ETH zürich

Lecture 9: Travelling Waves

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MSc Computational Biology 2019/20

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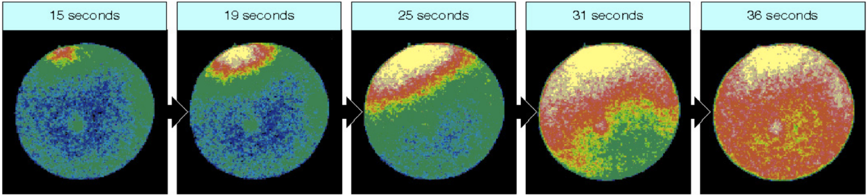

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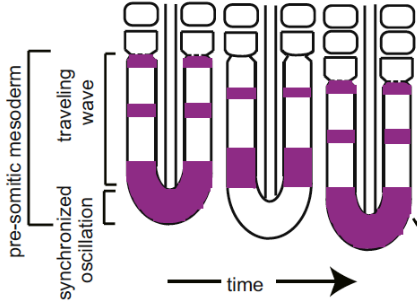
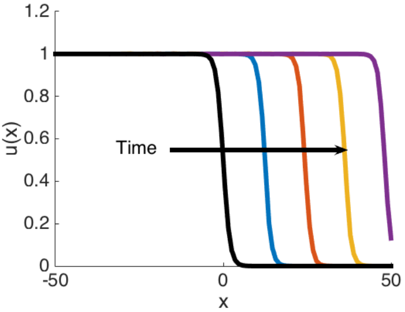


Travelling Wave



Travelling Wave

- travels without change of shape.
- if $u(x, t)$ represents a travelling wave, the shape of the solution will be the same for all time
- speed of propagation is a constant, which we denote c.

Reference Frame

If we look at this wave in a travelling wave frame moving at speed c then this wave will appear stationary.

Travelling Wave

In mathematical terms, $u(x,t)$ is a travelling wave that moves at constant speed c in the positive x-direction, if

$$u(x,t) = u(x-ct) = u(z), \qquad z = x - ct. \tag{1}$$

z is referred to as **wave variable**.

Biological Constraints

To be physically realistic $u(z)$ has to be bounded for all z and non-negative.

Example: Logistic Growth

Consider an ODE that describes logistic growth of the variable u,

$$\frac{du}{dt} = u(1-u). \tag{2}$$

The general solution with integration constant c is given by

$$u(x,t) = \frac{c\exp(t)}{1+c\exp(t)}. \tag{3}$$

If we chose as initial conditions

$$u(x,0) = \frac{1}{1+\exp(x)} \tag{4}$$

then we obtain

$$u(x,0) = \frac{c}{1+c} = \frac{1}{1+\exp(x)} \Rightarrow c = \exp(-x). \tag{5}$$

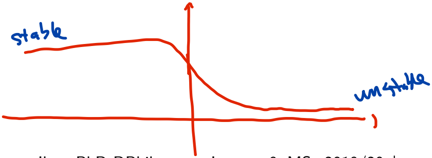
$$u(x,t) = \frac{c \exp(t)}{1 + c \exp(t)} \qquad \text{with} \qquad c = \exp(-x) \tag{6}$$

can be written as

$$u(x,t) = \frac{\exp(t-x)}{1 + \exp(t-x)}. \tag{7}$$

Using the **wave variable** $z = t - x$, we then have

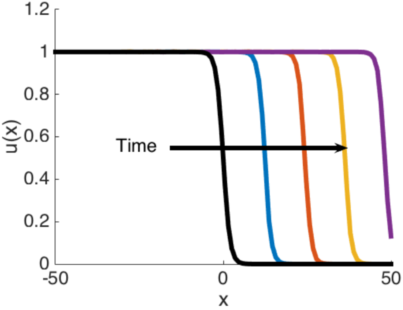
$$u(z) = \frac{\exp(z)}{1 + \exp(z)}. \tag{8}$$



Travelling Wave Solution

only depends on reaction kinematics
Not the substance diffusion.

$$u(z) = \frac{\exp(z)}{1 + \exp(z)}$$



If $z = x - t = const$ then the shape does not change, i.e. if $\frac{dx}{dt} = 1$.

The shape of the wave thus does not change if one travels with the wave at speed 1.

This wave depends on the initial conditions and is highly unstable.

Travelling Wave in one spatial dimension

In one spatial dimension, x, diffusion of a molecule with concentration $c(x, t)$ can be described as

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2}. \tag{9}$$

In mathematical terms, $u(x, t)$ is a travelling wave that moves at constant speed c in the positive x-direction, if

$$u(x, t) = u(x - ct) = u(z), \qquad z = x - ct. \tag{10}$$

z is referred to as **wave variable**.

PDE ⇒ Set of ODEs

$$u(x,t) = u(x-ct) = u(z), \qquad z = x - ct$$

can be rewritten as

$$\frac{du}{dz} \cdot \frac{dz}{dt} = \frac{du}{dz} \cdot -c$$

$$\begin{aligned} \frac{\partial u}{\partial t} &= -c\frac{du}{dz} \\ \frac{\partial u}{\partial x} &= \frac{du}{dz}. \end{aligned} \tag{11}$$

PDE ⇒ Set of ODEs

Partial differential equations in x and t become sets of ordinary differential equations.

