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Coupled Oscillators and Biological Synchronization

A subtle mathematical thread connects clocks, ambling elephants, brain rhythms and the onset of chaos

by Steven H. Strogatz and Ian Stewart

In February 1665 the great Dutch physicist Christiaan Huygens, inventor of the pendulum clock, was confined to his room by a minor illness. One day, with nothing better to do, he stared aimlessly at two clocks he had recently built, which were hanging side by side. Suddenly he noticed something odd: the two pendulums were swinging in perfect synchrony.

He watched them for hours, yet they never broke step. Then he tried disturbing them—within half an hour they regained synchrony. Huygens suspected that the clocks must somehow be influencing each other, perhaps through tiny air movements or imperceptible vibrations in their common support. Sure enough, when he moved them to opposite sides of the room, the clocks gradually fell out of step, one losing five seconds a day relative to the other.

Huygens's fortuitous observation initiated an entire subbranch of mathematics: the theory of coupled oscillators. Coupled oscillators can be found throughout the natural world, but they are especially conspicuous in living things: pacemaker cells in the heart; insulin-secreting cells in the pancreas; and neural networks in the brain and spinal cord that control such rhythmic behaviors as breathing, running and chewing. Indeed, not all the oscillators need be confined to the same organism: consider crickets that chirp in unison and congregations of synchronously flashing fireflies [see "Synchronous Fireflies," by John and Elisabeth Buck; SCIENTIFIC AMERICAN, May 1976].

Since about 1960, mathematical biologists have been studying simplified models of coupled oscillators that retain the essence of their biological prototypes. During the past few years, they have made rapid progress, thanks to breakthroughs in computers and computer graphics, collaborations with experimentalists who are open to theory, ideas borrowed from physics and new developments in mathematics itself.

To understand how coupled oscillators work together, one must first understand how one oscillator works by itself. An oscillator is any system that executes periodic behavior. A swinging pendulum, for example, returns to the same point in space at regular intervals; furthermore, its velocity also rises and falls with (clockwork) regularity.

Instead of just considering an oscillator's behavior over time, mathematicians are interested in its motion through phase space. Phase space is an abstract space whose coordinates describe the state of the system. The motion of a pendulum in phase space, for instance, would be drawn by releasing the pendulum at various heights and then plotting its position and velocity. These trajectories in phase space turn out to be closed curves, because the pendulum, like any other oscillator, repeats the same motions over and over again.

A simple pendulum consisting of a weight at the end of a string can take any of an infinite number of closed paths through phase space, depending on the height from which it is released. Biological systems (and clock pendulums), in contrast, tend to have not only a characteristic period but also a characteristic amplitude. They trace a particular path through phase space, and if some perturbation jolts them out of their accustomed rhythm they soon return to their former path. If someone startles you, say, by shouting, "Boo!", your heart may start pounding but soon relaxes to its normal behavior.

Oscillators that have a standard waveform and amplitude to which they return after small perturbations are known as limit-cycle oscillators. They incorporate a dissipative mechanism to damp oscillations that grow too large and a source of energy to pump up those that become too small.

A single oscillator traces out a simple path in phase space. When two or more oscillators are coupled, however, the range of possible behaviors becomes much more complex. The equations governing their behavior tend to become intractable. Each oscillator may be coupled only to a few immediate neighbors—as are the neuromuscular oscillators in the small intestine—or it could be coupled to all the oscillators in an enormous community. The situation mathematicians find

