Chapter 3

One-Dimensional Systems

In this chapter we describe geometrical methods of analysis of one-dimensional dynamical systems, i.e., systems having only one variable. An example of such a system is the space-clamped membrane having Ohmic leak current \( I_L \):

\[
C \dot{V} = -g_L(V - E_L) .
\] (3.1)

Here the membrane voltage \( V \) is a time-dependent variable, and the capacitance \( C \), leak conductance \( g_L \), and leak reverse potential \( E_L \) are constant parameters described in chapter 2. We use this and other one-dimensional neural models to introduce and illustrate the most important concepts of dynamical system theory: equilibrium, stability, attractor, phase portrait, and bifurcation.

3.1 Electrophysiological Examples

The Hodgkin-Huxley description of dynamics of membrane potential and voltage-gated conductances can be reduced to a one-dimensional system when all transmembrane conductances have fast kinetics. For the sake of illustration, let us consider a space-clamped membrane having leak current and a fast voltage-gated current \( I_{\text{fast}} \) with only one gating variable \( p \),

\[
C \dot{V} = -g_L(V - E_L) - g p(V - E) \quad \text{Leak} I_L - \text{fast} I_{\text{fast}}
\]
(3.2)

\[
\dot{p} = (p_\infty(V) - p)/\tau(V) ,
\] (3.3)

with dimensionless parameters \( C = 1, g_L = 1, \) and \( g = 1 \). Suppose that the gating kinetics (3.3) is much faster than the voltage kinetics (3.2), which means that the voltage-sensitive time constant \( \tau(V) \) is very small, that is, \( \tau(V) \ll 1 \) in the entire biophysical voltage range. Then the gating process may be treated as being instantaneous, and the asymptotic value \( p = p_\infty(V) \) may be used in the voltage equation (3.2).
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Figure 3.1: Solution of the full system (3.2, 3.3) converges to that of the reduced one-dimensional system (3.4) as $\tau(V) \to 0$.

to reduce the two-dimensional system (3.2, 3.3) to a one-dimensional equation:

$$C \dot{V} = -g_L(V - E_L) - \frac{\text{instantaneous } I_{\text{fast}}}{g_{\infty}(V)(V - E)}.$$  \hspace{1cm} (3.4)

This reduction introduces a small error of the order $\tau(V) \ll 1$, as one can see in Fig.3.1.

Since the hypothetical current $I_{\text{fast}}$ can be either inward ($E > E_L$) or outward ($E < E_L$), and the gating process can be either activation ($p$ is $m$, as in the Hodgkin-Huxley model) or inactivation ($p$ is $h$), there are four fundamentally different choices for $I_{\text{fast}}(V)$, which we summarize in Fig.3.2 and elaborate on below.

3.1.1 I-V Relations and Dynamics

The four choices in Fig.3.2 result in four simple one-dimensional models of the form (3.4):

$I_{\text{Na,p}}$-model, $I_K$-model, $I_h$-model, and $I_{\text{Kir}}$-model.

These models might seem too simple to biologists, who can easily understand their behavior just by looking at the I-V relations of the currents depicted in Fig.3.3 without
using any dynamical systems theory. The models might also appear too simple to mathematicians, who can easily understand their dynamics just by looking at the graphs of the right-hand side of (3.4) without using any electrophysiological intuition. In fact, the models provide an invaluable learning tool, since they establish a bridge between electrophysiology and dynamical systems.

In Fig. 3.3 we plot typical steady-state current-voltage (I-V) relations of the four currents considered above. Note that the I-V curve is nonmonotonic for \(I_{Na,p}\) and \(I_{Kir}\) but monotonic for \(I_K\) and \(I_h\), at least in the biophysically relevant voltage range. This subtle difference is an indication of the fundamentally different roles these currents play in neuron dynamics. The I-V relation in the first group has a region of “negative conductance” (i.e., \(I'(V) < 0\)), which creates positive feedback between the voltage and the gating variable (Fig.3.4), and plays an amplifying role in neuron dynamics. We refer to such currents as \textit{amplifying currents}. In contrast, the currents in the second group have negative feedback between voltage and gating variable, and they often result in damped oscillation of the membrane potential, as we show in chapter 4. We refer to such currents as \textit{resonant currents}. Most neural models involve a combination of at least one amplifying and one resonant current, as we discuss in chapter 5. The way these currents are combined determines whether the neuron is an \textit{integrator} or a \textit{resonator}.

### 3.1.2 Leak + Instantaneous \(I_{Na,p}\)

To ease our introduction into dynamical systems, we will use the \(I_{Na,p}\)-model

\[
C \dot{V} = I - g_L(V - E_L) - g_{Na} m_\infty(V)(V - E_{Na}),
\]

called \textit{persistent sodium model}, with

\[
m_\infty(V) = 1/(1 + \exp\{(V_{1/2} - V)/k\})
\]
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Depolarization

- Increase in inward current
- Increase in outward current

Hyperpolarization

- Decrease in inward current
- Decrease in outward current

Activation, m

Depolarization

- Increase in inward current

Hyperpolarization

- Decrease in inward current

Inactivation, h

Depolarization

- Increase in outward current

Hyperpolarization

- Decrease in outward current

Figure 3.4: Feedback loops between voltage and gating variables in the four models presented above (see also Fig. 5.2).

Throughout the rest of this chapter. (Some biologists refer to transient Na⁺ currents with very slow inactivation as being persistent, since the current does not change much on the time scale of 1 sec.) We obtain the experimental parameter values

\[
C = 10 \ \mu F, \quad I = 0 \ \text{pA}, \quad g_L = 19 \ \text{mS}, \quad E_L = -67 \ \text{mV}, \quad g_{Na} = 74 \ \text{mS}, \quad V_{1/2} = 1.5 \ \text{mV}, \quad k = 16 \ \text{mV}, \quad E_{Na} = 60 \ \text{mV}
\]

using whole-cell patch-clamp recordings of a layer 5 pyramidal neuron in the visual cortex of a rat at room temperature. We prove in exercise 3.3.8 and illustrate in Fig. 3.15 that the model approximates the action potential upstroke dynamics of this neuron.

Figure 3.5: (a) I-V relations of the leak current \( I_L \), fast Na⁺ current \( I_{Na} \), and combined current \( I(V) = I_L(V) + I_{Na}(V) \) in the \( I_{Na,p} \)-model (3.5). Dots denote \( I_0(V) \) data from layer 5 pyramidal cell in rat visual cortex. (b) The right-hand side of the \( I_{Na,p} \)-model (3.5).
Figure 3.6: Typical voltage trajectories of the $I_{Na,p}$-model (3.5) having different values of $I$.

The model’s I-V relation, $I(V)$, is depicted in Fig.3.5a. Due to the negative conductance region in the I-V curve, this one-dimensional model can exhibit a number of interesting nonlinear phenomena, such as bistability, i.e. coexistence of resting and excited states. From a mathematical point of view, bistability occurs because the right-hand-side function in the differential equation (3.5), depicted in Fig.3.5b, is not monotonic. In Fig.3.6 we depict typical voltage time courses of the model (3.5) with two values of injected DC current $I$ and 16 different initial conditions. The qualitative behavior in Fig.3.6a is clearly bistable: depending on the initial condition, the trajectory of the membrane potential goes either up to the excited state or down to the resting state. In contrast, the behavior in Fig.3.6b is monostable, since the resting state does not exist. The goal of the dynamical system theory reviewed in this chapter is to understand why and how the behavior depends on the initial conditions and the parameters of the system.

