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Extending the Basic Picture: Breaking Away

I play with arrangements that lie on the brink of instability to achieve lyrical motions.

—George Rickey, sculptor

Coordination and other similar function words such as integration and orchestration do enormous scientific duty in the behavioral and brain sciences. The word “coordination” seems to hold the key to everything that is going on at nearly every level of description. Although coordination is a word that often carries the onus of explanation, in my opinion it is a word that demands explanation. It trips off the tongue so easily as a way to connect things that, because of the natural tendency to focus on the things themselves, the significance of the *coordinative relations* between things is lost. One is reminded again of the words of the French mathematician Henri Poincaré, the discoverer of what we now call chaos, that “the aim of science is not things themselves, as the dogmatists in their simplicity assume, but the relations among things; outside these relations there is no reality knowable.”¹ As a nonmathematician, I’d say we need both, mindful of the possibility that what is a thing at one level may be relations among (different) things at another.

The aim of this chapter is to build on and elaborate the basic picture of coordination that emerged from our hand movement experiments in chapter 2 and the various generalizations described in chapter 3. There we saw in an enormously complex living system (the human being) contraction of the dynamics to an evolution equation involving the relative phase alone. I have to admit, although I find it quite beautiful, the picture drawn in chapters 2 and 3 is a bit idealized. This may be a natural, even mandatory, step on the road to understanding.

To a large degree all scientific progress rests on idealizations. Physics uses nature’s simplest atom, hydrogen, to illustrate the power of quantum mechanics. Chemistry and biology have their idealizations, too. The unit of inheritance is a very large molecule, DNA, which takes the geometrical form of the famous double helix deduced by Crick and Watson. The genome itself is far more complicated and dynamic than the static geometrical structure of DNA might lead us to believe. But none of this minimizes the significance of the

hydrogen atom and DNA as means of revealing important physical and biological insights at their respective levels of description.

So too, when we come to the problem of understanding coordination in complex living things, our torus with a coordination dynamics running around inside is a very simple idealized structure. But not so simple that it lacks essential properties. Already we've seen the importance of concepts such as symmetry (in determining basic modes of coordination), multistability (the coexistence of several coordination modes for the same parameter value), hysteresis, switching between modes at critical points, transition pathways, and all those predicted phenomena associated with fluctuations and dynamic instabilities. They allowed us to arrive at a primitive nonlinear structure for coordinated behavior. Now it is time to expand it.

To take the next step, imagine the following situation. An adult is walking along the beach with a small child. The two are not physically coupled (though they might be if they held hands), and they are not necessarily biologically coupled (though they probably are). Let's say, rather, that they are informationally coupled. Perhaps they are talking to each other, or one is telling the other a story. To remain together (coordinated), either one or both must adjust their step frequency and/or stride length. Unlike experienced lovers and dancing couples, synchronization is difficult unless one or both spontaneously adjust to the circumstances. For example, to keep up, the child may sometimes skip a step or the adult slow down just so the two can remain together. This form of coordination is far more variable, plastic, and fluid than pure phase locking. Certainly, *tendencies* toward phase and frequency synchronization are still present, but sometimes the phase slips before it is reset again to some regular rhythm.

How can we go about understanding this less rigid, more flexible form of coordination? The brilliant German physiologist Erich von Holst (figure 4.1) coined the term *relative coordination* for this kind of behavior:

Relative coordination is a kind of neural cooperation that renders visible the operative forces of the central nervous system that would otherwise remain invisible.²

In relative coordination, an *attraction* to certain phase relations among coordinating components may exist (which von Holst called the magnet or M effect) but it is offset by differences between the components themselves: In other words, individual biological components possess intrinsic properties that tend to persist even when the components are coordinating with each other (von Holst called this the maintenance tendency). Thus, relative coordination was the outcome of a latent and never-ending struggle between maintenance and magnet effects.

Given this beautiful but somewhat qualitative description, I believe that the phenomena von Holst discovered are enormously important in at least two senses. First, in modern-day jargon, relative coordination falls under the heading of correlated neuronal activity, which is suspected of playing a highly



Figure 4.1 Eric von Holst (1908–1962) in a picture taken in 1958. Von Holst was one of the most original systems physiologists and was a friend of K. Lorenz and the physicist W. Heisenberg. (Reprinted with permission from MIT Press)

influential organizing role in functions such as perception, memory, and learning, as well as the development and plasticity of structural-functional linkages in the nervous system.³ Striking coordinative relations also exist within and among cardiovascular, respiratory, and vegetative functions.⁴ Second, and more important at present, is that relative coordination suggests that biological systems have access to other dynamical mechanisms (beyond bifurcations or phase transitions) for going in and out of coherent states.

I connect the phenomenon of relative coordination to a generic feature of dynamical systems called *intermittency*. The difference between intermittency and phase transitions is that the phase transition mechanism uses an active process (a parameter change or fluctuation) to switch the system from one stable state to another. The intermittency mechanism does not. Rather, the system is poised *near* critical points where it can spontaneously switch in and out. Strictly speaking, in the intermittent regime it no longer possesses any stable states at all.

In this chapter I will show how intermittency may be built into the elementary laws of coordination. A great advantage of living near but not in phase-locked states is that the system is (meta)stable and flexible *at the same time*. I'll explain what this means shortly. However, before we get too far ahead of ourselves, let me explain what relative coordination is in a bit more detail. Then I'll show, by way of a specific experimental example, how to model it.

There won't be much fancy mathematics here; only a way of looking at old phenomena from a new point of view.

RELATIVE COORDINATION

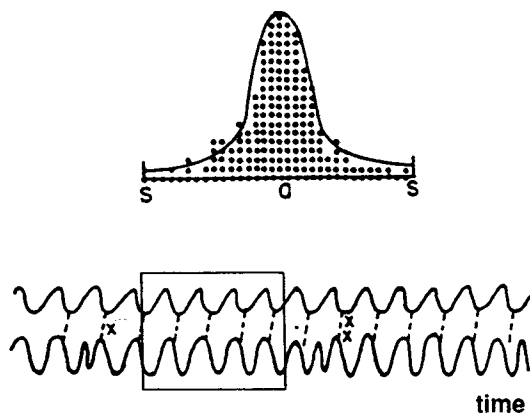
The time series displayed in figure 4.2 show the essential difference between absolutely and relatively coordinated behavior. The former, rigid and machine-like, involves phase relationships that are constant. The corresponding histogram has a single large peak concentrated at a single relative phase. Relative coordination, in contrast, displays *all* possible relative phase values in the S-S interval spanning 360 degrees ($0-2\pi$ radians) even though a common phase characteristic of absolute coordination is still present. I have drawn a box around the relative coordination time series to show how easy it is to make a mistake and confuse the two classes of coordination. (One always has to ward against the unconscious tendency to display the data that look the most orderly.) It would be quite easy, for example, to cut up the time series, as I have, and claim that mode locking or absolute coordination (phase and frequency synchronization) is observed!

But relative coordination is not mode locking. In particular, inside the box we see a *progressive* and *systematic* slippage in the phase relation between the components, and then when we increase the time scale of observation, the insertion of an extra step to keep the components together. It's just like the adult and child walking together. Rigid entrainment (absolute coordination), which reflects asymptotic convergence to a mode-locked attractor, may be more a feature of biological oscillator *models* than of reality.

(Broken) Symmetry Again

How ubiquitous is relative coordination in natural systems? The list is likely to be endless, in large part because the phenomenon is possible in any system containing two or more components whose frequencies couple nonlinearly. Yet by far the greatest attention has been given to absolute coordination or frequency locking, which was discovered over 300 years ago by Dutch physicist Christian Huygens when he noted that two pendulum clocks placed near each other tended to synchronize due to tiny coupling forces transmitted by vibrations in the wall on which they hung. Physicists James Glazier and Albert Libchaber have provided a representative list of the "almost bewilderingly common" occurrences of frequency locking in the natural world.⁵ It includes in mechanics, the damped driven pendulum; in hydrodynamics, the vortices behind an obstacle in a wind tunnel or an airplane wing, the dripping of a faucet, our familiar convective rolls, and the oscillations of acoustically driven helium; in solid-state physics, Josephson junctions and oscillations in other materials; in chemistry, the Belousov-Zhabotinsky and many other reactions; and in biology, cardiac rhythms, brain rhythms, slime molds, and menstrual cycles.⁶ To this one could add electrically stimulated giant squid axons, neural

a Relative Coordination



b Absolute Coordination

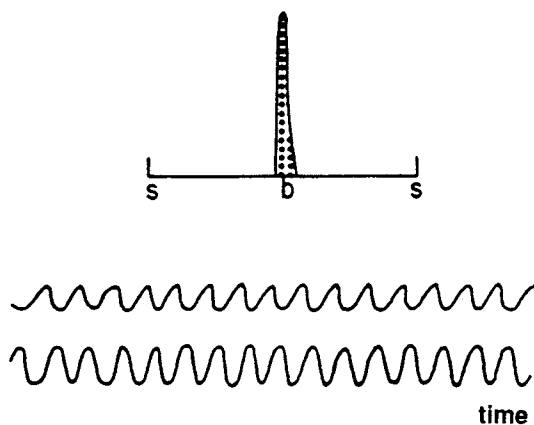


Figure 4.2 (a) Relative coordination. (*Top*) The distribution of possible phase relations between two signals. (*Bottom*) The corresponding time series from which the phase relation is extracted. The distance from S to S on the abscissa spans the phase interval 0 to 2π rad. The signals come from pectoral (upper time series) and dorsal (lower time series) fin movements of a fish. (b) Absolute coordination. Distribution of phase relations and corresponding time series as described in (a). (Adapted from reference 2.)

and muscle membrane oscillations, locomotor-respiratory rhythms, speech-hand movement patterns, and cell populations in primate and cat visual, auditory, and sensorimotor cortex, to name just a few examples in neuroscience and psychology.⁷

But how is this more plastic and fluid form of organization called relative coordination to be understood? The basic reason for relative (rather than absolute) coordination is that the component parts of complex biological

systems are seldom identical, thereby introducing *broken symmetry* into coordination dynamics. Nature thrives on broken symmetry for its diversity, and coordination it turns out, is no exception. As we'll see, any influence that causes the components of the system to differ is a potential source of symmetry breaking. Handedness and hemispheric differences in the brain are obvious examples.

Coordination often occurs between different structural components, as in the case of speech, for example, or between the same components put together for different functions (e.g., playing the piano versus playing the flute). In general, symmetry breaking occurs when different (neuro)anatomical structures, each possessing a different intrinsic frequency, must be coordinated. Alternatively, task requirements may dictate that some response must be coordinated in a particular fashion with an environmental event. Just this situation provided an experimental insight that enabled my colleagues and me to understand relative coordination as a consequence of broken symmetry in the coordination dynamics, and to formulate the corresponding law.⁸

Action-Perception Patterns: An Example

I once described this experiment to a professor of music who told me that I had (re)discovered a test used at the Juilliard School in New York City to evaluate musical talent. I have no idea whether this is true or not. According to my source, sometimes it is difficult to decide between two prospective pupils so the following test is conducted. "Clap *between* the metronome beats," the student is instructed, as the teacher turns the knob on the metronome, making it go faster. The one who keeps out of time the longest wins!

In our experiment the task for the subject was to synchronize peak flexion of the index finger with a metronome in two modes of coordination: on the beat and off the beat. For each mode, the pacing frequency was monotonically increased (or, in another condition, decreased). Figure 4.3 shows representative plots of the relative phase between the metronome and the hand for the off the beat, syncopated condition. Several different kinds of patterns are observed.

