# The glycolytic oscillator

- without spatial diffusion
- with spatial diffusion — in 1D, in 2D

[problems 7.19 and 11.15c in EK with extras]
For a description of this biochemical reaction, see page 304 in EK.

Model for: substrates $\longrightarrow$ F6P $\to \ldots \to$ ADP $\to$ products
F6P: $f(t)$, ADP: $g(t)$

f and g functions of time t only in first model:

$$\begin{cases} \dfrac{df}{dt} = \delta - kf - fg^2 \\ \dfrac{dg}{dt} = kf + fg^2 - g \end{cases}$$

$\delta > 0,\ k > 0$ constants

Analyze this system!

Steady states

$$\begin{cases} \delta - k\bar{f} - \bar{f}\bar{g}^2 = 0 \\ k\bar{f} + \bar{f}\bar{g}^2 - \bar{g} = 0 \end{cases} \quad \text{add} \Rightarrow \delta - \bar{g} = 0 \Rightarrow \bar{g} = \delta \text{ and } \bar{f} = \frac{\delta}{k+\bar{g}^2} = \frac{\delta}{k+\delta^2}$$

$\Rightarrow (\bar{f},\bar{g}) = \left(\frac{\delta}{k+\delta^2}, \delta\right)$ is the only steady state.

Stable? Jacobian:

$$J(f,g) = \begin{pmatrix} -k-g^2 & -2fg \\ k+g^2 & 2fg-1 \end{pmatrix} \Rightarrow J(\bar{f},\bar{g}) = \begin{pmatrix} -k-\delta^2 & -\frac{2\delta^2}{k+\delta^2} \\ k+\delta^2 & \underbrace{\frac{2\delta^2}{k+\delta^2} - 1}_{=\frac{\delta^2-k}{k+\delta^2}} \end{pmatrix} = J$$

$$\det J = (k-\delta^2) + 2\delta^2 = k + \delta^2 > 0$$

$$\operatorname{Tr} J = -(k+\delta^2) + \frac{\delta^2-k}{k+\delta^2} = \frac{-(k+\delta^2)^2 + \delta^2 - k}{k+\delta^2} < 0 \text{ if } \delta^4 + 2k\delta^2 + k^2 - \delta^2 + k > 0$$

$$\Longleftrightarrow \left(\delta^2 + k - \tfrac{1}{2}\right)^2 > \tfrac{1}{4} - 2k, \text{ condition for stability}$$

always satisfied if $k > \frac{1}{8}$

Signs of J: $J \sim \begin{pmatrix} - & - \\ + & \frac{\delta^2-k}{k+\delta^2} \end{pmatrix} \Rightarrow$ positive feedback (to g) if $\delta^2 > k$.

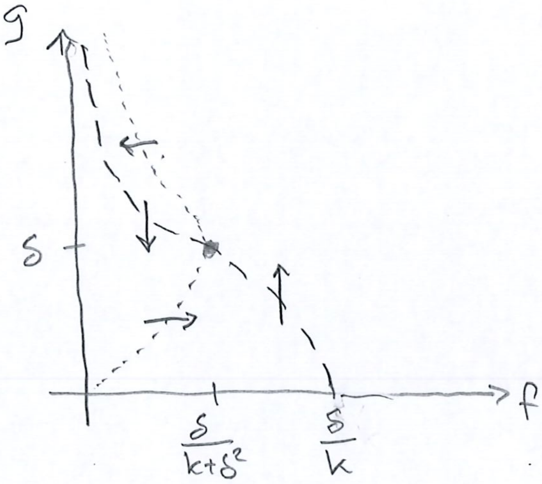
Phase space

f-nullcline $f = \frac{\delta}{k+g^2}$ ---

g-nullcline $f = \frac{g}{k+g^2}$ ......

