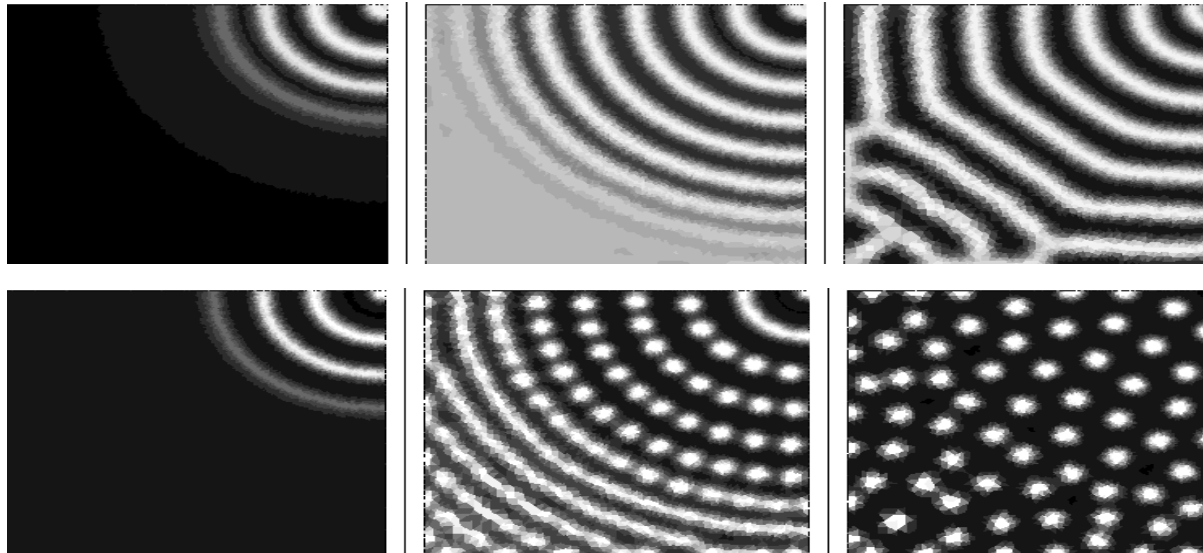
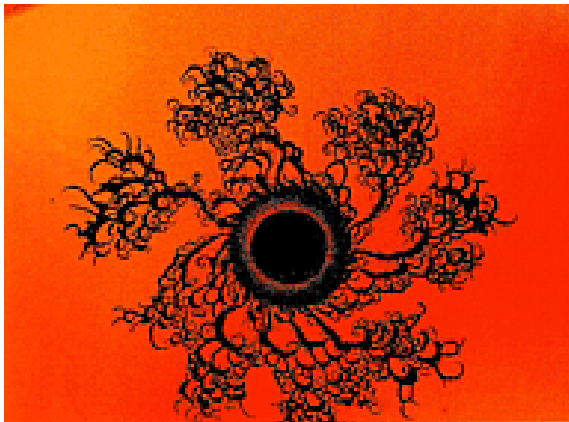


Traveling pulses and branching patterns

Benoît Perthame



WHY



Bacterial colonies. Top S. Serror (CNRS-Paris-Sud). Bottom K. Ben Jacob (TAU)

WHY

Lecture 1. Parabolic models and pulse propagation

Lecture 2. The hyperbolic Keller-Segel model and branching pattern

Lecture 2bis. V. Calvez (Keller-Segel and asymmetric pulses)

Lecture 3. Another example of concentration Darwin evolution

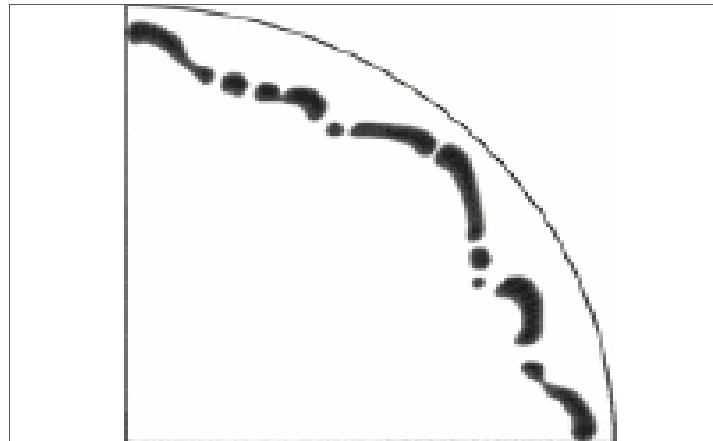
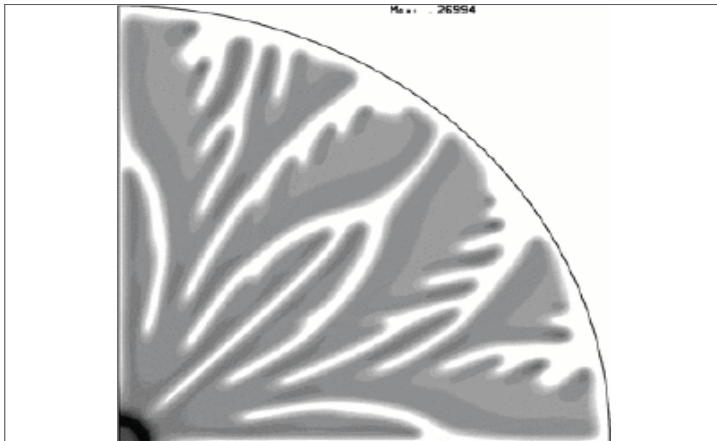
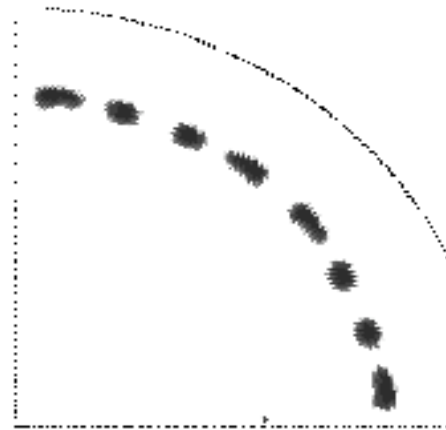
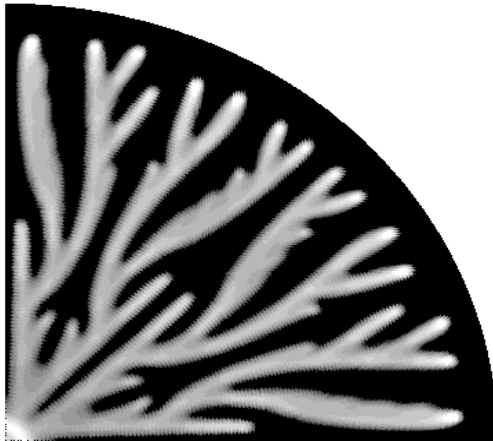
Dentritic patterns

