Introduction to Dynamical Systems and Applications in Neuroscience

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What is a Dynamical System?

We can start with an informal definition:

Definition (Dynamical System)

A *dynamical system* is a system whose state is uniquely specified by a set of variables and whose behavior is described by predefined rules.

Dynamical systems can be seen everywhere, from a pendulum, population growth, motions of planets, to biochemical systems in the human body. The motivation behind the theory is trying to understand how systems will behave as $t \to \infty$ or $t \to -\infty$.

First-order ODEs

Dynamical systems can be either in **discrete** time steps or **continuous** time line. They have the respective mathematical formulations:

Definition (First-order Dynamical System)

$x_t = F(x_{t-1}, t)$ for discrete dynamical system and $\frac{dx}{dt} = F(x, t)$ for continuous systems where $x(t) \in \mathbb{R}^d$ and $F : \mathbb{R}^d \to \mathbb{R}^d$

From the definitions:

- F is a function/mapping determining rules by which the system changes states over time, usually an iterative map for discrete steps and a differential equation for the continuous case
- x or x_t is the state variable of the system at time t, can be scalar or vector These are only the first-order versions, higher order systems include higher order terms $(\frac{d^2x}{dt^2}, \frac{d^3x}{dt^3}, \ldots)$.

Phase Space Analysis

We can study the behavior of dynamical systems with **phase spaces**.

Definition (Phase Space and Phase Plane)

A *phase space* of a dynamical system is a theoretical space where every state of the system is mapped to a unique spatial location.
A *phase plane* is the space of a two-dimensional system.

These graphs visually represent how a dynamical system is changing with respect to one variable, which might provide more insights into the dynamics than equations.

Example: The Pendulum

We can consider the classic pendulum problem and use Newton's equation to get a system of ODEs:

$$\dot{\theta}(t) = v(t)$$

$$\dot{v}(t) = -sin(\theta)$$

The phase plane plots allow us to see how the pendulum will end up despite all the possible starting angles and velocities.

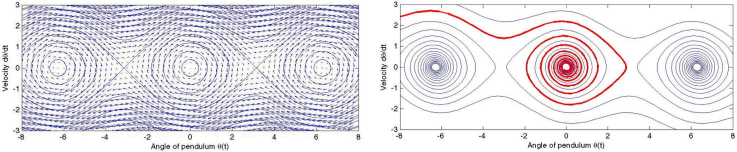


Figure: Phase plane between angle and velocity of pendulum: (left) ideal case, no friction, (right) pendulum with friction

Fixed Points

When analyzing dynamical systems, one of the first things to consider are the **fixed points**. These are points where the system can stay the same over time.

Definition (Fixed Points (also Equilibrium Points or Steady States))

If $x_0 \in \mathbb{R}^d$ is a zero of F, $F(x_0) = 0$, then x_0 is a *fixed point* and has constant solution $x(t) = x_0$.

For the pendulum example, the rest position of $\theta = 0$ is a fixed point. These fixed points are important theoretically because they serve as constant references that we can use to understand the evolving space space. With this knowledge, we can manipulate the system to be in certain desirable states from the fixed points.

Stability

Fixed points can be **stable** or **unstable**, depending on whether perturbations around these points remain bounded or grow unbounded.

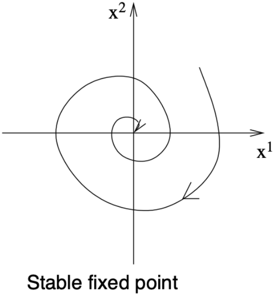


Figure: Example of a stable and unstable fixed point

The Jacobian Matrix

For systems with dimensions higher than one, we rely on the **Jacobian matrix** to define properties such as stability and bifurcation:

Definition (Jacobian Matrix)

For the mapping $F : \mathbb{R}^d \to \mathbb{R}^d$ with $\mathbf{x} \in \mathbb{R}^d$, the *Jacobian matrix* is defined as

$$\mathbf{J} = \begin{bmatrix} \frac{\partial f_1}{\partial x_1} & \cdots & \frac{\partial f_1}{\partial x_d} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_d}{\partial x_1} & \cdots & \frac{\partial f_d}{\partial x_d} \end{bmatrix}$$

Stability Defined

Definition (Stable Fixed Point)

With continuously differentiable $F : \mathbb{R}^d \to \mathbb{R}^d$ with fixed point x_0 and eigenvalues λ_i of Jacobian matrix $J_x(F)$.
If $\|\lambda_i\| < 1$ for all i then x_0 is a *stable fixed point*.
If $\|\lambda_i\| > 1$ for at least one i then x_0 is an *unstable fixed point*.
If $\|\lambda_i\| = 1$ for some i then the Jacobian test is inconclusive.

Bifurcations

Bifurcation means splitting in two. When considering long-term behavior of a system, we might observe changes in parameter that cause slight changes in the system, and there can be slight parameter changes that cause drastic, qualitative changes in the behavior.
That slight change is characterized by *critical threshold*, or the parameter value at which bifurcation occurs.

