e. The solution is **chaotic** when $r = 4$. One property of chaos is **sensitive dependence on initial conditions.** Compare a solution starting from $x_0 = 0.3$ with one starting at $x_0 = 0.30001$. Even though they start off very close, they soon separate and become completely different. Why might this be a problem for a scientific experiment?

48. Consider the discrete-time dynamical system

$$x_{t+1} = e^{ax_t}$$

for the following values of the parameter a. Use your computer to graph the function and the diagonal to look for equilibria. Cobweb starting from $x_0 = 1$ in each case.

a. $a = 0.3$.

b. $a = 0.4$.

c. $a = 1/e$.

49. Consider the equation describing the dynamics of selection

$$p_{t+1} = \frac{sp_t}{sp_t + r(1 - p_t)}$$

but with two cultures 1 and 2. In 1, the mutant does better than the wild type, and in 2 the wild type does better. In particular, suppose that $s = 2.0$ and $r = 0.3$ in culture 1 and that $s = 0.6$ and $r = 2.0$ in culture 2. Define discrete-time dynamical systems f_1 and f_2 to describe the dynamics in the two cultures.

a. Graph the functions f_1 and f_2 along with the identity function. Find the first five values of solutions starting from $p_0 = 0.02$ and $p_0 = 0.98$ in each culture. Explain in words what each solution is doing and why.

b. Suppose you change the experiment. Begin by taking a population with a fraction p_0 of mutants. Split this population in half, and place one half in culture 1 and the other half in culture 2. Let the bacteria reproduce once in each culture, and then mix them together. Split the mix in half and repeat the process. The updating function is

$$f(p) = \frac{f_1(p) + f_2(p)}{2}.$$

Can you derive this? Plot this updating function along with the identity function. Have your computer find the equilibria and label them on your graph. Do they make sense?

c. Use cobwebbing to figure out which equilibria are stable.

d. Find one solution starting from $p_0 = 0.001$ and another starting from $p_0 = 0.999$. Are these results consistent with the stability of the equilibria? Explain in words why the solutions do what they do.

1.11 An Excitable Systems: The Heart

We can use cobwebbing and equilibria to study a simplified model of the heart. Our goal is to understand how simple changes in the parameters of a heart can produce heartbeat patterns called **second-degree block.** With these syndromes, people's hearts either beat half as often as they should or beat normally for a while, skip a beat, and return to beating. These conditions are solutions for the same model that describes a normal heartbeat, but with different parameter values.

1.11.1 A Simple Heart

Figure 1.11.1 shows the basic apparatus for beating of the heart. The sinoatrial node (SA node) is the pacemaker, sending regular signals to the atrioventrical node (AV node). The AV node then tells the heart to beat if conditions are suitable.

The AV node can be thought of as keeping track of the condition of the heart with an electrical potential. Denote the potential after responding to a signal from the SA node as V_t. Two processes go into updating this potential. During the time τ between signals from the SA node, the electrical potential of the AV node decays exponentially at rate α. Setting $\hat{V}_t$ to be the potential of the AV node just before receiving the next signal from the SA node,

$$\hat{V}_t = e^{-\alpha\tau} V_t$$

(Figure 1.11.2). Whether the heart beats depends on the state of the AV node when a signal arrives. If the potential $\hat{V}_t$ is too high, the heart has not had enough time to recover from the last beat, and the AV node ignores the signal. Otherwise, the AV node accepts the signal, tells the heart to beat, and increases its potential by u.

