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## Self-organization and pattern formation

### Sheet 2

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## Exercise 6 – Bogdanov-Takens bifurcation

In the Lecture and previous exercises, we've explored saddle-node and Hopf bifurcations. The upcoming pair of exercises will delve into scenarios where these bifurcations converge at a specific location within the parameter space. Such convergence points, often referred to as organizational centers, play a pivotal role in shaping the phase space structure. They embody the essential characteristics of the phase space structure that emerge due to the bifurcation. Analyzing the dynamics in both parameter space and phase space around these points is crucial, a process known as "unfolding the bifurcation." This concept is analogous to the cusp bifurcation discussed in the lecture.

Consider the following two dimensional system

$$\begin{aligned}\partial_t x(t) &= y(t) := f(x, y), \\ \partial_t y(t) &= a + by(t) + x(t)^2 - x(t)y(t) := g(x, y).\end{aligned}\tag{1}$$

Use the provided *Mathematica* notebook to explore the dynamics of the system described in equation (1). Visualize the nullclines, flow, invariant manifolds, and trajectories, adjusting the parameters  $a$  and  $b$  using the 'Manipulate[]' function. This hands-on approach will help you control the presence of saddle-node and Hopf bifurcations. Throughout this exercise, we will develop a bifurcation diagram based on these parameters to systematically classify the system's behavior across different regimes.

- a)** Derive an expression for the fixed points and corresponding eigenvalues of this two-component dynamic system.
- b)** Identify the relationship between  $a$  and  $b$  that leads to a saddle-node bifurcation. Sketch the corresponding bifurcation line in parameter space and mark the number of fixed points in each region.
- c)** Show that one fixed point is consistently a saddle. The other fixed point experiences a Hopf bifurcation. Establish the conditions for  $a$  and  $b$  that lead to Hopf bifurcation and illustrate the Hopf bifurcation line on your sketch.
- d)** At which point in parameter space do the Hopf bifurcation and the saddle-node meet? This bifurcation is called the Bogdanov-Takens bifurcation.

e) Pick  $a$  and  $b$  such that you have a limit cycle (e.g.  $a = -0.2$  and  $b = -0.4$ ) and slowly increase  $b$  with the given Mathematica notebook. The system now undergoes a Homoclinic bifurcation. Describe the behavior of the system before, after and at the bifurcation, in particular what happens to the limit cycle. Describe how the fixed points, their stability throughout this bifurcation.

f) Use the Mathematica notebook to approximate the bifurcation line for the Homoclinic bifurcation, i.e. pick values for  $a$  between  $-0.5$  and  $-0.02$  and the corresponding value for  $b$  for which the Homoclinic bifurcation occurs. Include your approximated bifurcation line in your sketch.

## Exercise 7 – Bogdanov-Takens bifurcation: Unfolding the homoclinic orbit

To analyze the homoclinic bifurcation of the system more closely, we apply a blow-up transformation in the vicinity of the Hopf bifurcation. This rescaling “zooms in” on the parameter region near the Bogdanov–Takens point. The goal of the blow-up is to separate contributions of different order: after rescaling, one obtains a leading-order system that captures the essential bifurcation structure, while higher-order terms appear as small perturbations. In this way, the dominant dynamics (such as the homoclinic orbit) can be studied independently from small corrections. The parameters are transformed as follows:

$$a \rightarrow -4\epsilon^4, \quad b \rightarrow \mu\epsilon^2.$$

a) Argue how this transformation makes sense from your observation in the last exercise. Then find the appropriate scaling factors for  $x$ ,  $y$ , and  $t$  to derive the following system of equations:

$$\begin{aligned} \partial_{\tilde{t}}\tilde{x} &= \tilde{y}, \\ \partial_{\tilde{t}}\tilde{y} &= -4 + \tilde{x}^2 + \epsilon\tilde{y}(\mu - \tilde{x}). \end{aligned} \tag{2}$$

Find  $\tilde{x}$ ,  $\tilde{y}$ , and  $\tilde{t}$ , respectively.

