Step in Time

Exploring the mathematics of synchronously flashing fireflies

By IVARS PETERSON

As the evening light fades, the myriad fireflies perched in a tree on a riverbank in Thailand begin tuning up for their nightly light show. One emits a burst of light; then another firefly flashes, and another, and so on, creating a random pattern of twinkling lights.

But it doesn't take long for neighboring fireflies to begin coordinating their flashes. The synchrony spreads rapidly to larger and larger clumps in the tree – and within half an hour, the entire swarm acts as a unit, flashing about once every second in nearly perfect unison.

The firefly's ability to control the timing of its flashes has long intrigued biologists. In particular, the rhythmic, synchronized flashing by the males – observed mainly among Southeast Asian species and rarely in North American species – has sparked a variety of field and laboratory studies. This remarkable phenomenon has also attracted the attention of mathematicians interested in elucidating the underlying mechanisms that compel a set of independent oscillators to become synchronized.

Recent theoretical work inspired by the firefly example focuses on the emergence of synchrony in the special case where oscillators, whether biological or physical, communicate by firing pulses. Mathematicians Renato E. Mirollo of Boston College and Steven H. Strogatz of the Massachusetts Institute of Technology have now created an abstract, idealized mathematical model of this type of behavior and have proved that under certain circumstances, pulse-coupled oscillators operating at the same frequency but starting at different times will always become synchronized.

"People have had a hard time figuring out the general mechanism of synchronization," says Arthur T. Winfree, a mathematical biologist at the University of Arizona in Tucson. Mathematical models like the one developed by Strogatz and Mirollo may provide useful insights into the dynamical behavior of a wide range of pulse-driven oscillating systems.

"Fireflies supply the right picture," Strogatz says. "They don't make themselves known to the others until the instant they go off, and it's only for that instant that they interact." Each firefly then responds to such flashes by gradually shifting its rhythm to achieve synchrony.

Few species other than fireflies and humans display a propensity for rhythmic communal synchronization. On a cellular level, however, such behavior appears in many biological systems. For example, the heart's pacemaker cells coordinate their electrical activity to maintain a beat, and networks of neurons in the brain keep time and respond to certain rhythms.

"There's a whole spectrum of possible [mathematical] models, from very detailed models, which include all the physiology and all the anatomy, to much more stylized models that try to capture the essence," says mathematician Charles S. Peskin of New York University in New York City. "The strength of what [Strogatz and Mirollo] did is in making [their model] general enough to be more likely applicable to a real situation."

At the same time, mathematical techniques – even when applied to simplified models – have their limitations. "The mathematical analysis of mutual synchronization is a challenging problem," Mirollo and Strogatz report in the December 1990 SIAM JOURNAL OF APPLIED MATHEMATICS. "It is difficult enough to analyze the dynamics of a single nonlinear oscillator, let alone a whole population of them."

The thread of research leading to Strogatz and Mirollo's proof started with Peskin's attempt in 1975 to model the way heart cells coordinate their electrical signals to generate a heartbeat. Applying ideas developed by other researchers to explain how nerve cells synchronize their activity in response to a stimulus, Peskin examined the case of two oscillators – representing two heart cells – that influence each other via their own signals.

In Peskin's grossly simplified model, each electrical pulse from one oscillator kicks its companion a small step up toward the threshold voltage at which that oscillator normally fires. Thus, each oscillator fires and resets itself at intervals influenced by the repeated signals from the other oscillator. At some stage, an oscillator that happens to be very close to its threshold senses a signal from its companion that induces it to fire immediately. From that point on, the signals from the two oscillators lock together and remain synchronized.

To make this model work, however, Peskin had to include a crucial proviso. He had to assume that an oscillator "leaked" when it neared the threshold, and that the leakage affected its readiness to fire. In other words, the closer an oscillator came to its firing threshold, the smaller an effect a given kick from its companion would have.

With this condition in place, Peskin proved mathematically that for almost all initial conditions, two oscillators would eventually get in sync. He went on to conjecture, based on his model of two cells, that the same mechanism leads to synchronization of any number of identical oscillators.

"That's actually a very strong conjecture – that no matter how they were started, they would always synchronize," Strogatz says. "With all these cells interacting, you might think that something very complicated could happen ... and that the system would never settle down or that it might break up into different groups, with individuals synchronized within a group but different groups staying out of step."

Strogatz first came across Peskin's work on synchronized electrical signals among pacemaker cells while thumbing through a book by Winfree on the geometry of biological time. Intrigued by the reference, he looked up Peskin's original paper on the subject.

"The conjectures were neat," Strogatz says. "But it was clear that his results were incomplete."

Strogatz got Mirollo interested in the problem, and together they developed a modified version of Peskin's model that could encompass any number of oscillators. Like Peskin, they assumed that all the oscillators behaved identically and that each was directly coupled to, or influenced by, all the others. But they expressed Peskin's "leakiness" constraint in a more general form, specifying only that the rise of an oscillator toward threshold follows an upward curve that gradually becomes less and less steep.

Computer simulations involving 100 oscillators provided the first evidence that a system of oscillators started at random times will eventually reach synchrony. The simulations showed that an individual oscillator initially receives many conflicting signals, but as their collective behavior evolves, oscillators begin to clump together in groups that fire at the same time. As these groups acquire more oscillators, they produce larger collective pulses, which gradually bring other, out-of-sync oscillators to the brink of threshold even faster. Large groups grow at the expense of smaller ones. Ultimately, only one huge group remains, and the entire population of oscillators becomes synchronized.

"We tried many different initial conditions, and the system always ended up synchronizing," Strogatz says. "That gave us a little confidence that [the original conjecture] was going to be a true theorem."