The subject shown in figure 4.3A would win no prizes at Juilliard. Beginning in syncopation (strict syncopation would fall on the dotted line, i.e., relative phase = $\pm \pi$), spontaneous switching to synchronization (relative phase = 0) occurs near the end of the first plateau. He can't keep time for very long, at least, off the beat. After that, the subject sustains synchronization (on the beat, in phase with the metronome) for the remainder of the run. The time series shown in figure 4.3B is similar: here again there is a transition from one mode to the other, but at higher frequencies a new phenomenon occurs. Synchronization is lost and the relative phase "wraps" continuously in the interval between 0 and 2π radians. This means that the subject can no longer maintain a one-to-one relation with the metronome. In figure 4.3C the subject keeps the syncopation mode very stably until at higher frequencies the relative phase

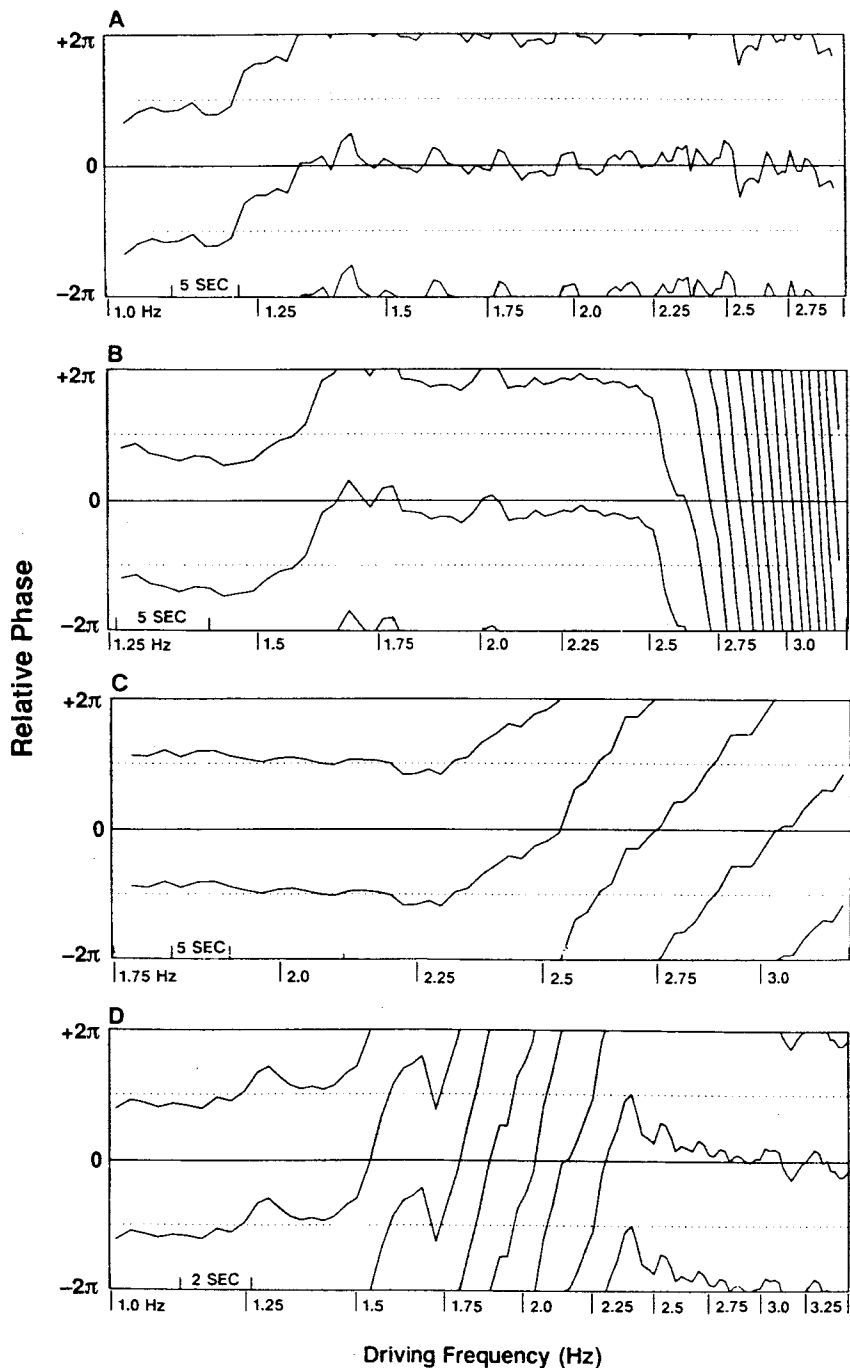


Figure 4.3 Representative plots showing relative coordination between hand and metronome in the Juilliard experiment of Kelso, Del Colle, and Schöner.⁸ Relative phase is normalized to the unit interval $[0, 2\pi]$ and the plot is duplicated in the interval $[-2\pi, 0]$. The tendency for phase attraction persists even though the oscillatory components exhibit different periodicities. The characteristic features are interspersed intervals of strict mode lockings, occasional phase wandering, and longer epochs of phase wandering as metronome frequency is increased.

starts to slip. Notice that this is a *directed*, not random, drift with brief pockets (the little flat parts) of *nearly* mode-locked behavior. Finally, in figure 4.3D we observe syncopation followed by slow drift and eventual synchronization.

The phenomena shown in figure 4.3B through D are typical of relative coordination or what a dynamicist would call loss of entrainment (phase and frequency desynchronization). The tendency is for phase attraction to persist even though the oscillatory components exhibit different periodicities. Typical features associated with desynchronization are interspersed intervals of nearly mode-locked behavior and occasional phase wandering, with longer epochs of phase wandering as the system is forced to coordinate itself at higher movement frequencies.

One's belief in the scientific method is enhanced when a given set of findings is confirmed or replicated by others, especially if it happens to be in a slightly different paradigm. In this case, Wimmers, Beek, and Van Wieringen used a visual tracking task rather than an auditory-motor task, but found the same basic transitions as reported here, including critical fluctuations. They didn't, however, look for any relative coordination effects.⁹

RELATIVE COORDINATION EXPLAINED

By now the reader will have noted the similarity among coordination of hand movements, coordination between people, and coordinating one's action with an environmental event. Comparing these cases one can appreciate that biological coordination is essentially a synthetic process; it deals with how the components are coupled together independent of the material structure of the components themselves and the physical nature of the coupling. This is not to say that the specific components do not constrain or shape coordinative patterns and the pattern dynamics. In the action-perception case, metronome and limb are obviously different components. As a consequence, we can no longer assume symmetry of the dynamics under the operation $\phi \rightarrow -\phi$. The fact is that any situation that creates differences between the interacting elements is a potential source of symmetry breaking.¹⁰ Moreover, as we will see in later chapters different functional requirements arising, for example, due to environmental demands, intentionality and learning (chapters 5 and 6) break the symmetry of the relative phase dynamics.

To accommodate relative coordination effects in the action-perception example requires only a single, apparently trivial change in the HKB symmetric coordination law described in chapter 2. The manifold consequences of this symmetry-breaking step, however, turn out to be subtle and nontrivial. The sole change we have to make is to include a term, $\delta\omega$, that takes into account intrinsic differences between the frequency that the moving limb generates spontaneously (call it ω_0) and the metronome frequency (call it ω).¹¹ This term is derived, of course, from a detailed (coupled) oscillator analysis, which the reader is spared here. When uncoupled, the individual components behave according to their respective (natural) frequencies. If $\delta\omega$ is the frequency differ-

ence, the rate of phase change between the components is just this difference. When coupled, the modified, symmetry-breaking version of the phase dynamics reads as¹²

$$\dot{\phi} = \delta\omega - a \sin \phi - 2b \sin 2\phi.$$

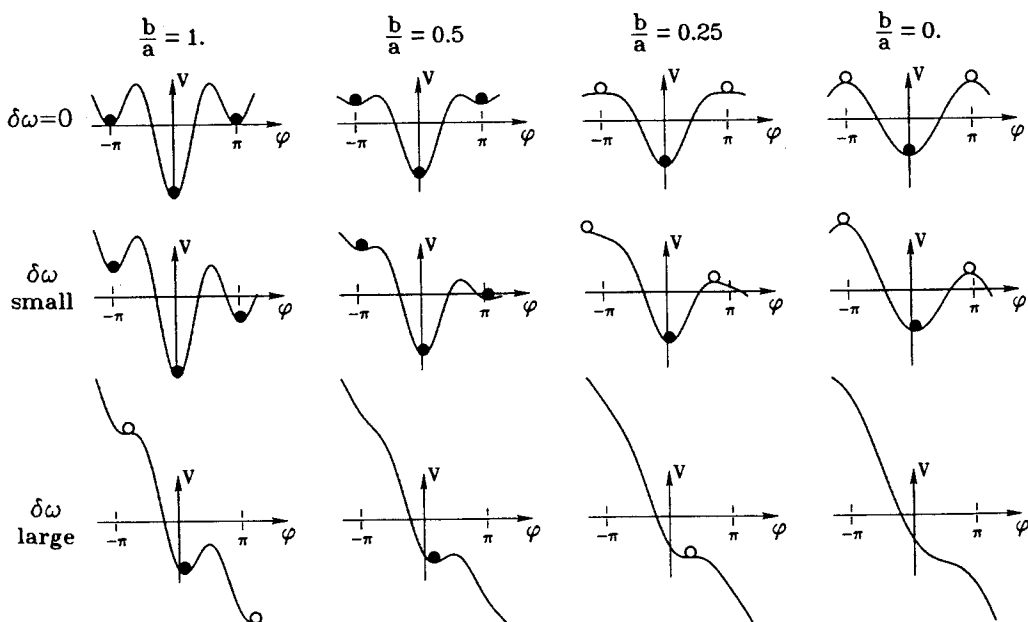
It is easy to see that if $\delta\omega = 0$, this is just the original symmetric-coordination law. For small values of $\delta\omega$ one can obtain phase locking as before, but the fixed points are slightly shifted away from the pure in-phase and antiphase patterns of coordination.

Our new equation corresponds to motion in a potential

$$V(\phi) = -\phi\delta\omega - a \cos \phi - b \cos 2\phi,$$

which is plotted in figure 4.4. (The minus signs allow us to interpret the potential as a landscape with attractor states at the minima for positive $\delta\omega$, a and b .) This picture and others that follow tell the whole story.

The effect of the first (linear) term is to tilt the whole curve along the line $V = -\phi\delta\omega$. For a given movement frequency, as $\delta\omega$ is increased, there is a point at which the curve loses its stable fixed points (minima of the potential), the system is no longer phase locked—synchronization is lost, and running or wrapping solutions predominate. The exact point at which the detuning



$$V(\phi) = -\delta\omega \phi - a \cos \phi - b \cos 2\phi$$

Figure 4.4 The potential, $V(\phi)$, of the coordination dynamics with broken symmetry. The region around each local minimum acts like a well that weakly traps the system into a coordinated state (see text). Black balls correspond to stable minima of the potential, white balls symbolize unstable states.

parameter, $\delta\omega$, causes the running solution to appear, and whether it appears at all, depends on the other parameters, a and b . This simply reflects the fact that *both* the frequency difference, $\delta\omega$, and the basic frequency of coordination affect the onset of the running solution.

The reader will remember from our previous analysis that the ratio b/a expresses the relative importance of the intrinsic phase attractive states at $\phi = 0$ and $\phi = \pi$, or 180 degrees. Note that in figure 4.4 the local minima serve to trap the system into one of the intrinsic phase states, depending on the initial condition. Then as parameters are changed, only the coordination mode near $\phi = 0$ remains, until eventually, when even that localized well becomes shallow (figure 4.4, bottom), the system escapes and runs. This behavior is especially interesting because even though all the stable fixed points are gone, *remnants* of the minima remain. One can imagine the system re-siding in these valleys for variable times before continuing to run depending on the curvature of this washboard potential.

Figure 4.5 shows the behavior of the relative phase in time corresponding to the potential pictures of figure 4.4. The running solutions have a fine

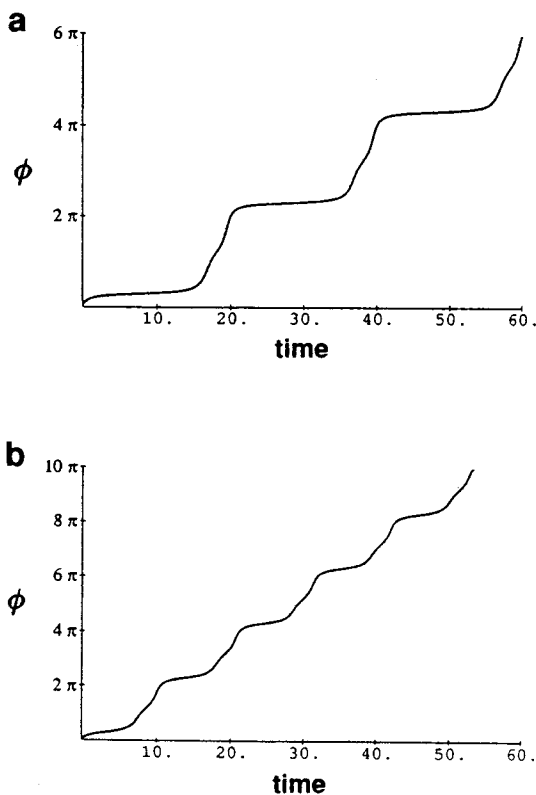


Figure 4.5 Running solutions in which there is still a tendency to maintain preferred phase relations. (a) The system is closer to a stable fixed point (mode-locked state) and therefore stays longer than in (b), where the plateaus are of shorter duration.

structure, spending more time at those relative phase values where the force, the derivative of ϕ with respect to time ($\dot{\phi}$) is minimal. This reproduces exactly the phenomenon of relative coordination. Although there is no strict mode locking and the system is nonstationary, it displays a partial form of coordination *in between* rigid mode locking and completely uncoordinated behavior. The reason there is a longer flat portion in figure 4.5a than figure 4.5b is that the system is closer to the stable fixed point near $\phi = 0, 2\pi, 4\pi$, and so on in the former than the latter. The closer the system is to the fixed point, the longer it hangs around. And the reason, of course, that the system runs (ϕ ever increasing) is that the component frequencies are no longer the same. Eventually, one component takes an extra step, and then both are nearly, but never totally, locked again.

