

NONLINEAR DYNAMICAL SYSTEMS

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The concepts and techniques developed by mathematicians, physicists, and engineers to characterize and predict the behavior of nonlinear dynamical systems are now being applied to a wide variety of biomedical problems. This chapter serves as an introduction to the central elements of the analysis of nonlinear dynamics systems. The fundamental distinctions between linear and nonlinear systems are described and the basic vocabulary used in studies of nonlinear dynamics introduced. Key concepts are illustrated with classic examples ranging from simple bistability and hysteresis in a damped, driven oscillator to spatiotemporal modes and chaos in large systems, and to multiple attractors in complex Boolean networks. The goal is to give readers less familiar with nonlinear dynamics a conceptual framework for understanding other chapters in this volume.

1. INTRODUCTION

The latter half of the twentieth century saw remarkable advances in our understanding of physical systems governed by nonlinear equations of motion. This development has changed the scientific worldview in profound ways, simultaneously supplying a dose of humility—the recognition that deterministic equations do not guarantee quantitative predictability—and a great deal of insight into the qualitative and statistical aspects of dynamical systems. One of the byproducts has been the realization that the mathematical constructs developed for modeling simple physical systems can be fruitfully applied to more complex systems, some of which are of great interest to the biomedical community. Examples range from electrical signal propagation in cardiac tissue, where one

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might well expect physical theory to play a significant role, to the logic of neural networks or gene regulation, where the role of physical/mathematical modeling may be less obvious.

The establishment of a connection between physical theory and biomedical observations generally involves a combination of fundamental physical reasoning and *a posteriori* model validation. The field of nonlinear dynamics is of crucial importance for both purposes. It provides both the techniques for analyzing the equations of motion that emerge from the physical theory and a useful language for framing questions and guiding the process of model validation (as noted by Shalizi, Part II, chapter 1, this volume). Because the concept of a nonlinear dynamical system is rich enough to encompass an extremely broad range of processes in which the future configurations of a system are determined by its past configurations, the methods of analysis developed in the field are useful in a huge variety of contexts.

To appreciate the validity of a particular research result involving the application of nonlinear dynamical theory and properly interpret the specific conclusions, it is important to grasp the broad conceptual basis of the work. The purpose of this chapter is to explain the meaning and crucial consequences of nonlinearity so as to provide an operational understanding of the principles underlying the modeling discussed in other chapters. (Almost all of the chapters in the present volume rely on techniques and approaches whose roots lie in the development of nonlinear dynamics as a discipline. The chapters by Subramanian and Narang [Part III, chapter 2.2], Lubkin [Part III, chapter 3.1], Tabak [Part III, chapter 5.2], Solé [Part III, chapter 6.2], and Segel [Part III, chapter 4.1] all make direct reference to nonlinear dynamical models of precisely the sort discussed here.) Along the way, certain fundamental terms will be defined and illustrated with examples, but the reader interested in the details of the mathematics will have to look elsewhere. Two excellent textbooks that do not require familiarity with mathematical concepts beyond basic calculus are (28) and (3). For treatments of more advanced topics, a good place to start is (25).

Nonlinear dynamics enters the biomedical literature in at least three ways. First, there are cases in which experimental data on the temporal evolution of one or more quantities are collected and analyzed using techniques grounded in nonlinear dynamical theory, with minimal assumptions about the underlying equations governing the process that produced the data. That is, one seeks to discover correlations in the data that might guide the development of a mathematical model rather than guess the model first and compare it to the data. (See the chapter by Shalizi [Part II, chapter 1] in this volume for a discussion of time-series analysis.) Second, there are cases in which symmetry arguments and nonlinear dynamical theory can be used to argue that a certain simplified model should capture the important features of a given system, so that a phenomenological model can be constructed and studied over a broad parameter range. Often this leads to models that behave qualitatively differently in different regions

of parameter space, and one region is found to exhibit behavior quite similar to that seen in the real system. In many cases, the model behavior is rather sensitive to parameter variations, so if the model parameters can be measured in the real system the model shows realistic behavior at those values, and one can have some confidence that the model has captured the essential features of the system. Third, there are cases in which model equations are constructed based on detailed descriptions of known (bio)chemistry or biophysics. Numerical experiments can then generate information about variables inaccessible to physical experiments.

In many cases, all three approaches are applied in parallel to the same system. Consider, for example, the problem of fibrillation in cardiac tissue. At the cellular level, the physics of the propagation of an electrical signal involves complicated physicochemical processes. Models involving increasingly realistic descriptions of the interior of the cell, its membrane, and the intercellular medium are being developed in attempts to include all the features that may give rise to macroscopic properties implicated in fibrillation. (See, for example, articles in (5).) At the same time, recognizing the general phenomenon of action potential propagation as similar to chemical waves in reaction-diffusion systems allows one to construct plausible, though idealized, mathematical models in which phenomena quite similar to fibrillation can be observed and understood (10,11)). These models can then be refined using numerical simulations that incorporate more complicated features of the tissue physiology. In parallel with these theoretical efforts, experiments on fibrillation or alternans in real cardiac tissue yield time series data that must be analyzed on its own (with as little modeling bias as possible) to determine whether the proposed models really do capture the relevant physics (13).

Almost all mathematical modeling of biomedical processes involves a significant computational component. This is less a statement about the complexity of biomedical systems than a reflection of the mathematical structure of nonlinear systems in general, even simple ones. Indeed, in large measure the rise of nonlinear dynamics as a discipline can be attributed to the development of the computer as a theoretical tool. Though one can often prove theorems about general features of solutions to a set of nonlinear equations, it is rarely possible to exhibit those solutions in detail except through numerical computation. Moreover, it is often the case that the numerical simulation has to be done first in order to give some direction to theoretical studies. Though the catalogue of well-characterized, generic behaviors of deterministic nonlinear systems is large and continues to grow, there is no *a priori* method for classifying the expected behavior of a particular nonlinear dynamical system unless it can be directly mapped to a previously studied example.

Rather than attempting a review of the state of the art in time-series analysis, numerical methods, and theoretical characterization of nonlinear dynamical systems, this chapter presents some of the essential concepts using a few exam-

ples. Section 2 presents the vocabulary needed for the description of dynamical systems of any type, linear or nonlinear, large or small, continuous or discrete. Section 3 presents the fundamental ideas relevant for understanding the behavior of small systems, i.e., systems characterized by a small number of dynamical variables. It begins with a discussion of the concept of nonlinearity itself, then proceeds to build on it using two canonical examples: the damped, driven oscillator and the logistic map. In section 4 new issues that arise in large systems are introduced, again in the context of two characteristic examples: the cardiac system and the Boolean model of genetic regulatory networks. It is hoped that these discussions will provide a context that will help readers understand the import of other chapters in this book.