Let V_c be the threshold potential (Figure 1.11.3). If $\hat{V}_t > V_c$, the heart is not ready to beat and

$$V_{t+1} = \hat{V}_t \quad \text{if } \hat{V}_t > V_c.$$

If $\hat{V}_t \le V_c$, the AV node responds and tells the heart to beat, and

$$V_{t+1} = \hat{V}_t + u \quad \text{if } \hat{V}_t \le V_c.$$

To translate this description into a discrete-time dynamical system, we must write V_{t+1} entirely in terms of V_t, eliminating the $\hat{V}_t$ terms. Because $\hat{V}_t = e^{-\alpha\tau}V_t$, the two cases can be summarized as

$$V_{t+1} = \begin{cases} e^{-\alpha\tau}V_t & \text{if } e^{-\alpha\tau}V_t > V_c \\ e^{-\alpha\tau}V_t + u & \text{if } e^{-\alpha\tau}V_t \le V_c. \end{cases}$$

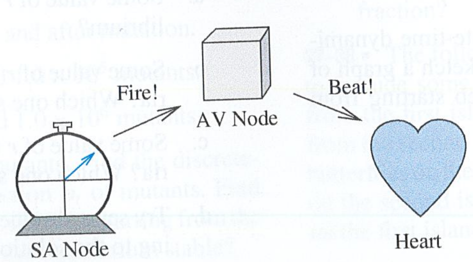


FIGURE 1.11.1
A mathematician's version of the heart

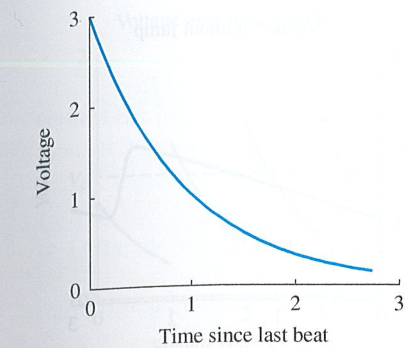


FIGURE 1.11.2
The exponential decay of voltage between beats

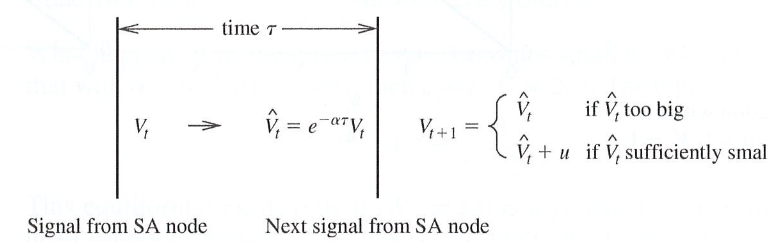


FIGURE 1.11.3
Schematic diagram of the potential of the AV node

For convenience we substitute the new parameter c for $e^{-\alpha\tau}$. A value of c near 1 means that the potential decays very little, and a value of c near 0 means that the potential decays a great deal (Figure 1.11.4).

Example 1.11.1 The Relation Between c, α, and τ

If $\tau = 1$ and $\alpha = \ln(3) = 1.099$, then $c = e^{-\alpha\tau} = 1/3$. The potential decays to 1/3 of its initial value between beats.

Example 1.11.2 The Relation Between c, α, and τ

If $\tau = 1$ and $\alpha = \ln(1.5) = 0.405$, then $c = e^{-\alpha\tau} = 2/3$. The potential decays less, to 2/3 of its initial value between beats, because α is smaller.

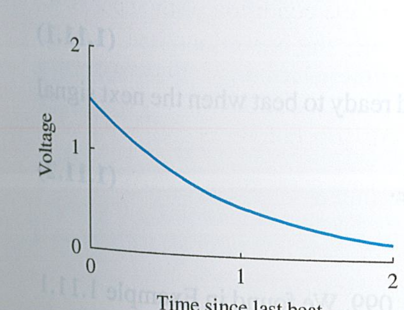


FIGURE 1.11.4
Graph of the potential of the AV node without beating

Using this new notation,

$$V_{t+1} = \begin{cases} cV_t & \text{if } cV_t > V_c \\ cV_t + u & \text{if } cV_t \le V_c. \end{cases}$$

This updating function is graphed with $u = 1$, $c = 0.4$ and $V_c = 1$ in Figure 1.11.5.

This function, unlike those we have studied hitherto, has a jump (where $cV_t = V_c$). This jump reflects the sharp response threshold. In the real heart, the threshold is not precise, and the two branches of the updating function are connected (Figure 1.11.6).

