12.5 Exploration: Neurodynamics

One of the most important developments in the study of the firing of nerve cells or neurons was the development of a model for this phenomenon in giant squid in the 1950s by Hodgkin and Huxley [23]. They developed a four-dimensional system of differential equations that described the electrochemical transmission of neuronal signals along the cell membrane, a work for which they later received the Nobel prize. Roughly speaking, this system is similar to systems that arise in electrical circuits. The neuron consists of a cell body, or *soma*, which receives electrical stimuli. This stimulus is then conducted along the *axon*, which can be thought of as an electrical cable that connects to other neurons via a collection of synapses. Of course, the motion is not really electrical, because the current is not really made up of electrons, but rather ions (predominantly sodium and potassium). See [15] or [34] for a primer on the neurobiology behind these systems.

The four-dimensional Hodgkin-Huxley system is difficult to deal with, primarily because of the highly nonlinear nature of the equations. An important breakthrough from a mathematical point of view was achieved by Fitzhugh [18] and Nagumo *et al.* [35], who produced a simpler model of the Hodgkin-Huxley model. Although this system is not as biologically accurate as the original system, it nevertheless does capture the essential behavior of nerve impulses, including the phenomenon of *excitability* alluded to below.

The Fitzhugh-Nagumo system of equations is given by

$$x' = y + x - \frac{x^3}{3} + I$$
$$y' = -x + a - by$$

where a and b are constants satisfying

$$0 < \frac{3}{2}(1-a) < b < 1$$

and I is a parameter. In these equations x is similar to the voltage and represents the *excitability* of the system; the variable y represents a combination of other forces that tend to return the system to rest. The parameter I is a stimulus parameter that leads to excitation of the system; I is like an applied current. Note the similarity of these equations with the van der Pol equation of Section 12.3.

1. First assume that $I = 0$. Prove that this system has a unique equilibrium point (x_0, y_0). *Hint:* Use the geometry of the nullclines for this rather than

explicitly solving the equations. Also remember the restrictions placed on a and b.

2. Prove that this equilibrium point is always a sink.
3. Now suppose that $I \neq 0$. Prove that there is still a unique equilibrium point (x_I, y_I) and that x_I varies monotonically with I.
4. Determine values of x_I for which the equilibrium point is a source and show that there must be a stable limit cycle in this case.
5. When $I \neq 0$, the point (x_0, y_0) is no longer an equilibrium point. Nonetheless we can still consider the solution through this point. Describe the qualitative nature of this solution as I moves away from 0. Explain in mathematical terms why biologists consider this phenomenon the "excitement" of the neuron.
6. Consider the special case where $a = I = 0$. Describe the phase plane for each $b > 0$ (no longer restrict to $b < 1$) as completely as possible. Describe any bifurcations that occur.
7. Now let I vary as well and again describe any bifurcations that occur. Describe in as much detail as possible the phase portraits that occur in the I, b–plane, with $b > 0$.
8. Extend the analysis of the previous problem to the case $b \leq 0$.
9. Now fix $b = 0$ and let a and I vary. Sketch the bifurcation plane (the I, a–plane) in this case.

EXERCISES

1. Find the phase portrait for the differential equation

$$x' = y - f(x), \quad f(x) = x^2,$$
$$y' = -x.$$

Hint: Exploit the symmetry about the y-axis.

2. Let

$$f(x) = \begin{cases} 2x - 3 & \text{if } x > 1 \\ -x & \text{if } -1 \leq x \leq 1 \\ 2x + 3 & \text{if } x < -1. \end{cases}$$

Consider the system

$$x' = y - f(x)$$
$$y' = -x.$$

(a) Sketch the phase plane for this system.
(b) Prove that this system has a unique closed orbit.