Definition (Bifurcation)

A *bifurcation* is a qualitative, topological change of a system's phase space that occurs when some parameters are slightly varied across their critical thresholds.

Important applications of bifurcations in dynamical systems are in studying excitation of neurons, transitions of ecosystems, or information in computer memory.

Bifurcations

There are two categories of bifurcations: local and global. We focus on local bifurcations, which can be detected with local information around the equilibrium point. This can be defined mathematically:

Definition (Local Bifurcation)

Local bifurcations occur when eigenvalues λ_i of the Jacobian matrix at an equilibrium point satisfy:

- $\|\lambda_i\| = 1$ for some i, and $\|\lambda_i\| < 1$ otherwise (for discrete case)
- $Re(\lambda_i) = 0$ for some i, and $Re(\lambda_i) =<$ otherwise (for continuous case)

Hopf Bifurcation

One particular type of bifurcation is the **Hopf bifurcation**. It is a local bifurcation where a stability switch in a system leads to a **limit-cycle** appearing around a fixed point.

Definition (Hopf Bifurcation)

Let J_0 be the Jacobian of a continuous dynamical system evaluated at fixed point x_0. Suppose all eigenvalues of J_0 have negative real parts except for one conjugate nonzero imaginary pair $\pm i\beta$.
A *Hopf bifurcation* occurs when these two imaginary eigenvalues cross the imaginary axis because of a parameter change in the system.

Limit Cycle and Stability

We also give an informal definition of limit cycles:

Definition (Limit Cycle)

A *limit cycle* is a closed trajectory in the phase plane such that other trajectories spiral toward it (either from the inside or outside) as $t \to \infty$.

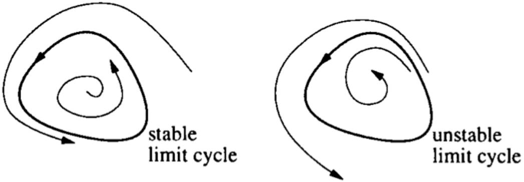


Figure: A stable and unstable limit cycle

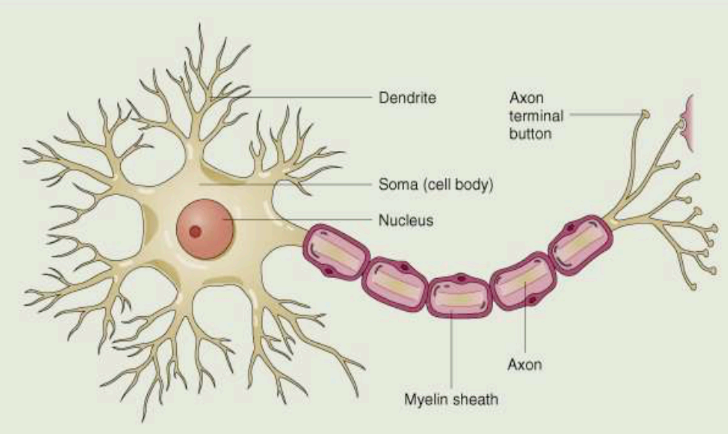
Neuroscience and Dynamics

One important application of the study of dynamical systems is in context of neuroscience, since modeling of the brain provides valuable insights in how complex processes such as thought, memory, vision, or motor control are derived from individual or populations of working neurons. In order to control all the processes that are needed to regulate a living animal, the brain is organized anatomically into regions.

Neurons are specialized cells of the nervous system that receive sensory input from the environment, transmit and relay information to other intermediates, and output motor commands to muscles.

Excitability of Neurons

Despite being in different locations and having vastly different functions, neurons still communicate with each other through the propagation of **action potentials**.



The Action Potential

The action potential, a transient electrical signal, is transmitted from one neuron's **axon hillock** to another neuron's **dendrites**. Action potentials occur when the membrane potential on the cell fluctuates ("depolarizes") rapidly, causing adjacent areas to depolarize and propagate further. The electrical activity comes from movement of ions such as K^+, Na^+, Cl^-, across the membrane.
These ions are able to move due to ion channels (e.g. potassium channel, sodium channel) that are embedded in the membrane and will selectively pass current. These channels are voltage-gated, meaning they are sensitive to the membrane potential and will predictably open or close upon specific voltages.

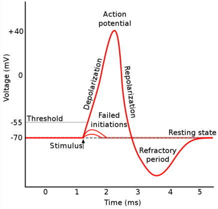


Figure: Plot showing the phases of an action potential

The Hodgkin-Huxley Model

Hodgkin and Huxley were neuroscientists who used voltage-clamp experiments, allowing membrane potential to be controlled, formulated a quantitative description of how action potentials could be generated. The model is a system of 4 equations, relating variables like voltage (V) to the individual conductances of each ion and leak currents ($\bar{g}_{Na}/\bar{g}_K/\bar{g}_L$).