2. DYNAMICAL SYSTEMS IN GENERAL

The term **dynamical system** refers to any physical or abstract entity whose configuration at any given time can be specified by some set of numbers, called **system variables**, and whose configuration at a later time is uniquely determined by its present and past configurations through a set of rules for the transformation of the system variables. Two general types of transformation rules are often encountered. In **continuous-time systems** the rules are expressed as equations that specify the time derivatives of the system variables in terms of their current (and possible past) values. In such cases, the system variables are real numbers that vary continuously in time. The Newtonian equations of motion describing the trajectories of planets in the solar system represent a continuous-time dynamical system. In **discrete-time systems** the rules are expressed as equations giving new values of the system variables as functions of the current (and possibly past) values. Though classical physics tells us that all systems are continuous-time systems at their most fundamental level, it is often convenient to use descriptions that describe the system configurations only at a discrete set of times and describe the effects of the continuous evolution as discrete jumps from one configuration to another.

A set of equations describing a continuous-time dynamical system takes the form

$$\dot{\mathbf{x}}(t) = \mathbf{f}(\mathbf{x}(t); \mathbf{p}, t). \quad [1]$$

Here the components of the vector \mathbf{x} are the system variables and the vector \mathbf{f} represents a function of all of the system variables at fixed values of the parameters \mathbf{p} . The overdot on the left indicates a first time derivative.¹ Note that \mathbf{f} can depend explicitly on time, as would be the case, for example, in a system driven by a time-varying external force. In some systems, time delays associated with

finite speeds of signal propagation cause \mathbf{f} to depend also on values of \mathbf{x} at times earlier than t .

In **spatially extended systems**, each system variable is a continuous function of spatial position as well as time and the equations of motion take the form of partial differential equations:

$$\frac{\partial x}{\partial t} = \mathbf{f}(\mathbf{x}, \nabla \mathbf{x}, \nabla^2 \mathbf{x}^2, \dots; \mathbf{p}, t), \quad [2]$$

where ∇ is the spatial gradient, ∇^2 is the Laplacian, and the dots represent higher-order derivatives of \mathbf{x} . The parameters \mathbf{p} may also be externally imposed functions of position, as would be the case for a system evolving in an inhomogeneous environment. (If the environment itself is affected by the system variables, however, then variables representing the environment become system variables rather than external parameters.)

A set of equations describing a discrete-time dynamical system takes the form

$$\mathbf{x}(t + 1) = \mathbf{F}(\mathbf{x}(t); \mathbf{p}t). \quad [3]$$

Here the function \mathbf{F} directly gives the new \mathbf{x} at the next time step, rather than the derivative from which a new \mathbf{x} can be calculated. The function \mathbf{F} is often referred to as a **map** that takes the system from one time step to the next.

In all cases, the evolution of the system is described as a motion in **state space**, the space of all possible values of the vector \mathbf{x} . A **trajectory** is a directed path through state space that shows the values of the system variables at successive times. The theory of dynamical systems is concerned with classifying the types of trajectories that can occur, determining whether they are robust against small variations in the system variables, categorizing the ways in which the possible trajectories change as parameters \mathbf{p} are varied, and developing techniques both for simulating trajectories numerically and inferring the structure of trajectories from incomplete sets of observations of the system variables. The most basic structures arising in the classification of state space trajectories—fixed points, limit cycles, transients, basins of attraction, and stability—will be explained below as they arise in the context of some simple examples.

3. LINEAR SYSTEMS AND SOME BASIC VOCABULARY

A **linear system** is one for which any two solutions of the equations of motion can be combined through simple addition to generate a third solution, given appropriate definitions of the zeros of the variables. The system of equations can be extremely complicated, representing large numbers of variables with all sorts

of logical structures associated with the connections between them, including complicated networks of causal relationships among variables, time delays between cause and effect, arbitrarily complex spatial inhomogeneities, or even externally imposed noise. The way to recognize a linear dynamical system is that its equations of motion will involve only polynomial functions of degree one in the system variables; there will be no products of different system variables or nontrivial functions of any individual variable. (Examples of nontrivial functions include squares or square roots, threshold functions that specify discontinuous switching of parameters as the system variables change, or quantities that have simple geometric interpretations but turn out to be complicated functions of the fundamental variables.) Gradients of any order may appear, however, as well as coefficients that are nontrivial functions of spatial position and time.²

For all types of linear systems, the constraint that the sum of any two solutions also must be a solution has profound consequences. Simply put, the full range of behavior of a linear system is understood as soon as its behavior in an infinitesimal region of its state space is understood. In the absence of an external driving force, there is one special solution to any linear system where the variables are time-independent—everything just sits still. This is called the **fixed point**. A trivial example is the equilibrium point of a weight hanging from an ideal spring in a perfectly uniform gravitational field. Here the system variables are the position and velocity of the weight, which can both be defined to be zero at the fixed point. Another example is the surface of a liquid that may have ripples governed by surface tension (capillary waves) described by a linear theory. The system variables here are a field representing the height of the liquid at all points in space and the time derivative of that field. Again, the system variables can be defined to be zero at the fixed point corresponding to a quiescent, flat surface.

When variables are defined so as to be zero at the fixed point, linearity implies that every solution can be multiplied by an arbitrary factor to yield another solution. Thus solutions with arbitrarily large amplitudes can be multiplied by an arbitrarily small factor to yield solutions infinitesimally close to the fixed point, indicating that the nature of solutions very near the fixed point determines all of the possible solutions. The situation is further simplified by the fact that solutions in the vicinity of the fixed point come in only three types—stable, unstable, and marginal.

In a linear **stable system**, all solutions asymptotically approach the fixed point as time progresses. The typical case is that beginning from any initial point in state space, the variables decay toward the fixed point by first rapidly approaching a particular line in state space and then relaxing exponentially along that line toward the origin.³ In an **unstable system**, all solutions that do not start exactly on the fixed point diverge from it exponentially at long times. The **marginal** case, in which the variables neither decay to zero nor diverge, occurs pri-

marily in "Hamiltonian" systems, in which conservation of energy prohibits convergence or divergence of nearby phase space trajectories. Such **dissipationless** systems are of great interest in quantum mechanics and statistical mechanics, but systems of interest in biomedicine always involve strongly **dissipative** processes, which include, for example, all processes involving frictional forces. Marginal stability then occurs only as a very special case where parameters have been carefully tuned, though there have been suggestions that marginal stability can reappear spontaneously in certain self-organizing nonlinear systems (2).

Now we are often interested in dissipative systems that are subjected to external driving of some sort, whether it be a steady input of energy or a driving with more complicated temporal structure. In such systems, the notion of a fixed point must be generalized to include steady or regularly repeating motions. For example, if the ceiling from which a weighted, damped spring is hanging were constantly oscillating up and down, the weight would not sit at a fixed point but could exhibit regular oscillations with a period that matches the oscillation of the ceiling. Such trajectories are called **limit cycles**, and, like fixed points, they may be stable or unstable.