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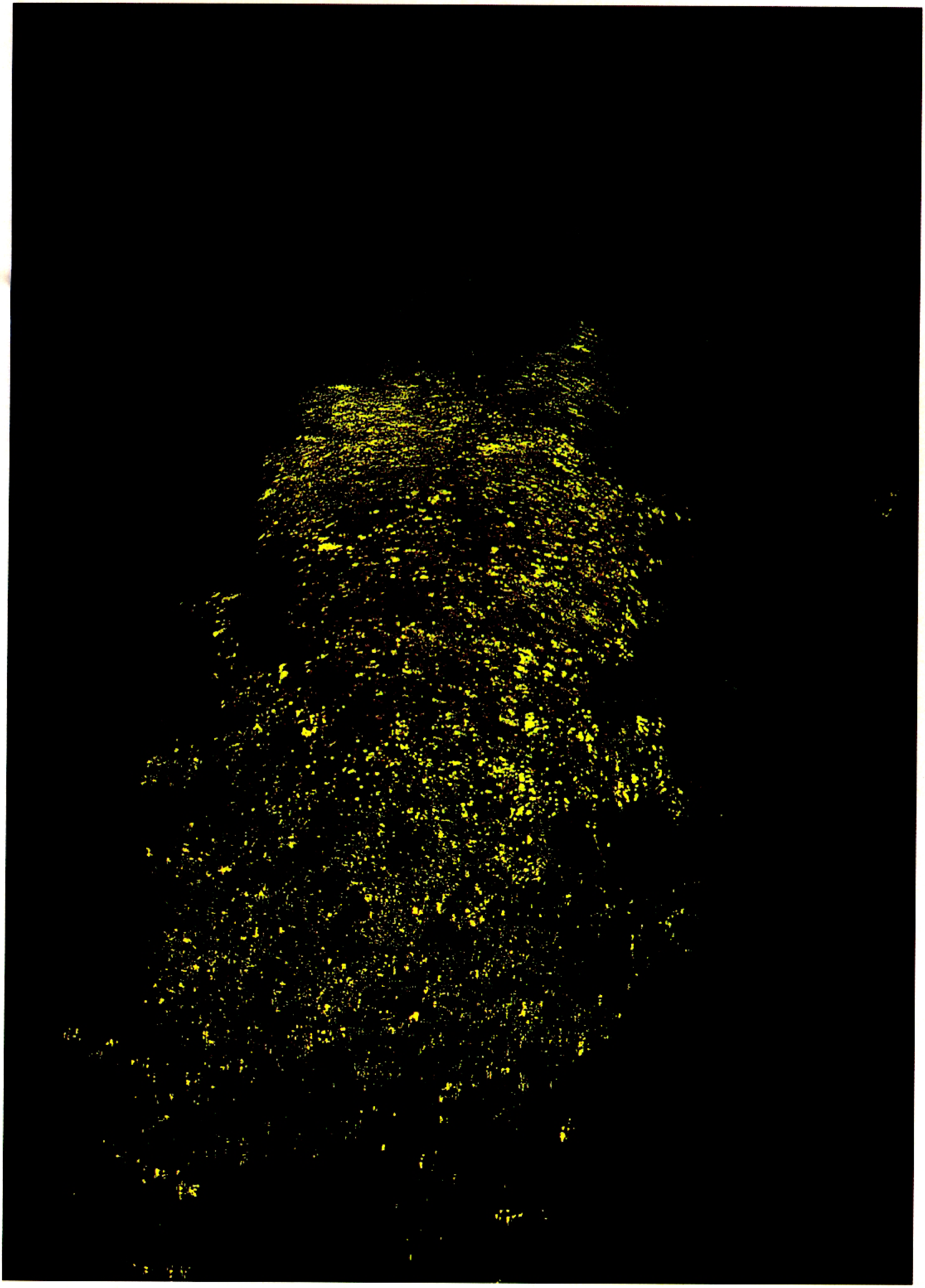
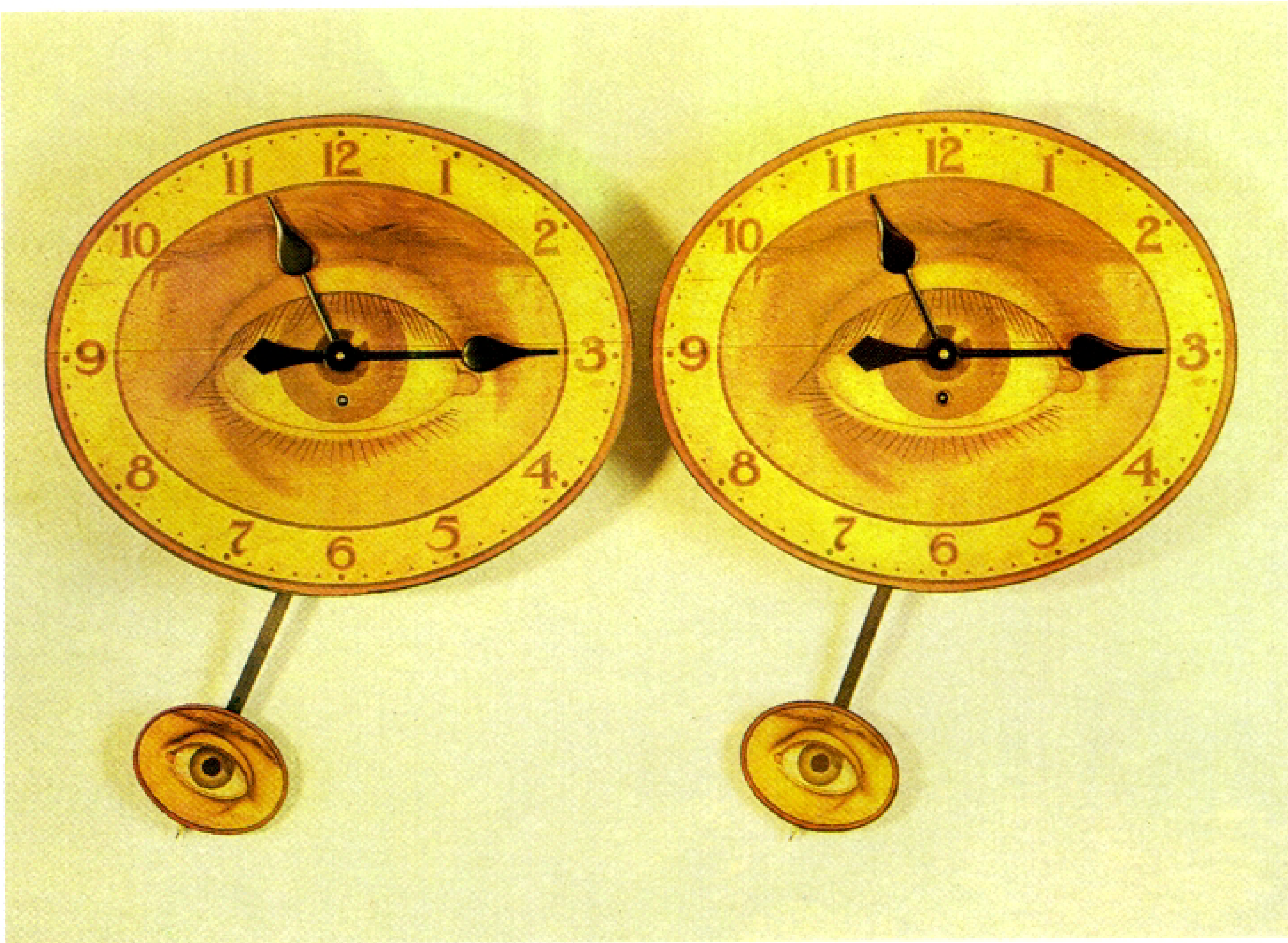
THOUSANDS OF FIREFLIES flash in synchrony in this time exposure of a nocturnal mating display. Each insect has its own rhythm, but the sight of its neighbors' lights brings that rhythm into harmony with those around it. Such couplings among oscillators are at the heart of a wide variety of natural phenomena.





