Peter Latham October 15, 2013

Linear analysis

Background

Many of the processes in computational neuroscience are modeled as ordinary differential equations. These equations have the form

$$\frac{dx_i}{dt} = F_i(\mathbf{x}) \tag{1}$$

where $\mathbf{x} = (x_1, x_2, ..., x_n)$ is an n-dimensional vector and F_i is some function. The x_i might, for instance, be voltage and gating currents in a Hodgkin-Huxley model, synaptic variables in a short term plasticity model, or firing rates in a network model. Except in very rare instances, this set of equations can't be solved analytically. We can, however, get some intuition into the dynamics by considering the fixed points and their stability. The "stability" part is where linear analysis comes in.

Linearizing equations

Linearizing Eq. (1) starts with finding a fixed point. Assume we've done that, and that the fixed point is at $\mathbf{x}_0$; that is, $F_i(\mathbf{x}_0) = 0$ for all i. We then Taylor expand around $\mathbf{x}_0$ by letting

$$\mathbf{x} = \mathbf{x}_0 + \delta\mathbf{x}\,, \tag{2}$$

or, in component form, $x_i = x_{0,i} + \delta x_i$. Inserting either of these expressions into Eq. (1), and noting that $dx_{0,i}/dt = 0$, we have

$$\frac{d\delta x_i}{dt} = F_i(\mathbf{x}_0 + \delta\mathbf{x})\,. \tag{3}$$

We then assume that $\delta\mathbf{x}$ is small and expand $F_i(\mathbf{x}_0 + \delta\mathbf{x})$ to first order,

$$F_i(\mathbf{x}_0 + \delta\mathbf{x}) \approx F_i(\mathbf{x}_0) + \sum_j \frac{\partial F_i(\mathbf{x}_0)}{\partial x_{0,j}}\,\delta x_j = \sum_j \frac{\partial F_i(\mathbf{x}_0)}{\partial x_{0,j}}\,\delta x_j \tag{4}$$

where the second equality follows because $F_i(\mathbf{x}_0) = 0$. It is useful to define the Jakobian matrix, $\mathbf{J}$, via

$$J_{ij} = \frac{\partial F_i(\mathbf{x}_0)}{\partial x_{0,j}} \,. \tag{5}$$

Then, replacing the "approximately equals" sign that appears in Eq. (4) by an equality (which is valid in the limit $\delta x_i \to 0$), Eq. (3) becomes

$$\frac{d\delta x_i}{dt} = \sum_j J_{ij} \delta x_j \,. \tag{6}$$

Alternatively, we can use vector notation and write

$$\frac{d\delta\mathbf{x}}{dt} = \mathbf{J} \cdot \delta\mathbf{x} \tag{7}$$

where $\mathbf{J}$ is a matrix with elements J_{ij} and "$\cdot$" is the standard dot product: $\mathbf{J} \cdot \delta\mathbf{x} = \sum_j J_{ij}\delta x_j$.

As with just about every equation, we solve this one by guessing. Our guess is that

$$\delta\mathbf{x} = \mathbf{v} e^{\lambda t} \tag{8}$$

where $\mathbf{v}$ is some (constant) vector. Inserting this into Eq. (6), and noting that $d\delta\mathbf{x}/dt = \lambda\mathbf{x}$, we have

$$\mathbf{J} \cdot \mathbf{v} = \lambda \mathbf{v} \,. \tag{9}$$

This is an eigenvalue equation, and it must be solved for both λ and $\mathbf{v}$. This is done in two steps. The first is to solve for λ. As we (should) know from linear algebra, Eq. (9) has a nontrivial solution (meaning a solution in which at least one of the elements of $\mathbf{v}$ is nonzero) if and only if

$$\mathrm{Det}[\mathbf{J} - \lambda\mathbf{I}] = 0 \tag{10}$$

where "Det" is the determinant and $\mathbf{I}$ is the identity matrix. If $\mathbf{J}$ is $n \times n$, then this equations has n different solutions – n different values of λ. For each of them there is a different eigenvector. Let us use λ_k to denote the k^{th} eigenvector and $\mathbf{v}_k$ to denote its corresponding eigenvector. Mathematically, λ_k and $\mathbf{v}_k$ are related via

$$\mathbf{J} \cdot \mathbf{v}_k = \lambda_k \mathbf{v}_k \,. \tag{11}$$

If we were interested only in stability, we would solve Eq. (10) for the λ_k, and then determine stability by looking at the real part of all of them: if the all the real parts were negative, then the fixed point is stable; if at least one is positive, then the fixed point is unstable. However, we are often interested in one more thing: the dynamics near the fixed point. That is, how does $\delta\mathbf{x}(t)$ evolve given that we know $\delta\mathbf{x}(0)$, its initial value?

