Mathematical Tools for Neuroscience (NEU 314)
Princeton University, Fall 2021
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Lecture 22-23: Dynamics

1 Dynamical systems in one variable

Dynamical systems in one variable involve ordinary differential equations (ODEs) of the form:

$$\frac{dx}{dt} = f(x) \tag{1}$$

which is equivalent to writing

$$\dot{x} = f(x). \tag{2}$$

What this specifies is a time-varying quantity $x(t)$ whose temporal derivative is the function $f(x(t))$ at each time point t. Typically we will specify an initial state x_0 at time $t = 0$. This indicates that the variable begins at value $x(0) = x_0$ and evolves from there according to the changes defined by $f(x)$.

The qualitative behavior of this model can be understood entirely by inspecting the graph of $f(x)$ vs. x:

- Regions where $f(x) > 0$: the derivative is positive, so $x(t)$ will increase (toward a fixed point or towards infinity).
- Regions where $f(x) < 0$: the derivative is negative, so $x(t)$ will decrease (towards a fixed point or towards negative infinity).
- **Fixed points**: points where $f(x)$ crosses the x axis, meaning $\frac{dx}{dt} = 0$. If x takes on such a value then it will remain there forever (because its derivative is zero), hence “fixed”.

We can classify fixed points as **stable** or **unstable** based on whether nearby points will converge towards or diverge away from the point.

In one dimension it is easy to determine stability of fixed points by visual inspection.

If the function $f(x) = \frac{dx}{dt}$ crosses the x axis with negative slope, the fixed point will be stable, because points to the left have positive derivative (meaning $x(t)$ increases towards the fixed point) and points to the right have negative derivative (meaning $x(t)$ will decrease towards the fixed point).

Conversely, if the function the x axis with positive slope, the fixed point will be unstable: points to the left have negative derivative (meaning $x(t)$ will decrease even further away from the fixed point) and points to the right have positive derivative (meaning $x(t)$ will increase away from the fixed point).

If $f(x)$ touches the x axis at a single point but does not cross it, then the fixed point is neither stable nor unstable.

2 Euler method for integrating a dynamical system

Of course, most dynamical systems that we encounter in neuroscience (or in real life) are nonlinear, and the vast majority of these systems do not have an analytical expression allowing us to write $x(t) = \textit{some expression}$. In such cases, we can still "solve" the ODE numerically by initializing $x(0) = x_0$ at time t_0 and just incrementing the value of $x(t)$ according to the information we have about its derivative.

The simplest numerical integration method for solving ODEs is known as Euler's method. This method comes about from making a "finite differencing" approximation to the derivative. If we recall from elementary calculus, the derivative of a function is defined as

$$\frac{dx}{dt} = \frac{x(t+\Delta) - x(t)}{\Delta} \tag{3}$$

in the limit that $\Delta \to 0$. If we instead set Δ to some finite value, then we obtain the Euler method for integrating a dynamical system. Namely, let

$$\frac{x(t+\Delta) - x(t)}{\Delta} = f(x(t)) \tag{4}$$

and solve this for $x(t + \Delta)$, the value of x at the next time step. This gives us:

$$\text{Euler's method:} \qquad x(t+\Delta) = x(t) + \Delta f(x(t)), \tag{5}$$

where Δ corresponds to the bin size used for integration.

3 Linear dynamical systems in one variable

Linear dynamical systems are simply those for which $f(x)$ is a linear function of x, namely:

$$\dot{x} = ax. \tag{6}$$

These kinds of systems are easy to analyze because they can have only a single fixed point (a linear function can only cross the x axis at a single point). And they can exhibit only two possible behaviors: if $a > 0$, the system is unstable, exhibiting exponential growth to infinity from any initial point that is not zero. If $a < 0$, the system is stable, exhibiting exponential decay from any initial point towards zero.

Technically, we could add a third condition, in which $a = 0$. This means the derivative is zero, so all points are stable. Wherever we initialize $x(t)$, it remains fixed there for all time.

Linear differential equations have a simple analytic solution. Namely, given initial condition $x(t) = x_0$ and $\dot{x} = ax$, we have solution:

$$x(t) = x_0 e^{at}. \tag{7}$$

It is simple to verify that the time derivative of $x(t)$ is

$$\frac{d}{dt}\, x_0 e^{at} = a\, x_0 e^{at} \tag{8}$$

which is indeed equal to $a \cdot x(t)$, as required. If $a < 0$ this exponent has negative sign, so $x(t)$ decays to zero, while for $a > 0$ it clearly blows up to infinity.