PENDULUM CLOCKS placed near each other soon become synchronized (*above*) by tiny coupling forces transmitted through the air or by vibrations in the wall to which they are attached. Dutch physicist Christiaan Huygens invented the pendulum clock and was the first to observe this phenomenon, inaugurating the study of coupled oscillators.

easiest to describe arises when each oscillator affects all the others in the system and the force of the coupling increases with the phase difference between the oscillators. In this case, the interaction between two oscillators that are moving in synchrony is minimal.

Indeed, synchrony is the most familiar mode of organization for coupled oscillators. One of the most spectacular examples of this kind of coupling can be seen along the tidal rivers of Malaysia, Thailand and New Guinea, where thousands of male fireflies gather in trees at night and flash on and off in unison in an attempt to attract the females that cruise overhead. When the males arrive at dusk, their flickerings are uncoordinated. As the night deepens, pockets of synchrony begin to emerge and grow. Eventually whole trees pulsate in a silent, hypnotic concert that continues for hours.

Curiously, even though the fireflies' display demonstrates coupled oscillation on a grand scale, the details of this behavior have long resisted mathematical analysis. Fireflies are a paradigm of a "pulse coupled" oscillator system: they interact only when one sees the sudden flash of another and shifts its rhythm accordingly. Pulse coupling is common in biology—consider crickets chirping or neurons communicating via electrical spikes called action potentials—but the impulsive character of the coupling has rarely been included in mathematical models. Pulse coupling is awkward to handle mathematically because it introduces discontinuous behavior into an otherwise continuous model and so stymies most of the standard mathematical techniques.

Recently one of us (Strogatz), along with Renato E. Mirollo of Boston College, created an idealized mathematical model of fireflies and other pulse-coupled oscillator systems. We proved that under certain circumstances, oscillators started at different times will always become synchronized [see "Electronic Fireflies," by Wayne Garver and Frank Moss, "The Amateur Scientist," page 94].

Our work was inspired by an earlier study by Charles S. Peskin of New York University. In 1975 Peskin proposed a highly schematic model of the heart's natural pacemaker, a cluster of about 10,000 cells called the sinoatrial node. He hoped to answer the question of how these cells synchronize their individual electrical rhythms to generate a normal heartbeat.

Peskin modeled the pacemaker as a large number of identical oscillators, each coupled equally strongly to all the others. Each oscillator is based on an electrical circuit consisting of a capacitor in parallel with a resistor. A constant input current causes the voltage across the capacitor to increase steadily. As the voltage rises, the amount of current passing through the resistor increases, and so the rate of increase slows down. When the voltage reaches a threshold, the capacitor discharges, and the voltage drops instantly to zero—this pattern mimics the firing of a pacemaker cell and its subsequent return to baseline. Then the voltage starts rising again, and the cycle begins anew.

A distinctive feature of Peskin's model is its physiologically plausible form of pulse coupling. Each oscillator affects the others only when it fires. It kicks their voltage up by a fixed amount; if any cell's voltage exceeds the threshold, it fires immediately. With these rules in place, Peskin stated two provocative conjectures: first, the system would always eventually become synchronized; second, it would synchronize even if the oscillators were not quite identical.

When he tried to prove his conjectures, Peskin ran into technical roadblocks. There were no established mathematical procedures for handling arbitrarily large systems of oscillators. So he backed off and focused on the simplest possible case: two identical oscillators. Even here the mathematics was thorny. He restricted the problem further by allowing only infinitesimal kicks and infinitesimal leakage through the resistor. Now the problem became manageable—for this special case, he proved his first conjecture.

Peskin's proof relies on an idea introduced by Henri Poincaré, a virtuoso French mathematician who lived in the early 1900s. Poincaré's concept is the mathematical equivalent of stroboscopic photography. Take two identical pulse-coupled oscillators, *A* and *B*, and chart their evolution by taking a snapshot every time *A* fires.

What does the series of snapshots look like? *A* has just fired, so it always appears at zero voltage. The voltage of *B*, in contrast, changes from one snapshot to the next. By solving his circuit equations, Peskin found an explicit but messy formula for the change in *B*'s voltage between snapshots. The formula revealed that if the voltage is less than a certain critical value, it will decrease until it reaches zero, whereas if it is larger, it will increase. In either case, *B* will eventually end up synchronized with *A*.

There is one exception: if *B*'s voltage is precisely equal to the critical voltage, then it can be driven neither up nor down and so stays poised at criticality. The oscillators fire repeatedly about half a cycle out of phase from each other. But this equilibrium is unstable, like a pencil balancing on its point. The slightest nudge tips the system toward synchrony.

Despite Peskin's successful analysis of the two-oscillator case, the case of an arbitrary number of oscillators eluded proof for about 15 years. In 1989 Strogatz learned of Peskin's work in a book on biological oscillators by Arthur T. Winfree of the University of Arizona. To gain intuition about the behavior of Peskin's model, Strogatz wrote a computer program to simulate it for any number of identical oscillators, for any kick size and for any amount of leakage. The results were unambiguous: the system always ended up firing in unison.

Excited by the computer results, Strogatz discussed the problem with Mirollo. They reviewed Peskin's proof of the two-oscillator case and noticed that it could be clarified by using a more abstract model for the individual oscillators. The key feature of the model turned out to be the slowing upward curve of voltage (or its equivalent) as it rose toward the firing threshold. Other characteristics were unimportant.

Mirollo and Strogatz proved that their generalized system always becomes synchronized, for any number of oscillators and for almost all initial conditions. The proof is based on the notion of "absorption"—a shorthand for the idea that if one oscillator kicks another over threshold, they will remain synchronized forever. They have identical dynamics, after all, and are identically coupled to all the others. The two were able to show that a sequence of absorptions eventually locks all the oscillators together.