Linear Parabolic PDEs

$$u_t = Du_{xx}. \tag{12}$$

Transformation of (x, t) to the wave variable $z = x - ct$ results with Eq. 11 in

$$DU'' + cU' = 0 \quad \Leftrightarrow \quad U(z) = A + B\exp\left(-cz/D\right), \tag{13}$$

where A and B are integration constants.

To be physically realistic $U(z)$ has to be bounded for all z and to be non-negative. Therefore, $B = 0$ as otherwise $U(z)$ becomes unbounded for $z \to -\infty$.

It can be shown more generally, that there are no physically realistic travelling wave solutions for linear parabolic PDEs.

Travelling Waves

To obtain travelling waves, we require an additional reaction term $f(u)$,

$$u_t = f(u) + Du_{xx}. \tag{14}$$

Transformation of (x, t) to the wave variable $z = x - ct$ then results with Eq. 11 in

2-order ODE

$$DU'' + cU' + f(u) = 0 \tag{15}$$

Example: Fisher Equation

Consider the Fisher equation

$$u_t = ku(1-u) + Du_{xx}. \tag{16}$$

This equation can be non-dimensionalized by using $1/k$ as timescale and $\sqrt{D/k}$ as length scale.

The non-dimensionalized Fisher equation reads

$$u_t = u(1-u) + u_{xx}. \tag{17}$$

Transformation to travelling wave coordinates

Consider the non-dimensionalized Fisher equation

$$u_t = u(1-u) + u_{xx}. \tag{18}$$

We write

$$u(x,t) = u(x-ct) = U(z), \qquad z = x - ct, \quad c \geq 0. \tag{19}$$

and upon substitution into Eqn.(55) we obtain

$$U'' + cU' + U(1-U) = 0 \tag{20}$$

PDE $\Rightarrow$ Set of ODEs

$$U'' + cU' + U(1-U) = 0$$

can be written as set of ODEs,

$$\begin{aligned} U' &= V \\ V' &= -cV - U(1-U). \end{aligned} \tag{21}$$

steady state

$V=0 \quad u=\{0,\underline{1}\} \Rightarrow 2$ steady state.

Stability of the steady state

Let

$$\vec{w} = \vec{x} - \vec{x}_s = (U - U_s, V - V_s)^T \tag{22}$$

be a small perturbation from the steady state

$$\vec{x_s} = (U_s, V_s)^T. \tag{23}$$

Stability of the steady state

The steady state is stable if the perturbation decays to zero for long times t, i.e. $\vec{w} \rightarrow 0$ as $t \rightarrow \infty$.

Perturbation at the steady state

Given

$$\begin{aligned} \frac{dU}{dt} &= \dot{U} = f(U, V) \\ \frac{dV}{dt} &= \dot{V} = g(U, V), \end{aligned} \tag{24}$$

we obtain for the dynamics of the perturbation

$$\frac{d\vec{w}}{dt} = \frac{d(\vec{x} - \vec{x_s})}{dt} = \begin{pmatrix} \dot{u}(t) - \dot{u}_s \\ \dot{v}(t) - \dot{v}_s \end{pmatrix} = \begin{pmatrix} f(u, v) - f(u_s, v_s) \\ g(u, v) - g(u_s, v_s) \end{pmatrix}.$$

Linearization around the steady state

$$
\begin{aligned}
f(u,v) &= \underbrace{f(u_s,v_s)}_{=0} + \frac{\partial f}{\partial u}\Big|_{ss}(u-u_s) + \frac{\partial f}{\partial v}\Big|_{ss}(v-v_s) + h.o.t. \\
g(u,v) &= \underbrace{g(u_s,v_s)}_{=0} + \frac{\partial g}{\partial u}\Big|_{ss}(u-u_s) + \frac{\partial g}{\partial v}\Big|_{ss}(v-v_s) + h.o.t.
\end{aligned}
$$

and

$$
\frac{d\vec{w}}{dt} = \frac{d(\vec{x}-\vec{x_s})}{dt} = \begin{pmatrix} \dot{u}(t) - \dot{u_s} \\ \dot{v}(t) - \dot{v_s} \end{pmatrix} = \begin{pmatrix} f(u,v) - f(u_s,v_s) \\ g(u,v) - g(u_s,v_s) \end{pmatrix}.
$$

Therefore,

$$
\frac{d\vec{w}}{dt} = \begin{pmatrix} f(u,v) - f(u_s,v_s) \\ g(u,v) - g(u_s,v_s) \end{pmatrix} = \begin{pmatrix} \frac{\partial f}{\partial u}\Big|_{u_s,v_s} & \frac{\partial f}{\partial v}\Big|_{u_s,v_s} \\ \frac{\partial g}{\partial u}\Big|_{u_s,v_s} & \frac{\partial g}{\partial v}\Big|_{u_s,v_s} \end{pmatrix} \begin{pmatrix} u - u_s \\ v - v_s \end{pmatrix}.
$$

