A Dynamic Systems Approach to Development.
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Chapter 1

Dynamic Pattern Formation: A Primer

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Morphology, embryology, evolution, developmental biology, neurobiology, physiology, and behavior are separate fields that now function largely in isolation of one another. Yet all deal, in one form or another, with structure or pattern formation processes. And all deal, in one form or another, with the fundamental issues of stability and change. Thus, separation of the disciplines does not necessarily negate the possibility that common principles may exist that underlie pattern formation and change. Although the details may differ, *events* on any chosen scale of description rely only upon interactions among components: words like *coordination* or *cooperation* express this fact. One may argue that rather than "things" (material ingredients) the coordinative relations or dynamical actions among things should be the primary focus of science.[1] If the universe were composed of noninteracting units that did not speak to one another, then there would be no need to understand pattern formation in physical, chemical, or biological systems. We would not be seeking principles of biological organization because, without interaction, chemistry and biology would simply not exist.

Given, then, the presence of interactions, what form do they take, i.e., what are the laws of coordination in complex biological systems? How do we find these laws, i.e., which, if any, strategies are useful? And what language is appropriate to express these laws? If structures or patterns represent coordinated states of affairs, how do we identify and define these collective states and specify the conditions guaranteeing their persistence and change? Unlike many physical and chemical systems where the important variables and equations are well-known, in living systems we have to find key observables and their dynamics (equations of motion).

In this primer we provide a language and a strategy for attacking the above questions. Our approach relies upon, and is inspired by, theories of spontaneous (self-organized) formation of patterns in nonequilibrium systems, especially Haken's (1977/1983) synergetics, the qualitative theory of dynamical systems (e.g., Guckenheimer and Holmes, 1983), and the theory of stochastic dynamics (e.g., Gardiner, 1983). For a long time, biologists have looked to concepts like self-organization and cooperative phenomena for insights into complexity, but it is only recently that the necessary theoretical tools have become available to place these concepts on a firm foundation. Intuitions like "the whole is greater than, or different from the sum of its parts" may thus be seen in a new light when the "whole" is characterized as a self-organized structure whose dynamics are capable of generating enormous behavioral complexity.

Before proceeding, we should mention that the application of dynamic concepts did not occur in a vacuum or because of James Gleick's bestseller *Chaos*, but rather was motivated in the context of specific experimental studies of biological coordination. We view this theoretical cum experimental analysis of coordination as a necessary *window*, even an essential step, into uncovering general principles. In this we complement other approaches to coordinative complexity[2] (see, e.g., contributions in Baskin and Mittenthal, 1992).

Where appropriate, we mention experimental examples as a means of illustrating the concepts with the aim of establishing a linkage between analytic tools and experimental data. But our main goal is to review some elementary concepts and techniques pertinent to the nonlinear dynamics of pattern formation. By and large, the primer is conceptual rather than mathematical, and is aimed at communicating with a biological audience. Before beginning we wish to stress that in the present approach, "understanding" is sought, not through some privileged scale of analysis but within the more abstract level of essential, biologically relevant variables and their dynamics *regardless of scale or material substrate*. There is no ontological priority of one observational scale over another. What is "macro" at one level can be "micro" at another. Molecules, for example, are macroscopic structures for the particle physicist and microscopic structures for the typical cell biologist. Here, it is the methodologic strategy and the reduction to (dynamically expressed) principles across levels of investigation that is the focus of our attention. Insight, within the present approach, is not necessarily gained by increasingly precise quantitative analysis (important though that may be) or by using increasingly complicated equations. Rather the aim is to account for a larger number of empirically observable features with a smaller number of theoretical concepts.

Dynamic Pattern Formation: General Remarks

Why should an understanding of structurally complex biological systems and their corresponding pattern complexity be sought in terms of organizational principles? One reason is that the same, reproducible patterns can be produced by many different material substrates and mechanisms. Even in physical systems a given pattern (e.g., Bénard convection cells) need not relate to a unique mechanism: examples in biology are nearly too numerous to mention (cf. Kelso and Schöner, 1987). To cite one instance, an extensive review in the well-developed field of invertebrate pattern generation reveals that there is a uniform *lack* of common neuronal mechanisms, despite similarities between the patterns generated (Selverston, 1988; p. 377). This fact, that many physical mechanisms may instantiate the same pattern, hints strongly of *universality*, that some underlying law(s) or rule(s) governs pattern formation. At the same time, biological structures are clearly multifunctional: the same set of anatomic components may support a variety of functions. Again, recent evidence from invertebrate central pattern generators shows that the same neural circuit can switch flexibly among different "functional states," and can reconfigure itself according to current conditions (e.g., Marder, 1989). Minimally, then, any principle(s) of pattern formation should handle *compositional complexity* on the one hand (e.g., how a given pattern is constructed from the interactions among a very large number of heterogeneous components) and *pattern complexity* on the other (e.g., multiple dynamical behaviors). Words familiar to biologists, such as (multi)*stability* (ability to persist under various environmental conditions) and *flexibility* (ability to adjust to changing internal or external conditions) should be fundamental features of any organizational principles. The "forces," or generic processes (e.g., competition), that lead to pattern *selection* should also be clear.

In the last decade or so, tremendous progress in understanding pattern formation in open, nonequilibrium physical, chemical, and biochemical systems has been made (see, e.g., Collet and Eckmann, 1990; Kuramoto, 1984; Nicolis and Prigogine, 1977; Babloyantz, 1986). In particular, synergetic construction principles (Haken, 1975; 1977/1983) have established the concepts of instability, fluctuations, and slaving as crucial to understanding and predicting the spontaneous (self-organized) occurrence of order in complex systems. Synergetics deals typically with equations of the following form:

$$(1) \quad \dot{\mathbf{q}} = \mathrm{N}(\mathbf{q}, \text{parameters, noise})$$

where the dot denotes the derivative with respect to time, $\mathbf{q}$ is a potentially high dimensional state vector specifying the state of system Eq. (1), and N is a nonlinear function of the state vector and may depend on a number of parameters (including time) as well as random forces acting on the system.

In general, when parameters in Eq. (1) change continuously, the corresponding solutions of Eq. (1) also change continuously. However, when a continuous change in the control parameter crosses a critical value (or critical point) the system may change qualitatively, or discontinuously. *These qualitative changes are frequently associated with the spontaneous formation of ordered spatial or temporal patterns.* This process of self-organization always arises via an *instability*. The emergence of pattern and pattern switching or change arise solely as a result of the cooperative dynamics of the system (the function N in Eq. [1]) with no specific ordering influence from the outside and no homunculus-like pattern generator (note the noun form) inside. Examples include the formation of convection rolls or hexagons in the Bénard system, vortex formation in the Taylor system, the onset of lasing in the laser, the formation of concentration patterns in certain chemical systems such as the Belousev-Zhabotinski reaction, reaction-diffusion systems, and the well-studied Turing instability, which has served as a model of morphogenesis. In all these cases, near the vicinity of critical regions (i.e., near an instability) the system's macroscopic behavior is dominated by just a few collective modes, the so-called *order parameters*. The latter are the only variables needed to describe the evolving self-organized state exhaustively. This compression of degrees of freedom (*df*) referred to as the *slaving principle* has been given an exact mathematical form by Haken for a large class of systems (for a discussion of these and many additional examples, see, e.g., Haken, 1977/1983; 1983, and references therein. A related approach is developed in a recent book by Nicolis and Prigogine [1989]. The mathematically oriented text by Murray (1989) contains a number of worked-out examples. A good review of the slaving principle is provided by Wunderlin [1987]).

The spontaneous formation of patterns in nonequilibrium systems may be understood as special solutions of the system's dynamics (Eq. [1]) that allow for a much lower dimensional description. Patterns emerging at *nonequilibrium phase transitions* (the term preferred by physicists) or *bifurcations* (the mathematical term) are defined in terms of *attractors* of the collective variable dynamics. We define and discuss these terms more fully below. It suffices to note at this point that attractors of the collective variable dynamics exist because nonequilibrium systems are *dissipative*: many independent trajectories with different initial conditions converge in time to a certain limit set or attractor solution. Stable fixed point, periodic limit cycle, and chaotic solutions are thus all possible in the *same* system (e.g., Eq. [1]), depending on parameter values. We have a glimpse, then, of one of nature's themes for handling different kinds of complexity. Vast *compositional complexity* is compressed at critical points (as demonstrated by the slaving principle of nonequilibrium phase transition theory). The resulting low-dimensional pattern dynamics are nonlinear, thus giving rise to enormous *behavioral complexity*. This theme (cf. Kelso, 1988) thus embraces both the disorder-order and order-order principles advocated by Schrödinger (1945) in *What Is Life?* and adds the evolutionary order-disorder principle.

Of course, from a scientific point of view, life (and its understanding!) is not so easy. The reason is that in most biological systems the state vector $\mathbf{q}$, its dynamics, the nature of the parameters, and the noise sources are largely unknown. The path from the microscopic dynamics of Eq. (1) to the understanding of macroscopic pattern formation in terms of collective order parameters is therefore not accessible to theoretical analysis. Moreover, it is not clear that biological systems possess the hierarchy of time scales necessary for the slaving mechanism of order formation. Consider, for instance, the typical time for synaptic integration ($\sim$10 ms) and compare it to typical reaction times ($\sim$100 ms) that may involve macroscopic movement of the entire organism. These times are not clearly separated although they refer to processes on very different spatial scales. Biological order formation poses challenges to theory also with respect to flexibility, in that biological systems are able to synthesize a tremendous number of different patterns, often continuously (consider, e.g., visual perception). As different such patterns are formed, the components of the biological system may stabilize qualitatively different relationships, e.g., the same neurons in a central pattern generator may stabilize synchronous activity in one pattern and alternating activity in another (e.g., Mpitsos and Cohan, 1986).

On the other hand, it has proven possible to learn from, and build upon the foundation provided by theories of nonequilibrium pattern formation by using an alternative approach to biological order, namely one in which the nature and dynamics of the low dimensional order parameters are first empirically determined. Phase transitions (or bifurcations) are a key part of this strategy, constituting a special entry point for developing theoretical understanding. The reason is that qualitative change allows a clear distinction of one pattern from another, thereby allowing the identification of collective variables for different patterns and the pattern dynamics (stability, loss of stability, etc.). *Near critical points the essential processes governing a pattern's stability, flexibility, and even its selection, can be uncovered.* Theoretically motivated measures (fluctuations, relaxation times, dwell times near the critical point, etc.; see below) are available to elucidate these processes and allow tests of theoretical predictions. In addition, the *control* parameters that promote instabilities can be discovered. Different levels of description can be related through a study of component dynamics and their coupling. In a companion paper, we apply this strategy to our chief experimental model system which involves the study of coordination in humans as a way to discover laws and principles of biological self-organization. In what follows, we provide a more detailed explication of the approach, particularly its reliance on concepts of low dimensional systems.[3]

General Definitions

Let $x_1, x_2, \ldots, x_n$ be the collective variables characterizing a complex biological system. Then the *phase space* is a n-dimensional Euclidean space spanned by the vector $x = (x_1, x_2, \ldots, x_n)$ with x_i ($i = 1, 2, \ldots, n$) assuming all permissible values. A *dynamical* *system* is a system of equations stipulating the temporal evolution of x. If x is a continuous function of time, then the dynamics of x is typically defined by a set of first-order ordinary differential equations (ODEs)

$$(2) \quad \dot{x} = \mathbf{F}(\mathbf{x})$$

where $\dot{x}$ denotes the derivative with respect to time and $\mathbf{F}(\mathbf{x})$ gives the vector field. ODEs are frequently encountered in biology, especially when $\mathbf{F}$ specifies a nonlinear oscillator. There is another important class of dynamical systems which appear as difference equations or maps:

$$(3) \quad x_{t+1} = \mathrm{G}(x_t)$$

Here "time" t is discrete and assumes integer values. A trajectory (orbit) of the map is $x_0, x_1, x_2, \ldots$. That is, given x_0, the map gives x_1; given x_1, Eq. (3) gives x_2; and so on. This type of system has found applications in ecology, most notably in insect population problems. Later we argue that certain forms of Eq. (3) also provide a natural framework for understanding multifrequency processes in biology and behavior (DeGuzman and Kelso, 1991; Kelso and DeGuzman, 1988).

