Computational Neuroscience 2012 – Lecture 1 (part A)

The overall goal of this course is to teach you how to formulate and solve problems in computational neuroscience. The field of nonlinear dynamics is critical to this endeavor. For instance, the transition from a silent to an active neuron can involve loss of stability of a fixed point and the emergence of a limit cycle according to different mechanisms referred to as bifurcations. In this lecture I will cover these concepts. Because for the study of nonlinear dynamics one often has to resort to numerical methods I will also tell you about root finding and integration of ordinary differential equations (ODEs). Most of the material covered in this lecture can be found in “Nonlinear dynamics and Chaos” by Steven Strogatz, as well as in many of the other books on nonlinear dynamics.

**Example ODE**: $y’ = ry(1 - y/K)$.

This is the logistic equation and $y$ could be the number of animals, $K$ the carry capacity and $r$ a positive growth rate, $x$ is the independent variable and represents time. The first factor is a growth term and the second factor an inhibiting term. The prime denotes the derivative $y’ = dy/dx$. In the Newton notation one also uses a dot above the variable if the derivative is with respect to time: $\dot{y} = dy/dt$.

Let’s get some intuition for this equation. If the equation was $y’ = ry$, like for small $y$ values, then the solution would be $y(x) = y_0 e^{rx}$. Which in turn means that the approximation used to obtain this solution will become invalid quickly. Hence to study the solution to this equation we will need to use numerical methods.

**The Euler & Modified Euler method**

We will use the general notation $y’ = f(x,y)$. Our goal is to predict from the value of $y$ at $x$, the value $y + dy$ for a higher value of $x = x + dx$. The increment in $y$ is given by $dy = f(x,y)dx$. The Euler method consists of taking many of these small steps (we use $h=dx$):

\[
x_n = x_0 + nh
\]

\[
y_{n+1} = y_n + hf(x_n, y_n)
\]

As Figure 1 shows, this method is not that good when $f$ varies strongly during the time course of one step. The error made during one step is of the order $h^2$, but since these errors accumulate across integration steps, the global error is $h$.

![Figure 1. The Euler method yields large errors because the derivative can change rapidly during one integration step.](image)

The modified Euler method takes a step ahead (indicated by the tilde on $y$), to see how the derivative has changed, and then makes the final step according to the mean of the derivative at the start and the end of the step. This method has a local
error of $h^3$ and thus a global error of $h^2$. This means that halving the step size $h$ makes the solution 4 times more accurate.

$$x_n = x_0 + nh$$

$$\tilde{y}_{n+1} = y_n + hf(x_n, y_n)$$

$$y_{n+1} = y_n + \frac{1}{2} h(f(x_n, y_n) + f(x_{n+1}, \tilde{y}_{n+1}))$$

The Euler method is not a good method, and should only be used for exploratory simulations. Figure 3 shows why. For every numerical operation there is a round off error. It stands to reason that the global effect is proportional to the number of steps taken, that is $T/h$, where $T$ is the integration interval. The error for the Euler method is proportional to $Ch+T/h$, whereas for Modified Euler is proportional to $Dh^2+T/h$. It makes no sense to reduce the step size too much, because round-off error will at some point dominate the error. Hence, there is a sweet spot for the step size, namely the $h$ value for which the error is minimal. The error at the sweet spot for Euler is much higher than for Modified Euler. The Modified Euler method is one of a class of algorithms known as Runge-Kutta (RK) methods. In professional code a combination of 4th and 5th RK with adaptive steps is used. In Matlab use the function ode45 for this purpose.

**Self-test 1.** Write out explicitly the Euler and Modified Euler method for the logistic equation.

**Example – continued.** To study the logistic equation, we start at $x=0$ from different $y$ values and determine its behavior by sketching (Figure 4) or actual integration of the trajectories (please try). Starting from $y=0$, the $y$-value stays zero. Starting from $y=K$, the solution also stays there. When $0<y<K$, the derivative is always positive and the solution increases until it reaches $y=K$. Likewise when $y>K$, the derivative is always negative, hence the solution converges to $y=K$.

Figure 2. Modified Euler is comprised of two steps

Figure 3. Modified Euler leads to a smaller error.

Figure 4. Trajectories of the logistic equation.
The points $y=0$ and $y=K$ are special: solutions that reach these points stay there. Hence we call them fixed points. There is a difference between them, trajectories close to $y=0$, move away from $y=0$, whereas trajectories close to $K$, go closer to them. The former is therefore referred to as an unstable fixed point (FP) and the latter as a stable one.

The dynamics can be more succinctly summarized using only the $y$-axis, with arrows indicating the direction of the $y$-change, fixed points as circles, open circle unstable and close circle stable.

Fixed points can be found directly by solving for $y'=0$. Setting $f(x,y)=f(y)=ry(1-y/K)=0$. We indeed get $y=0$ and $y=K$. For more complicated forms of $f(y)$ you will need a root finder, with which we will deal with shortly.