See plots for

1. $\delta^2 = \frac{3}{4}, k = \frac{1}{4}$ (stable)
2. $\delta^2 = \frac{3}{8}, k = \frac{1}{8} \Rightarrow \operatorname{Tr} J = 0$
   oscillating values

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Now, add diffusion, first 1D

The functions are $f(t,x)$ and $g(t,x)$, and the system

$$\begin{cases} f_t = \delta - kf - fg^2 + D_1 f_{xx} \\ g_t = kf + fg^2 - g + D_2 g_{xx} \end{cases}$$

The spatially uniform steady state is $(\bar{f}, \bar{g}) = \left(\frac{\delta}{k+\delta^2}, \delta\right)$, which is stable for $D_1 = D_2 = 0$ if $(\delta^2 + k - \frac{1}{2})^2 > \frac{1}{4} - k$.

We have diffusive instabilities if $(D_1 > 0, D_2 > 0)$

$$a_{11} D_2 + a_{22} D_1 > 2\sqrt{D_1 D_2 \det A} \quad \text{, where } A = J(\bar{f}, \bar{g}) \Rightarrow$$

$$-(k+\delta^2) D_2 + \frac{\delta^2 - k}{k+\delta^2} D_1 > 2\sqrt{D_1 D_2 (k+\delta^2)} \quad (*)$$ Condition for diffusive instability.

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Difficult to simplify but $\delta^2 > k$ is necessary to satisfy (*).

Take $\delta^2 = \frac{3}{4}, k = \frac{1}{4} \Rightarrow$ stable if $D_1 = D_2 = 0$.

We get $A = \begin{pmatrix} -1 & -3/2 \\ 1 & 1/2 \end{pmatrix} \Rightarrow \det A = 1$ and $\operatorname{Tr} A = -\frac{1}{2}$, (*) becomes

$$-D_2 + \frac{1}{2} D_1 > 2\sqrt{D_1 D_2} \Rightarrow \frac{D_1}{D_2} - 2 > 4\sqrt{\frac{D_1}{D_2}}$$

$\left( x - 2 = 4\sqrt{x} \Rightarrow (x-2)^2 = 16x \Rightarrow x^2 - 20x + 4 = 0 \Rightarrow x = 10 \pm \sqrt{96} \approx 19.8 \right)$

$\Rightarrow \frac{D_1}{D_2} > 19.8$ gives diffusive instability

(note that here $a_{11} < 0, a_{22} > 0 \Rightarrow D_1 > D_2$)

Take $D_1 = 1$, $D_2 = 0.05$ $\Rightarrow$ $\frac{D_1}{D_2} = 20 > 19.8$

With $0 < x < L_x$ and no-flux BC, there are unstable modes $e^{\sigma t} \cos \frac{m\pi x}{L_x}$ (with $\sigma > 0$) if

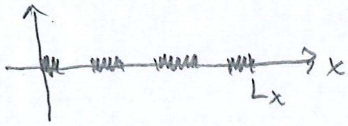
$$q_m^2 - \Delta < \frac{m^2 \pi^2}{L_x^2} < q_m^2 + \Delta \quad , \quad q_m^2 = \frac{a_{11} D_2 + a_{22} D_1}{2 D_1 D_2} = \frac{-0.05 + 0.5}{0.1} = 4.5$$

$$\Delta = \sqrt{q_m^4 - \frac{\det A}{D_1 D_2}} = \sqrt{4.5^2 - 20} = 0.5$$

$$\Rightarrow 4 < \frac{m^2 \pi^2}{L_x^2} < 5$$

Take $L_x = 2\sqrt{2}\pi$ for a simple value $\Rightarrow 4 < \frac{m^2}{8} < 5 \Rightarrow 32 < m^2 < 40$

$\Rightarrow m = 6$ only value, 1D pattern




$\cos \frac{6\pi x}{2\sqrt{2}\pi}$

Diffusion in 2 spacedimensions

Functions $f(t,x,y)$ and $g(t,x,y)$.