Strogatz and Mirollo relied heavily on geometric arguments to establish the conditions under which synchrony could be achieved. The resulting proof clearly demonstrates that synchrony is actually the rule for mathematical models in which every oscillator interacts with every other oscillator under the conditions Strogatz and Mirollo specify.

"The strength of this work is the proof that this behavior can emerge under a certain range of conditions," Peskin says.

The Strogatz-Mirollo model, however, contains a number of simplifications that cloud its applicability to a swarm of real fireflies. For example, critics argue that not all fireflies of a given species flash at precisely the same rate, and it's unlikely that every firefly sees the flash of every other firefly.

"The question is: How different can [individual fireflies] be and still synchronize?" Peskin says. "The most important thing to do in the future is to generalize [the model] to the case where you have a population of oscillators that are not quite identical."

Experiments involving different species of Southeast Asian fireflies show that each species tends to have a characteristic flashing frequency despite small differences among individuals in that group. "Fireflies [of a particular species] have a fairly narrow [frequency] window," says biologist Frank E. Hanson of the University of Maryland Baltimore County in Catonsville. "They don't pay any attention to anything flashing at a rate outside that window."

Hanson and others have observed overlapping swarms of two different firefly species flashing synchronously at independent rates. They note, however, that although the flashes ordinarily have fairly uniform intensities, durations and delays, no single swarm ever really achieves perfect synchrony.

Mathematicians are also taking a closer look at what happens when each oscillator interacts directly with only a few neighbors rather than with the whole population. One possibility is that such a group would generate distinctive, nonsynchronous patterns of firing. In fact, observers have noticed waves of flashing in firefly congregations, especially when a population is spread out over a large tree or in a string of bushes along a riverbank.

Strogatz and Mirollo have tried some computer simulations to explore the effects of limited-range interactions in their model. "Strangely, we never saw any waves in our model," Strogatz says. "We always saw synchrony."

This led them to conjecture that the oscillators in their model – even when limited to interacting with close neighbors – would always synchronize, and that the system would never show waves. "That could be completely wrong," Strogatz says. "We don't know yet."

Indeed, apparently small changes in the rules governing a mathematical model can lead to radically different results. Mathematician G. Bard Ermentrout of the University of Pittsburgh has studied coupling in a ring of identical oscillators, and he finds that he gets a stable traveling wave rather than synchrony.

Ermentrout has also extended his model to two-dimensional networks. "I can now prove the existence and stability of rotating spiral waves in two-dimensional arrays with nearest-neighbor coupling," he says.

But in all this mathematical modeling, the issue comes down to whether a given model actually captures key aspects of the behavior of biological oscillators. "There are certainly an awful lot of real biological systems that do mutually synchronize," Winfree says. "Whether they do it by the mechanism involved in this pulse-coupled theory seems to me an important question that ought to be pursued."

"There are many different ways of synchronizing," Ermentrout says. "While Strogatz and Mirollo did a really nice job on their particular model, it doesn't help explain many types of oscillators."

For instance, the model postulates that pulses and responses are instantaneous, and it specifies that sensed pulses always advance an oscillator toward threshold. However, even among fireflies, pulses clearly have a finite duration, and field studies by biologists have revealed that in some species of fireflies, such signals can either advance or delay firing.

"Mathematicians remain in the dark about these more subtle aspects of firefly synchronization," comments mathematician Ian Stewart of the University of Warwick in Coventry, England, in the April 18 NATURE.

Equally subtle is the more general problem of determining whether a biological oscillator really responds to a string of sharp pulses or instead interacts continuously with its neighbors. "It's an open scientific question whether certain examples are really pulse-coupled as opposed to continuously coupled," Strogatz says.

Nonetheless, the work of Strogatz and Mirollo does shed some light on mechanisms that lead to synchronization. Their generalization of Peskin's leakiness property, for instance, "is a realistic feature of the model," Peskin says. "Biological membranes have a resistive character. They have channels that allow current to leak."

This leakiness plays roughly the same role as friction does in mechanics and resistance does in electricity, he adds. In effect, it allows two oscillators to forget their past firing patterns so that they can come together.

Mathematicians who attempt to understand biological oscillators face difficult mathematical questions. "It would be very desirable to start building in a little more reality," Strogatz says. But, as so often happens in mathematics, "one problem may turn out relatively easy to solve, and everything else in every direction around [it] is hard."

Researchers also have much more to learn about biological oscillators. Firefly behavior alone is remarkably diverse and complex, and has so far eluded thorough understanding. For instance, biologists originally suggested that the synchronized displays of the males serve as riverside beacons for females, who fly in to mate, then fly down to dry land to lay their eggs. But subsequent research showed that several other factors may be involved.

Over the past 50 years, investigators have learned a great deal about the synchronous rhythmic flashing of fireflies, says John Buck, an emeritus biologist with the National Institutes of Health, who in 1938 wrote the first general review of their behavior. "At the same time, its mysteries have multiplied," he notes in the September 1988 QUARTERLY REVIEW OF BIOLOGY. "Each step of physiological elucidation has revealed new black boxes, and each behavioral insight has left major puzzles yet unsolved."

Future progress in understanding biological oscillators may depend on greater cooperation between mathematicians and biologists. "Best of all would be to collaborate with a biologist who actually measures things in, say, fireflies, against which we could check the quantitative predictions of mathematical models," Strogatz says.

Ermentrout has already mined some of the data collected by Hanson, Buck and their co-workers for evidence supporting his firefly models. But that's just a beginning. Mathematical models also make predictions that can be tested in the field.

Says Hanson, "Perhaps [Ermentrout] and I could go back to New Guinea or someplace like that, with some carefully designed experiments to probe these systems." □