

8 Spatiotemporal patterns (Murray: Ch. 12.1; Murray II: Ch. 1.8-1.9)

In Lecture 6 we saw that a **one-dimensional reaction diffusion equation may show wave-like solutions**. The reaction-diffusion equation for two coupled concentrations $n_1(\mathbf{x}, t)$ and $n_2(\mathbf{x}, t)$, reaction terms f_1 and f_2 , and diffusion constants D_1 and D_2

$$\begin{aligned}\frac{\partial n_1}{\partial t} &= f_1(n_1, n_2, \mathbf{x}, t) + D_1 \nabla^2 n_1 \\ \frac{\partial n_2}{\partial t} &= f_2(n_1, n_2, \mathbf{x}, t) + D_2 \nabla^2 n_2\end{aligned}, \quad (1)$$

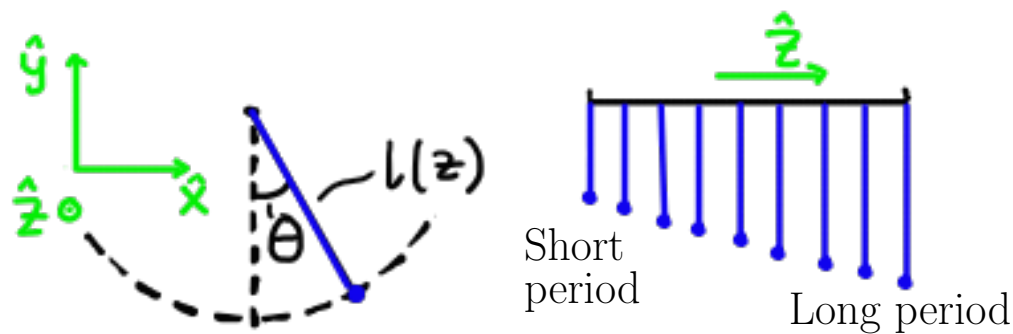
often has even more intricate dynamics. As seen in the last lecture, it allows for spontaneous formation of stationary patterns via the diffusion-driven instability. In this lecture we will consider **formation of spatiotemporal patterns in the form of spiral waves**.

8.1 Waves in uncoupled oscillators (M 12.1)

As a simplest example of a mechanism for spatio-temporal wave formation of the concentrations n_1 and n_2 in Eq. (1), consider a case where diffusion is negligible ($D_1 = D_2 = 0$) and where f_1 and f_2 depend explicitly on a single spatial coordinate z . At each value of z , the system has an independent growth equation. A simple example from mechanics is obtained by denoting $n_1 = \theta$, $n_2 = \omega$ and letting $f_1 = \omega$, $f_2 = -\frac{g}{l(z)}\theta$ (g is gravitational acceleration):

$$\frac{\partial \theta}{\partial t} = \omega, \quad \frac{\partial \omega}{\partial t} = -\frac{g}{l(z)}\theta. \quad (2)$$

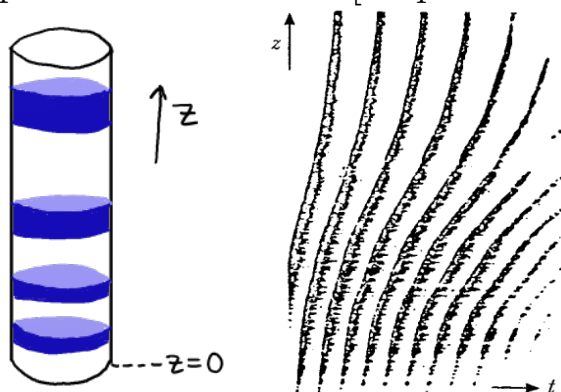
For each value of z these equations describe the angular motion of a simple pendulum of length $l(z)$.



By choosing $l(z)$ appropriately, this system shows wave patterns. Similar behaviour is observed in spatial distributions of biological (limit-cycle) oscillators. These oscillators are often coupled to some degree, a case we will consider in a later lecture. **An example of a system consisting of uncoupled oscillators is given by the Belousov-Zhabotinsky reaction**, which we study in detail below.

8.1.1 Example: Belousov-Zhabotinsky reaction

The BZ reaction was introduced in Lecture 4. It is a chemical oscillator: the ratio of concentrations of the reactants oscillates (in contrast to the spatial angular coordinate in the pendulum above). Adding an appropriate dye allows for visualization of the concentration of one of the reactants. If stirred, the color of the entire sample periodically changes due to oscillations in the concentration of the reactant. If instead left unstirred in a vertical cylinder, spatial patterns form: coloured bands form at the bottom of the cylinder, and rise slowly to eventually fill the cylinder with non-homogeneously distributed bands. Illustration of band positions after some time (left) and experimental space-time dependence of bands [Kopell and Howard (1973)] (right):



[Right panel from Fig. 12.1b in Murray, *Mathematical Biology I* (2003)]