### 3.2 Dynamical Systems

In general, dynamical systems can be continuous or discrete, depending on whether they are described by differential or difference equations. Continuous one-dimensional dynamical systems are usually written in the form

$$\dot{V} = F(V), \quad V(0) = V_0 \in \mathbb{R}.$$  \hspace{1cm} (3.6)

For example,

$$\dot{V} = -80 - V, \quad V(0) = -20,$$

where $V$ is a scalar time-dependent variable denoting the current state of the system, $\dot{V} = V_t = dV/dt$ is its derivative with respect to time $t$, $F$ is a scalar function (its output is one-dimensional) that determines the evolution of the system, e.g., the right-
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\( V(t) = E_L + (V_0 - E_L)e^{-gL/C} \)

Figure 3.7: Explicit analytical solution \( V(t) = E_L + (V_0 - E_L)e^{-gL/C} \) of the linear equation (3.1) and corresponding numerical approximation (dots) using Euler’s method (3.7).

hand side of (3.5) divided by \( C \); see Fig.3.5b. \( V_0 \in \mathbb{R} \) is an initial condition, and \( \mathbb{R} \) is the real line, that is, a line of real numbers (\( \mathbb{R}^n \) would be the \( n \)-dimensional real space).

In the context of dynamical systems, the real line \( \mathbb{R} \) is called the phase line or state line (phase space or state space for \( \mathbb{R}^n \)) to stress the fact that each point in \( \mathbb{R} \) corresponds to a certain, possibly inadmissible state of the system, and each state of the system corresponds to a certain point in \( \mathbb{R} \). For example, the state of the Ohmic membrane (3.1) is its membrane potential \( V \in \mathbb{R} \). The state of the Hodgkin-Huxley model (see section 2.3) is the four-dimensional vector \( (V, m, n, h) \in \mathbb{R}^4 \). The state of the \( I_{Na,p} \)-model (3.5) is its membrane potential \( V \in \mathbb{R} \), because the value \( m = m_\infty(V) \) is unequivocally defined by \( V \).

When all parameters are constant, the dynamical system is called autonomous. When at least one of the parameters is time-dependent, the system is nonautonomous, denoted as \( \dot{V} = F(V, t) \).

“To solve equation (3.6)” means to find a function \( V(t) \) whose initial value is \( V(0) = V_0 \) and whose derivative is \( F(V(t)) \) at each moment \( t \geq 0 \). For example, the function \( V(t) = V_0 + at \) is an explicit analytical solution to the dynamical system \( \dot{V} = a \). The exponentially decaying function \( V(t) = E_L + (V_0 - E_L)e^{-gL/C} \) depicted in Fig.3.7, a solid curve, is an explicit analytical solution to the linear equation (3.1). (Check by differentiating).

Finding explicit solutions is often impossible even for such simple systems as (3.5), so quantitative analysis is carried out mostly via numerical simulations. The simplest procedure to solve (3.6) numerically, known as the first-order Euler method, replaces (3.6) with the discretized system

\[
\frac{[V(t + h) - V(t)]}{h} = F(V(t))
\]

where \( t = 0, h, 2h, 3h, \ldots \), is the discrete time and \( h \) is a small time step. Knowing the current state \( V(t) \), we can find the next state point via

\[
V(t + h) = V(t) + hF(V(t))
\]

Iterating this difference equation starting with \( V(0) = V_0 \), we can approximate the analytical solution of (3.6) (see the dots in Fig.3.7). The approximation has a noticeable error of order \( h \), so scientific software packages, such as MATLAB, use more sophisticated high-precision numerical methods.
In many cases, however, we do not need exact solutions, but qualitative understanding of the behavior of (3.6) and how it depends on parameters and the initial state $V_0$. For example, we might be interested in the number of equilibrium (rest) points the system could have, whether the equilibria are stable, their attraction domains, etc.

### 3.2.1 Geometrical Analysis

The first step in the qualitative geometrical analysis of any one-dimensional dynamical system is to plot the graph of the function $F$, as in Fig. 3.8 (top). Since $F(V) = \dot{V}$, at every point $V$ where $F(V)$ is negative, the derivative $\dot{V}$ is negative, and hence the state variable $V$ decreases. In contrast, at every point where $F(V)$ is positive, $\dot{V}$ is positive, and the state variable $V$ increases; the greater the value of $F(V)$, the faster $V$ increases. Thus, the direction of movement of the state variable $V$, and hence the evolution of the dynamical system, is determined by the sign of the function $F(V)$.

The right-hand side of the $I_{\text{leak}}$-model (3.1) or the $I_{\text{Na},p}$-model (3.5) in Fig. 3.8 is the steady-state current-voltage (I-V) relation, $I_{L}(V)$ or $I_{L}(V) + I_{Na,p}(V)$ respectively, taken with the minus sign, see Fig. 3.5. Positive values of the right-hand-side $F(V)$ mean negative I-V, corresponding to a net inward current that depolarizes the membrane. Conversely, negative values mean positive I-V, corresponding to a net outward current that hyperpolarizes the membrane.
3.2.2 Equilibria

The next step in the qualitative analysis of any dynamical system is to find its equilibria or rest points, that is, the values of the state variable where

\[ F(V) = 0 \quad (V \text{ is an equilibrium}). \]

At each such point \( \dot{V} = 0 \), the state variable \( V \) does not change. In the context of membrane potential dynamics, equilibria correspond to the points where the steady-state I-V curve passes zero. At each such point there is a balance of the inward and outward currents so that the net transmembrane current is zero, and the membrane voltage does not change. (Incidentally, the part libra in the Latin word aequilibrium means balance).

The \( I_K \)- and \( I_h \)-models mentioned in section 3.1 can have only one equilibrium because their I-V relations \( I(V) \) are monotonic increasing functions. The corresponding functions \( F(V) \) are monotonic decreasing and can have only one zero.

In contrast, the \( I_{Na,p} \)- and \( I_{Kr} \)-models can have many equilibria because their I-V curves are not monotonic, and hence there is a possibility for multiple intersections with the \( V \)-axis. For example, there are three equilibria in Fig.3.8b corresponding to the resting state (around \(-53 \) mV), the threshold state (around \(-40 \) mV), and the excited state (around 30 mV). Each equilibrium corresponds to the balance of the outward leak current and partially (rest), moderately (threshold), or fully (excited) activated persistent Na\(^+\) inward current. Throughout this book we denote equilibria as small open or filled circles, depending on their stability, as in Fig.3.8.

3.2.3 Stability

If the initial value of the state variable is exactly at equilibrium, then \( \dot{V} = 0 \) and the variable will stay there forever. If the initial value is near the equilibrium, the state variable may approach the equilibrium or diverge from it. Both cases are depicted in Fig.3.8. We say that an equilibrium is asymptotically stable if all solutions starting sufficiently near the equilibrium will approach it as \( t \to \infty \).

