1 Dynamical Systems

We consider two types of dynamical systems:

1. Flows (I will use ordinary differential equations)

$$\begin{array}{c} \frac{d\vec{x}}{dt} = \vec{f}(\vec{x}, t) \\ \vec{x}(0) = \vec{x}_0 \end{array} \tag{1}$$

2. Maps

$$\begin{array}{c} \vec{x}_{n+1} = \vec{f}(\vec{x}_n) \\ \vec{x}_0 \text{ is known} \end{array} \tag{2}$$

A fixed point for a flow is a point $\vec{x}_0 \in \mathbb{R}^N$ such that $\vec{f}(\vec{x}_0) = 0$. A fixed point for a map is a point $\vec{x} \in \mathbb{R}^N$ such that $\vec{x} = \vec{f}(\vec{x})$.

A major part of studying a dynamical system is determining the behavior of the system near fixed points. This problem often reduces to the behavior of a linear system:

$$\begin{array}{c} \frac{d\vec{x}}{dt} = A\vec{x} \\ \vec{x}(0) = \vec{x}_0 \end{array} \tag{3}$$

The only fixed point for this system is the fixed point at $\vec{x} = 0$.

We need to define a few things. A *vector space* V contains vectors such that if $\vec{v} \in V$ and $\vec{w} \in V$ then $\vec{v} + \vec{w} \in V$ and $c\vec{v} \in V$. We will define a vector space as a *span*, where

$$V = \text{span}\{\vec{v}_1, ..., \vec{v}_M\}$$

so that any vector in V can be written as a linear combination,

$$\vec{v} = c_1\vec{v}_1 + ... + c_M\vec{v}_M.$$

If

$$\sum_i^M c_i\vec{v}_i = 0$$

only when $c_1 = c_2 = ... = c_M = 0$ then the vectors $\vec{v_i}$ are said to be *linearly independent*.

An *eigenvalue* of A is a scalar, $\lambda \in \mathbb{C}$, such that $A\vec{v} = \lambda\vec{v}$ for some $\vec{v} \in V$, which we call the *eigenvector* corresponding to λ.

We will assume that the matrix $A \in \mathbb{R}^{N\times N}$ has N linearly independent eigenvectors, corresponding to N eigenvalues,

$$A\vec{v}_i = \lambda_i \vec{v}_i.$$

Let $\vec{x}(0) = \vec{x}_0$. Since we have a full set of linearly independent eigenvectors, we can decompose as

$$\vec{x_0} = \eta_1 \vec{v}_1 + ... + \eta_N \vec{v}_N$$

and so we can write the linear system as

$$\vec{x}' = A(\eta_1(t)\vec{v}_1 + ... + \eta_N(t)\vec{v}_N)$$

$$\begin{aligned}\frac{d}{dt}\eta_1(t)\vec{v}_1 + \frac{d}{dt}\eta_N(t)\vec{v}_N &= A(\eta_1(t)\vec{v}_1 + ... + \eta_N(t)\vec{v}_N) \\ &= \eta_1(t)\lambda_1\vec{v}_1 + ... + \eta_N(t)\lambda_N\vec{v}_N\end{aligned}$$

Since the eigenvectors are linearly independent, we can write this as N separate (uncoupled) differential equations,

$$\frac{d}{dt}\eta_i(t) = \lambda_i \eta_i(t)$$

which have solutions

$$\eta_i(t) = e^{\lambda_i t}\eta_i(0).$$

If all of the eigenvalues are less than zero, then all of the solutions will go to zero, and the fixed point at the origin is said to be *asymptotically stable.*

Often, the eigenvalues can be complex. Consider

$$\left(\begin{array}{c} x \\ y \end{array}\right)' = \begin{bmatrix} a & -b \\ b & a \end{bmatrix} \left(\begin{array}{c} x \\ y \end{array}\right)$$

The matrix has eigenvalues $a \pm \imath b$. We set $z = x + \imath y$ and the above system becomes

$$z' = (a + \imath b)z.$$

Next, we put this into polar coordinates by letting $z = re^{\imath\theta}$. Substituting into the previous equation

$$z' = r'e^{\imath\theta} + \imath\theta' re^{\imath\theta} = (a + \imath b)re^{\imath\theta}$$

and so

$$r' + \imath\theta' r = (a + \imath b)r$$

Collecting like terms gives

$$r' = ar$$
$$\theta' = b$$

So, if the real part of the eigenvalues are less than zero, the fixed point is asymptotically stable, and the approach to the fixed point is a spiral - the frequency of which is determined by the imaginary part of the eigenvalue.