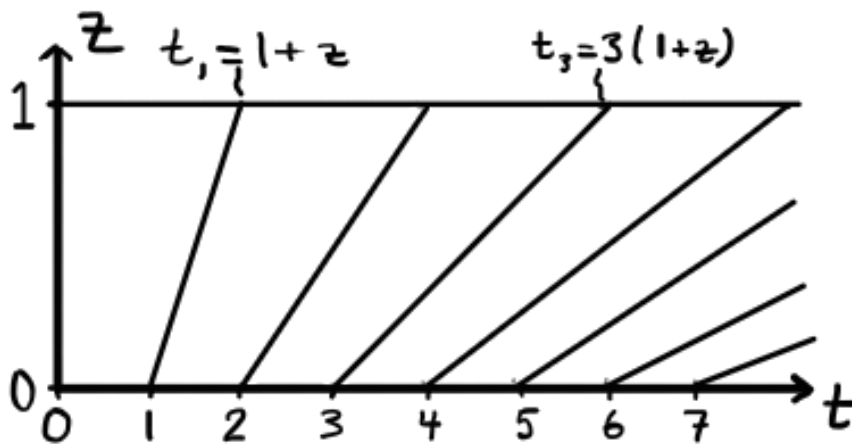
Model: Let each position z in the cylinder be an independent chemical oscillator (undergoing the Belousov-Zhabotinsky reaction) with period time T that depends on z (for instance due to temperature variation, or a concentration gradient in one of the chemicals in the z -direction).

Use the **phase of oscillation** $\phi(z, t)$ to characterise the state of each oscillator. An oscillator of period time T forms a closed periodic orbit γ in phase space (the space of chemical concentrations n_1, n_2). Assuming an initial coordinate $(n_1(0), n_2(0))$ on γ when $t = 0$, all succeeding points $(n_1(t), n_2(t))$ on γ can be parameterized by t . Use the phase $\phi(z, t) = \phi_0(z) + 2\pi t/T(z)$ to parameterize the state of the oscillator at z . $\phi(z, t)$ increases with 2π as t increases by a multiple of the period time $T(z)$:

$$\phi(z, t + nT(z)) = 2\pi n + \phi(z, t),$$

with integer n . To understand the structure of bands, introduce **wave fronts**: Regions of constant phase (points in this one-dimensional case).

As an explicit example, assume initial phase $\phi_0(z) = 0$, and $T(z) = 1 + z$. At times $t_n = nT(z) = n(1 + z)$ the n :th wave front (the wave front with $\phi = 2\pi n$) reaches the height $z = 1$ in the cylinder:



- The oscillator at $z = 0$ is in phase (returns to the original concentration) every time unit [$T(z=0)=1$], the oscillator at $z = 1$ is in phase every second time unit [$T(z = 1) = 2$].
- The speed $v_n(z)$ at which the n :th wave front move is given by

the slopes of the lines in the figure above:

$$v_n(z) \equiv \left[\frac{dz}{dt} \right]_{\phi=2\pi n} = \frac{1}{n}.$$

- For fixed t there will be more and more bands in the cylinder the larger t is, and the bands are denser at small z . This essentially explains the observed pattern in the experiment.

This is an example of purely kinematic pattern formation (diffusion, convection etc. are negligible). Nothing actually moves, it is just the relative phases that varies. In contrast, in systems with coupled oscillators the phase and frequency of individual oscillators may change due to the interaction. Such systems often exhibit synchronisation (next lecture).

8.2 Spiral waves (MII 1.8)

In addition to travelling waves and the kinematic waves above, reaction-diffusion equations in higher dimensions can show spiral waves. These occur naturally in many biological, physiological and chemical systems, some examples are:

1. Beluosov-Zhabotinski reaction
2. Neural activity in brain
3. Electrical impulses in heart
4. Signalling patterns of slime mould

Example: Spiral wave in concentration in a BZ reaction



- For a fixed time, contour lines of concentration form a spiral.
- As time goes, the spiral is rotating.
- Curves of constant concentration (phase) describe wave-fronts of the wave.

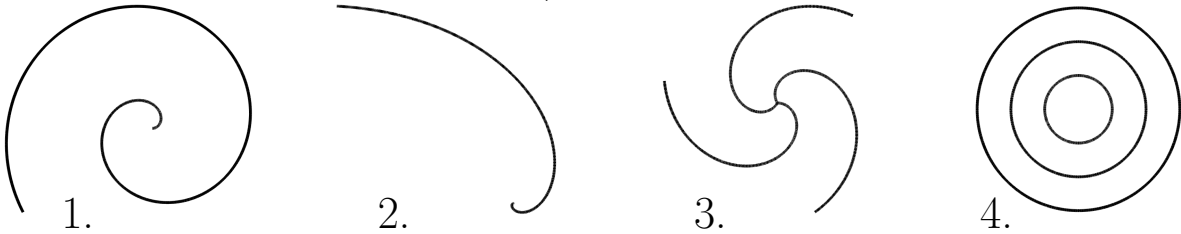
8.2.1 Simple rotating spiral

It is natural to describe a rotating spiral in two spatial dimensions by polar coordinates r , θ at time t . The phase ϕ of a simple rotating spiral is

$$\phi(r, \theta, t) = \frac{2\pi t}{T} + \underbrace{\psi(r) \pm m\theta}_{\phi_0(r, \theta)} \quad (3)$$

with constant angular frequency $\Omega = 2\pi/T$ (change sign of first term to change direction of rotation), radial dependence $\Psi(r)$, number of arms m , and \pm in front of m decides chirality of the spiral. Analogous to the patterns in Section 8.1, regions of constant phase describe wave fronts of the spiral wave (one-dimensional curves here).