We can use the graphical method for finding equilibria as intersections with the diagonal to study this discrete-time dynamical system. Each piece of the updating function is a line with slope $c < 1$. There are two possible pictures. Either the upper branch of the updating function crosses the diagonal at an equilibrium (Figure 1.11.7a),

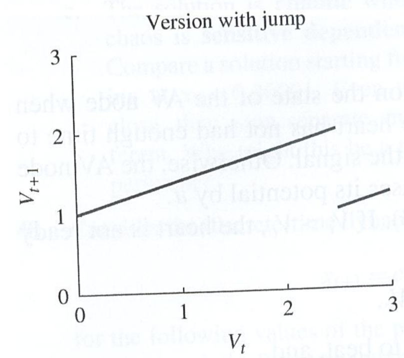
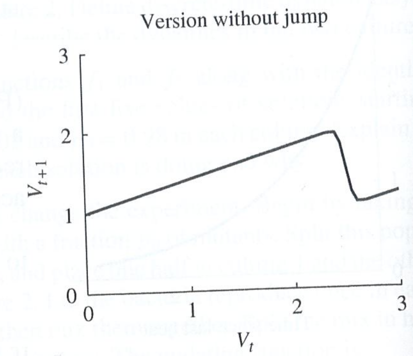


FIGURE 1.11.5
The updating function for the potential of the AV node

FIGURE 1.11.6
A smoothed updating function for the potential of the AV node



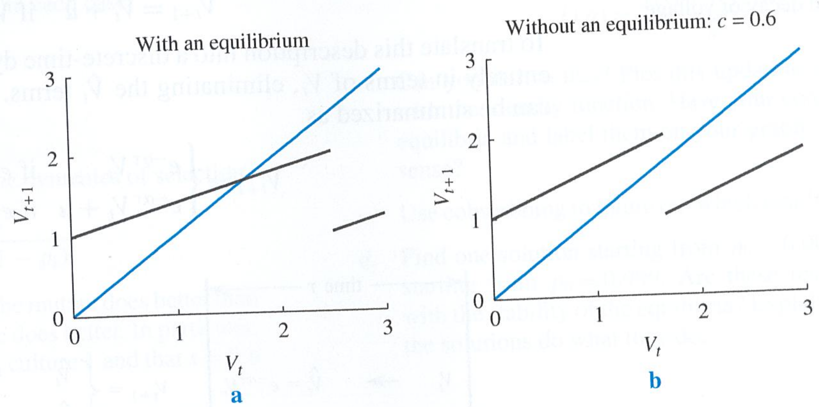


FIGURE 1.11.7
The heart updating function with and without an equilibrium: $u = 1$, $V_c = 1$.

or the diagonal sneaks through the gap between the two branches and there is no equilibrium at all (Figure 1.11.7b).

What does this equilibrium mean? An equilibrium is a point where different processes balance. In the present case, an equilibrium represents a value of the potential where the decay (by a factor of c) is exactly balanced by the response to the signal (an increase of u). This means that the heart will beat steadily.

What are the algebraic conditions for an equilibrium? An equilibrium is a value of V_t that solves $V_{t+1} = V_t$. The heart must proceed through the cycle

$$V_t \overset{\text{decay}}{\longrightarrow} \hat{V}_t = cV_t \overset{\text{decay}}{\longrightarrow} cV_t + u = V_t$$

and end up where it started. Setting V^* to be the equilibrium, we can solve

$$V^* = cV_t + u$$

to find

$$V^* = \frac{u}{1-c}. \tag{1.11.1}$$

This equilibrium exists only if the heart is indeed ready to beat when the next signal comes, or if

$$cV^* = c\frac{u}{1-c} \leq V_c. \tag{1.11.2}$$

Example 1.11.3 Case Where Heart Beats with Every Signal

Suppose that $u = 1$, $V_c = 1$, $\tau = 1$, and $\alpha = \ln(3) = 1.099$. We found in Example 1.11.1 that $c = e^{-\alpha\tau} = 1/3$. The equilibrium is