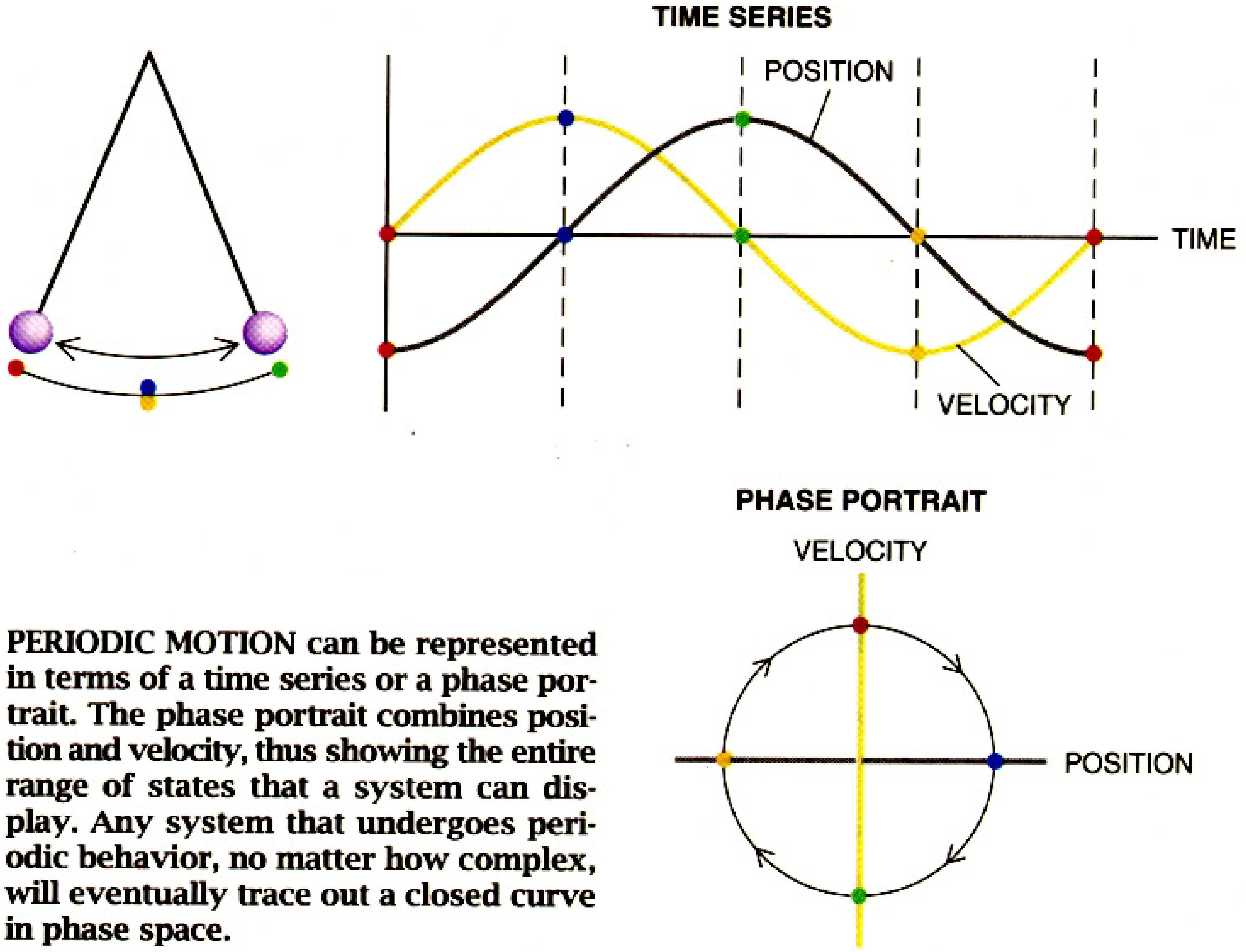
Although synchrony is the simplest state for coupled identical oscillators, it is not inevitable. Indeed, coupled oscillators often fail to synchronize. The explanation is a phenomenon known as symmetry breaking, in which a single symmetric state—such as synchrony—is replaced by several less symmetric states that together embody the original symmetry. Coupled oscillators are a rich source of symmetry breaking.

Synchrony is the most obvious case of a general effect called phase locking: many oscillators tracing out the same pattern but not necessarily in step. When two identical oscillators are coupled, there are exactly two possibilities: synchrony, a phase difference of zero, and antisynchrony, a phase difference of one half. For example, when a kangaroo hops across the Australian outback, its powerful hind legs oscillate periodically, and both hit the ground at the same instant. When a human runs after the kangaroo, meanwhile, his legs hit the ground alternately. If the network has more than two oscillators, the range of possibilities increases. In 1985 one of us (Stewart), in collaboration with Martin Golubitsky of the University of Houston, developed a mathematical classification of the patterns of networks of coupled oscillators, following earlier work by James C. Alexander of the University of Maryland and Giles Auchmuty of the University of Houston.