Stable fixed points and limit cycles are called **attractors**, as trajectories in state space eventually flow toward them and then stay very close to them at long times. If we begin observing a system when it is far from its attractor and watch for a long time, we will be able to detect its motion toward the attractor for a while, but at some point it will be so close to the attractor that we can no longer resolve the difference. The portion of the trajectory over which we can observe progress toward the attractor is called a **transient**. The set of points in state space that lie on transients associated with a particular attractor is called the **basin of attraction** of the attractor. In a stable linear system, all points in state space lie in the same basin of attraction. In other words, for any initial configuration of the system variables, the ultimate fate of the system is the same fixed point or limit cycle.

4. NONLINEAR EFFECTS IN SIMPLE SYSTEMS

Linear systems are often studied in great detail. They can be solved exactly and hence make for good textbook problems; and linear equations can be used as good approximations to nonlinear ones in situations where the trajectories stay very close to a stable fixed point or limit cycle. They cannot capture, however, many of the most important qualitative features of real systems.

In a **nonlinear system**, the equations of motion include at least one term that contains the square or higher power, a product of system variables (or more complicated functions or them), or some sort of threshold function, so that the addition of two solutions does *not* yield a valid new solution, no matter how the

system variables are defined. *All physical systems describable in terms of classical equations of motion are nonlinear.* (The quantum mechanical theory of atoms and molecules is a linear theory: the connection between it and the comparatively macroscopic processes at the cellular level and larger is beyond the scope of the present discussion.) In all real systems, deviations of large enough amplitude require nonlinear terms in the relevant model. There is no such thing as a truly linear spring or a waves on a fluid obeying a perfectly linear equation of motion. This is why the study of nonlinear dynamics has such broad relevance.

The consequences of nonlinearity are profound. Most importantly, nonlinear systems may contain multiple attractors, each with its own basin of attraction. Thus the fate of a nonlinear dynamical system may depend on its initial state, and a whole new set of phenomena arises associated with the way in which basins of attraction shift as parameters are varied.

Nonlinearity can also give rise to an entirely new type of attractor. Limit cycles in nonlinear systems may be quite complicated, circling around in a bounded region of state space many times before finally closing on themselves. It is even possible (and quite common) for a trajectory to be confined to a region of state space where there are no stable limit cycles or fixed points. The system then appears to follow an irregular trajectory that is said to lie on a **strange attractor**. The trajectory comes arbitrarily close to closing on itself, but never quite does, and two identical systems that come arbitrarily close to each other in state space diverge rapidly thereafter. A strange attractor is the state space structure associated with the phenomenon known as **chaos**.

Finally, in spatially extended systems nonlinearities can give rise to **pattern formation**, the spontaneous creation of attractors with nontrivial spatial structure in a system with no externally imposed inhomogeneities. (See (33,8,20) for textbook treatments of pattern formation and spatiotemporal structures in large systems. For more technical treatments from a physics perspective, see (17,6,4)). Examples include the formation of stripes or spots in chemical reaction-diffusion systems and excitable media, which find applications in such processes as butterfly wing coloration and cardiac electrodynamics.

The essential features of nonlinear systems can be illustrated with the simplest of examples, the driven, damped oscillator. Figure 1 shows a picture of the system. We assume the spring is nonlinear: it gets stiffer under compression and softer under extension. With an appropriate definition of the zero of x , the position of the mass, the equation of motion can be written as $m\ddot{x} = -\gamma\dot{x} + k(h-x) + k'(h-x)^2$, where m , γ , k , and k' are constants and h is the deviation of the ceiling from its average height. Defining $z = \dot{x}$, the equation of motion can be written as two coupled equations in a two-variable state space: $\dot{v} = -\gamma v - k(h-x) + k'(h-x)^2$ and $\dot{x} = v$. We will consider cases in which the ceiling oscillates according to $h = \alpha \sin(\omega t)$.

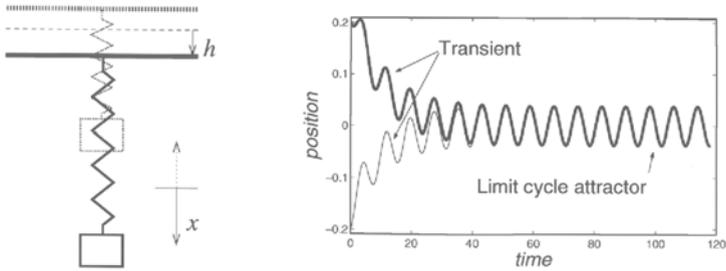


Figure 1. A simple nonlinear dynamical system. Left: A mass is attached to the ceiling by a spring. The force exerted on the mass by gravity and the spring together is $k(h - x) + k'(h - x)^2$, where h is the displacement of the ceiling from its nominal height and x is the displacement of the mass from its resting position. The solid and dotted images represent the spring and mass at different times during a cycle in which the ceiling is oscillating. Right: Two time series for the linear case $k' = 0$.

Figure 1 also shows the behavior of the mass when $k' = 0$, which makes the system linear. Two time series are shown for a particular choice of the drive frequency ω , and one sees that the long term behavior in the two cases is identical. The difference between the two curves in the early stages corresponds to transients that depend on the details of the initial configuration. The behavior that is reached in the long term is called a limit cycle attractor.

When $k' = 0$, one can see immediately from the equations that the strength of the drive, α , is not an important parameter in determining the qualitative structure of the motion. The solution for a given α can simply be rescaled by multiplication so as to correspond to a different value of α .

When k' is nonzero, so that the system is nonlinear, one often finds behavior similar to that shown in Figure 1, i.e., convergence of all transients (in the domain of initial conditions of interest) to the same solution. In the nonlinear case, however, it is possible to see quite different behavior. Figure 2 shows one simple nonlinear effect: one can have two different long term solutions for a single value of the system parameters. The differences produced by different initial conditions in this case are not limited to transient effects. This phenomenon of **bistability** is a generic feature of nonlinear dynamics, and its presence in all sorts of biomedical systems indicates that nonlinearities play a fundamental role in their function.

The presence of bistability in a system raises the question of which initial conditions will lead to which orbit, or which points in state space lie in which basin of attraction. Even for systems as simple as the damped, driven oscillator,

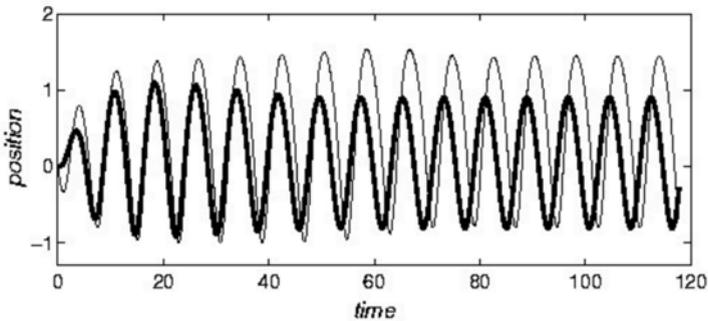


Figure 2. Two time series for the same system as in Figure 1, but with parameters set such that two different long time solutions exist. Which solution is realized depends upon the choice of initial conditions.

the boundaries in state space of the basins of attraction can be quite complex, making it extremely difficult to predict which orbit the system will eventually reach from a specified initial configuration. (See chapter 5 of (24) for details.) In studying more complicated systems, one often finds multiple attractors with basins of attraction that can vary widely in size.