To answer that, we need the full expression for $\delta\mathbf{x}(t)$, which is

$$\delta\mathbf{x}(t) = \sum_k a_k \mathbf{v}_k e^{\lambda_k t} \tag{12}$$

where the a_k are constant. It is easy to verify that this does indeed satisfy Eq. (7). Our job now is to find the coefficients, a_k. To do that, we introduce adjoint (or left) eigenvectors. These, which we denote $\mathbf{v}_k^\dagger$, obey the equations

$$\mathbf{v}_k^\dagger \cdot \mathbf{J} = \lambda_k \mathbf{v}_k^\dagger\,. \tag{13}$$

If $\mathbf{J}$ is symmetric, then the adjoint eigenvectors are equal to the eigenvectors; otherwise, they aren't. The really important fact about them is that they form an orthogonal basis, in the sense that they can be chosen so that

$$\mathbf{v}_k^\dagger \cdot \mathbf{v}_l = \delta_{kl} \tag{14}$$

where δ_{kl} is th Kronecker delta: $\delta_{kl} = 1$ if $k = l$ and 0 otherwise.

As an aside, orthogonality is easy to show, at least when all the eigenvectors are different:

$$\mathbf{v}_k^\dagger \cdot \mathbf{J} \cdot \mathbf{v}_l = \lambda_k \mathbf{v}_k^\dagger \cdot \mathbf{v}_l = \lambda_l \mathbf{v}_k^\dagger \cdot \mathbf{v}_l\,. \tag{15}$$

The first equality follows from Eq. (13); the second from Eq. (11). The second equality tells us that if $\lambda_k \neq \lambda_l$, then $\mathbf{v}_k^\dagger \cdot \mathbf{v}_l = 0$. So, if no two eigenvalues are the same, so that $\lambda_k \neq \lambda_l$ implies that $k \neq l$, then it follow that $\mathbf{v}_k^\dagger \cdot \mathbf{v}_l = 0$ whenever $k \neq l$. Forcing $\mathbf{v}_k^\dagger \cdot \mathbf{v}_k$ to be 1 is just a matter of choosing a normalization.

To see why all this is useful, dot both sides of Eq. (12) with $\mathbf{v}_l^\dagger$, use the orthogonality condition given in Eq. (14), and evaluate the expression at $t = 0$. This gives

$$\mathbf{v}_l^\dagger \cdot \delta\mathbf{x}(t) = a_l \tag{16}$$

Inserting this into Eq. (12) (and changing l to k), we see that

$$\delta\mathbf{x}(t) = \sum_k \mathbf{v}_k \mathbf{v}_k^\dagger \cdot \delta\mathbf{x}(0)\, e^{\lambda_k t}\,. \tag{17}$$

This is a nice expression. More importantly, it is also often very useful. That's because at long times the right hand side is dominated by the largest eigenvalue; in that case Eq. (17) is reduced to one term.

Note that by evaluating Eq. (17) at time $t = 0$, we have

$$\sum_k \mathbf{v}_k \mathbf{v}_k^\dagger = \mathbf{I}\,. \tag{18}$$

Moreover, differentiating Eq. (17) once with respect to time, evaluating the expression at $t = 0$, and using Eq. (7), we see that

$$\sum_k \lambda_k \mathbf{v}_k \mathbf{v}_k^\dagger = \mathbf{J}\,. \tag{19}$$

(There are easier ways of showing this; for instance, by showing that the eigenvalues and eigenvectors of the left and right hand sides of Eq. (19) are the same.) It is also not hard (for instance, by taking more time derivatives) to show that

$$\sum_k \lambda_k^n \mathbf{v}_k \mathbf{v}_k^\dagger = \mathbf{J}^n \tag{20}$$

where $\mathbf{J}^n$ means take n dot products: $\mathbf{J}^n \equiv \mathbf{J} \cdot \mathbf{J} \cdot ...$ with $\mathbf{J}$ appearing n times on the right hand side. All of this is mind-numbingly useful; you should remember it.

The 2-D case

This is next!