Stability of an equilibrium is determined by the signs of the function \( F \) around it. The equilibrium is stable when \( F(V) \) changes the sign from “plus” to “minus” as \( V \) increases, as in Fig.3.8a. Obviously, all solutions starting near such an equilibrium converge to it. Such an equilibrium “attracts” all nearby solutions, so it is called an attractor. A stable equilibrium point is the only type of attractor that can exist in one-dimensional continuous dynamical systems defined on a state line \( \mathbb{R} \). Multidimensional systems can have other attractors, e.g., limit cycles.

The differences between stable, asymptotically stable, and exponentially stable equilibria are discussed in exercise 18 at the end of the chapter. The reader is also encouraged to solve exercise 4 (piecewise continuous \( F(V) \)).
3.2.4 Eigenvalues

A sufficient condition for an equilibrium to be stable is that the derivative of the function $F$ with respect to $V$ at the equilibrium is negative, provided the function is differentiable. We denote this derivative here by

$$\lambda = F'(V), \quad (V \text{ is an equilibrium; that is, } F(V) = 0)$$

and note that it is the slope of the graph of $F$ at the point $V$ (see Fig. 3.9). Obviously, when the slope, $\lambda$, is negative, the function changes the sign from “plus” to “minus”, and the equilibrium is stable. Positive slope $\lambda$ implies instability. The parameter $\lambda$ defined above is the simplest example of an eigenvalue of an equilibrium. We introduce eigenvalues formally in chapter 4 and show that they play an important role in defining the types of equilibria of multidimensional systems.

3.2.5 Unstable Equilibria

If a one-dimensional system has two stable equilibrium points, then they must be separated by at least one unstable equilibrium point, as we illustrate in Fig. 3.10. (This may not be true in multidimensional systems.) Indeed, a continuous function $F$ has to change the sign from “minus” to “plus” somewhere in between those equilibria; that is, it has to cross the $V$-axis at some point, as in Fig. 3.8b. This point would be an unstable equilibrium, since all nearby solutions diverge from it. In the context...
of neuronal models, unstable equilibria lie in the region of the steady-state I-V curve with negative conductance. (Please, check that this is in accordance with the fact that $F(V) = -I(V)/C$; see Fig.3.5.) An unstable equilibrium is sometimes called a repeller. Attractors and repellers have a simple mechanistic interpretation depicted in Fig.3.11.

If the initial condition $V_0$ is set to an unstable equilibrium point, then the solution will stay at this unstable equilibrium; that is, $V(t) = V_0$ for all $t$, at least in theory. In practice, the location of an equilibrium point is known only approximately. In addition, small noisy perturbations that are always present in biological systems can make $V(t)$ deviate slightly from the equilibrium point. Because of instability, such deviations will grow, and the state variable $V(t)$ will eventually diverge from the repelling equilibrium the same way that the ball set at the top of the hill in Fig.3.11 will eventually roll downhill. If the level of noise is low, it could take a long time to diverge from the repeller.

### 3.2.6 Attraction Domain

Even though unstable equilibria are hard to see experimentally, they still play an important role in dynamics, since they separate attraction domains. Indeed, the ball in Fig.3.11 could go left or right, depending on which side of the hilltop it is on initially. Similarly, the state variable of a one-dimensional system decreases or increases, depending on which side of the unstable equilibrium the initial condition is, as one can clearly see in Fig.3.8b.

In general, the basin of attraction or attraction domain of an attractor is the set...
Figure 3.12: Two attraction domains in a one-dimensional system are separated by the unstable equilibrium.

of all initial conditions that lead to the attractor. For example, the attraction domain of the equilibrium in Fig.3.8a is the entire voltage range. Such an attractor is called global. In Fig.3.12 we plot attraction domains of two stable equilibria. The middle unstable equilibrium is always the boundary of the attraction domains.

### 3.2.7 Threshold and Action Potential

Unstable equilibria play the role of thresholds in one-dimensional bistable systems, i.e., in systems having two attractors. We illustrate this in Fig.3.13, which is believed to describe the essence of the mechanism of bistability in many neurons. Suppose the state variable is initially at the stable equilibrium point marked “state A” in the figure, and suppose that perturbations can kick it around the equilibrium. Small perturbations may not kick it over the unstable equilibrium so that the state variable continues to be in the attraction domain of “state A”. We refer to such perturbations as subthreshold.

In contrast, we refer to perturbations as superthreshold (or suprathreshold) if they are large enough to push the state variable over the unstable equilibrium so that it becomes attracted to the “state B”. We see that the unstable equilibrium acts as a threshold that separates two states.

The transition between two stable states separated by a threshold is relevant to the mechanism of excitability and generation of action potentials in many neurons, which is illustrated in Fig.3.14. In the $I_{Na,p}$-model (3.5) with the I-V relation in Fig.3.5 the existence of the resting state is largely due to the leak current $I_L$, while the existence of the excited state is largely due to the persistent inward Na$^+$ current $I_{Na,p}$. Small (subthreshold) perturbations leave the state variable in the attraction domain of the rest state, while large (superthreshold) perturbations initiate the regenerative process – the upstroke of an action potential – and the voltage variable becomes attracted to the excited state. Generation of the action potential must be completed via repolarization,
Figure 3.13: Unstable equilibrium plays the role of a threshold that separates two attraction domains.
which moves $V$ back to the resting state. Typically, repolarization occurs because of a relatively slow inactivation of $\text{Na}^+$ current and/or slow activation of an outward $\text{K}^+$ current, which are not taken into account in the one-dimensional system (3.5). To account for such processes, we consider two-dimensional systems in the next chapter.

Recall that the parameters of the $I_{\text{Na},p}$-model (3.5) were obtained from a cortical pyramidal neuron. In Fig.3.15 left, we stimulate (in vitro) the cortical neuron by short (0.1 ms) strong pulses of current to reset its membrane potential to various initial values, and interpret the results using the $I_{\text{Na},p}$-model. Since activation of the $\text{Na}^+$ current is not instantaneous in real neurons, we allow variable $m$ to converge to $m_{\infty}(V)$, and ignore the 0.3-ms transient activity that follows each pulse. We also ignore
Figure 3.16: Membrane potential bistability in a cat TC neuron in the presence of ZD7288 (pharmacological blocker of $I_h$. (Modified from Fig. 6B of Hughes et al. 1999).

Figure 3.17: Bistability and hysteresis loop as $I$ changes.

the initial segment of the downstroke of the action potential, and plot the magnification of the voltage traces in Fig.3.15 (right). Comparing this figure with Fig.3.8b we see that the $I_{Na,p}$-model is a reasonable one-dimensional approximation of the action potential upstroke dynamics. It predicts the value of the resting ($-53\,\text{mV}$), the instantaneous threshold ($-40\,\text{mV}$), and the excited ($+30\,\text{mV}$) states of the cortical neuron.

