Mathematical Neuroscience; Tutorial 3

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1 Theoretical Exercises

These are exercises in dynamical systems theory. You will encounter these features so often that it will be useful to pay special attention to these.

1. We check a few statements regarding the Hopf bifurcation using the Hopf normal form. This is the simplest model exhibiting the Hopf bifurcation. A topological equivalence can be made between this model and an application for parameters close to the Hopf bifurcation point. The cubic nonlinearity is the essential term that you have to include in the description. We will not prove that here.

   - Verify that the system
   $$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} \alpha x - \omega y + (cx - dy)(x^2 + y^2) \\ \omega x + \alpha y + (cy + dx)(x^2 + y^2) \end{pmatrix}. \tag{1}$$
   in polar coordinates reads $r' = r(\alpha + l_1 r^2)$ and $\theta' = \omega + pr^2$. Express l_1, p in terms of c and d.
   Recall the transformation $r' = \frac{1}{r}(xx' + yy')$ and $r' = \frac{1}{r^2}(xy' - yx')$.
   - The branch corresponding to periodic orbits is given by $r^* = \sqrt{-\alpha/l_1}$. Characterize the stability in terms of the sign of l_1.
   - Approximate the period for small α.

2. We verify how the periods of periodic orbits depend on the parameter as the parameter gets close to a homoclinic bifurcation. You may also find bits of this exercise in exercises 8,9,14 of Chapter 3. We consider the following two cases: In both cases, there is some global return time T_g depending on

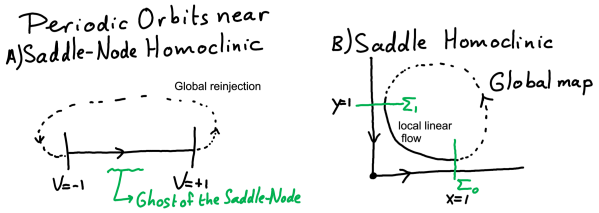

Figure 1: The geometry of periodic orbits near a saddle-node homoclinic (A) and a saddle-homoclinic (B). There is local flow that is slow, and a global return map.

   properties of the model that are less important. Here we focus on the slow dynamics near the (ghost of the) equilibria. We need to find the time it takes to go from section Σ_0 to Σ_1, see the figures.

   - **Saddle-node Homoclinic** As a model system we use the normal form for the saddle-node bifurcation with global reinjection. We take the equation $V' = V^2 + I$ with $I > 0$ to describe the dynamics on the slowest critical part for $|V| < 1$, once $V = 1$ is reached we set it to $V = -1$. Separate variables and integrate to determine the time system needs to move from $V = -1$ to $V = +1$. Show the period is $T \sim \frac{\pi}{\sqrt{I}} + T_g$.

- **Saddle Homoclinic** For the saddle-node homoclinic the dynamics is essentially one-dimensional, simplifying the analysis. In this case, we need to find the periodic orbit as a fixed point of a Poincaré map, which we construct as the composition of two maps, one local P_0 and one global P_1. We start with coordinates $(1, y_0)$ on Σ_0 and map this to the point $(x_1, 1)$ on Σ_1 with $x_1 = ay_0 + b$. The parameter a is positive, but not too important. Note that if $b = 0$, then we have a homoclinic orbit as the point $(1, 0)$ is mapped to $(0, 1)$. Hence, b plays the role of the parameter here. Near the saddle, we approximate the local dynamics by the linear system

  $$x' = \nu x, \qquad y' = -\mu y,$$

  where $\mu > \nu > 0$. The latter defines the local map P_0. The composition of P_1 and P_0 tells us how y_0 is mapped to a point y_1. We define the so-called saddle quantity $r = \mu/\nu$.