4 Higher-dimensional dynamical systems

In many settings in neuroscience we are interested in multi-dimensional dynamical systems, such as those governing the evolution of spike rates of a group of neurons. In this case, the dynamic variable is a vector, and we write

$$\dot{\vec{x}}(t) = f(\vec{x}(t)), \tag{9}$$

where $\vec{x}$ is the vector

$$\vec{x}(t) = \begin{bmatrix} x_1(t) \\ \vdots \\ x_n(t) \end{bmatrix} \tag{10}$$

and f specifies the vector of derivatives of each component, given by

$$\dot{\vec{x}}(t) = \begin{bmatrix} \frac{dx_1}{dt} \\ \vdots \\ \frac{dx_n}{dt} \end{bmatrix}. \tag{11}$$

In class we visualized the behavior of some hypothetical 2-dimensional dynamical systems by visualizing their **flow fields** or **vector fields**. Such fields show you the direction the system will move from any point (x_1, x_2) in the 2D plane.

In this view, stable fixed points are (once again) points where $f(\vec{x})$ is the zero vector, meaning there is no change in $x(t)$ if it is initialized at such a point. Stable fixed points are ones for which all the flow field arrows point towards the fixed point, while unstable fixed points are ones for which the field arrows point away.

4.1 Line attractors

In multiple dimensions, new kinds of attractors besides stable fixed points become possible. A particularly important form is known as a line attractor, defined to a 1-dimensional line in the state space along which $f\vec{x})$ is zero along its entire length. Initialized anywhere in the immediate vicinity of a line attractor, the system will converge to a point on the line attractor, but different initial points will lead to different points along the attractor. Line attractors play an important role in the theory of neural circuits, where they are implicated in the theory of working memory and neural integration (e.g., for maintaining stable eye position after a saccadic eye movement).

4.2 Multi-dimensional linear dynamics

A multidimensional linear dynamical system is one for which the dynamics can be written as a linear matrix equation:

$$\dot{\vec{x}} = A\vec{x} \tag{12}$$

for some matrix A.

The behavior of such systems can be understood entirely in terms of the eigenvectors and eigenvalues of A. Remember that an eigenvector is defined as a vector $\vec{v}$ for which

$$A\vec{v} = \lambda\vec{v}, \tag{13}$$

that is A times the vector produces a rescaled version of the same vector, where eigenvector λ indicates the amount of the rescaling.

The eigenvectors of a linear dynamical system can be used to understand its behavior because we can decompose any state $\vec{x}$ as a superposition of eigenvectors:

$$\vec{x} = \sum w_i \vec{v}_i \tag{14}$$

for some weights w_i, and we can then think about how the system acts on each of those eigenvectors:

$$\dot{\vec{x}} = A\vec{x} = A(\sum w_i \vec{v}_i) = \sum w_i (A\vec{v}_i) = \sum w_i \lambda_i \vec{v}_i. \tag{15}$$

Here, the independent time evolution $v(t)$ for each eigenvector is often referred to as an *eigenmode* of the system.

We can determine the stability or instability of the system from its eigenvalues. In particular, if the real part of $real(\lambda_i) < 0$, the system decays to zero along this mode, just as in 1D dynamical systems. If on the other hand the real part $real(\lambda_i) > 0$, we have exponential growth along this eigenmode. The system is therefore stable only if ALL eigenvalues of A have real part less than zero.

Although we have not encountered them previously in this course, it turns out the eigenvalues of A can also be complex valued, so that we write $\lambda_i = a + ib$. Now a is the real part of the eigenvalue and b is the complex part. What does b tell us about the behavior of the system? It turns out that complex part of the eigenvalue gives rise to *rotation*, with the magnitude of b telling us the speed of the rotation (or oscillation).

From this we can see that multi-dimensional linear dynamical systems can have richer dynamical behavior than one-dimensional ones. One dimensional systems can only explode to infinity or decay to zero. Multi-dimensional systems, however, can explode, decay, and rotate. (They can of course also spiral down to zero if a¡0 and b is non-zero, or spiral out to infinity if a¿0 and b is non-zero). A "saddle" results when some eigenvalues have real part ¡0 and others have real part ¿ 0.

Although linear dynamical systems are quite restricted compared to the much richer space of nonlinear systems, the theory of linear systems is fundamental to the analysis of nonlinear dynamics. This is because the primary way that one analyzes the behavior of nonlinear dynamical systems is to linearly expand it (i.e., approximate it by its first order Tayler expansion) in the neighborhood of a fixed point and ask whether the corresponding linear system is stable or unstable.

5 Wong & Wang 2006