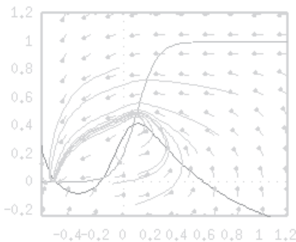

Chapter 4

Dynamics

4.0.1 Introduction to dynamical systems

Dynamical systems theory provides a powerful tool for analyzing nonlinear systems of differential equations, including those that arise in neuroscience. This theory allows us to interpret solutions geometrically as curves in a phase space. By studying the geometric structure of phase space, we are often able to classify the types of solutions that the model may exhibit and determine how solutions depend on the model's parameters. For example, we can often predict if a model neuron will generate an action potential, determine for which values of the parameters the model will produce oscillations and compute how the frequency of oscillations depends on parameters.

In this chapter, we introduce many of the basic concepts of dynamical systems theory using a reduced 2-variable model: the Morris-Lecar equations. Although this model is considerably simpler than the Hodgkin-Huxley equations, it still exhibits many important features of neuronal activity. For example, the Morris-Lecar model generates action potentials, there is a threshold for firing and the model displays sustained oscillations at elevated levels of an applied current. By considering a reduced model, we can more easily explain the geometric mechanisms underlying each of these phenomena. Moreover, we can introduce important mathematical concepts such as phase space analysis, bifurcation theory, oscillations and stability theory. Each of these concepts plays a fundamental role in the analysis of more complex systems discussed throughout the book.

4.0.2 The Morris-Lecar model

One of the simplest models for the production of action potentials is a model proposed by Kathleen Morris and Harold Lecar. The model has three channels: a potassium channel, a leak, and a calcium channel. In the simplest version of the model, the calcium current depends instantaneously on the voltage. Thus, the

Morris-Lecar equations (ML) have the form:

$$C_m \frac{dV}{dt} = I_{app} - g_l(V - E_l) - g_k n(V - E_K) \quad (4.1)$$
$$-g_{Ca} m_\infty(V)(V - E_{Ca}) \;\equiv\; I_{app} - I_{ion}(V, n)$$
$$\frac{dn}{dt} = \phi(n_\infty(V) - n)/\tau_n(V)$$

where

$$m_\infty(V) = \frac{1}{2}[1 + \tanh((V - V_1)/V_2)]$$
$$\tau_n(V) = 1/\cosh((V - V_3)/(2V_4))$$
$$n_\infty(V) = \frac{1}{2}[1 + \tanh((V - V_3)/V_4)].$$

Here, $V_{1,2,3,4}$ are parameters chosen to fit voltage clamp data.

The solutions shown in Figure 4.1 demonstrate that the Morris-Lecar model exhibits many of the properties displayed by neurons. Here the parameters are listed in Table 4.0.2 under the Hopf case. Figure 4.1A demonstrates that the model is *excitable* if $I_{app} = 60$. That is, there is a stable constant solution corresponding to the resting state of the model neuron. A small perturbation decays to the resting state, while a larger perturbation, above some threshold, generates an action potential. The solution $(V_1(t), n_1(t)) \equiv (V_R, n_R)$ is constant; V_R is the resting state of the model neuron. The solution $(V_2(t), n_2(t))$ corresponds to a subthreshold response. Here, $V_2(0)$ is slightly larger than V_R and $(V_2(t), n_2(t))$ decays back to rest. Finally, $(V_3(t), n_3(t))$ corresponds to an action potential. Here, we start with $V_3(0)$ above some threshold. There is then a large increase of $V_3(t)$ followed by $V_3(t)$ falling below V_R and then a return to rest.

Figure 4.1B shows periodic solutions of (ML). The parameter values are exactly the same as before; however, we have increased the parameter I_{app}, corresponding to the applied current. If we increase I_{app} further, then the frequency of oscillations increase; if I_{app} is too large, then the solution approaches a constant value.

In the following, we will show how dynamical systems methods can be used to mathematically analyze these solutions. The analysis is extremely useful in understanding when this type of model, for a given set of parameters, displays a particular type of behavior. The behavior may change as parameters are varied; an important goal of bifurcation theory, which we describe below, is to determine when and what type of transitions take place.

4.0.3 The phase plane

Every solution $(V(t), n(t))$ can be viewed as a curve, or trajectory (or orbit), in the (V, n)-plane parametrized by time, t. The (V, n)-plane is called the *phase plane*; for higher dimensional systems, this is called the *phase space*. Of course, not every curve in the phase plane represents a solution of the differential equations. It will be convenient to write (4.1) as

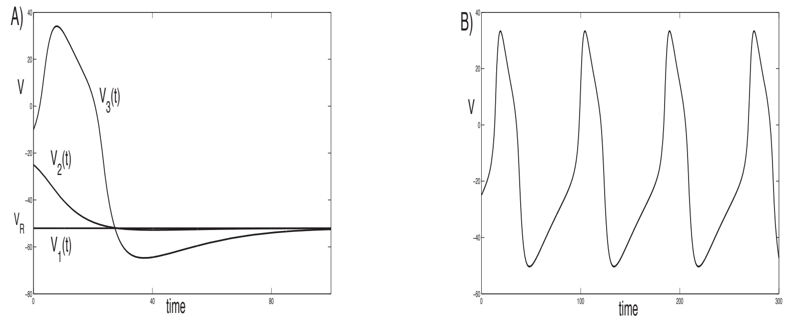

Figure 4.1. *Solutions of the Morris-Lecar equations. Parameters are listed in Table 4.0.2, the Hopf case. A) A small perturbation from rest decays to the resting state, while a larger perturbation generates an action potential. Here,* $I_{app} = 60$*. B) A periodic solution of (ML). Here,* $I_{app} = 100$.

Table 4.1. *Morris-Lecar parameters; the current,* I_{app}*, is a parameter.*

Parameter	**Hopf**	**SNLC**	**Homoclinic**
ϕ	0.04	.067	0.23
g_{Ca}	4.4	4	4
V_3	2	12	12
V_4	30	17.4	17.4
E_{Ca}	120	120	120
E_K	-84	-84	-84
E_L	-60	-60	-60
g_K	8	8	8
g_L	2	2	2
V_1	-1.2	-1.2	-1.2
V_2	18	18	18
C_m	20	20	20

$$\frac{dV}{dt} = f(V,n)$$
$$\frac{dn}{dt} = g(V,n). \tag{4.2}$$

A trajectory corresponds to a solution if it has the property that at every point (V, n) along the trajectory, the vector $(f(V, n), g(V, n))$ is tangent to the trajectory.

Two important types of trajectories are *fixed points* (sometimes called *equilibria*) and *closed orbits*. At a fixed point, $f(V_R, n_R) = g(V_R, n_R) = 0$; this corresponds to a constant solution. Closed orbits correspond to periodic solutions. That is, if $(v(t), n(t))$ represents a closed orbit, then there exists $T > 0$ such that