Perturbation at the steady state

$$\frac{d\vec{w}}{dt} = \begin{pmatrix} \left.\frac{\partial f}{\partial u}\right|_{u_s,v_s} & \left.\frac{\partial f}{\partial v}\right|_{u_s,v_s} \\ \left.\frac{\partial g}{\partial u}\right|_{u_s,v_s} & \left.\frac{\partial g}{\partial v}\right|_{u_s,v_s} \end{pmatrix} \vec{w} = J\vec{w}$$

If the eigenvectors of J form a complete eigenbasis

$$J\vec{v_i} = \lambda_i \vec{v_i}$$

then we can solve for $w\vec{(t)}$ as

$$\vec{w}(t) = \sum_i w_i(t)\vec{v_i} \qquad \text{and} \qquad w_i(t) = w_i(0)\exp(\lambda_i t)$$

such that

$$\vec{w}(t) = \sum_i w_i(0)\vec{v_i}\exp(\lambda_i t).$$

$w_i(0)$ is a constant that is determined by the initial perturbation, i.e. $\vec{w}(0) = \sum_i w_i(0)\vec{v_i}$.

Stability of Steady States

$$\begin{aligned} U' &= V \\ V' &= -cV - U(1-U). \end{aligned}$$

To determine the stability of the steady states

$$(U,V) = (0,0); \qquad (U,V) = (1,0), \tag{25}$$

we need to determine the eigenvalues

$$\lambda_{\pm} = \frac{1}{2}\left(tr(J) \pm \sqrt{tr(J)^2 - 4det(J)}\right) \tag{26}$$

of the Jacobian,

$$J = \begin{pmatrix} 0 & 1 \\ -(1-2U^*) & -c \end{pmatrix}. \tag{27}$$

Stability of Steady States

$c < 0 \Rightarrow$ No steady state

$$\vec{w}(t) = \sum_i w_i(0)\vec{v}_i \exp(\lambda_i t)$$

$$\lambda_\pm = \frac{1}{2}\left(tr(J) \pm \sqrt{tr(J)^2 - 4det(J)}\right); \qquad J = \begin{pmatrix} 0 & 1 \\ -(1-2U^*) & -c \end{pmatrix}$$

Steady states: $tr(J) = -c < 0$; $\det(J) = (1 - 2U^*)$

problems w/ negative values

1. $(U^*, V^*) = (1, 0)$: saddle node $\det(J) = (1 - 2U^*) = -1 < 0$
   - 1 positive and 1 negative eigenvalue
2. $(U^*, V^*) = (0, 0)$: stable $\det(J) = (1 - 2U^*) = 1 > 0$
   - node (2 real, negative eigenvalues) if $c \geq 2$
   - spiral (2 conjugate complex eigenvalues with negative real part) if $c < 2$.

Con.

$-a + bi$

Phase Plane Analysis

- Determine Nullclines
- Determine Steady States
- Determine Stability of Steady States
- Determine Trajectories and Phase Vectors

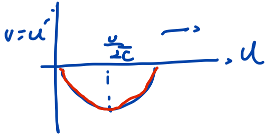
Nullclines and Steady States

$$
\begin{aligned}
U' &= V = 0 \\
V' &= -cV - U(1-U) = 0. \qquad (28)
\end{aligned}
$$

Nullclines:

The U-nullcline is given by $V = 0$ =

The V-nullcline is given by $V = -\frac{U(1-U)}{c}$ =>



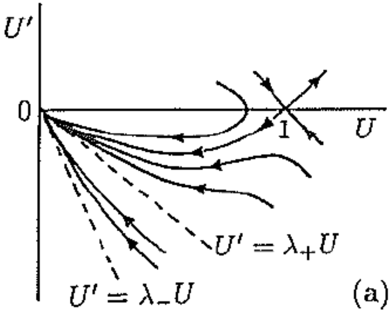
Steady states: (U,V) = (0,0) and (U, V) = (1,0).

and it's related to the slope ⇐ $V = \frac{U}{2c}$ reaches max

Phase Plane

Fisher Equation:

$$\begin{aligned} U' &= V \\ V' &= -cV - U(1-U). \end{aligned}$$



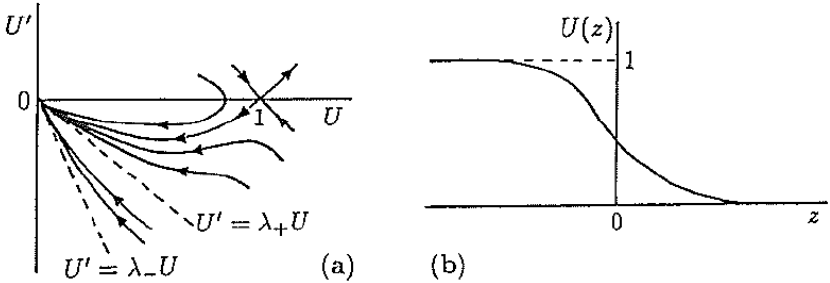
Steady States:

1. $(U^*, V^*) = (1, 0)$: saddle node
2. $(U^*, V^*) = (0, 0)$: stable st st

Phase Plane Trajectory:

$$\frac{dV}{dU} = \frac{-cV - U(1-U)}{V}$$

Phase Plane



Since U can assume negative values if there is a stable spiral at $(U^*, V^*) = (0, 0)$ we require $c \geq 2$ for physically realistic travelling wave solutions.

