II. Nonlinear ODES

If all differential equations were linear, then life would be easier but not so interesting. Most of the models that arise in real physical systems involve nonlinearities and as a consequence a much broader range of behavior is possible such as <u>chaos</u> and <u>oscillations</u>. We will continue building our simple membrane model by adding a nonlinear voltage-dependent conductance. This conductance is due to calcium. The equation is

$$C\frac{dV}{dt} = I + g_l(V_L - V) + g_{Ca}m_{\infty}(V)(V_{Ca} - V)$$

where

$$m_{\infty}(V) = .5(1 + \tanh((V - V_1)/V_2))$$

This equation is already too difficult to solve analytically so one sees the advantage of numerical and qualitative techniques. (Actually, you can write the solution down in terms of an integral which you cannot evaluate except numerically!)

The ODE file for this equation in the old style is

```
# One fast persistent calcium channel
# Here is the equation
dv/dt=(i+gl*(vl-v)+gca*minf(v)*(vca-v))/c
#and the initial condition
V(0)=-60
# and the calcium current
aux ica=gca*minf(v)*(v-vca)
# and the parameters
param vl=-60,vca=120
param i=0,gl=2,gca=4,c=20
param v1=-1.2,v2=18
# and the functions
minf(v)=.5*(1+tanh((v-v1)/v2))
done
```

I have attempted to make comments which tell you what is going on. There are 2 new things here. **Auxiliary** quantities and **User defined** functions. Since functions are really important we will cover them first.

User defined functions.

User defined functions are declared just like you would write them. They can have up to 9 arguments. Thus the function **minf** has 1 argument and is a squashing function. A function of 2 variables, say, f(x,y) = exp(x) *sin(y) would be written as

```
f(x,y)=exp(x)*sin(y)
```

Auxiliary quantities.

We saw in the previous example that it was possible to add new <u>columns</u> to the <u>Data Browser</u> window. This is fine if you think of something you want to compute while in XPP. But the **auxiliary** declaration allows you to incorporate quantities that are not explicitly solutions to differential equations but instead some combinations of them. They are declared by starting the line with **aux** followed by the name of the quantity an equal sign and the definition. Now when you run this, you will be able to save the value of the calcium current and plot it as a function of time.

Homework 1.3

Add another auxiliary variable to your file which tracks the leak current, $gl^*(V-VL)$.

Fixed quantities

In the above examples, the calcium current is computed twice: once in the definition of the right-hand side and another time as an auxiliary quantity. While for this simple example, it probably doesn't matter (unless you are running on a PC with no math coprocessor) there are plenty of times when it will. If you were writing a program in C or FORTRAN you might define an intermediate quantity and use it to save on computation time. In XPP, this is done with **fixed** quantities that are declared by typing **name=formula** into the file. Fixed quantities are always evaluated before the right-hand sides are evaluated and are evaluated in the order that they are defined.

Thus, a faster version of the ode is

```
# One fast persistent calcium model with fixed quantities
# Here is the equation
dv/dt=(i+gl*(vl-v)-icaf)/c
#and the initial condition
V(0)=-60
# and the calcium current as a fixed quantity
icaf=gca*minf(v)*(v-vca)
# make ica available to look at
aux ica=icaf
# and the parameters
param vl=-60, vca=120
param i=0,gl=2,gca=4,c=20
param v1=-1.2, v2=18
# and the functions
minf(v)=.5*(1+tanh((v-v1)/v2))
done
```

NOTE XPP complains if things have the same names, thus, I have not named the AUXILIARY and the FIXED variables the same thing.

You have now learned the essential components of an ODE file:

- Declaration of differential equations
- Declaration of parameters
- Fixed variables
- Auxiliary quantities
- User defined functions
- Initial conditions

Most applications use no more than this.

Homework 1.4

Consider the nonlinear pendulum

$$ml\frac{d^2x}{dt^2} = -ml\sin(x) - f\frac{dx}{dt}$$

Rewrite this as a pair of first order differential equations. The frictionless energy of the system is given by:

$$E = \frac{1}{2}ml^2 \left(\frac{dx}{dt}\right)^2 + mgl(1 - \cos(x))$$

Write an ODE file for it in the old style and then in the new style. Keep track of the energy with an auxiliary variable. Assign some positive values to all of the parameters and some random initial conditions. Answer!