A feature generically associated with bistability is **hysteresis**, the dependence of the observed solution on the direction in which a parameter is varied. For example, Figure 3 shows curves indicating the amplitude of oscillation of the mass in our simple model as the drive frequency ω is slowly ramped up and then down. For small ω and large ω there is only one attractor. In the intermediate range, however, there are two (plus an unstable periodic orbit that is not seen). During the upswing, the system stays in the basin of one of the attractors until that attractor is destroyed, at which point it is attracted to the stable orbit of significantly different amplitude. During the downswing, the same process happens in reverse, except that the jump occurs at a lower value of ω .

The jump to a different solution in a hysteretic system is an example of a **bifurcation**. More generally, the theory of bifurcations describes the transitions that occur between structurally different solutions as a system parameter is varied. Such transitions may correspond to the creation or destruction of fixed points or simply to changes in the stability properties of existing fixed points. In the oscillator example, one may observe a bifurcation upon variation of any of the parameters k , k' , γ , α , or ω . The precise values of the parameters at which a bifurcation occurs are called a **critical point** in parameter space. The mathematical theory of how solutions can be created or destroyed as parameters are varied is well developed and full of beautiful structures (12,24,25,28).

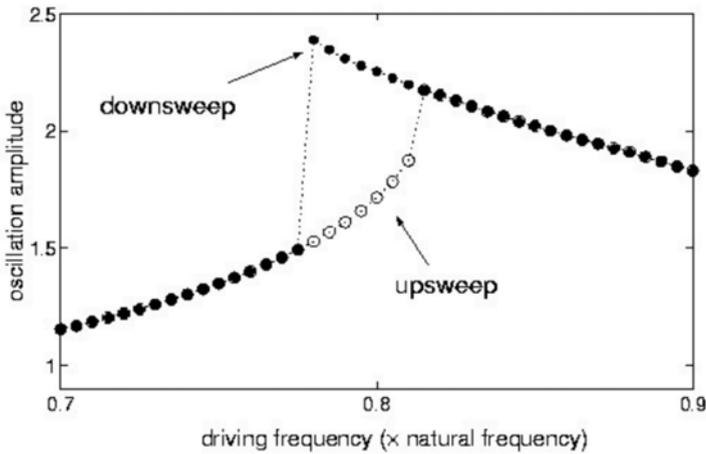


Figure 3. The limit cycle amplitudes for different values of the driving frequency in a nonlinear oscillator. The solid circles correspond to oscillations observed as the driving frequency is slowly ramped up from 0.7. The open circles correspond to oscillations observed as the driving frequency is slowly ramped down from 0.9. The dotted lines are guides to the eye. The drive frequency is measured in units of the natural frequency of the linear oscillator. The time series shown in Figure 2 correspond to the two limit cycles that coexist at a driving frequency of 0.8 for $\gamma = 0.18$, $k = 1$, $k' = 0.5$, and $\alpha = 0.3$.

As mentioned above, nonlinear dynamical systems sometimes exhibit chaos, motion that never settles into a fixed point or limit cycle. The system stays confined to a finite region of state space, but never returns precisely to one of the points it has visited before. In fact, almost all dynamical systems are chaotic for some range of parameter values and our simple driven oscillator is no exception. An example of a chaotic orbit in this system is shown in Figure 4.

Much attention has been devoted to the characterization of strange attractors. Three aspects of the theory are of particular interest for practical purposes. The first is the determination of the **dimension of the attractor**. The attractor itself is a geometric object, a set of points in state space, that has a dimension which can be non-integral, sometimes called a **fractal dimension**. Most importantly, the dimension is finite and lower than the dimension of the full state space. Its origin in a set of deterministic equations for a relatively small number of variables makes it fundamentally different from the erratic trajectories associated with random, or stochastic, processes. This raises the possibility that an experimentally observed time series suggesting erratic, unpredictable behavior actually arises from a deterministic, though nonlinear, set of equations. A beauti-

ful theorem shows that the important topological features of strange attractors can be reconstructed from a time series measurement of a single variable (30). One can construct the state space structure of the attractor using time-delayed values of that variable rather than synchronous measurements of all of the system variables. The reconstruction is said to be **embedded** in a space of dimension equal to the number of time delays used and the theorem says that as long as the embedding dimension is large enough, the topological features of the trajectory will be accurately reconstructed. (See (24) for a discussion of embedding.) This has led to the development of a number of computational tools for analyzing time series data to determine whether a system can be modeled using a small number dynamical variables or not, though prohibitive difficulties are almost always encountered if more than about 10 variables are required. (Aspects of this sort of time-series analysis are discussed in the preceding chapter by Shalizi.)

The second item of interest is the characterization of the strength of the chaos (its degree of unpredictability) via the **Lyapunov exponents**. Suppose a system is following a trajectory in state space that is a long time solution to the equations of motion. We imagine an almost exact copy of the system at time $t = 0$. The copy has exactly the same parameter values as the original—it is the same system—but the variable values at $t = 0$ differ by a tiny amount from the original. In a chaotic system, the difference between the variable values in the copy and the original will grow (on average) with time. Ignoring short-time scale fluctuations, the difference between a given variable, say x , in the two systems will grow exponentially: $\delta x = \delta x_0 \exp(\lambda t)$. The quantity λ , with dimensions of 1/time, is called the Lyapunov exponent.⁴

A large λ indicates rapid divergence of nearby trajectories, which implies that prediction of future values of the variables requires extremely precise knowledge of the present values. The consequence of exponential divergence is that accurate prediction becomes prohibitively difficult over times larger than a few times λ^{-1} . This is only a quantitative issue: chaos does *not* imply some mysterious new source of randomness of the type, say, that is found in measurements on quantum systems. Nevertheless, the mathematics of exponential growth makes a qualitative difference in practice for would-be predictors of the motion. The increase in precision of measurement required to make accurate predictions is so rapid within the desired time interval covered that useful long-time prediction is impossible.

The third item of interest is the nature of the transition to chaos as a parameter is varied, i.e., the type of bifurcation that leads to the emergence of a strange attractor. Perhaps the most celebrated result in chaos theory is the proof by Feigenbaum that all discrete maps in a broad class go through a quantitatively identical transition, dubbed the **period-doubling route to chaos** (9). In a period-doubling bifurcation, a periodic orbit undergoes a change in which only every other cycle is identical. One then still has a periodic orbit, but its period is twice

as long as the original. The deviations from the original simple orbit can grow larger as the bifurcation parameter is ramped further, eventually leading to a second period-doubling bifurcation, so that the new orbit has a period that is four times longer than the original. In fact, an entire period-doubling cascade can occur within a finite range of the bifurcation parameter, leading finally to a chaotic attractor. Feigenbaum showed that the sequence of bifurcations has a structure that is the same for a large class of discrete maps. The details of the particular map under study become irrelevant as we approach the end of the period-doubling cascade.