The Bifurcation Structure

The phenomena of relative coordination can readily be understood in dynamic language. Consider the plot of $\dot{\phi}(d\phi/dt)$ versus ϕ (figure 4.6) for a fixed frequency difference, $\delta\omega$, as the coupling ratio b/a is varied. (It might be useful to compare the same plot for the symmetric case; see figure 2.8). Once again,

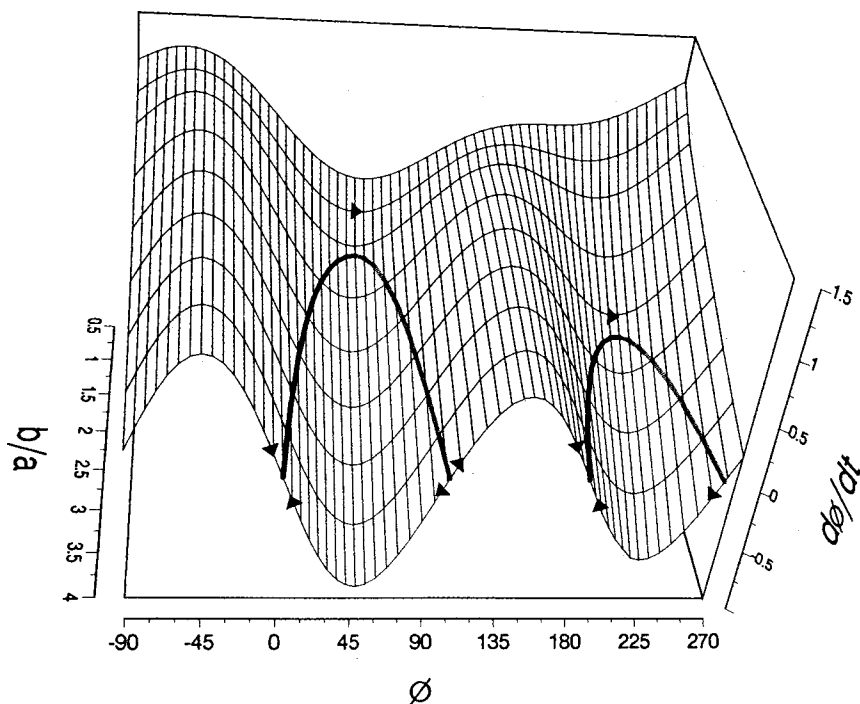


Figure 4.6 The broken symmetry version of the coordination dynamics with the parameter, $\delta\omega \neq 0$. When the symmetry of the coordination dynamics is broken, inverse saddle node bifurcations are seen. Eventually no stationary solutions exist (see text for definitions and discussion).

the system contains stationary patterns or fixed points of ϕ where the time derivative $\dot{\phi}$ is zero and crosses the ϕ axis. When the slope of $\dot{\phi}$ is negative, the fixed points are stable and attracting; when the slope is positive, the fixed points are unstable and repelling. Arrows in figure 4.6 indicate the direction of flow. Thick solid and dashed lines signify stable and unstable fixed points that establish the boundaries of the system's basin of attraction.

Now the multiple manifestations of broken symmetry in the coordination dynamics emerge. The bifurcations in this asymmetric system are called *saddle node* bifurcations ("saddle" referring to the repelling direction, "node" to attracting direction). On the right side of the figure around $\phi \approx 180$ degrees, stable and unstable fixed points coalesce onto a tangent, causing a transition to the only other stable fixed point available near $\phi = 0$ and then, *by exactly the same mechanism*, the last remaining stable fixed point disappears.

The broken symmetry law generates rich dynamics. Whereas the stable fixed points in the symmetric case do not change their value as the control parameter is varied (cf. figure 2.8) *systematic drift* is evident in the asymmetric case as parameters change. Moreover, due to the greater slope of the function surrounding the fixed point near $\phi = 180$ degrees, it is theoretically easier for the system to transit to the other stable fixed point in one direction (ϕ increasing from ~ 180 deg) than the other. Experiments by Jeka confirmed these drift and *transition path* predictions by directly manipulating the asymmetry between arms and legs using different loads applied to the limbs. Dagmar Sternad and colleagues used the hand-held pendulum paradigm to establish the systematic effect on relative phase due to frequency differences between the limbs.¹³

Loss of Entrainment

In figure 4.6 it is easy to see that as the function is flattened by decreasing a control parameter, stationary solutions eventually disappear. In this regime (exemplified by the solitary arrow at the top of the figure) there is no longer any phase or frequency locking, a condition called *loss of entrainment* or *desynchronization*. Such desynchronization is not present in the symmetric version of the coordination dynamics, but is again a consequence of symmetry breaking. Desynchronization does not always mean irregular behavior; its magnitude depends on how close the system is to its critical points, which depends on all three parameters, $\delta\omega$, a , and b (see figure 4.4). This simply reflects the fact that in broken symmetry coordination dynamics, both the frequency difference between components and the basic frequency of coordination are control parameters affecting the onset of the running solution.

Intermittency

When the saddle nodes vanish, indicating loss of entrainment, the coordination system tends to stay near the previously stable fixed point. It's as though

the fixed point leaves behind a remnant or a phantom of itself that still affects the overall dynamical behavior. Thus, in figures 4.4, 4.5, and 4.6 there is still attraction to certain phase relations even though the relative phase itself is unstable ($\dot{\phi} > 0$). Such behavior is especially significant because it shows that although there is no longer any strict mode locking, a kind of partial coordination exists in which the order parameter is temporarily trapped. Motion hovers around the ghost of the previously stable fixed point most of the time, but occasionally escapes along the repelling direction (phase wandering). A histogram of the phase relation in this intermittent regime of the coordination dynamics contains all possible phase values, but concentrates around preferred phase relations (the previously stable fixed points) exactly as shown in figure 4.2 and 4.3 for relative coordination!¹⁴

As a scientist, there are occasions—usually few and far between—when one gets an insight or reaches a level of understanding about a problem that gives one a feeling of genuine delight and satisfaction. One of them was when I realized the theoretical connection between relative coordination, which I'd studied for many years, and the dynamical mechanism of intermittency, one of the generic processes found in low-dimensional dynamical systems near tangent or saddle node bifurcations.¹⁵ What's the excitement about? Well, there are a few reasons.

One is that relative coordination has been described for over sixty years without a satisfactory explanation. So an intermittency mechanism for relative coordination seems like an idea whose time has come, and is certainly worth exploring. Another reason is that the connection between relative coordination and intermittent dynamics suggests that biological systems tend to live near the *boundaries* separating regular and irregular behavior. They survive best, as it were, in the margins of instability. Several authors, notably the theoretical biologist Stuart Kauffman, have proposed a similar idea independently in an entirely different context, namely "rugged fitness" models of adaptive evolution. I'm coming from a direction that Kauffman admittedly eschews—whole organisms acting in their environment—but, as others have pointed out, the similarities are quite compelling.¹⁶

Why should a biological system occupy the strategic position near boundaries of mode-locked states rather than residing inside them? The answer given by the intermittency theory of relative coordination is that by residing near the edge, the system possesses both flexibility and metastability. There is *attraction* (the ghost of the fixed point), but no longer any attractor.

ABSOLUTE AND RELATIVE COORDINATION UNIFIED

Both relative and absolute coordination fall out of the broken symmetry version of the coordination dynamics. Obviously, the solid lines in figure 4.6 depict absolutely coordinated phase- and frequency-locked states. Relative coordination exists in the intermittent regime, just beyond mode-locking regions, where stable (attracting) and unstable (repelling) fixed points collide.

The symmetric version of the coordination law sires only absolute coordination; the asymmetric version provides a single coherent theory of both absolute and relative coordination. Which version holds depends on the system's symmetry. These basic coordinative forms emerge as two sides of the same coin, inhabiting different regimes of the same underlying law.

The broken symmetry dynamics encompasses all the effects we encountered in chapter 3 where the coordinative interactions were mostly among dissimilar components, including multistability, the coexistence of several coordination modes for the same parameter value; switching among modes at a critical parameter value due to dynamic instability; and hysteresis, where the coordination mode observed depends on which direction parameters are changing and so forth. But in addition to these effects—in some sense as vestiges of them—there is a further transition from absolute to relative coordination.

The individual components now express themselves freely, and/or the coupling between them is not strong enough to suppress their individuality completely. Only *tendencies* to coordinate in a strict fashion remain. When coordination slips, extra steps have to be inserted to keep the pattern cohesive. And then, if it's pushed further, the whole system breaks up and becomes desynchronized. Only a shadow of its previous coordination remains. Like in some marriages attraction fades, here due to the weakened curvature of a mathematical function. The mind boggles.

RELATED MODELS: FIREFLIES, LAMPREYS, AND LASERS

Nancy Kopell and Bard Ermentrout are two applied mathematicians who have worked extensively on coupled nonlinear oscillator models of biological systems. Their goal is to develop a body of mathematics that can help biologists decide whether differences they observe are crucial or not. Their approach is complementary to that taken here: these investigators work with so-called robust classes of equations and, within that framework, sort out which features are essentially universal and which depend on further structure. "Further structure" means adding more terms to the equations. Coming more from an experimental background that is inspired by the physical concepts of synergetics, I look for robust phenomena and seek a minimal, bare-bones set of principles (mathematically instantiated, of course) that embraces as many of the phenomena as possible. Although simplicity is an admirable sought-after property of mathematical models, a fine line exists between the goal of simplicity and omitting important details. Nevertheless, it is generally agreed that the best theories are those that explain the known facts and predict new facts of the same kind. Insight isn't necessarily gained by making mathematical models more complicated. Again, it comes down to determining variables that are essential and their dynamics. Here I'll describe two situations in which an identical model successfully captures certain key phenomena, although certainly not all the particulars. Then I'll make some remarks about the relation

of these models to our coordination dynamics, although by the end it should be pretty obvious.

The astute reader may have connected many of the coordinative phenomena discussed thus far with one of the most spectacular sights in all of nature: the synchronous flashing of huge swarms of fireflies that occurs in places such as Malaysia and Thailand. These insects have the ability to synchronize their flashing with either an outside signal or with other fireflies of the same species. A propensity for rhythmic communication is evidently shared by humans and fireflies. Of course, on a cellular level, as we'll see, such behavior is not only ubiquitous but important, as in the case of pacemaker cells that coordinate their electrical activity to maintain the heartbeat.

Ermentrout and John Rinzel consider firefly entrainment as a problem of entraining the free-running firefly oscillator (of a certain periodicity) with a stimulus (a *Zeitgeber*) of a different period.¹⁷ Fireflies differ considerably in terms of their flashing periodicity, but the typical interval between flashes is about a second. As long as the periods of the firefly and the *Zeitgeber* are close enough, the creature will entrain and flash at a distinct phase of the stimulus cycle (exactly like my Juilliard experiment). But if the periods (the inverse of frequency) are too different, the firefly reaches the limit of its entrainment ability, and desynchronization occurs. In many cases, this loss of entrainment is only transient (intermittency?), but in other cases, the firefly-stimulus phase difference may cycle repeatedly through all values, a phenomenon known as phase walk-through in the firefly literature (see figures 4.3 and 4.5). Phase walk-through, of course, occurs because the discrepancy between the natural period of firefly flashing and the *Zeitgeber* period is too large.

Ermentrout and Rinzel model firefly entrainment, its transient loss, and phase walk-through with the following one-variable model for the phase dynamics:

$$\dot{\phi} = \delta\omega - a \sin(\phi),$$

where $\delta\omega$ is the frequency difference, and a measures the relative influence of the *Zeitgeber* on the firefly. Figure 4.7 shows the phase dynamics when entrainment occurs (top) and when the entrainment limit is reached, giving rise to phase walk-through (bottom). In the former case, ϕ has a stable fixed point near zero (where $\dot{\phi}$ crosses the x -axis); in the latter, due to increasing $\delta\omega$, the function is lifted off the line and entrainment (the stable fixed point) is lost. Note, however, that the relative phase changes very slowly close to the horizontal axis, increasing beyond the shaded interval. Note also that the bifurcation is a saddle node, stable and unstable fixed points moving toward each other, colliding, and then disappearing, exactly as in the analysis of my Juilliard experiment.

Ermentrout and Rinzel's model is even simpler than our coordination dynamics, because, at least as described, it does not exhibit multistability, bistable to monostable phase transitions, or hysteresis. Nor does it consider the role of stochastic fluctuations. Nevertheless, it is a beautiful little model

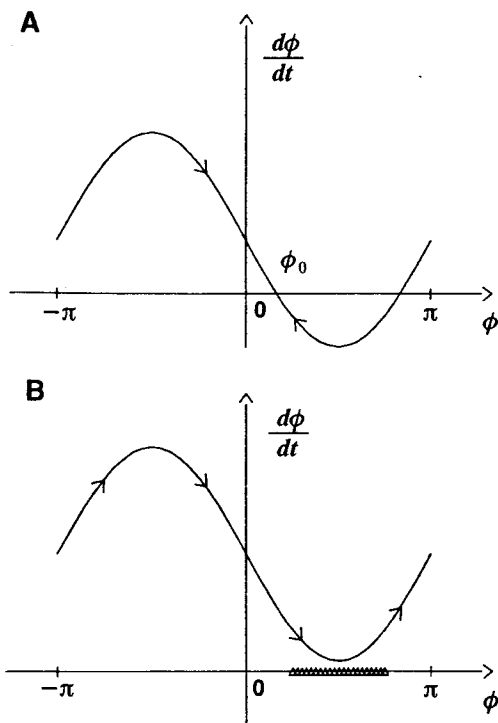


Figure 4.7 Dynamics of phase relation in Ermentrout and Rinzel's model of firefly entrainment. (A) Entrainment occurs at ϕ_0 where stimulus and pacemaker periods are close. When the function lifts off the horizontal axis (B) there is no longer any stable phase relation. Phase walk-through occurs, and ϕ continually increases, although slowly in the shaded interval. (Reprinted by permission from the American Physiological Society.)

that occupies its own niche in the spectrum of possible mathematical models. I like it because it prunes away all the details, including all the physiology and anatomy of these tiny creatures, but captures the essence of their relation to each other and to the environment.