Write an ODE file for the single variable continuous time Hopfield model

$$\tau \frac{da}{dt} = -a + w f(a) + i$$

where

$$f(a) = 1/(1 + e^{-\beta(a-\theta)})$$

Use beta=2, theta=1, i=0, tau=1, w=1, a(0)=0. Answer!

Multiple equilibria and hysteresis

Now that you undestand the essentials of creating an ODE file, we will explore some more of the features of the program. Recall that we wish to explore:

$$C\frac{dV}{dt} = I + g_l(V_L - V) + g_{Ca}m_{\infty}(V)(V_{Ca} - V)$$

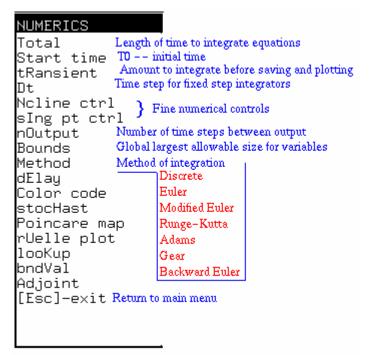
where

$$m_{\infty}(V) = .5(1 + \tanh((V - V_1)/V_2))$$

Fire the file up by clicking on the equation. As usual the main window and the others will show up on the screen. Let's take a look at a very important set of menus:

Numerics Menu

Click (U) or on the $\underline{\mathbf{n}(\mathbf{U})\mathbf{merics}}$ part of the main menu (*i.e.* type "U") and a new menu will appear.



This menu is very important as it sets the parameters for all of the numerical algorithms in XPP. Details of the commands for this are found by clicking on the title of this section. I will briefly summarize the other most important commands for you. For the present example, the voltage can reach up to 120 mV. XPP attempts to prevent numerical overflow by stopping a calculation when any variable or auxiliary quantity exceeds a **Bound** that is set by the user. The default when XPP fires up is **100** which is less than what we would like. Set the **Bound** to 1000 by clicking on (B) and adding a 0 to make the global bount 1000 instead of 100. Type (Enter) when you are done. Next, we want to integrate for at least 200 msec so change the amount of time to integrate to 200. Do this by clicking on (T) for **Total** and changing the 20 to 200 and typing (Enter).

Now is a good time to take a look at other things in this menu. The time step for integration **Dt** is set by clicking on (D) and chjanging it. If **Dt** is negative, then the program integrates bakwards in time. The default is **Dt=0.05**. For this simple problem, set **Dt=.2** by clicking (D), typing .2, and then (Enter). **n(O)ut** is important as it tells XPP how frequently you want output to plot and browse. It is set to 1 by default thus, you will get output every 0.05 msec in these examples. The **t(R)ansient** tells the program how long to integrate before saving and plotting the numbers. This is useful for integrating out transient effects. **Start time** tells the integrator what the starting time is. It is set to 0 by default and is totally irrelevant for *autonoumous* differential equations that do not have time explicitly in them. Finally, **Method** tells the program which method to use to integrate the equations. The default is Adams-Bashforth predictor corrector. The **Gear** method is the only presently available method in XPP which uses an *adaptive* step size. It will integrate *stiff* differential equations which are impossible to integrate using standard means. It is a very robust integrator. The other integrators are well-known and can be found in any book on numerical methods. **Modified Euler** is sometimes called Heun's method.

Having set the global bounds and the total integration time, return to the main menu by clicking (Esc). Set the window size by clicking (W) (W) to bring up the window box. Change it so that the X-axis goes from 0 to 200 and the y-axis from -150 to 150. Click on (Ok) or type (Tab) to enter the results. Type (I) (G) to integrate the equations. You should see a straight line across the screen. We started essentially at rest. Now type (I) (N) to manually enter new initial conditions. You will be asked for the initial voltage. Type in -20. You should see a decay to the rest state just like you saw in the linear problem. Now start with initial data of V=-10. Click (I) (N) again and then type in -10. Aha! the voltage does not decay; instead it increases to a new level of around 50 mV. This is an example of multi-stability. Nonlinear systems are often characterized by the existence of multiple stable behaviors. This cannot happen with linear differential equations (unless they are degenerate.)