### 3.2.8 Bistability and Hysteresis

Systems having two (many) coexisting attractors are called bistable (multistable). Many neurons and neuronal models, such as the Hodgkin-Huxley model, exhibit bistability between resting (equilibrium) and spiking (limit cycle) attractors. Some neurons can exhibit bistability of two stable resting states in the subthreshold voltage range, for example, $-59\,\text{mV}$ and $-75\,\text{mV}$ in the thalamocortical neurons (Hughes et al. 1999) depicted in Fig.3.16, or $-50\,\text{mV}$ and $-60\,\text{mV}$ in mitral cells of the olfactory bulb (Heyward et al. 2001), or $-45\,\text{mV}$ and $-60\,\text{mV}$ in Purkinje neurons. Brief inputs can switch such neurons from one state to the other, as in Fig.3.16. Though the ionic mechanisms of bistability are different in the three neurons, the mathematical mechanism is the same.

Consider a one-dimensional system $\dot{V} = I + F(V)$ with function $F(V)$ having a
cubic N-shape. Injection of a DC current $I$ shifts the function $I + F(V)$ up or down. When $I$ is negative, the system has only one equilibrium, depicted in Fig.3.17a. As we remove the injected current $I$, the system becomes bistable, as in Fig.3.17b, but its state is still at the left equilibrium. As we inject positive current, the left stable equilibrium disappears via another saddle-node bifurcation, and the state of the system jumps to the right equilibrium, as in Fig.3.17c. But as we slowly remove the injected current that caused the jump and go back to Fig.3.17b, the jump to the left equilibrium does not occur until a much lower value corresponding to Fig.3.17a is reached. The failure of the system to return to the original value when the injected current is removed is called \textit{hysteresis}. If $I$ were a slow $V$-dependent variable, then the system could exhibit relaxation oscillations depicted in Fig.3.17d and described in the next chapter.

### 3.3 Phase Portraits

An important component in the qualitative analysis of any dynamical system is reconstruction of its \textit{phase portrait}. It depicts all stable and unstable equilibria (as black and white circles, respectively), representative trajectories, and corresponding attraction domains in the system’s state/phase space, as we illustrate in Fig.3.18. The phase portrait is a geometrical representation of system dynamics. It depicts all possible evolutions of the state variable and how they depend on the initial state. Looking at the phase portrait, one immediately gets all important information about the system’s qualitative behavior without even knowing the equation for $F$.

![Phase Portrait and Function F(V)](image)

Figure 3.18: Phase portrait of a one-dimensional system $\dot{V} = F(V)$. 

3.3.1 Topological Equivalence

Phase portraits can be used to determine qualitative similarity of dynamical systems. In particular, two one-dimensional systems are said to be topologically equivalent when the phase portrait of one of them, treated as a piece of rubber, can be stretched or shrunk to fit the other one, as in Fig. 3.19. Topological equivalence is a mathematical concept that clarifies the imprecise notion of “qualitative similarity”, and its rigorous definition is provided, for instance, by Guckenheimer and Holmes (1983).

The stretching and shrinking of the “rubber” phase space are topological transformations that do not change the number of equilibria or their stability. Thus, two systems having different numbers of equilibria cannot be topologically equivalent and, hence, they have qualitatively different dynamics, as we illustrate in Fig. 3.20. Indeed, the top system is bistable because it has two stable equilibria separated by an unstable one. The evolution of the state variable depends on which attraction domain the initial condition is in initially. Such a system has “memory” of the initial condition. Moreover, sufficiently strong perturbations can switch it from one equilibrium state to another. In contrast, the bottom system in Fig. 3.20 has only one equilibrium, which is a global attractor, and the state variable converges to it regardless of the initial condition. Such a system has quite primitive dynamics, and it is topologically equivalent to the linear system (3.1).
3.3.2 Local Equivalence and the Hartman-Grobman Theorem

In computational neuroscience, we usually face quite complicated systems describing neuronal dynamics. A useful strategy is to replace such systems with simpler ones having topologically equivalent phase portraits. For example, both systems in Fig.3.19 are topologically equivalent to $V = V - V^3$ (readers should check this), which is easier to deal with analytically.

Quite often we cannot find a simpler system that is topologically equivalent to our neuronal model on the entire state line $\mathbb{R}$. In this case, we make a sacrifice: we restrict our analysis to a small neighborhood of the line $\mathbb{R}$ (e.g., a neighborhood of the resting state or of the threshold), and study behavior locally in this neighborhood.

An important tool in the local analysis of dynamical systems is the Hartman-Grobman theorem, which says that a nonlinear one-dimensional system

$$\dot{V} = F(V)$$

sufficiently near an equilibrium $V = V_{eq}$ is locally topologically equivalent to the linear system

$$\dot{V} = \lambda (V - V_{eq}) ,$$

provided the eigenvalue

$$\lambda = F'(V_{eq})$$

at the equilibrium is nonzero, that is, the slope of $F(V)$ is nonzero. Such an equilibrium is called hyperbolic. Thus, nonlinear systems near hyperbolic equilibria behave as if they were linear, as in Fig.3.21.

It is easy to find the exact solution of the linearized system (3.8) with an initial condition $V(0) = V_0$. It is $V(t) = V_{eq} + e^{\lambda t}(V_0 - V_{eq})$ (readers should check by differentiating). If the eigenvalue $\lambda < 0$, then $e^{\lambda t} \to 0$ and $V(t) \to V_{eq}$ as $t \to \infty$, so that the equilibrium is stable. Conversely, if $\lambda > 0$, then $e^{\lambda t} \to \infty$ meaning that the initial displacement, $V_0 - V_{eq}$, grows with time and the equilibrium is unstable. Thus, the linearization predicts qualitative dynamics at the equilibrium, and the quantitative rate of convergence/divergence to/from the equilibrium.

If the eigenvalue $\lambda = 0$, then the equilibrium is non-hyperbolic, and analysis of the linearized system $\dot{V} = 0$ cannot describe the behavior of the nonlinear system. Typically, non-hyperbolic equilibria arise when the system undergoes a bifurcation, i.e., a qualitative change of behavior, which we consider next. To study stability, we need to consider higher-order terms of the Taylor series of $F(V)$ at $V_{eq}$. 

Figure 3.21: Hartman-Grobman theorem: The nonlinear system $\dot{V} = F(V)$ is topologically equivalent to the linear one $\dot{V} = \lambda (V - V_{eq})$ in the local (shaded) neighborhood of the hyperbolic equilibrium $V_{eq}$. 

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3.3.3 Bifurcations

The final and most advanced step in the qualitative analysis of any dynamical system is the bifurcation analysis. In general, a system is said to undergo a bifurcation when its phase portrait changes qualitatively. For example, the energy landscape in Fig. 3.22 changes so that the system is no longer bistable. The precise mathematical definition of a bifurcation will be given later.

Qualitative change of the phase portrait may or may not necessarily reveal itself in a qualitative change of behavior, depending on the initial conditions. For example, there is a bifurcation in Fig. 3.23 (left), but no change of behavior, because the ball remains in the attraction domain of the right equilibrium. To see the change, we need to drop the ball at different initial conditions and observe the disappearance of the left equilibrium. In the same veins, there is no bifurcation in Fig. 3.23 (middle and right) – the phase portraits in each column are topologically equivalent, but the apparent change of behavior is caused by the expansion of the attraction domain of the left equilibrium or by the external input. Dropping the ball at different locations would result in the same qualitative picture – two stable equilibria whose attraction domains are separated by the unstable equilibrium. When mathematicians talk about bifurcations, they assume that all initial conditions could be sampled, in which case bifurcations do result in a qualitative change of behavior of the system as a whole.