MIMURA's model

$$\left\{ \begin{array}{l} \frac{\partial}{\partial t} n(t, x) - d_1 \Delta n = r n \left(S - \frac{\mu n}{(n_0 + n)(S_0 + S)} \right), \\ \frac{\partial}{\partial t} S(t, x) - d_2 \Delta S = -r n S, \\ \frac{\partial}{\partial t} f(t, x) = r n \frac{\mu n}{(n_0 + n)(S_0 + S)} \end{array} \right.$$

The dynamics is driven by the source terms, i.e., by bacterial growth/nutrient consumption.

Dendritic patterns



Dentritic patterns

Intuitive explanation

- Nutrient is consumed by the active cells and reaches a low level in the colony
- Cells at the front have an advantage for multiplication
- This enhances any perturbation

Dendritic patterns

This model, as well as other variants are based on the Gray-Scott chemical reaction

$$\begin{cases} \frac{\partial}{\partial t}u - d_u\Delta u = u(u^{n-1}v - \mu), \\ \frac{\partial}{\partial t}v - d_v\Delta v = -u^n v, \\ \frac{\partial}{\partial t}f(t, x) = \mu u^n. \end{cases}$$

Here $n = 1, 2, \dots$ plays the role of ignition temperature.

Levin and Kessler model is

$$\frac{\partial}{\partial t}u - d_u\Delta u = u(h(u)v - \mu),$$

$$h(u) = 0 \quad \text{for} \quad u < u_{\text{threshold}}.$$

Dendritic patterns

This model, as well as other variants are based on the Gray-Scott chemical reaction

$$\begin{cases} \frac{\partial}{\partial t}u - d_u\Delta u = u(u^{n-1}v - \mu), \\ \frac{\partial}{\partial t}v - d_v\Delta v = -u^n v, \\ \frac{\partial}{\partial t}f(t, x) = \mu u^n. \end{cases}$$

Here $n = 1$ makes a big difference with $n = 2\dots$ or Levin and Kessler model or Mimura model.

Dentritic patterns

Traveling pulse for Gray-Scott

$$\begin{cases} -\sigma u' - d_u u'' = u(v - \mu), & u(\pm\infty) = 0, \\ -\sigma v' = -uv, & v(-\infty) = v_-, \quad v(+\infty) = v_+. \end{cases}$$

Theorem (PES, BP ongoing) Let (μ, v_-, v_+) be such that

$$v_- < \mu < v_+, \quad \mu \ln(v_-) - v_- = \mu \ln(v_+) - v_+,$$

Then, for all speeds

$$\sigma > \sigma^* := 2\sqrt{v_+ - \mu}$$

there is a unique traveling pulse and v is increasing.

Dentritic patterns

Some references

Golding-Koslovsky-Ben Jacob

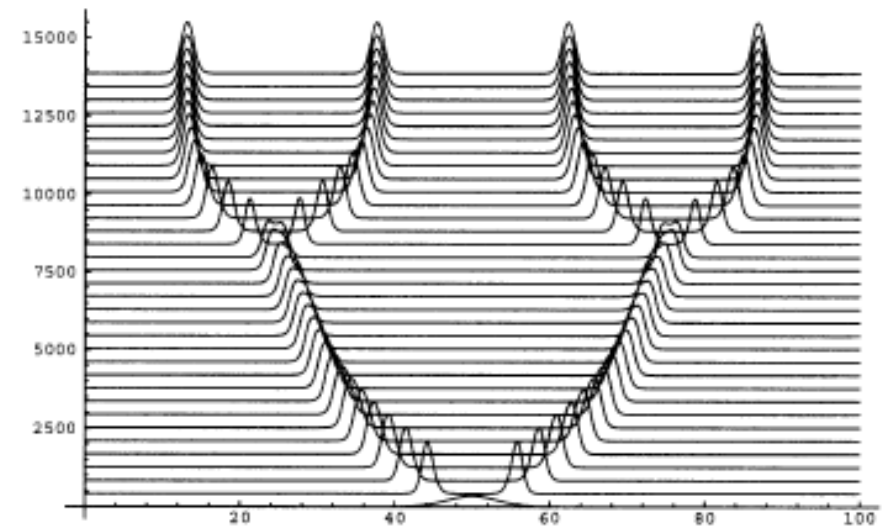
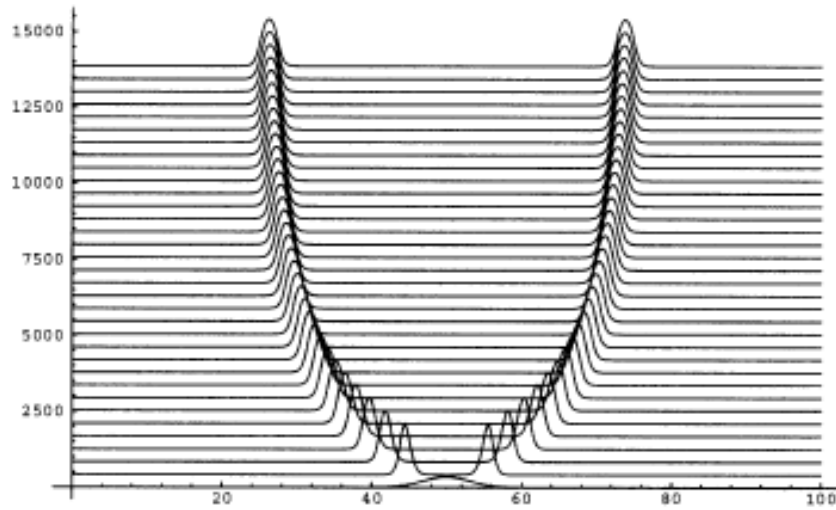
Muratov-Osipov, Doelman-Eckhaus-Kaper-Gardner