$$V^* = \frac{1}{1-c} = \frac{1}{1-1/3} = 1.5.$$

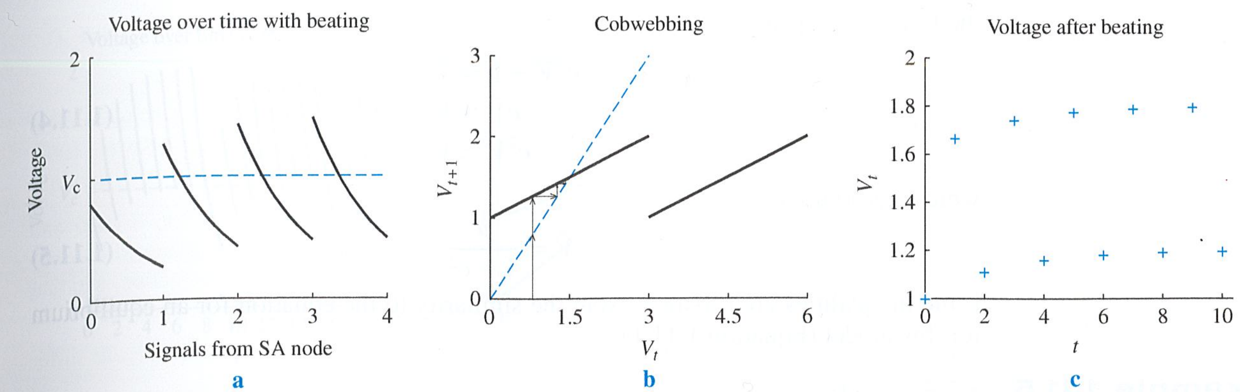


FIGURE 1.11.8
The behavior of a heart with an equilibrium

This equilibrium exists only if $cV^* = 0.5$ is less than $V_c = 1$. Because it is, the heart will beat every time, with voltage decaying from 1.5 to 0.5 between beats and increasing back to 1.5 on the beat (Figure 1.11.8a).

Example 1.11.4 Case Where Heart Fails to Beat with Every Signal

What happens if α, the recovery rate, becomes smaller? We found in Example 1.11.2 that with $\alpha = \ln(1.5) = 0.405$, then $c = e^{-\alpha\tau} = 2/3$. The equilibrium is

$$V^* = \frac{1}{1-2/3} = 3.0$$

This equilibrium exists only if $cV^* = 2.0$ is less than $V_c = 1.0$. Because it is not, the heart cannot beat every time. If α is too small, the AV node recovers too slowly from one signal to be ready to respond to the next. Similarly, if the time τ between beats is decreased by too much, the heart might not have time to recover, and there will be no equilibrium. The AV node cannot respond to every signal when signals from the SA node arrive too frequently. The more complicated dynamics that result are our next topic.

1.11.2 Second-Degree Block

When the heart fails to beat in response to every signal from the SA node, the condition is called **second-degree block**. In one type, called **2:1 AV block**, the heart beats only with every other stimulus. In another, called the **Wenckebach phenomenon**, the heart beats normally for a while, skips a beat, and then resumes normal beating and repeats the cycle. Our model of the heart can help us understand these two conditions.

Graphically, 2:1 AV block corresponds to the situation in Figure 1.11.9. There is no equilibrium. The potential of the AV node alternates between a high value and a low value. When high, the potential does not decay sufficiently to respond to the next signal. After another cycle (time τ), however, the potential has reached a low enough value to respond.

To find the conditions for 2:1 AV block, we use techniques similar to those used to find an equilibrium. Suppose the potential is V_t just after beating (Figure 1.11.9). If the node responds to the second signal but not the first

$$V_t \overset{\text{decay}}{\longrightarrow} cV_t \overset{\text{signal ignored}}{\longrightarrow} cV_t \overset{\text{decay}}{\longrightarrow} c^2V_t \overset{\text{signal obeyed}}{\longrightarrow} c^2V_t + u. \tag{1.11.3}$$

If the potential after these two full cycles comes back exactly to where it started, the heart beats with every other signal, producing 2:1 AV block. The updated potential after two cycles matches the original potential if V_t is equal to some value $\bar{V}$ that satisfies the following equations

$$c^2\bar{V} + u = \bar{V}$$
$$c\bar{V} > V_c \qquad (1.11.4)$$
$$c^2\bar{V} < V_c$$

which has solution

$$\bar{V} = \frac{u}{1-c^2}, \qquad (1.11.5)$$

if the inequalities are satisfied. Note the similarity to the equation for an equilibrium for this model (Equation 1.11.1).