To illustrate the importance of sampling all initial conditions, let us consider the in
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Figure 3.23: Bifurcations are not equivalent to qualitative change of behavior if the system is started with the same initial condition or subject to external input.

vitro recordings of a pyramidal neuron in Fig.3.24. We inject 0.1-ms strong pulses of current of various amplitudes to set the membrane potential to different initial values. Right after each pulse, we inject a 4-ms step of DC current of amplitude $I = 0$, $I = 16$, or $I = 60$ pA. The case of $I = 0$ pA is the same as in Fig.3.15, so some initial conditions result in upstroke of the action potential, while others do not. When $I = 60$ pA, all

Figure 3.24: Qualitative change of the upstroke dynamics of a layer 5 pyramidal neuron from rat visual cortex (the same neuron as in Fig.3.15).
initial conditions result in the generation of an action potential. Clearly, a change of qualitative behavior occurs for some $I$ between 0 and 60.

To understand the qualitative dynamics in Fig.3.24, we consider the one-dimensional $I_{Na,p}$-model (3.5) having different values of the parameter $I$ and depict its trajectories in Fig.3.25. One can clearly see that the qualitative behavior of the model depends on whether $I$ is greater or less than 16. When $I = 0$ (top of Fig.3.25), the system is bistable. The resting and the excited states coexist. When $I$ is large (bottom of Fig.3.25) the resting state no longer exists because the leak outward current cannot balance the large injected DC current $I$ and the inward Na$^+$ current.

What happens when we change $I$ past 16? The answer lies in the details of the geometry of the right-hand-side function $F(V)$ of (3.5) and how it depends on the
Figure 3.26: Saddle-node bifurcation: As the graph of the function $F(V)$ is lifted up, the stable and unstable equilibria approach each other, coalesce at the tangent point, and then disappear.

Parameter $I$. Increasing $I$ elevates the graph of $F(V)$. The higher the graph of $F(V)$ is, the closer its intersections with the $V$-axis are, as we illustrate in Fig. 3.26, which depicts only the low-voltage range of the system. When $I$ approaches 16, the distance between the stable and unstable equilibria vanishes; the equilibria coalesce and annihilate each other. The value $I = 16$, at which the equilibria coalesce, is called the bifurcation value. This value separates two qualitatively different regimes. When $I$ is near to but less than 16, the system has three equilibria and bistable dynamics. The quantitative features, such as the exact locations of the equilibria, depend on the particular values of $I$, but the qualitative behavior remains unchanged no matter how close $I$ is to the bifurcation value. In contrast, when $I$ is near to but greater than 16, the system has only one equilibrium and monostable dynamics.

In general, a dynamical system may depend on a vector of parameters, say $p$. A point in the parameter space, say $p = a$, is said to be a regular or non-bifurcation point, if the system's phase portrait at $p = a$ is topologically equivalent to the phase portrait at $p = c$ for any $c$ sufficiently close to $a$. For example, the value $I = 13$ in Fig. 3.26 is regular, since the system has topologically equivalent phase portraits for all $I$ near 13. Similarly, the value $I = 18$ is also regular. Any point in the parameter space that is not regular is called a bifurcation point. Namely, a point $p = b$ is a bifurcation point if the system's phase portrait at $p = b$ is not topologically equivalent to the phase portrait at a point $p = c$ no matter how close $c$ is to $b$. The value $I = 16$ in Fig. 3.26 is a bifurcation point. It corresponds to the saddle-node (also known as fold or tangent) bifurcation for reasons described later. It is one of the simplest bifurcations considered in this book.
3.3.4 Saddle-Node (Fold) Bifurcation

In general, a one-dimensional system

$$\dot{V} = F(V, I),$$

having an equilibrium point $V = V_{sn}$ for some value of the parameter $I = I_{sn}$ (i.e., $F(V_{sn}, I_{sn}) = 0$), is said to be at a saddle-node bifurcation (sometimes called a fold bifurcation) if the following mathematical conditions, illustrated in Fig.3.27, are satisfied:

- **Non-hyperbolicity.** The eigenvalue $\lambda$ at $V_{sn}$ is zero; that is,
  $$\lambda = F_V(V_{sn}, I_{sn}) = 0 \quad (at \ V = V_{sn}),$$
  where $F_V$ denotes the derivative of $F$ with respect to $V$; that is, $F_V = \partial F / \partial V$. Equilibria with zero or pure imaginary eigenvalues are called non-hyperbolic. Geometrically, this condition implies that the graph of $F$ has horizontal slope at the equilibrium.

- **Non-degeneracy.** The second-order derivative with respect to $V$ at $V_{sn}$ is nonzero; that is,
  $$F_{VV}(V_{sn}, I_{sn}) \neq 0 \quad (at \ V = V_{sn}).$$
  Geometrically, this means that the graph of $F$ looks like the square parabola $V^2$ in Fig.3.27.

![Figure 3.27: Geometrical illustration of the three conditions defining saddle-node bifurcations. Arrows denote the direction of displacement of the function $F(V, I)$ as the bifurcation parameter $I$ changes.](image-url)
• **Transversality.** The function $F(V, I)$ is non-degenerate with respect to the bifurcation parameter $I$; that is,

$$F_I(V_{sn}, I) \neq 0 \quad \text{(at } I = I_{sn}),$$

where $F_I$ denotes the derivative of $F$ with respect to $I$. Geometrically, this means that as $I$ changes past $I_{sn}$, the graph of $F$ approaches, touches, and then intersects the $V$-axis.

Saddle-node bifurcation results in appearance or disappearance of a pair of equilibria, as in Fig.3.26. None of the six examples on the right-hand side of Fig.3.27 can undergo a saddle-node bifurcation because at least one of the conditions above is violated.

The number of conditions involving strict equality (“=” ) is called the *codimension* of a bifurcation. The saddle-node bifurcation has *codimension-1* because there is only one condition involving “=” ; the other two conditions involve inequalities (“≠”). Codimension-1 bifurcations can be reliably observed in systems with one parameter.

It is an easy exercise to check that the one-dimensional system

$$\dot{V} = I + V^2$$

is at saddle-node bifurcation when $V = 0$ and $I = 0$ (readers should check all three conditions). This system is called the *topological normal form* for saddle-node bifurcation. The phase portraits of this system are topologically equivalent to those depicted in Fig.3.26, except that the bifurcation occurs at $I = 0$, and not at $I = 16$.

### 3.3.5 Slow Transition

All physical, chemical, and biological systems near saddle-node bifurcations possess certain universal features that do not depend on particulars of the systems. Consequently, all neural systems near such a bifurcation share common neurocomputational properties, which we will discuss in detail in chapter 7. Here we take a look at one such property – slow transition through the ruins (or ghost) of the resting state attractor, which is relevant to the dynamics of many neocortical neurons.

