On a normal form for one-dimensional excitable media

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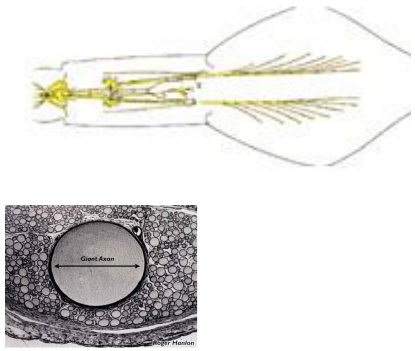
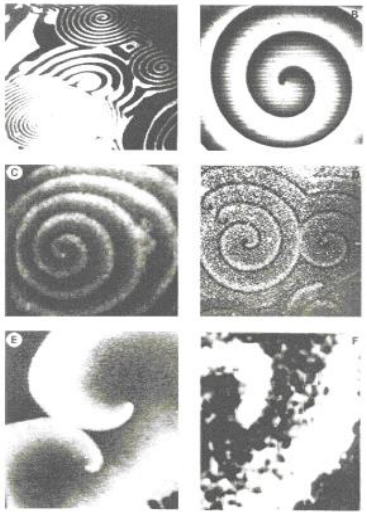
dedicated to Lorenz Kramer

Excitable Media

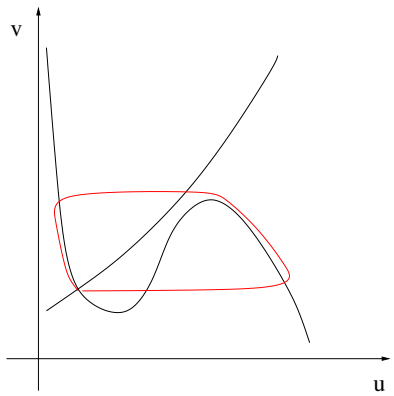
Excitable media are often found in chemical and biological systems. Examples are the the Belousov-Zhabotinsky reaction, catalytic CO-oxidation, cardiac and nerval tissue, slime mold aggregation and intracellular Ca^{+}-waves.





Excitable Media

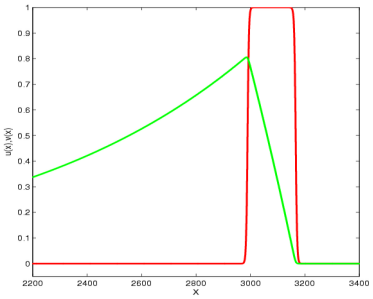
An element of an excitable medium returns to its initial state after a burst of activity initiated by a supercritical external perturbation

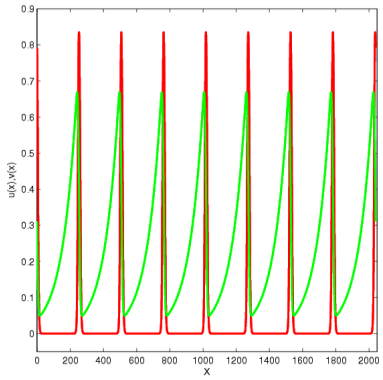


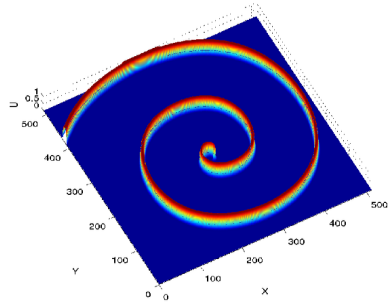
Reaction-diffusion equations for an activator u and an inhibitor v

$$\begin{aligned} \partial_t u &= D\Delta u + u(1-u)(u-u_s-v) \\ \partial_t v &= \epsilon(u-av) \end{aligned}$$

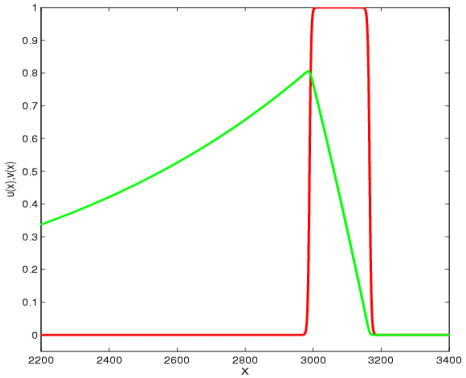
Generically one observes pulses in 1D and spirals in 2D.