  - Determine the flying time, i.e., the time an orbit starting from a point $(x_1, 1)$ on Σ_1 needs to reach Σ_0.
  - Show that $y_1 = (ay_0 + b)^r$ and that $y \approx b^r$ is a fixed point for sufficiently small b.
  - Show that the period of the periodic orbit for I small satisfies $T \sim T_g + \dfrac{-1}{\nu} \log b$.

2 One-parameter Bifurcation Diagrams for the Morris-Lecar Model using MatCont

In this tutorial, you will perform bifurcation analysis of the Morris-Lecar model

$$\begin{cases} C_M V' = & -g_{Ca} m_\infty (V - E_{Ca}) - g_K n (V - E_K) - g_L (V - E_L) + I_{app}, \\ \tau_n(V) n' = & (n_\infty(V) - n). \end{cases} \tag{2}$$

After this tutorial, you have learned how to

- enter a system into MatCont and to perform simulations,
- determine a branch of equilibria using numerical continuation in one parameter,
- determine a branch of periodic orbits starting from either a Hopf bifurcation or a simulation,
- import and plot the data.

MatCont is designed for numerical bifurcation analysis of smooth autonomous systems. It will, however, not show nullclines, and simulations for some non-autonomous systems are possible. Resets as for the Leaky-Integrate-and-Fire-model are not supported.

2.1 Getting started with MatCont

We assume you have downloaded the MatCont package from SourceForge, and extracted the package into some folder. Change your Matlab working folder to this folder, i.e. the folder containing the file matcont.m. **For**

2.1.1 Setting up the System

Type ”matcont” from the Matlab command line to start up the toolbox. The main window appears, and possibly others too if some other system is already active. We want system (2) to be available in MatCont, and to define this system we choose in the main window **Select** $\rightarrow$ **System** $\rightarrow$ **New**, see Figure 2(left). We then fill in all the fields according to Figure 2(right), or see the listing below for all fields.

```
Name          MorrisLecar
Coordinates   V,n
Parameters    phi,gCa,V3,V4,Iapp
Equations
ECa=120
EK=-84
EL=-60
gK=8
gL=2
V1=-1.2
V2=18
CM=20
minf=(1+tanh((V-V1)/V2))/2
taun=1/cosh((V-V3)/(2*V4))
ninf=(1+tanh((V-V3)/V4))/2
V'=(-gCa*minf*(V-ECa)-gK*n*(V-EK)-gL*(V-EL)+Iapp)/CM
n'=phi*(ninf-n)/taun
```

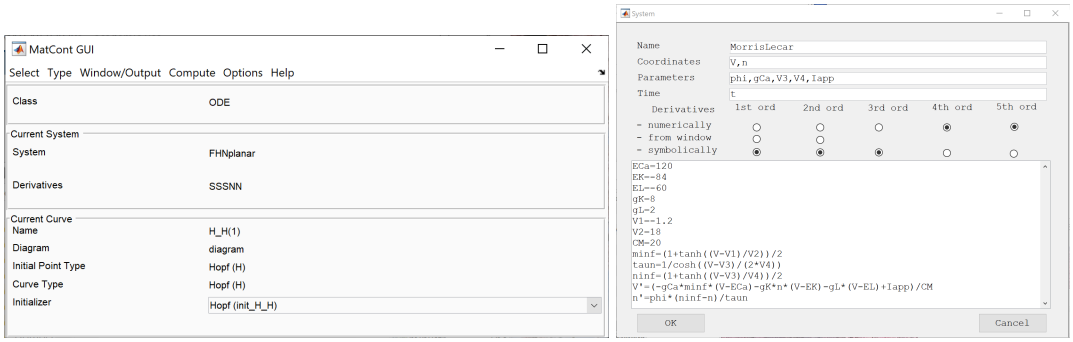

Figure 2: Left: The main MatCont window starting from some arbitrary system. Right: Entering the equations for the Morris-Lecar model.

If you have access to the Symbolic Toolbox in MATLAB, then select symbolic derivatives up to order three. If not, MATCONT will use finite differences to determine certain derivatives. When you are ready, press "OK".