To see a sequence of period-doubling transitions leading to chaos, one need look no farther than our simple nonlinear oscillator. Figure 4 shows a set of solutions, with $k = 1$, $k' = 0.5$, $\gamma = 0.5$, and $\omega = 0.8$, for four different values of the drive amplitude α . The time series on the top row show that bifurcations occur as the drive amplitude is varied. At some critical point between the first and second panels ($\alpha = 0.7$ and $\alpha = 0.76$) the solution undergoes a structural change. It begins with a limit cycle with some period (the exact value is unimportant). It then changes to a limit cycle that has a period approximately twice as long as the original. In terms of the original, every other cycle looks different. In a periodically forced system such as this one, the second limit cycle is often called a "2:1 state," referring to the fact that there are two periods of the driver for every one period of the limit cycle. By the time we get to the third panel, the 2:1 state has itself undergone a period-doubling bifurcation, leading to a 4:1 state. In between the third and fourth panels, an infinite sequence of period doublings has occurred, leading, finally, to a strange attractor and its trademark erratic time series.

The bottom row of Figure 4 shows a view of the same motion that clarifies the nature of the bifurcations a bit. Each of these plots is a projection of the trajectory corresponding to the time series above it. In the present case, the state space is three dimensional, the three dimensions corresponding to the position and velocity of the mass and the position of the ceiling. The figures show the projection of a path through the 3D space onto a 2D plane. Here the differences between the four solutions are easier to see at a glance.⁵

A standard method for analyzing such a situation is through the construction of a discrete **return map** from its current position in state space to its position one drive period later. This is the theoretical equivalent of taking a movie of the motion with a strobe light that flashes in synchrony with the ceiling oscillations. In that movie, the ceiling will appear to sit still, while the weight will jump from point to point according to the map. If the weight is on a simple limit cycle as described above, it will appear fixed in the movie. In this way, we see that a periodic orbit of a continuous-time system corresponds to a fixed point of a discrete-time system.⁶ The motion of the system in the strobed movie is said to occur on a **Poincaré section** of the state space. For practical and analytical

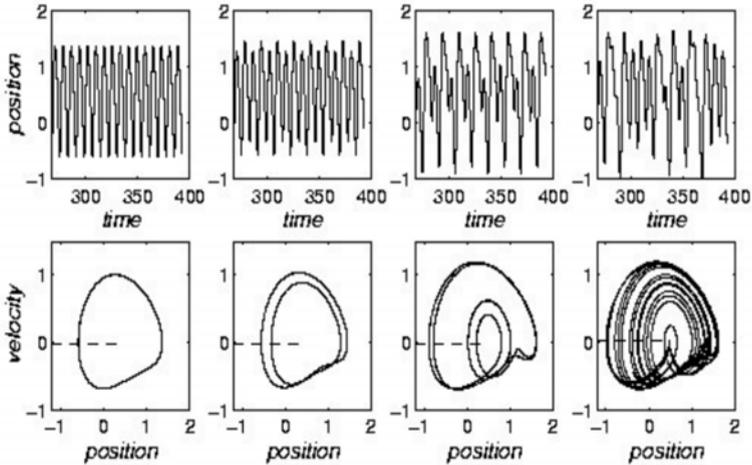


Figure 4. The period doubling route to chaos in the oscillator with $k = 1$, $k' = 0.5$, $\gamma = 0.5$, and $\omega = 0.8$ for $\alpha = 0.700, 0.760, 0.794$, and 0.810 . Top: time series of the position (x vs. t). Bottom: phase space plots (\dot{x} vs. x).

reasons, one often works directly with a discrete map that takes one point on the Poincaré section into the next, rather than the underlying differential equations.

Since the system is deterministic, the map that takes one point to the next is unique. In the oscillator example above, the Poincaré section may be taken to be the half plane corresponding to the points where the phase of the drive has some chosen value. The dashed line drawn on the lower set of plots in Figure 4 schematically represents the projection of this plane onto the $x - \dot{x}$ plane. As time progresses, the system keeps looping around the state space in a clockwise direction, passing through the Poincaré section once every time around. Each time the section is crossed, the position and velocity of the oscillator are observed. In the present case (and many others) it is sufficient to keep track of only one variable, say the position at each piercing of the Poincaré section. In this way we obtain a discrete sequence of x values, x_n . A return map f defined by $x_{n+1} = f(x_n; \alpha)$ can then be constructed, where we write α explicitly to indicate that the map depends on the bifurcation parameter.

For the simple limit cycle on the left, the system returns to the same point on every cycle. For this value of α , the fixed point x^* satisfying $x^* = f(x^*)$ is stable. For the second case shown in the figure, x_n will alternate between two values. In this case it is the map f^2 (two successive applications of f) that has a

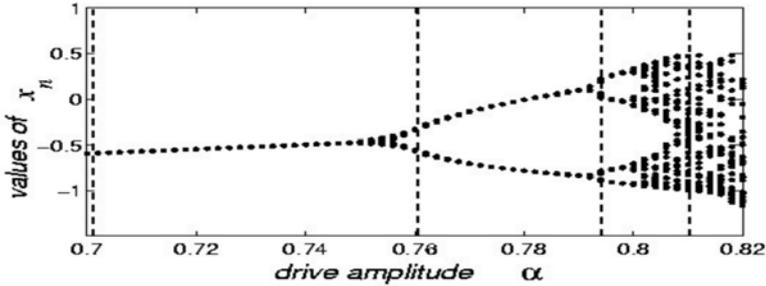


Figure 5. The bifurcation diagram for the oscillator with $k = 1$, $k' = 0.5$, $\gamma = 0.5$, and $\omega = 0.8$, in the range $\alpha = (0.7, 0.82)$. The dashed vertical lines indicate the values of α used in Figure 4.

fixed point. Though it cannot be seen from these figures, there may still be a fixed point of f in this system, but it has become unstable at this value of α . For the chaotic orbit on the right, the sequence x_n will contain an infinite number of different points (assuming we can wait long enough to collect them). Moreover, there are infinitely many values of m for which f^m has a fixed point. These fixed points cannot be literally on the attractor—if the system were ever to hit one of these points exactly, it would stay on the associated periodic orbit—but they are infinitesimally close to it. These periodic orbits are said to be **embedded** in the strange attractor, and their presence has been exploited both for control purposes and for the derivation of mathematical properties of the strange attractors. (See (24) for details.)