Example 1.11.5 2:1 AV Block

In Figure 1.11.9, we have set $u = V_c = 1.0$ and $c = 2/3$, corresponding to the second case considered above. We have seen that there is no equilibrium. Equation 1.11.5 implies that $\bar{V} = 1.8$. We can follow the dynamics through a complete cycle, finding

$$\bar{V} = 1.8 \overset{\text{decay}}{\longrightarrow} c\bar{V} = 1.2 \overset{\text{signal ignored}}{\longrightarrow} c\bar{V} = 1.2 \overset{\text{decay}}{\longrightarrow} c^2\bar{V} = 0.8 \overset{\text{signal obeyed}}{\longrightarrow} c^2\bar{V} + u = 1.8.$$

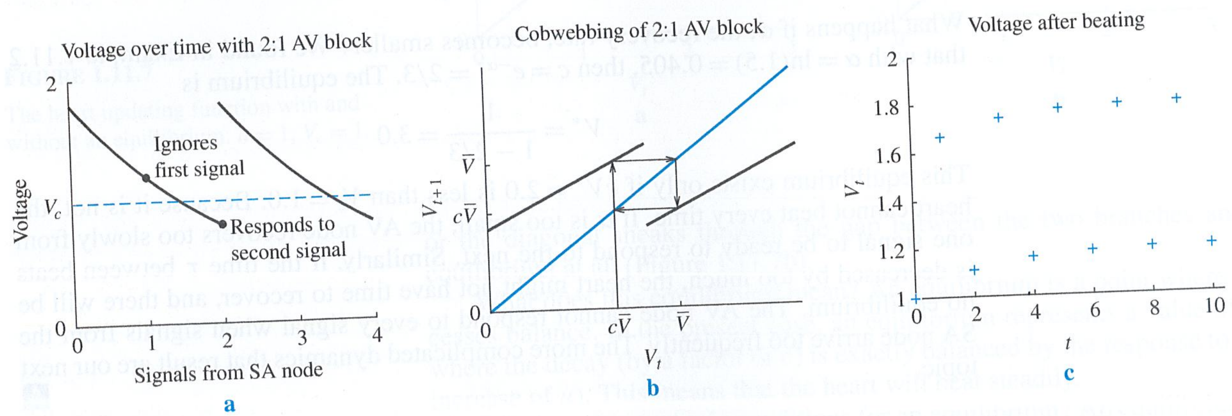


FIGURE 1.11.9
The dynamics of 2:1 AV block

The AV node does not respond to the first signal because $1.2 > V_c = 1.0$, but is ready to respond to the second and return to its original potential.

1.11.3 The Wenckebach Phenomenon

With the parameter values $u = V_c = 1$, we can compute the conditions on c for the existence of an equilibrium. The equation for an equilibrium is

$$V^* = \frac{1}{1-c}$$

requiring that $cV^* \le 1$ (Equation 1.11.2). The equilibrium at V^* exists only if

