Pattern formation in biological systems

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Pattern formation

The study of pattern formation deals with the visible, orderly outcomes of self-organization and the common principle behind similar patterns

Examples

- Animal markings (zebra);
- Phyllotaxis (the arrangement of the leaves on the stem of a plant, etc.); (2 pics on-line)
- Bacterial colonies growth; (2 pics on-line)
- ...

Analysis

- find a model PDE of the form

$$\frac{\partial \psi}{\partial t} = N(\psi, t),$$

where $N(\psi, t)$ is nonlinear differential operator;

- search for solution in the form

$$\psi = \sum_{j=1}^{m} A_j(t) \exp i[\vec{k}_j \vec{x} - \omega_j t], \quad A_j \neq \text{const}_j;$$

- reduce an initial nonlinear PDE to a system of nonlinear ODEs (ordinary differential equations) with variables $A_j(t)$;
- study the system of nonlinear ODEs by standard methods of the theory of dynamical systems and establish the conditions of regular and chaotic behaviour.

Example: Swift-Hohenberg Equation

Swift-Hohenberg equation has the form

$$\psi_t = \varepsilon\psi - (\nabla^2 + 1)^2\psi + g_1\psi^2 - \psi^3$$

and describes pattern formation under the convective heat transport (e.g. growth of algae on the surface of a lake depends on the air temperature which is changing according to the day time).

Two movies on-line

Basic Notions about PDEs

Given:

$$a\frac{\partial^2\psi}{\partial x^2} + b\frac{\partial^2\psi}{\partial x\partial y} + c\frac{\partial^2\psi}{\partial y^2} + d\frac{\partial\psi}{\partial x} + e\frac{\partial\psi}{\partial y} + f\psi = g$$

Definitions:

- a, b, c, d, e, f, g do not depend on $\psi \Rightarrow$ *linear* PDE, example:

$$\frac{\partial^2\psi}{\partial x^2} + 4e^x\frac{\partial\psi}{\partial y} = y^2$$

- a, b, c, d, e, f, g depend on $\psi \Rightarrow$ *nonlinear* PDE, example:

$$\frac{\partial^2\psi}{\partial x^2} - \frac{\partial^2\psi}{\partial y^2} = \psi^3$$

Mathematical Classification of PDEs based on the FORM of EQUATIONS

Method of Characteristics:

$$a\frac{\partial^2\psi}{\partial x^2} + b\frac{\partial^2\psi}{\partial x\partial y} + c\frac{\partial^2\psi}{\partial y^2} = F(x, y, \psi, \frac{\partial\psi}{\partial x}, \frac{\partial\psi}{\partial y}) \Rightarrow$$

$$\frac{\mathbf{d}x}{\mathbf{d}y} = \frac{b}{2a} \pm \frac{1}{2a}\sqrt{b^2 - 4ac}$$

Three Types of PDEs:

- $b^2 < 4ac$, elliptic PDE: $\psi_{xx} + \psi_{yy} = 0$
- $b^2 > 4ac$, hyperbolic PDE: $\psi_{xx} - \psi_{yy} - x\psi_x = 0$
- $b^2 = 4ac$, parabolic PDE: $\psi_{xx} - 2xy\psi_y - \psi = 0$
- "Bad" example - Tricomi equation: $y\psi_{xx} + \psi_{yy} = 0$

Each type of PDE demands special type of initial/boundary conditions for the problem to be well-posed.

The problem is well-posed if:

- the problem has exactly one solution for given initial/boundary conditions (uniqueness)
- a small change in initial/boundary conditions produces a small change in the solution (stability)

If a problem is not well-posed, its solution is useless for applications:

- there exists more than one solution $\Rightarrow$ a model has no predictive power
- the solution is unique but small changes in data lead to big changes in the solution $\Rightarrow$ a model has no predictive power (measurement error)

Common types of boundary/initial conditions:

- Dirichlet conditions: the function ψ is given on the boundary.
- Neumann conditions: when we specify the normal derivative $(\nabla\psi)_n = \frac{\partial\psi}{\partial x}$.
- Robin (mixed) conditions: a combination of ψ and $(\nabla\psi)_n$ are given.
- Cauchy (initial) conditions: ψ and $\frac{\partial\psi}{\partial t}$ are given at some initial value of t.

Example of an ill-posed problem:

Let us consider equation

$$\frac{\partial^2 \psi}{\partial t^2} = \frac{\partial^2 \psi}{\partial x^2}$$

with Dirichlet type boundary conditions

$$\psi(0, t) = 0, \quad \psi(\pi, t) = 0,$$

and

$$\psi(x, 0) = 0, \quad \psi(x, \pi) = 0.$$

Looking for solutions of the form $\psi(x, t) = X(x)T(t)$ we find that any function of the form

$$\psi(x, t) = A \sin(nx) \sin(nt)$$

with integer n gives a solution. Thus there are infinitely many solutions to the problem! It is ill-posed.