For travelling waves to exist we require one stable node and one saddle node.

A key question at this stage is:

- What kind of initial conditions $u(x, 0)$ will evolve to a travelling wave solution?
- And, if such solution exists, what is its wave speed c?

Initial conditions & Wave Speed

Kolmogoroff et al (1937) proved that if $u(x, 0)$ has compact support,

$$u(x,0) = u_0(x) \geq 0, u_0(x) = \begin{cases} 1 & \text{if} \quad x \leq x_1 \\ 0 & \text{if} \quad x \geq x_2 \end{cases} \tag{29}$$

where $x_1 < x_2$ and $u_0(x)$ is continuous in $x_1 < x < x_2$, then the solution $u(x, t)$ of the Fisher Equation evolves to a travelling wave solutions with $c = c_{min} = 2$.

More general Initial Conditions

For other initial data the solution critically depends on the behaviour of $u(x, 0)$ as $x \to \pm\infty$.

To see this, consider the leading edge of the evolving wave where since u is small $u^2 << u$ such that

$$u_t \sim u + u_{xx}. \tag{30}$$

Consider now as initial condition

$$u(x, 0) \sim A \exp(-\alpha x); \quad \alpha > 0 \quad \text{as} \quad x \to \infty. \tag{31}$$

We then have

$$u(x, t) = A \exp(-\alpha(x - ct)) \tag{32}$$

if

$$\alpha c u = u + \alpha^2 u \quad \Rightarrow \quad c = \frac{1}{\alpha} + \alpha \tag{33}$$

Wave Speed depends on Initial Conditions

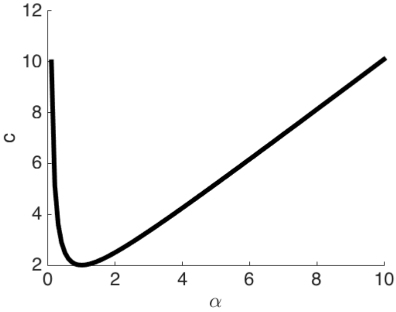
For initial condition

$$u(x,0) \sim A \exp\left(-\alpha x\right) \quad \text{as} \quad x \to \infty$$

the wave speed

$$c = \frac{1}{\alpha} + \alpha$$

depends on the initial conditions $\alpha > 0$.



General Equation

$$u_t = f(u) + u_{xx} \qquad u(x,0) \sim A\exp(-\alpha x), \quad \alpha > 0 \tag{34}$$

can be linearized as

$$u_t = f'(u)u + u_{xx} \qquad u(x,0) \sim A\exp(-\alpha x) \tag{35}$$

with solution

$$u(x,t) = A\exp(-\alpha(x-ct)) \tag{36}$$

if

$$\alpha c u = f'(u)u + \alpha^2 u \tag{37}$$

i.e.

$$c = \frac{f'(u)}{\alpha} + \alpha \tag{38}$$

The minimal travelling wave speed

The minimal wave speed of

$$c = \frac{f'(u)}{\alpha} + \alpha \tag{39}$$

can be determined as

$$c_{min} = 2\sqrt{f'(u)} \tag{40}$$

by differentiating c with respect to α

$$\frac{dc}{d\alpha} = -\frac{1}{\alpha^2} f'(u) + 1 = 0 \Rightarrow \alpha = \pm\sqrt{f'(u)} \tag{41}$$

The travelling wave solution

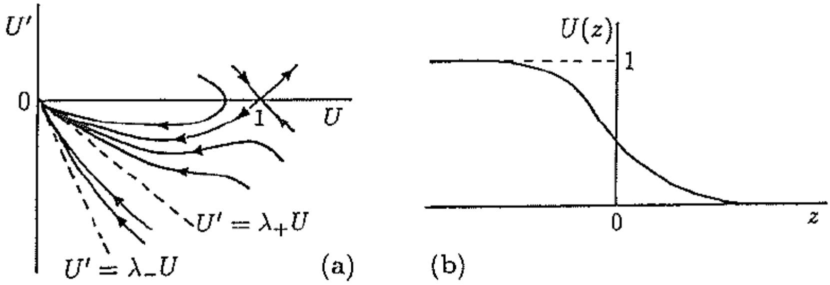
$$u_t = f(u) + u_{xx} \qquad u(x,0) \sim A\exp(-\alpha x), \quad \alpha > 0 \tag{42}$$

with $f(u)$ having two zeros u_1, $u_2 > u_1$

If $f'(u_1) > 0$ and $f'(u_2) < 0$ wavefront solutions monotonically evolve with u going monotonically from u_1 to u_2 with wave speed

$$c \geq c_{min} = 2\sqrt{f'(u)} \tag{43}$$

The flatter the wave, the faster it moves



Recall that the V-nullcline is given by $V = -\frac{f(U)}{c}$.

