Stochastic Travelling Waves in Neural Tissue

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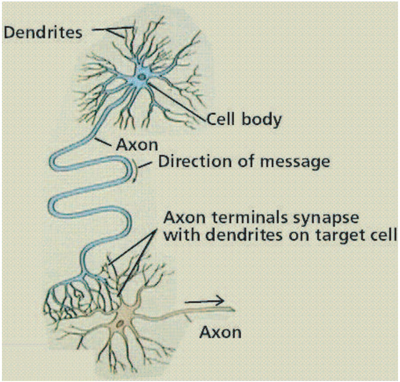
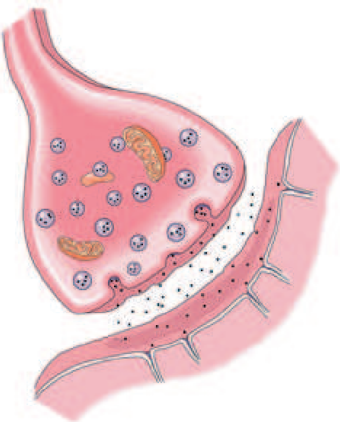
- Computing stochastic travelling wave (Nagumo)
- Baer-Rinzel model and SDS model
- Filtering - low pass filter

Neurons and Synapses





... interested in travelling wave propagation

Deterministic Nagumo - axon wave propagation

$$u_t = \Big[u_{xx} + u(1-u)(u-\alpha)\Big] \quad u(x,t) \in \mathbb{R},\ x \in \mathbb{R},\ t > 0$$

where $\alpha \in (0, \frac{1}{2})$.

- Explicit TW solution connecting $u \equiv 1$ and $u \equiv 0$

$$u_{\text{det}}(x - \lambda t) = \left(1 + e^{\frac{\lambda t - x}{\sqrt{2}}}\right)^{-1}, \quad \text{wavespeed} \quad \lambda = \sqrt{2}\,(\tfrac{1}{2} - \alpha)$$

- Suppose we have a TW with wavespeed λ for

$$u_t = \Big[u_{xx} + f(u)\Big].$$

Into co-moving frame $u(x,t) = u(x - \lambda t, t)$

$$u_t = u_{xx} + \lambda u_x + f(u), \quad x \in \mathbb{R}, \quad t \geq 0 \qquad (1)$$

of which the travelling wave u is a stationary solution ($u_t = 0$).

Deterministic case II

$$u_t = \left[u_{xx} + f(u) \right] \quad u(x,t) \in \mathbb{R},\ x \in \mathbb{R},\ t > 0.$$

- What if we do not know wavespeed or if wavespeed a func. of t?

Co-moving frame : unknown position $\gamma(t)$ and wavespeed $\lambda(t)$
$u(x,t) = u(x - \gamma(t), t)$

$$u_t = u_{\xi\xi} + \lambda(t) u_\xi + f(u)$$

Position of wave $\gamma(t) = \int_0^t \lambda(s) ds$.

Have an extra variable $\lambda(t)$ – add a phase condition $0 = \psi(u, \lambda)$.

Example phase condition :
Given a reference function $\hat{u}$, min $\|u - \hat{u}\|_2^2$.

Stochastic Nagumo

Effects of noise

$$du = \Big[u_{xx} + u(1-u)(u-\alpha)\Big]\,dt + (\nu + \mu u(1-u))dW(t)$$

on large finite domain $[0, L]$, Dirichlet BC's.
Multiplicative noise : $\nu = 0$, $\mu \neq 0$ – parameter α (wave speed).

- Assume Wiener processes of the form

$$W(x,t) \;=\; \sum_{n\in\mathbb{Z}} b_n\phi_n(x)\beta_n(t)\;, \qquad \beta_n \text{ iid Brownian motions.}$$

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- White in time and correlated in space: length scale ξ
$$C(x) = \frac{1}{2\xi} = \exp\left(-\pi x^2/4\xi^2\right).$$
- Space-time white

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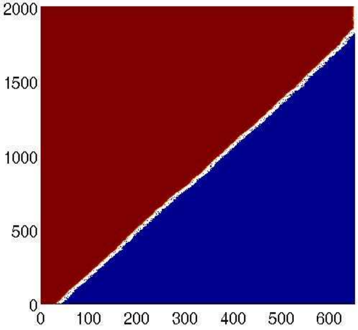
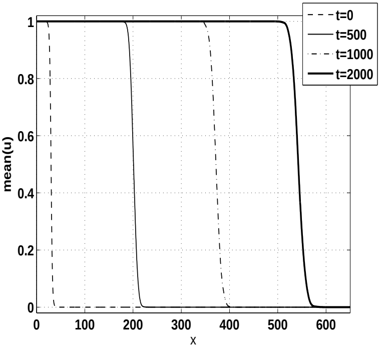
- Ito & Stratonovich Noise.

Stochastic Travelling wave





Typically :

▶ Reference to deterministic wave (eg small noise, mean profiles) Mikhailov, Schimansky–Geier & Ebeling '83

▶ Evolution of a level set : eg sFKPP Tribe, Elworthy& Zhao, Mueller & Sowers & Doering,

▶ Wavespeed increases with noise intensity (Stratonovich). [Armero, Sancho, Lacasta, Ramirez-Piscina, Sagues, 1996]

For reviews see for example : Garcia-Ojalvo & Sancho or Panja

Freezing a Stochastic Travelling wave

$$du = \Big[u_{xx} + f(u)\Big]\, dt + g(u,t) dW(t)$$

1) Add convection term to freeze wave

$$du = \Big[u_{xx} + f(u) + \lambda u_x\Big]\, dt + g(u,t) dW(t),$$

2) For some reference function $\hat{u}$ want : $\min \|u - \hat{u}\|_2^2$

- SPDE has a travelling wave u if there exists a rv λ s.t.

$$\begin{aligned} du &= [u_{xx} + \lambda(t) u_x + f(u)]\, dt + g(u) dW, \quad u(0) = u^0 \\ 0 &= \langle \hat{u}_x, u - \hat{u} \rangle \end{aligned} \tag{2}$$

- $\lambda(t)$ "instantaneous" wave speed
- Wavespeed : $\Lambda(t) = \frac{1}{t} \int_0^t \lambda(s) ds$
- Shift noise : $z_1 = x + ct$, $z_2 = y + ct$ then $E(dW(z_1, s) dW(z_2, t)) = C(x + cs - y - ct)\delta(t - s)$.