Maps and ODEs are intrinsically related to each other. In particular, maps can arise in ODEs in the form of a Poincaré surface of section as illustrated in figure 1.1. The plane S is the designated surface of section, and Λ denotes a trajectory of the ODE. Every time Λ pierces S going downward (points P_1, P_2, and P_3 in the figure), the corresponding coordinates in the plane are recorded. Clearly the coordinates of P_1 uniquely determine those of P_2, and the coordinates of P_2 uniquely determine those of P_3, and so on. Thus there exists a map G such that $P_{n+1} = \mathrm{G}(P_n)$. In the special case of

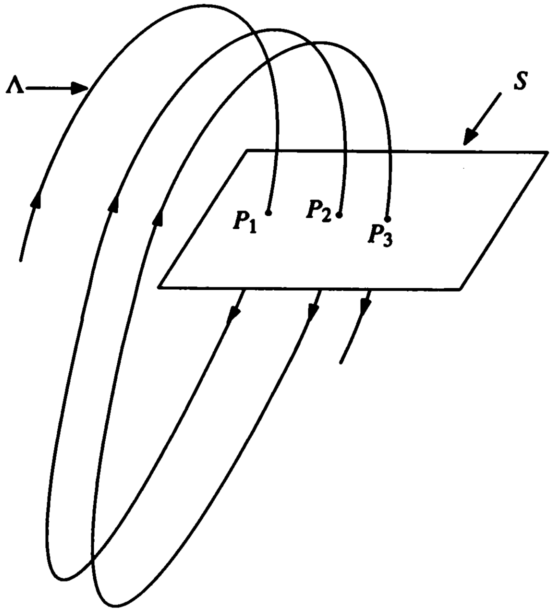

Figure 1.1
Poincaré surface section for an ordinary differential equation (ODE). See text.

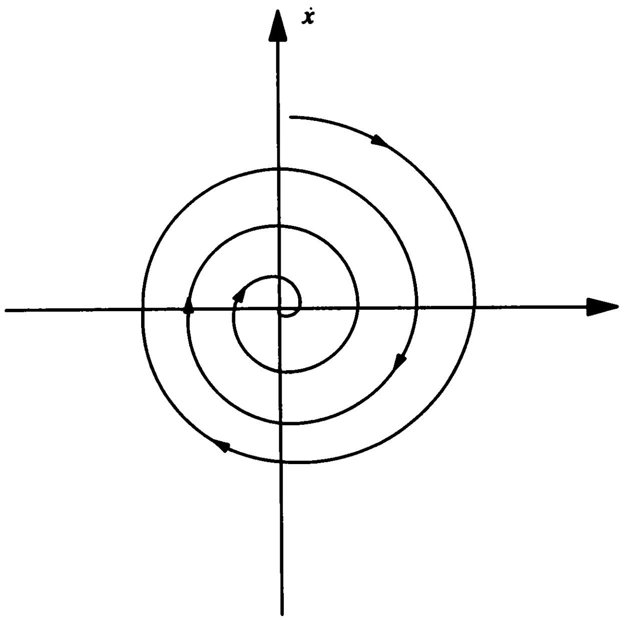

Figure 1.2
The origin is the fixed point attractor for a damped pendulum.

periodically forced ODEs the Poincaré map can be interpreted as resulting from strobing the system at times $t_n = nT$ where T is the forcing period. Note that although maps and ODEs differ in respective analysis techniques, together they provide complementary means for studying nonlinear dynamic systems.

A *dissipative system* is one whose phase space volume decreases (dissipates) in time. As a consequence of this, dissipative systems are usually characterized by the presence of attractors. An *attractor* is a subset of the phase space to which initial conditions converge asymptotically as time $t \to \infty$. For example, for a damped pendulum, oscillations induced by an initial displacement from equilibrium will wind down and eventually come to a halt. The attractor in this case is a *fixed point* at rest (figure 1.2). (Pictures like the one shown in figure 1.2 are often referred to as *phase portraits*.)

A self-excitatory system usually exhibits a *limit cycle* as its attractor. Figure 1.3 shows one such attractor on which the dynamics are periodic. When a system is on a limit cycle, it oscillates with a certain frequency and amplitude that are a function of system parameters only, not of the initial conditions. The stability of this attractor is revealed by the fact that trajectories outside the limit cycle spiral inward, while trajectories inside spiral outward toward the limit cycle. *Quasi-periodicity* arises in higher dimensional systems. Topologically, a quasi-periodic attractor is defined by an m-dimensional torus (T^m). Figure 1.4 shows an example for $m = 2$. The quasi-periodic dynamics on a torus exhibits two or more incommensurate frequencies.

Higher dimensional ODEs ($n > 2$) or maps of any dimensionality may also exhibit *deterministic chaos*, a type of irregular dynamical behavior resembling that of random noise. The presence of chaos in physical systems is ubiquitous and has been demonstrated extensively (see Hao, 1990, and references therein). Recent evidence suggests that chaos may also play an important part in certain biological functions (Başar, 1990;

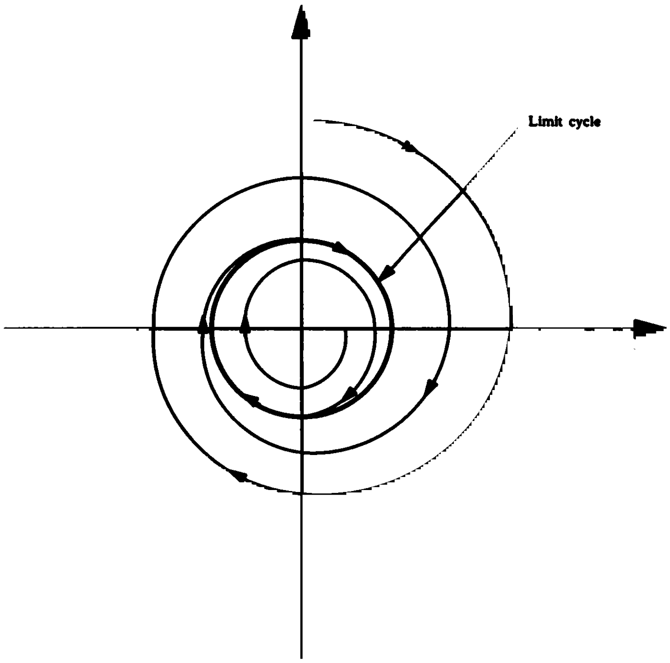

Figure 1.3
A limit cycle attractor.

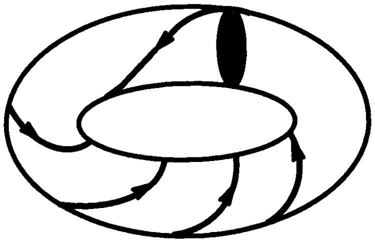

Figure 1.4
A torus attractor.

Glass and Mackey, 1988). We touch briefly on this subject below (see Circle Maps and Intermittency), but otherwise leave more detailed discussions to the burgeoning literature.

Related to the idea of attractors is the concept of *basin of attraction*. A given attractor's basin of attraction refers to the region in phase space in which almost all initial conditions converge to the attractor. Several attractors with different basins of attraction may also coexist, a feature called multistability. Multistability, the coexistence of several collective states for the same value of the control parameter, is an essential property of biological dynamics.

The term *transient* defines the segment of a trajectory starting from its initialization in the basin of attraction until it settles onto the attractor. Mathematically, transients are generally infinite. The reason is because a typical trajectory approaches the attractor only in the limit $t \rightarrow \infty$. In practice, transients are bound to be finite due to finite experimental resolution. For example, let us assume our experimental resolution is ε. Then, for the damped pendulum shown in figure 1.2, the transient may be regarded as that segment of the trajectory which occurs before the trajectory reaches the circle of radius ε around the origin.

Equations (2) and (3) often depend on *control parameters*. For a damped pendulum, the strength of the gravitational field and the friction coefficient may be considered as such control parameters. For biological systems, control parameters are usually not readily identified, hence detailed analysis of the circumstances is required.

When a parameter p changes smoothly, the attractor, in general, also changes smoothly. When the parameter passes through a critical point $p = p_c$, however, an abrupt change in the attractor takes place. This phenomenon, as mentioned above, is called a *bifurcation*, or *nonequilibrium phase transition* in physical theories of pattern formation. As we have stressed, bifurcations are particularly important for the investigation of complex biological systems, both methodologically and conceptually (see Bifurcations below).

A Simple Example

We begin with the simplest possible case, an overdamped one-dimensional oscillator. Simple though it is, it nevertheless is a useful vehicle for explaining most of the relevant concepts. The equation of motion is

$$(4) \quad \dot{x} = f(x) + \text{noise}$$

$$(5) \quad \phantom{\dot{x}} = -dV(x)/dx + \text{noise}$$

The phase space in this case is the entire x-axis. In mechanical terms, x is the position of a point particle in the potential landscape, $f(x)$ is the force, and $V(x)$ is the potential producing the force. As will become clear, the presence of noise in Eq. (4) is of both conceptual and practical importance. For the moment, however, we concentrate on the deterministic part of Eq. (4).

A typical potential $V(x)$ is shown in figure 1.5. The extrema of $V(x)$, x_1, x_2, and x_3 in figure 1.5 are points of vanishing force, giving rise to *steady-state* solutions. For initial conditions near a minimum of the potential, the resulting trajectories approach the minimum in a fashion resembling that of a point particle moving in a "very sticky" well. Near a maximum, on the other hand, trajectories are repelled away from that point. Consequently, the maximum is called a *repeller*. For the potential in figure 1.5, x_1 and x_3 are fixed point attractors and x_2 is a fixed point repeller.[4] The basin of attraction for x_1 is $-\infty < x < x_2$ and that for x_3 is $x_2 < x < \infty$. Repellers always lie on the boundary of basins of attraction. On the x-axis of figure 1.5 we have drawn the attractors, the repeller, and the directions of flow (the set of all possible trajectories) in the various regions. The whole picture constitutes a phase portrait albeit in this case a very trivial one. Implementing a dynamical theory means mapping the reproducibly observed states of a system (i.e., those that occur independent of initial conditions) onto attractors of a corresponding dynamic model. Thus, *stability* is a central concept. How does one determine stability of dynamic patterns?

Measures of Stability: Relaxation Time, Fluctuations

Stability can be measured in several ways. (1) If a small perturbation applied to a system drives it away from its stationary state, x_f, the time for the system to return to

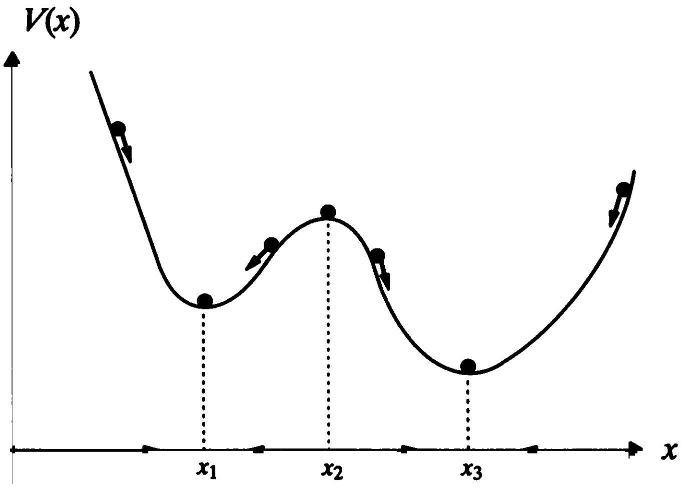

Figure 1.5
A bistable potential with point attractors at x_1 and x_3 and a repeller at x_2. On the x-axis (phase space) the flow directions are indicated.

its stationary state is independent of the size of the perturbation (as long as the latter is sufficiently small). This "local relaxation time" (local with respect to the attractor) is therefore an observable system property that measures the stability of the attractor state. Mathematically:

$$(6) \quad x(t) = x_f + \varepsilon e^{-t/\tau_{rel}}$$

where ε is the size of the perturbation.[5] The smaller τ_{rel} is, the more stable is the attractor. The case $\tau_{rel} \rightarrow \infty$ corresponds to a loss of stability. Figure 1.6 illustrates these relationships.