Of course, the model leaves out many subtle aspects of firefly synchronization. Recent work addressed some of these, including how synchronization occurs in a very large population of fireflies regardless of when they start flashing.¹⁸ This research shows that synchronization is the rule in a system of numerous identical oscillators regardless of initial conditions. But many questions remain. For example, what happens when the population of oscillators is not identical? Do traveling waves occur? What is the nature of the coupling mechanism? and so forth.

The lamprey is a strange beast: it's a bona fide vertebrate like humans; and it swims like a fish, but lacks fins and other complicated appendages. As far as we know, the lamprey swims with just one basic pattern of alternation between local opposing muscles. It turns out that neurobiologists, like Avis Cohen and Sten Grillner, can isolate the animal's spinal cord and keep it alive in a bath containing various compounds that acts as neurotransmitters.¹⁹ This

makes the lamprey a great preparation for studying how the vertebrate nervous system generates patterns of neural activity (see chapter 8). The motor patterns of the intact lamprey and the isolated spinal cord are basically the same, raising hopes that the study of this creature might help us better understand spinal cord injuries in humans.

The overall organization of lamprey pattern generation is believed to be that of a chain of segmental neural oscillators coupled across the creature's spinal cord. This gives the strict alternation pattern that produces a traveling wave up and down the cord. The lamprey needs only four segments to generate the traveling wave (the adult has about 100) and two to produce alternating activity. So, as far as theoretical modeling is concerned, we're back in the ballpark of nonlinearly coupled oscillators. Cohen, Kopell, and colleagues are world-famous for their work on modeling central pattern generation using systems of coupled oscillators.²⁰ There's more to this than meets the eye, but what I like is that they have come up with a remarkably simple model for the lamprey that is formally similar to that of firefly entrainment. Considering each pair of segmental oscillators, they show that a phase-locked, alternating pattern will occur if the difference between the oscillator frequencies is small relative to the coupling between them. They also show transitions from drifting to phase-locked motion between two oscillators of different frequencies, ω_1 and ω_2 , when the coupling is increased. Their model reads as follows:

$$\dot{\phi} = (\omega_1 - \omega_2) - (a_{12} + a_{21}) \sin \phi,$$

where ϕ represents the phase lag between the oscillators, and a_{ij} is the coupling between them.

Notice that the lamprey model is of exactly the same form as the firefly entrainment model, but the coupling is different. Whereas the *Zeitgeber* to firefly coupling is one-way (the *Zeitgeber* drives the firefly but not the other way around), the segmental oscillators of the lamprey are *mutually coupled*, each affecting the other's behavior. Thus, in the Rand et al. model, if the net coupling ($a_{12} + a_{21}$) is positive or excitatory, oscillator 1 (the faster one) leads. If the coupling is negative or inhibitory, the slower oscillator leads. This model provides a mechanism for reversing direction of motion from forward to backward by simply changing the relative frequencies of the oscillators.

I don't know if lampreys swim backward, but I do know why I find these models of firefly entrainment and lamprey coordination interesting. First, they are simple and aesthetically pleasing. Second, they show that the same basic principles of coordination are in operation for very different kinds of things. Third, they exhibit the same behavioral patterns—phase locking and entrainment, relative coordination, and desynchronization—but by very different physiological mechanisms. All the patterns of firefly entrainment and lamprey pattern generation boil down to mathematical patterns of symmetry breaking in coupled oscillators. Was it Einstein or Wigner who asked why mathematics works so well to describe nature?

Excerpt from—Haken, H. et al. (1967).

Theory of laser noise in the phase-locking region.

Zeitschrift für Physik, 206, 369–393.

The essential noise source in lasers is so-called spontaneous emission noise which is of quantum mechanical nature. We have shown in previous papers (Haken, 1965) that spontaneous emission noise may be introduced from first principles by using quantum mechanical Langevin forces. In the present paper, we derive for the most complicated example, namely the self-mode locking, the basic equation for the relative phase including noise. As we will show, this equation has the form

$$\dot{\psi} = \delta - \beta \sin \psi + f(t),$$

where the fluctuating Langevin force $f(t)$ represents white noise and is gaussian. *The treatment of one example makes clear that this force is quite universally determined for all kinds of frequency locking phenomena (italics mine) (p. 371).*

Chronology aside, why didn't Haken, Bunz, and I use the simpler coordination law characteristic of lampreys and fireflies to model the basic forms of observed coordination within persons, between persons, and between organisms and environments? The equation is well known to Haken. Nearly thirty years ago he and his colleagues derived it from quantum mechanics (see box). But the simpler equation does not exhibit multistability, the fact that the two basic modes of coordination, in-phase and antiphase, may be produced for the same parameter value. Nor does it produce order-order transitions. For this the $\sin 2\phi$ term is necessary. Multistability, as I've stressed, is the dynamical equivalent of multifunctionality in biology: organisms meet the same functional or environmental requirements in different ways. How else might one imagine writing one's name with one's hand, one's big toe, or one's nose?

INSTABILITY AND THE NATURE OF LIFE: THE INTERMITTENCY MECHANISM EXPOSED

The title of this section, at least the part before the colon, is stolen from an old paper by Arthur Iberall and Warren McCulloch, each one a seminal thinker.²¹ Their article, which reads like a primitive poem, resonates with the intermittency theme that I want to expand in this section. I will quote only a few sentences to convey the essence:

An essential characteristic of a living system is its marginal instability.... As a result, the motor systems of the organism are plunged into intermittent search modes to satisfy all of its hungers.

The living system unfolds its states, posture by moment. In each posture (the action of the body on the body) the system is temporarily locked into an orbital constellation of all its oscillators. The psychological-physiological "moment" then changes from instant to instant.

The function of the central nervous system with its memory, communications, computational and learning capabilities is to ... modulate the system into behavioral modes.

This language must seem terribly outdated and vague to the sophisticated reader, but to me it has a solid ring of truth, nay, inspiration. McCulloch and Ibbert's admittedly qualitative emphasis on instability, nonlinearity, information compression, and collective behavioral modes was ahead of its time. Of course, my primary reason for including them here is that I like the idea that organisms are "plunged into intermittent search modes." One of the goals now is to put more clothes on the frame of intermittency because it will be crucial later when I discuss perception (chapter 7) and the brain (chapter 9). The other is to deal with "orbital constellations" of oscillators whose frequencies are not locked one to one (1 : 1).

So far all the situations I've described deal with one-to-one coordination between the interacting components. Yet in many cases in living systems the components are not so coordinated. Staying within the context of rhythmic activity, it's possible for the components to be coordinated stably with other frequency ratios, such as 2 : 1 or 3 : 2, or the frequency relation may even be irrational, giving rise to quasi-periodicity. How do we understand these multi-frequency situations, and where does intermittency come in? Our coordination law as it stands doesn't handle such situations, which are actually quite widespread.

From Continuous Flows to Discrete Maps

Our coordination dynamics is written as an ordinary differential equation (ODE), the conventional way in which many physical laws are stated. Of

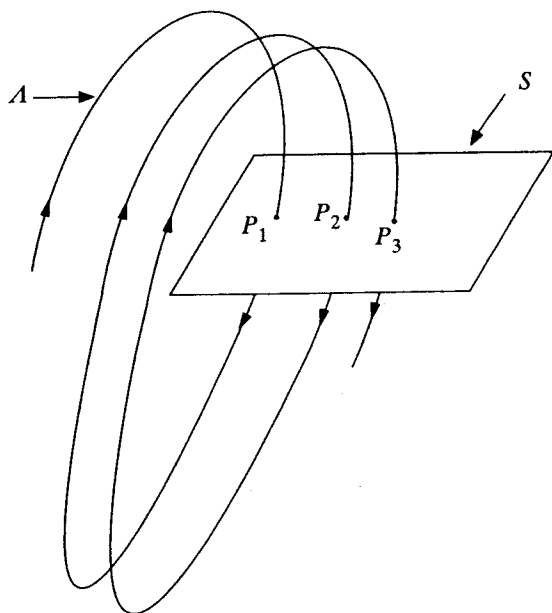


Figure 4.8 Poincaré surface of section for an ODE (see text).

course, it's possible to extend this law to accommodate oscillations of different frequencies, but this is quite complicated, technically speaking. Earlier, I mentioned an important class of dynamical system called *difference equations* or *maps*. It is this tool that I will use here as a simpler way to gain understanding of multifrequency processes and intermittent behavior in neurobiology and behavior. Instead of flowing continuously, as in ODEs, time is a discrete integer in maps. Maps and ODEs are intrinsically related to each other. In particular, Poincaré comes up again because the way they are related is named after him (Poincaré return maps and Poincaré cross-sections).

Just to get the idea, figure 4.8 shows a smooth trajectory Λ of an ODE. The plane S is designated as a surface of section and is pierced every time the trajectory cuts it, shown as the points P_1 , P_2 , and P_3 in the figure. Obviously, the point P_1 is related to the point P_2 which is related to P_3 and so on. Thus, a map G exists such that $P_{n+1} = G(P_n)$. We can learn a lot from such maps—physicists and mathematicians already have—because they can capture many important aspects of the real situation. Of course, the map that we will use is for the relative phase, ϕ , the collective variable that captures the coordination between nonlinearly coupled components. We call this the HKB or phase-attractive map because it's a reduction of the nonlinear oscillator model formulated by Haken, Bunz, and me (see box).

Instead of studying the entire trajectory on a 2-frequency torus, we simply encode the entire dynamics in the form of a map, $\phi_{n+1} = F(\phi_n)$. This return map is a map of the circle onto itself. It is easy to study by plotting ϕ_{n+1} versus ϕ_n as parameters are varied. The best way to do that is on a computer. Some people even believe that because we have computers, differential equations, especially in areas such as biology and the social sciences, might be supplanted by discrete maps, which are better suited to the digital computer. Whether this happens or not, of course, hinges on how well such maps model the phenomena of interest.

The Discrete Nature of Coordination

In our case, we don't need the digital computer to motivate introducing the phase-attractive map. The reason is that coordination itself is often of a discrete nature. For example, when we look at bursts of activity in muscle or brain recordings (and, incidentally, many other kinds of records), event *onsets* in different components are often related to each other. In other situations, it may be a well-defined peak of activity that enables analysis of coordination. The way we calculate relative phase is usually but not always discrete and local (see figure 2.5). In such cases, detailed trajectory information is disregarded because the essential information for coordination is localized around discrete regions. In our studies of multilimb coordination in humans, Jeka and I found that the relative phase converges only at certain points for a trot or a pace. Peter Beek noticed the same feature in skilled jugglers.

FROM FLOWS TO MAPS

How may a pair (or a system) of N -coupled nonlinear oscillators be reduced to a map for the relative phase only? The phase of each oscillator, θ_i , is viewed as living on a circle, $0 \leq \theta_i < 2\pi$, rotating at a frequency, ω_i , and a period, $2\pi/\omega_i$ (figure 4.9). Since motion is confined to a circle, there is no distinction between one oscillation and the next. The shape of the waveform and its content, which may be important at the oscillator level, is ignored. That is one price that has to be paid in this kind of analysis. A system of N oscillators will inhabit N circles, but here I just show two (step 1). Mathematically, the product of N circles is an N -dimensional torus T^N . For the case of $N = 2$ the state space is a 2-torus, T^2 (step 3). The bridge between steps 1 and 3 is a square (step 2) in which the phase of each oscillator is displayed on the horizontal and vertical axes in the interval $[0, 2\pi]$. A constant relative phase, ϕ , between the oscillators, ($\phi = \theta_2 - \theta_1$), is reflected by a straight line: this is called phase locking. It is quite possible, even usual, for each oscillator to complete a cycle in the same time, but the phase difference between them may not be constant. This is called phase entrainment. The vertical plane in step 4 cuts the torus at some reference time, "freezing," as it were, the motion of one oscillator, but allowing us to see where its partner strikes it every time it traverses the torus. Each strike makes a point on the circle, allowing the entire dynamics to be encoded in the form of a return map in which each iteration takes a point, ϕ_n , on the circumference of the circle to the next point, ϕ_{n+1} . The problem of coupled oscillators is thus reduced from a flow on the torus to the study of a map from the circle to itself, $\phi_{n+1} = F(\phi_n)$.

We might expect coordination with the external environment to be of a discrete nature in situations where there are heavy constraints on timing; for example, when getting on an escalator one has to step at the right moment or one can fall on one's nose. Even on neurobiological grounds, a discreteness assumption seems valid. Neurons either fire or they don't. And they communicate with each other by releasing discrete packets of neurotransmitter in a quantal fashion.

Treating the dynamics in terms of a return map is tantamount to saying the system is highly *dissipative*. All other variables are subservient, as it were, to the collective variable. Discrete phase dynamics therefore represents the contraction of a higher- to a lower-dimensional space. Even our bagel—the two-oscillator torus—is reduced from a state space of four variables (x and \dot{x} for each oscillator) to just one, the relative phase.