To summarize, for a linear system of ODE's

$$\vec{x}' = A\vec{x}$$

the fixed point at the origin is stable is the real part of the eigenvalues of A are negative. If the eigenvalues are complex, the approach will be a spiral. If the eigenvalues are real, orbits will approach the origin along the eigenvectors, where the relative sizes of the eigenvalues determines which dominates.

2 Bifurcations

I will make this section brief. First, the basic bifurcations that happen for flows

- The fold bifurcation (or saddle node, or tangent bifurcation) has the normal form (simplest system where the bifurcation can occur)

  $$\frac{dx}{dt} = \alpha + x^2.$$

  At $\alpha = 0$ there is a fold bifurcation. For $\alpha < 0$ there are two fixed points (one stable and one unstable). As α crosses zero, these two fixed points collide and are annihilated. The conditions for the fold bifurcation at $\alpha = 0$ and $x = 0$ for the system

  $$x' = f(x, a)$$

  are

  $$f(0,0) = 0$$
  $$\lambda = f_x(0,0) = 0$$
  $$f_{xx}(0,0) \neq 0$$
  $$f_\alpha(0,0) \neq 0$$

The first of these conditions is the fixed point condition. The second is the condition on the eigenvalue, and that a change in stability (and more) is taking place. The third condition ensures that that f is concave (either up or down, depending on which direction the bifurcation occurs) so that there is never a continuum of points. The fourth condition ensures that the system changes as α crosses through the bifurcation value.

The fold bifurcation is important in modeling, in particular conductance based modeling of neurons. It provides a mechanism to switch from resting (at the stable fixed point) to firing (elimination of fixed points so that the orbit escapes. The transition from resting to firing via this mechanism is called *type I excitability*, and has some distinct properties.

- The Hopf bifurcation has the normal form

$$
\begin{aligned}
x_1' &= \alpha x_1 - x_2 - x_1(x_1^2 + x_2^2) \\
x_2' &= x_1 + \alpha x_2 - x_2(x_1^2 + x_2^2)
\end{aligned}
$$

which is a linear part with complex eigenvalues $\alpha \pm \imath$, and a nonlinear part that is always pushing opposite of the variable - when $x_1 <$ then $x_1(x_1^2 + x_2^2) > 0$ and vice-versa. If we set $z = x_1 + \imath x_2$ then we get

$$
z' = (\alpha + \imath)z - z|z|^2.
$$

Finally, we set $z = \rho e^{\imath\phi}$ to get

$$
\begin{aligned}
\rho' &= \rho(\alpha - \rho^2) \\
\phi' &= 1
\end{aligned}
$$

When $\alpha < 0$ then there is only one fixed point for ρ, the origin. For $\alpha > 0$ the fixed point at the origin is still there, but it is unstable and there is now a periodic solution, which is stable.

The conditions for the Hopf bifurcation at a fixed point $x = 0$ and a parameter $\alpha = 0$ for the system

$$
x' = f(x, \alpha)
$$

are

$$
\begin{aligned}
f(0, 0) &= 0 \\
\lambda_{1,2}(0) &= \pm\imath\omega_0
\end{aligned}
$$

The Hopf bifurcation provides another mechanism for excitability, where a resting point can be excited onto a periodic solution, which for many conductance based models of neurons corresponds to spiking. This mechanism of excitability also exhibits distinct properties.

The bifurcations for maps occur when the eigenvalues cross the unit circle. When, as a function of a parameter, and eigenvalue crosses at 1, a fold bifurcation occurs. This fold is very similar to the fold for flows, also creating or annihilating fixed points via some tangency. When the eigenvalue crosses at some complex value of the unit circle, a Neimark-Sacker bifurcation occurs. This is the discrete analog to the Hopf bifurcation for flows, where periodic solutions are created and destroyed. Because these are so similar to the corrsponding bifurcations for flows, I won't spend any more time dealing with them here.

Of note is that for maps, a periodic solution is possible for a one dimensional system. This does not occur for flows. Because of this difference, there is a bifurcation that is exclusive to maps - the flip bifurcation. This bifurcation occurs when the crossing of the unit circle occurs at -1. The normal form for the flip bifurcation is

$$x_{n+1} = -(1+\beta)\eta + \eta^3$$

There will be an exercise on the flip bifurcation, so I won't say any more here.

3 Phase response curves, phase locking, and averaging

Let $X(t)$ be some quantity that is oscillating with period T. We define the *phase* of the oscillator

$$\theta = \frac{t}{T}$$

so that, for example, $\theta = 3$ would indicate that X has undergone three cycles.

We want to know what happens when the oscillator is subjected to an external input during the phase. We are assuming that the coupling and inputs are *weak*, which means that input to the oscillator only perturbs the phase (rather than knocking the orbit off of the limit cycle into a qualitatively different behavior).