The stability of a FP is defined in terms of the effects of a small perturbation. When a perturbation becomes smaller over time, that is, the solution returns to the fixed point, then the fixed point is stable. Otherwise, it is unstable. Let’s consider a small perturbation denoted by $\delta y = y - y^*$ (the fixed point is indicated by an asterisk), then the linearized differential equation becomes $\delta y' = f(y^* + \delta y) \approx f(y^*) + f'(y^*)\delta y = \alpha \delta y$ (note that the first term vanishes at the fixed point, alpha is short hand for the derivative at the fixed point). Hence the solution is $\delta y = \delta y_0 e^{\alpha t}$. When $\alpha > 0$, the perturbation increases over time, thus the fixed point is unstable. When $\alpha < 0$, the perturbation decreases over time, thus the fixed point is stable. When $\alpha = 0$, we cannot conclude anything about the stability, because we will have to consider the effects of higher order terms in the perturbation.

**Example – continued.** We rewrite the equation slightly into $y' = f(y) = y(r - y)$. The fixed points are found by setting $f(y) = y(r - y) = 0$ and are $y=0$ and $y=r$. The stability is determined by substituting these values in the derivative $f'(y) = r - 2y$, yielding for $y=r$, $f'(r) = r - 2r = -r$, hence stable for positive $r$ and unstable for negative $r$, whereas for $y=0$, $f'(0) = r$, which means it is unstable for positive $r$ and stable for negative $r$. Hence the stability of the fixed points exchanges at $r=0$ as shown in Figure 6. We say that a bifurcation (specifically transcritical bifurcation) has taken place and, which is best displayed in a bifurcation diagram.

![Figure 5. Fixed points of logistic equation.](image)

![Figure 6. Stability of fixed points](image)

![Figure 7: Transcritical bifurcation. The fixed point position is plotted versus bifurcation parameter $r$](image)
It is useful to be able to recognize other standard bifurcations.

In the **saddle-node** bifurcation a stable and an unstable fixed point approach each other closer and closer until they both disappear at the bifurcation point. Near the bifurcation point systems with this type of behavior can be described by the ODE $y' = r + y^2$.

In the **supercritical pitchfork** there is one stable fixed point for $r<0$ which loses it stability at $r=0$ at which point two stable fixed points get added. The canonical behavior is described by $y' = ry - y^3$. This means that the system goes through a smooth transition at $r=0$ because the amplitude of the new fixed points increase as a square root of $r$.

The **subcritical pitchfork** is a more dangerous transition. For negative $r$ there is one stable fixed point at $r=0$ and two unstable ones. At $r=0$, the stable fixed point loses its stability, at the same time the other two fixed points disappear. This means that if the system is at $y=0$ for $r<0$, then when $r>0$ it will diverge to infinity, that is explode. The system near the bifurcation point is described by $y' = ry + y^3$.

**Example.** Consider the dynamical system $y' = -y + \beta \tanh y$. What type of bifurcation would you encounter when beta is varied? To answer this question we first need to determine the location of the fixed points by solving $y' = -y + \beta \tanh y = 0$. There always is a solution at $y=0$, and as the figure illustrates, when beta is large enough, three solutions. It is not possible to explicitly give the value of the nonzero roots. These will have to be found numerically, for instance, via Newton's method.
**Newton's method.** The goal is to solve the equation \( f(y) = 0 \). Let's assume we are at \( y_n \) for which \( f(y_n) \neq 0 \). We want to find a new point \( y_{n+1} = y_n + h \) that is closer to zero. This is achieved by setting the first order Taylor expansion to zero: \( f(y_{n+1}) = f(y_n + h) = f(y_n) + hf'(y_n) = 0 \). Hence \( h = -f(y_n)/f'(y_n) \) or \( y_{n+1} = y_n - f(y_n)/f'(y_n) \). Newton's method is very fast because it converges quadratically to a root that means that the number of correct digits doubles with each iteration. It also means that it is unstable (consider what happens when \( f'(y) = 0 \)).

**Example continued.** Hence, to find the fixed points we need to iterate

\[
y_{n+1} = y_n - \frac{(-y_n + \beta \tanh y_n)}{(-1 + \beta / \cosh^2 y_n)}.
\]

The derivative at those points is \( f'(y) = -1 + \beta / \cosh^2 y \).

**Self-test 2:** Determine the stability of the fixed points as a function of beta. What kind of bifurcation takes place? Could you have guessed that by considering an expansion in \( r=1-\beta \)?

Fixed points also exist in the dynamics of two-dimensional phase space, but in addition it is possible to have so called limit cycles. These are an essential concept for describing neural dynamics.