Implementation : SPDAE on $[0, L]$

$$
\begin{aligned}
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$$

Discretize in space (eg finite differences $A \approx \Delta$ etc)

- Ito: Semi–implicit Euler–Maruyama scheme in time gives :

$$
\begin{aligned}
u^{n+1} &= u^n + \Delta t\, [Au^n + \lambda^n D_{\lambda^n} u^n + f(u^n)] + g(u^n)\Delta W_n \\
0 &= \langle \hat{u}_x, u^{n+1} - \hat{u} \rangle
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where $\Delta W_n = (W(t_{n+1}) - W(t_n))$ is our Brownian increment

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- Stratonovich : semi-implicit Euler–Heun

$$z = u^n + g(u^n)\Delta W_n$$
$$u^{n+1} = u^n + \Delta t\left[Au^{n+1} + \lambda^n D_{\lambda^n} u^n + f(u^n)\right] + \frac{1}{2}\left(g(z) + g(u^n)\right)\Delta W_n$$
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$$0 = \langle \hat{u}_x, u^{n+1} - \hat{u} \rangle$$

Other time discretizations possible - eg
[Moro,'08]: adapt g for numerical instabilities at $u \equiv 0$ and $u \equiv 1$.

Frozen Nagumo Multiplicative Noise, $\alpha = 0.25$

Wavespeeds for SPDAE are computed from random variable $\lambda(t)$

$$E\lambda(t), \quad \Lambda(t) = \frac{1}{t}\int_0^t \lambda(s)ds, \quad E\Lambda(t), \quad \Lambda = \frac{1}{T_2 - T_1}\int_{T_1}^{T_2} E\Lambda(t)dt.$$

Ex : Ito space-time white noise 1000 realizations ,
$T_1 = 100,\ T_2 = 200$

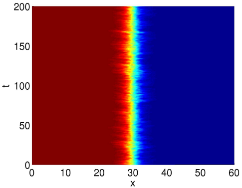
	$\mu = 0$	$\mu = 0.0625$	$\mu = 0.25$	$\mu = 0.5$	$\mu = 1$
Λ	0.3534	0.354	0.355	0.358	0.377

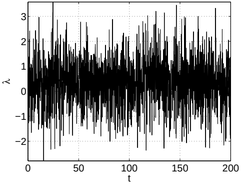
Let us validate results with

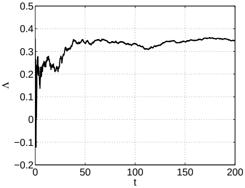
- Ito Noise
- Reference function: $\hat{u} = u_{\text{det}}$
- Initial data : $u^0 = u_{\text{det}}$

Frozen Nagumo Multiplicative, $\mu = 0.5$

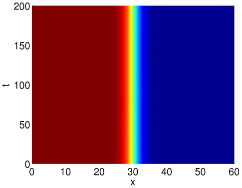
Single realization $\lambda(t)$ $\Lambda(t)$

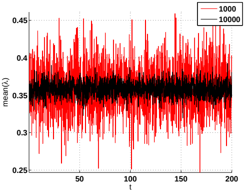


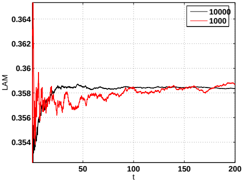




And means over 1000 and 10000 realizations:







Mean $E\lambda(t)$ $E\Lambda(t)$

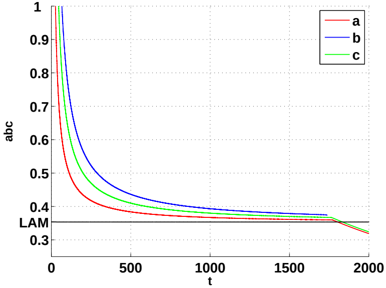
Comparison with SPDE

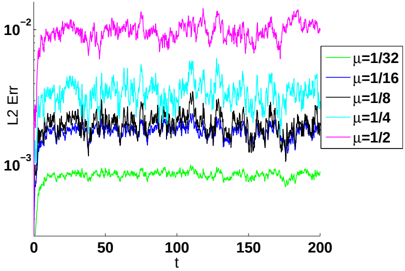
For SPDE wavespeeds compute $a(t)/t$, $b(t)/t$, $c(t)/t$

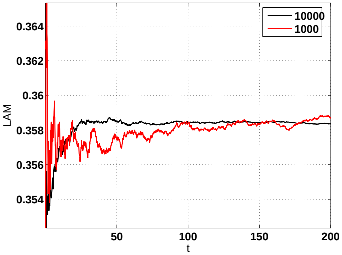
$$a(t) := \sup\{z : u(x,t) = u_-, x \le z\}$$

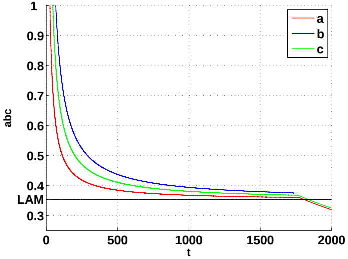
$$b(t) := \sup\{z : u(x,t) = u_+, x \ge z\}$$

$$c(t) := \sup\{z : u(x,t) = (u_- + u_+)/2, x \le z\}.$$









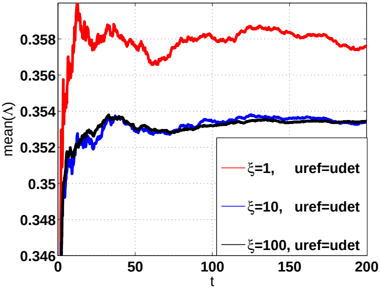
	$\mu = 0$	$\mu = 0.5$
Λ (SPDAE)	0.3534	0.3587
Λ (SPDE)	0.3531	0.3544
Analytic	0.3536	

Extrapolation of a, b, c gives under estimate of Λ.
See increase in wavespeed with noise.

Spatial correlation

$$W(x,t) = \sum_{n\in\mathbb{Z}} b_n \phi_n(x)\beta_n(t) \ , \qquad \beta_n \text{ iid Brownian motions.}$$

Exponential decay in b_n. White in time.