A useful way to exhibit the types of bifurcations that occur in a given system is to form a **bifurcation diagram** from the return map. Sets of values of x_n are collected for many different values of the bifurcation parameter and plotted on a single figure, as shown in Figure 5. Each vertical slice of the figure shows all of the x_n 's observed for the corresponding value of α . The sequence of period doubling bifurcations is visible, and is a common structure in systems with only a few variables. Two other features common to experiments are visible in the figure. First, at the critical point for the first period doubling bifurcation (near $\alpha = 0.76$), the data are slightly smeared out. This is because near the transition the 1:1 limit cycle is just barely stable, which in turn implies that the transient relaxation to the limit cycle is very long. The plot was made by integrating the equations of motion up through about 50 cycles and recording data from the last 40 cycles. In the present case, the smearing could easily be reduced by waiting

longer before recording the data; the plot is presented as it is to illustrate the general point that slow relaxation near the critical point makes it more difficult to get clean data there. Second, the chaotic region above $\alpha \approx 0.81$ appears rather sparsely filled. Again, this is partly because the runs from which data were gathered only covered 40 cycles of the drive. For longer runs, the data for a given α would form rather dense bands with some visible gaps. Experimental data similar to Figure 5, however, would constitute clear evidence of chaotic behavior.

The presence of a period-doubling route to chaos in a wide variety of systems, together with the recognition that simple bifurcations can be classified into generic types, is very encouraging. It means that many of the features of nonlinear dynamical systems are **universal**, that is, they are independent of the quantitative details of a model. There are now several other routes to chaos that have been characterized, including quasiperiodic attractors that finally give way to chaos, and intermittent behavior in which long periods of nearly regular behavior are interrupted by chaotic bursts (17,23). This type of universality allows educated guesses about how to construct models that exhibit the features observed in experiments.

A basic vocabulary of bifurcations and transitions to chaos is now well developed, and one's first inclination upon observing chaos in an experiment should be to classify its onset as a particular known type. The known classification scheme is not exhaustive, however, and there continue to be cases in which theoretical understanding requires exploring the mathematics of new types of transitions. This is particularly true in systems with very many variables or systems described by partial differential equations that lead to complex patterns.

5. TWO TYPES OF COMPLEXITY: SPATIAL STRUCTURE AND NETWORK STRUCTURE

Thus far the discussion has been limited to systems with only a few degrees of freedom. The effects of nonlinearity become much more difficult to characterize or predict when many degrees of freedom interact. The complexity of the solutions can become overwhelming, in fact, and many fundamental mathematical questions about such systems remain open. Nevertheless, the language and techniques of nonlinear dynamics are helpful in formulating fruitful questions and reporting results.

There are two different ways in which a system can involve a large number of degrees of freedom, both of which are commonly encountered in biomedicine. First, a system can be spatially extended, consisting of a few variables that take on different values at different spatial points. Though such systems may be described by just a few PDEs, the solutions can involve spatial structures of exceedingly complex form. A steadily driven chemical reaction, for example, can display ever-changing patterns of activity as spiral waves are continually formed

and destroyed by propagating wavefronts. As one might expect, there is a whole zoo of observed patterns and bifurcations in such systems, obtained both from physical experiments and numerical simulations on systems as diverse as vertically vibrated layers of sand, layers of fluid heated from below, chemical reaction-diffusion systems, and optical systems involving broad laser beams in feedback loops containing nonlinear elements. Studies of such systems appear to be relevant for explaining pattern formation on butterfly wings, cardiac alternans and fibrillation, and the behavior of neuronal tissue, to name just a few examples.

Not all spatially extended systems show dynamics qualitatively different from simple systems of a few variables. Typically, there is a length scale associated with the spatial patterns one sees in a snapshot of the system. This could be, for example, the average width of stripes observed in a stationary or moving pattern or the size of a square in a checkerboard pattern. If the system is not too large compared to this characteristic length, the dynamics generally takes the forms discussed in section 3.

To analyze spatiotemporal dynamics, one often tries to define new variables that make the problem as simple as possible. These variables take the form of spatially varying functions of the natural field variables, and these functions are called **modes** of the system. Choosing a useful set of modes can be difficult, though in some cases symmetry considerations make the task easier. For example, when the equations of motion are unchanged by uniform spatial shifts, it is often useful to use a Fourier decomposition, in which the modes are simple sine waves of different wavelength. In other cases it may be natural to define modes associated with spatial structures whose amplitudes grow or shrink particularly rapidly or capture salient features of the observed patterns.

The partial differential equations of motion are then transformed into ordinary differential equations governing the amplitudes of the different modes. In the case of systems that are not too large compared to their characteristic length scale, one usually finds that all but a few of the mode amplitudes decay rapidly to zero. The long time dynamics of the system is then well represented by coupled ordinary differential equations for a few variables and the methods of section 3 can be applied even though the corresponding spatiotemporal behavior may look rather complicated.

If the system is *large* compared to the natural length scale of the spatial pattern, the situation becomes substantially more complex. Figure 6 shows a snapshot of the convection pattern in a fluid heated from below. PDEs used to model this system reproduce the observed behavior very well, and the phenomenon is now known as "spiral defect chaos" (7,19). The spiral structures in the pattern move around in erratic ways, and theoretical understanding of the motion is far from complete. It can be extremely difficult, for example, to answer one of the most fundamental questions about observed erratic behavior: Does it correspond to a strange attractor or just to an extremely long transient?

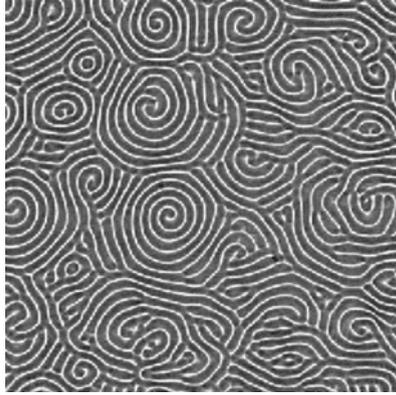


Figure 6. Spiral defect chaos: an example of spatiotemporal chaos in a system that is large compared to the characteristic length scale of the pattern (the width of the stripes). Image courtesy of G. Ahlers.

The theory of spatiotemporal pattern formation and chaos in large systems spans several loosely connected approaches. One is to study the dynamics of isolated typical structures. For example, one can study the speed with which a single pulse moves and spreads through an otherwise homogeneous medium. Another is to look carefully at critical points where universal bifurcation structures can be identified. An example of this is the onset of stripe structures in a homogeneous medium, such as the regions of sinking and upwelling in a fluid heated from below, or the development of chemical patterns in reaction-diffusion systems. Still another is to analyze the **short-time Lyapunov exponents** and associated modes of instability. These exponents do not quite have the same meaning as the true Lyapunov exponents, but are similar in spirit. The true exponents are defined as global properties of the full limit cycle or strange attractor. The short time exponents describe the local stability properties of a trajectory over a finite time interval and the modes associated with positive short-time exponents can reveal the locations in a pattern where instabilities will make prediction difficult over near term.

Still another theoretical approach to complex spatiotemporal behavior is to identify local structures that control the evolution of the pattern and try to describe their collective behavior in statistical terms. Often, the objects of interest are "defects" in an otherwise regular pattern. In spiral defect chaos, for example, it is known that there is another attractor consisting of uniform stripes, so it is tempting to think of the core of a spiral can be thought of as a defect in a stripe pattern. For topological reasons, the defect (a left-handed spiral, say) cannot be

removed except by drifting off the boundary of the system or annihilating with another defect of opposite topological sign (a right-handed, spiral). The dynamics of the system may be described as a changing pattern of defect locations. Since the behavior of dissipative nonlinear dynamical systems with many degrees of freedom resembles in several ways the behavior of systems treated by statistical mechanics, the language of statistical mechanics sometimes creeps into discussions of deterministic nonlinear dynamical systems. In particular, bifurcations are sometimes referred to as **phase transitions**.

