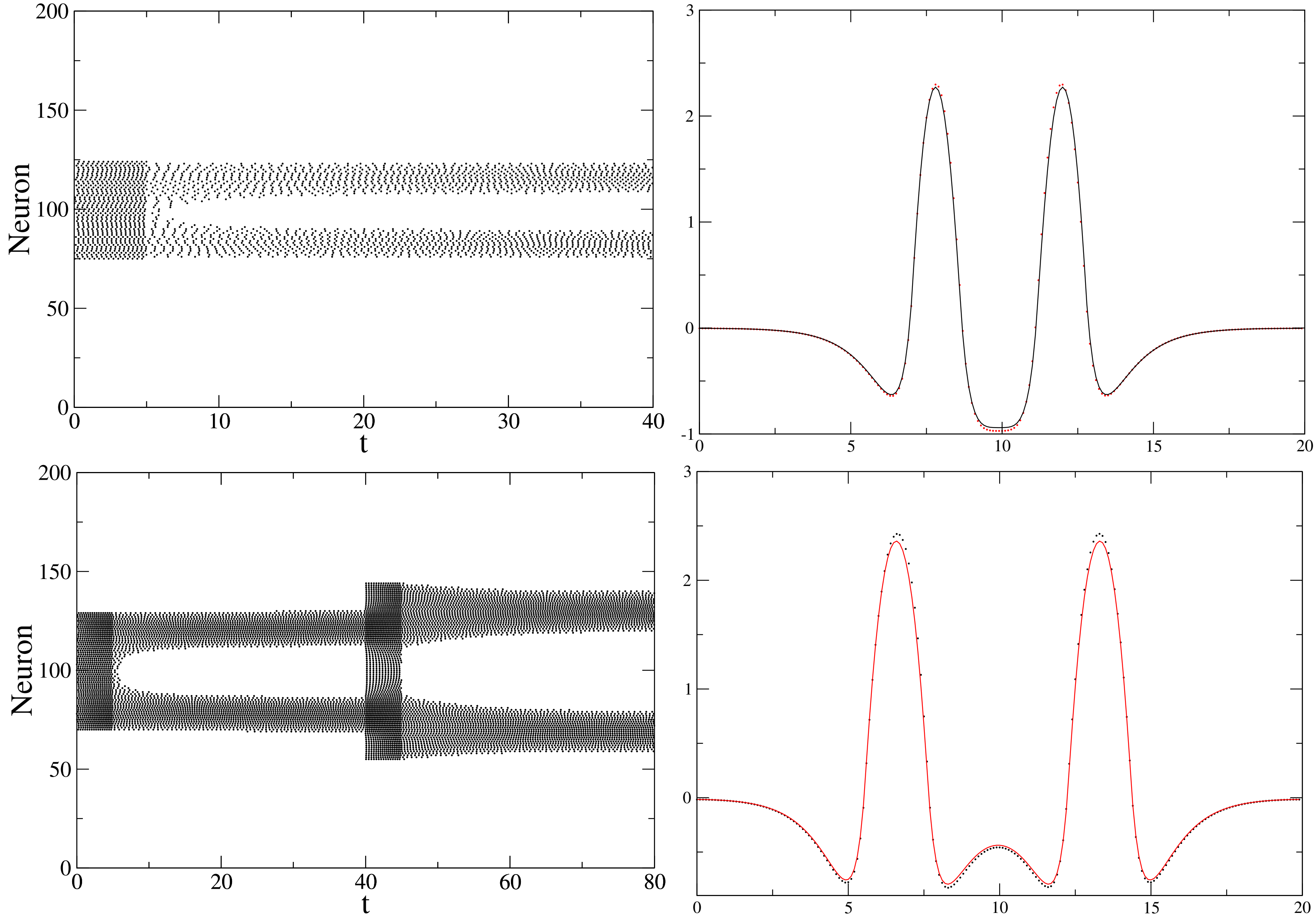
$I = 0.786 \; A = 1.8 \; a = 1.6$

Multistability





Double Bumps $I = 7.74 \; A = 2.8 \; a = 2.65$

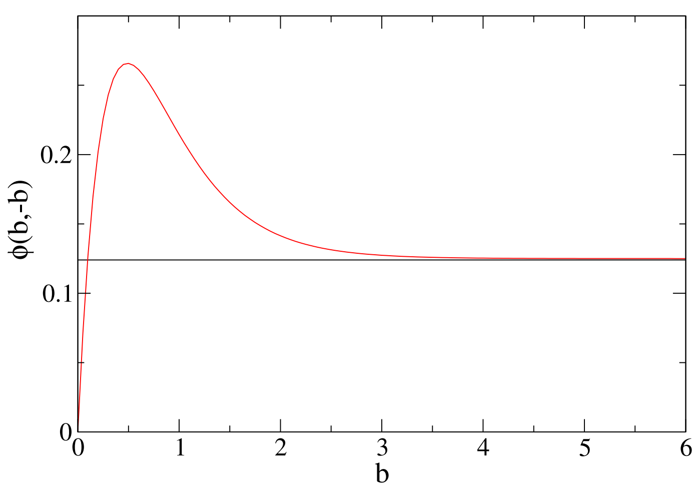


Discreteness and Marginal Stability

- Discreteness can stabilize marginal modes
- Consider pulse of width b in Amari equation

$$u(x) = \phi(x,b), \quad u_T = \phi(b,b)$$

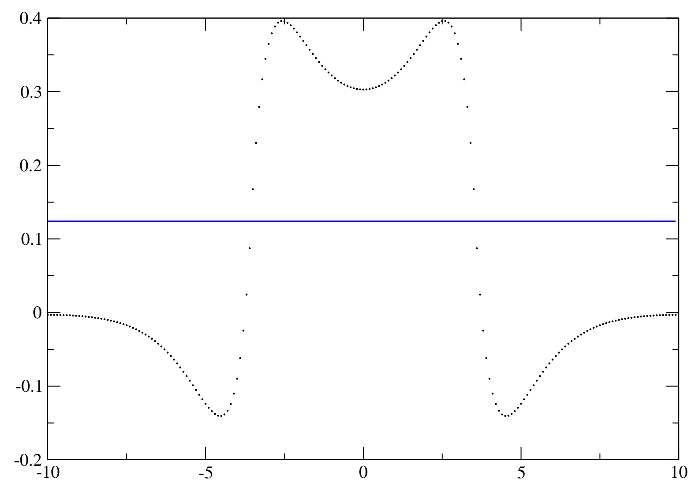
$$\phi(x,b) = \int_{-b}^{b} Ae^{-a|x-y|} - e^{-|x-y|} dy$$



Dimple case

$A = 1.8 \ a = 1.6 \ u_T = 0.124$

- Discretization gives stability to marginal modes since neurons adjacent to edge are below threshold by $\partial_x \phi(x = b, b)dx \sim (A - 1)dx$



- Since $\phi(b, -b) - u_T \sim 0.001$, to eliminate discreteness effect need adjacent neuron to be above threshold. i.e. $(A - 1)dx < 0.001$
- Thus $dx < 0.00125$ or need $> 16,000$ neurons in simulation