With these preliminaries over, we can get down to business. Our phase-attractive circle map

$$\phi_{n+1} = f(\phi_n) = \phi_n + \Omega - K/2\pi \{1 + A \cos(2\pi\phi_n)\} \sin(2\pi\phi_n) \pmod{1} \quad (4.10)$$

turns out to be a function of three parameters, the meaning of which is inferred from general properties of circle maps as well as corresponding parameters in the continuous differential form of the coordination dynamics proposed by Haken et al. Thus, Ω is the frequency ratio of the components, K is the strength of coupling between components, and the parameter A is a measure of the relative stability of the intrinsic phase states, $\phi = 0$ and $\phi = \pi$.²² The way the map works is illustrated in figure 4.10. One feeds some

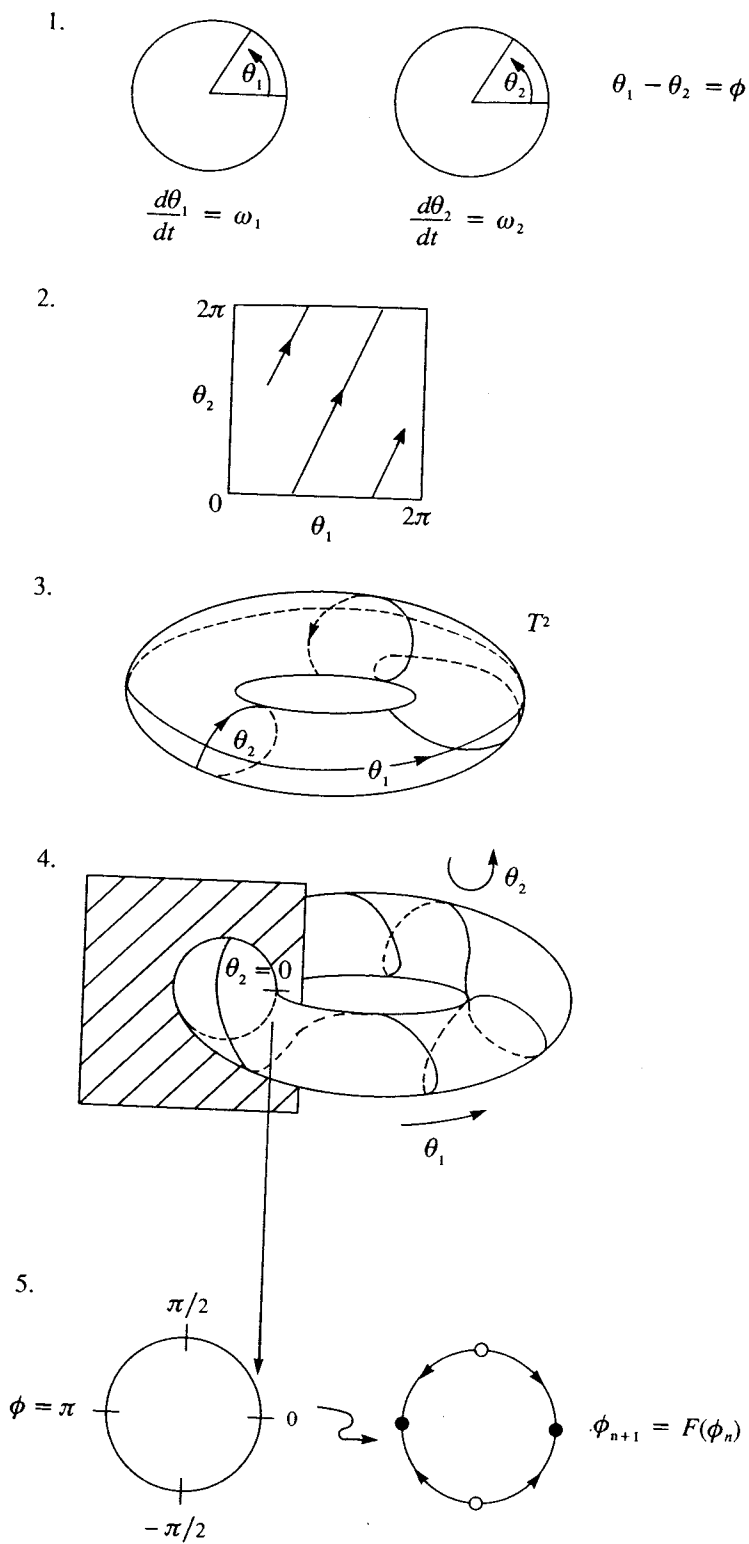


Figure 4.9 From flows to maps (see box for steps 1 to 5).

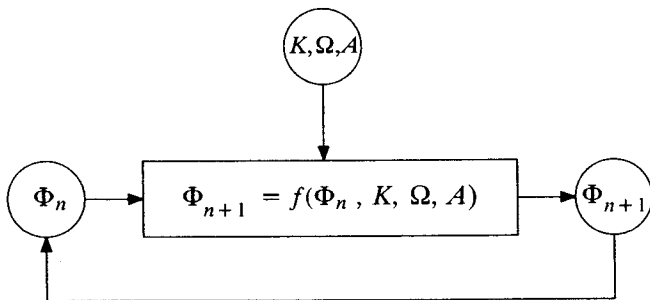


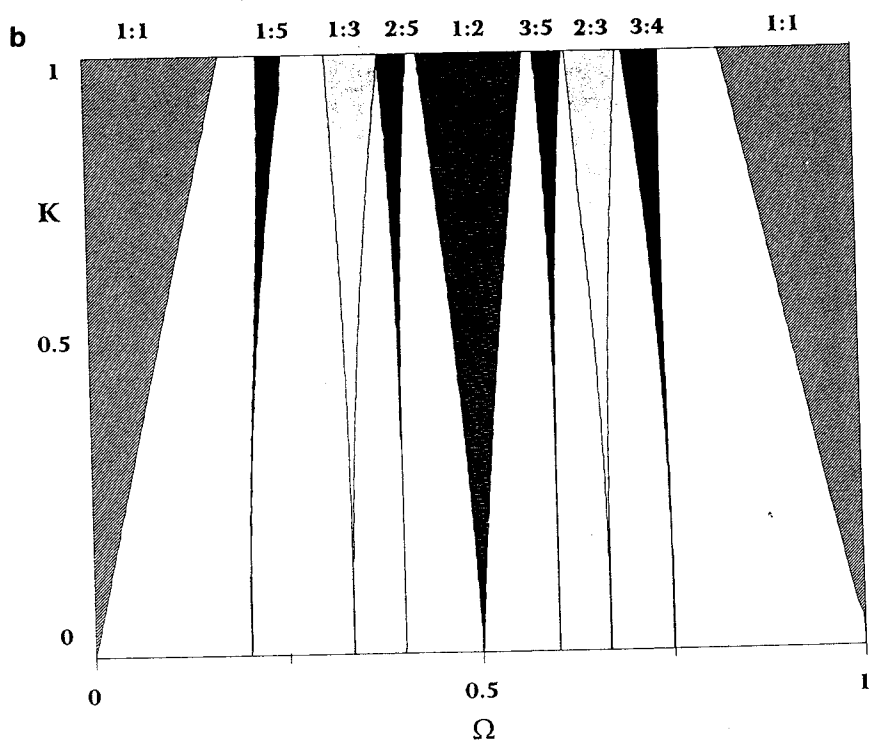
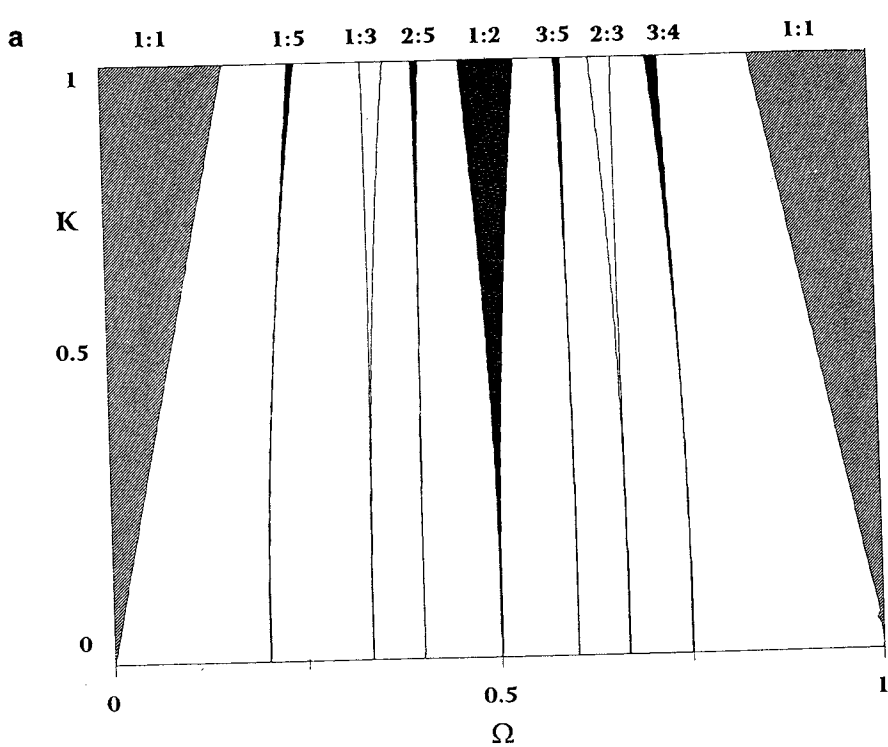
Figure 4.10 How iteration of the phase-attractive circle map works. See text for explanation.

initial phase, ϕ_n , as input into the function, then computes the output, ϕ_{n+1} , which is then fed back into the function in an iterative fashion. In short, by studying the properties of our phase map we can more readily understand how coupled oscillators behave, especially when the component frequencies are different and the coupling is subject to change.

Multifrequency Stability

Everything that we've observed for 1 : 1 coordination (e.g., bistability to monostability phase transitions) can be reproduced by the map. But there's a wealth of other phenomena besides, due to the presence of the Ω and K parameters. Consider, for instance, the ubiquity of low-order frequency ratios in physiology, neurobiology, and psychology.²³ Just to get the idea across, try tapping 2 : 1 with your two hands. Some people find it easier than others, and it depends on which hand beats the faster rhythm. (By now the reader has become an experimental psychologist and has tried these tasks with left-versus right-handers; musicians versus nonmusicians; brain-damaged versus normals; under the influence of alcohol ... ad infinitum.) Many studies of temporal organization in humans, especially by Michael Peters in Canada, Jeff Summers in Australia, Peter Beek in Holland and Diana Deutsch and others in the United States, have shown that the low-order ratios (1 : 1, 2 : 1, 3 : 2, etc.) are easier to perform than higher-order ones (4 : 3, 5 : 3 ...). I confess to feeling a secret pleasure with such results. Here is the most complex system of all, the human brain, yet a typical person is only able to perform, stably at least, low-integer frequency ratios between the hands!

Ignoring questions about skilled musicians and learning for the moment, the fundamental reason for this restriction has to do with the *structural stability of the rational frequency ratios*.²⁴ Structural stability means that slight modification of the system does not alter the stability of ratios. It accounts for similar behavior across very different systems, such as clock mechanisms, moon-earth phase locking, walking and breathing in humans, electrically stimulated nerve membranes, frequency locking in mammalian visual cortex, and so on.



Numerical studies of coupled oscillators or circle maps allow us to calculate the size of mode-locked regions. Technically, the asymptotic value of the frequency ratio is called the *winding number*, W , and is, in fact, the measured frequency ratio between the oscillators. When W is a rational number, the underlying oscillations are mode-locked or frequency synchronized. When W is irrational, which means it cannot be expressed as the ratio of two integers, the oscillations are desynchronized. The outcome is either quasi-periodicity or chaos.

Figure 4.11 (see also plate 3) shows why low-integer frequency ratios are ubiquitous in nature and why they are the easiest for humans to perform. The wedges emanating from the horizontal axis, called *Arnol'd tongues* after the Russian mathematician who first described them, correspond to pure mode locking. Tongues represent regions of the (K, Ω) parameter space that have asymptotic solutions to our phase map equation. In between these tongues are quasi-periodic regions where the frequency ratios are irrational. As K increases above zero, the width of each locking increases, culminating in a situation where locked states fill the entire interval (see below). The widest mode-locked regions correspond to low-frequency ratios and are the most (structurally) stable and attractive. Because of their width, any parameter variation inside these larger Arnol'd tongues will not kick the system somewhere else. As a consequence, fat Arnol'd tongues containing the $2:1$, $3:1$, $3:2 \dots$ coordination modes are relatively easier to perform than slim ones ($4:3$, $5:2 \dots$).²⁵

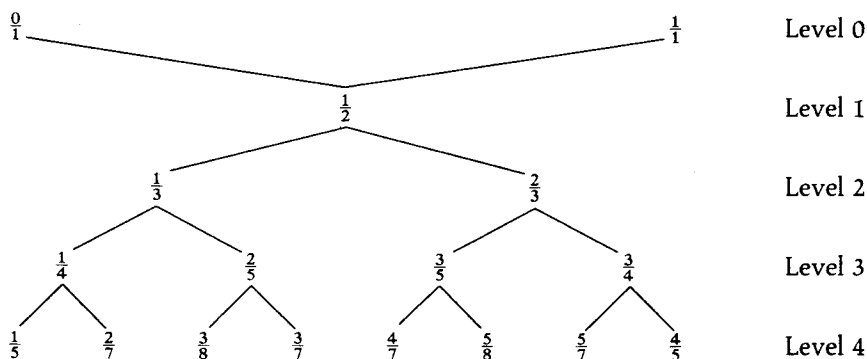
The Farey Tree: Hierarchical Complexity

Notice in plate 3 and to a lesser extent in figure 4.11 how the widths of the mode-locked regions are ordered. Scanning from left to right, the biggest tongues order as

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

This *Farey sequence* represents an increasing succession of rational numbers p/q such that $q \leq n$ where $n = 4$ in this case. It is possible to order the mode-locked regions (the rational numbers between 0 and 1) into a hierarchy called the *Farey tree*. The power of mathematics shows up again: the branching structure of the tree encapsulates all the possible mode-lockings in this entire class of dynamical systems. To grow the tree, start with the parents $0/1$ and $1/1$. Add the numerators and denominators together according to the formula $p/q \oplus p'/q' \equiv p + p'/q + q'$, forming successive levels as follows:

Figure 4.11 Arnol'd tongues for the phase-attractive circle map showing mode-locked regions for some of the lower-order (non-1:1) mode-locked regions. (a) $A = 0$ yields the familiar result for the sine circle map. (b) $A = 0.5$ produces a widening effect on the tongues. In both cases, the relative widths of the tongues provide a basis for the differential stability and complexity of multifrequency coordination. Quasi-periodic dynamics exists between the tongues.