**Example.** Consider \( \ddot{x} + x = 0 \) and let's define \( y = \dot{x} \) (we altered the notation a bit for convenience: the dot stands for the time derivative and \( y \) and \( x \) are now the dependent variables). We can then write this second order differential equation as two coupled first order equations:

\[
\begin{align*}
\dot{y} &= \ddot{x} = -x \\
\dot{x} &= y
\end{align*}
\]

or in vector form

\[
\begin{pmatrix}
\dot{x} \\
\dot{y}
\end{pmatrix} =
\begin{pmatrix}
0 & 1 \\
-1 & 0
\end{pmatrix}
\begin{pmatrix}
x \\
y
\end{pmatrix}
\]

One solution is (depending on initial conditions and ignoring initial phase):

\[
\begin{align*}
x(t) &= A\cos t \\
y(t) &= -A\sin t
\end{align*}
\]
This is a circle in phase space, which looks like a limit cycle, except that the amplitude $A$ is not fixed will be changed by a perturbation. We can make a real limit cycle by fixing the radius. Consider first the same problem in polar coordinates

\[
\begin{align*}
x &= \rho \cos \theta \\
y &= \rho \sin \theta
\end{align*}
\]

and set the time derivative equal to the equation of for the circle:

\[
\begin{align*}
\dot{x} &= \rho \cos \theta - \rho \dot{\theta} \sin \theta = y = \rho \sin \theta \\
\dot{y} &= \rho \sin \theta + \rho \dot{\theta} \cos \theta = -x = -\rho \cos \theta
\end{align*}
\]

This is a linear equation for the derivative of rho and theta

\[
\begin{pmatrix}
\cos \theta & -\rho \sin \theta \\
\sin \theta & \rho \cos \theta
\end{pmatrix}
\begin{pmatrix}
\dot{\rho} \\
\dot{\theta}
\end{pmatrix}
= \rho
\begin{pmatrix}
\sin \theta \\
-\cos \theta
\end{pmatrix}
\]

whose solution is

\[
\begin{align*}
\dot{\rho} &= 0 \\
\dot{\theta} &= -1
\end{align*}
\]

We generate a limit cycle by altering the equation for rho

\[
\begin{align*}
\dot{\rho} &= \mu \rho - \rho^3 \\
\dot{\theta} &= \omega + b \rho^2
\end{align*}
\]

The limit cycle is then given by

\[
\begin{align*}
\rho &= \sqrt{\mu} \\
\theta &= (\omega + b\mu)t
\end{align*}
\]

It is stable because small perturbations away from the limit cycle return to it.

**Intermezzo.** Determination of stability of fixed points in 2D systems. Consider the following set of equations

\[
\begin{align*}
\dot{x} &= f(x,y) \\
\dot{y} &= g(x,y)
\end{align*}
\]

Null clines are the lines on which one variable does not change. Thus, the x nullcline is given by $f(x,y)=0$, or $y=h(x)$ (if the relationship can be inverted), whereas the y
nullcline is given by \( g(x,y)=0 \), or \( y=k(x) \). The fix point is the intersection of nullclines, where all the derivatives are zero \( f(x^*,y^*)=g(x^*,y^*)=0 \).

The stability of the fixed point is again defined in terms of the stability of perturbations, but now the perturbations are two dimensions:

\[
(\delta x, \delta y) = (x - x^*, y - y^*)
\]

the evolution of a perturbation is given by

\[
\frac{d}{dt}(\delta x, \delta y) = \begin{pmatrix} f(x^*,y^*) \\ g(x^*,y^*) \end{pmatrix} + \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix} \begin{pmatrix} \delta x \\ \delta y \end{pmatrix} = \nabla F(x^*, y^*) \delta x
\]

where \( F \) is the vector function having \( f \) and \( g \) as components. We can simplify this by substituting the values for the derivatives at the fixed point

\[
\frac{d}{dt}(\delta x, \delta y) = A \delta x
\]

with

\[
A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}.
\]

We first consider the case \( b=c=0 \). Depending on the sign of \( a \) and \( d \), and whether they are nonzero there are four general cases: stable fixed point, unstable fixed point, as well as the new cases saddle point, and degenerate (when one of \( a \) & \( d \) is

![Figure 13. Stabilities possibilities for a diagonal matrix A.](image-url)
The general case with nonzero $b$ and $c$ can be brought in the same simple form using eigenvectors:

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix} = V \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix} V^T$$

where $V$ has the corresponding eigenvectors as columns.

In this case new stability possibilities occur, because the eigenvalues determined via $\det(A - \lambda I) = 0$ can be complex. They are given by

$$\lambda_\pm = \mp \frac{1}{2} \tau \pm \frac{1}{2} \sqrt{\tau^2 - 4\Delta},$$

where $\tau = TrA = a + d$ and $\Delta = \det A = ad - bc$. The solution for the time course of the perturbation, expressed in the new coordinate system defined by the eigenvectors, would be

$$\delta x(t) = e^{\mu t} \cos \omega t,$$

$$\delta y(t) = e^{\mu t} \sin \omega t$$

(ignoring initial phase and amplitude),

where $\mu = \text{Re} \lambda_*$ and $\omega = \text{Im} \lambda_*$. This leads to spirals (Figure 14).

Figure 15 where the type of solution is plotted as a function of the trace and determinant of the stability matrix $A$ is very helpful for analysis of stability.

![Figure 14. Perturbations spiral towards or away from the fixed point.](image)

![Figure 15. Type of fixed point as a function of the trace and determinant of the derivative matrix at the fixed point.](image)