Equation type + boundary/initial conditions

- parabolic: One initial (Cauchy)+ some boundary condition(s). **Heat conduction:**
  $$\triangle\psi = \alpha^{-1}\psi_t,$$
  α is heat conductivity.
- elliptic: Dirichlet/Neumann/Robin. **Laplace equation:**
  $$\nabla^2\psi = 0,$$
  (note that operator $\nabla^2\psi$ is commonly written as $\triangle$ in pure mathematical texts)
- hyperbolic: One initial (Cauchy) + some boundary condition(s), **Wave equation:**
  $$\triangle\psi = c^{-2}\psi^2_{tt},$$
  in acoustics c is sound speed, in electrodynamics of varying fields c is light speed, etc.

Physical Classification of PDEs, based on the FORM of SOLUTIONS

Zero Step: Two Types of Variables

Time variable t and
space variable x or $\vec{x} = (x_1, ..., x_n)$
PDE is then said to be of **(1+1)-order** or **(1+n)-order**.

First Step: Linear PDE, constant coefficients, arbitrary order

Suppose that this LPDE has a wave-like solution (Fourier harmonic)

$$\psi(x, t) = A \exp i(kx - \omega t)$$

with amplitude A, wave-number k and wave frequency ω.

How to compute frequency (I)

Let us regard a linear PDE

$$\psi_{tt} + \alpha^2 \psi_{xxxx} = 0$$

and make some preliminary calculations:

$$\psi_t = \frac{\partial}{\partial t}\psi = \omega(-i)A \exp i(kx - \omega t),$$

$$\psi_{tt} = \frac{\partial}{\partial t}(\frac{\partial}{\partial t}\psi) = (\omega(-i))^2 A \exp i(kx - \omega t) = -\omega^2 A \exp i(kx - \omega t),$$

$$\psi_x = \frac{\partial}{\partial x}\psi = kiA \exp i(kx - \omega t),$$

$$\dots\dots\dots,$$

$$\psi_{xxxx} = \frac{\partial^4}{\partial x^4}\psi = (ki)^4 A \exp i(kx - \omega t) = k^4 A \exp i(kx - \omega t).$$

How to compute frequency (II)

After substituting these results into initial PDE one gets:

$$0 = \psi_{tt} + \alpha^2 \psi_{xxxx} =$$
$$= -\omega^2 A \exp i(kx - \omega t) + \alpha^2 k^4 A \exp i(kx - \omega t),$$

which leads to the equation for frequency $\omega(k) = \pm\alpha k^2$.

Definiton of dispersion

Dependence frequency on wave vector, $\omega = \omega(k)$, is called **dispersion function** (or dispersion relation, or just dispersion) if ω is real-valued function $\quad \omega = \omega(k): \quad \mathrm{d}^2\omega/\mathrm{d}k^2 \neq 0 \quad$.

General form of dispersion function

Substitution of $\partial_t = -i\omega, \quad \partial_x = ik$ into LPDE transforms it into a **POLYNOMIAL** on ω and k.

Examples

$$\psi_t + \alpha\psi_x + \beta\psi_{xxx} = 0 \quad \Rightarrow \; \omega(k) = \alpha k - \beta k^3$$

$$\psi_{tt} + \alpha^2\phi_{xxxx} = 0 \quad \Rightarrow \; \omega^2(k) = \alpha^2 k^4$$

$$\psi_{tttt} - \alpha^2\psi_{xx} + \beta^2\psi = 0 \quad \Rightarrow \; \omega^4(k) = \alpha^2 k^2 + \beta^2$$

Definitions

- A linear PDE with wave-like solutions are called **evolutionary dispersive** LPDE
- A nonlinear PDE with dispersive linear part are called **evolutionary dispersive** NPDE.

Summary

- We have constructed a one-to-one correspondence between linear (evolution) PDE $L(\psi) = 0$ of arbitrary order allowing a wave solution $\psi(\vec{x}) = A \exp i(\vec{k}\vec{x} - \omega t)$ and some polynomial P which defines dispersion function $\omega = \omega(\vec{k})$.
- In case of several space variables we have a polynomial $P(\frac{\partial}{\partial t}, \frac{\partial}{\partial x_1}, ..., \frac{\partial}{\partial x_n}) = 0$ and condition of non-zero second derivative of the dispersion function takes a matrix form:

$$\left|\frac{\partial^2 \omega}{\partial k_i \partial k_j}\right| \neq 0.$$

  The number of variables of dispersion function ω coincides with the number of space variables of the initial PDE.
- Given dispersion function allows us to re-construct the corresponding linear PDE.