The statistical approach is very tempting to physicists. The tools of statistical mechanics have been spectacularly successful in analyzing phase transitions in equilibrium systems, and they become more and more accurate as system size increases. They are based on the idea that the details of how a system moves in its very high-dimensional state space are unimportant for making statistical predictions about the states it is likely to be found in. Unfortunately, the fundamental assumptions of statistical mechanics are strongly violated in the driven, dissipative systems of biomedical interest. At present, there is increasing evidence that statistical mechanics can account for the behavior of a number of deterministic systems far from equilibrium. Examples include coupled discrete maps that undergo bifurcation that are quantitatively similar to equilibrium phase transitions (18), and sheared granular materials like sand in which effective temperatures can be defined for describing the wanderings of individual grains in space and time (16). These applications of statistical mechanics are as yet poorly understood, however, and in the absence of a fundamental theory of nonequilibrium pattern formation, theoretical insight comes largely from numerical simulation of model equations and analysis of the generic types of behavior on a case by case basis.

Construction of an appropriate model for a spatially extended dissipative system involves a healthy dose of intuition as well as a few constructive principles. One generally begins with the selection of the simplest PDE that incorporates the symmetries and general features of the physical system. This may be a known set of equations that is selected either because its solutions seem to match the observed behavior qualitatively or because the underlying physics of the system is expected to be in the same universality class. One then simulates the system numerically and attempts to find a regime in parameter space where the spatiotemporal dynamics is roughly reminiscent of the real system. Analysis of the model can then lead to hypotheses about the effects of varying parameters in the real system. To obtain more accurate predictions, one then adds terms to the model that alter the detailed behavior without changing the big picture. Given the complexity of types of bifurcations that can occur in large systems, however, one often discovers new and unexpected attractors, or one finds that detailed models just don't work and aspects of the physics that were thought to be irrelevant actually must be included in order to obtain reasonable representations of the true dynamical attractors. A good example of progress of this sort is

the modeling of cardiac electrodynamics, which is being approached from several directions simultaneously. The construction of PDE models based on detailed understanding of the physiology of cardiac tissue (26), the construction and simulation of PDE models reproducing realistic patterns of spatiotemporal activity (10,34), and the construction of ODE models or discrete maps reproducing bifurcations observed in small pieces of cardiac tissue (31), are all being brought to bear in a grand attempt to explain the onset and characteristics of arrhythmias from simple period doubling to fibrillation.

The second way in which complexity can enter the world of nonlinear dynamics is through the sheer abundance of distinct variables and the logical, or causal, relations among them. Even without taking into account the spatial distribution of concentrations of molecules, for example, the immune system or the metabolic network in a cell can exhibit surprising behavior due to nonlinear interactions among the concentrations of distinct types of molecules. The nature of these connections, and in particular the topology of the network representing them, has become a central theme in current research. As yet, rather little is understood about the dynamical processes that occur within such large networks containing many feedback loops. Our purpose here is just to illustrate the way in which nonlinear dynamics becomes the natural language for discussing the behavior of complex systems of this sort.

Consider the problem of modeling the regulatory network that governs gene expression in a cell. At its most basic level, the cell can be thought of as a dynamical system of interacting biomolecules produced through the mechanisms of gene expression. In this picture, the future chemistry of a cell is determined by which genes are expressed at any given moment. The products of transcription and translation of genes interact in extraordinarily complicated ways and act back on the processes of transcription and translation so as to influence which genes are expressed at a later time. To model this system the nonlinear dynamist might begin by defining the system variables to be the levels of expression of each gene. Thus the life history of a cell becomes a trajectory through a state space of dimension equal to the number of genes in the network.

Modeling of the detailed interactions among all of the proteins and nucleic acids in the cell would make for a horrifically complicated mathematical system, from which it would be very difficult to glean any useful insights. Instead, one can hope (and perhaps expect) that many features of the state space trajectories are universal, i.e., that they do not depend on the details of the interactions. One is then led to devise models that retain the general logical structure of genetic regulatory networks but are defined by interactions simple enough to be efficiently simulated and studied analytically. One approach, pioneered in the context of genetic regulatory networks by Kauffman (14,15) is to assume that gene expression level is a Boolean variable and that the logical relations among different genes' activities are essentially random. As it turns out, the behavior of

such networks is surprisingly complex and suggestive, and is a subject of active research.

Boolean functions describing the switching of system variables between binary values can be thought of as an approximation of a map corresponding to a very complicated set of differential equations for the underlying physical processes. These functions, which must produce a binary output given some set of binary inputs, are strongly nonlinear. Since the system variables can only have two distinct values, the notion of a state corresponding to the sum of two other distinct states is not even well defined. Even in this extreme situation, however, the concepts of nonlinear dynamics provide a useful framework for discussing network behavior. Here we present a bare-bones description of this framework as an illustration of how the concepts discussed above enter the discussion.

A Boolean network is a collection of N logic gates, each having some fixed number of inputs, K_i , and one binary output, σ_i , where $i = 1, \dots, N$ indexes the gates. The inputs to a gate are a subset of size K_i of the outputs from all of the gates. Each gate is also characterized by a truth table T_i that determines σ_i as a function of the inputs. On each (discrete) time step, all of the gates apply their truth tables to their inputs and update their outputs accordingly. Each T_i is assumed to be selected randomly from a weighted distribution of all the possible truth tables with K_i inputs. To complete the definition of the model, one must specify the K_i 's and the procedure for choosing which σ_i 's act as inputs to a given gate. The best studied cases are networks in which all K_i are the same and the choice of which gates are inputs to any given gate is completely random. The result is a "random Boolean network" (RBN), sometimes referred to as a "Kauffman net."

The system variables in an RBN are simply the values of the outputs of the gates. The parameters of a particular model network are the choices of which outputs serve as inputs to each gate and which Boolean function is assigned to each gate. Instead of specifying all of these parameters explicitly, however, we specify a random procedure for choosing them. The number of inputs to each gate and the probabilities assigned to each of the different truth tables are taken as the parameters of the model. Note that when we discuss the behavior of the model at a certain set of parameter values, we are now talking about the average or typical behavior of a whole class of individual RBNs—those constructed according to a specified probabilistic procedure—rather than the detailed behavior of one specific dynamical system. (For more on probabilistic procedures for constructing the wiring diagrams of biological networks, see this volume, Part II, chapter 4, by Wuchty, Ravasz, and Barabási.)

In an RBN, the trajectory associated with the differential equations becomes a sequence of vertices in a state space that is a discrete set of points. If there are N gates in the network, each point in state space is an N -dimensional vector. Now because the number of distinct states is finite, the total number of possible states being 2^N , the sequence must eventually arrive at a point that has been vis-

ited before. From then on, it must cycle on the same loop forever. This means that, strictly speaking, all attractors on any Boolean network are periodic limit cycles. When N is very large, however, 2^N is astronomically huge and these cycles can become extremely long.