2.1.2 Initial Simulations towards an equilibrium

We will now perform a simulation such that the orbit approaches an equilibrium. This will serve as initial data for the continuation. In the Main window set the *Type* of the Initial Point to *Point*, see Figure 3(top). The Curve Type has changed to *Orbit* automatically. Two windows appear, called Starter and Integrator.[1] We can enter initial conditions and parameter values. We choose $\phi = 0.067$, $g_{Ca} = 4$, $V_3 = 12$ $V_4 = 17.4$ and set $I_{app} = 30$. This parameter setting corresponds to the so-called SNIC-case. For the initial condition, we choose $V = -37$ and $n = 0.03$ close to the stable equilibrium. For the integrator settings we set *Interval=300* to ensure we see sufficient transient tim, see Figure 3 for all fields. It is time to perform the simulation; Press *Compute*|*Forward* in the Main window. Quickly, a pop-up window with messages appears, and the simulation has finished. Now that we have performed the simulation, we will visualize the orbit in the (V, n)-phase plane via *Window/Output*|*Graphic*|*2D plot*. A new window appears, and by clicking on *MatCont*|*Layout* we can set the Axis properties. Select *MatCont*|*Redraw Curve*. The result may look a bit cluttered as initial transients are also plotted, see Figure 4. We could also have opened the plot window first before simulating, but plotting during simulation or continuation can be rather slow. Redo the computation for slightly higher values of the initial potential. For $V_0 > -24$, you will first see an action potential before the system returns to rest. Once more, the Morris-Lecar model is an excitable system. You have now

[1] If for some reason they do not appear, then right-click in the lower (curve) part of the main MatCont window, and select them in the Pop-up menu.

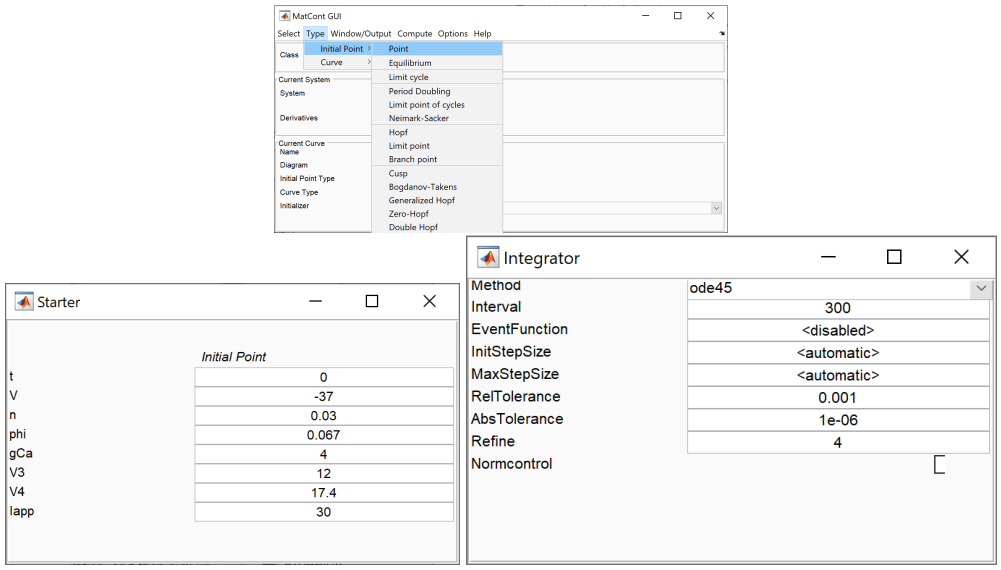

Figure 3: Top: Selecting the type for the initial point. Bottom: Numerical values and Integrator settings.

entered the Morris-Lecar model into MatCont, and used it to perform some simulations. If you would have set I_{app} to higher values, then the outcome is different. We will now slowly build up to that analysis.