Making another window

Lets look at the calcium current. Create a new window by clicking (H) (C). This invokes the HalfWindow command a stupid name that is a holdover from the DOS version where the window was split in half. Grab the lower corner of the window and make it larger. Note that the window has a small square in the upper left corner that tells you it is the current plotting window. Now in the main window click (X) to choose what to plot versus time and type ICA (Enter) at the prompt. Recall that ICA is the name you gave the calcium current. You will see the calcium current plotted in the new window as a function of time. Note that it is negative and so it is an inward current. To make the voltage window the active plotting window, click the mouse inside the graph and the little square will show up on the voltage window. Make the calcium window active again. Now click the right mouse button somewhere in the picture and look at the region underneath the picture in the the main window, the info area. You should see a pair of numbers that indicate the point on the graph where you clicked. This is how you can figure out approximate values of points on your graphs. Find the time at which the calcium current is most negative. (It is about -4.7 msec.)

Homework 1.5

Make the voltage window the plotting window by clicking on it. You saw above that if you start with V=-20 then the voltage goes to an equilibrium value of about -60. If you start with V=-10 it goes to a high voltage of about 60 mV. This suggests that between -20 and -10 there is a critical value of voltage which acts as a threshold and any potential below threshold goes to the low state and above goes to the high state. Find this value, V^* Then use the (S) (G) option to find the **singular point** or **equilibrium** value of voltage that is the threshold. (Answer **No** to both questions that XPP asks.) Is this stable? Such a point separates the set of initial voltages into two groups: (i) those which tend to the lower voltage $V < V^*$ and (ii) those which tend to the upper voltage $V > V^*$. These two half lines are called **the domain of attraction** of the lower and upper equilibria.

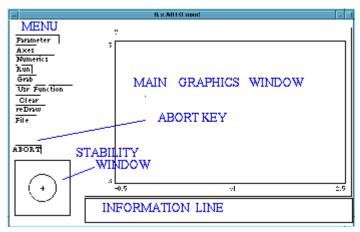


AUTO for the first time

One of the main goals of nonlinear dynamics is the study of how systems depend on parameters. The study of the parametric dependence of differential equations is called **continuation** and the analysis of how solutions appear and disappear as parameters vary is called **bifurcation theory** from the Latin word *bifurkus* for branching.

The program <u>AUTO</u> is one of the best continuation packages available and allows you to study the behavior of nonlinear dynamical systems as a function of parameters. It is part of XPP so that you can easily go between the two programs. The interface to regular AUTO involves writing lots of different FORTRAN programs, compiling them, and then running them. In this version, everything is done interactively.

To use AUTO you have to <u>prepare</u> your file by starting at a known steady state. When I=0 the lower steady state is -59.446. Thus start an integration with V(0)=-59.446. (I) (N) and enter the voltage at the prompt. Now you have a good guess for a steady state. It helps often to then type (I) (L) a few times - (this integrates using the end values of the previous simulation and places you even closer to a stable equilibrium.) Click (F) (A) to bring up the AUTO window. You will see a window like this:



There are 4 regions in the window. A majority of it is taken up by the main graphics window where the bifurcation diagram is drawn. Below this is the information window. This is used when you have found the bifurcation window and are traversing the different branches. It tells you about stability of the branch, the values of the parameters, and the nature of special points. the left are the menus which let you tell AUTO

- The <u>parameters</u> you want to vary
- The dimensions and what you want to plot on the axes
- The <u>numerical</u> parameters that control AUTO
- <u>User defined</u> special points at, say, a particular period or value of a parameter
- What to <u>save</u> such as the graph of the diagram, the actual orbits, etc.
- When to **ABORT** a calculation

Finally, the little square with a circle in it summarizes the <u>stability</u> information of the solutions. All stable modes lie in the circle and unstable ones out of the circle.

Assuming you are still with me, we will now use AUTO to compute the steady state voltage as a function of the current. (This can be done by hand since this is a scalar differential equation. Thus, it might seem that we are

killing a problems.)

with a shotgun. However, the basic method we use here can be easily used for other

You should have set the initial data for the voltage to V=-59.446 and the current I=0. All other paremeters should be at their default values. (To make sure of this, go to the main XPP window and type (P). At the **Parameter** prompt, type the word **default** and the parameters will be set to their originals.)

Now click the AUTO window so that it is active. Click on the (Parameter) window and you will see a list of 5 parameters. These are the parameters that AUTO will recognize. We want to vary the current, **I** and since the current **I** is among these parameters, we don't have to change anything. Just click on (Ok).