$$\frac{c}{1-c} \le 1.$$

We can solve for c, finding

$$c \le 1 - c$$
$$2c \le 1$$
$$c \le 0.5.$$

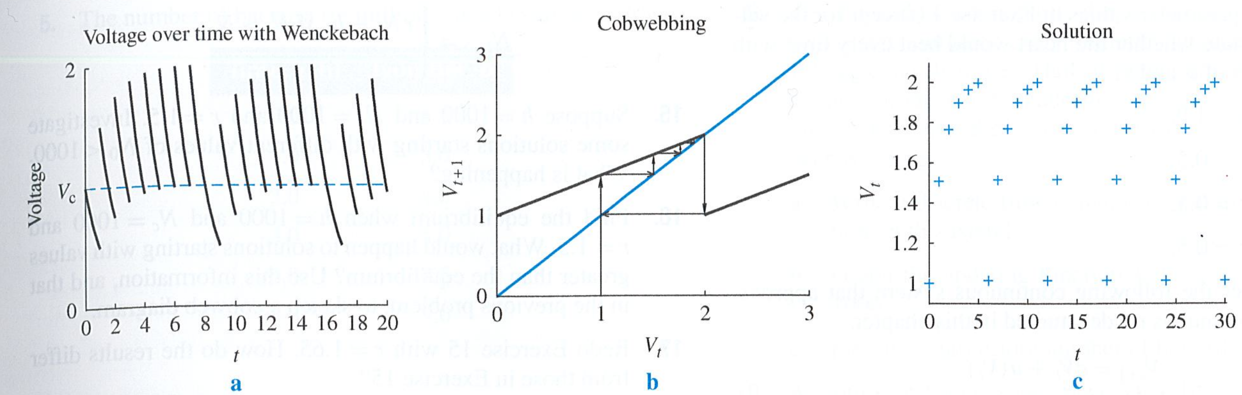


FIGURE 1.11.10
The Wenckebach phenomenon

The value $c = 1/3$ that produced an equilibrium and normal beating (Figure 1.11.8) is well below this value. The value $c = 2/3$ that produced 2:1 AV block (Figure 1.11.9) is well above this value. What happens if c is only slightly above 0.5 and the heart can nearly recover?

Figure 1.11.10 shows the behavior of the system when $c = 0.5001$, a hair above the threshold for existence of an equilibrium. The heart beats 12 times, building up to a higher and higher potential. Eventually, the potential becomes too high, the AV node cannot recover, and the heart fails to beat. After this rest, the potential drops, and the process begins again. This is the Wenckebach phenomenon.

Actual measurements of the Wenckebach phenomenon correspond in part to this model, but show that the heart beats a bit more slowly before missing a beat. Why might this be the case? Our model assumes that the SA node sends out precise pulses at precise times. If the signals from the SA node take a little while to build up, an AV node at low potential will respond right at the beginning of a signal from the SA node. An AV node close to the threshold will be slower and might respond near the end of the signal from the SA node, delaying the heartbeat slightly. This slowing indicates that the AV node will soon exceed the threshold and that the heart will miss a beat.

Summary A simplified model of the heart includes two phases: decay of potential in the AV node (recovery from the last beat) and response to a rhythmic signal from the SA node. We derived conditions for the heart to beat properly with each signal and showed that if the recovery time is not long enough, two types of **second-degree block** can result. In the first, **2:1 AV block**, the heart beats with every other signal. In the second, the **Wenckebach phenomenon**, the heart misses a beat only occasionally.

1.11 Exercises

Applications

1–4 ▪ In the following circumstances, compute $\hat{V}_t$ and V_{t+1} and state whether the heart will beat.

1. $V_c = 20.0$ mV, $u = 10.0$ mV, $c = 0.5$, $V_t = 30.0$ mV.
2. $V_c = 20.0$ mV, $u = 10.0$ mV, $c = 0.6$, $V_t = 30.0$ mV.
3. $V_c = 20.0$ mV, $u = 10.0$ mV, $c = 0.7$, $V_t = 30.0$ mV.
4. $V_c = 20.0$ mV, $u = 10.0$ mV, $c = 0.8$, $V_t = 30.0$ mV.

5–8 ▪ Describe the long-term dynamics in each of the given cases. Find which ones will beat every time, which display 2:1 AV block, and which show some sort of Wenckebach phenomenon.

5. The case in Exercise 1.
6. The case in Exercise 2.
7. The case in Exercise 3.
8. The case in Exercise 4.

9–12 ▪ Use the parameter values in Exercise 1 (except for the values of c), and state whether the heart would beat every time with the given values of α and τ.

9. $\alpha = 1.0, \tau = 1.0$.

10. $\alpha = 1.0, \tau = 0.5$.

11. $\alpha = 2.0, \tau = 0.5$.

12. $\alpha = 0.5, \tau = 0.5$.