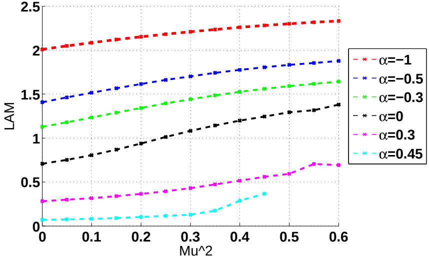


Correlated (smoother) noise – reduces wave speed.

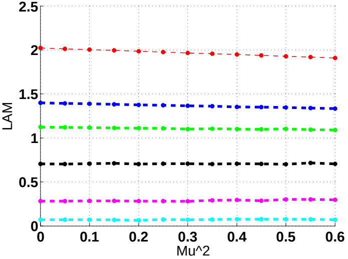
Stratonvich vs Ito noise

Λ vs Noise intensity for different nonlinearities.

Stratonovich



Ito



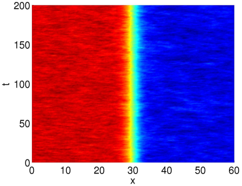
For

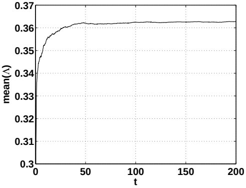
Ito noise wavespeed not strictly increasing with noise intensity.

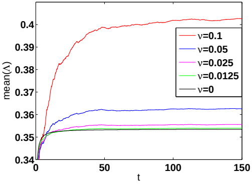
Additive noise

Can not use a, b, c to readily determine position of the wave.
(In general travelling wave may only exist for a finite time)

$\alpha = 0.25$, $\nu = 0.05$





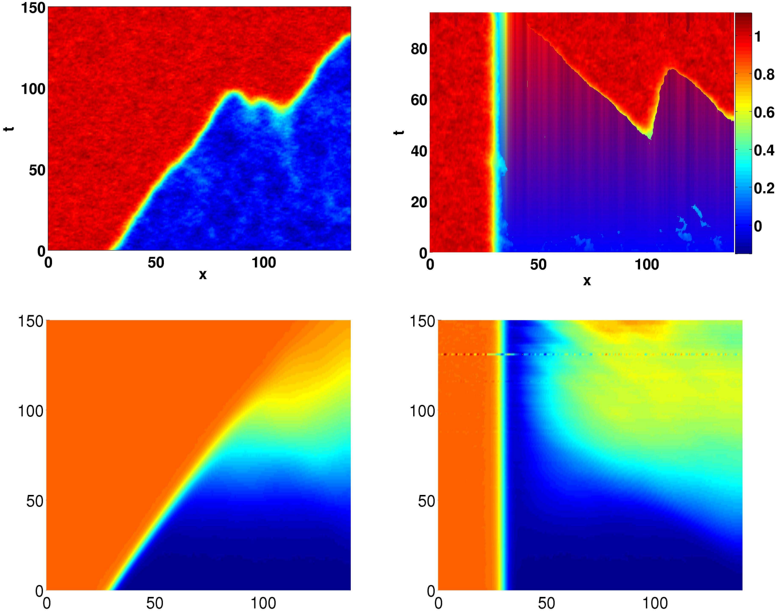


1 realization $\Lambda(t)$ $E\Lambda(t)$ for different intensities.

With additive noise - new waves will nucleate

Additive noise $\alpha = 0.1$, $\nu = 0.05$

Nucleation of new waves :



Weaker notion

SPDAE for Tarvelling wave :

$$du = [u_{xx} + \lambda(t)u_x + f(u)]\,dt + g(u)dW, \quad u(0) = u^0$$
$$0 = \langle \hat{u}_x, u - \hat{u} \rangle$$

An example of a weaker version :

$$du = [u_{xx} + \Lambda(t)u_x + f(u)]\,dt + g(u)dW, \quad u(0) = u^0$$
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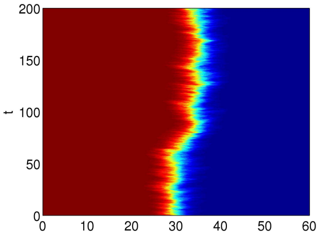

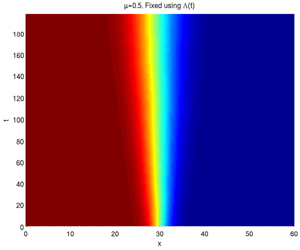

Summary

- Can define stochastic travelling wrt reference $\hat{u}$.
- Results agree with those by direct simulation of SPDE

Some adavantages of method

  - Efficient : smaller domain
  - Faster convergence than via level sets a, b, c.
- Disadvantage of method
  - Maybe the need for a reference solution uref
  - Need careful implementation - numerical instability - large convection

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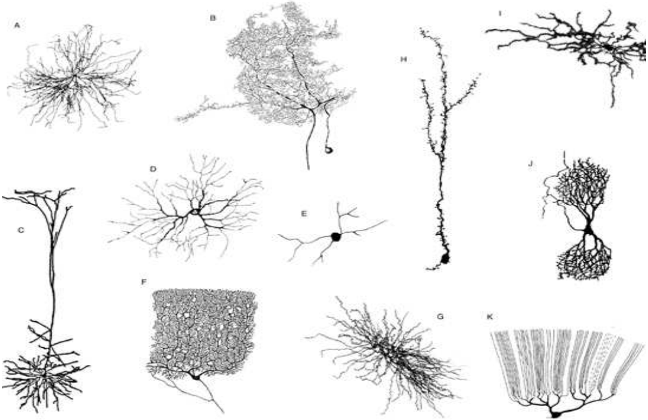
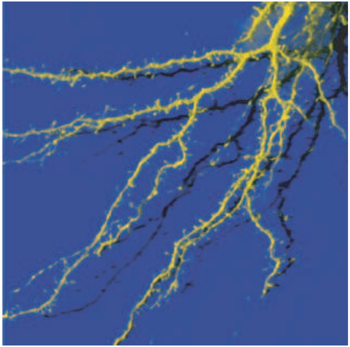
apply in another neural model