System $\begin{cases} f_t = \delta - kf - fg^2 + D_1 (f_{xx} + f_{yy}) \\ g_t = kf + fg^2 - g + D_2 (g_{xx} + g_{yy}) \end{cases}$

With $0 < x < L_x$, $0 < y < L_y$, and no-flux BC, unstable modes $e^{\sigma t} \cos \frac{m\pi x}{L_x} \cos \frac{n\pi y}{L_y}$, appear if

$$Q_m^2 - \Delta < \left(\frac{m^2}{L_x^2} + \frac{n^2}{L_y^2}\right)\pi^2 < Q_m^2 + \Delta$$

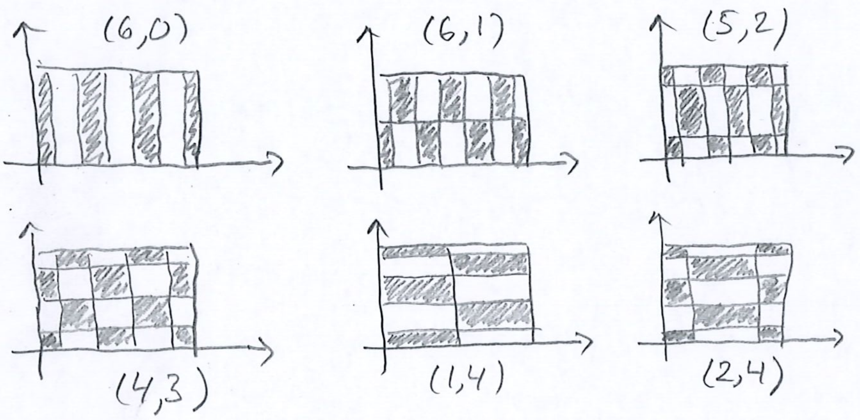
, $Q_m$ and $\Delta$ exactly as for 1D ($Q^2 = q_1^2 + q_2^2$)

Same choice of values of constants, and $L_y = 2\pi$ $\Rightarrow$

$$4 < \frac{m^2}{8} + \frac{n^2}{4} < 5 \Rightarrow 32 < m^2 + 2n^2 < 40$$

$\Rightarrow$ allowed values are

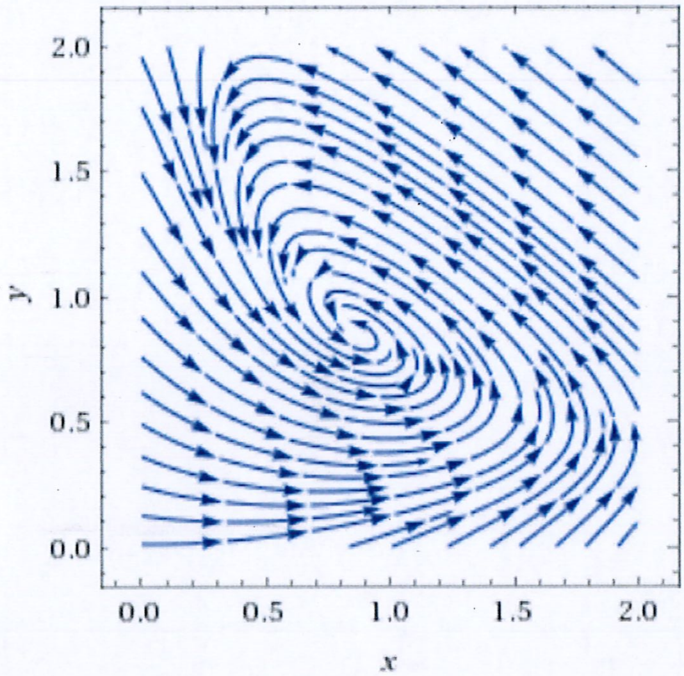
$(m,n) = (6,0), (6,1), (5,2), (4,3), (1,4), (2,4)$ $\Rightarrow$ 6 patterns can form