Level 1 is created by the Farey sum $0/1 \oplus 1/1 = 1/2$. The branches of level 2 are given by $0/1 \oplus 1/2 = 1/3$ and $1/1 \oplus 1/2 = 2/3$... and so on. Notice in figure 4.11 and plate 3 the lowest denominator tongues are the widest. No wonder they are the easiest to get into and stay in. In our theory, pattern stability and complexity are related to the level in the Farey tree hierarchy and are inversely proportional to tongue width.

Multifrequency Transitions

How does the Arnol'd tongue structure envisage *transitions* in coordination between multifrequency states? How does the rhythm change? In principle, all the system has to do is cross from one tongue to the other. This might sound easier than it looks. It is clear, for example, that a system buried deep inside one of the tongues is pretty stable despite parameter changes or the influence of noise. As I said before, this fact is significant for rationalizing the dominance of the low-order frequency ratios. But it is also obvious that the width (stability) of the mode-locked regions plays a role in determining which patterns are easiest to switch into and out of.

In our experiments, spontaneous transitions are far more likely from the less stable frequency ratios to the more stable frequency ratios than vice versa, just as the Farey tree would predict.²⁶ This may be one of the reasons why people (even the best musicians) have to practice so hard to produce intricate rhythms: any little noise will kick the system into one of the more stable ("easier") Arnol'd tongues. Learning complex rhythms in this context involves stabilizing higher-order frequency ratio states (there's much more to it than that, of course, as we'll see in chapter 6). Just getting into these thin Arnol'd tongues is tricky. The fat ones are far stickier.

Between the tongues sprouting from $K = 0$ in figure 4.11, the dynamics are quasi-periodic, the frequency ratio is irrational. As K increases, the Arnol'd tongues widen and eventually touch each other on the *critical surface*. Above the critical surface, the tongues overlap and the system can display chaos (see box and plate 3).

Tongue overlapping is a necessary but not sufficient condition for chaos. For example, as you can see in plate 3, it is possible to stay in a 2 : 1 ratio far

THE CASE OF THE CRINKLED TORUS

The *most* irrational ratio or winding number is the golden-mean, $(\sqrt{5} - 1)/2$, which is the easiest place to observe quasi-periodicity experimentally. Why? Because it's the *least* likely to lock into a low denominator tongue (rationality, as it were!). The golden mean therefore is the last exit before irrationality turns into chaos. A beautiful physical experiment by Albert Libchaber—one of my favorites ever—was conducted on Rayleigh-Bénard convection in a small mercury-filled rectangular cell.²⁷ After an *oscillatory instability* was set up, producing a well-defined frequency of rolling motion (f_1) in the cell, Libchaber et al. injected a small alternating current of a certain amplitude and frequency, f_2 . The experiment resembles someone stirring a pot of soup while heating it on a stove. Since f_1 is time independent, locking behavior can be studied by manipulating current amplitude and f_2 . The entire Arnol'd tongue structure can then be beautifully mapped out and all the circle map predictions tested. By far the strongest image imprinted on my mind is near the critical surface where the two frequencies have been set up at the golden mean and the nonlinear coupling (by the current amplitude) increased. The 2-torus starts to break down, and the attractor becomes stretched and crinkled, indicating the onset of chaos (figure 4.12). Extra dimensions start to make themselves felt. Turbulence (high-dimensional behavior) is just over the horizon, and you can *feel* it in this picture.

beyond the point at which the tongues overlap. Notice, however, how the shape of the Arnol'd tongues and the overall complexity of the space depends on parameters. For instance, for fixed K and Ω , the variation of the intrinsic parameter, A , raises and lowers the critical surface, hence affecting the onset of chaos. The variation of these parameters determines the width of the stable mode-locked regions consequently delaying or accelerating irregular behavior. A familiar (by now) message appears in a different guise: *where the system lives in parameter space dictates the complexity of its behavior.*

The Devil's Staircase

A universal feature of maps such as our phase-attractive circle map is that at the critical surface the mode-locked tongues fill up the line. This is called the *Devil's staircase*.²⁸ The reason is that if you blow up or magnify any piece of it, you see the same thing. So, in some sense, dear pilgrim, you'll never make it to the top! Tom Holroyd did an interesting numerical experiment calculating the widths of the tongues in our map by plotting the winding number against Ω for various values of A and K . Below the critical surface, the length of the mode-locked regions is less than 1, and so the Devil's staircase is incomplete. But the smaller the steps you take the smaller the gap between mode lockings, until, at criticality, there is no longer any room for quasiperiodicity, and the staircase is said to be complete.

Figure 4.13 shows the complete staircase for three sets of different parameter values for our map. The similarity between the staircases is compelling, attesting to the universality property of these kinds of dynamical systems.

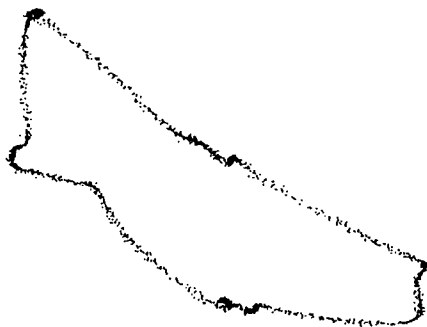


Figure 4.12 The crinkled torus observed in Libchaber's Bénard convection experiment. The winding number is close to the golden mean, and breakdown of the torus is imminent. (Reprinted with kind permission of The Royal Society)

Physicists take universality to be crucial, because without it they would not be able to predict the results of experiments in systems in which the underlying map (the dynamics) is unknown. Of course, this is usually, if not always, the case in biology and behavior.

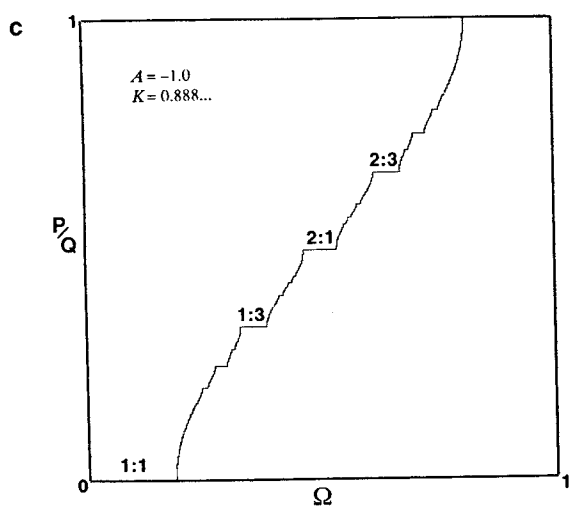
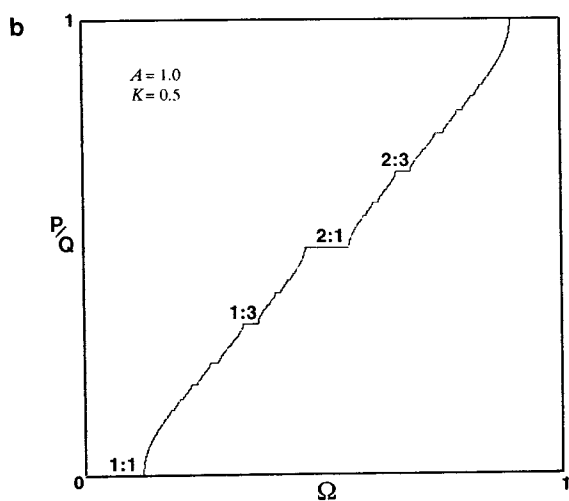
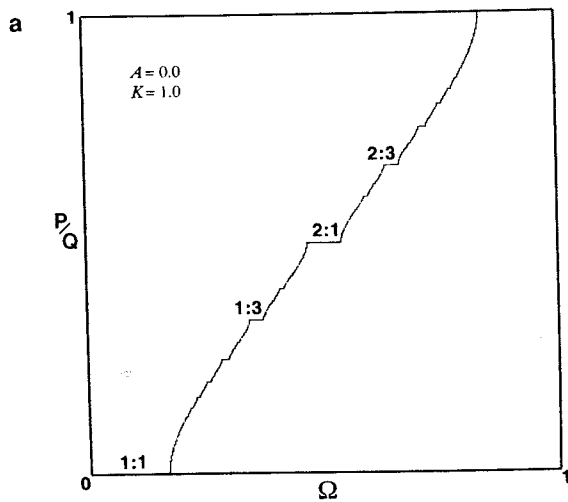
When one examines these staircase plots in figure 4.13 one sees differences as well. In particular, the *relative* width of the tongues changes with the phase-attractive term, A , our intrinsic parameter. I find it interesting that a parameter derived from our phase-transition experiments that reflects the bistability of the phase states at $\phi = 0$ and π changes the size, for example, of the 2 : 3 ratio relative to 1 : 2.

Although it's well-nigh impossible to manipulate all the Arnol'd tongues in any biological experiment, never mind on humans, some years ago Gonzalo DeGuzman and I obtained results that are at least consistent with the mode-locking picture²⁹ (see below). Very similar results were obtained recently using different procedures.³⁰ Taken collectively, this work demonstrates the potential power of the dynamical account of multifrequency coordination. But a lot more could be done to unpack further Iberall and McCulloch's "orbital constellations."

Life at the Edge

The greatest flexibility is afforded a coordinative system when it is near the tongue boundaries where transitions to other modes are easily effected. The reason is that mode lockings in the phase-attractive map are created and destroyed through tangent or saddle node bifurcations that occur at the boundaries of Arnol'd tongues (cf. chapter 1). In other words, for motion on a

Figure 4.13 The Devil's staircase. At the critical surface, Arnol'd tongues completely fill the Ω -axis, except for a set (the Cantor set) of measure zero. The width of the mode-locked intervals is dependent on the parameters A and K . (a) $A = 0$, $K = 1.0$; (b) $A = 1.0$, $K = 0.5$; (c) $A = -1.0$, $K = 0.888 \dots$



torus, transition pathways are by intermittency, the dynamical mechanism I proposed earlier for relative coordination. What does intermittency look like in our map, and does it really produce the relative coordination effect? For a change, let's do the analysis quantitatively with numbers.

I present an example in figure 4.14 in which I vary the values of Ω near the period 1 boundary, that is, near a 1 : 1 phase and frequency-synchronized state. The boundary in this case ($A = 0$) is defined by $K = 2\pi\Omega$. For $K = 0.6$, the saddle node bifurcation occurs at $\Omega_c = 0.6/2\pi \approx 0.0455$. Figure 4.14a shows the function $f(\phi)$ intersecting the diagonal line at two points: ϕ^- and ϕ^+ , where ϕ^- is a fixed point (mode locked) attractor and ϕ^+ is a fixed point repeller ($\Omega = \Omega_c - 0.03$). Initial conditions other than exactly $\phi = \phi^+$ converge to ϕ^- as $n \rightarrow \infty$. As Ω increases, ϕ^- and ϕ^+ approach each other and coalesce when $\Omega = \Omega_c$ (figure 4.14b). For $\Omega = \Omega_c + 0.01$ beyond the boundary of the Arnol'd tongue, ϕ^- and ϕ^+ cease to exist (figure 4.14c), and the system exhibits either mode lockings with higher-frequency ratios or quasi-periodic motion, depending on the exact location of Ω . If Ω is decreased, then the reverse sequence of events is observed.