13–14 ▪ Consider the following continuous system that approximates the discontinuous model studied in this chapter.

$$V_{t+1} = cV_t + u(V_t)$$

where

$$u(V_t) = \frac{2(1-c)}{1+V_t^n}$$

for the following values of n. Find the equilibria and their stability as a function of c, and describe the dynamics.

13. Suppose $n = 2$. Show that $V_t = 1$ is an equilibrium. Sketch a graph and cobweb with $c = 1/4$. Does the equilibrium seem to be stable?

14. Suppose $n = 4$. Show that $V_t = 1$ is an equilibrium. Sketch a graph and cobweb with $c = 1/4$. Does the equilibrium seem to be stable?

15–18 ▪ Population models with thresholds can also have unusual behavior. Evaluate the following models where individuals emigrate when the population is overly crowded. In particular, suppose h individuals leave if the population is larger than some critical value N_c

$$N_{t+1} = \begin{cases} rN_t - h & \text{if } N_t > N_c \\ rN_t & \text{if } N_t \le N_c. \end{cases}$$

15. Suppose $h = 1000$ and $N_c = 1000$ and $r = 1.5$. Investigate some solutions starting with different values of $N_0 < 1000$. What is happening?

16. Find the equilibrium when $h = 1000$ and $N_c = 1000$ and $r = 1.5$. What would happen to solutions starting with values greater than the equilibrium? Use this information, and that in the previous problem, to sketch a cobweb diagram.

17. Redo Exercise 15 with $r = 1.65$. How do the results differ from those in Exercise 15?

18. Find the equilibrium when $h = 1000$ and $N_c = 1000$ and $r = 1.65$. Can you explain why solutions that start below the equilibrium can shoot off to infinity?

Computer Exercises

19. Study the dynamics of Exercises 1–4 for values of c ranging from 0.4 up to 1.0. Are there any cases where the behavior is neither 2:1 AV block nor the Wenckebach phenomenon? How would you describe these behaviors.

20. What happens to the dynamics of the example illustrated in Figure 1.11.10 if c is made even closer to 0.5? What does it look like on a cobwebbing diagram? If $c = 0.5000000000001$, do you think it would be possible to distinguish the Wenckebach phenomenon from normal beating? Is it?

Supplementary Problems

1. Suppose you have a culture of bacteria, where the density of each bacterium is 2.0 g/cm^3.

a. If each bacterium is $5\mu m \times 5\mu m \times 20\mu m$ in size, find the number of bacteria if their total mass is 30 grams. Recall that $1\mu m = 10^{-6}$ meters.

b. Suppose that you learn that the sizes of bacteria range from $4\mu m \times 5\mu m \times 15\mu m$ to $5\mu m \times 6\mu m \times 25\mu m$. What is the range of the possible number of bacteria making up the total mass of 30 grams?

2. Suppose the number of bacteria in a culture is a linear function of time.

a. If there are 2.0×10^8 bacteria in your lab at 5 P.M. on Tuesday, and 5.0×10^8 bacteria the next morning at 9 A.M., find the equation of the line describing the number of bacteria in your culture as a function of time.

b. At what time will your culture have 1.1×10^9 bacteria?

c. The lab across the hall also has a bacterial culture where the number of bacteria is a linear function of time. If they have 2.0×10^8 bacteria at 5 P.M. on Tuesday, and 3.4×10^8 bacteria the next morning at 9 A.M., when will your culture have twice as many bacteria as theirs?

3. Consider the functions $f(x) = e^{-2x}$ and $g(x) = x^3 + 1$.

a. Find the inverses of f and g, and use these to find when $f(x) = 2$ and when $g(x) = 2$.

b. Find $f \circ g$ and $g \circ f$ and evaluate each at $x = 2$.

c. Find the inverse of $g \circ f$. What is the domain of this function?

4. A lab has a culture of a new kind of bacteria where each individual takes 2 hours to split into three bacteria. Suppose that these bacteria never die and that all offspring are OK.

a. Write an updating function describing this system.

b. Suppose there are 2.0×10^7 bacteria at 9 A.M. How many will there be at 5 P.M.?

c. Write an equation for how many bacteria there are as a function of how long the culture has been running.

d. When will this population reach 10^9?