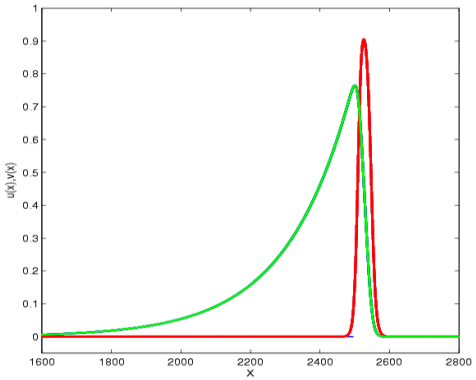






The focus here is on one-dimensional excitable media





$\longrightarrow$ increasing ϵ $\longrightarrow$

Saddle-Node

Goal : Find a simple equation ("normal form") which accounts for all bifurcations.

$$\partial_t X = -\mu - gX^2 - \beta(\gamma + X(t-\tau) + \gamma_1 X(t))$$

where $\beta = \beta_0 \exp(-\kappa\tau)$

I. Properties of the normal form

- Saddle-node bifurcation

$$\bar{X}_{SN} = -\frac{\beta}{2g}(1+\gamma_1) \quad \text{where} \quad \bar{\mu}_{SN} = \frac{\beta^2}{4g}(1+\gamma_1)^2 - \beta\gamma$$

(note $L \to \infty$ recovers with $\beta \to 0$ the old saddle-node $X = 0$ at $\mu = 0$)

- Homogeneous subcritical Hopf bifurcation

Study stability of homogeneous stationary solution w.r.t perturbations of the form $\delta X \exp(\sigma t)$

$$\sigma + 2g\bar{X} + \beta\gamma_1 + \beta e^{-\sigma\tau} = 0 \, .$$

Hopf bifurcation: $\sigma = i\omega$

$$\omega = \beta \sin \omega\tau \qquad \bar{X}_{HH} = -\frac{\beta}{2g}(\cos \omega\tau + \gamma_1)$$

$\beta\tau > 1$ needed (coupling strong enough)

- Bogdanov-Takens point

$$\beta\tau = 1 \text{ where } \omega\tau \to 0$$

At bifurcation we have a slowing down of the dynamics:

$$X(t-\tau) = X(t) - \tau\partial_t X(t) + (\tau^2/2)\partial_{tt} X(t) + \mathcal{O}(\tau^3)$$

Equation for the deviation from the stationary solution

$$\begin{aligned} \partial_t \mathcal{X} &= Y \\ \partial_t Y &= -aY - b\mathcal{X} - \frac{2g}{\tau^2\beta}\mathcal{X}^2 \end{aligned}$$

with $a = 0$ when $\beta\tau = 1$.

- Inhomogeneous pitchfork bifurcation

Consider now a periodic wave train with distinct members

$$\partial_t X_l = -\mu - g X_l^2 - \beta(\gamma + X_{l-1}(t-\tau) + \gamma_1 X_l(t))$$

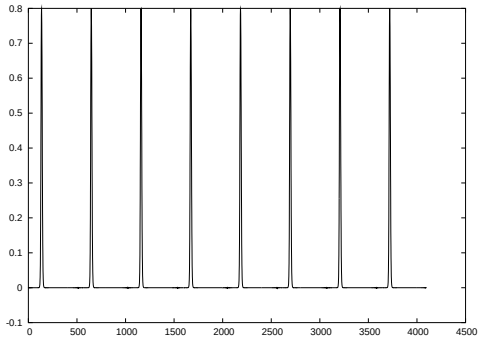
Linearize around homogeneous stationary solution

$$X_l = \bar{X} + \delta e^{\sigma t} e^{ipl} \quad \text{and} \quad X_{l-1} = \bar{X} + \delta e^{\sigma t} e^{ip(l-1)}$$