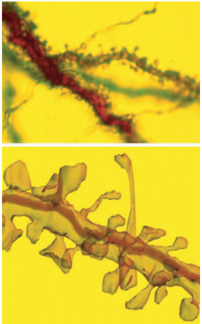
Many forms of Neurons

www.dendrite.org



Dendrites and spines



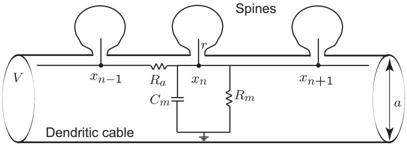


(synapses.mcg.edu)

- Spines provide surface area for synapses from other neurons
- $\approx$ 80% excitable synapses at dendritic spines in cortex
- Evidence for plasticity in spines
- Involved in : learning, memory, logic computation, pattern matching, temporal filtering

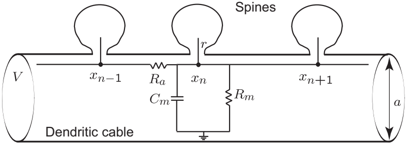
Baer-Rinzel Model

[J Neurophys, 65, 1991]



- Couples continuum of active spines to a passive (diffusive dendrite).
- Spine-head dynamics modelled by Hodgkin-Huxley (HH) equations.
- Can be extended to include branching, tapering etc

Baer-Rinzel Model:

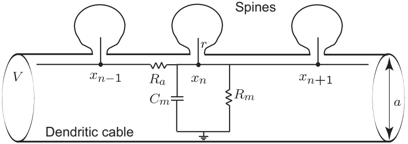


[J Neurophys, 65, 1991]

- Cable Equation :

$$\pi a C_m V_t = \frac{\pi a^2}{4R_a} V_{xx} - \frac{\pi a}{R_m} V + \rho \frac{\hat{V} - V}{r}$$

Baer-Rinzel Model:



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- Cable Equation :

$$\pi a C_m V_t = \frac{\pi a^2}{4R_a} V_{xx} - \frac{\pi a}{R_m} V + \rho \frac{\hat{V} - V}{r}$$

- Spine Dynamics :

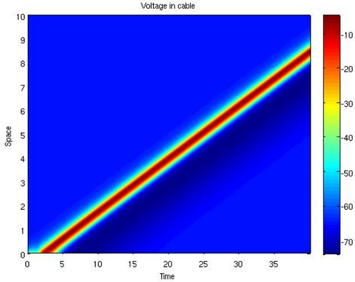
$$\begin{aligned} \hat{V}_t &= -I(\hat{V}, m, n, h) - \frac{\hat{V} - V}{r} \\ \tau_X X_t &= X_\infty - X, \qquad X \in \{m, n, h\} \end{aligned}$$

$$I(\hat{v}, m, n, h) = g_K n^4 (\hat{V} - V_K) + g_{Na} h m^3 (\hat{V} - V_{Na}) + g_L (\hat{V} - V_L)$$

L Leakage, K potassium, Na Sodium Conductance variables m, n, h take values between 0 and 1.

Baer-Rinzel

Deterministic BR supports travelling wave solutions



Baer-Rinzel

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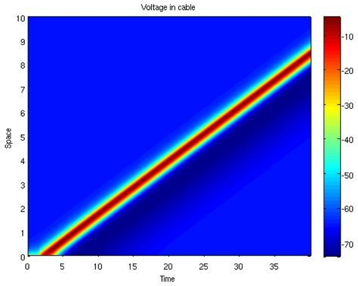

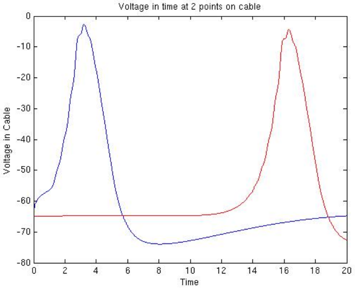

Baer-Rinzel

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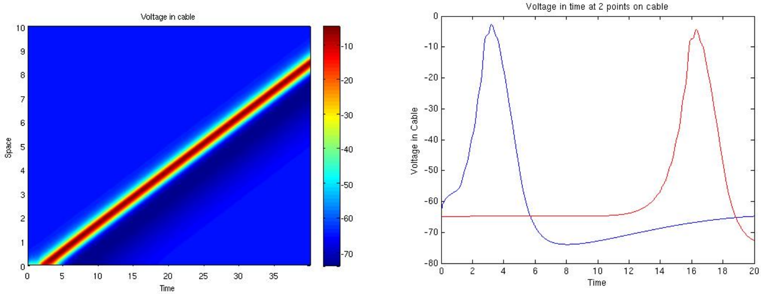


PDE : $u_t = u_{xx} + f(u)$

Can put into a travelling frame: $\xi = x - \lambda t$ for wavespeed λ

$$u_t = u_{\xi\xi} + \lambda u_\xi + f(u), \quad x \in \mathbb{R}, \quad t \geq 0$$

For a travelling wave with constant wspeed λ: $u_t = 0$

$$0 = u_{\xi\xi} + \lambda u_\xi + f(u), \quad x \in \mathbb{R}, \quad t \geq 0.$$

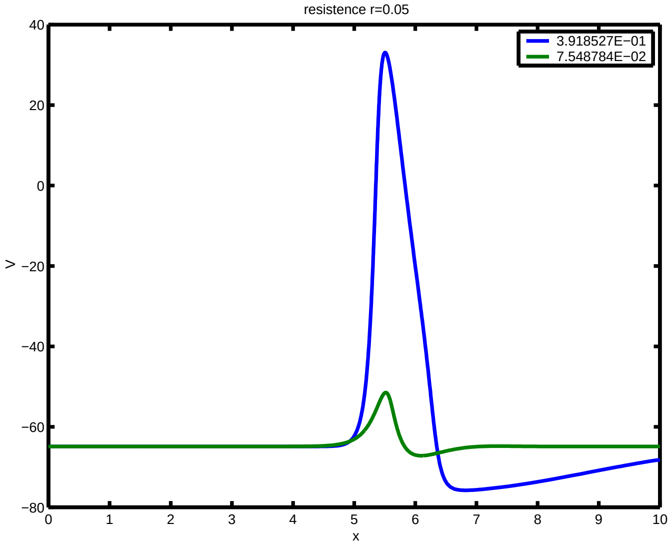
Travelling wave I

Transform Baer-Rinzel to TW frame: $\xi = ct - x$ with speed c :
6D system

$$
\begin{aligned}
V' &= W \\
W' &= cW + g_L(V - V_L) - \rho(\hat{V} - V)/r \\
c\hat{V}' &= g_L(V_L - \hat{V}) - (\hat{V} + V)/r - g_K n^4(\hat{V} - V_k) \\
&\quad -g_{Na} h m^3(\hat{V} - V_{Na}) \\
c\tau_X X' &= X_\infty - X, \qquad X \in \{m, n, h\}
\end{aligned}
$$