In Fig.3.28 we show the function $F(V)$ of the system (3.5) with $I = 30$ pA, which is greater than the bifurcation value 16 pA, and the corresponding behavior of a cortical neuron (compare with Fig.3.15). The system has only one attractor, the excited state, and any solution starting from an arbitrary initial condition should quickly approach this attractor. However, the solutions starting from the initial conditions around $-50$ mV do not seem to hurry. Instead, they slow down near $-46$ mV and spend a considerable amount of time in the voltage range corresponding to the resting state, as if the state were still present. The closer $I$ is to the bifurcation value, the more time the membrane potential spends in the neighborhood of the resting state. Obviously, such a slow transition cannot be explained by a slow activation of the inward Na$^+$ current, since Na$^+$ activation in a cortical neuron is practically instantaneous.
Figure 3.28: Slow transition through the ghost of the resting state attractor in a cortical pyramidal neuron with $I = 30$ pA (the same neuron as in Fig.3.15). Even though the resting state has already disappeared, the function $F(V)$, and hence the rate of change, $\dot{V}$, is still small when $V \approx -46$ mV.

The slow transition occurs because the neuron or the system (3.5) in Fig.3.28 is near a saddle-node bifurcation. Even though $I$ is greater than the bifurcation value, and the resting state attractor is already annihilated, the function $F(V)$ is barely above the $V$-axis at the “annihilation site”. In other words, the resting state attractor has already been ruined, but its “ruins” (or its “ghost”) can still be felt, because

$$\dot{V} = F(V) \approx 0 \quad \text{(at attractor ruins, } V \approx -46 \text{ mV)},$$

as one can see in Fig.3.28. In chapter 7 we will show how this property explains the ability of many neocortical neurons, such as the one in Fig.3.29, to generate repetitive action potentials with small frequency, and how it predicts that all such neurons, considered as dynamical systems, reside near saddle-node bifurcations.
3.3.6 Bifurcation Diagram

The final step in the geometrical bifurcation analysis of one-dimensional systems is the analysis of bifurcation diagrams, which we do in Fig.3.30 for the saddle-node bifurcation shown in Fig.3.26. To draw the bifurcation diagram, we determine the locations of the stable and unstable equilibria for each value of the parameter \( I \) and plot them as white or black circles in the \((I,V)\) plane in Fig.3.30. The equilibria form two branches that join at the fold point corresponding to the saddle-node bifurcation (hence the alternative name fold bifurcation). The branch corresponding to the unstable equilibria is dashed to stress its instability. As the bifurcation parameter \( I \) varies from left to right, passing through the bifurcation point, the stable and unstable equilibria coalesce and annihilate each other. As the parameter varies from right to left, two equilibria – one stable and one unstable – appear from a single point. Thus, depending on the direction of movement of the bifurcation parameter, the saddle-node bifurcation explains disappearance or appearance of a new stable state. In any case, the qualitative behavior of the systems changes exactly at the bifurcation point.

3.3.7 Bifurcations and I-V Relations

In general, determining saddle-node bifurcation diagrams of neurons may be a daunting mathematical task. However, it is a trivial exercise when the bifurcation parameter is the injected DC current \( I \). In this case, the bifurcation diagram, such as the one in Fig.3.30, is the steady-state I-V relation \( I_\infty(V) \) plotted on the \((I,V)\)-plane. Indeed, the equation

\[
C\dot{V} = I - I_\infty(V) = 0
\]
states that \( V \) is an equilibrium if and only if the net membrane current, \( I - I_\infty(V) \), is zero. For example, equilibria of the \( I_{Na,p} \)-model are solutions of the equation

\[
0 = I - (g_L(V - E_L) + g_{Na,m_\infty}(V - E_{Na}))
\]

which follows directly from (3.5). In Fig. 3.31 we illustrate how to find the equilibria geometrically: We plot the steady-state I-V curve \( I_\infty(V) \) and draw a horizontal line with altitude \( I \). Any intersection satisfies the equation \( I = I_\infty(V) \), and hence is an equilibrium (stable or unstable). Obviously, when \( I \) increases past 16, the saddle-node bifurcation occurs.

Note that the equilibria are points on the curve \( I_\infty(V) \), so flipping and rotating the curve by 90\(^\circ\), as we do in Fig. 3.32 (left), results in a complete saddle-node bifurcation diagram. The diagram conveys all important information about the qualitative behavior of the \( I_{Na,p} \)-model in a very condensed manner. The three branches of the S-shaped

Figure 3.31: Equilibria are intersections of the steady-state I-V curve \( I_\infty(V) \) and a horizontal line \( I = \text{const.} \).
Bistability

Monostability

Bifurcation

Tangent Point

Figure 3.33: Bifurcation in the $I_{Na,p}$-model (3.5). The excited state and the threshold state coalesce and disappear when the parameter $I$ is sufficiently small.

curve, which is the $90^\circ$-rotated and flipped copy of the N-shaped I-V curve, correspond to the resting, threshold, and excited states of the model. Each slice $I = \text{const}$ represents the phase portrait of the system, as we illustrate in Fig.3.32 (right). Each point where the branches fold (max or min of $I_\infty(V)$) corresponds to a saddle-node bifurcation. Since there are two such folds, at $I = 16 \text{ pA}$ and at $I = -890 \text{ pA}$, there are two saddle-node bifurcations in the system. The first one, studied in Fig.3.25, corresponds to the disappearance of the resting state. The other one, illustrated in Fig.3.33, corresponds to the disappearance of the excited state. It occurs because $I$ becomes so negative that the Na$^+$ inward current is no longer strong enough to balance the leak outward current and the negative injected DC current to keep the membrane in the depolarized (excited) state.

Below, the reader can find more examples of bifurcation analysis of the $I_{Na,p}$- and $I_{Kr}$-models, which have nonmonotonic I-V relations and can exhibit multistability of states. The $I_K$- and $I_h$-models have monotonic I-V relations, and hence only one equilibrium state. These models cannot have saddle-node bifurcations, as the reader is asked to prove in exercise 13 and 14.
Figure 3.34: Magnification of the I-V curve in Fig. 3.31 at the left knee shows that it can be approximated by a square parabola.

3.3.8 Quadratic Integrate-and-Fire Neuron

Let us consider the topological normal form for the saddle-node bifurcation (3.9). From $0 = I + V^2$ we find that there are two equilibria, $V_{\text{rest}} = -\sqrt{|I|}$ and $V_{\text{thresh}} = +\sqrt{|I|}$ when $I < 0$. The equilibria approach and annihilate each other via saddle-node bifurcation when $I = 0$, so there are no equilibria when $I > 0$. In this case, $\dot{V} \geq I$ and $V(t)$ increases to infinity. Because of the quadratic term, the rate of increase also increases, resulting in a positive feedback loop corresponding to the regenerative activation of the $\text{Na}^+$ current. In exercise 15 we show that $V(t)$ escapes to infinity in a finite time, which corresponds to the upstroke of the action potential. The same upstroke is generated when $I < 0$, if the voltage variable is pushed beyond the threshold value $V_{\text{thresh}}$.