When explored systematically, τ_{rel} reveals the critical parameter values at which one pattern loses stability and another pattern spontaneously emerges. (2) A second measure of stability is related to the noise sources indicated in Eq. (4). Any real system described by low dimensional dynamics will be composed of, and be coupled to, many subsystems. These act to a certain degree as *stochastic forces* on the collective variables (cf. Gardiner, 1983; Haken, 1977/1983, section 6.2). The presence of stochastic forces and hence of *fluctuations* of the macroscopic variables is not merely a technical issue, but is of both fundamental and practical importance (cf. Haken, 1977/1983, section 7.3). In the present context, the stochastic forces act as continuously applied perturbations and therefore produce deviations from the attractor state. The size of these fluctuations as measured, for example, by the variance or standard deviation (SD) of x around the attractor state, is a measure of the stability of this state. The more stable the attractor, the smaller the mean deviation from the attractor state for a given strength of stochastic force. Such a situation is illustrated in figure 1.7.

Without elaborating on the details, it is worth mentioning that the relaxation time may also be determined from fluctuation measures (e.g. by measuring the line width of the spectral density function; see Kelso, Schöner, Scholz, and Haken, 1987). All of the above statements can, of course, be made exact and quantitative (see Haken, 1983, for many examples; and Schöner, Haken, and Kelso, 1986, for a specific example related to biological coordination).[6]

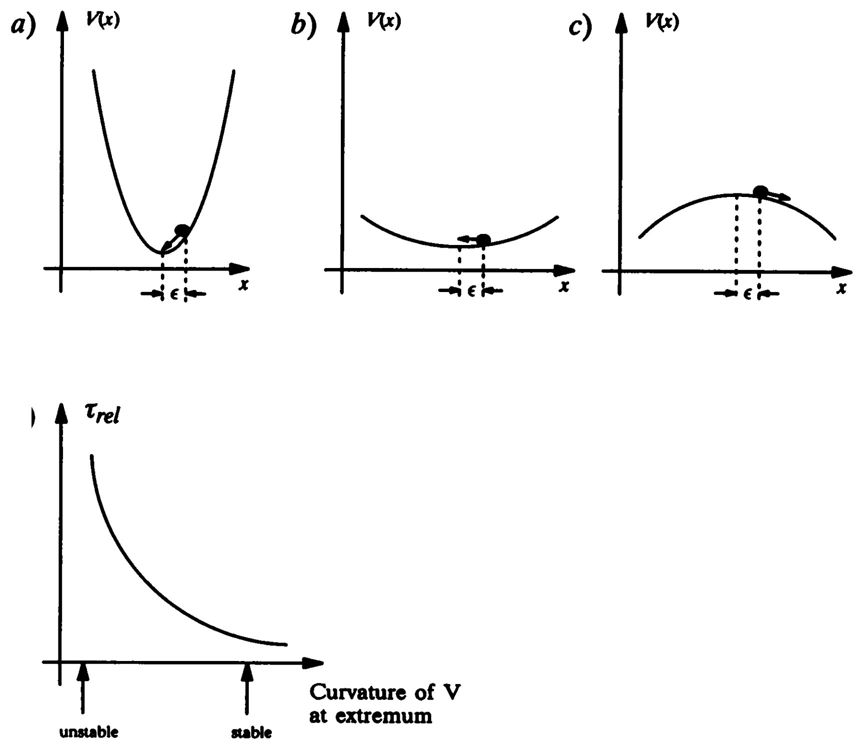

Figure 1.6
a) In a steep potential, the system relaxes quickly from a small perturbation of size ε. *b*) In a shallower potential (smaller curvature at the minimum) the relaxation after the same perturbation as in *a*) takes longer due to the smaller restoring force exerted. *c*) When the potential has a maximum, the system does not return to an unstable state after perturbation. *d*) When the shape of the potential is changed by varying a parameter, thus changing the stability of a stationary state, τ_{rel} reflects this change.

Loss of Stability: Critical Slowing Down, Critical Fluctuations

How can a dynamic system change its behavior, defined in terms of its attractors, stabilities, etc.? As indicated in Eq. (1) the dynamical equations usually depend on parameters. As these parameters change, the dynamics change. Often a small change in some parameter results in a small change of the dynamics. However, at certain critical points, the dynamics may also change qualitatively, e.g., the stability of an attractor is lost.

Such changes of stability are, of course, reflected in stability measures. A simple example, schematically illustrated in figure 1.8, shows that as the potential deforms due to scaling of its parameters, the minimum in question becomes shallower and shallower. Then, at the critical point, it becomes completely flat (having collided with a neighboring maximum). Beyond the critical point, the original minimum vanishes. Accordingly, relaxation time increases as the minimum flattens out, and then, as the system switches, decreases sharply to the small value corresponding to the other stable, stationary state. The strong increase in relaxation time is called *critical slowing down.*[7] The flattening of the potential is also seen as an enhancement of fluctuations (so-called *critical fluctuations*). Thus, the shallower potential has a less restraining in-

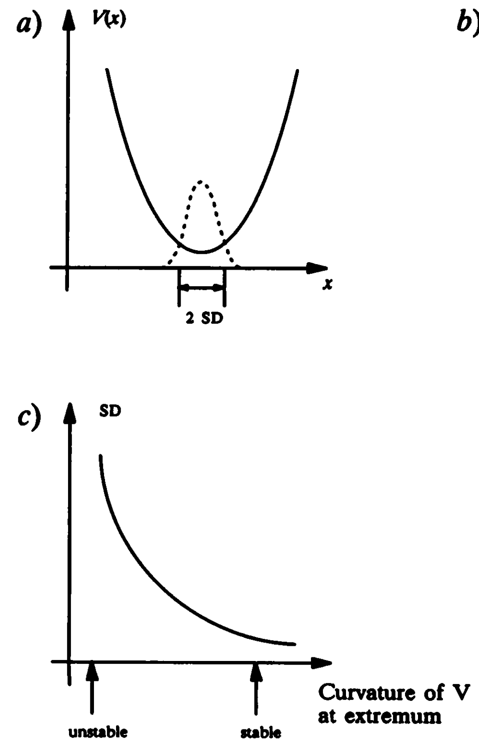

Figure 1.7
a) The width of the probability distribution (*dashed line*), as measured by the standard deviation (*SD*), is a measure of stability. It is smaller for a more pronounced minimum of the potential *a*) than for a shallower potential *b*). *c*) If one varies the shape of the potential experimentally, the SD exhibits the corresponding change in stability.

fluence on the fluctuations, thereby allowing the system to be, on the average, further away from the minimum.

These features of critical slowing down and critical fluctuations are characteristic of *instabilities*. Their experimental detection represents strong evidence not only that observed patterns correspond to attractor states but also that the switching between attractors is due to loss of stability. Once again, these predictions have been worked out in quantitative detail in the case of biological coordination (for reviews, see Schöner and Kelso, 1988a, and Jeka and Kelso, 1989).

Time Scales Relations

Obviously the presence of fluctuations is important for some aspects of critical behavior. In this section, we explain how they are quite fundamental to the consistency of a dynamic modeling approach, especially to transitions and the ability to change patterned states. We mentioned earlier that any realistic low-dimensional model of a complex system must include noise. The presence of noise, however, renders the interpretation of observed states as attractor states of a dynamical system nontrivial. This situation is most obvious in the bistable case illustrated in figure 1.9. In the presence of noise, the system, initially prepared in the state x_1, will, after a sufficiently

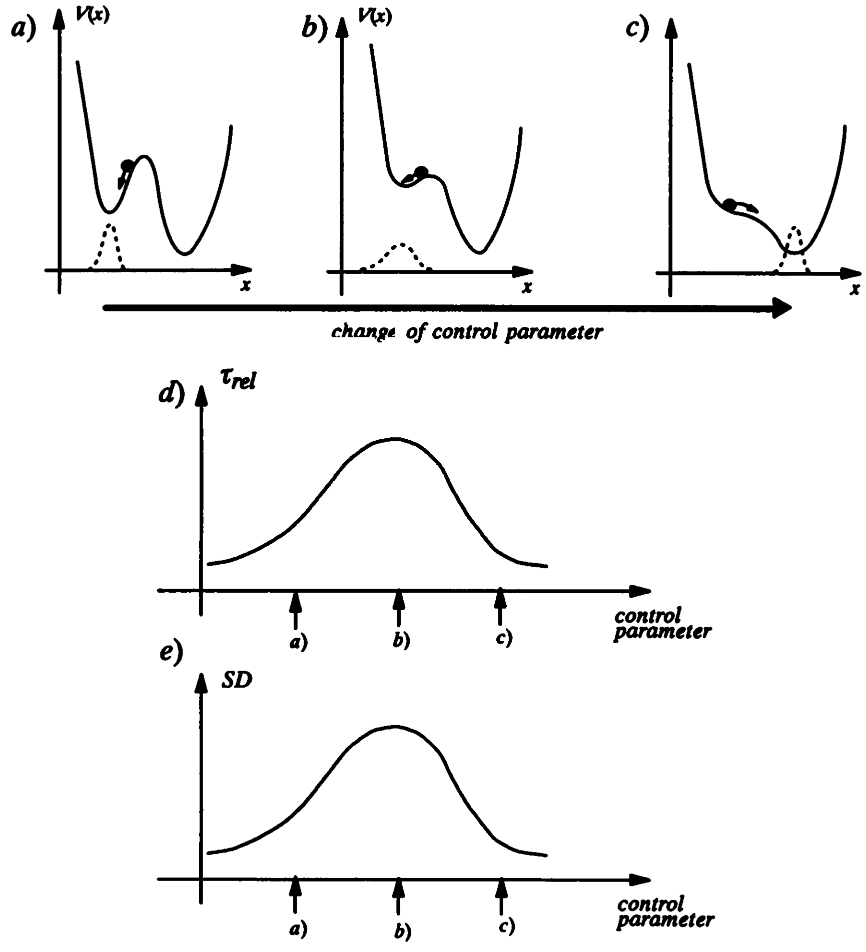

Figure 1.8
a) A bistable potential (——) with a local probability distribution (- - - -). Local relaxation is fast. *b*) One minimum has flattened out as a control parameter is changed to a critical value. Local relaxation is slow, and the local probability distribution is very wide. *c*) As the control parameter is increased beyond the transition, the system switches to another available stable stationary state. Local relaxation and the probability distribution now refer to this new stable state. *d*) Relaxation time is plotted as a function of the control parameter (the approximate locations of the situations *a*), *b*), and *c*) are indicated.) The maximum, as the system goes through the transition, indicates critical slowing down. *e*) The standard deviation (*SD*) as a function of the control parameter, the maximum of which reveals critical fluctuations.

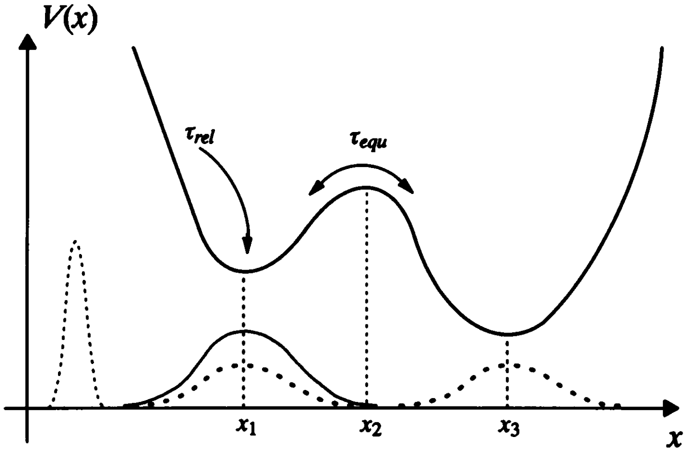

Figure 1.9
Illustration of time scales in a bistable potential. An initial distribution (- - - - - - -) relaxes to an intermediate local distribution (——) around a stationary state x_1 on the time scale τ_{rel}. This local distribution relaxes to the stationary distribution (- - -) on a time scale τ_{equ} that is determined largely by the typical time it takes to climb over the potential hill.

long time and with nonzero probability, switch over to state x_3. Indeed, the stationary probability distribution that describes the system after a sufficiently long transient time will be a bimodal distribution with some probability mass at x_1 and some at x_3. Is, then, the state x_1 not really a stable state? To answer this question a discussion of three types of *time scales* is necessary. The first one is the previously discussed local relaxation time, τ_{rel}; a second is the typical time scale on which the system is *observed*, τ_{obs} (i.e., the time interval over which data are statistically analyzed); and a third time scale is the so-called *equilibration time* (or global relaxation time), τ_{equ}. The last is defined as the time it takes the system to achieve the stationary probability distribution from a typical initial distribution. In a bistable situation such as that shown in figure 1.9, τ_{equ} is determined mostly by the typical time it takes to cross the potential hill. If these time scales fulfill the following relation,

$$(7) \quad \tau_{rel} \ll \tau_{obs} \ll \tau_{equ}$$

(local stationarity), then the interpretation of observed states as attractors is consistent. That is, the system has relaxed to an attractor on the observed time scale, but is not yet distributed over all coexisting attractors according to the stationary probability distribution. When stationary states in an experimental system are referred to, what is meant is that the time-scales relation Eq. (7) is obeyed.