A surprising aspect of RBNs is the existence of two qualitatively different behaviors for different parameter regimes. A parameter q_1 can be defined that corresponds to the probability that changing the value of one randomly selected input to a randomly selected gate will result in a change in the output of that gate (27). A qualitative change in the network behavior is observed as q_1 is varied, which can be accomplished by changing K or changing the weights of the different truth tables. For small values of q_1 , typical networks have only a few attractors; almost all of the gates wind up stuck on one value or the other and the duration of the attractor cycles are short. For larger values of q_1 , a number of gates of order N remain active and the cycles are extremely long. The attractors in the two regimes also have markedly different stability properties. In the case of small q_1 , small externally imposed perturbations, like changing the output value of a single gate for one time step, have little effect. The system quickly returns to the original attractor. For large q_1 , on the other hand, small perturbations often place the system in the basin of a different attractor. The regime in which one observes short, stable cycles is called "ordered," and the region with exponentially long, attractors that are sensitive to small perturbations is called "chaotic." The latter term is meant to emphasize the erratic nature of the attractors over many times steps, but is not a rigorous description of the attractors over the tremendously long times associated with their cycle durations.

RBNs at the critical value of q_1 exhibit a unique balance of attractor stability and flexibility (15). The discovery of these special and totally unanticipated properties of critical RBNs is an indication of the power of the nonlinear dynamics conceptual framework. Even though these specific RBN models are not faithful representations of real biological processes, they reveal nonlinear dynamical structures that are likely to arise also in models that incorporate more realistic details, and therefore suggest new ways of understanding of the integrated behavior of the genome.

6. DISCUSSION AND CONCLUSIONS

This chapter is intended only to establish some of the vocabulary of nonlinear dynamics and give some indication of the rich behaviors that fall within its domain. Many important phenomena have been neglected entirely to this point. Three stand out as requiring some comment, however brief: the effects of stochastic processes; the role of boundary conditions; and the phenomena of frequency locking and synchronization.

Dynamical systems are, by definition, deterministic. They are therefore capable of exhibiting exquisitely detailed mathematical structures, and one might well ask whether these structures survive in the presence of stochastic influences, or **noise**. Conversely, dynamical systems with rather mundane behavior could respond in unexpected ways in the presence of noise. The theory of noisy dynamical systems, which in many cases is studied under the heading of non-equilibrium statistical mechanics, is a rich topic in its own right and is likely to be highly relevant for understanding some biomedical processes. It is also true, however, that the effects of noise can often be safely neglected, either because the details washed out by the noise are on such a fine scale as to be uninteresting, or because the feedback elements in the system allow it to operate reliably even when noise is a strong influence.

In spatially extended dynamical systems, boundary conditions can play a crucial role in determining the nature of the solutions to equations describing a bulk material. The same PDE can exhibit very different solutions when the boundary conditions are changed, and the realistic modeling of a system may depend just as much on getting the boundary conditions right as it does on modeling the bulk process. This often means having to understand the physics of a material or interface that was originally thought to be external to the system. Many analytical and numerical studies of PDEs are performed on domains that are artificially modeled as having no boundaries, like a torus. This is often quite useful, but care must be taken in applying intuition from these studies to the interpretation of experiments.

Phase locking is a phenomenon that occurs when two autonomous systems that oscillate at different natural frequencies are weakly coupled. While for extremely weak coupling there exist **quasiperiodic** trajectories of the coupled system that never exactly repeat but do not have the positive Lyapunov exponents associated with chaos, slightly stronger coupling tends to cause the two original systems to lock into a periodic trajectory in which the ratio of the periods of oscillation of the two original systems is a rational number. The most famous case of this is the phase locking of the moon's rotation about its axis to its orbit around the earth, which is why we on earth always see the same side of the moon. When elements are added to a system to induce phase locking, or when a large number of systems become phase locked in a 1:1 pattern, the phenomenon is sometimes called **synchronization**. In studying natural systems where synchronization is observed, it may be helpful to keep in mind the fact that it could be a straightforward consequence of nonlinear dynamics principles (29).

Finally, in an age in which the control and manipulation of biological systems is attracting so much interest and speculation, it is worth noting that there is a vast and growing literature on the **control** of dynamical systems. In this context, control means applying signals, hopefully of low power, in order to get a system to follow a desired trajectory in state space. (Two useful textbooks for basic elements of control theory are (21,22).) This may mean steering the system

from one attractor to another, keeping the system on a trajectory that is unstable in the absence of control, or combinations of the two. One example of a biomedical problem that naturally involves control theory, but also pushes its current limits, is the prevention of cardiac arrhythmias in humans (see Part III, chapter 3.3, by Glass.) Here one has a spatially extended system large enough to support complex spatiotemporal activity, though the desired behavior is a simple, regular heartbeat. There is some reason to hope that nonlinear dynamics models will provide useful descriptions of cardiac electrodynamics and new ideas for suppressing instabilities associated with certain types of arrhythmias. Recent work has focused on the onset of alternans (period doubling) in paced cardiac tissue (31) and the manipulation or destruction of spiral waves in excitable media models (1).

The world of nonlinear dynamical systems is full of complex structures and surprising behavior. There is now a well-developed language for characterizing all sorts of attractors and bifurcations as parameters are varied. The classification schemes will (probably) never be complete, however, and studies of systems as complex as living tissues and biological networks (metabolic, genetic, immunological, neuronal, ecological) are highly likely to uncover new mathematical structures. Systems with strongly stochastic elements or many interacting variables will require further connections to be made between nonlinear dynamics proper and statistical mechanics. As indicated by many of the chapters in this volume, all of these concepts can and should be brought to bear in the study of biomedical systems.

6. NOTES

1. If the equations of motion contain a second derivative of x_j , say, the above form is recovered by defining $x_2 = \dot{x}_1$ and writing \dot{x}_2 wherever the second derivative of x_j appeared in the equations.

2. The coefficients are the external parameters designated by \mathbf{p} above.

3. It is possible, however, for there to be an initial increase in some variables before the ultimate relaxation toward the origin occurs. This can happen when the eigenvectors associated with significantly different modes are **non-normal** (not perpendicular to each other in state space). See (32) for a discussion of this effect and presentation of several examples.

4. Strictly speaking, this is a bit of a misnomer, as an exponent should not be a dimensionful quantity. The physically relevant quantity is the Lyapunov exponent λ multiplied by some characteristic time in the system.

5. Note that at points where the trajectory appears to cross itself it must be really separated in the third dimension since the future behavior is unique once an initial point in state space is given.

6. The situation is simple when driving is explicitly exhibited and is strictly periodic. For other systems, the strobe may have to be triggered in a slightly more subtle way. It has to flash when a system variable passes through a particular value, rather than at precisely equal time intervals, but the basic idea is the same.

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