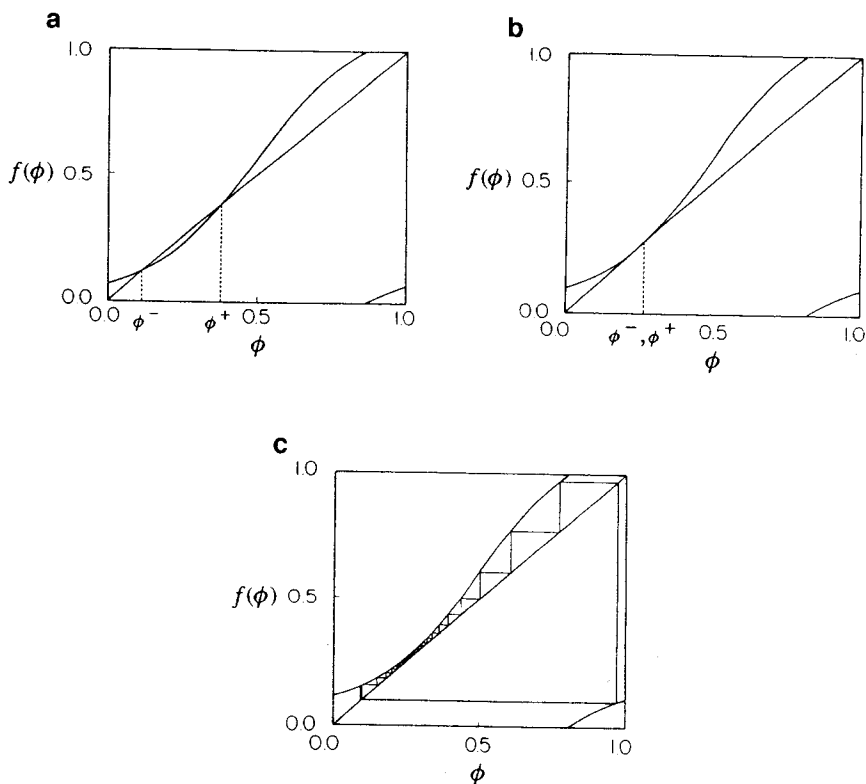


Figure 4.14 Intermittency in the phase-attractive map. Shown is the function $f(\phi)$ for three values of Ω . ϕ^- and ϕ^+ correspond to stable and unstable fixed points of the map. Notice in (b) the two coalesce at a saddle node bifurcation and then lift off in (c), giving rise to intermittent dynamics (see text).

The narrow corridor between the function $f(\phi)$ and the diagonal line in figure 4.14c induces what the French physicists Yves Pomeau and Paul Manneville call *type I intermittency*.³¹ The dynamical behavior is as follows. Inside the channel, iterates of the map move very slowly, 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. That is, *phase slippage* occurs and there is no longer any mode locking, because the fixed points have disappeared. Only a faint trace of them remains.

The appearance of phase slippage means that between two channel crossings one of the oscillators gains a period: exactly the phenomenon of *relative coordination* (see again figure 4.2a). Slips in phase occur because of the unstable direction: the system escapes to explore other regions of its space before

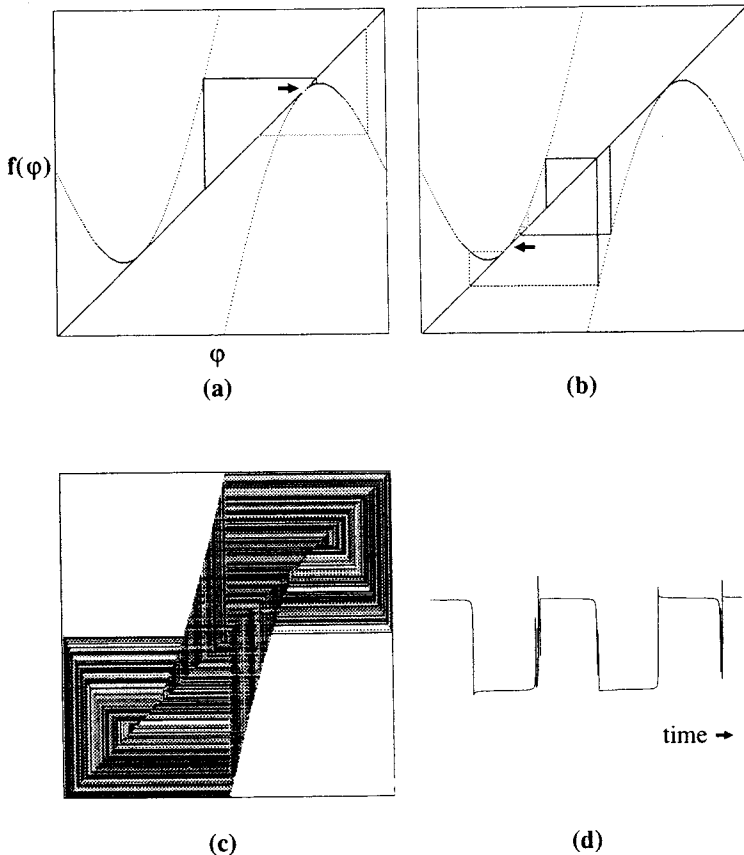


Figure 4.15 Intermittency in the chaotic regime of the phase-attractive circle map. In (a) there is a stable fixed point on the right lobe which attracts initial conditions (see arrow). (b) same as (a) except attraction is to a fixed point on the left lobe. (c) When the function is lifted off the diagonal, spontaneous switching between the fixed points occurs via a chaotic transient, as shown by the time series in (d).

wandering back into the channel (due to the 2π periodicity of ϕ), where it visits once more the remnant of the fixed point. It is just like the father walking along with his small child who, because of their intrinsically different cycle periods, must either slow down (father) or add steps (child) to keep pace with each other. The father-child system is poised near the ghost of mode-locked states (fixed points), relatively but not absolutely coordinated. The main dynamical mechanism (figure 4.14b) is the coalescence of stable (attracting) and unstable (repelling) directions in the coordination dynamics. Both stabilizing and destabilizing processes must, it seems, coexist.

When we move into the chaotic region of the dynamics the same basic mechanism is present. In figure 4.15 I show the map in the noninvertible region beyond the critical surface, where the torus breaks down. For $\Omega = 0.5$, that is, a 2 : 1 frequency ratio, and strong coupling there is a double “hump,”

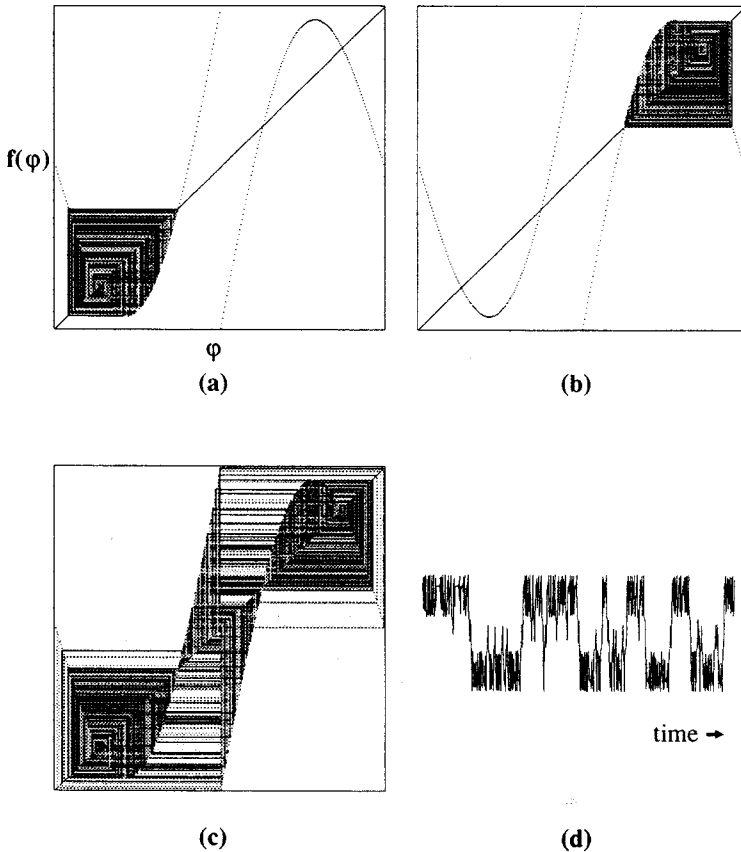


Figure 4.16 Chaotic-chaotic transitions in the phase-attractive circle map. (a) shows a chaotic attractor in the left lobe of the state space, (b) shows a different chaotic attractor in the right lobe, and (c) shows a connection between them, creating a two lobed attractor in which motion jumps spontaneously from one lobe to the other. Note in the time series (d) that motion is chaotic in each lobe.

each containing a stable fixed point. Which one is observed depends on initial conditions (figure 4.15a and b). When the function is lifted slightly off the line (figure 4.15c) the system escapes through a portal, jumping between the two nearly mode-locked states, via a chaotic transient. Figure 4.15d shows the corresponding time series. Such a process may well underlie the kind of perceptual switching that occurs when observers view ambiguous figures like the Necker cube (see Chapter 7) as well as the intermittent switching observed in ion channel kinetics (see chapter 8).

Finally, our map may possess two *chaotic attractors* with independent basins of attraction.³² A random initial condition falls into one of the attractors and stays there (figure 4.16a and b). With a small parameter change, a single two-lobed attractor emerges, composed of the two original attractors connected through small portals in the phase space. A chaotic trajectory is followed inside one of the lobes until it escapes and falls into the other lobe (figure 4.16c). The time series in figure 4.16d illustrates the way the system switches randomly back and forth between these states. Although fluctuations are obviously important in biological systems, these switches are actually deterministic and not the result of noise. The slightest parameter change causes escape from the basin of one chaotic attractor to the other, reminiscent of conceptual leaps.³³

Experimental Windows on Intermittency

Much of von Holst's work on the nature of order in the central nervous system was performed on *Labrus*, a fish distinguished by the fact that it swims smoothly using rhythmic fin movements but keeps its main body axis immobile. Von Holst referred to this preparation, in true Germanic style, as his *precision apparatus* (italics his). The time series shown in figure 4.2 are from *Labrus*. The coordination is either at (absolute) or near (relative) 1 : 1 mode locking.

I have a "precision apparatus" too, custom made and especially configured for driving and monitoring the movements of the two hands simultaneously.³⁴ In a series of experiments done with Gonzalo DeGuzman we manipulated the frequency ratio between the two hands. It is very difficult to require a subject to produce high-order frequency ratios on demand. My idea was to drive one finger passively using a torque motor while the other finger maintained a base rhythm. This allowed us to scan the frequency ratio in small steps (0.1 Hz) every 20 seconds or so from just below 1 : 1 to just above 2 : 1. We found beautiful evidence for intermittent dynamics in the human sensorimotor system.

A typical time series from the experiment is shown in figure 4.17. The required frequency ratio is set near 2 : 1, not 1 : 1 as in figure 4.2. The input signal used to drive the torque motor is on top. The *actual trajectory* of the driven hand is in the middle. Notice it does not exactly follow the driver. The free hand, moving at its base rhythm, is on the bottom. Enhancement of the

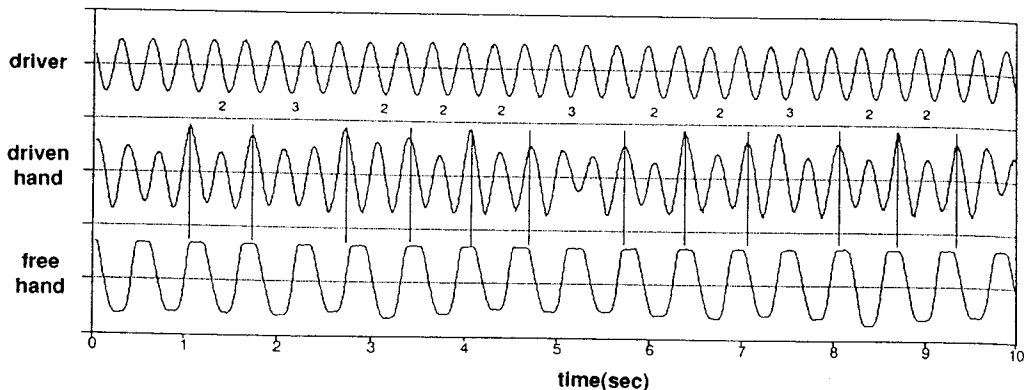


Figure 4.17 Relative coordination near a 2:1 required frequency ratio. Trajectories of the input signal used to drive the torque motor (*top*), the actual motion produced by the driven hand (*middle*), and the free hand (*bottom*). Enhancement of the peaks near in-phase regions points to the discrete nature of the coordination. Occasional but systematic slips are evident when the enhanced peak extends beyond the broadened peak of the free hand (3 steps instead of 2).

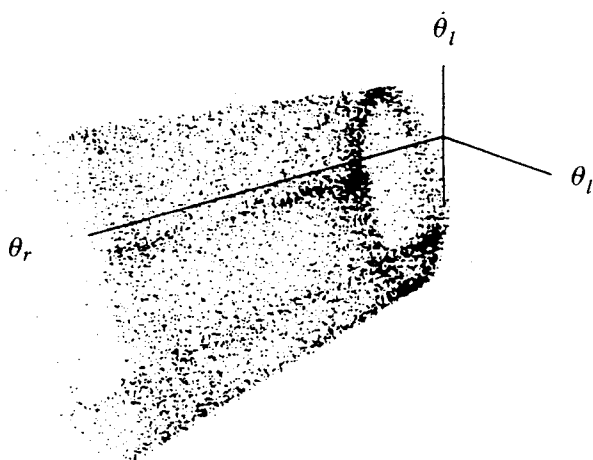


Figure 4.18 Phase space portrait of a 2:1 case in the Kelso and DeGuzman experiment. θ_l and θ_r correspond to the angular position of the left and right hands; $\dot{\theta}_l$ is the angular velocity of the left hand. the dark bands show phase concentration around 0 and π . The length of these bands is due to flattening of the right-hand trajectories at the crests and troughs.

peaks near in-phase coordination attests once more to the discrete nature of coordination. More important here, however, is that the driven hand adjusts its trajectory to sustain the natural tendency to be in phase with the slower free hand. Follow the vertical lines on figure 4.17 from left to right. Occasional slips occur when the position of the enhanced peak extends beyond the broadened peak of the free hand. Three steps instead of two! This experimental system, our little window into life, resides on the edge of the mode-locked state, not in it.