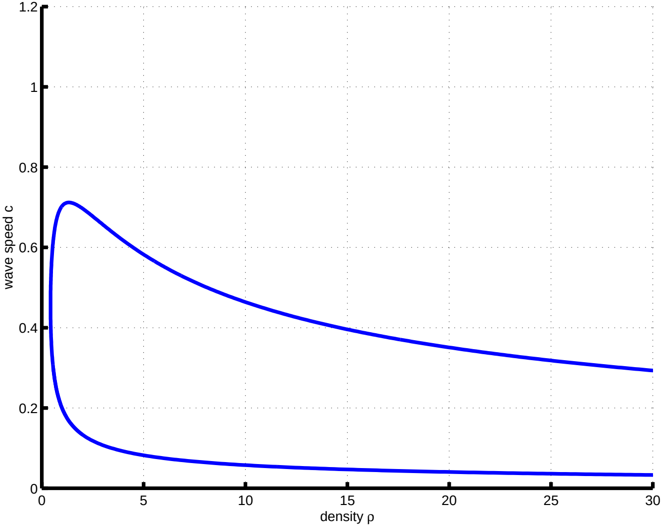
(ugly)
Unique Fixed point :
5D stable manifold
1D unstable manifold

Travelling wave I



Resistence $r = 0.05$ $H1$: Fast and slow wave below.

Travelling wave I



Resistence $r = 0.05$ $H1$: Fast and slow wave below.

Baer-Rinzel and noise

We can consider effects of noise on wave propagation

- Synaptic noise
- Cable noise

Modify the PDE to include space-time noise

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Modify the PDE to include space-time noise

- Eg: Voltage fluctuation in cable membrames

$$\mathrm{d}V = \left[DV_{xx} - \frac{V}{\tau} + Dr_a\rho(x)\frac{\widehat{V} - V}{r} \right] \mathrm{d}t + \mu_V \mathrm{d}W(t,x),$$

- Interpret noise in the Ito/Stratonovich sense.

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- Interpret noise in the Ito/Stratonovich sense.
- Assume Wiener process W are of the form

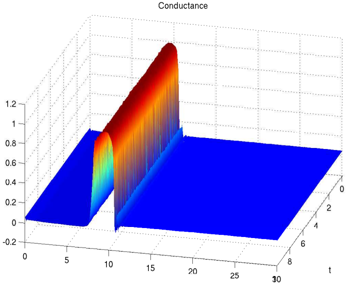
$$W(t,x) = \sum_{n\in\mathbb{Z}} b_n\phi_n\beta_n(t) \;, \qquad \beta_n \text{iid Brownian motions.}$$

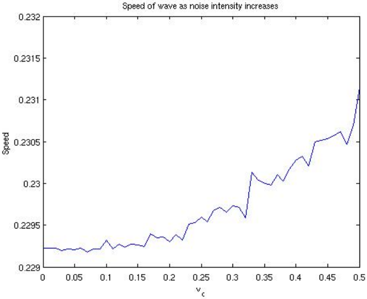
$$\sum_{n\in\mathbb{Z}} e^{2\alpha|n|}|b_n|^2 < \infty \;.$$

Parameter α : correlation length scale and smoothness.

Baer-Rinzel Travelling wave - FROZEN

Mult. Strat. noise in HH spine dynamics





Stratonovich–Ito correction

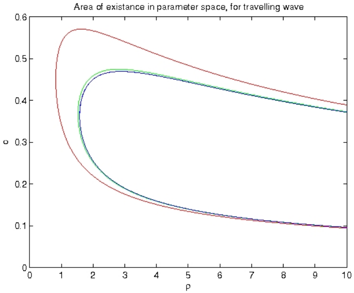
Start with Statonovich noise - exponential correlation

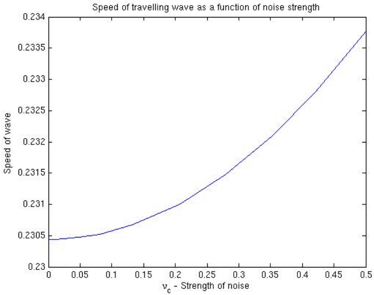
$$du = (f(u))\,dt + g(u) \circ dW$$

- Take out 'systematic' contribution of noise :
  changes nonlinear term.

$$du = \left(f(u) + \frac{C}{2} g'(V) g(V) \right) dt + g(u) dW$$

Now assume noise small to get deterministic system [Garca-Ojalvo & Sancho].



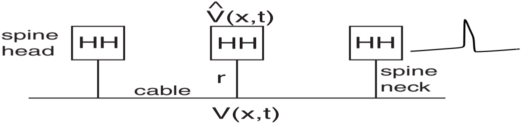


Baer-Rinzel :

- Can see range of parameters for existence of wave
- Small noise
  - – wave exists for wider parameter set
  - – speeds increases

Baer-Rinzel Discrete Model

[J Neurophys, 65, 1991]



- Cable Equation :

$$\pi a C_m V_t = \frac{\pi a^2}{4R_a} V_{xx} - \frac{\pi a}{R_m} V + \rho(x) \frac{\hat{V} - V}{r}$$

