Biological physics, fall 2013, IST Austria

Lecture week 11: Dynamical systems (TB)

1. Nonlinear dynamics
   - The general framework of dynamical systems can be used to describe (“model”) many phenomena in biology, including gene regulation networks, neuronal networks, population dynamics etc.
   - A (continuous) dynamical system is described by a set of equations of the form: \( \dot{x} = f(x) \), where the function \( f \) can be nonlinear. More generally, \( f \) can depend explicitly on time, \( \dot{x} = f(x, t) \).
   - If \( f \) is sufficiently smooth, solutions to these equations exist and are unique. The solutions \( x(t) \) are called trajectories. It is straightforward to obtain these solutions numerically, e.g. by using Euler’s forward integration method \( \dot{x}(t + \Delta t) = f(x(t))\Delta t \) starting at an initial position \( x(t = 0) = x_0 \).
   - If \( f \) is a linear function of \( x \) it is relatively easy to calculate a complete solution. However, many real-world phenomena are nonlinear. For nonlinear functions \( f \), the system is harder to study. Dynamical systems theory provides a framework for analyzing such nonlinear systems systematically.
     - Examples:
       - Growth of a population of bacteria: \( \frac{dN}{dt} = gN \), with the cell number \( N \) and the growth rate \( g > 0 \). The solution of this linear equation is \( N(t) = N_0 \exp(gt) \).
       - An example for a nonlinear dynamical system is given by the logistic growth equation: \( \frac{dN}{dt} = gN (1 - N/K) \). Here, \( K \) is the carrying capacity which is the maximum population size that can be sustained (e.g. due to limited nutrient availability).
   - The fixed points of a dynamical system are points \( \bar{x} \) for which \( \dot{x} = f(x) = 0 \).
     - Stability of fixed points: a fixed point \( \bar{x}_* \) is stable (an attractor) if the system returns to \( \bar{x}_* \) upon any small perturbation \( \delta x \), i.e. trajectories starting at \( \bar{x}_* + \delta x \) return to \( \bar{x}_* \) for \( t \to \infty \) for any \( \delta x \), provided that \( \|\delta x\| \) is sufficiently small.
     - Example: the logistic growth equation \( \frac{dN}{dt} = gN (1 - N/K) \) has a stable fixed point at \( N = 0 \) and a stable fixed point at \( N = K \).
   - Linear stability analysis provides a systematic way to test if a fixed point \( \bar{x}_* \) is stable. Using \( \bar{x} = \bar{x}_* + \delta x \), we linearize the system around \( \bar{x}_* \): \( \frac{d\delta x}{dt} = \dot{\delta x} = \bar{f}(\bar{x}_*) = \bar{f}(\bar{x}_* + \delta x) = \bar{f}(\bar{x}_*) + D\bar{f}(\bar{x}_*) \cdot \delta x + O(\|\delta x\|^2) \). Here, \( D\bar{f}(\bar{x}_*) \) is the Jacobian matrix (for one-dimensional systems, the Jacobian is simply the first derivative \( df/dx \) evaluated at \( x = \bar{x}_* \)). Since \( \bar{f}(\bar{x}_*) = 0 \), we have \( \frac{d\delta x}{dt} = D\bar{f}(\bar{x}_*) \cdot \delta x + O(\|\delta x\|^2) \). The stability of the fixed point \( \bar{x}_* \) is determined by the Eigenvalues of the Jacobian \( D\bar{f}(\bar{x}_*) \):
     - A fixed point is stable (an attractor) if the real part of all Eigenvalues of \( D\bar{f}(\bar{x}_*) \) is smaller than 0.
     - ... unstable if the real part of at least one Eigenvalue of \( D\bar{f}(\bar{x}_*) \) is greater than 0.
• ... a repellor if the real part of all Eigenvalues of $D\hat{f}(\hat{x}_*)$ is greater than 0.
• ... a saddle if the real part of at least one Eigenvalue of $D\hat{f}(\hat{x}_*)$ is greater and that of at least one Eigenvalue of $D\hat{f}(\hat{x}_*)$ smaller than 0.
• ... marginal if the real part of at least one Eigenvalue is 0.
• The Eigenvalues of $D\hat{f}(\hat{x}_*)$ also determine the time scale of relaxation towards the fixed point: for an attractor $\hat{x}_*$, the inverse of the real part of the largest Eigenvalue is the relaxation time.
• In one dimension, the dynamics of the linearized system is given by \[ \frac{d\delta x}{dt} = \lambda \delta x \] with $\lambda = df/dx|_{x=x_*}$, and the solution is simply $\delta x(t) = \delta x_0 e^{\lambda t} = \delta x_0 e^{\text{Re}(\lambda)t}$.
• Examples:
  • Lotka-Volterra model of species competition (see Strogatz book p. 155 for this example)
  • The basin of attraction of a (stable) fixed point $\hat{x}_*$ is the set of initial points $\hat{x}_0$ whose trajectories lead to $\hat{x}_*$ for $t \to \infty$.
  • Using a phase portrait, we can understand key qualitative properties of the dynamics of a system without having a complete solution. For each initial point $\hat{x}_0$ in phase space, the dynamical system defines a trajectory $\hat{x}(t)$. A phase portrait consists of these trajectories for many (ideally all) initial points. In practice, we can calculate many trajectories numerically and simply draw them.
    • Even without resorting to numerical solutions, key features of a phase portrait can be captured. In particular, we can draw:
      • The fixed points (stable and unstable).
      • The trajectories near the fixed points (obtained from linear stability analysis).
    • An educated guess for the complete phase portrait can then often be made, making use of the fact that different trajectories never intersect (because the solutions are unique).
  • Closed orbits are periodic solutions which return to the same point $\hat{x}$ in phase space after a time $T$, i.e. $\hat{x}(t+T) = \hat{x}(t)$.
    • Example: Harmonic oscillator $m\ddot{x} + kx = 0$. We convert this second order differential equation into a dynamical system by introducing $\dot{x} = v$. A solution of this system is $x(t) \sim \sin(\omega t), v(t) \sim \cos(\omega t)$. Hence, the trajectories are closed orbits in phase space.
    • If we introduce a damping term, the system becomes $m\ddot{x} + \mu \dot{x} + kx = 0$, and the trajectories become spirals that converge on the stable fixed point $(x, v) = (0,0)$.
  • Poincaré-Bendixson theorem: In two dimensions, if a trajectory is confined to a closed bounded region, and there are no fixed points inside this region, then there is a closed orbit inside.