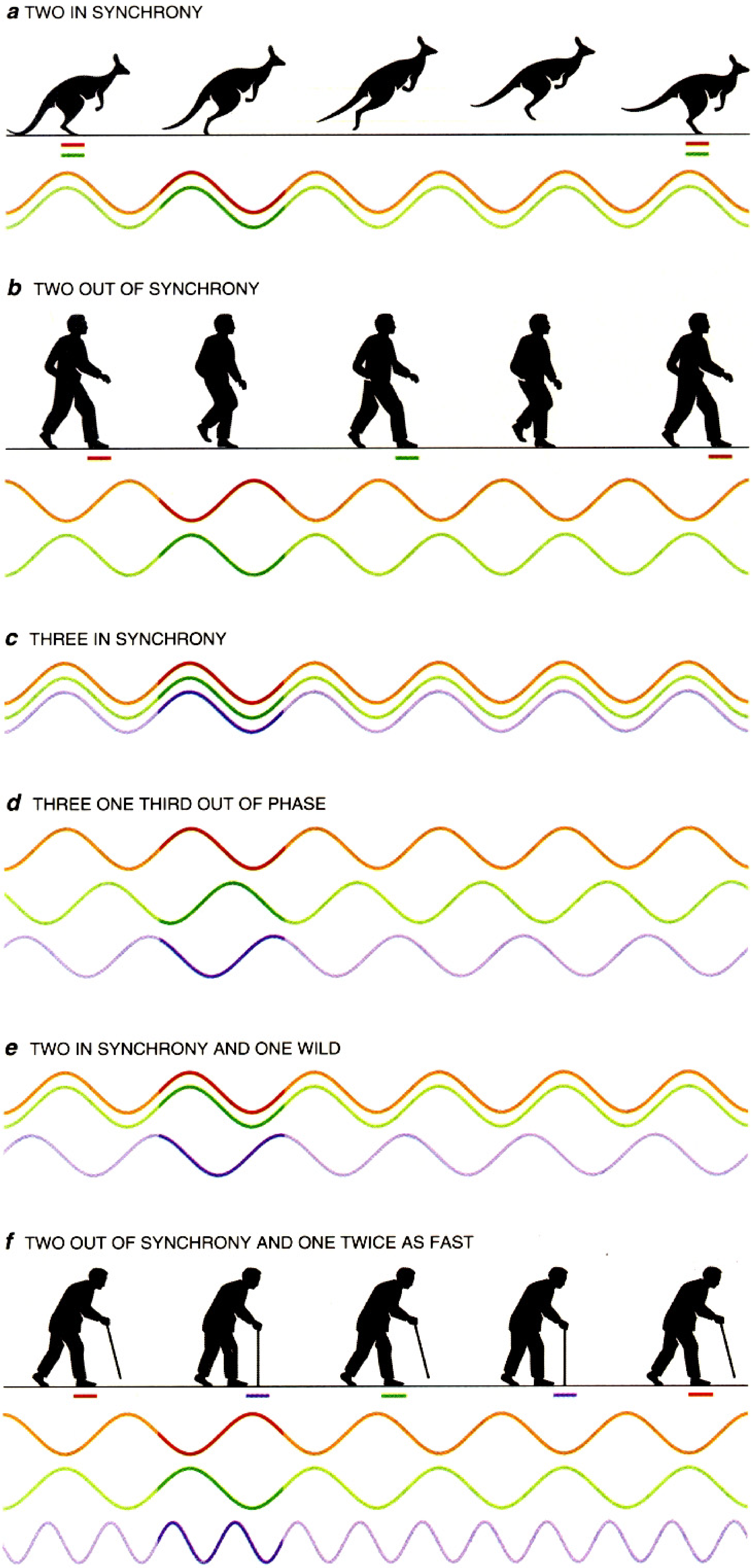
The classification arises from group theory (which deals with symmetries in a collection of objects) combined with Hopf bifurcation (a generalized description of how oscillators "switch on"). In 1942 Eberhard Hopf established a general description of the onset of oscillation. He started by considering systems that have a rest point in phase space (a steady state) and seeing what happened when one approximated their motion near that point by a simple linear function. Equations describing certain systems behave in a peculiar fashion as the system is driven away from its rest point. Instead of either returning slowly to equilibrium or moving rapidly outward into instability, they oscillate. The point at which this transition takes place is termed a bifurcation because the system's behavior splits into two branches—an unstable rest state coexists with a stable oscillation. Hopf proved that systems whose linearized form undergoes this type of bifurcation are limit-cycle oscillators: they have a preferred waveform and amplitude. Stewart and Golubitsky showed that Hopf's idea can be extended to systems of coupled identical oscillators, whose states undergo bifurcations to produce standard patterns of phase locking.

For example, three identical oscillators coupled in a ring can be phase-locked in four basic patterns. All oscillators can move synchronously; successive oscillators around the ring can move so that their phases differ by one third; two oscillators can move synchronously while the third moves in an unrelated manner (except that it oscillates with the same period as the others); and two oscillators may be moving half a phase out of step, while the third oscillates twice as rapidly as its neighbors.

The strange half-period oscillations that occur in the fourth pattern were a



PERIODIC MOTION can be represented in terms of a time series or a phase portrait. The phase portrait combines position and velocity, thus showing the entire range of states that a system can display. Any system that undergoes periodic behavior, no matter how complex, will eventually trace out a closed curve in phase space.



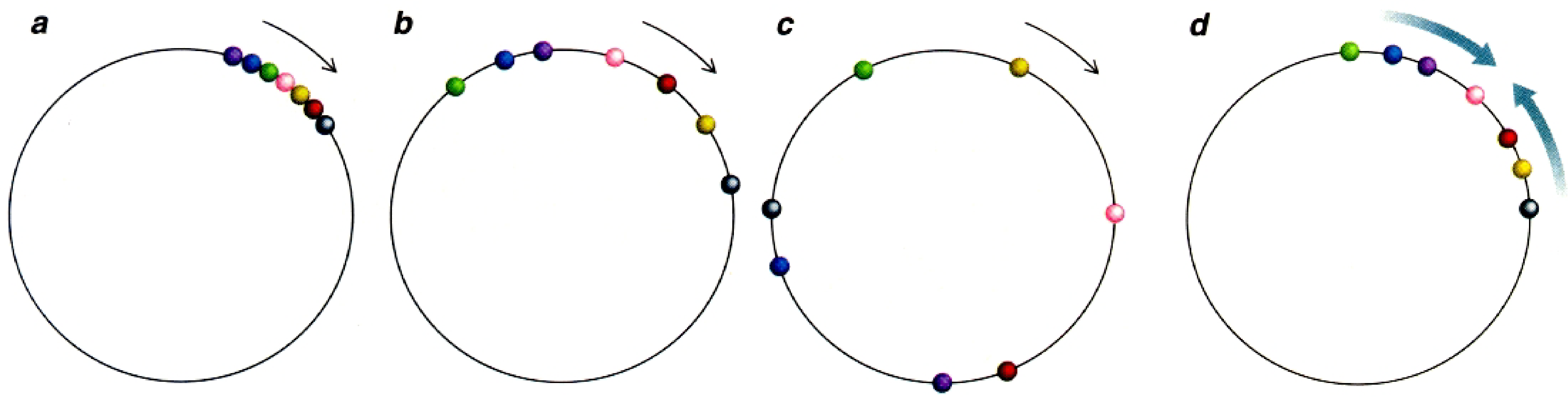
surprise at first, even to Stewart and Golubitsky, but in fact the pattern occurs in real life. A person using a walking stick moves in just this manner: right leg, stick, left leg, stick, repeat. The third oscillator is, in a sense, driven by the combined effects of the other two: every time one of them hits a peak, it gives the third a push. Because the first two oscillators are precisely antisynchronous, the third oscillator peaks twice while the others each peak once.