Dispersive and non-dispersive PDEs

- Partitioning of all evolutionary PDEs into two classes - dispersive and non-dispersive is constructed.
- This partition is not complementary to a standard mathematical one:
  (a) most hyperbolic PDEs do not have dispersive wave solutions but hyperbolic equation $\psi_{tt} - \alpha^2 \bigtriangledown^2 \psi + \beta^2 \psi = 0$ has them.
  (b) equation $\psi_{tt} + \alpha^2 \phi_{xxxx} = 0$ can not be classified as hyperbolic, parabolic or elliptic but belongs to the class of dispersive PDEs.
- In this way PDEs are able to generate only *polynomial* dispersion relations. In some cases a PDE with special initial/boundary conditions may generate a transcendental dispersion function such like

$$\omega(k) = k \tanh \alpha k.$$

Famous evolutionary dispersive NPDEs

- Swift-Hohenberg Equation: $\psi_t = \varepsilon\psi - (\nabla^2 + 1)^2\psi + g_1\psi^2 - \psi^3$
- Boussinesq Equation: $\psi_{tt} + (\psi_{xx} + \psi^2)_{xx} = 0$
- Korteweg-de Vries Equation (KdV): $\psi_t + \psi_{xxx} - 6\psi\psi_x = 0$
- Kadomtsev-Petviashvili Equation (KP): $(\psi_t + 6\psi\psi_x + \psi_{xxx})_x + 3\psi_{yy} = 0$
- Schrödinger Equation: $i\psi_t + \psi_{xx} + f(|\psi|)\psi = 0$
- Zakharov System of Equations:

$$i\psi_t + \psi_{xx} - \psi\varphi = 0, \quad \varphi_{tt} - \varphi_{xx} - |\psi|^2_{xx} = 0$$

- .... (many!)

Linear PDE $L(\phi) = 0$: superposition principe

If $A_j \exp i[\vec{k}_j\vec{x} - \omega_j t]$, $\quad \jmath = 1, 2, .., n$ are solutions of $L(\phi) = 0$, than

$$\sum_{j=1}^{m} A_j \exp i[\vec{k}_j\vec{x} - \omega_j t], \quad A_j = \mathrm{const}_j,$$

is also solution of $L(\phi) = 0$ (with notation $\omega(\vec{k}_j) = \omega_j$)

Nonlinear PDE $L(\psi) + N(\psi) = 0$: Generalized Poincare theorem

A nonlinear PDE $L(\psi) + N(\psi) = 0$ **can be linearized** if the algebraic equation

$$p_1\omega_1 + p_2\omega_2 + \cdots + p_m\omega_m = 0, \quad p_1, p_2, .., p_m \in \mathbb{Z}. \tag{1}$$

has no solutions. This is **algebraic equation**.

Resonance conditions

Equations

$$p_1\omega_1 + p_2\omega_2 + \cdots + p_m\omega_m = 0, \tag{2}$$

$$p_1\vec{k}_1 + p_2\vec{k}_2 + \cdots + p_m\vec{k}_m = 0, \tag{3}$$

with $p_1, p_2, .., p_m \in \mathbb{Z}$. Eqs.(2) are called **resonance conditions**.

Examples

Usually in applications (biological, medical, physical) we have often

$$\begin{cases} \omega_1 + \omega_2 = \omega_3, \\ \vec{k}_1 + \vec{k}_2 = \vec{k}_3, \end{cases} \quad \text{or} \quad \begin{cases} \omega_1 + \omega_2 = \omega_3 + \omega_4, \\ \vec{k}_1 + \vec{k}_2 = \vec{k}_3 + \vec{k}_4, \end{cases} \tag{4}$$

with $\vec{k}_j = (m_j, n_j), \quad m_j, n_j \in \mathbb{Z}$ and
$\omega \sim (m^2+n^2)^{1/4}, \quad (m^2+n^2)^{3/4}, \quad \frac{m}{n^2+m^2+1}, \quad (m^2+n^2)^{-1/2}, \ldots.$

Next lecture

In the next lecture we will learn some general methods for finding integer solutions of resonance conditions (4).

Control questions

- Is Fourier harmonic $A \exp i(\vec{k}\vec{x} - \omega t)$ with constant A a solution of linear or nonlinear PDE?
- Does the superposition principle work for linear or nonlinear PDEs?
- Are the coefficients of evolutionary dispersive nonlinear PDE constant or not?
- Do we need linear or nonlinear PDE to compute dispersion function?
- Is dispersion ω a function of integer or real variables?
- How many scalar equations we need to describe resonance conditions (4)?