M. Ward-Kolokolnikov-Wei

Mimura (Masuda)

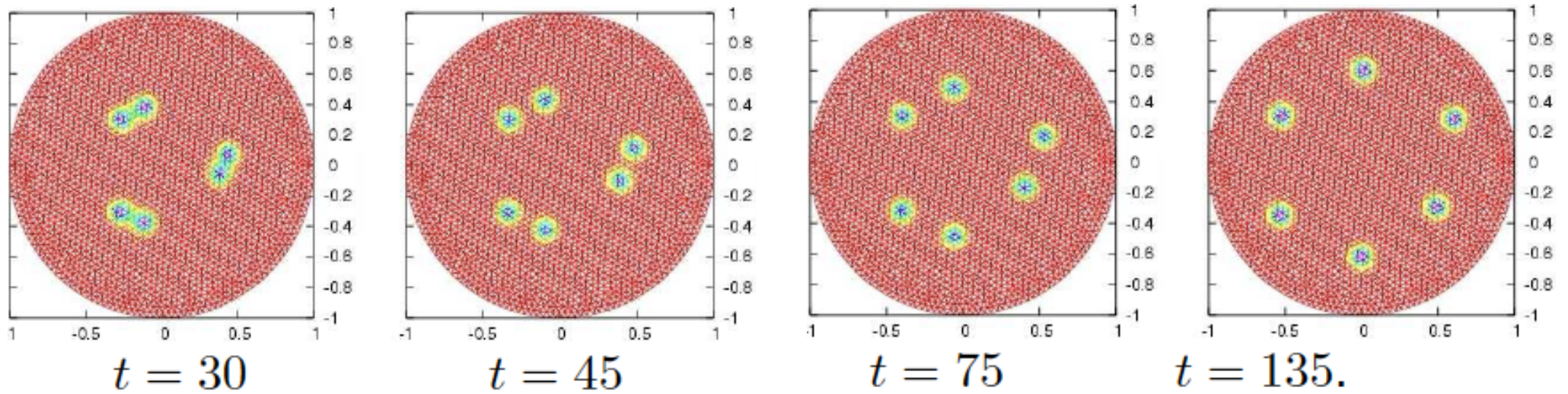
Elliptic case : Del Pino, Kowalczyk

Dendritic patterns



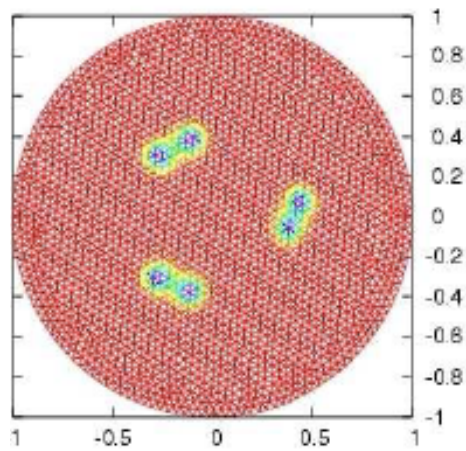
Pulse splitting in GS system (from DoelmanEckhaus-Kaper, SIAP)

Dentritic patterns

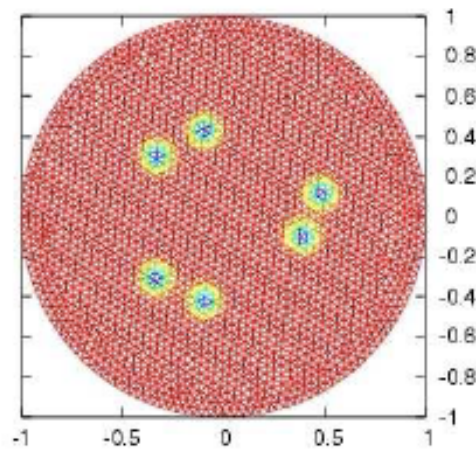


Pulse splitting in 2D GS system (from M. Ward)