2.2 Equilibrium Continuation in One Parameter

First, we want to see how the position of the equilibria change as we change the applied current I_{app}. Continuation starts from a certain point type X, where X could denote EP=equilibrium, H=Hopf, LP= Limit Point, LC=Limit Cycle and so. We then compute a certain solution branch Y, and the result will be stored in a file X_Y(n).mat with the label n indicating the number of computed branches of that type. In this case, we want to compute an EP_EP branch in MatCont with one free parameter.

2.2.1 Preparing the continuation

First, we need to get the initial data, we click *View Result* in the Control window, and select the last point of the simulation, see Figure 5. This final point is close to the equilibrium, and provides good starting data. Alternatively, you may type the coordinates of $V = -42$ and $n = 0.002$ into the Starter window directly. Approximations will do, it is not necessary to specify all digits. Next, we set the Initial Point Type to Equilibrium Point in the Main window. The Curve Type changes to Equilibrium (EP) automatically. These steps are shown in Figure 5.

For the continuation we have to specify which parameter we want to vary. Click on the radio button next to *Iapp* in the Starter window. To speed up the continuation, we change *MaxStepsize* to 0.5 in the Continuer window. The default settings for all other fields are fine. During the continuation we want to see what the result looks like. Change the Layout of the 2DPlot to show the parameter I_app from -20 to 140, and the potential V from -80 to 40.

We are ready to run the continuation. In the Main window, select *Compute|Forward*. In the Control window a few message appear, press "Resume" to continue. With *Compute|Extend*, you can extend the branch until you have reached $I_{app} = 140$. These steps will give you the branch in one direction, so also select *Compute|Backward* to get the branch that leaves the 2DPlot on the left. If all is well, you will now have a plot as in Figure 6(right).