The theory of symmetrical Hopf bifurcation makes it possible to classify the patterns of phase locking for many different networks of coupled oscillators. Indeed, Stewart, in collaboration with James J. Collins, a biomedical engineer at Boston University, has been investigating the striking analogies between these patterns of phase locking and the symmetries of animal gaits, such as the trot, pace and gallop.

Quadruped gaits closely resemble the natural patterns of four-oscillator systems. When a rabbit bounds, for example, it moves its front legs together, then its back legs. There is a phase difference of zero between the two front legs and of one half between the front and back legs. The pace of a giraffe is similar, but the front and rear legs on each side are the ones that move together. When a horse trots, the locking occurs in diagonal fashion. An ambling elephant lifts each foot in turn, with phase differences of one quarter at each stage. And young gazelles complete the symmetry group with the pronk, a four-legged leap in which all legs move in synchrony [see "Mathematical Recreations," by Ian Stewart; SCIENTIFIC AMERICAN, April 1991].

More recently, Stewart and Collins have extended their analysis to the hexapod motion of insects. The tripod

SYMMETRY BREAKING governs the ways that coupled oscillators can behave. Synchrony is the most symmetrical single state, but as the strength of the coupling between oscillators changes, other states may appear. Two oscillators can couple in either synchronous or antisynchronous fashion (*a*, *b*), corresponding roughly to the bipedal locomotion of a kangaroo or a person. Three oscillators can couple in four ways: synchrony (*c*), each one third of a cycle out of phase with the others (*d*), two synchronous and one with an unrelated phase (*e*) or in the peculiar rhythm of two oscillators antisynchronous and the third running twice as fast (*f*). This pattern is also the gait of a person walking slowly with the aid of a stick.



NONIDENTICAL OSCILLATORS may start out in phase with one another (as shown on circle *a*, in which 360 degrees mark one oscillation), but they lose coherence as the faster ones move ahead, and the slower ones fall behind (*b*, *c*). A simple coupling force that speeds up slower oscillators and slows down faster ones, however, can keep them all in phase (*d*).

gait of a cockroach is a very stable pattern in a ring of six oscillators. A triangle of legs moves in synchrony: front and back left and middle right; then the other three legs are lifted with a phase difference of one half.

Why do gaits resemble the natural patterns of coupled oscillators in this way? The mechanical design of animal limbs is unlikely to be the primary reason. Limbs are not passive mechanical oscillators but rather complex systems of bone and muscle controlled by equally complicated nerve assemblies. The most likely source of this concordance between nature and mathematics is in the architecture of the circuits in the nervous system that control locomotion. Biologists have long hypothesized the existence of networks of coupled neurons they call central pattern generators, but the hypothesis has always been controversial. Nevertheless, neurons often act as oscillators, and so, if central pattern generators exist, it is reasonable to expect their dynamics to resemble those of an oscillator network.

Moreover, symmetry analysis solves a significant problem in the central-pattern generator hypothesis. Most animals employ several gaits—horses walk, trot, canter and gallop—and biologists have often assumed that each gait requires a separate pattern generator. Symmetry breaking, however, implies that the same central-pattern generator circuit can produce all of an animal's gaits. Only the strength of the couplings among neural oscillators need vary.

So far our analysis has been limited to collections of oscillators that are all strictly identical. That idealization is convenient mathematically, but it ignores the diversity that is always present in biology. In any real population, some oscillators will always be inherently faster or slower. The behavior of communities of oscillators whose members have differing frequencies depends on the strength of the coupling among them. If their interactions are too weak, the oscillators will be unable to achieve synchrony. The result is incoherence, a cacophony of oscillations. Even if started in unison the oscillators will gradually drift out of phase, as did Huygens's pendulum clocks when placed at opposite ends of the room.

Colonies of the bioluminescent algae *Gonyaulax* demonstrate just this kind of desynchronization. J. Woodland Hastings and his colleagues at Harvard University have found that if a tank full of *Gonyaulax* is kept in constant dim light in a laboratory, it exhibits a circadian glow rhythm with a period close to 23 hours. As time goes by, the waveform broadens, and this rhythm gradually damps out. It appears that the individual cells continue to oscillate, but they drift out of phase because of differences in their natural frequencies. The glow of the algae themselves does not maintain synchrony in the absence of light from the sun.