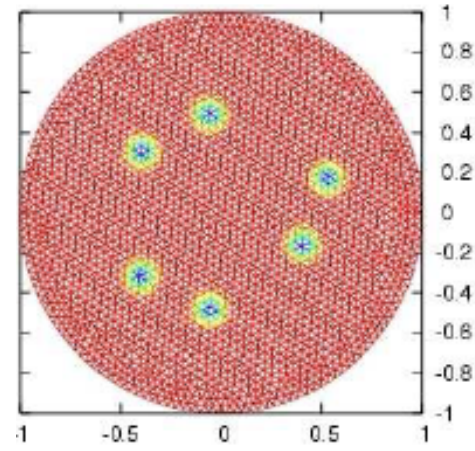
Dentritic patterns



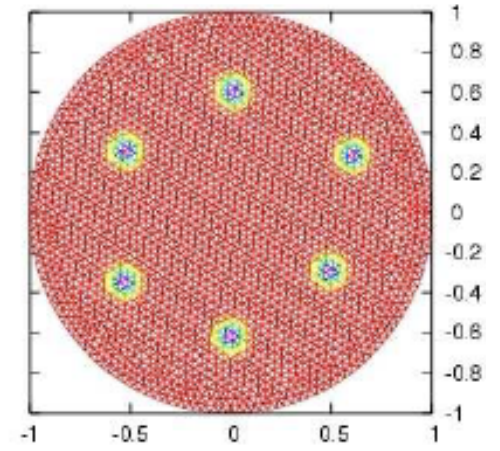
$t = 30$



$t = 45$



$t = 75$



$t = 135.$

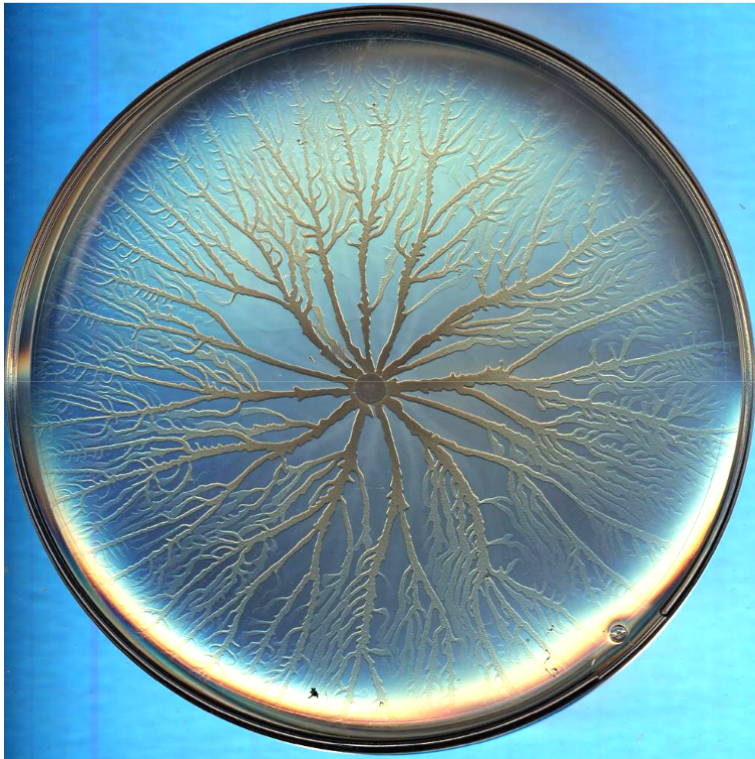
Pulse splitting in 2D GS system (from M. Ward)

A conservative model with branching

New experiments are done on rich media.

Are there models based on other ingredients that achieve this type of patterns ?

A conservative model with branching



Experiments by B. Holland and S. Serror, CNRS Paris-Sud

A conservative model with branching

The shortcoming of Keller-Segel system

$$\begin{cases} \frac{\partial}{\partial t}n(t, x) + \operatorname{div}[\chi n \nabla c] = \Delta n, & x \in \mathbb{R}^d, t \geq 0, \\ -\Delta c + c = n, \\ n(t, x) = n^0(x). \end{cases}$$

A conservative model with branching

The shortcoming of Keller-Segel system

$$\begin{cases} \frac{\partial}{\partial t}n(t, x) + \operatorname{div}[\chi n \nabla c] = \Delta n + n(1 - n), & x \in \mathbb{R}^d, t \geq 0, \\ -\Delta c + c = n, \\ n(t, x) = n^0(x). \end{cases}$$

Theorem (G. Nadin, BP, L. Ryzhik)

For χ small enough, there is a traveling wave.

For χ large enough the K.-S. equation is unstable in the sense of Turing.

A conservative model with branching

The hyperbolic Keller-Segel system (Dolak, Schmeiser)

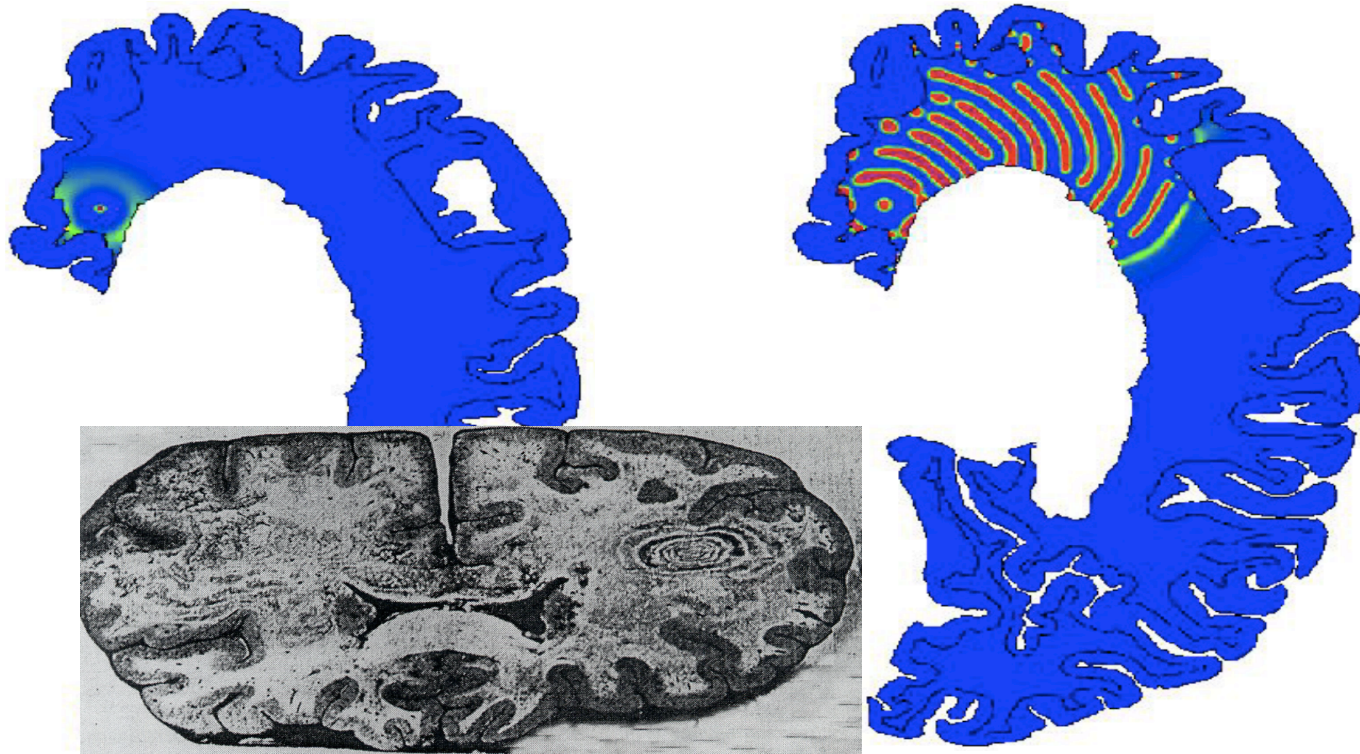
$$\begin{cases} \frac{\partial}{\partial t} n(t, x) + \operatorname{div}[n(1-n)\nabla c] = 0, & x \in \mathbb{R}^d, t \geq 0, \\ -\Delta c + c = n, \\ n(t, x) = n^0(x), & 0 \leq n^0(x) \leq 1, \quad n^0 \in L^1(\mathbb{R}^d). \end{cases}$$

Interpretation

- $n(t, x)$ = bacterial density ,
- $c(t, x)$ = chemical signalling (chemoattraction),
- $n(1-n)$ represents something like quorum sensing,
- random motion of bacteria is neglected

A conservative model with branching

Related to the Keller-Segel model but no point concentrations



By V. Calvez, B. Desjardins, H. Khonsari on multiple sclerosis

A conservative model with branching

$$\left\{ \begin{array}{l} \frac{\partial}{\partial t} n(t, x) + \operatorname{div} [n(1 - n) \nabla c - n \nabla S] = 0, \quad x \in \mathbb{R}^d, t \geq 0, \\ -d_c \Delta c + c = \alpha_c n, \\ \frac{\partial}{\partial t} f(t, x) - d_f \Delta f = \alpha_f n + f(1 - f) \\ \frac{\partial}{\partial t} S(t, x) - d_S \Delta S + S = \alpha_S (n_{\text{mother colony}} + f + n). \end{array} \right.$$

- n = swarmer cells,
- f = follower (supporter) cells,
- c = short range 'attractant'
- S = long range signal (surfactant?)