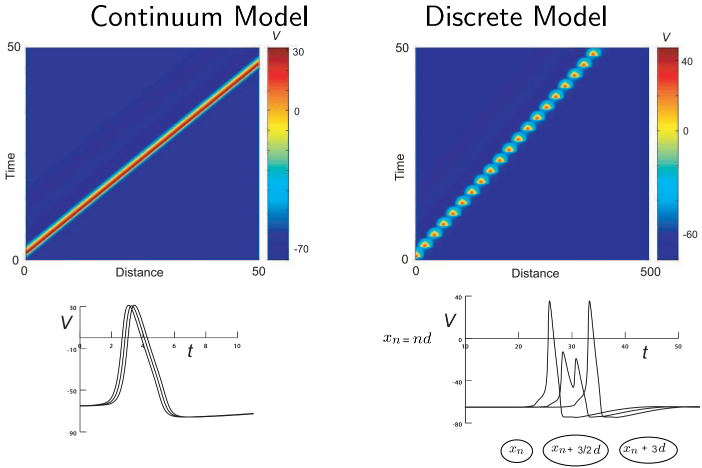
- Spine Dynamics :

$$\begin{aligned} \hat{V}_t &= -I(\hat{V}, m, n, h) - \frac{\hat{V} - V}{r} \\ \tau_X X_t &= X_\infty - X, \qquad X \in \{m, n, h\} \end{aligned}$$

- Discrete set of spines at $x = x_n$: $\rho(x) = \sum_n \delta(x - x_n)$

d := distance between spines

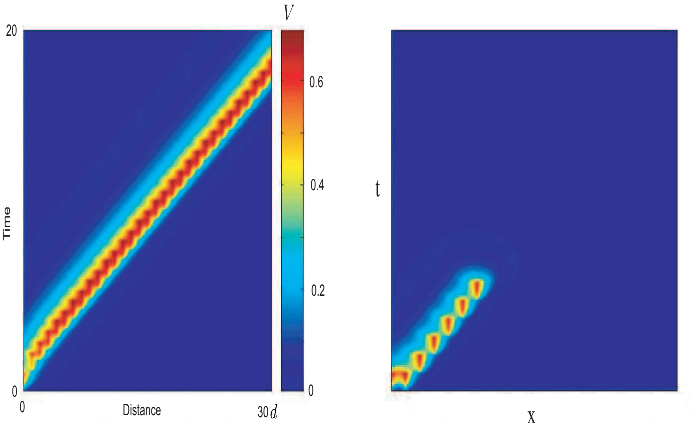
Example solutions



$$\rho(x) = Const \qquad\qquad \rho(x) = \sum_n \delta(x - x_n).$$

(Found : by solving coupled ODEs and cable equation)

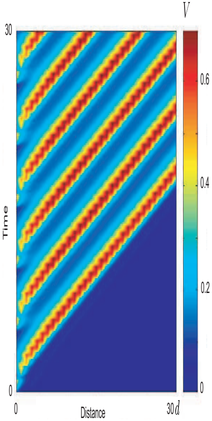
Vary parameters : eg spine distance

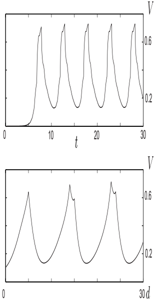


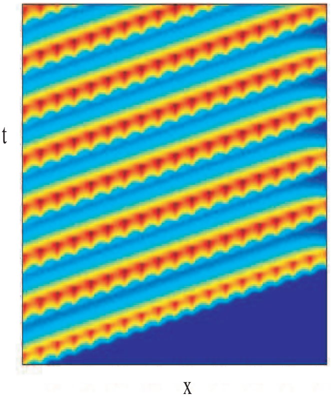
(L. of LP) $d = 0.6$, , Propagation failure (R. of LP) $d = 0.95$

Periodic travelling waves

Reduce refractory time : eg $\tau_R = 5$





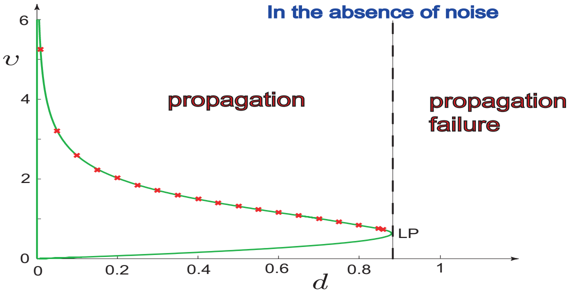


SDS and Noise

- Stochastic gating of ion channels
- Voltage fluctuation in cable membrames

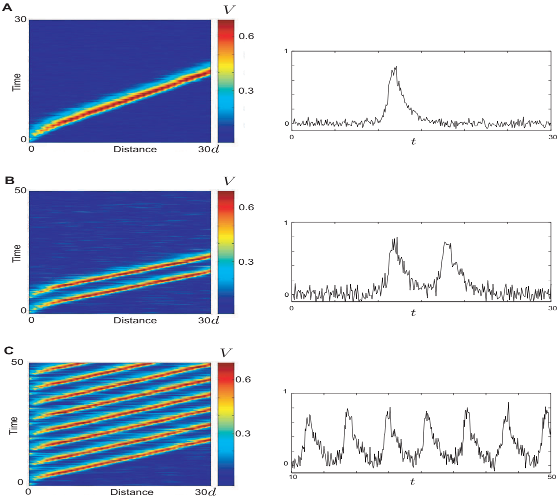
$$\mathrm{d}V = \left[D\Delta V - \frac{V}{\tau} + Dr_a\rho(x)\frac{\widehat{V} - V}{r} \right] \mathrm{d}t + \mu_V \mathrm{d}W(t,x),$$

$$\mathrm{d}U_n = \left[\frac{V_n}{\widehat{C}r} - \varepsilon_0 U_n - h\sum_m \delta(t - T_n^m) \right] \mathrm{d}t + \mu_U \mathrm{d}W(t,x).$$



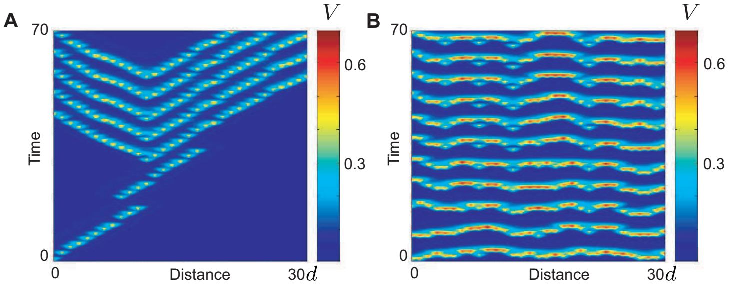
Noise induced propagation: $d = 1$, $\mu_U = 0$

Increasing μ_V: $\mu_V = 0.4, 0.8, 0.81$.