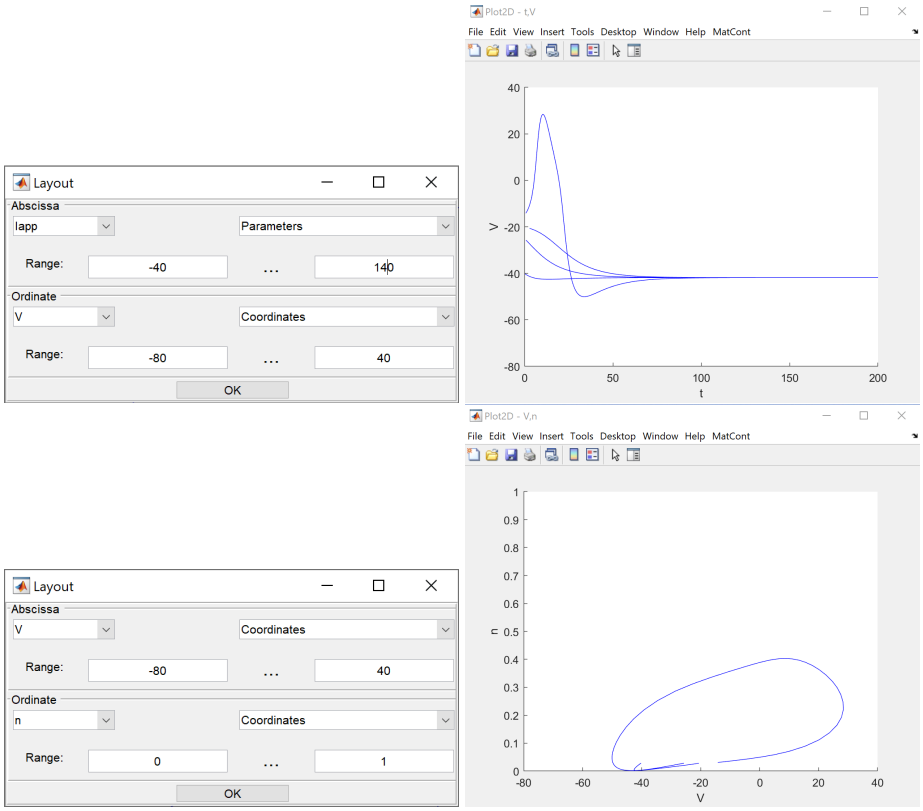

Figure 4: Top, left: Setting the Layout for the 2D Plot. Top, Right: Bottom, left: Layout for phase plane projection. Bottom, right: Simulated orbits projected onto the (V, n)-plane with transients towards the equilibrium. Initial conditions $n_0 = 0.03$ and $V_0 \in \{-40, -25, -20, -15\}$. Only starting from $V_0 = -15$ we get a spike.

2.2.2 Inspecting the continuation results

Now that we have obtained our plot it is time to inspect the result. Have a look at the command line of the main window. You see a message regarding the timing and some information about special points. The array x is the continuation variable consisting of the coordinates of the equilibrium and the parameter we are varying, i.e., I_{app}. We observe the following messages

- **LP** at $I_{app} = 39.96$ has been detected. The normal form coefficient a is nonzero, i.e. the bifurcation is non-degenerate. Note that the sign of a does not matter.
- A neutral saddle **H** is found at $I_{app} = 36.64$. Here the two real eigenvalues of the saddle equilibrium satisfy $\lambda_1 + \lambda_2 = 0$. Hence, the testfunction for a Hopf bifurcation vanishes. As there is no change in stability or some other qualitative change in dynamics, this is not a bifurcation.
- Another **LP** at $I_{app} = -9.95$ has been detected with nonzero normal form coefficient a, i.e. the bifurcation is non-degenerate.
- A Hopf bifurcation **H** is found for $I_{app} = 97.64$ with positive first Lyapunov coefficient l_1, i.e., the bifurcation is subcritical and a branch of unstable periodic orbits emerges from this Hopf point.

You have now computed a branch of equilibrium points in one parameter and detected a few bifurcations. A few remarks before we move on to the Hopf point.

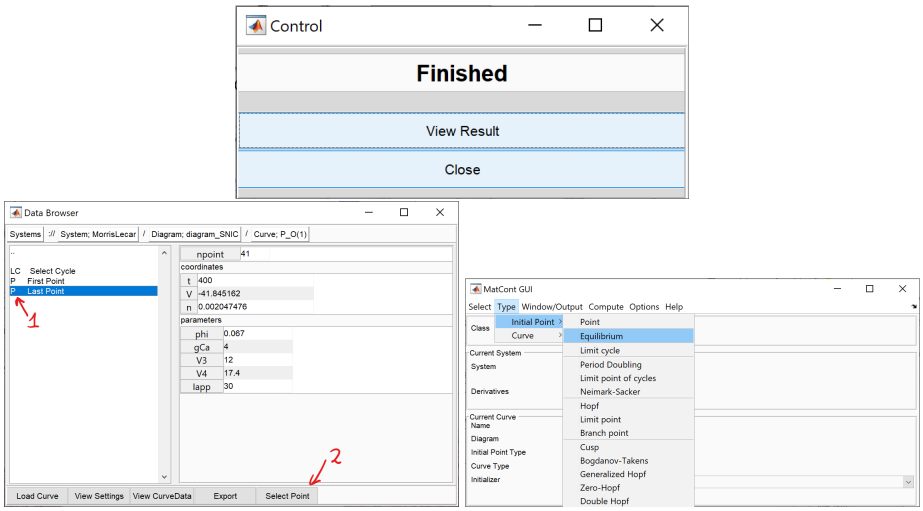

Figure 5: Top: Message window when the simulation has finished. Clicking "View Result" opens the Data Browser. Bottom, left: The Data Browser allows to inspect various settings of a solution curve and lists special points. Bottom, right: selecting an equilibrium point as Initial Point Type.