A conservative model with branching

show movies now

Traveling pulses

Numerical instabilities can be observed on reduced systems

$$\begin{cases} \frac{\partial}{\partial t} n(t, x) + \operatorname{div}[n(1-n)\nabla c - n\nabla S] = 0, & x \in \mathbb{R}^d, t \geq 0, \\ -d_c \Delta c + c = \alpha_c n, \\ \frac{\partial}{\partial t} S(t, x) - d_S \Delta S + \tau_S S = \alpha_S n. \end{cases}$$

And check for traveling pulses

$$\begin{cases} -\sigma n' + [n(1-n)c' - nS']' = 0, & x \in \mathbb{R}, \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' - d_S S'' + \tau_S S = \alpha_S n. \end{cases}$$

Traveling pulses

$$\begin{cases} -\sigma n' + [n(1-n)c' - nS']' = 0, & x \in \mathbb{R}, & n(\pm\infty) = 0, \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' - d_S S'' + \tau_S S = \alpha_S n. \end{cases}$$

$$\begin{cases} -\sigma n + n(1-n)c' - nS' = 0, & x \in \mathbb{R}, \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' - d_S S'' + \tau_S S = \alpha_S n. \end{cases}$$

$$\begin{cases} \bullet & -\sigma + (1-n)c' - S' = 0, & x \in [0, L], \\ \bullet & n \equiv 0, \text{ for } x \notin [0, L], \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' - d_S S'' + \tau_S S = \alpha_S n. \end{cases}$$

Traveling pulses

$$\left\{ \begin{array}{l} -\sigma n' + [n(1-n)c' - nS']' = 0, \quad x \in \mathbb{R}, \quad n(\pm\infty) = 0, \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' - d_S S'' + \tau_S S = \alpha_S n. \end{array} \right.$$

$$\left\{ \begin{array}{l} -\sigma n + n(1-n)c' - nS' = 0, \quad x \in \mathbb{R}, \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' - d_S S'' + \tau_S S = \alpha_S n. \end{array} \right.$$

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Traveling pulses

$$\begin{cases} -\sigma n' + [n(1-n)c' - nS']' = 0, & x \in \mathbb{R}, & n(\pm\infty) = 0, \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' - d_S S'' + \tau_S S = \alpha_S n. \end{cases}$$

$$\begin{cases} -\sigma n + n(1-n)c' - nS' = 0, & x \in \mathbb{R}, \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' - d_S S'' + \tau_S S = \alpha_S n. \end{cases}$$

$$\begin{cases} \bullet & -\sigma + (1-n)c' - S' = 0, & x \in [0, L], \\ \bullet & n \equiv 0, \text{ for } x \notin [0, L], \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' - d_S S'' + \tau_S S = \alpha_S n. \end{cases}$$

Traveling pulses

Special case 1. Steady states,

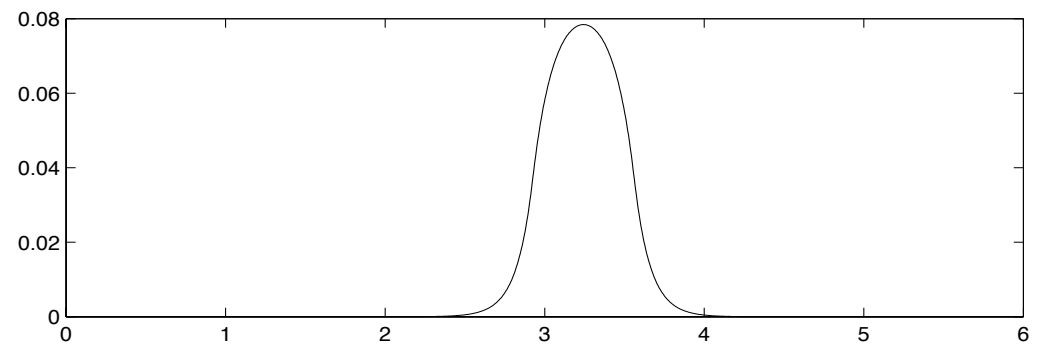
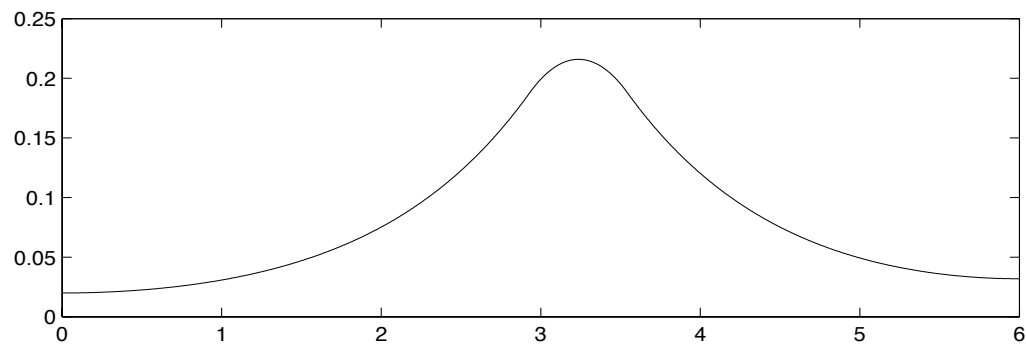
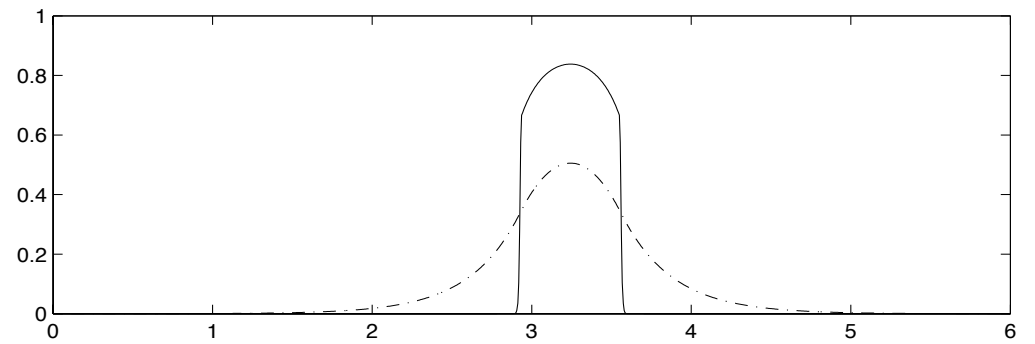
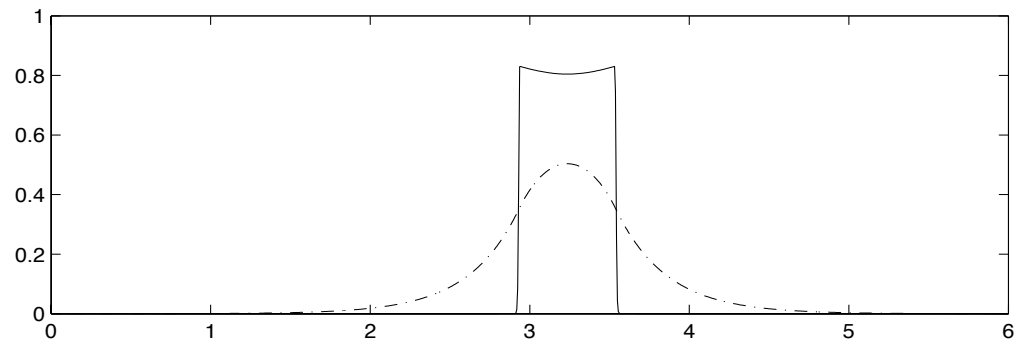
$$\left\{ \begin{array}{l} \bullet \quad (1 - n)c' - S' = 0, \quad x \in [0, L], \\ \bullet \quad n \equiv 0, \text{ for } x \notin [0, L], \\ -d_c c'' + c = \alpha_c n, \\ -d_S S'' + S = \alpha_S n. \end{array} \right.$$