b) For convenience, we rename  $\tilde{t} \rightarrow t$ ,  $\tilde{x} \rightarrow x$ , and  $\tilde{y} \rightarrow y$  for the rest of the exercise. For  $\epsilon \rightarrow 0$  you can interpret the dynamics (2) as a energy conserving system of a frictionless mass point moving in a potential  $V = 4x - x^3/3$ . Use the expression for the total energy  $E = y^2/2 + V(x)$  to sketch the possible orbits of the conservative system in  $(x, y)$ -phase space. Find the energy of the homoclinic orbit which starts and ends exactly at the local maximum of  $V(x)$ . Show that  $x_h(t) = 2(1 - 3/\cosh(t)^2)$  is the homoclinic trajectory of (2) for  $\epsilon = 0$ .

c) As discussed in the previous exercise, for the singular point  $\epsilon = 0$ , the dynamics (2) can be interpreted as a energy conserving system of a frictionless mass point moving in a potential  $V = 4x - x^3/3$ . Any (however small) value of  $\epsilon$  will break this property, because the driving/friction-term  $\epsilon y(\mu - x)$  will perturb the orbits over time. In particular, the homoclinic orbit (where  $\mu = \mu_h$ , you don't need to find the value of  $\mu_h$  in this part) of the energy conserving system will in general be perturbed such that it does return exactly to the maximum of  $V(x)$ , i.e. picks up a net energy difference as it traverses the orbit.

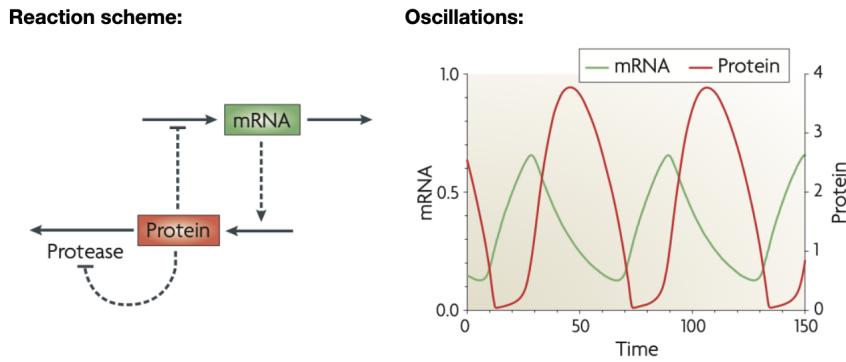


Figure 1: This figure is adapted from Novak, B. and Tyson, J. J. (2008). *Nature Reviews*, 9(12), 981-991. Left: Schematic representation of a negative-feedback loop in which mRNA and protein regulate each other's synthesis and degradation. The dynamics of this system are described by a set of kinetic equations that capture how the feedback strength and molecular interactions can lead to oscillatory behavior. Right: Simulated sustained oscillations in mRNA and protein concentrations corresponding to the parameter set that produces a limit cycle solution. These oscillations illustrate how feedback and nonlinearity can generate rhythmic gene expression in a self-sustained manner.

Sketch a situation where it gains some energy and a situation where it loses some net energy difference along the trajectory.

d) We can use the analogy to a mass point moving in a potential to determine the homoclinic bifurcation line: The homoclinic orbit only remains homoclinic (return to its starting point) if the energy picked up due to the driving/friction-term along the homoclinic orbit vanishes. First, show that

$$\delta E = \varepsilon \int_{-\infty}^{\infty} dt (\partial_t x_h)^2 (\mu - x_h) \quad (3)$$

is the energy picked up due to the driving/friction-term along the homoclinic orbit  $x_h(t)$ . Then, use the condition  $\delta E = 0$  to determine the critical value  $\mu_{\text{crit}}$  for which the homoclinic orbit occurs.

*Hint:* Use Mathematica to evaluate the net energy integral.

e) Transform the parameters back to the original parameter space  $(a, b)$  to add your approximation of the homoclinic bifurcation line to the bifurcation diagram. Are your values found in the last exercise agrees with the approximation?