Condition for stationary instability (ie. $\sigma = 0$)

$$\bar{X} = -\frac{\beta}{2g}(\gamma_1 + \cos p - i \sin p) \ .$$

==> either $p = 0$ (old saddle-node) or $p = \pi$ (every second pulse dies)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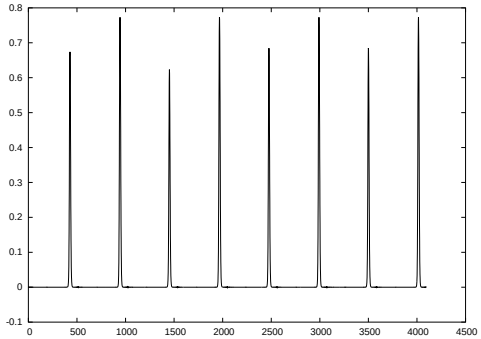
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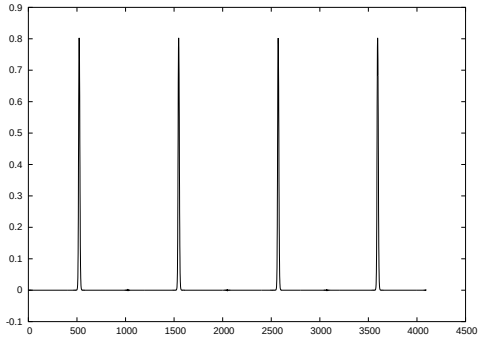
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Two populations of pulses X and Y:

$$\begin{aligned}\partial_t X &= -\mu - gX^2 - \beta(\gamma + Y(t-\tau) + \gamma_1 X(t)) \\ \partial_t Y &= -\mu - gY^2 - \beta(\gamma + X(t-\tau) + \gamma_1 Y(t))\end{aligned}$$

Stationary solutions: old homogeneous friend $X = Y$ and additional alternating mode $\bar{X}_a = -\bar{Y}_a + \frac{\beta}{g}(1-\gamma_1)$

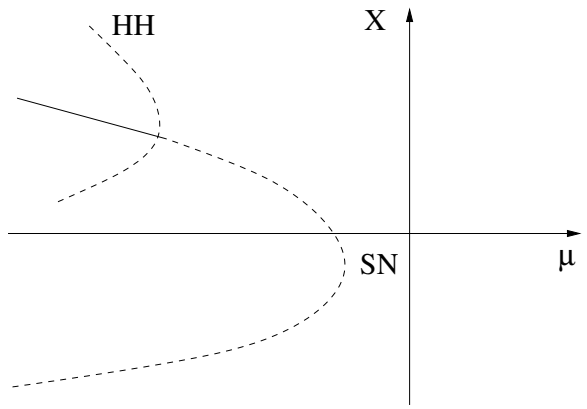
==> subcritical pitchfork bifurcation

$$\mu_{PF} = \frac{1}{4}\frac{\beta^2(1+\gamma_1)^2}{g} - \frac{\beta^2}{g} - \beta\gamma = \bar{\mu}_{SN} - \frac{\beta^2}{g} \qquad X_{PF} = Y_{PF} = \frac{\beta}{2g}(1-\gamma_1)$$

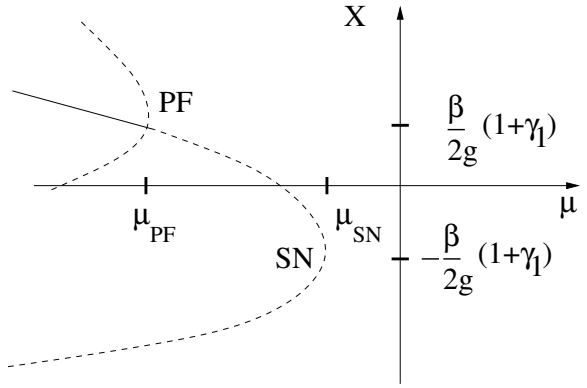
(Note: Hopf bifurcation possible but comes after pitchfork bifurcation)

Summary

Single pulse in a ring:



Wave train in a ring:



Alternans????

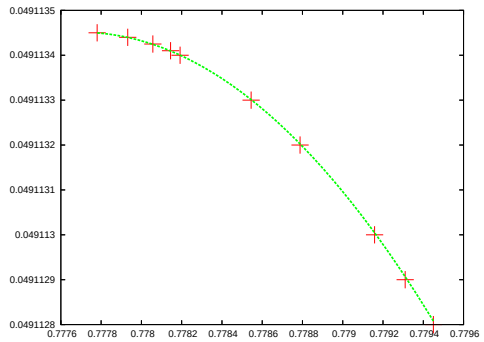
II. Determination of the parameters of the normal form

$$\partial_t X = -\mu - gX^2 - \beta(\gamma + X(t-\tau) + \gamma_1 X(t))$$

$$\text{where } \beta = \beta_0 \exp(-\epsilon a \tau) = \beta_0 \exp(-\epsilon a \frac{(L-l)}{c_0})$$