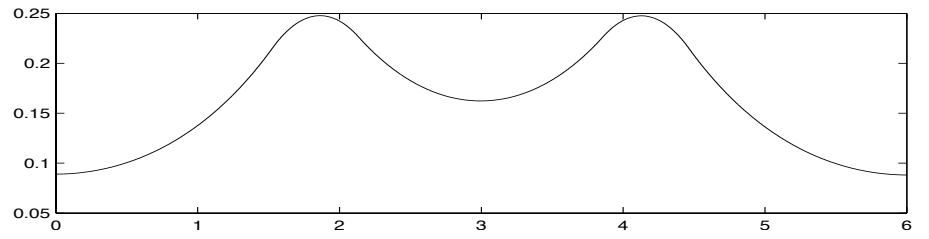
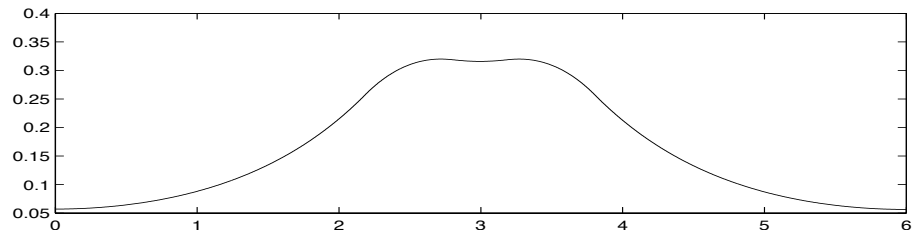
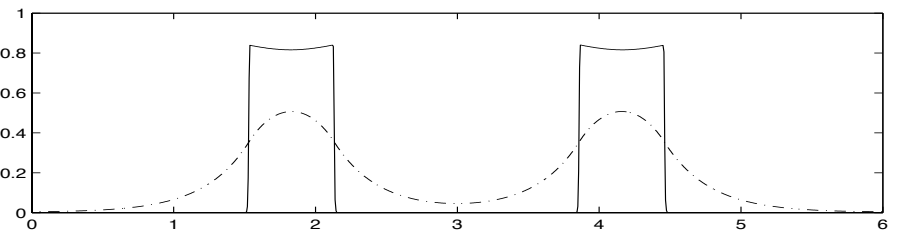
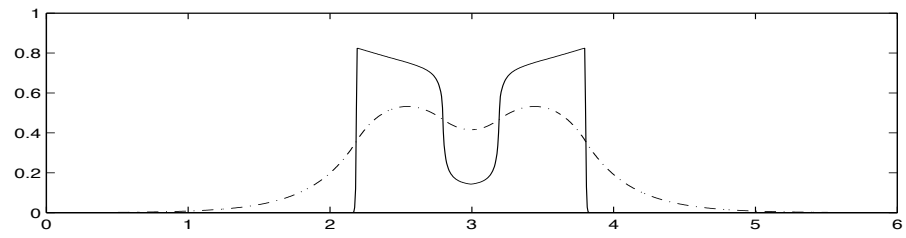
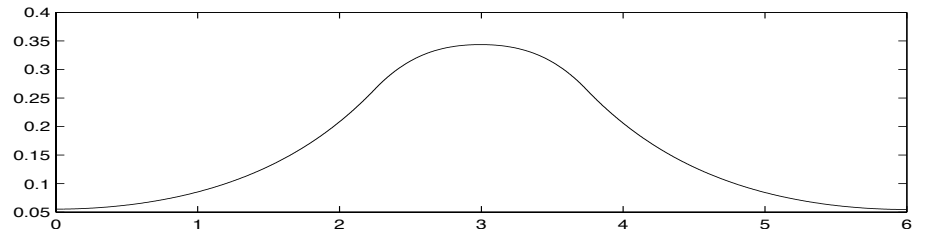
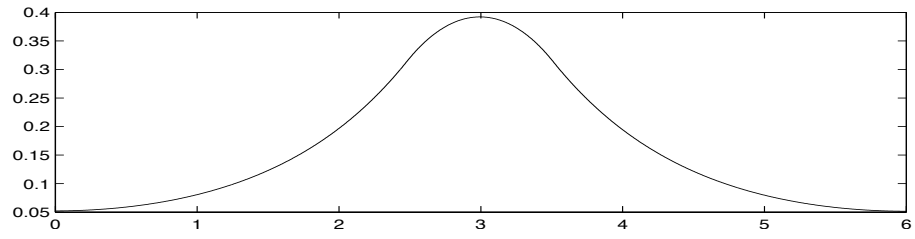
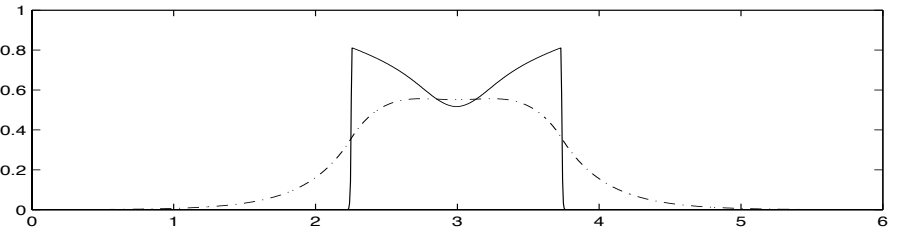
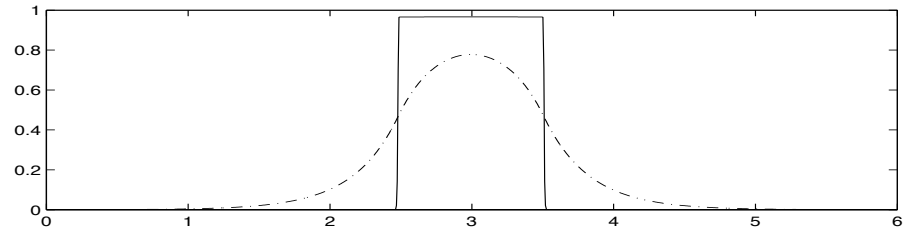
Theorem For