It is important to realize that much of the work in dynamic modeling of biological systems uses deterministic models only and thus implicitly makes the assumption that Eq. (7) holds (see, e.g., the contributions to the 1982 symposium on nonlinearity in brain function edited by Garfinkel and Walter, 1983, for typical examples). To neglect fluctuations and assume Eq. (7) throughout is dangerous, however, because (a) the relation Eq. (7) breaks down at critical points; (b) fluctuations are an important feature of bifurcation phenomena; and (c) fluctuations are essential in bringing about transitions. Before examining the first and third points in some detail, let us add as an aside that the analysis of fluctuations allows one (in cases where Eq. [7] is or is not valid) to test explicitly the consistency of dynamic modeling as well as certain nontrivial theoretical predictions. The analysis of fluctuations is thus crucial to employing dynamical language in a scientific way, i.e., one in which constructs are operationally defined and open to experimental test.

We have seen how, when a transition is approached, local relaxation time increases while global relaxation time decreases (e.g., figure 1.8). At the critical point, however, both are of the same order as the observed time and one can see the transition. Thus, at the transition point, the time scales relation Eq. (7) is violated and an additional time scale assumes importance, namely the *time scale of parameter change*, τ_p. This reflects the fact that in all biological systems, the control parameter that brings about the instability is itself changed in time. The relation of the time scale of parameter change to the other system times plays a decisive role in predicting the nature of the phase transition. If, for example,

$$(8) \quad \tau_{rel} \ll \tau_p \ll \tau_{equ}$$

then the system changes state only as the old state actually becomes unstable, as was assumed in figure 1.8. The features of critical slowing down and critical fluctuations discussed in connection with figure 1.8 are predicted, as well as jumps and hysteresis (among other features) .

If, on the other hand,

$$(9) \quad \tau_{rel} \ll \tau_{equ} \ll \tau_p$$

then the system, with overwhelming probability, always seeks out the lowest potential minimum. It therefore switches state before the old state actually becomes unstable. [Note: In catastrophe theory, these two different transition behaviors are sometimes referred to as conventions, although they can, of course, be derived from the observationally accessible relations Eq. (8) and Eq. (9) (see, e.g., Gilmore, 1981). Failure to treat fluctuations renders catastrophe theory incomplete in this respect].

Finally, let us clarify the role of fluctuations per se, in effecting transitions. In so-called symmetry breaking transitions (in which a minimum turns into a maximum, with two symmetric new minima emerging), stochastic forces are obviously necessary if the system is to change state at all. Without such forces, the system may well stay in its now unstable state (the new maximum of V) "unaware," as it were, of its surroundings (cf. figure 1.10). Aside from such a fundamental role, fluctuations also determine the speed at which a transition takes place. For example, it is possible to predict theoretically how long the switching behavior will actually take (the *mean switching time*, cf. Schöner et al., 1986). A related concept is that of *mean first passage time*, i.e., the length of time on average, before the system first changes state when the parameters are fixed. Again, detailed comparisons of theory (e.g., Schöner et al., 1986) and experimental observations (e.g., Kelso and Scholz, 1985; Kelso et al., 1987; Scholz, Kelso, and Schöner, 1987) have been carried out (see also Schöner and Kelso, 1988b; Kelso, Scholz, and Schöner, 1988).

Bifurcations

Bifurcations come in various forms and guises. For example, as parameters vary, *pitchfork* and *saddle-node* bifurcations may take place. We illustrate both bifurcations next .

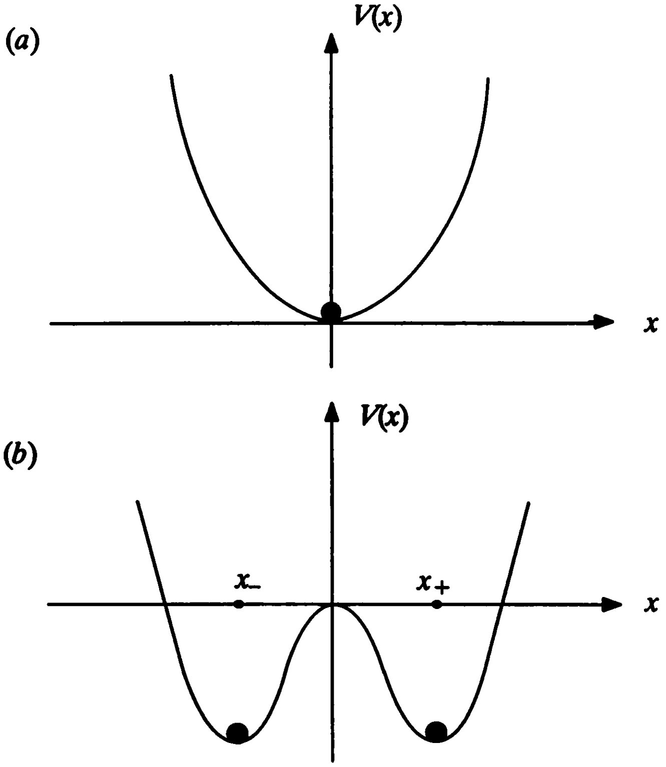

Figure 1.10
The potential $V(x) = ax^2 + bx^4$. (a) $b > 0$ and $a > 0$; (b) $b > 0$ and $a < 0$.

Pitchfork Bifurcation A simple nontrivial potential exhibiting a pitchfork bifurcation is

$$V(x) = ax^2 + bx^4 \tag{10}$$

where a and b are control parameters and $V(x)$ possesses a *reflection symmetry* (i.e., the system is invariant under the transformation $x \to -x$). Let $b > 0$, then for $a > 0$, the origin $x = 0$ is a minimum and the only fixed point attractor (figure 1.10a). For $a < 0$, however, $x = 0$ becomes a local maximum and two new minima, $x_+ = \sqrt{-a/b}$ and $x_- = -x_+ = -\sqrt{-a/b}$, come into existence (figure 1.10b). This qualitative change is called a pitchfork bifurcation in which $a = a_c = 0$ is the critical point. For $b < 0$, a pitchfork bifurcation with a flipped potential proceeds from $a < 0$ to $a > 0$. System dynamics for both $b > 0$ and $b < 0$ are represented collectively in figure 1.11 where the entire parameter plane (a, b) is partitioned into four different regions according to the shape of the potential. The diagrams shown in figure 1.11 are called *phase diagrams* which establish a one-to-one correspondence between the system dynamics and regions in the parameter plane. As a result, we can predict the behavior and the change of behavior in the system as parameters vary in the plane. Along the arrow shown in figure 1.11 we obtain the *bifurcation diagram* (figure 1.12), in which solid lines indicate stable fixed points and dashed lines unstable fixed points. Note that the appearance of the bifurcation diagram in figure 1.12 resembles that of a pitchfork.

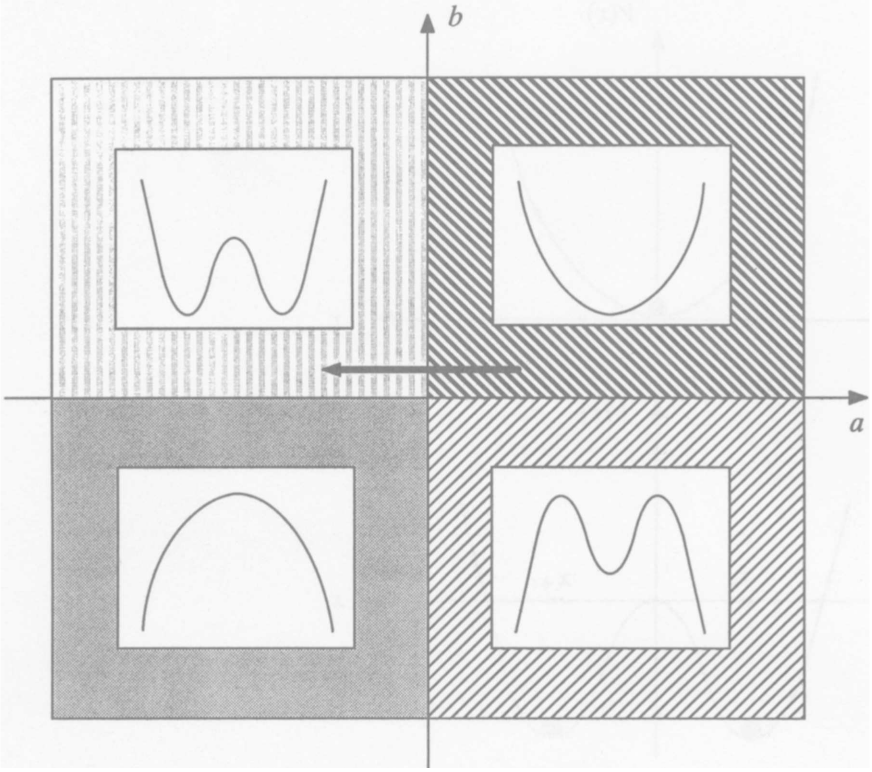

Figure 1.11
Phase diagram for the potential $V(x) = ax^2 + bx^4$ with parameters a and b. The different regions in the parameter plane (a, b) correspond to regimes with different forms of the potential, indicated schematically. The *arrow* corresponds to a path in parameter space (see text).

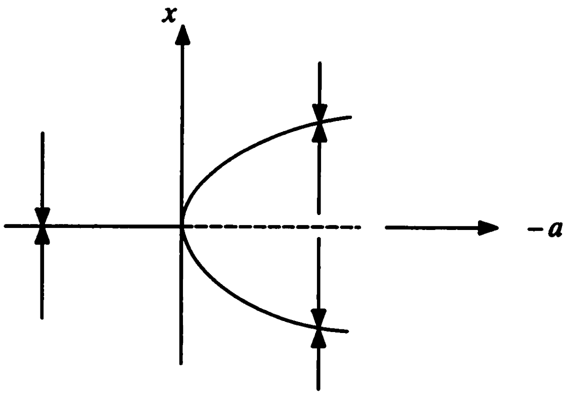

Figure 1.12
Bifurcation diagram along the *arrow* in figure 1.11.

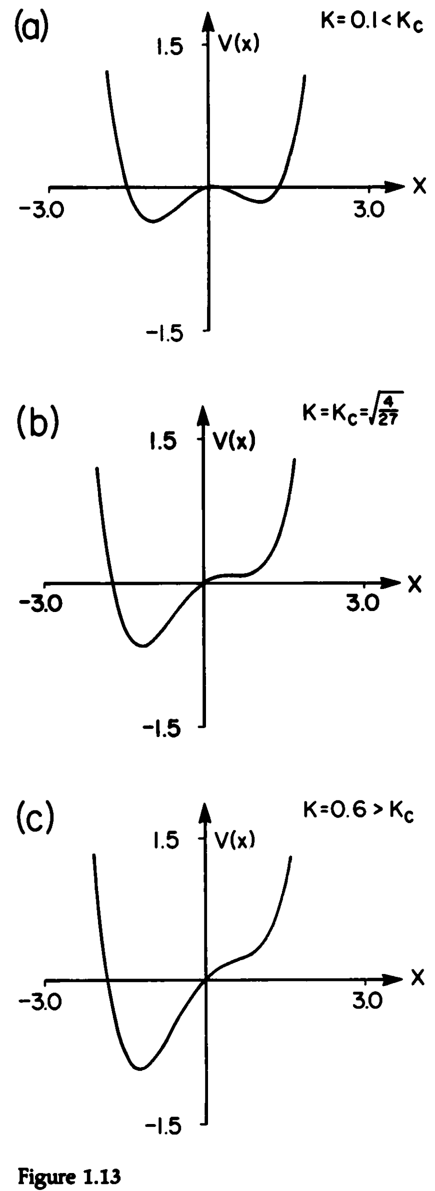

Figure 1.13
Potential landscape defined by Eq. (11) for three values of *K*.