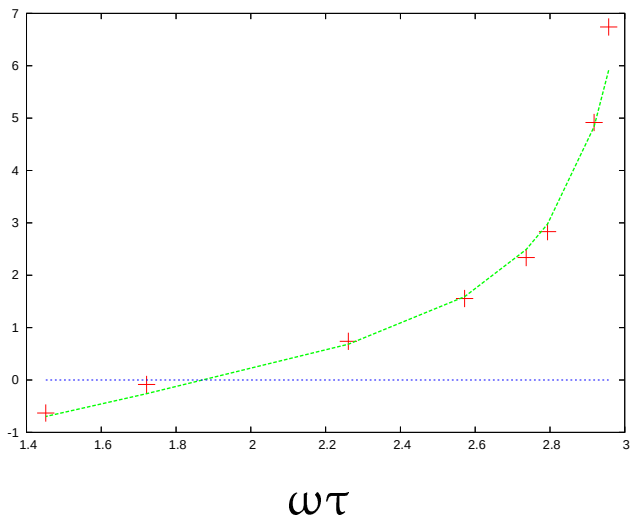
II.a Numerical simulations

- l is due to finite width of pulse. $l = 35$.
- $\mu = \alpha(\epsilon - \epsilon_c)$ and g via saddle-node of the isolated pulse



$\alpha = 1.455$ and $g = 0.31$

- γ_1 via $\frac{\bar{X}_{HH}}{\omega} = -\frac{1}{2g}(\cot(\omega\tau) + \gamma_1 \sin^{-1}(\omega\tau))$



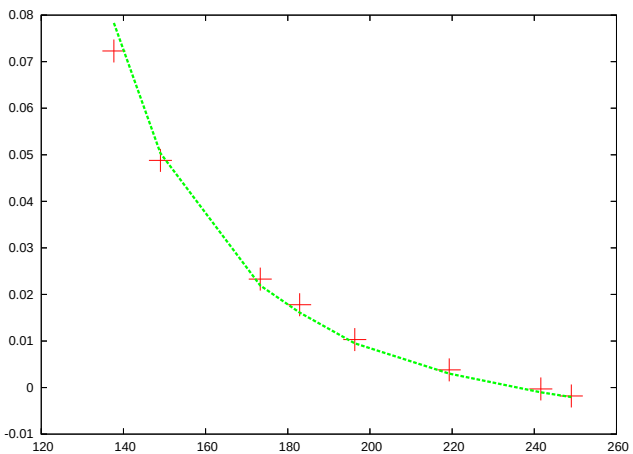
$==> \gamma_1 = 0.31$

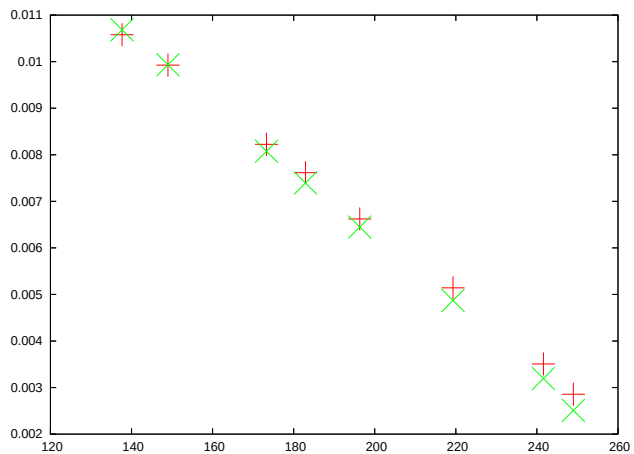
- β_0 and γ via shift of the saddle-node:

$$\mu + \delta + g(X - \xi)^2 = \mu + gX^2 + \beta_0\, e^{-\epsilon a \frac{L-l}{c_0}} (\gamma + (1 + \gamma_1)X)$$

$$==> \gamma = 0.2 \text{ and } \beta_0 = 0.60$$

- CHECK: Do the parameters which have been obtained via the properties of the stationary solution also describe the Hopf bifurcation?





II.b Test function approach

Goal Determine the parameters directly from the PDE. We need to describe the behaviour of the pulse correctly at least close to the saddle-node.

The usual approach is asymptotics. BUT close to the saddle-node the pulse looks like a bell-shaped function and not like a front.

We choose u of the general form

$$u(x,t) = f_0(t)U(\eta)\ , \eta = w(t)x$$

where $U(\eta)$ is chosen as a symmetric, bell-shaped function.