- L small
 - or $|d_c - d_S| + |\alpha_c - \alpha_S|$ small
- there is a unique solution $n \in C(0, L)$.

Traveling pulses

Special case 1. Steady states,





Traveling pulses

Special case 2. $d_S = 0$, $\tau_S = 0$,

$$\left\{ \begin{array}{l} \bullet \quad -\sigma + (1-n)c' - S' = 0, \quad x \in [0, L], \\ \bullet \quad \quad \quad n \equiv 0, \quad \text{for } x \notin [0, L], \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' = \alpha_S n. \end{array} \right.$$

$$n = \begin{cases} 1, & 0 \leq x \leq L, \\ 0, & \text{otherwise} \end{cases}$$

$$-\sigma S' = \alpha_S n, \quad \forall x, \quad \sigma = -S' \text{ for } x \in [0, L],$$

$$\implies \sigma = \sqrt{\alpha_S}, \quad \sigma = -S' \quad x \in [0, L], \quad S' = 0 \text{ for } x \notin [0, L],$$

Traveling pulses

Special case 2. $d_S = 0$, $\tau_S = 0$ (stability)

Theorem These waves are stable if and only if

$$c'(0) > \sqrt{\alpha}, \quad c'(L) < 0.$$

See the problem as an hyperbolic system (as **T. LI, Z. WANG**).

$$\begin{cases} \frac{\partial}{\partial t} n + [n(1-n)c' - nS_x]_x = 0, & x \in \mathbb{R}, \\ \frac{\partial}{\partial t} S = \alpha_S n. \end{cases}$$

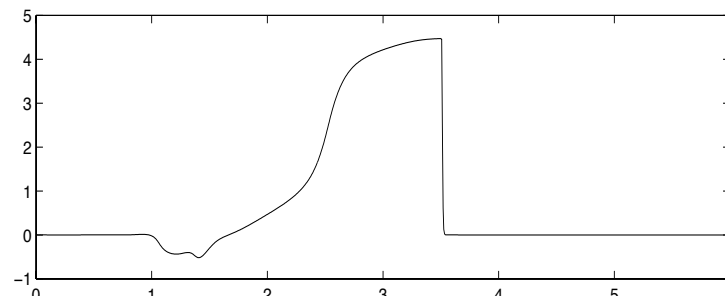
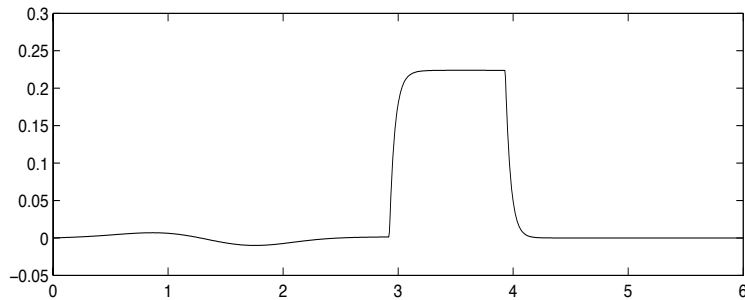
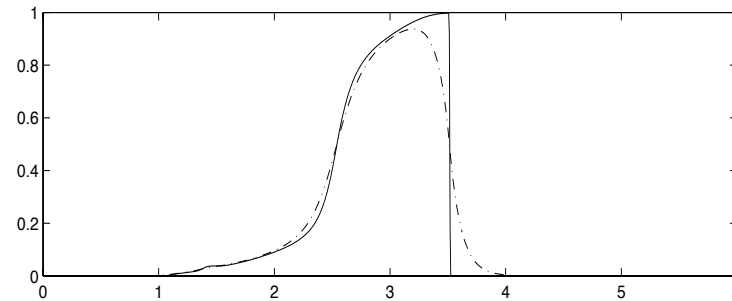
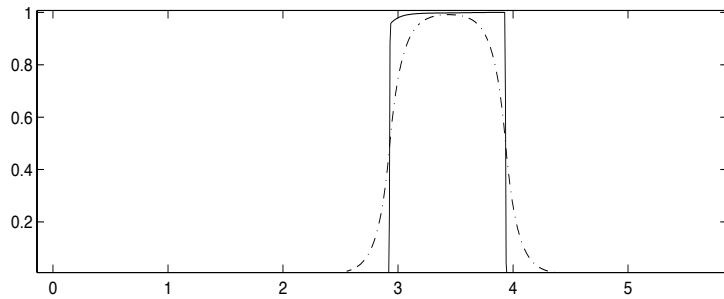
$$\begin{cases} \frac{\partial}{\partial t} n + [n(1-n)c' - nv]_x = 0, \\ \frac{\partial}{\partial t} v - \alpha_S n_x = 0. \end{cases} \quad v := S_x$$

And check the Lax entropy condition.