Glycolytic oscillato–

| stream plot | $(0.866 - 0.25\,x - x\,y^2,\ 0.25\,x - y + x\,y^2)$ | $x = 0$ to $2$ <br> $y = 0$ to $2$ |
|---|---|---|

Plot:

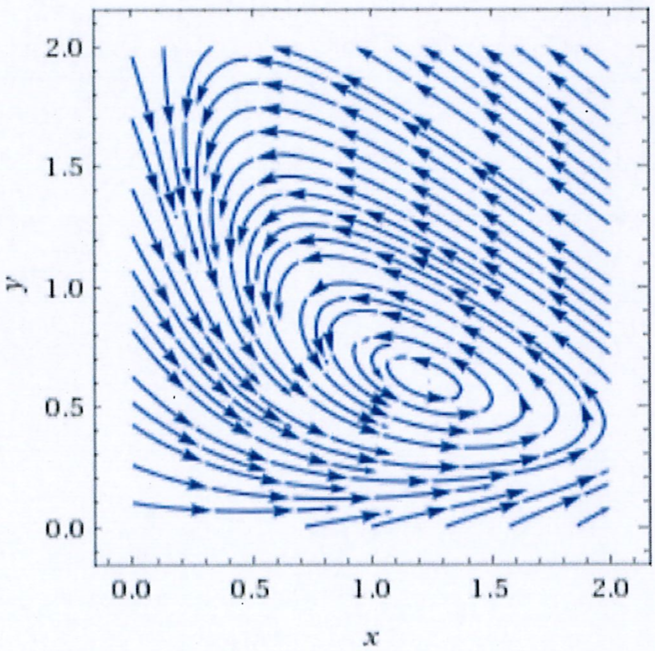



$\delta^2 = \frac{3}{4}, k = \frac{1}{4},$

$(\bar{f}, \bar{g}) = \left(\frac{\sqrt{3}}{2}, \frac{\sqrt{3}}{2}\right)$, stable

| stream plot | $(0.61237 - 0.125\,x - x\,y^2,\ 0.125\,x - y + x\,y^2)$ | $x = 0$ to $2$ <br> $y = 0$ to $2$ |
|---|---|---|

Plot:




$\delta^2 = \frac{3}{8}, k = \frac{1}{8}$

$(\bar{f}, \bar{g}) = \left(\sqrt{\frac{3}{2}}, \frac{\sqrt{3}}{2\sqrt{2}}\right)$

Tr J = 0 limit case

oscillating values

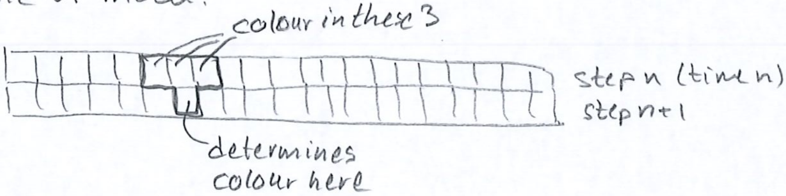
## Cellular automata

Simple rules can create complex or chaotic patterns.

Philosophy : nature governed by simple rules (e.g. S. Wolfram)

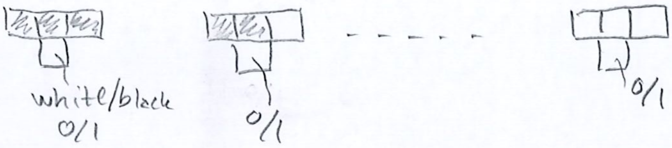
[see EK page 542-543]

Example of model:




each box 0 or 1 (or white or black)

Possible rules




→ 8-digit binary number, $2^8 = 256$

→ rules 0 to 255

Check in Wolfram Alpha, type "rule 37" and a pattern appears.

Initial condition is  (one black box)

Most rules give simple/trivial patterns, but some give more complex, fractal, or even chaotic

You should try, e.g. rules

$2, 7, 25, \underbrace{122, 126, 153}_{\text{fractal}}, \underbrace{137, 30}_{\text{chaotic (?)}}$