Next, we want to set up the ranges of the diagram for plotting. Click on (Axes) and a menu will appear. We want to plot the maximum and minimum of the voltage versus the parameter, so we choose the default of **HiLo.** A new window will appear into which we type the necessary information. We want the "Y axis" to be the voltage, so we should type **V** for that entry. The main parameter is the current so change **VL** to **I**. We want the current to vary from -225 to 60 so use these values for **Xmin** and **Xmax** respectively. Finally, the voltage will range from -200 to 100 so type in these values for **Ymin** and **Ymax** respectively and then click on (Ok). Summarizing, the entries of interest should look like this:

Y axis: VMain Par. : I

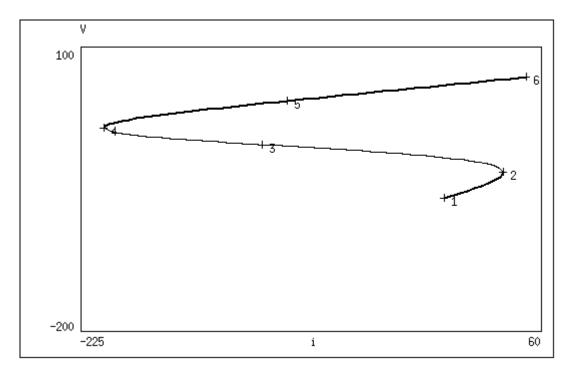
Xmin: -225Ymin: -200Xmax: 60Ymax: 100

(*How did I know what range?* I ran this diagram extending the ranges until I got the full picture. Thus, *practice and playing around are the best tools.*)

Now, AUTO needs to know some numerical stuff. Click on (Numerics) and a window comes up with many entries. Look at <u>the numerical</u> description in the <u>AUTO</u> part of this tutorial. For now make sure of the following:

- $D_S = .02$
- Nmax=400
- NPr=200
- Dsmax = 2.5
- Par Min = -220
- Par Max = 50
- Norm Max = 1000

and then click on (OK). You are ready to roll! Click on (Run) and then click on (Steady state). If you did it right, you will be rewarded with the diagram (or a very similar picture):



If you did not get this, then you should try again. Reset the diagram by clicking (File) (Reset Diagram) and answering yes. Go back to the main XPP window and reset the initial data to V=-59.446 and I=0. Then repeat the above steps.

Assuming that you now have the diagram, lets <u>traverse</u> the diagram to see what we have computed. Click on (Grab) and a cross-hair should appear on your diagram. (*NOTE* If you do not see a cross-hair then you should run XPP with the -xorfix option. That is, XPP should call xppaut -xorfix instead of just xppaut See the documentation for details.) Use the left and right arrow keys to move along the diagram. As you move, the information window at the bottom tells you stuff about the solutions such as the parameter values, the voltage value and the value of a secondary parameter. As you move along the diagram, the stability is displayed in the stability window. A quick summary of stability is seen from the diagram itself. **Thick solid lines indicate stable**

fixed points, thin are unstable fixed points. **Solid circles are stable periodic solutions** and open circles are unstable periodics.

You can move through the diagram very rapidly by using the (TAB) key which only jumps to the <u>special points</u>. When you grab a **special** point, then you can do lots of other things with AUTO. Move to the point labeled 1. We will continue this curve in the negative I direction. Press the (Enter) key to accept this point. (When you (Enter) on a grabbed point, it sets all the dependent variables to the corresponding values and the relevant parameters to their values. If the point is a **special** point, it also tells AUTO information about the nature of the point.) Now we have "grabbed" the starting point in our curve. AUTO has already traced out the curve in the positive I diresction. Click on the (Numerics) menu again. In the slot labeled **Ds** change **0.02 to -.02** so that AUTO will try to go in the other direction. Click on (Ok) to leave the numerics window and click on (Run). A branch should appear that continues until around I=-220. It is solid.

This is a complete diagram of the voltage-current relationship. There are two interesting values of the current. Traverse the diagram by clicking (Grab) and moving the crosshairs. The special point labeled 2 is denoted in the information window as **LP** meaning that it is a limit point. It occurs at I=36.79 A similar point at I=-210.5 is also a limit point. Both of these **limit points** are also called **saddle-nodes** or **turning point** bifurcations. They represent values of the parameter at which a pair of solutions comes together to form one solution. Note that the two values of current delimit the range in which there are two stable possible voltages. For -210.5 < I < 36.8 there are three steady states, two of which are stable, separated by an unstable steady state (cf. Homework 1.5) Thus imagine you start at the lower steady state. As you increase the current, the voltage rises until you hit I=36.8. There is a sudden increase in the potential from about -32 mV to +64mV. Now decrease the current. The potential stays high until you cross I=-210.5 at which point the potential drops precipitously. The appearance of two stable steady states gives rise to *this* phenomena which is known as **hysteresis**.