5. The number of bacteria (in millions) in a lab are as follows

Time, t (h)	Number, b_t
0.0	1.5
1.0	3.0
2.0	4.5
3.0	5.0
4.0	7.5
5.0	9.0

a. Graph these points.

b. Find the line connecting them and the time t at which the value does not lie on the line.

c. Find the equation of the line and use it to find what the value at t would have to be to lie on the line.

d. How many bacteria would you expect at time 7.0 hours?

6. The number of bacteria in another lab follows the discrete-time dynamical system

$$b_{t+1} = \begin{cases} 2.0b_t & b_t \le 1.0 \\ -0.5(b_t - 1.0) + 2.0 & b_t > 1.0 \end{cases}$$

where t is measured in hours and b_t in millions of bacteria.

a. Graph the updating function. For what values of b_t does it make sense?

b. Find the equilibrium.

c. Cobweb starting from $b_0 = 0.4$ million bacteria. What do you think happens to this population?

7. Convert the following angles from degrees to radians and find the sine and cosine of each. Plot the related point both on a circle and on a graph of the sine or cosine.

a. $\theta = 60°$.

b. $\theta = -60°$.

c. $\theta = 110°$.

d. $\theta = -190°$.

e. $\theta = 1160°$.

8. Suppose the temperature H of a bird follows the equation

$$H = 38.0 + 3.0\cos\left(\frac{2\pi(t-0.4)}{1.2}\right)$$

where t is measured in days and H is measured in degrees C.

a. Sketch a graph of the temperature of this bird.

b. Write the equation if the period changes to 1.1 days. Sketch a graph.

c. Write the equation if the amplitude increases to 3.5 degrees. Sketch a graph.

d. Write the equation if the average decreases to 37.5 degrees. Sketch a graph.

9. The butterflies on a particular island are not doing too well. Each autumn, every butterfly produces on average 1.2 eggs and then dies. Half of these eggs survive the winter and produce new butterflies by late summer. At this time, 1000 butterflies arrive from the mainland to escape overcrowding.

a. Write a discrete-time dynamical system for the population on this island.

b. Graph the updating function and cobweb starting from 1000.

c. Find the equilibrium number of butterflies.

10. A culture of bacteria has mass 3.0×10^{-3} grams and consists of spherical cells of mass 2.0×10^{-10} grams and density 1.5 grams/cm^3.

a. How many bacteria are in the culture?

b. What is the radius of each bacterium?

c. If the bacteria were mashed into mush, how much volume would they take up?

11. A person develops a small liver tumor. It grows according to

$$S(t) = S(0)e^{\alpha t}$$

where $S(0) = 1.0$ gram and $\alpha = 0.1$/day. At time $t = 30$ days, the tumor is detected and treatment begins. The size of the tumor then decreases linearly with slope of -0.4 grams/day.

a. Write the equation for tumor size at $t = 30$.

b. Sketch a graph of the size of the tumor over time.

c. When will the tumor disappear completely?

12. Two similar objects are left to cool for one hour. One starts at 80°C and cools to 70°C and the other starts at 60°C and cools to 55°C. Suppose the discrete-time dynamical system for cooling objects is linear.

a. Find the discrete-time dynamical system. Find the temperature of the first object after 2 hours. Find the temperature after 1 hour of an object starting at 20°C.

b. Graph the updating function and cobweb starting from 80°C.

c. Find the equilibrium. Explain in words what the equilibrium means.

13. A culture of bacteria increases in area by 10% each hour. Suppose the area is 2.0 cm^2 at 2:00 P.M.

a. What will the area be at 5:00 P.M.?

b. Write the relevant discrete-time dynamical system and cobweb starting from 2.0.

c. What was the area at 1:00 P.M.?

d. If all bacteria are the same size and each adult produces two offspring each hour, what fraction of offspring must survive?

e. If the culture medium is only 10 cm^2 in size, when will it be full?