A concentration showing a simple rotating spiral can be written as $n(r, \theta, t) = F(\phi)$, where F is a 2π -periodic function. The following examples show lines of constant concentration (wave fronts) at $t = 0$ (curves show $\phi = 0, 2\pi, 4\pi, \dots$):



1. **Archimedian spiral** $\psi \propto r$, $m = 1$, ‘ $-$ ’ sign in Eq. (3)
2. **Logarithmic spiral** $\psi \propto \ln r$, $m = 1$, ‘ $-$ ’ sign in Eq. (3)
3. **3-armed Archimedian spiral** $\psi \propto r$, $m = 3$, ‘ $+$ ’ sign in (3)
4. **Target pattern** $\psi \propto r$, $m = 0$

Some observations:

- For fixed r and t , the spiral has an m -fold symmetry
- For fixed (r, θ) , a wave front passes through every $\frac{T}{m}$ time unit.

8.2.2 Spiral waves in oscillatory reaction systems (MII 1.9)

In the previous section a mathematical description of wave fronts of spiral waves was introduced. This description in terms of a phase $\phi(r, \theta, t) = \Omega t \pm m\theta + \psi(r)$ can be used to search for spiral waves in reaction-diffusion equations in two spatial dimensions, similar to how we used the wave variable $z = x - ct$ to search for travelling waves in reaction diffusion equations in one spatial dimension. An example of a reaction diffusion equation for two concentrations n_1 and n_2 allowing spiral-wave solutions is the ‘ λ - ω reaction system’

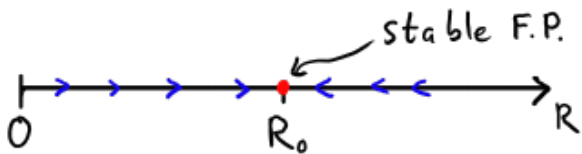
$$\frac{\partial}{\partial t} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix} = \begin{pmatrix} \lambda(R) & -\omega(R) \\ \omega(R) & \lambda(R) \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix} + D \nabla^2 \begin{pmatrix} n_1 \\ n_2 \end{pmatrix}$$

with $R = \sqrt{n_1^2 + n_2^2}$ and λ, ω are real functions of R .

Homogeneous solutions (n_1 and n_2 independent of the spatial coordinates) to this system often show oscillations. To see this, transform the concentrations (n_1, n_2) to polar coordinates $n_1 = R \cos \phi$, $n_2 = R \sin \phi$

$$\begin{aligned} \frac{\partial R}{\partial t} &= \frac{n_1 \frac{\partial n_1}{\partial t} + n_2 \frac{\partial n_2}{\partial t}}{R} = \lambda(R)R + D(\nabla^2 R - R|\nabla \phi|^2) \\ \frac{\partial \phi}{\partial t} &= \frac{n_1 \frac{\partial n_2}{\partial t} - n_2 \frac{\partial n_1}{\partial t}}{R^2} = \omega(R) + D \left(\frac{2}{R} \nabla R \cdot \nabla \phi + \nabla^2 \phi \right) \end{aligned} \quad (4)$$

In the homogeneous case ($D \rightarrow 0$), the n_1 - n_2 -system has a limit-cycle if $\lambda(R)R$ has a stable steady state at some $R = R_0$



The limit-cycle oscillator has phase $\phi(\mathbf{x}, t) = \phi_0(\mathbf{x}) + \omega(R_0)t$.

Adding diffusion, the system allows for travelling plane wave solutions along the x -axis on the form $R = \alpha = \text{const.}$ and $\phi = \omega(\alpha)t - \sqrt{\lambda(\alpha)/D}x$ (follows by insertion into Eq. (4)). The stability of these travelling wave solutions depends on the form of λ and ω and analysis is in general non-trivial.

Adding diffusion may also allow for spiral wave solutions. Search for rotating spirals on the form

$$\begin{aligned} R(r, \theta, t) &= f(r) \\ \phi(r, \theta, t) &= \Omega t + m\theta + \psi(r) \end{aligned}$$

with spatial polar coordinates $x = r \cos \theta$, $y = r \sin \theta$ (the angular coordinate in n_1 - n_2 -space is the phase ϕ) and with suitable boundary conditions. Using numerical solutions of the resulting partial differential equations, rotating spirals have been found for different choices of $\lambda(R)$ and $\omega(R)$, one simple example being $\lambda(R) = 1 - R^2$ and $\omega(R) = -\beta R^2$ with $\beta > 0$ showing 1-armed or 2-armed spirals when $\beta = 1$ (Kuramoto & Koga 1981). For higher values of β the wave fronts become chaotic.

Spiral waves are also observed in many reaction-diffusion models that are not on the form of the λ - ω reaction system above. See for example the work of Dwight Barkley or the classification of the Gray-Scott model.