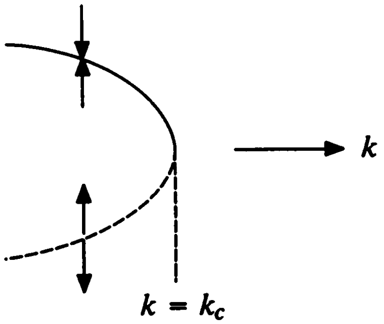

Figure 1.14
Schematic bifurcation diagram for a saddle-node bifurcation.

Saddle-Node Bifurcation and Hysteresis The terms *saddle* and *node* have their origin in higher dimensional systems. In the present situation, a saddle simply refers to a repeller and a node refers to an attractor. Unlike pitchfork bifurcations, saddle-node bifurcations occur in more generic situations where the presence of local reflection symmetry is not required. This asymmetry is easily accommodated by adding a linear term to the potential Eq. (10), i.e.,

$$(11) \quad V(x) = kx + ax^2 + bx^4$$

where k may be considered as the parameter specifying the degree of asymmetry. If we fix $a = -1/2$ and $b = 1/4$ and consider the system behavior as a function of increasing k, then the following set of events take place. (1) When $k > 0$ is very small, the potential landscape becomes slightly tilted but otherwise remains unchanged in terms of the composition of attractors and repellers (figure 1.13a). (2) The steady-state solutions drift in the phase space as k increases from 0. (3) At $k = k_c = \sqrt{4/27}$, an attractor and a repeller coalesce (figure 1.13b). (4) For $k > k_c$, the coalescing solutions cease to exist and only one fixed-point attractor remains in the system (figure 1.13c). Steps (2), (3), and (4) constitute the phenomenology of a saddle-node bifurcation and $k = k_c = \sqrt{4/27}$ is the critical point. figure 1.14 shows the schematic bifurcation diagram. If we reverse the direction of k, then a reverse sequence of events takes place.

Now let us examine the *hysteresis effect*. Specifically, we consider the system dynamics for both increasing and decreasing k. Figure 1.15 schematically illustrates the collective states of the system, where the directions of parameter variation are indicated by the arrows. A striking feature revealed by the figure is that there exists an overlapping region, $-k_c < k < k_c$, in which, depending on the directions of k, the system can rest in either one of two possible states. At $k = k_c$ and $k = -k_c$, the system switches to a different state signifying the end of the coexistence of two distinct attractors.

From an empirical point of view, the coexistence of multiple attractors may be regarded as evidence of nonlinearity, and it is manifested by the hysteresis effect. In the quest for a better understanding of biological dynamics, the role of hysteresis can hardly be exaggerated. Finally, we note that there is only one further bifurcation that can be observed in one-dimensional ODEs, namely the transcritical bifurcation in which two fixed point solutions exchange stability (cf. Guckenheimer and Holmes,

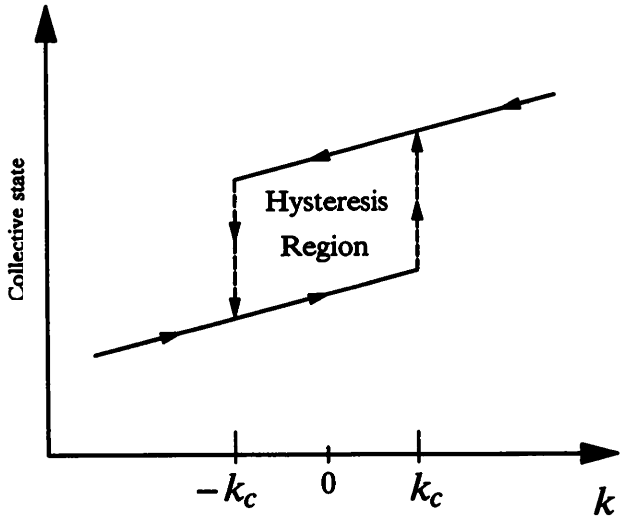

Figure 1.15
Schematic illustration of hysteresis.

1983, p. 145). To accommodate more sophisticated biological dynamics we must look beyond one-dimensional phase space.

Hopf Bifurcations in Self-excitatory Systems A self-excitatory system is one in which rhythmic motions can be generated spontaneously as a parameter passes a certain critical value. Mathematical mechanisms underlying such transitions are provided by Hopf bifurcations (see Marsden and McCracken, 1976, for a comprehensive review of Hopf bifurcations and their applications).

Supercritical Hopf bifurcation Consider the following two-dimensional ODE in polar coordinates

(12a) $\dot{r} = br(a - r^2)$

(12b) $\dot{\theta} = 2\pi f$

where a and $b > 0$ are parameters and f is the frequency of revolution in the θ direction. The relation between the Cartesian coordinates x and y and polar coordinates τ and θ can be expressed as (figure 1.16)

(13a) $x = r\cos\theta$

(13b) $y = r\sin\theta$.

For $a \leq 0$, the origin $r = 0$ is a stable fixed point attracting all initial conditions in the plane. Trajectories starting from any nonzero initial conditions spiral toward the origin as shown in figure 1.17a. (The origin $r = 0$ is sometimes called a *stable focus.*) Near the origin the relaxation dynamics obeys

(14) $r(t) = r(0)e^{-t/\tau_{rel}}$

where $\tau_{rel} = -1/ab$ is the relaxation time ($a \neq 0$). For $a > 0$, the origin loses stability and a limit cycle attractor appears at $r = \sqrt{a}$ (figure 1.17b). This phenomenon is called

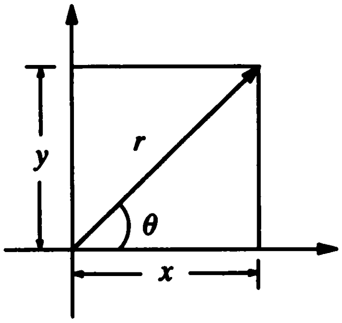

Figure 1.16
The relationship between the Cartesian coordinates x, y, and polar coordinates r, θ.

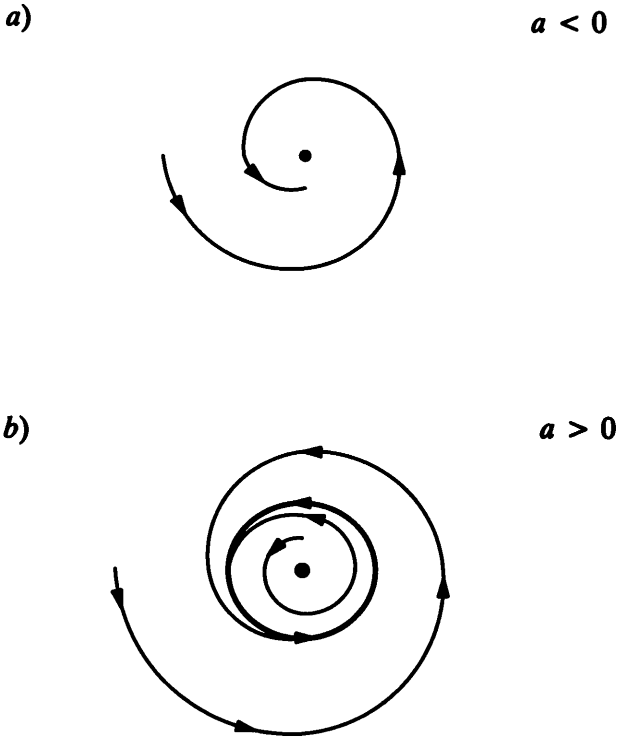

Figure 1.17
a) Fixed point attractor at the origin. *b*) Limit cycle attractor at $r = \sqrt{a}$ [cf. Eq. (12)].

a *supercritical Hopf bifurcation*, or *soft excitation*. The term *soft excitation* refers to the fact that the limit-cycle attractor emerges gradually from the origin. Initial conditions inside and outside the circle, $r = \sqrt{a}$, spiral toward the circle. Trajectories on the circle execute periodic (rhythmic) oscillations of period $T = 1/f$. The local relaxation dynamics toward the limit cycle is determined by

$$(15) \quad \delta r(t) = \delta r(0)e^{-t/\tau_{rel}}$$

where $\delta r(t) = r(t) - \sqrt{a}$ and $\delta r(0) = r(0) - \sqrt{a}$ are both small quantities and $\tau_{rel} = 1/(2ab)$ is the relaxation time.

Subcritical Hopf bifurcation A different scenario for generating rhythmic oscillations occurs in the following system:

$$(16a) \quad \dot{r} = br(a + 2r^2 - r^4)$$

$$(16b) \quad \dot{\theta} = 2\pi f.$$

Figure 1.18 shows the phase portraits for three different situations. For $a < -1$, $r = 0$ is a fixed point attractor attracting all the initial conditions in the plane (figure 1.18a). For $a > -1$, a stable limit cycle appears at $r = [1 + (1 + a]^{1/2})^{1/2}$, and for $-1 < a < 0$, an unstable limit cycle also exists at $r = [1 - (1 + a)^{1/2}]^{1/2}$ (figure 1.18b). At $a = 0$, the origin becomes unstable by absorbing the unstable limit cycle, and for $a = 0$, the system exhibits finite amplitude oscillations (figure 1.18c). The bifurcation of the origin is called a *subcritical Hopf bifurcation*. From a global perspective we have a *hard excitation* transition to oscillation at $a = 0$. The term *hard excitation* refers to the fact that oscillations appear at $a = 0$ with finite amplitude. As a is decreased from above 0, the finite amplitude oscillations persist until $a = -1$. Below $a = -1$, the oscillation suddenly disappears. Thus for $-1 < a < 0$ there exist two stable attractors, implying that the hysteresis effect will be observed if the parameter is systematically increased and then decreased.

Hopf bifurcations are important mechanisms for living systems to self-generate rhythmic oscillations from resting steady states. Interestingly, such self-generated rhythms can be turned on and off by varying a single parameter.

Synchronization and Relative Phase Dynamics

Synchronization and entrainment are commonly observed phenomena (e.g., van der Pol, 1922; Winfree, 1980; Kuramoto, 1984; Ermentrout and Rinzel, 1984; Kopell, 1988). In this primer we are particularly interested in their occurrence in nonlinear *coupled* oscillators. In neurobiology, groups of interacting neurons may be considered as coupled oscillators. One possible mechanism involves mutually inhibitory coupling with postsynaptic rebound, which may lead to sustained periodic oscillations (Glass and Mackey, 1988). Limit cycle oscillations arise also in populations of neurons that have excitatory and inhibitory coupling (e.g., Wilson and Cowan, 1973). Animal activities such as walking and running require individual limbs to execute rhythmic motions. If we use coupled nonlinear oscillators to model the coordinative limb dynamics, then the parameters reflecting the coupling strength and the frequency (such as the pace of oscillation) stipulate the formation of different patterns of coordination. Furthermore, smooth change in the parameters may induce transitions (bifurcations) among the coordination patterns. For example, a horse may spontaneously switch

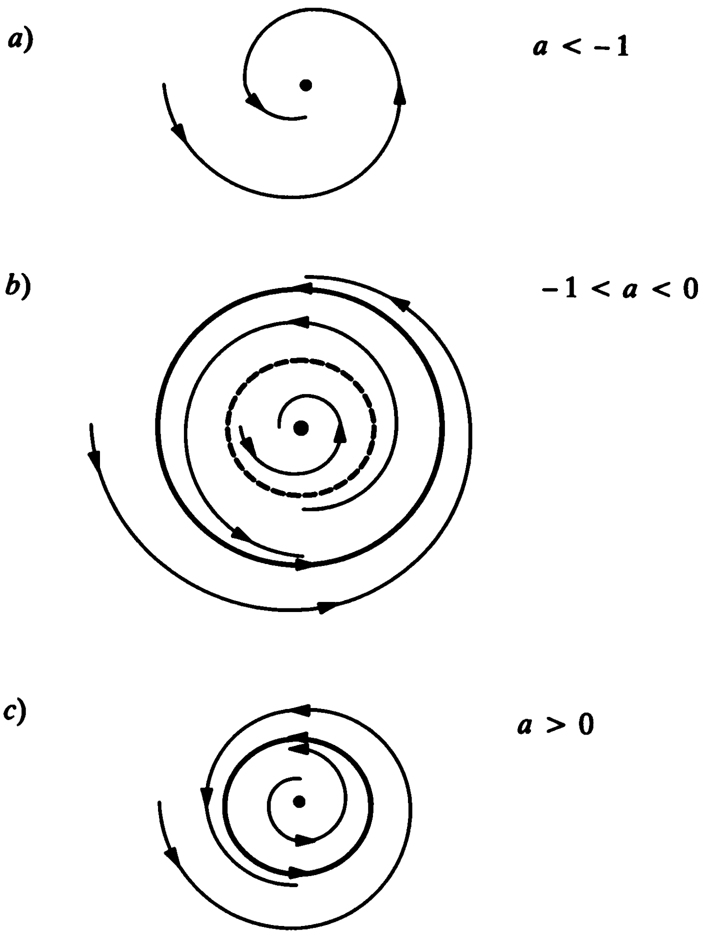

Figure 1.18
Phase portraits of Eq. (16) for three different values of a.

from walking to trotting as the speed of free running passes a certain threshold (for theory, see Schöner, Jiang, and Kelso, 1990; for experiments see Kelso and Jeka, 1992).