Considering infinite values of the membrane potential may be convenient from a purely mathematical point of view, but this has no physical meaning and there is no way to simulate it on a digital computer. Instead, we fix a sufficiently large constant $V_{\text{peak}}$ and say that (3.9) generated a spike when $V(t)$ reached $V_{\text{peak}}$. After the peak of the spike is reached, we reset $V(t)$ to a new value $V_{\text{reset}}$. The topological normal form for the saddle-node bifurcation with the after-spike resetting,

$$\dot{V} = I + V^2, \quad \text{if } V \geq V_{\text{peak}}, \quad \text{then } V \leftarrow V_{\text{reset}}$$

is called the quadratic integrate-and-fire neuron. It is the simplest model of a spiking neuron. The name stems from its resemblance to the leaky integrate-and-fire neuron $\dot{V} = I - V$ considered in chapter 8. In contrast to the common folklore, the leaky neuron is not a spiking model because it does not have a spike generation mechanism, i.e., a regenerative upstroke of the membrane potential, whereas the quadratic neuron does. We discuss this and other issues in detail in chapter 8.

In general, the quadratic integrate-and-fire model could be derived directly from the equation $CV = I - I_\infty(V)$ through approximating the steady-state I-V curve near
the resting state by the square parabola $I_\infty(V) \approx I_{sn} - k(V - V_{sn})^2$, where $k > 0$ and the peak of the curve $(V_{sn}, I_{sn})$ could easily be found experimentally (see Fig. 3.34). Approximating the I-V curve by other functions – for example $I_\infty(V) = g_{\text{leak}}(V - V_{\text{reset}}) - k e^{bV}$, results in other forms of the model, such as the exponential integrate-and-fire model (Fourcaud-Trocme et al. 2003), which has certain advantages over the quadratic form. Unfortunately, the model is not solvable analytically, and it is expensive to simulate. The form $I_\infty(V) = g_{\text{leak}}(V - V_{\text{leak}}) - k (V - V_{\text{th}})^2 + x_+$, where $x_+ = x$ when $x > 0$ and $x_+ = 0$ otherwise, combines the advantages of both models. The parameters $V_{\text{peak}}$ and $V_{\text{reset}}$ are derived from the shape of the spike. Normalization of variables and parameters results in the form (3.10) with $V_{\text{peak}} = 1$.

In Fig. 3.35 we simulate the quadratic integrate-and-fire neuron to illustrate a number of its features, which will be described in detail in subsequent chapters using conductance-based models. First, the neuron is an integrator; each input pulse in Fig. 3.35 (top), pushes $V$ closer to the threshold value; the higher the frequency of the input, the sooner $V$ reaches the threshold and starts the upstroke of a spike. The neuron is monostable when $V_{\text{reset}} \leq 0$ and can be bistable otherwise. Indeed, the first spike in Fig. 3.35 (middle) is evoked by the input, but the subsequent spikes occur because the reset value is superthreshold.

The neuron can be Class 1 or Class 2 excitable, depending on the sign of $V_{\text{reset}}$. 

---

**Figure 3.35**: Quadratic integrate-and-fire neuron (3.10) with time-dependent input.
Suppose the injected current $I$ slowly ramps up from a negative to a positive value. The membrane potential follows the resting state $-\sqrt{|I|}$ in a quasi-static fashion until the bifurcation point $I = 0$ is reached. At this moment, the neuron starts to fire tonic spikes. In the monostable case $V_{\text{reset}} < 0$ in Fig.3.35 (bottom), the membrane potential is reset to the left of the ghost of the saddle-node point (see section 3.3.5), thereby producing spiking with an arbitrary small frequency, and hence Class 1 excitability. Because of the recurrence, such a bifurcation is called saddle-node on invariant circle. Many pyramidal neurons in mammalian neocortex exhibit such a bifurcation. In contrast, in the bistable case $V_{\text{reset}} > 0$, not shown in the figure, the membrane potential is reset to the right of the ghost, no slow transition is involved, and the tonic spiking starts with a nonzero frequency. (As an exercise, explain why there is a noticeable latency [delay] to the first spike right after the bifurcation.) This type of behavior is typical in spiny projection neurons of neostriatum and basal ganglia, as we show in chapter 8.

**Review of Important Concepts**

- The one-dimensional dynamical system $\dot{V} = F(V)$ describes how the rate of change of $V$ depends on $V$. Positive $F(V)$ means $V$ increases; negative $F(V)$ means $V$ decreases.

- In the context of neuronal dynamics, $V$ is often the membrane potential, and $F(V)$ is the steady-state I-V curve taken with the minus sign.

- A zero of $F(V)$ corresponds to an equilibrium of the system. (Indeed, if $F(V) = 0$, then the state of the system, $V$, neither increases nor decreases.)

- An equilibrium is stable when $F(V)$ changes the sign from “plus” to “minus”. A sufficient condition for stability is that the eigenvalue $\lambda = F'(V)$ at the equilibrium be negative.

- A phase portrait is a geometrical representation of the system’s dynamics. It depicts all equilibria, their stability, representative trajectories, and attraction domains.

- A bifurcation is a qualitative change of the system’s phase portrait.

- The saddle-node (fold) is a typical bifurcation in one-dimensional systems. As a parameter changes, a stable and an unstable equilibrium approach, coalesce, and then annihilate each other.
Bibliographical Notes

There is no standard textbook on dynamical systems theory. The classic book *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields* by Guckenheimer and Holmes (1983) plays the same role in the dynamical systems community as the book *Ion Channels of Excitable Membranes* by Hille (2001) plays in the neuroscience community. A common feature of these books is that they are not suitable for beginners.

Most textbooks on differential equations, such as *Differential Equations and Dynamical Systems* by Perko (1996), develop the theory starting with a comprehensive analysis of linear systems, then applying it to local analysis of nonlinear systems, and then discussing global behavior. To get to bifurcations, the reader has to go through a lot of daunting math, which is fun only for mathematicians. Here we follow an approach similar to that in *Nonlinear Dynamics and Chaos* by Strogatz (1994). Instead of going from linear to nonlinear systems, we go from one-dimensional nonlinear systems (this chapter) to two-dimensional nonlinear systems (next chapter). Rather than burdening the theory with a lot of mathematics, we use the geometrical approach to stimulate the reader’s intuition. (There is plenty of fun math in exercises and in later chapters.)

Exercises

1. Consider a neuron having a Na$^+$ current with fast activation kinetics. Assume that inactivation of this current, as well as (in)activations of the other currents in the neuron are much slower. Prove that the initial segment of action potential upstroke of this neuron can be approximated by the $I_{Na,p}$-model (3.5). Use Fig.3.15 to discuss the applicability of this approximation.

2. Draw phase portraits of the systems in Fig.3.36. Clearly mark all equilibria, their stability, attraction domains, and direction of trajectories. Determine the signs of eigenvalues at each equilibrium.

![Phase Portraits](image_url)

Figure 3.36: Draw a phase portrait of the system $\dot{V} = F(V)$ with shown $F(V)$.

3. Draw phase portraits of the following systems:

   (a) $\dot{x} = -1 + x^2$,  


(b) $\dot{x} = x - x^3$.

Determine the eigenvalues at each equilibrium.

4. Determine stability of the equilibrium $x = 0$ and draw phase portraits of the following piecewise continuous systems:

(a) $\dot{x} = \begin{cases} 2x, & \text{if } x < 0 \\ x, & \text{if } x \geq 0 \end{cases}$

(b) $\dot{x} = \begin{cases} -1, & \text{if } x < 0 \\ 0, & \text{if } x = 0 \\ 1, & \text{if } x > 0 \end{cases}$

(c) $\dot{x} = \begin{cases} \frac{-2}{x}, & \text{if } x \neq 0 \\ 0, & \text{if } x = 0 \end{cases}$

5. Draw phase portraits of the systems in Fig. 3.37. Which of the pairs in the figure correspond to topologically equivalent dynamical systems?