Traveling pulses

Special case 2. $d_S = 0$, $\tau_S = 0$ (structural stability)

Theorem Still when $c'(0) > \sqrt{\alpha}$, $c'(L) < 0$, these waves are stable for d_S small.



Traveling pulses

Special case 3. $L \approx 0$

$$\left\{ \begin{array}{l} \bullet \quad -\sigma + (1 - n)c' - S' = 0, \quad x \in [0, L], \\ \bullet \quad n \equiv 0, \quad \text{for } x \notin [0, L], \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' - d_S S'' = \alpha_S n. \end{array} \right.$$

$$n = 1 + \frac{\sigma + S'}{c'}$$

Difficulty

- $c'(x_0) = 0$ at a single point
- Choose $\sigma = S'(x_0)$

Traveling pulses

Special case 3. $L \approx 0$

$$\begin{cases} n = 1 + \frac{\sigma + S'}{c'} \\ -d_c c'' + c = \alpha_c n, \\ -\sigma S' - d_S S'' = \alpha_S n. \end{cases}$$

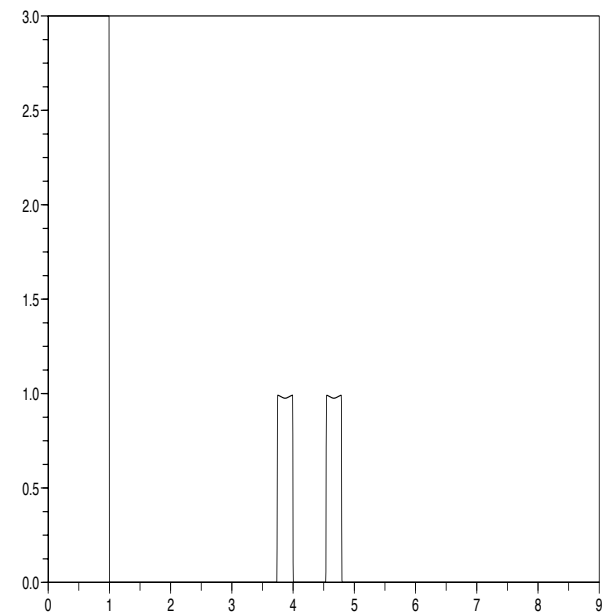
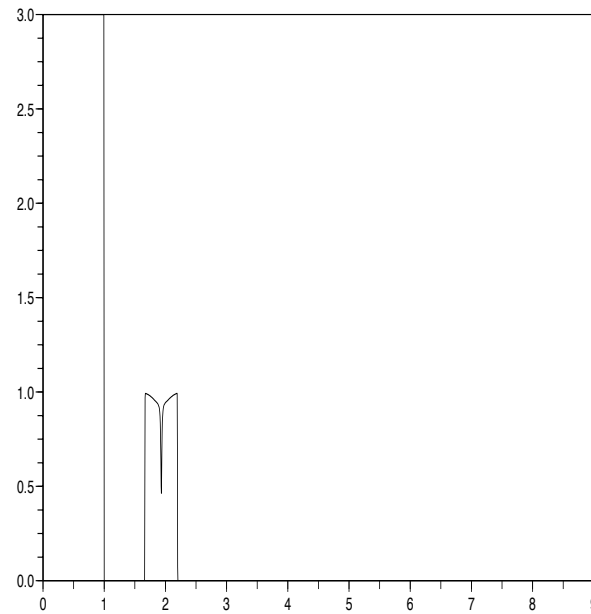
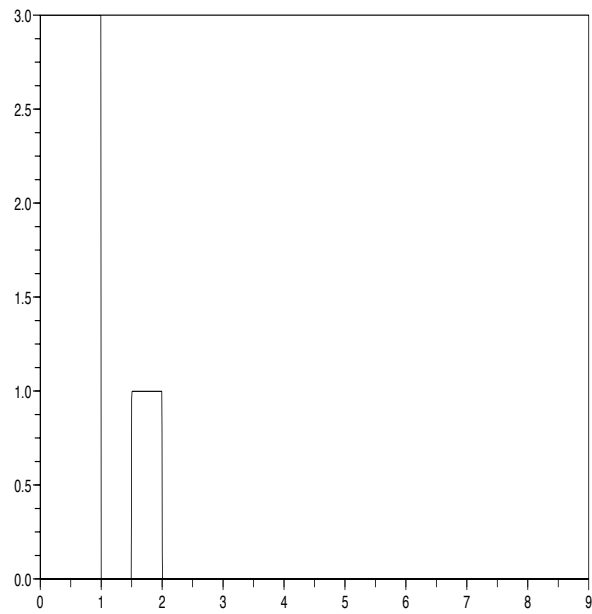
Difficulty • $c'(x_0) = 0$ at a single point • Choose $\sigma = S'(x_0)$.

Theorem For $L \approx 0$ there is a unique solution $n \in C(0, L)$

- c is convex in $[0, L]$
- S is decreasing in $[0, L]$
- Find a fixed point $n \mapsto 1 + \frac{\sigma + S'}{c'}$

Traveling pulses

Special case 3. $L \approx 0$



Conclusion

$$\left\{ \begin{array}{l} \frac{\partial}{\partial t} n(t, x) + \operatorname{div} [n(1 - n) \nabla c - n \nabla S] = 0, \quad x \in \mathbb{R}^d, t \geq 0, \\ -d_c \Delta c + c = \alpha_c n, \\ \frac{\partial}{\partial t} f(t, x) - d_f \Delta f = \alpha_f n + f(1 - f) \\ \frac{\partial}{\partial t} S(t, x) - d_S \Delta S + S = \alpha_S (n_{\text{mother colony}} + f + n). \end{array} \right.$$

This system creates branching patterns.

A reduced hyperbolic Keller-Segel system explains how instabilities can occur on traveling pulse solutions for n .

Thanks to my collaborators

A.-L. Dalibard, V. Calvez

C. Schmeiser, M. Tang, N. Vauchelet

A. Daerr

B. Holland and S. Serror