An important aspect to note in the above examples is that all the participating oscillators evolve with a single frequency. This situation is usually referred to as 1:1 frequency *synchronization* or *mode-locking* (these two terms together with *entrainment* are used interchangeably here). Dynamic patterns are now defined by the relative phases among the oscillators. A typically observed phenomenon is that the relative phases converge asymptotically on certain fixed relationships (*phase-locking*) which appear as attractors in the space of relative phases. We illustrate this with a simple idealized example. Let two oscillators be synchronized at a common frequency ω with sinusoidal trajectories

$$(17a) \quad x_1 = A \sin(\omega t + \phi_1)$$

$$(17b) \quad x_2 = B \sin(\omega t + \phi_2).$$

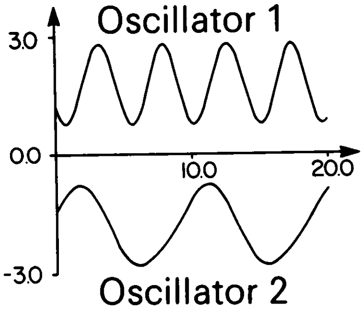

Figure 1.19
Oscillator 1 (*above*) and oscillator 2 (*below*) exhibit a 2:1 frequency synchronization.

Under suitable conditions the relative phase $\phi = \phi_2 - \phi_1$ may be regarded as a collective variable obeying the following equation of motion:

$$(18)\quad \dot{\phi} = f(\phi) = -dV(\phi)/d\phi.$$

Different attractors of Eq. (18) then give rise to different phase-locked dynamic patterns. Switching among these patterns can be analyzed using the methods developed in the section entitled Bifurcations. Thus, with the aid of a collective variable such as relative phase, the higher dimensional problem of coupled nonlinear oscillators reduces to the study of a one-dimensional ODE.

The study of coordination at both neural and behavioral levels demonstrates the value of relative phase dynamics. In the case of human bimanual coordination, the relative phase between the underlying oscillatory components has been rigorously shown to be a collective variable in the 1:1 frequency-synchronized situation (Haken, Kelso, and Bunz, 1985). For more complex forms of coordination, symmetry arguments and group theory are employed to study the classification of various coordination patterns and transitions among these patterns (Schöner, Jiang, and Kelso, 1990; for an amusing and insightful treatment, see Stewart, 1991).

Much richer dynamics occurs in multifrequency synchronization paradigms. Consider the case of two initially uncoupled self-excitatory oscillators. The difference between their respective natural frequencies, $\Delta\omega = \omega_1 - \omega_2$, can be viewed as a control parameter. If the coupling is weak and $\Delta\omega$ is very small, the oscillators are expected to be 1:1 entrained with each other. As $\Delta\omega$ increases, transition to desynchronization takes place at a critical point. In the desynchronization region, the system typically exhibits quasi-periodic dynamics. That is, the amplitude and the phase of the oscillation vary slowly and the Fourier spectra for the time series display two or more incommensurate fundamental frequencies. If ω_1 is close to $2\omega_2$, multifrequency synchronization at 2:1 may occur, in which the time interval for one oscillation in oscillator 2 is the same as that for two oscillations in oscillator 1 (figure 1.19). If the coordinates of oscillator 1 are $(x, \dot{x})$ and those of oscillator 2 are $(y, \dot{y})$, then the plots x vs. y are called *Lissajous figures*. For 1:1 frequency synchronization, the Lissajous figure is typically a circle (figure 1.20a), whereas for 2:1 frequency synchronization, the corresponding Lissajous figure can exhibit a figure 8 (figure 1.20b).

An important mathematical example displaying multifrequency mode-locking is the periodically forced van der Pol oscillator

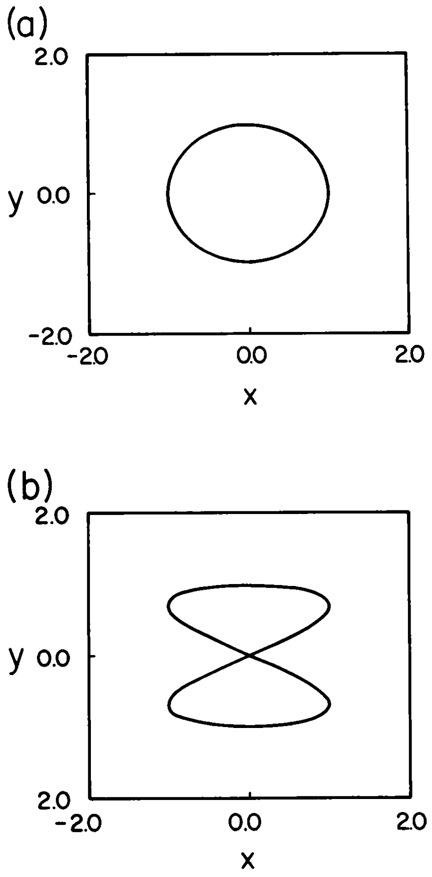

Figure 1.20
Lissajous figures for (*a*) 1 : 1 and (*b*) 2 : 1 frequency synchronization.

$$(19) \quad \ddot{x} - \varepsilon(1 - x^2)\dot{x} + x = B\cos(\nu t)$$

The term $B\cos(\nu t)$ in this case may be regarded as the output of another oscillator whose dynamics is not affected by x. If $B = 0$, the two oscillators are totally decoupled, and the van der Pol oscillator possesses a unique limit cycle attractor whose frequency is denoted by ω_0. For different values of ν and B, the attractors of Eq. (19) and the sinusoidal driving may be mode-locked at different frequency ratios as shown in figure 1.21. Between the mode-locking regions, one may find parameter values for which the dynamics of Eq. (19) is quasi-periodic.

Of course, coupled nonlinear oscillators also give rise to spatial and spatiotemporal structures. A good example is the Belousev-Zhabotinski (B-Z) reaction which consists of a recipe of multiple reactants that, instead of relaxing to equilibrium, exhibit rhythmic alterations in the form of wave patterns. The latter correspond to gradients of phase (for an excellent discussion and analysis, see Murray, 1989; for beautiful illustrations of phase gradients and other rhythmically generated structures, see Winfree, 1987). The B-Z reaction shares many common features with excitable media, including the nerve membrane. Traveling waves, e.g., of chemical concentration, appear to

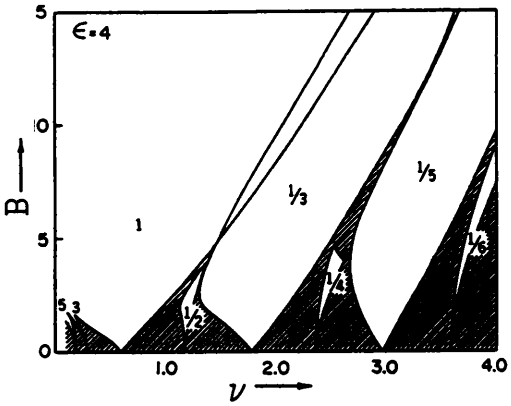

Figure 1.21
Phase diagram for the van der Pol oscillator [Eq. (19)]. [Reproduced with permission from Hayashi (1964).]

play a key role in developmental processes and reaction-diffusion systems in general. A famous example is the so-called Turing instability. Turing (1952) showed that spatially heterogeneous patterns of chemical or morphogen concentration can arise in an otherwise homogeneous system owing to reaction and diffusion. A local perturbation to one of the (slowly diffusing) catalytic agents produces standing waves. Once again, low level noise from the surroundings or internally generated molecular fluctuations are sufficient to "trigger" the development of pattern.[8] Recent experiments on the chlorite–iodide–malonic acid–starch reaction in a gel reactor (Castets, Dulos, Boissonade, and De Kepper, 1990) provide convincing evidence of the stable patterns predicted by Turing.

Circle Maps and Intermittency

It is important to note that in the multifrequency regimes, Eq. (18) is no longer an adequate description for the relative phase dynamics. Alternative methods use discrete maps.

Consider the phase space $(x, \dot{x})$ of a nonlinear oscillator and the associated polar coordinates (r, θ). If the system is periodically driven, then discrete maps for the variable (r, θ) may be derived by strobing the system at time $t_n = nT$, where $T = 2\pi/\nu$ is the driving period (see General Definitions above). Specifically, let the point on a trajectory at time t_n be (r_n, θ_n) and the point on the same trajectory at time t_{n+1} be (r_{n+1}, θ_{n+1}), then the following relations hold:

$$(20a) \quad r_{n+1} = R(r_n, \theta_n)$$

$$(20b) \quad \theta_{n+1} = \Theta(r_n, \theta_n).$$

This two-dimensional map of (r, θ) may be further simplified if the dissipation in the system is very strong. In that case, the dependence of Θ on r may be neglected and Eq. (20b) reduces to a one-dimensional map on a circle (θ is an angular variable)

$$(21) \quad \theta_{n+1} = f(\theta_n) = \theta_n + \Omega + g(\theta_n).$$

The issue concerning the validity of reducing Eq. (20) to Eq. (21) has been addressed in the literature. The results show that the mode-locking properties of coupled oscillators in certain regions of the parameter space are essentially encoded in the circle maps (Glazier and Libchaber, 1988, and references therein). The advantage of studying circle maps is that they are low-dimensional and hence permit more detailed analysis.

A much-studied example of circle maps takes the following concrete form:

$$(22)\quad \theta_{n+1} = f(\theta_n) = \theta_n + \Omega - \frac{K}{2\pi}\sin(2\pi\theta_n)$$

where K represents the strength of nonlinearity, Ω is the ratio between the natural frequencies of the uncoupled oscillators, i.e., $\Omega = \omega_0/v$. The θ-circle in Eq. (22) is assumed to be of unit length (instead of 2π). We henceforth refer to Eq. (22) as the circle map.

(A different form of circle maps is studied in the companion paper where the map is defined as

$$(23)\quad \theta_{n+1} = \theta_n + \Omega - \frac{K}{2\pi}(1 + A\cos 2\pi\theta_n)\sin 2\pi\theta_n$$

Equation (23) is called the "phase attractive" circle map which has been used to model the properties of multifrequency coordination of behavior [DeGuzman and Kelso, 1991; Kelso and DeGuzman, 1988].)

To study the circle map Eq. (22) we need to introduce a few concepts. The *winding number* W for a trajectory $\{\theta_n\}$ of Eq. (22) is defined as

$$(24)\quad W \equiv \lim_{n\to\infty} \frac{\theta_n - \theta_0}{n}$$

which is, in fact, the measured frequency ratio of the two coupled oscillators. Specifically, W as a rational number implies that the underlying oscillators are mode-locked or synchronized. If W is irrational, then the oscillators are desynchronized. More precisely, they exhibit quasiperiodicity or chaos. For $K \leq 1$, the circle map is characterized by a unique winding number W (Devaney, 1989). For $K > 1$, however, W is not always well defined. In particular, trajectories starting from different initial conditions may yield different winding numbers. In this primer we focus mainly on the region $K < 1$. The region $K > 1$ is explored in Glass, Guevara, Shrier, and Perez (1983) and Zeng and Glass (1989).