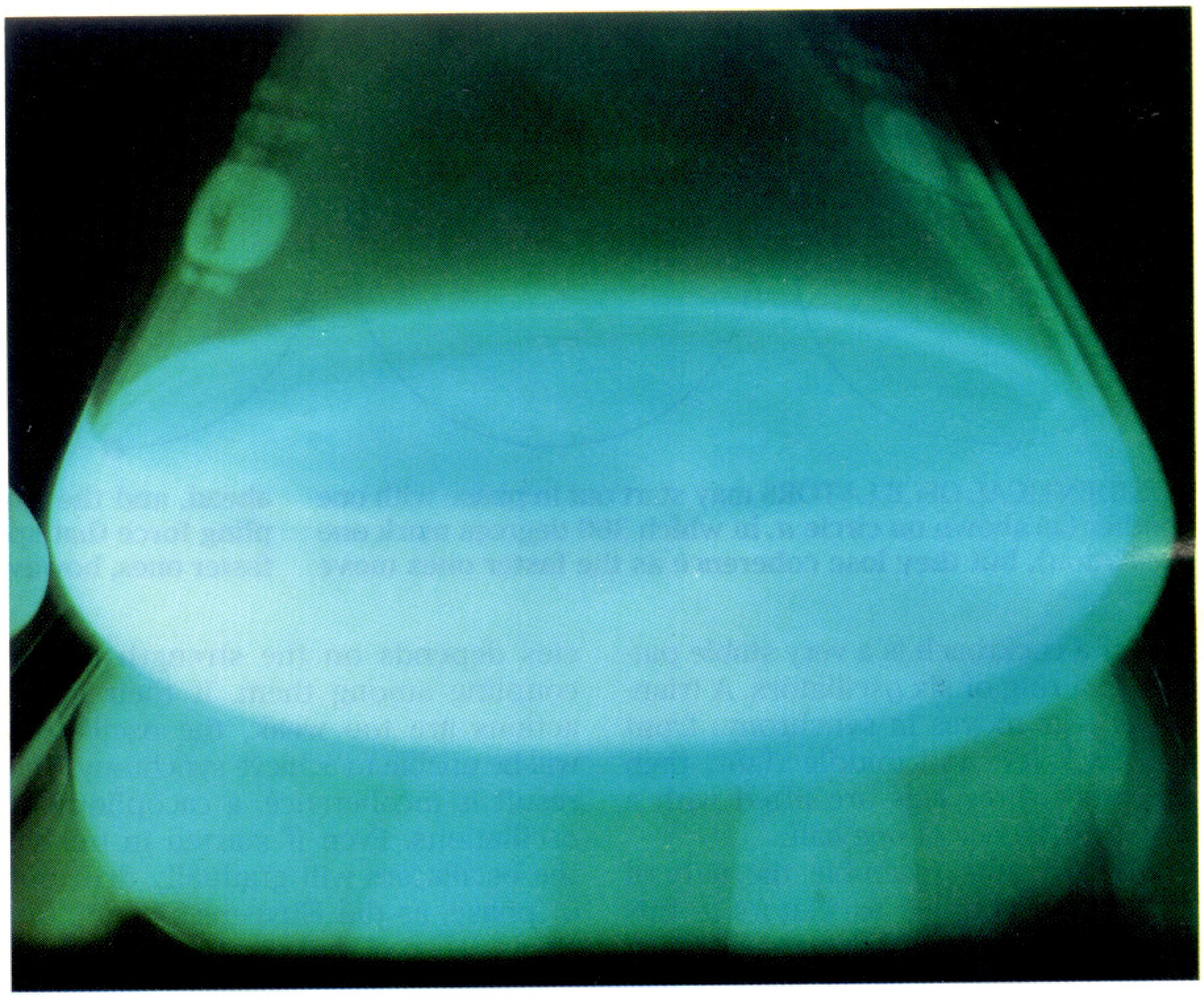
In other oscillator communities the coupling is strong enough to overcome the inevitable differences in natural frequency. Polymath Norbert Wiener pointed out in the late 1950s that such oscillator communities are ubiquitous in biology and indeed in all of nature. Wiener tried to develop a mathematical model of collections of oscillators, but his approach has not turned out to be fruitful. The theoretical breakthrough came in 1966, when Winfree, then a graduate student at Princeton University, began exploring the behavior of large populations of limit-cycle oscillators. He used an inspired combination of computer simulations, mathematical analysis and experiments on an array of 71 electrically coupled neon-tube oscillators.