Moreover, $\frac{dU}{dz} = V = -\frac{f(U)}{c}$.

Thus the flatter the wave, the faster it moves.

Stability of travelling wave Solutions

Introduce perturbation around travelling wave solution

$$u(z,t) = u_c(z) + \omega v(z,t) \qquad 0 < w \ll 1 \tag{44}$$

The travelling wave solution $u_c(z)$ is stable if

$$\lim_{t\to\infty} v = 0. \tag{45}$$

If

$$\lim_{t\to\infty} v = \frac{du_c}{dz}. \tag{46}$$

then there are small translations along the x-axis.

Stability of travelling wave Solutions

$$u(z,t) = u_c(z) + \omega v(z,t) \qquad 0 < \omega \ll 1 \tag{47}$$

Ansatz:

$$v(z,t) = g(z)\exp\left(-\lambda t\right) \tag{48}$$

Determine eigenvalues to evaluate long-term behaviour of $v(z,t)$.

Waves in 3D

Ansatz: transform to spherical coordinate system

$$\begin{aligned} x &= r\cos(\psi)\sin(\theta) \\ y &= r\sin(\psi)\sin(\theta) \\ z &= r\cos(\theta) \end{aligned}$$

$\psi \in [0, 2\pi)$ the azimuthal angle, and $\theta \in [0, \pi]$ the polar angle.

Spherical coordinate system

$$u(t, x, y, z) = u(t, r\cos(\psi)\sin(\theta), r\sin(\psi)\sin(\theta), r\cos(\theta))$$

The diffusion equation then reads

$$\frac{du}{dt} = f(u) + D\Delta_s u. \tag{49}$$

where Δ_s is the spherical Laplace operator,

$$\Delta_s = \frac{1}{r^2}\frac{\partial}{\partial r}\left(r^2\frac{\partial}{\partial r}\right) + \frac{1}{r^2\sin(\theta)}\frac{\partial}{\partial \theta}\left(\sin(\theta)\frac{\partial}{\partial \theta}\right) + \frac{1}{r^2\sin^2(\theta)}\frac{\partial^2}{\partial \psi^2}. \tag{50}$$

Axisymmetry

$$\Delta_s = \frac{1}{r^2}\frac{\partial}{\partial r}\left(r^2\frac{\partial}{\partial r}\right) + \frac{1}{r^2\sin(\theta)}\frac{\partial}{\partial\theta}\left(\sin(\theta)\frac{\partial}{\partial\theta}\right) + \frac{1}{r^2\sin^2(\theta)}\frac{\partial^2}{\partial\psi^2}.$$

In case of axisymmetry,

$$\frac{\partial}{\partial\theta} = 0 \qquad \frac{\partial}{\partial\psi} = 0$$

The spherical Laplace operator then simplifies to

similar to 1D

$$\Delta_a = \frac{\partial^2}{\partial r^2} + \frac{1}{r}\frac{\partial}{\partial r} \tag{51}$$

Transformation to travelling wave coordinates

$$u_t = u(1-u) + \frac{1}{r}u_r + u_{rr} \tag{52}$$

$\frac{\partial}{\partial r}$ $\frac{\partial^2}{\partial r^2}$

We write

$$u(r,t) = u(r-ct) = U(z), \qquad z = r - ct, \quad c \geq 0. \tag{53}$$

$$\begin{aligned} \frac{\partial u}{\partial t} &= -c\frac{du}{dz} \\ \frac{\partial u}{\partial r} &= \frac{du}{dz} \end{aligned} \tag{54}$$

but $\frac{1}{r}$ cannot be transformed.

Axisymmetric form of Fisher equation

$$u_t = u(1-u) + \frac{1}{r}u_r + u_{rr} \tag{55}$$

$\Rightarrow$ does not become an ordinary differential equation in the variable $z = r - ct$.

$\Rightarrow$ does not possess travelling wavefront solutions in which a wave spreads out with constant speed, because of the u_r/r term.

$\Rightarrow$ wavespeed $c(r)$ is a function of r: increases monotonically with r and reaches $c(r) \sim 2$ for r large.

The calcium-stimulated-calcium release mechanism

Elevated levels of Ca^{2+} in the cytoplasm stimulate further release of Ca^{2+} from the endoplasmatic reticulum (ER) and sarcoplasmatic reticulum (SR) where available.

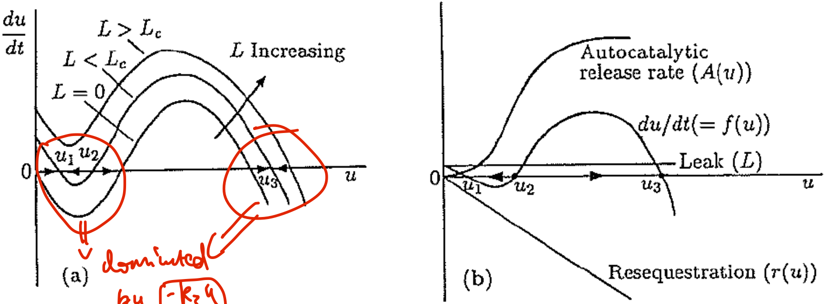
The kinetics for Ca^{2+} can therefore be described by the following phenomenological model