NOTE This hysteresis in the *I-V* curve is essential for neurons and one can see how it is then possible to get oscillatory behavior. Indeed, suppose that we make the current a varible such that when the voltage is low, the current increases and when it is high, it decreases. Then the voltage will oscillate making up and down jumps at the limit points.

Two parameter curves and the "Cusp catastrophe"

AUTO (and XPP) allow you to study two parameter curves of special points. That is, we have seen that for GCA=4 there are limit points at I=36.8,-210.5. What about GCA=3 or other values of GCA. We could of course, change GCA and redo this calculation. Instead, we can fix our attention to the limit point and just compute the values of I for each value of GCA at which there is a limit point. Lets do that now. Grab special point number 2. (Click (Grab) and (Tab) to it, then hit (Enter).) Click on (Axes and choose (Two par) to do a two parameter bifurcation. We will look at the appearance of limit points for 0 < GCA < 10 and extend the current to a slightly more positive value.

- Change the entries in he Axis window to:
 - Y-axis: V
 - o Main Parm: I
 - o 2nd Parm: gca
 - o Xmin: -225
 - Ymin: 0
 - o Xmax: 100
 - Ymax: 10
- Click (Ok) after making these changes. In two parameter bifurcations, the "Y-axis" entry is ignored and just "2nd Parm" entry becomes the Y-axis for the graph.
- Now click on (Numerics) and change (Par Max) to 100. Click (Ok) and we are ready to roll.
- Click on (Run) and a thinline that runs off the screen will appear. This is a curve of values of (I,GCA) at which there is a limit point.

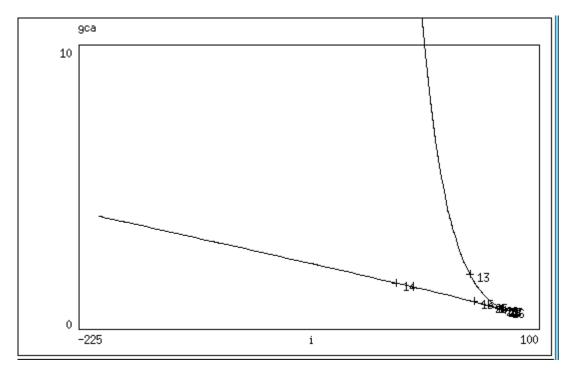
• Now focus on the information window and click (Grab) until you once again are on special point 2 (You wont see anything on the graph which is why I told you to focus on the info window.) Type (Enter) to accept the point.

- Click on (Numerics) and then change **Ds from -.02 to 0.2** and then click on (Ok.)
- Now click on (Run) and the branch will continue down and to the right until it stops. This is the "complete" curve of (I,GCA) points corresponding to the first limit point.

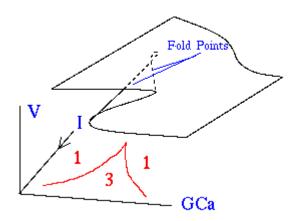
Now, we want to do this for the other limit point, special point 4.

- Click on (Grab) and (Tab) 3 times to get special point 4 and type (Enter) to accept it.
- Now before starting, note that you may want to click on (ABORT) while the curve is running as it gets numerically treacherous near the end. Thus, if you see a build-up of lots of numbers, click on the (ABORT). Now click on (Run) and the other branch will appear. Click on (ABORT) to stop the calculation.

If you have done this correctly, you will see something like



The two branches of limit points meet at a cusp point. Within the region bounded by the two curves, there are **three** rest states and outside of them there is **one.** A three-dimensional representation of this looks like:



This completes the analysis of a model with a single nonlinear conductance. You should click on (File) (Reset Diagram) and click (Yes) at the prompt. This will delete all the files that AUTO creates when running a bifurcation diagram

Homework 1.6

A one-dimensional neural net is described by the following equations:

$$\frac{dV}{dt} = -V + \frac{1}{1 + e^{-(wV - \theta)}}$$

- Write an ODE file for this model. Hint: See Homework 1.4b.
- Set w=6, thet a=5 and find the equilibria. How many are there?
- Compute a 1 parameter bifurcation curve using *theta* as the parameter varying it between -8 and 8. Use DsMax=.05 in the AUTO calculation. What are the limit points. What is the range of hysteresis?

Still not ready to give up?



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