Noise induced propagation: $d = 1$, $\mu_V = 0$

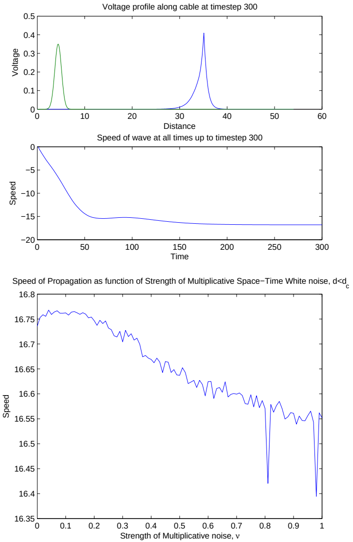
Increasing $\mu_U = 0.17, \mu_U = 0.4$.

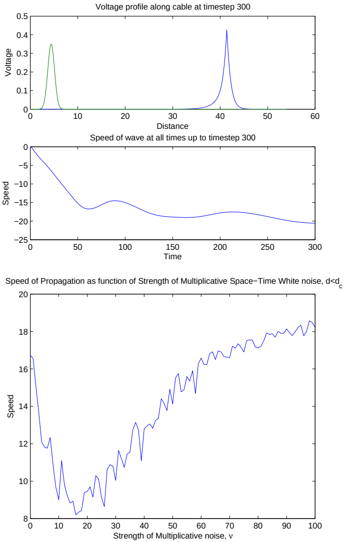


More sensitive to noise in the spine heads.

'Freezing' the SDS

Small ($\mu = 0.6$) and large ($\mu = 80$) noise.
Deterministic propagates.

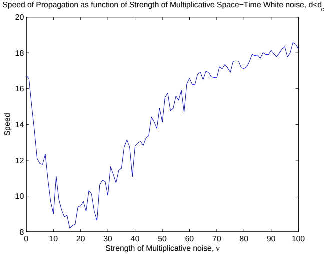




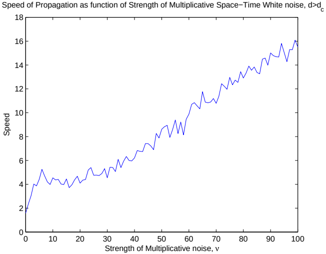
SDS speeds

Computed by freezing:

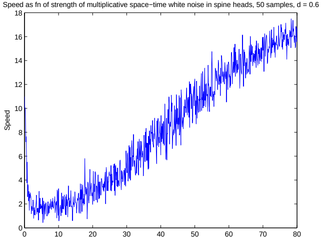
Det Propagates

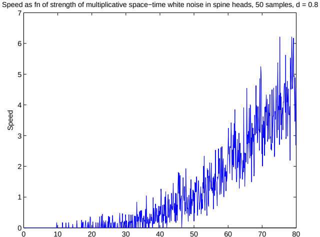


Noise Induced



Computed by level set :





Summary

Noise in Baer–Rinzel and SDS

- speeds wave propagation in cable
- induces wave propagation
- compared level set approach
- compared to 'small noise'

Filtering

Rose and Fortune : looked at weakly electric fish [1996,1997,1999]

- Looked at response to temporal stimuli in neurons

Show that spiny neurons with a broad dendritic tree act as low pass filter.

Filtering

Rose and Fortune : looked at weakly electric fish [1996,1997,1999]

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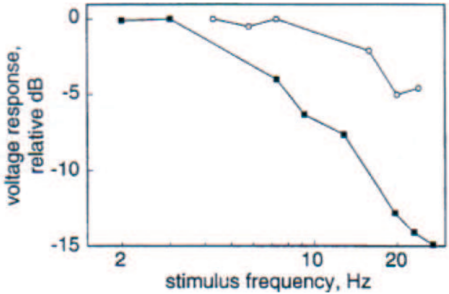
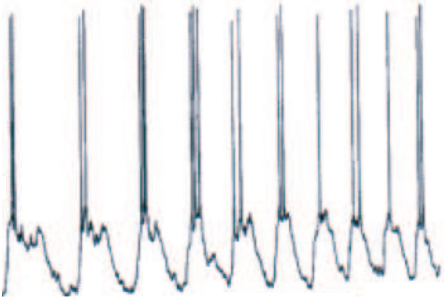
Show that spiny neurons with a broad dendritic tree act as low pass filter.

- Observed in SDS model ? — note we have no soma or branches here.