Note that the inhibitor can be solved for directly.

(*GAG & Lorenz Kramer, Chaos,* **14** *855 (2004), Shakti Menon & GAG, PRE* **71**, *066201 (2005), Steve Cox & GAG, submitted*).

Idea: Restrict the solutions to the solution space of test functions $u(x,t) = f_0 U(wx - ct)$

The tangent space, associated with this ansatz is spanned by:

$$\partial u/\partial f_0 = U \qquad \text{and} \qquad \partial u/\partial w = x U_x$$

Minimize the error caused by restricting to this space:

$$\begin{aligned} \langle -u_t + Dw^2 u_{\eta\eta} + u(1-u)(u-u_s-v) | U \rangle_{u=f_0 U(\eta)} &= 0 \\ \langle -u_t + Dw^2 u_{\eta\eta} + u(1-u)(u-u_s-v) | \eta U' \rangle_{u=f_0 U(\eta)} &= 0\,, \end{aligned}$$

$\Rightarrow$

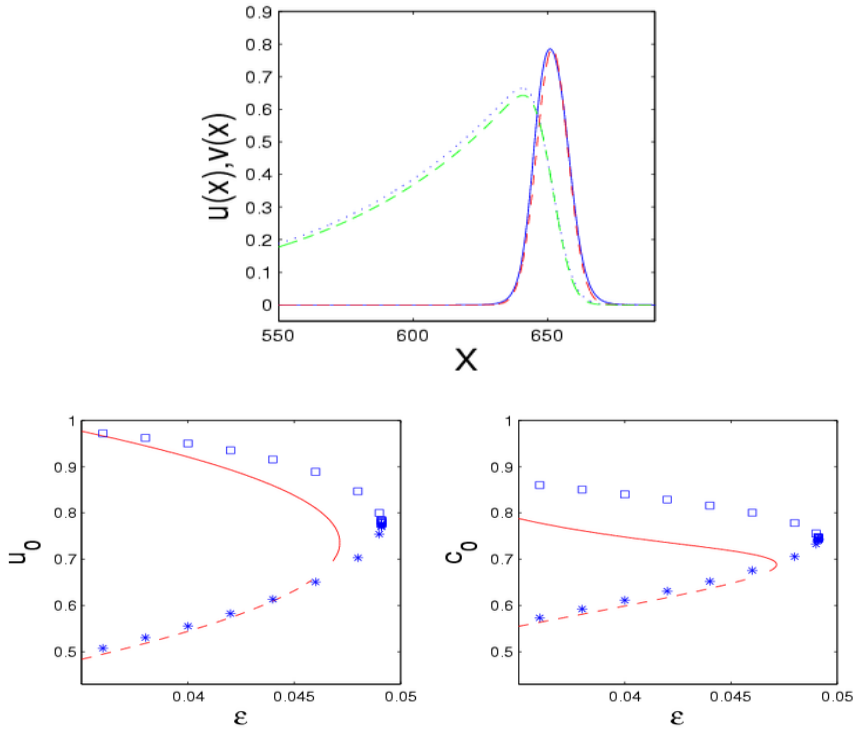
$$\begin{aligned} \langle U^2 \rangle \frac{\dot{f}_0}{f_0} &= -2Dw^2 \langle U'^2 \rangle - u_s \langle U^2 \rangle - \frac{\epsilon}{c_0 w} \langle U^2 V \rangle f_0 + \frac{7}{9}(1+u_s)\langle U^3 \rangle f_0 \\ &+ \frac{1}{2} a (\frac{\epsilon}{c_0 w})^2 \langle U^2 \eta V \rangle f_0 + \frac{7}{6} \frac{\epsilon}{c_0 w} \langle U^3 V \rangle f_0^2 - \frac{1}{3} a (\frac{\epsilon}{c_0 w})^2 \langle U^3 \eta V \rangle f_0^2 - \frac{5}{4} \langle U^4 \rangle f_0^2 \\ \langle U^2 \rangle \frac{\dot{w}}{w} &= -2Dw^2 \langle U'^2 \rangle + \frac{1}{3}(1+u_s)\langle U^3 \rangle f_0 + \frac{1}{3} \frac{\epsilon}{c_0 w} \langle U^3 V \rangle f_0^2 - \frac{1}{2} \langle U^4 \rangle f_0^2 \\ &+ a (\frac{\epsilon}{c_0 w})^2 \langle U^2 \eta V \rangle f_0 - \frac{2}{3} a (\frac{\epsilon}{c_0 w})^2 \langle U^3 \eta V \rangle f_0^2 \end{aligned}$$