$$c_M \frac{dV}{dt} = -\bar{g}_{Na} m^3 h (V - E_{Na}) - \bar{g}_K n^4 (V - E_K) - \bar{g}_L (V - E_L)$$

$$\frac{dn}{dt} = \phi[\alpha_n(V)(1-n) - \beta_n(V)n]$$

$$\frac{dm}{dt} = \phi[\alpha_m(V)(1-m) - \beta_m(V)m]$$

$$\frac{dh}{dt} = \phi[\alpha_h(V)(1-h) - \beta_h(V)h]$$

Note: $E_{Na}/E_K/E_L$ = equilibrium potentials, α/β = rate constants for channel opening/closing, gating variables $n, m, h \in (0, 1)$, and ϕ = temperature factor

HH Solution

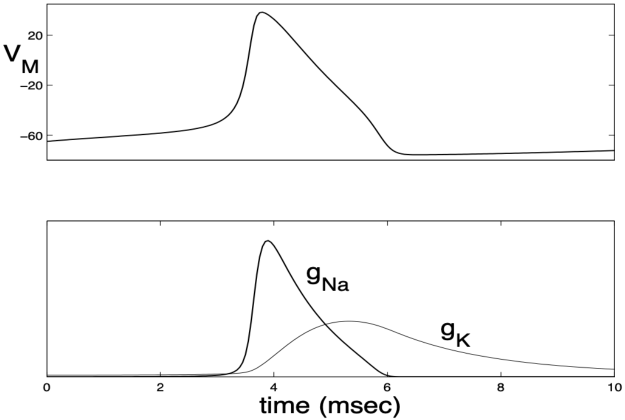


Figure: The top figure shows the solution to the HH equations, the shape of an action potential. The bottom shows the conductance of Na and K channels during the course of the action potential. This reveals the mechanics behind the action potential.

Mechanism behind the Action Potential

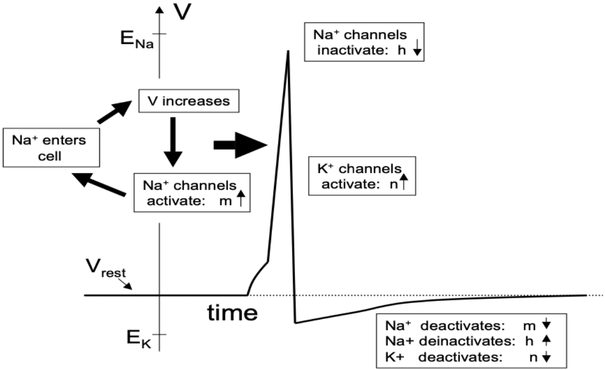


Figure: Figure illustrating mechanism behind the action potential and why it has that shape. The upstroke is due to Na channels activating, followed by their quick inactivation. The down-stroke is largely up to K channels for hyperpolarization.

The Morris-Lecar Model

Another model for the production of action potentials, the Morris-Lecar model considers three channels: potassium channel, calcium channel, and a leak channel. This model is popular since it is regarded as a two-dimensional system (as opposed to the 4-dimensional HH model). The assumption behind using this two-dimensional model is that true higher-order systems can be projected onto a two-dimensional phase plane without altering any topological properties of the phase space.

$$C_m \frac{dV}{dt} = I_{app} - g_l(V - E_L) - g_k n(V - E_K) - g_{Ca} m_\infty(V)(V - E_{Ca})$$

$$\frac{dn}{dt} = \phi(n_\infty(V) - n)/\tau_n(V)$$

ML Solution

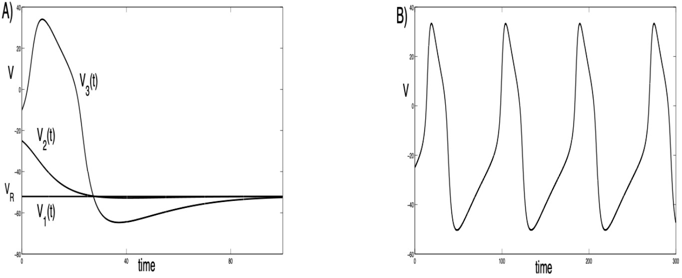


Figure: (V,n)-plane: (left) small perturbation from rest decays to resting state ($V_2(t)$) while larger perturbation generates action potential ($V_3(t)$);(right) periodic solution from Hopf bifurcation

Fixed Points of ML

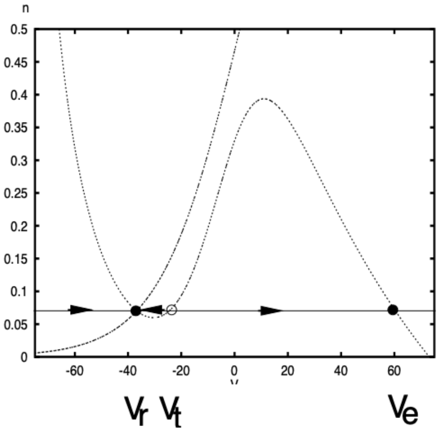


Figure: Filled-in dots are stable fixed points, representing resting potential V_r and peak of action potential V_e. Open dot is unstable fixed point, signifying the threshold voltage needed for an action potential V_t

References

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