The *Lyapunov exponent* Λ is defined as

$$(25)\quad \Lambda = \lim_{k\to\infty} \frac{1}{k}\sum_{n=1}^{k} \ln|f'(\theta_n)|$$

which measures the rate of exponential divergence or convergence of two trajectories with slightly different initial conditions (figure 1.22), thus providing a criterion for delineating different types of attractors in the system. In particular, $\Lambda < 0$ implies that the map has a periodic attractor and, consequently, the underlying coupled oscillators are in a mode-locked state. $\Lambda = 0$ means that the dynamics is quasi-periodic and the attractor occupies the entire unit circle. $\Lambda > 0$ depicts a situation in which two nearby trajectories exponentially diverge from each other regardless of how closely situated are the respective initial conditions (see figure 1.22). In this case, the system is said to exhibit *sensitive dependence on initial conditions*, a fact often viewed as the hallmark of chaotic dynamics.

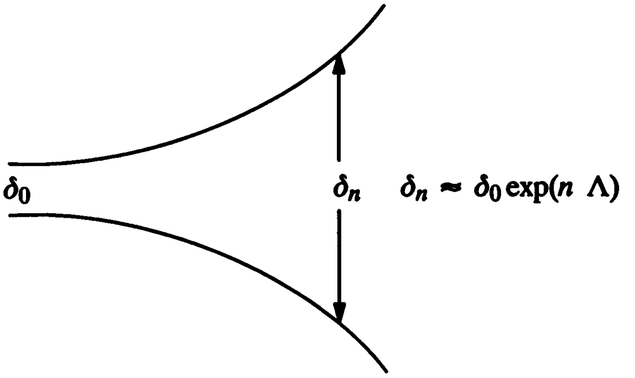

Figure 1.22
Schematic illustration of the Lyapunov exponent Λ. $\Lambda > 0$ for the case shown.

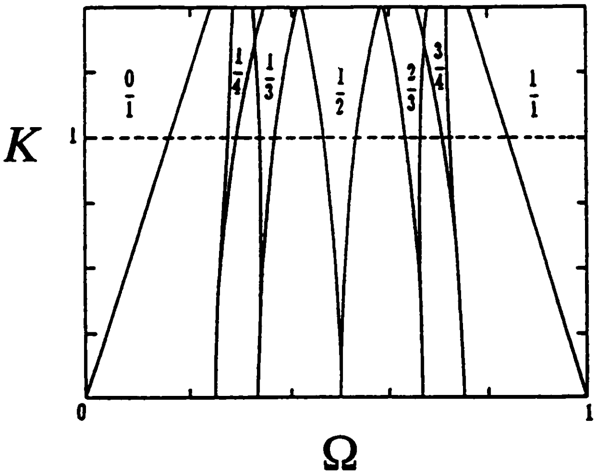

Figure 1.23
The $\Omega - K$ parameter plane for the circle map Eq. (22) (schematic). After Hao (1990).

Now let us examine the parameter plane of the circle map (figure 1.23). If $K = 0$ in Eq. (22), then $W = \Omega = \omega_0/v$, and the situation is simple. The map exhibits either periodic (synchronized) or quasi-periodic motions, depending on whether Ω is rational or irrational. Finite K introduces nonlinearity in the system and causes a given periodic orbit to persist for a range of Ω values. The result is the Arnold tongue structure of the $\Omega - K$ plane shown in figure 1.23, which is the phase diagram for the circle map. Inside each Arnold tongue there is a unique attracting periodic trajectory and its winding number satisfies the mode-locking condition: $W = m/n$ with m and n being integers. The orbit of the periodic attractor is composed of n distinct θ values: $\theta_1, \theta_2, \ldots, \theta_n$, such that $\theta_2 = f(\theta_1)$, $\theta_3 = f(\theta_2)$, $\ldots$, $\theta_n = f(\theta_{n-1})$, and $\theta_{n+1} - \theta_1 = m$.[9] Between the tongues the winding number W is irrational and the dynamics is quasi-periodic ($\Lambda = 0$). As K increases, the Arnold tongues widen and eventually touch each other on the critical curve $K = 1$. Above this critical curve, the tongues overlap and the system can display chaos.

It is interesting to note that the phase diagram of the circle map (see figure 1.23) and that of the van der Pol oscillator (see figure 1.21) exhibit remarkable similarity. In particular, the order of occurrence of various mode-locking tongues in figure 1.21 surveyed from right to left is the same as that in figure 1.23 surveyed from left to right. The reversal of order in the two diagrams is caused by the reciprocal relationship between Ω and ν, i.e., $\Omega \sim 1/\nu$. Mathematically, this order of occurrence of the mode-locking tongues is given by the so-called *Farey sequences*. An n-Farey sequence is the increasing succession of rational numbers p/q with $q \leq n$. An example for $n = 4$ is

$$0/1,\ 1/4,\ 1/3,\ 1/2,\ 2/3,\ 3/4,\ 1/1$$

(see figure 1.23). As shown in the works of Herman (see e.g., Bergé, Pomeav, and Vidal, 1984), the universality of frequency locking derives from the structural stability of the rational frequency ratios. *This accounts for similar behavior across very different systems* (e.g., clock mechanisms, moon-earth phase locking, walking and breathing in humans, externally stimulated nerve membranes, frequency locking in mammalian visual cortex, etc.).

Periodic attractors are created and destroyed in the circle map through saddle-node bifurcations (see above) which occur at the boundaries of the Arnold tongues. We show an example in figure 1.24 in which we vary the values of Ω near the boundary of the Arnold tongue with winding number $W = 0/1$ while keeping K as a constant. The boundary in this case is defined by

$$(26) \quad K = 2\pi\Omega$$

For $K = 0.6$, the saddle-node bifurcation occurs at $\Omega_c = 0.6/2\pi \approx 0.0955$. Figure 1.24a shows the function $f(\theta)$ intersecting the diagonal line at two points: θ^- and θ^+, where θ^- is a fixed point attractor and θ^+ is a fixed point repeller ($\Omega = \Omega_c - 0.03$ in figure 1.24a). Initial conditions other than $\theta = \theta^+$ converge to θ^- as $n \to \infty$. As Ω increases, θ^- and θ^+ approach each other and coalesce when $\Omega = \Omega_c$ (figure 1.24b). For $\Omega = \Omega_c + 0.01$ beyond the boundary of the Arnold tongue, θ^- and θ^+ cease to exist (figure 1.24c), and the system exhibits either periodic orbits of higher period or quasi-periodic orbits, depending on the exact location of Ω. If Ω is decreased, then the reverse sequence of events is observed.

The narrow channel between the function $f(\theta)$ and the diagonal line in figure 1.24c induces interesting dynamical behavior called *type I intersmittency* (Pomeau and Manneville, 1980). The phenomenology is the following. Inside the channel, iterates of the map move very slowly (see figure 1.24c), giving rise to the impression that the fixed point attractor was already in place (from the point of view of decreasing Ω). After exiting the channel, the trajectory takes large strides for a number of times before reentering the channel. Figure 1.25 shows the time series θ vs. n for a typical initial condition ($\Omega = \Omega_c + 0.0001$ in this case). During the time course the trajectory in figure 1.25 spends most of the time near the narrow channel, which is clearly shown in the bifurcation diagram (figure 1.26) where the Ω values are plotted in the horizontal direction and in the vertical direction we plot 500 iterates of the map for each value of Ω. The dark area in the figure corresponds to the θ interval most frequently visited by the trajectory and this interval is precisely where the channel is situated.

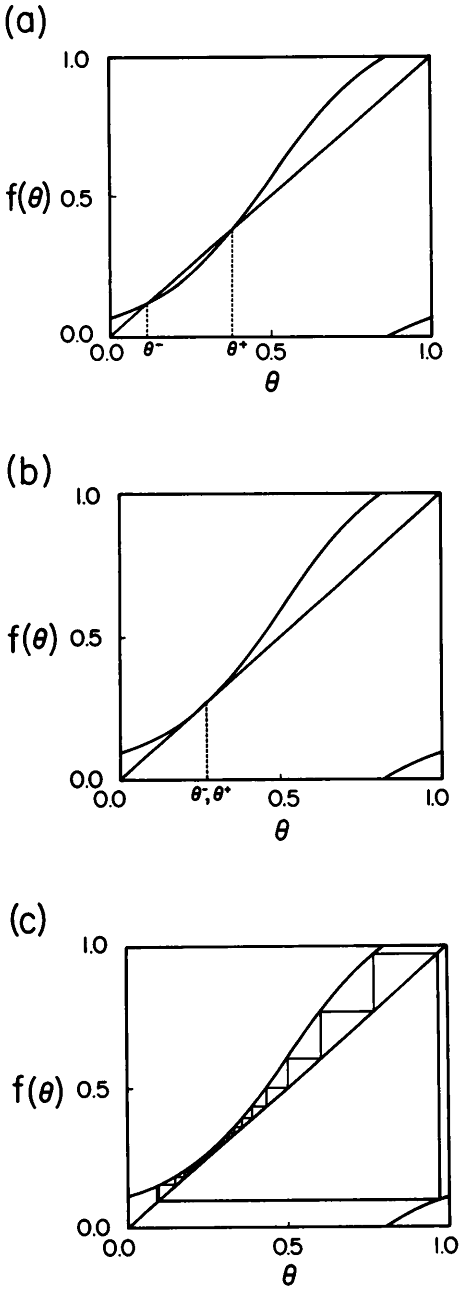

Figure 1.24
Function $f(\theta)$ for three values of Ω. (*a*) $\Omega = \Omega_c - 0.03$; (*b*) $\Omega = \Omega_c$; (*c*) $\Omega = \Omega_c + 0.01$ (see text).

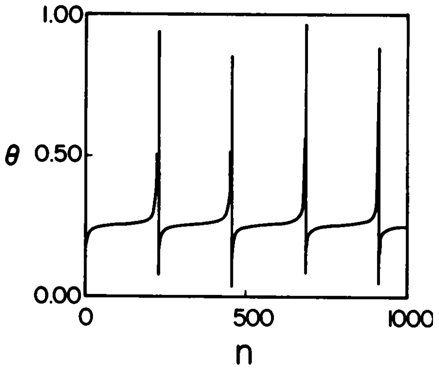

Figure 1.25
The time series for an intermittent trajectory ($\Lambda = 0$).

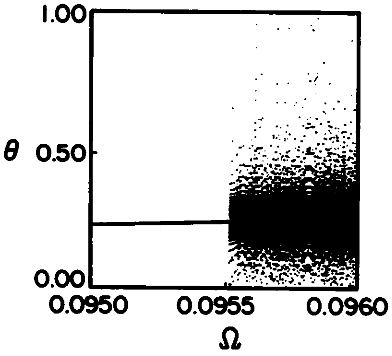

Figure 1.26
Bifurcation diagram for the circle map. The range of Ω straddles the boundary of the Arnold tongue (0/1). ($K = 0.6$).

The intermittent dynamics seen in figure 1.25 is quasi-periodic with $\Lambda = 0$. An often cited example of chaotic intermittency happens in the following one-dimensional logistic map

$$(27)\quad x_{n+1} = h(x_n) = ax_n(1 - x_n)$$

where x may be considered as a variable proportional to the population of a certain type of insect and a is the control parameter representing the environment. For $0 < a < 4$, Eq. (27) maps the unit interval [0, 1] into itself.