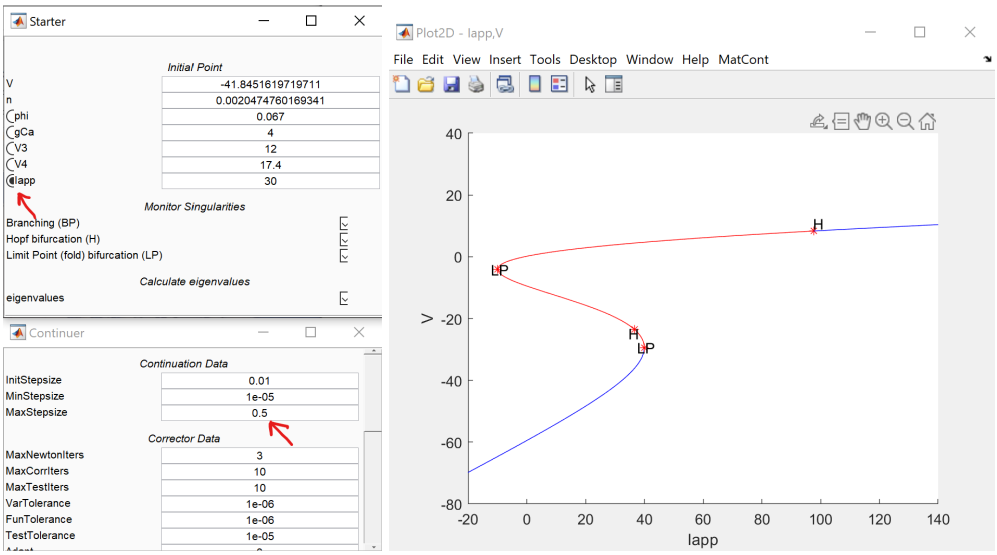

Figure 6: Left: Settings for the Equilibrium Continuation. Right: Result of computing the equilibrium branch in both directions.

- MatCont will overwrite old curves if you compute too many of the same type. If you want to keep a certain solution branch, it is best to rename the file. The DataBrowser allows you to do that from within MatCont at the diagram level (the level is shown at the top). Select the curve and then click the *Rename* button on the bottom. Rename your two **EP_EP** branches to *EPforward* and *EPbackward*.

- For one-parameter continuations, we can display the stability of various branches. In the Plot2D window, select *MatCont|Plot Properties* and for the empty field *EP if unstable* enter *'Color', 'red', 'linestyle', '-'*. Next redraw the diagram, and the part of the equilibrium branch between the lower **LP** and the upper **H** turns red. This implies that equilibrium for the corresponding value of I_{app} is unstable.

2.3 Continuation of a Limit Cycle in One Parameter

The Hopf bifurcation leads to periodic orbits and provides a natural starting point to find this branch of limit cycles.

2.3.1 Setting up Continuation of the Limit Cycle from a Hopf Point

We show another way of selecting the initial point. In the Main window we go to the Data Browser via *Select*|*Initial Point*. The Data Browser opens and we select the EP-branch with the Hopf point. If necessary, you can switch to the other branch by clicking on *Diagram* at the top, and then selecting the other curve. Then select the Hopf point, see Figure 7(right). In the Main window the Curve Type is Limit Cycle (LC). If not, you set it using the Initializer drop down box below it. In the Starter window, make sure that the radio buttons for I_{app} and the Period are ticked. You cannot change the Maximum Stepsize of during a continuation. As this run may take some time, you can choose to set the *MaxStepsize* in the Continuer window to 1.5 to speed it up.