## Exercise 8 – Biochemical Oscillations

Biochemical oscillations, play crucial roles in various biological processes like metabolism, cell signaling, and growth. In this exercise, we will study a gene-regulatory-network (GRN) able to describe how circadian rhythms arise in the expression of a protein through phase space analysis and oscillations. We consider two concentrations: the mRNA concentration  $M$  and the protein concentration  $P$ .

a) The first key ingredient to obtain an oscillator is a protein  $P$  that represses the transcription of its own gene (for example, PER in the circadian control system of fruit

flies<sup>1</sup>). Transcription is modulated by a signal density  $S$ . Another key ingredient is that the protein  $P$  can be degraded by a protease, denoted  $E$ . The time evolution equations for the mRNA  $M$  and the protein  $P$  reads:

$$\frac{dM}{dt} = k_1 S \frac{K_d}{K_d + P} - k_2 M \quad (4)$$

$$\frac{dP}{dt} = k_3 M - k_4 E \frac{P}{K_m + P} \quad (5)$$

See Fig. 1 for a visualization of the key ingredients. What are the meanings of the different coefficients  $k_1, k_2, k_3, k_4, K_d$  and  $K_m$ ?

*Hint: Consider the two limits of  $P \rightarrow \infty$  and  $P \rightarrow 0$  when interpreting the meaning of the various terms. You might find it useful to look up Michaelis-Menten kinetics.*

**b)** Assume, for simplification, that  $k_1 = k_2$  and  $k_3 = k_4$  and  $K_d = K_m$ . Show that you can nondimensionalize the equations, such that you get a set of equations of the form

$$\frac{dX}{d\tau} = S \frac{1}{1 + Y} - X, \quad (6)$$

$$\frac{dY}{d\tau} = \tilde{k}X - \tilde{k}E \frac{Y}{1 + Y}. \quad (7)$$

What are the rescaled parameters  $\tilde{k}$ ,  $\tau$ ,  $X$  and  $Y$  in terms of the old parameters.

**c)** How many fixed point do Eqs.(6), (7) have? Solve for the fixed points and classify them by using the trace determinant criteria from the lecture.

**d)** Sketch the phase portrait of the system, by sketching the nullclines by hand. Then use the provided mathematica file, to plot the two nullclines and additionally study the sign of the time derivatives of  $X$  and  $Y$  and plot a few trajectories in phase space. Are there oscillations? If yes, are these damped or sustained? Argue how you can connect the stability of the fixed point found above with the oscillations being damped or sustained.

**e)** To sustain the oscillations, we must introduce a positive feedback parameter into the system. In particular, we assume that protein  $P$ , in addition to binding to its own gene regulatory site and downregulating its own expression, can bind to protease  $E$  and thereby inhibit its activity. Biologically, this is motivated by the fact that proteins often regulate their own degradation by binding to and transiently inactivating the proteases responsible for their turnover. Such sequestration reduces the effective protease activity when the protein concentration is high, thereby introducing a positive feedback that can help sustain oscillations. The new equations read:

$$\frac{dM}{dt} = k_1 S \frac{K_d^p}{K_d^p + P^p} - k_2 M \quad (8)$$

$$\frac{dP}{dt} = k_3 M - k_5 P - k_4 E \frac{P}{K_m + P + K_1 P^2} \quad (9)$$

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<sup>1</sup>Tyson, J. J., Hong, C. I., Thron, C. D., and Novak, B. (1999)). A simple model of circadian rhythms based on dimerization and proteolysis of PER and TIM. *Biophysical journal*, 77(5), 2411–2417.

The term describing the transcription of the mRNA is now raised to the  $p$ -order, indicating whether  $Y$  binds to the DNA sequence as a monomer, dimer or trimer and so on. In what limit does the newly introduced terms inhibit the activity of  $E$ ? Can you motivate the additional terms in the equations?

**f)** Numerically find the fixed points of (8), (9). Using the provided mathematica file, plot the two nullclines and study the sign of the time derivatives of  $M$  and  $P$ , plot a few trajectories in phase space. Using the Poincaré-Bendixon theorem, the stability of the fixed point and the qualitative behavior of the vector field argue whether you expect a limit cycle or not. Make a comparison with the Rho GTPases phase space studied in the lecture.

Your solutions should be handed in in moodle by **Wednesday, November 05<sup>th</sup> 2025, 10 am.**