2. Bifurcations
  • The qualitative structure of the flow can change abruptly as a parameter of the system is varied. Such abrupt changes are called “bifurcations.”
  • In a saddle-node bifurcation, a stable and an unstable fixed point annihilate as a parameter is varied.
Example: \( dx/dt = r + x^2 \). For \( r < 0 \) this system has a stable fixed point at \( x = -\sqrt{|r|} \) and an unstable fixed point at \( x = \sqrt{|r|} \). For \( r > 0 \), there are no fixed points. Thus, the system has a saddle-node bifurcation at \( r = 0 \).

- Importantly, such bifurcations are generic, i.e. there are only relatively few different types of bifurcation. For example, for any dynamical system that has a saddle-node bifurcation, the dynamics “looks” like \( dx/dt = r + x^2 \) near this bifurcation upon suitable rescaling of the system variables. This is called the normal form of the bifurcation. (Here, we do not go into the depth that would be required to make this statement precise; see Crawford review below for details.)

- In a Hopf bifurcation, a fixed point loses stability as a limit cycle is created.
  - A limit cycle is an isolated closed orbit. Here, “isolated” means that trajectories in close proximity of the limit cycle are not closed, but spiral towards or away from the limit cycle.
    - Like a fixed point, a limit cycle can be stable or unstable. It is stable if all trajectories starting near the limit cycle converge on the limit cycle for long times.
  - Example: \( \frac{dr}{dt} = \mu r - r^3, \frac{d\theta}{dt} = \omega + br^2 \) (using polar coordinates \( x = r \cos \theta, y = r \sin \theta \)).
    - This system has a fixed point at \( r = 0 \). Linear stability analysis shows that this fixed point is stable for \( \mu < 0 \) and unstable for \( \mu > 0 \). The two Eigenvalues of the Jacobian matrix have a nonzero imaginary part and cross the imaginary axis from left to right at \( \mu = 0 \). This behavior is a hallmark of a Hopf bifurcation.
    - The trajectories near the fixed point are stable spirals that converge on \( r = 0 \) for \( \mu < 0 \). They change into spirals that converge on a limit cycle for \( \mu > 0 \).
    - The frequency of the limit cycle oscillation is approximately \( \text{Im}(\lambda) = \omega \). This result holds in general for Hopf bifurcations.

- There are two different types of Hopf bifurcation:
  - In a supercritical Hopf bifurcation, the limit cycle stays near the fixed point that lost stability as long as the control parameter is near the critical value \( \mu = 0 \). The example discussed above is a supercritical Hopf bifurcation.
  - In a subcritical Hopf bifurcation, the trajectory jumps to a distant limit cycle as soon as the control parameter crosses the critical value \( \mu = 0 \).
    - Example: \( \frac{dr}{dt} = \mu r + r^3 - r^5, \frac{d\theta}{dt} = \omega + br^2 \)
    - Subcritical bifurcations show hysteresis which means that large amplitude oscillations do not disappear when the control parameter is reduced back below the critical value \( \mu = 0 \). The stable limit cycle only disappears at a lower value of \( \mu \) in what is called a saddle-node bifurcation of cycles where it is annihilated in a collision with an unstable limit cycle.

- Example: In the bullfrog ear, sensory cells called “hair cells” detect sound waves. Each of these cells has a so-called “hair bundle” which is an active oscillator that can amplify low amplitude sound waves. It has been suggested that such oscillators may be tuned to the critical point of a Hopf bifurcation. This scenario is plausible because
such a sensory system should certainly not oscillate spontaneously in the absence of sound, i.e. if it exhibits a Hopf bifurcation it should not be tuned above the critical value. On the other hand, being tuned close to the point where spontaneous oscillations occur ensures strong amplification of low amplitude sounds. Such a mechanism could explain how hair cells can detect sounds that carry less energy than the background noise. For details, see Camalet reference below.

References / further reading:

- S Strogatz book
- Advanced: Crawford, Rev Mod Phys, 1991
- Advanced: S Camalet, PNAS, 2000