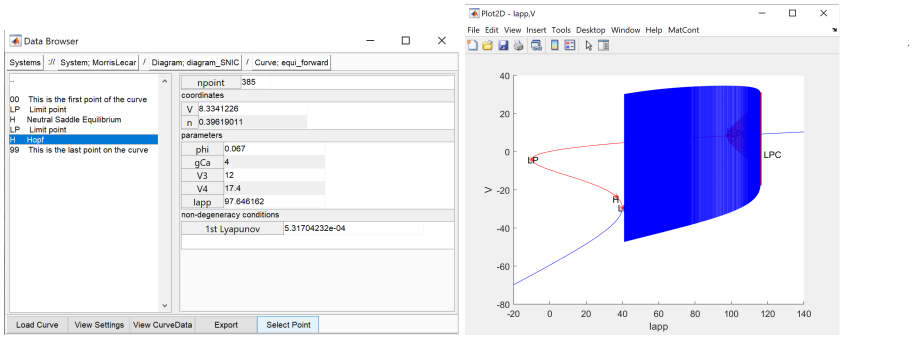

Figure 7: Left: Selecting the Hopf Point as Initial Point. Right: Result of the continuation.

We are ready for the continuation, and press *Compute*|*Forward*. Immediately, an LPC will be reported. This is exactly at the Hopf point where the test function for a limit point of cycles (saddle-node bifurcation of periodic orbits) vanishes. You can ignore it, and press *Resume*. Another LPC will be detected, and resume the continuation. You may extend the run at least once until the parameter I_{app} gets close to the **LP**-point at $I_{app} = 39.96$.

2.3.2 The bifurcation diagram

In essence, you have now computed Figure 3.6(left) from the book. With a little more effort you can polish the graph, see also the commands below. This bifurcation diagram tells us rather precisely what dynamics to expect. For $I < 40$, the system is excitable. The system is at rest, but a perturbation may induce an action potential. For $40 < I < 97$, the system shows periodic oscillations continuously. The frequency of the oscillations increases as I increases. For $98 < I < 115$, the system is bistable. There is an oscillation, but an equilibrium with high value of V is stable too. For $I > 115$, the system exhibits depolarization block.

It is instructive to plot the period as well. Then notice that compared to figure 3.6 panel, a branch seems missing. In the book they decided not to plot the frequency of the unstable part. You can repeat these steps to obtain the diagrams for the Hopf and Homoclinic cases.

2.4 Data Plot from Command Line

All continuation data is stored in .mat-files. This can be imported into the MATLAB workspace for manual editing. Here it necessary to be aware of the meaning of the variables.

- x: the continuation variable. For equilibria the state variables and the parameter at the end. For periodic orbits, it contains first all state variables of the discretization, then at the end period and the parameter, in that order.
- v: tangent vector to the solution branch, useful internally, not so much for plotting.
- s: structure indicating bifurcation and other special points.
- h: information on the continuation, stepsizes and testfunctions for bifurcations.
- f: For periodic orbits it first mentions the mesh for the time discretization. If computed, at the end it contains the eigenvalues for equilibria or Floquet multipliers for periodic orbits, i.e. the stability information.

To plot some of the features of the previous bifurcation diagram, you can use the following commands. Modify as you wish, e.g., the file names.

```
load Systems\MorrisLecar\diagram\EPforward.mat
%Plot the stable and unstable branches with different colors
figure; hold on;
range1=[s(1).index:s(2).index];
range2=[s(2).index:s(5).index];
range3=[s(5).index:s(6).index];
plot(x(3,range1),x(1,range1),x(3,range3),x(1,range3),'Color','blue');
plot(x(3,range2),x(1,range2),'Color','red');
plot(x(3,[s.index]),x(1,[s.index]),'Marker','*','Linestyle','none');
%
load Systems\MorrisLecar\diagram\LimitCycles.mat
%To plot the minimal and maximal value of V along the LC-branch as function of Iapp
plot(x(end,:),min(x(1:2:end-2,:)),x(end,:),max(x(1:2:end-2,:)))
xlabel('I_{app}');ylabel('V');
hold on;
%To plot the period of the Limit cycles as function of Iapp
figure;plot(x(end,:),x(end-1,:)); xlabel('I_{app}');ylabel('period T');
```