$$\dot{u} = A(u) - r(u) + L = f(u) \tag{56}$$

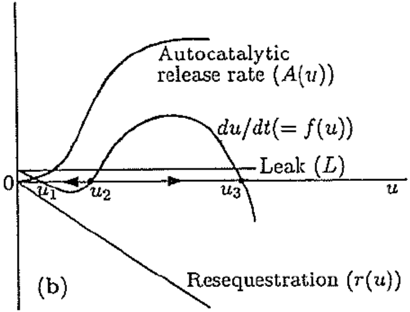
$A(u) = \frac{k_1 u^2}{k_2 + u^2}$: autocatalytic Ca^{2+} accumulation
$r(u)$: linear resequestration process
L: constant leakage flux

Graphical Analysis

$$\dot{u} = \frac{k_1 u^2}{k_2 + u^2} - k_3 u + L = f(u)$$



dominated by $\boxed{-k_3 u}$



Importantly $f(u)$ has three zeros, and in the following we will consider a simplified version, i.e.

$$f(u) = A(u - u_1)(u_2 - u)(u - u_3), \qquad u_1 < u_2 < u_3, \qquad A > 0.$$

Since Ca^{2+} can diffuse we have to consider a reaction-diffusion equation to adequately describe the Ca^{2+} kinetics and we thus have

$$\dot{u} = f(u) + D\frac{d^2u}{dx^2}. \tag{57}$$

As before we write

$$u(x,t) = u(x-ct) = U(z), \qquad z = x - ct, \quad c \geq 0. \tag{58}$$

and upon substitution into Eqn.(57)

$$DU'' + cU' + f(U) = 0 \tag{59}$$

$$DU'' + cU' + f(U) = 0 \tag{60}$$

Given the flat shape of the wave at $\pm\infty$, we need to have $U' = 0$ at $U = u_1$ and $U = u_3$.

Ansatz:

$$U' = \frac{dU}{dz} = \alpha(U - u_1)(U - u_3) \tag{61}$$

Not to calculate u_1 u_3 explicitly.

We differentiate again with respect to z and obtain

$$U'' = \frac{dU'}{dz} = \alpha(2U - u_1 - u_3) \cdot U'. \tag{62}$$

With $f(u) = A(U - u_1)(u_2 - U)(U - u_3)$ upon substitution into Eq. 60

$$\underbrace{D\alpha(2U - u_1 - u_3)U'}_{DU''} + \underbrace{c\alpha(U - u_1)(U - u_3)}_{cU'} + \underbrace{A(U - u_1)(u_2 - U)(U - u_3)}_{f(U)} = 0.$$

We factor out $(U-u_1)(U-u_3)$ and obtain

$$(U-u_1)(U-u_3)\left[D\alpha^2(2U-u_1-u_3)+c\alpha-A(U-u_2)\right]=0,$$

which we can rewrite as

$$(U-u_1)(U-u_3)\left[(2D\alpha^2-A)U-[D\alpha^2(u_1+u_3)-c\alpha-Au_2]\right]=0.$$

To be zero for all U, we require
$2D\alpha^2-A=0$ and $D\alpha^2(u_1+u_3)-c\alpha-Au_2=0$, such that

$$\alpha=\sqrt{\frac{A}{2D}},\qquad c=\sqrt{\frac{AD}{2}}(u_1-2u_2+u_3). \tag{63}$$

speed

integration cons.

If α and c satisfy Eq. 63, then we obtain as solution for Eq. 57

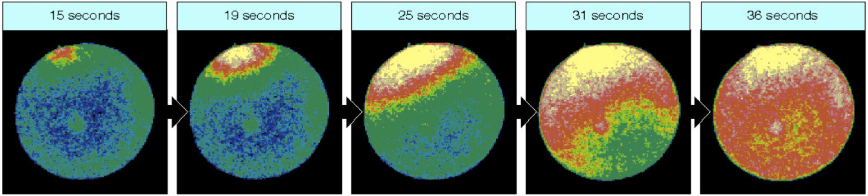
$$U(z) = \frac{u_3 + K u_1 \exp\left(\alpha(u_3 - u_1)z\right)}{1 + K \exp\left(\alpha(u_3 - u_1)z\right)} \tag{64}$$

where K is an integration constant that determines the origin in the z-plane.

Note that the sign of c depends on the reaction kinetics, i.e. on u_1, u_2, u_3.

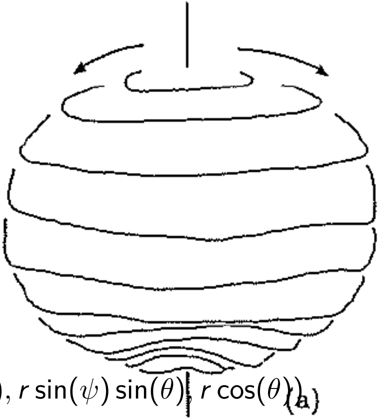
Calcium Waves on Amphibian Eggs

Models by Cheer et al (1987) and Lane et al (1987)



A number of wave-like events can be observed upon fertilization. There are for example both chemical and mechanical waves which propagate on the surface of many vertebrate eggs. These waves arise from a combination of local reactions and long-range diffusion.