Figure 4.18 shows a 3-D plot of a 2 : 1 condition in which the position and velocity of the driven hand occupy the x - and y -axes, and the position of the free hand is plotted continuously on the z -coordinate. The reason a nice limit cycle is observed is because the driving torque is sufficiently large that the hand has to follow it. Two bands of phase concentration on the driven cycle show up clearly around $\phi = 0$ and π . This is because in this case the free hand visits these states for prolonged periods of time before wandering away. The length of the dark bands is due to flattening of the free hand trajectories at the crests and troughs of its motion. Here we see the same relative coordination effect produced in a different way that nevertheless attests to the mutual cooperation between the components.

When I first presented these results in 1987 at one of Hermann Haken's famous Elmau meetings (this one on neural and synergetic computers) I remarked, paraphrasing Arnold Mandell:

Neurobiological dynamical systems lack stationarity: their orbital trajectories visit among and jump between attractor basins from which (after relatively short times) they are spontaneously "kicked out" by their divergent flows.

Using the map, it is easy to plot the relative phase distributions corresponding to mode-locked and intermittent regimes of the coordination dynamics. One look at these distributions strengthens the theory that absolute and relative coordination, the two basic dynamic forms, correspond to mode locking and intermittent regimes of the coordination dynamics. The reader can prove this by iterating our map on a computer and plotting a histogram of the phases visited. That's what is displayed in figure 4.19 for parameters that are set near 2 : 1 (i.e., $\Omega \approx 0.5$). The map is iterated 10,000 times and plotted after removal of any initial transients. Three distributions are shown, with the same number of data points in each. Relative phase $[0, 2\pi]$ is on the horizontal axis expressed on the unit interval $[0, 1]$. As the frequency ratio parameter is brought closer to 2 : 1, the peaks near $\phi = 0$ (~ 0.1) and $\phi = \pi$ (~ 0.5) become higher and narrower. The system still visits all possible phase states, but less so than when it is farther away from the mode-locked state. Were one to enter the 2 : 1 Arnol'd tongue without adding a little noise, two straight lines exactly at the absolutely coordinated phase states would be observed with approximately the same number of points (~ 5000) in each. Comparison with von Holst's phase distributions in figure 4.2 is irresistible.

Anticipation ...

The trajectories displayed in figures 4.2 and 4.17 exhibit a phenomenon that one might call, for want of a better word, *anticipation*. Notice as the vertical lines progressively strike the broadened peaks in figure 4.17 (third row) they reach a point at the edge where we *know* an extra step is going to be inserted. The system itself is clearly sensitive to the fact that if it doesn't adapt quickly, coordination and communication will be lost. Literally, in our system, it will behave irrationally. How do we understand this anticipatory effect?

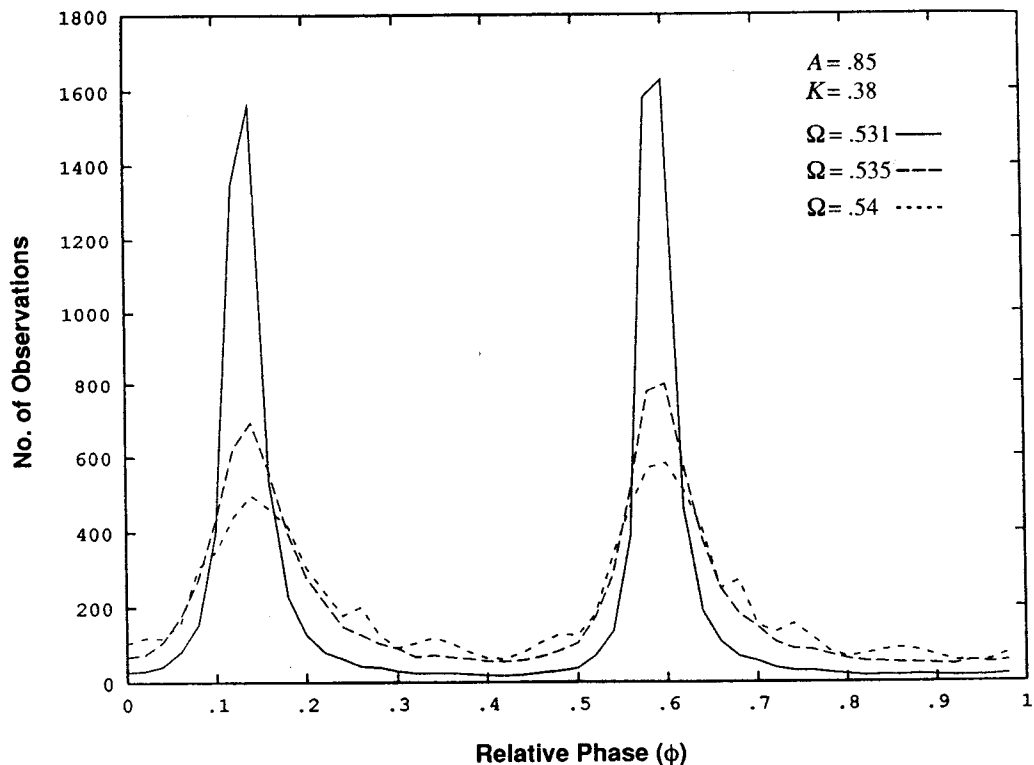


Figure 4.19 Histogram of the relative phase distributions in the intermittent regime of the phase-attractive map near a frequency ratio of 2:1 ($\Omega = .5$). Notice the peaks become smaller and more dispersed as the frequency ratio moves away from the 2:1 mode-locked state.

Referring back to figure 4.14c, note that close to the tangent bifurcation, the relative phase concentrates and slows. Phase attraction persists because the iterates are trapped in the corridor separating the function and the 45-degree line. Obviously, as the system approaches closer and closer to the fixed point, the time spent in the channel gets longer and longer (critical slowing in another guise!). This phase gathering has an anticipatory quality about it. Even though the motion is quasi-regular, it is easy to predict where and when the mode-locked state is going to reveal itself.

A good way to see this is through the corresponding bifurcation diagrams shown in figure 4.20. The bifurcation parameter, K , in this case, is varied along the x -axis and the relative phase, ϕ , is on the y -axis. The fuzzy area corresponds (mostly) to quasi-periodic motion because the frequency ratio between the components is irrational. By the way, the gaps inside the fuzziness are higher-order, very thin, mode-locked regions. Notice, however, that the progressive darkening anticipates the upcoming stable solution (the single line), which indicates that coordination is trapped or mode locked 1:1 in figure 4.20a or 2:1 in figure 4.20b.

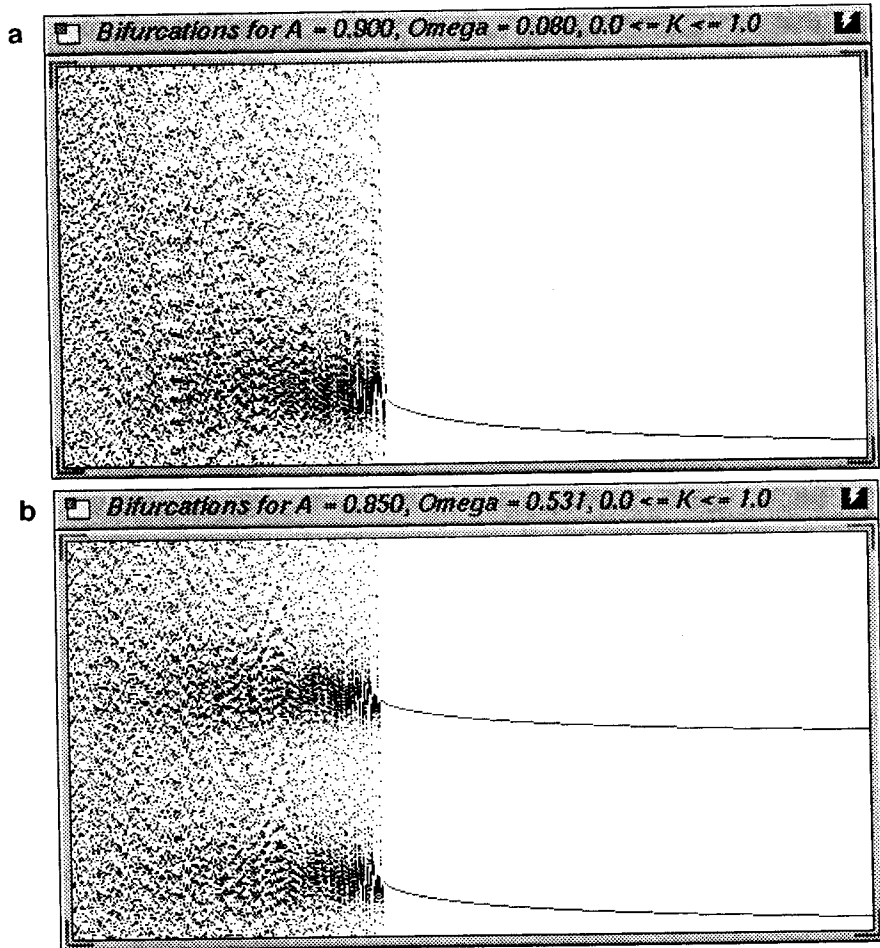


Figure 4.20 Anticipation? Bifurcation diagram showing the phase behavior when crossing the Arnol'd tongues at (a) 1:1 and (b) 2:1 for fixed A and increasing K . Progressive darkening “anticipates” upcoming stable solutions (single lines), which indicate that coordination is trapped or mode locked.

The main point is that the system spends more time near a particular phase as it approaches a critical point, giving rise to an enhanced phase density that specifies the locus of the upcoming state. Critical slowing (the darkening effect) is thus a predictor of upcoming transitions. Somewhat facetiously (but not entirely), I refer to this aspect of the coordination dynamics as an anticipatory dynamical system (ADS).³⁵ An ADS stays in contact with the future by living near critical points.

POSTSCRIPT

For me, there can hardly be a more powerful image of the central thesis here—that materially complex biological systems may exhibit low-dimensional,

but complex dynamical behavior—than the demonstrated tendencies for humans to exhibit limited forms of spatiotemporal organization among themselves or their components. Although I hesitate to use the heady language of universality, nevertheless, a remarkable, possibly quite profound, connection seems to exist among physical, biological, and psychological phenomena. “Phenomenon” is often a dirty word in the softer sciences, somehow suggesting failure to come to grips with “mechanisms” and settling instead for “description.” Often mechanisms for a given phenomenon are sought at lower levels in the interior workings of the system. That view may be flawed if lower levels also turn out to be governed by the same kinds of self-organized dynamical principles or generic mechanisms shown to be at work here.

In this book, I use the word *phenomenon* very much in the style of physics, to refer to observations obtained under specific circumstances including an account of the entire experiment.³⁶ This does not mean one cannot go beyond the specifics of the experiment to some deeper theoretical framework. The phenomena of absolute, and, to a lesser degree, relative coordination have been around a long time: their connection to concepts of self-organization in nonequilibrium systems and their expression in terms of dynamical laws is, I think, quite recent. Up to now, the early discoveries of von Holst and his generally valid descriptions of biological coordination, even though widely recognized, were not accompanied by a successful theoretical treatment. This had to wait for the concepts of synergetics to handle cooperative interactions, and the appropriate mathematical tools of nonlinear dynamical systems to formalize them.

In this chapter it has been difficult to contain my excitement at the recognition of unity between features of complex coordination phenomena that previously appeared quite unconnected. Absolute and relative coordination, the two basic dynamic forms, correspond to mode locking and intermittency, now unified in a single theory. Both absolute and relative coordination spring from a basic symmetry in the collective variable, relative phase. Symmetries run the laws of physics and are always tied to conservation principles. The mathematical language of symmetries dominates all the way from the conservation of momentum and energy in classical physics to the fundamental particles of quantum mechanics. Does a new conservation principle underlie coordination? Perhaps. The concept of stability seems equally if not more important, because, as shown here, coordinative states may possess equivalent symmetry yet not be equally stable.

It is the breaking of symmetry that gives rise to the complex of phenomena collectively called relative coordination. Phase slippage and the injection of additional steps correspond to the intermittent regime of the coordination dynamics. The main *generic mechanism* is the coalescence near tangent bifurcations of stable (attracting) and unstable (repelling) fixed points in the coordination dynamics. In this flexible, intermittent regime, systems exhibit phase

attraction but not phase locking or phase entrainment. The collective variable is nonstationary, it does not converge asymptotically.

When Mozart wrote to his father about three piano concertos he had just completed, he is reported to have said, "They are exactly between too hard and too easy: the connoisseurs will find satisfaction, but the nonexperts will feel content without knowing why." That's relative coordination, in between the hard and the easy, the regular and the irregular where the creative pulse beats.