At $a = a_c = 1 + \sqrt{8}$, the logistic map undergoes a saddle-node bifurcation in which a periodic attractor and a periodic repeller, both of period 3, are created. figure 1.27 shows the function $h^3(x) = h(h[h(x)])$ for three values of a: $a = 3.82 < a_c$, $a = a_c \approx 3.8282$ and $a = 3.84 > a_c$. Each of the three narrow channels in figure 1.27a resembles that in figure 1.24c. But the attractor corresponding to figure 1.27a has a positive Lyapunov exponent, i.e., $\Lambda > 0$. As a result, the iterates of the map between two successive passages through the narrow channels are erratic and unpredictable. Figure 1.28 shows the time series x vs. n of a typical trajectory for $a = 3.82819 < a_c$. Let us define the reinjection time t to be the number of iterates between exiting one of the

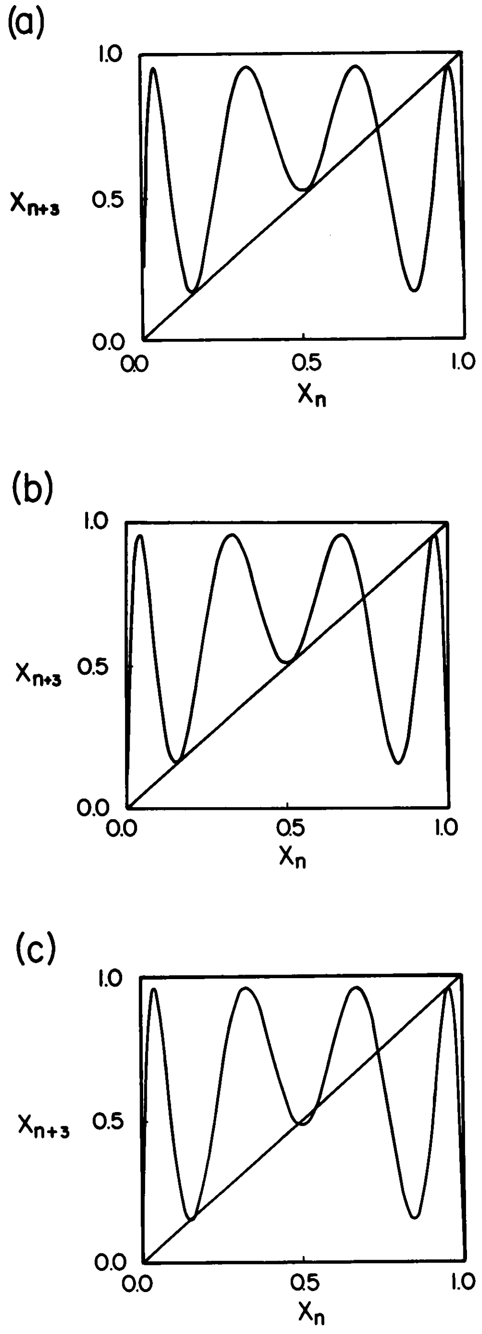

Figure 1.27
Saddle-node bifurcations in the logistic map. (*a*) $\alpha < \alpha_c$. (*b*) $\alpha = \alpha_c$, (*a*) $\alpha > \alpha_c$.

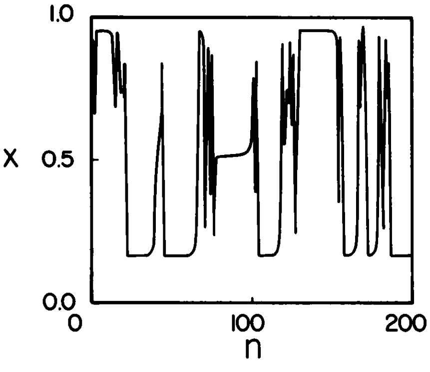

Figure 1.28
The time series for an intermittent trajectory ($\Lambda > 0$).

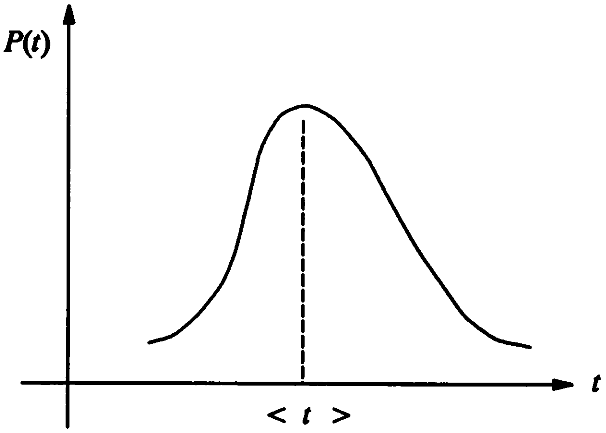

Figure 1.29
Schematic illustration of the probability distribution of the reinjection time t.

channels and reentering another (cf. figure 1.27a). Then t can be treated as a stochastic variable whose probability distribution is shown schematically in figure 1.29. A quantitative measure of intermittency is the average reinjection time $\langle t \rangle$ which is found to scale with the parameter a as

$$(28) \quad \langle t \rangle \sim \frac{1}{|a - a_c|^{\alpha}}$$

where $\alpha = 1/2$.

Intermittency is observed in a variety of different natural systems ranging from turbulent fluids to chemical reactions (see Bergé et al., 1984, for examples). We have found indications of intermittent dynamics in sensorimotor (Kelso, DelColle, and Schöner, 1990) and multifrequency (Kelso, DeGuzman, and Holroyd, 1991a,b) coordination. The broader implications of intermittency, where the system is poised near a fixed point but not actually in it, are explored elsewhere (see also Kelso, 1991; Kelso and DeGuzman, 1988; Kelso et al., 1991a,b; Mandell, 1983).

Synopsis

In scientific modeling, a variety of different observations are often accounted for by a specific model. Here our considerations focus on very general principles that pertain to dynamic pattern formation and change on several different scales of observation. The main idea behind the present approach is to view pattern formation, on a given level of observation, in terms of coordination dynamics. Now we briefly summarize the essential, stripped-down aspects of these (abstract, level-independent) dynamics. Specific extensions are developed elsewhere (e.g. Kelso et al., 1991a,b).

1. Spatiotemporal patterns are characterized by low-dimensional collective variables or order parameters which define stable and reproducible relationships among the system's elements. What constitutes an element is based on a functional decomposition at a chosen level of description. Nonlinear interactions among the elements produce patterns.
2. As a first step, observable patterns are mapped onto attractors of the order parameter dynamics, using the strategy of phase transitions. Thus, the dynamics are dissipative.
3. The order parameter dynamics may give rise to pattern complexity, i.e., additional features not seen or understood before may appear. For example, partially ordered spatiotemporal patterns may correspond to the intermittent regime of the coordination dynamics (Kelso and DeGuzman, 1991, 1992; Kelso and Ding, 1992).
4. Biological boundary conditions act as parameters on the coordination dynamics. A parameter that moves the system through different patterns is called a *control parameter*, which may be quite unspecific to the resulting patterns. (On the other hand, specific parametric effects are also expected in biological systems, e.g., specific environmental or learning requirements. These are treated in mathematical detail elsewhere, however, e.g., in Schöner and Kelso, 1988c,d).
5. The spontaneous (self-organized) emergence of pattern arises through instability. Fluctuations are always probing the stability of patterned states in open systems and are conceptually crucial. Similarly, switching from one pattern to another is often connected to instability.
6. Competitive processes lead to pattern selection. For example, the relative values of parameters in Eq. (23) determine the patterns observed. Interestingly, one of the parameters (A) represents intrinsic constraints (e.g., attraction to certain "preferred" relative phases) and the other (K) represents external influences.

On a final, somewhat speculative note, we are reminded of recent work in evolution which suggests that it is the dismantling of intrinsic (genotypic) constraints (described by terms such as "internal balance," "genetic homeostasis") that effects speciation (Mayr, 1982). For example, rapid changes in mollusc sequence under the stress of an evaporating Lake Turkana produced a major "developmental instability," a breakup of genetic homeostasis. Accompanying these points of rapid taxa change was a significant elevation of phenotypic variance (Williamson, 1981). If Lake Turkana's drought is viewed (in dynamic language) as an environmental control parameter, and the "cohesion of the genotype" corresponds to the intrinsic, collective variable dynamics characterizing morphologically stable states, then speciation may be viewed as a self-organized pattern formation process.

Under appropriate time scales assumptions, the theory of nonequilibrium pattern formation predicts critical fluctuations near instabilities. It is tempting to interpret the enormous phenotypic variance preceding the emergence of new species as a striking confirmation of this prediction. In any case, it is hard to ignore the analogy between speciation and the present (elementary) concepts of dynamic pattern formation. This does not say, of course, that the conventional neo-Darwinian dogma in which new species (forms) arise by accumulating slight, successive variations in the genotype is wrong. But it does suggest that autonomous self-organization processes (the basic principles and language of which we present here) may play an important role.

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Notes

1. Two unlikely bedfellows shared this viewpoint. Witness Henri Poincaré (1905): "... the aim of science is not things themselves, as the dogmatists in their simplicity imagine, but the relations among things; outside these relations there is no reality knowable." And D'Arcy-Thompson (1917): "The *things* which we see in the cell are less important than the *actions* we recognize in the cell." This latter view was considered so outdated that it was omitted in J. T. Bonner's (1961) abridgment of Thompson's *On Growth and Form* (Harrison, 1988). A still broader viewpoint is that the classic dichotomy between structure and function may be one of appearance only. A unified treatment would treat structure and function on the same terms, viz., as dynamical processes separated only by the numerous time scales on which they live. Although a detailed mathematical description of such a unified view is beyond the Scope of this primer, elsewhere we have established an analogous linkage between the (relatively) slow time-scale dynamics of learning and the faster time scale of behavior itself (Schöner, Zanone, and Kelso, 1992; Zanone and Kelso, 1992).
2. For example, Kauffman (1990 p. 82) asks: "How a complex system of interacting genes *coordinating* one another's activities behaves and what must be supposed in order to obtain anything like plausible *coordinated* behavior" (*italics* ours). He then idealizes the activity of the element, the gene in this case, as an on/off binary device, and proceeds to some surprising conclusions regarding order formation (*sans* selection) in model genetic systems. We chose a particular experimental model system and level of description (Kelso, 1981; 1984) in order to pursue the possibility that principles of coordination lie at the level of dynamic patterns (or forms, cf. von Holst, 1939/1973; Goodwin, preprint). Once the laws at the pattern level are found, they can be derived as self-organized stable states of coupled nonlinear dynamics among the individual components (Haken, Kelso, and Bunz, 1985).
3. It is interesting to note that complex, biological systems containing very many *df* often appear to live (at least part of the time) in lower-dimensional spaces. Boundary conditions (e.g., functional context, environmental constraints, energetic requirements) appear to play the role of pinning the system onto a low-dimensional manifold without any slaving in the classic sense. Other examples are synchronization and entrainment in systems of nonlinear oscillators which can often be characterized in terms of phase coupling (see Synchronization and Relative Phase Dynamics below).
4. Sometimes it is said that point attractors are boring and nonbiological, but this in our opinion depends on what the point attractor refers to. Here the contest refers to fixed points of the collective variable dynamics which may capture the essential aspects of the phenomena under study. In other contexts,

whole patterns may be defined in terms of point attractors, as in artificial neural networks for pattern recognition and associative learning (for a recent review, see Haken, 1991).

5. Time scales arc generally defined with respect to time dependences governed asymptotically by exponential functions as indicated in Eq. (6). Exceptions arc the time scale of observation and the time scale of parameter change defined below.
6. Deterministic dynamics in the chaotic regime may show typical times that do not converge exponentially, but rather as stretched exponentials or powers of time with fractional exponents (Shlesinger, 1988; see also Mandell and Kelso, 1991). Regardless of the form convergence takes, τ_{rel} is still a key quantifiable property of any complex system.
7. The term is borrowed from the field of critical phenomena or second order equilibrium phase transitions (see, e.g., Ma, 1976). Note that here, in contrast to equilibrium systems, the growth of relaxation time is bounded by stochastic switching so that one deals with a strong increase but not a singularity of relaxation time.
8. Turing (1952) considered the case of a system just beginning to leave a homogeneous condition, hence the first appearance of pattern, as "the exception rather than the rule. Most of an organism, most of the time, is developing from one pattern into another, rather than from homogeneity into a pattern." (p. 72) The dynamics we outline here emphasizes the latter case, as do our experimental studies of order-order transitions. Interestingly, Schrödinger (1945) advocated an order-order transition principle as the essential distinction between living and nonliving systems. In the context of open, nonequilibrium systems this is no longer necessary.
9. Two points with integer difference in their coordinates appear as the same point on the circle of unit length. Conventionally, periodic orbits in the circle map are discussed in the sense of *modulo* 1 which means that we only consider the fractional part of θ. Under this convention, we may assert that $\theta_{n+1} = \theta_1$.

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