Suppose an input to the system, in the form of a δ pulse, arrives at phase $\theta = \theta_0$. The phase of the oscillator changes. Let $T_1(\theta)$ be the time of the next peak. We define the phase shift as

$$\Delta\theta = \frac{T - T_1(\theta)}{T}$$

If T_1 arrives sooner than the regularly scheduled peak, then the phase has been advanced. Conversely, if T_1 is longer than T, then the phase has been delayed. So, $\Delta\theta < 0$ corresponds to a phase delay, and $\Delta\theta > 0$ corresponds to a phase advance. The graph of $\Delta\theta$, as a function of θ, is called the *phase response curve (PRC)*.

We are going to use the PRC to solve two problems. The first is whether or not the oscillator will train to a periodic stimulus. Suppose there is an input that arrives every P time units. Let θ_n be the phase of the oscillator right before the nth stimulus. We want to know what the phase of the oscillator will be right before the $n+1$th stimulus. Since we know the input occurs at phase θ_n. we know that the phase right after the input will be

$$\theta_{n^+} = \theta_n + \Delta(\theta_n).$$

To get to the next stimulus, just advance the phase by P/T:

$$\theta_{n+1} = \theta_n + \Delta(\theta_n) + \frac{P}{T}.$$

Now, we want to know whether or not the oscillator will train to this periodic stimulus. We define M:N phase locking as M "spikes" for every N "inputs" (and it means exactly locked). Here, we will focus on $M:1$ phase locking ($N \neq 1$ is too hard). For each stimulus, we want the phase of the oscillator to advance M times. So, we want $\theta_{n+1} = \theta_n + M$. We solve

$$\theta + M = \theta + \Delta\theta + \frac{P}{T}$$

to get

$$\Delta\bar{\theta} = M - \frac{P}{T}.$$

If this solution exists, then the oscillator does train to the stimulus in an $M:1$ fashion.

The next step is to determine if the phase locked solution is stable. To do this, linearize the map

$$\left.\frac{\partial f}{\partial \theta}\right|_{\theta=\bar{\theta}} = 1 + \Delta'(\bar{\theta})$$

and so if $-2 < \Delta'(\bar{\theta}) < 0$ the phase locked solution will be stable. Note here that since the phase response curve is a periodic function, if there is one solution, then there has to be another (unless there is a tangency), and so if there is a solution, then there is a stable solution (might not be the same one).

The second problem that we address using the PRC is synchronization of (weakly) coupled oscillators. We will consider these in terms of the phase of the oscillators, writing

$$\begin{aligned} \theta_1' &= 1 + H(\theta_2 - \theta_1) \\ \theta_2' &= 1 + H(\theta_1 - \theta_2) \end{aligned} \tag{4}$$

If we assume a pulse stimulus, as we have thus far, then when θ_2 finishes a phase and "fires", the phase θ_1 will be altered. This happens as a step function (the integral over a delta function). To avoid this discontinuity, we find the integral of the the function H over an entire period, and then average over the period, substituting something continuous for something not continuous.

When θ_2 crosses the firing threshold, we know that $\theta_1 = T - (\theta_2 - \theta_1)$. Let $\phi = \theta_2 - \theta_1$. The phase shift of θ_1 will be given by $\Delta(T - \phi)$ - the PRC evaluated at $T - \phi$. To average this over an entire period, we write H as

$$H(\phi) = \frac{1}{t}\int_0^T \Delta(t)\delta(t+\phi)dt.$$

We can determine the steady state phase relationship between the oscillators:

$$\phi' = \theta_2' - \theta_1' = H(-\phi) - H(\phi) = -2G(\phi),$$

where G is the odd part of H. Since G is odd, $G(0) = 0$ and so a synchronous solution exists. For it to be stable requires $G'(0) > 0$.

Let

$$V^*(t) = \lim_{a\to 0}\frac{\Delta(t,a)}{a}$$

where a is the amplitude of the stimulus. The function V^* is called the infintesimal PRC, which we can use to extrapolate the PRC values for different amplitude stimuli. We can use this to address the problem when the stimulus is not a δ pulse. A common way to model synaptic inputs is be using an α function, for example

$$\alpha(t) = \alpha_0 t e^{-\beta t}.$$

The synaptic current is then written

$$\alpha(t)(V_{syn} - V(t)),$$

where V_{syn} is the reversal potential. We can compute the coupling function

$$H(\phi) = \frac{1}{T}\int_0^T V*(t)\alpha(t+\phi)(V_{syn} - V(t))dt$$

and so we can determine the steady state phase relationships between cells.