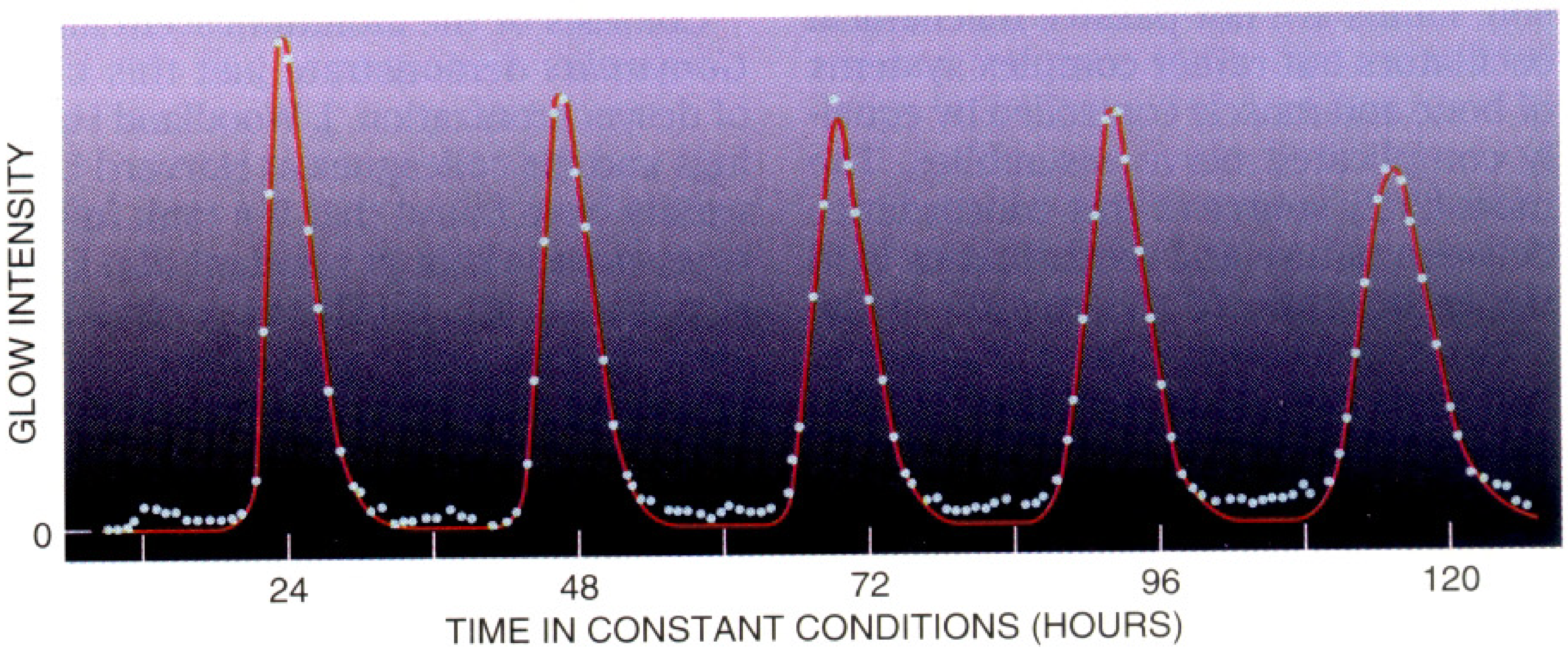
Winfree simplified the problem tremendously by pointing out that if oscillators are weakly coupled, they remain close to their limit cycles at all times. This insight allowed him to ignore variations in amplitude and to consider only their variations in phase. To incorporate differences among the oscillators, Winfree made a model that captured the essence of an oscillator community by assuming that their natural frequencies are distributed according to a narrow probability function and that in other respects the oscillators are identical. In a final and crucial simplification, he assumed that each oscillator is influenced only by the collective rhythm produced by all the others. In the case of fireflies, for example, this would mean that each firefly responds to the collective flash of the whole population rather than to any individual firefly.

To visualize Winfree's model, imagine a swarm of dots running around a circle. The dots represent the phases of the oscillators, and the circle represents their common limit cycle. If the oscillators were independent, all the dots would eventually disperse over the circle, and the collective rhythm would decay to zero. Incoherence reigns. A simple rule for interaction among oscillators can restore coherence, however: if an oscillator is ahead of the group, it slows down a bit; if it is behind, it speeds up.

In some cases, this corrective coupling can overcome the differences in natural frequency; in others (such as that of *Gonyaulax*), it cannot. Winfree found that the system's behavior depends on the width of the frequency distribution. If the spread of frequencies is large compared with the coupling, the system always lapses into incoherence, just as if it were not coupled at all. As the spread decreases below a critical value, part of the system spontaneously "freezes" into synchrony.

Synchronization emerges cooperatively. If a few oscillators happen to synchronize, their combined, coherent signal rises above the background din, exerting a stronger effect on the others.





GONYAULAX **luminescent algae (*top*) change the intensity of their glow according to an internal clock that is affected by light. If they are kept in constant dim light, the timing of the glow becomes less precise because the coupling among individual organisms is insufficient to keep them in sync (*bottom*).**

When additional oscillators are pulled into the synchronized nucleus, they amplify its signal. This positive feedback leads to an accelerating outbreak of synchrony. Some oscillators nonetheless remain unsynchronized because their frequencies are too far from the value at which the others have synchronized for the coupling to pull them in.

In developing his description, Winfree discovered an unexpected link between biology and physics. He saw that mutual synchronization is strikingly analogous to a phase transition such as the freezing of water or the spontaneous magnetization of a ferromagnet. The width of the oscillators' frequency distribution plays the same role as does temperature, and the alignment of oscillator phases in time is the counterpart of an alignment of molecules or electronic spins in space.

The analogy to phase transitions opened a new chapter in statistical mechanics, the study of systems composed of enormous numbers of interacting subunits. In 1975 Yoshiki Kuramoto of Kyoto University presented an elegant reformulation of Winfree's model. Kuramoto's model has a simpler mathematical structure that allows it to be analyzed in great detail. Recently Strogatz, along with Mirollo and Paul C. Matthews of the University of Cambridge, found an unexpected connection between Kuramoto's model and Landau damping, a puzzling phenomenon that arises in plasma physics when electrostatic waves propagate through a highly rarefied medium. The connection emerged when we studied the decay to incoherence in oscillator communities in which the frequency distribution is too broad to support synchrony. The loss of coherence, it turns out, is governed by the same mathematical mechanism as that controlling the decay of waves in such "collisionless" plasmas.

The theory of coupled oscillators has come a long way since Huygens noticed the spontaneous synchronization of pendulum clocks. Synchronization, apparently a very natural kind of behavior, turns out to be both surprising and interesting. It is a problem to understand, which is not an obvious consequence of symmetry. Mathematicians have turned to the theory of symmetry breaking to classify the general patterns that arise when identical, ostensibly symmetric oscillators are coupled. Thus, a mathematical discipline that has its most visible roots in particle physics appears to govern the leap of a gazelle and the ambling of an elephant. Meanwhile techniques borrowed from statistical mechanics illuminate the behavior of entire populations of oscillators. It seems amazing that there should be a link between the violent world of plasmas, where atoms routinely have their electrons stripped off, and the peaceful world of biological oscillators, where fireflies pulse silently along a riverbank. Yet there is a coherent mathematical thread that leads from the simple pendulum to spatial patterns, waves, chaos and phase transitions. Such is the power of mathematics to reveal the hidden unity of nature.

FURTHER READING

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