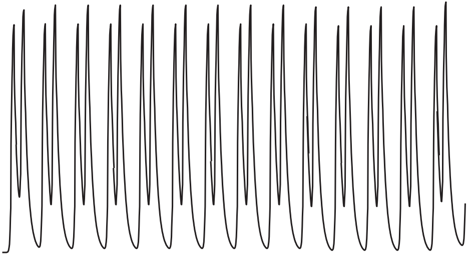


E.Fortune, G.Rose,
J Neuroscience, 1997

Dendrite potential

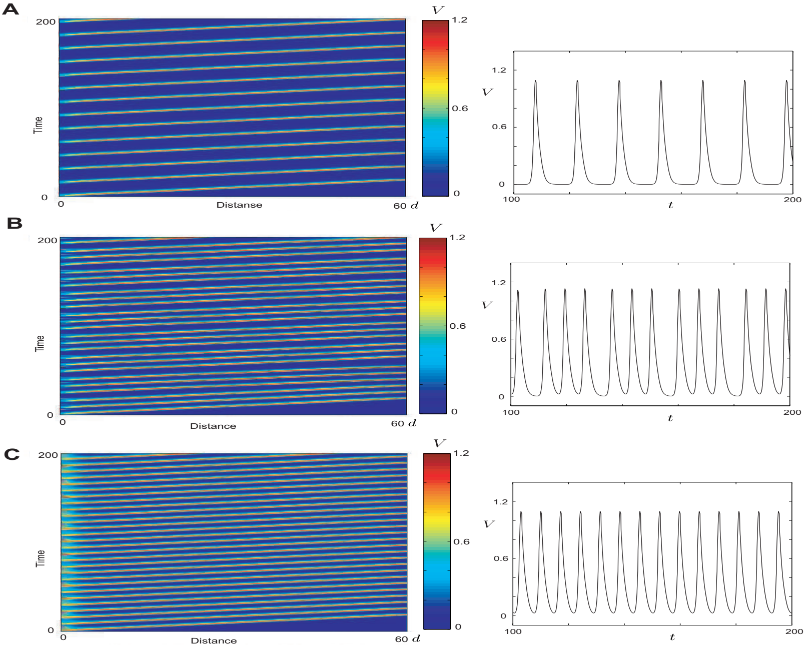


E.Fortune, G.Rose,
J Neuroscience, 1997



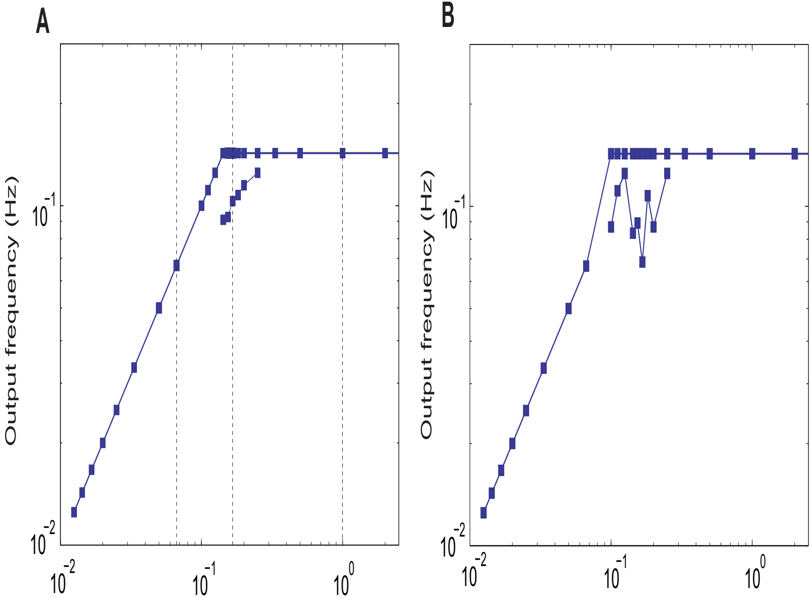
SDS model under the stimulus with constant frequency

$\tau_R = 7$

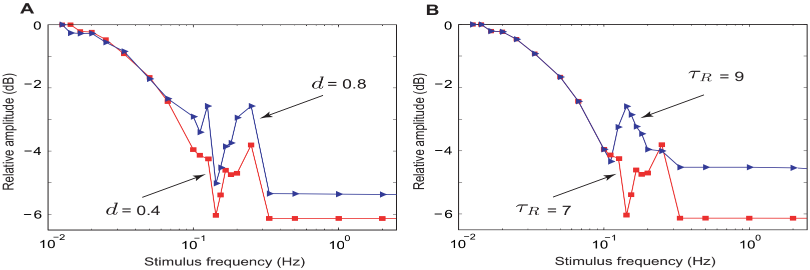


A
200
Time
0
0
Distanse
60 d
V
1.2
0.6
0
1.2
V
0.6
0
100
t
200
B
200
Time
0
0
Distance
60 d
V
1.2
0.6
0
1.2
V
0.6
0
100
t
200
C
200
Time
0
0
Distance
60 d
V
1.2
0.6
0
1.2
V
0.6
0
100
t
200

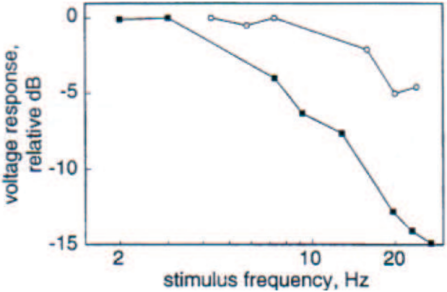
Frequency, $d = 0.4$ and $d = 0.8$



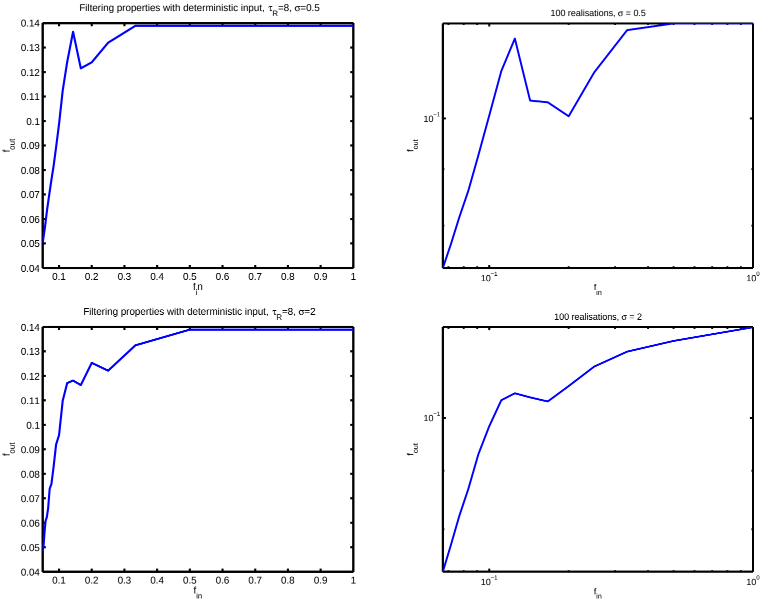
Amplitude



$d = 0.4 \& d = 0.8$ $\tau_R = 7 \& \tau_R = 9$



E.Fortune, G.Rose,
J Neuroscience, 1997



Filtering properties with deterministic input, τ_R=8, σ=0.5
0.14
0.13
0.12
0.11
0.1
0.09
0.08
0.07
0.06
0.05
0.04
f_{out}
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
f_in
100 realisations, σ = 0.5
10^{-1}
f_{out}
10^{-1}
10^{0}
f_{in}
Filtering properties with deterministic input, τ_R=8, σ=2
0.14
0.13
0.12
0.11
0.1
0.09
0.08
0.07
0.06
0.05
0.04
f_{out}
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
f_{in}
100 realisations, σ = 2
10^{-1}
f_{out}
10^{-1}
10^{0}
f_{in}

Summary

Freezing wave :

- Compute wave and wavespeed

Noise in Baer–Rinzel and SDS :

- speeds wave propagation in cable
- induces wave propagation
- compared level set approach
- compared to 'small noise'

Filtering:

- Filtering robust to noise
- Identify an 'operating regime' for filter