Isolated pulse

Stationary case:

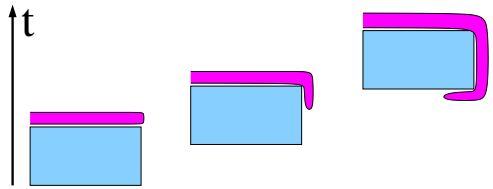
$$A(\Theta, \langle U \rangle, L) f_0^2 + B(\Theta, \langle U \rangle, L) f_0 + C(\Theta, \langle U \rangle, L) = 0 \quad \text{and} \quad w^2 = w^2(f_0, \Theta, \langle U \rangle, L)$$

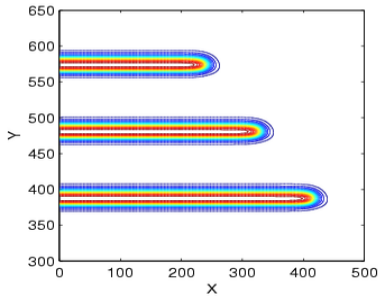
Take $L = \infty$ in the set of algebraic equations.



$D = 3 \quad a = 0.22 \quad b = 0.1$

Growing velocity and retracting fingers in two dimensional excitable media





previous work:

small ϵ-asymptotics by *Hakim & Karma, 1997*

dynamical systems approach by *Ashwin, Nicol & Melbourne, 1999*

Test function ansatz approach:

$$D\Delta u + c_0\partial_\eta u + c_g\partial_y u + \mathcal{F}(u,v) = 0 \qquad \text{and} \qquad c_0\partial_\eta v + c_g\partial_y v + \epsilon(u - a\ v) = 0$$

We introduce a product ansatz for the activator field

$$u(x,y) = f(y)U(\eta)$$

with test function $U(\eta)$ and shape function $f(y)$, and write $v(x,y)$ as an asymptotic expansion in powers of c_g

$$v(x,y) = \Theta g_0(y)V_0(\eta) + c_g\Theta g_1(y)V_1(\eta) + \mathcal{O}(c_g^2)$$

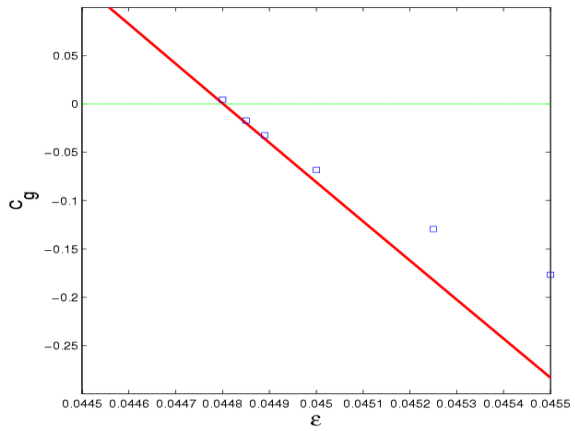
Comparison with numerical results:

We obtain by projection onto $U(\eta)$ for the growing velocity c_g:

$$c_g = \bar{c}_g \frac{1}{1 + \frac{1}{2} G_0 f_o + \frac{3}{10} G_1 f_o^2} \,,$$

where

$$\bar{c}_g = \sqrt{\frac{D}{2}} \sqrt{\frac{\langle U^4 \rangle - \Theta \langle U^3 V \rangle}{\langle U^2 \rangle}} (f_{0+} - 2 f_{0-}), \quad G_0 = -\Theta \frac{\langle U^2 V_1 \rangle}{\langle U^2 \rangle}, \quad G_1 = \Theta \frac{\langle U^3 V_1 \rangle}{\langle U^2 \rangle}$$



Summary

- "Derivation" of a "normal form" for one-dimensional excitable media
- Identification of three new bifurcations: homogeneous Hopf bifurcation, Bogdanov-Takens point and inhomogeneous pitchfork bifurcation
- The parameters of the normal form can be determined with comparison to numerical simulations of the full PDE; and (hopefully) by a test function approach directly from the PDE.
- Reduction of PDE's to a set of algebraic equations by a non-perturbative method.
- Stationary saddle-node bifurcations can be accurately described for isolated pulses, wave trains and for retracting fingers.