6. (Saddle-node bifurcation) Draw the bifurcation diagram and representative phase portraits of the system $\dot{x} = a + x^2$, where $a$ is a bifurcation parameter. Find the eigenvalues at each equilibrium.
Figure 3.38: The $I_{K_{ir}}$-model having injected current ($I$), leak current ($I_L$), and instantaneous K$^+$ inward rectifier current ($I_{K_{ir}}$) and described by (3.11). Inactivation curve $h_\infty(V)$ is modified from Wessel et al. (1999). Parameters: $C = 1$, $I = 6$, $g_L = 0.2$, $E_L = -50$, $g_{K_{ir}} = 2$, $E_K = -80$, $V_{1/2} = -76$, $k = -12$ (see Fig. 2.20).

7. (Saddle-node bifurcation) Use definition in section 3.3.4 to find saddle-node bifurcation points in the following systems:

   (a) $\dot{x} = a + 2x + x^2$,
   (b) $\dot{x} = a + x + x^2$,
   (c) $\dot{x} = a - x + x^2$,
   (d) $\dot{x} = a - x + x^3$ (Hint: Verify the non-hyperbolicity condition first.),
   (e) $\dot{x} = 1 + ax + x^2$,
   (f) $\dot{x} = 1 + 2x + ax^2$,

where $a$ is the bifurcation parameter.

8. (Pitchfork bifurcation) Draw the bifurcation diagram and representative phase portraits of the system $\dot{x} = bx - x^3$, where $b$ is a bifurcation parameter. Find the eigenvalues at each equilibrium.

9. Draw the bifurcation diagram of the $I_{K_{ir}}$-model

   \[
   CV = I - g_L(V - E_L) - g_{K_{ir}}h_\infty(V)(V - E_K),
   \]  

   using parameters from Fig. 3.38 and treating $I$ as a bifurcation parameter.

10. Derive an explicit formula that relates the position of the equilibrium in the Hodgkin-Huxley model to the magnitude of the injected DC current $I$. Are there any saddle-node bifurcations?

11. Draw the bifurcation diagram of the $I_{Na,p}$-model (3.5), using parameters from Fig. 3.39 and treating
Figure 3.39: The $I_{Na,p}$-model with leak current ($I_L$) and persistent Na$^+$ current ($I_{Na,p}$), described by (3.5) with the right-hand-side function $F(V)$. Parameters: $C = 1$, $I = 0$, $g_L = 1$, $E_L = -80$, $g_{Na} = 2.25$, $E_{Na} = 60$, $V_{1/2} = -20$, $k = 15$ (see Fig.2.20).

Figure 3.40: The $I_K$-model with leak current ($I_L$) and persistent K$^+$ current ($I_K$), described by (3.12). Parameters: $C = 1$, $g_L = 1$, $E_L = -80$, $g_K = 1$, $E_K = -90$, $V_{1/2} = -53$, $k = 15$ (see Fig.2.20).

(a) $g_L$ as a bifurcation parameter, or
(b) $E_L$ as a bifurcation parameter.

12. Draw the bifurcation diagram of the $I_{Kir}$-model (3.11), using parameters from Fig.3.38 and treating

(a) $g_L$ as a bifurcation parameter, or
(b) $g_{Kir}$ as a bifurcation parameter.

13. Show that the $I_K$-model in Fig.3.40

\[
C \dot{V} = -g_L(V - E_L) - g_K m^4(V)(V - E_K).
\]

cannot exhibit saddle-node bifurcation for $V > E_K$. (Hint: Show that $F'(V) \neq 0$ for all $V > E_K$.)
Figure 3.41: The $I_h$-model with leak current ($I_L$) and “hyperpolarization-activated” inward current $I_h$, described by (3.13). Parameters: $C = 1$, $g_L = 1$, $E_L = -80$, $g_h = 1$, $E_h = -43$, $V_{1/2} = -75$, $k = -5.5$ (Huguenard and McCormick 1992).

14. Show that the $I_h$-model in Fig.3.41,

$$ C \dot{V} = -g_L(V - E_L) - g_h h_\infty(V)(V - E_h), \tag{3.13} $$

cannot exhibit saddle-node bifurcation for any $V < E_h$.

15. Prove that the upstroke of the spike in the quadratic integrate-and-fire neuron (3.9) has the asymptote $1/(c - t)$ for some $c > 0$.

16. (Cusp bifurcation) Draw the bifurcation diagram and representative phase portraits of the system $\dot{x} = a + bx - x^3$, where $a$ and $b$ are bifurcation parameters. Plot the bifurcation diagram in the $(a, b, x)$-space and on the $(a, b)$-plane.

17. (Gradient systems) An $n$-dimensional dynamical system $\dot{x} = f(x)$, with $x = (x_1, \ldots, x_n) \in \mathbb{R}^n$ is said to be gradient when there is a potential (energy) function $E(x)$ such that

$$ \dot{x} = -\text{grad } E(x), $$

where

$$ \text{grad } E(x) = (E_{x_1}, \ldots, E_{x_n}) $$

is the gradient of $E(x)$. Show that all one-dimensional systems are gradient. (Hint: See Fig.3.11.) Find potential (energy) functions for the following one-dimensional systems

(a) $\dot{V} = 0$,  \hspace{1cm}  (b) $\dot{V} = 1$,  \hspace{1cm}  (c) $\dot{V} = -V$,
(d) $\dot{V} = -1 + V^2$,  \hspace{1cm}  (e) $\dot{V} = V - V^3$,  \hspace{1cm}  (f) $\dot{V} = -\sin V$.

18. Consider a dynamical system $\dot{x} = f(x)$, $x(0) = x_0$.

(a) Stability. An equilibrium $y$ is stable if any solution $x(t)$ with $x_0$ sufficiently close to $y$ remains near $y$ for all time. That is, for all $\varepsilon > 0$ there exists $\delta > 0$ such that if $|x_0 - y| < \delta$ then $|x(t) - y| < \varepsilon$ for all $t \geq 0$. 
(b) Asymptotic stability. A stable equilibrium \( y \) is *asymptotically stable* if all solutions starting sufficiently close to \( y \) approach it as \( t \rightarrow \infty \). That is, if \( \delta > 0 \) can be chosen from the definition above so that \( \lim_{t \rightarrow \infty} x(t) = y \).

(c) Exponential stability. A stable equilibrium \( y \) is said to be *exponentially stable* when there is a constant \( a > 0 \) such that \( |x(t) - y| < \exp(-at) \) for all \( x_0 \) near \( y \) and all \( t \geq 0 \).

Prove that (c) implies (b), and (b) implies (a). Show that (a) does not imply (b) and (b) does not imply (c). That is, present a system having stable but not asymptotically stable equilibrium, and a system having asymptotically but not exponentially stable equilibrium.

19. (\( I_{\text{NMDA}} \)-model) Show that voltage-dependent activation of NMDA synaptic receptors in a passive dendritic tree with a constant concentration of glutamate is mathematically equivalent to the \( I_{\text{Na,p}} \)-model.