Waves are on the surface of a sphere, i.e. Ca^{2+} wavefront is a ring that is propagating over the surface.



We therefore consider diffusion in 3 dimensions and use the spherical coordinate system, i.e.

$$u(t,x,y,z) = u(t, r\cos(\psi)\sin(\theta), r\sin(\psi)\sin(\theta), r\cos(\theta))$$

$\psi \in [0, 2\pi)$ the azimuthal angle, and $\theta \in [0, \pi]$ the polar angle.

The diffusion equation then reads

$$\frac{du}{dt} = f(u) + D\Delta_s u. \tag{65}$$

where Δ_s is the spherical Laplace operator,

$$\Delta_s = \frac{1}{r^2}\frac{\partial}{\partial r}(r^2\frac{\partial}{\partial r}) + \frac{1}{r^2\sin(\theta)}\frac{\partial}{\partial\theta}(\sin(\theta)\frac{\partial}{\partial\theta}) + \frac{1}{r^2\sin^2(\theta)}\frac{\partial^2}{\partial\psi^2}. \tag{66}$$

Given the inherent symmetries the spherical Laplace operator simplifies to

$$\Delta_s = \frac{1}{r^2\sin(\theta)}\frac{\partial}{\partial\theta}(\sin(\theta)\frac{\partial}{\partial\theta}) = \frac{1}{r^2}\left(\frac{\partial^2}{\partial\theta^2} + \cot(\theta)\frac{\partial}{\partial\theta}\right). \tag{67}$$

sensible

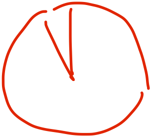
what to do ?

using 3-polynomial equation:

Cheer et al (1987) use the phenomenological description $f(u) = A(u-u_1)(u-u_2)(u-u_3)$ where A is a positive parameter to describe the excitable kinetics. At each fixed θ we obtain a wavefront solution of the form

$$u(\theta, t) = U(z), \qquad z = R\theta - ct. \tag{68}$$

?



We therefore have

$$DU'' + \left(c + \frac{D}{R}\cot(\theta)\right)U' + f(U) = 0 \tag{69}$$

This equation can be solved in the same way as Eqn.(59) as long as we set $\theta =$ const. We then obtain for the wave speed in analogy to Eqn.(63)

$$c = \sqrt{\frac{AD}{2}}(u_1 - 2u_2 + u_3) - \frac{D}{R}\cot\theta. \tag{70}$$

$$c = \sqrt{\frac{AD}{2}(u_1 - 2u_2 + u_3)} - \frac{D}{R}\cot\theta.$$

The wave speed thus increases as the wave moves from the animal pole ($\theta = 0$) to the vegetal pole ($\theta = \pi$).

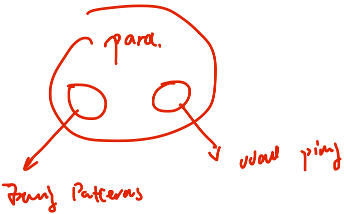
In reality calcium waves slow down as they move towards the vegetal pole. There must therefore be important cortical properties that have been neglected by the model and which prevent the speeding up tendencies for propagating waves on the surface of a sphere.

Wave Pinning

Wave Pinning

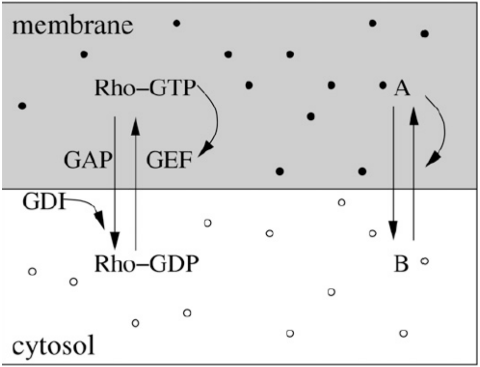
Wave Pinning

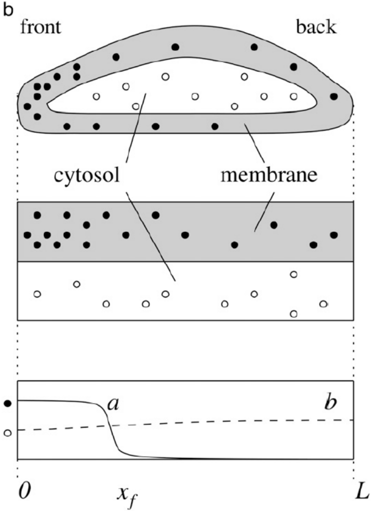
If a travelling wave eventually halts, the phenomenon is referred to as **wave pinning**.



Example: Cell Polarization

Membrane translocation cycle of a typical Rho family GTPase. The inactive cytosolic form (B) diffuses much faster than the active membrane-bound form (A) and is approximately uniformly distributed.





Mori et al. Biophys J 94, 3684-3697, (2008).

Conserved System

加多少减多少

$$\frac{\partial a}{\partial t} = D_a \frac{\partial^2 a}{\partial x^2} + f(a, b)$$
$$\frac{\partial b}{\partial t} = D_b \frac{\partial^2 a}{\partial x^2} - f(a, b)$$

with $Db \gg D_a$ and $f(a, b)$ leading to bistability (at least two stable steady states (a_-, b_-), (a_+, b_+)), e.g.

$$f(a, b) = b\left(k_0 + \frac{\gamma a^2}{K^2 + a^2}\right) - \delta a$$

For details, see Mori, Y., Jilkine, A. & Edelstein-Keshet, L. Wave-pinning and cell polarity from a bistable reaction-diffusion system. Biophys J 94, 3684-3697, doi:10.1529/biophysj.107.120824 (2008).

Single Variable Case (fixed b)

$$\frac{\partial a}{\partial t} = D_a \frac{\partial^2 a}{\partial x^2} + f(a, b)$$

with $f(a, b)$ leading to bistability (at least two stable steady states $(a_-,\ a_+)$.

Suppose a develops a propagating front on $0 < x < L$, sufficiently far from the boundaries. Then we can approximate a region of validity by $-\infty < z < \infty$. Let

$$A(z) = A(x - ct) = a(x, t).$$

$$A'' + cA' + f(a, b) = 0$$

Wave Speed

$$A'' + cA' + f(a,b) = 0$$

Multiply by A' and integrate from $-\infty$ to ∞

bounded => zero at -/+ ∞

$$\int_{-\infty}^{\infty} A'(A'' + cA' + f(a,b))dz = 0$$

Since $A'(\pm\infty) = 0$ (flat part of wave) and $A(-\infty) = a_-$ and $A(\infty) = a_+$, this integrates to give

steady state at "bound"

$$c\int_{-\infty}^{\infty} [A']^2 dz = -\int_{-\infty}^{\infty} f(a,b)A'dz = -\int_{a_-}^{a_+} f(a,b)dA$$

$$c = \frac{\int_{a-}^{a+} f(a,b)da}{\int_{-\infty}^{\infty} \left(\frac{\partial A}{\partial z}\right)^2 dz}$$

Wave Speed

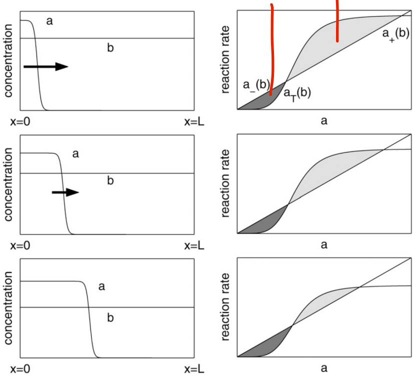
Wave Speed

$$c(b) = \frac{\int_{a-}^{a+} f(a,b)da}{\int_{-\infty}^{\infty} \left(\frac{\partial A}{\partial z}\right)^2 dz}$$

The denominator is always positive, while the numerator changes sign dependent on b.

Conditions for Wave Pinning

what are those compartments ?



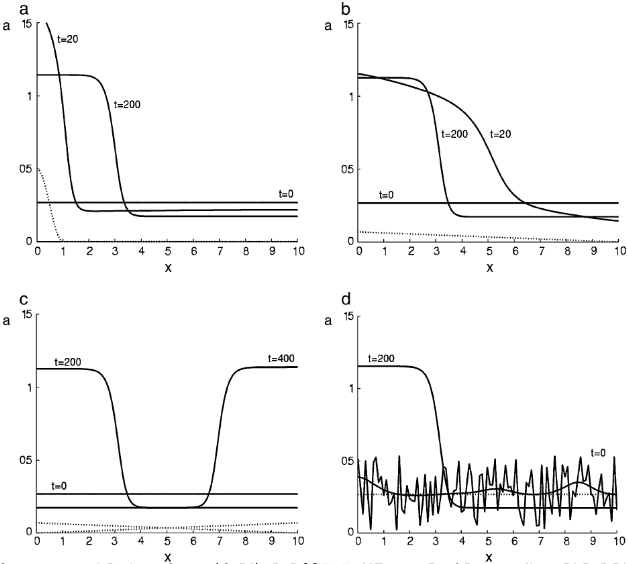
Mori, Y., Jilkine, A. & Edelstein-Keshet, L. Biophys J 94, 3684-3697, (2008).

- At least two stable steady states for $b_{min} < b < b_{max}$
- $\int_{a-}^{a+} f(a,b)da$ changes sign at $b = b_c$

$$c(b) = \frac{\int_{a-}^{a+} f(a,b)da}{\int_{-\infty}^{\infty} \left(\frac{\partial A}{\partial z}\right)^2 dz}$$

Pattern formation much faster than by diffusion (Turing Pattern)!!

Example for Wave Pinning



Dashed line: initial conditions

Mori, Y., Jilkine, A. & Edelstein-Keshet, L. Biophys J 94, 3684-3697, (2008).

Thanks!!

Thanks for your attention!

Slides for this talk will be available at:
`http://www.bsse.ethz.ch/cobi/education`